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A review of mangrove and seagrass ecosystems and their linkage to fisheries and fisheries management

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**A review of mangrove and seagrass ecosystems
and their linkage to fisheries and fisheries
management**

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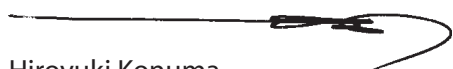
Foreword

In the tropical and sub-tropical regions of Asia, mangrove and seagrass habitats provide habitat for a wide range of species and plants, for some or all of their lifecycle. Many of these species are exploited for food and are the target of both artisanal and commercial fisheries. Mangroves provide a wide range of ecosystem services which are incidental to fisheries production, but important to coastal environments and the livelihoods of coastal populations. Mangroves provide a diverse range of fishery products, seed stock for some forms of aquaculture, forest products, timber and wildlife. The non-fishery ecosystem services of mangroves can include erosion control, mitigation of pollution and protection from storm or tsunami events.

There is a widely held perception that mangrove and seagrass habitats underpin fish and shrimp fishery production by acting as a nursery habitat for commercially important fisheries species. However, the decline or degradation of these habitats and their apparent role in the lifecycle of fish and invertebrates gives rise to the question as to why large cumulative losses of these habitats have not been matched by commensurate declines in fishery production of these commercial species.

This review brings together the findings in the scientific literature on the extent of mangrove and seagrass habitat and any relationships they may have to fisheries production. In doing so, it reveals that some popular perceptions regarding the role of mangroves and seagrass in fisheries production may be overstated or incorrectly interpreted. The review also finds that the linkages between fisheries and mangrove or seagrass vary both according to species and life stage and needs to be evaluated on a case by case basis. This does not diminish the value of mangrove and seagrass habitats and emphasizes the need for a more holistic approach to the management of coastal environments and the fisheries within them. This approach must adequately take into account the complexity and interactions between adjoining habitats, and the overarching need to manage fishing activity, especially fishing effort.

This review provides an excellent overview of our state of knowledge of how mangrove and seagrass habitats interact with fisheries and concludes with recommendations on where our knowledge must be strengthened. In particular, the review concludes that studies on species specific life histories, and on the ecological connectivity between adjacent biotopes, are needed to clarify more explicitly the nature of any relationship between mangrove and seagrass habitats and fish or shrimp populations. It is expected that further studies using more sophisticated methods and statistical techniques will clarify more explicitly the nature of any relationship between mangrove and seagrass habitats and fish populations.



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Summary

This report is based on a review of the literature on the extent of mangrove and seagrass habitats and their relationship to fisheries production. The review focused on the apparent conundrum that despite there being a widely held perception that these habitats support fisheries production by acting as nursery habitats for commercially important fisheries species, in most cases large cumulative losses of habitats have not been matched by commensurate declines in fish production.

In order to explore the relationship between fisheries production and mangrove and seagrass habitats, the review addressed the following questions:

- To what extent are mangroves and seagrass important as fisheries habitats for fish caught directly in these habitats or for subsequent fisheries production?
- What attributes of mangrove and seagrass environments contribute to their value as fisheries habitats?
- What aspects of mangroves and seagrasses attract and/or maintain larval and juvenile populations of fish and invertebrates?
- Are there quantitative or qualitative links between changes in the extent or quality of mangrove and seagrass areas and fish production (yield)?
- If so, what is the relative importance for fisheries production of qualitative aspects of mangrove and seagrass habitats compared with the extent or area of these habitats?
- Is it possible to distinguish between changes to fisheries production resulting from factors such as natural and seasonal variation, changes in fishing effort, and overfishing as opposed to changes in the extent and/or quality of mangrove and seagrass habitats?
- What trophic resources are available in, or derived from, mangroves and seagrasses?
- What measures are available to enhance, or expand, existing fisheries habitats?
- What evidence exists to indicate that habitat enhancement will result in increased fisheries production (or biodiversity, more generally)?
- What information gaps exist?

The review led to the conclusion that the pervasive view of the link between extent of habitat and fisheries production does not universally apply. Instead, there appears to be support in many cases for fish production differing between feeding guilds and species over space and time.

Analyses were complicated by environmental variability, individual species variability, large variations in catches from year to year, inadequate or unreliable data for fish catches and sometimes extent of habitat, and substantial changes in habitat extent over long time frames, although nearly all research studies were conducted over shorter periods.

Broad generalizations based on statistical inferences (correlations and regressions) about links between extent of habitat and fisheries production appear to be unsound and when they are corrected to take into account autocorrelations between variables, the results show different relationships.

Finally, a number of information needs are identified, especially studies on species-specific life histories, and on the ecological connectivity between adjacent biotopes, that if addressed could clarify more explicitly the nature of any relationship between mangrove and seagrass habitats and fish populations.

1. Introduction

Mangrove and seagrass ecosystems are widespread coastal and estuarine environments found in tropical and subtropical latitudes. These ecosystems provide habitat, shelter and food for numerous organisms, including some species that support important nearshore fisheries. This biotic interaction between mangroves and seagrasses and nearshore fisheries has often been invoked as grounds for mangrove conservation and sustainable use.

Over the past 50 years, approximately 30 percent of global mangrove cover has been lost.¹ It is also estimated that 30 percent of seagrass areas has been lost in the past 30 years. Much of this loss has occurred in the Asian region. These declines have caused concern because capture fisheries production is believed to constitute the major value of marketed products, and a basis for subsistence fishing from non-degraded mangrove forests.

The link between mangrove and seagrass areas and fisheries production is based on the well-established perception that these habitats serve as nursery areas for fisheries species. Many studies in various parts of the world suggest that these habitats provide a sheltered environment, protection from predators, supply abundant and diverse food and physically intercept and concentrate planktonic larvae.

It is now widely accepted that these habitat attributes of mangroves and seagrasses have an influence on the survival and recruitment of juvenile fishes and crustaceans, and that some of these species are important to commercial and subsistence fisheries.

These species are either exploited directly in seagrass or mangrove systems (e.g. shellfish, crabs, shrimp, some mangrove associated fish species) or further away from these systems where the juveniles have migrated to underpin the adult population (e.g. to coral reefs, or to other inshore coastal habitats). The mangroves and seagrasses also are thought to provide the food web support for fisheries species.

Despite strong inferential evidence, including correlations between production in some types of fisheries and the presence of mangrove and seagrass habitats, recent reviews of the literature² have shown that the direct effects of changes in mangroves and seagrasses on fisheries have not been unequivocally demonstrated.

The important questions that have emerged relate to the “missing links” between occurrence of juveniles of fish and crustacean species in mangroves and seagrass ecosystems and their ultimate contribution to adult populations. What is the relative importance of these ecosystems with respect to fish production, compared to other factors such as natural changes in abundance, seasonal or interannual variations, effects of fishing or targeting of larvae or broodstock? This point, in turn, raises the question of the role of connectivity between habitats as another potential influence on fish production both in terms of the effect on recruitment and how rehabilitation of these habitats may best be undertaken.

¹ Alongi (2002)

² Manson *et al.* (2005); Blaber (2007 and 2009)

This report elaborates the linkages between mangrove and seagrass ecosystems to fisheries productivity and diversity (coastal/inshore and offshore) and their relative importance within the broader context of fisheries management and habitat conservation. More specifically, this report:

- reviews past and recent literature to synthesize the information relating to the role of mangrove and seagrass ecosystems in the recruitment and abundance of aquatic species important to fisheries (both subsistence and commercial);
- reviews documented impacts on fisheries and species resulting from habitat change/removal/restoration, and compares this with the relative impact of other fishing effects;
- assesses objectively the likely benefits of habitat rehabilitation (e.g. what sort of rehabilitation is likely to have an effect and which species are most likely to be affected) in relation to other fishery management measures;
- provides guidance on ways to capture the positive effects of mangrove and seagrass ecosystems within a broader framework of fishery management; and
- provides policy advice for the Asia-Pacific region in relation to best practices for managing fisheries and mangrove/seagrass ecosystems.

2. Elements of the conundrum

Mangroves and seagrasses have long been considered important habitats for underpinning coastal fisheries, based on providing a sheltered physical environment, protection from predators, a physically complex structure that enhances the entrapment of planktonic larvae,³ and an abundance of food. In particular, these habitat characteristics appear to be of special significance to larval and juvenile fish and invertebrate species, resulting in these habitats being almost universally viewed as “nursery areas”⁴

This section frames the questions that need to be answered in order to elucidate whether mangrove and seagrass habitats function in support of fisheries, including those fisheries for which they may not be particularly significant.

2.1 The nursery area concept

It became generally recognized in studies of estuarine habitats in the second half of the twentieth century, that these areas often contained higher numbers or densities of juvenile fish and/or crustaceans and molluscs than other habitat types and so estuaries were termed nursery areas. By 2011, the development of the nursery concept had become so pervasive that it assumed considerable scientific authority. The nursery concept gradually became refined over time to apply to components of the estuary, then to assemblages of species, then to individual species.⁵

In a review of 75 major research papers concerned with mangrove and seagrass habitats and their associated fish and crustacean populations, 38 of the studies (>50 percent of the total) related to mangrove and/or seagrass habitats as nursery areas, based on the presence of juvenile fish and/or crustaceans.⁶ This provides an indication of the extent to which the nursery concept of estuarine habitats has become an embedded paradigm in the discourse on fisheries.

More recently, there has been a tendency to consider an area as a nursery if a juvenile fish or invertebrate species occurs at higher densities, avoids predation more successfully, or grows faster than in a different habitat. Most of the studies have focused on density of juveniles as a proxy for their contribution to the adult population.⁷

There are a number of definitions of nursery in the literature, ranging from simple to complex:

Simple definition:

A nursery is an area or habitat where there are higher concentrations of larvae and juveniles.

Simple definition:
A nursery is an area or habitat where there are higher concentrations of larvae and juveniles.

³ Chong, Sasekumar and Wolanski (1996)

⁴ Bell *et al.* (1984); Pollard (1984); Baran and Hambrey (1998); Manson *et al.* (2005); Faunce and Serafy (2006)

⁵ Beck *et al.* (2001)

⁶ The 38 papers comprised: twenty-three papers on mangroves; four papers on seagrasses; six papers on mangroves and seagrasses and five papers on experimental field studies of attributes of mangroves or seagrass habitats that supplied nursery values.

⁷ Beck *et al.* (2001)

This simplistic approach has been challenged and a more rigorous definition of a nursery area has been outlined.⁸ This definition states that a habitat is a nursery for juveniles of a species if its contribution per unit area to production of recruits to adult populations is greater on average, than production in other habitats in which juveniles occur.

Intermediate definition:
A nursery is an area or habitat where, on average, juveniles make a larger contribution per unit area to the recruitment of the adult population compared to other areas where juveniles occur.

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A nursery is an area or habitat where, on average, juveniles make a larger contribution per unit area to the recruitment of the adult population compared to other areas where juveniles occur.

This definition also has limitations because it focuses only on the comparison between areas, and does not take into account possible changes in sources of recruits over time. In particular, one area may produce more recruits during one period, and another formerly less productive area may produce more recruits at another time. It also does not take into account that many species show tidal/diurnal feeding movements among multiple habitats and are thus not restricted to a single nursery.

The definition of a nursery has been further refined to include the contribution of juveniles to the adult population, taking into account the unit area coverage of the particular habitat type, rather than total area.⁹

Complex definition:

A nursery is an area or habitat where, on average, juveniles make a larger contribution per unit area to the recruitment of the adult population, and overall contribute more recruits to the population than other areas where juveniles occur. (Dahlgren *et al.* 2006)

Both of these approaches can lead to differing conclusions regarding which habitat types are nurseries for particular species. More importantly, they are static measures – snapshots – that do not allow for changes over time.

Complex definition:
A nursery is an area or habitat where, on average, juveniles make a larger contribution per unit area to the recruitment of the adult population, and overall contribute more recruits to the population than other areas where juveniles occur. (Dahlgren *et al.* 2006)

The effect of scale is important when defining habitats.¹⁰ It is possible to consider nursery habitats as single structural habitats (i.e. sand, seagrass or mangrove), as single geographic units (i.e. a reef or estuary), or possibly as aggregations of structural units across various scales.

The scale of any habitat or collection of habitats is also determined by the natural history of the particular species being considered (e.g. those species such as *Cheilinus undulatus*, which moves from seagrass to coral reefs, or *Scarus guacamaia*, which moves from mangroves to coral reefs during their life-cycle).¹¹

It appears that the most effective means of assessing the juvenile contribution of a habitat (i.e. nursery value) is to directly measure the movement of individuals from juvenile habitat to the adult population using tags or natural or artificial markers.¹²

⁸ Beck *et al.* (2001)

⁹ Dahlgren *et al.* (2006)

¹⁰ Sheaves, Baker and Johnston (2006)

¹¹ Sheaves, Baker and Johnston (2006); Layman *et al.* (2006); Dorenbosch *et al.* (2006)

¹² Gillanders *et al.* (2003); Dahlgren *et al.* (2006)

Unfortunately, this type of research is uncommon and there is limited data available.¹³ As a result, mangroves and seagrasses are alluded to as nurseries simply because they support a relatively high abundance of juvenile individuals.

It is difficult to assess the production (based on abundance, growth, and survival) and export of individuals that utilize habitats of interest.¹⁴ Any one of these factors is difficult to measure and to measure all four simultaneously may not be possible in most situations.

As a result, there is a lack of information that can be used to quantitatively demonstrate the role of mangroves and seagrasses in supporting secondary production.¹⁵ This is particularly the case for fish, based on the more rigorous definitions of nursery habitats described above.¹⁶ This difficulty has led one group of researchers to conclude:¹⁷

“Until these data are gathered, the case for identifying flooded mangrove forests as critical nursery habitat for transient fishes and decapods remains equivocal.”

The effort that has been exerted to quantify the general nursery values of habitats is considerably greater than the effort directed towards species-specific life-history studies. An illustration of this¹⁸ comes from the First International Symposium on Mangroves as Fish Habitat published in the *Bulletin of Marine Science*. Of 60 abstracts from the symposium, 20 considered nursery/trophic functions of mangroves, 30 dealt with other topics, such as management, new techniques and habitat restoration and the remaining seven dealt with species-specific life-histories (all Caribbean species).

Life-history studies are essential to elucidate the different relationships that different species have with various habitats or biotopes. Until species-specific relationships are adequately known, it is not possible to assess how many species:

- are critically dependent on mangroves or seagrasses as nursery areas;
- facultatively use mangroves or seagrasses as nursery areas; or
- opportunistically use mangroves or seagrasses as feeding areas.

2.2 The “single habitat” approach

A further difficulty is that until recently most attempts to identify nursery habitats have relied on a “single habitat” approach¹⁹ in which a single structural habitat type is sampled, or compared with another single habitat type (e.g. mangroves, seagrasses, mudflats and creek banks have been studied and/or compared as though they are uniform habitats or biotopes).

“The most effective means of assessing the nursery value of a habitat, is to directly measure the movement of individuals from juvenile habitat to the adult population using tags or natural or artificial markers.”

¹³ Sheridan and Hays (2003)

¹⁴ Faunce and Layman (2009)

¹⁵ Sheridan and Hays (2003)

¹⁶ Beck *et al.* (2001); Dahlgren *et al.* (2006)

¹⁷ Sheridan and Hays (2003), p. 456

¹⁸ Serafy and Araújo (2007)

¹⁹ Meynecke, Lee and Duke (2007a)

This difficulty with comparisons arises because investigators have included different elements in their studies. Not all seagrass beds are equivalent, mudflats significantly differ in their sedimentological characteristics, and not all mangroves provide the same goods and services.²⁰

In order to provide some consistency and comparability, this review applies some definitions for these various biotopes (see below). It should be noted that these might differ from the definitions used in the actual research studies (in the cases where these were actually provided).

