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Seasonal Changes in Metabolism of Four South Temperate
Marine Fishes

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Abstract

GENERALLY speaking, the fishes included in this study demonstrate a loss of sensitivity to temperature during the warm season, such sensitivity being measured in terms of metabolic rate in the upper range of temperature tolerance.

Forsterygion varium and *F. robustum* show a clear relationship between size and metabolic rate, following cold history. With warm history these species show no significant relationship between size and metabolic rate. Hence, in these two species the small animals can make a better adjustment to cold than can the large ones, but acclimation to heat is not size related.

In *Pseudolabrus celidotus* there is, in some seasons, an extreme inverse relationship between size and metabolic rate. It is indicated that this species develops unusual metabolic regulatory mechanisms. The metabolic-rate temperature curve becomes flattened during the warm season.

INTRODUCTION

THE metabolic rate of poikilothermic (i.e., "cold-blooded") animals depends upon the environmental temperature. Very approximately, it has been generally considered that an increase of 10° C. results in a doubling of the metabolic rate, over the normal range of temperature tolerated by a given species. The increase of metabolic rate with temperature rise is logarithmic. This relationship is commonly expressed as the temperature coefficient or Q_{10} , the factor by which metabolic rate increases with a 10° temperature rise. Measurements of metabolic rate at different temperatures demonstrate the degree of dependence of metabolism upon temperature and have been termed "acute" measurements by Bullock (1955) in his review of the subject.

The relationship between metabolic rate of poikilothermic animals and environmental temperature is complicated by the phenomenon of thermal acclimation. After transfer to a lower temperature, an animal usually shows the expected depression of metabolic rate, followed after several days or weeks by a return approximately to the original level. A similar compensation of metabolism, but

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in the opposite direction of course, may be expected to follow transfer to a higher temperature. Thus, any metabolic study must consider the thermal history of the animals if the study is to be ecologically meaningful. Fry (1957) has reviewed metabolism and some aspects of thermal acclimation in fishes.

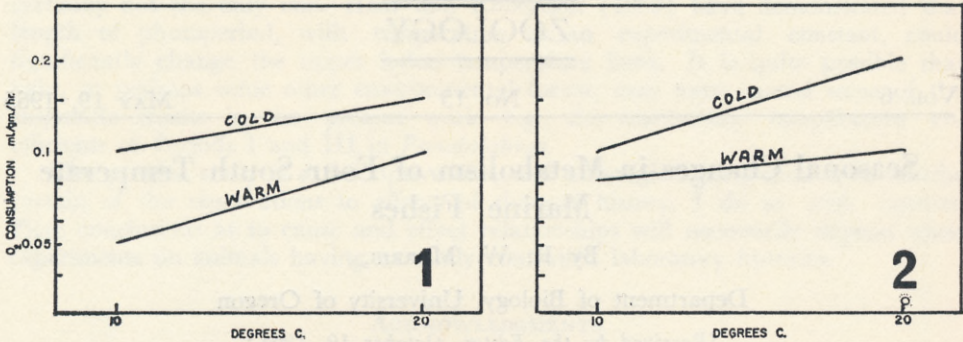


FIG. 1.—Differences generally observed between rate-temperature curves of cold- and warm-acclimated poikilotherms. See text.

FIG. 2.—Differences between rate-temperature curves of cold- and warm-acclimated specimens of certain species such as *Carassius vulgaris*. See text.

Bullock (1955) used the expression "acute" measurement of Q_{10} to indicate that a Q_{10} value had been derived from data on activity measured not only at the temperature to which the animal had been acclimated but also at other temperatures within the physiological range. He reviewed a large body of data which showed that the acutely measured Q_{10} of poikilotherms is significantly lower following a period of cold history than if such measurements are made after a period of warm history. We can illustrate a hypothetical example in Fig. 1. Here, metabolic rate, expressed as ml. O_2 consumed per gram of body weight per hour, is plotted against temperature ("rate-temperature" plot) for two groups of animals. One group, labelled "cold", was acclimated to 10° C. and the other group, labelled "warm", was acclimated to 20° C. The oxygen consumption of the cold-acclimated animals was the same (0.10 ml. O_2 /gm./hr. when measured at the 10° C. acclimation temperature as that of the warm-acclimated animals when the latter were measured at their 20° C. acclimation temperature. Hence, the long-term Q_{10} would be 1.0, showing perfect metabolic compensation in this hypothetical case. The processes of acclimating to high temperatures tend to lower the metabolic rate at those high temperatures and, conversely, acclimation to cold tends to increase the metabolic rate at low temperatures. Thus, within limits, thermal acclimation helps the animal to maintain the rate of the system at a more uniform level than would otherwise be possible. The physiological mechanisms underlying acclimation are not understood. Although I have not seen such a degree of acclimation ability as appears in this hypothetical example, I do have a considerable body of data from laboratory studies of *Aequidens portalegrensis* which demonstrates that this species can make an almost perfect metabolic adjustment over the temperature range from 24 to 30° C. The long-term Q_{10} approximates 1.0 over this range. *A. portalegrensis* is a tropical fish, native to Brazil. It belongs to the family Cichlidae. There are no published accounts of the ecology of this species.

