

Among-individual niche variation of a marine top predator species, the bull shark (*Carcharhinus leucas*), suggests diverse functional roles within coastal food webs



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Introduction

- Predators may induce numerous direct and indirect effects in food webs
- Most studies of these effects have used a “species”-based approach
 - i.e., individuals within a predator species have same **trophic niche*** (network of trophic interactions)
- This approach could mask important variation in the way *predator individuals* affect community and ecosystem properties

*Elton (1927) *Animal Ecology*

Introduction

- e.g., just **five** killer whale individuals (*Orcinus orca*) switching their diets from pinnipeds to sea otters (*Enhydra lutris*) may have
 - triggered declines in otter populations* that...
 - ultimately led to collapse of kelp ecosystems in the northeastern Pacific‡



*Williams et al. (2004) *Ecology*

‡Estes et al. (1998) *Science*

Introduction

- Studies addressing possibility that top-down effects might vary as function of individual differences in trophic interactions needed
- First step: document among-individual trophic niche variation
- Juvenile bull sharks in an undeveloped subtropical estuary



The Bull Shark



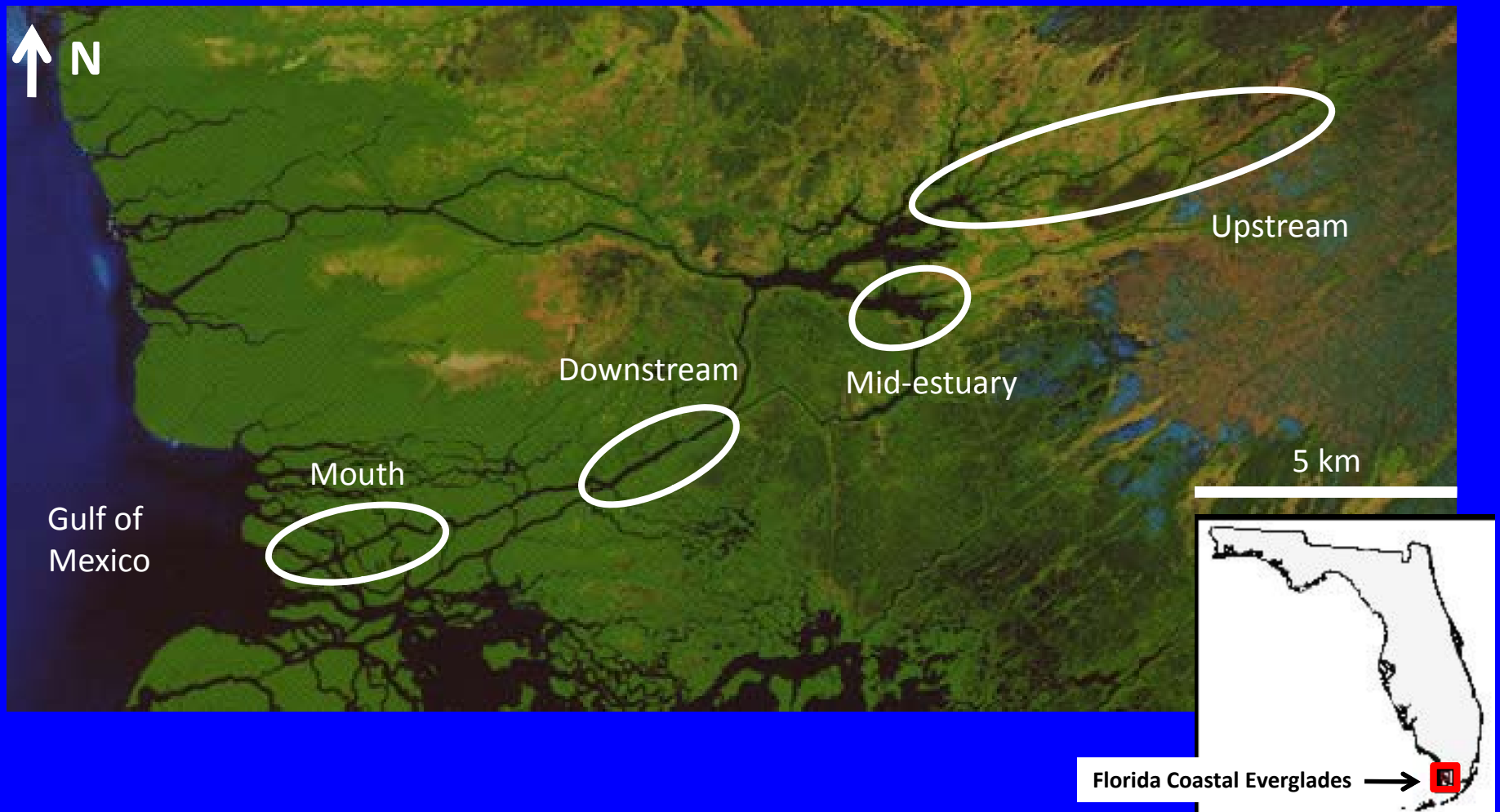
- Shallow tropical/subtropical distribution
- Large: to 3.4 m (~11 ft)
- Broad diet (teleosts, marine mammals, sharks)
- Threat to humans
- Euryhaline

