The Temperature Tolerances of Three Species of Marine Fishes

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ABSTRACT

The temperature tolerances of three species of marine fishes—*Menidia menidia* (common silverside), *Pseudopleuronectes americanus* (winter flounder), and *Spheroides maculatus* (northern swellfish)—have been determined. Following calculation of the median tolerance limit for various exposure times over a range of acclimation temperatures, the thermal tolerance was determined on a square graph by plotting lethal temperature against acclimation temperature. The tolerances determined are: 715°C squared for *M. menidia*; 635°C or 685°C squared for *P. americanus*, with cold tolerance limits of 1°C or 0°C, respectively; and 550°C squared for *S. maculatus*.

Introduction. Temperature probably has greater bearing on fishes than any other environmental factor. Fry (1947) has presented two experimental procedures for assessing the temperature tolerance of fishes. The first method, which requires exposure of the organism to continuous and progressively higher or lower temperatures until death occurs, is rapid, convenient, and requires little apparatus. Unfortunately, this method does not permit isolation of the time and temperature variables. However, in the past this method has yielded valuable results in preliminary comparisons involving marine organisms (Vernon 1899, Huntsman and Sparks 1924, and Battle 1926). With the second method, the organism is subjected to various thermostatically controlled constant temperatures. This method, although more time-consuming, does permit isolation of the time and temperature variables. Thus, this approach appears to provide temperature data that permit better appraisal of the sur-

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vival requirements of a fish in its natural environment, insofar as temperature is concerned.

The three marine species used in these experiments, representing three orders, are: (i) *Pseudopleuronectes americanus* (winter flounder)—Pleuronectiformes, (ii) *Menidia menidia* (common silverside)—Mugiliformes, and (iii) *Spheroides maculatus* — Tetraodontiformes.

Methods and Procedure. All fish used in these experiments were taken from local waters: *M. menidia* from March through June 1964, *S. maculatus* from July through September 1964, and *P. americanus* from May through July 1963 and 1964. All specimens were held prior to acclimation and experimentation in 200-gallon tanks at room temperatures of 17.5°C to 18.5°C for periods ranging from two to 30 days, during which time *Venus mercenaria* (hard clam) was fed to them daily. (The fish were not fed during acclimation or experimentation.)

The seawater employed was obtained at high tide from the inlet at Belmar, New Jersey. Its salinity in the tanks ranged between 29‰ and 31‰; salinity was determined with a salinometer (Industrial Instruments, Model Rs52).

Prior to experimentation, each fish was gradually acclimated. In general, the changes from room temperature to the prescribed acclimation temperature proceeded at a rate of about 1°C/hour. Fish that were acclimated to 14°C and 21°C were held at these temperatures for 24 hours prior to the experiment. Fish acclimated to 7°C, 10°C, and 28°C were held at these temperatures for periods ranging from two to five days.

All experiments were performed in ten gallons of standing seawater, which was well aerated with compressed air. During the experiments, the water temperature was under thermostatic control (Fenwall Thermoswitch, Model 17502-0) and did not deviate from the stated value by more than ±0.5°C. Low temperatures were obtained by placing a ten-gallon tank (used for the experiments) in a 20-gallon bath aquarium, and the water in the bath aquarium was then circulated through a cooling unit (Heat-X Inc., Model OOP-40) by means of a centrifugal pump. When a series of low temperatures was desired, the water was passed from tank to tank through glass U-shaped syphons. To determine heat tolerance, 500-watt immersion heaters (stainless steel custom fashioned) were employed. To reduce the effect of changes in the dissolved-oxygen concentration during the experiments, the water was vigorously aerated.

M. menidia and *P. americanus* were usually treated in groups of ten, but occasionally groups of five were employed. Because of its size, *S. maculatus* was treated in groups of only five. Two hundred and sixty-five *M. menidia*, 180 *P. americanus*, and 175 *S. maculatus* were employed in these experiments. The number of specimens that survived was recorded in periods of 1, 3, 6, 24, 48, and 72 hours. The mean lengths and weights were recorded after the

fish expired or after the experiment was terminated. In all experiments, a specimen was presumed to be dead when no respiratory movements could be detected.

