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The feeding ecology and trophic role of the northern pipefish, Syngnathus fuscus, in a lower Chesapeake Bay seagrass community

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THE FEEDING ECOLOGY AND TROPHIC ROLE OF THE NORTHERN PIPEFISH, *SYNGNATHUS FUSCUS*, IN A LOWER CHESAPEAKE BAY SEAGRASS COMMUNITY

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

Clifford H Ryer

1981

APPROVAL SHEET

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ABSTRACT

The purpose of this study is to examine the feeding ecology and trophic role/importance of the northern pipefish, Syngnathus fuscus, in a lower Chesapeake Bay seagrass community.

The study incorporates; 1) examination of stomach contents in conjunction with prey abundance data, inorder to arrive at conclusions concerning the food preferences of S. fuscus, 2) determination of daily feeding periodicities and stomach evacuation parameters, thus allowing for the determination of a daily ration for S. fuscus, 3) examination of size relationships between S. fuscus and it's major prey species, 4) estimation of pipefish densities at the study site, and 5) examination of the trophic importance of S. fuscus via estimation of the annual quantities of specific prey species consumed at the study site, and comparison of these values with estimated production values for the prey populations.

It is suggested, that while S. fuscus consumes only moderate portions of the annual production of it's prey species, it may serve to modulate the production of these prey species by feeding predominantly upon small individuals, thus effectively altering the age-class stucture of the prey population, and assumably the production charactoristics as well.

THE FEEDING ECOLOGY AND TROPHIC ROLE OF THE NORTHERN PIPEFISH, *SYNGNATHUS FUSCUS*, IN A LOWER CHESAPEAKE BAY SEAGRASS COMMUNITY

INTRODUCTION

In recent years numerous studies have been undertaken to examine the structural and functional ecology of seagrass ecosystems (Adams, 1976a, 1976b; Brook, 1975; Carr and Adams, 1973; Fenchel, 1977; Heck and Orth, 1980; Kikuchi, 1974; Marsh, 1973, 1976; Orth, 1973, 1976; Orth and Heck, 1980; Stoner, 1979).

Seagrasses provide a carbon source for a rich detrital pathway that furnishes energy to a host of invertebrate infaunal and epifaunal species (Fenchel, 1977; Klug, 1980). These organisms then serve as food for higher tropic levels, including commercially important species (Car and Adams, 1973; Adams, 1976; Stoner, 1979; Nilsson, 1969).

Aside from providing the basis for a dynamic trophic pathway, seagrass also provides a structurally complex habitat whose faunal assemblage may be entirely different from nearby unvegetated sites. Many juvenile fish species, as well as adults, seasonally occupy grassbeds, where they find refuge from predation as well as abundant food resources (Adams, 1976a, 1976b; Orth and Heck, 1980).

Of the many fish species inhabiting grassbeds along the Gulf coast and southeast coast of the United States, the pinfish, *Lagadon rhomboides*, is typically one of the most abundant, and is considered by many investigators (Adams, 1976a,b,c; Nelson, 1979; Stoner, 1979) to be the dominant predator upon motile epifauna, exerting extensive control over the distribution and abundance of this assemblage. However, pinfish are rare, or absent, from grassbeds north of the Cape Hatteras faunal divide. Orth and Heck (1980) also noted the relatively greater abundance of epifaunal amphipods and isopods from Chesapeake Bay grassbeds, when compared to more southerly grassbeds, and have speculated that the presence of Lagadon may account for depressed pericarid densities to the south.

This speculation implies that there is no ecological replacement of Lagadon in Chesapeake Bay grassbeds. Preliminary data indicated that the only fish species present from the Chesapeake Bay which may serve to replace the pinfish is the northern pipefish, *Syngnathus fuscus* (Ryer, unpublished data). *S. fuscus* has a continuous distribution from Nova Scotia to northern Florida, occurring in a variety of habitats (Herald, 1965). Mercer (1973), studying pipefishes in the lower Chesapeake Bay, found *S. fuscus* to feed primarily upon mysid shrimp, isopods, caprellid amphipods, and gammarid amphipods.

This study was undertaken to examine and define the interaction between *S. fuscus* and its prey species in a lower Chesapeake Bay seagrass ecosystem. Identification of these interactions should help in determining what role *S. fuscus* plays in controlling the abundance of prey species, as well as contrasting the predatory role of *S. fuscus* with that of *L. rhomboides* in southern grassbeds.

Description of Study Sites

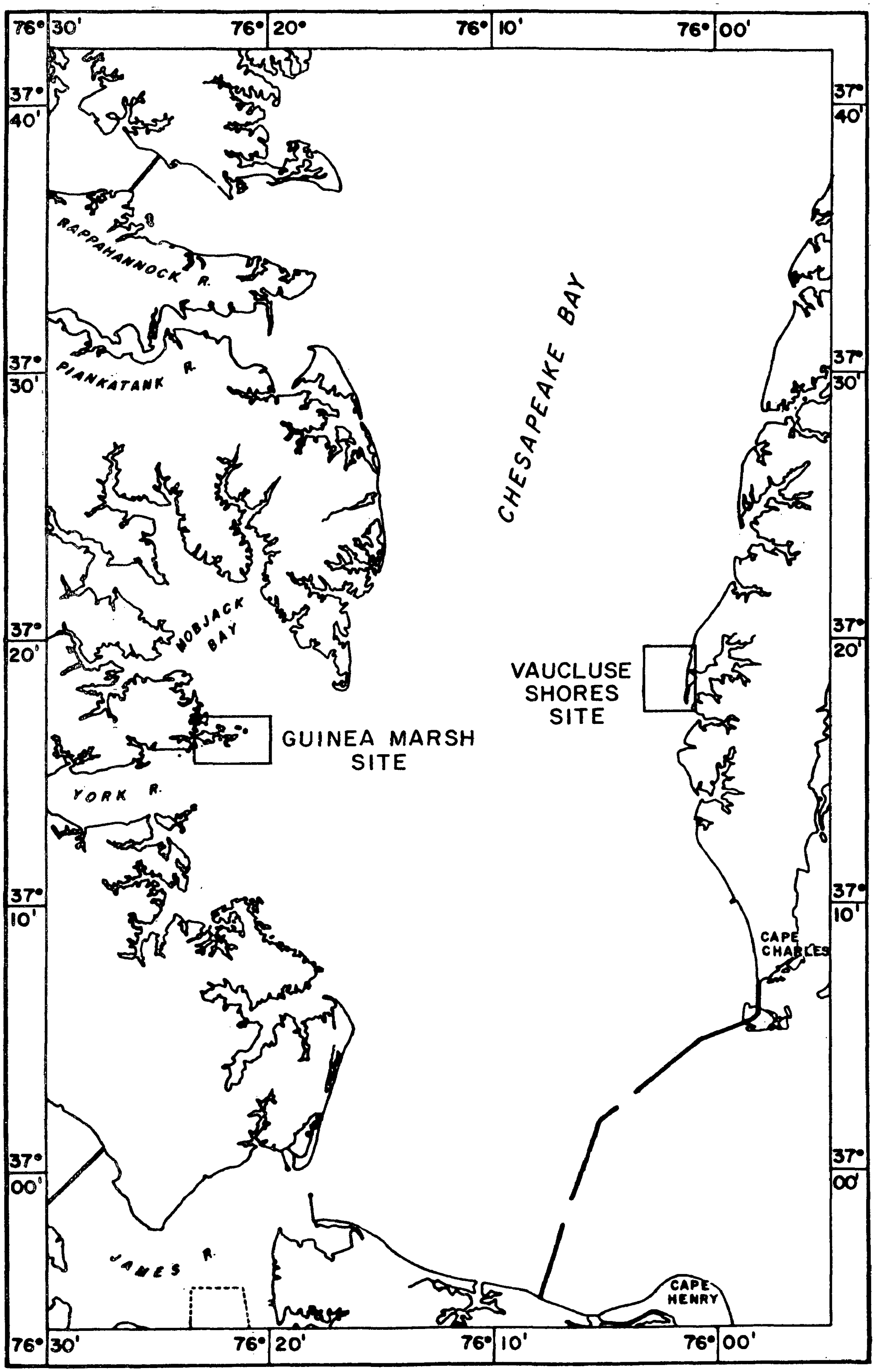
Two shoal areas in the lower Chesapeake Bay, both supporting extensive beds of submerged aquatic vegetation, served as collection sites for the different aspects of this study. The first site, identified as Vaucluse Shores, is located on the western side of the Delmarva Peninsula at the mouth of Hungars Creek (approximately 37°25'N latitude, 75°59'W longitude). There are approximately 2,105,000 m^2 of bottom covered by vegetation at this site with widgeon grass, Ruppia maritima, dominating the shallow areas (<0.3 m MLW), eelgrass, Zostera marina, dominates the deeper areas (>1.0 m MLW), with a mixture of the two species at intermediate depths. The Submerged Aquatic Vegetation (SAV) is bordered by the shoreline and a sandbar, located 500 to 700 m offshore.

The second site, only utilized for one segment of this study, was located at the mouth of the York River next to Guinea Marshes. This extensive shoal area is almost entirely vegetated by eelgrass. There are approximately 3,087,600 m^2 of bottom covered by Zostera marina at the site.

Both sites (Fig. 1) are nearly identical with regards to the faunal assemblage they support, both in terms of species and faunal abundance (Diaz, R. J. and Fredett, T. in preparation; Orth and Heck, 1980; Van Montfrans, Orth and Ryer, in preparation).

FIGURE 1.

Location Of Study Sites In The Lower Chesapeake Bay, Virginia.


76° 30'
76° 20'
76° 10'
76° 00'
37° 40'
37° 30'
37° 20'
37° 10'
37° 00'
RAPPAHANNOCK R.
PIANKATANK R.
CHESAPEAKE BAY
MOBJACK BAY
VAUCLUSE SHORES SITE
GUINEA MARSH SITE
YORK R.
CAPE CHARLES
JAMES R.
CAPE HENRY

METHODS AND MATERIALS

Collection of Fish for Abundance and Stomach Analysis

Fish were collected monthly from the Vaucluse Shores site, from May through November 1979, during daylight hours. May and June collections were conducted using a 4.9 meter otter trawl with 1.9 cm mesh wings and 0.6 cm mesh cod end liner. Fish for all subsequent collections were obtained using a venturi suction dredge apparatus in conjunction with a 0.98 m^2 fiberglass dropnet ring. Four to six replicate samples were taken on each sampling date using the suction dredge. Fish were preserved in 10% buffered formalin, later rinsed, and transferred to 70% ETOH prior to examination. Total length and wet weight were recorded for each individual.

Syngnathus fuscus possesses a relatively undifferentiated gastrointestional tract, and in order to avoid examination of highly digested and fragmentary food items, the first half of the gut tube length was arbitrarily defined as the stomach and examined under a dissecting microscope. *S. fuscus* typically ingests prey as discrete, intact particles, and as such, food items were generally identifiable to the species level. In cases where species level identification was not possible, items were classified into higher taxonomic categories. Fragmented and/or highly digested animals remains were saved and identified to the taxonomic group from which they were derived. All prey items were enumerated and later sorted into larger taxonomic groups for dry weight determinations.

Selectivity

Selectivity indices were calculated for major prey species using stomach analysis data from this study and prey abundance data taken from concurrent studies on the macroinvertebrates species at the Vaucluse Shore site (Diaz, R. J. and Fredette, T., in preparation; Van Montfrans, Orth and Ryer, in preparation).

A number of selectivity indices have been reported in the literature (Ivlev, 1961; Allen, 1941; Hess and Schwartz, 1940; Jacobs, 1974; Gabriel, 1978). The natural log of the modified forage ratio, L (Gabriel, 1978), was chosen because of its ease of calculation and the availability of a standard error of L. The index is calculated as:

$$L = \ln \frac{p_1 q_2}{p_2 q_1}$$

where p_1 = fraction of the diet comprised by a given prey species

q_1 = fraction of the diet comprised by all other prey species

p_2 = fraction of food in the environment comprised by the given prey species.

q_2 = fraction of food in the environment comprised by all other prey species

L is symmetrically distributed about a mean of 0 and ranges from 0 to $+\infty$ in the case of positive selection, and from 0 to $-\infty$ in the case of negative selection. p_1q_2/p_2q_1 is, coincidently, the odds ratio proposed by Fleiss (1973), for which a standard error is available. Therefore a standard error of L can be calculated as:

$$S.E.(L) = \frac{1}{n_1p_1q_1} + \frac{1}{n_2p_2q_2}$$

where n_1 = the total number of prey in the diet sample

n_2 = the total number of food organisms in the environmental sample

and p_1, q_1, p_2, and q_2 are as previously defined.

The significance of L can be tested by comparison of Z values with values found in a table of areas of the normal curve (z distribution), where:

$$Z = \frac{L(\text{observed}) - L(\text{expected})}{S.E.(L)}$$

In typical cases, L (expected) will always be equal to zero.

Prey Size Measurements

Meristics of prey taken from fish stomachs were performed upon four prey species: *Gammarus mucronatus*, *Caprella penantis*, *Erichsonella attenuata*, and *Idotea balthica*. Measurements were made for these species only during months when they were present in the gut in large enough numbers to allow for statistical treatment. Measurements were taken so as to allow results to be comparable with those of the Secondary Production work being conducted at Virginia Institute of Marine Science (Diaz, R. J. and Fredette, T., in preparation). For gammarid amphipods, the length from the base of the second antennae to the rear of the third body segment was recorded. For Caprellid amphipods, the length from the base of the second antennae to the rear of the second body segment was used. For Isopods, total length was measured. These data were analyzed by regressing fish size vs. prey size using a modified least squares model allowing for multiple y observations with each value of x.

Feeding Periodicity

Data on the feeding periodicity of *S. fuscus* were collected at the Guinea Marsh site on June 14, 1979, by sampling fish at 3 hour intervals throughout a 24 hour period. Fish were collected using a 4.9 m otter trawl with 1.9 cm mesh wings and 0.6 cm mesh cod end. For each sample, six fish were preserved in 10% buffered formalin and returned to the lab for processing. After measuring total length, the gut was removed and the contents deposited upon tared aluminum sheets for dry weight determination. Dry weight of both fish and stomach contents were determined by drying to constant weight at 58°C.

A second periodicity study was conducted at the Vaucluse Shores site on August 21, 1979. Only seven samples were taken during the 24 hour period (as compared to eight for Guinea Marsh, 6/14/79) at slightly less regular intervals.

Evacuation Rate Determinations

Evacuation rates were determined using the serial slaughter method of Windell (1967). Fish were collected at the Guinea Marsh site using a 4.9 m otter trawl on September 1, 1980, at a temperature of 24°C. The fish were brought to the laboratory where they were divided into three groups. Temperatures were changed at approximately 1°C per day until the final acclimation temperatures of 15°, 23°, and 27°C were reached. Fish were maintained for two to three weeks at the acclimation temperature and were fed daily upon gammaridian amphipods, primarily *Gammarus mucronatus*, prior to experimentation.

Fish were starved for three days prior to experiments to allow complete evacuation of the gut. To determine evacuation rates, each group was allowed to feed to satiation for one hour upon gammaridean amphipods, after which the fish were isolated from further contact with food. Groups of seven fish were then removed and sacrificed at 2 to 4 hour intervals, and both fish and gut contents prepared for dry weight determinations. Serial slaughter was continued at each temperature until visual observation of the guts indicated that they were completely evacuated. All fish were between 150 mm and 200 mm in total length and, as such, constituted only mature adult individuals.

For each temperature, results were examined as the geometric mean for seven values of the log (% body weight in GI tract +1). At each temperature, values were then least square regressed against time to obtain the evacuation rate B. Evacuation rates for each temperature were then least square regressed against temperature to obtain a model for temperature dependence of evacuation rate.

