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Experimental test of preference by a predatory fish for prey at different densities

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ABSTRACT

Preference for a particular prey implies that a behavioral choice is made by the predator, requiring an experimental approach to separate process from observed patterns in nature. For example, pink shrimp (Farfantepenaeus duorarum) and pinfish (Lagodon rhomboides) are dominant prey observed in the diet of juvenile gag (Mycteroperca microlepis) collected from natural habitats, but it is unclear whether their approximate equal representation is due to a lack of preference between the two. Furthermore, both prey are captured in high quantities as targeted (shrimp) and non-targeted (pinfish) components of a trawl fishery operating in the same seagrass habitats where juvenile gag are found, thus requiring examination as to whether reductions in prey densities affect consumption rates and preference. In the current study, I used laboratory feeding experiments and applied new analytical techniques derived in a series of recent papers published in this journal to examine preference by juvenile gag on these two morphologically and behaviorally different prey. Consumption rates were higher for shrimp than pinfish and were not related to the initial density of prey presented to gag. However, gag did not exhibit a feeding preference for either prey across 10 controlled comparisons. Experimental results in the laboratory therefore reflected patterns observed in the field for the diet of this predatory fish. Moreover, by examining the effects of reduced prey densities on food web processes, the approach used in this study may be applied to inform ecosystem-based management on indirect effects of fishing.

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1. Introduction

The influence of prey density on predator–prey dynamics forms a cornerstone of ecological study (e.g., Holling, 1966). A rich literature on the subject across a variety of marine fauna and ecosystems has shown predation rates (i.e., functional response) can increase, decrease, or remain unchanged when the density of prey is altered (e.g., reviews by Rodriguez et al., 1993 for invertebrates; Hixon and Webster, 2002 for fishes). Understanding how the direction and magnitude of preference for different prey varies across densities can inform ecologists on how changes to prey densities may influence food web dynamics. For example, strongly disproportionate changes in densities among prey species can drive generalist predators to switch apparent feeding preferences (Murdoch, 1969; Closs et al., 1999). Whether preference is affected by near proportionate changes in the densities of their prey has received far less attention.

Ecologists commonly use choice experiments to determine whether animals exhibit preference for a particular prey or habitat. By isolating the behavior of choice, these experiments can separate process from patterns observed in nature (Singer, 2000) and can inform us on a suite of topics concerning interaction webs and species–habitat relationships (reviewed in Roa, 1992). However, the procedures and analyses used to examine the behavioral response of preference by animals (e.g., for prey, habitat) have garnered tremendous attention and debate from ecologists. Peterson and Renaud (1989) pointed out several issues affecting the rigor of feeding experiments. For example, they criticized the use of two or more predators within an individual feeding trial due to the risk of interactive effects between predators (e.g., interference, facilitation) influencing the results. In addition, Peterson and Renaud (1989) highlighted the need for predator-free controls, an obvious necessity when the organism being consumed may incur an autogenic change (e.g., in mass) but also valuable for determining whether changes in prey abundance are attributable to non-predatory events (e.g., losses due to escape). It has also been emphasized that although some experiments infer preference by comparing consumption rates of different foods provided singly, the only way to actually examine a behavioral choice is to present the consumer with two or more food types simultaneously (Peterson and Renaud, 1989; Roa, 1992).

A series of recent papers published in this journal by Underwood and colleagues have further explored the appropriate procedures and analyses of feeding experiments. Underwood et al., (2004) suggest a commonly used, two-stage experimental approach to test preference. In the first stage, consumers are presented with a single type of food or prey. Consumption rates during this first stage therefore reflect "handling" times (e.g., search, capture, digestion) required by the consumer for a particular prey and provide estimates for the null hypothesis of no preference. In the second stage, consumers are

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presented with two or more prey. Statistical tests that follow determine whether observed consumption differs from expected consumption using information from both stages. However, this approach usually ignores sampling error associated with the first stage, leading to biased tests and greater potential for Type I errors. As a solution, Underwood and Clarke (2005) derived maximum likelihood estimators for the null values (i.e., expected consumption under no preference) that account for sampling error in both experimental stages. Null values are then compared against observed values using χ^2 contingency tables.

