SOME FACTORS AFFECTING DISTRIBUTION AND PRODUCTIVITY IN THE ESTUARINE AMPHIPOD *ANISOGAMMARUS PUGETTENSIS*

by

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B.Sc., University of British Columbia, 1972

A THESIS SUBMITTED IN PARTIAL FULFILMENT OF

THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

in the Department

of

Zoology

We accept this thesis as conforming to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA

April, 1975

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ABSTRACT

Factors affecting the distribution and productivity of the benthic estuarine amphipod Anisogammarus pugettensis (Dana) were examined. Data were obtained from field samples taken from Crescent Beach, British Columbia, between May 1973 and September 1974. Tolerances to selected physical factors, growth rates, oxygen uptake, and assimilation efficiency were measured in the laboratory. This species is present and appears to reproduce throughout the year at Crescent Beach. Distribution is affected by: avaoidance of temperature extremes and desiccation, which restrict the species to the middle intertidal zone and deeper at low tide; avoidance of anoxic and low oxygen waters; salinity intolerances, which restrict the species to outer estuarine areas; and food availability. Productivity within inhabited areas is affected mainly by temperature, and food quantity and quality. Productivity will be greatest in warm months. Growth rates, growth efficiencies, and reproductive ability are high compared to values reported for other species. A. pugettensis is an omnivore, capable of eating a wide variety of foods. These data indicate that this species is an important consumer organism in the estuarine environment. The wide tolerances to physical factors, broad diet, and high productivity will make it suitable for mariculture impoundments, if it can be shown that the cultured fish will show high growth rates when feeding on these amphipods.

TABLE OF CONTENTS

Page

ABSTRACT i

TABLE OF CONTENTS ii

LIST OF TABLES v

LIST OF FIGURES vi

ACKNOWLEDGEMENTS viii

I. INTRODUCTION 1

II. DESCRIPTION OF A. PUGETTENSIS 3

III. FIELD STUDIES 7

A. Description of Collecting Site 7

B. Methods 10

1. Collection of Samples 10

2. Brood Size vs. Female Size Relationship 11

C. Results 11

1. Length-Frequency Data for Samples 12

2. Relative Numbers of Males, Females, and Reproductive Females 19

3. Size of Adults 21

4. Relationship between Brood Size and Female Size 21

IV. LABORATORY STUDIES 26

A. Methods 26

1. Maintenance of Amphipods 26

2. Length-Weight Relationships 26

3. Tolerance Experiments 27

Page

4. Effect of Temperature on Incubation Time 28

5. Effects of Temperature and Salinity on Growth .. 29

6. Effects of Temperature, Salinity, and Oxygen Levels on Oxygen Consumption 29

7. Feeding Experiments 31

8. Growth Efficiencies 34

B. Results 36

1. Length-Weight Relationships 36

2. Tolerance Experiments 36

3. Effectoof Temperature on Incubation Time 42

4. Effects of Temperature and Salinity on Growth .. 42

5. Effects of Temperature, Salinity, and Oxygen Levels on Oxygen Consumption 45

6. Feeding Experiments 50

7. Growth Efficiencies 61

V. DISCUSSION 76

A. Factors Affecting Distribution 76

B. Factors Affecting Productivity 79

C. Productivity of A. pugettensis 84

D. Importance to Mariculture 92

VI. LITERATURE CITED 95

VII. APPENDICES 99

A. Data for individual field samples 99

B. Means and Sample standard deviations for length vs. age data of males and females at different temperatures and salinities 105

Page

C. Oxygen uptake of individual animals at different acclimation and test temperatures ... 109

LIST OF TABLES

Page

I. Percentages of males, total females, and reproductive females among adults in field samples 20

II. Survival at high temperatures after 24 h exposure 41

III. Survival at high and low salinities after 24 h exposure 41

IV. Survival in anoxic conditions induced by the addition of sodium sulfite 41

V. The effect of salinity (10° C) on the relationship between oxygen uptake per animal and dry body weight ... 49

VI. Assimilation efficiencies of adults 64

VII. Assimilation efficiencies of plant foods by benthic amphipods 86

LIST OF FIGURES

Page

1. Diagram of adult A. pugettensis 4
2. Map of Crescent Beach area 8
3. Length-frequency data for field samples 13
4. Temperature and salinity data obtained at sampling times 16
5. Size of reproductive females collected at Crescent Beach 22
6. Brood size vs. female size data for animals collected at Crescent Beach 24
7. The relationship between head length and dry weight 37
8. The relationship between dry weight and ash-free dry weight 39
9. Growth in head length at different temperatures and salinities 43
10. The effect of acclimation and test temperatures on oxygen consumption 46
11. Oxygen consumption in decreasing oxygen levels at 10° C . 51
12. Growth in head length with various foods 53
13. Egestion rates (mg C/day) at 20° C 62
14. Growth in dry weight at 10 and 20° C (24‰) 66
15. Growth rate vs. body weight at 10 and 20° C (24‰) 68
16. Oxygen uptake vs. body weight at 10 and 20° C (24‰) ... 70
17. Assimilated rations vs. body weight at 10 and 20° C (24‰) 72
18. Net growth efficiency (K_2) vs. body weight at 10 and 20

Page

°C (24‰) 74

ACKNOWLEDGEMENTS

I thank Dr. T. R. Parsons for providing supervision and facilities for this study. A. B. Norton, D. Kirk, C. L. Tsuyuki, and C. A. Bawden provided much valuable assistnace. Amphipod specimens were identified by D. Laubitz and Dr. E. L. Bousfield of the National Museum of Canada, and Dr. C. D. Levings of the Pacific Environment Institute. The manuscript was critically read by Drs. J. R. Stein and A. G. Lewis. I was supported by a postgraduate scholarship from the National Research Council of Canada.

I. INTRODUCTION

Amphipods (class Crustacea, subclass Malacostraca, superorder Peracarida) are common organisms in shallow marine environments (Barnard 1969). On the British Columbia coast, amphipods are often found in large numbers. In the Squamish estuary, amphipods are extremely abundant in sedge rhizomes, and are the major food of juvenile salmon and other fishes in the estuary (Goodman and Vroom 1972; Levings 1973). At Bamfield, amphipods are the most important food for shallow subtidal fishes (B. Leaman, personal communication). Large numbers of amphipods are often found in polluted waters adjacent to pulp mills (Waldichuk and Bousfield 1962; Harger and Nassichuk 1974).

These observations indicate that amphipods are widely distributed, highly productive, and an important part of food webs in estuarine environments in British Columbia. However, there is a lack of experimental evidence to confirm these observations. In the present study, field samples were taken, and laboratory experiments conducted, in order to examine factors affecting distribution and productivity in a benthic estuarine amphipod.

Another object of this study was to determine if a benthic estuarine amphipod would be useful in salmon mariculture impoundments. If a mariculture impoundment contains an animal that can grow and produce as part of the natural food web, and which can be eaten by salmon, then the high costs of adding artificial fish feeds can be largely reduced or eliminated (Powers 1973). Shallow-water benthic amphipods may be suitable in this role for the following reasons: they may naturally occur in impoundments (Powers 1973); because they are adapted to an environment characterized by fluctuating conditions,

and can exist in polluted conditions (see above), they should be able to tolerate the environmental fluctuations that may occur in a shallow impoundment (Brown and Parsons 1972); they appear to have a broad diet (Kinne 1959; Martin 1966; Levings 1973), so their food requirements can be easily met; their often large numbers (see above) indicates high productivity (which is needed for high fish production); and they are an important food for juvenile salmon in the natural environment (see above). These qualities must be confirmed in any amphipod species that would be present in an impoundment in order to determine the feasibility of amphipod-salmonid mariculture.

The present study examined certain aspects of the ecology of Anisogammarus pugettensis (Dana), a common amphipod of the British Columbia coast (Waldichuk and Bousfield 1962). Data were obtained concerning factors affecting its distribution and productivity, and these findings were related to its suitability for mariculture. The effects of selected factors on distribution were determined from field data on abundance, temperature, and salinity, laboratory measurements of tolerances to certain physical factors, and the ability of various foods to support survival and growth. The effects of selected factors on productivity were determined from estimates of growth efficiency and reproductive ability under various conditions. Growth efficiencies were estimated from laboratory measurements of growth, oxygen uptake, and assimilation efficiency. Reproductive ability was estimated from brood sizes and the occurrence of reproductive animals and young in field samples, and laboratory measurements of incubation time and growth. Growth efficiencies and reproductive ability were compared to data obtained by other authors for amphipods and other aquatic animals. Field samples were taken from May 1973 to September

1974 at Crescent Beach, British Columbia.

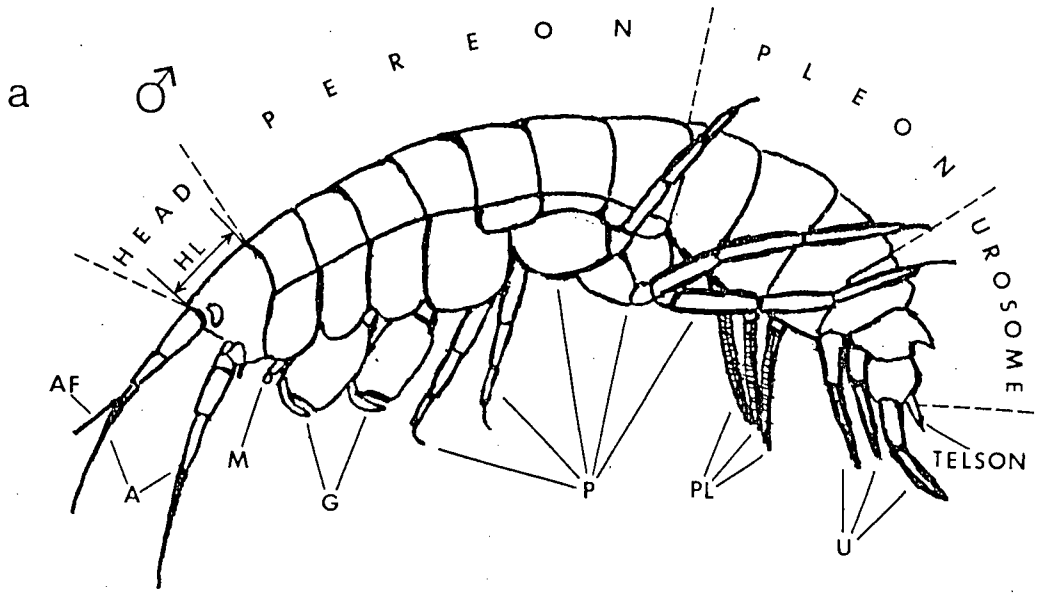
II. DESCRIPTION OF A. PUGETTENSIS

Anisogammarus pugettensis (Dana) is a gammarid amphipod found in cold, slightly brackish, shallow waters from Alaska to central California (Barnard 1954; Light et al. 1954; Waldichuk and Bousfield 1962). It occurs at 30 m depth in polluted waters near a pulp mill near Prince Rupert (Waldichuk and Bousfield 1962).

Adults are diagrammed in Fig. 1 (see also Barnard 1954). Mature males are usually larger than females. Sexes can be distinguished by the size of the gnathopods (Fig. 1) and by the presence or absence of oostegites (not shown). Gnathopods are used for grasping food and other objects; pereopods are used for walking and for clinging to seaweeds or other surfaces; pleopods are used for swimming and ventilation of gills. Gills (not shown) are found on the appendages of pereon segments 2-6. Oostegites, found on the appendages of pereon segments 2-5, form the marsupium (brood pouch) in mature females. Food objects are broken up by the gnathopods and mandibles. Mandibles have cutting and grinding (molar) surfaces (Barnard 1954).

Mating is similar to that of other gammarid amphipods (see Hynes 1955; Kinne 1959). Copulation in A. pugettensis is preceded by a period of precopula, lasting for from less than 1 day to 7 or more days, in which the male holds the female's anterior body segments with his gnathopods. Precopula appears to be initiated by a random collision between a male and female. The female sometimes breaks away from the male before copulation has taken place; this probably occurs most often early in the female's molt cycle. Copulation follows molting by the female. The male and female then separate

Figure 1. Diagram of adult A. pugettensis. (a) male; (b) female. A, antennae (2 pairs); AF, accessory flagellum (on 1st antennae); G, gnathopods (2 pairs); HL, head length; M, maxillipeds(1 pair); P, pereopods (5 pairs); PL, pleopods (3 pairs); U, uropods (3 pairs).


a
♂
PEREON
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HEAD
HL
UROSOME
AF
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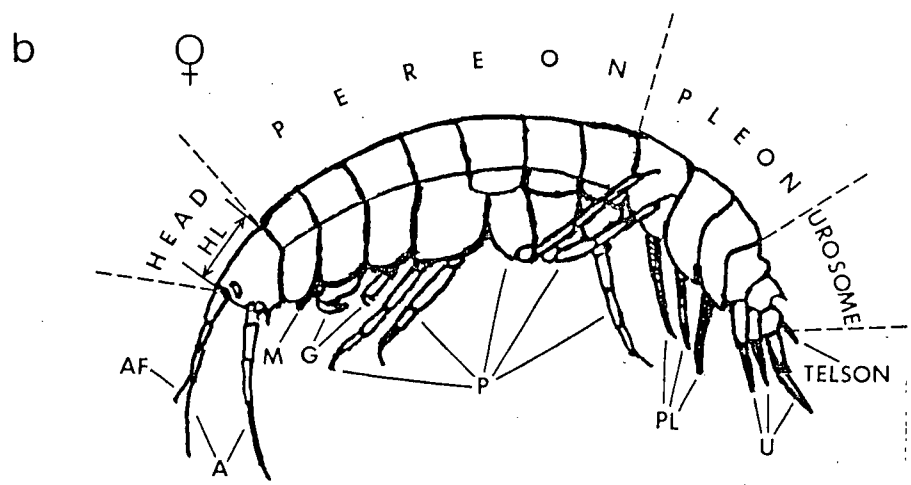
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and the female ovulates, resulting in a mass of blackish eggs (each ca. 0.4 mm diameter) in the marsupium. The female carries the embryos until just after hatching. During the development of the embryos, females frequently beat their pleopods to ventilate the marsupium. Young are released over a period of 1-3 days, just before, or at, the next female molting.

Newly released young have basically the same extermal appearance as adults (except there is no sexual dimorphism in gnathopods, and oostegites are absent), with a head length of ca. 0.25 mm. Growth occurs via a series of molts. Molts are eaten after molting. Although not measured directly, data from growth studies and the recovery of some molts indicate that 7-10 molts are required to attain maturity (0.9-1.2 mm head length).

Females in precopulatare sometimes carrying a brood. Following the next female molt, any remaining young from this brood are released and copulation occurs, followed by ovulation. In other cases, females have a resting period of at least 1 molt cycle between successive broods. The potential number of broods per female was not measured; some individuals had 3 broods in the laboratory, but more may be possible.

In the field and in laboratory cultures, the amphipods are not easily seen. They are usually clinging to seaweeds or are under rocks, shells, or other objects. Behavioral observations indicate an attraction to objects to which they can cling.

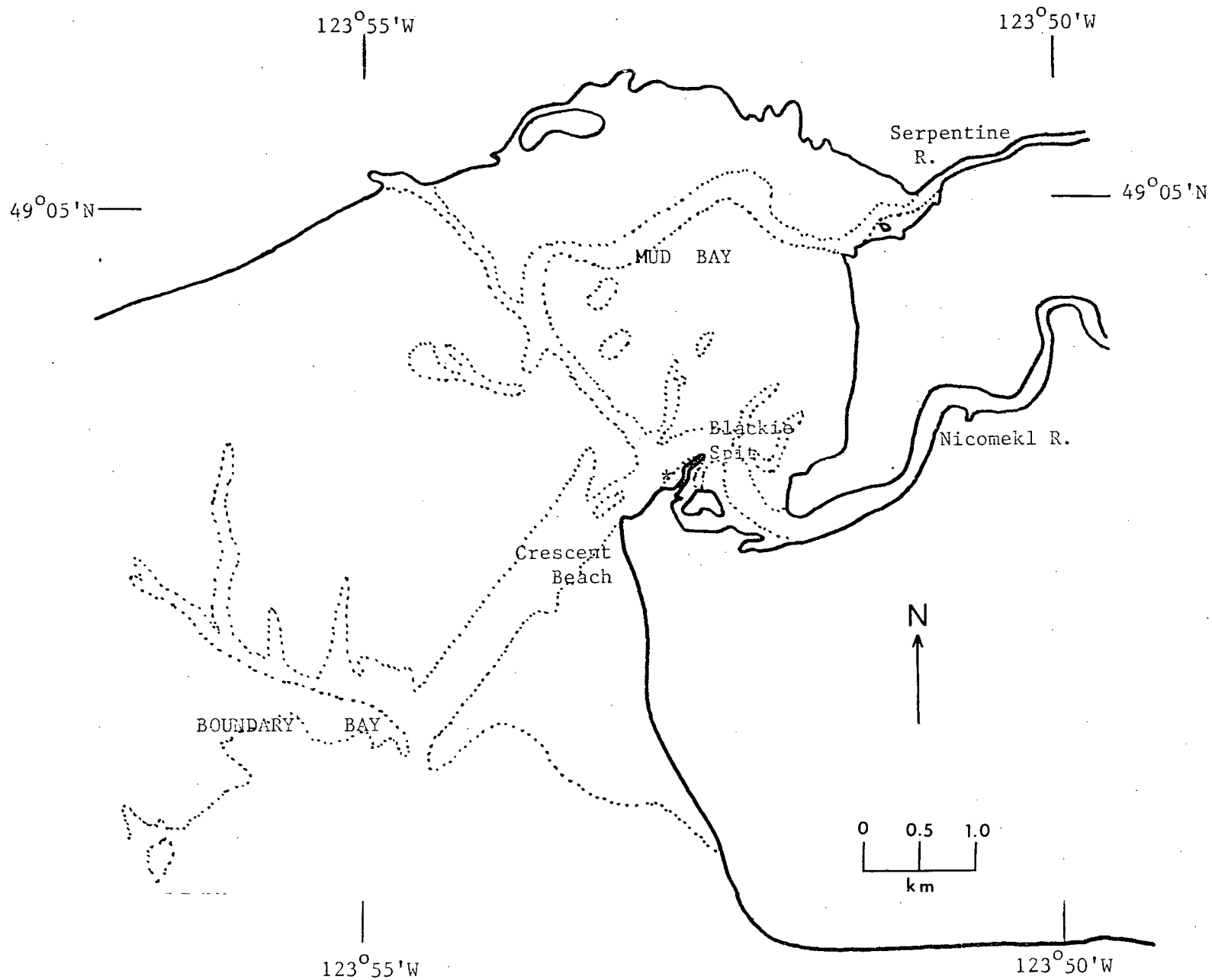
III. FIELD STUDIES

A. DESCRIPTION OF COLLECTING SITE

Samples were taken on the northwest side of Blackie Spit at Crescent Beach, British Columbia (49°04'N, 122°53'W; Fig. 2). This area is shallow with extensive mudflats exposed at low tide. Maximum depth is ca. 3 m below lower low water. The beach area is sandy in the high intertidal zone, becoming muddy in the lower zones. Living macroflora consists mainly of Zostera marina L. (low on the beach) and Enteromorpha spp. (mostly high on the beach). Small, shallow, ephemeral, muddy tidepools (up to ca. 1 m diameter, 20 cm deep) are present in the middle and lower intertidal zones at low tide. These pools usually contain dead strands of Zostera, especially in winter and spring. Small cast-up clumps (up to ca. 1 m long of unattached seaweeds, mainly dead Zostera and Enteromorpha, occur throughout the intertidal zone, especially in spring and summer. Clumps of dead Zostera are present at the highest high water line throughout the year. Large amounts of an unattached red alga, Chondria decipiens Kylin, covered most of the beach from August to early October in 1973 and 1974. A thin coating of benthic diatoms often covers much of the mud surface (identified by D. Kirk as Licomorpha sp.).

The intertidal epifauna includes several amphipod species. Anisogammarus pugettensis (Dana) is the most common species. Others include, in approximate order of abundance: Allorchestes angustus Dana, Anisogammarus confervicolus (Stimpson), Atylus collingi (Gurjanova) (mainly in winter), Corophium sp. (mainly in spring), and Amphithoë valida Smith (mainly in spring). Harpacticoid copepods are common in tidepools. Other intertidal epifauna include hermit

Figure 2. Map of Crescent Beach area. *, sampling site on Blackie Spit; ———— , high tide line; -------- , low tide line. (Redrawn from map 92 G/2 W, edition 3, Canada Department of Mines and Technical Surveys, 1961).


123°55'W
123°50'W
Serpentine R.
49°05'N
49°05'N
MUD BAY
Blackie Spit
Nicomekl R.
Crescent Beach
N
BOUNDARY BAY
0 0.5 1.0
km
123°55'W
123°50'W

crabs (Pagurus sp.), the snails Nassarius obsoletus Say and Batillaria zonalis (Brugière), and the barnacle Balanus glandula Darwin. Sculpins (Oligocottus maculosus) sometimes occur in tidepools.

A. pugettensis is the only common amphipod in subtidal trap samples (see methods below). Pricklebacks (Anoplarchus purpurescens) are found subtidally.

B. METHODS

1. Collection of Samples

Monthly samples (May 1973-September 1974) were taken from the middle and lower intertidal zones at low tide. A. pugettensis was collected from tidepools using small, fine-mesh dip nets (6 cm diameter), bulb pipettes (inner diameter 8 mm), by hand, or by collection of the plant material to which the amphipods were attached. During the late spring and early summer, especially in 1974, amphipods were more commonly found in small clumps of seaweeds (unattached Enteromorpha and Zostera) in the middle and lower intertidal zones. Amphipods were removed by hand or by collection of seaweed. Up to 3 hours were spent in collecting a sample; the longest sampling times occurred when the fewest amphipods were present.

A few samples were taken from the shallow subtidal area in April to July 1974 using a trap consisting of 2 connected wire cages (each ca. 30 X 20 X 20 cm, openings ca. 1.5 cm), one containing small styrofoam chips and the other containing small stones; each cage was baited with Enteromorpha and Zostera. The trap was tied to a piling and allowed to rest on the bottom at a depth of ca. 2 m below the low intertidal zone. It was sometimes noted that amphipods would leave the trap as it was being lifted to the surface.

The amphipods and seaweeds from each collection were brought to the laboratory in 2 l vacuum flasks. Live individuals of A. pugettensis were sexed, measured for head length (Fig. 1), females were checked for the presence of eggs or embryos, and mating pairs were noted. Amphipods were sexed according to the size of the gnathopods (see Fig. 1). This method is accurate for large animals, but is less reliable for the size class in which the amphipods first mature (head length 0.9-1.1 mm). The minimum size of reproductive females in field samples was used as an estimate of the minimum size at maturity. Animals classed as reproductive females were females in precopula and females carrying eggs, embryos, or young.

When large numbers of A. pugettensis were collected, only a subsample of 70-140 animals was measured.

2. Brood Size vs. Female Size Relationship

For some samples, some of the ovigerous (bearing eggs or embryos) females were isolated and either preserved in formalin or kept alive in the laboratory until the young were released. In the latter situations, individual females were kept in 100-200 ml seawater and provided with excess food (Enteromorpha intestinalis). The numbers of eggs, embryos, or young were counted, and the female's head length measured.

C. RESULTS

Quantitative estimates of the population size at Crescent Beach were not obtained because of the extreme patchiness of distribution (in space and in time) in the intertidal zone. Any population estimates

must also include subtidal individuals.

The numbers of amphipods collected in each month depended upon the number of samples taken in each month, the time spent collecting each sample (the time was inversely related to the numbers present), and the type of habitat sampled (see below), as well as the numbers actually present. Because of this, and because only subsamples were measured when large numbers were collected, the total numbers and the numbers of adult males, females, and reproductive females shown in the results are not indicative of the actual numbers present in each month. For data concerning reproductive females, in some months not all ovigerous females shown in the length-frequency data had their broods measured, while in other months, data were obtained for reproductive females from samples or subsamples not included in the length-frequency data.

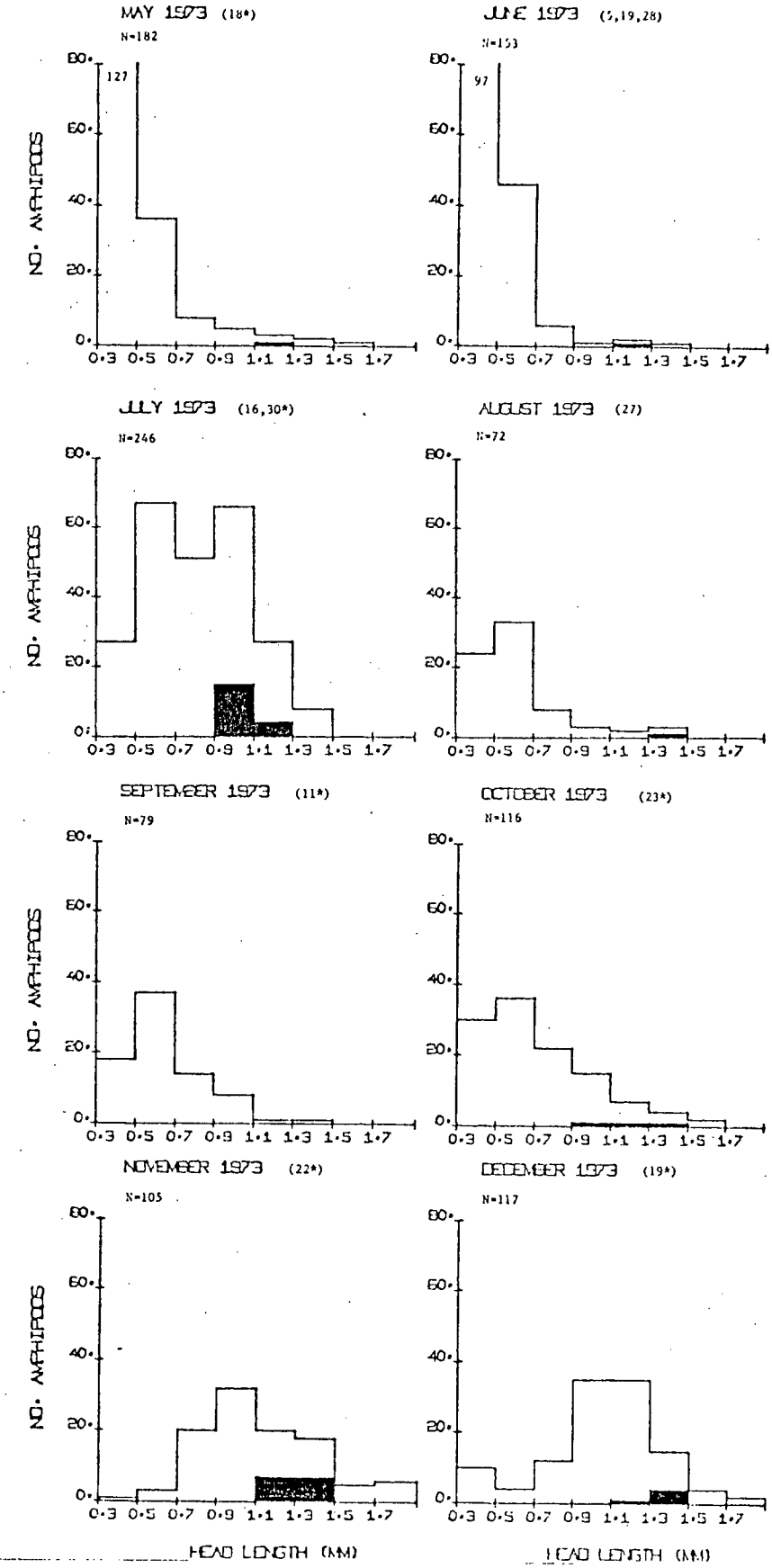
1. Length-Frequency Data for Field Samples

The length-frequency data for field samples for May 1973 to July 1974 are shown in Fig. 3 (see also Appendix A). The temperatures and salinities in tidepools at sampling times are shown in Fig. 4 (also Appendix A). Temperatures ranged from 5-24° C, salinities from 19-27‰. The low temperatures in November 1973 to early February 1974 were partly due to the night sampling times during this period.

a. Late October 1973 to April 1974

During this period, all samples were taken from tidepools containing strands of dead Zostera, from exposed Zostera beds, or from cast-up clumps of seaweeds. In November, December, and early February, the relative scarcity of small size classes was probably due

Figure 3. Length-frequency data for field samples. All samples in any one month are pooled (see Appendix A). Individuals with head lengths less than 0.3 mm are not included. The largest size class represents individuals 1.7 mm and larger. Solid bars represent reproductive females (ovigerous or mating females). The numbers in parentheses following the month are the dates on which samples were taken; *, indicates a subsample.


