Experimental test of preference by a generalist piscivore on morphologically- and behaviorally- different prey

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ABSTRACT

Generalist predators can have wide diet breadths that are influenced by the relative abundance of different prey available to them, making it difficult to determine prey preference from field observations. To ascertain preference, controlled experimentation is required that accounts for prey-specific variation in the time it takes to search, capture, and consume the prey; all of which can be affected by its morphology and behavior. Based on previous stomach content studies, Pinfish, *Lagodon rhomboides* and Clown Gobies, *Microgobius gulosus*, comprise a substantial proportion of the diet of Spotted Seatrout, *Cynoscion nebulosus*, despite strong differences in the morphology and behavior of these prey. Pinfish are demersal, deep-bodied fish that form loose aggregations with strong dorsal- and anal-fin spines that shoal in large aggregations, whereas Clown Gobies are benthic, shallow-bodied fish with weaker fin spines and are solitary but evenly distributed over the substrate. We conducted controlled, laboratory feeding experiments to test prey preference by Spotted Seatrout for these two common prey. Spotted Seatrout did not exhibit a feeding preference for either Pinfish or Clown Gobies, despite the strong differences in morphology and behavior. However, we observed higher consumption rates of the Clown Goby, but not the Pinfish, during 24-hour trials compared to those lasting 48 hours. This suggests that the densities of a solitary prey, but not a shoaling one, may have influenced search times by the generalist predator. Our experiments highlight the complexities of feeding behaviors by a generalist predator in highly dynamic ecosystems.

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1. Introduction

Predators must find, capture, and consume their prey, and theoretically, do so in a manner that will confer optimal energetic benefits (Brechbuhl et al., 2011; Gill, 2003). Foraging arenas of generalist predators can include a suite of prey that differ in morphology, behavior and microhabitat association (Ahrens et al., 2012). To maintain optimality, generalist predators have highly plastic search and capture abilities which can allow for a wide range of prey types (Closs et al., 1999; Eubanks and Denno, 2000). Under natural conditions where multiple prey are available to the predator, such plasticity requires some level of choice (Eubanks and Denno, 2000; Jackson and Underwood, 2007). That is, the predator must make behavioral decisions about whether to hunt and attempt to capture one prey versus another (Eubanks and Denno, 2000; Jackson and Underwood, 2007; Underwood et al., 2004).

The behavioral choice of prey preference is a complex relationship between the predator and the prey that should not be interpreted based solely on association, i.e., we cannot infer preference based on field observations from electivity studies (Alldredge et al., 1998; Lechowicz, 1982). Experimental protocols for examining prey preference have been a highly contentious topic over the past few decades (Jackson and Underwood, 2007; Stallings, 2010; Underwood et al., 2004) and early efforts incorrectly assumed preference based on the relative prevalence of certain prey in a predators diet (Underwood et al., 2004). Because the time it takes to find, consume, and digest an item may differ among prey types, preference can be confounded by handling times. Thus, a two-stage approach was developed, the first with only one prey type offered (no choice possible) and the second with more than one prey offered (choice possible). This approach allows the researcher to account for handling times and associated sampling error in the first stage (expected consumption), eliminating inflated Type-I errors associated with traditional methods (Underwood and Clarke, 2005). Following this two-stage approach, we tested for preference by a generalist, euryphagic piscivore on two common prey found in their diet, which differ morphologically, behaviorally, and with microhabitat association (Lassuy, 1983; McMichael and Peters, 1989; Simonsen and Cowan, 2013; Wenner and Archambault, 1996).

Spotted Seatrout, *Cynoscion nebulosus*, are ecologically- and economically-important predators found in the coastal waters from

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the Yucatan Peninsula, throughout the Gulf of Mexico, and as far north as the Chesapeake Bay (Wenner and Archambault, 1996). They spend their entire life in vegetated areas such as seagrass beds, saltmarshes, and mangrove roots and exhibit limited movements (Iverson and Tabb, 1962). Like other piscivorous fishes, juvenile Spotted Seatrout transition from a diet comprising small crustaceans (e.g., copepods, mysids) to one of larger crustaceans (e.g., penaeid shrimp) and finally fishes (Hall-Scharf, 2014; McMichael and Peters, 1989; Peebles and Hopkins, 1993; Wenner and Archambault, 1996).

