AN ABSTRACT OF THE THESIS OF

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Title: OXYGEN CONSUMPTION OF THREE SPECIES OF SEA

URCHINS AT DIFFERENT TEMPERATURES

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Metabolic rate-temperature responses of three related

species of sea urchins were determined using oxygen consumption

rate measurements. The three species used were Strongylocen-

trotus purpuratus, Strongylocentrotus franciscanus, and Allocen-

trotus fragilis. All measurements were made using an oxygen

macro-electrode, physiological gas analyzer, and sealed respiratory

container. Two series of experiments--field-acclimatized and

temperature-acclimated--were conducted. In each case, oxygen

consumption was determined at 3° intervals over a temperature

range extending from 6° to 24°.

The results of the field-acclimatized animals, maintained in

the laboratory for only short periods after collection, are consistent

with the temperature fluctuations of the respective habitats. The

benthic A. fragilis did not possess any rate-temperature independ-

ence. The partly intertidal S. franciscanus possessed little

independence. The largely intertidal S. purpuratus possessed a

great deal of rate-temperature independence, especially from 12°

to 21°.

S. purpuratus and S. franciscanus were used in the tempera-

ture acclimation study. Both species were maintained at 9° and 18°

for a month. The results of both species clearly show "reverse"

compensation--i.e. the rate mean of the warm-acclimated animals

exceeds that of the cold-acclimated animals at the same test

temperature. Temperature-acclimated S. purpuratus possessed

considerable temperature compensation. Cold-acclimated animals

had greater rate-temperature independence between 9° and 15°,

whereas warm-acclimated animals had greater independence

between 15° and 24°. Temperature-acclimated S. franciscanus

possessed little temperature compensation. Cold-acclimated

animals had no rate-temperature independence. Warm-acclimated

animals had some independence over the upper end of the tempera-

ture range tested.

Comparison of the "field-acclimatized" metabolic rate-

temperature curve with the appropriate "temperature-acclimated"

curves suggests that summer-acclimatized S. purpuratus is more

warm-acclimated and summer-acclimatized S. franciscanus is

more cold-acclimated.

Oxygen Consumption of Three Species of
Sea Urchins at Different Temperatures

by

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INTRODUCTION

Physiological variation may take place at many levels of biological organization, from the molecular to the organismic (Prosser, 1955). Bullock (1955), Fry (1958), Prosser (1964, 1967), and others address themselves specifically to physiological responses to variation in temperature. Distinctions are made among the terms acclimation, acclimatization, and adaptation. Physiological acclimation refers to a compensatory change in response to a single, laboratory-controlled environmental identity. Such responses may be quite transient. Acclimatization is a compensatory response induced by any number of factors in the natural surroundings of an organism. Such variations may operate throughout a life span and even affect subsequent generations. Adaptation refers to changes operating at the phylogenetic (genotypic) level. Although the use of these terms in the literature is often ambiguous and often not as specified above, the above distinctions will be used operationally throughout the present paper.

The survival of variants rests with their ability to cope with the extremes of an environment as opposed to the average conditions (Prosser, 1955, 1957, 1964). Prosser (1967) distinguishes between

"resistance adaptation" and "capacity adaptation". The former is a response which permits survival at the extremes of an environmental identity, whereas the latter is said to operate within the "normal" range of the identity. The corresponding terms "resistance acclimation" and "capacity acclimation" are used to refer to physiological adjustments occurring under controlled laboratory conditions.

One type of measurement which can be made for intraspecific and intrageneric population comparisons is the determination of the rate of a biological process as a function of a given environmental factor. Results from such studies impart information about the nature of capacity acclimation (Prosser, 1957). Detection of possible interpopulation differences may be revealed by comparing coefficients, such as the Q_{10}, which measure the slope of the rate function.

Various patterns of temperature acclimation responses are possible (Bullock, 1955; Prosser, 1955, 1958, 1964; Precht, 1958; Prosser and Brown, 1961). In most instances, cold-acclimated organisms are described as having higher rate values accompanied by lower temperature coefficients compared to warm-acclimated forms. The importance of knowledge of thermal history is stressed for studies which deal with temperature acclimation.

Temperature compensatory responses in rate processes are known to occur under several conditions of acclimatization. Lati-

tudinal rate compensation is described for the pumping rate of

Mytilus californianus (Rao, 1953), the heart rate of Acmaea

limatula (Segal, 1956), and the oxygen consumption rate of Uca

pugnax (Vernberg, 1959). A temperature compensatory response

in the heart rate of A. limatula from different levels of the inter-

tidal is discussed by Segal (1956). Segal (1956) has also described

a lower temperature coefficient for winter forms compared with

summer forms over the same temperature range. Pickens (1965)

has studied temperature acclimation of Mytilus californianus and

Mytilus edulis heart rates.

The effects of various factors (organismic and environmental)

upon echinoid metabolism have been noted. These factors include

body size, the nutritional state, the reproductive cycle, environ-

mental oxygen, salinity, temperature, and habitat. Fuji (1962)

notes a greater food intake (expressed as a body weight percentage)

by the smaller Strongylocentrotus intermedius and concludes that

the smaller animals have a higher level of metabolism. Farman-

farmaian (1966) observes that the oxygen consumption of Strongylo-

centrotus purpuratus is approximately halved following a month of

starvation. Giese et al (1966) mention that the oxygen consumption

rate of S. purpuratus is rather constant regardless of the gonad

index when expressed per unit wet weight. If the rate is expressed

per unit nitrogen, it is observed to decrease with increases in the

gonad index. Johansen and Vadas (1967) conclude that S. purpuratus, Strongylocentrotus franciscanus, and Strongylocentrotus droebachiensis are able to regulate their oxygen consumption over a wide range of oxygen tensions. Critical oxygen tensions in the range of 60 to 70 mmHg were obtained by these authors. Only slight changes in the oxygen consumption of S. purpuratus are noted in salinities ranging from 70 to 120% sea water (Giese and Farmanfarmaian, 1963). Significant decreases are observed at salinities beyond this range. Lewis (1968) reports significantly lower oxygen consumption rates for infaunal (burrowing) sea urchins compared to epifaunal species. Brissus unicolor and Mellita sexiesperforata comprised the former group, and Echinometra lucunter, Tripneustes esculentus, and Diadema antillarum comprised the latter. A sixth species, Eucidaris tribuloides (a cidarid--lacking peristomial gills), is said to have a rate intermediate between those of the infaunal and epifaunal groups and significantly different from either of them. Farmanfarmaian and Giese (1963) conducted a study on temperature acclimation in S. purpuratus. Although a shift in the oxygen consumption rate was noted, the temperature coefficients in the range from 5° to 20° for both acclimated groups increased with increases in temperature. This contrasts with the usual pattern of decreasing Q_{10}'s with increasing temperature (Precht, 1958).

The purpose of the present investigation was to compare the extent of physiological temperature adaptation, through measurement of the metabolic rate-temperature relationship, in three sea urchin species occupying different ecological niches in the intertidal and offshore waters. The species investigated were S. purpuratus, S. franciscanus, and Allocentrotus fragilis. The extent of laboratory-induced capacity acclimation was investigated for two of the species, S. purpuratus and S. franciscanus. In all instances, the determination of oxygen consumption rates of whole animals was used as an index of metabolic activity.

MATERIALS AND METHODS

Collection and Maintenance of Animals

Specimens were collected from several different locations. *Strongylocentrotus* *purpuratus* was obtained from Yaquina Head (approximately 44° 39' N) and Whale Cove (approximately 44° 47' N). *Strongylocentrotus* *franciscanus* was collected from North Cove, Cape Arago (approximately 43° 17' N), Whale Cove, and Stonewall Bank (a rocky shoal some 55 to 60 m deep and 24 km offshore). *Allocentrotus* *fragilis* was dredged with an otter trawl from depths of 150 and 200 m (Newport line benthos stations NAD 6N, 44°N, and NAD 8, 44° 39.1' N, respectively).

Since the present study is interspecific in nature, no particular attention was directed to the microgeographic distribution of a species at any collecting site. Animals were collected only if a cursory examination showed them to be responsive to external stimuli and generally healthy. Since the metabolic rate results were corrected to a standard size animal, as described later, no effort was made to control the size of the animals collected. A considerable size range was thus used for each of the species, but especially S. franciscanus. S. franciscanus, except for the individuals which were dredged, was obtained from the uppermost regions of its vertical distribution. The assumption was made

that the individuals used are generally representative of the total, largely subtidal, distribution.

Two series of experiments were conducted. In one, metabolic rate determinations were made over a range of temperatures on animals kept in laboratory tanks for only short periods after collection. These will hereafter be called field-acclimatized animals. In the second series of tests sea urchins were acclimated for 30 days to a low and a high temperature, and the metabolic rate of the acclimated animals was determined over the same range of temperature as for the field-acclimatized animals. These will henceforth be called temperature-acclimated animals.

The field-acclimatized animals were maintained in aerated fiberglass or fiberglass-lined wooden holding tanks for periods of three to eight days. Several A. fragilis were maintained up to 12 days due to the infrequent opportunities to collect them. The holding tank temperature for S. purpuratus and S. franciscanus ranged from $11^{\circ}C$. to $14^{\circ}C$. That for A. fragilis was maintained at $9^{\circ}C$. The laboratory salinity to which all of the field-acclimatized animals were subjected ranged from 29‰ to 35‰. These animals were not fed any macroscopic material. Presumably, some level of nutrition was maintained by assimilating various microscopic organic materials. All of the sea water used, however, was passed through a gradient gravel filter which placed

a size limit upon this organic matter.