MAY 1973 (18*)
N=182
127
JUNE 1973 (5,19,28)
N=153
97
JULY 1973 (16,30*)
N=246
AUGUST 1973 (27)
N=72
SEPTEMBER 1973 (11*)
N=79
OCTOBER 1973 (23*)
N=116
NOVEMBER 1973 (22*)
N=105
DECEMBER 1973 (19*)
N=117
NO. AMPHIPODS
0 20 40 60 80
0·3 0·5 0·7 0·9 1·1 1·3 1·5 1·7
HEAD LENGTH (MM)

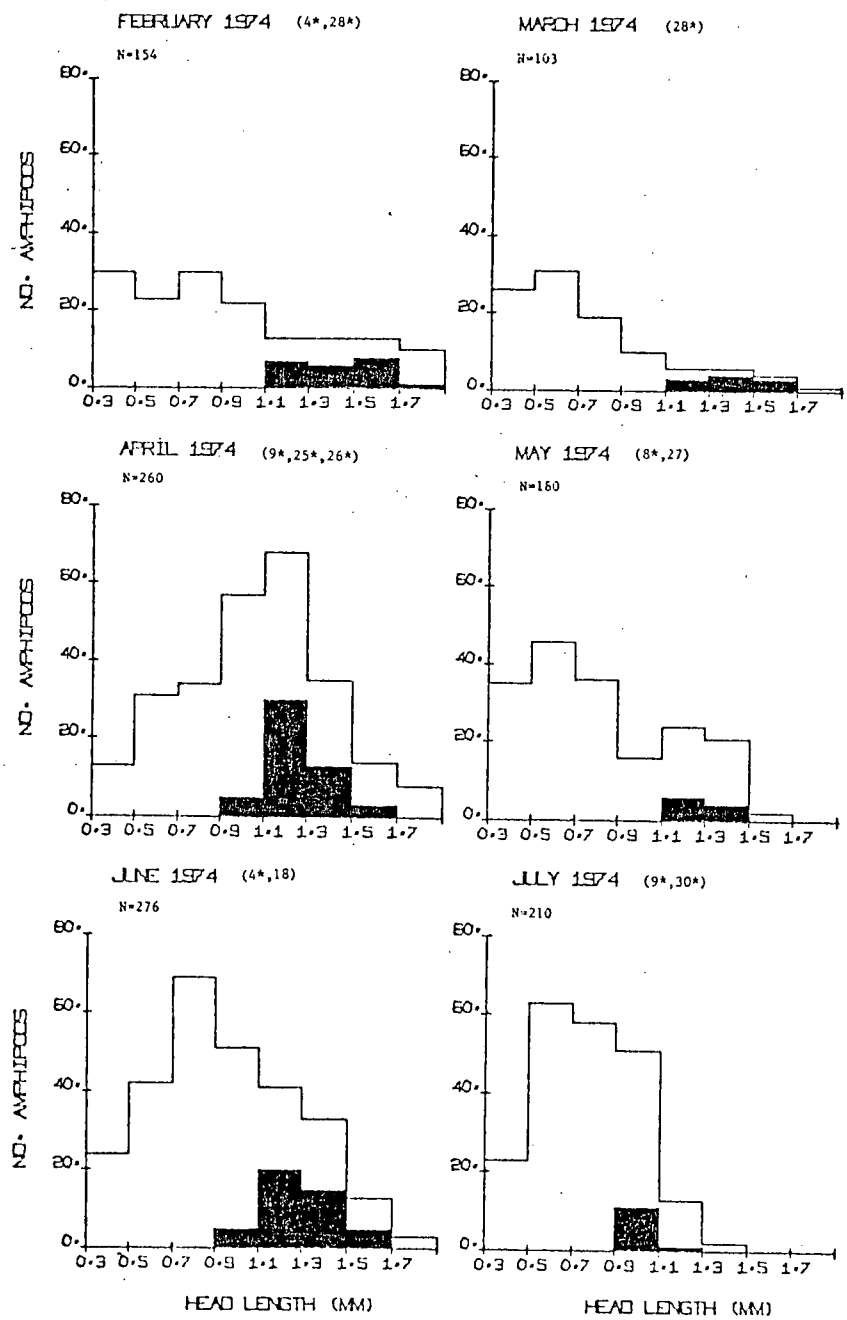
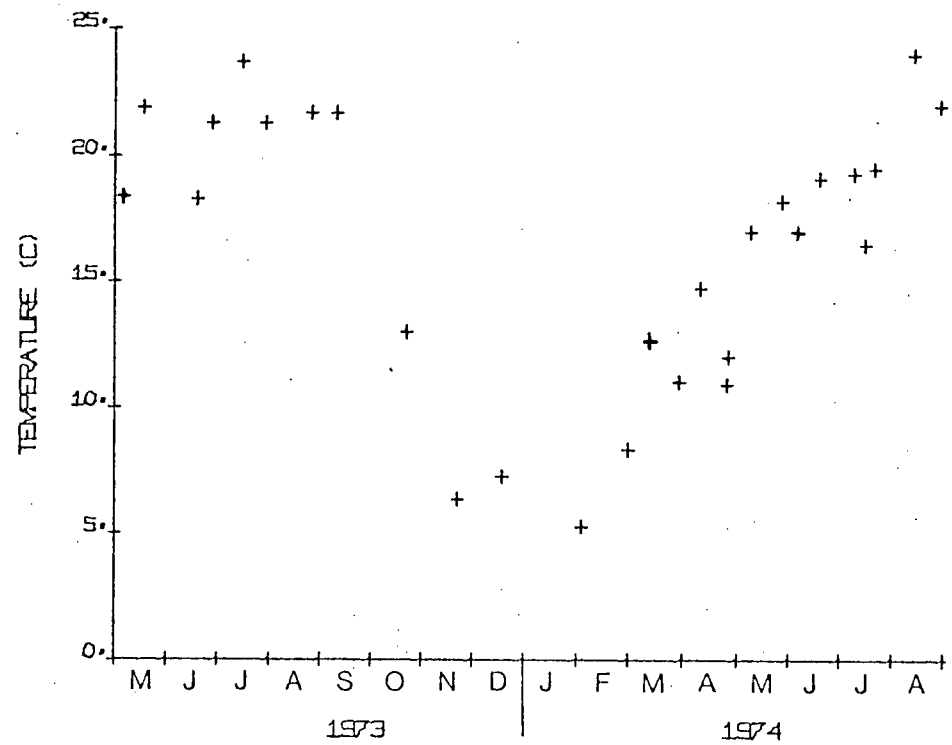
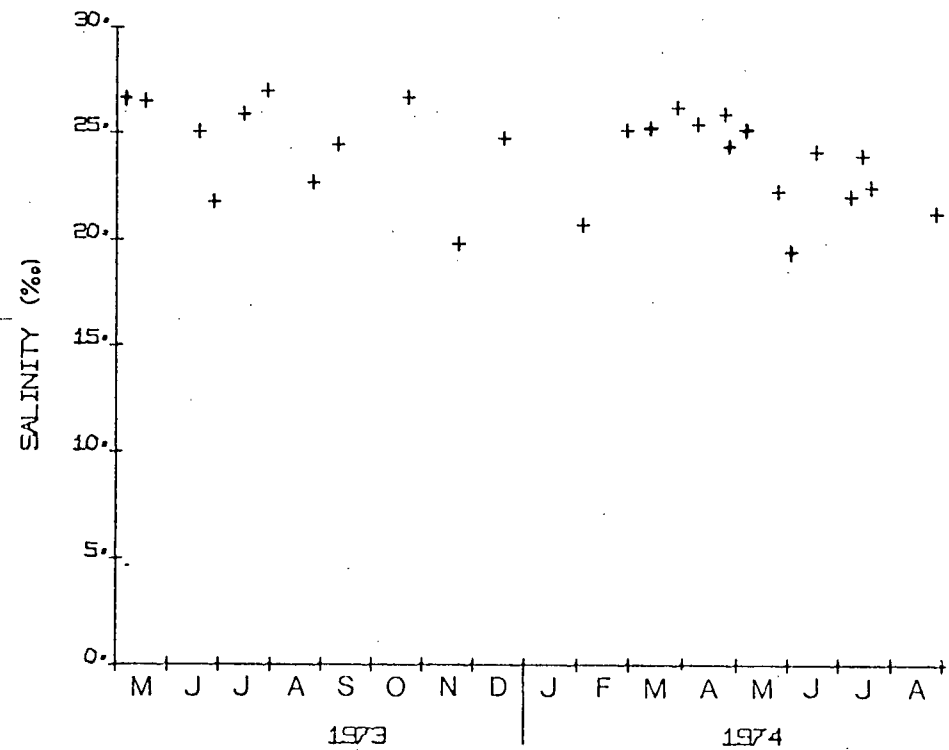

FEBRUARY 1974 (4*,28*)
N=154
MARCH 1974 (28*)
N=103
APRIL 1974 (9*,25*,26*)
N=260
MAY 1974 (8*,27)
N=160
JUNE 1974 (4*,18)
N=276
JULY 1974 (9*,30*)
N=210
NO. AMPHIPODS
0 20 40 60 80
0·3 0·5 0·7 0·9 1·1 1·3 1·5 1·7
HEAD LENGTH (MM)

Figure 4. Temperature and salinity data obtained at sampling times. Each point represents the mean of 2 or more tidepools in the middle or lower intertidal zone.

a FIELD TEMPERATURES



b FIELD SALINITIES



to the reduced visibility at night; young that were found were accidentally taken by pipette or were on strands of seaweed that were carried back to the laboratory.

A. pugettensis was abundant in tidepools in these months, and tidepools were also abundant. Reproductive females and young were present throughout this period. No samples were taken in January 1974. However, reproductive females and young were present in December 1973 and February 1974, and adults and young were found in this area in January 1973 (D. Kirk, personal communication). These data indicate that reproducing adults and young probably occurred in January 1974.

b. Late April to July

During this period (both years), tidepools did not contain as much Zostera as in winter months. A. pugettensis was also less abundant in tidepools; adults were especially scarce, except on July 30, 1973 when tidepools containing Zostera were present. However, on some days during this period, few amphipods were found even when tidepools with Zostera were present. As a result, in May and June 1973, when only tidepool samples were taken, the samples were almost entirely composed of young.

In July 1973 and May-July 1974, amphipods were also collected intertidally from clumps of cast-up seaweeds (Zostera and Enteromorpha), and in late April 1974, from exposed Zostera beds in the low intertidal zone. Samples from these habitats often contained high densities of A. pugettensis including many adults and older juveniles. These seaweed clumps were not present in winter months. A. pugettensis was absent from the dead Zostera at the highest high water line at

all times of the year.

Subtidal samples were taken from a depth of ca. 2 m below low intertidal zone in late April-June 1974. In these samples, large numbers of A. pugettensis often occurred. These were predominantly adults; young may have been present, but were difficult to detect and remove from the trap. In some trap samples, few amphipods were found. This appeared to be the result of removal of the seaweed bait, possibly by grazing amphipods. On April 25 and June 4, 1974, large numbers were found subtidally when few were present intertidally (very few in pools, few clumps of seaweed present). If the different types of samples for late April to July are combined, it is seen that adults, including reproductive remales, and young were present throughout this period.

c. August to Early October

During these months (both years) only intertidal samples were taken. However, seaweed clumps of Zostera and Enteromorpha were absent; tidepools were also scarce, and contained little seaweed. During this period, the entire beach (except the highest parts) was covered with a mat of unattached Chondria. The intertidal samples taken at this time usually contained few A. pugettensis, and when found, there were few adults (including few reproductive females).

2. Relative Numbers of Males, Females, and Reproductive Females

The percentages of males, total females, and reproductive females among adults in field samples are shown in Table I. Male: female ratios were variable, but usually close to unity. Errors in these values may be due to the small sample sizes in some months, and the incorrect sexing of smaller adults. Reproductive females

Table I. Percentages of Males, Total Females, and Reproductive Females in Adults in Field Samples.

Month	No. Adults	% Males	% Total Females	% Reproductive Females
1973:				
May	11	64	36	9
Jun	3	67	33	33
Jul	88	52	48	22
Aug	8	38	62	13
Sep	5	40	60	0
Oct	24	67	33	13
Nov	49	59	41	29
Dec	56	57	43	9
1974:				
Feb	49	47	53	45
Mar	17	35	65	59
Apr	148	48	52	34
May	57	61	39	18
Jun	132	55	45	34
Jul	66	67	33	18
Aug	2	0	100	100

were ca. 50% or more of the total females in all months in which at least 10 females were collected; an exception was December 1973. Almost all non-reproductive females were in the smallest adult sizes (see Appendix A); therefore, many of these may have been immature or incorrectly sexed, resulting in underestimates of the ratios of reproductive females to total females.

3. Size of Adults

As shown in Fig. 5, the minimum, mean, and maximum sizes of reproductive females changed over the year, being smallest in July, and largest in February and March. Sufficient data were not obtained for August, September, or January. A similar seasonal size trend appeared to occur in mating males, but there was insufficient data to confirm this. The smallest mating male collected had a head length of 1.2 mm (June 1974). The largest individual collected was a 2.1 mm male (February 1974).

4. Relationship between Brood Size and Female Size

Brood size vs. female size data for each month are shown in Fig. 6. There was a general increase in brood size with female size, but with much variability. Some of the largest females had relatively small broods. Females collected in June 1974 had larger broods at all female sizes up to 1.5 mm than in any other month. Average brood sizes per female were calculated for months in which 8 or more ovigerous females were measured. The averages were: Oct/73, 46; Nov/73, 59; Mar/74, 72; Apr/74, 55; May/74, 49; Jun/74, 88; Jul/74, 30.

Figure 5. Size of reproductive (ovigerous or mating) females collected at Crescent Beach. Results averaged for each month. Data are presented for months in which 5 or more reproductive females were collected. Δ , means; vertical distance from mean to nearest horizontal mark represents one sample standard deviation; outer marks represent the range of values obtained; numbers beside triangles represent the numbers of individuals measured in each month.

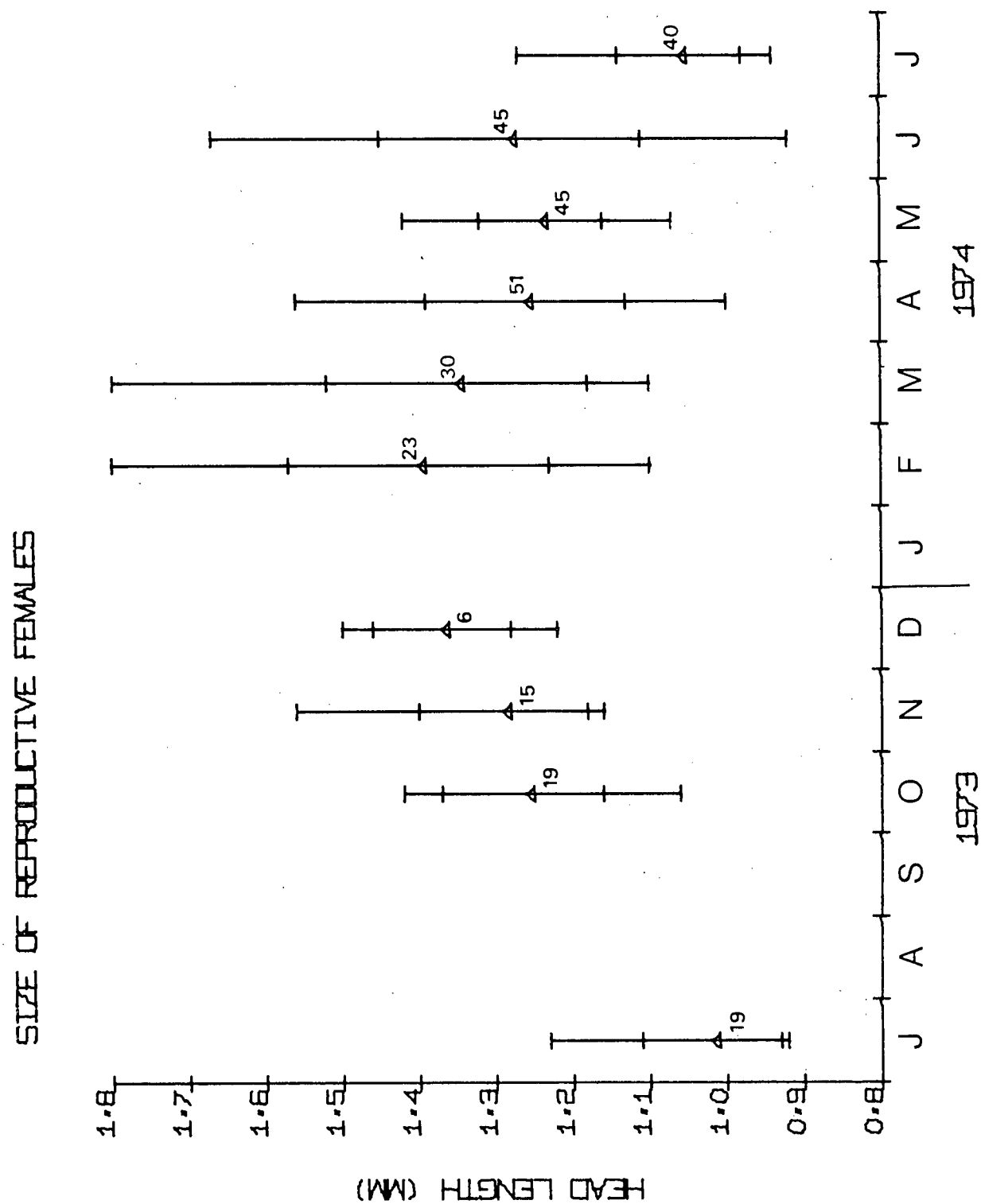
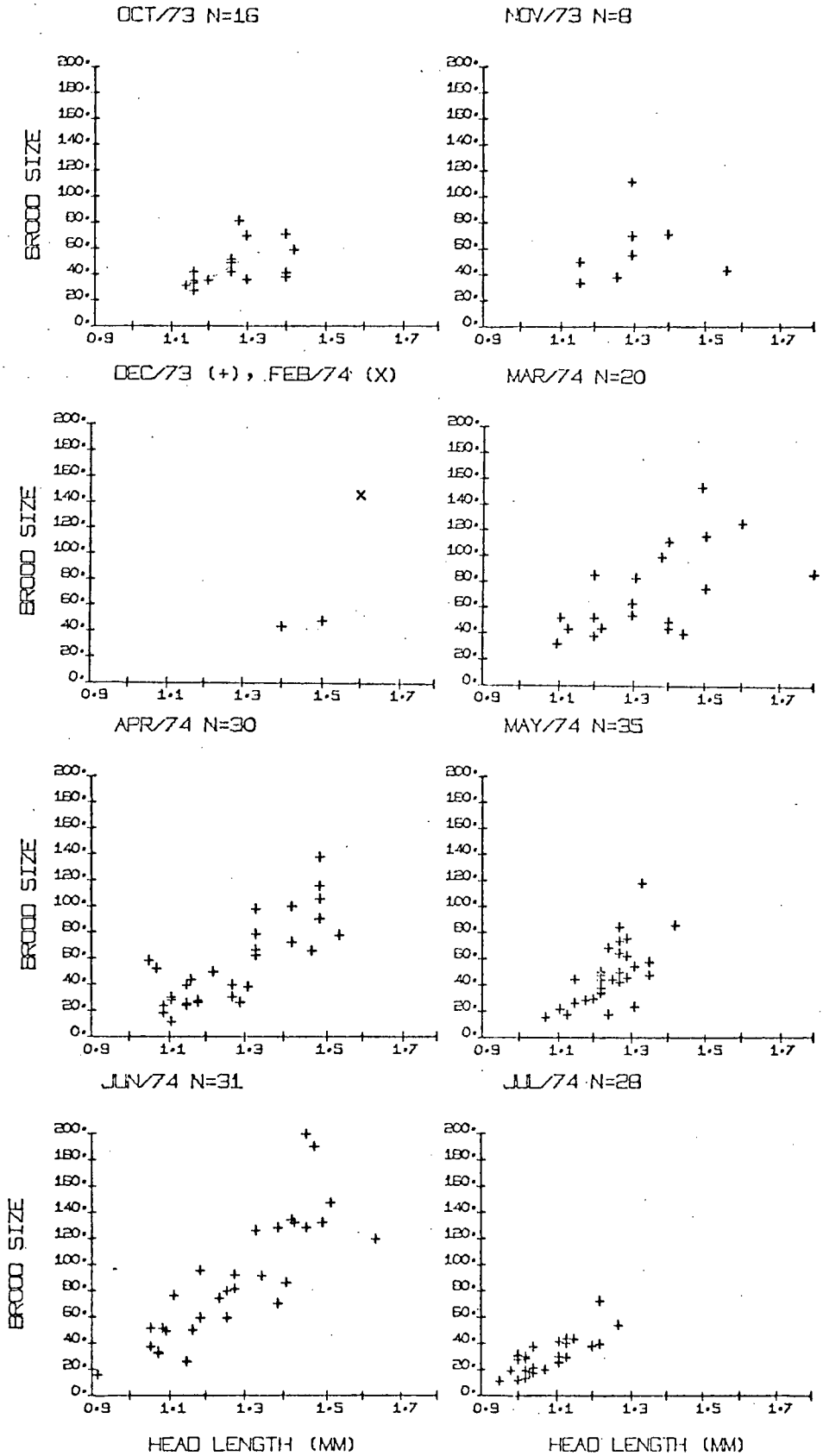

SIZE OF REPRODUCTIVE FEMALES
HEAD LENGTH (MM)
1.8
1.7
1.6
1.5
1.4
1.3
1.2
1.1
1.0
0.9
0.8
J A S O N D J F M A M J J
1973
1974
19
40
45
45
51
30
23
6
15
19

Figure 6. Brood size versus female size data for animals collected at Crescent Beach. Each point represents one female.


OCT/73 N=16
NOV/73 N=8
DEC/73 (+), FEB/74 (X)
MAR/74 N=20
APR/74 N=30
MAY/74 N=35
JUN/74 N=31
JUL/74 N=28
BROOD SIZE
HEAD LENGTH (MM)
0·9
1·1
1·3
1·5
1·7

IV. LABORATORY STUDIES

A. METHODS

1. Maintenance of Amphipods

Amphipods were maintained in the laboratory at 10 and 20° C. The medium was unfiltered seawater (ca. 24-28‰). The amphipods were kept in glass stacking dishes and beakers of various sizes, ranging in volume from 100 ml (for 1-2 animals) to 1 l (several animals). Mass cultures were kept in glass aquaria (5-10 l seawater) and plastic dishes (ca. 6 l). Cultures were not usually aerated; this resulted in mortalities in some mass cultures when the water became fouled (i.e., cloudy, with a surface scum) by rotting algae, or when cultures were overcrowded. Enteromorpha (collected at Crescent Beach) was provided in excess amounts for food. Small rocks and plant material (Enteromorpha and Zostera) served as refuges. Cultures were illuminated 13 h/day.

Under laboratory conditions mating occurred spontaneously. However, broods did not always develop to hatching. The reasons for these brood failures were not determined.

Recently hatched young sometimes became caught in the surface film where they died if not removed. This usually occurred with ca. 10-25% of the young in a brood, although sometimes, almost an entire brood became caught.

2. Length-Weight Relationships

The head length to dry weight relationship for A. pugettensis was determined from measurements of animals from laboratory cultures. Dry weights were obtained by rinsing animals in distilled water and

then drying them at 60° C overnight. The ash content was obtained by heating animals in a muffle furnace at 600° C for 4-6 h. The carbon content of animals was estimated as one-half of the ash-free dry weight (see Parsons and Takahashi 1973).

3. Tolerance Experiments

In all tolerance experiments, animals were acclimated for at least 2 weeks to 10 or 20° C (24‰) and provided with excess food (Enteromorpha).

For the determination of high temperature tolerances, individuals were placed in 150 ml beakers containing 100 ml filtered seawater (pore size 0.45 µm) at the temperature of acclimation (24‰). The beakers were then placed in a water bath set at the test temperature (24, 27, or 30° C). Animals were left at the test temperature for 24 h, then returned to the acclimation temperature, and checked for survival 16 h later. Low temperature tolerances over 24 h were not determined.

For salinity tolerance tests, individuals were transferred directly from the acclimation temperature and salinity to ca. 100 ml filtered seawater at the test salinity (0, 3, 5, 7, and 40‰; no temperature change). After 24 h, animals were returned to 24‰. Survival was checked 16 h later. Low salinities were obtained by dilution of seawater at room temperature.

In the temperature and salinity tolerance experiments, the LD_{50}-24 h was the temperature or salinity that resulted in the deaths of 50% of the tested animals after 24 h exposure.

An indication of the tolerance to anoxic conditions was deter-

mined from the survival of individuals in 5 ml filtered seawater (10 or 20° C, 24‰) to which ca. 0.5 mg Na_2SO_3 had been added. Sodium sulfite removes oxygen from solution, but is also poisonous in high concentrations. Therefore, these tests may show the effects of the poison as well as the effects of anoxia. The animals were exposed to these conditions for 1, 2, or 3 h. The animals were then transferred to aerated seawater and survival was checked 16 h later.

Survival out of water in moist air was measured by blotting animals on filter paper to remove excess water, and then placing them in a 150 ml beaker (no water) which was placed in a sealed 600 ml beaker to which 100 ml seawater was added. Survival was checked hourly (less frequently near the start and end of the experiment).

Survival of animals in the absence of food was determined by placing individuals in ca. 100 ml filtered seawater, without food (at the acclimation temperature and salinity). Survival was checked daily.

In the anoxia, survival out of water, and survival without food experiments, the LT_{50}^{50} was the time required for 50% of the tested animals to die.

In all tolerance experiments, the criterion for death was the absence of movement when touched.

4. Effect of Temperature on Incubation Time

The incubation time was measured as the time in days from copulation until the first young were released by the female. Mating pairs were isolated in 100-250 ml seawater at 10 and 20° C (24‰) and

supplied with excess amounts of Enteromorpha. After copulation, the male was removed.

5. Effects of Temperature and Salinity on Growth

Growth of young from the time of release from the female to adult size was measured at 10 and 20° C in filtered seawater at 24-28, 18-21, and 12-14‰. Animals were fed excess amounts of Enteromorpha. Experiments at 10° C were continued for 15 weeks, and those at 20° C for 12 weeks. Experiments were conducted in transparent plastic, compartmentalized boxes (Vlchek Plastics "Trans-box" P824), with one animal/compartment. Each compartment was 5.3 X 5.3 X 5.3 mm, filled with ca. 100 ml seawater.

Experimental animals were from broods released in the laboratory within 48 h prior to the start of each experiment. Each animal was measured (head length) and moved to a clean container with fresh filtered seawater and excess food every 7 days. Periodic checks were made between measurement times to check food supplies and to note deaths.

6. Effects of Temperature, Salinity, and Oxygen Levels on Oxygen Consumption

Oxygen consumption was measured with a YSI Model 53 Biological Oxygen Monitor (2 Ag-Pt electrodes, KCl electrolyte, and Teflon membranes). The experimental chambers were glass vials filled with 4-10 ml filtered seawater, depending upon the size of the animal tested and the test temperature. The experimental chamber was divided into 2 portions by a nylon screen (mesh size ca. 0.5 mm).

One amphipod was placed in the lower chamber, and a magnetic stirring bar was placed in the upper chamber; the tip of the electrode protruded into the upper chamber (similar to the set-up of Teal and Halcrow 1962). A control chamber, identical to the experimental vials except that no amphipod was present, was run concurrently with each experimental chamber. The experimental and control chambers were placed in a constant temperature water bath. Tests were done in subdued light. Following each test, dry weights of amphipods were obtained (see section IV.A.2).

For tests of the effects of temperature and salinity on the oxygen uptake, animals were kept at the acclimation temperatures and salinities, and provided with excess food, for at least 2 weeks prior to the tests, and were kept in the experimental vials at the test temperatures and salinities for ca. 30 min prior to the tests.

The water in experimental and control chambers was approximately saturated with oxygen at the start of the temperature and salinity tests, and was not allowed to fall to less than 70% saturation. Tests were run until the animal showed a constant oxygen uptake rate for ca. 30 min. Although the animals were restricted in their movements by the size of the chambers, the action of the stirring bar in moving the water usually stimulated the amphipod to become active, although the amount of activity varied greatly between individuals. Oxygen uptake was expressed in µl/h and µl/mg dry wt/h.

To test for the effects of temperature on oxygen consumption, amphipods acclimated to 10° C were tested at 0, 5, 10, 20, and 25° C, and animals acclimated to 20° C were tested at 5, 10, 20, 25, and 30° C (24‰). Individuals were warmed or cooled to the test temperatures

(where necessary) over ca. 10-15 min. Q_{10} values were calculated as

$$\log Q_{10} = (10(\log V_2 - \log V_1))/(t_2 - t_1) \quad (1)$$

(base 10 logs) where V_2 and V_1 are the rates at temperatures t_2 and t_1 (Winberg 1971).

To test the effects of salinity on respiration rates, amphipods were acclimated at 10° C to 24, 18, or 12 ‰, and then tested at the acclimated temperature and salinity. Also, some animals acclimated to 24‰ were moved directly into 12‰ and tested at this salinity after 30 min.

The effect of the environmental oxygen level on the oxygen uptake rate at 10° C (24‰) was measured by recording the decrease in the oxygen level caused by an amphipod placed in a closed test chamber (4 ml filtered seawater). The water was stirred throughout the tests The water was close to oxygen saturation at the start of each test. Each test lasted for ca. 6-8 h. Animals were acclimated to 10° C, 24‰ for at least 2 weeks, and were placed in the test chamber ca. 1 h prior to the start of measurements. Seven adults were tested, and the results averaged. Oxygen uptake was calculated at 10% oxygen saturation intervals. In order to compare results from different sized animals, oxygen consumption rates at each oxygen level were expressed as percentages of the rate shown by the same animal at 80% oxygen saturation (this is approximately the oxygen level in the temperature and salinity effect experiments). Oxygen utilization rates (oxygen uptake/h/oxygen available) were calculated.

7. Feeding Experiments

a. Feeding Experiments with Adults

Four to six adults were placed in a small stacking dish (ca. 250 ml filtered seawater, 10 or 20° C, 24‰) with excess amounts of a food type. Survival of amphipods, disappearance of food, and presence of fecal pellets were examined over 1 week to determine acceptability of foods. Three or more trials were done for each food. The foods tested were: "Tetramin Staple Flake Food" (tropical fish feed); "Clarke's New-Age Crumbles" (trout pellet feed); frozen brine shrimp (Artemia), frozen fish flesh (juvenile sockeye salmon); the seaweeds Ulva sp., Enteromorpha intestinalis, Fucus sp., Chondria decipiens, and dead Zostera marina (all collected at Crescent Beach); clumps of benthic diatoms (predominantly Nitzschia sp.; collected from seawater aquaria); and detritus collected from the substrate of tidepools at Crescent Beach (particles mostly < 0.1mm diameter). Plant foods had various microorganisms associated with them.

b. Effect of Food Type on Growth

Young were fed from the time of release from the female up to adult size, on the same foods as in section IV.A.7b, except that Chondria was not tested. Some animals were given a food choice consisting of brine shrimp, Enteromorpha, benthic diatoms, and Zostera. Fish and seaweeds were given in small pieces, especially to young animals. Experiments were done at 10 and 20° C (24‰). Experimental vessels and measurement procedures were as in section IV.A.5.

Because there were insufficient numbers of each sex for each food type, and because many amphipods died at sizes too small to allow sexing, the data for both sexes are combined and presented until an average head length of 0.9 mm was attained, or until all animals died. Both sexes grow at approximately the same rate up to this size, which is the minimum adult size.

c. Egestion Rates

Animals were acclimated to 20° C (24‰) with excess food (Enteromorpha) for at least 2 weeks. Individuals were then placed in 100 ml filtered seawater (20° C, 24‰) with excess Enteromorpha. Fecal pellets were removed by Pasteur pipette after 24 h, rinsed in isotonic ammonium formate (to remove adventitious salts), dried at 60° C, and weighed.

d. Assimilation Efficiencies

Animals were acclimated at 10 or 20° C (24‰) with excess Enteromorpha intestinalis for at least 2 weeks. Assimilation efficiencies for adults feeding on E. intestinalis at 10 and 20° C (24‰), and on the benthic diatom mixture at 10° C (24‰) were measured by two methods. For both foods, associated microorganisms were probably ingested along with the plant material.

The first method used the radioisotope ^{14}C. Plant foods were incubated for 1 week in enriched filtered seawater medium containing $NaHCO_3$ labelled with ^{14}C (20 μCi/250 ml medium). The labelled food was rinsed several times in filtered seawater before being used. Individual animals plus excess amounts of labelled food were placed in sealed 125 ml Erlenmyer flasks containing 140 ml filtered seawater. Flasks were incubated in the dark for 10-16 h (depending on the feeding rate). Each animal was then transferred to a second flask containing unlabelled food to allow the animal to clear its gut of labelled food. After 7-16 h, the experiment was terminated. The amounts of ^{14}C in solution, in feces in both flasks, and in the animal were measured by liquid scintillation counting. Feces and animals were rinsed in filtered seawater before measurement. The amount of ^{14}C released by labelled food in the absence of feeding amphipods, and the amount of

^{14}C released into the medium by labelled feces, were measured in control experiments. The assimilation efficiency (A, %) was calculated as

$$A = \frac{s + a}{s + a + f} \cdot 100 \qquad (2)$$

where s was the activity in solution in both flasks combined (corrected for controls), a was the activity of the animal, and f was the activity in feces in both flasks combined (corrected for controls). The corrected value of s was assumed to represent label released by the animal due to respiration or excretion.