2.3 The challenge

Despite the inferred strong links between mangrove and seagrass habitats and fisheries species, quantitative evidence for a change in these habitats resulting in a change in associated fisheries production remains elusive.

In order to critically evaluate the generally held views of links between these habitats and subsequent fisheries production, and assist in enhancing any attributes that may improve fisheries, the following questions must be addressed:

- To what extent are mangroves and seagrass important as fisheries habitat for fish caught directly in this habitat or for subsequent fisheries production?
- What attributes of mangrove and seagrass environments contribute to their value as fisheries habitat?
- What aspects of mangroves and seagrasses attract and/or maintain larval and juvenile populations of fish and invertebrates?
- Are there quantitative or qualitative links between changes in the extent or quality of mangrove and seagrass areas and fish production (yield)?
- If so, what is the relative importance for fisheries production of qualitative aspects of mangrove and seagrass habitats compared with the extent or area of these habitats?
- Is it possible to distinguish between changes to fisheries production as a result of factors such as natural and seasonal variation, changes in fishing effort, and overfishing as opposed to changes in the extent and/or quality of mangrove and seagrass habitats?
- What trophic resources are available in, or derived from, mangroves and seagrasses?
- What measures are available to enhance, or expand, existing fisheries habitats?
- What evidence exists to indicate that habitat enhancement will result in increased fisheries production (or biodiversity, more generally)?
- What information gaps presently exist?

To address these questions, the recent literature was critically reviewed and the opinion of a panel of experts in the field (see Acknowledgements) was also sought.

²⁰ Ewel, Twilley and Ong (1998)

3. Mangroves as a structural fisheries habitat

3.1 Mangrove habitat

Defining what constitutes “mangrove habitat” is a challenge because of the diversity and variability of features that occur within the inundated, forested areas such as creeks, mudflats, saltflats, or partially forested areas with dwarfed or sparsely distributed trees. The landward boundaries of mangrove habitats are also problematic, particularly where the mangrove forest grades into another forest system, such as lowland rainforest, where the change may be gradual and virtually imperceptible. The definition of mangrove habitat adopted for this report is as follows:

Mangrove habitats are tidally inundated forests whether dense or sparse, and the associated tidal creeks and creek banks within the vegetated areas. This does not include mudbanks or sandbanks that are separated from the vegetated areas, or mangrove lands and that have been cleared/deforested.

3.2 Fisheries values of mangrove habitats

Mangrove systems, including their contained waterways, provide habitat for fish and crustacean species that have formed the basis of fisheries throughout the world.²¹ For example:

- Fish catches in mangrove waterways of the Philippines²² ranged from 1.3 to 8.8 kg hr⁻¹ throughout the year and the fish biomass of the total catch was positively correlated with the carbon content of the sediments and the mangrove litterfall.
- A study of three different mangrove areas over two years in southeast India²³ has reported that luxuriant mangroves supported a catch of 11 kg of shellfish per hectare per day and 4.5 kg of finfish per hectare per day, and that these catches are much greater than those from sparse mangroves in the same region.

This is not confined to fish species, as crustaceans and shellfish species are also commonly harvested within and around mangroves. Several species of penaeid shrimps are dependent on mangrove forests for shelter during their juvenile stages²⁴ (e.g. *Penaeus indicus*, *P. merguensis*, *P. monodon*, *P. subtilis*, *P. brasiliensis*, and most species of *Metapenaeus*).

Collecting molluscs such as oysters (*Saccostrea* spp.) and cockles (*Anadara* spp.) is an important subsistence activity in many mangrove areas.

Brushpark fisheries, consisting of mangrove sticks or branches placed in shallow waters in and around mangrove habitats, have independently developed in many mangrove regions and all show slight variations on the same theme.²⁵ These small, artificial mangrove thickets attract fish partly

Evidence for linkages between mangroves and offshore habitats by animal migration is still scarce, but essential for management and conservation purposes.

²¹ Saenger, Hegerl and Davie (1983); Hamilton and Snedaker (1984); Matthes and Kapetsky (1988)

²² Pinto (1987)

²³ Kathiresan and Rajendran (2002)

²⁴ MacNae (1974); Vance *et al.* (1990); Vance *et al.* (1996); Primavera (1998); Kenyon *et al.* (2004); Meagher *et al.* (2005)

²⁵ Saenger (2002)

by the availability of food (organisms attached to the plant material) and partly by the protection and shelter offered by the thickets. When a sufficient number of fish have congregated in the brushpark, it is enclosed with encircling nets and the fish harvested. Other designs, such as the brushpark traps used in the Republic of South Africa, guide the fish to a terminal trap where they are easily harvested. Various forms of brushparks are known in the People's Republic of Bangladesh, the Republic of Benin, the Federative Republic of Brazil, the People's Republic of China, the Republic of Ecuador, the Republic of Madagascar, the United Mexican States (Mexico), Independent State of Papua New Guinea, the Republic of South Africa, and the Democratic Socialist Republic of Sri Lanka.

Comparisons of fish densities between Old World mangrove sites have generally supported the contention that there is a nursery function for mangrove habitats, but often with high variance in the nursery value of mangrove habitat in any one region.²⁶ Even so, controversy remains about the importance of mangrove forests as nursery habitats for fish and invertebrates with several authors²⁷ concluding that:

“The evidence for linkages between mangroves and offshore habitats by animal migration is still scarce, but highly needed for management and conservation purposes.”

Although numerous studies²⁸ have now demonstrated that mangrove proximity influences the assemblages of fish and invertebrates, particularly juveniles, considerable variation in fish densities has been reported at different locations, and at least in one case, in adjacent habitats. Moreover:

- Studies that reported high densities of juvenile fish included locations at Gazi Bay, Kenya;²⁹ Florida, United States;³⁰ Queensland, Australia;³¹ Luzon, Philippines.³²
- Studies that reported low densities of juvenile fish in mangroves included different locations at Gazi Bay, Kenya;³³ subtropical Queensland, Australia;³⁴ Palmar, Ecuador;³⁵ and Iriomote Island, Japan.³⁶
- In temperate mangroves in Australia, a study showed that fish assemblages in mangroves differed from assemblages on mudflats 500 metres away,³⁷ but neither total abundance nor species richness differed significantly between mangroves and mudflats. Importantly, mangrove proximity did not influence fish distribution at a habitat scale.

²⁶ Daniel and Robertson (1990)

²⁷ Sheridan and Hays (2003); Manson et al. (2005); Nagelkerken *et al.* (2008, p. 155)

²⁸ Nagelkerken *et al.* (2000); Hindell and Jenkins (2004); Dorenbosch *et al.* (2004, 2006); Verweij *et al.* (2006); Mumby and Hastings (2008); Nagelkerken (2009)

²⁹ Crona and Rönnböck (2007)

³⁰ Thayer, Colby and Hettler (1987)

³¹ Robertson and Duke 1990a and Vance *et al.* (1996)

³² Rönnböck *et al.* (1999)

³³ Huxham, Kimani and Augley (2004)

³⁴ Halliday and Young (1996)

³⁵ Shervette *et al.* (2007)

³⁶ Nanjo *et al.* (2011)

³⁷ Payne and Gillanders (2009)

It must be emphasized that the composition of mangrove fish assemblages is determined by a combination of factors³⁸ that include the structural diversity of the habitat, the hydrological features (tidal range, current speeds, turbidity and salinity) and the nature of adjacent waters. As a result, the fish assemblage in any mangrove system is usually unique because of these site-specific factors and differences in their relative importance.

3.3 Factors underpinning mangrove habitat value

Mangroves are an important habitat for juvenile fish and shrimp.³⁹ Various attributes of mangroves that might be involved have been suggested including protection from predators by structural features or turbidity, the abundant availability of organic detritus and other food, and the generally sheltered, shallow and osmotically-favourable conditions.⁴⁰ The mangrove root system is also an important habitat for numerous species of epiphytic fauna and flora that form temporary feeding areas for fish from adjacent habitats.⁴¹

The relative importance of these various factors has generally been inferred indirectly from habitat use patterns by juvenile and small fish and/or their predators.⁴² For example:

- the sheltering effects of mangrove vegetation structures, such as complex above-ground roots, are mainly supported by results showing higher densities of juvenile and small fishes, or lower densities of carnivores in mangrove habitats than in unvegetated habitats;⁴³ and
- higher fish densities were found among standing pneumatophores than among hanging prop-roots, but there was no relationship with root surface area.⁴⁴

Such differences in fish densities, however, do not directly support the sheltering effects of mangrove vegetation structures, as these differences may result from other aspects of habitat preference, for example:

- some studies found that densities of small fishes are not always higher amongst complex vegetation microhabitats in mangrove estuaries;⁴⁵ and
- habitat preferences also vary considerably among different fish species, with some fishes occurring mainly in structurally complex habitats, suggesting that the sheltering function of mangrove vegetation structures may differ considerably among fish species.

What features of mangrove estuaries underpin the habitat value of mangrove-fringed waterways, particularly to larval, juvenile and small fish species and crustaceans?

Habitat preference is related to shelter from predation and availability of food.

³⁸ Blaber (2007)

³⁹ Lugendo *et al.* (2007a)

⁴⁰ Blaber, Brewer and Salini (1989); Sasekumar *et al.* (1992); Ruiz, Hines and Posey (1993); Blaber (1997); Primavera (1997); Ley *et al.* (1999); Laegdsgaard and Johnson (2001); Verweij *et al.* (2006); Rypel, Layman and Arrington (2007)

⁴¹ Thayer, Colby and Hettler (1987)

⁴² Beck *et al.* (2001); Manson *et al.* (2005)

⁴³ Blaber (2000)

⁴⁴ Rönnböck *et al.* (1999)

⁴⁵ e.g. Smith and Hindell (2005); Payne and Gillanders (2009)

Substrate provides biofilms and epiphytic fouling as a food source.

Recently, various experimental approaches have cast further light on the most important features underpinning the habitat value of mangroves to juvenile fish and crustaceans.

An experimental study⁴⁶ in Moreton Bay, southeastern Queensland tested the relative importance of three factors (structure, reduced predation and food) affecting the attractiveness of mangrove habitats to juvenile fish. Following the use of artificial mangrove root structures in the field and in the laboratory, it was found that structure was not usually attractive on its own, independent of other factors, such as association of structure with food. There was only a slight increase in fish numbers when structure was added. However, artificial root structures with accumulated algae attracted four times the number of juvenile fish, compared with unfouled structures, or no structure. The gut contents of the fish in the study matched the invertebrates found on algae that are epiphytic on mangrove pneumatophores.

It is important to note that although fish numbers did not differ significantly between treatments, there were significant differences in community structure indicating variation in habitat selection criteria between species of fish. Five species were more abundant in fouled stakes, suggesting that they were seeking food, whereas other species were attracted to stakes whether they were fouled or not, indicating that they were seeking shelter.

The presence of predators increases the preference for mangroves as shelter.

In tests on predation, juveniles of five species of fish that previously avoided shelter actively sought shelter when predators were added. Thus, predation pressure influenced habitat choice in juveniles fishes. However, larger fish did not seek shelter when predators were added to their tank, as they are apparently less vulnerable to predators.

In field studies,⁴⁷ it was found that the relative refuge value of seagrasses and mangroves were similar, but species richness and abundance of juvenile fish were greater in mangroves, suggesting greater accessibility to food. Feeding rates of larger fish were greater on the mudflats, which is the preferred habitat for these larger fishes. It was concluded that for juvenile fish entering an estuary, habitat selection is driven by risk of predation and availability of food. The preference for mangroves is because they provide more food and equivalent protection to seagrasses.

This also seems to be the case for shrimp, whereby structure often reduced predation pressure on shrimp by fish.⁴⁸

There are differences in function between night and day.

In another comprehensive study in Curaçao,⁴⁹ field experiments were undertaken to elucidate which factors make mangroves and seagrasses attractive habitats for juvenile reef fishes. These experiments used artificial seagrass leaves and artificial mangrove roots to provide structure, shade and food. The study concluded that:

- Diurnally active herbivores and zoobenthivores were primarily attracted by food.

⁴⁶ Laegdsgaard and Johnson (2001)

⁴⁷ Laegdsgaard and Johnson (2001)

⁴⁸ Macia *et al.* (2003)

⁴⁹ Verweij *et al.* (2006)

- Nocturnally active zoobenthivores and a piscivore were attracted by structure that offered some protection from predation.
- Although the importance of the various factors differed between feeding guilds and species during the day, all three factors – structure, food and shade – contributed significantly to the attractiveness of mangroves and seagrass beds to juvenile reef fish.

Comparisons of relative predation rates of juveniles of three fish species in mangrove root areas and unvegetated sand areas were undertaken using a tethering technique⁵⁰ in Iriomote Island, Japan.

Two of the prey species inhabited both the complex mangrove-root and unvegetated sand areas, although with different behavioural patterns. It is worth noting that the mangrove-root area harboured significantly greater numbers of resident piscivorous fishes, which suggests that the potential risk of predation in such areas is not necessarily low, a result also found in another study.

This casts some doubt on the general notion that more structurally complex microhabitats have lower predation mortality. However, the result obtained for the mangrove-root area specialist, *Apogon amboinensis*, showed significantly lower mortality rates in mangrove-root areas than in unvegetated sand areas. It was concluded that:

“The lower mortality rate of *A. amboinensis* in such a predator-rich area may be due to their anti-predator tactic associated with mangrove structural complexity, sheltering behind mangrove roots when disturbed by predators. The similar mortality rates of the other two species between microhabitats may have resulted from anti-predator tactics independent of mangrove vegetation structure, such as rapid flight and cryptic body coloration.”⁵¹

Artificial mangrove units (AMUs) have been used empirically to test the effects of water depth and sheltered waters on the attractiveness of mangrove prop-roots as fish habitat in the Caribbean.⁵² Although AMUs showed somewhat different fish densities than in natural mangroves, the experimental results nevertheless provide useful insights into those factors determining mangrove use by fishes, although (as the authors suggest) the broad application of these findings to all mangrove ecosystems should be done with caution.

To the extent that AMUs mimic real mangrove roots, the hypothesis that mangrove prop-roots are an attractive fish habitat because they are located in relatively shallow water of embayments can be rejected: AMUs located at greater depths attracted a higher number of fish and fish species.

Similarly, the hypothesis that mangroves are an attractive fish habitat because of sheltered water conditions can be rejected as AMUs placed in less sheltered locations, such as on coral reefs, attracted the same, or even higher numbers of fish and fish species. However, when the AMUs were

All fish utilize shelter from structures in the water, but only species that depend on mangroves as juveniles require the presence of mangrove structures to sustain their population.

⁵⁰ Nanjo *et al.* (2011)

⁵¹ Hammerschlag, Morgan and Serafy (2010)

⁵² Nagelkerken and Faunce (2008)

removed from the embayment, there was complete collapse of those species that used mangroves when juveniles: only mangrove nursery species showed a strong association with the complex structure provided by the mangroves. Water depth and shelter showed no differences in density or assemblages.

Subsequent studies⁵³ in Caribbean mangroves, used AMUs with different root architecture (including root length, vertical root orientation and three-dimensional root configuration) to investigate various fish community variables (abundance, number of species and community composition). Root length and three-dimensional structure had no effect on fish community variables. However, vertical pipe orientation had a significant effect, with AMUs with standing pipes showing higher total fish abundance and number of species than AMUs with hanging pipes. There were differences in fish usage of the pipe (root) structures, with demersal fish mainly occupying standing pipes and semi-pelagic fish occupying hanging pipes.

