

Chapter 11

Sources of Variation that Affect Perceived Nursery Function of Mangroves

Craig H. Faunce and Craig A. Layman

Abstract Mangroves are considered among the most productive ecosystems on the planet. While mangroves provide numerous critical ecosystem services to surrounding environments, there is particular interest in the role of mangroves as nursery habitats for fish and decapods. Despite this interest, scientific consensus regarding the role of mangroves as nurseries remains elusive. In this chapter, we identify four principal sources of variability that underlie conflicting conclusions regarding the function of mangroves as nursery habitat. We provide brief sketches of the reasons why these sources of variability may affect the role of mangroves as nursery habitat, drawing particularly on recent empirical advances in the field, and conclude with a conceptual model summarizing the different levels at which the nursery function of mangroves is evaluated.

‘It is time that we biologists accept diversity and variability for what they are, two of the essential features of the biological world. We would be wise to restructure our search for orderly patterns in the natural world. We should stop thinking primarily in terms of central tendencies . . . Variation among and within species is fundamental to organisms. Analysis of variation can offer insights just as surely as can traditional delineation of central tendencies.’ (Bartholomew 1986).

Keywords Variance · Nursery · Biogeography · Hydrology · Conceptual model

11.1 Introduction

Mangroves are considered among the most productive ecosystems on the planet, and provide numerous other critical ecosystem services (Costanza et al. 1997, see Chapter 16). They often are believed to augment fishery production in estuaries and

C.H. Faunce (✉)
National Marine Fisheries Service, Alaska Fisheries Science Center, 7600 Sand Point Way NE,
Seattle, Washington, USA
e-mail: Craig.Faunce@noaa.gov

adjacent areas due to the abundant food resources and protection from predators that they may provide (see papers in Serafy and Araujo 2007, and Chapter 10). Of particular interest is the role that mangroves may play as nursery habitat, and thus the way mangroves are inter-connected with other ‘back reef’ habitats through the export of fish biomass (Adams et al. 2006). However, the extent to which mangroves serve as nurseries, or serve a mangrove nursery function, remains a subject of much debate in the scientific literature (Blaber 2007). We believe that much of the disagreement regarding their value as nursery habitat stems directly from the underlying variability in mangrove systems (Ewel et al. 1998, Blaber 2007), as well as the way in which the systems are studied. In the present chapter, we will outline some of these sources of variability, and discuss how they explicitly affect the interpretation of mangroves’ role as nursery habitat.

Variability in abiotic and biotic variables is an intrinsic property of biological systems (Bartholomew 1986). Yet scientists seek to identify general rules, laws, or theories that would unite scientific inquiry across these sources of variability. The study of mangrove ecology/biology is no exception. For example, there seems to be a pervasive desire to provide a singular answer to the question: ‘are mangroves nursery habitats?’ Yet there is likely no simple answer to this question. Mangroves are likely critical nursery habitat in some instances, and have no nursery function in others.

In this chapter, we identify four principal sources of variability that underlie the conflicting conclusions regarding the function of mangroves as nursery habitat. The first is related to how researchers define nursery habitat and mangrove ecosystems, and the next three deal with intrinsic sources of biological variability: variation in space (geomorphology, habitat type, and configuration), variation in time (hydrodynamics, time of day), and variation in species (assemblage vs. species-level analyses). This is not intended as another comprehensive review of the important functions mangroves play with respect to nursery function and fishery production (e.g., Sheridan and Hays 2003, Faunce and Serafy 2006, Blaber 2007, Nagelkerken 2007, see Chapter 10). Instead, we endeavor to provide targeted examples of how variability may lead to different conclusions regarding the role of mangroves as nursery habitat. We hope the end result will be that researchers explicitly consider each of these sources of variability (and others) when evaluating the role of mangroves as nursery habitat.

11.2 Variation in Definitions

11.2.1 What Defines a Nursery?

One of the reasons that researchers have reached different conclusions regarding the role of mangroves as nursery habitat relates to the specific definition of ‘nursery’ that has been employed (Table 11.1). Historically, nurseries were regarded as those areas that supported a higher density or abundance of immature fishes than other

Table 11.1 A summary of different connotations of the term ‘nursery’

Definition	Description	Source
Historical connotation	A habitat type which supports a higher density or abundance of juvenile individuals than other habitat types	–
Predation/food-based	A habitat must provide adequate protection from predators or a food source which is both varied and concentrated	Thayer et al. (1978)
Juvenile contribution function	Nursery habitats for a particular species are those that contribute a greater than average number of individuals to the adult population on a per-unit-area basis in comparison to other habitat types used by juveniles	Beck et al. (2001)
Effective juvenile habitat	A habitat type is considered a nursery if, for a particular species, it contributes a greater proportion of individuals to the adult population than the mean level contributed by all habitats used by juveniles	Dahlgren et al. (2006)
Essential fish habitat	Those waters and substrate necessary to fish for spawning, breeding, feeding, or growth to maturity	NOAA (1996)

adjacent habitats. This criterion allows much latitude in attributing the nursery label to a particular habitat type and provides no standardized guide for evaluation. In this context, the methodologies employed to estimate faunal densities are critical to assessment of nursery function, and identifying nursery habitat often may depend as much on the sampling method employed as the underlying biological or ecological drivers. And since methodologies often are not employed in a fashion that allows direct comparisons among habitat types (Faunce and Serafy 2006), it is not surprising that many different conclusions have been reached regarding the role of mangroves as nursery habitat.

The lack of rigor in defining nursery habitat led Beck et al. (2001) to propose a more stringent set of criteria: ‘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.’ In this context, nursery habitats could support greater production through increased density, growth, survival, or export of juveniles. The main limitation of this definition is that area coverage of habitat types is not considered, so one habitat type may support fewer individuals per unit area, but yet still be the most important contributor in absolute numbers to an adult population. To this end, Dahlgren et al. (2006) suggested that in some contexts it may be useful to identify ‘effective juvenile habitats’: a habitat for a particular species that contributes a greater proportion of individuals to the adult population than the mean level contributed by all habitats used by individuals, regardless of area coverage. Different conclusions can be reached regarding which habitat types are nurseries depending on which of these two approaches is employed (e.g., see the example outlined in Dahlgren et al. 2006).

Despite the suggestion that a standard, quantifiable, framework is essential to adequately determine whether a habitat functions as a nursery (Beck et al. 2001, Dahlgren et al. 2006), the majority of studies rely on the historical connotation of the term. That is, mangroves are nominally alluded to as 'nurseries' simply if they support a relatively high abundance of juvenile individuals. This is likely due to the difficulty in assessing the production (based on abundance, growth, and survival) and export of individuals that utilize habitats of interest. Any one of these factors is challenging to measure alone, and to measure all four simultaneously may be impossible in many situations (although there are some recent attempts toward this end, see Koenig et al. 2007, Valentine-Rose et al. 2007, Faunce and Serafy 2008a). As such, there is a dearth of information that can be used to quantitatively infer mangroves' role in supporting secondary production based on the more stringent definitions provided by Beck et al. (2001) and Dahlgren et al. (2006).

For the remainder of this chapter, we will follow the nursery definition of Beck et al. (2001). As such, we endeavor to point out some of the sources of variability that affect the estimation of the density, growth, mortality, or export of juveniles within coastal habitat types, and how these sources of variability may contribute to the lack of an established consensus of whether mangrove habitat functions in a nursery role.

