# SOME ASPECTS OF THE BIOLOGY OF SEA STARS ASTERIAS VULGARIS VERRILL AND LEPTASTERIAS POLARIS (MULLER AND TROSCHEL) IN NEWFOUNDLAND WATERS



MING-HSIUNG KAO

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# SOME ASPECTS OF THE BIOLOGY OF SEA STARS ASTERIAS VULGARIS VERRILL AND LEPTASTERIAS POLARIS (MÜLLER AND TROSCHEL) IN NEWFOUNDLAND WATERS

by

© Ming-hsiung Kao, B.Sc., M.Sc.

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ABSTRACT

The comparative respiratory metabolism of Asterias vulgaris and Leptasterias polaris was determined by oxygen consumption measurements in both whole organisms and excised tissues under different temperatures. Oxygen consumption was measured by using Winkler's method for whole organisms and by the Warburg technique for excised tissues. Various levels of some important environmental factors influencing the oxygen consumption of whole sea stars were evaluated. Statistical analyses were applied to estimate and compare the effect of these factors on respiration in both species of sea stars.

The relation between the body weight of sea stars and oxygen consumption was expressed as a logarithmic linear regression. Regression lines of oxygen consumption of whole sea stars rise from 0°C to 15°C. The mean slope of the regression line was 0.72-0.89 for A. vulgaris; and 0.75-0.92 for L. polaris. There is no significant difference in oxygen consumption of whole sea stars between the sexes within a species. L. polaris has a lower oxygen consumption than A. vulgaris except in the larger L. polaris at 15°C. The oxygen consumption rate of sea stars is dependent on the ambient oxygen content in the sea water. The relationship showed a curvilinear instead of simple

linear correlation as general oxyconformer invertebrates do. The oxygen consumption rate decreases as the pH value in sea water is changed from normal sea water. The oxygen consumption rate of sea stars decreased more sharply with pH values above that of normal sea water (toward basic) compared to pH value below that of normal sea water. A. vulgaris is more sensitive than L. polaris to the pH effect. Salinity changes above or below the salinity of normal sea water also reduced oxygen consumption rate. Short-term food deprivation does not affect the oxygen consumption of sea stars. The oxygen consumption rate of various tissues in sea stars showed a tendency similar to that of whole sea stars, but the slopes varied greatly for different tissues. Some regression lines are not significant at the 5% level. It may be due to the different relative weights of various organs. Coelomic fluid exhibited the lowest oxygen uptake because there are few living cells in the fluid. The mature gonad of male sea stars indicate positive correlation between body weights and the oxygen consumption rate. This is as expected because the mature and full grown sea star would more likely possess active sperm.

The moving speed of A. vulgaris is faster than that of L. polaris and is more sensitive to temperature change. The moving speed of sea stars is not related to body weight, but righting response time is a function of body

weight. The smaller sea stars require less time to right themselves. When both species employed the same righting method, there was no significant difference between them. However, most larger sizes of L. polaris quite often applied the tulip method which consumes more time than the rest. Temperature does affect the uptake of amino acids. A. vulgaris appears to have better absorption capacity at high temperature. On the other hand, L. polaris exhibits better ability at low temperature. A. vulgaris is distributed from Southern Labrador to Cape Hatteras. This species can be found in shallow water in Northern North America, but south of Long Island Sound, it is not found along the shore. Temperature limits their distribution to deeper and cooler water in more southern regions. Therefore, it is classified as a boreal species. On the other hand, L. polaris occurs from the high Arctic region to Nova Scotia, and can be recognized as an Arctic species.

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# INTRODUCTION

Several large predatory species of asteroids are found in the northwestern Atlantic Ocean. Among these, Asterias forbesi (Desor) is found from the Gulf of Mexico to Maine (Coe, 1912; Galtsoff and Loosanoff, 1939; Gray et al., 1968) and Asterias vulgaris Verrill from Cape Hatteras to Newfoundland. A. vulgaris is considered by some authors (Tortonese, 1963; O'Brien, 1972) to be the same species as Asterias rubens Linnaeus, which occurs in the northeastern Atlantic Ocean and off West Greenland. However in view of their distinct distributions and minor morphological differences, they are considered distinct species in this thesis, since the appropriate experimental cross-breeding has not been done. This seems to be the opinion of the most current literature. The third species in the northwestern Atlantic Ocean is the circumpolar species Leptasterias polaris (Müller and Troschel) which extends as far south as Nova Scotia.

Thus both A. vulgaris and L. polaris occur in Newfoundland waters and are readily obtained and available for study. The present thesis compares some of their respiratory physiology and other characteristics to determine if these can account for their different distributions.

Environmental temperature is generally considered the most important factor influencing distribution. Hence its effect on the routine metabolism of whole animals and selected tissues were compared by measuring oxygen uptake at various temperatures. The influence of salinity, oxygen content and pH of the sea water on oxygen uptake were also examined to determine their effects.

The activity of the animals at various temperatures was compared by measuring righting responses and the rate of locomotion. Feeding activities were observed in the laboratory and the uptake of food compared by measuring the rate of uptake of labelled amino acids at various temperatures.

The respiratory physiology of echinoderms has been studied by a number of investigators (Meyer, 1935; Smith, 1940; Farmanfarmaian, 1959; Giese, 1966, 1967; Percy, 1971, Webster, 1972, etc.), but most works dealt with echinoids and relatively few details in them have been concerned with asteroids. In particular, the oxygen consumption of A. vulgaris and L. polaris has been neglected.

Many careful oxygen consumption studies have been conducted on a range of animals including at least 14 asteroids from temperate North America to New Zealand (Webster, 1972), but few investigations have been done for boreal forms, and these strongly suggest the need for a detailed examination of this aspect of the physiology of

northern species. Unfortunately, most of the reported measurements were on one or a few individuals and at a single temperature thus permitting no calculations of derived parameters. Metabolism reflects the energy expenditure of an organism. Of the several methods of analyzing metabolic processes, the choice of determining the oxygen consumption in relation to body weight follows the practice of most investigations in this field (Zeuthen, 1953; Barlow, 1961; Beamish, 1964, etc.).

The investigations presented in this thesis extend current knowledge about echinoderms into the northern regions of the biosphere and with sufficient detail to permit calculation of such important characteristics as temperature coefficients.

Meyer (1935) undertook an exhaustive study of respiration and its relationship to different environmental factors in one species of sea star, A. rubens which is distributed in northern European waters. Unfortunately, she did not carry out statistical analysis to establish the relationship between body weight and oxygen consumption of sea stars. Farmanfarmaian (1966) pointed out that most papers which have reported on size versus respiration in echinoderms had too little data and were not adequate to give the precise relationship. So the present study intends to determine relationships more precisely as described above and also to compare interspecifically with greater

accuracy, by using regression analyses to test this relationship in the two species studied here.

Studies of temperature effects on the respiration of these two species are conspicuously absent from the literature. Scholander et al. (1953) summarized results obtained from a number of species taken in Arctic and warm waters. The Arctic forms as a rule have higher oxygen consumption than related southern forms when measured at the same intermediate temperature. Measured at their normal environmental temperatures, many warm-water forms showed a higher respiration rate than do the cold water forms. They concluded that three main possible homeostatic adaptations of metabolic rate might occur: (a) by parallel displacement of the metabolic-temperature curve with maintenance of normal temperature sensitivity, (b) by a low $Q_{10}$, whereby the overall temperature sensitivity is low, and (c) by selection of a constant environment. However, Vernberg (1959a) measured metabolic-temperature curves of fiddler crabs from different climatic regions (temperate and tropical zone species) at temperature below 12°C. Those from the temperate zone had a higher metabolic rate than did the tropical species. In contrast, at higher temperatures no systematic difference could be correlated with geography, although interspecific differences did exist. The different shape of the metabolic-temperature curve suggested that the temperature

did not uniformly affect the metabolic rate, but that certain temperatures were more critical than others. In order to understand whether the southerly distributed species, A. vulgaris would in fact have a lower metabolic rate than the northern species L. polaris at the same temperature, the metabolism-temperature relationships should be considered. Furthermore, slope values of respiration with body weight could be examined under the influence of different temperatures. Therefore the temperature effect on respiration will also be investigated in this thesis.

Sea stars are obligate aerobes and mostly occur only where ambient oxygen tensions are normally at high levels. In fact, the oxidative metabolic rate of most species conforms to the pressure of oxygen available in sea water. On the other hand, Johansen and Petersen (1971) studied the oxygen consumption of the cushion star Pteraster tesselatus Ives, and reported that its respiration rate was independent of ambient oxygen tension down to about the range of 70 mm Hg due to possession of a unique pumping mechanism which allows P. tesselatus to satisfy its needs for respiratory gas exchange in a manner uniquely different from that in all other sea stars. Recently, Shick (1976) also found that the mud star Ctenodiscus crispatus (Retzius) could regulate oxygen consumption to lower oxygen levels (10 to 25 mm Hg) at temperatures between 10°C and 12°C.

Maloeuf (1937) indicated that the oxygen consumption of A. forbesi was strictly dependent on the oxygen tension in sea water and Hyman (1955) also showed that the sea star Patiria miniata (Brandt) was dependent upon the oxygen content in sea water, but Mangum and Van Winkle (1973) found that A. forbesi was an oxygen regulator. So far no information has been obtained or studies made for either species used in the present study.

The influences of salinities and pH values of sea water on the oxygen consumption has been indicated by Farmanfarmaian (1966), but this still remains unclear and controversial. A. rubens (Binyon, 1972) and A. vulgaris (Smith, 1940) can tolerate a salinity of 14 °/oo and upward. Again there are no reports or papers concerned with the effects of salinities and pH on oxygen consumption for A. vulgaris and L. polaris. Therefore further investigations are required and some pertinent data are provided herein; the effect of pH and salinity on oxygen consumption of sea stars will be evaluated in this study also.

It is known that sea stars can stand prolonged food deprivation and that long-term deprivation reduces oxygen consumption (Feder, 1959). Unfortunately, the temperature control in our laboratory would not permit an experiment of long-term period, but a comparison has been achieved of A. vulgaris and L. polaris after food deprivation for 10 days. During the winter sea stars are more subject to food

deprivation, hence, an experimental temperature of 0°C was chosen which approximated the winter water temperature.

The publications contributing the most valuable information on echinoderm tissue respiration are by Farmanfarmaian (1959), Giese (1966), Percy (1971), Belman and Giese (1974). Giese (1966) pointed out that little information on tissue respiration was found in the literature. He reported that tissue respiration in two species of asteroids only involved a general investigation and with no consideration of temperature and body weight effects. He and Belman (1974) studied the oxygen consumption of the Antarctic sea star Odontaster validus Koehler; they emphasized on the contribution of the body wall to the oxygen consumption of the whole sea star in only a small range of temperature. Many well known physiologists attempted to relate the body weights and oxygen consumption rate of tissues, but so far no conclusive assessments have been obtained. Most studies dealt with homeothermic organisms; therefore, whether sea stars, poikilothermic organisms, would follow a similar pattern as homeothermic organisms should also be considered.

Sea stars are slow moving invertebrates, the movement of their body results from the operation of tube feet of one or several rays. Some sea stars have terminal suckers to increase adhesion. Most asteroids tend to move about to avoid physical stress or to seek food. Feder and Christensen (1966) gave some information about

the rate of locomotion of various sea stars from several authors' reports but unfortunately there are very little data available on the effect of temperature on moving speed. So, an attempt was made to study this aspect.

The righting movement of sea stars is their ability to right themselves when they are placed on their aboral side; detailed descriptions of this subject have already been reviewed by Hyman (1955), Reese (1966), Pells and Gonor (1975). In general, the righting reactions of sea stars fall into three categories: somersaulting, folding over, and raising their arms like a tulip. Most works dealing with the righting response of sea stars were only concerned with some aspects, such as the nature of the stimulus that evokes righting, variation in behavior, how the direction of light affects the righting reaction and some other factors such as substratum, depth of water and temperature, etc.; but the comparison of the righting response between species with respect to time, temperature and body weight has received little attention. Variation in the righting response in different species may be due to diversity of morphology.

Sea stars unlike most sea urchins are carnivorous; their diet consists of high protein content food (e.g., mussel, oyster, barnacle, etc.) which are digested initially into various amino acids and later assimilated into different tissues and organs, therefore their amino acid uptake

should be a good indicator of food uptake processes. The digestive gland of sea stars serves primarily for nutrient absorption, although most tissues of sea stars have been demonstrated to be able to take up labelled amino acids from incubative solutions (Stephens and Schinste, 1961; Ferguson, 1964, 1967, 1979; etc.). The uptakes of labelled amino acid in A. vulgaris and L. polaris are compared at different temperatures in the present study in an attempt to determine if the differences are correlated with difference in their geographic distribution.

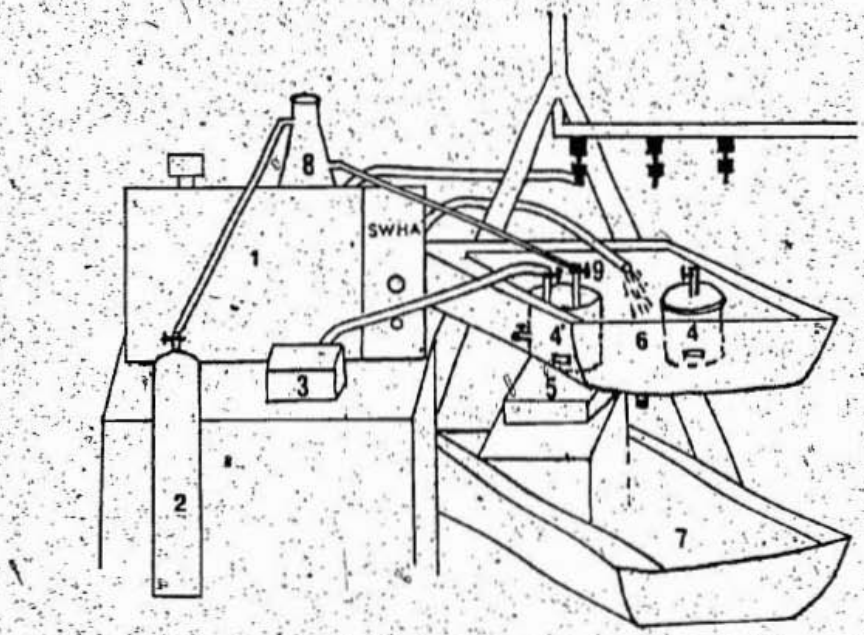
## MATERIALS AND METHODS

### I. Collecting Sites and Handling Sea Stars

Sea stars L. polaris and A. vulgaris were collected from Logy Bay, St. Phillips, Flatrock and Bay Bulls areas near St. John's, Newfoundland (47°N/52°W). They were maintained in an aerated running sea water holding tank at the Marine Sciences Research Laboratory, Logy Bay. For experimental purposes, unpolluted sea water coming directly from the bay to the laboratory was filtered by gauze and passed through a plastic heat-exchange coil lying in a constant-temperature bath which could be manipulated to the desired temperature with a sensitivity of ±0.3°C (Heat Exchange Model SWHX by Neslab Instrument Inc.). Constant temperature sea water from the bath was passed to the experimental tank, then to the holding tank (see Fig. 1). The temperature in the holding tank was about 0.5°C higher than that in the experimental tank, a negligible difference. When fresh sea stars were collected, they were placed in the holding tank which was immediately adjusted to the same water temperature as in the collection locality in the field. An acclimation period of at least one day under laboratory conditions was permitted prior to further adjustment. Sea stars in the holding tank were fed with

Fig. 1

Diagram of Respiratory chambers with related apparatus.




1. Heat Exchange.
2. Nitrogen Cylinder.
3. Oxygen Analyser
4. Respiratory chamber for (1) & (2).
4'. Respiratory chamber for (3).
5. Magnetic Stirrer.
6. Experimental Tank.
7. Holding Tank.
8. Constant Level Chamber.
9. Clamp.

mussels Mytilus edulis Linnaeus. All sea stars were examined under a stereoscopic microscope in order to remove all amphipoda (Caprella unica Mayer) on the surface (dermal skin) of A. vulgaris. Caprellids are symbiotic on A. vulgaris (McCain, 1968), and were not observed on L. polaris. They were prevalent in summer. Only perfect specimens were used, and specimens with damaged or regenerated arms were discarded. At the completion of experimentation, the sea stars were carefully blotted by paper towels and immediately weighed, then were dissected to determine sex by examining the gonads. However, if any gonad was infected by parasitic ciliates (Orchitophyra stellarum Cépède) the results obtained with that particular sea star were discarded. Many sea stars were used repeatedly at different temperatures, Nile blue sulfate solution was used to label the sea star by marking different parts of the body and the arms.

## II. Whole Sea Star Respiration

### (1) Determination of Oxygen Consumption of Whole Specimens

Different body sizes of sea stars were utilized for the respiration studies. Experimental sea stars were not fed for at least 24 hours before the experimental period. Oxygen consumption was determined on a single specimen by placing it in a closed respiratory chamber, the size of which depended on the size of the specimen.

The respiratory chamber (Fig. 1) was closed with a rubber lid, making sure no air bubbles were trapped inside. This was done by pressing the rubber lid down on the filled respiratory chamber, so that sea water from the respiratory chamber would rise slightly in the rubber tube mounted on top of the rubber lid. A clamp was used to close the rubber tube, thus trapping about 1.0 or 1.5 ml of sea water. In order to obviate stratification of dissolved oxygen in the respiratory chamber the sea water was mixed constantly by means of a magnetic stirrer placed under perforated plate at the bottom of the respiratory chamber. Immediately before introducing the experimental sea star into the respiratory chamber a 5 ml sample of sea water was taken by a syringe. The oxygen content was determined titrimetrically according to the unmodified Winkler method, then the whole respiratory chamber was completely immersed in the experimental tank. At the termination of each experiment sea water samples were extracted from the respiratory chamber directly into a syringe through a needle which pierced through the rubber lid. In so doing, it was necessary to release the clamp on the rubber tube, to equalize the internal and external pressures, for otherwise the sea water samples could not be withdrawn. The oxygen content was then determined again. In each experiment the net volume of sea water in the respiratory chamber, i.e., water volume excluding sea

star, was determined by volumetric flask and graduated cylinder.

(2) Determination of Oxygen Consumption of Whole Specimens at Different Temperatures

Oxygen consumption was measured at four different temperatures: 0°C, 5°C, 10°C, and 15°C. In order to eliminate lengthy periods of temperature acclimation and the confounding effects of the previous thermal history of sea stars, the animals collected from different temperatures at different seasons were acclimated to the nearest temperature as listed above, e.g., animals collected at temperature 3°C from the collection site were maintained one day in the holding tank which was adjusted to 3°C, then the temperature of the holding tank was raised at approximately 1°C every 24 hours up to 5°C. The animals were held at 5°C for several days before experiments were begun. Experiments at 0°C were performed in the winter, because of the limited capacity of the instruments to reduce temperature to that extent. Water temperatures in Newfoundland winter are below 0°C and it was feasible then to allow the temperature to rise to 0°C in the laboratory, and to maintain it there during acclimation and experimentation.

(3) Determination of Oxygen Consumption of Whole Specimens at Different Oxygen Content in the Sea Water

Oxygen uptake was measured at hourly intervals in a closed cylindrical respiratory chamber which was made of

plexiglass, and contained approximately 1 liter of filtered sea water coming from a glass container. After a sea star was placed in the respiratory chamber, the chamber was closed by a rubber lid on which a rubber tube was connected to a glass container with about 3 liters of sea water. Nitrogen gas from a nitrogen cylinder was bubbled through the sea water in the glass container (constant level chamber) in order to decrease the oxygen content to the desired concentration. In this manner the pH of sea water was not markedly affected. Sea water in the respiratory chamber was replaced at hourly intervals by fresh sea water from the constant level chamber and used sea water was replaced through an outlet on the bottom of the respiratory chamber. A Galvanic cell oxygen analyzer (by Precision Scientific Co. Cat. No. 68850) with a sensitivity of ±0.1 mg/l was mounted on the rubber lid. In order to maintain optimal sensitivity of the electrode, the sea water was also constantly mixed by means of a magnetic stirrer under a perforated plate. The galvanic cell oxygen analyzer was read visually at hourly intervals. In each experiment the oxygen analyzer was calibrated in oxygenated sea water in which the oxygen was determined titrimetrically by using the unmodified Winkler method. Comparisons between Winkler titration and the oxygen analyzer were within a range of ±1%. If they did not agree, the membrane of the probe from the oxygen analyzer was replaced immediately.

(4) Determination of Oxygen Consumption of Whole Specimens at Different pH Values

The same apparatus as described above was employed in this experiment, but the pH of sea water was adjusted in the constant level chamber and was reduced by adding HCl to sea water. Sea water in the respiratory chamber was withdrawn from the outlet and its pH value was determined by using a Corning pH meter (Model 7). The pH of sea water could only be raised up to 10 before the precipitation of $Mg(OH)_2$ would occur. This precipitate would cover the body surface of the sea star, at this point interference with the penetration of the oxygen might cause incorrect results and the experiments were terminated. The method of acidification and basification of sea water followed the techniques suggested by Kokubo (1962).

(5) Determination of Oxygen Consumption of Whole Specimens at Different Salinities

The apparatus used above was also used in this study. The salinity of sea water was gradually changed either by the addition of distilled water to decrease salinity or by the introduction of sea salts to increase salinity. Salinities were determined by a Salinity Refractometer (American Optical Corporation No. 10419) and checked by using the Mohr technique as suggested by Strickland and Parsons (1965). The silver nitrate solution was standardized against normal sea water "Eau de Mer Normale" which was supplied by the Laboratoire Hydrographique

Charlottenlund, Denmark.

(6) Determination of Oxygen Consumption of Whole Sea Stars after 10 Days Food Deprivation

Sea stars were kept in a tank with filtered running sea water maintained at 0°C. Sea stars were not fed for 10 days, and measurements of oxygen consumption of sea stars were performed to examine any significant difference.

III. Determination of the Freezing Point of the Coelomic Fluid in Sea Stars at Varying Salinities of Sea Water

The sea stars were placed in 1000 cc of sea water. Coelomic fluid was drawn by hypodermic needle through the dorsal surface of a sea star arm. The salinity of the coelomic fluid obtained from the sea star and of the sea water surrounding the sea star was measured by using a refractometer. The salinities were then converted into freezing points for comparison with the literature by using Sea Water Temperature and Density Reduction Tables by W.B. Zerbe (U.S. Government Printing Office, Washington, 1953); alternatively readings of refractive index could be converted to the freezing point directly by using conversion tables supplied by the American Optical Company.

IV. Tissue Respiration

The oxygen consumption of various tissues was measured by the direct method using a refrigerated Warburg

Manometer (by Precision Scientific Company). The organs and tissues studied were pyloric caecum, gonad, tube feet, stomach, body wall and coelomic fluid.

Following an adaptation period of 2-3 days, experimental sea stars were removed from the water tank, quickly blotted with a paper towel and weighed. A 5 cc disposable sterile syringe was used to withdraw coelomic fluid from the aboral side of a sea star, this coelomic fluid was then immediately filtered through fine gauze. Fresh tissues were cut freehand with a sharp razor blade or scissors, then gently blotted with a filter paper before being placed in Warburg flasks.

The calibration of the flasks (approximately 15 ml) and the manometers followed the procedure described in Hawk's Physiological Chemistry 14th edition, 1965. In the main compartment each flask contained 1 ml of coelomic fluid mixed with 2 ml of natural sea water as the medium, or freshly prepared tissue with 3 ml natural sea water. Natural sea water used as the medium in the flask was filtered through filter paper and sterilized by boiling and then adjusted to the original salinity by introducing distilled water. The center well of the flask contained 0.2 ml of 20% KOH solution and flared filter paper (Whatman No. 40), the top of which projected 1-2 mm above the rim of the center well so as to be better able to absorb carbon dioxide in the gas space of the flask.

After the tissues were placed in the flasks, the flasks and manometers were sealed with petroleum jelly and placed in a water bath with a thermal control accuracy of ±.02°C. The flasks and manometers were shaken for 10 minutes at a shaking amplitude of 120 oscillations per minute to allow temperature and pressure equilibrium. Measurements were made at 15-minute intervals for a minimum time period of two hours. Manometric determinations were at temperatures of 5°C and 15°C. Oxygen consumption was expressed in terms of µls per mg of wet weight per hour.

V. The Determination of Moving Speed and Righting Response Time of Sea Stars

The moving speed of sea stars was determined as follows: an arm of a sea star was held with the bare hand at a marked point on a smooth plastic substratum, then released, simultaneously stimulating the sea star with a needle. The moved distances were determined from the marked point to the spot reached by the same arm of the sea star in one minute. Only movements in a straight line direction were recorded. If the sea star moved in a zigzag or circular direction the data were discarded. Different sizes of sea stars were used in this study.

The procedure for determining righting response time was as follows: by using the bare hand a sea star was placed on a flat surface in the observation aquarium with the aboral side on the bottom of the aquarium. The righting response time of a sea star was measured as the sea star turned over with tube feet of all arms touching

the surface of the aquarium. Different sizes of sea stars were selected for the trial. Three righting methods were employed by both species and comparison of the righting time for both species were made, only applied to the same righting method. To determine the relationship between body weight and righting response time or moving speed, the results were subject to correlation and regression analyses, and student's t test.

VI. Labelled Amino Acid Uptake of Tissues at Different Temperatures

The sea stars were treated as described previously at temperatures of 0°C and 15°C and were not fed for two days prior to experimentation. Minced pyloric caeca (0.5 g) were incubated in 2 ml of filtered sea water containing 25λ of $C^{14}$ alanine (specific activity 175 mc/m mole, New England Nuclear Corporation) for three hours at the desired temperature. The reaction vessels were flushed with an oxygen:carbon dioxide (95:5) mixture every half an hour. The tissues were treated sequentially as follows: (1) Centrifugation at 5K for five minutes in a Beckman TJ6 centrifuge and the supernatant was discarded; (2) the tissue was washed twice with 2 ml of sea water containing 1 mg/ml alanine to remove any non-specific absorption of radioactive amino acid on the outer surface of the tissue; (3) after, the tissue was homogenized in 2 ml of sea water, an equal volume of 20% trichloroacetic

acid was added, and stirred to precipitate the proteins; (4) after 10 minutes at 5°C, the homogenate was centrifuged and the precipitate was washed twice with 10% trichloroacetic acid; (5) the precipitate was extracted with chloroform to remove lipids; (6) the precipitate was later dissolved in 2 ml of 0.5N NaOH with heating.

Radioactive incorporation was determined by pipetting an aliquot (50 µl) of the above solution into scintillation vials with 10 ml of Riaflour (New England Nuclear Corporation). The vials were cooled to 4°C in the dark for two hours and the radioactivity was determined on a Parkard Tri-carb liquid Scintillation Spectrometer.

Protein concentration of the solution was estimated in terms of absorbance at 280 nm using a UV spectrophotometer.

VII. Statistical Analysis

Multiple regressions were employed to analyze the data and regression lines were estimated by running Ordinary Least Squares using the Shazam computer package (White, 1978). This package reference provides a special feature including hypothesis testing on linear combination of coefficients (e.g., to test the hypothesis that $a - a' = 0$ for the intercepts and $b - b' = 0$ for the slopes).

Indicator variables which had no numerical scales (e.g., sex, species, etc.) were introduced to the model

and provide a flexible device to deal with the class in data. Separate regressions can be combined in one regression with indicator variables, and tests for comparing the regression function for different classes of indicator variable can be clearly seen on the tests of the regression coefficient in a general linear model. Indicator variables methods were described by several authors (Wesolowsky, 1976; Neter and Wasserman, 1974; etc.). Hypothetical example as follows a general regression model $Y_{ij}=a_{ij}+b_{ij}X_{ij}$ (i=1=A.v,# i=2=L.p##) (j=1=female, j=2=male) contains four separate regressions through classes

$Y_{11} = a_{11} + b_{11} X_{11}$ ..... for A.vulgaris (female)

$Y_{12} = a_{12} + b_{12} X_{12}$ ..... for A.vulgaris (male)

$Y_{21} = a_{21} + b_{21} X_{21}$ ..... for L.polaris (female)

$Y_{22} = a_{22} + b_{22} X_{22}$ ..... for L.polaris (male)

When all samples are pooled together a multiple linear regression with indicator variables method was derived. This will yield fitted regressions as described above. A multiple linear regression would be:

$$Y = a_{11} + b_{11} X + \sum_i \sum_j (a_{ij} - a_{11}) D_{ij} + \sum_i \sum_j (b_{ij} - b_{11}) D_{ij} X$$

where $i \neq 1$, and $j \neq 1$, $D_{ij}$ is defined as an indicator variable taking the value of 1 for the particular combination of species and sex, and zero otherwise. Hence a multiple linear regression in the following represents a detailed

#A.v denoted for Asterias vulgaris from now on.
##L.p denoted for Leptasterias polaris from now on.

model derived from the above.

$$Y = a_{11} + b_{11} X + (a_{12} - a_{11}) D_{12} + (b_{12} - b_{11}) D_{12} X + (a_{21} - a_{11}) D_{21} + (b_{21} - b_{11}) D_{21} X + (a_{22} - a_{11}) D_{22} + (b_{22} - b_{11}) D_{22} X$$

$Y_1 = a_{11} + b_{11} X$ .... for A.vulgaris (female)

$Y_2 = a_{11} + b_{11} X + (a_{12} - a_{11}) D_{12} + (b_{12} - b_{11}) D_{12} X$

when $D_{12} = 1$, 0 otherwise

.... for L.polaris (male)

$Y_3 = a_{11} + b_{11} X + (a_{21} - a_{11}) D_{21} + (b_{21} - b_{11}) D_{21} X$

when $D_{21} = 1$, 0 otherwise

.... for L.polaris (female)

$Y_4 = a_{11} + b_{11} X + (a_{22} - a_{11}) D_{22} + (b_{22} - b_{11}) D_{22} X$

when $D_{22} = 1$, 0 otherwise

.... for L.polaris (male)

Multiple comparison among means were based on the Student-Newman-Koul test (Sokal and Rohlf, 1969). The t-test was employed only for the difference between two means. The standard convention was followed in that levels of statistical significance for F values or t values were denoted significant with symbol * for the 5% level and N.S. for no significance.

## RESULTS AND DISCUSSION

### (1) & (2) The Effect of Temperature on Oxygen Consumption of Whole Specimens with Respect to Body Weight and Sex in Different Species

It is to be expected that oxygen consumption of the organisms will vary with body size. The total oxygen consumption (µl/animal/hr)# increases with body weight, but the rate of oxygen consumption (µl/g/hr) decreases with increasing body weight. Also, oxygen consumption of aquatic organisms is closely related to the water temperature. The oxygen consumption of sea stars like all poikilothermic organisms increases linearly with body weight when plotted on a double logarithmic grid. The relationship has been described as an exponential curve $Y = aX^b$ by many physiologists (Zeuthen, 1953; Prosser, 1961; Newell, 1970; etc.), where Y is oxygen consumption of brganism, X is body weight of organism, a is the intercept and b represents the slope. If b = 1 it means oxygen consumption of the organism increases directly proportional to the body weight; usually values may vary from 0.55 to 1. In the present study the relationship between body weight and oxygen consumption of sea stars was considered for the two species at four different temperatures, 0°C, 5°C, 10°C and 15°C. The Ordinary Least Square method was employed to fit logarithmic transformations of exponential curve. The

#Oxygen consumption refers to total oxygen consumption (µl/animal/hr.)

data show that the oxygen consumption of sea stars increases with body weight along a logarithmic line of slope ranged from 0.72 to 0.89 for A. vulgaris; and 0.75 to 0.92 for L. polaris.

Multiple regression analysis was used. The calculated equation for 0°C was expressed as follows by using OLS in the Shazam computer package:

Y = the expected $\log_e$(µl) oxygen consumption per hour

X = the $\log_e$ body weight in grams

$D_{ij}$ = indicator variable

$$i = \begin{cases} 1 = \text{A. vulgaris} \\ 2 = \text{L. polaris} \end{cases}$$

$$j = \begin{cases} 1 = \text{female} \\ 2 = \text{male} \end{cases}$$

$$\log_e Y = 2.9819 + 0.8189 \log_e X - \quad \text{...A.vulgaris (female)}$$
$$(0.0267)$$

$$0.2479D_{22} - 0.0567D_{22}\log_e X - \quad \text{...L.polaris (male)}$$
$$(0.1771) \quad (0.0399)$$

$$0.2495D_{12} + 0.0692D_{12}\log_e X - \quad \text{...A.vulgaris (male)}$$
$$(0.2223) \quad (0.0511)$$

$$0.6011D_{21} + 0.03669D_{21}\log_e X \quad \text{...L.polaris (female)}$$
$$(0.2453) \quad (0.0575)$$

Numbers in parentheses are standard error of estimations.

$R^2$ (coefficient of determination) = 0.9689.

Standard error of estimate = 0.1034.

Analysis of Variance

| | SS | DF | MS | F |
|---|---|---|---|---|
| Explained | 32.017 | 7 | 4.5738 | 427.649* |
| Unexplained | 1.0267 | 96 | 0.0107 | |
| Total | 33.044 | 103 | 0.3208 | |

Hypothesis Test: between intercepts; and regression coefficients.

| Hypothesis | t ratio | Hypothesis | t ratio |
|---|---|---|---|
| $a_{11} = a_{12}$ | -1.1224 (N.S.) | $b_{11} = b_{12}$ | 1.3526 (N.S.) |
| $a_{11} = a_{21}$ | 2.4501* | $b_{11} = b_{21}$ | 0.63859 (N.S.) |
| $a_{22} = a_{12}$ | 0.007 (N.S.) | $b_{22} = b_{12}$ | 2.385* |
| $a_{22} = a_{21}$ | 1.402 (N.S.) | $b_{22} = b_{21}$ | 1.585 (N.S.) |

significance level $p < 0.05$.

$\text{Log}_e Y = 2.9819 + 0.8189 \log_e X$ ... A. vulgaris (female)
(when $D_{22}=0$, $D_{12}=0$, $D_{21}=0$)

$\text{Log}_e Y = 2.734 + 0.7622 \log_e X$ ... L. polaris (male)
(when $D_{22}=1$; 0 otherwise)

$\text{Log}_e Y = 2.7324 + 0.8881 \log_e X$ ... A. vulgaris (male)
(when $D_{12}=1$; 0 otherwise)

$\text{Log}_e Y = 2.3708 + 0.8556 \log_e X$ ... L. polaris (female)
(when $D_{21}=1$; 0 otherwise)

} at 0°C indicated in Table 1

The same principal was applied to calculate the regression line for both sexes in both species at 5°C, 10°C and 15°C, as summarized in Table 1.