Habitat structure and shade increase epifauna (on the sediment surface and structures) but not infauna (within the sediments).

Habitat structure has also been shown to influence the benthic faunal community of mangroves. Manipulative experiments in Trang Province, Thailand⁵⁴ show that mangrove structural complexity (specifically canopy shade and root structures) enhanced the mangrove epifauna, but not the infauna. This enhancement was a result of shading and light attenuation effects, leading to conditions that mimic the conditions in undisturbed mangrove vegetation. Following 18 months of observation, species richness and abundance of epifauna were found to have increased under shade and shade plus structure treatments. However, structure and shade manipulations did not significantly influence infaunal variables.

Similar responses were reported from eight-year old mangrove plantations in Kenya,⁵⁵ with the re-establishment of an algal flora on pneumatophores and an increase in the epifauna with increasing shade.

Salinity changes might be a significant unrecognized impact in mangrove areas.

The significance of salinity in mangroves and associated waterways has rarely been evaluated critically. The Sine Saloum estuary in Senegal has been subject to drought since the 1970s and as a result has become a “reversed estuary” with salinity increasing upstream, reaching maximal levels of 100 parts per thousand. A three-year study⁵⁶ of the juvenile fish community was undertaken to ascertain whether the estuary still functioned as a nursery area for important fish stocks. The study also provided an opportunity to determine the relative importance of estuarine processes (particularly freshwater mixing) and mangroves on the nursery function. Based on the findings from Sine Saloum estuary, the study concluded that:

“Good estuarine conditions alone are sufficient for good nursery function but mangrove alone is not.”⁵⁷

⁵³ Nagelkerken *et al.* (2010)

⁵⁴ Kon, Kurokura and Tongnunui (2010)

⁵⁵ Crona, Rönnböck and Holmgren (2006)

⁵⁶ Vidy (2000)

⁵⁷ Vidy (2000, p.50)

The nursery role of mangrove estuaries is depressed when insufficient freshwater inflow occurs. A principle reason for this is that the egg and larval stages of some fish and shrimps are neither able to tolerate high salinity, nor able to regulate osmotically or ionically; they must occur in waters of physiologically appropriate salinities. These species are consequently reliant on estuarine brackish waters for egg and larval survival. Other species that rely on higher salinities may move out from mangroves during the wet season.⁵⁸

In summary, it is clear from these studies that mangrove habitats provide food sources, structure that shelters from predation, and physical properties of light and shade that support juveniles of fish species, and to that extent act as important juvenile habitats. In making this general conclusion, however, it must be remembered that many of the responses were different between different fish and shrimp species. For particular species, environmental attributes other than mangrove structure such as fluctuations in and absolute values of salinity, water temperature and oxygen content could be more important in determining fish assemblages or abundances.

3.4 Larval entrapment

There is some evidence that the hydraulic structure of mangroves enhances the entrapment of larvae, particularly penaeid shrimp mysis larvae.⁵⁹ This evidence shows that wind is not important for the shoreward transport of larvae, but that the dominant mechanism is via tidal currents with a strong cross-shore component. The larvae are washed into mangrove creeks where they become concentrated by lateral trapping at high tide, with such entrapment significantly amplified during spring tides. A conclusion of the above research was that if mangroves were to be removed, then

“not only will the channels silt ... but up to 50 percent less prawn larvae (from the spawning grounds) may be advected into southern Klang Strait and the loss rate of these larvae thereafter may double. This should measurably decrease the value of the prawn fishery.”⁶⁰

Mangroves play a function in trapping penaeid larvae distributed along coastlines.

⁵⁸ Lugendo *et al.* (2007b)

⁵⁹ Chong, Sasekumar and Wolanski (1996)

⁶⁰ Chong, Sasekumar and Wolanski (1996, p. 21)

4. Seagrasses as a structural fisheries habitat

4.1 Definitions and limitations

Seagrass beds, consisting of about 60 species of marine angiosperms worldwide, are found in shallow coastal waters throughout tropical and temperate oceans. Seagrasses all have prostrate stems buried in sand or mud and produce ribbon-like leaves on erect branches that can vary in length from less than a millimetre to half a metre or more. As a result, seagrass beds can be dense and of complex structure (e.g. *Enhalus acoroides*, *Cymodocea serrulata*, *Syringodium isoetifolium*, *Thalassia hemprichii* and *Thalassodendron ciliatum*) or may be sparse and/or of diminutive species such as *Halodule uninervis*, *Halophila ovalis* and *Zostera capricorni*. For this report, seagrass habitats are defined as marine meadows containing dense or sparse, complex or short grass-like vegetation, and New World species are treated as equivalent to Indo-Pacific species.

As with mangroves, the concept of “nursery function” of seagrass beds has been derived from the numerous studies that report higher densities of juvenile animals, particularly fish and shrimp/prawns, in seagrass beds than in adjacent unvegetated areas. The original nursery concept proposed that entire estuaries were nurseries and only subsequently elaborated into specific habitats (or biotopes) within an estuary acting as nursery areas. It is contended⁶¹ that the concept of a nursery must go beyond the numbers of juveniles and that a more holistic understanding of a nursery should incorporate considerations such as:

- higher survival, perhaps due to reduced predation;
- higher specific growth rates, due to the abundance of food resources; and
- the combined effects of these factors that are likely to result in more juveniles reaching the adult stage.

4.2 Fisheries values of seagrass meadows/beds

Seagrass meadows offer protection from larger predators to juvenile and small fish and larval shrimps, recycle nutrients, stabilize sediments and produce and export detritus.⁶²

The differentiation into leaves, stems and blades and the existence of epiphytic algae increases the complexity of the habitat and thus the range of different types of species that can occur.⁶³ The numerical abundance of species of invertebrates and fish within seagrass beds generally greatly exceeds adjacent unvegetated areas.⁶⁴

Evaluation of nursery functions of seagrass should go beyond numbers of animals and include effects on survival, nutrition and reduced predation.

⁶¹ Heck, Hayes and Orth (2003)

⁶² Kneib (1987); Heck, Nadeau and Thomas (1997); Heck, Hayes and Orth (2003); Heck and Orth (2006)

⁶³ Ooi *et al.* (2011)

⁶⁴ Ferrell and Bell (1991); Connolly (1994); Haywood, Vance and Loneragan (1995); Lee, Fong and Woo (2001)

Structure, rather than intrinsic properties of seagrass, seems to be the important determinant of the habitat value of seagrass beds.

A meta-analysis⁶⁵ of seagrass studies found that abundance, growth and survival of juvenile fish and crustaceans were higher in seagrass than in unstructured habitats, but not significantly greater when compared with other structured habitats such as oyster reefs or macro-algal beds. The conclusion of the meta-analysis was that structure *per se* rather than some intrinsic property of the seagrasses, was the important determinant of the habitat value of seagrass beds.

Benthic invertebrates within seagrass areas show higher diversity and abundance and/or higher biomass of species compared with unvegetated areas,⁶⁶ although it has been found⁶⁷ that differences in these parameters could also occur between dense and sparse seagrass beds.

In subtropical Florida, populations of macro-invertebrates in mangroves were higher than in seagrass or non-vegetated areas,⁶⁸ but in temperate seagrass beds in New Zealand, the densities and species richness of macro-invertebrates were higher than in adjacent biotopes, including those in mangroves and unvegetated sandflats.⁶⁹

Benthic enrichment of nutrients in seagrass beds is the result of a number of factors:⁷⁰

- seagrasses bind sediment with their root structures;
- the baffling effect of seagrass leaves accelerates accretion of fine material;
- seagrasses, through their enhancement of fine sediment accumulation, also play a significant role in nutrient cycling;
- seagrasses appear to accumulate nutrients (particularly organic forms) to a much higher level than bare sandy sediments in which seedlings become established;
- seagrasses have the means for efficiently removing nutrients from their leaves prior to leaf shedding; and
- seagrasses have functional roots and are thus able to take up nutrients both from the water column and from the sediments.

Apart from accumulating and cycling nutrients, seagrasses also contribute to nutrient export. Large masses of fruit and leaves are dispersed from seagrass areas and there is evidence that some nutrients leach out of the blades and are absorbed by epiphytic algae and diatoms. With the inclusion of the effects of grazing, particularly by fish and amphipods, there is the impression that there is a net loss of nutrients from the system. However, the input of detritus from epiphytes and the animals that inhabit seagrass areas, together with the somewhat reduced fine sediments that accumulate amongst seagrasses and bind nutrients, probably more than compensates for the apparent nutrient losses. Studies at Inhaca Island, Mozambique have shown that nutrient input from seagrass litter exceeds that from mangrove litter at the same location.⁷¹

⁶⁵ Heck, Hayes and Orth (2003)

⁶⁶ Bloomfield and Gillanders (2005)

⁶⁷ van Houte-Howes *et al.* (2004)

⁶⁸ Sheridan (1997)

⁶⁹ Alfaro (2006)

⁷⁰ Larkum, McComb and Sheppard (1989); Stapel *et al.* (1996)

⁷¹ de Boer (2000)

Seagrass beds increase nutrient enrichment of sediments and release significant amounts of nutrients to surrounding waters.

Commercial and recreational fisheries species are associated with seagrass beds including a range of shrimps (*Penaeus esculentus*, *P. semisulcatus*, *P. latisulcatus*, *Metapenaeus ensis*, *M. endeavori* and *M. bennettiae*), and numerous species of fish.⁷²

In addition, seagrass beds are important nursery areas for the Indian Ocean island wrasse, *Cheilinus undulatus*, the adults of which occur on coral reefs⁷³ and for the puerulus larvae and juveniles of rock lobsters (*Panulirus argus* in the Caribbean;⁷⁴ *Panulirus ornatus* in northern Australia⁷⁵).

4.3 Factors that underpin seagrass habitat value

As mentioned above, seagrass beds are characterized by highly variable structural complexity, including variable seagrass height, shoot density and plant biomass.⁷⁶ This complexity is generally considered the major factor responsible for faunal richness of seagrass habitat, in that it:

- provides a refuge against predators;
- attenuates strong water movements through sediment binding and baffling; and
- provides a range of varied microhabitats, and supplies a variety of food resources.

A review of “within patch structural complexity” concludes⁷⁷ that the protection from predation is one of the more important benefits derived from seagrass habitats. However, the response to seagrass complexity varies considerably between species and this will be discussed further in Chapter 11.

⁷² MacNae (1974); Pollard (1984); Bell and Pollard (1989); Macdonald (1991); Coles *et al.* (1993); Connolly (1994); Loneragan *et al.* (1998); Nagelkerken *et al.* (2001); Heck, Hayes and Orth (2003)

⁷³ Dorenbosch *et al.* (2006)

⁷⁴ Acosta and Butler (1997)

⁷⁵ Dennis, Skewes and Pitcher (1997)

⁷⁶ Ooi *et al.* (2011)

⁷⁷ Horinouchi (2007)

5. The importance of mangroves in nearshore food webs

5.1 The Florida model

The early studies in the Caribbean suggested that mangroves provide the primary carbon source fuelling detrital-based food webs and therefore that they represented the major route of energy flow in such systems.⁷⁸

These early models considered that solar energy and tidal dynamics were the principal factors in the amounts of nutrients generated and exported from mangroves. The internal biotic processes of litter and nutrient cycling were not considered, or thought to be insignificant. This modelling approach has become known as the Florida model.⁷⁹

This model is based on the assumption that leaf herbivory is a minor factor in nutrient cycling. An early example of this estimated a mean grazing effect on Florida mangrove leaves of only 5.1 percent of the total leaf area (range 0–18 percent on a leaf area basis).⁸⁰ Later work⁸¹ suggests that despite considerable geographic and interspecific variation, there is considerable leaf herbivory in mangroves, and this is likely to exert marked effects at the individual and community levels. Similarly it has been shown that *in situ* peat formation in mangroves comprises a substantial carbon sink.⁸²

5.2 Beyond the Florida model

The Florida model of organic matter production and fate provided the theoretical framework for mangrove trophic studies into the early 1990s.

Mass balance approaches estimated litter export from northeastern Australian⁸³ and Malaysian⁸⁴ mangrove systems, based on the difference between the rate of litter production and the amount remaining on the forest floor after high tide. According to the Florida model, any missing biomass was assumed to have been exported by tidal flow.

This assumption was challenged by studies of mangrove litter dynamics in northeastern Australia and Malaysia, and by the use of stable isotope analysis over traditional gut content analysis in determining real pathways of energy flow in mangrove ecosystems.⁸⁵ Studies using stable isotopes suggest that these early attempts at mass balance calculations must be interpreted with caution as particulate organic carbon (POC) of both marine and mangrove origin are present and cannot be distinguished on mass balance considerations alone.⁸⁶

The Florida model, an important (if flawed) early paradigm, overemphasized the export of mangrove material and underestimated internal cycling processes such as herbivory, peat formation or *in situ* reprocessing and decomposition.

⁷⁸ Golley, Odum and Wilson (1962); Heald (1971); Odum (1971) Odum and Heald (1972), (1975a and 1975b); Twilley (1995)

⁷⁹ Lee (1999)

⁸⁰ Heald (1969)

⁸¹ Reviewed by Saenger (2002)

⁸² Ong (1993)

⁸³ Boto and Bunt (1981)

⁸⁴ Gong and Ong (1990)

⁸⁵ Lee (1999)

⁸⁶ Rezende *et al.* (1990)

Internal cycling processes, such as leaf grazing by sesarmid crabs, drive the functioning and biodiversity of mangrove habitats and underpin their resilience.

A considerable amount of mangrove primary production is retained within internal, herbivorous and coprophagous pathways, rather than exported to external detrital pathways.

Subsequent investigations of the same system demonstrated that biotic processes within the system accounted for a significant fraction of the missing biomass.⁸⁷ Some of the missing biomass had been reprocessed by sesarmid crabs, which could remove about 28 percent of the litter produced in mixed *Rhizophora* forests.⁸⁸

Similar findings were subsequently reported from mangroves in Southeast Asia,⁸⁹ southeastern Africa,⁹⁰ and in other Australian mangroves.⁹¹ Recent studies in Ecuador have also demonstrated that crabs consume considerable quantities of mangrove leaf litter even in high tidal range neo-tropical systems.⁹²

5.3 Internal cycling

Amphipods play a significant role in litter reprocessing in mangroves. A study has shown that large populations (up to 7 000 m⁻²) of the amphipod *Parhyale hawaiiensis* occur in the mangroves of northeastern Australia.⁹³ Using measurements of faecal production as an index of feeding rate, it was shown that this amphipod could consume large quantities of decomposing *Rhizophora stylosa* leaves, with maximal faecal production in the order of 1 700 mg.dry weight.g⁻¹ amphipod.d⁻¹, depending on favourable salinity and food source conditions. Feeding rates were not significantly different over the salinity range 15-35‰, although significant decreases were noted at further extremes, i.e. 10 and 40‰.