11.2.2 What Defines a Mangrove Forest?

There have been several attempts to provide a framework for the study of mangrove forests. These frameworks were considered necessary after it was recognized that several different forest types, each with their own physical configuration and production properties, could result from identical mangrove communities exposed to different abiotic regimes. Lugo and Snedaker (1974) and later Lugo (1980) described six types of Florida mangrove forest based on topographic location and geomorphologic form. Moving across a landscape in an upland direction, these forests include those: (1) completely inundated by daily tides (overwash; up to 7 m tall), (2) fringing emergent shorelines (fringe; up to 10 m tall), (3) along flowing waters (riverine; up to 18 m tall), (4) located in a depression behind a berm (basin; up to 15 m tall), (5) located in extreme environments, e.g., poor water exchange (dwarf, or 'scrub'; less than 2 m tall; Fig. 11.1), and (6) located on 'peat islands' within the Everglades (hammock; up to 5 m tall). Woodroffe (1992) developed a more general classification system in Australia that included river-dominated, tide-dominated, and interior mangrove forests. Extending these works, Ewel et al. (1998) developed a hybrid classification scheme used (which we use hereafter): tide-dominated systems are termed fringe mangroves, river-dominated mangroves are termed riverine mangroves, and interior mangroves are termed basin mangroves.

Forest-type is rarely defined in studies of mangrove-associated fauna. Yet differences in forest type have important implications on our perceived value of mangroves as nursery habitats because each forest type serves a different ecological function and is utilized by different motile fauna. For example, because they connect

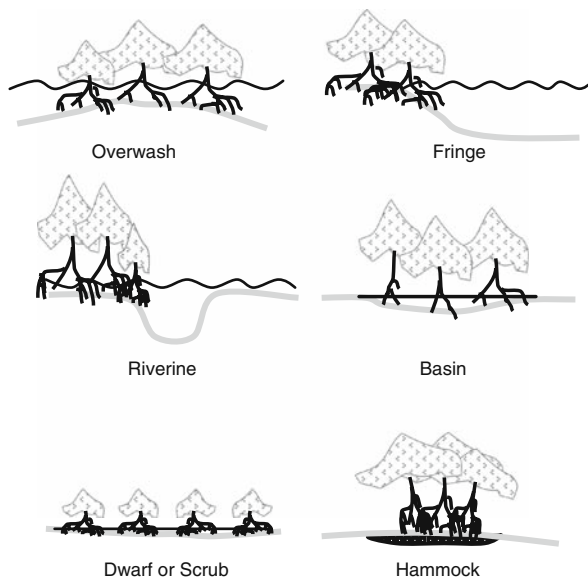


Fig. 11.1 Schematic cross-section view of various forest-type architectures exhibited from a single species of mangrove (*Rhizophora mangle*) in south Florida (following Lugo 1980)

upstream freshwater sources and downstream estuarine waters, riverine mangroves are used opportunistically as a conduit for motile fauna on seasonal, lunar, or daily tidal cycles. However, the same static patch of riverine mangrove may experience a suite of salinities throughout a tidal cycle or season. Consequently, identical locations of habitat may be inhabited by animals from freshwater, estuarine, or marine guilds, and decisions as to the relative importance of the mangle in the lives of fishes becomes an ever-changing target that must be carefully qualified. In contrast, basin-type forests are inundated much less often, but for longer duration than fringing forests (Lewis 2005). These forests are utilized during the flooded period by small-bodied (<100 mm) individuals that include juveniles of estuarine and marine spawning species and resident species that spend their entire lives within the mangle. The dynamics of these fauna are strongly driven by water levels. Within a seasonally flooded Florida mangle, density, biomass, and ultimately secondary production of fishes were positively related to water level and flooding duration (Lorenz 1999). However as water levels decrease, animals must seek deep water refugia at the edges of riverine or fringe forests or be stranded, causing negative correlations between abundance metrics and water levels in these forest types (e.g., Faunce et al. 2004, Serafy et al. 2007). Thus upper basin-type forests function as fish nurseries when flooded, and as important food sources during subsequent dry periods for animals such as birds. Because they are both speciose and abundant, resident fauna are largely responsible for trends in assemblage metrics (e.g., species richness and total abundance). For example, in the Philippines it was found that the density of fishes among stands of different mangrove species and distance to open water were

greatest within the upper (shallow) *Avicennia* portions (Rönnbäck et al. 1999). The remainder of our discussion will focus on variation in animal use of well-studied fringing forests.

11.3 Spatial Variation

11.3.1 Geographic Regions

The common ancestry of mangroves has resulted in the global distribution between the 20 °C aquatic isotherms (Alongi 2002), yet individual regions have unique oceanographic and geologic histories. Spalding et al. (1997) identified five regions based on present-day geomorphology and biodiversity of mangrove forests: Australasia (Australia, Papua New Guinea, New Zealand, and the South Pacific islands), South and Southeast Asia (Pakistan to the west, China and Japan to the northeast, including Indonesia), East Africa and the Middle East (Iran to South Africa eastwards, including the islands in the Indian Ocean), West Africa, and the Americas (north, central, and south). Based on mangrove forest composition and richness, West Africa is most similar to the Americas (hereafter Western Atlantic), and East Africa to the Indo-Pacific (hereafter Indo-Pacific), with the latter group roughly three times more speciose than the former (Hogarth 2007).

The divide between the Western Atlantic and the Indo-Pacific is reflected in the current body of literature on mangrove use by motile fauna, with generally all studies within the former accepting the paradigm that mangroves serve a nursery function, and challenges to this paradigm arising from studies conducted in the latter. Such differences in opinion can be explained by the differences in the spatial configuration of shelves, habitat configuration, and/or hydrology between regions.

11.3.2 Shelf Configuration

The availability of mangroves to juveniles determines their nursery value. For species that spawn offshore, availability of mangrove habitats depends directly on the amount of submerged shoreline, the location of reproduction relative to mangroves, the prominent oceanographic conditions during and after the spawn, and the larval duration. These factors are substantially influenced by bathymetry. Obligate-group and pair-group spawning strategies have evolved within functionally and taxonomically related species in the Caribbean region (e.g., Lutjanidae: snappers). Which strategy prevails is related to local differences in shelf slope and resultant mangrove area. In obligate-group spawning, fish aggregate *en masse* at very specific geographic locations to reproduce, and these locations are near local gyres that ideally retain larvae nearshore for a period of time approximating their average larval duration (Heyman et al. 2005, Paris et al. 2005). This spawning strategy is

largely documented in locations with limited emergent coastline and steep shelves with limited available hard-bottom promontories, e.g., Belize, southwest Cuba, and the lower Florida Keys.

Because the area of mangrove relative to alternative submerged habitats is relatively small, and the presence and persistence of gyres needed for favorable larval advection are variable, spawning on promontories may be a very risky reproduction strategy if juveniles require mangrove-lined bays to survive. Parrish (1989) proposed that mangrove-lined embayments act as 'waiting rooms' that collect excess larvae from species that spawn offshore, and that the majority of offspring necessary for the maintenance of adult populations are resident to the reef. Parrish (1989) also postulated that mangrove residence may act to mitigate the negative effects of poor juvenile recruitment to adulthood within reef environments. Thus, while juveniles of marine-spawning species on steep slopes do utilize mangroves, their reliance on these systems does not appear to be obligate and they likely do not function as nurseries in this context.

