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Studies of pipefish foraging in simulated seagrass habitats

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College of William and Mary - Virginia Institute of Marine Science

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STUDIES OF PIPEFISH FORAGING IN SIMULATED SEAGRASS HABITATS

A Dissertation

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

Doctor of Philosophy

by

Clifford H. Ryer

1987

APPROVAL SHEET

This dissertation is submitted in partial fulfillment of

the requirements for the degree of

Doctor of Philosophy

_____
Clifford H. Ryer

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ABSTRACT

Laboratory experiments determined the effects of two levels of habitat complexity upon pipefish (Syngnathus fuscus) foraging for amphipods. Habitats were composed of equal densities of either narrow (low complexity) or wide (high complexity) leafed artificial seagrass. The response to habitat, as measured by rate of encounter with amphipods, probability of attack after encounter, probability of success after attack, and overall rate of amphipod consumption, was determined for combinations of two fish size classes and three amphipod size classes. Small fish did not respond to decreased habitat complexity, while large fish did. Small fish apparently did not experience visually inhibitive effects in either habitat, while large fish had their visual fields impinged upon in the wide leaf habitat and encountered fewer amphipods. There was a general trend for encounter rate to increase with amphipod size. Large fish attack probability was positively related to amphipod size in the narrow leaf habitat, but negatively related to amphipod size in the wide leaf habitat. Small fish attack probability was negatively related to amphipod size in both habitats. This pattern of attack probabilities was predicted by a conceptual model of prey vulnerability which considers prey size relative to the predator, and size-specific refugia. Success was negatively related to a ratio of prey size to fish size, and showed no overall effect of habitat. Large pipefish in seagrass meadows could maximize energy intake by utilizing areas where vegetation is sparse or patchy. Pipefish have flexible behaviors, allowing them to minimize unsuccessful attacks. Due to their position in the structure of vegetation, amphipods have a distribution of vulnerabilities; a criterion by which pipefish select prey.

Size-selective predation on gammarid amphipods by pipefish (Syngnathus fuscus) was examined utilizing simulation modeling and laboratory experimentation. Three computer simulation models were developed: 1) a mechanistic model based on empirically derived size-dependent mechanisms of pipefish-amphipod interaction, 2) an optimal diet breadth model in which the rate of energy intake is maximized, and 3) an optimal diet breadth model where switching from energy maximization to time minimization occurs as consumption becomes limited by gastric processing (i.e. satiation). None of these models successfully accounted for the observed pattern of prey size selection. Pipefish concentrated their feeding upon smaller, energetically more profitable amphipods, in excess of what was predicted by either the mechanistic or optimal diet breadth models. This pattern of selection was evident through out 4 hour feeding bouts, indicating that diet breadth compression did not occur.

It is suggested that pipefish may use a simple tactical rule for size-selection when multiple prey are simultaneously encountered: attack the energetically most profitable prey. The possible relevance of this proposed mechanism of prey selection for planktivorous fish is discussed.

STUDIES OF PIPEFISH FORAGING IN SIMULATED SEAGRASS HABITATS

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PREFACE

Fish foraging ecology: a perspective

While our knowledge of fish foraging ecology has benefited from
a diversity of fish foraging studies, the concentration by numerous
investigators has been on "model predators". For freshwater the best
example of a "model predator" is the bluegill sunfish, _Lepomis
macrochirus_. The pinfish, _Lagodon rhomboides_, is ecologically very
similar to sunfishes, and has been adopted as a model predator in
many marine studies. The most notable advances to be derived
through the study of model predators has been the development of
quantitative models of prey selection and encounter. The seminal
work of Werner and Hall (1974) was the first to compare observed
patterns of prey consumption against a realistic null model of prey
encounter to identify active selection for specific prey by sunfish.
Prior studies of fish foraging were primarily descriptive or employed
"selectivity indices": active selection for or against particular
prey determined by mathematical indexes that compare observed
consumption against the relative abundances of all prey categories in
the environment (Ivlev 1961, and references therein). However, such
indices ignore the possibility that some prey, by virtue of their
size, coloration, or behavior, might be encountered less frequently
by fish than other equally abundant prey.

Werner and Hall's model of prey encounter, the "reactive field
volume model" (RFVM), is based upon the fact that larger prey can be
seen at greater distance (i.e. the reactive distance) than smaller
prey (Northmore et al. 1978). Hence, the rate at which a particular

sized prey is encountered will be proportional to the volume of a sphere (the reactive field volume: RFV) with a radius equal to the reactive distance. The RFV increases roughly in proportion to the cube of prey size. Werner and Hall compared observed prey consumption (Daphnia spp.) by bluegills from laboratory and field studies and noted that as overall prey abundance increased, fish consumed proportionately more large prey than could be explained by the RFVM. Large Daphnia were shown to be more profitable (i.e. net energy gain by fish per unit time spent handling prey) than small Daphnia, and the authors concluded that bluegills were maximizing energy intake by preferentially consuming large Daphnia; i.e. foraging optimally. Subsequent studies using bluegills, as well as other fish, have reported similar results (Werner and Hall 1977; Stein 1977; Gibson 1980; Werner and Mittelbach 1981; Mittelbach 1981, 1983, 1984; Stein et al. 1984).

O'Brien et al. (1976) have suggested the "apparent size hypothesis" (ASH) as an alternative mechanistic explanation for selection of large prey by bluegills and other planktivorous fish. Rather than actively choosing prey to maximize energy intake, a process that requires fish to know the profitabilities of prey as well as their absolute abundances, fish instead use a simple tactical rule of thumb: "select the prey that, either by virtue of absolute size or proximity to the fish, appears to be largest at the instant the fish initiates its search for food". At low prey densities the predictions of the RFVM and ASH are identical. As prey densities increase simultaneous encounters start to occur, with fish beginning to show apparent preference for larger prey: the same observation

which Werner and Hall (1974) attributed to optimal foraging by bluegills.

The debate between proponents of optimal foraging and the apparent size hypothesis continues, and despite continued research (Gibson 1980; Eggars 1982; Wetterer and Bishop 1985; Bence and Murdoch 1986) no consensus has emerged. Perhaps the root of this debate is division over whether animals are capable of employing strategies, as opposed to tactics. A strategy, such as optimal foraging, requires that individual decisions be made in the context of an overall plan where their is a distinct objective. In contrast, a tactic is less flexible, utilizing a criterion, or set of criteria to arrive at a response to a specific circumstance. Most importantly, unlike a strategy a tactic is not dependent upon past experience or future expectations: decisions are independent. In any case, both strategies and tactics may be viewed as adaptive responses to changing environmental conditions which may contribute to fitness.

Physical factors in the environment may modify fish foraging. Turbid water is characteristic of many marine, estuarine and freshwater systems and depending upon characteristics of both predator and prey, is known to modify predator-prey dynamics. Vinyard and O'Brien (1976) found that turbidy decreased the reactive distance of bluegills for Daphnia, with the decrease being greatest for larger Daphnia, indicating that turbidy may reduce the effects of prey size upon encounter rates. In contrast, Boehlert and Morgan (1985) found feeding by larval herring to be facilitated by increased turbidity. As larval herring have short reactive distances (compared

to larger fish such as _Lepomis_), turbidy was suspected as having provided a contrasting background against which prey (rotifers) were more visible. In fact, factors that affect visibility of prey, such as pigmentation and prey motion, may have dramatic effects upon predator-prey encounter rates (Zaret and Kerfoot 1975; Zaret 1980a, 1980b). Therefore, turbid waters may be areas were feeding by larval fish is facilitated, while predation from visual piscivorous predators is relaxed, since these predators rely upon detecting prey at greater distances where turbidity becomes inhibitive. Finally, the effects of turbidity may depend upon behavioral characteristics of both predator and prey. Turbidity increased the rate of predation by southern flounder, _Paralichthys lethostigma_, upon brown shrimp, while predation by pinfish, _Lagodon rhomboides_, was decreased (Minello, Zimmerman, and Martinez 1987). Pinfish rely exclusively upon vision to encounter and pursue prey, and are therefore negatively affected by turbidity. Flounder, on the other hand, use an ambush tactic which depends upon the close proximity of prey, and is therefore unaffected by turbidity. In fact, shrimp activity was found to increase with turbidity, facilitating flounder feeding.

Another area in which advances have recently occurred deals with the effects of habitat complexity upon fish foraging. Quantitative models describing fish foraging have been developed primarily for open-water systems. Physical structure, such as submerged vegetation, has a mediatory effect upon predator-prey dynamics in both marine and freshwater systems and has been the topic of numerous studies. Predator foraging efficiency decreases with increasing vegetation, frequently with thresholds at which efficiency decreased

abruptly (Nelson 1979; Heck and Thoman 1981; Savino and Stein 1982; Coull and Wells 1983). Since invertebrate prey density usually increases with vegetation density, energy intake for fish predators may therefore be greatest at intermediate vegetation levels just below these thresholds (Cooper and Crowder 1979; Crowder and Cooper 1982).

The mechanisms responsible for decreased foraging efficiency is decreased in vegetation are only now being resolved. Visual interference by vegetation may decrease that distance at which prey are detected, decreasing rates of encounter (Savino and Stein 1982). This may be compounded by microhabitat utilization where prey inhabit spaces between grassblades, thereby further decreasing their visibility, and perhaps their vulnerability to fish (Wellborn and Robinson 1987). In addition, some prey have elaborate behavioral responses to perceived predators that make use of physical characteristics of the vegetation to decrease their vulnerability (Main 1987).

Sunfish have also been extensively studied with respect to mediation of habitat use by predation risk. Bluegills shift their use of habitats as the availability of prey changes: choosing to forage in the habitat that provided the highest net rate of energetic intake (Werner et al. 1983a). However, sunfish are risk sensitive in their habitat use (Werner et al. 1983b). Large bluegills are relatively invulnerable to predation by piscivorous fish and foraged in the open water column where consuming zooplankton provided the highest energy return (as opposed to nearby vegetated habitats). Small bluegills, at greater risk from predators, trade-off better

foraging in the open water for lower risk of predation along the edges of vegetation.

The advances in fish foraging ecology made over the last two decades should now be subjected to a period of critical re-evaluation. The usefulness of general models and principles in ecology is determined by their applicability under various conditions and in dissimilar systems. It needs to be determined whether existing models developed for simplified model predator-prey systems are useful in predicting foraging behavior of other fish species, in more complex habitats. The present study was undertaken to examine and model the foraging behavior of the northern pipefish, Syngnathus fuscus, consuming gammarid amphipods in laboratory simulated seagrass habitats.

The pipefish-amphipod predator-prey system

Seagrasses are a conspicuous feature of shallow water marine and estuarine habitats along much of the east and gulf coasts of North America. These habitats are characterized by high densities of both invertebrate and vertebrate species (Orth 1977). Free-living epifaunal amphipods, a dominant food item for many resident and transient fish species, are characterized by highest density during late winter or spring (Nelson 1980; Fredette and Diaz 1986). Declining densities coincide with the arrival of numerous fish and predatory invertebrates (Adams 1976; Heck and Orth 1980; Orth and Heck 1980), and seasonal lows in amphipod abundance occur when these predators have reached their peak densities, suggesting that amphipod abundance may be largely controlled through predation. Seagrass

amphipod populations are highly productive (Fredette and Diaz 1986) and may serve as major agents of energy transfer to higher trophic levels.

The northern pipefish, *Syngnathus fuscus*, occurs from Florida northward to Nova Scotia (Dawson 1982). The body is very elongate and tapers to a long straight tail. The mouth is terminal to a long tube-like snout. *S. fuscus* rarely exceeded 230 mm total length, with typical adult sizes of 100 - 200 mm, although a specimen of 305 mm has been reported (Nichols and Breder 1927). Color varies from a dark green to olive brown, with some degree of dark banding on body and tail. While found in a number of different habitats, *S. fuscus* is most abundant in seagrass meadows (*Zostera marina*, *Ruppia maritima*) from May through November, after which migration to deeper bay and/or channel areas is presumed to occur (Hildebrand and Schroeder 1928, Mercer 1973, Ryer 1981). Typical of Syngnthidae, females deposit eggs in the male's brood pouch: a membranous marsupium located on the ventral surface of the tail, posterior to the vent, where juvenile fish mature until released at a size of 1 cm. In the Chesapeake Bay region breeding occurs from May through October, with an apparent peak in May and early June. It is probable that males only spawn once; when maintained in aquaria they tend to languish and die shortly after the release of young (Ryer personal observation). Sexual maturity is reached in approx 12 months (Bigelow and Welsh 1925). *S. fuscus* feeds primarily upon small crustaceans (Mercer 1973, Ryer 1981): amphipods, isopods, calanoid copepods, and shrimp, and is a visually directed feeder having a distinct diurnal feeding periodicity (Ryer and Boehlert 1983).

Although not consumed by any predators in large numbers, S. fuscus is probably infrequently consumed by a number of resident and transient species (Brooks et al. 1981).

Among resident seagrass fishes known to prey upon gammarid amphipods, the pinfish, Lagodon rhomboides, is perhaps the most throughly studied (Carr and Adams 1973; Nelson 1979; Stoner 1979, 1980, 1982). Prior to shifting to omnivory, and finally herbivory as adults (Livingston 1982), juvenile pinfish are epifaunal predators, and may exercise considerable control over the amphipod populations upon which they feed (Stoner 1982). Not unlike freshwater sunfishes (Werner and Hall 1979; Mittelbach 1981), juvenile pinfish are large relative to most of their prey, being able to consume, and in larger fish showing preference for, the largest amphipods available (Nelson 1979). While abundant from North Carolina southward, L. rhomboides is rarely found in the Chesapeake Bay, where the northern pipefish is the dominant piscine predator upon epifaunal amphipods (Brooks et al. 1981). Unlike pinfish, due to morphological constraints placed upon them by their trophic apparatus (i.e. small mouth and elongated tube-like snout) pipefish consume predominantly the smaller sized amphipods available. During the spring the amphipod Gammarus mucronatus is at peak abundance and pipefish consume them to the exclusion of other available prey. Ryer and Orth (1987) calculated that during this time pipefish consume numbers of amphipods m^{-2}, on a monthly basis, that exceed the average amphipod density, thus indicating that predation by pipefish may have significant effects upon amphipod population dynamics. Ryer (1981) estimated that pipefish may consume as much as 30% of the yearly production produced

by the portion of the G. mucronatus population which is vulnerable to pipefish predation (i.e. smaller amphipods).

Dissertation objectives

Two broad areas of fish foraging ecology are addressed by this dissertation. Chapter 1 examines the effect that vegetation has upon predator-prey interactions. As many of the afore mentioned studies have demonstrated that predator-prey interactions may be very different in vegetated v.s. unvegetated habitats, this study is more narrowly concentrated on examining mechanisms of interaction within simulated seagrass habitats. This study also examines hypotheses dealing with the effects of vegetation architecture. Chapter 2 deals with models of prey size selection by pipefish. Three models, each increasingly complex and requiring greater information processing capabilites on the part of the fish, are considered: 1) mechanistic model - prey consumption is determined by prey abundances and size dependent mechanistic interactions, 2) optimization model - fish select that range of prey sizes that maximize the rate of energy intake, 3) diet breadth compression model - diet breadth and associated rates of energy intake are linked with a model of gastric processing capability.

CHAPTER 1

PIPEFISH FORAGING AND THE EFFECT OF ALTERED HABITAT COMPLEXITY

INTRODUCTION

Much attention in freshwater and marine systems has been directed towards the effects of habitat complexity upon predator-prey dynamics. In the absence of some spatial or temporal heterogeneity, predator-prey systems may be unstable, as exemplified by simple laboratory systems where both prey and predator go extinct (Gause 1934). Numerous physical aspects of aquatic habitats provide structural complexity: substrate (Stein 1977; Lipcius and Hines 1986; Smith and Coull 1987), litter (Ware 1972), worm-tubes (Bell and Coen 1982), emergent macrophytes (Vince et al. 1976; van Dolah 1978), and submerged macrophytes (Coen et al. 1981; Crowder and Cooper 1982; Stoner 1979, 1982; Coull and Wells 1983). The effect of artificial structure upon predator-prey interaction has also been examined (Glass 1971; Brock 1979; Nelson 1979; Heck and Thoman 1981; Marinelli and Coull 1987; Russo 1987). With few exceptions (Marinella and Coull 1987) predator efficiency decreases with increasing habitat complexity, and there may be a threshold above which predator efficiency decreases abruptly (Nelson 1979; Heck and Thoman 1981; Savino and Stein 1982; Coull and Wells 1983). In addition, prey density usually increases with increasing habitat complexity, resulting in peak predator feeding and growth rates at intermediate complexities (Cooper and Crowder 1979; Crowder and Cooper 1982).