The quality of organic matter is also enhanced by biotic reprocessing within mangroves, particularly by sesarmid crabs.⁹⁴ The faecal pellets of sesarmid crab contain finely fragmented mangrove material. These are low in deterrent chemicals such as tannins, and are readily colonized by microbes, thereby comprising the basis of a coprophagous food chain both in the mangrove benthos and among such planktonic consumers as copepods.⁹⁵

Insect herbivory is also widespread in mangroves, although accounting for only about 2 to 3.5 percent of the annual net above-ground primary production.⁹⁶

When taken together with the activities of crabs and amphipods, it seems clear that a considerable amount of mangrove primary production is retained within internal, herbivorous pathways rather than exported to external, detrital pathways suggested by the Florida model. It seems, therefore, that biotic reprocessing within mangroves may be more important than the export of leaf material from mangrove systems, at least on a regional basis.⁹⁷

⁸⁷ Boto (1982); Boto, Alongi and Nott (1989); Robertson, Daniel and Dixon (1991)

⁸⁸ Robertson (1986)

⁸⁹ Lee (1989)

⁹⁰ Micheli, Gherardhi and Vannini (1991); Emmerson and McGwynne (1992); Steinke, Rajh and Holland (1993)

⁹¹ Micheli (1993a and 1993b); Imgraben and Dittmann (2008)

⁹² Twilley *et al.* (1997)

⁹³ Poovachiranon, Boto and Duke (1986)

⁹⁴ Nielson and Richards (1989); Lee (1999 and 2008); Kristensen *et al.* (2008)

⁹⁵ Lee (1999); Kristensen *et al.* (2008)

⁹⁶ Lee (1991)

⁹⁷ Lee (1999)

When internal reprocessing is taken into account, organic export remains sizeable in some systems but considerably less than the total production.

According to the Florida model the principal energy pathway was considered to be from mangrove leaf detritus to bacteria and fungi and then to detritivores, which, in turn, were consumed by carnivores. This pathway was concluded from gut content analysis, which had revealed that more than 20 percent of material contained in the digestive tracts of all herbivores and omnivores in the estuarine mangrove system of Florida contained mangrove detritus. However, the ingestion of detritus does not necessarily imply any direct assimilation (energy transfer) of that material.

Initially, stable carbon isotope ratios ($\delta^{13}\text{C}$) were used to study assimilation, although later work has additionally used stable nitrogen ($\delta^{15}\text{N}$) and/or sulphur ($\delta^{34}\text{S}$) isotope ratios. As mangroves are depleted in ^{13}C (because ^{12}C is preferentially fixed in photosynthesis) the ratio of $^{13}\text{C}/^{12}\text{C}$ becomes more negative in mangroves and in organisms feeding on, and assimilating, mangrove organic matter. This conclusion is supported by various studies, for example:

- Mangrove detritus in the guts of inshore and offshore marine consumers in Malaysia was identified, however there was no isotopic evidence for any mangrove assimilation by offshore marine consumers.⁹⁸
- In a similar study, inshore juvenile shrimp showed limited mangrove carbon assimilation.⁹⁹
- Another study (using two isotopes) showed that the fiddler crab *Uca vocator* from a mangrove-fringed, land-locked lagoon in Puerto Rico differentially assimilated material from ingested sediments.¹⁰⁰ Benthic micro-algae were preferentially assimilated over mangrove detritus, indicating that the presence of mangrove detritus in the gut does not constitute evidence of an energy pathway.
- A study of three species of fiddler crabs (*Uca borealis*, *U. arcuata* and *U. lactea*) and several species of polychaetes in Taiwan Province of China,¹⁰¹ similarly showed that although mangrove carbon was the largest source at their study sites, it was not as important a source of assimilation to these consumers as particulate organic matter, benthic micro-algae and the wetland grass *Imperata cylindrica*.
- Other sesarimid crabs have also been shown not to depend on mangrove organic matter for their nutritional needs.¹⁰²

Penaeid shrimps, some of which are closely associated with mangroves, have been assumed to benefit from mangrove detritus. However, it has been shown that *Penaeus notialis*, *P. subtilis* and *P. brasiliensis* in a mangrove-fringed lagoon in Puerto Rico contained less than 25 percent detrital material in their diets, the bulk of which consisted of capitellid polychaetes and amphipods.¹⁰³

⁹⁸ Rodelli *et al.* (1984)

⁹⁹ Loneragan, Bunn and Kellaway (1997)

¹⁰⁰ France (1998)

¹⁰¹ Hsieh *et al.* (2002)

¹⁰² Lee (2005)

¹⁰³ Stoner and Zimmerman (1988)

Mangrove carbon production is considerable but may be less important than particulate organic matter, benthic micro-algae and non-mangrove wetland plants.

Although the carbon source in shrimps is dependent on their location within the estuary, the direct contribution of mangroves to the shrimp food web was insignificant.

Shrimp fishery catches and those of some fish species appear to be correlated with intertidal areas of mangroves; this seems, however, to be more related to structure rather than feeding.

Using three isotope ratios ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$), the amounts of carbon from mangroves, seagrasses and macro-algae/sediment incorporated into penaeid shrimps in northern Australia, particularly those species commonly associated with mangrove habitats e.g. *Penaeus merguensis*, were studied. Although the carbon source in shrimps depended a little on their location within the estuary, it was concluded that the direct contribution of mangroves to the shrimp food web was insignificant.¹⁰⁴

A study of the distribution, density and species composition of juvenile shrimps in three mangrove zones on the southeastern coast of India, found that shrimps were in higher densities in mangrove-lined waters than in neritic waters.¹⁰⁵ Using decomposing mangrove leaves in litter traps as shrimp larval attractors, it was found that there was about a threefold increase in catches around traps than in controls.

It was also found that larval shrimp catches gradually increased to a maximal abundance after between 30 and 40 days of decomposition. This increased catch coincided with the build-up of microbial biomass, including a significant increase in nitrogen-fixing azotobacters on the surface of the decomposing leaves, and it was concluded that the increase in nitrogen provided greater nutritional value to the juvenile shrimps.

Earlier studies, using correlation analyses, had indicated that penaeid shrimp standing stocks (yields) in particular correlated with intertidal vegetation,¹⁰⁶ mangrove areas¹⁰⁷ or length of mangrove shoreline.¹⁰⁸

Since then, a considerable body of data has been collected to suggest that shrimp and fish catches can be correlated with the available areas of intertidal vegetation, particularly mangroves. Correlations have been found for shrimp catches in the Philippines¹⁰⁹ and a review of the shrimp catches from 38 areas around the world and have found a highly significant relationship.¹¹⁰ There are also a number of clear cases of similar relationships in relation to finfish catches.¹¹¹

Extent of intertidal area, rather than areas of mangrove tree cover, seems to be a more important factor for shrimp yield.

Although statistically significant relationships between some species and mangroves have been demonstrated, the assumption of direct subsidy via mangrove detritus, (which is the central tenet of the Florida model), remains unconvincing, *but the role of the structured habitat provided by mangroves appears to be increasingly significant*. There are, however, increasing questions about the validity of correlative studies in elucidating causal linkages between fish production and mangrove area.¹¹²

A more recent re-evaluation¹¹³ of shrimp yield and mangrove data using principal-components analysis (which overcomes many of the statistical

¹⁰⁴ Loneragan *et al.* (1997)

¹⁰⁵ Rajendran and Kathiresan (2004)

¹⁰⁶ Turner (1977)

¹⁰⁷ Martosubroto and Naamin (1977); Loneragan *et al.* (2005)

¹⁰⁸ Staples, Vance and Heales (1985)

¹⁰⁹ Paw and Chua (1989)

¹¹⁰ Pauly and Ingles (1986)

¹¹¹ Blaber, Brewer and Salini (1989); Chong *et al.* (1990); Paw and Chua (1989); de Graaf and Xuan (1998)

¹¹² Robertson and Blaber (1992); Blaber (2009)

¹¹³ Lee (2004)

problems of auto-correlations inherent in correlation analyses) has shown that shrimp yield is most strongly related to the tidal amplitude.

In turn, this finding suggested that shrimp catch is influenced by the amount of intertidal area available and not merely by the area of mangroves.

Moreover, no significant relationship was noted between shrimp catch and relative mangrove area. Stable isotope studies support this view and have shown that the proportion of mangrove matter used as food for shrimps declines farther offshore, where phytoplankton and micro-algae form the bulk of a shrimp diet.

With fish, it was reported from a mangrove inlet in northeastern Australia that five main trophic pathways could be identified on the basis of $\delta^{13}\text{C}$ values of the various trophic levels:¹¹⁴ one based on both mangrove and micro-phytobenthos, one on plankton, two on both micro-phytobenthos and seagrass, and one based predominantly on seagrass, mediated by epibenthic invertebrates.¹¹⁵ The relatively greater reliance on the assimilation of seagrass from the diminutive *Halophila ovalis* when compared with that from mangroves, strongly supports the finding¹¹⁶ that seagrass herbivory is more pronounced in tropical systems.

Clearly, it seems that *in situ* degradation and recycling within mangroves is sizeable and the export of mangrove material, either as macro-detritus (leaves and wood) or as micro-detritus (particulate organic matter or dissolved organic carbon) is highly variable.¹¹⁷ This is particularly dependent upon the hydrodynamics of the estuaries and the mangrove-nearshore environment.¹¹⁸ Within estuaries, the axial convergence will tend to move macro-detritus upstream,¹¹⁹ whereas the stable coastal boundary layer water will reduce the extent of any outwelling from mangroves to offshore areas.¹²⁰

A more recent review of the use of stable isotope ratios, highlighted a number of methodological problems with these measures, particularly the failure to take the ^{13}C -depletion of estuarine phytoplankton into account.¹²¹ This review concluded that there was little evidence that mangrove carbon contributes substantially to faunal communities, either in tidal mangrove creeks or adjacent waters. This suggests that future studies need to sample all necessary components, including the estuarine phytoplankton, and to supplement these measurements with complementary chemical tracers, such as lignin-derived phenols.

Export of detritus – particulate or dissolved organic matter – is highly variable between systems, and this export is limited to immediate coastal areas.

¹¹⁴ The $\delta^{13}\text{C}$ value is a measure of the ratio of stable isotopes ^{13}C : ^{12}C .

¹¹⁵ Abrantes and Sheaves (2009)

¹¹⁶ Vonk, Christianen and Stapel (2008)

¹¹⁷ Robertson and Daniel (1989); Lee (1995); Mfiling *et al.* (2005); Rezende *et al.* (2007)

¹¹⁸ Wolanski *et al.* (1992); Stieglitz and Ridd (2001)

¹¹⁹ Stieglitz and Ridd (2001)

¹²⁰ Wolanski *et al.* (1992)

¹²¹ Bouillon *et al.* (2008)

5.4 Mangrove outwelling: hydraulic and biotic export

Most studies conducted in macrotidal mangrove communities suggest that mangroves serve as net exporters of organic carbon and nutrients, but that the amounts involved are highly variable in space and time.¹²²

There are, however, also reports of mangroves acting as net importers of organic carbon and nutrients, storing large proportions of litter production for *in situ* decomposition, mainly as a result of a restricted inundation regime.¹²³

A study of a mangrove system in Bragança, northern Brazil¹²⁴ investigated the driving forces behind the coastal outwelling of nutrients and organic matter from mangroves. It concluded that the tidal range and porewater concentrations were the major driving forces behind coastal outwelling. It was suggested (on the basis of equilibrated fluxes) that outwelling probably occurs only from mangroves where the nutrient concentration in porewater exceeds the demands of the benthic community and trees. This phenomenon is caused by rapid sediment accumulation rates or by high N-fixation rates. Importantly, outwelling only occurs in macrotidal regions where porewater can flow in considerable amounts to tidal creeks and the ocean.¹²⁵

The fate of this outwelling of organic matter and nutrients to mangrove creeks and nearshore areas is largely unknown.¹²⁶

Mangrove creeks and nearshore areas are known to act as nursery areas for some species of juvenile fish,¹²⁷ spiny lobsters,¹²⁸ and shrimp.¹²⁹ However, this function is largely dependent on the physical habitat conditions, including such features as the highly complex structure of the habitat with roots and pneumatophores offering shelter, turbidity and an array of osmotic refuges. The evidence for a direct trophic subsidy to this nursery function of mangrove creeks and nearshore areas from mangrove leaves or detritus is minimal, at best.¹³⁰

Indirect trophic subsidies cannot be ruled out at present. For example a study¹³¹ of mangrove inlets and creeks in Selangor, Malaysia, showed that they are the habitat for 119 species of fish and nine species of shrimps. The majority of fish and all shrimps sampled in the inlets were juveniles. This study concluded that:

¹²² Lee (1995); Simpson, Gong and Ong (1997); Dittmar and Lara (2001); Rezende *et al.* (2007); Kristensen *et al.* (2008)

¹²³ Twilley, Lugo and Patterson-Zucca (1986); Flores-Verdugo, Day and Briseno-Duenas (1987); Lee (1990); Alongi *et al.* (1998); Ayukai *et al.* (1998)

¹²⁴ Dittmar and Lara (2001)

¹²⁵ Dittmar and Lara (2001)

¹²⁶ Alongi (1998); Kristensen *et al.* (2008)

¹²⁷ Thayer *et al.* (1987); Robertson and Duke (1987, 1990a and 1990b); Laegdsgaard and Johnson (1995); Kimani *et al.* (1996); Halliday and Young (1996); Ley *et al.* (1999)

¹²⁸ Acosta and Butler (1997); Dennis *et al.* (1997)

¹²⁹ Staples (1980a and 1980b); Vance *et al.* (1990); Primavera (1998); de Graaf and Xuan (1998); Ahmad Adnan *et al.* (2002)

¹³⁰ Loneragan *et al.* (1997)

¹³¹ Sasekumar *et al.* (1992)

Tidal range and macrotidal regions, where porewater can flow in considerable amounts to tidal creeks and the ocean, are the major driving forces behind coastal nutrient outwelling from mangroves.

- “mangroves support fisheries by providing habitat and food”;
- the presence of juvenile shrimps in mangroves may be attributed to three main factors: shelter from predators, high food abundance, and turbidity; and
- whilst juvenile prawns may not derive nutrition directly from mangrove detritus,¹³² it is apparent that significant quantities of mangrove carbon are being assimilated through secondary sources.¹³³

More recent studies have shown that mangrove carbon may be assimilated by fish feeding on species, such as sesarimid crabs that feed directly on mangrove leaves¹³⁴ or through the utilization of faecal material from crabs by copepods.¹³⁵

The concept of biotic export from mangroves has not been critically evaluated, although it is often inferred.¹³⁶ It consists of ontogenetic migrations (as for example in barramundi, *Lates calcarifer*), where juveniles feed amongst mangroves and increase in biomass, which is then exported as the young adults move to the mouths of estuaries to spawn.

Biotic export can also result when young adults are washed out of mangrove waterways by monsoonal rains (as for example in banana shrimps, *Penaeus merguensis*¹³⁷ or by the larval export of grapsid and portunid crabs.

Although there are individual studies¹³⁸ providing direct evidence of export of fish from mangroves to adjacent coral reefs using stable isotope analysis, to date there are no comprehensive, quantitative estimates of the amount of biomass that is exported out of any particular area of mangrove.

It remains difficult to evaluate the role of biotic export compared with hydraulic export, or recycling within the system. Such data are urgently needed.

Although juvenile shrimps may not derive nutrition directly from mangrove detritus, significant quantities of mangrove carbon may be assimilated through secondary sources, including reprocessed mangrove material (e.g. crab faeces) as well as epiphytic or associated organisms (e.g. algae and amphipods).

Biotic export (nutrients bound in living material) from mangroves has not been critically evaluated and its relative significance, compared with hydraulic export and recycling, remains unknown.