RESULTS

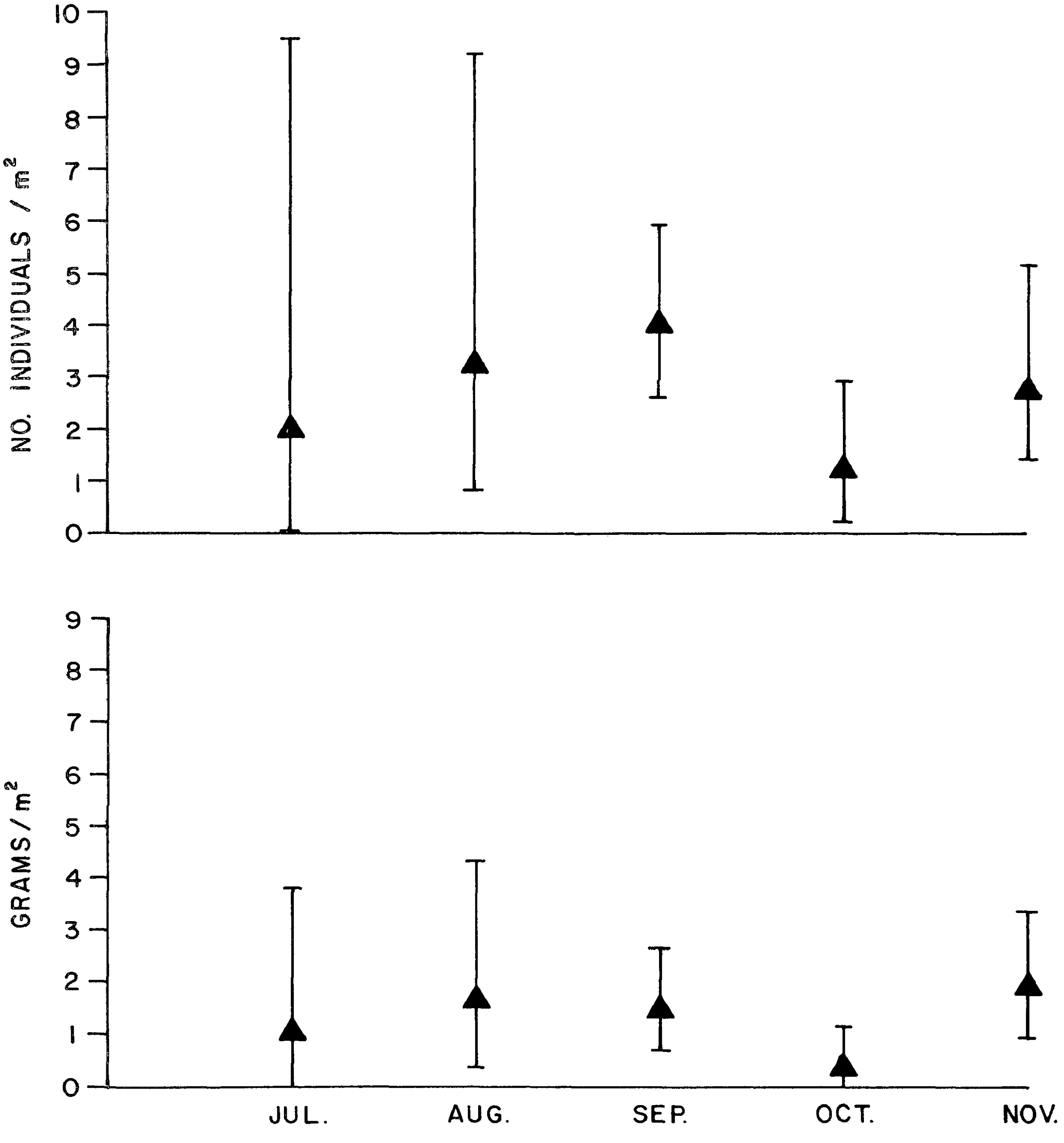
Pipefish Abundance

Trawl samples taken in the deeper (1.0 to 2.0 m) Zostera dominated portion of the study indicated that Syngnathus fuscus was present in the Vaucluse Shores grassbed from April through November. However, due to the filiform body morphology of S. fuscus, it was felt that trawl samples would severely underestimate population densities of S. fuscus. On several occasions pipefish were observed wriggling out of the cod mesh end of the trawl as it was hauled to the boat. This was particularly true for individuals less than 100 mm in total length.

Although covering less area, suction dredge samples are believed to provide a more reliable estimate of pipefish densities, due to their more quantitative nature. S. fuscus was first observed in samples collected from the mixed area in July (Fig. 2), and remained relatively constant in both no. of individuals/m^2 and grams wet weight/m^2 from July through November. S. fuscus was absent from December collections. The observed densities of S. fuscus during the period of July through November were not significantly different (ANOVA, oneway $p < 0.05$), and mean monthly density of 2.57 ind/m^2 and 1.260 grams wet wt/m^2 was calculated for the study area during this period.

FIGURE 2.

Density of Syngnathus Fuscus, Geometric Means and 95% Confidence Intervals


10
9
8
7
6
5
4
3
2
1
0
NO. INDIVIDUALS / m²
9
8
7
6
5
4
3
2
1
0
GRAMS / m²
JUL.
AUG.
SEP.
OCT.
NOV.

Feeding

A total of 136 guts were examined to determine the food habits of *S. fuscus*. Of these, only three fish possessed empty guts. Monthly information on the diet of *S. fuscus* in terms of raw numbers, % composition, % frequency of occurrence, and % dry weight are presented in Tables 1, 2, 3 and 4, respectively. For convenience these values have been integrated into a single index value using a modification of the Pinkas et al. (1971) Index of Relative Importance (IRI). The IRI values were calculated as:

$$IRI = (\%N + \%wt.)\ \%F)/200$$

where

%N = percent composition of a prey group in the gut

%wt. = percentage by dry weight of a prey group in the gut, and

%F = Frequency of Occurrence of the prey group among guts.

20,000 is the maximum value possible for (%N + %wt.) %F. Therefore, division by 200 normalizes the IRI to a scale of 0-100. IRI values are presented in Table 5.

During May, fish fed primarily upon *Gammarus mucronatus* and *Caprella penantis*, together comprising over 89% of the total prey weight consumed and yielding IRI's of 64.93 and 18.10, respectively. In June *G. mucronatus* and *C. penantis* continued to dominate in terms of weight composition (63.7%), but fell in IRI ranking to 8.54 and 4.45, respectively. This was the result of a dramatic increase in the numbers of calanoid copepods consumed by *S. fuscus*, comprising only

Table 1. Diet of *Syngnathus fuscus*, in numbers of individual of encountered taxa, by month. *n = number of* stomachs sampled.

	May n=18	Jun n=23	Jul n=15	Aug n=25	Sep n=24	Oct n=9	Nov n=22	Total n=136
Calanoid Copepods	2	461	3204	3109	240	21	87	7124
Gammarus mucronatus	367	32	1	0	1	0	0	401
Microprotopus raneyi	12	2	2	3	0	0	0	19
Ampithoe longimana	10	13	0	2	7	4	0	36
Cymadusa compta	0	0	1	0	1	0	1	3
Ampelisca sp.	0	0	0	10	0	0	0	10
Gammaridae	52	52	1	35	84	41	8	273
Corophiidae	0	0	0	0	0	1	0	1
Caprella penantis	133	38	0	0	0	0	0	171
Paracaprella tenuis	1	9	0	4	8	6	0	28
Erichsonella attenuata	0	1	1	31	84	18	7	142
Idotea balthica	3	18	11	0	4	1	1	38
Edotea triloba	0	0	1	12	6	2	0	21
Paracerceis caudata	0	0	0	1	1	2	0	4
Mysid shrimp	0	1	0	1	0	0	26	28
Balanus improvisus	7	0	0	0	0	0	0	7
Oxyruostylis smithi	0	0	0	0	1	0	0	1
Nereis succinea	0	2	1	0	0	0	0	3
Crepidula convexa	0	0	0	0	0	1	0	1
Harpacticoid Copepods	0	0	0	0	55	1	0	56
Foraminifera	0	0	0	14	19	2	0	35
Ostracods	10	4	0	0	53	0	0	67
Totals	597	633	3223	3222	564	100	130	8469

Table 2. Diet of *Syngnathus fuscus*, % representation of encountered taxa, by month. n = number of stomachs sampled.

	May n=18	Jun n=23	Jul n=15	Aug n=25	Sep n=24	Oct n=9	Nov n=22	Total 136
Calanoid Copepods	0.34	72.83	99.41	96.49	42.55	21.0	66.92	84.12
Gammarus mucronatus	61.47	5.06	0.03	0	0.18	0	0	4.73
Microprotopus raneyi	2.01	0.32	0.06	0.09	0	0	0	0.22
Ampithoe longimana	1.68	2.05	0	0.06	1.24	4.0	0	0.43
Cymadusa compta	0	0	0.03	0	0.18	0	0.77	0.04
Ampelisca sp.	0	0	0	0.31	0	0	0	0.12
Gammaridae	8.71	8.21	0.03	1.09	14.89	41.0	6.15	3.22
Corophiidae	0	0	0	0	0	1.0	0	0.01
Caprella penantis	22.28	6.00	0	0	0	0	0	2.02
Paracaprella tenuis	0.07	1.42	0	0.12	1.42	6.0	0	0.33
Erichsonella attenuata	0	0.16	0.03	0.96	14.89	18.0	5.38	1.68
Idotea balthica	.50	2.84	0.34	0	0.71	1.0	0.77	0.45
Edotea triloba	0	0	0.03	0.37	1.06	2.0	0	0.25
Paracerceis caudata	0	0	0	0.03	0.18	2.0	0	0.05
Mysid shrimp	0	0.16	0	0.03	0	0	20.00	0.33
Balanus improvisus	1.17	0	0	0	0	0	0	0.08
Oxyruostylis smithi	0	0	0	0	0.18	0	0	0.01
Nereis succinea	0	0.32	0.03	0	0	0	0	0.04
Crepidula convexa	0	0	0	0	0	1.0	0	0.01
Harpacticoid Copepods	0	0	0	0	9.75	1.0	0	0.66
Foraminifera	0	0	0	0.43	3.37	2.0	0	0.41
Ostracods	1.68	0.63	0	0	9.40	0	0	0.79

Table 3. Diet of *Syngnathus fuscus*, in % frequency of occurrence of encountered taxa among guts, by month.

	May n=18	Jun n=23	Jul n=15	Aug n=25	Sep n=24	Oct n=9	Nov n=22
Calanoid Copepods	11.11	56.52	93.33	68.00	75.00	55.56	36.36
Gammarus mucronatus	100.00	30.43	6.67	0	4.17	0	0
Microprotopus raneyi	22.22	8.70	13.13	4.00	0	0	0
Ampithoe longimana	16.67	17.39	0	8.00	20.83	22.22	0
Cymadusa compta	0	0	13.33	0	4.17	0	4.55
Ampelisca sp.	0	0	0	8.00	0	0	0
Gammaridae	38.89	43.48	6.67	24.00	37.50	66.67	27.27
Corophiidae	0	0	0	0	0	11.11	0
Caprella penantis	83.33	47.83	0	0	0	0	0
Paracaprella tenuis	5.56	21.74	0	8.00	20.83	33.33	0
Erichsonella attenuata	0	4.35	6.67	32.00	62.50	55.56	4.55
Idotea balthica	11.11	34.78	13.33	0	8.33	11.11	4.55
Edotea triloba	0	0	6.67	12.00	20.83	11.11	0
Paracerceis caudata	0	0	0	4.00	4.17	22.22	0
Mysid shrimp	0	4.35	0	4.00	0	0	50.00
Balanus improvisus	22.22	0	0	0	0	0	0
Oxyruostylis smithi	0	0	0	0	4.17	0	0
Nereis succinea	0	4.35	0	0	0	0	0
Crepidula convexa	0	0	0	0	0	11.11	0
Harpacticoid Copepods	0	0	0	0	12.50	11.11	0
Foraminifera	0	0	0	16.00	16.67	22.22	0
Ostracods	38.89	4.35	0	0	20.83	0	0

Table 4. Diet of *Syngnathus fuscus*, in % dry weight representation of major taxa, by month.

	May n=18	Jun n=23	Jul n=15	Aug n=25	Sep n=24	Oct n=9	Nov n=22
Calanoid Copepods	0.03	5.11	87.33	58.34	9.02	1.68	4.23
Gammarus mucronatus	68.38	51.09	1.89	0	-	0	0
Microprotopus raneyi	0.93	0.60	0.13	-	0	0	0
Ampithoe longimana	-	14.40	0	0.93	-	-	0
Caprella penantis	21.16	12.61	0	0	0	0	0
Paracaprella tenuis	-	1.96	0	1.17	1.10	0.42	0
Erichsonella attenuata	0	1.96	0.54	23.34	49.72	61.76	51.64
Idotea balthica	0.10	6.58	7.68	0	3.31	-	0.47
Edotea triloba	0	0	0.94	4.55	0.74	2.52	0
Mysid shrimp	0	0.27	0	1.28	0	0	39.67
Amphipods	5.13	1.47	1.48	3.15	13.63	11.34	3.99
Polychaete	0	3.91	-	0	0	0	0
Other Prey	4.20	-	0	7.24	22.47	22.27	0

\- indicates presence of prey taxa, however dry weights were not determined due to small quantity of animal material.

Table 5. Diet of *Syngnathus fusus*, Index of relative Importance (IRI), by month.

	May n=18	Jun n=23	Jul n=15	Aug n=25	Sep n=24	Oct n=9	Nov n=22
Calanoid Copepods	0.02	22.03	87.13	52.35	19.34	6.30	12.94
Gammarus mucronatus	64.93	8.54	0.06	0	0	0	0
Microprotopus raneyi	0.33	0.04	0.01	0	0	0	0
Ampithoe longimana	0	1.43	0	0	0	0	0
Caprilla penantis	18.10	4.45	0	0	0	0	0
Paracaprella tenuis	0	0.37	0	0.05	0.26	1.07	0
Erichsonella attenuata	0	0.05	0.02	3.93	20.19	22.16	1.30
Idotea balthica	0.03	1.64	0.53	0	0.17	0	0.03
Edotea triloba	0	0	0.03	0.30	0.19	0.25	0
Mysid shrimp	0	0.01	0	0.03	0	0	14.92
Amphipods	3.92	2.10	0.10	0.49	8.78	22.29	1.74
Polychaete	0	0.53	0	0	0	0	0
Other Prey	1.76	0	0	0.78	10.39	8.13	0

5.11% of the dry wt., but which received an IRI value of 22.03 due to their large %N and %F. *Ampithoe longimana* and *Idotea balthica* also occurred during June accounting for 21% of the dry weight, but also received low IRI's (1.43 and 1.64, respectively) due to the large numerical dominance of calanoid copepods.

By July, *S. fuscus* had switched to feeding almost exclusively upon calanoid copepods comprising 87.33% of the dry wt. and 99.41% number of prey. This resulted in the highest IRI (87.13) observed for any prey group during this study. This pattern continued through August, with calanoid copepods receiving an IRI of 52.64. *Erichsonella attenuata* first appeared in pipefish guts during July, accounting for 23.34% of the dry weight, but having an IRI of only 3.98 due to its low numerical dominance. By September, calanoid copepod had decreased in both % numbers and % weight, resulting in an IRI of 9.02. Meanwhile, *E. attenuata* accounted for 49.72% of the dry wt. and received an IRI of 20.19. During September, amphipoda (generally juvenile Gammaridae unidentifiable to species) were taken in relatively high numbers (14.89%) and totaled 13.63% dry wt. resulting in an IRI of 8.78.

During October, *E. attenuata* continued as the dominant prey item with an IRI of 22.16 and accounting for 61.76% of the dry weight consumed. Juvenile amphipods received an IRI of 22.29 and accounted for 11.34% dry weight.

In November, mysid shrimp (primarily *Neomysis americana*) appeared in large number in the guts comprising 20.00% and 39.67% of the

% numbers and % dry weights, respectively, resulting in an IRI of 14.92. *E. attenuata* continued to dominate guts in terms of % dry weight (51.64) but declined in % numbers, causing a lowering of the IRI to 1.30. This was the result of the reappearance of large numbers of calanoid copepods (66.92%). While calanoid copepods contributed only 4.23% of the dry weight total because of their large numbers, they received an IRI of 12.94.

A generalized overview of seasonal importance for combined prey categories is presented in Fig. 3.

Prey Abundance

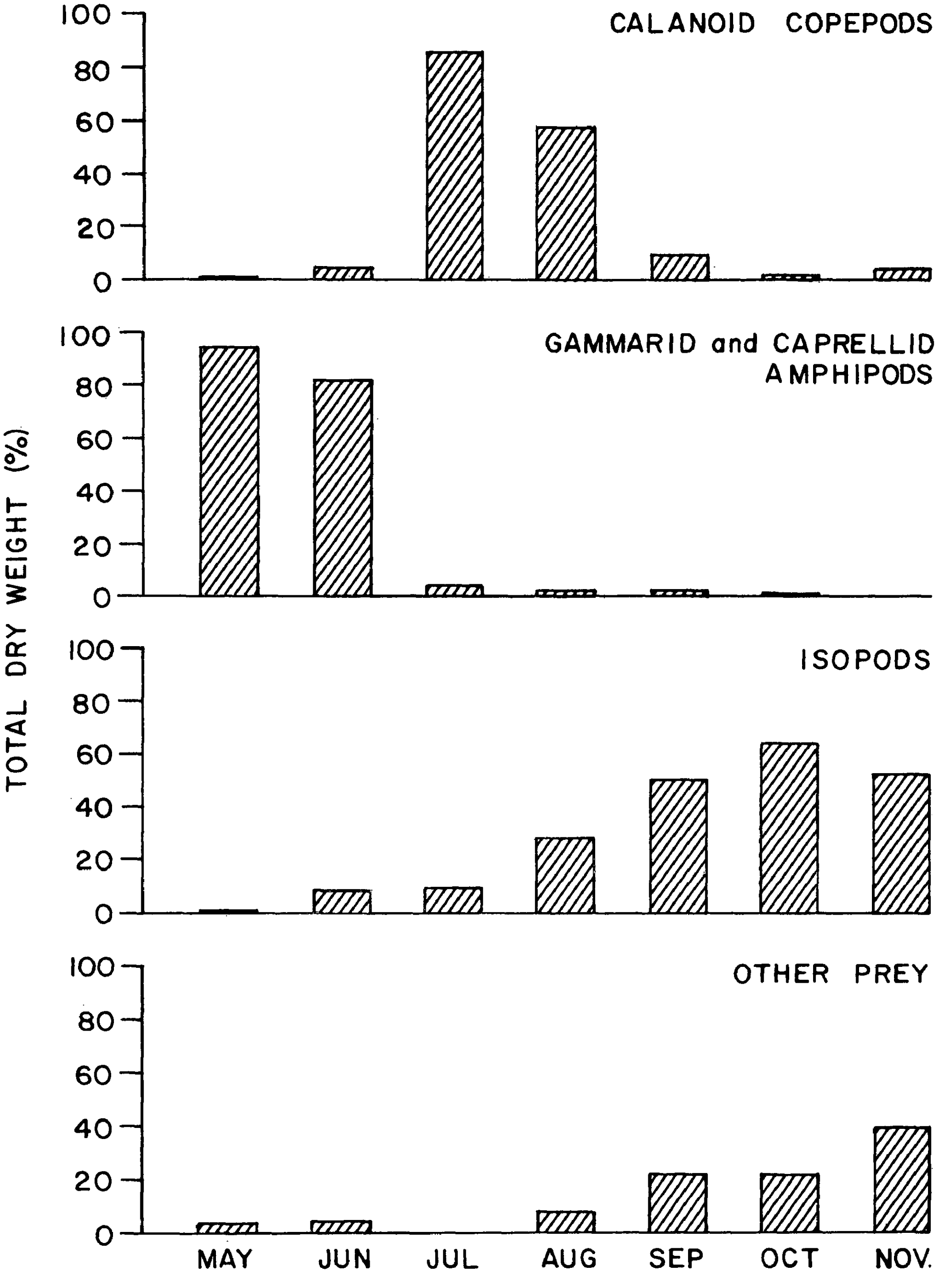
Complete monthly abundance data were available for only five prey groups: calanoid copepods (Myers et al., in preparation), *G. mucronatus*, *E. attenuata*, *I. balthica*, and *E. triloba* (Diaz, R. J. and Fredette, T., in preparation). Abundance data for the majority of other prey categories was available from June, September, and November (Van Montfrans, Orth and Ryer, in preparation). These data are presented in Table 6. Copepod densities were relatively low in May and June (413/m^3 and 564/m^3), but increased dramatically in July to a peak density of 26,992/m^3. During August, September, and October, densities remained relatively stable (10008, 5787, and 10610/m^3) before decreasing to a low of 116/m^3 in November.