In addition to guiding study of food webs, prey preference studies can inform resource managers wishing to implement an ecosystembased approach to predict the consequences of reductions to prey densities on species of management concern. Nonselective fishing practices can reduce the densities of both targeted and non-targeted (i.e., bycatch) organisms. For example, trawl fisheries for shrimp are notorious for having high levels of bycatch that can equal or exceed catch rates of targeted species (Diamond, 2004). One such trawl fishery operates in shallow seagrass beds in Florida (USA) and targets penaeid shrimps (especially pink shrimp; Farfantepenaeus duorarum, Penaeidae). The fishery uses rollerframe trawls to capture juvenile shrimp that are in turn sold to bait houses that supply recreational fishermen (Upton et al., 1992). As with other trawl fisheries (e.g., commercial food shrimp), rollerframe hauls can include high quantities of bycatch (Meyer et al., 1999). However, bycatch in the rollerframe fishery tends to be limited to relatively small animals due to the presence of metal rods ("excluder bars") placed vertically every 5 cm across the opening of the trawls (Stallings et al., 2009). Although larger, higher trophic-level predators inhabiting the seagrass beds are not captured in high quantities, reductions to their prey populations may have unanticipated effects on food web dynamics.

Juvenile gag (Mycteroperca microlepis, Serranidae) are a generalist predator inhabiting the same seagrass beds where the rollerframe fishery occurs. As older juveniles and adults, gag themselves are the target of recreational and commercial fisheries and are both overfished and experiencing overfishing (NMFS, 2009). Thus, understanding how changes in their prey populations affect feeding choice is a practical matter of interest to resource managers. The diet of larger juveniles is dominated by an approximate equal representation of penaeid shrimp and fishes (Bullock and Smith, 1991; Mullaney and Gale, 1996); primarily pink shrimp and pinfish (Lagodon rhomboides, Sparidae) respectively, in our study system (Stallings et al., In press). Both prey species are captured in high quantities by the rollerframe trawls (Meyer et al., 1999). Therefore reductions to the densities of these important prey may have indirect effects on the feeding behavior of this predatory fish. In the current study, I use new analytical techniques and ask whether juvenile gag show a behavioral preference for the consumption of pink shrimp or pinfish, and whether both choice and consumption rates are affected by prey density.

2. Materials and methods

2.1. Study organisms and experimental venue

Gag are a warm-temperate grouper inhabiting coastal waters of the western Atlantic Ocean and Gulf of Mexico. After a larval period lasting approximately 45 days, they settle to seagrass beds in the spring and remain there until autumn when they emigrate to shallow, nearshore reefs located further offshore. Growth in juvenile gag is fast during their seagrass stage ($\geq 1 \text{ mm d}^{-1}$; Ross and Moser, 1995; Mullaney and Gale, 1996; Stallings et al., In press), possibly due to the combined effects of abundant prey available to them in seagrass (reviews by Hemminga and Duarte, 2000; Gillanders, 2006), their voracious feeding behavior (Adams, 1976a; Nelson, 1979) and high ecological efficiency (Adams, 1976b). Like many fishes that ultimately become piscivores (Mittelbach and Persson, 1998), their diet transitions from numerous, small invertebrates to fewer but larger prey as gag attain larger sizes (Mullaney and Gale, 1996; Stallings et al., in press).

Pink shrimp and pinfish are among the most abundant animals found in seagrass beds of the northeastern Gulf of Mexico during the summer months when juvenile gag are present (Livingston, 1982; C. D. Stallings unpublished data). Pinfish are primarily active during daylight with peak activity during crepuscular hours (Sogard et al., 1989). Pink shrimp are nocturnally active (Fuss, 1964), but also exhibit high activity levels during crepuscular periods (Reynolds and Casterlin, 1979). Although pinfish and shrimp exhibit different diel activity patterns, the two species appear at near equal representation in the diet of juvenile gag, a predominantly diurnal predator (Stallings et al., In press).

