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# The Roles of Large Top Predators in Coastal Ecosystems: New Insights from Long Term Ecological Research

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# THE ROLES OF LARGE TOP PREDATORS IN COASTAL ECOSYSTEMS

## New Insights from Long Term Ecological Research

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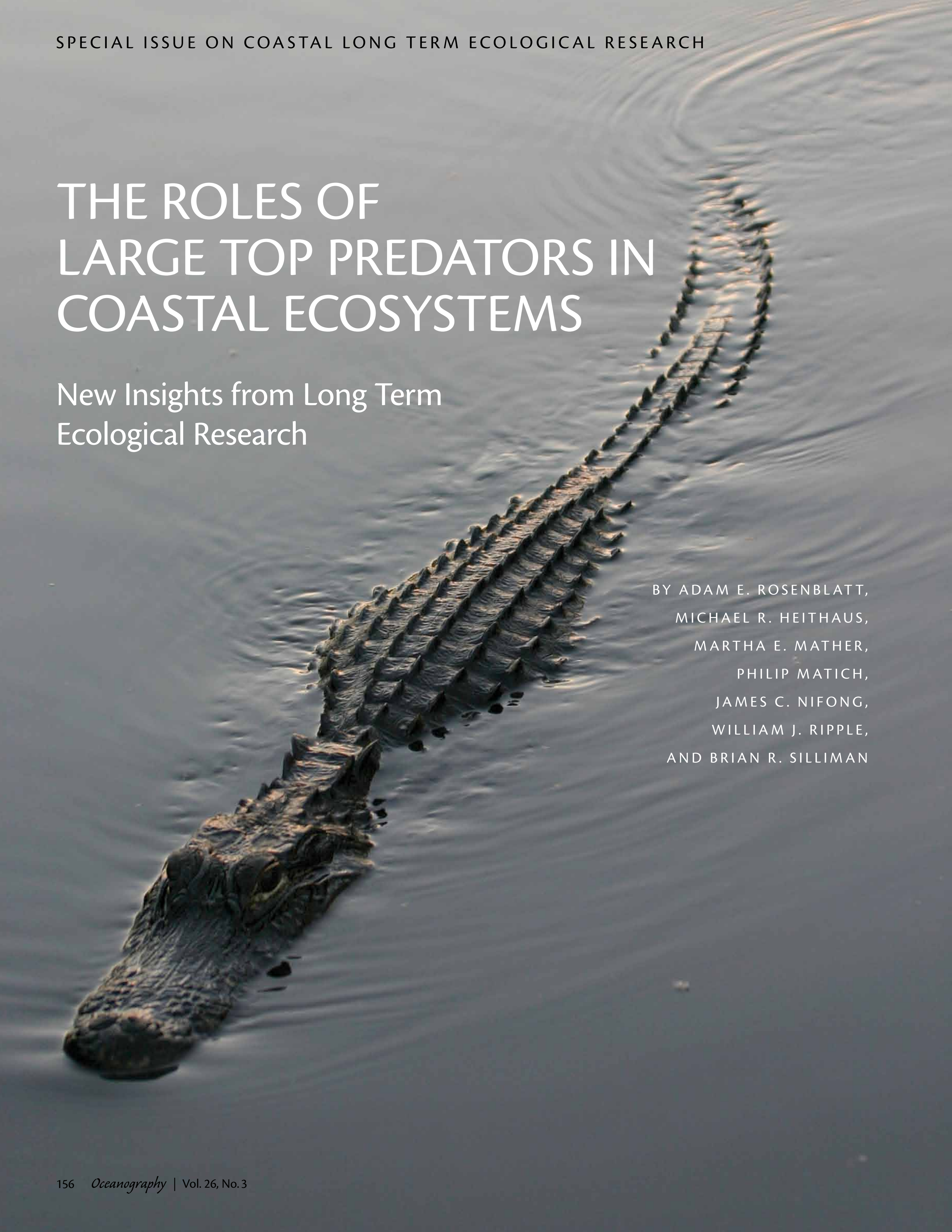

ABSTRACT. During recent human history, human activities such as overhunting and habitat destruction have severely impacted many large top predator populations around the world. Studies from a variety of ecosystems show that loss or diminishment of top predator populations can have serious consequences for population and community dynamics and ecosystem stability. However, there are relatively few studies of the roles of large top predators in coastal ecosystems, so that we do not yet completely understand what could happen to coastal areas if large top predators are extirpated or significantly reduced in number. This lack of knowledge is surprising given that coastal areas around the globe are highly valued and densely populated by humans, and thus coastal large top predator populations frequently come into conflict with coastal human populations. This paper reviews what is known about the ecological roles of large top predators in coastal systems and presents a synthesis of recent work from three coastal eastern US Long Term Ecological Research (LTER) sites where long-term studies reveal what appear to be common themes relating to the roles of large top predators in coastal systems. We discuss three specific themes: (1) large top predators acting as mobile links between disparate habitats, (2) large top predators potentially affecting nutrient and biogeochemical dynamics through localized behaviors, and (3) individual specialization of large top predator behaviors. We also discuss how research within the LTER network has led to enhanced understanding of the ecological roles of coastal large top predators. Highlighting this work is intended to encourage further investigation of the roles of large top predators across diverse coastal aquatic habitats and to better inform researchers and ecosystem managers about the importance of large top predators for coastal ecosystem health and stability.