A pair-group spawning strategy is employed by dominant snapper within low-relief continental geomorphologies within the Caribbean (e.g., southeastern Florida, northeastern Cuba, Yucatan peninsula). For example, *Lutjanus griseus* (known locally as mangrove snapper) has evolved a life history strategy to take advantage of the comparatively larger areas of emergent vegetation proximate to broad shelves. This species is capable of spawning in pairs or in groups of <20 individuals; small aggregations can form at numerous, less-specified, locations, and individuals are commonly found in mangroves at most post-larval stages (Serafy et al. 2003, Faunce et al. 2007). Therefore, the reliance on mangroves for the maintenance of healthy adult populations of fish and decapods may be greater within continental low-relief systems with large mangrove area than within steep-sloped insular systems with less mangrove area. Indeed, when data for the same genera (*Lujanidae* and *Haemulidae*) residing in mangroves are compared, groupings based on either continental (low relief) or insular (high relief) geomorphologies are evident (Fig. 11.2).

11.3.3 Habitat Configuration

Because they can tolerate a variety of abiotic conditions, mangroves occur in many different areas of coastal and estuarine ecosystems. It is important that the relative position, area, and configuration of the mangrove patch, as well as the developmental stage of the individual, be considered when determining nursery value of mangrove habitat. Because they are located closest to marine source populations, mangroves along oceanic-facing shorelines are more likely to receive marine-derived post-larval recruits than other mangrove locations. Yet, unlike locations within bays, ocean-facing shorelines within much of the Caribbean lack sufficient sediment (due to erosion), and mangrove roots may penetrate into the water only a few centimeters. Thus, along ocean-facing shorelines, their availability (relative area

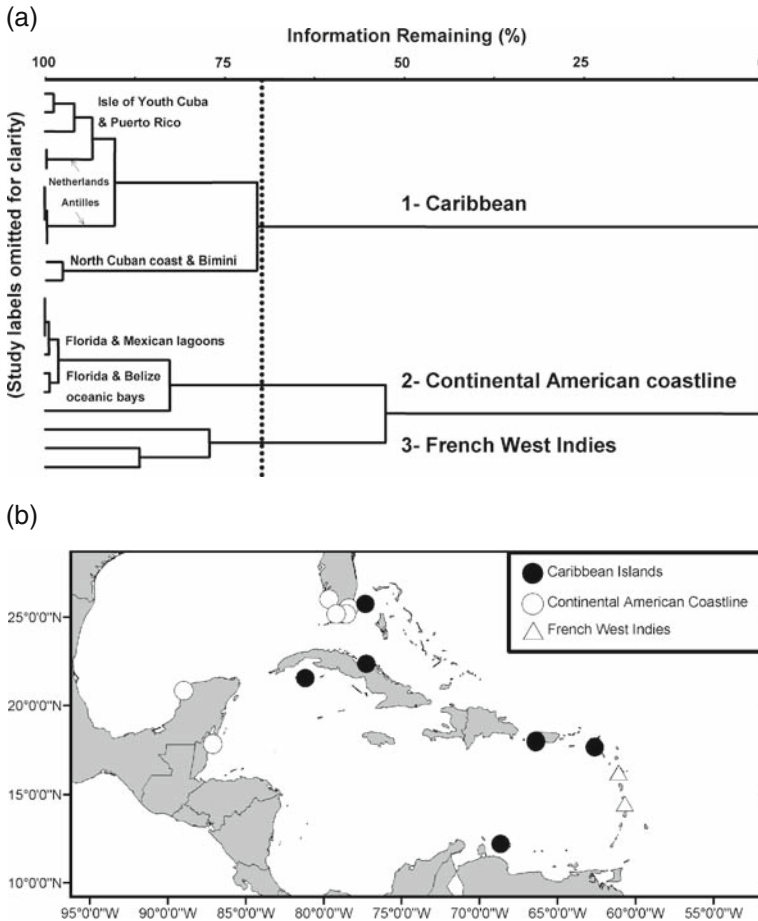


Fig. 11.2 Summary of data for snappers (Lutjanidae) and grunts (Haemulidae) reported from 21 studies conducted within Florida-Caribbean mangroves vetted from the literature (1971–2005) following Faunce and Serafy (2006). Density or biomass were relativized to maximum within each study and entered into agglomerative cluster analysis using Bray-Curtis distances with flexible beta (–0.25) linkage (a). Indicator Species Analysis (Dufrene and Legendre 1997) identified three groups that are related to shelf configuration (b). The species *Haemulon flavolineatum* and *Lutjanus apodus* distinguished the Caribbean group, *L. griseus* distinguished the continental American group, and *H. bonariense*, *H. aurolineatum*, and *L. jocu* distinguished the French West Indies group

coverage) may be comparatively low. In cases where mangrove roots are submerged enough to create fish habitat, comparative study has demonstrated that oceanic fringes are utilized much more than their availability would suggest, indicating positive selection for this shoreline type (Faunce and Serafy 2008b).

Compared to oceanic fringes, a much greater proportion of our current knowledge of fish and decapod use of mangroves comes from studies conducted within

inlets and protected bays. It follows that for species of marine origin, the accessibility of mangroves would not only be influenced by proximity of shoreline to spawning locations (described above), but also by the width and depth of the bay-ocean interface, local currents, and tidal flow. A decline in total abundance and richness of reef-associated demersal fishes has been observed with distance inland from the outer bay mouth in the Caribbean (Nagelkerken et al. 2000a), Brazil (Araujo et al. 2002), Africa (Little et al. 1988), and the Indo-Pacific (Quinn 1980, Blaber et al. 1989, Hajisamae and Chou 2003). Because the pool of available species is likely larger within offshore areas relative to bays, comparisons of total species, total density, and species-specific density will result in a negative relation between these metrics and distance of the mangrove patch from marine source waters.

Given the variation in geomorphology and hydrology described above, it follows that different basins within a single system may vary substantially in their physical and environmental properties, and this will be reflected in animal use patterns. Robertson and Duke (1987) were among the first to propose that each mangrove embayment may be considered its own unit, and that nursery function changes from unit to unit. Ley et al. (1999) first provided evidence consistent with this hypothesis by showing that distinct fish assemblages existed within three connected embayments with varying levels of freshwater flow in Florida. These results compare well with those reported from northeastern Australia, where it has been demonstrated that faunal assemblages can be delimited largely based on characterization of estuaries by catchment hydrology (tide or wave dominated), configuration of estuary mouth, substrate, and mangrove area (Ley 2005). Characterization of a nursery will depend on whether the species under investigation is of freshwater or marine origin, and where the mangle is located relative to fresh and marine water sources.

Mangroves are not the only habitat available to fish and decapods within subtropical and tropical bays, and the relative importance of mangroves compared to other structurally complex habitats is a major focus of current research (Faunce and Serafy 2006). Comparisons of fish size has revealed larger size-class occurs within mangroves than seagrass beds in Florida (Eggleston et al. 2004, Faunce and Serafy 2007) and Curaçao (Nagelkerken et al. 2000a, b, Cocheret de la Morinière et al. 2002). From these observations it has been concluded that mangroves act as secondary habitats for fishes of the region, and it is for this reason that the evaluation of mangroves as nursery habitat need to be carefully considered. For species that undergo ontogenetic habitat shifts, e.g., from seagrass to mangroves to coral reefs, comparisons of relative abundance between habitats are flawed because population dynamics dictate that the smallest and youngest individuals will have the greatest absolute abundance (Ricker 1975). In this example, even for equally-sized patches, total abundance will be lower in mangroves compared to seagrass beds, and yet higher within mangroves compared to coral reefs. This situation, i.e. where seagrass beds comprise the greatest area and contain a greater absolute number of animals relative to mangroves, may explain why comparisons by Sheridan and Hays (2003) failed to find a nursery function role for mangroves.

