6.04 Trophic Interactions in Coastal and Estuarine Mangrove Forest Ecosystems

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Abstract

Mangrove habitats are among the most productive ecosystems on the Earth. Their low vegetational diversity belies a remarkable richness of associated species and trophic interactions. This contribution summarizes what is known about these interactions. Information on interaction strengths, top-down versus bottom-up control, and the consequences of species interactions for community structure is only available for a few systems. At a more fundamental level, our understanding of the relative contributions of different sources of primary productivity and the patterns and mechanisms of their exploitation by herbivores, detritivores, and deposit feeders remains quite limited. Even less is known about the movement of carbon, nitrogen, and other elements through mangrove food webs to higher trophic levels. Long-standing paradigms asserting minimal consumption of living plant tissues by herbivores and the paramount role of mangrove detritus as fuel for secondary production of crustaceans and fish are being challenged by data gathered with newer methodologies, most notably, stable isotope analysis. Much remains to be learned about the role of mangroves as nurseries for juvenile life history

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stages and the trophic links between mangroves and neighboring ecosystems. Ongoing and future investigations of these processes that employ a balanced mix of quantitative observation and field experiments promise to generate exciting new insights about mangrove community and ecosystem processes, and at the same time inform general food-web theory.

6.04.1 Introduction

In his book, The Log from the Sea of Cortez, Steinbeck (1951: 123) painted a stark picture of trophic interactions in mangroves:

> As the tide came up we moved upward in the intertidal towards the mangrove trees, and the foul smell of them reached us. They were in bloom, and the sharp sweet smell of their flowers, combined with the filthy odor of the mud about their roots, was sickening. But they are fascinating to look into. Huge hermit crabs seem to live among their stilted roots; the black mud, product of the root masses, swarms as a meeting place for land and sea animals. Flies and insects in great numbers crawl and buzz about the mud, and the scavenging hermit crabs steal secretly in and out and even climb into the high roots.
>
> We suppose it is the combination of foul odor and the impenetrable quality of the mangrove roots which gives one a feeling of dislike for these salt-water-eating bushes. We sat quietly and watched the moving life in the forest of the roots, and it seemed to us that there was stealthy murder everywhere. On the surf-swept rocks it was fierce and hungry and joyous killing, committed with energy and ferocity. But there it was like stalking, quiet murder. The roots gave off clicking sounds, and the odor was disgusting. We felt that we were watching something horrible. No one likes the mangroves.

With all due literary respect to Steinbeck, many scientists, naturalists, subsistence, sport, and commercial fishers, and indigenous coastal cultures appreciate the uniqueness of mangrove forests and greatly value the resources they afford. In this chapter, we examine trophic interactions in mangrove habitats. Our primary focus is on interactions that occur within forest stands and contiguous habitats (i.e., seagrass beds, tidal flats, channels, and creeks), but we also provide an overview of trophic linkages with nearshore and offshore communities. The low tree species diversity of mangrove forests, as compared to species-rich upland rainforests, belies a diverse assemblage of consumers. In part, this surprising richness in consumers derives from the ecotonal nature of mangrove habitats, which occupy the interface of marine and terrestrial habitats, and provide resources to consumers from both environments, as well as those endemic to mangroves. There are countless trophic interactions in this habitat, many of them only anecdotally documented; relatively few have been rigorously quantified or investigated experimentally. Linkages and relative strengths of interactions are poorly understood, as compared to better-studied habitats like the temperate rocky intertidal zone (Paine, 1980, 1992; Menge et al., 1994; Wootton and Emmerson, 2005), kelp forests (Estes and Palmisano, 1974; Estes et al., 1978; Estes and Duggins, 1995), rivers (Power et al., 1985; Power, 1990), lakes (Carpenter et al., 1987; Carpenter and Kitchell, 1988), rainforest (Asquith et al., 1997; Fine et al., 2004), small tropical islands (Spiller and Schoener, 1988, 1990, 1994), and deserts (Brown et al., 1986; Polis, 1991; Heske et al., 1993). In fact, our knowledge of trophic interactions in mangroves lags well behind our understanding of these relationships in the marine (e.g., corals, reefs, and seagrass beds) and terrestrial (e.g., rainforest) environments that border them. This is likely due to their relative inaccessibility and the inhospitable abiotic and biotic conditions they present to field researchers. In this chapter, we focus on the better-studied trophic interactions in mangrove ecosystems (**Figure 1**). Our treatment of this topic has been informed by several excellent recent reviews that consider trophic interactions in mangrove forests (e.g., Kathiresan and Bingham, 2001; Cannicci et al., 2008; Nagelkerken et al., 2008; Alongi, 2009a, 2009b; Feller et al., 2010).

6.04.2 What Are Mangrove Forests?

To set the stage for our discussion of trophic relationships in mangrove habitats, we begin by describing this forest type and its environment. Mangroves are the characteristic vegetation type of low-energy intertidal shores and estuaries throughout the tropics and much of the subtropics (Tomlinson, 1986). With the exception of a few locales in the Southern Hemisphere, they are distributed between the winter 20 °C north and south isotherms (Duke, 1992). Mangrove is a vegetation type rather than a taxonomic grouping, and is comprised of trees, shrubs, palms, and ground ferns that grow in the intertidal zone, generally above mean sea level (Duke, 1992). Numerous families are represented in any particular assemblage, and many species have terrestrial relatives. Mangroves share the ability to grow and reproduce in tidally flooded soils, which exhibit wide fluctuations in water-saturation, salinity, oxygen availability, and hydrogen sulfide concentrations on daily, seasonal, and annual timescales. Mangrove forests are typically low in plant diversity, especially compared to neighboring upland rainforest. The tree species richness of mangrove forests varies from about 3 to 5 in the Caribbean to as many as 35–40 species in the Indo-Pacific region. Authors differ somewhat in their definition of what is a true mangrove versus a mangrove associate, but following Duke's (1992) classification scheme, there are 69 mangrove species, worldwide, including putative hybrids, with representatives in 20 plant families. Twenty-seven genera include mangrove species, with 17 being comprised exclusively of mangroves.

The physiognomy of mangrove habitats undoubtedly influences the assemblage of associated consumers. Generally speaking, there is a tree or palm canopy layer, with a notably sparse, open understory, comprised of young-of-the-year mangrove tree seedlings, and some saplings, shrubs, ferns, vines, and sedges. The nontree components tend to be more abundant in less-saline areas near the upland edges of the forest. A number of investigators have commented on the depauperate nature of the mangrove understory (Janzen, 1985; Corlett, 1986; Lugo, 1986; Snedaker and Lahmann, 1988), suggesting a variety of hypotheses to explain the sparse undergrowth. Even so, the trees themselves can add considerable structure to the understory; this is particularly true of lower intertidal forests dominated by *Rhizophora* spp. The dense tangle of aerial prop roots provides hard substrate for attachment of epibionts, protection from strong wave surge, pathways for animal movement above the water or muddy benthos, and a

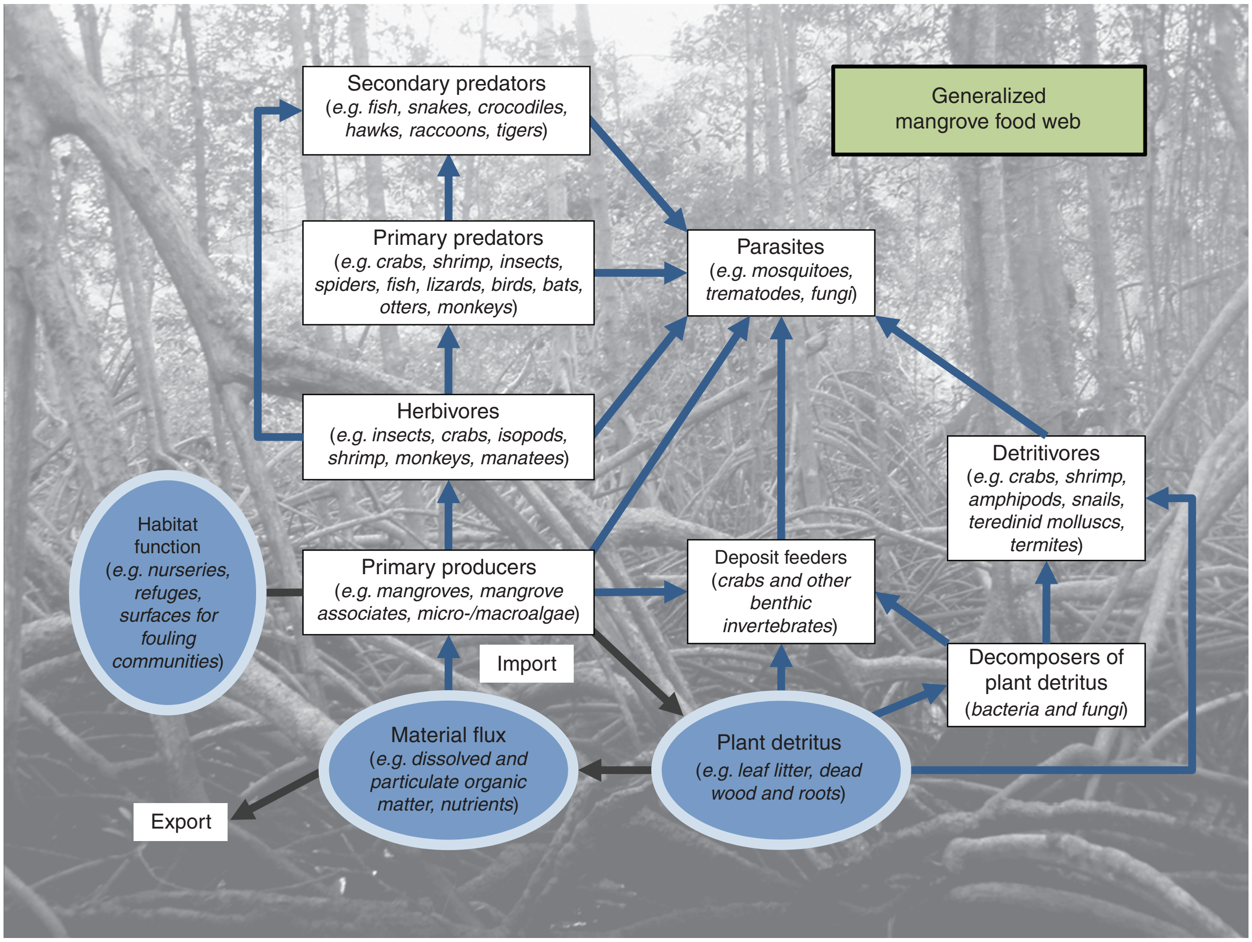

Figure 1 Generalized mangrove food web, highlighting the major trophic interactions discussed in this chapter. Blue arrows indicate direct trophic interactions from resource to consumer. Gray arrows indicate non-consumptive transformation or movement of materials. The functional role of mangrove vegetation as habitat is also indicated (background photo by EMD: Playa Barqueta, Panama).

three-dimensional (3D) physical refuge from mobile predators for invertebrates and fishes.

Mangroves grow in a wide range of soil types, from nutrient-poor, carbonate sand to highly organic fine mud to dense peat. The finer sediments are oxygen poor with high concentrations of hydrogen sulfide. In areas free of riverine influence, soil salinity tends to increase with distance from the shoreline, due to higher levels of evaporation at upper intertidal levels, especially at locales with a marked dry season. Mangroves possess a variety of morphological and physiological traits that allow them to establish and grow in these seemingly harsh conditions. Species vary in their tolerance of differing physicochemical conditions (Tomlinson, 1986; Smith, 1992; Krauss et al., 2008).

Mangrove forests have been classified into various types based on their physiognomy, spatial position in the intertidal, functional characteristics, and geomorphic setting (Lugo and Snedaker, 1974; Woodroffe, 1992; Ewel et al., 1998). In this chapter, we will use the forest categories of Lugo and Snedaker (1974): overwash, fringe, riverine, basin, scrub/dwarf, and hammock forests. This scheme was developed for the relatively species-poor forests of the Neotropics, and may not be as effective for describing the diverse forests of the Old World (Woodroffe, 1992); however, it is satisfactory for our purposes. Overwash stands grow on small low islands or narrow projections of the mainland that are completely overwashed by high tides. Fringe forest grows along the seaward edge of the habitat and experiences daily inundation by tides and wave action during storms (Figure 2). Riverine forest occupies the

Figure 2 Fringe *Rhizophora mangle* forest (Punta Galeta, Panama; photo by WPS).

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Figure 3 Basin *Avicennia germinans* forest (Punta Galeta, Panama; photo by WPS).

floodplain along the edges of rivers and creeks, and typically has the tallest canopy trees. These stands are regularly flushed by fresh river water or tidally influenced, low-salinity estuarine waters. Basin forests are located inland of fringing or riverine stands, often in shallow depressions behind a raised berm (**Figure 3**). Tidal inundation is infrequent, usually associated with extreme tidal events or storms. Rainfall runoff, mixed with some tidal waters, often ponds in these areas during the rainy season. Despite this, repeated cycles of dry season evaporation causes high soil salinity. Scrub/Dwarf forest occurs landward of fringe forest in nutrient-poor, saline soils; they experience limited flooding by higher tides and no wave action (**Figure 4**). Recruitment of new trees is rare, so individuals tend to be old and stunted, with typical canopy heights of 1.5 m, or less. Finally, hammock forests, an inland basin forest type unique to the Florida Everglades, grow on raised islands of mangrove-derived peat, which have built up over depressions in the underlying limestone substrate. This stand type is isolated from tidal or riverine influence; water availability and soil salinity are controlled by rainfall, runoff, and evaporation.

Finally, we would be remiss in not pointing out that mangrove habitats are some of the most endangered on the planet. Once occupying 75% of the world's sheltered tropical coastlines and estuaries (estimated to have been more than 200 000 km^2; Chapman, 1976; Spalding et al., 2010), much of the world's original mangrove cover has now been lost to urban, industrial, and touristic development, conversion to agriculture, aquaculture, pollution, hydrological alterations, accelerating sea-level rise, and clear-cutting for forest products, among other types of habitat degradation (Farnsworth and Ellison, 1997b; Alongi, 2002; Gilman et al., 2008; Spalding et al., 2010; **Figure 5**). The most up-to-date estimate of the current worldwide extent of mangrove forest, based on detailed analysis of Landsat satellite imagery, is 137 760 km^2 (Giri et al., 2011), substantially below other recent estimates of 150–180 000 km^2 (e.g., Valiela et al., 2001; FAO, 2010; Spalding et al., 2010). Thus, roughly a third of the world's mangrove forests have been destroyed in the second half of the twentieth century (Alongi, 2002). Consistent with this value, Valiela et al. (2001) estimated that over the last 20 years, mangrove forests have declined by 35%. Worldwide rates of mangrove destruction average about 2% yr^{-1}, exceeding those documented for rainforest and coral reef habitats. Such analyses have given rise to the dire prediction that viable mangrove habitat could disappear altogether within the next 100 years (Duke et al., 2007). Efforts to halt and reverse this trend will require rigorously collected and widely communicated information on the processes that structure and maintain mangrove communities, including key trophic relationships, and their linkage to resources and ecosystem functions valued by society.

Although the classification of organisms into distinct trophic levels is often an unrealistic portrayal of community structure (e.g., Polis and Strong, 1996), it can still provide a useful framework for discussion of trophic interactions.

Figure 4 Dwarf *Rhizophora mangle* forest (Bocas del Toro, Panama; photo by I.C. Feller).

Figure 5 Mangrove stand clear-cut for port development (Coco Solo, Panama; photo by WPS).

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Therefore, we refer to the following trophic categories: primary producers, decomposers, detritivores, herbivores, predators, and secondary predators. Note that many consumer species are omnivorous and thus do not fall cleanly into one trophic level; in these cases, we group organisms by their primary food sources. We also discuss the fouling communities that inhabit mangrove prop roots and the role of mangroves as nursery grounds and refuges from predation.

6.04.3 Net Primary Productivity of Mangrove Forests

Mangrove forests are typically characterized as highly productive ecosystems. The carbon that fuels mangrove food chains derives from primary production by the mangroves themselves and by associated benthic or epiphytic algae, as well as phytoplankton carried into the forest by tidal flow from neighboring embayments and seaward habitats such as seagrass beds. This primary production is supplemented by allochthonous phytodetritus, transported by tidal flow, creeks and rivers, or by surface runoff from upland terrestrial habitats (Bouillon et al., 2002a, 2004b; Kristensen et al., 2008).

Gross primary production (GPP) is the total amount of carbon fixed by autotrophic organisms in an ecosystem. In forests, carbon fixation occurs by photosynthesis, and gross primary productivity is the rate at which carbohydrate biomass accumulates per unit area. Mangroves, mangrove-associated vascular plants and mosses, and benthic and epiphytic algae are the key autochthonous primary producers in mangrove ecosystems. Net primary production (NPP), the energy that is potentially available to other trophic levels, is the difference between GPP and total plant and algal respiration in an ecosystem. While this definition is straightforward, direct estimates of this difference between gross production and respiration from field measurements of gas exchange are technically and logistically challenging, and extrapolation from leaf-level measurements to whole canopy estimates is compromised by assumptions, compounding errors, and uncertain relationships (Bunt et al., 1979; Ryan, 1991; Clough, 1992; Clark et al., 2001a). Several alternative methods of NPP estimation have been devised. The most commonly used is the summation method (Kira and Shidei, 1967; Clark et al., 2001a) by which NPP for a specified interval is estimated as the sum of (1) the quantity of new organic matter that is retained by living plants at the end of the interval and (2) the amount of new organic matter that was produced but lost by plants during the interval to mortality and consumption by herbivores. Stated more simply,

$$\mathrm{NPP} = G + H + L$$

where NPP is the net primary productivity (Mg or t dry mass or C unit area^{-1} time interval^{-1}; most commonly expressed as Mg or t dry mass or C ha^{-1} yr^{-1}); G the growth increment during the interval; H the consumption by herbivores during the interval; and L the mortality other than herbivory during the interval.

In practice, most studies of NPP in mangroves ignore losses to herbivory, assuming it to be insignificant (see Section 6.04.4.1). Mortality is most commonly estimated as fine litterfall (i.e., fallen leaves, propagules, inflorescences, and twigs). Some early studies used annual litterfall as a proxy for NPP when data on biomass increments were unavailable (e.g., Teas, 1979), a practice that can greatly misestimate net primary productivity, depending on the assumed conversion factor between litterfall and NPP (Day et al., 1987; Clough, 1987, 1992; Kristensen et al., 2008).

Belowground root growth, grazing on roots, litter production from roots, and the release of dissolved organic carbon (DOC) via root exudates are seldom quantified (Clough, 1992). Consequently, most estimates of mangrove NPP are for aboveground parts only. Our inability to readily incorporate belowground productivity is an important omission; mangrove carbon production and sinks may be greatly underestimated (Bouillon et al., 2008a). Root biomass of tropical mangroves, including prop roots, buttresses, pneumatophores, and fine roots, accounts for 19–49% (median = 30%, $n = 12$) of tree biomass (Komiyama et al., 2008). By comparison, roots account for 14–34% (median = 17%, $n = 39$) of upland tropical tree biomass (Jackson et al., 1996; Cairns et al., 1997; Mokany et al., 2006). Therefore, mangroves generally allocate a greater proportion of their biomass to roots than terrestrial trees. To date, very few studies have directly measured mangrove root productivity. McKee and Faulkner (2000) used the implanted soil core technique to measure the production of new roots over a 12-month period in *Rhizophora mangle* stands at sites in southwest Florida. Their estimates of g C m^{-2} yr^{-1} from four sites were equivalent to 60–70% of the annual input of carbon from leaf fall at those sites. A similar in-growth core technique was employed by Gleason and Ewel (2002) to compare root production by *Sonneratia alba*, *Bruguiera gymnorrhiza*, and *Rhizophora apiculata* on the island of Kosrae, Federated States of Micronesia. Production varied significantly among the species, with *S. alba* producing fine roots at 8.4–9.6× the rate of the other two species, which did not differ in root in-growth rates. The authors were unable to compare these production rates to components of aboveground production for lack of data. Sánchez (2005) measured fine root production at eight sites within the Rookery Bay National Estuarine Research Reserve in southwestern Florida using the same in-growth core technique. Root production rates varied from 106 to 842 g m^{-2} yr^{-1}. By comparison, leaf litter production in the same plots varied from 101 to 263 g m^{-2} yr^{-1}, with the ratio of root to litter production varying from 0.6 to 8.0. Assuming there are no serious artifacts of the in-growth core technique, these studies demonstrate that root growth represents a very substantial contribution to forest productivity, and calls for additional quantitative studies of *in situ* root production.

Summation estimates of aboveground NPP (or ANPP) calculate the growth component of production, that is, the change in tree biomass for a given increment in diameter, using empirically derived allometric equations that relate diameter at breast height (DBH) to mass (Komiyama et al., 2008). Adding litter production values, and assuming that herbivory is negligible, yields an estimate of ANPP. This is probably the most reliable method of estimating ANPP, but requires intensive, long-term monitoring of the target stand to gather multiyear measurements of increments in DBH and litterfall (Clough et al., 1997; Alongi, 2009b). It is not well suited to large-scale surveys or short-term comparative studies, especially in remote areas.

A technique that better lends itself to survey studies of productivity is the light attenuation method, first developed by Bunt et al. (1979) (also see Boto et al., 1984), and later modified by Clough (1997) and Clough et al. (1997). This method is based on the well-documented relationship between NPP and the amount of light absorbed by a forest canopy, which in turn is closely related to the canopy leaf-area index or LAI (i.e., total one-sided green leaf area per unit ground area). LAI is usually estimated indirectly from measurements of the attenuation of light as it passes through the canopy. The LAI value is then combined with measurements of canopy photosynthesis to estimate daytime net photosynthetic production (see Clough et al. (1997) for a detailed description of both the original and revised methods). As useful as this approach may be, it is important to recognize that it does not produce an estimate of NPP. It measures the amount of carbon fixed by net photosynthesis in the canopy (gross photosynthesis minus respiration) during daylight hours. Examples of mangrove studies employing this method include Robertson et al. (1991), Clough et al. (1997), Clough (1998), Cox and Allen (1999), and Alongi et al. (2000, 2005).

A number of authors have compiled lists of published estimates of net productivity for various mangrove stands around the world (e.g., Sherman et al., 2003; Komiyama et al., 2008; Alongi, 2009b). **Table 1** lists 22 estimates of mangrove ANPP from 10 studies that used the summation method, pooling the annual biomass growth increment and litterfall. One of these studies (Ross et al., 2001) used detailed data on leaf demography and turnover rate, instead of litterfall data, to estimate the mortality component. The estimates of ANPP in **Table 1** are quite variable, ranging from 3.99 to 27.00 Mg dry wt ha^{-1} yr^{-1}, with mean and median values of 14.33 and 13.10, respectively. Less productive stands tend to be dwarf, scrub, or basin forms, growing in soils that are either subject to frequent evaporative drying and therefore highly saline, or waterlogged and anaerobic, with high concentrations of hydrogen sulfide. Fringe stands, which experience regular tidal flushing, or riverine stands, which grow in less saline soils, exhibit higher ANPP values. Other factors known to influence mangrove productivity are soil nutrient availability (Onuf et al., 1977; Boto and Wellington, 1983, 1984; Boto et al., 1984; Feller, 1995; Feller et al., 2002, 2003; Lovelock et al., 2004; Naidoo, 2009; Medina et al., 2010; Reef et al., 2010), species-specific growth patterns, and latitude/temperature (Duke, 1990; Saenger and Snedaker, 1993; Stuart et al., 2007). Some of the variations among ANPP estimates are probably due to uncontrolled inter-annual variation in climate or hydrological conditions that affect growth, or differences in the age and density of the stands.

Fringe, riverine, and some basin mangrove stands generally have higher ANPP than their terrestrial counterparts. Among the 39 estimates of ANPP compiled by Clark et al. (2001b) from old-growth tropical upland forests, only one forest, located in Ivory Coast, had an estimated ANPP greater than 10 Mg dry wt ha^{-1} yr^{-1}. The maximum ANPP of 14.3 Mg dry wt ha^{-1} yr^{-1} recorded from that site is equal to the mean value of the mangrove estimates in **Table 1**. The median value for the 39 tropical upland forests was 5.6 Mg dry wt ha^{-1} yr^{-1}, and those values were adjusted upward to include estimated losses to consumers and volatilization of organic compounds, components that are missing from the mangrove estimates.

Other primary producers in mangrove ecosystems include benthic micro- and macroalgae, as well as phytoplankton. Benthic purple photosynthetic bacteria, which thrive in anaerobic sediments, also contribute to ecosystem productivity (Vethanayagam, 1991), but to what degree is unknown. Algae and cyanobacteria are common epiphytes on mangrove prop roots, stems, and pneumatophores (e.g., Rodriguez and Stoner, 1990; Steinke and Naidoo, 1990; Ellison and Farnsworth, 1992; Farnsworth and Ellison, 1996; Laursen and King, 2000; Naidoo et al., 2008; see Ellison and Farnsworth (2001) for additional examples). Their contribution to overall ecosystem productivity varies with the forest setting. In areas with a dense forest canopy and little open water, the understory is shaded and the water in river and creek channels is usually highly turbid, so algal productivity is low (Alongi and Sasekumar, 1992; Robertson et al., 1992; Alongi, 1994). Phenolic compounds in the DOC leached from leaf litter may also inhibit benthic diatom growth (Alongi and Sasekumar, 1992). By contrast, in more open lagoonal settings, with expansive shallow areas of open, relatively clear water, phytoplankton and benthic algal production are substantially higher, in some locations representing roughly half of ecosystem primary productivity (Day et al., 1982; Robertson and Blaber, 1992). The standing biomass of cyanobacteria and algae growing on prop roots of *R. mangle* around the edge of a large shallow lagoon on the coast of Puerto Rico was only slightly less than the biomass of annual litterfall of mangrove leaves (Rodriguez and Stoner, 1990); assuming a realistic turnover rate of 4–5 times a year, cyanobacterial and algal productivity would substantially exceed by several fold that of the mangroves. This projection is consistent with stable isotope analyses that show cyanobacteria to be the primary carbon source for macro-infauna, shrimp, and crabs. Bouillon et al. (2002a, 2004a) described a striking counter example to the generalization that algal productivity contributes relatively little to trophic processes in mangrove stands. Their stable isotope analysis showed that local and imported algal sources were a major source of carbon for benthic invertebrate consumers in mangrove-lined creeks near the mouth of the Gautami Godavari River, on the east coast of India. Why this site exhibits this unusual pattern of resource exploitation remains to be determined.

