ALIENS IN PARADISE: A COMPARATIVE ASSESSMENT OF INTRODUCED AND NATIVE MANGROVE BENTHIC COMMUNITY COMPOSITION, FOOD-WEB STRUCTURE, AND LITTER-FALL PRODUCTION.

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ABSTRACT

Mangrove benthic community ecology and food-web structures in introduced and native mangroves were examined in detail in this dissertation. Introduced mangroves support a diverse macrofaunal community, primarily composed of polychaetes, oligochaetes and amphipods. The dominance of introduced and cryptogenic fauna in mangrove sediments indicates that mangroves may facilitate the persistence and spread of introduced species in Hawaii.

Examination of mangrove food webs indicated that the relative importance of mangrove detritus to detritivores differed in introduced and native mangrove communities. Based on $\delta^{13}C$ and $\delta^{15}N$ stable isotopic analysis, it was determined that few Hawaiian detritivores appear to rely on mangrove leaves for their diets. Based on $\delta^{15}N$, it appeared that particulate organic matter and/or benthic microalgae, rather than mangrove detritus, supported infauna from Hawaiian mangroves. In addition, significant differences in stable isotopic values of sandflat and mangrove sediment infauna suggest a landscape driven shift in stable carbon isotopic values to more depleted, possibly mangrove-influenced values with increased penetration into the interior of mangroves.

Mangrove food-webs were explored in more detail in native mangrove forests on Kosrae, Micronesia. Mangal contribution to the diets of the mangrove crab, *Scylla serrata*, ranged from 70-100% for Okat and Utwe watersheds. In contrast, crabs collected from the Lelu watershed had a lower percentage of mangal contribution (53-73%), and higher $\delta^{13}C$ and $\delta^{34}S$ indicating that these crabs may forage more on adjacent reef flats, resulting in enriched tissue isotopic values. Mangrove faunal associates, including

grapsid crabs and benthic infauna, served as important food sources for the crabs, as indicated by their corresponding $\delta^{13}C$ and $\delta^{15}N$ values. Discriminant analysis indicated that mangrove crabs restrict their movement to within their resident watershed.

Based on four months of litter sampling on Oahu, it was concluded that introduced mangroves in Hawaii export a greater proportion of litter relative to native forests in Puerto Rico. Export differences between sites may be a function of the physical environment (e.g., width of the forest) and rainfall patterns.

To conclude, the research presented in this dissertation enhances our understanding of the benthic community ecology and food-web structure in introduced and native mangrove communities.

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CHAPTER 1. INTRODUCTION

Elucidating the role mangroves play in structuring faunal communities, including community composition and food-web structure, is fundamental to understanding the importance of mangroves in near-shore, sub-tropical and tropical ecosystems. Mangrove root systems perform similar functions as other dense aquatic vegetation by providing cover from predators and extending the availability of hard substrate for encrusting fauna such as barnacles and bivalves (Shokita et al. 1989; Alongi and Sasekumar 1992). In addition, mangroves act as dramatic ecosystem engineers (c.f., Jones et al. 1997) by altering water flow and trapping sediments, limiting coastal erosion (e.g., from storms), contributing to the formation of new islands, and extending shorelines (Chapman and Ronaldson 1958; Bird 1971; Odum 1971; Lugo and Snedaker 1974; Woodroffe 1992). While much has been learned about mangrove ecosystems (Robertson and Alongi 1992; Hogarth 1999; Naylor et al. 2000), many aspects of mangal ecology deserve further study, including the structure of food webs, processes of detrital decomposition, and impacts of mangroves as invading species (Alongi and Sasekumar 1992; Robertson and Alongi 1992; Twilley et al. 1997; Fry and Ewel 2003). This dissertation is a comparative study of the ecological impacts of mangroves in invaded and native habitats.

Background

Mangroves are opportunistic trees or shrubs that grow in the intertidal zone along tropical and subtropical coasts and estuaries (Stoddart 1980; Wester 1981). Mangrove stands typically develop into swampy forests, called "mangals", which are among the

most productive of marine habitats (Crisp 1975; Duarte and Cebrian 1996; Alongi 1998). Mangals occupy ≥ 60% of tropical coastlines (Duke 1992, 2002), making them essential components of low-latitude coastal ecosystems. They produce renewable resources for humans (e.g., wood, charcoal, tannins for hide processing and ink production) and provide habitats for commercially important fishes and invertebrates (Lugo and Snedaker 1974; Thayer et al. 1987; Odum 1988; Rezende et al. 1990; Vance et al. 1990, 1996, 2002). In addition, mangroves limit coastal erosion by trapping sediments, and buffering intense wave and storm energy (Chapman and Ronaldson 1958; Bird 1971; Odum 1971; Woodroffe 1992).

Mangrove introduction history in Hawaii

The Hawaiian Islands have no native mangrove species, primarily due to extreme geographic isolation and young geologic age. Between 1902 and 1946, seven species of mangroves were introduced from Florida, the Bahamas, and the Philippines to Hawaii (Molokai and Oahu) primarily to stabilize shorelines and secondarily to provide forage for bees (Munro 1904; MacCaughey 1917; Degener 1945, 1946; Wester 1981; Allen 1998). Three of the introduced mangrove species (*Rhizophora mangle* from Florida, *Bruguiera sexangula* from the Philippines, and *Conocarpus erectus* from Florida and the Bahamas) have proliferated, but only *R. mangle* maintains viable, abundant populations on all the main Hawaiian Islands (Wester 1981; Allen 1998). *Bruguiera sexangula* maintains small stands on Oahu. *C. erectus* occurs occasionally on Oahu, Lanai, and Maui (Wagner et al. 1990; Allen 1998) and has become a popular ornamental tree in the Hawaiian Islands. The red mangrove, *R. mangle* inhabits large portions of low-energy

Hawaiian coastlines (e.g., the lagoons of south Molokai, Kaneohe Bay, and Keehi Lagoon) as well as the banks of streams and drainage channels (e.g., in Pearl Harbor and along the Ala Wai Canal, Figure 1) (Wester 1981; Allen 1998). *Rhizophora mangle* has high dispersal capabilities, broad environmental tolerances, and few natural enemies in Hawaii (Allen 1998; Cox and Allen 1999; Steele et al. 1999); as a result, the mangrove habitat appears to be expanding rapidly in Hawaii (D'Iorio et al. 2003). While introduced mangroves fundamentally alter Hawaiian coastal ecosystems, their effects on sediment community structure, species invasions, and detrital food webs have not been evaluated.

Potential Impacts of Invasive Mangroves

Prior to the recent invasion of mangroves (and other exotic plant species), the high to mid-intertidal zone of Hawaii lacked vascular plants (Wester 1981; Allen 1998). The introduction of vascular plants, particularly mangroves, to intertidal habitats can dramatically alter a variety of ecologically important habitat characteristics (e.g., Posey 1988, 1993; Callaway and Josselyn 1992; Levin et al. 1996; Levin and Talley 2000; Talley and Levin 2001). Major environmental parameters altered by mangal development typically include rates of water flow, sediment grain size and organic-matter content, oxygen and sulfide concentrations (both in bottom- and pore-waters), salinity, and the availability of hard substrates (Alongi 1987; Robertson and Alongi 1992). All of these factors can substantially influence the structure and dynamics of benthic communities (see reviews by Sanders 1969; Gray 1974; Rhoads 1974; Boesch 1977; Pearson and Rosenberg 1978; Nowell and Jumars 1984; Weston 1990; Posey et al. 1993, 1997; Snelgrove and Butman 1994; Arrow et al. 2000; Levin and Talley 2000).

Hawaiian soft-sediment community composition is very likely to be altered by the presence of introduced mangroves. Native mangroves in Southeast Asia and Florida are typically colonized by specific, potentially co-evolved, fauna having few species in common with sand or mud-flat ecosystems (Sasekumar 1974; Frith 1977; Sheridan 1997). In contrast, because mangroves were recently introduced to Hawaii without their co-evolved fauna, Hawaiian mangrove habitats appear to lack the extensive fauna typical of native mangrove stands (Walsh 1967; Kay 1987), and may be ecologically underutilized (i.e., have open niche space). Invasive species with broad environmental tolerances may readily colonize these open niches. Thus, mangroves may facilitate the establishment of exotic species in Hawaii, especially near sources of species introductions via ballast water and ship-hull fouling (e.g., Carlton and Geller 1993; Coles et al. 1999), such as Honolulu and Pearl harbors. It is therefore quite feasible that Hawaiian mangals provide a haven for introduced species which may in turn threaten the ~500 species of marine and estuarine benthos endemic to Hawaii, possibly by competing for space, food resources, and/or a combination of these factors (Kay 1987; Eldredge and Miller 1997; Eldredge and Evenhuis 2002).

Mangals may also influence surrounding coastal habitats by exporting large quantities of organic matter, or detritus (Leach and Burgin 1985; Twilley et al. 1986, 1997; Robertson and Alongi 1992; Duarte and Cebrian 1996). In Hawaii, *R. mangle* stands are likely to outwell unusually large amounts of detritus in part because Hawaiian mangroves lack mangrove-specific herbivores that can limit mangrove recruitment, growth, and ultimately, productivity (Cox and Jokiel 1996; Yap 1998; Steele et al. 1999). In addition, Hawaiian mangrove forests lack the leaf-eating crabs (Coles et al. 1999,

personal observations) that bury and recycle a large proportion of the leaf litterfall (up to 79%) within native mangrove forests (Robertson 1986; Camilleri 1992; Robertson et al. 1992; Kwok and Lee 1995; Twilley et al. 1997; Hogarth 1999). Therefore, mangroves in Hawaii may produce a large amount of litter fall available for tidal export to adjacent coastal waters. Mangrove litter degradation and export is a function of many factors, including mangrove production, *in situ* consumption by fauna, freshwater runoff, tidal inundation and frequency. Thus, mangrove litter export rates in Hawaii may vary depending on these factors.

Outwelling mangrove detritus may have a negative impact on surrounding faunal communities in Hawaii. Mangrove detritus, particularly that of *R. mangle*, is rich in tannins (Robertson 1988; Kimura and Wada 1989; Sessegolo and Lana 1991; Lee 1999). Tannins are toxic to many fish and bacteria (Mahadevan and Muthukumar 1980), generally deter herbivores (Tahvanainen et al. 1985; Valiela 1995), interfere with the feeding and digestion of detritivores (McMillan 1984; Neilson et al. 1986; Poovachiranon et al. 1986; Alongi 1987; Lee 1999), and cause reduced densities and diversities of benthic meiofauna and macrofauna (Tietjen and Alongi 1990; Alongi and Christoffersen 1992; Lee 1999). In addition, mangrove litter is typically low in nutritional quality compared to other marine detrital sources (e.g., marine phytodetritus, benthic microalgae), having a high C:N ratio and relatively high lignin content (Giddins et al. 1986; Robertson 1988; Robertson et al. 1992). The poor nutritional quality of mangrove detritus may perpetuate the dominance of pioneering infaunal assemblages in mangrove-forest sediments(Alongi and Christoffersen 1992; Sheridan 1997). The introduction of tannin-rich, low-quality mangrove litter to detrital food webs in Hawaii has the potential

to alter the structure and dynamics of coastal communities. Such alterations are especially likely because, until very recently, Hawaiian benthos occupying the high to mid intertidal zone have not been exposed to a significant input of marine vascular-plant detritus.

Despite the > 100 yrs of mangrove presence in the Hawaiian Islands, little is understood about the benthos inhabiting mangroves in Hawaii. In a limited, largely qualitative study of mangrove benthos, Walsh (1963, 1967) found only harpacticoid copepods, nematodes, and insects in sediment-grab samples from mangals on Oahu; these are typically considered dominant meiobenthos in native mangrove forests (Alongi 1987; Alongi and Christoffersen 1992; Gee and Somerfield 1997; Gwyther and Fairweather 2002). In contrast, infaunal macrobenthos (retained on a 0.5 mm sieve) in native mangrove habitats in Asia, Australia, and North and South America are generally dominated by oligochaetes, polychaetes, amphipods and molluscs (Sasekumar 1974; Frith 1977; Alongi and Sasekumar 1992; Lana et al. 1997; Sheridan 1997). While Walsh's (1963, 1967) data seem to indicate a markedly unusual infaunal assemblage, Walsh used sampling techniques that differed substantially from the other studies, making comparisons problematic. In a technical report, Bigelow et al. (1989) described infaunal macrobenthos (retained on a 3 mm sieve) consisting of polychaetes and mollusks (> 3 mm) in Hawaiian mangroves on Molokai. Thus, at higher taxonomic levels, the macrofauna currently inhabiting Hawaiian mangroves appear to resemble those of native mangrove forests. While not intensively studied by Walsh (1963, 1967), infaunal benthos can carry out important functions in both mangal and non-mangal coastal habitats, e.g., serving as food for commercially important species, shredding detritus, aerating reduced

sediments, and stimulating detrital decomposition (e.g., Levinton 1982; Parsons et al. 1985; Robertson and Alongi 1992). Thus, it is critical to evaluate the species, biomass and food-web structure of infaunal communities in Hawaiian mangals as a first step in assessing the impacts of mangroves on Hawaiian coastal ecosystems. The present study is the first quantitative assessment of the impact of invading mangroves on benthic community structure, species diversity, and marine food webs in the Hawaiian coastal zone.

Objectives

The primary objective of my dissertation research was to understand the roles introduced mangroves play in structuring Hawaiian soft-sediment communities. Specifically, I wished to examine the community ecology and food-web structure in introduced mangroves and compare these with other soft-sediment ecosystems in Hawaii, and with native mangrove forests found elsewhere. The results of research addressing these goals are presented in five chapters which cover the soft-sediment infaunal and epifaunal community structure of introduced mangroves, their corresponding food webs, how these food webs compare to native mangroves, and lastly, the fate of mangrove litter production in Hawaii and Puerto Rico. An additional food-web study was conducted exclusively in native mangroves in order to better understand the trophic structure in native mangrove communities. The organization of this dissertation is as follows.

Dissertation Organization

In **Chapter 2**, the habitat characteristics, and epifaunal and infaunal community structure of Hawaiian mangrove benthic communities are described and compared to other soft-sediment ecosystems in Hawaii. This is the first study to elucidate the role of invasive mangroves in structuring Hawaiian coastal ecosystems. Ultimately, these observations provide information on the effect of vascular aquatic plants on coastal benthic communities, by predicting plant-sediment modifications, plant-infaunal community interactions, and providing a tropical analog to the largely temperate-focused invasive plant research.

Chapter 3 describes the importance of mangal-derived detritus in coastal foodwebs, and compares the trophic structure in introduced Hawaiian mangrove communities with native mangrove communities in Puerto Rico using stable carbon and nitrogen isotope analysis. A majority of food-web studies in mangroves have focused on fish and epibenthos, while few studies have examined mangrove infauna. This chapter estimates the proportional utilization of mangal detrital sources in coastal food webs, including mangrove infauna.

Chapter 4 describes the feeding and movement of the mangrove crab, *Scylla serrata*, in native mangrove communities on Kosrae, Federated States of Micronesia. This research emphasizes the utility of a broad range of environmental measurements, including trace metal and cation analyses, in combination with stable isotope methods, to help define habitat and diet characteristics of mangrove fauna. In addition, I estimate mangal contribution to crab diets in native mangrove ecosystems.

In **Chapter 5,** mangrove litter production, standing stock, leaf decomposition, and the fate of leaf litter are compared in introduced and indigenous mangroves in Hawaii and Puerto Rico. I describe differences in leaf decomposition and turnover rates, and discuss the implications of these differences to Hawaiian coastal ecosystems.

Chapter 6, the final chapter of my dissertation, is a synthesis of the conclusions from this research. The controversial role of mangrove detritus as an important dietary source is discussed, including comparisons to existing models of unstructured and mangrove food-webs by Isaacs (1972) and Odum and Heald (1975), respectively. Functions of mangroves (both introduced and native) as an important habitat for a variety of organisms are examined. I conclude the chapter with new questions raised by this study and recommendations for future research.

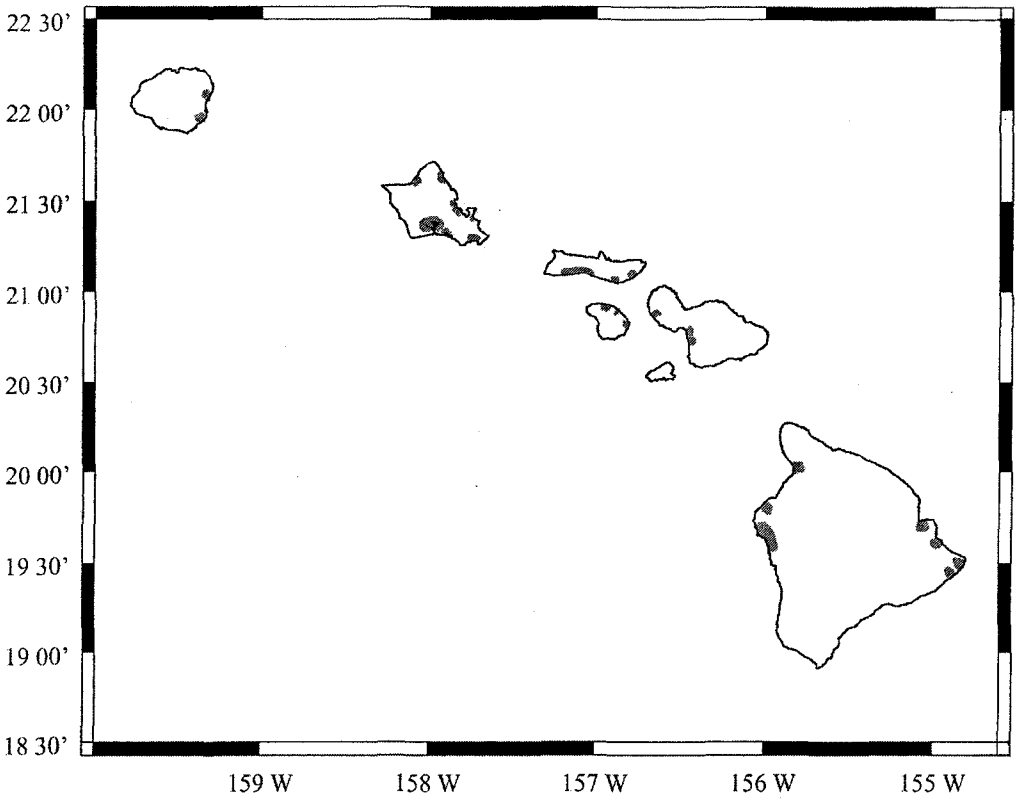

Figure 1. Approximate locations of known mangrove stands in Hawaii are delineated in gray. Map is updated from Wester (1981) and Allen (1998).

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CHAPTER 2. BENTHIC COMMUNITY STRUCTURE IN AN INTRODUCED HABITAT: MANGROVES IN THE HAWAIIAN ISLANDS.

Abstract

Species introductions provide an unusual opportunity to examine factors that regulate community composition. Mangroves, including *Rhizophora mangle*, were introduced to the Hawaiian Islands in 1902, and have subsequently spread extensively in tidal wetlands. To date, however, little is understood regarding the community composition and functional dynamics of these new habitats. I sampled introduced mangroves and sandflat assemblages to examine the impacts of mangroves on Hawaiian soft-sediment communities. Mangrove sediments were generally enriched in organic carbon, had higher pore-water salinities, and were composed of smaller median grain sizes than sandflat habitats. Emergent mangrove roots were colonized by a variety of encrusting organisms including the introduced barnacles *Chthamalus proteus*, *Balanus reticulatus*, and *Balanus amphitrite*, and the introduced sponges *Suberites zeteki, Sigmadocia caerulea,* and *Gelloides fibrosa*. The dominant mangrove sediment macrofauna, in terms of both densities and species numbers, included polychaetes, oligochaetes, and amphipod crustaceans. Mangrove habitats had higher macrobenthic species richness and diversity than sandflat communities. Dominant trophic groups in mangrove sediments included omnivores, suspension feeders, and surface- and subsurface deposit feeders. The mangrove sediment infauna was dominated by non-tube dwellers and burrowing forms. In addition, higher densities and proportions of cryptogenic and introduced species macrofauna were collected from mangrove transects

than from sandflat controls, indicating that invasive mangroves facilitate the persistence of non-native infauna in Hawaii. Introduced mangroves in Hawaii are directly modifying the infaunal community composition, potentially by enhancing the structural complexity of the Hawaiian coastal environment. Because macrobenthos provide a variety of ecosystem services, e.g., serving as prey for fish, birds and invertebrates, and promoting detrital decomposition, mangrove-induced changes in sediment community composition may have far-reaching consequences in Hawaii.

Introduction

The impact of introduced species on native communities has received increased attention in recent years (Diamond and Case 1986; Pieterse and Murphy 1990; Mooney and Hobbs 2000). In particular, plant invasion of coastal wetlands throughout the world is a rapidly growing problem (Posey 1988; Callaway and Josselyn 1992; Posey et al. 1993). Habitat modification and degradation have increased the susceptibility of wetlands to invasions by providing open niches to be colonized by opportunistic plant species. Invading species may alter nutrient cycling and change habitat characteristics (Posey et al. 1993; Talley and Levin 2001). Changes in vegetation associated with plant invasion provide the opportunity to study plant effects on faunal communities, including those related to provision of three-dimensional habitat structure and to alteration of hydrodynamic and depositional regimes (Eckman 1983, 1990; Peterson et al. 1984; Fonseca et al. 1992). When introduced plants invade previously unvegetated habitat, there can be substantial changes in faunal community composition, as observed with the introduction of Japanese eelgrass, *Zostera japonica,* in Oregon and Washington, (Posey

1988) and with the invasion of Pacific mudflats by the Atlantic cordgrass *Spartina alterniflora* (Niera et al., submitted). In this study, I examined the effects of an introduced aquatic vascular plant, *Rhizophora mangle*, on benthic community composition and coastal wetland habitat characteristics in Hawaii. Prior to mangrove introduction, the high to mid-intertidal zone of Hawaii essentially lacked vascular plants (Wester 1981).

Following its introduction to Molokai, Hawaii, in 1902, *Rhizophora mangle* (MacCaughey 1917; Degener 1945, 1946) has developed monospecific stands throughout the main Hawaiian Islands, as a result of both continuous propagule production and dispersal, as well as a paucity of mangrove herbivores and propagule (mangrove seedling) predators (Allen 1998; Cox and Allen 1999; Steele et al. 1999). In Hawaii, *Rhizophora mangle* has colonized the full marine tidal range, including the high intertidal, where typically it would be out-competed by other mangrove species in native forests (Lugo and Snedaker 1974). *Batis maritima,* an introduced salt-marsh succulent, is often found in the high-salinity dry zone on the landward margin of mangrove fringe forests (D'Iorio et al. 2003).

The effects of *Rhizophora mangle* spread on intertidal communities in Hawaii are likely to be substantial and may include the alteration of important habitat characteristics (Levin et al. 1996, 1998). Fundamental habitat parameters altered by aquatic vascular plant development (both native and introduced) typically include above and below-ground plant biomass, the availability of hard substrates, rates of water flow, sediment granulometry and organic-carbon content, oxygen and sulfide concentrations in bottom- and pore-waters, and salinity (Alongi 1987; Robertson and Alongi 1992; Levin and Talley 2000). Alterations of these parameters can substantially influence the structure and

dynamics of soft-sediment communities, allowing aquatic vascular plants (e.g., mangroves) to function as major ecosystem engineers (see reviews by Sanders 1969; Rhoads 1974; Gray 1974; Boesch 1977; Pearson and Rosenberg 1978; Nowell and Jumars 1984; Weston 1990; Robertson and Alongi 1992; Snelgrove and Butman 1994; Levin and Talley 2000).

Plant vegetation can enhance, or at least alter, infaunal densities through a variety of mechanisms (Orth 1977; Orth et al. 1991). Mangrove root systems, like other dense aquatic vegetation, provide cover from predators (Peterson et al. 1979; Boesch and Turner 1984; Orth et al. 1984; Baird et al. 1985; Reise 1985; Lee and Kneib 1994), baffle currents, and provide hard substrates for encrusting fauna (e.g., barnacles and bivalves) (Shokita et al. 1989). By reducing water flow, the root structure traps fine and organic-rich sediments transported by currents or produced *in situ* from mangrove litter (Chapman and Ronaldson 1958; Bird 1971). Modification of sediment particle size and organic content can influence the infaunal species found in sediments (Rhoads and Young 1970). Reduced particle size and increased sediment organic content can affect the densities of deposit-feeding animals and the filtering ability and densities of suspension feeders (Peterson et al. 1984). Lana and Guiss (1991) found high diversity and species richness in *Spartina alterniflora* relative to unvegetated wetlands, with a positive correlation between increased macrofaunal abundance, organic matter and decreased sediment grain size. Thus, infaunal abundance, biomass, and species richness within mangrove communities are likely to be influenced by mangrove root structure, sediment grain size and organic content, and may differ from non-mangrove, unvegetated sandflat habitats.

While introduced mangroves may fundamentally alter Hawaiian coastal ecosystems, their effects on native benthic communities and species invasions in Hawaii have not been evaluated. Sasekumar (1974), Frith (1977), and Sheridan (1997) reported that mangroves in Southeast Asia are a habitat for a specific fauna with limited species overlap with sand or mud-flat biotopes. Because mangroves were very recently introduced to Hawaii, native infauna may be poorly adapted to this new habitat. For example, the endangered Hawaiian stilt typically forages within sandflats and on the seaward edge of mangrove forests, but generally does not forage within mangrove prop roots (Rauzon et al. 1997; Rauzon and Drigot 2002). Hawaiian native birds may avoid foraging in introduced trees because of variations in microhabitats and prey abundances (Greenburg 1983; Clout and Gaze 1984). In the only published study of the Hawaiian mangrove fauna, Walsh (1967) concluded that Hawaiian mangroves were a substantially under-utilized habitat, i.e., that they contained a variety of open niches. Such open niches may be readily colonized by invading species with broad tolerances (Orians 1986). Thus, mangroves could provide invader "footholds," facilitating the establishment of exotic species in Hawaii, especially near sites of species introductions via ballast water (Carlton and Geller 1993), such as Honolulu, Pearl, and Hilo Harbors. Hawaiian mangroves may provide a haven for introduced species that ultimately may threaten the ~500 species of marine and estuarine invertebrates endemic to Hawaii (Kay 1987; Eldredge and Miller 1997). In order to evaluate mangrove impacts on Hawaiian coastal communities, it is important to determine whether open niches are being filled by introduced species or by native fauna increasingly able to colonize mangrove habitats.

In this study, I examined the effects of the invasive *Rhizophora mangle* on benthic habitat characteristics, and epifaunal and infaunal community structure. Specifically, field sampling was conducted to test the following hypotheses:

1. *Mangrove invasion of unvegetated tidal flats leads to increased below-ground plant biomass, decreased median grain size, and increased pore-water salinities and sediment organic-carbon content.*

2. *These changes in environmental parameters are associated with changes in macrofaunal community structure and species composition; Hawaiian mangrove benthic communities have lower infaunal densities and species richness than adjacent sandflats and other coastal Hawaiian sandflat substrates.*

3. *Hawaiian mangroves harbor a high proportion of introduced and cryptogenic species compared to non-mangrove sandflats.*

Study Sites and Methods

Samples were collected in mature *Rhizophora mangle* mangrove communities located in Kaneohe Bay, Oahu (21° 27' 42" N, 157° 50' 29" W) and near Kapuaiwa Grove, Molokai (21° 05' 52" N, 157° 03' 10" W) Hawaii (Figure 1). Kaneohe Bay was colonized by *R. mangle* in ~1920 and has some of the largest mangrove stands on Oahu

(Devaney 1982). *Rhizophora mangle* was introduced to the south shore of Molokai in 1902, and this island has the oldest, most extensive mangrove stands in the Hawaiian archipelago. Infaunal and epifaunal benthos and sediments were sampled in July and August 1999 in each of three habitats: mangrove stands, adjacent sandflats, and sandflats at distances > 1.5 km from mangroves.

Samples were collected along 3 randomly located transects running perpendicular to the mangrove forest edge. Samples were taken at six points along each transect: at distances of 8, 2, and 0.5 m from the forest edge within the mangrove forest, and at similar distances from the forest edge on the adjacent sandflat (Figure 2). Sampling was also conducted at control sandflats (non-mangrove sites) in Kaneohe Bay and Molokai 1.5 km from the nearest mangrove stand. Each control non-vegetated sandflat was sampled along 3 randomly located transects established at the same tidal elevations as for sampled mangrove habitats, and samples were collected at six distances along these transects: 3 along the same tidal-elevation as interior mangrove stations (named "control upper" or CU) and 3 along the same tidal-elevations as sampling sites in the adjacent sandflats ("control lower" or CL). Specific mangrove stands and control sandflat sites were chosen to have roughly comparable habitat size, location (i.e., within the same bay for Kaneohe Bay and on the same south coast for Molokai), and sediment grain size.

Densities of epifauna, large biogenic features, and mangrove roots were counted within 0.5 m^2 quadrats placed over each sampling site (Sasekumar 1974). Quadrat counts included number of mangrove roots, all visible epifauna, and the number and size of burrow openings. Salinity was measured using a refractometer (± 2 psu) for porewater extracted from syringe samples taken in the upper 5 cm of sediment at low tide.

Two sediment cores were collected from each sampled site for infaunal analysis and sediment properties. Sediment cores (33 cm^2 in area and 5 cm deep) for macrofaunal analysis were collected and horizontally sectioned into 0-2 cm and 2-5 cm intervals, and preserved in 10% formalin prior to sieving. In the laboratory, samples were washed through nested sieves (1000 μm and 500 μm) to allow comparison to previous mangrove studies (Broom 1982; Alongi and Hanson 1985; Alongi 1987; Shokita et al. 1989; Alongi and Christoffersen 1992; Schrijvers et al. 1996; Gee and Somerfield 1997; Sheridan 1997; Schrijvers et al. 1998; Morrisey et al. 2003; Ellis et al. 2004). Animals retained on sieves were sorted under a dissecting microscope, identified to the lowest possible taxon, and transferred to ethanol for storage. After identification, animals were blotted and weighed using a microbalance to determine biomass. Hardparts of molluscs were removed prior to weighing. Macrofaunal species were assigned to trophic, domicile, and mobility groups (Appendix A) based on Barnard (1969), Barnes (1980), Fauchald and Jumars (1979), Kukert and Smith (1992), and Sheridan (1997). Belowground plant material was removed from macrofaunal cores, dried at 60°C to a constant weight (~ 1-2 days) and weighed to determine belowground biomass.

Sediment cores were sectioned horizontally into 0-2 and 2-5 cm intervals for sediment grain-size distribution, sediment organic-carbon and total nitrogen content, and the intervals were then homogenized, subsampled for analyses, and frozen at –20°C. Organic carbon and total nitrogen content of the sediments were determined using a Carlo Erba 1108 CHN Analyzer after carbonate material was dissolved using sulfurous acid (Verardo et al. 1990). A portion of sediment for grain size analysis was digested with hydrogen peroxide to remove organic material and subsequently wet sieved through

2000 μm (to remove large plant material and collect rubble/large grain sizes) and 63-μm sieves. Size fractions (>2000 μm, 2000- 63 μm and < 63 μm) were dried at 60°C for 1-2 d, weighed, and percent rubble (>2mm), sand (63 μm ≤ x < 2mm), and silt/clay (< 63 μm) calculated.

In order to evaluate Hawaiian mangroves as a habitat for introduced/cryptogenic macrofauna (hypothesis 3), species lists for Hawaiian mangroves were compared with existing lists of introduced species for the state of Hawaii (Eldredge and Miller 1997; Eldredge and DeFelice 2000). The abundances and proportions of introduced/cryptogenic species were also compared among mangrove, adjacent sandflats and sandflat control habitats.

One-way ANOVA comparisons were conducted within and between sites (4 sites: Oahu mangrove and control transects, and Molokai mangrove and control transects) over the full tidal elevation range from 8 m within mangroves to 8 m out onto adjacent sandflats. All distances are given from the forest boundary or corresponding boundary as illustrated in Figure 2. Within a mangrove site, paired comparisons were made between locations occurring at distance from the mangrove boundary; i.e., 8 m inside mangrove (M) versus -8 m outside on adjacent sandflat (AS), 2 m inside mangrove versus -2 m outside on adjacent sandflat, and 0.5 m inside mangrove versus -0.5 m outside on adjacent sandflat (Figure 2). "Negative" distances correspond to sampling locations on adjacent, lower tidal elevation sandflats. The "negative" labeling is used throughout the text to aid with spatial analysis. Paired comparisons were also made between mangrove and control transects at similar tidal elevations; i.e., 8 m inside mangrove versus 8 m

control upper, 2 m inside mangrove versus 2 m control upper, etc. F-tests were used to determine significant differences in all measured variables between mangrove and control sandflat sites, and within sites (i.e., inside mangroves versus adjacent sandflats) for each island (Molokai and Oahu) ($\alpha = 0.05$). Comparisons of macrofaunal and environmental variables between islands, sites (mangrove versus control sandflats), and elevations (e.g., 8, 2, 0.5, -0.5, -2, and -8 m) were made using a nested ANOVA (elevations nested within four sites) with a-posteriori Bonferroni tests ($\alpha = 0.05$). All data were tested for heteroscedasticity (inequality of variances among samples) using Bartlett's test for homogeneity of variances (Sokal and Rohlf 1969; 1995). As a result of this test, all proportion data were arcsin-square-root transformed, and numeric data were square-root transformed prior to statistical analysis in order to achieve homogeneity of variances. All data presented in tables and figures are untransformed means, and faunal data have been converted to a per square meter basis for comparative purposes.

Macrofaunal diversity was examined using Biodiversity Pro and PRIMER Statistical Software (McAleece et al. 1999; Clarke and Warwick 2001) by using number of species (S), normalized species richness per core ($d = S-1/\ln N$, where N= number of individuals), Shannon-Weiner Information index (H'; log base 2), evenness (J') per core, and rarefaction, for infaunal sediment cores pooled within elevations. Similarities and differences in macrofaunal communities were examined using non-metric multidimensional scaling (MDS), based on Bray-Curtis similarity indices. Pairwise comparisons were made between mangrove and control transects in each of the four sites using Analysis of Similarity (ANOSIM; to obtain p-values). Similarity percentages (SIMPER) determined the percent dissimilarity/similarity and the taxa responsible for

differences between groups. All multivariate analyses were performed using PRIMER Statistical Software on square-root transformed macrofaunal data, in order to allow all macrofauna species/biomass to contribute to the similarity while also retaining the importance of more abundant species (Clarke and Warwick 2001).

Results

Vegetation characteristics and sediment properties.

Above-ground aerial root densities within mangroves ranged from 4 to 75 roots m^{-2} (Figure 3). Although there was no significant difference in root densities between mangrove sites (Oahu and Molokai), Oahu mangroves had significantly greater below-ground plant biomass than Molokai mangroves (Table 1). Both root densities and below-ground biomass were higher than in adjacent sandflats (Figure 3), given that the non-vegetated sandflat controls had neither roots nor below-ground plant biomass. Total organic carbon in sediments was ~ 2.5 times higher in mangrove than in adjacent sandflats (a-posteriori Bonferroni test, $p=0.004$ for Molokai). Total organic carbon in Molokai mangrove sediments was ~ 2 times higher than Oahu sediments (Nested ANOVA, $p < 0.001$). Total nitrogen was similar among sites on Oahu (Figure 4), but significantly higher in Molokai mangroves than adjacent sandflats ($p<0.001$ for 8 m and 2 m paired comparisons) and sandflat controls ($p <0.001$). Between islands, Molokai had significantly higher sediment organic carbon content (ANOVA, $p<0.001$) for both mangrove and sandflats.

Oahu mangrove sediments were composed of proportionately more percent sand than sandflat controls ($p<0.001$), whereas sandflat controls had 50 times more rubble than mangrove sites ($p<0.001$) (Figure 5). Molokai mangrove sediments were composed of more silt/clay and less sand then adjacent sandflats ($p= 0.002$ for silt/clay, $p= 0.001$ for sand, mangrove transects) (Figure 6). Pore-water salinities ranged from 26 to 42 ‰ for mangrove sediments and 13 to 33 ‰ for sandflat controls. Mangrove pore-water salinities were higher than in sandflat controls ($p<0.001$, Oahu) and Molokai mangrove sediment transects had the highest salinities ($p<0.001$) of all four sites. Overall, mangrove sediments contained a greater proportion of smaller grain sizes and higher pore-water salinities than control sandflats.

MDS and ANOSIM analysis of sediment and vegetation parameters revealed significant differences among the environments for mangrove and control transects. For Oahu, mangrove sediments versus adjacent sandflats and sandflat controls were equally dissimilar (ANOSIM P=0.001, SIMPER ~ 40%) (Table 2, Figure 7). On Molokai, mangroves were most distinct from adjacent sandflats (ANOSIM P=0.01, SIMPER 17-48%). Mangrove transect environmental parameters (elevations nested within islands) differed on Oahu and Molokai (ANOSIM P=0.002, SIMPER 54%). The abundance of root material, belowground biomass, and differing sediment grain size were responsible for ~ 96% of the dissimilarities between mangrove and control transects from Oahu and Molokai.

Epifauna/biogenic features

Epifauna present in mangrove habitats consisted of barnacles, sponges and zooanthids. Barnacle species included the introduced species *Chthamalus proteus*, *Balanus reticulatus*, and *Balanus amphitrite.* Total barnacle densities were highest in the Oahu mangroves (233.3 barnacles per root) (Table 3). The introduced crab *Panopeus lacustris* was also found in Oahu mangrove roots. Although barnacles were occasionally observed on Molokai mangrove roots, none was found on the roots within sampled transects. Sponges found attached at the base of mangrove roots included the introduced species *Suberites zeteki, Sigmadocia caerulea,* and *Gelloides fibrosa.* The sponge areal coverage ranged from 0.3 to 4 % cover for Molokai and Oahu mangroves. In addition, both large (0.5 cm diameter) and small (0.1cm) burrows were present at each site. Epifauna from adjacent sandflats and sandflat controls included amphipods, crabs, gobies, medusae, and shrimp. Total epifauna were most abundant in the sandflats adjacent to Molokai mangroves relative to Oahu adjacent sandflats and sandflat controls.

Infaunal macrobenthos

Abundance, composition, and diversity

Densities of total macrofauna ranged from 39,000 to 109,000 individuals m^{-2} in mangrove sediments, from 11,000 to 42,000 individuals m^{-2} for adjacent sandflats, and from 12,000 to 134,000 individuals m^{-2} for sandflat control transects (Figure 8). Mangrove infaunal densities were higher than adjacent sandflats for both Oahu and Molokai ($p<0.001$). Highest densities overall occurred in the mangrove and sandflat control sites on Oahu (Table 1, $p < 0.001$). Densities from sandflat control stations were

higher than mangrove sites on Oahu ($p<0.001$). Total macrofaunal biomass ranged from 2.4 to 7.7 g wet wt. m^{-2} and did not differ significantly for the Molokai transects. For Oahu, biomass was significantly higher at 2 m inside mangroves than 2 m on adjacent sandflat and 8 m control lower (CL) biomass was higher than at the mangrove transect at the same tidal elevation.

Major macrofaunal taxa in terms of relative abundance within mangrove sediments from Oahu included amphipods (17-58 %), polychaetes (10-36%), especially sabellids, and enchytraeid (4-6%) and tubificid (18-37%) oligochaetes (Figure 9). Other taxa included insecta, hydrozoa, ectoprocta, and bryozoa. Adjacent sandflats were composed mostly of these same major taxa with the notable absence of enchytraeid oligochaetes. In terms of relative abundance, Oahu sandflat controls were dominated by polychaetes (77-88%), primarily sabellids (62-80%), followed by capitellids (4-9%), spionids (2-2.5%) and syllids (1-2%). Tubificid oligochaetes ranged from 7-10 %, and amphipods in control sandflats were dominated by one species, *Neomicrodeutopus cf. makena* (4-13 %).

In contrast, mangrove taxa from Molokai were not dominated by amphipods, but by polychaetes (33-70%) and enchytraeid (0 –15%) and tubificid (19-53%) oligochaetes (Figure 10). The suite of polychaetes included sabellids (10-24%), capitellids (0-4%), cirratulids (5-8%), spionids (10-23%) and syllids (1-9%). Other taxa included tanaids (1-2%) and sipunculids (0 to 14%). Adjacent sandflats were similar in major taxonomic composition, but contained an additional suite of polychaetes including ophelids (8-15 %) and oweniids (0-4%). Molokai sandflat control sediments were dominated by polychaetes

(43-66%), primarily capitellids, chaetopterids, questids, sabellids, and spionids. All adjacent sandflats and sandflat controls lacked enchytraeid oligochaetes.

Mangrove transects were characterized by a greater abundance of enchytraeid oligochaetes and sabellids (Table 2, $p < 0.001$), and higher proportions of spionids relative to sandflat controls. MDS and ANOSIM analysis of macrofaunal assemblages and biomass for all four sites and elevations revealed significant differences in macrofaunal assemblages between mangroves, adjacent sandflats and sandflat control sites (Table 4, Figure 11). For Oahu, mangrove sediments versus adjacent sandflats and sandflat controls were equally dissimilar (ANOSIM, $p \leq 0.002$, % similarity = 29-60%) (Table 4, Figure 11). Differences between mangrove and sandflat controls could be attributed to the abundant amphipods, syllids, hydrozoans, and enchytraeids (*Marionina coatesae)* in mangrove sediments versus sabellids (*Potamilla* sp. 1 and 2) and nemerteans in sandflat controls. On Molokai, mangrove sediment infauna were more obviously distinct from adjacent and sandflat controls (Table 4 and Figure 11). Differences could be attributed to the abundance of tubificid oligochaetes, opheliid, capitellid, and syllid polychaetes, and tanaid crustaceans in mangrove sediments, and the overwhelming abundance of *Corophium insidiosum* in sandflat control sediments. Mangrove transects between Oahu and Molokai were significantly different in their associated infauna (ANOSIM $p=0.002$, SIMPER 13 %). These differences were primarily due to the dominance of *Corophium insidiosum*, *Neomicrodeutopus cf. makena*, hydrozoans, tanaids, enchytraeid oligochaetes, and sabellids in Oahu mangrove sediments versus opheliid and spionid polychaetes in Molokai mangroves. The same dissimilarity patterns were present in the biomass from each site (Table 4 and Figure 11).

Species richness per sediment core was highest within Molokai mangrove communities, (Table 5). In addition, diversity (d, Shannon-Weiner H') and evenness (J') were highest at both mangrove and sandflat transects in Molokai, compared to Oahu ($p<0.001$). Mangrove taxonomic richness (S) was greater than control sandflats on Molokai ($p=0.033$). The highest diversity (Shannon-Weiner H') from Oahu transects was observed at 2 and 0.5 m inside mangroves ($p=0.017$) and 0.5 on adjacent sandflats, corresponding to the mangrove forest boundary. Total species richness per site, standardized to number of individuals using rarefaction (Hurlbert 1971), also showed higher diversity within mangroves relative to sandflat controls on the same island (Figure 12). Molokai mangrove macrofaunal diversity appeared to be higher than in Oahu mangroves, and mangrove community diversity from both islands were higher than control sandflat sites.

Eighty-seven macrofaunal taxa were found in the mangrove, adjacent sandflat, and control sandflat habitats throughout this study (Appendix B). Of these, only 4 taxa were found in common among all sites: *Exogone* sp. E, *Malacoceros* sp., *Potamilla* sp. 1, and nemerteans. Thirty-six taxa were exclusive to Molokai transects, and 15 were exclusive to Oahu transects. Thirty-six taxa were found in mangrove transects (including mangrove and adjacent sandflats) and 11 in sandflat control sites. Of the 36 taxa found within mangrove transects, 21 were found only in mangrove sediments, 6 were exclusive to adjacent sediment flats, and only 9 taxa were found in common between habitats. Between each island, there were 5 taxa found only in Oahu mangroves and 16 taxa found within Molokai mangroves only (Table 6).

Trophic modes, Lifestyles (domicile and mobility groups), and Introduction status

Mangrove infaunal communities on both islands were characterized by significantly higher densities of omnivores, surface deposit feeders and suspension feeders than adjacent sandflats (Table 1). Mangroves also had greater densities of omnivores relative to sandflat controls ($P<0.001$) (Figure 13). Oahu mangroves had significantly greater densities of omnivores relative to adjacent sandflats. Oahu sandflat controls were dominated by one feeding type, suspension feeders (71-80%), and greater densities of carnivores, suspension feeders, and subsurface deposit feeders were found in Oahu control sandflats relative to mangrove transects.

In general, mangrove sediments at 8 m on Oahu and mangrove transects on Molokai had greater densities and proportions of burrowers than sandflat controls (Figure 14). Domicile type differed in proportion of tube dwellers and non-tube dwellers at each site. Non-tube dwellers dominated the mangrove transects on Molokai and Oahu compared to sandflat control transects (Figure 15). In addition, a significantly greater abundance of non-tube dwelling forms was found in mangrove sediments on Oahu (8 m interior) than in adjacent sandflats or sandflat controls (Table 1, $p<0.001$). In contrast, Oahu sandflat controls had a greater proportion of tube-dwelling fauna, primarily sabellid polychaetes.

Lastly, mangrove transects had greater densities and proportions of cryptogenic and introduced species than sandflat controls (Oahu, $p<0.001$, Molokai, $p< 0.012$) (Figure 16). In addition, densities of native fauna were lower in Oahu mangroves relative to sandflat controls, although the densities of native fauna were higher in mangroves from both islands than in adjacent sandflats ($p=0.027$, densities, $p=0.001$, proportion data).

ANOSIM and SIMPER results for trophic, domicile, mobility, and biogeographic status indicated significant dissimilarity between sites on a functional level (trophic mode, mobility, etc.), complementing the dissimilarities found in densities, biomass, and environmental parameters (Table 7). Comparing mangrove transects versus control sandflats, percent similarities ranged from 60 to 75%. Thus, mangroves are characterized by omnivores and surface deposit feeding forms, high densities of tube dwellers (Oahu), non-tube dwellers (Molokai), burrowers, and cryptogenic and introduced species.

Discussion

Mangrove influence on sediments and fauna

Mangrove invasion into previously unvegetated Hawaiian sandflats has changed habitat properties by increasing above and below-ground plant biomass, pore-water salinity, sediment organic carbon content, the availability of hard substrate for encrusting organisms, and by decreasing sediment grain size. These results are consistent with the first hypothesis, that *mangrove invasion of unvegetated tidal flats leads to increased below-ground plant biomass, decreased grain size, and increased pore-water salinities and sediment organic carbon content.* MDS and SIMPER results indicate that the mangrove environment is quite distinct from control, non-vegetated sandflats, given that the percent similarity ranged from 17-66 % for mangrove versus adjacent sandflat comparisons, while adjacent sandflats and sandflat controls were very similar (81-95%, Table 2). The primary parameters responsible for the differences are all functions of mangrove presence: below-ground biomass, root density, and sediment organic carbon. These changes in habitat parameters are reflected in the macrofaunal density and

composition in mangrove-invaded and control sandflat transects. Increases in sediment infaunal densities and taxonomic richness in proximity to mangrove forests ran contrary to the proposed hypothesis: *Hawaiian mangrove benthic communities have lower infaunal densities and reduced species richness than adjacent sandflats and other coastal Hawaiian sandflat substrates.*

Changes in macrofaunal composition in invaded mangroves involved a distinct shift towards more abundant oligochaetes in the interior of mangroves and a dominance by polychaetes on the adjacent sandflats. In addition, mangrove sediments had reduced densities of carnivores and tube builders, and an increase in burrowing, omnivorous, and surface-deposit feeding forms. Increases in burrowing forms were attributable to the dominance of oligochaetes in interior mangrove sediments. Concurrent with the increase in burrowing forms (Figures 14) was the increase in below-ground plant biomass (Figure 3), typically consisting of a dense mat of capillary roots. This root mat may promote the persistence of oligochaetes (especially enchytraeids) (Levin et al. 1998), while inhibiting larger burrowing forms. While small burrowing taxa were abundant in Hawaiian mangroves (e.g., oligochaetes and *Capitella capitata*), non-burrowing and tube-building taxa (e.g. sabellids and *Corophium* amphipods) contributed more to densities and species number to the 2 and 0.5 m interior mangrove locations. The seaward (from interior mangrove to adjacent sandflat) increase in tube-builders, particularly sabellid polychaetes, may result from lesser root mat dampening of water flow, promoting suspension feeding. However, sabellids were abundant in both mangrove and control transects, suggesting that these taxa are well distributed in the intertidal zone. Mangroves also serve as a hard substrate for encrusting barnacles and sponges. More epifauna (both

root- and non-root associated) were observed along mangrove transects than at sandflat controls.

A rich faunal assemblage inhabits mangrove sediments in Hawaii. Of the 87 taxa collected, 40% were found only in mangrove transects, and over half of these were found actually within mangrove sediments. A large percentage of these fauna were introduced and cryptogenic. Differences in species source pools between islands may partly explain community differences. Thus, introduced mangroves in Hawaii harbor significant proportions of introduced and cryptogenic species, as hypothesized.

Of the 21 mangrove-specific taxa collected, *Aphelocheta molinaris*, *Monticellina* sp. 1-6, Polydora sp. 1, and *Marionina coatesae* have not been previously reported from the Hawaiian Islands. Frith (1977) and Sheridan (1997) found little taxonomic overlap of sediment infauna between mangroves and other habitats in Thailand and Florida, including sandflats. Therefore, introduced mangroves may be mimicking native mangrove forests in that they are providing a niche for specific organisms not found elsewhere in the Hawaiian Islands.

Mangrove infaunal diversities in Hawaii were similar to native mangrove forests (Table 8, Figure 17) (Frith 1977; Guerreiro et al. 1996; Sheridan 1997; Ellis et al. 2004), although it should be noted that diversity levels in native mangroves span an extremely broad range. Using the same sampling techniques, macrofaunal densities in native Puerto Rico mangroves ranged from 32,000 to 57,000 individuals m^{-2} (versus 39,000 to 108,000 individuals m^{-2} in Hawaii), and the fauna was dominated by capitellid polychaetes and oligochaetes (e.g., enchytraeids and tubificids), with small proportions of insect larvae and nemerteans (Demopoulos, unpub. data). Patterns similar to these in introduced

Hawaiian mangroves with respect to infaunal domicile and trophic groups are evident in native forests, including a dominance of burrowing forms and the following trophic groups: surface-deposit feeders, abundant suspension feeders and few carnivores in mangrove sediments (Wells 1984; Sheridan 1997). Enhanced infaunal diversity with greater distance into mangrove forest has also been observed in native mangroves. Hart and Chindah (1998) observed a landscape gradient in infaunal diversity, with values increasing from the low to high intertidal zone. They attributed this pattern to decreasing exposure of the benthos to predators as a result of increased protection from mangrove roots. Frith (1977) found enhanced species richness in the *Rhizophora* zone relative to adjacent mudflats, and credited these patterns to an increase in shade, substrate moisture, attachment points, and abundance of organic detritus in the forest, all functioning to provide a favorable habitat for colonizing benthos. In other words, mangrove spatial heterogeneity may increase availability of microhabitats for a variety of infaunal benthos, facilitating enhanced diversity and infaunal densities.