## INTRODUCTION

Among the processes regulating population, community, and ecosystem dynamics are at least four major interdependent processes that operate over short time scales (i.e., excluding evolutionary and geologic processes, which generally have longer time scales): (1) "bottom-up" forces such as primary production, nutrient dynamics, and energy cycles; (2) "top-down" forces such as predation, risk effects, and trophic cascades; (3) nonpredatory interactions, including facilitation and inter- and intraspecific competition for resources; and (4) both pulse and press disturbance events such as fires, wave action, storms, floods, and droughts (Sousa, 1984; Estes et al., 2001; Bruno et al., 2003; Terborgh and Estes, 2010; Turner, 2010). The varying strengths of these interacting processes have been debated throughout the history of modern ecology (e.g., Power, 1992; Estes et al., 2001; Bruno et al., 2003; Meserve et al., 2003; Bando, 2006; Reed et al., 2011), but it has gradually become clear that all four processes are present to some degree in virtually every ecosystem on the planet, with the relative importance of each being somewhat context dependent (e.g., Zhang and Adams, 2011). Human actions have modified these forces across ecosystems in countless minor and major ways for many millennia, likely even prior to recorded history (Rule et al., 2012). However, in recent history, human impacts on these forces have been larger in scope and magnitude and have occurred more rapidly than ever before because of massive increases in human population and resource consumption, leading to human dominance of many global ecological processes (Imhoff et al., 2004; Schlesinger, 2006; Strong and Frank, 2010).

Though human actions have affected all four processes, top-down processes have been particularly strongly altered through over-hunting of large top predators and habitat destruction, leading Estes et al. (2011) to suggest that the loss or marginalization of top predator populations "is arguably humankind's most pervasive influence on the natural world." The loss or diminishment of top-down control can have dramatic consequences on ecosystem structure and function because top predators help regulate population, community, and ecosystem dynamics through consumption of prey, altering the behavior of prey through risk effects, initiating trophic cascades, and altering nutrient and biogeochemical cycles (Goldschmidt et al., 1993; Estes and Duggins, 1995; Pace et al., 1999; Terborgh et al., 2001; Heithaus et al., 2008; Beschta and Ripple, 2009; Schmitz et al., 2010; Estes et al., 2011; Burkholder et al., 2013). For example, the extirpation of large top predators on the Kaibab Plateau in northern Arizona in the early twentieth century caused irruption (sudden rapid increase) of the mule deer (*Odocoileus hemionus*) population, leading to over-browsing, a reduction in woody browse cover, and eventually famine among the deer (Leopold, 1943; Binkley et al., 2006). Similarly, in Yellowstone National Park, the extirpation of wolves (*Canis lupus*) in the early twentieth century led to an increase in the elk (*Cervus elaphus*) population, a concomitant decrease in the recruitment of deciduous tree species, and related effects on ecosystem structure and function (Ripple and Beschta, 2012). Also, on predator-free islands artificially created by the construction of a hydroelectric dam in Venezuela in the 1980s, herbivore densities increased 10 to 100-fold relative to the mainland, and the plant communities on the islands were severely negatively impacted (Terborgh et al., 2001). Lastly, recent research shows that predatory spiders can even indirectly affect the nutrient content of soils and plant-litter decomposition rates through fear of predation by their grasshopper prey (Hawlena et al., 2012).

Coastal areas contain some of the highest densities of humans on the planet and have been heavily developed as a result (Small and Nicholls, 2003), causing coastal aquatic large top predator populations to be particularly vulnerable to human actions (Jackson et al., 2001; Ferretti et al., 2010). Given the high productivity and importance of coastal areas to human populations (Barbier et al., 2011), it is crucial to understand the roles of large top predators in these systems so that we can predict the potential consequences of their extirpation and marginalization for coastal ecosystem structure and function, and to manage conservation efforts where possible. Yet, relatively few long-term studies of the roles of large top predators in coastal aquatic habitats have been conducted (but see examples below), leaving a significant gap in our understanding of the underlying top-down mechanisms potentially regulating coastal aquatic population, community, and ecosystem dynamics. Here, we review what is known about the roles of large top predators in coastal aquatic systems and present a synthesis of recent work from three coastal eastern US Long Term Ecological Research (LTER) sites where long-term studies have revealed insights into what appear to be common themes relating to the roles of large top predators in these systems. Our hope is that highlighting this work will encourage further investigation of the roles of large top predators across diverse coastal aquatic habitats and better inform researchers and ecosystem managers about the importance of large top predators for ecosystem health and stability.

