No bull: Juvenile bull sharks may play diverse functional roles in coastal food webs

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Introduction

- Predators may induce numerous direct and indirect effects in food webs

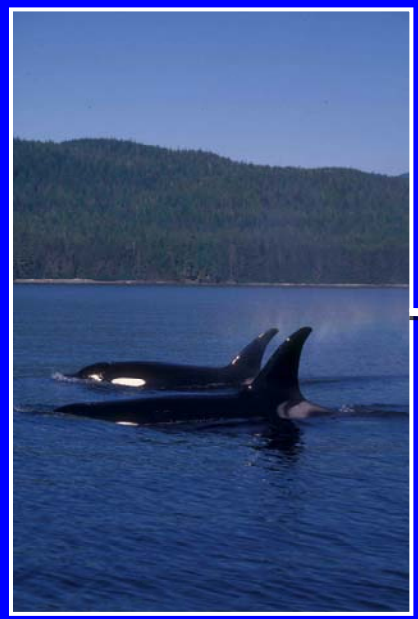
- Most studies of these effects have used a "species"-based approach
  - i.e., individuals within a predator species have same **trophic niche*** (network of trophic interactions)

- 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

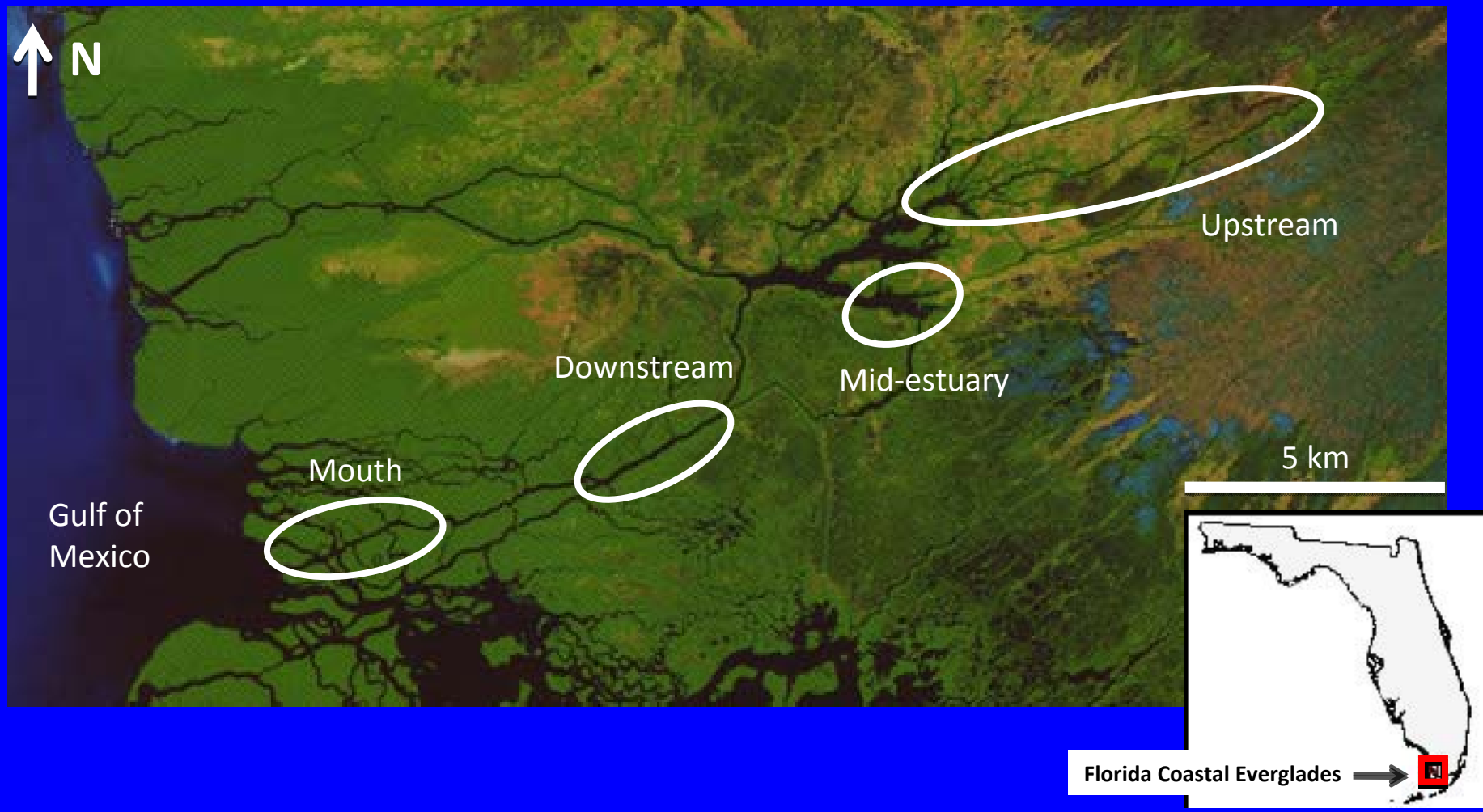
The Bull Shark

- 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
- 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



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

Handling Protocol

- All sharks…
- Tagged, measured, sexed
- Muscle tissue sample collected using biopsy punch (0.5 cm^2, lateral to first dorsal fin)

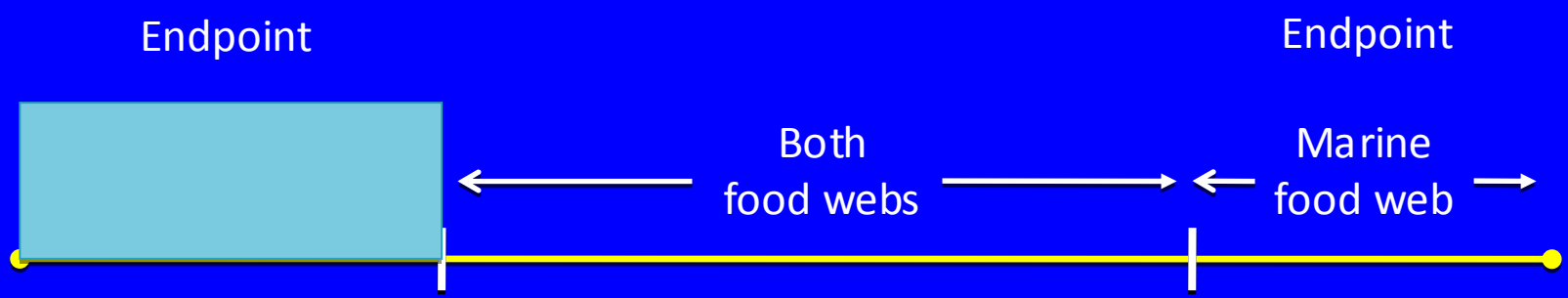
Stable Isotopic Analysis

- 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 $\delta^{15}N$) exhibit stepwise enrichment with trophic transfers, estimate trophic position
  - Ratios of carbon isotopes (^{13}C to ^{12}C, or $\delta^{13}C$) vary among primary producers but not trophic transfers, identify ultimate sources of dietary carbon (trophic niche)
- Bull shark muscle tissue turnover rate: 100s of days
  - $\delta^{15}N$ & $\delta^{13}C$ identify long-term differences in resource use
- ANOVA to test for effects of length, sex, season, site on $\delta^{15}N$, $\delta^{13}C$

Defining Food Web "Endpoints"

- **Goal**: Determine extent to which juvenile bull sharks feed in freshwater vs. marine food webs
- Defined ranges of $\delta^{13}C$ representative of producers and consumers existing solely in freshwater and marine food webs
- Establishment of isotopic carbon boundaries ("endpoints") to distinguish sharks feeding exclusively in marine or freshwater food webs from those in both

Defining Food Web "Endpoints"



