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# The ecological basis for economic value of seafood production supported by mangrove ecosystems

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**Abstract**

The undervaluation of natural products and ecological services generated by mangrove ecosystems is a major driving force behind the conversion of this system into alternative uses. This trend of undervaluation is partly due to the difficulty involved in placing a monetary value on all relevant factors, but lack of ecological knowledge and a holistic approach among those performing the evaluation may be even more important determinants. This article identifies and synthesizes ecological and biophysical links of mangroves that sustain capture fisheries and aquaculture production. Fish, crustacean and mollusc species associated with mangroves are presented and the ecology of their direct use of this system is reviewed. Through a coastal seascape perspective, biophysical interactions among mangroves, seagrass beds and coral reefs are illustrated. The life-support functions of mangrove ecosystems also set the framework for sustainable aquaculture in these environments. Estimates of the annual market value of capture fisheries supported by mangroves ranges from US$750 to 16 750 per hectare, which illustrates the potential support value of mangroves. The value of mangroves in seafood production would further increase by additional research on subsistence fisheries, biophysical support to other ecosystems, and the mechanisms which sustain aquaculture production. 

*Keywords:* Mangroves; Coastal seascape; Ecological services; Capture fisheries; Aquaculture; Economic evaluation

## 1. Introduction

In an ecologically illiterate world, the economic value of natural products and ecosystem services generated by mangrove forests is generally underestimated (Saenger et al., 1983; Hamilton and Snedaker, 1984; Hamilton et al., 1989; Lal, 1990; Barbier, 1994). As a consequence mangrove ecosystems have become prime candidates for conversion into large scale development activities,

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Table 1
Natural products and ecological services of mangrove ecosystems[a]

| | |
|---|---|
| *Natural products* | |
| Fuel | |
| | Firewood |
| | Charcoal |
| | Alcohol |
| Construction | |
| | Timber for scaffolds and heavy construction |
| | Beams, poles, flooring, panelling, etc. |
| | Boat building |
| | Dock piling |
| | Thatch, matting |
| Fishing | |
| | Poles for fish traps |
| | Fish attracting shelters |
| | Fishing floats |
| | Fish poison |
| | Tannins for net and line preservation |
| Food and beverages | |
| | Fish |
| | Crustaceans |
| | Molluscs |
| | Other fauna |
| | Vegetables from propagules, fruit and leaves |
| | Sweetmeats from propagules |
| | Condiments from bark |
| | Sugar |
| | Honey |
| | Cooking oil |
| | Tea substitutes |
| | Alcohol |
| | Vinegar |
| | Fermented drinks |
| Household items | |
| | Furniture |
| | Glue |
| | Wax |
| | Household utensils |
| | Incense |
| | Matchsticks |
| Textiles, leather | |
| | Fur, skins |
| | Synthetic fibres (e.g. rayon) |
| | Dye for cloth |
| | Tannins for leather preservation |
| Other products | |
| | Fish, shellfish and mangrove roots for aquarium trade |
| | Medicines from bark, leaves, fruits and seeds |
| | Fodder for cattle, goats and camels |
| | Fertilisers |
| | Lime |
| | Paper |
| | Raw material for handicraft |
| | Cigarette wrappers |

Table 1 (Continued)

| |
|---|
| *Ecological services* |
| Protection against floods, hurricanes and tidal waves |
| Control of shoreline and riverbank erosion |
| Biophysical support to other coastal ecosystems |
| Provision of nursery, breeding and feeding grounds |
| Maintenance of biodiversity and genetic resources |
| Storage and recycling of organic matter, nutrients and pollutants |
| Export of organic matter and nutrients |
| Biological regulation of ecosystem processes and functions |
| Biological maintenance of resilience |
| Production of oxygen |
| Sink for carbon dioxide |
| Water catchment and groundwater recharge |
| Topsoil formation, maintenance of fertility |
| Influence on local and global climate |
| Habitat for indigenous people |
| Sustaining the livelihood of coastal communities |
| Heritage values |
| Cultural, spiritual and religious values |
| Artistic inspiration |
| Educational and scientific information |
| Recreation and tourism |

[a] Sources: Saenger et al., 1983; Hamilton and Snedaker, 1984; Ruitenbeek, 1994; Costanza et al., 1997.

such as agriculture, aquaculture, forestry, salt extraction and infrastructure. More than 50% of the world's mangroves have been removed (World Resources Institute, 1996), and for the Asia-Pacific region an annual deforestation rate of 1% is considered to be a conservative measure (Ong, 1995). Mangroves formerly occupied $\approx 75\%$ of tropical coasts and inlets (Farnsworth and Ellison, 1997), but today they only line $\approx 25\%$ of the world's tropical coastlines (World Resources Institute, 1996). Evaluation of the importance of mangroves for society requires insight into the flow of products and services within the social system of coastal communities, and how they are linked and influenced by domestic and international markets and institutions. It also requires insight into the biophysical links within and between mangroves and other ecosystems for the generation of natural products and ecological services, many of which are harvested or enjoyed outside the mangrove system. Although it will not be possible to place a monetary value on all relevant factors, they must be recognized explicitly and incorporated into the discussion of management alternatives for mangrove forests.

Mangroves provide a wide range of ecological services like protection against floods and hurricanes, reduction of shoreline and riverbank erosion, maintenance of biodiversity, etc. (Table 1). These services are key features which sustain economic activities in coastal areas throughout the tropics. In addition to the multiple ecological services provided by mangrove ecosystems, ranges of direct and indirect natural products from mangroves are vital to subsistence economies and provide a commercial base to local and national economies (Table 1). Commercial and traditional products range from timber to charcoal, and from tannins to medicines. Moreover, a number of food products are harvested directly within the mangrove system through hunting, gathering, and fishing operations.