## ROLES OF LARGE TOP PREDATORS IN COASTAL SYSTEMS: WHAT DO WE KNOW?

The limited number of studies that have investigated the long-term roles of large top predators in coastal systems offer fascinating insights into coastal population, community, and ecosystem dynamics. Perhaps the most well-known long-term study is that of sea otters (*Enhydra lutris*) within the kelp forests of the Aleutian archipelago (Estes and Duggins, 1995). Over 15 years, researchers surveyed kelp forests along a sea otter density gradient and found that where sea otter populations were healthy and at or near equilibrium density, their herbivore prey, sea urchins (*Strongylocentrotus* spp.), were unable to overgraze kelp, and as a result kelp forests were able to thrive. Conversely, in areas where sea otters were absent, likely because of overexploitation, sea urchin populations were much larger and kelp was less abundant. This research showed that trophic cascades (i.e., when predators indirectly affect lower trophic levels through interactions with their prey; Paine, 1980) can be very strong in coastal systems, and that prey consumption by large top predators can be key for regulating ecosystem structure and stability. These conclusions are supported by other studies of losses of large top predators from coastal systems, such as overfishing of cod (*Gadus morhua*) in the Gulf of Maine and overhunting of marine mammals in the Baltic Sea, each of which led to serious "trophic-level dysfunction" and possible ecological regime shifts (Steneck et al., 2004; Österblom et al., 2007), and overfishing of large sharks along the US eastern seaboard, which Myers et al. (2007)

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hypothesized may have led to predation release of cownose rays (*Rhinoptera bonasus*) and a concomitant collapse of the bay scallop (*Argopecten irradians*) fishery, a major prey of cownose rays.

Another important long-term study (15+ years) of the effects of large top predators on ecosystems was carried out in Shark Bay, Australia (Heithaus et al., 2012). Researchers used the seasonal presence of tiger sharks (*Galeocerdo cuvier*) in the bay as a natural experiment to investigate the effects of predator presence on prey behaviors and the seagrass community. They found that a variety of tiger shark prey altered their behaviors and habitat use in the presence of sharks to balance risk of predation and their own foraging. Experimental manipulations suggested that these behavioral changes cascade to the seagrass community, altering their biomass, structure, composition, and nutrient dynamics (Burkholder et al., 2013). Together, these studies from a variety of coastal systems showed that large top predators can exert strong top-down effects on coastal ecosystem dynamics through both direct consumption and indirect predation risk effects, and that losses of large top predators can have severe consequences for coastal food web stability. However, recent research in other systems suggests that top predators may play significant roles in other aspects of ecosystem dynamics, such as nutrient cycling and transport (Schmitz et al., 2010) and habitat connectivity (Polis et al., 2004; Darimont et al., 2009). Given the high mobility and relatively large appetites of many coastal large top predators, we were interested in investigating whether they had the potential to play such roles and, if so, what the possible consequences for ecological theory and ecosystem management and conservation could be. Here, we present some of our early findings.

## COASTAL EASTERN US LTER STUDIES: INSIGHTS INTO THE ROLES OF LARGE TOP PREDATORS

Large top predator research began at the Plum Island Ecosystems (PIE) site, Massachusetts, with the study of striped bass (*Morone saxatilis*) in 1999. Bull shark (*Carcharhinus leucas*) research began at the Florida Coastal Everglades (FCE) site in 2005 and expanded to include American alligators (*Alligator mississippiensis*) in 2007 and bottlenose dolphins (*Tursiops truncatus*) in 2011. Alligator research at the Georgia Coastal Ecosystems (GCE) site began in 2007. At all three sites (Figure 1), our research has focused primarily on movement, habitat use, and feeding patterns (Figure 2) and how biotic and abiotic factors affect them. We have identified three major themes that appear to be common to all three sites: (1) predators acting as mobile links between disparate habitats, (2) predators potentially affecting nutrient and biogeochemical dynamics through localized behaviors, and (3) individual specialization of large top predator behaviors.

