Feeding chronology, daily ration, and the effects of temperature upon gastric evacuation in the pipefish, *Syngnathus fuscus*[1]

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Synopsis

Feeding chronology, daily ration, and the effects of temperature upon gastric evacuation were examined in the pipefish, *Syngnathus fuscus*, from field and laboratory data. *S. fuscus* displayed a pattern of diurnal feeding, characteristic of syngnathids. Daily ration calculations yielded estimates of 4.0 and 4.4% body weight per day, which are comparable to estimates for other teleosts. Evacuation rate was found to be temperature dependent, with more rapid evacuation with increasing temperature. In addition, evacuation rate was found to be positively correlated with gut content. Slowing of evacuation rate with decreasing gut content may allow for increased assimilation efficiency during periods of low food availability. Daily ration, although controlled by the temperature dependence of evacuation rate, may also be controlled by prey abundance; fish maximize food intake during periods of high prey availability, and maximize upon assimilation during periods of low prey availability.

Introduction

Field studies dealing with the feeding ecology and trophic dynamics of fish communities are often hampered by a lack of information regarding the dietary requirements of fish species. Examination of stomach contents gives evidence of food preferences, but provides no information on the total quantity of food consumed on a daily basis, particularly as temperature varies on a seasonal basis. Such information can prove particularly helpful in studies of energetics and growth, but data of this type are relatively scarce, especially for estuarine species. The present study was undertaken to de-termine the diel feeding chronology, daily ration, and the effects of temperature upon gastric evacuation in the northern pipefish, *Syngnathus fuscus*.

The northern pipefish ranges from the Gulf of St. Lawrence to Florida and into the Gulf of Mexico; over this relatively broad geographic range the temperatures encountered by this species range from 6.2 to 27.0° C (Hardy 1978). In the Chesapeake Bay this species is most active and abundant in shallow waters from May to November, at temperatures from 12° C to 30° C (Ryer 1981) During the months in deeper, colder water, this species is apparently in a state of torpor, lying on the bottom (Wicklund et al. 1968). Thus food resources during the warmer months when the fish are active may play a disproportionately large role in supporting seasonal patterns of growth an reproduction.

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[1] Contribution number 1035 of the Virginia Institute of Marine Science of the College of William and Mary.

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Materials and methods

Fish were collected from two sites in the lower Chesapeake Bay, Virginia (Fig. 1.). The Guinea Marsh site is an extensive shoal area, almost entirely vegetated by eelgrass (*Zostera marina*) and located adjacent to the mouth of the York River. The second site, Vaucluse Shores, is on the western side of the Delmarva Peninsula at the mouth of Hungars Creek. This area is dominated by widgeon grass, *Ruppia maritima*, in the shallows (0.1 to 0.3 m MLW). Eelgrass dominates the deeper areas (1.0 m MLW), with a mixture of the two species at intermediate depths. Both sites support faunal assemblages which are nearly identical with respect to species composition and abundance (Heck & Orth
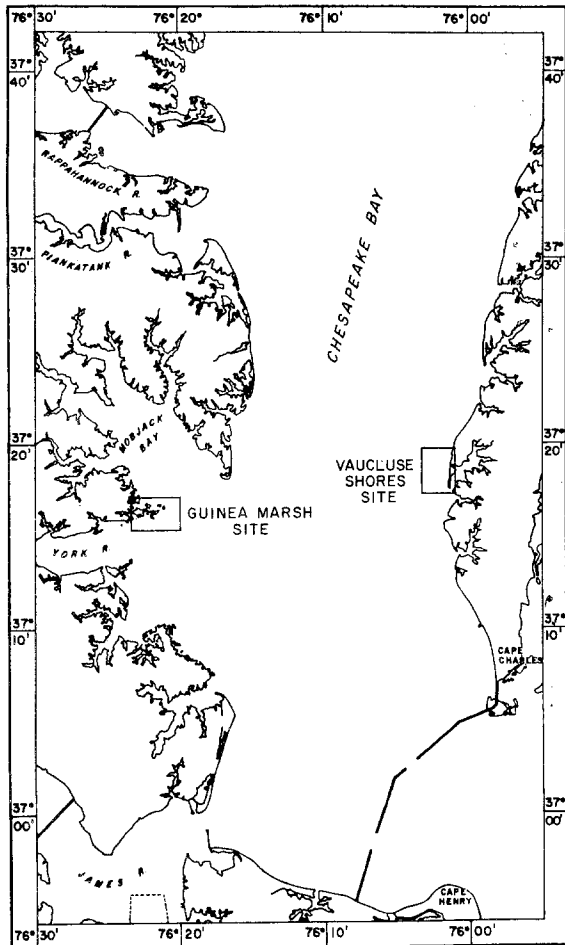

Fig. 1. Location of the Guinea Marsh and Vaucluse Shores study sites in the lower Chesapeake Bay, Virginia.

