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Studies on oxygen uptake in ctenophores

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Metabolic activity as a function of (1) body size and surface area, (2) temperature, (3) digestion and starvation, and (4) reduction of comb plates was studied for *Pleurobrachia pileus* Fabr. For *Beroe gracilis* Künne and *Bolinopsis infundibulum* Müller only items (2) and (3) were investigated. In studies on respiration versus body size, the regression coefficients for *Pleurobrachia* were around 0.8 at 2, 8, 12, 18 and 24°C. The Q_{10} coefficients were 2.72 for *Pleurobrachia*, 3.56 for *Beroe* and 3.73 for *Bolinopsis* with body weights (fresh) of 0.2, 0.3 and 1.08 g, respectively. In *Beroe* O_2 consumption was elevated at the moment of swallowing prey and during its digestion, and probably also at the time of egg production. Individuals without comb plates consumed O_2 at a lower rate than normal *Pleurobrachia*.

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1. Introduction

Ctenophores occur in great masses in the North Sea at certain times of year (Greve 1969). It has been shown that the occurrence of different species of ctenophores is determined by their food habitats: *Beroe gracilis* Künne feeds on *Pleurobrachia pileus* Fabr., and *Beroe cucumis* Fabr. on *Bolinopsis infundibulum* Müller (Greve 1971). *Pleurobrachia* and *Bolinopsis*, in turn, are important predators of zooplankton, including fish larvae (Fraser 1970, Lebour 1922, 1923).

In view of their ecological importance it is appropriate to measure the O_2 uptake of these ctenophores. A few measurements have been made of O_2 consumption in ctenophores, but only in members of the genus *Pleurobrachia: P. bachei* (Hirota unpubl.), *P. pileus* (Lazarewa 1961, 1962) and *P. globosa* (Rajagopal 1963).

This report gives some data on O_2 uptake for the four ctenophore species listed above, and especially emphasizes metabolic activity as a function of (1) size and surface area, (2) temperature, (3) nutritional condition (feeding, starvation), and (4) reduction of comb plates. In *Pleurobrachia* all aspects were studied, but in *Bolinopsis* and *Beroe gracilis* shortage of material caused restriction of studies to items (2) and (3).

2. Material and methods

The ctenophores used in the experiments were caught with a 280 μm plankton net in the waters surrounding Heligoland. The samples were transferred from the net to containers the same day, and stored at different salinities and temperatures for at least 1 day.

In order to investigate metabolic activity as a function of food consumption the animals were offered fresh food (copepods for *Pleurobrachia* and *Pleurobrachia* for *Beroe gracilis*). The starvation experiments were performed in Greve's plankton *kreisel*, with double cuvette (Greve 1972). The animals were left without food for up to 10 days. They were acclimated to the experimental temperature and salinity for at least 24 h. *Pleurobrachia* without combs were obtained from a tank containing *Pleurobrachia* and copepods.

The apparatus for measuring O_2 consumption was essentially as described by Gyllenberg (1973). The O_2 electrode was a Clark-type electrode manufactured by Radiometer, connected to a digital pH meter (PHM 72 Mk2), and to a recorder (Servogor S, Metrawatt). The electrode is very sensitive (10^{-11} A), and consequently the flow of water through it can be maintained at a very low speed (1 ml·h^{-1}). The instrument is described in detail in the Radiometer instruction manual and by Lessler (1972). The electrode was calibrated with sodium sulphite and oxygen-saturated air. For details of calibration and calculation of measurements, see e.g. Bulnheim (1972).

The temperature in the glass container, the respiration chamber and the O_2 electrode was regulated with a cryostat (Colora-Lorch/Württ KT20K). The respiration chamber (about 100 ml) was constructed from Plexiglass. Its shape provided a spiral current of water through the chamber. A lid with holes at the top of the chamber prevented the tentacles of the animal from being sucked into the outlet tube. The measurement error normally remained within ± 10 per cent. Measurements were always made on single specimens down to 4 mm in diameter. With smaller animals the errors incurred would have been too large and the experimental readings unreliable. The animals were kept in the respiration chamber until O_2 consumption rates became constant. Generally the readings during the first hour were discarded. Control measurements were always taken before and after each run.