Bull Sharks in Fresh Water



- Females venture into estuaries to pup
- Neonates and juveniles continue to use freshwater
 - Often found far upstream
- Explanation
 - Safety from larger sharks
- Our questions
 - Do juvenile sharks feed on freshwater resources while upstream?
 - If so, is there variation with respect to this tendency?

Shark River Estuary



Florida Coastal Everglades →

Longline Sampling



ca. 500m longline equipped with 50 Mustad size 12/0 tuna circle hooks

Fishing Protocol

- Sampling allocated evenly across 4 sites, seasons
- Longlines deployed from dawn to dusk
- Soak time = 1 hour
- Bull sharks caught processed immediately
- All released in good condition



Handling Protocol



- Sharks brought alongside boat
- Tagged, measured, sexed
- Muscle tissue sample collected using biopsy punch (0.5 cm², lateral to first dorsal fin)

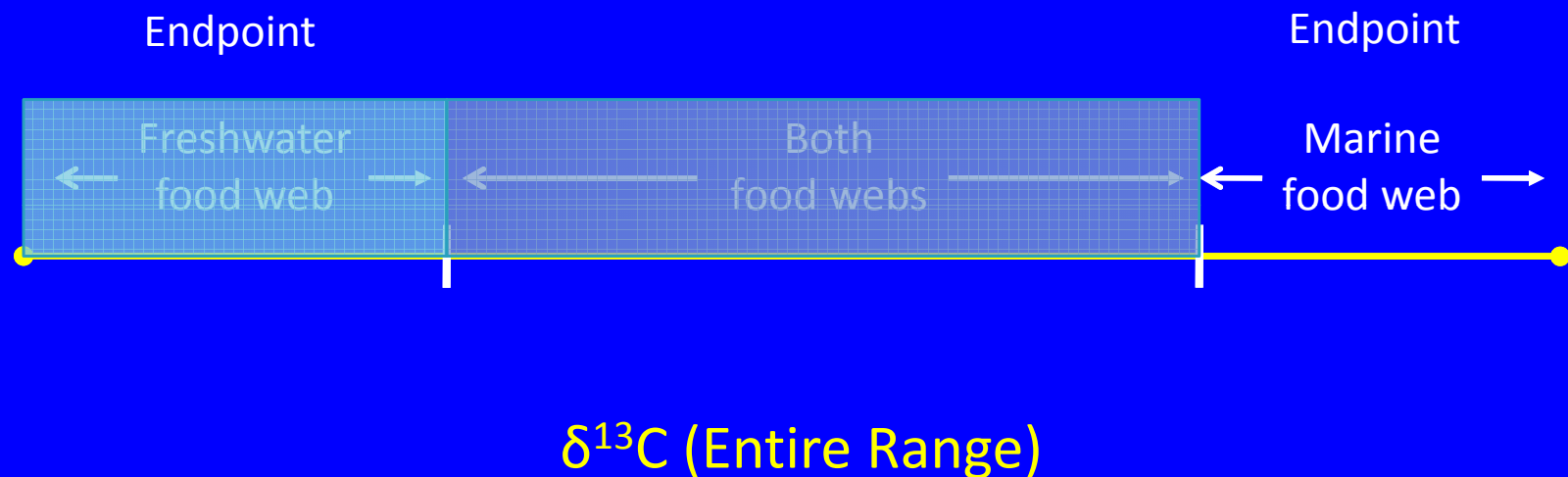
Stable Isotopic Analysis

- Muscle samples used to generate stable carbon (C) and nitrogen (N) isotopic signatures
- Stable isotopic analysis: provides time- and space-integrated representation of trophic ecology
 - Ratios of nitrogen isotopes (^{15}N to ^{14}N , or $\delta^{15}\text{N}$) exhibit stepwise enrichment with trophic transfers, estimate trophic position
 - Ratios of carbon isotopes (^{13}C to ^{12}C , or $\delta^{13}\text{C}$) vary among primary producers but not trophic transfers, identify ultimate sources of dietary carbon (organism's trophic niche)
- Bull shark muscle tissue turnover rate: 100s of days
 - $\delta^{15}\text{N}$ & $\delta^{13}\text{C}$ identify long-term differences in resource use
- ANOVA to test for effects of length, sex, season, site on $\delta^{15}\text{N}$, $\delta^{13}\text{C}$

Defining Food Web “Endpoints”

- **Goal:** Determine extent to which juvenile bull sharks feed in freshwater vs. marine food webs
- Defined ranges of $\delta^{13}\text{C}$ representative of producers and consumers existing solely in freshwater and marine food webs
- Establishment of isotopic carbon boundaries (“endpoints”) to distinguish individuals feeding exclusively in marine or freshwater food webs from those exploiting both
 - i.e., to distinguish specialized from generalized trophic niches

Defining Food Web “Endpoints”



- Exhaustive search of the literature*, own analysis

*Loftus 2000, Fry and Smith 2002, Chasar et al. 2005, Cornett 2006, Williams and Trexler 2006

Results

- Muscle tissue samples from 79 juvenile bull sharks
 - Largest reported database of stable isotope values for any elasmobranch
- Sizes ranged from 72 to 190 cm (total length)
- 1:1 sex ratio



