Diet variation of a generalist fish predator, grey snapper *Lutjanus griseus*, across an estuarine gradient: trade-offs of quantity for quality?

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This study examined diet, prey quality and growth for a generalist fish predator, grey snapper *Lutjanus griseus*, at five sites across an estuarine gradient in the Loxahatchee River estuary, Florida, U.S.A. *Lutjanus griseus* diets shifted from dominance by low quality, intertidal crabs upstream to an increased reliance on higher quality shrimp, fishes and benthic crabs downstream. Frequency of *L. griseus* with empty stomachs was higher at downstream sites. *Lutjanus griseus* growth rates did not vary among sites. Results indicate that *L. griseus* may be able to compensate for lower quality prey upstream by consuming more, and thus individuals are able to maintain similar levels of energy balance and growth rates across the estuarine gradient. Elucidating mechanisms, such as compensatory feeding, that enable generalist species to remain successful across habitat conditions are critical to understanding their organismal ecology and may facilitate predictions about the response of generalists to landscape alteration.

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INTRODUCTION

Being able to maintain a positive energy balance is necessary for growth and reproduction. Optimal foraging models predict that animals should forage in ways that maximize their net energy intake (MacArthur & Pianka, 1966; Schoener, 1971; Stephens & Krebs, 1986). For example, prey that require longer handling or search times should have higher energy content to be profitable. When comparing across trophic guilds, species consuming higher-quality prey that may require more energy to capture (*e.g.* piscivores) often feed less frequently than species that consume lower-quality resources (*e.g.* herbivores) (Arrington *et al.*, 2002; Vinson & Angradi, 2011). Such variation in diet quality and frequency of feeding also exists within species, particularly for generalists, which are able to exploit a wide range of resources.

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Generalization is associated with trading-off the costs and benefits of being able to use diverse resources (Futuyma & Moreno, 1988). For instance, specializing in high-quality resources is profitable when they are abundant. Being able to consume lower-quality resources when competition for resources is high, or when resources vary greatly through time or space, however, may allow fitness to be maintained (Stephens & Krebs, 1986; Futuyma & Moreno, 1988). One mechanism by which generalist species may be able to compensate for lower-quality food is by increasing the quantity of food resources consumed. This compensatory feeding strategy has been demonstrated for many taxa when environmental conditions limit the availability of high quality forage (Targett & Targett, 1990; Rueda *et al.*, 1991; Pennings *et al.*, 1993; Taillon *et al.*, 2006). The mere presence of compensatory feeding, however, does not necessarily mean that similar levels of individual fitness are maintained, and little is known about the efficacy of compensatory feeding strategies in higher-order consumers such as predatory fishes [but see Kadin *et al.* (2012) and Schrimpf *et al.* (2012) for examples with seabirds].

Many predatory fishes are considered generalists with respect to both habitat and diet. In particular, species associated with ecotones, such as estuaries, are often faced with numerous potential prey resources. Grey snapper *Lutjanus griseus* (L. 1758), an ecologically important fisheries species common throughout Florida and the Caribbean (Starck & Schroeder, 1970), can tolerate a wide range of salinities (Serrano *et al.*, 2011) and inhabits a diverse suite of habitats including seagrass beds, oyster reefs, mangroves and man-made habitats (Eggleston *et al.*, 2004; Tolley & Volety, 2005; Faunce & Serafy, 2007). *Lutjanus griseus* diets have been reported to be highly variable in space and time (Starck & Schroeder, 1970; Rutherford *et al.*, 1983; Hettler, 1989; Layman *et al.*, 2007; Yeager & Layman, 2011). Because *L. griseus* can consume a variety of prey items of varying quality across their range, they represent a good model for examining how predatory fishes may deal with varying resource quality.

The objective of this study was to investigate foraging trade-offs of *L. griseus* across an estuarine gradient. Differences in prey resource pools were linked to growth rates in order to explore potential drivers of foraging trade-offs. Specifically, it was hypothesized that (1) diet composition and quality would vary across the estuarine gradient, (2) quantity of prey consumed would be inversely related to prey quality and (3) growth rates would be similar across sites if compensatory feeding was found.

MATERIALS AND METHODS

STUDY SITE

The Loxahatchee River (26° 57′ N; 80° 06′ W) is located on the south-east coast of Florida, U.S.A., flowing into the Atlantic Ocean through Jupiter Inlet (Fig. 1). The river drains a 700 km^2 catchment, of which 63% is still dominated by natural habitats (South Florida Water Management District, 2006). Diverse habitats are found across this landscape, changing from riverine cypress swamps upstream to marine-dominated mangrove and seagrass habitats closer to the mouth. The wet season in South Florida generally spans May to October, when rainfall and freshwater inflow reach annual peaks. This study focused on five sites across the estuarine gradient representing the range of habitats utilized by *L. griseus* within this estuary (see Table I for site descriptions). Sites span an 11 km gradient across this ecotone and represent a significant environmental gradient for *L. griseus*, ranging from nearly fresh to fully marine waters.
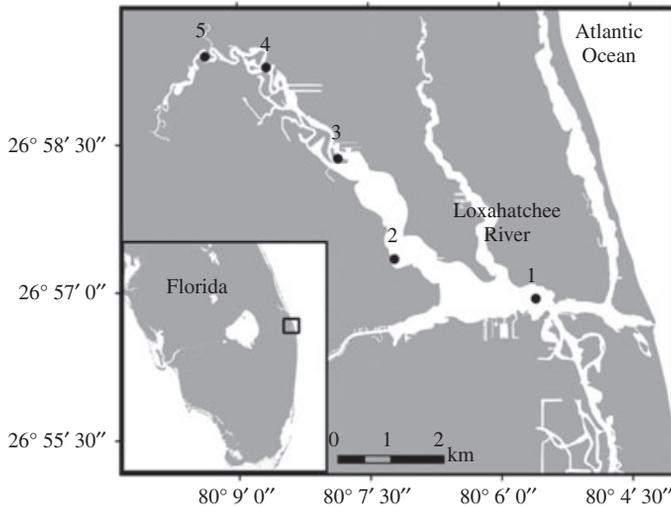
FIG. 1. Map of the Loxahatchee River and estuary. The five study locations are indicated (●): site 1, Bird Island; site 2, Eagle's Nest; site 3, Oyster Island; site 4, Boy Scout Camp; site 5, Kitching Creek.