Submerged aquatic vegetation is a conspicuous feature of the shallow waters of many freshwater and marine systems. Mechanistic models of fish foraging that account for visual reactive field volumes (Werner and Hall 1974), prey visibility (Zaret and Kerfoot 1975), prey motion (Zaret 1980a) and the apparent size of prey

(O'Brien et al. 1976) have been developed for zooplanktivorous fish. Similar models which account for visual (Savino and Stein 1982; Main 1985, 1987) and physical (Orth 1977; Stein 1977; Virnstein 1977; Reise 1978; Nelson 1979; Blundon and Kennedy 1982) inhibitory effects of vegetation, as well as predator detection (Petranka et al. 1987), avoidance (Main 1987; Petranka et al. 1987) and escape capabilities of prey (Savino and Stein 1982; Main 1987), have yet to be developed for vegetated habitats.

The northern pipefish (Syngnathus fuscus) is a common inhabitant of vegetated shallows along much of the North American east coast (Dawson 1982). Field and laboratory studies of pipefish (Syngnathus fuscus) foraging and prey selection (Ryer 1987; Ryer and Orth 1987) have generated hypotheses concerning mediation of predator-prey interactions by habitat complexity. First, seagrass decreases the distance at which predators can detect prey, thereby reducing encounter rates. Second, the probability of an encounter resulting in initiation of attack will depend upon perceived vulnerability of individual prey. Vulnerability is determined by the relative sizes of predator and prey and by the ability of the prey to effectively utilize available refugia. The effectiveness of refugia will depend upon refuge architecture and the relative size of predator and prey: a refuge from larger predators may not be an effective refuge from smaller predators. Therefore, changes in habitat complexity will have size-specific effects upon the ability of predators to attack prey. Third, to forage more efficiently, predators have flexible behavior patterns designed to minimize unsuccessful attacks.

Therefore, patterns of success across prey sizes should remain uniform regardless of habitat.

I tested these hypotheses by examining pipefish-amphipod interactions (2 fish sizes and three amphipod sizes) at two levels of habitat (artificial seagrass) complexity. Various investigators have used different measures of vegetation complexity: biomass (Heck and Wetstone 1977; Orth 1977; Stoner 1980), shoot/blade density (Homziak et al. 1982), surface area (Stoner and Lewis 1985), and surface-to-volume ratio (Coull and Wells 1983). I wished to define habitat complexity in terms that are directly related to mechanisms of pipefish-amphipod interaction. I have observed gammarid amphipods to preferentially occupy the spaces between the basal portions of artificial seagrass blades, effectively reducing their conspicuousness and vulnerability to pipefish. I reasoned that changing the width of grassblades would affect the ability of pipefish to visually locate amphipods, as well as affecting amphipod vulnerability once encounter had occurred. These are both mechanisms of predator-prey interaction. I therefore chose to define habitat complexity in terms of leaf width: narrow leaf = low-complexity, wide leaf = high-complexity. Encounter rates, probabilistic attack and success, and consumption rates were quantified, providing a mechanistic approach to the study of predator-prey interactions in structurally complex habitats.

MATERIALS AND METHODS

Animal collection and maintenance

Pipefish were obtained from eelgrass (Zostera marina) meadows
located at the mouth of the York River, in the lower Chesapeake Bay.
Fish were held in static, subsand-filtered 38 L aquaria, with a
uniform density (60 shoots, 4 leaves/shoot, mean leaf length=11 cm)
of 5 mm wide artificial eelgrass (polypropylene ribbon). Pipefish
were held for a minimum of 1 week prior to experimentation, fed a
mixed diet of gammarid amphipods and Artemia nauplii, and were
assigned individual identification numbers to follow their
experimental history and growth.

Two Gammarus spp. were used interchangeably as prey: G.
mucronatus, an inhabitant of eelgrass and algal communities (Fredette
and Diaz 1986), and G. palustris, and intertidal marsh inhabitant
(van Dolah 1978). These amphipods are morphologically very similar
(Bousfield 1973), and like most free-living vegetation dwelling
amphipods, are highly thigmotactic (Nagle 1968; van Dolah 1978;
Stoner 1980). Preliminary experimentation indicated that both
preferred to occupy spaces between basal portions of grassblades, and
interacted with pipefish in identical manners. I concluded that prey
species would have no effect upon experimental outcomes. Amphipods
were kept in static, subsand-filtered aquaria and fed frozen chopped
spinach. Pipefish and amphipods were kept at temperatures of 24-25°C
and experienced natural photoperiod.

Experimental design and procedures

The experimental design employed was a full factorial: two
levels of habitat complexity, two fish size classes, and three
amphipod size classes. All trials were conducted in aerated static 38
L aquaria with sand substrate, artificial eelgrass, an overhead
aquarium light to provide consistent illumination, and filtered (1
um) York River water (salinity range 16-24 ppt). The high-complexity
habitat treatments consisted of 60 shoots/aquarium (4 leaves/shoot,
mean shoot length=11 cm) of artificial eelgrass (5 mm wide
polypropylene ribbon). This shoot density (480 m^{-2}), while on the
low side of reported Z. marina densities (Orth 1977), provided enough
habitat complexity to keep amphipods from congregating in aquarium
corners, but still allowed detailed behavioral observations. The
low-complexity habitat consisted of an equal number of identically
constructed shoots, but made with 1.7 mm wide ribbon. Thus, the low-
complexity habitat had 33% of the surface area of artificial grass in
the high-complexity habitat, and was composed of shoots with narrower
leaves.

Fish size classes were small (110-130 mm) and large (180-200 mm
total length). No fish was used more than once within a cell of the
factorial design; due to limited supply, some fish were used more
than once between cells. Amphipod size classes were small (mean
size=4.8 mm), medium (6.1 mm), and large (7.0 mm total length from
base of 2nd antennae to the tip of uropods). Amphipods were sorted
by mechanical sieving. By repeated sieving and discard of amphipods
from intervening sieves, overlap between classes was eliminated.
Amphipods showed no adverse effects as a result of the sieving

process.   Six trials for each combination of habitat, fish size, and
prey size were conducted.

Trials were run during morning hours with a maximum of 8 per
day. Twenty-four hours prior to experimentation, fish were isolated
in experimental aquaria (1 fish per aquarium) without prey, assuring
a uniform starvation period.   Twelve hours prior to experimentation
50 amphipods were added to each aquarium and immediately covered with
opaque black plastic.   As pipefish are visual feeders (Ryer and
Boehlert 1983; personal observation), amphipods were given an
acclimation period without risk of predation.

Trials were conducted individually and serially, allowing direct
observation of all predator-prey interactions.   After removal of the
aquarium cover, a trial began and data recording was initiated when a
fish first attacked an amphipod, or positioned itself for attack.   A
trial was continued until: fish stopped foraging (see description of
foraging behavior below), until the trial exceeded 20 min, or until
$\pm$25% of the amphipods were consumed.   Hence, prey densities and
distributions did not change greatly during a trial, and fish did not
become satiated, which may cause changes in predator-prey
interactions (Kislalioglu and Gibson 1976; Bence and Murdoch 1986).
Trials where fish did not display typical foraging behavior were
discarded and repeated.   Fish were observed from a distance of 50 cm
in a darkened room and did not appear to respond to my presence.
Data were entered with the remote keyboard of a microcomputer running
an event recording program.   An encounter between fish and amphipod
was defined by the simultaneous fixation by the fish of both eyes
upon the amphipod.   An attack was defined by attempted consumption of

an amphipod through a forward thrust of the head with a concurrent inward sucking through the snout. An attack was considered successful when the amphipod was captured and swallowed.

Statistical analysis

Four dependent variables were were quantified:

1) Encounter Rate - the number of amphipods encountered min^{-1} (not including time spent in positioning, pursuit, or handling of prey),

2) Attack probability - the proportion of encountered amphipods which were attacked,

3) Success probability - the proportion of attacked amphipods which were captured and consumed,

4) Consumption rate - the number of amphipods consumed min^{-1}, inclusive of positioning, pursuit, and handling   time.

Examination of normal deviates plotted against ranked observations (rankit plot, Sokal and Rohlf 1981) indicated that dependent variables were normally distributed. Attack and success probabilities were homoscedastic (Cochrans's C-test, Sokal and Rohlf 1981). Natural log transformation (ln(x+1)) of encounter rates resulted in homoscedasticity. Despite use of several common transformations (ln, log, sqrt, arcsin), consumption rates remained heteroscedastic. Attack probabilities, success probabilities, and transformed encounter rates were analyzed by analysis of variance (ANOVA, Sokal and Rohlf 1981), with habitat, fish size, and prey size as independent variables. To further examine significant interactions between independent variables, data were separated by

fish size (large v.s. small) and analyzed separately by two-way
ANOVA. Consumption rates were tested for effect of fish size
(Kruskal-Wallis nonparametric ANOVA, Sokal and Rohlf 1981), and then
separated by fish size. Natural log transformed consumption rates
for small and large fish were homoscedastic, and were analyzed
separately by ANOVA. Examination of residuals for all dependent
variables indicated that no fish which was used more than once showed
a tendency toward consistently high or low response. I therefore
conclude that re-use of fish resulted in no significant experimental
bias. For any statistical test, the null hypothesis of no effect was
rejected at $p \leq 0.05$.

RESULTS

General foraging behavior

When aquarium covers were removed at the initiation of a trial
fish were lying motionless on the bottom or suspended within the
artificial eelgrass. After several seconds to several minutes fish
became active, after exhibiting periodic gill clearing behavior
(prolonged expansion of the opercular chamber). Conversely,
amphipods appeared to have been active during the acclimation period,
as many were exposed on the bottom or swimming. These quickly
redistributed themselves to the spaces between basal portions of
blades by the time fish began to forage.

Pipefish foraging behavior is characteristic and entails slow
swimming or snake-like movements along the bottom with frequent
pauses (up to a minute), during which the head is slowly moved up and
down and side to side. This appears to be methodical examination of
the surroundings, with examination of individual shoots for prey.
Detection of an amphipod involved sudden fixation of both eyes upon
the amphipod and a rapid closing of the distance between fish and
prey. This was followed by a variable period of positioning (1-20
sec), as the fish examined the amphipod and attempted to get within
striking distance ($\pm$1 cm). Sometimes fish backed away from the prey,
but returned to initiate an attack. Attack consisted of a quick
thrusting forward of the head to bring the mouth to within 2-6 mm of
the amphipod, combined with a rapid expansion of the buccal and
opercular chambers. The propensity to attack seemed to depend upon
the amphipod's degree of physical exposure. Amphipods nestled deep
between the basal portions of grassblades were often scrutinized and

abandoned, while exposed amphipods were more often attacked. Amphipod movement also appeared to result in a higher probability of attack.

Prior to an attack, amphipods did not obviously alter their behavior as a fish drew near. Fish could approach to within several mm of amphipods without disturbing them. However, unsuccessful attack led to evasive behavior by amphipods: rapid swimming. Amphipods fleeing through vegetation were rarely pursued, or only pursued for short distances (5-10 cm). Fish held in nonvegetated aquaria often pursued and repeatedly attacked amphipods. Small amphipods were usually sucked directly through the snout and swallowed in 1-2 sec. Larger amphipods often became stuck in the mouth or snout and took longer to swallow, requiring numerous gulps, and resulting in longer handling times.

Encounter, attack, success and consumption

ANOVA indicated a significant effect of habitat, fish size, and prey size upon encounter rate, a significant interaction between habitat and fish size, and a significant 3-way interaction (Table 1, Fig. 1). Two-way ANOVA for small fish showed no effect of habitat upon encounter rate, a significant effect of prey size, and no interaction between habitat and prey size. Two-way ANOVA for large fish indicated a significant effect of habitat, no effect of prey size, and a significant interaction between habitat and prey size. Small fish showed the same response of in both habitats: increasing encounter rate with increasing prey size. Large fish had different responses to the two habitats: no effect of prey size in the wide

Table 1. Summary of analysis of variance (ANOVA) for natural log transformed (ln(x+1)) encounter rates.

Three-way ANOVA

Source	SS	df	F	Sig
Habitat	1.442	1	32.493	.000
Fish Size	1.377	1	31.026	.000
Prey Size	.391	2	4.401	.016
Hab X Fish	.706	1	15.907	.000
Hab X Prey	.903	2	1.052	.355
Fish X Prey	.038	2	.430	.652
Hab X Fish X Prey	.378	2	4.263	.019
Unexplained	2.663	60		

Two-way ANOVA: Large fish

Habitat	2.083	1	45.408	.000
Prey Size	.143	2	1.556	.228
Hab X Prey	.327	2	3.567	.041
Unexplained	1.376	30		

Two-way ANOVA: Small fish

Habitat	.065	1	1.516	.228
Prey Size	.286	2	3.335	.049
Hab X Prey	.145	2	1.685	.202
Unexplained	1.287	30		

Figure 1. Mean ($^+_-$ 1 standard error) encounter rates (encounters
min^{-1}) of pipefish with amphipods across two habitats (wide and
narrow leaf), two fish sizes, and three amphipod sizes.

Large Fish   **Small Fish**

Legend
- - - - - Narrow Leaf
——— Wide Leaf

ENCOUNTERS PER MINUTE

3.0
2.5
2.0
1.5
1.0
.5

5 6 7   5 6 7

AMPHIPOD SIZE (in mm)
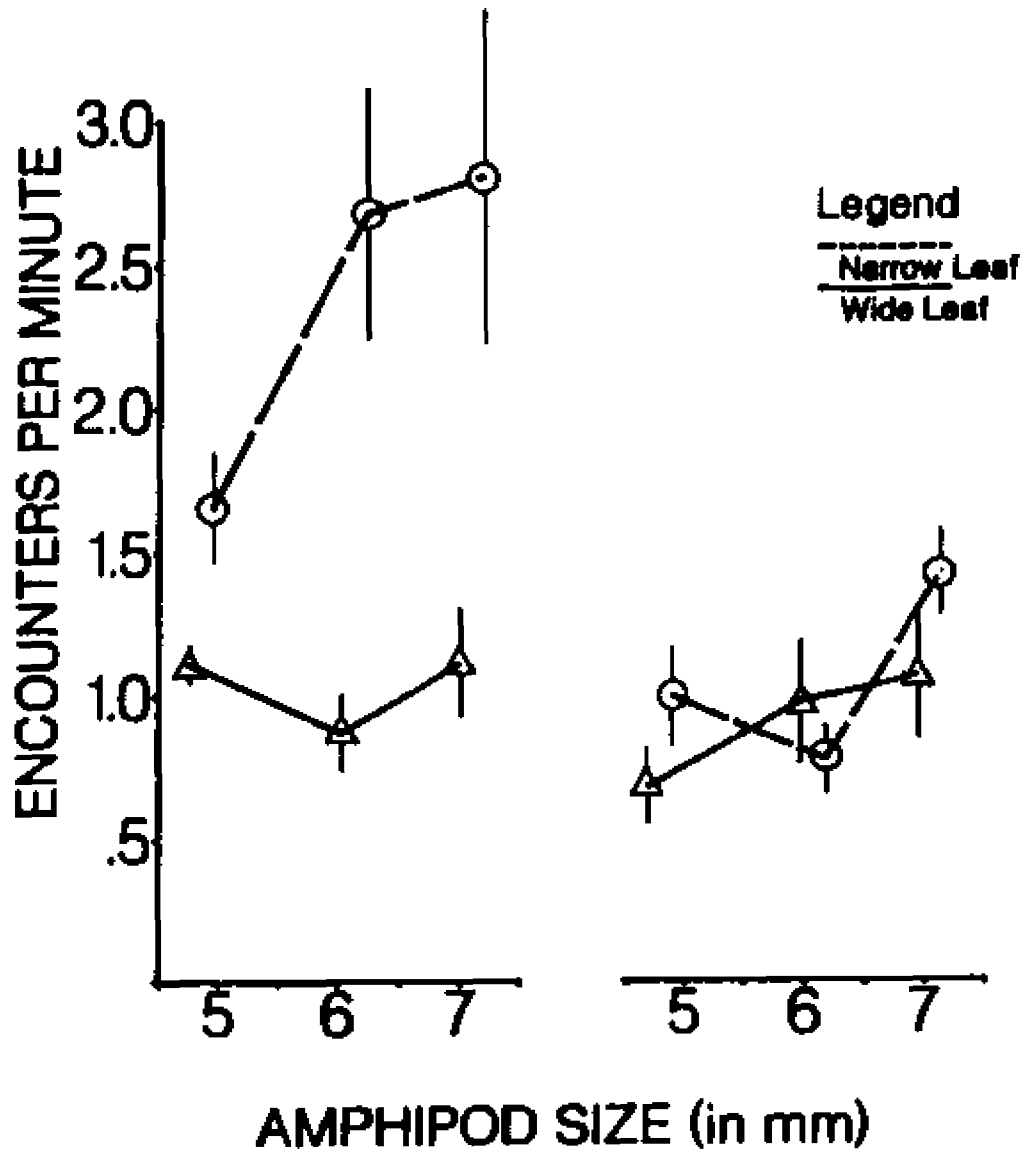
leaf (high-complexity) habitat, and increasing encounter rate with increasing prey size in the narrow leaf (low-complexity) habitat. Small fish in both habitats, and large fish in the wide leaf habitat, showed encounter rates of comparable magnitude. These fish reacted to amphipods at short distances (<10 cm), and foraged in a slow deliberate manner. Large fish foraging in the narrow leaf habitat had higher encounter rates, reacted to amphipods from a greater distance (<15 cm), and foraged more rapidly.