The faunal diversity in mangrove sediments in Hawaii was enhanced by the abundance of cryptogenic oligochaete taxa. Oligochaetes are typically the numerical dominant taxon in native mangrove sediments, and appear to be important contributors to the remineralization of organic material (Erseus 1999) and to the production of higher trophic levels by serving as food for crustaceans and fish (Giere and Pfannkuche 1982). Schrijvers et al. (1997) concluded that oligochaetes may also compete for nutritional resources with the epibenthos in an *Avicennia* mangrove forest in Kenya. Oligochaetes in the present study included similar taxa and species found in native mangrove forests in Kenya, e.g., Phallodrilinae sp., *Thalassodilides cf. gurwitschi*, *Marionina coatesae*,

Tectidrilus bori, *Smithsonidrilus capricornae*, and *Ainudrilus* sp. These taxa are associated with fully marine environments (e.g., Phallodrilinae sp.), low salinities (*Ainudrilus* sp.), and/or organically enriched sediments (*T. gurwitschi, S. capricorane, T. bori*) (Erseus 1999). *Tectidrilus bori* and *Thalassodilides cf. gurwitschi* were both associated with mangrove and sandflat sediments on Molokai, where the sediments were typically enriched in organic carbon relative to Oahu sediments. Enchytraeid oligochaetes were exclusively found in mangrove sediments in Hawaii, which possibly reflects their terrestrial and plant-associated environmental preferences, as the mangroves were located on the landward edge of the transects (Healy and Walters 1994). However, based on salinities, both mangrove sites were fully marine habitats, suggesting that this typically terrestrial family most likely contains species adapted to more marine habitats.

Densities and proportions of cryptogenic and introduced fauna were greater in mangroves than control sandflats in Hawaii, with native species more abundant in control sandflats. Reduced densities of native fauna in mangroves may be a result of specific functions of the new habitat. For example, native taxa may be inhibited by root and leaf exudates, which can be rich in tannins (Sessegolo and Lana 1991). Tannins are known to be toxic to many organisms and can interfere with the feeding and digestion of detritivores, potentially decreasing population densities of infauna (McMillan 1984; Poovachiranon et al. 1986; Alongi 1987; Tietjen and Alongi 1990). In addition, mangrove litter is typically low in nutritional quality, having a high C:N ratio (Giddins et al. 1986; Robertson 1988). The poor nutritional quality of mangrove detritus has been implicated as a factor in perpetuating the dominance of pioneering infaunal assemblages in mangrove sediments (Alongi and Christoffersen 1992). Thus, the introduction of

mangrove detritus may inhibit the colonization of native fauna via toxic tannins and facilitate the persistence of opportunistic introduced and cryptogenic fauna with broad environmental tolerances (e.g., capitellids, oligochaetes).

The ability of vascular plant cover, density, and composition to influence the structure and function of wetlands and enhance habitat complexity and heterogeneity is well documented (Lana and Guiss 1991; Leonard and Luther 1995; Levin and Talley 2000). For example, higher macrobenthic densities and species richness were associated with *S. alterniflora* relative to unvegetated wetlands (Lana and Guiss 1991; Netto and Lana 1999). Densities of dominant polychaetes in these habitats were found to be positively correlated with live below-ground biomass (Lana and Guiss 1992). It was suggested that the plant material is used as a physical refuge rather than for food. Roots and rhizomes from seagrasses have been found to protect infauna from predators, possibly leading to enhanced infaunal abundance (Posey 1988; Posey et al. 1993). Root exudates may also stimulate microbial growth and subsequent grazing by infauna (Teal and Wieser 1966). Introduced mangroves may provide a refuge for fauna by offering protection from abiotic disturbance (e.g., desiccation) and physical barriers to some predators (e.g., birds and juvenile fish) (c.f., Sasekumar 1974; Sheridan 1997). Therefore, enhanced species richness and densities in introduced mangrove habitats in Hawaii relative to unvegetated adjacent sandflats agree well with existing data demonstrating the effects of vegetation on marine macrobenthos (Bertness et al. 2000).

Consequences of Mangrove invasion

As climate and land-use patterns change world wide, mangrove distribution patterns are also very likely to change. Mangrove invasion of new habitats is particularly likely if global warming yields expansion of tropical and subtropical climate zones, and if coastal erosion and runoff yield the formation of new intertidal flats. For example, native mangroves in New Zealand are expanding beyond their "native range" by invading new intertidal flats formed as a result of increased estuarine sedimentation resulting from deforestation of upland habitats (Woodroffe 1982; Young and Harvey 1996). Ellis et al. (2004) reported that the habitat areas of black mangrove expanded by ~ 50 % in 45 years into previously unvegetated intertidal flats, ultimately resulting in the loss of sandflats. The ecological effects and public perception of mangrove habitat expansion in New Zealand have been varied; mangroves may increase fisheries production and diversity and help to prevent coastal erosion, but as in Hawaii, they interfere with recreational and commercial use of the shore, and displace other habitats (e.g., mud and sandflats) that also have significant ecological value (Morrisey et al. 2003). Because of the potential expansion of mangrove habitats due to climate warming and increased coastal sedimentation, our study of the effects of mangrove introduction on coastal ecosystems may have broad applications.

Future Work

Mangroves in Hawaii colonize the feeding and nesting grounds of native and migratory bird populations (Rauzon and Drigot 2002). However, the specific diet of

most of these birds remains unknown. To assess the impacts of mangrove introduction on the food resources of the Hawaiian avifauna, it would be extremely useful to evaluate the importance of the dominant species of sandflat and mangrove benthos in the diets of wetland birds in Hawaii.

While this research had no temporal component, it provides a framework from which future research and experiments can be generated, and temporal variation in the differences observed may be evaluated. The present study did not experimentally manipulate any specific mechanisms that may cause changes in the sediment and faunal properties when *Rhizophora* invades. Plant-sediment interactions can be complex, involving changes in current speed, turbulence and shear, irradiation, sedimentation rate, litter deposition, evaporation, salinity (Chung 1990), and oxygen concentrations (Osenga and Coull 1983; Lana and Guiss 1991). These can affect sediment particle size, erosion or accretion, organic content, nutrients, redox conditions, and sulfide concentrations. Future experiments that manipulate *Rhizophora* and its associates would be required to un-"mangal" the relative importance of above and below ground plant biomass, sediment organic matter, particle size, redox conditions, and nutrient exchange to the macrobenthos.

Conclusions

Rhizophora mangle habitats in Hawaii supported a dense sediment infaunal community primarily composed of polychaetes, oligochaetes and amphipods. There are significant community differences within and among mangrove stands in Hawaii, possibly as a consequence of differences in sediment organic carbon content, salinity

ranges, predation refuges, hard substrate availability, and grain size distributions. Higher macrofaunal densities and enhanced diversity are associated with mangrove sediments relative to adjacent sandflats. Differences in species composition between islands may be a result of differential access to species source pools. The dominance of cryptogenic and introduced species in mangrove sediments indicates that while introduced mangroves in Hawaii are providing similar ecosystem services to mangroves in other parts of the world (e.g., providing a habitat for a diverse fauna, both root and sediment associated), they also facilitate the persistence and spread of introduced species, which may ultimately have an impact on the ~ 500 estuarine and marine endemic species in Hawaii.

Table 1. Results of nested analysis of variance (ANOVA) for (A) environmental and (B) macrofaunal variables as compared with elevations nested within mangrove and control sandflat sites (Oahu and Molokai).

		Site		Elevation (Site)	
		P	F	P	F
A. Environmental variables					
Above-ground properties					
Root density		0.936	0.007	0.001	6.34
Sediment properties					
Bg plant biomass		0.003	5.371	0.011	8.16
Total Organic Carbon		< 0.001	25.197	0.001	3.02
Total Nitrogen		< 0.001	37.29	< 0.001	6.03
% Rubble		< 0.001	40.31	NS	0.80
% Sand		< 0.001	48.13	< 0.001	5.77
% Silt/Clay		< 0.001	58.06	< 0.001	20.69
Salinity		< 0.001	97.34	NS	0.30
B. Macrofaunal variables					
Biomass		NS	1.13	NS	1.49
Density		< 0.001	78.19	< 0.001	3.88
Taxon richness		0.056	2.70	NS	1.20
Oligochaeta	#	< 0.001	23.37	< 0.001	3.47
	%	< 0.001	20.19	0.023	2.03
Tubificidae	#	< 0.001	21.66	< 0.001	3.02
	%	< 0.001	19.46	0.034	1.91
Enchytraeidae	#	< 0.001	15.69	< 0.001	7.19
	%	0.007	4.53	< 0.001	3.44
Polychaeta	#	< 0.001	122.46	< 0.001	3.76
	%	< 0.001	53.39	NS	1.68
Capitellidae	#	< 0.001	31.31	NS	0.96
	%	NS	2.49	NS	0.68
Sabellidae	#	< 0.001	169.19	< 0.001	4.79
	%	< 0.001	116.46	0.002	2.78
Spionidae	#	0.006	4.64	< 0.001	3.94
	%	< 0.001	22.05	0.011	2.25
Syllidae	#	NS	1.82	NS	1.50
	%	< 0.001	26.33	NS	1.43

Table 1. Cont.		Site		Elevation (Site)	
		P	F	P	F
Crustaceans	#	< 0.001	56.92	< 0.001	3.46
	%	< 0.001	36.72	NS	1.73
Amphipods	#	< 0.001	63.09	< 0.001	3.37
	%	< 0.001	41.02	NS	1.40
Insects	#	NS	1.65	NS	0.57
	%	NS	1.23	NS	0.72
Nemerteans	#	0.001	6.33	NS	0.71
	%	0.001	4.17	NS	0.83
Hydrozoa	#	< 0.001	8.37	0.029	1.96
	%	0.033	3.15	NS	0.86
Ectoprocta	#	NS	1.70	0.476	1.25
	%	NS	1.81	0.476	1.81
Sipunculids	#	0.042	2.95	0.006	2.42
	%	0.039	3.02	0.030	1.95
Molluscs	#	0.002	5.55	NS	0.21
	%	0.001	6.46	NS	0.24
Trophic Groups					
Carnivore	#	0.001	6.07	NS	1.60
	%	< 0.001	22.14	0.026	1.99
Suspension Feeder	#	< 0.001	109.62	< 0.001	5.12
	%	< 0.001	74.28	< 0.001	3.55
Omnivore	#	< 0.001	20.68	< 0.001	3.14
	%	< 0.001	20.28	0.010	2.28
Surface-deposit feeder	#	0.001	7.28	0.001	3.02
	%	< 0.001	16.70	0.046	1.82
Sub-surface deposit feeder	#	< 0.001	18.73	NS	0.96
	%	< 0.001	4.77	NS	1.37
Domicile Groups					
Non-tube dweller	#	< 0.001	18.27	0.011	2.26
	%	< 0.001	19.43	0.005	2.48
Tube-dweller	#	< 0.001	81.43	< 0.001	4.84
	%	< 0.001	19.43	0.005	2.50

Table 1. Cont.		Site		Elevation (Site)	
		P	F	P	F
Mobility Groups					
Burrower	#	< 0.001	25.45	0.001	3.04
	%	< 0.001	21.93	0.011	2.31
Non-burrower	#	< 0.001	71.58	< 0.001	4.28
	%	< 0.001	21.77	0.010	2.34
Biogeographic status					
Cryptogenic/Introduced	#	< 0.001	23.30	0.001	3.91
	%	< 0.001	26.17	0.002	2.73
Native	#	< 0.001	111.99	< 0.001	3.42
	%	< 0.001	48.13	0.030	1.95
Unknown	#	< 0.001	21.14	0.015	2.15
	%	NS	5.93	NS	1.33

Table 2. Comparisons of environmental parameters from the mangrove and sandflat habitats within 4 sites. Shown are pairwise Analysis of Similarity (ANOSIM) and SIMPER between-site percent similarities and R statistics. Distances refer to meters from forest or habitat boundary. 8, 2, and 0.5 m distances in interior mangrove and control habitat upper and 8, 2, and 0.5 m distances on adjacent sandflats and control habitat lower were taken at the same tidal elevations. M= mangrove, AS= adjacent sandflat, CU = control upper, CL= control lower.

		ANOSIM		SIMPER
Pairwise Comparisons		P	R statistic	% Similarity
Interior Mangrove versus Adjacent Sandflat				
Oahu	8 m	0.01	1	30.6
	2 m	0.01	0.963	24.6
	0.5 m	0.05	-0.111	66.4
Molokai	8 m	0.01	1	16.7
	2 m	0.01	1	22.8
	0.5 m	0.01	0.889	48.3
Control Upper versus Control Lower				
Oahu	8 m	0.08	-0.296	81.4
	2 m	0.06	-0.037	82.4
	0.5 m	0.1	-0.259	87.8
Molokai	8 m	0.1	-185	92.6
	2 m	0.08	-0.116	94.2
	0.5 m	0.08	-0.259	95.4
Mangrove transects versus sandflat control transects				
Oahu ithin sites		0.002	0.937	41.7
8 m -M v. CU		0.01	1	25.9
2 m- M v. CU		0.01	0.852	22.5
0.5 m M v. CU		0.01	0.593	18.8
-0.5 AS v. CL		0.01	0.556	30.8
-2 AS v. CL		0.01	0.593	65.8
-8 m AS v. CL		0.01	1	81.0
Molokai ithin sites		0.002	0.687	54.3
8 m -M v. CU		0.01	1	14.8
2 m- M v. CU		0.01	1	20.2
0.5 m M v. CU		0.01	0.889	35.7
-0.5 AS v. CL		0.01	1	75.8
-2 AS v. CL		0.01	0.593	91.4
-8 m AS v. CL		0.01	0.333	89.5

Table 2 Cont.		ANOSIM		SIMPER
		P	R statistic	% Similarity
Mangrove Transects				
Oahu versus Molokai	'ithin sites	0.002	0.535	54.4
	8 m- M	0.01	1	79.3
	2 m - M	0.01	0.852	84.2
	0.5 m - M	0.02	0.296	72.1
	-0.5 m -AS	0.01	0.519	46.8
	-2 m -AS	0.01	0.825	91.0
	-8 m-AS	0.01	1	93.3
Sandflat Control Transects				
Oahu versus Molokai	'ithin sites	0.002	1	72.9
	8 m -CU	0.01	1	72.0
	2 m -CU	0.01	1	76.7
	0.5 m -CU	0.01	1	70.5
	-0.5 m -CL	0.01	1	79.0
	-2 m -CL	0.01	0.63	65.1
	-8 m -CL	0.01	0.741	74.4

Table 3. Epifauna and biogenic features from 0.5 m^2 quadrat counts conducted in mangroves, adjacent sandflats, and sandflat controls on Oahu and Molokai. Presence/absence (P/A) of 1 mm burrows are indicated. A = amphipods, C= crabs, M= medusa, Z = zoanthids, S= shrimp, and G= gobies.

	Burrows 1 mm	0.5 cm (# m^{-2})	Barnacles (# per root)	Sponge % area	Other epifauna (# m^{-2})	
Mangrove Transects	P/A	Mean	Mean	Mean	Mean	Type
Oahu						
8-M	yes	0.0	2.3	0.00	0.0	
2-M	yes	7.7±3.8	233.3±66.7	1.3±0.7	0.0	
0.5-M	yes	5.7±2.8	136.3±85.8	4.0±3.1	0.0	
0.5-AS	yes	0.0	33.3±33.2	0.3±0.3	0.3±0.3	A, C, M
2-AS	yes	0.0	0.0	0.00	0.7±0.3	A, C, M
8-AS	yes	0.0	0.0	0.00	0.3±0.3	A, C, M
Molokai						
8-M	no	23.7±4.9	0.0	0.00	1.0±0.6	C, Z
2-M	no	46.0±17.0	0.0	3.3±3.3	10.0±5.8	C, Z
0.5-M	no	47.3±24.0	0.0	0.7±0.7	1.0±1.0	C, Z
0.5-AS	yes	51.3±29.5	0.0	0.00	9.0±5.2	S, G
2-AS	yes	38.7±15.7	0.0	0.3±0.3	1.0±0.6	S, G
8-AS	yes	75.7±15.9	0.0	0.00	0.0	
Control Transects						
Oahu						
8-CU	yes	10.0±2.5	0.0	0.00	0.0	
2-CU	yes	20.0±4.9	0.0	0.00	0.0	
0.5-CU	yes	12.7±7.3	0.0	0.00	0.0	
0.5-CL	no	19.3±7.9	0.0	0.00	2.3±1.5	G, A
2-CL	no	10.3±6.1	0.0	0.00	0.0	
8-CL	no	14.0±4.0	0.0	0.00	0.0	
Molokai						
8-CU	no	32.7±10.9	0.0	0.00	0.0	
2-CU	no	45.0±15.1	0.0	0.00	0.0	
0.5-CU	no	43.3±13.6	0.0	0.00	0.0	
0.5-CL	no	53.0±16.2	0.0	0.00	0.0	
2-CL	no	37.3±14.7	0.0	0.00	0.0	
8-CL	no	39.0±16.1	0.0	0.00	0.0	

Table 4. Comparisons of densities and biomass of macrofaunal assemblages from the mangrove and sandflat habitats within 4 sites. Shown are pairwise Analysis of Similarity (ANOSIM) and SIMPER between-site percent similarities and R statistics. Distances refer to meters from forest or habitat boundary. 8, 2, and 0.5 m distances in interior mangrove and control upper and 8, 2, and 0.5 m distances on adjacent sandflats and control lower were taken at the same tidal elevations. M= mangrove, AS= adjacent sandflat, CU = control upper, CL= control lower.

		ANOSIM		SIMPER
Pairwise Comparisons		P	R statistic	% Similarity
A. Density				
Interior Mangrove versus Adjacent Sandflat				
Oahu	8 m	0.01	1	37.1
	2 m	0.01	0.852	41.8
	0.5 m	0.04	0.074	59.8
Molokai	8 m	0.01	0.926	21.9
	2 m	0.01	1	21.9
	0.5 m	0.01	0.222	42.0
Control Upper versus Control Lower				
Oahu	8 m	0.02	0.481	74.8
	2 m	0.04	0.148	74.8
	0.5 m	0.08	-0.222	80.5
Molokai	8 m	0.07	-0.074	36.4
	2 m	0.07	-0.148	36.3
	0.5 m	0.08	-0.259	50.2
Mangrove transects versus sandflat control transects				
Oahu	Elevations nested within sites	0.002	0.685	40.5
	8 m -M v. CU	0.01	1	37.0
	2 m- M v. CU	0.01	1	52.4
	0.5 m M v. CU	0.01	1	47.7
	-0.5 AS v. CL	0.01	1	38.5
	-2 AS v. CL	0.01	0.963	29.9
	-8 m AS v. CL	0.01	0.926	38.7

Table 4 cont.		ANOSIM P	R statistic	SIMPER % Similarity
Mangrove transects versus sandflat control transects				
Molokai	Elevations nested within sites	0.001	0.841	17.7
	8 m -M v. CU	0.01	1	12.2
	2 m- M v. CU	0.01	1	7.6
	0.5 m M v. CU	0.01	0.889	18.7
	-0.5 AS v. CL	0.01	1	16.9
	-2 AS v. CL	0.02	0.222	30.0
	-8 m AS v. CL	0.01	0.778	16.6
Mangrove Transects				
Oahu vers	Elevations nested within sites	0.002	0.935	13.2
	8 m- M	0.01	1	34.2
	2 m - M	0.01	1	22.6
	0.5 m - M	0.01	1	12.9
	-0.5 AS	0.01	1	11.9
	-2 AS	0.01	1	22.0
	-8 m AS	0.01	1	12.0
Sandflat Control Transects				
Oahu vers	Elevations nested within sites	0.002	1	15.7
	8 m -CU	0.01	1	18.0
	2 m -CU	0.01	1	12.1
	0.5 m -CU	0.01	1	15.2
	-0.5 CL	0.01	1	18.6
	-2 CL	0.01	0.815	17.1
	-8 m CL	0.01	0.63	22.5
B. Biomass				
Mangrove versus Sandflat Controls				
Oahu		0.002	0.524	39.7
Molokai		0.001	0.428	18.8
Mangrove site similarities				
ıs Molokai		0.001	0.656	14.5

Table 5. Macrofaunal taxon richness (S, d), evenness (J'), diversity (H'), d = S-1/log N. Error represent 1 standard error. S= number of species per core (33 m^2). Solid line represents boundary as in Figure 2.

Mangrove Transects	Elevation	S	d	J'	H'(log_2)
Oahu	8-M	8.7 ± 1.9	1.43 ± 0.36	0.56 ± 0.11	1.77 ± 0.48
	2-M	14.3 ± 1.7	2.18 ± 0.25	0.65 ± 0.04	2.45 ± 0.05
	0.5-M	15.7 ± 1.7	2.46 ± 0.17	0.57 ± 0.07	2.23 ± 0.22
	-0.5-AS	11.0 ± 3.1	1.82 ± 0.42	0.61 ± 0.11	1.97 ± 0.26
	-2-AS	7.3 ± 0.3	1.46 ± 0.01	0.67 ± 0.07	1.92 ± 0.22
	-8-S	9.0 ± 0.6	1.87 ± 0.15	0.69 ± 0.05	2.19 ± 0.20
Molokai	8-M	12.3 ± 0.9	2.57 ± 0.21	0.66 ± 0.01	2.39 ± 0.06
	2-M	16.0 ± 1.5	2.90 ± 0.26	0.69 ± 0.02	2.77 ± 0.15
	0.5-M	14.3 ± 1.8	2.85 ± 0.48	0.71 ± 0.11	2.74 ± 0.54
	-0.5-AS	11.0 ± 1.5	2.67 ± 0.44	0.75 ± 0.10	2.61 ± 0.49
	-2-AS	12.0 ± 1.0	3.04 ± 0.30	0.88 ± 0.04	3.14 ± 0.05
	-8-S	11.0 ± 2.5	2.92 ± 0.55	0.86 ± 0.04	2.89 ± 0.14
Sandflat Control					
Oahu	8-CU	11.0 ± 1.7	1.59 ± 0.27	0.46 ± 0.05	1.55 ± 0.16
	2-CU	9.3 ± 0.9	1.45 ± 0.24	0.57 ± 0.03	1.83 ± 0.18
	0.5-CU	10.0 ± 1.0	1.53 ± 0.19	0.62 ± 0.07	2.03 ± 0.15
	-0.5-CL	8.7 ± 0.7	1.32 ± 0.11	0.52 ± 0.07	1.61 ± 0.17
	-2-CL	11.3 ± 1.3	1.86 ± 0.32	0.60 ± 0.05	2.10 ± 0.19
	-8-CL	11.7 ± 0.3	1.87 ± 0.06	0.61 ± 0.06	2.15 ± 0.20
Molokai	8-CU	10.0 ± 2.5	2.42 ± 0.38	0.80 ± 0.04	2.56 ± 0.15
	2-CU	9.7 ± 3.2	2.28 ± 0.59	0.77 ± 0.08	2.28 ± 0.22
	0.5-CU	10.0 ± 2.5	2.68 ± 0.53	0.89 ± 0.02	2.90 ± 0.36
	-0.5-CL	11.0 ± 1.5	2.64 ± 0.28	0.81 ± 0.01	2.77 ± 0.13
	-2-CL	10.7 ± 2.2	2.61 ± 0.54	0.79 ± 0.06	2.63 ± 0.25
	-8-CL	10.3 ± 1.5	2.63 ± 0.34	0.85 ± 0.07	2.81 ± 0.16

Table 6. Taxa found exclusively in mangrove transects, including adjacent sandflats, or only in mangrove sediments.

Island	Location	Identification
Oahu	mangrove sediments	*Pseudopolydora antennata*
		Marionina coatesae
		Phallodrilinae sp.
		Chironomidae larvae
		Insect sp. C
Oahu	mangrove and adjacent sandflats	*Ehlersia hyperioni*
		Bivalve sp. 1
		Amphipod sp. A
		Insect sp. D
		Insect sp. E
Molokai	mangrove sediments	*Aphelocheta molinaris*
		Monticellina sp. 1
		Monticellina sp. 2
		Monticellina sp. 3
		Monticellina sp. 4
		Monticellina sp. 5
		Monticellina sp. 6
		Amphiglena mediterranea
		Potamilla sp. 3
		Caraziella reishi
		Pseudopolydora corallicola
		Lumbrineris dentata
		Mesochaetopterus sagittarus
		Paraonella sp. A
		Polydora sp. 1,
		Enchytraeidae sp. 2
Molokai	mangrove and adjacent sandflats	*Myriochele oculata*
		Myriochele sp. 1
		Myriochele sp. 2
		Polycirrus sp. 1
		Tectidrilus bori
		Tubificid sp. 1
		Eriopisa hamakua
		Tanaid sp. B
		Pionosyllis spinsetosa
		crab zoea

Table 7. Comparisons of trophic, domicile, mobility, and biogeo groups from the mangrove and sandflat habitats within 4 sites. Shown are pairwise Analysis of Similarity (ANOSIM) and SIMPER between-site percent similarities and R statistics. Elevations were nested within sites.

	ANOSIM		SIMPER
Trophic group	P	R statistic	% Similarity
Mangrove versus Sandflat Controls			
Oahu	0.002	0.357	70.85
Molokai	0.002	0.541	60.34
Mangrove site similarities			
Oahu versus Molokai	0.002	0.412	57.89
Domicile group			
Mangrove versus Sandflat Controls			
Oahu	0.087	0.134	74.75
Molokai	0.002	0.694	65.26
Mangrove site similarities			
Oahu versus Molokai	0.050	0.269	65.6
Mobility group			
Mangrove versus Sandflat Controls			
Oahu	0.041	0.244	72.97
Molokai	0.017	0.321	72.12
Mangrove site similarities			
Oahu versus Molokai	0.078	0.202	65.36
Biogeo group			
Mangrove versus Sandflat Controls			
Oahu	0.002	0.517	66.94
Molokai	0.002	0.170	71.02
Mangrove site similarities			
Oahu versus Molokai	0.002	0.122	64.84

Table 8. Macrofaunal taxon richness (S, d), diversity (H', Fisher's a), evenness (J'), in introduced and native mangroves. S= number of species per core, densities per core, d = S-1/log N. Error represents 1 standard error. Samples were sieved on 0.5 mm mesh sieves.

Site	S	d	J'	H'(log_2)	Core area	Source
Oahu	20.0 ± 2.0	3.3 ± 0.3	0.6 ±0.02	2.6± 0.1	33 cm^2	This study
Molokai	30.0 ± 1.7	6.0 ± 0.5	0.7± 0.04	3.5 ± 0.3	33 cm^2	This study
Australia	35-65	0.00	0.00	0.00	6.6cm^2	Alongi and Christoffersen, 1992
Florida	38-56	4 to 8	0.00	0.00	78.5cm^2	Sheridan 1997
New Zealand	3.7-6.6	0.74-1.51	0.00	0.00	78.5 cm^2	Morrisey et al., 2003
Hong Kong	17.65	2.30	0.48	1.64	269 cm^2	Lee 1999
New Zealand	3.08	1.19	0.00	0.00	113 cm^2	Ellis et al. 2004
New Zealand	6.21	1.65	0.00	0.00	113 cm^2	Ellis et al. 2004
India	0.00	0.00	0.80	2.43	40 cm^2	Sunil Kumar 1995

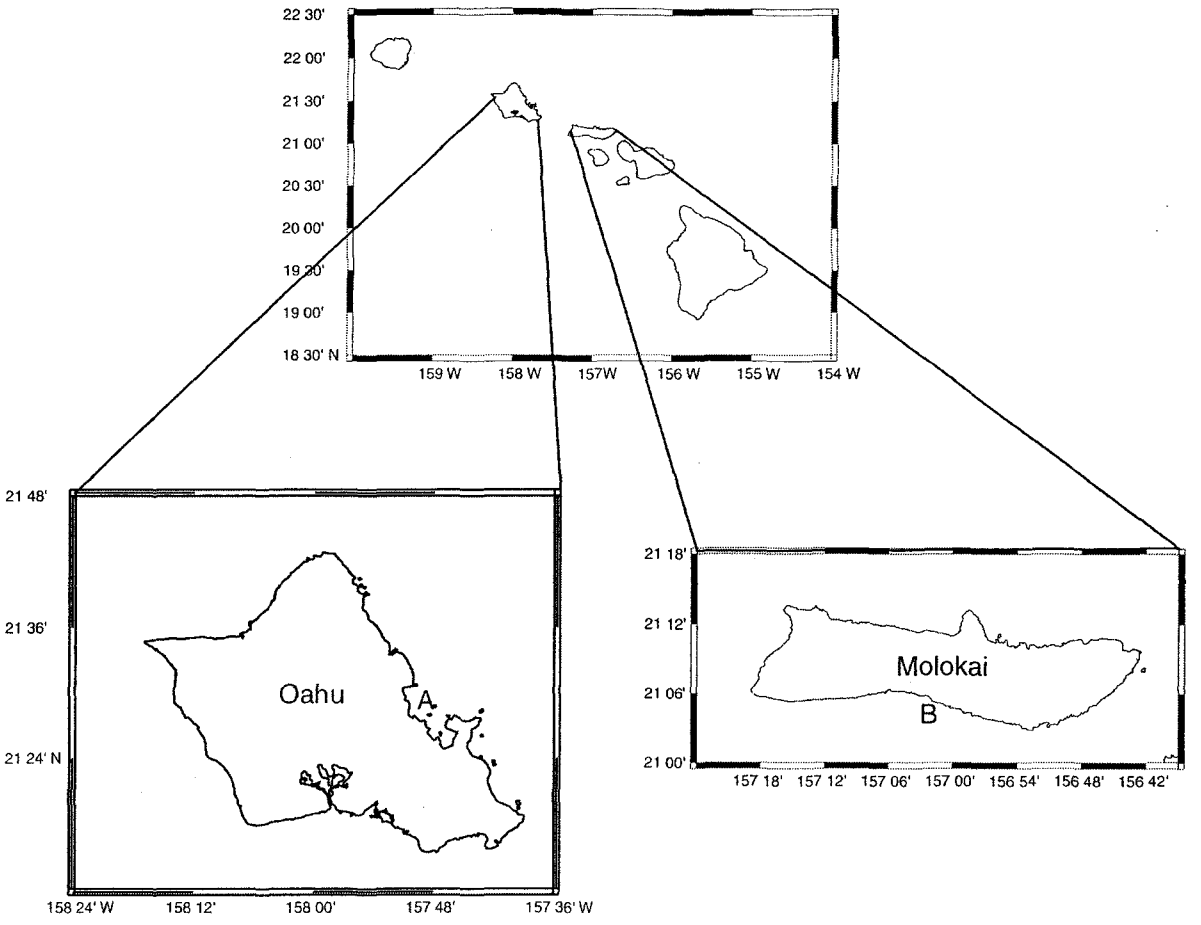
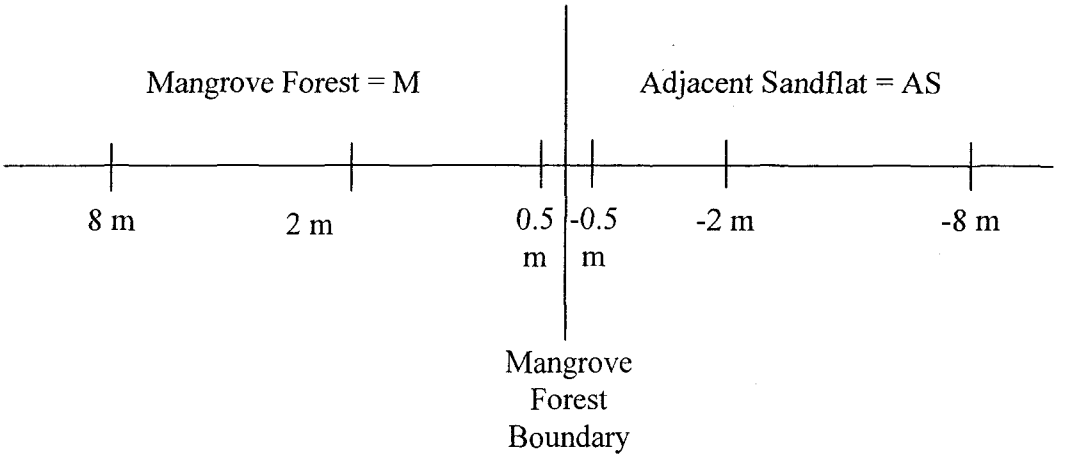


Figure 1. Locations of sampling stations on Oahu and Molokai, Hawaii.

A.



B.

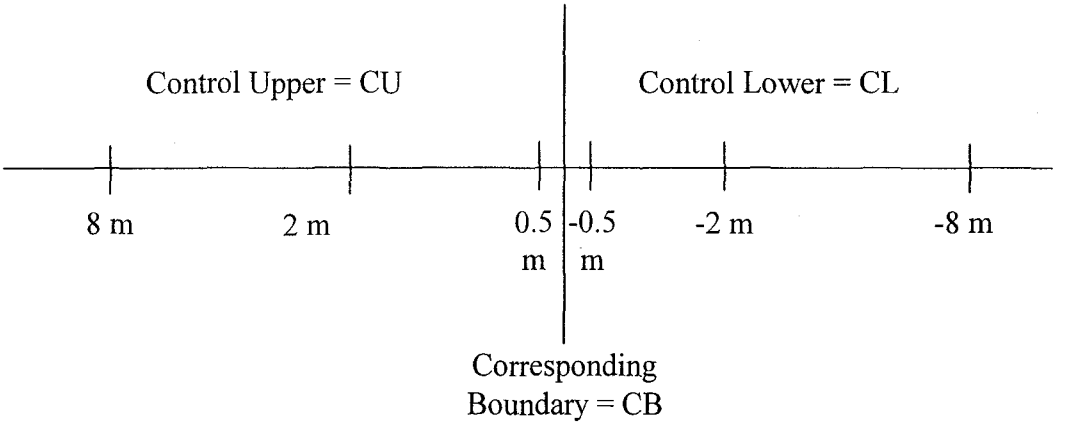


Figure 2. Sampling design in mangrove (A) and control (B) transects.

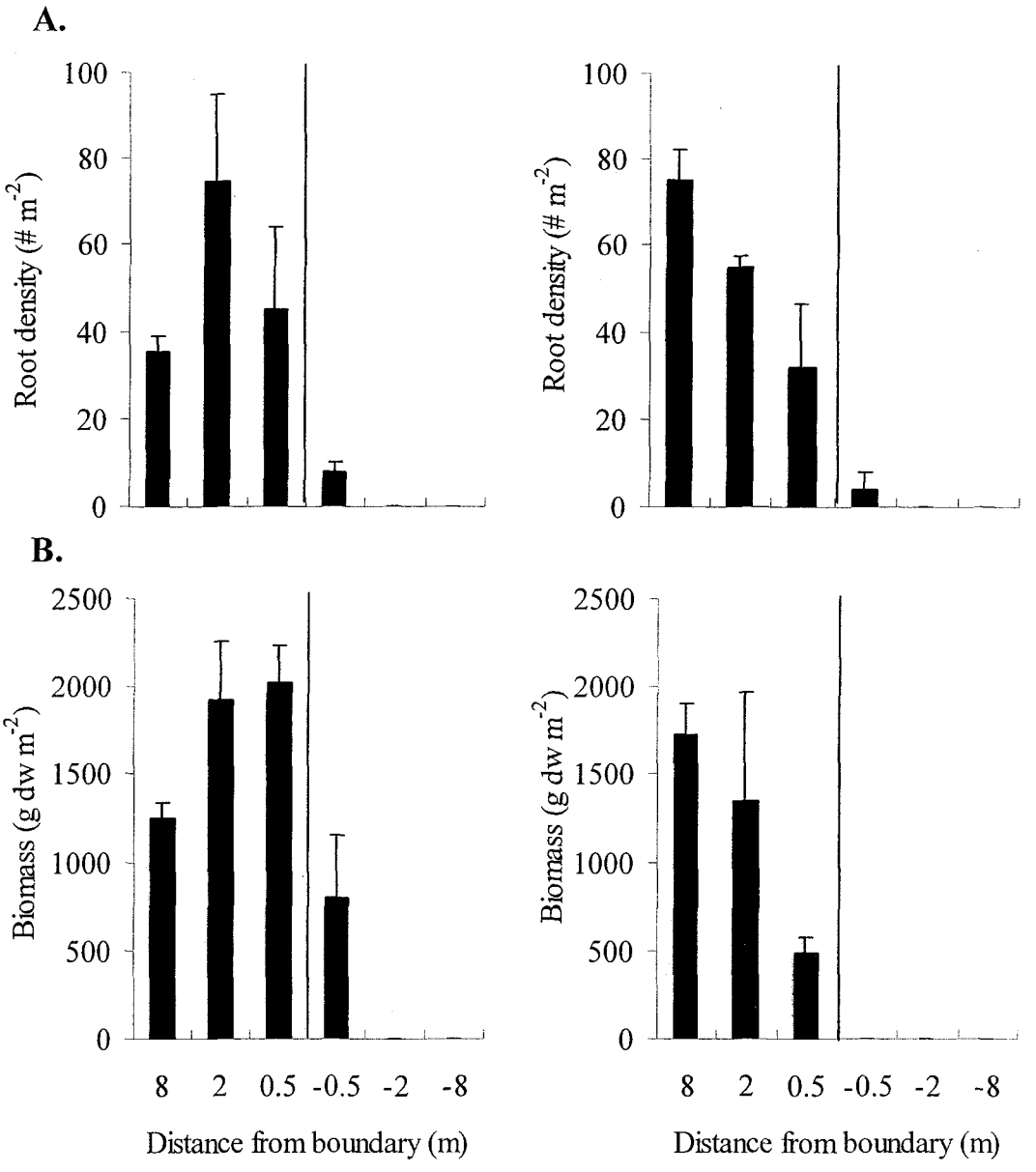


Figure 3. Mean (± 1 SE) root density (A) and below-ground biomass (B) found in mangroves and adjacent sandflats. Vertical line represent forest boundary as in Figure 2.

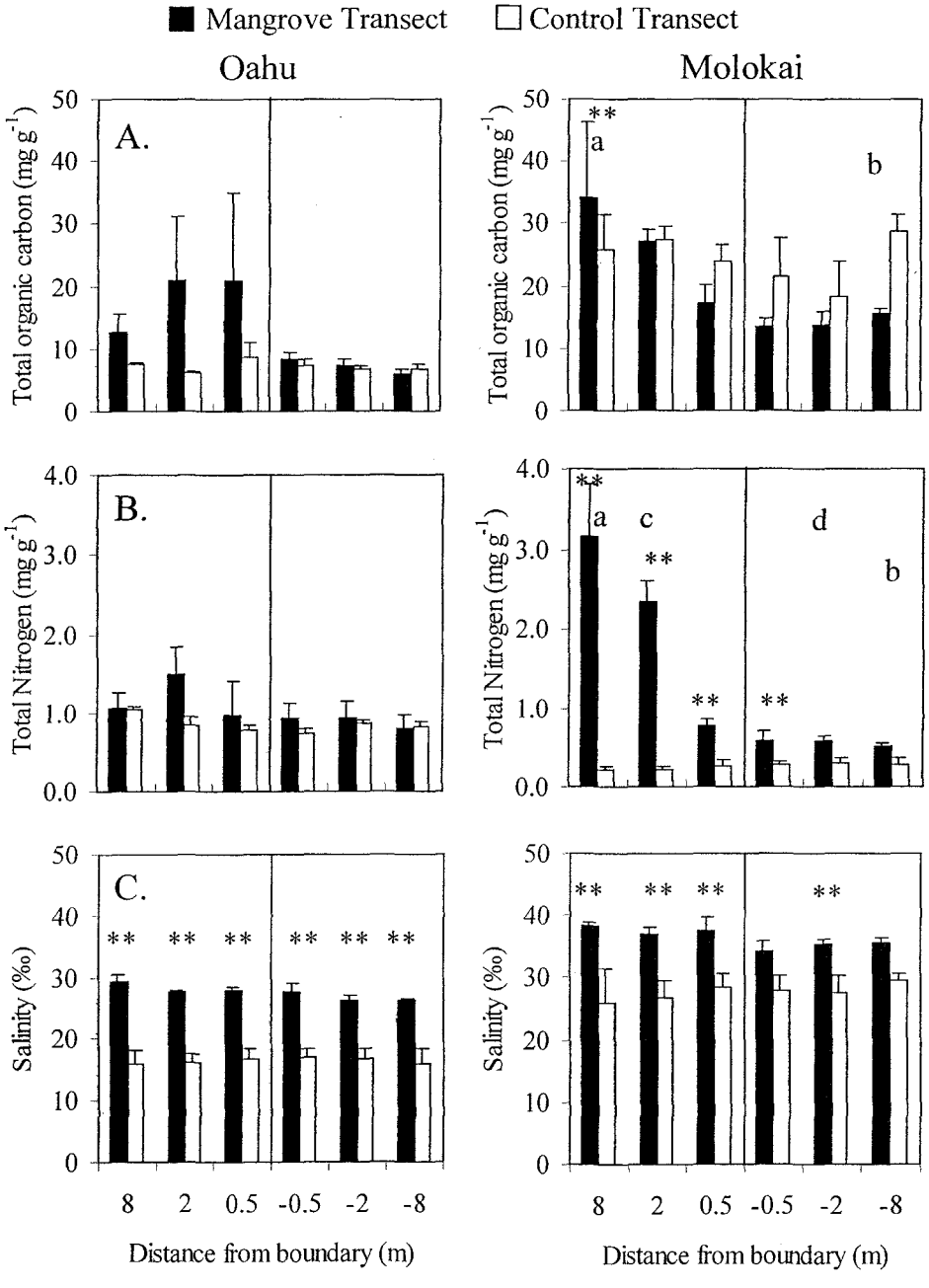


Figure 4. Mean (± 1 SE) (A) sediment organic carbon, (B) sediment total nitrogen, and (C) pore-water salinity found in mangrove and control transects on Oahu and Molokai. Letters a and b, c and d indicate significant differences between elevation pairs 8 and –8 m (e.g., 8 m inside mangroves compared to 8 m on adjacent sandflat), and 2 and –2 m, respectively. ** indicate significance for comparisons between mangrove and control sandflat transect samples at the same tidal elevations. $\alpha = 0.05$ from ANOVA f-tests between mangroves and adjacent sandflats, and mangroves and sandflat controls. Vertical line corresponds to boundary as in Figure 2.

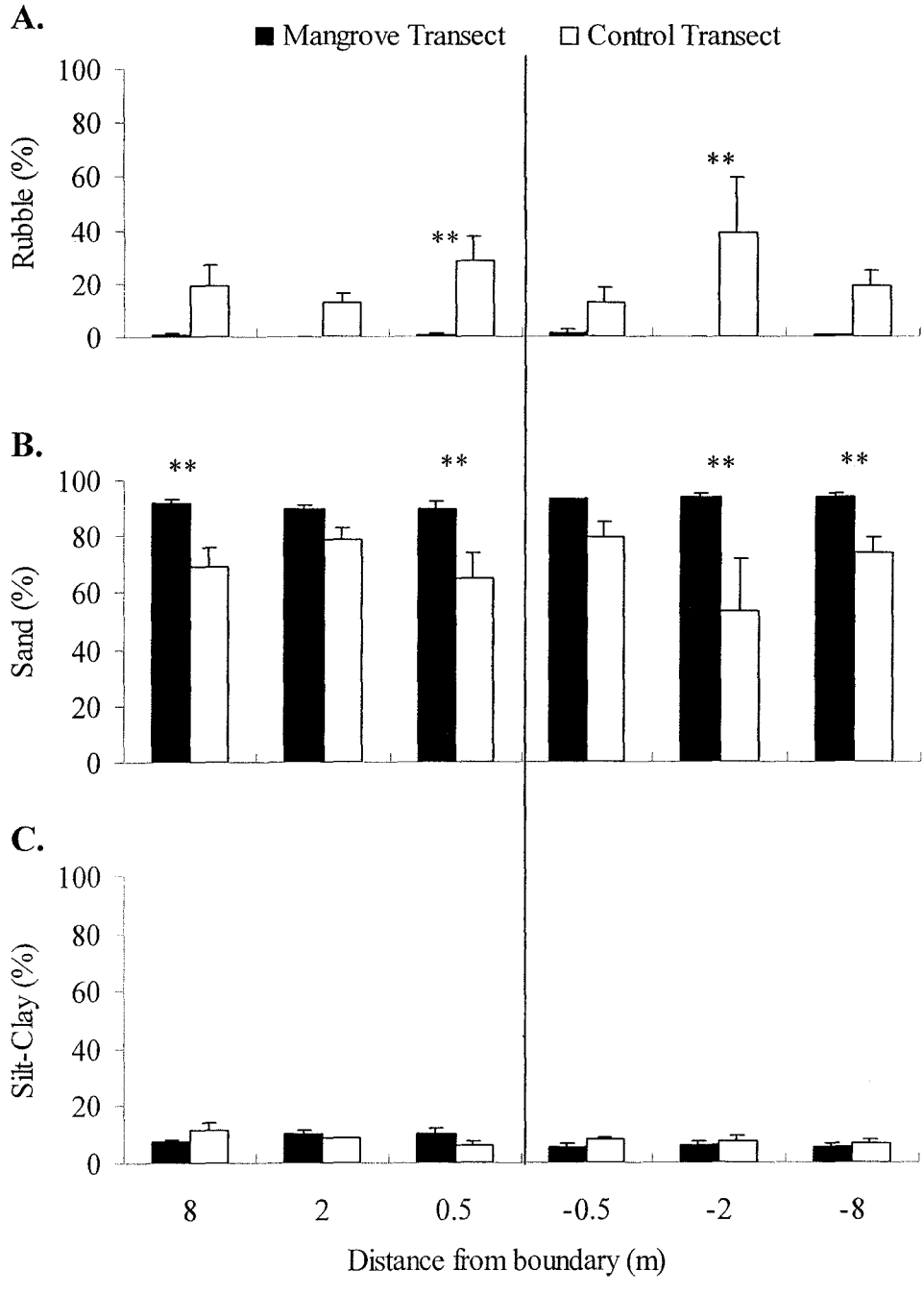


Figure 5. Mean (± 1 SE) (A) percent rubble, (B) percent sand, and (C) percent silt-clay found in Oahu mangroves, adjacent sandflats, and sandflat controls. ** indicate significance for comparisons between mangrove and control sandflat transect samples at the same tidal elevations, with $\alpha < 0.05$ from ANOVA f-tests between mangroves and adjacent sandflats, and mangroves and sandflat controls. Vertical line corresponds to boundary as in Figure 2.

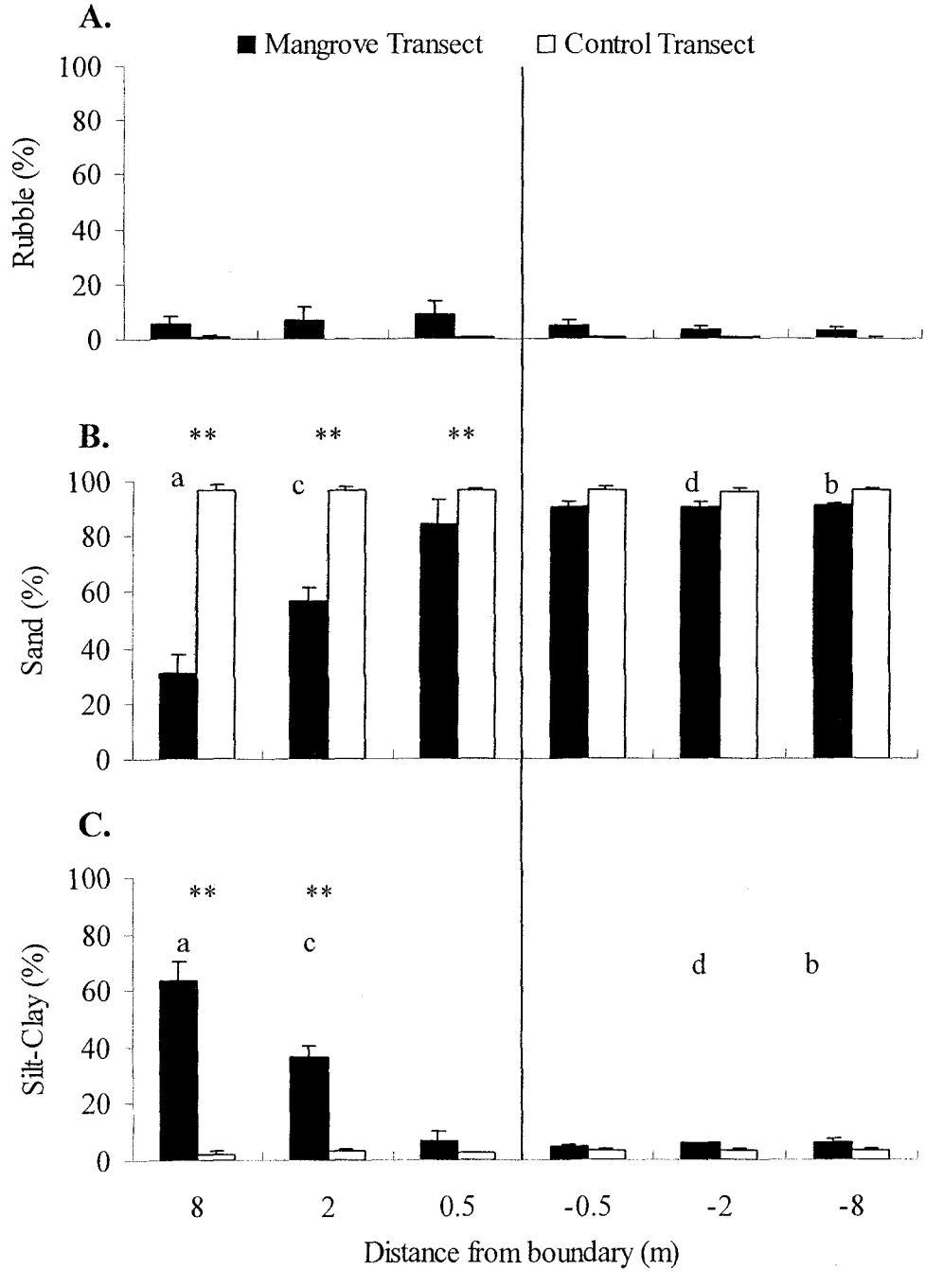


Figure 6. Mean (± 1 SE) (A) percent rubble, (B) percent sand, and (C) percent silt-clay found in Molokai mangroves, adjacent sandflats, and sandflat controls. Letters a and b, c and d indicate significant differences between elevation pairs 8 and –8 m (e.g., 8 m inside mangroves compared to 8 m on adjacent sandflat), and 2 and –2 m, respectively. ** indicate significance for comparisons between mangrove and control sandflat transect samples at the same tidal elevations, with $\alpha < 0.05$ from ANOVA f-tests between mangroves and adjacent sandflats, and mangroves and sandflat controls. Vertical line corresponds to boundary as in Figure 2.