Table 1. Regression lines for oxygen consumption of sea stars under different temperature.

| | | 0°C | | 5°C | | 10°C | | 15°C | |
|---|---|---|---|---|---|---|---|---|---|
| | | $R^2$ = 0.9689 | | $R^2$ = 0.9334 | | $R^2$ = 0.9905 | | $R^2$ = 0.9596 | |
| | | SE = 0.1034 | | SE = 0.1216 | | SE = 0.0434 | | SE = 0.0913 | |
| | | F = 427.649* | | F = 206.316* | | F = 1506.09* | | F = 379.680* | |
| | | Intercept | Slope | Intercept | Slope | Intercept | Slope | Intercept | Slope |
| Species | Sex | $a_1$ | $b_1$ | $a_2$ | $b_2$ | $a_3$ | $b_3$ | $a_4$ | $b_4$ |
| A.vulgaris | Female | 2.9818 | 0.8189 (0.1022) | 3.6538 | 0.8010 (0.1375) | 3.8744 | 0.7833 (0.0495) | 4.2077 | 0.7742 (0.0678) |
| L.polaris | Male | 2.7340 | 0.7623 (0.1064) | 3.5908 | 0.7511 (0.1054) | 3.4572 | 0.8672 (0.0389) | 4.0059 | 0.8073 (0.0583) |
| A.vulgaris | Male | 2.7324 | 0.8882 (0.0970) | 3.9091 | 0.7342 (0.1346) | 3.8660 | 0.7820 (0.0453) | 4.4333 | 0.7231 (0.1009) |
| L.polaris | Female | 2.3708 | 0.8557 (0.0854) | 3.4405 | 0.7926 (0.0522) | 3.4111 | 0.8768 (0.0292) | 3.7992 | 0.8559 (0.0565) |

Numbers in brackets are standard error of estimates . $S_{\log x \cdot \log y}$

Table 2. Hypothesis Testing for Comparison of Intercepts and Slope between Sex and Species Under Different Temperature ($p < 0.05$).

| | 0°C | | 5°C | | 10°C | | 15°C | |
|---|---|---|---|---|---|---|---|---|
| Species and Sex | t ratio Intercepts a-a' | t ratio Slopes b-b' | t ratio Intercepts a-a' | t ratio Slopes b-b' | t ratio Intercepts a-a' | t ratio Slopes b-b' | t ratio Intercepts a-a' | t ratio Slopes b-b' |
| A.vulgaris female-A.vulgaris male | 0.2479(N.S.) | -0.0567(N.S.) | 0.234(N.S.) | 1.1682(N.S.) | -0.0958(N.S.) | 0.0641(N.S.) | 1.134(N.S.) | -1.0988(N.S. |
| A.vulgaris male-L.polaris male | 0.0070(N.S.) | -2.385* | -1.251(N.S.) | 0.284(N.S.) | -4.354* | 3.955* | 5.155* | 4.969* |
| A.vulgaris female-L.polaris female | -0.6011(N.S.) | 0.0367(N.S.) | -0.6169(N.S.) | -0.1019(N.S.) | -4.113* | 3.5772* | -1.5789(N.S.) | 1.3170(N.S.) |
| L.polaris male-L.polaris female | -1.402(N.S.) | -1.585(N.S.) | 0.4300(N.S.) | 0.4900(N.S.) | 0.362(N.S.) | 0.323(N.S.) | -1.063(N.S.) | 1.135(N.S.) |

Table 3. Hypothesis testing for comparison of intercepts and slopes between temperatures within the species ($p < 0.05$).

| | A.vulgaris | (female) | L.polaris | (male) | A.vulgaris | (male) | L.polaris | (female) |
|---|---|---|---|---|---|---|---|---|
| | t ratio | t ratio | t ratio | t ratio | t ratio | t ratio | t ratio | t ratio |
| | Intercepts | Slopes | Intercepts | Slopes | Intercepts | Slopes | Intercepts | Slopes |
| Temperature | a-a' | b-b' | a-a' | b-b' | a-a' | b-b' | a-a' | b-b' |
| 0°C-5°C | 3.5380* | -0.4148(N.S.) | 4.5636* | -0.2535(N.S.) | 4.8737* | -2.7648* | 5.3337* | -1.3213(N.S.) |
| 5°C-10°C | 1.007(N.S.) | 0.352(N.S.) | -0.609(N.S.) | -2.246* | 0.214(N.S.) | -1.047(N.S.) | 0.139(N.S.) | -1.671(N.S.) |
| 10°C-15°C | -1.423(N.S.) | 0.167(N.S.) | 0.431(N.S.) | 1.130(N.S.) | -2.856(N.S.) | 1.305(N.S.) | -1.897(N.S.) | 0.430(N.S.) |

Table 2 shows that the regression lines are not significantly different between sexes within the species at each temperature. Percy (1971) found that summer acclimatized sea urchins with slopes from 0.68 to 0.75, were slightly different from winter acclimatized ones with slope values ranging from 0.56 to 0.8, but he observed no significant differences within a species. However, the results in the present studies indicate that there are significant differences between species in slopes and/or intercepts.

Temperature had a greater effect on the slope in several cases of the male of both species only, but not the female in either species; slopes, therefore, are fairly constant. Intercepts show the greatest increase from $0^{\circ}C$ to $5^{\circ}C$, then level off at $10^{\circ}C$, and increase again at $15^{\circ}C$. In the case of the male of A. vulgaris, the slope was gradually decreased except at $10^{\circ}C$ where it increased instead. In the female of A. vulgaris, the slopes became less as temperature increased. Table 3 indicates that the slopes of the regression line in the male of A. vulgaris show a significant difference between $0^{\circ}C$ and $5^{\circ}C$ only. The slopes of the male in L. polaris seem to be quite constant as the temperature rises except at $5^{\circ}C$. Increments of intercept increase sharply at $0^{\circ}C$ and $5^{\circ}C$, then remain constant, while the slope in the male of L. polaris keep almost constant except at $5^{\circ}C$ where it is lower. Table 3 also shows that the slope of the regression line in the male of L. polaris significantly different between $5^{\circ}C$-$10^{\circ}C$ only.

Overall, the oxygen consumption of L. polaris is more dependent on body weight at higher temperature than at lower temperatures. Regression lines of oxygen consumption of whole sea stars rise from 0°C to 15°C and remain approximately parallel as shown in Fig. 2-5 for logarithmic transformations of exponential curves and Fig. 12-19 for non-log, transformations of exponential curves.

Fairly constant slopes were reported in some fish to represent the effect of body weight on oxygen consumption by some investigators (Job, 1954; Beamish, 1964). Fry (1957) pointed out that most species of fish showed a standard rate of oxygen consumption related to the body weight raised to a power of approximately 0.8. Certain species, however, have been found to conform to the surface area law. The relation of the standard rate of oxygen consumption to body size is essentially independent of temperature. Scholander et al. (1953) also showed the same proportionate response in oxygen consumption with increase in temperature for different size of insects, but Barlow (1961) recognized that values of the slope (b) may vary with temperature for several gobiids. He reported b values were higher in the range from 10°C to 17°C than in the range 21°C to 31°C. Newell (1970) (his personal communication with Barnes) reported that the effect of temperature on the log respiration rate/log body size regression line for Balanus showed different slopes at different temperatures. Some factors may alter b values, e.g., genetic

make-up, race, sex, growth nutrition state as pointed out by Hoar (1966). However, by reviewing the effects of food and temperature on the relation between metabolism and body weight in fish, Paloheimo and Dickie (1966a) concluded that the experimental evidence points strongly to a value of b of about 0.8 under natural conditions; they still know very little about the corresponding levels of metabolism. In the present study, L. polaris had a lower oxygen consumption compared to A. vulgaris over the entire measured temperature range except at 10°C and 15°C, where larger body sizes of L. polaris had higher oxygen consumption than A. vulgaris. Such differences could primarily be due to the differences in activity between the species. Vernberg and Vernberg (1970) studied the oxygen consumption in nine species of marine crabs; they concluded that active species had higher oxygen consumption than similar sizes of less active species.

Observations were carried out in the laboratory (Emerson, 1974) and it was found that feeding rates of A. vulgaris were much higher than those for L. polaris. The moving speed of A. vulgaris was also higher at 0°C and 15°C in spite of body weight. Occasionally if mussels were not supplied in time A. vulgaris would feed on L. polaris, which seems vulnerable to attack by A. vulgaris and Crossaster papposus (Linnaeus). My observations reveal that the frequency of A. vulgaris in moving from one area to another was higher than L. polaris. These activities

imply that A. vulgaris may require more energy to maintain their higher metabolic processes. $Q_{10}$ values in Table 4 clearly show that oxygen consumption of both species greatly increases between 0°C and 5°C. In the case of L. polaris $Q_{10}$ gradually decreases to 15°C, in other words, the smaller $Q_{10}$ values at higher temperature intervals in L. polaris agrees with the typical pattern of the biological processes (Prosser, 1973). The reduced $Q_{10}$ values at higher temperature could save energy, but $Q_{10}$ values of A. vulgaris were higher at temperatures of 10°C-15°C. This could be explained under optimal temperature, the activities would increase and contribute to higher $Q_{10}$. Scholander et al. (1953) suggested that there seem to be three main possible avenues along which homeostatic adaptation of the metabolic rate might occur: (1) by parallel displacement of the metabolic-temperature curve with maintenance of normal temperature sensitivity; (2) by a low $Q_{10}$, whereby the overall temperature sensitivity is low; and (3) by selection of a constant environment. Based on metabolic-temperature curves of a number of unrelated species of Arctic and tropic poikilotherms, they concluded that in no case had it been shown that organisms were adapted to fluctuations in temperature by having a low respiratory $Q_{10}$, by being metabolically insensitive to temperature change. It seems to be that the metabolic-temperature curve displacement and lower respiratory $Q_{10}$ did not fit into the present series, therefore the selection of a microclimate is the most reliable way. Relation

between body weight of sea stars and $Q_{10}$ are quite complex as shown in Fig. 6, but there is a tendency for $Q_{10}$ values to decline with increasing body weight except in the male of L. polaris between 5°C and 10°C; between 10°C and 15°C; in the female of L. polaris between 5°C and 10°C; and in the male of A. vulgaris between 5°C and 10°C. Rao and Bullock (1954) reviewed $Q_{10}$ with relation to body size and habitat temperature in poikilotherms. They postulated that $Q_{10}$ may increase with body size but they also cautiously stated that this may not be necessarily always true. However, Percy (1971) in his study of sea urchins, showed some irregularity. Newell (1970, personal communication with Barnes) indicated a decreased $Q_{10}$ value with an increase in size in barnacles. The present study agrees with Percy and Newell's observations and also showed some irregularities. The temperature sensitivity of oxygen consumption in L. polaris and A. vulgaris as shown in Fig. 7 indicates the curves of L. polaris are not displaced to the left of that for A. vulgaris. Also, both sexes of A. vulgaris have lower $Q_{10}$ than those for L. polaris. Unfortunately, there is no evidence that A. vulgaris inhabits more stable thermal regions.

Fig. 2

Regression lines of oxygen consumption on body weight at $0^{\circ}C$, $5^{\circ}C$, $10^{\circ}C$ and $15^{\circ}C$ for the female of Asterias vulgaris (from Table 1).

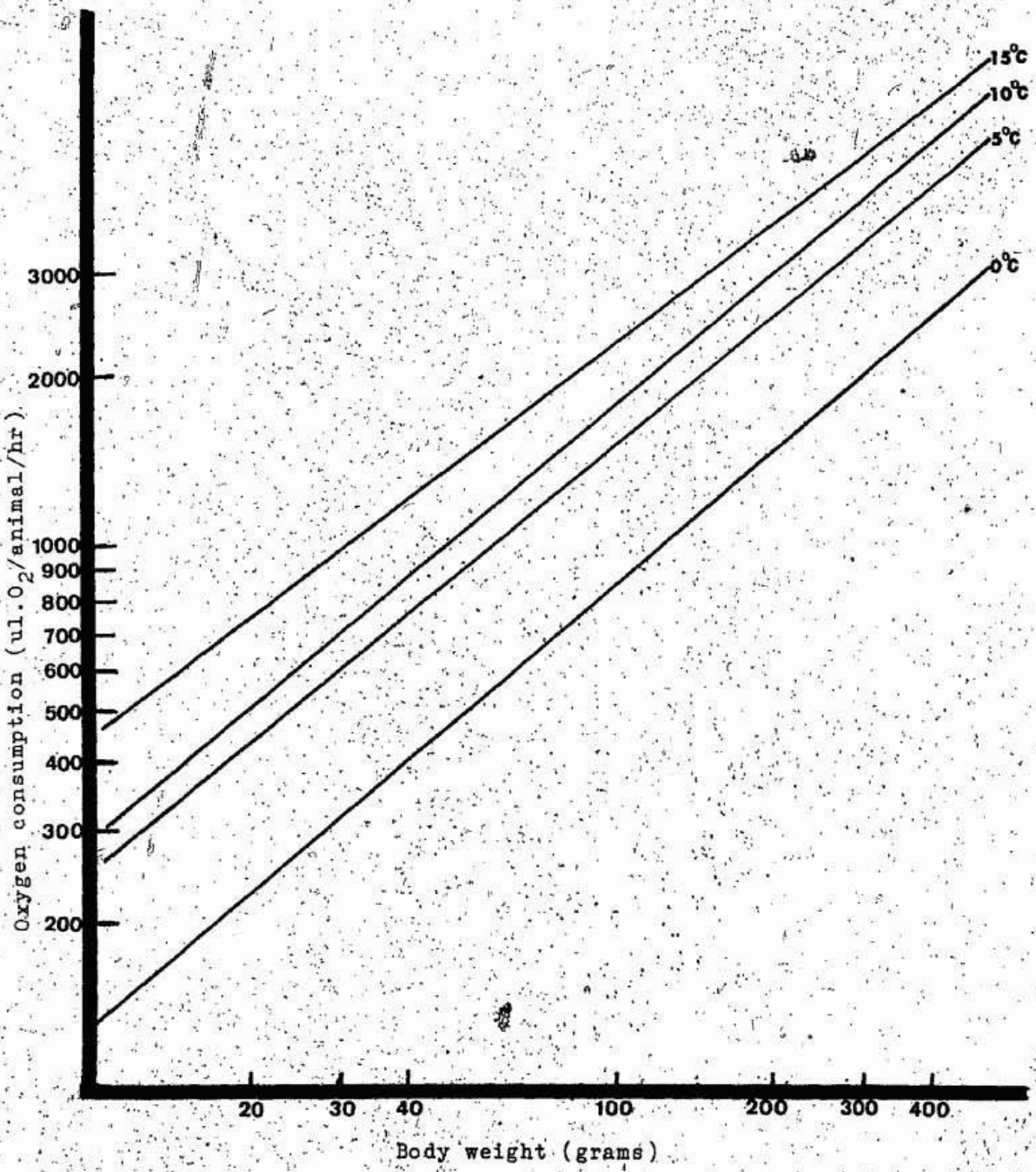

15°c
10°c
5°c
0°c
3000
2000
1000
900
800
700
600
500
400
300
200
Oxygen consumption (ul.$O_2$/animal/hr)
20
30
40
100
200
300
400
Body weight (grams)

Fig. 3

Regression lines of oxygen consumption on body weight at 0°C, 5°C, 10°C and 15°C for the female of Leptasterias polaris (from Table 1).

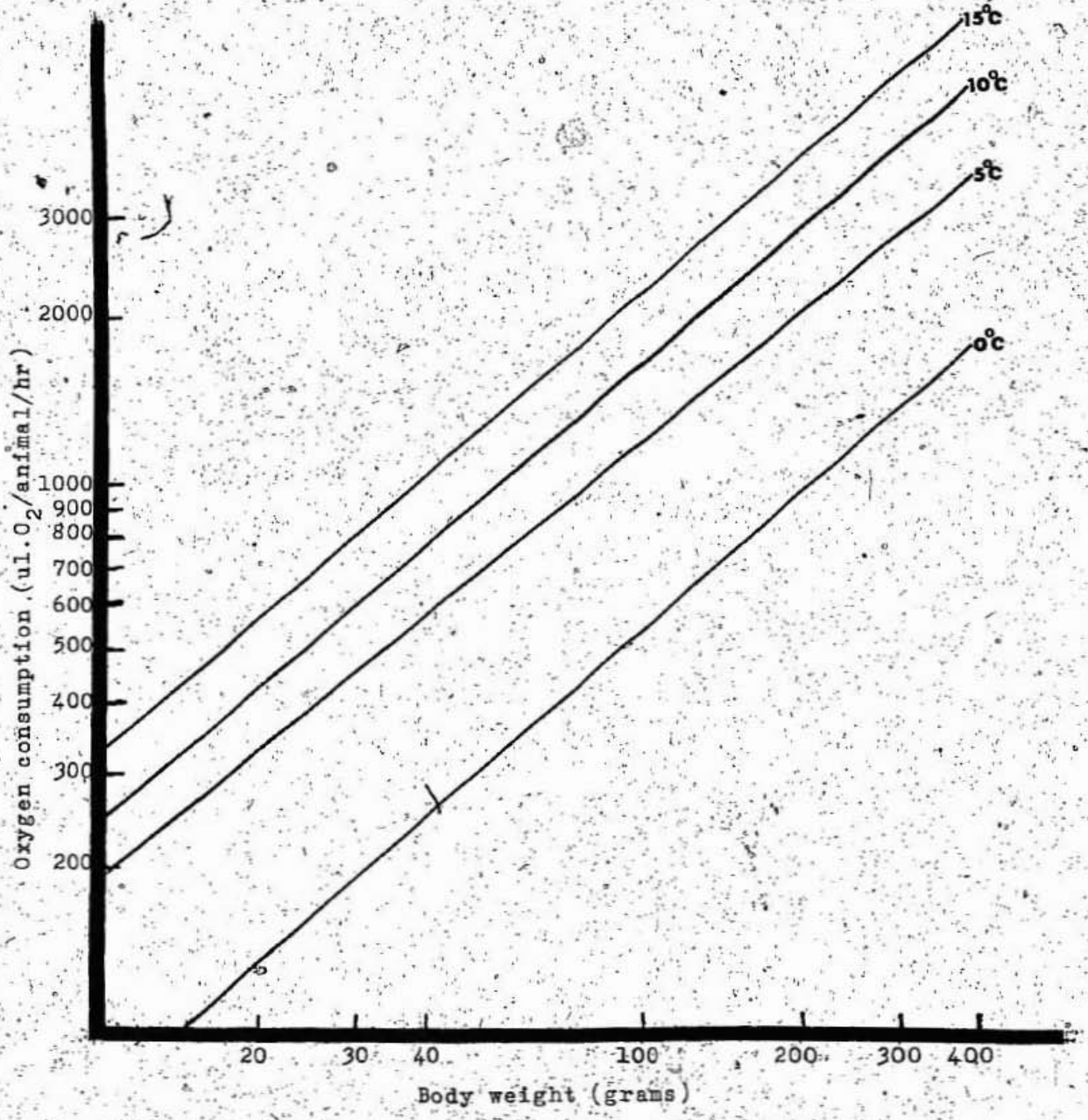

15°c
10°c
5°c
0°c
3000
2000
1000
900
800
700
600
500
400
300
200
Oxygen consumption (ul.$O_2$/animal/hr)
20
30
40
100
200
300
400
Body weight (grams)

Fig. 4

Regression lines of oxygen consumption on body weight at 0°C, 5°C, 10°C and 15°C for the male of Leptasterias polaris (from Table 1).

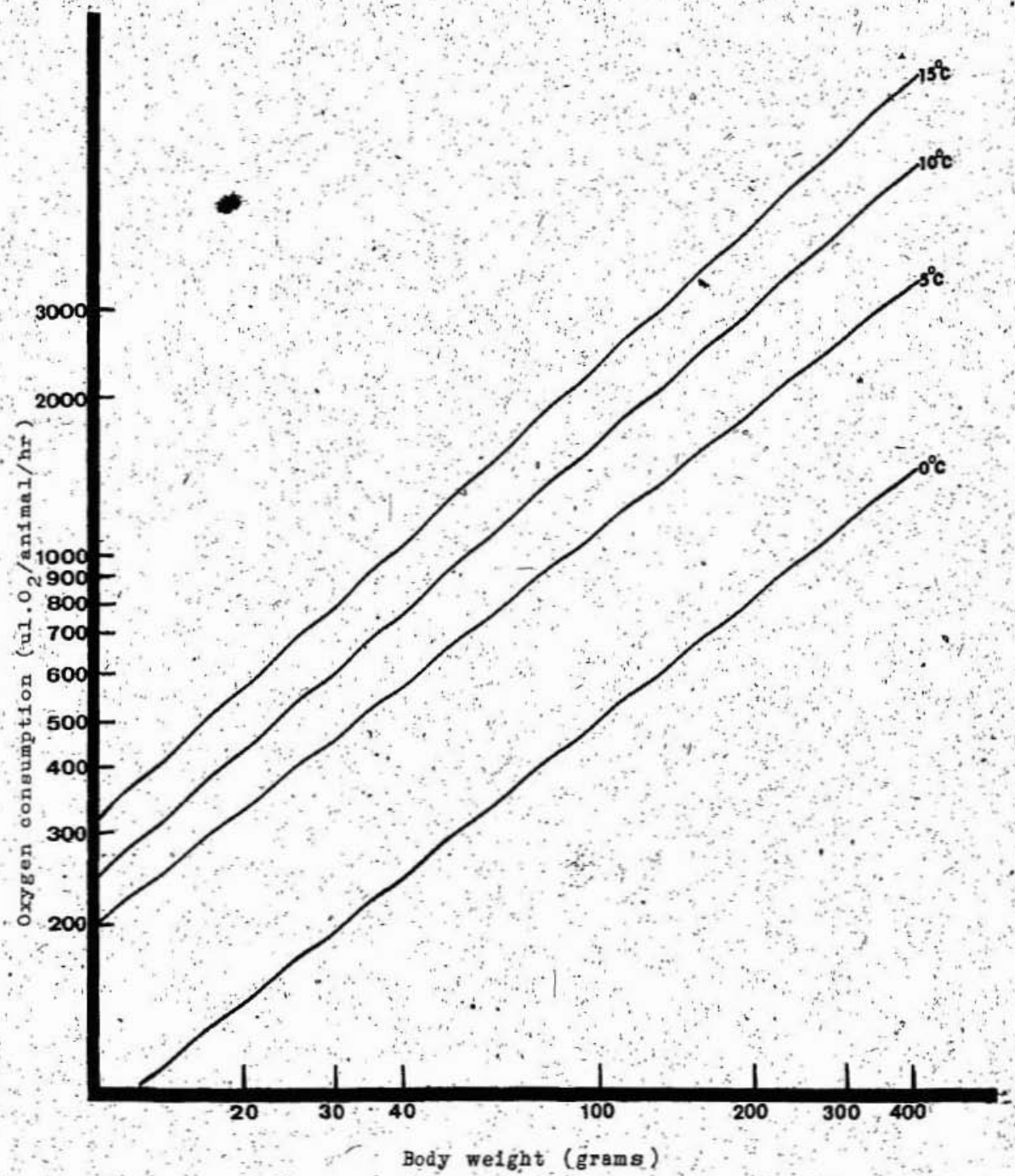

15°C
10°C
5°C
0°C
3000
2000
1000
900
800
700
600
500
400
300
200
Oxygen consumption (ul.O2/animal/hr)
20
30
40
100
200
300
400
Body weight (grams)

Fig. 5

Regression lines of oxygen consumption on body weight at 0°C, 5°C, 10°C and 15°C for the male of Asterias vulgaris (from Table 1).

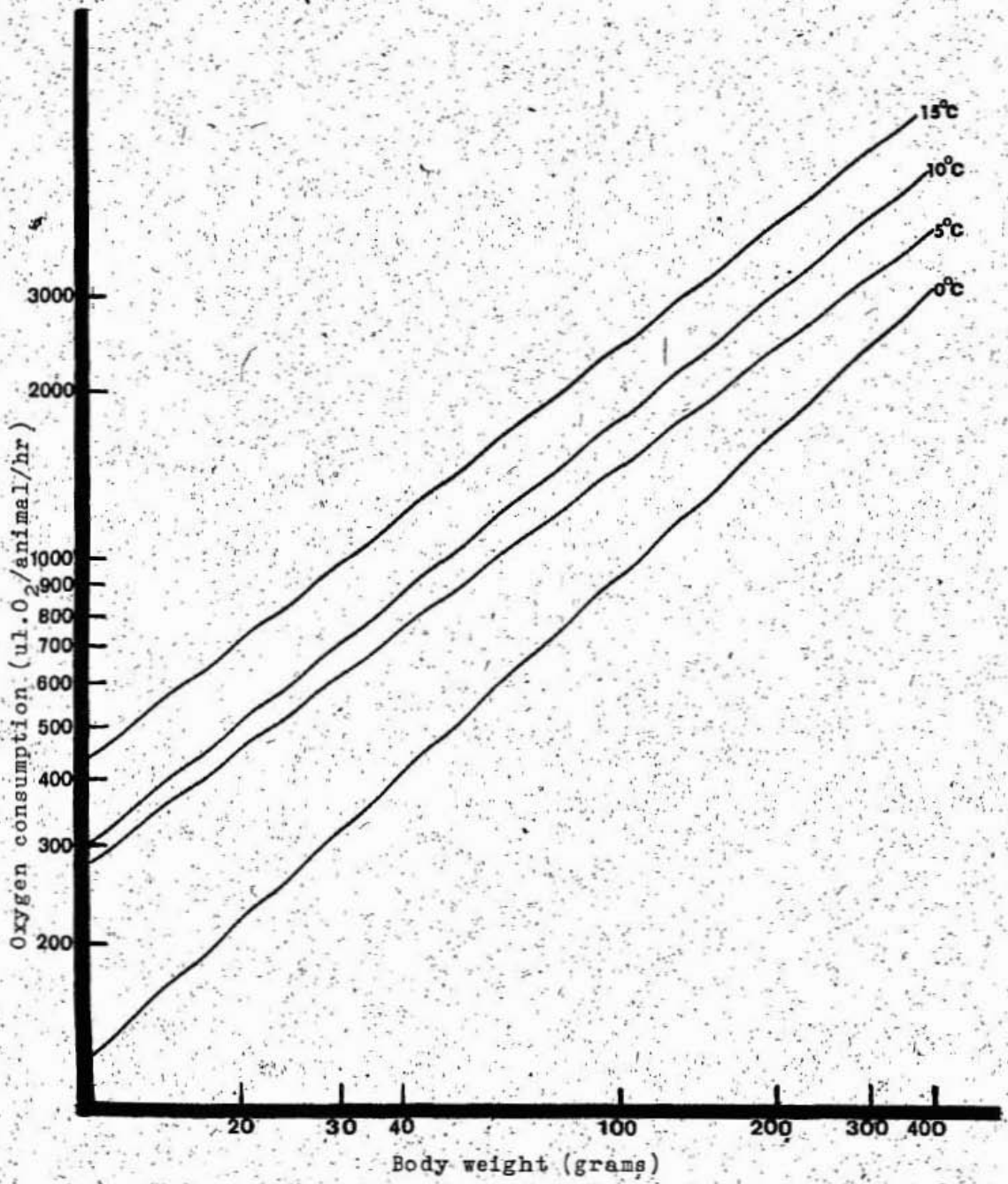

15°c
10°c
5°c
0°c
3000
2000
1000
900
800
700
600
500
400
300
200
Oxygen consumption (ul.$O_2$/animal/hr)
20
30
40
100
200
300
400
Body weight (grams)

Table 4. $Q_{10}$ values.

| Species | Sex | Body Wt. | Temperature 0°C-5°C | Temperature 5°C-10°C | Temperature 10°C-15°C |
|---|---|---|---|---|---|
| A.vulgaris | female | 40g | 3.35 | 1.36 | 1.82 |
| | | 80g | 3.28 | 1.32 | 1.80 |
| | | 120g | 3.23 | 1.32 | 1.78 |
| | | 160g | 3.20 | 1.30 | 1.77 |
| | | 200g | 3.17 | 1.29 | 1.77 |
| L.polaris | male | 40g | 5.11 | 1.80 | 1.77 |
| | | 80g | 5.04 | 2.11 | 1.90 |
| | | 120g | 5.00 | 2.33 | 1.96 |
| | | 160g | 4.97 | 2.49 | 2.06 |
| | | 200g | 4.93 | 2.62 | 2.11 |
| A.vulgaris | male | 40g | 3.35 | 1.30 | 2.01 |
| | | 80g | 2.72 | 1.39 | 1.85 |
| | | 120g | 2.41 | 1.45 | 1.77 |
| | | 160g | 2.20 | 1.49 | 1.71 |
| | | 200g | 2.06 | 1.52 | 1.67 |
| L.polaris | female | 40g | 5.34 | 1.77 | 1.85 |
| | | 80g | 4.88 | 1.96 | 1.82 |
| | | 120g | 4.65 | 2.11 | 1.78 |
| | | 160g | 4.48 | 2.22 | 1.76 |
| | | 200g | 4.36 | 2.30 | 1.74 |

Fig. 6

The effect of body weight, sex, and temperature on $Q_{10}$ coefficient for the respiration of *Asterias vulgaris* and *Leptasterias polaris*.

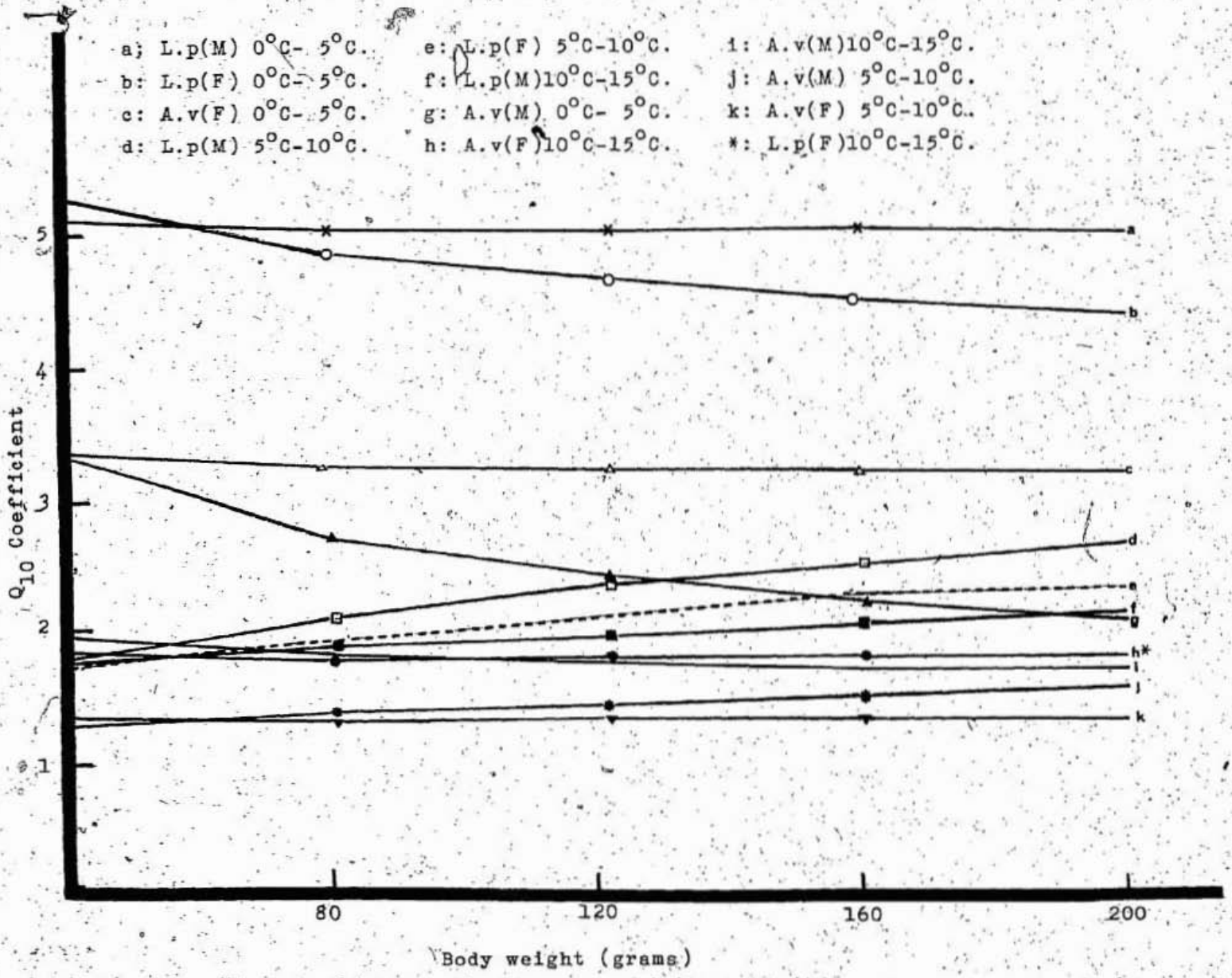
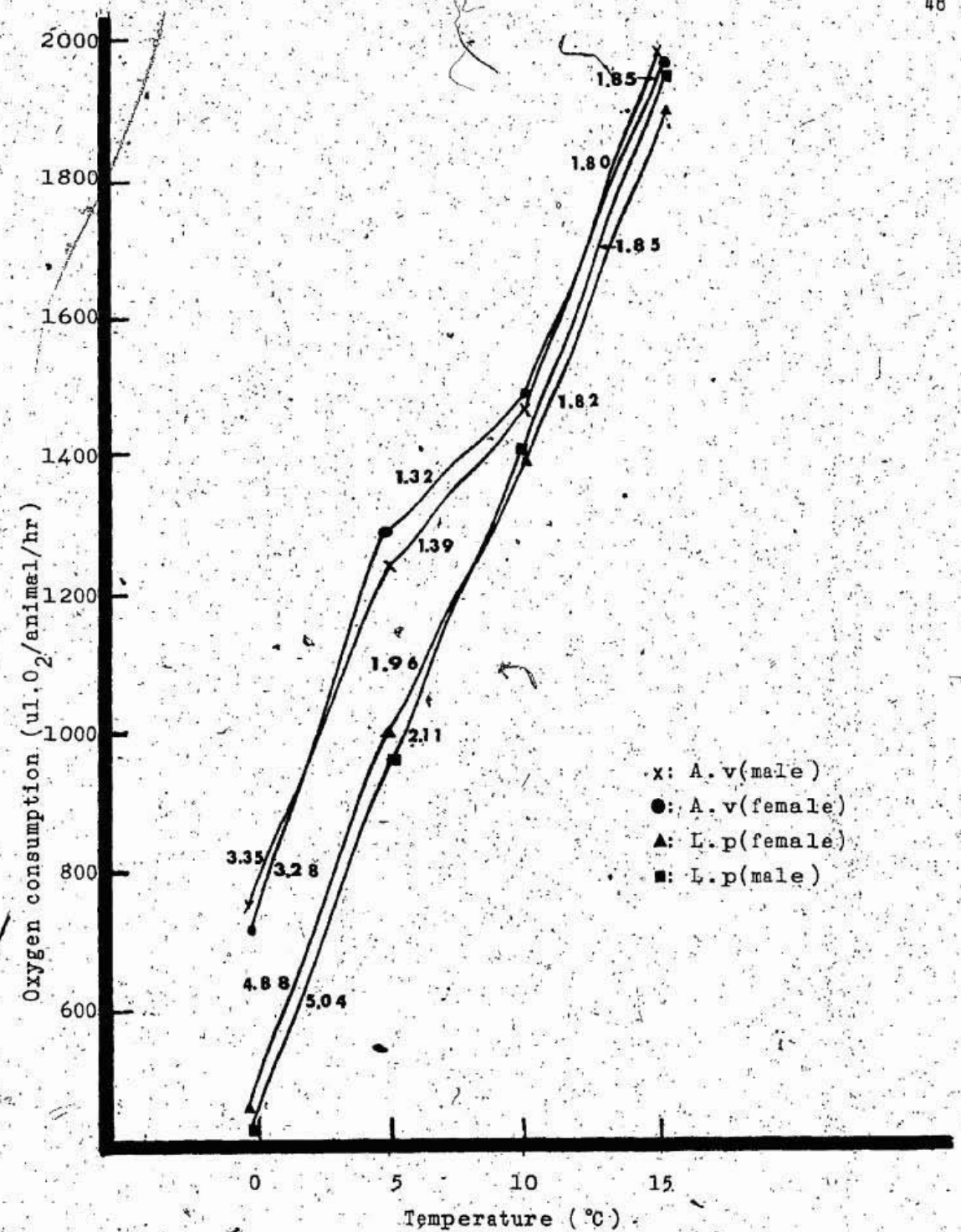

a; L.p(M) 0°C- 5°C.
b: L.p(F) 0°C- 5°C.
c: A.v(F) 0°C- 5°C.
d: L.p(M) 5°C-10°C.
e: L.p(F) 5°C-10°C.
f: L.p(M)10°C-15°C.
g: A.v(M) 0°C- 5°C.
h: A.v(F)10°C-15°C.
i: A.v(M)10°C-15°C.
j: A.v(M) 5°C-10°C.
k: A.v(F) 5°C-10°C.
*: L.p(F)10°C-15°C.
Q10 Coefficient
1
2
3
4
5
80
120
160
200
Body weight (grams)

Fig. 7

Temperature sensitivity of oxygen consumption in both sexes of *Leptasterias polaris* and *Asterias vulgaris* (based on specimens of the 80 g sea stars). $Q_{10}$ values given for each temperature interval.


