# Energy flow to two abundant consumers in a subtropical oyster reef food web

Lauren A. Yeager · Craig A. Layman

**Abstract** Oyster reefs are among the most threatened coastal habitat types, but still provide critical habitat and food resources for many estuarine species. The structure of oyster reef food webs is an important framework from which to examine the role of these reefs in supporting high densities of associated fishes. We identified major trophic pathways to two abundant consumers, gray snapper (*Lutjanus griseus*) and crested goby (*Lophogobius cyprinoides*), from a subtropical oyster reef using stomach content and stable isotope analysis. The diet of gray snapper was dominated by crabs, with shrimp and fishes also important. Juvenile gray snapper fed almost entirely on oyster reef-associated prey items, while subadults fed on both oyster reef- and mangrove-associated prey. Based on trophic guilds of the gray snapper prey, as well as relative $\delta^{13}C$ values, microphytobenthos is the most likely basal resource pool supporting gray snapper production on oyster reefs. Crested goby had omnivorous diets dominated by bivalves, small crabs, detritus, and algae, and thus were able to take advantage of prey relying on production from sestonic, as well as microphytobenthos, source pools. In this

way, crested goby represent a critical link of sestonic production to higher trophic levels. These results highlight major trophic pathways supporting secondary production in oyster reef habitat, thereby elucidating the feeding relationships that render oyster reef critical habitat for many ecologically and economically important fish species.

**Keywords** Diet · Estuary · *Lutjanus griseus* · *Lophogobius cyprinoides* · Stable isotope analysis

## Introduction

Oyster reefs have suffered severe declines worldwide as a result of overharvest and anthropogenic habitat degradation, driving oysters to the brink of ecological extinction in many temperate estuaries (Jackson et al. 2001; Beck et al. 2009). Yet oyster reefs remain one of the most important estuarine habitat types because of the number of ecosystem services they provide. One such service includes the provision of habitat structure, as oysters form structurally complex reefs, thereby providing refuge for diverse communities of fishes and invertebrates (Tolley and Volety 2005; Boudreaux et al. 2006; Shervette and Gelwick 2008). Many of these organisms are direct food resources for commercially important species, such as blue crabs (Portunidae) and striped bass (Moronidae) (Harding and Mann 2001, 2003; Grabowski et al. 2008). As

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such, the structure of oyster reef food webs can provide a context to evaluate one of the important ecosystem services that these habitats provide.

Two food web approaches are typically employed to explore trophic relationships: interaction webs and energy flow webs (Paine 1980; Polis and Winemiller 1996). Interaction models are usually based on controlled experimental manipulations to determine the per capita impact of one species on another (Paine 1992). Most studies of oyster reef food webs have utilized this approach (Grabowski 2004; Fodrie et al. 2008; Grabowski et al. 2008; O'Connor et al. 2008). Alternatively, food web models developed using direct dietary information or stable isotope values depict the flow of energy among species in an ecosystem. Such "energy flow models" are most useful for understanding which production sources and trophic pathways support particular species of interest (Paine 1980; Winemiller and Polis 1996; Layman et al. 2005). An energy flow approach has rarely been taken in studies of oyster reef food webs (but see Dame and Patten 1981; Lenihan et al. 2001; Wilson et al. 2009), and thus, underlying trophic pathways supporting consumers are typically only inferred from functional relationships for many oyster reef systems. Furthermore, most studies examining trophic relationships in oyster reef food webs are restricted to temperate reefs and little is known about oyster reef food webs in subtropical settings.

In this study, we use an energy flow approach to identify important trophic pathways supporting the production of fish consumers. We combine stomach content and stable isotope data to analyze the trophic role of these consumers. Direct diet observation through stomach content analysis provides detailed information on typical prey items. However, stomach content analysis gives only a snapshot of an individual's diet and may bias the importance of individual taxa toward the most common or those with longer residence times in the gut. Conversely, stable isotope analysis is widely employed in food web studies to provide insight into an individual's integrated diet over longer time scales (Layman and Post 2008). The $\delta^{13}C$ value (derived from the ratio of $^{13}C$ to $^{12}C$) often varies among primary producers with different photosynthetic pathways and is useful in inferring basal carbon resource pools supporting a consumer, since there is little change with trophic transfers (Peterson and Fry 1987; Wada et al. 1991; Post

2002). Alternatively, the $\delta^{15}N$ value (derived from the ratio of $^{15}N$ to $^{14}N$) becomes more enriched with each trophic transfer and therefore is useful in estimating trophic position within a food web (Cabana and Rasmussen 1996; Vander Zanden and Rasmussen 1999; Post 2002). We use these two complementary techniques to gain insight into the major trophic pathways that support the production of consumers.