The temperature-acclimated animals (S. purpuratus and S. franciscanus) were acclimated at 9°C. and 18°C. for a minimum of 30 days. The salinity ranged from 24.5‰ to 34.5‰. During the initial two weeks of acclimation these animals were fed macroscopic algae. For the remainder of the acclimation period, no attempt was made to feed them.

Metabolic Rate Measurements

Rate of oxygen consumption was determined by measuring changes in the oxygen tension of a closed and sealed container in which the animal was placed. The animals were submerged in sea water at all times. A Beckman Spinco oxygen macro-electrode in conjunction with a physiological gas analyzer (Beckman Spinco model 160) was used to determine the oxygen tension. The electrode consists of a platinum wire cathode and a silver wire anode.

Calibration involves the determination of oxygen tensions of reference solutions (preferably the extremes) on the analyzer. The calibration solutions used were samples of the sea water in which the studies were made. An oxygen free reference solution was obtained by the addition of Oxsorbent (Burrell Corporation, catalog no. 39-710) to sea water. An air-saturated calibration solution was obtained by extensive aeration of a sea water sample.

The meter setting for the latter solution was calculated from the
following formula, in which air was considered to be 20.95%
oxygen:

$$\text{mmHg } O_2 = 0.2095 \text{ X (barometric pressure less water vapor partial pressure at the temperature of measurement)}$$

Several features of the respiratory containers were con-
sidered desirable. Among these were a secure seal, ease in
opening and closing, and an assortment of sizes to match those of
the animals. Various "Tupperware" products have proved quite
suitable in these respects (Figure 1). A magnetic stirring bar
was placed at the bottom of each container and was used in all
studies to provide for uniform temperature and oxygen tension
values. The desired experimental temperature was maintained by
placing the container in a large volume water bath maintained to
$\pm$ 0.10°C.

Richards and Corwin (1956) provide a nomogram with which
one may correlate temperature and salinity to the amount of oxygen
dissolved in water at saturation. With values for both the tension
and concentration (mls/L) of the oxygen in air-saturated water,
one may determine the concentration of oxygen equivalent to a
change in the tension from the following relationship:
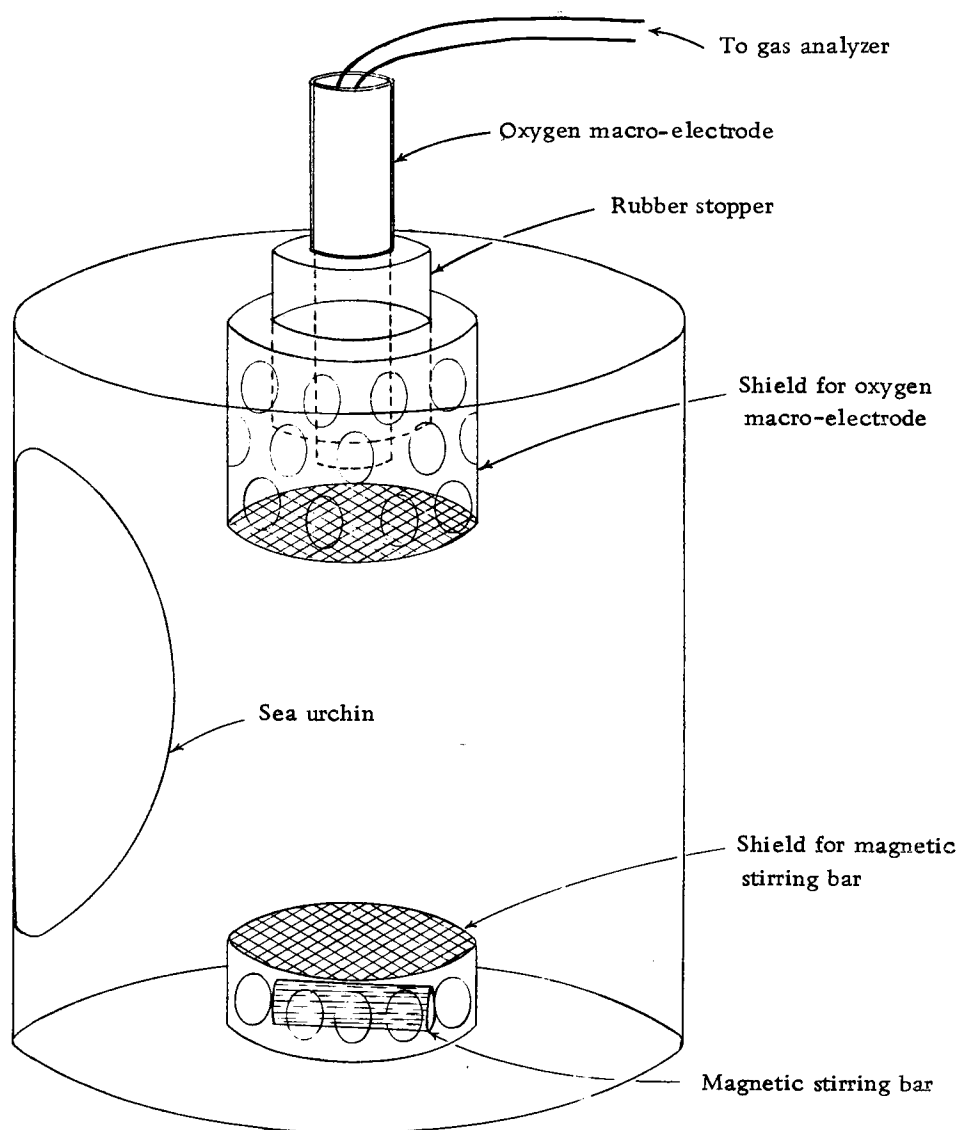
Figure 1. Respiratory Container.

(A) mls O_2/L at
     saturation
     _____

(B) calculated meter
     setting at satura-
     tion in mmHg

(X) O_2 consumed in mls/L
     in given time interval
     _____

(Y) mmHg consumed in
     given time interval

Thus: X = A/B times Y

And: X times volume of respiratory container minus
      sea urchin volume in liters equals mls O_2 con-
      sumed during an interval of time

The temperature range used was 6°C. to 24°C., with mea-
surements of metabolic rate made at increments of 3°C. The
same protocol was followed for field-acclimatized and temperature-
acclimated animals. Sea urchins were placed in the respiratory
containers overnight for equilibration purposes. After each change
in temperature, a one hour period for equilibration preceded the
actual measurements of oxygen uptake. Three to six determinations
were made at each temperature. The oxygen tension of the sea
water in the respiratory containers was never allowed to fall below
75 mmHg and in practically all cases did not reach this level.

The rates of oxygen consumption used in the present study
are probably "routine", as defined by Fry (1957). Occasionally,
an animal was observed to move rapidly about the respiratory
container, or at least to display excessive podial and spine move-
ment. During such intervals a considerable increase in oxygen
consumption was observed. Whenever the oxygen consumption

rate determined during these intervals was more than double that of any other rate under the same conditions, the former was discarded.

Subjecting an animal to each of the seven test temperatures used together with the requisite equilibration and measurement time constituted approximately 13 to 14 hours. To ascertain the existence of possible respiratory rhythms during the experimental period, several S. purpuratus and S. franciscanus were placed in the respiratory containers, and their oxygen consumption rates were determined over a 13 to 17 hour period. A scarcity of A. fragilis precluded a similar control experiment for this species. A possible respiratory rhythm coinciding with the tidal cycle by this benthic species seems less likely, however, than that for either of the Strongylocentrotus species involved.

Results are expressed in microliters of oxygen consumed per gram of weight per hour (μL/g wet/hr) and in microliters of oxygen consumed per gram of "soft tissue" dry weight per hour (μL/g dry/hr). The "soft tissue" dry weight was obtained by initially determining the total dry weight. Each animal was dried at 70°C. until no further weight loss was noted. Secondly, the dry "inorganic" weight for each animal was determined subsequent to placing it in a muffle furnace (500°C.) for a pre-determined amount of time--eight hours for S. purpuratus and A. fragilis and

generally 24 hours for S. franciscanus. The dry "soft tissue"

weight was assumed to be the difference.

RESULTS

A preliminary test was carried out without an animal in the
respiratory container, and there was no apparent change in the oxy-
gen tension of filtered sea water at 15° for an interval of 45 minutes.
This period of time is more than twice as long as any interval during
which sea urchin oxygen consumption was observed. Consequently,
errors from instrument drift and/or microorganismic respiration
were considered negligible.

Metabolic rates of three Strongylocentrotus purpuratus and two
Strongylocentrotus franciscanus urchins were determined over long
periods of time at 12°. The results are graphed in Figures 2 and 3.
All tables and figures are at the end of the chapter. Although occa-
sional large fluctuations in rate occurred (especially in S. purpura-
tus control animal 1), reasonably stable rates were observed for
long periods. High initial rates for S. purpuratus control animal 3
may be partly due to insufficient equilibration time. The appropriate
rate and tidal information is presented in Appendix A. Metabolic
rates of the smaller species, S. purpuratus, were greater than those
of S. franciscanus, as expected from the well-established effect of
size on metabolic rate (Zeuthen, 1953; Hemmingsen, 1960; Prosser
and Brown, 1961). The periods of measurement for each of the
control animals encompassed more than a complete tidal cycle. No

predictable cycling of the oxygen consumption rate is evident when the results from all of the control animals are examined. No obvious correlation, for example, appears between the metabolic rate of any control animal and the tidal cycle. Circadian or tidal rhythms, therefore, were not considered to have significant effects on the results during the periods of measurement.

