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ELSEVIER

Journal of Experimental Marine Biology and Ecology 357 (2008) 109–120

**Journal of
EXPERIMENTAL
MARINE BIOLOGY
AND ECOLOGY**

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Experimental assessment of trophic impacts from a network model of a seagrass ecosystem: Direct and indirect effects of gulf flounder, spot and pinfish on benthic polychaetes

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Received 6 June 2006; received in revised form 14 June 2007; accepted 31 December 2007

Abstract

Trophic cascades are predicted to occur when the abundance of predators is increased, directly reducing the abundance of the intermediate prey and indirectly increasing the abundance of the prey at the base of a food web. Mixed trophic impact analysis of a network model developed for Apalachee Bay, near St. Marks, FL, USA predicted such a trophic cascade, in that increased abundance of juvenile gulf flounder *Paralichthys albigutta* (\bar{x} = 149 mm SL, effective trophic level 3.9) should have a negative impact on juvenile spot *Leiostomus xanthurus* (\bar{x} = 30 mm SL, effective trophic level 2.9) and a positive impact on benthic polychaetes (effective trophic levels 2.3 for deposit feeders and 3.0 for predatory polychaetes) in *Halodule wrightii* seagrass beds. We tested the predictions of the mixed trophic impact analysis by manipulating the abundance of the high trophic-level species (juvenile gulf flounder) in a cage-exclusion study in the North River, near Harkers Island, NC, USA. We compared the polychaete communities in St. Marks, FL and Harkers Island, NC, and showed that they are 51% similar (Jaccard's Index) at the family level, with the same eight dominant families (Nereidae, Capitellidae, Syllidae, Spionidae, Cirratulidae, Terebellidae, Sabellidae, and Maldanidae) present in both locations. We used 24 open-bottom cages to enclose the benthos and its seagrass-associated animal communities. We manipulated each cage by assigning it to one of the following treatments: (1) inclusion of fishes in upper and intermediate trophic levels (1 juvenile gulf flounder and 10 juvenile spot, the flounder+spot treatment); (2) inclusion of the intermediate predator (10 juvenile spot with no gulf flounder, the spot-only treatment); and (3) no fish added (unmanipulated controls). Core samples taken within the cages provided pre- and post-experimental measures of polychaete density and biomass, and the difference in density and biomass were used as response variables. At the end of the experiment, we collected, weighed, and analyzed the gut contents of all juvenile spot present in the cages. Juvenile pinfish (*Lagodon rhomboides*, \bar{x} = 30 mm SL) were present at the end of the study, having arrived as larvae or being trapped during cage set-up, and these fish were also examined, because they also eat polychaetes and their natural densities exceeded our introduced spot densities. Significant differences among treatments were detected for the polychaete family Terebellidae for both the change in density and biomass (pre-experiment – post-experiment). Densities of the Terebellidae changed in the direction predicted by the network model's impact analysis, declining in the cages with spot added compared with the control cages. Analyses of the other response variables (post-experiment spot and pinfish densities and biomass, difference between pre- and post-experiment polychaete densities and biomass for other families, and post-experiment spot and pinfish stomach content biomass) showed no significant differences among treatments. Several variables (Nereidae densities, pinfish densities and biomass, and pinfish stomach content biomass) varied between cages with low and high seagrass cover (significant blocking effect, $P < 0.001$). Nereidae densities declined significantly in cages with high (73%) rather than with low coverage (31% cover) of seagrass. Pinfish density and biomass were significantly greater in the high seagrass cages at the end of the experiments ($P < 0.001$), suggesting that dense seagrass attracted them. We conclude that the high density of pinfish in dense seagrass was responsible for the decline in density of the Nereidae. The direct effect of intermediate predators (pinfish feeding on polychaete prey) can be influenced by preferential recruitment of fishes to structurally complex habitats. The direction of change of indirect effects, but not the magnitude, in multi-trophic-level food webs can be predicted by the mixed trophic impact analysis of network models. However, these indirect effects are likely to be small in magnitude relative to direct effects and may be difficult to detect experimentally, especially in low-power experimental caging studies with natural fluctuations in recruitment rates of competitor species.

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Keywords: Mixed trophic impacts; Network analysis; Seagrass beds

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1. Introduction

It is not often clear what will happen in a given ecosystem if species are added, removed or their abundance altered. Removal or addition of species (through fishery harvests or due to species introductions) can have impacts on food webs that extend across several trophic levels based on theoretical analyses (Ulanowicz and Puccia, 1990; Yodzis, 2000; Libralato et al., 2006) and experimental results (Heck et al., 2006). This phenomenon, in which a top predator is removed by harvest, its intermediate prey increases due to a direct effect, and the intermediate prey's prey declines due to an indirect impact, has been termed a trophic cascade (Paine, 1980; Lodge et al., 1994; Schindler et al., 1996).

Trophic cascades are relevant to multi-species management of fisheries, where the decline in abundance of a harvested species can affect the predators that consume it and the prey that it consumes. In Southeastern USA, flounders (*Paralichthys* sp.) are the subject of intense commercial and recreational fishing pressure, which removes 1.8–2.7 million kg of fish per year (O'Bannon, 2002; NMFS, personal communication). One aspect of this fishery that needs examination is the impact of the removal of flounders from the food web, both direct effects (on flounder prey populations) and indirect effects (on the rest of the species in the ecosystem). For example, Yodzis (2000) has shown that indirect effects (or diffuse effects) as a result of fishing can cause changes to the abundances of other species throughout the food web. It would be useful if a mathematical model could be used to predict what changes in species biomass would occur as a result of a change in flounder biomass caused by fishery harvests.

One such modeling approach includes ecological network models (Kay et al., 1989; Baird and Ulanowicz, 1989), which incorporate all possible trophic interactions among species, and may be used to predict trophic impacts and what could happen if species abundances are changed (Ulanowicz and Puccia, 1990). Various alternative approaches to the analysis of trophic structure include experimental removal or addition studies (Connell, 1961; Virnstein, 1977; Lubchenco, 1978; Paine, 1980; Leber, 1985), development of topological food web models (Goldwasser and Roughgarden, 1993; Hall and Raffaelli, 1993; Polis, 1994), and trophic cascade models (Lodge et al., 1994; Schindler et al., 1996). Although all of these experiments and models make predictions about the impact of a change in a species abundance on other species in a given ecosystem, only network analysis provides a method for quantifying the expected change in abundances due to direct and indirect effects (Ulanowicz and Puccia, 1990). Until now, no attempt has been made to experimentally verify the predictions of an ecological network model. Here, we experimentally test the predictions of the mixed trophic impacts model of the St. Marks seagrass food web (Baird et al., 1998; Christian and Luczkovich, 1999; Luczkovich et al., 2002; Luczkovich et al., 2003).

