The Activity and Catchability of the Lobster (*Homarus americanus*) in Relation to Temperature[1]

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ABSTRACT

The activity (walking rate) of lobsters acclimated to various temperatures increased from 2 to 10°C. and from 20 to 25°C. but was constant between 10 and 20°C. Lobsters acclimated to low temperatures were most active above the acclimation temperature. Those acclimated to intermediate and high temperatures were most active at the acclimation temperatures. Experimental fishing of a relatively constant stock showed that the catch per 100 standard trap hauls (index of catchability) was linearly related to temperature. Slope of line is, however, dependent on stock density. Catchability is shown to be proportional to activity minus a constant. This relationship permits use of catch per unit effort and accumulated catch data to estimate lobster populations.

INTRODUCTION

Where abundant, the lobster is the object of an intensive fishery with the stocks subjected to exploitation rates of 35 to 80% (Wilder, 1947). To provide the biological basis for management of this fishery, long-term population studies have been conducted. One of the more important parameters to be estimated in such studies is the absolute abundance of the stock. Various methods involving the use of tagged or marked individuals are possible but each is subject to error and is often costly. An alternative method suggested by DeLury (1947, 1951) is based on a relationship between catch per unit of effort and the accumulated catch. A basic assumption of this method is that "catchability", defined as the proportion of the population captured by one unit of effort, remains constant throughout the sampling period. General observations, however, suggest that the catchability of lobsters varies with temperature. If so, the relationship between catch per unit of effort and accumulated catch should be modified accordingly.

With lobsters, which are caught almost exclusively in baited traps, catchability is presumably related to activity. As a first approach to a study of catchability the activity of lobsters acclimated to and tested over a wide range of temperatures was measured in a series of laboratory experiments. A more direct index of catchability involved systematic fishing at regular intervals over an 8-month period in an area where the stock was relatively constant. Finally, the two sets of data were examined together to determine the relationship between activity and catchability.

ACKNOWLEDGMENTS

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I. ACTIVITY

Fry and Hart (1948a) demonstrated differences in the activity of goldfish depending partly on the temperature acclimation of the specimen. McLeese (1956) has shown that lobsters have the ability to acclimate and has demonstrated the importance of this in connection with lethal temperatures. It was assumed therefore that acclimation should be considered in the study of activity of lobsters.

Lobsters of both sexes, 23 to 25 centimetres total length, were obtained locally for these tests. They were held in aerated sea water at a series of constant temperatures between 2 and 25°C. until fully acclimated. In 3 weeks at high temperatures lobsters acclimate fully to a temperature change of about 9°C. (McLeese, 1956). However, Brett (1946) found that the rate of acclimation for goldfish depended on the general level of temperature, being slowest at low temperatures. To allow for a possible slower rate of acclimation at low temperatures, lobsters were held for at least 2 months for acclimation to temperatures below 20°C. and for at last 1 month at 20°C. and higher. Temperature control during acclimation was usually within 1°C. of the stated temperature. Variations slightly in excess of these limits occurred infrequently, were of short duration, and had no appreciable effect on the level of acclimation.

The rate of walking in response to a bright light was used as a measure of activity. The rate for one lobster was calculated from the total distance and time taken for 10 trips in a planed soft-wood trough 10 feet long by 8 inches by 8 inches ($305 \times 20 \times 20$ cm.) inside dimensions. The walking rate for a given set of test conditions was then taken as the median walking rate of 7 to 15 lobsters. Since the distribution of walking rates for individual lobsters departed from a normal distribution at low and high temperatures, when some animals failed to walk, the median is used rather than the arithmetic mean.

A General Electric RF12 reflector photoflood lamp held 2 feet (60 cm.) directly above the lobster was the stimulus. The light was directed slightly posteriorly, producing a strong gradient of light at the head region of the animal with the darkest area in front of the lobster. The lobster responded by walking forward away from the light. The stimulus was kept essentially constant by moving the light as the lobster proceeded. As shown by preliminary tests, the photoflood lamp produced the most consistent response. In 3 cases lobsters readily completed 10 trips in response to the photoflood lamp. Subsequently they failed to respond uniformly to light sources up to 100 watts but resumed walking when the photoflood lamp was substituted. Lobsters did not respond consistently to either food or diffuse light.