Capture fisheries production is believed to constitute the major value of marketed products from an unexploited mangrove forest (Hamilton et al., 1989), and the support to commercial, recreational and subsistence fisheries is well documented. For instance, 80% of all marine species of commercial or recreational value in Florida, USA, have been estimated to depend upon mangrove estuarine areas for at least some stage in their life cycles (Hamilton and Snedaker, 1984). In Fiji (Hamilton and Snedaker, 1984) and in India (Untawale, 1986), approximately 60% of the commercially important coastal fish species are directly associated with mangrove environments. The relative contribution of mangrove-related species to total fisheries catch can also be significant, constituting 67% of the entire commercial catch in eastern Australia (Hamilton and Snedaker, 1984), 49% of the demersal fish resources in the southern Malacca Strait (Macintosh, 1982), 30% of the fish catch and almost 100% of shrimp catch in ASEAN countries (Singh et al., 1994). Positive correlations have also been demonstrated between mangrove cover and municipal fisheries landings (Camacho and Bagarinao, 1987) as well as penaeid shrimp catches (Turner, 1977; Staples et al., 1985; Pauly and Ingles, 1986). In addition to commercial fisheries, coastal subsistence economies in many developing countries are heavily dependent upon sustainable harvest of fish and shellfish from mangroves. The median fisherman density of about 5.6 fishermen per $km^2$ in mangrove environments is considerably higher than in other fished systems as is the yield per unit area (Matthes and Kapetsky, 1988). Because a large portion of the world's human population lives in coastal or estuarine areas, e.g. 70% of the population in South East Asia (Pauly and Chua, 1988), the importance of fishery activities as a source of food and income cannot be overstated.

Another aspect of mangroves as life-support systems is their role in sustaining mollusc, fish, and shrimp aquaculture. Land based pond farming of fish and crustaceans in former mangrove areas has a long tradition in many countries, and dates back some 500 years to rearing of milkfish (*Chanos chanos*) in Indonesia (Schuster, 1952). In recent decades, aquaculture activities have intensified dramatically, particularly for high-value crops like penaeid shrimps. Conversion of mangrove forests into shrimp farms has grown to such an extent that today it constitutes the main threat to mangroves in many countries (Hamilton et al., 1989; Primavera, 1998). Ironically, the productivity of these aquaculture systems is heavily dependent on surrounding mangroves which provide seed, food inputs, clean water, etc. (Hamilton and Snedaker, 1984; Larsson et al., 1994; Beveridge et al., 1997). Failure to acknowledge this life-support function of mangroves is one explanation for the boom-and-bust pattern of shrimp aquaculture. The lifespan of most semi-intensive and intensive ponds seldom exceeds 5–10 years (Gujja and Finger-Stich, 1996), and 70% of previously productive ponds have been abandoned in Thailand (Stevenson, 1997).

This article identifies and synthesizes ecological and biophysical links of mangroves that sustain seafood production (Fig. 1). By illuminating the 'hidden' support of mangroves to capture fisheries and aquaculture, these human activities are put into an ecosystem framework. Without this understanding it is difficult, if not impossible, to sustainably manage mangroves and the natural products and ecological services associated with this coastal ecosystem. This ecological knowledge can also serve as a conceptual framework for economic evaluations of mangrove ecosystems in supporting seafood production. First, I identify fish, crustacean and mollusc species associated with mangroves and review the ecology of their direct use of mangroves. This is followed by a section on biophysical interactions between mangroves and other coastal ecosystems, relations often forgotten in mangrove management. The ecological goods and services constituting a prerequisite for sustainable aquaculture in mangrove environments are outlined before discussing economic valuations of seafood production supported by this system. To illustrate the potential support value of mangroves in fish and shellfish production, productivity and market value of some fisheries are presented. The undervaluation of mangroves, originating in ecological illiteracy and in the difficulties involved in placing a monetary value on generated natural products and ecological services, is also discussed.

## 2. Fish, crustaceans and molluscs associated with mangroves

Fishery species which use mangroves as habitat can be classified into permanent residents, spending their entire life cycle in mangrove systems, and temporary residents, associated with mangroves during at least one stage in their life cycle (Ogden and Gladfelder, 1983). The latter can be divided into obligate or incidental users. The broad application of these definitions has been widely de-

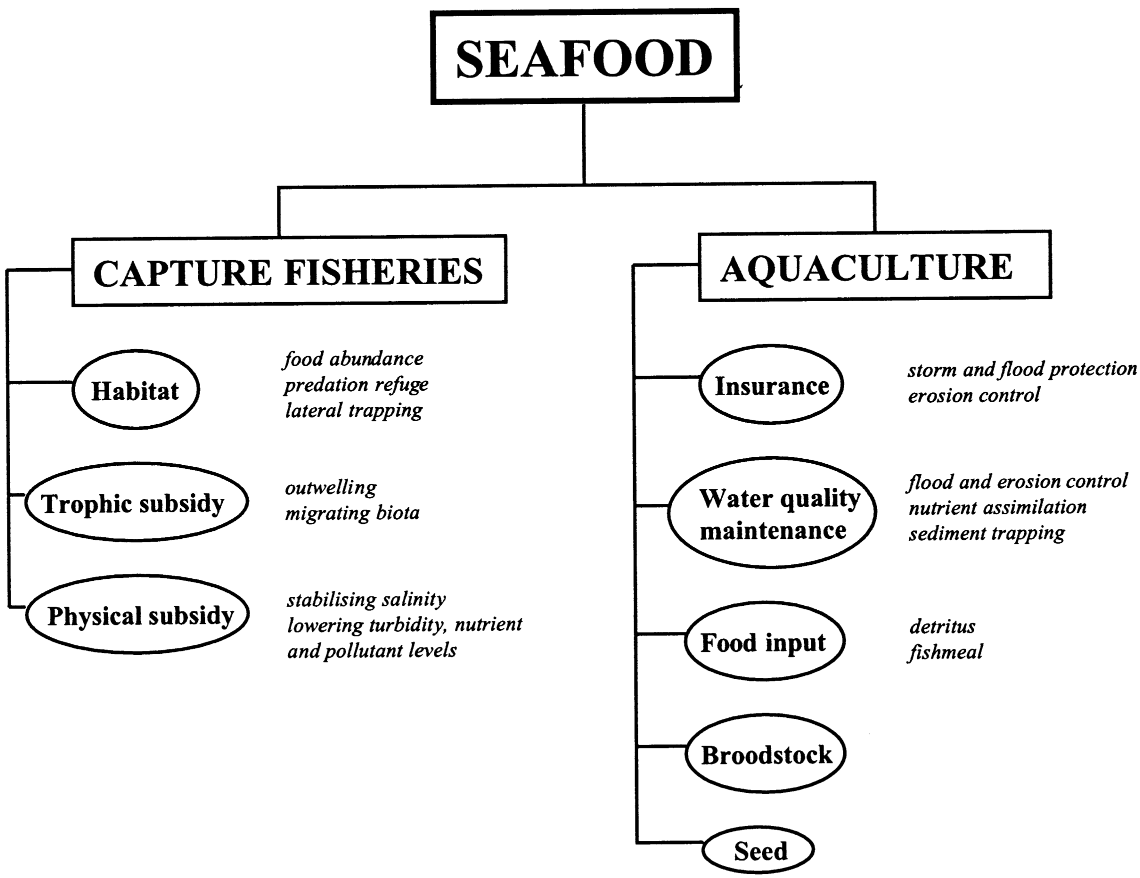


Fig. 1. Seafood production generated by mangrove ecosystems: direct biophysical support to capture fisheries, and natural products and ecological services sustaining aquaculture.