1980, Orth & Heck 1980, unpublished data).

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

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

Evacuation rates were determined using the serial slaughter method of Windell (1967). Fish were collected at the Guinea Marsh site using a 4.9 m otter trawl on September 1, 1980, at a temperature of 24° C. The fish were brought to the laboratory where they were divided into three groups. Temperatures were changed at approximately 1° C per day until the final acclimation temperatures of 15°, 23°, and 27° C were reached. Fish were maintained for 2 to 3 weeks at the acclimation temperature and were fed daily upon gammaridean amphipods, primarily *Gammarus mucronatus*, prior to experimentation. This species is one of the preferred prey of *S. fuscus* in the lower Chesapeak Bay (Ryer 1981).

Fish were starved for 3 days prior to experiments to allow complete evacuation of the gut. Each group of fish was allowed to feed to satiation for one hour upon gammaridean amphipods, after which the fish were isolated from further contact with food. Groups of seven fish were then removed and sacrificed at 2 to 4 hour intervals, and both fish and gut contents prepared for dry weight determinations. Serial slaughter was continued at each temperature until visual observation of the guts indicated that they were completely evacuated. All fish were between 150 mm and 200 mm in total length and, as such, constituted only mature adult individuals.

Results

Feeding periodicity

S. fuscus displayed a cyclical 24 h feeding pattern that was similar during both sampling dates at the two different locations (Fig. 2). The largest quantities of food were present in guts just prior to dusk, with a gradual decline from dusk to a minimum level just prior to dawn, and an increase from dawn to mid-day the following day. Covariate analysis of this data, with food weight as the dependent variable and fish weight as the covariate showed time to have a significant ($p < 0.05$) effect upon food weight. Data were also examined to determine if there might be any tidal effect superimposed on this diel pattern; however, covariate analysis failed to demonstrate any such tidal effect.

In Fig. 2 the quantity of food from pipefish guts is expressed as percent body weight. Elliott (1979) has objected to the use of such proportions for the examination of daily energy intake, presumably because allometric growth patterns may result in significant error when comparing fish of different sizes. However, in our samples, fish did not vary greatly in 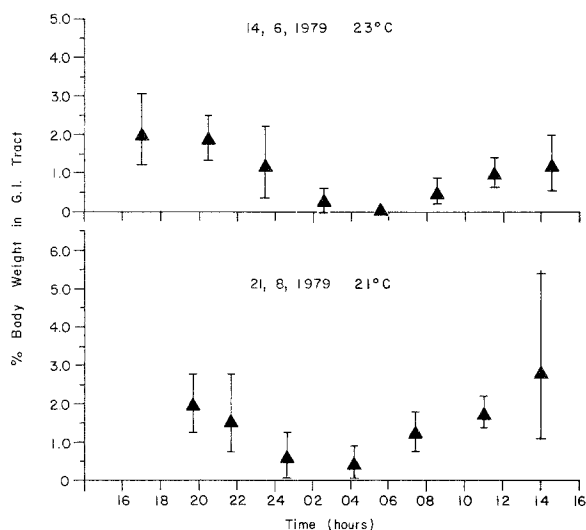size (mean length = 162 mm, range 125 to 201 mm) and covariate analysis showed no effect of fish weight on this percentage. In addition, while some error may result, such percentages provide a useful index for the comparison of species on an energetic basis.

Gastric evacuation

Fish ate readily at all three temperatures, with no significant difference in maximum meal size but with more rapid evacuation with increasing temperature (Fig. 3, Table 1). The quantity of food evacuated was a constant proportion of the food in the gut at any time. Time required to completely evacuate a meal was 30.2 h at 15° C, 14.1 h at 23° C, and 10.3 h at 27° C (Fig. 3, Table 1). Regression of evacuation rate constants against temperature (Fig. 4) can be used to predict evacuation rates at any temperature range for estimation of daily ration.