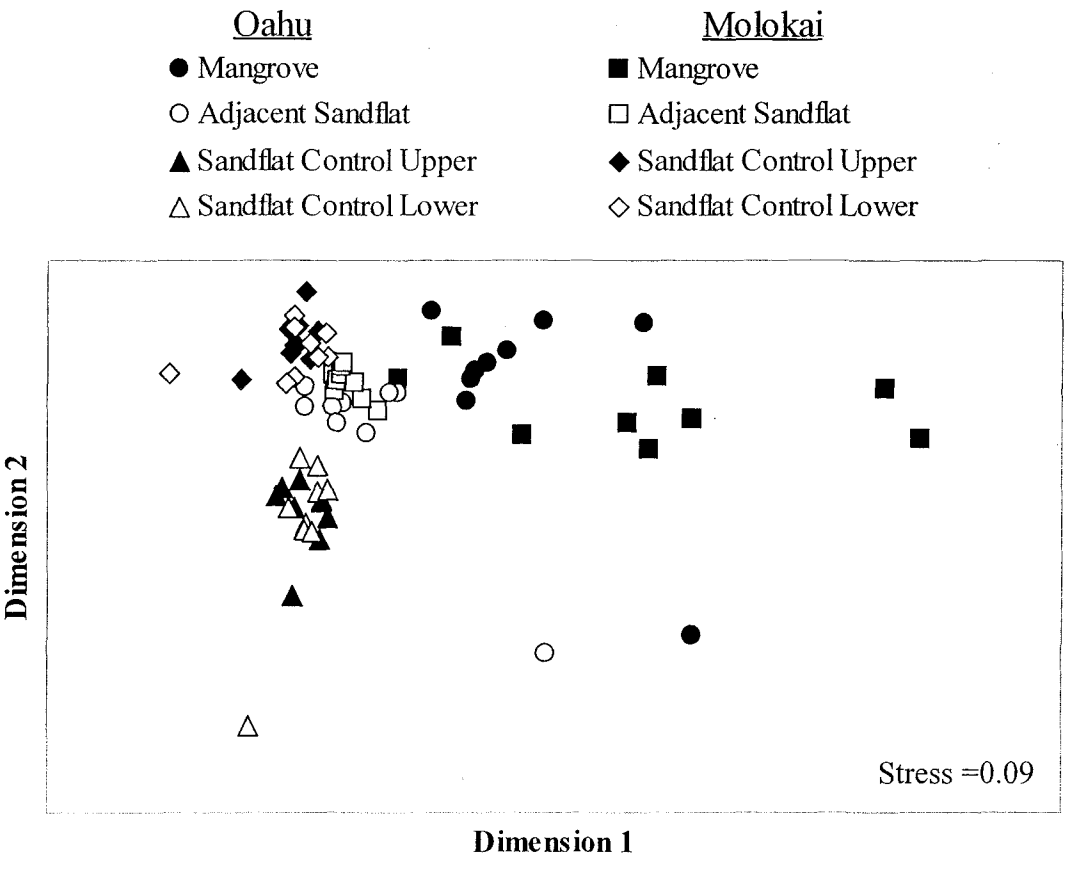


Figure 7. Multidimensional scaling of environmental parameters from mangrove, adjacent sandflats, and non-mangrove sandflat controls. Figure symbols as follows: Molokai mangrove and adjacent sandflats are solid and open squares, Oahu mangrove and adjacent sandflats are solid and open circles, control sandflats are solid and open diamonds (Molokai) and triangles (Oahu). Sandflat control upper and lower correspond to the same tidal elevation ranges as in mangrove and adjacent sandflat habitat, respectively. Each point represents the environmental parameters measured within one core.

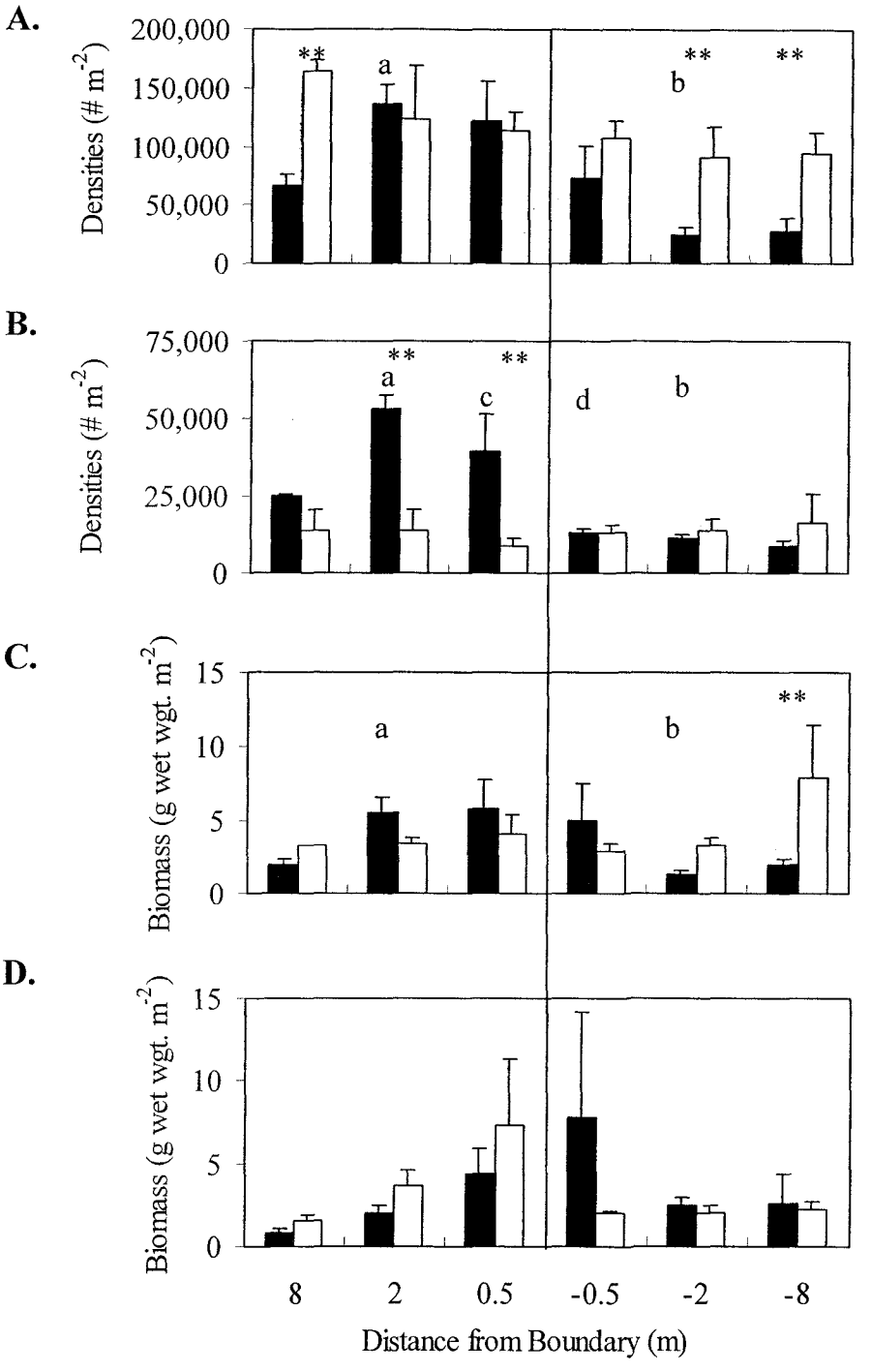


Figure 8. Macrofaunal densities (A and B), and biomass (C and D), from Oahu and Molokai, respectively. Error bars represent standard error of three samples. Letters a and b, c and d indicate significant differences between elevation pairs 2 and –2 m (e.g., 2 m inside mangroves compared to 2 m on adjacent sandflat), and 0.5 and –0.5m, respectively. ** indicate significance for comparisons between mangrove and control sandflat transect samples at the same tidal elevations, with $\alpha < 0.05$ from ANOVA f-tests between mangroves and adjacent sandflats, and mangroves and sandflat controls.

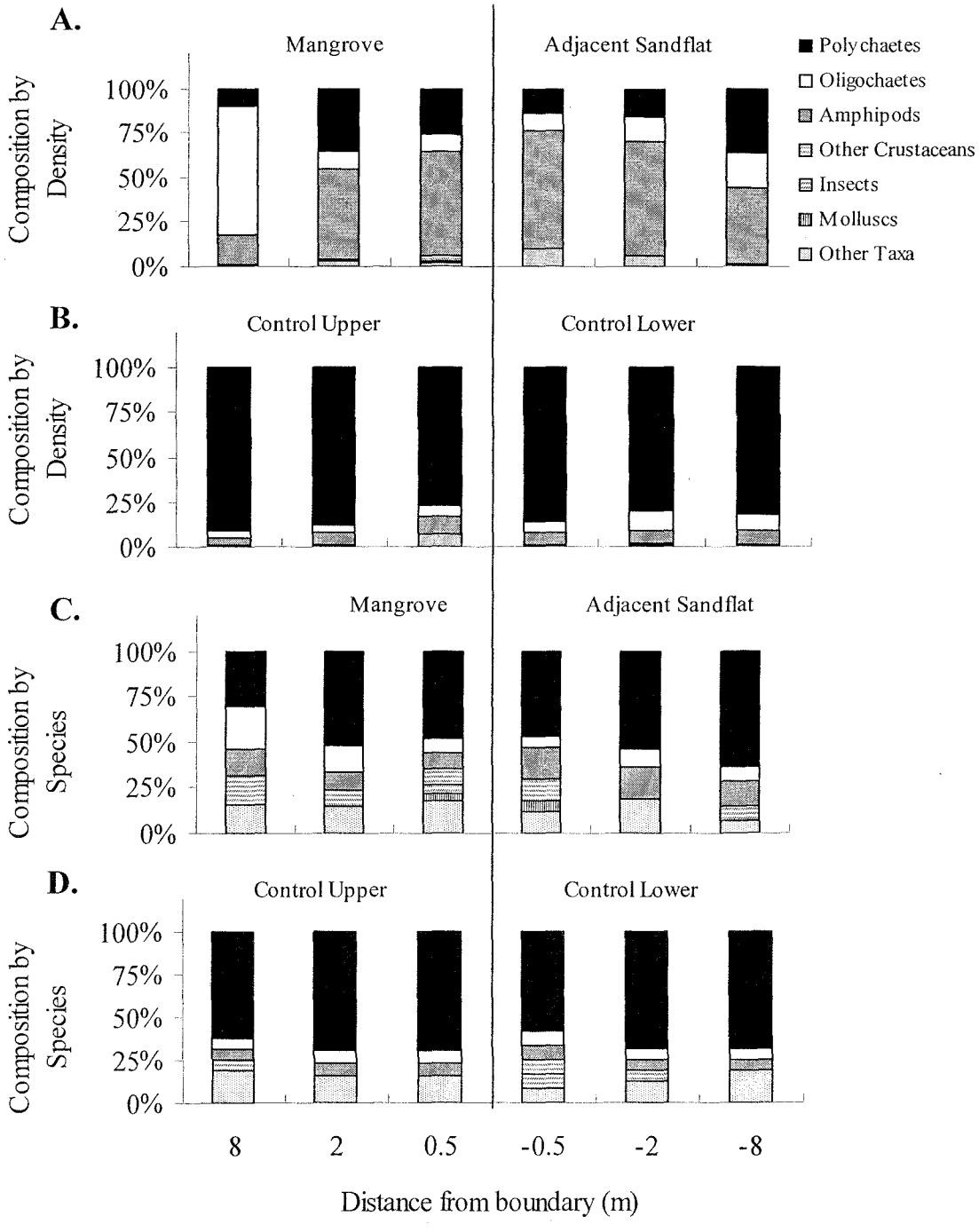


Figure 9. Proportion of taxa by macrofaunal densities (A and B) and species (C and D) from Oahu mangrove and control transects, respectively. Vertical line corresponds to the boundary between mangrove and adjacent sandflats or control upper and control lower elevations. See figure 2 for clarification.

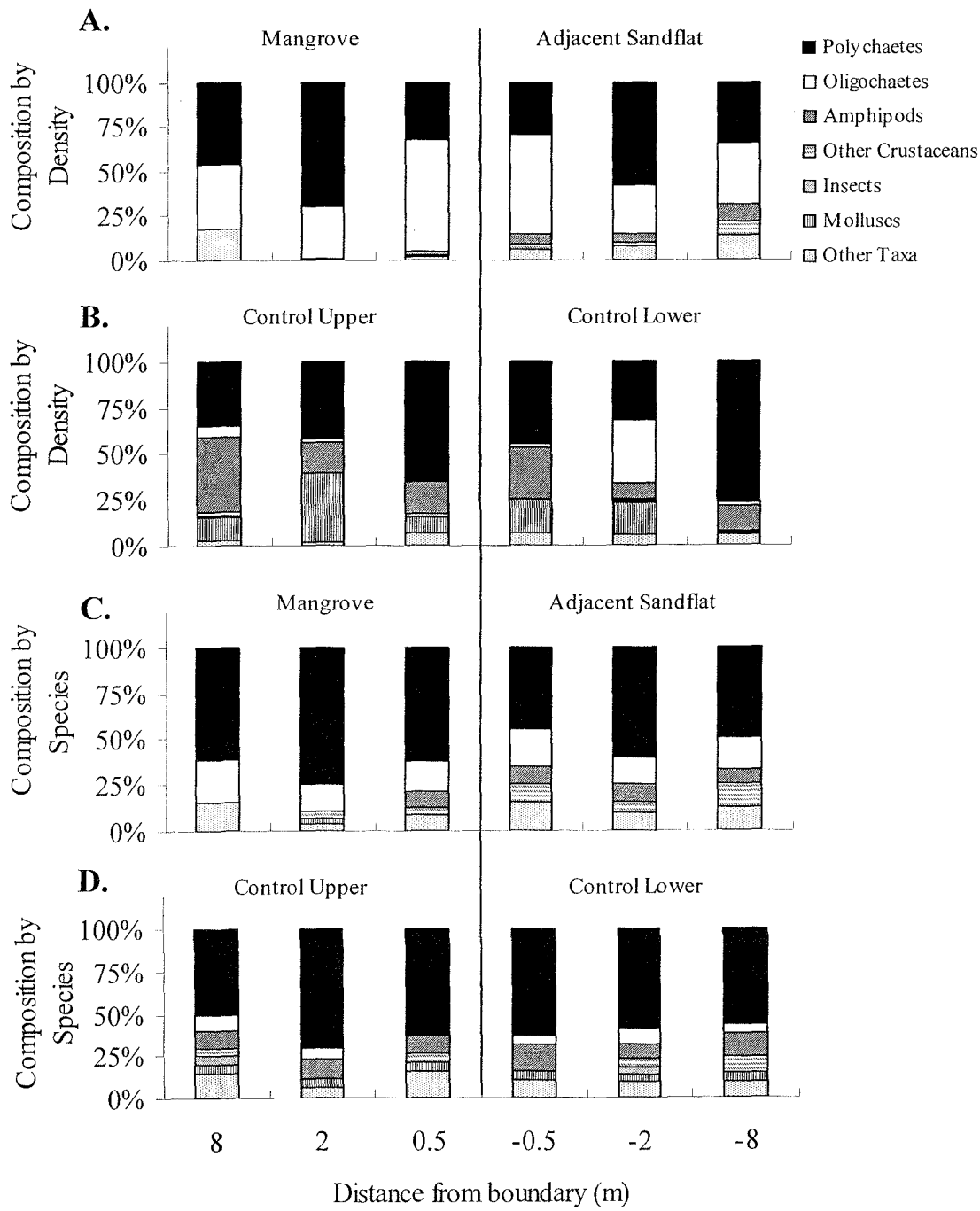


Figure 10. Proportion of taxa by macrofaunal densities (A and B) and species (C and D) from Molokai mangrove and control transects, respectively. Vertical line corresponds to the boundary between mangrove and adjacent sandflats or control upper and control lower elevations. See figure 2 for clarification.

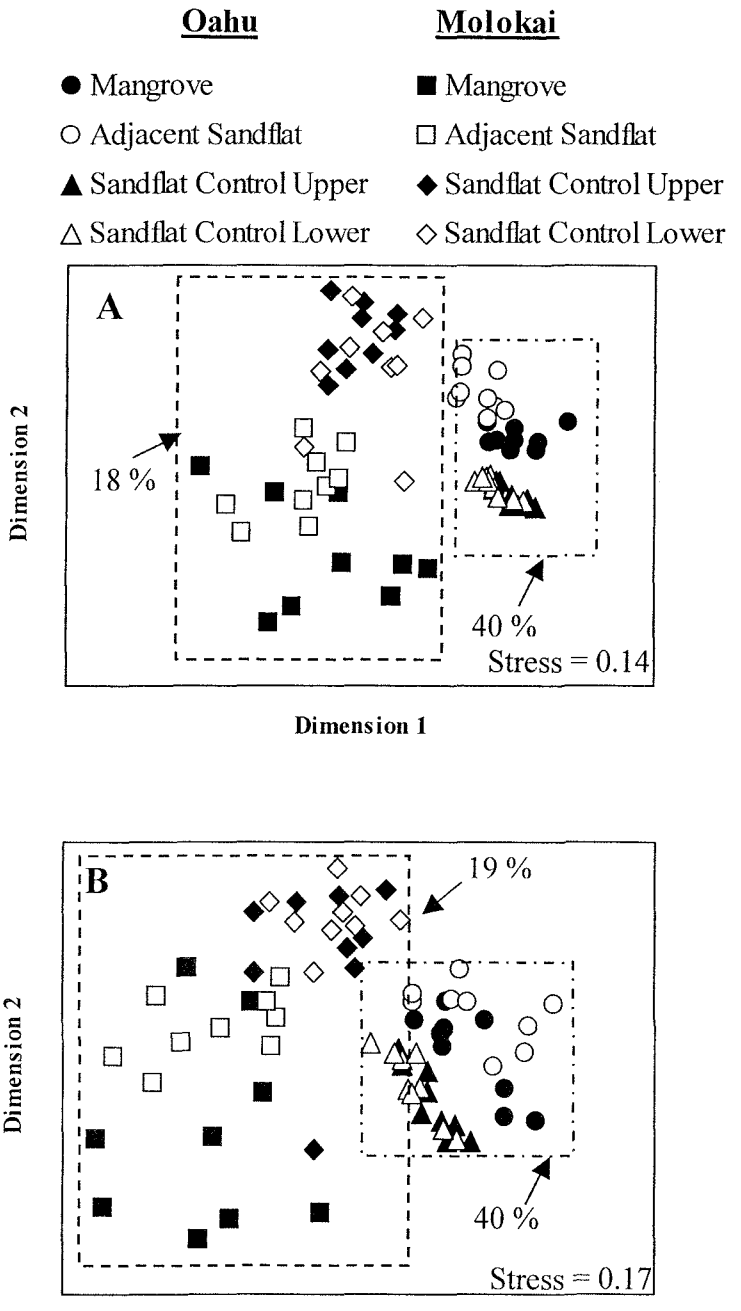


Figure 11. NMDS results of macrofaunal abundances (A) and biomass (B) from mangroves, adjacent sandflats, and sandflat controls. Each point represents the assemblage/biomass within one core. Dashed rectangles represent mangrove-sandflat control comparisons. Percent similarities are from SIMPER results in Table 4.

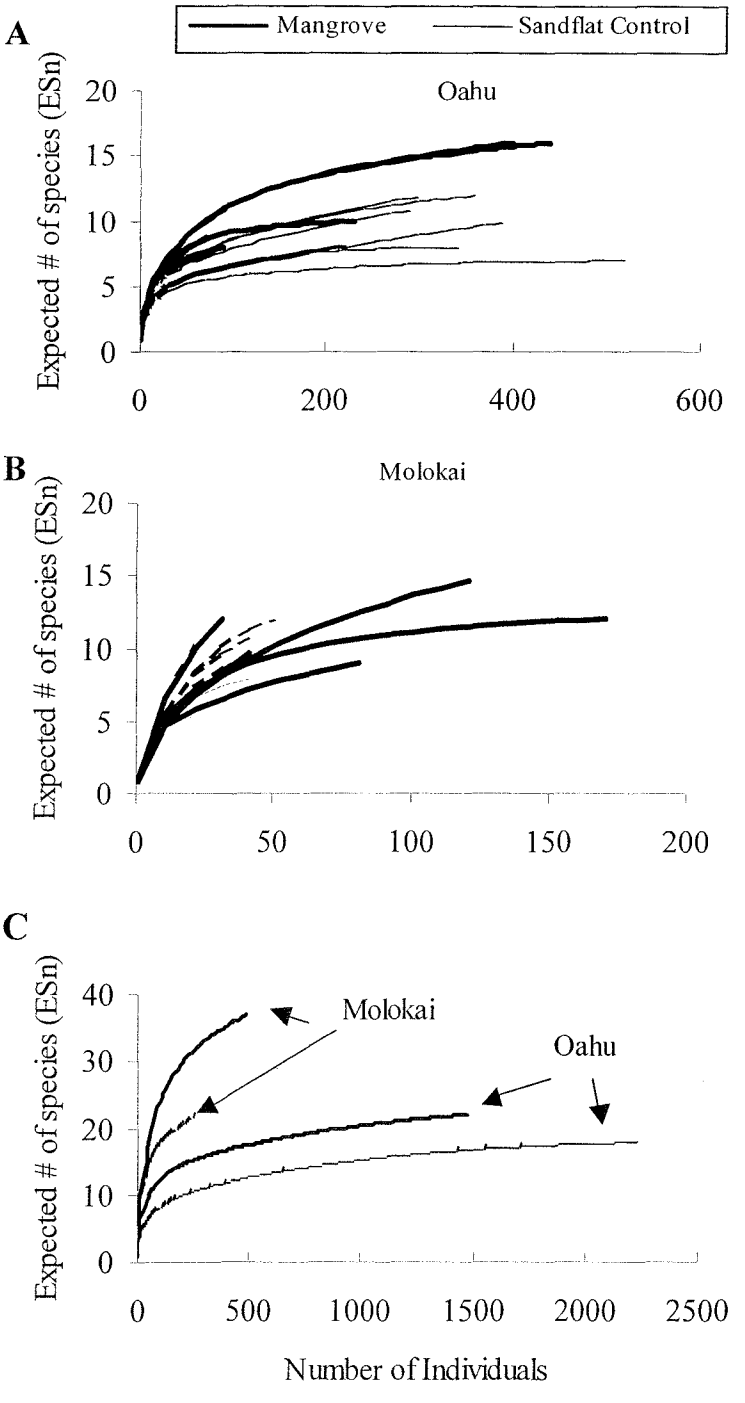


Figure 12. Rarefaction curves of macrofauna from the mangrove and control sandflat transects for Oahu (A) and Molokai (B). Each line represents data from each elevation, pooled from three replicate samples. (C) pooled elevation data by site (mangrove and control on Molokai and Oahu, respectively). Curves are generated by pooling data from each of the 4 sites, thus there is no within-site replication.

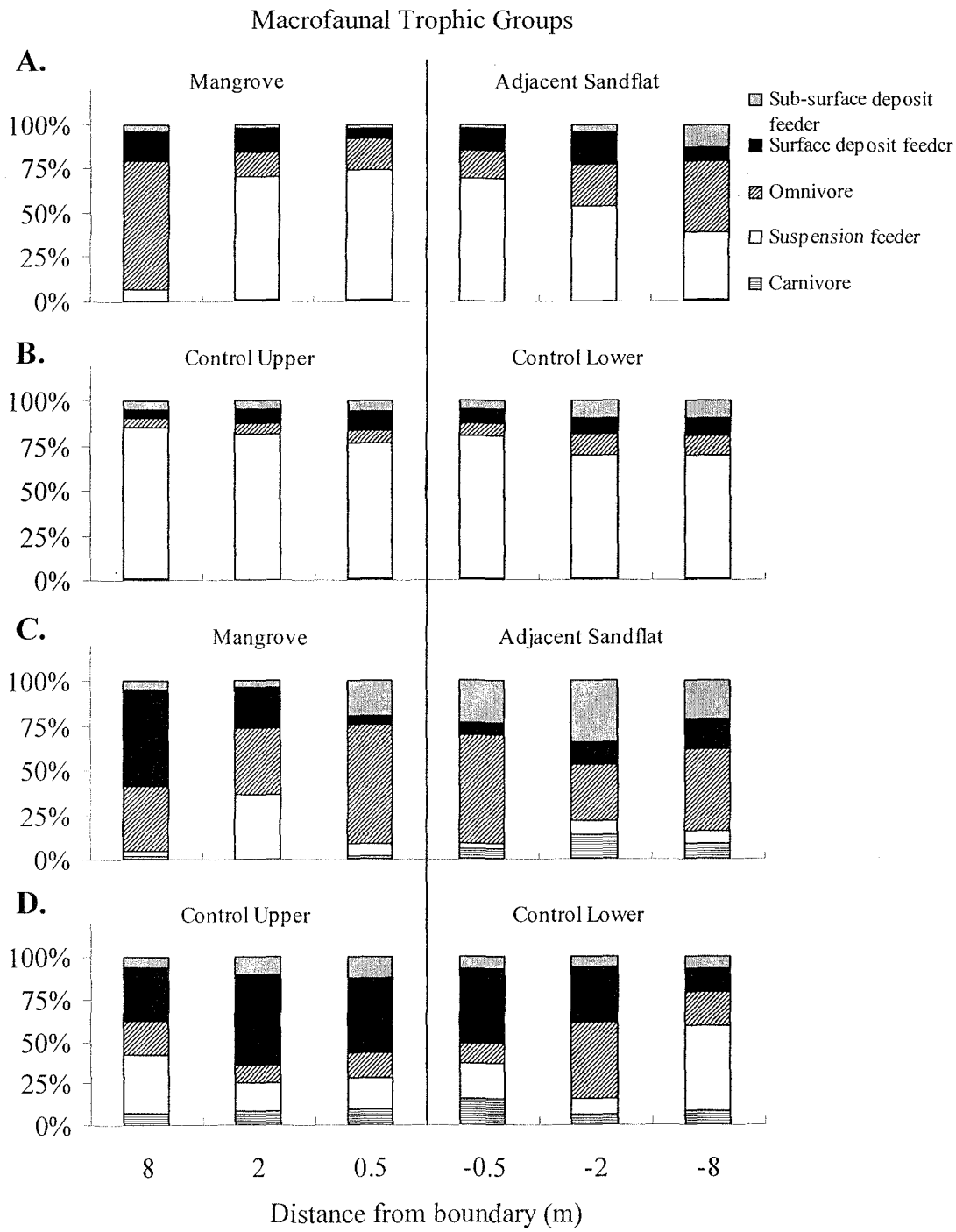


Figure 13. Percent composition of macrofaunal trophic groups from mangrove and control transects in Oahu (A and B) and Molokai (C and D), respectively. Vertical line corresponds to the boundary between mangrove and adjacent sandflats or control upper and control lower elevations. See figure 2 for clarification.

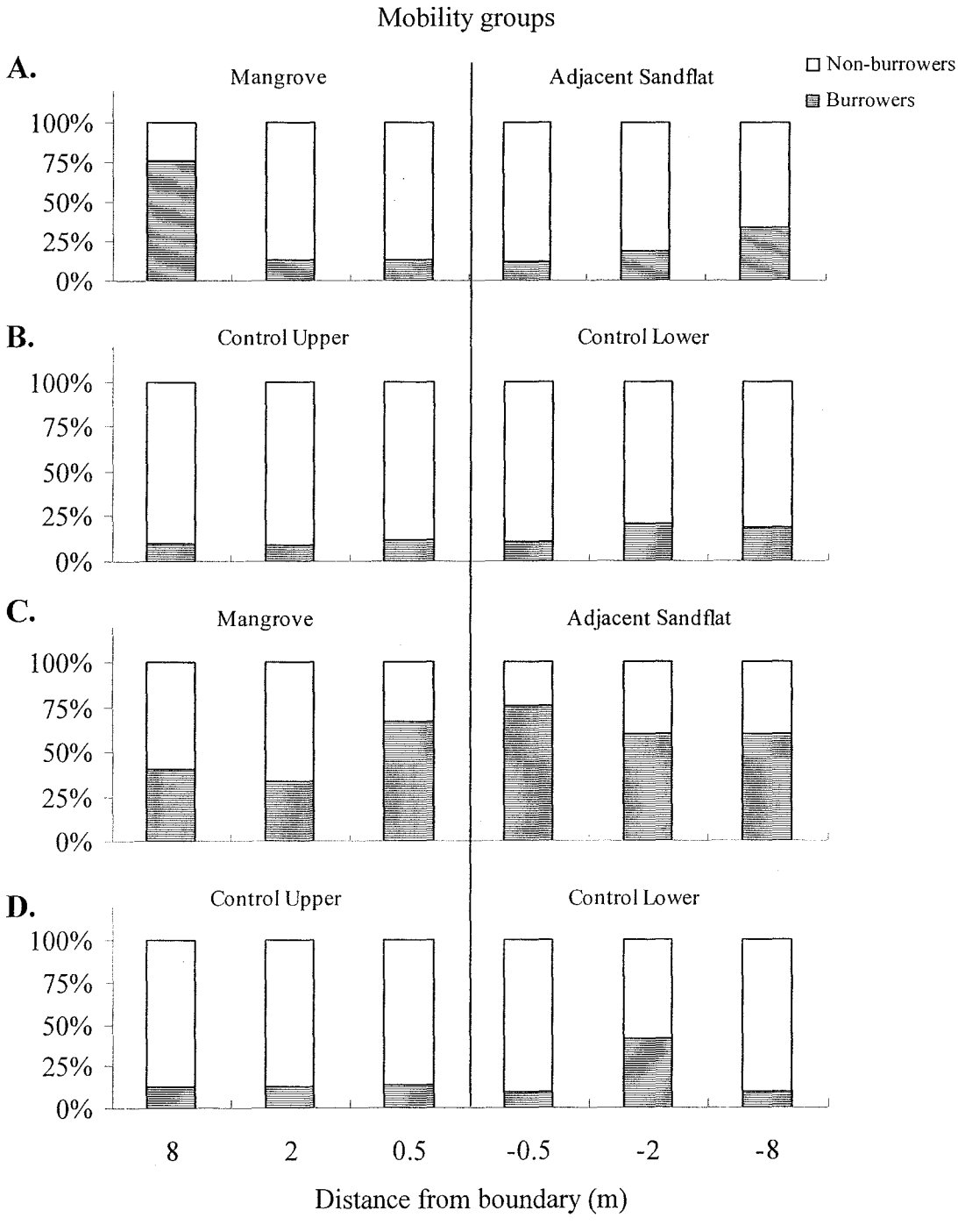


Figure 14. Percent composition of mobility groups from mangrove and control transects in Oahu (A and B) and Molokai (C and D), respectively. Vertical line corresponds to the boundary between mangrove and adjacent sandflats or control upper and control lower elevations. See figure 2 for clarification.

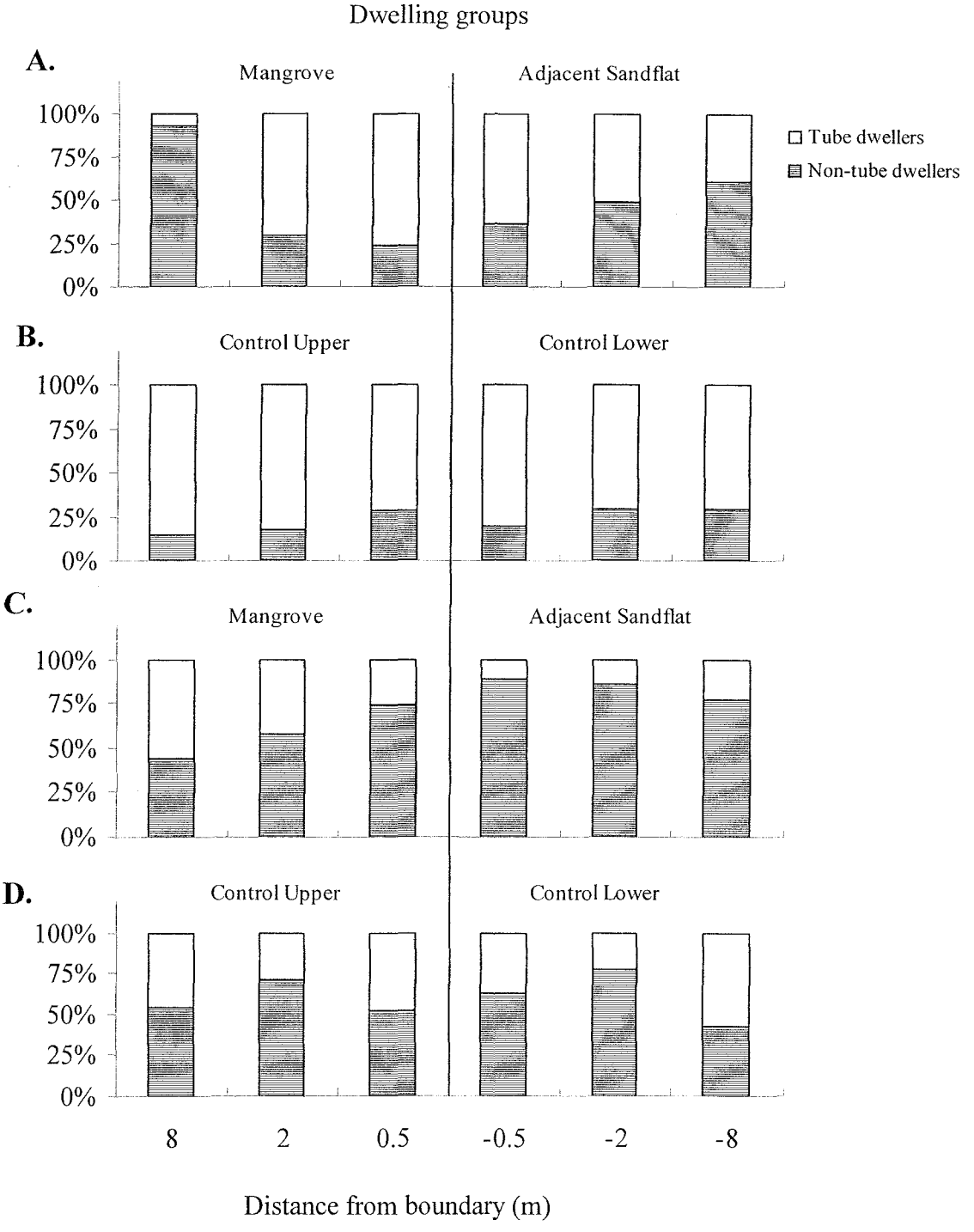


Figure 15. Percent composition of dwelling groups from mangrove and control transects in Oahu (A and B) and Molokai (C and D), respectively. Vertical line corresponds to the boundary between mangrove and adjacent sandflats or control upper and control lower elevations. See figure 2 for clarification.

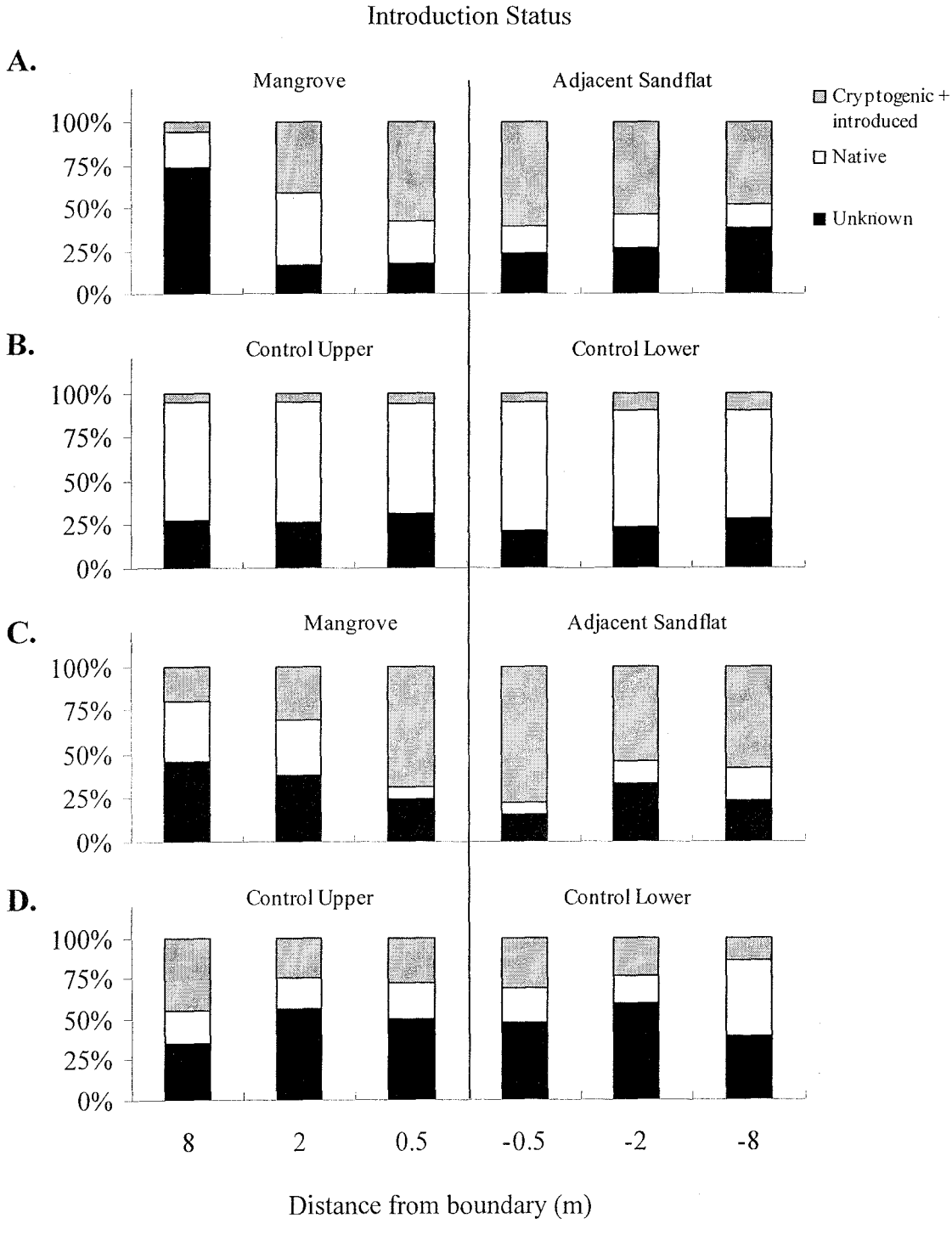


Figure 16. Percent composition of introduction status from mangrove and control transects in Oahu (A and B) and Molokai (C and D), respectively. Vertical line corresponds to the boundary between mangrove and adjacent sandflats or control upper and control lower elevations. See figure 2 for clarification.

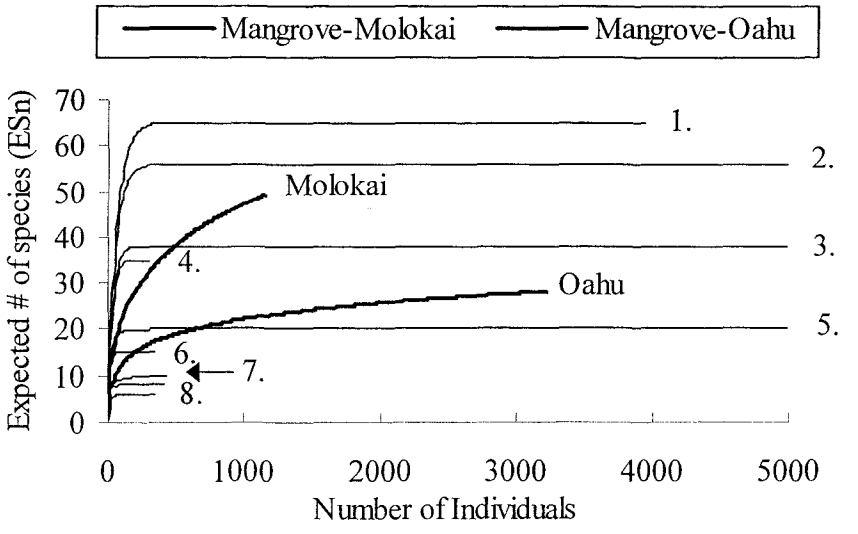


Figure 17. Rarefaction curves of macrofauna from the introduced and native mangrove forests (C). 1 and 4 = Alongi and Christoffersen (1992); 2 and 3 = Sheridan (1997); 5= Lee (1999); 6 = Sasekumar and Chong (1998); 7 = Ellis (2004); 8 = Morrisey (2003).

Appendix A. Trophic mode, domicile, mobility, and biogeographic status for all the infauna collected in mangroves, adjacent sandflats, and control sites on Oahu and Molokai. Letter key: SF=suspension feeder, sdf=surface deposit feeder, omni=omnivore, ssdf=sub-surface deposit feeder, carni=carnivore, tdw=tube-dweller, ntdw=non-tube dweller, b=burrower, nb=non-burrower, u=unknown, n=native, c=cryptogenic, and introduced = introduced species.

ANNELIDA	Trophic mode	Domicile	Mobility	Biogeostatus
Polychaeta				
Amphiglena mediterranea	SF	tdw	nb	u
Aphelochaeta cf molinaris	sdf	ntdw	nb	u
Arabella sp. 1	omni	ntdw	b	u
Armandia intermedia	ssdf	ntdw	b	c
Brania cf. furcelligera	omni	ntdw	nb	u
Brania cf. rhopalophora	omni	ntdw	nb	n
Brania spp.	omni	ntdw	nb	n
Capitella capitata	ssdf	ntdw	b	c
Carazziella cf. reishi	sdf	tdw	nb	n
Decamastus sp. 1	ssdf	ntdw	b	u
Decamastus sp. 2	ssdf	ntdw	b	u
Dipolydora cf. normalis	sdf	tdw	nb	u
Ehlersia cf. hyperioni	carni	ntdw	nb	u
Exogone longicornis	omni	ntdw	nb	u
Exogone sp. 1	omni	ntdw	nb	u
Exogone sp. E	omni	ntdw	nb	u
Lumbrineris cf dentata	omni	ntdw	b	u
Lysidice sp. 1	omni	tdw	b	u
Malacoceros sp. 1	sdf	tdw	nb	c
Marphysa corallina	omni	tdw	b	n
Mediomastus californiensis	ssdf	ntdw	b	u
Mediomastus sp. 1	ssdf	ntdw	b	u
Mesochaetopterus cf sagittarius	sdf	tdw	nb	n
Monticellina sp. 1	sdf	ntdw	nb	u
Monticellina sp. 2	sdf	ntdw	nb	u
Monticellina sp. 3	sdf	ntdw	nb	u
Monticellina sp. 4	sdf	ntdw	nb	u
Monticellina sp. 5	sdf	ntdw	nb	u
Monticellina sp. 6	sdf	ntdw	nb	u
Myriochele oculata	ssdf	tdw	nb	u
Myriochele sp. 1	ssdf	tdw	nb	u
Myriochele sp. 2	ssdf	tdw	nb	u

Appendix A cont.	Trophic mode	Domicile	Mobility	Biogeostatus
Nematonereis unicornis	omni	tdw	b	n
Paraonella sp. A	ssdf	ntdw	b	u
Pionosyllis spinesetosa	carni	ntdw	nb	u
Polychaete larva	omni	ntdw	nb	u
Polycirrus sp.1	sdf	tdw	nb	n
Polydora sp. 1	sdf	tdw	nb	u
Potamilla cf. linguicollaris	SF	tdw	nb	u
Potamilla sp. 1	SF	tdw	nb	n
Potamilla sp. 2	SF	tdw	nb	u
Potamilla sp. 3	SF	tdw	nb	u
Potamilla sp. 4	SF	tdw	nb	u
Pseudopolydora cf. antennata	sdf	tdw	nb	n
Pseudopolydora corallicola	sdf	tdw	nb	n
Questidae	ssdf	ntdw	b	u
Rhynchospio sp.1	sdf	tdw	nb	n
Sabellidae sp.	SF	tdw	nb	u
Scyphoproctus djiboutiensis	ssdf	ntdw	b	n
Sphaerosyllis cf. centroamericana	omni	ntdw	nb	n
Spiochaetopterus cf costarum	sdf	tdw	nb	u
Syllidae sp.	omni	ntdw	nb	u
Typosyllis cf. variegata	carni	ntdw	nb	u
Typosyllis cornuta	carni	ntdw	nb	n
OLIGOCHAETA				
Enchytraeidae				
Enchytraeidae sp.2	omni	ntdw	b	u
Cf. *Marionina coatesae*	omni	ntdw	b	u
Tubificidae				
Ainudrilus sp.	omni	ntdw	b	u
Phallodrilinae sp.	omni	ntdw	b	u
Smithsonidrilus capricornae	omni	ntdw	b	u
Tectidrilus cf. bori	omni	ntdw	b	c
Thalassodrilides cf. gurwitschi	omni	ntdw	b	c
Tubificid sp. 1	omni	ntdw	b	u
ARTHROPODA				
Crustacea				
Amphipoda				
Corophium insidiosum	SF	tdw	nb	introduced
Eriopisa sp. A	omni	ntdw	nb	u
Eriopisella sechellensis upolu	omni	ntdw	nb	n
Gammaridae sp. A	omni	ntdw	nb	u
Neomicrodeutopus cf makena	sdf	ntdw	nb	n

Appendix A cont.	Trophic mode	Domicile	Mobility	Biogeostatus
Nuuanu cf amikai	omni	ntdw	nb	n
Other Crustaceans				
Metopograpsus sp.	omni	ntdw	nb	n
Apanthura inornata	omni	ntdw	nb	n
Isopod sp. A	omni	ntdw	nb	u
Munnidae sp. A	omni	ntdw	nb	u
Sphaeromatidae sp. A	omni	ntdw	nb	u
Anatanais insularis	omni	tdw	nb	n
Apseudes n. sp. moniker	omni	tdw	nb	introduced
Leptochelia dubia	omni	tdw	nb	introduced
caridean shrimp	omni	tdw	nb	u
crab zoea	omni	tdw	nb	u
Insecta				
Chironomidae larvae	sdf	ntdw	nb	u
Insect sp. A	sdf	ntdw	nb	u
Insect sp. c	sdf	ntdw	nb	u
Insect sp. d	sdf	ntdw	nb	u
Insect sp. f	sdf	ntdw	nb	u
Technomyrmex albipes	sdf	ntdw	nb	introduced
Sipunculid	sdf	tdw	nb	u
Nemertean	carni	ntdw	nb	u
Hydrozoa	SF	ntdw	nb	u
Bryozoa/Ectoproct	SF	ntdw	nb	u
Platyhelminthes	carni	ntdw	b	u
MOLLUSCA				
Gastropod sp. 1	sdf	ntdw	nb	u
Bivalve sp. 1	SF	ntdw	nb	u

Appendix B. Mean density (no. individuals m^{-2}) of macrofaunal taxa in mangroves, adjacent sandflats, and control sandflat sites on Oahu and Molokai.