¹³² Stoner and Zimmerman (1988)

¹³³ Sasekumar *et al.* (1992, page 206)

¹³⁴ Sheaves (2000)

¹³⁵ Lee (1997); Werry and Lee (2005)

¹³⁶ Saenger (1994)

¹³⁷ Staples and Vance (1986); Staples (1991); Vance *et al.* (1998)

¹³⁸ e.g. Nakamura *et al.* (2008)

6. The importance of seagrasses in nearshore food webs

Seagrass beds support distinct fish assemblages and generally higher fish densities and number of species,¹³⁹ when compared with bare sand or mudflat habitats.

Seagrasses in temperate and warm temperate waters are a direct source of food for a limited number of organisms, e.g. isopods, sea urchins, abalone, and some fish species (Odacidae, Monacanthidae, Tetraodontidae and Girellidae, Labridae, parrot fish, surgeonfish, leatherjackets and garfish). Seagrasses in the tropics are grazed by green turtles and dugong and in shallow water, waterfowl feed on *Zostera*.

Overall, however, grazing probably accounts for less than 5 percent of total production, although some studies¹⁴⁰ suggest a greater proportion is lost to fish grazing and it has been estimated¹⁴¹ that scarid parrotfishes consume an average of four times the daily growth of *Thalassia hemprichii* and *Enhalus acoroides*.

Stable isotope research has focused more critical attention on carbon assimilation, as with few exceptions it was generally held that the grazing of seagrasses, although limited, led to direct assimilation. Research studies using stable isotopes have subsequently revealed that assimilation of seagrass material was minimal, with greater assimilation of epiphytic algal material.¹⁴²

It is possible that there might be significant differences in the trophic role of tropical seagrasses when compared with temperate seagrasses.¹⁴³ It seems that tropical seagrasses have higher leaf production and faster turnover rates, lower fibre concentrations and higher carbohydrate concentrations than temperate seagrasses.¹⁴⁴ This increases the palatability and nutritional value of tropical seagrasses, giving them a more significant trophic role. In a study in Sulawesi, Indonesia, using stable isotopes, it was found that a large number of fauna species depended on seagrass material, including crustaceans, holothurids and herbivorous fish. These species had $\delta^{13}\text{C}$ values comparable to seagrass material, showing they predominantly (>50 percent) assimilated material originating from seagrasses.

Seagrass material can be incorporated directly by herbivores or omnivores via detritus by detritivores or indirectly via predation on the former species. Thus, small crustaceans incorporate seagrass carbon into their tissues and form an important part of the diet of fish species in tropical seagrass meadows.¹⁴⁵

Epiphytic algal material may be a more significant source of nutrients than seagrass itself.

Direct grazing of tropical seagrasses may contribute more to nutrients than in temperate zones.

¹³⁹ Ferrell and Bell (1991)

¹⁴⁰ e.g. Heck and Valentine (2006)

¹⁴¹ Unsworth *et al.* (2007b)

¹⁴² Yamamuro (1999); Lepoint *et al.* (2000); Moncreiff and Sullivan (2001); Smit *et al.* (2005, 2006)

¹⁴³ Vonk, Christianen and Stapel (2008)

¹⁴⁴ Dawes and Lawrence (1980); Klumpp, Howard and Pollard (1989)

¹⁴⁵ Lugendo *et al.* (2006); Unsworth *et al.* (2007a); Vonk, Christianen and Stapel (2008)

Seagrasses can also provide material for the detrital food chain. Initially, there is leaching of dissolved organic carbon from cut or broken leaf material into the water column. This is followed by mechanical breakdown of the remaining leaf material by turbulence or repeated ingestion, forming particulate organic carbon (POC). Some POC is removed by filter feeders. In turn, bacterial and fungal decomposition of POC occurs and this attracts bacteria-consuming microfauna and other detrital feeders. These microfaunal species become prey for larger animals.

7. Estuarine habitat connectivity

Mangroves and seagrasses and their special features can be considered as a particular case of an estuarine environment,¹⁴⁶ characterized by intermittently brackish tidal areas.

These estuarine environments are generally characterized by high productivity, which forms the base of a food web where zooplankton, mysids and shrimp provide abundant and diversified trophic resources to postlarvae and juvenile fish. High primary productivity is based on mangrove and seagrass litter, supplemented by the activity of benthic cyanobacteria, diatoms, microalgae, amphipods, copepods and epiphytic algae on mangrove roots, which in turn, allows the development of particularly dense zooplanktonic, then micro- meio- and macro-benthic fauna.¹⁴⁷

7.1 The importance of variety and connectivity of habitats

It should be noted that there are differences between mangroves and seagrasses in the fishery benefits they deliver.¹⁴⁸ For example, seagrasses often dominate in subtidal waters with higher clarity and are often seasonal in abundance, distinguishing their potential contribution to juvenile fish survival from that of mangroves, which mostly occupy more turbid settings with consistent structural complexity.

These differences are complementary and are likely to underpin the importance of the connectivity of these biotopes. There is increasing evidence of the important role of the estuarine mosaic, i.e. the close juxtaposition of different biotopes such as mangroves, seagrasses, coral reefs, mudflats and sandflats and rocky reefs.

The connectivity of these biotopes significantly enhances their ecological or functional values.¹⁴⁹ For example, studies have shown that:

- two species of penaeid shrimps were more abundant in tropical seagrass beds close to mangroves than in seagrass beds that were further away;¹⁵⁰
- seagrass beds close to mangroves had more fish species and fish numbers than beds far from mangroves;¹⁵¹ and
- more fish species used mangroves with adjacent continuous seagrass beds, than used mangroves with adjacent patchy seagrasses or unvegetated mudflats.

Furthermore, in the Caribbean, species richness and abundance of fish were significantly higher in seagrass beds of bays containing mangroves than in bays without mangroves,¹⁵² but were lower in mangroves and

The connectivity of different biotopes such as mangroves, seagrasses, coral reefs, mudflats and sandflats and rocky reefs significantly enhances their ecological or functional value as fisheries habitats.

¹⁴⁶ Baran and Hambrey (1998)

¹⁴⁷ Baran and Hambrey (1998); Alongi (2009)

¹⁴⁸ Lee, personal communication (2012)

¹⁴⁹ Fortes (1988); Yáñez-Arancibia, Dominguez and Dya (1993); Hemminga *et al.* (1994); Sheaves and Molony (2001)

¹⁵⁰ Skilleter *et al.* (2005)

¹⁵¹ Jelbart, Ross and Connolly (2007)

¹⁵² Nagelkerken *et al.* (2000 and 2001); Cocheret de la Morinière *et al.* (2002); Dorenbosch *et al.* (2004)

seagrass beds when compared with inshore and offshore coral reefs in Puerto Rico.¹⁵³

On Hainan Island, China, it was found that although fish abundance, biomass and species richness were lower in vegetated mangrove areas than on treeless mudflats and creeks, the mangrove estuarine mosaic of all three biotopes was a very attractive habitat for juvenile and small fish.¹⁵⁴

7.2 Importance of mangroves and seagrass for reef associated species

Studies in the Caribbean have indicated that seagrasses and mangroves form important nursery areas for fish, whose adults are confined to coral reefs.¹⁵⁵ Conversely, mangroves were found to be important habitats for relatively few species of coral reef fish in the Indo-West Pacific.¹⁵⁶

There is substantial variation in the use of mangroves by the juveniles of reef-associated fish species.

In the Indian Ocean, many juveniles of coral reef-associated fishes occur at high densities in mangroves, and there is an ontogenetic habitat shift from shallow- to deep-water habitats.¹⁵⁷ It was found that ontogenetic habitat shifts were not consistent across the localities studied and it was concluded that further insights can only be obtained with studies at various spatial and temporal scales to document accurately the spatial, seasonal and interannual variability in habitat use of each fish species. In fact, the low juvenile habitat fidelity suggested that ontogenetic habitat use is very flexible, and highly adaptable.

Ontogenetic habitat switches are known to occur in some species of fish and crustaceans between mangroves and seagrasses and other estuarine biotopes.¹⁵⁸ It appears that olfactory cues can be involved:¹⁵⁹ for example, megalopae of the blue crabs, *Callinectes sapidus*, orientate to nursery areas with seagrass beds using specific habitat odours,¹⁶⁰ and larval and juvenile fish are able to distinguish water plumes as chemical roadmaps to nursery habitats e.g. in the Apogonidae:¹⁶¹ French grunts, *Haemulon flavolineatum*¹⁶² and Spangled emperors, *Lethrinus nebulosus*.¹⁶³

The importance of the estuarine mosaic can be seen from a consideration of the habitat shifts juvenile fish undergo to maximize benefits:¹⁶⁴

“For small fish arriving at the estuary as post-larvae, the most important pressures governing habitat selection and/or differential survival among habitats are the risk of predation and the availability of food, both of which relate to the nature of physical structure.

¹⁵³ Aguilar-Perera *et al.* (2008)

¹⁵⁴ Wang *et al.* (2009)

¹⁵⁵ Cocheret de la Morinière *et al.* (2002); Mumby *et al.* (2004); Dorenbosch *et al.* (2006); Adams *et al.* (2006)

¹⁵⁶ Quinn and Kojis (1985); Thollot and Kulbicki (1989); Blaber and Milton (1990); Nakamura *et al.* (2008)

¹⁵⁷ Kimirei *et al.* (2011)

¹⁵⁸ Cocheret de la Morinière *et al.* (2002)

¹⁵⁹ Arvedlund and Kavanagh (2009)

¹⁶⁰ Forward *et al.* (2003)

¹⁶¹ Atema, Kingsford and Gerlach (2002); Gerlach *et al.* (2007)

¹⁶² Huijbers *et al.* (2008, 2012)

¹⁶³ Arvedlund and Takemura (2006)

¹⁶⁴ Laegdsgaard and Johnson (2001 p. 250)

Mangrove forests provide structure at an intermediate scale in which capture of invertebrate food prey by juvenile fish species appears optimal and risk from piscivorous predators is reduced. In other habitats within the estuary, such as seagrass beds, there is equal protection from predators but foraging success is reduced and therefore seagrass beds are less suitable for post-larval fish. With increased size, juvenile fish switch to mudflat habitats as their foraging success in mangroves is reduced (presumably because the complex structure of the mangrove forests becomes restrictive of foraging) and the fish become less vulnerable to predators and are able to forage in relative safety on the more open mudflats [or indeed on coral or rocky reefs].”

In a novel approach, the link between total catch, catch per unit effort (CPUE) and habitat of 21 species groups of fish and crustaceans commercially fished in Queensland was investigated.¹⁶⁵ The study looked at the catch data in relation to the various characteristics of estuarine habitats such as size and structural connectivity. This quantified the patterning of mapped benthic habitat types (including mangroves, saltmarsh and shallows, inclusive of seagrass beds).

Although the authors recognized some inherent limitations of the study, the findings strongly suggest that coastal wetland connectivity is significant to inshore fisheries. The connectivity indices for mangroves, saltmarsh and shallows explained from 30 to 70 percent of the variance in the data, emphasizing the importance of connected tidal wetlands as fisheries habitat.¹⁶⁶ Fish species clearly used a number of habitats or biotopes, with the overall catch and CPUE being dependent on the whole estuarine mosaic rather than any single habitat, and that to date, “the significance of mud- and sandflats has been greatly underestimated in broad scale analyses.”¹⁶⁷

The logical consequence of the importance of habitat mosaics, connectivity and complementarity of adjacent biotopes for species richness and fishery yield is significant for consideration of the scale and design of marine reserves and/or protected areas.

Ideally, to gain maximum benefit for fisheries purposes, the data strongly support that such areas should include not just mangroves and seagrasses, but also adjacent mudflats and sandflats and reef areas. The seaward extent of such areas should be determined on a case-by-case basis.

Tidal wetland habitat connectivity is significant to inshore fisheries with connectivity indices for mangroves, saltmarsh and channels explaining from 30 to 70 percent of the variance in the fish catch data.

The significance of mud- and sand-flats has been greatly underestimated in broadscale analyses.

¹⁶⁵ Meynecke, Lee and Duke (2007 and 2008); Meynecke *et al.* (2007)

¹⁶⁶ Meynecke, Lee and Duke (2008)

¹⁶⁷ Meynecke *et al.* (2007 p. 787)

8. Loss of mangroves and seagrasses: causes and extent

The global coverage of mangroves in 2005 was estimated to be 15.2 million hectares¹⁶⁸ and the annual rate of net loss of mangroves has slowed from about 1 percent in the 1980s to 1990s¹⁶⁹ to about 0.7 percent in 2000–2005.¹⁷⁰ The principal cause of this loss appears to be “human pressure on coastal ecosystems”¹⁷¹ where the competition for land for aquaculture, agriculture, infrastructure and tourism is often high.

Natural hazards such as cyclones, storms and floods, and tsunamis make a minor contribution to mangrove losses. However, the green coastal buffer provided by mangroves contributes significantly to the overall protective function of dense forests.¹⁷²

Clearing of mangrove forests modifies a number of ecosystem processes,¹⁷³ including increased algal biomass production because of increased light and temperature, decrease in the organic content of sediment, and an increase in the level of consumption of algae by herbivorous fish. Similarly, partial clearing of mangroves (e.g. thinning) also affects temperature and light conditions and is correlated with significantly lower fish densities.¹⁷⁴

Reliable data on seagrass losses are not available, although numerous regional studies have documented significant seagrass losses.¹⁷⁵ Most recent estimates of seagrass losses are that they are being lost at the rate of 1 to 1.5 percent per year, or about 30 percent of the global seagrass area since 1980.¹⁷⁶

Some of these losses are the result of major human activities such as dredging, siltation or pollution (including nutrient enrichment), whereas others have resulted from natural occurrences such as major flooding, erosion or cyclonic disturbances.¹⁷⁷

In March 1985, tropical cyclone Sandy crossed the coastline of the Gulf of Carpentaria, severely damaging or destroying 151 km² of the original 183 km² seagrass beds,¹⁷⁸ consisting largely of luxuriant beds of *Enhalus acoroides*, which supported the greatest density of juveniles of *Penaeus esculentus*. Regrowth was slow and dependent on seed stored in the sediments.

Recolonization was first noted in 1987, and by 1988 about 20 percent of the seagrass beds had recovered, with limited recolonization by 1990.

¹⁶⁸ FAO (2007); Spalding, Kainuma and Collins (2010)

¹⁶⁹ Spalding, Blasco and Field (1997); Blasco, Aizpuru and Gers (2001); FAO (2007)

¹⁷⁰ FAO (2007)

¹⁷¹ FAO (2007 p. ix)

¹⁷² Saenger (2011)

¹⁷³ Granek and Ruttenberg (2008)

¹⁷⁴ Scott *et al.* (2007)

¹⁷⁵ Sheridan and Hays (2003); Gillanders (2006); Duarte (2009)

¹⁷⁶ Dennison (2009)

¹⁷⁷ Preen, Lee Long and Coles (1995)

¹⁷⁸ Poiner *et al.* (1992)

Logbook data for catches of *P. esculentus* showed that from 1980 to 1984, mean annual catches were about 250 tonnes, but in 1985 to 1990 the catches in the affected areas were about 40 tonnes compared to 200 tonnes in unaffected areas.¹⁷⁹

Although no data on fishing effort were presented, the trawl catches appear to support the general view that seagrass beds are an important habitat supporting shrimp catches. Loss of seagrass beds could also result in a loss of species richness and abundance, especially for organisms that rarely occur in other habitats.¹⁸⁰

The *P. esculentus*-seagrass relationship appears to be only one of the factors influencing the catch of *P. esculentus*, with a strong relationship with rainfall also being involved.