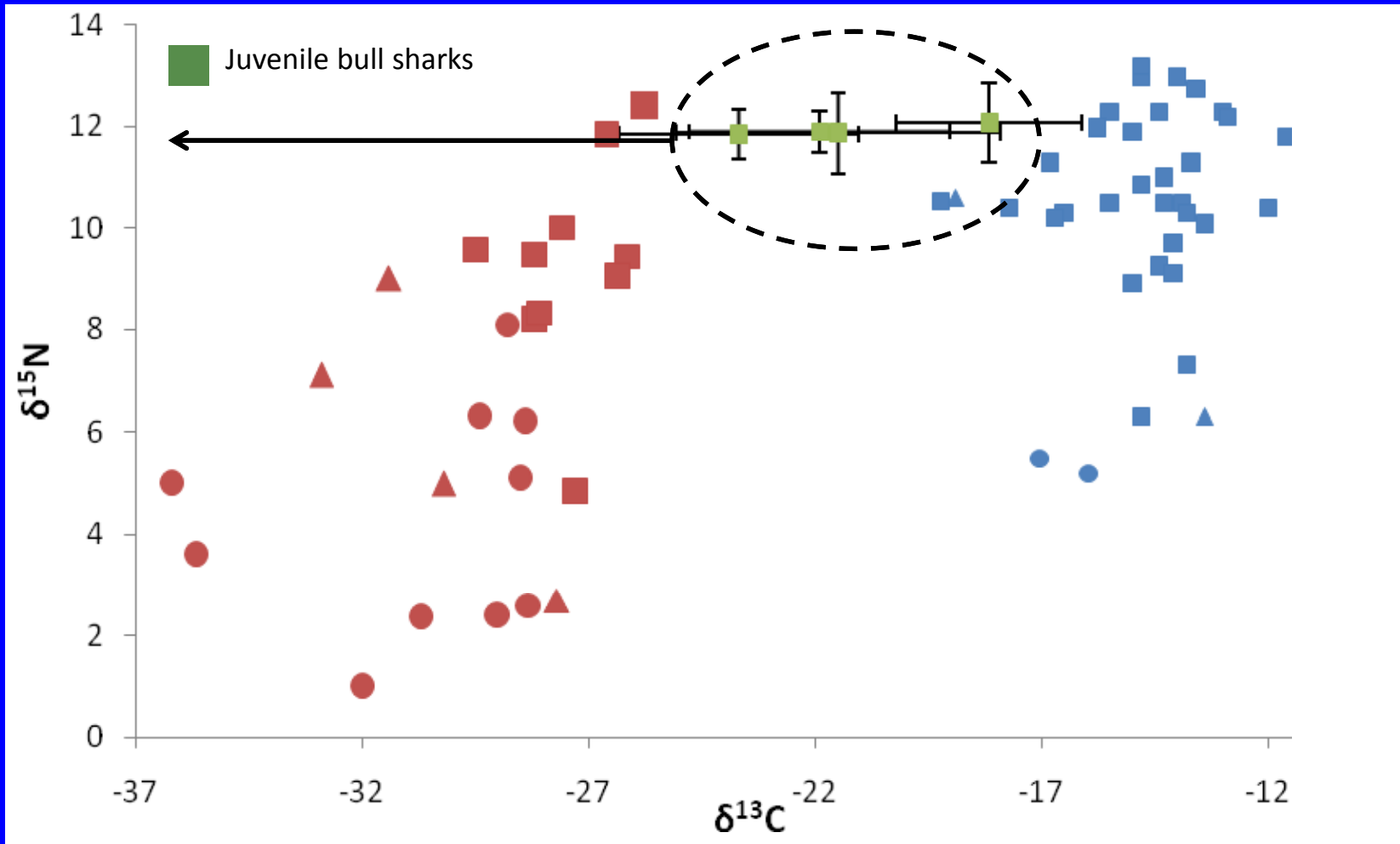
Mean Isotopic Ratios for Bull Sharks

- No significant variation in stable nitrogen isotope ($\delta^{15}\text{N}$) signatures with respect to
 - length ($F_{1,78} = 0.24$, $P = 0.6$)
 - sex ($F_{1,78} = 0.76$, $P = 0.8$)
 - season (wet versus dry) ($F_{1,78} = 0.61$, $P = 0.4$)
 - site ($F_{3,78} = 0.44$, $P = 0.7$)