bated and criticised (Potter et al., 1990). In addition to the difficulty involved in defining the degree of dependence, fish and shellfish species associated with mangroves are in some cases not confined to particular families or even genera (Robertson and Blaber, 1992). For instance, many genera contain closely related species whose adults co-occur offshore, but which do not all use mangroves as nursery. The importance of mangroves to economically important organisms was highlighted through a biogeographic analysis by Matthes and Kapetsky (1988), which associated particular life stages of these organisms to mangrove environments. This kind of information is, however, limited in many areas due to lack of adequate research.

### 2.1. Fish

Few fish species are permanent residents in mangroves, but numerous marine species use mangroves as nursery grounds (Robertson and Blaber, 1992). Fish species richness has been reported to be as high as almost 200 species in mangrove-dominated estuaries and embayments in Australia and India (reviewed by Robertson and Blaber, 1992). A large number of teleost (bony fish) species that utilise mangrove areas as larvae, juveniles, or adults are captured by fishermen either inshore or offshore (economically important families are listed in Table 2). Highly valued food and game fish that have a close association with mangroves in the Indo-West Pacific include mullets (*Liza*, *Mugil*), groupers (*Epinephelus*), snappers (*Lutjanus*), tarpons (*Megalops*), sea-perch (*Lates*, *Centropomus*) and catfish (e.g. *Arius*, *Tachysurus*) (Macintosh, 1982). In addition to teleosts, a great number of shark and ray species can also be found in mangrove environments (Matthes and Kapetsky, 1988).

Table 2
Fish families that utilise mangroves as habitat during their life cycle and are of economic importance to fisheries[a]

| |
|---|
| Megalopidae (tarpons) |
| Chanidae (milkfish) |
| Clupeidae (herrings, sardines, pilchards) |
| Engraulidae (anchovies) |
| Ariidae (sea catfishes) |
| Plotosidae (eel catfishes) |
| Mugilidae (mullets) |
| Centropomidae (barramundi, snooks) |
| Serranidae (groupers, sea basses) |
| Sillaganidae (sillagos) |
| Carangidae (king fishes) |
| Leiognathidae (soapies) |
| Lutjanidae (snappers) |
| Gerridae (mojarras) |
| Haemulidae (rubberlips, grunts) |
| Sparidae (breams) |
| Polynemidae (threadfins) |
| Scianidae (drums, croakers) |
| Mullidae (goat fishes) |
| Cichlidae (cichlids) |
| Gobiidae (gobies) |
| Scatophagidae (scatties) |
| Siganidae (rabbit fishes) |
| Sphyraeinidae (barracudas) |
| Stromateidae (ruffs) |
| Cynoglossidae (tonguefishes) |

[a] Sources: Macnae, 1974; Hamilton and Snedaker, 1984; Matthes and Kapetsky, 1988; Singh et al., 1994.

### 2.2. Crustaceans

Mangroves are important nursery areas for many commercially important shrimp and crab species throughout the tropics (Macnae, 1974; Dall et al., 1990). In terms of value per unit catch and total value of catch, the penaeid shrimps are among the most important resources for coastal fisheries worldwide (Dall et al., 1990). Many species of palaemonid shrimps are also associated with mangroves, including the commercially important giant freshwater shrimp, *Macrobrachium rosenbergii* (Macnae, 1974; Matthes and Kapetsky, 1988; Singh et al., 1994). Mangroves also support vast numbers of small shrimp of which *Acetes* spp. (Sergestidae) are the most important to fisheries (Macnae, 1974; Macintosh, 1982). These shrimps are partially dried and made into a fermented paste that forms a key ingredient in South East Asian cooking.

The mangrove crab fauna is of major ecological and economic importance (Macnae, 1974; Macintosh, 1982; Matthes and Kapetsky, 1988), including the high-priced mangrove mud crab, *Scylla serrata*. Distributed from eastern Africa to the central Pacific, this crab is abundant enough to support local fisheries and aquaculture operations throughout the Indo-West Pacific region. In addition to *S. serrata* there are minor fisheries for some of the larger species of mangrove sesarmid crabs in Burma and Thailand. In the Eastern Pacific, Twilley et al. (1993) reported that in Ecuadorian mangroves the ocypodid crab, *Ucides occidentalis*, occupies a similar fishery niche as *S. serrata* in the Indo-West Pacific.

### *2.3. Molluscs*

Mangrove estuarine areas often support an abundance of mollusc species that are largely sessile in nature and constitute an important insitu fishery (Macnae, 1974; Macintosh, 1982; Hamilton and Snedaker, 1984; Matthes and Kapetsky, 1988; personal observation). Edible species of oysters, mussels, cockles, and gastropods are collected extensively for local consumption, usually by the families of local fishermen. Mangrove roots and lower parts of trunks provide substrate for oysters and mussels. Because these animals are filter feeders, they are confined to microhabitats below mean high water, and are usually only abundant in areas adjacent to open water (Macintosh, 1982; Menzel, 1991). The blood clam, *Anadara granosa*, and other cockles can be found in large numbers in mudflats on mangrove strands, where it lies partially buried in the sediment (Macintosh, 1982).

Historically the natural stocks of molluscs have been more than sufficient to meet market demands, resulting in no incentive for culturing molluscs like oysters, mussels and cockles (Macintosh, 1982; Hamilton and Snedaker, 1984). However, this situation has changed dramatically in many countries, due to overcollection and loss of previously productive mollusc beds through habitat destruction, pollution, etc. In many areas the harvestable yields are augmented by the provision of artificial substrates in the form of rafts, simple stakes, or ropes placed in the shallow waters of mangrove estuaries for settlement and growth of bivalve molluscs (Hamilton and Snedaker, 1984).