A similar effect of seagrass on shrimp catches was seen in Exmouth Gulf, Western Australia after the almost total loss of seagrasses¹⁸¹ in 1999. There was a drop in brown tiger prawn catch from 400 tonnes to 80 tonnes, with a subsequent slow catch recovery as the seagrass recovered.

¹⁷⁹ Poiner *et al.* (1992)

¹⁸⁰ Bloomfield and Gillanders (2005)

¹⁸¹ Loneragan *et al.* (2004, 2012 and personal communication, 2012)

9. Expansion of mangroves and seagrasses: causes and extent

9.1 Expanding mangrove habitats through rehabilitation

Although there are a few examples of natural increases of mangroves due to siltation (e.g. in the Bay of Bengal), most of the recent increase in mangrove area has been achieved through mangrove rehabilitation initiatives.¹⁸²

As a result, despite gradual overall global mangrove losses, replanting efforts of mangrove and seagrass habitats in recent years have resulted in some expansion of these biotopes in selected regions (e.g. Bangladesh,¹⁸³ Viet Nam¹⁸⁴ and Kenya¹⁸⁵).

Anthropogenic mangrove rehabilitation raises two major concerns:¹⁸⁶

- What measures of success should be used to assess these projects?
- How can the ecological functionality of rehabilitated/created mangroves be measured?

9.2 Ecosystem function in restored mangrove habitats

The goal of any mangrove rehabilitation initiative is to restore ecological functioning to something similar to the pre-disturbed state (e.g. natural regeneration and self-maintenance). Measuring such functionality is difficult and time-consuming, and there have been few studies of rehabilitation programmes that have achieved the full range of ecological functions displayed by natural mangrove systems, although recovery in many projects often is relatively complete after three to five years.

In a study of the faunal, floral and sedimentological properties of two different age stands of *Avicennia marina* stands in New Zealand,¹⁸⁷ older (>60 years) and younger (3 to 12 years) stands showed a clear separation on the basis of environmental characteristics and benthic macrofauna. The number of faunal taxa was generally larger at younger sites, and the number of individuals of several taxa was also larger at these sites.

As these mangrove stands mature, the focus of faunal diversity shifted from the benthos to epiphytic fauna, such as insects and spiders. Differences in the faunas were coincident with differences in the nature of the sediment; in older stands, the sediments were more compacted and contained more organic matter and leaf litter. Interestingly, mangroves in the younger stands were able to take up more N and P than those in older stands, presumably because of less root competition in the younger stands. Overall, the study concluded that younger and older stands have significantly different functional characteristics, which should be considered in planning and management.

In mangrove rehabilitation, the recovery of many ecological functions displayed by natural mangrove systems is relatively complete after three to five years.

¹⁸² Field (1996); Walters *et al.* (2008)

¹⁸³ Saenger and Siddiqi (1993)

¹⁸⁴ Hong (1996)

¹⁸⁵ Crona and Rönnböck (2007)

¹⁸⁶ Bosire *et al.* (2008)

¹⁸⁷ Morrissey *et al.* (2003)

A review¹⁸⁸ of mangrove rehabilitation projects on the eastern Australian coast, ranging in age from 1 to 18 years examined each of the replanted areas in terms of survival rates of plants, natural regeneration and general health of the plantation. For the eight-year old plantations (7 hectares in Ballina in the northeastern coast of New South Wales), additional detailed studies were carried out on fish usage at high tides, fish food availability, and short-term (marker horizons) and long-term (sequential topographic surveys) accretion rates in planted and control areas. It was found that within four years, the planted areas showed comparable results to the control areas in all the studied aspects.

It is expected that ecosystem functioning in relation to soil processes may take somewhat longer to reach comparable levels to natural undisturbed mangroves. Nevertheless, it should be noted that:

- N-fixation in mangroves provides one useful measure of the state of ecosystem functioning in damaged and rehabilitated mangrove ecosystems.¹⁸⁹
- In Thailand, the concentrations of soil organic carbon were found to be a useful indicator of the functioning of rehabilitated mangroves in abandoned shrimp ponds.¹⁹⁰

The structural development and biogeochemical functioning of replanted and natural mangrove forests were compared within the same physiographic setting in southwest Florida.¹⁹¹ Two sites, replanted in 1982 and 1990 respectively were compared with adjacent natural mangrove forests that had been undisturbed for 50 to 60 years. Despite being planted initially with *Rhizophora mangle*, both replanted sites were also naturally colonized by *Laguncularia racemosa* and *Avicennia germinans*. The replanted forests were dense but immature, with lower basal area and stand height, and higher tree density when compared with the reference forests. By the time the replanted stands were at an age of 6 to 13 years, structurally they were still at the pioneer stage, but there were only a few biogeochemical differences. Some interesting results of other studies are shown below:

- Recovery of fish populations to similar species composition and density as reference sites was accomplished within three to five years in a review of four studies in the United States.¹⁹²
- In Florida,¹⁹³ fish and macrobenthos had become re-established within two years in a mangrove-rimmed embayment, once tidal flows were restored.
- Similarly, fish diversity increased rapidly with increasing age of replanted mangrove habitat.¹⁹⁴
- In Kenya,¹⁹⁵ fish densities and mean fish biomass were indistinguishable from natural mangroves and an eight-year old

¹⁸⁸ Latif (1996)

¹⁸⁹ Vovides *et al.* (2010)

¹⁹⁰ Matsui *et al.* (2010)

¹⁹¹ McKee and Faulkner (2000)

¹⁹² Lewis (1992)

¹⁹³ Vose and Bell (1994)

¹⁹⁴ Barimo and Serafy (2003)

¹⁹⁵ Crona and Rönnböck (2007)

replanted area, and replanted mangroves of Gazi Bay harboured a significant number of commercially important species (15 of the 20 most abundant fish species) as juveniles suggesting that their function as nursery habitats for nekton had been restored.

- A study on crustacean and molluscan epifauna¹⁹⁶ from variously aged replanted mangrove areas around Ranong, Thailand noted that four to seven years old plantations showed no significant difference compared to old growth mangroves. However, it was reported that ten-year old plantation areas following tin-mining, showed poor signs of recovery – presumably because of the intense sediment upheaval that has stripped away the mud, leaving gravel and a substantially changed hydrology.

Because of the importance of the estuarine mosaic for species richness and fishery yields as outlined in Chapter 7, consideration should be given to including reconstruction of non-mangrove estuarine biotopes where this is feasible (e.g. in depositing dredge spoil to create shallows or mudflats).

9.3 Ecosystem function in rehabilitated seagrass habitats

As with mangroves, the principal objective of seagrass rehabilitation is to restore ecological functioning to make it similar to the pre-disturbed state.

Relatively few studies have been undertaken¹⁹⁷ of replanted seagrass beds as there have been relatively few successful examples. Most studies of the functionality of seagrass beds have been undertaken by comparing natural seagrass areas with disturbed/degraded seagrass areas, which have been recolonized naturally following the re-establishment of suitable conditions. In these cases, the recolonization and recovery of the seagrass bed has occurred within two to five years.¹⁹⁸ These studies show that:

- fish assemblages between natural and transplanted seagrass beds up to four years old showed no significant differences in community composition;
- species richness seemed to remain lower in 31-year old recolonized seagrass beds during the winter season; and
- restored seagrass beds appeared to function as fish habitat within a few years, providing suitable habitats for juvenile and small, adult fishes.

Seagrass recovery can take two to five years, and habitat function returns within a few years.

¹⁹⁶ Macintosh, Ashton and Havanon (2002)

¹⁹⁷ e.g. McLaughlin *et al.* (1983); Fonseca *et al.* (1990)

¹⁹⁸ Poiner *et al.* (1992); Brown-Peterson *et al.* (1993); Preen, Lee Long and Coles (1995); Campbell and McKenzie (2004)

10. Other means of enhancing existing habitat

10.1 Retaining mangrove functionality

It has been suggested¹⁹⁹ that a considerable proportion of mangrove functionality might be retained when a mangrove area is reduced (e.g. 75 percent of nursery function might be retained in 50 percent of the original area). There are, however, relatively few studies on this aspect of the functionality of mangrove habitats in relation to remnant areas.

It has been shown that thinning of the frontal fringing mangroves and clearing of inland mangroves resulted in highly significant reductions in fish densities.²⁰⁰ This seems to contradict the view that a reduction in area does not result in comparable loss of functionality for fish. However, this investigation was carried out in what were termed “oceanic mangroves associated with patch reefs” in the Caribbean, and may not be comparable to estuarine-type mangroves of the Indo-West Pacific.

It has been found that mangroves fringing deeper water appear to retain more functionality than inland, shallower, intertidal mangroves.²⁰¹ It is therefore possible that provided the majority of mangrove loss was confined to the inland margins, and that deeper fringing areas were left intact, “much of the functional value could be retained.”²⁰²

10.2 Maximizing fishery benefits from fishing reserves/no take zones

Another approach that has evolved over the past decade is the adoption of no-take or no fishing zones or reserves as a means of protecting some stocks or to restore fish stocks by allowing migration into adjacent areas. First demonstrated on Sumilon Island, Philippines,²⁰³ no-take reserves resulted in the export of pelagic larvae that settle in areas outside the reserve, and in spillover of adults emigrating from areas where stocks have been reduced by fishing mortality.

In the Gulf of Aquaba, Egypt,²⁰⁴ a network of no-take reserves covering mangroves and coral reefs, resulted in an increase in abundance of lethrinids and serranids in the reserves within five years and increased the mean catch per unit effort within the adjacent fished areas by about two-thirds over the same period.

Although this study did not distinguish the effects of proximity to nursery areas from those of protection from fishing in the reserves, other studies²⁰⁵ have found that for biomass of juvenile fish, the proximity to nursery areas far outweighs the effects of protection from fishing, and for the biomass of large-bodied fish there was an increase both with fishing protection and proximity to nurseries in that order.

Limiting loss of mangroves to the inland margins and maintaining deeper fringing areas may retain much of the functional value.

Protected areas or ‘no-take’ reserves ideally should include a mosaic of estuarine or coastal biotopes to maximise fisheries benefits.

¹⁹⁹ Kapetsky (1985)

²⁰⁰ Scott *et al.* (2007)

²⁰¹ Vance *et al.* (1996)

²⁰² Blaber (2007, p. 466)

²⁰³ Russ (1985)

²⁰⁴ Galal, Ormond and Hassan (2002)

²⁰⁵ Nagelkerken, Grol and Mumby (In press)

Based on these studies, and as previously noted (see Chapter 7), protected areas or no-take reserves ideally should include a mosaic of estuarine or coastal biotopes to maximize fisheries benefits. This is an important consideration since, in many cases, marine protected areas exclusively focus on a single biotope (mangrove, or seagrass or coral reef) and do not include adjacent areas. This would be an inherent limitation on the effectiveness of a protected area in delivering benefits to fisheries productivity or conservation.

11. Is there a link between fisheries production and changes in the extent of mangrove and seagrass habitat?

There are clear linkages between mangroves and seagrass beds and different life stages of many fish and crustacean species. There are complex interactions within mangrove and seagrass ecosystems and between associated biotopes (e.g. mudflats, coastal waters). It is therefore difficult to demonstrate unequivocally that there are quantitative links between the extent of mangroves and seagrasses and fisheries production.

It is equally difficult to demonstrate conclusively that decreases in mangrove and seagrass areas result in reduced production of those species that utilize them at some stage of their life cycle, most often as juveniles.²⁰⁶

As discussed in Chapter 5 (section 5.3), although many studies purport to show this relationship, most rely on statistical inference, usually correlation or regression, to support the link.²⁰⁷ The weaknesses of this approach have been recognized by some authors who identify autocorrelation of the factors being examined as an important limitation.²⁰⁸

The tendency of research studies to focus principally on the nursery function of mangroves and seagrasses has further complicated efforts to demonstrate linkages to fisheries production. This is because of the need to establish a link between the presence of juvenile fish in the nursery habitat and their contribution to the adult population (which often inhabits an adjacent habitat. See discussion in Chapter 2). It is extremely difficult to establish this sort of linkage by direct means, although one specific study successfully used stable isotopes in tissue and otoliths to demonstrate the linkage between seagrass beds and coral reefs for the yellowtail snapper *Ocyurus chrysurus*.²⁰⁹

In view of these issues and limitations, what can be said about linkages between the extent of mangroves and seagrasses and fisheries production?

It is becoming clear that the widely held generalized view that mangroves and/or seagrasses underpin fisheries production through their role as nursery areas appears unlikely to apply in all cases. The emerging evidence is that of normal biological variability:

- some species are dependent on these habitats, or on the food webs they provide;
- other species variously utilize mangrove and/or seagrass habitats or other habitats at different stages of their life-cycle; and
- some species are flexible in their habitat use and are not dependent on the presence of mangroves and/or seagrass habitats.

²⁰⁶ e.g. Blaber *et al.* (1989); Gilbert and Janssen (1997); Baran and Hambrey (1998); Manson *et al.* (2005); Blaber (2007 and 2009)

²⁰⁷ Turner (1977); Staples, Vance and Heales (1985); Pauly and Ingles (1986); Paw and Chua (1989); Ley (2005)

²⁰⁸ e.g. Robertson and Blaber (1992); Lee (2004); Blaber (2007 and 2009)

²⁰⁹ Verweij *et al.* (2008)

The widely held, generalized view, that mangroves and/or seagrasses underpin fisheries production through their role as nursery areas appears unlikely to apply in all cases.

Overlying the biological variability is the difficulty of conducting quantitative field-based sampling studies of fish species²¹⁰ and the difficulty of using fisheries production statistics for comparative purposes.

The concerns and issues about the nursery function of mangroves and seagrasses and their importance in underpinning fisheries production have been covered by a number of authors²¹¹ and can be broadly summarized as follows:

- Most mangroves are located in developing countries where food security and local livelihoods often override conservation and management considerations.
- Links between reduction in mangrove area and fishery production are unclear because of the possible effects of fishing pressure. This is especially the case where fishing effort increased during the same period of declining mangrove coverage.
- In the same manner, increased fishing effort of push nets and trawl across seagrass beds, prevents a clear indication of the primary cause of declining fishery production.
- It is difficult to link fisheries catch statistics to particular mangrove areas.
- There is high variation within data sets including areas of mangrove forest, commercial catch records, fishing pressure and variation in the natural environment in temperature, rainfall, ocean currents, salinity.
- No simple generalization relating the nursery function of mangroves and seagrasses to their importance in underpinning fisheries production has been demonstrated.
- Fish diversity in mangroves varies at a wide range of scales from global to local levels. Each of these scales can interact to determine the species composition in any one system.
- Many closely related fish species can have markedly different ecological requirements.
- The dependence on mangrove for many species may be overstated: an incidental association with shallow, turbid areas of varying salinity may also account for fish distribution patterns. For other species the dependence is more assured, but the species may not form significant fisheries.
- The results drawn from site-specific studies cannot be generalized and applied to large areas in different geomorphic, climatic or zoogeographic settings.
- Although studies that rely on correlations and regressions may demonstrate statistically significant relationships, these may not be due to causation. This is because the variables used are often strongly correlated with each other.
- A wide range of variables influence species assemblages at the local level and there is increasing evidence of the importance of connectivity between adjacent habitats.
- The restoration of mangrove or seagrass habitats is unlikely to restore fisheries productivity, unless other effects, such as fishing pressure, are addressed.