Having established that mangrove ecosystems are highly productive, key questions are: (1) how and where does that organic matter move through mangrove food webs, and (2) does it subsidize consumer populations in adjacent habitats?

6.04.4 The Fate of Mangrove and Algal Organic Matter

Primary production either is consumed by herbivores or pathogens, or enters the pool of dead organic matter as detritus. The vast majority of past research on mangrove ecosystem dynamics has focused on the importance of mangrove detritus as a resource base for food webs, but recent studies suggest that the significance of herbivory on living leaves, flowers, stems, and propagules has been underestimated. Since herbivory may in some instances limit the amount of mangrove organic matter that enters the pool of detritus, we will start by reviewing what is known about the impact of herbivores on living mangrove biomass and then consider the dynamics of mangrove organic matter that escapes primary consumers, senesces, and falls to the forest floor. The fate of algal biomass in mangrove ecosystems has been much less studied, but from the examples presented above and others we described below, the contribution of benthic micro- and macro-algae, and phytoplankton, to

Table 1 Estimates of annual net aboveground primary productivity (ANPP) and litterfall for a variety of mangrove forest stands in the Atlantic/Caribbean/Eastern Pacific (ACEP) and Indo-West Pacific (IWP) regions

Region	*Mangrove type*	*Predominant genera*	*Ht (m)*	*ANPP*	*Litterfall (Lf)*	*Lf % of ANPP*	*Reference*
ACEP							
Dominican Republic	Fringe	*Rhizophora, Laguncularia, Avicennia* mix	24	16.80	10.20	60.71	Sherman et al., 2003
Dominican Republic	Basin	*Rhizophora, Laguncularia, Avicennia* mix	24	23.60	12.80	54.24	Sherman et al., 2003
Florida	Dwarf	*Rhizophora*	1	8.10	N/A		Ross et al., 2001
Florida	Fringe	*Rhizophora*	4	26.10	N/A		Ross et al., 2001
Mexico	Riverine	*Avicennia* (all three present)	20	24.58	12.52	50.94	Day et al., 1987
Mexico	Fringe	*Rhizophora* (all three present)	6	16.06	8.35	51.99	Day et al., 1987
Mexico	Basin	*Avicennia, Rhizophora*	6	6.95	4.96	71.37	Day et al., 1996
Mexico	Basin	*Avicennia*	4	3.99	3.07	76.94	Day et al., 1996
Mexico	Basin	*Avicennia*	6	6.12	4.10	66.99	Day et al., 1996
Guadeloupe	Scrub	*Rhizophora, Avicennia, Laguncularia mix*	?	6.10	5.77	94.59	Imbert and Rollet, 1989
Guadeloupe	Scrub	*Rhizophora, Avicennia* mix	?	6.30	3.75	59.52	Imbert and Rollet, 1989
Guadeloupe	Fringe	*Rhizophora, Avicennia, Laguncularia* mix	?	21.20	13.44	63.40	Imbert and Rollet, 1989
Guadeloupe	Upper intertidal	*Avicennia*	?	7.60	6.08	80.00	Imbert and Rollet, 1989
Guadeloupe	Upper intertidal	*Laguncularia*	?	13.10	8.79	67.10	Imbert and Rollet, 1989
IWP							
Malaysia	Upper intertidal	*Rhizophora*	21	23.64[a]	10.20	43.15	Ong et al., 1995
Malaysia	Fringe	*Rhizophora*	~30	17.70	11.00	62.15	Putz and Chan, 1986
Indonesia	Plantation	*Rhizophora*	5.9	22.30	8.25	37.00	Sukardjo and Yamada, 1992
Thailand	Fringe	*Rhizophora*	11	27.00	6.70	24.81	Christensen, 1978
Sri Lanka	Riverine	*Rhizophora*	4.5	13.00	5.52	42.46	Amarasinghe and Balasubramaniam, 1992
Sri Lanka	Riverine	*Avicennia, Rhizophora*	4.5	11.15	6.24	55.96	Amarasinghe and Balasubramaniam, 1992
Sri Lanka	Fringe	*Rhizophora*	3.9	8.75	4.41	50.40	Amarasinghe and Balasubramaniam, 1992
Sri Lanka	Fringe	*Avicennia*	3.9	5.14	3.74	72.76	Amarasinghe and Balasubramaniam, 1992
			Mean	14.33		59.32	
			Median	13.10		60.12	

[a] Carbon productivity value converted to dry mass, assuming dried wood is 50% carbon.

All studies employed the summation method of estimation, as described in the text. Litterfall and ANPP are in dry mass (Mg ha^{-1} yr^{-1}). Canopy height (Ht) is indicated, if provided in the source.

mangrove food webs can be substantial in some environmental settings.

6.04.4.1 Herbivory on Mangroves

Mangrove leaves, flowers, stems, and propagules are fed upon by a variety of insects, crabs, and mammals. For reasons discussed below, methodological issues have precluded a clear consensus concerning the magnitude of their impact on mangroves. This trophic interaction begs additional rigorous investigation.

6.04.4.1.1 Folivory

As noted earlier, it has been a long-standing dogma that mangrove leaves are little grazed by insects or other herbivores because they have high concentrations of defensive chemicals, particularly soluble tannins. In fact, a recent review of productivity estimates for mangrove forests (Komiyama et al., 2008: 135) unambiguously reiterates this view: "it may be generally argued that herbivory is not important in mangroves because of their high tannin content." However, compared to other vegetation types, there have been relatively few studies of leaf consumption rates in mangroves, and, as discussed below, most have drawn their estimates from discrete samples of standing leaf damage, a questionable method that tends to underestimate actual rates of folivory (Lowman, 1984; Coley and Barone, 1996; Burrows, 2003). Moreover, it is well known from studies of insect–plant interactions in other systems that tannins are not an absolute barrier to insect herbivory, and that numerous factors besides leaf chemistry influence rates of folivory (Bernays, 1981; Martin and Martin, 1984; Martin et al., 1987; Bernays and Graham, 1988; Bernays et al., 1989). Studies that have monitored mangrove leaf condition over time (e.g., Onuf et al., 1977; Feller, 1995; Burrows, 2003) have observed a diversity of herbivores and significant leaf damage (**Figure 6**).

Insects. Burrows (2003) reviewed published studies of insect folivory in mangroves. He compiled a list of 26 studies, most of them examining members of the widespread genera, *Avicennia* and *Rhizophora*. Several of these studies assessed damage on species of other genera as well. Of the 26 studies, 19 provide estimates of the proportion of leaf area consumed. Seventeen of the 19, including three studies that resampled the study trees multiple times, computed their estimates from measurements of standing damage in discrete samples of mature, fully flushed leaves. Such snapshot estimates do not account for disproportionate expansion of grazed holes in immature leaves due to leaf growth (e.g., Farnsworth and Ellison, 1993; but see Lowman, 1987); ignoring this confounded process, in effect, equates hole expansion with herbivory, causing an overestimation of grazing rates. On the other hand, measurement of the area missing from mature leaves does not account for leaves that are eaten completely or abscised due to damage. Comparisons of this method with estimates from leaves that are marked as buds or when first flushed and then monitored through time to maturity or disappearance found that estimates from standing mature leaves underestimated actual leaf area loss by 38–81% (Lowman, 1984; Coley and Barone, 1996; Burrows, 2003). The degree of underestimation in the 17 discrete sampling estimates cannot be determined and is likely to vary somewhat in each case. Putting this methodological problem aside, the median rate of leaf area damage among the 13 published estimates for tropical populations of *Avicennia* spp. was 7.6%, varying from 1.1% to 14.8%. Two temperate zone populations of *Avicennia marina* from New Zealand had 0.0% and 2.6% damage. Among the 23 estimates for *Rhizophora* spp., all from tropical sites, the median rate of leaf area damage was 5.0%, varying from 0.2% to 12.4%. These median values exclude two cases of extended leptidopteran grazer outbreaks discussed below. Those studies that sampled a given species from multiple sites or years, often detected substantial spatial or temporal variation (usually two- to fivefold) in leaf damage.

Figure 6 *Junonia genoveva* larva feeding on *Avicennia germinans* leaf (Punta Galeta, Panama; photo by A. Varma).

Measurements of discrete damage rates in other genera of mangrove have yielded similarly low rates of leaf area removal. Lee (1991) and Tong et al. (2006) studied insect herbivory on *Kandelia obovata* (previously *K. candel*, Rhizophoraceae) near Hong Kong. Lee (1991) observed temporal variation in standing leaf damage in his single study plot over the 21-month study, ranging from 8.1% to 12.4%, with an average of 10.3%. In their 13-month study, Tong et al. (2006) measured monthly rates of leaf area loss ranging from 2.1% to 6.5% (averaging 3.9%) at one site, and 1.6% to 3.8% (averaging 2.3%) at the other. Lacerda et al. (1986) measured a 3.2% loss of leaf area for a *Laguncularia racemosa* population on the coast of Brazil. Ditzel Faraco and Lana (2004) measured average leaf area loss to grazing by insects and the sesarmid crab, *Aratus pisonii*, of 4.3% for *L. racemosa* in a subtropical mangrove forest in SE Brazil. Their estimates of 3.2% for *Avicennia schaueriana* and 2.4% for *R. mangle* in the same site are consistent with the results from studies summarized by Burrows (2003). Menezes and Peixoto (2009) assessed standing damage by insects, crabs, and mollusks to mature leaves at a site in Sepetiba Bay in southeastern Brazil. Loss of leaf area to herbivory was 12.1%, 8.3%, and 6.2% in *L. racemosa*, *A. schaueriana*, and *R. mangle*, respectively. Again, the values for *Avicennia* and *Rhizophora* are consistent with those reported by Burrows (2003). Rates of herbivory on *Laguncularia* were higher than those measured by the earlier Brazilian studies. Finally, Kathiresan (2003) estimated herbivory from discrete damage measurements for 10 mangrove species in the Pichavarum mangroves, on the southeast coast of India. Mean leaf area damage ranged from 0.7% to 12.0%; the five species in the Rhizophoraceae averaged 1.8%, while the two members of Avicenniaceae averaged 10.7%, fitting the pattern seen in Burrows (2003) compilation of earlier studies. For these 10 species, leaf area loss was highly negatively correlated ($r = 0.91$) with concentrations of total soluble tannins.

Two of the 17 studies compiled by Burrows (2003) are particularly noteworthy for the large number of species on which folivory rates were assessed. Johnstone's (1981) study of folivory on mangroves in mixed species stands in Papua, New Guinea, is probably the earliest published measurement of insect herbivory on mangroves. Examining standing damage in samples of 25 mature leaves collected from 1 to 14 individuals of 23 different mangrove species distributed among multiple stands, his species-specific estimates of mean % area eaten ranged from 0.2% to 14.2% (averaged across sites), with a grand mean of 6.8%. The maximum eaten in a single sample from an individual plant was 18.3%. Johnstone noted that his estimates from mature leaves did not account for expansion of holes first grazed in immature leaves, due to leaf growth. On the other hand, his measurements of the area missing from mature leaves did not account for leaves that are eaten completely or abscised due to damage. Assuming a 50% underestimation of leaf area removal rates, and roughly accounting for the leaf expansion problem, the average consumption might be 12–14%, with some species experiencing as much as a 25–30% loss.

In a second multi-species study, Robertson and Duke (1987a) visually scored standing damage (% leaf area missing) on between 50–100 leaves collected from replicate trees of 25 species of mangroves in three forests near Townsville in North Queensland, Australia. The mean leaf area missing was highly variable among mangrove species, ranging from 0.8–32.4% (averaged across sites), but less so among sites (averaged across species, range of 5.1–8.8%). These estimates potentially suffer from the same methodological issues as Johnstone's, but Robertson and Duke (1987a) corrected for hole expansion using data from young expanding leaves punched with holes of known size and observed low rates of entire leaf disappearance from samples of marked newly flushed leaves of three species (*Rhizophora stylosa*: 0.0%, *Ceriops tagal*: 3.3%, and *A. marina*: 6.7%) monitored for a period of 3 months. On this basis, they concluded that their survey technique did not greatly underestimate actual rates of leaf consumption. Overall, Robertson and Duke (1987a: 6) estimated that insect folivores consumed on average only about 2.1% of leaf primary production by the dominant forest trees at their study sites, concluding that "grazing insects appear to be relatively unimportant in transferring energy and materials in mangrove forests…"

As noted earlier, these discrete estimates of damage due to folivory may not accurately measure actual rates of loss. The one study that has followed the fates of leaf buds or newly emerged leaves through to fully expanded maturity recorded substantially higher rates of leaf consumption by insects. In the most rigorous investigation of mangrove folivory to date, Burrows (2003) measured rates of leaf area consumption for *A. marina* and *R. stylosa* at two sites in North Queensland, Australia. He followed the fates of 3202 *A. marina* and 3382 *R. stylosa* marked, newly emerged leaves to maturity over a period of 4 months, visually estimating the percent of total leaf area missing. His visual estimates were highly correlated with actual removal rates measured on 25 leaves of each species using an image analysis system. *R. stylosa* suffered 7.5–13.2% leaf area loss, while 28.5–36.1% of *A. marina* leaf area was consumed. For both species, this damage fell most heavily on young leaves. In the case of *R. stylosa*, mature leaves were rarely attacked, while older leaves of *A. marina* experienced significant damage and rates of loss. By comparison, concurrent discrete sampling estimates of leaf area damage by herbivorous insects were considerably lower, by about 61–76%, than those measured from longitudinal monitoring: 3.8–4.2% for *R. stylosa* and 6.8–8.5% for *A. marina*.

Rates of loss of entire leaves to insect consumption or abortion due to insect damage were 5.0–8.3% for *R. stylosa* and 19.3–29.5% for *A. marina*; these rates are substantially higher than those observed by Robertson and Duke (1987a). Importantly, loss of leaf material through premature abscission of damaged leaves was as great as that lost to direct consumption. Loss of entire leaves to herbivory reduced leaf longevity estimates by 4–5% and 12–13% for *R. stylosa* and *A. marina*, respectively. It appears that estimates of leaf damage and loss due to insect folivores are highly method dependent and that many, if not most, estimates in the literature underestimate true values. Without additional data from studies employing the longitudinal technique for measuring rates of herbivory, it is not possible to reach a general conclusion about the impact of insect herbivores on mangrove leaf area and biomass.

Burrows (2003) also assessed the degree to which herbivorous insects damaged apical buds and tips, destroying leaves before they emerged. Such damage was most often caused by moth larvae or weevils. Destruction of leaf buds resulted in greater loss of potential leaf biomass than the damage suffered by emerged leaves. Leaf bud feeding has effects of similar magnitude in populations of *R. mangle* in Florida (Onuf et al., 1977) and Belize (Feller, 1995; Feller and Chamberlain, 2007), where the bud moth (*Ecdytolopha* sp: Olethreutidae) tunnels into and feeds in apical buds. Damage to apical buds can also lead to shoot death and loss of inflorescences. Death of apical buds, and redirection of growth to previously suppressed lateral buds, sometimes causes marked changes in tree architecture.

The most spectacular impacts of insect folivores are observed during occasional outbreaks of some lepidopteran species, often specialist feeders. These outbreaks have occurred on a variety of host mangrove species including *A. marina*, *Avicennia alba*, *Avicennia germinans*, *R. stylosa*, and *Excoecaria agallocha*. Most of these events have simply been reported in short notes (see examples cited in Burrows, 2003), but the following cases, from both the Atlantic/Caribbean/Eastern Pacific region (ACEP) and the Indo-West Pacific region (IWP), have been documented in greater detail. In Hong Kong, mass defoliation of *A. marina* by larvae of the moth, *Nephopterix syntaractis* (Lepidoptera: Pyralidae), has been frequently observed since the late 1960s and recorded annually since

1986 (Anderson and Lee, 1995). The events are strongly seasonal, beginning in April–May; caterpillar densities rise rapidly, and within 3 months, the trees are defoliated (> 75% of leaf area removed). Caterpillar densities begin to decline precipitously within 3–4 weeks of the onset of the outbreak, and flushing of new leaves rapidly regenerates the canopy. Experimental exclusion of the larvae with insecticide has demonstrated strong negative effects on leaf biomass and flower and propagule production. Duke (2002) monitored a 2-year-long outbreak of the moth, *Doratifera stenosa* (Lepidoptera: Limacodidae), in *R. stylosa* stands in central Queensland, Australia. The larvae fed in aggregations, consuming about 30–40% of canopy leaves each year.

Similar events have been documented in the ACEP. Gara et al. (1990) observed an outbreak of the bagworm, *Oiketicus kirbyi* (Lepidopetera: Psychidae), in mixed forests of *Rhizophora mangle*, *Avicennia germinans*, *Laguncularia racemosa* and *Conocarpus erectus* on the coast of Ecuador. Bagworms defoliated 1200 ha of forest in about an 8-month period. Ellison and Farnsworth (1996) observed an outbreak of larvae of the butterfly *Phocides pigmalion* (Hesperiidae) on saplings of *R. mangle* fringing small islets off the coast of Belize. Each sampled sapling had more than seven larvae, and many lost >50% of their standing leaf biomass. On the Ajuruteua Peninsula of Brazil's Amazon coast, *A. germinans* forests experience complete defoliation every 2 years due to *Hyblaea pura* (Hyblaeidae) caterpillars. The caterpillars feed exclusively on *A. germinans*, greatly decreasing litter fall. Nutrients are returned to the soil as frass rather than leaf litter (Fernandes et al., 2009). Much of the frass and associated leaf fragments are exported to the estuary with the next spring tide, and fishermen report higher shrimp catches in these moth outbreak years, apparently a consequence of the increased organic inputs to the estuary (Wolff et al., 2000). The conditions that induce these population eruptions are not known, but their occurrence runs counter to the dogma that populations of tropical species are more stable than their temperate counterparts.

A corollary of the perception that mangroves suffer little herbivory is that few species of grazers exploit them. This is certainly not the case for insects, as documented by surveys conducted in a variety of geographic locales. For example, Murphy (1990) found 102 species of insect herbivores feeding on 21 species of mangroves in Singapore, with lepidopterans and coleopterans predominating. Some of the mangrove genera such as *Avicennia* and *Sonneratia* support relatively distinctive herbivore assemblages. Farnsworth and Ellison (1991) observed over 66 species of insect folivores feeding on *R. mangle* and *A. germinans* at two study sites in Belize; the two host species supported entirely distinct assemblages of insects. Tong et al. (2006) found 24 species of insect herbivores feeding on *K. obovata* (previously *K. candel*) at two sites near Hong Kong. Five orders of insects were represented, with Lepidoptera being the primary folivores. Veenakumari et al. (1997) recorded 197 phytophagous insect species, representing 63 families and nine orders, feeding on living and dead tissues of mangroves on the Andaman and Nicobar Islands in the Bay of Bengal. Lepidoptera comprised over half the species. Eighty-seven percent of the herbivores appeared to be monophagous. Burrows (2003) documented 61 species of insects feeding on his two study species, *R. stylosa* and *A. marina*, with only four species in common between the two host plants. Clearly, the insect herbivore assemblages of mangroves are rich in species.

Crabs. Most mangrove crabs forage on the forest floor, feeding on detritus, macroalgae, living invertebrates, carrion, or diatoms and microbes in fine sediments. Some of these species will also feed on freshly released propagules (see below) and green leaves and stems of mangrove seedlings. A few of the latter species will also climb up into the vegetation at night to feed on green leaves in young trees and on the lower branches of mature trees (e.g., the sesarmid crabs, *Episesarma versicolor and E. mederi*; Sivasothi, 2000; Offenberg et al., 2004, 2006). There are four sesarmid species, however, that are arboreal in habit, rarely, if ever, coming to the forest floor. One of these, *Selatium brockii*, feeds on algae growing on tree trunks (Sivasothi, 2000), but the other three feed predominantly on fresh green leaves in the canopy. These species are *A. pisonii*, native to the ACEP (Warner, 1967), *Parasesarma* (formerly *Sesarma*) *leptosoma* of the IWP (Vannini and Ruwa, 1994; Dahdouh-Guebas et al., 1999; Emmerson et al., 2003; Emmerson and Ndenze, 2007), and *Armases elegans* of West Africa (Green (1986) as cited in Fratini et al., 2005). All three species share morphological characteristics that facilitate vertical clinging and climbing, including a flattened body, long propodi and short, sharp dactyli, and triangular carapace. *A. pisonii* and *A. elegans* are phylogenetically quite close, and the genera may be sister taxa (Fratini et al., 2005).

A. pisonii feeds primarily on green leaves of *R. mangle* (**Figure 7**), although it will consume small amounts of fresh leaf matter from other mangrove species, including *A. germinans*, *L. racemosa*, and *Pelliciera rhizophorae* (Beever et al., 1979; Erickson et al., 2003; E. Dangremond, personal observation). It occurs in mangrove swamps from Florida to Brazil on the Atlantic coast of the Americas, and on the Pacific coast, from Sonora to Peru and in Baja California. A high percentage of *R. mangle* leaves can be damaged by *A. pisonii*, but the frequency of damage varies considerably among sites. Beever et al. (1979) reported that between 4.5% and 80.6% (median = 35.3%) of the leaves at the 11 sites they monitored in southern Florida were damaged by crab grazing. On the other hand, the amount of leaf area damaged by crab grazing was fairly low, ranging from 0.4% to 7.1% (median = 2.2%) across the same sites. Using a similar sampling technique,

Figure 7 Mangrove tree crab, *Aratus pisonii*, on *Rhizophora mangle* leaf (Punta Galeta, Panama; photo by WPS).

Ditzel Faraco and Lana (2004) estimated a leaf area consumption rate of 2.2–5.4% by the combination of *A. pisonii* and insects herbivores in mangroves of Paranagua Bay, in southeastern Brazil. Both these estimates came from discrete sampling of standing damage, so may underestimate the actual impact of *A.pisonii* grazing, as discussed above for discrete estimates of insect damage. However, following the fates of marked leaves, Feller and Chamberlain (2007) measured very similar rates of leaf damage (lifetime leaf area damage of 3–10%) by herbivores on *R. mangle* at their study site on Twin Cays, Belize; they attributed the damage largely to grazing by *A. pisonii*. Though often referred to as an herbivore, *A. pisonii* is actually an opportunistic omnivore, occasionally feeding on fish and insects when available (Beever et al., 1979; Diaz and Conde, 1988; Erickson et al., 2008). Since animal tissue is higher in N content than plant matter, omnivory might allow crabs to compensate for the low leaf N found in *R. mangle* (Erickson et al., 2004). Beever et al. (1979) observed *A. pisonii* feeding on *P. pygmalion* (skipper caterpillars), *Orocharis* sp. and *Tafalisca lurida* (crickets), and *Coccotrypes* (formerly *Poecilips*) *rhizophorae* (scolytid beetles) in addition to mangrove leaves.

P. leptosoma is the only species of the Indo-Pacific region that climbs to the tops of tall mature trees (*Rhizophora mucronata*, *B. gymnorhiza*, and *C. tagal*) to feed on fresh, green leaves (Dahdouh-Guebas et al., 1999). This behavior has a distinct temporal rhythm. Crabs make two daytime forays to the canopy, one in the morning (ascend at 06:00, descend by 10:00) and another in the late afternoon/early evening (ascend at 16:00, descend by 19:00), returning to lower aerial roots of the tree (Vannini and Ruwa, 1994). Dozens, sometimes hundreds, of crabs migrate synchronously up, and then down, a tree trunk. They exhibit fidelity to a particular tree, to one or a few branches on which they feed, and to crevice refuges at the tree's base (Cannicci et al., 1996a, 1996b). A comprehensive, adaptive explanation for these migrations and their timing remains elusive. While midday high temperatures and desiccation may force crabs out of the canopy, their second descent in the evening is not explained by heat stress. That crabs only migrate in daytime, not at night, is also inconsistent with harsh abiotic conditions being the primary driver of the phenomenon. Avoidance of predators near the base of the tree may play some role, but Cannicci et al. (1996a, 1996b) observed no instances of predation on the crabs.

Monkeys. Proboscis monkeys (*Nasalis larvatus*) inhabit the mangroves of Borneo. Salter et al. (1985) identified leaves of *S. alba*, *A. alba*, *B. gymnorrhiza*, and *Rhizophora* spp. to be the most important food items in the diet of proboscis monkeys, but Yeager (1989) later examined the monkeys' diets in more detail and found a broad diet of at least 55 plant species, many of which were not mangrove plants. Proboscis monkeys are not restricted to mangroves, but use a wide variety of habitat types including riparian forests and tend to prefer higher forests where available (Salter et al., 1985).

Because of the high salt content of mangrove leaves, buds, and flowers, animals that are not adapted to live in mangroves have to alter their behavior to deal with salt when they are using mangroves for food. In Zanzibar, a population of red colobus monkeys (*Procolobus kirkii*) that live exclusively in a *R. mucronata* forest adopted the behavior of frequent water drinking. These monkeys feed on leaves of *R. mucronata*, *S. alba*, and *A. marina*. *Rhizophora* leaves have higher tannin contents than *Avicennia*, and for this reason monkeys often avoid eating the midribs of mature *Rhizophora* leaves (Nowak, 2008).

Manatees. In a review of the foods and feeding habits of wild and captive Sirenia, Best (1981) summarized evidence that in estuarine environments of Suriname and Brazil, the West Indian manatee (*Trichechus manatus*) consumes the young shoots and leaves of *Avicennia nitida*, *R. mangle*, and *L. racemosa*. They have also been observed feeding on *R. mangle* in Senegal. In French Guiana, mangrove estuaries are the main habitat of *T. manatus*, where they browse shoreline vegetation including *R. mangle* leaves, in addition to consuming other aquatic plants (de Thoisy et al., 2003; Spiegelberger and Ganslosser, 2005). Manatees also consume *R. mangle* leaves in shallow mangrove lagoons in Florida (E. Dangremond, personal observation). The degree to which mangrove leaves contribute to manatee diets or sustenance is not known.

