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THE EFFECT OF TEMPERATURE ON THE FEEDING RATE OF THE ROUGH OYSTER DRILL, *EUPLEURA CAUDATA* (SAY)

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THE EFFECT OF TEMPERATURE ON THE FEEDING RATE OF THE ROUGH OYSTER DRILL, *EUPLEURA CAUDATA* (SAY) [1]

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ABSTRACT

Feeding rates of Eupleura caudata *(Say) were studied at a series of controlled water temperatures. The negligible consumption of young* Crassostrea virginica *and* Mulinia lateralis *at 10.0°C indicates that this temperature is near the lower limit for predatory activity. Feeding rates increased with increasing temperature from 10.0 to 27.5°C, and decreased when the temperature was increased from 27.5 to 30.0°C. Feeding rates were maximum at 25.0 and 27.5°C. Drills consumed more* M. lateralis *than* C. virginica *at all experimental temperatures although physical differences between the prey may account for this disparity. Drills were cannibalistic in the presence of alternative food sources throughout the range of temperature studied. Cannibalism increased as the temperature and feeding rates increased and the highest incidence of cannibalism was at optimum feeding temperatures (25.0 and 27.5°C). Ovipositing drills discriminated between the two prey organisms as substrata for capsular attachment; they deposited egg capsules readily on the valves of* C. virginica *but only infrequently on the valves of* M. lateralis.

INTRODUCTION

The marine prosobranch gastropods, *Eupleura caudata* (Say) and *Urosalpinx cinerea* (Say), are two of the more serious predators of the Eastern oyster, *Crassostrea virginica.* Economic losses caused by these muricid gastropods have led a number of investigators to study various aspects of the ability of the drills to consume prey organisms. Although numerous studies have been made of *U. cinerea,* very little attention has been given to the activities of *E. caudata* (Carriker, 1955), and no evaluation of the voracity of *E. caudata* under controlled laboratory conditions has been reported.

Much of what is known about the destructiveness of *E. caudata* came from field observations in several, separate geographical areas. Haskin (1935)[2], in his preliminary investigations at Barnegat Bay, New Jersey, found that *E. caudata* consumed prey at about the same rate as *U. cinerea.* Galtsoff, Prytherch and Engle (1937) reached the same conclusion with drills from Delaware Bay but suggested that *U. cinerea* was the more serious predator because of its greater abundance. MacKenzie (1961) reported that *E. caudata* collected from the York River, Virginia, began feeding at approximately 12.5°C. These authors, however, presented little quantitative information and almost no data on the effect of temperature on the feeding of *E. caudata.*

The present study was initiated to determine estimates of the feeding rates of *E. caudata* from Long Island Sound at a series of controlled water temperatures. Using an experimental procedure similar to that used by Hanks (1957) with *U. cinerea,* it was possible to determine the feeding rates of *E. caudata* at several temperatures and compare the feeding rates of the two drill species

[1] Adapted from portions of a thesis submitted to Southern Connecticut State College in partial fulfillment of the requirements for the degree of Master of Science.

[2] Haskin, H. H. 1935. Investigations on the boring and reproductive activities of the oyster drills, *Urosalpinx cinerea* (Say) and *Eupleura* sp. Unpub. Rep U. S. Bur. Fish.

indigenous to Long Island Sound. Observations on drill mortalities and on substrata used for egg capsule attachment were included.

METHODS

Oyster drills *(E. caudata)* and young oyster spat *(C. virginica)* were collected in Long Island Sound in the vicinity of the Norwalk Islands, Norwalk, Connecticut, an area extensively used for farming oysters. During July and August 1967, when the majority of animals were collected, the bottom salinities and temperatures averaged 27.0 ppt and 22.2°C. Coot clams *(Mulinia lateralis)* were collected from the intertidal area of Fort Trumbull Beach, Milford, Connecticut, in August and September 1967.