Although the oxygen tension in the containers fluctuated between 75 and 160 mmHg, there was no correlation between the oxygen consumption rate and the ambient oxygen tension for any control animal. Some of the highest rates were observed at the lowest oxygen tensions, and, conversely, some low rates were recorded when the partial pressure of oxygen was high.

A summary of the results for the field-acclimatized animals is given in Tables 1 and 4. The oxygen consumption rate-temperature curves are presented in Figure 4 as semilog plots. The rates for S. purpuratus, S. franciscanus, and Allocentrotus fragilis are expressed as $\mu L/g$ dry/hr corrected to correspond to 5.0 g, 20.0 g, and 2.0 g animals, respectively. The effect of size upon metabolism is well documented (Zeuthen, 1947, 1953; Hemmingsen, 1960; Prosser and Brown, 1961). Farmanfarmaian (1966) cites the results of several investigations dealing with echinoderms which illustrate this phenomenon. The weight-standardized rates used in all rate-temperature curves were calculated by determining the linear

regression equation from the mean rates of all animals under a given set of conditions (species, temperature, and thermal history). The pertinent data for these equations are provided in Appendix B.

Metabolic rates of field-acclimatized S. purpuratus and A. fragilis were consistently greater than those of the larger species, S. franciscanus (Figure 4). Rates of A. fragilis increased consistently with increases in temperature. Rates of S. franciscanus rose consistently with temperature from 6° to 18°, but some temperature independence from 18° to 24° is suggested. A Q_{10} of 1.13 was obtained for the interval 18° to 21°. The rates of S. purpuratus rose with temperature from 6° to 12° and 21° to 24° but increased very little (or failed to rise) from 12° to 21°. The results for the field-acclimatized animals indicate temperature independence of the metabolic rate of S. purpuratus from 12° to 21° (Figure 4). Q_{10}'s in this temperature range varied from 0.779 to 1.60 (Table 4). Little evidence of rate-temperature independence is suggested from the Q_{10}'s for either S. franciscanus or A. fragilis.

The results for temperature-acclimated S. purpuratus are presented in Tables 2 and 4 and Figure 5. Cold-acclimated animals had rates of 130, 166, and 248 $\mu L/g$ dry/hr, and warm-acclimated animals had rates of 185, 277, and 286 $\mu L/g$ dry/hr at 12°, 15°, and 18°, respectively. All of these rates differ by more than two standard errors. The cold-acclimated rate-temperature curve

thus represents a shift (translation) to the right of the warm-accli-

mated curve. Such a phenomenon is called "reverse" or "paradoxi-

cal" acclimation (Precht, 1958; Prosser, 1967). Between 9° and

15° the cold-acclimated group had lower Q_{10}'s than the warm-

acclimated group. This situation was reversed between 15° and 24°

with the warm-acclimated animals showing almost complete rate-

temperature independence.

The results for temperature-acclimated S. franciscanus are

presented in Tables 3 and 4 and Figure 6. A reverse acclimation

again is quite evident. The cold-acclimated rate-temperature

curve displays a translation to the right of the warm-acclimated

curve and also some counterclockwise rotation. Cold-acclimated

animals had average rates of 38.3, 62.1, 82.2, 106, 144, and 196

μ L/g dry/hr, and warm-acclimated animals had average rates of

85.2, 104, 144, 170, 200, and 258 μL/g dry/hr at 6°, 9°, 12°,

15°, 18°, and 21°, respectively. All of the rates differ by more

than two standard errors.

In Figures 7 and 8 the rate-temperature curves of the field-

acclimatized animals are plotted with those of the temperature-

acclimated groups. Realizing that animals recently collected from

their natural surroundings obviously represent an entirely different

environmental history than those kept under controlled laboratory

conditions for a month, two overall impressions are worth noting.

For S. purpuratus (Figure 7) the field-acclimatized curve roughly

parallels the warm-acclimated results, especially in the upper part

of the testing range. In S. franciscanus (Figure 8) the field-accli-

matized pattern more nearly resembles that for the cold-acclimated

group, especially at the lower and intermediate testing tempera-   .

tures.

Table 1. Oxygen Consumption Rate-Temperature Results for Field-
Acclimatized Sea Urchins:

Strongylocentrotus purpuratus (7/31/68 - 9/6/68)
dry "organic" weight range = 4.59-9.25 g
dry "organic" weight mean = 6.96 g

Temperature	Number of Animals	Oxygen Consumption Rate $\mu L/g$ dry/hr*	Standard Error of Rate
6°	12	91.0	1.21
9°	12	154	1.10
12°	12	218	1.08
15°	12	217	1.09
18°	12	250	1.10
21°	12	232	1.13
24°	12	303	1.15

Strongylocentrotus franciscanus (6/17/68 - 11/4/68)
dry "organic" weight range = 15.41-109.87 g
dry "organic" weight mean = 49.1 g

6°	12	21.4	1.30
9°	12	40.4	1.19
12°	12	77.0	1.08
15°	12	106	1.15
18°	12	146	1.09
21°	12	152	1.10
24°	12	180	1.09

Allocentrotus fragilis (10/19/68 - 10/28/68)
dry "organic" weight range = 1.29-390 g
dry "organic" weight mean = 2.22 g

6°	6	69.9	1.61
9°	6	100	1.26
12°	6	140	1.18
15°	6	199	1.12
18°	6	311	1.17
21°	5	393	1.06
24°	5	482	1.04

The symbol * indicates that the oxygen consumption rates are for
5.0, 20.0, and 2.0 gram animals of S. purpuratus, S. franciscanus,
and A. fragilis, respectively.

Table 2. Oxygen Consumption Rate-Temperature Results for
Temperature Acclimated <u>Strongylocentrotus</u> <u>purpuratus</u> .

Cold (9°) Acclimated (9/4/68 - 11/18/68)
dry "organic" weight range = 0.53-7.23 g
dry "organic" weight mean = 4.84 g

Temperature	Number of Animals	Oxygen Consumption Rate μL/g dry/hr*	Standard Error of Rate
6°	10	61.1	1.14
9°	10	96.1	1.16
12°	10	130	1.11
15°	10	166	1.07
18°	10	248	1.03
21°	10	326	1.10
24°	10	395	1.09

Warm (18°) Acclimated (9/5/68 - 11/11/68)
dry "organic" weight range = 3.20-4.61 g
dry "organic" weight mean = 3.70 g

6°	6	55.7	1.39
9°	6	85.1	1.14
12°	6	185	1.12
15°	6	277	1.35
18°	6	286	1.17
21°	6	327	1.18
24°	6	370	1.13

The symbol * indicates that the oxygen consumption rates are
for 5.0 gram animals.

Table 3.   Oxygen Consumption Rate-Temperature Results for
Temperature Acclimated <u>Strongylocentrotus</u> <u>franciscanus</u>.

Cold (9°) Acclimated (9/13/68 - 10/18/68)
dry "organic" weight range = 1.42-90.79 g
dry "organic" weight mean = 41.6 g

Temperature	Number of Animals	Oxygen Consumption Rate μL/g dry/hr*	Standard Error of Rate
6°	6	38.3	1.18
9°	6	62.1	1.18
12°	6	82.2	1.18
15°	6	106	1.15
18°	6	144	1.26
21°	6	196	1.22
24°	6	276	1.14

Warm (18°) Acclimated (9/10/68 - 11/2/68)
dry "organic" weight range = 1.02-56.21 g
dry "organic" weight mean = 19.9 g

6°	6	85.2	1.18
9°	6	104	1.29
12°	6	144	1.21
15°	6	170	1.21
18°	6	200	1.25
21°	6	258	1.22
24°	6	269	1.19

The symbol * indicates that the oxygen consumption rates are for
20.0 gram animals.

Table 4. Q_{10} Values for Oxygen Consumption Rate-Temperature Relationships.

Temperature Range	Strongylocentrotus purpuratus Q_{10}	Strongylocentrotus franciscanus Q_{10}	Allocentrotus fragilis Q_{10}
	Field-Acclimatized Animals		
6°-9°	5.75	8.25	3.35
9°-12°	3.19	8.55	3.02
12°-15°	0.985	2.86	3.24
15°-18°	1.60	2.95	4.43
18°-21°	0.779	1.13	2.17
21°-24°	2.44	1.77	1.97

	Temperature Range	Cold (9°) Acclimated Q_{10}	Warm (18°) Acclimated Q_{10}
	Temperature-Acclimated Animals		
Strongylocentrotus purpuratus	6°-9°	4.52	4.10
	9°-12°	2.71	13.3
	12°-15°	2.26	3.85
	15°-18°	3.85	1.12
	18°-21°	2.47	1.56
	21°-24°	1.90	1.50
Strongylocentrotus franciscanus	6°-9°	5.01	1.97
	9°-12°	2.55	2.95
	12°-15°	2.32	1.71
	15°-18°	2.78	1.72
	18°-21°	2.80	2.35
	21°-24°	3.13	1.14