To measure the temperature tolerance of a given species, the upper and lower median tolerance limit—defined as that temperature by and at which 50% of the experimentals can no longer live for a designated exposure period—was determined by a simple procedure recommended by Douderoff (1942). Five or ten fish, after direct transference from the acclimation tank to the test tank, were subjected to a temperature known from preliminary tests to have been close to the tolerance limit. Using the known total number of survivors at the end of the various designated time intervals, the tolerance limit was estimated by interpolation. This involved (i) plotting the experimental data on semilogarithmic coordinate paper, with test temperature laid off on the logarithmic scale and survival percentage on the arithmetic scale, (ii) connecting with a straight line the two points that represent survival percentages at two successive test temperatures that are lethal to more than half and to less than half of the experimentals, and (iii) noting the concentration that corresponds to 50% survival on the graph. After the upper and lower limits were determined for a series of acclimation-temperature levels, the limits were plotted so that the entire thermal tolerance of the species could be displayed (Fry et al. 1942). The lethal temperature (Tlm at 48 hours) was then plotted against the acclimation temperature on a square graph that has an additional line drawn at an angle of 45° to the axis; this line indicates where the lethal and acclimation temperatures are identical.

The two lethal-temperature lines, together with portions of the axis, and the perpendicular line from the junction of the upper-lethal and acclimation temperatures enclose an area that represents all tolerable thermal possibilities of the species. This area was determined with a planimeter (Ott Compensating Polar Planimeter, Model 83699); a degree centigrade squared is the unit.

Results. The data obtained for all three species are presented in Tables I–VI, and the results are depicted diagrammatically in Figs. 1–3. The tabular data were employed in preparing the figures.

The behavior of the specimens, when transferred from an acclimation tank to a test tank with high temperatures, was in general similar to that described by Hathaway (1927) for several species of freshwater fishes. This behavior included all or most of the following effects: (i) an increase in general activity, (ii) disturbances in equilibrium, which might be evidenced by surfacing, darting, floating, imbalance, persistent fin movement, tail elevation, or swimming into the side of the tank, and (iii) increased respiratory movement.

In all three species the disturbances in equilibrium from heat shock usually occurred within one minute following transference, and in cases of exposure to extreme temperature changes it was necessary to cover the tank to prevent

Table I. Per cent survival of *Menidia menidia* at various low temperatures in relation to preceding acclimation. Tlm refers to the estimated lower median tolerance limits.

Accl. temp. (°C)	Test temp. (°C)	No. of Fish	Mean length (cm)	Mean weight (g)	Percentage surviving after 1 hr.	3 hr.	6 hr.	24 hr.	48 hr.	72 hr.	Tlm
28	15	10	8.6	4.3	100	100	100	100	100	100	
28	10	10	8.8	4.7	100	100	90	90	80	80	
28	8	10	8.8	4.9	90	60	60	40	30	30	
28	7	10	8.7	4.6	60	20	00	00	00	00	
					–	7.8	7.9	8.3	8.7	8.7	Tlm
21	7	5	8.9	4.8	100	100	100	100	100	100	
21	5	10	9.0	5.2	100	100	100	90	90	70	
21	4	10	9.0	5.1	70	60	60	40	40	40	
21	3	10	8.7	4.8	50	50	20	20	10	10	
21	2	5	8.7	4.6	00	00	00	00	00	00	
					3.0	3.0	3.7	4.2	4.2	4.3	Tlm
14	5	10	8.6	4.7	100	100	100	100	100	90	
14	3	10	9.2	4.9	100	100	100	80	80	60	
14	2	10	8.3	5.1	100	100	90	80	80	50	
14	1	5	8.6	4.6	00	00	00	00	00	00	
					1.4	1.4	1.5	1.5	1.8	2.0	Tlm
7	2	10	8.7	4.6	100	100	100	100	90	90	
7	1	5	9.1	5.0	80	00	00	00	00	00	
					–	1.4	1.4	1.4	1.5	1.5	Tlm

Table II. Per cent survival of *Menidia menidia* at various high temperatures in relation to preceding acclimation temperature. Tlm refers to the estimated upper median tolerance limits.