We focused our study on two of the most abundant consumers found on subtropical oyster reefs: (1) the predatory gray snapper (*Lutjanus griseus* Linnaeus 1758) and (2) the omnivorous crested goby (*Lophogobius cyprinoides* Pallas 1770). Gray snapper is one of the most ecologically important species in subtropical estuaries of the southeast United States and the Caribbean region, as well as an important fishery species (Layman and Silliman 2002; Serafy et al. 2003; Layman et al. 2007; Pittman et al. 2007; Valentine-Rose et al. 2007b). Crested goby are one of the most numerically dominant fish species on subtropical oyster reefs (Tolley et al. 2006) and thus likely play an important role in their structure and dynamics. Our objectives were to describe the trophic pathways supporting gray snapper and crested goby and, simultaneously, reveal detail as to the structure of the overall oyster reef food web.

## Materials and methods

### Study site

The Loxahatchee River (26°57′ N, 80°06′ W) is located on the southeast Atlantic coast of Florida, United States of America, draining a 620-km$^2$ watershed and connecting to the ocean through Jupiter Inlet. The Northwest Fork of the Loxahatchee River has been nationally designated a Wild and Scenic River, making it the first river in Florida to hold such a designation (Chapter 83–358, Laws of Florida, approved June 1983). Sixty-three percent of the watershed is still dominated by natural environments (South Florida Water Management District 2006). The Loxahatchee River and estuary encompass diverse aquatic habitats including freshwater cypress swamps, mangrove shorelines, seagrass beds, and oyster reefs. Oyster reefs are common in the mesohaline section of the river (Fig. 1). A 2008
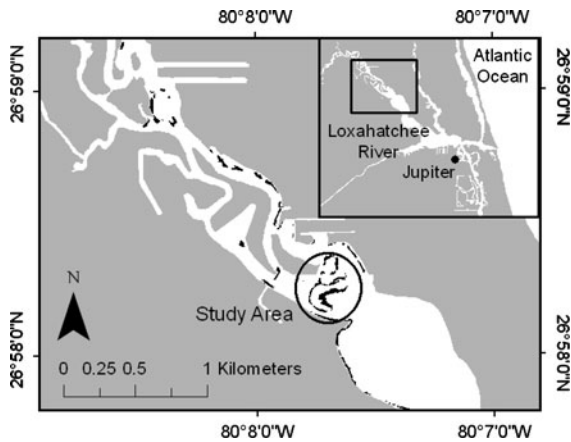
Fig. 1 Map of the Northwest Fork of the Loxahatchee River. Areas in *black* represent oyster reefs

survey of oyster reef habitat by the Loxahatchee River District mapped 91 oyster reefs covering more than 60,000 $m^2$ (Howard and Arrington 2008). The present study will focus on an area of extensive natural oyster habitats surrounding mangrove islands (26°58′16 N, 80°07′41 W) in the Northwest Fork of the river (Fig. 1).

Study species

Gray snapper is an important estuarine species and is a conspicuous predator in multiple estuarine habitat types. They are often associated with mangroves, seagrass, and coral reef environments (Eggleston et al. 2004; Layman et al. 2004; Faunce and Serafy 2007; Valentine-Rose et al. 2007a; Faunce and Serafy 2008a, b), and also are abundant on oyster reefs (Tolley and Volety 2005). This species supports economically important recreational and small-scale commercial fisheries (Valentine-Rose et al. 2007b). Gray snapper are known generalists with respect to both trophic role (Layman et al. 2007) and physiological tolerances (Serrano et al. 2007). Juveniles are one of the most numerically dominant fishes on oyster reefs in the Loxahatchee River, Florida (C. Layman, unpublished data), and likely play an important role in the estuarine food web.

Crested goby is one of the most abundant fish species on subtropical oyster reefs (Tolley et al. 2006) and is the dominant benthic fish consumer in terms of biomass in the study area (Layman, CA, unpublished data). Crested goby are suspected to

have omnivorous diets (Darcy 1981). Furthermore, crested goby may serve as important prey for piscivores in oyster reef food webs, including gray snapper (Odum and Heald 1972). For this reason, they may represent an important energy flow pathway to higher-order consumers, including commercially important fishery species.