## 3. Mangroves as habitat for fish and shellfish

Mangroves dominate the intertidal zone of tropical deltas, lagoons, and estuarine coastal systems that receive significant inputs of exogenous material, but they can also be found colonizing the shoreline of carbonate platforms, developing from little or no terrestrial run-off (Duke, 1992; Twilley et al., 1993, 1996). Local variations in topography and hydrology result in the differentiation of ecological types of mangroves such as riverine, fringe, basin, overwash and dwarf forest (Lugo and Snedaker, 1974). The combination of different geomorphological settings, each with a variety of ecological types, contributes to the diversity of mangrove ecosystems, and their specific characteristics of structure and function (Duke, 1992; Twilley et al., 1993, 1996).

Mangroves are characterized by high abundance of fish, crustaceans and molluscs. Fish standing stock, ranging from 4 to 25 g $m^{-2}$ in intertidal mangrove habitat (reviewed by Rönnbäck et al., 1999), is much higher in mangrove habitat compared to adjacent coastal habitats (Robertson and Duke, 1987; Thayer et al., 1987; Blaber et al., 1989; Morton, 1990; Robertson and Duke, 1990). For instance, Robertson and Duke (1987) found mangroves in northern Australia to contain four to ten times higher fish abundance compared to adjacent seagrass habitats, and Thayer et al. (1987) reported fish to be 35 times more abundant in Florida mangroves compared to adjacent seagrass beds.

Several complementary hypotheses have been proposed to explain why many fish and invertebrate species utilise mangroves during at least one stage of their life cycle. The three most widely accepted explanations relate to food abundance, shelter from predation, and the hydrodynamic ability of mangroves to retain immigrating larvae and juveniles (Fig. 1). Spatiotemporal variations in the availability of food and shelter, and retention capacity, affect the quality of individual mangrove microhabitats for fish and shellfish. Identification of prime nursery and feeding grounds is therefore of central importance to mangrove conservation and management.

### 3.1. Food abundance

Because of the high primary productivity in mangrove systems (Birkeland, 1985; Robertson and Blaber, 1992), it has been suggested that fish and invertebrates occupying mangrove habitats do so mainly to utilise the food resource (Boesch and Turner, 1984; Robertson and Blaber, 1992; Singh et al., 1994). Primary production can be attributed to several sources: the trees themselves, their associated epiphytes (ongrowth), other larger plants, phytoplankton (microscopic, floating plants), and benthic microalgae. Carbon fixed by the trees is likely to be the main carbon source for fauna in systems with turbid waters and a relatively high proportion of forest to open water (Robertson et al., 1992). Where mangroves occur as fringing vegetation along coastal lagoons, or on small islands in relatively clear water, food webs are likely to be more complex (Robertson et al., 1992).

A crucial argument for the food supply hypothesis is that mangrove forests provide a higher abundance of food than adjacent coastal ecosystems. This was proven to be the case in a mangrove-lined estuary in northeastern Australia (reviewed by Robertson et al., 1992). During the major recruitment period of most fish into the system, zooplankton-feeding fish dominated the fish community. The diet of most juvenile fish caught during this recruitment period was dominated by crab larvae, which were two orders of magnitude more abundant in mangrove waterways compared to adjacent nearshore habitats.

Odum and Heald (1975) suggested that the principal flow in mangrove food web was mangrove leaf litter → saprophytic community (microbial decomposition) → detritus consumers → lower carnivores → higher carnivores. Annual leaf litterfall can be substantial; in northeastern Australia litterfall has been estimated at 8–10 t dry weight per ha, with a maximum of up to 20 t dry weight per ha (Clough, 1992). The mangrove crab fauna can consume or store 30–80% of this litterfall (Robertson et al., 1992). These crabs are consumed by fishes, and therefore constitute an important link at the primary consumer level in food webs, beginning with mangrove plant production and leading to higher level consumers harvested by humans. Small-sized sergestid and palaemonid shrimp, which feed mostly on mangrove detritus (Odum and Heald, 1972; Macintosh, 1982), are other key organisms in mangrove food webs by virtue of their immense abundance and their importance as prey for fish and shellfish (Xiao and Greenwood, 1993).

Stable isotope studies have indicated that seagrass, macroalgae and phytoplankton might be more important than mangrove leaf detritus as carbon source for some fish and invertebrate species (Primavera, 1996; Loneragan et al., 1997). For these species the role of mangroves as habitat may be more a result of the predation refuge offered or the lateral trapping capacity, rather than the food abundance.

### 3.2. Predation refuge

Mangrove environments function as predation refuges for larvae and juveniles of many fish and invertebrates (Boesch and Turner, 1984; Robertson and Blaber, 1992; Singh et al., 1994). For penaeid shrimps the major cause of mortality in estuaries and coastal areas is predation rather than food supply or physico-chemical factors (Dall et al., 1990). Minello et al. (1989) concluded that the number of postlarvae entering estuaries only partially explained the variability in recruitment of brown shrimp, *Penaeus aztecus*, to the fishery. Rather, the mortality of young life stages within the nursery habitat appeared critical in determining recruitment levels.

Juvenile fish and shrimp have been found to move substantial distances into the mangrove forest habitat at high tide (Vance et al., 1996; Rönnbäck et al., 1999), where they gain protection from predation by larger fish, which remain in or near mangrove waterways (Vance et al., 1996). The structural complexity resulting from mangrove roots, debris, and other vegetational structures of the intertidal habitat enhances the refuge aspect. Shelter is also created through shallow environments, high turbidity, and soft muds suitable for burrowing, all as a result of the sediment-trapping capacity of mangroves. These physical characteristics should be of major importance in reducing predation rates on ebb tides, when juvenile fish and shrimp concentrate in the open water of mangrove waterways. The shelter function of mangroves has also been attributed to lower abundance of large carnivorous fish compared to coral reef ecosystems (Section 4.1).

### *3.3. Lateral trapping*

About 70% of all marine invertebrate larvae are pelagic, and these adaptations facilitate dispersal and colonization (Thorson, 1950). Planktonic larvae spawned offshore, but utilising mangroves as nursery habitats, e.g. many penaeid shrimp, face the problem of recruitment to and retention in this coastal ecosystem. The lateral trapping hypothesis focuses on the role of mangroves as a retention area for immigrating early life stages that would otherwise be swept away by currents and tidal action (Chong, 1995; Chong et al., 1996). The presence of mangroves greatly increases the residence time of the water, which is particularly prominent in the upper reaches of flat, wide mangrove forests with high-complexity waterways (Wolanski and Ridd, 1986). This reflects the need for extensive and wide mangrove forests in retaining immigrating young stages of fish and invertebrates of direct and indirect importance to fisheries and aquaculture.

