1981

Fish predator-prey interaction in areas of eelgrass (Zostera marina)

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Recommended Citation

Lascara, Joseph, "Fish predator-prey interaction in areas of eelgrass (Zostera marina)" (1981). *Dissertations, Theses, and Masters Projects.* Paper 1539617518.
https://dx.doi.org/doi:10.25773/v5-7wrj-6447

FISH PREDATOR-PREY INTERACTIONS
IN AREAS OF
EELGRASS (_ZOSTERA MARINA_)

A Thesis
Presented to
The Faculty of the School of Marine Science
The College of William and Mary in Virginia

In Partial Fulfillment
Of the Requirements for the Degree of
Master of Arts

by
Joseph Lascara
1981

APPROVAL SHEET

This thesis is submitted in partial fulfillment of
the requirements for the degree of

Master of Arts

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ACKNOWLEDGEMENTS

I would like to express thanks to my major professor, Dr. John V. Merriner, for his assistance and guidance. I am also indebted to Dr. George W. Boehlert, for his advice in designing the experimental laboratory system, and for his continued support throughout this project. Also, thanks to Dr. Robert J. Orth, Dr. Carl H. Hershner and Dr. Christopher S. Welch for contributing their time and effort to the betterment of this study.

I thank my fellow workers Deane Estes, Hugh Brooks, Tom Munroe and Mike Rathbone for their help in making field sampling a learning and memorable experience.

I am grateful to Nancy Peters, Sharon Pyatt and Wanda Hebert, their clerical assistance was of considerable help.

Special thanks to my parents and family for their continued support during what became a rather lengthy extension of my eduational career.

Thank you M.P. for always being a friend.

To Cathy Meyer, for her constant encouragement and inspiration, many thanks.

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ABSTRACT

An integrated field and laboratory program was employed to investigate fish predator-prey interactions in areas of eelgrass, Zostera marina. Distribution and food habits of three abundant piscivores were determined from monthly gill net captures in vegetated and adjacent non-vegetated sampling sites in the lower Chesapeake Bay during 1979 and 1980. Predator abundance varied with respect to habitat and time of day. Equal effort vegetated to non-vegetated capture ratios were approximately 1:3 for bluefish, Pomatomus saltatrix, 3:1 for weakfish, Cynoscion regalis, and 5:1 for summer flounder, Paralichthys dentatus. Distinct peak captures occurred during daylight in the non-vegetated habitat for bluefish and during twilight and night in the vegetated habitat for weakfish. Eelgrass resident prey were present in stomach contents from each of the three predator species, indicating that some feeding had occurred in the vegetated habitat. Eelgrass blades, believed to be incidentally ingested as prey were captured within the vegetative canopy, were present in both bluefish and summer flounder stomach contents but were absent in weakfish.

Specific predator-prey interactions were analyzed qualitatively and quantitatively in a laboratory setting with varying habitat complexity. Both vegetative cover and light intensity influenced predator activity and prey capture success. Weakfish consumed fewer prey, Leiostomus xanthurus and Menidia menidia, as percent area of artificial vegetative cover increased. Similiarly, fewer M. menidia were consumed by summer flounder as vegetative cover increased. However, due to respective capture and avoidance behaviors, summer flounder captured fewer L. xanthurus in non-vegetated experiments than in any vegetated experiments. In general, prey which remained at the conclusion of an experiment were those which were oriented within the vegetation. Peak feeding activity occurred during morning and evening twilight for weakfish, and during morning hours between 0800 and 1200 for summer flounder.

Data indicate that eelgrass beds were utilized as refuge habitats for prey fishes as well foraging grounds for predators. Prey which orient within the eelgrass canopy, out of the visual predators' sight, suffer least from predation. However, both crepuscular and lie-in-wait predators appear to be effective in capturing prey which migrate from vegetative cover. Schooling, as a capture tactic by predators or as an escape tactic by prey, may be inhibited by the presence of vegetation.

Integration of field and laboratory studies is suggested as being the most effective method for evaluating specific fish predator-prey behavioral interactions.

FISH PREDATOR-PREY INTERACTIONS
IN AREAS OF
EELGRASS (*ZOSTERA MARINA*)

INTRODUCTION

Eelgrass, Zostera marina, beds are generally considered to play important trophic and refuge roles for many species of fish in estuarine and coastal marine ecosystems (Ried, 1954; Kikuchi, 1974; Hellier, 1962; Briggs and O'Conner, 1971; Carr and Adams, 1973; Adams, 1976a; Orth and Heck, 1980). Through stomach content analysis, researchers have demonstrated that many resident fish species of eelgrass areas are heavily dependent on the associated fauna and flora as a source of food (Adams, 1976b; Robertson, 1977). However evidence that structurally complex eelgrass habitats provide small fishes refuge from predation is largely inferential (Colwell and Fuentes, 1975; Cooper and Crowder, 1979). In addition, the extent to which these areas are utilized as foraging grounds by large transient piscivorous fish is not well established.

Field and laboratory studies have indicated that physical structures may affect predator-prey interactions. Shelter from predation appears to be the most important factor in the formation of fish communities which gather around floating material in the open ocean (Gooding and Manguson, 1967). In laboratory studies testing the effectiveness of floating kelp (Macrocystis pyrifera) in reducing predation, Mitchell and Hunter (1970) noted that prey were pursued less often, for shorter periods, and were captured less frequently when kelp was present than when it was absent. Sullivan and Atchison (1978) noted that fathead minnows, Pimephales promelas, used artificial vegetation extensively when the predator, the largemouth bass, *Micropterus salmoides*, changed positions in the experimental tank. They observed that prey vulnerability was influenced by the presence of cover. Other investigators have demonstrated that the physical structure of macrophyte standing crop, including eelgrass, may be important in mediating predatory fish behavior and thus decrease predatory success (Vince et al., 1976; Nelson, 1979; Stoner, 1979).

Other studies, however, have indicated that vegetative cover affords little or no protection to prey. Mauck and Coble (1971) found that the relative vulnerability of several prey fish species to northern pike, *Esox lucius*, predation was the same in experiments with and without vegetative cover. Johannes and Larkin (1961) noted that redside shiners, *Richardsonius balteatus*, pursued *Gammarus* amphipods deep within weed (*Chara*) beds. Thus, behavior and morphology of both predators and prey may override the influence of habitat structure.

The theoretical framework for investigations of predator-prey interactions has been established (Emlen, 1966; MacArthur and Pianka, 1966; Griffiths, 1975). Natural selection may favor predators which feed as energy maximizers. Simply stated, a predator should optimally obtain the greatest caloric yield per unit time spent in search, capture and consumption of prey. The use of vegetative cover by prey fish may have population survival value as a protective habitat which serves to increase energy spent relative to energy gained by the predator. Glass (1971), studying the predation energetics of largemouth bass found that energy expenditure per attack increases rapidly in more densely structured environments. In addition, natural selection may act to enforce the association of prey with vegetative cover: susceptible prey will be consumed while less available prey will remain to reproduce.

Recently, researchers have attempted to integrate field and laboratory studies in evaluating the behavioral interrelationships of fishes and their prey in structurally complex habitats (Vince et al., 1976; Nelson, 1979). Direct field observations, traditionally conducted in clear tropical waters (Hobson, 1965, 1968, 1972, 1973; Majors, 1977; McFarland et al., 1979) by SCUBA are difficult at best in turbid nearshore or estuarine waters. In these areas, field sampling for stomach content analysis, diel catch frequencies, habitat preference or other parameters in conjunction with controlled laboratory experiments may prove most effective in determining specific predator-prey interactions.

This study assessed the ecological significance of submerged aquatic vegetation, SAV (principally, *Z. marina*), in fish predator-prey relationships. The extent to which SAV is utilized as a refuge habitat by prey fishes and as a foraging grounds for piscivorous predators was investigated through both field and laboratory studies. Specific predator-prey interactions of fish species from a lower Chesapeake Bay SAV system were analyzed qualitatively and quantitatively in a laboratory setting with varying habitat complexity. Field sampling was conducted to determine spatial and temporal movements and feeding habits of the predator species in and around SAV. Selected predator and prey species provided contrast in habitat selection and feeding strategies. Juvenile spot, *Leiostomus xanthurus*, an abundant SAV resident, and Atlantic silverside, *Menidia menidia*, an abundant bay-wide resident, served as prey species. Bluefish, *Pomatomus saltatrix*, weakfish, *Cynoscion regalis*, and summer flounder, Paralichthys dentatus, all species of major commercial and recreational importance, served as representatives of the Bay piscivore guild.

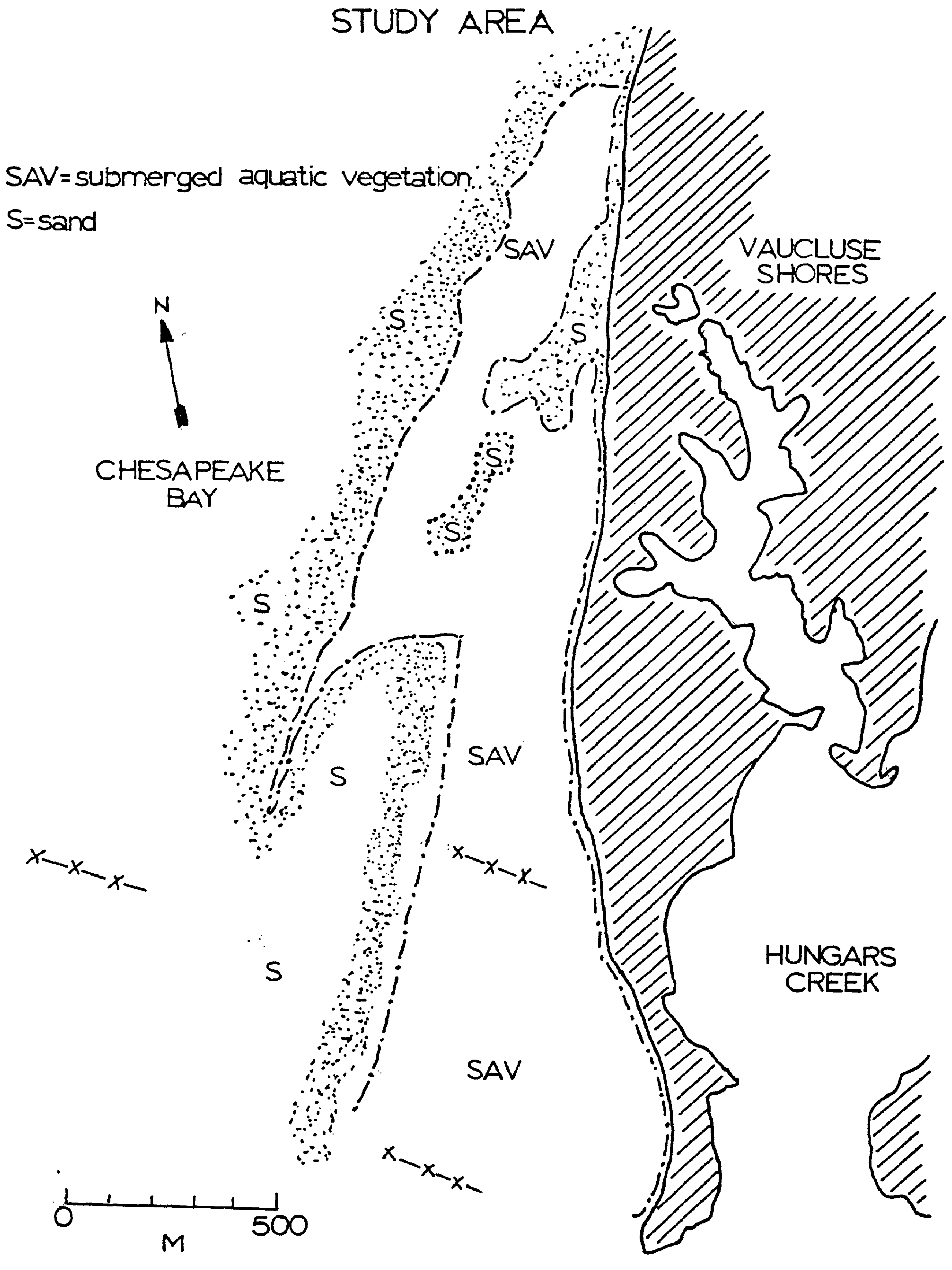
MATERIALS AND METHODS

Field Study

The study site, a 260 hectare SAV bed (mixed eelgrass and widgeon grass, Ruppia maritima) was located in southeastern Chesapeake Bay (approximately 37°51'N latitude, 76°51'W longitude). The area was bounded by Hungar's Creek to the south, a sand bar to the north and west, and land (Vaucluse Shores) to the east. Gill net sampling was conducted on a monthly basis from March through November 1979 and from March through September 1980. Gill nets were set and fished every four hours over a 24-hour period along the transects depicted in Figure 1. Two nets were fished over the vegetated habitat and one over the non-vegetated habitat. For quantitative comparisons the vegetated habitats were combined and averaged. The non-vegetated site was approximately 750-1000 meters west of the SAV bed. Nets were 60 meters long and fished 1.8 meters off the bottom. In 1979, each net was comprised of two thirty meter sections of 12.7 and 17.8 cm stretch mesh monofilament. Low catch in the 17.8 cm mesh net necessitated a change to 8.9 cm mesh for the 1980 sampling program. Due to these differences in sampling gear catch data for the two years were analyzed separately. Average depths in which the nets were set varied from 0.5-1.5 meters within the grass bed to 1.5-2.5 meters over the sand bar.

Bluefish, weakfish and summer flounder were measured (standard length, SL in mm) and weighed (gms). Stomachs were removed, labelled

Figure 1. Location of sampling site in lower Chesapeake Bay, Virginia. Gill net transects depicted by hatch marks.


STUDY AREA
SAV=submerged aquatic vegetation
S=sand
N
CHESAPEAKE BAY
SAV
S
S
S
S
S
S
SAV
S
SAV
VAUCLUSE SHORES
HUNGARS CREEK
0
500
M

and preserved in 10% buffered formalin solution for later laboratory analysis, or when time permitted, were analyzed in the field. Contents were identified to species, enumerated and measured whenever possible. Data were tabulated as percent occurrence and percent number for each taxonomic category. Percentages represent the proportion of the stomachs containing food for each species captured in each habitat.

Laboratory Study

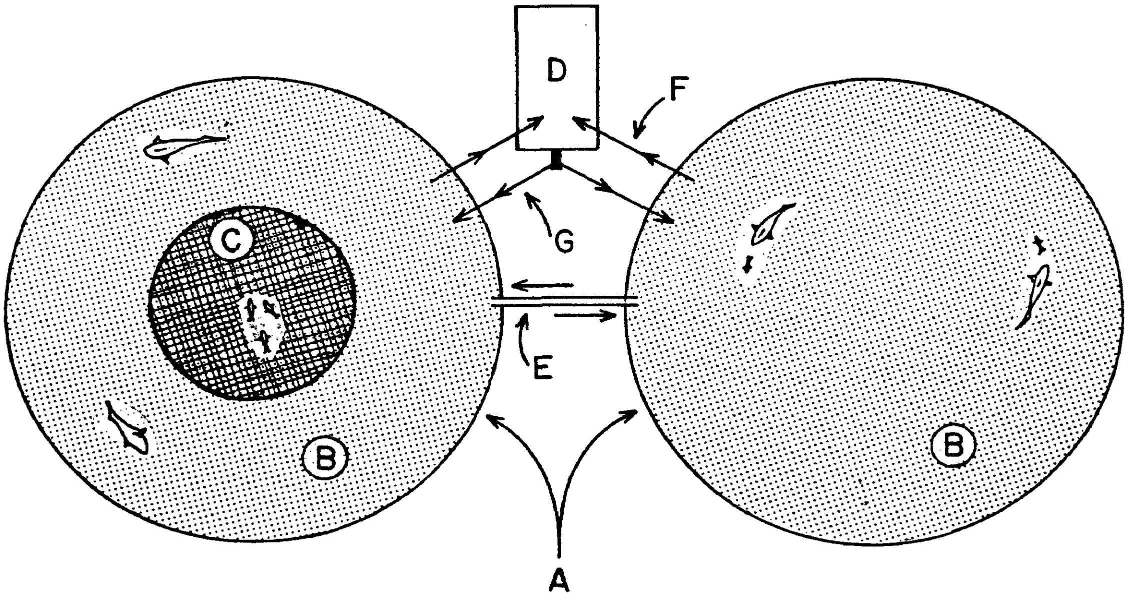
Experiments were conducted in two identical 4 m diameter by 1 m deep double-lined light blue wading pools (Figure 2). A water depth of 0.9 m (approx. 10,000 liters/tank) was maintained in the pools. This was the maximum depth at which water could be held to prevent predators from jumping out of the pool confines. Each tank bottom was covered with a layer of coarse sand (3-4 cm).

Observations were made from atop a 1.5 m stand adjacent to the experimental tanks. The stand was covered with black plastic and observation portals were arranged such that the entire water column of both tanks was visible to the observer.

Seawater System. A closed, recirculating water system was employed. The high turbidity of local York River water severly inhibited observations making the use of flow-through seawater system unsuitable.