STUDY SPECIES

Lutjanus griseus may be considered generalist with respect to both diet and habitat use. Juvenile (<100 mm standard length, L_S) and sub-adult (100–250 mm L_S) *L. griseus* often use estuarine habitats as nurseries (Eggleston *et al.*, 2004; Tolley & Volety, 2005; Faunce & Serafy, 2007). While some adult (>250 mm L_S) *L. griseus* may move offshore, many remain estuarine residents throughout their life (Faunce & Serafy, 2008*a*). In the Loxahatchee, adult *L. griseus* are observed in some deeper regions of the estuary near the inlet, but are uncommon at the five focal sites in this study. Reported diets for *L. griseus* are most often dominated by crustaceans and fishes, although prey species and relative importance of various prey items vary widely (Starck & Schroeder, 1970; Harrigan *et al.*, 1989; Hettler, 1989; Layman & Silliman, 2002).

Data from acoustic telemetry studies within the Loxahatchee indicate that *L. griseus* do not regularly move between the five study sites (C. A., Layman, unpubl. data). Furthermore, previous tagging studies on daily movements of *L. griseus* from mangrove habitats in Florida and The Bahamas have found that they generally move <100 m between daytime resting habitat and adjacent soft-bottom feeding areas (Luo *et al.*, 2009; Hammerschlag-Peyer & Layman, 2010). Distances between study sites ranged between 1·5 and 3·2 km and thus movement among sites by *L. griseus* individuals should be limited.

DATA COLLECTION

Lutjanus griseus were collected for growth and diet analysis by fishing with single hook rod and reel baited with frozen penaeid shrimp during June to September in 2007–2009. Mustad brand fish hooks of different sizes (sizes 6, 4 and 2, http://www.mustad.no/) were used to target fish over a range of body sizes at each site. A total of 267 *L. griseus* were caught, ranging in L_S from 54 to 204 mm, comprising all juvenile and sub-adult individuals. Fish were euthanized using a high dose of eugenol (Sladky *et al.* 2001; Cotter & Rodruck, 2006). The L_S of each individual was measured to the nearest mm. Stomach contents of each *L. griseus* were extracted and identified to the lowest taxonomic level possible. When necessary, stomach contents were brought back to the laboratory and identified with the aid of a dissecting microscope. Volume of prey items in *L. griseus* stomachs was estimated by volumetric displacement in water with a graduated cylinder. Otoliths were extracted from the fish and returned to the laboratory for ageing. Fin tissue was taken for isotope analysis.

TABLE I. Description of the five study sites in the Loxahatchee River estuary, FL, U.S.A. Salinity (mean and range) reported for summer months (June to September) corresponds to the sampling period in this study. Temperature and salinity data courtesy of the Loxahatchee River District and based on averages over 2007–2009

Site number	Site name	Distance from mouth of estuary (km)	Mean annual temperature (° C)	Mean annual salinity	Mean (range) salinity for summer months	Site description
1	Bird Island	2·6	25·3	32	30 (11–36)	Red mangrove *Rhizophora mangle* islands bordered by sub-tidal channels and mud flats with sparse seagrass
2	Eagle's Nest	5·3	25·7	27	22 (3–34)	*Rhizophora mangle* and concrete rip-rap shoreline bordered by patches of muddy bottom and oysters
3	Oyster Island	6·8	25·7	16	12 (0–28)	*Rhizophora mangle* islands surrounded by extensive oyster reefs
4	Boy Scout Camp	9·9	25·7	8	3 (0–13)	*Rhizophora mangle* shorelines bordered by muddy bottom with sparse oyster clumps
5	Kitching Creek	13·1	24·5	5	1 (0–6)	Freshwater cypress *Taxodium distichum* and riverine *R. mangle*-lined shoreline, bordered by muddy bottom

Additional *L. griseus* were sampled non-lethally for stomach contents (to reduce the number of fish sacrificed) (Layman & Winemiller, 2004). These fish were anaesthetized using eugenol and forced to regurgitate their stomach contents by pressing the abdomen while using a metal spatula to help invert the stomach (Hammerschlag-Peyer & Layman, 2012). This method was found to be effective at removing all the stomach contents in 98% (49/50) of individuals of the congeneric schoolmaster *Lutjanus apodus* (Walbaum 1792) of similar size to the fish in this study (Hammerschlag-Peyer & Layman, 2012). A fin clip was also taken from these *L. griseus* for stable isotope analysis. After sampling their stomach contents, fish were placed in a holding tank filled with water from the study site and allowed to recover before being released.

DIET ANALYSIS

To assess the frequency of feeding and quantity of food consumed across sites, the frequency of non-empty stomachs and the total volume of food in *L. griseus* stomachs were analysed. For these analyses, only *L. griseus* captured during the morning (0830–1200 hours, $n = 212$ individuals) were used because *L. griseus* feed primarily at night (Starck & Schroeder, 1970; Luo *et al.*, 2009). First, effects of fish L_S and site within the estuary on the frequency of non-empty stomachs were tested with logistic regression (Sokal & Rohlf, 2012). Because differences were found among sites, whether distance from the mouth of the estuary predicted the proportion of *L. griseus* with non-empty stomachs was tested using linear regression. Next, a general linear model (GLM) was used to test whether total food volume (excluding *L. griseus* with empty

stomachs) could be predicted by site or L_S (Sokal & Rohlf, 2012). As a measure of effect size, η^2 values were calculated, which represent the proportion of unique variation explained by individual predictor variables. Whether distance from the mouth of the estuary predicted the mean stomach content volume (for fish with non-empty stomachs) at each site was tested using linear regression.