G. mucronatus showed a pattern of spring peak abundance, with 1227/m^2 during May. By June, densities had decreased to 404/m^2, with relatively low densities from July on through November. *E. attenuata*

FIGURE 3.

Consumption of Major Prey Catagories

by Month in % Dry Weight



TOTAL DRY WEIGHT (%)
CALANOID COPEPODS
GAMMARID and CAPRELLID AMPHIPODS
ISOPODS
OTHER PREY
0
20
40
60
80
100
MAY
JUN
JUL
AUG
SEP
OCT
NOV.

Table 6. Prey abundance, in individuals per m^2, by month.

	May	Jun	Jul	Aug	Sep	Oct	Nov
*Calanoid Copepods	413	564	26992	10008	5787	10610	116
Gammarus mucronatus	1227	404	123	96	81	50	171
Microprotopus raneyi	---	818	---	---	0	---	0
Ampithoe longimana	---	30	---	---	20	---	0
Cymadusa compta	---	104	---	---	787	---	994
Ampelisca abdita	---	97	---	---	82	---	497
Corophiidae	---	0	---	---	0	---	82
Caprella penantis	---	151	---	---	0	---	31
Paracaprella tenuis	---	386	---	---	60	---	435
Erichsonella attenuata	790	1803	1246	1992	1600	2015	938
Idotea balthica	11	192	382	115	48	92	134
Edotea triloba	180	532	712	1684	712	1800	1754
Paracerceis caudata	---	0	---	---	---	---	0
Nereis succinea	---	3132	---	---	2368	---	4865
Balanus improvisus	---	50109	---	---	286	---	540
Oxyruostylis smithi	---	16	---	---	0	---	0
Crepidula convexa	---	410	---	---	18194	---	47100

* in individuals per m^3

showed a pattern of high abundance through the summer and early fall, with peak abundance occurring during the month of October. Both I. balthica and E. triloba showed variable abundance through the period of this study, with no clear cut patterns.

Although other species were seasonally abundant as eelgrass epifauna, e.g., Nereis succinea, Balanus improvisus, and Crepidula vonvexa, they were not preferred prey items, as they were not frequently encountered in S. fuscus guts.

Selectivity Indices

The natural log of the forage ratio was calculated for all major prey species taken by S. fuscus during June, September and November, as complete prey abundance data were available for these months only. Results and their statistical significance are presented in Table 7. In several instances, a prey species which was routinely taken by S. fuscus from other collections was absent from guts during a particular month. Because of the nature of the calculations which derive the L values, these species, which were known to be preyed upon by S. fuscus, would have received L values of zero, indicating no selection. Obviously these species were selected against by S. fuscus, and in order to have this fact reflected by the L values, one individual of each such species was arbitrarily defined as having been taken by the fish during these months.

Table 7. Natural logs of Jacobs forage ratio (L) and Standard Errors (S.E.) for major prey species taken by _S. fuscus_.

	June		September		November	
	L	S.E.(L)	L	S.E.(L)	L	S.E.(L)
Calanoid Copepods	+0.4651**	0.1134	-0.0680	0.1161	+1.5612**	0.3219
Gammarus mucronatus	-0.3504*	0.1892	-1.1304	1.0076	-1.1815	1.0081
Microprotopus raneyi	-3.6800**	0.7094	0	0	0	0
Ampithoe longimana	+1.3048**	0.3350	+2.1903**	0.4426	0	0
Cymadusa compta	-2.4672*	1.0058	-3.3234**	1.0021	-2.7577**	1.0057
Caprella penantis	+0.7407**	0.1871	0	0	0	0
Paracaprella tenuis	-1.539**	0.3401	+1.2267**	0.3804	-2.0598*	1.0063
Erichsonella attenuata	-4.8920**	1.0013	+0.2309*	0.1280	-0.8306*	0.3937
Idotea balthica	-0.2017	0.2505	+0.7669	0.5233	-0.9452	1.0089
Edotea triloba	-4.0076**	1.0019	-1.4547**	0.4136	-3.1192**	1.0055

* $p < 0.05$
** $p < 0.01$

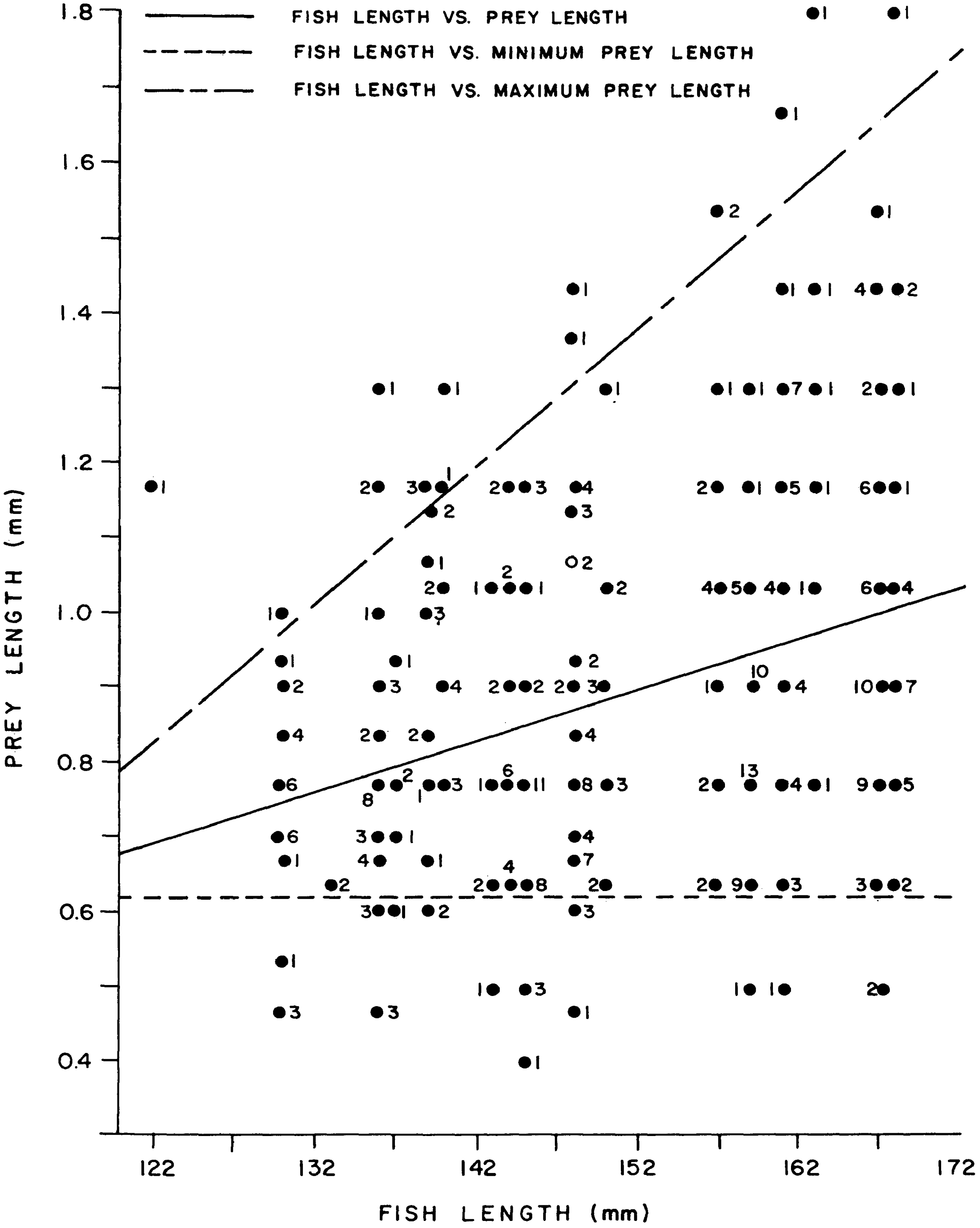
Predator-Prey Size Relationships

Prey length measurements were recorded for C. penantis, E. attanuata, G. mucronatus and I. balthica for months when these prey items were numerous enough in guts to allow for statistical analysis. Prey lengths were recorded for G. mucronatus and C. penantis, from May samples, G. mucronatus, C. penantis and I. balthic from June and E. attenuata from September. For each species-month the following combination of Least-Squares Regression analysis was performed: fish length vs. prey length, fish length vs. minimum prey length (the smallest prey item taken from each stomach), and fish length vs. maximum prey length (the largest prey item from each stomach). These regressions are presented in Figs. 4, 6, 8, 10, 12, 13 and in summary Table 8.

Regression statistics for G. mucranous (5/79) indicated a highly significant positive relationship between fish length and prey length (R-correlation coefficient) and a resultant line with a slope significantly different from zero (T-test, see Table 8 for summary statistics). The minimum prey length regression line showed no significant correlation and had a slope not significantly different from zero. For this reason the minimum regression line has been plotted as a 0-slope line in Fig. 4. Regression of maximum prey lengths resulted in a line with significant correlation as well as significant slope. These results indicate a situation where larger fish, while able to consume larger prey items, also continue to feed

FIGURE 4.

Regression Lines for Size Comparisons Between *Gammarus Mucronatus* and *Syngnathus Fuscus*.



FISH LENGTH VS. PREY LENGTH
FISH LENGTH VS. MINIMUM PREY LENGTH
FISH LENGTH VS. MAXIMUM PREY LENGTH
PREY LENGTH (mm)
FISH LENGTH (mm)
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
122
132
142
152
162
172
1 1
1
2 1
1 1 1 4 2
1
1 1 1 1 1 1 7 1 2 1
1 2 3 1 2 3 4 2 1 5 1 6 1
2 3
1 O2
2 1 2 1 2 4 5 4 1 6 4
1 1 3
1 1 2
2 3 4 2 2 2 3 1 10 4 10 7
4 2 2 4
6 8 2 1 3 6 1 11 8 3 2 13 4 1 9 5
6 3 1 4
1 4 1 4 7
2 2 8 2 2 9 3 3 2
3 1 2 3
1
1 3 1 1 2
3 3 1
1

Table 8. Summary statistics for regressions of predator-prey size relationships.

	Fish Length vs.	# of fish	Mean Prey Length	Slope	Intercept	R^2	R Correlation Coefficient	Sign. of R	Probability of Greater (+)
Gammarus	Prey length	348	0.884	0.006	-0.087	0.102	0.319	0.01	0.0001
mucronatus	Min. Prey length	18	0.610	-0.004	1.153	0.082	0.286	no sign.	0.2504
5/79	Max. Prey length	18	1.293	0.018	-1.399	0.644	0.802	0.01	0.0001
Gammarus	Prey length	32	1.173	0.008	0.028	0.634	0.796	0.01	0.0001
mucronatus	Min. Prey length	7	0.885	0.001	0.728	0.064	0.253	no sig.	0.5853
6/79	Max. Prey length	7	1.272	0.009	0.238	0.854	0.924	0.01	0.0029
Caprella	Prey length	133	1.818	0.017	-0.630	0.123	0.351	0.01	0.0001
penantis	Min. Prey length	14	1.456	0.026	-2.301	0.272	0.522	0.05	0.0556
5/79	Max. Prey length	14	2.543	0.013	0.564	0.160	0.400	no sig.	0.1564
Caprella	Prey length	38	1.816	0.009	0.683	0.239	0.489	0.01	0.0018
penantis	Min. Prey length	11	1.360	-0.002	1.540	0.020	0.141	no sig.	0.6779
6/79	Max. Prey length	11	2.087	0.023	-7.465	0.764	0.874	0.01	0.0004
Erichsonella	Prey length	52	4.195	0.068	-5.130	0.298	0.546	0.01	0.0001
attenuata	Min. Prey length	7	2.230	0.003	1.765	0.029	0.170	no sig.	0.7127
9/79	Max. Prey length	7	5.676	0.097	-7.465	0.636	0.797	0.01	0.0316
Idotea	Prey length	17	2.305	0.013	0.612	0.790	0.889	0.01	0.0001
balthica	Min. Prey length	8	2.225	0.010	0.861	0.795	0.892	0.01	0.0029
6/79	Max. Prey length	8	2.334	0.011	0.851	0.725	0.851	0.01	0.0073

upon smaller prey, resulting in an increase in prey size range with increased fish size.

Figure 5 compares the size frequency distribution of G. mucronatus taken from field samples with the size frequency distribution from S. fuscus guts. The field population of G. mucronatus is dominated by smaller individuals, less than 2 mm, comprising over 77% of the total population. However, significant numbers of larger individuals (>2.0 mm) are present. In contrast, G. mucronatus taken from S. fuscus guts include no individuals greater than 2 mm, and only 3% of the population is greater than 1.5 mm. Approximately 66% of the gut population fell in the 0.5-1.0 mm size range as compared to only 36% for the field population. Comparison of these two size frequency distributions using G-test (Sokal and Rohlf, 1969) conclude that the distributions are significantly different ($p<0.005$). Therefore, during May, S. fuscus was preying upon the smaller size classes of G. mucronatus present in the sample areas.

Results of regression analysis for G. mucronatus during June (Fig. 6) were essentially the same as those for May (Fig. 4). However, examination of size frequency distribution for field and gut population (Fig. 7) showed a field population consisting almost exclusively of individuals less than 2.0 mm. Consequently, the gut population resembled the field population rather closely, and the G-test shows no significant difference between the populations ($p<0.05$).

FIGURE 5.

Comparison of Size Distributions for *Gammarus Mucronatus* (5/79) from Field and Gut Collections.

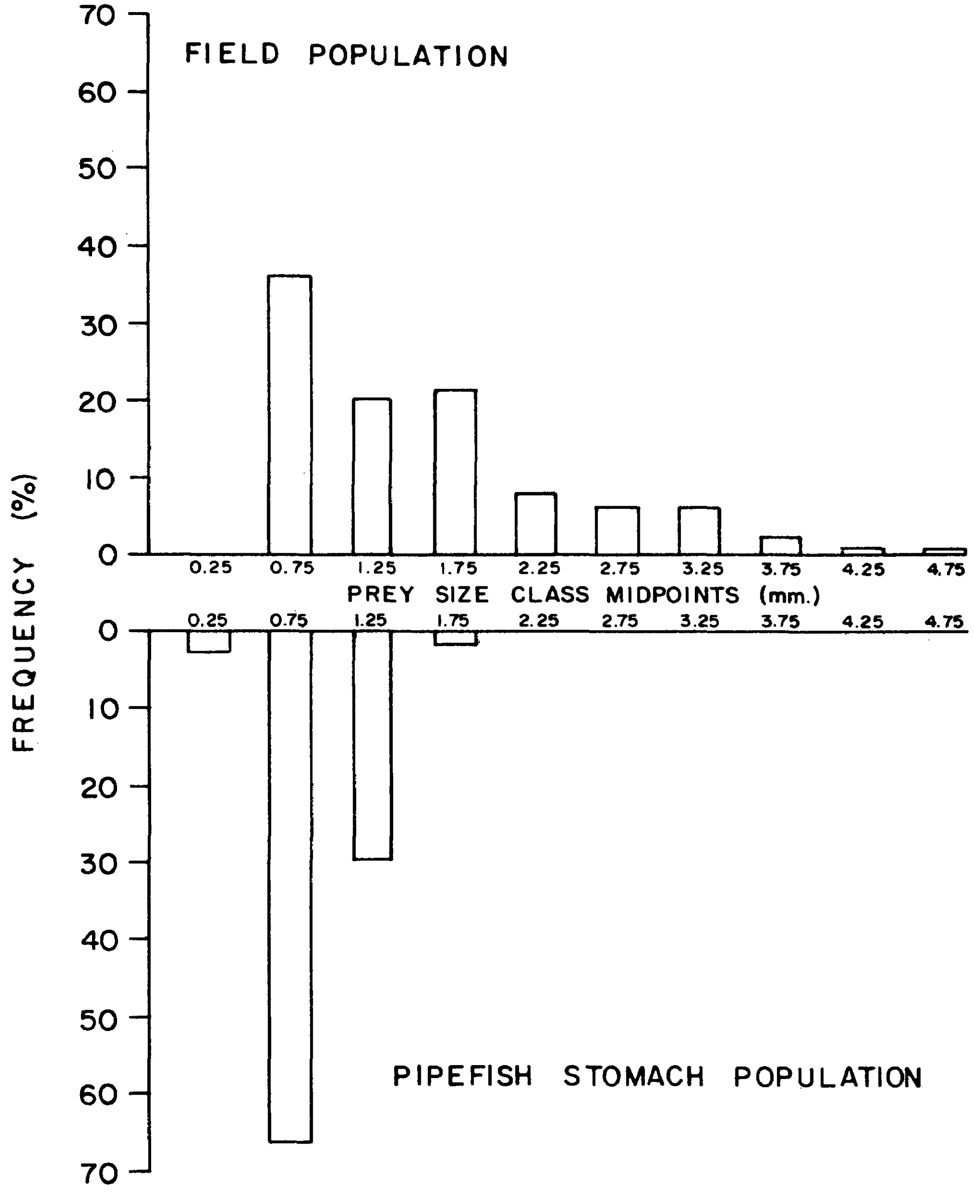

FIELD POPULATION
PIPEFISH STOMACH POPULATION
FREQUENCY (%)
PREY SIZE CLASS MIDPOINTS (mm.)
0.25
0.75
1.25
1.75
2.25
2.75
3.25
3.75
4.25
4.75
70
60
50
40
30
20
10
0

FIGURE 6.