Figure 2. The Relationship Between Oxygen Consumption Rate and Elapsed Time for <u>Strongylocentrotus purpuratus</u> Control Animals.
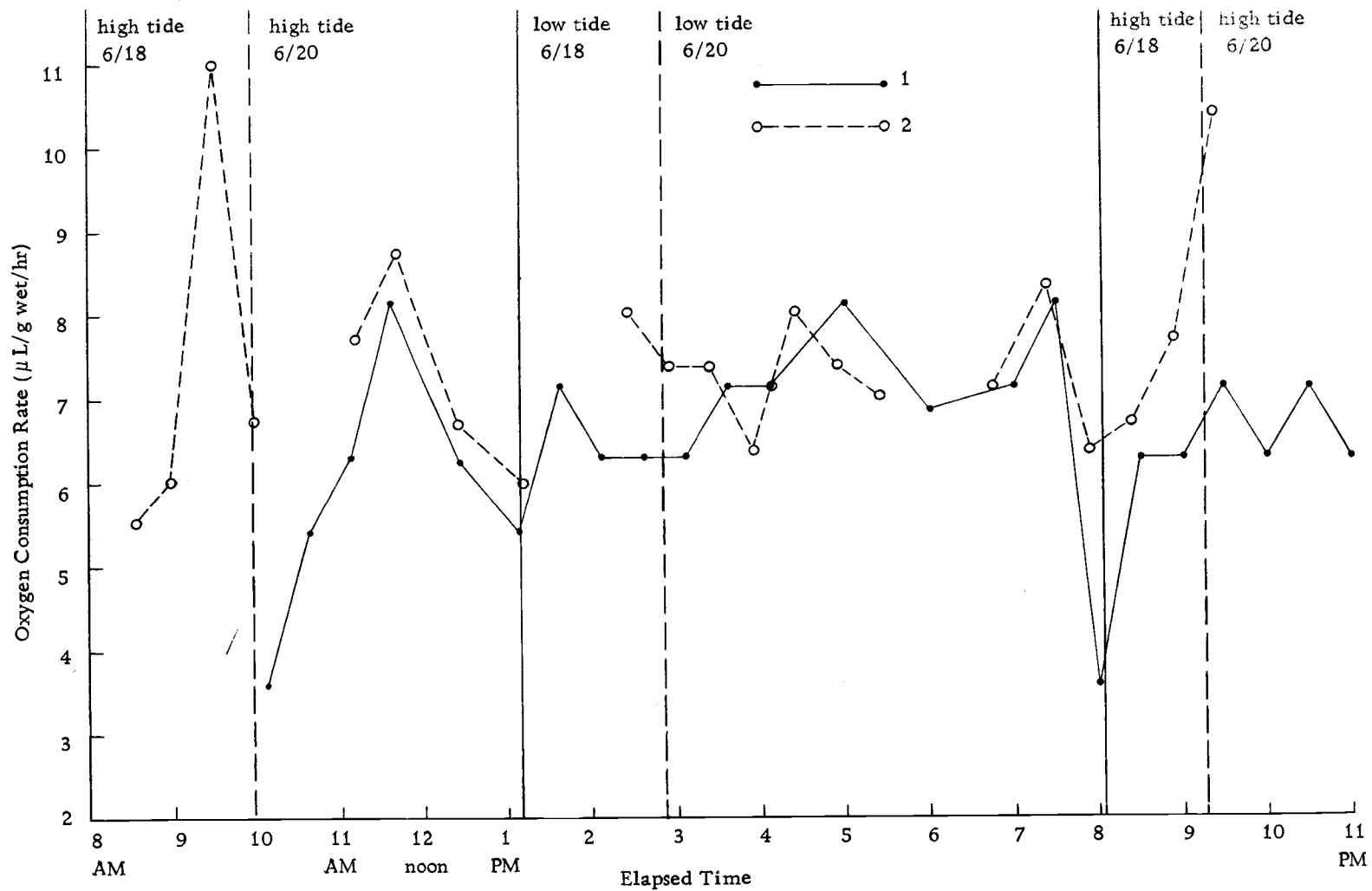
Figure 3. The Relationship Between Oxygen Consumption Rate and Elapsed Time for <u>Strongylocentrotus franciscanus</u> Control Animals.
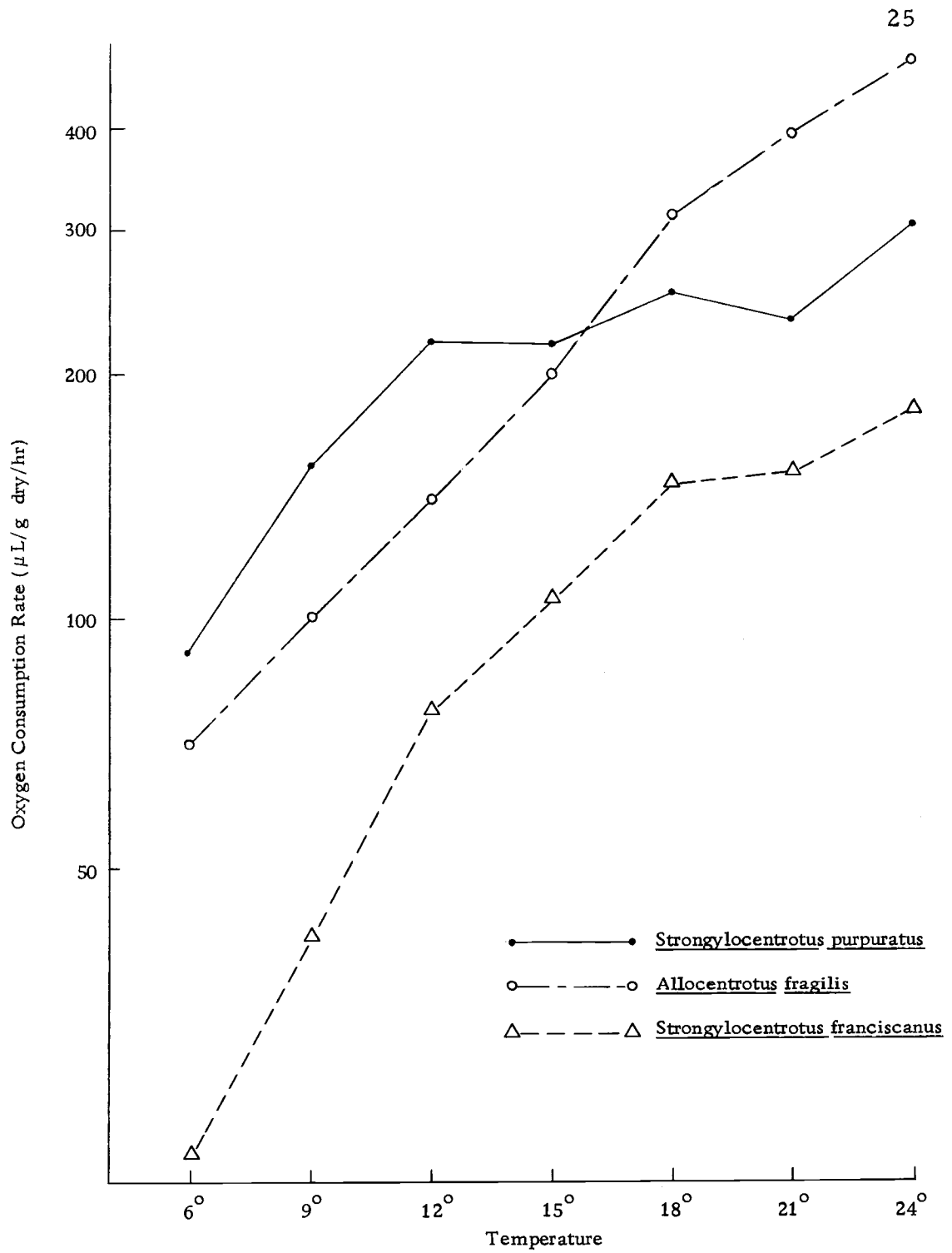
Figure 4. Oxygen Consumption Rate-Temperature Curves for Field-Acclimatized Sea Urchins.
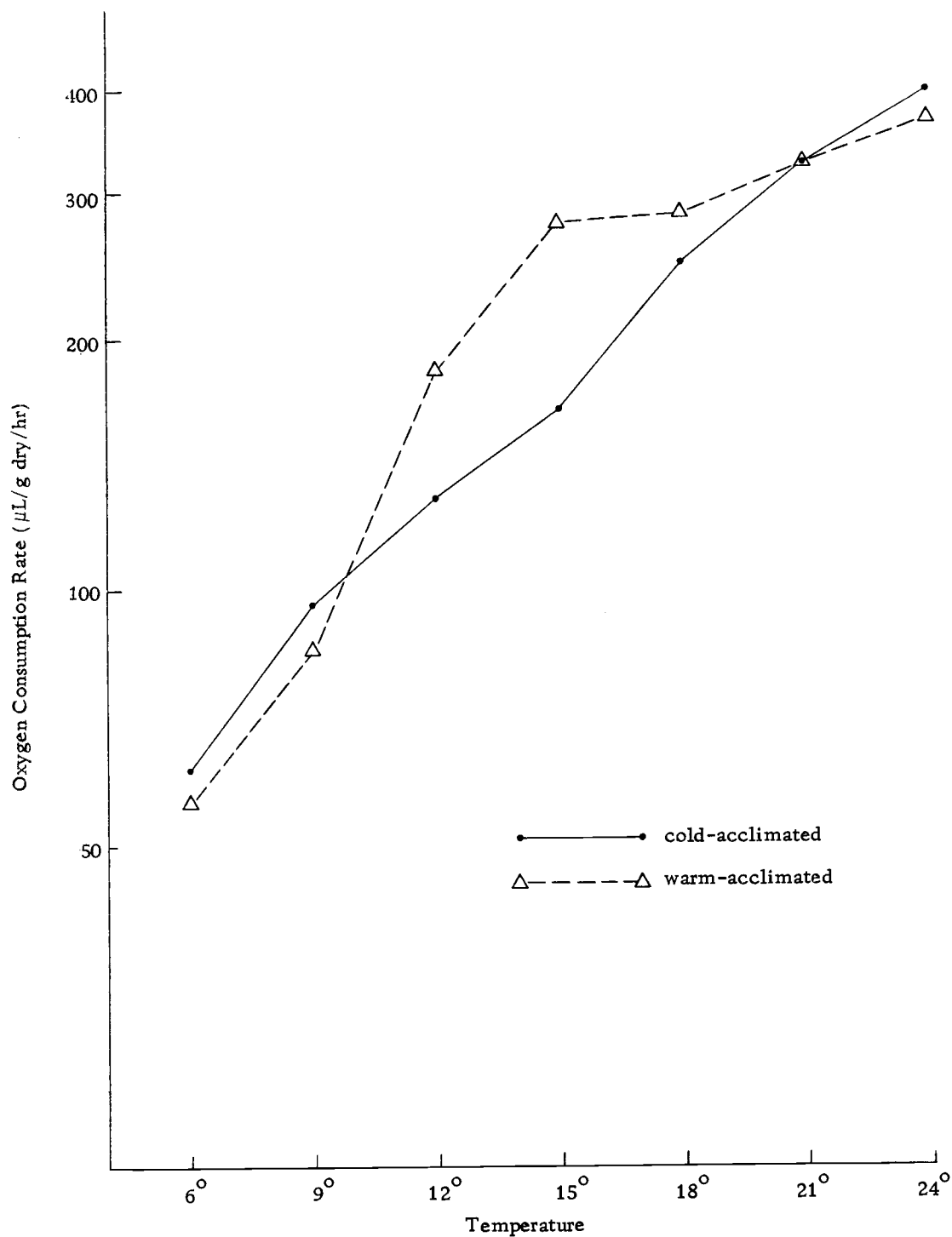
Figure 5. Oxygen Consumption Rate-Temperature Curves for Temperature-Acclimated