Estuarine water was passed through a filter bag (5 mm) before entering the experimental system. Water was continuously pumped from the bottom of the two experimental tanks and an adjacent 1.5 m diameter by 1 m deep prey holding tank into a filter box (1.5 by 1.5 by 1.0 m) used as a biological filter to remove potentially toxic waste materials

Figure 2. Schematic of laboratory seawater system. A. 2-1 m deep x 4 m diameter experimental tanks. B. Coarse sand substrate. C. Artificial vegetation. D. Biological filter. E. Siphon hose maintaining equal water levels in the two tanks. F. Water pumped from tank to biological filter. G. Water gravity fed through biological filter and back into tank.


D
F
C
G
E
B
B
A

(Arnold et al., 1978). Intake hoses were shielded to prevent damage to prey fish and fouling of pump impellers. Water was distributed over the surface of the filter medium by horizontal 7.6 cm PVC pipe with 0.5 cm diameter holes in two rows at 45° from the bottom. Water then passed through a 10 cm layer of coarse sand, a 10 cm layer of crushed oyster shell, and a 20 cm layer of gravel. The filtered seawater then entered a 5.1 cm PVC effluent pipe below the filter bed and gravity fed back into each tank (Figure 2). Equivalent water levels were maintained by siphoning action through 5.2 cm plastic vacuum hoses connecting the tanks. No metallic materials were permitted to contact the seawater at any point in the system. Approximately 50% of the water volume was replaced each week with 'new' river water.

Dissolved oxygen was maintained at or near saturation through the use of conventional aquarium airstones and airpumps. Salinity was checked routinely with a refractometer. Water was heated during winter months by a 3000 watt aquarium heater, and cooled during the summer by ambient air conditioned room temperatures.

Artificial Seagrass. Green polypropylene ribbon, 5 mm wide was used as artificial eelgrass. A specific gravity of 0.6 allowed the artificial grass blades to stand naturally in the water column. The ribbon was affixed to ¼" square mesh black plastic screen. Average and high density mats were constructed having 875 blades/m^2 and 1750 blades/m^2, respectively. These values correspond to observed field densities for *Z. marina* in the lower Chesapeake Bay (R.J. Orth, pers comm., Virginia Institute of Marine Science, Gloucester Point, Virginia). Mats were anchored with a 0.75 m square of 1.9 cm sand-filled PVC pipe. Mats were placed in the tanks a minimum of 12 hours before initiation of an experiment. The coarse sand substrate was pushed over the edges of the mat to provide a smooth transition from non-vegetated to vegetated areas.

Lighting. Black vinyl plastic enclosed the study area, allowing only minimal, indirect, outside light penetration. The artificial lighting system approximated natural light conditions with regard to intensity and duration. Lights were controlled by a series of automatic time switches. First AM light was provided by two banks of double 40 watt daylight flourescent lamps situated below tank level. This provided low intensity indirect lighting of approximately 10 foot candles at the water surface. After 30 minutes, a set of two 60 watt soft white incandescent bulbs was illuminated. Next, a single 100 watt soft white incandescent bulb located directly over each tank was switched on. The three sets of lights remained on together during the day. Since Verheijen and DeGroot (1967) reported that high light intensities could inhibit normal activity in flatfish and because preliminary experiments showed much the same for weakfish, maximum daylight intensities were held to 100 fc at the water surface. In the evening the light series switched off in reverse order for the night period. To maintain natural seasonal day length conditions photoperiod was maintained at L:D 12:12 for predator-Atlantic silverside experiments during mid-March through mid-April and at L:D 15:9 for the predator-spot experiments from mid-June through mid-July.

Experimental Animals. Experimental fish, both predator and prey, were caught in the lower York River estuary by a variety of methods, including: (1) hook and line; (2) 16 and 30 foot otter trawl; and (3) 50 foot beach seine. Fish were quickly moved to acclimation tanks minimizing handling whenever possible.

Predator species were acclimated to experimental conditions for a minimum of 30 days. During this period predators were fed a variety of live prey fish. Prey species were acclimated for minimum period of 14 days. Both prey species were fed Purina Trout Chow^R, which they readily consumed. Care was taken to avoid use of prey fish with signs of abnormal swimming behavior or ectoparasites.

Preliminary experiments were conducted to establish the sizes and numbers of both predators and prey. Predators were selected such that the confines of the tanks did not severely inhibit their ability to pursue and capture prey. Four predators, standard lengths (SL) 27-30 cm, were placed in each tank. A larger number of predators could surround and herd prey. Fewer predators would reduce the number of feeding behaviors which could be observed per unit time and allow for a less complete behavioral characterization. Prey were of a size small enough to be captured and consumed yet not so small as to be unattractive. Spot ranged from 50-65 mm SL and silversides ranged from 60-80 mm SL. To establish the number of prey to be used with this experimental design, prey were offered individually each day for one week with no vegetative cover present. At least twelve prey were consumed each day during this period. Therefore, the number of prey used in each experiment was set at twelve. A decrease in the number of prey consumed was assumed to be a result of increased time and energy spent by the predator in search, pursuit and capture (due to prey schooling or orientation within vegetation).

Four bluefish were held in the experimental tanks for a two month period. During this time bluefish were fed a variety of prey including Atlantic silversides and Atlantic menhaden, Brevoortia tyrannus. The confines of the experimental system disrupted the natural bluefish feeding behavior. No formal quantitative bluefish-prey-eelgrass experiments were conducted, but several qualitative observations are presented in the results section.

Experiments. Prey were moved from the acclimation tank 12 hours before initiation of tests and placed in 0.5 m diameter clear plexiglass 'acclimation cylinders' to minimize prey disorientation upon release. These cylinders were suspended by pully system over the center of each experimental tank. A fine mesh clear plastic screen in the bottom of the cylinders allowed water to enter freely. From within the cylinders prey had a full 3-dimensional view of the experimental tank, including predators and grass when present. The lower ¼ of the cylinder was hinged and equipped with a release mechanism. At initiation of each experiment the release mechanism was tripped and the cylinder opened (Figure 3). The entire apparatus was then hoisted out of the water. All operations were conducted manually from the observation stand.

Each predator-prey combination was tested in triplicate against five substrate variations (Figure 4):

(1) 'N' - no artificial grass, bare sand substrate

(2) 'A' - average density artificial grass, 1 m^2 mat in center of tank, 875 blades/m^2, 7.5% area covered

Figure 3. Prey release sequence. A. Prey are placed in to clear plexiglass cylinders 12 hours prior to initiation of an experiment. B. From the observation blind the release mechanism is manually triggered and the cylinder opens. C. A pulley system suspended over the center of the tank allows the observer to remove the entire apparatus from the water column.

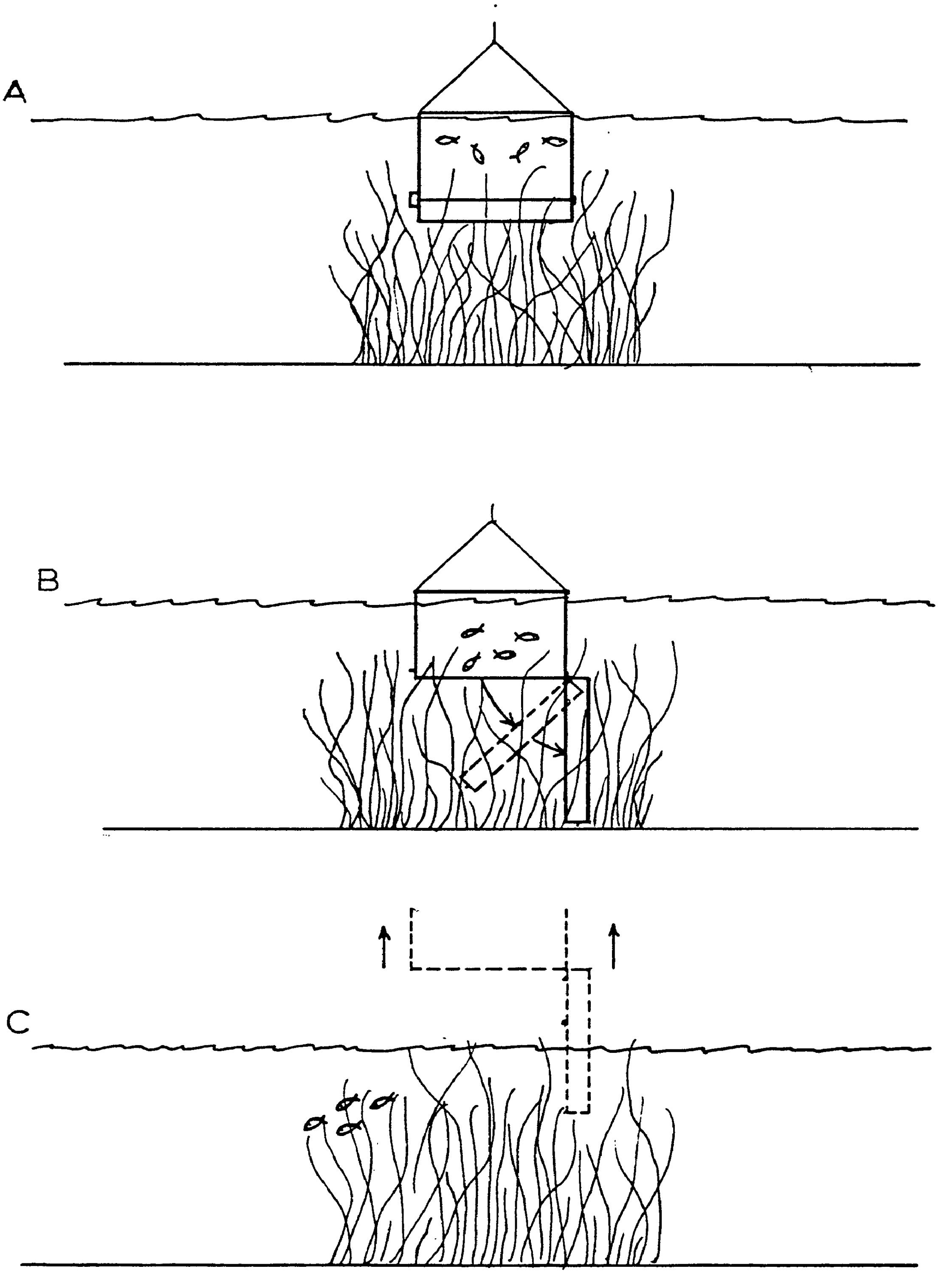
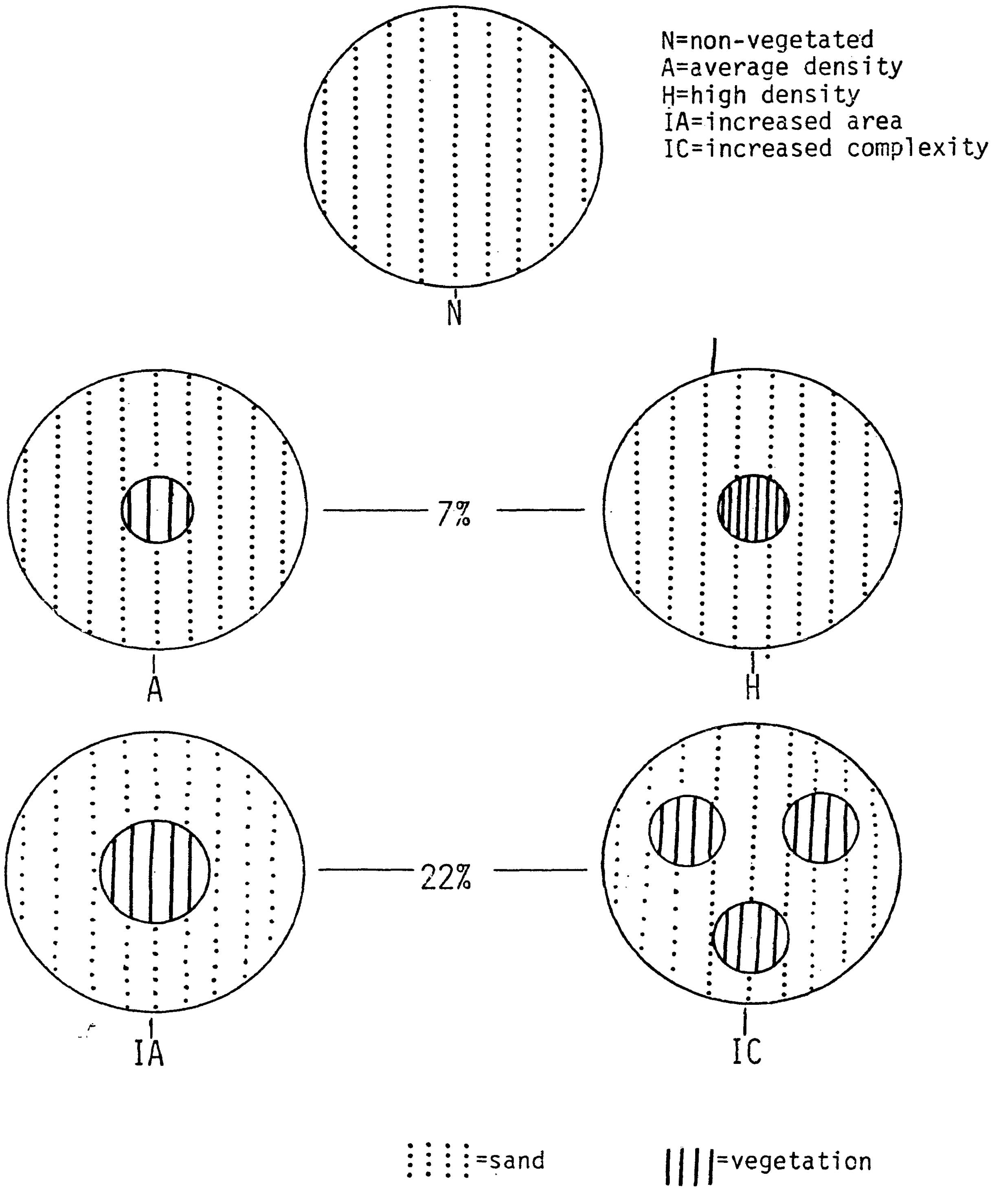

A
B
C

Figure 4. Diagram of the five experimental vegetative treatments. Average and high densities of artificial vegetation refer to observed eelgrass, *Z. marina*, field densities of 875 and 1750 blades/m^2, respectively, (Orth, pers. comm.). At the 22% area vegetative cover level 3-1 m^2 mats were arranged together in the center of the tank (increased area) and evenly about the tank (increased complexity).


N=non-vegetated
A=average density
H=high density
IA=increased area
IC=increased complexity
N
7%
A
H
22%
IA
IC
=sand
=vegetation

(3) 'H' - high density artificial grass, 1 m^2 mat in center of tank, 1750 blades/m^2, 7.5% area covered

(4) 'IA' - increased area, three-1 m^2 mats placed together in center of tank, 2-1750 and 1-875 blades/m^2 mats, 22% area covered

(5) 'IC' - increased complexity, three-1 m^2 mats evenly spaced about tank, 2-1750 and 1-875 blades/m^2 mats, 22% area covered

To minimize learning by predators experimental treatments were randomly ordered. One hour observations were made during morning and evening light transition and midday full-light periods. Surviving prey were enumerated at these times. Predator and prey activity levels, orientation with respect to artificial eelgrass and capture-avoidance strategies were also noted. All remaining prey were removed at the conclusion of each experiment. Predators were starved for a 24-hour period prior to initiating the next experiment. Predator-Atlantic silverside experiments were conducted for 12 hours from first to last daylight. Predator-spot experiments were conducted for a 24 hour period in order to include an assessment of night feeding habits.

The median test, a nonparametric procedure (Conover, 1971), was employed for statistical examination of experimental data. The median number of prey consumed among the 5 predator-prey combinations tested were compared. Significance was chosen to be the alpha=0.05 level.

RESULTS

Field

The numerically dominant adult teleostean predators in the 1979 and 1980 gill net catch data were bluefish, weakfish, and summer flounder (Appendix I). Preliminary analysis indicated no significant difference in catch numbers for the three predator species over the two vegetated sampling sites. Thus, for comparative purposes, gill net captures for the two areas were combined and averaged to yield a representative SAV habitat value.

Bluefish. A total of 157 bluefish, average length 450 mm SL, were captured from April to November (1979 and 1980). Water temperature at time of capture ranged from 11 to 29° C. Bluefish were caught more frequently over the non-vegetated, sand bottom habitat in both 1979 and 1980. Equal effort sand to SAV catch ratios for bluefish were 3.6 and 1.8 for 1979 and 1980, respectively (Figure 5). Five of the 26 gill net sets containing bluefish constituted greater than 50% of the total catch over the sand bottom habitat (Figure 6). These five sets contained between 6 and 17 bluefish, averaging 10.2 per set. The majority, 88%, of sets capturing bluefish over SAV contained 3 or less fish. At no time were more than 5 bluefish captured in a single 4 hour SAV set.

General diel catch frequency trends are similar for bluefish in 1979 and 1980 sampling program. Sand and SAV catches are shown

Figure 5. Equal effort capture ratios over the sand and SAV sampling sites for bluefish, weakfish and summer flounder (1979 and 1980).

