Some Factors Influencing Predation by the Flatworm, *Stylochus ellipticus* (Girard), on Oysters

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ABSTRACT: Some of the effects of low temperature, low salinity, prey size, and predator source on the predatory activity of *Stylochus ellipticus* on oysters were investigated in the laboratory.

Lowering temperatures below 10 C resulted in a progressive decrease in predation. Salinities as low as 5 $^{0}/_{00}$, approximately the lower limit of tolerability of the oysters, appeared to give no lasting decrease in predation. As an oyster predator, *S. ellipticus* primarily attacked small individuals but large worms (20 mm long) killed oysters as long as 61 mm.

S. ellipticus from seven localities were observed in the laboratory for differences in predatory activity on oysters and barnacles. An obvious preference for one or the other prey species was demonstrated by worms from each locality. Worms from higher salinities preferred barnacles, whereas those from lower salinities preferred oysters. Prey preference might be correlated with a comparatively greater abundance of barnacles in higher salinities and oysters in lower salinities. This relationship could be consistent with the hypothesis of "ingestive conditioning," which states that a predator develops a tendency to respond more readily to effluents from a given invertebrate prey species after ingestion of living tissues of that species.

Introduction

Hopkins (1949, 1950) found approximately 160 references to predation by marine flatworms. Among those listed is Stylochus ellipticus, a species widely distributed on the Atlantic and Gulf Coasts of the United States and commonly associated with barnacles and oysters (Hyman, 1940). Its activity as a predator on the oyster, Crassostrea virginica, has been studied by Pearse and Littler (1938), Nelson (1939), and Webster and Medford (1959), who presented circumstantial evidence of predation by S. ellipticus on oysters in the Middle Atlantic area. Loosanoff (1956) and Provenzano (1959) showed that S. ellipticus from West Tisbury Great Pond, Martha's Vineyard, Massachusetts, readily killed and ate oyster spat in the laboratory and in the field, respectively.

In view of the potential danger that this widespread flatworm poses to the commercially valuable oyster, it is important that factors influencing its feeding habits be investigated. This paper presents experimental data concerning some effects of temperature, salinity, and prey size on the predatory activity of *S*. *ellipticus* on oysters and the influence of predator source on the choice by *S*. *ellipticus* between oysters and barnacles as prey.

Worms from the original Milford Harbor collection were identified as *S. ellipticus* by Dr. Libbie H. Hyman of the American Museum of Natural History. Worms from other sources were identified as *S. ellipticus* by the senior author, using the Milford Harbor specimens as homeotypes.

Materials and Methods

All of the experiments were carried out in pans containing 6 liters of filtered, standing sea water changed three times a week. Since *S. ellipticus* is euryhaline (Pearse and Wharton, 1938; Landers and Toner, 1962), all of the temperature experiments were performed in undiluted $(27-28 \ ^{0}/_{00})$ water from Milford Harbor after a suitable acclimation time, i.e., when all signs of distress in the worms had disappeared, regardless of the salinity at the 56

source when the worms were collected. (Signs of distress in *S. ellipticus* transferred abruptly to low salinities have been described by Landers and Toner [1962] as a loss of color, sluggishness, and the production of abnormal amounts of mucus). Salinity experiments were carried out at room temperature. Here again, the worms were acclimated to the experimental salinities before being put in pans with oysters.

Oysters used in all experiments were collected from Milford Harbor and were acclimated for several days prior to any experiments involving lowered salinities. We made no attempt to measure the degree of acclimation produced by this treatment.

All of the barnacles came from Milford Harbor. Cursory examination indicated that we used two species, *Balanus improvisus* and *Balanus eburneus*, indiscriminately.

In every experiment equal numbers of each species involved were put in each pan. This was usually 10 individuals but on two occasions 8 of each were used. The initial number was maintained throughout an experiment by replacing dead individuals with live ones. When oysters and barnacles were compared as prey, they were put in the same pans. An amount of Chlorella sp. and Phaeodactylum tricornutum mixture that could be cleared from the water by the filterfeeders within 24 hours was added daily to each pan. Normal activities of the experimental animals, such as the production of feces by the oysters, sweeping movements of the barnacles' cirri, and escape movement of the worms when disturbed, were assumed to be signs of a healthy environment in which predation could occur.