The acutely measured Q_{10} is an index of the nature and magnitude of response to a sudden temperature change. In the cold-acclimated group of Fig. 1, the metabolic rate increased from 0.10 (ml. O_2 /gm./hr.) at 10° C. to 0.15 at 20° C. Thus the acutely measured Q_{10} is equal to 1.5. The rate of the warm-acclimated animals drops from 0.10 at 20° C. to 0.05 at 10° C., giving an acutely measured Q_{10} of 2.0. A semi-logarithmic rate-temperature plot (Fig. 1) has the advantage in that the slopes of the curves are readily interpreted in terms of Q_{10} . Bullock (1955) concluded that, as a general rule for poikilotherms, the relative positions and slopes of the rate-temperature curves of cold- and warm-acclimated animals are of the form shown in Fig. 1. Thus, the curves of cold-acclimated animals are higher and flatter than are those of warm-acclimated animals. I have found such acclimation-induced changes in several species of fishes.

Suhrmann (1955), however, found a different acclimation response in the crucian carp, *Carassius vulgaris*. In this species she found that the rate-temperature curve of oxygen consumption was higher for cold-acclimated than for warm-acclimated fish, but that the Q_{10} was increased as a result of cold history. Considering only the upper portion of the range of temperature tolerance, we can diagrammatically illustrate the positions of the rate-temperature curves of *Carassius* as in Fig. 2.

The two types of acclimation response (Figs. 1 and 2) differ fundamentally. In the first general type, it is the cold-acclimated system that shows the lower sensitivity to temperature change, whereas in the second type the warm-acclimated system is less responsive to temperature change. Implications of these differences will be treated further in the Discussion.

Suhrmann's (1955) findings indicated that in the crucian carp there was quite a different physiological response to thermal history than had been found in other poikilothermic vertebrates. In recent studies of other fishes, I have found the acclimation responses of a catfish, *Ictalurus natalis*, to be similar to those of the crucian carp. Measured acutely over the upper range of tolerance, cold-acclimation results in a high flat curve, acclimation to a high temperature results in a low flat curve, and acclimation to an intermediate temperature results in a curve of intermediate level but having a much steeper slope than the curves representing the two extremes of acclimation temperature.

The present study represents a portion of a continuing survey conducted in order to see whether or not it will be possible to formulate generally applicable rules relating acclimation type to either phylogeny or ecology. Collateral investigations of a more analytical nature are currently in progress.

MATERIALS AND METHODS

An initial survey of the Fortobello vicinity indicated a large number of species that would be of considerable interest. In consideration of the probable availability of sufficient numbers of specimens of suitable sizes, the study was limited to four species.

Collecting was done either with a small dredge or by angling. The specimens were kept in running seawater in the laboratory for from one to five days prior to use in an experiment. Since the laboratory seawater was pumped every day and there was a high rate of flow through the system, holding temperatures did not differ significantly from the natural temperatures. Density of the seawater used in the experiments was sampled periodically. These samples showed no indication

of appreciable dilution at any time during the study. The Otago Harbour has no river system to speak of. Gonads of larger specimens of each of the four species studied were examined during the course of the investigation. None of them was found to be sexually active.

Metabolic rate was respirometrically measured in a volumetric apparatus recently described (Morris, 1963). Constant temperature of the water bath was maintained with ice water and heaters controlled through a Fenwal thermostwitch.

The temperatures over which measurements were made were intended to cover approximately 10° to 15° C. of the upper range of tolerance. Preliminary investigations indicated that the upper lethal limit of these species was approximately 30° C. Experimental temperatures covered the range from 12° to 28° C. The upper range of tolerance is the range of interest in this study, since it is here that metabolic changes due to acclimation will be most conspicuous.

In the experimental routine a fish was placed in the respiration chamber and the chamber was flushed with oxygen. Respiration and compensation chambers were closed and about 30 minutes were allowed for equilibration. Then followed a one-hour period for measurement of oxygen consumption. The fish was then removed and weighed. The volumes of oxygen measured were reduced to STP, and in the following account, metabolic rate is expressed as ml. O₂ consumed/gm. (wet weight) /hr.