Regression Lines for Size Comparisons Between Gammarus Mucronatus and Syngnathus Fuscus (6/79).

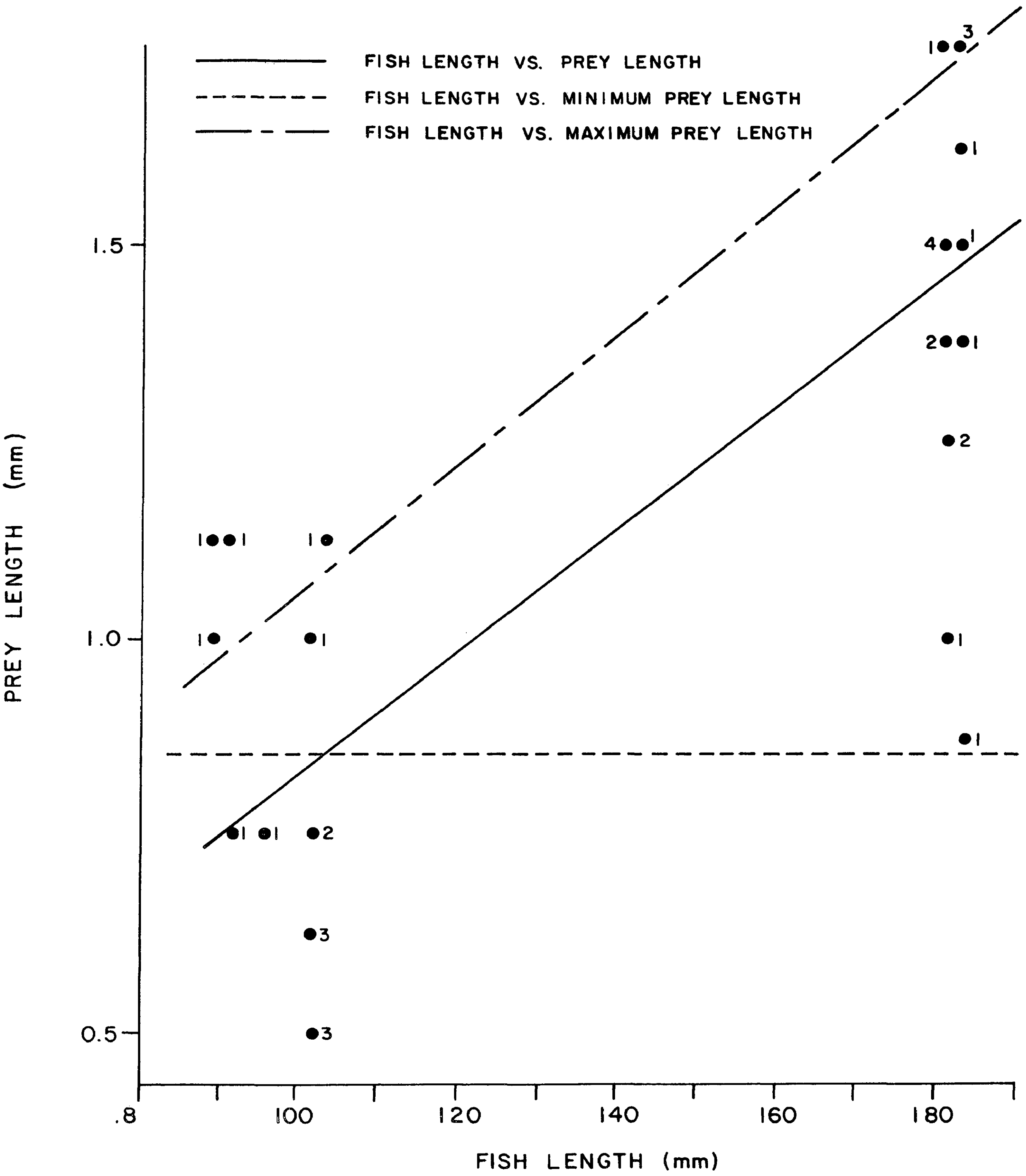
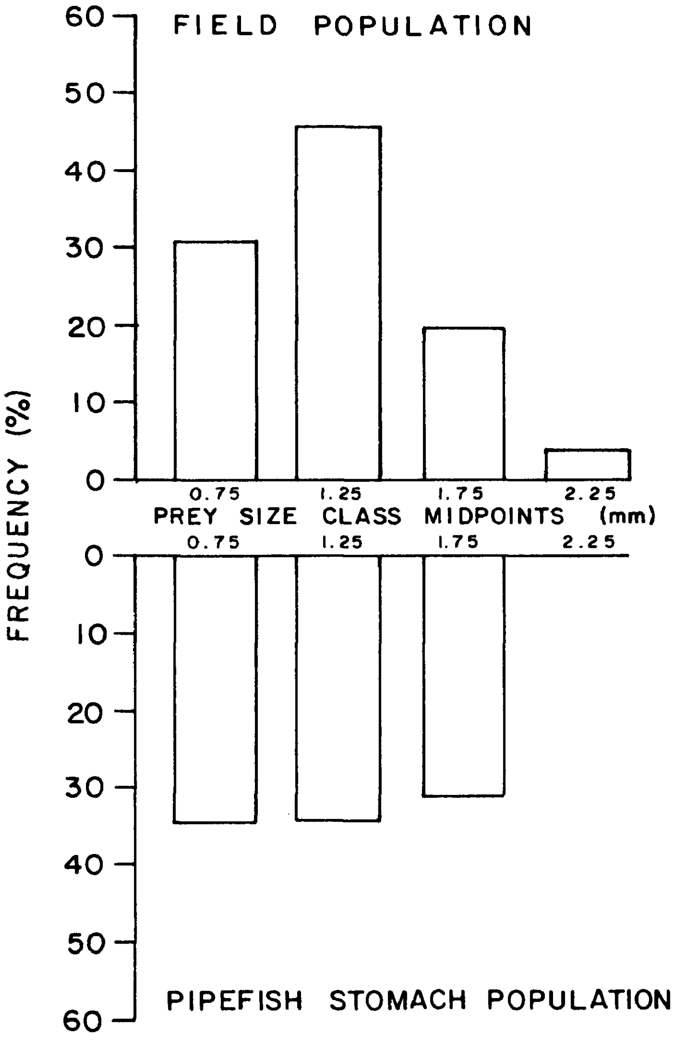

FISH LENGTH VS. PREY LENGTH
FISH LENGTH VS. MINIMUM PREY LENGTH
FISH LENGTH VS. MAXIMUM PREY LENGTH
PREY LENGTH (mm)
1.5
1.0
0.5
.8
100
120
140
160
180
FISH LENGTH (mm)
1
3
1
4
1
2
1
2
1
1
1
1
1
1
1
1
1
1
2
3
3

FIGURE 7.

Comparison of Size Distributions for *Gammarus Mucronatus* (6/79) from Field and Gut Collections.


FIELD POPULATION
FREQUENCY (%)
60
50
40
30
20
10
0
0.75
1.25
1.75
2.25
PREY SIZE CLASS MIDPOINTS (mm)
0
0.75
1.25
1.75
2.25
10
20
30
40
50
60
PIPEFISH STOMACH POPULATION

Examination of regession analysis for *E. attenuata* in September (Fig. 8) showed a pattern similar to that for *G. mucronatus*. Both prey length and maximum prey length regressions showed significant positive correlation and were significantly different from 0-slope regressions, but the minimum regression showed no significant correlation and was not significantly different from an 0-slope regression. This again indicated an increase in the size range of prey available to fish as they increased in size. *S. fuscus* are again apparently feeding primarily upon the smaller size classes of *E. attenuata* present in the field (Fig. 9). G-test analysis of these two distributions indicates a significant difference ($p<0.005$).

I. balthica (6/79) demonstrated a pattern not observed for *G. mucronatus* or *E. attenuata* (Fig. 10). All three regressions (prey length, minimum prey length, and maximum prey length) were found to be positively correlated and significantly different from a 0-slope regression. Slope values were 0.013, 0.010, and 0.011 for prey L, min. L and max L, respectively. These results indicated that as fish increased in size they selected larger prey items and discontinued feeding upon smaller items. Examination of size frequency data (Fig. 11) showed that fish chose 85% of their food items from the 1-3 mm size class, whereas only 12% of the field population fell into this size range. Approximately 50% of the field population was beyond a size where *S. fuscus* did not feed upon them. Comparison of these two distributions using the G-test showed them to be significantly different ($p<.005$).

FIGURE 8.

Regression Lines for Size Comparisons Between *Erichsonella Attenuata* and *Syngnathus Fuscus* (9/79).

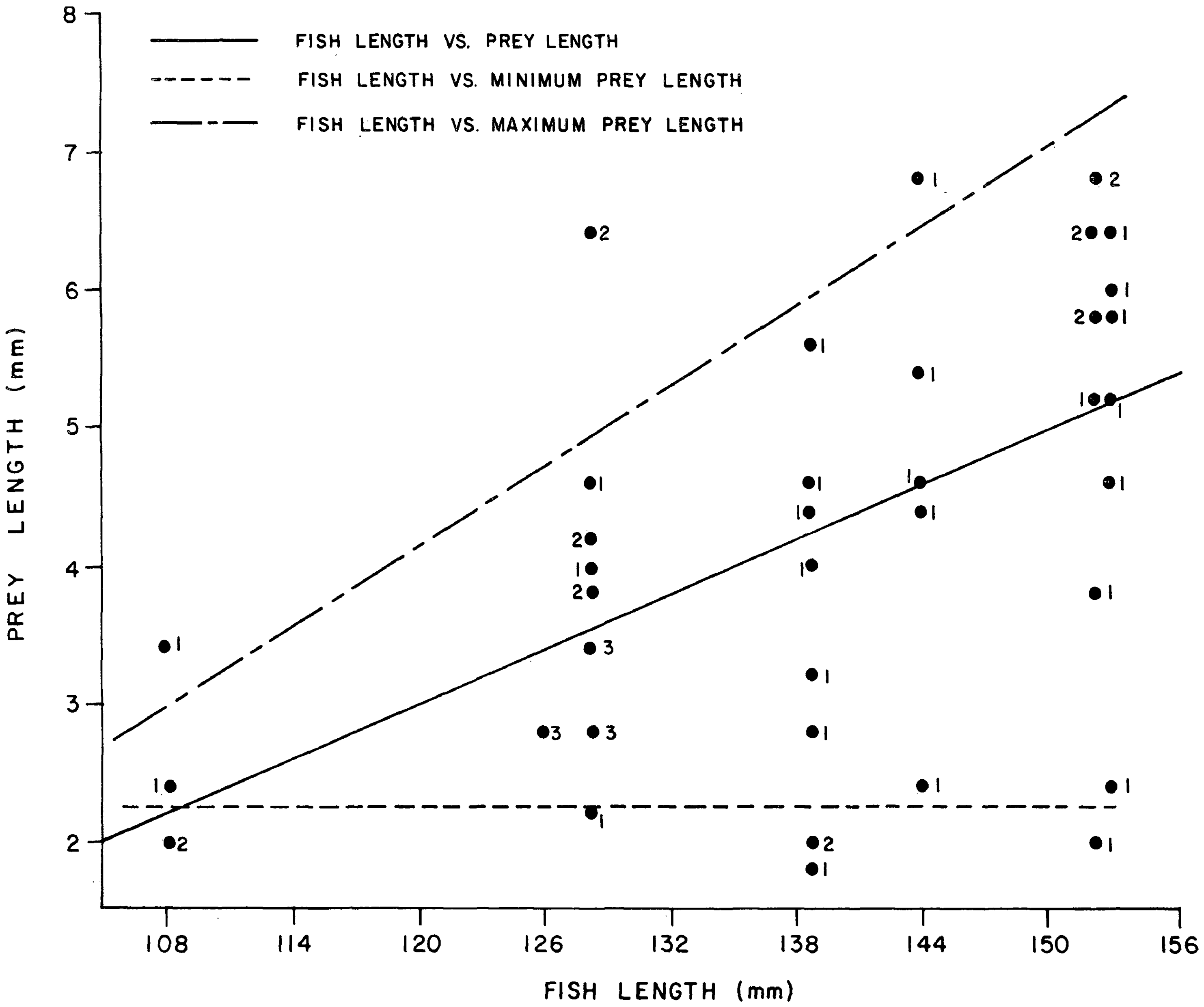

FISH LENGTH VS. PREY LENGTH
FISH LENGTH VS. MINIMUM PREY LENGTH
FISH LENGTH VS. MAXIMUM PREY LENGTH
PREY LENGTH (mm)
FISH LENGTH (mm)
8
7
6
5
4
3
2
108
114
120
126
132
138
144
150
156
1
2
3

FIGURE 9.

Comparison of Size Distributions for *Erichsonella Attenuata* (9/79) from Field and Gut Collections.

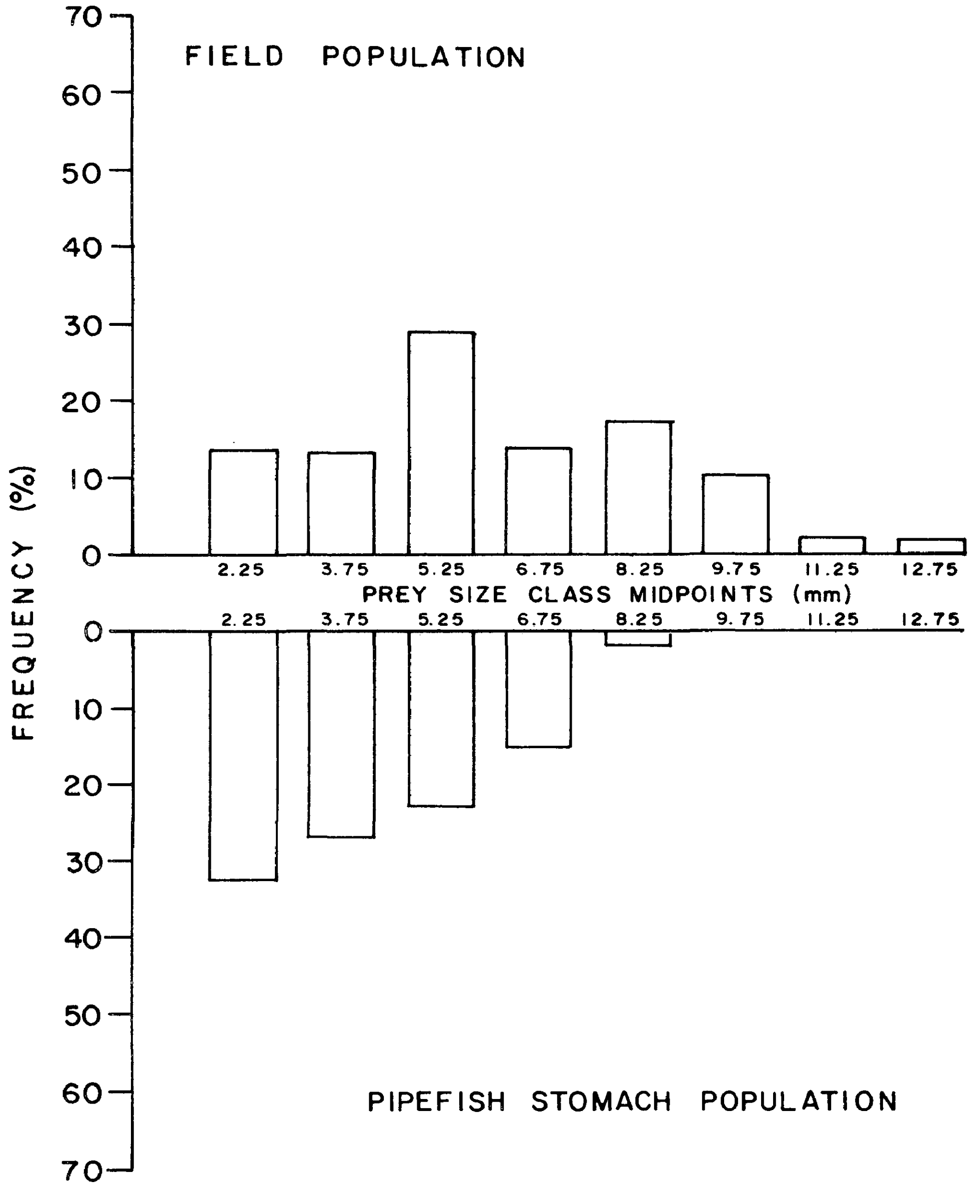

FIELD POPULATION
PIPEFISH STOMACH POPULATION
FREQUENCY (%)
PREY SIZE CLASS MIDPOINTS (mm)
70
60
50
40
30
20
10
0
2.25
3.75
5.25
6.75
8.25
9.75
11.25
12.75

FIGURE 10.

Regression Lines for Size Comparisons Between *Idotea Balthica* and *Syngnathus Fuscus* (6/79).