Daily ration calculation

For the calculation of daily rations, the method of Peters & Kjielson (1975) was adopted. Because the absolute evacuation rate is dependent upon the quantity of food present in the gut, a fish which exhibits periodic feeding will evacuate food at various rates throughout the day. For any given quantity of food in the gut, the equation
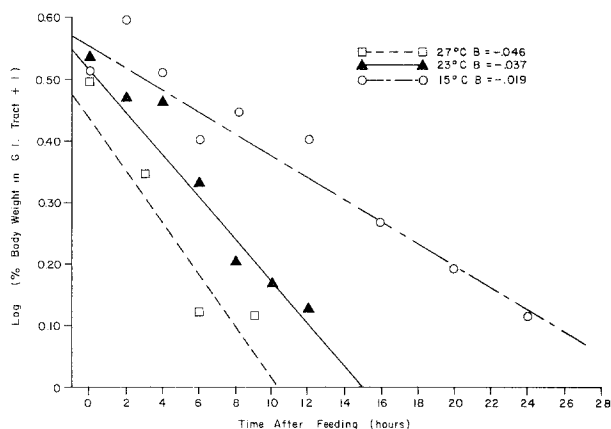
$$\frac{dC}{dt} = -2.303 \ BC$$

Fig. 2. Feeding chronology of the northern pipefish for 14 June 1979 at Guinea Marsh and 21 August 1979 at the Vaucluse Shores site. Geometric means and 95% confidence intervals for % body weight in gastrointestinal tract by sampling intervals.

Fig. 3. Regression of gut contents against time at 15, 23 and 27° C for the determination of evacuation rate constants (B).

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

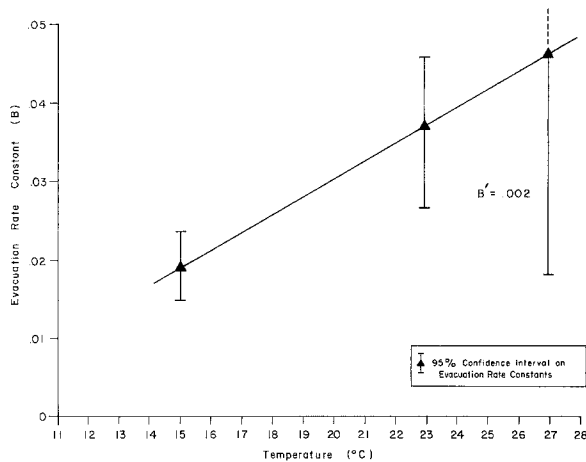|	15° C	23° C	27° C
Evacuation equation	Y = 0.573 − 0.019 X	Y = 0.522 − 0.037 X	Y = 0.475 − 0.046 X
Number of fish	28	49	63
Coefficient of determination (r²)	0.928	0.952	0.908
Estimate of unevacuated food (% dry body weight) at:			
0 h	2.74	2.56	1.99
6 h	1.88	1.14	0.58
12 h	1.21	0.28	—
24 h	0.31	—	—
Time to complete evacuation:			
	30.2 h	14.1 h	10.3 h

Fig. 4. Regression of evacuation rate constants (B) against temperature, with 95% confidence intervals for the evacuation rate constants determined at 15, 23, and 27° C. B′ indicates slope of regression.

will provide an estimate of the instantaneous evacuation rate, where C = gut contents (% dry body weight + 1), B = the evacuation rate constant for the given temperature, and t = time (Peters & Kjielson 1975).

In order to calculate daily rations, evacuation rate constants were calculated (from Fig. 4) for the temperatures (21° C and 23°C) encountered during the two feeding chronology studies. These values were then utilized to calculate the instantaneous evacuation rate for each sample time during the chronology studies (Fig. 2). These values provided

estimates of the food being evacuated at any sample time throughout the 24 h period. By averaging consecutive pairs of evacuation rates, the average evacuation per hour for the given time interval was obtained. These average rates were multiplied by the number of hours between each sample to arrive at an estimate of the total quantity of food evacuated during the particular interval. The total quantity of food evacuated over 24 h, which served as an estimate of the daily ration, was obtained by summing the quantities evacuated during each interval.

These calculations provided daily ration estimates of 4.0 and 4.4% body weight per day for the observed feeding periodicities of 14 June 1979 and 21 August 1979, respectively.