Accl. temp. (°C)	Test temp. (°C)	No. of fish	Mean length (cm)	Mean weight (g)	Percentage surviving after 1 hr.	3 hr.	6 hr.	24 hr.	48 hr.	72 hr.	Tlm
28	30	5	8.9	4.6	100	100	100	100	100	100	
28	32	10	9.0	5.2	100	100	100	90	70	70	
28	34	10	8.7	4.4	50	20	00	00	00	00	
					34.0	33.0	32.9	32.8	32.5	32.5	Tlm
21	28	10	9.1	5.1	100	100	100	100	90	90	
21	30	10	8.7	4.3	100	100	90	80	80	70	
21	31	10	9.0	4.9	70	50	50	40	40	20	
21	32	10	9.0	5.2	20	20	00	00	00	00	
					31.4	31.0	31.0	30.7	30.7	30.4	Tlm
14	23	10	8.7	4.1	100	100	100	100	100	100	
14	25	10	8.5	4.5	100	80	80	60	60	50	
14	27	10	8.9	4.8	80	50	50	40	40	30	
14	29	10	9.1	5.1	40	20	20	20	20	10	
					28.4	27.0	27.0	26.0	26.0	25.0	Tlm
7	20	10	9.0	4.7	100	100	80	80	80	80	
7	22	10	8.8	4.5	100	80	80	60	60	50	
7	24	10	8.7	4.4	70	50	30	30	20	20	
					–	24.0	23.0	22.6	22.5	22.0	Tlm

Table III. Per cent survival of *Pseudopleuronectes americanus* at various low temperatures in relation to preceding acclimation temperature. Tlm refers to the estimated upper median tolerance limits.

Accl. temp. (°C)	Test temp. (°C)	No. of fish	Mean length (cm)	Mean weight (g)	Percentage surviving after 1 hr.	3 hr.	6 hr.	24 hr.	48 hr.	72 hr.	Tlm
28	7.0	10	6.3	3.6	100	100	100	80	80	70	
28	6.0	10	6.0	3.4	100	100	90	70	60	50	
28	4.0	10	6.9	4.2	80	70	70	50	20	20	
					–	–	–	4.0	5.4	6.0	Tlm
21	6.0	5	6.7	3.7	100	100	100	100	100	100	
21	4.0	5	6.5	3.6	100	100	100	100	100	80	
21	2.0	10	6.5	3.5	100	80	80	70	70	60	
21	1.0	10	7.1	4.2	100	70	70	50	50	40	
					–	–	–	1.0	1.0	1.4	Tlm
14	2.0	5	7.0	4.1	100	100	100	100	80	80	
14	1.0	5	6.6	3.5	100	100	100	100	100	80	
					–	–	–	–	–	–	Tlm
7	1.0	5	6.8	3.8	100	100	100	100	100	100	
					–	–	–	–	–	–	Tlm

Table IV. Per cent survival of *Pseudopleuronectes americanus* at various high temperatures in relation to preceding acclimation temperature. Tlm refers to the estimated upper median tolerance limits.

Accl. temp. (°C)	Test temp. (°C)	No. of fish	Mean length (cm)	Mean weight (g)	Percentage surviving after 1 hr.	3 hr.	6 hr.	24 hr.	48 hr.	72 hr.	Tlm
28	29.0	10	10.5	12.8	100	100	80	70	70	60	
28	30.0	10	11.0	14.7	80	60	30	30	10	00	
					–	–	29.6	29.5	29.3	29.1	Tlm
21	26.0	10	10.7	13.5	100	100	100	100	90	90	
21	28.0	10	11.3	14.9	50	30	20	20	20	20	
21	29.0	10	10.2	12.6	20	20	10	00	00	00	
					28.0	27.5	27.3	27.3	27.0	27.0	Tlm
14	23.0	10	9.5	12.1	100	90	90	80	80	80	
14	24.0	10	8.6	10.3	80	80	60	50	50	40	
14	26.0	10	9.4	12.5	40	40	20	20	20	20	
					25.5	25.5	24.5	24.0	24.0	23.7	Tlm
7	20.0	5	10.6	12.8	100	100	100	100	100	100	
7	22.0	10	11.1	14.9	80	70	70	50	50	50	
7	24.0	10	9.7	12.3	30	10	00	00	00	00	
					23.2	22.8	22.7	22.0	22.0	22.0	Tlm