11.4 Temporal Variation

11.4.1 Hydrology

A temporal perspective also reveals intrinsic differences in the function of mangrove ecosystems in the Western Atlantic and the Indo-Pacific. In the latter region, there is greater influence of freshwater from larger catchments and dramatic changes in water level with tidal flow. These differences at the bay scale translate into great differences in the nature of variation in habitat availability to motile fauna. In the two often studied portions of the Western Atlantic, Southeast Florida, and the Caribbean islands, smaller tidal ranges result in the availability (i.e., inundation) of structurally-heterogeneous habitats (largely fringe mangroves) nearly year-round (Provost 1973). Under this temporal regime, animals are able to reside and select between different microhabitats best suited for their survival, and a positive relationship between depth and body size is apparent (Dahlgren and Eggleston 2000). In contrast, large tidal fluctuations (>2 m) can completely drain and re-flood mangrove forests twice daily in portions of the Indo-Pacific (Wolanski et al. 1992, Blaber 2000). This dynamic forces fishes and shrimps to reside within subtidal riverine forests and adjacent mudflats during ebb periods, and rapidly utilize basin mangroves during flood periods (Wassenberg and Hill 1993, Lugendo et al. 2007). Under such a regime, it becomes apparent why animal assemblages in mangroves are more similar to mud flats than to coral reefs in such areas, and how segregation of prey from predators may be poorly maintained (Thollot and Kulbicki 1988, Sheaves 2001, Baker and Sheaves 2006).

11.4.2 Time of Day

Another source of variation relevant to mangroves' nursery function is the time of day sampling is conducted. Comparisons between day- and night-time use of mangroves have consistently demonstrated that this habitat is predominantly utilized during the former period (Rooker and Dennis 1991, Nagelkerken et al. 2000c). This has major implications, since virtually all observations of mangroves are taken during the day. Results of multifactorial experiments demonstrate that the relative influence of structure, food, and shade in attracting fishes is dependent upon the diurnal activity of the species; artificial mangrove units with structure and shade were the most attractive to nocturnally active zoobenthivores compared to diurnally active herbivores (Verweij et al. 2006a). For the former taxa, assimilation of energy and resultant growth are the result of foraging in adjacent habitats such as seagrass beds (Loneragan et al. 1997, Cocheret de la Morinière et al. 2003). For this reason, the proximity of a mangrove stand to suitable nocturnal feeding areas (inter-patch distance) may, at least partially, explain why the mangroves support a higher density of fish during the day. It follows that the value of mangroves as nursery habitat may be over-estimated in systems with extensive connectivity among different habitats.

11.5 Species Variation

11.5.1 Variation Among Species

Each mangrove system may be inhabited by different species, and the number of shared species will be conditional on a variety of factors. Nonetheless, the literature is rich in examples of studies that have concluded that mangroves are not nursery habitats because of few shared species between mangroves and adjacent habitats. The most prominent comparison is between mangroves and coral reefs, and this may be one of the primary reasons opinions differ over whether mangroves are nursery habitats (Table 11.2). Blaber et al. (1985) cited that only 22 of over

Table 11.2 Summary of studies (in chronological order, 1971–present) we feel have made important statements counter to the paradigm that mangroves are nursery habitats. Although some of these studies examined both fish and decapods, all statements pertain to mangroves as nursery habitats for fish. Geographic region following Spalding et al. (1997)

Author	Location	Region	Rationale
Blaber and Blaber (1980)	Trinity Inlet system, Australia	Australasia	Fish assemblages result of quiet water, not mangrove presence
Blaber et al. (1985)	Dampier region, Northwest Australia	Australasia	Only 22 of 1,000 species on shelf occur as juveniles within the estuary
Robertson and Duke (1987)	Alligator Creek, Australia	Australasia	Only 3 of top 30 species of commercial importance
Thollot and Kulbicki (1988)	Saint-Vincent Bay, New Caledonia	Australasia	Overlap in species present between mangroves and reef low (13) compared to soft-bottom and coral reef (92) First to state the interaction between mangroves and coral reefs has been overstated
Blaber and Milton (1990)	Solomon Islands, Western Pacific	Australasia	Only 8–9% of snappers of marine origin
Chong et al. (1990)	Selangor, Malaysia	South and Southeast Asia	Fishes found within mangroves ubiquitous within estuary
Weng (1990)	Moreton Bay, Australia	Australasia	Only 5 of 86 species within mangroves were of marine origin, and only two of these of commercial importance
Dennis (1992)	La Parguera, Puerto Rico	Americas	Proposes fundamental difference between mangroves on islands and their counterparts on continental margins First to state value of mangroves as fish nurseries has been overstated in Caribbean

1,000 species that occur on the northeast Australian shelf were found in mangroves. Thollot and Kulbicki (1988) found that there was little overlap in faunal assemblages between mangroves and coral reefs in New Caledonia and concluded that linkages between the two were exaggerated. Similar conclusions have been drawn by Blaber and Milton (1990), Weng (1990), and Lin and Shao (1999). All of these studies have been conducted in the Indo-Pacific. Although not widely acknowledged, similar observations have been made in the Western Atlantic. For example, in southeastern Florida less than ten of over 70 species within mangroves can be considered reef fishes (Ley et al. 1999). Thus, for both the Indo-Pacific and Western Atlantic, when assessed at the level of *entire* fish assemblages, mangroves do not appear to be significant nurseries for coral reef fishes.

How then did such widely different opinions on the function of mangroves as nursery habitats evolve between the Indo-Pacific and the Caribbean? One explanation may be the level at which the majority of studies in the regions are conducted. Whereas studies from the Indo-Pacific have stressed the lack of congruence in faunal composition between mangroves and coral reefs at the assemblage-level, many studies from the Caribbean basin focus on the nursery function of mangroves with respect to particular species. For example, in the Florida Keys, mangroves contain the greatest densities of gray snapper (*Lutjanus griseus*) and barracuda (*Sphyraena barracuda*) relative to other available habitats (Eggleston et al. 2004). The relative abundance of *Haemulon flavolineatum*, *H. sciurus*, and *Lutjanus apodus* was greater within mangroves than within six other biotopes in Curaçao (Nagelkerken et al. 2000a). Further, the presence of bays containing mangroves has been shown to be positively related to adult fish stocks of certain species. Offshore Curaçao, the densities of grunts (*H. sciurus*), snapper (*L. analis*, *L. apodus*, *L. mahogoni*, *O. chrysurus*), parrotfish (*Scarus coeruleus*), and barracuda (*Sphyraena barracuda*) are greater on coral reefs adjacent to bays containing seagrass beds and mangroves than on coral reefs adjacent to bays without these habitats (Dorenbosch et al. 2004). Similarly, adult biomass of grunts (*H. sciurus*, *H. flavolineatum*, *H. plumieri*), and snapper (*O. chrysurus*, *L. apodus*) have been shown to be substantially greater in proximity to 'rich' mangrove forests than near 'mangrove scarce' areas (Nagelkerken et al. 2002, Mumby et al. 2004). This trend is not simply indicative of mangroves of the Western Atlantic; recent studies using the species-based approach have concluded that mangroves in the Indo-Pacific also contribute to the maintenance of healthy adult populations located in other habitats (Dorenbosch et al. 2005, 2006, Lugendo et al. 2005).