The water flow was kept constant with the aid of an infusion pump (Unita IIB, Braun-Melsungen), and later with a peristaltic pump. The speed of flow was adjusted so that the animals generally consumed less than 5 % of the O_2 available.

Sterilized sea water was used in all experiments. Bacterial respiration through Seitz filters KO-00 and K5 was only 0.5—0.6 × 10^{-4} ml · h^{-1}, thus amounting to 1/20th of the smallest O_2 consumption values in the experiments.

3. Results

A. O_2 consumption versus size and temperature

O_2 consumption generally bears an exponential relation to body weight. This relationship has been fully confirmed by many authors (Bertalanffy 1957, Hemmingsen 1960). Mathematically it is expressed by the allometric equation $y = ax^b$, where y = O_2 consumption, x = weight, and a and b are constants. This relation is demonstrated in Figs. 1—2, where the allometric curves at five different temperatures are plotted for *Pleurobrachia pileus* individuals. These curves show that O_2 consumption per unit weight is proportionally higher for young individuals than for adults.

The temperature range selected (2—24°C, Fig. 1) is that to which *Pleurobrachia* individuals are generally exposed. In the starvation experiments the pre-adaption period was kept at 24 h for each temperature. Data points deviating from the curve illustrate individual variation. High regression coefficients (Figs. 1—2) show the dependence of O_2 consumption on body size.

The value of b is close to 0.8 in *Pleurobrachia*, thus being intermediate between the values expected for surface-dependent and weight-dependent O_2 consumption.

The results referred to give the O_2 consumption for routine metabolic rates (RMR, see Kinne 1971). Therefore only values after adaptation for 1 h in the respiration chamber could

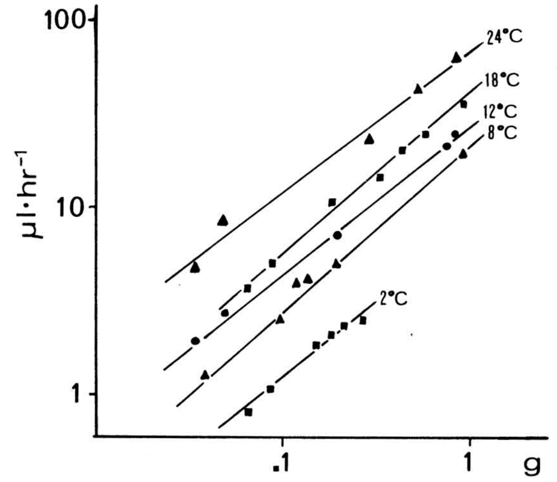

Fig. 1. The relation between O_2 consumption and body weight in *Pleurobrachia pileus* at selected temperatures. The measurements were made after acclimation for 1 day. The regression lines are as follows:

2°C $\log y = 0.801 \log x - 1.499$ ($r = 0.990$)
8°C $\log y = 0.858 \log x - 1.256$ ($r = 0.998$)
12°C $\log y = 0.780 \log x - 0.922$ ($r = 0.995$)
18°C $\log y = 0.852 \log x - 0.954$ ($r = 0.995$)
24°C $\log y = 0.753 \log x - 0.432$ ($r = 0.992$)

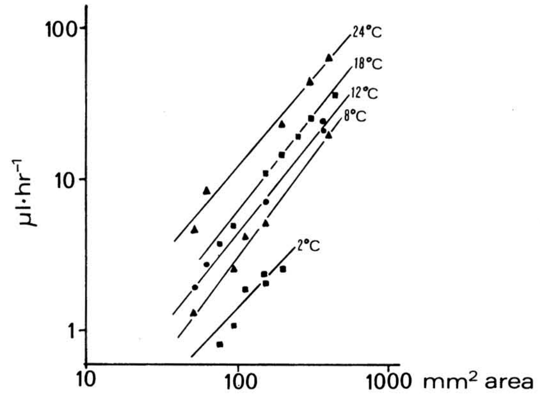

Fig. 2. The relation between O_2 consumption and surface area in *Pleurobrachia pileus* at selected temperatures. The regression lines are as follows:

