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AN EVALUATION OF THE EVIDENCE FOR LINKAGES BETWEEN MANGROVES AND FISHERIES: A SYNTHESIS OF THE LITERATURE AND IDENTIFICATION OF RESEARCH DIRECTIONS

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Abstract There is a widely-held paradigm that mangroves are critical for sustaining production in coastal fisheries through their role as important nursery areas for fisheries species. This paradigm frequently forms the basis for important management decisions on habitat conservation and restoration of mangroves and other coastal wetlands. This paper reviews the current status of the paradigm and synthesises the information on the processes underlying these potential links. In the past, the paradigm has been supported by studies identifying correlations between the areal and linear extent of mangroves and fisheries catch. This paper goes beyond the correlative approach to develop a new framework on which future evaluations can be based. First, the review identifies what type of marine animals are using mangroves and at what life stages. These species can be categorised as estuarine residents, marine-estuarine species and marine stragglers. The marine-estuarine category includes many commercial species that use mangrove habitats as nurseries. The second stage is to determine why these species are using mangroves as nurseries. The three main proposals are that mangroves provide a refuge from predators, high levels of nutrients and shelter from physical disturbances. The recognition of the important attributes of mangrove nurseries then allows an evaluation of how changes in mangroves will affect the associated fauna. Surprisingly few studies have addressed this question. Consequently, it is difficult to predict how changes in any of these mangrove attributes would affect the faunal communities within them, and, ultimately, influence the fisheries associated with them. From the information available, it seems likely that reductions in mangrove habitat complexity would reduce the biodiversity and abundance of the associated fauna, and these changes have the potential to cause cascading effects at higher trophic levels with possible consequences for fisheries. Finally, there is a discussion of the data that are currently available on mangrove distribution and fisheries catch, the limitations of these data and how best to use the data to understand mangrove-fisheries links and, ultimately, to optimise habitat and fisheries management. Examples are drawn from two relatively data-rich regions, Moreton Bay (Australia) and Western Peninsular Malaysia, to illustrate the data needs and research requirements for investigating the mangrove-fisheries paradigm. Having reliable and accurate data at appropriate spatial and temporal scales is crucial for mangrove-fisheries investigations. Recommendations are made for improvements to data collection methods that would meet these important criteria. This review provides a framework on which to base future investigations of mangrove-fisheries links, based on an understanding of the underlying processes and the need for rigorous data collection. Without this information, the understanding of the relationship between mangroves and fisheries will remain limited. Future investigations of mangrove-fisheries links must take this into account in order to have a good ecological basis and to provide better information and understanding to both fisheries and conservation managers.

Introduction

The basis for the paradigm that mangroves are important for coastal fisheries

The paradigm and the challenge

There is a widely held paradigm that mangroves are critical for sustaining production in coastal fisheries because they act as important nursery areas for fisheries species. The role of mangroves as nursery habitats is widely accepted (e.g., Blaber 2000, Kathiresan & Bingham 2001) and this paradigm is used as the basis for important management decisions on habitat conservation and restoration (Beck et al. 2001). There is also an assumption that the area of mangrove habitat in an estuary translates to the secondary production and catch of commercial fisheries (Baran 1999). This paradigm predicts that the loss of mangrove habitat would then lead to a reduction in, or total loss of, fisheries production.

This paper reviews the current status of the paradigm that mangroves are critical for sustaining the production of coastal fisheries and synthesises the information on the processes underlying the interactions between mangroves and the marine fauna that use them. The evidence underpinning this paradigm and its application as a management principle are also assessed. The need for testing the paradigm and for quantifying the links between estuaries and their associated fauna has recently been highlighted (e.g., Blaber 2000, Beck et al. 2001, Mumby et al. 2004) and potential methods for doing this are discussed. This review, as summarised in Figure 1, goes beyond the simple correlative approach taken in past studies of mangrove-fisheries links. It aims to develop a new framework describing the evidence for the underlying mechanisms of mangrove-fisheries links and identifying how this evidence should be used in designing future research and management strategies.

A comprehensive review of the literature showed that considerable work has been done on certain aspects of the mangrove-fisheries relationship (e.g., abundances of juvenile fishes within mangrove habitats), whereas little work has been done in other areas (e.g., growth and survival rates within these habitats). Much of the work has been carried out on Australian mangroves, with relatively few studies elsewhere and this bias is reflected in the review which draws heavily on these Australian examples. Useful information can, however, also be drawn from an expansive literature, mainly from North America, on the nursery values of other coastal habitats (especially saltmarsh and seagrass) in both temperate and tropical waters and these studies are included in this review where relevant. Despite the volume of work describing habitat-fisheries relationships, it is only recently that significant attempts have been made to draw together all the available information on links between mangroves and fisheries into a broad and meaningful framework (e.g., Blaber 2000, Sheridan & Hays 2003). The current review aims to develop this framework further.

Nursery role concept

Nursery areas for fishes and invertebrates have been regarded as any areas inhabited by the juveniles of a species, often with the adults living in distinctly separate habitats. Under this definition, all areas of habitat are considered important in contributing recruits to the adult population. For

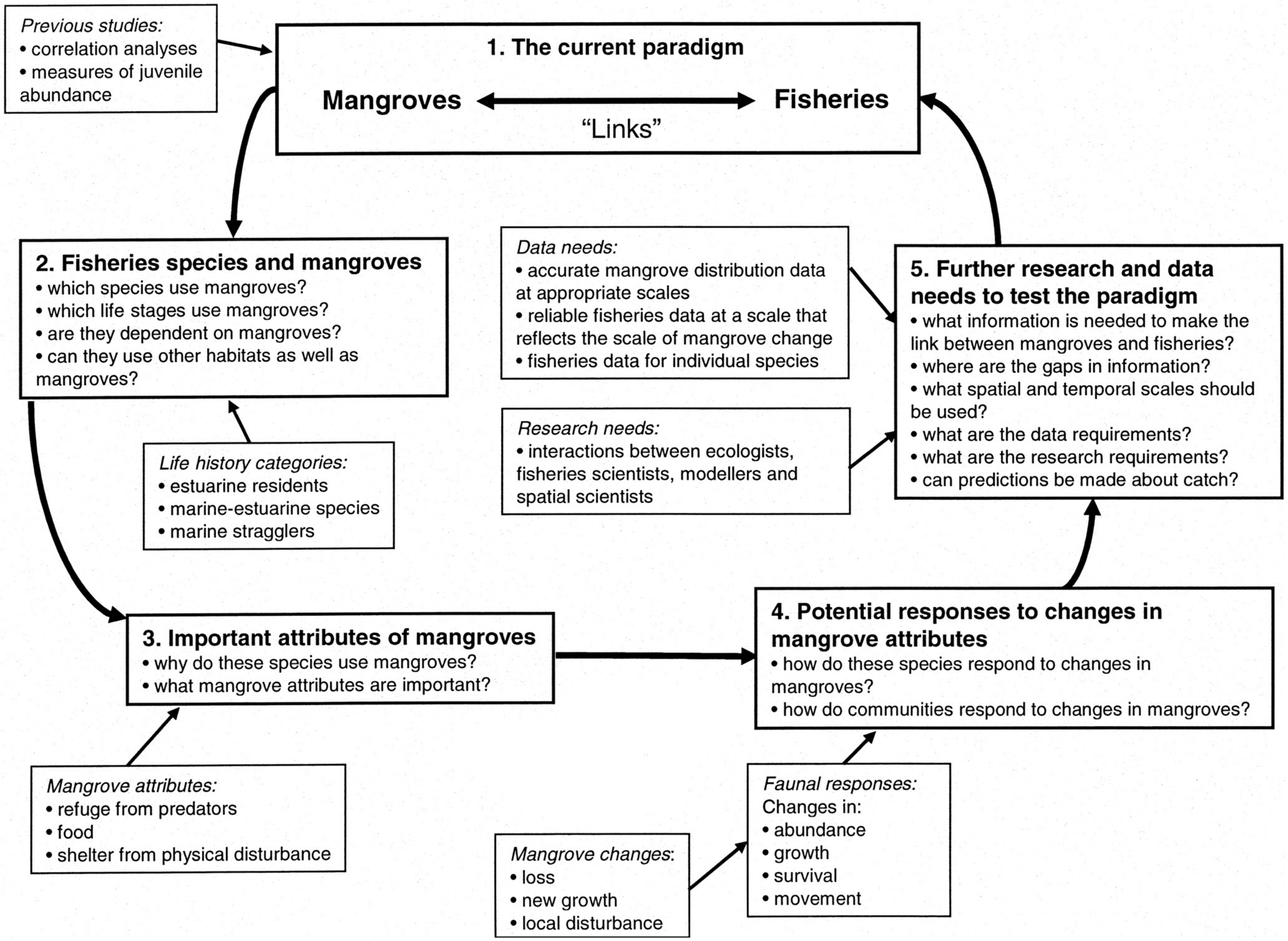

Figure 1 The conceptual framework describing a new approach to mangrove-fisheries links.

example, all mangrove habitats may be regarded as having equal nursery value for certain fish species. Recently, this classical view has been challenged on the grounds that all juvenile habitats may not be contributing equally as nurseries (Beck et al. 2001).

Beck et al. (2001) propose a stricter definition of nurseries: "a habitat is a nursery for juveniles of a particular species if its contribution per unit area to the production of individuals that recruit to adult populations is greater, on average, than production from other habitats in which juveniles occur". Under this definition, not all juvenile habitats are regarded as nurseries. Nurseries are a subset of all possible juvenile habitats and are the most productive of these habitats in terms of the supply of recruits to adult populations and, therefore, to fisheries. Recruits, in this definition, are animals that enter an adult population and subsequently reproduce.