For attack probability, ANOVA indicated significant effects of habitat and fish size, a significant interaction between habitat and fish size, and a significant interaction between habitat and prey size (Fig 2, Table 2). Two-way ANOVA indicated no effect of habitat or prey size, or their interaction for small fish. For large fish, Two-way ANOVA indicated a significant effect of habitat, no effect of prey size, and a significant interaction between habitat and prey size. Two-way ANOVA for small fish indicated no effect of habitat, prey size, or their interaction upon attack probability. Although the effect of prey size upon attack probability for small fish was not significant (p=0.051), there was a strong trend for decreasing attack probability with increasing prey size, regardless of habitat. Attack probability increased with increasing prey size for large fish in the wide leaf habitat, but decreased with increasing prey size in the narrow leaf habitat. A relative size ratio (prey size/fish snout length (measured from mouth to corner of eye)) was used to standardize various amphipod-fish combinations. In the narrow leaf habitat attack probability decreased with increasing size ratio. In the wide leaf habitat highest attack probabilities occurred at

Table 2. Summary of analysis of variance (ANOVA) for attack
probabilities.

Three-way ANOVA

Source	SS	df	F	Sig
Habitat	.123	1	3.996	.050
Fish Size	.194	1	6.310	.015
Prey Size	.062	2	1.012	.369
Hab X Fish	.213	1	6.948	.011
Hab X Prey	.265	2	4.324	.018
Fish X Prey	.191	2	3.105	.052
Hab X Fish X Prey	.124	2	2.026	.141
Unexplained	1.841	60		

Two-way ANOVA: Large fish

Habitat	.330	1	12.632	.001
Prey Size	.020	2	.379	.688
Hab X Prey	.375	2	.187	.003
Unexplained	.783	30		

Two-way ANOVA: Small fish

Habitat	.006	1	.176	.677
Prey Size	.233	2	3.301	.051
Hab X Prey	.015	2	.212	.810
Unexplained	1.058	30		

Figure 2. Mean ($\pm$ 1 standard error) attack probability (attacks encounters^{-1}) for large and small fish in the two habitats.

Large Fish   Small Fish

SIZE RATIO

.4   .5   .6   .7 .8 .9 1.0

Legend
Narrow Leaf
Wide Leaf

ATTACKS\ENCOUNTERS

.9
.8
.7
.6
.5

5   6   7   5   6   7
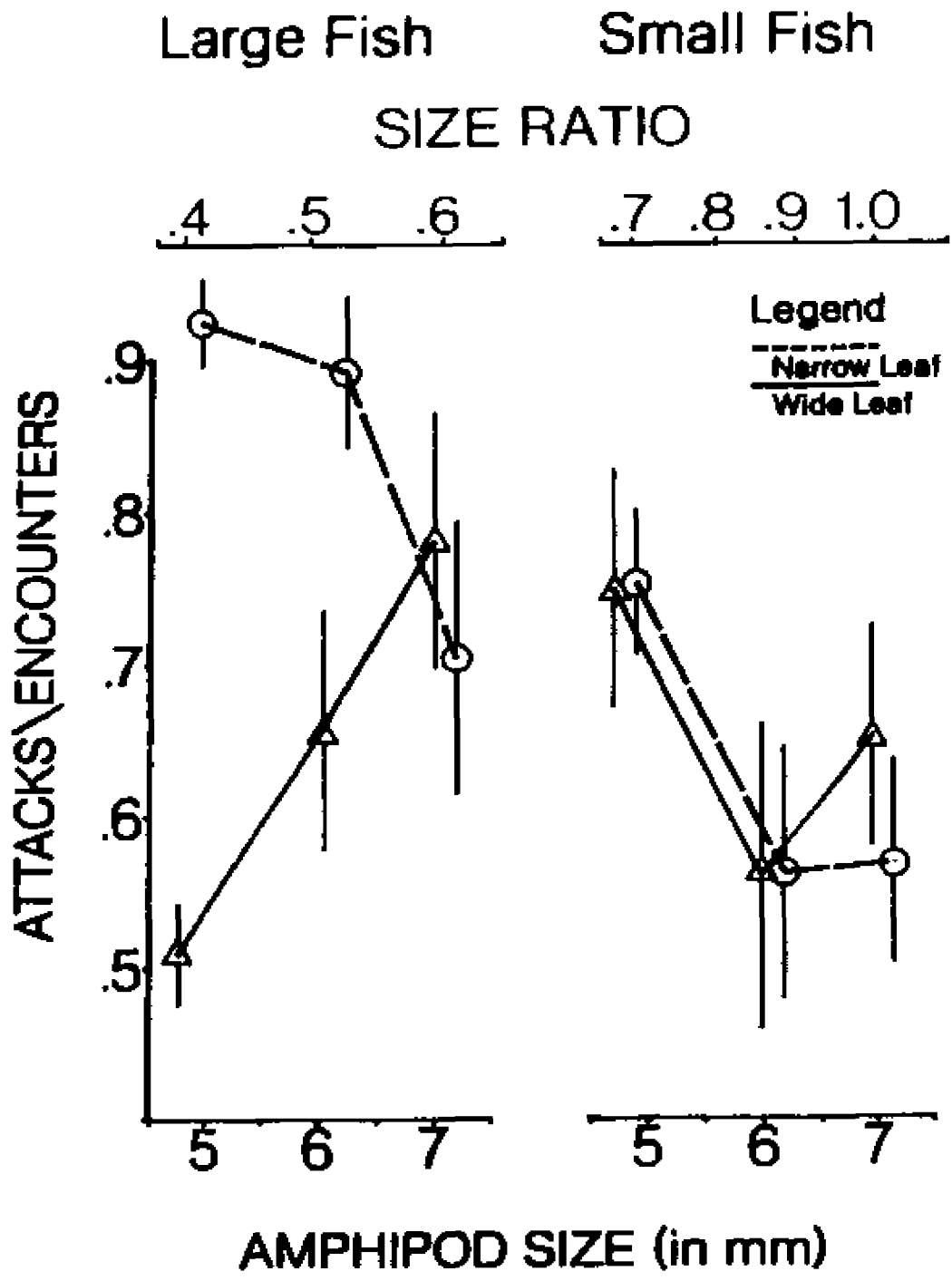
AMPHIPOD SIZE (in mm)

intermediate size ratios (large amphipod/large fish, small
amphipod/small fish).

ANOVA indicated a no effect of habitat upon success, but
significant effects of fish size, prey size, interaction between
habitat and prey size, and interaction between fish and prey size
(Table 3, Fig. 3). Two-way ANOVA indicated no effect of habitat,
prey size, or their interaction upon success for large fish. Two-way
ANOVA for small fish indicated no effect of habitat, a significant
effect of prey size, and no significant interaction. Success tended
to decrease with increasing prey size in both habitats, although this
trend was not significant for large fish (p=0.077). Overall,
success probability decreased with increasing size ratio.

Kruskal-Wallis ANOVA indicated a significant effect of fish size
upon the rate of amphipod consumption (Table 4, Fig. 4). Two-way
ANOVA for large fish indicated a significant effect of habitat, but
no effect of prey size or interaction between habitat and prey size.
Two-way ANOVA for small fish indicated no effect of habitat, or the
interaction between habitat and prey size, but a significant effect
of prey size. Large fish demonstrated higher consumption rates in
the the narrow leaf habitat across prey sizes. Small fish
demonstrated decreasing consumption rates with increasing prey size
in both habitats.

Table 3. Summary of analysis of variance (ANOVA) for success probabilities.

Three-way ANOVA

Source	SS	df	F	Sig
Habitat	.002	1	.053	.818
Fish Size	.978	1	25.076	.000
Prey Size	1.083	2	13.885	.000
Hab X Fish	.037	1	.937	.337
Hab X Prey	.337	2	4.322	.018
Fish X Prey	.546	2	6.998	.002
Hab X Fish X Prey	.029	2	.375	.689
Unexplained	2.340	60		

Two-way ANOVA: Large fish

Habitat	.028	1	.937	.341
Prey Size	.167	2	2.792	.077
Hab X Prey	.092	2	1.532	.232
Unexplained	.897	30		

Two-way ANOVA: Small fish

Habitat	.011	1	.220	.642
Prey Size	1.462	2	15.195	.000
Hab X Prey	.275	2	2.856	.073
Unexplained	1.443	30		

Figure 3. Mean ($\pm$ 1 standard error) success probability

(successes attacks^{-1}) for large and small fish in the two

habitats.

Large Fish   Small Fish

SIZE RATIO

.4   .5   .6   .7 .8 .9 1.0

SUCCESSES\ATTACKS

.8

.6

.4

.2

Legend

Narrow Leaf
Wide Leaf

5   6   7   5   6   7

AMPHIPOD SIZE (in mm)
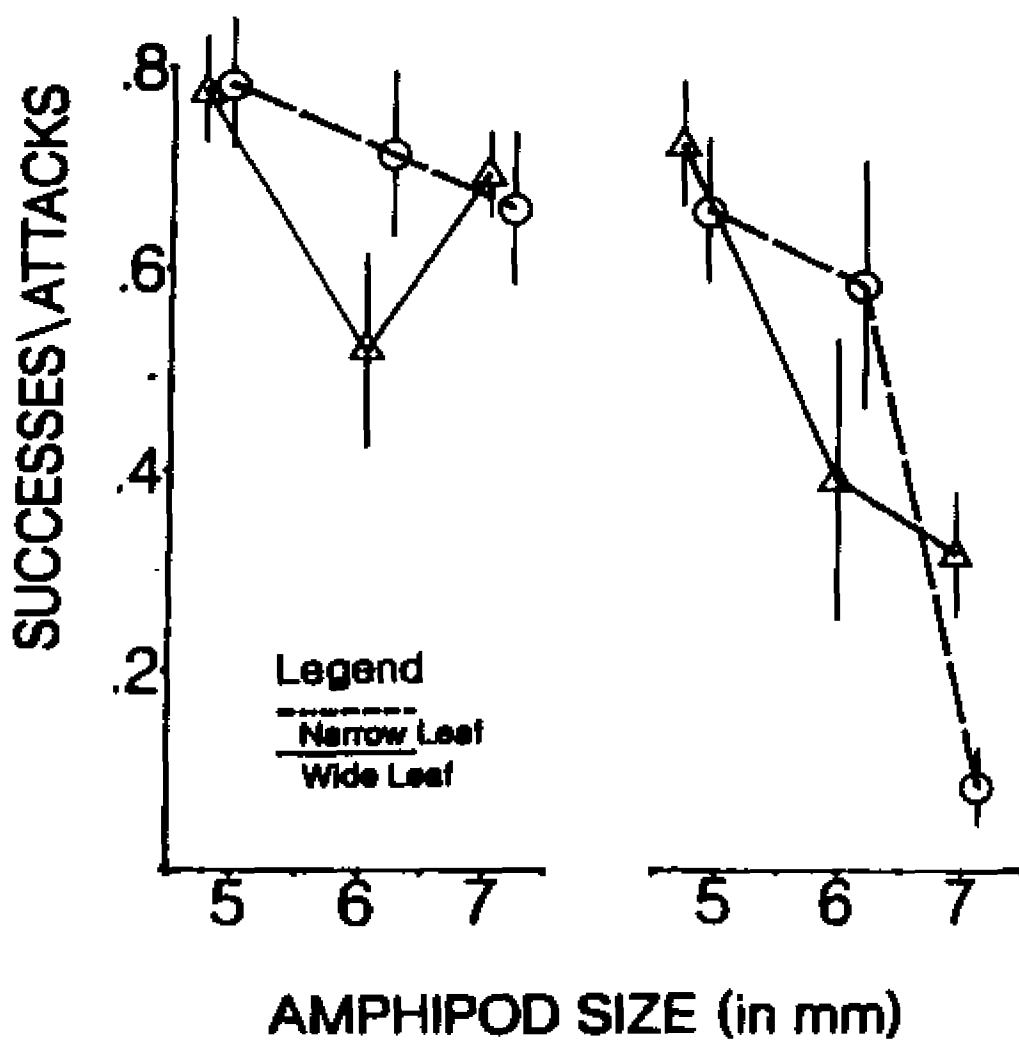
Table 4. Summary of statistical analysis of natural log (ln(x+1)) transformed consumption rates.

Kruskal-Wallis One-way ANOVA

	Mean Rank	Cases
Small fish	23.39	36
Large fish	49.61	36

Chi-square=28.258

p=0.000

Two-way ANOVA: Large fish

Source	SS	df	F	Sig
Habitat	1.662	1	27.506	.000
Prey Size	.020	2	.163	.850
Hab X Prey	.270	2	2.231	.125
Unexplained	1.812	30		

Two-way ANOVA: Small fish

Habitat	.001	1	.107	.746
Prey Size	.261	2	9.772	.001
Hab X Prey	.055	2	2.068	.144
Unexplained	.401	30		

Figure 4. Mean ($\pm$ 1 standard error) amphipod consumption rates
(amphipods eaten min^{-1}) for large and small fish in the two
habitats.