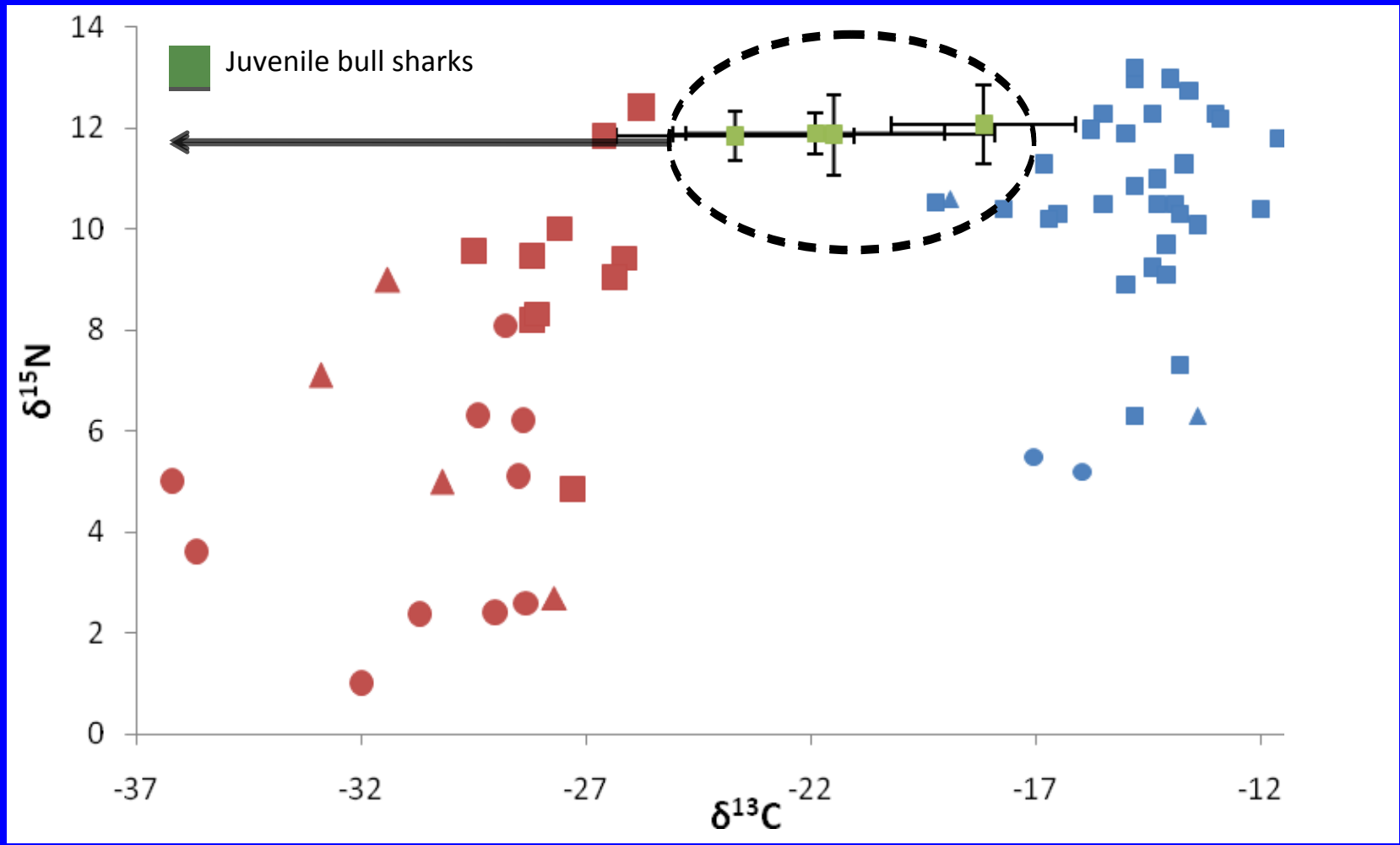
Results

- 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 ($\delta^{15}N$) 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