The success of recruitment from nursery habitats to adult populations depends on several factors, all of which contribute in varying degrees to overall production. First, the nursery must be accessible to settling larvae or post-larvae and this will depend on hydrodynamic processes over a range of spatial scales. After settlement, the value of a nursery habitat is further measured in terms of juvenile density, survival, growth and movement to adult habitats (Beck et al. 2001, Sheridan & Hays 2003). Failure of any one of these processes can lead to a lack of recruits back to the adult population.

In most studies, only the abundance or density of juveniles within a habitat is quantified, with the assumption that areas with more juveniles will provide a greater contribution to the adult population. However, juvenile abundance may not always reflect adult abundance (Beck et al. 2001) and attempts to evaluate the importance of nursery areas should ideally incorporate measures of all four factors. Survival, growth and movement are much harder to measure than abundance and are often ignored or overlooked (Sheridan & Hays 2003), although some recent papers have attempted to address this problem, e.g., survival and growth (Stoner 2003), movement between juvenile and adult habitats (Gillanders et al. 2003, Mumby et al. 2004, see also the review on seagrass nurseries in Heck et al. 2003).

Mangrove habitats within estuaries

Mangroves are just one of the habitats found in estuaries and shallow coastal waters, although in many tropical areas they are the dominant estuarine habitat type (Blaber 2000). The functional services provided by mangroves (e.g., food, shelter, high primary production) are often the same as those provided more generically by estuarine and nearshore environments and it may be difficult to separate the contribution of mangroves to biodiversity and fisheries from that of estuaries themselves (Loneragan et al. in press). Despite the difficulties associated with separating the roles of mangroves from those of estuaries, this is a necessary step for management; separation of the roles could determine how habitats are protected and at what temporal and spatial scales.

It is also important to note that fishes and crustaceans only use mangroves for a proportion of the tidal cycle (e.g., 8–10 h in any 24–h period; Vance et al. 2002, Skilleter & Loneragan 2003, Pittman & McAlpine 2003) and, therefore, other adjacent habitats must be important during the low tide. The depth and duration of tidal inundation will vary considerably among sites. These factors are likely to influence both the movement of animals into the mangroves and their ability to use the resources therein (Meager et al. 2003).

Only a subset of species that use estuaries as nurseries are mangrove-dependent, i.e., they require mangrove habitats at some stage of their life cycle (the concept of mangrove dependency is discussed further in the next section, pp. 000–000). The degree of dependency on either mangroves or estuaries varies between species, locations and regions. The juveniles of some species, such as banana prawns (*Penaeus merguiensis* and *P. indicus*), are found almost exclusively in mangrove-lined creeks (Staples et al. 1985, Vance et al. 1998, Rönnbäck et al. 2002, Kenyon et al. in press) and are described as being highly mangrove-dependent (see following section, pp. 000–000). Other

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species of fishes and invertebrates may be able to use other estuarine habitats such as seagrass, saltmarsh and mudflats, and may not be so dependent on mangroves. However, even if the juveniles are capable of using alternative habitats, there is some evidence that mangroves confer advantages in the growth and survival of juveniles of some species, compared with other habitats (Mumby et al. 2004).

Some of the species that use mangroves as nurseries are important in commercial and/or recreational fisheries. It has been estimated that over two-thirds of the world's harvest of fish and shellfish are directly linked to estuarine habitat in this manner (Robertson & Blaber 1992). Rönnbäck (1999) listed the proportion of mangrove-related species in fisheries around the world: e.g., Florida (80%), Fiji and India (60%), eastern Australia (67%), Malacca Strait (49%) and southeast Asian countries (fish catch 30%, prawn catch nearly 100%). In Malaysia, it was estimated that 32% of the 1981 fish harvest could be linked to mangroves, whereas in the Philippines, about 72% of the catch between 1982 and 1986 was associated with mangroves (Paw & Chua 1991). In Australia, estuarine ecosystems, such as mangroves, seagrasses and shallow-water habitat, are critical to about 75 and 70% of fish and crustacean species in the fisheries of Queensland (Quinn 1992) and New South Wales (Pollard 1976, 1981), respectively. This value is lower for southwestern Australia (20%) and Australia as a whole (32%) but still represents a large total catch (Lenanton & Potter, 1987).

Support for the concept of mangroves as nursery areas has come from two main sources. First, numerous studies have documented greater abundances of juvenile species in mangroves than in other estuarine and inshore habitats in various places around the world, e.g., Australia (Robertson & Duke 1987, Laegdsgaard & Johnson 1995, 2001), Malaysia (Chong et al. 1990), Belize (Sedberry & Carter 1993), and the Carribean (Nagelkerken et al. 2001, Nagelkerken & van der Velde 2002). However, as discussed above, juvenile abundance does not always reflect adult abundance, and further studies of survival, growth and movement to adult habitats are needed. Second, several studies have found correlations between the extent of mangroves and the catch in nearby fisheries (Table 1). Although in some cases these correlations are quite strong, and infer some link between mangroves and fisheries, they cannot be used to assume causality. Furthermore, few attempts have been made to assess the ecological framework that would explain such correlations from the perspective of the biology of the organisms involved and hence allow predictions to be made about the effects of disturbance and loss of mangroves on fisheries catches and productivity.

Existing Correlations

The strongest correlations between mangrove extent and commercial catch are those for mangrove area and penaeid prawns. Penaeid prawns are the most economically valuable fishery resource associated with mangroves (Rönnbäck 1999) and there are several studies that have investigated correlations between the magnitude of prawn catches and the area of mangroves in tropical regions of the world (Table 1). These studies assumed that the correlations demonstrated the role of mangroves as nurseries for juvenile prawns, but there was no discussion of the causal mechanisms that might underlie the relationships. Without some consideration of underlying mechanisms, it is not possible to move towards predictive models of how changes to mangroves might affect fisheries around the world.

Furthermore, most of these correlations are based on the total catch of all prawns, not the catch of those prawn species known to be mangrove dependent. The inclusion of prawn species that use habitats other than mangroves will influence the strength of the correlations and may mask the true interaction between mangroves and the prawns that use them.

Pauly & Ingles (1986), using data from a worldwide survey and two additional studies in Indonesia and the Philippines, found significant relationships between mangrove area, production of prawn fisheries and latitude (Table 1). Latitude itself does not affect faunal abundance, rather it

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Table 1 Published relationships between mangroves and fisheries production (after Baran 1999).

Relationship	r^2 (n)	Region	Reference
Prawns			
Catch / VA = $158.7e^{-0.070(\text{Latitude})}$	0.54 (27)	Worldwide tropical	Turner 1977
Catch / VA = $159e^{-0.063(\text{Latitude})}$	0.64 (14)	Western hemisphere tropical	Turner 1977
$\text{Log}_{10}\text{Catch} = 2.41 + 0.4875\log_{10}\text{VA} - 0.0212$ latitude	NA	Worldwide tropical	Pauly & Ingles 1986
Catch = 5.473 + 0.1128 MA	0.89 (NA)	Indonesia	Martosubroto & Naamin 1977
Log_{10} Catch = 0.8706 $\log_{10}$ MA – 0.0575	0.61 (18)	Philippines	Paw & Chua 1991
Catch = 0.5682 MA + 636.8	0.89 (10)	Peninsular Malaysia	Sasekumar & Chong 1987
P. merguiensis catch = 1.074 ML + 218.3	0.58 (6)	Gulf of Carpentaria, Australia	Staples et al. 1985
Log_{10} white prawn catch = 0.7623 $\log_{10}$ MA + 1.2263	0.66 (18)	Philippines	Paw & Chua 1991
Fishes			
LnCatch = 0.496Ln MA + 6.070	0.48 (10)	Gulf of Mexico	Yanez-Arancibia et al. 1985
Log_{10}Carangids = 0.8082$\log_{10}$MA + 0.9896	0.53 (18)	Philippines	Paw & Chua 1991
Log_{10}Mugilids = 0.7361$\log_{10}$MA – 0.4091	0.40 (20)	Philippines	Paw & Chua 1991
Log_{10}Siganids = 0.9505$\log_{10}$MA + 1.1462	0.66 (12)	Philippines	Paw & Chua 1991
Log_{10}Serranids = 0.4734$\log_{10}$MA + 1.1530	0.40 (18)	Philippines	Paw & Chua 1991
Log_{10}Lutjanids = 0.5337$\log_{10}$MA + 0.7972	0.34 (15)	Philippines	Paw & Chua 1991
Total fishes and prawns			
Catch = 0.4304$\log_{10}$MA + 0.0575	0.4 (34)	Philippines	Paw & Chua 1991
Catch = 0.5948 $\log_{10}$MA + 1.8045	0.45 (39)	Philippines	Paw & Chua 1991
Catch = 0.449 MA + 0.614 engine capacity + 654 social incentive	0.95 (NA)	Vietnam	de Graaf & Xuan 1998
Catch = 2.97 MA – 18,700	0.88 (5)	Vietnam	de Graaf & Xuan 1998

Notes: VA = area of intertidal vegetation, MA = mangrove area, ML = mangrove length, NA = not available

is a surrogate for a number of possible climatic, geological and hydrographical variables. The inverse relationship between catch per hectare and latitude could be attributed to a number of factors including temperature, food availability and changes in the growth rates of the prawns (Turner 1977) but the relative importance of these factors, and the mechanisms by which they may operate, have not been investigated further.

The linear extent of mangrove-lined estuaries has been used as an alternative index of the available mangrove nursery, rather than total area (Staples et al. 1985; Table 1). Staples et al. (1985) found a positive correlation between the linear extent of mangroves in the estuaries of the Gulf of Carpentaria, northern Australia, and the mean annual banana prawn catch over 10 yr in the adjacent region of the fishery. The relationship was not consistent over different regions; removing one region (Limmen Bight, western Gulf of Carpentaria), made the correlation much stronger ($r^2 = 0.92$). Other environmental factors, such as freshwater flows, may influence the catches in this region more strongly than the extent of habitat.