Mean Isotopic Ratios for Bull Sharks

Trophic Position

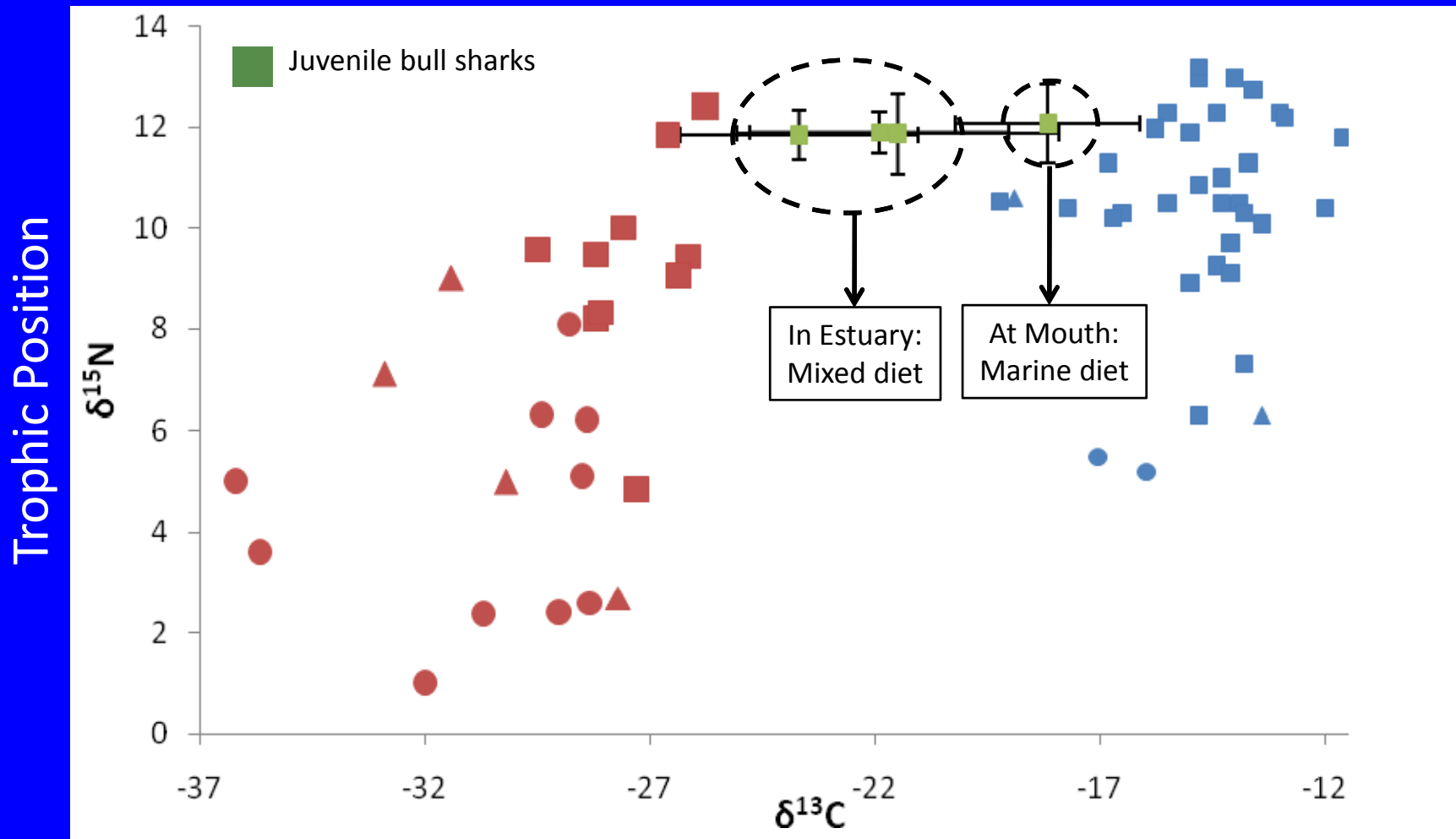


Source of Dietary Carbon (■ Freshwater vs. ■ Marine)

Mean Isotopic Ratios for Bull Sharks

- No significant variation in stable carbon isotope ($\delta^{13}\text{C}$) signatures with
 - length ($F_{1,78} = 1.76, P = 0.2$)
 - sex ($F_{1,78} = 2.90, P = 0.1$)
 - season ($F_{1,78} = 1.41, P = 0.2$)
- **But**, sharks captured at the mouth of estuary were more ^{13}C -enriched than those caught at sites farther upstream ($F_{3,78} = 7.60, P = 0.0002$)

Mean Isotopic Ratios for Bull Sharks



Source of Dietary Carbon (■ Freshwater vs. ■ Marine)