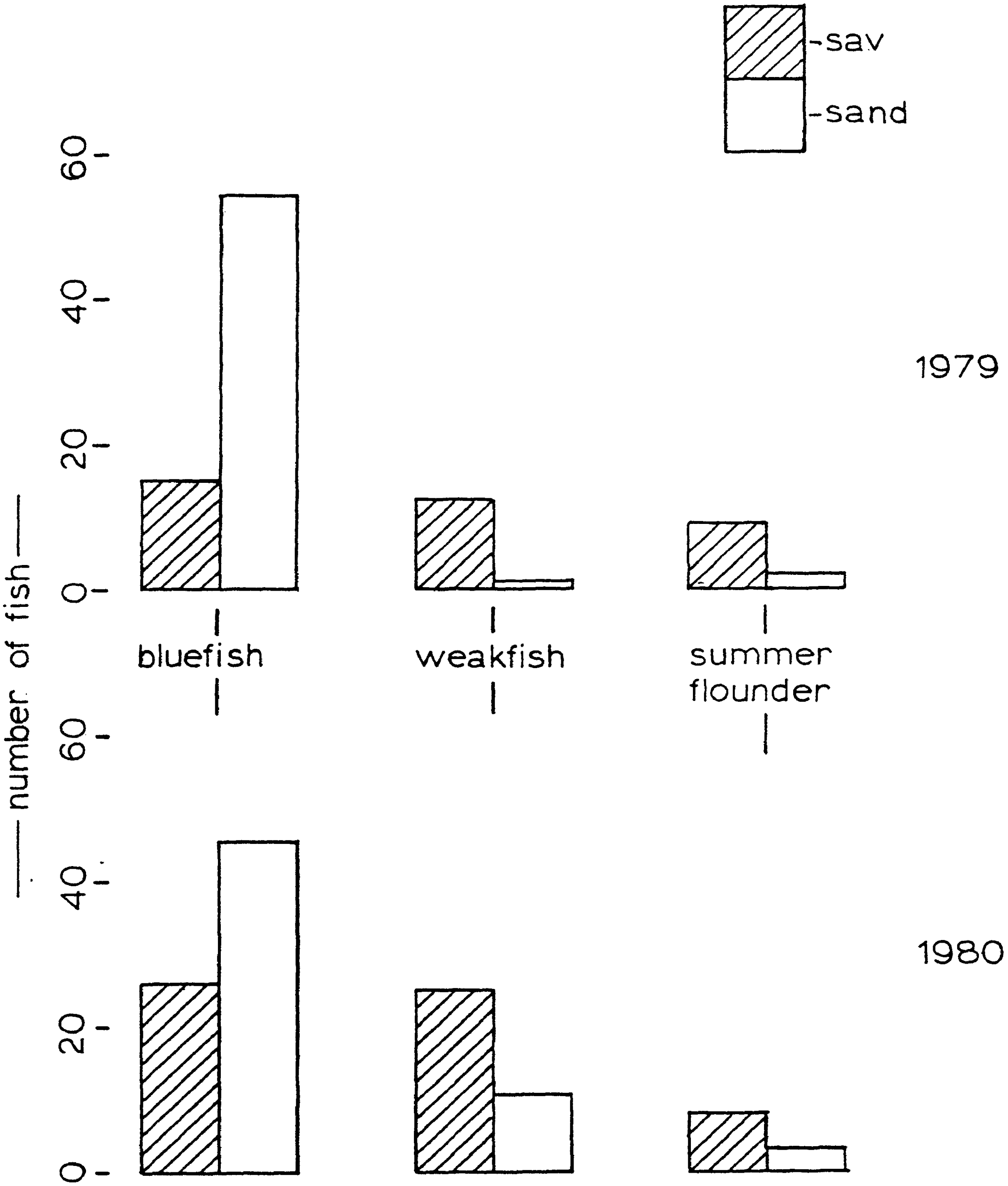
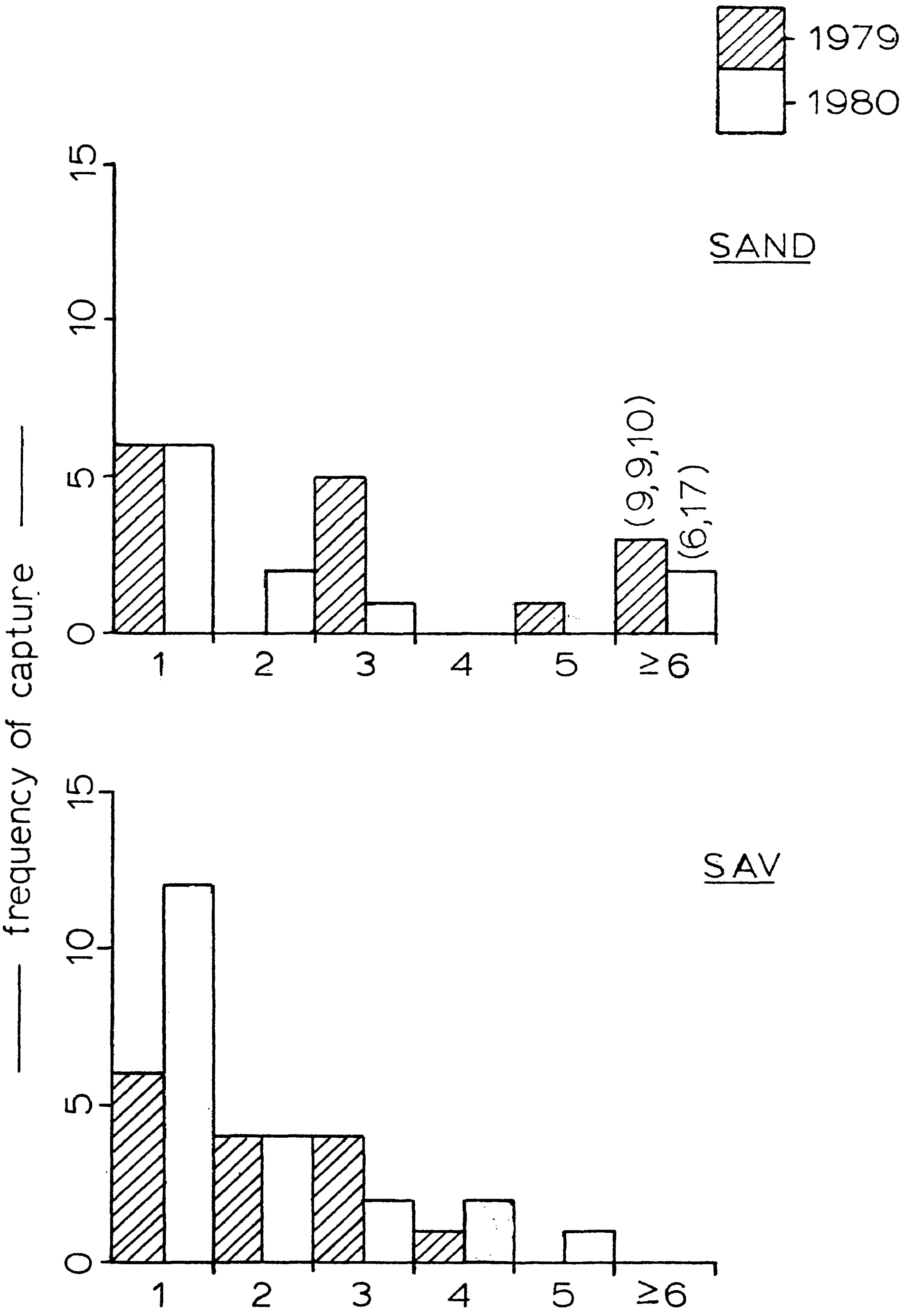

-sav
-sand
60
40
20
0
number of fish
1979
bluefish
weakfish
summer flounder
60
40
20
0
1980

Figure 6. The number of bluefish captured per 4 hour set in the 2-60 m gill nets fished over the SAV site and the single 60 m net fished simultaneously over the sand site.


1979
1980
SAND
SAV
frequency of capture
0
5
10
15
1
2
3
4
5
≥6
(9,9,10)
(6,17)
number of bluefish captured / 4 hr.*

separately for each of the two years (Figure 7 and 8). Maximum catch over the sand habitat occurred between 1200 and 2000 hours. This peak accounted for a large portion of the total diel catch (43% in 1979, 74% in 1980).

Over the SAV habitat, bluefish catch frequency exhibited no distinct diel pattern in 1979. Relatively low numbers were caught throughout the 24 hour period. In 1980, greater numbers were observed between 1200 and 1600 and between 2000 and 2400.

Atlantic menhaden (Brevoortia tyrannus), sand shrimp (Crangon septemspinosa), spot and mullet (Mugil cephalus) were the dominant food items of the bluefish examined. Order of dominance depended upon habitat and method of presentation (Table 1). Sixty-one percent of the stomachs from bluefish captured over the sand habitat contained menhaden while 6% contained sand shrimp and 6% spot. Menhaden also dominated on a numerical basis, representing 58% of the total prey items. Over the vegetated habitat, menhaden were the most frequently occurring food item (31%) followed by spot (12%), mullet (12%) and sand shrimp (8%). The numerically dominant food item over the vegetated habitat was sand shrimp (54%). Stomachs from bluefish captured over SAV contained a total of 7 prey species while stomachs from those captured over sand contained 3 prey species. Eelgrass was found in 3 stomachs, all from bluefish captured over SAV.

Weakfish. A total of 89 weakfish, average length 403 mm SL, were captured from April to September (1979 and 1980). Water temperature at the time of capture ranged from 14 to 28° C. Weakfish were

Figure 7. Diel catch frequency for bluefish captured by gill net over the sand sampling site. Equal fishing effort was maintained during each 4 hour interval. Captures for 1979 and 1980 sampling programs are shown separately due to different net mesh sizes employed. Points represent aggregate captures for each 4 hour interval.

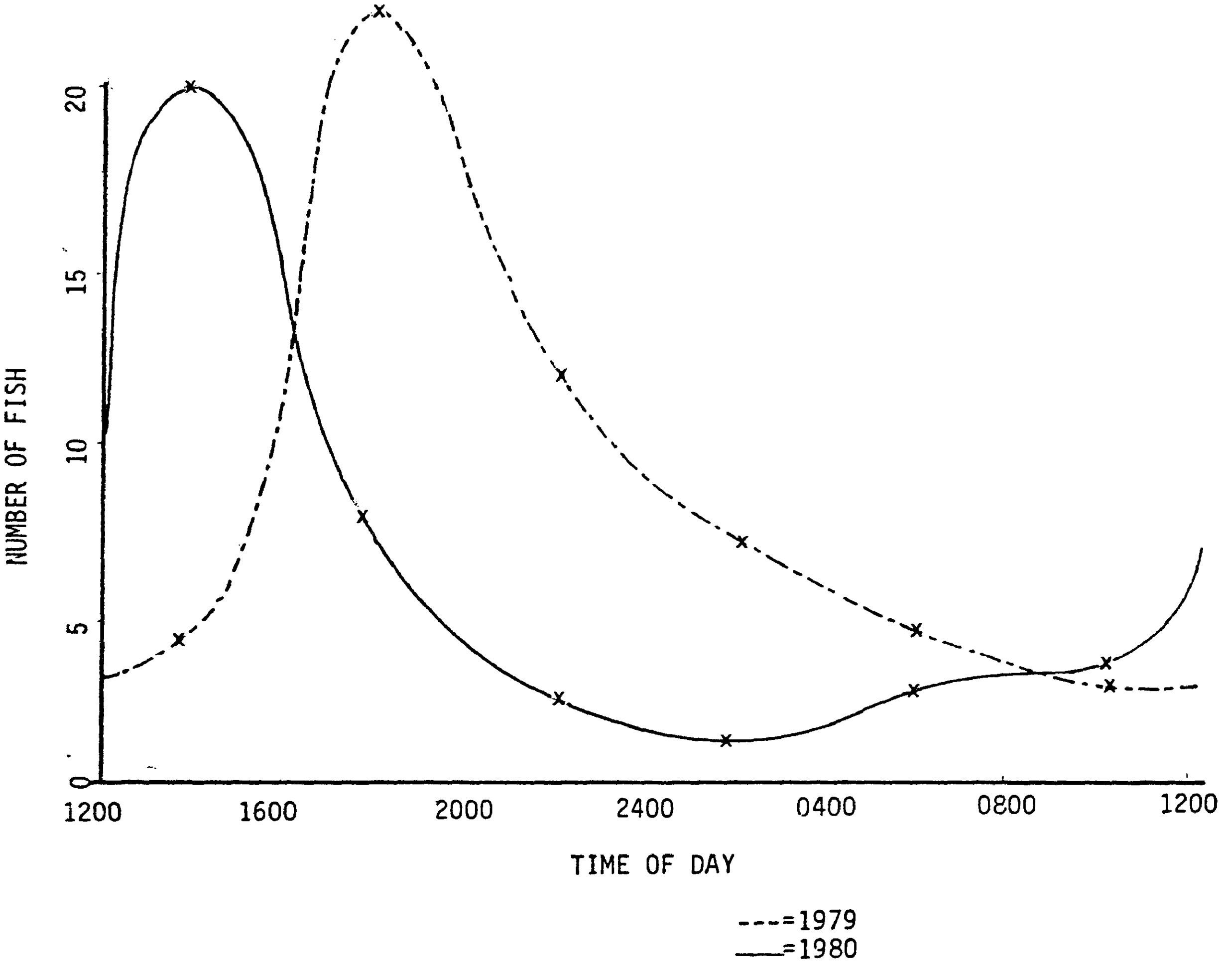

NUMBER OF FISH
0
5
10
15
20
1200
1600
2000
2400
0400
0800
1200
TIME OF DAY
----=1979
——=1980

Figure 8. Diel catch frequency for bluefish captured by gill net over the SAV sampling site. Equal fishing effort was maintained during each 4 hour interval. Captures for 1979 and 1980 sampling programs are shown separately due to different net mesh sizes employed. Points represent aggregate captures for each 4 hour interval.

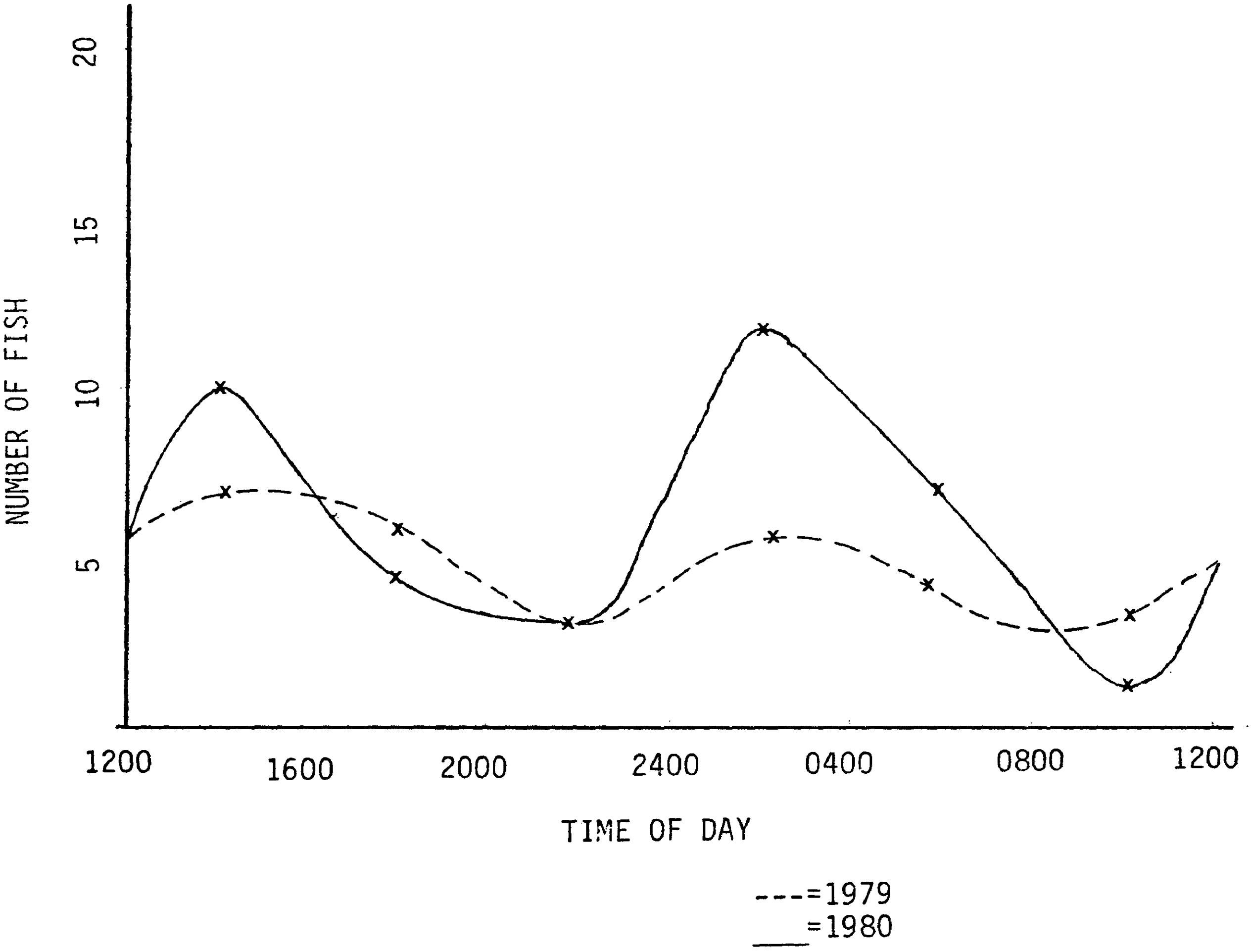

NUMBER OF FISH
20
15
10
5
1200
1600
2000
2400
0400
0800
1200
TIME OF DAY
----=1979
____=1980

TABLE 1. Percent occurrence, and percent number of food items in the stomachs of bluefish, containing food, which were captured over the sand and SAV sampling sites.