Pinfish, *Lagodon rhomboides*, and Clown Gobies, *Microgobius gulosus*, are common in some of the same vegetated habitats where Spotted Seatrout are found. These two species also comprise a substantial portion of the diet of Spotted Seatrout based on stomach content studies (Fish and Wildlife Research Institute–Fisheries Independent Monitoring, unpublished data, W. Fletcher, pers. obs.), yet they differ markedly in morphology, behavior, and microhabitat use. Pinfish have a laterally-compressed shape, strong dorsal- and anal-fin spines, tend to aggregate in shoals, and usually reside within the middle to lower water column. They can be found in vegetated areas, near bridges and pilings, and near hard-bottom habitats in marine to freshwater salinities (Carpenter, 2002). Clown Gobies have a dorsoventrally-compressed shape with weaker fin spines, are solitary and benthic, and reside in muddy and vegetated estuaries at marine to freshwater salinities (Carpenter, 2002; Schofield, 2003). Using controlled laboratory experiments, this study examined whether Spotted Seatrout had a prey preference between these morphologically- and behaviorally- different prey, Pinfish and Clown Gobies, which had been previously observed in stomach analyses.

2. Materials and methods

2.1. Study organisms and experimental venue

All fish were collected by research staff from the Florida Fish and Wildlife Conservation Commission's Fish and Wildlife Research Institute as part of the Fisheries-Independent Monitoring and Marine Finfish Biology programs. Collections were made in Tampa Bay with 21.3-m seines, 121.9-m seines, 183-m center bag seines, and 6.1-m otter trawls. Captured organisms were placed in holding tanks containing aerated seawater and transported to the aquarium laboratory located at University of South Florida's College of Marine Science. In the laboratory, Pinfish were held in a 621-l tank, Clown Gobies in a 208-l tank, and Spotted Seatrout in 1200-l and 890-l tanks. Each holding tank was supplied with flow-through water from Tampa Bay and was equipped with aerators to promote adequate oxygenation (DO ≥ 6.5 mg/l) and heaters to ensure constant temperature (26.7–28.3 °C). The collection and housing of animals adhered to University of South Florida's Institutional Animal Care and Use Committee guidelines (Protocol No. 4193).

Feeding trials were conducted in 890-l circular tanks with flow-through seawater which were maintained at the same oxygen levels and temperature as the holding tanks. To simulate natural habitat, we created artificial seagrass units from green polypropylene ribbon (16-cm height × 0.25-cm width). The density (3500 blades m^{-2}) of the artificial seagrass mimicked that of *Halodule wrightii*, which is a common habitat of juvenile spotted seatrout in Tampa Bay (Flaherty et al., 2009; Flaherty-Walia et al., 2014). The artificial seagrass was attached to a weighted, plastic mesh placed in the bottom of the feeding trial tanks.

2.2. Prey preference experiments

A two-stage experimental design was used to test preference by Spotted Seatrout between the two prey species. In stage 1, Spotted Seatrout were offered one prey species only: Pinfish or clown gobies. In stage 2, spotted seatrout were simultaneously given both pinfish and Clown Gobies. The initial density of prey was kept consistent among treatments at 12 individuals per feeding trial. Thus the three

combinations of prey were: 1) stage 1–12 Pinfish, 2) stage 1–12 Clown Gobies, and 3) stage 2–6 Pinfish and 6 Clown Gobies. To ensure that a temporal artifact, such as prey switching, was not masking a true prey preference (Jaworski et al., 2013; Micheli, 1997; van Baalan et al., 2001), the two-stage feeding trials were conducted at two time intervals (24 versus 48 h). Five rounds of trials were run for 24 h (N = 15) and five were run for 48 h (N = 15).

Pilot feeding trials (N = 8) were conducted to determine the size range of prey that Spotted Seatrout could successfully consume. Pinfish measuring 16–32% and Clown Gobies measuring 12–25% of the standard length (SL) of Spotted Seatrout were readily consumed. Because the size range of Clown Gobies collected was limited to less than 40 mm SL, sizes of both prey used in feeding trials were limited to less than 40 mm SL to eliminate potential confounding effects of prey size on consumption and preference.