Collections of juvenile gag, pinfish, and pink shrimp were made with both otter and rollerframe trawls towed at a standard rate of 1.8 km/h for short durations (\leq 5 min). The captured organisms were immediately placed in sorting tanks containing aerated seawater from the collection site and non-targeted animals were released. Gag, pinfish, and pink shrimp were separated by species, placed in holding tanks with aerated seawater, and brought back to the Florida State University Coastal and Marine Laboratory (FSUCML) where they remained separated in 1130 L rectangular tanks (305 cm length×61 cm width×61 cm depth) with flow-through seawater. Live pink shrimp were also purchased from local bait dealers that had made collections in nearby seagrass beds. All experimental animals were held for 2–7 days prior to being introduced to experimental feeding tanks (see Section 2.2 for additional information on acclimation times).

Feeding experiments were conducted in 445 L circular tanks (90 cm diameter \times 70 cm height) with flow-through seawater. Artificial seagrass (35 cm height \times 0.8 cm width green nylon ribbon) attached to weighted, plastic mesh was placed on the bottom of the tanks. The shape, size and density (470 blades per m²) of the artificial seagrass mimicked that of the dominant turtle grass (*Thalassia testudinum*) habitat present in the grass beds adjacent to the FSUCML, where experimental animals were collected.

2.2. Prey preference experiments

To test for preference by juvenile gag between shrimp and pinfish, I used a two-stage experimental design. Gag were given either shrimp or pinfish alone in stage 1 and both prey in stage 2. In addition, I tested whether the initial density of prey (12 versus 24 individuals) affected consumption rates and preference. This substitutive and additive experiment consisted of six combinations of the prey composition by density treatment (1: stage 1 – 12 shrimp only; 2: stage 1 – 12 pinfish only; 3: stage 2 – 6 shrimp and 6 pinfish together; 4: stage 1 – 24 shrimp only; 5: stage 1 – 24 pinfish only; and 6: stage 2 – 12 shrimp and 12 pinfish together).

Pilot feeding trials (N=12) were conducted to determine the size range for each prey that juvenile gag could successfully consume (i.e., predator–prey size ratios). In fishes, this ratio is commonly measured as the size of the prey relative to the length of the fish (Scharf et al., 2000). Pink shrimp measuring 8–15% (carapace length) and pinfish measuring 20–33% (standard length) of gag standard length were readily consumed, therefore prey in experimental feeding trials were restricted to these respective ranges.

Gag (standard lengths = 16.9-21.4 cm) were placed singly into experimental tanks for a 96-hour acclimation period prior to feeding trials, during which they were fed *ad libitum*. Prey composition (i.e., shrimp only, pinfish only, shrimp and pinfish together) provided to each gag during the acclimation period matched that of the ensuing experimental period to avoid a confounding effect of experience on

choice (Micheli, 1997). Following acclimation, all remaining prey were removed and gag were starved for 24 h to standardize hunger.

After the starvation period, prey were added through an upright PVC pipe (7.6 cm diameter) temporarily placed in the center of the tank. The pipe allowed prey to swim safely to the bottom, thus allowing them to reach the shelter of the artificial seagrass without being immediately consumed by the gag. Feeding trials lasted 48 h, after which remaining prey were removed and counted. The number of prey consumed was then calculated as the initial abundance minus the number of remaining prey. Each feeding event was conducted with a unique individual gag and unique sets of prey. The entire study involved five rounds of feeding trials with each round represented by a single replicate for each of the six prey-density combinations randomly allocated among experimental tanks (N = 30). Following Peterson and Renaud (1989), I also ran three trials lacking gag for each prey-density combination (N=18) to control for non-predatory changes in prey density. All trials were conducted within a four-week period in late summer when water temperature (mean = 27.9 °C: SE = 0.12), salinity (mean = 29.4 ppt; SE = 0.32), and dissolved oxygen (mean = 5.8 ppm; SE = 0.09) remained stable.

2.3. Statistical analyses

Using the data from stages 1 and 2 of the feeding trials and maximum likelihood equations derived by Underwood and Clarke (2005; Section 2.4 and Appendix A.3), I estimated the null expectations of no preference. Observed consumption was then compared with expected values using χ^2 tests. This relatively new analytical technique has previously been used to test habitat selection in diadromous fishes (Hale et al., 2008) and prey-size preference in a reef crab (Jackson and Underwood, 2007). A total of 10 comparisons were made (five low prey density and five high prey density) and individual tests consisted of similarly sized gag (e.g., the smallest with the smallest, largest with the largest) (Table 1).