Because positive relationships between fishery yield and mangrove area has been demonstrated for shrimps and fishes (see review by Manson et al. 2005 and Chapter 15), some have used economic importance as a basis for making decisions as to the relevance of mangroves as nursery habitat. This approach is often problematic because ecological factors relevant to individuals of a population (e.g., growth and survival) are different from factors influencing the population maintenance with respect to fishery yield (e.g., catch and effort regulations). In addition, what species are exploited will vary based on location and the type (gear, size, and technology) of the fishery. In Southeast Florida, for example, recreational landings outnumber those

from the commercial sector, shifting the label of ‘economically important species’ towards groupers, snappers, and grunts (i.e., fishes which utilize bays with seagrass beds and mangroves; Ault et al. 1998). In contrast, Robertson and Duke (1987) concluded that Australian mangroves were not important nursery habitats because only three of the top 30 species in total catch were of commercial importance, and Dennis (1992) concluded that the role of mangroves in Puerto Rico may be over-estimated since mangrove dependent species made up a small portion of commercial catches.

11.5.2 Variation Within Species

Another source of variation that confounds attributing nursery function to mangrove habitat is intraspecific variation in habitat utilization, behavior, or diet. Species long have been treated as homogenous units, with intraspecific variation among individuals regarded as non-existent or unimportant. Yet increasing evidence, across a broad range of taxa, suggest that intraspecific variation in niche characteristics may be substantial, and critical to include in ecological models (Bolnick et al. 2003, Bolnick et al. 2007). Ecology of tropical and sub-tropical organisms is no exception, e.g., almost all of the examples in this book seek to identify patterns at the level of ‘species’ or ‘population’, tacitly ignoring important aspects of intraspecific variation.

For species that undergo ontogenetic habitat shifts, the life-history stage of the individual must be qualified for adequate comparison of nursery value. For ingressing larvae from marine sources, mangroves may offer an attractive habitat for settlement (compared to bare substrates) because of their structural complexity. However, while modeling exercises indicate that mangroves may create complex currents that act as a hydrodynamic ‘trap’ for incoming larvae in the case of prawns (Wolanski and Sarenski 1997), relatively few eggs and larval fishes have been collected within mangroves compared to other habitats or life-stages in India (Krishnamurthy and Jeyasslan 1981), Australia (Robertson and Duke 1990), Puerto Rico (Dennis 1992), and Brazil (Barletta-Bergan et al. 2002). Mangroves appear to be utilized much more by individuals after settlement, and as we have discussed, comparison of size-distributions reveals that mangroves likely act as a secondary habitat in the Caribbean after seagrass beds for many species. However, while species-specific comparisons of abundance among different habitats have been extensively conducted, evaluation of how different life-history stages are distributed within patches of the same habitat has been rarely studied. In southeastern Florida, comparison of mangrove shoreline use by two marine fishes revealed that juveniles (age 0), sub-adults (<50% maturity), and adults were physically sorted along a bay-ocean gradient >10 km, with juveniles almost exclusively present near the bay-ocean mouth and adults restricted to inland portions (Faunce and Serafy 2007). Such patterns are likely due to an expansion of home range and mobility with body size, as well as intraspecific variation in habitat utilization among individuals.

11.5.3 Variation Among Individuals

Intraspecific variation can occur at a much finer scale. Even individuals of the same species and size (or age) class, which are ‘resident’ to the same habitat or area, may develop diverse behavioral (and presumably dietary) patterns (e.g., Verweij et al. 2006b). Such variation rarely is incorporated into the study of purported nursery habitats. We present a simplistic empirical example of individual habitat choice in Fig. 11.3. These data are drawn from an extensive acoustic telemetry monitoring program (Vemco equipment system) on Abaco Island, Bahamas (see <http://www.adoptafish.net/>). Individual fishes had acoustic transmitters surgically implanted into their body cavity, and stationary receivers recorded each time the ‘tagged’ fishes passed within their detection range (for more detail on such methodologies see Szedlmayer and Schroepfer (2005)). Such studies provide for remote monitoring of fishes, and a means by which to assess their habitat utilization and presumed foraging excursions. In Fig. 11.3, we depict the proportion of time two *Lutjanus cyanopterus* (cubera snapper) spent at different locations within an intertidal, mangrove-dominated, creek system. Each fish was tagged on the same day, was approximately the same size, and each spent the majority of daylight hours associated with a subtidal sinkhole adjacent to a mangrove stand. At night, each fish

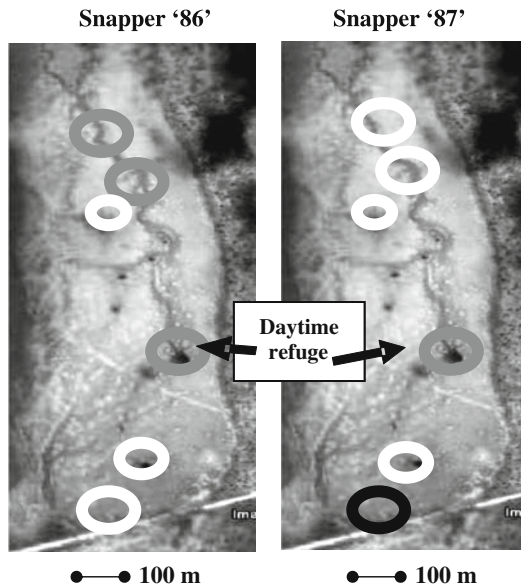


Fig. 11.3 Proportion of time (white <5%, gray 5–50%, black >50%) over a two week period two cubera snapper (*Lutjanus cyanopterus*) spent at different locations in a mangrove-lined intertidal creek system (Abaco Island, Bahamas). Both fishes are daytime residents to the same subtidal habitat, but exhibit distinct nighttime movement patterns. Snapper ‘86’ moves upstream at night and snapper ‘87’ downstream (presumably related to feeding movements). Data from www.adoptafish.net, and based on an acoustic telemetry monitoring system. Size of the symbols represents approximate detection range of telemetry receivers

exhibited a distinct behavioral pattern. Over the same two week period, fish '86' repeatedly moved upstream at night, whereas fish '87' moved downstream. Presumably, this reflects differential utilization of proximate habitats to feed. When scaling up from two fish to an entire population, it is easy to envision how such variation among individuals renders it difficult to assess which habitats may serve as nurseries for an entire species.

In presumed 'generalist' species, intraspecific variation in habitat utilization and foraging behaviors likely increases with increasing heterogeneity of the environment (Layman et al. 2007). That is, the more diverse the habitat mosaic (e.g., seagrass, macroalgal beds, rocky reefs, etc.), and the more diverse the associated food resources, the more likely that intraspecific variation in feeding behaviors may develop. In this context, perhaps *individuals* is the level at which habitat utilization and nursery function should be evaluated. In seeking generalities for an entire species, we may be in danger of oversimplification when attributing a single habitat as *the* 'nursery' for a species. Especially for those species which are characterized by high intraspecific variation in behaviors or dietary patterns, answering the question 'are mangroves nursery habitat?' becomes yet more complicated.