Assimilation efficiencies were also measured by the method of Conover (1966). This method is based on the assumption that the ash fraction of the food is not assimilated by the animal. The assimilation efficiency (U, %) was calculated as

$$U = \frac{F - E}{(1 - E)F} \cdot 100 \qquad (3)$$

where F is the ratio of the ash-free dry weight to the dry weight in the food, and E is the same ratio for the feces. Amphipods were kept in filtered seawater and provided with excess food. Feces were collected after 24 h with a Pasteur pipette, rinsed several times in isotonic ammonium formate, dried overnight at 60° C, and weighed. Ash weights were determined by heating feces at 450° C for ca. 5 h. Feces from 4-6 animals were combined into a single sample.

8. Growth Efficiencies

The net growth efficiences (K_2, %) were estimated for animals raised on Enteromorpha at 10 and 20° C in 100% seawater as

$$K_2 = \frac{G}{G + T} \cdot 100 \qquad (4)$$

where G was the growth rate and T was the metabolic rate, both expressed

in mg C/day (Winberg 1971).

The growth rate (G) was estimated from the growth experiment data (section IV.B.4). Growth in length was converted to growth in dry weight and carbon content using the length-weight relationships (section IV.B.1). Growth rates were estimated over weekly intervals. The absolute growth rate (mg C/day) was estimated as

$$G(\text{mg C/day}) = \frac{C(2) - C(1)}{t(2) - t(1)} \tag{5}$$

and the weight-specific growth rate, as a percentage of the total body carbon per day, was estimated as

$$G(\%) = \frac{\ln C(2) - \ln C(1)}{t(2) - t(1)} \tag{6}$$

(ln = natural logs) where C(1) and C(2) were the carbon contents of the animals at times t(1) and t(2) (Winberg 1971).

The absolute (in mg C/day) and weight-specific (in % body C/day) metabolic rates (T) were estimated from the oxygen uptake rates for animals acclimated and tested at 10° C and acclimated and tested at 20° C (24‰). Oxygen uptake in volume of oxygen was converted to mg carbon by the formula

$$\text{mg C} = \text{ml } O_2 \cdot \frac{12}{22.4} \cdot RQ \tag{7}$$

with RQ assumed to be 1 (Parsons and Takahashi 1973).

The assimilated ration was estimated as the sum of growth (G) and metabolism (T).

The gross growth efficiences (K_1, %) were estimated as

$$K_1 = A \cdot K_2 \tag{8}$$

where A was the assimilation efficiency.

B. RESULTS

1. Length-Weight Relationships

The relationship between head length and dry body weight is shown in Fig. 7. The relationship between dry body weight and ash-free dry body weight is shown in Fig. 8.

2. Tolerance Experiments

a. Temperature

The survival after 24 h exposure to high temperatures is shown in Table II. The LD_{50}-24 h was between 24 and 27° C for animals acclimated to 10° C, and between 27 and 30° C for animals acclimated to 20° C. Animals could be kept several weeks at 5-20° C. See also section IV.B.5a.

b. Salinity

The survival of animals after 24 h exposure to high and low salinities is shown in Table III. The low salinity LD_{50}-24 h at 10° C (animals acclimated to 10° C, 24‰) was between 3 and 5‰, and at 20° C (animals acclimated to 20° C, 24‰), between 5 and 7‰. At both temperatures, the high salinity LD_{50}-24 h was greater than 40‰. Animals could be kept several weeks at 12-28‰ (10 or 20° C).

c. Low Oxygen

The survival of animals at 10° C in anoxic conditions (caused by the addition of sodium sulfite) is shown in Table IV. The LT_{50} was between 2 and 3 h. At 20° C, 8 individuals were tested for 1 h; 4 of these survived. At both temperatures, once anoxic conditions were established, all individuals became paralyzed, and remained so throughout the exposure.

Figure 7. The relationship between head length and dry weight for *A. pugettensis*. (Base 10 logarithms)

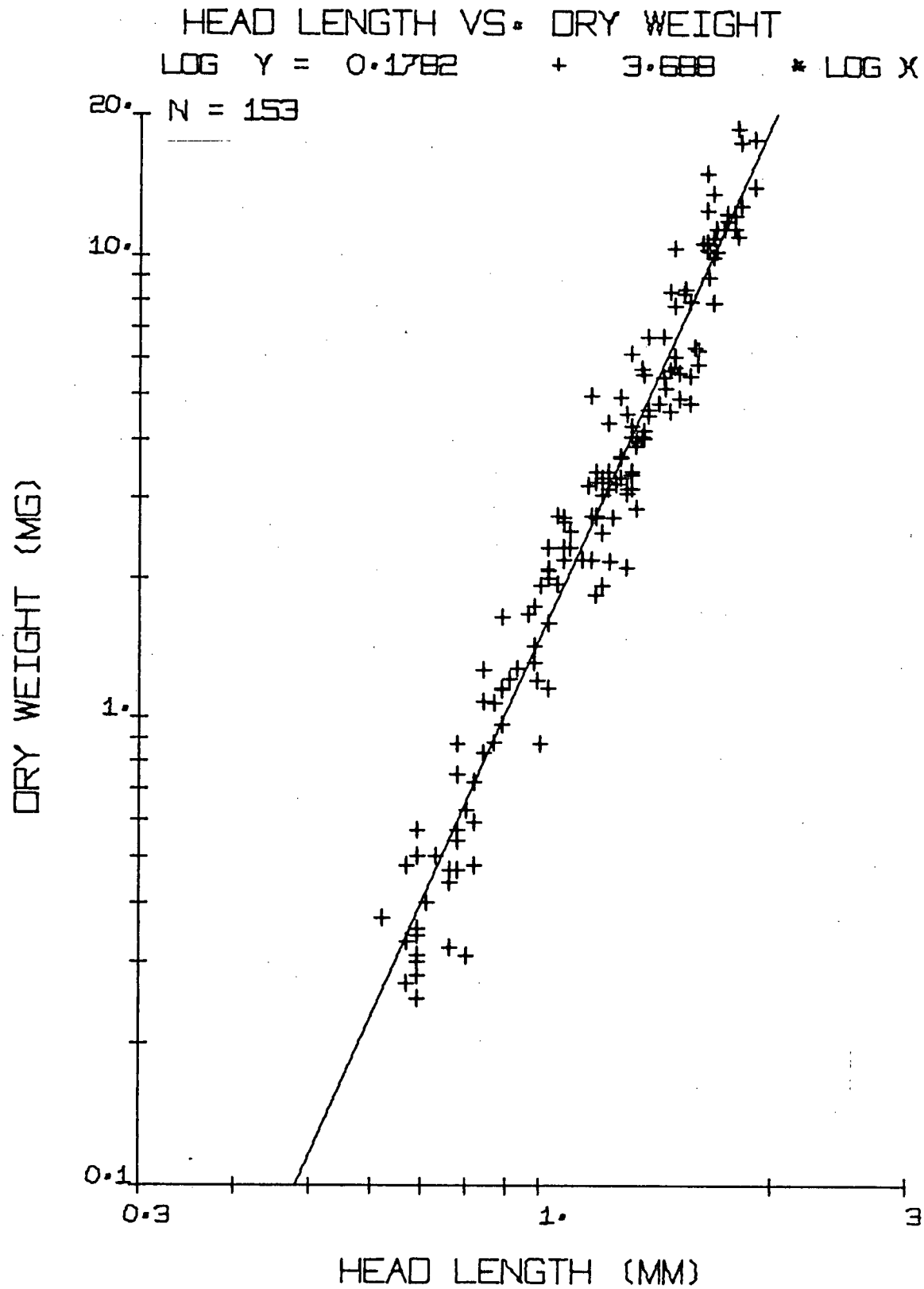

HEAD LENGTH VS. DRY WEIGHT
LOG Y = 0.1782 + 3.688 * LOG X
N = 153
20.
10.
1.
0.1
0.3
1.
3.
DRY WEIGHT (MG)
HEAD LENGTH (MM)

Figure 8. The relationship between dry weight and ash-free dry weight in A. pugettensis. (Base 10 logarithms)

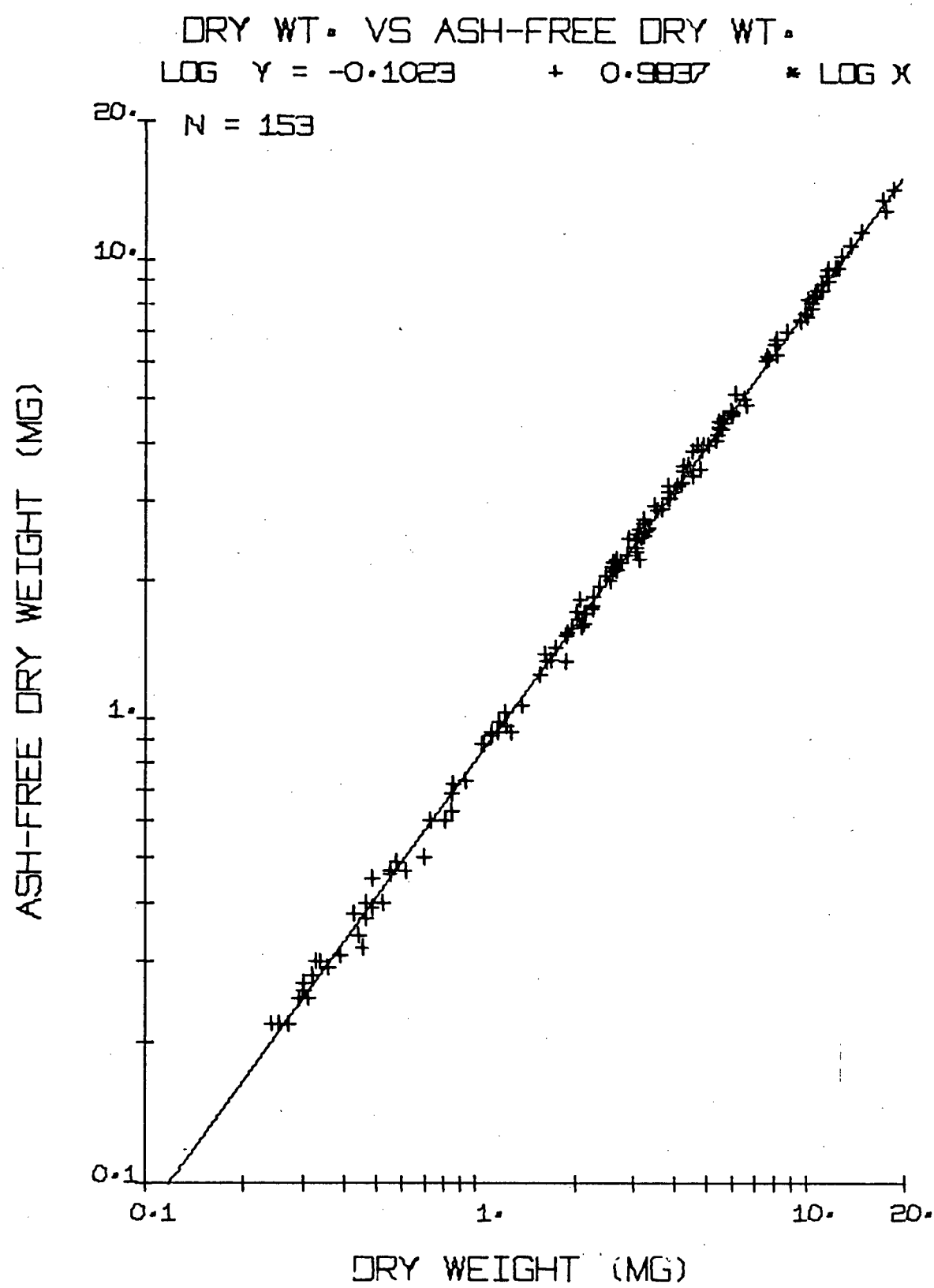

DRY WT. VS ASH-FREE DRY WT.
LOG Y = -0.1023 + 0.9837 * LOG X
N = 153
20.
10.
1.
0.1
0.1
1.
10.
20.
ASH-FREE DRY WEIGHT (MG)
DRY WEIGHT (MG)

Table II. Survival at high temperatures after 24 h exposure (24‰).

Test Temperature (°C)	Acclimation to 10° C n	Acclimation to 10° C Number Surviving	Acclimation to 20° C n	Acclimation to 20° C Number Surviving
24	16	14	16	16
27	16	6	16	16
30	16	0	16	0

Table III. Survival at high and low salinity after 24 h exposure.

Test Salinity (‰)	Acclimation to 10° C, 24‰ n	Acclimation to 10° C, 24‰ Number Surviving	Acclimation to 20° C, 24‰ n	Acclimation to 20° C, 24‰ Number Surviving
0	18	0	18	0
3	18	8	18	0
5	18	12	18	5
7	18	18	18	16
40	18	17	18	10

Table IV. Survival in anoxic conditions induced by the addition of sodium sulfite (10° C, 24‰).

Duration of Exposure	n	Number Surviving
1	9	9
2	9	6
3	9	2

d. Survival in Moist Air

The LT_{50} for survival in moist air was 32-33 h at 10° C (range, 26-98 h; n = 10), and 15-17 h at 20° C (range, <14-25 h; n = 10).

e. Survival in the Absence of Food

The LT_{50} for survival in the absence of food was 17-20 days at 10° C (range, 9-35 days; n = 11), and 6-11 days at 20° C (range, <6-15 days; n = 8). In starved animals, material in the anterior part of the gut was not egested as fecal pellets, but appeared to disappear from the gut gradually over a number of days. This material was probably assimilated to a higher degree than in normally fed individuals.

3. Effects of Temperature on Incubation Time

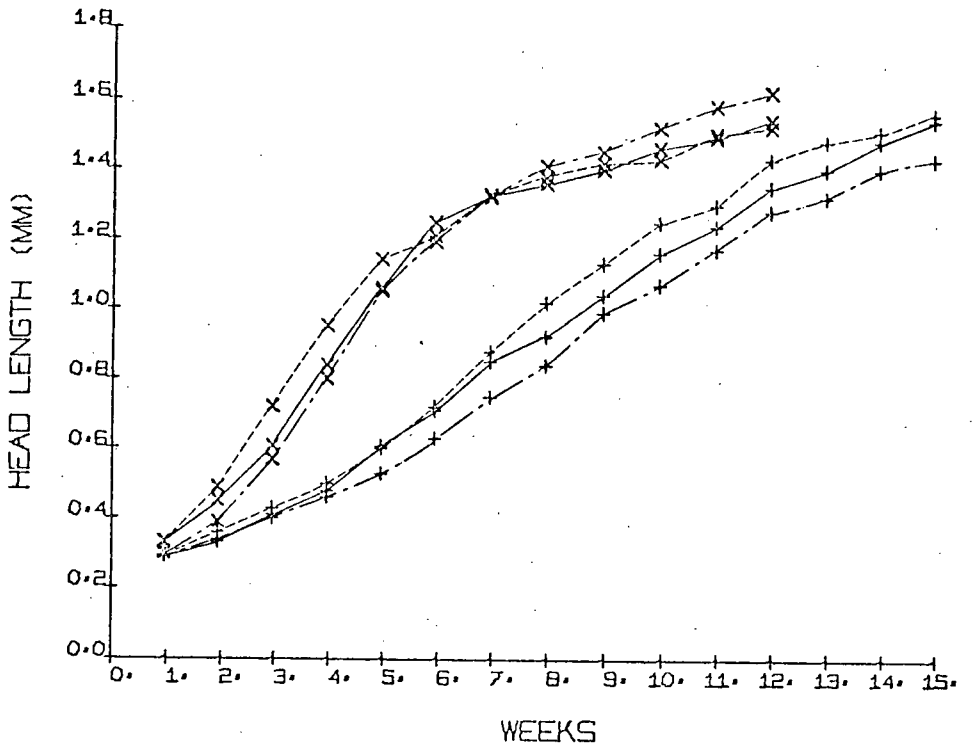
For broods that developed from fertilization to release from the female in the laboratory, the incubation time was 14-16 days (n = 9) at 10° C, and 9-10 days (n = 14) at 20° C. This represents a Q_{10} for the average brood development rate of ca. 1.5.

4. Effects of Temperature and Salinity on Growth

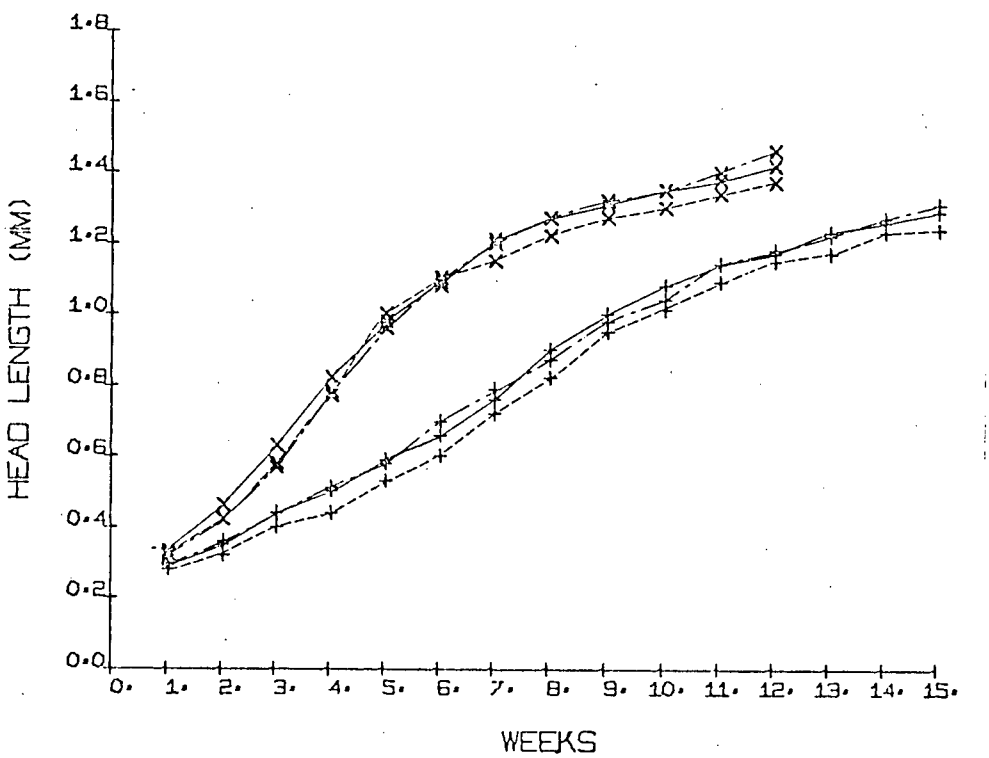
The growth in head length of animals feeding on Enteromorpha at different temperature-salinity combinations is shown in Fig. 9 and Appendix B. These figures show only results for animals that survived to the end of the experiment. There was no effect of temperature or salinity on survival up to 0.9 mm head length (67-76% survival, not including animals caught on surface film). Mortality between 10 and 15 weeks age was 4% at 10° C, and at least 29% at 20° C (the latter figure may be low, since not all 20° C animals were kept alive past 12 weeks age).

Figure 9. Growth in length at different temperatures and salinities. Mean values. (See Appendix B). Food: Enteromorpha intestinalis. +, 10° C; x, 20° C; ———, 24-28‰; —— - ——, 18-21‰; -----, 12-14‰.

a MALES



b FEMALES



Males and females showed similar growth rates up to ca. 0.8-0.9 mm head length (except at 12-14‰), after which males grew faster than females.

Salinities of 12-28‰ had no marked effect on growth at 10 or 20° C. Temperature did have a large effect on growth at all salinities. The time required to reach 0.9 mm head length averaged 8-9 weeks at 10° C, and 4-5 weeks at 20° C. This represents a Q_{10} for average growth from time of release from female up to 0.9 mm of ca. 1.9.

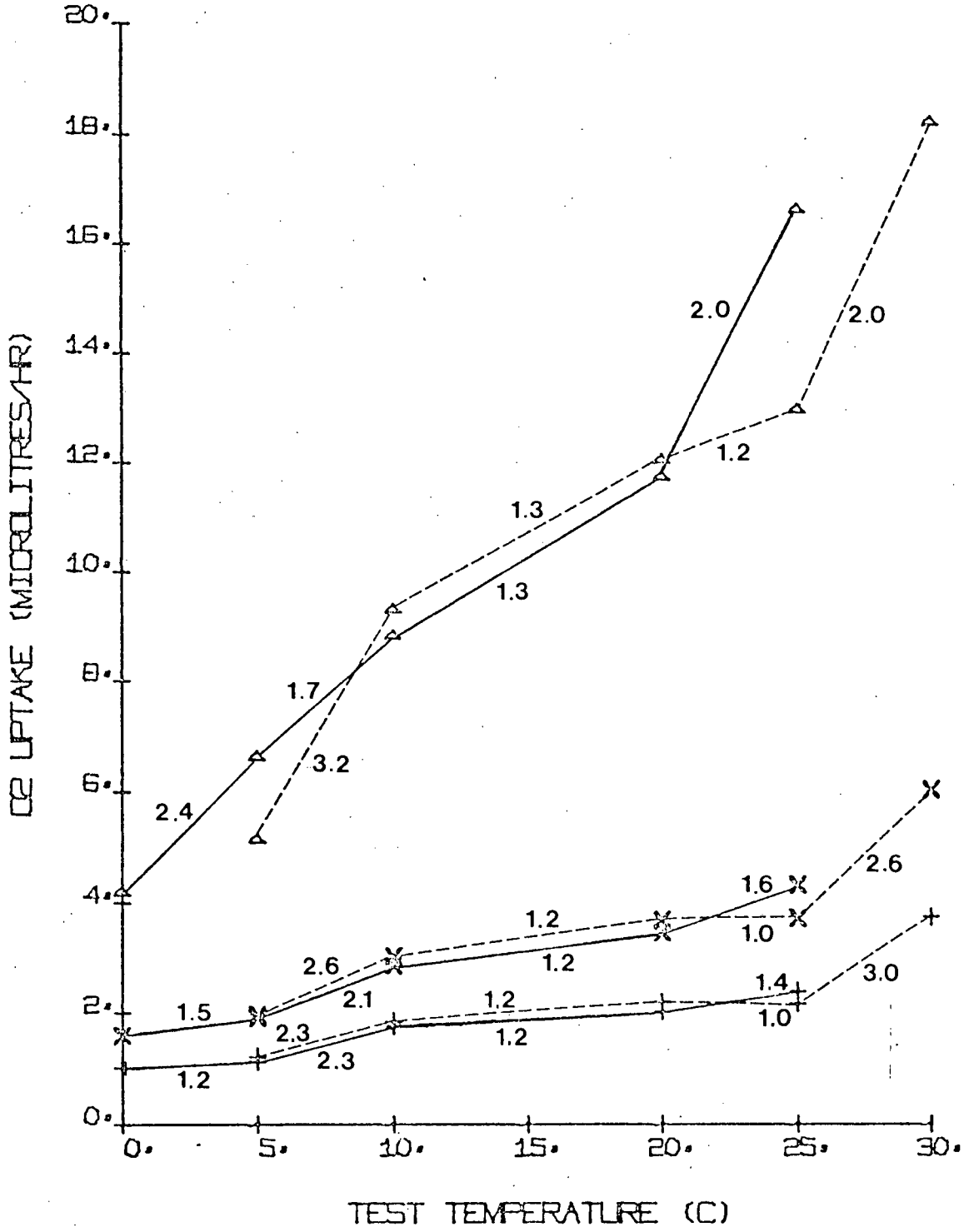
5. Effects of Temperature, Salinity, and Oxygen Levels on Oxygen Consumption

The relationship between oxygen uptake and dry body weight was a log-log relationship with oxygen uptake per animal increasing with increasing weight; weight-specific oxygen uptake decreased with increasing body weight (Appendix C). Data includes both sexes; there was no apparent effect of sex on oxygen uptake (except as a result of size differences).

a. The Effect of Temperature

Increased test temperatures resulted in increased oxygen consumption (Fig. 10). There was also greater activity at higher test temperatures. Acclimation temperatures had no significant effect on the oxygen uptake at test temperatures of 10 or 20° C. At high test temperatures, the lower acclimation resulted in higher oxygen uptake, especially in larger individuals; at 30° C, animals acclimated to 10° C become paralyzed. In tests at 5° C, the higher acclimation temperature resulted in lower oxygen consumption by larger animals,

Figure 10. The effect of acclimation and test temperature on oxygen consumption. Salinity, 24‰. Values were obtained from Appendix D. ———, animals acclimated to 10° C; -----, animals acclimated to 20° C; +, 0.5 mg dry body weight; x, 1.0 mg dry body weight; Δ, 5.0 mg dry body weight; numbers on graph are Q_{10} values between the two nearest test temperatures for animals acclimated to the same temperature.


O2 UPTAKE (MICROLITRES/HR)
TEST TEMPERATURE (C)
0
2
4
6
8
10
12
14
16
18
20
0
5
10
15
20
25
30
2.4
1.7
1.3
2.0
3.2
1.3
1.2
2.0
1.5
2.6
2.1
2.3
1.2
1.2
1.2
1.6
1.0
2.6
1.2
1.4
1.0
3.0
1.2
2.3

but little difference for smaller individuals; at 0° C, animals acclimated to 20° C became paralyzed. The Q_{10} values are shown in Fig. 10. Values were low between test temperatures of 10 and 20° C, increasing at test temperatures outside this range. The Q_{10} between 10 and 20° C for animals acclimated to the test temperature was 1.3 for animals of 0.5-5.0 mg dry weight.

b. The Effect of Salinity

Short or long term exposures to salinities of 12-24‰ did not affect the relationship between oxygen uptake and body weight at 10° C (Table V).

c. The Effect of Oxygen Level

The oxygen uptake rate fell as the oxygen level fell in these short term tests except below a certain oxygen level. Below this level the amphipods showed a constant, low oxygen uptake rate until near zero oxygen levels (less than 2% saturation) were reached, after which, no oxygen uptake occurred. During the constant uptake and zero uptake stages, the animals remained paralyzed, showing no activity other than occasional twitching of the pleopods; at higher oxygen levels, animals did show activity. If moved to aerated water soon after paralysis occurred, animals usually recovered immediately; after 1 h or more paralyzed, recovery did not occur. This implies a shorter tolerance to anoxic conditions than in the sodium sulfite tests (section IV.B.2c); this can be attributed to the stress conditions experienced by animals in the present tests in the low oxygen conditions prior to the onset of paralysis. The level at which paralysis occurred ranged from 28% to less than 2% oxygen saturation. This variability may be related to acclimated

Table V. The effect of salinity (at 10° C) on the relationship between oxygen uptake per animal and dry body weight. Regression equations are of the form

$$\text{Log } T = a + b(\text{Log } W)$$

where T is the oxygen uptake in microlitres of oxygen per animal per hour, W is the dry body weight in mg, a is the y-intercept, and b is the slope of the line; logarithms are base 10. Analysis of covariance: comparison of slopes, p = 0.46; comparison of y-intercepts, p = 0.53. Common slope: 0.73.

Acclimation Salinity (‰)	Test Salinity (‰)	n	a	b	r^2
12	12	19	0.55	0.67	0.84
18	18	14	0.36	0.92	0.76
24	24	15	0.48	0.74	0.93
24	12	16	0.47	0.72	0.82

oxygen conditions (these were not strictly controlled).

The change in oxygen uptake rates in decreasing oxygen levels is shown in Fig. 11a. The oxygen utilization rates are shown in Fig. 11b. The higher utilization rates shown at low oxygen levels, even when paralyzed, may be partly due to the constant stirring of the medium during the tests.

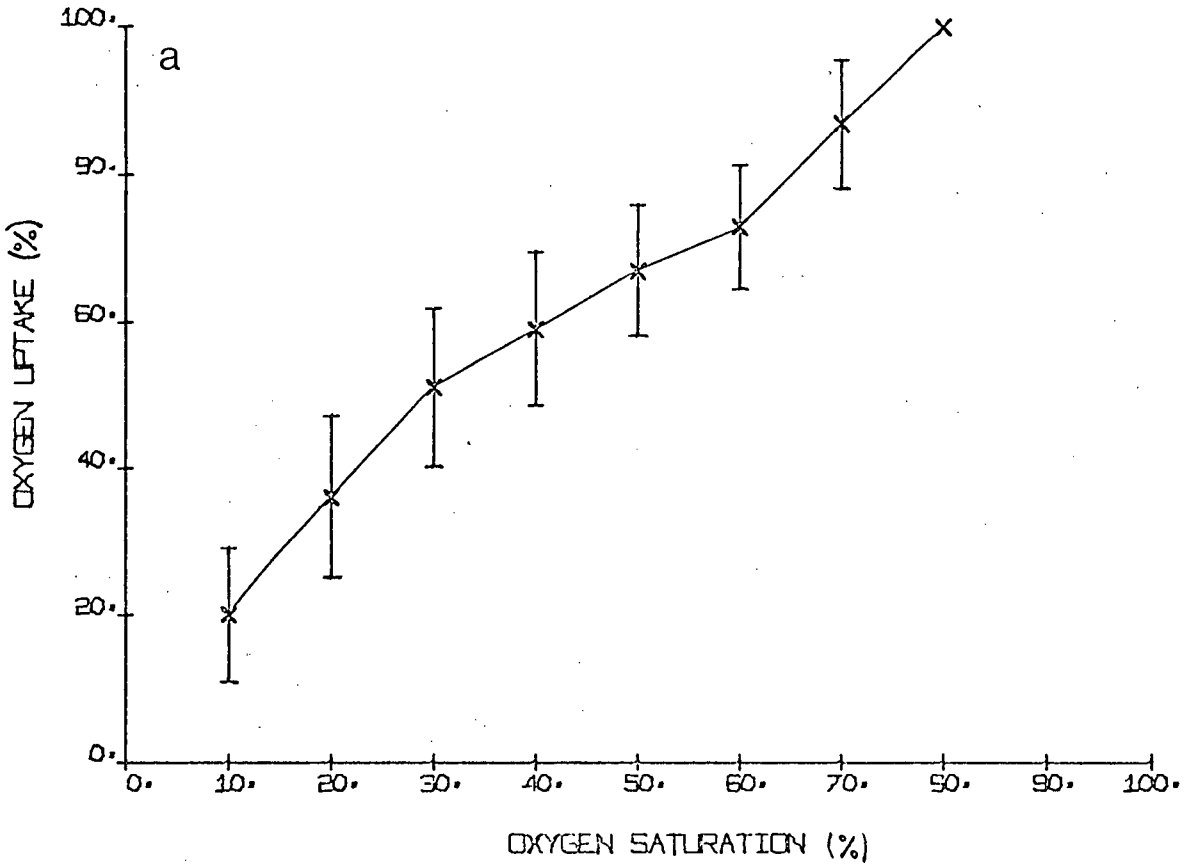
6. Feeding Experiments

a. Feeding Experiments with Various Foods

The survival (not including animals dead on surface film) and growth of young on various foods are shown in Fig. 12. Growth was faster at 20° C than at 10° C with all foods. The best growth and survival of young among individual foods was shown with Enteromorpha and benthic diatoms. These foods were also usually eaten by adults. For Enteromorpha, small thalli were best for youngest amphipods. In another experiment with the same benthic diatoms, 0.9 mm head length was reached at between 3 and 4 weeks age (cf. 5 weeks in the present study) with 4 of 5 surviving (Chang and Parsons 1975; note : diatom species was Nitzschia, not Pseudonitzschia).