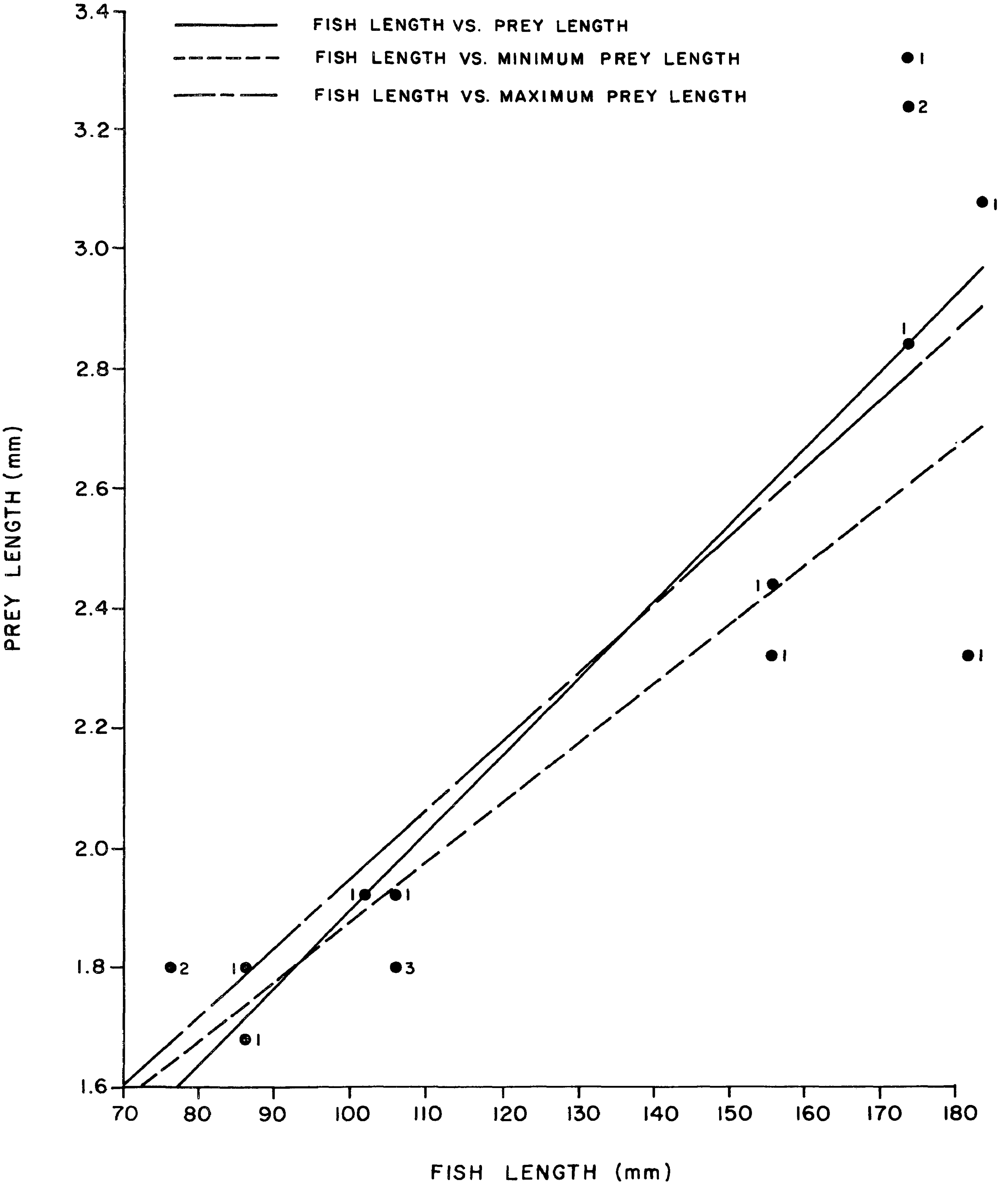
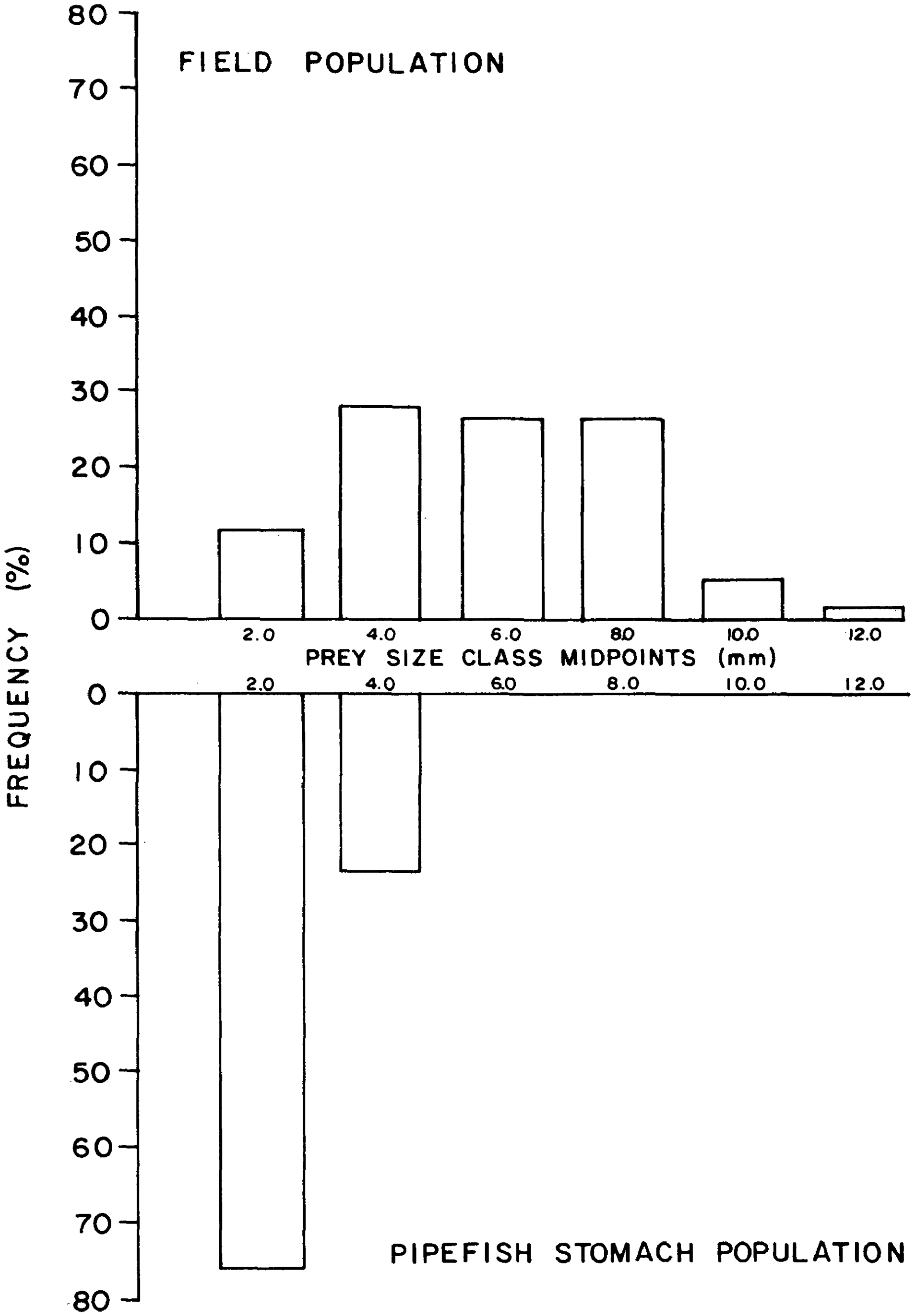

FISH LENGTH VS. PREY LENGTH
FISH LENGTH VS. MINIMUM PREY LENGTH
FISH LENGTH VS. MAXIMUM PREY LENGTH
PREY LENGTH (mm)
3.4
3.2
3.0
2.8
2.6
2.4
2.2
2.0
1.8
1.6
FISH LENGTH (mm)
70
80
90
100
110
120
130
140
150
160
170
180
1
2
1
1
1
1
1
1
1
1
2
1
3
1

FIGURE 11.

Comparison of Size Distributions for *Idotea Balthica* (6/79) from Field and Gut Collections.


FIELD POPULATION
PIPEFISH STOMACH POPULATION
FREQUENCY (%)
PREY SIZE CLASS MIDPOINTS (mm)
80
70
60
50
40
30
20
10
0
2.0
4.0
6.0
8.0
10.0
12.0

Regression analysis for *C. penantis* from May (Fig. 12) showed a significant relation for prey length, but no significant relationship for either minimum or maximum prey lengths.

Analysis for *C. penantis* from June (Fig. 13) showed the same pattern found for *G. mucronatus* and *E. attenuata*, with both prey L and max prey L being significant. Unfortunately, no size distribution information from field populations was available for either May or June *C. penantis* samples.

Feeding Periodicity

S. fuscus displayed a cyclical 24 hour feeding pattern that was similar during both sampling dates at the two different locations (Fig. 14). The largest quantities of food were present in guts just prior to dusk, with a gradual decline from dusk to a minimum level just prior to dawn, and an increase from dawn to mid-day the following day; this pattern is indicative of diurnal feeding.

Gut Evacuation

Fish ate readily at all three temperatures, with no significant difference in maximum meal size but with more rapid evacuation with increasing temperature (Fig. 15, Table 9). The quantity of food evacuated is a constant proportion of the food in the gut at any time. Time to completely evacuate a meal required a 30.2 hour at 15°C, 14.1 hour at 23°C, and 10.3 hour at 27°C (Fig. 15, Table 9). Regression of evacuation rates against temperature (Fig. 16) can be used to predict

FIGURE 12.

Regression Lines for Size Comparisons Between *Caprella Penantis* and *Syngnathus Fuscus* (5/79).

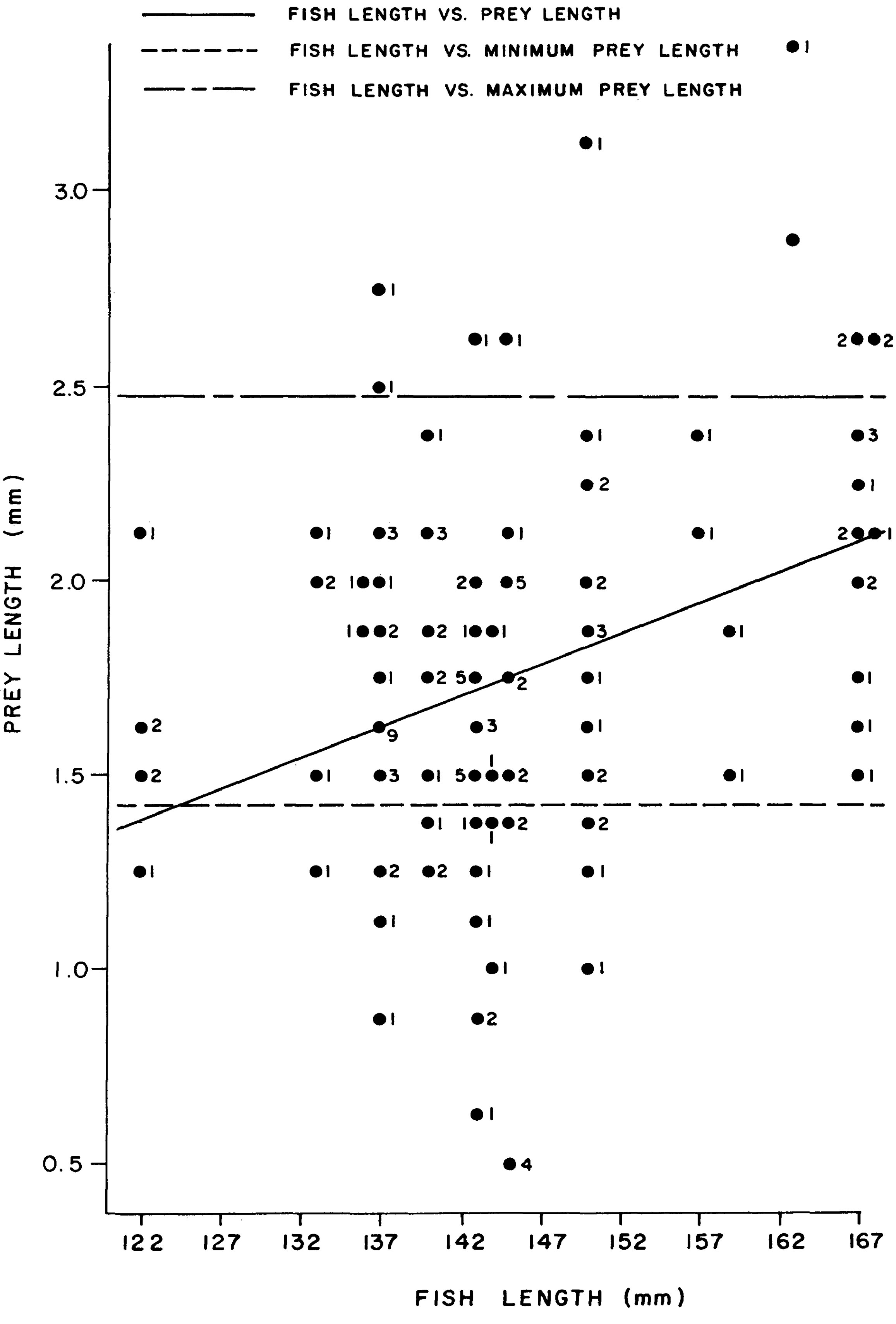

FISH LENGTH VS. PREY LENGTH
FISH LENGTH VS. MINIMUM PREY LENGTH
FISH LENGTH VS. MAXIMUM PREY LENGTH
PREY LENGTH (mm)
3.0
2.5
2.0
1.5
1.0
0.5
122
127
132
137
142
147
152
157
162
167
FISH LENGTH (mm)

FIGURE 13.

Regression Lines for Size Comparisons Between _Caprella_ _Penantis_ and _Syngnathus_ _Fuscus_ (6/79).

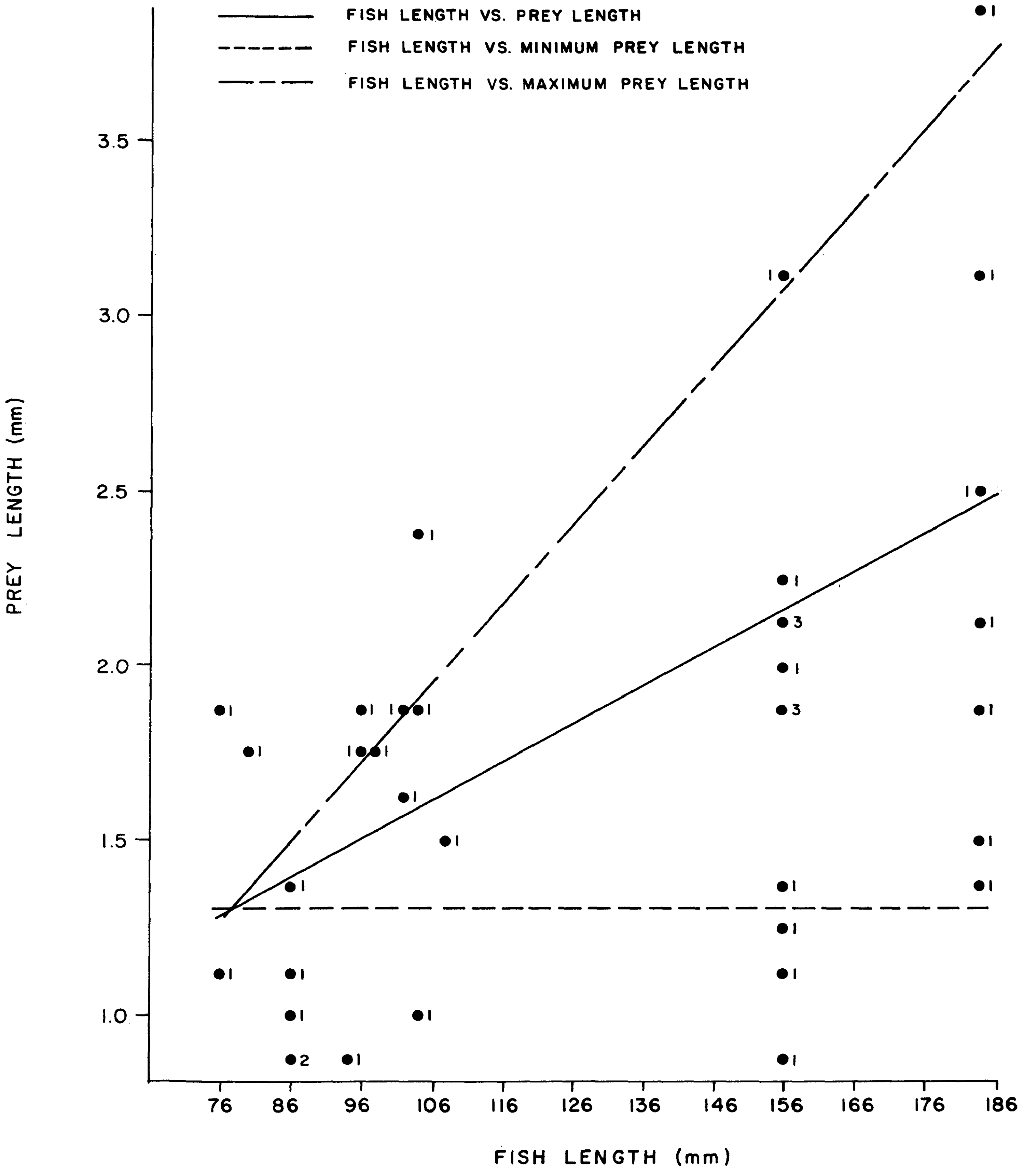

FISH LENGTH VS. PREY LENGTH
FISH LENGTH VS. MINIMUM PREY LENGTH
FISH LENGTH VS. MAXIMUM PREY LENGTH
PREY LENGTH (mm)
3.5
3.0
2.5
2.0
1.5
1.0
76
86
96
106
116
126
136
146
156
166
176
186
FISH LENGTH (mm)

FIGURE 14.