	SAND (N=26)		SAV (N=26)	
Food Item	% occurrence	% number	% occurrence	% number
Vegetation				
Zostera marina			11.5	-
Invertebrates				
Gastropoda	-	-	3.8	1.8
Crangon septemspinosa	7.7	6.4	7.7	53.6
Callinectes sapidus	-	-	3.8	1.8
Fish				
Brevoortia tyrannus	57.6	61.3	30.7	14.3
Leiostomus xanthurus	3.8	6.4	11.5	5.4
Mugil cephalus	-	-	11.5	5.4
Atherinidae	3.8	1.8	-	-
Unid. fish remains	30.7	25.8	34.7	16.1

captured more frequently over the SAV habitat than over the sand habitat in both years. Equal effort, sand to SAV capture ratios for weakfish were 1:12.5 for 1979 and 1:2.5 for 1980 (Figure 5).

Considering only 4 hour sets in which weakfish were captured, 1 to 2 individuals per set predominated (Figure 9). Only 5 of the 52 total sets capturing weakfish contained 4 or more individuals. The two largest single set captures were 6 and 8 weakfish, both occurring over the vegetated habitat. Only one 4 hour set over sand contained greater than two weakfish.

Diel catch frequency patterns over the SAV habitat for weakfish are similar for both sampling years (captures over the sand bottom habitat were too few for comparative purposes) (Figure 10). Peak catch periods over the SAV area occurred between 2000 and 2400 hours. Approximately 33% of all weakfish (32% in 1979 and 40% in 1980) were captured during this 4 hour period. Low numbers of individuals were captured between 0800 and 1600 hours and for the two years combined only 5% of the total catch was taken in this period.

Dominant food items of weakfish examined were anchovies (_Anchoa mitchilli_), sand shrimp, blue crabs (_Callinectes sapidus_) and spot (Table 2). Anchovies occurred most frequently (44%) while sand shrimp were numerically dominant (60%) in stomachs of weakfish captured over the sand bottom habitat. Over SAV, sand shrimp and blue crabs were the most frequently occurring food items (35% and 38%, respectively). Numerically, sand shrimp (21%), blue crabs (20%), anchovies (17%) and spot (16%) dominated. Stomachs from weakfish captured over the sand

Figure 9. The number of weakfish captured per 4 hour set in the 2-60 m gill nets fished over the SAV site and the single 60 m net fished simultaneously over the sand site.

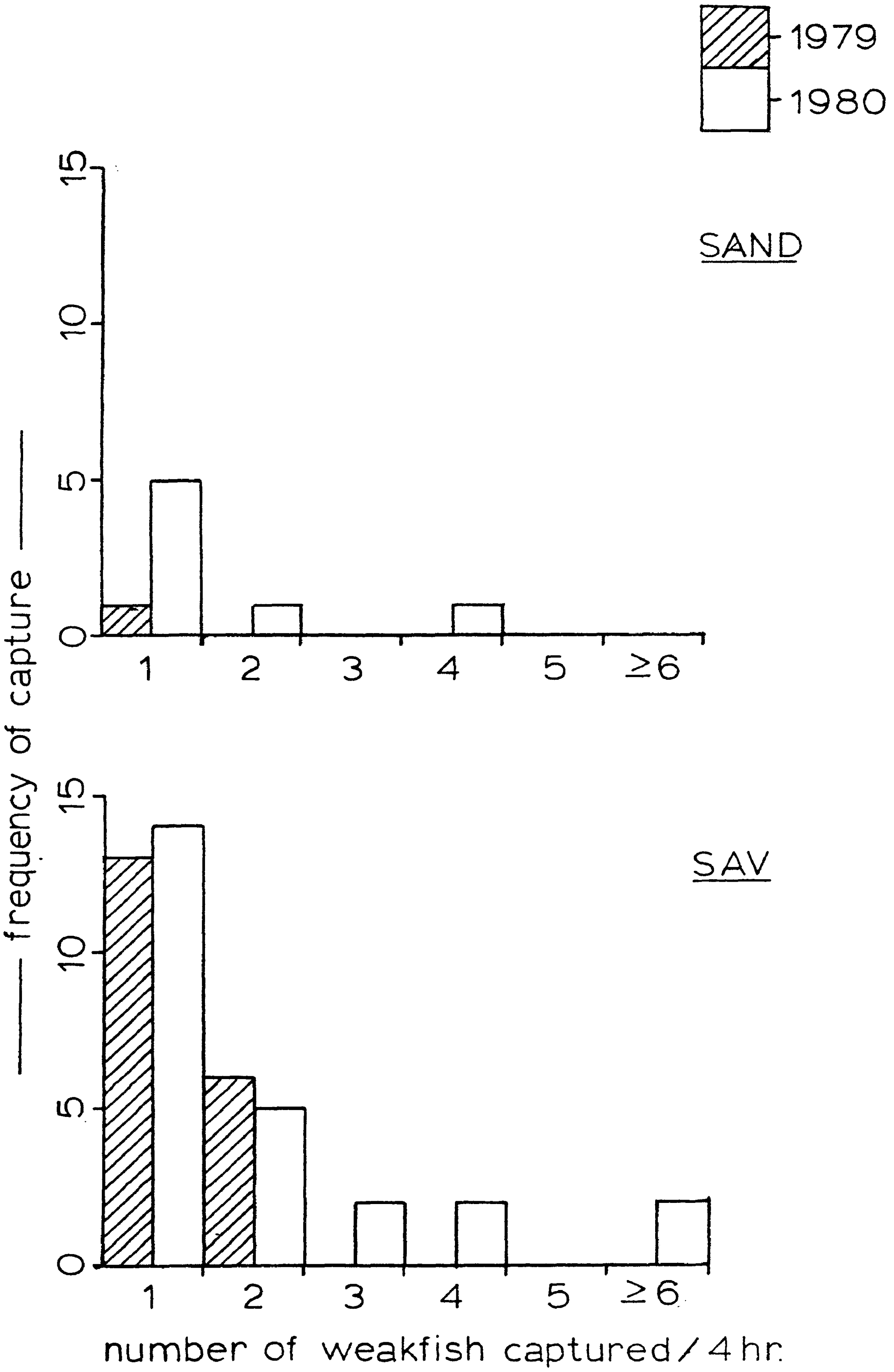

1979
1980
SAND
SAV
frequency of capture
0
5
10
15
1
2
3
4
5
≥6
number of weakfish captured / 4 hr.

Figure 10. Diel catch frequency for weakfish captured by gill net over the SAV sampling site. Equal fishing effort was maintained during the 4 hour interval. Captures for 1979 and 1980 sampling programs are shown separately due to different net mesh sizes employed. Points represent aggregate captures for each 4 hour interval.

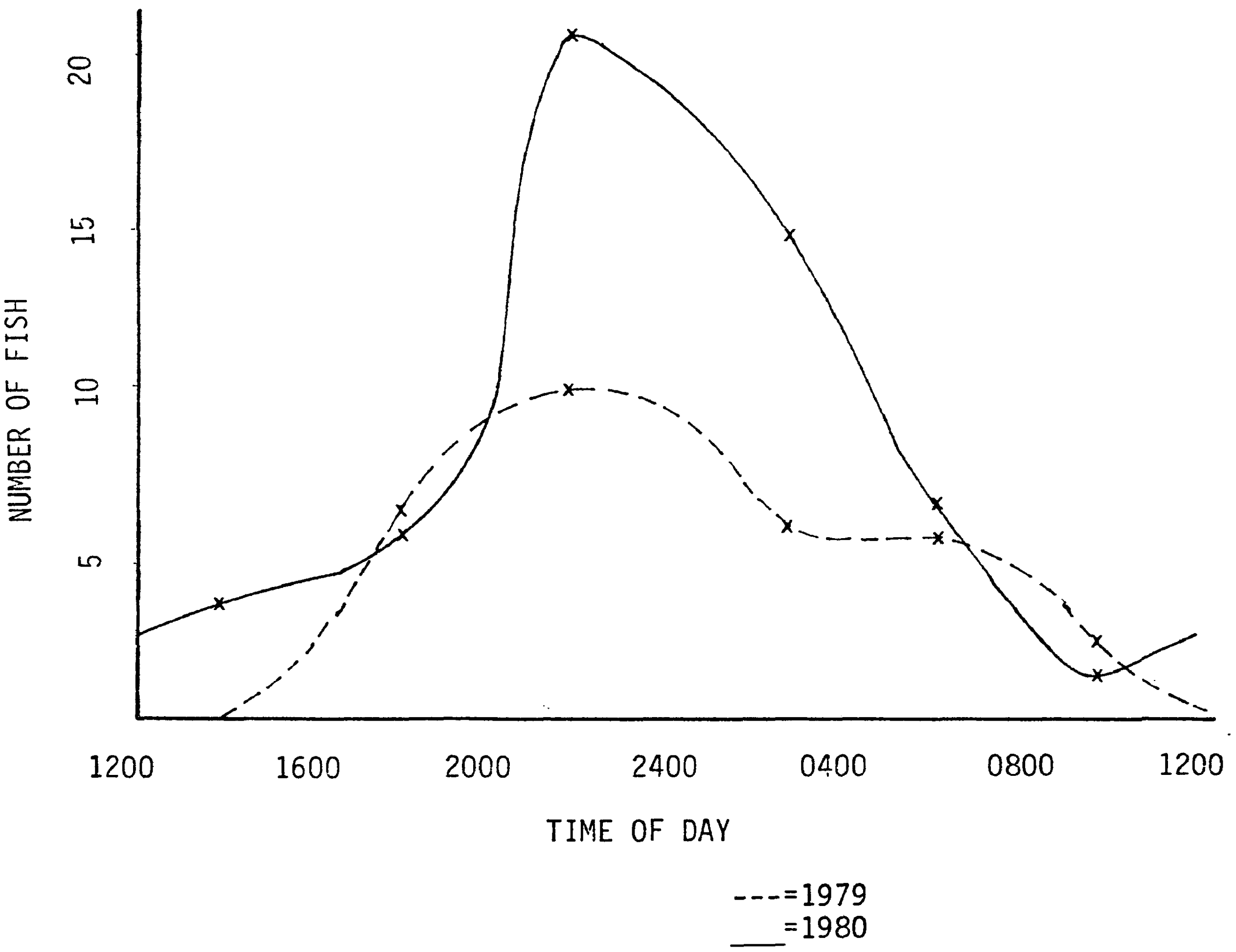

NUMBER OF FISH
20
15
10
5
1200
1600
2000
2400
0400
0800
1200
TIME OF DAY
----=1979
____=1980

TABLE 2. Percent occurrence and percent number of food items in the stomachs of weakfish, containing food, which were captured over the sand and SAV sampling sites.

Food Item	SAND (N=9) % occurrence	SAND (N=9) % number	SAV (N=29) % occurrence	SAV (N=29) % number
Invertebrates				
Crangon septemspinosa	11.1	60.0	34.5	20.5
Callinectes sapidus	11.1	2.8	38.0	19.9
Fish				
Anchoa sp.	44.4	25.7	24.1	17.4
Brevoortia tyrannus	11.1	2.8	13.9	2.9
Leiostomus xanthurus	-	-	17.2	15.5
Menidia menidia	-	-	3.4	2.1
Syngnathus fuscus	-	-	3.4	2.1
Unid. fish remains	33.3	8.5	27.6	6.1

habitat contained a total of 3 prey species while stomachs from those captured over SAV contained 7 prey species.

Summer Flounder. A total of 45 flounder, average length 274 mm SL, were captured at water temperatures ranging from 19.5 to 26.5^{o} C from May to October (1979 and 1980). A small percentage (7%) of these were taken over the sand bottom habitat (Figure 5). Flounder were captured in each of the six 4 hour sampling periods. No distinct temporal pattern was discerned from the available data.

Only seven of the total flounder captured contained identifiable stomach contents. Prey items included spot, pipefish (*Syngnathus fuscus*), sand shrimp, grass shrimp (*Palaemonetes vulgaris*) and eelgrass. Stomach contents of flounder captured over the SAV sampling site by both gill netting and otter trawling from 1978 through 1980 reflected similar food habits (VIMS EPA-SAV Final Report). Tabulated by percent weight of prey items in the 26 stomachs analyzed, spot dominated (56%), followed by unidentified fish (31%). Fifty-eight percent of the stomachs contained mysid shrimp (*Neomysis americanus*), 42% contained sand shrimp and 17% contained spot and eelgrass.

Laboratory

Salinity varied between 16 and 20% and water temperature was maintained at 22± 2^{o} C over the duration of the experiments. Remaining prey were enumerated at the completion of each experiment and used to assess the predator's relative capture success at each of the five vegetated treatments.

Weakfish captured more prey, of both species, in the non-vegetated treatments than in any vegetated treatment (Figure 11). Little difference in capture success occurred between the average and high density vegetative treatments (7% area covered) in either weakfish-prey combination. Greatest within treatment variation occurred in increased area and increased complexity experiments. Weakfish captured the fewest prey in the increased complexity treatment (Table 3). Progressively fewer prey, of both species, were captured as the amount (% area) of artificial grass increased (Figure 12). This trend is most pronounced in the weakfish vs spot experiments where the percentage of prey surviving rises from zero for non-vegetated to 15 for 7% covered to 40 for 22% covered.

Summer flounder captured all silversides in the non-vegetated, high and average density treatments (Figure 13). Capture success dropped only at the 22% vegetative cover level, IA and IC treatments. Flounder captured the fewest silversides in the increased area treatment. The general trend in percentage of prey survival vs percentage vegetative cover is reversed in the flounder vs spot experiments (Figure 12). Here, flounder captured fewer spot in the non-vegetated treatment than in any vegetated treatment.

The median test, a non-parametric procedure, was employed for statistical examination of data (Table 4). My null hypothesis (H_0) was no difference among the treatments in the median number of prey consumed. Test results indicated H_0 is rejected (p=0.95) for the weakfish vs spot experiments. Although statistical analysis with the median test does not isolate differences between specific

Figure 11. The number of prey consumed by weakfish in each of the 3 replicates for the 5 vegetative treatments. The horizontal bar represents the median observation, the vertical bar represents high and low observations and indicates the range among the 3 values.

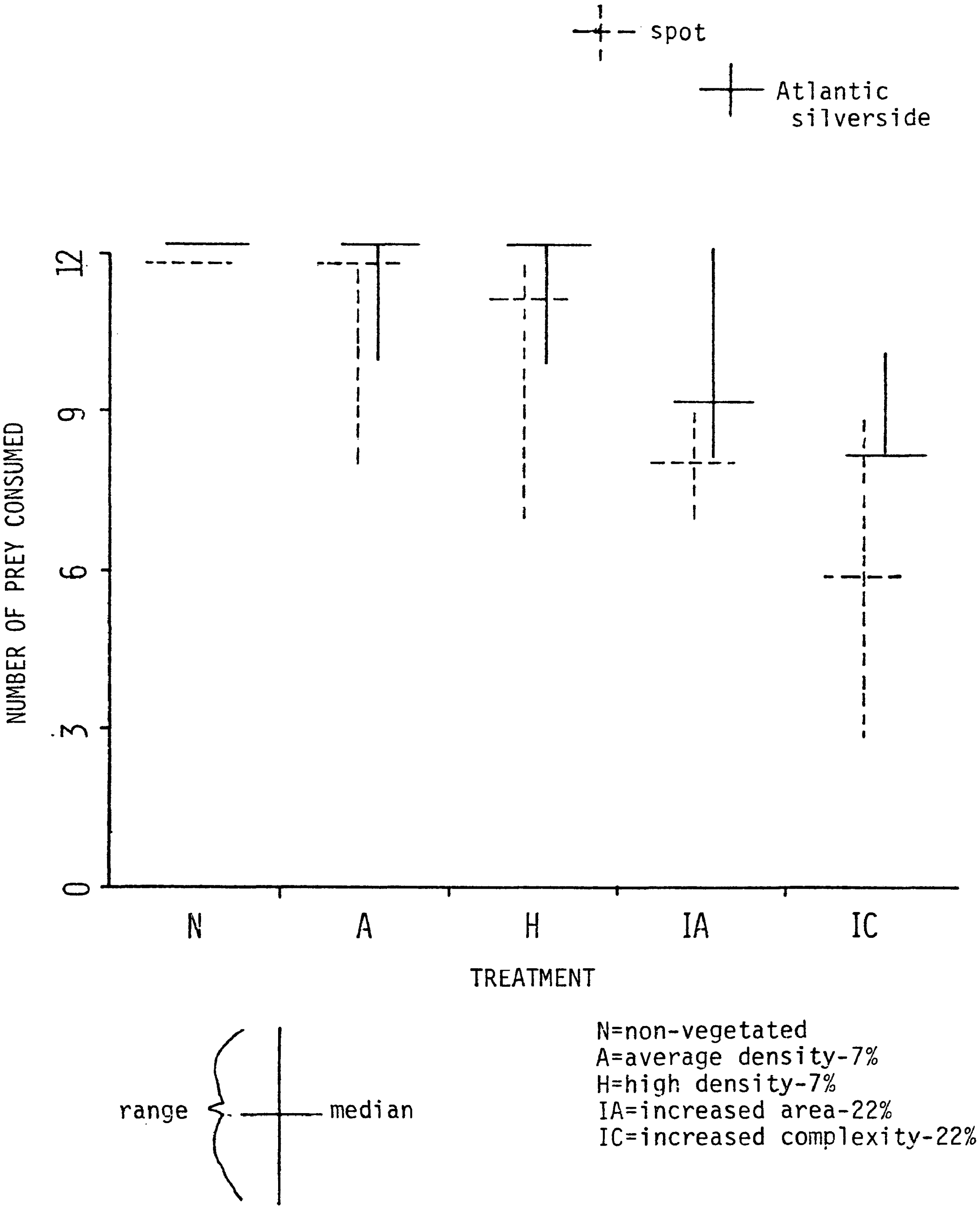

spot
Atlantic silverside
NUMBER OF PREY CONSUMED
0
3
6
9
12
N
A
H
IA
IC
TREATMENT
range
median
N=non-vegetated
A=average density-7%
H=high density-7%
IA=increased area-22%
IC=increased complexity-22%

TABLE 3. Average number of prey consumed for 3 replicates of each vegetative treatment.