There was variability in results with both young and adults feeding on Fucus. This appeared to be due to variability in the texture of the Fucus used in the experiments: soft, rotting plant was eaten by adults, and supported growth of young; fresh plant was not eaten. Ulva and dead Zostera were usually not eaten by adults; neither alga supported growth of young animals to 0.9 mm head length, although Zostera did support survival for several weeks, but with poor growth. Chondria was not ingested by adults;

Figure 11. Oxygen consumption in decreasing oxygen levels at 10° C. (a) x-axis, oxygen level as a percentage of the saturation level; y-axis, oxygen uptake as a percentage of the consumption per animal per hour shown by the animal at 80% saturation. (b) x-axis, percent oxygen saturation; y-axis, oxygen utilization expressed as the oxygen uptake per animal per hour divided by the amount of oxygen in the test vessels, in percent. Individuals were allowed to consume the oxygen in a closed container until no oxygen was left; oxygen uptake rates were calculated at 10% intervals of oxygen saturation. x, mean of 7 animals; vertical bars represent one sample standard deviation on either side of the mean.


a
OXYGEN UPTAKE (%)
100.
90.
60.
40.
20.
0.
0.
10.
20.
30.
40.
50.
60.
70.
80.
90.
100.
OXYGEN SATURATION (%)

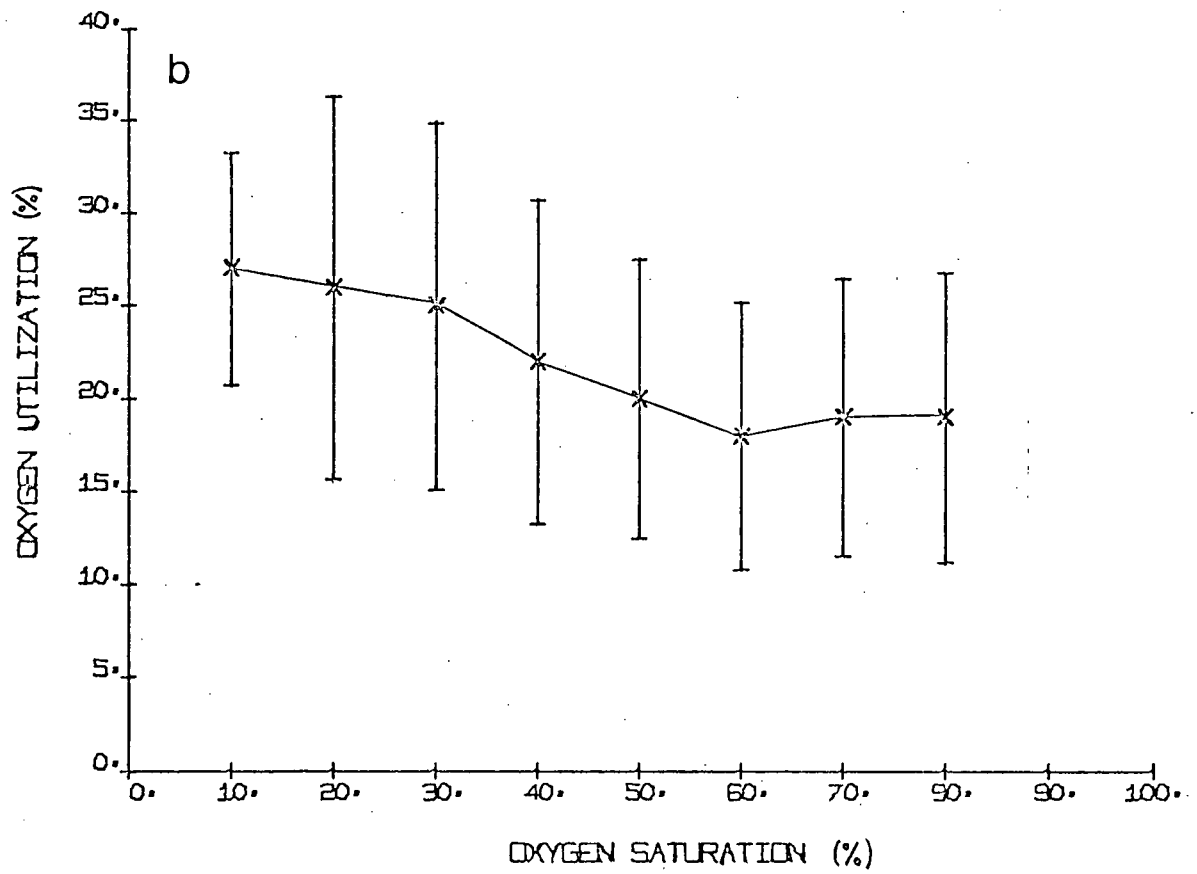
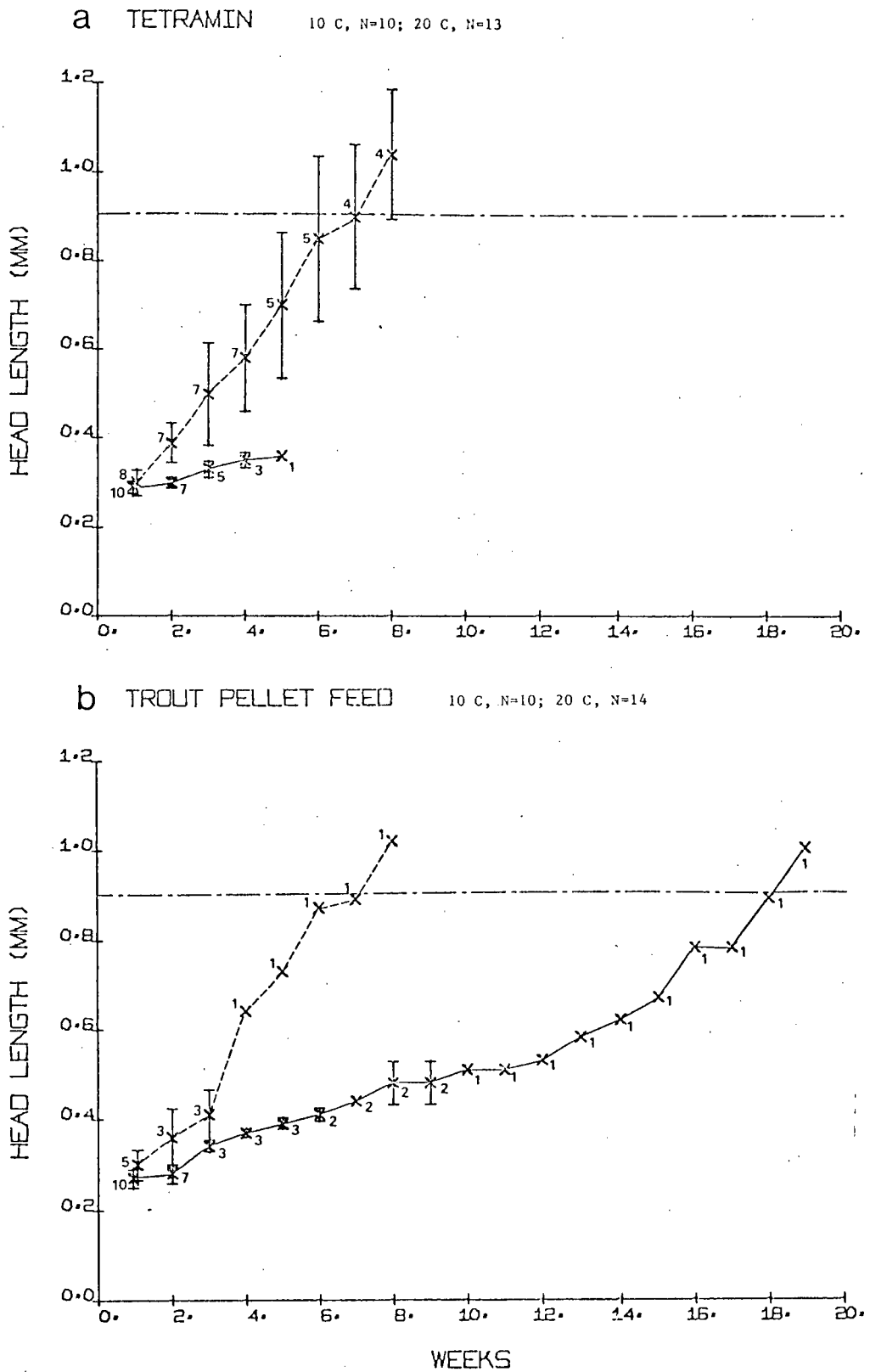
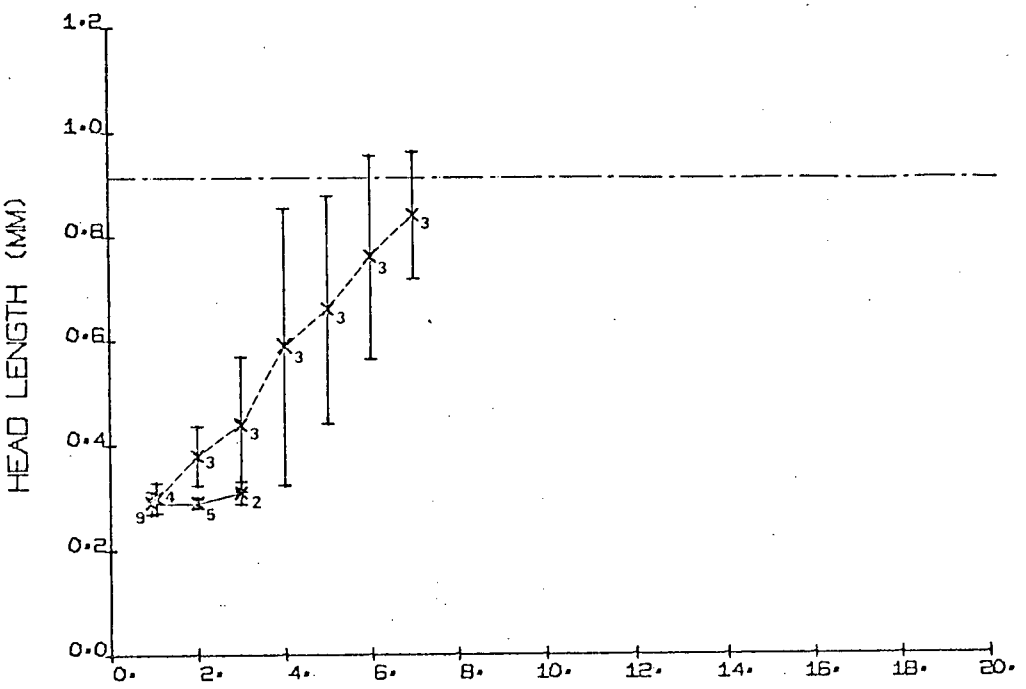

b
OXYGEN UTILIZATION (%)
40.
35.
30.
25.
20.
15.
10.
5.
0.
0.
10.
20.
30.
40.
50.
60.
70.
80.
90.
100.
OXYGEN SATURATION (%)

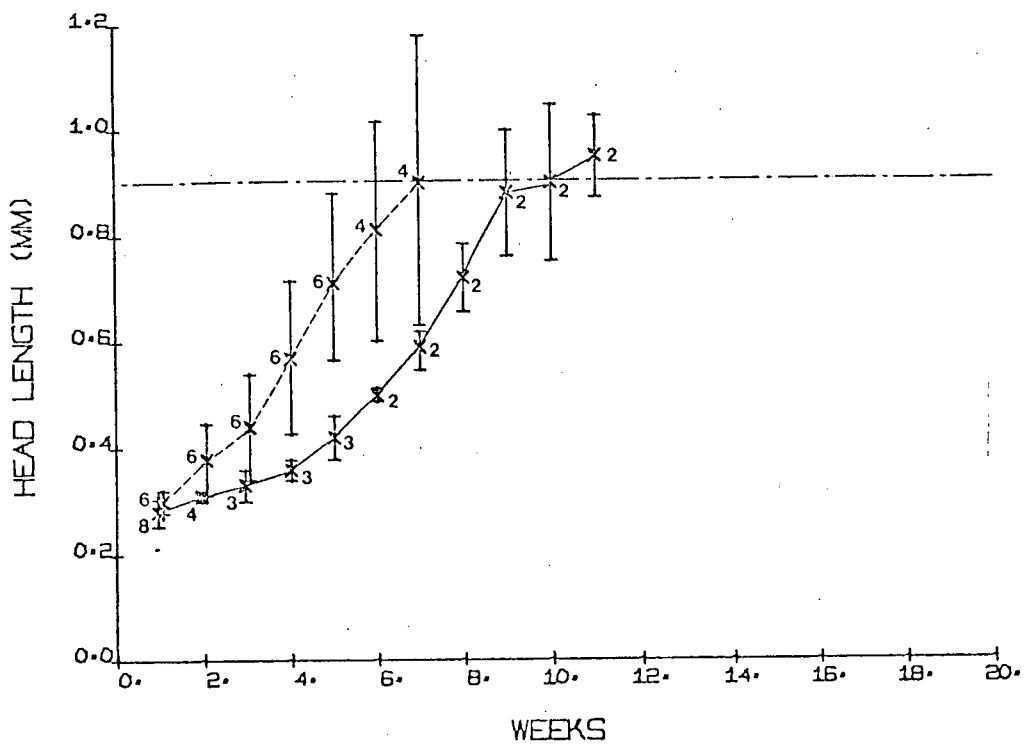
Figure 12. Growth in head length with various foods. Experiments were continued until an average head length of 0.9 mm was attained (or until all individuals died if this occurred first). x, mean; ———, 10 C (24‰); -----, 20 C (24‰); — - —, 0.9 mm head length. Number beside mean is the number of animals surviving. Vertical lines represent one sample standard deviation on either side of the means. Animals that died on the surface film not included.


a TETRAMIN 10 C, N=10; 20 C, N=13
HEAD LENGTH (MM)
1·2
1·0
0·8
0·6
0·4
0·2
0·0
0·
2·
4·
6·
8·
10·
12·
14·
16·
18·
20·
b TROUT PELLET FEED 10 C, N=10; 20 C, N=14
HEAD LENGTH (MM)
WEEKS

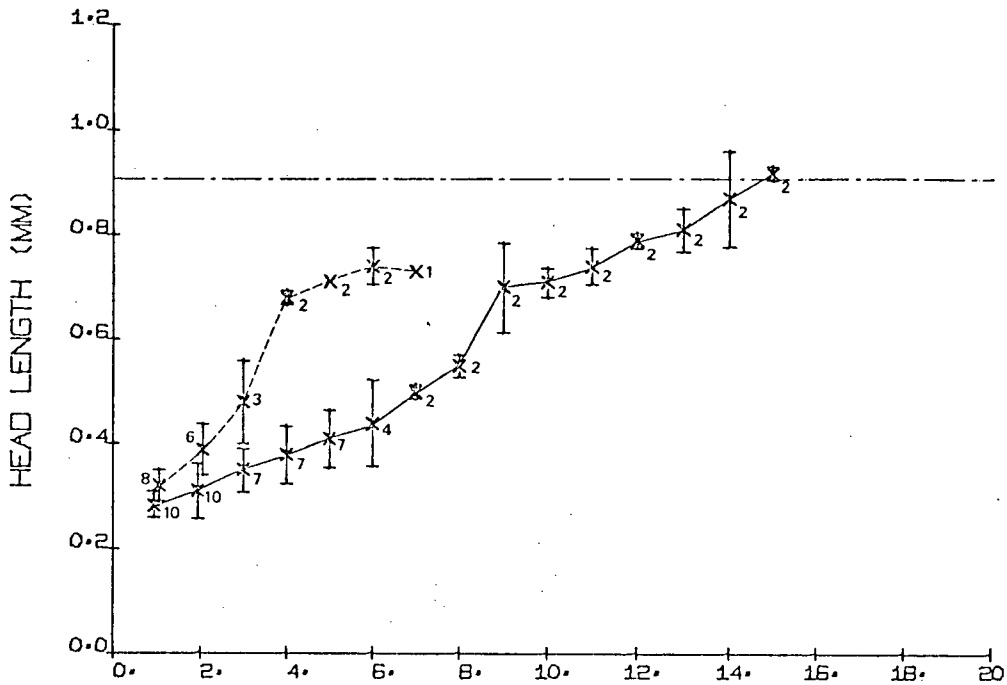
c FISH (FROZEN) 10 C, N=10; 20 C, N=14



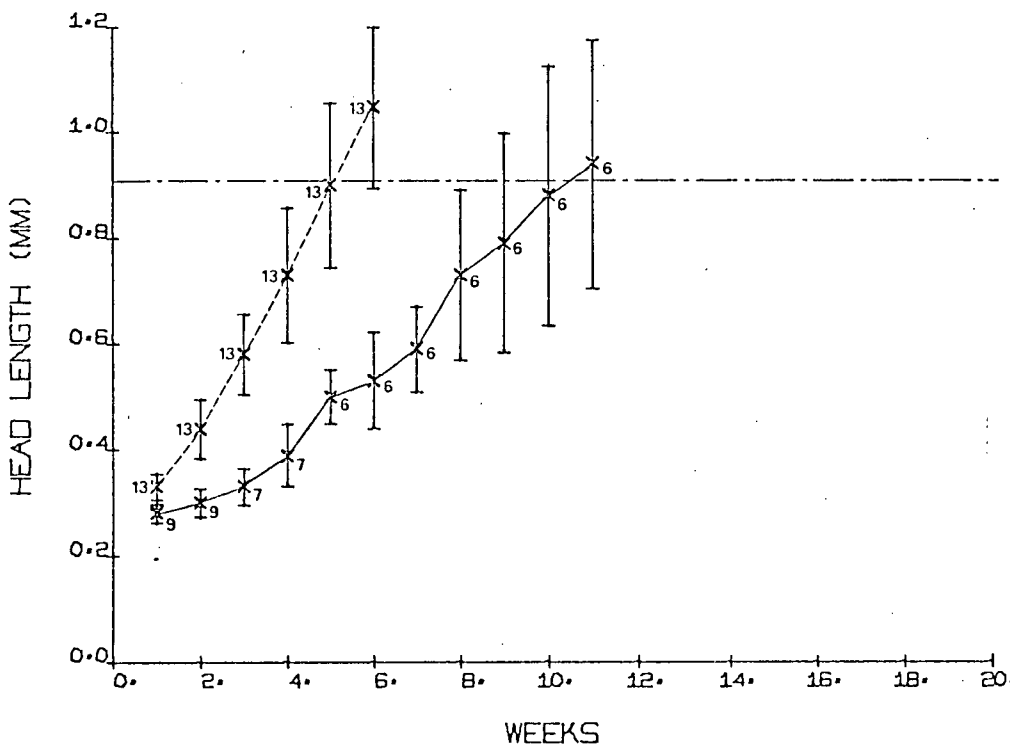
d FROZEN BRINE SHRIMP 10 C, N=10; 20 C, N=14



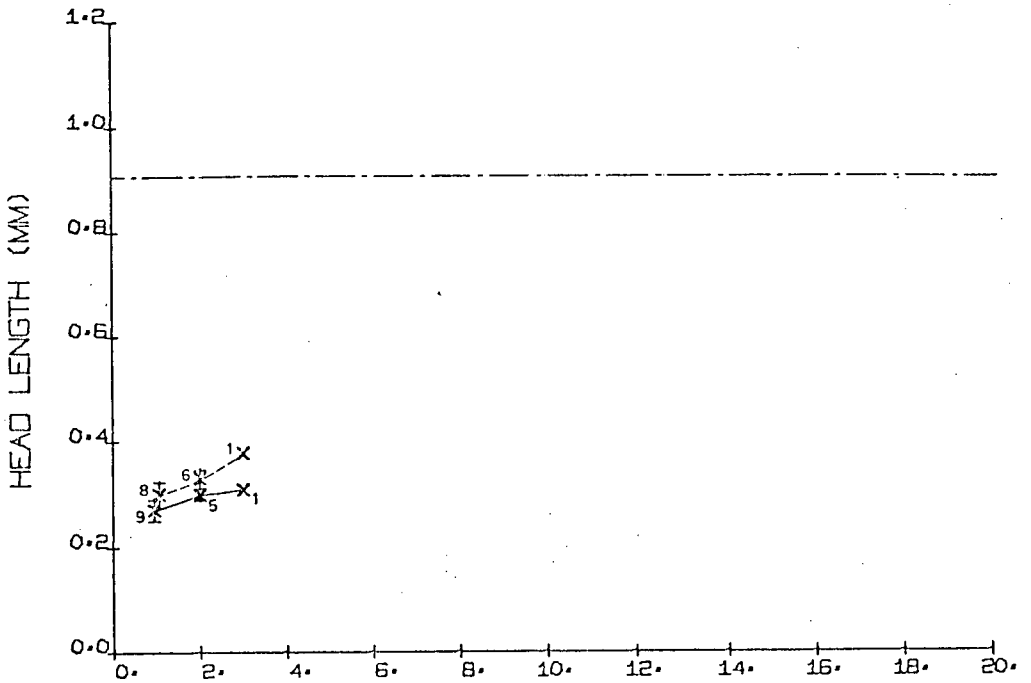
e FUCUS 10 C, N=10; 20 C, N=14



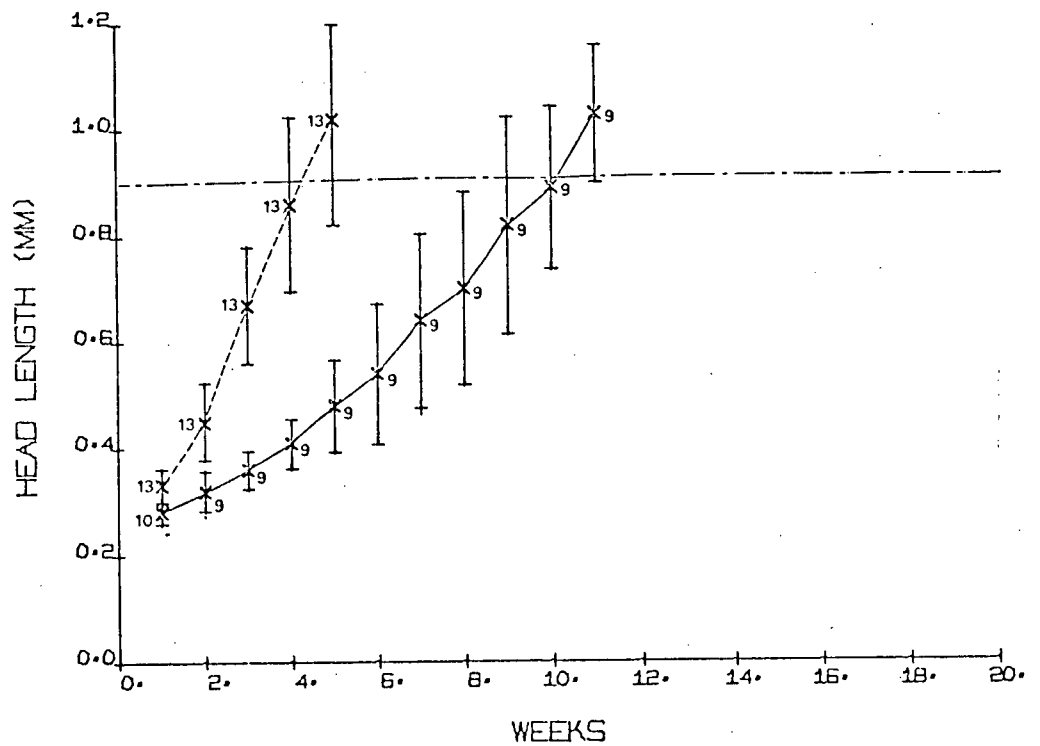
f DIATOMS 10 C, N=9; 20 C, N=14



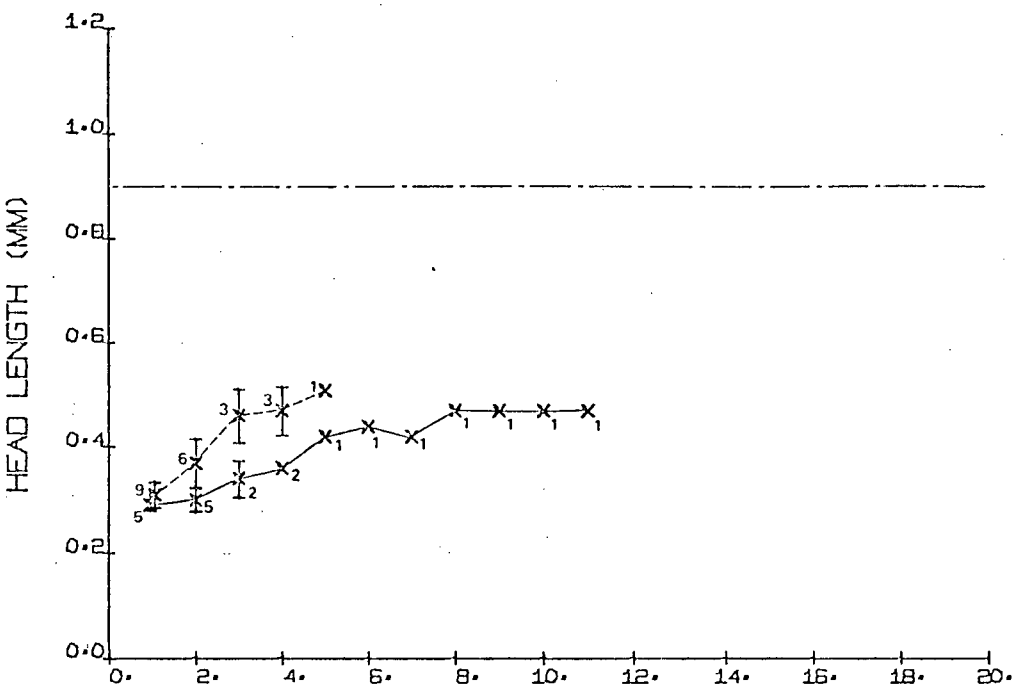
g ULVA 10 C, N=10; 20 C, N=16



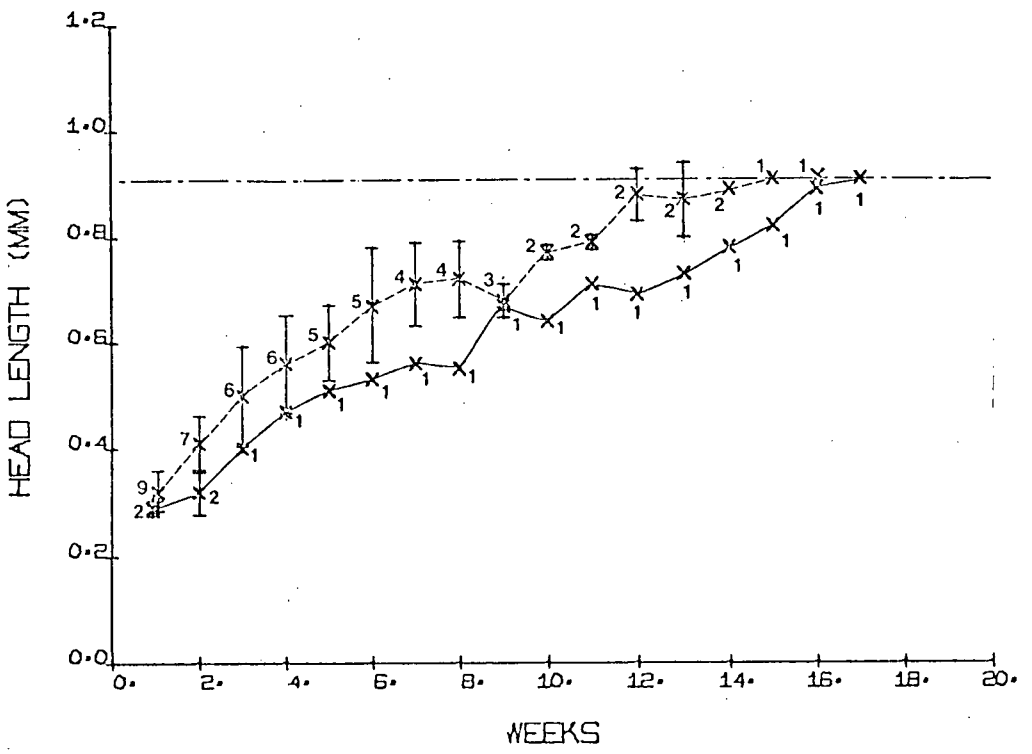
h ENTEROMORPHA 10 C, N=10; 20 C, N=14

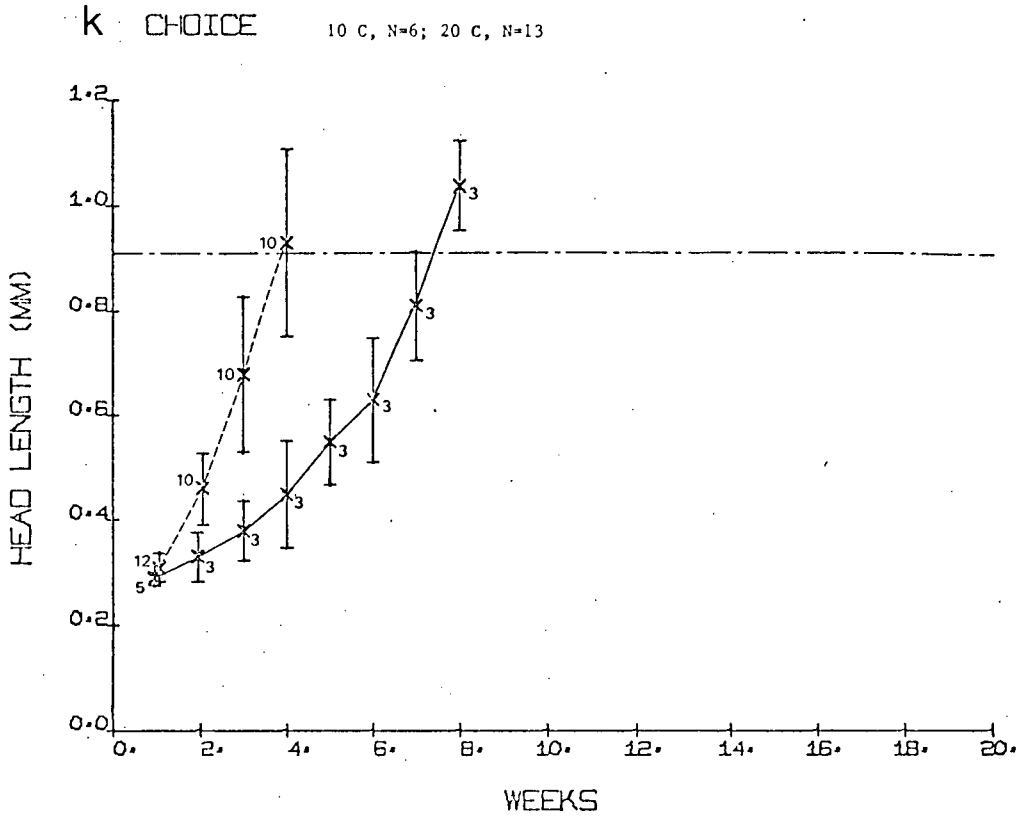


i ZOSTERA 10 C, N=6; 20 C, N=14



j DETRITUS 10 C, N=6; 20 C, N=12




k CHOICE
10 C, N=6; 20 C, N=13
HEAD LENGTH (MM)
1.2
1.0
0.8
0.6
0.4
0.2
0.0
0.
2.
4.
6.
8.
10.
12.
14.
16.
18.
20.
WEEKS
12
5
10
10
10
3
3
3
3
3
3

in an earlier experiment, some young survived 6 weeks on this plant, but with poor growth (maximum head length attained, 0.6 mm; Chang and Parsons 1975). The survival of some animals for several weeks with Zostera and Chondria was probably due to ingestion of epiphytic organisms, as the host plant was not reduced by grazing. On plants that were ingested, epiphytes may also be a nutritional source.