2000
1800
1600
1400
1200
1000
800
600
Oxygen consumption (ul. $O_2$/animal/hr)
0
5
10
15
Temperature (℃)
1.85
1.80
1.85
1.82
1.32
1.39
1.96
2.11
3.35
3.28
4.88
5.04
x: A.v(male)
●: A.v(female)
▲: L.p(female)
■: L.p(male)

Recently, many physiologists employed multiple linear regression to relate respiration rate to several independent variables, e.g., body weight, temperature, or oxygen content in water, etc. (Wohlschlag, 1967; Percy, 1971; May, 1972; etc.). Therefore the results for the above were also treated in the form as follows:

$$\text{Log}_e Y = a_{11} + b_{11}\log_e X + c_{11}T + \sum\sum_{ij}(a_{ij}-a_{11})D_{ij}$$

$$+ \sum\sum_{ij}(b_{ij}-b_{11})D_{ij}\log_e X + \sum\sum_{ij}(c_{ij}-c_{11})D_{ij}T$$

or

$$\text{Log}_e Y = a_{11} + b_{11}\log_e X + c_{11}T +$$

$$(a_{12}-a_{11})D_{12} + (b_{12}-b_{11})D_{12}\log_e X + (c_{12}-c_{11})D_{12}T +$$

$$(a_{21}-a_{11})D_{21} + (b_{21}-b_{11})D_{21}\log_e X + (c_{21}-c_{11})D_{21}T +$$

$$(a_{22}-a_{11})D_{22} + (b_{22}-b_{11})D_{22}\log_e X + (c_{22}-c_{11})D_{22}T$$

here Y = the expected $\log_e$ µl oxygen consumption per animal

X = the $\log_e$ weight in grams

T = temperature (°C)

$D_{ij}$ = indicator variables

$a_{ij}$; $b_{ij}$; $c_{ij}$ are regression coefficients

i = species { 1 = A. vulgarus; 2 = L. polaris }

j = sex { 1 = female; 2 = male }

The calculated equation was expressed as follows by Shazam computer package:

$$\underset{(0.0239)}{\text{Log}_e\ Y = 3.1671 + 0.7975\ \log_e X} \underset{(0.0026)}{+ 0.0666T} \quad \ldots \underline{A.vulgaris}\ (\text{female})$$

$$\underset{(0.1503)}{-0.4366D_{22}} \underset{(0.0338)}{+0.0008D_{22}\log_e} \underset{(0.0035)}{X + 0.0284D_{22}T} \ldots \underline{L.polaris}\ (\text{male})$$

$$\underset{(0.1535)}{+0.1530D_{12}} \underset{(0.0344)}{-0.0234D_{12}\log_e} \underset{(0.0035)}{X - 0.0057D_{12}T} \ldots \underline{A.vulgaris}\ (\text{male})$$

$$\underset{(0.2009)}{-0.5528D_{21}} \underset{(0.0467)}{+0.0385D_{21}\log_e} \underset{(0.0038)}{X + 0.0241D_{21}T} \ldots \underline{L.polaris}\ (\text{female})$$

Numbers in parentheses are standard error of estimations

$R^2 = 0.8856$ Standard error of estimate = 4.885

Analysis of Variance

| | SS | DF | MS | F |
|---|---|---|---|---|
| Explained | 171.08 | 11 | 15.553 | 704.544* |
| Unexplained | 9.5366 | 432 | 0.0221 | |
| Total | 180.62 | 443 | 0.4077 | |

Hypothesis Test: between intercepts and regression coefficients

| Hypothesis | t ratio | Hypothesis | t ratio | Hypothesis | t ratio |
|---|---|---|---|---|---|
| $a_{11}=a_{12}$ | 0.9977(NS) | $b_{11}=b_{12}$ | -0.6798(NS) | $c_{11}=c_{12}$ | -1.6286(NS) |
| $a_{11}=a_{21}$ | -2.7512* | $b_{11}=b_{21}$ | 0.8245(NS) | $c_{11}=c_{21}$ | 6.3505* |
| $a_{22}=a_{12}$ | -3.887* | $b_{22}=b_{12}$ | 0.704(NS) | $c_{22}=c_{12}$ | 10.007* |
| $a_{22}=a_{21}$ | 0.582(NS) | $b_{22}=b_{21}$ | -0.808(NS) | $c_{22}=c_{21}$ | 1.142(NS) |

$\log_e Y = 3.1671 + 0.7975 \log_e X + 0.066T$ ...A. vulgaris (female)(1)'

(when $D_{22}=0$, $D_{12}=0$, $D_{21}=0$)

$\log_e Y = 2.7305 + 0.7983 \log_e X + 0.095T$ ...L. polaris (male)(2)'

(when $D_{22}=1$; 0 otherwise)

$\log_e Y = 3.3201 + 0.7741 \log_e X + 0.0609T$ ...A. vulgaris (male)(3)'

(when $D_{12}=1$; 0 otherwise)

$\log_e Y = 2.6143 + 0.836 \log_e X + 0.0907T$ ...L. polaris (female)(4)'

(when $D_{21}=1$; 0 otherwise)

Regression lines in Figs. 8, 9, 10 and 11 are based on the above equations (1)', (2)', (3)' and (4)'. This provided poor fit because the interaction between temperature body weight effect is not considered in the model. Secondly, if $T \leq 0^{\circ}C$, log T would be meaningless unless °Kelvin is used instead. The data showed that the oxygen consumption increased with body weight along a logarithmic line of slope range from 0.77 to 0.79 for A. vulgaris and 0.79 to 0.84 for L. polaris within the temperature range from 0°C to 15°C. There are significant differences between species, but not sexes within the species, and regression lines are not parallel. However, this method only provided a rough estimation.

Fig. 8

Regression lines of oxygen consumption of the female of Asterias vulgaris under different temperature (based on equation (1)').

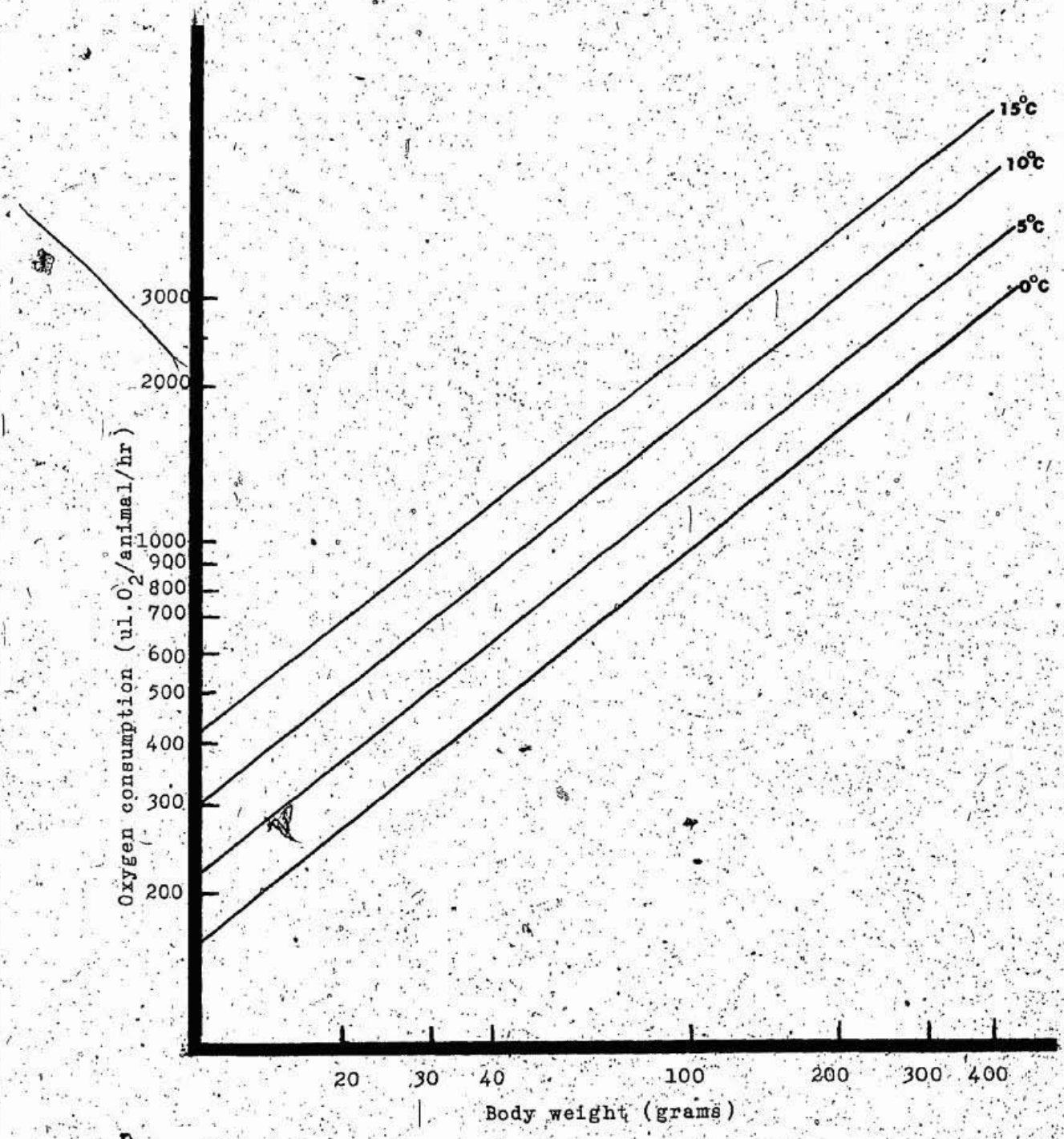

15°c
10°c
5°c
0°c
3000
2000
1000
900
800
700
600
500
400
300
200
Oxygen consumption (ul.$O_2$/animal/hr)
20
30
40
100
200
300
400
Body weight (grams)

Fig. 9

Regression lines of oxygen consumption of the male of Leptasterias polaris under different temperatures (based on equation (2)').

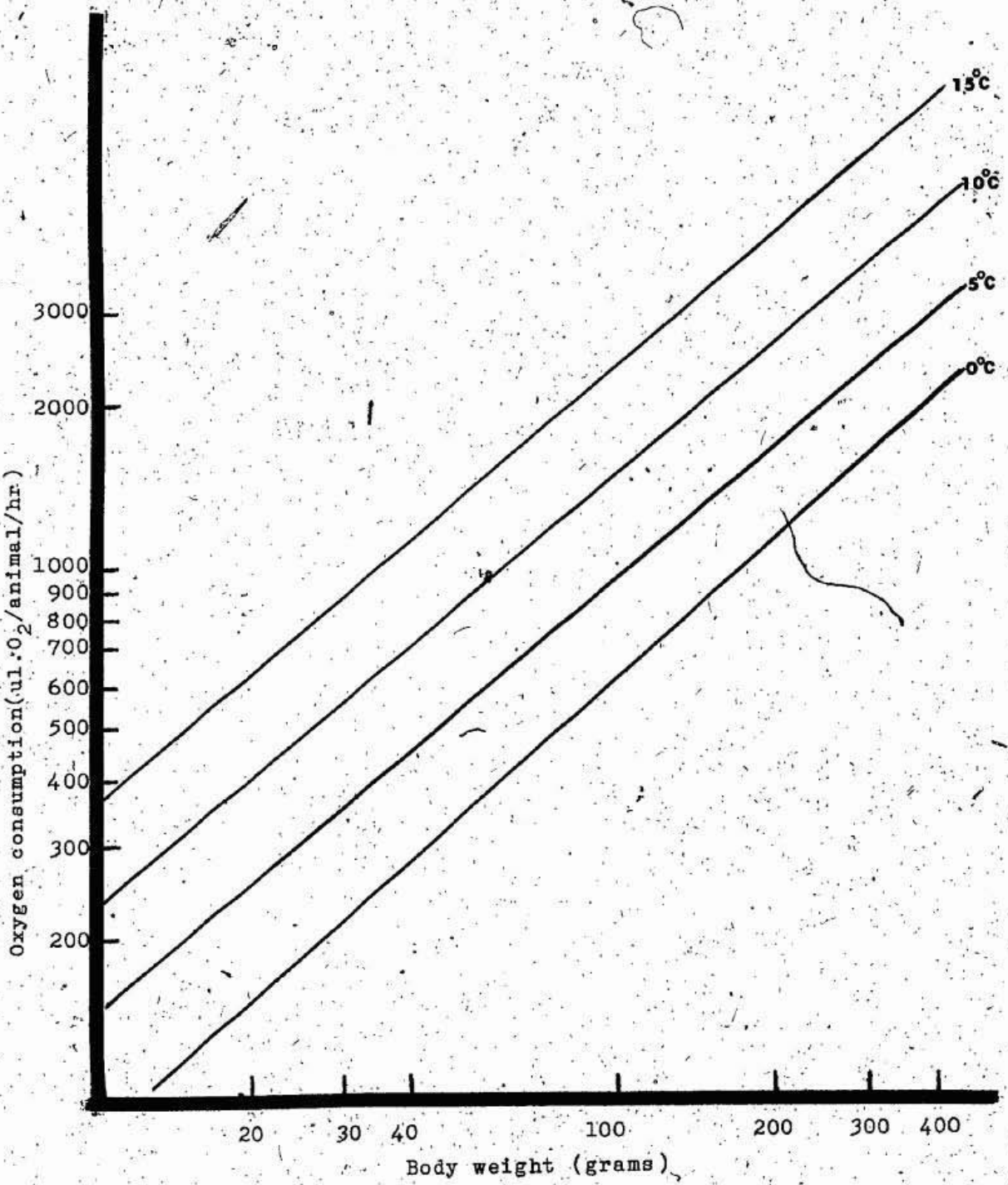

15°C
10°C
5°C
0°C
3000
2000
1000
900
800
700
600
500
400
300
200
Oxygen consumption(ul.$O_2$/animal/hr)
20
30
40
100
200
300
400
Body weight (grams)

Fig. 10

Regression lines of oxygen consumption of the female of Leptasterias polaris under different temperature (based on equation (4)').

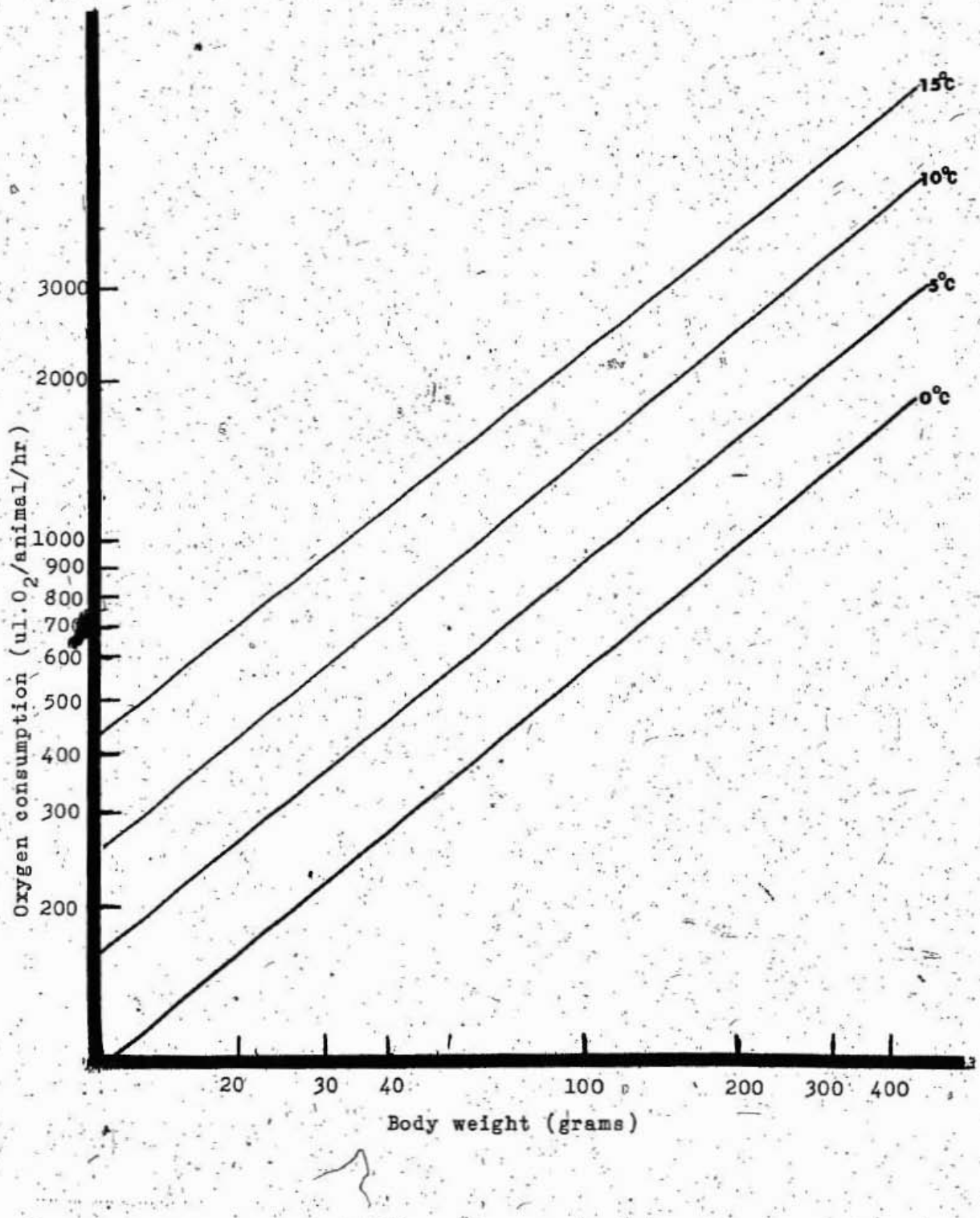

15°c
10°c
5°c
0°c
3000
2000
1000
900
800
700
600
500
400
300
200
Oxygen consumption (ul.$O_2$/animal/hr)
20
30
40
100
200
300
400
Body weight (grams)

Fig. 11

Regression lines of oxygen consumption of the male of *Asterias vulgaris* under different temperatures (based on equation (3)').

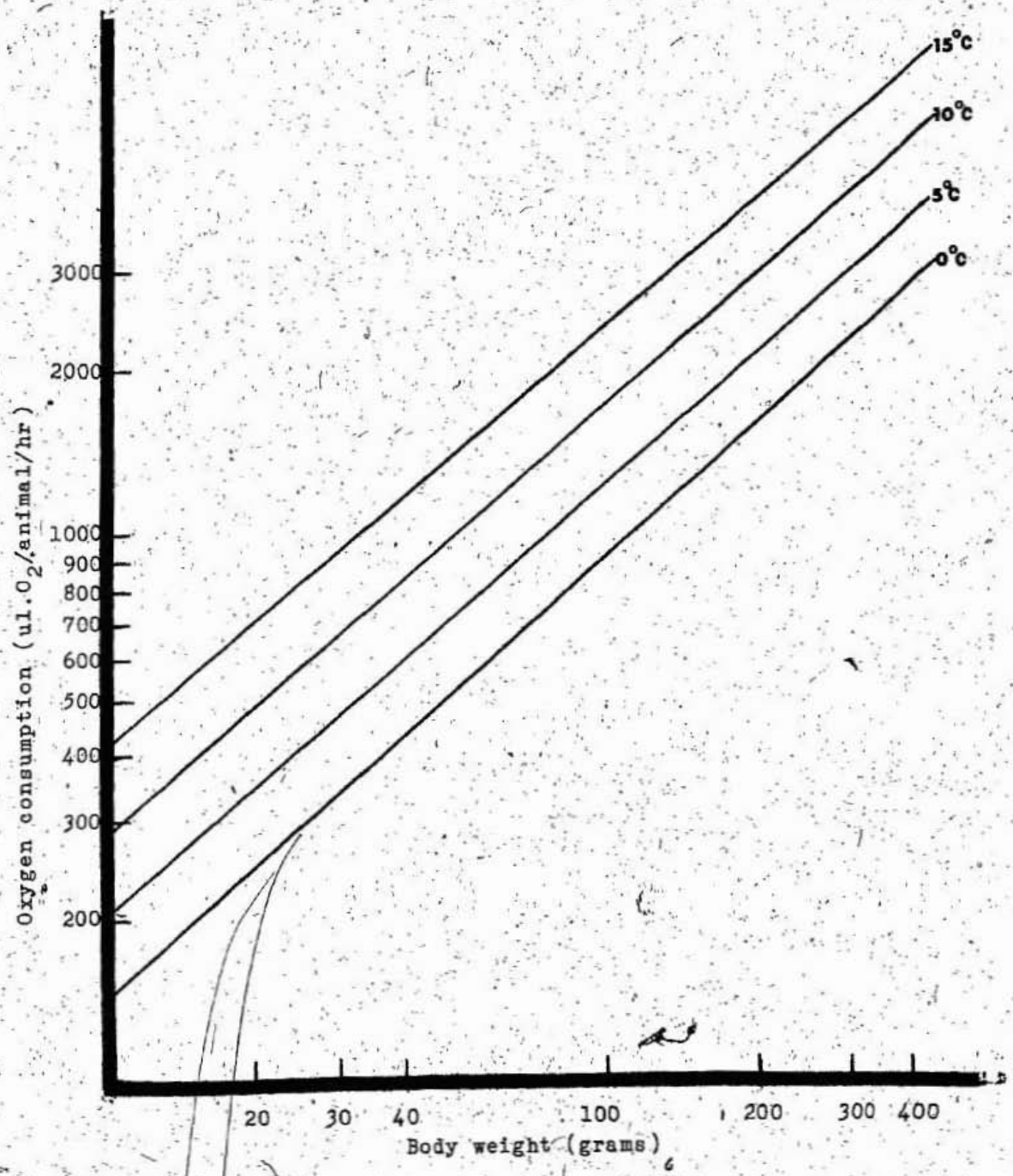
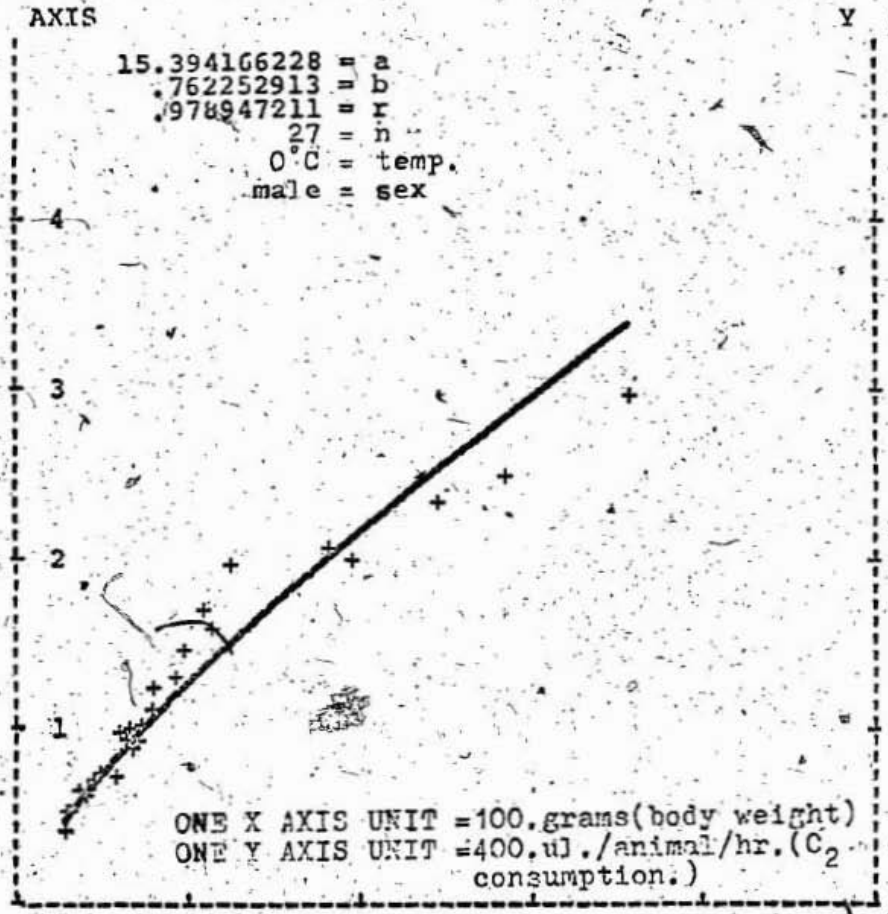

15°c
10°c
5°c
0°c
3000
2000
1000
900
800
700
600
500
400
300
200
Oxygen consumption (ul.$O_2$/animal/hr)
20
30
40
100
200
300
400
Body weight (grams)

Fig. 12

Regression lines of oxygen consumption on body weight at 0°C for Leptasterias polaris.

LEAST SQUARE FIT - POWER CURVE ($y = ax^b$)



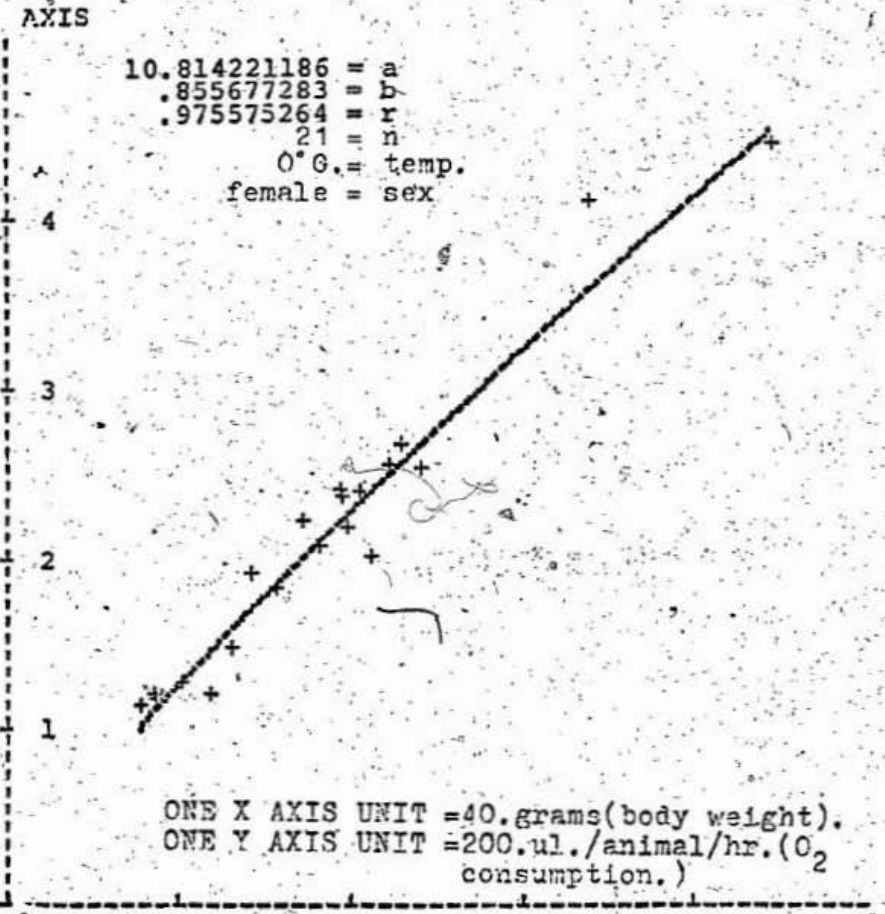
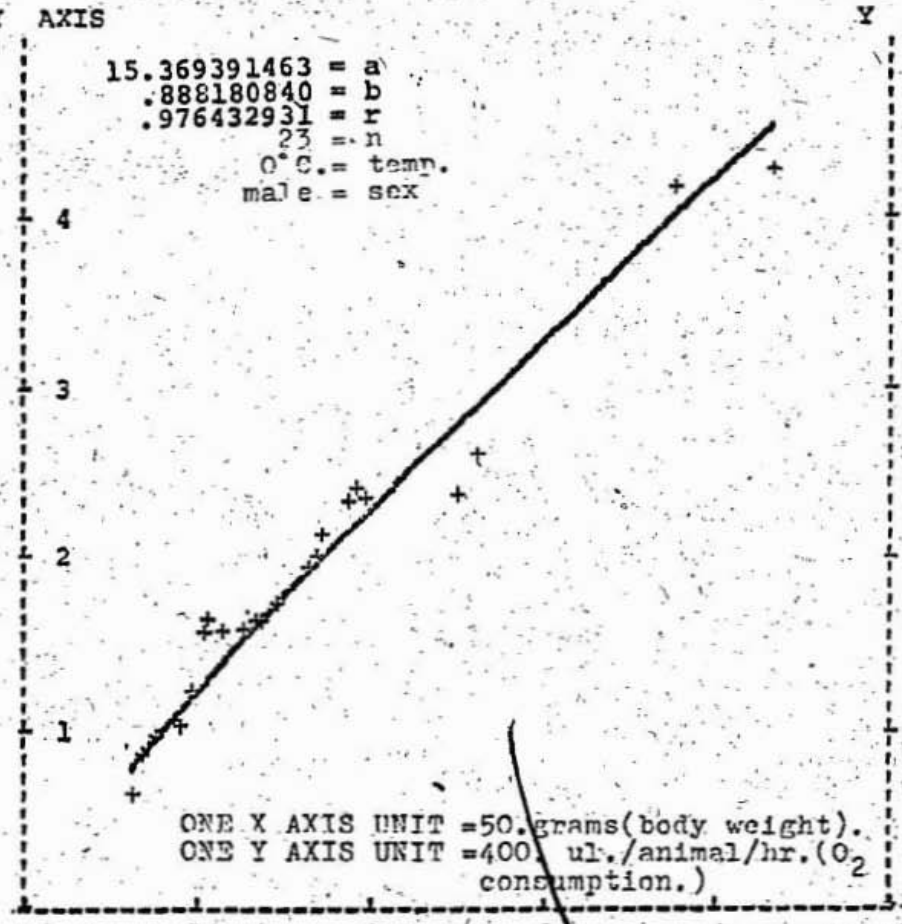



Fig. 13

Regression lines of oxygen consumption on body weight at $0^{\circ}C$ for Asterias vulgaris.

LEAST SQUARE FIT - POWER CURVE ($y = ax^b$)



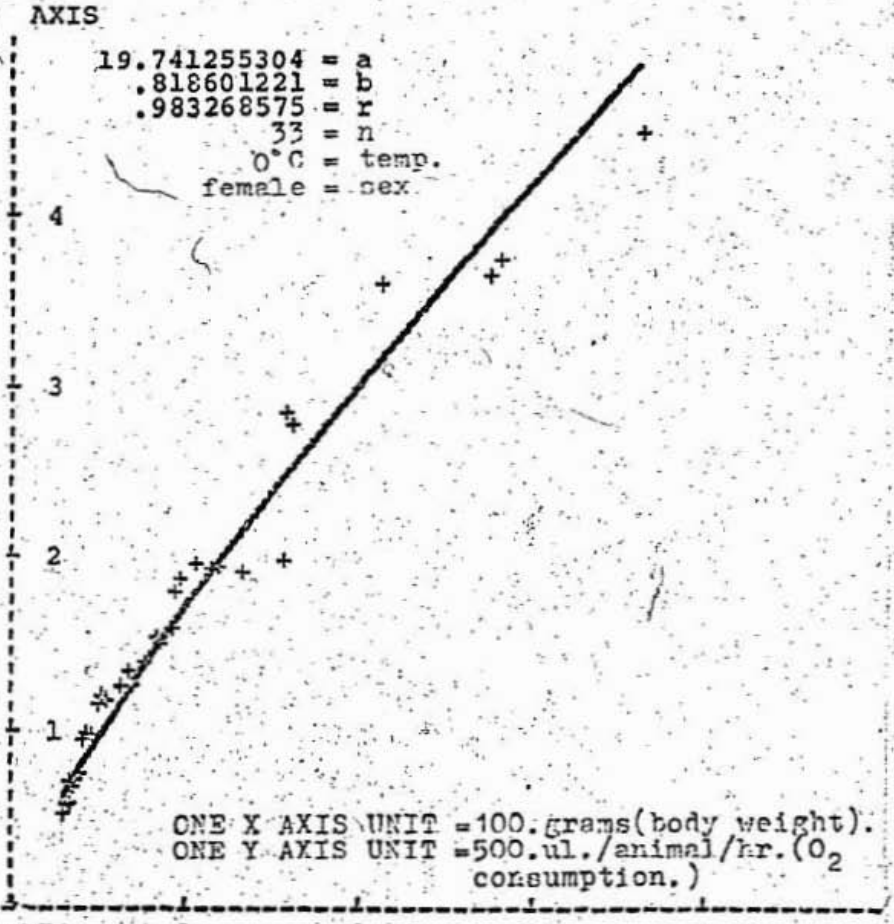



Fig. 14.

Regression lines of oxygen consumption on body weight at 5°C for *Leptasterias polaris*.

LEAST SQUARE FIT - POWER CURVE ($y = ax^b$)

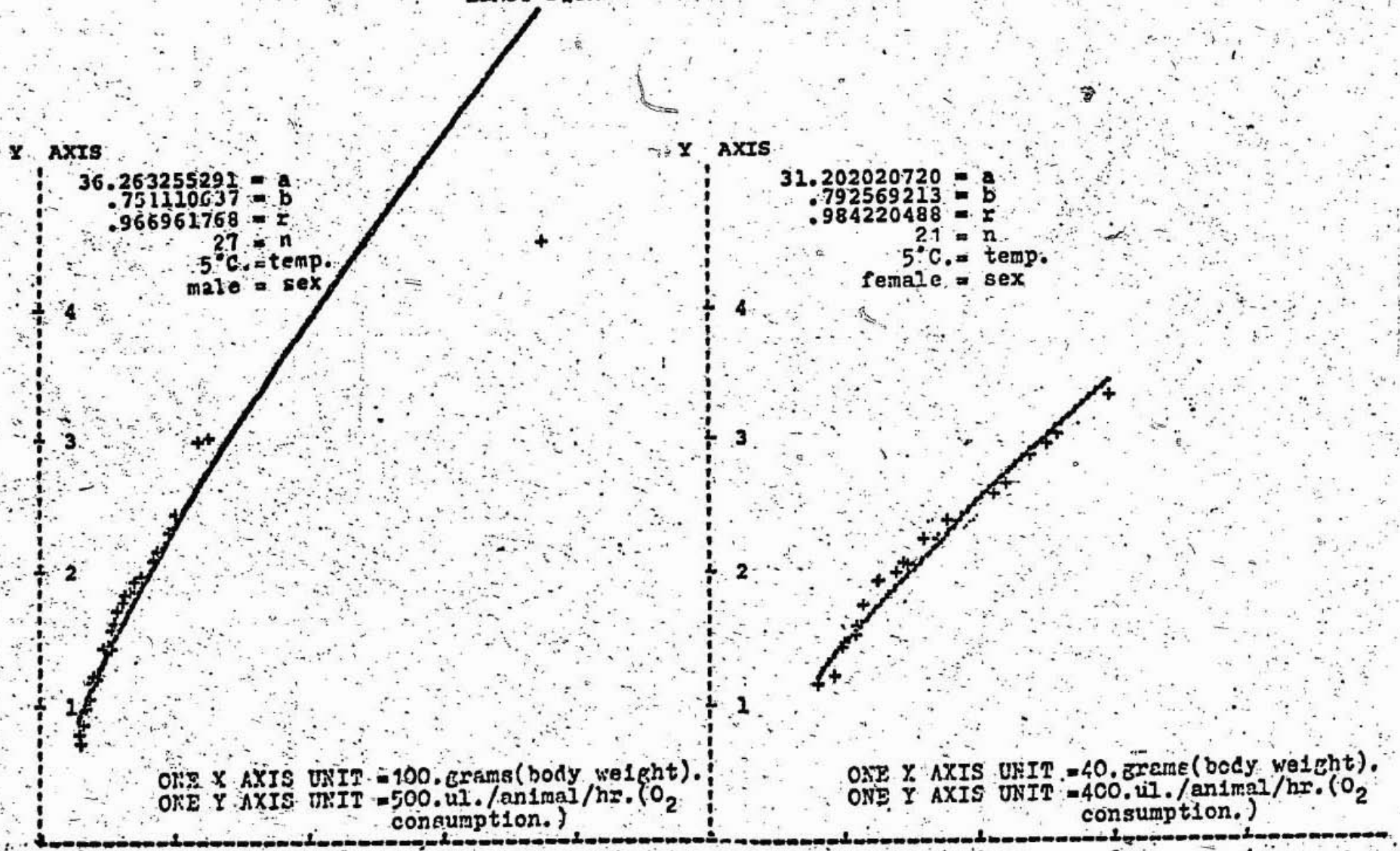


Fig. 15

Regression lines of oxygen consumption on body weight at $5^{o}C$ for Asterias vulgaris.