## 4. Biophysical interactions with other coastal ecosystems

Although mangroves, seagrass beds, and coral reefs can exist in isolation from each other, they commonly form integrated ecosystems of high productivity that generate a diversity of ecological services (Moberg and Folke, this issue). Many of these ecological services constitute an important support to the productivity and sustainability of capture fisheries and aquaculture operations. A coastal seascape perspective, where the biophysical interactions among mangroves, seagrass beds and coral reefs are acknowledged (Fig. 1), is therefore a prerequisite for the management and economic evaluation of seafood production from individual systems.

### *4.1. Animal migrations*

The larvae and juveniles of many fish and shellfish species utilise mangroves or seagrass beds as nursery grounds, whereafter they emigrate to other systems as adults or subadults (Ogden and Gladfelder, 1983; Parrish, 1989). This strategy should increase the survival rates and recruitment success of commercially valuable species harvested in other ecosystems, such as coral reefs and pelagic zones (Parrish, 1989). In this respect, the ability of mangroves to passively retain or actively attract immigrating larvae and juveniles is of critical importance to capture fisheries.

Given the high abundance of young organisms and their relative vulnerability during migrations, larger carnivorous fish are attracted to mangroves from surrounding systems such as coral reefs (Ogden and Gladfelder, 1983). Coral reef fish and invertebrate communities also include herbivores, whose feeding migrations are quantitatively important wherever reefs and vegetated habitats cooccur (Birkeland, 1985; Parrish, 1989; see also Holmlund and Hammer, in this issue).

### *4.2. Outwelling*

Much of the mangrove leaf production is unexploited by terrestrial animals and instead becomes available to surrounding waters through litterfall (Robertson et al., 1992). Large amounts of leaf litter are normally retained within the forest, but the rest is exported to nearshore areas as organic carbon and nutrients. This outwelling has long been considered to play an important role in enhancing production in other systems in the coastal seascape, and has been widely used as an argument for mangrove conservation (Parrish, 1989; Lee, 1995). However, mangrove leaf detritus is relatively refractory to decomposition and direct assimilation by fauna, and thus its importance to the productivity of surrounding systems has also been questioned (Rodelli et al., 1984; Birkeland, 1985; Lee, 1995).

The magnitude and direction of material fluxes between mangroves and adjacent coastal systems depends on the geomorphological setting, hydrodynamics, soil and vegetation types, the time frame of observation, and the substance in question (Robertson et al., 1992). Estimates of dissolved material fluxes between mangroves and nearshore areas vary widely and range from net imports of 73 kg/ha per year to exports of 443 kg/ha per year (reviewed by Robertson et al., 1992). In a detailed study in tropical Australia, the annual export of particulate organic matter was found to be 3322 kg/ha (reviewed by Robertson et al., 1992). However, this estimate does not include the movement of animal biomass, an aspect usually overlooked in mangrove mass balance studies (Robertson et al., 1992). Those species which spend their larval and juvenile phase in the mangroves but migrate to other habitats as adults may represent one important source of carbon input originating from mangrove primary production (see also Holmlund and Hammer, this issue). This is the case in north-eastern Australia, where many clupeid species, of no or low importance to capture fisheries, become prey for commercially important fish species like mackerel, once they leave their mangrove nursery (Robertson and Duke, 1990).

### 4.3. Physical interactions

Mangroves, seagrasses, and coral reefs interact by modifying their physical environment. Reefs function as a hydrodynamic barrier, dissipating wave energy and creating waters of low energy on the landward side (Ogden and Gladfelder, 1983; Birkeland, 1985; Ogden, 1997). This is of major importance to seagrass beds and mangroves, which thrive in the presence of those barriers. The reciprocal dependence on mangroves relates to the ability of this system to control coastal water quality (Ogden and Gladfelder, 1983; Birkeland, 1985; Ogden, 1997). The long residence time of water inside mangrove environments buffers the magnitude and frequency of salinity fluctuations in the coastal zone. Fresh water stored in mangroves may be lost through evapotranspiration as well as dissolving excess salt in mangrove sediment, reducing the volume of undiluted freshwater that reaches the coast. Another important feature of mangroves, and to a lesser degree also seagrass beds, is the trapping of particulate matter and assimilation of nutrients in river run-off. Mangroves also influence coastal water quality, while functioning as a flood control mechanism and as an effective binder of shoreline and riverbank sediments, thereby reducing erosion or scouring by waves and currents.

The influence of mangroves in stabilising water quality in the coastal zone can be of major importance to the functioning of nearby coral reefs. Sediments and accompanying nutrients are a major threat to coral reefs, which require oligotrophic (nutrient poor) waters of low turbidity for vigorous growth (Kühlmann, 1988; Goureau et al., 1997). The clearing of watersheds for agriculture, industry and tourism, and the destruction of coastal estuaries, seagrass beds and mangrove forests, acting as sediment traps, are therefore among the most damaging influences on coral reefs around the world (Ogden, 1997).

Do mangroves function as a net source or sink of particulate matter and nutrients? As mentioned previously, mangroves export part of their primary production as organic carbon and nutrients and thus fertilise adjacent waters, but at the same time mangroves are said to control water quality by trapping and assimilating sediments, organic material, and nutrients. The possible confusion about whether mangrove forests are net exporters or importers generally results from observations at different time scales (Robertson et al., 1992). The export of particulate carbon from mangrove systems can be substantial. During dry periods, with insignificant river run-off, the export of mangrove detritus could be important in sustaining production in adjacent systems. On the other hand, during periods of significant run-off, the trapping and assimilating functions of mangroves reduce fluctuations in salinity, turbidity and nutrient levels in coastal waters, and thus lower the stress on adjacent coastal ecosystems. This illustrates the importance of understanding and accounting for the spatiotemporal dynamics of the ecosystem that generates a flow of essential products and services.

## 5. The role of mangroves in sustaining aquaculture production

Mangroves support various types of aquaculture through a wide variety of mechanisms (Fig. 1). They help control erosion and protect against floods and hurricanes, and thus help protect aquaculture operations against these natural disturbances. The importance of these ecological services to aquaculture production depends upon the vulnerability of the site to disturbances and may be extremely valuable in certain areas, creating an incentive to preserve mangrove greenbelts along shorelines and riverbanks.