2°C $\log y = 1.0577 \log x - 1.9843$ ($r = 0.9090$)
8°C $\log y = 1.3015 \log x - 2.1229$ ($r = 0.9955$)
12°C $\log y = 1.2187 \log x - 1.8091$ ($r = 0.9931$)
18°C $\log y = 1.2406 \log x - 1.7097$ ($r = 0.9962$)
24°C $\log y = 1.1529 \log x - 1.2459$ ($r = 0.9929$)

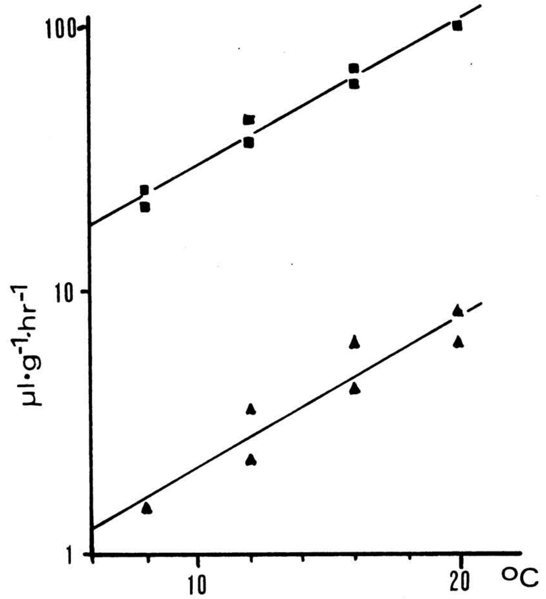

Fig. 3. O_2 consumption ($\mu l \cdot g^{-1}$ fresh wt) as a function of temperature in *Beroe gracilis* (squares) and *Bolinopsis infundibulum* (triangles). The coefficients for the regression lines are given in Table 1.

Table 1. Calculated variables describing oxygen consumption (μl $0_2 \cdot g^{-1} \cdot h^{-1}$) as a function of temperature (°C) in *Pleurobrachia* with and without combs, and in *Bolinopsis* and *Beroe*. *a* = intercept of the regression line on the y axis, *b* = regression coefficient (slope), *r* = correlation coefficient, Q_{10} = temperature coefficient, indicating rise in y for 10°C rise in x, m = mean body weight in g, n = number of specimens measured.

species	a	b	r	Q_{10}	m	n
P. pileus						
– with combs	10.3	0.040	0.951	2.72	0.201	15
– without combs	2.61	0.047	0.786	2.95	0.211	13
B. gracilis	8.47	0.055	0.989	3.56	0.300	7
B. infundibulum	0.58	0.057	0.960	3.73	1.083	8

be used. During adaptation the respiratory rate increased 3- to 4-fold, reflecting an active metabolic rate (AMR), which could be verified by visual observation.

Owing to shortage of experimental animals no investigation could be made on the relation of O_2 consumption to body weight in the other ctenophores, and only the relation to temperature was studied in these species (see Fig. 3). In the experiments with *Beroe gracilis* and *Bolinopsis infundibulum* the temperature-induced increase in respiration was very much lower in *Bolinopsis* than in either *Pleurobrachia* or *Beroe*. This may reflect the fact that *Bolinopsis* needs less energy for capturing its prey. Also, the adaption time was rather short in these experiments, only 2—6 h.

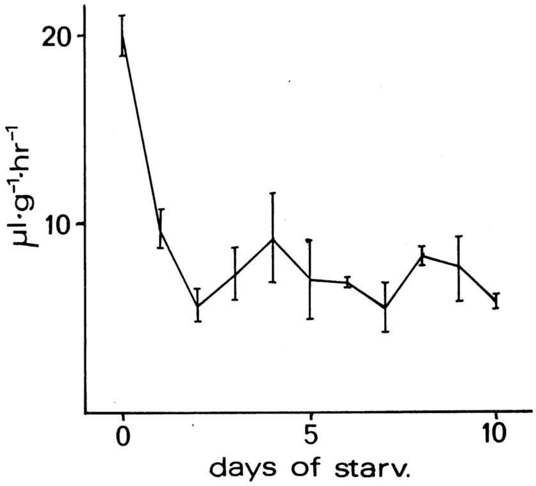

Fig. 4. Time course of O_2 consumption during starvation in *Pleurobrachia pileus* at 8 °C (number of replicates =5). The first value at the start of the experiment is measured during food digestion.