Individual variation can be reflected in the resultant chemical composition of various organs or hard parts such as otoliths. For example, comparison of the signatures deriving from the juvenile portion of the otolith relative to the adult portion can yield information on the relative contribution of individuals from bays containing mangroves to the adult populations located elsewhere. The estimated contribution of nearshore habitats (expressed as a percentage of the total adult population that inhabited bays as juveniles) is estimated at 41% for blue grouper (*Achoerodus viridis*), 32–65% for stone flounder (*Platichthys bicoloratus*), 7–53% for snapper (*Pagrus suratus*), and 40% for *Haemulon flavolineatum* (Gillanders and Kingsford 1996, Yamashita et al. 2000, Gillanders 2002, Chittaro et al. 2004). Because contribution of individuals from mangroves is not 100%, it can be concluded that while bays containing mangroves contribute individuals to the adult population, such contributions are limited. Because mangroves are not the only source of recruits to offshore populations of adult marine fishes, it appears that the export of individuals from mangroves provide *enhancement* (and not maintenance) of offshore populations of certain species, as originally proposed by Bardach (1959) and later Parrish (1989).

11.6 Conclusions

The sources of variability outlined herein are only a partial list of the myriad of factors that affect the role of mangroves as nursery habitat. Two important themes have emerged relevant to mangrove nursery function: (1) attribution of nursery function is influenced by how 'nursery' or 'mangrove ecosystem' is defined, and (2) the importance of mangroves as nursery habitat is dependent on ecological, biological, and hydrological factors that operate at multiple scales. Recent studies have made great strides toward developing more rigorous frameworks for precise quantification and

categorization of the most important nursery habitats for various organisms (Beck et al. 2001, Dahlgren et al. 2006). Yet even these frameworks remain limited in many ways, largely because of the difficulty in estimating the production (based on abundance, growth, and survival) and export of individuals that utilize mangroves (or other habitats). We hope this chapter will encourage researchers to state more explicitly their study approach (definitions and analysis focus) and to acknowledge how resultant opinions regarding the importance of mangroves as nurseries stem from real underlying differences among mangrove ecosystems or species of interest.

So where does the future lie? In Fig. 11.4, we outline two parallel frameworks for identifying: (1) ‘essential fish habitat’ (NOAA 1996), and (2) the levels of study outlined in this chapter at which nursery function can be evaluated. These frameworks are analogous in that the endpoint (highest level) each requires a diverse suite of detailed information (from lower levels). Yet most existing data sets fall far short of these rigorous requirements. As has been emphasized throughout this chapter, much study on the nursery function of mangroves remains at the ‘assemblage-’ and ‘species-’ levels, i.e., identifying which species are present and their relative abun-

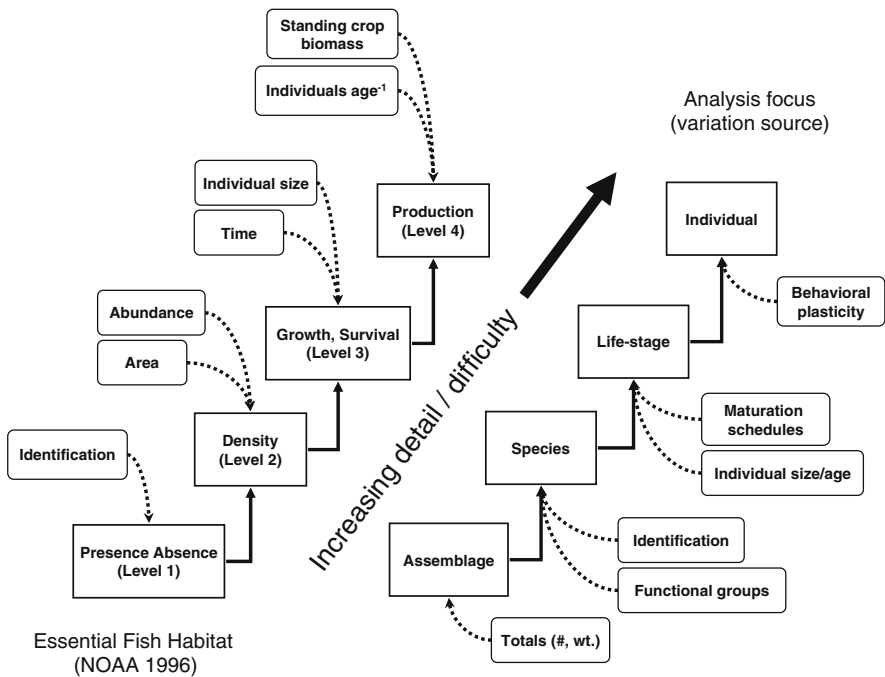


Fig. 11.4 Scheme depicting the parallels between the four levels of information used to assess essential fish habitat by the US Federal Government (left) and the levels of analysis focus described herein to assess the nursery value of mangroves. Each framework is designed so that the analysis of each successive tier (box, solid arrows) poses additional data requirements, some examples of which are illustrated in ovals with dashed arrows. Abbreviations: # = number of fish, wt. = weight of fish

dance among a range of potential habitats. Yet the most robust investigations of the nursery value of mangroves require far more extensive and specific data. As scientists continue to move toward compiling these data sets, we hope that an understanding of the inherent sources of variability in attributing nursery function will remain at the forefront of such efforts.

References

- Adams A, Dahlgren C, Kellison GT et al (2006) The juvenile contribution function of tropical backreef systems. *Mar Ecol Prog Ser* 318:287–301
- Alongi DM (2002) Present state and future of the world's mangrove forests. *Environ Conserv* 29:331–349
- Araujo FG, De Azevedo MCC, Silva MA et al (2002) Environmental influences on the demersal fish assemblages in the Sepetiba Bay, Brazil. *Estuaries* 25:441–450
- Ault JS, Bohnsack JA, Meester GA (1998) A retrospective (1979–1996) multispecies assessment of coral reef fish stocks in the Florida Keys. *US Fish Bull* 96:395–414
- Baker R, Sheaves M (2006) Visual surveys reveal high densities of large piscivores in shallow estuarine nurseries. *Mar Ecol Prog Ser* 323:75–82
- Bardach J (1959) The summer standing crop of fish on a shallow Bermuda reef. *Limnol Oceanogr* 4:77–85
- Barletta-Bergan A, Barletta M, Saint-Paul U (2002) Community structure and temporal variability of ichthyoplankton in North Brazilian mangrove creeks. *J Fish Biol* 61:33–51
- Bartholomew GA (1986) The role of natural history in contemporary biology. *BioScience* 36:324–329
- Beck MW, Heck KL, Able KW et al (2001) The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *Bioscience* 51:633–641
- Blaber SJM, Blaber TG (1980) Factors affecting the distribution of juvenile estuarine and inshore fish. *J Fish Biol* 17:143–162
- Blaber SJM (2000) *Tropical estuarine fishes: ecology, exploitation, and conservation*. Blackwell Science Ltd., London
- Blaber SJM (2007) Mangroves and fishes: issues of diversity, dependence, and dogma. *Bull Mar Sci* 80:457–472
- Blaber SJM, Milton DA (1990) Species composition, community structure and zoogeography of fishes of mangrove estuaries in the Solomon Islands. *Mar Biol* 105:259–267
- Blaber SJM, Young JW, Dunning MC (1985) Community structure and zoogeographic affinities of the coastal fishes of the Dampier Region of north-western Australia. *Aust J Mar Freshw Res* 36:247–266
- Blaber SJM, Brewer DT, Salini JP (1989) Species composition and biomasses of fishes in different habitats of a tropical northern Australian estuary: their occurrence in the adjoining sea and estuarine dependence. *Estuar Coast Shelf Sci* 29:509–531
- Bolnick DI, Svanbäck R, Fordyce JA et al (2003) The ecology of individuals: incidence and implications of individual specialization. *Am Nat* 161:1–28
- Bolnick DI, Svanbäck R, Araujo M et al (2007) More generalized populations are also more heterogeneous: comparative support for the niche variation hypothesis. *Proc Natl Acad Sci USA* 104:10075–10079
- Chittaro PM, Fryer BJ, Sale PF (2004) Discrimination of French grunts (*Haemulon flavolineatum*, Desmarest, 1823) from mangrove and coral reef habitats using otolith microchemistry. *J Exp Mar Biol Ecol* 308:169–183
- Chong VC, Sasekumar A, Leh MUC et al (1990) The fish and prawn communities of a Malaysian coastal mangrove system, with comparisons to adjacent mud flats and inshore waters. *Estuar Coast Shelf Sci* 31:703–722

