NOTE

THE IMPACTS OF RED MANGROVE (*RHIZOPHORA MANGLE*) DEFORESTATION ON ZOOPLANKTON COMMUNITIES IN BOCAS DEL TORO, PANAMA

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Deforestation impact studies have generally focused on tropical rainforests or temperate coniferous woodlands. However, extensive clear-cutting is currently occurring in a wide-ranging, but far less recognized habitat: the world's mangrove forests. These coastal forests thrive in areas of low wave action and high sediment availability, where mangrove trees develop dense and productive ecosystems (Alongi, 2002). Extensive aerial and subtidal prop root networks, a dense canopy, and varying water conditions allow these forests to support unique assemblages of flora and fauna.

Even as mangrove deforestation continues to alter coastlines, these forests are increasingly recognized as important nursery habitats and feeding grounds for many larval, juvenile and adult fish and invertebrate species (e.g., Nagelkerken et al., 2001, 2002; Mumby et al., 2004; Nagelkerken and van der Velde, 2004). Larval populations of a wide variety of marine species recruit to these sheltered, structurally complex, shaded and nutrient-rich ecosystems (Krishnamurthy, 1982; Dennis, 1992). Whether zooplankton communities differ between intact and cleared mangrove areas is unknown.

Structural complexity should affect flow and hence food availability and larval retention rates. However, results from different systems are inconsistent. In kelp forests, structural complexity inhibits deposition of suspended particles, possibly reducing food availability for benthic organisms and retarding zooplankton dispersal (Eckman et al., 1989). As with inhibited flow in kelp forests, Toffart (1983) suggests that there is a rapid decrease in species diversity from the seaward edge of a mangrove forest towards the shore because of reduced flow. This would particularly affect less active swimmers. However, few direct measurements of zooplankton inside and outside mangroves exist (e.g., Ambler et al., 1991).

Mangroves may be preferred settlement sites for some highly mobile species that can actively select this habitat. Capacity for swift directional travel among zooplankton (Luckenbach and Orth, 1992; Ferrari et al., 2003) may allow these species to actively select mangrove habitat over less complex, more open environments (i.e., cleared mangrove areas). Low flow in mangroves may increase (or decrease) zooplankton abundance and create retention zones where zooplankton can develop near suitable adult habitat (Paula et al., 2004). Zooplankton survival may be high in mangroves due to favorable substrate and increased niches (due to root complexity), greater food availability, and reduced predation (Laegdsgaard and Johnson, 1995; Cocheret de la Morinière et al., 2004). The dense mangrove root networks retain nutrients and sediments carried in runoff from adjacent land or produced in situ, having the dual effect of fueling productivity (Bouillon et al., 2000) and creating murky water conditions, reducing visibility for predators. The structural complexity of mangrove roots may provide settling larvae with shelter from predators and open water currents. On the other hand, differences in structural complexity within man-

grove forests may also lead to variable larval supply and diversity within different areas of intact mangroves (Krumme and Liang, 2004; Osore et al., 2004).

To date few studies have examined zooplankton communities in mangrove habitats (but see Ambler et al., 1991; Paula et al., 2001; Barletta-Bergan et al., 2002; Osore et al., 2004). In this study, we examined the effects of mangrove habitat loss on zooplankton communities by comparing diversity, abundance, and community composition between areas cleared of mangroves and areas with intact mangroves in the Bocas del Toro region of Panama. We tested the hypothesis that different meroplankton and holoplankton communities inhabit intact and cleared mangrove environments. Because higher complexity habitats are sometimes characterized by higher biological diversity (i.e., Kohn and Leviten, 1976; Taniguchi and Tokeshi, 2004; Gratwicke and Speight, 2005a,b; Kostylev et al., 2005; Lassau et al., 2005; Le Hir and Hily, 2005), we expected to find higher diversity in the intact mangrove habitat.