Fish feeds and animal flesh were readily eaten by adults. Some young grew to maturity on these foods, but growth was slower (especially for trout pellet feed), and survival was poor, especially for the smallest amphipods. In an earlier experiment, 0.9 mm was reached in 5-6 weeks at 20° C with pellet feed and turbot flesh (cf. present study) with poor survival (Chang and Parsons 1975). Deaths in older animals fed fish feeds and flesh were due to fouling of the medium when too much food was added. Other animals foods could also be eaten; cannibalism sometimes occurred in cultures, especially when other food was scarce; molts were eaten after each molting. Very few fecal pellets were produced when fed animals flesh; with plant foods, numerous fecal pellets were egested.

Tidepool detritus supported slow growth of young animals to mature size, but with poor survival. The amount of detritus that was supplied may have contained insufficient organic matter.

Animals supplied with a choice of frozen brine shrimp, Enteromorpha, benthic diatoms, and Zostera showed slightly faster growth than animals fed Enteromorpha or diatoms alone; numbers were insufficient to determine if this difference was significant. At 10° C, survival with the food choice was low; this was due to fouling of the medium by the brine shrimp. Brine shrimp was the

first eaten by adults; Enteromorpha (small thalli) and diatoms were first eaten by young; Zostera was usually not eaten, except by some adults when all other foods had been eaten.

Enteromorpha also supported reproduction in laboratory cultures. The ability of other foods to support reproduction was not studied.

b. Egestion Rates

Egestion rates over 24 h at 20° C were extremely variable (Fig. 13). Qualitative observations indicated that feeding and egestion rates were higher at 20° C than at 10° C. Preliminary experiments over 2 and 3 days also showed large variability in egestion rates.

c. Assimilation Efficiencies

The estimates of assimilation efficiency of organic matter by adult A. pugettensis feeding on Enteromorpha and diatoms are shown in Table VI. For Enteromorpha, both methods produced nearly identical results. The variability within each method was large. The assimilation efficiency at 20° C was significantly lower than that at 10° C (t-test, $p = 0.01$, for ^{14}C results). For diatoms, the two methods produced quite different results; the ^{14}C method gave much higher efficiencies.

7. Estimates of Growth Efficiency

a. Growth Rates

Growth in length when fed Enteromorpha at 10 and 20° C in 24‰ (see Fig. 11), converted to growth in dry body weight, is shown in Fig. 14. The absolute and weight-specific growth rates, in mg C/day, calculated over weekly intervals, are shown in Fig. 15. Absolute growth rates increased at a decreasing rate as body weight increased.

Figure 13. Egestion rates (mg C/day) at 20° C. Food: Enteromorpha intestinalis. Fecal pellets were collected after 24 h. The carbon content of the fecal pellets was assumed to be one-half the ash-free dry weight. The dry weights of the amphipods were obtained by conversion of head lengths (see Fig. 7). x, males; +, females.

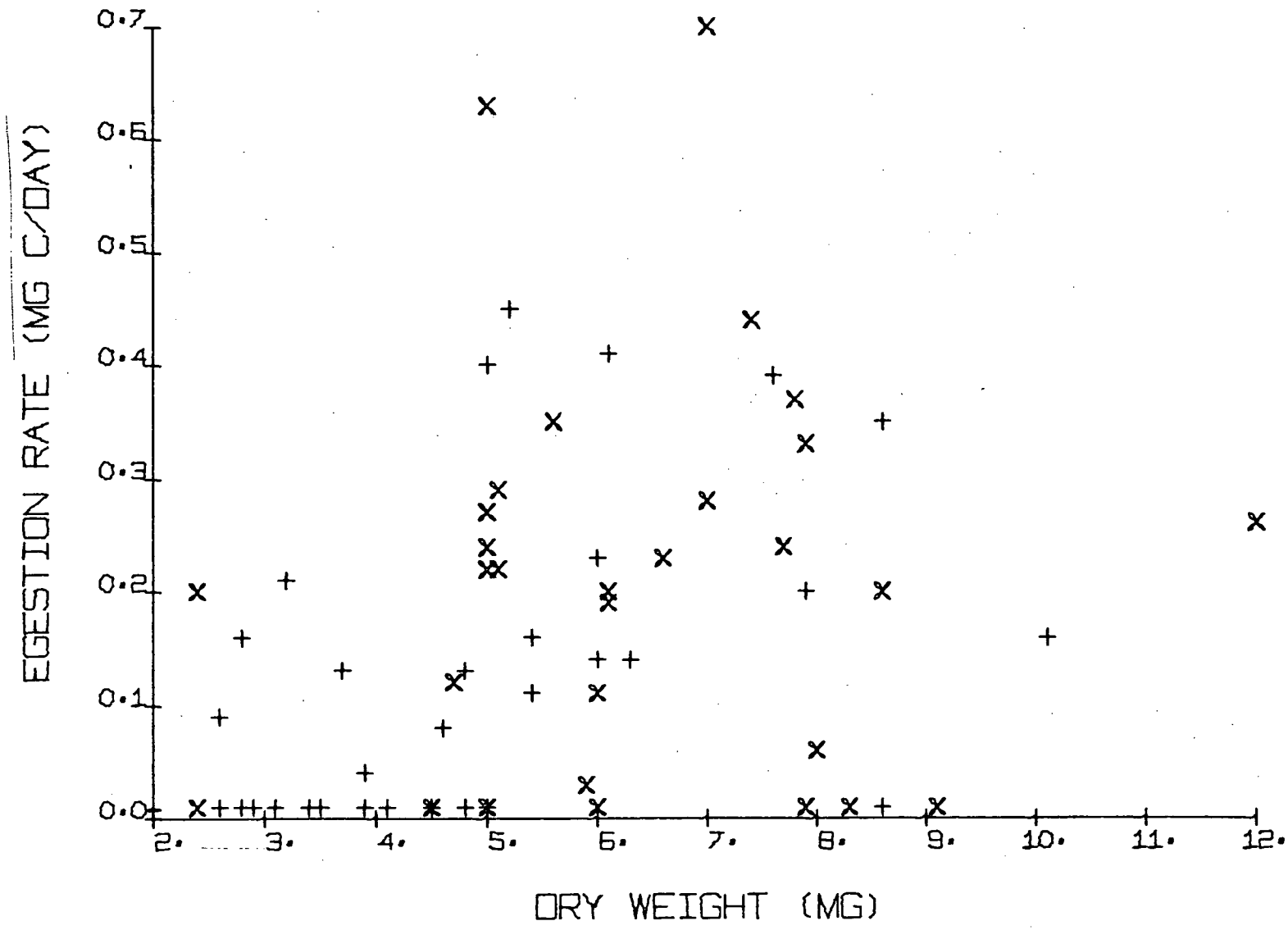

T = 20 C
EGESTION RATE (MG C/DAY)
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
2.
3.
4.
5.
6.
7.
8.
9.
10.
11.
12.
DRY WEIGHT (MG)

Table VI. Assimilation efficiencies (A) of adults.

Food; ash content in % ($\bar{x}$±SD)	Temp. (C)	^{14}C Method[1] n	Dry wt. amphipods ($\bar{x}$±SD)	A (%) ($\bar{x}$±SD)	Conover Method[2] n	A (%) ($\bar{x}$±SD)
Enteromorpha intestinalis (17.1±3.48)	10	14	5.4±0.87	77±9.4	8	77±6.4
Enteromorpha intestinalis (17.1±3.48)	20	14	5.5±1.00	68±9.1	8	66±15.2
Benthic diatoms (Nitzschia sp.) (45.8±3.34)	10	10	5.0±0.66	82±6.0	5	46±5.3

[1] n is the number of individuals; dry wt. estimated from head length

[2] n is the number of trials; each trial represents the pooled results of 4-6 adults

Weight-specific growth rates decreased at a decreasing rate as body weight increased. Males showed higher growth rates than females, especially at body weights greater than ca. 1 mg dry weight (which is the approximate minimum size of mature females). Growth rates were higher at 20° C than at 10° C for animals smaller than ca. 3.5 mg dry weight; for larger animals, growth rates were higher at 10° C.

b. Metabolic Rates

The oxygen uptake rates at 10 and 20° C in 24‰ seawater (from Appendix C), expressed in mg C/day (males and females combined) are shown in Fig. 16. Absolute metabolic rates increased at a decreasing rate as the body weight increased; weight-specific rates decreased at a decreasing rate as body weight increased. Oxygen uptake rates were higher at 20° C than at 10° C.

c. Assimilated Ration

The absolute and weight-specific assimilated rations, as estimated by the sum of the growth and oxygen uptake rates, are shown in Fig. 17. The absolute assimilated ration increased at a decreasing rate as body weight increased; the weight-specific assimilated ration decreased at a decreasing rate as body weight increased. The assimilated ration was higher for males than for females, except at the smallest sizes. At 20° C, the assimilated ration was higher than at 10° C, but at weights greater than ca. 3.5 mg, the values at 10° C approached those at 20° C.

d. Growth Efficiencies

The net growth efficiencies (K_2) are shown in Fig. 18. The values of K_2 show a general decrease with increasing body weight.

Figure 14. Growth in dry weight at 10 and 20° C (24‰). Food: Enteromorpha intestinalis. Data converted from data in Fig. 9 (see Fig. 7). The minimum size of adults is ca. 1 mg. x, males; +, females; ———, 10° C; -----, 20° C.

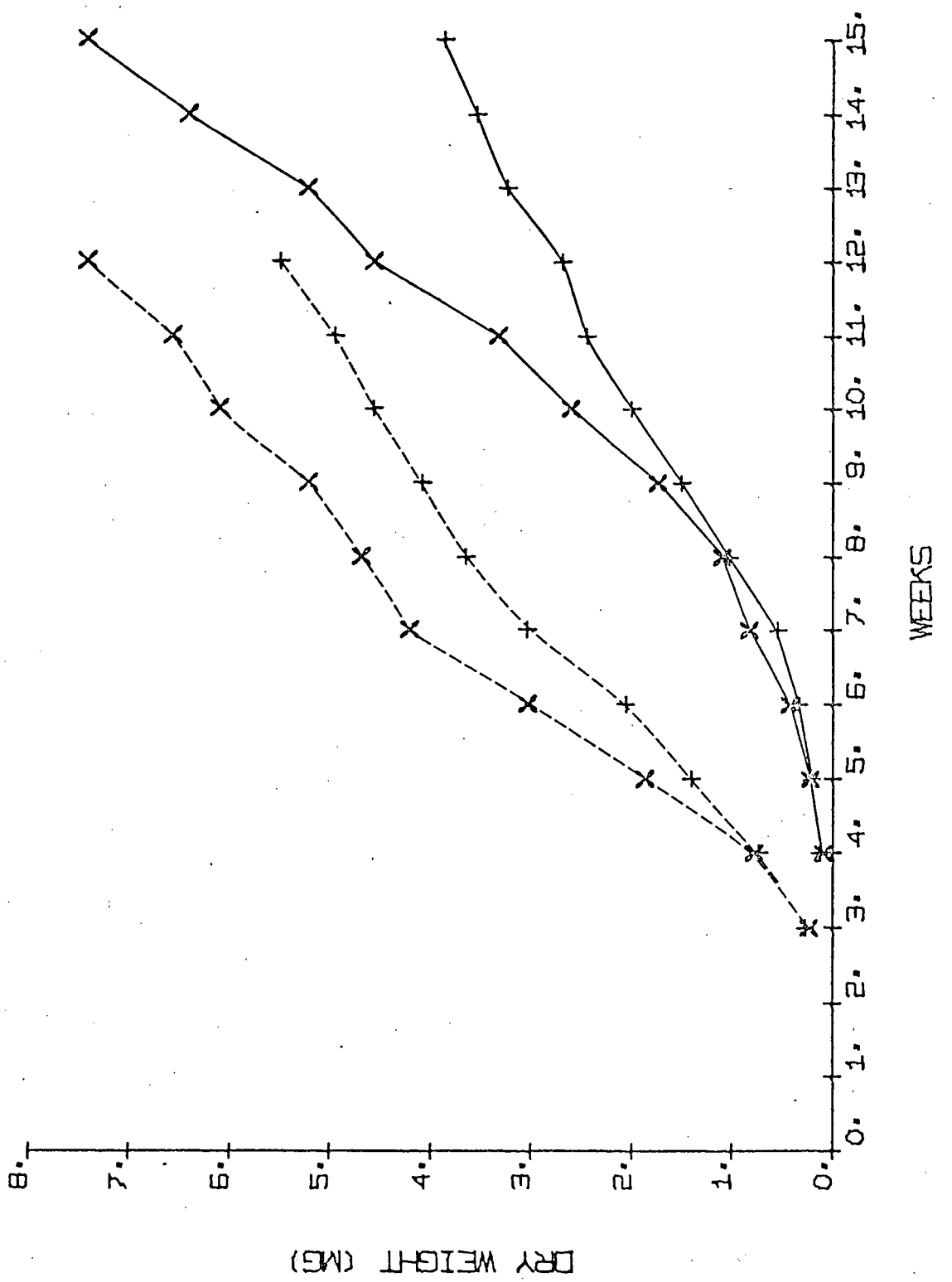
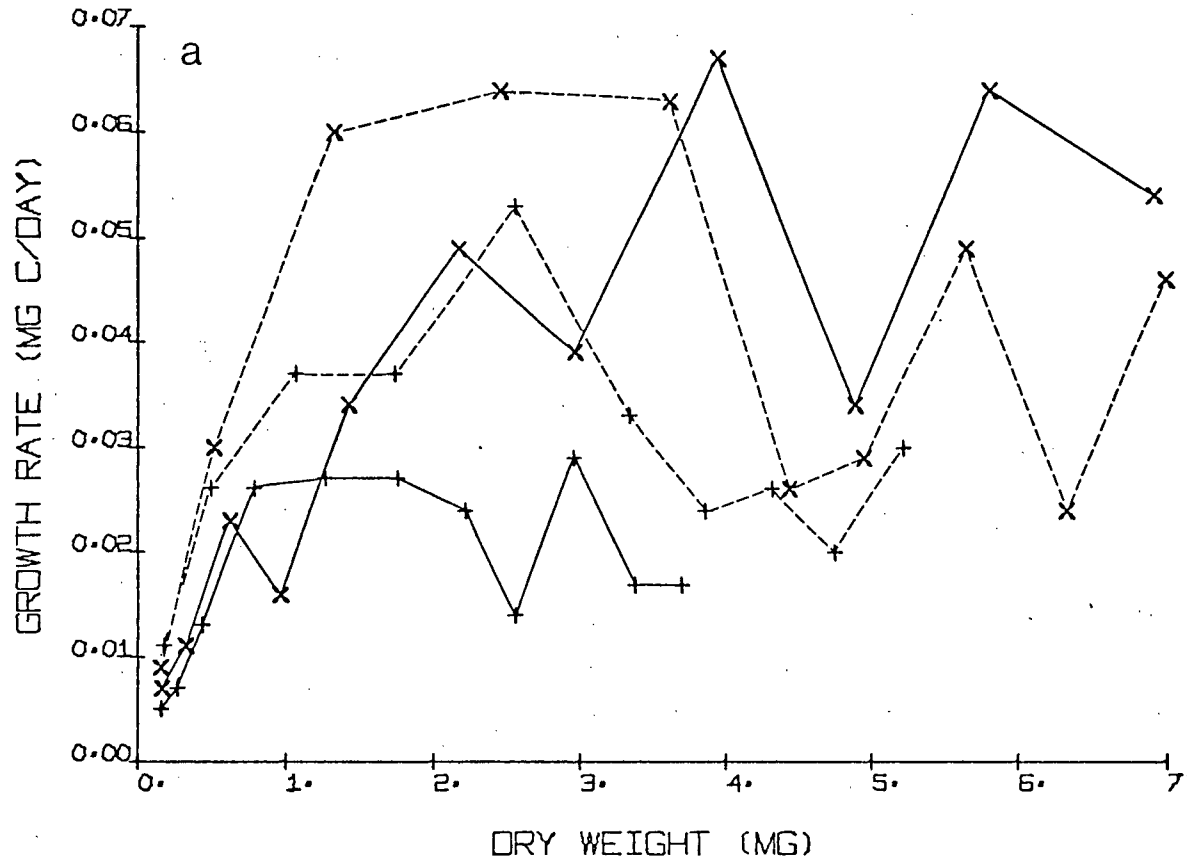

DRY WEIGHT (MG)
WEEKS
0.
1.
2.
3.
4.
5.
6.
7.
8.
9.
10.
11.
12.
13.
14.
15.

Figure 15. Growth rate vs. body weight at 10 and 20° C (24‰). Food: Enteromorpha intestinalis. Rates were calculated from the data shown in Fig. 14. Fig. 15a: growth rate in mg C/day vs. dry body weight. Fig. 15b: growth rate as a percentage of the total body C/day vs. dry body weight. x, males; +, females; ———, 10° C; -----, 20° C.


a
GROWTH RATE (MG C/DAY)
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0.00
0.
1.
2.
3.
4.
5.
6.
7.
DRY WEIGHT (MG)

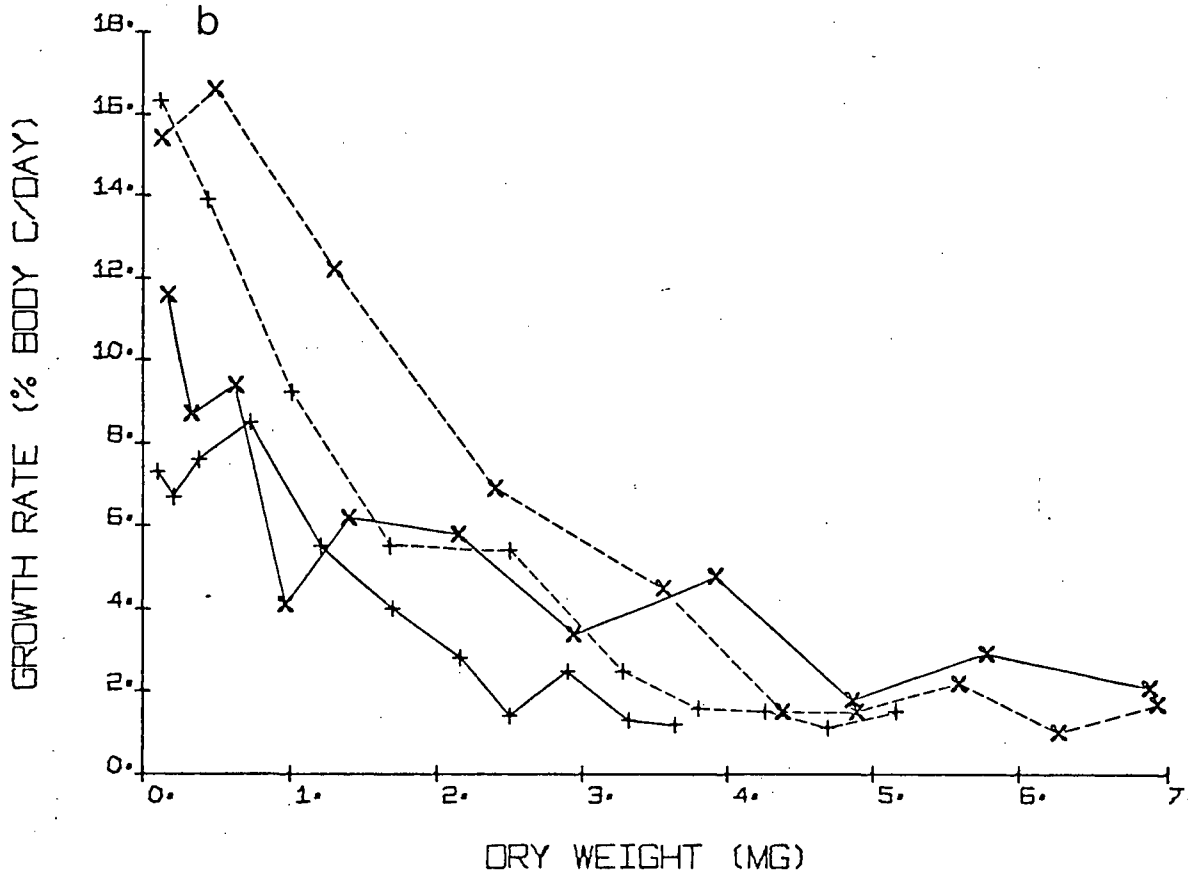
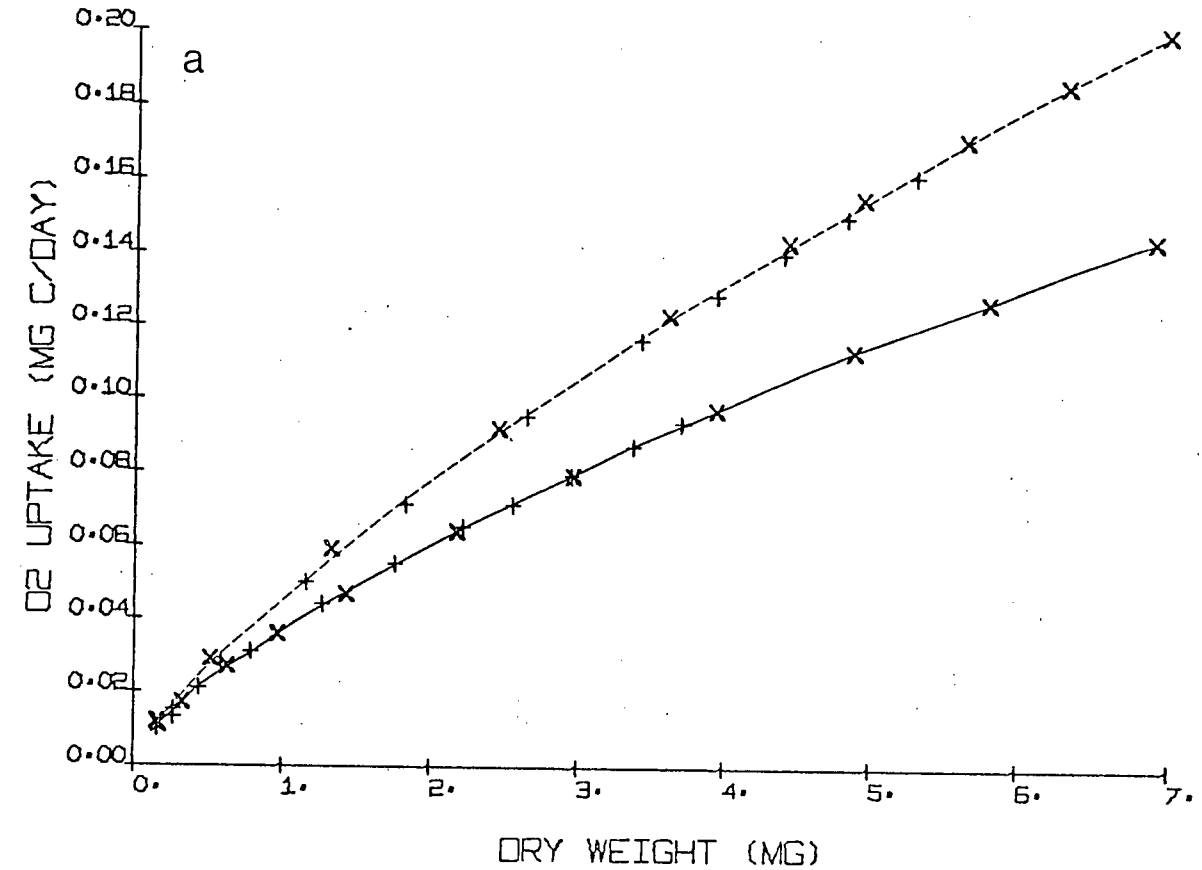

b
GROWTH RATE (% BODY C/DAY)
18.
16.
14.
12.
10.
8.
6.
4.
2.
0.
0.
1.
2.
3.
4.
5.
6.
7.
DRY WEIGHT (MG)

Figure 16. Oxygen uptake vs. body weight at 10 and 20° C (24‰). Rates were calculated from data in Appendix C. Males and females of the same size were assumed to show similar rates. Fig. 16a: oxygen uptake in mg C/day vs. dry body weight. Fig. 16b: oxygen uptake as a percentage of the total body C/day vs. dry body weight. x, males; +, females; ———, 10° C; -----, 20° C.


a
O2 UPTAKE (MG C/DAY)
0.20
0.18
0.16
0.14
0.12
0.10
0.08
0.06
0.04
0.02
0.00
0.
1.
2.
3.
4.
5.
6.
7.
DRY WEIGHT (MG)

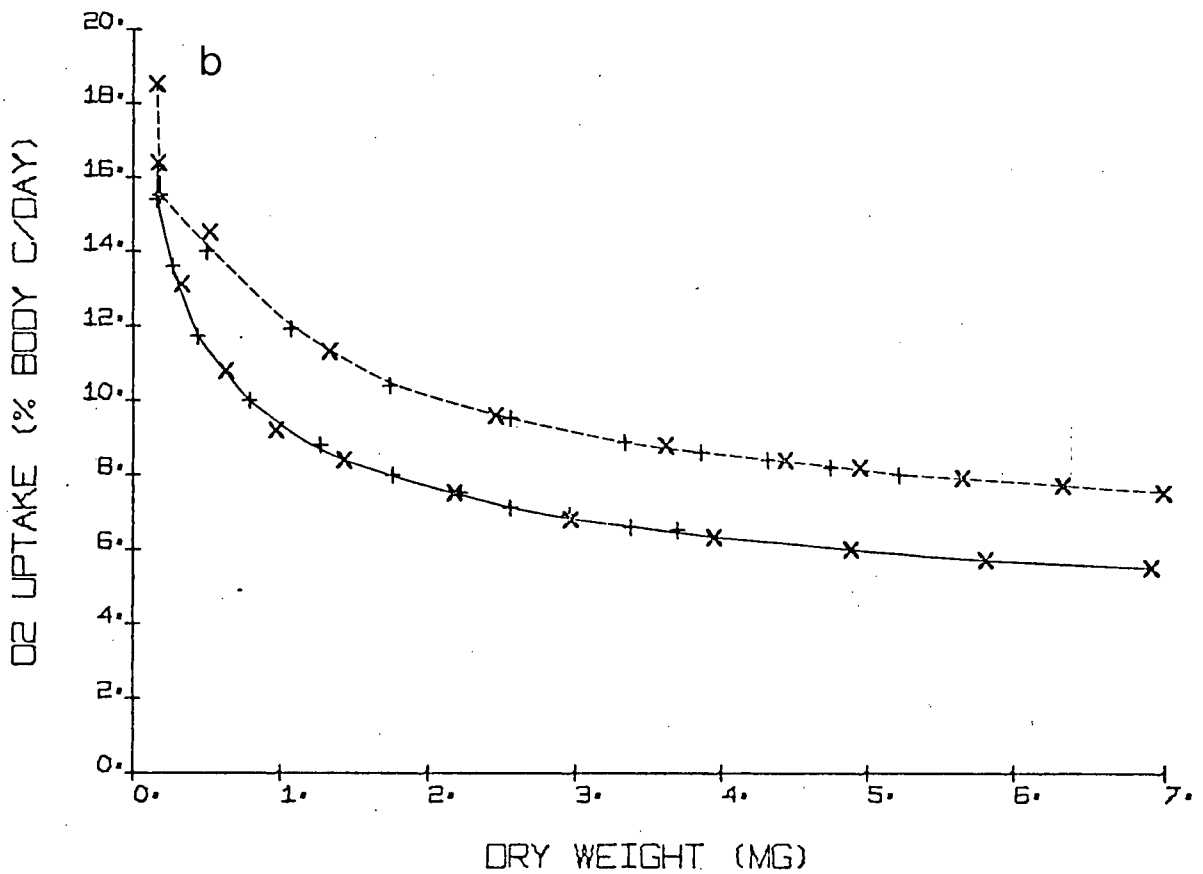
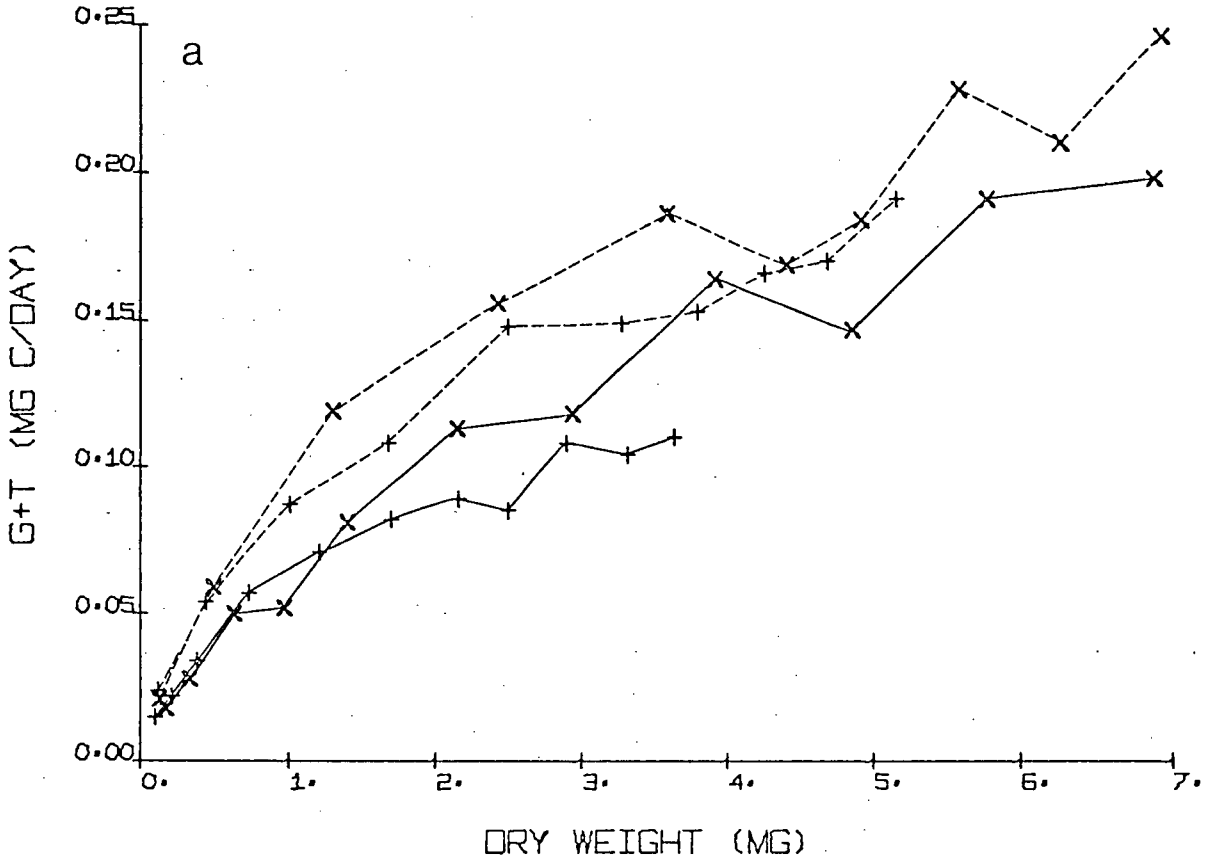

b
O2 UPTAKE (% BODY C/DAY)
20.
18.
16.
14.
12.
10.
8.
6.
4.
2.
0.
0.
1.
2.
3.
4.
5.
6.
7.
DRY WEIGHT (MG)