Large Fish **Small Fish**

AMPHIPODS PER MINUTE

2.0
1.6
1.2
.8
.4

Legend
- - - - - - -
Narrow Leaf
Wide Leaf

5 6 7   5 6 7

AMPHIPOD SIZE (in mm)
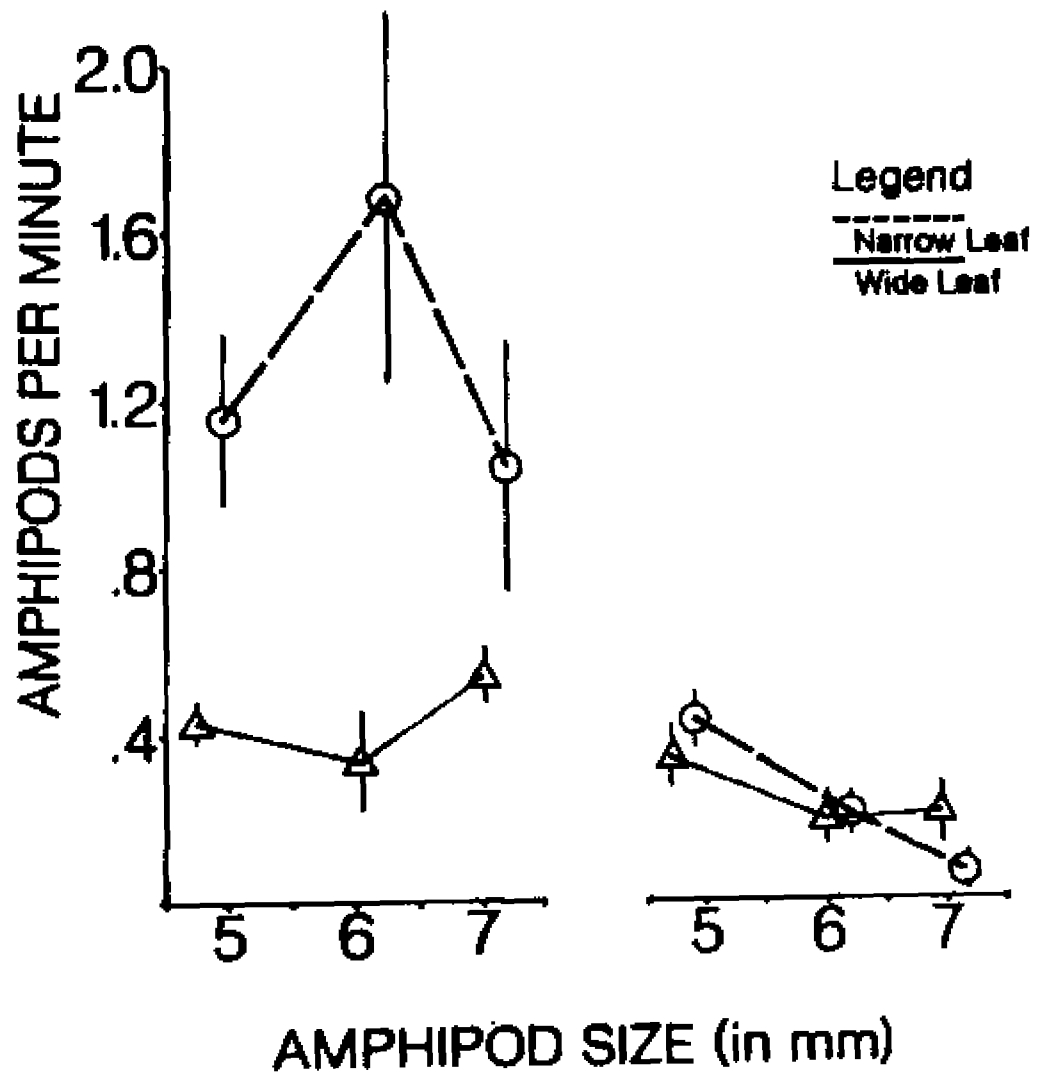
DISCUSSION

The approach of this study was to divide predator efficiency into separately measurable components or mechanisms: encounter, attack and success. The change in grassblade architecture from wide to narrow leaves was predicted to have separate and independent effects upon these mechanisms. Encounter rates should have increased with decreased vegetation complexity (blade width). Amphipods should have been more visible positioned between narrow as opposed to wide leaves. Also, the lowered total vegetation surface area of narrow leaves should have impinged less than wide leaves upon the distance at which amphipods were detected. The distance at which fish react to prey increases with prey size, with the reactive field volume (RFV) roughly proportional to the cube of prey size (Werner and Hall 1974; O'Brien et al. 1976; Gibson 1980; Eggers 1982; Wetterer and Bishop 1985). However, it should be noted that the shape of this volume will depend upon water depth, and/or fish position in the water column. For a bottom swimming fish like S. fuscus a hemispherical volume seems more appropriate. Encounter rate for a fish-amphipod size combination will be proportional to the product of prey density and the reactive field volume. In its original formulation (Werner and Hall 1974) the reactive field volume model (RFVM) was developed as a null model of prey encounter to be compared with observed patterns of prey selection. In the present study fish were presented only one prey size in any experiment. As a result, here the RFVM is considered a model of prey encounter, not a model of prey selection. There was a general trend, although not significant for all fish-habitat combinations, for encounter rate to increase

with amphipod size. This may be attributable to two related factors. Larger amphipods were probably seen at greater distance and were therefore encountered more often. Also, larger amphipods may have been more conspicuous between grass blades. An impression as to the relative importance of these factors may be gained by an examination of the effect of habitat upon encounter rates of small fish.

Small fish showed no response to change in habitat, indicating that neither increased RFV or increased visibility of amphipods, due to decreased shelter quality, facilitated encounter. In contrast, Stoner (1982) found amphipods to be more readily detected by pinfish on the narrow (<1 mm) blades of _Halodule wrightii_ than on wider (>6 mm) blades of _Thalassia testudinum_. Unfortunately, as Stoner did not standardize his treatments according to vegetation surface area or shoot density it is unclear whether this response was the result of altered RFV or shelter quality. Small pipefish may have small reactive volumes that were not impinged upon by either habitat. It also appears that the pipefish's methodical foraging tactic is efficent across a range of habitat complexities, and for the levels of habitat complexity examined here, increased quality of hiding places between wider leaves did not lower an amphipod's chances of being detected.

Large fish in the wide leaf habitat had encounter rates comparable to small fish, but had greatly increased encounter rates in the narrow leaf habitat. This did not appear to be the result of increased search speed. Instead, these fish reacted to amphipods at greater distance. I suggest that greater eye size in these fish resulted in greater reactive distance. Reactive distance will depend

upon visual acuity, which is in turn dependent upon eye size. Increase in eye size results in larger pupillary aperture and a larger retinal image, and since the decrease in retinal resolving power is proportionately less than the increase in retinal image, visual acuity increases with increasing eye size (Northmore, Volkmann, and Yager 1978). In the narrow leaf habitat visual interference from vegetation may have reduced the RFV of large fish to a size comparable to the RFV of small fish. Reduced visual interference in the narrow leaf habitat allowed large fish to utilize their greater visual capabilities. Hence, there may be size-specific thresholds of vegetation density at which vision becomes restricted. Other authors have suggested that threshold effects exist (Glass 1971; Ware 1972; Vince et al. 1976; van Dolah 1978; Nelson 1979; Coen et al. 1981; Heck and Thoman 1981; Stoner 1982; Crowder and Cooper 1982). Assuming large fish have discriminatory capabilities similar to those of small fish, within the limits of their respective RFVs, it is probable that increased reactive volume, and not lowered shelter quality for amphipods, was the primary cause of increased encounter in the narrow leaf habitat.

An alternative explanation of these results involves size dependent risks, as perceived by pipefish, associated with foraging in the two habitats. Small fish, possibly at greater risk from predators, might forage more slowly than large fish in the narrow leaf habitat, adopting a strategy of "movement minimization" (Pough and Andrews 1985), as doing so would make them less conspicuous. But as no pipefish-predators were used in this experiment, this would imply that pipefish have a fairly rigid repertoire of behavior. This

implication does not conform to the emerging pattern of plasticity of behavioral response which has been demonstrated for both vertebrate (Werner et al. 1983a, 1983b, Petranka et al. 1987) and invertebrate prey (Holomuzki personal communication).

Probabilistic attack can depend upon a number of factors: hunger level (Kislalioglu and Gibson 1976, Bence and Murdoch 1986), prey profitability (Werner and Hall 1974, Eggers 1977), apparent size of prey (O'Brien et al. 1976, Wetterer and Bishop 1985), and prey motion (Zaret 1980a). I sought to minimize the effects of changing hunger level (i.e. satiation) through uniform pre-trial starvation and by keeping experimental trials short in duration. I assume that profitability is determined by amphipod size, which I have controlled. I further assume that apparent size, as a criteria for selection between simultaneously encountered prey, is not relevant in the context of this study. Amphipod densities were low, so that simultaneous encounters did not occur often. When they did, multiple amphipods were encountered upon a single shoot, and being of the same size, probably had comparable apparent sizes. In such instances I noted that amphipod motion often drew attack from pipefish. Main (1985) also reported that both _Syngnathus floridae_ and _Lagodon rhomboides_ concentrated attacks upon moving, as opposed to motionless prey.

Another factor relevant to pipefish foraging involves the probability of an attack resulting in consumption of the prey. Pipefish often unsuccessfully attack prey, and often decline to attack encountered prey. If foraging tactics are contributors to fitness and natural selection acts upon them, predators should

develop behaviors that eliminate, or minimize unsuccessful attacks. Therefore, probabilistic attack should be related to the chances for success. I suggest that for this study probabilistic attack was determined by two interacting and often opposing factors: the relative size of amphipod and fish, and size-dependent ability of amphipods to utilize available refugia. Leaf architecture was expected to have size-specific effects upon probability of attack once an amphipod had been detected. Narrow leaves would afford little protection to amphipods, regardless of size, and probabilistic attack would decrease with increasing size of amphipods relative to pipefish size. Wide leaves would afford greater protection to amphipods when the fish was large relative to the amphipod: a large fish would not be able to get its mouth close enough to attack a small amphipod nestled far down between grassblades, where as a small fish would. This implies that there may be a relative size (amphipod/fish size) threshold below which attack probabilities decrease as amphipods become less vulnerable due to refugia use, and above which attack probability also decreases as amphipods become less vulnerable due to larger relative size. This would give rise to a humped distribution of attack probabilities, with peak probability of attack at intermediate size ratios.

The attack probabilities for the two habitats match the predictions of this model. In the wide leaf habitat, as prey became smaller relative to the predator, the more vulnerable they became, until a refuge threshold was reached, after which they became increasingly less vulnerable. In the narrow leaf habitat the refuge threshold was eliminated. Only two fish sizes and three amphipod

sizes were used in this study. The prey-predator size ratios for the two fish sizes were disjunct (i.e no overlap) and it could be argued that the observed results are due to distinct behavioral differences between the two fish sizes, irrespective of relative size considerations. However, in a concurrent study (Ryer 1987) I augmented the data for the wide leaf habitat with one additional amphipod size class (7 mm) and one fish size class (160 mm), resulting in six additional amphipod-fish size combinations. There was overlap of amphipod-fish size ratios between each fish size class, and the additional means also conformed to the predicted humped distribution. Stein (1977) found small crayfish to be preferentially consumed by smallmouth bass on sand substrates, while intermediate size crayfish were consumed on pebble substrates. As in the present study, small prey were able to decrease their vulnerability by retreating into the spaces between structure, taking advantage of size dependent refuges.

I also noted in this study that Gammarus spp. appeared to be unaware of, or did not respond to fish until attacked. Main (1987) demonstrated that a marine shrimp, Tozeuma carolinense, displays elaborate avoidance behaviors in response to approaching predators. Yet, avoidance behavior may be subtle, and need not occur at the time of encounter. It has been demonstrated that both vertebrate (Petranka et al. 1987) and invertebrate prey (Holomuzki personal communication.) can detect fish predators by chemical cues, and modify their distributions. Since most amphipods were between basal portions of blades, microhabitat preference for these locations may be an adaptation to decrease susceptibility to predators. Wellborn

and Robinson (1987) demonstrated that odonate larvae positioned in the axil areas of _Sagittaria platyphylla_ plants are less susceptible to predation by sunfish than exposed larvae. For amphipods, microhabitat selection and refuge utilization appear to be more important in mediating predation than post-encounter avoidance behaviors.

A final prediction of this study was that behavioral plasticity in pipefish (attack probability) would minimize unsuccessful attacks, giving rise to consistent patterns of success, independent of habitat. The probability of predator success will be related to escape capabilities of prey (Swift and Fedorenko 1975; O'Brien 1979; Scott and Murdoch 1983; Bence and Murdoch 1986), mechanical limitations of the predator such as mouth gape (Zaret 1980b, Scott and Murdoch 1983), and degree of prey vulnerability. Many of the prey species consumed by _S. fuscus_ have a broad range of sizes, and mouth gape puts an upper limit upon prey sizes consumed in the field (Ryer and Orth 1987). Larger amphipods, when attacked, often were not sucked fully into the mouth and escaped by rapidly swimming away. It appears that vegetation enhanced the escape capabilities of amphipods by allowing them to get out of the visual field of pipefish. I have observed pipefish to pursue and repeatedly attack amphipods in aquaria without any vegetation, but in the two vegetated habitats examined here pipefish rarely pursued amphipods after an unsuccessful attack. For epifaunal and swimming prey, the ability to escape a pursuing predator by placing obstructions in its visual field, may be one of the chief mediatory effects of increased habitat complexity. In the present study habitat type had no overall effect

upon success probabilities, although for two specific amphipod-
pipefish combinations there appears to have been an effect of
habitat. Prey size had less of an effect upon large fish than small
fish. This indicates the the relationship between relative size and
success may be nonlinear: success decreases slowly at first with
increasing prey size, and then more rapidly as prey approach the
maximum the fish is capable of consuming.

The rate at which predators consume prey is a function of the
rate of prey encounter, vulnerability or accessibility of prey, and
the ability of the predator to capture prey. In turn, each of these
steps in the foraging sequence may be dependent upon predator size,
prey size, habitat complexity, and their interactions. Other studies
have examined how vegetation density affects predator efficiency
(Nelson 1979; Coen et al. 1981; Heck and Thoman 1981; Savino and
Stein 1982; Stoner 1982), but have not necessarily provided an
understanding of how habitat complexity affects the fundamental, more
mechanistic, aspects of foraging. In this study, conclusions based
solely upon results of consumption rates would have overlooked many
of the more interesting effects of prey size, predator size, and
habitat complexity.

Recent literature demonstrates that fish tend to maximize their
rates of energy aquisition, through both prey selection (Werner and
Hall 1974; Stein 1977; Mittelbach 1983) and habitat use (Werner and
Hall 1979; Mittelbach 1981; Werner et al. 1981; Crowder and Cooper
1982). Based upon the findings presented here it would appear that,
provided other factors such as prey density and predatory risk are
comparable between habitats, larger sized pipefish would be able to

maximize rates of encounter with prey by occupying sparsely or patchily vegetated areas. Similarly, choice of vegetation with narrower, or otherwise simpler architecture, would increase the proportion of prey actually available to fish. The conceptual model for pipefish attack probability presented here, may be generally applicable, and prove useful in the study of other predator-prey interactions in structured habitats. It also demonstrates that prey, even though they are of the same size, may be perceived as fundamentally different by predators, as a result of their vulnerability. This has particularly important implications for optimization studies, where all prey of a given size are usually assumed to be uniformly available to the predator. If, for a given prey size or species, there is a distribution of vulnerabilities due to differential use of habitat complexity, this distribution must be taken into account in the calculation of prey profitabilities. Finally, the fact that success probability for amphipod-fish size combinations remained relatively uniform across habitats, despite changing prey encounter rates and vulnerabilities, indicates that pipefish may be utilizing flexible foraging tactics to maintain consistent patterns of success.

CHAPTER 2

PREY SIZE SELECTION BY PIPEFISH: A COMPARISON OF
MECHANISTIC AND OPTIMAL FORAGING MODELS.

INTRODUCTION

A major premise of modern ecology is that natural selection favors organisms that maximize design criteria related to overall fitness. Design criteria may be structural, such as the length of a limb, or they may be behavioral. Foraging strategies, a class of behavioral criteria that are often assumed to be major contributors to overall fitness, have received a great deal of attention in the last two decades, and when integrated with the concept of "optimization" has led to the generation of a large body of literature referred to as "optimal foraging theory". A wide diversity of visually oriented vertebrate and invertebrate species are seemingly capable of altering their foraging behavior, either with respect to prey or patch selection, to maximize energy intake (Pyke, Pulliam, and Charnov 1977; Krebs and McCleery 1984; and references therein).