Deteriorating water quality in mangrove environments can have serious impacts on the marketability and sustainability of mollusc (Menzel, 1991; Beveridge et al., 1997) and shrimp aquaculture (Macintosh and Phillips, 1992; Beveridge et al., 1997). Therefore, the ability of mangroves to maintain good water quality, i.e. to abate fluctations in salinity and turbidity, reduce concentrations of pollutants, and control nutrient levels in coastal waters cannot be overstated. Larsson et al. (1994) estimated the mangrove ecosystem area needed to sustain a Colombian semi-intensive shrimp farm. The area of mangrove lagoons providing clean water to the ponds was estimated to be seven times larger than the shrimp pond, a figure that would increase with higher intensity of the farming system. Robertson and Phillips (1995) estimated that 22 ha of mangrove forest would be required to filter the nitrogen and phosphorus loads from effluents produced per hectare of intensive shrimp pond. However, it should be stressed that the environmental effects of this loading are virtually unknown, suggesting the use of the precautionary principle on this matter (Troell et al., 1999). Furthermore, the establishment of shrimp aquaculture usually results in massive mangrove deforestation and degradation in the area. As a consequence, the size of remaining mangroves are too small to assimilate all nutrients released, which increases the risk of self-pollution and subsequent collapse of the shrimp farm. The filtering capacity of mangroves can only be used successfully if the density of shrimp ponds is sufficiently low and ponds are located either towards the landward edge of the forest or on terrestrial areas inland.

The high productivity of mangrove forests provides food inputs to aquaculture systems. Organic material and nutrients can either be exported to adjacent open water habitat, where they enhance the production of cultured molluscs, or they can serve as a more direct input to landbased farming systems with suitable logistics. Larsson et al. (1994) estimated that bacterial and fungal films on mangrove leaf detritus made up 30% of shrimp food, corresponding to a mangrove area four times the size of the semi-intensive pond. Fish and invertebrates dependent on mangroves can also serve as feed inputs to aquaculture, either as direct ‘trash fish’ input or as ingredients in formulated feeds.

Perhaps the most important link between mangroves and aquaculture is the natural production of larvae and juveniles—or seed as they are known to the aquaculturist—of farmed species (FAO/NACA, 1995). Some countries have developed hatcheries for seed production of certain species, whereas many countries still depend on wild seed for stocking. Wild seed is either collected from natural habitat and subsequently placed in aquaculture systems, or allowed to enter farming systems naturally through tidal entry of fish and crustaceans into land-based systems, or by settling of mollusc seed on artificial substrates.

The productivity of mangrove mollusc culture can be severely limited by low availability of seed (Hamilton and Snedaker, 1984; Menzel, 1991), which is aggravated by the destruction and deterioration of natural spatfall (larvae production) areas, i.e. mangroves. For milkfish, *C. chanos*, the principal tropical marine fish species reared in coastal mangrove ponds, shortage of wild seed can also be a serious constraint to increased production (Macintosh, 1982). In the Larsson et al. study, the largest support system by far was the mangrove nursery area for shrimp postlarvae, which ranged between ten and 160 times the area of a semi-intensive shrimp farm, depending on the quantity of wild-caught postlarvae, stocking densities in ponds and larval density in the mangrove. Therefore, the destruction of mangrove habitat will exacerbate existing shortages of postlarval shrimp, which is the primary constraint on increased production of cultured shrimp in many countries (FAO/NACA, 1995). The development of hatcheries for cultured shrimp and fish species may have reduced the dependence on mangroves to produce seed, but has increased demand for wild-caught female spawners instead. The deforestation of mangroves has also led to a shortage of broodstock, resulting in movements of animals (including exotic strains and species) within and between countries and with implications for spread of disease and dilution of wild genetic material (Beveridge et al., 1997).

## 6. The economic significance of mangroves in seafood production

### *6.1. Capture fisheries*

Below I review economic evaluations of mangroves in sustaining capture fisheries production. Studies which fail to provide adequate information on how the value was derived or lack reasonable methodology are not included. Original calculations, based on productivity estimates for some fisheries, are also presented. The objective is to outline the potential of some fisheries, rather than assigning an economic value to all mangrove-associated fisheries. Economic values predominantly represent gross financial benefits, and are calculated by using market prices to assign values.

Comparing market values from previous studies needs to be done with some caution, due to differences in inflation rates and in market prices of the same fishery products between countries. Therefore, the productivity by biomass should be included in the presentation, but unfortunately this is not always the case. Economic valuation is also context-specific. To ask about the value of a hectare of mangrove without relating it to a specific decision situation is not very meaningful from a standard economic perspective (Barbier et al., 1994).

One major weakness of previous evaluations of mangroves and capture fisheries production is the number and type of fisheries included in the analysis. The economic value of mangroves is usually underestimated, since only one or a few species of commercial importance are included in the evaluation, not acknowledging the large number of fish and shellfish species associated with mangroves. This is in part due to the fact that many species are harvested outside mangrove environments, even if they are dependent upon this system during early life stages. Hence, the important link between mangroves and harvested fish and shellfish is not always perceived. Another reason is that a significant proportion of the fisheries catch is non-marketed subsistence harvest, which is not included in national fishery statistics. Due to lack of reliable catch data, the actual value of subsistence fisheries is usually underestimated. However, some studies have illuminated its significant importance. The contribution of subsistence fisheries to total catch supported by mangroves was estimated to 10–20% in Sarawak (Bennett and Reynolds, 1993), 56% in Fiji (Lal, 1990), and 90% in Kosrae (Naylor and Drew, 1999). Therefore, any economic analysis trying to estimate the value of mangroves to fisheries, without recognizing their contribution to subsistence economies, will be incomplete.