To examine shifts in the composition of *L. griseus* diets across sites, diets were assessed based on both the volume and number of prey items from different taxonomic groups ($n = 267$ individual *L. griseus*). Prey items were grouped into taxonomically similar categories such that each group represented at least 5% of the total diet (by volume in ml and number) across all sites ($n = 8$ groups). A multivariate analysis of variance (MANOVA) was used to test whether the volume of major prey groups in *L. griseus* stomachs differed among sites (Johnson & Wichern, 2007). Next, a χ^2 test of independence was used to test if the number of individuals from different prey groups varied among sites (Sokal & Rohlf, 2012). If significant results were obtained for the MANOVA or χ^2 test of independence, *post hoc* tests [one-way analyses of variance (ANOVAs) and examination of standardized residuals (Beasley & Schumacker, 1995), respectively] were used to determine which sites and prey taxa were driving the differences. Additionally, prey were categorized by their primary habitat type: intertidal, benthic or pelagic based on life-history information and observations of prey behaviour and habitat use at the study sites. A MANOVA and χ^2 test of independence were used to test whether the volume and number of prey, respectively, from different habitat types varied among sites.

Carbon stable isotope analysis was used to examine shifts in basal carbon resource pools for *L. griseus* among sites. $\delta^{13}C$ is known to vary among producers from different photosynthetic pathways, but changes little with trophic transfers, and as such is often used to trace the basal carbon resource pool of consumers (Layman *et al.*, 2012). Because of the diverse array of producers present in estuarine mangrove systems, it is often not possible to identify individual producers as the ultimate source of production, but $\delta^{13}C$ can be useful in separating general carbon source groups (*e.g.* marine- *v.* estuarine-derived production) (Layman, 2007). A sub-set of *L. griseus* collected in 2009 was used for stable isotope analysis (between 11 and 15 individuals per site). The analysis focused on *L. griseus* collected in one year to reduce the potential for temporal variation in isotopic signatures of carbon resource pools biasing results. Fin tissue was processed for $\delta^{13}C$ according to Post *et al.* (2007). To test whether there was a shift in basal resource pool across sites, $\delta^{13}C$ of *L. griseus* fin tissues were compared among sites using a Kruskal–Wallis non-parametric ANOVA, as data did not meet assumptions of normality ($P < 0.05$) (Sokal & Rohlf, 2012). The relationship between mean $\delta^{13}C$ and distance to the mouth was tested with linear regression.

PREY QUALITY ANALYSIS

Individuals of prey species were collected separately based on taxa identified from *L. griseus* stomachs. Prey species were collected from benthic, intertidal and pelagic habitats throughout the estuary using a variety of methods (nets, traps and by hand). Proximate composition of prey taxa [per cent water, lipid, lean mass (protein) and inorganic components] was used to assess prey quality (Van Pelt *et al.*, 1997). Per cent water was determined by subtracting wet mass from the dry mass (DM) after drying whole organisms at 60° C. Each organism was then ground to a powder with a mortar and pestle and a sub-sample of the homogenized powder was taken. Per cent total lipid in the tissue was determined gravimetrically by solvent extraction following the Bligh–Dryer method (Bligh & Dyer, 1959), modified for use with the less toxic dichloromethane:methanol (2:1) solvent according to Erickson (1993). Per cent lean mass (primarily protein) and inorganic material were found after burning lipid-extracted tissue in a furnace at 550° C for 4 h. Per cent inorganic material was found by weighing the remaining ash and the amount of lean mass was calculated by subtraction (Van Pelt *et al.*, 1997).

Energy density (in kJ g^{-1} DM) for different prey items was calculated based on proximate composition and published energy values for lipid and lean mass (Schmidt-Nielson, 1997). Differences in energy density among prey taxa were tested with a one-way ANOVA (Sokal & Rohlf, 2012). Prey were then divided into high-energy (mean energy density of $21-22$ kJ g^{-1} DM) and low-energy density (mean energy density of $12-17$ kJ g^{-1} DM) groups. A MANOVA was used to test whether the volume of high- and low-energy density prey consumed by *L. griseus* differed

among sites (Johnson & Wichern, 2007). To test whether the frequency (number of prey items) at which *L. griseus* consumed high- and low-energy density foods differed among sites, a χ^2 test of independence was used.

AGE AND GROWTH ANALYSIS

Lutjanus griseus age was determined by examination of annual rings on sagittal otoliths. Annual rings were examined on whole otoliths immersed in water under a dissecting microscope using reflected light and counted by two readers (L.A.Y. and C.M.H.-P.) (Morales-Nin, 1992). Counts were made blind with no knowledge of fish size. The average per cent error between readers was 3·8% (Beamish & Fournier, 1981) and the sample was excluded if counts between readers differed. Fish were aged to fractions of a year based on the month captured, where 1 August was always considered the start of the year as this represented the peak spawning time of *L. griseus* in South Florida (Denit & Sponaugle, 2004).

Growth curves were created based on size and age data of *L. griseus* from sites 1, 3 and 5, the only sites with sufficient sample sizes to develop the curves ($n = 91$ fish). Linear growth models regressing age (decimal years) and L_S (mm) best fit observed data. Because fish used in this study were mostly juveniles and sub-adults, linear growth models were most appropriate (Rutherford *et al.*, 1983; Faunce & Serafy, 2008b). Growth analysis was restricted to fish between 1 and 4 years old as this age range was well represented at all sites. A GLM was used to determine whether size at age and growth rates differed among sites (Sokal & Rohlf, 2012). All statistical tests were performed in SAS v. 9.3 (SAS Institute; www.sas.com), except the χ^2 tests which were performed in SPSS v. 21.0 (IBM Corp.; http://www-01.ibm.com/).