### Highly Mobile Top Predators May Connect Disparate Coastal Habitats

Many large top predator species are highly mobile, maintain large home ranges, and exhibit seasonal shifts in habitat use. These attributes often result in interaction of large top predators with a wide diversity of prey and habitats and theoretically promote ecosystem stability (Rooney et al., 2006). Predators have the potential to link prey populations and habitats through three main pathways (Polis et al., 1997): directly transporting nutrients between habitats (e.g., Holtgrieve and Schindler, 2011), indirectly affecting nutrient transport

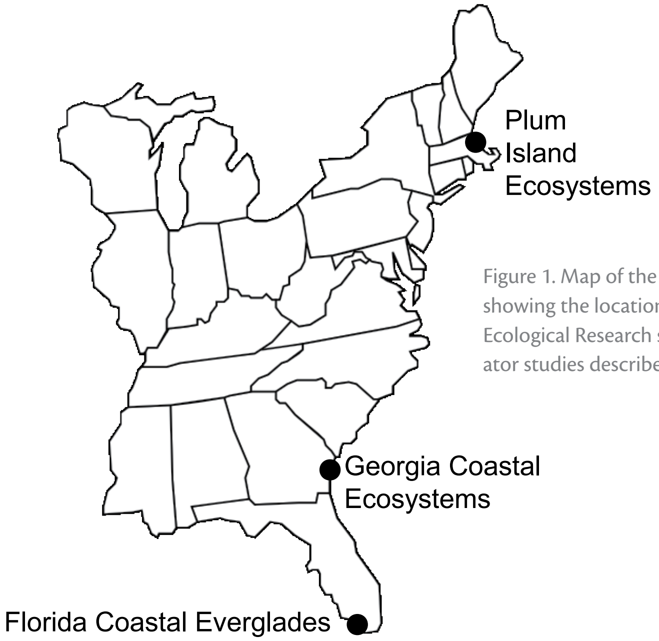

Figure 1. Map of the eastern United States showing the locations of the three Long Term Ecological Research sites where the large top predator studies described in the text take place.

between ecosystems by affecting prey that transport nutrients (e.g., Croll et al., 2005; Maron et al., 2006), and subsidizing their diets in one ecosystem, which then can affect their top-down or competitive interactions in another habitat (e.g., Sabo and Power, 2002; Lancaster et al., 2008). However, the majority of what is known about these pathways comes from short-term studies that consider the interactions of smaller-bodied mesopredators. Though mesopredators can and do link ecosystems through movements and feeding behaviors, large top predators appear to be unique in that a relatively small number of individuals can potentially link ecosystems through their movement and feeding behaviors and as a result significantly alter ecosystem dynamics (e.g., Estes et al., 1998).

Studies across our three coastal eastern US LTER sites suggest that highly mobile top predators have the potential to be important links among habitats and ecosystems over a variety of spatial and temporal scales. In the oligotrophic Shark River Estuary (SRE; Childers

Figure 2. (A) An American alligator (*Alligator mississippiensis*) on Sapelo Island, GA, with a Global Positioning System unit attached to its neck. (B) A juvenile bull shark captured in the Shark River Estuary, FL, with an identity tag attached to its dorsal fin. (C) Researchers drawing blood from a bull shark (*Carcharhinus leucas*) in the Shark River Estuary, FL. (D) Researchers drawing blood from an alligator in the Shark River Estuary, FL. We applied stable isotope analysis to the blood to elucidate top predator feeding patterns.

et al., 2006) of FCE, about half of the alligators regularly travel long distances (15–25 km) from freshwater/estuarine habitats to marine habitats to feed, then travel back to freshwater/estuarine habitats to restore their osmoregulatory balance (Rosenblatt and Heithaus, 2011). In fact, over two years, nine alligators alone made 244 round trips between the different habitats (Rosenblatt and Heithaus, 2011). Similarly, many juvenile bull sharks captured in the freshwater/estuarine waters of the SRE feed on a diverse mix of marine/estuarine/freshwater taxa, suggesting that these sharks move between the different habitats of the SRE and link them through trophic interactions (Matich et al., 2011). Such behaviors by these large, mobile consumers may lead to transport of limiting nutrients from relatively nutrient-rich marine habitats to oligotrophic freshwater/estuarine habitats, which could affect community composition of primary producers. For example, FCE is a phosphorus (P)-limited system (Childers et al., 2006) in which additions of as little as 3–13 $\mu$g $L^{-1}$ of P can lead to replacement of periphyton communities, the basal resource for much of the freshwater Everglades, by filamentous green algae (Noe et al., 2001). Fasting alligators alone excrete on average 7 mg of P per kg of body weight per day in their urine (Coulson and Hernandez, 1964), and actively feeding alligators presumably would excrete even more. If alligators transported even a fraction of this P from marine areas to freshwater areas repeatedly over time, it could potentially alter local freshwater primary production. Therefore, including estimates of consumer-mediated nutrient inputs (from these, and other, large-bodied and highly mobile predators) could be important for understanding biogeochemical cycles and primary productivity, especially in oligotrophic systems.