The experiments on the influence of temperature, salinity, and prey size on predation were continued for 10 days after predation was first observed. This was sufficient to take the worms well beyond their first peak of predatory activity in any environment that we tested. A "first peak" of predation was observed to be common to every experiment in which predation occurred and consisted of a concentration of predatory activity during the first 2 to 4 days after predation started, followed by a decrease in activity thereafter. The absence of food during conditioning periods prior to the start of many of the experiments may have accentuated this

initial burst of predatory activity but we noticed the same phenomenon in worms given prey less than 24 hours after they were collected (Landers, unpublished data).

The length of the worms was measured from head to tail by calipers to the nearest millimeter while the animals were moving on a flat surface. Oyster length was considered to be the greatest linear dimension from umbone to bill. Barnacles were sized by measuring the long axis of the carapace opening. We tried to maintain size uniformity within each group of experimental animals throughout our observations to minimize the influence of size variation between predator and prey. Except where otherwise noted, the worms were approximately 10 mm long and the oysters 15 mm long. The carapace opening of the barnacles was about 4 mm long.

The experiments on prey selection by *S. ellipticus* were continued for several days after predation was first noted to give the worms ample opportunity to attack both prey species.

Control pans of prey with no worms were included with each experiment.

Observations and Results

Influence of Temperature and Salinity

Landers and Toner (1962) suggested that some environmental control of predation by *S. ellipticus* on oysters may exist in areas where periods of low salinity or low water temperature slow the worm's movements. With this suggestion in mind, we observed the effects of these two factors on worms from West Tisbury Great Pond.

Since we had seen heavy predation in stock trays earlier at 12 C (Landers, unpublished data), we limited our low-temperature observations to 11 to 5 C. Observations were also made at room temperature (21-22 C) as a standard for comparison since this is within the range at which movement of *S. ellipticus* is at its maximum (Landers and Toner, 1962). Based on the pooled results of four experiments in which predation at each temperature category listed in Table 1 was observed at least twice, we concluded that predation started before the end of the first day at

	nset of predation number of days to first kill)	Rate of predation (number of spat killed per day per 10 worms)	
21-22	1	0.60	
10-11	1	0.50	
9-10	2	0.32	
7-8	2	0.33	
6–7	4	0.27	
5-6	6	0.14	

TABLE 1. Effect of temperature on predatory activity of S. ellipticus on oysters at a salinity of $27-28^{0}/_{00}$.

¹Computed only for days after onset of predation.

21-22 C and at 10-11 C. The rate of predation was also approximately the same at the two temperatures-0.60 and 0.50 oysters killed per day per 10 worms, respectively. Below 10 C, days-to-first-kill increased and predation rate decreased with decreasing temperature, reaching 6 days and 0.14 spat killed per day per 10 worms, respectively, at 5-6 C. None of the control oysters died at any of the experimental temperatures. These data agree well with the observations of Landers and Toner (1962), who found a noticeable slowdown in movement of S. ellipticus at about 10 C and further decreases at lower temperatures.

The effects of salinity on predation were observed in two experiments at each of the following salinities: 27-28, 15, 7.5, 5, and 2.5 $^{0}/_{00}$. Predation started by the end of the first day of each experiment at salinities of 7.5 $^{0}/_{00}$ and above, but not until 3 or more days at 5 $^{0}/_{00}$. The rate of predation, on the other hand, fluctuated with differences in salinity and was as high as 5 $^{0}/_{00}$, once predation started, as at 27-28 $^{0}/_{00}$ (Table 2). The data for 2.5 $^{0}/_{00}$ were inconclusive. Worms survived at this salinity but the oysters, including controls, died within a week after the experiments were begun. Worms were seen moving slowly about and occasionally feeding on dead spat but there was no evidence of predation. Except for the death of those in $2.5 \ ^{0}/_{00}$, only one other control oyster (in $5^{0}/_{00}$) died during these experiments.

These data indicated that under the existing experimental conditions the predatory activity of S. *ellipticus* on oysters was retarded at temperatures below 10 C but that salinities as

	Onset of predation (number of days) to first kill)	Rate of predation ¹ (number of spat killed per day per 10 worms)
27-28	1	0.60
15	1	1.00
7.5	1	0.90
5	3 or more	0.80

 TABLE 2. Effect of salinity on predatory activity of S.
 ellipitcus on oysters at 21–22 C.