		M			AS	
OAHU MANGROVE TRANSECTS	8	2	0.5	-0.5	-2	-8
POLYCHAETES	6869	48889	31313	10303	3939	10000
Capitellidae	2828	3737	3131	1616	1010	3535
Capitella capitata	2828	3737	3131	1616	1010	3535
Decamastus sp. 1	0	0	0	0	0	0
Decamastus sp. 2	0	0	0	0	0	0
Mediomastus sp. 1	0	0	0	0	0	0
Mediomastus californiensis	0	0	0	0	0	0
Scyphoproctus djiboutiensis	0	0	0	0	0	0
Chaetopteridae	0	0	0	0	0	0
Mesochaetopterus cf sagittarius	0	0	0	0	0	0
Spiochaetopterus cf costarum	0	0	0	0	0	0
Cirratulidae	0	0	0	0	0	0
Aphelochaeta cf molinaris	0	0	0	0	0	0
Monticellina sp. 1	0	0	0	0	0	0
Monticellina sp. 2	0	0	0	0	0	0
Monticellina sp. 3	0	0	0	0	0	0
Monticellina sp. 4	0	0	0	0	0	0
Monticellina sp. 5	0	0	0	0	0	0
Monticellina sp. 6	0	0	0	0	0	0
Eunicid	0	202	505	303	0	404
Lysidice sp. 1	0	0	0	0	0	101
Marphysa corallina	0	202	303	101	0	202
Nematonereis unicornis	0	0	202	202	0	101
Lumbrineridae	0	0	0	0	0	0
Lumbrineris cf dentata	0	0	0	0	0	0
Oenonidae	0	0	0	0	0	0
Arabella sp. 1	0	0	0	0	0	0
Ophelidae	0	0	0	0	0	0
Armandia intermedia	0	0	0	0	0	0
Oweniidae	0	0	0	0	0	0
Myriochele oculata	0	0	0	0	0	0
Myriochele sp. 1	0	0	0	0	0	0
Myriochele sp. 2	0	0	0	0	0	0
Paraonidae	0	0	0	0	0	0
Paraonella sp. A	0	0	0	0	0	0
Questidae	0	0	0	0	0	0
Sabellidae	3939	41010	21717	3030	202	707
Amphiglena mediterranea	0	0	0	0	0	0

Appendix B. cont.		M			AS	
OAHU MANGROVE TRANSECTS	8	2	0.5	-0.5	-2	-8
Potamilla sp. 1	3434	36970	19697	3030	202	606
Potamilla sp. 2	505	3232	1818	0	0	101
Potamilla sp. 3	0	0	0	0	0	0
Potamilla sp. 4	0	0	0	0	0	0
Potamilla cf. linguicollaris	0	808	202	0	0	0
Sabellidae sp.	0	0	0	0	0	0
Spionidae	101	1111	1111	2222	606	0
Carazziella cf. reishi	0	0	0	0	0	0
Dipolydora cf. normalis	0	0	0	0	0	0
Polydora sp. 1	0	0	0	0	0	0
Malacoceros sp. 1	101	1010	909	2121	505	0
Pseudopolydora cf. antennata	0	101	0	0	0	0
Pseudopolydora corallicola	0	0	0	0	0	0
Rhynchospio sp.1	0	0	202	101	101	0
Syllidae	0	2828	4848	3131	2121	5354
Brania cf. furcelligera	0	101	0	0	0	0
Brania cf. rhopalophora	0	0	0	0	0	0
Brania spp.	0	0	0	0	0	0
Ehlersia cf. hyperioni	0	0	0	0	0	0
Exogone sp. 1	0	0	0	0	0	0
Exogone sp. E	0	909	3535	2121	1616	4646
Exogone longicornis	0	0	0	0	0	0
Pionosyllis spinesetosa	0	0	0	0	0	0
Sphaerosyllis cf. centroamericana	0	1717	909	1010	505	404
Typosyllis cornuta	0	101	404	0	0	303
Typosyllis cf. variegata	0	0	0	0	0	0
Syllidae sp.	0	0	0	0	0	0
Terribellidae	0	0	0	0	0	0
Polycirrus sp.1	0	0	0	0	0	0
Polychaete larva	0	202	808	606	0	101
OLIGOCHAETES	48485	13434	11919	7172	3434	5354
Enchytraeidae	7980	2424	404	0	0	0
Cf. *Marionina coatesae*	7980	2424	404	0	0	0
Enchytraeidae sp.2	0	0	0	0	0	0
Tubificidae	40505	11010	11515	7172	3434	5354
Tubificid sp. 1	0	0	0	0	0	0
Thalassodrilides cf. gurwitschi	0	0	0	0	0	0
Phallodrilinae sp.	707	404	0	0	0	0
Ainudrilus sp.	39798	10606	11515	7172	3434	5354
Smithsonidrilus capricornae	0	0	0	0	0	0

Appendix B. cont.		M			AS	
OAHU MANGROVE TRANSECTS	8	2	0.5	-0.5	-2	-8
Tectidrilus cf. bori	0	0	0	0	0	0
CRUSTACEA	11414	70505	75152	48182	15657	12020
AMPHIPOD	11414	68283	71010	47778	15657	12020
Neomicrodeutopus cf makena	10909	16667	5051	7071	4040	2222
Corophium insidiosum	505	51616	65960	40606	11616	9798
Eriopisella sechellensis upolu	0	0	0	0	0	0
Eriopisa sp. A	0	0	0	0	0	0
Nuuanu cf amikai	0	0	0	0	0	0
Gammaridae sp. A	0	0	0	101	0	0
Metopograpsus sp.	0	202	0	0	0	0
Sphaeromatidae sp. A	0	0	0	0	0	0
Munnidae sp. A	0	0	0	101	0	0
Isopod sp. A	0	0	0	0	0	0
Apanthura inornata	0	0	0	0	0	0
Leptochelia dubia	0	0	101	0	0	0
Anatanais insularis	0	2020	4040	303	0	0
Apseudes n. sp. moniker	0	0	0	0	0	0
caridean shrimp	0	0	0	0	0	0
crab zoea	0	0	0	0	0	0
MOLLUSCA	0	0	101	101	0	0
Gastropod sp. 1	0	0	0	0	0	0
Bivalve sp. 1	0	0	101	101	0	0
INSECTA	202	0	303	0	0	101
Insect sp. A	0	0	0	0	0	0
Technomyrmex albipes	101	0	0	0	0	0
Insect sp. c	101	0	0	0	0	0
Insect sp. d	0	0	0	0	0	101
Insect sp. f	0	0	0	0	0	0
Chironomidae larvae	0	0	303	0	0	0
Sipunculid	0	0	0	0	0	0
Nemertean	202	404	101	0	0	101
Hydrozoa	202	2828	1212	101	909	0
Bryozoa/Ectoproct	0	0	1414	6667	505	0
Platyhelminthes	0	303	101	0	0	0

Appendix B. cont.	CU			CL		
OAHU CONTROL TRANSECTS	8	2	0.5	-0.5	-2	-8
POLYCHAETES	148586	109091	88283	91717	73939	77576
Capitellidae	8282.8	5858.6	5960	4545	8283	8081
Capitella capitata	8080.8	5757.6	5960	4545	7980	7677
Decamastus sp. 1	0	0	0	0	0	0
Decamastus sp. 2	0	0	0	0	0	0
Mediomastus sp. 1	202.02	0	0	0	202	303
Mediomastus californiensis	0	101.01	0	0	101	101
Scyphoproctus djiboutiensis	0	0	0	0	0	0
Chaetopteridae	0	0	0	0	0	0
Mesochaetopterus cf sagittarius	0	0	0	0	0	0
Spiochaetopterus cf costarum	0	0	0	0	0	0
Cirratulidae	0	0	0	0	0	0
Aphelochaeta cf molinaris	0	0	0	0	0	0
Monticellina sp. 1	0	0	0	0	0	0
Monticellina sp. 2	0	0	0	0	0	0
Monticellina sp. 3	0	0	0	0	0	0
Monticellina sp. 4	0	0	0	0	0	0
Monticellina sp. 5	0	0	0	0	0	0
Monticellina sp. 6	0	0	0	0	0	0
Eunicid	303.03	505.05	404	202	505.1	303
Lysidice sp. 1	202.02	101.01	101	202	303	0
Marphysa corallina	0	404.04	303	0	0	303
Nematonereis unicornis	101.01	0	0	0	202	0
Lumbrineridae	0	0	0	0	0	0
Lumbrineris cf dentata	0	0	0	0	0	0
Oenonidae	0	0	0	0	0	0
Arabella sp. 1	0	0	0	0	0	0
Ophelidae	0	0	0	0	303	606.1
Armandia intermedia	0	0	0	0	303	606.1
Oweniidae	0	0	0	0	0	0
Myriochele oculata	0	0	0	0	0	0
Myriochele sp. 1	0	0	0	0	0	0
Myriochele sp. 2	0	0	0	0	0	0
Paraonidae	0	0	0	0	0	0
Paraonella sp. A	0	0	0	0	0	0
Questidae	0	0	0	0	0	0
Sabellidae	138990	101212	79091	84949	62727	64848
Amphiglena mediterranea	0	0	0	0	0	0
Potamilla sp. 1	102828	75556	59596	71212	53232	49798
Potamilla sp. 2	31818	21818	17273	11111	8586	13535

Appendix B. cont.	CU			CL		
OAHU CONTROL TRANSECTS	8	2	0.5	-0.5	-2	-8
Potamilla sp. 3	0	0	0	0	0	0
Potamilla sp. 4	0	0	0	0	0	0
Potamilla cf. linguicollaris	0	0	0	0	0	0
Sabellidae sp.	4343.4	3838.4	2222	2626	909.1	1515
Spionidae	202.02	505.05	1414	707.1	1616	1616
Carazziella cf. reishi	0	0	0	0	0	0
Dipolydora cf. normalis	0	0	606.1	0	0	101
Polydora sp. 1	0	0	0	0	0	0
Malacoceros sp. 1	202.02	505.05	808.1	707.1	1515	1515
Pseudopolydora cf. antennata	0	0	0	0	0	0
Pseudopolydora corallicola	0	0	0	0	0	0
Rhynchospio sp.1	0	0	0	0	101	0
Syllidae	808.08	1010.1	1414	1313	505.1	2121
Brania cf. furcelligera	101.01	0	0	0	0	0
Brania cf. rhopalophora	0	0	0	0	0	0
Brania spp.	0	0	0	0	0	0
Ehlersia cf. hyperioni	0	0	0	0	0	0
Exogone sp. 1	0	0	0	0	0	0
Exogone sp. E	606.06	808.08	1111	1111	505.1	1818
Exogone longicornis	0	0	0	0	0	0
Pionosyllis spinesetosa	0	0	0	0	0	0
Sphaerosyllis cf. centroamericana	101.01	101.01	303	202	0	303
Typosyllis cornuta	0	0	0	0	0	0
Typosyllis cf. variegata	0	0	0	0	0	0
Syllidae sp.	0	101.01	0	0	0	0
Terribellidae	0	0	0	0	0	0
Polycirrus sp.1	0	0	0	0	0	0
Polychaete larva	0	0	0	0	0	0
OLIGOCHAETES	6666.7	4949.5	6667	6364	9394	8384
Enchytraeidae	0	0	0	0	0	0
Cf. *Marionina coatesae*	0	0	0	0	0	0
Enchytraeidae sp.2	0	0	0	0	0	0
Tubificidae	6666.7	4949.5	6667	6364	9394	8384
Tubificid sp. 1	0	0	0	0	0	0
Thalassodrilides cf. gurwitschi	0	0	0	0	0	0
Phallodrilinae sp.	0	0	0	0	0	0
Ainudrilus sp.	6666.7	4949.5	6667	6364	9394	8384
Smithsonidrilus capricornae	0	0	0	0	0	0
Tectidrilus cf. bori	0	0	0	0	0	0

Appendix B. cont.	CU			CL		
OAHU CONTROL TRANSECTS	8	2	0.5	-0.5	-2	-8
CRUSTACEA	7373.7	9494.9	10909	7576	7071	7677
AMPHIPOD	7373.7	9494.9	10909	7475	6970	7677
Neomicrodeutopus cf makena	7373.7	9494.9	10909	7475	6970	7677
Corophium insidiosum	0	0	0	0	0	0
Eriopisella sechellensis upolu	0	0	0	0	0	0
Eriopisa sp. A	0	0	0	0	0	0
Nuuanu cf amikai	0	0	0	0	0	0
Gammaridae sp. A	0	0	0	0	0	0
Metopograpsus sp.	0	0	0	0	0	0
Sphaeromatidae sp. A	0	0	0	0	101	0
Munnidae sp. A	0	0	0	0	0	0
Isopod sp. A	0	0	0	0	0	0
Apanthura inornata	0	0	0	0	0	0
Leptochelia dubia	0	0	0	0	0	0
Anatanais insularis	0	0	0	0	0	0
Apseudes n. sp. moniker	0	0	0	0	0	0
caridean shrimp	0	0	0	101	0	0
crab zoea	0	0	0	0	0	0
MOLLUSCA	0	0	0	0	0	0
Gastropod sp. 1	0	0	0	0	0	0
Bivalve sp. 1	0	0	0	0	0	0
INSECTA	101.01	0	0	101	0	0
Insect sp. A	0	0	0	0	0	0
Technomyrmex albipes	0	0	0	0	0	0
Insect sp. c	0	0	0	0	0	0
Insect sp. d	0	0	0	0	0	0
Insect sp. f	101.01	0	0	101	0	0
Chironomidae larvae	0	0	0	0	0	0
Sipunculid	101.01	0	0	0	0	101
Nemertean	1010.1	505.05	808.1	909.1	1010	505.1
Hydrozoa	101.01	303.03	0	0	303	101
Bryozoa/Ectoproct	0	0	7273	0	0	0
Platyhelminthes	0	0	0	0	0	0

Appendix B. cont.		M			AS	
MOLOKAI MANGROVE TRANSECT	8	2	0.5	-0.5	-2	-8
POLYCHAETES	11616	37273	12929	3939	6667	3131
Capitellidae	606.06	1616.2	404	1010	1111	606.1
Capitella capitata	404.04	1313.1	101	1010	1010	404
Decamastus sp. 1	202.02	202.02	303	0	101	101
Decamastus sp. 2	0	101.01	0	0	0	101
Mediomastus sp. 1	0	0	0	0	0	0
Mediomastus californiensis	0	0	0	0	0	0
Scyphoproctus djiboutiensis	0	0	0	0	0	0
Chaetopteridae	101.01	404.04	101	0	0	0
Mesochaetopterus cf sagittarius	101.01	0	0	0	0	0
Spiochaetopterus cf costarum	0	404.04	101	0	0	0
Cirratulidae	101.01	9090.9	606.1	0	0	0
Aphelochaeta cf molinaris	0	101.01	0	0	0	0
Monticellina sp. 1	0	0	101	0	0	0
Monticellina sp. 2	0	5050.5	404	0	0	0
Monticellina sp. 3	0	3737.4	101	0	0	0
Monticellina sp. 4	0	101.01	0	0	0	0
Monticellina sp. 5	101.01	0	0	0	0	0
Monticellina sp. 6	0	101.01	0	0	0	0
Eunicid	0	101.01	0	0	0	0
Lysidice sp. 1	0	0	0	0	0	0
Marphysa corallina	0	101.01	0	0	0	0
Nematonereis unicornis	0	0	0	0	0	0
Lumbrineridae	0	101.01	0	0	0	0
Lumbrineris cf dentata	0	101.01	0	0	0	0
Oenonidae	0	0	0	0	0	0
Arabella sp. 1	0	0	0	0	0	0
Ophelidae	0	0	1212	1515	1414	1313
Armandia intermedia	0	0	1212	1515	1414	1313
Oweniidae	0	101.01	5859	505.1	101	0
Myriochele oculata	0	101.01	2424	0	101	0
Myriochele sp. 1	0	0	3434	303	0	0
Myriochele sp. 2	0	0	0	202	0	0
Paraonidae	303.03	0	0	0	0	0
Paraonella sp. A	303.03	0	0	0	0	0
Questidae	202.02	0	0	0	1313	0
Sabellidae	505.05	19091	2525	101	404	606.1
Amphiglena mediterranea	303.03	0	0	0	0	0
Potamilla sp. 1	0	14141	2020	0	404	505.1
Potamilla sp. 2	0	0	0	0	0	0

Appendix B. cont.		M			AS	
MOLOKAI MANGROVE TRANSECT	8	2	0.5	-0.5	-2	-8
Potamilla sp. 3	101.01	202.02	0	0	0	0
Potamilla sp. 4	0	4545.5	404	0	0	101
Potamilla cf. linguicollaris	101.01	101.01	0	101	0	0
Sabellidae sp.	0	101.01	101	0	0	0
Spionidae	9191.9	2626.3	1111	404	909.1	303
Carazziella cf. reishi	808.08	1515.2	0	0	0	0
Dipolydora cf. normalis	0	0	0	0	0	0
Polydora sp. 1	1010.1	0	0	0	0	0
Malacoceros sp. 1	0	101.01	1111	404	909.1	202
Pseudopolydora cf. antennata	0	0	0	0	0	0
Pseudopolydora corallicola	7373.7	1010.1	0	0	0	0
Rhynchospio sp.1	0	0	0	0	0	101
Syllidae	505.05	4141.4	1111	404	1414	303
Brania cf. furcelligera	0	0	101	101	101	0
Brania cf. rhopalophora	0	0	0	0	0	0
Brania spp.	0	0	0	0	0	0
Ehlersia cf. hyperioni	0	0	0	0	0	0
Exogone sp. 1	0	0	0	0	0	0
Exogone sp. E	0	4040.4	808.1	0	101	0
Exogone longicornis	202.02	0	0	0	101	101
Pionosyllis spinesetosa	0	0	0	101	707.1	101
Sphaerosyllis cf. centroamericana	101.01	101.01	0	0	0	0
Typosyllis cornuta	202.02	0	202	202	404	0
Typosyllis cf. variegata	0	0	0	0	0	101
Syllidae sp.	0	0	0	0	0	0
Terribellidae	101.01	0	0	0	0	0
Polycirrus sp.1	101.01	0	0	0	0	101
Polychaete larva	0	0	0	0	0	0
OLIGOCHAETES	8787.9	15758	24545	7273	3030	3030
Enchytraeidae	4040.4	0	0	0	0	0
Cf. *Marionina coatesae*	0	0	0	0	0	0
Enchytraeidae sp.2	4040.4	0	0	0	0	0
Tubificidae	4747.5	15758	24545	7273	3030	3030
Tubificid sp. 1	101.01	0	101	101	0	101
Thalassodrilides cf. gurwitschi	4343.4	13939	12121	4646	1313	2626
Phallodrilinae sp.	0	0	0	0	0	0
Ainudrilus sp.	101.01	808.08	0	0	0	0
Smithsonidrilus capricornae	101.01	202.02	404	303	404	101
Tectidrilus cf. bori	101.01	808.08	11919	2222	1313	202

Appendix B. cont.		M			AS	
MOLOKAI MANGROVE TRANSECT	8	2	0.5	-0.5	-2	-8
CRUSTACEA	0	101.01	1212	1212	808.1	1616
AMPHIPOD	0	0	505.1	707.1	606.1	909.1
Neomicrodeutopus cf makena	0	0	202	505.1	505.1	505.1
Corophium insidiosum	0	0	0	0	0	0
Eriopisella sechellensis upolu	0	0	303	202	101	404
Eriopisa sp. A	0	0	0	0	0	0
Nuuanu cf amikai	0	0	0	0	0	0
Gammaridae sp. A	0	0	0	0	0	0
Metopograpsus sp.	0	0	0	0	0	101
Sphaeromatidae sp. A	0	0	0	0	0	0
Munnidae sp. A	0	0	0	0	0	0
Isopod sp. A	0	0	0	0	0	101
Apanthura inornata	0	0	0	0	0	0
Leptochelia dubia	0	0	0	0	0	0
Anatanais insularis	0	0	0	0	0	0
Apseudes n. sp. moniker	0	101.01	707.1	404	202	505.1
caridean shrimp	0	0	0	0	0	0
crab zoea	0	0	0	101	0	0
MOLLUSCA	0	101.01	0	0	0	0
Gastropod sp. 1	0	101.01	0	0	0	0
Bivalve sp. 1	0	0	0	0	0	0
INSECTA	0	0	0	0	0	0
Insect sp. A	0	0	0	0	0	0
Technomyrmex albipes	0	0	0	0	0	0
Insect sp. c	0	0	0	0	0	0
Insect sp. d	0	0	0	0	0	0
Insect sp. f	0	0	0	0	0	0
Chironomidae larvae	0	0	0	0	0	0
Sipunculid	4040.4	0	0	0	0	606.1
Nemertean	202.02	0	505.1	303	505.1	101
Hydrozoa	101.01	101.01	0	202	404	0
Bryozoa/Ectoproct	0	0	0	0	0	0
Platyhelminthes	101.01	0	101	202	0	505.1

Appendix B. cont.		CU			CL	
MOLOKAI CONTROL TRANSECTS	8	2	0.5	-0.5	-2	-8
POLYCHAETES	4949.5	5858.6	5556	5960	4343	12424
Capitellidae	808.08	1313.1	707.1	707.1	707.1	1010
Capitella capitata	0	0	0	0	101	0
Decamastus sp. 1	0	0	101	0	0	0
Decamastus sp. 2	202.02	505.05	404	202	0	606.1
Mediomastus sp. 1	0	0	0	0	0	0
Mediomastus californiensis	0	0	0	0	0	0
Scyphoproctus djiboutiensis	606.06	808.08	202	505.1	606.1	404
Chaetopteridae	0	101.01	606.1	505.1	303	101
Mesochaetopterus cf sagittarius	0	0	0	0	0	0
Spiochaetopterus cf costarum	0	101.01	606.1	505.1	303	101
Cirratulidae	0	0	0	0	0	0
Aphelochaeta cf molinaris	0	0	0	0	0	0
Monticellina sp. 1	0	0	0	0	0	0
Monticellina sp. 2	0	0	0	0	0	0
Monticellina sp. 3	0	0	0	0	0	0
Monticellina sp. 4	0	0	0	0	0	0
Monticellina sp. 5	0	0	0	0	0	0
Monticellina sp. 6	0	0	0	0	0	0
Eunicid	0	0	0	0	101	0
Lysidice sp. 1	0	0	0	0	0	0
Marphysa corallina	0	0	0	0	0	0
Nematonereis unicornis	0	0	0	0	101	0
Lumbrineridae	0	0	0	0	0	0
Lumbrineris cf dentata	0	0	0	0	0	0
Oenonidae	0	101.01	0	0	0	0
Arabella sp. 1	0	101.01	0	0	0	0
Ophelidae	0	0	0	0	0	0
Armandia intermedia	0	0	0	0	0	0
Oweniidae	0	0	0	0	0	0
Myriochele oculata	0	0	0	0	0	0
Myriochele sp. 1	0	0	0	0	0	0
Myriochele sp. 2	0	0	0	0	0	0
Paraonidae	0	0	0	0	0	0
Paraonella sp. A	0	0	0	0	0	0
Questidae	101.01	101.01	404	303	101	202
Sabellidae	101.01	606.06	808.1	303	707.1	7071
Amphiglena mediterranea	0	0	0	0	0	0
Potamilla sp. 1	101.01	404.04	707.1	202	505.1	5152
Potamilla sp. 2	0	0	0	0	0	0

Appendix B. cont.		CU			CL	
MOLOKAI CONTROL TRANSECTS	8	2	0.5	-0.5	-2	-8
Potamilla sp. 3	0	0	0	0	0	0
Potamilla sp. 4	0	202.02	101	101	202	1212
Potamilla cf. linguicollaris	0	0	0	0	0	0
Sabellidae sp.	0	0	0	0	0	707.1
Spionidae	1414.1	1616.2	1616	1717	1111	808.1
Carazziella cf. reishi	0	0	0	0	0	0
Dipolydora cf. normalis	101.01	0	0	0	0	101
Polydora sp. 1	0	0	0	0	0	0
Malacoceros sp. 1	1313.1	1616.2	1616	1717	1111	707.1
Pseudopolydora cf. antennata	0	0	0	0	0	0
Pseudopolydora corallicola	0	0	0	0	0	0
Rhynchospio sp.1	0	0	0	0	0	0
Syllidae	2525.3	2020.2	1414	2424	1313	3232
Brania cf. furcelligera	0	0	0	0	0	0
Brania cf. rhopalophora	0	101.01	0	0	202	202
Brania spp.	0	0	0	0	202	0
Ehlersia cf. hyperioni	0	0	0	202	0	0
Exogone sp. 1	101.01	101.01	101	0	0	0
Exogone sp. E	0	0	303	505.1	606.1	2020
Exogone longicornis	1515.2	1010.1	707.1	707.1	202	303
Pionosyllis spinesetosa	0	0	0	0	0	0
Sphaerosyllis cf. centroamericana	101.01	0	0	0	0	0
Typosyllis cornuta	707.07	808.08	303	808.1	101	707.1
Typosyllis cf. variegata	0	0	0	202	0	0
Syllidae sp.	101.01	0	0	0	0	0
Terribellidae	0	0	0	0	0	0
Polycirrus sp.1	0	0	0	0	0	0
Polychaete larva	0	0	0	0	0	0
OLIGOCHAETES	707.07	202.02	0	202	4646	404
Enchytraeidae	0	0	0	0	0	0
Cf. *Marionina coatesae*	0	0	0	0	0	0
Enchytraeidae sp.2	0	0	0	0	0	0
Tubificidae	707.07	202.02	0	202	4646	404
Tubificid sp. 1	0	0	0	0	0	0
Thalassodrilides cf. gurwitschi	202.02	0	0	0	1212	404
Phallodrilinae sp.	0	0	0	0	0	0
Ainudrilus sp.	0	0	0	0	0	0
Smithsonidrilus capricornae	505.05	202.02	0	202	3434	0
Tectidrilus cf. bori	0	0	0	0	0	0

Appendix B. cont.	CU			CL		
MOLOKAI CONTROL TRANSECTS	8	2	0.5	-0.5	-2	-8
CRUSTACEA	5959.6	2323.2	1717	3737	1313	2323
AMPHIPOD	5757.6	2323.2	1515	3737	1212	2121
Neomicrodeutopus cf makena	1010.1	606.06	707.1	1212	505.1	909.1
Corophium insidiosum	4747.5	1717.2	808.1	2424	707.1	1111
Eriopisella sechellensis upolu	0	0	0	0	0	0
Eriopisa sp. A	0	0	0	101	0	0
Nuuanu cf amikai	0	0	0	0	0	101
Gammaridae sp. A	0	0	0	0	0	0
Metopograpsus sp.	0	0	0	0	0	0
Sphaeromatidae sp. A	0	0	0	0	0	0
Munnidae sp. A	0	0	0	0	0	0
Isopod sp. A	0	0	0	0	0	0
Apanthura inornata	202.02	0	0	0	101	101
Leptochelia dubia	0	0	0	0	0	0
Anatanais insularis	0	0	0	0	0	0
Apseudes n. sp. moniker	0	0	0	0	0	0
caridean shrimp	0	0	202	0	0	101
crab zoea	0	0	0	0	0	0
MOLLUSCA	1818.2	5151.5	707.1	2424	2424	202
Gastropod sp. 1	1818.2	5151.5	707.1	2424	2424	202
Bivalve sp. 1	0	0	0	0	0	0
INSECTA	101.01	0	0	0	101	0
Insect sp. A	101.01	0	0	0	0	0
Technomyrmex albipes	0	0	0	0	101	0
Insect sp. c	0	0	0	0	0	0
Insect sp. d	0	0	0	0	0	0
Insect sp. f	0	0	0	0	0	0
Chironomidae larvae	0	0	0	0	0	0
Sipunculid	101.01	0	101	0	101	202
Nemertean	101.01	303.03	404	808.1	707.1	707.1
Hydrozoa	0	0	0	0	0	0
Bryozoa/Ectoproct	0	0	0	101	0	0
Platyhelminthes	202.02	0	101	0	0	0

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CHAPTER 3. FOOD-WEB STRUCTURE IN INTRODUCED AND NATIVE MANGROVE COMMUNITIES; A HAWAII-PUERTO RICO COMPARISON.

Abstract

The importance of detrital pathways through infaunal and epifaunal food webs in introduced and native *Rhizophora mangle* forests was examined using a dual isotope approach and a two source mixing model. Only the nematode community and nereid polychaetes from native mangrove forests exhibited stable isotopes consistent with a mangrove-derived diet, based on the trophic-level fractionation of 0-1 ‰ for $\delta^{13}C$ and 3-4 ‰ for $\delta^{15}N$. Certain infauna (tubificid oligochaetes) had $\delta^{13}C$ values consistent with mangrove leaves, but were depleted in ^{15}N, suggesting their ultimate nitrogen source was characteristically low in ^{15}N, and was possibly N_2-fixing bacteria. Several infauna and epifauna from both native and introduced mangroves had stable isotopes values falling between mangrove and particulate organic matter (POM) and benthic microalgae (BMA) sources, potentially indicating a mixed diet. Tubificid oligochaetes and nematodes from the oldest mangrove forest on Molokai, Hawaii were the only infauna from introduced mangroves with stable isotope values similar to mangrove leaves. The remaining benthos from Hawaii were enriched in ^{13}C and ^{15}N relative to mangrove leaves and were significantly enriched compared to benthos from native mangrove forests, indicating that these organisms are not feeding on mangrove-derived material and differ from native forests. Differences between introduced and native mangrove forest food webs may be a

result of differential availability and utilization of mangrove versus non-mangrove primary food sources.

Introduction

Plant invasions into estuaries are a growing problem (Posey 1988; Callaway and Josselyn 1992; Posey et al. 1993). The impacts of introduced plants, including vascular plants, on tidal wetlands have been studied mostly in temperate wetlands (Posey 1988; Ruiz et al. 1997; Rice et al. 2000; Adam 2002). Vascular plant introductions to intertidal habitats can dramatically alter rates of water flow, sediment grain size and organic-carbon content, and oxygen and sulfide concentrations (both in bottom- and pore-waters). In addition, introduced plants can increase habitat complexity and sediment stability (Orth 1977; Posey 1987) and possibly provide a source of detrital and dissolved organic food (Kikuchi 1980; Alongi 1987; Posey 1988; Robertson and Alongi 1992; Levin and Talley 2000). Based on studies conducted in native vascular plant communities, all of these factors can substantially influence the structure, dynamics, and food webs of faunal communities (see reviews by Sanders 1969; Rhoads 1974; Gray 1974; Boesch 1977; Pearson and Rosenberg 1978; Nowell and Jumars 1984; Weston 1990; Robertson and Alongi 1992; Snelgrove and Butman 1994; Leonard and Luther 1995; Levin and Talley 2000), and therefore vascular plants in intertidal habitats can function as major ecosystem engineers (cf. Jones et al. 1997). The significant and rapid vegetation change associated with plant invasions provides the opportunity to examine the effects of these plants on faunal communities (Talley and Levin 2001), and more specifically, food-web structure.

In 1902, *Rhizophora mangle*, a mangrove broadly distributed in the New World and South Pacific, was introduced from Florida to southern Molokai, Hawaii to stabilize the shoreline (MacCaughey 1917; Degener 1945; 1946) and has subsequently spread naturally to the remaining Hawaiian Islands. *Rhizophora mangle* has high dispersal capabilities, broad environmental tolerances, and few natural enemies in Hawaii (Allen 1998; Cox and Allen 1999; Steele et al. 1999); as a consequence, mangroves have expanded rapidly into large portions of low-energy coastlines (e.g., the lagoons of south Molokai and Kaneohe Bay) as well as the banks of streams and drainage channels (e.g., in Pearl Harbor, Allen 1998). What remains unknown is how mangrove benthic communities compare to native mangrove forests and the role mangrove detritus plays in the food webs of each community.

It is difficult to predict the impact of mangroves on detrital food webs in Hawaiian coastal ecosystems. Prior to the recent invasion of mangroves, the intertidal zone of Hawaii generally lacked extensive vascular plants (Wester 1981; Allen 1998). Sasekumar (1974) and Frith (1977) reported that mangroves in Southeast Asia are a habitat for a specific, potentially co-evolved, fauna with limited species overlap between mangroves and sand or mud-flat biotopes. Because mangroves were recently introduced to Hawaii without their faunal associates or co-evolved fauna, detritivores colonizing Hawaiian mangrove habitats may not be adapted to consuming mangrove detritus, particularly detritus from *R. mangle*, which is rich in tannins (Sessegolo and Lana 1991). Tannins are toxic to many fish and bacteria (Mahadevan and Muthukumar 1980), and can interfere with the feeding and digestion of detritivores (McMillan 1984; Poovachiranon et al. 1986; Neilson et al. 1986; Alongi 1987). In addition, mangrove litter is typically low

in nutritional quality compared to other marine detrital sources (e.g., marine phytoplankton), having a high C:N ratio and relatively high lignin content (Giddins et al. 1986; Robertson 1988; Robertson et al. 1992). Therefore, it is conceivable that mangrove detritus may have a negative impact on infaunal and epifaunal communities in Hawaii (Alongi and Christoffersen 1992), or at the very least be underutilized by local detritivores. The introduction of tannin-rich, low-quality mangrove litter to detrital food webs in Hawaii has the potential to alter the food-web structure of coastal communities. Such alterations are especially likely because, until very recently, Hawaiian benthos occupying the high to mid-intertidal have not been exposed to detritus from marine vascular plants.

While introduced mangroves may fundamentally alter Hawaiian coastal ecosystems, their effects on detrital food webs in Hawaii have not been evaluated. Several studies have suggested the important role of native mangrove detritus may play in adjacent and coastal systems and food webs (Odum and Heald 1975; Twilley 1988; Watayakorn et al. 1990; Robertson et al. 1992). Odum and Heald (1975) used a model of a mangrove-detritus based food web to suggest that mangrove leaves, via microbial decomposition, were the dominant food source for detritivores, relative to phytoplankton and benthic microalgae. In contrast, recent studies using stable isotope analyses suggest that these systems may be more complex, with the role of benthic microalgae and phytoplankton previously underestimated (Stoner and Zimmerman 1988), and with mangroves not contributing significantly to coastal food webs (Stoner and Zimmerman 1988; Newell et al. 1995; Primavera 1996).

Most food-web stable isotope studies have focused on mangrove fish and epibenthos, including crabs, shrimp, and root encrusting organisms (e.g., barnacles, oysters etc.) (Stoner and Zimmerman 1988). However, stable isotopes have rarely been used to infer feeding patterns of smaller macroinvertebrates (Rodelli et al. 1984; Bouillon et al. 2002) and only on a few specific invertebrates (Slim et al. 1997; France 1998). Very few studies have examined mangrove sediment infauna (Bouillon et al. 2002). Infaunal benthos carry out important functions in both mangrove and non-mangrove coastal habitats, e.g., serving as food for higher trophic levels, detrital shredders, and stimulators of detrital decomposition (Levinton 1982; Parsons et al. 1985; Robertson and Alongi 1992). However, detailed knowledge of infaunal trophic position, resource partitioning and feeding ecology is lacking (Riera et al. 1996; Moens et al. 2002). Infauna are generally considered opportunistic consumers; they rely most heavily on what is produced from local sources (Peterson et al. 1985; Deegan and Garritt 1997). Therefore, it is conceivable that infauna would be the most likely candidate for mangrove detritus consumers and assimilators, since mangrove leaves and detrital material typically are the most abundant local food sources available in mangroves. If infauna are consuming and assimilating mangrove-derived material, then their $\delta^{13}C$ values should be similar to mangrove leaf material, with ~ 1‰ enrichment, given that the ratio of carbon isotopes ($\delta^{13}C$) changes very little as carbon is transferred through food webs (DeNiro and Epstein 1978; 1981; Rounick and Winterbourn 1986; Peterson and Fry 1987; France and Peters 1997; McCutchan et al. 2003). In contrast, $\delta^{15}N$ of infauna should be 3-4‰ enriched relative to mangrove leaves, and $\delta^{15}N$ can be used to estimate trophic position (DeNiro

and Epstein 1981; Minagawa and Wada 1984; Peterson and Fry 1987). In addition, infaunal stable isotopes may differ from root and mobile epibenthos, both in introduced and native mangrove forests, where epibenthos may preferentially utilize suspended material and/or benthic microalgae rather than mangrove detritus. Alternatively, infauna may rely on phytodetritus deposited on the sediment surface or sediment-dwelling benthic microalgae growing *in situ*, which would be consistent with the findings of previous salt marsh stable isotope studies of sediment infauna (Currin et al. 1995) and mangrove stable isotope studies of mobile or root epibenthos (Stoner and Zimmerman 1988; Newell et al. 1995; Primavera 1996).

Macroinvertebrates, e.g., polychaetes, oligochaetes, crabs and gastropods, are considered important in terms of carbon cycling within mangroves and carbon transfer to adjacent waters (Robertson et al. 1992), and as food sources for foraging fish and shrimp. Therefore, it is critical to evaluate the food-web structure of infaunal communities in mangroves as a first step in assessing the impacts of introduced mangroves on Hawaiian coastal ecology and food webs, including assessing the relative utilization of vascular plant detritus as a food source. This study is the first to use stable carbon and nitrogen isotope analyses to evaluate the trophic dynamics in introduced mangrove communities in Hawaii in comparison to native mangrove communities. This work is directly applicable to ongoing research evaluating the relative importance of introduced and native vascular plant detritus to coastal food webs (Carman and Fry 2002). My goal was to evaluate the role mangrove detritus plays in infaunal and epifaunal food webs. Data were collected in three mangrove communities and an isotope-mixing model was used to test the following hypotheses:

1. *Infauna have stable isotope values consistent with mangrove detritus whereas epifauna (both sediment- and root-associates) have stable isotope values consistent with either mixed diets or with phytoplankton and/or benthic microalgae assimilation.*
2. *Infaunal and epifaunal trophic structure in Hawaiian mangroves differs markedly from food-web structures in islands with indigenous mangroves (e.g., Puerto Rico).*

Materials and methods

Description of study sites- Samples were collected in mature *Rhizophora mangle* mangrove communities located on Oahu (21° 27' 42" N, 157° 50' 29" W) and Molokai (21° 05' 52" N, 157° 03' 10" W) Hawaii, and Puerto Rico (17° 57' 40" N, 66° 13' 05" W) (Figure 1). Kaneohe Bay was colonized by *R. mangle* ~ 1930 and has some of the largest mangrove stands on Oahu (Devaney 1982). Molokai has the oldest, most extensive mangrove stands in the Hawaiian archipelago (Allen 1998). The mangrove area at the National Estuarine Research Reserve at Jobos Bay, Puerto Rico (Fig. 1) is among the largest in Puerto Rico, and Jobos Bay is the largest forest (11 km^2) on the south coast of Puerto Rico (Cintron et al. 1978), containing native *Rhizophora mangle* forests, as well as three other mangrove species. The tidal range is ~ 0.3 m for all three sites.

Field sampling- Samples of vegetation, surface sediments, and fauna (both infauna and epifauna) were collected during the Summer of 2001. Sediment infauna were collected with at least 5 replicate core tubes (33 cm^2 x 2 cm) at each of the sites. Sediment cores were collected from 8 and 16 m inside Molokai mangroves, 8 m within Oahu mangroves, and at the same tidal elevation inside mangroves in Puerto Rico. In addition, sand-flat sediments were collected at 8 m from the mangrove fringe boundary, adjacent to the mangrove communities at each site.

Sample preparation- Mangrove leaves of various ages were collected. Fresh, green leaves of the same age were collected from the second leaf from the terminal bud, and yellow leaves, both attached and fallen, were also collected from mangrove trees and surface sediments. In addition, macroalgae and seagrasses were collected, sorted to remove epiphytes, and washed with 10% HCl to dissolve carbonate. Suspended particulate organic matter (POM) was collected by filtering 180 mL of seawater adjacent to the sampling stations onto pre-combusted GFF filters. Suspended POM was used as a proxy for phytoplankton stable-isotope content; however, in addition to phytoplankton, detrital material and zooplankton were also most likely collected on the filters. Paired sediment and filter samples were collected at each station such that one sample was acidified with 1 N HCl to remove inorganic carbon (e.g., HCO_3^-) and the other for $\delta^{15}N$ was not acidified, as the acid treatment has been reported to affect $\delta^{15}N$ values (Bunn et al. 1995). Surface sediments were collected and processed for benthic microalgae (BMA) using the LUDOX extraction technique (Levin and Currin 2002). Previous studies have used nitex mesh netting on the sediment surface to allow motile diatoms to migrate away

from the sediments through to the top layer of the mesh. In mangrove sediments, however, this technique proved less than optimal, due to sediment contamination via resuspension and deposition of fine-grained, flocculent sediment on the mesh surface. The LUDOX technique allowed for clean separation of the BMA material from sediments.

Infaunal samples were processed as in Carmen and Fry (2002). Infaunal cores were sectioned at 0-2 cm intervals and were either sorted live or preserved in 10% formalin prior to sieving. Laboratory gloves were used at all times during the infauna processing to minimize C and N contamination. In the laboratory, samples were washed through nested sieves (300 and 45 μm) to remove sediment and assist with identification. Infauna were rapidly sorted, pooled to species level when possible, and transferred to clean Petri dishes containing deionized water. Infauna were then cleaned, transferred to tin cups containing ~ 2 μl of deionized water, dried in the oven at 60°C, crimped, and analyzed for $\delta^{13}C$ and $\delta^{15}N$ as described below. Infauna collected and analyzed were the dominant taxa present in the mangrove sediments as determined from the species composition of the core samples. A minimum of 5 μg C and 10 μg N are required per sample for stable isotopic analysis (Peterson and Howarth 1987), therefore, for smaller species (e.g., polychaetes, oligochaetes, and other invertebrates), 5-100 animals were pooled per sample. For epifauna, here defined as sediment and root-associated animals > 0.5 cm, soft tissue from gastropods, barnacles, and crab chelae were dissected, rinsed with distilled water, and frozen until further analysis. Whenever possible, a minimum of three replicate samples was analyzed for each species.

All samples were dried at 60°C, and, with the exception of infauna and filter samples, ground to a fine powder and subsampled for $\delta^{13}C$ and $\delta^{15}N$. Whole filter samples were placed in tin cups and analyzed as follows.

Isotope analysis- Isotope analyses were conducted at the University of Hawaii isotope laboratory using a Thermoquest/CE Instruments Automated Elemental Analyzer (model 1110 Nc 2500) interfaced to a Finnegan MAT Delta-S stable isotope ratio mass spectrometer via a Finnigan MAT ConFlo II interface. Stable isotopic values were expressed as δ values:

$$\delta X\ (‰) = [(R_{SAMPLE}/R_{STANDARD})-1] \times 10^3$$

where X is ^{13}C or ^{15}N and R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Carbon results are given in ‰ units as $\delta^{13}C$ versus PeeDee Belemnite (PDB) and nitrogen results are given as $\delta^{15}N$ versus air N_2. Following isotope analysis, preserved infaunal samples were corrected for formalin preservation by adding 1‰ to $\delta^{13}C$ values of each preserved sample (Sarakinos et al. 2002).

To determine if mangrove leaves served as potential sources of carbon or nitrogen for particular infauna and epifauna, trophic shift boxes were constructed by the following methods. Trophic-level fractionation of 0-1 ‰ for $\delta^{13}C$ and of 3-4 ‰ for $\delta^{15}N$ were added to the range of isotope values for mangrove leaves (Post 2002; McCutchan et al. 2003) . Organisms that use mangrove leaves for nutrition were expected to fall into the trophic shift box.

IsoError 1.04 (Phillips and Gregg 2001) was used to estimate proportional contribution of mangrove-derived material to benthic food webs. This method accounts for the variability of the mixture (consumer) and the source stable isotope values. Mean and standard deviations of $\delta^{13}C$ values for consumers, mangrove leaves, POM, and BMA were used for these calculations.

Statistics

Multivariate analysis of variance (ANOVA, Type IV) was used to compare isotopic values for both elements among producer groups within Oahu, Molokai, and Puerto Rico mangrove sites, and within and between infaunal and epifaunal consumers for each mangrove community. Multivariate ANOVA was also used to compare isotopic values between wetlands (Molokai, Oahu, and Puerto Rico). All analyses included an interaction term, and significance level was $\alpha = 0.05$. Bonferroni post-hoc significance tests were used to test differences in mean values from the various multiple comparisons (e.g., taxa specific stable isotope comparisons) (Sokal and Rohlf 1969; 1995). Non-parametric Kruskal Wallis median and Kolmogorov-Smirnov tests were used for paired comparisons of non-normal data (Sokal and Rohlf 1969). All statistical analyses were performed using SPSS Statistical software.

Results

Primary Producers and Sediments

Mangrove leaves, POM, BMA, macroalgae, and sediment stable carbon and nitrogen isotope data are reported in Table 1. *Rhizophora mangle* green leaf $\delta^{13}C$ ranged from –28.2 to –30.2 ‰ and $\delta^{15}N$ from 2.2 to 9.3 ‰. Molokai mangrove leaves were significantly enriched in $\delta^{13}C$ and $\delta^{15}N$ relative to Oahu leaves (ANOVA, p=0.000,0.033, respectively). In general, leaf $\delta^{15}N$ was significantly greater in Hawaii than Puerto Rico (ANOVA, p<000). When comparing leaf age overall by combining data from the three sites (green versus yellow versus detritus), green leaves were significantly depleted in $\delta^{15}N$ compared to older leaves (ANOVA, p=0.003 for yellow leaves, 0.005 for detritus). Leaf percent organic carbon and nitrogen were similar among the three sites, ranging from 41-45 % (org. C) and percent nitrogen decreased from 1.5 for green leaves to 0.3 for detritus (Table 2).

POM $\delta^{13}C$ values did not vary significantly between sites, ranging from –22.0 to –21.1 ‰. However, POM from Hawaii was significantly enriched in ^{15}N compared to Puerto Rico, (p=0.005 and 0.003 for Molokai and Oahu, respectively). There was no significant difference in stable isotopic values of benthic microalgae (BMA) between Molokai and Puerto Rico. There was insufficient N in the BMA samples for $\delta^{15}N$ analysis.

Seagrass and macroalgae $\delta^{13}C$ ranged from –9.3 ‰ for *Thalassia testudinum* to –33.6‰ for an unidentified red-filamentous alga, and $\delta^{15}N$ values ranged from 0.9 ‰ for *Diplanthera wrigthii* to 9.9 ‰ for *Centroceras clavulatum*. In general, macroalgae were significantly depleted in ^{13}C on Molokai compared to Oahu ($p=0.000$) and Puerto Rico ($p=0.000$), and enriched in ^{15}N relative to Puerto Rico ($p<0.000$).

Mangrove sediment percent organic carbon content ranged from 17.5% for Puerto Rico to 0.57% for Oahu and total percent nitrogen from 0.76 % (Puerto Rico) to 0.08 % for Oahu (Table 2). Molokai mangrove sediments have intermediate levels of organic carbon (5.0 %) and total nitrogen (0.2 %). Sediment $\delta^{13}C$ ranged from –20.5 ‰ on Oahu to –26.5 ‰ for Puerto Rico, and $\delta^{15}N$ from 2.2 ‰ (Puerto Rico) to 9.7 ‰ (Molokai). Overall, sediments from Oahu were significantly more enriched in ^{13}C than Puerto Rico ($p=0.008$) and Molokai ($p<0.000$). In general, Hawaii mangrove sediments mirrored the patterns in $\delta^{15}N$ leaf data with higher $\delta^{15}N$ compared to Puerto Rico (p=001, Molokai, 008, Oahu). Mangrove sediments were depleted in ^{13}C relative to adjacent sandflat sediments on Molokai (-25.3 versus –15.6 ‰, Table 2). However, Oahu mangrove and sandflat sediment $\delta^{13}C$ and $\delta^{15}N$ were similar.

Stable isotope composition of invertebrates

Sediment Infauna- Stable isotope data for sediment infauna are summarized in Table 3. For all three sites, only nematodes and nereid polychaetes from Puerto Rican mangroves had stable isotopic values falling within the trophic shift box, indicating nereid and

nematode values were consistent with a 100 % mangrove leaf diet (Figure 2). Extremes in mangrove infaunal $\delta^{13}C$ values were found in nematodes from Puerto Rico, ranging from –38 ‰ to –25.0 ‰, as illustrated in the large spread in isotopic values in Figure 2. The range in $\delta^{13}C$ values corresponds to samples collected at different locations in the mangrove. Nematodes were significantly depleted in ^{13}C relative to oligochaetes ($p=0.015$) and capitellid polychaetes ($p=0.004$) and enriched in ^{15}N compared to oligochaetes ($p=0.000$), capitellid polychaetes ($p=0.000$), and nereids ($p=0.001$). The oligochaete community (multiple species) had $\delta^{13}C$ values similar to mangrove leaves (-27.9 ± 0.1 ‰), but were depleted in ^{15}N ($\delta^{15}N = 3.3 \pm 0.6$ ‰). Other infauna exhibited similar patterns; specifically, nereid polychaetes and Enchytraeidae sp. 1 (oligochaetes) $\delta^{13}C$ values were consistent with mangrove leaves, but their $\delta^{15}N$ values (3.8 ± 0.3 ‰ and 1.8 ± 0.5 ‰, respectively) were lower than mangrove leaves (yellow = 5.9, detritus=5.6 ‰). In contrast, capitellid polychaetes and Tubificidae sp. 1 and 2 (oligochaetes) had stable carbon isotopic values intermediate between POM/BMA and mangrove leaves. In addition, oligochaetes were significantly depleted in ^{15}N relative to capitellid and nereid polychaetes ($p=0.007$ and 0.009, respectively).

For Hawaii, all mangrove sediment infauna were enriched in ^{13}C relative to mangrove leaves. From Molokai, Tubificidae sp. 1 (oligochaetes) average $\delta^{13}C$ values were higher, but due to large variability, there was isotopic overlap with mangrove leaf $\delta^{13}C$. Nematodes and Tubificidae sp. 2 $\delta^{13}C$ values were between mangrove leaves and POM/BMA. The remaining infauna, including capitellid and paraonid polychaetes, enchytraeid oligochaetes, sipunculids, and tanaids, had $\delta^{13}C$ values similar to POM

and/or BMA values. Nematodes were significantly enriched in ^{15}N, similar to Puerto Rico, compared to oligochaetes ($p=0.000$, capitellids ($p=0.001$), sipunculids ($p=0.020$), and tanaids ($p=0.000$). Oligochaetes were significantly depleted in ^{15}N relative to syllids ($p=0.007$) and ^{13}C compared to paraonids ($p=0.031$) and sipunculids ($p=0.038$). Lastly, syllids were significantly enriched in ^{15}N compared to tanaids ($p=0.018$).

Extremes in sediment infaunal $\delta^{13}C$ values from Oahu mangroves ranged from -19.3 ± 0.9 ‰ for nematodes to -14.2 ± 0.6 ‰ for *Corophium insidiosum*. As with the other two mangrove sites, nematodes were significantly enriched in ^{15}N compared to the other infauna: oligochaetes ($p=0.004$), sabellids *Potamilla* sp. (0.003), and *Corophium insidiosum* ($p<0.001$). Oligochaetes were also enriched in ^{15}N relative to *Corophium insidiosum* ($p<0.001$). Lastly, *Corophium insidiosum* was significantly enriched in ^{13}C compared to all mangrove sediment infauna from Oahu: oligochaetes ($p<0.001$), nematodes ($p<0.001$), and sabellids *Potamilla* sp. ($p<0.001$).

Epifauna- Mangrove epifaunal stable isotope data are summarized in Table 4. No epifaunal taxa had stable isotopes consistent with a mangrove-leaf diet as predicted by the trophic shift box (Figure 3). For Puerto Rico, sesarmids, xanthids, *Uca* sp., and *Melampus* sp. had $\delta^{13}C$ values that were intermediate between mangrove leaves and POM/BMA. The blue crab *Callinectes sapidus* and remaining root-associated epifauna, e.g., *Mytilus* sp., unidentified green sponge, *Tedania ignis*, *Balanus eburneus*, B. reticulatus, *Littoraria* sp., and *Crassostrea rhizophorae*, all had $\delta^{13}C$ values consistent with POM/BMA or were enriched in ^{13}C relative to these primary producers. There was a

significant difference between the root-dwelling and sediment-dwelling epifauna $\delta^{15}N$ and $\delta^{13}C$ values (two-sample Kolmogorov-Smirnov Test, $p=0.003$, $p<0.001$).

Similar patterns were present for Hawaii epifauna, with stable carbon isotopic values either similar to POM/BMA or enriched in $\delta^{13}C$ relative to these possible food sources.

Hawaii versus Puerto Rico

Separation between the three mangrove communities was evident in the infaunal stable isotopic values and less clear with the epifaunal results (Figure 4). In general, after combining infauna stable isotope results for each site, infaunal $\delta^{13}C$ was highest on Oahu, followed by Molokai, and lastly Puerto Rico ($p = 0.004$). For $\delta^{15}N$, the same trend existed. Although Oahu and Molokai were not significantly different ($p>0.301$), both were enriched in ^{15}N relative to Puerto Rico ($p < 0.001$). When stable isotopes from sediment infauna from the three sites were compared (Figures 5 and 6), $\delta^{13}C$ and $\delta^{15}N$ values decreased from Oahu to Molokai to Puerto Rico, reflecting the general pattern from the sediment infaunal stable isotope results described above. Stable isotope patterns for epifauna are similar to those of the infauna; sediment-associated epifauna from both Hawaii sites were enriched in ^{15}N and ^{13}C relative to Puerto Rico ($p<0.001$). In contrast, there was no difference in stable isotopic values of mangrove root-associated epifauna in introduced and native mangroves (Figures 5 and 6).

Infauna collected in Puerto Rico from sandflats on the seaward side of the mangroves had significantly higher stable $\delta^{13}C$ values than those collected inside the

mangroves (Kruskal Wallis median test, $p < 0.001$, Figure 5). The same pattern persisted for Hawaii sandflat infauna (Kruskal Wallis median test, $p=0.001$).

Infauna versus Epifauna

Infauna were significantly depleted in ^{13}C compared to epifauna from Molokai and Puerto Rico ($p<0.001$ for both). Infauna were depleted in ^{15}N relative to epifauna from Puerto Rico ($p<0.001$). No significant difference was found for stable carbon or nitrogen isotopic values between epifauna and infauna from Oahu ($p>0.937$, 0.999, respectively).

2-source Mixing model (IsoError results)

Specific infauna and epifauna from Puerto Rico had $\delta^{13}C$ values between two major primary producers or food sources (Figure 7). These animals included the following infauna: nematodes, oligochaete community (mixture of species), enchytraeid and tubificid oligochaetes, nereids, capitellid community (mixed species) and *Capitella* spp., and the following epifauna: xanthids, sesarmids, *Uca* sp., and *Melampus* sp. (gastropod). The two-source mixing model "IsoError" was used to estimate relative contributions of mangrove leaves versus POM, and mangrove leaves versus BMA to these consumers' diets and the results, including the mean and associated ranges are summarized in Table 5. Nematodes were the only organism with both $\delta^{15}N$ and $\delta^{13}C$ consistent with a diet of mangrove leaves, with the proportional contribution from mangroves was 100 %. Because certain nematodes from Puerto Rico had lower $\delta^{13}C$

values relative to mangrove leaf $\delta^{13}C$ values, the proportional contribution of POM/BMA to their diet was 0% (0-20%, 95% C.I.). As $\delta^{13}C$ values increased from Oligochaete community (mixed species) to Capitellids and Tubificids, the estimated proportional contribution of mangrove leaves to the diet decreased from 98 % (90-100 %, 95% C.I) to 43 % (35-51 %, 95% C.I), using POM as the second endmember. For epifauna, mangrove contribution was greatest in sesarmid crabs at 62% (52-72%, 95% C.I.) and decreased to 41% (36-46%, 95% C.I.) for xanthid crabs. Average BMA $\delta^{13}C$ values were used in the mixing model because BMA were another likely food source for these organisms and the proportional contribution was consistent with the results for POM. However, BMA $\delta^{13}C$ values were more variable (± 3.0 ‰), and thus resulted in a wider range of estimated proportions.

For Molokai, the relative contribution of mangrove leaves to the diet of Tubificidae sp. 1 oligochaetes was 80% (0-100 %, 95% C.I.). The proportional contribution of mangroves decreased to 27% (0-94%, 95% C.I.) for nematodes collected from 8 m inside the mangrove forest.