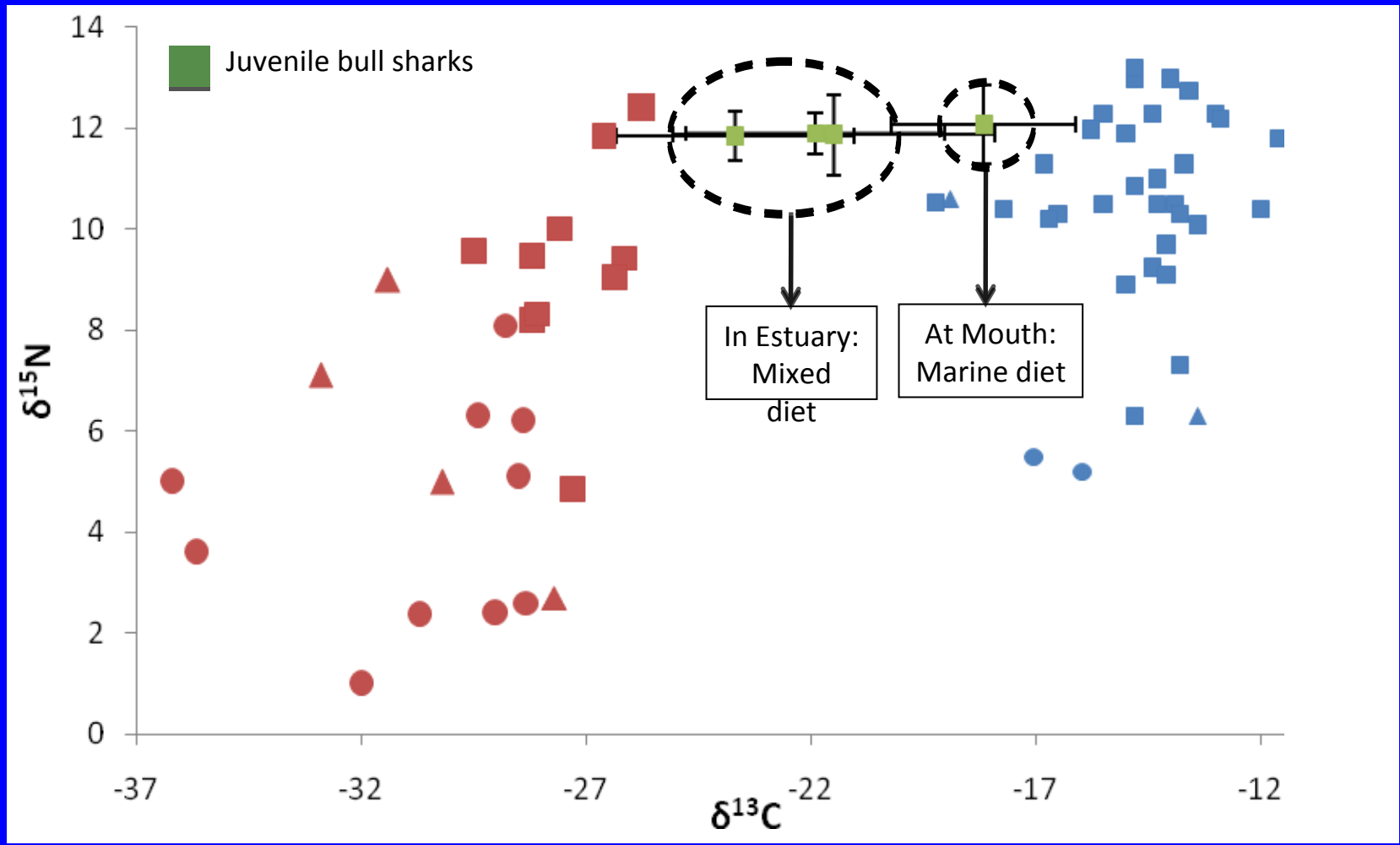


Mean Isotopic Ratios for Bull Sharks

- No significant variation in stable carbon isotope ($\delta^{13}C$) 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)