Figure 17. Assimilated ration vs. body weight at 10 and 20° C (24‰). The assimilated ration was estimated as the sum of growth (Fig. 15) and metabolism (Fig. 16). Fig. 17a: assimilated ration in mg C/day vs. dry body weight. Fig. 17b: assimilated ration as a percentage of the total body C/day vs. dry body weight. x, males; +, females; ———, 10° C; -----, 20° C.


a
0·25
0·20
0·15
0·10
0·05
0·00
G+T (MG C/DAY)
0·
1·
2·
3·
4·
5·
6·
7·
DRY WEIGHT (MG)

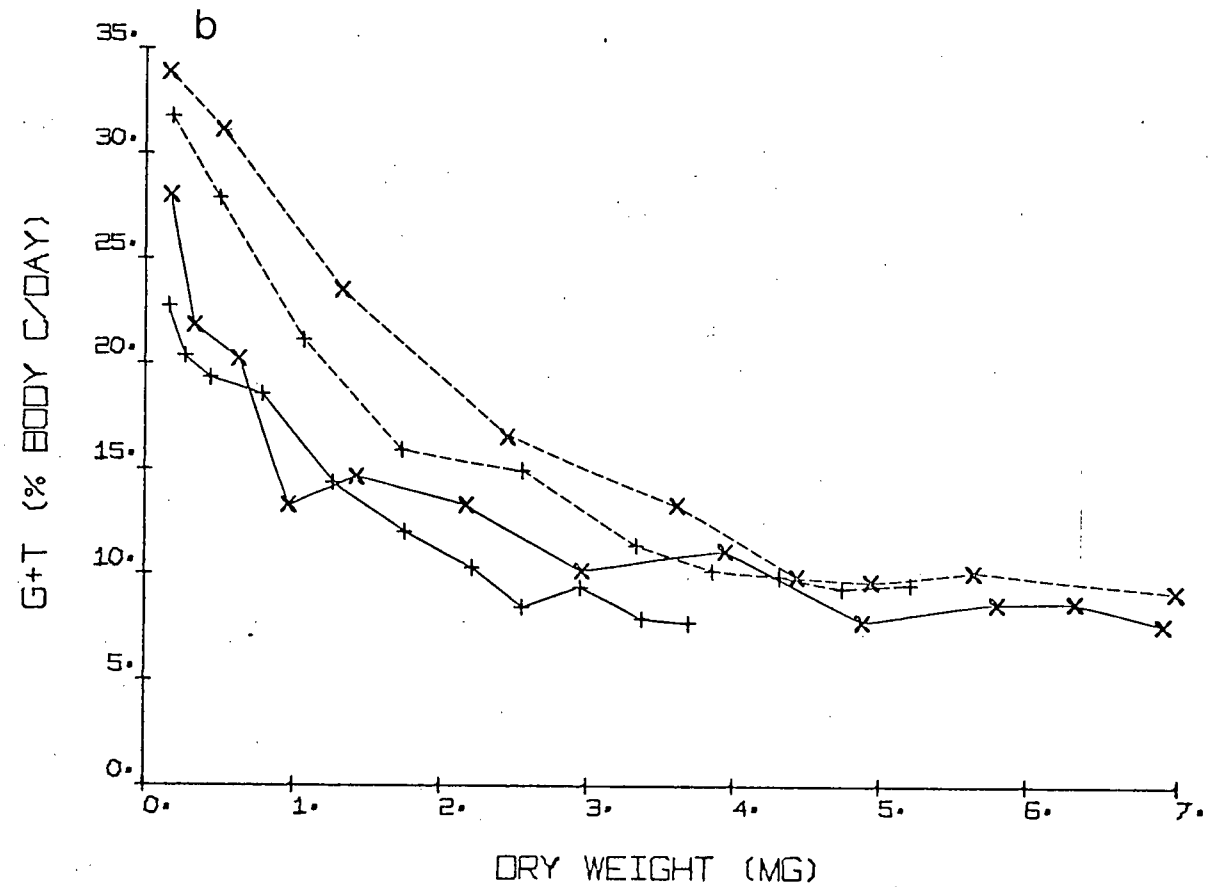
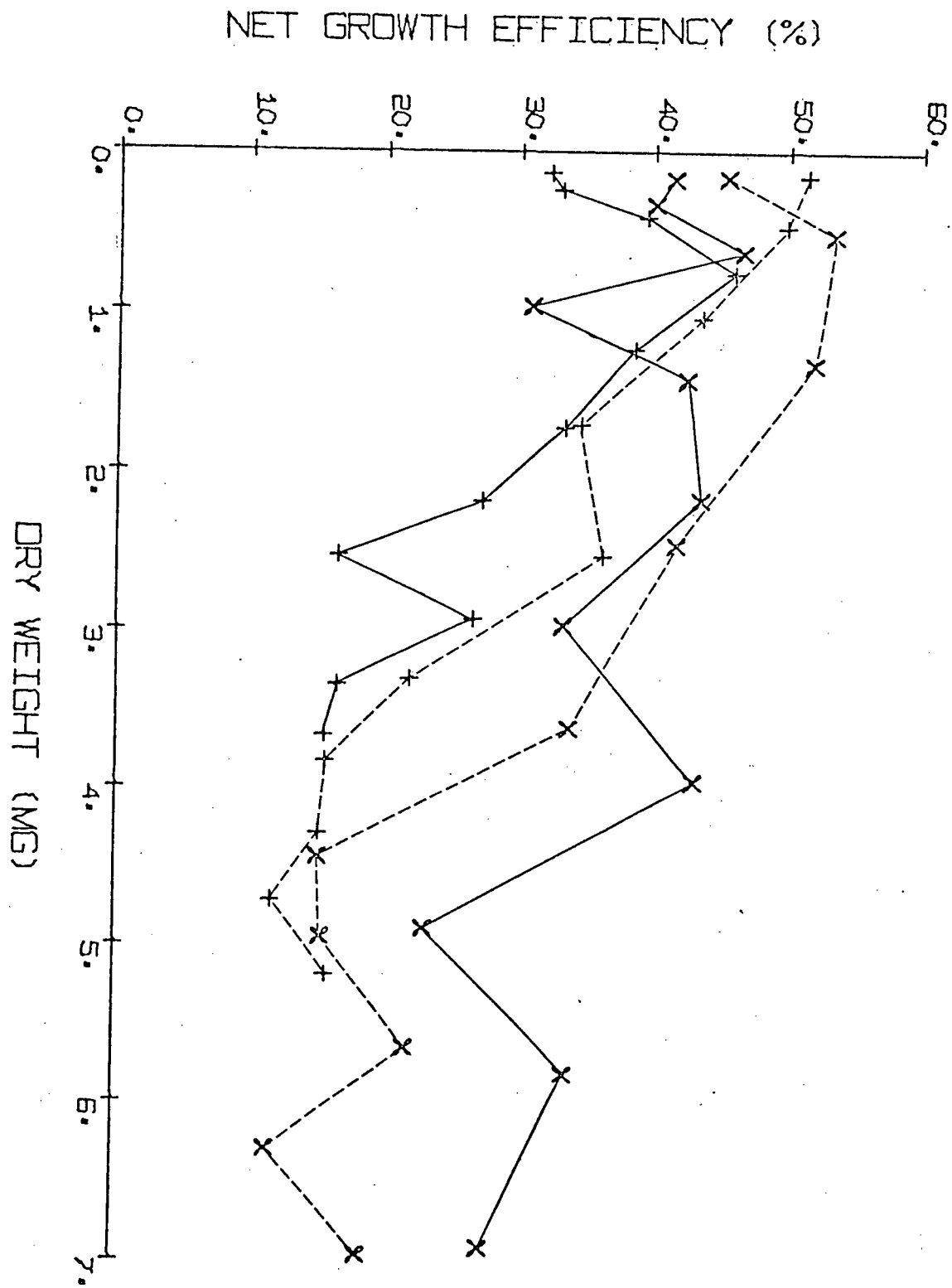

b
35·
30·
25·
20·
15·
10·
5·
0·
G+T (% BODY C/DAY)
0·
1·
2·
3·
4·
5·
6·
7·
DRY WEIGHT (MG)

Figure 18. Net growth efficiency (K_2) vs. dry body weight at 10° and 20° C (24‰). Net growth efficiencies in percent were estimated as the growth rate (Fig. 15) divided by the sum of the growth and metabolic rates (Fig. 17). Food: Enteromorpha intestinalis. x, males; +, females; ———, 10° C; -----, 20° C.


NET GROWTH EFFICIENCY (%)
0.
10.
20.
30.
40.
50.
60.
DRY WEIGHT (MG)
0.
1.
2.
3.
4.
5.
6.
7.

However, at body weights less than ca. 0.5 mg, there appeared to be an increase in K_2 with increasing body weight (a K_2 vs. weight curve exhibiting a hump at smaller sizes was found in Pontogammarus maeoticus; Soldatova 1970; Makarova and Zaika 1971). Males showed higher K_2 values than females, especially at sizes greater than 1 mg. At 20° C, K_2 values were higher than at 10° C for animals smaller than ca. 3 mg; animals greater than 3 mg showed higher K_2 values at 10° C.

For the time from hatching until 0.9-1.0 mm head length (ca. 1 mg dry wt.) is attained, the overall K_2 values were similar in males and females, and higher at 20° C (males, 50%; females, 45%) than at 10° C (males, 39%; females, 40%). The maximum K_2 values shown were 46-47% at 10° C (at 0.6-0.8 mg dry wt.) and 51-53% at 20° C (at 0.02-0.05 mg).

If the assimilation efficiencies obtained for 5 mg adults also apply to smaller individuals, then gross growth efficiencies (K_1) could be estimated as 30-31% at 10° C and 30-34% at 20° C (assuming assimilation efficiencies of 77% at 10° C and 67% at 20° C) for growth up to 0.9-1.0 mm head length on Enteromorpha.

V. DISCUSSION

A. FACTORS AFFECTING DISTRIBUTION

A. pugettensis was found in the middle and lower intertidal zones in tidepools, seaweed clumps, and Zostera beds. The amphipods were also found subtidally in seaweeds in the trap. The temperature tolerances of A. pugettensis were more than adequate for survival in the temperature range recorded in the middle and

lower intertidal zones at Crescent Beach during sampling times in this study. Temperatures outside the recorded range can occur in this area: temperatures greater than the 24 h high temperature tolerance (24-27° C) can occur in summer, but infrequently, and for only a short part of the day (during a daytime low tide); tidepool temperatures of 0°C or less can occur in winter, and freezing of tidepools rarely occurs (see Husted 1969). The wide tolerance range (tolerance to freezing was not examined) plus the ability to adjust this range according to the acclimation temperature indicate that temperature will rarely cause mortality in the middle intertidal zone and deeper. However, temperature may be a reason for the absence of A. pugettensis from the high intertidal zone at low tide. In this zone, the duration of low tide exposure is longer. As a result, exposure to temperature extremes (including freezing conditions) will be greater than in lower regions of the beach.

Avoidance of desiccation may be another reason for the absence from the higher intertidal zone at low tide. Desiccation could be avoided during a low tide intertidally in tidepools or in moist air within seaweed clumps. In the high intertidal zone, tidepools were absent, and seaweed clumps may become dried out (and uninhabitable) as a result of the longer exposure time, especially in summer temperatures (these clumps were mostly absent in winter).

The 24 h salinity tolerance range was much wider than the range of recorded field salinities. The one week low salinity tolerance was ca. 11‰ (Chang and Parsons 1975). Salinities outside the recorded range may occur as a result of evaporation in tidepools in summer, or precipitation, but these salinities should rarely

be of a magnitude or duration that would cause mortalities. The intolerance to low salinities may limit A. pugettensis to outer estuarine areas where salinities are higher. This probably acts in combination with competition from species that are adapted to lower salinities. In other areas, A. pugettensis is found in relatively high salinities; on the west coast of Vancouver Island, and in Porpoise Harbor near Prince Rupert, this species is found in salinities of 27-32‰ (Bousfield 1958; Waldichuk and Bousfield 1962).

Oxygen levels at Crescent Beach were not measured. In similar shallow marine environments, low oxygen or anoxic conditions frequently occur (Broekhuysen 1935; Wieser and Kanwisher 1959). In the laboratory, most adults survived less than 3 h in anoxia. All were paralyzed during anoxia, and some became paralyzed at oxygen levels as high as 28% saturation. The survival time in anoxia is similar to that of Gammarus oceanicus, although this latter species remains active in anoxic conditions until just before death (Wieser and Kanwisher 1959). In cultures, ovigerous female A. pugettensis beat their pleopods more frequently than did other individuals, indicating a greater oxygen need by embryos.

Wieser and Kanwisher (1959) note that highly mobile animals, such as amphipods, do not need a high tolerance of anoxic conditions because of their ability to detect and avoid such areas. This ability has been shown in Gammarus oceanicus and G. pulex (Cook and Boyd 1965; Costa 1966). A. pugettensis appears to have a similar ability; much activity was shown just after sodium sulfite was added to the medium, indicating an avoidance reaction to low oxygen (or to sodium sulfite); in laboratory cultures in which the medium had

become fouled, some individuals were found above the water surface on the walls of the culture dishes, indicating an attempt to avoid the fouled waters (this behavior was not seen in normal cultures); in the polluted waters of Porpoise Harbor, A. pugettensis occurred mainly in bottom waters where oxygen levels were greater than 30% saturation, and mostly avoided the near-surface waters where oxygen levels were less than 10% saturation (Waldichuk and Bousfield 1962).

Animals can only exist where food of adequate quality and quantity is available. Because of the broad diet, and ability to survive several days without food, A. pugettensis may inhabit a wide variety of food environments. However, food can still affect distribution. The amphipods were not found in tidepools without seaweeds; they were scarce intertidally when seaweed clumps (other than Chondria, which was not acceptable as food) and tidepools with seaweeds were absent; they were abundant in seaweeds in the subtidal trap on some days when seaweeds and amphipods were scarce intertidally; they were scarce in the subtidal trap when it contained no seaweeds. This association of amphipods with seaweeds thus appears to be related to food (as well as to dessication and the attraction of amphipods to solid surfaces).

In summary, food, temperature, dessication, salinity, and oxygen are important factors affecting distribution. The wide tolerances and broad diet allow the species to be widely distributed.

B. FACTORS AFFECTING PRODUCTIVITY

Within the tolerated environment, fluctuations in physical factors can affect productivity. Changes in salinity within the range 12-24‰

did not seem important. In the laboratory, short- or long-term salinity changes in this range had no effect on oxygen consumption, and long-term exposure to different salinities did not affect growth. Large seasonal changes in salinity were not recorded at Crescent Beach.

There may be large diel fluctuations in oxygen levels in shallow coastal waters (Broekhuysen 1935). Short-term changes in oxygen levels affect oxygen consumption, with uptake decreasing as oxygen levels decrease. A similar pattern is reported in some other coastal-water crustaceans, while others are able to maintain constant oxygen uptake over a wide range of oxygen levels (van Weel et al. 1954; Walshe-Maetz 1956; Vernberg 1972). There may be smaller seasonal changes in oxygen levels (e.g. see Bawden et al. 1973). The effects of such long-term changes in oxygen levels on productivity were not examined, although there were lower oxygen levels at 20° C than at 10° C in laboratory experiments (colder water has a higher oxygen carrying-capacity).

Temperature is the most important physical factor affecting production. Large seasonal and diel fluctuations in temperature do occur, and temperature does affect production. Animals acclimated to 10 or 20° C had Q_{10} values of 1.2-1.3 for oxygen uptake at 10 and 20° C. These low values indicate an adaptation to a variable temperature environment; various invertebrates adapted to the less variable pelagic environment have Q_{10} values of 1.6-3.6 (Ikeda 1970; Kinne 1970). Warm-acclimated A. pugettensis maintained low Q_{10} values up to 25° C (which is near the maximum that would be experienced). The high Q_{10} values at low test temperatures would probably be lower in

animals acclimated to winter temperatures, since it is only during winter that near-zero temperatures occur.

Growth rates up to adult size, including embryonic development rates, were much higher at 20° C than at 10° C. The large temperature effect on growth and small effect on metabolism result in much higher growth efficiencies (up to adult size) at 20° C.

Data from field samples indicated other effects of temperature on growth. In warmer months, the minimum, mean, and maximum sizes of mature animals were smaller than in colder months. A temperature effect on maximum size was also indicated in laboratory experiments. Animals larger than ca. 3.5 mgg had higher growth rates, and appeared to have longer life spans, at 10° C than at 20° C. This should result in a larger final size at lower temperatures. Similar temperature effects on incubation period, growth rate to maturity, maximum size, and life span have been reported in many marine invertebrates (see Kinne 1970).

Because brood size increased with female size, average brood sizes were smallest in July, when females were smallest. Winter females did not have the largest average brood sizes, despite the large female sizes, because of the relatively small broods in the largest (>1.5mm head length) females. The largest average brood sizes were in June, when females were relatively large, and average brood sizes were larger at all female sizes than in other months.

From August to early October, the numbers of reproductive females collected were insufficient to allow determination of their reproductive capacity. Young animals were present in these months (1973), indicating that reproduction was occurring. The scarcity

of adults in intertidal collections in these months appeared to be due to the scarcity of suitable habitats (the beach was covered with Chondria); more adults may have been recovered if subtidal collections had been made in these months.

The shorter incubation time, faster growth of young, and the smaller size at maturity, result in a potentially greater frequency of broods in warmer months. This, combined with the large broods in June, means that the greatest productivity should occur in this month. In the warmest months, July and August, the effect of small broods resulting from small female size should be overcome by an increased frequency of broods at the higher temperatures; productivity should be higher than in colder months.

Temperature also affects feeding. The assimilated ration per individual (as estimated from the sum of growth and metabolism) was higher at 20° C than at 10° C, and the assimilation efficiency was lower. Therefore the total ration must be higher at 20° C. Also, the smaller size of animals in warmer months results in a higher weight-specific ration than for animals in colder months. These factors, combined with the greater productivity of the population in warmer months will result in a larger food consumption (by the population) than in colder months.

The quantity of available food affects productivity. With reduced food supplies, growth and metabolism must be reduced, and therefore productivity is reduced. Below a certain food level, survival will also be reduced. Quantity of available food should be greatest in warm months, when primary production is greatest.

The type of food also affects growth and survival. The ability

to ingest foods depends upon the texture of foods. Plants with firm textures cannot be eaten, but after decay they may soften and become acceptable. A similar effect of texture on food acceptability occurs in Marinogammarus (Martin 1966). The decay of plant tissue is accompanied by increased colonization of microorganisms which may increase the nutritional value of the food as well as causing further decay. The size of food was also a factor. The feeding apparatus of A. pugettensis can handle pieces of seaweeds or animal foods and clumps of diatoms, but is less able to handle fine, loose detritus. Amphipods fed animal foods alone did not show as high growth and survival rates as did those fed both animal and plant foods or certain plant foods alone. A need for plant food for maximum growth and survival also occurs in Gammarus duebeni (Kinne 1959).

No quantitative measurements were made of the food supply for A. pugettensis at Crescent Beach. Zostera was the most common macrophyte, but in the laboratory, dead strands of this plant were not eaten by young, and only occasionally by adults. Strands in a more advanced state of decay may be acceptable. Enteromorpha, the next most abundant macrophyte, allowed high growth and survival in the laboratory. It was present in the field (mainly spring and summer), but the standing stock was never large, possibly because of grazing by amphipods. Chondria was present in large quantities for a short part of the year, but was not eaten. Other macrophytes were not common. Clumps of benthic diatoms resulted in high growth and survival rates in the laboratory; a thin layer of diatoms often covered much of the mud at Crescent Beach (although they were not

the same species as those in the laboratory). Diatoms may be important, with bacteria and other microorganisms, as epiphytic material which can be grazed off Zostera or ingested along with Enteromorpha. In coastal environments, epiphytes are important food sources for invertebrates including amphipods (Barnard 1969; Odum 1971). Flesh from dead and some live animals can be eaten, especially by adults; the availability of animal food is unknown. The abundant detritus may be utilized to some extent. The broad diet and the ability to survive several days without food mean that food requirements for survival are easily met. However, because of the effect of food type and quantity on growth and survival, productivity is affected by food.

In summary, temperature and food are the most important factors affecting productivity. Warmer temperatures allow faster growth and greater frequency of reproduction. Food supply should also be larger in warm months. Therefore, productivity should be highest in warmer months.

C. PRODUCTIVITY OF ANISOGAMMARUS PUGETTENSIS

Productivity depends on growth and reproduction. Net growth efficiencies were calculated from data on metabolism and growth. Oxygen consumption by A. pugettensis is in the range of values shown by other amphipod species (see Ivanova 1972; for comparison, wet weight of A. pugettensis is ca. 4 times the dry weight). Growth rates of A. pugettensis are higher than that shown by many Atlantic amphipods. The 28-35 days at 20° C and 49-63 days at 10° C required by A. pugettensis to attain the minimum adult size compares with 130 days at 15° C for Marinogammarus marinus (Vlasblom 1969) and 150-180

days at 18-20° C for Gammarus duebeni (Kinne 1959). G. zaddachi and G. salinus show slightly higher rates (ca. 25 days at 19-20° C; Kinne 1960, 1961) than A. pugettensis. Calculated net growth efficiencies for growth of A. pugettensis to maturity on Enteromorpha are above average compared to values for other aquatic organisms (see Sushchenya 1970; Winberg 1971).

Gross growth efficiencies were calculated from assimilation and net growth efficiencies. Assimilation efficiencies for 5 mg adult A. pugettensis feeding on Enteromorpha (measured by ^{14}C and Conover methods) and on benthic diatoms (^{14}C method) were high, as other authors (using various methods) have found for benthic amphipods feeding on similar foods (Table VII). The Conover method probably underestimated the assimilation efficiency of benthic diatoms by A. pugettensis because of the assumption that the ash fraction of food is not assimilated; this assumption appears invalid (Tsikhon-Lukanina et al. 1968; Forster and Gabbott 1971). Therefore this method will understimate assimilation efficiency, especially in foods with high ash contents such as the benthic diatom mixture (ash was 45% of dry weight; in Enteromorpha ash was 18%). Assimilation efficiencies of A. pugettensis feeding on animal flesh were not measured, but the scarcity of fecal pellets when feeding on flesh indicated higher efficiencies than with plant foods. In other marine Crustacea, assimilation efficiencies of 90% or more occur with animal food (Tsikhon-Lukanina et al. 1968; Ivleva 1970).

In this study, assimilation efficiencies were measured only in adults averaging 5 mg dry weight. Larger (10 mg) A. pugettensis have a lower assimilation efficiency (Table VII). Data from other amphipods (Table VII) indicate that young should have assimilation

Table VII. Assimilation efficiencies (A) of plant foods by benthic amphipods.

Food	Amphipod	Temp. (C)	Sal. (‰)	A (%)	Method	Reference
Enteromorpha intestinalis	Anisogammarus pugettensis (5 mg adults)	10	24	77	^{14}C and Conover	present study
		20	24	67	^{14}C and Conover	
Enteromorpha intestinalis	Anisogammarus pugettensis (10 mg)	10	28	59	^{14}C	Chang and Parsons 1975
Enteromorpha sp.	Anisogammarus pugettensis (old juveniles)	11	23	75	^{14}C-^{51}Cr dual label	W.A. Heath, unpubl.
Enteromorpha sp.	Pontogammarus maeoticus (1 mg)	22-24	14	85-90	dry wt. & nitrogen of food & feces	Karpevich 1946
Cladophora (live)	Pontogammarus maeoticus	24				
	juv. 0.9 mg	24	12	81	calorific value of	Soldatova
	adults 9 mg	24	12	76-81	food & feces	et al. 1969
Cladophora (dead)	Pontogammarus maeoticus					
	juv. 0.8 mg	24	12	61	calorific value of	Soldatova
	adults 6 mg	24	12	64	food & feces	et al. 1969

Table VII. Continued

Food	Amphipod	Temp. (C)	Sal. (‰)	A (%)	Method	Reference
Cystoseira (dead)	Orchestia bottae					
	young		ST*	50	not given	Suschenya
	adults		ST	32	not given	1970
clumps of benthic diatoms (Nitzschia sp.)	Anisogammarus pugettensis (5 mg adults)	10	24	82	^{14}C	present
		10	24	46	Conover	study
Skeletonema costatum on filter paper	Anisogammarus pugettensis (old juveniles)	11	23	90	^{14}C-^{51}Cr dual label	W.A. Heath, unpubl.
Navicula sp. in sediment	Hyalella azteca (0.6-0.8 mg)	15	FW**	75	^{14}C	Hargrave 1970
epiphytes on Chara sp. (17% ash)	Hyalella azteca (0.6-0.8 mg)	15	FW	72	gravimetric	Hargrave
		15	FW	73	Conover	1970
		15	FW	80	protein content of food & feces	

* ST = semi-terrestrial
** FW = freshwater

efficiencies equal to, or greater than, adults. If assimilation efficiencies of young are assumed equal to 5 mg adults, then the estimated gross growth efficiencies for growth of A. pugettensis to 1 mg on Enteromorpha are above average compared to values obtained for various Crustacea (see Sushchenya 1970).

Makarova and Zaika (1971) note that growth efficiencies have been calculated by different formulas that are not strictly comparable; e.g. net growth efficiencies calculated as $K_2 = G/G+T$ are not equal to estimates using $K_2 = G/AR$ (where G is the growth rate, T is the oxygen uptake rate, A is the assimilation efficiency, and R is the ration), since G+T underestimates AR by the amount of energy lost in molting, excretion, and production of young. Therefore, K_2 estimates using the former formula (as in the present study) may be greater than estimates using the latter formula.

It was originally planned to estimate the ration also from the measurements of assimilation efficiency and egestion rates. However, egestion rates were too variable to be of use for this purpose. Many of the animals showed egestion rates much higher than would be expected on the basis of the values of assimilation efficiency, growth, and metabolism, while other individuals did not feed during the test period. To overcome this variability in feeding rates, fecal pellets should be collected daily for several days in succession, and averaged over the period.

Soldatova (1970) estimated that the energy expenditure in molting in Pontogammarus maeoticus was 18% of the weight increase for younger animals, and higher in older animals; over the entire life span, 8% of the total assimilated energy was used in molting, 5% in

weight gain, and 87% in metabolism. Mathias (1971) estimated the energy of molting to be 40% of the energy of growth, or 8% of the total assimilated energy, in a population of Hyalella azteca. Molting rates of A. pugettensis were not directly measured. Molting rates of adult females could be estimated from the incubation period, since molting occurred just before ovulation, and just after the hatching of young; this was also found for H. azteca (Mathias 1971). This would mean a molt interval of about 10 days at 20° C and 15-17 days at 10° C for adult female A. pugettensis. Molt intervals for younger animals are probably shorter (see Kinne 1959; Vlasblom 1969).

If it is assumed that ca. 9 molts are required for A. pugettensis to reach 0.9-1.0 mm head length (1 mg), if each molt is 10-20% of the dry body weight at the time of molting for larger animals and a larger percentage of smaller animals (see Mathias 1971; Ivleva 1970), and if the calorific value (or carbon content) per dry weight of molts is 1/3-1/2 that of dry body tissue (see Soldatova 1970; Mathias 1971), then the energy value of molts during growth to maturity would be 10-30% of the weight gain. However, because A. pugettensis (and other amphipods; Martin 1966; Barnard 1969) usually ingest each molt after molting, not all of the energy value of the molts is lost. As a result, the effect of neglecting the energy loss in molting in the estimation of assimilated ration and growth efficiencies should not be important in the period of rapid growth up to maturity. For large animals, the energy value of molts becomes equal to or greater than the energy gain in growth, and assimilated rations will be significantly underestimated (growth

efficiency will be overestimated) if molting is ignored.

Energy losses due to the excretion of soluble organic substances were not measured for A. pugettensis. Excretion is usually considered to be negligible relative to the energy of oxygen consumption (e.g. Soldatova 1970; Sushchenya 1970). If this is true, then the error in the growth efficiency estimates due to the omission of this energy loss would not be great. However, Hargrave (1971) found the energy of excretion to be of the same order of magnitude as that of oxygen consumption in Hyalella azteca.

No young were produced in the growth experiments of the present study. Therefore, K_2 values for adult females are not representative of reproducing adults. If production of young is considered an energy loss, then K_2 values for reproducing females would be lower than in the present study. If production of young is considered as part of growth, then K_2 values for reproducing females should be similar to, or possibly higher than, values for males (cf. Fig. 18).

The brood sizes of A. pugettensis (average 30-88) were larger than those of most Atlantic amphipods (e.g. Sexton 1928; Cheng 1942; Kinne 1959, 1960, 1961; Steele and Steele 1969, 1970, 1972; Vlasblom 1969); larger broods (average 140-150) were found in Gammarus locusta (Sexton 1928). As in other species, brood size increased as female size increased. There were indications of a decrease in brood size in the largest female A. pugettensis. This occurs in some species of Gammarus, and can be attributed to senility in older (larger) females (Cheng 1942; Kinne 1961). If the dry weight of newly hatched A. pugettensis is estimated as 0.009 mg (extrapolated from Fig. 7), then each brood represents an average of 12-20% of female weight.