Similarly, at GCE, alligators repeatedly move between freshwater ponds/wetlands and estuarine habitats, potentially linking these geographically distinct areas through nutrient transport and trophic interactions. For FCE and GCE, movements of consumers occur over scales of tens of kilometers and hours to days. In contrast, at PIE, striped bass use the estuary as a feeding ground but depart during the fall, thereby potentially coupling PIE with other coastal habitats at scales of tens to hundreds of kilometers over many months (Mather et al., 2009, 2013, in this issue). Large-scale migrations of bass likely export nutrients from PIE, and prey in PIE may alter striped bass predation in other ecosystems.

Although cross-boundary movements of the large predator populations at FCE, GCE, and PIE generally occur consistently across years (e.g., Rosenblatt and Heithaus, 2011), the degree of habitat coupling likely varies in magnitude and relative importance both annually and seasonally. For example, potential habitat coupling at FCE is linked to seasonal fluctuations in salinity for alligators, with downstream movements concentrated in the wet season when salinities are lower (Rosenblatt and Heithaus, 2011). Extreme events also appear to be important. In 2010, an abnormally long cold period at FCE killed or forced out almost all the juvenile bull sharks in the SRE (Matich and Heithaus, 2012). The impacts of this event on shark demographics, trophic interactions, and their ecological roles are currently being assessed.

Studies from other systems that have examined the potential roles of large top predators in nutrient translocation between ecosystems and their possible ability to link the population dynamics of prey in different habitats have shown similar results. Brown bears (*Ursus arctos*) in Alaska, through the relocation of salmon carcasses from streams to riparian areas and the consumption and excretion of salmon-derived nutrients, are responsible for up to 24% of riparian nitrogen budgets (Helfield and Naiman, 2006). Also, orcas (*Orcinus orca*) in the Aleutian archipelago triggered declines in coastal sea otter populations in the 1990s after the disappearance of their preferred oceanic prey, Steller sea lions (*Eumetopias jubatus*) and harbor seals (*Phoca vitulina*), ultimately resulting in significant changes to kelp ecosystems and suggesting that orcas act as mobile links between largely unrelated prey populations (Estes et al., 1998). Furthermore, arctic foxes in the Aleutian archipelago can reduce seabird-mediated nutrient inputs from the ocean to terrestrial areas, causing grassland habitats to shift to dwarf shrub/forb-dominated ecosystems (Croll et al., 2005; Maron et al., 2006).

## Top Predators Potentially Contribute to Bottom-up Components of Coastal Ecosystems Through Localized Behaviors

Top-down and bottom-up drivers of environmental processes are strongly linked in many ecosystems. For example, freshwater consumers, through the coupled processes of consumption and excretion, can recycle nutrients such as nitrogen (N) and P at rates similar to other nutrient sources and contribute to heterogeneity in nutrient dynamics (Vanni, 2002). In the specific case of upper trophic levels, large top predators may contribute to the creation of heterogeneous nutrient patterns in ecosystems through their own nutrient recycling, inducing behavioral modifications (e.g., habitat shifts) in prey species that affect the distribution of nutrients (Schmitz et al., 2010). For example, caiman (Alligatoridae) in the central Amazon are hypothesized to recycle vital nutrients through consumption and excretion in areas where primary production is low, thereby stimulating the local food web and enabling the next generation of fish to grow and develop (Fittkau, 1970, 1973). Also, even short-term concentrations of nutrients excreted by piscivorous seabirds at artificial roosting sites can alter the composition and biomass of seagrass communities over multiple decades (Herbert and Fourqurean, 2008). Such potential interactions between top predators and biogeochemical cycling may enable large top predators to strongly influence the structure, composition, and spatial patterns of local areas through participation in bottom-up processes.

In the context of coastal eastern US LTER research, we have documented the potential for such interactions between top predators and biogeochemical cycles at local sites. Striped bass at PIE congregate at sites with physically complex habitat, likely because of dense aggregations of prey at these sites (Kennedy, 2013). This behavior could create hotspots of foraging and nutrient recycling, thereby providing more abundant nutrients to primary producers. Similarly, bull sharks at FCE, along with both estuarine and marsh consumers, increase their use of freshwater parts of the SRE during the dry season when marsh prey move into the SRE as a refuge from marsh drydown, potentially recycling and concentrating nutrients in this oligotrophic area (e.g., Boucek and Rehage, 2013; Matich and Heithaus, 2013).