Linear extent was regarded as a better index of available habitat than total area, because prawns access the mangrove forest through the mangrove-water interface as they move in and out with the tide (Vance et al. 1996, 2002). Similarly, research on the relationship between saltmarsh and brown shrimp (*Penaeus aztecus*) in the southern U.S. has suggested that the marsh-water interface is the important part of the marsh habitat for the brown shrimp (Browder et al. 1989). These studies attempted to take into account the mechanisms of the relationship between intertidal vegetation and prawns, by recognising the way that prawns access mangroves and salt marshes from adjacent waterways. This represents a shift in the approach to mangrove-fisheries correlations because it attempts to consider the basis for the relationship in order to determine the most appropriate data to be used.

There are fewer clear cases of correlations between the magnitude of commercial finfish catches and the extent of mangroves (Table 1). For example, in the Philippines, a positive, but weak, correlation was found between mangrove area and the catch of four families of commercial fish (Paw & Chua 1991; Table 1). Again, there was little or no discussion of the ecological mechanisms underlying the relationships, beyond the basic assumption that the mangroves are providing nursery habitats for juvenile fishes.

Correlative relationships, while inferring a link between mangroves and fisheries, do not necessarily establish causality. A causal link between the abundance of juvenile penaeids and the spatial extent of mangroves has never been established experimentally (Robertson & Blaber 1992) and there is no direct evidence anywhere for a significant drop in catches caused by the reduction in area of mangrove habitat. However, it is known that mangroves harbour greater densities of juvenile fishes than adjacent areas (Robertson & Duke 1987, Robertson & Blaber 1992, Laegdsgaard & Johnson 1995, 2001), and that juveniles of some species, such as *P. merguiensis,* are found almost exclusively in mangrove habitats (Staples et al. 1985). To understand whether there is a causal linkage between the extent of mangrove habitat and the magnitude of associated fisheries requires a knowledge of the processes behind these interactions. The remainder of this review describes a sequence of steps that can be used to gain a better understanding of these mangrove-fisheries interactions (Figure 1). The first step in this framework is to identify what type of marine animals are using mangroves and at what life stages (see the following section).

Interaction of fishery species with, and dependence on, mangroves

Fishes and invertebrates use estuarine and inshore habitats in a number of ways: some are only occasional visitors, some use them only at certain life stages, whereas others reside permanently in the estuaries (Lenanton & Potter 1987, Potter et al. 1990, Potter & Hyndes 1999, Whitfield 1999). These differences in life history behaviours may influence the nature of any interactions between species and their habitats. A number of different life cycle categories can be identified depending on the ways (temporally and spatially) that species use estuaries.

Some species use a range of environments, including offshore, inshore and estuarine regions. From an estuarine perspective, those that are found only occasionally in estuaries have been termed marine stragglers (Potter & Hyndes 1999, Whitfield 1999) and are regarded as having no dependence on estuaries or mangroves.

A second group of species, termed marine-estuarine species, use inshore areas and estuaries for significant periods of time, often during the juvenile phase. Several marine-estuarine species have juveniles that are only found amongst mangroves: these have been termed mangrove-dependent species (e.g., the banana prawn *P. merguiensis*; Staples et al. 1985, Vance et al. 1996). Some catadromous species travelling between freshwater and marine habitats also use mangrove habitats at certain life stages (e.g., barramundi *Lates calcarifer*; Russell & Garrett 1983).

A final grouping is the true estuarine species that complete their entire life cycle within estuaries. These species are clearly estuarine dependent but many are small and short lived (e.g., members of the Gobiidae and Atherinidae, Blaber et al. 1989, Potter & Hyndes 1999, Whitfield 1999, Blaber 2000) and few contribute directly to fisheries; they will not be discussed further. Instead, the focus will be on the marine-estuarine category that includes a number of economically important species.

Marine-estuarine species

The life cycles of species in this category vary but can be described by the following generalised sequence. Typically, the adults of these species spawn off shore, producing eggs which disperse in the water column for varying lengths of time. The eggs then develop into planktonic larvae, which move, or are carried by currents, into inshore and estuarine waters. The post-larval or early juvenile stages then settle in estuarine habitats. The length of time spent in these habitats varies between species, between regions, and even between individuals, and also depends on environmental factors such as temperature, season, salinity and rainfall. After spending time in estuarine habitats, the subadults or adults migrate varying distances out of the estuary, and back towards the offshore areas. This generalised life cycle applies to a number of fisheries species, e.g., banana prawns (*Penaeus merguiensis*) (Dall et al. 1990), sea mullet (*Mugil cephalus*), whiting (*Sillago* spp.) and flathead (*Platycephalus* spp.) although the specific details vary between the different species. In South Africa, 39% of the total number of fish species found in estuaries belonged to this category (Whitfield 1999).

Mangrove-associated species

Mangroves are found within estuarine and coastal waterways in tropical and subtropical areas. The fauna found in mangroves is therefore also associated with estuarine and coastal waters, making it difficult to separate the importance of mangroves in their life cycle with other features of these water bodies (see further discussion in next section). However, it is known that the importance of mangroves in the life cycles of inshore species varies among species. Some species appear to use mangroves almost exclusively, e.g., banana prawns, *Penaeus merguiensis* and *P. indicus* (Staples et al. 1985, Rönnbäck et al. 2002, Kenyon et al. in press), rainbow parrotfish *Scarus guacamaia* (Mumby et al. 2004), while others use alternative habitats in addition to mangroves, e.g., barramundi (Russell & Garrett 1983).

A marine-estuarine species with a strong mangrove dependency is the white banana prawn (*Penaeus merguiensis*), with the juveniles being found exclusively in mangroves and along mangrove-lined mudbanks (Staples et al. 1985, Dall et al. 1990, Rönnbäck et al. 2002). Adult white banana prawns are the basis of a high-value commercial fishery in southeast Asia and in northern and eastern Australia (e.g., worth AU $50 million a year in Australia's northern prawn fishery), where this species has been well studied (e.g., Staples 1980a,b, Staples & Vance 1986, Haywood & Staples 1993, Vance et al. 1998). The closely related red-legged banana prawn (*P. indicus)* appears to have a similar dependence on mangroves (Loneragan et al. 2002, Rönnbäck et al. 2002, Kenyon et al. in press). Both species have strong links with mangroves, as the juveniles are found only in mangrove habitats. There are few other species for which such a strong dependence on mangroves has been established.

There is much less evidence for the dependence of other commercially important species on mangroves than for banana prawns. For example, the barramundi has been regarded as a mangrove-associated fish but the role of mangroves as a nursery for barramundi is not clear. It is an important commercial and recreational fish in many regions throughout the tropical and subtropical Indo-West Pacific region (Russell & Garrett 1985). Although their life cycle has been documented in several countries, e.g., Papua New Guinea (Moore 1982) and Australia (Russell & Garrett 1983, 1985), there remains a lack of knowledge about the use of nursery habitats by various juvenile stages of barramundi. In general, barramundi follow the generalised life cycle of a catadromous species, using inshore marine waters as spawning grounds and freshwater and estuaries as juvenile and subadult habitats. However, unlike the banana prawn, they can use a range of supralittoral habitats within estuaries, including tidal pools, gutters, floodplains and billabongs as well as mangroves (Russell & Garrett, 1983). They may, therefore, be regarded as estuarine related rather than mangrove dependent and a more detailed understanding of their nursery habitat use is required before habitat associations can be confirmed.

Summary

Fish and invertebrate species clearly use mangrove habitats in a variety of ways, at different stages of their life cycles and for different lengths of time. The level of mangrove dependency therefore varies depending on the species of interest, the life history of the species, and the proportion of the life history spent in the mangroves. Step 3 of the framework (Figure 1) investigates why these different species and life stages use mangroves, what benefits are gained by using this habitat and which attributes of mangroves contribute to the increased abundance, survival, growth and movement of these animals.

Attributes of mangroves likely to be important for fisheries species and the question of whether these can be separated from estuarine attributes in general

The evidence presented in the foregoing sections shows that a number of fisheries species use estuarine habitats as juvenile nurseries. Key questions underlying why estuaries, and mangroves in particular, are important as nurseries for these fish and crustacean species include: What benefits can be gained from spending their juvenile life stage in mangrove habitats? Which particular mangrove attributes are attractive to the juveniles that live in them? Do other estuarine habitats provide the same or complementary benefits to these species? Is it possible to separate the nursery attributes of mangroves from the more general attributes of estuaries?

AU: Is this what you meant?

The nursery role of shallow inshore waters, estuaries in general and estuarine habitats other than mangroves has long been recognised, e.g., sheltered shallow coves (Dulcic et al. 2002), rocky shores (Henriques & Almada 1998), salt marshes (Boesch & Turner 1984), seagrass (Heck et al. 1997), seagrass, corals and mangroves (Hatcher et al. 1989) and it is difficult to separate the value of mangroves from broader estuarine values or even shallow inshore waters. Mangroves and estuaries share features such as shallow water, reduced wave action, high organic content in the sediment, high primary production and the provision of protection from predators, which may all contribute to their role as nurseries. These processes could, therefore, also be functions of other estuarine habitats. What is currently unknown, and needs to be determined, is whether mangroves fulfill these roles differently from other estuarine habitats such as seagrass, saltmarsh, sandbanks and mudflats. More detailed information is required for individual species because the relative roles will vary between species.

AU: Seagrass again?

The exact role of mangroves as nursery areas is not clearly understood but a number of hypotheses have been proposed to try to explain this role (Robertson & Blaber 1992, Blaber 2000). The three main hypotheses are that mangroves provide juveniles with (1) a refuge from predators, (2) an abundance of food and (3) shelter from physical disturbances. These three hypotheses are not mutually exclusive and are likely to be interlinked. All three may play a role in creating effective nurseries and the relative importance of each will vary with different species.