Aerated water at the appropriate test temperature flowed through the trough during the tests. For tests departing from the acclimation temperature, lobsters were transferred to the test temperature at least 1 hour before testing to allow them to equilibrate to the test temperature. The tests were conducted in a darkened room, the tank was painted dull black and the observer was shielded to reduce external stimuli as much as possible.

The results are summarized in Table I. When a series of 10 observations were arranged in increasing order of magnitude, the 3rd and 8th observations were taken as indicative of the range. The 1st and 7th, 2nd and 7th, 2nd and 8th, 3rd and 9th, 3rd and 10th, 4th and 10th, 5th and 11th observations were

TABLE I. Median walking rates of lobsters (ft./min.) for various acclimation and test temperatures. The number of lobsters in each test and the ranges for the medians are given (1 ft./min. = 30.48 cm./min.).

	TEST TEMPERATURE, DEGREES CENTIGRADE						
	2	5	10	15	20	25	28
	ACCLIMATION TEMPERATURE 2° C.						
Median	7.2	8.9	8.1	4.5	...	...	...
No.	12	9	11	10	...	...	...
Range	6.0–9.5	5.5–13.0	6.5–15.5	0.0–9.5	...	...	...
	ACCLIMATION TEMPERATURE 5°C.						
Median	8.3	9.5	12.4	11.6	0.0	0.0	...
No.	10	15	9	10	8	9	...
Range	8.0–10.0	8.0–11.0	11.0–14.0	11.5–15.0	0.0–15.0	0.0–9.5	...
	ACCLIMATION TEMPERATURE, 10°C.						
Median	6.9	12.1	16.4	16.4	14.5	14.6	...
No.	10	10	13	10	10	10	...
Range	6.0–8.0	11.0–14.0	16.5–17.5	12.5–18.0	13.5–16.5	12.0–18.2	...
	ACCLIMATION TEMPERATURE 15°C.						
Median	0.0	8.1	15.1	17.1	17.3	10.1	...
No.	10	10	10	10	10	10	...
Range	0.0	6.5–9.0	11.4–16.5	16.5–18.5	14.5–18.5	9.0–15.0	...
	ACCLIMATION TEMPERATURE 20°C.						
Median	0.0	0.0	9.1	14.4	16.5	14.3	...
No.	10	8	7	9	10	10	...
Range	...	0.0–4.5	5.4–10.5	9.6–17.8	14.0–19.0	13.8–17.5	...
	ACCLIMATION TEMPERATURE 25°C.						
Median	...	...	0.0	14.8	20.6	23.5	19.8
No.	...	...	10	10	10	10	10
Range	...	...	0.0	14.0–16.5	20.0–21.5	22.0–25.0	19.0–23.4

	8° acclimation, tested at 8°C.	22.5° acclimation, tested at 22.5°C.
Median	13.8	21.9
No.	10	10
Range	10.0–15.0	20.0–25.0

used for a series of 7, 8, 9, 11, 12, 13 and 15 observations respectively. These ranges are also confidence limits for the medians, that is the medians will lie within the stated limits at least 9 times out of 10. The actual probabilities range from 0.89 to 0.97, depending on the number of observations (Mood, 1950).

The activity of lobsters fully acclimated to the test temperatures is plotted in Fig. 1. From this curve, activity in relation to acclimation temperature is seen to have 3 phases. As the acclimation temperature increases, up to 10°C. the