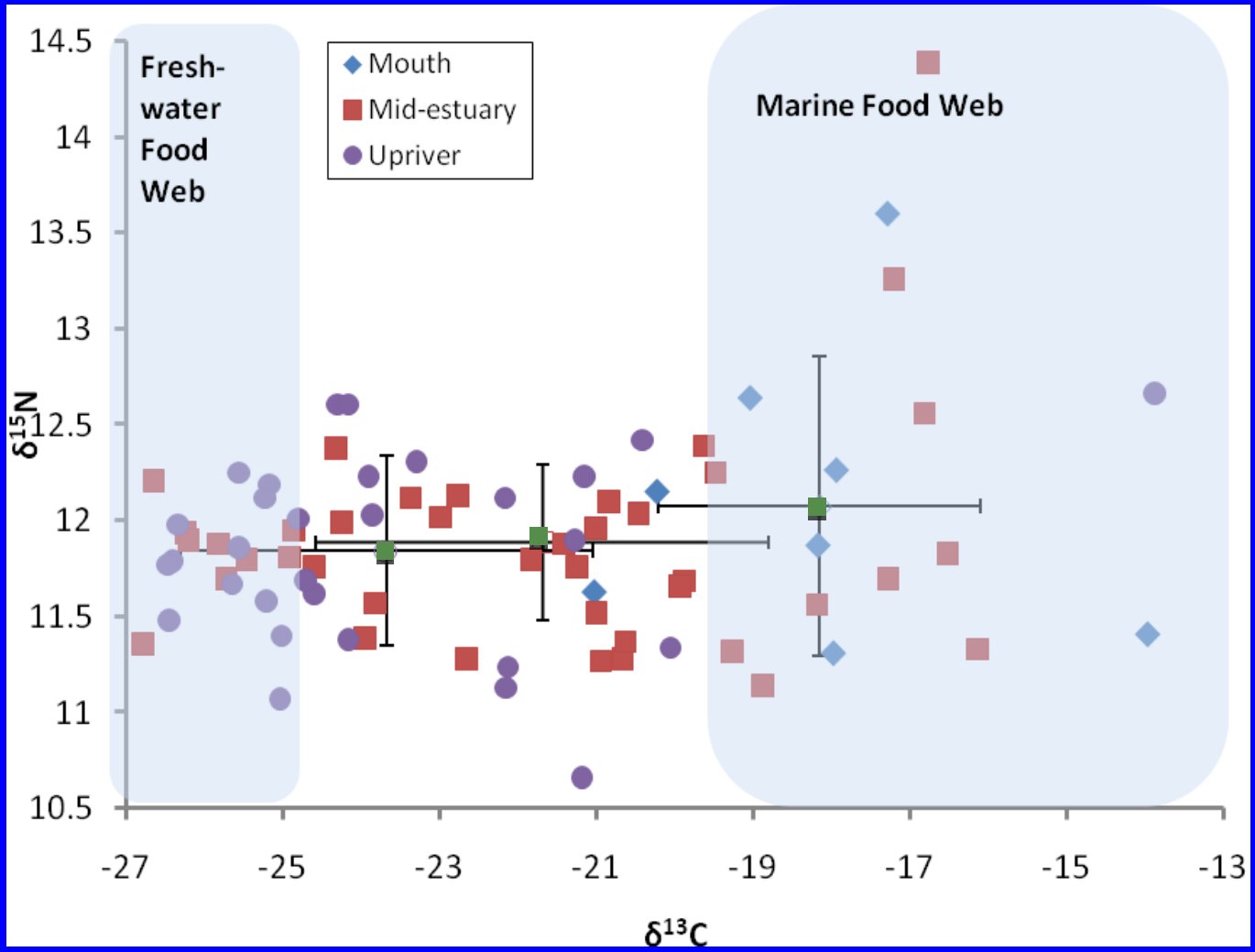
Mean Isotopic Ratios for Bull Sharks



Trophic Position

Source of Dietary Carbon (Freshwater vs. Marine)