Data collection

All fishes were collected from one oyster reef (∼2,000 $m^2$ area) at the study site. Gray snapper were collected during the summers of 2008 and 2009 using hook and line fishing. Upon capture, snapper were euthanized using an overdose of eugenol. Stomach contents were extracted by dissection, all prey items identified to the lowest taxonomic level possible, and content volume estimated using graduated cylinders. Additional individuals were collected and anesthetized using eugenol. These snapper were sampled nonlethally using stomach regurgitation following methods modified from Layman and Winemiller (2004) and finally released. Goby were collected for stomach content analysis during the summer of 2008 using benthic tray "traps" filled with oyster shell (Rodney and Paynter 2006). Goby were euthanized, and stomach contents were analyzed in the laboratory under a dissecting microscope and volume estimated as above.

Fin tissue for stable isotope analysis was collected from a subset of snapper used for stomach content analysis. Fin tissue was used so the tissue type was consistent among all individuals, because muscle was not taken from individuals sampled nonlethally. The $\delta^{13}C$ and $\delta^{15}N$ of gray snapper fin and muscle tissue are highly correlated within individuals ($\delta^{13}C$ fin = 1.11($\delta^{13}C$ muscle) + 2.73, $R^2 = 0.95$; and $\delta^{15}N$ fin = 0.998 ($\delta^{15}N$ muscle) + 0.459, $R^2 = 0.93$, $N = 37$ individuals; C.A. Layman, unpublished data). Using these relationships, the small correction was made from gray snapper fin isotope values to that of muscle values, as muscle tissue was used for other fish species in this study. Crested goby were collected from the summers of 2008 and 2009, and muscle tissue was used for isotope analysis.

Based on the results of stomach content analysis, identified taxa (Table 1) were collected from oyster reef habitat for stable isotope analysis using benthic tray traps described above. Live oyster (*Crassostrea virginica*) and ribbed mussels (*Guekensia demissa*)

**Table 1** Isotope values and sample size for oyster reef fauna

| Taxa | | $\delta^{13}$C | $\delta^{15}$N | $N$ |
|------|------|------|------|------|
| Common Name | Scientific name | | | |
| Periwinkle | *Littorina* sp. | −24.4 (1.1) | 2.3 (2.0) | 5 |
| Green mangrove tree crab | *Aratus pisonii* | −23.6 (0.73) | 5.6 (0.84) | 7 |
| Fiddler crab | *Uca* sp. | −21.1 (0.74) | 6.1 (1.2) | 3 |
| Ribbed Mussel | *Guekensia demissa* | −26.7 (0.20) | 6.9 (0.27) | 4 |
| Green porcelain crab | *Petrolisthes armatus* | −23.6 (0.73) | 7.1 (0.19) | 6 |
| Shore crab | *Pachygraspus transversus* | −21.2 (0.61) | 7.2 (0.03) | 3 |
| Juvenile mud crabs | Xanthidae | −20.3 (1.0) | 7.2 (0.31) | 8 |
| Black-fingered mud crab | *Eurypanopeus* sp. | −21.2 (0.74) | 7.8 (0.37) | 10 |
| Eastern oyster | *Crassostrea virginica* | −25.8 (1.2) | 8.0 (0.30) | 4 |
| White mullet | *Mugil curema* | −13.3 (1.4) | 8.6 (1.0) | 3 |
| Black-fingered mud crab | *Panopeus* sp. | −22.2 (1.6) | 8.9 (0.66) | 16 |
| Barnacle | *Balanus* sp. | −22.3 (1.2) | 9.1 (0.46) | 2 |
| Snapping shrimp | *Alpheus* sp. | −22.9 (0.79) | 9.2 (0.40) | 10 |
| Striped mullet | *Mugil cephalus* | −13.5 (1.8) | 9.6 (1.2) | 2 |
| Pinfish | *Lagodon rhombiodes* | −21.8 (0.23) | 10.9 (0.29) | 2 |
| Other Goby | *Gobiosoma* sp. | −24.6 (0.32) | 11.0 (0.68) | 3 |
| Checkered puffer | *Sphoeroides testudineus* | −24.1 (0.87) | 11.2 (0.25) | 34 |
| Sheepshead | *Archosargus probatocephalus* | −21.0 (3.6) | 11.3 (0.43) | 2 |
| Frillfin goby | *Bathygobius soporator* | −23.4 (0.96) | 11.4 (0.40) | 10 |
| Mojarra | *Eucinostomus* sp. | −22.9 (1.1) | 11.6 (0.69) | 10 |
| Mojarra | *Diapterus* spp. | −22.0 (2.0) | 11.7 (0.51) | 4 |
| Sailor's choice | *Haemulon parra* | −20.5 | 11.9 | 1 |
| Schoolmaster | *Lutjanus apodus* | −20.0 | 12.4 | 1 |
| Highfin blenny | *Lupinoblennius nicholosi* | −23.4 | 12.6 | 1 |
| Jack | Carangidae | −20.3 (0.79) | 12.6 (0.36) | 2 |
| Dog snapper | *Lutjanus jocu* | −20.7 (0.07) | 13.3 (0.30) | 2 |
| Crested goby | *Lophogobius cyprinoides* | −23.0 (0.55) | 11.7 (0.34) | 11 |
| Gray snapper | *Lutjanus griseus* | −22.7 (1.4) | 12.4 (0.75) | 46 |