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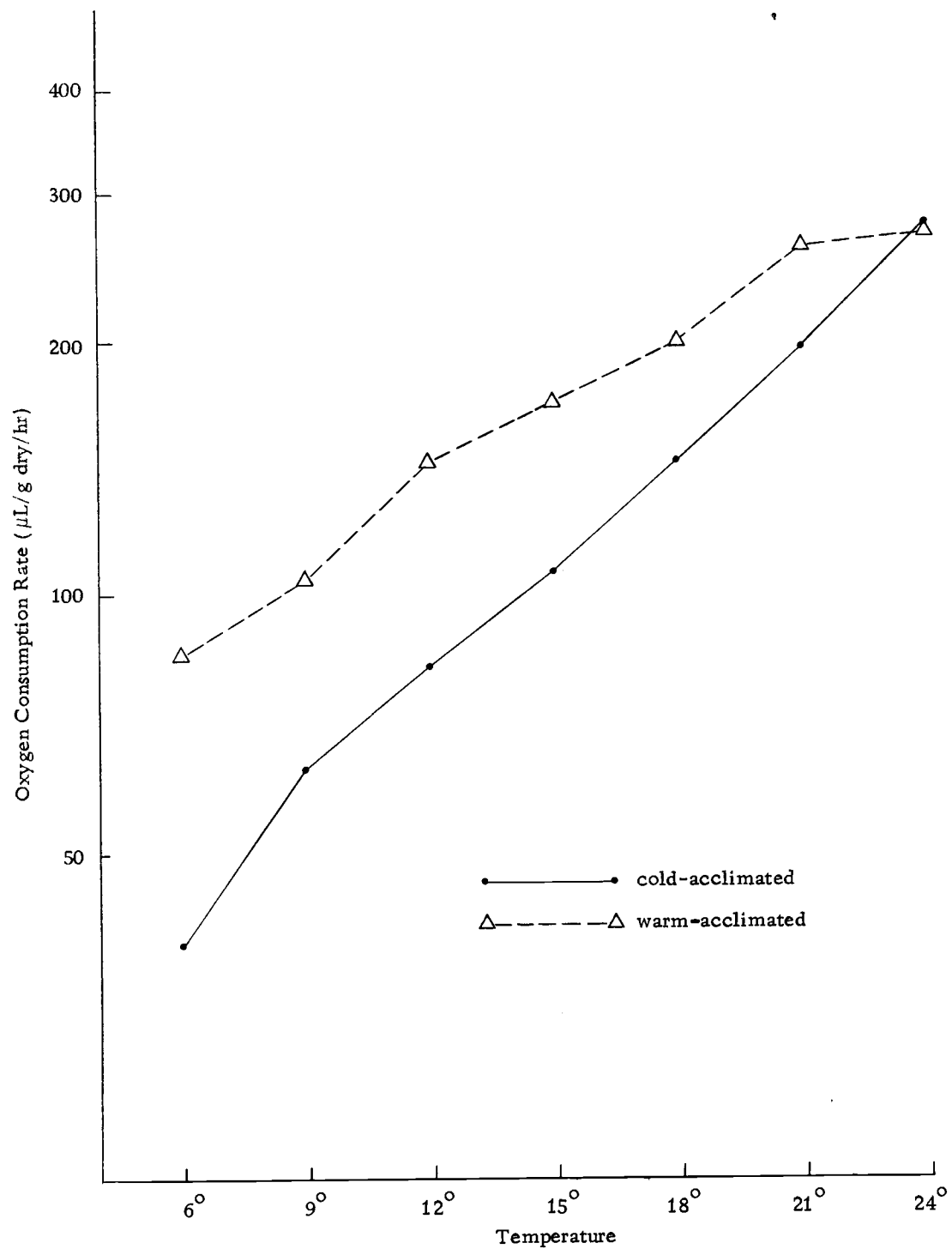
Figure 6. Oxygen Consumption Rate-Temperature Curves for Temperature-Acclimated
Strongylocentrotus franciscanus.
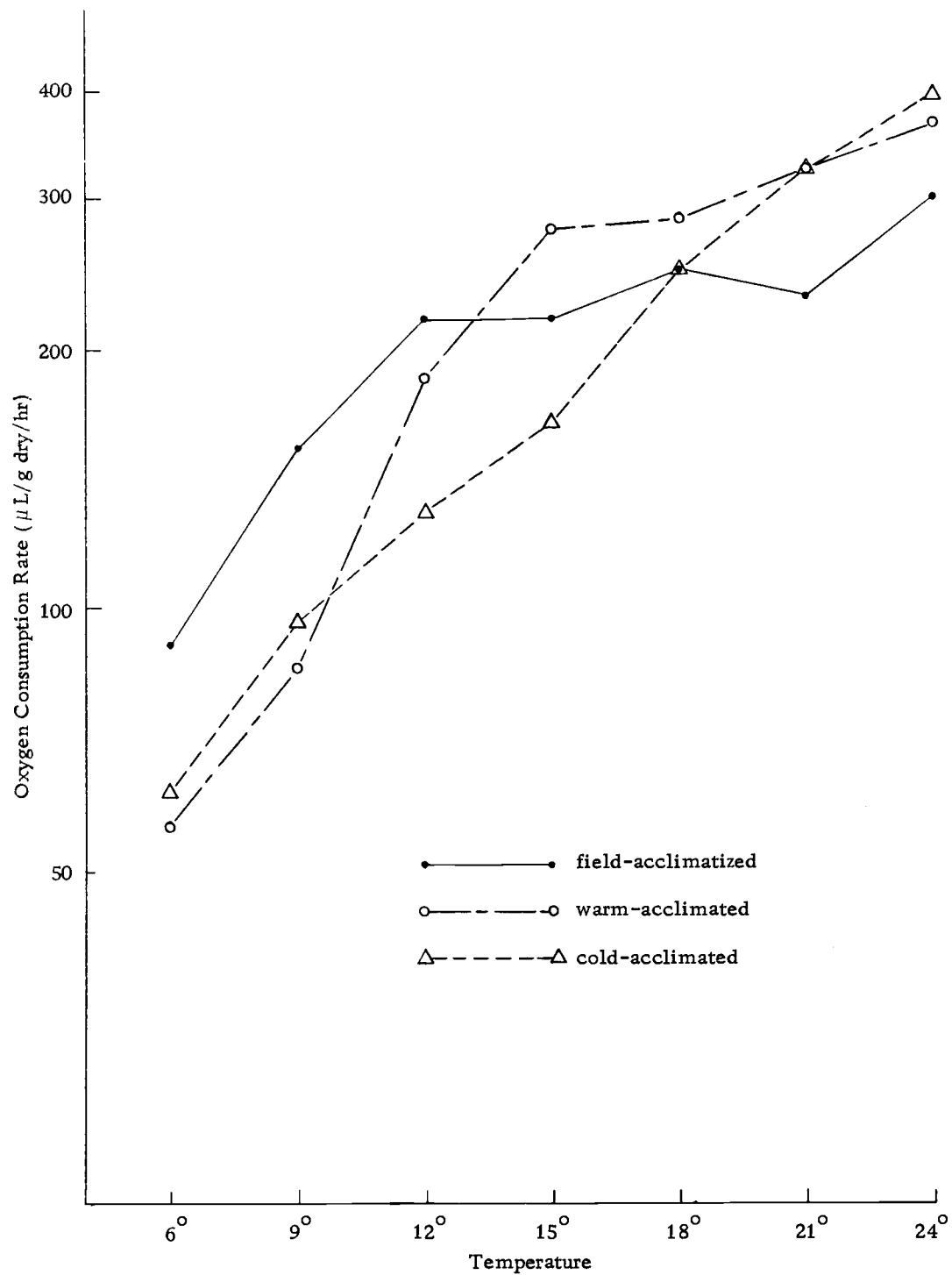
Figure 7. Oxygen Consumption Rate-Temperature Curves for _Strongylocentrotus purpuratus._
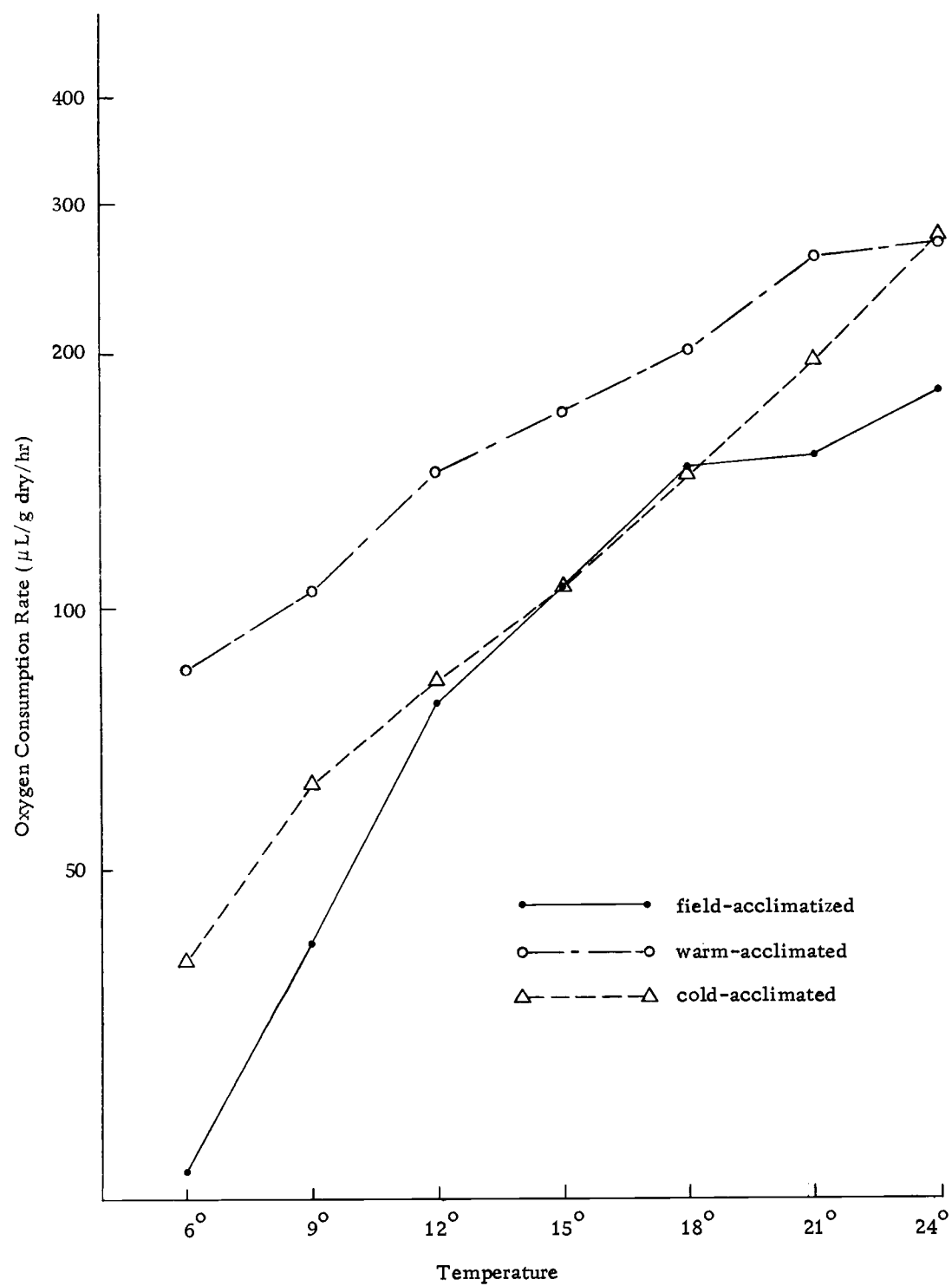
Figure 8. Oxygen Consumption Rate-Temperature Curves for <u>Strongylocentrotus</u> <u>franciscanus.</u>