RESULTS

DIET COMPOSITION

The probability of an *L. griseus* having a non-empty stomach varied among sites (logistic regression, d.f. = 4, $W = 12 \cdot 1$, $0 \cdot 05 > P > 0 \cdot 01$), but was not related to L_S (logistic regression, d.f. = 1, $W = 2 \cdot 6$, $P > 0 \cdot 1$). The proportion of *L. griseus* with food in their stomachs was positively related to distance from the mouth of the estuary [linear regression; $r^2 = 0 \cdot 90$, $0 \cdot 05 > P > 0 \cdot 01$; Fig. 2(a)]. Total stomach content volume for *L. griseus* with food in their stomachs did not vary among sites (GLM, $F_{4,139} = 1 \cdot 3$, $P > 0 \cdot 1$, $\eta^2 = 0 \cdot 04$), but was positively related to L_S (GLM, $F_{1,139} = 8 \cdot 2$, $0 \cdot 01 > P > 0 \cdot 001$, $\eta^2 = 0 \cdot 06$). The stomach content volume was not related to distance from the mouth of the estuary [linear regression; $r^2 = 0 \cdot 21$, $P > 0 \cdot 1$; Fig. 2(b)].

Lutjanus griseus diets were composed of 16 prey taxa across the five sites, including (ordered from most to least abundant): mud crab (Xanthidae, 20·7%), fiddler crab *Uca* spp. (18·6%), mangrove tree crab *Aratus pisonii* (11·0%), blue crab *Callinectes sapidus* (5·9%), penaeid shrimp (Penaeidae, 4·1%), shore crab *Pachygraspus transversus* (3·1%), palaemonid shrimp (Palaemonidae, 2·8%), isopod (Isopoda, 2·8%), plant material (2·1%), anchovy *Anchoa* sp. (1·7%), green porcelain crab *Petrolisthes armatus* (1·7%), snapping shrimp *Alpheus* sp. (1·4%), mojarra *Eucinostomus* spp. (0·7%), crested goby *Lophogobius cyprinoides* (Pallas 1770) (0·7%), mussel (Mytilidae, 0·3%) and amphipod (Amphipoda, 0·3%). The remaining 22·1% of prey in *L. griseus* stomachs could not be identified to this level of taxonomic resolution.

There was a difference among sites in *L. griseus* diet composition, as analysed with binned prey categories [listed in Fig. 3(a)] based on volume (MANOVA, $F_{32,890} = 4 \cdot 9$, $P < 0 \cdot 001$) and number (χ^2 test, d.f. = 20, $\chi^2 = 283 \cdot 2$, $P < 0 \cdot 001$). *Post hoc* tests revealed that this difference was driven by an increased reliance on shrimp and
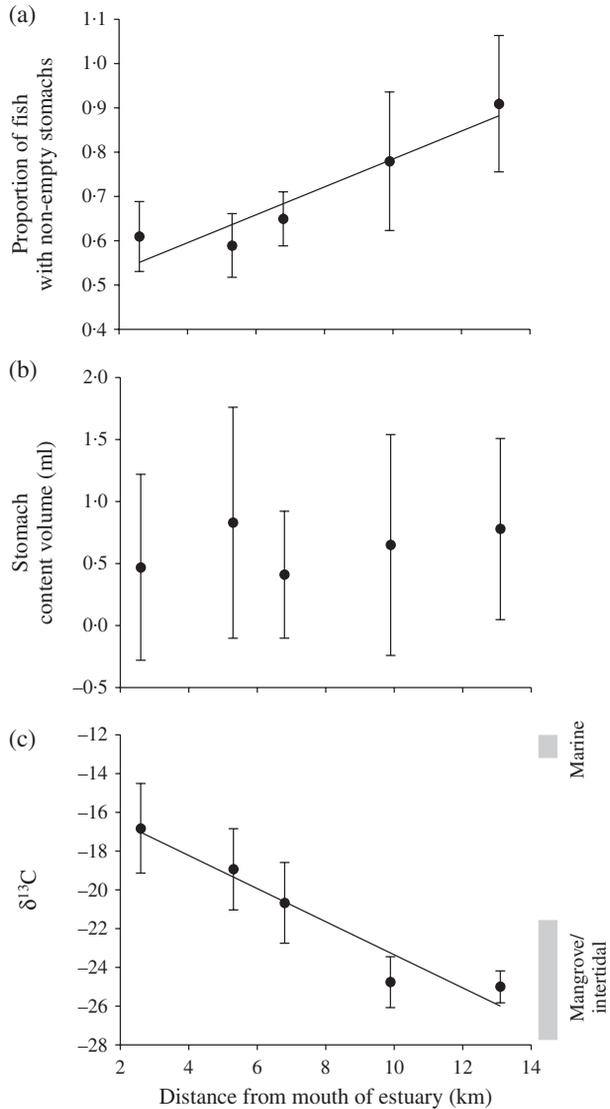
FIG. 2. Aspects of *Lutjanus griseus* diet along an estuarine gradient: (a) mean ± S.D. proportion of *L. griseus* with non-empty stomachs ($y = 0.03x + 0.47$), (b) mean ± S.D. total food volume in *L. griseus* stomachs and (c) mean ± S.D. δ^{13}C of *L. griseus* fin tissue from five sites along the gradient ($y = -0.85x - 14.81$). (c) Ranges of δ^{13}C values from marine or mangrove and intertidal carbon source pools in the estuary (Yeager & Layman, 2011) are given (■).