Table V. Per cent survival of *Spheroides maculatus* at various low temperatures in relation to preceding acclimation temperature. Tlm refers to the estimated low median tolerance limits.

Accl. temp. (°C)	Test temp. (°C)	No. of fish	Mean length (cm)	Mean weight (g)	Percentage surviving after 1 hr.	3 hr.	6 hr.	24 hr.	48 hr.	72 hr.	Tlm
28	16.0	5	15.3	75.8	100	100	100	100	100	100	
28	14.0	10	14.7	72.2	90	90	90	90	80	80	
28	12.0	10	15.9	79.3	80	60	60	40	10	10	
28	10.0	10	14.9	74.0	80	10	00	00	00	00	
					–	11.6	11.7	12.3	13.0	13.0	Tlm
21	12.0	5	14.2	69.7	100	100	100	100	80	80	
21	10.0	10	14.6	74.8	90	70	70	70	50	30	
21	8.0	10	15.6	78.9	50	30	30	20	00	00	
					8.0	9.0	9.0	9.2	10.0	10.7	Tlm
14	10.0	5	13.8	62.3	100	100	100	100	100	100	
14	8.0	10	15.1	72.8	90	80	80	60	40	20	
14	6.0	10	14.6	67.4	60	10	10	00	00	00	
					–	7.1	7.1	7.7	8.4	8.8	Tlm
10	7.5	5	14.2	64.9	100	100	100	80	60	20	

Table VI. Per cent survival of *Spheroides maculatus* at various high temperatures in relation to preceding acclimation temperature. Tlm refers to the estimated upper median tolerance limits.

Accl. temp. (°C)	Test temp. (°C)	No. of fish	Mean length (cm)	Mean weight (g)	Percentage surviving after 1 hr.	3 hr.	6 hr.	24 hr.	48 hr.	72 hr.	Tlm
28	31.0	5	14.6	72.4	100	100	100	100	100	80	
28	32.5	10	15.4	76.9	90	80	80	80	60	50	
28	33.5	10	14.7	77.3	90	60	60	40	20	00	
					–	–	–	33.2	33.0	32.5	Tlm
21	30.0	5	15.1	70.3	100	100	100	100	100	100	
21	31.0	10	14.3	70.9	100	80	80	80	60	60	
21	32.0	10	15.6	80.3	100	70	70	50	30	20	
					–	–	–	32.0	31.4	31.2	Tlm
14	27.0	5	14.6	69.0	100	100	100	100	100	100	
14	30.0	5	14.0	62.2	100	80	60	60	60	60	
14	32.0	10	15.3	68.7	80	20	10	00	00	00	
					–	31.0	30.5	30.2	30.2	30.2	Tlm
10	25.0	5	15.3	79.6	100	100	100	100	100	100	
10	30.0	10	14.2	64.7	80	70	60	40	20	00	
					–	–	–	29.2	28.2	27.5	Tlm