Such adaptive behaviors can have profound impacts upon community dynamics, with perhaps the best documented example being found in the study of lake zooplankton communities. Selection of large zooplankters by fish results in the competitive release of smaller zooplankton species which often dominate lacustrine systems (Brooks 1968; Brooks and Dodson 1965). In the absence of planktivorous fish these systems are dominated by competitively superior large zooplankton species. The selection of large prey under conditions of high prey density conforms to the predictions of optimal foraging theory (Werner and Hall 1974; Mittelbach 1981). However, there may be an alternate explanation for observed prey size preference by

planktivorous fish. The "apparent size hypothesis" (O'Brien et al. 1976) states that rather than making decisions with respect to rates of energy intake, fish use a simple tactical "rule of thumb": choose the apparently largest prey in the visual field. The predictions of these two models; optimization vs. apparent size, are similar over a range of prey sizes and densities, which has made experimental differentiation between them difficult (Gibson 1980; Eggers 1982; Wetterer and Bishop 1985).

Submerged aquatic macrophytes form a conspicuous and important habitat type in both freshwater and marine systems. Predator efficiency generally decreases with increasing vegetation density and/or complexity (Heck and Thoman 1981; Crowder and Cooper 1982). But the mechanisms by which this occurs are poorly understood (Main 1987; Ryer 1987; Welborn and Robinson 1987). The northern pipefish (Syngnathus fuscus) is an abundant inhabitant of vegetated shallows in the Chesapeake Bay (Mercer 1973; Orth and Heck 1980; Ryer 1981). Pipefish consume small crustaceans, with gammarid amphipods being preferred by adult fish (Mercer 1973; Ryer and Orth 1987). Examinations of guts have indicated that pipefish consume predominantly small amphipods (Ryer and Orth 1987), despite their ability to consume larger individuals. This is markedly different from the pattern of selection for large prey exhibited by many microcarnivorous fish species (Werner and Hall 1974; Nelson 1979; Zaret 1980b; Mittelbach 1981). An ecologically pertinent question is whether this pattern is the result of mechanistic processes or active prey size selection by pipefish? Additionally, if pipefish are

actively selecting for small prey, does this behavior conform to predictions of selection models developed for open-water habitats?

In this paper I will examine the usefullness of two optimal foraging models, as well as a mechanistic alternative model, for describing prey size selection by _Syngnathus_ _fuscus_, in a simulated seagrass habitat.

The Models

Mechanistic model

This model allows for no preference for one prey size over another. Patterns of prey consumption are determined by fish and prey size, and their effects upon rates of encounter, probabilities of attack, and success. It is assumed that estimates of these variables, from experiments where different predator-prey size combinations are examined separately, may be used to construct sub-models of encounter, attack, and success that predict the behavior of fish feeding on mixed-size prey populations. The mechanistic model, is the result of the compounding effects of these sub-models:

$$C_{ij} = B_{ij}A_{ij}S_{ij} \tag{1}$$

where C_{ij} is consumption, by fish size i, of amphipod size j (amphipods ingested min^{-1}), B_{ij} is the rate of encounter, A_{ij} is the probability of attack, and S_{ij} is probability of success. This is operationally similar to functional response models (Holling 1959) when handling time is small enough to be ignored, with the shape of the curve being dependent upon density dependence of encounter.

The reactive field volume model (RFVM) has been generally adopted as a null model of prey encounter (Werner and Hall 1974; Eggers 1982; Wetterer and Bishop 1985; Newman 1987) against which strategies of prey selection may be tested. The distance at which prey can be detected increases with prey size, resulting a greater reactive volume and higher encounter rates for large prey. Similarly, increased eye size also results in increased visual acuity, giving rise to a larger reactive volume (Northmore et al. 1978). For the purposes of the mechanistic model, the effects of prey size, prey density, and fish size on encounter rate (B_{ij}) are accounted for by fitting a general multiple regression model to experimental data.

Once a prey has been detected (i.e. encounter), a fish may react in one of two ways: attack, or continue searching. Assuming that other factors such as prey movement and crypsis are equal, the decision to attack will depend upon prey vulnerability: the relative ease with which the prey may be extracted from the habitat and consumed. The probability of attack is proportional to the mean vulnerability of amphipods of that size. Vulnerability is the product of two opposing functions: relative size-inferred and habitat-inferred vulnerability. As an amphipod increases in size relative to a pipefish, it becomes increasingly difficult to capture and consume. Given that behaviors of both amphipods and pipefish remain the same over a range of sizes, as the ratio of amphipod to fish size increases, the vulnerability of amphipods decreases. However, increasing relative size also makes amphipods more vulnerable. Amphipods reduce their vulnerability to predators by

positioning themselves between the basal portions of leaves, and
amphipods that are small relative to fish are able to get far enough
down between leaves so that they are relatively invulnerable.
Amphipods that are large relative to fish, although positioned
between leaves, are still vulnerable: the fish can get it's snout
into the refuge space. Dependent upon refuge architecture, there
will be a critical size ratio threshold above which amphipods are
highly vulnerable, and below which decreasing relative size results
in decreasing vulnerability. Balancing of these opposing functions
results in a distribution of vulnerabilities characterized by highest
vulnerability at intermediate size ratios, and decreasing with either
increasing or decreasing size ratio. However, if amphipods are too
large to make effective use of refuges (e.g. leaves are very narrow),
then vulnerability will be determined by the relative size of
amphipod and fish, regardless of refuge. Ryer (1987) has
demonstrated that changes in attack probabilities, in response to
changing refuge architecture, qualitatively match the predictions of
this model. A mathematical representation of the attack probability
(A_{ij}) sub-model is

$$A_{ij} = [(1 - \frac{R_{ij}}{M})(\frac{R_{ij}}{Q})]^L \tag{2}$$

where R_{ij} is amphipod size/fish size ratio, M is the largest ratio at
which attack occurs, Q is the ratio below which amphipod
vulnerability is decreased through use of refugia, and L is a curve

shaping coefficient. Also the function has imposed constraints: if $R_{ij} > M$, then $R_{ij}/M = 1$, and if $R_{ij} > Q$, then $R_{ij}/Q = 1$.

The probability of successful attack (S_{ij}) is related to the relative size of the fish and amphipod, and can be described by:

$$S_{ij} = [(\frac{W - R_{ij}}{W})]^K \tag{3}$$

where W is the maximum size ratio at which attacks are successful, and K is a curve shaping coefficient. As before, the equation has imposed constraints: if $R_{ij} > W$, then $R_{ij} = W$.

Energy maximization/optimization model

This model is similar to optimal foraging models developed for other predators (Werner and Hall 1974; Charnov 1976; Mittelbach 1981). The net rate of energetic intake can be described by

$$E_n/T = \frac{\sum_{i=1}^{n} (A_{ij} B_{ij} V_{ij})}{1 + \sum_{i=1}^{n} (A_{ij} H_{ij})} \tag{4}$$

where
$$V_{ij} = S_{ij}(ae_i) \tag{5}$$

E_n is the energy available (calories) from prey (i=1..n) during time interval T, V_{ij} is the energetic value (calories) of an amphipod to pipefish, H_{ij} is handling time, a is the assimilable fraction of

amphipod energy content, and e_i is the energy content (calories) of
amphipods. A_{ij}, B_{ij}, and S_{ij} are as previously defined.

The optimal diet maximizes energy intake. Prey sizes are ranked
according to profitability (V_{ij}/H_{ij}) and then added to the diet until
energetic intake is maximized. The assimilable fraction of prey
energy (a) is assumed to be independent of fish and prey size, and a
value of 0.7 was adopted (Mittelbach 1981). The energy content of
amphipods was assumed to be linearly related to amphipod body mass,
and estimated using a value of 4050 cal g dry wt^{-1} (Cummins and
Wuycheck 1971) and equations relating amphipod size and weight
(Fredette and Diaz 1986). All other parameters in the model were
determined as part of this study.

This model differs from others by inclusion of attack
probabilities (A_{ij}) and success probabilities (S_{ij}), which are also
attributes of the mechanistic model. Pursuit time, pursuit costs,
and search costs have been eliminated. Pipefish do not pursue
amphipods, which appear unaware of impending attack and make no
attempt to flee (Ryer 1987). Search is a slow process and is assumed
to represent a negligible energetic cost when compared with gains
associated from individual prey. In any case, all amphipods are
searched for simultaneously, utilizing the same strategy.

Diet breadth compression model

A second class of optimization models deals with time-
minimization (Schoener 1971). Time-minimizers select prey or prey
patches so as to minimize the time required to collect a set quantity
of energy. A predator might shift during a foraging bout, from

energy-maximization to time-minimization. During the initial stage of foraging the gut is empty and the predator selects prey to maximize intake (energy-maximization). As foraging continues, the rate of intake becomes limited by the gut passage (gastric processing). The predator now selects prey to minimize the time required to acquire the amount of food that can be accommodated by the gastric system. The result is a shift in optimization strategy, with concomitant diet breadth compression.

A simple model of gastric processing capabilities can be derived:

$$I_{max} = G_{max} - G \tag{6}$$

where I_{max} is the maximum quantity of food (g dry wt) that can be consumed during T, G_{max} is the gut capacity, and G is gut content (g dry wt). The gut content at time t (G_t) can be expressed as

$$G_t = G_{t-1} + I + P \tag{7}$$

where I is the quantity of food consumed and P is the quantity evacuated during the last time interval. As is typical of fish which consume large numbers of small prey (Jobling 1987), gastric evacuation in pipefish is dependent upon gut content and temperature, and is best described by a negative exponential function (Ryer and Boehlert 1983):

$$P = G_{t-1} - G_{t-1}e^{2.303TZ} - 1 \tag{8}$$

where Z is the evacuation rate constant. The temperature dependence of Z has been quantified (Ryer and Boehlert 1983):

$$Z = 0.002(N) - 0.015 \qquad (9)$$

where N is temperature in degrees centigrade.

This gastric processing model is linked with an optimization model (presented above) to predict switching from energy-maximization to time-minimization. As long as consumption is limited by aquisition from the environment (E_n/T, Eq. 4), energy will be maximized. But as gastric processing becomes limiting (I_{max}/T), the foraging strategy will shift to time minimization.

MATERIALS AND METHODS

Collection and holding of animals

Pipefish were collected from eelgrass (Zostera marina) meadows and held in undergravel filtered 38 l aquaria with a uniform density of artificial eelgrass (polypropylene ribbon) for a minimum of 1 week (maximum 4 weeks) prior to use in trials. Fish were fed a mixed diet of gammarid amphipods and 48 hour Artemia nauplii. Individual identification numbers were assigned to each fish so the experimental histories could be followed. Two Gammarus spp. were used in trials: G. mucronatus (collected from eelgrass) and G. palustrus (collected from Spartina alterniflora marshbanks). Both species are morphologically very similar (Bousfield 1973), and as is typical for free-living vegetation dwelling gammarids, are highly thigmotactic (Nagle 1968; van Dolah 1977; Stoner 1980). Both species preferred to occupy spaces between basal portions of grassblades, and interacted with pipefish in identical manners. I concluded that prey species would have no effect upon experimental outcomes. Amphipods were kept in undergravel filtered aquaria with sand substrate, and fed frozen, chopped spinach. Both pipefish and amphipods were kept at temperatures of 24-25°C, and experienced natural photoperiods.

Model parameter estimation

Experiments to determine the effect of fish and amphipod size on encounter rate, probabilities of attack and success, and handling time were set up according to a factorial design, employing 3 fish and 4 amphipod size-classes. All trials were conducted in aerated, static 38 l aquaria with sand substrate, artificial eelgrass, and an

overhead aquarium light to assure uniform illumination. River water (salinity range 16-24 ppt) was filtered (1 um) prior to use. Artificial eelgrass consisted of 60 shoots/aquaria (4 leaves/shoot, mean shoot length=11 mm) of artificial eelgrass (5 mm wide polypropylene ribbon). This density of shoots corresponds roughly to 480 shoots m^{-2}, and although low compared to reported field densities of _Zostera_ _marina_ (Orth 1977), provided enough habitat complexity to keep amphipods from congregating in aquarium corners, and still allowed observation of fish-amphipod interactions.

Fish size classes were small (110-130 mm), medium (150-170 mm), and large (180-200 mm total length). Fish were not used more than once within a treatment. However, due to limited supply, some fish were occasionally used more than once between treatments. Amphipods were sorted by mechanical sieving: class 1 (mean size=4.8 mm), class 2 (6.1 mm), class 3 (7.0 mm), and class 4 (9.6 mm, total length from base of 2nd antennae to the tip of uropods). Each size class represents the mean size retained in particular sieves. Repeated sieving, and discard of amphipods from intervening sieves eliminated any overlap between classes. Amphipods showed no apparent adverse effects due to sieving. For each combination of fish and prey size, six trials were conducted.

Trials were run during morning hours (maximum of 8 per day). Twenty-four hours prior to the trials, fish were introduced to the experimental aquaria (1 per aquarium). Twelve hours prior to trials, 50 amphipods were added and the aquaria immediately covered with black plastic. This allowed amphipods an acclimation period during which there was no risk of predation: pipefish are visual feeders

(Ryer and Boehlert 1983; personal observation). Trials were conducted individually and serially, thereby allowing observation of each trial. After the aquarium cover was removed and the aquarium light turned on, data recording was initiated when a fish first acknowledged a prey by attacking or by positioning in preparation to attack. A trial was terminated when: the fish stopped foraging (see description of foraging behavior below), the duration of the experiment exceeded 20 min, or 25% of the prey were consumed. The last criteria was included to insure that amphipod densities and distributions were not greatly altered, and the pipefish did not become satiated. Fish were observed at a distance of 50 cm in a darkened room, and my presence did not appear to effect fish behavior. Trials in which fish did not display typical foraging behavior (as described in results) were discarded and repeated. Data were keyed into a remote keyboard of a microcomputer running an event recording program. In this manner time sequencing and outcomes of all predator-prey encounter were recorded.

An encounter occurred when pipefish acknowledged an amphipod by simultaneously fixing both eyes upon it. An attack consisted of an attempt to consume the amphipod by thrusting forward the head with a concurrent inward sucking through the snout. An attack was successful when the amphipod was ingested.

In addition to the data generated from the above factorial design, 6 measurements of handling time for large fish feeding on class 5 (11.0 mm) amphipods were conducted. Handling time was the time starting when the amphipod was sucked into the mouth, and ending when it had been swallowed, gulping motions had ceased, and normal

gill ventilation began. After each experiment notes on foraging behavior were recorded.

Data were examined for conformation to the general assumptions of analysis of variance (ANOVA, Sokal and Rohlf 1981). Examination of normal deviates plotted against ranked observations (Rankit plot, Sokal and Rohlf 1981) indicated that data for encounter rate, attack, and success probability were normally distributed. Natural log (ln) transformation of handling time data resulted in normality. Encounter rates and attack probabilities were homoscedastic (Cochrans's C-test, Sokal and Rohlf 1981). Success probabilities were heteroscedastic due to high variance in one cell. Examination of observations from this cell revealed an extreme outlier (> 3 standard deviations from the mean). During 20-min this fish attacked only 4 amphipods (range of 9-22 for rest of fish in cell) and was 100% successful (mean cell success 39%). Elimination of this point, on the basis of it being an extreme outlier and due to the small number of individual observations from which it was derived, resulted in homoscedasticity. Variances were highly heterogeneous for handling times and could not be corrected through transformation (log, square root, arcsine). This was due to the high variance associated with the six class 5 amphipod measurements. Omitting these points, the remaining data set was homoscedastic when natural log transformed.

Residuals for each data set were examined to determine if the repeated use of fish might have resulted in non-independence of error terms. Fish which were used more than once were not characterized by

consistently high or low responses. I therefore concluded that repeated use of fish resulted in no experimental bias.

Statistical test results were considered significant at $p<0.05$. When analyses indicated significant effect of, or interactions between independent variables, generalized models were fit to the data using an iterative nonlinear least-squares regression approach (SAS ref). The solution was chosen that maximized the ratio of explained to total sums of squares. For handling time, the class 5 amphipod observations were re-admitted to the data set prior to model fitting.