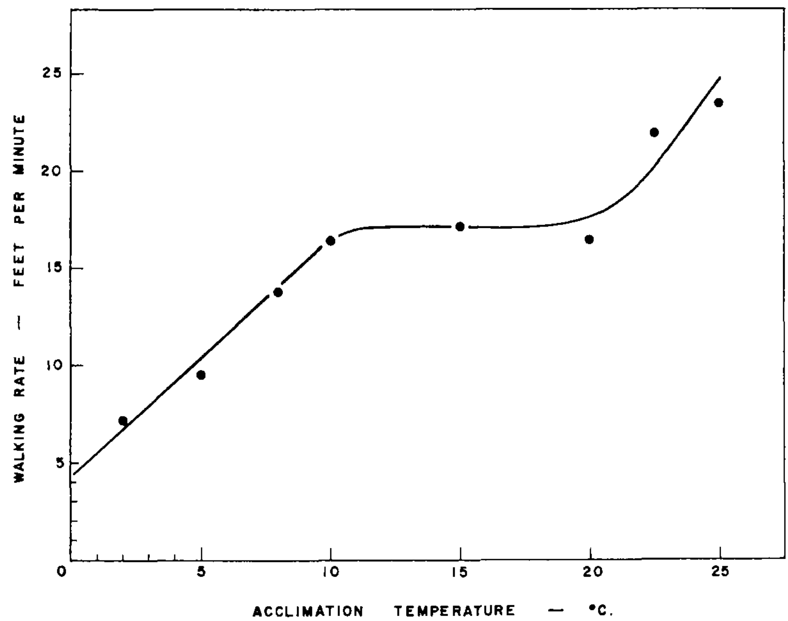

FIG. 1. Activity of lobsters tested at various acclimation temperatures.

level of activity rises rapidly. Activity remains essentially constant for acclimation temperatures between 10° and 20°C. However, the level of activity again increases at acclimation temperatures above 20°C. In general, it has been found that the acclimated activity of fish follows either of two patterns. In one, peak activity occurs at a temperature below the lethal temperature, and in the other, activity progressively increases up to the lethal temperature. These patterns of activity are associated with different relationships between active and standard respiration rates or scope for activity (Fry, 1947; Fry and Hart, 1948a,b; Graham, 1949). The pattern of activity for the lobster, with its rapid increase in activity at temperatures above 20°C., appears to differ from both of these patterns.

The activity of lobsters exposed to sudden temperature changes both upwards and downwards from the acclimation level is shown in Fig. 2. Arrows show upper lethal temperatures and estimated lower lethal temperatures (McLeese, 1956).

Lobsters acclimated to low temperatures (2° and 5°C.) are capable of moderate activity only, regardless of temperature, and attain maximum levels of activity (9 and 13 ft./min.) at temperatures a few degrees above the acclimation temperature. Those acclimated to intermediate temperatures (10°C.) are inactive at low temperatures and attain maximum levels of activity (16 to 17 ft./min.) at the acclimation temperature. For lobsters acclimated to high temperatures (15 to 25°C.) activity is curtailed at low temperatures but reaches a maximum at the acclimation temperature. Activity falls rapidly at higher temperatures, presumably being zero at the upper lethal temperatures.