		Treatment				
Predator	Prey	N	A	H	IA	IC
Weakfish	Spot	12	10.7	10	8	6
	Atlantic silverside	12	11.3	11.3	9.7	8.7
Summer flounder	Spot	6	9.3	10	8	9
	Atlantic silverside	12	12	12	10	11

N = non-vegetated
A = average density, 7% area covered
H = high density, 7% area covered
IA = increased area, 22% area covered
IC = increased complexity, 22% area covered

TABLE 4. Median test results. H_o-the median number of prey consumed does not differ significantly among the 5 vegetative treatments. H_o is rejected when the value of the calculated statistic exceeds the critical value at = 0.05.

Predator vs Prey	Calculated Statistic	H_o
Summer flounder vs Atlantic silverside	6.64	accept
Weakfish vs Atlantic silverside	7.49	accept
Summer flounder vs Spot	4.24	accept
Weakfish vs Spot	10.27	reject

Critical value at = 0.05- 9.48

Figure 12. Percentage of prey remaining at 0%, 7% and 22% areal vegetative cover for each predator-prey combination. Data points are connected to indicate possible trends, not exact biological relationships.

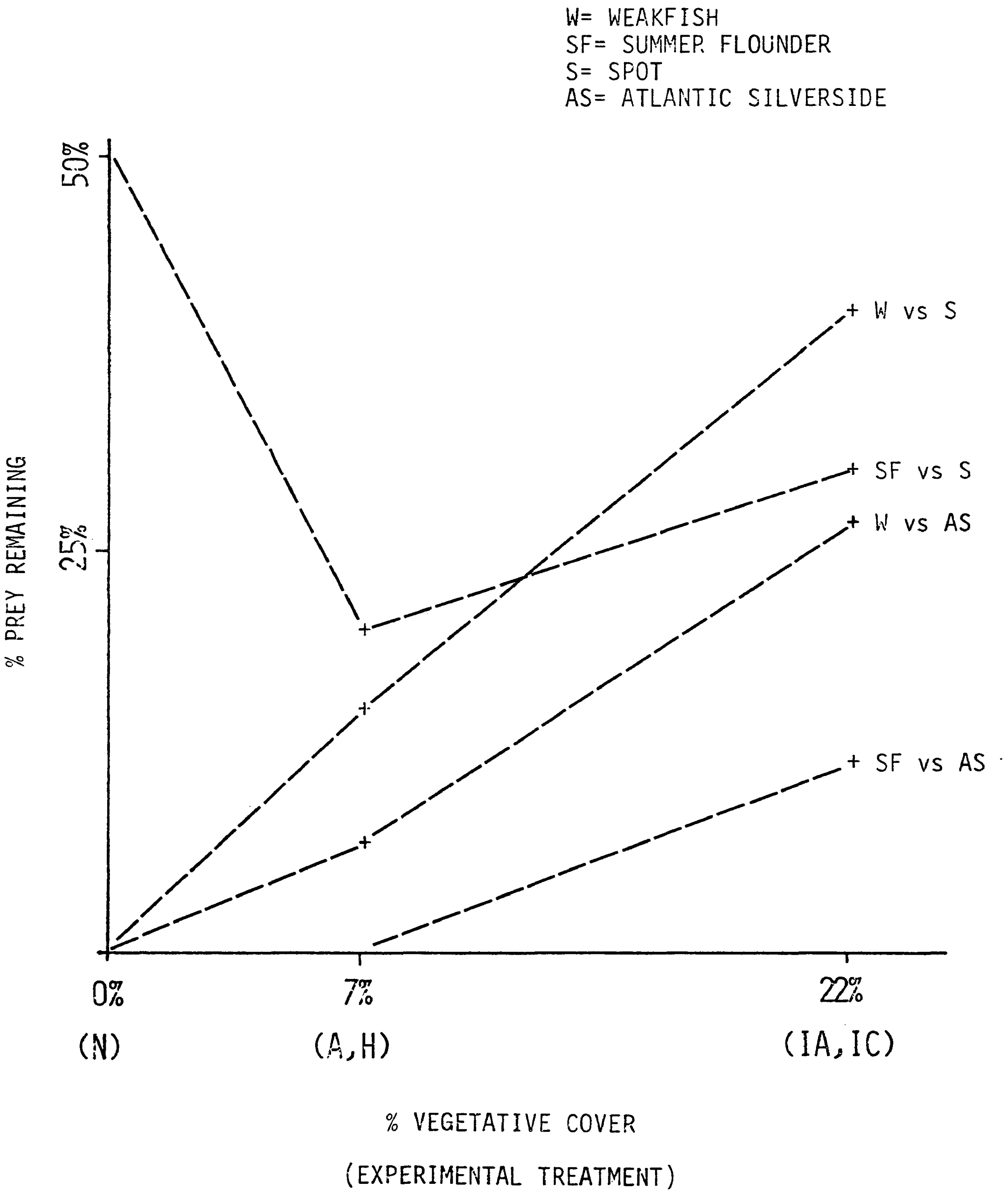
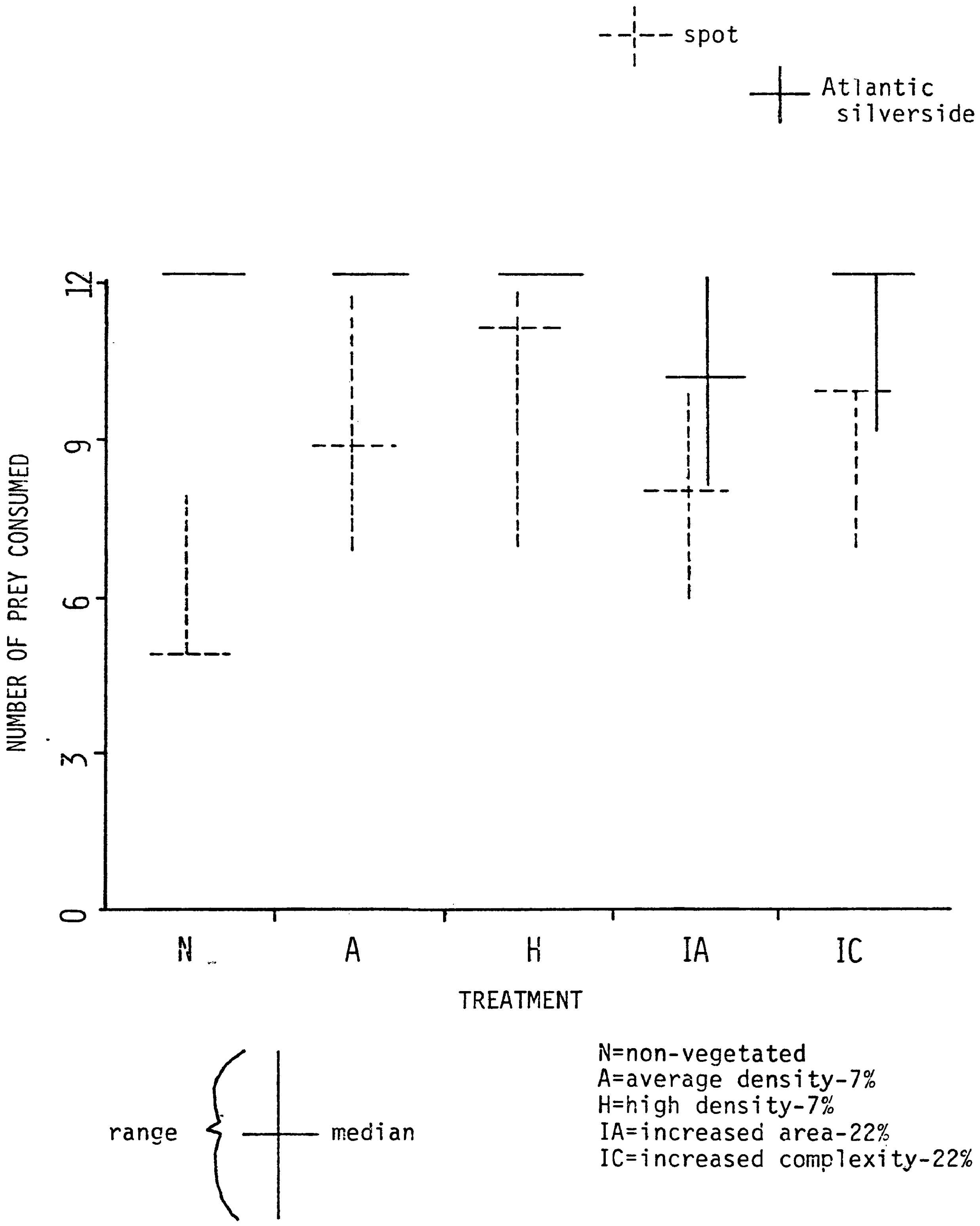

W= WEAKFISH
SF= SUMMER FLOUNDER
S= SPOT
AS= ATLANTIC SILVERSIDE
% PREY REMAINING
50%
25%
W vs S
SF vs S
W vs AS
SF vs AS
0%
(N)
7%
(A,H)
22%
(IA,IC)
% VEGETATIVE COVER
(EXPERIMENTAL TREATMENT)

Figure 13. The number of prey consumed by summer flounder in each of the 3 replicates for the 5 vegetative treatments. The horizontal bar represents the median observation, the vertical bar represents high and low observations and indicates the range among the 3 values.



N=non-vegetated
A=average density-7%
H=high density-7%
IA=increased area-22%
IC=increased complexity-22%

treatments (Conover, 1971), visual inspection of illustrated data (Figure 11), revealed most apparent differences occurred between the non-vegetated and increased complexity treatments. No significant differences occurred among treatments for the other predator-prey combinations.

Behavioral Observations

Bluefish. Bluefish schooled continuously during observation periods. Individuals broke off from the school only to pursue prey or when startled by outside stimuli. Prey were consumed both whole and in portions. Small prey were generally consumed whole. Other individuals were cleanly severed and only the posterior portion was consumed. The anterior portion was often immediately consumed by another bluefish. On occasion, the uneaten, severed portion reached the sand bottom where it was later picked up and consumed. Remnants of mutilitated prey also remained untouched on the bottom. Captures were observed only after high-speed pursuits. This observation is similar to that reported by Olla et al. (1970). Bluefish did not move through vegetation during any observation period.

Weakfish. Weakfish exhibited three distinct activity patterns: (1) resting, (2) swimming, and (3) feeding. These patterns were observed to correlate well with changes in diel illumination intensities. While resting, weakfish hovered near the bottom. Stabilized by slow repetitive pectoral and caudal fin motions, little change in vertical or horizontal positioning occurred. Resting was observed only at night under near total darkness (flashlights were occasionally used to observe night-time activity).

Swimming was observed at all light intensities and generally occurred throughout the daylight period. Weakfish would often swim slowly back and forth along a short section of the pool for hours at a time during maximum light intensity periods.

Feeding was observed during all lighted periods, but was most intense at very low light levels. Yawning, mouth wide agape and opercles extended (see Rasa, 1972), was observed in most experiments and often marked the transition from swimming to feeding. During a feeding period fish generally swam actively about the entire tank. At light intensities too low for visual observation (lowest lighted levels) weakfish could be heard popping or splashing the water surface. These noises were assumed to be related to feeding activity since similar noises occurred when a weakfish rapidly beat the caudal fin and turned downward after an attack at the water surface. No feeding related noises were audible at total darkness.

The prey capture sequence exhibited by weakfish is outlined in Figure 14. Active pursuit followed visual fixation and orientation towards prey. Once within striking distance, about 20-50 cm, the caudal fin beat rapidly and the weakfish lunged forward and upward, jaws agape and opercles spread. Prey were taken whole, generally around the midsection. Upon capturing prey, weakfish rapidly turned, leveled and then slowed. At this point pharyngeal-esophageal motions occurred as the weakfish ingested the prey.

Although artificial eelgrass did not alter the basic elements of prey capture by weakfish, the sequence of visual fixation-prey capture

Figure 14. Feeding behavior sequence for summer flounder and weakfish.

<table>
<tr><th></th><th>SUMMER FLOUNDER</th><th>WEAKFISH</th></tr>
<tr><td>search</td><td>ACTIVE SWIMMING, CAN BE COMBINED WITH GLIDING
OR
LYING ON BOTTOM, HEAD RAISED, EYES SCANNING</td><td>ACTIVE SWIMMING</td></tr>
<tr><td>contact</td><td colspan="2">PREY ENTER PREDATOR VISUAL FIELD</td></tr>
<tr><td>orient</td><td colspan="2">PREDATOR TURNS IN DIRECTION TOWARDS PREY</td></tr>
<tr><td>approach</td><td>FLOUNDER SWIMS (WATER COLUMN) OR CRAWLS (BOTTOM), TOWARDS PREY, SLOWS (BOTH CASES) AT "STRIKING DISTANCE"* FROM PREY</td><td>SWIMS SLOWLY TO POSITION AT "STRIKING DISTANCE" OR RAPIDLY IN SWOOPING MOTION</td></tr>
<tr><td>attack</td><td>EYES FIXED ON PREY, DORSAL AND ANAL FINS FLEXED, CAUDAL FIN RAPIDLY BEATS, FLOUNDER LUNGES AT PREY JAWS OPEN, OPERCLES SPREAD</td><td>EYES FIXED ON PREY, CAUDAL FIN RAPIDLY BEATS, WEAKFISH SPRINGS AT PREY, JAWS OPEN OPERCLES SPREAD, RAPID CHANGES IN DIRECTION MAY OCCUR DURING ATTACK PHASE</td></tr>
<tr><td>capture</td><td>GENERALLY TAKE FISH WHOLE POSTERIO-ANTERIORALLY, RETURN TO BOTTOM WHERE JAW MOVEMENTS OCCUR ASSOCIATED WITH PHARENGEO-ESOPHAGAL SWALLOWING ACTIVITY</td><td>GENERALLY TAKE FISH WHOLE, OFTEN DORSO-VENTRALLY, LEVEL AND SLOW IN WATER COLUMN, JAW MOVEMENTS FOR HANDLING PREY FROM MOUTH TO GUT</td></tr>
</table>

*Olla et al., (1972)- 5-10cm, depending on prey size and behavior.

was interrupted. Open water pursuits often ended on the perimeter of the vegetated area as prey moved into the grass and out of sight. Weakfish moved through and directly over the grass in all vegetated treatments. Captures were observed within the grass when weakfish were able to maintain or obtain visual fixation (similar to flounder). Captures also occurred directly over or alongside the grass.

Illumination intensity and vegetative cover affected weakfish feeding activity and capture success. In non-vegetated experiments weakfish captured 55% of all silversides during the first hour, the remaining 44% were captured by the midday observation. Feeding activity was most intense during the first hour and generally persisted to a lesser extent until all silversides were consumed. At the 7% vegetative cover level, A and H treatments, weakfish captured 86% of all silversides by the midday observation (54% during the first hour). Feeding activity waned to a low point during afternoon hours (no captures) and increased during the last hour, light transition period (8% captured). At the 22% vegetative cover level, IA and IC treatments, weakfish captured 68% of all silversides during morning and evening light transition periods. Capture success was greatest (39%) during the evening period, following the time lights began to dim until near total darkness.

Enumeration of remaining spot in vegetated experiments was not possible. Spot oriented deep within artificial vegetation and could not be seen from the observation stand. Only by removing artificial vegetation at the conclusion of the experiment could an exact numerical count be made. Thus, only general diel feeding activity was noted in vegetated experiments. In non-vegetated experiments weakfish feeding activity began shortly after introduction of spot and continued into the midday observation until all individuals were captured. An increase in swimming activity occurred during evening low light hours even though no prey remained. In vegetated treatments, especially increased area and increased complexity, feeding activity was much greater during both morning and evening low light periods than during full daylight periods.