The reproductive capacity depends on the frequency of broods as well as on brood size. One factor affecting frequency of broods is the length of the incubation period. The 9-10 days at 20° C and 14-16 days at 10° C for A. pugettensis was shorter than that found for many species of amphipods (see Thurston 1970); e.g. G. duebeni required 12.5 days at 20° C and 29 days at 10° C (Kinne 1959). The incubation time for A. pugettensis was about the same as that shown by Marinogammarus marinus (Vlasblom 1969) and G. salinus (Kinne 1960).

If female A. pugettensis ovulated at each molt, then a brood could be produced about every 10-11 days at 20° C and every 15-17 days at 10° C, with broods becoming successively larger in any one female (except in the largest females). Hynes (1955) states that most amphipods are capable of producing several broods in succession, one at each molt, although an occasional brood may be missed (Sexton 1928). However, 28-90 days (mean, 50) separate successive ovulations of Marinogammarus marinus at 15° C (this is greater than the average length of one molt cycle; Vlasblom 1969). Sufficient data were not obtained to allow estimation of the average time between successive broods in female A. pugettensis. In the laboratory, one female had 3 successive broods (in 3 molt cycles), while other females did not mate before the end of a molt cycle in which a brood was developing, so that at least one molt cycle would occur before the next ovulation. In field collections, some females were observed to be in precopula while already carrying a brood, indicating that another ovulation would occur at the next molt. The great majority of the larger females in the field samples were ovigerous. It appears that broods at

successive molts occur in natural conditions, but a resting interval of at least one molt cycle between broods is probably not uncommon.

Field data indicate that reproduction occurs throughout the year at Crescent Beach, since either reproductive females or young are present in all months. Many Atlantic amphipods show a resting stage (not due to temperature), during which no reproduction occurs, at some part of the year (Steele 1967). However, other species, such as Gammarus chevreuxi and Marinogammarus marinus reproduce throughout the year (Sexton 1928; Vlasblom 1969).

In summary, A. pugettensis shows a large brood size, probably a high frequency of broods, reproduction throughout the year, high growth rates, and high growth efficiencies. This should result in a large, highly productive population, especially in warmer months when growth rates, brood frequency, and food supplies should be highest.

This potentially high productivity, combined with the broad diet, indicates an important role for A. pugettensis as a consumer in higher salinity estuarine environments. The amphipod is probably an important prey species for various fishes, although no studies of predation on A. pugettensis were done. Sculpins and blennies, which are known to eat amphipods in shallow coastal waters (e.g. Husted 1969; B. Leaman, personal communication), are present at Crescent Beach. In Mamquam Channel in the Squamish estuary, large numbers of A. pugettensis are eaten by juvenile salmon (Levings 1973).

D. IMPORTANCE TO MARICULTURE

An object of this study was to determine the suitability of

A. pugettensis in a salmon mariculture impoundment. The data indicate that many of the qualities wanted for an organism in an impoundment food chain are shown by this species. The tolerances to physical factors were wide, and should be sufficient to survive fluctuations in impoundment conditions. Productivity should be high. Reproduction should occur throughout the year in the impoundment. The broad diet can mean a large food supply for the amphipods. In a shallow artificial upwelling impoundment, such as that suggested by Brown and Parsons (1972), a dense layer of phytodetritus (clumps of phytoplankton that has sunk to the bottom, bacteria, and organic slimes) is produced. In the present study (also W.A. Heath, personal communication), A. pugettensis could utilize similar foods (clumps of diatoms) with high assimilation efficiencies and high growth rates. The amphipods could also eat dead or disabled fish, thus preventing deterioration of water conditions, while obtaining food.

An essential requirement for successful mariculture is that the cultured fish show high growth rates when feeding on the amphipod. This was not examined in the present study. As noted above, A. pugettensis is an important part of the diet of juvenile salmon feeding in the Mamquam Channel. In preliminary experiments, juvenile sockeye and coho salmon fed on a diet of frozen A. pugettensis for at least 2 weeks. Some growth was shown, but longer-term experiments would be needed to verify the suitability of A. pugettensis as food. In freshwater environments, salmonids can grow on similar amphipod species. Surber (1935) raised rainbow and brook trout fingerlings (ca. 20 g wet weight) up to 100 g size in 5 months time, with live Gammarus fasciatus (average dry weight 3.3 mg each) as the sole food.

The conversion rate of dry weight of food to wet weight of fish was a high 1.2, and the fish showed better coloration than was normally found in hatchery and wild populations. If similar results can be shown for marine or estuarine amphipods and anadromous salmonids then amphipod-salmonid impoundment mariculture should be feasible.

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APPENDIX A.

Data for individual field samples. Samples were classed according to size, sex, and reproductive state. Time, temperature, salinity, and habitat data are presented.

Appendix A. Numbers of A. pugettensis in field samples. (T, total; M, males; NF, non-reproductive females; RF, ovigerous or mating females; *, subsample)

Date;Time[1]	18/V/73;1200				5/VI/73;1430				19/VI/73;1325			
Temp.;Sal.[2]	21.9° C;26.3‰								18.3° C;25.1‰			
Habitat	Tidepools				Tidepools				Tidepools			
Head length (mm)	T	M	NF	RF	T	M	NF	RF	T	M	NF	RF
0.30-0.49	127				75				7			
0.50-0.69	36				16				9			
0.70-0.89	8				3							
0.90-1.09	5	2	3	-	1							
1.10-1.29	3	2	-	1								
1.30-1.49	2	2	-	-								
1.50-1.69	1	1	-	-								
1.70+												
Total	182*				95				16			

Date;Time	28/VI/73;0925				16/VII/73;1155				30/VII/73;1130			
Temp.;Sal.	21.3° C;21.8‰				23.7° C;25.9‰				21.3° C;27.0‰			
Habitat	Tidepools				Tidepools				Tidepools			
Head length (mm)	T	M	NF	RF	T	M	NF	RF	T	M	NF	RF
0.30-0.49	15				10				7			
0.50-0.69	21				32				27			
0.70-0.89	3				19				21			
0.90-1.09					9	2	2	3	31	9	8	5
1.10-1.29	2	1	-	1	2	1	-	1	13	9	1	3
1.30-1.49	1	1	-	-	1	1	-	-	4	4	-	-
1.50-1.69												
1.70+												
Total	42				73				103*			

[1] time is the predicted time of the low tide (Pac. Std. Time)
[2] temperature and salinity data for intertidal collections are the averages of 2 or more tidepools.

Date;Time	30/VII/73;1130				27/VIII/73;1030				11/IX/73;1020			
Temp.;Sal.	21.3° C;27.0‰				21.7° C;22.7‰				21.7° C;24.5‰			
Habitat	Seaweeds				Tidepools				Tidepools			
Head length (mm)	T	M	NF	RF	T	M	NF	RF	T	M	NF	RF
0.30-0.49	10				24				18			
0.50-0.69	8				33				37			
0.70-0.89	11				8				14			
0.90-1.09	26	6	11	7	3	1	2	-	8	1	2	-
1.10-1.29	12	11	1	-	2	-	2	-	1	-	1	-
1.30-1.49	3	3	-	-	3	2	-	1	1	1	-	-
1.50-1.69												
1.70+												
Total	70*				72				79*			

Date;Time	9/X/73;0915				23/X/73;0900				22/XI/73;2205			
Temp.;Sal.	11.5° C				13.0° C;26.7‰				6.4° C;19.8‰			
Habitat	Tidepools				Tidepools and Seaweeds				Tidepools and Zostera beds			
Head length (mm)	T	M	NF	RF	T	M	NF	RF	T	M	NF	RF
0.30-0.49					30				1			
0.50-0.69					36				3			
0.70-0.89					22				20			
0.90-1.09					15	6	4	1	32			
1.10-1.29					7	5	1	1	20	10	3	7
1.30-1.49					4	3	-	1	18	8	3	7
1.50-1.69					2	2	-	-	5	5	-	-
1.70+												
Total	Few seen				116*				105*			

Date;Time	19/XII/73;2020				4/II/74;2135				28/II/74;1600			
Temp.;Sal.	7.3° C;24.8‰				5.3° C;20.7‰				8.3° C;25.2‰			
Habitat	Tidepools				Tidepools				Tidepools			
Head length (mm)	T	M	NF	RF	T	M	NF	RF	T	M	NF	RF
0.30-0.49	10				16				14			
0.50-0.69	4				8				15			
0.70-0.89	12				2				28			
0.90-1.09	35				3				19			
1.10-1.29	35	18	16	1	10	2	3	5	3	1	-	2
1.30-1.49	15	8	3	4	10	4	1	5	3	2	-	1
1.50-1.69	4	4	-	-	9	5	-	4	4	-	-	4
1.70+	2	2	-	-	9	9	-	-	11	--	--	1
Total	117*				67*				87*			

Date;Time	11/III/74;1340				28/III/74;1435				9/IV/74;1305			
Temp.;Sal.	12.3° C;25.3‰				11.0° C;26.3‰				14.7° C;25.5‰			
Habitat	Tidepools				Tidepools				Tidepools			
Head length (mm)	T	M	NF	RF	T	M	NF	RF	T	M	NF	RF
0.30-0.49					26				9			
0.50-0.69	no collection				31				23			
0.70-0.89	made; some				19				23			
0.90-1.09	young and				10				24			
1.10-1.29	adults seen,				6	2	1	3	15	8	2	5
1.30-1.49	including				6	2	-	4	12	6	1	5
1.50-1.69	reproductive				4	1	-	3	1	1	-	-
1.70+	females				1	1	-	-	2	2	-	-
Total					103*				109*			

Date;Time	25/IV/74;1325				25/IV/74;1325				26/IV/74;1410			
Temp.;Sal.	10.9° C;26.0‰				12.0° C;24.0‰				12.0° C;24.5‰			
Habitat	Tidepools				Subtidal trap				Zostera beds (few in pools)			
Head length (mm)	T	M	NF	RF	T	M	NF	RF	T	M	NF	RF
0.30-0.49									4			
0.50-0.69									8			
0.70-0.89					1				10			
0.90-1.09					16	5	3	2	17	2	8	3
1.10-1.29					36	9	7	20	17	8	4	5
1.30-1.49					17	9	-	8	6	6	-	-
1.50-1.69					8	7	-	1	5	2	1	2
1.70+					3	3	-	-	3	3	-	-
Total	Few				81*				70*			

Date;Time	8/V/74;1235				8/V/74;1235				27/V/74;1535			
Temp.;Sal.	17.0° C;25.3‰								18.2° C;22.3‰			
Habitat	Seaweeds, some in tidepools				Subtidal trap, no bait left				Tidepools			
Head length (mm)	T	M	NF	RF	T	M	NF	RF	T	M	NF	RF
0.30-0.49	3								32			
0.50-0.69	41								5			
0.70-0.89	33								3			
0.90-1.09	15	6	3	-					1	1	-	-
1.10-1.29	24	10	8	6	mostly adults							
1.30-1.49	20	15	1	4					1	1	-	-
1.50-1.69	2	2	-	-								
1.70+												
Total	138*				30 (approx.)				42			

Date;Time	4/VI/74;1100				4/VI/74;1100				18/VI/74;0950			
Temp.;Sal.	17.0° C;19.6‰								19.1° C;24.2‰			
Habitat	Seaweeds (few in pools)				Subtidal trap				Seaweeds (few in pools)			
Head length (mm)	T	M	NF	RF	T	M	NF	RF	T	M	NF	RF
0.30-0.49	18								6			
0.50-0.69	14				4				24			
0.70-0.89	9				7				49			
0.90-1.09	12	5	5	-	10	1	5	4	27	16	5	-
1.10-1.29	5	3	11	1	28	10	-	18	5	5	-	-
1.30-1.49	7	6	-	1	26	12	-	14				
1.50-1.69	2	1	-	1	10	6	-	4				
1.70+					2	2	-	-				
Total	67				87*				111			

Date;Time	18/VI/74;0950				24/VI/74;1420				9/VII/74;1400			
Temp.;Sal.	19.5° C;20.5‰								19.3° C;22.1‰			
Habitat	Subtidal trap, no bait left				Seaweeds (few in pools)				Seaweeds (few in pools)			
Head length (mm)	T	M	NF	RF	T	M	NF	RF	T	M	NF	RF
0.30-0.49									16			
0.50-0.69	none mea				none measured				44			
0.70-0.89	4				but many found				27			
0.90-1.09	2	1	-	1	including many				18	10	2	6
1.10-1.29	3	2	-	1	ovigerous				4	3	-	1
1.30-1.49					females				1	1	-	-
1.50-1.69	1	1	-	-								
1.70+	1	1	-	-								
Total	11								110*			

Date;Time	22/VIII/74;1315				30/VII/74;0950				13/VIII/74;0715			
Temp.;Sal.	19.6° C;22.6‰											
Habitat	Seaweeds (few in pools)				Seaweeds (few in pools)				Seaweeds, tidepools			
Head length (mm)	T	M	NF	RF	T	M	NF	RF	T	M	NF	RF
0.30-0.49					7							
0.50-0.69	none measured,				19							
0.70-0.89	but many found				31							
0.90-1.09	including many				33	20	8	5				
1.10-1.29	ovigerous				9	9	-	-				
1.30-1.49	females				1	1	♀	-				
1.50-1.69												
1.70+												
Total					100*				Few			

Date;Time	29/VIII/74;0915				13/IX/74;0845			
Temp.;Sal.	22.0° C;21.3‰				23.0° C			
Habitat	Seaweeds (none in pools)				Seaweeds, tidepools			
Head length (mm)	T	M	NF	RF	T	M	NF	RF
0.30-0.49								
0.50-0.69	2							
0.70-0.89	1							
0.90-1.09	2	-	-	2				
1.10-1.29								
1.30-1.49								
1.50-1.69								
1.70+								
Total	5				0			

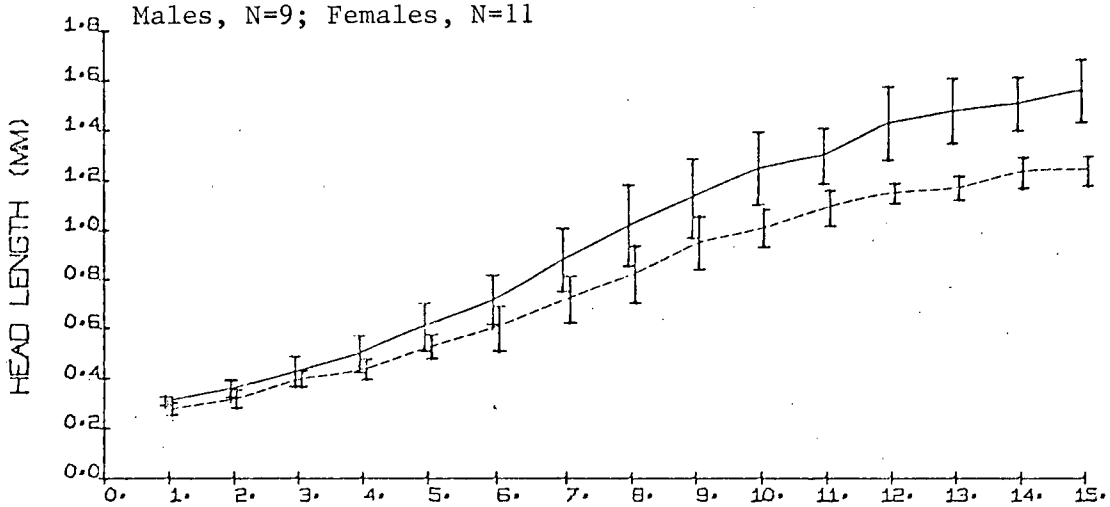
APPENDIX B.

Means and sample standard deviations for length vs. age data of males and females at different temperatures and salinities (food: Enteromorpha intestinalis).

Appendix B. Head length vs. age in weeks. ———, males; -----, females (lines connect weekly means); vertical lines represent one sample standard deviation on either side of the means.

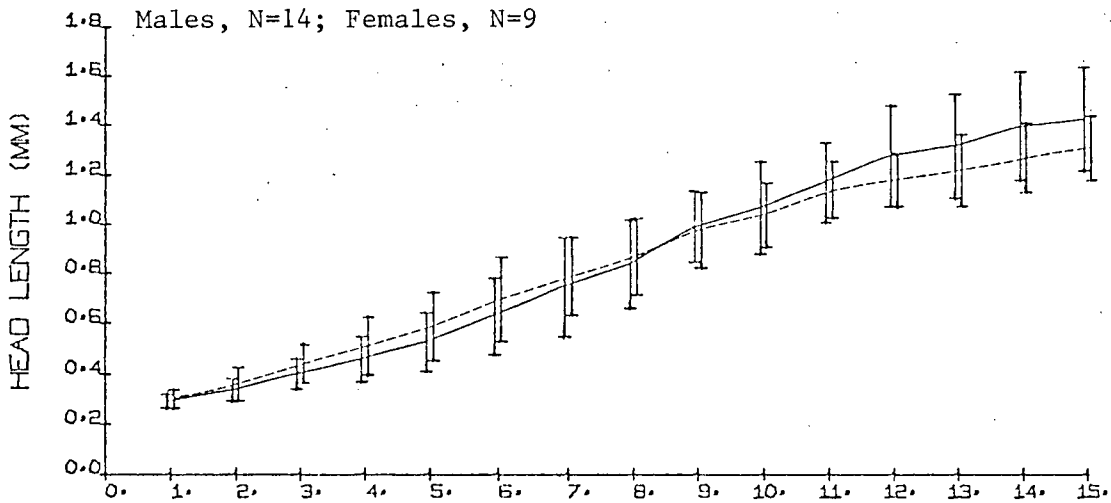
a 10 C, 12-14‰

Males, N=9; Females, N=11



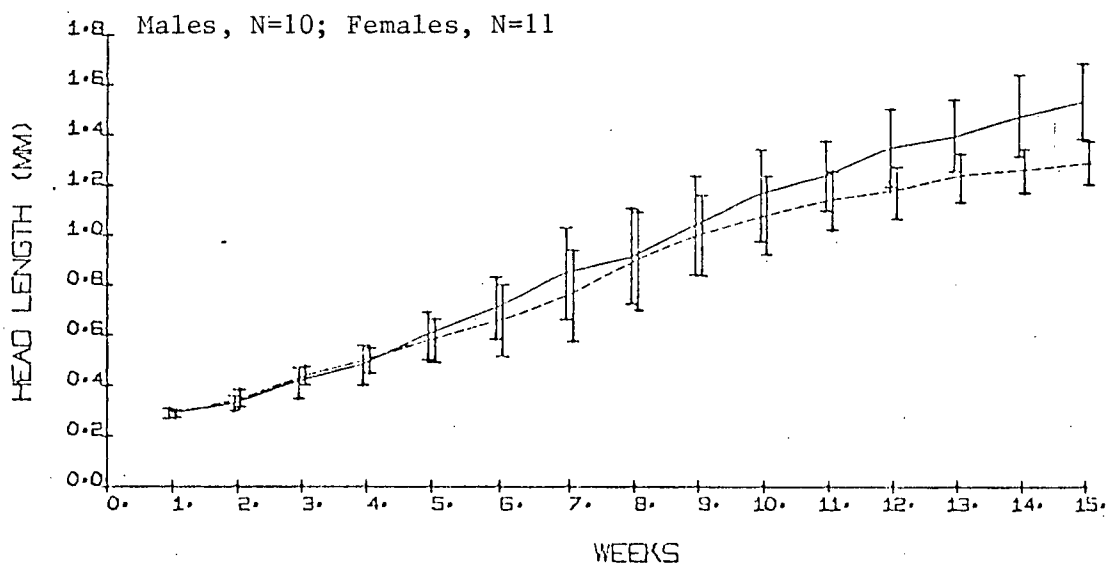
b 10 C, 18-21‰

Males, N=14; Females, N=9



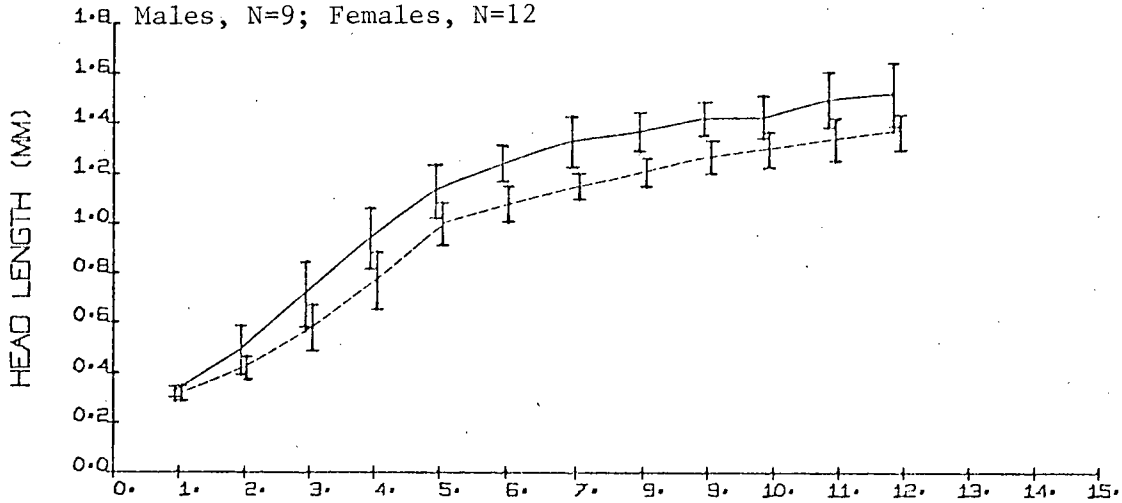
c 10 C, 24-28‰

Males, N=10; Females, N=11



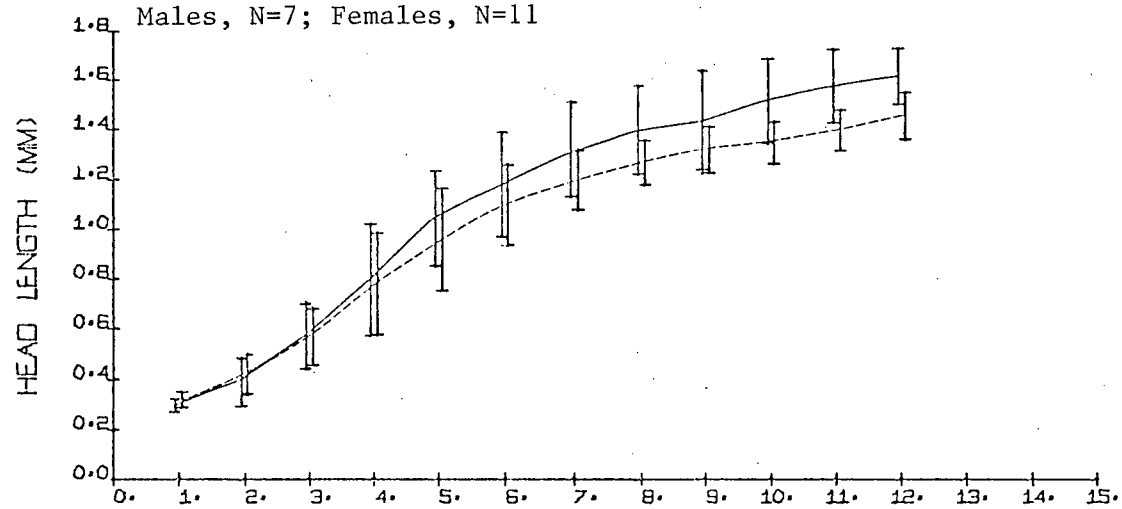
d 20 C, 12-14‰

Males, N=9; Females, N=12



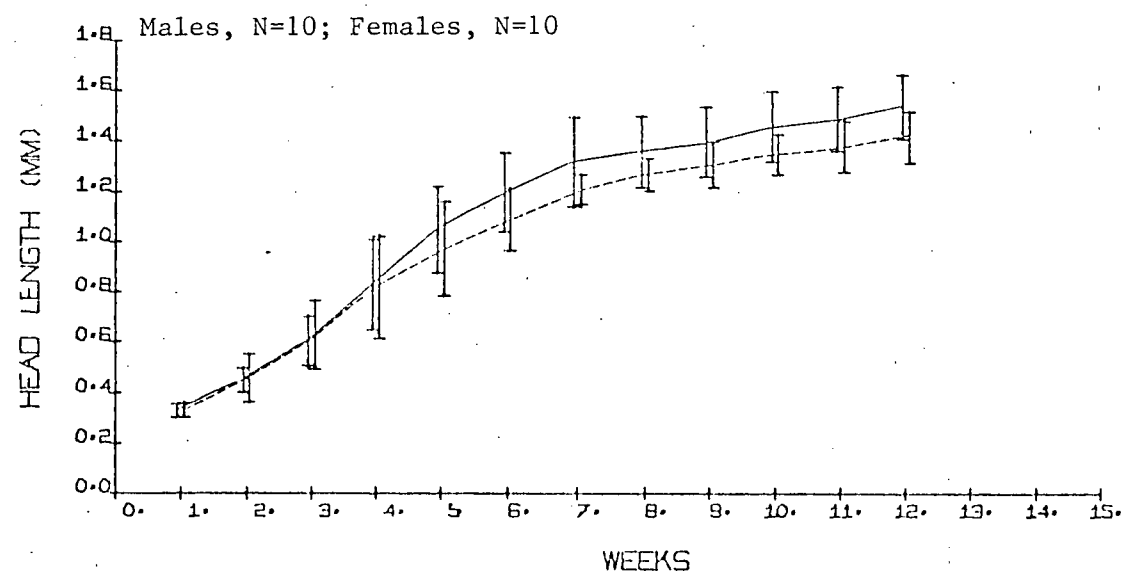
e 20 C, 18-21‰

Males, N=7; Females, N=11



f 20 C, 24-28‰

Males, N=10; Females, N=10

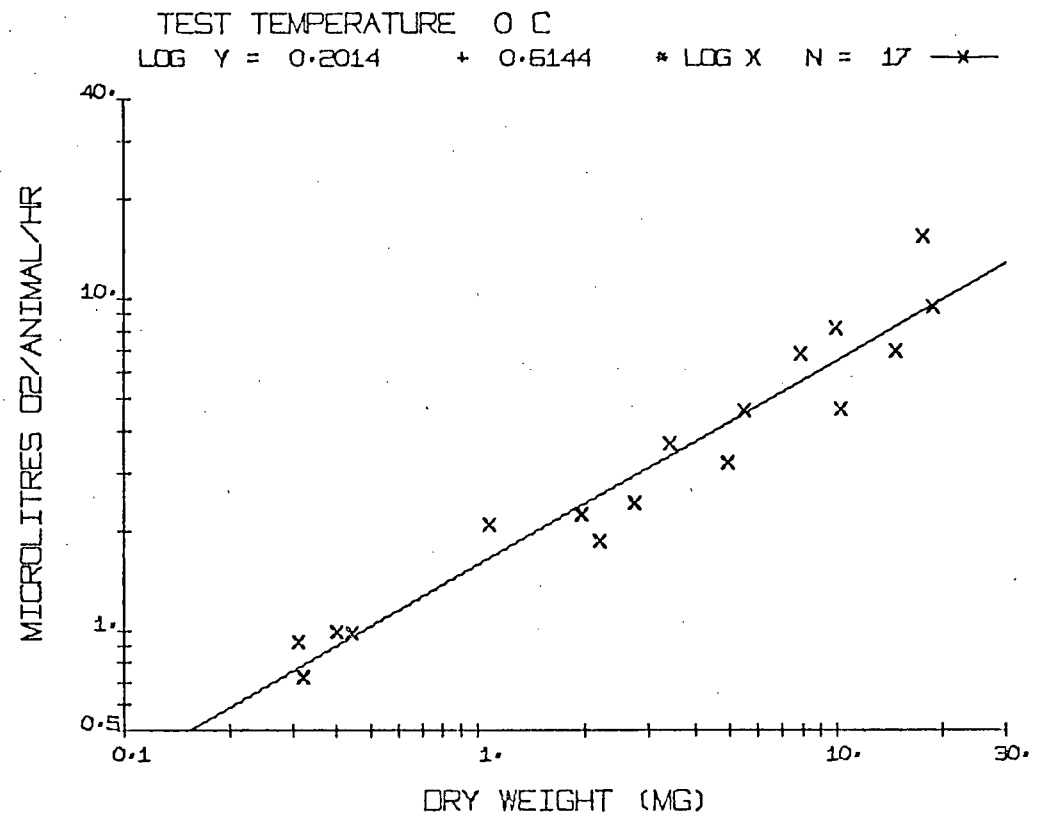


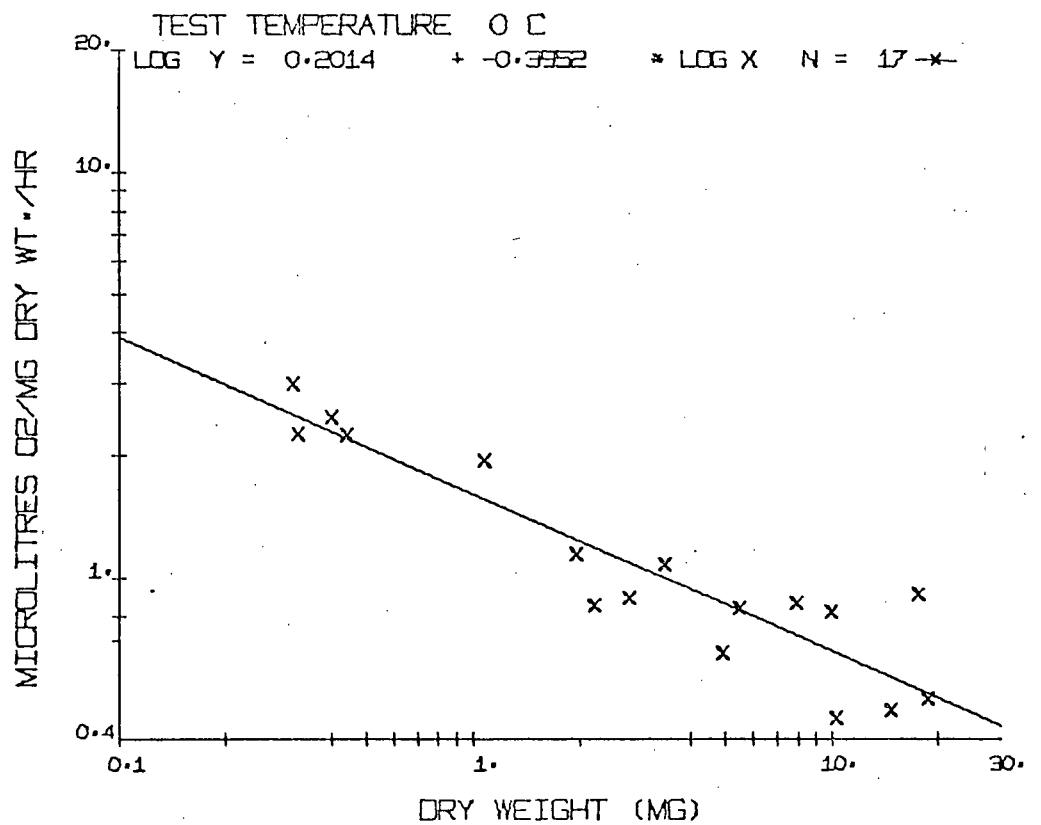
APPENDIX C.