- Cocheret de la Morinière E, Pollux BJA, Nagelkerken I et al (2002) Postsettlement life cycle migration patterns and habitat preference of coral reef fish that use seagrass and mangrove habitats as nurseries. *Estuar Coast Shelf Sci* 55:309–321
- Cocheret de la Morinière E, Pollux BJA, Nagelkerken I et al (2003) Ontogenetic dietary changes of coral reef fishes in the mangrove-seagrass-reef continuum: stable isotopes and gut-content analysis. *Mar Ecol Prog Ser* 246:279–289
- Costanza R, d'Arge R, deGroot R et al (1997) The value of the world's ecosystem services and natural capital. *Nature* 387:253–260
- Dahlgren CP, Eggleston (2000) Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. *Ecology* 81:2227–2240
- Dahlgren CP, Kellison GT, Adams AJ et al (2006) Marine nurseries and effective juvenile habitats: concepts and applications. *Mar Ecol Prog Ser* 312:291–295
- Dennis GD (1992) Island mangrove habitats as spawning and nursery areas for commercially important fishes in the Caribbean. *Proc Gulf Caribb Fish Inst* 41:205–225
- Dorenbosch M, van Riel MC, Nagelkerken I et al (2004) The relationship of reef fish densities to the proximity of mangrove and seagrass nurseries. *Estuar Coast Shelf Sci* 60:37–48
- Dorenbosch M, Grol MGG, Christianen MJA et al (2005) Indo-Pacific seagrass beds and mangroves contribute to fish density and diversity on adjacent coral reefs. *Mar Ecol Prog Ser* 302:63–76
- Dorenbosch M, Grol MGG, Nagelkerken I et al (2006) Seagrass beds and mangroves as potential nurseries for the threatened Indo-Pacific humphead wrasse, *Cheilinus undulatus* and Caribbean rainbow parrotfish, *Scarus guacamaia*. *Biol Conserv* 129:277–282
- Dufrêne M, Legendre P (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol Monogr* 67:345–366.
- Eggleston, DB, Dahlgren C, Johnson EG (2004) Fish density, diversity and size-structure within multiple back-reef habitats of Key West National Wildlife Refuge, USA. *Bull Mar Sci* 75:175–204
- Ewel KC, Twilley RR, Ong JE (1998) Different kinds of mangrove forests provide different goods and services. *Glob Ecol Biogeogr* 7:83–94
- Faunce CH, Serafy JE (2006). Mangroves as fish habitat: 50 years of field studies. *Mar Ecol Prog Ser* 318:1–18
- Faunce CH, Serafy JE (2007) Nearshore habitat use by gray snapper (*Lutjanus griseus*) and bluestriped grunt (*Haemulon sciurus*): environmental gradients and ontogenetic shifts. *Bull Mar Sci* 80:473–495
- Faunce CH, Serafy JE (2008a) Growth and secondary production of an eventual reef fish during mangrove residency. *Estuar Coast Shelf Sci* 79:93–100
- Faunce CH, Serafy JE (2008b). Selective use of mangrove shorelines by snappers, grunts, and great barracuda. *Mar Ecol Prog Ser* 356:153–162
- Faunce CH, Serafy JE, Lorenz JJ (2004) Density-habitat relationships of mangrove creek fishes within the southeastern saline Everglades (USA), with reference to managed freshwater releases. *Wetlands Ecol Manage* 12:377–394
- Faunce CH, Ault E, Ferguson K et al (2007) Reproduction of four Florida snappers with comparisons between an island and continental reef system. In: Barbieri L, Colvocoresses J (eds) Southeast Florida reef fish abundance and biology. Five-year performance report to the U.S. Fish and Wildlife Service. Florida Fish and Wildlife Research Institute, St. Petersburg
- Gillanders BM (2002) Connectivity between juvenile and adult fish populations: do adults remain near their recruitment estuaries? *Mar Ecol Prog Ser* 240:215–223
- Gillanders BM, Kingsford MJ (1996) Elements in otoliths may elucidate the contribution of estuarine recruitment to sustaining coastal reef populations of a temperate reef fish. *Mar Ecol Prog Ser* 141:13–20
- Hajisamæ S, Chou LM (2003) Do shallow water habitats of an impacted coastal strait serve as nursery grounds for fish? *Estuar Coast Shelf Sci* 56:281–290
- Heyman, WD, Kjerfve B, Graham RT et al (2005) Spawning aggregations of *Lutjanus cyanopterus* (Cuvier) on the Belize Barrier Reef over a six year period. *J Fish Biol* 67:83–101

- Hogarth, PJ (2007). The biology of mangroves and seagrasses. Oxford University Press, London
- Koenig CC, Coleman FC, Eklund A et al (2007) Mangroves as essential nursery habitat for goliath grouper (*Epinephelus itajara*). Bull Mar Sci 80:567–586
- Krishnamurthy K, Jeyasslan MJP (1981) The early life history of fishes from Pichavaram mangrove ecosystem of India. In: Lasker R, Sherman K (eds) The early life history of fish: recent studies. The second ICES symposium. Conseil International Pour L'Exploration de la Mer Palegade 2–4, Copenhagen, Denmark
- Layman CA, Quattrochi JP, Peyer CM et al (2007) Niche width collapse in a resilient top predator following ecosystem fragmentation. Ecol Lett 10:937–944
- Ley JA (2005) Linking fish assemblages and attributes of mangrove estuaries in tropical Australia: criteria for regional marine reserves. Mar Ecol Prog Ser 305:41–57
- Ley JA, McIvor CC, Montague CL (1999) Fishes in mangrove proproot habitats of northeastern Florida Bay: distinct assemblages across an estuarine gradient. Estuar Coast Shelf Sci 48:701–723
- Lewis RR (2005) Ecological engineering for successful management and restoration of mangrove forests. Ecol Eng 24:403–418
- Lin HJ, Shao KT (1999) Seasonal and diel changes in a subtropical mangrove fish assemblage. Bull Mar Sci 65:775–794
- Little MC, Reay PJ, Grove SJ (1988) Distribution gradients of ichthyoplankton in an East African mangrove creek. Estuar Coast Shelf Sci 26:669–677
- Loneragan NR, Bunn SE, Kellaway DM (1997) Are mangroves and seagrasses sources of organic carbon for penaeid prawns in a tropical Australian estuary? A multiple stable isotope study. Mar Biol 130:289–300
- Lorenz JJ (1999) The response of fishes to physicochemical changes in the mangroves of northeast Florida Bay. Estuaries:500–517
- Lugendo BR, Pronker A, Cornelissen I et al (2005) Habitat utilisation by juveniles of commercially important fish species in a marine embayment in Zanzibar, Tanzania. Aquat Living Resour 18:149–158
- Lugendo BR, Nagelkerken I, Kruitwagen G et al (2007) Relative importance of mangroves as feeding habitat for fish: a comparison between mangrove habitats with different settings. Bull Mar Sci 80:497–512
- Lugo AE, Snedaker SC (1974) The ecology of mangroves. Annu Rev Ecol Syst 5:39–64
- Lugo AE (1980) Mangrove ecosystems: successional or steady state? Biotropica 12:65–72
- Manson FJ, Loneragan NR, Skilleter GA et al (2005) An evaluation of the evidence for linkages between mangroves and fisheries: a synthesis of the literature and identification of research directions. Annu Rev Oceanogr Mar Biol 43:483–513
- Mumby PJ, Edwards AJ, Arias-Gonzales JE et al (2004) Mangroves enhance the biomass of coral reef fish communities in the Caribbean. Nature 427:533–536
- Nagelkerken I (2007) Are none-stuarine mangroves connected to coral reefs through fish migration? Bull Mar Sci 80:595–607
- Nagelkerken I, Dorenbosch M, Verberk WCEP et al (2000a) Importance of shallow-water biotopes of a Caribbean bay for juvenile coral reef fishes: patterns in biotope association, community structure and spatial distribution. Mar Ecol Prog Ser 202:175–192
- Nagelkerken I, van der Velde G, Gorissen MW et al (2000b) Importance of mangroves, seagrass beds and the shallow coral reef as a nursery for important coral reef fishes, using a visual census technique. Estuar Coast Shelf Sci 51:31–44
- Nagelkerken I, Dorenbosch M, Verberk WCEP et al (2000c) Day-night shifts of fishes between shallow-water biotopes of a Caribbean bay, with emphasis on the nocturnal feeding of Haemulidae and Lutjanidae. Mar Ecol Prog Ser 194:55–64
- Nagelkerken I, Roberts CM, van der Velde G et al (2002) How important are mangroves and seagrass beds for coral-reef fish? The nursery hypothesis tested on an island scale. Mar Ecol Prog Ser 244:299–305