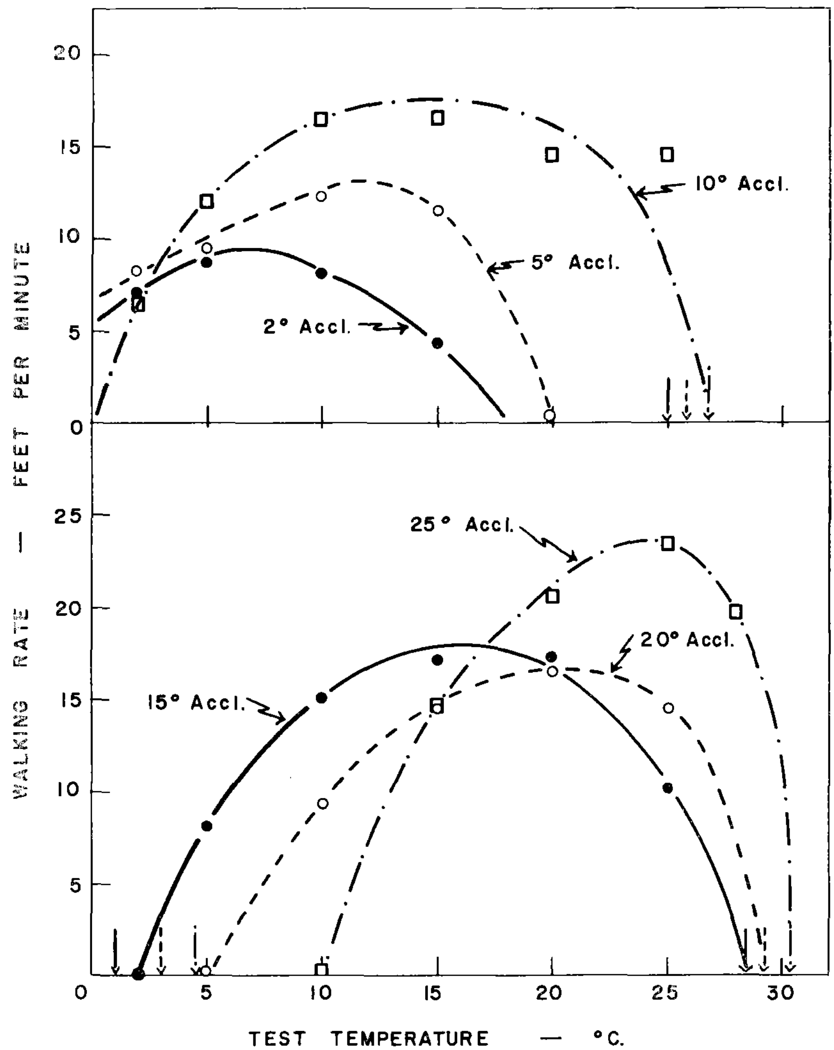

FIG. 2. Activity of lobsters acclimated to various temperatures and tested at a series of temperatures. Arrows on the abscissa indicate upper and lower lethal temperatures.

Brett (1956) pointed out the importance of sufficient activity at near lethal temperatures for continued existence of the animal. Activity as expressed by walking rate is closely related to the ability to feed, compete and to escape predation, all factors necessary for continued survival of the lobster. The temperatures at which activity becomes zero at the various acclimation levels have been plotted on the thermal tolerance diagram (Fig. 3) for the lobster (McLeese, 1956). The diagram encloses temperatures which the lobster can tolerate indefinitely. The area within the diagram is divided into a large zone of activity

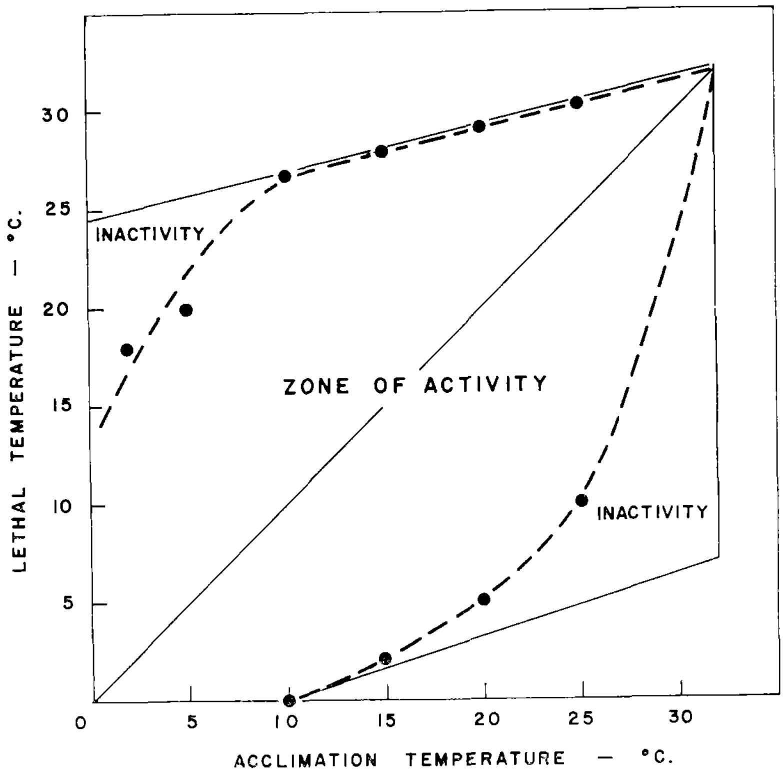

FIG. 3. Thermal tolerance diagram for the lobster showing zones for activity and inactivity. Circles show temperatures of zero activity.

in the central region and two smaller zones of inactivity near the margins. Continued existence of the lobster would not be possible in the zones of inactivity although the temperatures themselves are not lethal.

Throughout this discussion it has been assumed, if not demonstrated otherwise, that activity becomes zero at the lethal temperatures. The lethal temperatures as used here define the zone of temperatures beyond which animals cannot live indefinitely. They can live for short times at lethal temperatures, these times being called resistance times by Fry (1947), but any activity beyond these temperatures would be of short duration and is considered to be zero in this paper. The zone of activity may be interpolated above and below the range of experimental points since activity at the ultimate upper and lower lethal temperatures—the highest or lowest level to which the lethal temperatures can be raised or lowered by thermal acclimation—will be zero. The ultimate upper lethal temperature is 32°C. The ultimate lower lethal temperature, although not experimentally determined, can be taken as the freezing point of sea water, approximately –1.8°C.