Leaf characteristics and folivory. A variety of leaf characteristics influence the vulnerability of mangrove leaves to herbivores, including their chemical composition (e.g., secondary defensive compounds, nutrients, and salts), toughness, and water content. These characteristics vary among species, between populations of a given species growing in different locations, and ontogenetically as leaves mature (Coley, 1983; Lacerda et al., 1986; Smith, 1987a; McKee, 1995a; Coley and Barone, 1996; Burrows, 2003). The relationship between these leaf characteristics and rates of herbivory on mangrove leaves is not well understood. As noted above, newly flushed leaves generally suffer higher rates of herbivory. These young leaves are less tough, have higher water content, and higher nitrogen concentrations (lower C/N ratios) than mature, fully expanded leaves, all of which would make them more palatable, nutritious, and attractive to herbivores. Young, expanding leaves of tropical rainforest trees typically have higher concentrations of phenolic or other secondary compounds than older leaves (Coley and Barone, 1996), but levels of these compounds do not necessarily correlate with rates of herbivory (Coley, 1983). We know of no studies that have compared concentrations of secondary chemical compounds in living mangrove leaves of differing age and degree of expansion. As discussed below, detritus-feeding crustaceans often, but not always, avoid recently abscised senescent leaves, which contain higher concentrations of tannins than leaves in a more advanced state of decay.

There have been insufficient comparative studies of herbivory on mangrove species that differ in leaf chemical and physical characteristics to isolate the key features that determine herbivore preferences. However, supplementation of nutrient availability from natural sources (bird rookeries) or experimental manipulations has been shown to enhance the nutritional quality of *R. mangle* leaves and new shoots, and increase the rates of herbivory by some insect herbivores (e.g., the bud moth *Ecdytolopha* sp. and the leaf mining moths, *Marmara* spp. (Gracilariidae)), but not others (Onuf et al., 1977; Feller, 1995; Feller and Chamberlain, 2007). On the other hand, Farnsworth and Ellison (1991) did not detect a difference in rates of herbivory between mangroves used as a bird rookery and other nonenriched stands.

A clear example of a mechanical morphological defense against insect herbivores is seen in buttonwood (aka grey mangrove), *Conocarpus erectus*, a high intertidal or semi-terrestrial

ACEP species. It exists in two morphs, one with pubescent silver leaves and the other with nearly glabrous green leaves (with some intermediates). The silver morph has dense, tiny, hair-like structures called 'trichomes' on its leaf surfaces and suffers less insect herbivory than the green glabrous morph (Schoener, 1987, 1988; Spiller and Agrawal, 2003; Agrawal and Spiller, 2004). In an archipelago of small islands in the Bahamas, the silver form is more common on larger islands where insect herbivores are more abundant, and is less common on islands with dense populations of entomophagous *Anolis* lizards, compared to islands lacking lizards (Schoener, 1987, 1988). Following severe hurricane defoliation, resprouting foliage of the silver morph is nonpubescent and suffers heavy insect grazing as a result; within a year, these plants regenerate pubescent leaves (Spiller and Agrawal, 2003; Agrawal and Spiller, 2004). *Conocarpus* has extrafloral nectaries on its petioles, which attract ant mutualists that prey on insect herbivores. The silver morph produces few and smaller extrafloral nectaries than the green morph and attracts fewer ants; experimental exclusion of ants resulted in higher herbivory on green leaves, but no change in the damage to silver leaves (Piovia-Scott, 2011a, 2011b). Thus, the value of the mutualism varies with the level of plant investment in morphological defense.

6.04.4.1.2 Leaf galling

Leaf galling midges (Diptera: Cecidomyiidae) are common on *Avicennia* in both the ACEP and the IWP. In a mangrove forest in northeast Brazil, the rate of attack by these leaf gallers on *A. germinans* increases as interstitial soil salinity increases. Though *Avicennia* has a higher salinity tolerance than other co-occurring mangrove species (e.g., *R. mangle* and *L. racemosa*), it becomes stressed in hypersaline environments and is more vulnerable to insect attack (Gonçalves-Alvim et al., 2001). Burrows (2003) found 10 species of cecidomyiid gall midges on *A. marina* at two sites in northern Queensland, Australia, but this group was entirely absent from *R. stylosa* leaves. Galls are rare on *Rhizophora* spp. worldwide (Burrows, 2003). Similarly, Murphy (1990) reported that *Avicennia* spp. are frequently galled by mites and cecidomyiid flies in Singapore, but described no examples of galling on *Rhizophora* spp.

The gall-inducing mite, *Brachendus enodis* (Acari: Eriophyidae), attacks *L. racemosa* on the central Brazilian coast (Santos-Mendonça et al., 2009). Leaves with galls were found to have higher concentrations of phenols than ungalled leaves. Rates of folivory by a grasshopper and caterpillar were lower on galled leaves, suggesting that galling induces secondary chemicals that deter other phytophagous insects.

6.04.4.1.3 Stem boring

In Belize's Twin Cays mangroves, at least 35 species of wood-eating (xylophagous) beetles and moths have been found on *R. mangle, A. germinans*, and *L. racemosa* (Feller and Mathis, 1997; Rützler and Feller, 1999). Their effects on the forest canopy can be substantial; for example, the wood-boring cerambycid beetle, *Elaphidion mimeticum*, kills *R. mangle* branches, opening small gaps, averaging 12 m^2, in forest canopy (Feller and McKee, 1999). These gaps comprise approximately 22% of the canopy in fringing stands on small mangrove islands off the coast of Belize, and increase light availability and soil temperature on the forest floor. Probably as a consequence, mangrove seedlings have higher survival rates in these areas than under the adjacent closed canopy. In a more comprehensive examination of the impact of this borer and a co-occurring congener, Feller (2002) determined that the girdling, pruning, and hollowing activities of these beetles killed over 50% of the fringe *R. mangle* canopy. Tree canopy architecture is changed as a result, and branches that are girdled by beetle tunneling produce more flowers and propagules. Green-leaf litterfall increases as branches are killed. Burrows (2003) also noted the significant mortality of twigs and branches caused by wood-boring cerambycids feeding on *R. stylosa* in Queensland, Australia.

Veenakumari et al. (1997) reported a large proportion of borers among the mangrove insects of the Andaman and Nicobar Islands in the Bay of Bengal. The same is true for the phytophagous mangrove insects of Singapore (Murphy, 1990). One unusual example is the chrysomelid beetle *Monolepta aff. bicavipennis*, which bores into *A. alba* pneumatophores, forming galleries that are protected from seawater flooding by accumulated frass.

Other borers that have a potentially large effect on forest structure are marine isopods and scolytid beetles. The isopods bore into the tips of young *R. mangle* prop roots below the water line, while the beetle does so to emergent roots. Surveys by Simberloff et al. (1978) at sites in southeast Florida, the Florida Keys, and the Pacific coast of Costa Rica found that between 23% and 86% of the submerged root tips had been attacked by isopods (*Sphaeroma terebrans* and *Limnoria* sp.). While some roots are killed, many adventitiously branch at the site of damage, increasing the overall number of viable root tips. Perry (1988) and Perry and Brusca (1989), also worked on the Pacific coast of Costa Rica, where they observed a strong negative impact of boring by the isopod *Sphaeroma peruvianum* on the growth of *R. mangle* aerial roots: 50% reduction in growth rate and a 62% loss of net root production. However, as observed by Simberloff et al. (1978), isopod damage did induce branching, resulting in a 35% increase in new root tips. A more recent study by Brooks and Bell (2001, 2002, 2005) found that isopods occupied, on average, 60% (range: 25–86%) of the intertidal aerial roots of *R. mangle* across eight sites in Upper Tampa Bay, Florida. As in earlier studies, they observed that prop roots commonly branch in response to isopod damage; however, repair of the damage by tissue in-growth, without new root initiation, was a more frequent outcome in their study sites. Simberloff et al. (1978) and others have hypothesized that this enhancement of both the number and the spatial spread of prop roots stabilizes the tree, making it less vulnerable to falling over in storms or high flow, and could accelerate mangrove island growth.

High rates of prop root boring by isopods (primarily *Phycolimnoria clarkae*) have also been observed in *R. mangle* in Belize (Ellison and Farnsworth, 1990, 1996). Depending on the site and time of sampling, between 21% and 38% of the aerial roots were attacked by isopods, closely tracking temporal patterns of new root production. Such attacks greatly decreased rates of root elongation. In these study sites, however, there was no evidence that isopod damage had a stimulatory effect on prop root branching.

Boring by the scolytid beetle *Coccotrypes* (formerly *Poecilips*) *rhizophorae* (**Figure 8**) and other insects into the distal ends of young prop roots above the waterline has much the same effect

Figure 8 Stem-boring scolytid beetle, *Coccotrypes rhizophorae* (Punta Galeta, Panama; photo by A. Varma).

as isopod attack (Simberloff et al., 1978). This damage also induces branching of the root, with a net increase in the number of living root tips that grow down into the water. Murphy (1990) observed the same effect of *C. rhizophorae* boring on prop root branching by *Rhizophora* spp. in Singapore. As described below, *C. rhizophorae* is also a very important propagule and seedling predator in Neotropical mangrove forests, as is its congener, *C. fallax*, in the IWP.

6.04.4.1.4 Leaf mining

In Belize, fringe and dwarf red mangrove hosts four undescribed species of microlepidopterans (*Marmara* spp., Gracilariidae). One mines in leaves, one in shoot periderm, one in propagule periderm, and one in aerial root periderm (Feller, 1995). Plant nutrient status can strongly affect their population density. In a fertilization experiment conducted in dwarf *R. mangle* stands on Twin Cays, Belize, the shoot periderm feeder infested 100% of the P and NPK fertilized plants, but none of the N fertilized or control plants. *R. mangle* is P limited at this site; the addition of this nutrient enhanced plant growth, while also increasing rates of leaf miner attack.

Murphy (1990) reported numerous leaf-mining species from Singapore mangroves. The leaf-mining moth, *Phyllocnistis* (Gracillariidae), regularly attacks all species of *Avicennia*. Burrows (2003) found three leaf-mining species in *A. marina* and seven species in *R. stylosa* in Queensland, Australia. By contrast, Veenakumari et al. (1997) found only six species in their survey of the 16 species of mangroves on the Andaman and Nicobar Islands in the Bay of Bengal.

6.04.4.1.5 Sap feeding

Sap feeding is a less conspicuous, but common mode of herbivory in mangroves. A diverse array of hemipterans feed on leaf or stem sap (Burrows, 2003). Scale insects (Diaspididae) and planthoppers (Flatidae) are particularly common sap feeders on *R. stylosa* and *A. marina* in Queensland, Australia (Burrows, 2003). Psyllids (Psyllidae) have been reported from *Sonneratia* in the Andaman and Nicobar Islands (Veenakumari et al., 1997) and Southeast Asia (Burckhardt, 1991). Considerable leaf area loss (37%) is caused by psyllids (*Telmasylla* sp.: Calophyidae and *Leuronota* sp.: Triozidae) that attack and gall expanding leaves of *A. germinans* on Twin Cays, Belize (Feller et al., 2007). On the Caribbean coast of Panama, psyllids (*Limbopsylla laguncularia*e: Psyllidae) commonly infest seedlings of *L. racemosa*, and appear to be a contributing factor to high rates of first-year mortality (W. Sousa, personal observation). The scale insect *Aulacaspis marina* (Diaspididae) is a serious pest that attacks and kills large numbers of *R. mucronata* seedlings planted in reforestation projects in Indonesia (Ozaki et al., 1999).

A survey of host records from around the world indicates 20 sap-feeding insect species from *Avicennia* spp. and 21 from *Rhizophora* spp. (Burrows, 2003). However, studies of local assemblages find far fewer species on *Avicennia* than on *Rhizophora* (Murphy, 1990; Veenakumari et al., 1997; Burrows, 2003). This difference has been attributed to the deterrent effect of excreted salt on the surface of *Avicennia* leaves (Murphy, 1990: 125).

6.04.4.1.6 Florivory

Herbivores damage flowers in addition to leaves. *A. pisonii* eats buds and flowers of *R. mangle* in Belize (Farnsworth and Ellison, 1991). Larvae of a phycitine moth (Pyralidae) consumed 15.6–35.1% of *A. marina* flower buds at three sites in subtropical southeastern Australia (Clarke, 1992). Murphy (1990) described numerous examples of moth larvae and larval and adult beetles feeding on the flower buds of *Avicennia* spp. and other genera in the mangrove forests of Singapore.

In mangroves of southeastern Brazil, the crab *Armases angustipes* (Grapsidae) feeds on flowers of the epiphytic bromeliad *Aechmea pectinata*. This species of bromeliad is pollinated by three different hummingbird species: *Thalurania glaucopis*, *Amazilia fimbriata*, and *Ramphodon naevius* (Trochilidae). The presence of a crab on an inflorescence of *A. pectinata* decreases hummingbird visits, and as a result fewer inflorescences set fruit (Canela and Sazima, 2003).

Mites are another type of florivore in mangroves, though very little is known about their ecology or their effects on the reproductive success of trees that they inhabit. Seeman and Walter (1995) found the ameroseiid mite *Afrocypholaelaps africma* eating the nectar and pollen of *Aegiceras cornicuiatum* in northern Queensland. These mites are sometimes packed into pollen baskets of the honeybee *Apis mellifera* and may incidentally become a nutritional supplement for the bees. Otherwise, female mites carrying eggs use the bees as phoretic carriers, dispersing from flower to flower. Other consumers of flower products include bats, birds, moths, butterflies, bees, wasps, flies, and other small insects. Many of these visitors are drinking nectar from the flowers and may serve as pollinators (e.g., Tomlinson et al., 1979; Kondo et al., 1987, 1991; Clarke and Myerscough, 1991; Noske, 1993, Sun et al., 1998; Ge and Sun, 1999; Raju et al., 2006; Raju and Karyamsetty, 2008; Jonathan and Raju, 2009). However, mangrove pollination syndromes are mostly inferred from floral morphology; there are few detailed studies of the pollination biology and breeding systems of mangroves (Tomlinson, 1986).

6.04.4.1.7 Propagule predation

Predispersal. Mangrove propagules are attacked by herbivorous insects while they are still developing on the parent tree and after they have dropped to the forest floor. Predispersal insect propagule predators are predominantly moth and fly larvae, and adult and larval beetles; their rates of infestation can be quite high. The phenomenon has been observed in mangroves around the world and varies in magnitude among species and sites (Farnsworth and Ellison, 1997a). Several intensive studies have quantified attack rates for IWP mangroves. Robertson et al. (1990) measured rates of predispersal predation for 12 species of mangroves across 12 sites in tropical Queensland, Australia. Between 2.1% and 92.7% of a species' propagules had been attacked at a site; for six species (*A. marina*, *B. gymnorrhiza*, *B. parviflora*, *Heritiera littoralis*, *Xylocarpus australasicus*, and *X. granatum*), rates of insect attack on propagules exceeded 40% at all sampled locations. Clarke (1992) quantified insect damage to mature *A. marina* propagules at 15 sites spread over a wide latitudinal range from Victoria to southern Queensland along the east coast of Australia. The larva of a phycitine moth (Pyralidae) was the predominant predispersal predator. Rates of attack varied greatly among sites (10.1–62.5%), with no clear latitudinal pattern. The median rate of 21.1% was lower than Robertson et al. (1990) measured in their more northern tropical sites (59.1–64.8% attacked). In a forest near Clarke's Sydney site, Minchinton and Dalby-Ball (2001) quantified damage to *A. marina* propagules by larvae of the mangrove fruit fly *Euphranta marina* (Tephritidae) and the mangrove plume moth *Cenoloba obliteralis* (Tineodidae). They found that 53% of the propagules in the tree, 69% of abscised propagules, and 80% of the cotyledons of newly established seedlings had been attacked by these insects. Krauss and Allen (2003) observed that 93% of *B. gymnorrhiza* propagules at a site on the island of Kosrae, Federated States of Micronesia, had been attacked by insect borers.

Fewer studies of predispersal propagule predation have been conducted in the ACEP. Over the course of the fruiting season, Onuf et al. (1977) monitored rates of infestation of *R. mangle* propagules by the scolytid beetle, *C. rhizophorae*, in two fringing stands on the Atlantic coast of Florida, USA (also see Devlin, 2004). These stands differed in the level of nutrient input from guano produced by roosting birds. The percentage of propagules infested with beetles increased over the period of observation (June–October), reaching 100% at the high-nutrient site and 43.2% at the low-nutrient site. Farnsworth and Ellison (1997a) recorded attack rates of 3.2–64.3% of marked *R. mangle* propagules at various times throughout the year at three study sites. The agents of damage were unspecified. Damaged propagules were more likely to prematurely abscise than undamaged ones (40.5% and 27.6%, respectively). Sousa et al. (2003) examined insect damage in freshly released propagules of *A. germinans*, *L. racemosa*, and *R. mangle* at a site on the Caribbean coast of Panama. Rates of predispersal insect attack on *A. germinans* propagules ranged from 46.7% to 100.0% (median = 90.0%) for collections from individual trees. *L. racemosa* propagules were attacked at lower rates than *Avicennia*; per tree rates ranged from 3.3% to 56.7% (median = 33.3%). *A. germinans* propagules were fed on by larvae of a weevil (*Stenobaris* sp., Curculionidae), pyralid moth (Pyralidae), and agromyzid fly (*Phytoliriomyza* sp., Agromyzidae), which often burrowed into and fed extensively throughout the fleshy cotyledons, sometimes damaging the embryonic axis. *L. racemosa* propagules were attacked by larvae of a noctuid moth (Noctuidae), which bore through the cork-like seed coat to feed on the developing tissues. Only the scolytid beetle, *C. rhizophorae*, was observed to feed on *R. mangle* propagules prior to their release from the parent tree. Rates of attack were 20.9% and 22.1% in samples collected in two successive years. Mated female beetles burrow through the epidermis of the hypocotyl and lay clusters of eggs in the cortex and central pith. Upon hatching, the larvae greatly extend and enlarge the parental tunnel, as they rapidly mature; persistent infestations consume much of the interior of the propagule (**Figure 9**).

Figure 9 *Rhizophora mangle* propagules damaged by the scolytid beetle, *Coccotrypes rhizophorae* (Punta Galeta, Panama; photo by WPS). Propagules have been cut open to reveal galleries created by beetle feeding. Developing larvae can be seen in the larger cavities.

The extent of damage to propagule tissues varies with the species of mangrove and insect predator. The consequence of this damage for propagule survival, establishment as a seedling, and seedling growth also varies (Sousa et al., 2003). For some species of mangrove, the impact on propagules is all or none; attacks that penetrate the outer layers of the propagule inevitably kill the embryo by destroying vital meristematic or conductive tissues. For most species, however, the effects are more graded, depending on the extent of the damage. In these cases, while extensive loss of tissue may kill a propagule or prevent it from rooting, damage is more typically sublethal, causing only partial loss of cotyledonary, cortical, or pith tissue. The partially consumed propagule can still develop into a rooted seedling. In this case, the loss of tissue may lead to reduced seedling growth (Robertson et al., 1990; Minchinton and Dalby-Ball, 2001; Sousa et al., 2003), with the magnitude of lost growth correlated with the degree of tissue damage. However, in some cases there is apparently no measurable effect on establishment or seedling performance (Robertson et al., 1990; Krauss and Allen, 2003).

Neither birds nor bats are known to feed on mangrove propagules. Frugivorous bats that are observed in mangroves are likely using them as a corridor for movement between

Figure 10 The grapsid crab, *Goniopsis cruentata*, feeding on a dispersing *Rhizophora mangle* propagule (Punta Galeta, Panama; photo by A. Varma).

Figure 11 The ocypodid crab, *Ucides cordatus*, is the major detritivore and propagule predator in low intertidal ACEP forests (Punta Galeta, Panama; photo by I Herriott).

patches of upland terra firma forest, where attractive, nutritious fruit is plentiful (Andrade et al., 2008).

Postdispersal. In addition to feeding on living and decaying leaves (see below), crabs are voracious consumers of dispersing mangrove propagules (**Figure 10**). Following in the footsteps of Smith's (1987a, 1987b) pioneering experimental study of patterns of propagule predation by crabs on the shores of Missionary Bay, Hinchinbrook Island in Queensland, Australia, there have been dozens of studies employing some variant of his tethering method for measuring rates of postdispersal, crab predation on mangrove propagules. Allen et al. (2003) compiled a list of 16 such studies (including Smith's) investigating a total of 20 mangrove species in numerous locations around the world. Our search of the more recent literature on mangroves revealed no additional studies of this type. The length of time that tethered propagules were monitored varied widely among these 16 studies, ranging from 4 to 90 days, making it difficult to standardize rates of consumption for comparison. As expected, cumulative predation rates do increase significantly with the length of monitoring ($r = 0.442$, $P < 0.001$). Unstandardized cumulative rates of removal ranged from near zero to 100%, with a median of 57.7% for a median monitoring period of 18 days. This wide range in propagule predation rates is not surprising given all the potential sources of variation among these studies, including species of mangrove, species of herbivorous crabs, geographic location, hydrological and geomorphic settings, tidal height, season, tethering technique and duration, and many other factors. Nonetheless, more than half the studies measured propagule consumption rates exceeding 50% in less than 3 weeks, demonstrating a substantial impact of herbivorous crabs on the pool of dispersing diaspores. Several other common patterns emerge. Predation rates can vary spatially along the tidal gradient, often reflecting a corresponding gradient in the density and species composition of crabs. For example, Sousa and Mitchell (1999) found that, over a 28-day period, crabs consumed 33.6% of propagules tethered in low intertidal, mixed *R. mangle*/*L. racemosa* stands, but only 4.8% of those tethered in high intertidal *A. germinans* stands. The key difference was in the crab assemblages that characterized the two stand types. In the low intertidal zone, there are dense populations of the herbivorous crabs, *Ucides cordatus cordatus* (**Figure 11**) and *Goniopsis cruentata* (**Figure 10**); in the upper intertidal, these crabs are rare and deposit-feeding fiddler crabs, *Uca* spp. (**Figure 12**), predominate. Other studies have documented spatial variation in crab predation along the tidal gradient, but the patterns are idiosyncratic, tied to local tidal patterns, geomorphology, and crab distributions (e.g., Smith, 1987a, 1987b; Smith et al., 1989; Osborne and Smith, 1990; McKee, 1995b; McGuinness, 1997; Clarke and Kerrigan, 2002). Crabs

Figure 12 Fiddler crabs, *Uca* spp., are major deposit-feeders in ACEP mangrove forests (Punta Galeta, Panama; photo by A. Varma).

generally exhibit preferences for certain species of propagules over others. For example, when *Avicennia* propagules are available, they are generally preferred to the propagules of other species. Presumably, this is because *Avicennia* propagules are largely comprised of fleshy, easily consumed cotyledons, which are relatively rich in nitrogen and simple sugars, and low in fiber, total phenolics, gallotannins, and condensed tannins (Smith, 1987a; McKee, 1995b). By contrast, propagules of species in Rhizophoraceae, which are less preferred by herbivorous crabs, are hard, fibrous, and have high tannin content.

Smith (1987a, 1988, 1992) and co-workers (Smith et al., 1989) proposed that spatial variation in the intensity of this differential propagule predation might be sufficient to explain the zonation of mangrove species along the tidal gradient. In a number of instances, they observed that a species suffered higher rates of predation in forest stands where conspecifics were rare or absent, and survived better where conspecifics dominated the canopy. These observations inspired the general hypothesis, referred to as the dominance-predation model (Smith et al., 1989), that selective crab predation maintains characteristic patterns of mangrove tree zonation by preventing, or greatly reducing, the establishment of certain species' seedlings at particular tidal elevations. Subsequent investigations in a variety of locales have found that while patterns of predation on propagules of *Avicennia* spp. are sometimes consistent with the model, the tidal distributions of most other species are not explained by the predicted inverse relationship between propagule predation rates and representation in the forest canopy (McKee, 1995b; Dahdouh-Guebas et al., 1998; McGuinness, 1997; Sousa and Mitchell, 1999; Clarke and Kerrigan, 2002). In a number of instances, propagules of a given species suffer highest predation in areas where adults are most abundant in the canopy. Nevertheless, crabs account for a large proportion of propagule and young seedling mortality, and thereby influence patterns and rates of forest regeneration.

Insect larvae that initially established in propagules predispersal may continue to consume tissue as the propagules disperse and develop into rooted seedlings (Minchinton and Dalby-Ball, 2001; Minchinton, 2006), and fresh attacks on propagules and developing seedlings occur on the forest floor. Snails have also been observed to feed on dispersing propagules (Smith et al., 1989; McKee, 1995b; Slim et al., 1997; Dahdouh-Guebas et al., 1998; Fratini et al., 2001).

6.04.4.2 Detritivory and Decomposition in Mangroves

Living mangrove biomass that is not consumed by herbivores or pathogens eventually dies and falls to the forest floor, where it becomes available to detritivores and decomposers. Litterfall represents a large proportion of the mangrove ANPP; for the studies in **Table 1**, it ranges from 24.8% to 94.6% (median of 60.1%). Leaves are the dominant component of this litter. Tracing the pathways by which this organic matter is consumed or stored in mangroves and adjacent habitats has been the focus of much of the research in this ecosystem since the mid-1970s.

6.04.4.2.1 Outwelling hypothesis

A long-standing paradigm concerning the fate of mangrove productivity is the 'outwelling hypothesis'. The origins of this idea can be found in early mass balance models of energy budgets for salt-marsh ecosystems in the southeastern US (e.g., Teal, 1962), which indicated substantial export of organic detritus to adjacent estuaries, where it was thought to support dense populations of detritivores, and secondary and tertiary consumers, in turn. The concept was formalized and the moniker outwelling coined by Odum (1968); for a historical perspective on the concept and a consideration of early evidence pro and con (see Odum (1980, 2000); also Nixon, 1980; Childers et al., 2000). While Golley et al.,'s (1962) study of the ecological metabolism of a fringing *R. mangle* stand in Puerto Rico was the first to quantify net export of mangrove-derived organic matter to nearshore waters, it was Odum and Heald's (1972, 1975) detailed study of the trophic interactions in the *R. mangle*-dominated North River Basin estuary on the southwest coast of Florida that most clearly detailed the outwelling process as it might apply to mangrove ecosystems. This particular site is heavily forested with limited expanses of open water, so benthic algae and phytoplankton were sparse, making mangrove leaf litter the primary source of organic carbon. Odum and Heald (1975) observed that when mangrove leaves fall to the forest floor, they are colonized, decomposed, and C- and N-enriched by bacteria, fungi, and protozoa. Resident detritivores and omnivores feed on the decaying leaves, further fragmenting them into fine particles. Odum and Heald (1975) estimated from field measurements that about half the detrital material produced in the forested basin was exported as suspended particles in ebbing tidal flow to surrounding bays and inshore waters, where they postulated that it fueled detritus-based food chains. Consistent with this dynamic, they found that "more than 20 percent of the material contained in the digestive tracts of all of the organisms classified as herbivores and omnivores was detritus of a vascular plant origin, usually mangrove leaf" (Odum and Heald, 1975: 273). According to the outwelling scenario, detritivores and omnivores would in turn be eaten by lower carnivores, with carbon of detrital origin eventually being assimilated into higher carnivores at the top of the food chain. The carbon from ingested detritus that does not make its way into higher trophic levels is recycled as fecal pellets that are consumed by benthic deposit or filter feeders. While Odum and Heald (1972, 1975) did not systematically quantify dissolved organic matter, the few samples they took showed high concentrations in outflowing water, indicating yet another form of outwelled mangrove carbon.