The experimental programme was reasonably continuous over the period from November 5, 1962 to April 25, 1963. At the conclusion of the study the raw data were divided into three periods on the basis of the record of daily shore temperatures at the Portobello laboratory. This record appears in Fig. 3, and the three study periods are designated by Roman numerals. Fig. 3 shows that Period I

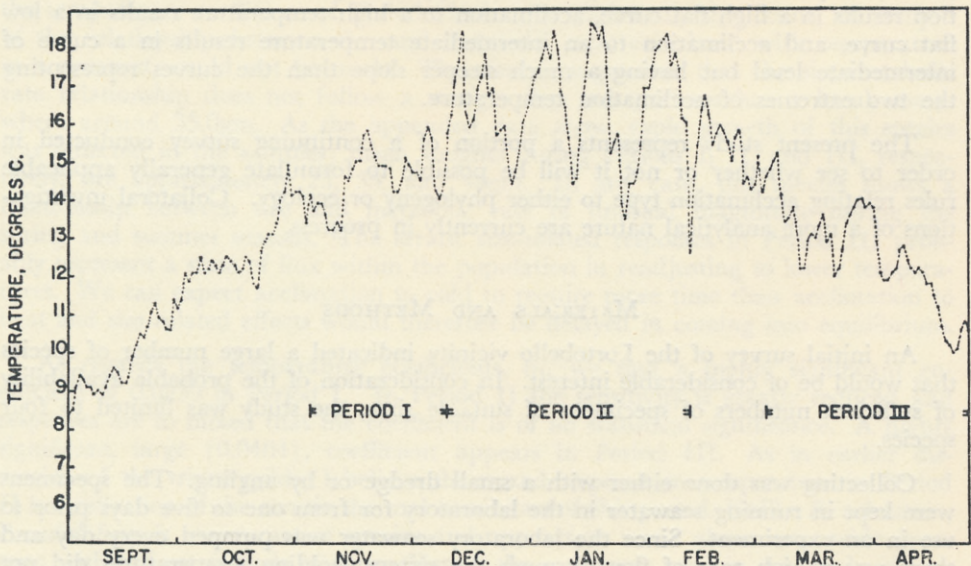


FIG. 3.—Daily shore temperature record, 1962-63, at the Portobello Marine Biological Laboratory. Periods of study are indicated by Roman numerals.

included those data from fishes having a recent thermal history that was entirely below 16° C. During the several weeks prior to and throughout that period the water temperature was rising steadily but did not fluctuate to any great extent. Period I extended from 5 November to 10 December 1962. Period II extended from 11 December 1962 to 12 February 1963 and, as the graph shows, was a time of high and extremely variable temperatures. From 13 February to 4 March 1963, sampling was suspended. Period III included 5 March to 25 April 1963, and was one of falling temperatures and minimal fluctuations.

The data were treated to consider oxygen consumption as a function of temperature and body size. A multiple regression was calculated for the data on each species for each of the three study periods. The equation,

$$Y = a + b_1X_1 + b_2X_2,$$

was used. Y represents the log estimated oxygen consumption in ml./gm./hr. The Y intercept, a, is the log. estimated oxygen consumption in ml./gm./hr. at 0° C., by a fish weighing 1.0gm. The variable, X₁, is the temperature in degrees C., X₂ is the log weight (gm.) and b₁ and b₂ are their respective partial regression coefficients. Statistical significance of each equation was determined by analysis of variance and of each partial regression coefficient (b₁ or b₂) by *t* tests. Statistical procedures are from Mather (1951).

The species selected for study were:

- Forsterygion capito* (Jenyns)
- Forsterygion varium* (Bloch & Schneider)
- Forsterygion robustum* (Clarke)
- Pseudolabrus celidotus* (Bloch & Schneider)

For each of the four species there is a graphic presentation of the metabolic rate-temperature curve for each of the periods of study. These appear in Fig. 4 and are representative of specimens of mean weight of the respective samples. Corrections were made for weight according to the partial regression coefficient. Since in some cases one or the other of the partial regression co-efficients (b₁ or b₂) was not statistically significant, these rate-temperature curves illustrated can be considered only as approximations of actual conditions of the samples.

The choice of species gave three closely related ones which it was hoped would yield information on the degree of consistency of metabolic performance within a narrow phylogenetic group. It has long been recognized that ecological evolution has not always paralleled phylogenetic lines and that within any given taxon there may be an extensive proliferation of ecological types. These trypterygiid fishes occupy habitats similar to those occupied by a number of species of Cottidae which I have studied at approximately the same latitude (ca. 45°) North. A comparison of these two groups was of particular interest. *Pseudolabrus celidotus* was chosen for study because of its great numbers and apparent success. Since it appears to be of rather recent tropical origin and has so successfully invaded high latitudes, I considered it likely that it might show something unusual in its metabolic rate-temperature relationships.