Spotted Seatrout (135 mm to 288 mm SL) were individually placed in the holding tanks for a 96-hour acclimation period prior to feeding trials. During the acclimation period, Spotted Seatrout were fed *ad libitum* and, to avoid any confounding effects of experience on prey choice, were given the prey composition (i.e., Pinfish only, Clown Gobies only, Pinfish and Clown Gobies together) that matched what they were provided during their ensuing experimental period (Micheli, 1997).

Before feeding trials began, the Spotted Seatrout were transferred to the experimental tanks and starved for 24 h to standardize level of hunger. After the starvation period for the Spotted Seatrout, prey were added to experimental tanks through a temporary, 6.3-cm diameter PVC pipe to allow them to swim safely to the bottom and reach the shelter provided by the artificial seagrass. Feeding trials lasted either 24 h (N = 15) or 48 h (N = 15), as described above. Once trials were complete, the artificial seagrass was washed with seawater to ensure all remaining prey were removed and counted. A screen was then placed over the drains of tanks and once they were empty of water, prey were counted again to ensure both counts matched. Any losses of prey were assumed to be due to predation by the Spotted Seatrout and this was further tested with four control trials that lacked the predator. Each feeding trial was conducted using different individual Spotted Seatrout and prey to ensure independence (Jackson and Underwood, 2007). Each round of trials consisted of similarly-sized Spotted Seatrout. All trials were conducted over a 10-week period from June to August 2012, during which salinity (24–27), temperature (26.7 °C–28.3 °C), and DO (>6.5 mg/l) remained stable.

2.3. Statistical analysis

Following the maximal likelihood equations developed by Underwood and Clarke (2005, Section 2.4 and Appendix A.3), we used the data collected from stages 1 and 2 of the feeding trials to calculate the null expectation of no preference for both the 24-hour and 48-hour trials separately. The number of consumed prey was compared to the expected prey values using χ^2 tests. Five comparisons were made for 24-hour trials and five comparisons were made for 48-hour trials (total of 10 comparisons) (Table 1).

3. Results

In the predator-free control trials, 100% survival of both Pinfish and Clown Gobies was observed, indicating that any losses of prey during the feeding trials were attributable to predation by Spotted Seatrout. All Spotted Seatrout readily consumed their assigned prey during both acclimation periods and experimental trials. In no experimental trials did the Spotted Seatrout consume all prey offered.

No preference was detected for either prey at $\alpha = 0.05$ for all ten trials (Table 1). However, a higher consumption rate (number eaten per hour) of Clown Gobies was observed during the 24-hour trials compared to the 48-hour trials (Fig. 1), both in the no-choice stage 1 ($t_8 = 4.05$, $P = 0.004$) and choice-possible stage 2 ($t_8 =$

Table 1
Tests for prey preference by Spotted Seatrout for either Pinfish or Clown Gobies. Notation follows that of Underwood and Clarke (2005).

Trial	M_1	M_2	m_1	m_2	N	Obs n_1	Obs n_2	Exp m_1	Exp m_2	Exp n_1	Exp n_2	χ^2	P
1	12	12	9	7	12	4	3	9.0	7.0	3.9	3.1	0.00	0.966
2	12	12	8	6	12	2	3	7.7	6.4	2.7	2.3	0.48	0.490
3	12	12	8	5	12	4	2	8.1	4.9	3.7	2.3	0.05	0.823
4	12	12	6	7	12	3	4	5.9	7.1	3.2	3.8	0.02	0.882
5	12	12	7	5	12	5	3	7.1	4.9	4.8	3.2	0.04	0.846
6	12	12	9	5	12	5	3	9.0	5.1	5.1	2.9	0.01	0.929
7	12	12	7	4	12	4	2	7.1	3.9	3.9	2.1	0.02	0.900
8	12	12	6	3	12	4	3	5.8	3.3	4.4	2.6	0.16	0.688
9	12	12	5	3	12	2	2	4.8	3.3	2.4	1.6	0.18	0.673
10	12	12	9	5	12	2	4	8.5	5.8	3.6	2.4	1.85	0.174

M_1 = total number of Clown Gobies available to predator in stage 1.
M_2 = total number of Pinfish available to predator in stage 1.
m_1 = number of Clown Gobies eaten in stage 1.
m_2 = number of Pinfish eaten in stage 1.
N = total number of prey (both species) available to predator in stage 2.
n_1 = total number of Clown Gobies eaten in stage 2.
n_2 = total number of Pinfish eaten in stage 2.