In the laboratory the drills were placed in 60-liter fiber glass aquaria, each supplied with a separate continuous flow of sea water at a temperature of 22.5°C and a salinity of 26.5 ppt. After 1 week of acclimatization the stock of drills was randomly divided, one group for each temperature to be studied, and placed in separate aquaria. The temperature of the water entering each aquarium was adjusted 1.0°C per day until one aquarium was maintained at each of the five temperatures to be studied. Drills were maintained for replacement stocks in these conditioning aquaria throughout the experiments. The young *C. virginica* and *M. lateralis* used as prey organisms were not temperature acclimated but were held in running water aquaria at 22.5°C and 26.5 ppt until used in the study.

Five temperature stations were established, each consisting of a polyethylene mixing cylinder held above the drain table on a wooden platform, and two fiber glass trays (35 cm x 48 cm x 11.5 cm) on the drain table. By adjusting the rate of flow from hot and cold sea-water outlets to the cylinders, the required temperature was maintained at each station (Loosanoff, 1949). The flow of water to the cylinders was adjusted so that overflow was continuous, thus keeping the water level and head pressure constant in all cylinders. A Y-tube at the bottom outlet of each cylinder supplied approximately 2 liters of water per minute to each of the two fiber glass trays.

Both trays at each station contained 20 adult *E. caudata* with a mean shell height of 24.4 mm, and either 60 oyster spat in 4 or 5 clusters (mean length 24.8 mm) or 70 clams (mean length 16.4 mm). By providing two species of bivalves as prey it was possible to compare the rates of prey consumption at different temperatures. *M. lateralis* was used as the secondary prey species on the basis of C. L. MacKenzie's (personal communication) field observations of heavy natural predation by *E. caudata* on the coot clam. The water temperatures at the five stations were maintained at 10.0, 15.0, 20.0, 25.0 and 30.0 $\pm$ 1.0°C. The salinity was maintained at 26.0 $\pm$ 1.5 ppt and probably did not have a significant influence on the feeding rates at the various temperatures. During the experiment the trays were covered with small-mesh nylon netting to prevent escape of the drills. The experiment consisted of five 10-day trials. The trays were examined at the end of each trial and the number of prey consumed and number of dead drills determined. After the trays were cleaned, the original number of drills and prey was restored by replacements from the aquarium stocks.

A second experiment was conducted to determine more accurately the optimum feeding temperature of *E. caudata*. Four stations were established and maintained at 22.5, 25.0, 27.5 and 30.0 $\pm$ 1.0°C. This study also consisted of five 10-day trials in which the same experimental procedures described above were used.

RESULTS AND DISCUSSION

Relation of feeding rate to temperature

The first experiment showed that the rates at which *E. caudata* consumed *C. virginica* and *M. lateralis* varied with changes in temperature (Table 1). At 10.0°C, drills fed very little (0.02 oyster or 0.05 coot clam per drill per trial), and attacked (attempted perforation) prey organisms only occasionally. Locomotor activity was limited; the drills generally remained stationary and firmly attached to a substratum. Movement was relatively slow (approximately 0.35 cm/min) and entailed limited podial extension. No copulation or ovipositing was seen. These observations seemed to indicate that 10.0°C may be near the lower temperature limit for normal activities of *E. caudata* indigenous to Long Island Sound.

The feeding rate gradually increased with each increase in temperature from 10.0 to 25.0°C. At 25.0°C the largest number of both prey species (1.34 oysters and 2.23 clams per drill per trial) was consumed and the highest percentage of drills feeding (55%) was observed. At 30.0°C, however, the feeding rate decreased noticeably, and the drills were relatively immobile and weakly attached to the trays. Egg deposition also was reduced considerably. Although feeding was still moderate at 30.0°C, this temperature may be near the upper limit for some activities of the drills.