More recently, Elliott & Persson (1978) derived a method of estimating daily food consumption for fish. Their first model incorporates the assumptions of constant food consumption and exponential evacuation; the same assumptions are inherent in the earlier method of Peters & Kjielson (1975). In fact, both methods utilize similar calculations, with the Peters-Kjielson method summing evacuation through 24 h, while the Elliott-Persson method utilizes evacuation as a correction in the calculation of consumption. When we applied the Elliott-Persson calculations to our data we arrived at daily ration estimates at 3.2 and 3.5 percent body weight for 14 June 1979 and 21 August 1979 respectively. These estimates are 20 percent lower than those derived through the Peters-Kjielson method.

Discussion

Examination of feeding chronology data (Fig. 2) demonstrates that S. fuscus is a diurnal predator feeding only slightly, if at all, at night, thereby demonstrating a distinct feeding periodicity. Jenkins & Green (1977) have criticized the use of the term 'periodicity' in cases where the diel pattern has not been repeatedly demonstrated. Despite having conducted a mere two chronology studies, we feel confident in our conclusions regarding this matter. This is also supported by personal observation in aquaria where pipefish show strong visual orientation to potential prey. In addition, eye structure in syngnathids, characterized by relatively few rods, many cones, and a fovea, is apparently adapted to acute diurnal vision (Engstrom 1963).

The observed dependence of evacuation rate upon gut content and temperature show the patterns characteristic of teleosts (Fange & Grove 1979). Temperature alters the rate of gastric evacuation, probably in response to the temperature dependence of metabolism and enzyme activity (Paloheimo & Dickie 1966). Slowing of evacuation rate with decreasing gut content may serve to allow increased assimilation efficiency during periods of low food availability. Solomon & Braefield (1972), for example, observed lowered assimilation efficiency with increasing ration in perch. In larval herring, which have a straight tube gut similar to that of S. fuscus, food is evacuated at a rate which increases with increasing prey density. Moreover, assimilation efficiency should decrease under these conditions, since Werner & Blaxter (1980) noticed that the state of digestion decreased with increasing density of prey, with occasional defecation of live prey at the highest prey density tested. Thus when prey availability is high, a common occurrence in spring and summer months in the habitat of S. fuscus (Ryer 1981), total food consumed may not only be a function of gut volume and satiation, but rather a function of prey availability. Under conditions of high prey density, although assimilation efficiency may decrease, it is assumed that the total energy gained would increase due to the greater number of prey items processed; further, with decreasing assimilation efficiency there may be

a concomitant increase in net growth efficiency (Welch 1968, Carefoot 1976). Although S. fuscus lives in Zostera beds in relatively shallow water, during certain months its prey is predominantly planktonic calanoid copepods which reach very high densities (Ryer 1981). Pipefish thus serve as an agent in the transfer of carbon from planktonic to benthic food webs in shallow water estuarine areas.

Calculated daily rations for S. fuscus are similar to those reported for other teleosts (Fange & Grove 1979). Peters & Kjielson (1975) examined the daily ration for several larvae of estuarine fish from the southeastern United States. They estimated daily rations of 2.5%, 4.9% and 4.3% of dry body weight per day for pinfish, menhaden, and spot, respectively. As the larvae transformed to juveniles and changed diet, the respective rations became 9.5%, 13.5%, and 10.1%. These higher rations were associated with increasing proportions of inorganic matter in the diet, and the organic proportion of the ration was probably similar to that of the larval stages (Peters & Kjelson 1975) and to that of the adult pipefish in the present study; S. fuscus rarely consumes inorganic matter (Ryer 1981). For silversides, which possess straight guts without stomachs (as in pipefish), Adams (1976) noted daily rations from 1.23% body weight (15° C) to 3.72% body weight (25° C).

Evacuation rate determined for S. fuscus is clearly dependent upon temperature (Fig. 3, 4, Table 1). Since the full rations consumed at the three temperatures of measurement were similar (0 h, Table 1) daily ration will therefore increase with increasing temperature if food is in excess. The estimates of daily ration noted in the present study (4.0 and 4.4% dry body weight per day) were determined at two similar temperatures (23° and 21° C, respectively); since the lower observed daily ration occurred at higher temperature, food availability may have been greater at the Vaucluse Shores site in June as compared to the Guinea Marsh site in August. Although prey abundance data were not available for the Guinea Marsh site, available data for the Vaucluse Shores site showed several highly preferred prey species (gammarid and caprellid amphipods) to be more abundant during June (Ryer 1981). At lower environmental tempera-