A second experiment was conducted to determine the effect of amphipod density upon encounter rate. Class 2 amphipods were presented to large pipefish at densities of 25, 50, and 100 amphipods per aquaria, with 6 trials at each density. In all other respects trials were conducted as described above. A Rankit plot indicated data were normally distributed. Cochran's C-test indicated that data were homoscedastic and the effect of amphipod density tested by ANOVA. Data were modeled using linear regression (Sokal and Rohlf 1981).

Simulation models

Models were simulated on an Apple IIe microcomputer. Input to the models included simulation duration, stomach fullness at the being of the simulation, water temperature, number of fish aquarium^{-1}, fish length, and the number of amphipods in each size class (1 mm incremental classes). All three models were linked to the model of gastric evacuation. For both the mechanistic and simple

optimization models, when intake from the environment exceeded the processing capabilities of the gut, the rate of consumption was determined by gastric processing. This prevented fish from consuming unrealistic (as determined by the gastric model) numbers of amphipods. However, in both models the relative contribution of the various amphipod size classes to consumption remained proportional to those of the maximum intake. In the case of the diet breadth compression model, limitation of intake by gastric processing resulted in the partial or complete elimination of amphipod size classes from the diet, starting with the amphipod class ranked lowest in profitability. All equations were iterated at 0.1 hour intervals, with correction of amphipod abundance for losses due to pipefish predation.

Determination of size preference

To determine prey size preference and provide a data set against which to judge model predictions, a separate experiment was conducted on pipefish prey size selectivity. This experiment was conducted prior to completion of the simulation models, and hence was not designed with apriori knowledge of amphipod densities and size distributions that would be predicted to result in active size selection by pipefish. Amphipods were segregated into size classes by sieving. Size classes were re-mixed in fixed proportions to create 6 replicate groups of 140 amphipods. This density of amphipods (140 aquarium^{-1}) corresponds to roughly 1680 m^2, and is higher than field densities ($\sim$1000 m^2) at which pipefish have been observed to display disproportionate consumption of small amphipods

(Ryer and Orth 1987). One group was chosen at random and preserved for later measurement. Ten pipefish (mean size=154 mm total length, range 144-161) were introduced to the aquaria (2 fish per aquarium) 24 hour prior to the beginning of the experiment. The remaining 5 groups of amphipods were introduced to aquaria 12 hours prior to the experiment and the aquaria immediately covered. Experiments started when covers were removed. After 4 hours fish were removed, frozen, and guts removed. Pipefish have an undifferentiated gastric system resembling a straight tube. Studies with neutral red dyed amphipods have indicated that amphipods remain in the gut tube in the same order in which they were consumed (Ryer, unpublished data). As amphipods were removed from the gut they were measured under a dissecting scope equipped with an ocular micrometer. The serial order of amphipods in the gut was recorded.

Size preference was calculated for pairs of fish that occupied the same aquaria using the index developed by Manly (1972) and Chesson (1978):

$$\alpha_i = \frac{\ln(\frac{R_i}{N_i})}{\sum_{j=1}^{k} \ln(\frac{R_j}{N_j})} \tag{10}$$

where α_i ranges between 0 and 1. N_i and R_i are the number of prey size i at the beginning and end of the experiment, and k is the number of prey size classes. The condition of no selection is 1/k. This index is appropriate under conditions when prey consumed during an experiment are not replaced, and Manly (1974) has demonstrated

that α_i is approximately normally distributed. Preferences (α_i) were determined to be homoscedastic (Cochran's C-test) and examination of a Rankit plot indicated a normal distribution. Data were analysed for the effect of amphipod size using ANOVA and Student-Newman-Keuls (SNK) test (Sokal and Rohlf 1981).

Size frequency distributions of amphipods from guts were tested for homogeneity, pooled, and tested for goodness of fit (G-test, Sokal and Rohlf 1981) of predictions. To determine whether size preference changed during the 4 hour feeding interval, amphipods from each gut were divided into 4 groups based upon their position in the gut tube (1st quarter, 2nd quarter, etc.), pooled, and compared using a Chi-square test (Sokal and Rohlf 1981).
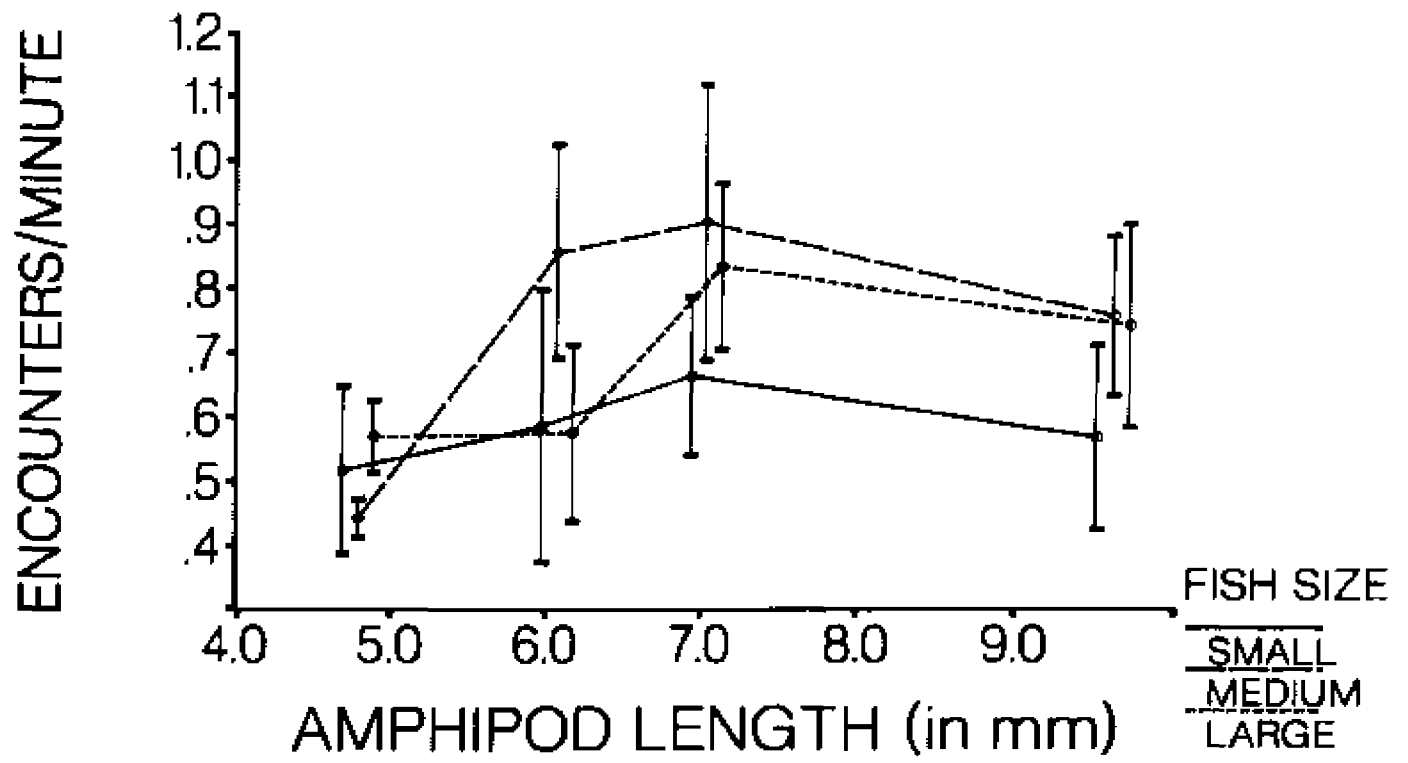
RESULTS

General foraging behavior

Pipefish use a tactic of slow and deliberate movement. Fish move several centimeters along the bottom and then pause for up to a minute and examine the surroundings. This examination is characterized by slow swaying (up and down, side to side) of the forward portion of the body. Pipefish are efficient at detecting amphipods that are well hidden between grassblades. When an amphipod is detected the pipefish moves to within 2 cm and arches the forward portion of the body to position the head in a downward tilted angle. Prey capture is accomplished by a rapid upward and forward thrusting of the snout to bring it within mm of the prey, accompanied by inward sucking produced by rapid expansion of the buccal and opercular chambers. For a more detailed description of foraging behavior see Ryer (1987).

Encounter, attack, and success

There was a trend toward increasing encounter rate with increasing amphipod size (Fig. 1), but ANOVA indicated no significant effect of either amphipod size, fish size, or their interaction (results of all statistical tests are presented in appendix). Amphipod density (Fig. 2) had a significant effect (ANOVA, p=0.004) upon encounter rate. Simple linear regression adequately described the effect of amphipod density on encounter rate (B_{ij} = 0.012(D) + 0.040, r^2=0.602, where D equals amphipod density).

Figure 1. The effect of amphipod size (total length in mm) and fish
size (small - 110-130 mm, medium - 150-170 mm, large - 180-200
mm total length) upon rates of pipefish-amphipod encounter
(means $\pm$ 1 SE).

The probability of a given encounter resulting in attack, as a function of prey to predator size ratio (amphipod total length divided by pipefish snout length: measured from mouth to eye), is presented in Fig. 3. Results of ANOVA indicate that individually neither fish or amphipod size had a significant effect on attack probability. The interaction between fish and amphipod size was significant (p=0.009). Equation 1 was used to model attack probabilities: $A_{ij}=[(1-(R_{ij}/3.83))(R_{ij}/0.61)]^{1.44}$, ratio of explained to total sums of squares=0.941.

The probability of an attack being successful, as a function of size ratio is presented in Fig. 4. Fish and amphipod size had significant effects upon probability of success (p=0.001 and p<0.001 respectively). The interaction between fish and prey size was not significant. Equation 2 was used to model this pattern: $S_{ij}=[(1.163-R_{ij})/1.163]^{0.7}$, explained to total sums of squares ratio of 0.868. For comparison, these data were also modeled using a linear, multiple regression equation fit by the iterative least squares approach, with amphipod and fish length as independent variables: $S_{ij}=O(-.109)+F(.004)+.660$, explained to total sums of squares ratio of 0.873, where O and F are amphipod and fish size respectively. The ratio based model was considered superior due to it's explanatory nature, and was adopted for use in the simulation model.

Handling times were highly variable, but had a pattern similar to that demonstrated for other fish (Werner and Hall 1974; Kislalioglu and Gibson 1976) i.e. handling times were positively