Alligators at FCE and GCE also may influence local nutrient dynamics. For example, at FCE we have observed alligators consuming such common aquatic prey as blue crabs (*Callinectes sapidus*) on the banks of the SRE at vegetated "haul-out" sites. If nutrients from the crab carcasses or from alligator excretions accumulate over time because of fidelity to these well-used sites, then they may become hotspots as well, potentially altering vegetation dynamics. At GCE, alligators show site fidelity for dens in freshwater areas; therefore, the dens have the potential to also become nutrient hotspots.

Unfortunately, although the concentrations and site fidelity of top predators we have observed at specific locations have the potential to influence biogeochemistry, these data are rarely collected (but see Schmitz et al., 2010). However, studies in other systems suggest that the large top predators at our sites may indeed be important local recyclers of nutrients. For example, alligators create and maintain water-filled holes in the freshwater marsh areas of FCE (Palmer and Mazzotti, 2004). These "alligator holes" provide refuges for the alligators themselves when the surrounding marshes dry up during the dry season in south Florida, but they also provide valuable refuges for other aquatic organisms (Craighead, 1968; Palmer and Mazzotti, 2004). Caiman, close relatives of alligators, reside in similar seasonal lakes in the Amazon rainforest and may consume 0.6–0.8% of their body weight per day and excrete daily 0.2–0.3% of their body weight as vital nutrients (e.g., P, N, calcium, potassium), thereby recycling nutrients for use by primary producers (Fittkau, 1973). If alligators consume and excrete nutrients, especially P, at similar rates in alligator holes, they could be important but overlooked components of local nutrient cycles in FCE and possibly elsewhere, especially given the unique vegetation communities supported by alligator holes (Campbell and Mazzotti, 2004).

## Top Predator Populations May Contain Individuals that Vary Substantially in Their Behaviors and Ecological Roles

Although ecologists have long recognized that individuals within a population vary in their behavior because of sexual, morphological, and ontogenetic differences, only recently has individual variation, separate from these factors, been considered in ecological and evolutionary studies (Bolnick et al., 2003; Araujo et al., 2011; Dall et al., 2012). This type of intrapopulation variation in behavioral patterns has been variously termed contingents (Secor et al., 2001; Mather et al., 2010; Pautzke et al., 2010), behavioral syndromes (Sih et al., 2012), personalities (Ogden, 2012), and individual specializations (Bolnick et al., 2003; Araujo et al., 2011). Common individual behavioral differences include boldness-shyness, avoidance-exploration, aggressiveness-passivity, and sociability-asociability (Conrad et al., 2011), and individual specialization can lead to differences in foraging/movement tactics and prey selection (Bolnick et al., 2003; Araujo et al., 2007). Behavioral specialization can thus have important ecological implications (Bolnick et al., 2003; Sih et al., 2012) and can potentially affect habitat connectivity and nutrient recycling via top predator populations. The ultimate factors that contribute to individual behavioral variability are not yet fully understood, but may include learning (e.g., Estes et al., 2003), adaptive morphological/physiological plasticity, and differential genetic and epigenetic expression (Dall et al., 2012).

At all of our sites, there is evidence for individual specialization within populations of top predators. Acoustic tracking and stable isotope analysis reveal that alligators at FCE display several distinct and consistent movement and habitat use patterns that are linked to differences in trophic interactions (Rosenblatt and Heithaus, 2011), with bull sharks displaying similar behaviors. Fifty-six percent of alligators and 30% of bull sharks repeatedly commuted between freshwater/estuarine and marine habitats to feed, while other individuals remained in freshwater/estuarine areas year-round and never entered marine areas (Figure 3c; Rosenblatt and Heithaus, 2011). Similarly, GPS telemetry and stable isotope analysis of the blood of adult alligators at GCE showed that some individuals repetitively traveled to and from estuarine habitats to isolated upland freshwater wetlands and ponds; in contrast, other individuals chiefly used freshwater ponds and wetlands, never traveling to estuaries (Figure 3b). In addition, stable isotope analysis suggests that bull sharks at FCE display a wide range of behavioral types. Despite occurring in the same habitats, some individuals are dietary generalists while others specialize in either marine or estuarine/freshwater prey (Matich et al., 2011). Striped bass at PIE also exhibit individual behavioral specialization in that seasonally resident striped bass formed distinct foraging contingents that consistently used different areas of PIE throughout summer and fall even though there were no differences in the size of bass in the different groups