LEAST SQUARE FIT - POWER CURVE ($y = ax^b$)

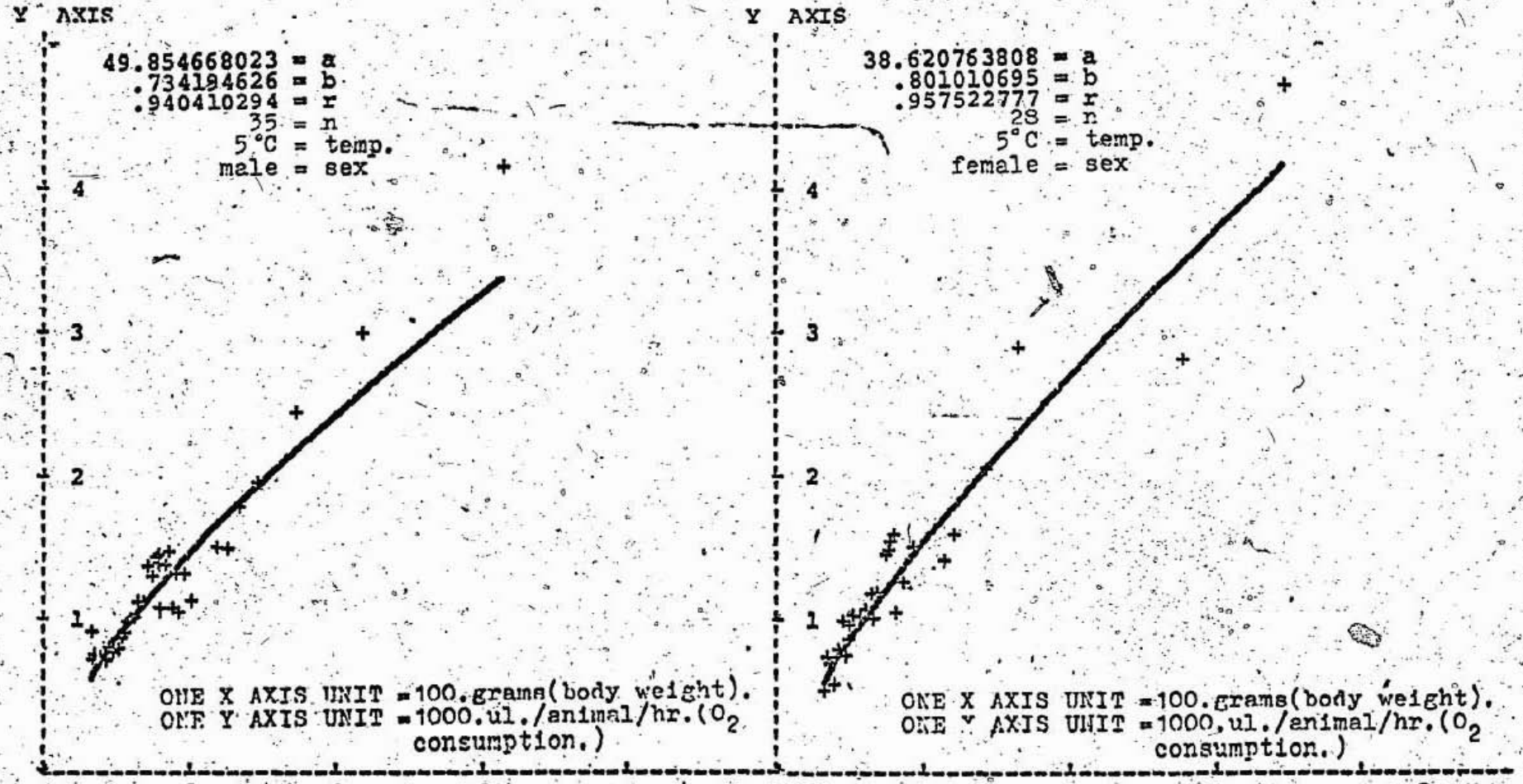
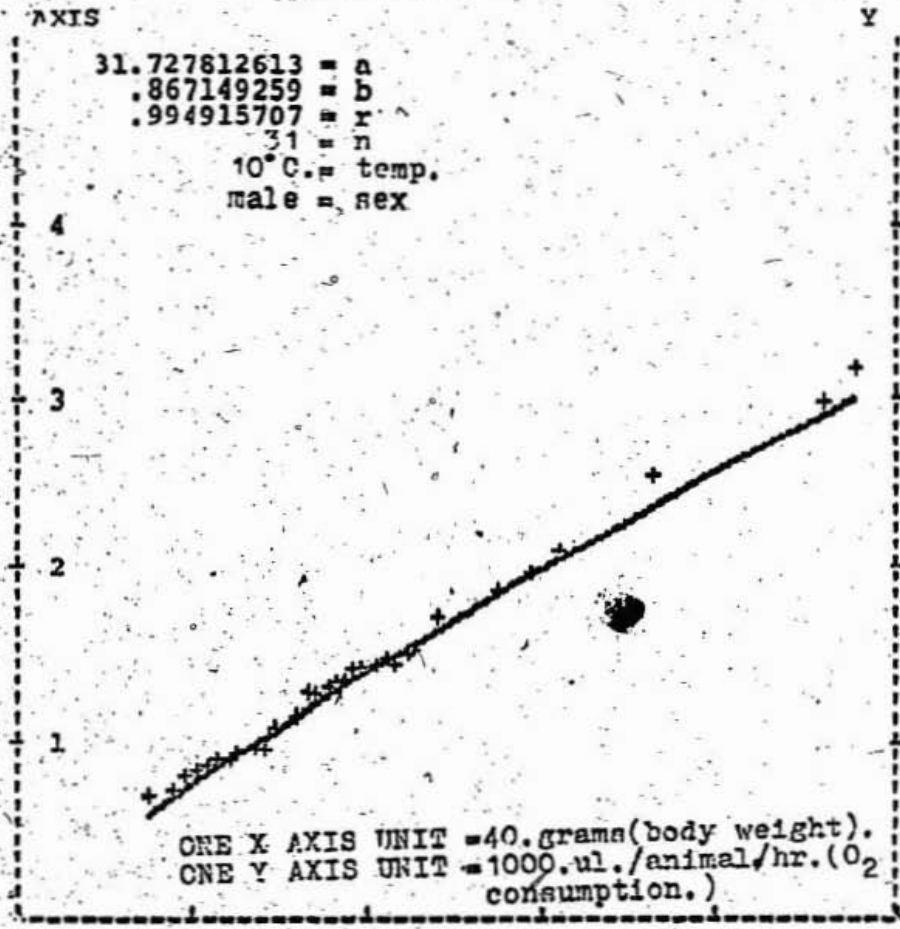


Fig. 16

Regression lines of oxygen consumption on body weight at 10°C for Leptasterias polaris.

LEAST SQUARE FIT - POWER CURVE ($y = ax^b$)



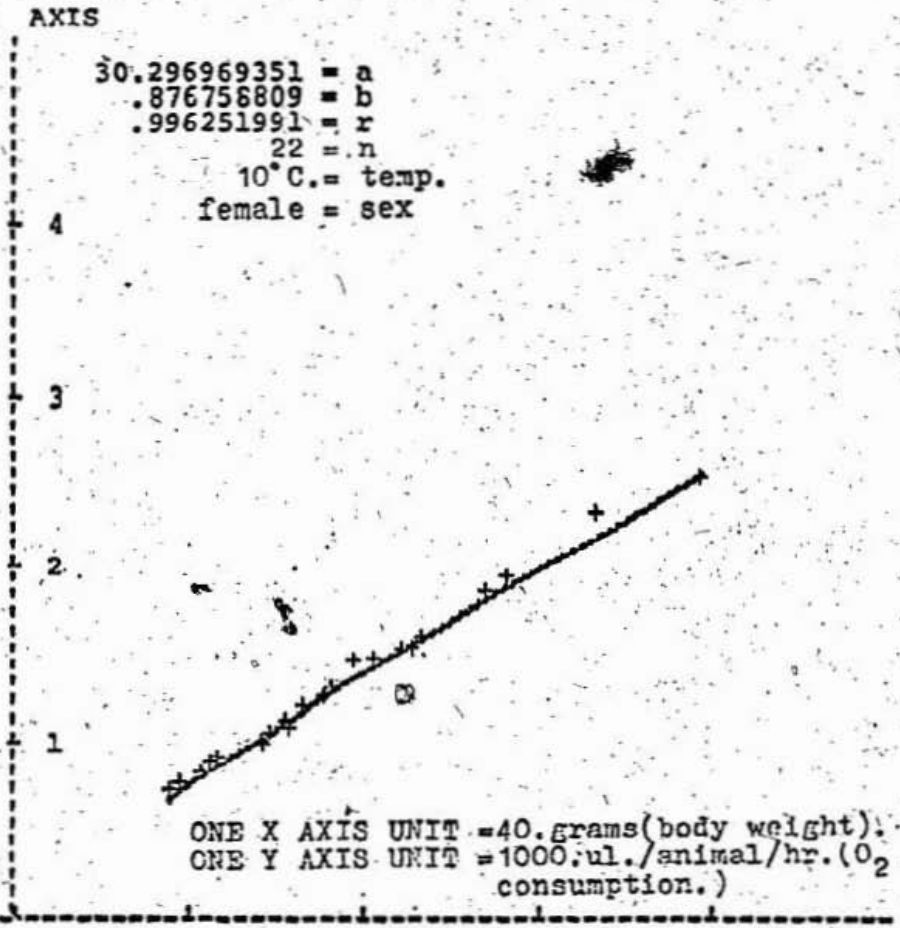
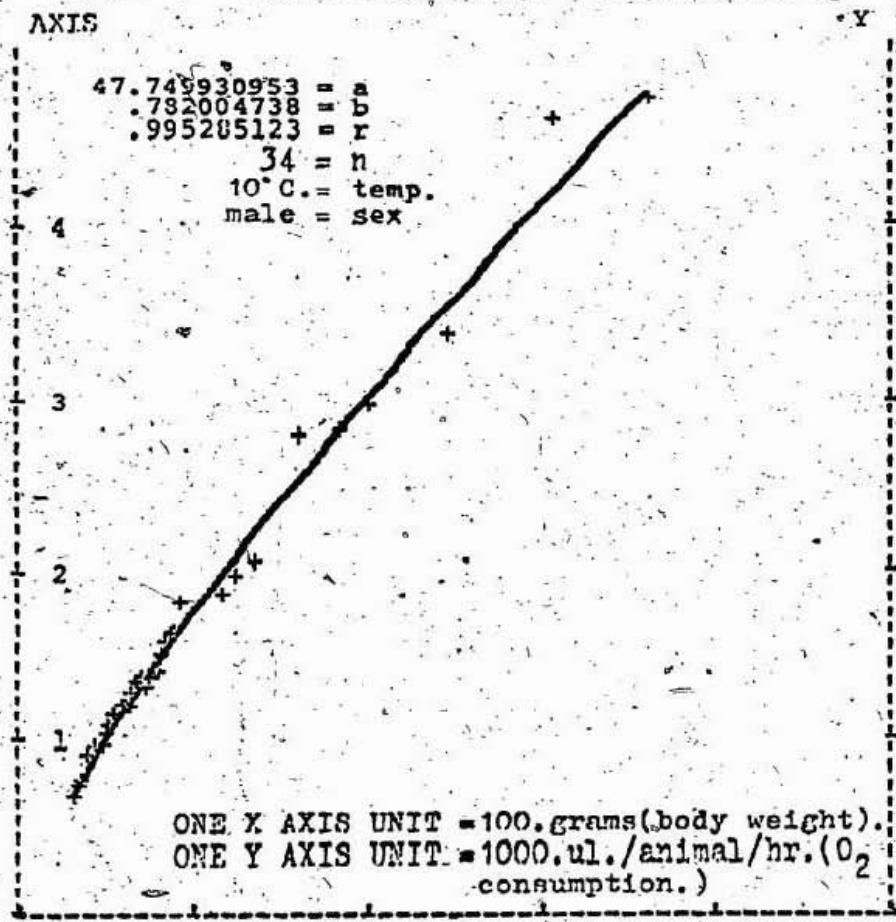



Fig. 17

Regression lines of oxygen consumption on body weight at 10°C for Asterias vulgaris.

b

LEAST SQUARE FIT - POWER CURVE ($y = ax^b$)



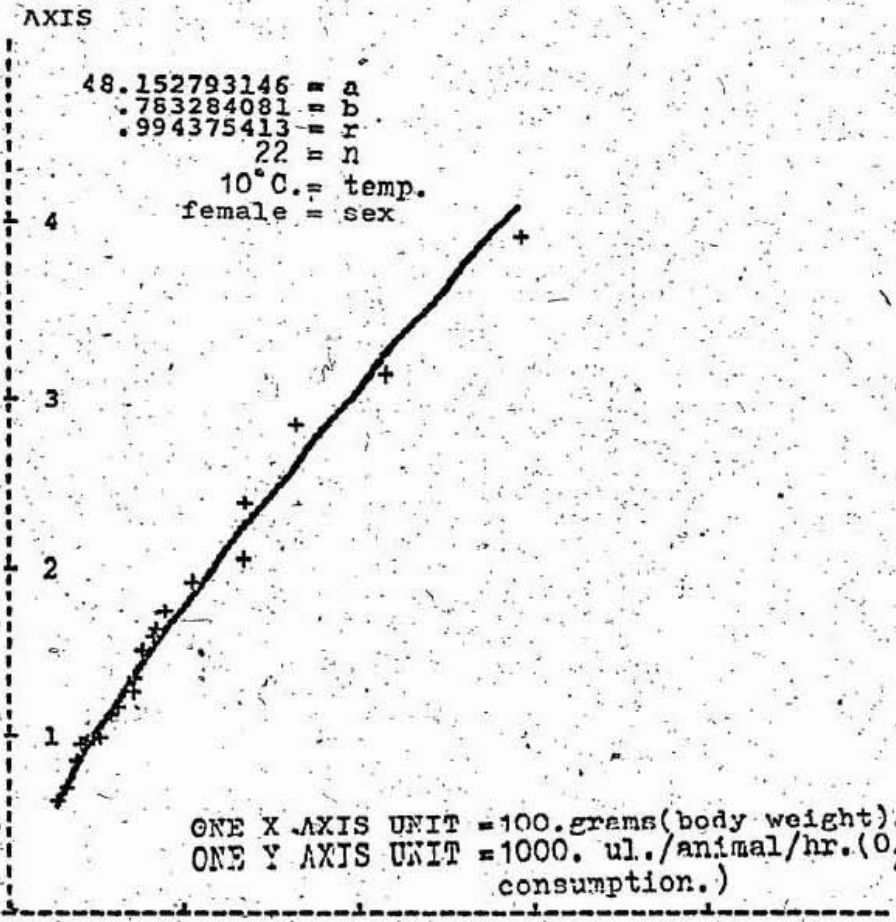
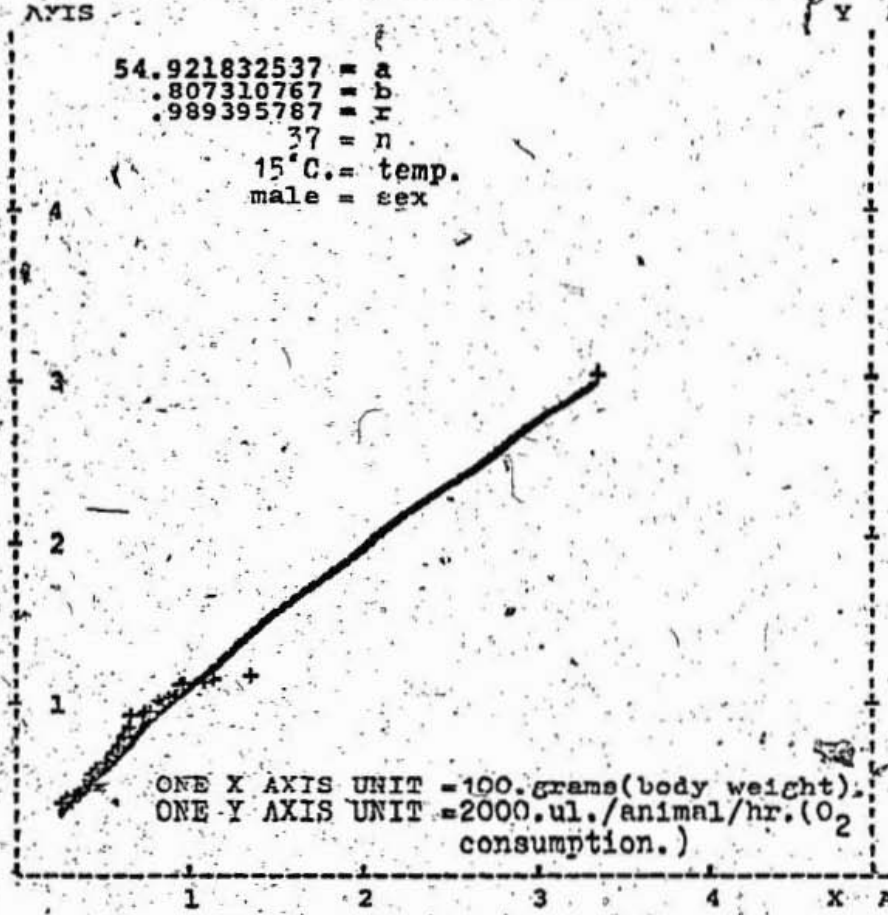



Fig. 18

Regression lines of oxygen consumption on body weight at 15°C for Leptasterias polaris.

LEAST SQUARE FIT - POWER CURVE ($y = ax^b$)



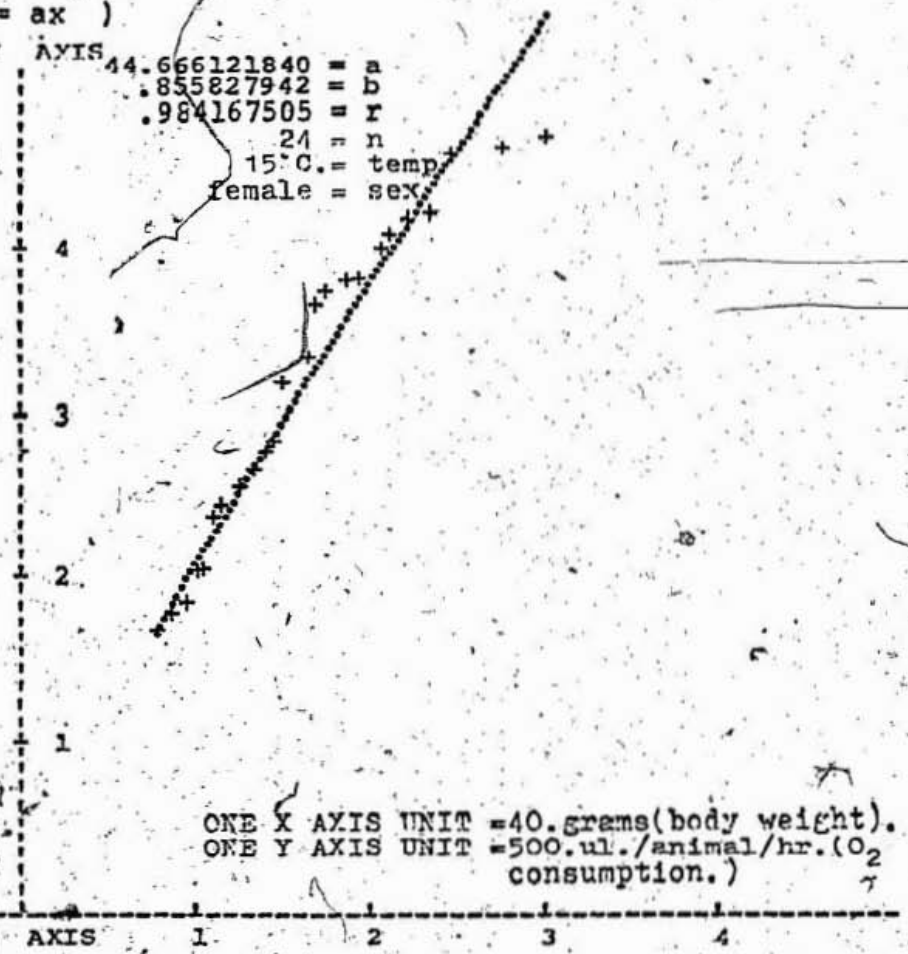
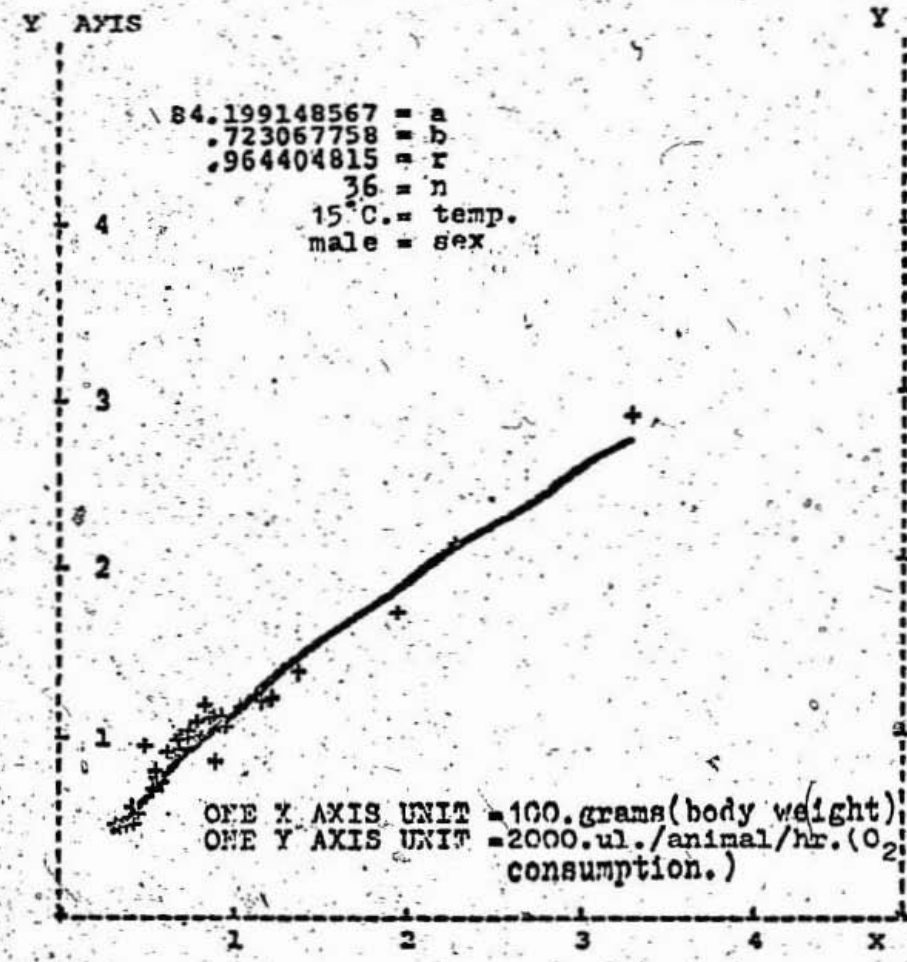
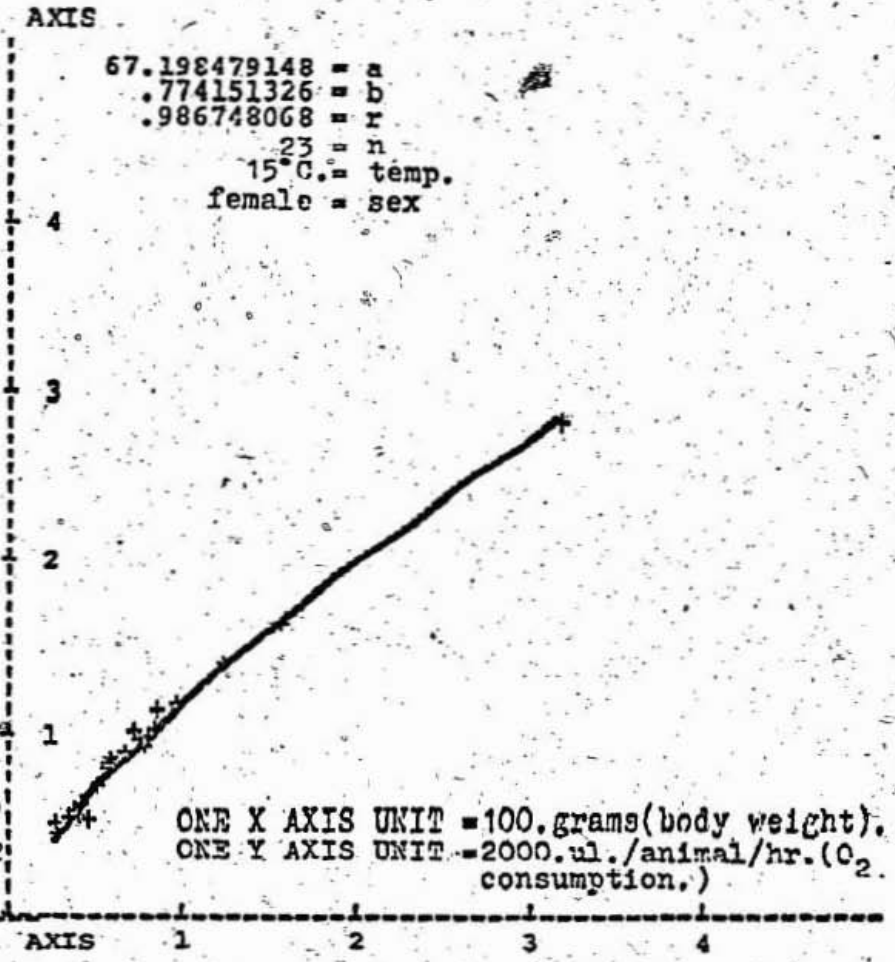



Fig. 19

Regression lines of oxygen consumption on body weight at 15°C for Asterias vulgaris.

LEAST SQUARE FIT - POWER CURVE ($y = ax^b$)



(3) The Influence of Oxygen Content upon the Rate of Oxygen Consumption in Sea Stars

If a bivariate relationship is simply unknown and a scattergram suggests clear deviation from linearity, one way to handle this type of non-linear condition is through the use of a polynomial function (Kim, 1975). The data fitted to Tang's (1933) hyperbolic equation and semi-logarithm curve produced very poor results. Therefore, the selection of a fitted equation in this study followed Mangum and Van Winkle's (1973) suggestion. The equation selected for best fit is a polynomial model. The correlation of the oxygen consumption rate with oxygen content in sea water implies the following relationship and the quadratic model (second degree polynomial) was found to be the best solution.

$$Y/X = a_{11} + b_{11}P + c_{11}P^2 + \sum_{ij}\sum(a_{ij}-a_{11})D_{ij} + \sum_{ij}\sum(b_{ij}-b_{11})D_{ij}P + \sum_{ij}\sum(c_{ij}-c_{11})D_{ij}P^2$$

here Y = oxygen consumption (μl/animal/hr)

X = body weight in grams

P = oxygen content in sea water (ml/l)

$D_{ij}$ = indicator variable

a, b and c are regression coefficients

i = species { 1 = A. vulgaris, 2 = L. polaris }

j = sex { 1 = famale, 2 = male }

The calculated equation was expressed as follows by Shazam computer package.

$Y/X = 11.429 + 2.3171p + 0.0043p^2$ ...A.vulgaris (female)
(1.5961)(0.8224) (0.0874)

$3.1238D_{22} + 1.6961D_{22}p - 0.2419D_{22}p^2$ ...L.polaris (male)
(2.1781) (1.1208) (0.1188)

$0.5220D_{12} + 0.0901D_{12}p - 0.0305D_{12}p^2$ ... A.vulgaris (male)
(2.2033) (1.1263) (0.1195)

$3.2957D_{21} + 1.9224D_{21}p - 0.2627D_{21}p^2$ ... L.polaris (female)
(2.078) (1.0828) (0.1156)

The numbers in parentheses are standard error.

$R^2 = 0.5757$ Standard error of estimate = 4.5615

Analysis of Variance

| | SS | DF | MS | F |
|---|---|---|---|---|
| Explained | 11690 | 11 | 1062.7 | 51.075* |
| Unexplained | 8614.4 | 414 | 22.808 | |
| Total | 20305 | 425 | 47.776 | |

Hypothesis Test: between intercepts and regression coefficients.

| Hypothesis | t ratio | Hypothesis | t ratio | Hypothesis | t ratio |
|---|---|---|---|---|---|
| $a_{11}=a_{12}$ | -0.2369(NS) | $b_{11}=b_{12}$ | 0.0800(NS) | $c_{11}=c_{12}$ | -0.2552(NS) |
| $a_{11}=a_{21}$ | -1.586(NS) | $b_{11}=b_{21}$ | 1.7755(NS) | $c_{11}=c_{21}$ | -2.2730** |
| $a_{22}=a_{12}$ | -1.226(NS) | $b_{22}=b_{12}$ | 1.483(NS) | $c_{22}=c_{12}$ | -1.846(NS) |
| $a_{22}=a_{21}$ | 0.086(NS) | $b_{22}=b_{21}$ | 0.218(NS) | $c_{22}=c_{21}$ | 0.1880(NS) |

$Y/X = 11.429 + 2.3171p + 0.0043p^2$ ...A.vulgaris (female)
(when $D_{22}=0$; $D_{12}=0$; $D_{21}=0$)

$Y/X = 8.3052 + 4.0132p - 0.2376p^2$ ...L.polaris (male)
(when $D_{22}=1$; 0 otherwise)

$Y/X = 10.907 + 2.4072p - 0.0262p^2$ ...A.vulgaris (male)
(when $D_{12}=1$; 0 otherwise)

$Y/X = 8.1333 + 4.2395p - 0.2584p^2$ ...L.polaris (female)
(when $D_{21}=1$; 0 otherwise)

Hyman (1929) reported that the oxygen consumption rate of sea stars below normal ambient oxygen tension in sea water is highly dependent on the oxygen content of the sea water. Meyer (1935), Maloeuf (1938), Prosser (1961) and Belman and Giese (1974) also indicated that some species of Asterias were oxygen conformers, but Johansen and Petersen (1971) described the ability of the sea star Pteraster tesselatus to regulate oxygen uptake based on the active irrigation of the dermal branchiae in the nidamental cavity and thus compensate for decreased ambient availability. The data shown in the figure by Maloeuf (1938) were quite different from those of Belman and Giese (1974). The former more likely agreed with Mangum and Van Winkle's (1973) report which indicated a second degree polynomial curve, fit to a semilogarithmic curve. Unfortunately, quantitative data in their paper were not presented; therefore, it is very difficult to find a suitable relationship. The results for the present study also showed a

non-linear relationship so that a polynomial model was selected as described above. As mentioned by Maloeuf (1938), there was no critical point. Therefore, it is probable that both species L. polaris and A. vulgaris are oxygen conformers, unable to control their oxygen consumption unlike Pteraster where there is a nidamental cavity through which it can pump sea water, up to 90% of its total oxygen uptake being obtained through active ventilation (Johansen and Petersen, 1971). The oxygen consumption rate of the female of A. vulgaris is significantly different from that of L. polaris. Although the oxygen consumption of the males of A. vulgaris compared to those of L. polaris, do not reach a significant difference level, we can still detect the difference, if a different probability is selected. There is no significant difference between males and females within A. vulgaris. The figures 20-23 show that the response to decreasing the rate of oxygen consumption from the decreasing oxygen content in the sea water is not so abrupt. A low oxygen content in sea water does not immediately reduce their activities. It was observed that sea stars in sea water of low oxygen content did not withdraw or protrude the tube feet except those in sea water containing less than 1.5 ml/l oxygen.

It is interesting that brooding behavior is found in L. polaris, not A. vulgaris. This brooding activity is shown by most arctic and subarctic species and may

play a very important role in the survival of the embryo. While brooding, the animal stays in one place and becomes very inactive, and will not consume food. Also my observations found the movement of A. vulgaris was greater than that of L. polaris. Only on very few occasions did I see A. vulgaris stay in one place over a two day period, but this was quite common for L. polaris. Obviously the fact L. polaris has brooding behavior may lead to a lower metabolic rate.

The oxygen consumption rate of A. vulgaris shown in the figures 20-23 indicates more sensitivity to lower oxygen content in sea water than in L. polaris. It is quite possible that the higher activity of A. vulgaris demands a higher oxygen uptake and therefore this species is more responsive to lower oxygen contents in sea water.

Mangum and Van Winkle (1973), and Van Winkle and Mangum (1975) proposed a quadratic model to describe the effect of oxygen content on oxygen consumption rate in different marine invertebrates. They postulated that the quadratic coefficient $B_2$ was an index of oxyregulation and reported that the higher negative values of the index appeared to signify a greater regulatory ability. By viewing the results on page 78 in contrast to the data from the common sea star Asterias forbesi, the blood sea star Henricia sanguinolenta (O.F. Muller), and the infaunal mudstar Ctenodiscus crispatus it is clear that A. vulgaris has a poorer regulatory ability than any of the above species

and that L. polaris is equipped with better regulatory capacity than A. vulgaris and the above species.

Shick (1976) pointed out that the mudstar C. crispatus probably encountered prolonged hypoxia and high $H_2S$ condition routinely, so that they are more resistant to hypoxia and $H_2S$ than any of the epifaunal species of Asterias. His study demonstrated that closely related animals inhabiting lower or less predictable oxygen environments possess greater resistance to hypoxia. He cautiously concluded that the degree of regulatory ability for oxygen consumption of asteroids from different environmental oxygen levels can be considered as adaptation to low or unpredictable oxygen conditions, but this phenomenon still remains ambiguous.

It is very difficult to explain why L. polaris has better regulatory capacity. Mangum and Van Winkle (1973) suggested that three factors determined the magnitude in aquatic invertebrates of the regulatory ability of oxygen consumption at different oxygen levels of ambient water: (1) The degree of impermeability of the exoskeleton insulating internal oxygen consuming tissues from their external oxygen source; endoskeletons also may somewhat reduce permeability; (2) differences in tissue metabolism; (3) efficiency of the circulatory system. L. polaris may possess more endoskeleton and lower tissue metabolism than A. vulgaris, and both species lack an active ventilation mechanism such as occurs in Pteraster tesselatus and

Ctenodiscus crispatus. This still cannot explain why L. polaris is a stronger regulator (page 78) than A. vulgaris.

It is possible that the regulatory mechanism is not just dependent on one factor. Examination of Shick's (1976) report would show that C. crispatus is furnished with a ventilation mechanism but has a lower index of oxyregulation than A. vulgaris.

Fig. 20

The influence of oxygen content in sea water on the rate of oxygen consumption for the male of Leptasterias polaris.