Discussion

Primary Producers and Sediments

Stable isotopic values for mangrove leaves from all three sites were typical for terrestrial C_3-plants and were within the range reported for leaves of various mangrove

species (Stoner and Zimmerman 1988; Rao et al. 1994; Newell et al. 1995; Loneragan et al. 1997; Marguillier et al. 1997; Bouillon et al. 2002). Leaf $\delta^{15}N$ increased with age as % N decreased in the leaves, possibly a result of withdrawal of ^{14}N-nitrogen in senescing yellow leaves still attached to trees, leading to increased $\delta^{15}N$ values for yellow leaves, a pattern which has been observed in mangrove leaves from Florida (Fry and Smith 2002). Benthic microalgae $\delta^{13}C$ values differed from mangrove leaves, and were within ranges reported for BMA from other mangrove and salt-marsh studies (France 1998; Stoner and Zimmerman 1988; Currin et al. 1995; Newell et al. 1995; Dittel et al. 1997; Page 1997; Dehairs et al. 2000; Bouillon et al. 2002; Moens et al. 2002). Although BMA samples were insufficient for $\delta^{15}N$ analysis, data from other mangrove studies have produced BMA $\delta^{15}N$ values ranging from 0.5 to 6.0 (Bouillon et al. 2002). POM $\delta^{13}C$ and $\delta^{15}N$ values from each site are within reported ranges for phytoplankton stable carbon and nitrogen isotopic values from mangroves (Mohan et al. 1997; Bouillon et al. 2002). Macroalgae $\delta^{13}C$ and $\delta^{15}N$ are similar to reported values, including the unidentified red alga found attached to mangrove roots on Molokai (-33.6 ‰ $\delta^{13}C$) (Fry et al. 1982; Zieman et al. 1984; Stoner and Zimmerman 1988; Lin et al. 1991; Bouillon et al. 2002).

Sediment stable isotopic values increased from Puerto Rico to Molokai to Oahu, which may result from differences in the source of organic matter in the sediments. For Puerto Rico and Molokai, sediment $\delta^{13}C$ values were close to mangrove leaves, indicating that $\delta^{13}C$ was mainly controlled by C_3 vascular plants rather than phytoplankton (Hseih et al. 2002). However, for Oahu, there was a large discrepancy between mangrove leaf $\delta^{13}C$ values (average -29.4 ‰, Figure 2) and underlying

sediments (-20.5 ± 0.4 ‰, Figure 2, Tables 1 and 2). Oahu sediment $\delta^{13}C$ was similar to POM (-21.1 ‰), and 2.4 ‰ higher in $\delta^{15}N$, indicating that phytoplankton (as approximated by suspended particulate organic matter measurements) may be a major component of sediment organic matter in the Oahu mangroves (Table 2). Sediment ^{13}C enrichment relative to mangrove leaves has been reported in other studies (Rodelli et al. 1984) and may reflect substantial deposition of suspended matter, including phytoplankton, from adjacent waters (Bouillon et al. 2002). The trends in sediment stable isotopes have further implications to be discussed below.

Stable Isotope Composition of Invertebrates

Infauna- Nematodes and nereid polychaetes from Puerto Rico were the only infauna having stable isotopes consistent with a diet derived from mangrove leaves. Nematodes are typically the most abundant taxon within estuarine wetland communities (Rao 2002). However, very little is known about their feeding ecology and trophic position (Montagna 1995). Nematode feeding types include grazers of microalgae/bacteria (Montagna 1995; Riera et al. 1996) and non-selective deposit feeders (Carman and Fry 2002), but there are also omnivorous and predaceous forms, sometimes found in aggregates on organic detritus (Moens et al. 2002). In their study of salt marsh food webs, Carman and Fry (2002) found a species specific variation in consumption of vascular plant detritus (*Spartina*) by nematodes and copepods, with a seasonal shift toward *S. alterniflora* detritus during the winter months. Therefore, some nematodes do consume and assimilate vascular plant detritus. Nematodes had the highest $\delta^{15}N$ for all sites, suggesting that either they are feeding at the top of the food chain or rely on a

primary substrate enriched in ^{15}N. Studies of salt marsh nematodes suggest high feeding selectivity, via grazing on bacteria and BMA, but enriched ^{15}N values indicate that trophic pathways to nematodes are less straightforward (Moens et al. 2002). Other possible food sources for nematodes include microbes that colonize mangrove leaves as they decay, (e.g., bacteria and ciliates) (Zhou 2001; Dorothy et al. 2003). The proportional contribution of mangroves to nematode diet was 100%. However, some nematode $\delta^{13}C$ values were less than those of mangrove leaves, so they may be feeding on other, ^{13}C depleted, organic sources. The large range in nematode $\delta^{13}C$ values may result from the consumption of sulfur oxidizing bacteria or ciliates with characteristically depleted ^{13}C values. Carbon fixation fueled by energy derived from sulfide oxidation supports food webs at deep sea hydrothermal vents where $\delta^{13}C$ values between -27 ‰ and -37 ‰ are routinely observed (Fisher 1990). Colonial ciliates with sulfide-oxidizing ectosymbiotic bacteria (mangrove peat associates) (Ott 1996) are one possible food source, which could help explain both the depleted $\delta^{13}C$ and enriched $\delta^{15}N$ values (Moens et al. 2002). It is interesting to note that none of the other higher order consumers (e.g., crabs) had $\delta^{15}N$ values consistent with a diet of nematodes, despite their purported importance as a food item for estuarine organisms (Coull et al. 1995). Although the sampling was extensive, this study may have missed specialized nematode consumers. To my knowledge, this is the first study to report nematode stable isotopic values for mangrove communities, and confirmation of these results in other mangrove settings are needed.

In contrast with the high $\delta^{15}N$ values from nematodes, infauna with low $\delta^{15}N$ (2-4‰), e.g., nereid polychaetes and oligochaetes, may be low trophic level primary consumers ($\delta^{15}N$ <1‰, Peterson and Howarth 1987; Hsieh et al. 2002). For example, oligochaetes may be utilizing mangrove leaves for their carbon substrate, as estimated by the trophic mixing model, but their low $\delta^{15}N$ may result from relying on N_2-fixing bacteria for their nitrogen requirements. These bacteria are abundant in mangrove sediments (Hicks and Silvester 1985; Mann and Steinke 1989; Boto and Robertson 1990). Tubificid oligochaetes have been classified as subsurface deposit feeders, while enchytraeidae oligochaetes have been known to feed on vascular plant detritus (Levin, pers. comm. 2003). However, oligochaetes can be generally classified as omnivorous feeders, consuming and assimilating whatever primary detrital sources are available. Nereid polychaetes, although they represent a variety of feeding types: omnivores, herbivores, and carnivores (Fauchald and Jumars 1979; Hseih et al. 2002), had isotopic values similar to mangrove-leaf $\delta^{13}C$ and $\delta^{15}N$, suggesting that they may be herbivorous leaf consumers. Capitellid and tubificid oligochaetes had intermediate isotopic values between mangrove leaves and POM/BMA, again consistent with sediment $\delta^{13}C$, indicating that their food may also be detritus from multiple sources. Capitellids are generally regarded as relatively non-selective deposit feeders (Fauchald and Jumars 1979), so as they feed on the sediment surface, they potentially consume a variety of primary sources, including mangrove leaf material and benthic microalgae, as well as detritus from other sources and sediment organic matter. Capitellids from the mangrove lagoon at Laguna Joyuda, Puerto Rico had higher $\delta^{13}C$ values compared to the current

study, ranging from –23.9 to –18.9 ‰ (Stoner and Zimmerman 1988). Given the spatial heterogeneity in consumers' $\delta^{13}C$ in this study and others, (Rodelli et al. 1984; Peterson and Howarth 1987; Deegan and Garritt 1997; Wainright et al. 2000), there may be various foods available to infaunal consumers in different mangrove microhabitats (Hseih et al. 2002).

Epifauna- No epifaunal consumers had stable isotopic values consistent with a pure mangrove-leaf diet as predicted by the trophic shift box. This was not surprising given results from previous stable isotope studies on mangrove macroinvertebrates (see above). *Uca* sp. are generally regarded as bacterial and/or microalgal feeders (Rodelli et al. 1984) and sesarmids are classified as omnivores/herbivores (Dahdouh-Guebas et al. 1999). Both of these crabs had $\delta^{13}C$ values similar to previously reported values from another mangrove lagoon in Puerto Rico (average -24.9 and -25.3, respectively) (Stoner and Zimmerman 1988; France 1998). Therefore, the only epifaunal organisms with carbon isotopic values similar to mangroves are those closely associated with the trees and sediments in Puerto Rico, e.g., xanthids, sesarmids, *Uca* sp., similar to results from Laguna Joyuda mangroves (Stoner and Zimmerman 1988).

Gastropods, including *Melampus* sp. and littorinids are generally classified as deposit feeders (Plaziat 1984). *Melampus* sp. stable isotopic values were between mangrove leaves and POM/BMA, indicating they may feed on a mixture of these sources, although their $\delta^{15}N$ values were depleted relative to these primary producers. Salt marsh *Melampus* congeners are described as detrital feeders, having isotopic values consistent with a diet from a mixture detrital sources (Page 1997). Lastly, *Melampus* sp.,

tubificids and capitellids are probably feeding on similar resources, given their isotopic similarity. Herbivorous gastropods (*Terebralia palustris*) from other mangrove communities have $\delta^{13}C$ values that reflected mangrove leaves (Marguillier et al. 1997). Littorinid gastropods use their radula to scrape organic material either from the sediment or mangrove root surface and specific food sources for these taxa can include microepiphytes (Reid 1986; Blanco and Cantera 1999), and cyanobacteria (Kohl and Shearer 1980). *Metapograpsus messor* typically display $\delta^{13}C$ values similar to the littorinids, because littorinids are a major part of the crab diet (Reid 1986). However for Hawaii, data from these crabs are 3‰ enriched in $\delta^{13}C$ relative to *Littoraria scabra*, the dominant littorinid on mangrove roots, suggesting that they are feeding on different food sources, possibly small infauna or are selecting for some specific component of the POM/BMA pool that is isotopically distinct from the littorinids. Food sources for the xanthid crabs from Oahu could include shrimp, among other mobile benthos.

Epifauna from Puerto Rico mangroves were divided into two distinct groups based on both their stable isotopic values and microhabitat/mobility: mobile sediment dwellers and mangrove root encrusting organisms. The diet of sediment-associated epifauna may be a mixture of mangrove detritus and POM/BMA, as suggested by their stable isotopic values and results from the mixing model calculations. Sesarmid, *Uca*, and xanthid crab species also had stable isotopic values consistent with certain sediment infauna (capitellids at -25/-26 ‰ and tubificids at -23.8‰), with about 2-4‰ trophic enrichment in ^{15}N, indicating that infauna may also be part of their diet. This may also explain why these epifauna may have intermediate $\delta^{13}C$ values: they are consuming

infauna with intermediate stable carbon isotopic values. However, *Uca vocans* and *Uca polita* from other native mangrove forests were found to be bacterial/protozoan feeders (Dye and Lasiak 1986) based on gut analysis and exclusion experiments.

Root-associated invertebrates, from both Hawaii and Puerto Rico, including particle-feeding sponges, barnacles and mussels, were isotopically similar to POM, with the requisite 3-5‰ enrichment in $\delta^{15}N$. Thus, mangrove carbon appeared to be assimilated by some, either directly or via secondary consumption, while still other primary sources formed a major part of the diet for others. In contrast, stable isotopic values for epifauna from Hawaii (Table 4, Figure 3) seem to show a progressive stepwise enrichment from POM/BMA to higher trophic levels. Thus, epifauna from Hawaiian mangroves may be deriving their nutrition from non-mangrove sources, possibly from deposited or suspended phytoplankton and/or from *in situ* production of sediment BMA. The overall spread of $\delta^{13}C$ data from -24.9 ‰ to -12.9 ‰ and minimal overlap in epifaunal stable isotopic values indicates that these organisms are feeding on multiple food sources with differing stable isotopic values. As a result, there may be little niche overlap of food resources, because the root-encrusted and sediment associated fauna re situated in different substrates, potentially exposed to different sources in both native and introduced mangrove communities. Generally, mangrove studies have suggested a limited role for mangrove-derived material in coastal food webs, where the sphere of influence of mangroves is restricted to within a mangrove forest or near mangrove waterways (Fry 1984; Zieman et al. 1984; Dittel et al. 1997; Marguillier et al. 1997; Lee 2000; Chong et al. 2001; Thimdee et al. 2001; Bouillon et al. 2002).

Despite significant differences in $\delta^{13}C$ values between native and introduced mangrove fauna, there was one general pattern among the three communities, i.e., that the root-dwelling epifauna from Puerto Rico and the epifaunal community (root and sediment associates) from Hawaii all appear to have POM/BMA based diets. Other studies have indicated that the production of benthic algae in native mangrove communities may be comparable to mangrove production, possibly accounting for the observed reliance on BMAand lack of mangrove utilization in local food webs (Stoner and Zimmerman 1988; Rodriquez and Stoner 1990).

There is still one outstanding question regarding mangrove food webs (Fry and Ewel 2003): if an organism is fed a diet exclusively of mangrove leaves, what will their stable isotopic values be? The general assumption for fractionation at each trophic step is 0-1 ‰ for $\delta^{13}C$ and 3-4 ‰ for $\delta^{15}N$ but there is some uncertainty in the isotopic shift between trophic levels (Fry and Sherr 1984; Peterson et al. 1985; Peterson and Howarth 1987). The only experiment published tested this hypothesis by feeding amphipods mangrove detritus and analyzing their $\delta^{13}C$ value. Most did not thrive, and others were enriched approximately 3 ‰ relative to mangroves (Zimmerman, unpubl. data; Zieman et al. 1984). Terrestrial feeding experiments on oligochaetes reported an substantial increase in 3-4 ‰ for $\delta^{13}C$ of oligochaetes relative to their vascular plant food source (tree leaves) (Spain et al. 1990; Schmidt et al. 1997). If trophic fractionation of $\delta^{13}C$ is 3 ‰, rather than close to 1 ‰, then most published mangrove food-web studies have underestimated the proportional contribution of mangroves to marine food webs. In addition, there are examples of consumers that ingest detrital material yet exhibit different $\delta^{13}C$ values than

detritus, suggesting a preferential assimilation of a specific component of the detritus, e.g., microbes, via microbial stripping, within the total organic matter pool (Zieman et al. 1984). Mixing model approximations suggest that further feeding experiments are needed to clarify the role of mangrove detritus in the diets of infaunal benthos.

Infauna versus epifauna

Results from Puerto Rico and Molokai appear to support the first hypothesis, *infauna have stable isotopic values consistent with mangrove detritus whereas epifauna (both sediment- and root-associates) have either mixed diets or those consistent with phytoplankton and/or benthic microalgae assimilation*, with stable carbon isotopes apparently separating infauna and epifauna; so it would seem likely that these two communities are feeding on different food sources. However, for Molokai, $\delta^{15}N$ does not separate communities, suggesting that they are feeding at similar trophic levels, or that some infauna are feeding on ^{15}N enriched primary sources while others feed at higher trophic levels resulting in indistinguishable $\delta^{15}N$ values. Results from Oahu mangroves do not support our hypothesis, suggesting that there is overlap in food resource utilization by Oahu mangrove infauna and epifauna.

Hawaii versus Puerto Rico

All else being equal, if all the mangrove food webs were the same, then one would expect no isotopic differences in infauna from one mangrove community to the next, whether introduced or native. However, when comparing these mangrove communities, infaunal and epifaunal trophic structure in introduced mangroves differs

from native mangroves, as hypothesized. In the native mangrove forest, both sediment infauna and sediment-associated epifauna derived some of their nutrition from mangroves based on the stable isotopic values and mixing model results (Table 5). In contrast, only a few infaunal species exhibited some dependence on mangrove leaves from Molokai, and for Oahu, there were no species that had stable isotopic values consistent with a pure mangrove diet. What are the possible reasons behind this differential pattern among mangrove communities?

The distinct separation between Hawaii and Puerto Rico infaunal stable isotopic values may be a result of regional differences in environmental parameters, and/or specific functional differences between introduced and native mangrove forest food-web structure resulting from mangrove forest age. Environmental differences, e.g., mangrove forest size, tidal flushing and sediment organic matter can affect community assemblages and food webs (Hseih et al. 2002; Fry and Ewel 2003). Differences in stable isotopic values can stem from the concentration and type of organic matter remaining *in situ* versus outwelling to surrounding communities. The proportion of outwelling of mangrove detritus and, more specifically, carbon depends primarily on the geomorphology and tidal characteristics of the ecosystem (Lee 1999). In addition, proximity to open bays and phytoplankton primary production can result in isotopic differences among communities (Chong et al. 2001). More specifically, shading and high turbidity can reduce phytoplankton primary production, which may result in increased reliance on mangrove detritus as a food source (Wainright et al. 2000). Sediment organic carbon and nitrogen content (and C/N ratios) were highest in Puerto Rico, decreasing to Molokai, and then to Oahu (Table 2). The inverse pattern is evident for stable isotopes of

sediments and, consequently, of infauna, where $\delta^{13}C$ and $\delta^{15}N$ decrease from Oahu to Puerto Rico (Figures 8, 9). These results indicate that sediment organic matter for Puerto Rico is primarily of a mangrove origin, while sediments from Oahu are more likely composed of *in situ* BMA production and/or imported phytoplankton from the adjacent embayment (Kaneohe Bay). Molokai mangrove sediments appear to be some combination thereof. Given that there are both concentration and isotopic differences in sediment organic matter between the three communities, it is useful to examine the mangrove introduction history in Hawaii and how forest age may have an effect on sediment organic matter accumulation and thus have an impact on the base of mangrove food webs.

Mangroves have the ability to colonize many different substrates, and following colonization, create soil several meters thick via allogenic peat accumulation and allochtonous sedimentation (Brady and Lee Wilson 1971). Mangrove peat accumulates as a result of decreased decomposition under anaerobic conditions (Middleton and McKee 2001). Over the past century, mangroves have colonized many areas of coastal Hawaii, resulting in the rapid accretion of soils and seaward progradation of the shoreline (~0.1 to 6 cm/yr) across the reef flat (Thom 1967; D'Iorio et al. 2003). As the forest ages from the youngest (Oahu) to oldest (Molokai), there is possibly a corresponding increase in sediment and peat accumulation (Callaway et al. 1997). Overtime, the corresponding sediment $\delta^{13}C$ and $\delta^{15}N$ values should decrease as the mangrove peat accumulates.

In addition, the concentration and rate of organic matter accumulation and export from introduced mangroves is unknown. Mangroves in Hawaii produce large quantities of litterfall (Cox and Jokiel 1996), therefore the potential for substantial exports may be

high, depending on restrictions in connections to open water. Mangrove leaf litter production was high, but long-term sediment accumulation of leaf litter at the Oahu mangrove site was much less pronounced than for Puerto Rico (Demopoulos 2004). Therefore, there are differences in sediment organic matter accumulation between these introduced and native mangrove forests, which may be age dependent. Research conducted on restored and introduced vascular plants in salt marsh communities also report an increase in organic matter accumulation with marsh age (0-10 yrs) and resulting shifts in benthic community structure and food webs (Levin and Talley 2000; Talley and Levin 2001). Interestingly, Molokai mangrove sediment isotopic values closely reflect those of mangrove leaves, but despite ~ 100 years of mangrove forest development, few Hawaiian detritovores appear to be relying solely on mangrove detritus, suggesting that organisms have not adapted to feeding on this new vascular plant detrital source. Thus, there are distinct trophic differences between introduced and native mangrove forest food webs.

Data presented here demonstrate the food-web complexity present in both introduced and native mangroves. This study provides the first evidence of mangrove detrital utilization by nereid polychaetes and nematode benthos. However, valid generalizations regarding mangrove detrital utilization continue to be elusive. Isotopic tracer addition studies have been very useful in clarifying linkages between detrital inputs and transfer to higher trophic levels (Hall 1995; Blair et al. 1996), but similar work has yet to be attempted using mangrove detritus.

Significant differences in stable isotopic values of sandflat and mangrove sediment infauna suggest a landscape-driven shift in stable carbon isotopic values to

more depleted, possibly mangrove-influenced values with increased penetration into the mangrove interior (Figure 5). These landscape gradients in stable isotopes have been reported for other native mangrove forests (Dehairs et al. 2000; Fry and Smith 2002), suggesting that introduced mangrove trees may be functioning similarly to other native forests as an organic matter source. For Hawaii and Puerto Rico, it appears where sampling was conducted in landscape-similar fringing systems, there is a large-scale isotopic shift, from native mangroves (depleted ^{13}C) to introduced mangroves (enriched ^{13}C), potentially resulting from different successional stages represented in each mangrove community and/or from mangrove introduction history in Hawaii. This case study of mangrove food-web ecology may provide insight into the variations of food webs from early to late succession forest development. In other words, mangrove forest age may be an important factor in understanding the development of mangrove detritus-based food webs. More importantly, the significant differences between introduced and native mangrove forest food webs suggest that fauna residing in introduced mangroves (Hawaii) are possibly mal-adapted to feeding on mangrove-derived material. Whereas vascular plant detritus supports detritivores in native mangrove forests, mangrove detritus remains underutilized (i.e. unassimilated) in Hawaiian detrital food webs. Plant introductions may dramatically change a variety of ecosystem parameters and continue to be a rapidly growing issue worldwide. However, my results indicate that coastal food webs in Hawaii appear to remain differentially affected by mangrove introduction. Further research on the functional attributes of mangrove communities (e.g., above and below-ground plant biomass, benthic community composition) is needed in order to more completely assess the impact of mangrove introduction to coastal communities.

Table 1. Stable isotopic values for primary producers collected in mangroves on Oahu, Molokai, and Puerto Rico. Data are mean δ values (± 95% confidence intervals).

	Oahu		Molokai		Puerto Rico	
	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
MANGROVE LEAVES						
Rhizophora mangle						
Green	-30.0 ± 0.6	6.0 ± 0.4	-28.2 ± 0.8	7.1 ± 0.6	-30.2 ± 0.6	2.2 ± 1.3
Yellow	-29.7 ± 0.2	7.3 ± 0.5	-27.5 ± 0.9	9.3 ± 1.2	-29.0 ± 0.2	5.9 ± 1.0
Detritus	-28.5 ± 0.7	7.7 ± 0.6	-28.3 ± 0.9	8.9 ± 0.6	-28 ± 0.4	5.6 ± 0.5
Avicennia germinans						
Green					-26.4±0.3	6.4 ± 0.4
yellow					-27.20	2.40
Laguncularia racemosa						
Green					-28.4 ± 0.5	4.6 ± 0.2
Yellow					-27.47	4.21
POM	-21.1 ± 0.6	4.1 ± 0.6	-22 ± 1.1	4.2 ± 0.01	-21.6 ± 0.2	1.1 ± 0.3
BMA			-20.7 ± 2.9		-21.6 ± 3.0	
SEAGRASS						
Thalassia testudinum					-9.3	2.6
Thalassia testudinum detritus					-10	2
MACROALGAE						
Diplanthera wrigthii					-9.5	0.9
Acanthophora specifica					-18.9	3.2
Caulerpa sertularioides					-17.6 ± 1.4	3.7 ± 2.0
Udotea flabellum					-14.9 ± 0.7	1.3 ± 0.1
Centroceras clavulatum					-19.20	9.90
Gracilleria tikvahiae					-19.00	4.70
Brown algae					-17.5	3.4
Unid. algae					-12.8	2.7
Root epiphytes					-23	2.5
Sargassum polyphyllum	-13.9 ± 0.7	5.9 ± 1.6				
Red algae	-18.3 ± 0.6	8.8 ± 1.6				
Green Algae	-15.6 ±1.6	6.8 ± 0.5				
Spyridia filamentosa	-16.0 ± 1.0	8.1 ± 0.7	-21.7 ± 1.6	8.1 ± 0.6		
Ulva rigida			-19.2 ± 0.6	9.1 ± 0.5		
Enteromorpha flexuosa			-20.9 ± 0.3	8.8 ± 1.2		
Red-filamentus algae			-33.6 ± 0.8	7.2 ± 0.3		

Table 2. Mean (± 1 S.E.) percent organic carbon, percent total nitrogen, and c/n ratios for mangrove leaves, benthic microalgae, and sediments collected in mangroves and sandflats, including sediment $\delta^{13}C$ and $\delta^{15}N$ values (± 1 S.E.).

	Oahu			Molokai			Puerto Rico		
	% C	% N	C/N	% C	% N	C/N	% C	% N	C/N
Mangrove Leaves									
Green	44.0±0.2	1.07±0.02	41	40.8±1.3	1.07±0.06	43	44.4±0.7	1.54±0.04	29
Yellow	42.7±0.5	0.38±0.01	112	40.7±0.7	0.38±0.01	141	44.5±0.9	0.40±0.01	112
Detritus	42.9±0.5	0.40±0.01	108	40.5±0.8	0.40±0.01	146	46.8±0.4	0.41±0.02	114
BMA						9.4			8.6

Sediments	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
Mangroves	-20.5 ± 0.4	6.5 ± 0.2	-25.3 ± 1.6	9.7 ± 3.9	-26.5 ± 0.4	2.2 ± 0.4
Sandflats	-19.8±0.3	7.4±0.1	-15.6±0.1	7.0±.1		

Sediments	% C	% N	C/N	% C	% N	C/N	% C	% N	C/N
Mangroves	0.57±0.09	0.075±0.001	7.6	4.95±1.42	0.281±.056	17.5	17.91±0.51	0.76±0.05	23.5
Sandflats	0.27±0.01	0.057±0.003	4.9	0.17±0.02	0.043±0.001	4			

Table 3. Stable isotopic values for infauna collected in the mangroves and sandflats on Oahu, Molokai, and Puerto Rico. Data are mean δ values (± 95% confidence intervals). Sediments from Molokai mangroves were collected at interior distances of a= 16 m, b=8 m.

	Oahu (n= 1-3)		Molokai (n=1-4)		Puerto Rico (n=4)	
	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
INFAUNA - Mangrove						
Nematoda	-19.3 ± 0.9	12.7 ± 0.4	-22.9 ± 1.4a	11.0 ± 0.5	-29.5 ± 2.5	6.0 ± 0.5
			-23.3 ± 0.2b	11.1 ± 0.6		
Oligochaetes						
Community					-27.9 ± 0.1	3.3 ± 0.6
Enchytraeidae sp. 1	-19.0 ± 0.6	9.4 ± 1.0	-21.7 ± 0.8a	6.2 ± 1.3	-26.5 ± 0.5	1.8 ± 0.5
			-20.4 ± 0.5b	6.4 ± 0.6		
Tubificidae sp. 1	-18.2 ± 0.6	9.1 ± 1.3	-25.8 ± 3.0a	7.1 ± 1.9	-23.8 ± 0.4	2.6 ± 0.3
Tubificidae sp. 2			-23.8b	8.9		
Capitellidae						
Community					-26.1 ± 0.3	4.8 ± 0.2
C. capitata	-17.7	8.4	-18.6a	6.7	-25.0 ± 0.7	2.5 ± 0.3
			-20.7 ± 1.4b	7.8 ± 0.9		
Syllidae			-19.8 ± 0.2a	9.5 ± 0.3		
Sabellidae- c.f. *Potamilla* sp.	-18.3 ± 0.2	7.5 ± 0.1				
Spionidae-*Pseudopolydora* sp.			-18.1b	9.2		
Paraonidae- *Paraonella* sp.			-18.4 ± 0.7b	8.7 ± 0.6		
Nereidae					-27.0 ± 0.5	3.8 ± 0.3
Sipunculid- cf. *Onchnesoma* sp.			-18.5 ± 0.5b	8.3 ± 0.3		
Amphipoda- *Corophium insidiosum*	-14.2 ± 0.6	4.8 ± 0.8				
Tanaids			-18.9 ± 0.1b	6.3 ± 0.02		
INFAUNA - Sandflat						
Oligochaete Community	-15.97	9.34			-14.2 ± 0.9	2.1 ± 0.4
Capitella spp.	-15.5	10.9			-13.9 ± 0.1	3.5 ± 1.6
Nematoda					-15.2 ± 0.2	4.2 ± 0.3
Syllidae					-16.1 ± 1.9	3.2 ± 0.6
Sabellidae					-16.4 ± 0.04	1.7 ± 0.1
Spionidae-*Rhynchospio* sp.			-14.3 ± 0.4	10.3 ± 0.7		
Ophelidae-*Armandia intermedia*			-13.6 ± 0.9	9.2 ± 0.4		

Table 4. Stable isotopic values for epifauna collected in mangroves on Oahu, Molokai, and Puerto Rico. Data are mean δ values (± 95% confidence intervals).

	Oahu (n=1-6)		Molokai (n=5)		Puerto Rico (n=1-5)	
	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
Epifauna						
Molluscs						
Siphonaria normalis			-19.7 ± 0.7	8.5 ± 0.1		
Mytilus sp.					-20.0 ± 0.3	4.9 ± 0.4
Crassostrea rhizophorae					-17.8 ± 0.5	5.5 ± 0.8
Melampus sp.					-24.7 ± 1.0	2.1 ± 0.3
Littoraria sp.					-16.40	4.10
Littoraria scabra	-19.8 ± 0.4	4.5 ± 1.2	-21.0 ± 0.7	6.1 ± 1.2		
Crustaceans						
Cthamalus proteus	-17.6 ± 0.7	9.9 ± 0.2				
Balanus reticulatus			-15.2 ± 0.2	8.8 ± 0.2	-18.0 ± 0.3	5.5 ± 0.2
Balanus amphitrite	-17.2 ± 0.1	10.2 ± 0.2				
Balanus eburneus					-17.8 ± 0.7	5.9 ± 0.6
Balanus sp.					-17.2 ± 1.9	5.6 ± 0.2
Uca sp.					-24.9 ± 0.7	6.1 ± 1.2
Sesarmid sp. 1					-25.3 ± 0.5	6.3 ± 0.7
Metapograpsus messor			-17.9 ± 1.9	7.2 ± 0.9		
Metapograpsus thukuhar	-16.6 ± 1.0	9.6 ± 0.5				
Xanthidae sp.1					-23.7 ± 0.2	7.9 ± 0.4
Panopeus lacustris	-15.4	12.1				
Thalamita crenata	-13.2 ± 1.2	11.3 ± 0.6	-14.4 ± 1.1	9.7 ± 0.7		
Callinectes sapidus					-21.2 ± 0.3	7.9 ± 0.6
Scylla serrata	-12.5 ± 4.3	11.3 ± 0.2	-14.2 ± 2.9	8.7 ± 1.4		
Gonodactylus falcatus			-12.9 ± 0.3	12.0 ± 0.4		
Penaeid shrimp	-16.1 ± 0.3	8.4±0.4	-16.1 ± 0.9	9.3 ± 0.4		
Porifera						
Suberites zeteki	-20.4 ± 0.5	8.6 ± 0.2	-14.8 ± 0.3	8.8 ± 0.3		
Tedania ignis					-19.4 ± 0.1	5.3 ± 0.8
Sigmadocia caerulea			-14.8 ± 0.1	8.6 ± 0.3		
Gelloides fibrosa -	-19.0 ± 0.3	7.5 ± 0.2	-15.5 ± 0.1	7.3 ± 0.5		
Uni. Green sponge					-19.9 ± 0.1	4.4 ± 0.2
Other						
Tunicates					-19.6 ± 0.3	3.7 ± 0.1
Zoanthus pacificus			-19.8 ± 0.6	8.1 ± 0.3		

Table 5. Summary of the single element (carbon) mixing model results for infauna and epifauna from Puerto Rico and Molokai using mangroves, POM and BMA as endmembers. For Puerto Rico, endmember $\delta^{13}C$ values were as follows: $\delta^{13}C$ for mangrove leaves = -28.1, for POM = -20.6, and for BMA = -20.6. For Molokai, endmember $\delta^{13}C$ values for mangrove leaves = -27, for POM = -21.0, and for BMA = -19.7. These values were adjusted for trophic fractionation of 1‰.

	Mean tissue	Mangrove:POM		Mangrove:BMA	
	$\delta^{13}C$	% Mangrove	95% C.L(%)	% Mangrove	95% C.L(%)
PUERTO RICO					
Infauna					
Nematode Community	-29.5	100	80-100	100	80-100
Oligochaete Community	-27.9	98	90-100	98	90-100
Nereids	-27.0	86	76-95	86	74-97
Oligochaete- Enchytraeidae spp.	-26.5	79	69-89	79	65-94
Capitellid community	-26.1	74	66-81	74	56-91
Capitella spp.	-25.0	59	47-70	59	21-96
Oligochaete- Tubificidae spp.	-23.8	43	35-51	43	0-94
Epifauna					
Sesarmid sp.	-25.3	62	52-72	62	35-90
Uca sp.	-24.9	57	44-71	57	25-89
Melampus sp.	-24.7	54	34-75	54	22-87
Callinectes sapidus	-24.2	48	41-55	48	2-95
Xanthidae sp.	-23.7	41	36-46	41	0-93
MOLOKAI					
Infauna					
Oligochaete- Tubificidae sp1.	-25.8	80	0-100	84	17-100
Nematode Community-16 m	-23.3	39	26-52	49	4-95
Nematode Community- 8 m	-22.6	27	0-94	40	0-91

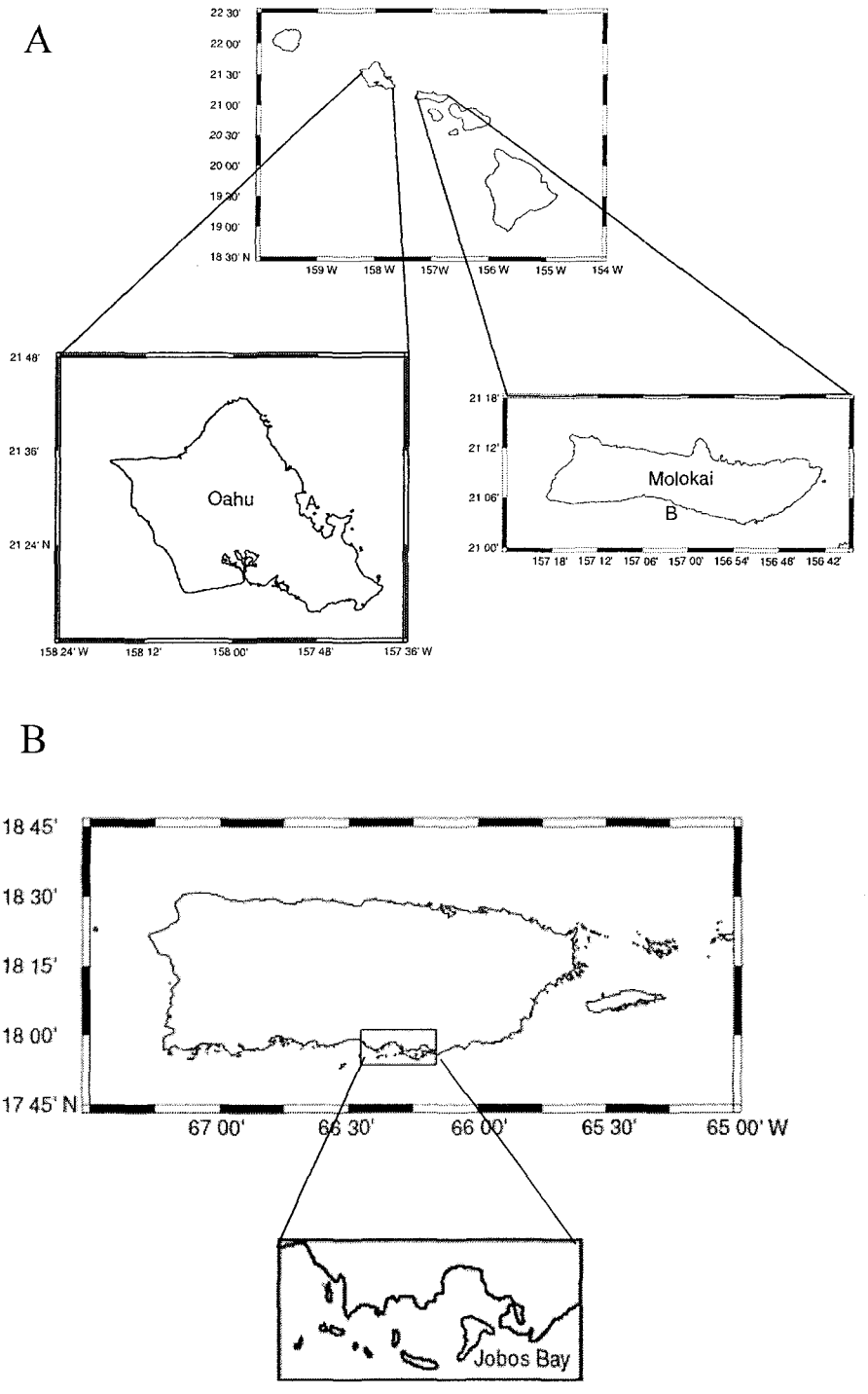

Figure 1. Locations of sampling stations on Oahu and Molokai, Hawaii (A) and Jobos Bay, Puerto Rico, (B).

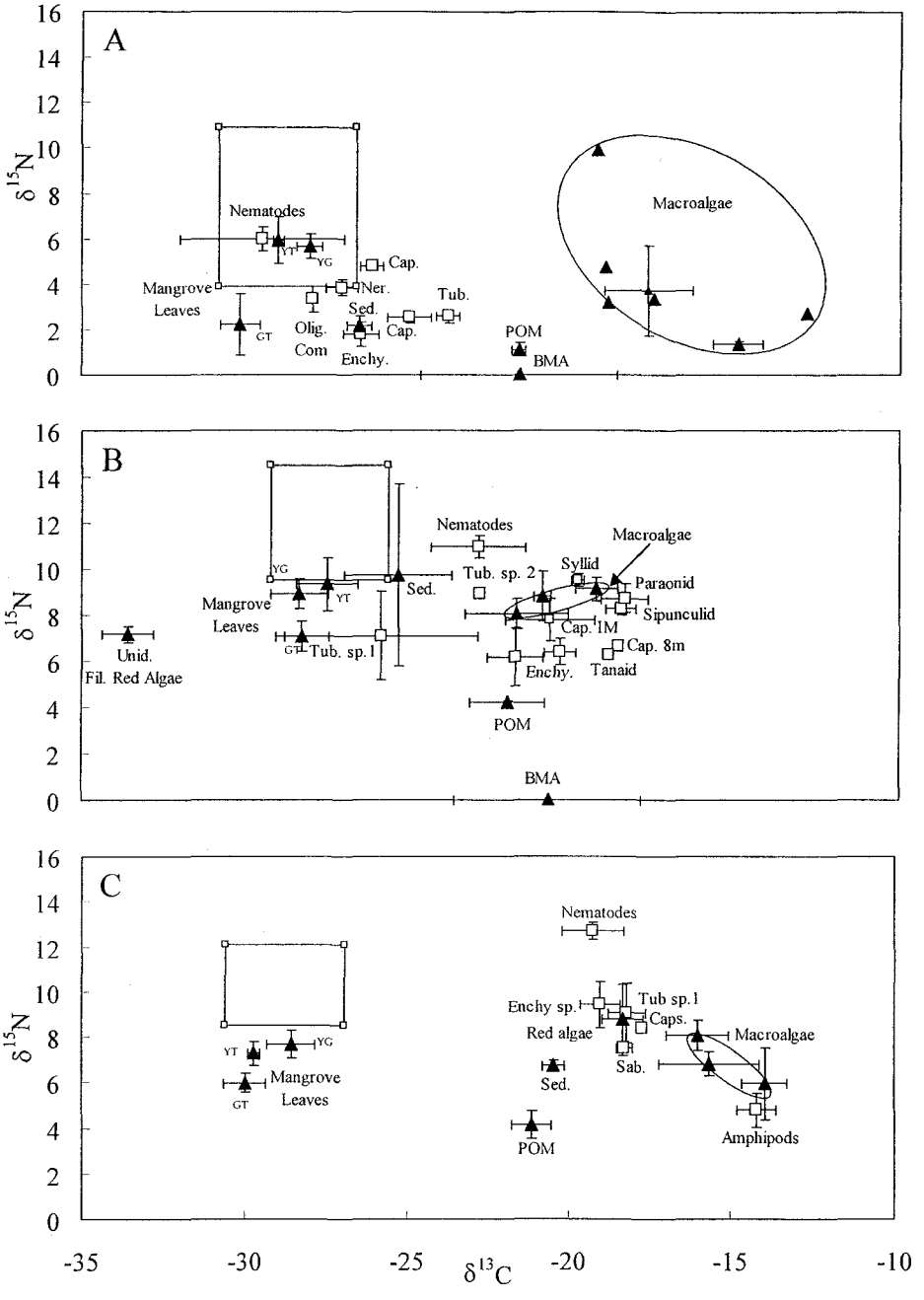

Figure 2. $\delta^{15}N$ and $\delta^{13}C$ of different primary producers (solid triangles) and sediment infauna (open squares) from native mangrove communities in A) Puerto Rico and introduced mangrove forests in B) Molokai and C) Oahu. A trophic shift box was illustrated for expected stable isotope values for infauna consuming mangrove leaves. For benthic microalgae (BMA), only $\delta^{13}C$ values are plotted. Error bars are 95% confidence limits. Abbreviations are as follows: GT = green tree leaves (mangroves), YT= yellow tree leaves, YG= detritus (yellow leaves from the ground), Olig. Com.= Oligochaete community, Enchy sp.=Enchytraeidae, Tub. Sp. 1/2 = Tubificidae sp. 1 and 2, Caps= Capitellidae, Sab = Sabellidae, c.f. *Potamilla* spp., Ner.=Nereid, Sed.= Sediments. Ellipse delineates macroalgae stable isotope values.

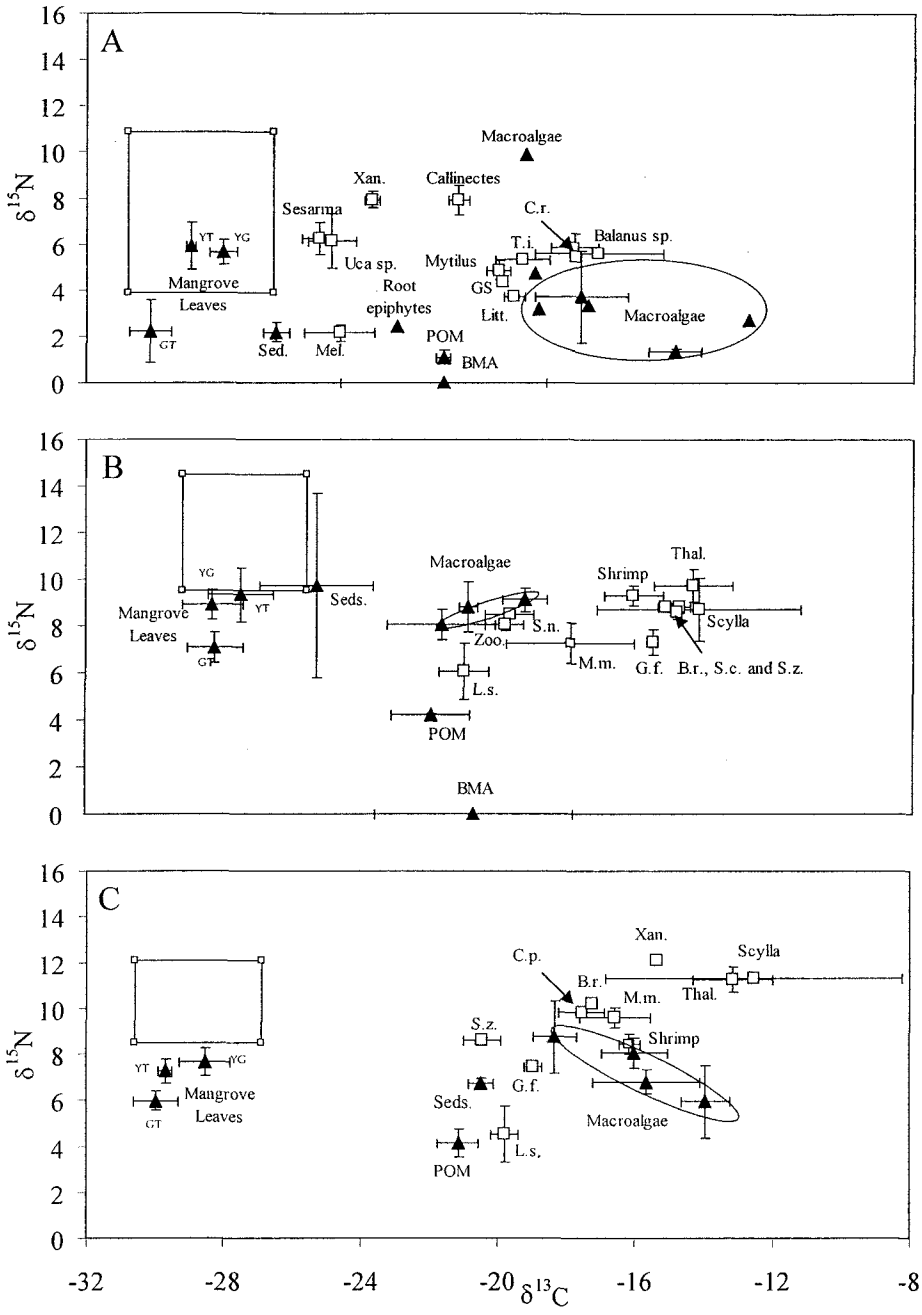

Figure 3. $\delta^{15}N$ and $\delta^{13}C$ of different primary producers (solid triangles) and mangrove epifauna (open squares) from native mangrove forests in A) Puerto Rico and introduced mangrove communities in B) Molokai and C) Oahu. A trophic shift box is illustrated for expected stable isotope values for epifauna consuming mangrove leaves. For benthic microalgae (BMA), only $\delta^{13}C$ values are plotted. Error bars are 95% confidence limits. Abbreviations are as follows: GT = green tree leaves (mangroves), YT= yellow tree leaves, YG= detritus (yellow leaves from the ground), Xan.= Xanthidae, Mel.= *Melampus* sp., GS = green sponge, T.i. = *Tedania ignis*, Litt. = *Littoraria* sp., L.s.= *Littoraria scabra*, C.r.=*Crassostrea rhizophorae*, B.r. = *Balanus reticulatus*, S.c. = *Sigmadocia caerulea*, S.z.=*Suberites zeteki*, S.n.=*Siphonaria normalis*, Zoo. = zooanthids, M.m.=*Metapograpsus messor*, G.f.=*Gelloides fibrosa*, Thal. =*Thalamita crenata*, C.p.=*Cthamalus proteus*, Sed.= Sediments. Ellipse delineates macroalgae stable isotope values.

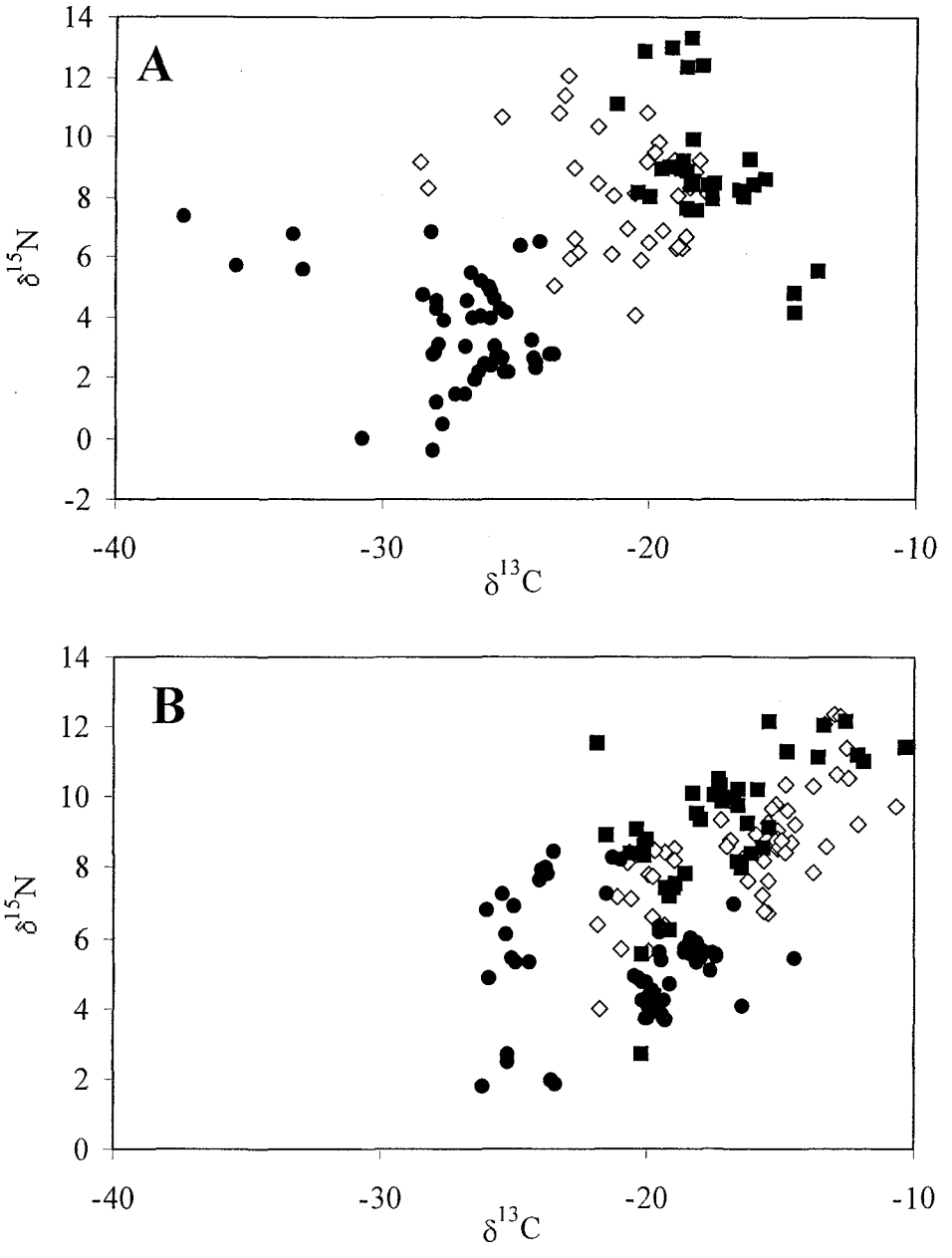

Figure 4. $\delta^{15}N$ and $\delta^{13}C$ from all measurements of infauna (A) and epifauna (B) from introduced mangrove communities on Oahu (solid squares) and Molokai (open diamonds), and native mangrove forests in Puerto Rico (solid circles).