METHODS

STUDY AREA.—This study was conducted adjacent to Isla Colón in the Bocas del Toro Province off the Caribbean coast of Panama. The coastline at the study area was characterized by red mangrove, *Rhizophora mangle* Linneaus, 1773 trees, except where stands had been removed for agriculture, construction, or viewsheds. Cleared mangrove areas ranged from 100 to 300 m in length along the shore and were bordered on either end by intact mangrove habitat. Mangrove removal occurred approximately 8 yrs prior to our study. Intact mangrove areas were characterized by submerged prop roots colonized by oysters, sponges, sporadic coral heads, and, infrequently, epibiotic algae, with occasional unforested channels between trees. Cleared areas were similar to forested areas in depth and distance from the shoreline, but they lacked the complex 3-dimensional underwater root structure (generally limited to a few remaining snags), overhead cover under the mangrove canopies, and high sediment levels and nutrients resulting from organic production of a healthy mangrove community (Krishnamurthy, 1982; Granek, 2006). Mangrove-removed areas were characterized by submerged decaying prop roots on the substrate with significant macroalgal growth inshore and seagrass (*Thalassia testudinum*) growth further from shore. Tidal exchange in the region is small: ~50 cm and not variable between forested and nonforested areas.

Six sites on Isla Colón were selected for this study because they met the following criteria: (1) at least 100 m long stretch of cleared *R. mangle* adjacent to stretches of at least 100 m of intact red mangroves; (2) fringing or patch coral reefs within 100 m of the seaward edge; and (3) > 2 km from major human development or construction, to exclude potential immediate anthropogenic sources of nutrients. Nearby development in the study region was limited, primarily consisting of subsistence farming and mangrove clear-cutting. Commercial and industrial development was > 10 km from all sampling sites. Below, we refer to areas of intact mangrove as +mangrove areas and to areas cleared of mangroves as −mangrove areas.

ZOOPLANKTON SAMPLING.—Previous assessments demonstrate that community composition differs between light trap and plankton tow sampling (Hickford and Schiel, 1999; Porter et al., 2002). Because zooplankton display a range of swimming abilities and photosensitivity, we simultaneously used light traps and plankton tows to assess zooplankton communities in the +mangrove and -mangrove areas. Positively phototactic swimming zooplankton are drawn into light traps, while non-phototactic and slow-moving or negatively phototactic zooplankton are more effectively sampled by plankton tows (Doherty, 1987). In June 2004, sampling was conducted for six nights around the new moon, the period of the lunar cycle when fish and invertebrate spawning is most common, and therefore, when the larval community is likely at its peak density (McFarland et al., 1985). We began collections 2 d prior to and continued 3 d after the new moon. Two sites were sampled per night (two intact and their

two associated cleared areas), and each site was sampled twice in the course of the study (n = 12 site × night combinations) using both sampling methods simultaneously.

Zooplankton Light Traps.—Zooplankton light traps have the potential to trap positively phototactic, mobile organisms (Watson et al., 2001; Porter et al., 2002). The light trap design was based on that used by Roegner et al. (2003). The traps were constructed using 7.6-l (2 gal) clear plastic water jugs, inverted, with an attached, 220-μm, mesh-lined cod-end made of perforated PVC tubing (Fig. 1). A yellow glow stick, suspended inside the bottle from the top of each inverted trap, was used as a light source. Three funnel-shaped entry points were available to zooplankton in the bottle's sides, each leading inward to a hole measuring approximately 1 cm in diameter. The small size of entry points and the funnel shapes were designed to limit, as much as possible, the ability of zooplankton to leave the traps after entering. Zooplankton were flushed into the cod-end of the trap when it was lifted from the water.

Traps were deployed for 1 hr after sunset, between 1900 and 2030. In intact mangrove areas, light traps were anchored by suspended dive weights within the root structure approximately 1–1.5 m above the substrate. In the cleared areas, traps were deployed within the area previously occupied by mangroves.