Summer Flounder. The feeding behavior of summer flounder, preying on two species of shrimp (*Crangon septemspinosa* and *Palaemonetes vulgaris*) is well documented (Olla et al., 1972). In this study summer flounder exhibited similar feeding behavioral characteristics preying on fish (Figure 14). Thus, described here are specific flounder-fish prey-eelgrass interrelations and those behaviors in addition to noted descriptions.

Flounder moved into artificial eelgrass (one or more times) in 15 of the total 24 vegetated experiments. Movements into the grass generally occurred when (1) visual fixation upon prey was maintained during a pursuit initiated outside the grass, or (2) visual fixation upon prey occurred during search initiated outside the grass. Pursuits into the eelgrass were made by both swimming and crawling. Several captures within the grass were recorded and on occasion artificial eelgrass was severed and ingested with the prey. Flounder also oriented on the bottom, alert yet motionless, near the grass-sand interface. From this position flounder made burst attacks at prey as they moved from the eelgrass. The angle of these sudden, rapid motions varied from horizontal (along the bottom directly in front of flounder) to vertical (directly over the flounder in the water column). This behavior was not observed by Olla et al. (1972).

Peak feeding activity (search-pursuits/unit time) generally occurred during daylight hours between 0800 and 1200. In experiments with no vegetation present flounder captured 89% of all silversides during the initial hour of the 12 hour experimental period. With vegetation present 72% were captured during this same period. No changes in feeding activity were discernable as a direct result of changing light intensities. A general decrease in feeding related activity occurred towards midday although searching behavior often continued after all silversides were consumed. With no vegetation present all silversides were consumed by the midday observation. No silversides were consumed, in any treatment between the midday and evening observations. Flounder generally remained in sedentary positions, often partially or entirely buried in the sand substrate. Although flounder occasionally swam around the pool perimeter, pursuits of remaining silversides were infrequent during this period.

General diel feeding activity followed a similar trend in the 24-hour flounder-spot experiments. Since spot frequently oriented deep within artificial grass, enumeration of remaining individuals during observation periods was precluded. Peak activity occurred during morning periods and decreased by midday irrespective of number of prey remaining or vegetative cover. Individuals buried (indicative of lowered state of responsiveness from which feeding related activity does not occur, Olla et al., 1972) most often during afternoon and night periods. While some night feeding did occur (as demonstrated by prey enumeration between last visible evening light and first visible morning light in non-vegetated treatments) such feeding did not account for a significant number of prey captures.

Silversides. Silversides generally schooled in the upper 30 cm of the water column during daylight hours. Both polarized (individuals oriented in the same direction with even spacing) and non-polarized (random orientation) schooling structures were observed.

Under attack, the polarized school broke-up and then reformed as the predator passed. Occasionally individuals became disoriented and spatially separated from the school. These individuals were then most susceptible to predation.

Silversides often evaded a direct attack by jumping out of the water. Jumping occurred most frequently at very low light intensities, when attacks by weakfish were most frequent.

Silversides were observed to form non-polarized, inactive schools directly over the artificial eelgrass. Schools did not move through the grass. Only individual silversides were observed within the grass. These fish hovered within the grass for periods ranging from several minutes to several hours. All individuals remaining at the end of an experimental period were oriented either within or directly above the artificial grass mats. Neither schools nor individual silversides oriented to the artificial eelgrass in the absence of predators.

Spot. Spot exhibited several distinct behavioral modes: schooling, "huddling", orienting within eelgrass, and resting. Fish generally schooled 1-3 cm above the bottom although schools were occasionally observed in mid-water and near the surface.

Spot also huddled near the bottom. As a circular shaped group, huddling spot oriented randomly with respect to neighboring fish, but generally faced toward the outside of the circle. When approached by a predator while in this formation the group broke-up, moved around to the sides and rehuddled behind the predator.

Spot frequently oriented within the artificial eelgrass. Several observations were made of schools dispersing and fleeing for the vegetated areas. As many as 9 spot were observed huddling within the vegetation. Individuals isolated from the school also moved into the grass.

During periods of near total darkness spot were widely dispersed over the bottom of the tank. Individuals hovered, virtually motionless both within the grass and over the bare sand substrate. In the absence of predators spot schooled and oriented to eelgrass less frequently.

DISCUSSION

Experimental Design

Laboratory conditions may have distorted the effects which eelgrass would have on predator-prey interactions in the wild. Restricted space within the experimental system was the most "abnormal" condition affecting both predator and prey. Under such conditions prey have limited possibilities of escaping from predators (Neill and Cullen, 1978). Individuals, especially those isolated from schools, are more susceptible to predation. In the wild these individuals have the additional possibility of escape. Predators such as bluefish, which use straightforward, rundown prey capture tactics are certainly also space limited (as evidenced by high speed collisions with the tank walls). In addition, the clear, filtered water in experimental tanks differed from the often turbid Bay waters. Such conditions could increase the distance at which predators are able to visually contact prey.

Despite drawbacks, the use of an experimental system in assessing predator-prey interactions does provide certain advantages over direct field observations. According to DeBoer (1980) the ideal design for studying the causation of behavior is one in which the fish is subjected to a single specific external stimulus. Noting changes in behavior in response to this external stimulus can lead to a better understanding of the internal factors controlling the behavior. Such conditions cannot be easily reached in the field, where salinity, temperature, diel light regime and other parameters are subject to continuous fluctuation. Behaviors can be studied and compared under only relatively similar external field situations, In the laboratory, experiments can be replicated until the observer is satisfied that exhibited behaviors have valid implications in the natural environment. Also, time, often a factor in the field (due to weather, expenses, etc.) is not as limiting a factor to the observer in the laboratory.

Neither laboratory experiments nor field studies concerning predator-prey interactions should be conducted exclusive of the other. For example, field sampling can provide information concerning predator food habits. Yet, without observational data specific attack and escape behaviors can only be inferred. Integration of field and laboratory programs in this study increased the number of factors sampled and observed and allowed for a more complete description of predator-prey-eelgrass interrelationships.

Learning (here meaning advantages gained by familiarity to experimental conditions and design) can bias results of laboratory experiments. By removing animals after each experiment and replacing them with individuals recently captured in the wild learning would be minimized. Also, behavioral characterizations would be based on a larger sample of the natural population. Two important factors, handling and acclimation, make such procedures unsatisfactory. Handling, capture and movement to the laboratory, can cause physical injury which in turn can alter behavior. Animals placed in experimental tanks must be acclimated and observed for periods sufficiently long to assure that they are in good condition. Also, considerable time (15 days for weakfish) may be required before an animal in a simulated environment will readily consume live prey.

Learning by predators did not seem to affect the efficiency with which prey were captured. If learning had affected the predator's capture efficiency chronological ordering of capture data should reflect this trend. Data indicated that no such trend occurred, increases and decreases of captures within treatments occurred with similar frequency.

Predator capture success was not appreciably different between equal areas of vegetation with different blade densities (e.g. high vs. average density treatments). Vince et al. (1979) noted that fewer prey were consumed by the salt marsh killifish (*Fundulus heteroclitus*) in densely vegetated high marsh (*Spartina patens*) habitat relative to the less densely vegetated low marsh (*Spartina alternaflora*) habitat and concluded that decreased mobility of the predators in the dense vegetation reduced hunting success. In the present study a distinct trend towards increased prey survival as the percent area with vegetative cover increased was evident in three of the four predator-prey combinations (Figure 12). Thus, in addition to possibly decreasing predator mobility, the increased vegetative cover apparently decreased the probability of visual contact and subsequent attack-capture sequences.

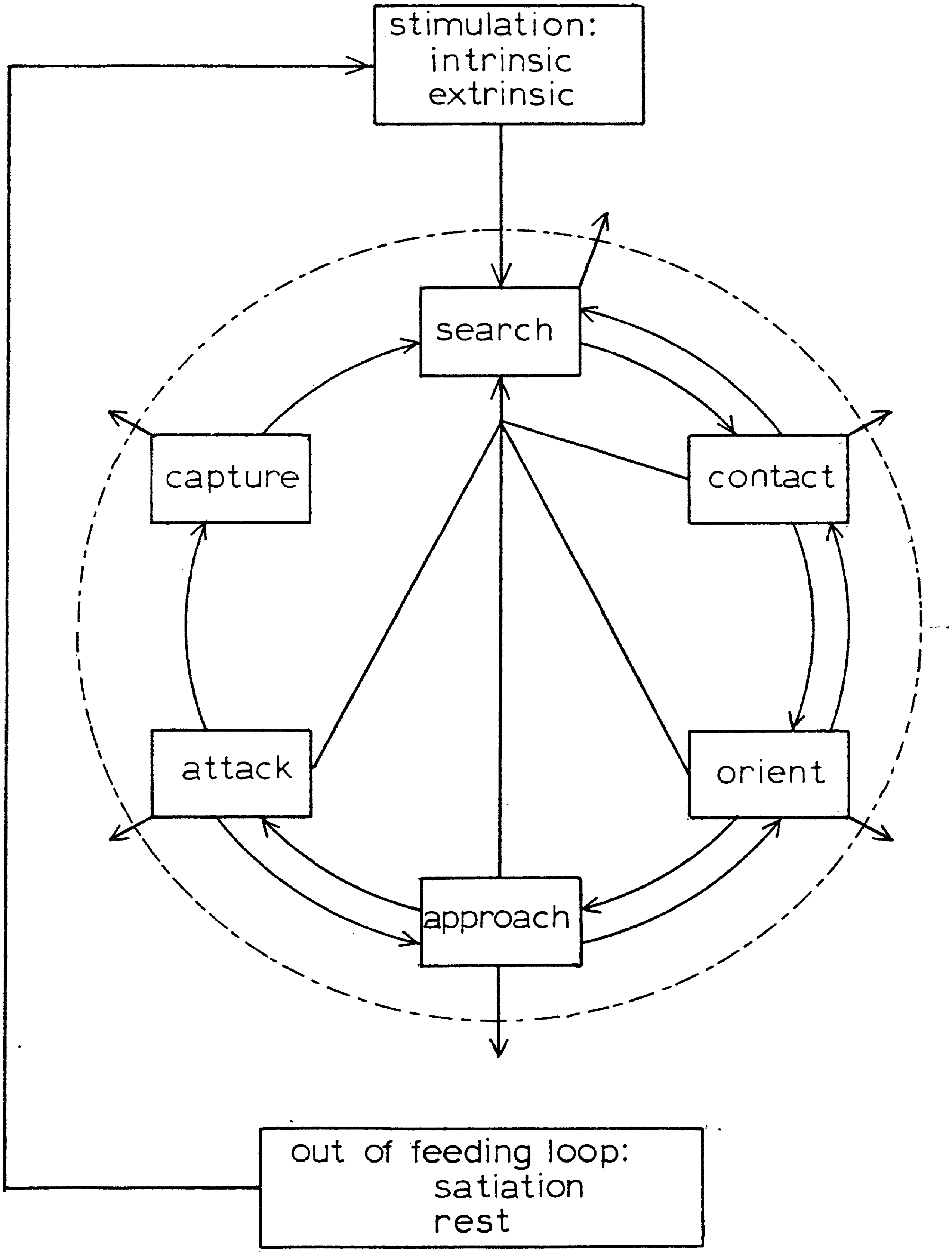
Predators

The extent to which the predators in this study foraged over either the vegetated or non-vegetated sampling sites was difficult to determine from field stomach content data alone since these highly motile predators could quickly cover the entire expanse of the SAV bed. The presence of identifiable prey in stomach contents was not conclusive evidence that feeding occurred in the habitat over which the predator was captured. However, the presence of certain prey species, previously characterized as eelgrass residents (e.g. those which utilize the beds for food and protection), coupled with additional field and laboratory information, was useful in determining a probable location and manner in which feeding occurred.

A conceptualized model of the feeding behavior sequence exhibited by summer flounder and weakfish under laboratory conditions in this study is presented in Figure 15. Triggered by intrinsic (hunger) and extrinsic (sensory receptors) stimuli the predator enters the search mode. Once contact (usually visual) is made, the predator orients directionally, approaches, attacks and captures the prey. The rate at which the sequence proceeds is variable and dependent on size and behavior of both predator and prey. Failure or inability by the predator to complete the sequence and capture prey may result from 1) prey schooling (predator unable to maintain visual orientation on a single prey), 2) loss of visual orientation to prey (e.g. prey escapes into structural cover such as vegetation or 3) low predator motivation (feeding intention behaviors displayed by satiated predator). Exit from the sequence occurs when the predator becomes satiated or requires rest.

Bluefish. Bluefish feeding behavior has been examined in both laboratory and field studies (Olla at el., 1970; Olla and Studholme, 1972; Oviatt, 1977). This species exhibits voracious pelagic feeding habits, consuming a large variety of prey fishes (Sykes and Manooch,

Figure 15. Conceptualization of feeding behavior sequence for summer flounder and weakfish. Exit from the feeding sequence (arrows leaving broken circle) occurs when the predator becomes satiated, requires rest or yields low energetic returns/expenditures.


stimulation:
intrinsic
extrinsic
search
capture
contact
attack
orient
approach
out of feeding loop:
satiation
rest

1979). Shaw (1979) noted that schooling bluefish swim rapidly through prey schools, randomly mutilating and consuming individuals. She concluded that such predatory behavior seemed aimed at dispersing the prey schools, isolating individuals which are then easier to capture. Few studies document bluefish feeding habits in and around SAV. Orth and Heck (1980) suggested that bluefish and other large piscivores may be trophically important transient components of the SAV fish community. This study indicates that bluefish is an important predator species over both vegetated and non-vegetated sampling sites.

Bluefish exhibited distinctly different patterns of distribution and abundance over the adjacent SAV and sand habitat sampling sites. While common, with respect to other piscivores, over both habitats, roughly 3 bluefish were captured over sand for every 1 over SAV. Gill net data indicated bluefish entered and moved through the eelgrass bed singly or in small groups of 2-3 individuals. At the non-vegetated site several larger single set (4 hr) captures, containing as many as 17 individuals, indicated the occurrence of schooling.

Diel abundance patterns also differed between habitats. Bluefish were present in relatively low abundance during both day and night periods in the SAV habitat. Over the non-vegetated site however, a distinct peak in catch occurred during afternoon and evening hours (1200-2000 hours). This peak corresponded well with the occurrence of large single set captures. Olla and Studholme (1971) suggested that bluefish, using vision as a primary sense in feeding, would be most efficient at locating and capturing prey during daylight hours when light intensities permit highest visual acuity.

Observed diel and interhabitat differences in distributional patterns may be related to distinct feeding behavioral modes employed over each habitat. Coincident, abundant catches of bluefish and menhaden and the high percent occurrence (83%) of menhaden in stomach contents indicated that schooling bluefish fed predominatly on schooling prey over the sand bottom habitat. This feeding behavior was not evident over the SAV site. Here, the diet of the solitary foraging bluefish was broadened, possibly reflecting the constraints of structural complexity, and contained a greater percentage of the SAV residents spot and juvenile blue crabs. Structurally complex environments can lead to increased search and pursuit times which in turn can lead to increased diet breadth (Cooper and Crowder, 1979).

Field and laboratory data reflect the possible means by which SAV affects bluefish-prey interactions. By serving as a partial visual and acoustic barrier which interferes with normal schooling behavior, SAV could inhibit the feeding strategy exhibited by schooling bluefish over the non-vegetated habitat. Shaw (1969) and Cahn (1972) found that when fish were separated by an acoustic barrier the typical hydrodynamic flow patterns were interrupted and characteristic spacing of the school was upset. I postulate that the preferred bluefish feeding strategy (maximizing energetic returns/expenditures) is that observed over the sand habitat. Interference in the SAV beds leads to an alternate feeding mode in which individual bluefish feed on a large variety of indivdual prey items.

Weakfish. Morphology, life history, general food habits, reproduction and development of weakfish have been all documented (Welsh and Breder, 1923; Massmann, 1958, 1963; Merriner, 1975, 1976; Chao and Musick 1977; Wilk, 1979). Lacking, however, is information concerning ecological aspects such as feeding behavior, particularly as related to SAV communities. Data from this study indicate weakfish are important top carnivores in the SAV habitat.

Weakfish exhibited distinct patterns of distribution and abundance with respect to habitat. Weakfish were the numerically dominant teleostean piscivore taken over the SAV habitat. In contrast, nets fished over the sand habitat yielded fewer individuals than those fished simultaneously over SAV. The high SAV to sand capture ratio suggest a possible weakfish preference for the eelgrass habitat.

Weakfish apparently traversed the SAV sampling site singly or in small groups. Eighty-six percent of all 4-hour SAV gill net sets which captured weakfish contained 1-2 individuals. Only 2 sets captured greater than 4 individuals (6 and 8). Large single set captures, indicative of schooling behavior, did not occur.

A distinct diel catch pattern was evident for weakfish captured over SAV. Eighty-two percent (61 fish) were captured during the dusk, night and dawn period between 2000 and 0800 hours. Visual avoidance of gill nets by weakfish during daylight hours was probably of minor importance in shaping the observed catch patterns since bluefish, another highly sight oriented predator (Olla et al., 1970), were caught most frequently during daylight hours.

The presence of certain prey species in weakfish stomachs indicated the probable habitat over which feeding occurred. Merriner (1973) noted that the foods of weakfish may include any locally abundant organism of appropriate size. Juvenile spot and juvenile blue crabs were considerably more abundant in the SAV site than at adjacent non-vegetated sampling sites (VIMS EPA SAV, 1980) and spot were believed to use the eelgrass beds as nursery grounds (Adams, 1976b). The high percent occurrence of crabs (40%) and spot (18%) in stomachs in weakfish captured in the SAV bed indicated that at least some feeding occurred there.