Figure 2. The effect of amphipod density (#/aquaria) upon rates of pipefish-amphipod encounter (means $^+_-$ 1 SE). Trials were conducted using large pipefish (180-200 mm total length) and class 2 amphipods (6 mm mean total length). Regression: B_{ij} = 0.012(Density) + 0.040, r^2=0.602.
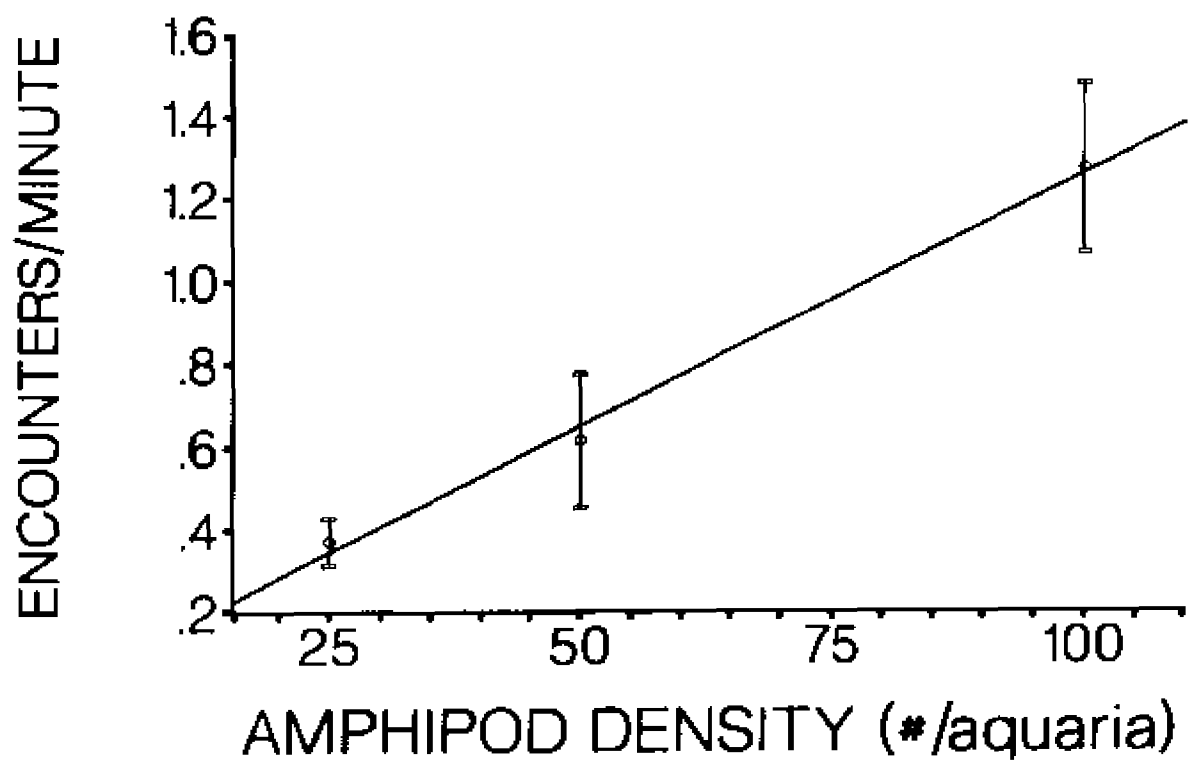
Figure 3. Probability of attack (means $^+_-$ 1 SE) as a function of the prey-predator size ratio. The size ratio is amphipod size (mean total length for a size class in mm) divided by pipefish snout length: the distance (in mm) from the tip of the mouth to the corner of the eye. The line is the attack probability sub-model (equation 1.) fit by iterative nonlinear least-squares regression.
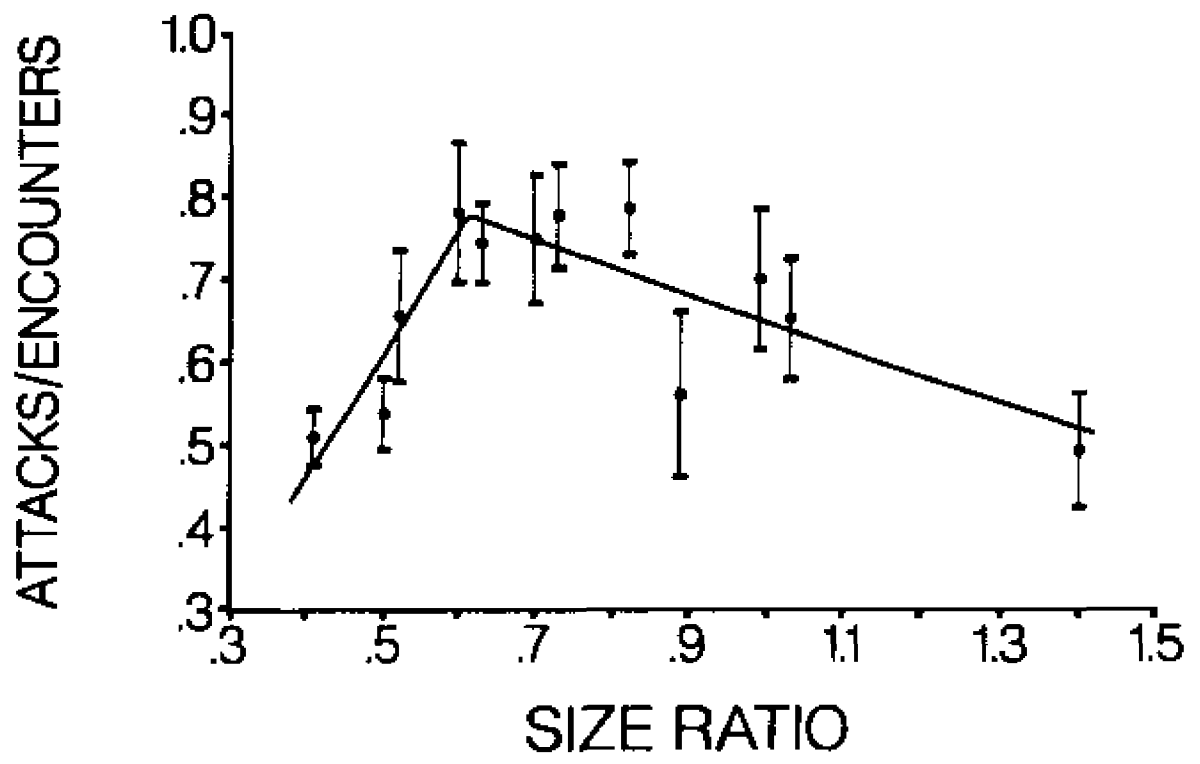
Figure 4. Probability of an attack being successful (means $\pm$ 1 SE) as a function of the prey-predator size ratio. The size ratio is amphipod size (mean total length for a size class in mm) divided by pipefish snout length: the distance (in mm) from the tip of the mouth to the corner of the eye. The line is the success probability sub-model (equation 2) fit by iterative nonlinear least-squares regression.
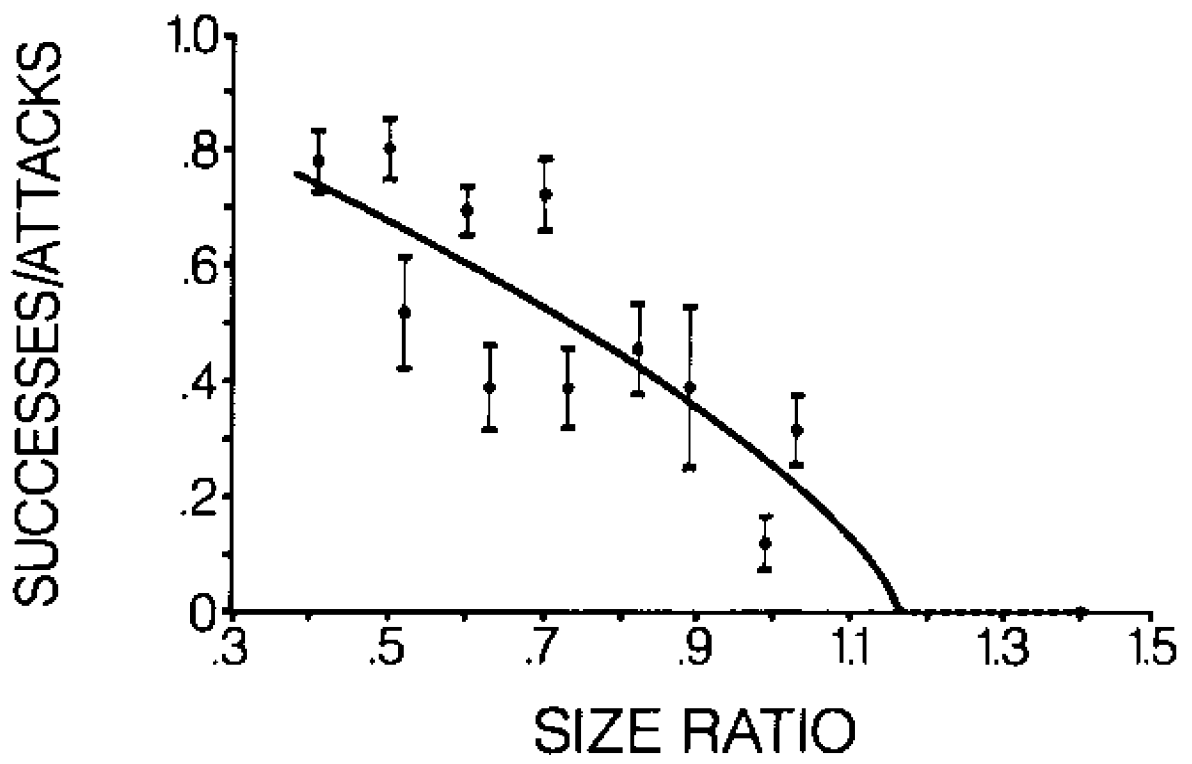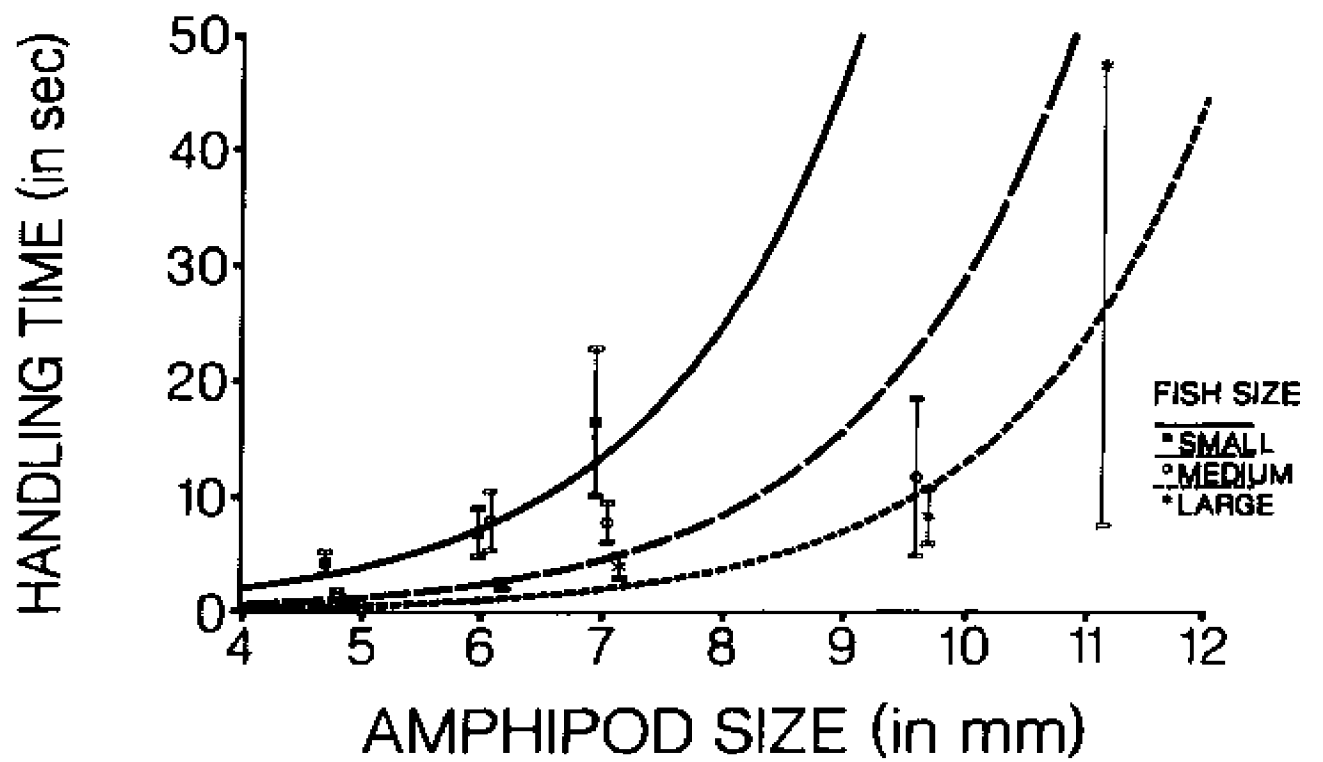
Figure 5. Handling time (means $\pm$ 1 SE) as a function of amphipod

size (means total lengths for size classes in mm) and pipefish

size (small - 110-130, medium - 150-170, and large - 180-200 mm

total length). An exponential model: handling time =

$4.576e^{-0.027(\text{fish length}) + 0.617(\text{amphipod length})}$, was fit by

iterative nonlinear least-squares regression.

related to prey size, and negatively related to predator size (Fig. 5). ANOVA indicated significant effects of both amphipod size (p<0.001) and fish size (p<0.001), with no significant interaction. Small amphipods were sucked into the mouth and swallowed in a single sucking action. Larger amphipods often became lodged in the snout and required numerous gulping motions before they were finally swallowed. This was exaggerated in some instances when the amphipod was sucked into the mouth in a sideways position, resulting in it becoming folded over in the snout. Several models were considered to describe handling times (linear, exponential, and power functions) with an exponential function being chosen, as it gave the best fit: $H_{ij}=4.576(exp((-0.027)F+(0.617)0))$, ratio of explained to total sums of squares = 0.204.

Prey size preference

Pipefish consumed an average of 24 amphipods each (min=19, max=28, SD=2.48). At the beginning of the experiment pipefish foraged actively, attacking the majority of encountered amphipods. Amphipods were most often attacked within seconds of encounter. By the second hour, while still actively foraging, fish appeared to attack a lower proportion of encountered amphipods. Prey were often scrutinized for up to 30 sec and then abandoned. The pooled size-frequency distribution for amphipods from pipefish guts (Fig. 6b) is skewed towards the predominance of small amphipods (4-5 mm). All fish showed this pattern (heterogeneity G-test, p>0.05), which was significantly different (G-test, p<0.05) from expected frequencies

Figure 6. Comparison of size frequency distributions of a) amphipods available at the beginning of experiment, b) amphipods removed from pipefish guts, c) predictions of mechanistic model (and energy-maximization model), and d) predictions of gastric linked optimization model.

AVAILABLE

OBSERVED
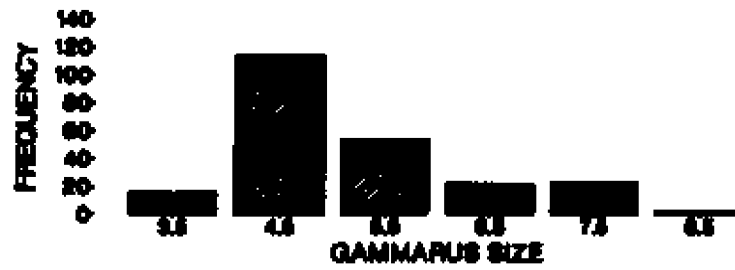
MECHANISTIC

COMPRESSION

based upon the sizes of available amphipods (Fig. 6a).

ANOVA indicated that amphipod size had a highly significant (p<0.001) effect upon preference ($_i$, Fig. 7). Amphipods in the 4-6 mm size range were significantly preferred (p<0.05, SNK) over amphipods greater than 6 mm. Amphipods less than 4 mm were not in evidence in the diet beyond what would be expected from random selection.

Simulation model predictions

Predictions of the mechanistic model (Fig. 6c) indicated that smaller amphipods would be utilized more extensively than large amphipods, due to the effects of the attack and success probabilities. The observed amphipod size-distribution from guts was significantly different (G-test, p<0.05) from the expected frequencies of the mechanistic model. This model was unable to account for the magnitude of the preferential consumption by pipefish of small amphipods.

Amphipod ca. 4 mm in length were most profitable to pipefish, regardless of fish size (Fig. 8). In this formulation of profitability the metabolic costs of handling prey are ignored. Calculations utilizing handling costs estimated as 100 times the standard basal metabolism of several freshwater (Brett and Groves 1979) and an estuarine fish (Brooks 1985) indicate that handling cost is insignificant compared with the energetic gain derived from even the smallest amphipods utilized in this study. Due to higher success probabilities and lower handling times, amphipods of a given size

Figure 7. Preference (Manly's α) (means $\pm$ 1 SE) as a function of amphipod size. The reference line at α =1.67 is the level of neutral preference at which prey are consumed in proportion to their abundance in the environment.
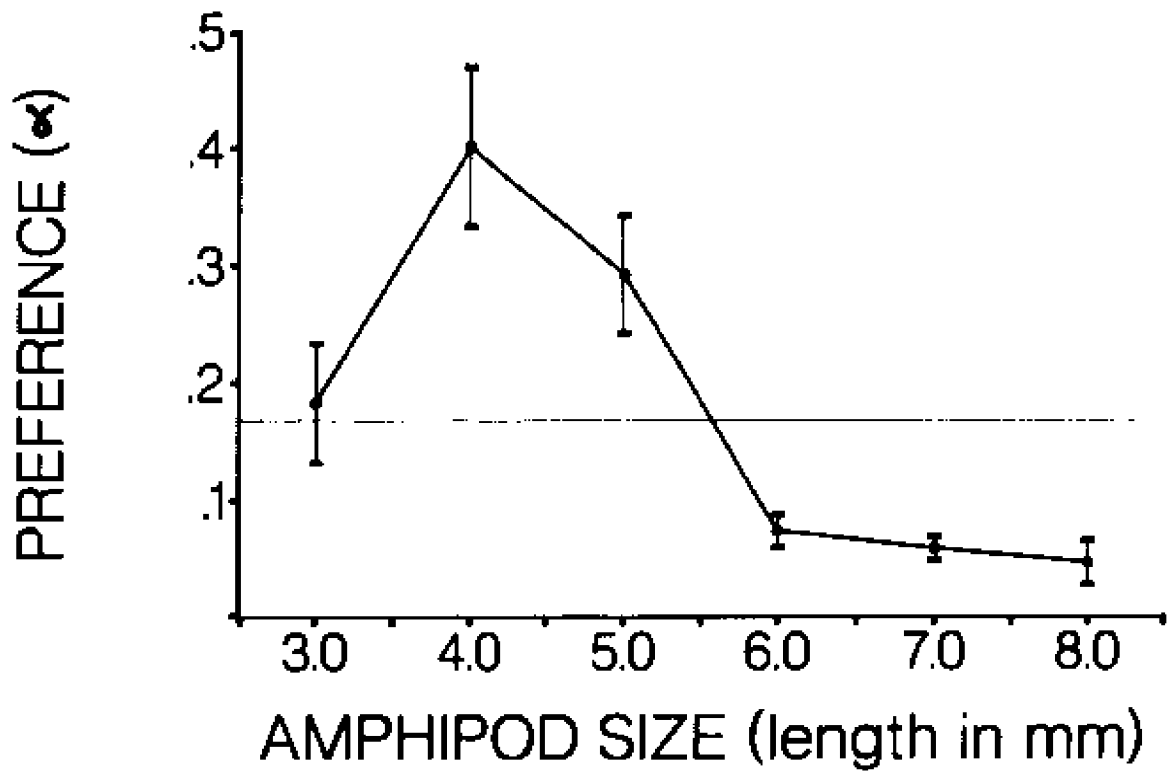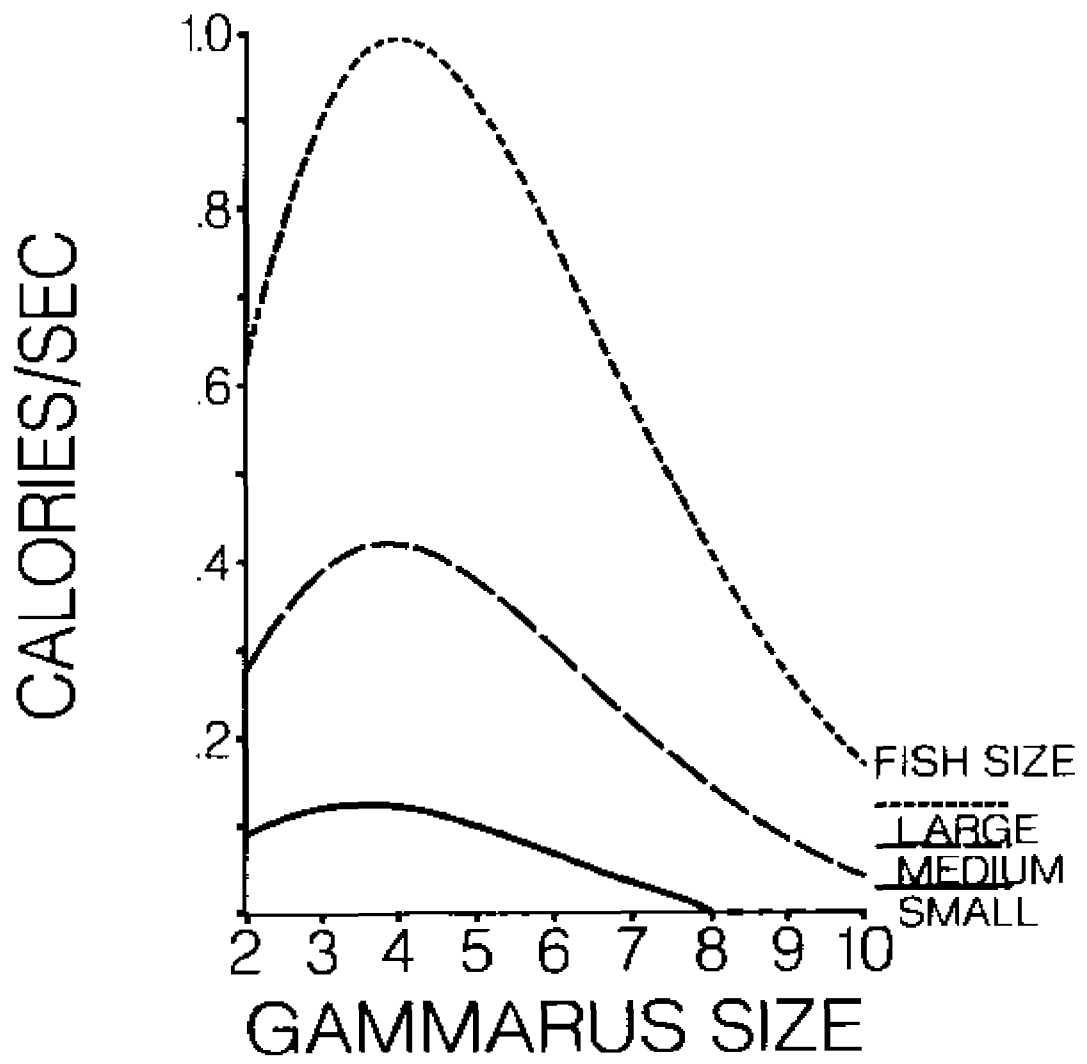
Figure 8.   Estimated profitability (in calories per second) of
amphipods to pipefish.

were more profitable to large fish than to small fish. The energy maximization optimization model predicted frequencies identical to those of the mechanistic model: utilizing all sizes yielded the highest rate of energy intake. There was no energetic gain achieved by ignoring lower ranked (large) amphipods in order to be ready for subsequent encounters with more valuable amphipods (smaller). All amphipod sizes should have been utilized, subject only to mechanistic limitations.