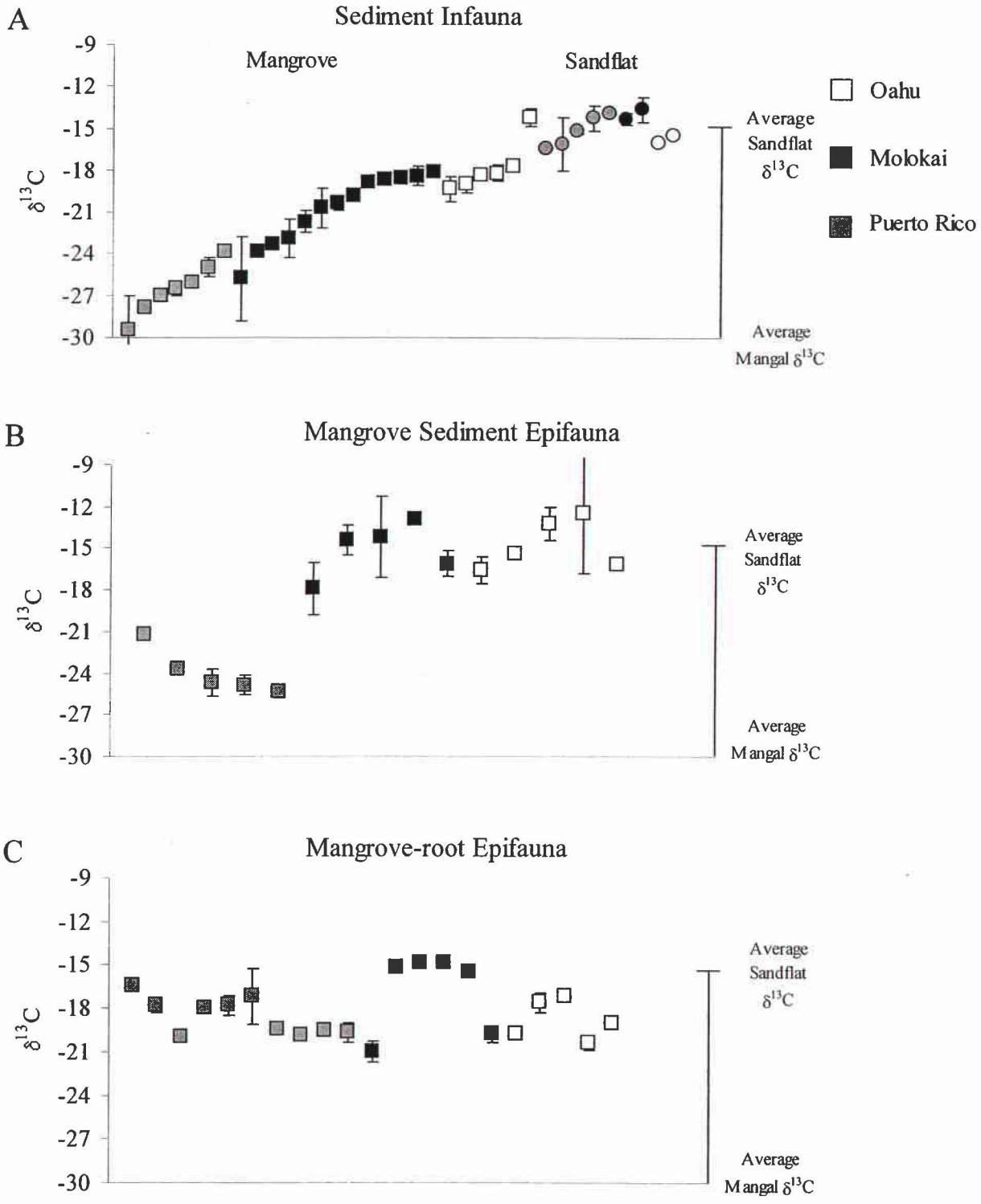

Figure 5. $\delta^{13}C$ measurements from sediment infauna, from both mangroves and sandflats (A), mangrove sediment epifauna (B), and mangrove root-associated epifauna (C). Solid line separates stable isotope measurements in mangrove sediments from sandflat sediments. Error bars represent 95% confidence limits.

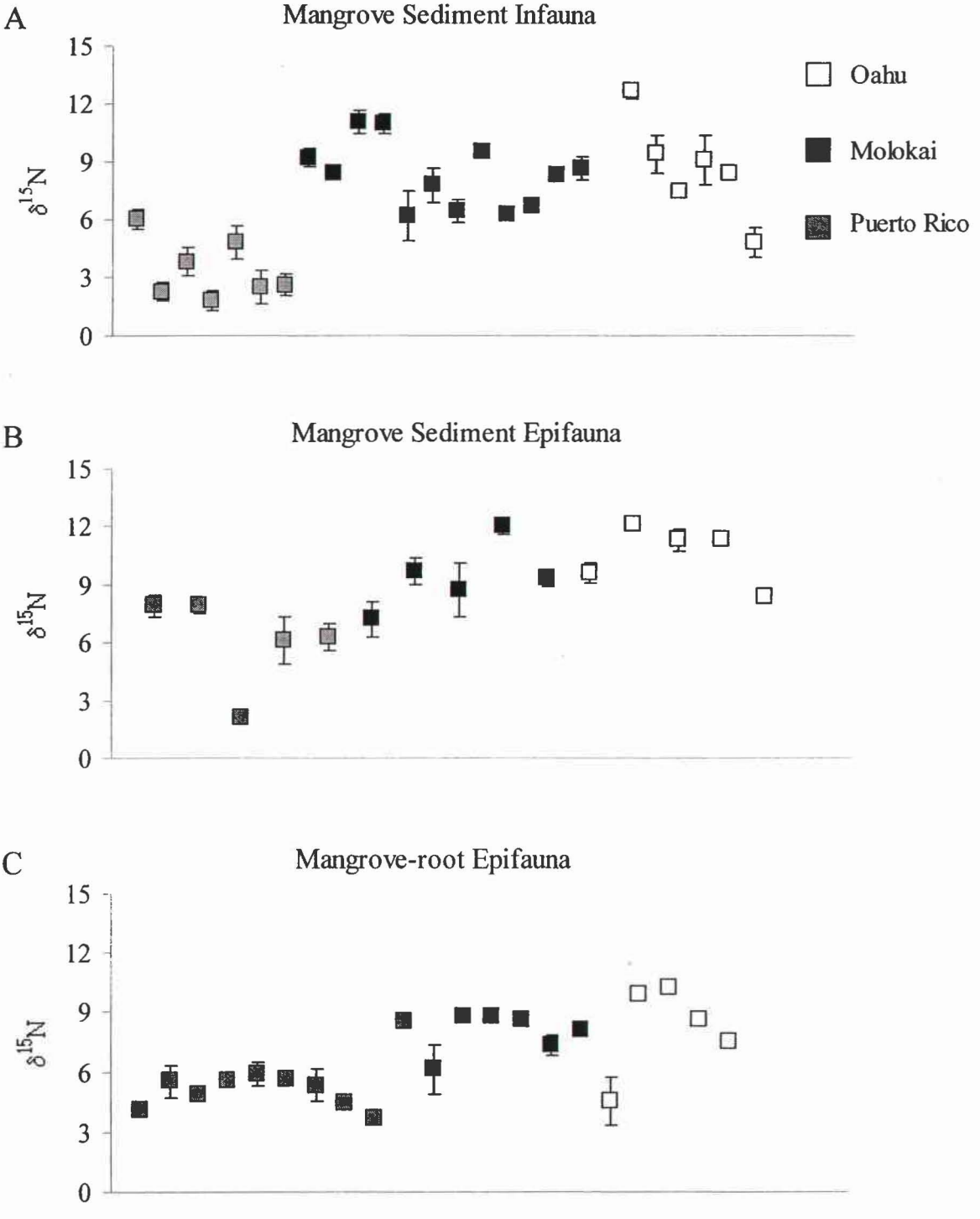

Figure 6. $\delta^{15}N$ measurements from sediment infauna (A), sediment epifauna (B), and root-associated epifauna (C) from mangroves. Error bars represent 95% confidence limits.

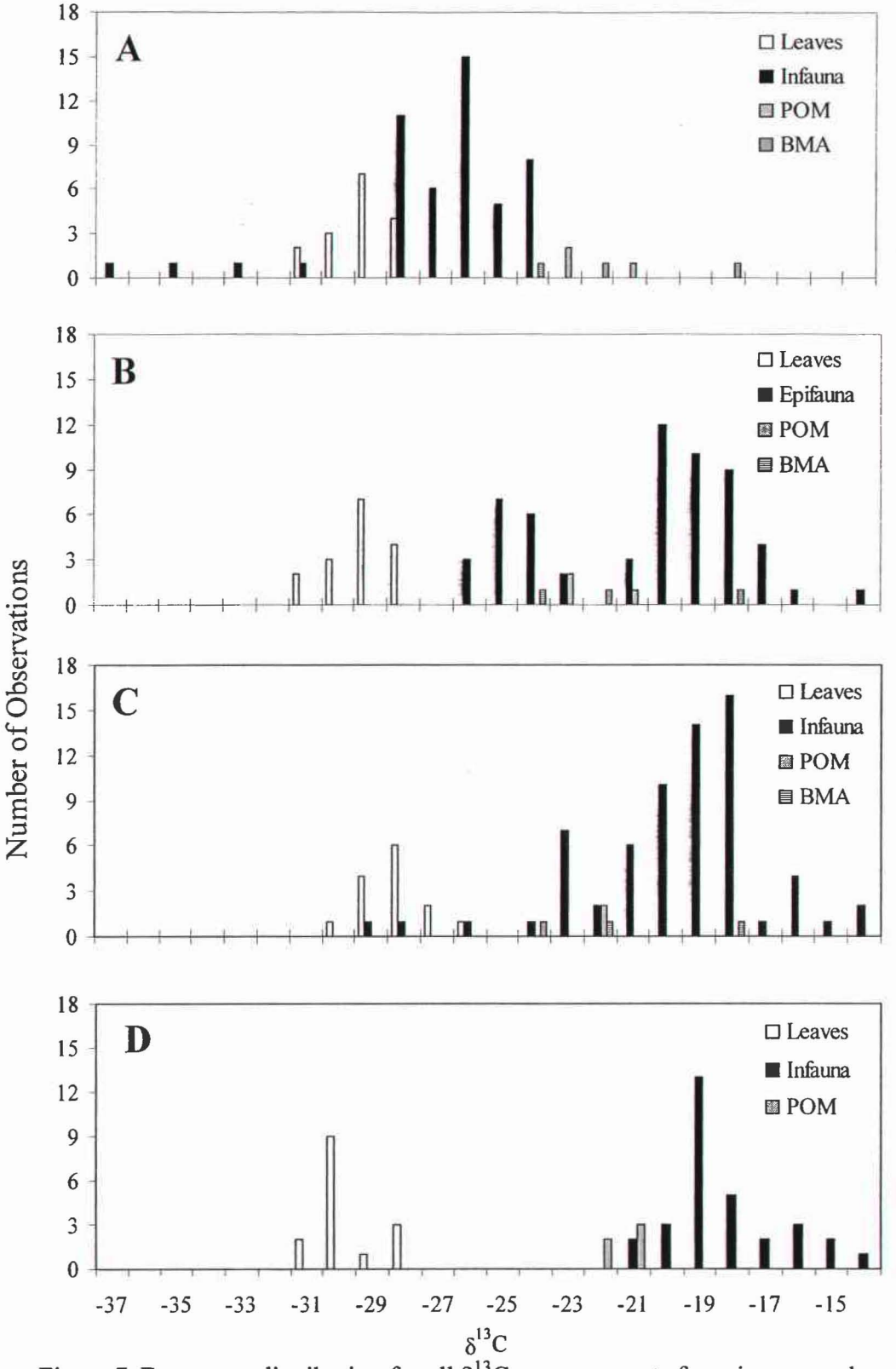

Figure 7. Frequency distribution for all $\delta^{13}C$ measurements for primary producers and infauna (A) and epifauna (B) from Puerto Rico, and infauna from Molokai (C) and Oahu (D).

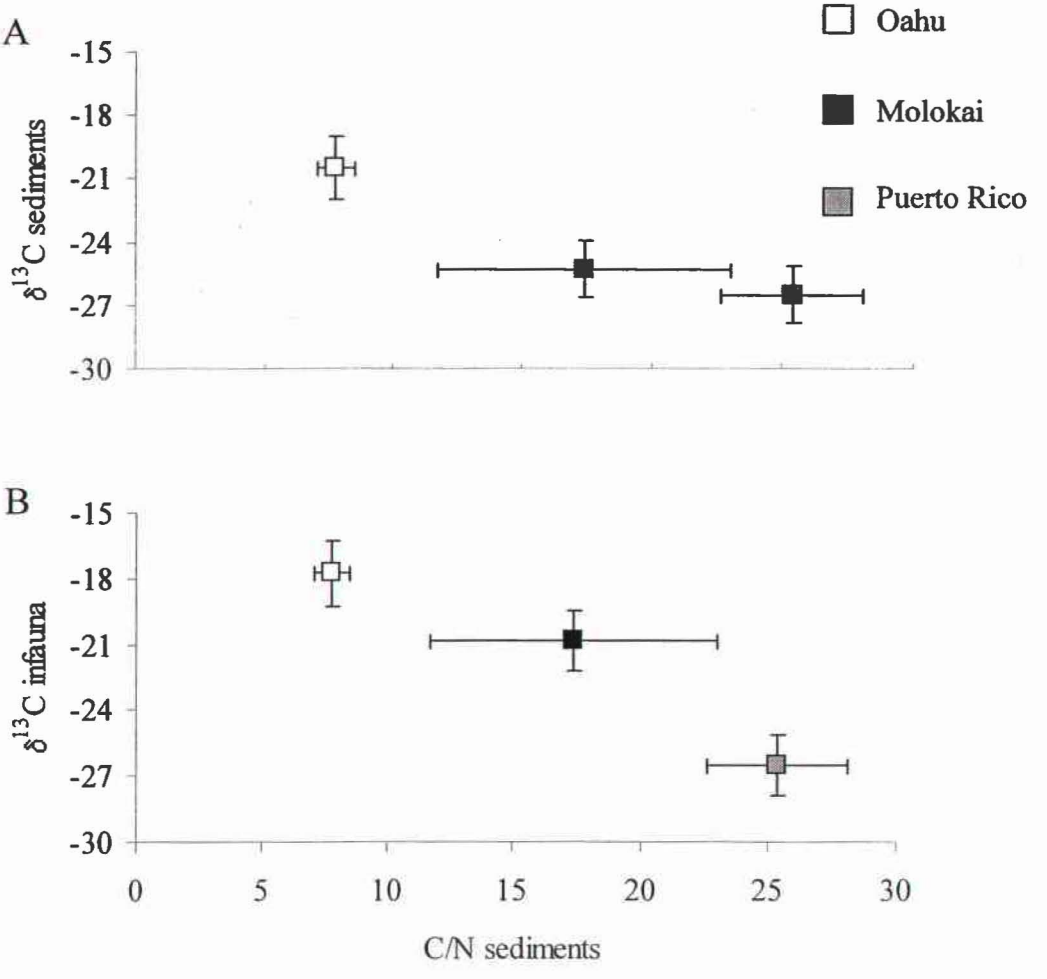

Figure 8. Sediment C/N ratios versus sediment $\delta^{13}C$ (A) and infauna $\delta^{13}C$ measurements (B). Error bars represent 95% confidence limits.

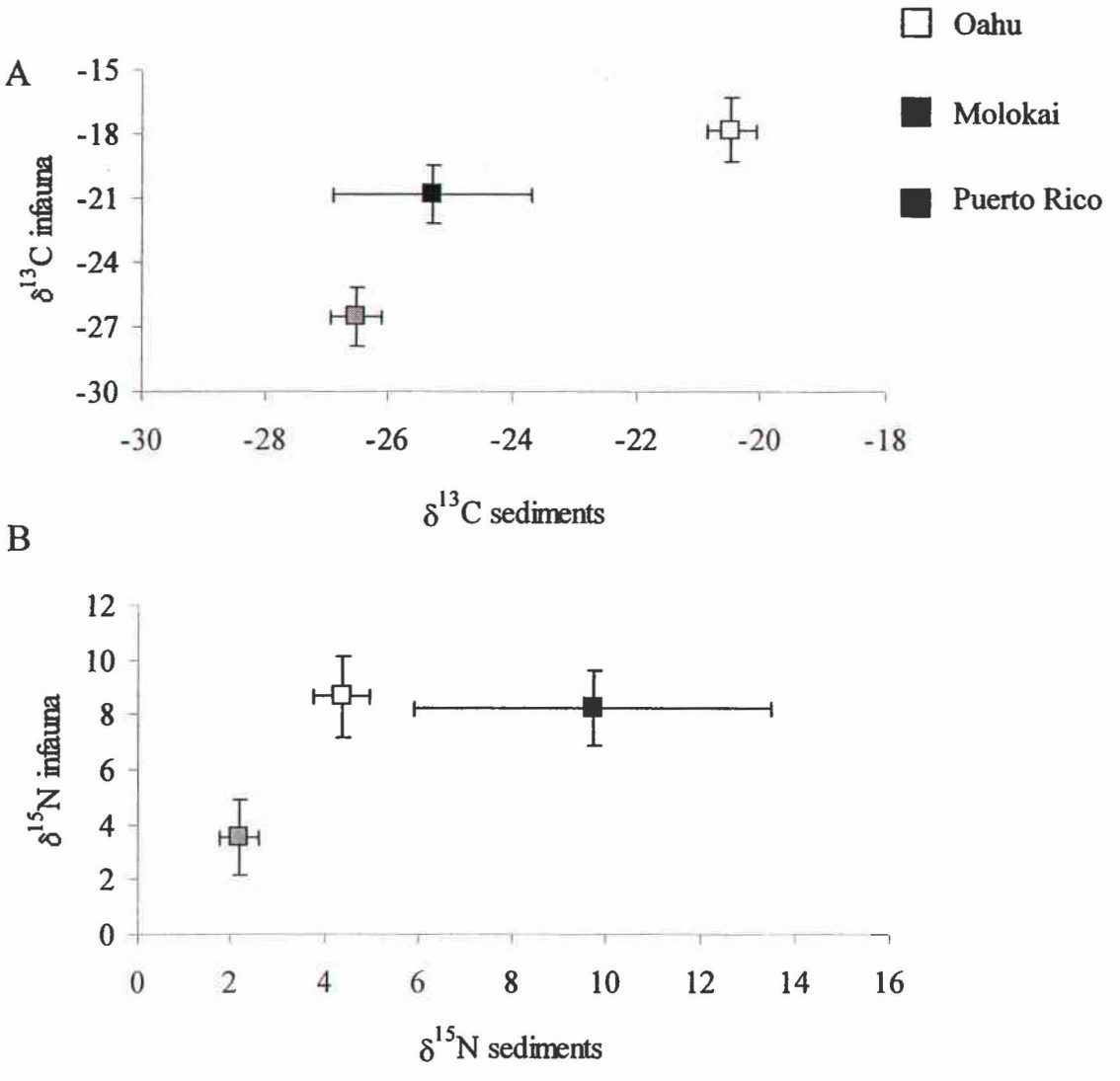

Figure 9. A) $\delta^{13}C$ values of sediments versus $\delta^{13}C$ of infauna, B) $\delta^{15}N$ values of sediments versus $\delta^{15}N$ of infauna from Puerto Rico, Molokai, and Oahu. Error bars represent 95% confidence limits.

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CHAPTER 4. TROPHIC LINKAGES AND CRAB MOVEMENT WITHIN MICRONESIAN MANGROVE FORESTS

Abstract

The mangrove crab, *Scylla serrata,* is an important component of mangrove fisheries throughout the Indo Pacific. Understanding crab feeding, reproduction and residency should assist in management of these fisheries. Stable isotope analyses can help trace crab movement and feeding behavior in mangroves and adjacent reefs where this crab is found. To better understand crab behavior, I sampled three mangrove-dominated watersheds, Lelu, Okat, and Utwe, on Kosrae, Micronesia. Samples of *S. serrata* and their potential food sources were analyzed for stable carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$), and sulfur ($\delta^{34}S$) isotopes. In addition, *S. serrata* crab tissues were analyzed for phosphorus and the following cations and trace elements: K, Ca, Mg, Na, Mn, Fe, Cu, Zn, and B. Crab tissues from Utwe watershed had significantly greater concentrations of Cu and P than Lelu and Okat, whereas crabs from Lelu had higher concentrations of Mn, Ca, and Mg than Utwe crabs. Discriminant analysis indicated that 90.8 % of the crabs remain in each watershed as distinct populations, not moving significantly among watersheds. Crab stable isotopic values indicated potential differences in foraging behavior among watersheds. Specifically, crabs from Lelu had higher $\delta^{13}C$ and $\delta^{34}S$ values, with average values of -21.8‰ and 7.8‰, respectively. These crabs may forage primarily on adjacent reef flats, thus yielding enriched isotope values. Crabs from Okat and Utwe had lower $\delta^{13}C$ and $\delta^{34}S$ values than those from Lelu, but similar to values expected from animals

feeding within mangrove swamps (mangal), e.g., on infaunal benthos that had average $\delta^{13}C$ values near –26.5 ‰. Isotope mixing model (IsoError) results support these conclusions, with the greatest mangal contribution to *Scylla serrata* diet occurring in Okat (91-100 %) and Utwe (71-100 %) watersheds, and a more balanced usage of mangrove and reef-flat habitats in Lelu (53-73 %). Isotope contrasts among the three watersheds correspond to extent of mangrove swamp development, with the strongest mangal signals occurring at Utwe, which has extensive forests. Thus, sustainability of *Scylla serrata* on Kosrae appears to rely on isolated populations residing in different watersheds, with habitats that differ ecologically and in harvesting pressure.

Introduction

The mangrove crab, *Scylla serrata* (also known as the mud crab), is the basis for important local fisheries around the Indo-Pacific region, where it inhabits mangrove forests and adjacent reefs. In Kosrae, Federated States of Micronesia, mangrove crabs provide 55 % of the ~ $1 million in goods harvested annually in mangroves (Naylor and Drew 1998). *Scylla serrata* is one of the largest estuarine crabs found in tropical, subtropical and warm temperate areas where it inhabits saltwater estuaries and mangrove forests. Because of their large size, high meat yield, and delicate flavor, these crabs are a valued source of food and income throughout their native range and are commercially important in the tropical Indo-Pacific (Escritor 1972; Varikul et al. 1972; Robertson and A. Kruger 1994; Keenan et al. 1998; Trino et al. 1999).

Scylla serrata life history and feeding patterns are very similar to many other near-shore, benthic crustaceans (cf., Fry et al. 2003) in being characterized by three kinds of movement: small scale movement around relatively permanent burrows in areas of sufficient food availability, free-range foraging within a 1-2 km area without returning to a fixed point each day, and a spawning migration by females up to 95 kilometers offshore (Arriola 1940; Macnae 1968; Hill 1975, 1978, 1994; Perrine 1978; Hyland et al. 1984; Robertson 1996; Akil and Jiddawi 1999). Studies conducted in other mangrove communities suggest that mangrove crabs, with the exception of spawning females, travel small distances throughout their adult lives, freely moving within local mangrove and reef-flat communities (Hill 1978, 1994; Perrine 1978; Hyland et al. 1984; Robertson 1996; Akil and Jiddawi 1999).

In recent years, the *S. serrata* population on Kosrae has apparently decreased, possibly a result of increased clearing of mangrove trees and decreased suitable habitat. It remains unclear whether mangrove loss has been linked to lower fisheries yields of *S. serrata*. Despite the economic importance of *S. serrata* to the Kosraean economy, habitat and dietary requirements and the impact of harvesting on crab population dynamics remain unknown. Without this information, it is difficult to assess the long-term sustainability of mangrove crab harvesting in Kosrae and throughout the Indo-Pacific region. In addition, factors that control crab movement are not well known, although results from mark and recapture studies in Kosrae suggest that these swimming crabs are essentially resident, remaining within 1-2 km of catch and release sites (Bonine et al. submitted). In order to learn more about the movements and diets of *S. serrata*, I used population census data to follow the adult movement patterns, and stable isotope, cation,

phosphorus, and trace metal analysis to approximate the extent of adult crab movement in mangrove and adjacent reef-flat communities (cf., Fry 1981; Fry et al. 1999, 2003).

Animals acquire their stable ^{13}C, ^{15}N, and ^{34}S compositions from their food sources, where $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ values are similar to their diets, with a corresponding 0-1 ‰ enrichment for $\delta^{13}C$ and $\delta^{34}S$, and 3-4 ‰ enrichment for $\delta^{15}N$ for each increase in trophic position (DeNiro and Epstein 1978; DeNiro and Epstein 1981; Minagawa and Wada 1984). Stable isotope values reflect time-integrated diets, depending on the metabolic rate of the tissue being measured (Tieszen et al. 1983). Animal muscle tissue turns over more slowly than blood, for example, on the order of 1 month versus a few days (e.g., Fry et al. 1999, 2003). The expectation is that stable isotope markers from crab muscle tissue will reflect diets of the past month for adult crabs that are growing slowly (e.g., Fry et al. 1999, 2003). Crabs that feed in the same location for several weeks would be expected to have relatively uniform isotope compositions, in equilibrium with site diets, whereas crabs that move among different habitat types and/or sites may have more varied isotopic compositions, i.e., more variation among individual crab isotopic values within a population (e.g., Fry et al. 1999, 2003). If *S. serrata* feed exclusively in mangroves, with little movement between habitats, it should have stable isotope compositions similar to those of animals that spend their adult life stages in mangroves (e.g., some grapsid crabs and benthic infauna). Stable isotopes of mangrove infauna (essentially residents) may provide useful "endmembers", or mangal (mangrove ecosystem) source contributions to *S. serrata* nutrition. Likewise, if *S. serrata* feed exclusively in adjacent reef-flats, one may expect their stable isotopic compositions to be in equilibrium with those animals that spend their entire life histories in the reef-flat

sediment environment. Therefore, changes in habitat use may be reflected in corresponding changes or increased variability in stable isotopic compositions. Also, animals acquire their trace metal and cation concentrations via uptake from the surrounding environment and from their diet (Reinfelder and Fisher 1994; Rainbow and Black 2002). Trace metal and cation concentrations can differ spatially, and thus concentrations from animal tissues may reflect that chemical variability among crab habitats (Rainbow et al. 2000) as well as crab movement patterns and habitat residency.

Many studies have focused on the diets and feeding ecology of crabs (Nakasone et al. 1985; Lee 1989; Thimdee et al. 2001), but very few have assessed the significance of isotopic variations in crabs inhabiting systems with various natural food sources (Rodelli et al. 1984; Thimdee et al. 2001; Bouillon et al. 2002). Based on gut content analysis, direct observation, and some stable isotope work, *Scylla* has been described as an opportunistic scavenger, herbivore, and carnivore (Arriola 1940; Thimdee et al. 2001, 2004). Specific food sources include detritus and, usually, slow-moving benthic animals: e.g., bivalves, snails, small crabs, and polychaetes. Mangrove crabs are considered the top predator in mangrove systems and may act as a keystone species controlling the distribution and zonation of grapsid crabs and clams (Hill 1978, 1979; Thimdee et al. 2001).

This study provides an opportunity to test the contribution of mangrove systems as a refuge for commercially important crab species. The goal was to understand adult *S. serrata* feeding habits, movement and residency. Data were collected from three watersheds on Kosrae, and an isotope mixing model was used to test the following alternative hypotheses: 1) *Muscle stable isotope, trace metal, and cation compositions*

suggest that adult S. serrata *restrict their movement to within a single watershed,* and 2) *Muscle stable isotopic compositions and mixing model calculations are consistent with* S. serrata *moving and foraging between mangrove and adjacent reef-flat habitats.*

Materials and Methods

Study site description

This study was conducted in June 2002 on the island of Kosrae, a 112 km^2 volcanic island in the Federated States of Micronesia (5°16' to 5°22'N, 162°54' to 163°02' E; Figure 1). Mangroves occupy ⅔ of the island's shoreline, consisting of a belt of vegetation up to 750 m thick. Eight species of mangroves are found in these forests: *Bruguiera gymnorrhiza, Heritiera littoralis, Lumnitzera littorea, Nypa fruticans, Rhizophora apiculata, R. mucronata, Sonneratia alba,* and *Xylocarpus granatum*. The seaward side of mangrove forests consists of fringing reefs, ranging from 50 m in width on the windward side, up to 500 m on leeward coast. Annual mean temperature is 27°C, and annual rainfall is high and not distinctly seasonal, ranging from 5000-6000 mm (Merlin et al. 1993). Study sites were located in distinct watersheds in three municipalities, Utwe, Lelu, and Okat (Figure 1), and each watershed had comparable water temperatures, salinities, and dissolved oxygen concentrations (Table 1).

Sample collection and preparation

In order to determine the stable isotopic values of various primary producers the following collections were made. Mangrove trees and surrounding sediments were

sampled for live green, shade leaves and decaying brown leaves. Pooled samples containing a mixture of species (n=20 leaves) collected randomly from separate trees in the mangrove understory were used to obtain site averages for green, shade leaves. Brown leaves, containing a mixture of shade leaves and sun leaves that grow on the sun-exposed side of the mangrove forest, were collected at random from the sediment surface and pooled (n= 20 leaves). In addition, suspended particulate organic matter (POM) was collected by filtering 300 mL of seawater adjacent to the sampling stations onto pre-combusted GFF filters (Fry et al. 1991). Surface sediments were collected and processed for benthic microalgae (BMA) chlorophyll content. Approximately 1 cm^3 of surface sediment was extracted in 5 mL of cold acetone for 24 hrs in the dark. Extracted chlorophyll was adsorbed and dried on pre-combusted GFF filters. Previous studies have used nitex mesh netting on the sediment surface to allow motile diatoms to migrate away from the sediments through to the top layer of the mesh. In mangrove sediments, however, this technique proved less than optimal due to sediment contamination via resuspension and deposition of fine-grained, flocculent sediment on the mesh surface. The acetone extraction was free of fine sediment and detrital material. Acetone, however, can co-extract other pigments (Wright et al. 1997), possibly confounding stable isotope values. Because samples from each site were treated the same, the extracts provided a baseline stable isotope value for benthic microalgae.

Mangrove crabs (*Scylla serrata*) were collected in each watershed in order to evaluate habitat residency and crab movement patterns. Crabs were caught in mangrove habitats using 6 baited traps. Traps were left overnight for a total of 4 consecutive trapping nights per watershed. Sex, carapace width, and weight were recorded for each

crab caught. Small crabs were collected from surface sediments and tree roots. Reef-associated crabs, e.g., *Thalamita crenata,* were also collected from adjacent reef-flats and baited traps.

Sediments for infauna were collected from mangroves and outer-reef-flat habitats. Infaunal samples were processed as in (Carman and Fry 2002) as follows. Infaunal sediments were preserved in 10% formalin prior to sieving. Laboratory gloves were used at all times during the infauna processing to minimize C and N contamination. In the laboratory, samples were washed through nested sieves (300 and 45 μm) to remove sediment, and infauna were rapidly sorted, pooled to species level when possible, cleaned with deionized water, and transferred to tin capsules for $\delta^{13}C$ and $\delta^{15}N$ analysis. Infauna The dominant taxa of infauna present in the mangrove sediments were collected and analyzed, as determined from the species composition of previously collected core samples (Demopoulos, unpublished data). Minimum aliquots of 5 μg C and 10 μg N are required per sample for stable isotopic analysis (Peterson and Howarth 1987). Consequently, for smaller species (e.g., polychaetes, oligochaetes, and other invertebrates) 5-100 animals were pooled per sample. Soft tissue from gastropods, barnacles, and *S. serrata* chelipeds were dissected and rinsed with distilled water. Whole chelipeds, including muscle and chitin tissues combined, from *S. serrata* and other crabs (grapsids, fiddlers, and *Thalamita crenata*) were analyzed separately for stable isotopes. In addition, stomach contents from smaller grapsid crabs collected inside mangrove forests were analyzed to evaluate isotopic variability in different tissue types. Whenever possible, a minimum of three replicate samples was analyzed for each species per watershed.

All samples were dried at 60 °C and, with the exception of infauna and filter samples, ground to a fine powder and subsampled for $\delta^{13}C$ and $\delta^{15}N$. *Scylla serrata* tissue samples were also subsampled for $\delta^{34}S$ analysis. Whole filter samples were placed in tin cups and analyzed as follows.

Isotope analysis

Samples were analyzed for C, N, and S isotopic compositions referenced to PeeDee Belemnite (PDB), atmospheric N, and Canyon Dioblo Troilite, respectively (Peterson and Fry 1987). Analyses were performed using an elemental analyzer interfaced to a Finnegan MAT Delta-S stable isotope ratio mass spectrometer via a Finnigan MAT ConFlo II interface. Reproducibility was monitored using several organic reference standards (Fry, personal communication 2003). Following isotope analysis and ratio calculations, preserved infaunal samples were corrected for formalin preservation by adding 1‰ to $\delta^{13}C$ values of preserved sample (Sarakinos et al. 2002).

Crab Tissue Cation Analysis

Crab muscle tissue was subsampled for phosphorus, trace metal and cation analysis (K, Ca, Mg, Na, Mn, Fe, Cu, Zn, and B) using inductively coupled plasma – atomic emission (ICP-AE). Samples were first digested in acid and then run with standards according to Kalra (1998).

Statistical Analyses

Comparisons among stable isotopic values and watersheds were conducted using Pearson's product moment correlation and univariate ANOVA tests. Bonferroni post-hoc significance tests were used to test differences in mean isotope values from the various multiple comparisons, with an experiment-wise significance level of $\alpha = 0.05$ (Sokal and Rohlf 1969, 1995). In order to distinguish differences based on crab movement versus crab size, non-parametric median tests were used to test for differences in *S. serrata* weights and carapace widths across watersheds (Sokal and Rohlf 1969). Discriminant analysis was used to test for differences in crab tissue isotope, phosphorus, trace metal, and cation compositions among the three watersheds (McLachlan 1992). Groupings of the crab samples were identified based on the untransformed tissue data analyzed for the following components: P, K, Ca, Mg, Na, Mn, Fe, Cu, Zn, B, $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$. All statistical analyses were performed using SPSS statistical software.

Estimated Habitat Contribution

In order to evaluate habitat contribution (mangal versus reef-flat) to *S. serrata* isotope values, I averaged stable carbon isotope values for animals residing exclusively in mangroves or reef-flats, including adult sediment infauna (polychaetes, oligochaetes, nematodes, and clams) and small grapsid crabs. These adult organisms are assumed to spend their juvenile and adult developmental stages in either reef-flat or mangrove habitats and thus provide endmembers for both habitat types. IsoError 1.04, an isotope modeling program, (Phillips and Gregg 2001) was used to estimate the percent contribution of habitat type (reefs versus mangal) to *S. serrata* isotope values. This

method accounts for the variability of the mixture (consumer) and the source (reef versus mangal endmember) stable isotope values. Mean and standard deviations of $\delta^{13}C$ values for *S. serrata* and endmembers from each watershed were used for these calculations.

Estimated Scylla serrata *Diet*

To determine possible food sources for *S. serrata*, diet ranges from stable isotope results were estimated by the following methods. Assumed trophic-level fractionations of 0-1 ‰ for $\delta^{13}C$ and of 2.4-3.4‰ for $\delta^{15}N$ were subtracted from the range of isotope values for *S. serrata* (Post 2002; McCutchan et al. 2003). Potential prey items for *S. serrata* are expected to fall within the area estimated for crab diet.

Tissue type comparisons

Before comparing crab tissue stable isotope data, I needed to evaluate any isotope differences between combined chitin plus muscle tissue samples and pure muscle samples for *S. serrata*. I analyzed separately whole chelipeds (combined muscle + chitin) and muscle tissue for stable isotopes. The average $\delta^{13}C$ of muscle and muscle plus chitin samples was -22.2 ‰, ranging from -24.5 to –19.3 ‰ for muscle samples and -23.6 ‰ to -20.8 for muscle plus chitin samples (Table 2). For $\delta^{15}N$, average muscle samples were 7.8 ‰ (6.2 to 9.0 ‰) and $\delta^{15}N_{muscle+chitin}$= 6.7 ‰ (4.9 to 8.1 ‰). There was no significant difference in $\delta^{13}C$ between sample types, so no correction was used for

stable carbon isotope values from non-*Scylla* crab values. However, crab muscle samples were enriched in ^{15}N by an average of 0.9 ‰, so a correction factor of 0.9 ‰ was added to $\delta^{15}N$ isotope values for non-*S. serrata* crab samples prior to plotting isotope data and estimating dietary contributions to *S. serrata*.

Results

Primary Producers and Sediments

Mangrove leaves, POM, BMA, root epiflora, and sediment stable carbon and nitrogen isotope data are reported in Table 2. Green leaf $\delta^{13}C$ values ranged from –37.3 ‰ to –34.1 ‰ and $\delta^{15}N$ from 1.3 ‰ to 3.6 ‰. Brown leaf $\delta^{15}N$ were similar to green leaves and sediments, ranging from 1.9 ‰ to 2.9 ‰, but average $\delta^{13}C$ values (–33.1 ‰) were enriched in ^{13}C relative to the green shade leaves and depleted relative to surface sediments. There were no significant differences in stable isotopic values of benthic microalgae (BMA) among watersheds. Stable $\delta^{13}C$ values from acetone extracts and non-extracted material were similar; thus, it was concluded that the extracted material was representative of benthic microalgae stable $\delta^{13}C$ values. BMA acetone extracts provided insufficient N for $\delta^{15}N$ analysis.

Patterns Across Watersheds

All crab muscle tissue raw data can be found in Appendices A and B. Crab carapace size and weight differed among watersheds (Table 3), and results from non-parametric median tests indicated that Utwe had the largest crabs, both in weight and carapace width, compared to Okat and Lelu (df =2, for weight, p=0.006, for width, p=0.007). The sizes of crabs from Okat were evenly distributed, whereas crabs from Lelu were among the smallest adults collected overall.

Some stable isotopic values of crabs overlapped among watersheds (Figure 2). All stable isotopic values from each watershed were positively correlated ($p < 0.001$), with the exception of $\delta^{13}C$ versus $\delta^{15}N$ from Utwe ($r^2 = 0.217$, $p=0.107$). Average isotope values were distinct among watersheds, with Lelu more enriched in ^{13}C, ^{34}S, and ^{15}N, than Utwe, and with Okat having intermediate values (Table 2). Mean values from each watershed were significantly different for each stable isotope ($df_{total}= 66$, $df_{model}=2$, for $\delta^{15}N$, $F = 20.902$, $p<0.001$, for $\delta^{34}S$, $F = 32.85$, $p<0.001$, and for $\delta^{13}C$ $F=52.204$, $p<0.001$). Bonferroni post-hoc comparisons yielded significant differences for all three stable isotopes, with crabs from Lelu and Okat more enriched in heavier isotopes than Utwe crabs ($p<0.001$ for Lelu and Utwe, $p<0.006$ for Okat and Utwe). In addition, crabs from Lelu were more enriched in both ^{13}C and ^{34}S than Okat crabs ($p<0.001$).

Discriminant analysis yielded distinct separations of muscle tissue data ($\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$, P, K, Ca, Mg, Mn, Fe, Cu, and Zn) among the Lelu, Okat, and Utwe watersheds (Figure 3). Almost all of the samples (90.8 %) were correctly classified into each separate watershed. Only two significant canonical discriminant functions were returned by the analysis, with significance of Wilks' Lambda at $p < 0.001$ for both functions 1 and 2. Function 1 largely separated Lelu from Okat and Utwe watersheds, and function 2 essentially separated Okat from Utwe watershed.

An examination of the values of the standardized canonical discriminant function coefficients helped identify variables that were influential in discriminating the three watersheds. Higher stable isotope values ($\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$) and manganese concentrations were strongly positively correlated with function 1 (Table 4). In contrast, negative coefficients were obtained for zinc, copper, and phosphorus concentrations. Function 2 showed a positive correlation with copper and percent potassium and was negatively correlated with $\delta^{15}N$, percent magnesium and calcium. These variables were important in characterizing crabs from the various watersheds and habitat conditions. In particular, Utwe crabs had significantly greater concentrations of copper and phosphorus then Lelu and Okat crabs (Table 5) (ANOVA, $p<0.001$ for copper and $p=0.032$ and 0.029 for phosphorus at Lelu and Okat, respectively). In addition, Utwe crabs had notably greater concentrations of zinc then Lelu crabs, at a level bordering on statistical significance (ANOVA, $df_{total}= 66$, $df_{model}=2$, $p=0.051$). Lelu crabs had higher concentrations of manganese, calcium and magnesium then Utwe crabs (ANOVA, $df_{total}=$

66, df_{model}=2, p=0.055, 0.006, and 0.007, respectively) and higher potassium concentrations than in Okat crabs (p=0.013).

To distinguish patterns due to food web (stable isotopes) versus environment (cations, trace metals, and phosphorus) among crabs from different watersheds, the same discriminant analysis was run for stable isotopes separately from environmental parameters. The results were similar to the combined discriminant analysis (Figure 3), and only six samples (9%) were not classified correctly. In contrast, after running the discriminant analysis for cations, trace metals, and phosphorus, 18 samples (27.7%) were not classified correctly. However, there was a significant separation among the watersheds by environmental parameters and by stable isotope values.

Size and gender-related patterns became evident when all of the crabs from the three watersheds were analyzed together. Smaller crabs (carapace width) were more enriched in ^{13}C, ^{34}S, and depleted in ^{15}N than larger crabs ($p < 0.05$). In addition, less massive crabs (in g) were more enriched in ^{34}S than more massive crabs, p=0.043. Carapace width was positively correlated with concentrations of zinc, copper, sodium, and sulfur, whereas it was negatively correlated with iron, manganese, and calcium. Thus, larger sized crabs had greater concentrations of zinc, copper, sodium and sulfur. Overall, male *S. serrata* were significantly more massive than females (p<0.001). In addition, a few (n=3) gravid females were collected from Okat and Lelu; these are not often collected inshore.

Crab size (weight and width) was significantly correlated with stable carbon, nitrogen, and sulfur isotope data (Table 6), using combined data from the watersheds. However, after separating these data by watershed, only Lelu crab size was significantly

correlated with isotope data (Table 6). In order to evaluate if size was a direct predictor of isotope patterns, i.e., as crab size increases, so does its $\delta^{15}N$ value, regression analysis was re-run on normalized *S. serrata* $\delta^{15}N$ data. *Scylla serrata* $\delta^{15}N$ values were normalized by subtracting the average $\delta^{15}N$ values for available prey items (e.g., mangrove sediment infauna and small crabs, Utwe = 3.7 ‰, Okat= 4.75 ‰, Lelu = 4.8 ‰) from each *S. serrata* $\delta^{15}N$ value. This calculation corrected crab isotope data for differences in $\delta^{15}N$ values attributable to variations in $\delta^{15}N$ of prey items across sites. The subsequent linear regression was not significant (r^2=0.002 and 0.013, for width and weight, respectively). Thus, there was no significant relationship between crab size and stable isotopic values, after correcting for site differences.

Within Watershed Habitat Comparisons

There was a large ^{13}C difference between inshore fauna collected from mangroves, including sediment infauna and grapsid crabs, versus those collected from adjacent reef-flats (Table 2). On average, $\delta^{13}C$ difference was 5.0 ‰, 10.6 ‰, and 12.2 ‰ for Utwe, Okat, and Lelu fauna respectively. I calculated mangal $\delta^{13}C$ endmembers from each watershed by averaging isotope values for sediment infauna and grapsid crabs, with $mangal_{Utwe}$= –27.2 ‰, $mangal_{Okat}$ = -25.9 ‰, and $mangal_{Lelu}$ = -27.1 ‰. Adjacent reef-flat $\delta^{13}C$ endmembers were also calculated: $reef\text{-}flat_{Utwe}$= -21.7 ‰, $reef\text{-}flat_{Okat}$ = –15.9 ‰, and $reef\text{-}flat_{Lelu}$= –14.9 ‰. Using these endmembers, IsoError mixing model

results estimated the average percent contribution of mangals to mangrove crabs as 86 % for Utwe, 95% for Okat, and 65% for Lelu (Figure 4).

Scylla serrata diets

Stable isotope data for fauna from mangroves and adjacent reef-flats are summarized in Table 2. Grapsid crabs, including *Metapograpsus latifrons*, Grapsid sp. 1, and *Parasesarma plicatum* stomach contents were depleted in ^{13}C relative to their chelipeds and were consistent with sediment $\delta^{13}C$ values. Based on the range of stable carbon and nitrogen isotope values for *S. serrata* and trophic fractionation of 0-1‰ for ^{13}C and 2.4-3.4 ‰ for ^{15}N, the small crabs *Parasesarma plicatum* and *Metapograpsus latifrons* collected from Lelu and Okat mangroves, plus whelks collected only from Okat, had stable carbon and nitrogen isotopes consistent with *S. serrata* estimated diet (Figure 5). For Utwe, various sediment infauna, including bivalves, oligochaete sp. 2 and sabellid polychaetes, had stable isotope values consistent with inferred food sources for *S. serrata*.

Discussion

Watershed Use

If adult crabs were moving among watersheds, one would expect more isotopic variability and possibly more homogeneous trace metal and cation concentrations in crab

tissues. In contrast, adult *Scylla serrata* stable isotopic compositions increased from Utwe to Okat to Lelu, indicating a discrete isotopic difference among watersheds that was also reflected in crab tissue phosphorus, trace metal and cation concentrations. These results appear to support the first hypothesis, that *muscle stable isotope, trace metal, and cation compositions suggest that adult* Scylla serrata *restrict their movement to within a single watershed.* Mark and recapture results and *Scylla* life histories support these patterns, indicating a high recapture rate for Kosrae (Bonine et al. submitted), with recaptures occurring within 1-2 km from the location of initial capture (Hill 1975; Perrine 1978; Bonine et al. submitted). Other studies indicate that once post-larval crabs return from the sea to the intertidal, only limited interchange occurs with neighboring populations (Macnae 1968; Hill et al. 1982). Crabs may migrate down shore as they grow, and harvesters find adult crabs within mangrove channels and in burrows within mangrove forests, as well as feeding on reef flats at low tide (e.g., Macnae 1968; Hill et al. 1982). Feeding occurs usually at night (cf., Hill 1978, 1980; Nandi and Dev Roy 1992), and crabs can travel an average nightly distance of 200-900 m (Hill 1978). If the neighboring watersheds are separated by unsuitable habitat, e.g., discontinuous non-mangrove or reef-flat, as is the case with Utwe, Lelu, and Okat watersheds, then no exchange is expected between adult populations (Hyland et al. 1984). Stock of adults in an area is therefore most likely dependent on the number of crabs reaching maturity within that same system (cf., Hyland et al. 1984).

Crab tissue trace metal, cation, and phosphorus concentrations among watersheds most likely reflect environmental differences in availability and uptake by crabs that are driven by the composition of source materials and their chemical reactivity in the

mangrove environment. Lelu crabs were enriched in manganese, calcium, and magnesium, whereas Utwe crabs had higher concentrations of zinc, copper, and phosphorus. Salinity can affect the bioavailability and subsequent uptake of trace elements by crabs (Hall and Anderson 1995; Wright 1995; Burke et al. 2003). Inter-site differences in salinity measured at one time during June 2002, however, were not significant, although Utwe was characterized by lower average salinity than Lelu (Table 1). In addition, Fe, Zn, and Cu are abundant in volcanic sediments (e.g., 5-10 % for Fe, 150-250 ppm for Zn and Cu), and can become bioavailable via direct uptake from the surrounding environment and through diet, e.g., enzymatic digestion of sediments and/or sediment associated organisms including infauna and crabs.

Differences among estuaries may also reflect patterns of organic matter source contributions, differentiating mangal from reef-flat/marine sources. In a previous food-web study on Kosrae using stable isotopes, Benstead et al.(submitted) estimated the relative contribution of marine and terrestrial organic matter sources to commercially important fish and crabs. They found that the highest marine contribution to fish and crab diets occurred where there was a restricted reef-flat and a narrow mangrove belt, similar to Lelu. In contrast, mangrove contribution was highest at the extensive mangrove forest site near Utwe. Due to extensive seagrass meadows and mangrove forests, Okat was intermediate in mangrove versus marine contribution (Benstead et al. submitted). Explicit differences in environmental parameters among watersheds help define habitat use by these crabs.

The largest *Scylla* were found in Utwe, with maximum widths at 182 mm corresponding to previous population studies of *Scylla* on Kosrae (maximum carapace

width of 200 mm) (Bonine et al. submitted). Results of size differences among watersheds and between sexes correspond to previous trapping results (Bonine et al. submitted). Both male and female *S. serrata* frequently use burrows for shelter during high daytime temperatures (cf., Hill 1980) and protection during molting and mating (Perrine 1978). Burrow density is strongly correlated with mangrove habitat width and crab population density (Bonine et al. submitted); thus the importance of mangrove habitat as a refuge for these crabs is evident.

Habitat Use

Residency can be considered in a broader view as habitat use, and one important step in evaluating residency was finding appropriate control groups whose isotope values would definitely reflect residency. I selected groups of annelid worms and crabs that remain in mangrove forests or reef-flats for most of their life histories, with stable isotope values assumed to be in equilibrium with their respective habitats. If *Scylla* were to live and feed strictly within mangroves, one would expect this behavior to be reflected in tissue isotope values that centered around the same compositions as the "resident mangrove fauna," e.g., grapsid crabs and infauna, with little isotopic variability. However, stable isotope compositions and mixing model approximations indicated there were watershed-level differences in habitat utilization, and the importance of mangrove habitat varied from site to site. These results supported the second hypothesis: *muscle stable isotopic compositions and mixing model calculations are consistent with* S. serrata's *moving and foraging freely between mangrove and adjacent reef-flat habitats.*

Stable isotope data from inshore and offshore *Scylla* populations in other parts of the world indicate a gradient in $\delta^{13}C$ values from ^{13}C-depleted inshore to ^{13}C-enriched offshore (Thimdee et al. 2001; Rodelli et al. 1984). The isotopic gradients between habitat types appear to concur with Ogden's (1988) description of a "coastal seascape," where multiple habitats make up coastal environments, and each compartment performs different roles and provides a variety of ecosystem services (Benstead et al. submitted).

Scylla serrata Diet

Previous diet studies of *Scylla* indicate that grapsid crabs and mollusks are a major component of *S. serrata* gut contents, whereas shrimp and fish are less important, possibly because they are fast moving prey (Hill 1976). *Scylla serrata* may feed on grapsids because of their larger mass and higher energy content than other prey organisms (Hill 1979). In addition, *S. serrata* food-web studies using stable isotopes indicate that food sources may change as the crab matures from juvenile to adult life stages. For example, Thimdee et al., (2001) found that small *S. serrata* are omnivorous, mostly feeding on small crabs and plant materials, while medium and large sizes are primarily carnivores, obtaining their carbon sources from slow moving invertebrates (grapsid crabs, shrimps, mollusks, worms and small fish). Their conclusions were based on stable isotopic similarities between *S. serrata* and potential food sources, and on an observed increase in mean $\delta^{15}N$ with increasing carapace width. However, medium and large size groups were not significantly different (100-139 mm vs. 140-179 mm). In the present study, there is no significant relationship between *S. serrata* size and normalized

$\delta^{15}N$ values, indicating that the collections were of mature crabs, ranging from 115-182 mm in size, feeding at similar trophic levels.

This stable isotope study of *S. serrata* diet appears to confirm the dietary importance of benthic invertebrates, including grapsid crabs and sediment-associated annelids. Additional prey items may include mangrove clams, e.g., *Anodontia endentula* (Figure 5, Table 2) (Perrine 1978), generally restricted to the Utwe watershed. Clams had low $\delta^{34}S$ (-9.3 ‰) and $\delta^{13}C$ (-33.3 ‰) values. *Scylla serrata* in Utwe watershed may feed on a mixed diet of isotopically depleted, yet abundant clams and isotopically enriched reef-flat fauna, resulting in intermediate crab-tissue isotope values (Figure 5).