3. Results

In the gag-free controls, I observed 100% survivorship across the six prey (i.e., shrimp only, pinfish only, shrimp and pinfish) and density (i.e., 12, 24) combinations, indicating that any losses in the gag-present trials could be attributed to predation. All juvenile gag consumed prey during both acclimation and experimental feeding periods. On average, gag consumed more shrimp than fish across all choice and density combinations (Fig. 1; Table 2). When choice was not possible, consumption rates were independent of initial prey density for both shrimp ($t_8 = 1.4$; P = 0.20) and fish ($t_8 = 0.16$; P = 0.88).

Preference was not detected for either prey at $\alpha = 0.05$ across all ten χ^2 tests (Table 1). However, the two tests comprising the smallest gag for the low and high initial prey densities resulted in marginally significant preference for shrimp (P = 0.07).

Table 1

Sizes (cm S.L.) of juvenile gag used in feeding trials according to prey and abundance combinations. Comparisons used to test for prey preference were made among gag of similar sizes.

Test	Pink shrimp	Pinfish	Both	Initial # of prey
1	16.9	17.7	17.3	12
2	18.4	18.5	18.2	12
3	19.0	18.7	19.1	12
4	19.7	19.8	19.5	12
5	20.1	19.8	20.0	12
6	17.2	17.5	16.9	24
7	19.0	18.4	18.3	24
8	19.2	18.7	19.0	24
9	20.2	19.7	19.6	24
10	21.4	20.1	20.3	24



Fig. 1. Consumption rates (number eaten 48 h^{-1}) of pink shrimp and pinfish by juvenile gag under different choice (columns) and initial prey density (rows) scenarios.

4. Discussion

Using a two-stage experimental approach and recently developed formulae that account for sampling error in each stage, I have demonstrated that juvenile gag do not display preference between two of their most common prey. The absence of choice between prey occurred despite marked differences in the morphology and behavior of the prey species. Moreover, the results were consistent across two initial prey densities. Experimental results therefore reflected patterns observed from stomach contents of gag collected from their natural habitats and also indicate the feasibility of mesocosm studies using this predatory fish.

When sampling error from the first experimental stage (i.e., no choice trails) was incorporated into null expectations, none of the χ^2 comparisons indicated preference. However, the outcome of the study was very different when I conducted *post hoc* comparisons using the same feeding trials while ignoring the sampling error from the first experimental stage. Six of the 10 comparisons produced significant χ^2

Table 2

Tests for prey preference by juvenile gag for either pink shrimp or pinfish. Observed (Obs) and null (Exp) values are given. Notation is defined below the table and follows that of Underwood and Clarke (2005).

Test	M_1	M_2	m_1	m_2	Ν	Obs	Obs	Exp	Exp	Exp	Exp	χ^2	Р
						n_1	n_2	m_1	m_2	n_1	n_2		
1	12	12	4	8	12	4	1	5.1	7.2	2.1	2.9	3.39	0.065
2	12	12	5	5	12	5	3	5.4	4.6	4.3	3.7	0.30	0.585
3	12	12	7	2	12	2	1	6.9	2.2	2.3	0.7	0.15	0.695
4	12	12	6	4	12	6	1	6.6	3.1	4.8	2.2	1.33	0.249
5	12	12	5	3	12	5	3	5.0	3.0	5.0	3.0	0.00	-
6	24	24	9	6	24	6	0	10.1	4.5	4.1	1.9	3.30	0.070
7	24	24	7	5	24	4	1	7.6	4.3	3.2	1.8	0.73	0.394
8	24	24	6	6	24	7	2	7.1	4.7	5.4	3.6	1.69	0.193
9	24	24	8	3	24	6	0	8.7	2.0	4.9	1.1	1.95	0.163
10	24	24	4	3	24	4	1	4.6	2.4	3.3	1.7	0.68	0.408

 M_1 = total number of shrimp available to predator in stage 1.

 M_2 = total number of pinfish available to predator in stage 1.