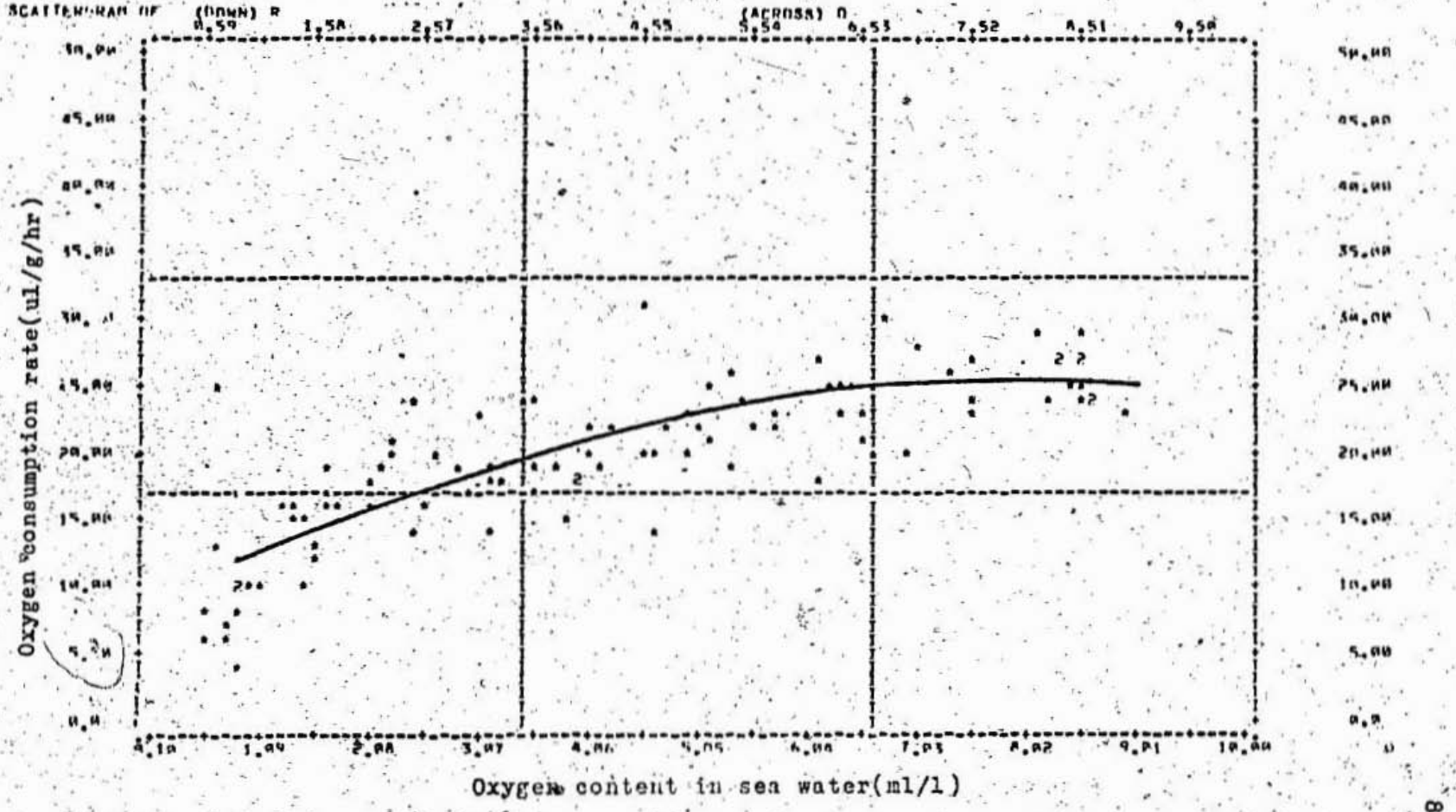

SCATTERGRAM OF (DOWN) R (ACROSS) O
0.59 1.58 2.57 3.56 4.55 5.54 6.53 7.52 8.51 9.50
Oxygen consumption rate(ul/g/hr)
Oxygen content in sea water(ml/l)

Fig. 21

The influence of oxygen content in sea water on the rate of oxygen consumption for the female of Leptasterias polaris.

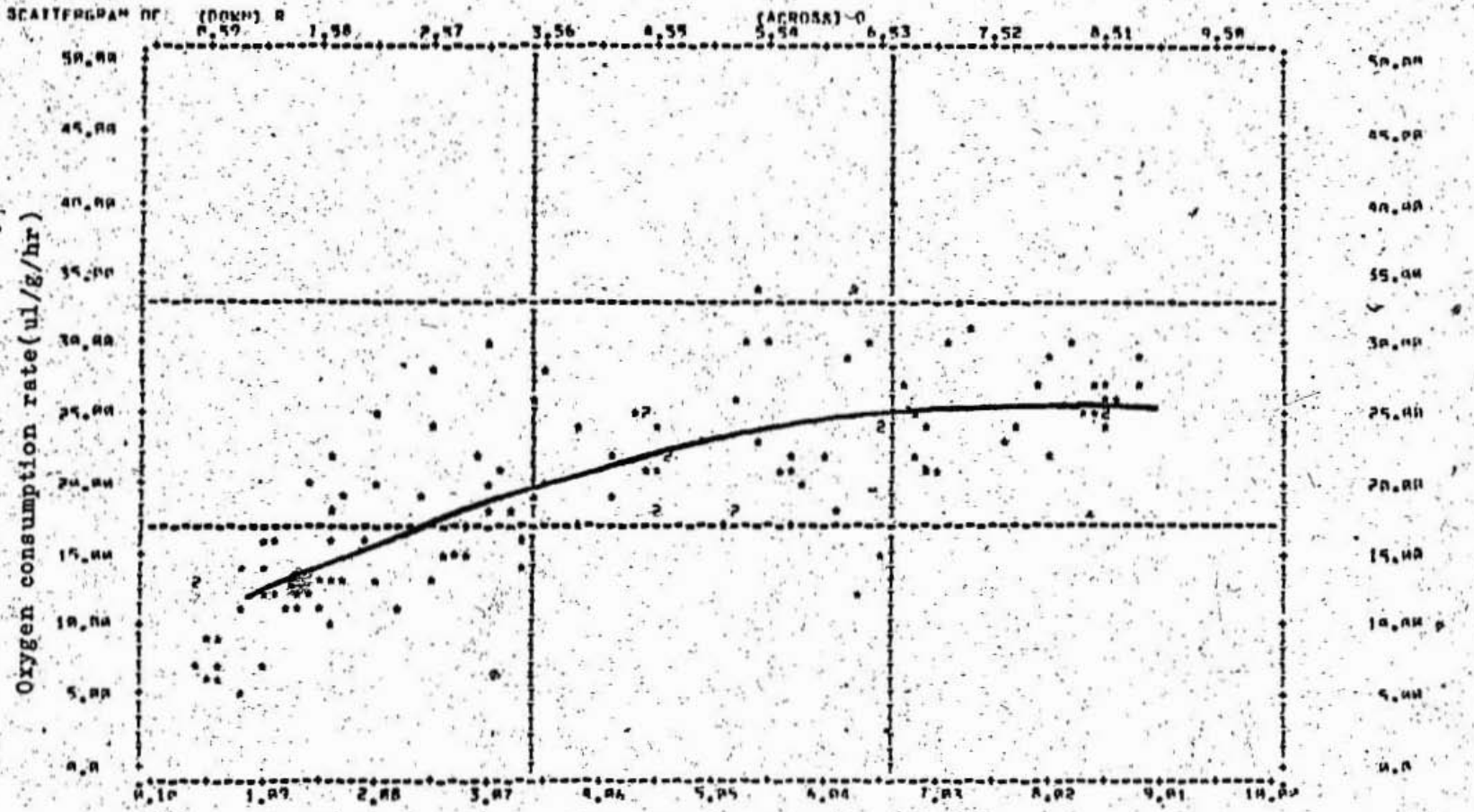

SCATTERGRAM OF (DOWN) R (ACROSS) O
Oxygen consumption rate(ul/g/hr)
Oxygen content in sea water(ml/l)

Fig. 22

The influence of oxygen content in sea water on the rate of oxygen consumption for the male of Asterias vulgaris.

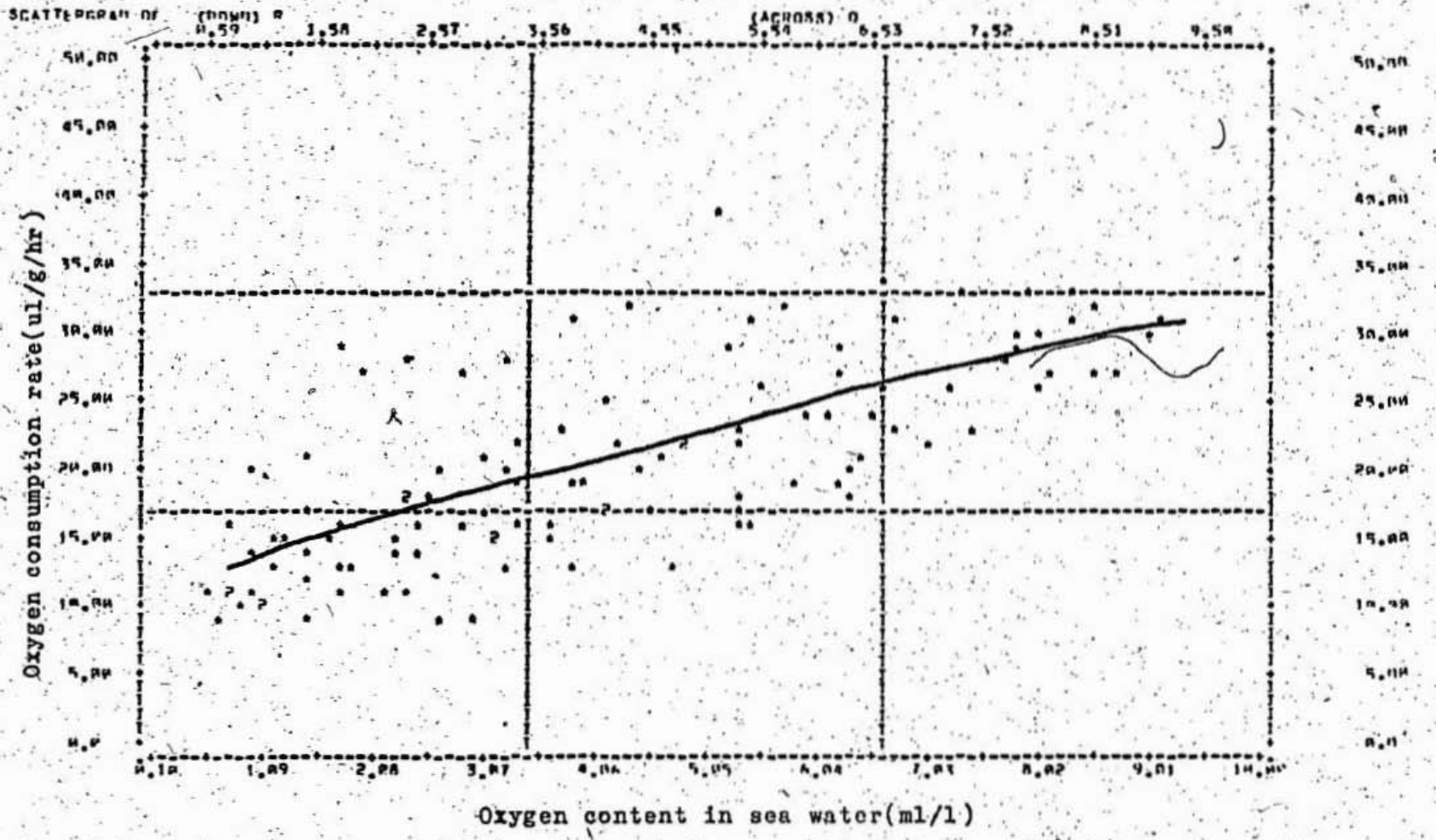
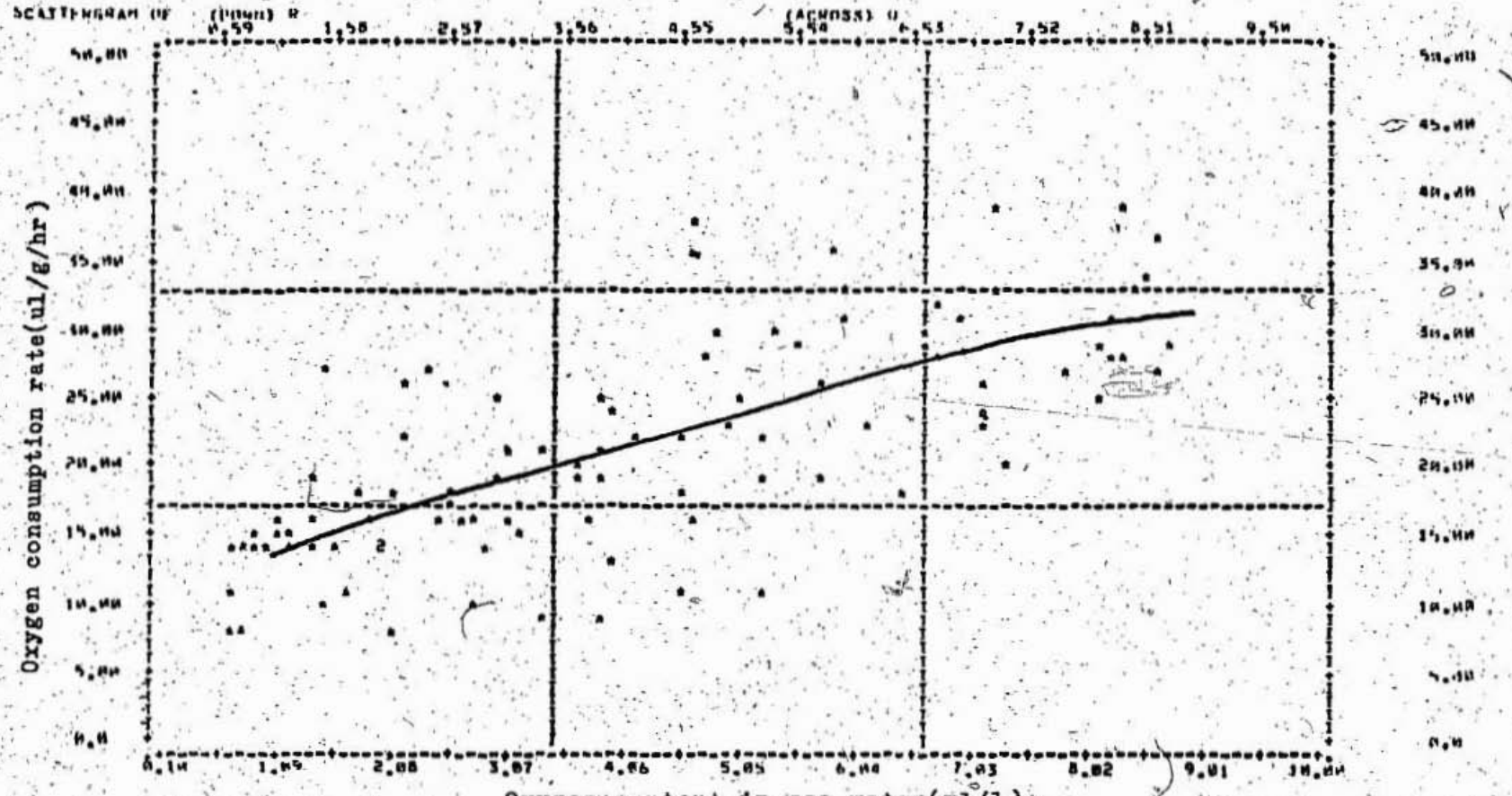

SCATTERGRAM OF (DOWN) R (ACROSS) O
0.59
1.58
2.57
3.56
4.55
5.54
6.53
7.52
8.51
9.50
50.00
45.00
40.00
35.00
30.00
25.00
20.00
15.00
10.00
5.00
0.0
0.10
1.09
2.08
3.07
4.06
5.05
6.04
7.03
8.02
9.01
10.00
Oxygen consumption rate(ul/g/hr)
Oxygen content in sea water(ml/l)

Fig. 23

The influence of oxygen content in sea water on the rate of oxygen consumption for the female of Asterias vulgaris.


Oxygen consumption rate(ul/g/hr)
Oxygen content in sea water(ml/l)

(4) The pH Effect on the Rate of Oxygen Consumption

The oxygen consumption rate of sea stars under different pHs indicates that a non-linear relationship exists between them. It was found that a piecewise linear model gave a better fit than a polynominal model, because the latter had a high degree of multicollinearity on the independent variable. This may lead to imprecision in the estimation of relationship, so that the piecewise linear regression was employed (Neter, 1974). A scattergram shows that oxygen consumption rate is the highest at pH = 8 over the entire measured range (Figs. 24-27). The general model was expressed as follows:

$$\frac{Y}{X} = a_{11} + b_{11}(pH-8)pH' + c_{11}pH + \sum_{ij}\sum (a_{ij}-a_{11})D_{ij} + \sum_{ij}\sum (b_{ij}-b_{11})D_{ij}(pH-8)pH' + \sum_{ij}\sum (c_{ij}-c_{11})D_{ij}pH$$

here Y = oxygen consumption (µl/animal/hr)

X = body weight (grams)

pH = pH values of sea water

pH' = if pH ≥ 8 then pH' = 1
if pH < 8 then pH' = 0

$D_{ij}$ = indicator variables

$a_{ij}$; $b_{ij}$; $c_{ij}$ are regression coefficients

i = species { 1 = L. polaris
2 = A. vulgaris

j = sex { 1 = female
2 = male

Fig. 24

The pH effect on the rate of oxygen consumption for the female of Leptasterias polaris.

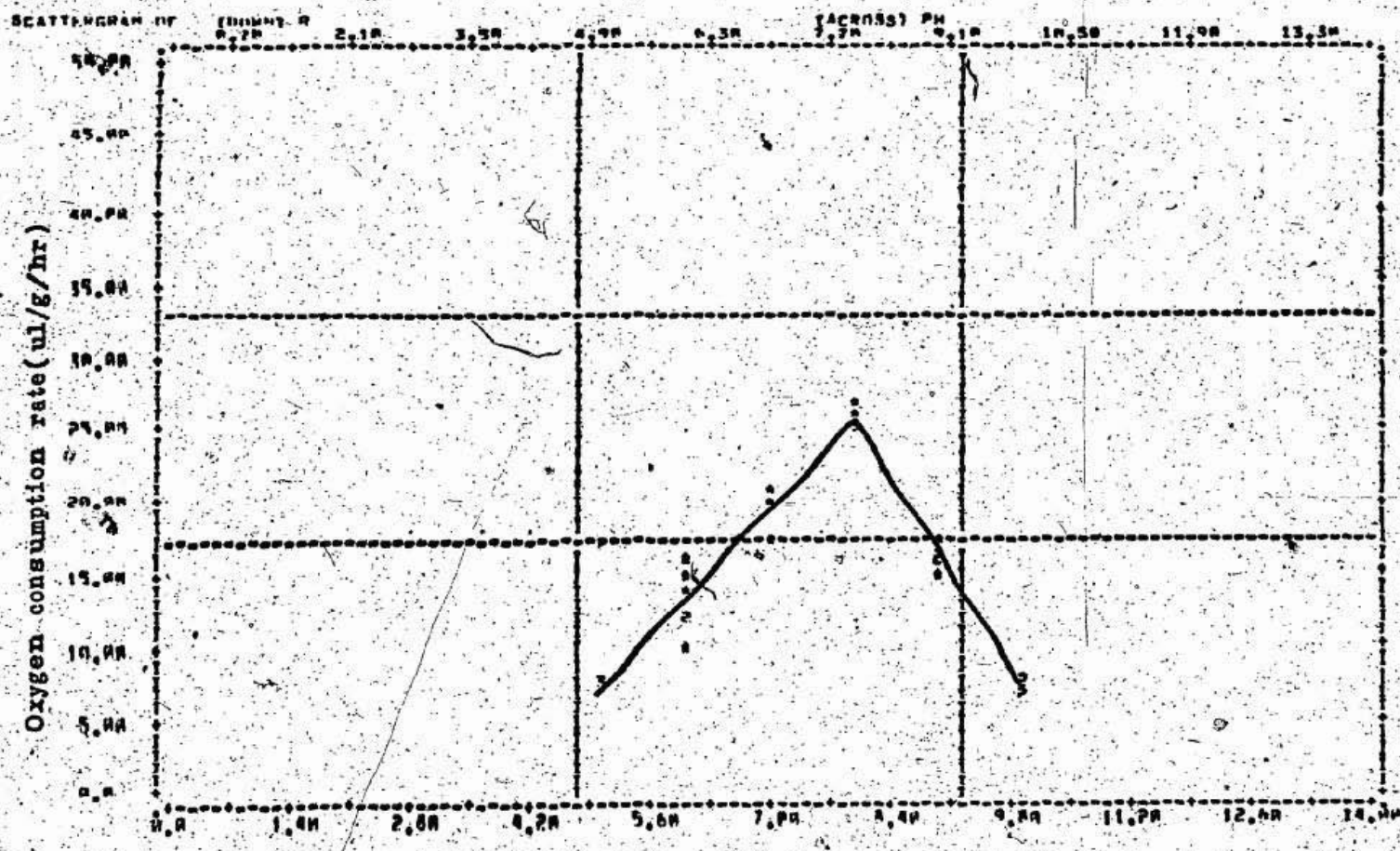

Oxygen consumption rate( ul/g/hr)
pH

Fig. 25.

The pH effect on the rate of oxygen consumption for the male of Leptasterias polaris.

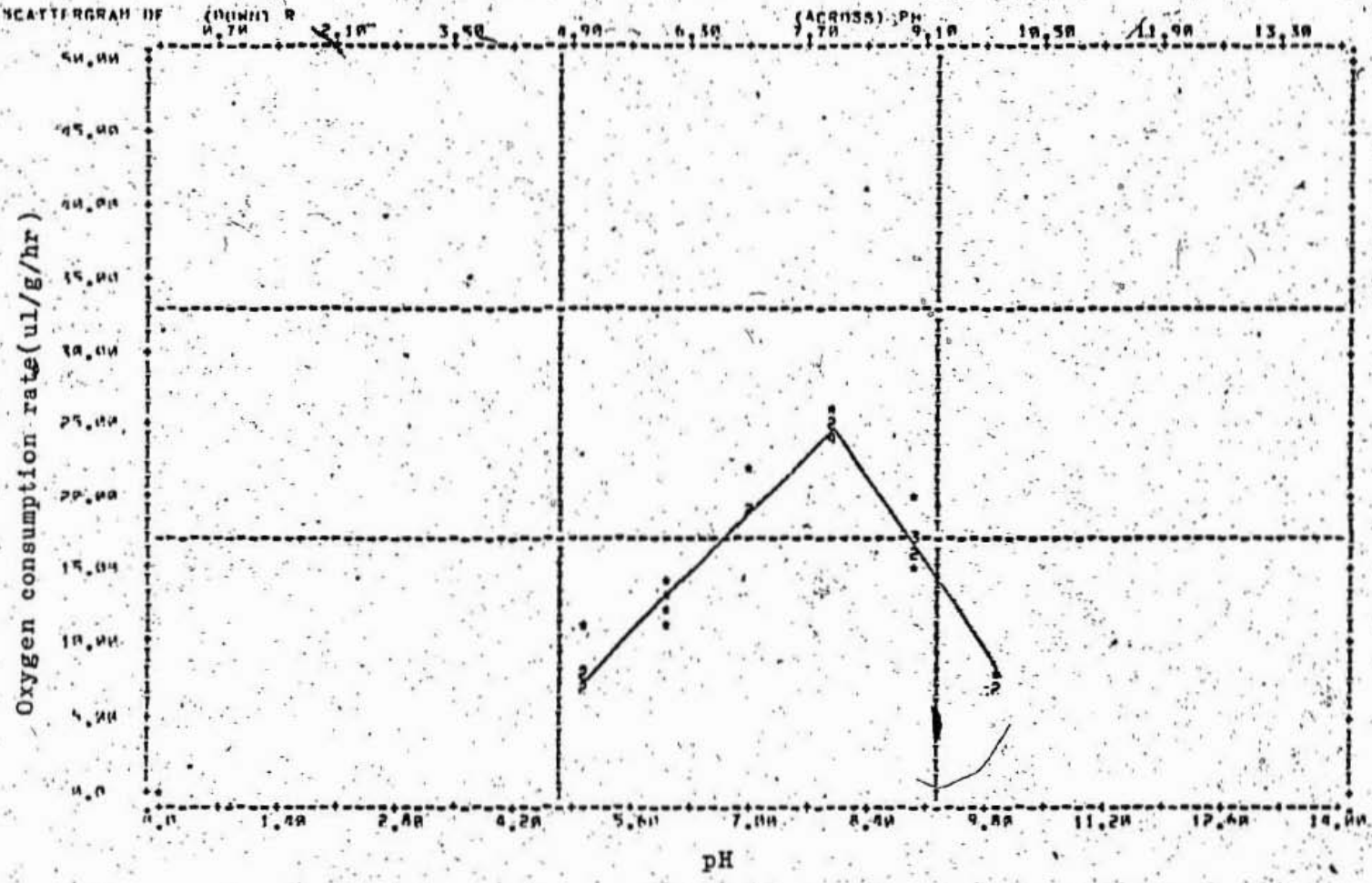

SCATTERGRAM OF (DOWN) P
(ACROSS) PH
Oxygen consumption rate(ul/g/hr)
pH

Fig. 26

The pH effect on the rate of oxygen consumption for the female of Asterias vulgaris.

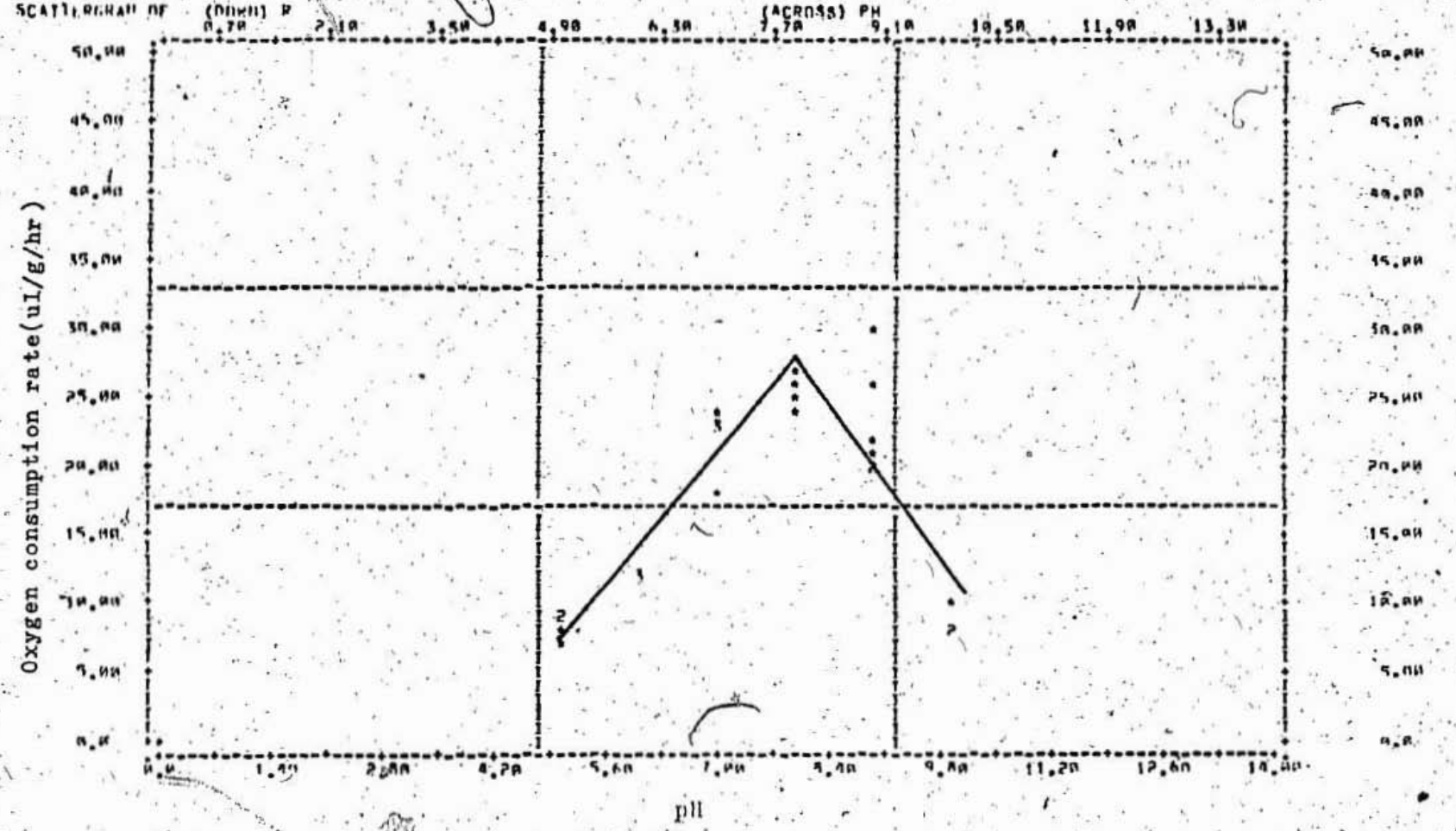
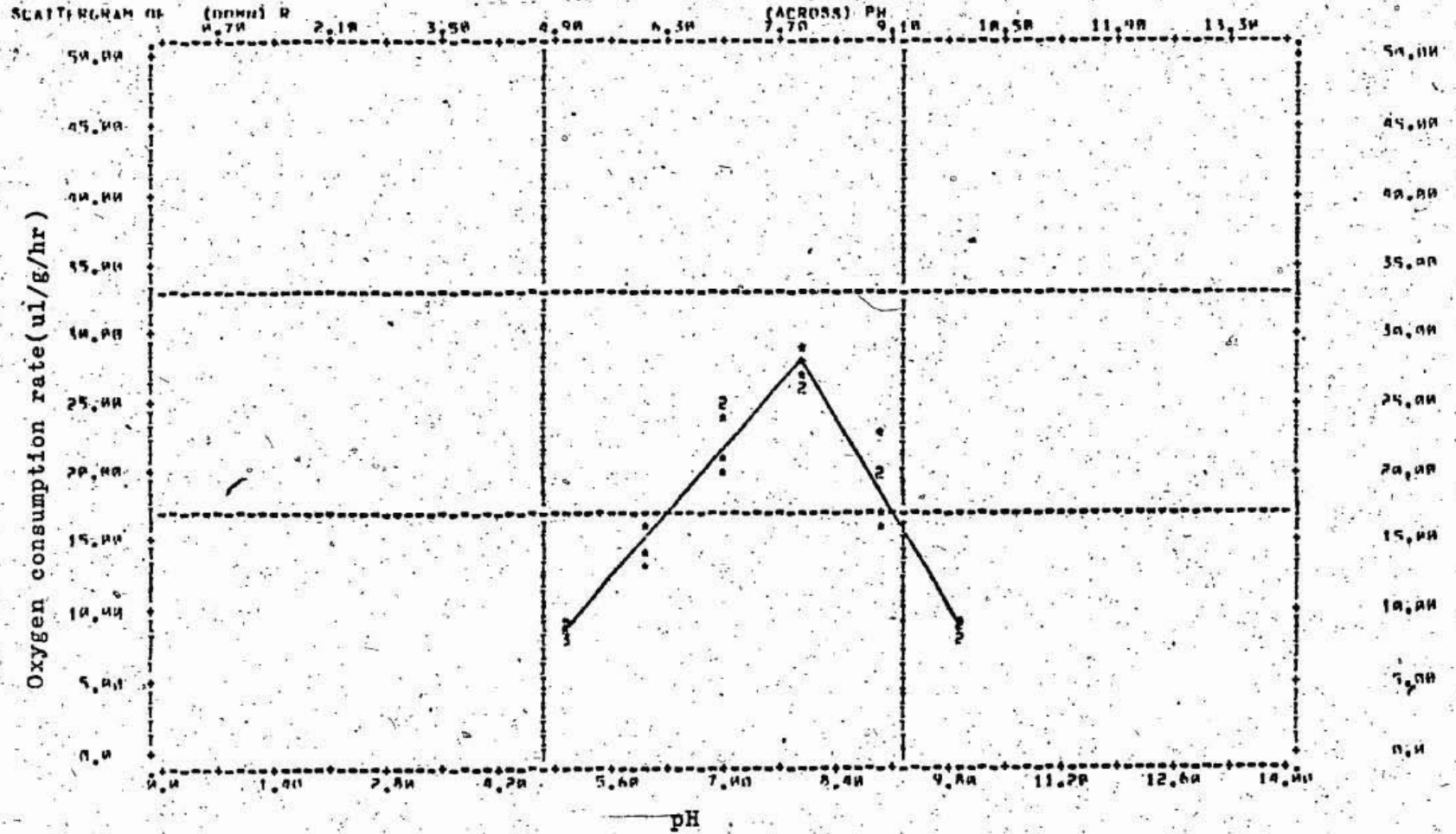

SCATTERGRAM OF (DOWN) P
(ACROSS) PH
0.7R
2.1R
3.5R
4.9R
6.3R
7.7R
9.1R
10.5R
11.9R
13.3R
50.0R
45.0R
40.0R
35.0R
30.0R
25.0R
20.0R
15.0R
10.0R
5.0R
0.0
Oxygen consumption rate(ul/g/hr)
1.4R
2.8R
4.2R
5.6R
7.0R
8.4R
9.8R
11.2R
12.6R
14.0R
pH

Fig. 27

The pH effect on the rate of oxygen consumption for the male of Asterias vulgaris.


SCATTERGRAM OF (DOWN) R
(ACROSS) PH
Oxygen consumption rate(ul/g/hr)
pH

The following results have been obtained by using multiple regression in Shazam computer program.

$\frac{X}{Y}$ = -21.629 - 14.758 (pH-8) pH' + 5.8591 pH + ....L.polaris (female)

(2.9966) (0.9425) (0.4356)

$1.217D_{12}$ - $0.8229D_{12}$(pH-8) pH' - $0.2247D_{12}$pH - .L.polaris (male)

(4.0265) (1.3415) (0.5876)

$5.2441D_{21}$ - $0.1674D_{21}$(pH-8) pH' + $1.0091D_{21}$pH - ..A.vulgaris (female)

(4.3358) (1.4337) (0.6369)

$2.7470D_{22}$ - $1.5054D_{22}$(pH-8) pH' + $0.7199D_{22}$pH ..A.vulgaris (male)

(4.4757) (1.3833) (0.6491)

$R^2$ = 0.9133; standard error of estimate = 2.1739

Analysis of Variance

| | SS | DF | MS | F |
|---|---|---|---|---|
| Explained | 4676.7 | 11 | 425.15 | 89.967* ($p < 0.05$) |
| Unexplained | 444.21 | 94 | 4.7256 | |
| Total | 5.120.9 | 105 | 48.770 | |

Hypothesis Test: between intercepts and regression coefficients.

| Hypothesis | t ratio | Hypothesis | t ratio | Hypothesis | t ratio |
|---|---|---|---|---|---|
| $a_{11} = a_{12}$ | 0.3022(NS) | $b_{11} = b_{12}$ | 0.6134(NS) | $c_{11} = c_{12}$ | -0.3824(NS) |
| $a_{11} = a_{21}$ | -1.2095(NS) | $b_{11} = b_{21}$ | -0.1167(NS) | $c_{11} = c_{21}$ | 1.5843(NS). |
| $a_{22} = a_{12}$ | 0.927(NS) | $b_{22} = b_{12}$ | 1.673(NS) | $c_{22} = c_{12}$ | -1.518(NS) |
| $a_{22} = a_{21}$ | -0.547(NS) | $b_{22} = b_{21}$ | 0.904(NS) | $c_{22} = c_{21}$ | 0.432(NS) |

$\frac{Y}{X} = -21.6290 + 5.85910\ pH - 14.758\ (pH-8)\ pH'$ ...L.polaris (female)

(when $D_{22} = 0$, $D_{12} = 0$, $D_{21} = 0$)

$\frac{Y}{X} = -20.4120 + 5.6344\ pH - 13.9351\ (pH-8)\ pH'$ ...L.polaris (male)

(when $D_{12} = 1$; 0 otherwise)

$\frac{Y}{X} = -26.8731 + 6.8682\ pH - 14.9254\ (pH-8)\ pH'$ ...A.vulgaris (female)

(when $D_{21} = 1$; 0 otherwise)

$\frac{Y}{X} = -24.3760 + 6.5790\ pH - 16.2634\ (pH-8)\ pH'$ ...A.vulgaris (male)

(when $D_{22} = 1$; 0 otherwise)

Farmanfarmaian (1966) quoted Meyer's (1935) paper, and remarked that A. rubens maintained a constant rate of oxygen consumption in the pH range from 5.5 to 7.8. Above this range, the rate of oxygen consumption increased up to pH 9 at which point it fell rapidly and stopped at pH 10.5. Below pH 5.5 the respiration rate was reduced and ceased at pH 4.5. Hiestand (1940) demonstrated that variations of the pH of sea water caused marked variations in the rate of oxygen consumption in the holothurian Thyone briareus (Lesueur) and pointed out that the relationship of oxygen consumption to pH is directly proportional over values from pH 5.4 to 8.8. No attempt was made to raise the pH above this level due, he said, to formation of a precipitate. However, precipitation does not occur until near pH 10 (Kukubo, 1968; Kao, 1970), so his measurements may have been in error. Ozaki (1970 summarized the results from various authors' reports and constructed

a generalized figure (Fig. 28) describing the relationship between pH and oxygen consumption of various species of fish. It was explained as follows:

(1) If pH is changed slightly from the normal condition, the oxygen consumption would increase initially and then return to the normal condition again. The higher initial oxygen consumption was induced by changing pH to excite the fish.