Taxa are ordered by increasing $\delta^{15}$N values, with the two focal consumers listed at the bottom. If more than one measurement was taken for a given taxon, the mean delta-value (standard deviation) is reported

were also collected by hand from the site. Additional invertebrates and primary producers were collected from mangrove prop roots and the intertidal zone. Encrusting algae was collected by hand from mangrove prop roots. Seston (suspended organic matter and plankton) was filtered from water collected at the site with pre-combusted glass fiber filters (0.7 μm). Benthic algae and associated organic material (hereafter referred to as microphytobenthos) were collected by hand by scraping the top 1-mm surface of intertidal sediments. Red mangrove (*Rhizophora mangle*) and white mangrove (*Lagunculara racemosa*) leaves were collected from live trees. Other fish species were collected with hook and line fishing to determine isotope values of other predators for comparison with gray snapper and crested goby (Table 1). All collections were made in the summers of 2008 and 2009 to reduce seasonal variability in isotope values and seasonal differences in prey abundance.

For all mollusks, only the soft tissue was extracted for isotope analysis. For arthropods, the whole organism was used, but separate analyses were done for $\delta^{13}$C and $\delta^{15}$N with the sample for $\delta^{13}$C being first acidified to remove inorganic carbon. Similarly, all

tissue was acidified before $\delta^{13}C$ analysis for seston, microphytobenthos, and epiphytic algae mats. All tissue samples were processed and analyzed for $\delta^{13}C$ and $\delta^{15}N$ isotopic content following Post et al. (2007). A quantitative model, such as IsoSource (Phillips and Gregg 2003), was not used to identify the exact proportions of resource pools supporting consumers because our sampling of primary producers was not sufficient to encompass primary producer spatial and temporal variability in isotope values. But snapshot $\delta^{13}C$ values of primary producers provide a valuable complement to information gained from direct stomach content and isotope data on consumers (Layman and Post 2008).

Data analysis

Consumer diets were analyzed based on the proportion of prey from various taxonomic groups. Because body size can affect the diet and trophic role of consumers (Werner and Gilliam 1984) and gray snapper collected in this study spanned a large range in body size, we divided them into juvenile (<100 mm SL) and subadult (100–200 mm SL) groups following Faunce and Serafy (2007). The diets of juvenile gray snapper, subadult gray snapper, and crested goby were compared using the Schoener index (1968) of diet overlap:

$$D = 1 - \frac{1}{2} \sum |p_{ij} - p_{ik}| \qquad (1)$$

where $D$ is the diet overlap and $p_{ij}$ and $p_{jk}$ are the proportions of the $i$th prey taxa for species/group $j$ and $k$, respectively. Diets with overlap less than $\sim 60\%$ typically are considered to be biologically different (Zaret and Rand 1971; Mathur 1977; Wallace 1981). Additionally, prey were categorized according to their primary habitat: (1) benthic, oyster reef-associated, or (2) intertidal, mangrove-associated, based on their collection locations and extensive observations of prey behavior at the site. None of the prey taxa are commonly found in both habitat types. The proportion of prey from each habitat was compared among juvenile gray snapper, subadult gray snapper, and crested goby with a chi-squared test. Stomach contents from unknown sources were excluded in this analysis.