Plankton Tows.—Diver-pulled plankton tows were conducted in the vicinity of the traps for 1 min (approximately 20 m) during the time period in which the light trap was deployed. The 200-μm mesh plankton net had an opening diameter of 30 cm. In intact mangrove areas, the net was pulled through partially open waters found behind the most seaward trees and through small channels within the mangrove forest. Tows were conducted as close to the light traps as feasible within the root structure, given the size of the net. In the cleared mangrove areas, the tows were pulled along a straight line, parallel to shore and adjacent to light traps. All tows were pulled at a similar speed, during calm nights, so that water flow was consistent between + and −mangrove areas to control for water volume sampled.

Sample Processing.—The contents of the cod-ends of the traps and tows were preserved in 2%–4% formalin solution. A light microscope was used for sample identification to count all individuals in each sample and identify them to phylogenetic order when possible. Deca-
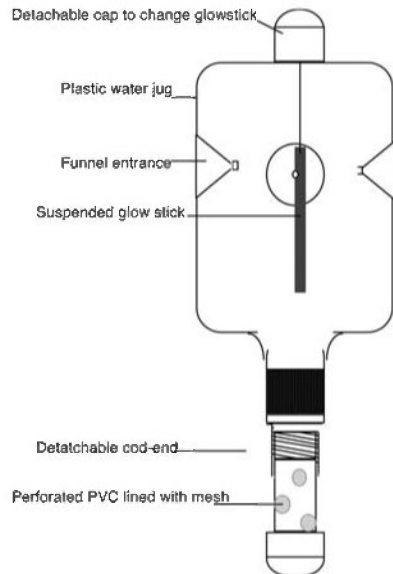

Figure 1. Diagram of larval trap design (modified from Roegner et al., 2003; not to scale). Our design utilized a smaller bottle, glow stick instead of fluorescent bulb, and modified cod end.

pods were further categorized by developmental (i.e., zoea, megalopae, or postlarval) and re-
productive stage.

STATISTICAL ANALYSIS.—Prior to analysis, data were log transformed for analysis of vari-
ance (ANOVA) tests and square-root transformed for non-parametric multidimensional
scaling analysis to meet model assumptions. Three-factor ANOVA was used to determine
how much of the variability in taxonomic abundance was accounted for by physical location
(site), mangrove presence (+mangrove vs −mangrove), and sampling night. A Shannon-Wein-
er diversity index was used to determine differences in taxon diversity between +mangrove
and −mangrove areas. A non-parametric multidimensional scaling analysis (nMDS) was
run to examine differences between communities at each site, and whether +mangrove sites
were more similar to each other than to −mangrove sites. A paired t-test compared overall
zooplankton abundance in the samples. All analyses were run separately for light trap and
plankton tow data. Communities were then separated into meroplankton and holoplankton,
and a nMDS was run for each sub-community (meroplankton; holoplankton). A single fac-
tor ANOVA was used to test how high temperature events differed between -mangrove and
+mangrove habitat.

<div align="center">RESULTS</div>

LIGHT TRAPS.—In light trap samples, abundance of meroplankton taxa includ-
ing amphipods, isopods, ostracods, crab and mysid postlarvae, and *Daphnia* were
greater in +mangrove areas (ANOVA: $P < 0.05$; Fig. 2A; see online Appendix 1);
Daphnia, crab megalopae and isopod abundance also varied by site and/or night.
Abundance of three meroplankton taxa (crab zoeae, shrimp zoeae and megalopae,
and polychaetes) and two holoplankton taxa (copepods and cumaceans) were greater
in −mangrove areas (Fig. 2A, online Appendix 1); cumacean abundance also varied
by site. For all other taxa sampled in light traps, there was no difference in taxon
abundance between + and −mangrove areas (Fig. 2A). Total zooplankton abundance
was not significantly different between +mangrove (mean = 2479 ± 596) and −man-
grove (mean = 9857 ± 3801) areas (Paired t-test: $t = -1.8141$, $df = 10$, $P = 0.10$).