Hypothesis 1: Refuge provided by structural complexity, shallowness and turbidity

Evidence for the protective role of mangroves comes from studies showing that few large piscivorous fish enter mangroves at high tide (Blaber et al. 1989, Vance et al. 1996, 2002, Rönnbäck et al. 1999, Meager 2003); thus smaller animals are able to escape their predators by entering the mangrove forest. This refuge effect may be caused by a number of factors. The structural complexity of submerged vegetation, shallow water and/or turbidity can provide significant refuges from predators, especially for small, mobile animals (Robertson & Duke 1987, Robertson & Blaber 1992, Rönnbäck 1999, Nagelkerken et al. 2000a,b). These characteristics are commonly found in a number of estuarine-associated habitats, particularly mangroves, seagrass beds and salt marshes.

AU: Change ok?

Structural complexity

Mangroves are the most structurally complex of the estuarine habitats, because of their trunks, branches, prop roots, buttresses, pneumatophores and fallen debris (e.g., leaves, branches and logs). These structures provide protection for small animals in several ways: they reduce prey visibility, lower the encounter rate of predator and prey, and limit the ability of predators to search for and capture prey (Rönnbäck et al. 1999, Meager et al. in press). In addition, exported mangrove detritus on the bottom of mangrove waterways is likely to serve as a useful shelter from predation, for example for juvenile penaeid prawns (Robertson & Blaber 1992). At low tide, when the structure of mangrove trees is not available as a refuge, fallen trees and branches in mangrove creeks may provide some shelter from predation (Robertson 1988, Sheaves 1992, 1996).

Lower predation rates will improve the effectiveness of a nursery area in several ways. If predation rates are low, the survival of individuals increases and hence population abundance increases. Growth will also potentially be increased because less time is spent hiding from predators and more time can be spent on foraging and feeding (Sih 1992, Heck et al. 2003). Thus, three of the essential functions of an effective nursery *sensu* Beck et al. 2001 (greater abundance, higher survival and faster growth) are likely to be found for some species in mangroves.

A number of laboratory experiments have added support for the refuge value of complex structures, by investigating the behaviour of fishes and crustaceans in vegetated (real or artificial) and unvegetated areas, with or without predators present (see review by Heck & Crowder 1991). In general, the results of these studies indicate that predation rates are lower in vegetated than unvegetated areas (Werner et al. 1983, Kenyon et al. 1995, Primavera 1997, Laegdsgaard & Johnson 2001) and lower amongst more structurally complex vegetation than less complex vegetation (Vince et al. 1976, Heck & Thoman, 1981, Kenyon et al. 1995). For example, juvenile fishes of a number of species actively sought shelter amongst artificial structures in a tank in the presence of predators but moved away from the structures when predators were absent (Werner et al. 1983, Laegdsgaard & Johnson 2001). In experiments with juvenile banana prawns (*Penaeus merguiensis*), more prawns sheltered in heterogeneous, complex structures in the presence of predators (*Lates calcarifer*) than in predator-free situations (Meager et al. in press).

Shallow waters

Larger predators may be unable to penetrate into shallow waters, thus creating another form of refuge for smaller fishes and crustaceans (Boesch & Turner 1984, Ruiz et al. 1993, Blaber 2000). This idea is supported by the work of Ruiz et al. (1993) who found higher abundances of small species (e.g., *Palaemonetes pugio*, *Crangon septemspinosa*, *Fundulus heteroclitus*) and lower abundances of large predatory species (*Callinectes sapidus*, *Leiostomus xanthurus* and *Micropogonias undulatus*) with decreasing water depth in Chesapeake Bay, U.S.

Vance et al. (1996) and Rönnbäck et al. (1999) found that small fishes and prawns moved into more shallow waters while larger fishes remained in deeper water at the fringes of the mangroves.

The greatest densities of juvenile prawns at low tide are found in small mangrove creeks and gutters which may be inaccessible to larger predators (Bell et al. 1984). Laboratory experiments have also shown that small fishes have a preference for shallow water in the presence of predators (Posey & Hines 1991).

By entering shallow water to escape from fish predators, small fishes and prawns may be increasing their vulnerability to predation by birds (Blaber 2000). However, within the mangrove forest this risk is reduced, due to the protection given by the mangrove canopy and the structure of roots and trunks, which may make it more difficult for birds to forage.

Shallowness is an attribute of inshore coastal waters and estuaries as well as mangroves and, once again, it is very difficult to separate the functional values of these different habitats. There is not enough information to determine whether the role of shallow waters in mangroves is different from shallow waters in the other habitats. It is likely that fish communities differ between shallow unvegetated areas and shallow mangrove areas in diversity, size of individuals and trophic structure (Williamson et al. 1994, Laegdsgaard & Johnson 1995, 2001). However, what this means for their relative nursery values is not clear.

Turbidity and shade

Underwater visibility is decreased by both high turbidity and shade beneath the mangrove canopy (Cocheret de la Morinière et al. 2004). The turbid, shaded water often found around mangroves may therefore provide an additional refuge from visual predators (Blaber & Blaber 1980, Cyrus & Blaber 1987, Kneib 1987, Whitfield 1999). Juvenile fishes appear to be attracted to turbid areas and may use the turbidity gradient to locate nursery areas (Blaber & Blaber 1980). Abundances of some fish species have been found to be higher in areas of higher turbidity (Blaber 2000), although a higher abundance does not necessarily prove their effectiveness as nurseries (see p. 000). However, very high turbidity may negatively affect processes such as fish egg survival, hatching success, feeding efficiency and growth rate (Whitfield 1999). The relative growth, survival and ontogenetic movements of animals in turbid versus non-turbid waters are not known.

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While the importance of turbidity as a form of refuge has been suggested by some studies, others indicate that it may not be the main factor in the nursery function of mangroves. In the Dampier region of Western Australia, the water around mangroves is as clear as in nearby open shore areas, yet fish abundances are greater in the mangroves than other habitats (Blaber et al. 1985). Similarly, in Moreton Bay, southeast Queensland, juvenile abundances were higher in mangroves than in other habitats (seagrass and mudflats) but turbidity did not vary between the different habitats (Laegdsgaard & Johnson 1995). Turbidity was not found to be an important factor influencing the fish communities in shallow estuarine waters in Singapore (Hajisamae & Chou 2003) and, in South Africa, some low turbidity estuaries were found to have a higher number of fish species than more turbid estuaries (Whitfield 1999). In these cases, it is likely that turbidity is less important than the structure and/or food provided in the mangrove or estuary habitat. However, this has not been examined in any more detail nor tested experimentally.

The turbidity of creeks and gutters adjacent to mangroves may provide a refuge for juveniles at low tide when they must move out of the mangroves. It is likely that both shallowness and turbidity contribute to this role, but the relative importance of each is not known, and will vary depending on both the prey and predator species.

Hypothesis 2: Availability of food

Nutrient levels and primary productivity are generally high in mangrove systems, and it is thought that food for juvenile fishes and crustaceans is more abundant in mangroves than in other coastal habitats (Hutchings & Saenger 1987, Robertson & Blaber 1992, Laegdsgaard & Johnson 2001). Nutrients are brought into mangrove ecosystems from upstream (freshwater inflows) and from seaward (tidal mixing) and they are concentrated by lateral trapping within the mangroves (Wolanski et al. 2001). Primary productivity generated within the mangrove forest itself can be attributed to several sources including mangrove trees, epiphytes, phytoplankton and benthic microalgae (Rönnbäck 1999). This primary productivity forms the basis of a food web providing abundant and diverse trophic resources to higher consumers (Baran & Hambrey 1998).

It was once believed that mangrove primary production drove offshore fisheries production through the outwelling of nutrients (Odum & Heald 1972, Robertson & Blaber 1992, Lee 1995). However, recent studies using stable isotope analysis indicate that this is not the case (Rodelli et al. 1984, Newell et al. 1995, Loneragan et al. 1997, Chong et al. 2001) and that mangrove-derived nutrients only contribute directly to the food-webs of animals (e.g. prawns) within mangrove-lined creeks (Loneragan et al. 1997). To date, it has not been conclusively shown whether or not outwelling of nutrients from mangroves contributes to offshore production.

Some studies have suggested that small fishes and prawns consume most of their food when in the mangroves. For example, banana prawns feed mainly during high tide, when they are able to forage in the mangroves (Wassenberg & Hill 1993). In experimental work in Moreton Bay, Laegdsgaard & Johnson (2001) found that small juvenile mullet (*Liza argentea*) and whiting (*Sillago* spp.) had significantly fuller guts when located in mangroves than in seagrass or on mud flats. This may be because there is more food available in the mangroves than in the adjacent habitats, or there may be more time available for feeding in the mangroves, due to reduced predation.

Many juvenile fishes are zooplanktivores and a large component of their diet in the mangroves is crab larvae (Robertson & Duke 1987, Rönnbäck 1999). These crab larvae are therefore an important indirect link in the food web of mangroves resulting in nutrients being exported from the mangroves. The crab larvae are much more abundant in mangroves and adjacent waterways than in other inshore and estuarine habitats because of lateral trapping (Robertson & Blaber 1992). In the absence of mangroves, this important food source would be more dispersed and therefore less efficiently foraged by small fish predators.

Mangroves produce a large quantity of leaf litter. Most animals are not able to assimilate this directly and require bacterial enrichment to take place before consumption. However, sesarmid crabs can directly consume mangrove leaves and may consume or store 30–80% of the litterfall (Rönnbäck 1999). These crabs are eaten by fishes, creating an important pathway for mangrove nutrients to enter food webs.

Whereas mangroves may be important feeding sites for juvenile fishes and prawns, there is little direct evidence that this is the primary reason for their nursery function (Robertson & Blaber 1992, Sheridan & Hays 2003). In addition, given that mangroves are only used for a limited time during the tidal cycle, it is likely that other sources of food must also be important.