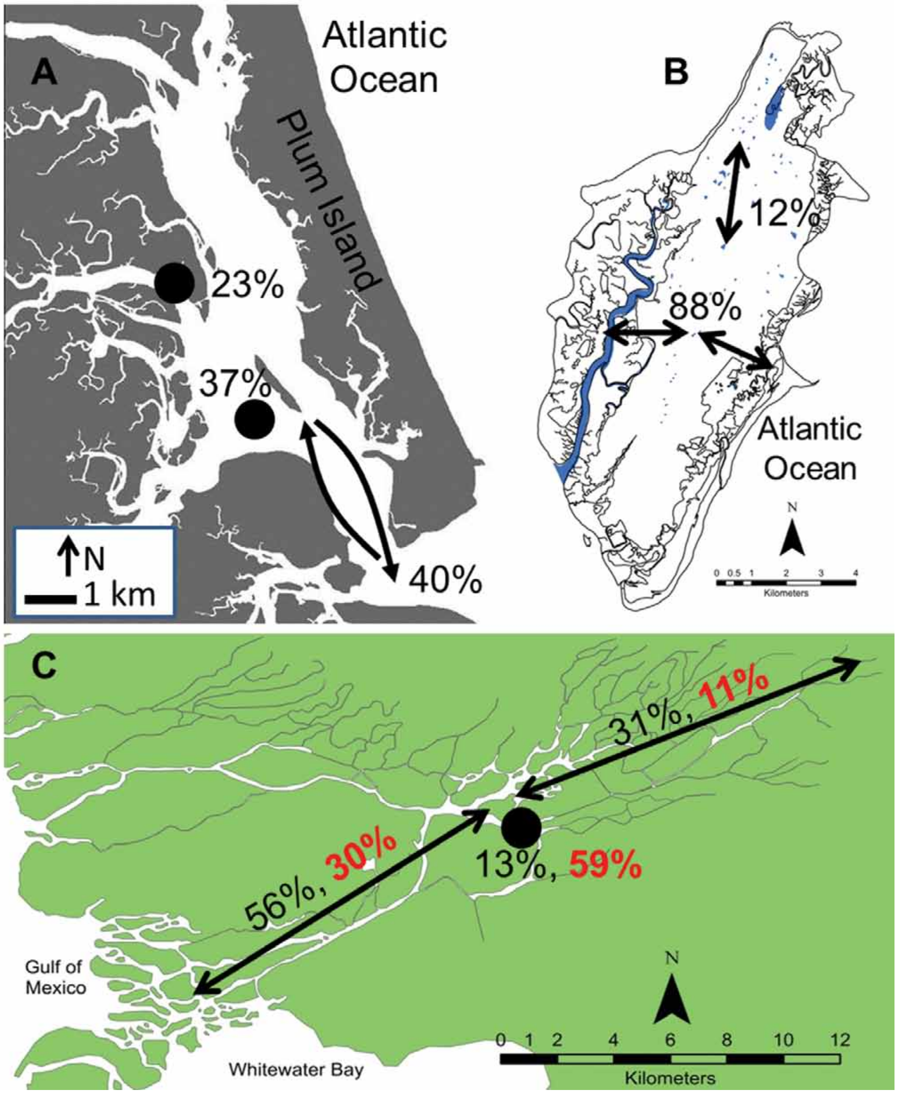

Figure 3. Detail maps of our three Long Term Ecological Research sites illustrating the variable movement patterns of large top predators. (A) Plum Island Estuary, MA. Dots represent locations where different striped bass (*Morone saxatilis*) foraging contingents remain during the feeding season, and arrows represent the foraging contingent that enters and then leaves the estuary. (B) Sapelo Island, GA. Arrows represent different groups of American alligators (*Alligator mississippiensis*) that either only move between different upland ponds/marshes or move between upland ponds/marshes and estuaries/marine habitats. (C) Shark River Estuary, FL, in the coastal Everglades. The dot represents an estuarine area where certain alligators and bull sharks (*Carcharhinus leucas*) remain resident year-round, and arrows represent other groups of alligators and bull sharks that either move between estuarine and marine habitats or between estuarine and freshwater habitats. In all maps, numbers indicate the percentage of the top predator population that exhibits each type of movement/habitat use behavior. In (C), black numbers correspond to alligators and red numbers correspond to bull sharks.

(Figure 3a; Pautzke et al., 2010). About 60% of these seasonally resident striped bass returned to PIE the following year after being detected in overwintering locations hundreds of kilometers away (Pautzke et al., 2010; Mather et al., 2013). This is surprising given that feeding site fidelity for migrants, which increases the potential benefits of local knowledge and specialized behavior, and might increase consumption of the local prey community, is rarely observed.