C. sapidus downstream, on xanthid crabs and *A. pisonii* in the mid-estuary and on *Uca* spp. upstream [Fig 3(a)]. The habitat source of *L. griseus* prey items also differed among sites based on both volume (MANOVA, $F_{12,654} = 4.9$, $P < 0.001$) and number (χ^2 test, d.f. = 8, $\chi^2 = 131.0$, $P < 0.001$). This difference was driven by an increased reliance on intertidal prey items, and a decreased reliance on benthic prey items, at upstream sites (4 and 5) compared to downstream sites [1 and 2; Fig. 3(b)].
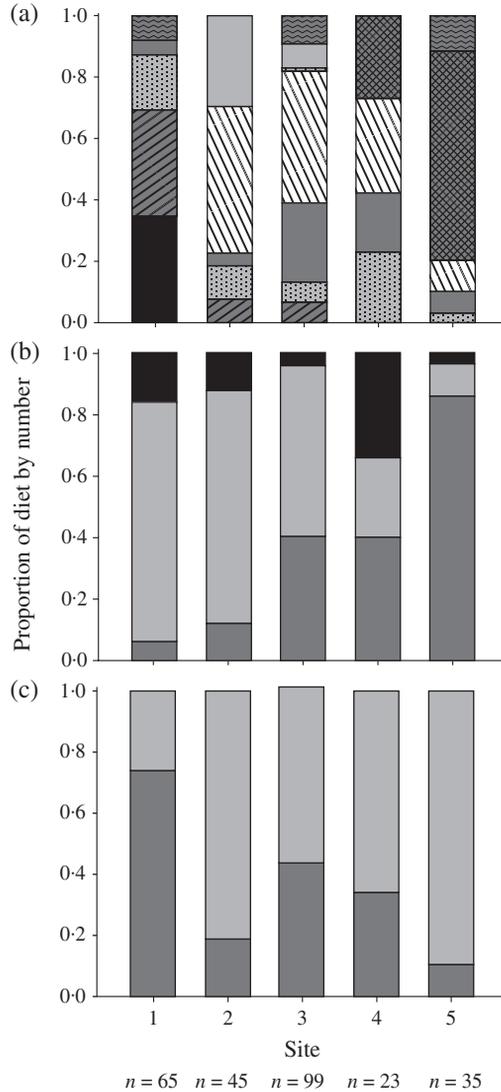
FIG. 3. Composition of *Lutjanus griseus* diets based on the number of prey items summarized by (a) major taxo-
nomic groupings of prey [other (▨), other crab (▢), *Uca* spp. (▨), *Aratus pisonii* (▨), xanthid crab (▨), fishes
(▨), shrimp (▨) and *Callinectes sapidus* (■)], (b) habitat source of prey items [pelagic (■), benthic (▢) and
intertidal (▨)] and (c) quality of prey from five study sites [low energy density (▢) and high energy density
(▨)]. Only data based on number are presented for simplicity, as patterns for diets based on volume of prey
were generally similar. Sample sizes (*n*) represent total number of *L. griseus* used for diet analysis from
each site.

The $\delta^{13}C$ of *L. griseus* fin samples differed among sites (Kruskall–Wallis test,
$H = 53{\cdot}4$, $P < 0{\cdot}001$). The mean $\delta^{13}C$ of *L. griseus* fin tissue was negatively related to
distance to the mouth [linear regression, $r^2 = 0{\cdot}93$, $0{\cdot}01 > P > 0{\cdot}001$; Fig. 2(c)]. This
shift probably corresponded to a shift from marine-derived production downstream to
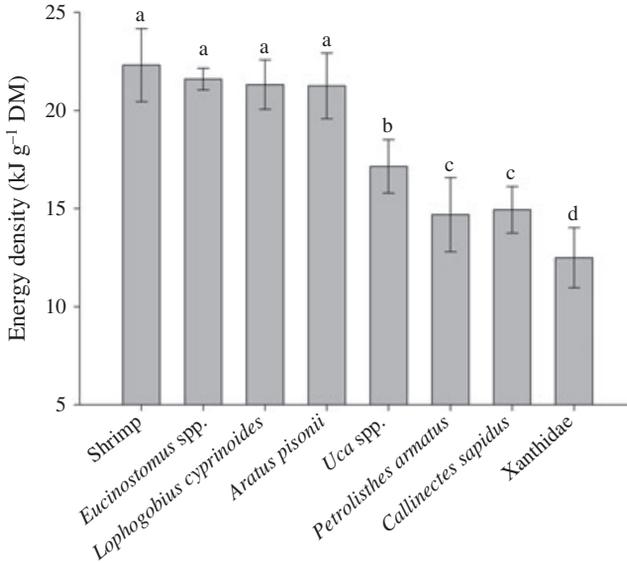mangrove- and estuarine-derived production upstream.

FIG. 4. Mean ± S.D. energy density (DM, dry mass) of *Lutjanus griseus* prey items. Similar lower-case letters denote groups that do not differ statistically at $\alpha = 0.05$.

PREY QUALITY

A total of 103 individuals from 10 prey taxa were processed to determine proximate composition (per cent water, lipid, lean mass and inorganic material). Energy density differed significantly among prey categories (ANOVA, $F_{7,87} = 81.3$, $P < 0.001$; Fig. 4). The volume of prey in *L. griseus* diets from high and low energy density groups did not differ significantly among sites (MANOVA, $F_{8,224} = 1.5$, $P > 0.1$). The number of prey from high and low energy density groups in diets, however, varied among sites [χ^2 test, d.f. = 4, $\chi^2 = 41.1$, $P < 0.001$; Fig. 3(c)]. Difference in the number of high and low energy density prey consumed was driven by a greater than expected number of high energy density prey consumed downstream (site 1) and more low energy density prey consumed upstream (site 5).

GROWTH

The L_S of *L. griseus* increased with age (GLM, $F_{1,85} = 15.3$, $P < 0.001$), but did not vary among sites (GLM, $F_{2,85} = 1.0$, $P > 0.1$). Growth rates ($L_S \times$ site) of *L. griseus* did not differ among the three sites examined (GLM, $F_{2,85} = 0.4$, $P > 0.1$; Fig. 5).

DISCUSSION

There was significant variation in the composition of *L. griseus* diets and the quality and quantity of prey consumed across the estuarine gradient. As may be predicted by optimal foraging models, the quality of prey consumed appeared to be inversely related to the quantity of prey consumed. *Lutjanus griseus* exhibited similar growth rates across sites, indicating that trading-off the quality and quantity of prey consumed may have
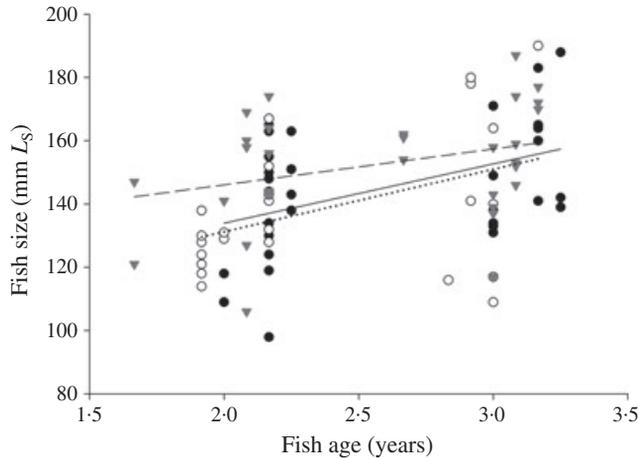
FIG. 5. Linear growth curves based on age and standard length (L_S) for *Lutjanus griseus* from three sites [site 1: $y = 18.7x + 96.5$ (●, —); site 3: $y = 19.8x + 91.7$ (○, ...); site 5: $y = 11.3x + 123.4$ (▼, – –)] along the estuarine gradient.