Lobsters acclimated at 10 to 15°C. show the greatest range of temperatures for activity. With a rise or fall in acclimation, the range of temperatures for activity decreases and finally reaches zero at the ultimate upper and lower lethal temperatures. This picture of the zone for activity is dynamic rather than static, because temperature changes departing from the acclimation levels will be accompanied by continual changes in acclimation.

II. CATCHABILITY

The limited stock of lobsters off the St. Andrews Biological Station in the estuary of the St. Croix River is relatively unattractive to commercial fishermen. Although the official lobster season extends from November 15 to June 24, commercial lobster fishing in this immediate area is usually limited to 5 or 6 boats that fish a few traps for several weeks in the fall and spring. The lobster population although small is relatively constant in comparison with areas where the fishery is intense. A further advantage of the area is that it is well sheltered and fishing is possible most days.

From mid-September to mid-April, 35 to 40 traps were fished for 6-day periods at approximately monthly intervals. The wooden traps were a type commonly used in the area and were equipped with a fishing head of hand-knitted nylon at one end and with one inner parlour head. They were approximately 42 inches (107 cm.) long, 26 inches (66 cm.) wide and 18 inches (46 cm.) high, outside dimensions. Lightly salted, sardine-size herring were used as bait throughout the experiment. The traps were set in 2 lines about 1 nautical mile (1.8 km.) long running parallel to and about 200 yards (180 m.) and 500 yards (460 m.) off shore. The inner line was set in 5 to 8 fathoms (9 to 15 m.), the outer in 10 to 16 fathoms (18 to 29 m.).

During the September fishing period the traps were deliberately moved about in an effort to find lobsters. For all subsequent fishing periods the traps were set as consistently as possible on the same grounds. As each trap was fished each day the condition of the trap was noted, the bait renewed, the lobsters measured, tagged, and promptly released close to the point of capture. Once or twice each day the bottom water temperature was taken with a reversing thermometer at an average depth of 10 fathoms (18 m.).

During the experimental fishing 265 lobsters were caught. Their carapace length, measured from the eye socket to the posterior margin of the carapace, ranged from 2.1 to 6.2 inches (5.3 to 15.7 cm.) and averaged 4.0 inches (10.2 cm.). Of these, 26 were recaptured in the experimental gear once, 3 were recaptured twice and 1 was recaptured 3 times to give a total of 35 recaptures. Commercial fishermen, who fished from November 15 to December 14 only, caught and removed 27 of the tagged lobsters.

For the 35 recaptures in the experimental gear, the average time between liberation and recapture was 25 days. The average straight line distance between release and recapture points was 0.1 nautical mile (0.2 km.). The 27 tagged lobsters returned by the commercial fishermen were reported to be free on the average for 27 days, and to have moved an average of 0.5 nautical mile (0.9 km.). The limited distribution of the experimental gear undoubtedly leads to an underestimate of the average movement, whereas inaccuracies in the fishermen's reports tend to overestimate it. It seems probable that the estimate of 0.3 nautical mile (0.6 km.) based on all recaptures, approximates the true average movement.

The tagged lobsters indicate that the number of catchable-sized lobsters in the experimental area is unlikely to be seriously affected by movements into or out of the area. Since moulting occurs principally during the summer months, recruitment through growth is unlikely to affect the numbers appreciably during the experimental period. Of 223 lobsters tagged to November 9, commercial fishermen caught 26 (11.6%) from November 15 to December 14 and presumably brought about a proportionate reduction in the stock. Natural mortality is believed to be low among the sizes of lobsters under consideration, particularly during the cold water period, and is assumed to have only a minor effect on the stock during the experimental period.

TABLE II. Catchability index of lobsters (adjusted catch per 100 trap hauls) in relation to temperature.