Overall zooplankton diversity in light traps was more than 50% higher in intact
mangrove areas relative to cleared areas (Shannon Weiner diversity index: intact =
1.4, removed = 0.92). Structural community differences between +mangrove and -
mangrove areas were revealed by nMDS analysis ($r^2 = 0.46$, Stress in randomized
runs: $P < 0.01$; Fig. 3A). Community differences in light traps were driven primarily
by higher abundance or presence in +mangrove areas of meroplankton including
amphipods, reproductive mysids, and porcellanid megalopae as well as *Daphnia* and
jellyfish. nMDS analysis examining only the meroplankton community demonstrat-
ed significant differences between +mangrove and -mangrove areas ($r^2 = 0.50$, Stress
in randomized runs: $P < 0.01$; Fig. 3B) as did an analysis of the holoplankton com-
munity ($r^2 = 0.42$, Stress in randomized runs: $P < 0.01$; Fig. 3C).

ZOOPLANKTON TOWS.—In plankton tows, several meroplankton taxa (including
amphipods, euphausids, mysids, and ostracods) were more abundant in +mangrove
than -mangrove areas (Fig. 2B; online Appendix 1) with some taxa being 10–100
times greater in +mangrove areas. For all other taxa sampled in plankton tows, there
was no significant difference in taxon abundance between + and -mangrove areas
(Fig. 2B). There was also no difference in the total zooplankton abundance between
+mangrove (mean = 351 ± 86) and −mangrove (477 ± 109) areas (Paired t-test: $t =
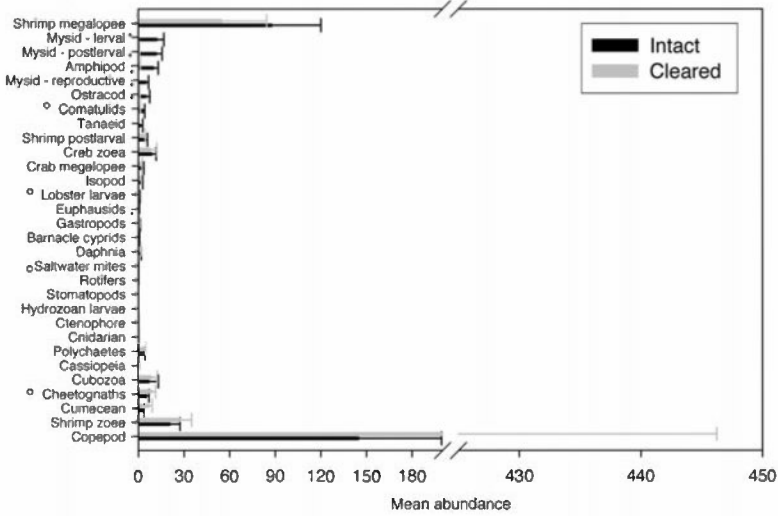1.3487$, $df = 10$, $P = 0.20$).

A. Trap
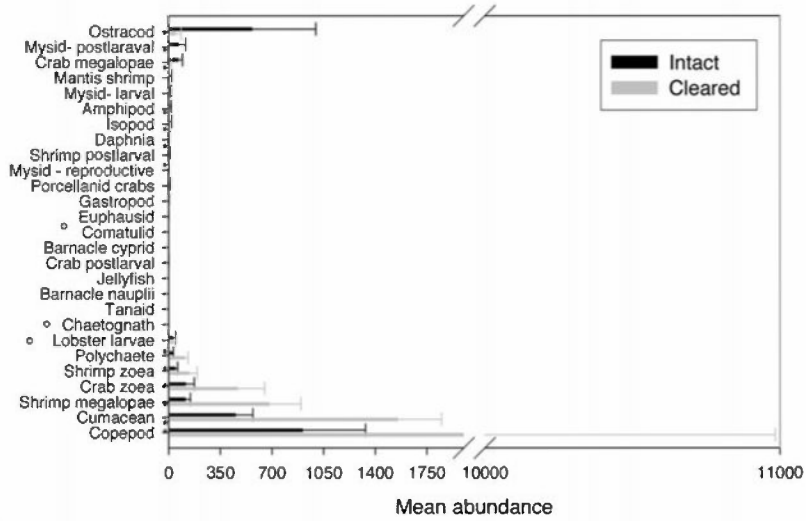
B. Tow

Figure 2. Difference in mean taxon abundance between +mangrove areas and −mangrove areas. * indicates significant difference ($P < 0.05$). ° indicate taxa that are not known as important food items for reef fish; all others are considered key food items for reef fish (Randall, 1967).