¹Computed only for days after onset of predation.

low as 5 $^{0}/_{00}$ produced only a temporary pause in predatory activity.

Some of the observed decrease in predatory activity must have been due to the slowing of the worm's movements at low temperatures and low salinities, as described by Landers and Toner (1962), but the effects of these factors on the shell movements of the oysters, which might alter their accessibility to attack, would also have to be considered in a definitive study of this predator-prey relationship. Loosanoff (Nat. Shellfish. Assoc. Convention Address, 1952) gave some information on this subject. He showed that there was a sharp decrease in shell movement of oysters from Long Island Sound transferred abruptly from $27^{\circ}/_{00}$ to salinities below $20^{\circ}/_{00}$, being more pronounced the greater the change in salinity, but he also noted some recovery of shell movement after the first six hours. He found that Long Island Sound oysters, conditioned for three months in the laboratory to salinities of 10 $^{\circ}/_{00}$ or 7.5 $^{\circ}/_{00}$, opened their shells at a much lower salinity than those kept in $27^{\circ}/_{00}$. As a result of these observations, he concluded that "oysters can get accustomed to a much lower salinity than the one in which they were grown".

Influence of Prey Size

Based on his observations of *S. ellipticus* from West Tisbury Great Pond in the laboratory, Loosanoff (1956) considered this worm to be more of an enemy to young oysters than to adults, but he also stated that these worms readily attacked oysters as large as 2.5 inches (63 mm) long. Provenzano (1959), on the other hand, gave 0.5-inch (12.5 mm) long as the largest oysters that he found apparently

preyed upon by *S. ellipticus* in West Tisbury Great Pond during the unusually severe spat mortality of 1956, but he did not make clear whether larger spat were present. He made no mention of any unusual mortality among adult oysters in the pond during this time.

We used worms from West Tisbury Great Pond and from the Tred Avon River in Chesapeake Bay for our observations on the influence of prey size on predation. Two experiments showed that worms from West Tisbury Great Pond, with a maximum length of 15 mm, successfully attacked oysters up to 49 mm long. In one experiment, worms about 20 mm long from the Tred Avon River killed oysters as large as 61 mm long. (None of the control oysters in the three experiments died.) In every experiment, however, more small than large oysters were killed (Table 3). We therefore concluded that when it preys on oysters, S. ellipticus is primarily an enemy of spat and seed.

Influence of Predator Source

Attempts to induce S. ellipticus to prey on oysters in the laboratory have not always been successful. For example, Pearse and Wharton (1938) found that although S. inimicus (the southern oyster "leech") from Apalachicola Bay, Florida, killed oyster spat in the laboratory, S. ellipticus collected from the same area did not, but did attack and eat barnacles. They concluded that S. ellipticus is not an enemy of healthy oysters, but since the worms did eat oyster meat, they may feed on sick and dying individuals. Investigators at the Virginia Institute of Marine Science, Gloucester Point, Virginia, also failed to induce predation on oysters by *S. ellipticus* from some local areas, although the worms did prey on barnacles and several species of bivalves other than oysters common in Chesapeake Bay (Dana Eldridge, personal communication).

Worms from Milford Harbor, no matter what season observed, never preyed on oyster spat in the laboratory; however, they always attacked barnacles (Landers, unpublished data). This observation led us to investigate the predatory activity of S. ellipticus from a number of localities along the Atlantic Coast of the United States on oysters and barnacles in the laboratory. The sources of these worms and their choices of prey under laboratory conditions are summarized in Table 4. We made no attempt to determine feeding rate for any of the groups of worms but only to ascertain whether predation occurred. In all of the experiments never did more than one individual of a control species die and in most experiments none.

These data suggest that populations of S. ellipticus may be separated into two categories, those that prey on oysters and those that do not. Why this is so is not clear, but the observations of Wood (1968) may give an explanation. In his discussion of prey preference by the oyster drill, Urosalpinx cinerea, he introduced the concept of "ingestive conditioning" to account for this gastropod's preference for a particular prey species. On the basis of his observations, Wood defined "ingestive conditioning" as the tendency of a

S. ellipticus	Experiment No.	Number of oysters of different lengths (mm) killed			
Source		12-25	26-38	39-51	52-64
West Tisbury Great Pond, Martha's Vineyard, Mass.	1 2	7 5	4 1	1 2	0 0
Tred Avon River, Chesapeake Bay, Md.	1		12-38 8	39-51 6	52-64 2

TABLE 3. Effect of oyster size on rate of predation by S. ellipticus at 21-22 C and 27-28 $^{0}/_{00}$.