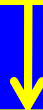
Trophic Niche Differentiation

- i.e., exploration of individual signatures revealed Three Niches

(1) Specialized niche: reliance on marine resources

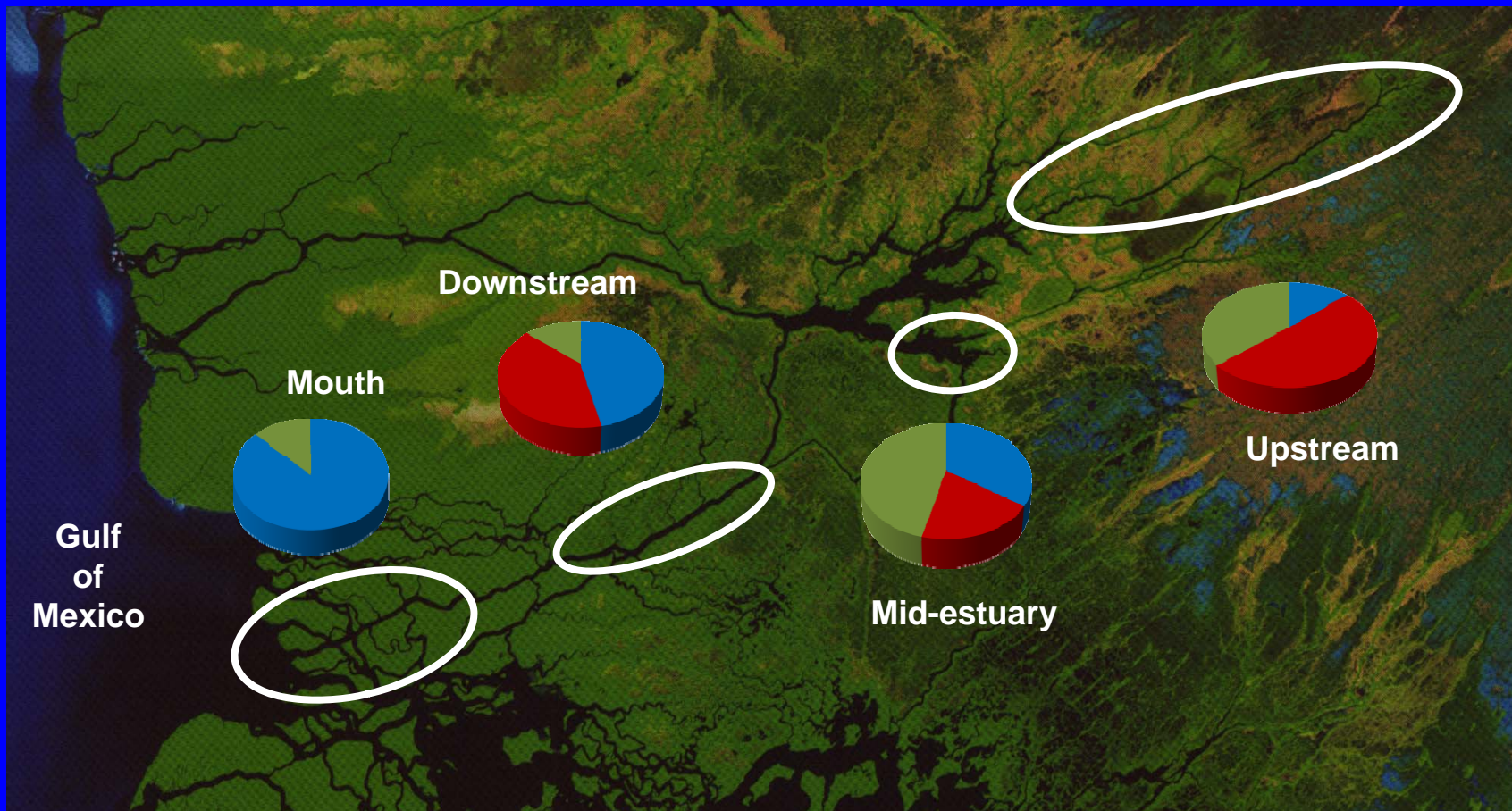
(2) Generalized niche: mixed diet

(3) Specialized niche: reliance on freshwater resources



Would have been missed had we relied on mean signatures

Distribution of Trophic Niches



Trophic Niche: Marine (Blue) Mixed (Green) Freshwater (Red)

Summary

- Juvenile bull sharks manifest 3 tropic niches
 - Marine or freshwater resource specialists, mixed diet
 - Freshwater niche missed without focus on individuals
- Niche variation not explained by size, sex, seasonal fluctuation
- Nor by location (space use)
 - 3 Niches at all upriver sites, individuals with marine niche 26 km upstream
- What is the explanation?

A Trade-off?

- Intraspecific variation in trophic niches can stem from unique set of trade-offs being associated with each niche*
- Likely the case for bull sharks in the Shark River
 - Marine river mouth is resource-rich but dangerous (predation by larger bull and lemon sharks)
 - Inside estuary, resources more scarce but predation risk is low
- This food-safety trade-off would promote niche diversity by
 - Allowing some individuals to exploit limited freshwater resources upstream in safety
 - While driving others to risk predation downstream for greater reward



*Bolnick et al. (2007) *PNAS*

Implications

- Our finding is notable for several reasons
- First, implicates bull sharks as **vectors** of nutrients into the nutrient-limited upper reaches of the Shark River
 - Juveniles transport nutrients (P) to depleted freshwater areas
- Second, first to document among-individual trophic niche variation in an elasmobranch within an age class
- Third, suggest that reliance on a small sample of individuals and/or a focus on mean trends could mask the diverse functional roles that predators play

Implications for Conservation

- Bull shark populations in the waters off of Florida appear to be in steep decline*
- Loss of bull sharks from these waters could lead to marine community reorganization
- Our results suggest that loss of bull sharks also could
 - alter nutrient dynamics in the upper reaches of the Shark River estuary
 - eliminate an important predator in freshwater food webs in these areas
- In general, ecological consequences of declines in large predators may be greater than is appreciated

*Heithaus et al. (2007) *CJFAS*

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WHERE DISCOVERIES BEGIN



Florida Coastal Everglades
Long Term Ecological Research



Questions