Hypothesis 3: Shelter and lateral trapping

Mangrove habitats are generally areas of low current speeds and low wave action, providing small juvenile animals with a benign physical environment in which to settle. The presence of mangroves increases the residence time of water, especially in flat, wide mangroves with complex waterways (Wolanski & Ridd 1986, Wolanski et al. 2001). Calm water appeared to be a requirement for some juvenile fish species in Moreton Bay, Australia, but not for others (Blaber & Blaber 1980), and no mechanism was proposed for why this might be.

Sheltered, calm water leads to the retention of planktonic larvae and post-larvae (Rönnbäck et al. 1999). In non-vegetated estuarine habitats, these early life stages are at risk of being swept away by currents but the trapping capacity of mangroves promotes their retention, thereby increasing their chances of settlement. The concentration of zooplankton (such as the crab larvae discussed above) in this way also provides a food source for planktivores within the mangroves.

Another form of lateral trapping associated with sheltered waters in mangrove waterways is sediment trapping, which promotes the deposition of soft sediments. This form of trapping results in a soft substratum into which invertebrates, such as prawns, can bury easily, thus providing another form of refuge from predators (Rönnbäck 1999).

Ontogenetic changes in habitat use

Mangroves provide nursery habitats for the juveniles of many species of fishes and invertebrates but as these juveniles grow they tend to move away from the mangroves, and from estuaries in general, towards their adult habitats. Relatively larger fish of the same species are found on mudflats and unvegetated areas in inshore and estuarine areas than in nearby mangroves (Chong et al. 1994, Laegdsgaard & Johnson 2001) and on coral reefs than in mangroves (Nagelkerken et al. 2000a,b, Cocheret de la Morinière et al. 2002, Mumby et al. 2004); these are likely to be subadult or adult fishes that are migrating out of the mangroves and into deeper waters. The bluestriped bass (*Haemulon sciurus*) appears to migrate through several ontogenetic changes in habitat, from seagrass to mangroves, then patch reefs and finally to forereefs in Belize (Mumby et al. 2004). A number of fish species in Bonaire, Netherlands Antilles, show a similar pattern of movement from mangrove and seagrass nurseries to deeper coral reefs. This migration can be either direct or stepwise from mangroves and seagrass to other shallow habitats within a bay to the outer coral reef (Cocheret de la Morinière et al. 2002).

These ontogenetic shifts in habitat use are likely to optimise growth and survival at each life stage and reduce intraspecific competition between size classes (Laegdsgaard & Johnson 2001). They may also be brought about by changes in the fish's dietary needs (Cocheret de la Morinière et al. 2003a,b). Having obtained food, shelter and refuge from predators in the mangroves, the juveniles may then reach a size where they are less vulnerable to predation, either directly because of their size or through greater mobility and the ability to escape from predators. At this stage, they can migrate away from the mangroves towards their adult habitats with a reduced risk of predation.

Summary

The evidence suggests that mangroves, and estuaries in general, fulfil a nursery role because they provide a refuge from predators, a source of nutrients and a benign environment in which the juveniles can develop. These three attributes are not mutually exclusive and the relative importance of each, which is currently unknown, is likely to vary among species. Experiments to test the relative importance of habitat structure and shade showed that, for one species of fish (*Haemulon sciurus*), both these factors were important, while another (*Ocyurus chrysurus)* was more influenced by the presence of shade (Cocheret de la Morinière et al. 2004). More experimental studies such as this are needed to determine the relative importance of all the possible factors for individual species.

Why is it important to investigate the relative values of these attributes? Because a change in any one of these attributes may affect the value of a habitat as a nursery and hence influence recruitment to the adult population and, ultimately, the fishery. This step, therefore, creates a link between present knowledge of mangrove usage by associated fauna and the ultimate effect on fisheries production caused by changes in mangrove distribution and extent (Figure 1). The information that is currently available on the importance of the nursery functions of mangroves can be used as the basis for habitat and fisheries management to optimise the conservation and resource values of coastal habitats. But, as the above discussion shows, there are still many gaps in present knowledge of these attributes and their functions An understanding of the effect of changes in these functions is necessary for habitat management and conservation, and for the development of predictive models of mangrove-fishery relationships. Based on the limited information available, the following section discusses the potential effects of changes to these nursery attributes on faunal communities.

The likely responses of fish and crustacean species to changes in mangroves

Many studies have looked at the effects of natural and human-induced changes on mangroves including the clearing of mangroves, the establishment of new mangroves, localised disturbances and changes in levels of nutrients or sediments (see reviews in Hutchings & Saenger 1987, Hatcher et al. 1989, Kathiresan & Bingham 2001, Valiela et al. 2001, Alongi 2002). These changes range in scale from local modifications (e.g., boardwalk construction, Kelaher et al. 1998) to regional impacts (e.g., oil spills, Duke et al. 1997), the total clearing of mangroves for the construction of prawn ponds (Valiela et al. 2001) and the global impacts of climate change (Alongi 2002). Some of these studies acknowledge, in an unspecific way, that these changes will somehow “affect” or “have consequences for” mangrove-related fauna. However, few studies have taken the next logical step and further investigated the subsequent effects of any of these changes on the faunal communities within the mangroves (Table 2). This type of information is critical for understanding and predicting changes in fauna as a result of changes in mangroves. For example, very little is known about how changes in mangrove habitat complexity affect the biodiversity and abundance of the associated fauna. However, even small-scale modifications to the physical structure of mangrove habitats are likely to produce significant effects on the diversity and abundance of macrobenthic organisms (Skilleter & Warren 2000).

Changes in mangrove habitats can affect their associated faunal communities in two ways. First, the structure of the communities may change, e.g., abundance, number of species and species composition. Second, functional aspects of the community, such as trophic groups, food webs, survival and growth characteristics could be affected. Existing studies focus on changes to the structure of faunal communities (Table 2), with no attention given to functional changes, presumably because these changes are more difficult to measure.

Mangrove loss

Many studies have documented the clearing of mangroves in numerous locations around the world (see reviews by Hutchings & Saenger 1987, Hatcher et al. 1989, Valiela et al. 2001, Alongi 2002) and in particular have focused on estimating the total area cleared, rates of clearing and, to a lesser extent, loss of sediments, erosion and changes in water quality. Some have stated that there will be consequences of mangrove clearing for the associated faunal community but only a few have gone into detail as to what these consequences may be for mangrove-related species (Table 2) and none has identified the resulting effect on fisheries.

The total clearing of mangroves will obviously have major impacts for the associated fauna, as well as for the mangroves themselves. Most or all of the potentially important attributes of mangroves as nursery habitats will be lost. Removal of mangrove trees will reduce the structural complexity of the habitat, also reducing potential refuges from predation. As the capacity for lateral trapping of sediments and slowing of currents is reduced, turbidity may decrease and changes in

Table 2 Studies of the effects of mangrove change on habitats and fauna

Type of change	Effect on habitat	Effect on fauna	Country	Reference
Mangrove loss				
Total clearing	Change in sediment grain size Higher water temperatures Changes in salinity Reduction in structure that provides refuges from predators	Decreased biodiversity Decreased densities of epifauna No decrease in density of infauna	Kenya	Fondo & Martens 1998
Total loss — loss of soft sediments	Bare habitat Soft sediments lost, only hard substrate remains	Lower abundance of postlarvae and juvenile prawns	Malaysia	Loneragan et al. in prep.
Loss of interior — fringe remains	Sediments retained	Abundance of postlarvae and juveniles similar to areas of no mangrove loss	Malaysia	Loneragan et al. in prep.
Total clearing	Loss of vegetation	Decrease in abundance and density Decrease in number of species Decrease in diversity	Malaysia	Hashim 2000
Mangrove disturbance				
Experimental manipulation	Removal of pneumatophores Removal of epiphytic algae	Fewer molluscs	Moreton Bay, Australia	Skilleter & Warren 2000
Presence of boardwalk	Fewer pneumatophores and epiphytic algae Fewer saplings (not significant)	Fewer molluscs species and individuals, and different spp composition More crabs and increased diversity	Moreton Bay, Australia	Skilleter & Warren 2000
Presence of boardwalk	Less compaction of sediment Fewer pneumatophores Lower leaf litter cover Lower proportion of root-material in sediment	More semaphore crabs	Sydney, Australia	Kelaher et al. 1998
Oil contamination	Loss of submerged roots creating a decrease of root surface for attachment	60% decrease in number of isopods on roots 40–50% decrease in number of juvenile spiny lobsters 65–90% decrease in number of oysters	Panama	Levings & Garrity 1994
Mangrove gain				
Natural establishment of new mangroves	Sediments less compacted Fewer pneumatophores Sediments contain less organic matter Sediments contain less leaf litter Leaves have higher N, P and Na Leaves have lower K and Ca	Higher number of faunal taxa Higher abundance of some benthic invert species Lower abundance of some benthic invert species More crab holes	New Zealand	Morrisey et al. 2003
Natural establishment of new mangroves	Difference in mangrove species Smaller tree height and diameter	Lower epifaunal biomass, abundance and diversity Higher infaunal biomass and abundance Lower infaunal diversity	Malaysia	Sasekumar & Chong 1998

Table 2 (continued) Studies of the effects of mangrove change on habitats and fauna

Type of change	Effect on habitat	Effect on fauna	Country	Reference
Establishment of new mangroves through rehabilitation	Lower heterogeneity Less developed soil structure Absence of mud lobster mounds	Higher faunal density and biomass Lower diversity Absence of mud lobsters Presence of *Littoraria* Fewer grapsid crabs More ocypodid crabs	Thailand	Macintosh et al. 2002

sediment type may occur. Similarly, the process of lateral trapping of nutrients will decline. Finally, the protection from wind and wave action provided by the mangroves will be lost. From organism, population and community aspects, the loss of these attributes will therefore have a great impact on the fauna.