2.45, $P = 0.040$). Consumption rates of Pinfish (Fig. 1) did not differ between the two trial lengths in either stage 1 ($t_8 = 2.00$, $P = 0.081$) or stage 2 ($t_8 = 0.85$, $P = 0.421$).

4. Discussion

By following the two-stage approach from Underwood and Clarke (2005), this study accounted for the time it took the Spotted Seatrout to find, consume, and digest the prey to infer preference. Despite the differences in morphology, behavior, and microhabitat use, Spotted Seatrout did not exhibit a preference for Pinfish or Clown Gobies. This was an intriguing outcome when considering the complexity of the predator–prey relationship and how Spotted Seatrout must hunt, capture, and consume these different prey (Gill, 2003; Jackson and Underwood, 2007; Wahl and Stein, 1988; Ware, 1972).

Spotted Seatrout would most likely employ different feeding strategies for hunting and capturing a Pinfish versus a Clown Goby. Spotted Seatrout are active hunters, but appear to use a combination of ambush, lie-and-wait, and chasing tactics (Juanes et al., 2002; Wenner and Archambault, 1996). In their natural environment, Spotted Seatrout actively search the edges of vegetated areas and oyster reefs while using eddies and drop-off points to wait for their prey (Wenner and Archambault, 1996). To capture a solitary, benthic prey such as the Clown Goby used in this study, the Spotted Seatrout likely used an active ambush tactic. Indeed, we observed that the Spotted Seatrout in

the holding tank oriented head down–tail up which may have conferred a benefit for finding benthic prey. Newly settled Spotted Seatrout orient in this head down manner possibly to blend in with the seagrass aided by a mid-body stripe which is lost in the older age classes (Fish and Wildlife Research Institute–Fisheries Independent Monitoring, R.E. Matheson Jr., pers. comm.). In contrast, to capture a shoaling prey such as the Pinfish, a lie-and-wait tactic may have been used. Interaction with the test tanks was avoided because we did not want to interfere with feeding behaviors, but classic C- and S-start feeding strikes on Pinfish were observed in the holding tanks (Hale, 2002). Spotted Seatrout in holding tanks were observed to lie-and-wait until the aggregations of Pinfish were in striking distance while Clown Gobies were often ambushed off the bottom. By using a combination of foraging tactics, Spotted Seatrout can take advantage of varying densities and availability of a wide range of prey.

Morphology and behavior of prey can each greatly affect handling time and thus ultimately affects the maximum energy return for the predator under the framework of optimal foraging theory. This study used Pinfish and Clown Gobies as they are both common prey to Spotted Seatrout despite having different morphological and behavioral characteristics. Pinfish are deeper bodied and have stronger dorsal- and anal-fin spines compared to Clown Gobies. These morphological characteristics would increase the handling time of the Pinfish possibly making them the more difficult to consume (Wahl and Stein, 1988). Unlike Clown Gobies which exhibit a solitary behavior, Pinfish often aggregate in shoals. Shoaling and schooling can reduce per capita mortality rates via predation (i.e., safety in numbers; Neill and Cullen, 1974; Seghers, 1974; Wahl and Stein, 1988) but also increases visibility, possibly making Pinfish more conspicuous to the Spotted Seatrout. Thus there was likely a tradeoff between search and capture between these two prey. Clown Gobies may be easier to capture but more difficult to find, whereas, Pinfish may be more difficult to capture but easier to find. This tradeoff may be further influenced by the relative density of the prey.