RESULTS

Forsterygion capito

Table 1 lists information relating to *F. capito*. As regards size, there are large negative coefficients in Periods II and III. However, the great amount of scatter, reflected in the large standard errors, renders size of no statistical significance in influencing metabolic rate.

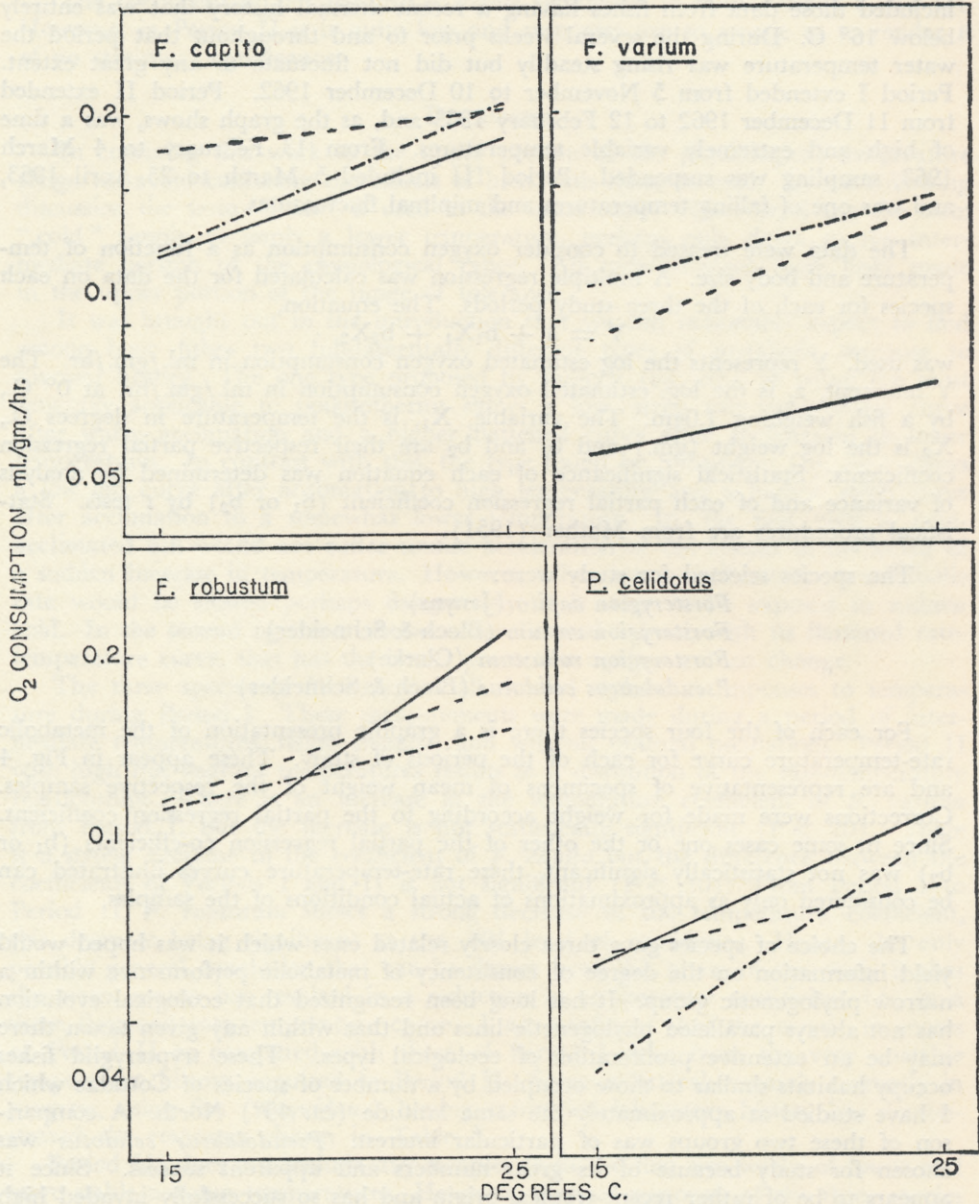


FIG. 4.—Oxygen consumption rate-temperature curves calculated as representative of specimens of mean weight of the respective samples. Curves are identified as to Study Period as follows: I, ———; II, - - - - ; III,

In collateral studies of the relationship between consistency of Q_{10} of oxygen consumption and stability of thermal history I have collected a large body of data showing that vagrant or oscillating acclimation temperature can, under certain conditions, lead to apparent nullification of the effect of temperature on metabolic rate. A few of these data appear in a later section of this paper. It

seems possible that in this species we might find a significant relationship between size and metabolic rate, or acclimation ability, if measurements were made after a period of carefully controlled thermal history.