However, the impacts on fisheries of the changes identified above have not been tested or documented although there is evidence for changes to faunal communities brought about by changes in sediment types due to the clearing of mangroves (Fondo & Martens 1998, Hashim 2000, Loneragan et al. in press). All of these studies found decreases in faunal abundance, number of species and/or species diversity where mangroves had been totally cleared and sediment grain size had changed (Table 2). It is difficult to interpret how these changes are brought about. In one example in Malaysia (Loneragan et al. in press), the loss of soft sediments may have prevented prawns from burying and so increased their vulnerability to predation. In this case, a reduction in the refuge value of the habitat caused a decrease in the abundance of postlarval and juvenile prawns (*Penaeus merguiensis*). In the same region, where mangroves were mostly cleared but with a narrow (<10 m) fringe of mangroves remaining, the soft sediments were retained and abundances of postlarval and juvenile prawns were similar to those in uncleared areas. In this case, the refuge value of the mangroves was retained, and the effects on prawns appeared to be minimal.

Studies that compare fish abundances in areas adjacent to mangroves against comparable areas without mangroves give an indication of what may happen to faunal communities and fisheries if mangroves are lost (Nagelkerken et al. 2001, 2002, Mumby et al. 2004). These studies have shown that the biomass of adults of several commercial species was higher where mangroves were adjacent to the adult coral reef habitats. Where there were no nursery habitats close to the reef habitats, many of these species were absent or present at low densities. This suggests that the removal of mangroves from these areas would result in lower abundances of adults and decreased fish catches. This outcome has been documented for the rainbow parrotfish *Scarus guacamaia*, which has a high dependency on the mangrove habitats and was fished commercially in Belize until the late 1970s (Mumby et al. 2004). On one reef, where all mangroves had been cleared in the 1960s, *S. guacamaia* became extinct, whereas on other, mangrove-rich reefs they survived at low densities despite heavy fishing.

Mangrove disturbance

Disturbance to mangroves (e.g., oil spills, trampling, construction of boardwalks and nutrient enrichment) can cause changes to the physical properties of a habitat, which may then affect the associated faunal community. Few studies have investigated these effects on the structure and function of mangrove communities (Table 2).

It is difficult to predict what the impacts of these disturbances on mangrove faunal communities might be. Studies on the impacts of oil contamination (Levings & Garrity 1994) and boardwalk construction (Kelaher et al. 1998, Skilleter & Warren 2000) all reported changes in species composition as a result of the disturbances. However, oil contamination was found to lead to a decrease in the abundance of all species investigated, whereas the response to boardwalk construction varied, depending on the species; some species showed an increase in abundance while others decreased (Table 2). The intensity, extent and duration of the disturbance will also influence the severity of the impact.

Once again, it would be useful to be able to identify the changes to the nursery attributes of mangroves (refuge, food and shelter) caused by these types of disturbance. A reduction in refuge value, changes in sediments and lower availability of food could account for some of the changes in species abundances and species composition found as a result of boardwalk construction (Kelaher et al. 1998, Skilleter & Warren 2000). Sediments in the vicinity of the boardwalks became less compacted, and there was a lower proportion of root material in the sediment (Kelaher et al. 1998). Close to the boardwalks there were fewer pneumatophores, fewer saplings, less epiphytic algae and a lower leaf litter cover (Kelaher et al. 1998, Skilleter & Warren 2000). These differences could result in less food being available for herbivores, and reduced protection for small animals under the leaf litter.

Mangrove gain

Mangroves can become established in areas where factors such as an increase in sedimentation have provided suitable habitats for seedlings to grow. These new areas of mangroves will then create potential habitat for fauna and will presumably take on the role of mangrove nurseries, providing refuge, food and shelter for juvenile fishes and invertebrates. How effective they are in this role compared with older mangroves will determine their relative nursery value.

One study in New Zealand has compared the sediments, flora and fauna of newly established mangroves (3–12 yr old) with those of long-standing (>60 yr) mangroves (Morrisey et al. 2003). In the younger mangroves, the sediments were less compacted and contained less leaf litter and organic matter. The mangroves themselves had fewer pneumatophores, and their leaves had higher levels of nitrogen, phosphorus and sodium, and lower levels of potassium and calcium. Differences were also apparent in the fauna: the number of taxa, the abundance of some benthic invertebrate species, and the number of crab holes were all higher in younger than in older mangroves. These results suggest that mangrove areas of different ages may have different functional values and therefore provide different levels of nursery potential.

Implications of mangrove change for faunal communities and for fisheries

While little information is available on the direct consequences for fauna, the existing studies indicate that there may be important impacts of changes to the structure of mangrove forest on their associated faunal communities. All of the changes have the potential to cause cascading effects at higher trophic levels (Skilleter & Warren 2000) with possible consequences for fisheries. Such cascading effects would be extremely hard to identify and even harder to measure.

None of the studies found in this review (Table 2) discusses how the identified changes to the faunal communities could affect fisheries catch. One study of seagrass communities in Florida, U.S., however, made the link between a perceived community change in the seagrass and fisheries catch (Sheridan et al. 1997). After the mortality of substantial portions of the seagrass (*Thalassia testudinum*), habitat heterogeneity increased due to the appearance of bare mud patches and areas of colonising seagrass species such as *Halodule wrightii*. Associated changes to the faunal community included a decrease in the standing crop and an increase in diversity. However, Sheridan et al. (1997) reported that there were no detectable changes in landings of commercial or recreational fisheries associated with the changes in habitat heterogeneity or the changes in community composition. A similar approach needs to be taken in mangrove studies to make the links between habitat and community changes and fisheries production.

From these few studies, it can be seen that changes or disturbances to mangroves, even localised low-impact modifications, can have effects on the structure and function of the faunal communities inhabiting them. Ultimately, this may have an impact on fisheries production for the species that are linked to these coastal habitats (Hatcher et al. 1989). To investigate the links between mangroves and fisheries production further, quantitative analyses are needed that take into account characteristics of the mangroves, faunal communities and fisheries at appropriate scales. For managers to make use of this information, there must be appropriate data on which to base their management decisions. The next section discusses what data are currently available at various spatial and temporal scales, the limitations of these data, how best to use the data to understand mangrove-fisheries links and, ultimately, how to optimise habitat and fisheries management. This section provides the final step in the framework for understanding mangrove-fisheries interactions (Figure 1), drawing together all the information collated in the previous sections and assessing how this can be used to quantify these interactions.

The use of existing data to predict the effects of mangrove change on fisheries production

Data issues for mangrove-fisheries links

The studies listed in Table 1 all identified relationships between mangroves and fisheries based on correlations rather than on an understanding of ecological processes. A more appropriate approach to understanding the linkages between mangroves and fisheries takes into account the underlying processes, such as those described in previous sections of this review and illustrated in Figure 1. Some of the limitations of the correlative approach were discussed in the first section of the review, and the following section looks at ways to improve on this approach.

The types of data that have previously been used in analyses of mangrove-fisheries links provide unreliable estimates of this relationship for a number of reasons, including (summarised from Turner 1977, Baran 1999):

1. Spatial information on where catches are made has not always been available and, when it was available, may not have been very accurate.
2. Mapping of intertidal vegetation was done at broad spatial scales (e.g., greater than 1:50,000) which are likely to be of varying accuracies.
3. The scale of fisheries data generally has not matched the scale at which changes in mangroves are occurring.
4. The spatial scales of both fisheries and mangrove data may have been too coarse to detect any ecological patterns.
5. The collection of fisheries catch data has been prone to under-reporting and, occasionally, over-reporting.
6. The species composition of the catch has not generally been available and groups of species tended to be included in the relationship, whether their life histories were linked to mangroves or not.

Each of these issues will be discussed with examples drawn from the worldwide literature, but focusing on two primary examples, Western Peninsular Malaysia and Moreton Bay, Australia (Figure 2). Western Peninsular Malaysia extends between about 1˚N to 6˚30 N with a coastline of

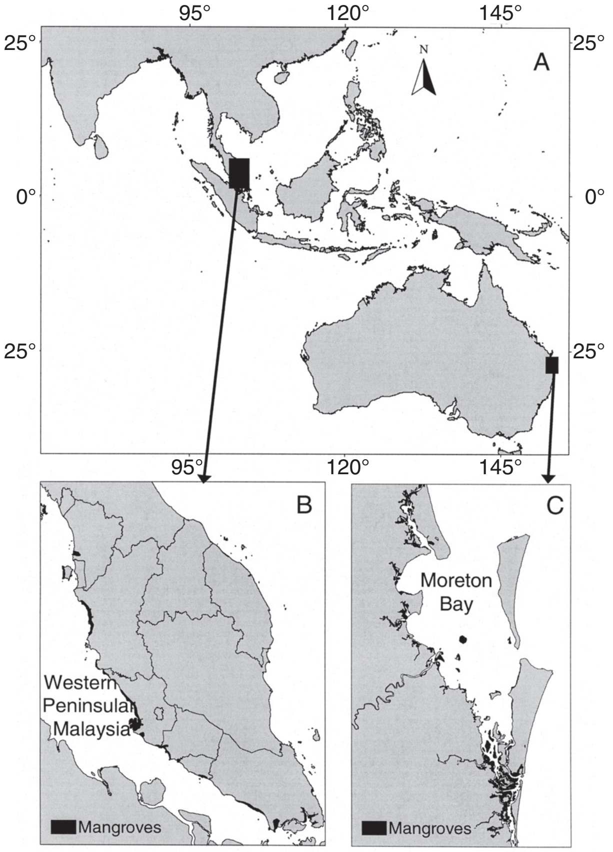

Figure 2 (A) SE Asia and Australasia, highlighting (B) mangrove distribution in western peninsular Malaysia (after Chan et al. 1993)and (C) mangrove distribution in Moreton Bay, Australia (after Manson et al. 2003).

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about 2000 km in length; links between prawn catches and mangrove extent in this area have been suggested by Loneragan et al. (in press). Moreton Bay is located in southeast Queensland, Australia, at approximately 27^{o}S, 153^{o}E. The bay is about 100 km long, and about 30 km wide at its widest point, with an average water depth of about 8 m. These two regions support both mangrove forests and significant fisheries. They are both relatively data-rich regions where work has previously been done on mangrove-fisheries interactions.