Feeding Periodicity, Geometric Means and 95% Confidence Intervals.

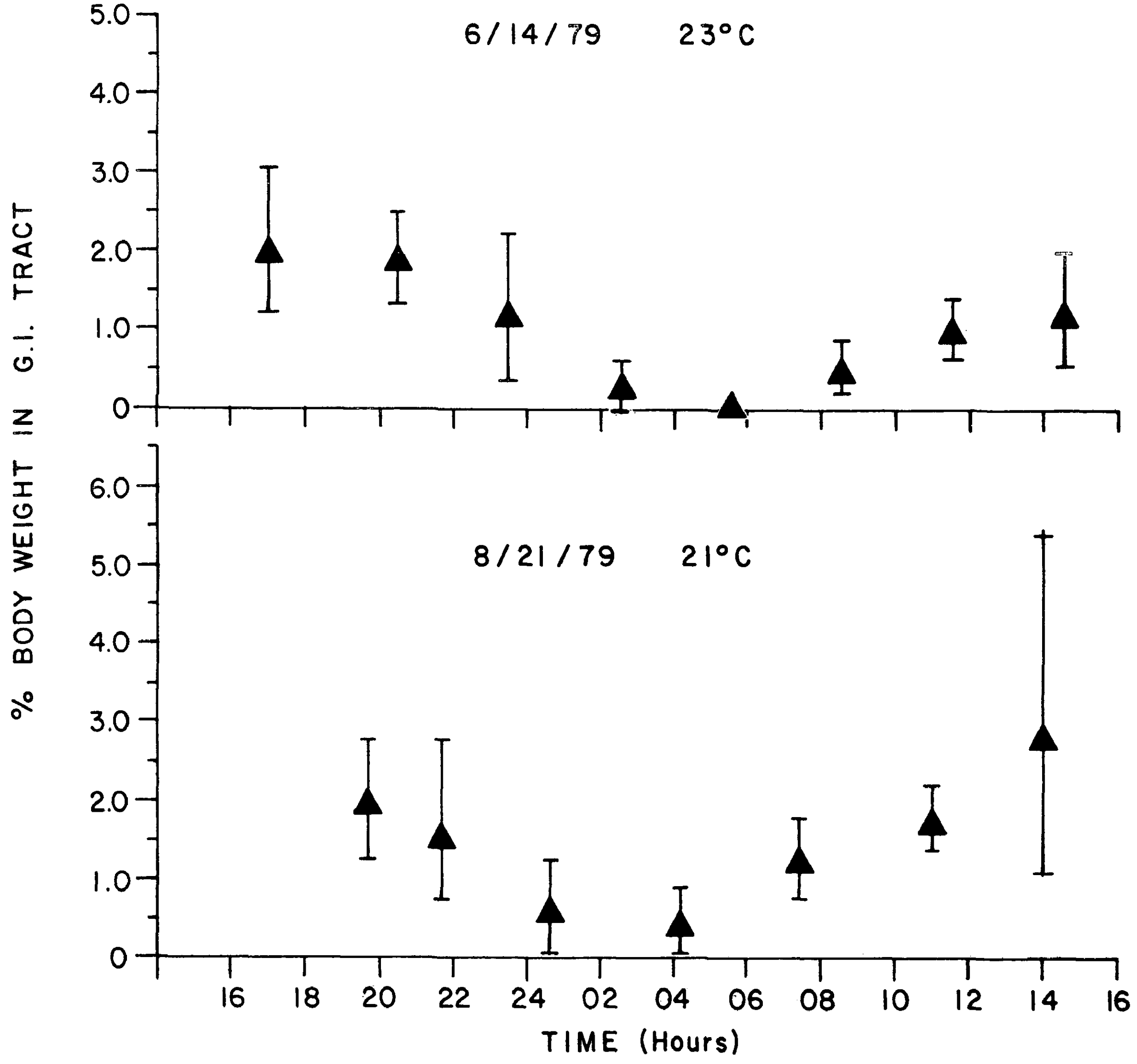
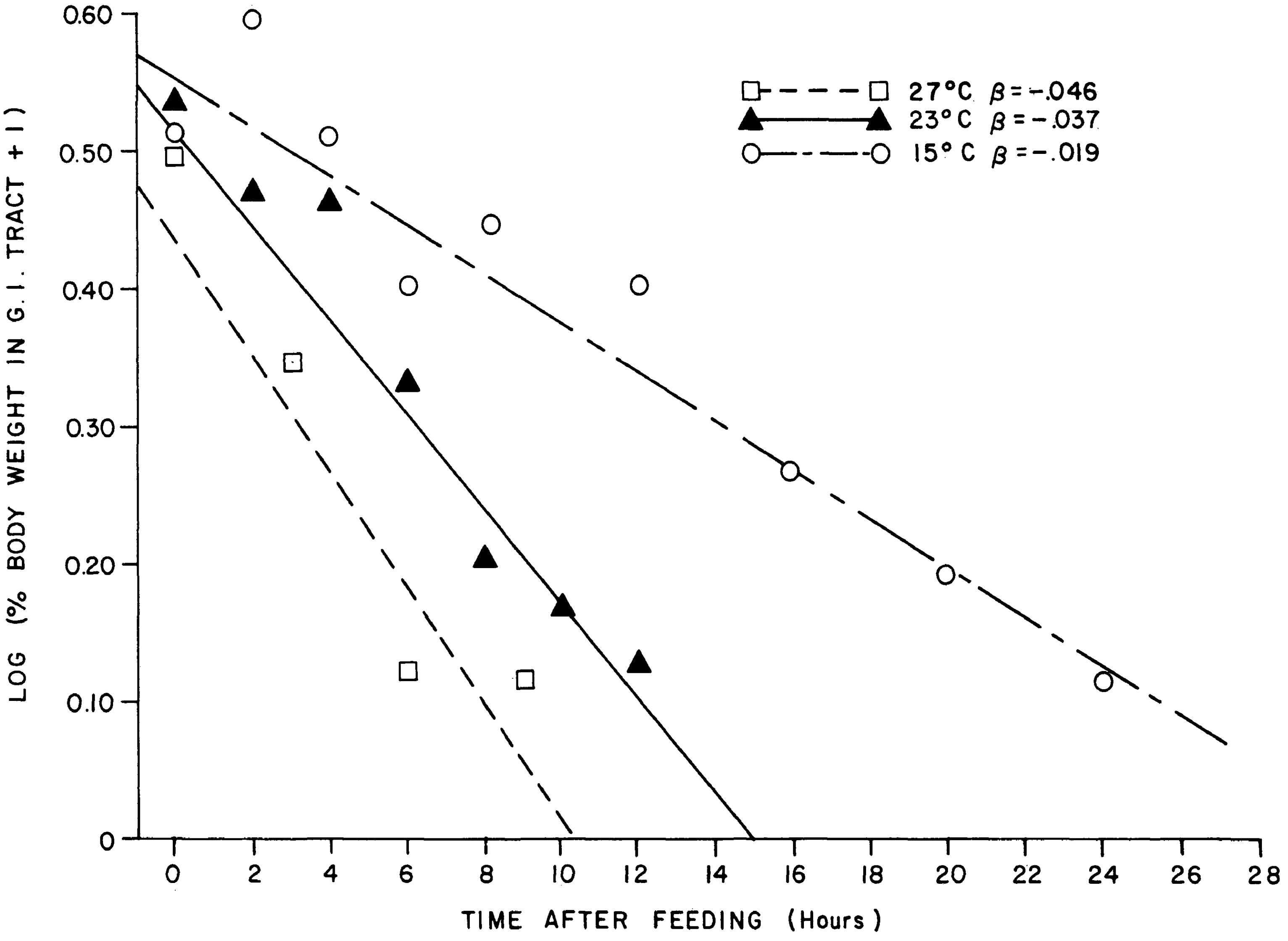

6/14/79 23°C
8/21/79 21°C
% BODY WEIGHT IN G.I. TRACT
5.0
4.0
3.0
2.0
1.0
0
6.0
5.0
4.0
3.0
2.0
1.0
0
16
18
20
22
24
02
04
06
08
10
12
14
16
TIME (Hours)

FIGURE 15.

Evacuation Regressions for 27°C, 23°C, and 15°C.



27°C β = -.046
23°C β = -.037
15°C β = -.019
LOG (% BODY WEIGHT IN G.I. TRACT + 1)
0.60
0.50
0.40
0.30
0.20
0.10
0
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
TIME AFTER FEEDING (Hours)

FIGURE 16.

Regression of Evacuation Rate

Constants vs Temperature.

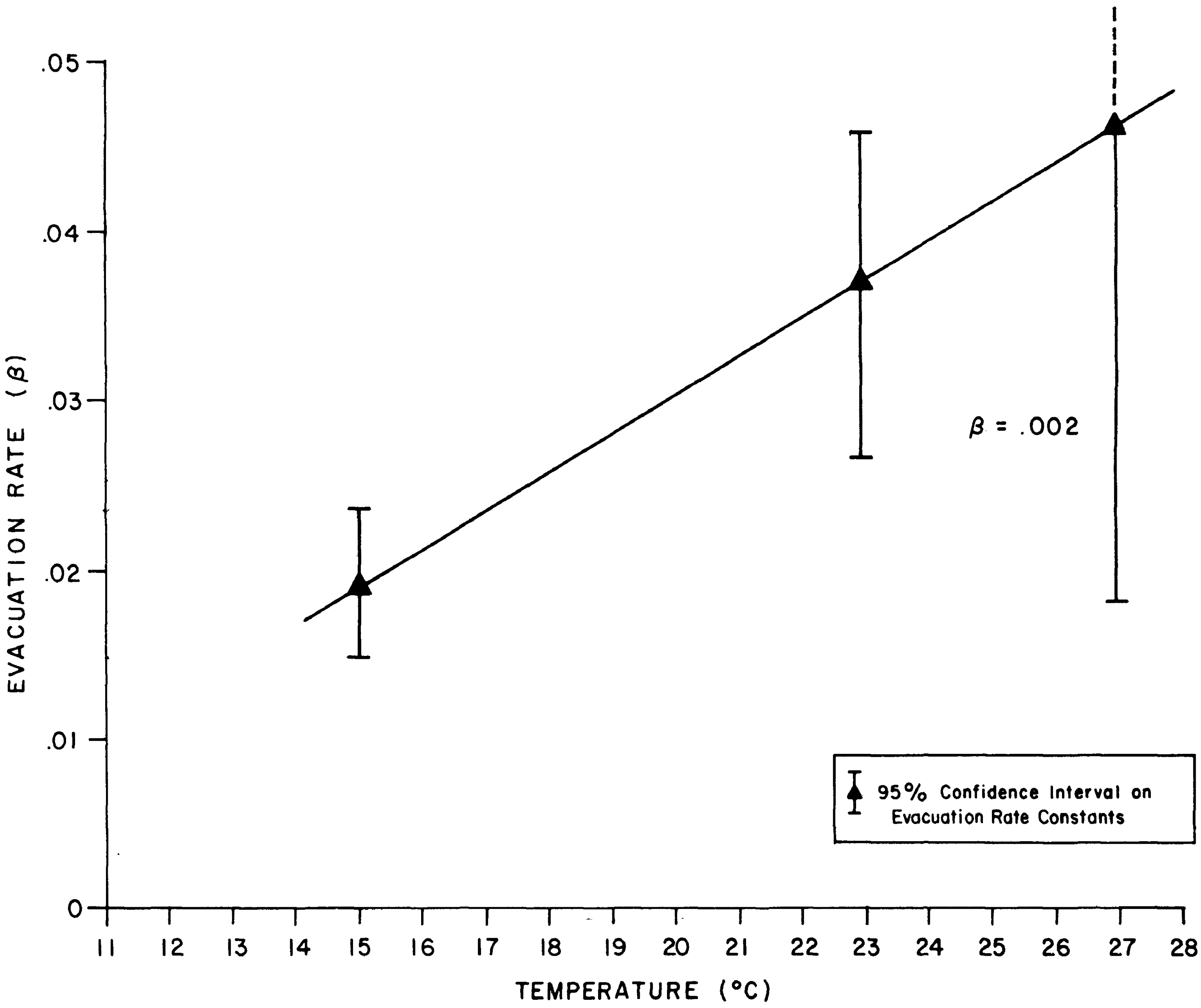

.05
.04
.03
.02
.01
0
EVACUATION RATE (β)
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
TEMPERATURE (°C)
β = .002
95% Confidence Interval on
Evacuation Rate Constants

Table 9. Gastric evacuation in *Syngnathus fuscus* as a function of temperature. In the regression equations Y = log (% dry body weight in stomach +1) and X = hours since feeding.

	15°C	23°C	27°C
Evacuation equation	Y=.573-.019X	Y=.522-.037X	Y=.475-0.46X
Number of fish	28	49	63
Coefficient of determination (r^2)	.928	.952	.908
Estimate of unevacuated food (% dry body weight) at:			
0 h	2.74	2.56	1.99
6 h	1.88	1.14	0.58
12 h	1.21	0.28	-
24 h	0.31		
Time to complete evacuation:			
	30.2 h	14.1 h	10.3 h

evacuation rates at any temperature range for estimation of daily ration.

Daily Ration Calculation

Because the absolute evacuation rate is dependent upon the quantity of food present in the gut, a fish which exhibits periodic feeding will evacuate food at various rates throughout the day. For any given quantity of food in the gut, the equation

$$\frac{dC}{dt} = 2.303\ BC$$

will provide an estimate of the instantaneous evacuation rate, where

C = gut contents (% dry body weight + 1)
B = the evacuation rate constant for the given temperature, and
t = time (Peters and Kjelson 1975).

In order to calculate daily rations, evacuation rate constants were calculated for the temperatures (21°C and 23°C) encountered during the two feeding periodicity studies. These values were then utilized to calculate the instantaneous evacuation rate for each sample time during the periodicity studies (Fig. 14). These values provided estimates for the food being evacuated at any sample time throughout the 24 hour period. By averaging consecutive pairs of evacuation rates, the average evacuation per hour for the given time interval was obtained. These average rates were multiplied by the number of hours between each sample to arrive at an estimate of the total quantity of food evacuated during the particular interval. The total quantity of food evacuated over 24 hour, which served as an estimate of the daily ration, was obtained by summing the quantities evacuated during each interval.

These calculations provided daily ration estimates of 3.996 and 4.378% body weight per day for the observed feeding periodicities of 6/14/79 and 8/21/79, respectively.

DISCUSSION

Seasonality and Abundance

Syngnathus fuscus has been shown to migrate seasonally, moving into the shallow vegetated shoreline areas in the spring, where they remain until the late fall when migration back to the deeper channel areas occurs (Hildebrand 1928; Mercer 1973; Orth and Heck 1980; Wicklund 1968). In the York River, Mercer (1973) found that *S. fuscus* moved into the shallows during March and April, reaching peak abundances during June. Offshore migration occurred during December. Orth and Heck (1980), working in the Vaucluse Shores grassbed during 1976 and 1977, found *S. fuscus* to first appear in trawl samples during late March of 1977. *S. fuscus* reached its peak abundance in July, followed by a gradual decrease in abundance until December, when *S. fuscus* disappeared from trawl samples. Data from the present study support this pattern of seasonal migration to and from nearshore vegetated areas by *S. fuscus*. During 1979, fish were first observed in the grassbed during May. *S. fuscus* remained in the Vaucluse Shores grassbed throughout the spring, summer and fall, until disappearing from samples in December.

Suction-dredge data from July through November yielded an average *S. fuscus* density of 2.57 individuals/m^2, or 1.260 grams wet weight/m^2. Adam (1976) examined the densities of numerous estuarine fish occupying two Zostera marina vegetated areas near Beaufort, NC. From his data, estimates of the average pipefish density for July through November at the two sites were 0.08 and 0.07 individuals/m^2 for the Phillips Island and Bougue Sound sites. By comparison, this study encountered S. fuscus densities over 30 times greater than did Adams in physically similar habitats.

This dramatic difference in S. fuscus density may result from fundamental differences in the structural aspects of the fish communities. Orth and Heck (1980) found only 20 of the 39 species listed by Adams (1976a) at the Vaucluse Shores site. The most obvious difference between these two assemblages was the absence or rarity of Lagodon rhomboides in the Vaucluse collections. L. rhomboides is a dominant species in southern grassbeds (Adams 1976a, 1976b; Hoese and Jones 1963; Cameron 1969; Tabb and Manning 1961), where it feeds primarily upon epifaunal animals, particularly amphipods and isopods (Adams 1976b; Young et al., 1976; Nelson, 1979b). Nelson (1979) experimentally demonstrated the importance of L. rhomboides as a predator upon amphipods. Orth and Heck (1980) have suggested the relative scarcity of L. rhomboides in the Chesapeake Bay to explain the generally higher densities of such epifaunal species in the Bay, as compared to more southerly grassbeds.

The absence of L. rhomboides may explain the higher observed densities of S. fuscus in the Chesapeake Bay. Two species utilizing the same food resources will be in direct competition, provided they are at least to some degree resource limited. It is logical to assume that in the absence of a competitor, a species will maintain higher densities than in the presence of a competitor, provided there are no other overriding factors controlling abundance. Brook (1975) studied the abundance and food habits of fish species inhabiting a Thalassia testudinum bed in Card Sound, FL. He noted what he considered the "anomolous" absence of L. rhomboides as a trophically dominant species in the Coral Sound. Brook also found three species of pipefish, S. scovelli, S. floridae, and Micrognathus crinigerus, to be among the most abundant fish species present. Suction dredge samples found M. crinigerus to have an average density of two individuals/m^2.