Overall zooplankton diversity in tows was more than 50% higher in +mangrove areas compared to -mangrove areas (Shannon Weiner diversity index: intact = 2.13, removed = 1.34). nMDS analysis revealed differences in zooplankton communities between +mangrove and -mangrove areas ($r^2 = 0.51$, Stress in randomized runs: P < 0.01; Fig. 3D). Community differences in plankton tows were primarily driven by higher abundances in +mangrove areas of holoplankton including *Daphnia*, jellyfish, and rotifer larvae; and meroplankton including comatulids, euphausids, hydrozoan
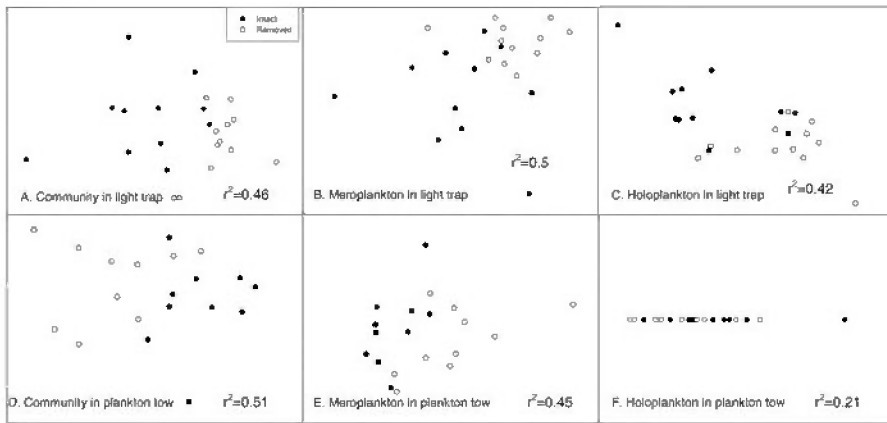
Figure 3. Nonparametric multidimensional scaling ordinations of differences in communities between intact and cleared mangrove areas from light traps (A–C) and plankton tows (D–F). Closed circles are +mangrove areas and open circles are -mangrove areas.

larvae, mantis shrimp, and snails. nMDS analysis examining only meroplankton revealed differences in communities between +mangrove and −mangrove areas ($r^2 = 0.45$, Stress in randomized runs: $P < 0.01$; Fig. 3E) although there was no difference in holoplankton communities between +mangrove and -mangrove areas ($r^2 = 0.21$, Stress in randomized runs: $P < 0.03$; Fig. 3F).

DISCUSSION

Taxonomic diversity of zooplankton communities, and, in particular, meroplankton, was different between adjacent areas with and without intact mangroves. We found that amphipods, euphausids, mysids, and ostracods were more abundant in undisturbed mangrove areas, regardless of sampling method. Crab megalopae and isopods were more abundant in light trap samples from undisturbed mangroves, whereas copepods, cumaceans, polychaetes, and crab and shrimp zoeae were more abundant in cleared areas. In addition to the dominant taxa sampled, less common taxa (e.g., jellyfish, comatulids, euphausids) also contributed to the patterns of community differences observed between intact and cleared areas, possibly due to their near or complete absence from cleared areas coupled with the high variability across samples for some more abundant species. Although light traps in +mangrove areas were likely sampling a smaller effective area than light traps in −mangrove areas due to decreased light penetration from roots and higher turbidity in +mangrove areas, the general patterns for these taxa were similar in both tows and traps, suggesting that the results are informative and a true representation of community differences. Furthermore, our use of higher order taxonomic groupings in the diversity analyses as well as the limited temporal scale of this study (seasonal, diel) may underestimate diversity differences at the generic or species level or across seasons between intact and cleared mangrove areas.