(2) With a greater change in pH, oxygen consumption rose initially, then reduced to a certain rate which was higher than the original oxygen consumption rate.

(3) With an even greater pH change, oxygen consumption intensified first, then gradually decreased to a level which was lower than the normal condition.

(4) With a change in pH more than in (3) oxygen consumption was enhanced at first, then declined to even lower than that in (3).

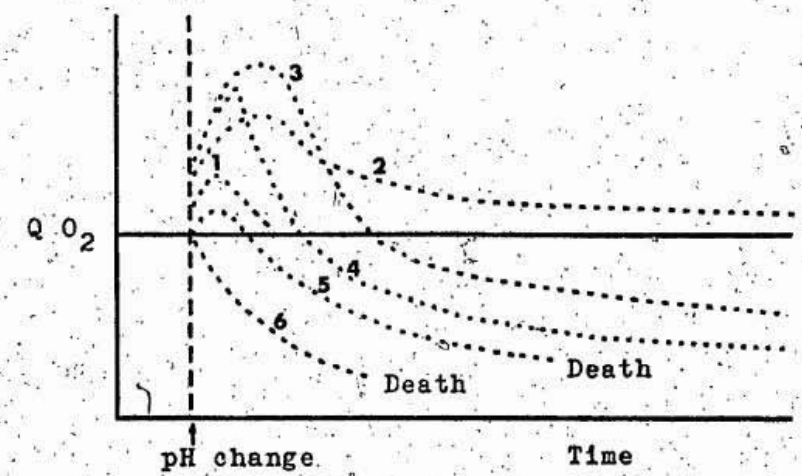
(5) When pH was changed more than in (4), oxygen consumption increased for only a very short period, then decreased for a brief period, subsequently resulting in death.

(6) If the pH change is greater than in (5), oxygen consumption decreased instead of increasing right from the start and finally death occurred.

A study of this typical figure revealed that the oxygen consumption rate was related to the degree of pH

Fig. 28

The effect of pH variation on the oxygen uptake in fish with time lapse (from Ozak, 1970).


Q O2
1
2
3
4
5
6
Death
Death
pH change
Time

change from the normal and the time elapsed, when oxygen consumption was measured. According to Buckingham and Freed (1976) the metabolic rate of the prosobranch snail (Viviparus contectoides Binney) is dependent on pH with two pH optima, at pH 7.1 and 8.9, with an intervening trough. They deduced that there are two sets of pre-existing enzyme systems with the different pH optima. They further stated that the relationship between pH and oxygen consumption in this species appeared to be the immediate rate compensation which was described by Hochochka and Somero (1973).

On the whole, by reviewing the above reports it is concluded that there is no generalization regarding the influence of different pH on oxygen consumption in poikilothermic organisms. Obviously, variations of oxygen uptake at different pH values are dependent on experimentation, species, initial pH, time lapse, etc. The response of sea stars to pH effects seems to be nervous stimulation (this indicates very rapid reaction).

As is shown in Figs. 24-27, the oxygen consumption rate of sea stars decreased with the change of pH, and this did not agree with Meyer's (1935) observation on A. rubens. This could be due to the different experimentation and her small sample size. The oxygen consumption rate of sea stars at pH values higher than 8 has a greater (absolute value) slope than below pH 8. Although statistical analysis indicated no significant difference between species and sex

within the species, we can still detect a slight difference between species but not sex within a species from the t test. The figures also illustrate that specimens of A. vulgaris are more responsive than L. polaris to pH judging from the different slopes. With moderate change of pH, A. vulgaris still maintains a higher oxygen consumption rate than L. polaris but further pH reductions had a more serious effect on the oxygen consumption of A. vulgaris than L. polaris and this phenomenon was not so obvious. It is possible that L. polaris may contain more $CaCO_3$ in the endoskeleton. Calcium carbonate neutralizes the acidic medium and therefore, as Farmanfarmaian pointed out, an acidic medium will have more effect on the oxygen consumption of A. vulgaris than on that of L. polaris.

With regard to the existence of immediate rate compensation between oxygen consumption and pH reported in the snail Viviparus contectoides (Buckingham and Freed, 1976), no comparable phenomenon is apparent in sea stars. By applying this explanation to Meyer's data, there should be some sets of pre-existing enzyme systems with different pH. optimums and the existence of an immediate rate compensation. However, a review of Hochachka and Somero's (1973) description of a three-time-course of response for metabolic compensation reveals that it refers to thermal regulation only and not to other environmental factors, so that immediate rate

compensation should be reconsidered.

Enzyme activities have optimal ranges of pH, but their existence with relation to higher oxygen consumption rate of organisms is still not fully understood. In other words, it does not necessarily follow that all of the metabolic processes should coincide in an optimum for one or two sets of enzyme activity. However, these two species of sea stars placed in a medium beyond optimum pH do reduce their oxygen consumption rate.

In fact, the stimulation by extreme pH media may cause paralysis of and even damage to the tissues of the sea star. Therefore, the sea star would not take up oxygen as in normal conditions and reduces oxygen consumption further.

(5) Influence of Salinity on the Rate of Oxygen Consumption of Sea Stars

The experimental data were roughly examined by scattergrams which reflected a non-linear pattern over the entire measured range. Oxygen consumption rates reached maxima at salinities of about 33 ‰, so that a piecewise linear regression was employed (Figs. 29-32). The equation of the regression line for the rate of oxygen consumption with varying salinities is:

$$\frac{Y}{X} = a_{11} + b_{11}(S-33)S' + c_{11}S + \sum_{ij}\sum (a_{ij}-a_{11})D_{ij} + \sum_{ij}\sum (b_{ij}-b_{11})D_{ij}(S-33)S' + \sum_{ij}\sum (c_{ij}-c_{11})D_{ij}S$$

here i = species $\begin{cases} 1 = \underline{A.\ vulgaris} \\ 2 = \underline{L.\ polaris} \end{cases}$

j = sex $\begin{cases} 1 = \underline{female} \\ 2 = \underline{male} \end{cases}$

Y = oxygen consumption (µl/animal/hr)

X = body weight (grams)

S = salinity of sea water

S' = If $S \geq 33$ then $S' = 1$
If $S < 33$ then $S' = 0$

$D_{ij}$ = indicator variables

$a_{ij}$; $b_{ij}$, $c_{ij}$ are regression coefficients

The calculated equation was expressed as follows by Shazam computer program:

$$\frac{Y}{X} = 0.8531 - 1.6356\ (S-33)\ S' + 0.7812\ S + \ldots \underline{A.\ vulgaris}\ (female)$$
$$(0.1238)\quad (0.1732)\qquad\qquad (0.0549)$$

$$0.1468D_{12} - 0.0570D_{12}(S-33)\ S' + 0.0025D_{12}S -$$
$$(1.753)\quad (0.2378)\qquad\qquad (0.0757)$$

$$\ldots \underline{A.\ vulgaris}\ (male)$$

$$0.0946aD_{21} - 0.3187D_{21}(S-33)\ S' - 0.0392D_{21}S -$$
$$(1.7116)\quad (0.2304)\qquad\qquad (0.0746).$$

$$\ldots \underline{L.\ polaris}\ (female)$$

$$1.3664D_{22} - 0.3535D_{22}(S-33)\ S' + 0.0055D_{22}S$$
$$(1.7413)\quad (0.2297)\qquad\qquad (0.0748)$$

$$\ldots \underline{L.\ polaris}\ (male)$$

Numbers in parenthesis are standard error

$R^2 = 0.8856$; standard error of estimate = 4.885.

Analysis of Variance

| | SS | DF | MS | F |
|---|---|---|---|---|
| Explained | 3354.7 | 11 | 323.16 | 66.153* (P<0.05) |
| Unexplained | 459.19 | 94 | 4.8850 | |
| Total | 4013.9 | 105 | 38.228 | |

Hypothesis Test: between intercepts and regression coefficients

| Hypothesis | t ratio | Hypothesis | t ratio | Hypothesis | t ratio |
|---|---|---|---|---|---|
| $a_{11} = a_{12}$ | 0.0838(NS) | $b_{11} = b_{12}$ | -0.2395(NS) | $c_{11} = c_{12}$ | 0.03265(NS) |
| $a_{11} = a_{21}$ | -0.0553(NS) | $b_{11} = b_{21}$ | -1.3833(NS) | $c_{11} = c_{21}$ | -0.5251(NS) |
| $a_{22} = a_{12}$ | 0.868(NS) | $b_{22} = b_{12}$ | 1.335(NS) | $c_{22} = c_{12}$ | -0.041(NS) |
| $a_{22} = a_{21}$ | 0.747(NS) | $b_{22} = b_{21}$ | 0.163(NS) | $c_{22} = c_{21}$ | -0.624(NS) |

$\frac{Y}{X} = 0.8531 - 1.6356\,(S-33)\,S' + 0.7812\,S$ ... *A. vulgaris* (female)

(when $D_{22} = 0$, $D_{12} = 0$, $D_{21} = 0$)

$\frac{Y}{X} = 0.9993 - 1.6929\,(S-33)\,S' + 0.7837\,S$ ... *A. vulgaris* (male)

(when $D_{12} = 1$; 0 otherwise)

$\frac{Y}{X} = 0.7585 - 1.9543\,(S-33)\,S' + 0.742\,S$ ... *L. polaris* (female)

(when $D_{21} = 1$; 0 otherwise)

$\frac{Y}{X} = -0.5133 - 1.9891\,(S-33)\,S' + 0.7867\,S$ ... *L. polaris* (male)

(when $D_{22} = 1$; 0 otherwise)

Tables 5a and 5b indicate that the freezing point of coelomic fluid of the sea stars (as a measure of salinity) is slightly lower than that of the ambient medium, but is not significantly different (by t test). Binyon (1970) recognized that A. rubens showed the same condition as above. Maloeuf (1938) suggested that echinoderms are entirely incapable of any osmoregulation. A slightly different freezing point between sea water and perivisceral fluid might be due to the Donnan effect, there being a slight amount of protein in the perivisceral fluid. He also found that the coelomic fluid of A. forbesi (this species was misquoted by Binyon, 1961, 1966, 1970 as A. rubens) had a slightly lower freezing point compared to that of the ambient concentrations of sea water. Giese (1966) also published some data on sea stars and reported that protein did exist in the body fluid of sea stars.

Sea stars are strictly marine organisms and conform osmotically to the surrounding medium in which they live (Prosser and Brown, 1961). The results from the above tables support this statement. Prosser and Brown (1961) pointed out,

> Success in fresh water required osmotic regulation of such order that high concentration of body fluids could be maintained against an extreme osmotic gradient: such regulation required active mechanisms for (1) lower permeability to water, (2) water elimination, (3) salt retention, (4) salt replacement. Freshwater animals differ from the marine in the degree of development of these regulating mechanisms.

Table 5a. The freezing point (°C) of ambient sea water and coelomic fluid in Asterias vulgaris

| Asterias vulgaris | Male<br>Body weight 90.32 g | Male<br>Body weight 114.26 g | Female<br>Body weight 105.49 g | Female<br>Body weight 112.17 g |
|---|---|---|---|---|
| Sea water | -2.1 -1.8 -1.0 -0.7 -0.35 | -2.0 -1.8 -1.4 -0.9 -0.65 | -2.2 -1.8 -1.5 -1.0 -0.5 | -2.0 -1.8 -1.4 -1.0 -0.4 |
| Coelomic fluid | -2.0 -1.85 -1.1 -0.8 -0.4 | -2.0 -1.8 -1.5 -1.1 -0.8 | -2.1 -1.85 -1.6 -1.1 -0.6 | -1.9 -1.8 -1.5 -1.05 -0.5 |
| t test between sea water and coelomic fluid | df = 4; t = 1.0887 (N.S.) (P<0.05) | df = 4; t = 2.25 (N.S.) (p<0.05) | df = 4; t = 1.29 (N.S.) (p<0.05) | df = 4; t = 0.8017 (N.S.) (p<0.05) |

Table 5b. The freezing point (°C) of ambient sea water and coelomic fluid in Leptasterias polaris

| Leptasterias polaris | Male<br>Body weight 183.25 g | Male<br>Body weight 156.81 g | Male<br>Body weight 87.93 g | Female<br>Body weight 109.57 g |
|---|---|---|---|---|
| Sea water | -2.0 -1.8 -1.3 -1.0 -0.4 | -2.2 -2.0 -1.8 -1.2 -1.0 | -2.2 -1.8 -1.4 -0.9 -0.6 | -2.25 -1.8 -1.2 -0.8 -0.3 |
| Coelomic fluid | -1.95 -1.8 -1.4 -1.1 -0.5 | -2.15 -1.9 -1.8 -1.35 -1.05 | -2.1 -1.9 -1.55 -0.95 -0.8 | -2.1 -1.8 -1.25 -0.85 -0.4 |
| t test between sea water and coelomic fluid | df = 4; t = 1.5811 (N.S.) (p<0.05) | df = 4; t = 0.2324 (N.S.) (p<0.05) | df = 4; t = 1.554 (N.S.) (p<0.05) | df = 4; t = 0.2324 (N.S.) (p<0.05) |

If sea stars had these mechanisms then they would have invaded freshwater in the course of their history. The results presented in the figures showed that both species had maximum respiratory rates when they were exposed to normal sea water (isoosmotic). In non-conforming aquatic invertebrates, when the surrounding medium is changed, the animal becomes hypertonic or hypotonic to the medium, and the respiratory rate is increased due to the energy required to perform osmo-regulation in order to maintain osmotic equilibrium. Non-regulatory animals, e.g., Asterias, Mytilus, Metridium, etc., respond to a change in salinity with a decrease in the respiratory rate (Potts and Parry, 1964). Kinne (1971) has classified four main types of respiratory mechanisms of marine and brackish water invertebrates in response to different salinities: (1) increased metabolic rate in sub-normal salinities within physiological range, (2) increased metabolic rate in both sub-normal and supra-normal salinities, (3) decreased metabolic rate in sub- and supra-normal salinities, and (4) a more or less constant metabolic rate with salinity variation. On the basis of these criteria, the present study as well as Potts and Parry's report (1964) clearly indicates that sea stars are stenohaline, belonging to Kinne's category (3). Numerous attempts have been made to explain these phenomena by several authors: Schlieper's (1958) "hydration theory"

suggested that salinity effects on the metabolic rate of invertebrates are the results of changes in the hydration of tissue which may affect the activity of enzymes. Flemister and Flemister (1951) suggested the increases in oxygen consumption rate of the brachyuran crab (Ocypode albicans Bosc) in hypotonic and hypertonic environments are the consequence of the extra energy required for osmoregulation. Loft (1956) concluded that the oxygen consumption rate of the prawn Palaemonetas varians (Leach) in different salinities were increased due to osmoregulatory mechanisms and some other processes.

McLusky (1969) found that no significant differences were present in the oxygen consumption of the euryhaline amphipod Corophium volutator (Pallas) in different salinities and suggested that the lack of any overt change in respiration rate might, however, conceal a shift of energy requirements within the animal. Production of urine hypo-osmotic to the blood under conditions of osmotic stress could greatly reduce the osmotic work of an animal so that no change in oxygen consumption in different salinities occurred. Potts and Parry (1964) suspected that the osmotic demand will increase the rate of oxygen consumption of organisms. They believed that the changes in metabolic rate are usually much too large to be attributed to osmotic regulation alone. They have calculated that the energy required for the crab Eriocheir sinensis (H. Milne Edwards) to perform osmoregulation in fresh water

was only 0.5% of the total metabolic energy, and postulated a number of reasons why the respiratory rate might vary with salinity in certain conditions. An adverse osmotic environment stimulates an animal to random movements or to escape movements. This causes the increase in the metabolic rate which occurs in some brackish water animals in both high and low salinities. It is the active crustaceans which respire most rapidly in these conditions rather than the more quiescent lamellibranchs or echinoderms. They assume by using Lowenstein's (1935) finding in the respiration of the amphipod Gammarus chevreuxii Sexton that the higher metabolic rate was due to less quiescence in more dilute medium.

However, sea stars are incapable of any osmoregulation (Binyon, 1961). It was noticed during reduction of salinity that the tube feet of the sea stars became immobile or inactive. Binyon (1971) suggested that the cause of temporary loss of activity of the tube feet could be due either to the neuromuscular junctions or to the contractibility of the muscles themselves. These two factors, the lack of osmoregulatory abilities and the temporary loss of activities could be responsible for the decreasing oxygen consumption rate during the reduction of salinities in the environment. When sea stars were placed in sea water where salinities were greater than the normal sea water, they behave differently than in reduced salinities, the tube

feet of these sea stars retract instead of protrude and the whole animal becomes immobile. The results suggested that both in hypotonic and hypertonic medium, the depression of oxygen uptake of sea stars could be explained as described above.

A comparison of both sexes of L. polaris with A. vulgaris showed that oxygen consumption in the two species are not significantly different at $p < 0.05$. On the other hand if we select a different probability level, we may be able to detect their difference. The oxygen consumption rate of A. vulgaris is higher than that of L. polaris, but it is not clear why this is so. There are many possible explanations. L. polaris appear to contain more endoskeleton which is mostly that of $CaCO_3$ and therefore more non-respiratory tissue and would consume less oxygen. The two species may be of different genetic make-up or different in enzyme systems and biochemical pathways of metabolism. There might be considerable differences in metabolic rate between species of the same size in the same habitat, very active forms such as the swimming crab Callinectes have higher basal metabolic rate than more sluggish forms such as the spider crab Libinia (Vernberg and Vernberg, 1970). As described previously, A. vulgaris is much more active than L. polaris. This probably leads to a partial explanation of the lower oxygen consumption of L. polaris than A. vulgaris.

According to Kinne's classification sea stars should be placed as stenohaline organisms, but Binyon (1966)

suggested that sea stars were more correctly classified as poikilosmotic and euryhaline because of their wide distribution in the Baltic and North Seas. Hence they could be considered as ecological euryhalinity osmoconformer.

With both species higher salinity has a more serious effect on the oxygen consumption rate than lower salinity. At 45‰ the oxygen consumption of A. vulgaris is much higher than that of L. polaris, but in low salinity there is no significant difference between the two species (Figs. 29-32). This suggests that at low salinities L. polaris and A. vulgaris have the same ability to adapt, but at higher salinities A. vulgaris has a greater tolerance. There was, however, no significant difference between sexes within a species.

(6) Short-Term Food Deprivation Effect on Oxygen Consumption of Sea Stars

The equation type used to estimate and compare both species is as follows:

$$\log_e Y = a_{111} + b_{111} \log_e X + \sum_{ijk}\sum\sum (a_{ijk}-a_{111})D_{ijk} + \sum_{ijk}\sum\sum (b_{ijk}-b_{111})D_{ijk} \log_e X$$

here i = species { 1 = A. vulgaris; 2 = L. polaris }

j = sex { 1 = female; 2 = male }

k = food { 1 = non-food deprivation; 2 = food deprivation }

Y = oxygen consumption (µl/animal/hr)

X = body weight

Fig. 29

The influence of salinity on the rate of oxygen consumption for the male of Leptasterias polaris.

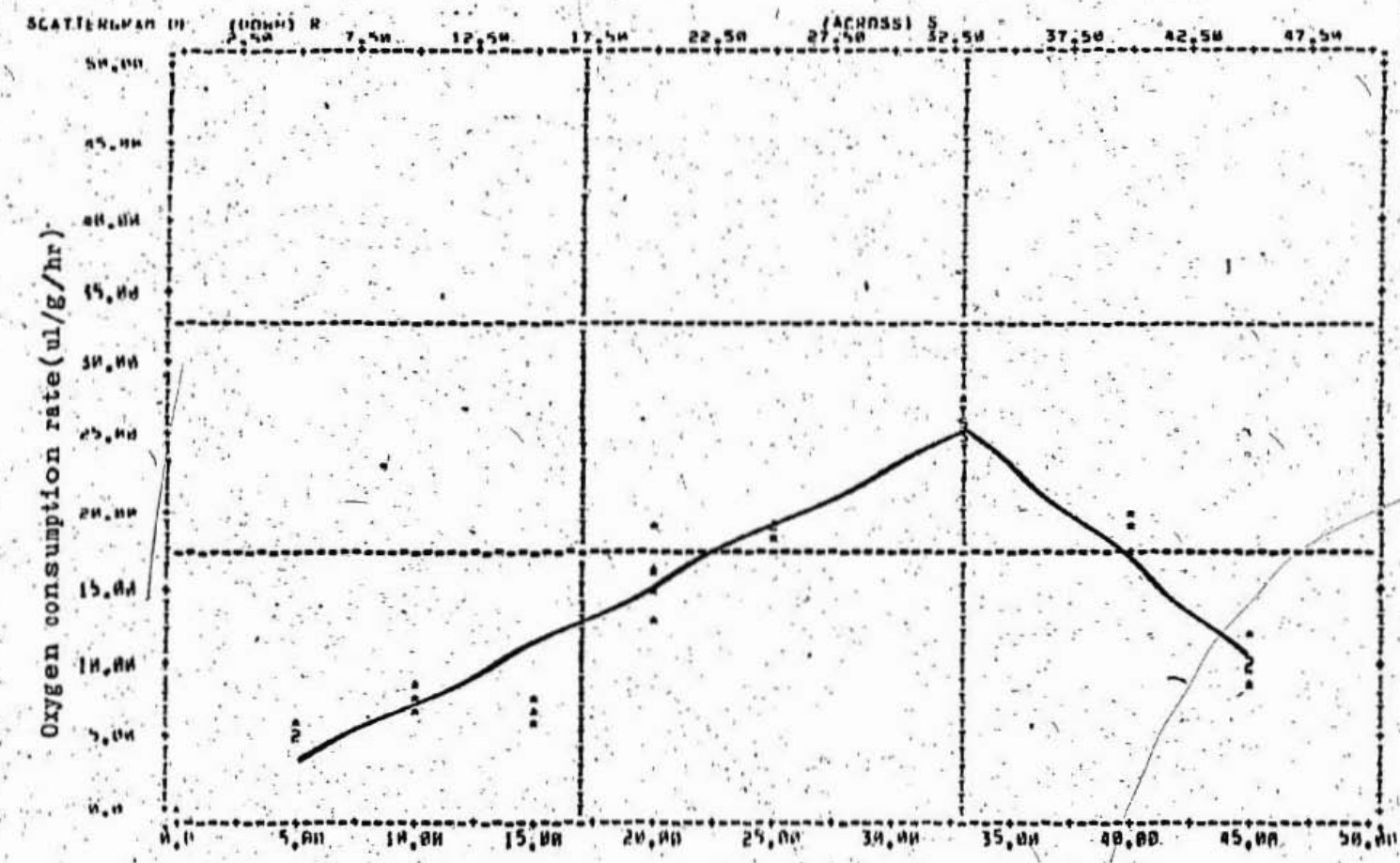

SCATTERGRAM OF (DOWN) R (ACROSS) S
2.50 7.50 12.50 17.50 22.50 27.50 32.50 37.50 42.50 47.50
Oxygen consumption rate(ul/g/hr)
0.00 5.00 10.00 15.00 20.00 25.00 30.00 35.00 40.00 45.00 50.00
Salinities(‰)

Fig. 30

The influence of salinity on the rate of oxygen consumption for the female of Leptasterias polaris.

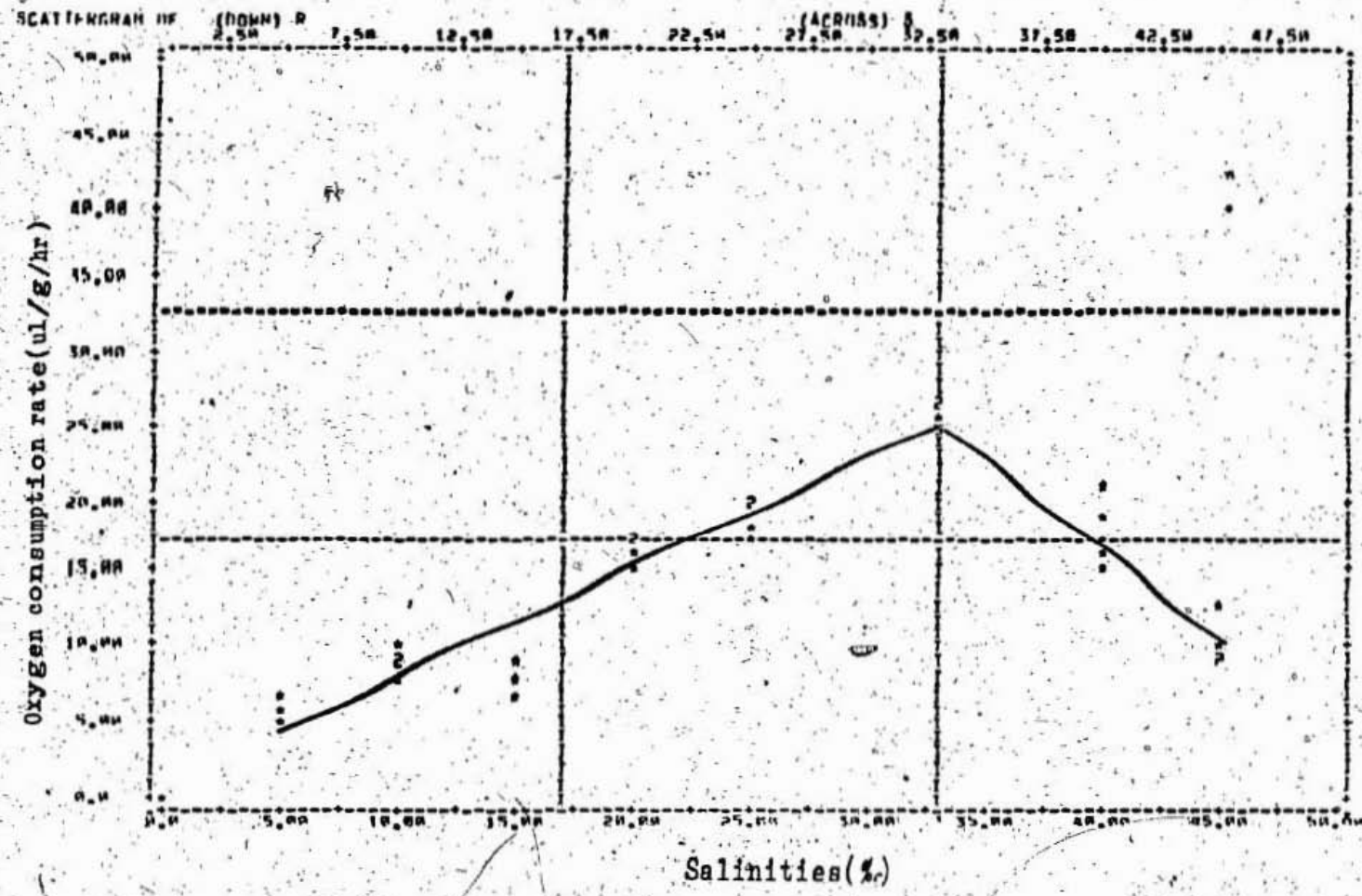

Oxygen consumption rate(ul/g/hr)
Salinities(‰)

Fig. 31

The influence of salinity on the rate of oxygen consumption for the female of Asterias vulgaris.

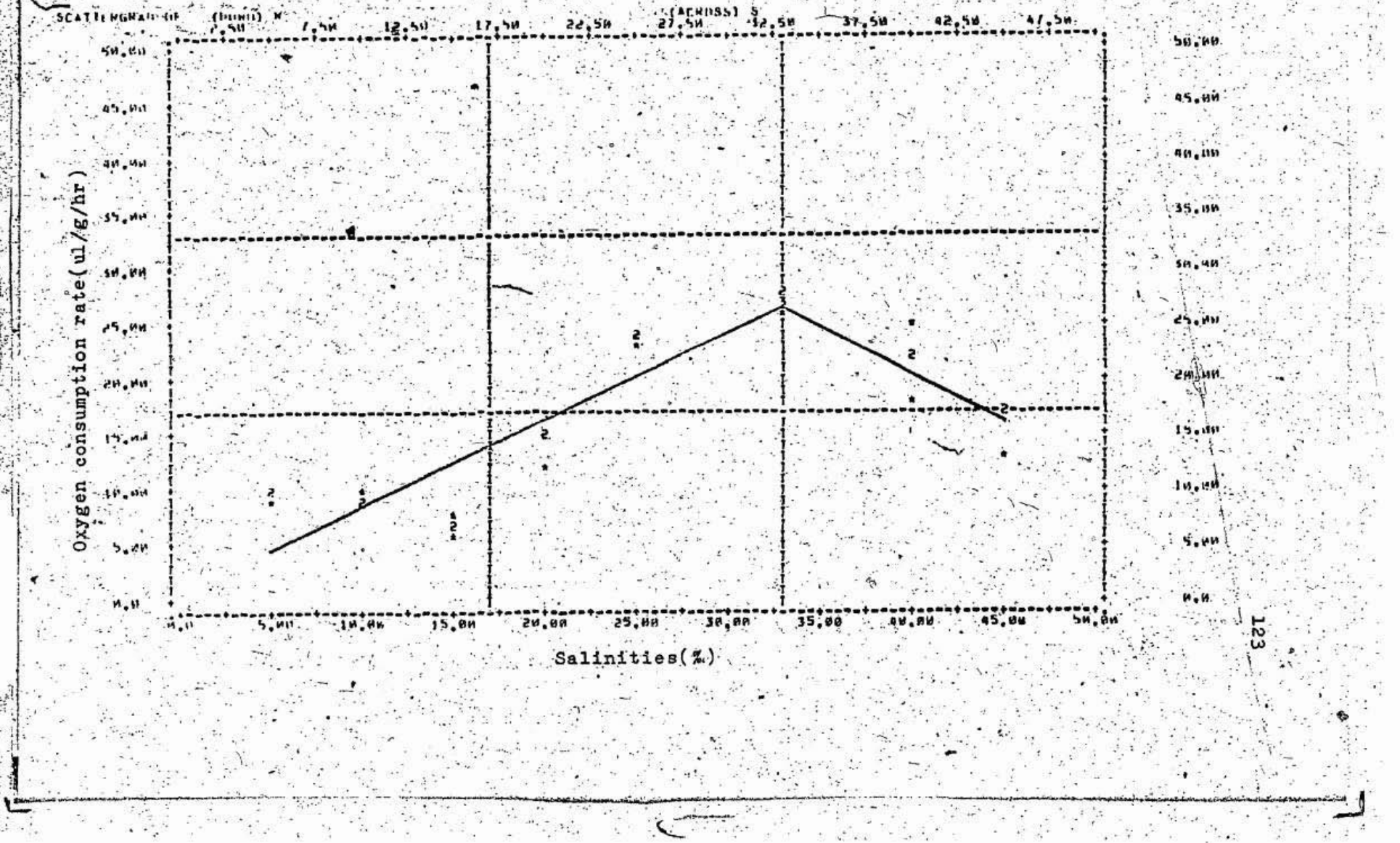
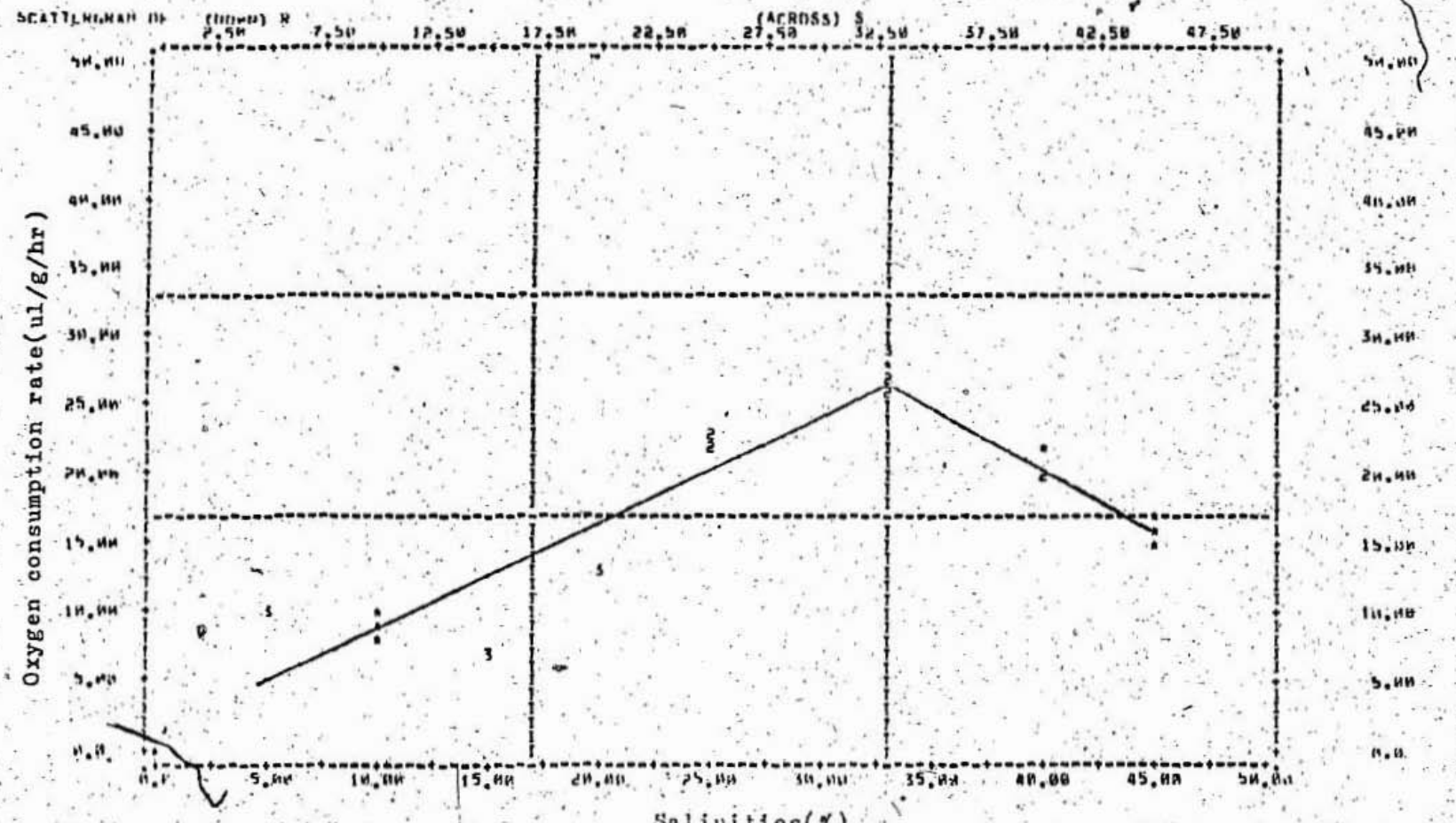

Oxygen consumption rate(ul/g/hr)
Salinities(‰)

Fig. 32

The influence of salinity on the rate of oxygen consumption for the male of Asterias vulgaris.


Oxygen consumption rate(ul/g/hr)
Salinities(%.)

$D_{ijk}$ = indicator variable for each combination of i, j, k, where $i \neq 1$, $j \neq 1$, $k \neq 1$, and $D_{ijk}$ is equal to one for the particular i, j and k in question and zero otherwise.

$a_{ijk}$; $b_{ijk}$; $c_{ijk}$ are regression coefficients.

The calculated equation was expressed as follows by Shazam computer program:

$\log_e Y = 2.9827 + 0.8186 \log_e X$ - ...A.vulgaris (female) N D#

(0.1142) (0.0257)

$0.3532 D_{122} + 0.0908 D_{122} \log_e X$ + ...A.vulgaris (male) D#

(0.2142) (0.0483)

$0.0073 D_{222} - 0.1199 D_{222} \log_e X$ - ...L.polaris (male) D

(0.1706) (0.0385)

$0.2503 D_{121} + 0.0696 D_{121} \log_e X$ - ...A.vulgaris (male) N D

(0.2142) (0.0493)

$0.2487 D_{221} - 0.0563 D_{221} \log_e X$ - ...L.polaris (male) N D

(0.1706) (0.0385)

$0.0808 D_{112} + 0.0121 D_{112} \log_e X$ - ...A.vulgaris (female) D

(0.1615) (0.0364)

$0.6761 D_{212} + 0.0523 D_{212} \log_e X$ - ...L.polaris (female) D

(0.2363) (0.0054)

$0.6011 D_{211} + 0.0369 D_{211} \log_e X$ ...L.polaris (female) N D

(0.2363) (0.0553)

# N D = non-food deprivation
D = food deprivation

The numbers in parentheses are standard error.