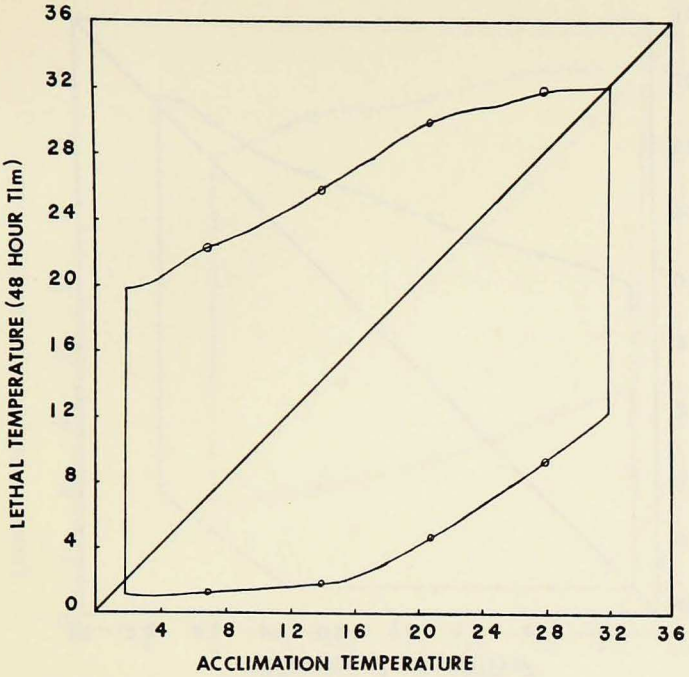

Figure 1. The thermal tolerence of *Menidia menidia* as displayed by plotting the lethal temperature against the acclimation temperature. Circles indicate calculated Tlm as determined from experimental data.

the fish from leaping out of the water. An increase in respiratory movement usually occurred within five to ten minutes after the test began. Labored respiration often continued for 24 hours, after which normal respiration usually returned with adjustment of the fish to the new temperature. However, if the hard and rapid respiration continued beyond 24 hours, death usually resulted before the test was completed. Recovery from heat shock was observed to occur in only *S. maculatus* and *M. menidia*—not in *P. americanus*. In some instances death occurred without a display of disturbance in equilibrium.

The behavior pattern of fishes subjected to extremely low temperatures usually included all or some of the following effects: (i) loss of equilibrium, (ii) an initial increase in respiration evidenced in faster and stronger opercular movement, and (iii) violent convulsive spurts and spasms. The reaction to cold shock occurred in two to five seconds following introduction of the fishes into the test tank. Oftentimes, death did not occur for periods ranging up to 48 hours following cold-shock symptoms. Recovery from cold shock occurred frequently in *M. menidia* and *P. americanus*, but only seldom in *S. maculatus*, which could not withstand temperatures below 8°C. Presumably, a longer acclimation period would lower this figure somewhat.

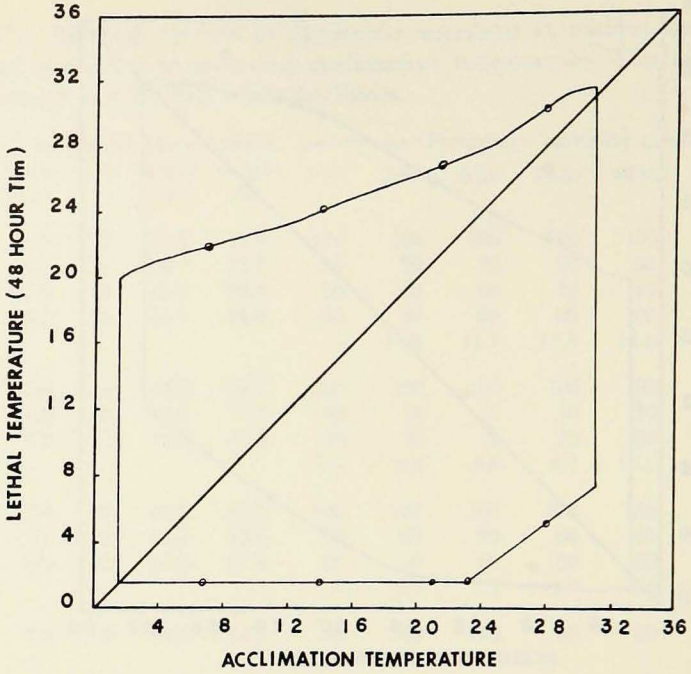

Figure 2. The thermal tolerance of *Pseudopleuronectes americanus* as displayed by plotting the lethal temperature against the acclimation temperature. Circles indicate calculated Tlm as determined from experimental data.