One of the analyses that can be performed in network analysis allows the calculation of positive and negative trophic impacts (mixed trophic impacts). Mixed trophic impacts are the direct and indirect impacts from other compartments affecting the biomass of a single compartment (Ulanowicz and Puccia,

1990). Direct impacts are the impacts of one compartment on another with which it shares a single pathway (one link away). This is analogous to the relationship between predator and prey. However, indirect impacts can occur between two compartments along multiple network paths through several possible compartments (two or more links distant from the focal node). Energy or biomass flows along trophic links are essential in estimating these impacts. For example, when a predator consumes prey, it reduces the predation on other species that are the food of the prey (indirect positive impact); trophic interactions of the prey and its competitors will be impacted in a similar way. When a predator consumes prey, it can also impact other predators of the prey by removing some of the available prey biomass (indirect negative impact). The relative importance of such indirect and direct pathways can be difficult to assess using qualitative methods alone. Mixed trophic impact analysis, which uses graph theory and biomass flows as measures of consumption to calculate all impacts along all trophic pathways, allows one to compute the relative magnitude of the direct and indirect trophic impacts, expressed as interaction coefficients, of one species on another (Ulanowicz and Puccia, 1990). These coefficients allow the calculation of the change in biomass in one species as a result of a change in biomass of another species in the network. Two major network modeling software packages can be used to perform mixed trophic impact analysis: the IMPACT module of NETWRK IV (Ulanowicz and Puccia, 1990) has been developed to compute the impact coefficients using a computer algorithm (available at <http://www.cbl.umces.edu/~ulan/ntwk/network.html>); also, ECOPATH 5.1 (<http://www.ecopath.org>) has a mixed trophic impact analysis module based on the Ulanowicz and Puccia (1990) equations.

For example, using the mixed trophic impact analysis on the network model of the Chesapeake Bay (Baird and Ulanowicz, 1989), the trophic impact coefficients for spot (*Leiostomus xanthurus*) on *Nereis* and other polychaetes are -0.002 and -0.004 respectively (Ulanowicz and Puccia, 1990). This suggests that an increase in spot biomass would cause a decrease in these prey groups due to both the direct and indirect predation effects. There are positive impacts as well; for example, the mixed trophic impact of spot on crustacean deposit feeders was calculated as $+0.003$. This positive indirect effect may be due to spot feeding on polychaetes, which are, in turn, the competitors of the crustacean deposit feeders (Ulanowicz and Puccia, 1990). Interestingly, the impact of spot on summer flounder (*Paralichthys dentatus*) is negative (-0.0092), which indicates that spot, even though they are directly prey of summer flounder and should have a positive impact, must compete with another prey of the summer flounder, are prey for competitors of summer flounder, or consume the same prey as summer flounder (Ulanowicz and Puccia, 1990).

Our work here was motivated by recent studies of a *Halodule wrightii* seagrass food web near St. Marks, Florida, which has been modeled using network analysis. The sampling design for that site was specific for network analysis and allowed for the construction of one of the most complex estuarine food webs obtained to date (Baird et al., 1998; Christian and Luczkovich, 1999; Luczkovich et al., 2002; Luczkovich et al., 2003). Mixed

trophic impact analysis indicated that in the St. Marks seagrass network model, juvenile gulf flounder (*Paralichthys albigutta*) and Atlantic needlefish (*Strongylura marina*) compartment had a large negative impact on pinfish (*Lagodon rhomboides*) (-0.0749) and spot (-0.218), while having a positive impact on predatory (0.0176) and deposit-feeding polychaetes (0.0194) (Table 1). These impact coefficients indicate that an increase in juvenile gulf flounder (or Atlantic needlefish) biomass would result in a decrease in pinfish and spot biomass (negative impacts) and an increase in predatory and benthic feeding polychaetes (positive impacts).

The goal of this research was to quantify experimentally the predictions made using mixed trophic impact analysis (with specific reference to the nodes juvenile gulf flounder, spot and polychaetes) calculated from the St. Marks seagrass network model. In this experiment, we included the network compartments (juvenile gulf flounder, spot, and polychaetes) modeled in St. Marks in January and February, but in a *H. wrightii* seagrass meadow at in an estuary in North Carolina, USA in April. We do not believe that the change in location was a significant factor, due to the well-established similarity of the ecological community of the *H. wrightii* seagrass meadows in these two areas. Peak fish recruitment of spot, pinfish and flounders occurs in the late winter and spring in the estuaries of North Carolina and in the Gulf of Mexico in Florida, with post-larvae arriving in the seagrass beds between February and April (Warlen and Burke, 1990; Sheridan and Livingston, 1983; Livingston, 1984). North Carolina is slightly later in the seasonal phenology and timing of fish recruitment, hence our experiment was 2 months later than the

modeled period at St. Marks. In addition, the rank order of abundance of polychaete species was similar in Apalachicola Bay, Florida *H. wrightii* meadows (Sheridan and Livingston 1983) and in *Zostera marina* meadows in Chesapeake Bay, Virginia (Orth, 1973); see the direct comparison of polychaete rank-order abundances in these two studies as described by Sheridan and Livingston (1983). Furthermore, the diets of gulf flounder, spot and pinfish are similar in North Carolina and Florida. In both areas, gulf flounder feed on spot (Overstreet and Heard, 1982; Burke, 1995; Ward, 1998; Christian and Luczkovich, 1999), spot feed mainly on polychaetes and amphipods (Billheimer and Coull, 1988; Ellis and Coull, 1989; Livingston, 1984) and pinfish feed mainly on copepods and amphipods and to a smaller extent, polychaetes (Carr and Adams, 1973; Stoner, 1980; Luczkovich and Stellwag, 1993; Miltner et al., 1994). Thus, our North Carolina experimental ecosystem, and importantly the trophic subsystem that we were interested in, mimicked that of the Florida seagrass bed.

We selected gulf flounder and spot to manipulate in a caging study in field experiments in Core Sound, North Carolina. We examined the impact of gulf flounder and spot additions and removals upon the change in polychaete density and biomass, while examining the stomach contents of fishes. Based on the network model mixed trophic impact analysis, we predicted that spot abundance would be lower, and change in polychaete abundance greater, in cages with gulf flounder added, compared with control cages. Unexpectedly, we observed the high levels of recruitment of pinfish to our cages with high percentage cover of seagrass, *H. wrightii*, so we also analyzed the impact of pinfish recruitment on the change in polychaete density.