$R^2 = 0.9718$; standard error of estimate = 0.0979

Analysis of Variance

| | SS | DF | MS | F |
|---|---|---|---|---|
| Explained | 63.415 | 15 | 4.2277 | 440.724* |
| Unexplained | 1.8418 | 192 | 0.0096 | |
| Total | 65.257 | 207 | 0.31525 | |

Hypothesis Test: between intercepts and regression coefficient.

| Hypothesis | t ratio | Hypothesis | t ratio |
|---|---|---|---|
| $a_{111} = a_{121}$ | -1.169 (N.S.) | $b_{111} = b_{121}$ | 1.4118 (N.S.) |
| $a_{111} = a_{112}$ | -0.5004(N.S.) | $b_{111} = b_{112}$ | 0.3329 (N.S.) |
| $a_{111} = a_{211}$ | 2.544* | $b_{111} = b_{211}$ | 0.6661 (N.S.) |
| $a_{122} = a_{222}$ | -1.63 (N.S.) | $b_{122} = b_{222}$ | 4.1500* |
| $a_{122} = a_{121}$ | -0.401 (N.S.) | $b_{122} = b_{121}$ | 0.3590 (N.S.) |
| $a_{122} = a_{112}$ | -1.272 (N.S.) | $b_{122} = b_{112}$ | 1.5990 (N.S.) |
| $a_{222} = a_{221}$ | 1.428 (N.S.) | $b_{222} = b_{221}$ | -1.5700 (N.S.) |
| $a_{222} = a_{212}$ | 2.817* | $b_{222} = b_{212}$ | -3.035* |
| $a_{121} = a_{221}$ | -0.07 (N.S.) | $b_{121} = b_{221}$ | 2.476* |
| $a_{221} = a_{211}$ | 1.453 (N.S.) | $b_{221} = b_{211}$ | -1.647 (N.S.) |
| $a_{112} = a_{212}$ | 2.519* | $b_{112} = b_{212}$ | -0.722 (N.S.) |
| $a_{212} = a_{211}$ | -0.257 (N.S.) | $b_{212} = b_{211}$ | 0.223 (N.S.) |

$\log_e Y = 2.9827 + 0.8186 \log_e X$ ....A.vulgaris (female) N D

(when $D_{122}$, $D_{222}$, $D_{121}$, $D_{221}$, $D_{112}$, $D_{212}$, $D_{211}$ equal to zero)

$\log_e Y = 2.6295 + 0.9095 \log_e X$ ....A.vulgaris (male) D

(when $D_{122} = 1$, 0 otherwise)

$\log_e Y = 2.9899 + 0.6987 \log_e X$ ....L.polaris (male) D

(when $D_{222} = 1$; 0 otherwise)

$\log_e Y = 2.7324 + 0.8882 \log_e X$ ....A.vulgaris (male) N D

(when $D_{121} = 1$; 0 otherwise)

$\log_e Y = 2.734 + 0.7623 \log_e X$ ....L.polaris (male) N D

(when $D_{221} = 1$; 0 otherwise)

$\log_e Y = 2.9019 + 0.8065 \log_e X$ ....A.vulgaris (female) D

(when $D_{112} = 1$; 0 otherwise)

$\log_e Y = 2.3066 + 0.8709 \log_e X$ ....L.polaris (female) D

(when $D_{212} = 1$; 0 otherwise)

$\log_e Y = 2.3817 + 0.8555 \log_e X$ ....L.polaris (female) N D

(when $D_{211} = 1$; 0 otherwise)

Most carnivorous animals are unable to withstand prolonged food deprivation, but Feder (1959) pointed out that Pisaster ochraceus (Brandt) could resist long periods of starvation, even longer than a year. From my observation, three A. vulgaris and three L. polaris were found to survive more than two months without feeding. Giese (1966) calculated that the storage of nutrients in sea urchins

could last 90 days. The results presented in Figs. 33 and 34 showed that 10 days of food deprivation did not affect the oxygen consumption in either species. This illustrates that the sea stars did not have to decrease oxygen consumption in order to meet short-term food deprivation.

Stephens and Schinske (1961) also found that both Henricia and Asterias can remove most glycine from a 2 μM solution in which they are kept for several hours. By using an autoradiographic method, Ferguson (1967) concluded that the absorption of environmental amino acids (and probably other compounds) by the epidermis of sea stars is an important and often the principal source of nutrition for the cells making up this tissue. Intermittent oral feeding satisfies the more general needs of the entire organism and especially of the internal organs. Obviously this provides the evidence that sea stars can absorb some nutrients directly from sea water in this manner if a sea star is kept in constant nutrient-rich sea water. It should be able to survive a long period of time without active feeding. Perhaps sea stars are sufficiently well equipped so that they need not find other mechanisms to compensate long periods of food deprivation. This would tend to support Feder's (1966) observations as described previously. Ferguson (1967) pointed out that it would be difficult to design an experiment in which sea stars were allowed to eat but were prevented from epidermal absorption.

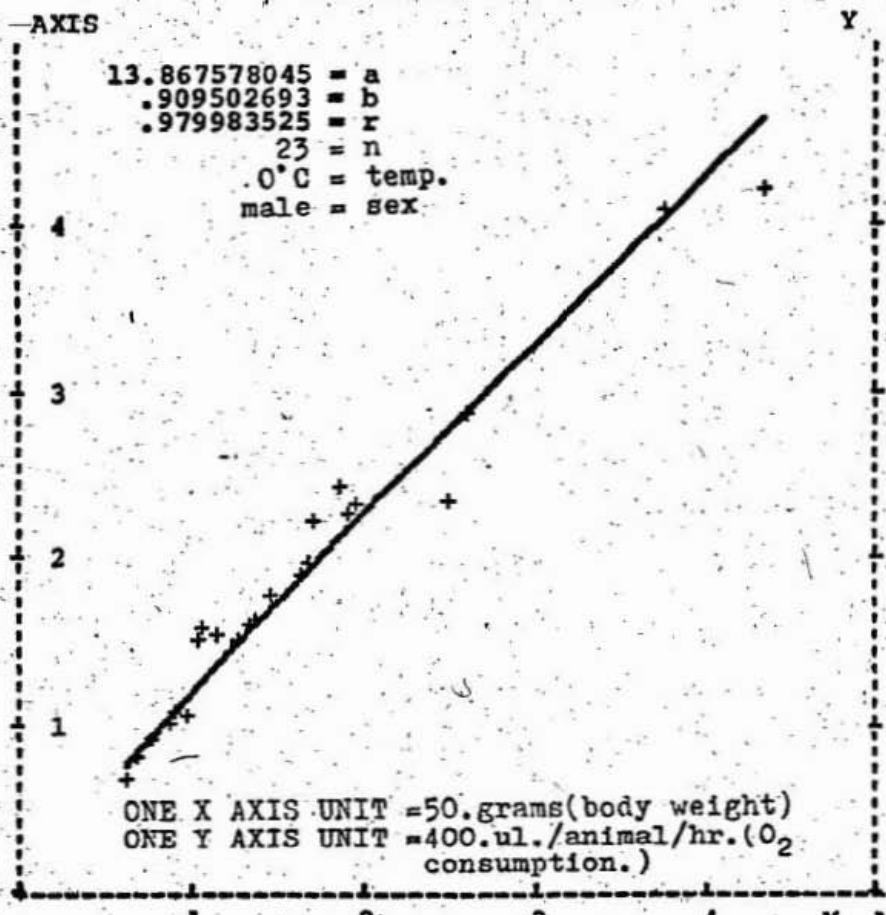
Epidermal absorption of nutritional material did occur, and it was reasonable to conclude that such absorption might be an important factor in the economy of these organisms.

Experimental data described herein illustrates that A. vulgaris and L. polaris have no significant differences both with and without short-term food deprivation. But the oxygen consumption of A. vulgaris when deprived of food is still higher than that of L. polaris, and this implies a possible disadvantage for survival in low temperature for A. vulgaris (Figs. 33-34). In winter few A. vulgaris are found near low water where most mussels live, and mussels are the main food source for A. vulgaris and L. polaris in this area. A. vulgaris migrates to deeper areas during the winter time possibly to avoid severe cold temperatures and rough seas. There, they would have difficulty in obtaining mussels, and it could be assumed that epidermal absorption of nutritional material may play an active role during this time. However, prolonged food deprivation may still affect their activities as Ferguson (1967) pointed out that epidermal absorption of exogenous nutrients was a continuous process while normal feeding was a discontinuous one. The latter provided nutrition for internal regions of body and the former nourished more external tissues. The two processes may balance each other. If the sea star were

Fig. 33

Regression lines of oxygen consumption on body weight at 10° 10 days food deprivation of Asterias vulgaris.

LEAST SQUARE FIT - POWER CURVE ($y = ax^b$)



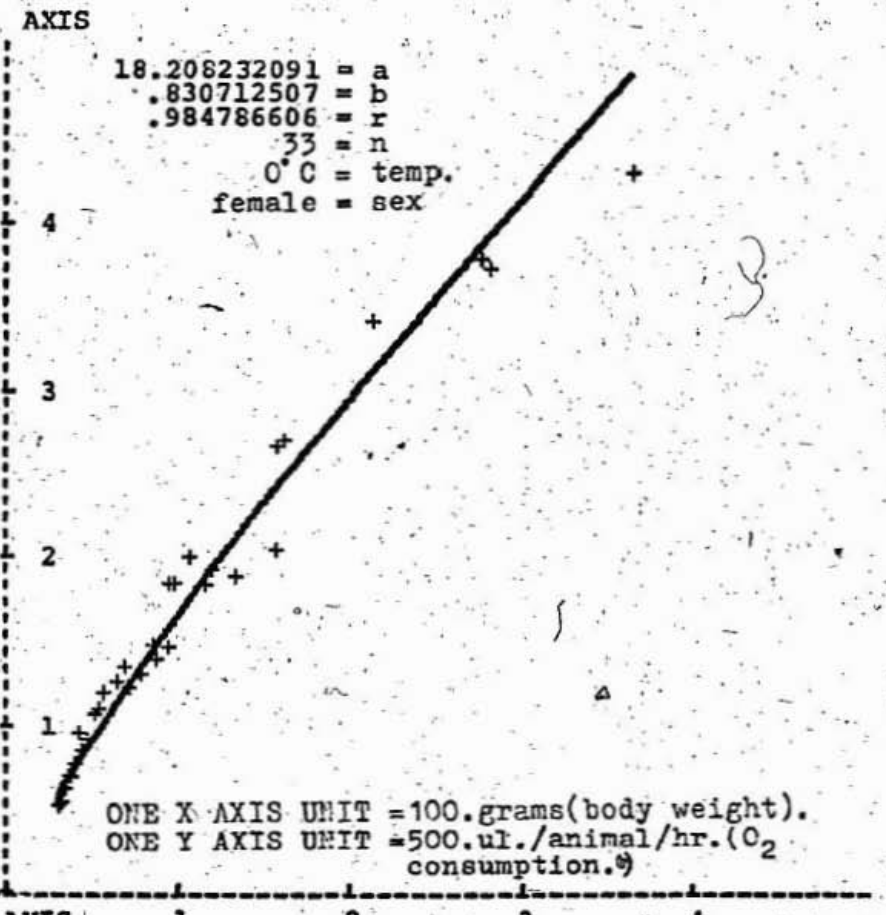
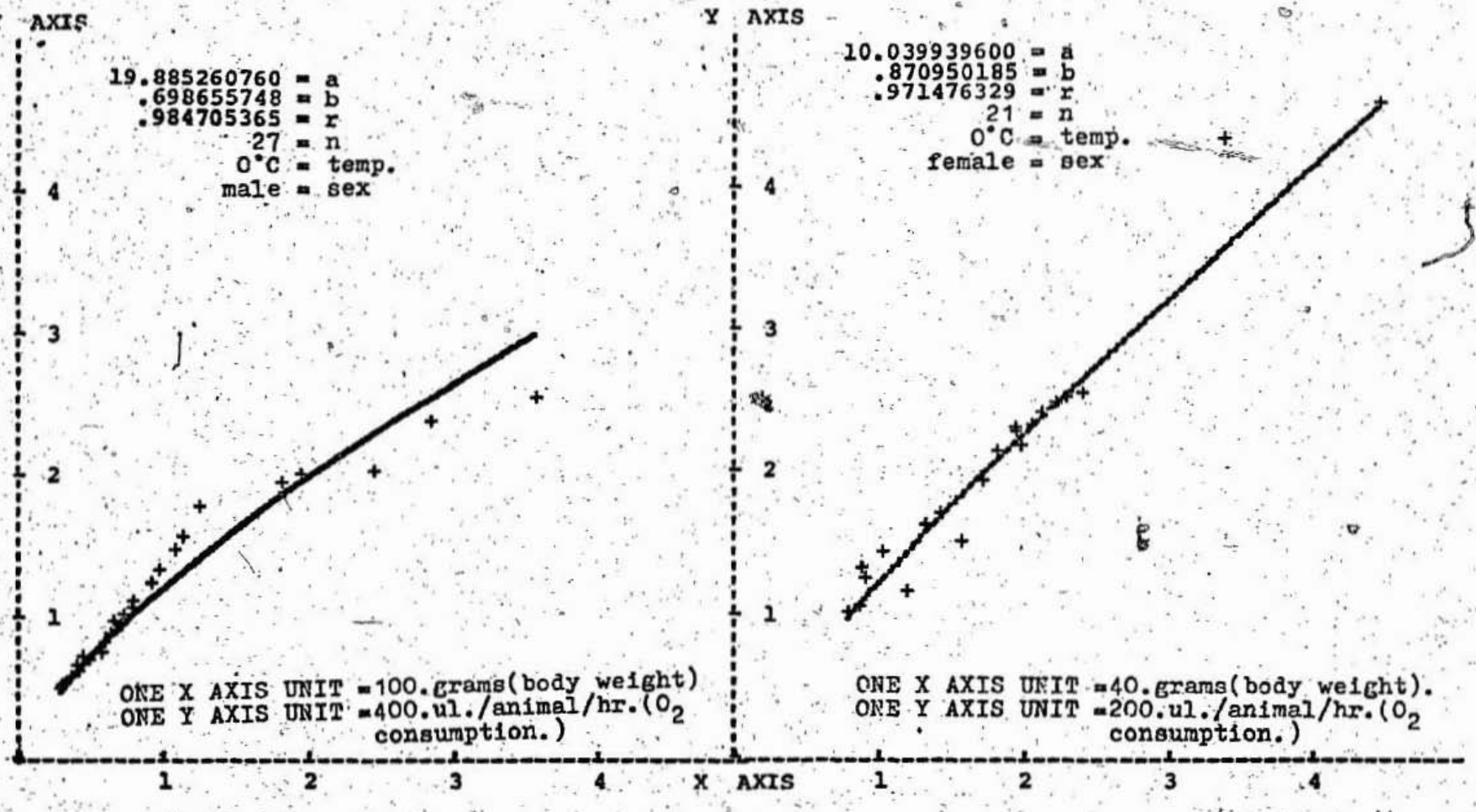



Fig. 34

Regression lines of oxygen consumption on body weight at 10 days food deprivation for Leptasterias polaris.

LEAST SQUARE FIT - POWER CURVE ($y = ax^b$)



prevented from utilizing either one of these sources it might not survive. Apparently, short-term food deprivation at lower temperature seems to have no serious effect on their major physiological activities, but long-term starvation may pose a threat for survival. Furthermore, A. vulgaris could not take up amino acids as well as L. polaris at lower temperature as shown later; also they still maintained higher oxygen consumption than L. polaris for short-term food deprivation. This gives some evidence to explain the distribution of A. vulgaris as limited to boreal regions and that it could not compete with L. polaris in high Arctic regions.

(7) Tissue Respiration

Krebs (1950) investigated the respiration of different mammalian tissues and reported that Q $O_2$ values of tissues in larger animals were usually somewhat lower than the homologous values of the smaller species, with some exceptions. No strict parallelism exists between the Q $O_2$ values of homologous tissues and the basal heat production per unit body weight of the intact animal. Bertalanffy and Pirozynski (1953) showed that the body sizes of organisms have a definite correlation with Q $O_2$ in certain tissues, but not in all. Weymouth et al. (1944) in their investigation on the relation between size and tissue respiration in the kelp crab and other crustaceans found

a decrease in oxygen uptake of tissues with increasing body sizes. Vernberg (1954) studied marine teleosts and agreed with Bertalanffy and Pirozynski's conclusion. Holmes and Scott (1960) noted that the respiration rates of gill and kidney tissues in the cutthroat trout decreased with increasing body weights (very low correlation coefficient and wide variation of values) but the exponent of body weights did not appear in keeping with the surface area rule (0.75).

Giese (1966 and 1967) remarked that the respiratory rate of both body wall and lantern of the sea urchin declined with an increase in body size, and in general, the respiration rates of various tissues of the sea urchin were proportional to their protein content. The data he presented on some sea stars and sea urchins showed body fluids with the lowest respiration rate and testes (mature?) with the highest rate.

Ferguson (1964) pointed out that coelomic fluid was the most important medium of transport and coelomocytes of A. forbesi did not store large amounts of nutrients. The lowest rate of respiration was found in the perivisceral fluid which was low in protein content and was known to have relatively few cells. This suggested that metabolically it was a relatively inert body component (Boolootian and Giese, 1958).

The results of the present study in Tables 6a and 6b show that 20 out of 48 regression lines of the log weight specific metabolism ($\log M = a + b \log W$) have no correlation. Moreover, the exponents with high variation do not always correspond to -0.25 or surface area rule (-0.34). It was surprising that the oxygen consumption rate of gonad tissue in the male of both species at a temperature of 15°C showed a positive regression coefficient, with (b -1) values of 0.73 for L. polaris and 0.68 for A. vulgaris respectively. The correlation coefficient also was significant at level $p < 0.05$. This could be explained if the sea stars used in the experiments were mature and there were more pronounced bursts of sperm activity in both species when the gonads were torn by scissors during experimentation. A greater body weight of the sea star would be likely to produce more sperm, which in turn would contribute to a higher oxygen consumption. The present study was somewhat similar to the previous reports (Krebs, 1950; Bertalanffy and Pirozynski, 1953; Holmes and Scott, 1960), and demonstrated a tendency for a general inverse relationship to exist between oxygen consumption rate by isolated tissues (in vitro) and body size. It still remains unknown if the wide variation of tissue respiration originated from exogenous or endogenous factors. However, the diversified results shown in Tables 6a and 6b created difficulties in comparing intraspecific and interspecific size dependence of tissue

Table 6a. Oxygen consumption rate of various tissues in relation to body weight at 15°C.

| Tissue | Species and Sex | L.polaris (female) | A.vulgaris (female) | L.polaris (male) | A.vulgaris (male) |
|---|---|---|---|---|---|
| | | #N = 21 | N = 32 | N = 17 | N = 20 |
| Gonad | a## | 0.2247 | 0.3624 | 0.0037 | 0.0048 |
| | b### | -0.0028 | -0.1399 | +1.2479 | +1.4051 |
| | r#### | -0.003 | -0.09 | +0.73* | +0.68* |
| Pyloric caecum | a | 1.4986 | 7.3468 | 1.6210 | 0.2763 |
| | b | -0.3967 | -0.8633 | -0.3927 | -0.0273 |
| | r | -0.53* | -0.73* | -0.60* | -0.14 |
| Coelomic fluid | a | 3.604 | 9.8506 | 2.0592 | 8.4429 |
| | b | -0.1676 | -0.0778 | -0.0964 | -0.0318 |
| | r | -0.27 | -0.16 | -0.21 | -0.06 |
| Tube feet | a | 0.5490 | 0.4966 | 0.7744 | 0.3075 |
| | b | -0.3995 | -0.2480 | -0.3770 | -0.1801 |
| | r | -0.77* | -0.20 | -0.62* | -0.38 |
| Stomach | a | 0.6970 | 1.7705 | 0.7246 | 1.1360 |
| | b | -0.3852 | -0.4710 | -0.3368 | -0.2521 |
| | r | -0.68* | -0.49* | -0.59* | -0.54* |
| Body wall | a | 0.2026 | -0.3657 | 0.2002 | 0.1912 |
| | b | -0.1162 | -0.2518 | -0.0998 | -0.0674 |
| | r | -0.26 | -0.42 | -0.29 | -0.20 |

#N = numbers of sea stars
##a = intercept
###b = slope
####r = correlation coefficient

Table 6b. Oxygen consumption rate of various tissues in relation to body weight at 5°C.

| Tissue | Species and Sex | L.polaris (female) | A.vulgaris (female) | L.polaris (male) | A.vulgaris (male) |
|---|---|---|---|---|---|
| | | #N = 19 | N = 20 | N = 17 | N = 18 |
| Gonad | a## | 0.1917 | 0.3744 | 0.0607 | 0.0816 |
| | b### | -0.4762 | -0.5654 | -0.1970 | -0.3031 |
| | r#### | -0.76* | -0.45* | -0.32 | -0.56* |
| Pyloric caecum | a | 0.4532 | 0.6687 | 0.216 | 0.9658 |
| | b | -0.5848 | -0.6883 | -0.4603 | -0.7733 |
| | r | -0.85* | -0.73* | -0.82* | -0.82* |
| Coelomic fluid | a | 2.7699 | 6.9737 | 1.4808 | 5.4172 |
| | b | -0.2036 | -0.3618 | -0.0677 | -0.3547 |
| | r | -0.45* | -0.42 | -0.37 | -0.58* |
| Tube feet | a | 0.2355 | 0.1179 | 0.0362 | 0.1496 |
| | b | -0.5109 | -0.2269 | -0.0941 | -0.4388 |
| | r | -0.66* | -0.29 | -0.26 | -0.46* |
| Stomach | a | 0.5320 | 0.4050 | 0.095 | 0.7499 |
| | b | -0.6815 | -0.5891 | -0.2691 | -0.7810 |
| | r | -0.75* | -0.57* | -0.47* | -0.78* |
| Body wall | a | 0.1911 | -0.0266 | 0.0338 | 0.0463 |
| | b | -0.5915 | -0.0566 | -0.2153 | -0.2460 |
| | r | -0.73* | -0.6 | -0.5* | -0.39 |

#N = numbers of sea stars
##a = intercept
###b = slope
####r = correlation coefficient

metabolism. Therefore a certain range in Table 7a and 7b (40-60g) of sea stars was selected to increase the reliability, and the Student-Newman-Koul test was performed in order to collate with differences between interspecies or intraspecies. Table 8 shows that oxygen consumption of coelomic fluid has the lowest oxygen consumption rate among the tissues within a species and is significantly different from the rest of the tissues. It is expected that the coelomic fluid has only a few living cells and thus would consume less oxygen. The gonads of the male in both species at 15°C had the highest rate, which was significantly different from the rest of the tissues. This has been explained previously. Although there was no significant difference in the oxygen consumption rate of body wall, tube feet, stomach, pyloric caeca and gonad (immature or at low temperatures), we can still detect that the body wall always has the lowest rate of oxygen consumption. The body wall possibly has a low oxygen consumption because the composition of the body wall is mostly non-living skeletal plate. When comparing the other tissues, gonads showed very low metabolism if they are immature or under lower temperature conditions. However, contrary to Giese's finding, the tube feet did not always show higher oxygen consumption rate, but the pyloric caecum showed the highest oxygen consumption rate. In fact these tissues--the tube feet, gonad (immature), stomach and pyloric caecum--indicated no significant difference among

Table 7a. Oxygen consumption rate (µl/mg/hr) of various tissues in sea star at temperature 5°C (body weight of sea star, range from 40 g to 60 g).

| Species & Sex | Body weight | Gonad | Pyloric caecum | coelomic fluid# | tube feet | stomach | body wall |
|---|---|---|---|---|---|---|---|
| | 46.29 | 0.028 | 0.042 | 1.416 | 0.029 | 0.040 | 0.017 |
| L.polaris | 51.97 | 0.031 | 0.040 | 1.204 | 0.025 | 0.032 | 0.022 |
| | 53.28 | 0.029 | 0.046 | 1.127 | 0.024 | 0.031 | 0.015 |
| (female) | 57.12 | 0.033 | 0.039 | 1.049 | 0.030 | 0.029 | 0.018 |
| | 58.36 | 0.032 | 0.045 | 0.386 | 0.036 | 0.036 | 0.015 |
| | 43.76 | 0.039 | 0.055 | 3.583 | 0.048 | 0.061 | 0.017 |
| A.vulgaris | 44.50 | 0.029 | 0.058 | 1.227 | 0.047 | 0.043 | 0.020 |
| | 48.39 | 0.044 | 0.038 | 1.246 | 0.050 | 0.027 | 0.019 |
| (female) | 48.50 | 0.060 | 0.047 | 1.365 | 0.094 | 0.067 | 0.033 |
| | 50.26 | 0.046 | 0.043 | 1.925 | 0.046 | 0.021 | 0.013 |
| | 45.81 | 0.027 | 0.036 | 1.197 | 0.026 | 0.045 | 0.015 |
| L.polaris | 47.26 | 0.025 | 0.037 | 1.257 | 0.025 | 0.032 | 0.020 |
| | 49.87 | 0.046 | 0.038 | 1.279 | 0.029 | 0.037 | 0.011 |
| (male) | 50.92 | 0.033 | 0.031 | 1.254 | 0.019 | 0.025 | 0.011 |
| | 58.34 | 0.025 | 0.033 | 1.096 | 0.022 | 0.031 | 0.020 |
| | 46.35 | 0.022 | 0.046 | 1.388 | 0.037 | 0.046 | 0.024 |
| A.vulgaris | 48.17 | 0.025 | 0.053 | 1.271 | 0.015 | 0.027 | 0.015 |
| | 54.78 | 0.026 | 0.037 | 1.062 | 0.019 | 0.038 | 0.018 |
| (male) | 56.42 | 0.027 | 0.040 | 1.179 | 0.034 | 0.029 | 0.026 |
| | 58.16 | 0.027 | 0.045 | 1.265 | 0.031 | 0.039 | 0.014 |

#µl/cc/hr $O_2$ consumption rate.

Table 7b. Oxygen consumption rate (µl/mg/hr) of various tissues in sea star at temperature 5°C (body weight of sea star range from 40 g to 60 g).

| Species & Sex | Body weight | Gonad | pyloric caecum | coelomic fluid# | tube feet | stomach | body wall |
|---|---|---|---|---|---|---|---|
| | 46.29 | 0.189 | 0.168 | 2.263 | 0.166 | 0.175 | 0.159 |
| L.polaris | 47.80 | 0.365 | 0.297 | 2.420 | 0.146 | 0.166 | 0.112 |
| | 49.00 | 0.095 | 0.135 | 2.313 | 0.140 | 0.146 | 0.129 |
| (female) | 53.00 | 0.213 | 0.305 | 1.625 | 0.139 | 0.165 | 0.175 |
| | 54.88 | 0.228 | 0.169 | 2.054 | 0.159 | 0.143 | 0.158 |
| | 45.25 | 0.284 | 0.227 | 9.292 | 0.194 | 0.429 | 0.105 |
| A.vulgaris | 46.45 | 0.127 | 0.221 | 7.928 | 0.158 | 0.280 | 0.135 |
| | 54.14 | 0.209 | 0.310 | 7.135 | 0.114 | 0.189 | 0.106 |
| (female) | 55.23 | 0.214 | 0.280 | 6.232 | 0.486 | 0.278 | 0.133 |
| | 58.49 | 0.289 | 0.198 | 6.285 | 0.324 | 0.394 | 0.137 |
| | 45.27 | 0.235 | 0.302 | 1.246 | 0.235 | 0.215 | 0.115 |
| L.polaris | 48.86 | 0.251 | 0.315 | 0.828 | 0.130 | 0.238 | 0.136 |
| | 51.54 | 1.205 | 0.403 | 1.137 | 0.176 | 0.209 | 0.140 |
| (male) | 52.71 | 0.266 | 0.311 | 1.624 | 0.183 | 0.194 | 0.128 |
| | 56.23 | 1.049 | 0.346 | 1.548 | 0.193 | 0.128 | 0.152 |
| | 42.85 | 0.682 | 0.271 | 9.584 | 0.139 | 0.509 | 0.123 |
| A.vulgaris | 47.52 | 0.353 | 0.261 | 8.541 | 0.159 | 0.426 | 0.168 |
| | 51.93 | 1.926 | 0.243 | 7.962 | 0.167 | 0.483 | 0.163 |
| (male) | 55.29 | 2.132 | 0.269 | 8.486 | 0.166 | 0.327 | 0.158 |
| | 56.74 | 2.410 | 0.274 | 7.399 | 0.142 | 0.415 | 0.161 |

#µl/cc/hr $O_2$ consumption rate

Table 8. Comparisons of oxygen consumption rate (µl/mg/hr) of various tissues in sea star within a species under temperatures 15°C and 5°C (based on body weight of sea star. Range from 40 g to 60 g; and the Student-Newman-Keuls test were used to measure difference among means. ($p < 0.05$)

| Species | Temp. | Sex | Tissues: | | | | | |
|---|---|---|---|---|---|---|---|---|
| L.polaris | 15°C | female | Body wall ##0.146 | Tube feet 0.1500 | Stomach 0.1590 | Pyloric caecum 0.2150 | Gonad 0.2180 | Coelomic fluid 2.135# |
| A.vulgaris | 15°C | female | Body wall 0.1232 | Gonad 0.2246 | Pyloric Caecum 0.247 | Tube feet 0.2550 | Stomach 0.314 | Coelomic fluid 7.3744# |
| L.polaris | 15°C | male | Body wall 0.1342 | Tube feet 0.1834 | Stomach 0.1968 | Pyloric caecum 0.3354 | Gonad### 0.6012 | Coelomic fluid 1.4766# |
| A.vulgaris | 15°C | male | Body wall 0.1546 | Tube feet 0.1546 | Pyloric caecum 0.2636 | Stomach 0.4320 | Gonad 1.5060### | Coelomic fluid 8.3948# |
| L.polaris | 5°C | female | Body wall 0.0174 | Tube feet 0.0288 | Gonad 0.0302 | Stomach 0.0336 | Pyloric caecum 0.0424 | Coelomic fluid 1.1564# |
| A.vulgaris | 5°C | female | Body wall 0.0204 | Gonad 0.0432 | Stomach 0.0438 | Pyloric caecum 0.0482 | Tube feet 0.0570 | Coelomic fluid 1.8692# |
| L.polaris | 5°C | male | Body wall 0.0154 | Tube feet 0.024 | Gonad 0.0312 | Stomach 0.0340 | Pyloric caecum 0.0350 | Coelomic fluid 1.2166# |
| A.vulgaris | 5°C | male | Body wall 0.0194 | Gonad 0.0254 | Tube feet 0.0272 | Stomach 0.0358 | Pyloric caecum 0.0442 | Coelomic fluid 1.233# |

#µl/cc/hr $O_2$ consumption rate

##Double underlines indicate not significantly different among them.

###Mature

them in terms of oxygen consumption rate.

Thus, it can be concluded that body wall and coelomic fluid consume less oxygen among the tissues within a species regardless of temperature. Table 9 shows that the difference of oxygen consumption in different tissues between species and sex are inconsistent, but overall A. vulgaris had a higher average oxygen consumption rate than L. polaris at two different temperatures. It is difficult to explain why the oxygen consumption rate of coelomic fluid of A. vulgaris at 15°C increased so much, but not in L. polaris. Is it possible for A. vulgaris to increase its activities of coelomocytes at this temperature which is almost the upper limit of L. polaris and in turn contribute to a higher oxygen consumption rate of coelomic fluid?

It is expected that high $Q_{10}$ values in gonads of male A. vulgaris and L. polaris (Table 10) especially in A. vulgaris is a particular case, because gonads in low temperatures are immature and inactive. The gonads of the male A. vulgaris are mature and sperm are actively functioning at higher temperatures, therefore high $Q_{10}$ values are obtained. On the other hand, $Q_{10}$ values in the male gonads of L. polaris are not as high as A. vulgaris. This could be because L. polaris in the range of body weight (40-60g) were not so mature, or it could be that the sperm were more active than in A. vulgaris.

Table 9. Comparisons of oxygen consumption rate (µl/mg/hr) in various tissues among sea stars under temperatures 15°C and 5°C (based on Table 1 and the Student-Newman-Keuls tests were used to measure difference among means $p < 0.05$)

| Temp. | Tissue | Species and Sex | | | |
|---|---|---|---|---|---|
| 5°C | Gonad | A.vulgaris (M)## | L.polaris (F)### | L.polaris (M) | A.vulgaris (F) |
| | | #### 0.0254 | 0.0302 | 0.0312 | 0.0432 |
| 5°C | Pyloric caeum | L.polaris (M) | L.polaris (F) | A.vulgaris (M) | A.vulgaris (F) |
| | | 0.0350 | 0.0424 | 0.0442 | 0.0482 |
| 5°C | Coelomic fluid# | L.polaris (F) | L.polaris (M) | A.vulgaris (M) | A.vulgaris (F) |
| | | 1.1564 | 1.2166 | 1.2330 | 1.8692 |
| 5°C | Tube feet | L.polaris (M) | A.vulgaris (M) | L.polaris (F) | A.vulgaris (F) |
| | | 0.0240 | 0.0272 | 0.0288 | 0.057 |
| 5°C | Stomach | L.polaris (F) | L.polaris (M) | A.vulgaris (M) | A.vulgaris (F) |
| | | 0.0336 | 0.0340 | 0.0358 | 0.0438 |
| 5°C | Body wall | L.polaris (M) | L.polaris (F) | A.vulgaris (M) | A.vulgaris (F) |
| | | 0.0154 | 0.0174 | 0.0194 | 0.0204 |
| 15°C | Gonad | L.polaris (F) | A.vulgaris (F) | L.polaris (M) | A.vulgaris (M) |
| | | 0.2180 | 0.2246 | 0.6012 | 1.5006 |
| 15°C | Pyloric caecum | L.polaris (F) | A.vulgaris (F) | A.vulgaris (M) | L.polaris (M) |
| | | 0.2150 | 0.2470 | 0.2636 | 0.3354 |
| 15°C | Coelomic fluid# | L.polaris (M) | L.polaris (F) | A.vulgaris (F) | A.vulgaris (M) |
| | | 1.4766 | 2.135 | 7.3744 | 8.3942 |
| 15°C | Tube feet | L.polaris (F) | A.vulgaris (M) | L.polaris (M) | A.vulgaris (M) |
| | | 0.1500 | 0.1546 | 0.1834 | 0.2550 |
| 15°C | Stomach | L.polaris (F) | L.polaris (M) | A.vulgaris (F) | A.vulgaris (M) |
| | | 0.159 | 0.1968 | 0.314 | 0.432 |
| 15°C | Body wall | A.vulgaris (F) | L.polaris (M) | L.polaris (F) | A.vulgaris (M) |
| | | 0.1232 | 0.1342 | 0.1460 | 0.1546 |

#µl/cc/hr $O_2$ consumption rate ###F = female

##M = male. #### Double underline indicates no significant difference among them.

Table 10. $Q_{10}$ values 5°C - 15°C (body weight 40 - 60 g)

| Species | Sex | Gonad | Pyloric caecum | Coelomic fluid | Tube feet | Stomach | Body wall |
|---|---|---|---|---|---|---|---|
| L.polaris | (F) | 7.2185 | 5.0708 | 1.8462 | 5.2083 | 4.7321 | 8.3908 |
| L.polaris | (M) | 19.2692 | 9.5829 | 1.2137 | 7.6417 | 5.7882 | 8.7143 |
| A.vulgaris | (F) | 5.1990 | 5.1245 | 3.9452 | 4.4737 | 7.1689 | 6.0392 |
| A.vulgaris | (M) | 59.0787 | 5.9638 | 6.8080 | 5.6838 | 12.0670 | 7.9691 |

at 5°C. $Q_{10}$ values of the tissues in the male of both species (if gonad is omitted due to active functional sperm) are higher than those for the female. Apparently, it seems to be that the males of both species were slightly more sensitive to the change of temperature; however, there is no evidence to confirm this phenomenon. $Q_{10}$ at the tissue level in both species showed no significant differences. Temperature coefficient characteristics showed that L. polaris is not more advantaged than A. vulgaris (a low $Q_{10}$ would indicate more success in adapting to low temperature). It may be true that $Q_{10}$ values at temperatures at 0°C and below 0°C display different characteristics.