Consumption rates of Clown Gobies, but not Pinfish, were higher in both stages 1 and 2 of the 24-hour trials compared to the two stages from the 48-hour trials. This may suggest that the predation rate by Spotted Seatrout was affected by the density of Clown Gobies, but not of Pinfish. Thus, as Clown Gobies were consumed during the first portion of the 48-hour trials, their density may have declined to a level below that conducive to predation by Spotted Seatrout (Ives et al., 1993). Given the solitary behavior of the Clown Goby, Spotted Seatrout may have lost a strong search image for them once their densities had been substantially reduced. In addition, when the densities of a preferred or more abundant prey becomes low, a predator may switch to consume a different species (Jaworski et al., 2013; Micheli, 1997; van Baalen et al., 2001). Under this proposed scenario, Spotted Seatrout
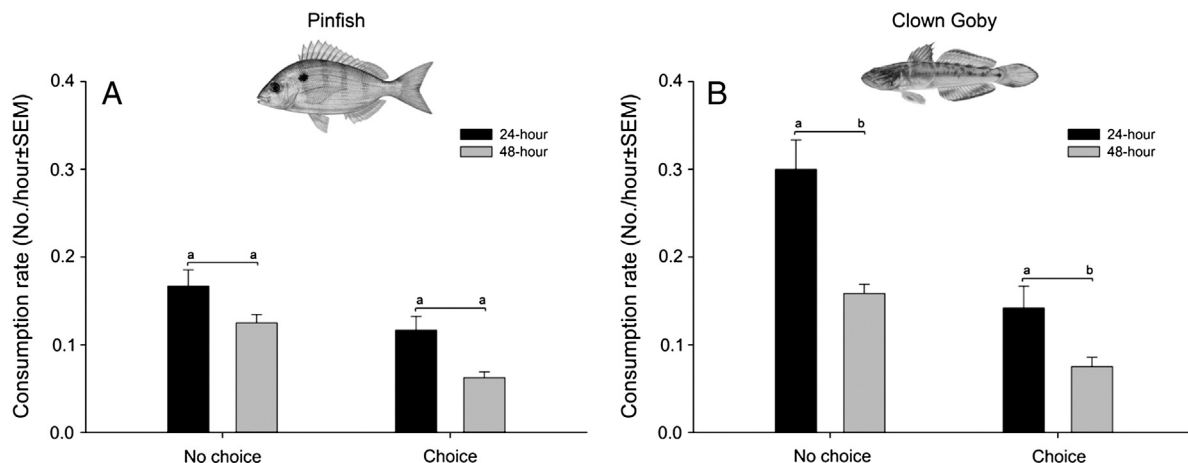
Fig. 1. Consumption rates (number eaten in 24- or 48-hours) of (A) Pinfish and (B) Clown Gobies.
Fish illustrations were kindly provided, with permission, by Diane R. Peebles (*Pinfish*) and Joseph Tomelleri (*Clown Goby*).

may have switched to feeding on Pinfish once the density of Clown Gobies was below a threshold. And, if prey switching did occur, a true preference may have been missed (Micheli, 1997). We also observed that in no trials did the Spotted Seatrout consume all prey offered. This per capita reduction may be a reflection of satiation by the predator (i.e., Type-I Functional Response; Murdoch, 1973).

In this study, Spotted Seatrout were restricted to only two types of prey, but, in their natural systems, have access to multiple species of prey with different levels of mobility. In addition, predatory fish that forage in clear, open water may rely on visual factors such as prey movement, prey size, and crypticity to locate prey; however, fish that forage in more turbid, estuarine environments may rely on a combination of visual and olfactory cues to locate their preferred prey in these low visibility environments (Chacin, 2014; Main, 1987; Seghers, 1974; Vinagre et al., 2008). An ongoing diet study of Spotted Seatrout collected from the Tampa Bay estuary, of the same size range used in our study, has identified that these fish consume prey from at least 11 different fish families, seven shrimp families, and three crab families (Fish and Wildlife Research Institute–Fisheries Independent Monitoring, unpublished data; pers. obs.). Practicing a generalist method of hunting for food would allow the different life-history stages of Spotted Seatrout to adapt to dynamic conditions, such as varying levels of turbidity and prey densities, which occur in the estuarine environment and in the associated fish communities (Bortone, 2003; Gerking, 1994; Llanso et al., 1998; Wilson et al., 2008). Conversely, generalist predators can select preferred prey based their size and abundance (Closs et al., 1999). The plasticity of a generalist predator, such as the Spotted Seatrout in our study, would be beneficial to the overall survival of the species in highly dynamic environments.

Understanding prey preference and diet of a predator is important to the management of ecosystems (Jackson and Underwood, 2007; Llanso et al., 1998; Underwood et al., 2004), especially with an economically-important species such as the Spotted Seatrout that uses the same estuary during all of its life-history stages. Knowing what a predator prefers and consumes can provide further insight into trophic dynamics and ecological patterns that can be applied to make predictions. Environmental impacts can alter food sources, and sound-management decisions can only be made when the effects of these changes on the predator of interest is understood. Therefore, information on prey preference is necessary for future ecosystem-based management.

Acknowledgments

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