Oxygen uptake of individual animals at different acclimation and test temperatures.

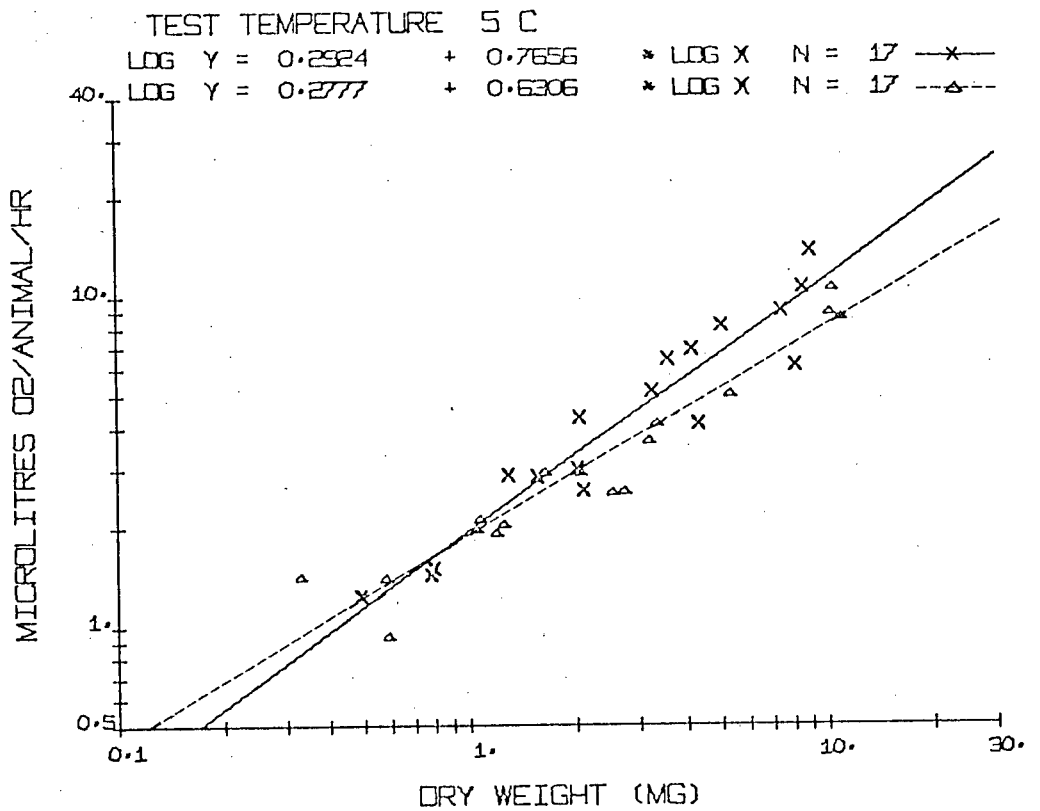
Appendix C. Top graphs: oxygen uptake/animal vs. dry body weight. Bottom graphs: oxygen uptake/dry body weight vs. dry body weight. x, animals acclimated to 10° C; Δ, acclimated to 20° C; ———, regression line for acclimation = 10° C; -----, regression line for acclimation = 20° C (base 10 logarithms).

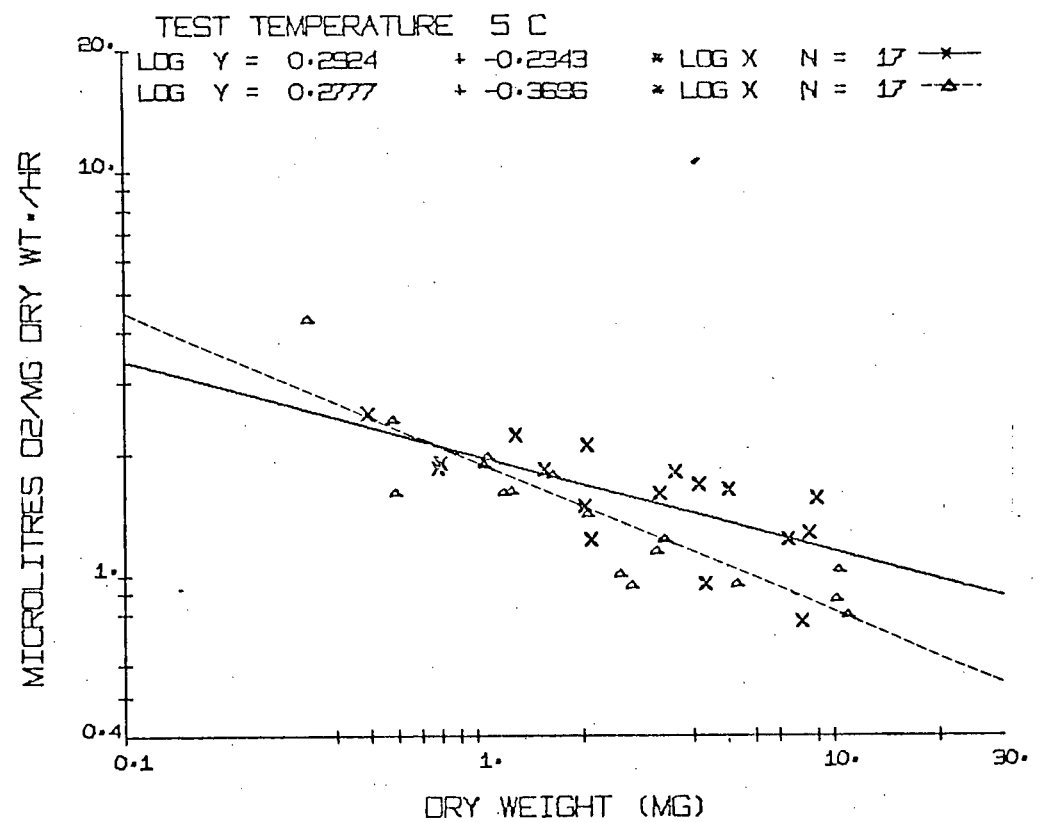
a


TEST TEMPERATURE 0 C
LOG Y = 0·2014 + 0·6144 * LOG X N = 17
MICROLITRES O2/ANIMAL/HR
40·
10·
1·
0·5
0·1
1·
10·
30·
DRY WEIGHT (MG)

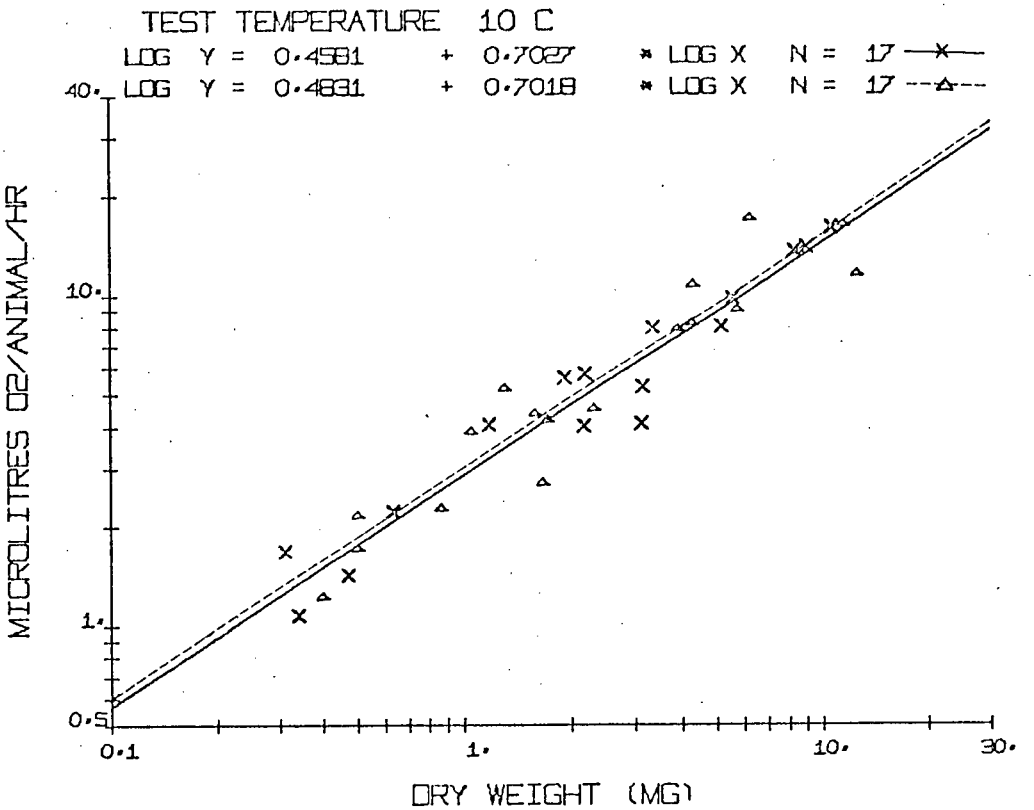

TEST TEMPERATURE 0 C
LOG Y = 0·2014 + -0·3952 * LOG X N = 17
MICROLITRES O2/MG DRY WT·/HR
20·
10·
1·
0·4
0·1
1·
10·
30·
DRY WEIGHT (MG)

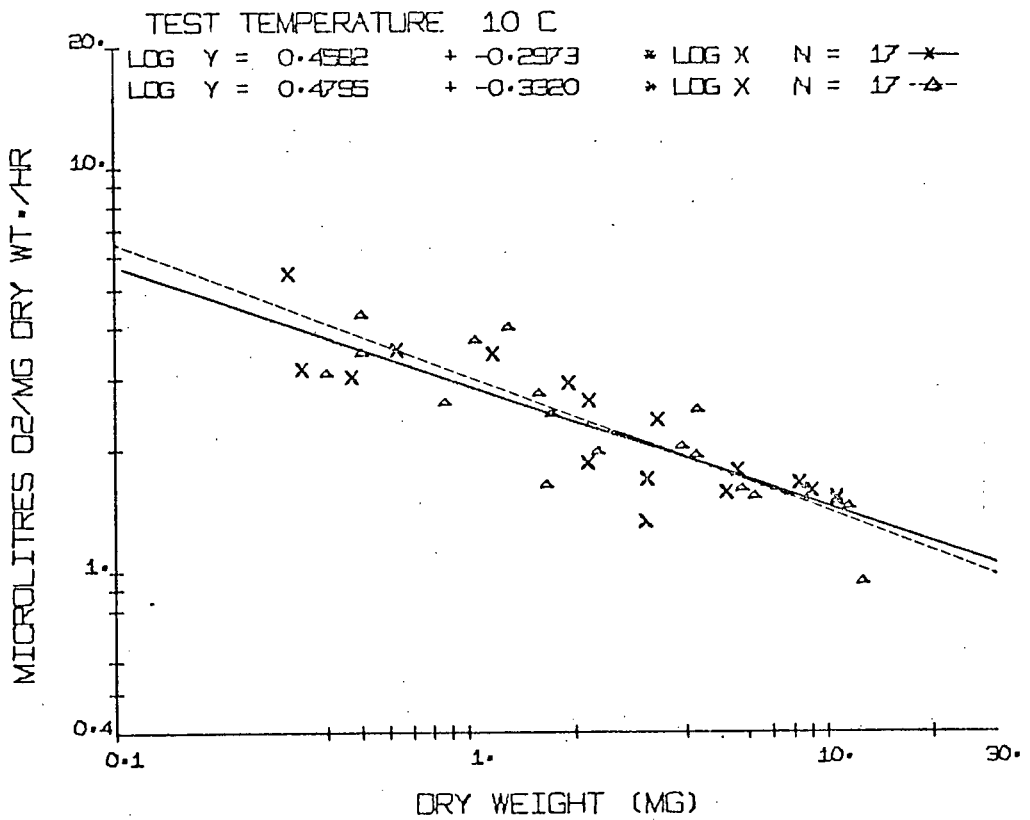
b


TEST TEMPERATURE 5 C
LOG Y = 0.2924 + 0.7656 * LOG X N = 17
LOG Y = 0.2777 + 0.6306 * LOG X N = 17
MICROLITRES O2/ANIMAL/HR
40.
10.
1.
0.5
0.1
1.
10.
30.
DRY WEIGHT (MG)

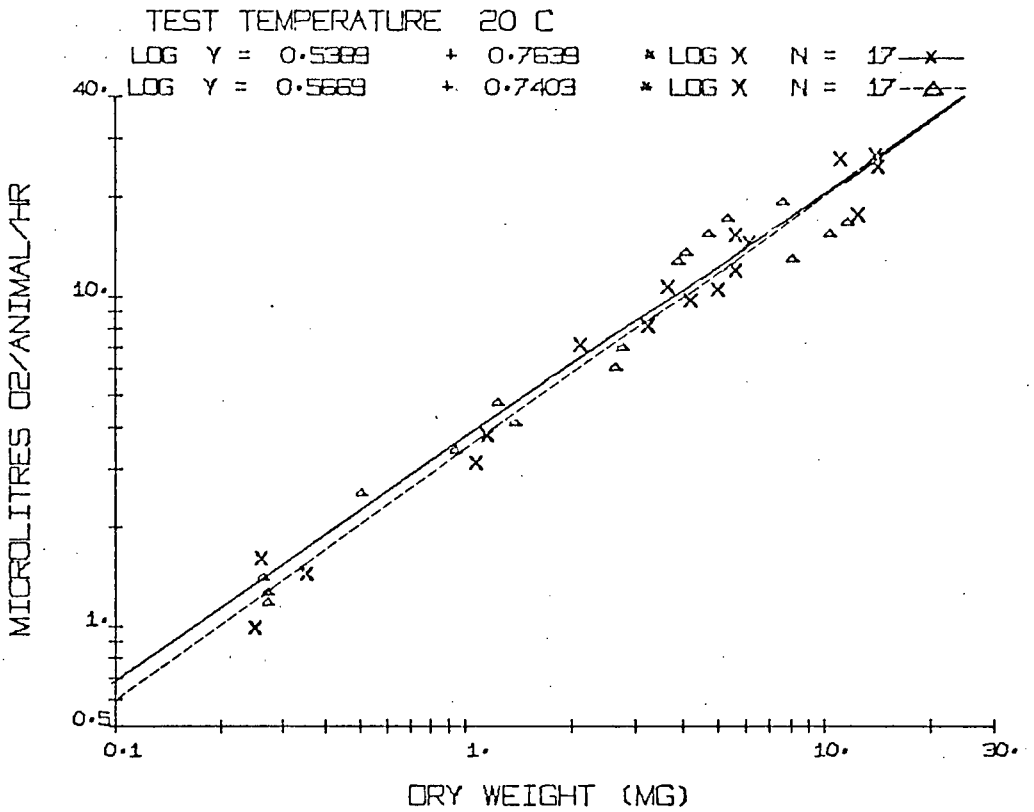

TEST TEMPERATURE 5 C
LOG Y = 0.2924 + -0.2343 * LOG X N = 17
LOG Y = 0.2777 + -0.3636 * LOG X N = 17
MICROLITRES O2/MG DRY WT./HR
20.
10.
1.
0.4
0.1
1.
10.
30.
DRY WEIGHT (MG)

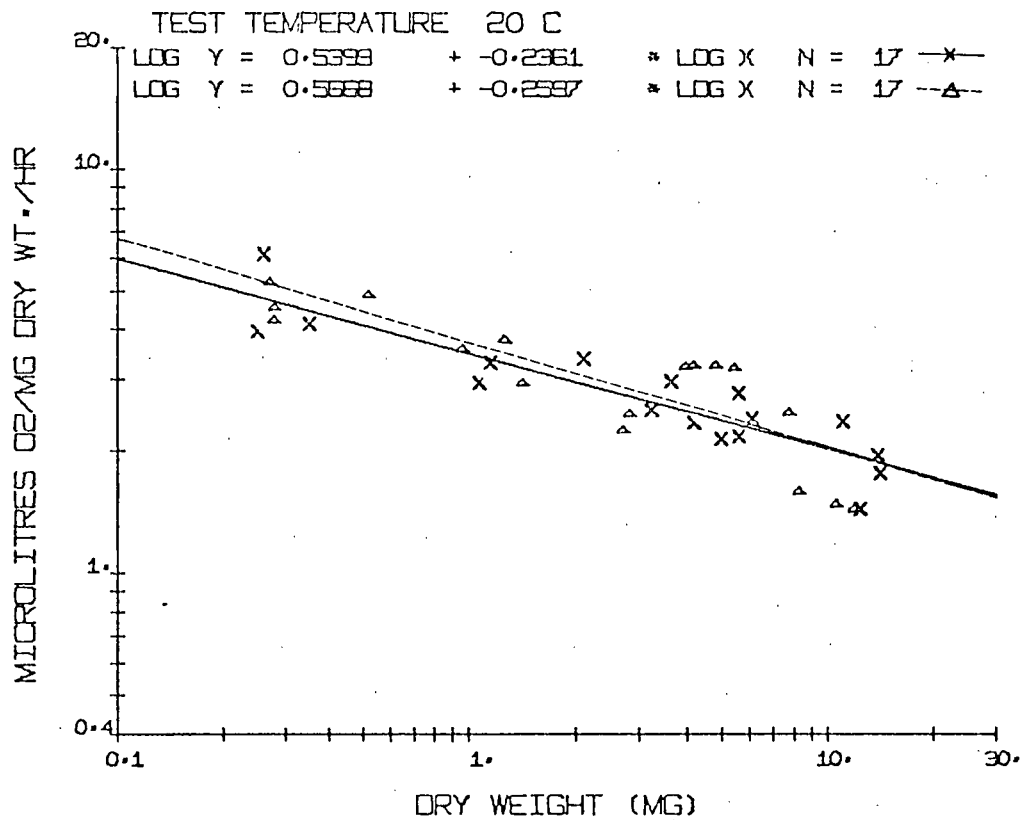
C


TEST TEMPERATURE 10 C
LOG Y = 0.4581 + 0.7027 * LOG X N = 17
LOG Y = 0.4831 + 0.7018 * LOG X N = 17
MICROLITRES O2/ANIMAL/HR
40.
10.
1.
0.5
0.1
1.
10.
30.
DRY WEIGHT (MG)

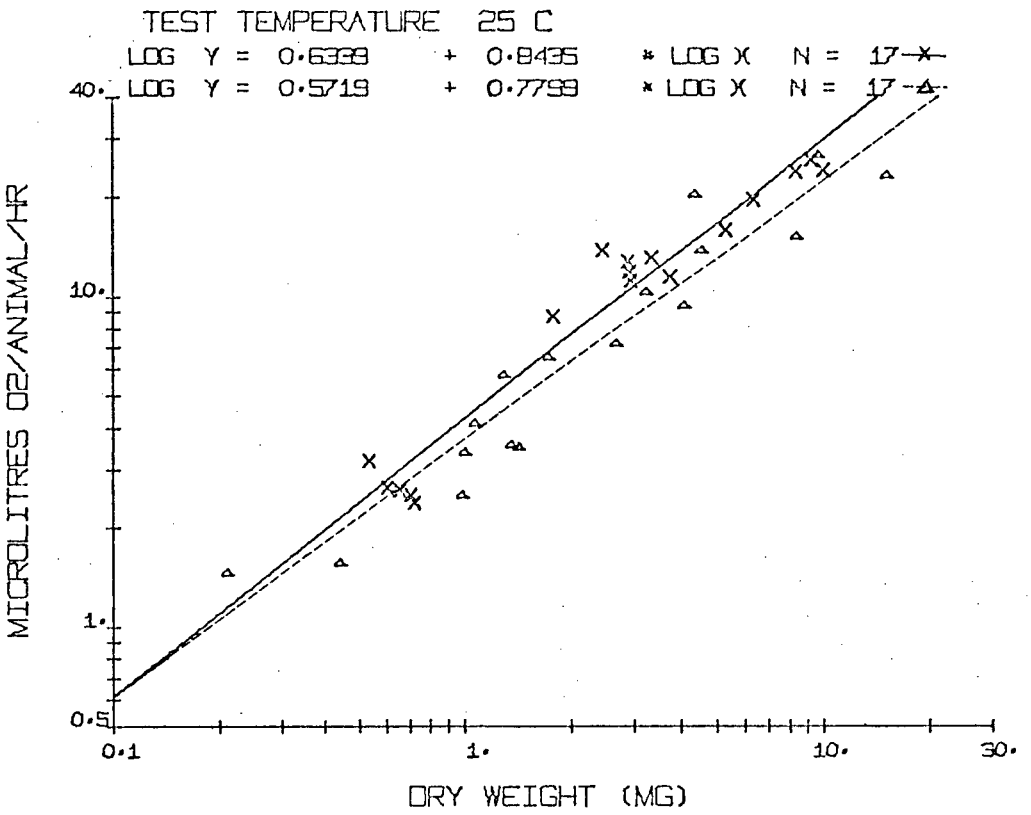

TEST TEMPERATURE 10 C
LOG Y = 0.4582 + -0.2973 * LOG X N = 17
LOG Y = 0.4795 + -0.3320 * LOG X N = 17
MICROLITRES O2/MG DRY WT./HR
20.
10.
1.
0.4
0.1
1.
10.
30.
DRY WEIGHT (MG)

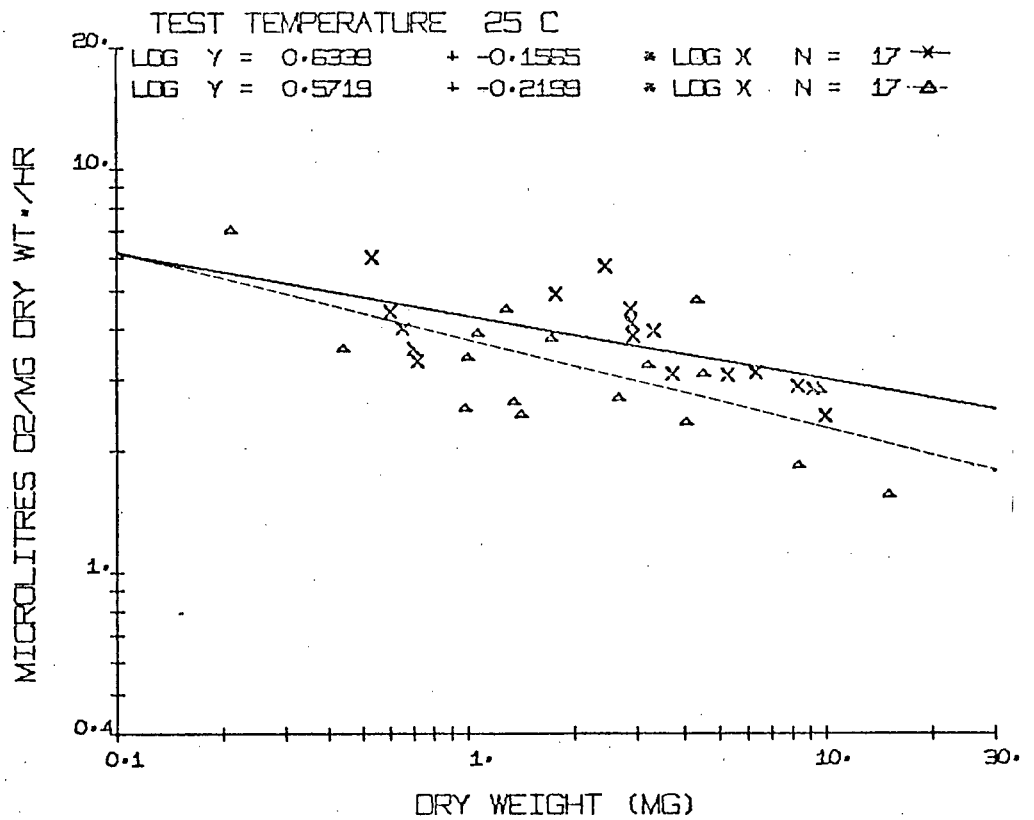
d


TEST TEMPERATURE 20 C
LOG Y = 0.5389 + 0.7639 * LOG X N = 17
LOG Y = 0.5669 + 0.7403 * LOG X N = 17
MICROLITRES O2/ANIMAL/HR
40.
10.
1.
0.5
0.1
1.
10.
30.
DRY WEIGHT (MG)

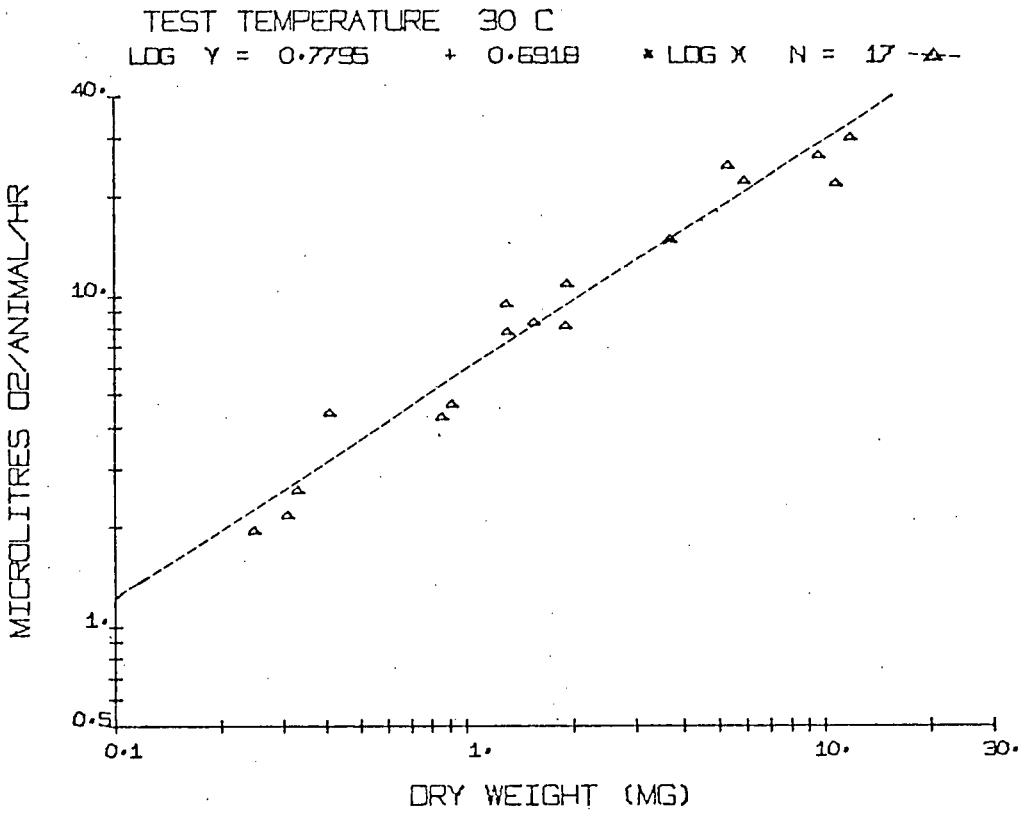

TEST TEMPERATURE 20 C
LOG Y = 0.5393 + -0.2361 * LOG X N = 17
LOG Y = 0.5668 + -0.2597 * LOG X N = 17
MICROLITRES O2/MG DRY WT./HR
20.
10.
1.
0.4
0.1
1.
10.
30.
DRY WEIGHT (MG)

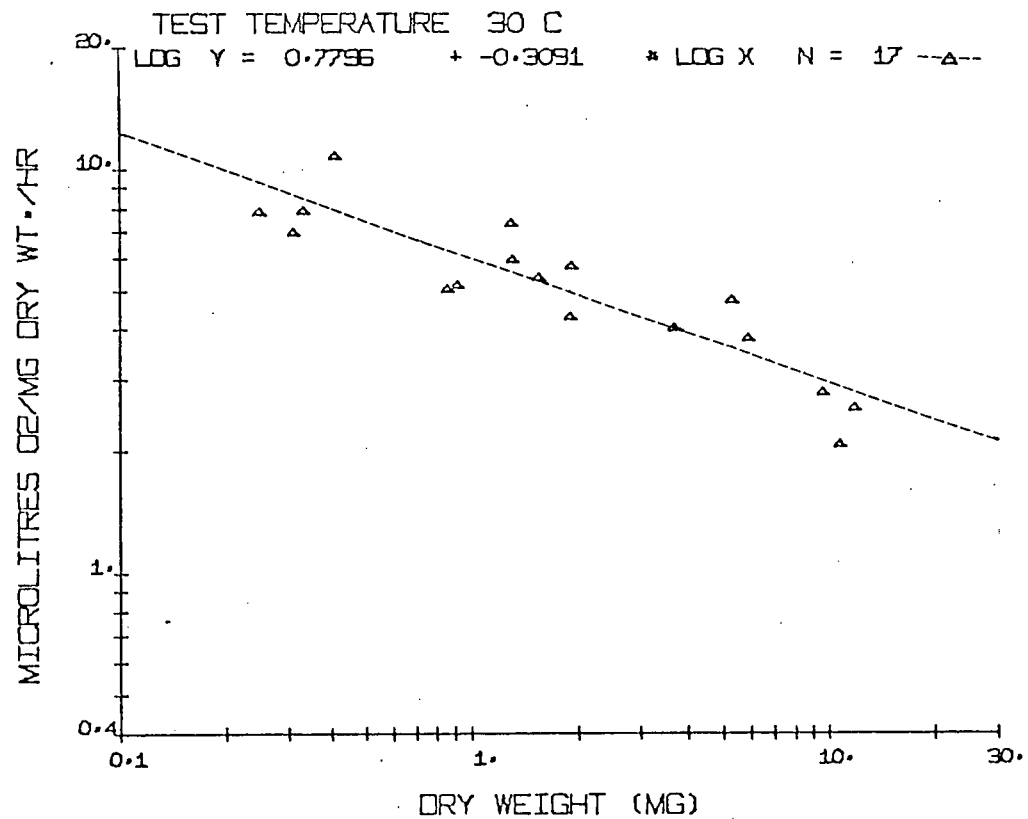
e


TEST TEMPERATURE 25 C
LOG Y = 0·6388 + 0·8435 * LOG X N = 17
LOG Y = 0·5719 + 0·7799 * LOG X N = 17
MICROLITRES O2/ANIMAL/HR
40·
10·
1·
0·5
0·1
1·
10·
30·
DRY WEIGHT (MG)


TEST TEMPERATURE 25 C
LOG Y = 0·6388 + -0·1565 * LOG X N = 17
LOG Y = 0·5719 + -0·2159 * LOG X N = 17
MICROLITRES O2/MG DRY WT·/HR
20·
10·
1·
0·4
0·1
1·
10·
30·
DRY WEIGHT (MG)

f


TEST TEMPERATURE 30 C
LOG Y = 0.7795 + 0.6918 * LOG X N = 17
MICROLITRES O2/ANIMAL/HR
40.
10.
1.
0.5
0.1
1.
10.
30.
DRY WEIGHT (MG)


TEST TEMPERATURE 30 C
LOG Y = 0.7795 + -0.3091 * LOG X N = 17
MICROLITRES O2/MG DRY WT./HR
20.
10.
1.
0.4
0.1
1.
10.
30.
DRY WEIGHT (MG)