Unanswered Questions

Several aspects of *S. serrata* life cycle remain unknown, including return migrations of females to the coast and the incidence of secondary spawnings by females (Heasman et al. 1985). The present study was the first to collect gravid *S. serrata* females in mangrove communities; egg-bearing females are not often collected inshore (Perrine 1978; Heasman et al. 1985). Three females were collected on the transition to a new moon, and two were collected during a new moon. These time periods follow the described trends in female migration following the lunar cycle, often peaking during the last quarter until just after the new moon (Perrine 1978; Heasman et al. 1985). Collection of ovigerous (gravid) females is an indication of migration out of the estuary into the open sea (Onyango 2002). Few gravid females were collected in this study, so generalizations about migration trends are tentative. Continued stable isotope and population studies on females will help define their feeding and migratory patterns.

Offshore spawning is an important mechanism for aiding larval dispersal (Ong 1966; Prasad and Neelakantan 1989; Hill 1994). However, crab larval supply dynamics among Kosraean watersheds remain a mystery, so it is unknown whether depleting the female population in one watershed will have a corresponding impact on the adjacent system. It would be useful to conduct genetic population studies in order to elucidate source populations to these watersheds. For instance, testing with mitochondrial DNA may evaluate whether female spawning is localized on certain reef patches.

Conclusions

On Kosrae, adult *Scylla serrata* generally move over small (1-2 km) spatial scales, primarily between mangrove forests and reef-flats, with little exchange occurring among separated watersheds. Sediment and tree-associated grapsid crabs and benthic infauna serve as important food sources for the crabs, and crab diets are restricted to fauna from mangrove habitats. Because *Scylla serrata* fishery sustainability on Kosrae appears to depend upon isolated populations residing in different watersheds, with habitats that differ ecologically and in harvesting pressure (Bonine et al. submitted), crabs and their habitat must be managed on a local scale to conserve burrow availability for mating and foraging *Scylla serrata*, and to protect microhabitats supporting crab diets.

Table 1. Temperature, salinity, and dissolved oxygen (DO) data collected from surface waters at each of the watersheds near crab trap locations for the duration of the trapping period. .

	Temperature (°C)	Salinity (‰)	DO (mg/L)
Okat	28.7 ± 0.5	29.6 ± 2.0	5.35 ± 0.25
Lelu	28.8 ± 0.4	30.1 ± 1.3	3.91 ± 0.56
Utwe	31.8 ± 0.4	26.8 ± 0.9	4.48 ± 0.59

Table 2. Stable isotopic values for primary producers, sediment, and fauna collected from mangroves and reefflats in Okat, Utwe, and Lelu watersheds. Data are mean δ values (± 95% confidence limits). * data are from Benstead et al., submitted. BMA-sunny samples were collected from sun exposed mangrove sediments and shade samples were collected in the shade. Numbers in parentheses correspond to sample size. Ephiphyte/epiflora data reflect either acetone extracted samples or whole samples.

	Utwe		Okat		Lelu	
	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
MANGROVE LEAVES						
Green (4)	-34.1 ± 1.0	1.3 ± 0.5	-35.6 ± 1.3	3.6 ± 0.8	-37.3 ± 0.2	2.9 ± 1.4
Brown (4)	-32.1 ± 0.5	2.9 ± 0.0	-34.1 ± 0.6	2.1 ± 0.8	-33.1 ± 0.7	1.9 ± 0.7
POM	-30.0 ± 0.6		-23.3 ± 0.9		-23.5	
BMA-acetone extracts (12)						
Interior-Sunny			-30.4 ± 0.1			
Interior-shade	-30.7 ± 0.3		-30.1 ± 0.5		-30.5 ± 0.2	
Bank	-30.4 ± 0.6	2.7 ± 1.6			-30.0 ± 0.1	
Root Epiphytes-whole (4)	-30.5 ± 0.3	1.7 ± 0.7				
Root Epiphytes-acetone extract (4)	-29.9 ± 1.8					
Rhizophora epiflora-whole (1)			-27.4	1.3		
Rhizophora epiflora-acetone extract (1)			-29.0			
Sonneratia epiflora-whole (1)			-27.0			
Sonneratia epiflora-acetone extract (1)			-27.1	2.2		
SEDIMENTS						
interior (4-5)	-28.1 ± 0.4	1.6 ± 0.2	-28.3 ± 0.1	2.4 ± 0.1	-27.9 ± 0.2	1.9 ± 0.5
bank (4-5)	-27.9 ± 0.1	1.9 ± 0.4			-28.0 ± 0.1	2.2 ± 0.5
MANGROVE FAUNA						
Molluscs						
*Anodontia edentula**	-33.0 ± 0.2	3.8 ± 0.3				
Bivalves (1)	-25.0	3.5	-26.6	2.3	-27.4	3.4
Whelks (1)			-23.0	4.0		
Crustaceans						
Grapsid crabs						
Metapograpsus latifrons (3)	-23.6 ± 2.2	2.6 ± 0.9	-26.2 ± 0.1	3.7 ± 0.5	-24.5 ± 0.9	3.9 ± 0.8
Metapograpsus latifrons -sc *(2-3)*	-27.4 ± 1.7	2.0 ± 0.7	-28.7 ± 0.5	4.0 ± 0.5	-28.7 ± 1.0	2.2 ± 0.7
Other tree crabs (2)	-19.7 ± 2.2	3.7 ± 0.4				
Other tree crabs-sc (2)	-24.2 ± 0.1	2.5 ± 1.2				
Parasesarma plicatum (2-5)	-25.0 ± 0.5	1.9 ± 0.1	-26.0 ± 0.3	3.8 ± 0.4	-23.9 ± 0.4	3.7 ± 0.7
Parasesarma plicatum -sc (2-5)	-29.1 ± 0.2	1.4 ± 0.6	-30.1 ± 1.6	3.3 ± 0.3	-29.2 ± 0.2	2.4 ± 0.6
Other crabs						
Fiddler Crab (1)			-22.3	3.3		
Scylla serrata- muscle (13-27)	-26.2 ± 0.7	5.7 ± 0.5	-24.7 ± 0.5	7.4 ± 0.4	-21.8 ± 0.6	7.8 ± 0.3
Scylla serrata- chitin + muscle					-22.2 ± 1.2	6.7 ± 0.6
Scylla serrata- chitin					-23.6 ± 1.4	3.2 ± 0.8
Fish						
Black snapper (2-9)					-20.9 ± 2.7	9.3 ± 0.9
Mudfish (2)					-23.9 ± 1.6	7.9 ± 1.0

Table 2. Cont.	Utwe		Okat		Lelu	
	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
Sediment infauna						
Nematodes (3-9)	-28.3 ± 1.7	5.8 ± 0.5	-26.5 ± 0.8	6.4 ± 0.3	-29.6 ± 0.4	5.7 ± 0.3
Oligochaetes						
sp. 1 (2-3)	-27.4 ± 0.1	1.3 ± 0.5	-26.7 ± 0.3	1.4 ± 0.7		
sp. 2 (3)	-27.5 ± 0.3	1.3 ± 0.3	-26.4 ± 0.8	2.7 ± 0.4	-27.4 ± 1.2	1.2 ± 0.9
Community (1-2)	-27.1	-2.5	-26.1 ± 0.4	1.4 ± 0.2	-28.6	-0.6
Capitellids (3)	-27.1 ± 0.4	0.4 ± 0.2	-26.5 ± 0.5	2.4 ± 0.5	-28.6 ± 0.9	0.1 ± 0.7
Sabellids (2-4)	-27.3 ± 0.2	2.1 ± 0.9	-25.3 ± 0.2	2.5 ± 0.8	-27.0 ± 0.3	2.4 ± 0.2
Syllids						
sp. 2 (2)	-27.5 ± 0.6	2.1 ± 0.9			-26.6 ± 0.9	3.1 ± 0.6
Community (1)	-27.2	2.5				
REEF-FLAT FAUNA						
Crustaceans						
Scylla serrata (1)			-24.6	7.4		
Thalamita crenata (4)	-22.8 ± 0.9	3.8 ± 0.5			-16.4 ± 1.2	6.9 ± 0.8
Sediment infauna						
Nematodes (3)	-21.0 ± 0.9	4.9 ± 1.4	-14.8 ± 1.0	4.0 ± 0.2	-14.4 ± 1.8	3.5 ± 0.2
Oligochaetes						
sp. 2 (2)	-22.4 ± 1.3	3.8 ± 0.7				
Capitellids	-22.2 ± 0.2	4.8 ± 0.3	-15.7 ± 1.9	3.7 ± 1.2		
Syllids						
sp. 1 (2-4)	-23.1 ± 0.4	6.2 ± 0.3	-12.6 ± 1.6	2.5 ± 2.0	-14.6 ± 0.6	5.9 ± 0.4
sp. 2 (2-3)	-20.8 ± 1.0	4.9 ± 0.9	-14.8 ± 0.6	3.0 ± 0.8	-15.4 ± 0.7	3.1 ± 2.1
sp. 3 (3)			-13.9 ± 1.3	2.5 ± 0.6		
Community (1-3)	-19.5	5.2			-13.7 ± 0.2	2.8 ± 0.6
Sabellids (4)			-17.6 ± 1.4	1.7 ± 0.8		

Table 3. Mean *Scylla serrata* weights and carapace widths from each of the three watersheds. Errors are standard errors.

	N	Weight (g)	Width (mm)
Utwe	13	833.8± 56.0	169.8± 2.9
Okat	27	738.7± 49.9	151.1± 2.6
Lelu	26	509.8± 46.3	140.0± 3.5

Table 4. Structure matrix containing correlation coefficient of each predicted variable with discriminant function.

Variable	Function 1	Function 2
$\delta^{13}C$	0.773	0.103
$\delta^{15}N$	0.656	-0.350
$\delta^{34}S$	0.627	-0.022
Mn	0.212	0.076
Zn	-0.164	0.162
Cu	-0.243	0.578
% K	0.151	0.324
% Ca	0.182	-0.319
% Mg	0.182	-0.318
% P	-0.170	0.299

Table 5. Stable isotope, cations, trace metals, and phosphorus concentrations from *Scylla serrata* muscle tissue from each watershed.

		Utwe	Okat	Lelu
$\delta^{13}C$	‰	-26.2± 0.7	-24.7± 0.4	-21.8± 0.6
$\delta^{34}S$		-3.8± 2.4	0.7± 1.4	5.8± 1.1
$\delta^{15}N$		5.7± 0.5	7.4± 0.5	7.8± 0.3
P	µmoles/g	322.3± 22.5	284.6± 9.1	303.6± 12.6
K		404.2± 54.5	350.8± 25.1	428.0± 27.9
Ca		75.4± 32.0	168.9± 36.4	192.1± 18.7
Mg		85.4± 10.4	111.7± 8.1	95.8± 7.1
Na		604.0± 64.7	748.6± 87.1	556.8± 84.2
Mn		0.05± 0.02	0.06± 0.02	0.13± 0.02
Fe		0.85± 0.21	1.32± 0.23	1.13± 0.88
Cu		0.76± 0.16	0.22± 0.07	1.13± 0.11
Zn		5.13± 0.35	4.43± 0.46	4.99± 0.38
B		0.62± 0.24	1.54± 0.80	0.73± 0.51

Table 6. Linear regression results for crab size (weight and width) versus stable isotope data.

		$\delta^{15}N$		$\delta^{13}C$		$\delta^{34}S$	
		r^2	p	r^2	p	r^2	p
All sites before correction	weight	0.051	0.069	0.113	0.006	0.15	0.001
	width	0.069	0.034	0.109	0.002	0.109	0.004
Utwe	weight	0.194	0.132	0.143	0.202	0.326	0.041
	width	0.012	0.717	0.04	0.512	0.02	0.645
Okat	weight	0	0.932	0.042	0.316	0.124	0.078
	width	0.027	0.421	0.004	0.760	0.066	0.205
Lelu	weight	0.362	0.001	0.224	0.015	0.427	0.001
	width	0.411	0.001	0.145	0.045	0.388	0.001

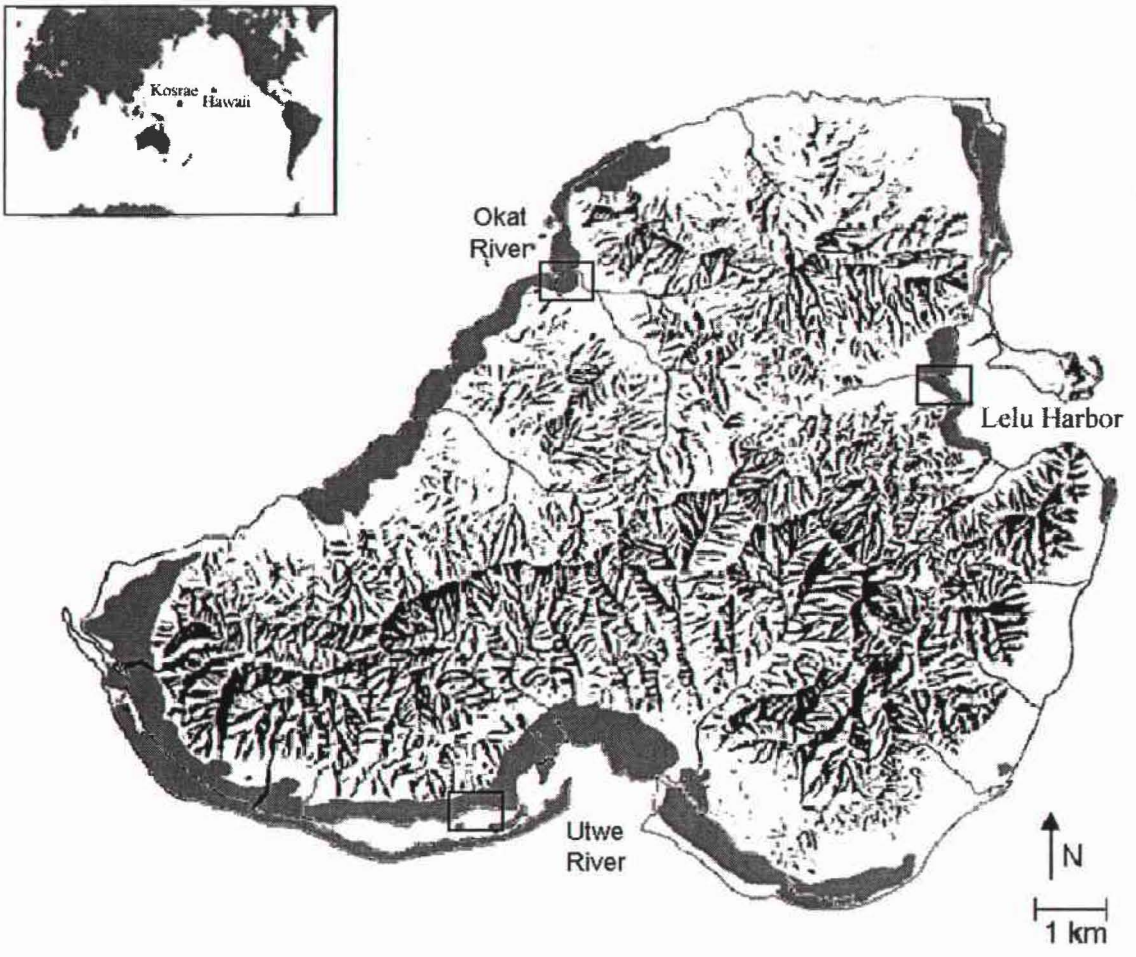

Figure 1. Location of sampling stations in three watersheds on Kosrae, Federated States of Micronesia. Mangrove areal coverage delineated in gray.

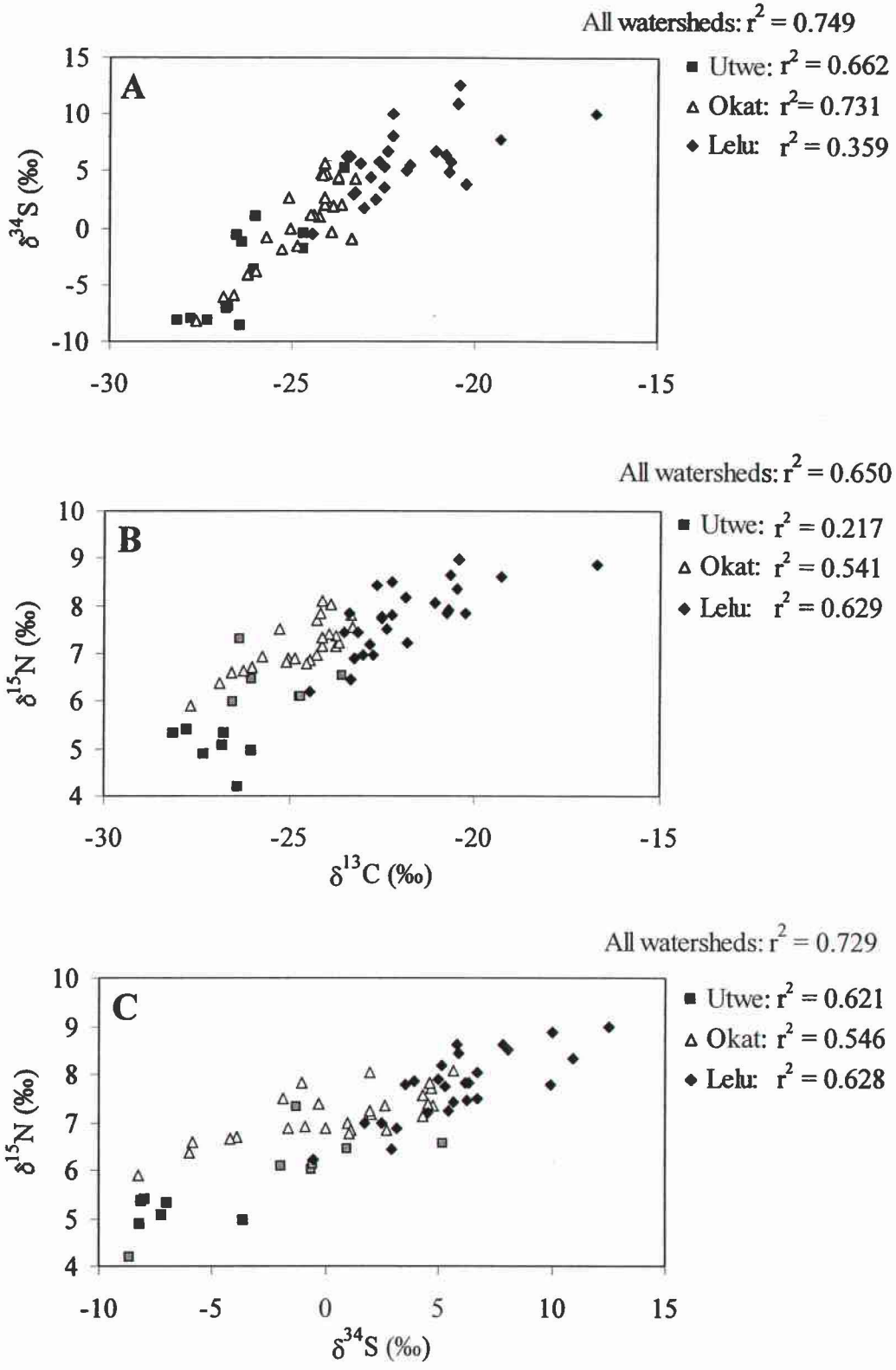

Figure 2. $\delta^{13}C$ versus (A) $\delta^{34}S$ and (B) $\delta^{15}N$, and $\delta^{34}S$ versus $\delta^{15}N$ (C) for *S. serrata* muscle tissue from all crabs analyzed in each watershed. r^2 values are significant at $p<0.001$.

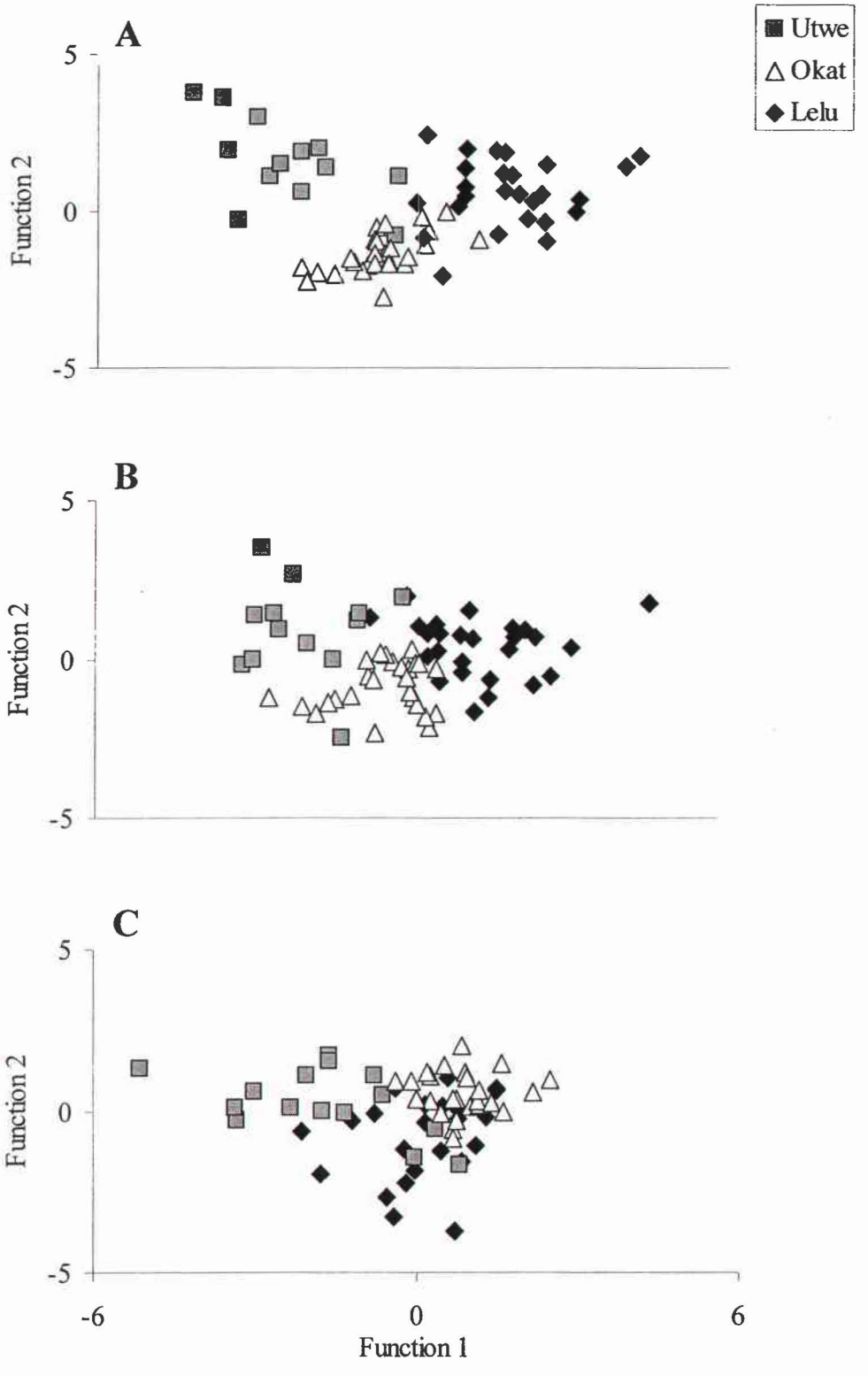

Figure 3. Results from the discriminant analysis of crab muscle tissue analysis for (A) stable isotopes, cations, trace metals, and phosphorus, (B) stable isotopes only, and (C) cations, trace metals, and phosphorus only.

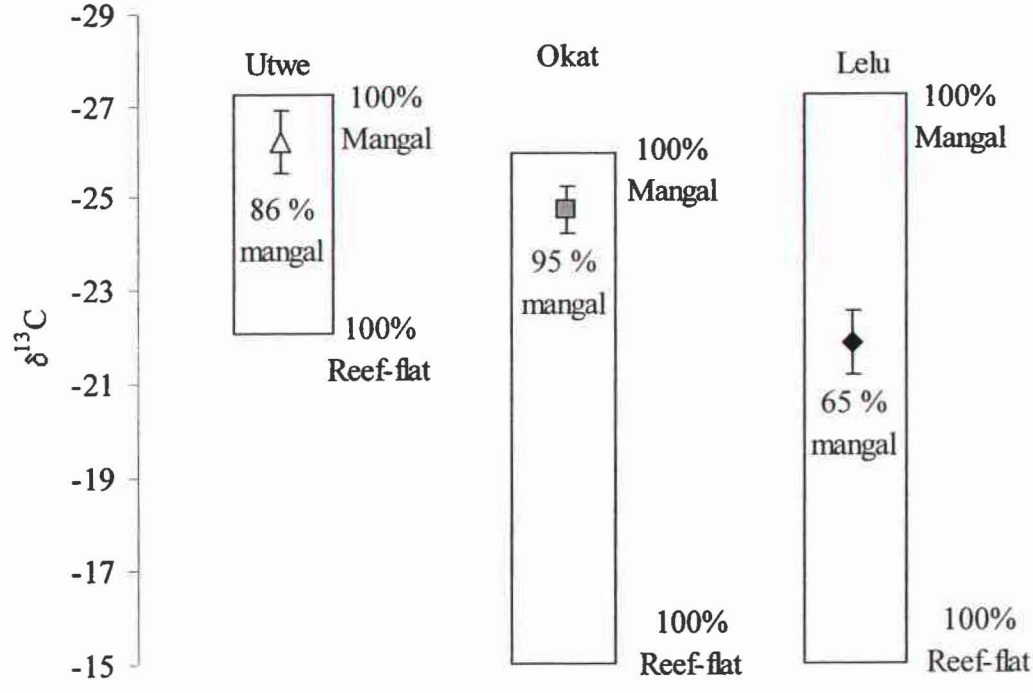

Figure 4. Results from IsoError analysis of *S. serrata* using mangal and reef-flat infauna and small crab $\delta^{13}C$ isotope values for habitat endmembers (see text for endmember values).

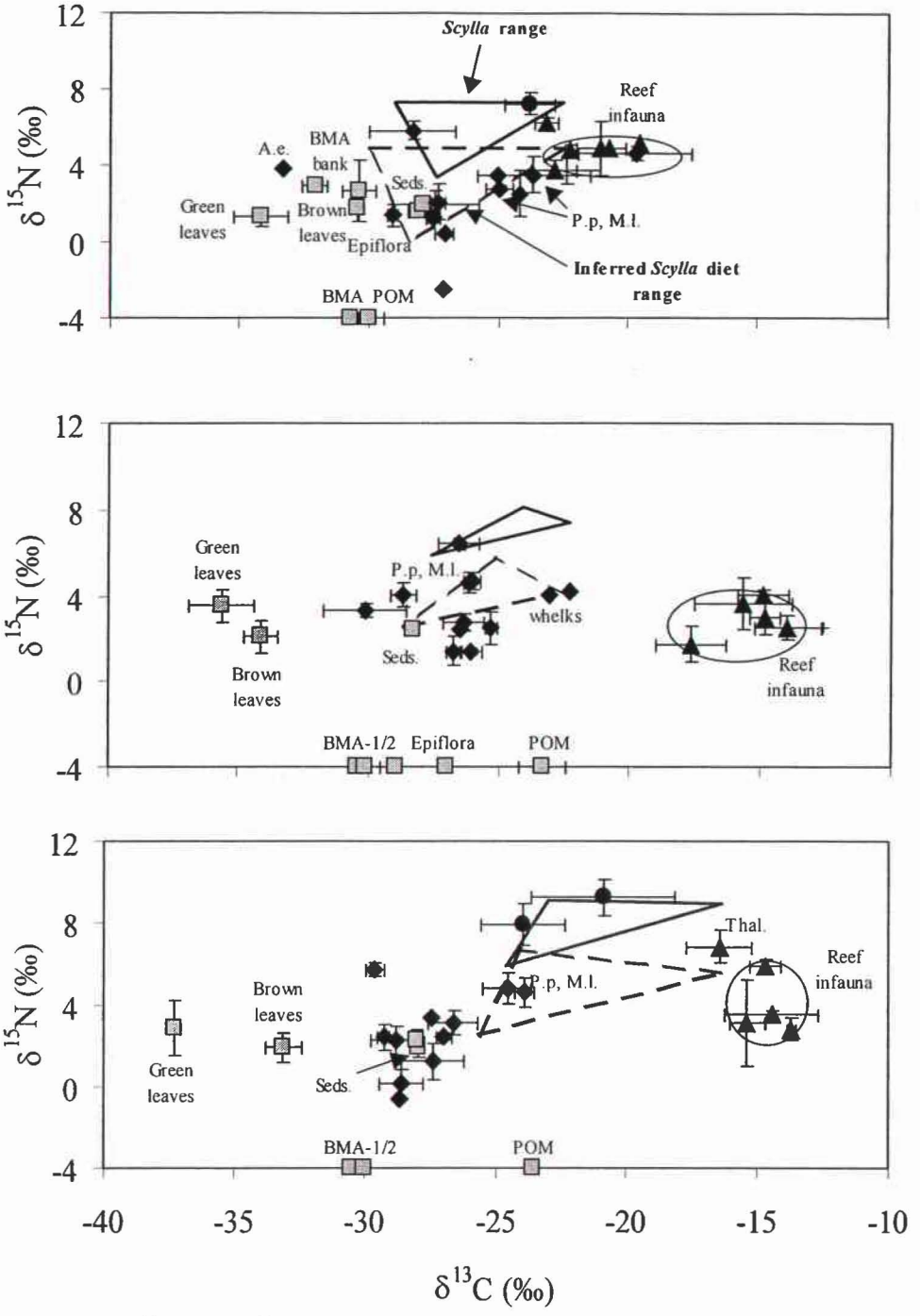

Figure 5. $\delta^{15}N$ and $\delta^{13}C$ of different primary producers (grey squares), and consumers including mangrove fauna (solid diamonds), fish (solid circles), reef fauna (solid triangles and *Scylla serrata* (range defined by solid-line triangle) for (A) Utwe, (B) Okat, (C) Lelu watersheds. Dashed triangle represents the inferred range of diet isotope values for *Scylla* estimated after subtracting trophic fractionations of 0-1 ‰ for ^{13}C and 2.4-3.4 ‰ for ^{15}N from measured *Scylla* values. P.p.= *Parasesarma plicatum*, M.l. = *Metapograpsus latifrons*. A.e. = *Anodondia edentula*, Thal. = *Thalamita crenata*. Data from BMA and POM are for $\delta^{13}C$ values, only.

Appendix A. Raw cation, phosphorus, and trace metal data from crab muscle tissues. Data are in μmol/g dry weight.

Sample ID	Site	P	K	Ca	Mg	Na	Mn	Fe	Cu	Zn	B
Je02-L58a	Lelu	303.6	428.0	192.1	95.8	556.8	0.13	1.13	1.13	4.99	0.73
Je02-L59a	Lelu	329.0	374.0	140.2	83.8	727.5	0.17	1.28	0.55	5.15	0.31
Je02-L60a	Lelu	330.8	388.3	126.9	86.0	510.8	0.18	2.41	0.98	4.88	0.13
Je02-L61a	Lelu	351.4	385.4	144.2	99.1	579.8	0.21	3.15	0.67	4.94	0.54
Je02-L62a	Lelu	351.0	416.5	163.2	88.6	698.1	0.06	1.40	0.49	5.10	0.30
Je02-L75a	Lelu	304.7	489.6	294.7	168.2	1423.3	0.12	2.03	0.28	3.38	3.95
Je02-L76a	Lelu	296.4	348.8	190.0	126.8	984.0	0.06	1.00	0.30	4.07	2.64
Je02-L77a	Lelu	272.8	421.2	90.4	91.9	772.9	0.02	0.52	0.13	5.13	0.66
Je02-L78a	Lelu	289.3	490.9	173.1	124.3	640.7	0.03	0.96	0.21	3.75	2.26
Je02-L79a	Lelu	223.1	545.3	150.6	105.8	473.6	0.12	12.67	0.17	2.97	3.64
Je02-L80a	Lelu	286.1	495.8	165.8	107.9	795.0	0.08	1.80	0.21	4.63	2.25
Je02-L81a	Lelu	257.9	449.7	145.0	96.4	595.3	0.06	1.38	0.70	4.34	1.63
Je02-L82a	Lelu	312.7	495.5	145.1	106.5	658.8	0.18	1.71	0.53	4.42	0.00
Je02-L83a	Lelu	288.1	556.7	169.0	108.5	774.8	0.03	1.10	0.24	4.04	0.94
Je02-L84a	Lelu	264.3	499.8	110.6	101.8	653.0	0.05	2.59	0.00	4.28	0.31
Je02-L97a	Lelu	345.7	310.0	198.3	109.7	574.1	0.08	1.61	0.07	5.23	2.66
Je02-L98a	Lelu	268.6	301.8	233.4	129.1	362.6	0.06	0.80	0.07	2.20	4.20
Je02-L99a	Lelu	247.4	356.3	146.2	91.8	471.6	0.07	2.35	0.17	5.06	0.74
Je02-L100a	Lelu	258.4	376.5	224.7	120.5	602.5	0.07	0.77	0.27	2.75	2.35
Je02-L101a	Lelu	297.5	383.0	99.6	102.5	699.2	0.05	1.24	0.28	4.99	0.87
Je02-L102a	Lelu	260.6	348.8	79.8	82.8	521.8	0.04	0.67	0.18	4.46	0.00
Je02-L103a	Lelu	264.3	389.6	155.8	123.1	824.8	0.04	1.07	0.10	2.83	3.11
Je02-L104a	Lelu	289.9	387.8	107.7	95.9	639.0	0.03	0.85	0.45	5.24	0.17
Je02-L105a	Lelu	263.4	544.8	182.0	123.5	1119.4	0.06	1.18	0.19	2.11	3.12
Je02-L106a	Lelu	280.6	461.7	90.7	104.8	711.1	0.05	0.86	0.72	5.37	0.95
Je02-L107a	Lelu	304.0	479.7	153.3	102.9	828.4	0.09	2.25	0.08	4.67	1.59
Je02-L64a	Utwe	333.1	418.7	27.1	67.5	417.7	0.04	1.01	0.72	5.42	0.05
Je02-L65a	Utwe	367.5	480.3	37.8	76.4	597.7	0.06	0.68	0.94	5.40	0.14
Je02-L66a	Utwe	345.3	467.0	38.0	80.2	600.5	0.02	0.68	0.88	5.72	0.39
Je02-L67a	Utwe	346.5	469.0	39.0	76.0	659.1	0.03	0.63	0.97	5.28	0.19
Je02-L68a	Utwe	371.8	435.4	46.8	81.1	624.7	0.03	0.72	1.51	5.37	0.73
Je02-L69a	Utwe	381.1	503.7	64.4	93.1	774.9	0.03	0.80	0.50	6.00	0.80
Je02-L74a	Utwe	229.0	608.6	257.1	145.2	871.3	0.08	0.83	0.52	3.76	0.64
Je02-L129a	Utwe	302.2	343.9	80.4	82.2	627.8	0.03	0.90	0.45	4.68	0.78
Je02-L130a	Utwe	296.6	281.8	91.1	81.9	527.2	0.15	1.97	0.51	5.94	1.77
Je02-L131a	Utwe	291.3	315.5	56.7	76.8	512.9	0.03	1.21	0.83	4.34	0.80

Appendix A. cont.

Sample ID	Site	P	K	Ca	Mg	Na	Mn	Fe	Cu	Zn	B
Je02-L132a	Utwe	308.5	296.9	98.9	88.3	596.9	0.04	0.45	0.79	4.66	0.47
Je02-L133a	Utwe	306.9	302.5	71.9	77.1	487.1	0.07	0.75	0.54	5.18	0.95
Je02-L134a	Utwe	310.1	331.0	70.5	83.9	554.7	0.02	0.46	0.70	4.94	0.40
Je02-L85a	Okat	265.1	308.5	171.5	108.5	650.5	0.03	1.18	0.12	5.27	0.46
Je02-L86a	Okat	264.6	376.9	104.8	87.6	799.9	0.02	0.60	0.34	5.91	0.00
Je02-L87a	Okat	315.1	329.0	133.2	100.3	528.4	0.08	0.40	0.56	5.51	0.02
Je02-L88a	Okat	294.4	442.2	159.2	110.7	956.7	0.04	1.32	0.27	4.84	0.69
Je02-L89a	Okat	303.7	421.8	184.5	126.0	1075.5	0.03	1.86	0.00	3.42	1.17
Je02-L93a	Okat	291.1	334.9	165.2	103.3	531.9	0.08	1.89	0.14	4.54	0.58
Je02-L94a	Okat	264.3	416.6	203.0	121.0	655.9	0.03	0.85	0.18	2.46	1.01
Je02-L95a	Okat	274.6	384.7	401.5	143.0	566.4	0.15	1.67	0.67	4.56	0.80
Je02-L96a	Okat	280.0	379.8	244.9	144.2	963.0	0.10	0.78	0.13	3.50	1.06
Je02-L108a	Okat	285.3	328.9	91.7	92.2	550.7	0.04	1.31	0.08	4.25	0.26
Je02-L109a	Okat	278.9	352.5	92.8	93.4	765.2	0.04	0.95	0.40	5.26	1.54
Je02-L110a	Okat	252.0	382.9	247.0	140.2	1059.3	0.06	1.85	0.00	3.94	0.45
Je02-L115a	Okat	270.5	380.2	141.9	108.7	1014.0	0.06	1.04	0.27	5.02	2.20
Je02-L116a	Okat	287.7	430.9	120.2	95.9	732.9	0.04	1.21	0.02	4.02	1.14
Je02-L117a	Okat	262.5	365.7	66.4	82.3	705.8	0.03	1.45	0.05	4.36	0.48
Je02-L118a	Okat	315.7	272.6	298.3	139.0	372.3	0.09	1.51	0.04	0.53	3.47
Je02-L119a	Okat	279.0	303.0	192.1	115.1	520.3	0.03	0.42	0.17	3.09	2.51
Je02-L120a	Okat	263.5	314.5	121.7	94.5	552.3	0.03	1.21	0.19	4.96	0.73
Je02-L121a	Okat	270.3	395.9	123.9	105.6	913.3	0.03	1.09	0.34	4.26	1.17
Je02-L122a	Okat	236.9	528.7	144.0	103.5	474.6	0.00	2.08	0.00	3.59	0.00
Je02-L123a	Okat	320.2	284.0	112.8	90.2	638.5	0.05	0.81	0.30	5.97	0.00
Je02-L124a	Okat	315.9	310.3	455.3	141.4	756.6	0.15	1.75	0.33	4.84	4.37
Je02-L125a	Okat	344.7	309.4	78.2	102.0	857.2	0.03	0.86	0.16	4.78	0.84
Je02-L126a	Okat	276.2	253.2	239.0	149.6	1404.4	0.14	2.76	0.52	3.85	10.64
Je02-L127a	Okat	299.1	263.1	52.1	87.1	654.3	0.03	1.11	0.11	4.66	1.36
Je02-L128a	Okat	288.9	249.8	73.7	87.3	624.2	0.02	0.90	0.18	5.72	1.38

Appendix B. Scylla serrata carapace width, weight, sex, and stable carbon, nitrogen, and sulfur isotope values. Female =1, male =2

Sample ID	Site	Width (mm)	Weight (g)	sex	$\delta^{15}N$	$\delta^{13}C$	$\delta^{34}S$
Je02-L58a	Lelu	116	260.8	1	6.9	-23.3	3.2
Je02-L59a	Lelu	159	456.3	2	8.5	-22.2	8.1
Je02-L60a	Lelu	127	318	2	7.7	-22.5	5.3
Je02-L61a	Lelu	122	239	1	8.1	-21.1	6.7
Je02-L62a	Lelu	157	804	2	7.9	-20.3	3.9
Je02-L75a	Lelu	179	910.5	2	9.0	-20.4	12.5
Je02-L76a	Lelu	158	855.7	2	7.8	-23.4	6.2
Je02-L77a	Lelu	155	860.9	2	8.3	-20.5	10.9
Je02-L78a	Lelu	120	268	1	7.2	-22.8	4.5
Je02-L79a	Lelu	109	159	2	6.2	-24.4	-0.5
Je02-L80a	Lelu	130	336.8	2	7.4	-23.5	6.2
Je02-L81a	Lelu	158	582	1	7.4	-23.1	5.7
Je02-L82a	Lelu	130	300.6	2	8.6	-19.3	7.8
Je02-L83a	Lelu	149	733.1	2	8.6	-20.7	5.8
Je02-L84a	Lelu	129	451.4	2	8.2	-21.9	5.1
Je02-L97a	Lelu	152	515.1	1	8.4	-22.6	5.9
Je02-L98a	Lelu	138	404.3	1	7.9	-20.7	4.9
Je02-L99a	Lelu	160	528	1	7.8	-20.8	6.4
Je02-L100a	Lelu	113	302.3	1	7.2	-21.8	5.5
Je02-L101a	Lelu	140	399.1	2	7.0	-23.0	1.8
Je02-L102a	Lelu	118	286.4	2	7.0	-22.7	2.5
Je02-L103a	Lelu	145	590.4	2	7.8	-22.5	3.6
Je02-L104a	Lelu	154	897.5	2	8.9	-16.7	10.0
Je02-L105a	Lelu	134	340.2	2	6.4	-23.3	2.9
Je02-L106a	Lelu	149	819.5	2	7.8	-22.2	10.0
Je02-L107a	Lelu	139	637.1	2	7.5	-22.4	6.7
Je02-L64a	Utwe	149	586	1	6.0	-26.5	-0.6
Je02-L65a	Utwe	171	981.1	2	5.1	-26.8	-7.2
Je02-L66a	Utwe	173	1228	2	4.2	-26.4	-8.7
Je02-L67a	Utwe	168	867.4	2	5.3	-28.1	-8.1
Je02-L68a	Utwe	171	811	1	4.9	-27.3	-8.2
Je02-L69a	Utwe	176	607.5	1	6.1	-24.7	-1.9
Je02-L74a	Utwe	175	940.4	2	7.3	-26.3	-1.3
Je02-L129a	Utwe	182	1140	2	5.4	-27.7	-8.0

Appendix B. cont.

Sample ID	Site	Width (mm)	Weight (g)	sex	$\delta^{15}N$	$\delta^{13}C$	$\delta^{34}S$
Je02-L130a	Utwe	180	848	1	6.5	-23.6	5.2
Je02-L131a	Utwe	163	825	2	5.3	-26.7	-7.0
Je02-L132a	Utwe	149	589	2	6.5	-26.0	1.0
Je02-L133a	Utwe	175	703	1	5.0	-26.0	-3.6
Je02-L134a	Utwe	175	713	2	6.1	-24.7	-0.5
Je02-L85a	Okat	155	837.8	2	6.9	-25.0	0.0
Je02-L86a	Okat	178	1242.3	2	7.8	-23.3	-1.0
Je02-L87a	Okat	132	413.2	2	7.7	-24.2	4.7
Je02-L88a	Okat	155	895.6	2	7.5	-25.3	-1.9
Je02-L89a	Okat	154	826.6	2	6.4	-26.9	-6.0
Je02-L93a	Okat	151	830	2	6.8	-25.1	2.7
Je02-L94a	Okat	153	825.1	2	6.6	-26.6	-5.9
Je02-L95a	Okat	139	526.4	2	7.0	-24.3	1.0
Je02-L96a	Okat	149	680.1	2	7.3	-24.1	4.8
Je02-L108a	Okat	149	600	2	6.9	-24.8	-1.6
Je02-L109a	Okat	171	1114	2	8.0	-23.9	1.9
Je02-L110a	Okat	151	734	2	6.8	-24.4	1.1
Je02-L115a	Okat	156	975	2	7.6	-23.3	4.3
Je02-L116a	Okat	151	831	2	6.7	-26.0	-3.9
Je02-L117a	Okat	155	886	2	5.9	-27.6	-8.3
Je02-L118a	Okat	115	241	2	7.1	-23.7	4.3
Je02-L119a	Okat	129	372	2	6.9	-25.7	-0.9
Je02-L120a	Okat	156	565	1	7.2	-24.1	2.1
Je02-L121a	Okat	150	680	2	7.2	-23.7	2.0
Je02-L122a	Okat	130	371	1	6.8	-24.5	1.1
Je02-L123a	Okat	158	692	2	8.1	-24.1	5.6
Je02-L124a	Okat	151	670	2	7.8	-24.1	4.6
Je02-L125a	Okat	152	739	2	7.4	-23.7	4.5
Je02-L126a	Okat	177	1341	2	6.6	-26.2	-4.2
Je02-L127a	Okat	150	421	2	7.4	-23.9	-0.3
Je02-L128a	Okat	160	780	2	7.3	-24.1	2.6

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CHAPTER 5. LITTER-FALL DYNAMICS IN NATIVE AND INTRODUCED MANGROVE FORESTS

Abstract

Mangroves are among the most productive coastal ecosystems in the world and can be significant sources of organic matter to coastal waters. The fate of mangrove litter was examined in introduced and native mangrove forests in Hawaii and Puerto Rico, respectively. Specifically, litter production, standing stock, turnover, and leaf decomposition were quantified in two mangrove forests. Litter production was higher in introduced mangroves, but leaf standing stock was greater in the native forests. In addition, leaf residence times were shorter in the introduced mangrove community in Hawaii compared to the native forest. These results suggest that mangroves in Hawaii export a greater proportion of litter relative to native forests. Standing stock results, sediment organic carbon, and the lack of leaf consumption via crabs all indicate that little mangrove carbon is retained within the introduced mangrove forest.

Introduction

Mangrove ecosystems are among the most productive communities of the world, with their global net primary production estimated at 1.1×10^{15} g C yr^{-1} (Duarte and Cebrian 1996). On average, 90% of the biomass produced in mangrove forests falls off the trees, and is either stored in the sediments, decomposed, or exported to adjacent

ecosystems (Duarte and Cebrian 1996). The fluctuation in leaf litter supply and retention in a system, including production, decomposition, and export, can have an impact on the secondary productivity and biogeochemistry of coastal ecosystems both inside and outside mangroves (Twilley 1988, 1995; Alongi et al. 1992; Robertson et al. 1992).

Mangroves were introduced to the Hawaiian Islands in 1902 and spread naturally to all of the main islands, leading to abundant populations of the red mangrove, *Rhizophora mangle*, along low energy coastlines. One aspect about mangrove communities in Hawaii that remains unknown is their productivity and potential export of mangrove leaf material to adjacent systems. In Hawaii, mangrove stands are likely to outwell unusually large amounts of detritus for two reasons: Hawaiian mangroves largely lack natural enemies (e.g., leaf grazers and propagule predators) that can limit mangrove recruitment and growth; Hawaiian forests thus can attain unusually high rates of productivity (Yap 1998; Cox and Allen 1999; Steele et al. 1999). Secondly, Hawaiian mangrove forests apparently also lack the leaf-eating crabs (Coles et al. 1999) that bury and recycle a large proportion of the leaf fall (up to 79%) within Old and New World mangrove forests (Robertson and Alongi 1992; Twilley et al. 1997). Therefore, a particularly large (but unknown) amount of litter fall is likely to be available for tidal export from Hawaiian mangrove habitats. Few studies exist on the degradation of mangrove litter (Steinke et al. 1983; Robertson 1988; Chale 1993; Mackey and Smail 1996; Twilley et al. 1997) and none have quantified the decomposition of leaves from introduced mangroves in Hawaii. Rates of decomposition can depend on leaching of water-soluble substances, water temperature, microbial action, and breakdown by macroinvertebrates (Crawford and Rosenberg 1984; Chale 1993; Twilley et al. 1997).

Therefore, conceptual models of litter dynamics in mangrove environments are useful for understanding the function of mangroves in coastal regions.

In the present study, litter production, standing stock, leaf turnover, and leaf decomposition were evaluated in introduced and native mangroves in Hawaii and Puerto Rico, respectively, in order to test the following hypothesis:

A greater proportion of mangrove litterfall is exported from introduced mangroves than from native mangroves.

Site descriptions

Samples were collected in mature *Rhizophora mangle* communities located in Kaneohe Bay, Oahu, Hawaii (21° 27' 42" N, 157° 50' 29" W) and Jobos Bay, Puerto Rico (17° 57' 40" N, 66° 13' 05" W) (Figure 1). Kaneohe Bay was colonized by *R. mangle* in ~ 1930 and has some of the largest mangrove stands on Oahu. The monospecific mangrove stand sampled in Kaneohe Bay, Oahu, contained ~ .06 km^2 of *Rhizophora mangle* forest. The mangrove area at the National Estuarine Research Reserve at Jobos Bay, Puerto Rico is among the largest in Puerto Rico. Jobos Bay is the largest forest (11 km^2) on the south coast of Puerto Rico (Cintron et al. 1978) containing native *Rhizophora mangle* forests (the dominant species), as well as three other mangrove species. The tidal range is ~ 0.3 m for both sites. Sediment percent organic carbon content ranged from 17.9% for Puerto Rico to 0.57% for Oahu and total percent nitrogen from 0.76 % (Puerto Rico) to 0.08 % for Oahu (Demopoulos 2004).

Materials and methods

Sample collection and processing:

To determine the fate of mangrove detritus, rates of litter fall, fallen litter standing stock, and leaf degradation/utilization rates were evaluated in Hawaii and Puerto Rico mangrove stands using the methods outlined by Twilley et al. (1997). A 100 m transect was established parallel to the shore 20 m inland from the mangrove forest edge, within each of the two sites. Mangrove litter fall was collected in 0.25 m^2 baskets supported 1.8 m aboveground. The bottom of each basket was constructed of fiberglass screening (1 mm mesh). Ten baskets were placed at random distances along a 100 m transect. Collections were made from Nov 2001–Oct 2002 in Puerto Rico, and litter-basket contents were removed monthly for 1 year. Unfortunately, mangroves were removed from the Hawaii study site prior to the completion of this study, limiting the monthly collections in Hawaii to May-Aug 2004. Litter standing crop was measured monthly at each of the sites by collecting litter from 0.1 m^2 quadrats on the forest floor. Each quadrat was randomly placed 3 m from one of the corners of a litter basket; a different corner was chosen for each subsequent trip. Material from the baskets and quadrats was collected with gloves to prevent contamination, separated into leaves, reproductive structures (flower, fruit), wood, and miscellaneous (included small pieces of mangrove debris), dried at 60°C to a constant weight (2-3 d) and weighed to the nearest 0.1 g.

To determine the rate of leaf litter removal by crabs from the forest floor, 10 freshly fallen leaves were marked with a white paint spot and placed in 4 m^2 areas near

the collection baskets during low tide. The number of leaves remaining after 2 hours was recorded (Twilley et al. 1997). This experiment was replicated at least four times at each site throughout the duration of the project.

Mangrove leaf degradation rates were determined by measuring the loss of dry mass from fiberglass bags. Fresh leaves (4-5 g wet weight) were collected from trees and placed in fiberglass bags (1 mm mesh, 20 x 20 cm). At basket # 3, 6, and 9, seven bags were placed 1 m apart on the forest floor along a transect located 4 m from the baskets. One bag was collected randomly from each basket monthly for 6 months in Puerto Rico and weekly for one month in Hawaii. The plant material was gently rinsed, dried at 60°C to a constant weight (2-3 d), and weighed to the nearest 0.1 g. Conversion of original wet leaf weight to dry weight was required in order to compare results with final leaf dry weights. Average conversion factors were evaluated from 25 fresh *Rhizophora mangle* leaves (4-5 g), dried to a constant weight at 60°C. The average conversion factor for Hawaii leaves was 44 ± 7% s.e. weight loss, and Puerto Rico was 38% ± 7% s.e.