Because gray snapper varied greatly in size and both consumers were collected in 2 years for stable

isotope analysis, we determined whether these two variables affected aspects of their diet. For gray snapper, the relationship between fish size and frequency of empty stomachs was tested with logistic regression, with year included as an additional predictor variable. Two separate Mixed Linear Models (PROC MIXED, SAS 9.2) were used to test for differences in $\delta^{13}C$ or $\delta^{15}N$ between gray snapper and crested goby. The effects of year (2008 and 2009), fish size, and interactions between fish species and year (species × year) and size (species × size) were included as additional predictor variables. In the event of a significant interaction term, least-square means with a Tukey–Kramer adjustment were calculated. Data were log-transformed when necessary to meet assumptions of normality (Kolmogorov–Smirnov test, $P > 0.05$ in all cases).

Results

Ninety-six gray snapper ranging in size from 54 to 190 mm standard length (SL) were collected during the summers of 2008 ($N = 44$) and 2009 ($N = 52$). Snapper were observed to have empty stomachs in 33% of individuals examined. The probability of a snapper having an empty stomach was not predicted by fish size ($W = 0.50$, $P = 0.5$) or collection year ($W = 0.66$, $P = 0.5$). Thirteen taxa were identified in snapper diets, including (ordered from most to least important as based on volumetric proportions) mangrove tree crab (*Aratus pisonii*), black-fingered mud crab (*Eurypanopeus* sp. and *Panopeus* sp.), grapsid crab (*Sesarma* sp.), snapping shrimp (*Alpheus* sp.), goby (Gobidae), ribbed mussel, isopod (Isopoda), amphipod (Amphipoda), grass shrimp (*Palaeomonetes* sp.), shore crab (*Pachygraspus transversus*), fiddler crab (*Uca* sp.), and plant material. Amphipod was only present in snapper diets in 2008 and fiddler crab in 2009, but was represented by only one individual in each case. The order of importance for the remaining prey taxa in snapper diets varied slightly between years, but this difference was largely the result of the proportion of juvenile snapper sampled relative to subadults sampled varying slightly between years and dietary differences between these two groups. Overall, snapper diets were dominated by crabs by volume (85.4%), with lesser contributions of fish (4.2%) and shrimp (2.8%).

Diet overlap between juvenile and subadult gray snapper was low (25.8%). Juvenile gray snapper diets were dominated by mud crabs (53.0% of diet by volume), whereas subadult diets had a larger proportion of green mangrove tree crabs (40.6%, Fig. 2a). Primary habitat of gray snapper prey items also differed between size classes (Fig. 2b). Juvenile diets were dominated by benthic, oyster reef prey items (93.0% of diet by volume, only 2 individual isopods were consumed by juveniles from mangrove habitat) while subadult gray snapper shift to a diet where the majority of prey items were from intertidal mangrove habitat (65.3%).

Fifty-four crested goby (26–52 mm SL) were collected for diet analysis in the summer of 2008. Goby had empty stomachs 63% of the time. Analysis of goby diets revealed seven distinct taxa, including (ordered from most to least important as based on volumetric proportions) mud crab, ribbed mussel, clams and other mussels (Bivalvia), detritus, green porcelain crab (*Petrolisthes armatus*), filamentous algae, and snapping shrimp *Alpheus* sp. Goby diets were dominated in volume by bivalves (35.3%), crabs (32.3%), and detritus and algae (23.5%). Diet overlap between crested goby and juvenile snapper, and

between crested goby and subadult snapper was low (25.8% and 19.8%, respectively). The source of goby prey was entirely from within benthic oyster habitat (100%). The proportion of prey from the two habitats (benthic, oyster vs. intertidal, mangrove) varied significantly between juvenile snapper, subadult snapper, and crested goby ($df = 2$, $\chi^2 = 140$, $P < 0.0001$).

The $\delta^{15}N$ values did not differ significantly between gray snapper and crested goby ($df = 1$, $F = 0.95$, $P = 0.3$), between years ($df = 1$, $F = 1.79$, $P = 0.2$), nor with fish size ($df = 1$, $F = 0.34$, $P = 0.6$). The $\delta^{13}C$ did not differ overall between species ($df = 1$, $F = 0.05$, $P = 0.8$) or with fish size ($df = 1$, $F = 0.94$, $P = 0.3$). There was a significant difference in $\delta^{13}C$ between years ($df = 1$, $F = 22.41$, $P < 0.0001$). However, this difference between years was driven by a significant interaction between species and year ($df = 1$, $F = 11.39$, $P = 0.002$) Post hoc tests revealed that $\delta^{13}C$ varied between years for gray snapper only ($P < 0.0001$), being more depleted in 2008 (mean $\pm$ SD $= -23.5 \pm 1.08$) when compared to 2009 ($-21.2 \pm 1.4$).