The outwelling of mangrove carbon to estuaries and coastal waters, where it subsidizes or maintains detritus-based food webs, was an appealingly intuitive concept, and provided a powerful argument for conserving mangrove habitats. That such detrital material might constitute an essential food resource for commercially important crustacean or fish populations (e.g. Turner, 1977) made the idea even more compelling. However, for nearly two decades following Odum and Heald's presentation of the idea, supporting evidence remained largely circumstantial (Lee, 1995), and examples came to light of mangrove systems that exhibited little net export of carbon and, in some cases, a net influx of carbon was observed. Moreover, studies began to reveal important missing components of the mangrove carbon dynamics story, namely, the large contribution of DOC to the total exported, the retention of nutrients and organic matter in porewater and their movement in groundwater flow, and the key role of crabs and other burrowing species in retaining detrital carbon within stands by consuming or burying it *in situ*.

The first step in testing the outwelling hypothesis is to measure or estimate the net movement of nutrients and organic detritus derived from mangroves. Early efforts to make such assessments either (1) directly sampled the particulate and dissolved organic matter being transported in flow out of, or into, a forest stand, or (2) estimated the net flux of organic matter using mass balance models. In the latter approach, production and consumption budgets are calculated, and imbalances are attributed to the import or export of material (Dame et al., 1986). Direct field measurements of the flux of organic matter are challenging due to the high spatial and temporal heterogeneity of these tidal systems, and the open nature of the habitat. The rigor of the sampling protocols and validity of extrapolated estimates are suspect in some cases (see Twilley (1985) for discussion).

Examination of the body of published direct measurements and mass balance estimates of carbon flux indicates that outwelling of mangrove organic matter occurs in most tidally inundated and riverine forests, but the degree varies substantially among sites, seasons, and years (Twilley, 1988; Lee, 1995). That said, outwelling is not a universal feature of mangrove habitats. Areas with restricted flow or infrequent tidal inundation may be net importers of organic matter or accumulate much of their litter fall, which is then processed by decomposers and detritivores *in situ* (e.g., Twilley, 1985; Twilley et al., 1986; Lee, 1990; Wolff et al., 2000). The role of geomorphology and hydrological regime in dictating the degree of outwelling exhibited by a particular site has become a common theme in discussions of the phenomenon (Odum et al., 1979; Odum, 1980, 2000; Twilley, 1985, 1988, 1995; Twilley et al., 1986; Lee, 1990). As Lee (1990: 461) puts it: "The precise role of the coastal wetland as a net importer or exporter of organic matter depends on the geomorphology of the habitat and the prevalent hydrology." Twilley and colleagues' (Twilley, 1985; Twilley et al., 1986) detailed studies of the exchange of organic carbon in two *A. germinans*-dominated basin mangrove forests in the Rookery Bay estuary of Southwest Florida provided a clear example of how topography and hydrology control the export of carbon and nutrients. These inland forests are separated from fringing stands by a raised berm, which allows only higher tides to enter the basin. Careful monitoring of the tidal regime and carbon fluxes revealed that 75% of exported carbon was in the dissolved form (DOC), derived from rapid leaching of carbon from *Avicennia* leaf litter submerged in the standing water that remained on the floor of the basin for two-thirds of the year. Export peaked during ebbing tides and following heavy rainfall events, and these processes jointly drove a seasonal cycle of export, which was highest in August–September, when nearly 46% of total export took place. Cumulative tidal amplitude each month was the best predictor of net export. Subsurface seepage of carbon also occurred, but at about a quarter the rate of surface export.

By comparison, fringe and riverine forests, which are regularly flushed by tides and river flow, have been shown to export substantially greater amounts of mangrove-derived, particulate carbon than basin forests (e.g., Heald, 1971; Boto and Bunt, 1981; Twilley, 1985, 1988; Twilley et al., 1997). Moreover, leaf litter production itself increases with the hydrologic energy of the site: riverine > fringe > basin > scrub/dwarf (Pool et al., 1975; Twilley et al., 1986; Twilley, 1988). The mechanism accounting for this relationship seems to be that higher water motion and more frequent porewater exchange increase soil aeration and nutrient supply, which together enhance leaf and, in turn, litter production. The influx of organically rich silts and clays further augments this productivity in riverine sites. By contrast, interior and higher intertidal sites, which experience little tidal or river inundation, are relatively unproductive due to high soil salinity, low nutrients, and other stressors, such as anoxia and associated hydrogen sulfide. Soil salinity and hydrogen sulfide concentrations tend to be inversely related to hydrologic energy (i.e., tidal flux or river flow). Therefore, it is the combination of the greater volume and frequency of inundation by tides and river water and the higher production of litter that result in fringe and riverine mangroves being greater sources of outwelled carbon and nutrients than more interior basin or scrub/dwarf forests. High temporal variation in the export of particulate and DOC and nutrients is also characteristic of these systems. Large pulses of outwelling are associated with spring tides and storm runoff (Twilley, 1985, 1988; Wolff et al., 2000; Schories et al., 2003).

6.04.4.2.2 Retention and recyling of carbon and nitrogen by detritivores and deposit feeders

The seaward transport of organic material by tides, river flow, and runoff is only one component of the processes that determine the degree of outwelling. Local, within-forest consumption, decomposition, and storage are key processes determining how much litter is available for export.

Detritus-feeding crustaceans. Summarizing data from the following studies, an average of 57% (range: 9–100%, median: 54.5%) of the annual biomass of leaves, propagules, and other fine litter that falls to the forest floor is consumed or buried by crabs (e.g., Leh and Sasekumar, 1985; Robertson, 1986; Lee, 1989; Robertson and Daniel, 1989b; Emmerson and McGwynne, 1992; Robertson et al., 1992; Micheli, 1993b; Steinke et al., 1993b; Slim et al., 1997; Twilley et al., 1997; Dahdouh-Guebas et al., 1998; Lee, 1998; Middleton and McKee, 2001; Ólafsson et al., 2002; Schories et al., 2003; Nordhaus et al., 2006; Chen and Ye, 2008; Kristensen, 2008; Thongtham et al., 2008). These rates vary among species of mangrove, among sites with different crab assemblages, with tidal height and geographic location, as well as other factors. Crabs of the family Sesarmidae (Grapsoidea) are the primary consumers of leaf litter in the IWP; genera include *Sesarma*, *Neosarmatium*, *Perisesarma*, *Parasesarma*, *Neoepisesarma*, and *Chiromantes*. *U. cordatus cordatus*, *Ucides cordatus occidentalis* (Ocypodoidea: Ucididae; **Figure 11**), and *G. cruentata* (Grapsoidea: Grapsidae; **Figure 10**) are the important litter consumers in the ACEP. This processing of litter by crabs conserves and recycles carbon and nitrogen within local stands, a factor that was overlooked in early models of mangrove carbon dynamics. Crabs consume about half the litter while foraging on the soil surface, and then drag the rest into their burrows, where it undergoes further leaching of tannins and decomposition (Kristensen, 2008), and additional consumption. As they feed on the decaying leaves, crabs shred and macerate them. Some of the fragments drop to the forest floor, but the ingested material passes through the crab's gut and is returned to the environment as partially digested fecal pellets. When feeding on decaying leaves, sesarmid and ocypodid crabs have a carbon assimilation efficiency of about 40–79%, so the pellets contain a considerable amount of organic material that can be exploited by smaller detritivores, deposit feeders, and decomposers (Giddins et al., 1986; Neilson and Richards, 1989; Lee, 1997; Thongtham and Kristensen, 2005; Werry and Lee, 2005; Nordhaus and Wolff, 2007; Kristensen, 2008).

Robertson (1987) hypothesized that crabs play a greater role in the recycling of mangrove leaf litter in the IWP compared to the ACEP, and that this difference was explained by the higher diversity and abundance of herbivorous crabs, especially sesarmids, in the IWP. To test this hypothesis, McIvor and Smith (1995) tethered leaves at sites in Rookery Bay, Florida to measure rates of removal, and also pitfall trapped to estimate crab abundance and species composition. They compared their results to pitfall trapping they conducted in tidally influenced areas near the mouth of the Murray River, in northeast Australia. The Rookery Bay leaf removal rates were compared to data from similar studies by Robertson (1986) and Robertson and Daniel (1989b) at sites in northeastern Australia. Pitfall trapping confirmed marked difference in crab assemblages between the sites. At Rookery Bay, the assemblage was composed largely of carnivorous xanthid crabs (*Eurytium limosum* and *Panopeus herbstii*) and deposit-feeding ocypodid (*Uca* spp.) crabs (90% of captured crabs), while herbivorous sesarmid (*Sesarma* spp.) crabs dominated (97% of captured crabs) at the Murray River site. None of the leaves tethered at Rookery Bay sites was removed by crabs, and only a very small number showed any signs of crab herbivory. By contrast, Robertson (1986) and Robertson and Daniel (1989b) reported 28–79% leaf removal by crabs. While the difference between these sites is clear and consistent with Robertson's hypothesis, subsequent studies at more tropical latitudes in the ACEP paint a different picture. In these areas, large, herbivorous ucidid crabs remove leaf litter at high rates, comparable to those measured in the IWP. In Guyana, *U. cordatus occidentalis* populations removed 100% of the daily leaf fall during the 9-month rainy season (roughly November–July); crabs were inactive and molting from August–October, so litter accumulated on the forest floor during this period (Twilley et al., 1997). Similarly, Nordhaus et al. (2006) estimated that *U. cordatus cordatus* populations consumed 81.3% of the daily leaf litter fall in a high intertidal forest in northern Brazil. At another site on the same peninsula, Schories et al. (2003) estimated that *U. cordatus cordatus* consumed 61% of the annual litter fall at mid-low intertidal levels. Middleton and McKee (2001) used leaf tethering experiments to estimate rates of leaf removal on Twin Cays, off the coast of Belize. In lower intertidal areas, where *U. cordatus cordatus* and *G. cruentata* are abundant, they measured high rates of leaf removal over the 23-day experiment: *A. germinans* (47%), *L. racemosa* (64%), and *R. mangle* (26%). In upper intertidal areas, where these herbivorous crabs were absent, and deposit-feeding *Uca* spp. dominated, almost no leaf tissue was consumed. With a broader geographical sampling of litter removal rates by crabs in the ACEP, there may prove to be less of a difference with IWP than Robertson (1987) thought.

Not surprisingly, the changing chemistry of decaying mangrove leaves is reflected in the grazing preferences of crabs. The C/N ratio of senescent leaves when initially dropped is quite high, ranging from about 47 to 100 (Giddins et al., 1986; Twilley et al., 1986; Robertson, 1988; Camilleri, 1989; Lee, 1997; Thongtham and Kristensen, 2005). As decomposition proceeds and microbial populations build up on the decaying leaves, the C/N ratio drops considerably. For example, Twilley et al. (1986) measured decomposition of senescent *R. mangle* and *A. germinans* leaves over a 148-day period at two sites in Rookery Bay, Florida, which differed in tidal inundation frequency. The lower elevation, near-river site (LENR), was inundated by 190 tides during the experiment, while the higher elevation, inland site (HEIS) was inundated by 127 tides. The C/N ratio of freshly fallen *R. mangle* leaves dropped from 98 to 33 at LENR and 98 to 43 at HEIS. The C/N ratio of *A. germinans* fell from 47 to 17 at LENR and 47 to 23 at HEIS. Tam et al. (1990) reported similar changes in C/N ratios during decomposition of mangrove leaves (*A. corniculatum*, *A. marina*, and *K. candel*) in a Hong Kong mangrove forest. Such shifts are partly due to the leaching of soluble organic carbon, as described above, but also due to the immobilization of N in the form of hydrolyzable amino acids and amino sugars in the accumulated microbes (Tremblay and Benner, 2006). Bacteria and their extracellular exudates also contribute lipids and fatty acids (Mfilinge et al., 2003). As noted earlier and discussed below, leaf tannin concentrations are also declining during this period, as is the C/P ratio (Nielsen and Andersen, 2003). When consumed, tannins bind with proteins in the ingested leaf material, making them less available to the herbivore or detritivore. If present in sufficient concentrations, tannins also inhibit the activity of digestive enzymes, either the animal's own, or those produced by endosymbionts, thereby reducing digestive efficiency (Swain, 1979).

Crabs require sufficient nitrogen in their diet to support growth, reproduction, and molting, and in theory, this is achieved by consuming foods with C/N of 17 or lower (Russell-Hunter, 1970). Consistent with this expectation, when offered leaves of a particular species in different states of decay, crabs generally prefer brown leaves that are in a more advanced state of decomposition than recently abscised senescent yellow or fresh green leaves. Preference for decayed leaves is thought to be related to their decreased tannin content and lower C/N ratio, which enhances their palatability, digestibility, and nutritional value. Similarly, when offered decaying leaves of different species, crabs usually selected those with lower C/N ratios and tannin concentrations (Giddins et al., 1986; Neilson et al., 1986; Camilleri, 1989; Lee, 1989, 1993; Steinke et al., 1993b; Kwok and Lee, 1995; Ashton, 2002; Thongtham and Kristensen, 2005; Ravichandran et al., 2007; Chen and Ye, 2008; Thongtham et al., 2008), but there are some clear exceptions to these patterns (Micheli et al., 1991; Micheli, 1993a, 1993b; Dahdouh-Guebas et al., 1997; Ashton, 2002; Nordhaus and Wolff, 2007).

Other crustaceans, such as the circumtropical amphipod, *Parhyale hawaiensis*, exhibit a very similar feeding preference for older, more decomposed mangrove leaf litter. In an estuary in northwest Australia, Poovachiranon et al. (1986) found dense populations of the amphipod living and feeding in mangrove leaf litter (mostly *R. stylosa*) on the forest floor. In laboratory feeding trials, when offered leaves in six different stages of decomposition and newly senescent leaves, feeding rates (measured by defecation rates) increased 25-fold from the least to most decomposed classes of leaves. Older leaf litter had higher concentrations of N and starch, and lower tannin, crude fiber, and toughness.

The C/N ratio of even the most decayed litter, however, rarely falls to a value of 17 or lower; in most cases the ratio is higher than this critical value by several fold. Yet, the diets of many species of mangrove crabs consist largely of this nutrient-poor leaf material. This paradox (Skov and Hartnoll, 2002) has led researchers to examine crab diets in more detail to learn whether they are also feeding on unknown nitrogen-rich foods (Thongtham and Kristensen, 2005). An early suggestion that crabs might obtain the required nitrogen by deposit feeding on benthic algae and bacteria in surface sediments (Robertson, 1986; Micheli, 1993a, 1993b; Bouillon et al., 2002a; Skov and Hartnoll, 2002) is not supported by analyses which indicate that crabs could not possibly consume enough sediment to obtain the nitrogen they need (Thongtham and Kristensen, 2005; Kristensen et al., 2010). However, carbon- and nitrogen-stable isotope signatures, stomach content analysis, feeding experiments, and field observations indicate that the diets of herbivorous crabs are substantially more diverse than previously thought (Beever et al., 1979; Giddins et al., 1986; Diaz and Conde, 1988; Micheli, 1993b; Steinke et al., 1993b; Kwok and Lee, 1995; Dahdouh-Guebas et al., 1997, 1999; Lee, 1998; Bouillon et al., 2002a; Erickson et al., 2003, 2008; Thongtham et al., 2008; Kristensen et al., 2010). Their nitrogen requirements beyond what can be assimilated from leaf litter seem to be met by a combination of algal grazing (filamentous algae and benthic diatoms) and supplementary consumption of animal tissue (crustaceans, mollusks, annelids, insects, and fish). The latter may provide about half the nitrogen required for growth and reproduction (Kristensen et al., 2010).

Detritus-feeding mollusks. Crabs and amphipods are not the only organisms that consume large quantities of mangrove leaf litter. Feeding by the intertidal gastropod, *Melampus coffeus*, greatly accelerates the decomposition of *Rhizophora* and *Avicennia* leaf litter at sites in Florida (Smith et al., 1989; Proffitt et al., 1993; McKee and Faulkner, 2000; Proffitt and Devlin, 2005). The potamidid snail, *Terebralia palustris*, has a similar impact on mangrove leaf litter in Africa (Slim et al., 1997; Fratini et al., 2004); snail populations consumed 10.5 leaves m^{-2} per tidal cycle in a Kenyan mangrove stand. Observations of antagonistic foraging interactions suggest that the sesarmid crab, *Neosarmatium smithi*, and *T. palustris* compete for decaying *R. mucronata* leaves (Fratini et al., 2000).

Deposit-feeding crabs. There are numerous taxa of infaunal and epifaunal deposit and filter feeders inhabiting the benthos of mangroves and adjacent tidal flats, including amphipods, isopods, tanaids, crabs polychaetes, oligochaetes, gastropods, bivalves, nemerteans, sipunculids, turbellarians, phoronids, and nematodes (e.g., Dye, 1983; Wells, 1983, 1984; Dye and Lasiak, 1986, 1987; Alongi, 1987a, 1990b; Stoner and Acevedo, 1990; Alongi and Sasekumar, 1992; Sheridan, 1997; Ashton et al., 2003; Alfaro, 2006; Lee, 2008; Nagelkerken et al., 2008; Printrakoon et al., 2008). Deposit-feeding fiddler crabs (*Uca* spp.; **Figure 12**) are often the most abundant and conspicuous macroinvertebrates on the mangrove forest floor, and one of the best studied. They are found throughout the tropics, attaining their highest species diversity in the Americas. Their densities can reach 70 crabs m^{-2} in some locations (MacIntosh, 1982; Hogarth, 2007; Koch et al., 2005). *Uca* spp. sift, sort, and consume a variety of organic matter from surface sediments (see Hogarth, 2007: 115–118, for a detailed description of feeding behavior and mechanism). Co-occurring species often exhibit distinct patterns of distribution along the tidal gradient and among sediment types, some species preferring to forage in organically rich muds and others in sandier sediments of lower organic content (e.g., Crane, 1975; Icely and Jones, 1978; Koch et al., 2005). The exact nature of the crabs' primary foods has been long debated, particularly the relative contributions of bacteria, microalgae, and detrital material. Dye and Lasiak (1986) examined the diets of two mangrove *Uca* spp. in Queensland, Australia. Gut contents indicated that fiddlers fed on bacteria, smaller diatoms, and protozoa. Assimilation efficiency for bacteria (98%) is far greater than for microalgae (31–41%), and fiddler crabs actively select the former over the latter (Dye and Lasiak, 1987). Most large algal cells and particulate mangrove detritus are filtered out or, if ingested, do not appear to be assimilated. Stable isotope ratios of *Uca vocator* collected along the mangrove-lined shoreline of a coastal lagoon in Puerto Rico indicate that the crabs feed mainly on nitrogen-fixing, blue–green algae, with little contribution from mangrove detritus (France, 1998).

Fiddler crabs are a key link between benthic primary producers and microbial decomposers and higher trophic levels in many mangrove food webs. This is especially well documented for the Caeté mangroves of Brazil, where four species of fiddler crabs account for about 11% of the total faunal biomass (Wolff et al., 2000), but almost 90% of total epibenthic production, due to their rapid growth and high turnover rates (Koch and Wolff, 2002). In turn, fiddler crabs are an important prey item for numerous species of crustaceans, birds, fish, and mammals (Wolff et al., 2000). Moreover, their extensive burrowing and foraging activities can enhance mangrove seedling growth and leaf production by: (1) oxygenating surface sediments, which lowers concentrations of toxic soil sulfides and (2) increasing soil porewater exchange, which flushes out salts (Nielsen et al., 2003; Kristensen and Alongi, 2006; Ferreira et al., 2007; Kristensen, 2008; Smith et al., 2009). Smith et al. (1991) demonstrated a comparable positive effect on mangrove growth by burrowing sesarmid crabs.

6.04.4.2.3 Litter decomposition

Leaves. Leaf litter decomposition is a central element of C and N dynamics in mangrove ecosystems and has a direct bearing on nutritional aspects of the crab–litter interaction (**Figure 13**). When senescent leaves fall to the forest floor, they may be rapidly consumed by crabs or other invertebrate detritivores. However, a sizeable fraction of the leaf fall may not be consumed immediately; detritivores could be in low abundance or inactive, crabs may store leaves underground in their burrows before eating them, or leaves may be transported by flow out of the reach of forest detritivores. These leaves undergo rapid chemical changes even before their characteristics are modified by microbially mediated decomposition (Kristensen et al., 2008; Alongi, 2009b). In the first 10–14 days they lose 20–40% of the organic carbon by leaching (Cundell et al., 1979; Feller and Master, 1980; Camilleri and Ribi, 1986; Neilson and Richards, 1989; Benner et al., 1990a, 1990b; Robertson et al., 1992; Steinke et al., 1993a). These leached soluble organic substances include sugars, tannins, and other

Figure 13 Submerged *Rhizophora mangle* leaf litter (Punta Galeta, Panama; photo by I. Herriott).

phenolic compounds. Much of this dissolved organic matter is rapidly exploited by bacteria and fungi, with a conversion efficiency of up to 94% under aerobic conditions with adequate nutrients (Benner et al., 1986). Assimilation efficiency is considerably lower (20–60%) below the sediment–water interface where oxygen concentrations are low and nutrients limiting (Boto et al., 1989). DOC leachate that is not immediately taken up by microbes will often flocculate into aggregates or flakes that are subsequently colonized and nutritionally enriched by microbes and then eaten by a variety of benthic invertebrate consumers (Fell and Master, 1980; Camilleri and Ribi, 1986; Robertson et al., 1992).

Bacterial, fungal, and diatom populations build up on leaf surfaces as tannin concentrations in leaf-tissues drop during decomposition (Cundell et al., 1979; Fell and Master, 1980; Giddins et al., 1986; Benner et al., 1988; Robertson, 1988; Steinke et al., 1990; Robertson et al., 1992; Hernes et al., 2001; Lin et al., 2007). The high concentrations of tannins found in the newly senescent leaves of most mangrove species likely inhibit initial microbial colonization and growth (Benoit and Starkey, 1968; Benner et al., 1986; Horner et al., 1988; Lee et al., 1990; Scalbert, 1991). However, leaching markedly reduces leaf tannin concentrations. For example, tannins comprised > 7% ash-free dry weight (AFDW) of *R. mangle* leaves that had been submerged for < 1week; after 6–7 weeks, tannin concentration had dropped to 0.5% AFDW. Thirty percent of tannins can be lost in a single day of soaking (Hernes et al., 2001).

What remains in leaf tissues after the leaching of soluble compounds are structural polymers referred to as 'lignocellulose'. In *R. mangle* leaves, these compounds comprise 48.5% of the dry weight (Benner and Hodson, 1985). Lignocellulose is a macromolecular complex of lignin and the polysaccharides cellulose and hemicellulose. Bacteria, oomycotes (water molds), and, to a lesser degree, true fungi are the primary degraders of lignocellulose (Bremer, 1995; Newell et al., 1987; Newell, 1996), which is indigestible to most animals. The polysaccharides are degraded by microbes twice as rapidly as lignin (Benner and Hodson, 1985). Microbial uptake of leached soluble organic components from decaying leaves can enhance breakdown of more recalcitrant lignocellulose components by fueling growth in microbial populations and/or by stimulating higher lignolytic metabolic activity (Lee et al., 1990).

Rates of leaf decomposition depend on numerous species-specific and environmental factors. Species (e.g., *Avicennia* spp., *Kandelia* spp., and *Sonneratia* spp.) with relatively high initial N concentrations, low C:N ratios, low lignocellulose, and low tannin concentrations are readily exploited by microbes and decay more rapidly than species (e.g., *Rhizophora* spp., *Ceriops* spp., and *Bruguiera* spp.) with relatively low N, high C:N, high lignocellulose, and high tannins (Twilley et al., 1986; Steinke and Ward, 1987; Robertson, 1988; Steinke et al., 1990; Turner, 1995; Wafar et al., 1997; Ashton et al., 1999; McKee and Faulkner, 2000; Middleton and McKee, 2001; Mfilinge et al., 2002; Kristensen et al., 2008; Alongi, 2009b). The same pattern is seen intraspecifically when local populations vary in N concentration and C:N ratio (Twilley et al., 1997). The positive correlation of decay rates with leaf nitrogen content is evidence that microbial populations are typically N limited.

Fragmentation and shredding of leaves by crabs or smaller detritivores such as amphipods, isopods, polychaetes, nematodes, and turbellarians (Camilleri, 1992; Middleton and McKee, 2001; Bosire et al., 2005) accelerate decomposition by increasing the surface area available to bacteria. Similarly, conversion of ingested leaves to fine particulate organic matter in the form of fecal pellets and their subsequent colonization by bacteria accelerates decomposition and enhances nutritional value to coprophagous consumers (Malley, 1978; Camilleri, 1992; Lee, 1997; Kristensen and Pilgaard, 2001; Werry and Lee, 2005; Kristensen, 2008). Bacteria abundance on ingested plant matter actually increases as it passes through the alimentary tracts of some crab species (Thongtham and Kristensen, 2005).

Environmental conditions also affect rates of leaf decomposition. Wet conditions facilitate leaching of soluble components and increase accessibility to microbes. As a consequence, decay rates are higher for submerged or frequently wetted leaves than for those deposited in dry sites. Therefore, leaves decay more rapidly in subtidal, frequently inundated low intertidal, or basin areas with standing water than in drier higher intertidal areas (Twilley et al., 1986; Steinke and Ward, 1987; Robertson, 1988; Sessegolo and Lana, 1991; Robertson et al., 1992; Middleton and McKee, 2001). Decomposition is also faster in wet than dry seasons (Twilley et al., 1986, 1997; Woitchik et al., 1997), and warm than cool seasons (Steinke and Ward, 1987). Biodegradation of lignin and polysaccharide components of lignocelluloses is greatly slowed by anaerobic conditions (Benner et al., 1984; Benner and Hodson, 1985); as a result, mangrove detritus has long residence times in anoxic sediments. For example, the half-life of lignin is > 150 years in anoxic mangrove sediments (Dittmar and Lara, 2001). How much carbon is stored in mangrove sediments is a critical question, particularly in light of global climate change and ongoing deforestation (Twilley et al., 1992; Bouillon et al., 2008a; Kristensen et al., 2008). The most recent analyses indicate that mangroves are among the most carbon-rich tropical forests and that their deforestation contributes substantially to carbon emissions (Donato et al., 2011; Kauffman et al., 2011).