Three major processes could be responsible, separately or in conjunction, for the difference in community structure between +mangrove and −mangrove areas: (1) differential proximity to source populations, (2) differential mortality, and/or (3) differential habitat preference among taxa. For taxa where adults inhabit and spawn

in mangrove habitats, proximity to such areas may well influence the relative abundance of early life stages. The community composition sampled in the two habitats could be affected by differential mortality through increased three-dimensional structure (Primavera, 1997; Sheridan and Hays, 2003) and turbidity in mangroves, both of which increase the ability of prey to escape or hide from predators, potentially increasing survival rates. Mangroves also provide shelter and protection for juvenile reef fish, including several zooplankton feeders (Randall, 1967), and are an important nursery and feeding area (Nagelkerken et al., 2001, 2002; Mumby et al., 2004; Nagelkerken and van der Velde, 2004). If the abundance of these juvenile planktivorous reef fish is greater in +mangrove areas (see Mumby et al., 2004), then predation pressure on zooplankton in mangrove areas should be high; however, it is unknown how lower predator abundance combined with reduced shelter against predators interact to affect the abundance of preferred prey items such as shrimp larvae, cumaceans, copepods, and polychaete worms in cleared areas where reef fish populations are purported to be lower (e.g., Mumby et al., 2004). Teasing apart the contribution of these conflicting mechanisms to differences in community structure between +mangrove and −mangrove areas necessitates further experimental investigation.

Habitat preference may also structure the zooplankton community. Mangrove habitat may be favorable to meroplankton because of lower thermal stress (Granek, 2006), increased structure for predator avoidance (Mohan et al., 1997; Kingsford et al., 2002), and greater food availability (Schwamborn et al., 2002). Zooplankton are capable of responding to temperature cues (Yurista, 2000; Metaxas, 2001; Ouimet, 2001; Bell and Weithoff, 2003), and thermally stressful events are significantly more frequent in −mangrove areas (Granek, 2006). Therefore, zooplankton may be attracted to the less thermally stressful environment of mangrove areas relative to cleared areas. Variation in swimming abilities among meroplankton (Holzman et al., 2005) may contribute to the taxonomic variability in intact mangrove areas, as only strong swimmers may be able to actively select mangrove root structure. Because meroplankton ultimately need to settle and holoplankton do not, holoplankton may be more patchily distributed across inshore habitats with varying benthic complexity (Ambler et al., 1991; Stewart, 1996) and swarming behavior in certain taxa may contribute to this patchiness (Ambler, 2002). Patchy distribution in the water column and micro-site differences may explain some of the observed between-site and -night variability. Our finding that meroplankton are more abundant in +mangrove areas whereas holoplankton are similar (in tows) or only slightly more abundant (in traps) in −mangrove areas supports this tenet.

The observed differences in zooplankton diversity and community composition between +mangrove and -mangrove areas suggest a potential impact of mangrove removal on coastal marine communities. Previous studies in diverse habitats demonstrate that habitat loss or transformation can lead to changes in community composition and species diversity (Boulinier et al., 2001; Silliman and Bertness, 2004; Stoner and Joern, 2004; Watson et al., 2004). Mangrove deforestation may change zooplankton communities due to a decrease in physical features, structure, changes in food availability, and water flow. Most zooplankton taxa sampled in this study are common or preferred food items for juvenile and adult reef fish (Randall, 1967; Fig. 2). Further research is needed to determine whether changes in zooplankton community composition observed in this study may lead to reduced food availability for

juvenile and adult reef fish feeding in mangrove habitat. The source of larval inver-
tebrates for adult populations on adjacent reefs may decline as the meroplankton
population shifts in nearby cleared mangrove areas. Further research is needed to
determine whether changes in zooplankton abundance and diversity cascades into
changes in fish communities on adjacent reefs following shifts in preferred prey items
subsequent to mangrove removal.

ACKNOWLEDGMENTS

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