The mean $\delta^{15}N$ value for other oyster reef-associated species ranged from 2.3 for periwinkle snails (*Littorina* sp.) to 13.3 for dog snapper (*Lutjanus jocu*). The $\delta^{15}N$ values of gray snapper and crested goby were among the highest measured (Table 1). Both consumers had intermediate $\delta^{13}C$ values compared to the range of $\delta^{13}C$ from all oyster reef fauna sampled ($-13.5$ to $-26.7$) and were within the range of prey items identified from diet analysis (Table 1; Fig. 3). While $\delta^{13}C$ values were variable for primary producers, seston were isotopically depleted compared to other producers (Fig. 3). Likely because of this depleted resource pool, filter-feeding bivalves were more depleted in $\delta^{13}C$ than all other oyster reef consumers.
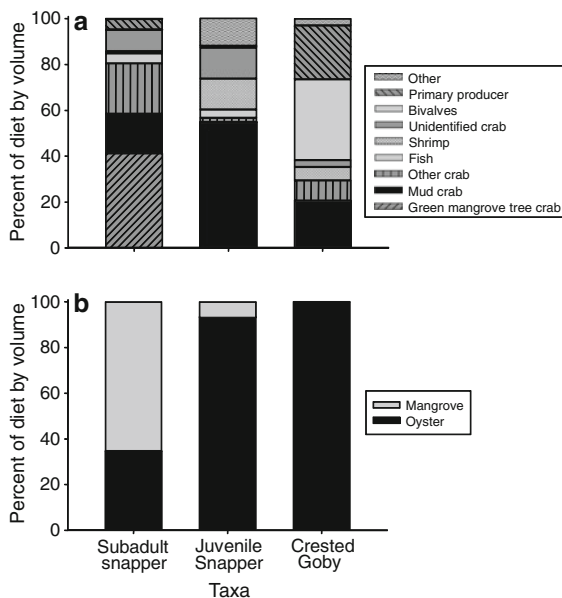


**Fig. 2** Composition diet (by volume) of two size classes of gray snapper (*Lutjanus griseus*) and crested goby (*Lophogobius cyprinoides*) based on prey items (**a**) and habitat source of prey (**b**). Primary producer prey category includes vascular plants, plant detritus and algae

## Discussion

Oyster reef-associated fauna were found to be important food resources for both gray snapper and crested goby. Gray snapper relied on food resources from both oyster reef and intertidal mangrove habitats, while crested goby diets were composed entirely of oyster reef fauna. Gray snapper at our study site shifted from a diet almost completely composed of oyster reef fauna as juveniles, to consuming a large
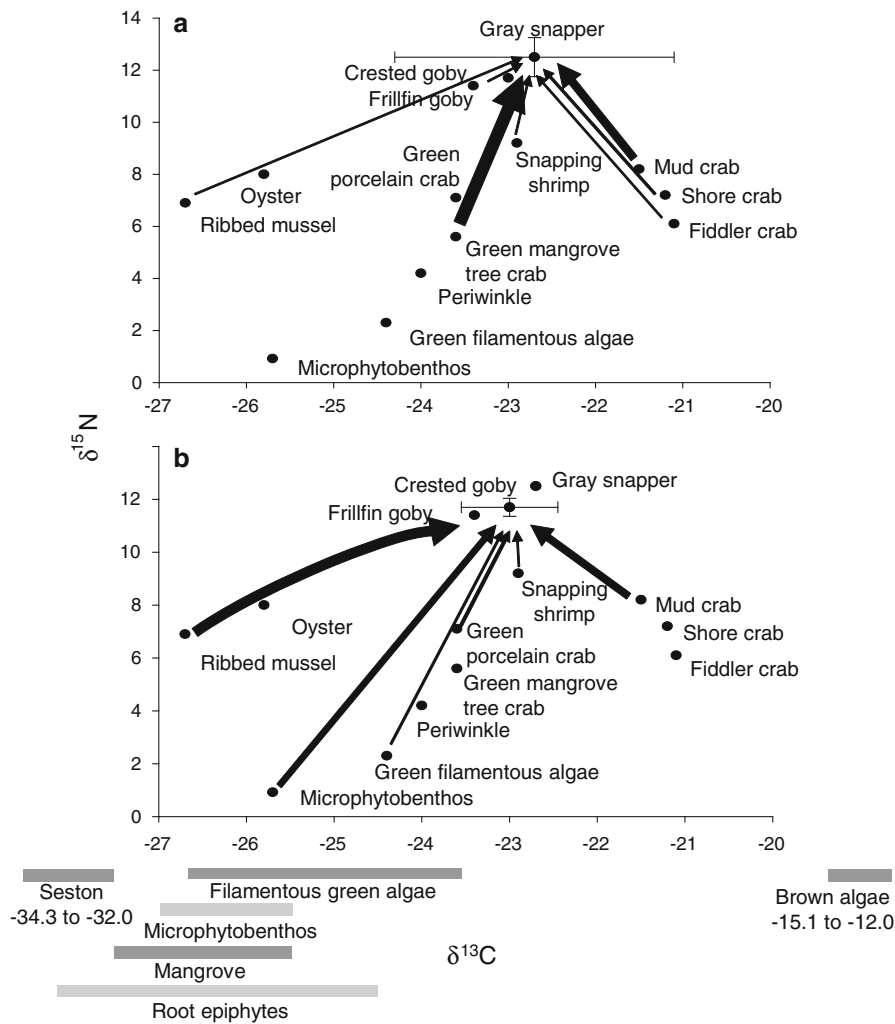
**Fig. 3** Model food web highlighting trophic pathways leading to gray snapper (*Lutjanus griseus*) (**a**) and crested goby (*Lophogobius cyprinoides*) (**b**). *Black dots* indicate mean isotopic value for each species. Bars around *gray snapper* and crested goby *dots* represent standard deviation. Error bars were omitted from other species for simplicity but are given in Table 1. *Arrows* indicate a direct trophic link as determined by stomach content analysis. The width of arrows leading to a consumer reflects the proportion (by volume) of that prey item in consumer diets. The $\delta^{13}C$ ranges of primary producers are represented by *gray bars* below the x-axis