The observed size-frequency distribution of amphipods from pipefish guts was not significantly different (G-test, $p > 0.05$) from frequencies (Fig. 6d) predicted by the diet breadth compression model. The model predicted a consumption of 40 amphipods per fish during the 4 hour experiment, as compared with an observed average of 24 amphipods per fish. This difference, while not large, indicates that either the rate of gastric evacuation or gastric capacity are not correct. However, the gastric model did not account for any lag time in evacuation: the time delay between the beginning of ingestion and the commencement of evacuation, or gut content weight loss, which also could have resulted in an over estimate of consumption.

The model also predicted that fish would initially forage to maximize energetic intake, and then shift to time minimization as energy intake became limited by gastric processing. At the beginning of the experiment fish should have foraged optimally: showing no active selection and excluding no prey size from the diet. As the gut filled, lower ranked prey (large amphipods) should have been dropped from the diet. The observed size frequency distributions of

amphipods taken from 4 positions along the gut length (Fig. 9) showed no significant change (Chi-square, p>0.05). Although the predicted cumulative prey size-frequency distribution matched the experimental data, the temporal sequence indicated no change in preference as a function of foraging time.

Figure 9. Observed size frequency distribution of amphipods from different portions of pooled pipefish guts. Amphipods from the 4th quarter were consumed at or near the beginning of the experiment, while amphipods from the 1st quarter were the last consumed.

1st QUARTER

2nd QUARTER
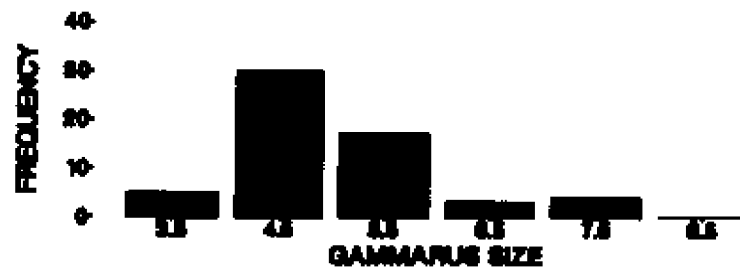
3rd QUARTER

4th QUARTER

Discussion

Prey size-selection observed in this study is similar to what
has been observed in the field. Ryer and Orth (1987) found pipefish
to consume predominantly smaller Gammarus mucronatus and Erichsonella
attenuata (an isopod) in a lower York River seagrass meadow, even
though both prey populations were dominated by larger individuals.
This pattern is conspicuously different than that which has been
documented for most micro-carnivorous fish species: selection for
the largest prey sizes available (Zaret 1980, and references
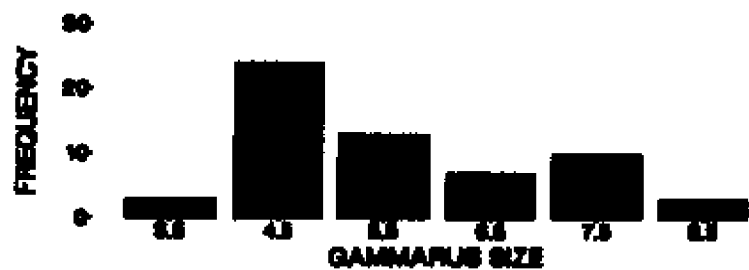therein).

Zaret (1980b) proposed a size-selective classification scheme
for aquatic predators of zooplankton based on the observation that
fish tend to prefer large prey, while invertebrate predators prefer
small prey. Preference is defined as disproportionate consumption of
prey, above and beyond what can be explained by relative abundance
(i.e. no consideration given to whether observed patterns are the
result of mechanistic considerations or deliberate behavioral
selection of prey). According to Zaret there are two functional
categories: "gape-limited" and "size-dependent" predators. Gape-
limited predators (fish) show a positive correlation between
preference and prey size until an upper limit of size is reached.
Prey at this limit are the largest the fish is capable of swallowing,
which is determined by mouth gape. Beyond this upper limit,
preference drops abruptly to zero. Size-dependent predators
(invertebrates), rather than being limited by the size of prey they
can ingest, are limited by their ability to successfully capture or

handle larger prey. Preference is a skewed bell-shaped curve. Peak preference occurs at smaller, or intermediate prey sizes, and decreases of with either increasing or decreasing prey size.

Scott and Murdoch (1983) have suggested that all aquatic predators, vertebrate and invertebrate alike, should display a size-dependent skewed bell-shaped pattern of preference, provided a full range of prey sizes are considered. This pattern had not been observed for fish predators because most examples are for planktivorous fish: zooplankton typically are not large relative to their fish predators. Preference curves lacking the descending tail at larger prey sizes that have been observed for planktivorous fish are due to truncated prey size distributions, lacking prey large enough to demonstrate the descending tail of preference. Bence and Murdoch (1986) have demonstrated that Gambusia affinis, a small microcarnivorous fish, exhibits a size-dependent pattern of preference when feeding on Daphnia. The results of this study also support this later contention. Pipefish displayed a preference for smaller sized amphipods, with amphipods greater than 6 mm being selected against ($\alpha_i < 0.167$). Figure 7 represents a portion of a skewed bell-curve. I assume that, had additional size-classes of smaller amphipods been examined, they would have further defined the ascending tail of the curve.

Discussion thus far has dealt with patterns of prey size utilization, with no attempt to differentiate between preference as a result of mechanistic considerations or active selection. From an ecological perspective it is desirable to determine the cause of such patterns. The mechanisms of interaction between predator and prey

are less well understood in vegetated habitats than in the water column. Vegetation decreases the rate at which predators encounter prey (Crowder and Cooper 1982; Savino and Stein 1982) and models of prey encounter like the reactive field volume model (RFVM) may be inappropriate for these highly structures environments (Ryer 1987). Instead, patterns of microhabitat utilization and behaviors demonstrated by prey that reduce rates of encounter, visibility, and vulnerability may dominate predator-prey interactions (Main 1987; Ryer 1987; Wellborn and Robinson 1987).

Our ability to discriminate patterns of active selection can only be as robust as the null models against which observed patterns of prey utilization are compared. The mechanistic model presented in this study was empirically derived, taking into account mechanisms of pipefish-amphipod interaction. The model assumes that prey behavior in populations of a single size-class is similar to that of mixed-size populations. It is possible that sexual or antagonistic interactions between amphipods of different size may result in changed rates of encounter, prey vulnerability, or pipefish success. In addition, the size preference experiment was conducted at a prey density roughly 3 times that used to experimentally examine mechanisms of interactions. van Dolah (1977) found that at high amphipod densities, large G. palustris often displace smaller individuals from preferred locations in the culmns of Spartina alterniflora. Presumably, such displacement results in higher vulnerability to predation. I observed amphipods exposed on the sediment or the surface of grassblades to be much more likely to be attacked than amphipods which were between grassblades. If

competition for refuges did occur, the smallest amphipods would be most likely to be evicted, increasing their vulnerability, and resulting in a disproportionate contribution of these amphipods to the diet. However, this is not supported by the preference indices, where amphipods in the range of 4-6 mm were preferred significantly over 3-4 mm amphipods. I have never observed such competitive displacement and conclude that the observed deviations in prey size utilization from the predictions of this model indicate that pipefish were actively selecting prey on the basis of size.

Prey size selection by pipefish did not conform to the predictions of the simple optimization model, as these predictions were identical to those of the mechanistic model: utilizing all prey size would have maximized energy intake. However, despite the invalidation of this model, the pattern of selection was qualitatively in agreement with the direction of predicted selection. There appears to have been some form of active selection by pipefish for the smaller, more profitable amphipods.

Qualitative, rather than quantitative agreement with predictions of optimization models has been noted for many predators: manifest as partial preference (here preference is taken to be synonymous with active selection (Krebs and McCleery 1984). These deviations have been ascribed to discrimination errors, learning limitations, runs of bad luck, simultaneous encounters, and inherent variation within and between individual predators. In all these instances predators have displayed broader than predicted diet breadth. In contrast, pipefish displayed greater selectivity than predicted, indicating that strict maximization of energetic intake was not the criteria directly

governing selection. _Gambusia_ has also been shown to select smaller, more profitable prey at densities where classical optimal foraging theory would have predicted no preferential consumption (Bence and Murdoch 1986). A possible explanation for the failure of the energy-maximization model may lie in its most basic assumption: fish forage so as to maximize energetic intake. Instead, fish may show preferences that are unrelated to prey profitability, selecting prey by other criteria.

Selection of prey may also be related to the physiological state of the predator. Bence and Murdoch (1986) found that _Gambusia_ alters its size-selective feeding behavior in response to its own satiation level. Satiated fish demonstrated higher selectivity for more profitable prey than did starved fish. Kislalioglu and Gibson (1976) have reported similar findings for sticklebacks. This indicates that maximization of energetic intake may not be the criteria used by satiated fish to make foraging decisions. It also implies that foraging strategies may be more flexible, over short time intervals, than has been previously recognised. The size selection experiment reported here was designed, taking advantage of the unique morphological characteristics of the pipefish gastric tract, to examine the possible occurrence of satiation related diet breadth compression. The diet breadth compression model predicted that pipefish would switch from energy-maximization to time-minimization, resulting in diet breadth compression. Although it accurately predicted overall size selection, this was entirely fortuitous, as pipefish did not display the predicted temporal sequence of change in

prey size selection. To the contrary, prey size selection by pipefish was constant over time.

I suggest that pipefish utilize a simple strategy of prey selection, or "rule of thumb", that gave rise to the observed results. O'Brien et al. (1976) concluded that sunfish attack the apparently largest prey in their visual field. Prey size selection by pipefish may be a simple mechanism akin to the apparent size rule: instead of attacking the largest prey when confronted with multiple prey, pipefish select the apparently most profitable. It should be noted that these two models yield identical results when the largest prey are most profitable. In the prey size selection experiment 140 amphipods were put into an 38 l aquaria with 60 artificial grass shoots. Amphipods usually position themselves between the basal portions of leaves. This resulted in multiple occupancy of these refugia. As such, pipefish often experienced encounters with multiple, mixed-sized amphipods. In such patches where amphipods are in close proximity to one another, apparent size will closely match absolute size, thereby eliminating the confusion between nearby small and distant large prey. Similarly, vegetation may provide a scale against which the absolute size of prey may be measured, a factor not present in the water column. When given a choice, consistently picking the amphipod that is most profitable could give rise to the observed pattern of selection. This tactic, while deviating from optimality (strict energy maximization) under conditions of moderate prey density, could result in good approximation of optimality under a broad range of conditions (low and high prey density). Pipefish utilizing this rule of thumb would be well predisposed to take

advantage of seasonal peaks in amphipod density, by selecting only more profitably sized amphipods, while still utilizing all amphipods during most of the year when amphipod densities are low. During the early spring when G. mucronatus is at its highest densities, pipefish consume predominantly small (2 to 4 mm) individuals (Ryer and Orth 1987).

The apparent size rule may in fact be a special case of a more general size-selective rule of thumb: select the apparently most profitable prey. When the most profitable prey are also the largest, as has been the case in most studies (Eggers 1982; Wetterer and Bishop 1985), these models are identical. At low prey densities fish will rarely simultaneously encounter multiple prey, and prey selection will closely follow the RFVM (i.e. no active selection). At high prey density, simultaneous encounters frequently occur, with large prey being actively selected due to their larger apparent size: i.e greater profitability. A different result is manifest when small prey are most profitable. Again, at low prey density selection will follow the RFVM. But at high prey density, distant large prey may often appear more profitable than nearby small prey, resulting in discrimination errors and a broader diet breadth than would be predicted by classic optimal foraging theory. The frequency of such discrimination errors will be dependent upon the predators ability to judge absolute, as opposed to apparent size. Gambusia is a planktivore for which small prey are most profitable (Bence and Murdoch 1986), and who's pattern of prey preference (as measured by Manly's preference index) remains constant with increasing prey density. While inconsistent with a strategy of choosing the

apparently largest prey, these results could be consistent with a strategy of choosing the apparently most profitable prey, provided discrimination errors occur.

Definitive evaluation of this hypothesis as a general mechanism of prey selection will necessarily await further examination of existing and future data, contrasting predator-prey interactions, over various prey densities, from cases in which the largest prey are most profitable, with instances where smaller and intermediate sized prey are most profitable. Similarly, further evaluation of this proposed mechanism of selection as it relates to pipefish foraging also awaits further experimentation, and a better understanding of amphipod spatial distribution under conditions of high density in vegetated habitats.

APPENDIX

I)   Summary of analysis of variance (ANOVA) encounter rates. Top:
ANOVA for effect of fish size and amphipod size upon encounter rate.
Bottom: ANOVA for effect of amphipod density upon encounter rate.

Source	SS	df	F	Sig
Fish	.299	2	1.196	.310
Amphipod	.773	3	2.060	.115
Fish by Amphipod	.373	6	.497	.808

Source	SS	df	F	Sig
Density	2.187	2	1.089	.004

II)   Summary of analysis of variance (ANOVA) for effects of fish size
and amphipod size upon probability of attack.

Source	SS	df	F	Sig
Fish	.085	2	1.435	.246
Amphipod	.175	3	1.972	.126
Fish by Amphipod	.559	6	3.147	.009

III) Summary of analysis of variance (ANOVA) for effects of fish size
and amphipod size upon probability of success.

Source	SS	df	F	Sig
Fish	.423	2	8.150	.001
Amphipod	1.424	3	18.298	.000
Fish by Amphipod	.303	5	2.337	.054

IV)   Summary of analysis of variance (ANOVA) for effects of fish size
and amphipod size upon natural log (ln) transformed handling time.

Source	SS	df	F	Sig
Fish	34.042	2	17.021	.000
Amphipod	84.891	3	27.715	.000
Fish by Amphipod	6.006	5	1.177	.320

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