The temperature coefficients, b_1 , are interestingly different in the three periods. Those of Periods I and III are both significant, their respective probabilities being $< .01$ and $< .001$. The temperature coefficient of Period II is very small, not statistically significant, and indicates a substantial loss of sensitivity between Period I and Period II.

Forsterygion varium

This is the largest species of the three from this genus that I studied. Here we see large negative size coefficients (Table 2). However, only that of the Period I sample is statistically significant, $P < .001$. Here, more clearly than in the case of *F. capito*, the apparent loss of effect of size on metabolic rate can be clearly related to the high and vagrant temperatures of Period II. A consistency of performance had still not been restored by Period III, indicating that the effects of exposure to the high temperatures of Period II were still affecting the system.

The temperature coefficients of Periods I and II are significant at the .01 and .02 levels of confidence, respectively. The increase of the coefficient from Period I to Period II is not significant ($< .20$). The coefficient of Period III is not significant, indicating that readjustment to lower, more stable temperatures had not come into equilibrium.

Forsterygion robustum

This was the most abundant benthonic species in the study area and permitted the most thorough sampling of any of the four species studied. A full range of sizes was consistently available and the sampling was better in regard to this variable also. Table 3 shows that there was a significant relationship between size and metabolic rate in study Period I. Size co-efficients were smaller in Periods II and III and are not significant.

The temperature coefficients of all three periods are significant, having probabilities of $< .001$, $< .001$, and $< .02$, respectively. From Period I to Period II there is a sharp drop in temperature sensitivity, the respective coefficients being 0.0407 and 0.0194. The difference between these coefficients is statistically significant at the .001 level of confidence. There is a slight further decrease in the temperature coefficient as one moves from Period II to Period III. However, this increase is not significant, $P < .20$.

The overall regression coefficients, R , of Periods I and II were found to be significantly different by an analysis of variance, $P < .01$.

Pseudolabrus celidotus

Data relating to this species appear in Table 4. In this fish we see in Period I a large negative size coefficient (-0.6059) which is highly significant, $P < .001$. However, Period II has again disrupted the consistency of performance and the negative size coefficient here, although larger than that of Period I, is significant only at the .05 level of confidence. In Period III the relationship between size and metabolic rate is lost, the coefficient being smaller and of no statistical significance.

The coefficient of temperature is highly significant in both Periods I and III. However, in Period II it is quite low and responses are so erratic as to render it of no statistical significance.

DISCUSSION

In confining this work to the upper portion of the physiological temperature range we avoid confusing the effects of heat with those of cold. In the following discussion the term "heat" is used in the usual sense. However, I use the term "cold" simply to imply a lower temperature, perhaps only down to the intermediate portion of the physiological range. All measurements have been made in the upper portion of the range of tolerance.

It was brought out in the introduction that we can reasonably expect to find among bony fishes two fundamentally different types of metabolic response to thermal history. The one type proposed by Bullock (*op. cit.*) as being the most generally applicable to poikilotherms shows a low, steep rate-temperature curve after warm acclimation and a higher flattened curve after acclimation to lower temperatures. In contrast with this, the type found by Suhrmann (*op. cit.*) shows a low flat curve after acclimation to high temperature and a higher, steep curve after acclimation to a somewhat lower temperature. In the first type a cold-acclimated fish would not suffer undue acceleration of the system in the event of a sudden increase in temperature. However, when warm-acclimated, its metabolic rate would be slowed perhaps dangerously, if it were to be exposed to sudden cold. In the second type it is the warm-acclimated animal, with its flattened rate-temperature curve, that has the better protection against sudden change.

The three species of *Forsterygion* all showed significant responses to temperature during Period I. These measurements were made during a period of intermediate temperatures, rising steadily, and without unusual oscillations. Period II with high but vagrant temperatures results in a disruption of the rate-temperature relationships. There is an increase in the temperature coefficient of *F. varium* from Period I, but the increase is not statistically significant ($P < .20$). There is a strong decrease in the coefficient of *F. capito* but the difference between the coefficients of Periods I and II is not significant ($P < .30$). From Period I to Period II, *F. robustum* shows a strong decrease in the temperature coefficient, this decrease being significant at the .001 level of confidence. Hence, the only possible general conclusion that can be drawn from this phase of the study is that the warm season has resulted in a reduction in temperature sensitivity—i.e., in a more flattened rate-temperature curve. I am confident that the erratic responses of Period II as compared with those of Period I arise from the very unstable temperature history acquired in Period II. Some collateral research currently in progress, using fish (*Aequidens*) having controlled laboratory history has demonstrated the responses shown in Table 5.