proportion of intertidal prey associated with mangroves as subadults. Therefore, oyster reefs may be most important to the production of newly settled, juvenile gray snapper. While juvenile gray snapper and crested goby both fed almost exclusively within the oyster matrix, they exhibited little diet overlap.

Relative predation risk may drive foraging patterns and habitat choice of organisms inhabiting oyster reefs (Werner and Hall 1988; Dahlgren and Eggleston 2000). Even though all fish were collected from within oyster reef habitat, subadult gray snapper were found

to forage in adjacent mangrove habitats. In our system, mangroves and oyster are in close proximity (the distance between mangrove prop root habitat and the oyster matrix ranges from 1 to 10 s of m), but the structure provided by the mangrove fringe is larger and devoid of clumps of oyster or other small structure. Furthermore, the mangrove fringe is only flooded at high tide, forcing fish back into the oyster matrix at low tide. Therefore, it is likely that body size contributes to the dietary differences between subadult snapper and juvenile snapper and crested

goby. Subadult gray snapper are larger, possibly allowing them to escape risk from gape-limited predators. It may be more risky for the smaller juvenile snapper and crested goby to leave the protection provided by the oyster matrix to feed in adjacent habitat. The ability of subadult gray snapper to leave the oyster matrix and feed within intertidal mangrove habitats at high tide could represent a critical resource subsidy for reef-associated organisms.

Previous food web studies in oyster reef habitats have been conducted from a different viewpoint, i.e., examining the per capita interaction strength among species. Such food webs in temperate oyster reefs focus on interactions linking filter-feeding bivalves to bivalve predators (e.g., mud crabs or oyster drills, *Stramonita haemastoma*), and then to top predators such as stone crabs (*Menippe* spp.) or oyster toadfish (*Opsanus tau*) (Grabowski 2004; Grabowski and Kimbro 2005; Hughes and Grabowski 2006; Fodrie et al. 2008; Grabowski et al. 2008). In particular, multiple studies have highlighted the importance of trophic cascades, where top predators can reduce predation by mud crabs on juvenile oysters (Grabowski 2004; Grabowski and Kimbro 2005; Grabowski et al. 2008). In our study, we also found that mud crabs may represent a critical link in the transfer of production to higher trophic levels, since they were important components of the diets of both gray snapper and crested goby. However, on the basis of the large difference in $\delta^{13}$C values, it seems unlikely that filter-feeding bivalves compose a large portion of mud crab diets in this system. Instead, other consumers, e.g., crested goby and checkered puffer (C. Layman, unpublished data), prey directly on filter-feeding bivalves. As such, piscivorous predators could be more important in controlling the abundance of bivalve predators in our study system, although these functional relationships warrant more study in subtropical oyster reef food webs.