allowed *L. griseus* to maintain a comparable energy balance and growth rate throughout the estuary. These results indicate that niche plasticity and compensatory feeding may be mechanisms through which *L. griseus* are able to thrive across gradients of resource quality and availability.

Lutjanus griseus diets shifted substantially across the estuarine gradient in terms of prey taxonomy and source habitat. Based on the identity of downstream prey, *L. griseus* fed mostly from soft-bottom habitats surrounding the mangrove island from which they were caught. In contrast, *L. griseus* upstream appeared to shift to a diet more heavily reliant on intertidal prey. Carbon isotope analysis of *L. griseus* tissue supported this diet shift, as carbon values of *L. griseus* upstream were more characteristic of intertidal food webs, while values of *L. griseus* downstream were reflective of more marine-based production (Yeager & Layman, 2011). The distribution of specific prey taxa did vary across sites (L. A. Yeager, pers. obs.) and much of the variation in diet composition is probably due to these differences. Most previous studies of *L. griseus* in mangrove and seagrass areas have reported diets dominated by penaeid and caridean shrimp, fishes and various crab species (xanthids, *A. pisonii* and *C. sapidus*) that are generally similar in composition to those from the mid- and downstream regions of the estuary in this study (Starck & Schroeder, 1970; Rutherford *et al.*, 1983; Hettler, 1989; Layman & Silliman, 2002). Most of these studies were conducted in higher salinity portions of estuaries. This study is among the first to report on diets of *L. griseus* across the euryhaline and oligohaline ranges. This may explain why *Uca* spp. had not previously been reported as a common diet item for *L. griseus*, but were found to comprise 68% of their diet from the most upstream site in this study.

The high incidence of empty stomachs downstream is similar to figures from previous studies on *L. griseus* diets. Hettler (1989) found that *L. griseus* in channels near seagrass beds had a much higher frequency (60%) of empty stomachs than *L. griseus* collected in more landward mangroves (31%). Similarly, Rutherford *et al.* (1983) found a high incidence of empty stomachs (58%) in sub-adult *L. griseus* from

nearshore mangrove and seagrass areas of Everglades National Park. In these two previous studies, *L. griseus* diets were dominated by penaeid shrimp, which were found to be a higher quality prey item based on energy content in this study. Together, results from all these studies may indicate that *L. griseus* which feed on higher quality prey may feed less frequently.

Differences in digestion rates and gut retention times among prey items could affect relative frequencies of different prey items observed in *L. griseus* stomachs. The presence of 'hard parts', prey size and energy content may all affect gut retention time and could bias estimates of the frequency of feeding (Hyslop, 1980). For the examination of frequency of non-empty/empty stomachs, however, analysis was restricted to *L. griseus* caught during mornings to reduce bias associated with differential digestion rates, as suggested by Starck & Schroeder (1970). Additionally, there were consistent differences in diets based on number of different prey items (which may be less sensitive than total volume, as a prey item would have to be completely digested in order to not be counted). Therefore, differences in digestion are probably not the only driver of differences in the frequency of feeding and relative importance of various prey items consumed across sites.

While it appears that *L. griseus* have a trade-off between quality and quantity of prey consumed across the estuarine gradient, much is still to be studied about the underlying mechanisms. Specifically, it is not known if differences in *L. griseus* diet across this gradient are due to differences in prey availability, prey choice or time spent foraging or both. The question remains at sites where the quality of prey consumed is high: why not consume more? Increased competition downstream may have resulted in lower per capita prey availability. Alternatively, if predator encounter rates were greater downstream, increased risk may have resulted in less foraging time or a smaller foraging range.

Other factors besides diet may affect growth of individual *L. griseus*. For example, environmental conditions such as temperature or salinity can affect physiological costs for *L. griseus*. Water temperatures varied little among the five sites, and thus probably had little effect on fish growth. Laboratory experiments have found that juvenile *L. griseus* growth varied little across salinities ranging from 5 to 45 (Wuenschel *et al.*, 2005). A previous study on costs associated with abrupt changes in salinity indicated that physiological stress in sub-adult *L. griseus* is unlikely to occur in salinities ranging between 5 and 50 (Serrano *et al.*, 2011). Furthermore, at very low salinities, *L. griseus* is still able to osmoregulate well, with little difference in plasma osmolality observed between fish held in fresh water (0) and those in marine water (30) within days of acclimation (Serrano *et al.*, 2011). Therefore, while the importance of abiotic factors cannot be excluded, variation in diet appears to be a more likely potential driver of *L. griseus* growth in this system.

While evidence of reduced growth for *L. griseus* associated with reduced forage quality was not found, this study focused only on naturally varying differences in forage quality. In contrast, in studies on fragmented tidal creek ecosystems in The Bahamas, *L. griseus* were found to have reduced growth rates and lower body condition when compared to those from unfragmented creeks (Rypel & Layman, 2008). In these fragmented systems, prey diversity was greatly reduced and *L. griseus* have a much smaller trophic niche width at these sites (Layman *et al.*, 2007). One hypothesis is that reduced prey diversity and abundance in fragmented systems prevent *L. griseus* from compensating for reduced quality by consuming more. This comparison may indicate that if

habitat degradation becomes too severe, foraging trade-offs may be inadequate to compensate for reduced forage quality or quantity.