²¹⁰ e.g. see the discussion in Payne and Gillanders (2009)

²¹¹ Lee (2004); Manson *et al.* (2005); Blaber (2007, 2009); Nagelkerken *et al.* (2008)

One of the ways of overcoming some of the deficiencies in fisheries catch data in examining the role of habitat on fish production is to conduct fisheries independent surveys. The problem (as alluded to above) is that many fisheries catch data sets collected by fisheries agencies to assist in making management decisions are variable in quality and their accuracy can be very difficult if not impossible to verify. There are at least two problems to address:

- There can be uncertainty about the level of confidence that can be placed on parts of a data set. This is due to difficulties the fishermen have in accurately reporting the species, weight and location of catches, or because the remote locations of fishermen make data collection difficult.
- There can be systematic biases in reported catch because of non-cooperation by fishermen. In this case the bias is overwhelmingly towards providing underestimates of catch to reduce tax, sell catch illegally, cheat on quota restrictions or to keep fishing locations and methods secret. However, in a few cases, the bias can be towards over-reporting catch, if for example, the management agency is going to use catch-history records to allocate fishing rights.

The problem of unreliability of fishermen's catch records is addressed by some management agencies insisting that observers accompany each fishing boat. This is an expensive and sometimes inconvenient option, more often employed when the catch potentially is very valuable.

This review undertook a wide literature search, however no relevant studies were found that clearly differentiated between fishing effects and habitat loss. It is virtually impossible to apportion the relative loss of fisheries production resulting from habitat loss compared with loss of production due to depletion of fish stocks caused by overfishing, based only on catch records. Both factors result in the loss of production but catch records cannot indicate the underlying causes. As suggested above, one possible way to address this issue is by use of fisheries independent surveys.

Fisheries independent surveys can be useful in distinguishing between changes in catch due to fishing pressure compared with changes in catch caused by environmental or habitat issues. For example, when sampling seagrasses or mangroves, if the survey methods collect all species there that are dependent on these habitats, both commercially harvested species and non-commercial species, synchronized fluctuations in the abundance of both groups would suggest that environmental variables were playing a significant role, whereas, decrease only in the commercially harvested species would suggest that fishing pressure may be playing the most important role. This is, of course, a simplification of the ecological complexity of seascapes, but the principle offers the prospect of separating the effects of overfishing from those caused by habitat loss when accounting for declines in commercial catch.

11.1 Case studies which illustrate these points

Life-stage variations and the differences between species limit the ability to attribute relative importance of different habitats.

A comparison²¹² was made of the occurrence of juveniles of two species of wrasses in seagrass beds and mangroves versus other shallow water habitat types on four islands in the western Indian Ocean and on a southern Caribbean island. Both species can attain a high biomass and have high commercial value for fisheries, despite the fact that they are on the red list for conservation.

The juveniles of the Indian Ocean island wrasse, *Cheilinus undulatus*, were found predominantly in seagrass beds, whereas adults were found only on coral reefs. Furthermore, the presence of seagrass beds resulted in significantly higher densities of adults on coral reefs in front of the seagrass habitats.

For the Caribbean rainbow parrotfish, *Scarus guacamaia*, juveniles occurred exclusively in mangroves, whereas adults were found only on coral reefs. No relationship between occurrence on coral reefs and distance to mangroves was observed and it was concluded that the scale for importance of mangroves was the whole island.

It was also concluded that there were ontogenetic shifts in habitat use as the fish grew, from occupation of juvenile (nursery) habitats to occupation of adult habitats. Although this study was broadened to 76 species around Tanzania and the island of Grande Comoros,²¹³ the results cannot be generalized to a uniform role of mangroves and seagrasses as juvenile habitat for coral-associated fishes. Furthermore, a quantitative link between juvenile and adult numbers has not been established.

Presence of juveniles in certain habitats does not always infer that these habitats are essential for that life-stage and may vary spatially and seasonally.

The weakness of the generalization regarding the presence of juveniles and nursery function is illustrated in the examination²¹⁴ of the spatio-temporal variability in ontogenetic habitat use by four species of tropical mangrove/seagrass associated coral reef fishes in Tanzanian waters.

The study ran across four seasons and at two spatially separated (more than 40 km apart) locations. There were two species of *Lethrinus*, and one each of *Lutjanus* and *Siganus*. These four species are both common and commercially important.

Across the study, juveniles of the four species had significantly higher relative densities in shallow water habitats (mangroves and seagrass beds) than in deepwater habitats (mudflats and coral reefs).

The opposite pattern was found for adults. This finding suggested that there was a strong and general pattern of ontogenetic habitat shift from juveniles to adults (and thus, by implication, that mangrove/seagrass habitats are essential to underpin adult populations in adjacent habitats).

²¹² Dorenbosch *et al.* (2006)

²¹³ Dorenbosch *et al.* (2005)

²¹⁴ Kimirei *et al.* (2011)

Despite this, specific habitat use patterns of juveniles and adults differed significantly in time and space.

Various species showed flexibility in juvenile and adult habitat use across seasons, years or at different locations. Some species showed shifts at one location but not at the other.

Whilst the study clearly showed the presence of ontogenetic habitat shifts for all four coral reef fish species; the detailed analysis of the data showed significant spatial, seasonal or interannual variability in habitat use patterns. The study concluded that this showed the difficulty of generalizing habitat use in such heterogeneous seascapes by fish species in different life stages.

Although the study is important for its findings on flexible habitat use, its findings of ontogenetic habitat use are only inferential in terms of fish production. This is because the study did not make a quantitative link between the presence of the juvenile fish and level of production of adults or on the extent of the habitat types and the size of the ontogenetically linked fish populations.

This demonstrates the limitations of generalized juvenile fish habitat/nursery area definitions based on density per unit area, in the absence of a time component.

A review²¹⁵ on the effects of within patch seagrass structural complexity on fishes found that different study methods yielded different results.

In general, seagrass habitats supported large numbers of fish species and individuals, and provided nursery habitats for juveniles of many species, including commercially important species, compared to unvegetated bare strata. However, some studies reported that adjacent bare strata supported the same numbers as seagrasses.

Fish responded in different ways to changes in seagrass height or density or clearance: sometimes with decreased abundance, but sometimes increases, or in other cases, no changes.

The review concluded that more studies on the effects of patch size, edge effects and within scale complexity were needed.

The scale and proximity of degraded and undisturbed habitats may limit determinations of effects of mangroves and seagrasses on fish.

The extent to which seagrass habitat loss leads to decline of fishery production is a complex issue.²¹⁶ From a review²¹⁷ of several studies of seagrass decline and associated loss of fish harvests, specific examples are:

- Eelgrass dieback in Europe and North America in the 1930s led to a dramatic decline in *Zostera marina* meadows but no decline in fisheries yields. Erosion of eelgrass habitats led to exposure of rocky substrates that were colonized by macro-algae that offered an alternative nursery habitat.

The loss of seagrass habitats may not result in declining fishery yields.

²¹⁵ Horinouchi (2007)

²¹⁶ Heck, Hayes and Orth (2003); Gillanders (2006); Loneragan (personal communication, 2012)

²¹⁷ Heck, Hayes and Orth (2003)

- Dramatic losses of turtlegrass, *Thalassia testudinum*, from Florida Bay in the late 1980s led to a small decline in pink shrimp, *Penaeus duorarum*. Despite no seagrass recovery, pink shrimp yield increased again after five years, following an increase in freshwater input and it seemed that low freshwater inputs played a major role in the decreased shrimp harvests in the early 1990s.
- With large eelgrass losses in Chesapeake Bay, it was expected that the harvest of blue crab, *Callinectes sapidus*, would also decline. This did not happen.

An investigation²¹⁸ into the effects of seagrass decline in Florida Bay compared ichthyoplankton composition and the ichthyofauna of the channel and basin habitats in 1984/85 and 1994–1996, using identical sampling techniques and sampling stations. The results were:

- although seagrass densities had decreased by as much as 100 percent, there were no observable changes in the total density of juvenile and small adult fishes in conjunction with the reductions in seagrass densities; and
- a shift in the fish fauna composition was observed, with an increase in planktivores and a decrease in canopy-dwelling or benthivorous species.

Habitat degradation/ changes must be analysed alongside fishing effects (such as changes in fishing effort), in order to elucidate their relative significance in terms of fishery decline or recovery.

An example from southern Australia²¹⁹ looks at seagrass losses and gains and commercial fish catches in Westernport Bay and in the Gippsland Lakes of Victoria, Australia.

In Westernport Bay, continuous catch data are available from 1914. Massive losses of seagrass occurred between 1970 and 1984, when approximately 180 km² of seagrasses were lost, with a total biomass reduction of about 85 percent. During that same period, commercial finfish catches from Westernport Bay declined by about 40 percent from a peak of 260 tonnes yr⁻¹ in the late 1960s to about 150 tonnes yr⁻¹ in the mid-1980s.

In the Gippsland Lakes, large seagrass losses occurred in the late 1910s, with subsequent recovery of these habitats in the early 1960s. There appears to be a decline and subsequent recovery in catches of some species, whose juvenile phases are associated with seagrass habitats. However, species not associated with seagrass appeared unaffected. This study concluded:

“As with Westernport Bay, catches of Gippsland Lake species not thought to be closely associated with local seagrass habitats showed no evidence of a major decline and subsequent increase during the period of major seagrass loss and recovery.”²²⁰

It is worth noting that the data show large annual variations in catches and the analyses do not take changing fishing effort into account, so that without further data or analysis, the conclusions remain tenuous.

²¹⁸ Thayer, Powell and Hoss (1999)

²¹⁹ Macdonald (1991)

²²⁰ Macdonald (1991 p.193)

The link between mangrove/seagrass habitats and fishery production was investigated on reefs in Belize and Mexico²²¹ associated with atolls, some of which lacked mangroves and some of which were “mangrove rich”.

The biomass of several commercially important species is more than double on those coral reefs where the adult habitat is connected to mangroves. It was found that the mangroves were unexpectedly important to reef fish communities, serving as an intermediate nursery habitat that may increase the survivorship of young fish.

In the study, there were significant differences between the structure of the reef fish communities from mangrove scarce and mangrove rich atolls. Mangrove extent was a dominant factor in the structure of reef fish communities.

One important finding was that mangrove extent partly explained patterns of reef fish community structure in fishes that are obligate reef species, not found in lagoon nursery areas. This suggests that mangroves supply other fish or forage species that enhance the obligate reef species numbers.

This study is important also because fishing pressure is rejected as a possible cause of the patterns observed: Lutjanid biomasses were greater in mangrove rich areas, despite higher fishing pressure there. This finding supports the contention that mangroves enrich reef fish communities in coral atoll islands.

This study infers that the doubling of biomass of commercially important fish species on mangrove-backed reefs would increase fisheries production, although no direct data for this link were provided.

On coral atoll islands, there are clear linkages between coral reef fish biomass and the occurrence of mangroves behind the reef.

A report²²² supporting some links between mangrove habitats and fisheries, discussed how fish and mangrove ecosystems are coupled in time and space.

This describes how mangroves and marshes in eastern Florida had been impounded in the 1950s as a mosquito control measure, then many years later reconnected by ditches to the tidal environment. Following impoundment, mangrove transient species and omnivores grazing on detritus vanished.

After reconnection of the mangrove habitats to tidal inundation by construction of ditches, these fish species re-established in even greater numbers than before impoundment.

It is argued that the important commercial and recreational species, namely snook, redfish, spotted sea trout and tarpon were impacted by loss of non-commercially important forage species due to the removal of juvenile habitat in mangrove areas: that loss of this habitat and general degradation of water quality have a stronger effect on populations of the

Mangroves may function as providers of prey/feed for commercially important fisheries species.

²²¹ Mumby *et al.* (2004)

²²² Lewis and Gilmore (2007)

commercially important species than fishing pressure. The authors cite another study, which found that:

“Only a small number of fish species examined in this study are of direct economic importance ... However, the valuable ... fisheries for barramundi are intimately linked to mangrove habitats ... our data show that more than 50 percent of the diet of sub-adult barramundi is composed of small fish which dominate the mangrove habitats.”²²³

This report is important in noting that mangrove habitat values for fishery production can include supporting commercially important species through provision of otherwise economically unimportant small species of fish (and juveniles) that are prey for the other species. By extension of this argument, mangroves could also indirectly support fisheries through provision of non-commercial invertebrate biomass.

Some species are consistently associated with mangroves, although other commercial species are more closely linked to areas of seagrass and mudflats. Increasing mangrove cover may occur at the expense of these habitats and negatively affect some target species.

Other work has provided a different perspective on the factors affecting fish assemblages in estuaries that reduces the emphasis on the importance of mangroves.

A study of estuaries in temperate eastern Australia²²⁴ used multivariate analyses of estuarine geomorphic variables to examine the relationship between estuary geomorphology and the extent of mangrove, seagrass and central mud basin. The study considered to what extent the area of each habitat type can be used to predict the commercial landings of fish and crustaceans.

Using the weight of fish caught and number of days fished in each estuary as a measure of effort, the study was limited to only those species that used the estuary at some stage. It was found that seagrass and mangrove areas were not significantly correlated, but seagrass and mangrove extents were associated with estuary type and maturity.

The major biotic predictors for fish catch were extent of seagrass and central mud basins. There was a demonstrated link between seagrass extent and the catch of shrimps, crabs, whiting, flathead and garfish, and this link was supported by ecological studies of the use of seagrass by these species, including as juveniles.

Other environmental variables were less important although a small group of species were consistently associated with mangroves.

It was concluded that the infilling of barrier estuaries is associated with an increase in mangrove area and a decrease in the areas of seagrasses and central mud basins. These changes can be directly related to variation in the commercial catch of fish and crustaceans that utilize these habitats in their postlarval stages.

²²³ Robertson and Duke (1990b)

²²⁴ Saintilan (2004)

A study of 11 large estuaries in tropical eastern Australia²²⁵ related patterns observed for estuarine fish assemblages to fundamental differences in physical forces (river, wave, tidal).

Overall, a substantial amount of variation (43 percent) in fish assemblages was related to catchment hydrology (rainfall, elevation), configuration of the estuary mouth, substrate and mangrove area. Other results were:

- tide-dominated systems located in drier catchments had greater mangrove area, wide deltaic mouths and muddy substrates and high fish diversity;
- wave-dominated systems located in higher rainfall catchments had constricted mouths, less mangrove area and sandy substrate and simpler fish assemblages; and
- true estuaries were relatively depauperate.

The study concluded that the general estuarine features generate physicochemical and biological processes that determine habitat use by tropical estuarine fishes.

Estuarine fish assemblages are determined by a range of factors: a substantial amount of variation is related to catchment hydrology (rainfall, elevation), configuration of the estuary mouth, substrate and mangrove area.

The difficulties of generalizing the value of mangrove habitats for underpinning fisheries production were highlighted as early as 1974, in a historic report on mangrove forests and fisheries.²²⁶

The review noted the variability and flexibility of habitat use by shrimp. Some species of penaeid shrimps are dependent on mangrove forests for shelter during juvenile stages (*Penaeus indicus*, *P. merguensis*, *P. monodon* and most species of *Metapenaeus*) although these will remain in backwaters and lagoons after the mangroves have been cleared.

The review notes that the problem of classifying the dependence of particular species on the one habitat type was:

“open-ended and incapable of a satisfactory solution. In one area, such as Mozambique or Madagascar, a correlation between certain penaeid species and mangroves appears to hold and one might say ‘no mangroves: no prawns’. But in another area such as the west coast of India the same prawns will remain even though the local [human] population has extirpated the mangroves.”²²⁷

The links between mangrove area and fisheries production were investigated showing landings of shrimp in countries around the Indo-Pacific in tonnes per year and area of mangroves in square kilometres (but with no data on fishing effort). Using these figures to calculate production per square km shows a very wide range of production: from 1.34 to 10.66 tonnes per square kilometre.