#### *6.1.1. Penaeid shrimp*

Penaeid shrimps are the most economically valuable fishery resource associated with mangroves, due to their abundance and very high market price. Positive correlations between offshore yield of shrimps and amount of mangrove forest in the nursery area have been demonstrated throughout the tropics (Table 3). Turner (1977) and Pauly and Ingles (1986) found a correlation between latitude and penaeid catch, with increasing catches towards the equator. Turner (1977) attributed this to temperature, food availability, and changes in the amount of time needed for shrimp growth in estuaries. Moreover, Pauly and Ingles (1986) found a logarithmic relationship between mangrove area and shrimp production, implying that the shrimp fisheries impact of reducing mangrove area becomes greater as the remaining area is reduced. Estimates of annual economic value per hectare of mangrove ranges from US$91 (1 ha of mangrove supports a penaeid fishery

Table 3
Annual production, market price and economic value per hectare mangrove for fisheries species utilising this habitat, linked with penaeid shrimp trawling or supported by mangrove outwelling

| Area | Production (kg/ha/yr) | Market price (US$/kg) | Value (US$/ha) | Source |
|---|---|---|---|---|
| *Crustaceans* | | | | |
| Penaeid shrimp | | | | |
| Indonesia | 16–165 | 7.00[f] | 112–1155 | Martosubroto and Naamin (1977) |
| Worldwide survey | 13–756[a] | 7.00[f] | 91–5292 | Turner (1977) |
| Peninsular Malaysia | 515 | 7.00[f] | 3.605 | Gedney et al. (1982) |
| Philippines | 130–350 | 7.00[f] | 910–2450 | Pauly and Ingles (1986) |
| Java, Indonesia | 161 | 7.00[f] | 1.127 | Naamin (1990) |
| Irian Jaya, Indonesia | 18 | 7.00[f] | 126 | Ruitenbeek (1994) |
| Perak, Malaysia | 670 | 7.00[f] | 4.690 | Singh et al. (1994); Chan et al. (1993) |
| Sumatra, Indonesia | 274 | 7.00[f] | 1.918 | Hambrey (1996) |
| Sergestid shrimp | | | | |
| Peninsular Malaysia | 63 | 0.30[f] | 19 | Gedney et al. (1982) |
| Malaysia | 29[b] | 0.30[f] | 9 | |
| Philippines | 113[b] | 0.30[f] | 34 | |
| Thailand | 89[b] | 0.30[f] | 27 | |
| Mangrove mud crab | | | | |
| Kowie, South Africa | 34 | 3.00[f] | 102 | Hill (1975) |
| Chanthaburi, Thailand | 13 | 3.00[f] | 39 | Christensen (1982) |
| Peninsular Malaysia | 15 | 3.00[f] | 45 | Gedney et al. (1982) |
| Andrah Pradesh, India | 17 | 3.00[f] | 51 | Macintosh (1982) |
| India, Madagaskar, Thailand | 17–23 | 3.00[f] | 51–69 | Sivasubramaniam and Angell (1992) |
| Kosrae, Micronesia | 64 | 5.50 | 352 | Naylor and Drew (1999) |
| *Fish* | | | | |
| Peninsular Malaysia | 549 | 1.00[f] | 549 | Gedney et al. (1982) |
| Fiji | 257 | 1.85 | 475 | Lal (1990) |
| Queensland, Australia | 5,840[c] | | 5330[h] | Morton (1990) |
| Perak, Malaysia | 900 | 0.80 | 713 | Singh et al. (1994); Chan et al. (1993) |
| *Molluscs* | | | | |
| Blood cockles | | | | |
| Perak, Malaysia | 500–750 | 0.28[g] | 140–210 | Macintosh (1982) |
| Edible molluscs | | | | |
| Negros Oriental, Philippines | 979 | 0.28[g] | 274 | NRMC and NMC (1986) |
| *Fish subsidised by penaeid trawlers* | 87–5,040[d] | 1.00[f] | 87–5040 | |
| *Discarded catch in penaeid fisheries* | 68–3,931[e] | 0.10[f] | 7–393 | |
| *Fish production from outwelling* | 3–33 | 1.00[f] | 3–33 | |

[a] Multiplied by a factor of 1.6 to convert 'head-off' to 'head-on' values (Pauly and Ingles, 1986).
[b] Mean catch (1992–1996) of sergestid shrimps (FAO, 1998) related to mangrove cover (Spalding et al., 1997).
[c] Fish standing stock.
[d] Trawl catch subsidised by penaeid shrimp fishery (667 kg fish:100 kg shrimp) (Turner, 1977).
[e] Catch ratio, 520 kg discarded catch:100 kg shrimps (Alversson et al., 1994).
[f] Assumed market price at present.
[g] Average market value of mussels in Southeast Asia in 1992 (FAO, 1995).
[h] Includes only large-sized marketable fish (valued at Australian $8380).

production of 13 kg) to US$5292 (1 ha supports 756 kg) (Table 3). This high variability in shrimp productivity can be attributed to regional variations in the quality of the mangrove nursery, underreporting of fisheries catch, underdeveloped or overdeveloped shrimp fisheries. In addition, shrimps landed in one area may have been caught in another, and thus the shrimp productivity in the landing area may be overestimated. The average annual penaeid production, based on 43 data sets (summarized in Table 3), is 162 kg/ha mangrove, estimated at US$1134 (based on a market price of US$7.00/kg). Moreover, because penaeid shrimp sales generate most of the revenues from mechanized trawling in developing countries, shrimps (and indirectly mangroves) effectively subsidise commercial fish harvesting efforts by these vessels, including fish species not using mangroves as habitat (Turner, 1977; Bennett and Reynolds, 1993). Trawl catch ratio between marketed fish and penaeids in Indonesia was 667 kg of fish for every 100 kg of shrimps trawled (Turner, 1977). In addition, the discarded catch from shrimp trawling has a potential value if landed and utilised for human consumption or processed into fish meal. The mean ratio of discarded to landed weight in shrimps is 5.20 globally, with a maximum recorded ratio of 14.7 for Trinidadian shrimp trawling (reviewed by Alversson et al., 1994). Roughly speaking, 1 ha of mangrove generating a penaeid fishery production of 162 kg, sustains a market value of US$2340 from penaeid shrimp fishery (US$1134), discarded catch (US$126), and subsidised trawl fisheries (US$1080) alone.

#### *6.1.2. Fish*

The market value of commercial fish species utilising mangroves as habitat ranges from US$475 to 5330 ha/year (Table 3). Morton (1990) based his calculations on field sampling from a subtropical mangrove in eastern Australia. Twice a month during a whole year, the same 3340-m$^2$ area of *Avicennia marina* was sampled with block nets. The total biomass of fish caught over the year was as high as 5840 kg/ha. From the total annual catch Morton (1990) made a conservative estimate of the market value, which equaled US$5330/ha mangrove. However, this value only included marketed fish value, and did not account for the numerous commercially important juveniles caught in the study. In Perak, Malaysia, 39 000 t of mangrove-dependent fish were landed in 1990, valued commercially at US$31 million (Singh et al., 1994). Divided by the areal extent of mangrove in this state (Chan et al., 1993), the annual production of fish would be 900 kg/ha, supporting a market value of US$713.