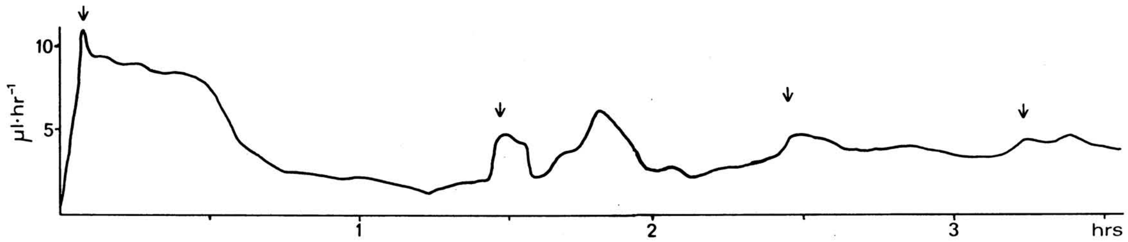

Fig. 5. Time course of O_2 consumption during digestion of one *Pleurobrachia pileus* by *Beroe gracilis*. The first arrow indicates when *Pleurobrachia* is swallowed, the second arrow indicates digestion, and the third and fourth arrows presumably indicate egg production.

B. Metabolic responses to environmental stress

Starvation and food digestion

The time course of digestion and starvation was studied in *Pleurobrachia pileus* (Fig. 4) and of digestion in *Beroe gracilis* (Fig. 5). The *Pleurobrachia* diagram indicates a high respiratory rate immediately after feeding, when the food particles are being digested. After this the respiratory rate falls to about half the initial value, and remains at this level for at least 10 days. The curve shows the relatively smaller decrease after starvation for 2—3 days, which has also been observed in *Calanus helgolandicus, Sagitta elegans* and *Acartia clausi* (Mayzaud 1976).

Fig. 5 shows the time course of digestion of one *Pleurobrachia* individual by *Beroe gracilis*. The initial peak, just after the *Beroe* swallowed its prey, represents the combined O_2 consumption of both *Beroe* and *Pleurobrachia*. The curve falls to a minimum when *Pleurobrachia* is enclosed in the oesophagus, and then increases to form two peaks when the actual digestion by *Beroe* is taking place. The slight increase in O_2 consumption after about 2.5 h is possibly related to production of eggs, either for formation of body protein, or for direct metabolism of the eggs. The curve then flattens out to a routine metabolic level.

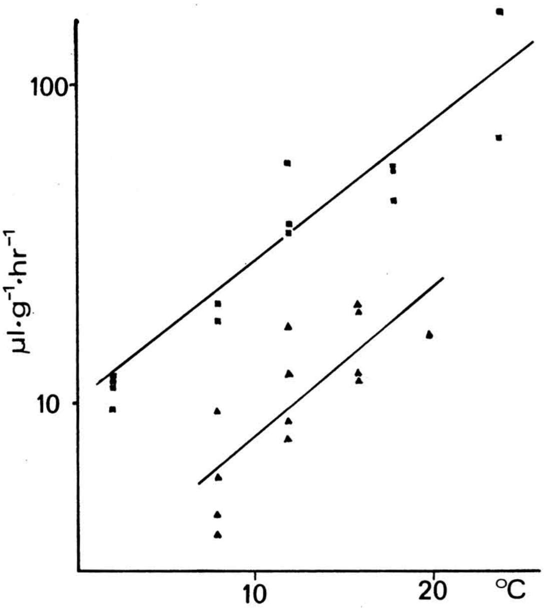

Fig. 6. O_2 consumption ($\mu l \cdot g^{-1}$ fresh wt) as a function of temperature in *Pleurobrachia* with (squares) and without (triangles) combs. The coefficients for the regression lines are given in Table 1.