2. Materials and methods

2.1. Site description

The site for the experiment was in the mouth of the North River in Core Sound near Harkers Island, North Carolina (N 34°43'28", W 76°34'48"), USA (Fig. 1). A small tidal creek bisected the site, and this creek divided the site into two blocks (each with six cages) for statistical purposes. This site had areas of seagrass (*H. wrightii* and *Z. marina*) beds where the experiments were conducted. Previous studies indicate that seagrass density may affect the densities of organisms utilizing seagrass beds (Kikuchi, 1974; Adams, 1976; Weinstein and Heck, 1979; Crowder and Cooper, 1982; Böstrom and Bonsdorff, 2000) and recruitment into seagrass beds (Jordan et al., 1996; Horinouchi and Sano, 1999; Horinouchi et al., 1999). To identify differences in seagrass density on either side of the tidal creek (the block effect), the density of seagrass was estimated using the random placement of a 0.8-m² ring along the same depth contour as the cages. Percent cover inside the ring was then approximated at each area sampled. One of the blocks (upstream of tidal creek) had higher seagrass density (>73% *Halodule* cover) and the other (downstream of tidal creek) had low seagrass density (sparse *Halodule*, <31% cover) (Fig. 2). The seagrass beds were 50 m from the shoreline and could be reached without using a boat. The site was 100 m from the nearest boat channel, which limited any disturbance by

Table 1

Mixed trophic impact coefficients from the St. Marks Bay network analysis for compartments having an effect from gulf flounder with an absolute value greater than 0.01

Compartment	Impacts upon gulf flounder	Effects from gulf flounder
Spot	0.477	-0.218
Zooplankton	0.148	-0.205
Gulf flounder and needlefish	-0.179	-0.179
Pinfish	-0.0141	-0.0749
Atlantic silverside and bay anchovy	-0.0293	-0.0478
Fish and crustacean eating birds	-0.00301	-0.0416
Red drum	-0.00894	-0.0199
Suspension-feeding polychaetes	-0.0289	-0.0158
Killifish	-0.00262	-0.0105
Predatory shrimp	-0.00763	0.0116
Herbivorous shrimp	0.00746	0.017
Predatory polychaetes	0.0229	0.0176
Deposit-feeding polychaetes	0.0222	0.0194
Raptors	-0.0152	0.0971

These are compartments that are impacted the most by gulf flounder (gulf flounder and needlefish are combined into one compartment in the St. Marks Bay network analysis) (Christian and Luczkovich, 1999).

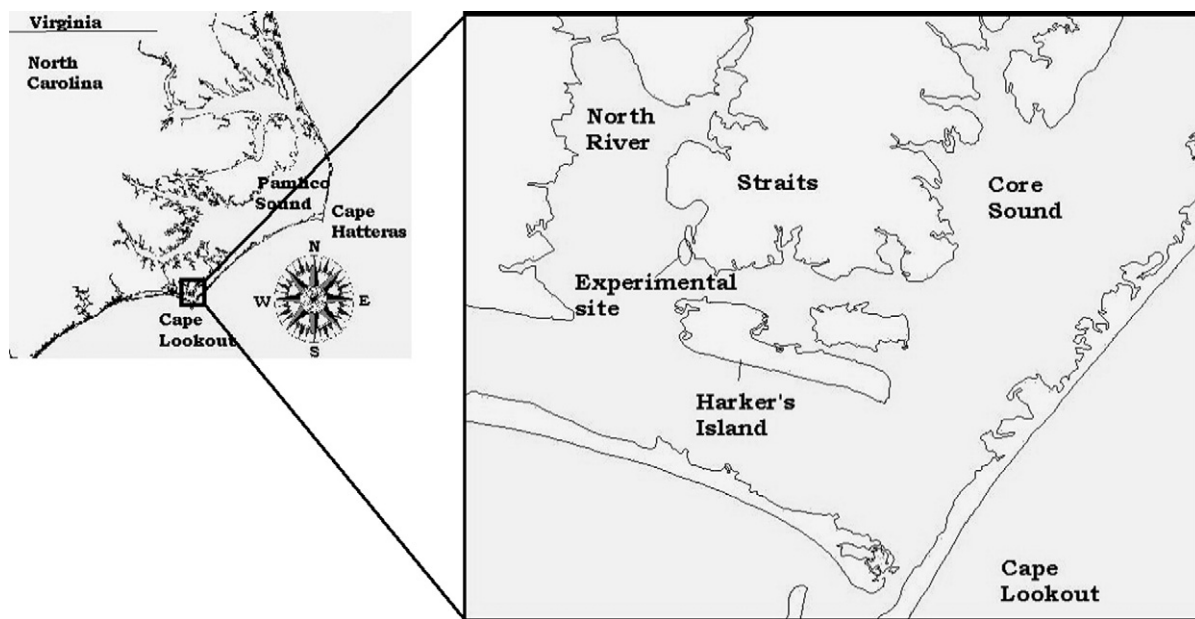


Fig. 1. Experimental site near Harkers Island, NC, U.S.A and surrounding area in eastern North Carolina.

vessels. The substrate was sand, which gulf flounder prefer over the muddy substrate found further upstream (Burke et al., 1991).

2.2. Cage design

The experiments were conducted in predator inclusion or exclusion cages 1.0-m high and 1.0-m diameter (0.785 m^2), constructed of 2.5-cm diameter flexible PVC tubing covered in a 3-mm mesh netting (to exclude predators and prevent escape), with a removable top that was tied shut with 20.5-cm cable ties. The cages were finished with a 15.2-cm wide, 3-mm thick fiberglass sheet around the base, which was submerged 5 cm into the sediment to control for migration of animals into the cages and escape by burrowing under the cages. The cages were open to the benthos to allow the fish to interact with the benthic invertebrates and round to control for any avoidance behavior by prey species aggregating in corners (Ellis and Coull, 1989; Leber, 1985).

2.3. Experimental design

The research was carried out in April 2002, during a period when spot and pinfish were numerous at this site. We added densities of 1 gulf flounder (1.3 m^{-2}) and 10 spot per cage ($12\text{--}13 \text{ m}^{-2}$), which are similar to previously described fish densities in North Carolina and Florida. Fish densities in the St. Marks seagrass beds in February 1994 averaged 10.1 m^{-2} for spot and average density of 8.1 m^{-2} for pinfish, but gulf flounder were much less common, with densities of 0.02 fish m^{-2} (Ward 1998). In North Carolina, the density of spot was between 5 and 30 fish m^{-2} in areas bordered by marsh or seagrasses (Stokesbury and Ross, 1997). Hovel et al. (2002) sampling in seagrass areas near Harkers Island, North Carolina, with throw traps showed that densities of pinfish were between 2 and 3 individuals m^{-2} in May and June and most likely they would have been higher in April. Wright et al. (1993) used

densities of spot (25–30 mm SL) ranging from 4 to 20 m^{-2} in an experimental study with southern flounder (*P. lethostigma*) predation in North Carolina estuaries. Hettler (1989) using a 10-m block net samples taken monthly in the Newport River, near Beaufort, NC 1986–1987 found that spot averaged $154.5 \times 10 \text{ m}^{-1}$, pinfish averaged $10.3 \times 10 \text{ m}^{-1}$, and gulf flounder averaged $0.1 \times 10 \text{ m}^{-1}$ of linear salt marsh edge, but did not report monthly values. Thus, the addition of 10 spot per cage fell within the range of natural levels of abundance of fishes in *H. wrightii* beds in the Southeastern USA at this time of year. However, our addition of one gulf flounder represented a relatively high density in these small cages; a single gulf flounder would have been found in larger area ($50\text{--}100 \text{ m}^2$) based on data from Hettler (1989) and Ward (1998). In order to restrict the effects of gulf flounder feeding on spot and pinfish and the indirect impact on polychaetes to a small area of bottom to study, we chose to use small cages with a single gulf flounder.