The predator's fuctional morphology coupled with the presence of eelgrass in stomach contents was suggestive of the manner in which prey were captured in areas of SAV. Stomachs from 1-2 year old sandbar sharks, Caracharhinus plumbeus, captured over eelgrass beds frequently contained soft-shell blue crabs along with varying amounts of eelgrass (VIMS EPA SAV, 1980). Unable to swim effectively and lacking the hard protective shell, molting crabs probably hide among the grass blades to avoid predation. Sandbar sharks probably feed deep within the SAV and incidentally ingested eelgrass along with the crabs. The mouth position of these sharks (underside the head) would facilitate this type of benthic predation. Conversely, weakfish mouth position (oblique) and the absence of eelgrass in stomachs containing SAV resident prey suggest that weakfish did not feed deep within the vegetation. Rather, as suggested by Chao and Musick (1977) weakfish feed "anterio-dorsally" and pelagically.

In laboratory experiments weakfish typically captured prey around the periphery of the artificial vegetation rather than deep within. Although weakfish occasionally pursued and captured prey within the vegetation, pursuits were generally terminated along the outer perimeters. Eelgrass apparently interrupted the visual fixation followed by prey capture feeding sequence exhibited by weakfish. Similarly, Johannes and Larkin (1961) noted that rainbow trout (Salmo gaidneri) remained some distance above grass (Chara) beds and would only attack individual Gammarus that appeared on the periphery of the grass.

Vegetative cover influenced weakfish capture success. Weakfish captured fewer prey, of both species, as the percentage of vegetative cover increased in laboratory experiments (Figure 12). The number of spot consumed by weakfish was significantly different among the vegetative treatments. The greatest differences occurred between the non-vegetated and the 22% vegetative cover treatments. Although the calculated statistic for the weakfish vs. silverside experiments was not significant (alpha = 0.05), a similar trend was evident.

The behavior of both predator and prey in relation to the artificial eelgrass largely determined the number of prey consumed in any treatment. The rapid turning, darting motions exhibited by feeding weakfish were effective in capturing both schooling and solitary individuals of both prey species. However, in all treatments with vegetation present a minimum of 2 prey survived in at least one replicate. The extent to which a prey species utilized eelgrass as a refuge apparently affected weakfish capture success. Spot exhibited a greater tendency to orient within eelgrass than did silversides and a greater percentage of spot survived each respective vegetative treatment. When attacked, both schooling and individual spot often swam into the artifical eelgrass. Spot remained virtually motionless within the grass and were apparently undetected by the weakfish. Conversely, silversides schooled in open water and when attacked the school dispersed with some individuals returning to the school and others remaining isolated from it. These isolated individuals were observed to be most susceptible to predation in my experiments and these findings are similar to those noted by Shaw (1970). Only individual silversides oriented within eelgrass, generally those isolated from the school or those remaining when most others had been consumed. Only those individuals which hid among the grass blades, remained at the conclusion of an experiment.

Time of day with its corresponding light intensity was a major factor regulating weakfish activity and feeding behavior. Under experimental laboratory conditions the three basic activity patterns exhibited by weakfish (i.e., resting, swimming, and feeding) followed discrete diel schedules.

Artificial vegetation altered diel feeding activity. In non-vegetated treatments feeding continued, irrespective of light intensity, until all prey were captured. With vegetation present feeding occurred almost exclusively during low lighted periods, possibly because search and pursuit yielded low energetic returns during daylight hours when prey were more likely to orient within eelgrass.

Increased feeding activity during low light periods in the laboratory and the higher night time gill net catch over the SAV bed suggest weakfish may be primarily a low light, crepuscular or nocturnal predator. Causal factors for concentrated feeding activity by predatory fishes during twilight have been suggested by several researchers (Major, 1977; Munz and McFarland, 1973; McFarland et al., 1979).

Hobson (1979) noted that tropical reef fish predation was most intense during the "quiet period", an interval of about 20 minutes during both morning and evening twilight. He postulated that crepuscular predators are successful because diurnal and nocturnal prey fishes on the reef are at a visual disadvantage during twilight. Possessing specialized visual structures, the twilight feeding piscivores have greater visual acuity and sensitivity during low light transition periods than either diurnal or nocturnal groups.

Specialized anatomical adaptations may account for the observed crepuscular feeding tendencies exhibited by weakfish. A reflecting layer, tapetum lucidum is present in the eyes of the congeneric species *Cynoscion nebulosus* and *C. arenarius* (Wang et al., 1981). The structure acts as a diffuse reflector allowing the fish to use available light more efficiently in periods of dim illumination. This process effectively increases visual sensitivity in environments where little light is available (Somiya, 1980).

Specific behavior patterns may further influence weakfish-prey interactions which occur in twilight or low light conditions. By positioning themselves below the prey, predators can distinguish the prey silhouette against the relatively light background of the twilight sky and within these periods prey are unable to detect predators in the dark waters below (Hobson, 1966, 1968).

I observed the above phenomenon frequently in the laboratory experiments. During twilight feeding episodes the prey were observed at the water surface whereas weakfish were visually undetectable less than

1-meter below. Popping, splashing noises documented that weakfish were detecting and feeding on prey positioned near the water surface. The relatively high capture success during this period indicated prey may have been visually disadvantaged, less able to detect attacking weakfish from below.

Weakfish were frequently caught over the SAV study site during twilight and night periods yet rarely occurred in daytime samples from SAV. Assuming that gill net avoidance during daylight hours is negligible, the question as to their daylight location remains. Local sport and commercial fishermen maintain that the main channel entrance of Hungar's Creek, adjacent to the SAV study area (Figure 1), provides the best daytime weakfish catches. Such spatial and temporal distribution might be expected (i.e., weakfish in deeper channel waters during the day and shallow eelgrass flats during low light periods). The dim light regimes under which weakfish are most effective predators occur at these times in these habitats.

In conclusion, field data and laboratory behavioral observations suggest that weakfish forage in SAV beds during the low light periods, probably capturing prey along the periphery of the SAV bed rather than deep within the vegetation proper.

Summer Flounder. Olla et al., (1972) observed that summer flounder, under laboratory conditions, exhibited a variety of behavioral tactics which allowed them to feed efficiently both in the water column and on the bottom. Powell and Schwartz (1979) described the food habits of the summer and southern flounders (_Paralichthys dentatus_ and _P. lethostigma_) in North Carolina estuaries. They reported that these species are well adapted for feeding on relatively large, motile prey including fishes and shrimp which are present throughout the water column.

Few studies have documented the predaceous habits of adult summer flounder in eelgrass beds. Previous sampling programs have been conducted over non-vegetated, sand or mud bottom habitats (Powell and Schwartz, 1977, 1979). Adams (1976) examined stomach contents of summer and southern flounder captured over eelgrass beds. Juvenile and larval fishes constituted 41% of the annual average food intake by weight of 39 individuals examined. However, the percentage of these 39 individuals which were summer flounder and the sizes of these individuals was not noted. Orth and Heck (1980) noted that summer flounder were regularly collected in low numbers in lower Chesapeake Bay eelgrass beds but did not include this species among those having a major predatory impact on the SAV community. Though summer flounder were apparently numerically underestimated by sampling methods employed in this study (relative to bluefish and weakfish), stomach content analysis and laboratory behavioral observations indicated that this species may be a major higher order consumer in the SAV community.

Flounder were captured during both day and night periods, and there were no conspicuous trends in diel abundance. Observations by Olla et al., (1972) indicated that flounder were primarily day-active. Captures at Vaucluse Shores were most frequent (3:1) over the vegetated habitat, reflecting a possible preference by summer flounder for this area of highly concentrated potential food items.

Gill net data and laboratory observations revealed that flounder entered and fed in areas of SAV. Although relatively few stomachs were examined, the presence of eelgrass and the prey species spot, pipefish (Syngnathus fuscus) and grass shrimp (all abundant eelgrass residents, VIMS EPA SAV Final Report, 1981) in stomachs from flounder captured over eelgrass indicated that feeding occurred in this habitat. In addition, stomach contents of flounder captured by 16' otter trawl in the same habitat reflected similar food habitats. The presence of eelgrass along with resident prey species indicated that flounder capture prey within the vegetation. In laboratory experiments flounder frequently entered the artificial eelgrass in pursuit of prey. On several occasions artificial eelgrass was incidentally severed and ingested as prey were attacked within the grass.

Behavioral and morphological adaptations and restrictions of both predator and prey may override the effect of SAV on specific interactions. Statistical analyses of experimental data indicated no significant difference in the median number of prey (of either species tested) consumed by flounder among the five experimental treatments, but do not reflect behavioral aspects of prey capture or predator avoidance relative to the artificial eelgrass. Flounder consumed fewer spot on the average in the non-vegetated treatment than in any vegetated treatment. In the absence of SAV, spot visually detected and avoided summer flounder. Through their morphological restrictions summer flounder were not able to execute the rapid turning motions necessary for successful capture of alterted schooling or huddling spot. Flounder effectively attacked and captured unsuspecting spot which were positioned directly in front, above or below them. Visually alerted "huddled" spot stayed in small groups and moved around to the sides and rear of the flounder, thus becoming less susceptable to capture. Fathead minnows exhibited a similar avoidance behavior when attacked by the largemouth bass (Sullivan and Atchison, 1978). In vegetated experiments flounder appeared to enchance their prey capture capabilities through strategic positioning relative to the artificial eelgrass. After lying motionless close to the perimeter of the artificial vegetation flounder would attack the individual spot which ventured too close, coming from within or the opposite side of the artificial SAV.

Implications of exhibited capture and avoidance behaviors differ from the 'a priori' notion that vegetation serves as a prey refuge. Flounder utilize the SAV as a "blind" and attack unsuspecting prey that enter within striking range. Thus, in a patchy SAV environment those prey which wander from within the confines of eelgrass may lose any distinct refuge advantage to such a predatory strategy.

Prey type (fish) and substrate (vegetation) utilized in this study differed from previously noted studies. These differences are believed to have elicited the observed summer flounder feeding behaviors which are additional to noted descriptions. Olla et al., (1972) did not observe summer flounder to attack prey (grass and sand shrimp) from the "head-up" position on the bottom without initiating active search (i.e., swimming or crawling). On several occasions I observed flounder lunging forward from this sedentary position to strike at and capture prey fish. As prey moved within striking distance the flounder would swim rapidly upward at angles up to 90^o from the bottom with exceptional quickness.

This strategy proved especially effective in capturing unsuspecting spot and implies that flounder are capable of a "lying-in-wait" method of prey capture.

Prey

Atlantic Silverside. Schooling appears to be the most important predator avoidance mechanism employed by silversides. Although every silverside was captured in each replicate of the non-vegetated treatment, schooling members were infrequently captured. Individual silversides which had become isolated from the school after an attack were frequently pursued and captured by both summer flounder and weakfish. The tendency of prey to quickly reform schools after an attack by a predator is an important factor in avoiding capture (Shaw, 1979).

When attacked by a predator silversides exhibited a greater tendency to school than to orient within the artificial SAV. Major (1977) termed the school a 'mobile biological refugium'. Schooling provides a means of cover seeking for those fish occupying unstructured open waters (Williams, 1964; Shaw, 1979). Frightened schools of silversides never hid among vegetation; however individual silversides which were either isolated from the school after an attack by a predator or remained after other members had been consumed, fled for the eelgrass. All individual silversides remaining at the end of an experiment were oriented either within or directly above the eelgrass. Neill and Cullen (1974) reported that the presence of vegetation helped single fish escape but provided little furthur benefit to fish which already had the protection of a school.

Spot. Huddling appeared to be an effective predator avoidance strategy employed by spot, especially in non-vegetated experiments.

Attacking predators were apparently unable to maintain visual fixation on an individual spot as the group dispersed.

Non-polarized schools of spot fled for vegetative cover when attacked. In contrast, non-polarized Atlantic silversides schools polarized when attacked and did not flee for cover. Thus, spot may form non-polarized schools as a low intensity fright response (i.e., in the presence of a predator); but when attacked, flight for vegetative cover appeared to be a primary predator avoidance mechanism.

General

That eelgrass beds serve as protective habitats for small prey fishes has long been inferred. This study revealed that, indeed, prey which remained within vegetative cover enhanced their chances for survival. However, data also suggest that predators utilize eelgrass beds as foraging grounds in ways which best fit their morphs and behaviors.

Several predatory strategies appear to be effective in areas of submerged aquatic vegetation. Heck and Orth (1980) suggested that the presence of vegetative cover would be less likely to reduce the efficiency of lie-in-wait predators. In this study summer flounder were observed lying-in-wait along the vegetative perimeter, effectively capturing prey which moved from within the grass. Thus, this tactic should be especially effective in patchy grass-bare sand areas. However, remaining inconspicuous in densely vegetated areas would be unlikely. As summer flounder moved through vegetation in laboratory experiments grass blades were matted down and essentially 'traced out' their body shape.

Crepuscular predators pose a threat to prey which migrate into the water column or out of the bed on a diel basis. Hobson (1979) has documented the high occurrence of crepuscular predation in tropical reef fish communities. Data presented here indicate that weakfish are particularly successful at foraging eelgrass beds during the twilight. However, further study must be conducted to determine the spectral sensitivity of retinal pigments for this species (see Hobson et al., 1981).

Little or no reduction in capture efficiency should occur in eelgrass beds for predators which utilize sensory receptors other than vision to locate and capture prey. Eelgrass may not be a barrier to sharks and rays which detect chemical or electrical emmisions from prey.

At least one example of predatory strategy can be cited which may be less successful in eelgrass beds. Schooling-feeding predators, such as bluefish, plunge into prey schools, dispersing individuals which are then easier to capture. Eelgrass could: 1) provide a barrier to efficient schooling by the predator (thus, reducing prey dispersal) and, 2) provide a means of cover seeking for disoriented prey. Either case would reduce predator efficiency.

Since variation in intraspecific avoidance behaviors could serve to increase predation, prey fish species should be expected to utilize either schooling or vegetative cover as primary avoidance tactics. In the present investigation, Atlantic silversides schooled continuously (obligate), in both polarized and non-polarized formations, and did not flee for artificial vegetation when attacked. Spot schooled occasionally (facultative) and oriented within eelgrass when attacked. Thus, one could predict that the presence of vegetation would not enhance predator avoidance efficiency of obligate schooling prey species. Facultative and non-schooling prey species should benefit from vegetative cover.

These are but a few examples of species-specific predator-prey-eelgrass interactions which require further investigation. They serve to illustrate the delicate balance which exists in natural predator-prey relations. Through evolutionary forces, the effective use of vegetative habitats as refugia by prey fishes has evoked effective predatory strategies for foraging in this habitat. Thus, the role of eelgrass beds as nursery habitats for small fishes must be expanded to include their importance as predator foraging grounds.

SUMMARY

1. Bluefish exhibited discrete distribution patterns and food habits over the non-vegetated and vegetated sampling sites. Data indicated that schooling bluefish fed predominantly on schooling prey over the non-vegetated habitat during daylight. Over the SAV habitat, where bluefish occurred singly or in small groups during both day and night, stomachs contained a variety of prey species including SAV residents.

2. Weakfish were the dominant teleostean piscivore captured over the SAV habitat occurring there predominantly during evening, night and early morning periods between 2000 and 0800. The relatively large number of spot, a SAV resident, in the diet of weakfish captured in the SAV habitat indicated foraging occurred there. Weakfish were rarely captured over the non-vegetated sampling site.

3. Although stomach content data indicated that summer flounder foraged in the SAV habitat, field observations revealed that their abundance, and thus, relative importance as a predator, was underestimated by gill net sampling. Due to their morphology summer flounder were rendered less susceptible, relative to bluefish and weakfish, to capture by gill nets employed in this study.

4. Under laboratory conditions, vegetative cover influenced weakfish prey capture success. Statistical results indicated that the number of spot consumed by weakfish varied significantly among the various vegetated

and non-vegetated treatments. Weakfish consumed fewer prey, spot and Atlantic silversides, as the percent area of artificial vegetative cover increased.

5. Diel light intensity variations regulated weakfish activity and feeding behavior in laboratory experiments. The three basic activity patterns exhibited by weakfish (resting, swimming and feeding) followed discrete diel schedules. Peak feeding activity occurred during morning and evening low light periods.

6. Due to their morphology, summer flounder exhibited limited success in capturing schooling prey. However, through strategic positioning relative to the artificial eelgrass summer flounder successfully captured individual prey. In addition to documented prey capture strategies summer flounder also exhibited a "lying-in-wait" tactic in which individuals rapidly lunged from a sedentary benthic position to attack prey without initiating pre-attack, active search movements.

7. Schooling was the major predator avoidance strategy employed by silversides. Upon attack schooling silversides dispersed and regrouped; those disoriented from the school were most susceptible to predation. Only individual silversides oriented within eelgrass.

8. To avoid predation, spot schooled, huddled and oriented within eelgrass. Both individuals and schools frequently moved into artificial vegetation.

9. Integration of field and laboratory programs can maximize the number of factors sampled and observed and provide a more complete understanding of predator-prey behavioral interrelationships.