Wood and roots. Decomposition of mangrove wood and roots is a slower process than that of leaf litter, due largely to the higher percentage of recalcitrant lignocellulose in the former tissues. The wood-decay process is biphasic, as it is for leaf litter; an initial phase of rapid leaching of soluble organic components (sugars, starches, proteins, and soluble tannins) is followed by a more gradual and prolonged period of saprophytic decay (Benner and Hodson, 1985; Robertson and Daniel, 1989a; Romero et al., 2005). From their long-term study of tree decomposition on Hinchinbrook Island in north Queensland, Robertson and Daniel (1989a) estimated that fallen trunks of mature *Rhizophora* (height 10–20 m) lose half their dry mass in 8.3 years, with 27.2% remaining after 15.7 years. Half the carbon in decaying trunks is lost in 6.5 years, with 18.4% remaining after 15.7 years. Not surprisingly, smaller diameter branches (≤1 cm) decay more quickly than larger trunks; 50% loss of dry mass and carbon occurs by 2.5 and 2.2 years, respectively. Even so, Middleton and McKee (2001) found that woody mangrove twigs decomposed much more slowly than leaves (51% of dry mass remaining after 540 days vs. 27% remaining after 230 days, respectively). Anaerobic conditions greatly slow (by a much as 10–30 times) the rate of wood decomposition (Benner and Hodson, 1985; Romero et al., 2005). Similar to decaying leaves, nitrogen content increases rapidly in the early stages of decomposition as saprophytes accumulate and N immobilization occurs (Robertson and Daniel, 1989b; Romero et al., 2005).

The assemblages of fungi that colonize decaying wood (**Figure 14**) can be quite diverse, but their biogeography, habitat distributions, host specificity, and functional biology are not yet well understood (Hyde and Jones, 1988; Steinke and Jones, 1993; Hyde and Lee, 1995). Hyde and Jones (1988) surveyed the fungal assemblages on mangrove driftwood, roots, and branches at two sites in the Seychelles archipelago off the east coast of Africa in the Indian Ocean. Their examination of 329 samples yielded 47 species of marine fungi: 37 *Ascomycotina*, one *Basidiomycotina*, and nine *Deuteromycotina*. Other collections of fungi from mangrove wood have yielded 32, 30, and 63 species at three locations in southwestern coast of the Malaysian peninsula (Jones and Tan, 1987; Tan and Leong, 1992; Alias et al., 1995; respectively), 41 species from a site in Singapore (Tan et al., 1989), and 55 species at a site on the Indian Ocean coast of South Africa (Steinke and Jones, 1993). Kohlmeyer et al. (1995) monitored colonization of submerged wood (stakes made from prop roots or branches) from four species of mangrove over a 2-year period at two sites off the coast of Belize. A total of 20 species of marine *Ascomycotina*, two *Basidiomycotina*, and six anamorphic fungi were identified from the experimental stakes. Fungal composition varied to some degree with site, water depth, and species of mangrove.

Figure 14 Wood decay fungus on a fallen mangrove tree (Punta Galeta, Panama; photo by WPS).

Contrary to the generalization by Kohlmeyer and Kohlmeyer (1979) that mangrove fungi exhibit little host specificity, Gilbert and Sousa (2002) found the assemblage of wood-decay polypore fungi in a mangrove forest on the Caribbean coast of Panama to be highly host specific, much more so than comparable assemblages in nearby upland rainforests.

Wood-boring organisms can greatly accelerate the decomposition process, by both directly consuming the dead wood and increasing the surface area accessible to microbial decomposers. The best studied of these are the ship worms (Mollusca: Teredinidae). Teredinid mollusks possess symbiotic, cellulolytic, nitrogen-fixing bacteria that facilitate the breakdown of lignocellulose and provide essential nutrients to the animals (Carpenter and Culliney, 1975; Waterbury et al., 1983). They rapidly recruit to submerged fallen wood and burrow extensively throughout the tissue, consuming > 50% by dry weight within just a few years (Robertson and Daniel, 1989a; Robertson, 1991; Kohlmeyer et al., 1995; Romero et al., 2005). Kohlmeyer et al. (1995) observed that the rate at which ship worms consumed submerged, experimental wood stakes was twice as great at a bird-roosting site with high nutrient availability as compared to a site without added nutrients.

Termites are common inhabitants of mangrove forests in both the IWP and the ACEP (e.g., Miller and Paton, 1983; Salick and Pong, 1984; Levings and Adams, 1984; **Figure 15**). Research on mangrove termites has largely focused on their foraging behavior, territoriality, and social systems (Levings and Adams, 1984; Adams and Levings, 1987; Atkinson and Adams, 1997; Adams et al., 2007; Atkinson et al., 2008). Very little is known about their impact on mangrove ecosystem processes beyond the fact that most species feed exclusively on dead wood, and possess flagellate protozoan endosymbionts in their hindguts, which facilitate digestion of lignocellulose (Inoue et al., 2000; Brugerolle and Radek, 2006). Nitrogen fixation by gut symbionts may also play a significant role in termite nutrition (Prestwich et al., 1980). One striking exception to the generalization that termites only forage on dead wood is *Coptotermes curvignathus*, an IWP species that feeds on living sapwood and appears to be a major cause of mortality in adult *R. apiculata* within the Matang mangrove forest reserve of Malaysia (Putz and Chan, 1986).

Figure 15 Termite nest (*Nasutotermes* sp.) on a *Rhizophora mangle* tree (Punta Galeta, Panama; photo by WPS).

Little is known about the effects of wood-boring insects, predominantly beetle larvae, on the decomposition of dead mangrove wood; however, they rapidly recruit in large numbers to newly dead trees (W. Sousa, personal observation). A variety of beetle families are represented among the xylophagous species that feed on dead wood (Hockey and Baar, 1988; Veenakumari et al., 1997).

Rates of root decomposition have been measured in several studies and are generally intermediate between leaves and wood, but closer to the latter. Working at several sites in southwest Florida, McKee and Faulkner (2000) measured about a 50% loss in dry weight of roots (diameter not stated) during the first year of decomposition in mesh litter bags. Of the three study species, *L. racemosa* roots tended to decompose more slowly than those of *R. mangle* or *A. germinans*, which did not differ in their rate of mass loss. By comparison, leaves of the three species were more than 90% decomposed within a year at most sites. Middleton and McKee (2001) monitored decomposition of *A. marina* and *R. mangle* roots on islands off the coast of Belize, deploying a mixture of fine (< 2 mm diameter) and coarse (> 10 mm diameter) roots enclosed in mesh bags at two different soil depths, at both lower and upper tidal elevations. Rates of mass loss were about 50% in 300 days, followed by slower decay over the next 284 days, when the study was ended. Over the entire period of 584 days, roots lost 60% of their mass; rates did not differ between the species, or with soil depth or tidal height. What remained was highly recalcitrant lignified epidermis of large roots (> 1 cm diameter), which is likely to accumulate over time as peat. By comparison, leaves placed in the lower intertidal were completely decomposed in 150 days. Poret et al. (2007) measured rates of decomposition of *R. mangle* roots (equal mixture of 1–4, 4–8, and 8–12 mm diameter roots) over 250 days at different soil depths at six sites in the Florida Everglades. Soil depth had no effect on decomposition rates, but rates differed considerably among sites, ranging from 25% to 50%. Higher decomposition rates were measured at sites with regular tidal flushing and higher soil redox potentials, as compared to sites that experienced prolonged inundation, more anoxic soil conditions, and possibly higher concentrations of soil sulfides and tannins. Huxham et al. (2010) compared rates of decomposition of roots (mixture of fine ≤3 mm diameter and coarse > 3 mm to ~9 mm) of three mangrove species (*A. marina*, *B. gymnorrhiza*, and *C. tagal*) in a Kenyan mangrove forest. Decomposition was monitored over 12 months at six sites along a tidal gradient. The effects of mixing roots from different species (*A. marina* and *C. tagal*) and fertilization (*B. gymnorrhiza*) with N and P were also evaluated. In addition, for *A. marina*, decay rates of fine and coarse roots were compared. Rates of decomposition (% dry weight lost after 1 year) differed among the species: *A. marina* (76%), *B. gymnorrhiza* (47%), and *C. tagal* (44%). Coarse roots of *A. marina* decomposed more slowly than fine roots. Decay also varied among sites, occurring more quickly in lower, frequently wetted locations than higher, drier areas. N-enriched roots decomposed more quickly than control roots; the addition of P did not affect decomposition rates. Mixing *A. marina* roots, which are relatively N-rich (C/N = 57), with N-poor *C. tagal* roots (C/N = 77) increased the rate of decomposition of the latter. This result and the enhancing effect of N fertilization indicate that decomposers are N limited in this system. Albright (1976) reported a similar enhancement of root decomposition with N, but not P, enrichment. Feller et al. (1999, 2002) found that fertilization with P (but not N) increased belowground decomposition rates in mangrove stands on islands off the coast of Belize. In this carbonate-rich setting, much of the dissolved inorganic P is bound to calcium and not available to plants or microbes.

Finally, studies in New Zealand and Australian mangroves also demonstrate lower rates of decomposition for *A. marina* roots as compared to leaves (Albright, 1976; van der Valk and Attiwill, 1984); in these studies, fibrous roots decomposed more slowly than main woody ones. Decomposition was slower for roots buried in anoxic soils compared to those on the sediment surface.

6.04.4.2.4 Does outwelled carbon and nitrogen fuel detritus-based food webs in adjacent habitats and farther offshore?

While detritivorous crabs, mollusks, and other benthic invertebrates consume decaying leaf litter and thereby enhance local retention and recycling of mangrove-derived carbon and nitrogen within forests, a considerable amount of mangrove particulate and dissolved organic matter is transported to neighboring habitats and farther offshore. As discussed earlier, these contributions vary greatly among mangrove systems depending on a suite of biological, geomorphologic, and climatological characteristics including, but not limited to, their NPP, volume, and areal extent of tidal exchange and river drainage/flushing, forest size in relation to watershed area, quantity and seasonal patterning of rainfall and associated runoff, storm activity, porewater volume and exchange, and rates of litter consumption by invertebrates (Twilley, 1988). Alongi (2009b) estimated that, on average, 32% of forest NPP is exported, with the largest amounts contributed by mangrove forests associated with major river systems (e.g., Fly River, Papua New Guinea) or estuaries with large tidal exchange (e.g., Darwin Harbor and Missionary Bay, Australia). In total, the export of particulate organic matter (POC) from mangroves could represent ~11% of the global export of terrestrial particulate matter (Jennerjahn and Ittekkot, 2002; Bouillon et al., 2008a). Similarly, Dittmar et al. (2006) estimated that DOC from mangroves represents ~10% of global terrestrial export. Both contributions are disproportionate to the land area covered by mangrove ecosystems (< 1%).

To what extent do near- and offshore food webs depend on this outwelled organic matter? Suffice it to say that the forest-feeds-the-ocean scenario is not as clear cut as originally conceived (Lee, 1995, 2005). Several reviews have rigorously analyzed available data (Robertson et al., 1992; Lee, 1995; Bouillon et al., 2004b, 2008b; Kristensen et al., 2008; Alongi, 2009b). Here, we present an overview of the present understanding of the phenomenon.

The method most commonly used to determine the fate of outwelled organic material is stable isotope analysis. This technique relies on ratios of naturally occurring stable isotopes as tracers for organic matter; the most commonly used tracers in mangrove studies are ratios of carbon ($^{13}C/^{12}C$ or $\delta^{13}C$), nitrogen ($^{15}N/^{14}N$ or $\delta^{15}N$), and sulfur ($^{34}S/^{32}S$ or $\delta^{34}S$) isotopes. In animals, each of these isotopic ratios is, in principle, closely tied to diet, and thus reveals the trophic position of consumers and consumed. Isotope ratios identify the organic matter that is assimilated into body tissues, not just ingested. They do not, however, demonstrate that the sampled population is limited by the assessed element.

By measuring isotopic signatures of mangrove inhabitants, researchers can, in theory, trace the flow of a chosen element through the mangrove and adjacent ecosystems, and describe the structure of the food web (e.g., Abrantes and Sheaves, 2009a). However, the success of these techniques rests on a number of key assumptions (Gearing, 1988; Fry and Smith, 2002; Fry and Ewel, 2003; Fry, 2006; Bouillon et al., 2008b): (1) that differences exist in the signatures of different primary producers, and that variation in these signatures from a given source does not overwhelm the average difference in signatures between sources, (2) that these differences are maintained or altered in a predictable way during decomposition, and (3) that changes in isotopic signatures (i.e., fractionation) during assimilation are consistent. Gearing (1988) and Bouillon et al. (2008b) provided detailed assessments of how well these assumptions are met in mangrove systems. In many instances, the assumptions could bear additional evaluation, particularly information on the degree of variation within a given source and shifts in ratios during assimilation. Such variation makes it all but essential to measure the stable isotope ratios of putative sources at each study location (e.g., Fry and Smith, 2002), as opposed to relying on values from the literature. Modern analyses often examine multiple isotopes, which can aid in quantifying trophic contributions from more than two sources (Lubetkin and Simenstad, 2004). Key to the success of this approach is the use of appropriate mixing models to estimate the proportionate contributions of different sources to a diet. This component of the analysis is one of the most challenging aspects of the method. One must identify and measure all primary sources, estimate intra-source variation in isotopic signatures, consider varying fractionation rates, and control error propagation in model calculations. To date, linear mixing models (e.g., Phillips, 2001; Phillips and Gregg, 2001, 2003; Phillips and Koch, 2002; Lubetkin and Simenstad, 2004; Phillips et al., 2005) have been most commonly employed in multi-source analyses, but Bayesian methods have recently been introduced as a means of explicitly addressing the uncertain, probabilistic nature of these multiple source analyses (e.g., Moore and Semmens, 2008; Jackson et al., 2009; Semmens et al., 2009; Parnell et al., 2010). Despite these technical issues and the need to more rigorously evaluate underlying assumptions, stable isotope methods have proved to be quite useful in testing the general expectations of the outwelling hypothesis, even if the details of mangrove-influenced, food-web dynamics have yet to be resolved.

The most commonly examined carbon sources in isotopic studies of mangrove trophic contributions are mangrove leaves, microalgae, macroalgae, and seagrasses. From a large collection of published values, Bouillon et al. (2008b) calculated the means and 25th and 75th percentiles of published $\delta^{13}C$ values for each of these sources: mangroves (–28.1; –29.4, –27.0), microalgae (–20.2; –23.0, –18.0), macroalgae (–18.9; –23.1, –16.4), and seagrasses (–12.1; –15.5, –10.7). Therefore, consumers with strongly depleted (more negative) isotope signatures are thought to depend most heavily on mangrove-derived carbon for their nutrition.

Stable isotope analyses have provided only limited support for a strong influence of mangrove carbon on organisms in neighboring and offshore habitats. Rodelli et al.'s (1984) study of a Malaysian mangrove and adjacent water bodies reported that there was very little isotopic signature of mangrove-derived carbon in organisms from coastal inlets < 2 km from the coast, and none from organisms in offshore water (2–18 km from the coast), whereas a mangrove carbon signature was clearly evident in organisms living within mangrove stands or in adjacent mudflats. Fleming et al. (1990) documented a very similar gradient in Biscayne Bay, Florida. Mangroves appeared to be a major contributor of carbon to heterotrophic organisms, such as crabs, snails, fishes, and oysters, only at a very restricted scale, within or immediately adjacent to forests. Outside the forest, the isotopic signatures of seagrass and other marine sources such as phytoplankton or seagrass epiphytes were the major sources. The isotopic signatures of wading birds reflected their foraging behavior; Great White Heron ratios matched those of seagrass-associated organisms, on which they primarily fed, while Roseate Spoonbills, which forage mainly on organisms associated with mangrove sediments and nearby mudflats, exhibited a mangrove carbon-dominated signature. An earlier, less extensive study by Zieman et al. (1984) at two sites in Florida showed a similar trend in $\delta^{13}C$ of the pink shrimp (*Penaeus duorarum*); a mangrove signature characterized shrimp from a mangrove-dominated mainland site at Rookery Bay, while a seagrass ratio was detected in shrimp from an offshore, seagrass-dominated site in the Florida Keys. In a mangrove-fringed lagoon in Puerto Rico, Stoner and Zimmerman (1988) found that juvenile penaied shrimp were omnivorous, feeding primarily on smaller benthic invertebrates (e.g., polychaetes and amphipods), with detritus constituting < 25% of their diet. Isotopic analysis indicated that both the juvenile shrimp and their detritivorous prey ultimately derived most of their carbon from benthic blue–green algae rather than mangrove detritus. Macia (2004) reported similar findings for penaied shrimp populations in a small mangrove-lined bay in Mozambique; shrimp appear to obtain the majority of their carbon from plankton and possibly benthic algae.

Hemminga et al. (1994) measured a sharp decline in mangrove detrital signature in sediments and seagrass tissue with distance from the mouth of a mangrove-dominated creek in a Kenyan estuary; only in the most landward seagrass zone, was δ^{13}C from mangroves detected; within 2 km of the forest, a mangrove signature was absent. Working in the Godavari delta mangrove ecosystem on the southeastern coast of India, Bouillon et al. (2002a, 2002b, 2004b) documented a similar gradient in δ^{13}C signatures, from more depleted in mangrove creeks to relatively enriched in an adjacent bay, but found isotopic evidence of marked selection for pelagic and benthic microalgal food sources by benthic invertebrates. Mangrove-derived and other terrestrial carbon was not a significant food source. Fry and Smith (2002) examined the contribution of mangrove carbon and nutrients to filter-feeding barnacles and mussels along the length of the Shark River estuary in south Florida. They found that mangroves supported up to 60% of the nutrition of filter feeders half-way up the estuary, an area which receives the greatest input from bordering mangrove swamps. By contrast, phytoplankton was a more important food source in the lower and upper reaches, peaking at 64% near the mouth of the estuary and 75% at the upriver terminus. Again, these data point to a more localized influence of outwelled mangrove organic matter than originally envisioned. Granek et al. (2009) documented a somewhat more widespread exploitation of mangrove carbon by coral reef invertebrates in Bocas del Toro, Panama. Organic matter from mangroves can comprise up to half of the organic matter incorporated into sessile reef animals such as corals, sponges, file clams, and feather duster worms. The contribution of mangrove carbon to isotopic signatures declined by about 40–50% over the first 250–300 m from the forest edge, but mangrove-derived carbon was detected in reef organisms living > 10 km from a mangrove forest. In most settings in which the impact of exported mangrove organic matter on detritus-based food webs has been examined, its influence is observed within a relatively short distance (< 1–2 km, and often only a couple of hundred meters) from source stands.

The rapid decline in the contribution of mangrove carbon to secondary production with distance from source areas is in many cases explained by the geomorphology and hydrodynamics of the system in question (Kristensen et al., 2008). Mangrove forests often surround partially enclosed bays or estuaries; in these settings, narrow openings to larger water bodies and eddying water currents will trap suspended particulate matter, resulting in its deposition in or near mangrove habitats. High-salinity plugs can also block exchange during seasons of low flow and a high evaporation (Wolanski, 1992). Even if the suspended particulate matter reaches coastal waters, it can be diverted by strong longshore currents (Jennerjahn and Ittekkot, 2002).

When such physical barriers to export are absent, as in estuaries with large tidal exchange or river flow, both particulate and dissolved organic matter are transported farther offshore. Isotopic analyses of offshore suspended particulate matter and sediments verify substantial concentrations of mangrove-derived particulate carbon as far as 10–12 km offshore in areas with strong tidal exchange or river flow (Rodelli et al., 1984; Robertson et al., 1992). However, as particulate organic matter moves offshore, it continues to be degraded, much of it converted to DOC (Dittmar et al., 2006). This adds to the exported pool of DOC that is leached from litter and roots and held in basins or subsurface porewaters until pumped seaward by tidal pressure (Twilley, 1985; Wafar et al., 1997; Bouillon et al., 2007).

Moran et al. (1991) estimated that 10% of the DOC in waters 1 km offshore of a mangrove forest on a small island in the Bahamas was of mangrove origin. Dittmar et al. (2006) showed that mangroves contributed most of the terrigenous DOC found in ocean waters off northern Brazil, and can be detected to the continental margin. In these cases, despite what seems an adequate supply of mangrove-derived carbon, it does not appear to represent much of a subsidy to offshore food webs. The modest incorporation of this material by offshore primary consumers is thought to be due to its refractory nature and poor nutritional quality (Rodelli et al., 1984; Alongi et al., 1989; Alongi, 1990a, 2009b; Robertson et al., 1992; Jennerjahn and Ittekkot, 2002; Dittmar et al., 2006; Kristensen et al., 2008) and, in some locations, the toxic effects of leached tannins (Alongi, 1987b). Dittmar et al. (2006) showed that sunlight efficiently destroyed dissolved aromatic molecules during transport offshore, removing about one-third of mangrove-derived DOC. The remainder was refractory to further microbial degradation.

These observations bear directly on a long-standing question concerning the relationship between mangrove habitat and the production of near- and offshore fisheries, especially for prawns. Because of the obvious economic and conservation implications, this relationship has been the subject of numerous investigations. Mangroves have been championed as both a nursery/refuge habitat and a nutritional source for these commercially important species. Early studies tested for correlations between various metrics of mangrove absolute or relative abundance and shrimp or finfish catch data; positive correlations of varying strength ($R^2 = 0.32–0.89$) were found in mangrove systems around the world (see Table 4.6 in Alongi (2009b); also Loneragan et al., 2005; Manson et al., 2005a, 2005b). However, the cause of these statistical relationships is unclear, and most of them derive from single factor analyses. Lee (2004) conducted a multivariate analysis using data from 37 countries, examining the combined influence of mangrove area, tidal amplitude, rainfall, temperature, human population size, length of coast line, and relative mangrove abundance (mangrove area per length of coastline) on prawn catch ($\mathrm{Mg\,yr^{-1}}$). To minimize multi-collinearity, the predictor variables were reduced to four orthogonal principal components that were used in a stepwise multiple regression to predict prawn catch. The best-fit model included two of the four principal components and explained 59.2% of the variance in the prawn catch data. The principal component with the highest explanatory power was positively correlated with tidal amplitude and population size. The effect of tidal amplitude could reflect a larger intertidal habitat area, greater exchange of nutrients and organic material, or greater productivity of benthic microalgae and other mudflat food sources. The positive effect of human population size could simply be that with more people to feed there is greater demand on the fishery. The second most important principal component was positively related to mangrove area and length of coastline, which are closely tied. The biological interpretation of this contribution is not clear; it could be evidence that mangroves are serving as important nursery habitat. On the other hand, the relative area of mangroves (a major element of a separate principle component), that is, how much mangrove occurs per length of coast, was not sufficiently related to catch to be included in the final model.

Manson et al. (2005a) conducted a similar multivariate regression analysis of the relationship between catch-per-unit-effort (CPUE) for several mangrove-related fishery species (e.g., banana prawns, mud crabs, and barramundi) in north-eastern Australia and various characteristics of mangroves along the region's coastline, as estimated from Landsat imagery for half-degree latitudinal sections. These characteristics included mangrove area, mangrove perimeter, number of patches, mean patch area, mean patch perimeter, length of coastline, ratio of mangrove area to length of coastline, area of shallow water, estuary perimeter, and latitude. For these species, which are associated with mangroves as juveniles or as permanent residents, CPUE was most closely tied to mangrove area and perimeter, area of shallow water, and latitude. Depending on the species, various combinations of these variables accounted for 37–70% of the variation in CPUE.

As a number of authors have pointed out, such correlations do not demonstrate a causal trophic relationship between the abundance of mangroves and nearshore fishery production. In fact, stable isotope studies (Newell et al., 1995; Primavera, 1996; Loneragan et al., 1997; Chong et al., 2001; Schwamborn et al., 2002; Abrantes and Sheaves, 2009b) indicate that the trophic link between mangroves and nearshore prawn populations is not very strong and more localized than had been thought. Newell et al. (1995), working on the west coast of Peninsular Malaysia, found that mangrove detritus contributes substantially to the nutrition of juvenile *Penaeus merguiensis*, which live in mangrove tidal creeks, where they also feed on benthic microalgae. However, neither the adults of this species nor the juveniles and adults of *Parapenaeopsis sculptilis*, which live offshore, show isotopic signatures consistent with feeding on particulate organic matter from mangrove. The isotope ratios of the offshore populations indicate consumption of phytoplankton. Primavera (1996) measured δ^{13}C of juveniles of four species of penaeid shrimp *(M. ensis, Penaeus indicus, P. merquiensis*, and *P. monodon)* collected along the banks of a riverine mangrove in central Philippines. The isotopic ratios pointed to shrimp obtaining their carbon primarily from feeding on phytoplankton and possibly epiphytic algae growing on pneumatophores, rather than mangrove detritus. Loneragan et al. (1997) examined the contributions of seagrasses, mangroves, macroalgae, and seston to the nutrition of several species of prawns (*Penaeus esculentus, P. semisulcatus, and Metapenaeus* spp.) in the Embley River estuary and adjacent offshore waters in north-eastern Australia. Their diet, as evaluated with a multiple-isotope analysis, varied with location in much the same manner as Newell et al. (1995) described. Juvenile prawns collected in seagrass beds had isotopic ratios closest to seagrass and algal epiphytes on seagrass, even though the beds were close to mangroves and mangrove detritus was present. The δ^{13}C values of juvenile prawns from an upstream mangrove creek were between those of mangrove detritus and seagrass, and close to those of macro-algae and seston. Adult penaeids collected offshore had isotopic ratios consistent with a mixed diet of seagrass, macroalgae, and seston. Mixing model results indicated that mangrove carbon represented the greatest proportion of the diet for juvenile prawns sampled from the mangrove creek (>60% in both the wet and the dry seasons), and comprised progressively less in juvenile prawns collected downstream toward the mouth of the estuary. Loneragan et al. (1997: 299) concluded that "although large amounts of mangrove and terrestrial carbon may be exported from the Embley River estuary, very little is assimilated by prawns in habitats away from the mangrove creeks, either in nearby seagrasses, or further away in offshore areas." Chong et al. (2001) conducted a multi-isotope study of juvenile prawn diets in the estuaries of the Matang mangroves in Malaysia. They estimated that mangrove organic matter contributed 84% of the assimilated carbon in the juvenile prawns living in the upper reaches of the estuary. The contribution of mangrove carbon to prawn tissues steadily declined in importance down the estuary. At 2 km away from the mangrove forest edge, mangrove carbon represented 15–25% of the total. Offshore, in shallow waters, 7–10 km from mangroves, the isotopic signature of mangroves was all but absent; prawns were feeding on phytoplankton and benthic microalgae. Schwamborn et al. (2002) measured isotopic ratios of planktonic larval and adult stages of the decapod crustaceans, *Lucifer faxon* and *Acetes americanus*, collected from various locations within the Itamaracá estuarine system in northeastern Brazil. While suspended mangrove particulate matter was plentiful, δ^{13}C values of both larvae and adults were typical of food webs based on microalgae, rather than carbon derived from mangroves. The same was true for two species of penaeid shrimp, a sardine species, and zoeal larvae of fiddler crabs and alpheid shrimp. The only species that exhibited ratios indicating considerable assimilation of mangrove carbon were mangrove oysters (*Crassostrea rhizophorae*), copepods (primarily, *Acartia lilljeborgi*), and zoeal larvae of a porcellanid crab (*Petrolisthes armatus*). Finally, Abrantes and Sheaves (2009b) found that mangrove detritus contributed very little to the juvenile diets of four penaeid prawn species in a mixed mangrove–salt-marsh floodplain habitat in north-east Australia.