Spatial and temporal scales of data collection and locational information

Temporal and spatial scales are important aspects of linking mangroves and fisheries data. It is crucial to look at ecological functions at scales that are appropriate to the ecosystem, species or process of interest. The scale of investigation can influence the ecological interpretation of data (Wiens 1989, Dungan et al. 2002). As the scale of observation changes, there may be changes to characteristics of the object or process of interest. For example, the population mean and the variance of the mean will change as the size of the sampling unit is changed (Dungan et al. 2002). Of particular relevance to the mangrove-fisheries paradigm is the fact that, as the unit sizes of two or more variables change, their covariance and correlation statistics also change (Openshaw 1984, Dungan et al. 2002). This is known as the “modifiable areal unit problem” (Openshaw 1984).

In terms of the mangrove-fisheries paradigm, it is therefore important to have appropriate and comparable scales of data for both fisheries and mangroves. Currently, the scale of the fisheries data is determined by the method of data collection from fishery logbooks or landings centres, whereas the scale of mangrove data is determined by vegetation mapping techniques, rather than a consideration of any ecologically meaningful relationships between mangroves and fisheries. According to the modifiable areal unit problem, this may result in erroneous correlations being detected. It is difficult to predict how the modifiable areal unit problem will operate at different scales but, at the very least, it is essential to be explicit about what scales are being used and why.

Despite the potential sources of inaccuracy in the data, studies have succeeded in detecting positive correlations between fisheries and mangroves at global and regional scales. The importance of the modifiable areal unit problem is not clear for these studies, but may have some influence on the resulting correlations, because the analyses are often based on the aggregation of data from finer scale sampling units. For these reasons, correlations at broad scales should be interpreted with caution until a better understanding of the mechanisms of the relationship, and of the effects of scale, are achieved.

The most appropriate scale for addressing mangrove-fisheries links would appear to be that at which changes to the mangroves are occurring. For example, in Moreton Bay, where mangroves are protected from extensive clearing, the changes in mangrove distribution are measured in tens to hundreds of hectares over a 25-yr period (Manson et al., 2003). In Malaysia, where clearing is more widespread and extensive, mangrove changes can be measured in thousands to tens of thousands of hectares over roughly the same period (Chan et al. 1993). Therefore, these two regions may require analyses at different spatial scales to enable detection of any effects of mangrove loss on fisheries catch.

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Spatial and temporal scales — mangrove data

The mapping of coastal vegetation, including mangroves, has been carried out around the world at a range of scales and using a number of different mapping techniques. For example, studies of mangrove-fisheries links (Table 1) have used a variety of data sources for this purpose, including topographic survey maps (Staples et al. 1985), forestry and soil-use maps (MacNae 1974, Martosubroto & Naamin 1977), and navigational charts (MacNae 1974). These data sources ranged in scale from 1:100,000 (Staples et al. 1985) to 1:2,500,000 (Martosubroto and Naamin 1977).

In Western Peninsular Malaysia, mangroves are found in sheltered waters all along the coastline with a total area of about 85,000 ha. In a study of mangrove-fisheries links in this region (Loneragan et al. in press), the extent of mangroves was derived from a range of sources (Chan et al. 1993) of varying resolution and accuracy. The reliability of these sources has not been verified and little information is available on where and how the data were derived. Nevertheless, it is clear that mangrove losses in this region over the past few decades can be measured in thousands or tens of thousands of hectares. For example, in the state of Johor alone, nearly 9000 ha of mangroves were lost between 1980 and 1990 (Chan et al. 1993).

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In Moreton Bay, there are about 15,000 ha of mangrove, particularly in the sheltered, southern sections of the bay, where there are numerous mangrove islands forming a deltaic pattern at the mouths of several rivers (Manson et al. 2003). Maps of the coastal habitats of this region are available at high spatial resolution and high accuracy. Aerial photographs for a number of dates are available for the entire region and used for the classification and mapping of coastal wetland habitats. For example, comprehensive aerial surveys of the region were carried out in 1973 at 1:12,000 and again in 1997 (ranging from 1:18,000 to 1:40,000) and used to create maps of coastal wetlands (Dowling & Stephens 1999). Overall loss of mangroves during this 24-yr period was about 200 ha. For smaller areas more frequently captured aerial photographs are available. For the

Logan River area of Moreton Bay, for example, aerial photographs are available at approximately decadal time periods since the 1940s (Manson et al. 2003). These time series data can be used for change detection analyses of the mangroves at fine spatial and temporal scales.

Several other sources of remote sensing data at a range of resolutions are available for mangrove mapping, including satellite imagery (e.g., Landsat Thematic Mapper (TM) — 30 m pixels; System Pour l'Observation de la Terre (SPOT) — 20 m pixels) and high resolution airborne multi- and hyperspectral imagery (e.g., Compact Airborne Spectrographic Imager (CASI) and Hymap — variable resolutions from centimetres up to tens of metres) (see reviews in Green et al. 1998, 2000). The scale of mapping, and the spatial resolution of any remote sensing technique used as a basis for this mapping, has a large effect on the accuracy of mangrove identification and the estimation of mangrove extents. In some cases, the characteristics of the mangroves themselves will determine which sensor must be used; for example, narrow bands of mangroves require the use of higher resolution techniques than wide areas of mangroves (Manson et al. 2001). The choice of mapping techniques should therefore be based on the careful selection of the most appropriate resolution for the issues under investigation and the characteristics of the mangroves in the area of interest and should be carefully matched to other relevant data.

Spatial and temporal scales — fisheries data

A number of productive fisheries are found along the coast of Western Peninsular Malaysia including both artisanal and commercial fisheries. Catch data are recorded at a number of landing centres along the coast. The mean annual landings of prawns in Western Peninsular Malaysia for 1981–1997 was about 55,000 t (Loneragan et al. in press). Malaysian fisheries data are collected as landings at various locations throughout the country. Information is very limited, therefore, on where and when the actual catches were made. Even with mangrove changes occurring at relatively broad scales (thousands to tens of thousands of hectares), these fisheries data may not be spatially accurate or precise enough for detecting potential mangrove-fisheries links.

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Moreton Bay supports a number of highly productive commercial fisheries (e.g., trawl, net, line, pot) with a combined mean annual catch of about 2,900 t (L. Williams, Queensland Department of Primary Industries, unpublished data). Spatial information on commercial catches in Queensland is mainly collected at the scale of half-degree latitude/longitude grids (equivalent to about 30 nautical miles). The whole of Moreton Bay is contained in just two of these grids. At this scale, a great deal of the positional information that would be useful for mangrove-fisheries studies is lost. However, the temporal scale of data collection is daily, which gives a good temporal series of data allowing analysis of daily, monthly, seasonal or annual catches.

AU: Year? Add to ref list?

The broad spatial scale of fisheries data collection limits its usefulness in mangrove-fisheries studies. In the Moreton Bay example, the spatial resolution of the fisheries data is too coarse to be able to align it effectively with the much higher resolution mangrove data. Data at the scale of tens of kilometres or less are required to match with the scale at which mangrove changes are occurring. In Queensland, fishers are being encouraged to record data using 6-nautical-mile grids rather than the 30-nautical-mile grids that have been the common practice. This improvement in spatial resolution would enhance the usefulness of the data for evaluating mangrove-fisheries links, and for use in other ecological studies.

Reliability of catch reporting

On a worldwide scale, the Food and Agriculture Organisation of the United Nations (FAO) has collected global fisheries statistics since 1950. Fishery statistics are provided to the FAO by member countries (Pauly et al. 2002) and the accuracy of the data is highly variable among countries.

Logbook collection methods vary among countries, with information being collected at different spatial and temporal resolutions, species groupings and level of reliability of recording. In some cases, catches are likely to be under-reported by fishers in order to avoid tax payments, to circumvent quotas and/or to conceal fishing in protected or closed areas (Turner 1977, Watson & Pauly 2001). However, in China, over-reporting has occurred because there was a need for state entities to achieve increased production levels (Watson & Pauly 2001). These inaccuracies in reporting of catches severely limit the current usefulness of fisheries data in mangrove-related studies.

In Malaysia, monthly commercial landings and fishing effort data are collected from a subset of the landing centres in each state by the Department of Fisheries. Summaries of the catch data are published in the Annual Fisheries Statistics. Inaccuracies in this reporting system may derive from errors due to the subsampling procedure and under-reporting of catch to protect information on prime fishing locations or to avoid tax (Loneragan et al. in press).

Commercial fisheries data for Moreton Bay are collected by the Queensland Department of Primary Industries (QDPI). This dataset is based on daily logbook records reported by commercial fishers and has been collected since 1988. Since 1990, this logbook data collection method has been regarded as reliable and accurate.

Reporting of species groups

As in many other regions of the world, Malaysian and Moreton Bay fisheries data are recorded by species groups or categories rather than by individual species. For example, in Western Peninsular Malaysia, data on prawns from the landings centres are recorded in a number of categories such as white prawns (*Penaeus merguiensis*, *P. indicus*, *P. penicillatus* and *P. latisulcatus*) and pink prawns/ greasyback prawns (*Metapenaeus affinis*, *M. ensis* and *M. intermedius*). Similarly, in Moreton Bay, some grouping of species occurs in the fisheries data, e.g., "bay prawns" includes greasyback (*M. bennettae*), school (*M. macleayi*), endeavour (*M. endeavouri*), hardback (*Trachypenaeus* spp.) and small king prawns (*Penaeus plebejus*) and the "whiting" group includes *Sillago ciliata*, *S. analis* and *S. maculata*.