Period III does not include any samples from the first two weeks of lower and more stable autumn temperatures. However, thermal responses of the three species differ substantially and, generally speaking, a new equilibrium had not been reached and vagaries of the summer period were still affecting the system. The processes of thermal metabolic acclimation are in themselves thermally dependent and cold acclimation is much more slowly acquired than is warm (Brett, 1956). In *F. capito* the temperature coefficient is highly significant in Period III and has increased greatly over the coefficient of Period II. In the other two species of *Forsterygion* there are no marked differences between the coefficients of Periods II and III.

Among the trypterygiid species the measurements of *F. varium* and *F. robustum* in Period I showed a significant relationship between size and metabolic rate.

Wohlschlag and Juliano (1959) are, to a degree, justifiably critical of metabolic studies of laboratory acclimated fishes as opposed to studies of fishes that have made such adjustments to environment under natural conditions. However, as their data abundantly show, natural conditions result in metabolic responses that are extremely difficult to evaluate because of the high degree of scatter. Even under laboratory conditions that are not carefully stabilized, metabolic responses to temperature change are so erratic as to render them statistically useless (Table V). And, in so many species, such is the degree of scatter of response of specimens from nature that enormity of necessary samples precludes the possibility of their study. In the present work erratic metabolic responses to temperature are apparent throughout the data, but in the case of *F. robustum*, which lent itself to the most thorough sampling programme, there is a clearly defined change in temperature sensitivity that can be related to season. In this species the warm season brought about a loss of thermal sensitivity (lower Q_{10}) in the upper ranges of tolerance. Neither of the other two species shows responses that demonstrate the presence of mechanisms that become sensitized (i.e., that show an increase in Q_{10}) in the warm season. Hence, the responses of these fishes show a closer relationship to those described by Suhrmann (*op. cit.*) than to those described by Bullock (*op. cit.*).

The size coefficients in Period I in *F. varium* and *F. robustum* show that in these species the smaller animals have a significantly greater ability to acclimate to cold than do the larger animals. Hence, the smaller ones can adjust their metabolic rate upward in the cold to a greater degree than can the larger fish. This is in line with what I found in *Aequidens* (Morris, 1962). Unlike the condition in *Aequidens*, however, we have no concrete evidence here that any of the three species of *Forsterygion* makes a size-related downward metabolic adjustment to heat since none of the size coefficients is statistically significant in Period II. Although the Period II size coefficient is larger in *F. capito* than that of Period I, this is not true of the other two species of *Forsterygion*. Consistency of metabolic performance as it might relate to size has undoubtedly been disturbed in Period II by thermal instabilities of this period. However, in *F. robustum*, the temperature coefficient of Period II is highly significant, $P < .001$, and since the size coefficient is smaller than in Period I and not significant, this appears to be good evidence that acclimation to heat is not size dependent. I think it is quite possible that experiments following carefully controlled history in *Forsterygion* will demonstrate that acclimation to heat is not size dependent in these species.

Although the species of *Forsterygion* considered in this paper occupy habitats that appear to be similar to those occupied by several species of Cottidae in the North Pacific, and the two groups are closer phylogenetically than would be *Forsterygion* and either *Carassius* or *Ictalurus*, affinities of their metabolic responses show quite a different situation. Awkward as this phylogenetic state of affairs may appear to be, it is very sound ecologically. The cottid fishes that I have studied along the west coast of the United States occupy waters that are well known for their thermal stability. Temperature records of both Hopkins Marine Station and Scripps Institution of Oceanography offer abundant evidence of this. These conditions are in sharp contrast with those of the waters of Otago Harbour where, during the summer, we can expect periodic changes in weather and hydrography to result in oscillations of temperature of considerable magnitude and of short period. Hence, the metabolic mechanism which loses sensitivity with warm acclimation is much better fitted to survive than would be one in which sensitivity increases with warm acclimation.

We may develop a better understanding of the results of this study if we consider some aspects of the general biology of the three species of *Forsterygion*. I was not able to make anything like a thorough study of the ecology of any of these fishes

but I did make some observations that appear to be relevant. *F. robustum* appears to be a very sedentary species with large numbers concentrated around boulders and among cobbles just below the level of low tide. Specimens are easily collected at the marine station wharf and most of the representatives of this species in the study came from that site. They were always abundant and continuous sampling was no problem. Thus, samples of this species are of more uniform background than are those of the others. This homogeneity of history gives, as a comparison of the tables shows, considerably more consistency of performance than in either of the other two species.