8. The Moving Speed and Righting Response Time of Sea Stars

(A) The Moving Speed of Sea Stars

As shown above, the moving speed of A. vulgaris is faster than L. polaris at each temperature. At the lower temperature (0°C), although the moving speed of A. vulgaris is higher than that of L. polaris, A. vulgaris has slowed down considerably more than L. polaris. This phenomenon perhaps indicates that A. vulgaris is still able to survive at the lower temperature; but is not so well adapted as L. polaris.

Table 11. Statistical analysis of moving speed and body weight with comparison between species under different temperatures.

| Species | Temp.(°C) | Average moving speed (cm/min.) ± standard deviation | Correlation coefficient (body wt. and moving speed) |
|---|---|---|---|
| A.vulgaris | 15 | 9.19 ± 2.19 | $r_{10;0.05} = -0.2957$ (N.S.) |
| L.polaris | 15 | 6.72 ± 2.29 | $r_{10;0.05} = -0.04$ (N.S.) |
| A.vulgaris | 0 | 5.40 ± 1.31 | $r_{18;0.05} = -0.1797$ (N.S.) |
| L.polaris | 0 | 4.32 ± 1.25 | $r_{22;0.05} = 0.2073$ (N.S.) |

For each species the moving speed at different temperatures or for each temperature. The moving speed of different species were compared by using t test.

In A.vulgaris (between 0°C & 15°C) $t_{df = 30} = 6.080$*

L.polaris (between 0°C & 15°C) $t_{df = 30} = 3.843$*

0°C (between A.vulgaris & L.polaris) $t_{df = 28} = 2.667$*

15°C (between A.vulgaris & L.polaris) $t_{df = 22} = 2.67$*

*Tested and found to be significant difference at p = 0.05.

(B) The Righting Response of Sea Stars

Table 12. Statistical analysis of righting response time and body weight (regression lines) with comparison between species under different temperature.

| No. | Species | Temp. (°C) | $a_i$ (intercept) | $b_i$ X (slope) | r (correlation coefficient) |
|---|---|---|---|---|---|
| 1 | A.vulgaris | 0 | 406.8954 | 4.2571 | 0.55* (N=18) |
| 2 | L.polaris | 0 | 377.8874 | 6.8431 | 0.68* (N=22) |
| 3 | L.polaris | 15 | -47.3734 | 4.12138 | 0.88* (N=10) |
| 4 | A.vulgaris | 15 | 53.9618 | 1.3397 | 0.79* (N=14) |

Hypothesis test: (same methods were used as described previously).

| | Hypothesis | t ratio | Hypothesis | t ratio |
|---|---|---|---|---|
| 1-2 | $a_1=a_2$ | -0.2408 (N.S.) | $b_1=b_2$ | 1.325 (N.S.) |
| 1-4 | $a_1=a_4$ | -3.208* | $b_1=b_4$ | -1.9712 (N.S.) |
| 2-3 | $a_2=a_3$ | 2.338* | $b_2=b_3$ | 0.981 (N.S.) |
| 3-4 | $a_3=a_4$ | -0.564 (N.S.) | $b_3=b_4$ | -1.137 (N.S.) |

The regression lines shown in Table 12 and Figs. 35 and 36 between species at each temperature do not show a statistically significant difference, but examination shows the t ratio of the slope between the two species at each temperature is much higher than the t ratio of the intercept. Even the slope between species at each temperature was not significantly different statistically. We can still detect that the larger specimens of A. vulgaris

Fig. 35

Regression lines of righting response time on body weight at 0°C for sea stars.

LINEAR REGRESSION ANALYSIS (y = a(0) + a(1)x )

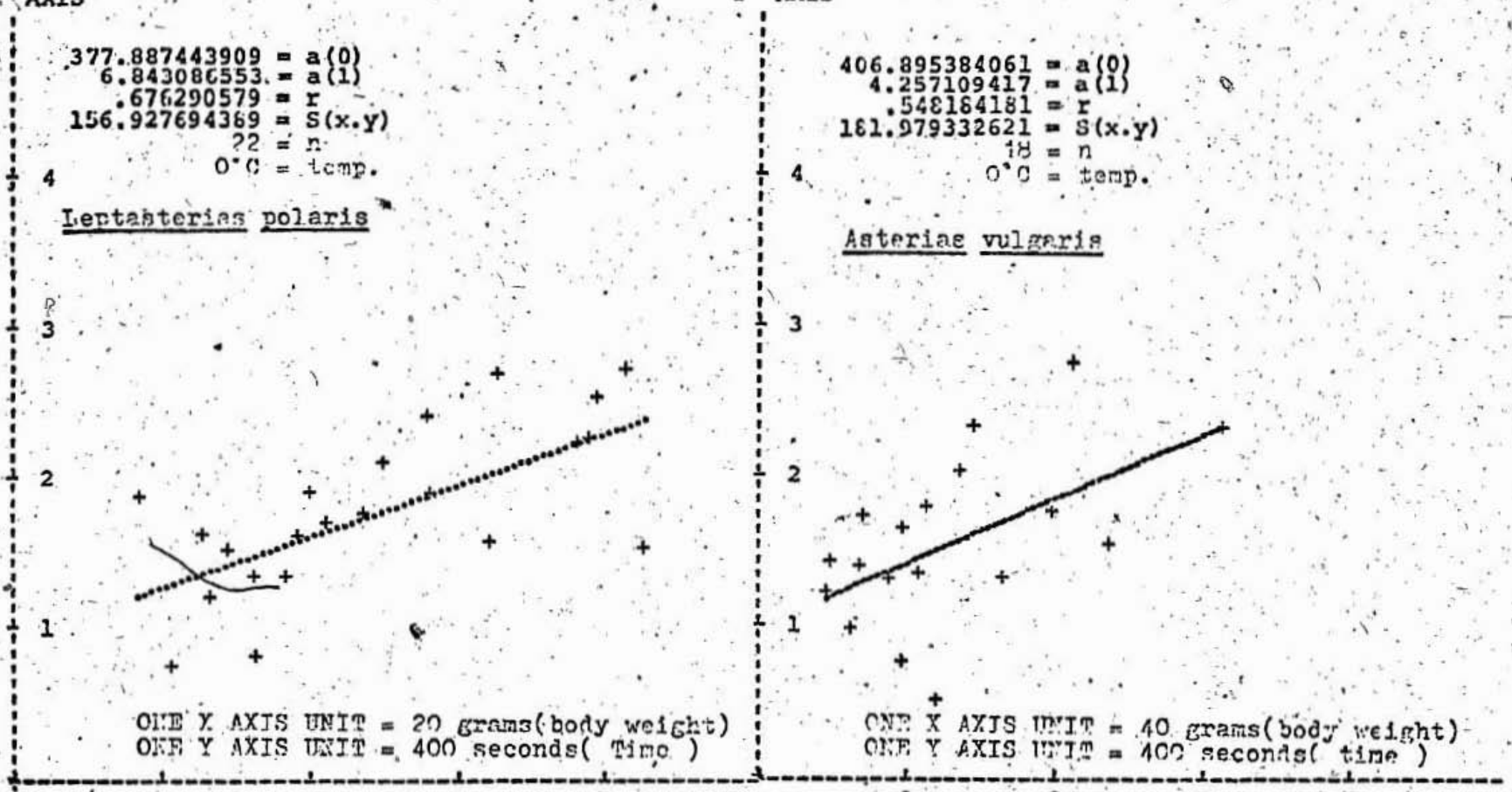


Fig. 36

Regression lines of $t_R$ righting response time on body weight at 15°C for sea stars.

LINEAR REGRESSION ANALYSIS (y = a(0) + a(1)x )

Y AXIS

-47.373358458 = a(0)
4.121383296 = a(1)
.883188967 = r
43.929274959 = S(x.y)
10 = n
15°C = temp.

Leptasterias polaris

ONE X AXIS UNIT = 40 grams(body weight)
ONE Y AXIS UNIT = 100 seconds( Time )

Y AXIS

53.961814662 = a(0)
1.339747913 = a(1)
.788074694 = r
47.503853492 = S(x.y)
14 = n
15°C = temp.

Asterias vulgaris

ONE X AXIS UNIT = 40 grams(body weight)
ONE Y AXIS UNIT = 100 seconds( Time )

X AXIS

required less righting time than L. polaris at the same temperature. This is due to the larger L. polaris being more calcified. They are stiffer and less flexible than A. vulgaris, so they have a longer righting time. However, temperature has the most predominant effect on righting reaction time over a wide range of body weight. This implies that at higher temperature the physiological activities are accelerated and the righting reaction time will be shorter within a certain range. Each regression line indicates that with an increase in body size there is an increase in righting reaction time within a species of asteroid. In this study, I should add observation that the larger L. polaris usually perform the tulip method for righting themselves. In this method, the righting time was longer. Some L. polaris even took more than two hours. This righting method would have less survival advantage. However, the tube feet of L. polaris are quite strong and their pulling capacity is higher than A. vulgaris (personal observation), therefore they would be less likely to be turned onto their aboral surface by physical factors (e.g., currents, turbulence, etc.), and this might compensate for the weak point described above.

(9) Labelled Amino Acid Uptake of Tissues at Different Temperatures

Data from preliminary experiments revealed that alanine uptake by pyloric caeca of sea stars is approximately linear for up to three hours. Therefore an incubation period of three hours was chosen for all subsequent

uptake experiments.

Uptake of amino acid was measured on groups of sea stars of approximately the same body size at 0°C and 15°C for both L. polaris and A. vularis (Table 13). Mean specific activity levels and standard deviations were as follows:

At 0°C were 354 cpm/$OD^{280}$ ± 21.2132 for A.vulgaris (N=4)

and 480 cpm/$OD^{280}$ ± 93.6098 for L.polaris (N=5)

At 15°C were 989 cpm/$OD^{280}$ ± 139.9220 for A.vulgaris (N=5)

and 814 cpm/$OD^{280}$ ± 59.2984 for L.polaris (N=5).

Student's t test was used to test for significant differences ($p < 0.05$) between the means, as shown in the table. The amino acid uptake of L. polaris was 1.36 times higher than that of A. vulgaris at 0°C. On the other hand, uptake in A. vulgaris was about 1.21 times higher than in L. polaris at 15°C.

The oxygen consumption rate of L. polaris is much lower than that of A. vulgaris at 0°C, but its uptake of amino acid is higher than in A. vulgaris. This implies that L. polaris may be able to channel some share of its food into protein assimilation and also that L. polaris may continue to function satisfactorily and even to grow in this lower thermal range. On the other hand, at the higher temperature (15°C), the metabolic rate of L. polaris is almost the same as that of A. vulgaris, as shown in the previous results, but the uptake of amino acid is reversed.

A review of the distribution of these two species indicates that L. polaris is a boreal and Arctic species

Table 13. Amino acid (alanine) uptake by the pyloric caecum of sea star.

| Temp. | Species | Sex | Body Weight | Specific Activity cpm/OD$^{280}$ 1 hr | 2 hr | 3 hr | |
|---|---|---|---|---|---|---|---|
| 0°C | A.vulgaris | Female | 54.71 | 256 | 280 | 329 | Average $\bar{X}$ = 354 (3 hr) |
| | A.vulgaris | Female | 58.24 | 160 | 440 | 374 | |
| | A.vulgaris | Male | 42.78 | | | 344 | Standard Deviation = 21.2132 (N=4) |
| | A.vulgaris | Male | 51.37 | | | 369 | |
| | L.polaris | Male | 60.53 | 411 | 473 | 593 | Average $\bar{X}$ = 480.4 (3 hr) |
| | L.polaris | Male | 64.33 | 369 | 537 | 565 | |
| | L.polaris | Male | 49.11 | | | 387 | Standard Deviation = 93.6098 (N=5) |
| | L.polaris | Male | 55.65 | | | 452 | |
| | L.polaris | Male | 61.70 | | | 405 | |
| 15°C | A.vulgaris | Female | 54.76 | 432 | 927 | 959 | Average $\bar{X}$ = 989.2 (3 hr) |
| | A.vulgaris | Male | 58.92 | 491 | 615 | 807 | |
| | A.vulgaris | Male | 65.10 | 522 | 906 | 1197 | Standard Deviation = 139.922 (N=5) |
| | A.vulgaris | Female | 45.09 | | | 969 | |
| | A.vulgaris | Female | 42.39 | | | 1014 | |
| | L.polaris | Male | 67.41 | 582 | 839 | 853 | Average $\bar{X}$ = 814.4 (3 hr) |
| | L.polaris | Male | 59.28 | 625 | 881 | 896 | |
| | L.polaris | Male | 56.70 | 368.9 | 639 | 793 | |
| | L.polaris | Female | 51.04 | | | 748 | Standard Deviation = 59.2984 (N=5) |
| | L.polaris | Female | 62.04 | | | 782 | |

t test for the difference of the mean between the species & between temp.within species

$t_{0°C}$(A.v.& L.p)=1.54 (N.S.) df = 7

$t_{15°C}$(A.v.& L.p.)=1.199 (N.S.) df = 8

$t_{A.v}$(0°C & 15°C)=0.263 (N.S.) df = 7

$t_{L.p}$(0°C & 15°C)=0.269 (N.S.) df = 8

t test for the difference of the mean between the species & between temp.within species

$t_{0°C}$(A.v.& L.p)=2.6129* df = 7

$t_{15°C}$(A.v.&L.p)=2.572* df = 8

t test for the difference of the mean between the species & between temp.within species

$t_{A.v}$(15°C & 0°C)=8.876* df = 7

$t_{L.p}$(15°C & 0°C)=6.739* df = 8

and is rarely found in regions above 15°C. Perhaps this temperature is the upper limit for its range, whereas A. vulgaris is a temperate species and at low temperature (0°C) probably approach their lower range limit. They may be able to tolerate a short-term period of exposure to upper or lower limits without any harm to their physiological function, but long-term existence under such conditions may lead to severe damage to physiological processes and pose a threat to its survival.

(10) The Geographic Distribution of Asterias vulgerias and Leptasterias polaris

Verrill (1895) reported that the distribution of A. vulgaris ranged from 0 to 350 fathoms (0-640m). He indicated that it could be found in shallow water from the eastern part of Long Island Sound to Labrador; in deep water it ranged southward as far as off Cape Hatteras. Gray et al. (1968) also showed that this species was distributed from Labrador to Cape Hatteras. However, Grainger (1964) in his report of the Blue Dolphin Expedition to Labrador, stated that existence of this species had not been verified from the Strait of Belle Isle or north of there, and therefore it was not properly a member of the Labrador fauna. A. vulgaris may be shown to reach Caribou Island in the Strait of Belle Isle, but it was doubtful that it reached farther northward from the above area. He did not include A. vulgaris in the list in his book

"Sea Stars of Arctic North America" (Grainger, 1966). Parkard (1863) collected this species near Caribou Island which is situated in the extreme northeast corner of the Gulf of St. Lawrence in Québec, near the entrance to the Strait of Belle Isle. On the other hand, A. vulgaris has been found at Cow Head, Northern Peninsula, Newfoundland (Lilly, 1968). Mr. Robert Hooper (personal communication), in his investigation at the entrance to the Strait of Belle Isle, mentioned that A. vulgaris did occur on the west coast of Newfoundland and at St. Anthony. He further stated that A. vulgaris was very widely distributed over the entire coast of Newfoundland, but he failed to find this species on the coast around the Québec and Labrador border, or further north. His account agreed with Grainger's (1964) statement.

Bousfield (1951) showed the distribution of certain pelagic Amphipoda in the Strait of Belle Isle was correlated with ocean currents. In general, the cold Labrador current flows into the Gulf along the north side of Belle Isle Strait, and warm water from the Gulf of St. Lawrence moves out to the Atlantic Ocean along the south side of the Strait. In a study of geostrophic currents in this area, Bailey (1958) and El-Sabh (1974), also reported an inward movement of Labrador coast water on the Labrador side and an outflow of the Gulf water on the Newfoundland side. A possible explanation why few A. vulgaris were found on the

Labrador side of the Strait of Belle Isle could be that the Labrador current would sweep any pelagic larvae of A. vulgaris (planktonic type) farther south. On the other hand, the outflow of Gulf water moving to the tip of the Northern Peninsula of Newfoundland is deflected by the main Labrador cold current and flows to the east coast of the Northern Peninsula, so that A. vulgaris is found in that area. Hence, A. vulgaris, just as the amphipods mentioned by Bousfield (1951), can be considered as an indicator of water from the Gulf of St. Lawrence. A. vulgaris can be found from Québec to Massachusetts around the shore, but farther south most A. vulgaris are found in deeper cold water. Ernst (1967) showed that A. vulgaris were distributed around the east coast (Atlantic side) of Long Island, New York, but not inside Long Island Sound, where he could collect only A. forbesi. He also collected some A. vulgaris along the New Jersey coast, but they were not as common as A. forbesi. Bell (quoted by Whiteaves, 1901) reported the presence of A. vulgaris at the entrance of Hudson Strait. This, however, is questionable because the low temperature would not be suitable for their survival, and his record is undoubtedly an error.

Tortonese (1963) proposed that A. vulgaris was conspecific to A. rubens. O'Brien (1973) in his Ph.D. thesis used the name A. rubens instead of these two species. Unfortunately, the few specimens of A. rubens and A. forbesi

that I have examined were not in good condition. Following Coe's classification, I found that A. rubens would be rather closer to A. vulgaris than to A. forbesi, especially in the presence of spines forming a rather distinct median longitudinal row on the aboral side of each ray. The row is indistinct in A. forbesi. Also the rays are pointed at the ends whereas the tips of A. forbesi are more rounded.

Loosanoff (1954) reported that the average length of the pelagic period of larva of A. forbesi was about 52 days. If A. vulgaris has a similar average time then this time period might be sufficient for transportation of the larvae across the Atlantic Ocean, so it is possible that A. rubens in Europe may have originated from North America.

Mortensen (1932) pointed out that A. rubens found on the west coast of Greenland might have come from Europe or from the Atlantic coast of North America, and suggested that A. rubens could have been transported there on the bottom of some ships, and that transportation of the larva to West Greenland by the currents seems very improbable. Mortensen further stated as follows:

> However, the matter is not so simple. The fact mentioned above that a large specimen of A. rubens was taken already in 1895 by the Ingolf Expedition off the Ameralik Fjord proves that its appearance in the Greenland Sea cannot be due to the increase in temperature in the very latest years. Also, the possible identity of the North American A. vulgaris with the North European A. rubens makes it quite possible that the species in question may have immigrated into the Greenland Sea from the North American coasts, not from the Europe seas.

> But whichever way it has come, the recent appearance of this sea star in the Greenland Sea is an event of very considerable zoogeographical interest.

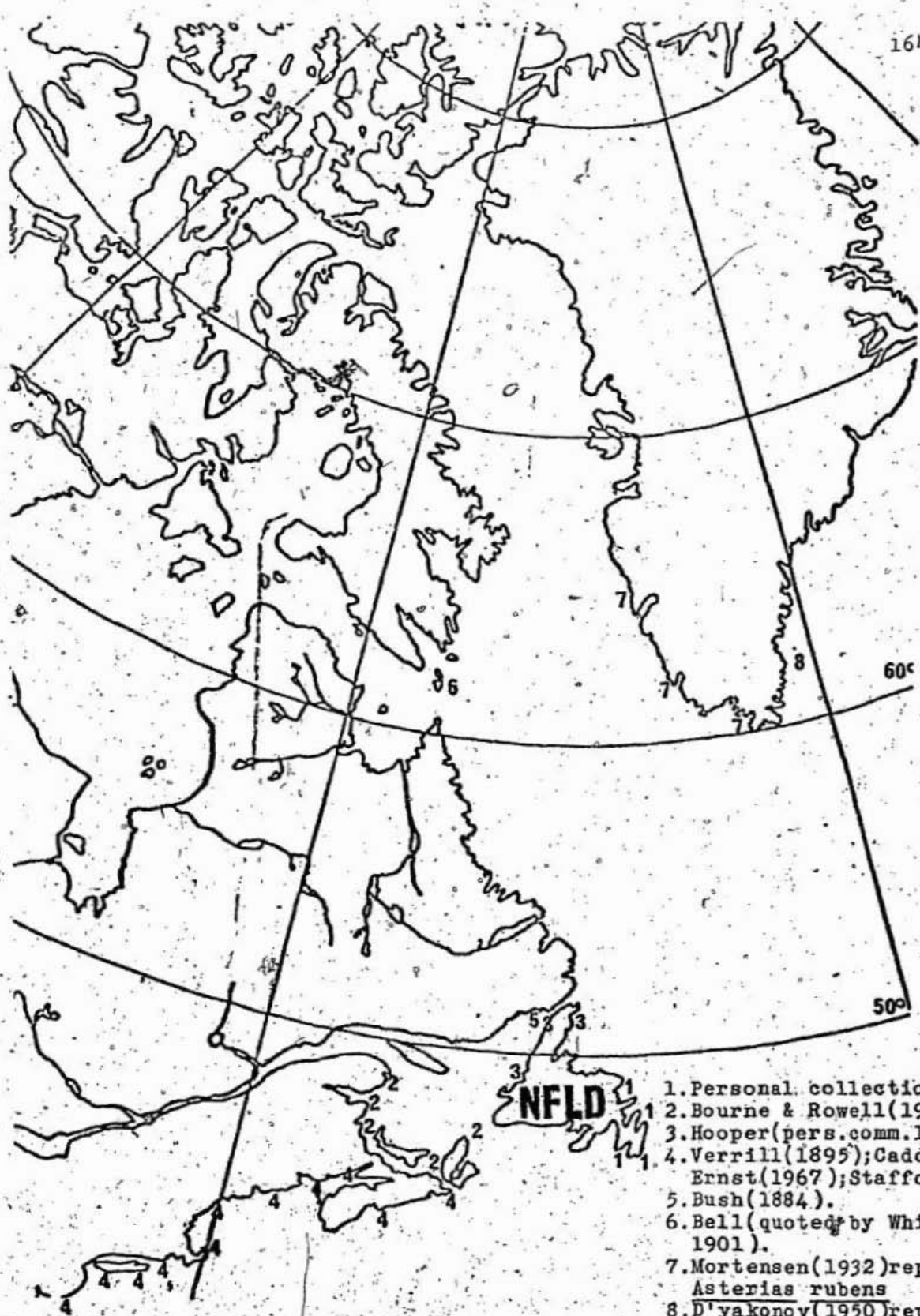
The question to be answered is why A. vulgaris are not found on the Labrador coast, but are found on the west coast of Greenland (if A. vulgaris = A. rubens). Transportation on a ship bottom seems highly unlikely since the adhesive power of A. vulgaris is rather weak and they would easily have been dislodged by the ship moving through the water. It seems possible that these two species avoid the high Arctic cold currents like the Labrador and Eastern Greenland current, and that the warmer Irminger current from Europe contribute to their presence off west Greenland.

L. polaris is a highly variable species. It has been reported as distributed from George's Bank and New England to Greenland (Verrill, 1895; Grainger, 1964), but a review of the literature shows that this species has been found in the Gulf of St. Lawrence, off the Nova Scotia coast (Atlantic side) and George's Bank, but not right on the coast of New England and New Brunswick. Apparently this species is adapted to cold temperatures and is only distributed in deep water further south. The larvae of L. polaris are brooded by the mother. This phenomenon is very common in Arctic and Antarctic species of sea stars. There are many advantages to brooding, as Chia (1964) suggested. Because the larvae of L. polaris

are not pelagic as are those of A. vulgaris, the surface movement of ocean currents would not affect its distribution as much as A. vulgaris. Instead, the warmer water temperatures do limit the distribution of this species farther south. This was shown on several occasions, when the water temperature in the laboratory went up to 22°C due to water pump failure. Most L. polaris were found dead, but not a single A. vulgaris died.

Fig. 37

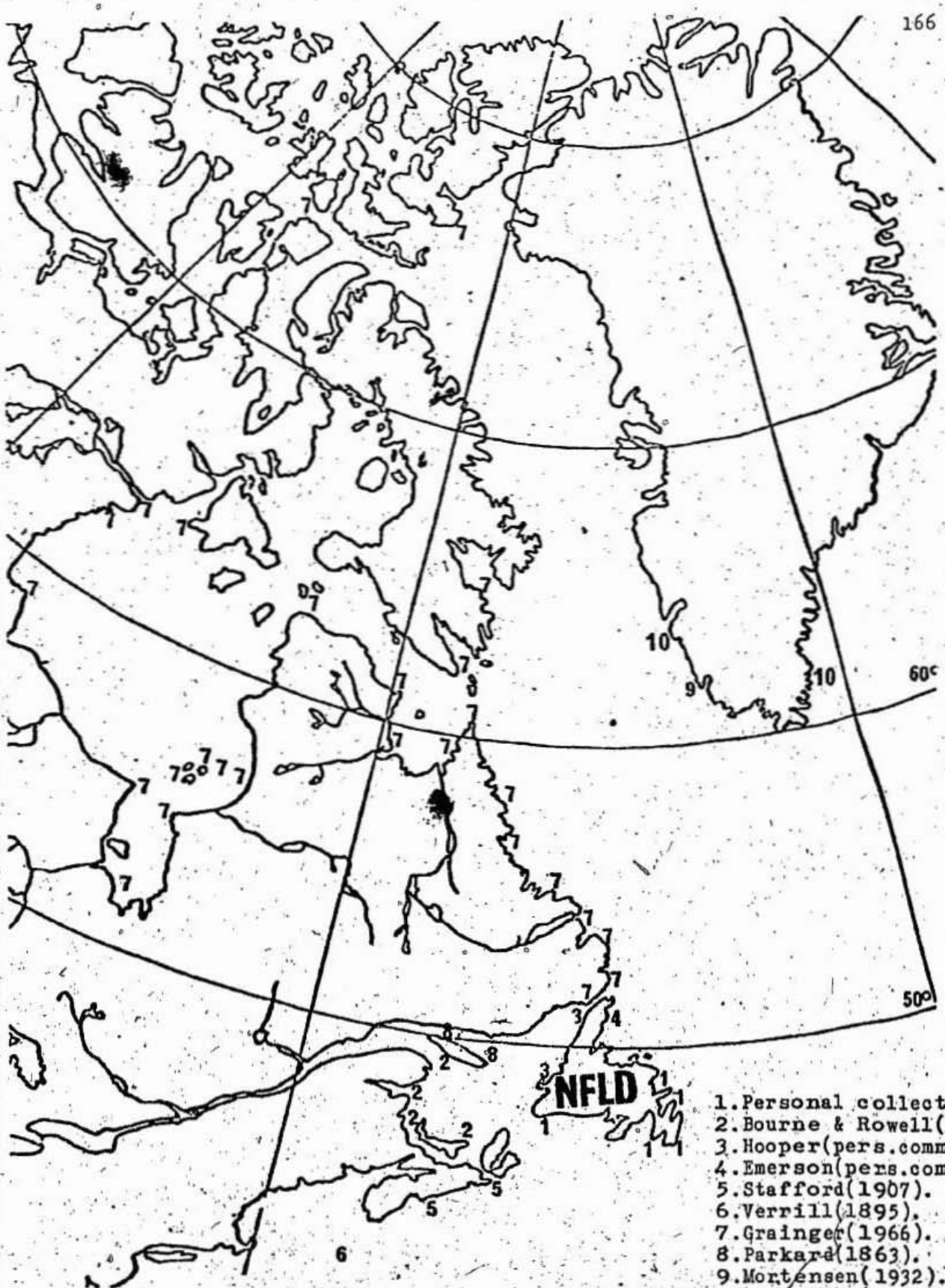
The distribution of Asterias vulgaris in Northern North America.




1. Personal collections.
2. Bourne & Rowell(1965).
3. Hooper(pers.comm.1978).
4. Verrill(1895);Caddy(1970); Ernst(1967);Stafford(1907).
5. Bush(1884).
6. Bell(quoted by Whiteaves 1901).
7. Mortensen(1932)reported Asterias rubens
8. D'yakonov(1950)reported Asterias rubens

Fig. 38

The distribution of Leptasterias polaris in Northern North America.




1. Personal collections.
2. Bourne & Rowell(1965).
3. Hooper(pers.comm.1978).
4. Emerson(pers.comm.1978).
5. Stafford(1907).
6. Verrill(1895).
7. Grainger(1966).
8. Parkard(1863).
9. Mortensen(1932).
10. D'yakonov(1950).

## GENERAL DISCUSSION

It is known that numerous environmental factors can modify or limit the distribution of organisms. The oxygen content in sea water limits the distribution of sea stars to some extent. Both A. vulgaris and L. polaris are epifaunal organisms and they do not usually experience a deficiency of oxygen (hypoxia) in their natural environment except that those living near an estuary may face some fluctuation of oxygen content in sea water. However, there was no great difference between the two species, hence to determine their distribution by means of the oxygen content in sea water seems to be unreasonable.

pH and salinity effects on respiration in both species also showed quite similar results. A. vulgaris (Smith, 1940) has been found in low salinity regions, but the respiratory mechanism of A. vulgaris is not much more efficient than that of L. polaris. In fact, six armed sea stars which must be L. polaris were also found in low salinity areas (Fletcher and Haggerty, 1975). One may suspect that in temperate regions environmental conditions vary more markedly than in the high Arctic; thus it is expected that the organisms from temperate regions would experience versatile environmental conditions and, in turn, have developed many

different adaptive mechanisms. However, as long as an osmoregulatory mechanism system is not developed there would be no route to have successfully invaded freshwater or land.

The present study indicates that temperature plays an important role in the distribution of sea stars. A. vulgaris and A. rubens are restricted to boreal and north temperate areas since they can tolerate low temperatures (below 0°C) during the wintertime, nevertheless, prolonged exposure to severe cold temperature environment may influence some activities compared to species with more northern distribution.

The difference of oxygen consumption between A. vulgaris and L. polaris at 0°C is much greater than at 15°C. A. vulgaris at low temperatures exhibited higher oxygen consumption and this suggests that they are not well adjusted to the expenditure of energy at this level in order to meet that condition as compared to L. polaris if food is limited. As a result, L. polaris are better equipped to survive in high Arctic regions, although interspecific differences do exist. Oxygen consumption of neither species decreases during short-term food deprivation and this could be considered as an unnecessary expenditure of energy. If they still maintain the same rate of oxygen consumption after prolonged food deprivation, L. polaris would be much more favored in terms of expenditure of energy, due to their lower metabolic rate.

Thermal insensitivity is not always the same for different organisms even if they occupy similar zones, reflecting different survival strategies. The moving speed of A. vulgaris is faster than that of L. polaris at each temperature, but A. vulgaris at low temperature were slowed down considerably; therefore, even their more aggressive activity in obtaining food would not be so effective in competing with L. polaris at low temperatures. The morphological feature of strong tube feet to hold onto the substratum utilized by L. polaris to compensate for their inefficient righting response can be considered to increase their survival and existence in the region with high turbulence or strong ocean currents. It is very interesting to find that L. polaris would aggregate to the area where sea water entered the circular tank with rather strong flowing speed. On the other hand, A. vulgaris tended to stay away from the above area. Apparently, A vulgaris avoids encountering strong turbulence or sea currents since their tube feet have weak adhesive ability. Sea stars take in energy into the body in the form of food through rather complicated physical and chemical processes, the temperature factor playing a very important role in these processes. Both species continue to feed at temperatures down to 0°C, but at low temperatures A. vulgaris shows a decrease in taking up amino acids as compared to L. polaris; this shows that temperatures do influence the amino acid uptake activities. Indirectly this may affect

the distribution range of sea stars owing to the temperature factor. Obviously, A. vulgaris could not withstand prolonged cold temperature as can L. polaris; and the latter shows comparatively lower activity in taking up amino acid at higher temperatures.

Asteroids distributed in Arctic and circumboreal regions often have non-pelagic larval development and some even possess brooding protection mechanisms to care for their young, as has been pointed out by Thorson (1950) for other bottom invertebrates in Arctic as well as Antarctic seas. He explained that the same ecological condition exists in both areas, with very limited periods of continuous phytoplankton production in connection with very low temperatures. He concluded that evolution in these areas would advance not only from a pelagic to a non-pelagic larval life, but also towards brood protection, from which the young start their free life at the bottom as late as possible. Thus, in my view, the animals reproducing in a non-pelagic way and brooding their eggs or larvae would also have a better chance of survival and of preventing their young from being carried away from the area by dominant sea currents.

When, therefore, the pelagic larvae of A. vulgaris in areas of the Strait of Belle Isle face the Labrador cold sea current they might be carried south by the current. Consequently, there will be some difficulties for A.

*vulgaris* to disperse northward toward the Labrador coast. Therefore, the lack of *A. vulgaris* in the Labrador coast region would be expected due to their poor adaptation toward cold temperatures and limitation of developing pelagic larvae. On the other hand, *L. polaris* only being found in deeper water from Nova Scotia (by farther south?) could be explained by their temperature requirements being the primary limiting factor, or that *L. polaris* is inferior to *A. vulgaris* and other asteroids in competing for food.

## SUMMARY

1. The effect of temperature on the respiration of whole specimens with respect to body size and sex in different species.

The oxygen consumption of sea stars like many poikilothermic organisms is closely dependent upon the water temperature. The results agree with this generalization that increasing temperature would induce a higher metabolism. The regression line of oxygen consumption against body weight of whole sea stars rises from 0° to 15°C. L. polaris has a low oxygen consumption compared to that of A. vulgaris over the entire measured temperature range. Such a difference could be due primarily to the difference in activities, high feeding rate, and moving speed of A. vulgaris. These activities imply that A. vularis requires more energy to maintain metabolic processes than L. polaris.

2. The effect of oxygen content upon the oxygen uptake rate of sea stars.

The oxygen consumption rate of the sea stars in this study is dependent on the oxygen content in sea water, and is not a simple linear relationship. Hence

the selection of best fitted equation followed Mangum and Van Winkle's (1973) suggestion. Most sea stars are oxygen conformers except Pteraster. No critical point as was mentioned by Maloeuf (1938) could be detected, the curve was quite different from that presented by Belman and Giese (1974).

3. The pH effect on oxygen consumption rate of sea stars.

The oxygen consumption of sea stars reached maximum at pH 8; above or below this value, it decreased. In sea water above pH 8, the respiration of sea stars decreases drastically, but in acidic sea water only moderately. A. vulgaris was more sensitive to pH effects than L. polaris.

4. Influence of salinity on the oxygen consumption rate of sea stars.

Sea stars strictly conform osmotically to the surrounding medium in which they live. The results supported this statement. Both species had a maximum oxygen consumption rate when they were exposed to normal sea water. Reduced or increased salinity induces temporary loss of activities, the animals become immobile, and the oxygen uptake decreases.

5. Food deprivation with relation to oxygen consumption of sea stars.

Most carnivorous animals are unable to withstand prolonged food deprivation, but sea stars are an exception. Giese (1966) reported that the storage of nutrients in sea urchins could last 90 days. Anderson (1966) and Ferguson (1964, 1979) reported that sea stars could remove amino acid from the solution in which they are kept. Sea stars are so well equipped that they need not find other mechanisms to compensate for a long period of food deprivation. In turn, the sea stars do not have to decrease oxygen uptake in order to meet short-term food deprivation as in hibernating animals.

6. The oxygen consumption of different tissues of sea stars at different temperatures.

In general, oxygen consumption rates of tissues decrease as body weight increases except in the gonad of the males of sea stars because the larger animal would be more mature, and active sperm consume more oxygen. Coelomic fluid which is low in protein content and is known to have relatively few cells has low oxygen consumption as expected.

7. The moving speed of L. polaris is slower and is not sensitive to temperature compared to A. vulgaris.

The moving speed of sea stars is not correlated to body weight but the righting response time is a function of body weight. The larger sea stars require a longer time to right themselves. There was no significant difference between species, if the same righting method is considered.

8. Temperature does affect amino acid uptake in sea stars. At high temperatures amino acid uptake in A. vulgaris is better than in L. polaris, but at low temperatures L. polaris performed better.

9. L. polaris is adapted to cold temperatures while A. vulgaris is a boreal and north temperate region sea star. The high Arctic region is not suitable for the existence of A. vulgaris due to many factors, e.g., current, physiological activity, temperatures, etc.

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