Classifying the dependence of particular species on a specific habitat type is almost impossible to determine.

²²⁵ Ley (2005)

²²⁶ MacNae (1974)

²²⁷ MacNae (1974, p. iii)

Without data on fishing effort, it is unclear if the variation in catches was due to differences in the support of mangrove areas or caused by differences in fishing effort.

To support the potential effects of fishing pressure, this report provided data on shrimp landings at three major ports in southern Thailand over three years (1968, 1969 and 1970). Over this period there was a doubling of fishing effort (measured in hours fished) and an approximate doubling of catch, so large variations in catch could easily have been the result of differences in fishing effort.

Fisheries of species that appear to depend on mangroves can be year round or highly seasonal. This will influence the relative importance of biophysical, climatic and other factors.

Commercial fishing activities that use (essentially) the same fishing method for a particular target species, may display significant differences between areas. This means that catch rates per unit of time and (by some measures) CPUE would vary enormously between these fisheries.

For example:

- In western peninsular Malaysia, landings of white (banana) shrimp are virtually constant throughout the year.²²⁸
- In eastern peninsular Malaysia, Sarawak and northern Australia, the fisheries are highly seasonal.
- In northern Australia, where approximately 80 percent of annual rainfall occurs during summer, approximately 90 percent of the shrimp catch is taken in the first two to four weeks of the season opening in April.

Even for a single fishing method, variations over time in effort, power and gear selectivity make interannual comparisons difficult. Consequently, attribution of relative effects of fishing compared with habitat change become even more tenuous.

The validity and use of comparative fish catch data is often a vexed issue for fisheries biologists and managers, even when comparing effort within a single fishery using only a single fishing method.

These data can be particularly problematic when they are needed for statistical comparisons on the effect of mangroves or seagrasses on fish production of different species over wide geographic areas.

Can fishing effort measured in kilogrammes of fish caught per day be used to compare effort on different species or in averages over multispecies catches?

For example, a day spent fishing for mud crabs by two fishermen working together might yield 50 to 100 kg of crabs.

- Can this then be combined with the results of fishing by a six person crew using a seine net to catch 10 000 kg of mullet in a day?
- What would the average of these two figures tell us about CPUE for the fisheries adjacent to a mangrove area?

²²⁸ Loneragan *et al.* (2005)

Even within a single fishery, fishing effort can change significantly over short periods of time and often in relatively intangible ways. For example, in a single species prawn fishery (*Penaeus latisulcatus*) in Gulf St. Vincent in South Australia, average fishing effort per licence holder (per boat) in the fleet doubled over an eight-year period because of increases in vessel length, increases in the power of their engines, changes to the type of fishing rig, increased hours fished per night and experience of the operators in the area.²²⁹

Another example of this point is drawn from marine capture fisheries in the Mekong Delta, in southern Viet Nam,²³⁰ where three phases in fishing are identified over a 20-year period. Over the same period (1976 to 1995), the area of mangrove declined by 23 percent (from 84 127 ha to 64 819 ha):

- 1975 to 1983: a decrease in fishing boat numbers because of the “boat people” exodus. CPUE (tonnes per horsepower per year) of the remaining boats increased, as did the total catch;
- 1983 to 1989: a slight increase in engine capacity, but the formation of government-initiated fishing cooperatives removed the incentive to fish, resulting in a decrease in CPUE and in total catch; and
- 1989 to 1995: introduction of a “free market” and increased availability of equipment. Total catch and engine capacity increased rapidly, but CPUE showed no increase. Production (total catch) between 1992 and 1995 increased by 27 percent. This increased catch was because of an increase in the number of boats by 85 percent and in engine capacity of the fleet by 100 percent. The statistics are based on total weight for all species and on all types of fishing vessels.

These comparisons demonstrate the difficulties of making inferences about the effect of mangrove loss on fisheries production given the complications of changes in fishing effort.

The reliability of fisheries data is a possible issue and was considered²³¹ looking at the relationship between shrimp landings and the extent of mangrove and shallow waters in western peninsular Malaysia.

It was found that the area of shallow water accounted for the greatest proportion of variation in landings of all shrimps and the mangrove-dependent white shrimp (banana prawn, *Penaeus merguensis*) in the state of Perak.

Landings of all shrimps and white shrimp in the nearby states of Selangor, Kedah and Johor, where there have been large losses (30 to 45 percent) of mangrove forest between 1980 and 1996, appear to have been maintained or increased. It was speculated that juvenile shrimps migrated to these waters from the larger areas of habitat off Perak.

Macro-economic and socio-economic effects in fisheries affect effort in fisheries.

Although satellite imagery now allows habitat cover to be estimated reasonably accurately, the landing data in many fisheries is of variable quality.

²²⁹ Byrne (1982)

²³⁰ de Graaf and Xuan (1998)

²³¹ Loneragan *et al.* (2005)

The reliability and accuracy of the fisheries data used in this study was questioned by the authors.²³² The issues they raised related to:

- the sub-sampling procedure used to estimate landings;
- identification of shrimps and estimation of weight in each category;
- errors in reporting landings: landings data could have been biased either way – under-reporting to protect locations of fishing spots or to avoid tax, or over-reporting to demonstrate that government policies were working; and
- the fact that no estimates were made of fishing effort in this study.

In a subsequent study²³³ reduced shrimp production (based on recorded catch landings) in western peninsular Malaysia between 1989 and 2003 was concluded to be associated with loss of mangroves. However, it should be noted that other factors may also have been affecting the landings. It is possible that fishing vessels shifted their catch landing to adjacent ports in Thailand where there were well-developed processing facilities and higher prices for catches. This emphasizes the importance of understanding the socio-economic dynamics of a fishery and behaviour of fishers. Sometimes, there is a perfectly good reason why catch landings change, which is unrelated to the state of the resource.

Much of the focus on mangrove and seagrass habitats as nursery areas for the support of commercially valuable fish species overlooks their importance in supporting subsistence fisheries.

Although not focusing specifically on mangrove and seagrass habitats, the importance of fish and invertebrates for subsistence living is illustrated by studies in the South Pacific, e.g. in Samoa²³⁴ and in Fiji.²³⁵ Household surveys conducted on the two main islands of Samoa showed fish were eaten on 2.7 days per week and over half of all Samoan households fished for subsistence at least once per week.²³⁶ On the island of Upolu, 64 percent of households ate all their catch and on Savaii, 75 percent ate all their catch. As well as fish, many species of invertebrates were caught and eaten, including snails, octopus, bivalves, crabs, sea cucumbers and sea urchins.

In a study of three villages on the banks of the Waidamudamu River on the island of Viti Levu, Fiji it was found that a majority of households (55 percent) retained a primarily subsistence existence relying on fishing for their protein.²³⁷ An average of 44 percent of households consumed fish each day.

Many of the species harvested from mangroves and seagrasses in subsistence fisheries are small fishes or juveniles of larger species and form part of the *in situ* fish catch or catch from adjacent areas relied on to supply protein to several million people living in tropical coastal areas. Rough estimates of the contribution of subsistence fisheries to total catch supported by mangroves range from 10 to 20 percent in Sarawak,

²³² Loneragan *et al.* (2005)

²³³ Chong (2006)

²³⁴ Zann (1999)

²³⁵ Zann and Zann (2008)

²³⁶ Zann (1999)

²³⁷ Zann and Zann (2008)

56 percent in Fiji and up to 90 percent in Kosrae (Federated States of Micronesia).²³⁸

These important contributions to mangrove habitat values are very hard to measure and so are frequently overlooked in studies of the fisheries value of mangrove habitats.

²³⁸ Rönnbäck (1999)

12. Principal findings and conclusions

12.1 Information needs

The following information needs have been identified during the preparation of this report. These are required to be addressed before greater insights and certainty can be offered on the nature of any relationship between mangrove and seagrass habitats and fish populations:

One of the important issues to consider in the search for links between habitats and fisheries production is the time frame over which changes to mangroves and seagrass habitats are occurring, compared with the time frames over which studies measure fish community structure and individual species abundances.

Ability to detect mangrove and seagrass loss compared to existing large variations in fisheries production – time frames.

Globally, the areas of mangroves and of seagrasses are estimated to be shrinking at about 1 percent per year. Therefore, significant losses of mangrove and seagrass areas are accumulating over time frames of about 50 years, although local changes might be faster or slower. There are, however, very few fisheries databases that capture fish community structures and individual species abundances over similar time frames, or databases covering areas where mangrove and/or seagrass losses are occurring. Similarly, there are few databases where changes in fishing effort that can significantly affect catches are monitored or known. This means that it is virtually impossible at this time, except in very limited areas, to link loss of huge areas of mangroves or seagrasses with commensurate declines in fisheries catches.

Another variable that can confound attempts to relate changes in the extent of mangrove or seagrass areas to change in fisheries catches is the apparently large natural fluctuations in fish populations.²³⁹

Natural fluctuation in fish stocks confounds attempts to link habitat loss to changes in the fishery.

It has been asserted that “stock biomass and catches of penaeid shrimp fluctuate primarily in response to recruitment variability, which is controlled by environmental forces that are believed to act on young shrimp in the estuarine nurseries”²⁴⁰ and that recruitment variability is high and unpredictable in estuarine marine resources (e.g. white shrimp catches varied more than 400 percent in the Gulf of Mexico).

This pattern is borne out in other studies of fish catches over long time periods. Data for total finfish catches from Westernport Bay in southeast Australia showed variation approaching 250 percent over a 50-year period. For individual species, such as King George whiting, there was a 500 percent variation in catch over the same period, and for black bream a variation of 450 percent.²⁴¹

²³⁹ Jones *et al.* (2010)

²⁴⁰ Houde and Rutherford (1993, p. 169)

²⁴¹ Macdonald (1991)

A study of marine recreational angling club records for finfish over a 30-year period around Ballina in southeastern Australia, during which fishing effort was relatively stable, showed catches varied 250 percent from lowest to highest catches.²⁴²

Relative contribution of patchy environments compared to the effects of widescale loss of mangroves and/or seagrasses.

Studies on the effect of mangrove and seagrass patchiness and habitat connectivity on fisheries production need to be carried out. This is of particular importance for the designation of marine protected areas or the design of networks of no-take fishing reserves. It is also, of course, of general significance for conservation of marine habitats.

Life-cycle studies for the main commercial species of fish and shrimps, including migration distances of larvae and juveniles for restocking adjacent areas.

Although life-cycles of some species are relatively well known, the majority of species important to commercial and subsistence fisheries and other species that support these groups have not been adequately documented. This includes any critical stages of development and the dynamics and flexibility of larval and juvenile stages. In addition, the ability of larvae and juveniles to migrate to adjacent areas remains unknown in most cases. Studies to elucidate these features are important for understanding the ability of species to restock depleted areas.

Development of techniques to identify and quantify links between juvenile fish and their adult populations: the role of ecological connectivity between adjacent biotopes.

The ecological connectivity between adjacent biotopes such as mangroves, seagrasses, coral reefs and mud banks is still developing as a field of study. This is emerging as a critical area for both recruitment of fish species (including crustaceans and molluscs) and for conservation in general.

Further refinement of tagging and marking techniques is needed to allow the quantification of recruitment to adult populations. An incidental benefit of such techniques is the ability to track success of restocking programmes by release of aquaculture grown stock.

Reliable and replicable quantitative fish sampling methods.

Standardization of sampling methods, and rigorous use of sampling techniques need to be applied more generally, and refined to improve their sampling confidence and reliability. This is crucial to quantify changes in fish populations and any relationship between fisheries production and the extent of mangrove and seagrass areas.

Better matching of fish catch statistical data gathering and areas of important fisheries habitat.

Fisheries agencies' statistical areas could be better aligned with areas of habitat that may contribute to fisheries production. This would also greatly contribute to the application of the ecosystem approach to fisheries management.

²⁴² Gartside, Harrison and Ryan (1999)

There are relatively few data on the extent of subsistence fishing in mangrove and seagrass areas even though subsistence fishing is known to be a vital source of protein for many coastal communities. Data on species caught and consumed, and the ability of mangrove and seagrass habitats to support these species are critically needed.

Focused effort on determining the importance of mangrove and seagrass habitats for subsistence fisheries.

To date, there is no comprehensive, quantitative estimate of the amount of biomass that is exported out of any particular area of mangroves. It remains difficult to evaluate the role of biotic export compared with hydraulic export, or recycling within the system and these data are urgently needed.

Quantifying biotic export.

12.2 Conclusions

The following conclusions are offered following our review of the nature of any relationship between mangrove and seagrass habitats and fish populations.

The general assumption of mangroves being nursery areas simply because of the ubiquitous presence of high densities of juvenile fishes is not universally supported. There now are a number of studies that show differences in species composition or density of individuals over time and/or geographic location within similar biotopes. In addition, the links between presence of juveniles and mature individuals expected to flow from nursery areas are in many cases missing or difficult to demonstrate.

Based on the limited data, it seems clear that the widely held, generalized view that mangroves and/or seagrasses underpin fisheries production through their role as nursery areas appears unlikely to apply in many cases.

The attraction of mangroves and seagrasses for juvenile fish and shrimps differs between feeding guilds and species and both factors (structural complexity and food) can contribute significantly but differently.

The direct trophic contribution of mangrove material to juvenile fish and crustaceans is minimal whereas that of tropical seagrass material is probably significant.

It is likely that the presence of biofilms, bacteria, epibenthos and faecal matter associated with mangrove and seagrass habitats make a substantial trophic contribution to juvenile and small fish and crustaceans.

In those instances where the effect of mangroves and seagrasses has been demonstrated to enhance fish production, it has been found to be limited to particular species at particular locations and particular times.

An illustration of this finding is that mangrove and seagrass habitats appear to be very important for some dependent species, either throughout their life cycle or for one or more particular stages of their life cycle. Some examples of these species include juveniles of king prawns (seagrasses) and banana prawns (mangroves), mudcrabs (mangroves) or at other stages of its life cycle, barramundi (mangroves).

Measuring the particular contribution of these habitats to species abundance, either within or adjacent to the habitats remains extremely challenging.

It is misleading to generalize that there is a prevailing effect of mangrove and seagrass areas, either as nursery areas or as enhancers of survival at other life cycle stages of most of the species that occur at sometime within them. Many studies have found weak evidence for the effect of mangroves/seagrass areas enhancing fish production, especially after statistical autocorrelations have been corrected.

The issue of whether mangrove and seagrass areas should be considered important in underpinning fisheries production needs to be evaluated on a case-by-case basis, without the distraction of the inappropriate use of inferential statistical links seeking to prove causation.

Greater understanding is gradually emerging from studies of inshore marine habitats (especially mangroves), regarding the importance of the support for fisheries provided by the complex food webs within them, rather than single species effects, and the effects of connectivity with adjacent habitats such as mud banks and coral reefs.

It is important to remember that mangroves provide a wide range of ecosystem services incidental to fisheries production, but central to the future of coastal environments, such as provision of seed stock for some forms of aquaculture, support of non-fisheries services such as erosion control, mitigation of pollution, mangrove forestry and protection from storm or tsunami events.²⁴³ This provision of a range of ecosystem services emphasizes the urgent need for a more holistic approach to the management of coastal environments and the fisheries within them. This approach must adequately take into account the complexity and interactions between adjoining habitats, and the overarching need to manage fishing activity.

It is expected that further studies using more sophisticated methods and statistical techniques will clarify more explicitly the nature of any relationship between mangrove and seagrass habitats and fish populations.

²⁴³ Saenger (2002); Walters *et al.* (2008)

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