Period	Trap hauls	Catch	Catchability index	Average bottom temperature
	no.	*no.*	*no./100 hauls*	*°C.*
Sept. 16–24/57	183	50	27.3	12.4
Oct. 7–12/57	175	103	58.8	11.5
Nov. 4–9/57	176	98	55.7	9.8
Dec. 9–14/57	175	26	16.6	6.5
Jan. 13–18/58	171	4	2.6	4.0
Mar. 10–17/58	177	8	5.1	2.8
Apr. 14–17/58	179	11	7.0	3.6

The catch and effort figures, together with average bottom water temperatures, are summarized in Table II for each fishing period. Traps not in fishing order when hauled are not included in the total. The catch includes recaptures. The catch per 100 standard (24-hour set) trap hauls is taken as the index of catchability. For the fourth and subsequent fishing periods the indices have been adjusted to allow for the estimated 11.6% reduction in stock by the commercial fishery. The low September index is not fully understood. The new, previously unused traps may have, as fishermen believe, adversely affected the catch. Some effort expended in September in searching for lobsters was relatively ineffective. Late summer moulting may also have reduced the September catch. In any case the September data are believed to be atypical and are not considered further. The data plotted in Fig. 4 indicate a linear relationship between catchability index and temperature over the range 3 to 12°C.

DISCUSSION

Although the catch per 100 standard trap hauls, used as an index of catchability, is linearly related to temperature over the range 3 to 12°C., the slope of the line depends on the stock density. Because of this, although the relationship is of general importance, it is not of direct applicability. The numerical

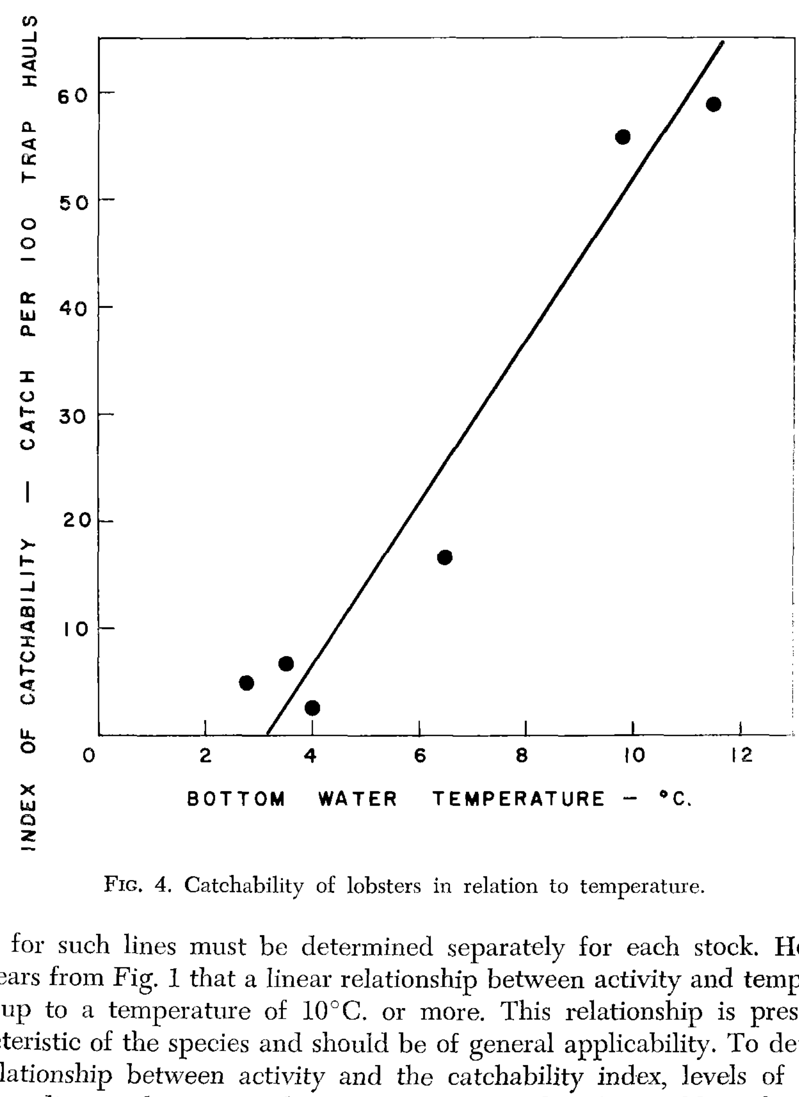

FIG. 4. Catchability of lobsters in relation to temperature.

values for such lines must be determined separately for each stock. However, it appears from Fig. 1 that a linear relationship between activity and temperature holds up to a temperature of 10°C. or more. This relationship is presumably characteristic of the species and should be of general applicability. To determine the relationship between activity and the catchability index, levels of activity corresponding to the average bottom temperatures listed in Table II have been interpolated from Fig. 1. These activity readings were then plotted in Fig. 5 against corresponding catchability indices. The relationship between activity and the catchability index is significant ($r = 0.974$, $P = 0.01$) and appears to be linear. According to this relationship the catchability index is proportional to activity minus a constant. This constant has been estimated graphically at 8.2. Observations based on the commercial winter fishery in southern Nova Scotia suggest that this figure is somewhat too high for that population.