F. capito was taken at high tide when specimens would come up into very shallow water along the edge. These were all taken by angling and I assume that their movement into the shallows constituted a feeding tour. They obviously wander around quite a lot, and they were available only sporadically. Hence, specimens were probably of quite diverse histories even within any given study period. The data certainly indicate this.

F. varium was taken from subtidal levels in or near the channel. Here again, samples were taken only sporadically and probably represent quite diverse histories. This species appear to move about over a wider territory than the other two members of the genus. It appears likely that it would be able to behaviorally protect itself against environmental vicissitudes to a greater extent than either of the other two since it lives in deeper water and moves about more.

The results of the study of *Pseudolabrus celidotus* are interesting in a number of ways. With a stable cold history, the coefficient of size is — 0.6059 and is highly significant ($P < .001$). With advance of the season to Period II the coefficient is larger but responses are more scattered and the probability rises ($P < .05$). With the return of the cold conditions of Period III the size effect is greatly reduced and the coefficient is of no statistical significance. Hence, in this species we see sweeping changes in size-metabolic rate relationships that can be related to season but not very clearly to thermal history. Since, as will be discussed in a later section, the temperature coefficient of Period II was not statistically significant, an analysis of the relationship between size and metabolic rate, calculated with temperature as a constant, could not be made. Therefore it is possible that the size-metabolic rate relationship does not follow a straight line but perhaps has a break somewhere around 35.0gm. As the appended data show, rapid growth of this species was reflected in the samples; mean weights during Periods I, II, and III, respectively, are approximately 25, 35, and 40gm. In any case, this species shows a relationship between size and metabolic rate of unusual magnitude during the spring and summer seasons. The erratic size-related responses in Period III probably represent a state of flux within the population in readjusting to lower temperatures. We can expect acclimation to cold to require more time than acclimation to heat and size-related effects would therefore be delayed in coming into equilibrium.

As regards the temperature coefficients, b_1 , we find a highly significant coefficient of 0.0259 in Period I. In Period II the sensitivity is greatly reduced and responses are so mixed that the coefficient is of no statistical significance. A highly significant, large (0.0404), coefficient appears in Period III. As in earlier discussion of the tripterygiids, I believe the mixed response to temperature in Period II is a reflection of the erratic thermal conditions of this period. Unlike *F. robustum*, *Pseudolabrus* is a very active species and appears to move about over wide areas even within short periods of time. Hence, the specimens used in this study in any given period undoubtedly represent quite different thermal histories, and I am confident that much of the erratic metabolic performance results from this fact.

TABLE I.—Information on *Forsterygion capito*. Data columns: (1) Study period. (2) Number of specimens. (3) Log mean weight of specimens. (4) Regression equation. (5) Multiple regression coefficient, R. (6) Standard error of R. (7) Probability of R. (8) Standard error of b_1 . (9) Probability of b_1 . (10) Standard error of b_2 . (11) Probability of b_2 .

| (1) | (2) | (3) | (4) | (5) | (6) | (7) | (8) | (9) | (10) | (11) |
|-----|-----|--------|---------------------------------------|--------|--------|------|--------|-------|--------|------|
| I | 12 | 0.5903 | $Y = -2.7032 + 0.0195X_1 + 0.1144X_2$ | 0.7704 | 0.0600 | <.01 | 0.0047 | <.01 | 0.1934 | <.70 |
| II | 14 | .4935 | $Y = -1.3744 + 0.0062X_1 - 0.4561X_2$ | .4435 | .1483 | >.20 | .0094 | >.90 | .3478 | <.30 |
| III | 11 | .5608 | $Y = -2.9041 + 0.0247X_1 - 0.3599X_2$ | .8852 | .0592 | <.01 | 0.0048 | <.001 | 0.1909 | <.10 |

TABLE II.—Information on *Forsterygion varium*. Data columns: (1) Study period. (2) Number of specimens. (3) Log mean weight of specimens. (4) Regression equation. (5) Multiple regression coefficient, R. (6) Standard error of R. (7) Probability of R. (8) Standard error of b_1 . (9) Probability of b_1 . (10) Standard error of b_2 . (11) Probability of b_2 .