Individual Isotopic Ratios



Trophic Niche Differentiation

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

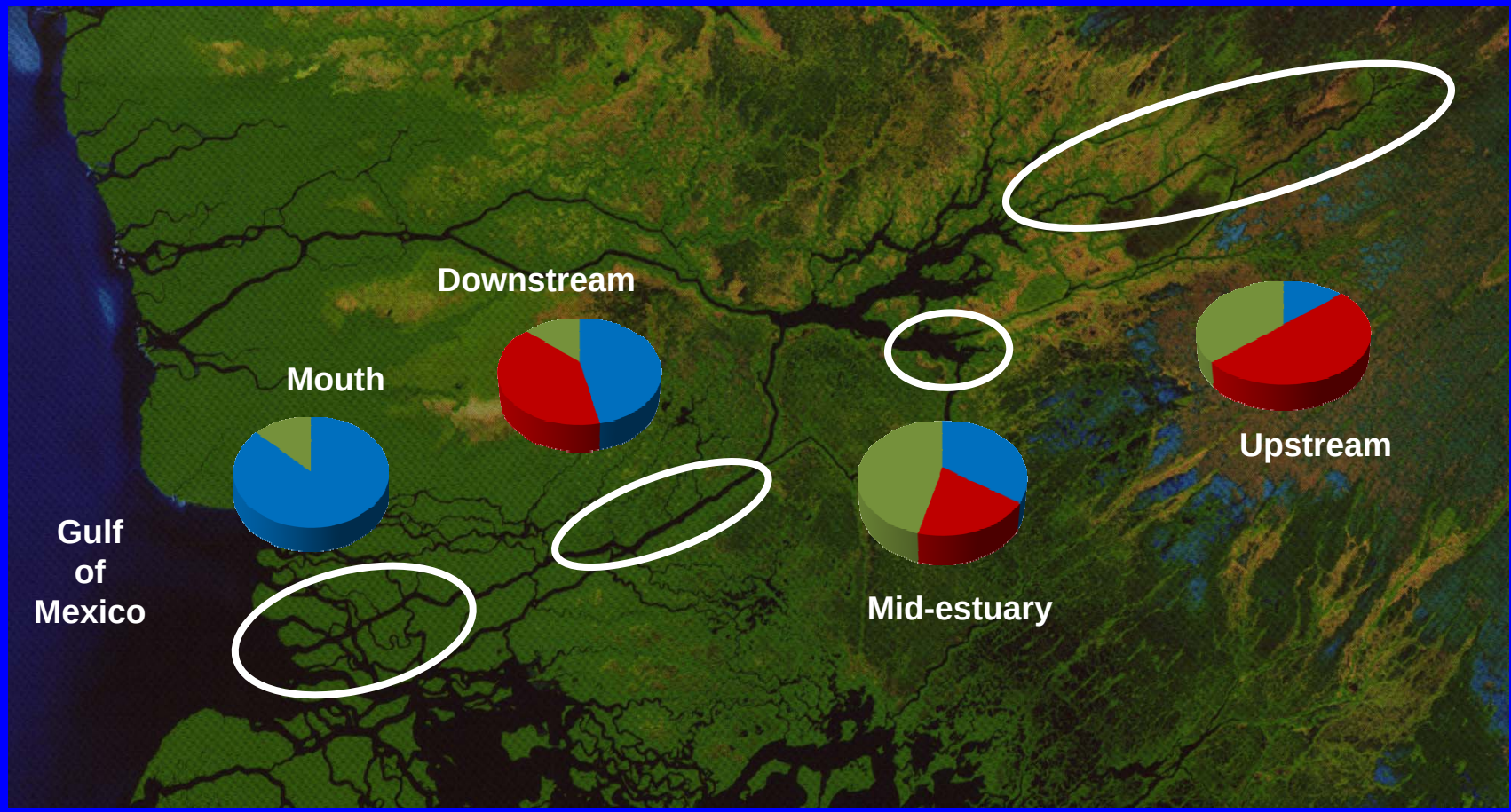
(1) Specialized niche: reliance on marine resources

(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
  - Two specialized, one generalized
  - Specialized freshwater niche missed without focus on individuals
- Niche variation not explained by size, sex, seasonal fluctuation
- Trophic niches showed little spatial segregation

Implications

- (1) Juvenile bull sharks as **vectors** of nutrients into the nutrient-limited upper reaches of the Shark River
  - e.g., P
  - Loss of bull sharks could alter upstream nutrient dynamics
- (2) Reliance on a small sample of individuals and/or a focus on mean trends could mask the diverse functional roles that predators play
- (3) Ecological consequences of declines in large predators may be greater than is appreciated
  - Loss of bull sharks could alter top-down forcing in marine *and* freshwater food webs

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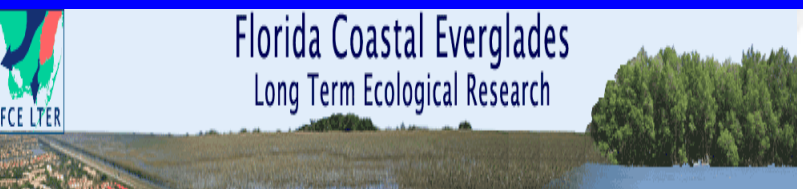

National Science Foundation
WHERE DISCOVERIES BEGIN

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


Lemon shark
(*Negaprion brevirostris*)

*Bolnick et al. (2007) *PNAS*