DISCUSSION

Comparative Echinoid Studies

The metabolic rates of the present study are generally in agreement with values obtained from other studies on echinoids (Spector, 1956; Farmanfarmaian, 1959; Giese et al, 1966; Johansen and Vadas, 1967). The somewhat higher rates obtained by Farmanfarmaian (1959) and Giese et al (1966) may partly result from the comparatively small animal size used.

Several authors describe various echinoids as being oxygen consumption "conformers" with regard to the relation between the oxygen consumption rate and oxygen tension (Hyman, 1929; Farmanfarmaian, 1959, 1966; Prosser and Brown, 1961). Steen (1965) mentions oxygen consumption regulation by Strongylocentrotus droebachiensis at 6° but conformity at 16°. More recently, Johansen and Vadas (1967) observed in several species of Strongylocentrotus that the oxygen consumption rate is independent of the ambient oxygen tension down to partial pressures of 60 to 70 mmHg. However, a close correlation between the oxygen consumption rate and the oxygen tension of the coelomic fluid was found.

The finding of oxygen consumption regulation by Strongylocentrotus purpuratus and Strongylocentrotus franciscanus (Johansen and Vadas, 1967) is indirectly supported by the results

from the control animals of the present study (Figures 2 and 3).

Determination of the oxygen consumption-oxygen tension relationship

was not an objective of the present study, and, consequently, support

for the critical oxygen tension range (60 to 70 mmHg) of Johansen

and Vadas (1967) is not offered. The partial pressure of oxygen was

never allowed to drop as low as this range.

Habitat Comparison

Mortensen (1943) and McCauley and Carey (1967) discuss the

echinoids indigenous to the central Oregon coast and offshore waters.

Ten species are cited by the latter authors. The species of the

present investigation, S. purpuratus, S. franciscanus, and

Allocentrotus fragilis, are all strongylocentrotids.

S. purpuratus is abundant in the intertidal region but also has

been dredged from depths as great as 64 m (Mortensen, 1943;

McCauley and Carey, 1967). The species is abundant on exposed

and partially protected rocky substrates. In such situations it is

presumably exposed to greater temperature stresses than are the

other strongylocentrotids of the study.

The distribution of S. franciscanus is more subtidal than that

of S. purpuratus (Mortensen, 1943; Swan, 1953; Ricketts and Calvin,

1966; McCauley and Carey, 1967). Although a considerable number

of S. franciscanus may be found in the intertidal region, its dis-

tribution extends from the low tide line to depths of at least 125 m.

S. franciscanus shows a distinct preference for rocky substrates.

A bathymetrical distribution of 50 to 1150 m is suggested

for A. fragilis (Mortensen, 1943; McCauley and Carey, 1967). The

substrate is said to consist of silts ranging from sands to clays.

In view of the above-mentioned distributions, S. purpuratus

presumably is exposed to the greatest temperature stress, and

A. fragilis is exposed to the least. A limited amount of temperature

data lends support to this assumption. Gonor (1968) found that

daily measurements of the sea surface temperature fluctuated con-

siderably more than did weekly measurements. The following

monthly temperature ranges for Agate Beach surf (approximately

44° 37' N) during the months of collection for the present investiga-

tion were determined from daily measurements:

May 1968	9.9°-15.0°
June 1968	7.8°-14.6°
July 1968	7.9°-15.6°
August 1968	8.5°-17.0°
September 1968	9.3°-15.6°
October 1967	12.3°-14.4°
November 1967	10.3°-13.2°

The temperature ranges for October and November were determined

from measurements made in 1967. Gonor (1968) mentions that the

summer temperatures of exposed rock surfaces generally are higher

than those of the adjacent sea. During the winter the temperatures

of these surfaces are lower than those of the water. As a conse-

quence, annual and diurnal temperature ranges of exposed surfaces

are considered to be considerably greater than those of the water.

Less information is available for the appropriate benthic

temperatures. Bottom temperature measurements taken during

the period of January 1967 to January 1969 for NAD 6N and NAD 8

averaged $8.20^{\circ} \pm 0.802$ and $7.58^{\circ} \pm 0.588$, respectively (Carey,

1969). In these examples, variation is expressed as standard

deviation.

Interpretation of the Results on Field-Acclimatized Animals

The rate measurements of the present study were acutely

determined. Morris (1962) notes that such determinations allow one

to assess the capacity of an organism to respond quickly to changes

in the environment. Such measurements on temperature-acclimated

animals are related to capacity acclimation (Prosser, 1967).

Field-acclimatized S. purpuratus appears to possess a con-

siderable degree of oxygen consumption-temperature independence.

The results of Tables 1 and 4 and Figure 4 suggest that from 12°

to 21° the metabolic rate is essentially independent of temperature.

Within this range the temperature coefficients (Table 4) were 0.985

($12^{\circ}-15^{\circ}$), 1.60 ($15^{\circ}-18^{\circ}$), and 0.779 ($18^{\circ}-21^{\circ}$). There is little to

suggest any temperature independence in the metabolic rate of the

field-acclimatized $\underline{S}$. $\underline{franciscanus}$.   There was a Q_{10} of 1.13 for

the 18° to 21° range, but the benefit of metabolic rate compensation

within this temperature range is not clear, since it is greater than

that to which the species is thought to be normally exposed. Field-

acclimatized $\underline{A}$. $\underline{fragilis}$ does not show metabolic rate-temperature

independence over any portion of the testing range. Further, as

seen in Table 4, there is less variation of temperature coefficients

than in the other species.   The highest Q_{10} was 4.43 (15°-18°), and

the lowest was 1.97 (21°-24°).

It is possible that insufficient time was allowed at each

temperature for the establishment of a stabilized rate.   Most of the

data collected for a given species at a given temperature, however,

were quite constant.   If the equilibration time was not adequate, one

would expect a high incidence of either rising or falling metabolic

rates while measurements were made at any one temperature.