#### *6.1.3. Coastal seascape perspective*

Through biophysical interactions, mangroves also support fisheries where the harvested species themselves never visit mangrove environments. The export of organic carbon and nutrients from mangroves constitutes a trophic subsidy to fisheries production. In an estuarine-lagoon system, the ratio of potential maximum sustainable fish yield to primary production by weight ranges from 0.0008 to 0.01 (Marten and Polovina, 1982). The potential fish yield supported by mangrove outwelling ranges from 3 to 33 kg/ha (Table 3), based on this ratio and a particulate carbon export of 3300 kg/ha per year (Robertson et al., 1992). The role of mangroves in maintaining coastal water quality indirectly supports the functioning and fisheries production of other ecosystems like coral reefs. Reefs have high fish standing stocks, and annual fisheries production has been estimated to be as high as 370 kg/ha (Alcala, 1988). Reef fisheries harvest many high-valued species, resulting in high market value for these fisheries. An excellent example of how to address the impact of sedimentation on coastal ecosystems is seen in a case study of resource-use conflicts, logging versus fisheries and tourism, carried out in Palawan, Philippines (Hodgson and Dixon, 1988). The competition between these industries was indirect through major ecosystem links. Erosion from coastal logging operations produced negative downstream effects on the marine ecosystem via sedimentation, and posed a threat to the viability of the coral reef tourism and the fishery industries. The results of this study were striking, with the gross revenues under the no-logging-option more than doubling those of the continued-logging-option (Hodgson and Dixon, 1988).

### 6.2. Aquaculture

The economic profit from aquaculture systems in mangrove environments is dependent on the support capacity of mangroves (Fig. 1). However, this 'free' support is not internalised in the market price of the product. The erosion control and protection against floods and hurricanes provided by mangroves could be valued by using the replacement cost of building hard protective structures in its place. In peninsular Malaysia, Chan et al. (1993) estimated this cost at US$3 million per kilometre coastline. Costanza et al. (1997) estimated the disturbance regulation to be worth US$1800/ha mangrove annually.

The susceptibility to self-pollution and subsequent collapse of aquaculture systems can be reduced if pond operation logistics enables the assimilation of effluents by surrounding mangroves. The value of this service should be compared with the cost involved in nitrogen and phosphorous reduction in conventional water treatment systems. The overall waste treatment function of mangroves has been estimated at US$6700/ha per year (Costanza et al., 1997).

Products like seed, broodstock and fishmeal ingredients have a market price, and if the productivity of these organisms is known, an economic value per mangrove area can be estimated. The opportunity cost of wild seed collection, resulting from discarded bycatch, should be included in an economic analysis of this activity. The collection of larvae and juveniles can be substantial in many countries. For instance, around 50 000 persons are involved in penaeid postlarvae collection in West Bengal, India (FAO/NACA, 1995). The favoured species for shrimp culture, i.e. *Penaeus monodon*, constitutes a very small proportion (down to 0.1%) of fish and invertebrate larvae in seed collector's catch (Primavera, 1998). Thus, the bycatch can be substantial, having significant negative impacts on biodiversity and capture fisheries production in the area.

## 7. Conclusion

This article illustrates the essential role of mangrove ecosystem in sustaining such human activities as capture fisheries and aquaculture. The amount of seafood production that can be supported by mangroves shows spatiotemporal variations throughout the tropics and subtropics. Therefore, when evaluating mangroves for seafood production or discussing management from a fisheries perspective, mangroves have to be viewed as dynamic ecosystems with non-linearities, thresholds and discontinuities (Costanza et al., 1993).

For crustaceans (penaeid shrimp, sergestid shrimps and mangrove mud crab), fish and molluscs that use mangroves as habitat the annual market value of fisheries per hectare mangrove ranges from US$750 to 11 280. If discarded catch in shrimp fisheries and other trawl fisheries subsidised by the penaeid fishery are included, the marketed value of fisheries dependent on mangroves ranges from US$850 to 16 750/ha per year. This value is eight to 170 times higher than previous capture fisheries values in the order of US$100 often used in cost-benefit analysis of management alternatives for mangroves (Christensen, 1982; Ruitenbeek, 1994; Janssen and Padilla, 1997). These lower market values must be considered as grave underestimates, given the information outlined in this article. Unfortunately, undervaluation is a major driving force behind the conversion of mangroves into alternative uses like shrimp pond farming. In part, this trend of undervaluation is due to the difficulty involved in placing a monetary value on some of the mangrove-related fisheries. Lack of ecological knowledge and a holistic approach among those performing the evaluation may be even more important determinants. Additional research is needed to identify fishery species directly or indirectly associated with mangroves, and to obtain reliable catch data for these. Estimates of fisheries production from mangroves have mainly focussed on penaeid shrimps, and there is a severe lack of good productivity estimates for other fishery species. Another serious shortcoming of economic valuations has been the inability to acknowledge the biophysical support from mangroves to seafood production in other systems. Recognizing the importance of mangroves to subsistence economies should also be self-evident when evaluating the production of fish and shellfish. However, the failure to take this non-commercial direct use value into account is often a major factor behind policy decisions that lead to overexploitation of mangroves (Barbier, 1994).

The life-support functions of mangroves set the framework for sustainable aquaculture in the tropical coastal seascape. Ecological illiteracy has, however, often caused the development of aquaculture systems like intensive shrimp farming, known for their ecological and socio-economic unsustainability (Macintosh and Phillips, 1992; Primavera, 1998). Ecological services, including flood and storm protection, erosion control, and water quality maintenance are crucial for the sustainability of aquaculture systems. In addition, low availability of seed or broodstock is a serious constraint to increased aquaculture production in many systems. Ironically, this is aggravated by the destruction of mangroves to accommodate aquaculture activities. Although the economic profit from aquaculture systems in mangrove environments depends on the support capacity of mangroves, the market price of the cultured product does not capture most of the goods and services provided by the mangrove ecosystems. These 'free' goods and services would require considerable amounts of energy and money if they were to be substituted with human technology based on fossil fuels. By internalising this 'free' support from mangroves, the market price of the product would increase significantly, thereby jeopardizing the economic sustainability of the aquaculture system itself.

Finally, it should be emphasized that this article has only focused on seafood production supported by mangrove ecosystems. Additional efforts to evaluate natural products and ecosystem services generated by mangroves (Table 1) would further demonstrate the dynamics of this system, and highlight its value and support to subsistence, local, and national economies. With increasing ecological and socio-economic knowledge, the conversion of mangroves into development activities whose social costs far outweigh their benefits should be reduced.

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