Overall, these studies do not demonstrate a consistently strong nutritional role for mangroves in supporting populations of commercially important shrimp populations. Only for juvenile stages living inside or quite close to the forest is the dietary contribution of mangrove carbon significant, and even in these areas the magnitude of the contribution varies from site to site, and among species of shrimp. This picture is further clouded by a potentially confounding gradient in δ^{13}C values for phytoplankton and microalgae that matches the pattern that has been attributed to a gradient in mangrove leaf litter exploitation: from depleted ratios in or near mangroves to enriched ratios offshore. Bouillon et al. (2004a, 2008b) argued that this coincident and parallel gradient prevents unambiguous assignment of mangrove carbon contributions to benthic invertebrate and shrimp nutrition. This uncertainty calls for more comprehensive and rigorous analysis of isotopic variation in space and time for each of the contributing sources.

6.04.5 Predation

There has been considerably less research on predator–prey interactions in mangroves than on detritivory or herbivory. Here, we summarize information on some of the better-studied invertebrate and vertebrate predators.

6.04.5.1 Invertebrate Predators

6.04.5.1.1 Crabs

While the bulk of the research on mangrove crabs has focused on the herbivorous or detritivorous taxa (many of which are actually omnivorous, as discussed earlier), there are a number of crab species that are carnivorous. Probably the best studied of these are the large portunid crabs, *Scylla* spp., which are common throughout the Indo-Pacific (Macnae, 1968). Four species of *Scylla* have recently been recognized (Keenan et al., 1998). Adults grow to 150 mm and larger in carapace width, and the species are heavily fished and reared in aquaculture (Keenan and Blackshaw, 1999; Walton et al., 2006). Juvenile crabs are resident in mangroves, remaining there throughout the tidal cycle, sheltering in burrows at low tide. Subadults occupy subtidal habitats at low tide, but move up into mangrove-lined tidal creeks and onto intertidal mudflats to forage at high tide. Adult crabs are predominantly subtidal in habit, but are occasionally observed foraging in the intertidal zone (Hill et al., 1982; Hyland et al., 1984; Walton et al., 2006). *Scylla* spp. feed nocturnally on gastropods, bivalves, grapsid crabs, and hermit crabs; they also appear to scavenge on dead fish and prawns (Hill, 1976). The density of adult *Scylla serrata* in a South African mangrove estuary was estimated at one per 124 m^2 (Hill, 1975). The impact of these mud crabs on prey populations has not been quantified.

In the ACEP, the burrowing mud crab *Eurytium limosum* (Xanthidae) fills a similar trophic role to *Scylla* spp., although it is a considerably smaller crab (10–43 mm carapace width). *Eurytium limosum* typically forages during high tide, but has been observed to feed on fiddler crabs during ebb tides (Wilson, 1989; Koch and Nordhaus, 2010). Stomach contents include mainly fiddler crab carapace fragments and modest quantities of polychaete and infaunal bivalve tissue. In a Jamaican mangrove swamp, the species was distributed fairly uniformly across the intertidal zone, its density ranging from 0.4 to 1.0 m^{-2} (Warner, 1969). As with *Scylla* spp., we know little about the impact of this predator on populations of its prey.

6.04.5.1.2 Ants

Mangrove insect assemblages include a variety of predatory taxa, including mantids, reduvid bugs, lacewings, beetles, flies, wasps, and ants (Veenakumari et al., 1997). Ants are the most abundant insects in mangrove forests (Simberloff and Wilson, 1969; Rützler and Feller, 1999; **Figure 16**). Assemblages of mangrove ant species may be quite diverse; for example, 16 species have been reported from an Australian mangrove (Clay and Andersen, 1996) and 22 species from a Brazilian mangrove (Lopes and Santos, 1996). Investigations of mangrove ants have examined their life histories, spatial distributions, nesting behavior, and competitive/territorial behavior, but relatively little is known about their role in structuring the community or ecosystem processes. Because ants are terrestrial animals and cannot tolerate prolonged periods of submergence, most ants in mangroves are arboreal and make their nests on the trees. These species are often distributed as mosaics of exclusive foraging territories, maintained by intra- and interspecific competition (Adams, 1994). The one known exception to the tree-nesting habit is the specialist mangrove ant, *Polyrachis sokolova*, which nests in the mud in the mangrove forests of Australia. The nests may be underwater for up to 3.5 h during high tides. To prevent total inundation of the nest and drowning of the animals inside, the ants leave loose soil outside the nest that is knocked into the nest entrances as the tide rises. This prevents water from entering and allows the ants inside the nest to survive on the air trapped inside (Clay and Andersen, 1996; Nielsen, 1997).

Figure 16 Large (~1.5 m-long), hanging nest (left) of the ant, *Azteca trigona*, and bell-shaped nest (right) of an associated wasp species (Punta Galeta, Panama; photo by I Herriott).

Mangrove ants are frequently observed preying on a variety of insects, but in only a few cases has their impact been quantified. Several studies have shown that ants can play a protective role for mangroves by reducing the numbers of herbivorous insects that feed on them. Offenberg et al. (2004) documented a negative correlation between the density of weaver ants (*Oecophylla smaragdina*) and levels of herbivory on *R. mucronata* leaves in a Thai mangrove forest. Trees lacking ants had more than 3 times the herbivore leaf damage of trees with ant nests. On trees with ants, leaves near the nest suffered less damage than those in other areas of the canopy. Most of the leaf damage was caused by chrysomelid beetles and sesarmid crabs; both were deterred by the presence of ants, and ants were observed preying on the beetles. Offenberg et al. (2006) showed that *R. mucronata* leaves with insect damage were more likely to be fed on by male crabs of the species *Episesarma versicolor* than intact leaves. Male crabs prefer to enlarge existing holes rather than make their own, possibly because piercing the leaf lamina is difficult with their large, thick claws.

Johnstone (1981) found a similar trend in a Papua New Guinea mangrove forest; trees lacking weaver ants appeared to suffer higher leaf herbivory than trees with ants, but the difference was not statistically significant. In this case, the comparison was for a pooled sample of leaves from 23 different species of mangroves, which undoubtedly introduced considerable variation in other leaf attributes that affect rates of herbivory. Ozaki et al. (2000) experimentally demonstrated in an Indonesian forest that two different mangrove ant species (*Monomorium joricola* and *Paratrechina* sp.) preyed on and suppressed populations of the coccinellid scale insect, *A. marina*, which infested seedlings of *R. mucronata*. Similarly, Cogni and Freitas (2002) observed 19 ant species visiting the extrafloral nectaries of *Hibiscus pemambucensis*, a shrub frequently found in mangrove forests of south-east Brazil. Eight of the species attacked termite larvae (*Nasutitermes*) that were introduced to the plants as insect bait and retrieved them to their nests. The authors interpreted these observations as evidence that ants were protecting the shrubs, although no information on rates of leaf damage was presented.

Some of the most interesting ant–plant interactions in mangroves involve the symbiosis of ants and particular types of epiphytic plants, called ‘ant plants’ (Huxley, 1978). Ant plants, or myrmecophytes, are restricted to the IWP and grow in a variety of habitats, including mangrove forests. Ants of the genus *Iridomyrmex* commonly inhabit myrmecophytes, though other types of ants can be found. Young plants of the genera *Myrmecodia* and *Hydnophytum* (both Rubiaceae) form chambered tubers out of swollen hypocotyls. Ants later nest in these chambers where they rear their larvae and pupae. They deposit waste materials on the chamber walls as small white swellings referred to as ‘warts’. The waste appears to serve as a source of nutrition for the plants, transferred to the plant through the warts (Huxley, 1978; Rickson, 1979). Sometimes organisms other than ants use myrmecophyte chambers, such as frogs, nematodes, mites, and fungi. Even skinks have been observed living in and laying eggs in *Hydnophytum*, where they also feed on developing ants.

A single ant colony may inhabit multiple myrmecophytes in neighboring trees. In Papua New Guinea mangroves, *Philidris* sp. is the dominant ant living in the mangrove epiphyte *Hydnophytum moseleyanum* (Maeyama and Matsumoto, 2000). These ants consume honeydew from diaspidid scale insects that they rear inside their nests. The ants also carry dead insects back to the nest, probably as a supplemental nitrogen source. The plants can absorb nutrients from the debris that their ant inhabitants store inside the cavities in the plant tubers. This mutualism is not obligate, as 38.5% of *H. moseleyanum* plants are unoccupied by ants.

Interactions between mangrove ferns and insects are rare and usually limited to herbivory, as ferns do not rely on pollinators. A few tropical ferns have hollow tubers that serve as ant domatia, but these ferns are found in rainforest habitat. The mangrove fern *Acrostichum danaeifolium*, found in *A. germinans* forests in the Gulf of Mexico, does not produce cavities or extrafloral nectaries to attract ants. However, because of a moth herbivore, *A. danaeifolium* becomes an involuntary host to ant species. Moth larvae hollow out cavities in the petiole and rachis of the fern leaves and these are colonized by at least ten different ant species; sometimes multiple species simultaneously inhabit the same leaves (Mehltreter et al., 2003). It remains unknown if other species of the *Acrostichum* genus have similar moth herbivores and/or ant associations.

6.04.5.1.3 Wasps

Wasps are abundant in mangroves (**Figure 16**) and prey on a variety of invertebrates, especially lepidopteran larvae; however, they have been little studied from a trophic ecology perspective. A comparative study of social vespid wasp assemblages in mangrove, rain forest, and lowland sandy habitats called ‘restingas’, on Itaparica Island on the central coast of Brazil, found wasp diversity to be strongly correlated with vegetational diversity (Santos et al., 2007). The species-poor, mangrove vegetation had the fewest wasp species of the three habitats.

Parasitoid wasps attack the eggs and larvae of a variety of insect hosts. Lepidopteran larvae are the most common prey of hymenopteran parasitoids, but other hosts include juvenile stages of dipteran, coleopteran, and homopteran species (Veenakumari et al., 1992; Feller and Chamberlain, 2007; W. Sousa, personal observation). In some settings, the parasitoid assemblage can be quite diverse. For example, in Veenakumari et al.’s (1997) survey of insects in mangroves on the Andaman and Nicobar Islands in the Bay of Bengal, they reared 43 species of hymenopterous parasitoids from the immature stages of collected insect herbivores.

As for nonparasitic wasps, relatively little is known about the direct effects of parasitoids on populations of their hosts, or their indirect effects on competitive or trophic relationships. However, the few studies that have quantified their impact suggest that the effect of parasitoids on host populations can be substantial. Gara et al. (1990) observed that parasitoids played a key role in suppressing an outbreak of defoliating bagworms (*O. kirbyi*) in an Ecuadorian mangrove forest. In their study of fertilization effects on dwarf *R. mangle* on islands off the coast of Belize, Feller and Chamberlain (2007) observed that parasitoids and other predators killed > 89% of the larvae of *Marmara* sp., a leaf-mining microleptidopteran.

6.04.5.1.4 Spiders

Spiders are common inhabitants of mangrove forest, but their role as predators in mangrove food webs has never been studied in detail. Like mangrove ants, they can be quite diverse. A survey of spiders in a small (2.5 ha) greenbelt mangrove strand in Cochin City on the west coast of India found 51 species of spiders, belonging to 40 genera and 16 families (Sebastian et al., 2006). Seven feeding guilds were represented, namely orb weavers (Araneidae, Tetragnathidae, and Uloboridae), stalkers (Oxyopidae and Salticidae), ground runners (Corinnidae and Lycosidae), foliage hunters (Clubionidae, Hersiliidae, Miturgidae, Pisauridae, Scytodidae, and Sparassidae), sheet-web builders (Linyphiidae), scattered-line weavers (Theridiidae), and ambushers (Thomisidae). Orb weavers and stalkers were the dominant guilds, representing 33% and 29%, respectively, of

Figure 17 The orb-weaving spider, *Nephila clavipes* (female; Punta Galeta, Panama; photo by WPS)

the total collection. A study of mangrove spiders at Morib, Selangor on the west coast of Peninsular Malaysia (Norma-Rashid et al., 2009) found 26 species, belonging to 10 families. In contrast to the Indian mangrove study, orb weavers were uncommon, comprising only 11% of the sample (all Tetragnathidae), while stalking spiders (Salticidae, Oxyopidae) represented 67% of the collections. The second most abundant group was the foliage-hunting Pisauridae (16%).

Orb-weaving *Nephila* spiders are widely distributed throughout the tropics and subtropics, and are common inhabitants of mangroves (**Figure 17**). They are well known for the large size of adult females, in comparison to diminutive males, and for weaving large conspicuous golden webs. Austin and Anderson (1978) studied a mangrove population of the Australian species, *Nephila edulis. Aegiceras corniculatum* and *A. marina* were the dominant tree species at the study site at Patonga, N.S.W. Samples of captured prey from webs revealed that these spiders fed exclusively on a diet of flying insects. Three species of leafhoppers comprised 90% of the prey; the remaining 10% included various hemipterans, dipterans, and hymenopterans.

Nephila spp. are infamous for their sexual cannibalism. Sexual cannibalism occurs when a female spider eats her mate after copulation or eats a potential mate before copulation. Despite the sacrifice of the male, sexual cannibalism may actually improve reproductive success of both sexes – the female gains nutritional benefits and thus improves the survival chances of her offspring and the genes they carry from both parents. In *N. plumipes*, another species that lives in Australian mangrove forests, small female spiders in poor condition are more likely to cannibalize mates than large female spiders in good condition. The choice to cannibalize improves the fertilization success of the copulation (Schneider and Elgar, 2001). In addition to eating members of its own species, *N. plumipes* eats a varied diet of flying insects from the Coleoptera, Diptera, Lepidoptera, and Hymenoptera (Herberstein and Elgar, 1994).

The large webs of *Nephila* spp. are commonly exploited by kleptoparasitic spiders of the genus *Argyrodes* (Theridiidae). Kleptoparastic species of *Argyrodes* do not construct their own webs; instead, they forage in *Nephila* webs, stealing prey. As many as 30 *Argyrodes* may exploit a single *Nephilia* web; the number of *Argyrodes* per web increases with host spider size, web size, and brightness of the web location (Koh and Li, 2002). This reduces *Nephila* weight gain, and increases their mortality, rate of web relocation, and web damage.

Wolf spiders (Lycosidae) are common members of the ground runner guild. Some species are able to run or glide across the water surface and dive to the bottom (W. Sousa, personal observation). The lycosid *Pardosa* from Malaysia is well adapted to this semi-aquatic life. Its hairy coat is water repellent; it sometimes shelters and may breed in air-filled burrows in the mud, and has been observed to feed on juvenile fiddler crabs (Stafford-Deitsch (1996) cited in Hogarth, 2007).

6.04.5.2 Vertebrate Predators

6.04.5.2.1 Fishes

Fishes representing a variety of consumer trophic levels live in mangrove habitat: planktivores, herbivores, omnivores, piscivores, and carnivores. These assemblages can be highly diverse. For example, Robertson and Duke's (1990) 13-month study of fish in forested areas, mudbanks, and tidal creeks of a small mangrove-lined estuary, Alligator Creek, in tropical northeastern Queensland, Australia, collected 128 species from 43 families. Numerically dominant species belonged to the families Engraulidae, Ambassidae, Leiognathidae, Clupeidae, and Atherinidae. Sasekumar et al. (1992) reported that mangrove inlets and creeks in Selangor, Malaysia served as habitat for 119 species of fish. Many of them prey on benthic invertebrates or plankton. Such high fish diversity is typical of IWP mangrove estuaries and exceeds that reported from tropical Atlantic mangrove systems, which is still substantial (Robertson and Blaber, 1992).

One important feature that influences the use of mangroves as fish habitat is the pattern of tidal flooding a particular area experiences. For example, in the Caribbean, the typical mean tidal range is less than 20 cm (Kjerfve, 1981), so fringing mangroves are often inundated and available to fishes for much of the tidal cycle. Probably as a consequence, the densities of fishes within fringing Caribbean mangroves are higher than those in adjacent seagrass and coral habitats (Nagelkerken, 2009). By contrast, in the IWP and on the Pacific coast of Central America, the mean tidal ranges are several meters in extent, making fringing stands effectively intertidal; they only become available to fish and prawns when a flooding tide reaches the forest (Vance et al., 1996; Lugendo et al., 2007; Krumme, 2009).

Vaslet et al. (2010) found that fish assemblages in rivers and mangrove islets in Guadeloupe were structured along an environmental gradient. Varying levels of water salinity determined the presence and abundance of freshwater, estuarine, and marine fish. Fish assemblages also varied by trophic level: carnivores were more abundant in mangrove islets near seagrass beds and planktivores were more abundant near coral reefs. Secondary predators reached their highest abundance near river mouths along the shore.

In the Matang mangrove system of Malaysia, zooplankton are abundant in both the mangrove estuary and nearshore waters, with copepods comprising >47% of the zooplankters (Chew and Chong, 2011). The relative abundance of copepod species changes along the gradient from offshore waters to upper estuary, reflecting species-specific responses to changing salinity, turbidity, and pH. Copepods are heavily preyed upon by

Figure 18 Interface of seagrass bed and fringe mangrove stand (Raja Ampat, West Papua, Indonesia; photo by P. Ryan).

Figure 19 Obicular cardinalfish (*Sphaeramia orbicularis*) swimming among *Rhizophora* prop roots (Raja Ampat, West Papua, Indonesia; photo by P. Ryan).

juveniles of numerous fish and shrimp species in the Matang estuary. In turn, juvenile prawns may experience strong predation pressure from estuarine piscivorous fish (Salini et al., 1990).

Studies in southeastern Australia (Jelbart et al., 2007) and Indonesia (Unsworth et al., 2008) found that the presence of mangroves affected the fish assemblages of neighboring seagrass beds (**Figure 18**). Fish density and species richness were higher in seagrass beds located near mangroves, as compared to more distant beds. At high tide, mangroves provide temporary feeding grounds for a component of the fish assemblage, but these foragers return to nearby seagrass beds at low tide, creating a trophic link between these two habitats. This exchange does not occur for more distant beds, including beds near coral reefs.

A number of studies have found that the densities of diurnally active fish species are highest close to mangroves, and decline with distance away from a stand (Nagelkerken, 2009; **Figure 19**). However, the pattern may not apply to nocturnal foragers. At their study site in southern Biscayne Bay, Florida, Hammerschlag and Serafy (2010) quantified the spatial distribution of fishes foraging at night with increasing distance from the mangrove edge across adjacent seagrass habitat. Species either showed no apparent change in density with distance or actually increased in density with distance from mangroves. Densities of most nocturnally foraging species were lowest at sampling stations closest to the mangrove edge, with the exception of the piscivore *Sphyaena barracuda*, which was most abundant at the mangrove–seagrass ecotone (**Figure 18**). Barracuda typically ambush their prey as they are migrating away from the protective cover of prop roots to forage in adjacent seagrass beds. Few nocturnal studies of fish distributions have been conducted, so it is premature to generalize this result, and the mechanisms generating these patterns are not well understood. Predation rates on experimentally tethered pinfish prey were twice as high at night, compared to daytime, so avoidance of predation does not explain the nocturnal foraging behavior of these species (Hammerschlag et al., 2010a, 2010b). However, rates of predation were highest near the mangrove edge and may explain why nocturnal foragers avoid that ecotone.

The charismatic mudskippers (Family Gobiidae: Subfamily Oxudercinae) are amphibious fish that live in IWP mangroves. The barred mudskipper, *Periophthalmus argentilineatus*, eats mostly small crustaceans such as copepods and amphipods as a juvenile. As the fish matures, its mouth enlarges and gut elongates, allowing bigger prey to be consumed. The mudskipper then shifts to eating polychaetes and mangrove crabs, aided by its amphibious lifestyle (Kruitwagen et al., 2007). Three large, predatory fishes of tropical lndo-Pacific estuaries, the groupers *Epinephelus coioides* and *E. malabaricus* and the snapper *Lutjanus argentimaculatus* feed heavily on sesarmid crabs (Sheaves and Molony, 2000).

We discuss additional examples of fish predator–prey interactions in a later section on mangroves as nursery grounds and refugia.

6.04.5.2.2 Birds

Mangroves are rich in bird diversity, in part because they grow at the interface of land and sea, attracting land birds, shorebirds, and seabirds. In the Sundarbans mangroves of Bangladesh, 315 bird species have been recorded (Hussain and Acharya, 1994). Other estimates of bird species richness in mangrove forests are 186 for Queensland, Australia (Saenger et al., 1977; Noske, 1996), 121 for Peninsular Malaysia (Nisbet, 1968; Noske, 1995), 125 for Guinea-Bissau, West Africa (Altenburg and van Spanje, 1989), 111 on the Pacific coast of Costa Rica (Barrantes, 1998), 104 in north-western Australia (Saenger et al., 1977; Noske, 1996), 94 in Surinam (Haverschmidt, 1965), 84 in Trinidad (Ffrench, 1966), 81 in Brazil (Mestre et al., 2007), and 42 in Singapore (Sodhi et al., 1997). Jayson (2001) recorded 41 bird species in an urban-influenced mangrove on the south-west coast of India. While many of these species are residents and breed in mangroves, only a modest number are mangrove specialists; most also feed or breed in adjacent habitats (Nagelkerken et al., 2008).

Luther and Greenberg (2009) consider 48 bird species to be mangrove endemics, because their life histories depend on mangrove habitats. These include five endangered species: the Madagascar Teal (*Anas bernieri*), the plain-flanked rail (*Rallus wetmorei*) of Venezuela, the mangrove hummingbird (*Amazilia boucardi*) of Costa Rica, the sapphire-bellied hummingbird (*Lepidopyga lilliae*) of Colombia, and the mangrove finch (*Camarhynchus heliobates*) of the Galápagos. Mangrove bird endemics, like those of other taxa, are geographically concentrated in the IWP, reflecting the diversity patterns of mangrove trees. Mangrove specialists differ in their feeding preferences: 51% feed primarily on insects, 27% feed on crabs, 16% feed on nectar, and 4% feed primarily on fish (Luther and Greenberg, 2009). The reason for the relatively small number of mangrove specialists is not known, but one possible explanation is that mangroves provide less opportunity for niche specialization than other tropical forests (Hogarth, 2007). This is because mangrove forests lack a true understory and have much lower plant diversity than tropical rainforests. The mangrove forest is structurally simple and thus provides fewer potential niches to exploit.

The birds occupying mangrove habitats are not all tropical; studies from Africa, Asia, and the Americas show that temperate zone birds use mangroves during their nonbreeding, migratory stays in the tropics (Cawkell, 1964; Haverschmidt, 1965; Ffrench, 1966; Nisbet, 1968; Altenburg and van Spanje, 1989; Sherry and Holmes, 1996; Hunt et al., 2005; Calvert et al., 2010). Migrants are predominantly insectivorous, feeding on flies, butterflies, beetles, ants, wasps, insect eggs and larvae, but the diets of some species include snails, spiders, isopods, centipedes, fish, frogs, and lizards (Lefebvre and Poulin, 1996; Warkentin and Morton, 2000). Lefebvre and Poulin (1997) examined differences in the diets of migrant and resident birds in mangroves of both the Pacific and the Caribbean coasts of Panama, separated by only 65 km. They found that migratory birds occurred in similar abundances on both coasts and were similarly distributed across various feeding guilds. However, the resident bird communities were different between the two coasts. The Caribbean site's resident community was comprised mostly of bark foragers, fly-catching and hovering insectivores, and frugivores. Frugivores fed on fleshy fruits available in adjacent upland habitats since mangrove propagules are not consumed by birds. On the Pacific, gleaning insectivores and granivores were more abundant. The differences in bird abundance were attributed to the differences in tidal amplitude and seasonality of rainfall between the two coasts, in addition to the adjacent habitats of the sites where the study was conducted. This work is supported by other studies by the same authors in Venezuelan mangroves, where the abundance of birds was related to food availability, with water availability a mediating factor (Lefebvre et al., 1994b).

Species such as the prothonotary warbler (*Protonotaria citrea*) and northern waterthrush (*Seiurus noveboracensis*) exhibit strong interannual site fidelity, with a substantial percentage of individual birds returning to mangrove sites that they occupied during the previous wintering period (Warkentin and Hernández, 1996; Reitsma et al., 2002). Site fidelity within a season varies considerably among species and local sites. Birds are not necessarily faithful to one site or habitat, but move between sites based on food availability (Lefebvre et al., 1994a; Lefebvre and Poulin, 1996). Extreme high tides or disturbance to the forest canopy can eliminate foraging sites and cause birds to abandon a local site in search of food (Reitsma et al., 2002). In general, the abundance of food may be more stable in mangroves than neighboring upland forest or scrub habitats because arthropod abundance in the flooded mangroves is less sensitive to seasonal variation in rainfall (Sherry and Holmes, 1996; Hunt et al., 2005). Studds and Marra (2005) conducted a novel removal experiment to directly assess the value of mangrove habitat to over-wintering American redstarts (*Setophaga ruticilla*). They removed behaviorally dominant individuals (mostly adult males) from black mangrove (*A. germinans*) stands in Jamaica and monitored the response of subordinates (mostly females and immature males) that had been relegated to living in neighboring, low quality, upland scrub habitat. The latter birds rapidly occupied the empty territories formerly held by dominant birds. These immigrants capitalized on the higher availability of insect prey in the mangroves; they maintained body mass from winter to spring, while birds on control scrub plots lost body mass, they departed earlier on spring migration and returned at a higher rate the following winter. This experiment and other observational studies suggest that greater food availability and relatively benign environmental conditions are key features that make mangroves an especially attractive over-wintering habitat for migratory birds.