tures, the daily ration should be considerably lower. At 15° C, for example, a fish filling the gut at the initiation of a 24 h diurnal feeding period would have been evacuated only 56% of the meal at the end of the period as compared to 89% at 23° and 100% at 27° C (Table 1). Thus the ration consumed at lower temperatures is limited by the rate of evacuation, as observed by Boehlert & Yoklavich (1983). During the colder months of the year, energy intake by S. fuscus must be severely restricted. At 10° C, for example, where Wicklund et al. (1968) noted torpor in this species, an extrapolation from our estimated evacuation rates (Fig. 3) would suggest that only 28% of a meal would be evacuated after 12 h. Thus instead of daily ration being a multiple of meal size as noted in the present study at 21° and 23°C, daily ration at low temperatures becomes a fraction of a single meal. If food is available, growth of S. fuscus during winter and spring months must be limited by slow digestion rate.

Acknowledgments

References cited

Adams, S.M. 1976. The ecology of eelgrass, Zostera marina (L.), fish communities. II. Functional analysis. J. Exp. Mar. Biol. Ecol. 22: 293–311.

Boehlert, G.W. & M.M. Yoklavich. 1983. Effects of temperature, ration, and fish size on growth of juvenile black rockfish, Sebastes melanops. Env. Biol. Fish. 8: 17–28.

Carefoot, T.H. 1967. Growth and nutrition of Aplysia punctata feeding on a variety of marine algae. J. Mar. Biol. Ass. U.K. 47: 565–590.

Elliott, J.M. & L. Perrson. 1978. The estimation of daily rates of food consumption for fish. J. Anim. Ecol. 47: 977–993.

Engstrom, K. 1963. Cone type and cone arrangement in teleost retina. Acta. Zool. 44: 179–243.

Fange, F. & D. Grove. 1979. Digestion. pp. 162–260. In: W.D. Hoar, D.J. Randall & J.R. Brett (ed.) Fish Physiology, Vol. 8, Academic Press, New York.

Hardy, J.D., Jr. 1978. Development of fishes of the mid-Atlantic Bight. Volume III, Anguillidae through Syngnathidae. U.S. Dept. of Interior, Fish and Wildlife Service, FWS/OBS–78/12. 458 pp.

Heck, K.L., Jr. & R.J. Orth. 1980. Structural components of eelgrass (Zostera marina) meadows in the lower Chesapeake Bay: decapod crustaceans. Estuaries 3: 289–295.

Jenkins, B.W. & J.M. Green. 1977. A critique of field methodology for determining fish feeding periodicity. Env. Biol. Fish. 1: 209–214.

Mercer, L.P. 1973. The comparative ecology of two species of pipefish (Syngnathidae) in the York River, Virginia. M.A. Thesis, School of Marine Science, College of William and Mary, Williamsburg. 37 pp.

Orth, R.J. & K.L. Heck, Jr. 1980. Structural components of eelgrass (Zostera marina) meadows in the lower Chesapeake Bay: fishes. Estuaries 3: 278–288.

Paoloheimo, J.E. & L.M. Dickie. 1966. Food and growth of fishes. III. Relations among food, body size, and growth efficiency. J. Fish. Res. Board Can. 23: 1209–1248.

Peters, D.S. & M.A. Kjielson. 1975. Consumption and utilization of food by various postlarval and juvenile fishes of North Carolina estuaries. pp. 448–472. In: L.E. Cronin (ed.) Estuarine Research, Vol. 1, Academic Press, New York.

Ryer, C.H. 1981. The feeding ecology and trophic role of the northern pipefish, Syngnathus fuscus, in a lower Chesapeake Bay seagrass community. M.A. Thesis, School of Marine Science, College of William and Mary, Williamsburg. 77 pp.

Solomon, D.J. & A.E. Braefield. 1972. The energetics of feeding, metabolism and growth of perch (Perca fluviatilis L.). J. Anim. Ecol. 41: 699–718.

Welch, H.E. 1981. Relationships between assimilation efficiencies and growth efficiencies for aquatic consumers. Ecology 49: 755–759.

Werner, R.G. & J.H.S. Blaxter. 1980. Growth and survival of larval herring (Clupea harengus) in relation to prey density. Can. J. Fish. Aquat. Sci. 37: 1063–1069.

Wicklund, R.I., S.J. Wilk & L. Ogren. 1968. Observations on wintering locations of the northern pipefish and spotted seahorse. Under. Nat. 5: 26–28.

Windell, J.T. 1967. Rate of digestion in fishes. pp. 151–173. In: S.D. Gerking (ed.) The Biological Basis of Freshwater Fish Production, Blackwell, Oxford. 495 pp.