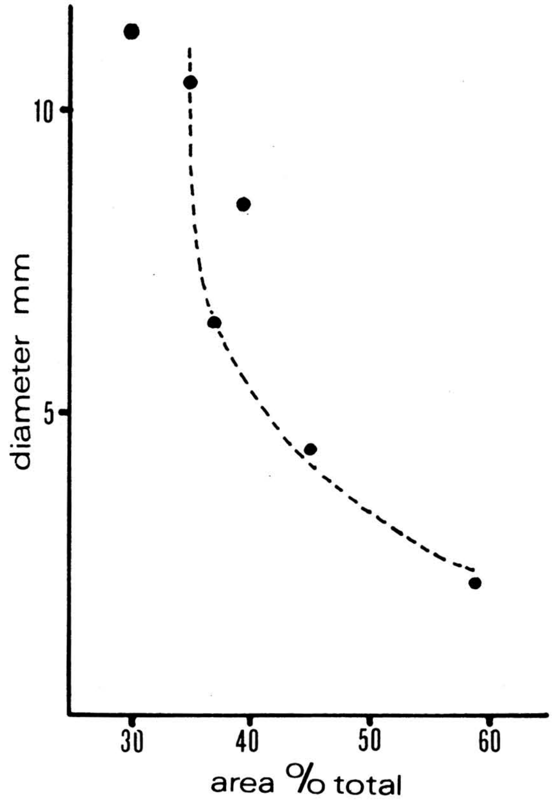

Fig. 7. Diameter of *Pleurobrachia pileus* as a function of the percentage of surface area occupied by combs.

Pleurobrachia without combs

In one large container *Pleurobrachia pileus* lost their combs, but were evidently still alive. These individuals were studied at a series of temperatures together with normal *Pleurobrachia* with combs. As Fig. 6 shows, the metabolism of these combless individuals is much reduced as compared with normal individuals. In order to investigate this phenomenon the proportion of the surface area occupied by the combs was calculated in *Pleurobrachia* of different sizes (Fig. 7). The 40 % loss of area does not in itself explain the reduction of O_2 consumption in the individuals lacking combs. In normal *Pleurobrachia* comb activity probably requires much energy expenditure.

4. Discussion

Many factors affect the respiration of poikilotherms. Of these factors body size, temperature, nutritional condition and malformations were investigated in this study.

Variations in regression coefficients due to such environmental factors as temperature are documented for crustaceans (Dehnel 1960, McFarland & Pickens 1965, Bulnheim 1972, 1974) and other invertebrates. The values normally lie between 0.67 and 1, indicating a variation somewhere between surface-related and weight-related respiration (Bulnheim 1974). The regression coefficient for *Pleurobrachia* appears to lie closer to surface-related metabolism. The fact that small individuals consume proportionally more O_2 than large individuals (cf. Ivlev 1961) carries an ecological corollary: During autumn and winter all *Pleurobrachia* individuals are large (Greve, unpubl.), whereas during spring and summer the predominating size-classes (comprising new offspring) are small. Small individuals need relatively more food to survive, and have relatively higher energy demands.

The reduced rate of metabolism in *Pleurobrachia* during starvation agrees well with the observations of many authors (see e.g. Nival *et al.* 1974). In *Sagitta elegans* and *Acartia clausi* respiration remains more or less constant after the initial decrease (Mayzaud 1976). This is also the case with *Pleurobrachia.* Probably *Pleurobrachia* individuals contain little lipid, in this respect resembling *Sagitta* and *Acartia* rather than *Calanus helgolandicus. Calanus* oscillates between periods of high- and low-lipid catabolism (Mayzaud 1976).

The energy requirements for metabolism seem to lie at higher levels in *Pleurobrachia* and *Beroe gracilis*, as compared with *Bolinopsis.* This may be explained by an optimization theory: *Beroe* and *Pleurobrachia* require energy to catch their prey.

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References

von Bertalanffy, L. 1957: Quantitative laws in metabolism and growth. — Quart. Rev. Biol. 32: 217—231.

Bulnheim, H.-P. 1972: Vergleichende Untersuchungen zur Atmungsphysiologie euryhaliner Gammariden unter besonderer Berücksichtigung der Salzgehaltsanpassung. — Helgoländer Wiss. Meeresunters. 23:485—534.