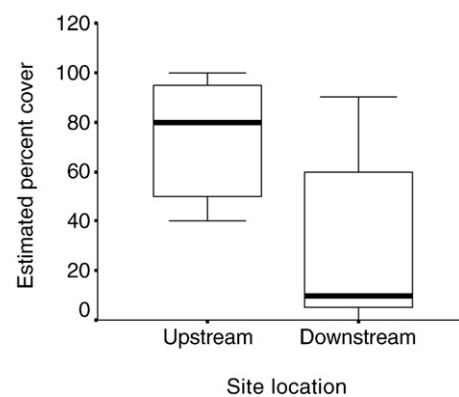


Fig. 2. Difference in seagrass cover between sites upstream and downstream of a tidal creek bisecting the experimental site, indicating higher seagrass cover upstream of the tidal creek (based on visual estimation of percent cover).

The treatment with 10 spot and one gulf flounder is referred to as “flounder + spot” treatment and the treatment with 10 spot and no gulf flounder is referred to as the “spot-only” treatment. The experiment also included a “control” with no fish introduced to the cage. We did not have a treatment with one gulf flounder and no spot added, because this was not a natural situation that we wanted to test (there was not a network model prediction for this situation, because flounder never occur without spot in natural communities). We acknowledge that this may be seen as an experimental design flaw by some readers, as the flounder addition alone may have changed the polychaete community through both direct and indirect effects. There were four replicate cages for each treatment, thus 12 cages were constructed and installed at the site, 6 on each side of the tidal creek (the blocking factor). Treatments were randomly assigned within each block to a cage.

Two trials were conducted in April 2002, so that a total of 24 cages (8 replicates per treatment) were used. We ran short-term experiments using two trials of seven days each, which allowed the cages to remain intact. These trials were shorter than the generation time for all species involved, a requirement for a short-term experiment on a food web (Yodzis, 1988). During mesocosm experiments, Ward (1998) was able to show significant differences between spot and pinfish density as a result of gulf flounder selective predation after 48 h. At the beginning of each trial, cages were placed in the seagrass beds and secured with mobile home tie-down anchors 24 h before introduction of the gulf flounder and spot. This method allowed the cage to settle into the substrate, after which, the anchors

were tightened into the substrate before introduction of the fish, to prevent any gaps between the substrate and the enclosure.

2.4. Collection methods

Polychaete samples were obtained from each cage at the beginning and end of each trial by taking three core samples from inside each cage with the use of a hand-held core sampler (7.6 cm inside diameter, to a depth of 10 cm). The cores were sieved through 500- μ m mesh in the field and placed in jars with rose bengal and 10% formalin. The pre-experimental cores were used to compare the polychaete community at Harkers Island with similar core samples taken at St. Marks, Florida in Jan and Feb 1994. The pre- and post-experimental difference in polychaete density and biomass within each cage was used as a response variable.

Juvenile gulf flounder were collected using a 12.2-m long, 2.5-cm mesh shrimp trawl in Core Sound, NC. After collection, the juvenile gulf flounder were transferred to a 25-liter transport tank and taken to the NOAA Laboratory in Beaufort. The juvenile gulf flounder were held in a 757-liter flow-through tank at the NOAA Laboratory to control for any mortality before being included in the experiment. At the beginning of each trial juvenile gulf flounder (\bar{x} = 149 mm SL \pm 36 s.d.) were transported to the experimental site and introduced to the cages assigned to the “flounder + spot” treatment. Juvenile spot (\bar{x} = 28 mm SL \pm 4 s.d.) were then collected using a 1.3-mm mesh beach seine from North River near the experimental site and introduced to cages on the same day. After introduction of fishes, the top of each cage was

Table 2

The polychaete community (based on taxa identified at the family level) of the *Halodule wrightii* seagrass beds at Harkers Island, North Carolina (experimental site) and at St. Marks, Florida (network model site)

Family	Harkers Island 7 Apr	Harkers Island 14 Apr	St. Marks no. m ⁻² Jan	St. Marks no. m ⁻² Feb	Harkers Island mean no. m ⁻²	St. Marks mean no. m ⁻²	Harkers Island %	St. Marks %
Spionidae	617	322	312.5	365.5	2928.8	339.0	45.10	11.61
Capitellidae	130	164	434.9	126.1	911.5	280.5	14.12	9.61
Syllidae	83	109	91.4	354.5	595.1	223.0	9.22	7.64
Cirratulidae	96	62	76.7	438.6	489.0	257.7	7.59	8.83
Nereidae	59	62	1154.9	274.1	375.6	714.5	5.81	24.48
Maldanidae	60	45	11	73.1	326.7	42.1	5.04	1.44
Poecilochaetidae	41	63	0	0.0	322.0	0.0	5.00	0.00
Sabellidae	11	26	62.1	252.2	114.2	157.2	1.78	5.38
Eunicidae	15	18	0	0.0	102.3	0.0	1.59	0.00
Terebellidae	10	14	561	0.0	74.4	280.5	1.15	9.61
Orbinidae	9	6	32.9	91.4	46.7	62.2	0.72	2.13
Opheliidae	10	3	0	0.0	40.7	0.0	0.62	0.00
Glyceridae	5	5	21.9	82.2	31.1	52.1	0.48	1.78
Phyllodocidae	3	6	0	0.0	27.8	0.0	0.43	0.00
Polynoidae	1	8	0	0.0	27.6	0.0	0.43	0.00
Flabelligeridae	7	1	0	0.0	25.1	0.0	0.38	0.00
Hesionidae	6	0	18.3	9.1	18.9	13.7	0.29	0.47
Onuphiidae	1	3	27.4	32.0	12.3	29.7	0.19	1.02
Lysaretidae	1	0	0	0.0	3.1	0.0	0.05	0.00
Paronidae	0	0	186.4	537.2	0.0	361.8	0.00	12.40
Pectinariidae	0	0	36.5	64.0	0.0	50.3	0.00	1.72
Serpulidae	0	0	109.6	0.0	0.0	54.8	0.00	1.88
Totals	1165	917	3137.5	2700.0	6476.1	2918.8	100.00	100.00

Numbers are densities in core samples (densities at Harkers Island taken with hand corers before fish introductions inside experimental cages, sum of 36 cores in April 2002; densities at St. Marks from the sum of 10 cores taken in January February 1994).

secured with plastic ties and the experiment was left to run for the seven-day period.

At the end of each trial, the spot and gulf flounder introduced in the cages were collected using a 0.0053 g/ml solution of crystalline rotenone in acetone. The cages were surrounded with a 2.0-m diameter × 1.0-m high circular barrier made of 3.0-mm thick fiberglass sheet supported on a 2.5-cm diameter polyethylene tubing frame. The rotenone solution was added to achieve a concentration of 0.28 ppm. The fishes were then collected with a 1.0-mm mesh dip net. After 20 min the bottom of each cage was dredged with the net to ensure all fish from the enclosure had been collected. In all cases except for a single fish in Trial 2, the gulf flounder were recaptured alive. The gulf flounder in that cage thus may not have been alive long enough to have an effect on the spot or polychaete biomass. We excluded the data from this cage when we analyzed the results.