This individual variability in top predator behavior has ecological implications that are important to both theory and coastal management. For example, if individual top predators are more mobile and exploratory or show preference for specific prey taxa, then these individuals could initiate trophic cascades over wider areas, transport more nutrients between habitats, or more strongly alter local nutrient dynamics than conspecifics. Such behavioral variation within a large top predator population could therefore contribute to variation in the ecological roles of large top predators across systems and contexts. Furthermore, failing to account for intrapopulation variation could result in misunderstanding population distributions, migratory timing, movement patterns, foraging behaviors, growth, mortality, and reproduction. For example, it is likely that not all subsets of coastal top predator populations will have the same effects on local prey populations, couple habitats in the same ways, or transport nutrients using the same pathways. In addition, predators that use specific locations within an estuary (Pautzke et al., 2010; Rosenblatt and Heithaus, 2011) or that move along the coast in distinct migratory contingents (Mather et al., 2010) may be differentially vulnerable to spatially explicit anthropogenic stressors such as fishing, hypoxia, and pollution. As a result, if this intrapopulation variation is not recognized, management and conservation efforts may not be successful in many cases. Whereas many behavioral specialization studies are short term and small scale, research at LTER sites can track the behavioral patterns of individuals over longer time spans and incorporate new individuals into studies as they recruit into the local population, allowing for long-term investigation of the drivers, prevalence, and ultimate impacts of behavioral specialization on ecosystems.

> “…A MORE COMPLETE UNDERSTANDING OF LARGE PREDATORS’ TOP-DOWN AND BOTTOM-UP EFFECTS WILL ENABLE US TO BETTER UNDERSTAND THEIR IMPORTANCE WITHIN ECOSYSTEMS AND HOW PREDICTED CHANGES ACROSS DIFFERENT LAND- AND SEASCAPES MAY AFFECT ECOSYSTEM DYNAMICS.”

## CONCLUSIONS AND FUTURE RESEARCH

At FCE, GCE, and PIE, we found evidence that predators such as striped bass, alligators, and bull sharks exhibit intrapopulation behavioral variability, may connect disparate habitats through trophic pathways, and may serve as vectors for the transport of nutrients and biomass across habitat boundaries, which is especially important in nutrient-limited systems. As climate and human-induced change continues to affect much of the natural world, especially coastal ecosystems (Jackson et al., 2001; Waycott et al., 2009), a more complete understanding of large predators’ top-down and bottom-up effects will enable us to better understand their importance within ecosystems and how predicted changes across different land- and seascapes may affect ecosystem dynamics. Because our work is still in its early stages, much of our focus has been on describing behaviors and trophic interactions within the boundaries of the LTER sites. This research has been greatly facilitated by working within the LTER framework because of the abundance of data it offers on physical and biogeochemical ecosystem parameters as well as knowledge of primary producer dynamics. For example, directly assessing prey abundance at FCE has been very difficult because of the relatively low densities of prey, lack of water visibility, and rocky benthos, making many different types of sampling methods difficult or impossible to employ. Despite this lack of prey data, we were able to link alligator and bull shark movements to likely feeding behaviors because of the detailed understanding of the SRE productivity gradient and P, N, primary producer, and organic matter dynamics enabled by the long-term research at FCE (Childers, 2006; Simard et al., 2006).

The next step in large top predator research at our sites is to begin more explicitly quantifying the impacts of predators on nutrient cycling and redistribution, and in initiating trophic cascades that might structure primary producer communities and ecosystem processes. For example, at non-LTER sites, exclosure/enclosure field experiments have led to an understanding of functional relationships between predators, prey, and primary producers (e.g., Schmitz, 2003). Similar experiments focusing on large top predators, properly scaled, would allow us to establish causality between specific large top predator behavioral patterns and ecosystem responses. In addition, quantifying feeding and excretion rates of large top predators in experimental and natural settings (Vanni, 2002) would enable better understanding of the potential contributions of large top predators to nutrient cycling and transport relative to other sources. Also, use of animal-borne imaging (Heithaus et al., 2001) would provide predator-eye views of coastal LTER sites and more accurately link specific feeding behaviors with different habitats.

Ultimately, our research suggests that the roles of large top predators in coastal systems may not be confined to strictly top-down processes. Through their wide-ranging movements, consistent habitat use patterns, and site fidelity, large top predators are also potentially capable of impacting bottom-up processes both directly through nutrient recycling and transport across systems, and indirectly through alteration of prey behaviors and habitat use that then affects nutrient dynamics. Furthermore, individuals in large top predator populations do not all exhibit the same behaviors. Instead, individuals may move or forage differently from conspecifics, and, therefore, individuals could potentially play different ecological roles within the same ecosystem. Also, these concepts are transferable and scalable across different ecosystems, so they should continue to be explored across a diversity of habitats to reveal insights into the ecological roles of large top predators in general. The attributes of coastal large top predator behavior described here will only be fully understood with more research across varied ecosystems and species, but coastal ecosystem managers and ecological modelers should begin incorporating more of the varied roles of coastal large top predators into their management strategies and simulations to arrive at more accurate and nuanced conclusions.

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