 $m_1 =$ number of shrimp eaten in stage 1.

 $m_2 =$ number of pinfish eaten in stage 1.

N = total prey available (both species) to predator in stage 2.

 $n_1 =$ number of shrimp eaten in stage 2.

 n_2 = number of pinfish eaten in stage 2.

tests indicating juvenile gag exhibited a preference for shrimp more often than they exhibited no preference. Such a high proportion of Type I errors is expected when the numbers of feeding trials and tests are relatively low, as is typical in preference experiments (Underwood and Clarke, 2005) including the current study. These results therefore underscore the importance of proper analyses of feeding experiments.

Preference for one prey over others implies an active, behavioral choice made by a predator. In the current study, consumption rates of shrimp were 23%–48% higher than that for pinfish during stage 1 feeding trials. It may be tempting to assume these results reflect a preference for shrimp. However, consumption rates from stage 1 lead to higher expected (null) values for shrimp in stage 2 trials, as derived from maximum likelihood equations. Higher consumption may reflect faster handling times required for juvenile gag to find, capture and ingest penaeid shrimp compared to fish. Shrimp moved liberally in three dimensions (i.e., horizontal and vertical planes) through the artificial seagrass while the pinfish tended to remain near the bottom. Therefore, differences in activity levels may have increased encounter rates with shrimp. However, gastric evacuation of crustacean prey can be much slower than that for fishes in serranids (e.g., Beukers-Stewart and Jones, 2004), and may have limited the maximum consumption rates for gag (Berens and Murie, 2008). Differences in digestion rates among various prey further highlight the shortcomings of inferring preference from patterns of diet data alone.

The impetus for this study was to attribute mechanism to patterns observed in the field using laboratory experiments that examine the behavior of choice. Prior stomach content analyses suggested juvenile gag undergo trophic shifts from diets comprising small invertebrate prey (e.g., amphipods, hypolytid shrimp) to larger epibenthic invertebrates (e.g., penaeid shrimp) and finally fishes during their first year (Bullock and Smith, 1991; Mullaney and Gale, 1996; Stallings et al., In press). Moreover, older juveniles and adult gag feed almost exclusively on fishes (Naughton and Salomon, 1985). I focused on young-of-year gag in the current study, involving only sizes reported to have mixed diets dominated by penaeid shrimp and fishes (i.e., transitional phase prior to piscivory). At the $\alpha = 0.05$ level, the feeding experiments provided no evidence of preference between the two prey for gag with standard lengths from 16.0 to 22.0 cm. However, it is worth noting that the feeding trails and χ^2 tests involving the smallest gag were marginally significant (i.e., two tests with P < 0.10), suggesting a weak preference for shrimp by the smallest individuals. Future feeding experiments could expand upon the range of juvenile gag sizes used in the current study to incorporate individuals that are both pre- and post-transitional periods to piscivory. Such an experimental design may elucidate process associated with diet shifts in predatory fishes.

Both preference and consumption rates were independent of initial prey density. Reductions in the densities of shrimp and pinfish by the rollerframe trawl fishery may therefore have little effect on these two components of gag feeding ecology, at least at the densities used in the current study. However, extreme reductions in the densities of important prey (e.g., from repetitive trawling) may reduce the carrying capacity for juvenile gag in local seagrass beds, thus limiting replenishment of adult populations. Management must therefore address factors that affect species throughout their life cycles, including both direct and indirect effects of fishing on juvenile stages (Stallings, 2008). Given that adult gag are intensively targeted by both commercial and recreational fisheries with annual landings averaging over 2400 metric tons in recent years (Turner et al., 2001, Coleman et al., 2004) and are both overfished and undergoing overfishing in the Gulf of Mexico (NMFS, 2009), accounting for unanticipated effects of fishing on juvenile stages is especially timely if sustainability is to be accomplished for this species. Identifying mechanism and quantifying predator-prey interactions is a necessary step in the recent calls for movement towards ecosystem-based management (Whipple et al., 2000, Garrison et al., in press). Studies that examine prey preference, such as that reported here, are one approach that can be used to better understand how changes in prey populations may influence food web dynamics and thus how management among different user groups may proceed.

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