In addition to spot and gulf flounder that we added, small fishes (<20 mm) including additional spot and pinfish (*L. rhomboides*) were recovered from some of the cages, including the “no fish” control treatment cages. These fishes either naturally recruited to our cages as larvae or were trapped during cage installation. Because these fishes naturally recruit into seagrass meadows in North Carolina and Florida as larvae at this time of year and prey on polychaetes after settlement (Luczkovich, 1988; Luczkovich and Stellwag, 1993; Luczkovich et al., 1995), we decided to include pinfish in the response variables (pinfish density, biomass and stomach content biomass).

2.5. Benthic sample analysis and stomach analysis procedures

The polychaetes were separated from the core samples and identified to family using Fauchald (1977), Day (1973) and Uebelacker and Johnson (1984). Fishes collected at the end of each trial were identified to species and placed into 5-mm SL size classes. Stomach contents from each fish were obtained and prey items identified, as digestive state would permit. We used a dissecting microscope at 40× magnification to make identifications. We estimated the dry biomasses of polychaetes by weighing a sample of worms of the same taxon and getting a dry mass/individual worm, then transforming the density counts obtained from core samples by this average mass per individual. Stomach content dry biomasses were estimated by weighing a small sample of prey items to obtain the average mass per prey item, and density counts within the stomachs of all fishes collected were then transformed by the average biomass per individual. Dry biomasses for fishes were obtained by weighing each fish separately. Dry biomasses were obtained in each case by placing the samples in an oven at 60 °C for 48 h, then weighing with a digital microbalance.

2.6. Statistical analysis

We used SYSTAT 11.0 to calculate similarity indexes (Jaccard's index) and analyses of variance (ANOVAs). We compared the communities of polychaetes (resolved to the taxonomic Family level) at St. Marks and Harkers Island using Jaccard's index of similarity. We compared the difference in

densities of polychaetes among treatments at the start and end of each experiment (difference in density = number per core at start – number per core at the end of each trial), so a positive response in this variable indicated a decline in density within each of the eight dominant families of polychaetes (i.e., >5% of the community at the start) that occurred at both St. Marks and Harkers Island. We compared the difference in polychaete density between treatments and blocks (high seagrass cover in Block 1 versus low seagrass cover in Block 2) using a two-way ANOVA test. ANOVAs were performed (randomized block design, with a Bonferroni-corrected post-hoc comparison test among the three treatment groups) on the following response variables: spot density and biomass, pinfish density and biomass, the difference in polychaete biomass, and stomach content biomass of prey taxa within the pinfish and spot. For

Table 3
Statistical table listing *F* and *P* values for ANOVA tests

Response variable	Factor	Degrees of freedom	<i>F</i>	<i>P</i>
Spot density	Treatment	2	1.411	0.271
	Block	1	0.763	0.395
	Treatment * Block	2	0.207	0.815
Pinfish density	Treatment	2	2.070	0.157
	Block	1	22.403	0.000*
	Treatment * Block	2	3.540	0.152
Stomach content biomass (spot and pinfish)	Treatment	2	1.740	0.205
	Block	1	16.056	0.001*
Polychaete biomass (All families)	Treatment * Block	2	1.844	0.188
	Treatment	2	2.019	0.141
	Block	1	1.043	0.311
Polychaete density difference (Dominant families)	Treatment * Block	2	2.878	0.064
	Treatment	2	1.480	0.236
	Block	1	1.007	0.319
Treatment * Block		2	3.258	0.045*
	<i>Dominant Polychaete families</i>			
	Capitellidae density difference	Treatment	2	0.319
Block		1	1.845	0.179
Treatment * Block		2	0.243	0.785
Cirratulidae density difference	Treatment	2	0.941	0.395
	Block	1	0.036	0.851
	Treatment * Block	2	0.485	0.618
Nereidae density difference	Treatment	2	0.396	0.675
	Block	1	5.051	0.028*
	Treatment * Block	2	0.959	0.389
Maldanidae density difference	Treatment	2	0.131	0.878
	Block	1	2.213	0.142
	Treatment * Block	2	0.420	0.659
Sabellidae density difference	Treatment	2	0.012	0.988
	Block	1	0.833	0.365
	Treatment * Block	2	0.793	0.457
Spionidae density difference	Treatment	2	0.937	0.397
	Block	1	0.191	0.663
	Treatment * Block	2	4.209	0.019*
Syllidae density difference	Treatment	2	0.857	0.429
	Block	1	1.503	0.225
	Treatment * Block	2	0.741	0.481
Terebellidae density difference	Treatment	2	3.541	0.035*
	Block	1	0.020	0.888
	Treatment * Block	2	1.907	0.157

Asterisks indicate significant differences $P < 0.05$.

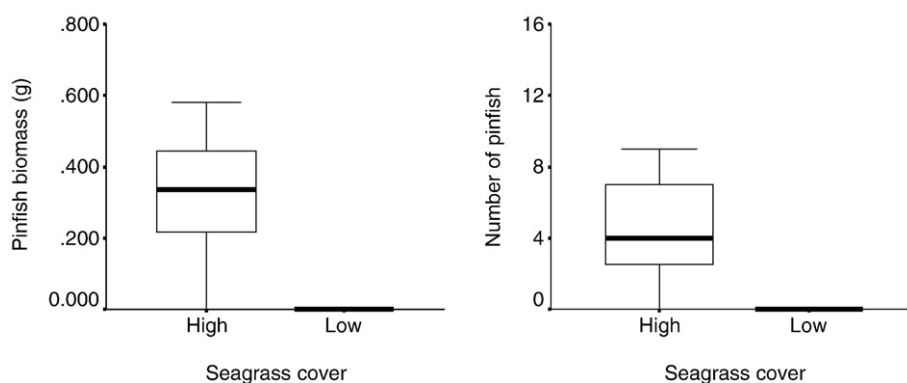


Fig. 3. Difference in pinfish density and biomass between sites with high and low seagrass cover, indicating higher density and biomass in areas with high seagrass cover.

these analyses, the two experimental trials were combined into a single analysis of variance because they were done within a few weeks of one another, and time was not a significant statistical effect in a preliminary ANOVA.