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This grouping of species makes it difficult to investigate mangrove-fisheries links, as different species will have different life history strategies (see pp. 000–000), will utilise different attributes of the mangroves (see pp. 000–000) and will respond to changes in environmental factors in different ways (see pp. 000–000). Data on individual species is needed for the assessment of fisheries production or for investigations on life history characteristics and habitat use.

Use of the data to predict the effect of mangrove change on fisheries catch

To achieve the ultimate goal of predicting the effects of mangrove loss and change on fisheries, datasets such as those discussed above must be used to evaluate and quantify the interactions between the fauna and the mangroves. If adequate data are available, and are used in conjunction with an understanding of the processes linking coastal habitats to fish populations, it should be possible to predict changes to fisheries catch when changes in mangrove distribution and extent occur. The prediction of fisheries catch in this way is the final step in the framework describing mangrove-fisheries links (Figure 1).

AU: Not on ref list.

AU: ?

Is it possible to carry out this step using existing data from data-rich regions such as Moreton Bay and Malaysia? Various types of mangrove change (total and partial clearing, conversion to canal estates, local disturbances, establishment of new mangroves, change in mangrove species) were identified in Moreton Bay by Manson et al. (2003) and in Western Peninsular Malaysia by Loneragan et al. (in press) and Haywood et al. (in prep). From the type of information collated in earlier sections of this review (pp. 000–000) on the potential effects of mangrove change on the

AU: Is perm necessary?

Table 3 Qualitative predictions of impacts on fauna and fisheries in Moreton Bay with changes in mangrove habitats between 1973 and 1997. Extent of mangrove change from Manson et al. (2003)

Change in mangroves	Area affected in Moreton Bay	Predicted effect on fauna	Predicted effect on fisheries
Total clearing	3800 ha	Decreases in abundance, density, species number, species diversity Change in community structure	Decrease in fisheries catch
Partial clearing	Unknown	Possible decreases in abundance, density, species number, species diversity Change in community structure	Possible decrease in fisheries catch
Conversion to canal estates	230 ha	Loss of juvenile habitat Decrease in abundance of commercial species	Decrease in fisheries catch
Local disturbance, e.g., boardwalks	Unknown	Localised decreases in abundance, density, species number, species diversity Change in community structure	Little impact on fisheries
Establishment of new mangroves	3600 ha	Change in community structure Possible increases in abundance, density, species number, species diversity	Increase in fisheries catch, if no extra effort
Change in mangrove species	1276 ha	Possible changes in community structure and species abundance	Possible change in abundance of species

associated fauna, speculation can be made on how the changes in mangroves of Moreton Bay may affect the fauna living within them (Table 3). Although a number of studies have looked at the species compositions in mangroves both in Moreton Bay (e.g., Laegdsgaard & Johnson 1995, 2001) and in Malaysia (e.g., Chong et al. 1990), no-one has investigated how these communities will be affected by mangrove change. Similarly, no one has looked at how any changes in the communities will affect fisheries production in these regions. This information needs to be collected and verified experimentally before definite conclusions can be made. Once the effect on the mangrove fauna can be identified, then it should be possible to predict the effect of mangrove change on fisheries. It is currently not possible to take this final step, even in an area such as Moreton Bay with relatively comprehensive data collection. Similar problems are likely to arise in other areas of the world where mangrove-fisheries links are under investigation; the problems will be even more severe in countries with less rigorous data collection methods.

Recommendations

The issues discussed above demonstrate the need for accurate, reliable and scale-specific datasets for evaluating mangrove-fisheries links. The interpretation of results from previous studies have been limited because they have not addressed these issues adequately. To improve the overall approach to mangrove-fisheries studies, the following recommendations are made. Specific examples have been drawn from Moreton Bay and Western Peninsular Malaysia but all of these points are relevant to other locations around the world.

Fisheries data

1. High spatial resolution data are required for good locational information. The spatial resolution of the dataset for Moreton Bay is very coarse (30-nautical-mile sections) and inappropriate when considering the scales at which habitat loss and change occur. These data may be useful for very broad-scale analyses but are generally not suitable for the finer-scale analyses needed for predicting the effects of habitat loss on fisheries. Some

data in Queensland are now collected at the 6-nautical-mile scale which greatly improves the usefulness of these data. The introduction of a Vessel Monitoring System, as is occurring in most fisheries in Australia, will produce data at a very fine scale. However, care will be needed in the analyses and use of these data because of confidentiality issues. Other countries (e.g., Malaysia) have much less detailed recording of positional information which limits the potential usefulness of these data for the types of ecological studies needed to address the mangrove-fisheries paradigm.

2. Consistently high temporal resolution of fisheries data collection are needed. Currently, the temporal resolution (daily) is good for most Australian fisheries and can be used for daily, monthly, seasonal or annual analyses of data. However, historical records (i.e., pre-1980s) are generally lacking. Fisheries in other countries often do not have such good temporal resolution.
3. Fisheries data need to be reliable as well as accurate. There is a large variation in the reliability of fisheries data, for the reasons discussed above (e.g., over- and under-reporting).
4. Knowledge of the movement, migration and home ranges of many fisheries species is needed, so that the scale of data collection is based on ecological significance rather than management convenience. Currently this knowledge is lacking, which imposes severe limitations on the use of fisheries data for mangrove-fisheries studies.

Mangrove data

1. The identification of the spatial and temporal scales of change in mangroves (e.g., disturbance, loss, new growth) is a prerequisite for studies of mangrove-fisheries links.
2. High spatial resolution data are crucial for defining the distribution and extent of mangroves at these scales. For some areas, such as Moreton Bay, data at fine spatial resolution (e.g., <10 m) are available (from field studies, aerial photographs, CASI, etc.) and can be used to detect changes at the appropriate spatial scale.
3. A regular and consistent time series of data would facilitate the assessment of changes in mangroves. In some areas, a temporal series of data is available (e.g., for the Logan River area of Moreton Bay there is a decadal series of aerial photographs (Manson et al. 2003)) but in most cases data are collected *ad hoc* and not following a specific time schedule.
4. The collection of data should be temporally and spatially consistent to allow comparisons between different parts of the world and between different periods. Mangrove data should also have consistent accuracy and reliability, and standardised classification systems. The current situation could be improved by the introduction of a standard protocol or set of guidelines for coastal habitat mapping, such as the use of national/international wetland inventories.
5. The potential for new and emerging technologies to be applied to mangrove studies must be recognised. For example, satellite images can be used to produce a time series of mangrove distribution, from high-spatial resolution (<5 m pixels) and moderate spatial resolution (5–30 m) image data. These data are collected at consistent temporal scales (e.g., 5–16 day intervals) and have varied capabilities for mangrove mapping (Green et al. 1996, 1998, 2000).

Conclusions

The role of mangroves as nursery habitats, although not well understood, is widely accepted and this has led to the establishment of the paradigm that mangroves are critical for sustaining production in coastal fisheries. Previous studies have attempted to find links between mangroves and fisheries by searching for direct correlations between the extent of mangroves and the size of fisheries catches AU: ? (pp. 000–000). Although strong correlations were found in some cases, these do not demonstrate a causal relationship. This approach makes no attempt to take into account the underlying mechanisms of potential mangrove-fisheries links or to find cause-and-effect relationships. It also fails to separate the role of mangroves from that of estuaries and shallow coastal waters in general.

A more thorough approach is required that takes into account the mechanisms underlying mangrove-fisheries links, and recognises interactions between mangroves and other estuarine and coastal habitats. This review is intended as a first step towards a better understanding of the role of mangroves as nursery habitats for fishery species, and forms a basis for future studies of mangrove-fishery interactions. It is divided into a number of sections, each of which is regarded as an important step towards a fuller understanding of the links between mangroves and fisheries.

Different species respond in different ways to changes in mangrove structure and function and it is clear that species need to be investigated individually in the future (pp. 000–000). The problems AU: ? associated with defining the concept of dependency on mangrove habitats is also discussed, along with the difficulties of separating the functions of mangrove habitats from other aspects of estuarine environments such as estuarine productivity and shallow, protected waters.

This issue of separating the functions of mangroves from those of estuaries in general was AU: ? dealt with further in pp. 000–000, where the attributes of mangroves which make them productive nursery habitats were reviewed. The important nursery roles of mangroves were identified as: the provision of refuge from predators (due to structural complexity, turbidity and shallow water), the availability of food, and the creation of a benign, sheltered environment. Changes to any one, or all, of these attributes may affect the nursery role of mangroves and therefore influence recruitment to the adult population and, ultimately, affect fishery production.

Possible responses to changes in mangrove structure and function were discussed in the next section (pp. 000–000). Although few studies have specifically measured the effect of changes to AU: ? mangrove structure and function on the faunal communities within them, enough evidence exists to suggest that these changes may have impacts at the local level. These impacts have the potential to cause cascading effects at higher trophic levels, which may then have consequences for fisheries.

The final step would be to link these changes in faunal communities with changes in fisheries AU: ? production (pp. 000–000). This linkage would allow the prediction of changes in catch based on changes to mangrove distribution and extent. However, appropriate data that would enable the evaluation of these ultimate effects on fisheries do not currently exist. An examination of the data from two regions, Moreton Bay in Australia and Western Peninsular Malaysia, show that even in these relatively data-rich areas the data are insufficient to allow predictions of fisheries change to be made. The data suffer from unreliability and inaccuracies in collection, and their usefulness is limited by their variable and generally low spatial and temporal resolutions. Improvements to data collection could lead to this final step in the understanding of mangrove-fisheries links being achieved.

The information collated in this review provides a framework on which to base future investigations of mangrove-fisheries links. The review emphasises the importance of understanding the processes underlying a possible relationship between mangroves and fisheries and recognises the need to identify changes in the function of mangrove habitats as well as changes to mangrove structure. Without this information, the understanding of the relationship between mangroves and fisheries will remain limited. Future investigations of mangrove-fisheries links must take this type of detail into account in order to develop greater ecological knowledge and to provide better information and understanding to both fisheries and conservation managers.

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