10. Based on integrated field and laboratory data hypotheses concerning specific predator-prey-eelgrass interrelationships can be formulated. These are:

a. Bluefish utilize non-schooling prey capture tactics within areas of SAV, consuming a variety of prey species including SAV residents.

b. Weakfish enter areas of SAV during low light intensity hours (twilight and night) capturing prey which are encountered in the water column along the periphery of the vegetation.

c. Summer flounder use lie-in-wait prey capture tactics, orienting on the bare substrate in patchy SAV areas and capture prey which wander from the vegetation. Active search prey capture tactics are also utilized.

d. Schooling Atlantic silversides do not utilize SAV areas as protective habitats. Individuals spatially separated from the school, however, may do so.

e. Spot utilize SAV areas as protective habitats by orienting within the vegetative canopy out of the predators visual field.

APPENDIX I

SUMMARY OF GILL NET DATA

The following table summarizes gill net capture data for *Cynoscion regalis*, *Pomatomus saltatrix* and *Paralichthys dentatus*. Catch-time equals set-time plus ½(pull-time minus set-time). All times are EST. SAV1 is the *Zostera marina* site and SAV2 is the mixed *Z. marina*-*Ruppia maritima* site. Food items were identified to species, enumerated and measured whenever possible.

Cynoscion regalis-1979

MONTH	CATCH TIME	TEMP °C	HABITAT	STANDARD LENGTH	FOOD ITEM
5	1130	21.5	SAV1	600	-
	1900	21.5	SAV2	540	-
	1930	21.5	SAV1	520	-
	2300	21.5	SAV2	500	-
	2345	21.5	SAV1	560	-
	0430	21.5	SAV1	580	*L. xanthurus*, *C. septemspinosa*. *C. sapidus*
	0500	21.5	SAND	260	-
6	1510	23.0	SAV1	360	-
	2010	20.5	SAV2	410	-
	2010	20.5	SAV2	330	*B. tyrannus*, unid. fish remains
	2020	20.5	SAV1	370	-
	0010	20.5	SAV2	410	-
	0020	20.0	SAV1	480	-
7	0200	26.5	SAV2	385	-
8	2055	25.0	SAV1	370	-
	2055	25.0	SAV1	430	-
	0100	25.0	SAV1	290	*Anchoa* sp.
	0100	25.0	SAV1	380	-
	0500	25.0	SAV2	300	-
	1510	21.0	SAV1	410	-
9	1835	21.5	SAV1	540	-
	1835	21.5	SAV1	265	-
	1835	21.5	SAV1	320	-
	1835	21.5	SAV1	355	*L. xanthurus*
	0630	21.0	SAV2	425	*C. septemspinosa*, unid. fish remains
	0630	21.0	SAV2	345	*M. menidia*, *B. tyrannus*

Cynoscion regalis-1980

MONTH	CATCH TIME	TEMP °C	HABITAT	STANDARD LENGTH	FOOD ITEM
4	1410	14.5	SAND	420	*A. mitchilli*-(3)
	1410	14.5	SAND	415	*A. mitchilli*
	1800	16.5	SAND	480	-
	1800	16.5	SAND	440	unid. fish remains
	1800	16.5	SAND	355	*C. sapidus* (15mm)
	1800	16.5	SAND	325	unid. fish remains
	2120	15.0	SAND	385	*A. mitchilli*-(2), unid. fish remains
	2200	15.0	SAV2	400	*A. mitchilli*-(2), *C. septemspinosa*
	0255	14.0	SAV2	345	-
	0300	14.0	SAV1	415	-
	0300	14.0	SAV1	370	*A. mitchilli*-(9)
	0300	14.0	SAV1	360	-
	0300	14.0	SAV1	375	*A. mitchilli*, *C. sapidus* (20mm), *C. septemspinosa*
	0300	14.0	SAV1	370	*A. mitchilli*-(2)
	0300	14.0	SAV1	395	*A. mitchilli*-(12)
	0555	12.5	SAND	370	-
5	1930	19.5	SAV1	320	*C. septemspinosa*
	2100	19.0	SAND	320	*A. mitchilli*
	2350	18.0	SAV2	395	-
	0405	19.0	SAV2	475	*C. septemspinosa*, unid. fish remains
	2130	19.0	SAV1	390	-
	2130	19.0	SAV1	485	unid fish remains
	2130	19.0	SAV1	475	-
	2130	19.0	SAV1	355	*C. septemspinosa*-(5), *L. xanthurus*-(15ind. 50mm ave.)
6	0140	20.0	SAV2	365	-
	0140	20.0	SAV2	405	*A. mitchilli*, *B. tyrannus*, *C. septemspinosa*
	0140	20.0	SAV2	355	-
	0215	20.0	SAV1	340	*B. tyrannus* (105mm)
	0710	20.0	SAV2	385	*L. xanthurus*-(7 ind. 80mm ave.)
	1840	20.0	SAV1	445	-
	2200	20.5	SAV1	375	-

Cynoscion regalis-1980 (cont.)

MONTH	CATCH TIME	TEMP °C	HABITAT	STANDARD LENGTH	FOOD ITEM
6	2200	20.5	SAV 1	347	-
	2225	20.5	SAND	400	*B. tyrannus*, *C. septimspinosa*-(20)
	2250	20.5	SAV 2	360	-
	2250	20.5	SAV 2	525	*L. xanthurus*
	2250	20.5	SAV 2	345	-
	2250	20.5	SAV 2	360	-
	2250	20.5	SAV 2	320	*C. septemspinosa*, unid. fish remains
	2250	20.5	SAV 2	380	-
	2250	20.5	SAV 2	390	-
	2250	20.5	SAV 2	360	-
7	2010	25.0	SAV 1	340	-
	0420	25.0	SAV 1	345	-
	0550	25.0	SAV 2	375	-
	1310	28.0	SAV 2	390	-
	1310	28.0	SAV 2	355	-
	1745	28.5	SAV 2	385	-
	2200	27.0	SAV 1	350	-
	2200	27.0	SAV 1	370	-
	2200	27.0	SAV 1	390	-
8	0100	25.0	SAV 1	410	*C. sapidus*-(<50mm)
	0100	25.0	SAV 1	440	-
	0130	25.0	SAV 2	465	*S. fuscus*, *C. septemspinosa*, *C. sapidus*-(<50mm)
	0130	25.0	SAV 2	465	*C. sapidus*-(<50mm)
	0130	25.0	SAV 2	550	*C. sapidus*-(<50mm),unid. fish remains
	0130	25.0	SAV 2	410	-
	0700	25.0	SAV 1	450	*C. sapidus*-(15 ind. 30mm ave.), unid. fish
	0700	25.0	SAV 1	405	*C. sapidus*-(2 ind. < 50mm)
	1040	25.0	SAND	345	*C. sapidus*-(8 ind. 25mm ave.)
	1400	25.0	SAV 1	415	*C. sapidus*-(45mm)
	1800	25.0	SAV 1	410	C. sapidus-(<50mm)

Pomatomus saltatrix-1979

MONTH	CATCH TIME	TEMP °C	HABITAT	STANDARD LENGTH	FOOD ITEM
5	1145	21.5	SAND	465	-
	1145	21.5	SAND	445	-
	1145	21.5	SAND	460	-
	1930	21.5	SAV1	710	unid. fish remains
	2045	21.5	SAND	740	unid. fish remains
	2300	21.5	SAV2	420	-
	2300	21.5	SAV2	320	-
	0400	21.5	SAV2	660	unid. fish remains
	0500	21.5	SAND	640	-
	0500	21.5	SAND	360	-
	0500	21.5	SAND	210	-
	0945	21.5	SAV1	340	-
6	1430	21.5	SAND	390	-
	1430	21.5	SAND	470	*B. tyrannus*
	1430	21.5	SAND	590	-
	1445	21.5	SAV2	340	-
	1445	21.5	SAV2	370	-
	1510	23.0	SAV1	830	-
	2020	20.5	SAV1	860	-
	2020	20.5	SAV1	870	*B. tyrannus*
	2335	18.0	SAND	320	-
	0010	20.0	SAV2	360	-
	0020	20.0	SAV1	530	*B. tyrannus*
	0020	20.0	SAV1	680	-
	0020	20.0	SAV1	480	unid. fish remains
	0830	21.0	SAV1	305	-
	0830	21.0	SAV1	295	-
8	1600	25.5	SAND	450	-
	1600	25.5	SAND	380	-
	1600	25.5	SAND	400	-

Pomatomus saltatrix-1979(cont.)

MONTH	CATCH TIME	TEMP °C	HABITAT	STANDARD LENGTH	FOOD ITEM
8	1600	25.5	SAND	410	-
	1600	25.5	SAND	590	*B. tyrannus*
	1600	25.5	SAND	590	unid. fish remains
	1600	25.5	SAND	470	*B. tyrannus*
	1600	25.5	SAND	470	*B. tyrannus*-(3)
	1600	25.5	SAND	460	-
	1600	25.5	SAND	410	-
	2000	24.5	SAND	420	*B. tyrannus*-(2)
	0100	25.0	SAV1	420	-
	0100	25.0	SAV1	385	-
	0530	25.0	SAND	500	unid. fish remains
9	1400	19.0	SAV2	335	-
	1400	19.0	SAV2	320	-
	1400	19.0	SAV2	340	-
	1400	19.0	SAV2	305	*L. xanthurus*
	1825	21.5	SAV2	350	unid. fish remains
	1825	21.5	SAV2	500	*L. xanthurus*, *M. cephalus*
	1825	21.5	SAV2	465	*M. cephalus*
	1845	21.5	SAV1	330	unid. fish remains
	0635	21.0	SAV2	515	*M. cephalus*, unid. fish remains
	0635	21.0	SAV2	420	-
	0635	21.0	SAV2	255	-
10	1820	21.0	SAV1	335	-
	1850	20.0	SAND	390	-
	1850	20.0	SAND	470	-
	1850	20.0	SAND	420	-
	2235	19.5	SAND	320	-
	0300	19.5	SAND	355	-
	0300	19.5	SAND	360	-
	0300	19.5	SAND	340	-
	0300	19.5	SAND	505	-

Pomatomus saltatrix-1979(cont.)

MONTH	CATCH TIME	TEMP °C	HABITAT	STANDARD LENGTH	FOOD ITEM
10	0300	19.5	SAND	360	-
	0620	19.5	SAND	335	-
11	1850	12.0	SAND	390	-
	1850	12.0	SAND	410	-
	1850	12.0	SAND	460	*B. tyrannus*-(2)
	1850	12.0	SAND	350	-
	1850	12.0	SAND	410	-
	1850	12.0	SAND	370	*B. tyrannus*
	1850	12.0	SAND	340	-
	1850	12.0	SAND	405	-
	1850	12.0	SAND	385	-
	2335	12.0	SAND	385	-
	2335	12.0	SAND	395	*B. tyrannus*
	2335	12.0	SAND	395	-
	2335	12.0	SAND	340	-
	2335	12.0	SAND	335	-
	2335	12.0	SAND	405	*B. tyrannus*
	2335	12.0	SAND	400	*B. tyrannus*
	2335	12.0	SAND	410	-
	2335	12.0	SAND	380	-
	0300	11.0	SAND	365	unid. fish remains
	0300	11.0	SAND	435	*B. tyrannus*
	0300	11.0	SAND	400	-

Pomatomus saltatrix-1980

MONTH	CATCH TIME	TEMP °C	HABITAT	STANDARD LENGTH	FOOD ITEM
4	1410	14.5	SAND	500	-
	1410	14.5	SAND	550	unid. fish remains
	1410	14.5	SAND	535	-
	1410	14.5	SAND	580	unid. fish remains

Pomatomus saltatrix-1980(cont.)

MONTH	CATCH TIME	TEMP ^{o}C	HABITAT	STANDARD LENGTH	FOOD ITEM
4	1410	14.5	SAND	520	-
	1410	14.5	SAND	545	*B. tyrannus*
	1410	14.5	SAND	540	*B. tyrannus*
	1410	14.5	SAND	525	-
	1410	14.5	SAND	610	-
	1410	14.5	SAND	700	-
	1410	14.5	SAND	585	unid. fish remains
	1410	14.5	SAND	525	-
	1410	14.5	SAND	565	*C. septemspinosa*
	1410	14.5	SAND	545	-
	1410	14.5	SAND	525	-
	1410	14.5	SAND	480	-
	1410	14.5	SAND	420	-
	1445	17.0	SAV2	415	-
	2120	15.0	SAND	730	-
	2145	15.0	SAV1	710	unid. fish remains
	0300	14.0	SAV1	375	*B. tyrannus*
5	0720	20.0	SAV2	515	*Z. marina*, unid. fish remains
	1520	19.5	SAV2	510	*B. tyrannus*
	1520	19.5	SAV2	505	-
	1520	19.5	SAV2	530	-
	1520	19.5	SAV2	525	*C. sapidus*, *Z. marina*
	1520	19.5	SAV2	525	unid. fish remains
	1530	19.5	SAV1	510	-
	1530	19.5	SAV1	485	-
	1540	19.5	SAND	390	-
	1920	19.5	SAV2	450	-
	1920	19.5	SAV2	535	-

Pomatomus saltatrix-1980(cont.)

MONTH	CATCH TIME	TEMP °C	HABITAT	STANDARD LENGTH	FOOD ITEM
5	1930	19.5	SAV1	505	*B. tyrannus*
	2100	19.0	SAND	480	-
	2100	19.0	SAND	465	-
	2350	18.0	SAV2	530	-
	0045	18.0	SAV1	460	*M. menidia*
	0045	18.0	SAV1	500	-
	0045	18.0	SAV1	400	*C. septemspinosa*-(8)
	0045	18.0	SAV1	520	-
	0405	19.0	SAV2	495	*B. tyrannus*
	0405	19.0	SAV2	520	*B. tyrannus*
	0415	19.0	SAV1	515	-
	0415	19.0	SAV1	485	*C. septemspinosa*-(20)
	0415	19.0	SAV1	295	-
	0825	18.5	SAND	440	-
	0825	18.5	SAND	450	*B. tyrannus*-(200mm)
	0825	18.5	SAND	370	*B. tyrannus*-(112mm)
6	0140	20.0	SAV2	270	-
	0140	20.0	SAV2	290	-
	0510	20.0	SAV2	520	*B. tyrannus*
7	0345	24.5	SAV2	325	-
	0420	24.5	SAV1	300	-
	0420	24.5	SAV1	315	-
	0420	24.5	SAV1	295	-
	0515	24.5	SAND	425	unid. fish remains
	0820	26.5	SAV1	285	-
	1335	28.5	SAND	345	-
	1335	29.0	SAND	335	-
	1700	29.0	SAND	330	*L. xanthurus*-(2)
	1700	29.0	SAND	345	-
	1700	29.0	SAND	310	-
	1700	29.0	SAND	330	-

Pomatomus saltatrix-1980(cont.)

MONTH	CATCH TIME	TEMP ^{o}C	HABITAT	STANDARD LENGTH	FOOD ITEM
7	1700	29.0	SAND	325	-
	1700	29.0	SAND	545	-
	1745	28.5	SAV2	325	-
8	0100	27.0	SAV1	485	Z. marina
	0100	27.0	SAV1	365	L. xanthurus, Gastropoda
	0100	27.0	SAV1	315	-
	0100	27.0	SAV1	380	-
	0030	27.0	SAND	395	-
	0730	27.0	SAND	500	-
	0730	27.0	SAND	515	-

Paralichthys dentatus-1979

6	0010	20.0	SAV2	220	-
8	1655	25.0	SAV1	260	-
	2055	25.0	SAV1	270	-
	0510	25.0	SAV1	275	-
	0510	25.0	SAV1	280	-
	1445	25.0	SAV1	290	-
	1445	25.0	SAV1	280	-
9	1825	21.5	SAV2	400	-
	1835	21.5	SAV1	325	-
	2225	21.5	SAV2	300	-
	0705	21.0	SAND	285	-
	0705	21.0	SAND	305	-
	1015	21.5	SAV2	280	-
	1015	21.5	SAV2	300	-
10	1420	21.5	SAV1	310	-
	0200	19.5	SAV2	295	-

Paralichthys dentatus-1979(cont.)

MONTH	CATCH TIME	TEMP °C	HABITAT	STANDARD LENGTH	FOOD ITEM
10	0215	19.5	SAV1	270	-
	0215	19.5	SAV1	285	-
	0215	19.5	SAV1	305	-
	0610	19.5	SAV2	250	-

Paralichthys dentatus-1980

MONTH	CATCH TIME	TEMP °C	HABITAT	STANDARD LENGTH	FOOD ITEM
5	1930	19.5	SAV1	185	-
6	0525	20.0	SAND	150	-
	2200	20.5	SAV1	290	-
7	0345	24.5	SAV2	215	*P. vulgaris*
	1530	24.5	SAV1	430	*L. xanthurus*
	1550	24.5	SAV2	255	-
	0820	26.5	SAV1	165	-
8	0700	25.0	SAV1	230	-
	0700	25.0	SAV1	265	-
	1000	25.0	SAV2	230	*S. fuscus*, *Z. marina*
	1000	25.0	SAV2	250	-
	1400	25.0	SAV1	250	-
	1400	25.0	SAV1	250	-
	1800	25.0	SAV1	280	-
	1800	25.0	SAV1	385	-

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