- NOAA (National Oceanic and Atmospheric Administration, National Marine Fisheries Service) (1996) Magnuson-Stevens Fishery Conservation and Management Act, as amended through October 11, 1996. NOAA technical memorandum NMFS-F/SPO, 121pp.
- Paris CB, Cowen RK, Claro R et al. (2005) Larval transport path-ways from Cuban snapper (*Lutjanidae*) spawning aggregations based on biophysical modeling. *Mar Ecol Prog Ser* 296:93–106
- Parrish JD (1989) Fish communities of interacting shallow-water habitats in tropical oceanic regions. *Mar Ecol Prog Ser* 58:143–160
- Provost MW (1973) Mean high water mark and use of tidelands in Florida. *Fla Sci* 36:50–66
- Quinn NJ (1980) Analysis of temporal changes in fish assemblages in Serpentine Creek, Queensland. *Environ Biol Fishes* 5:117–133
- Ricker WE (1975) Computation and interpretation of biological statistics of fish populations. *Bull Canadian Fish Res Board* 1–392
- Robertson AI, Duke NC (1987) Mangroves as nursery sites: comparisons of the abundance and species composition of fish and crustaceans in mangroves and other nearshore habitats in tropical Australia. *Mar Biol* 96:193–205
- Robertson AI, Duke NC (1990) Mangrove fish-communities in tropical Queensland, Australia: spatial and temporal patterns in densities, biomass and community structure. *Mar Biol* 104:369–379
- Rönnbäck P, Troell M, Kautsky N et al (1999) Distribution pattern of shrimps and fish among *Avicennia* and *Rhizophora* microhabitats in the Pagbilao Mangroves, Philippines. *Estuar Coast Shelf Sci* 48:223–234
- Rooker JR, Dennis GD (1991) Diel, lunar and seasonal changes in a mangrove fish assemblage off southwestern Puerto Rico. *Bull Mar Sci* 49:684–698
- Serafy JE, Araujo RJ (2007) First international symposium on mangroves as fish habitat – Preface. *Bull Mar Sci* 80:453–456
- Serafy JE, Faunce CH, Lorenz JJ (2003) Mangrove shoreline fishes of Biscayne Bay, Florida. *Bull Mar Sci* 72:161–180
- Serafy JE, Valle M, Faunce CH et al (2007) Species-specific patterns of fish abundance and size along a subtropical mangrove shoreline: an application the delta approach. *Bull Mar Sci* 80:609–624
- Sheaves MJ (2001) Are there really few piscivorous fishes in shallow estuarine habitats? *Mar Ecol Prog Ser* 222:279–290
- Sheridan P, Hays C (2003) Are mangroves nursery habitat for transient fishes and decapods? *Wetlands* 23:449–458
- Spalding M, Blasco F, Field C (1997) World mangrove atlas. The International Society for Mangrove Ecosystems (ISME), Okinawa
- Szedlmayer ST, Schroepfer RL (2005) Longterm residence of red snapper on artificial reefs in the northeastern Gulf of Mexico. *Trans Am Fish Soc* 134:315–325
- Thayer GW, Stuart HH, Kenworthy WJ et al (1978) Habitat values of salt marshes, mangroves, and seagrasses for aquatic organisms. In: Greeson PE, Clark JR, Clark JE (eds) *Wetlands functions and values: the state of our understanding*. American Water Resources Association, Washington DC
- Thollot P, Kulbicki M (1988) Overlap between the fish fauna inventories of coral reefs, soft bottoms and mangroves in Saint-Vincent Bay (New Caledonia). In: Choat JH, Barnes D, Borowitzka MA et al (eds) *Sixth International Coral Reef Symposium*, Townsville
- Valentine-Rose L, Layman CA, Arrington DA et al (2007) Habitat fragmentation decreases fish secondary production in Bahamian tidal creeks. *Bull Mar Sci* 80:863–877
- Verweij MC, Nagelkerken I, de Graaff D et al (2006a) Structure, food and shade attract juvenile coral reef fish to mangrove and seagrass habitats: a field experiment. *Mar Ecol Prog Ser* 306:257–268
- Verweij MC, Nagelkerken I, Wartenbergh SLJ et al (2006b) Caribbean mangroves and seagrass beds as daytime feeding habitats for juvenile French grunts, *Haemulon flavolineatum*. *Mar Biol* 149:1291–1299

- Wassenberg TJ, Hill BJ (1993) Diet and feeding behaviour of juvenile and adult banana prawns (*Penaeus merguensis* de Man) in the Gulf of Carpentaria, Australia. *Mar Ecol Prog Ser* 94:287–295
- Weng HT (1990) Fish in shallow areas in Moreton Bay, Queensland and factors affecting their distribution. *Estuar Coast Shelf Sci* 30:569–578
- Wolanski E, Mazda Y, Ridd P (1992) Mangrove hydrodynamics. In: Robertson AI, Alongi DM (eds) *Tropical mangrove ecosystems*. Coastal and Estuarine Studies 41. American Geophysical Union, Washington DC
- Wolanski E, Sarenski J (1997) Larvae dispersion in coral reefs and mangroves. *Am Sci* 85:236–243
- Woodroffe C (1992) Mangrove sediments and geomorphology. In: Robertson AI, Alongi DM (eds) *Tropical mangrove ecosystems*. Coastal and Estuarine Studies 41. American Geophysical Union, Washington DC
- Yamashita Y, Otake T, Yamada H (2000) Relative contributions from exposed inshore and estuarine nursery grounds to the recruitment of stone flounder, *Platichthys bicoloratus*, estimated using otolith Sr:Ca ratios. *Fish Oceanogr* 9:316–327