General Feeding Ecology

Leistomus xanthurus, S. fuscus, and Bairdiella chrysura are the three numerically dominant resident fish species inhabiting the Vaucluse Shore grassbed (Brooks et al. 1981; Orth and Heck 1980). Of these, S. fuscus was found to be the dominant predator of amphipod and isopod crustaceans. L. xanthurus, while being numerically dominant, was found to feed primarily upon infaunal organisms, with motal epifauna represented only by trace quantities in their diet. B. chrysura fed primarily upon mysid shrimp, Paleomonides vulgaris, and Crangon septemspinosa, and was only resident in the grassbed during the fall months.

When one considers the diverse assemblage of animals present in a Zostera habitat, it becomes apparent that S. fuscus feeds upon a relatively narrow spectrum of prey items, typically gammarid amphipods, caprellid amphipods, isopods, mysid shrimp, and calanoid copepods. Within this suite of prey species, S. fuscus tends to feed more heavily upon certain prey than would be predicted from prey abundance data, as evidenced by selectivity indices (Table 7). This may reflect active selection of various preferred prey by S. fuscus, or it may reflect prey availability. Measures of the abundance of prey species from the field do not necessarily reflect the abundance, or "availability", as percieved by the predator. The availability of a prey item will be controlled by physical and or behavioral characteristics of that species which will serve to determine its vulnerability to predation. Stoner (1979) found predation upon amphipods by L. rhomboides to be mediated by the structural complexity of the habitat (increasing seagrass surface area), and concluded that observed preference for certain amphipod species by L. rhomboides was directly attributable to differential availability among these prey species.

The 24 hour feeding periodicity studies establish S. fuscus as a daytime predator that visually orients towards prey items (corroborated by personal observation). This fact will automatically decrease the availability of some prey items that are primarily nocturnal in their activity and/or movement into and out of the grassbed. Paramount among this group is the mysid shrimp Neomysis americanus. This species has been shown (Brooks et al., 1981) to be primarily nocturnal in its activity, assumably migrating into the grassbed from the deeper sand bottoms after dusk. In 1978, N. americanus was determined to be the trophically most important food item to the majority of fish species present in the grassbed. In

1979, mysid shrimp were the dominant prey item for *B. chysura*, a nocturnal feeder (Brooks et al. 1981). However, due to temporal incompatibilities in their behavior, *N. americanus* had a low availability to *S. fuscus* and was only utilized extensively during the month of November, when mysid densities were assumably very high.

Calanoid copepods are believed to be a highly available prey, in that they have little or no ability to utilize the structural complexity of the grass habitat in order to avoid detection and entrapment by *S. fuscus*. Calanoid represent a very small energy package as compared to most other prey, but also require very little energy expenditure to consume in terms of pursuit, capture, and handling time. Calanoids were routinely taken by *S. fuscus*, to the exclusion of other prey during months of peak calanoid abundance. During July, calanoids accounted for 99.41% of the total prey taken by *S. fuscus*. At this time calanoids reached a density of approximately 27,000 individuals/m^3. However, other prey such as *E. attenuata* were present in fairly high abundances (1246 individuals/m^2), but were rarely taken by *S. fuscus*. During June and September calanoids were positively selected by pipefish, as evidenced by selectivity indices (Table 7). This disproportionate predation upon calanoids may have been the result of active selection and the development of a calanoid model search image by the pipefish. Emlen (1968) has suggested that predators will tend to specialize in their diets (not necessarily on usually "superior" foods) when food is abundant. However, this may also reflect the greater relative availability of calanoids as compared to other prey.

Gammarus mueronctus is envisioned as having low to moderate availability to *S. fuscus*. *G. mucronatus* was observed to display rapid "scurrying" behavior while foraging for food among detritus and algal encrusted *Zostera* blades. This type of rapid movement would certainly impart *G. mucronatus* with a high degree of visibility to potential predators. However, by virtue of its' speed and ability to utilize the structural complexity of the grass habitat, *G. mucronatus* is a relatively difficult prey to capture. *S. fuscus* in aquaria were observed to actively pursue *G. mucronatus* with the amphipod often finding refuge under dead leaves or among algal clumps. *G. mucronatus* was negatively selected for by *S. fuscus* during all three months (June, Spetember, November). But this selection was only statistically significant for June, during which *S. fuscus* fed extensively upon *G. mucronatus*, comprising 51% of the total food weight consumed. This negative selection of *G. mucronatus* may result from its lower relative availability when compared to other prey (i.e. calanoids). Indeed, as they comprised over 50% of the food weight consumed during June, *G. mucronatus* may have actually been positively selected for by *S. fuscus*, with this fact being overshadowed *G. mucronatus*'s lower availabilty, to which the selectivity index is blind.

Microprotopus raneyi was negatively selected in June, and absent from the study site during September and November. During June *M. raneyi* was present in densities roughly twice those of *G. mucronatus* and yet was utilized to a much lower extent by *S. fuscus*, with only two individuals taken. This vast difference in utilization is apparent in comparison of their selectivity indices; -0.3504 and -3.6800 for *G. mucronatus* and *M. raneyi*, respectively. *M. raneyi* is much smaller than *G. mucronatus*, and therefore may be of less interest to *S. fuscus*. *M. raneyi* may also have a lower availability. Unfortunately little information is available on the ecology of *M. raneyi* upon which speculation may be based.

Selectivity indices for the gammarid amphipods *Ampithoe longimana* and *Cymadusa compta* provide a puzzling case of selection by *S. fuscus*. Both species are nest-builders: constructing web-like nests of secretions and bits of algae on *Zostera* blades (Bousfield, 1973; Marsh, 1973). Both species feed upon diatoms and are of approximately the same size. Despite these similarities in their ecologies, *C. compta* was selected against by *S. fuscus* during months when it was present, and *A. longimana* was selected for. In addition, *C. compta* was the more numerous species, having densities of 104, 787 and 994 individuals/m^2 for June, September and November, respectively, compared to 30, 20 and 0 individuals/m^2 for *A. longimana* for the same months. Obviously there must be some overlooked aspects of the ecology of these species that render *A. longimana* much more susceptible to predation. Stoner (1979) also found *C. compta* much less available to *L. rhomboides* predation, when compared to other prey species, in a Florida seagrass bed.

A similar case as for *A. longimana* and *C. compta* arose in June for *Caprella penantis* and *Paracaprella tenuis*. *P. tenuis*, the more numerous species, was selected against while *C. penantis* was selected for. The only obviously discernible difference between these species is in size. P. tenuis is considerably smaller than C. penantis, and as such, may have been a less desirable or less detectable prey. Both species would be predicted to have a low availability due to their crytic body morphology and coloration. However, some additional factor in microhabitat preference by either species might also be involved.

The isopods E. attenuata, I. balthica, and E. triloba were considered to have relatively low availability due to their cryptic coloration (most individuals were either dark brown or green and, as such, blend very well with dead and living grass), as well as behavioral attributes. E. attenuata and I. balthica were observed to spend most of their time slowly moving along grass blades, assumably grazing upon periphyton and associated detritus, only occasionally attracting attention by swimming from blade to blade. E. triloba was observed to be primarily associated with the sediment surface and, as such, had less spatial overlap with S. fuscus which feeds primarily above the sediment surface, among the living grass.

E. triloba was negatively selected by S. fuscus, most likely due to its lower availability. I. balthica showed no significant selection, and E. attenuata was negatively selected in June and November and positively selected in September. This variability in the selection of E. attenuata is most likely related to the generally higher abundance of other positively selected prey items during June and November.

From the preceding discussion it becomes apparent that when availabilities of all the various prey species are considered relative to one another, calanoid copepods were clearly most available. This may explain their predominance during months of high abundance, despite their much smaller size and relatively lower food value per unit effort.

A further consideration that was not incorporated into the selectivity analysis involves the size of the prey relative to the predator. As will be discussed in the following sections pipefish are often unable to prey upon the entire prey population, as some prey individuals may be too large to be consumed. Obviously, these factors also influence the observed selectivity of fish predators, and must be accounted for in studies that attempt overall synthesis of predator-prey interactions.

Predator-Prey Size Relations

Examination of regression statistics for predator-prey size relations, prey size-frequency distributions from guts, and prey size frequency distributions from the field have led to some general conclusions concerning the predatory strategy employed by *S. fuscus*. The freshwater literature is rich with examples of size selective predation upon prey populations by planktivorous fish (Brooks and Dodson, 1965; Gailbraith, 1967; Brooks, 1968; and Wong and Ward, 1972; to name a few), and Nelson (1979) demonstrated size selection of prey by the estuarine species *L. rhomboides*. In all of these studies, fish were relatively large sized when compared to their prey, and tended to select the larger individuals available from the prey populations. The pipefish, however, is morphologically adapted for preying upon relatively small animals, as evidenced by its tube-like snout and small mouth gape. Prey capture is accomplished via darting motion towards the prey, accompanied by sucking action through rapid expansion of the buccal and opercular chambers. *S. fuscus* has been observed (Nelson 1979, personal observations) to pursue and attempt to consume large amphipods. However, such encounters typically resulted in prey escape, or at best, consumption of small portions of the prey, such as appendages.

Comparison of prey size frequency distributions from guts and the field indicate that in most cases *S. fuscus* fed upon the smaller individuals present within any prey population. For both *G. mucronatus* and *E. attenuata*, the individuals vulnerable to predation by *S. fuscus* (by virtue of their size) also constituted a numerical majority of the prey found in the environment. For *I. balthica*, the majority of individuals were beyond the size where *S. fuscus* fed upon them.

Examination of regression statistics for predator-prey size relations demonstrate a general pattern of positive correlation between *S. fuscus* size and prey size. However, for *G. mucronatus* (5/79, 6/79), *E. attenuata* (9/79) and *C. penantis* (6/79), increasing fish size resulted in an increase in the maximum prey size taken, but had no effect upon the minimum prey size taken, thus effectively causing predator size to be positively correlated with the range of prey sizes taken. According to popular optimal foraging theory (Emlen, 1968; Pulliam, 1974; Schoener, 1971; Stenseth, 1981; Iwasa et al., 1981), this is the expected pattern, provided the prey population is not heavily skewed towards the predominance of large prey. Given a fairly uniform prey size distribution, increase in predator size should not cause a dramatic increase in the rate of encounters with potential prey. In such an instance large predators will take large prey, but continue to take smaller prey as they continue to represent a sizable portion of the available prey community. But given the case of a prey community skewed towards the predominance of large individuals, a large predator may forego feeding upon small prey, as they are encountered less frequently, and may represent a smaller net energy gain when compared to a larger prey. This argument makes the general assumption that large prey do not require a significantly greater expenditure of energy to pursue, capture, and consume, than do small prey of the same species. This assumption is felt to be reasonable, considering the limited size range of animals upon which *S. fuscus* preys.

As will be discussed in the following section, the size relationship between *S. fuscus* and its various prey species may have geat importance in modulating the trophic interplay between them.

Periodicity, Evacuation, and Daily Ration

Examination of feeding periodicity demonstrates that *S. fuscus* is a diurnal predator, feeding only slightly, if at all, at night

(Fig. 14). This is also supported by personal observation in aquaria, where pipefish show strong visual orientation to potential prey.

The observed dependence of evacuation rate upon gut content and temperature show the patterns characteristic of teleosts (Fange and Grove 1979). Temperature alters the rate of food evacuation, probably in response to the temperature dependence of metabolism and enzyme activity (Paloheimo and Dickie 1966). Slowing of evacuation rate with decreasing gut content may serve to allow increased assimilation efficiency during periods of low food availability. Thus, when prey availability is high, a common occurrence in spring and summer months in the habitat of _S_. _fuscus_, total food consumed may not only be a function of gut volume and satiation, but rather a function of prey capture.

Calculated daily rations for _S_. _fuscus_ are similar to those reported for other teleosts (Fange and Grove 1979). Peters and Kjelson (1975) examined the daily ration for several postlarval estuarine fish from the southeastern United States. They estimated daily rations of 3.5%, 4.9%, and 4.3% of dry body weight per day for pinfish, menhaden, and spot, respectively. As the larvae transformed to juveniles and changed diet, however, the respective rations were 9.5%, 13.5%, and 10.1%. These higher rations were associated with increasing proportions of inorganic matter in the diet, however, and the organic proportion of the ration was probably similar to that of the larval stages (Peters and Kjelson 1975) and to that of the adult pipefish in the present study; _S_. _fuscus_ rarely consumes inorganic matter. For silversides, which possess straight guts without morphological stomachs (as in pipefish), Adams (1976) noted daily rations from 1.23% body weight (15°C) to 3.72% body weight (25°C).

Evacuation rate determined for *S. fuscus* is clearly dependent upon temperature (Figs. 15 and 16, Table 9). Since the full rations consumed at the three temperatures of measurement were similar (0 h, Table 1) daily ration will therefore increase with increasing temperature if food is in excess. The estimates of daily ration noted in the present study (3.996 and 4.378% dry body weight per day) were determined at two similar temperatures (23° and 21°C, respectively); since the lower observed daily ration occurred at higher temperature, food availability may have been greater at the Vaucluse Shores site in June as compared to the Guinea Marsh site in August. Although prey abundance data were not available for the Guinea Marsh site, available data for the Vaucluse Shores site showed several preferred prey species (gammarid and caprellid amphipods) to be more abundant during June. At lower environmental temperatures, the daily ration should be considerably lower.

Production Considerations

The food requirements of *S. fuscus* can now be related to the standing crop and production of the various dominant prey species in order to estimate the potential impact of this predation on the prey populations.

In order to calculate monthly and seasonal dietary demands for S. fuscus, the 4.187% daily ration is multiplied by the estimated density of S. fuscus (1.260 grams wet weight/m^2 or 0.323 grams dry weight/m^2), resulting in daily consumption of 0.014 grams dry weight/m^2/day. This extrapolates to approximately 0.434 gram dry weight/m^2/monthly or approximately 3.0 grams dry weight/m^2/year (assuming a 7 month residency period in the grassbed).

This total biomass demand can be apportioned to the various prey species on the basis of their respective contribution from the stomach analysis. Multiplication of the monthly consumption rate by the % dry weight contribution of each species provides an estimate of the total dry weight consumed per month for each prey species (Table 10).

Monthly biomass, size frequency distribution data, and yearly production estimates were available for E. attenuata, G. mucronatus, I. balthica, and E. triloba (Diaz, R. J. and Fredette, T., in preparation). Figures 17, 18, 19, and 20 contrast the estimated consumption of each species with their standing crop biomass in the grassbed.

As discussed earlier, E. attenuata is a major contributor to the diet of S. fuscus, particularly during the late summer and fall. As can be seen from Figure 17, E. attenuata maintains high standing crops during this period, with S. fuscus consuming an estimated 7%, 20%, 25%, and 29% of the standing crop in August, September, October, and November, respectively. E. attenuata produces an estimated 17,600 mg/m^2/yr, of which S. fuscus consumes 805 mg/m^2/yr, or 5% of the

Table 10. Prey consumption by month in milligrams (dry weight)

	May	Jun	Jul	Aug	Sep	Oct	Nov	Total
Calanoid Copepods	0	21	379	253	38	7	18	716
Gammarus mucronatus	297	215	8	0	--	0	0	520
Microprotopus raneyi	4	3	1	--	0	0	0	8
Ampithoe longimana	--	60	0	4	--	--	0	64
Amphipods (juv., etc.)	22	6	6	14	57	49	17	171
Caprella penantis	92	53	0	0	0	0	0	145
Paracaprella tenuis	--	8	0	5	5	2	0	20
Idotea balthica	0	28	33	0	14	--	2	77
Edotea triloba	0	0	4	20	3	11	0	38
Erichsonella altenuata	0	8	2	101	209	268	217	805
Mysids	0	1	0	6	0	0	167	174
Polychaetes	0	16	--	0	94	0	0	110
Other Prey	18	--	0	31	0	97	0	146
Totals	433	419	433	434	420	434	421	2994

FIGURE 17.

Erichsonella Attenuata Standing Crop and Estimated Monthly *S. Fuscus* Cropping.