3. Results

3.1. Polychaete community at Harkers Island

The community of polychaetes at Harkers Island, North Carolina (experimental site) and St. Marks Florida (network model site) showed similarities in terms of the dominant taxa present, although only 52% of the families were present at both locations (Jaccard's index=0.52) and the total densities were greater at Harkers Island (6476 m^{-2} versus 2919 m^{-2} at St. Marks; Table 2). Spionids were the most common family at Harkers Island, whereas Nereids were most common at St. Marks. If we consider those families >5% of the total density as the dominants, then the polychaete community at both locations was dominated by eight families: the Spionidae (45.1% at Harkers Island, 11.6% at St. Marks), Capitellidae (14.1% at Harkers Island, 9.6% at St. Marks), Syllidae (9.2% at Harkers Island, 7.6% at St. Marks), Cirratulidae (7.6% at Harkers Island, 8.8% at St. Marks), Nereidae (5.8% at Harkers Island, 24.5% at St. Marks), Maldanidae (5.0% at Harkers Island, 1.4% at St. Marks), Sabellidae (1.8% at Harkers Island, 5.4% at St. Marks), and Terebellidae (1.2% at Harkers Island, 9.6% at St. Marks) (Table 2). Other families that were less abundant but were present in both places included the Orbinidae, Glyceridae, Hesionidae, and Onuphiidae. There were some differences (the presence of a family at only one location), with large numbers of Paronidae at St. Marks (12.4% of the community), while Harkers Island had many members of the Poecilochaetidae (5.0%). Several less abundant families only occurred at one location (Acrocirridae, Lumbrineridae, Opheliidae, Phyllodocidae, Polynoidae, Flabelligeridae, Lysaretidae, Pectinariidae, and Serpulidae).

3.2. Experimental test of gulf flounder trophic impacts

3.2.1. Spot and pinfish density and biomass

The trophic impacts from the St. Marks model predicted that increases in gulf flounder biomass would have a negative impact

on both spot and pinfish biomass and a positive impact on predatory and deposit-feeding polychaete biomass. However, there were no significant differences due to adding gulf flounder in mean spot or pinfish density or biomass in the cages (ANOVA, $P=0.157$ for pinfish density, $P=0.392$ for pinfish biomass, $P=0.271$ for spot density, $P=0.973$ for spot biomass; Table 3). Interestingly, mean pinfish density and biomass was highest in cages with high seagrass cover ($\bar{x}=6.09\pm 4.01$ s.d.) and lowest in cages with low seagrass cover ($\bar{x}=3.00\pm 0.00$ s.d.), suggesting that pinfish recruited preferentially into those cages (ANOVA, $P<0.001$ for density and biomass) (Fig. 3). This was not the case for spot which appeared to not recruit differently to the different seagrass cover blocks (ANOVA, $P=0.395$ for density and $P=0.720$ for biomass; Table 3).

3.2.2. Polychaete change in density and biomass

There was no overall effect of fish addition treatments on total polychaete biomass (Table 3). Likewise, the mean polychaete difference in density (pre-post=density measured at start of experiment–density measured after experiment) for the eight dominant polychaete families was not significantly different among treatments (ANOVA, $P=0.236$) or between blocks (ANOVA, $P=0.319$; Table 3); however, there was a significant

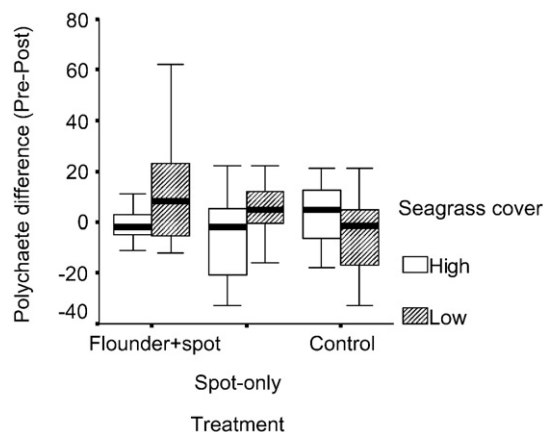


Fig. 4. Difference between pre- and post-experimental dominant polychaete family densities among treatments (fish additions) and blocks (high and low seagrass cover). Positive values are a reduction in density.

interaction effect between treatments and blocks ($P=0.045$; Fig. 4). When analyzed separately for each polychaete family, there was a significant treatment effect for Terebellidae density and biomass (ANOVA, $P=0.035$; Table 3 and Fig. 5). Bonferroni post-hoc comparisons showed a significant difference between the spot-only treatment and the control treatment (contrast, $P=0.030$), with no significant difference between spot-only and flounder+spot or flounder+spot and the control treatment. There was also a significant block effect for Nereidae density and biomass (ANOVA, $P=0.028$) (Table 3, Fig. 6), suggesting that the Nereidae declined in high seagrass cover irrespective of fish addition treatment.

3.2.3. Stomach contents

Together, pinfish and spot consumed mainly harpacticoid copepods (74% of diet) (Table 4). They also consumed gammarid amphipods (21% of diet), polychaetes (1% of diet), and crustacean remains (1% of diet), when considered as a pooled group of predators. Individually, spot consumed few amphipods (9% of diet) and polychaetes (2% of diet), eating mostly harpacticoid copepods (82% of the diet). Likewise, pinfish consumed mostly harpacticoid copepods (72% of diet) and very few polychaetes (1% of diet), but consumed higher amounts of amphipods than spot (23% of diet).

The total mass of all prey in stomach contents indicated that spot and pinfish did not consume significantly more benthic prey in cages where flounder were absent, although there was an interesting trend towards more prey being consumed in the spot-only treatment. The mean dry mass of the stomach contents of spot and pinfish combined did not differ among treatments, but there was a significant block effect due to seagrass cover (ANOVA, $P=0.001$; Table 3). This was also true for the pooled gut contents for pinfish alone, which showed a significant block effect (ANOVA, $P<0.001$); the gut contents for spot alone showed no significant block effects. The mean biomass of pinfish gut contents pooled across prey type was highest in the spot-only treatment ($\bar{x}=0.08164 \text{ g} \pm 0.10513 \text{ s.d.}$), intermediate in the flounder+spot treatment ($\bar{x}=0.06309 \text{ g} \pm 0.11059 \text{ s.d.}$) and lowest in the control ($\bar{x}=0.02489 \text{ g} \pm 0.04322 \text{ s.d.}$). This trend in high gut content biomass in the spot-only cages held for spot as well, where the

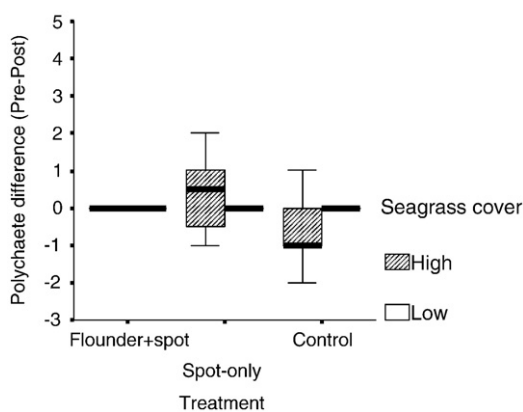


Fig. 5. Plot of difference between blocks with high and low seagrass density for changes in Terebellid density (density at beginning of experiment – density at end of experiment). Positive values are a reduction in density.