—»— 1974: Respiratory metabolism of *Idotea balthica* (Crustacea, Isopoda) in relation to environmental variables, acclimation processes and moulting. — Helgoländer Wiss. Meeresunters. 26: 464—480.

Dehnel, P. A. 1960: Effect of temperature and salinity on the oxygen consumption of two intertidal crabs. — Biol. Bull. (Woods Hole) 118: 215—249.

Fraser, J. H. 1970: The ecology of the ctenophore *Pleurobrachia pileus* in Scottish waters. — J. Cons. Int. Explor. Mer 33: 149—168.

Greve, W. 1969: Zur Ökologie der Ctenophore *Pleurobrachia pileus* Fabr. — Math. Naturwiss. Diss. Kiel, 137 pp.

—»— 1971: Ökologische Untersuchungen an *Pleurobrachia pileus* 1. Freilanduntersuchungen. — Helgoländer Wiss. Meeresunters. 22: 303—325.

—»— 1972: Ökologische Untersuchungen an *Pleurobrachia pileus.* 2. Laboratoriumsuntersuchungen. — Helgoländer Wiss. Meeresunters. 23: 141—164.

Gyllenberg, G. 1973: Comparison of the Cartesian diver technique and the polarographic method, an open system, for measuring the respiratory rates in three marine copepods. — Comment. Biol. 60: 1—13.

Hemmingsen, A. M. 1960: Energy metabolism as related to body size and respiration surfaces, and its evolution. — Rep. Steno Mem. Hosp. 9(2): 1—110.

Hirota, J. unpubl.: The relationship of respiratory rate to body size in the ctenophore *Pleurobrachia bachei* A. Agassiz. — Manuscript, Dept. of Oceanography, University of Washington, Seattle, Washington.

Ivlev, V. S. 1961: Experimental ecology and nutrition of fish. — New Haven, Yale University Press, 261 pp.

Kinne, O. 1971: Temperature: Invertebrates. — In: Kinne, O. (ed.): Marine ecology Vol. I. Environmental factors: 407—514. Wiley Interscience, London, New York, Toronto, Sydney.

Lazarewa, L. D. 1961: On the oxygen consumption of the ctenophore *Pleurobrachia pileus* O. F. Müller of different sizes as related to the temperature and salinity of the environment (in Russian). — Trudy Karadagsk. Biol.Sta. Akad.Nauk. USSR 17:85—96.

—»— 1962: Some ecological problems of the Black Sea ctenophore *Pleurobrachia pileus* O. F. Müller (in Russian). — Vopr. Ekol. Vysshaya Shkola, Moscow 5: 113—115.

Lebour, M. 1922: The food of plankton organisms. — J. Mar. Biol. Ass. U. K. 12: 644—677.

Lebour, M. 1923: The food of plankton organisms 2. —J. Mar. Biol. Ass. U. K. 13: 70—92.

Lessler, M. A. 1972: Macro- and micro-oxygen electrode techniques for cell measurement. — In: Prescott, D. M. (ed.), Methods in cell physiology. 5: 199—218. Academic Press, New York and London.

Mayzaud, P. 1976: Respiration and nitrogen excretion of zooplankton. IV. The influence of starvation on the metabolism and the biochemical composition of some species. — Mar. Biol. 37:47—58.

McFarland, W. W. & Pickens, P. E. 1965: The effects of season, temperature and salinity on standard and active oxygen consumption of the grass shrimp, *Palaemonates vulgaris* (Say). — Can. J. Zool. 43:571—585.

Nival, P., Malara, G., Charra, R., Palazzoli, I. & Nival, S. 1974: Etude de la respiration et de l'excrétion de quelques copépodes planktoniques (Crustacea) dans la zone de remontée d'eau profonde des côtes marocaines (Mission Cineca IV du N. O. Jean-Charcot: 20 juillet — 19 août 1973). — J. Exp. Mar. Biol. Ecol. 15:231—260.

Rajagopal, P. K. 1963: A note on the oxygen uptake of the ctenophore *Pleurobrachia globosa.* — Current Sci. (India) 32: 319—320.

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