In addition to serving as foraging grounds for terrestrial birds, mangroves are important habitats for waders and seabirds (**Figure 20**). At low tide, waders search the mud and seagrass beds for invertebrate prey. At high tide, they retreat to the mangrove roots or another area to wait for the mud surface to be exposed again. Herons, egrets, and kingfishers eat crabs and fish from the shallow waters. Larger seabirds often use mangrove trees to roost and nest, fishing for prey farther from shore (Hogarth, 2007). Seabirds vary in the extent to which they use the mangrove habitat; the magnificent frigate bird, *Fregata magnificens*, nests in the tops of *Avicennia* trees (Diamond, 1973), but other species may only visit mangroves to forage. In the Florida Everglades, egrets (*Casmerodius albus*) forage in the muddy fringe of the mangrove and white ibis (*Eudocimus albus*) feed in 5 cm of water in the interior mangrove areas (Wilson, 1989). The diet of white ibis feeding in


Figure 20 Egrets feeding along a mangrove channel (Punta Galeta, Panama; photo by A. Varma).

mangrove habitat of south Florida includes crabs, especially *Uca* spp., fish, polychaetes, isopods, and prawns (Kushlan and Kushlan, 1975).

In coastal wetlands of the Yucatan Peninsula, the diets of heron species reflect prey availability in their primary foraging habitats (coastal mangrove, inland mangrove, sawgrass, and coastal lagoon). The reddish egret (*Egretta rufescens*) and the tricolored heron (*E. tricolor*) most commonly forage in coastal mangroves, while the snowy egret (*E. thula*), great egret (*Casmerodius albus*), and great blue heron (*Ardea herodia*) feed primarily in inland mangrove swamps (Ramo and Busto 1993). All five waders feed mainly on fish, with the primary prey species varying by habitat and with predator size. The great blue heron consumes larger prey species than the other four, and its diet includes white ibis chicks. Snow egrets, great egrets, and tricolored heron also consume some invertebrates, including prawns. Miranda and Collazo (1997) documented the diets of some of the same species of wading birds in a Puerto Rican mangrove. At this site, snowy and great egrets feed predominantly on small fish and prawns, tricolor heron consumed only fish, and little blue herons (*E. caerulea*) feed exclusively on fiddler crabs (*Uca* spp.). In Brazil, the scarlet ibis (*Eudocimis ruber*) and the yellow-crowned night heron (*Nyctanassa violacea*) subsist on a diet of crabs. The scarlet ibis and the yellow-crowned night heron show some overlap of feeding niche, but the yellow-crowned night heron eats mostly *U. cordatus* whereas the scarlet ibis eats both *U. cordatus* and fiddler crabs (*Uca* spp.) (Martínez, 2004).

Butler et al. (1997) studied the densities of birds along coastal habitats on both the Pacific and the Caribbean coasts of Panama. Their surveyed habitats included sandy beaches, rocky beaches, mudflats, mudflats with mangroves, lagoons, shrimp ponds, and saltflats. They found densities of shorebirds, wading birds, and coastal seabirds were highest in mudflats backed by mangroves. The authors attributed this result to the high productivity of mangroves, providing many invertebrates and fish for birds to eat. However, they noted that similar mudflat/mangrove areas in other parts of Central America do not always support high densities of birds. Therefore, they suggest, it must be a combination of geomorphological and oceanic conditions that lead to the highly productive mangroves that support abundant bird densities in Panama.

An interesting note is that though mangroves support many bird populations, birds can sometimes have negative effects on the mangrove ecosystem. In Montserrat, West Indies, there was a steady die-off of *L. racemosa* and *A. germinans* where a large colony of cattle egrets (*Bubulcus ibis*) had established. The nesting behavior of the cattle egrets can be quite deleterious to the vegetation in which they nest. In the case of the Montserrat mangroves, cattle egrets systematically destroyed the trees by using all available material for nests, and building nests that were so heavy that supporting branches broke. Their own destructive behavior overharvested the local mangrove materials so that the birds had to build smaller and smaller nests and the forest no longer supports a cattle egret population (Arendt and Arendt, 1988).

Raptors are another conspicuous component of the mangrove avifauna, often foraging and nesting in mangroves. The Common Black Hawk (*Buteogallus anthracinus*) and the Rufous Crab-Hawk (*Buteogallus aequinoctialis)* are two common species in Neotropical mangroves. The Common Black Hawk is distributed from the southwestern United States, through Mexico, Central America, and northern South America to Guyana (Schnell, 1994). In mangroves, it feeds primarily on crabs, but has also been observed feeding on heron (Caldwell, 1986). It also feeds on a variety of small birds, small mammals, reptiles, frogs, land crabs, sea turtle hatchlings, bird eggs and nestlings, and carrion in more seaward and landward habitats. The Rufous Crab-Hawk is a common inhabitant of mangroves on the Atlantic coast of north-eastern South America, and feeds almost exclusively on crabs (Haverschmidt, 1962).

6.04.5.2.3 Reptiles

Most reptiles found in mangroves are also common inhabitants of neighboring marine, freshwater, or terrestrial habitats, although there are a small number of mangrove specialists.

Lizards. Several species of monitor lizards (*Varanus* spp.) are common in IWP mangroves, although they occupy other habitats as well. The semi-aquatic, rusty monitor lizard (*Varanus semiremax*) inhabits mangroves, as well as inland habitats, in Australia. Individuals living in mangroves eat crabs, fish, and small mammals, but during dry seasons have no source of water other than food and seawater. To tolerate dry conditions, *V. semiremax* secretes NaCl or KCl through a nasal salt gland (Dunson, 1974). The so-called mangrove monitor, *V. indicus*, also lives in a variety of habitats, but is common in mangroves. Like *V. semiremex*, it possesses salt-secreting glands, which allow it to live in brackish environments and consume marine prey. It is an arboreal climber and a strong swimmer, with a broad diet of lizards, insects, crabs, small mammals, and bird and reptile eggs (Losos and Greene, 1988). The semi-aquatic water monitor, *V. salvator*, has been found in mangroves in Thailand (Lauprasert and Thirakhupt, 2001), but its diet has not been described.

Ctenosaura bakeri (Iguanidae) is a mangrove specialist endemic to Utila Island, located 30 km off the coast of Honduras. Like most iguanids, *C. bakeri* is primarily an herbivore, consuming flowers, leaves, stems, and fruit, but it opportunistically feeds on arthropods and eggs. It has been observed eating smaller green iguanas (*Iguana iguana*) and geckos. Because it is limited to a small area of mangroves on Utila Island, *C. bakeri* is listed as critically endangered by the IUCN. Tree hollows of *A. germinans* provide nighttime sleeping areas for *C. bakeri*, and individuals use the same tree as a home for multiple years. Abundance of *C. bakeri* in sites around Utila is correlated with tree hole abundance, so it seems that availability of these retreats may be a limiting factor for this species (Gutsche, 2005).

Snakes. Snakes are common in mangroves, but few species are mangrove specialists; most use the habitat only as a foraging ground, where they feed on lizards, frogs, mammals, birds, fish, and bird eggs (Luiselli and Akani 2002,). Mangrove snakes can be arboreal, terrestrial, arboreal–terrestrial, semi-aquatic, and generalist. The mangrove water snake, *Nerodia fasciata compressicauda*, occurs in Florida mangroves, where it preys on a variety of fish species (Miller and Mushinsky, 1990). An analysis of gut contents revealed that *Cyprinodon variegatus* is the most commonly ingested prey, but the dietary contribution of other prey species changes as snakes grow larger and are able to ingest larger fish. The smaller fish species *Fundulus similis* and *F. grandis* are common in the diet of young snakes, but as the snakes grow larger, *Fundulus* spp. are replaced by the larger *Tilapia* sp., an introduced species.

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Figure 21 *Boa constrictor* resting among *Avicennia germinans* pneumatophores (Punta Galeta, Panama; photo by WPS).

Figure 22 American crocodile (*Crocodylus porosus*) basking on seagrass bed at low tide (Punta Galeta, Panama; photo by WPS).

We know relatively little about the ecology of other mangrove snakes. The mangrove cat snake, *Boiga dendrophila*, is a mildly venomous, arboreal colubrid snake that lives in Australian and Southeast Asian lowland rainforests and mangrove swamps, where it forages nocturnally on birds, mammals, snakes, lizards, frogs, and possibly invertebrates (Minton and Dunson, 1978). In the mangroves of southern Nigeria, the most extensive in Africa, *Python sebae*, along with the Nile crocodile, *Crocodylus niloticus*, has risen to the position of a top predator, following the extirpation of leopards from the region (Luiselli and Akani, 2002).

Boa constrictors (*Boa constrictor*) are commonly seen in Central American and Caribbean island mangroves (**Figure 21**), where they feed on lizards (e.g., black iguanas), birds, mammals, and possibly hatchling crocodiles (Platt et al., 1999, 2004; W. Sousa, personal observation). Boas can be found partially submerged in shallow standing water or on emergent ground (W. Sousa, personal observation).

Crocodilians. Crocodiles can be found in mangroves in both the IWP and the ACEP. They are usually threatened where they occur because of habitat loss and their potential danger to humans; occasionally they are killed for their skins (illegal in most countries) or for food. The saltwater crocodile, *Crocodylus porosus*, is a notable resident of the IWP and the largest living crocodile species (up to 6–7 m; Whitaker and Whitaker, 1989). In the ACEP, the American crocodile, *Crocodylus acutus*, is common and can grow to 5 m in length (**Figure 22**). It is distributed along the Atlantic and Pacific coasts, from Mexico, through Central America, to South America, reaching French Guiana, and in the Caribbean islands and southeast Florida (Thorbjarnarson, 1989). In Florida, where the species is very much endangered, most individuals occupy inland mangrove swamps, bays, and creeks during fall and winter, but move to more exposed shorelines and coves during the spring and summer breeding season (Kushlan and Mazzotti, 1989). *C. acutus* nest in holes or on mounds along beaches, creeks, and abandoned levees, often under shrubby mangrove cover (Ogden, 1978; Kushlan and Mazzotti, 1989). Female crocodiles return to the same breeding sites in consecutive years, enlarging the nest with each use. Human interference (shooting and disturbance) has driven them away from many nesting sites, and much of their habitat has been destroyed. Predation on eggs by raccoons also has a significant impact on reproductive success. In more central, less developed parts of its range, *C. acutus* is common in mangrove estuaries and lakes.

Crocodiles feed on a variety of vertebrate and invertebrate prey. Juvenile *Crocodylus porosus* in the mangrove-lined Klias River in Sabah, Malaysia feed predominantly on ocypodid crabs and prawns. Other food items include a single fish species, beetles, and cicadas (Sah and Stuebing, 1996). In northern Australia, juveniles of this species feed mostly on sesarmid and ocypodid crabs, shrimp, beetles, and rats. Occasionally, slow moving fish, such as gobies and mudskippers, are also consumed (Taylor, 1979; Webb et al., 1991). Larger *C. porosus* feed on mammals, birds, reptiles, and fish (Taylor, 1979). In *R. mangle*-lined lagoons on the Caribbean coast of Mexico, American crocodiles feed on fish, crabs, shrimp, insects (beetles and true bugs), birds (cormorants and ducks), and unidentified mammals (Villegas and Soto, 2008). Juvenile and subadult crocodiles favored, in order, fish, crustaceans, and insects, while adults consumed mainly mammals and birds, along with some crustaceans, fish, and insects. Caldwell (1986) observed predation on heron by *Crocodylus acutus* in mangroves on the Caribbean coast of Panama.

Juvenile crocodiles use mangroves and mangrove associates as shelter from predators and also as nesting spots. In a survey of *C. porosus* habitat in Sri Lanka, de Silva (2008) found yearlings resting above the water on branches of the mangrove associate tree, *Dolichandrone spathacea*. He described it as an ideal refuge because the branches hide the crocodiles from avian predators. Young crocodiles used low-lying branches of *Sonneratia caseolaris* and *Excoecaria agallorha* in a similar manner (de Silva, 2008). Stands of the mangrove fern, *Acrostichum aureum*, are favored nesting sites, and the leaves are often used in nest construction.

The common or spectacled caiman (*Caiman crocodiles*) is another crocodilian found in Neotropical mangroves (Gorzula and Seijas, 1989). Adults can grow to 2.5–3.0 m, and feed on fish, birds, turtles, crustaceans, and mammals. Juveniles consume smaller prey including fish, crustaceans, mollusks, and aquatic and terrestrial insects.

6.04.5.2.4 Amphibians

The salinity of mangrove waters and soils are inimical to most amphibians, but the southeast Asian frog, *Rana cancvivova*, is a remarkable exception to this rule (Elliott and Karunakaran, 1974). The species lives in both fresh and brackish swamps; its euryhaline capability derives from the presence of urea in its plasma, and the ability to elevate levels of urea to maintain osmotic balance in saltier environments. As its name conveys, this frog also has the unusual habit of feeding largely on sesarmid crabs in brackish habitats, including mangroves.

6.04.5.2.5 Mammals

Raccoons. Four species of raccoons live in or forage in Neotropical mangroves: *Procyon lotor*, *P. cancrivorus*, *P. pygmaeus*, and *P. lotor marinus*. *P. lotor* (**Figure 23**) is known to eat the arboreal sesarmid crab, *A. pisonii*, in Florida mangroves (Beever et al., 1979), though the frequency with which this occurs and its effects on crab population size are unknown. *P. lotor* forages in the mangroves of the Florida Everglades during winter low tides (December through March), digging for mud crabs and climbing through the prop roots and even into the lower canopy in search of *A. pisonii*. During these months, raccoons become the most important predator on crabs, preempting the predatory, swimming blue crab (*Callinectes sapidus*), which is more active in summer, and is the primary predator on mud crabs during that time of year. Wilson (1989) suggested that this seasonal shift in dominant predator explained behavioral changes in the crabs. In summer, crabs escape mudflat predators, including *C. sapidus*, by climbing up onto prop roots. By contrast, in winter, when raccoons frequented the forest, no mud-dwelling crabs climbed onto prop roots, and most *A. pisonii* remained high in the canopy, presumably reducing their risk of being eaten.

P. lotor also preys upon eggs of the American crocodile, *Crocodylus acutus*; raccoons search out nests and often consume all of the eggs (Ogden, 1978; Kushlan and Mazzotti, 1989). Nests in loose, porous sand were more vulnerable to raccoons than nests in denser, sun-baked soil. In addition to eggs, *P. lotor* also prey on juvenile crocodiles, and on at least three occasions even removed radio transmitters from juvenile crocodiles before gobbling them down! Where it occurs in mangrove, *P. cancrivorus* subsists mostly on crustaceans (Novaes (2002); as cited in Gatti et al., 2006), earning it the name 'crab-eating raccoon'. However, *P. cancrivorus* also lives in other coastal habitats, where it forages on fruit, insects, and small vertebrates (Gatti et al., 2006).

Figure 23 Juvenile raccoon (*Procyon lotor*) inside hollowed-out trunk of an old *Avicennia germinans* tree (Punta Galeta, Panama; photo by WPS).

Insectivorous and piscivorous bats. The most well-known piscivorous bat is *Noctilio leporinus*, the Neotropical fishing bat. It is distributed from southern Mexico to southern Brazil, and roosts near mangroves, lakes, and rivers. *N. leporinus* feeds on insects, crustaceans, and fish, and the composition of its diet changes seasonally (Brooke, 1994; Bordignon, 2006). In a Brazilian mangrove area, Bordignon (2006) found fish were the most common food source for *N. leporinus*, followed by insects and crustaceans. Fish eaten by *N. leporinus* included the silverside *Atherinella brasiliensis* (Atherinopsidae), the silver mullet *Mugil curema* (Mugilidae), sardines (Clupeidae), and anchovies (Engraulidae). The insects eaten were mostly moths (Lepidoptera), followed by beetles (Coleoptera). The majority of crustaceans eaten was shrimp (Palaemonidae), with a few crabs (Gecarcinidae). The relative frequency of each type of prey changed throughout the year – insects and crustaceans were only eaten during warmer months, perhaps because they were unavailable or harder to find in the cold winter months. There were also differences in diet between the sexes; females ate only insects during the spring (October to December), while males continued to eat fish, insects, and crustaceans during that period. Insects may be easier to catch in the spring than fish or crustaceans, and therefore preferred food items for mother bats feeding their young (Bordignon, 2006).

Andrade et al. (2008) sampled the bat assemblages in adjacent mangrove and terra firma forests in northern Brazil. They found slightly more bat species in mangroves (18 vs. 14), but there was extensive overlap in species composition. Most of the nine species that were exclusively caught in the mangrove forest were insectivorous or piscivorous.

Otters. Otters are common in mangroves of Southeast Asia (Hogarth, 2007) and parts of Africa (Angelici et al., 2005). Two species of otters, *Aonyx capensis* and *Lutra macullicolis*, are known to use mangroves in Nigeria. Both species have been found in freshwater and brackish water habitats, but *A. capensis* is more restricted to mangroves and brackish streams. *A. capensis* eats a variety of prey, including crabs, terrestrial mollusks, snakes, and small mammals. The high availability of crabs in mangrove habitats is thought to be why *A. capensis* seems to prefer mangroves to other habitats. Both species of otter are hunted and sold as bushmeat, and thus humans become a top predator of the mangrove food web (Angelici et al., 2005).

The Neotropical otter (*Lontra longicaudis*) inhabits mangrove swamps in Central and South America. The species is distributed from northwestern Mexico south to Uruguay and northeastern Argentina (Emmons and Feer, 1997). Predominant prey items of *L. longicaudis* in coastal areas of Brazil are fish, crustaceans, and mollusks; they opportunistically feed on insects, amphibians, reptiles, birds, and small mammals (Alarcon and Simões-Lopes, 2004; Carvalho-Junior et al., 2010). This otter occurs in mangroves on the Caribbean coast of Panama (W. Sousa, personal observation), but there is no specific information on its diet in this area.

Dolphins. Both freshwater and marine dolphins use mangrove areas. Asian freshwater dolphins are one of the world's most endangered species, and conservation of mangroves may be vital to their continued existence. In the Sundarbans mangroves of Bangladesh, both Irrawaddy dolphins (*Orcaella brevirostris*) and Ganges River dolphins (*Platanista gangetica gangetica*) occur in higher numbers than in rivers where they have been surveyed in India, Indonesia, Myanmar, and Cambodia (Smith et al., 2006). Ganges River dolphins are considered apex predators and subsist on a diet of fish alone; they feed on at least 16 species of fish found in the Ganges River. However, their populations have declined drastically in recent years due to pollution, poaching, dam construction, and overfishing of the dolphins' prey (Bashir et al., 2010). As of 2008, there were only 1800 Ganges River dolphins left in the wild (Behera et al., 2008).

In a study on bottlenose dolphins on the Pacific coast of Baja California (Mexico), Acevedo (1991) found the dolphins preferred to feed in channels alongside mangroves than areas without mangroves. The invertebrates and juvenile fish associated with mangroves feed larger fish, which then invite even larger fish, seabirds, and dolphins to hunt there. The attraction of dolphins to the mangrove channels, which have high fish densities, is a key trophic interaction connecting the mangrove ecosystem to the ocean ecosystem.

Monkeys. Omnivorous capuchin monkeys have been observed foraging on marine invertebrates in Neotropical mangroves. In a mangrove forest in the state of Maranhão in northeast Brazil, a tufted capuchin, *Cebus apella paella*, was seen using shells to break open and feed on the mangrove oyster, *C. rhizophorae*, which grows in clumps attached to the prop roots of *R. mangle* (Fernandes, 1991). The white-face capuchin monkey (*Cebus capucinus)* has also been reported to feed on mangrove oysters, which it opens by striking them with rocks (Hernández-Camacho and Cooper, 1976) and has been observed foraging for marine invertebrate prey on the forest floor in *R. mangle* forests on the Pacific coast of Darien Province, Panama (N. Duke, pers. comm.).

The long-tailed or crab-eating macaque (*Macaca fascicularis*) forages in IWP mangroves, where it feeds on mangrove parts (leaves, buds, flowers, fruits, roots, and bark) and a variety of marine and terrestrial invertebrates, including crabs (Grapsoidea: *Helice tridens*, *Metaplax longipes*, and *Sesarma bidens*, and Ocypodoidea: *Uca lactera*, *U. arculata*, and *U. crassipes*), shipworms (*Bankia saulii*), razor clams (*Solen gouldii*), octopus, sipunculid worms (*Phascolosoma arcuatum*), shrimp, wood-boring caterpillars (*Zeuzera* sp.), other insects, and frogs (Son, 2003, 2004).

Tigers. Though not often thought of as a typical mangrove resident, the Royal Bengal tiger (*Panthera tigris tigris*) can be found in the Sundarbans mangroves of Bangladesh and India. This is the largest single tract of mangrove forest in the world, covering approximately 10 000 km^2 (Gopal and Chauhan, 2006). It is estimated that 400–600 tigers inhabit the Sundarbans. The present-day diet of mangrove tigers consists primarily of chital (or spotted deer, *Axis axis*), which feed on *Avicennia* and *Sonneratia* leaves, and wild boars (*Sus scrofa*), which feed on roots (Sanyal, 1987; Reza et al., 2001; Khan, 2004; Gopal and Chauhan, 2006; Ahmad et al., 2009). The biomass of potential prey abundance in the Sundarbans is comparable to that of the best Indian peninsular tiger habitat. The tigers also prey upon marine organisms, including fish, crabs, turtles, and water monitor lizards. Mangrove tigers can swim across wide rivers, and may do so because their habitat shrinks with rising of the tide. Unfortunately, this habitat is particularly threatened by human activity such as logging and conversion to agricultural land. Conflict between tigers and humans has increased recently, as humans from adjacent villages enter the mangroves to hunt or harvest (Sanyal, 1987; Reza et al., 2002; Barlow, 2009). These encounters have earned the tigers the name 'man-eating tigers' (Gopal and Chauhan, 2006).

6.04.6 Parasitism

6.04.6.1 Mosquitoes

Humankind's favorite blood-sucking insect, the mosquito, is quite abundant in mangroves. Species diversity can be high; for example, 18 species of mosquito occur in the Pichavaram mangroves of southern India (Thangam and Kathiresan, 1993). The pools of stagnant water in tidal pools, rot holes in trees, and crab burrows provide ample breeding sites. When walking through a mangrove forest, one might wonder how a forest seemingly devoid of mammal life can support such a vibrant mosquito population. The answer is that mosquitoes sustain themselves on the mammals, birds, and even fish of the mangroves. In Australia, the mosquito species, *Aedes amesii*, was observed feeding on mudskippers, which means warm-blooded animals are not their only prey (Hutchings and Saenger, 1987). Fish predation can limit mosquito oviposition, resulting in smaller mosquito populations in mangroves with high fish densities (Ritchie and Laidlaw-Bell, 1994).

6.04.6.2 Trematodes

Many of the organisms living in soft-sediment estuarine environments, including mangrove habitats, are hosts to parasites, particularly helminth parasites, yet we know little about their impact on host population dynamics or community structure (Sousa, 1991). Two studies have shown that the prevalence of larval trematode infections in intermediate host, mudflat snails, increases with proximity to mangroves. Smith (2001) found that populations of the mangrove snail, *Cerithidea scalariformis*, had the highest prevalence of larval trematode infections in locations near dead mangrove snags, where wading birds, the definitive hosts of adult trematodes, frequently perched and defecated. Their droppings conveyed trematode eggs or miracidia larvae to snails on the mudflat below. Lafferty et al. (2005) documented a similar pattern, albeit on a larger spatial scale. The prevalence of larval trematode infections in populations of the estuarine snail, *Batillaria minima*, was positively correlated with the percent cover of mangroves within 25 m of 16 collection sites ($R^2 = 0.48$, $P = 0.003$). Although the authors were unable to quantify bird use of the mangrove vegetation, they hypothesized that, as in Smith's study, bird definitive hosts of the trematodes roosted in the trees, enhancing local transmission of the parasites to the intermediate host snails, which are relatively sedentary.

6.04.6.3 Pathogenic Fungi

In addition to their role as decomposers, some fungi are mangrove pathogens, attacking leaf and stem tissues. Probably the most notorious and controversial of these cases is the reported epidemic dieback of large areas of *Rhizophora* forest in The Gambia, West Africa, due to a gall-forming fungus (Teas and McEwan, 1982). Jiménez et al. (1985) argued that the authors had presented no rigorous evidence that a fungal pathogen was responsible for the mortality. In fact, the same or very similar gall-forming fungus, *Cylindrocarpun didymum*, can infect a high proportion of *Rhizophora* trees in Florida, Panama, and Costa Rica without causing noticeable mortality. Jiménez et al. (1985) attributed the extensive mortality in Gambian forests to the stresses associated with variable rainfall in an arid environment, rather than the fungus. This is not to say that pathogenic fungi are not a significant source of tree mortality. *R. mangle* experiences significant dieback and mortality due to the imperfect fungus *Cytospora rhizophorae*, which infects seedlings and trees through wounds caused by herbivores or physical damage (Wier et al., 2000). In southwestern Puerto Rico, Wier (2004) found cankers in association with dead branches and trunks, and estimated as much as 32% mortality due to *C. rhizophorae* infections. The presence of this fungus was correlated with proximity to arboreal nests of the termite *Nasutitermes costalis*. This termite inhabited 40% of injured red mangroves; Wier (2004) presented circumstantial evidence that the fungus is carried and disseminated by them. Spores germinate in wounds on branches and roots, and the developing cankers weaken trees as they grow, increasing the likelihood of mortality.

The polypore basidiomycete fungus *Phellinus swieteniae* mostly infects living *A. germinans* trees in forests on the Caribbean coast of Panama (**Figure 24**). It aggressively attacks live hosts, hollowing the trunks of many of the larger individuals. While the unique and extensive vascular system of *A. germinans* (Zamski, 1979) allows most trees to survive such attacks, growth and reproduction are likely reduced. Such heart rot is rarely seen in co-occurring *R. mangle* or *L. racemosa* trees (Gilbert and Sousa, 2002).

Figure 24 Pathogenic fungus (*Phellinus swieteniae*) infecting the trunk of an *Avicennia germinans* tree (Punta Galeta, Panama; photo by WPS).