The optimum feeding temperature for *E. caudata* was more accurately determined in the second experiment (Table 2). The rates at which both prey organisms were consumed increased as the water temperature increased from 22.5 to 25.0°C. At 25.0 and 27.5°C the feeding rates were similar; *E. caudata* consumed an average of ap-

TABLE 1. Average number of *Crassostrea virginica* and *Mulinia lateralis* consumed by *Eupleura caudata* per 10-day trial and the number consumed per drill per trial at a series of controlled water temperatures. [a]

Temperature °C	*C. virginica*		*M. lateralis*	
	Average per trial	Average per drill	Average per trial	Average per drill
10.0	0.40	0.02	1.00	0.05
15.0	5.20	0.26	11.20	0.56
20.0	13.80	0.69	29.80	1.49
25.0	26.80	1.34	48.60	2.23
30.0	17.80	0.89	20.80	1.04

[a] Twenty *E. caudata* were placed in trays at each temperature with either 60 oyster spat or 70 clams. See text for details.

proximately 1.54 oysters and 2.08 coot clams per drill per trial. At 30.0°C feeding had again declined to a rate below that observed for 22.5°C. Thus, the optimum temperature for prey consumption was between 25.0 and 27.5°C.

A comparison of the feeding of oyster drills on each prey species showed that more coot clams than oysters were consumed at all temperatures studied (Fig. 1). At the lower temperatures the

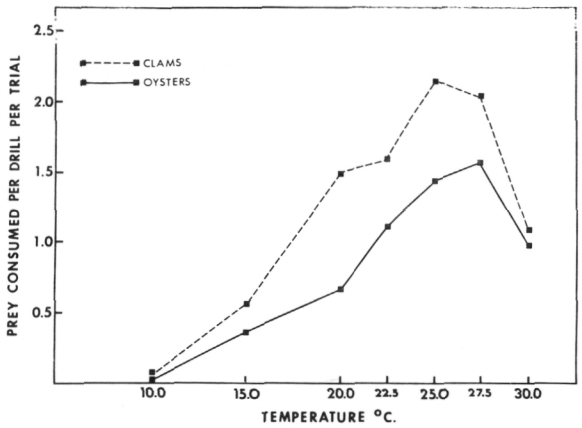

FIG. 1. *Feeding rates of* Eupleura caudata *on two prey species at a series of controlled water temperatures.*

drills consumed approximately twice as many clams as oysters, but this difference gradually decreased as the temperature and feeding rates increased. At the optimum feeding temperature the number of clams consumed was only 40% higher and at 30.0°C the disparity was reduced to about 10% (Experiments 1 and 2 combined).

Statistical evaluation (Student's t-test) revealed that all differences between the means of the feeding rates at progressively increasing temperature levels were significant at the 99% confidence level ($t>4.604$ with d.f. $= 4$) in Experiment 1 and (except for those at 25.0 and 27.5°C) at the 95% confidence level ($t>2.776$ with d.f. $= 4$) in Experiment 2.

Hanks (1957) reported a progressive increase in feeding of *U. cinerea* similar to that shown here for *E. caudata* and suggested that the optimum feeding temperature for this species was 25.0°C (27.5°C was not tested). He stated, however, that since water temperatures in Long Island Sound seldom reach 25.0°C or higher, oyster drills probably do not feed at the observed maximum rates in their natural environment. His results showed that *U. cinerea* consumed a larger number of oyster spat at all temperatures than the *E. caudata* observed in the present study. Although this difference could indicate that *U. cinerea* is the more voracious of the two drills, it is possible that *C. virginica* is a less attractive prey organism to *E. caudata.*

Relation of feeding rate to species of prey

The disparity between the rates at which the two prey organisms were consumed by *E. caudata* (Tables 1 and 2) could be considered evidence of a preference for the coot clam over the oyster. More clams than oysters were consumed at each temperature, but possibly certain physical factors were responsible for the disparity. Because of its larger size, *C. virginica* provided the attacking drill more food per kill than *M. lateralis.* Moreover, the greater ease with which the thinner shell of the clam can be penetrated may result in a higher frequency of successful attacks. Regardless of the effect of these factors it seems reasonably certain that *E. caudata* feeds on *M. lateralis* at least as readily as it does on *C. virginica.*

TABLE 2. Average number of *Crassostrea virginica* and *Mulinia lateralis* consumed by *Eupleura caudata* per 10-day trial and the number consumed per drill per trial at a series of controlled water temperatures.[a]

Temperature °C	*C. virginica*		*M. lateralis*	
	Average per trial	Average per drill	Average per trial	Average per drill
22.5	22.20	1.11	30.80	1.54
25.0	30.00	1.50	42.40	2.12
27.5	31.80	1.59	40.80	2.04
30.0	20.80	1.04	21.20	1.06

[a] Twenty *E. caudata* were placed in trays at each temperature with either 60 oyster spat or 70 clams. See text for details.