An additional leaf bag pilot experiment was established to evaluate decomposition rates based on exclusion of different size classes of organisms. Fresh leaves (1-2 g wet weight) were collected from trees and placed in bags (6 x 6 cm) of various mesh sizes (1, 0.5, 0.25, 0.13, and 0.030 mm). At basket #2, 3 bags of each mesh size were placed 1 m apart on the forest floor along a transect located 4 m from the basket. All bags were collected after one week in Puerto Rico. The leaves were processed as above.

Leaf turnover rates, including degradation, burial, and outwelling, were estimated based on leaf fall estimates and litter standing crop. Leaf turnover rates were estimated using the following equation:

Equation 1 $K_t = Lf/Lsc$

Where K_t is the turnover coefficient, Lf is the leaf litter fall in g m^{-2} d^{-1}, and L_{sc} is the leaf standing stock in g m^{-2}. This equation assumes the system is in steady state where leaf litter production equals leaf litter losses (Twilley et al. 1997). Kt values were monthly averages for 3 months of data.

Leaf degradation rate (K_d) was estimated using a single exponential model, which described litter weight loss with time:

Equation 2 $K_d = (\text{Ln } Mt_o - \text{Ln } Mt_n)/(t_n - t_o))$

where Mt_o=dry mass in degradation bag at to, Mt_n=dry mass in degradation bag at t_n, and $(t_o - t_n)$= duration of degradation study (days). Residence times were estimated from 1/k and half-times were estimated from 0.693/k (Olson 1963; Steinke and Ward 1987; Twilley et al. 1997). Leaf turnover based on leaf degradation experiments removes the influence of tidal export and consumption via large macrobenthos (> 1mm in size). K_d estimates were compared between sites based on 1 month of data. A negative-exponential model was also used to evaluate rates of degradation for the entire period of the decomposition study (Hawaii= 4 weeks, Puerto Rico = 7 months).

Rainfall data from Puerto Rico and Hawaii were accessed directly from the following data dissemination websites: cdmo.baruch.sc.edu/data_dissemination.html., www.prh.noaa.gov/hnl/hydro/hydronet/hydronet-data.php, and Hawaii rainfall data summaries in Scheinberg (2004).

Statistical analysis:

Standard errors were calculated from averaged monthly litter fall and litter standing stock (n=10 samples). For leaf degradation rates, K_d, standard error was calculated for 1 month of data based on n=3 replicate leaf-litter bagseach from Hawaii and Puerto Rico. Standard errors were calculated for K_t from monthly K_t estimates for 3 months of data (June-August) from both sites. Nested ANOVA analyses were used to compare native and introduced mangrove sites with months sampled nested within sites, and to compare temporal variation in litter components (leaves, wood, reproductive material, and miscellaneous) within a site. One-way ANOVA was used to assess temporal variability in the Puerto Rico samples. Pearson product-moment correlation was used to examine relationships between rainfall and litter standing stock and litterfall. Kruskal-Wallis median tests were used to test for significant differences in leaf degradation experiments when the data did not satisfy the assumptions for normality (Sokal and Rohlf 1969). Jonckheere-Terpstra non-parametric tests were used to test for differences in leaf degradation in different mesh-sized litter bags (Hollander and Wolfe 1973; Pirie 1983). All statistical tests were run using SPSS Statistical Software.

Results

Litterfall

Mean litterfall in Hawaii was 4.9 ± 1.9 g m^{-2} d^{-1} (18.0 ± 5.9 t ha^{-1} yr^{-1}). For the same time period (May-Aug. 2002), mean daily litterfall in Puerto Rico was 2.9 ± 0.2 g m^{-2} d^{-1} (10.7 ± 0.8 t ha^{-1} yr^{-1}) and for one year of sampling, 3.6 ± 0.4 g m^{-2} d^{-1} (13.2 ± 1.5 t ha^{-1} yr^{-1}). Most of the litterfall was attributed to leaves in Puerto Rico stands, whereas for Hawaii, nearly equal proportions of leaves and reproductive components constituted the leaf litter for July and August (Figure 2). Peak litterfall from four months of collections occurred in August 2002 in Hawaii, and July and August had the greatest amount of leaves, reproductive material, and miscellaneous detritus. October 2002 was the peak litterfall month in Puerto Rico (1 year sampling period), and temporal variation in total litter fall, leaves, and reproductive components was significant, with February and October 2002 producing the highest amounts and November 2001 the least amount of litter (Kruskal-Wallis median test, $p<0.001$). Leaf fall followed a bimodal pattern, increasing first from January and February, and secondly in September-October. The proportion of leaves always exceeded the other components throughout the year except for December (nested ANOVA, $p <0.001$). Reproductive material exceeded wood fall and miscellaneous material in November/December 2001 and January/October 2002. Reproductive material (flowers, propagules, etc.) was absent from the litter fall from May through August, whereas December had the greatest contribution (1.5 g m^{-2} d^{-1}).

Wood fall in Puerto Rico mangroves was greater than in Hawaii (paired t-test from 4 months, $p=0.054$). In contrast, Hawaiian mangroves had a significantly greater amount of reproductive material than did Puerto Rico (Kruskal-Wallis median test, $p=0.002$), and total litter production for the months May-August was greater in Hawaii than in Puerto Rico ($p=0.010$).

Rainfall and litter production/standing stock

There was no significant correlation between rainfall and litterfall or litter standing stock (Figure 3, Pearson correlation, $r = 0.204$, and 0.173, respectively).

Litter standing stock

Average monthly litter standing stock within mangroves in Hawaii, 58.9 ± 12.4 g m^{-2}, and in Puerto Rico was 204.2 ± 8.8 ($t = 3$ months), and 507.6 ± 36.8 g m^{-2} ($t=12$ months) (Figure 4). Of the total litter standing stock, leaves contributed 152.8 ± 17.6 g m^{-2} (28%) for Puerto Rico and 25.2 ± 6.0 g m^{-2} (41%) for Hawaii. Leaves and wood made up a significantly greater fraction of the litter standing stock compared to reproductive and miscellaneous material in Puerto Rican mangroves (Nested ANOVA, $p<0.001$). In Hawaii, a higher proportion of mangrove leaves was present in the standing stock litter, compared to wood, reproductive, and miscellaneous material (Nested ANOVA, $p<0.001$).

Significant temporal differences in leaf standing stocks were present in Puerto Rico, with standing stocks in July greater than August (One-way ANOVA, $F=8.514$,

p=0.001). In contrast to litter production rates, mangrove total- and leaf-litter standing stock were significantly greater in Puerto Rico than in Hawaii (t=3 months, Kruskal-Wallis median test, $p<0.001$).

Litter decomposition

After 30 days, mangrove leaves retained between 40-65 % of their original mass in both Hawaii and Puerto Rico (Figure 5), with no significant differences found between Hawaii and Puerto Rico leaf decomposition (t=30 days). A negative-exponential model fit to the decomposition data yielded higher decomposition rates (K_d) for Hawaii, based on 4 weeks of data than for Puerto Rico (7 months) (Table 1, Figure 5). In addition, there was no significant difference in leaf decomposition among different sized mesh bags (Figure 6) (Jonckheere-Terpstra test, $p> 0.05$). However, there was a noticeable trend towards increased percent mass loss with increased mesh size.

Leaf Turnover

Average leaf turnover, based on leaf degradation results after 4 weeks for both sites and using equation 2 (K_d) was 0.033 d^{-1} for Hawaii and 0.015 d^{-1} for Puerto Rico (Table 1). Leaf residence times ($1/k_d$) were twice as long in Puerto Rico (66.7 d) as in Hawaii (30.3 d). Leaf turnover (K_t) estimated from equation 1 integrates all of the ecological processes of leaf loss including tidal export, crab consumption, and leaf degradation. Average K_t values were greater than calculated K_d values for both Hawaii

(0.149 d^{-1}) and Puerto Rico (0.038 d^{-1}). Leaf turnover estimates based on K_t calculations were significantly higher for Hawaiian mangrove leaves than for Puerto Rico leaves (Kruskal-Wallis rank test, $p<0.05$).

Leaf removal by crabs

No leaves were removed by crabs during any of the observation periods at either site.

Discussion

Results from this study combined with Cox and Allen's (1999) > 1 year study indicate that mangrove litter production in Hawaii was higher than in native forests, (Figure 1). In addition, calculated leaf residence times ($1/k_t$) in Hawaii were ~ ½ those in Puerto Rico, in support of the hypothesis: *a greater proportion of mangrove litterfall is exported from introduced mangroves than from native mangroves.* Overall, more litter production, less standing stock, and lack of observed leaf consumption by crabs in Hawaii suggest that more material was exported from Hawaiian mangroves compared to those in Puerto Rico. In addition, sediment organic carbon content from Hawaii (0.57 %) is much less than Puerto Rico (17.9%), suggesting that very little mangrove-derived particulate organic carbon is retained within Hawaiian mangal sediments. Similar studies conducted in Puerto Rico agree with our results, with litter production rates close to 9.49 t ha^{-1} y^{-1} for *R. mangle* forests (Pool et al. 1975) (Table 2). Given that litter collections

and decomposition experiments in Hawaii were limited in duration, generalizing these results must be done cautiously. Proceeding with this caveat in mind, I will summarize possible reasons for high litter production in introduced mangrove forests.

A major contributor to the higher litterfall rates found in Hawaii was mangrove reproductive material, supplying up to 40% of the total litter production. In contrast, reproductive material in native mangroves, including in this study, constitute a relatively small portion of total litterfall, i.e., $\leq 20\%$ (Duke et al. 1981; Woodroffe 1982; Woodroffe and Moss 1984; Lopez Portillo and Ezcurra 1985; Amarasinghe and Balasubramaniam 1992). A high proportion of reproductive material was also found in Cox and Allen's (1999) study of Hawaiian mangrove productivity, and they attributed this to low pre-dispersal propagule predation by herbivores. In addition, they suggested that herbivorous insects or disease agents may not target mangrove buds and flowers in Hawaii, resulting in enhanced reproductive output.

An additional factor that may have contributed to higher Hawaiian litterfall rates is the small amount of leaf herbivory observed in introduced mangroves (Cox and Allen 1999). Leaf fall contributed 11.4 t ha^{-1} yr^{-1} in Hawaii, which is similar to Cox and Allen's (1999) estimates of leaf fall (10.2 t ha^{-1} yr^{-1}), but higher than the total litterfall for native mangrove stands (Pool et al. 1975; Twilley et al. 1986; Twilley et al. 1997). Herbivory in Hawaiian mangroves has been regarded as an insignificant control on leaf production, generally affecting less than 10% of the leaves (Cox and Allen 1999). In contrast, herbivore damage can affect up to 100% of *Rhizophora mangle* leaves in Belize (Farnsworth and Ellison 1991; 1993), resulting in 20-50% of leaf area loss in native mangrove forests.

Leaf turnover/residence times

Differences in litter export play a major role in determining the residence time of surface litter in mangroves (Twilley et al. 1986). Therefore, it can be misleading to rely solely on litter-bag experiments for determining residence times of litter in fringe mangroves because these experiments exclude the influence of macrobenthic consumption and tidal export (Twilley et al. 1986). The actual residence time of leaf litter (based on K_t) for Puerto Rico was < ½ that based on leaf degradation rates (K_d) alone, suggesting that export processes largely control the fate of leaf litter. Based on leaf degradation studies (K_d) and leaf turnover (K_t), the longest residence times occurred at Puerto Rico. Residence times based on K_d for Puerto Rico were similar to fringe forests in Ecuador (~ 0.3 yr), but K_t yielded residence times of 0.005 yr for Ecuador forests (Twilley et al. 1997). The shorter residence times, based on K_t, for the Ecuador forests were attributed to seasonal differences in rainfall patterns, with faster turnover occurring during the rainy season (Twilley et al. 1997). In contrast, no marked seasonal pattern was evident in our Puerto Rico data, but because these collections were only for 1 year, seasonal patterns may not become evident in such a short period.

Leaf residence time in Hawaii, based on K_d, was 5 times greater than from K_t, suggesting that export, not *in situ* degradation, is driving litter loss. Shorter residence times for leaves in Hawaii could be a result of environmental differences between the sites. For example, despite similar tidal regimes, there may be differences in runoff, flushing rates, and mangrove width between Hawaii and Puerto Rico. In 2002, annual rainfall in Kaneohe Bay, Hawaii (~ 1800 mm) (Scheinberg 2004) was much greater than

in Puerto Rico (~ 660 mm) (Demopoulos 2004). Greater freshwater runoff through Hawaiian mangroves could result in shorter leaf residence times and enhanced litter export (e.g., Twilley 1995). Alternatively, the relatively narrow mangrove area in the Hawaii site and consistent onshore winds from the northeast trades (Juvik and Juvik 1998) may force mangrove litter inland, leading to decreased litter standing stock in the low intertidal (cf., May 1999). The resultant "inwelling" and possible accumulation of litter on the landward margin of mangrove forests (Demopoulos pers. obs.) may facilitate further colonization of mangroves by the increased stabilization of the sediment environment (Robertson and Alongi 1992). Therefore, the fate of mangrove litter in Hawaii may be bi-directional, either fluxing inshore during consistent onshore winds or out to sea during high rains and runoff periods.

Litter decomposition rates in mangrove environments can be controlled by temperature, humidity, soil pH, aeration, the nature of plant material, microbial populations, and soil fauna (Lugo and Snedaker 1974). Slower leaf degradation rates in Puerto Rican mangroves may be a function of the sediment environment and litter standing stock. The large litter bank retained within the forest may create a reducing environment, where anaerobic decomposition processes tend to dominate, which can be slower than their aerobic counterparts (Boto 1982), although current literature indicates that anaerobic decomposition rates in mangroves vary and can be a function of the environment (e.g., temperature, humidity) (Mackey and Smail 1996).

Leaf turnover estimates based on K_t calculations take into account litter supply and standing stock. All else being equal, lower litter stocks will imply shorter residences, and, ultimately, greater export. However, there may be some seasonal fluctuations in

standing stock of leaf litter and litter production that remain unknown in Hawaii because this study was limited to the summer months. For example, litter-standing stock in Puerto Rico was noticeably reduced during the June-August period, which is associated with higher average rainfall. Increased rainfall can result in increased export of litterfall material (Twilley et al. 1997). However, results showed no significant correlation between monthly rainfall and litter standing stock or litterfall in Puerto Rico.

Despite relatively high litter production rates found in introduced mangroves, very little mangrove litter remains to decompose in the Hawaiian forest. Similar dynamic supply and export has been observed in mangrove communities in Papua New Guinea (Leach and Burgin 1985). Nonetheless, mangrove forests do exist in Hawaii containing dense accumulations of mangrove litter; these are found in protected harbors and low energy habitats (e.g., Pearl Harbor) with infrequent tidal inundation (Demopoulos personal observations; N. Duke, personal communication 2001). Thus, the fate of mangrove leaf litter in introduced mangroves may be more directly controlled by the hydrological/tidal environment than by the direct consumption of leaves by macrobenthos.

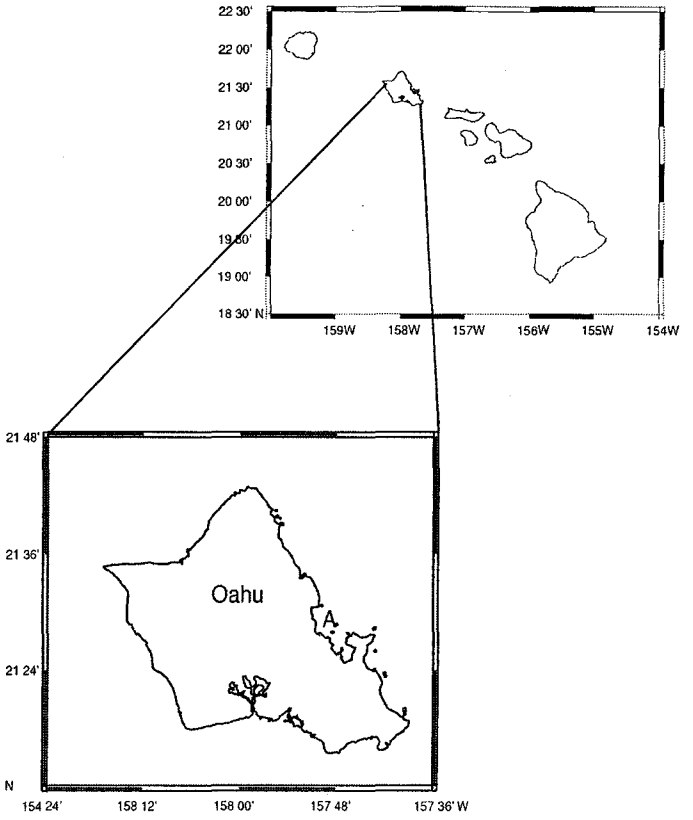
Table 1. Estimates of leaf litter turnover (day^{-1}) based on degradation rates (k_d= (Ln Mt_o-Ln Mt_n)/(t_n-t_o)); where Mt_o=dry mass in degradation bag at t_o, Mt_n=dry mass in degradation bag at t_n, (t_o-t_n)= duration of degradation study (days) compared to estimates based on leaf litter standing crop and leaf fall rates (k_t=Lf/Lsc); where Lf=mean leaf litter fall rate (daily mean), Lsc=mean leaf litter standing crop (annual mean). 1/k = leaf residence time. K_t values were calculated from monthly averages for June-Aug from both sites, and standard errors are based on average K_t values for n= 3 months. Standard error for K_d estimates are based on leaf degradation rates from 3 replicate leaf bags.

Site	k_d (1 mo)	k_t	$1/k_d$	$1/k_t$	$T_{0.5\text{-}kd}$	$T_{0.5}$-k_t	k_d entire study	Source
Hawaii	0.033±0.007	0.149±0.009	30.3	6.7	21.0	4.7	0.040	This study
Puerto Rico	0.015±0.003	0.038±0.005	66.7	26.3	46.2	18.2	0.007	This study
Ecuador		0.601±0.366	125.0	1.7	86.6	1.2	0.008	Twilley et al., 1997

Table 2. Total litterfall for mangrove stands.

Predominant Species	Location	Total Litterfall $t\ ha^{-1}\ yr^{-1}$	Source
Rhizophora mangle	Puerto Rico	13.2	This study
R. mangle	Oahu, Hawaii	18	This study
R. mangle	Oahu, Hawaii	25.2	Cox and Allen 1999
Mixed stands	Puerto Rico	9.49	Pool et al., 1975
Avicennia sp.	Australia	8.05	Duke et al., 1981
R. stylosa	Tuvalu	7.77	Woodroffe and Moss 1984
R. mucronata	Sri Lanka	6.24	Amarasinghe and Balasubramaniam 1992
A. germinans	Mexico	6.14	Lopez-Portillo and Ezcurra 1985
A. marina	New Zealand	8.1	Woodroffe 1982
R. stylosa	Australia	9.3	Duke et al., 1981
Ceriops tagal	Australia	7.52	Woodroffe et al., 1988
B. gymnorrhiza	Australia	8.61	Bunt 1982
Sonneratia alba	Australia	7.9	Duke et al., 1981
R. apiculata	Australia	11.15	Bunt 1982
B. parviflora	Australia	10	Duke et al., 1981
Monospecific stands	Florida	4.44	Twilley et al., 1986
Mixed stands	Florida	8.03	Twilley et al., 1986
R. stylosa	many sites	5.89-18.77	

A.



B.

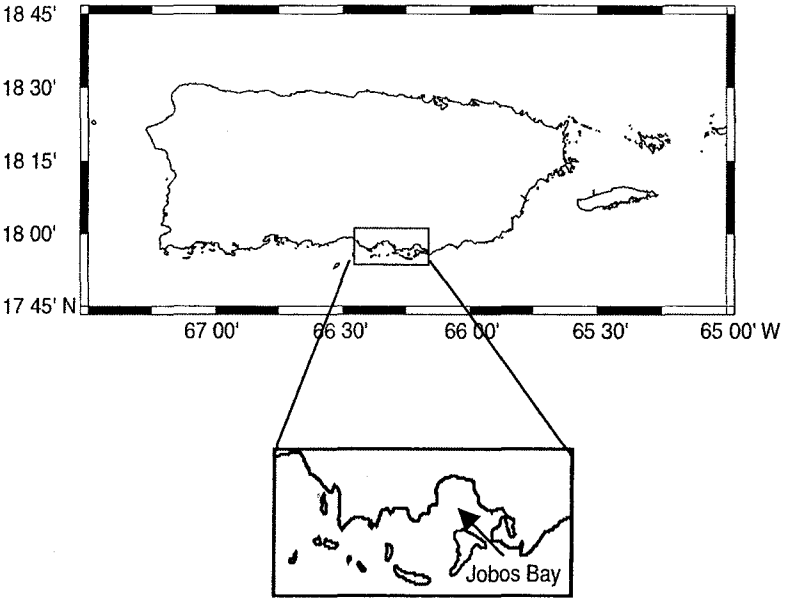


Figure 1. Locations of sampling stations on Oahu, Hawaii (A) and Puerto Rico (B).

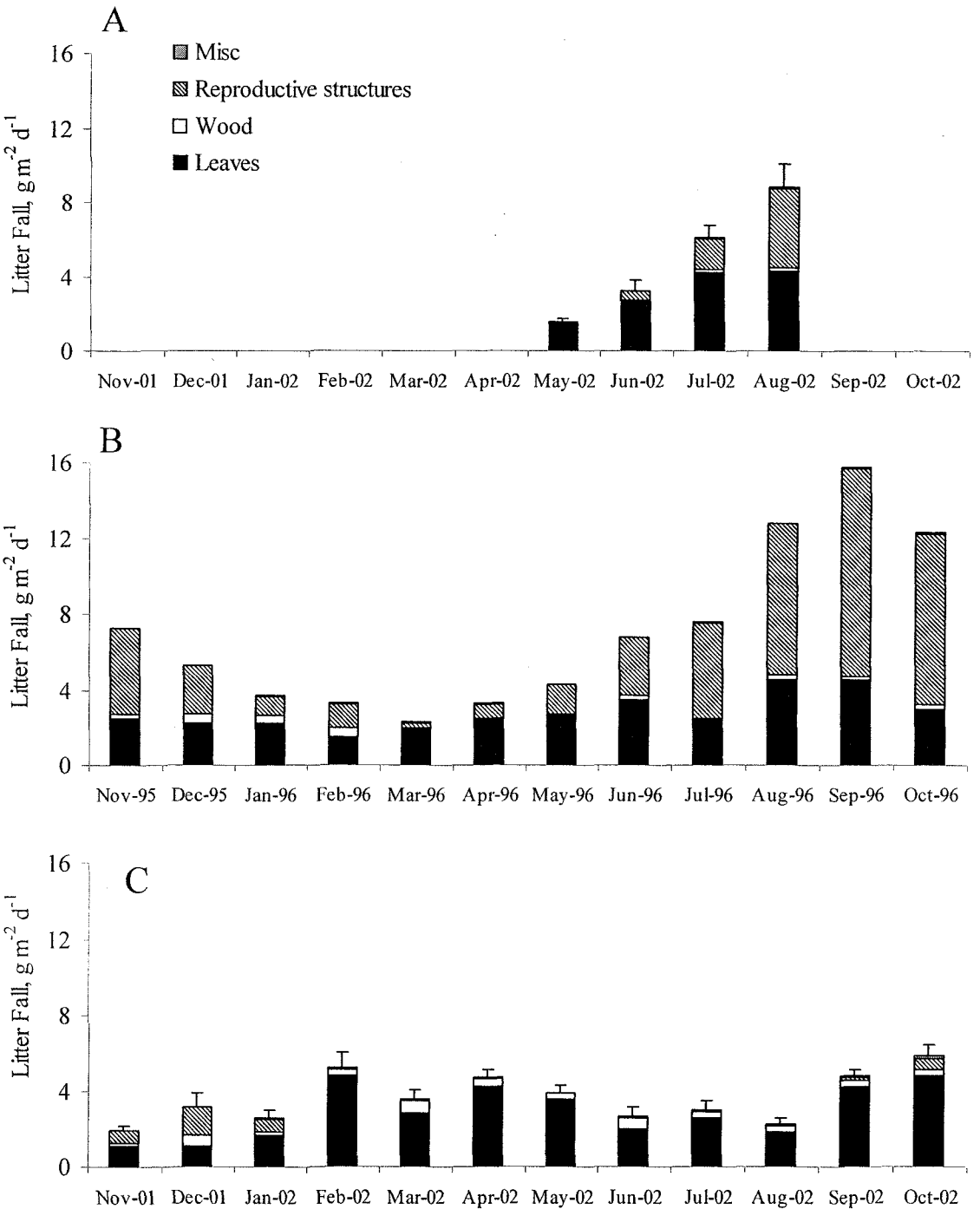


Figure 2. Monthly mangrove litter fall in g m^{-2} d^{-1} from Hawaii including (A) current study, (B) data from Cox and Allen, 1999, and (C) Puerto Rico (current study). Error bars on total monthly litterfall represent standard error.

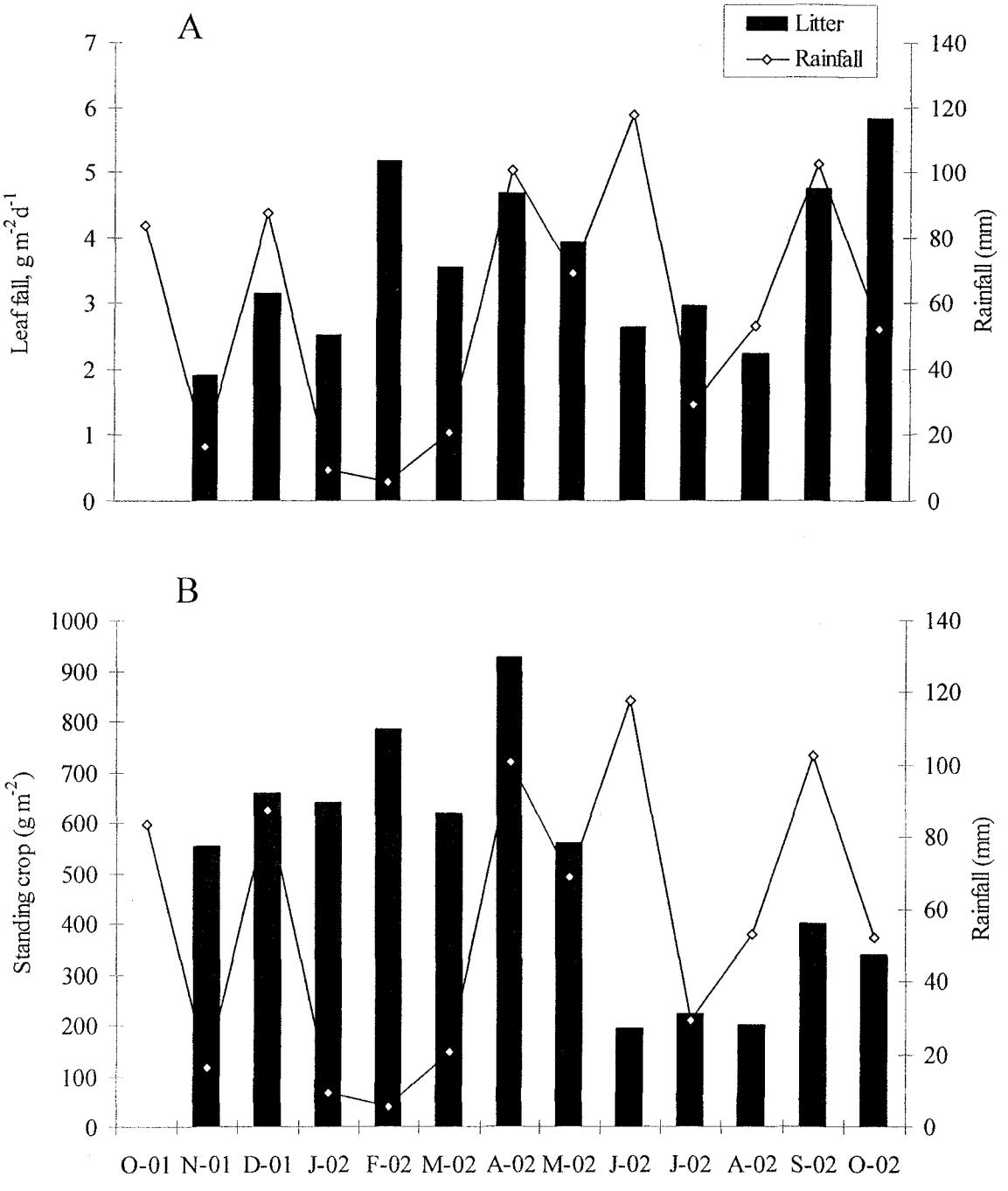


Figure 3. Monthly rainfall (mm) and mangrove litter fall (g m^{-2} d^{-1}) (A) and litter standing stock data (g m^{-2}) (B) from Puerto Rico.

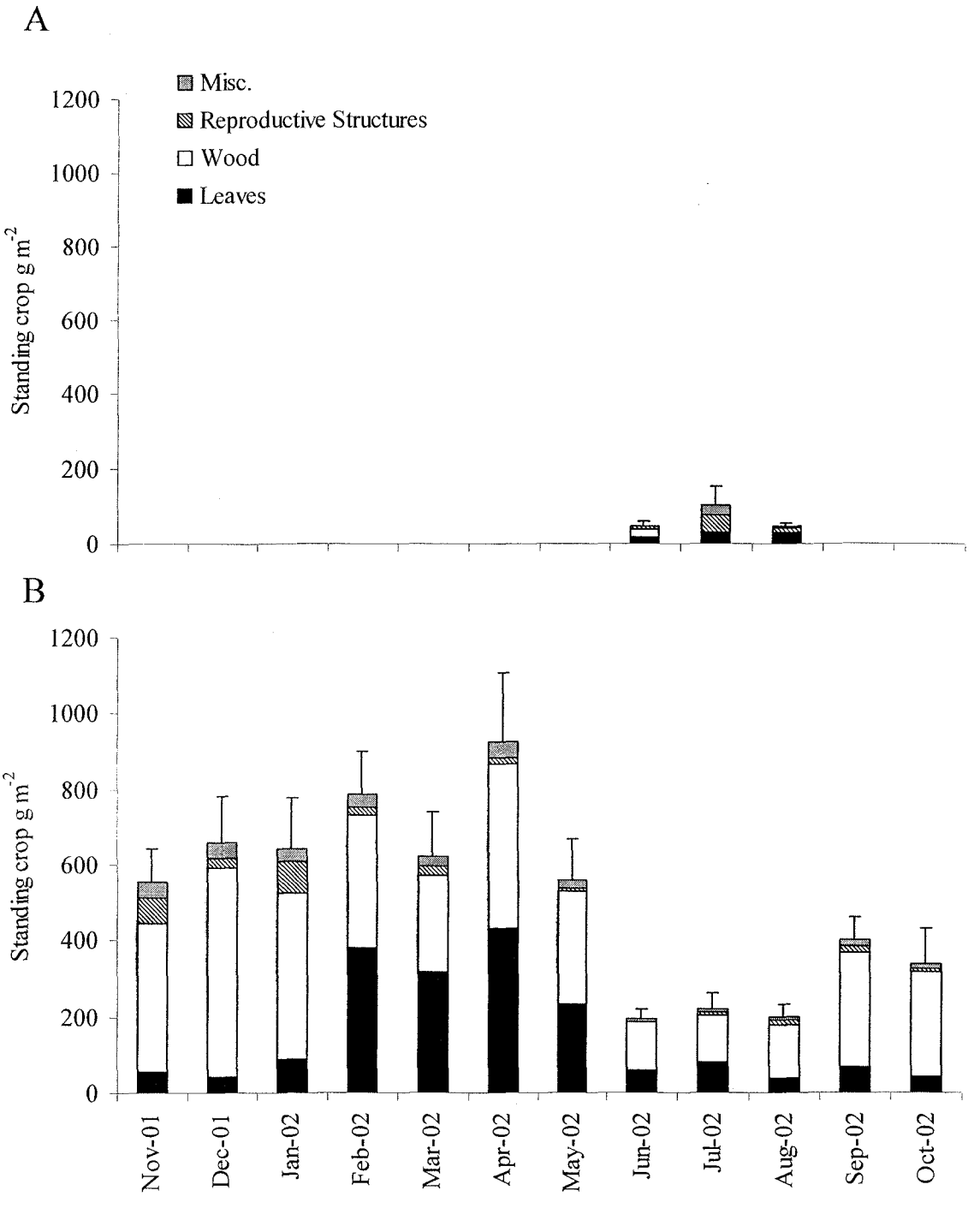


Figure 4. Monthly mangrove litter standing stock in g m^{-2} from (A) Hawaii, and (B) Puerto Rico. Error bars on total litter standing stock represent standard error.

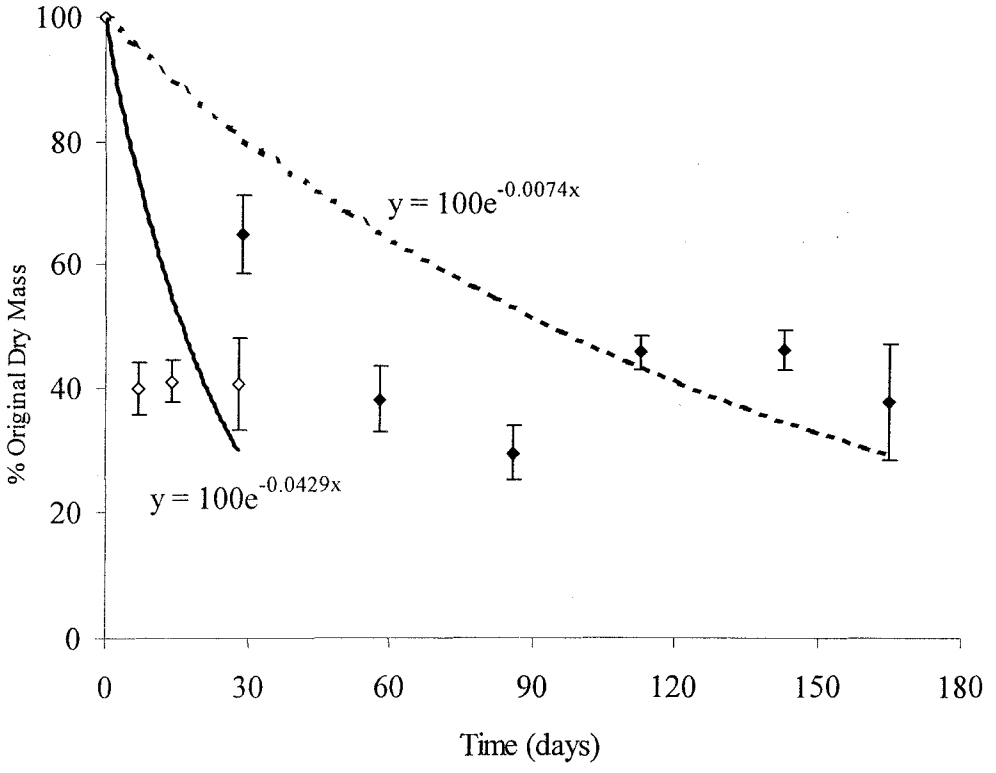


Figure 5. Mean loss in dry mass during the decomposition of *Rhizophora mangle* leaves from Hawaii (open diamonds) and Puerto Rico (solid diamonds). A negative exponential curve was fit to the data for Puerto Rico (dashed line) and Hawaii (solid line). Error bars represent standard error for n=3 litter bags per time point.

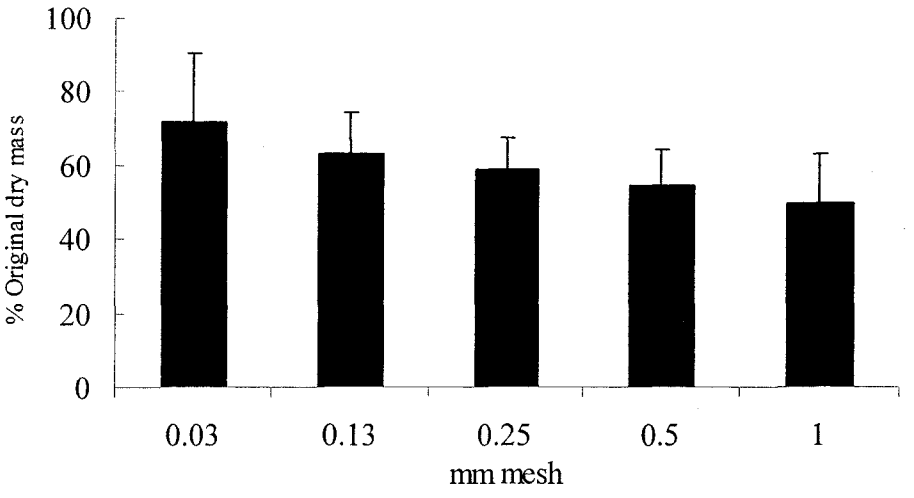


Figure 6. Mean changes in percent original dry mass over 1 week during the decomposition of *Rhizophora mangle* leaves from Puerto Rico from different mesh sized leaf bags. Error bars are standard error for three replicate litter bags.

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CHAPTER 6. CONCLUSIONS

The research presented in this dissertation enhances our understanding of the benthic community ecology and food-web structure in introduced and native mangrove communities. Specifically, these chapters provide new insights into: 1) mangroves providing a niche for marine exotics, 2) the limited role mangrove detritus plays in Hawaiian detritivore food webs, 3) food webs in native mangroves, including the diets, habitat fidelity, and movement patterns of the mangrove crab, *Scylla serrata*, and 4) comparative rates of mangrove litter production, degradation and export in introduced and native mangrove communities.

Habitat characteristics and benthic community structure in introduced mangroves

Rhizophora mangle habitats in Hawaii supported a dense and diverse assemblage of sediment macrofauna primarily composed of polychaetes, oligochaetes, and amphipods. The dominance of cryptogenic and introduced species in mangrove sediments indicates that mangroves may facilitate the persistence and spread of introduced species in Hawaii. Mangroves contained higher macrofaunal densities and enhanced diversity compared to non-vegetated sandflats. These observed community differences between mangroves and non-mangrove habitats may be a consequence of differing sediment organic carbon content and grain size, gradients in salinity, presence of below-ground biomass, and availability of hard substrates and predation refuges. Therefore, introduced mangroves in Hawaii are directly modifying the infaunal and epifaunal community composition, possibly as a result of the greater habitat complexity

and heterogeneity created by mangal development. Enhanced faunal diversities and densities (including for fish) have been observed in other native mangroves (Robertson and Blaber 1992). However, it is unknown whether mangrove forest structure supports high fish diversity in Hawaii.

Mangrove food webs

Introduced versus native mangroves

The relative importance of mangrove detritus to detritivores differs in introduced and native mangrove communities. Using $\delta^{13}C$ and $\delta^{15}N$ stable isotope analyses, it was determined that few Hawaiian detritivores appear to rely on mangrove leaves for their diets. Because mangroves were introduced relatively recently (~100 years ago), it is likely that sediment infauna and epifauna have not yet adapted to feeding on this new food source. Mangrove leaves are rich in tannins, which can be toxic to invertebrates and interfere with detritivore digestion (McMillan 1984; Neilson et al. 1986; Poovachiranon et al. 1986; Alongi 1987; Mahadevan and Muthukumar 1980). Based on $\delta^{15}N$ values, it appears that particulate organic matter and/or benthic microalgae, rather than mangrove detritus, support 2-3 trophic levels in Hawaiian mangroves.

Significant differences in stable isotope values of sandflat and mangrove sediment infauna suggest a landscape-driven shift in stable carbon isotope values to more depleted, possibly mangrove-influenced values with increased penetration into the mangrove interior of Hawaiian mangroves. Isotopic shifts are also observed in native mangroves in

Puerto Rico and Kosrae, suggesting that introduced mangrove trees may be functioning similarly to other native mangroves as an organic-matter source.

The consequences of mangrove-induced modification of the benthos may extend to higher trophic levels because macrobenthos can serve as prey for fish, birds and various invertebrates. However, the trophic relationships between mangrove infauna, epifauna, and more mobile fish and bird species in Hawaii remain unknown. Diets of mangrove-associated fish can vary among native mangrove forests depending on availability and species composition of prey (Robertson and Blaber 1992). Future food web studies of fish taxa coupled with my results will help elucidate trophic connections between mangrove infauna and mobile fish species in Hawaii. In addition, examining the diets of endangered aquatic birds in Hawaii will help assess whether the presence of mangroves in Hawaii modifies the relative abundances of major prey items for these birds.

Mangrove crab, Scylla serrata

Food-web structure and habitat usage by *Scylla serrata* in native mangroves were examined in Chapter 4. Estimated mangal contribution to *Scylla serrata* diet in the Pacific Island of Kosrae ranged from 70-100% for Okat and Utwe watersheds (Chapter 4). In contrast, crabs collected from the Lelu watershed had a lower percentage of mangal contribution (53-73%) and higher $\delta^{13}C$ and $\delta^{34}S$ values, indicating that these crabs may forage more on adjacent reef flats, resulting in enriched tissue isotopic values. Mangrove faunal associates, including grapsid crabs and benthic infauna, served as important food sources for the crabs, as indicated by their corresponding $\delta^{13}C$ and $\delta^{15}N$ values.

In general, mangrove crabs appeared to move over small spatial scales (1-2 km) feeding in mangrove forests and adjacent reefflats. In addition, the restriction of crab populations within watersheds was further supported by using additional tissue measurements, including trace metal, cation, and phosphorus analyses. Results from discriminant analysis indicated that crab-tissue stable isotope data alone separated the watersheds by 91%. Trace metal, cation, and phosphorus concentrations in crab tissue discriminated 73% of the watershed data. These results suggested that stable isotope analyses yielded the best separation, but if research resources are limited, environmental measurements (cost = $5/sample) in lieu of stable isotope analyses ($\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ combined =$25/sample) can provide useful insight into habitat and movement patterns of mangrove fauna.

Mangrove litter production and fate

Based on four months of data collected in Hawaii, litter production was higher in introduced mangroves, but leaf-standing stock was greater in the native forests (Chapter 5). In addition, leaf residence times were shorter in the introduced mangrove forests in Hawaii compared to native forests. After evaluating the standing stock results, sediment organic carbon, and the lack of leaf consumption via crabs, I concluded that very little mangrove litter is retained within the studied introduced mangrove forests and that mangroves in Hawaii can export a greater proportion of litter relative to native forests in Puerto Rico. However, anecdotal evidence that other mangroves in Hawaii have dense accumulations of mangrove litter (e.g., inland mangrove forests in Molokai and Pearl Harbor) suggests that the fate of mangrove litter in introduced mangroves may differ

from site to site, possibly as a function of the physical environment (e.g., width of the forest) and rainfall patterns.

The reduced availability of mangrove leaf material on the forest floor may explain the lack of observed dietary utilization by Hawaiian detritivores. Sediment organic carbon content in Molokai mangroves was higher than Oahu and the stable isotope values reflected organic material derived from mangroves. In addition, few organisms had $\delta^{13}C$ values consistent with mangrove-leaf material. These differences could be attributed to differing successional stages observed in introduced mangroves. For example, Odum (1971) described a change in food chains from grazing pathways to more complex detrital-based food webs as an ecosystem develops from early successional stages to a mature system. This pattern may be reflected as a succession from POM/BMA-reliant fauna in Oahu, to more mangrove detritus-based fauna in Molokai, to even greater reliance on mangrove detritus in the mature mangrove forests in Puerto Rico and Kosrae. As mangrove forests age from the more newly introduced communities on Oahu (~ 30 yrs), to older introductions on Molokai (<100 yrs), to mature forests elsewhere, there may be an associated increase in mangrove area and width, and a concomitant buildup an in mangrove leaf litter. This may result in a greater utilization of mangrove detritus by detritivores.

One issue that remains is whether Hawaiian mangroves host the suite of detritivores known to consume mangrove detritus, which are present in native mangroves. Detritus may accumulate in later successional stages or in different physical regimes in Hawaiian mangroves, but it still may not be utilized if species adapted to exploit mangrove detritus are absent. I found similar oligochaete and polychaete taxa in

both native and introduced mangroves, but have yet to find in both regions the same species that are known to assimilate mangrove detritus.

Implications for Hawaii and Mangrove Management Concerns

Rhizophora mangle has many attributes of a successful invader, including broad environmental tolerances, opportunistic growth strategies, wind pollination, viviparous reproduction, and high seedling dispersal capabilities (Lugo and Snedaker 1974; Tomlinson 1986). In addition, there is evidence that *Rhizophora* can self pollinate, which can allow pioneering species to become established when isolated from parental sources (Primack and Tomlinson 1980; Tomlinson 1986). As a result, some mangroves have been successful at invading the near-shore environment in Hawaii. Despite small-scale removal efforts, *Rhizophora* continues to spread exponentially in the Hawaiian Islands (Chimner et al. unpublished data). Given the high propagule production rate and a lack of propagule predators, the constant supply of seedlings enables the continued colonization and succession of mangrove communities statewide. Thus, coastal zone managers of mangroves in Hawaii are faced with two major challenges: 1) removal of mangrove roots and associated material and 2) follow-up control of mangrove seedlings. In addition, mangroves were introduced to reduce coastal erosion in areas denuded by cattle and various agricultural practices. However, despite the present emphasis put on mangrove removal, there has not been equivalent energy put into reducing upland erosion, e.g., the planting of upland native plants after mangrove removal. No study to date has examined post mangrove removal impacts on the sediment environment, including possible resuspension and run-off of surface sediments that are currently being trapped by

mangrove roots. In addition, the following questions remain regarding impacts of mangrove removal to Hawaiian coastal communities: 1) Do cleared wetlands return to assemblages found in non-vegetated sandflat substrates following mangrove removal, and if so, under what time scales? 2) Would mangrove removals result in the long-term decrease in population abundances of mangrove-associated introduced and cryptogenic species?

General mangrove food web structure

Evaluation of food-web structure can involve data from a variety of sources including examination of stomach contents and analyses of stable isotopes. For example, animal stomach contents may be dissected and the various connections between consumers and food sources ascertained to develop unstructured food-web models (Isaacs 1972). Odum and Heald's (1975) unstructured food-web model in mangroves illustrated the major pathway of energy from mangrove leaf detritus to bacteria/fungi, to detritus consumers, to lower carnivores, and finally, to higher carnivores. Key organisms in this food web were detritivorous nematodes, polychaetes and a few fishes. In contrast, stable isotope techniques seek to evaluate food-web structure and the connections between sources and consumers by focusing on sources rather than by sorting out stomach contents. Stable isotope research in mangroves has largely identified a limited role for mangrove detritus in near-shore food webs (Fry 1984; Zieman et al. 1984; Dittel et al. 1997; Marguillier et al. 1997; Lee 2000; Chong et al. 2001; Thimdee et al. 2001; Bouillon

et al. 2002). However, if an organism potentially consumes more than one food source, resulting in intermediate isotopic values, then relationships between mangrove detritus and detritivores can become obscure, often leading to the use of mixing models to explore the proportional contribution of different sources to consumer diets. The use of mixing models alone can often lead to ambiguous results, because they are based on stable isotope values from a limited number of sources (mixture of sources), (Phillips and Gregg 2001). Thus, a combined approach, using stable isotope mixing models and knowledge of feeding habits of organisms may result in more useful conclusions about trophic connections in detritus-based food webs.

Conceptual food-web models in mangroves may need to take a more ecosystem-level approach because it may be more useful to consider habitat use and residency in addition to food-web support in ascertaining mangrove importance in coastal communities (Fry and Ewel 2003). Utilizing this macroscopic rather than microscopic view of mangroves may help to better quantify the role mangroves play in coastal ecosystems. Stable-isotope data from introduced mangroves in Hawaii indicated that few organisms assimilate mangrove leaves. This was also the case in native mangroves in Puerto Rico, where only nematodes and nereids had stable isotope values consistent with diets of mangrove leaves. In contrast, stable isotope studies in Kosrae indicated that dependence on mangal subsidies might be a function of mangrove width and proximity to open embayments because the widest mangroves yielded the highest dietary contribution of mangroves to consumers. The approach taken with the Kosrae stable-isotope data was to choose mangal and reef-flat "residents", rather than using a mangrove-leaf focus, and then estimating proportional contributions of mangal to crab diets. Future isotope studies

in coastal ecosystems with large detrital reservoirs, including salt marsh communities, may do well to use this broader approach, rather than to focus only on leaf and/or plant material usage.

Ultimately, there are a number of assumptions typically made concerning mangrove contributions to consumer diets including the trophic fractionation factors of 0-1 ‰ for $\delta^{13}C$ and 3-4 ‰ for $\delta^{15}N$ (Rodelli et al. 1984; Stoner and Zimmerman 1988; Newell et al. 1995; Primavera 1996; Bouillon et al. 2002). The trophic fractionation associated with mangrove leaves remains unknown and my assumptions based on literature approximations may be underestimates. For example, fungal colonization and degradation of plant material can lead to 6 ‰ enrichment in ^{13}C (Fry and Ewel 2003). To evaluate trophic fractionation associated with feeders on mangrove litter, it would be useful to conduct feeding and growth experiments with mangrove leaves and infaunal organisms, carrying the infauna through several generations. If infauna require fungal and bacterial decomposition prior to consumption of mangrove detritus, this could then be demonstrated by measurements of $\delta^{13}C$ from feeding experiments. Assumptions of 0-1 ‰ for trophic fractionation of $\delta^{13}C$ in mangrove food webs may be incorrect, ultimately underestimating the importance of mangrove detritus in coastal food webs. Thus, feeding experiments with mangrove leaves should be performed on mangrove sediment infauna in order to better quantify the role of mangroves in detrital food webs.

Directions for future research

There are a number of questions regarding mangrove community ecology in general and the fate of mangroves in Hawaii that have been generated by this research. These include:

1. What are the stable isotopic values for organisms raised directly on mangrove leaves and what are the stable isotopic values of organisms that follow alternative trophic pathways, e.g., consumption of mangrove detritus after fungal decomposition?
2. What is the energetic role of benthos in tropical mangrove ecosystems? Specifically, what is the trophic role of microbes, meiofauna, and macrofauna in terms of actual amounts of biomass passed up the food chain?
3. Do sediment infauna enhance mangrove production, e.g., via aeration of roots in a suboxic environment?

It would be interesting to focus future experiments and research around these questions in order to better understand mangrove detrital pathways, trophic transfer, and animal-plant interactions within mangrove sediments.

Concluding remarks

Once considered to be a foul smelling wasteland filled with only predatory beasts, and a nuisance with few positive attributes (Bowman 1917; Davis 1940, 1942, 1943, 1946), mangroves are now recognized as productive and diverse habitats. In particular, native and introduced mangroves play a significant role in structuring benthic community

composition and coastal food webs. Introduced mangroves are so highly productive that future management of mangroves in Hawaii may need to focus efforts on the control of propagule production to limit the supply of new recruits colonizing open niches in the Hawaiian coastal zone.

In contrast, losses of native mangrove area worldwide are occurring rapidly, exceeding rates of 1% of mangrove forest total area per year (Umali et al. 1987; Hatcher et al. 1989). Over time, this attrition may lead to reduced patches of mangrove that are too small to support the diversity of organisms known to thrive in large-scale native forests (Hogarth 1999). Given the importance of the mangrove habitat to a variety of commercially important fish and invertebrates, and that size (e.g., width) of mangrove forest positively correlates with sizes of crabs and their mangrove habitat usage (see Chapter 4), it would appear that preserving mangrove habitat size and continuity will enhance the success of other mangrove faunal associates.

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