Fungi also damage and kill leaves. *R. mangle* has 10 known foliar pathogens, while *L. racemosa* has three and *A. germinans* only one (Farr et al., 1989; Gilbert et al., 2002). Variation in the susceptibility of different species to foliar pathogens may be related to the concentration of salt in and on their leaves. *R. mangle* is a salt excluder, so its leaves are not salty, and it is infected by a variety of pathogens. By contrast, *L. racemosa* and *A. germinans* secrete salt and their leaf tissues are saline; this may inhibit fungal spore germination or hyphal growth, and explain the resistance of these species' leaves to fungal attack (Gilbert et al., 2002).

See Hyde et al. (1998) for additional examples of fungal pathogens of living leaf and stem tissues in mangroves.

6.04.7 Provision of Substrate and 3D Structure

6.04.7.1 Substrate for Fouling Communities

The aerial prop roots of *Rhizophora* provide attachment space for a diverse assemblage of marine benthic organisms that recruit to the intertidal and especially subtidal surfaces of the roots (see photos in Rützler and Feller, 1996; **Figure 25**). This assemblage, referred to as a 'fouling community', is typically dominated by filter- and suspension feeders, and includes sponges, barnacles, bivalves, serpulid and sabellid polychaetes, sea anemones, hydroids, hard and soft corals, bryozoans, and tunicates, as well as algae (Sutherland, 1980; Bingham, 1992; Ellison and Farnsworth, 1992; Garrity and Levings, 1993; Goodbody, 1993, 2000, 2003, 2004; Levings and Garrity, 1994; Levings et al., 1994; Bingham and Young, 1995; Farnsworth and Ellison, 1996; Rützler and Feller, 1999; Diaz et al., 2004). Sponges and tunicates are often the predominant groups, and competition for space can be intense. The species composition, diversity, and structure of these assemblages vary considerably in space, both locally and geographically, and in time, especially in response to disturbances, such as low-salinity conditions following heavy rainfall (Goodbody, 1961) and strong tidal flows (Bingham and Young, 1995).

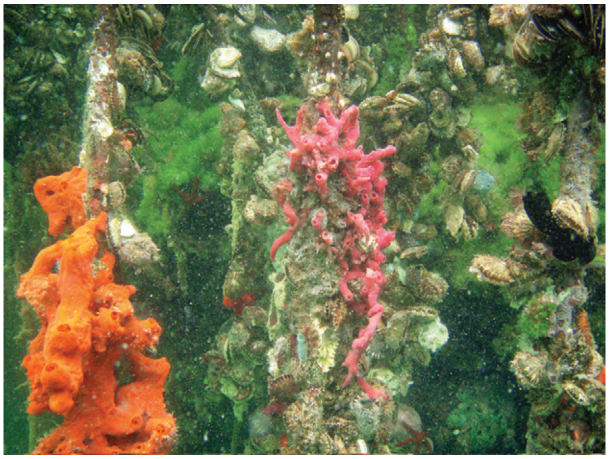

Figure 25 Fouling community growing on *Rhizophora mangle* prop roots. This assemblage includes sponges, bivalves, and algae (Bocas del Toro, Panama; photo by EMD).

A variety of trophic interactions among prop root dwelling organisms have been studied. Wulff (2000, 2005) investigated the causes of differences in the species composition of sponge assemblages on two *R. mangle* cays in Belize – Twin Cays and Pelican Cays. At Twin Cays, mangroves grow in peat banks, surrounded by open sediment and seagrass meadows, whereas the mangroves on Pelican Cays grow in peat that overlies a coral reef. At Pelican Cays, the assemblage was comprised of sponge species that commonly grow on coral reefs, while the species composition of the Twin Cays assemblage was typical of the majority of *Rhizophora* stands in the Caribbean, in which prop roots are embedded in soft sediment environments. Sponge-eating predators, especially seastars (*Oreaster reticulatus*) and angelfishes (*Pornacanthus arcuatus* and *P. paru*), were much more abundant at Pelican than Twin Cays, presumably because the complex microtopography of the coral reef at Pelican afforded shelter from higher-level predators. In addition, the piscivore, *Sphyaena barracuda*, was common at Twin Cays but rare at Pelican Cays. Wulff (2005) reciprocally transplanted (with controls) several species of sponge between habitats to compare habitat-specific growth rates, and protected half the transplants to Pelican Cays with cages to evaluate the impact of predators. Most sponges transplanted from Twin to Pelican Cays were consumed within 3 days, unless protected by cages; modest portions of two species remained, but had disappeared by 7 months. All control sponges at Twin Cays survived. Reef sponge species transplanted to Twin Cays were overgrown and competitively excluded by faster-growing resident species. Wulff highlighted the tradeoff between defenses against predators and growth rate in explaining the spatial variation in sponge assemblages between the two sites. In the predator-rich environment of Pelican Cays, coral reef sponge species, which are better defended chemically and morphologically against predators, persist and dominate, while in the low predation conditions at Twin Cays, faster-growing, less-defended species outcompete the slower-growing defended species for space on root surfaces.

Predation can also minimize the potentially damaging effects of some epifaunal species on prop roots. Barnacles (*Balanus* spp.) are a common member of prop root fouling assemblages. With strong recruitment and growth, barnacles can encrust the root surface and cover up many lenticels, inhibiting gas exchange. In this circumstance, barnacles can cause up to a 30% decrease in root growth rate and 52% decrease in net root production (Perry, 1988). However, on the Pacific coast of Costa Rica, predation by snails (*Thais kiosquiformis* and *Morula lugubris*) and a hermit crab (*Clibanarius panamensis*) strongly limits barnacle cover once a prop root has grown into contact with the bottom, allowing these predators access.

Despite the generally negative effects of epifauna, mangroves benefit from the presence of some fouling species. For example, facultative mutualisms exist between some species of sponges and the trees on whose roots they live. In Belize, Ellison et al. (1996) transplanted the sponges *Tedania ignis* and *Haliclona implexiformis* onto *R. mangle* roots and found that the presence of live sponges initiated nutrient exchange between sponge and tree through fine adventitious rootlets that penetrate the sponge tissue. Stable isotope analysis showed that these rootlets uptake nitrogen from the sponges, and the sponges obtain carbon from the tree roots. Presumably because of this carbon input, sponges grew better on roots than on polyvinyl chloride (PVC) tubes of the same diameter and depth as the roots. This does not occur with all root-fouling organisms, as no nutrient exchange was detected between mangrove roots and the red alga *Acanthophora spicifera*. Another benefit of root-fouling sponges and ascidians is that they prevent root-boring isopods from damaging the roots. When sponges and ascidians were experimentally removed from *R. mangle* roots, the roots had more damage from isopods and 55% lower growth than roots with protective sponge and ascidian cover (Ellison and Farnsworth, 1990, 1992).

6.04.7.2 Nursery Grounds, Refuge from Predation, or Both?

As our ability to trace the fate of mangrove elements through food webs and among habitats has radically improved with the application of stable isotope methods and more rigorous sampling of resource and consumer populations and their movements, the significance of mangroves as nursery or refuge habitats has become the subject of considerable debate. What has long been a rallying cry for mangrove conservation, that mangroves are important nursery grounds for fishes and crustaceans of economic and human nutritional importance, is now a much more nuanced discussion about geographic or regional variation in this role. Increasingly, field experimental methods are being used to elucidate the mechanisms for particular patterns of association between fish or prawns and mangroves.

Beck et al. (2001: 635) proposed the following definition of a nursery habitat: "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." This contribution may be reflected in any of several demographic features, including density, growth, survival, and/or rates of movement into the habitats favored by adults (Nagelkerken, 2009). Dahlgren et al. (2006) later suggested that this definition be expanded to include habitats that make a greater than average contribution to adult populations, even if not on a per-unit-area basis They introduced the term 'effective juvenile habitat' to describe this broader collection of above-average source areas. Sheaves et al. (2006) and Adams et al. (2007) commented further on these definitions.

The concept of mangroves as a nursery habitat emerged from the observation that juvenile densities of numerous species of prawns and fish are higher in mangroves than in adjacent nearshore seagrass or coral reef habitats (Odum et al., 1982; Robertson and Duke, 1987b, 1990; Thayer et al., 1987; Blaber et al., 1989; Vance et al., 1990; Laegdsgaard and Johnson, 1995; see review by Robertson and Blaber (1992); and critical comments on the evidence by Sheridan and Hays (2003)). The adults and juveniles of some of these species live exclusively in mangrove estuaries and so are permanently estuarine, but in most of the cases in which juveniles of a species are found concentrated in mangroves, the adults live and spawn outside the estuaries, and larvae or postlarvae are transported by incoming tides, or actively migrate, into the estuaries. These species are estuarine dependent, but not permanent residents. As the juvenile stages of these estuarine-dependent species of prawns and fish mature, they begin to move toward the mouths of estuaries (evidenced by shifts on size-structure) and then presumably to the near- or offshore habitats of the reproductive adult population. However, quantitative information on the movement of newly mature individuals into adult populations is very sparse, making it difficult to unambiguously designate particular habitats as nurseries (Sheridan and Hays, 2003; Verweij et al., 2007). Nagelkerken (2009) discussed the methodological challenges to accurately quantifying these spatial dynamics.

In any one assemblage of prawns or fish, species exhibit a range of dependency on mangroves. For example, in Bonaire (Leeward Antilles), high densities of juveniles from four commercially important fish species use mangroves as their primary habitat, and eight more species use mangrove habitat in addition to seagrass beds and coral reefs (Nagelkerken et al., 2000c; also see Nagelkerken et al., (2000a, 2001)). Similarly, Newell et al.'s (1995) study of the diet of prawns on the west coast of Peninsular Malaysia found that juvenile *Penaeus merguiensis*, which inhabit mangrove creeks, rely heavily on mangrove detritus for their nutrition. By contrast, adults of this species, and both the juveniles and the adults of the co-occurring *P. sculptilis*, which live offshore, do not appear to exploit mangrove detritus as a food source. While the majority of coral reef fish species do not rely on back-reef habitats (seagrasses or mangroves) for juvenile development, there is a strong dependency for some, as judged by the relative densities of juveniles found in different habitats (Nagelkerken et al., 2000a, 2000c; Dorenbosch et al., 2005; Lugendo et al., 2005; Nagelkerken, 2007). Additional indirect evidence that mangroves serve as nurseries for particular species comes from the observation that their adult densities in seagrass beds or on reefs are lower when there is no mangrove habitat for juveniles nearby (Nagelkerken et al., 2001, 2002; Dorenbosch et al., 2004, 2005, 2007; Mumby et al., 2004; Jelbart et al., 2007; Unsworth et al., 2008). Comparing IWP and ACEP systems, mangroves appear to serve as the primary nursery habitat for most of the ACEP fish species that live as adults on coral reefs and as juveniles in back-reef areas, while seagrass beds are the primary nursery habitat for comparable species in the IWP (Nagelkerken, 2009). As discussed earlier, this difference could reflect the large differences in tidal regimes in the two regions, and the degree to which mangroves provide fish habitat at low tide. However, as Nagelkerken (2009: 364) cautioned: "…we still know relatively little of the precise ontogenetic habitat shifts of decapods and fish among tropical coastal habitats."

Robertson and Blaber (1992) suggested three explanations for the use of mangroves by juvenile shrimp and fish. First, they may gain some protection from visual predators in the turbid water often associated with mangroves. Second, food availability to juveniles may be higher in mangroves than adjacent sand- or mudflats, seagrass beds, or coral reefs. Finally, the structural complexity of mangrove root systems, that is, prop roots, pneumatophores, and fallen logs and branches, shelters juveniles from predators. As Nagelkerken (2009) points out, these hypotheses are not mutually exclusive. For example, the 3D structure of prop roots may reduce the risk of predation, but also increase the surface area for growth of epibiont assemblages and associated prey species (Laegdsgaard and Johnson, 2001).

Evidence that juvenile fish suffer lower rates of predation due to the turbidity of mangrove waters is largely circumstantial (Robertson and Blaber, 1992). Blaber and Blaber (1980) observed positive associations for some species between juvenile recruitment and turbidity in a subtropical estuary in Queensland. Australia. Subsequent sampling studies in the Natal estuaries of southeastern Africa (Cyrus and Blaber, 1987a, 1987b) and the Embley Estuary in tropical northern Australia (Cyrus and Blaber, 1992) demonstrated statistically significant positive correlations between CPUE and turbidity for 35% (7/20) and 11% (5/45) of the species sampled, respectively. Lab preference trials offering fish a choice of different turbidity levels demonstrated preferences that were mostly consistent with the distributional patterns observed in the field (Cyrus and Blaber, 1987a, 1987c). Another observation that is consistent with the hypothesis is that piscivorous fish are more abundant in mangroves that receive little terrestrial runoff and therefore have clearer water (Blaber et al., 1985; Blaber, 1986). However, none of these studies presented data on actual rates of predation at sites or times of year that differed in water clarity, and an alternative explanation that turbidity was associated with higher levels of suspended food, as opposed to lower predation, was not evaluated. More recent studies of the influence of turbidity on juvenile distribution provide either no support for the hypothesis or no evidence that the response to turbidity is highly species specific (Macia et al., 2003; Johnston et al., 2007; Huxham et al., 2008).

The hypothesis that greater availability of food and faster growth in mangroves explains their attraction as habitat to the juveniles of certain species of fish and shrimp is also not well supported by available data (Nagelkerken, 2009). Sampling studies (plankton net hauls or sediment cores) generally find that prey availability is higher in seagrass beds than mangroves or coral reefs. The few studies that have compared juvenile growth in different habitats, often by enclosing fish in cages over specific substrates, have yielded mixed results. A few species grow faster in mangroves, but others grow better in coral, or over beds of macroalgae. In most cases, there was no detectable difference in growth between individuals living in mangroves and those occupying seagrass beds (e.g., Grol et al., 2008). The number of such studies is very small, however, so it is premature to generalize.

As noted earlier, the pattern of mangrove exploitation as foraging habitat by juvenile fish and shrimp is very much tied to the predominant tidal regime of the region. In areas like the Caribbean, with a very limited tidal range, a substantial portion of the fringing mangrove habitat is inundated and accessible at all times. In these areas, juveniles of numerous species forage across multiple habitats, and in the case of some nocturnal feeders regularly migrate at dusk from the daytime shelter of mangroves to neighboring seagrass beds and sand flats to feed on benthic invertebrates, suggesting that mangroves are not inherently richer in prey (Rooker and Dennis, 1991; Nagelkerken et al., 2000b; Nagelkerken and van der Velde, 2004a, 2004b; Verweij et al., 2006b; Nagelkerken, 2009; Hammerschlag and Serafy, 2010). For some species, there appear to be separate subpopulations of mangrove and seagrass bed feeders (Nagelkerken and van der Velde, 2004b) in the same location. Most species whose juveniles are typically associated with Caribbean seagrass beds appear to spend little or no time foraging in neighboring mangroves (Nagelkerken and van der Velde, 2004a, 2004b). Of 23 such species on Curaçao in the Leeward Antilles, plus two others whose juveniles are reef dwellers, only two species, one a herbivore and the other a carnivore, had isotopic signatures that indicated concentrated feeding in mangroves, while two other carnivore species foraged in both mangrove and seagrass habitats at some sites. Prey of the piscivore, *Sphyaena barracuda*, consisted of fish species schooling at interface of mangroves and seagrasses. Juveniles of the other 18 species of seagrass fish species showed no isotopic evidence of feeding in nearby mangroves.

By contrast, the large tidal ranges of the IWP mean that most mangroves are only inundated and accessible during high tide. This is when fishes and shrimp move from seagrass beds and deeper channels and creeks into the forest to feed (Sasekumar et al., 1984; Robertson and Duke, 1990; Vance et al., 1990, 1996; Sheaves and Molony, 2000). For this same reason, in coastal areas of the IWP, seagrass beds, rather than mangrove stands, serve as the primary nursery habitat for fishes (Nagelkerken, 2009). However, mangroves do appear to fill this role in larger estuary systems of the region (Blaber et al., 1989; Laegdsgaard and Johnson, 1995).

In summary, higher food availability and growth rates do not provide a general explanation for the higher abundance of juvenile fish and shrimps in mangrove habitats, but it is certainly an important factor in particular cases. Better information on the diets, foraging behavior, including movement, and growth rates of juveniles across the mosaic of shallow nearshore habitats is critical for a definitive evaluation of this hypothesis.

Lastly, is it the 3D structure of mangrove and associated lessening of predation risk that attracts juvenile fish and shrimp to mangroves? A number of studies have experimentally tested the effect of mangrove-mimicking structure, with and without fouling algal epibionts, on fish habitat choices. Laegdsgaard and Johnson (2001) found that more juvenile fish were attracted to structures that mimicked *Avicennia* trunks and pneumatophores than areas without structure, and that structures which had been allowed to develop a cover of algae attracted 4 times as many juveniles as clean structures. Algal cover afforded greater availability of invertebrate prey. Seven species exhibited a significant preference for the artificial structures; five of these selected the fouled structures, while two species simply chose structure over no structure. In laboratory trials, four out of five species avoided structure in the absence of a predator, but all of them sought shelter in the presence of a predator. The choice of habitats by adults of the same species were unaffected by the presence of the predator, presumably because they were of an invulnerable size. In the field, tethered individuals of *Sillago* spp. survived better over the period of one high tide in mangroves and seagrasses (both 91.5%) than on the open mudflat (37.5%). Similarly, Acosta and Butler (1997) studying habitat use by juvenile spiny lobster (*Panulirus argus*) in Belize, found that tethered newly settled individuals experienced considerably lower predation among *R. mangle* prop roots than in coral reef crevices or seagrass. Tethered larger juveniles had equal survival in mangroves and coral crevices, both higher than in seagrass. Primavera (1997) conducted mesocosm experiments to evaluate the role of mangrove habitat structure in mediating fish predation on juvenile prawns. Prey species were the greasyback shrimp (*M. ensis*), white shrimp (*P. merguiensis*), and tiger shrimp (*Penaeus monodon*); tested predators were sea bass (*Lates calcarifer*) and mangrove snapper (*Lutjanus argentimaculatus*). For some fish predator–prey prawn combinations, intermediate densities of *Sonneratia griffithii* pneumatophores reduced rates of prawn mortality compared to those observed in bare sand or sand with submerged coconut bract debris treatments, while other predators were largely unaffected by the presence of structure. The difference in outcome was related to predator behavior and speed; pneumatophores interfered with predation by the slow-moving mangrove snapper, but not the fast-swimming sea bass. Thus, the refuge effect of pneumatophores was contingent on several features of the system: pneumatophore density, the species of prawn, and species of fish predator. In a similar mesocosm experiment, Macia et al. (2003) examined the independent and interactive effects of pneumatorphore density (*A. marina*), water turbidity, prey density, and substrate type on rates of predation by the thorn fish (*Terapon jarbua*) predation on juvenile white shrimp (*P. indicus*) and brown shrimp (*Metapenaeus monoceros*). Focusing on their results with respect to pneumatophore density and water turbidity, they found that both features lessened rates of predation, but the exact patterns with respect to different densities of pneumatophores and levels of turbidity were complex and prey-species specific. It was unclear whether prey and/or predator behavioral responses to these features were responsible for the observed patterns of predation.

Several recent *in situ* experimental studies have attempted to tease apart the multifactorial influences of mangrove habitat structure on fish behavior and predation risk. A series of three related studies have employed artificial habitat units to investigate the influence of habitat structure and food availability on fish assemblages in a lagoonal setting on the island of Curaçao in the Leeward Antilles. Cocheret de la Morinière et al. (2004) installed open cage-like structures (1 m W × 1 m L × 0.8 m H) that offered varying degrees of spatial complexity (i.e., different densities of hanging PVC pipes that mimicked mangrove prop roots) and shading (i.e., varying the number of layers of black shading fabric on top of the structure) in a factorial design. The experiments units were positioned over monospecific seagrass beds of similar cover and length, and then numbers of individuals of recruiting species were recorded. Both spatial complexity and shade resulted in higher densities of fish, but the responses were both species- and foraging-style-specific. Diurnally active species preferred the most structurally complex units and moderate shade. The responses of nocturnally foraging species during daytime periods of sheltering varied by species; one preferred higher complexity and higher shade, while the other increased in abundance with added shading, but its abundance did not vary with structural complexity. Since the experimental units were kept clean of epibionts, variation in food availability was not a factor in the preference of fish for particular experimental treatments. Shelter from predation and/or high levels of ultraviolet (UV) radiation were suggested to be the primary factors motivating the choice of units offering complex structure and shade.

Expanding on the previous study, Verweij et al. (2006a) examined the effects of structure, food, and shade on the attraction of juvenile fish to mangroves and seagrass beds as compared to bare muddy substratum. They installed experimental units, very similar to those employed by Cocheret de la Morinière et al. (2004), that offered various combinations of imitation seagrass (plastic strips) and mangrove structure (hanging PVC pipes) and observed patterns of habitat selection by fish. Access to food was manipulated by offering structures that had developed a cover of algal epibionts and allowed fish access to the muddy substratum for foraging, and comparable structures that had been cleaned of epibionts and had a cotton sheet installed across the bottom of the structure to prevent benthic foraging. Light levels were manipulated by installing black shading fabric over half the replicates of each structural treatment. Fish responses varied with trophic category and diurnal versus nocturnal feeding habit. Diurnal herbivorous fish preferred more complex artificial habitats that had accumulated algal epibionts: mangrove plus seagrass > mangrove only > seagrass only or sand (see also MacDonald et al., 2008). Sunlit treatments had higher abundances of herbivores than shaded treatments. These species were observed feeding on attached algae, which were most abundant on the artificial mangrove roots and presumably in the unshaded treatments. Herbivores exhibited no habitat preference when cleaned structures were offered. As a group, fish species that forage diurnally on benthic invertebrates (zoobenthivores) showed no clear preference among the treatments. One exception to this pattern was a species that avoided treatments in which the bottom was covered with fabric, but showed no other discrimination with respect to structure or shade. Habitat selection by fish in these two trophic categories (diurnal herbivores and zoobenthivores) appears to be mainly a response to food availability, rather than shelter. However, the complex structure of mangrove roots undoubtedly provides immediate refuge in the event of a predator attack (Laegdsgaard and Johnson, 2001).

During daytime, fish species that forage for benthic or planktonic invertebrates in seagrass beds at night preferred to occupy experimental units that offered structure and shade, regardless of epibiont cover or access to the benthos. Artificial seagrass cover alone or the combination of seagrass and artificial mangrove prop roots were preferred in the absence of shade, but if shaded, as they would be under natural conditions, mangrove prop roots alone were equally attractive. These species rested but did not feed in the high-complexity units during the day. Similarly, the piscivore, *S. barracuda*, was attracted to structure of any kind (seagrass, mangrove, or the combination) regardless of epibiont cover, access to the benthos, or shade. Small individuals may have been reducing their risk of predation, but larger individuals were likely concealing themselves in the structure as a means of ambushing their primary prey, the schools of sardines, anchovies, and silversides that school at the interface between mangroves and seagrass beds.

Most recently, Nagelkerken et al. (2010) investigated in greater detail the effects of mangrove prop root architecture on the same fish assemblages. They installed the same type of artificial mangrove units with PVC pipes as roots, but varied structural features such as pipe length, orientation, and 3D complexity, and observed the effects on absolute and relative abundances of different fish species. All experimental units were shaded to mimic light levels below a mangrove canopy, and the substratum was covered with a cotton cloth to eliminate access to benthic food as a variable. The artificial units were cleaned every other day, so that differences in epibiont abundance would not influence fish choice. Surprisingly, neither pipe length nor the complexity of their spatial arrangement affected the composition of fish inhabiting the structures. However, pipe orientation (standing vs. hanging) had a large influence on composition, as did inter-pipe spacing. Fish abundance and species richness were higher with standing as compared to hanging artificial roots. Species-specific differences were also evident: demersal species preferred units with standing pipes, while the pelagic piscivore, *S. barracuda*, was more frequently observed in units with hanging pipes. The abundances of both demersal and semi-pelagic fish species decreased with greater inter-pipe distances, a response the authors interpreted as meaning that distance to refuge is a critical factor in the response of fish to mangrove prop root structure.

In sum, current evidence indicates that for some species of juvenile fish and prawns, the structural complexity afforded by mangrove prop and aerial roots and the shade of a fringing canopy are attractive, independent of food availability. Reduced risk of predation or avoidance of high UV levels may be the ultimate explanations for this habitat preference. In other cases, the availability of food organisms, either algal epibionts on submerged roots or small mobile invertebrates living amongst the epibionts, and/or the spatial heterogeneity created by epibionts are key attractants. Clearly, there is much more to be learned about the nature of mangroves' role as a nursery habitat (Adams et al., 2006). Faunce and Serafy (2006) reviewed 50 years of literature reporting the findings of field studies of mangrove fish assemblages. They examined over 111 fish surveys, with the goal of identifying general principles about the organization and dynamics of these assemblages. They found the methods, collected data, and analyses so inconsistent as to frustrate cross-study comparison. The studies tended to be short term, largely descriptive, and focused on assemblages of species, rather than the demographies and environmental and resource requirements of individual species and their populations. Very few studies provided species-specific estimates of abundance, growth, reproduction, and mortality, information that is essential to a comprehensive evaluation of the value of mangroves as fish habitat. Despite the weaknesses they identified in available data, Faunce and Serafy (2006: 2) conclude that "mangrove habitats likely play a variety of roles in the lives of associated fishes: feeding areas for some species or life stages, daytime refugia for others, nursery and/or nesting areas for yet more."

6.04.8 Concluding Remarks

Research on mangrove trophic interactions has rarely been framed as a test of theory in food-web ecology and, as a consequence, is seldom cited in textbooks or synthetic reviews as illustrating general principles. It is our hope that this chapter will help bring past and emerging research on mangrove trophic interactions to the attention of ecologists working in other habitats. As a study system, mangroves hold great promise for informing general ecological theory. For example, the environmental setting is tailormade for investigations of the importance of trophic subsidies among habitats to local population and community dynamics, that is, reciprocal exchanges among mangrove, coastal marine, riverine, and terrestrial habitats. Experimental manipulations of resource availability and the densities of consumers have demonstrated both bottom-up resource limitation and strong top-down consumer control in different compartments of the food web. Crabs are particularly strong interactors, exerting top-down control over litter dynamics and seedling recruitment in numerous mangrove forests. Finally, recent confirmation that mangroves are key sites of carbon storage has major implications for the prioritization of habitat protection and management efforts in response to accelerating climate change.

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