Generalist species are able to thrive in numerous ecological niches because of their plastic responses to biotic and abiotic environmental variation. Trade-offs such as compensatory feeding may be critical in allowing generalist species to deal with sub-optimal conditions. In light of the rapid rate of species loss and landscape change, it is critical to understand how, when and where generalist species may be able to undergo trade-offs in order to maintain critical functions of altered environments.

References

Arrington, D. A., Winemiller, K. O., Loftus, W. F. & Akin, S. (2002). How often do fishes "run on empty"? *Ecology* **83,** 2145–2151. doi: 10.1890/0012-9658(2002)083[2145:HODFRO]2.0.CO;2

Beamish, R. J. & Fournier, D. A. (1981). A method for comparing the precision of a set of age-determinations. *Canadian Journal of Fisheries and Aquatic Sciences* **38,** 982–983. doi: 10.1139/f81-132

Beasley, T. M. & Schumacker, R. E. (1995). Multiple regression approach to analyzing contingency tables: post hoc and planned comparison procedures. *Journal of Experimental Education* **64,** 79–93. doi: 10.1080/00220973.1995.9943797

Bligh, E. & Dyer, W. (1959). A rapid method of total lipid extraction and purification. *Canadian Journal of Biochemistry and Physiology* **37,** 911–917. doi: 10.1139/o59-099

Cotter, P. A. & Rodruck, K. J. (2006). Differential effects of anesthetics on electrical properties of the rainbow trout (*Oncorhynchus mykiss*) heart. *Comparative Biochemistry and Physiology A* **145,** 158–165. doi: 0.1016/j.cbpa.2006.06.001

Denit, K. & Sponaugle, S. (2004). Growth variation, settlement, and spawning of gray snapper across a latitudinal gradient. *Transactions of the American Fisheries Society* **133,** 1339–1355. doi: 10.1577/T03-156.1

Eggleston, D. B., Dahlgren, C. P. & Johnson, E. G. (2004). Fish density, diversity, and size-structure within multiple back reef habitats of Key West National Wildlife Refuge. *Bulletin of Marine Science* **75,** 175–204.

Erickson, M. C. (1993). Lipid extraction from channel catfish muscle: comparison of solvent systems. *Journal of Food Science* **58,** 84–89. doi: 10.1111/j.1365-2621.1993.tb03217.x

Faunce, C. H. & Serafy, J. E. (2007). Nearshore habitat use by gray snapper (*Lutjanus griseus*) and bluestriped grunt (*Haemulon sciurus*): environmental gradients and ontogenetic shifts. *Bulletin of Marine Science* **80,** 473–495.

Faunce, C. H. & Serafy, J. E. (2008a). Selective use of mangrove shorelines by snappers, grunts, and great barracuda. *Marine Ecology Progress Series* **356,** 153–162. doi: 10.3354/meps07231

Faunce, C. H. & Serafy, J. E. (2008b). Growth and secondary production of an eventual reef fish during mangrove residency. *Estuarine, Coastal and Shelf Science* **79,** 93–100. doi: 10.1016/j.ecss.2008.03.006

Futuyma, D. J. & Moreno, G. (1988). The evolution of ecological specialization. *Annual Review of Ecology and Systematics* **19,** 207–233. doi: 10.1146/annurev.ecolsys.19.1.207

Hammerschlag-Peyer, C. M. & Layman, C. A. (2010). Intrapopulation variation in habitat use by two abundant coastal fish species. *Marine Ecology Progress Series* **415,** 211–220. doi: 10.3354/meps08714

Hammerschlag-Peyer, C. M. & Layman, C. A. (2012). Factors affecting resource use variation for an abundant coastal fish predator, *Lutjanus apodus*, in a Bahamian wetland system. *Bulletin of Marine Science* **88,** 211–230. doi: 10.5343/bms.2011.1024

Harrigan, P., Zieman, J. C. & Macko, S. A. (1989). The base of nutritional support for the gray snapper (*Lutjanus griseus*): an evaluation based on a combined stomach content and stable isotope analysis. *Bulletin of Marine Science* **44,** 65–77.

Hettler, W. F. (1989). Food habitats of juveniles of spotted seatrout and gray snapper in western Florida Bay. *Bulletin of Marine Science* **44,** 155–162.

Hyslop, E. J. (1980). Stomach content analysis: a review of methods and their application. *Journal of Fish Biology* **17,** 411–429. doi: 10.1111/j.1095-8649.1980.tb02775.x

Johnson, R. A. & Wichern, D. W. (2007). *Applied Multivariate Statistical Analysis*, 6th edn. Upper saddle River, NJ: Pearson Education, Inc.

Kadin, M., Osterblom, H., Hentati-Sundberg, J. & Olsson, O. (2012). Contrasting effects of food quality and quantity on a marine top predator. *Marine Ecology Progress Series* **444,** 239–249. doi: 10.3354/meps09417

Layman, C. A. (2007). What can stable isotope ratios reveal about mangroves as fish habitat? *Bulletin of Marine Science* **80,** 513–527.

Layman, C. A. & Silliman, B. R. (2002). Preliminary survey and diet analysis of juvenile fishes of an estuarine creek on Andros Island, Bahamas. *Bulletin of Marine Science* **70,** 199–210.

Layman, C. A. & Winemiller, K. O. (2004). Size-based responses of prey to piscivore exclusion in a species-rich neotropical river. *Ecology* **85,** 1311–1320. doi: 10.1890/02-0758

Layman, C. A., Quattrochi, J. P., Peyer, C. M. & Allgeier, J. E. (2007). Niche width collapse in a resilient top predator following ecosystem fragmentation. *Ecology Letters* **10,** 937–944. doi: 10.1111/j.1461-0248.2007.01087.x

Layman, C. A., Araújo, M. S., Boucek, R., Harrison, E., Jud, Z. R., Matich, P., Hammerschlag-Peyer, C. M., Rosenblatt, A., Vaudo, J., Yeager, L. A., Post, D. M. & Bearhop, S. (2012). Applying stable isotopes to examine food web structure: an overview of analytical tools. *Biological Reviews* **87,** 545–562. doi: 10.1111/j.1469-185X.2011.00208.x

Luo, J. G., Serafy, J. E., Sponaugle, S., Teare, P. B. & Kieckbusch, D. (2009). Movement of gray snapper *Lutjanus griseus* among subtropical seagrass, mangrove, and coral reef habitats. *Marine Ecology Progress Series* **380,** 255–269. doi: 10.3354/meps07911

MacArthur, R. H. & Pianka, E. R. (1966). On optimal use of a patchy environment. *American Naturalist* **100,** 603–609.