A correlation of fish size to temperature tolerance has not been attempted. However, most of the *P. americanus* used were about 10 cm in length, and the 48-hour Tlm of 29.3°C is in close agreement with the range of upper lethal temperatures (29.1–30.4°C for 10-cm fish) reported by Huntsman and Sparks (1924).

The thermal tolerances obtained in this study were: 715°C squared for *M. menidia*; 635°C or 685°C squared for *P. americanus*, with cold tolerance limits of 1°C or 0°C, respectively;[2] and 550°C squared for *S. maculatus*.

Discussion and Conclusions. The importance of temperature to fishes has already been amply discussed by Brett (1956), who has also reported the temperature tolerance of many species. All of his observations were on freshwater species, except for *Girella nigricans*, an estuarine fish that had a value of 800°C squared assigned to it.

Of the three species observed here, temperature studies on only *P. americanus* have been reported previously. Huntsman and Sparks (1924) found different "death points" when flounders of different size were exposed to high temperatures: 27.8°C to 29°C for fish 30 cm long, and 29.1°C to 30.4°C for fish 10 cm

2. The low temperature apparatus did not function below 1°C.

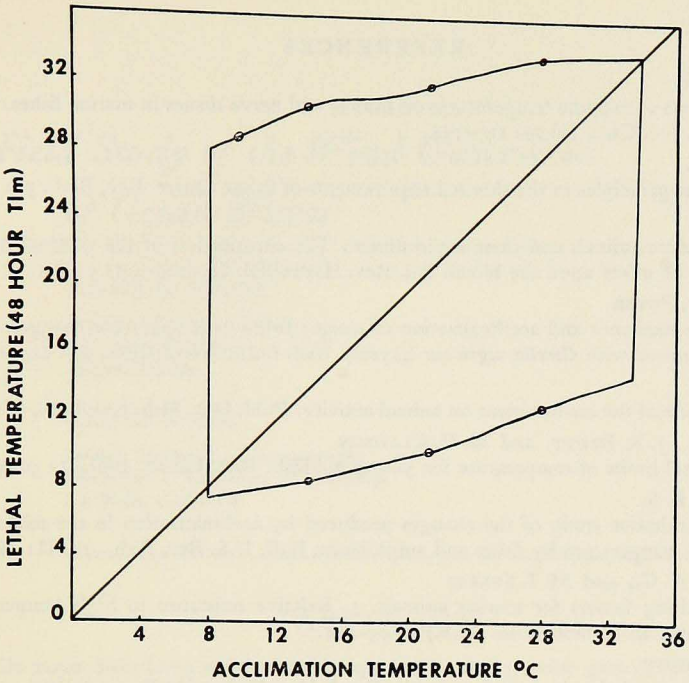

Figure 3. The thermal tolerance of *Spheroides maculatus* as displayed by plotting the lethal temperature against the acclimation temperature. Circles indicated calculated Tlm as determined from experimental data.

long. Battle (1926) has observed that the tissues of small *P. americanus* can withstand higher temperatures (1.0–1.7°C higher) than those of the larger specimens.

During the winter of 1946–1947 four species, "plaice, cod, whiting and dab," in the North Sea were apparently subjected to lethal temperatures (Simpson 1953, Vaux 1953). Simpson reported that continuous cold easterly gales caused rapid cooling of the surface water, and Vaux reported a low water temperature of −1.8°C. [The freezing point of the body fluids of teleosts lies mainly within a range of −0.5°C to −0.9°C (Dakin 1912, Krogh 1939, Kubo 1953).]

The thermal tolerance of *M. menidia*, *P. americanus*, and *S. maculatus* lies between that of the cold-water salmonoids and the warm freshwater teleosts. Brett has given thermal tolerances of 450°C to 529°C squared for five species of *Oncorhynchus*, and values of 1162°C and 1220°C squared, respectively, for warm freshwater species *Ictalurus nebulosus* and *Carassius auratus*.

Few cases of heat death of fishes in the natural environment have been recorded. But information on upper thermal tolerances becomes increasingly important with the increase in construction of more and larger power generating plants, including those with atomic reactors.

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