Inferences regarding trophic linkages made from stable isotope data may be ambiguous in estuarine food webs, since these webs are characterized by high species diversity and numerous basal resource pools (Layman 2007). Additionally, our sampling regime did not enable us to identify all sources of variability in isotope signatures (such as those driving differences in $\delta^{13}$C of gray snapper between years). However, the isotope data support information from consumer stomach content analysis, and by combing these two data sources, we were able to identify the most important pathways linking consumers in this oyster reef food web. In our study, production derived from sestonic sources via filter-feeding organisms did not appear to contribute substantially to the diet of snapper. Instead, benthic feeding crabs, that possibly derive energy from various microphytobenthos resource pools, seem to support snapper production. Conversely, crested goby did feed on filter-feeding bivalves and in doing so, represent a link from sestonic production into the benthic oyster reef food web. Exotic green porcelain crabs (Knott 1999), another filter-feeding organism, were also important components of the diet of crested goby. Stable isotope data suggest that green porcelain crabs have different diets than bivalve filter feeders, perhaps because filter feeders are known to partition food by particle size (e.g., Stuart and Klumpp 1984). As such, green porcelain crabs may represent an additional trophic pathway supporting secondary production in oyster reef food webs.

This study has focused on one large natural oyster reef, and as such, the transferability of these results across systems is largely unknown. However, we did focus on the largest natural reef within the estuary, which is similar in physiochemical conditions, habitat structure, and benthic community structure to other natural oyster reefs in the system (C. Layman, unpublished data). Additionally, oyster reef communities from our study site are similar to those of other subtropical reefs in Florida (Tolley and Volety 2005; Tolley et al. 2005). Creating an energy flow model represents a critical first step in the development of new hypotheses related to the structure and function of these subtropical reef-associated food webs. We assert that more studies on subtropical oyster reefs are warranted in order to better understand the overall structure of these subtropical oyster reef food webs.

In subtropical and tropical ecosystems, much study has focused on the role of "nursery habitats", i.e., habitats that typically provide abundant food and/or shelter from sources of mortality (Beck et al. 2001; Dahlgren et al. 2006). Although nursery species, such as gray snapper, are common on oyster reefs as juveniles (Tolley et al. 2005), oyster reefs do not receive the same attention as potential nurseries as do other structured habitats (e.g., seagrasses or mangrove). Herein, we have shown that oyster reefs provide important food resources for juvenile gray

snapper where they occur, as they are feeding almost entirely on prey from within the oyster matrix. In addition to providing adequate shelter, oyster habitat may provide more concentrated sources of prey when compared to other potential nursery habitats in the Loxahatchee River and other South Florida estuaries. Settlement size gray snapper have been found to recruit directly to oyster habitat (C. Layman, unpublished data), and other potential recruitment habitats, such as seagrass, are not common in the Loxahatchee. Recruitment substrate with suitable shelter may be a limiting factor for populations of nursery species (Shulman 1984; Shulman and Ogden 1987), especially in cases where the amount of suitable juvenile habitat is small compared to adult habitat (Halpern et al. 2005). Therefore, it is likely that available oyster reef habitat may be a bottleneck limiting gray snapper production and that oyster reefs are critical nursery habitat within this study system.

Oyster reef habitat in the Loxahatchee has suffered severe declines (Howard and Arrington 2008), similar to declines in many estuaries around the world. In the Loxahatchee estuary, this loss is primarily attributed to changing salinity regimes caused by the permanent opening of the Jupiter Inlet, as well as alteration of upstream freshwater inflows. The optimal salinity zone for oyster has shifted upstream, resulting in the death and subsequent burial of old oyster reefs. Oyster recruitment further upstream where salinities are optimal is now limited by available hard substrate. In other systems, oyster reef restoration has been shown to be an effective tool in increasing fish production (Peterson et al. 2003). Ongoing restoration of oyster habitat including increasing substrate for oyster settlement in the Loxahatchee may be critical to maintain ecosystem function (Beck et al. 2009). Our study illustrates the important role oyster reefs play in supporting fish production, in particular the juvenile stage of an important fishery species, and thus the importance of including oyster reef habitat in ecosystem-based management strategies.

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