| (1) | (2) | (3) | (4) | (5) | (6) | (7) | (8) | (9) | (10) | (11) |
|-----|-----|--------|---------------------------------------|-------|-------|-------|--------|------|--------|-------|
| I | 15 | 0.7984 | $Y = -2.8707 + 0.0122X_1 - 0.3960X_2$ | .8827 | .0729 | <.001 | 0.0045 | <.01 | 0.0865 | <.001 |
| II | 19 | .9678 | $Y = -2.8448 + 0.0224X_1 - 0.2628X_2$ | .7190 | .1134 | <.01 | 0.0057 | <.02 | 0.2069 | <.30 |
| III | 12 | .6977 | $Y = -1.0507 + 0.0153X_1 - 0.3837X_2$ | .7381 | .1102 | <.05 | 0.0084 | <.20 | 0.3271 | <.30 |

TABLE III.—Information on *Forsterygion robustum*. Data columns: (1) Study period. (2) Number of specimens. (3) Log mean weight of specimens. (4) Regression equation. (5) Multiple regression coefficient, R. (6) Standard error of R. (7) Probability of R. (8) Standard error of b_1 . (9) Probability of b_1 . (10) Standard error of b_2 . (11) Probability of b_2 .

| (1) | (2) | (3) | (4) | (5) | (6) | (7) | (8) | (9) | (10) | (11) |
|-----|-----|-------|---------------------------------------|-------|-------|-------|--------|-------|--------|------|
| I | 41 | .6175 | $Y = -2.5269 + 0.0407X_1 - 0.3262X_2$ | .8752 | .1065 | <.001 | 0.0038 | <.001 | 0.1165 | <.01 |
| II | 54 | .6650 | $Y = -2.8647 + 0.0194X_1 - 0.1359X_2$ | .5843 | .1476 | <.001 | 0.0042 | <.001 | 0.1356 | <.50 |
| III | 34 | .6567 | $Y = -2.9727 + 0.0109X_1 - 0.1171X_2$ | .5322 | .1020 | <.01 | 0.0040 | <.02 | 0.1800 | <.70 |

TABLE IV.—Information on *Pseudolabrus celidotus*. Data columns: (1) Study period. (2) Number of specimens. (3) Log mean weight of specimens. (4) Regression equation. (5) Multiple regression coefficient, R. (6) Standard error of R. (7) Probability of R. (8) Standard error of b_1 . (9) Probability of b_1 . (10) Standard error of b_2 . (11) Probability of b_2 .

| (1) | (2) | (3) | (4) | (5) | (6) | (7) | (8) | (9) | (10) | (11) |
|-----|-----|--------|---------------------------------------|-------|-------|-------|--------|-------|--------|-------|
| I | 27 | 1.4158 | $Y = -1.2576 + 0.0259X_1 - 0.6059X_2$ | .8272 | .0855 | <.001 | 0.0046 | <.001 | 0.0233 | <.001 |
| II | 41 | 1.5423 | $Y = -1.8262 + 0.0119X_1 - 0.7782X_2$ | .6127 | .2094 | <.001 | 0.0082 | <.20 | 0.3474 | <.05 |
| III | 24 | 1.6309 | $Y = -2.3276 + 0.0404X_1 - 0.1951X_2$ | .7551 | .1321 | <.001 | 0.0077 | <.001 | 0.1827 | <.30 |

TABLE V.—Relationship between stability of thermal history and consistency of metabolic response to temperature change in *Aequidens portalesgrensis*.

| Thermal History | No. of Specimens | Mean Q_{10} of O_2 Consumption Over Range, 24-27° C. | Range of Q_{10} | Standard Error |
|--|------------------|--|-------------------|----------------|
| 27° C. constant, 4 weeks | 10 | 1.69 | 0.80-2.28 | 0.4881 |
| 24-27° C., oscillating on a diurnal cycle, 4 weeks | 10 | 1.84 | 0.31-5.52 | 1.8120 |

It appears that we can safely generalize and say that *Pseudolabrus* responds to the warm season with a loss of temperature sensitivity.

Throughout this study I have sought to relate seasonal metabolic changes to thermal conditions. Although temperature history is generally conceded to be the most important single factor in bringing about such metabolic changes, it is certainly not the only one. Hoar and Robertson (1959) have demonstrated that length of photoperiod, with temperature as an experimental constant, could significantly change the upper lethal temperature limit. It is quite possible that light, or perhaps some other environmental factor, may have caused some of the enigmatic results in the present work—e.g., the contrasting temperature coefficients of Periods I and III in *Pseudolabrus*.

The present study is a descriptive one, and although I have tended to ascribe certain of the observations to effects of thermal history, I do so with caution. Firm conclusions as to cause and effect relationships will necessarily depend upon experiments on animals having carefully controlled laboratory histories.

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