As mentioned previously $\underline{S}$. $\underline{purpuratus}$ occupies the most

exposed habitat of the three species considered and would be ex-

pected to encounter considerable fluctuations in temperature within

a tidal cycle.   Gonor (1968) observes that the internal temperature

of exposed $\underline{S}$. $\underline{purpuratus}$ may be at least 10° in excess of that of

the sea surface.   The wide range of temperature (12° to 21°) over

which the metabolic rate of $\underline{S}$. $\underline{purpuratus}$ is relatively temperature

independent may have adaptive significance in permitting this sea

urchin to maintain a constant metabolic rate in the face of changing habitat temperatures.

Countless environmental and other factors affect an organism in its natural surroundings, and doubtless some are more important than others. McCauley and Carey (1967) emphasize that the distribution of echinoids may be affected by depth, substrate composition, food availability, predation, competition, and temperature.

Prosser (1955, 1964) discusses the sequence by which allopatric speciation may take place. Initially, environmental factors may induce phenotypic variation. Subsequent genetic change would then serve to establish strains through natural selection. Various topographic and/or distance barriers may bring about complete isolation. Subsequent reproductive and other significant interdeme differences would eventually appear likely. These factors would lead to the establishment of separate species, the integrity of which would be maintained should they later come into contact. Any two closely similar species, such as certain intrageneric forms, may well have undergone phylogenetic development, diverging from a common ancestor as proposed above. This could have occurred regardless of whether or not the distributions of the species presently overlap. The results of field-acclimatized animals do not detract from the possibility that physiological variation in the temperature-metabolism relationships of an "ancestral strongy-

locentrotid" may have at least partially contributed to the development of S. purpuratus, S. franciscanus, and A. fragilis as separate species.

Two points are worth mentioning in concluding the interpretation of the results on field-acclimatized animals. Neither the nutritional state nor the reproductive state of these organisms was considered in the determination of their respective metabolic rates, and either or both of these factors may have contributed to the variability of the results. Since none of these animals was fed anything macroscopic while in the laboratory, however, the nutritional states presumably were at low and somewhat uniform, but not minimal, levels. Absence of information on the reproductive states of these animals was partially offset by the fact that the metabolic rate measurements were made for all of the species during the summer and early fall.

Interpretation of the Results on Temperature-Acclimated Animals

Prosser (1967) states that laboratory acclimation studies may provide information on the extent of capacity acclimation by an organism to an environmental identity. In the present study, two acclimation groups (9° and 18°) were tested, for both S. purpuratus and S. franciscanus. The results of the metabolic rate-temperature relationships for each acclimated group are shown in Tables 2, 3,

and 4 and Figures 5 and 6. In both species there is a shift (trans-
lation) of the metabolic rate-temperature curve for the cold-accli-
mated animals to the right of that for the warm-acclimated group.
In addition, the cold-acclimated S. franciscanus curve exhibits
a counterclockwise rotation or displacement when compared with
that of the warm-acclimated group. Precht (1958) has termed such
responses reverse acclimation.

S. purpuratus appears to possess a greater capacity for
temperature compensation of metabolic rate than S. franciscanus.
A comparison of the Q_{10}'s of cold and warm-acclimated S. purpura-
tus (Table 4) indicates greater metabolic rate-temperature indepen-
dence for the cold-acclimated group between 9° and 15° and for the
warm-acclimated group between 15° and 24°. In S. franciscanus
high temperature coefficients, ranging from 2.32 to 5.01, charac-
terize the cold-acclimated animals and suggest the absence of any
metabolic rate-temperature independence. Somewhat lower Q_{10}
values were found for the warm-acclimated animals over the testing
range (Table 4), but only at the upper extreme of the range is there
a suggestion of metabolic rate-temperature independence (a Q_{10} of
1.14 from 21° to 24°).

Although the cold-acclimated S. purpuratus animals had
slightly higher metabolic rates at 6°, 9°, and 24° (Table 2 and
Figure 5) compared to the warm-acclimated animals, the differences

are not nearly as striking as are the differences at 12°, 15°, and 18° at which the warm-acclimated animals had the higher rates. The rate differences at all of these latter temperatures are greater than two standard errors. The temperature-acclimated S. franciscanus animals possessed metabolic rate differences (greater than two standard errors) between 6° and 21°. In each instance, the warm-acclimated rate was greater than the cold-acclimated rate (Table 3 and Figure 6).

Although reverse acclimation, or paradoxical change according to Prosser (1967), appears to lack adaptive significance, many instances of reverse acclimation are cited from temperature acclimation and acclimatization studies (Berg, 1953; Dehnel, 1960; Webb and Brown, 1961; Pickens, 1965; Roberts, 1967). "Secondary" factors are said to contribute to the phenomenon of reverse acclimation (Prosser, 1964; Pickens, 1965), but the factor or factors responsible for the reverse acclimation found in the temperature-acclimated S. purpuratus and S. franciscanus are unknown. Factors of the testing environment other than temperature were maintained at as constant levels as possible throughout the study. An unchanging light intensity was maintained during all metabolic rate measurements. Mechanical disturbances were few in number and of small magnitude. Although the salinity range during all temperature-acclimated rate measurements ranged from 24.5‰ to 34.5‰, the

salinity level was constant for the measurements of any single animal. Oxygen tension levels were maintained in keeping with the interpretations of Johansen and Vadas (1967).

Farmanfarmaian and Giese (1963) investigated the effects of temperature acclimation upon the oxygen consumption of S. purpuratus. A cold-acclimated group was maintained at 5°, and a control group was kept at 14° to 19°. Determinations of metabolic rate were made at 5°, 10°, 15°, and 20°. Unlike the results of the present study, the cold-acclimated rate-temperature curve underwent translation to the left--that is to say that the cold-acclimated rate was greater than that of the control group for any given test temperature. The results obtained by these authors show temperature coefficients rising with increase in temperature, contrary to what is usually observed (Precht, 1958). Farmanfarmaian and Giese (1963) used Warburg-Barcroft respirometry in their metabolic rate determinations, and small animals (13 - 26 g wet weight) were selected in order that they fit into the flasks. These were much smaller animals than those used in the present study. Although Ebert (1967) has observed negative growth by some specimens in a population of S. purpuratus, shrinkage appeared only in animals larger than those used by Farmanfarmaian and Giese (1963). It appears likely, therefore, that the animals used by Farmanfarmaian and Giese (1963) were considerably younger than the S. purpuratus

of the present investigation. Conceivably, during the ontogenetic development of S. purpuratus, a shift or translation of the metabolic rate may be of less importance in temperature acclimation, and rotation (a change in Q_{10}) becomes of greater importance.

Comparison of the rate-temperature curves of the temperature-acclimated (laboratory-acclimated) animals with those of the field-acclimatized animals serves to emphasize the degree to which temperature compensation may have taken place in nature. The warm-acclimated S. purpuratus curve parallels the field-acclimatized curve far better than does the cold-acclimated curve, particularly in the 15° to 24° temperature range (Figure 7). On the other hand, the cold-acclimated S. franciscanus curve better parallels the appropriate field-acclimatized curve than does that of the warm-acclimated animals. This is especially evident in the 12° to 18° temperature range (Figure 8). Conceivably, summer acclimatization of S. purpuratus involves an increasing metabolic rate compensation over the upper half of the temperature range tested. Seasonal acclimatization of the comparatively subtidal S. franciscanus does not appear to result in an enhanced ability to maintain rate-temperature independence at the higher temperatures. Realizing that animals recently collected from the field, in contrast to the laboratory-acclimated animals, have been subjected to a great variety of environmental stresses, it is none the less tempting to

suggest that summer S. purpuratus animals are essentially "warm-acclimated", whereas summer S. franciscanus animals display the metabolic characteristics of "cold-acclimated" animals. This would be consistent with the summer temperature ranges of the respective habitats.

The present study has served to describe the metabolic rate responses to temperature change and their apparent adaptive value for several strongylocentrotids from various habitats. Studies to disclose the possible effects of ontogenetic development upon the metabolic rate-temperature curve would be of considerable interest. Transplantation and breeding studies may help to disclose whether some of the variations are genetic or phenotypic. Additional studies to discover possible molecular mechanisms of temperature acclimation in these forms would be appropriate.

SUMMARY

1. Metabolic rate-temperature relationships for several species

    of sea urchins, from different habitats, were determined

    using oxygen consumption rate measurements.

2. Two groups of experiments were performed. In one, meta-

    bolic rates were determined over a range of temperatures

    on animals kept in the laboratory for short periods of time

    (field-acclimatized animals). In the second, sea urchins

    were acclimated to a low and a high temperature for 30 days

    (temperature-acclimated animals), and their metabolic rates

    were determined over the same temperature range as for the

    field-acclimatized animals.

3. The metabolic rate-temperature results for the field-accli-

    matized animals are consistent with the temperature fluctua-

    tions of their respective habitats. The benthic Allocentrotus

    fragilis did not possess any metabolic rate-temperature

    independence. The comparatively subtidal Strongylocen-

    trotus franciscanus had some independence at the upper end

    of the temperature range tested. The more-exposed Strongy-

    locentrotus purpuratus showed a great deal of metabolic rate-

    temperature independence with a range of independence ex-

tending from 12° to 21°.

4. Reverse acclimation (cold-acclimated rates less than warm-acclimated rates) was demonstrated in both temperature-acclimated S. purpuratus and S. franciscanus. Both cold-acclimated metabolic rate-temperature curves were shifted to the right of the respective warm-acclimated curves. This is contrary to the results on the majority of animals.