	Predation on		G_1::(4 (0/)	
Predator source	Oysters	Barnacles	Salinity (⁰ /00) at source	
Long Island Sound, Milford, Conn.	No	Yes	30+	
Milford Harbor, Conn.	No	Yes	26-28	
Lewis Gut, Bridgeport, Conn.	No	Yes	26+	
Cape Charles, Chesapeake Bay, Va.	No	Yes	27	
Bayville, Long Island, N. Y	Yes	No	24+	
Tred Avon River,				
Chesapeake Bay, Md.	Yes	No	9-12	
West Tisbury Great Pond,				
Martha's Vineyard, Mass.	Yes	Yes	10-25	

TABLE 4. Effect of predator source on predation by S. ellipticus on oysters and barnacles at 21-22 C and $27-28^{\circ}/_{00}$.

predator to respond more readily to effluents from a given invertebrate prey species after ingestion of living tissue of that species. If this is so, we suggest that a predator might become so conditioned to one prey species that it would refuse to attack another. Our observations on *S. ellipticus* predation in the laboratory appear to demonstrate this. Worms from six of the seven localities sampled preyed on either oysters or barnacles but not on both (Table 4).

Worms from West Tisbury Great Pond were the only ones that preyed on both oysters and barnacles; however, oysters were the preferred prey. In two experiments where oysters and barnacles were in the same pan, 7 spat and 1 barnacle, and 6 spat and 2 barnacles were eaten in 21 days and 28 days, respectively. In another experiment where only barnacles were available for the first 30 days, 3 were killed. Oyster spat were then added to the pan and 5 were eaten during the next 24 hours.

During several of our many attempts to induce S. ellipticus from Milford Harbor to prey on oyster spat, we obtained data which might be interpreted as additional evidence that this worm can become strongly conditioned to feeding on one kind of prey. On two occasions worms were given freshly opened spat daily for more than a week, in addition to live spat and barnacles which were always present. Only the barnacles were eaten. On several other occasions worms were denied barnacles for weeks. They shrunk and eventually died, apparently from starvation, even though oyster spat, which they never attacked, were available to them throughout these periods.

The data in Table 4 appear to show a relationship between preferred prey and salinity since all four localities providing worms which preferred barnacles have a consistently high salinity, although lower than oceanic, while two of the three areas providing worms that preyed on oysters have salinities that are consistently or periodically low. Actually, we know nothing about the effect of salinity on the food preference of S. ellipticus. However, if we extend Wood's hypothesis to S. ellipticus, we might expect this species to become conditioned to feeding on the most abundant food available since the worms would come into contact with it more frequently. We might then speculate that the apparent relationship in Table 4, between preferred prey and salinity, may actually reflect the comparative abundance of barnacles and oysters in these two types of salinity regimes. The one locality that appears to be an exception to this in Table 4 but may not be is Bayville, Long Island. Here we found worms preying on a dense population of hatchery-reared seed oysters on shells suspended from rafts in water that never has a salinity lower than about $24^{\circ}/_{00}$. The worms probably settled on the shells as metamorphosing larvae since adult S. ellipticus do not swim (Hyman, personal communication) and would have had difficulty getting to the oysters in any other way. Although we made no counts, we could see that oysters were abundant on the shells and barnacles were not. Barnacles were abundant on rocks and pilings in the area but since the shells bearing the seed oysters were put in the water after the peak of barnacle setting had passed, they collected relatively few barnacles. In this case, from the time they set on the shells the worms would have found oysters to be by far the most abundant food species available.

In summary, our observations on S. ellipticus prey preference show that when given a choice between oysters and barnacles, individuals from some localities exhibit a strong preference for oysters, whereas those from other localities have an equally strong preference for barnacles. This phenomenon may be interpreted as an example of "ingestive conditioning" but in the absence of direct proof this conclusion must remain tentative.

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