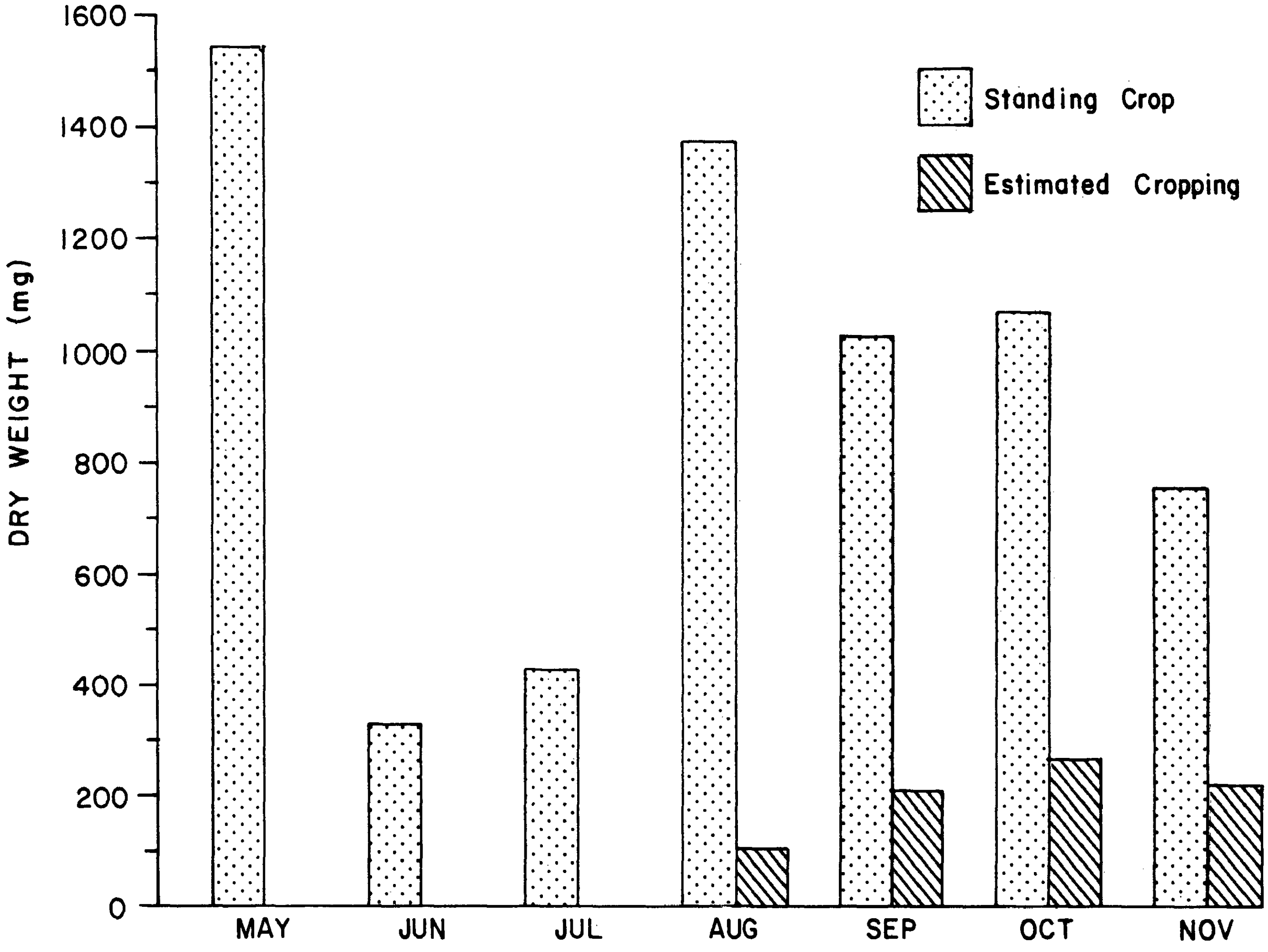

DRY WEIGHT (mg)
1600
1400
1200
1000
800
600
400
200
0
MAY
JUN
JUL
AUG
SEP
OCT
NOV
Standing Crop
Estimated Cropping

FIGURE 18.

<u>Gammarus</u> <u>Mucronatus</u> Standing Crop and Estimated Monthly <u>S</u>. <u>fuscus</u> Cropping.

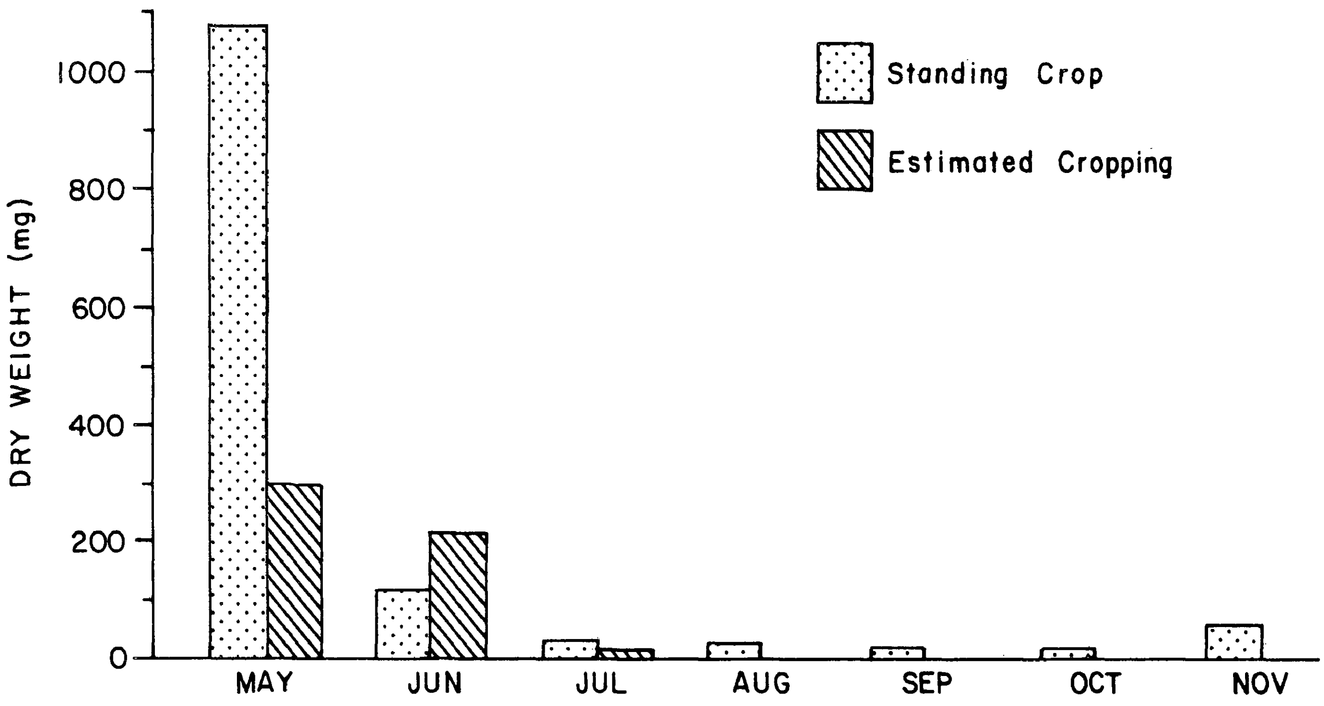

DRY WEIGHT (mg)
1000
800
600
400
200
0
MAY
JUN
JUL
AUG
SEP
OCT
NOV
Standing Crop
Estimated Cropping

FIGURE 19.

Idotea Balthica Standing Crop and
Estimated Monthly *S. fuscus* Cropping.

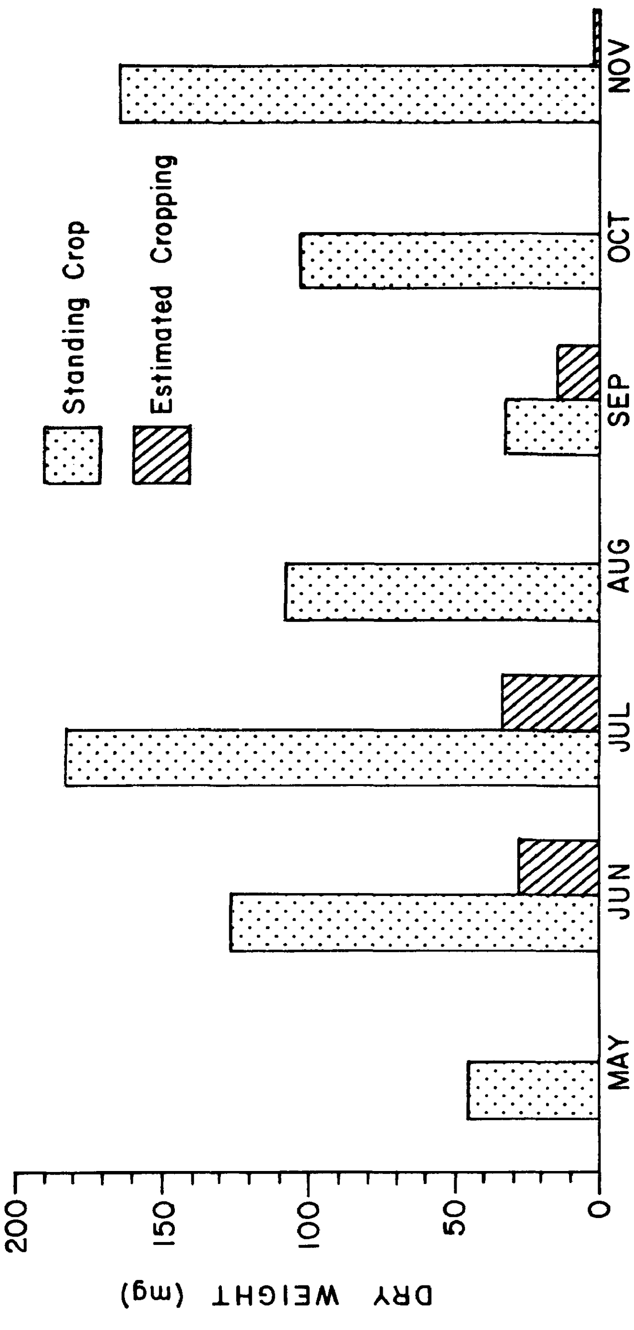
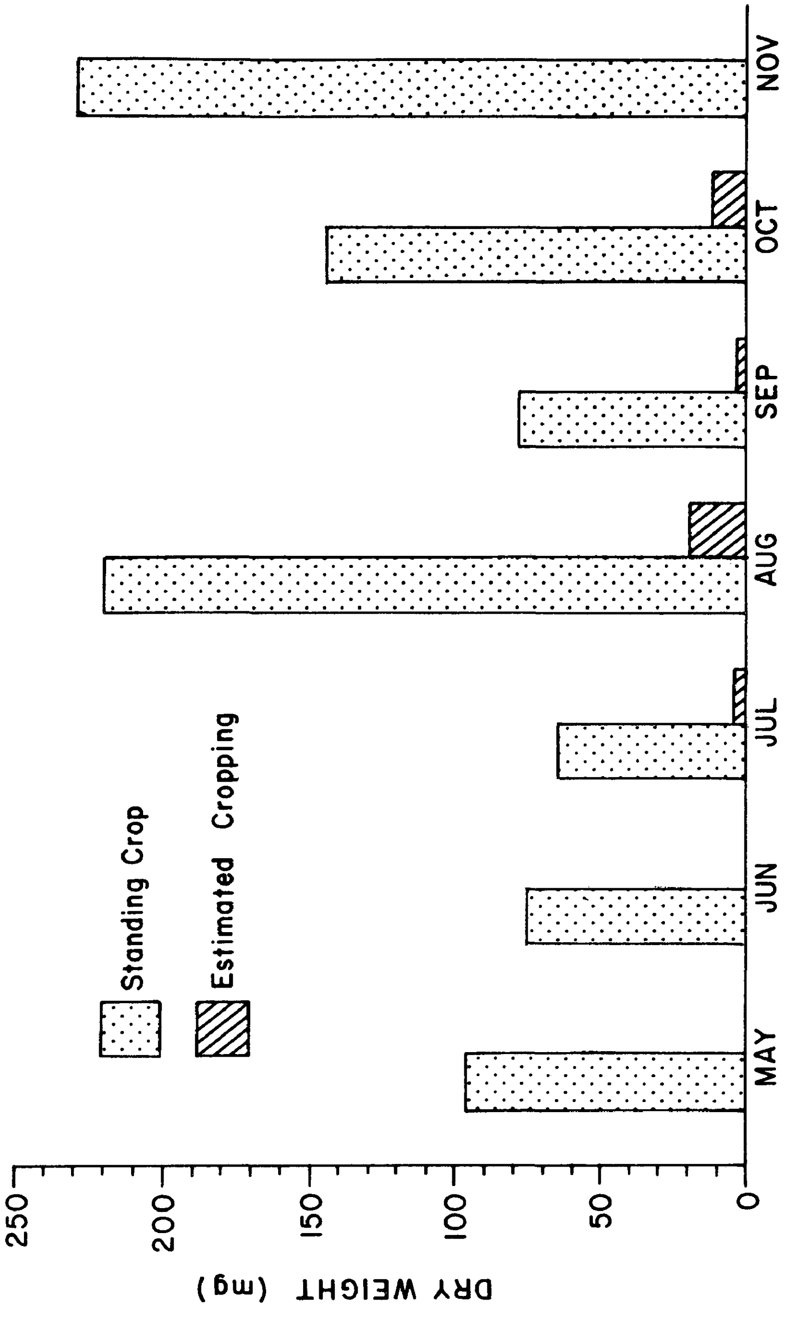

DRY WEIGHT (mg)
200
150
100
50
0
MAY
JUN
JUL
AUG
SEP
OCT
NOV
Standing Crop
Estimated Cropping

FIGURE 20.

Edotea Triloba Standing Crop and Estimated Monthly *S. fuscus* Cropping.


DRY WEIGHT (mg)
250
200
150
100
50
0
Standing Crop
Estimated Cropping
MAY
JUN
JUL
AUG
SEP
OCT
NOV

annual production. But gut size frequency data show that S. fuscus did not feed upon E. attenuata greater than 9 mm in total length. When this is taken into consideration, S. fuscus consumed 11%, 32%, 31%, and 46% of the vulnerable standing crop during August, September, October, and November. When this type of examination is extended to production parameters, the vulnerable portion of the prey population produces 3742 mg/m^2/yr, of which S. fuscus consumes 21%.

G. mucronatus was fed upon significantly by S. fuscus only during May and June, when the amphipod was very abundant. S. fuscus cropped off an estimated 28% of the standing crop during May, and 190% during June. The total yearly production of G. mucronatus was found to be 8,000 mg/m^2/yr, of which pipefish consumed an estimated 520 mg, or 7%. When only the predation vulnerable portion of the population is considered, based on the observations that S. fuscus consumed no G. mucronatus greater than 2 mm (head and first three segments), S. fuscus consumed 120% and 220% of the available standing crop in May and June, respectively. In terms of yearly production, S. fuscus consumed an estimated 30% of the production resulting from the portion of the population which was subject to predation.

Predation upon I. baltica was limited mostly to the summer months during its peak abundance. During June, July and September, S. fuscus consumed an estimated 22%, 18%, and 44%, respectively, of the total I. balthica standing crop. Alternatively, considering only the vulnerable portion of the population, these values become 200%, 89%, and 280% for the same months. In terms of yearly production, S.

fuscus consumed and estimated 8% of the total *I. balthica* production, or 34% of the production produced by the vulnerable size classes.

E. triloba was not utilized as extensively by *S. fuscus* as were other species, the reason for which have already been discussed. However, *S. fuscus* was estimated to have eaten roughly 2% of the annual *E. triloba* production. No size frequency data from guts were taken for *E. triloba*, so the effect of size limitations cannot be examined.

These four prey species combined account for 48% of the estimates *S. fuscus* production demand. In turn, this sum represents 5% of the total yearly production for these four species. The majority of production among these species occurs in the larger size classes, upon which *S. fuscus* is unable to feed. But *S. fuscus* is effectively helping to modulate the production of these prey populations by limiting recruitment of individuals into the larger size categories where the majority of production was found to occur (Diaz, R. J. and Fredette, T., in preparation).

The trophic role of *S. fuscus* in the lower Chesapeake Bay can be grossly compared to that of *L. rhomboides* in more southerly grassbed by examination of their densities. Thayer, Adams and LaCroix (1975) reported a mean yearly biomass of *L. rhomboides* to be 0.650 grams dry wt m^{-2}. This value is considerably higher than the 0.188 grams dry wt m^{-2} value for pipefish observed in this study. Given that both fish have comparable daily ration requirements, *L. rhomboides* would be expected to consume over three times the yearly food biomass consumed by S. fuscus. With respect to the effect of both species upon the distribution and abundance of the pericarids inhabiting the grassbed, this difference in yearly production demand is not so great, particularly when one considers that pinfish greater than 70 mm in length tend to become omnivors (Adams, 1976; Carr and Adam, 1973).

Beyond yearly production demands, the trophic roles of these two fish differ with respect to the size of prey they consume. S. fuscus feeds primarily upon the small prey available, while Lagodon selects for larger individuals. Prey species in Chesapeake Bay grassbeds would therefore be able to find refuge in size, allowing for the maintenance of a population structure with a large proportion of reproductive adults, while more southerly prey populations would be expected to be dominated by smaller individuals. Data comparing the size distribution of prey from such populations could be used to test this speculation.

CONCLUSIONS AND SUMMARY

1. This study has arrived at several conclusions concerning the trophic ecology of *S. fuscus*: *Syngnathus fuscus* is one of the most abundant resident fish species inhabiting the Vaucluse Shores grassbed. In addition, *S. fuscus* is the dominant fish-predator upon epifaunal amphipods and isopods at the study site.

2. Species upon which *S. fuscus* feeds include *G. mucronatus*, *M. raneyi*, *A. longimana*, *C. penantis*, *P. tenuis*, *I. balthica*, *E. triloba*, *E. attenuata*, *N. americanus*, and calanoid copepods. Together, these items comprise 91% of the *S. fuscus* diet (dry weight). *S. fuscus* is therefore rather specialized in its feeding, avoiding numerous other eipfaunal species showing high abundance in the grassbed.

3. Within the narrow suit of species upon which it preys, *S. fuscus* specializes upon particular species, whose availabilities assumably render them more susceptible to predation.

4. For many of the prey species examined, *S. fuscus* was found to feed primarily upon the smaller individuals present in the prey population. This is related to the small mouth gap of *S. fuscus*, which is morphologically specialized for handling small prey. For all prey examined, a positive correlation between *S. fuscus* size

and prey size was observed. Relationships between minimum prey size, maximum prey size, and prey size range were also observed. These data lend insight into the predatory strategy employed by *S. fuscus*. However, in order to derive firm conclusions concerning optimal foraging behavior, additional data are required.

5. The daily ration of *S. fuscus* was determined to be roughly 4% body weight/day. This value is in good agreement with estimates for other estuarine fish species.

6. Although *S. fuscus* does not consume large portions of the annual prey production, it may help to modulate the abundance and production of these species by preying exclusively upon the smaller prey size categories, thus preventing extensive recruitment of individuals into the larger size categories where most production occurred.

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