5. Considerable temperature compensation (as indicated by low Q_{10} values) was evident in temperature-acclimated S. purpuratus. There was greater metabolic rate-temperature independence between 9° and 15° for cold-acclimated animals, and the warm-acclimated group possessed greater independence between 15° and 24°. Temperature-acclimated S. franciscanus exhibited little or no rate-temperature independence for either acclimation group.

6. The indication of metabolic rate-temperature independence by both temperature-acclimated and field-acclimatized S. purpuratus and its comparative absence in both temperature-acclimated and field-acclimatized S. franciscanus are consistent with the temperature ranges of their respective habitats.

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APPENDICES

APPENDIX A.

Oxygen Consumption Rates and Other Pertinent Information for
Strongylocentrotus purpuratus Control Animals:

Control Animal 1			Control Animal 2		
128.1 g (wet)			150.1 g (wet)		
7.62 g (organic dry)			9.10 g (organic dry)		
Respiratory Rate (μL/g/hr)			Respiratory Rate (μL/g/hr)		
Time	wet	dry	Time	wet	dry
9:10	20.0	336.2	10:20	6.54	107.8
9:30	17.0	285.8	10:40	11.7	192.9
9:50 AM	12.3	206.8	11:00	10.5	173.1
2:57 PM	34.0	571.5	11:20	6.54	107.8
3:17	11.6	195.0	11:40 AM	14.4	237.5
3:37	16.2	272.3	12:00 M	10.5	173.1
3:57	19.3	324.4	12:20 PM	7.86	129.6
4:17	13.9	233.7	5:54	13.1	216.0
4:37	13.9	233.7	6:54	11.8	194.6
10:56	6.18	103.9	7:54	9.13	150.6
11:16	23.1	388.3	8:14	9.13	150.6
11:36	16.2	272.3	8:34	9.13	150.6
			8:54	11.7	192.9
7/30/68			9:14	10.5	173.1
high tide (6.8) 3:33 AM			9:34	13.1	216.0
low tide (0.5) 10:09 AM			9:54	5.24	86.41
high tide (7.4) 4:39 PM			10:19 PM	13.1	216.0
low tide (1.6) 11:03 PM			12:05 AM	9.13	150.6
			12:25	9.13	150.6
7/31/68			12:45	14.4	237.5
high tide (6.1) 4:33 AM					

APPENDIX A. (Cont.)

Oxygen Consumption Rates and Other Pertinent Information for
Strongylocentrotus purpuratus Control Animals:

Control Animal 3
157. 1 g (wet)
9. 01 g (organic dry)
Respiratory Rate (μL/g/hr)

Time	wet	dry	Time	wet	dry
8:15	17.7	308.7	5:13	6.75	117.7
8:25	15.2	265.1	5:55	6.87	119.8
8:35	12.7	221.5	6:35	7.57	132.0
8:45	7.57	132.0	7:27	7.19	125.4
9:45	17.7	308.7	8:05	6.75	117.7
9:55	12.7	221.5	8:20	8.40	146.5
10:05	10.1	176.1	8:35	6.75	117.7
10:15	10.1	176.1	8:50	6.75	117.7
11:37	5.04	87.90	9:05	5.07	88.42
11:47	7.57	132.0	9:20	8.40	146.5
11:57 AM	5.04	87.90	9:35	6.75	117.7
12:07 PM	7.57	132.0	9:50	6.75	117.7
12:17	5.04	87.90	11:10	6.33	110.4
12:27	7.57	132.0	11:48 PM	5.07	88.42
12:37	5.04	87.90	12:03 AM	8.40	146.5
12:49	5.07	88.42	12:18	3.36	58.60
1:04	5.07	88.42	12:33	10.1	176.1
1:19	6.75	117.7	12:48	6.75	117.7
1:34	6.75	117.7	1:03	6.75	117.7
2:30	5.07	88.42			
2:45	6.75	117.7	5/11/68		
3:00	6.75	117.7	low tide (-1.1) 6:15 AM		
3:12	5.04	87.90	high tide (6.5) 12:33 PM		
4:20	5.04	87.90	low tide (1.8) 5:51 PM		
4:30	5.04	87.90	high tide (8.7) 11:45 PM		
4:43	8.40	146.5	5/12/68		
4:58	6.75	117.7	low tide (-1.7) 7:03 AM		

Animals 1 and 2 were measured at 12.0° on 7/30/68. Animal 2
was also measured on 7/31/68. Animal 3 was measured at 11.25°
on 5/11/68 and 5/12/68.

APPENDIX A. (Cont.)

Oxygen Consumption Rates and Other Pertinent Information for
Strongylocentrotus franciscanus Control Animals:

Control Animal 1			Control Animal 2		
207.7 g (wet)			535.5 g (wet)		
15.41 g (organic dry)			38.20 g (organic dry)		
Respiratory Rate (μL/g/hr)			Respiratory Rate (μL/g/hr)		
Time	wet	dry	Time	wet	dry
10:07	3.60	48.53	8:33	5.53	77.53
10:37	5.39	72.66	8:58	6.01	84.26
11:07	6.31	85.06	9:28	11.0	154.2
11:37 AM	8.14	109.7	9:58	6.72	94.21
12:22 PM	6.26	84.38	11.10	7.73	108.4
1:07	5.39	72.66	11:40 AM	8.74	122.5
1:37	7.17	96.65	12:25 PM	6.70	93.93
2:07	6.31	85.06	1:10	6.01	84.26
2:37	6.31	85.06	2:25	8.03	112.6
3:07	6.31	85.06	2:55	7.40	103.7
3:37	7.17	96.65	3:25	7.40	103.7
4:07	7.17	96.65	3:55	6.39	89.59
5:00	8.14	109.7	4:25	8.03	112.6
6:00	6.88	92.74	4:55	7.40	103.7
7:00	7.17	96.65	5:25	7.02	98.42
7:30	8.14	109.7	6:46	7.15	100.2
8:00	3.60	48.53	7:23	8.37	117.3
8:30	6.31	85.06	7:53	6.39	89.59
9:00	6.31	85.06	8:23	6.72	94.21
9:30	7.17	96.65	8:53	7.73	108.4
10:00	6.31	85.06	9:23	10.4	145.8
10:30	7.17	96.65			
11:00	6.31	85.06			

6/18/68
    high tide (5.5) 7:03 AM
    low tide (1.1) 1:09 PM
    high tide (7.2) 8:03 PM
6/19/68
    low tide (1.4) 2:51 AM

6/20/68
    low tide (0.8) 3:51 AM
    high tide (5.2) 9:57 AM
    low tide (2.2) 2:51 PM
    high tide (7.6) 9:15 PM
6/21/68
    low tide (0.3) 4:39 AM

Animals 1 and 2 were measured at 12.0°. The former was mea-
sured on 6/18/68, and the latter was measured on 6/20/68.

APPENDIX B

Zeuthen (1953) correlates animal size and metabolism with

the following expression:

$$Y = a \, X^b$$

Y equals the metabolic rate.

X equals the size of the animal.

a equals the Y axis intercept.

b equals the power to which X is raised in order to
relate it to Y.

This relationship is logarithmic. A linear relationship is suggested

by taking the logarithm of both sides of the equation. Therefore,

$\ln Y = \ln a + b \cdot \ln X$. In order to correct for the size effect on

oxygen consumption, a linear regression analysis was performed

for all oxygen consumption rate means of similar species, tempera-

ture, and recent thermal history. Three digit symbols are used to

properly identify such conditions.

The left digit refers to the species.

1. Strongylocentrotus purpuratus
2. Strongylocentrotus franciscanus
3. Allocentrotus fragilis

The middle digit refers to the recent thermal history.

1. field-acclimatized
2. cold-acclimated (9°)
3. warm-acclimated (18°)

APPENDIX B. (Cont.)

The right digit refers to the temperature at which the oxygen consumption measurements were determined.

1. 6°
2. 9°
3. 12°
4. 15°
5. 18°
6. 21°
7. 24°

Code	ln a	b
111	3.940477	0.354323
112	4.743715	0.182316
113	5.300150	0.053096
114	5.476212	-0.058652
115	5.640811	-0.072787
116	5.001086	0.275599
117	5.860188	-0.091498
121	4.114675	-0.001515
122	5.042946	-0.296480
123	5.214753	-0.217893
124	4.947226	0.100758
125	5.508605	0.003324
126	6.244690	-0.285578
127	6.428575	-0.273549
131	1.361362	1.651907
132	5.315619	-0.541267
133	4.217287	0.622543
134	2.861262	1.715995
135	4.213159	0.895703
136	4.593140	0.743428
137	5.343411	0.353570

APPENDIX B. (Cont.)

Code	ln a	b
211	3. 142413	-0. 025326
212	3. 652362	0. 015861
213	4. 551867	-0. 069423
214	5. 243308	-0. 195092
215	5. 637653	-0. 217999
216	5. 503072	-0. 161736
217	5. 960484	-0. 256796
221	3. 218367	0. 142218
222	4. 300405	-0. 057339
223	4. 653295	-0. 081308
224	4. 987612	-0. 108444
225	5. 609189	-0. 213701
226	6. 074389	-0. 265401
227	6. 057854	-0. 145674
231	4. 819103	-0. 124752
232	4. 887070	-0. 079627
233	5. 807358	-0. 278862
234	6. 042189	-0. 303789
235	6. 354634	-0. 352061
236	6. 431754	-0. 292368
237	6. 321573	-0. 242510
311	5. 122140	-1. 263438
312	5. 107810	-0. 721470
313	5. 239238	-0. 429767
314	5. 182817	0. 160871
315	5. 517523	0. 320484
316	6. 052599	-0. 114042
317	6. 212921	-0. 047423