Morales-Nin, B. (1992). *Determination of Growth in Bony Fishes from Otolith Microstructure.* Rome: FAO Fisheries Department.

Pennings, S. C., Nadeau, M. T. & Paul, V. J. (1993). Selectivity and growth of the generalist herbivore *Dolabella auricularia* feeding upon complementary resources. *Ecology* **74,** 879–890. doi: 10.2307/1940813

Post, D. M., Layman, C. A., Arrington, D. A., Takimoto, G., Quattrochi, J. & Montana, C. G. (2007). Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia* **152,** 179–189. doi: 10.1007/s00442-006-0630-x

Rueda, A. A., Slansky, F. & Wheeler, G. S. (1991). Compensatory feeding response of the slug *Sarasinula plebeia* to dietary dilution. *Oecologia* **88,** 181–188. doi: 10.1007/bf00320809

Rypel, A. L. & Layman, C. A. (2008). Degree of aquatic ecosystem fragmentation predicts population characteristics of gray snapper (*Lutjanus griseus*) in Caribbean tidal creeks. *Canadian Journal of Fisheries and Aquatic Sciences* **65,** 335–339. doi: 10.1139/F07-192

Schmidt-Nielson, K. (Ed) (1997). *Animal Physiology: Adaptation and Environment*, 5th edn. New York, NY: Cambridge University Press.

Schoener, T. W. (1971). Theory of feeding strategies. *Annual Review of Ecology and Systematics* **2,** 369–404.

Schrimpf, M. B., Parrish, J. K. & Pearson, S. F. (2012). Trade-offs in prey quality and quantity revealed through the behavioral compensation of breeding seabirds. *Marine Ecology Progress Series* **460,** 247–259. doi: 10.3354/meps09750

Serrano, X., Serafy, J. & Grosell, M. (2011). Osmoregulatory capabilities of the gray snapper, *Lutjanus griseus*: salinity challenges and field observations. *Marine and Freshwater Behaviour and Physiology* **44,** 185–196. doi: 10.1080/10236244.2011.585745

Sladky, K. K., Swanson, C. R., Stoskopf, M. K., Loomis, M. R. & Lewbart, G. A. (2001). Comparative efficacy of tricaine methanesulfonate and clove oil for use as anesthetics in red pacu (*Piaractus brachypomus*). *American Journal of Veterinary Research* **62,** 337–342. doi: 10.2460/ajvr.2001.62.337

Sokal, R. R. & Rohlf, F. J. (2012). *Biometry: The Principles and Practice of Statistics in Biological Research*, 4th edn. New York, NY: W.H. Freeman and Company.

Starck, W. A. & Schroeder, R. E. (1970). Investigations of the Gray Snapper, *Lutjanus griseus*. Coral Gables, FL: University of Miami Press.

Stephens, D. W. & Krebs, J. R. (1986). *Foraging Theory*. Princeton, NJ: Princeton University Press.

Taillon, J., Sauve, D. G. & Cote, S. D. (2006). The effects of decreasing winter diet quality on foraging behavior and life-history traits of white-tailed deer fawns. *Journal of Wildlife Management* **70,** 1445–1454. doi: 10.2193/0022-541X(2006)70[1445:TEODWD]2.0.CO;2

Targett, T. E. & Targett, N. M. (1990). Energetics of food selection by the herbivorous parrotfish *Sparisoma radians*: roles of assimilation efficiency, gut evacuation rate, and algal secondary metabolites. *Marine Ecology Progress Series* **66,** 13–21. doi: 10.3354/meps066013

Tolley, S. G. & Volety, A. K. (2005). The role of oysters in habitat use of oyster reefs by resident fishes and decapod crustaceans. *Journal of Shellfish Research* **24,** 1007–1012. doi: 10.2983/0730-8000(2005)24[1007:TROOIH]2.0.CO;2

Van Pelt, T. I., Piatt, J. F., Lance, B. K. & Roby, D. D. (1997). Proximate composition of energy density of some North Pacific forage fishes. *Comparative Biochemistry and Physiology* **118A,** 1393–1398. doi: 10.1016/S0300-9629(97)00240-5

Vinson, M. R. & Angradi, T. R. (2011). Stomach emptiness in fishes: sources of variation and study design implications. *Reviews in Fisheries Science* **19,** 63–73. doi: 10.1080/10641262.2010.536856

Wuenschel, M. J., Jugovich, A. R. & Hare, J. A. (2005). Metabolic response of juvenile gray snapper (*Lutjanus griseus*) to temperature and salinity: physiological cost of different environments. *Journal of Experimental Marine Biology and Ecology* **321,** 145–154. doi: 10.1016/j.jembe.2005.01.009

Yeager, L. A. & Layman, C. A. (2011). Energy flow to two abundant consumers in a subtropical oyster reef food web. *Aquatic Ecology* **45,** 267–277. doi: 10.1007/s10452-011-9352-1

Electronic References

Rutherford, E. S., Thue, E. B. & Buker, D. G. (1983). *Population Structure*, *Food Habits*, *and Spawning Activity of Gray Snapper, Lutjanus griseus, in Everglades National Park*. Homestead, FL: South Florida Research Center. Available at http://digitalcollections.fiu.edu/sfrc/pdfs/FI90698302.pdf/ (last accessed 30 March 2014).

South Florida Water Management District (2006). *Restoration Plan for the Northwest Fork of the Loxahatchee River*. Jupiter, FL: Loxahatchee River District. Available at http://www.loxahatcheeriver.org/pdf/Restoration_Plan_Final.pdf/ (last accessed 30 March 2014).