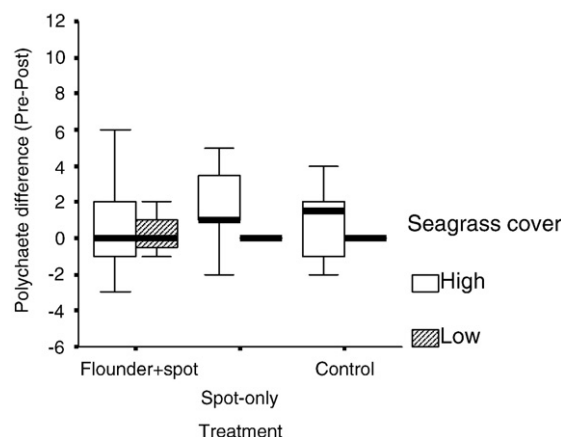


Fig. 6. Plot of difference between blocks with high and low seagrass density for changes in Nereid density (density at beginning of experiment – density at end of experiment). Positive values are a reduction in density.

contents pooled across prey type was also highest in the spot-only treatment ($\bar{x}=0.02348 \text{ g} \pm 0.048113 \text{ s.d.}$). However, in the case of spot, gut content biomass was intermediate in the control ($\bar{x}=0.00678 \text{ g} \pm 0.01509 \text{ s.d.}$) and lowest in the flounder+spot treatment ($\bar{x}=0.00333 \text{ g} \pm 0.00305 \text{ s.d.}$). This result indicates that more benthic fauna were removed by pinfish and spot in the spot-only treatment than in either the flounder+spot treatment or the control. However, as noted above, there was no significant treatment effect on mean prey mass in stomachs of spot and pinfish combined.

Table 4

Mean biomass and proportion (in parentheses) of prey items in gut contents by prey group for spot, pinfish and both, for each treatment and across all treatments

Prey group	Flounder+spot	Spot only	Control	Total
<i>Spot gut contents</i>				
Harpacticoid copepods	0.007 (0.21)	0.089 (0.92)	0.018 (0.66)	0.114 (0.82)
Gammarid amphipods	0.001 (0.07)	0.002 (0.02)	0.009 (0.33)	0.012 (0.09)
Polychaetes	0.001 (0.07)	0.002 (0.02)	0.000 (0.00)	0.003 (0.02)
Crustacean remains	0.001 (0.07)	0.002 (0.02)	0.000 (0.00)	0.003 (0.02)
Other	0.005 (0.33)	0.002 (0.02)	0.000 (0.00)	0.007 (0.05)
<i>Pinfish gut contents</i>				
Harpacticoid copepods	0.141 (0.63)	0.251 (0.76)	0.087 (0.85)	0.479 (0.72)
Gammarid amphipods	0.075 (0.33)	0.070 (0.21)	0.008 (0.08)	0.154 (0.23)
Polychaetes	0.000 (0.00)	0.002 (0.01)	0.000 (0.05)	0.003 (0.01)
Crustacean remains	0.003 (0.01)	0.001 (0.00)	0.000 (0.00)	0.004 (0.01)
Other	0.006 (0.02)	0.007 (0.02)	0.007 (0.07)	0.021 (0.03)
<i>Combined gut contents</i>				
Harpacticoid copepods	0.148 (0.62)	0.340 (0.80)	0.105 (0.81)	0.593 (0.74)
Gammarid amphipods	0.077 (0.32)	0.072 (0.17)	0.017 (0.13)	0.166 (0.21)
Polychaetes	0.001 (0.00)	0.004 (0.01)	0.000 (0.00)	0.006 (0.01)
Crustacean remains	0.003 (0.01)	0.004 (0.01)	0.000 (0.00)	0.007 (0.01)
Other	0.011 (0.05)	0.009 (0.02)	0.008 (0.06)	0.028 (0.04)

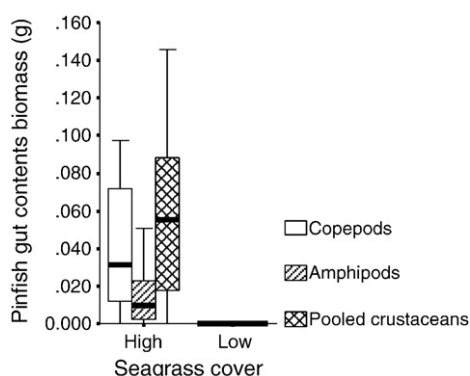


Fig. 7. Difference in biomass between cages with high seagrass cover vs. low seagrass cover amphipod, copepod and pooled crustacean obtained from pinfish gut content analyses.

We also looked at variation in the various prey categories in stomachs of spot and pinfish, and found that pinfish had more polychaetes in their guts in the spot-only treatment and in the high seagrass cover block. Interestingly, the mean polychaete biomass in pinfish stomach contents differed significantly among treatments (ANOVA, $P=0.043$) (Table 4), with the spot-only treatment having significantly greater amounts of polychaetes in the guts of pinfish than either the flounder+spot treatment (Fisher's LSD, $P=0.031$) or the control treatment (Fisher's LSD, $P=0.029$). Pinfish showed no significant differences among treatments for any other prey group and spot showed no significant treatment effects for any prey group. Pinfish gut content biomass of copepod and amphipod remains, as well as the pooled crustacean remains (including unidentified crustacean remains), showed a significant block effect from seagrass cover (ANOVA, $P<0.002$) with Block 1 fish (high density seagrass) having the greatest mean biomass in their stomachs (Fig. 7).

4. Discussion

The predictions of the mixed trophic impact indexes from the St. Marks network model were supported for one family of depositing–feeding polychaete. The addition of gulf flounder and spot had significant impacts on Terebellidae density and biomass, which declined when spot were introduced without gulf flounder. In an unpredicted result, the block effect (correlated with seagrass density) was highly significant for both Nereidae density and pinfish density, suggesting that pinfish recruited preferentially to these cages with high seagrass cover and Nereids were consumed in greater quantities by pinfish in cages placed in areas of high seagrass cover. Pinfish also consumed large amounts of harpacticoid copepods and gammarid amphipods, leading to the greater stomach content biomass in cages with higher seagrass cover. Taken together, the results indicate that pinfish and spot were predators on Terebellid polychaetes when gulf flounder were not present, while pinfish consumed Nereid polychaetes in the cages with high seagrass cover.

However, it appears that this significant treatment effect on polychaetes was due to the unanticipated effect of significantly

greater pinfish predation on polychaetes in the spot-only treatment. Why this occurred is not certain, but it may be due to a synergism between pinfish and spot feeding behaviors, with spot feeding making pinfish predation on polychaetes more likely to occur due to increased prey odors and activity (Luczkovich, 1988). In the presence of gulf flounder, this synergism disappeared and neither spot nor pinfish were observed to consume polychaetes in that treatment, indeed they had less prey in their guts overall.