The proportional relationship between activity and the catchability index can be used to correct catch per unit of effort data for varying catchability. Such corrections permit the use of the relationship between catch per unit of effort and accumulated catch for estimating lobster populations.

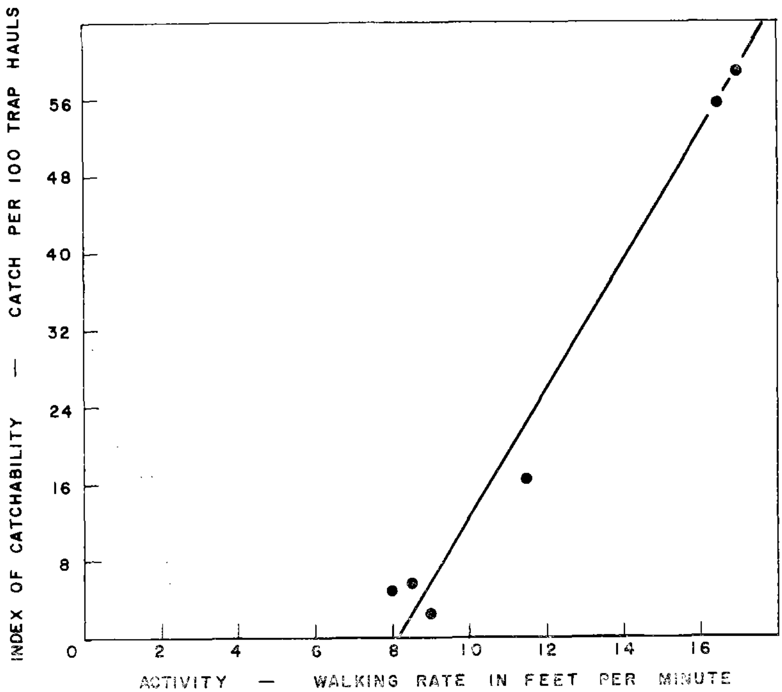

FIG. 5. Catchability of lobsters in relation to activity.

REFERENCES

BRETT, J. R. 1946. Rate of gain of heat-tolerance in goldfish (*Carassius auratus*). *Univ. Toronto Stud., Biol. Ser.*, No. 53; *Pub. Ontario Fish. Res. Lab.*, No. 64, 28 pp.

1956. Some principles in the thermal requirements of fishes. *Quart. Rev. Biol.*, **31**(2): 75–87.

DELURY, D. B. 1947. On the estimation of biological populations. *Biometrics*, 3(4): 145–167.

1951. On the planning of experiments for the estimation of fish populations. *J. Fish. Res. Bd. Canada*, **8**(4): 281–307.

FRY, F. E. J. 1947. Effects of the environment on animal activity. *Univ. Toronto Stud., Biol. Ser.*, No. 55; *Pub. Ontario Fish. Res. Lab.*, No. 68, 62 pp.

FRY, F. E. J., AND J. S. HART. 1948a. Cruising speed of goldfish in relation to water temperature. *J. Fish. Res. Bd. Canada*, **7**(4): 169–175.

1948b. The relation of temperature to oxygen consumption in the goldfish. *Biol. Bull.*, 94(1): 66–77.

GRAHAM, J. M. 1949. Some effects of temperature and oxygen pressure on the metabolism and activity of the speckled trout, *Salvelinus fontinalis*. *Canadian J. Res.*, D, **27**: 270–288.

MOOD, A. M. 1950. Introduction to the theory of statistics. McGraw-Hill Book Co., Inc. 433 pp.

MCLEESE, D. W. 1956. Effects of temperature, salinity and oxygen on the survival of the American lobster. *J. Fish. Res. Bd. Canada*, **13**(2): 247–272.

WILDER, D. G. 1947. The effect of fishing on lobster populations as determined by tagging experiments. *Fish. Res. Bd. Canada, Atl. Prog. Rept.*, No. 37, pp. 10–14.