Relation of cannibalism and mortality to temperature

Cannibalism among *E. caudata* occurred in many of the experimental trays and may have had a significant bearing on the results. The rate of cannibalism, like the rate of feeding, increased with temperature. The incidence of cannibalism was highest at 25.0 and 27.5°C, where maximum feeding on the prey species also occurred. Although cannibalism has been observed previously for *E. caudata* (Flower, 1954; C. L. MacKenzie, personal communication), this was the first instance where cannibalism was observed throughout the drill's thermal feeding range in the presence of alternative food sources. In all observations of active cannibalism, the predators were female drills. Probably the rate of cannibalism in the comparatively high drill population densities in these experiments does not occur frequently in the natural environment; thus, the cannibalism rates observed may be valid only in comparable population densities in nature.

The survival of *E. caudata* also appeared to be temperature-dependent. The range of temperatures studied was not sufficient to establish the thermal limits for drill survival, but the experiments did show that mortalities can occur at temperatures comparable with those occurring in natural waters. Drill mortalities were not appreciable below 20.0°C within the experimental period; the total average mortality ($\bar{x}$ mortality of the five trials) was only 3.0% during the five 10-day experimental periods at 20.0°C. The percentage mortality increased as the temperature increased and reached a peak of approximately 17.0% at 30.0°C. In most experiments cannibalism accounted for a relatively large part of the mortalities (20.0-66.0% of the recorded mortalities), especially at the optimum feeding temperatures, 25.0 and 27.5°C. Unknown causes, however, contributed to the observed mortalities, particularly at 30.0°C. It seems reasonable to conclude, therefore, that natural mortalities probably increase at 30.0°C and above.

Substrata used for capsular attachment

MacKenzie (1961), in his study of drills from the York River, Virginia, reported that *E. caudata* showed little preference in substratum for capsular attachment. He stated that the only apparent criteria for these substrata were that they be hard and free of fouling. In the present study the rates of egg-capsule deposition of *E. caudata* confined with two different prey organisms were not significantly different, although the substrata used for capsule attachment were markedly dissimilar. The *E. caudata* confined with *C. virginica* attached capsule clusters, almost exclusively, to the valves of the oyster spat. Drills confined with *M. lateralis*, however, rarely attached capsules to the shell surface; most capsules were attached to the sides and bottom of the tray, or on other drills. The ability of the drills to discriminate between substrata for attachment of egg capsules is worthy of further study.

SUMMARY AND CONCLUSIONS

1. The small number of attacks by *E. caudata* from Long Island Sound on prey organisms at 10.0°C indicates that this temperature is near the lower limit for feeding.

2. Feeding rates increased with each increase in temperature from 10.0-27.5°C, but decreased when the temperature was increased to 30.0°C.

3. Maximum feeding rates on both prey organisms *(C. virginica* and *M. lateralis)* were at 25.0 and 27.5°C.

4. Drills consumed more *M. lateralis* than *C. virginica* at all temperatures. Physical differences between the prey may account for some of this disparity.

5. Drills were cannibalistic in the presence of alternative food sources throughout the range of experimental temperatures. Cannibalism increased as feeding rate increased and was greatest at the optimum feeding temperatures. All cannibalistic drills observed were females.

6. *E. caudata* discriminated between the two prey organisms as substrata for capsular attachment. Ovipositing drills deposited egg capsules readily on the valves of *C. virginica* but only infrequently on the valves of *M. lateralis*.

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