The addition of gulf flounder did not cause a decline in spot and pinfish density and biomass, as compared with controls, in contrast with the predictions of the mixed trophic impact analysis model. The mixed trophic impact analysis predicted that spot and pinfish biomass would be lowest in gulf flounder addition cages. We can explain this by noting that there was recruitment or trapping of both spot and pinfish in the cages during the experiment, which may have masked the prediction of the mixed trophic impact analyses. With spot and pinfish recruiting to all cages, including the controls, the statistical effect of gulf flounder predation may not have been observable. Perhaps with modification to the cages (e.g., using a smaller mesh size), we could have prevented fish larvae from entering and observed this predicted effect. It is unknown if that cage modification would have produced an even greater indirect effect on polychaetes densities and biomass.

Network analysis assumes a steady state, but in field experiments, changes in the environment may cause results other than those predicted by the mixed trophic impacts analysis. Mixed trophic impacts for the St. Marks model were computed using the means for January and February, but do not account for the great deal of variability in the raw data from St. Marks from place to place and month to month (Baird et al., 1998). No confidence intervals are produced from the impact module of NETWRK IV, but the actual variance may be large. The results from our study were extremely variable, resulting in a significant difference for the contrast between the flounder+spot and the spot-only treatment for a single polychaete family. This may have been remedied by increasing the number of replicates. Also, the St. Marks network model does not account for shifts in behavior over time (dynamic component). The results of any network analysis or experiment must be matched in time or season. During summer, changes in prey density force spot from the seagrass beds in search of benthic prey (Hodson et al., 1981), while pinfish can utilize plant matter, which results in greater pinfish density in seagrass beds during the summer (Luczkovich and Stellwag, 1993; Ward, 1998). Also, as fish grow their diets change, and their behavior changes in the presence of a predator. Differences in fish biomass results for this study and the predictions made by the mixed trophic impacts for the St. Marks network model may be due to behavioral changes that are not incorporated into the network model. It is well known that a change in behavior of a prey fish occurs in the presence of a predator (Von Frisch, 1938; Pfeiffer, 1962; Holbrook and Schmitt, 1988; Jordan et al., 1996). Network models do not account for these behavioral changes at the current time, but this can be adjusted in further network model development.

Spot and pinfish were observed feeding primarily on harpacticoid copepods; the density of this prey item was most likely greater than the density of polychaetes in the experimental site. The St. Marks model showed a negative direct impact on polychaetes from spot and pinfish, even though the meiofauna was a larger proportion of the diet for these two species (Christian and Luczkovich, 1999). It does not follow that there would be a negative direct impact on meiofauna due to the foraging of spot and pinfish, because of the large biomass of meiofauna and the relatively small flow of biomass to spot and pinfish. However, Posey and Hines (1991) did find that omnivory can play a significant role in multi-trophic level interactions. It may be that omnivory was masking the results we expected to find. The impact of spot and pinfish foraging on meiofauna in our experiments deserves further study, and will be the subject of another paper.

The small size of the spot present in the cages may be another reason for the difference between our study and the predictions made by the St. Marks model. Spot show a shift in diet from zooplankton toward more benthic organisms with increasing size (Miltner et al., 1994). In this experiment the majority of spot recovered (61%) were less than 30 mm SL (\bar{x} = 23 mm SL \pm 8 s.d.). Polychaete remains were only found in the gut contents of three spot, all over 30 mm SL, while polychaetes only accounted for 1% of the gut contents for spot. These results indicate that most spot recovered from the cages were still actively feeding on harpacticoid copepods. Pinfish gut contents indicated that they, too, were preying mainly on copepods. Few polychaete remains were found in the pinfish guts, and pinfish have been shown to consume fewer polychaetes than spot at the sizes that were present in the cages (Carr and Adams, 1973; Stoner, 1980; Luczkovich and Stellwag, 1993).

Although unexpected, the recruitment of pinfish to the cages during the experiment deserves special mention. Pinfish recruited to the cages perhaps because they acted as a fish attracting device (FAD). FADs are often used to increase fish density by providing structure. This provides greater opportunity for fishing in areas around FADs compared to those areas over bare substrate. We also found that there was a greater density of pinfish in cages with high seagrass cover. It is possible that the higher rates of recruitment to these cages led to increased competition between pinfish and spot in such a confined area, which may have inhibited our ability to detect additional significant treatment effects.

However, we did find that percent cover of seagrass had a significant effect on pinfish density and biomass, as well as stomach content biomass. The site with higher percent cover had a significantly higher pinfish density, biomass and stomach content biomass. Böstrom and Bonsdorff (2000) were able to show that strong disturbances negatively impacted benthic fauna diversity in bare sand areas, while positively impacting complex seagrass bed habitats. Animals in bare areas were more susceptible to dispersal from strong wind events, while abundances in seagrass beds were more stable. This could have led to significant differences in post-settlement abundances between these two habitats indicating that habitat complexity strongly affected species abundances in seagrass beds versus bare areas.

Leber (1985) used caging experiments to demonstrate that predation, and refuge from it, are strong organizing forces in seagrass beds contributing to higher abundances in these habitats. He also found that for some species, microhabitat selection based on food availability and living space influenced the abundance patterns observed. Horinouchi and Sano (1999) had results that indicated that juvenile gobiid fishes associated with seagrass beds preferred sparse shoot density and often occurred in bare patches adjacent to seagrass beds, but were not found over bare areas with no seagrasses adjacent. In this study, areas where there were large unvegetated patches had significantly lower abundances of pinfish. This variation in the biomass of the pinfish as a result of seagrass density differences may suggest a need for greater replication when differences in seagrass density exist.

5. Conclusion

In this experiment we were able to show that the predictions based on the mixed trophic impacts from the St. Marks network analysis model could be detected for a single polychaete family. The effect that was predicted was small in magnitude, which made it difficult to detect with our low statistical power. It may be that the overriding effect that dominated the experiment was the direct impact of pinfish on harpacticoid copepods. It may also be that the differential recruitment of pinfish to areas with dense seagrass beds made it impossible to detect the results predicted for a greater number of polychaete families. Further research is needed to determine if the other impacts predicted by the mixed trophic impacts analysis from the St. Marks network analysis model can be verified by field experiments. Because natural variability is difficult to incorporate in the mixed trophic impacts analysis, large replicate size and longer experiments may also help in resolving the accuracy of the impacts predicted by the mixed trophic impacts analysis from the St. Marks network analysis model.

Acknowledgements

We would like to express our gratitude to the staff of the NOAA Beaufort Laboratory. Without the time, advice, equipment and lab space volunteered by the staff, this research would have been much more difficult to complete. We would especially like to thank James Morris, for the use of his lab space in analyzing the core samples and fish gut contents, and his brother Julius, who allowed us to collect gulf flounder from his shrimp trawler. I would also like to thank Dr. Kevin O'Brien for his statistical advice, and our reviewers, whose advice aided in a much improved manuscript. Finally, we would like to thank Anne Gloeckner and Dr. Jeff Ward DVM for sacrificing their much needed sleep in the early hours of the weekend to help collect benthic core samples. [SS]

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