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RELATIONSHIP BETWEEN RESPIRATION RATE AND BODY  
SIZE IN MARINE PLANKTON ANIMALS AS A FUNCTION OF  
THE TEMPERATURE OF HABITAT

Tsutomu IKEDA\*

It is generally known that the rate of oxygen consumption (metabolic rate) per unit body weight of animals increases with the decrease in body size of the animals. This concept was initiated from the finding of the "surface law" by Sarrus & Rameaux (1839), and many studies on this problem have been done on mammals and birds ever since (refer to the reviews of Krogh, 1916; Benedict, 1938; Kleiber, 1947; Prosser, 1961a). A detailed study on this subject (Kleiber, 1947) has shown that the metabolic rate is proportional to a given power function of body weight rather than to body surface. Weymouth *et al.* (1944) showed that this relationship is also applicable to poikilothermal animals according to experiments on a kelp crab, *Pugettia producta*. Zeuthen (1947), working on the marine micro-fauna, found a similar relationship. The review of Zeuthen (1953) extended this concept to organisms from bacteria to large mammals.

In regard to plankton animals, Raymont & Gauld (1951) first suggested that the rate of oxygen consumption in copepods is proportional to their body surface. This was confirmed by Gauld & Raymont (1953), Raymont (1959), Conover (1959) and Berner (1962). Conover (1960), working on copepods, amphipods and euphausiids, and Rajagopal (1962), working on a hydromedusa, ctenophores, copepods, decapods and a tunicate, stated that the log respiration is well correlated to the log dry body weight of animals. Recently this relationship was reported on copepods by Haq (1967) and Comita (1968), and on euphausiids by Small, Hebard & McIntire (1966), Small & Hebard (1967), Paranjape (1967) and Pearcy *et al.* (1969).

The present investigation was made in an attempt to obtain the relationship between the rate of oxygen consumption (respiration) and the body size (weight) in various marine plankton animal groups from three different areas, boreal, temperate and tropical seas.

Before going further, the author wishes to express his sincere thanks to Prof. S. Motoda, Faculty of Fisheries, Hokkaido University, for his continuing guidance and encouragement. Thanks are also due to Assoc. Prof. T. Kawamura and Dr. T. Minoda, Faculty of Fisheries, Hokkaido University, for their generosity in giving many valuable suggestions during the work. The author is especially grateful to Prof. T. Tsujita and Assoc. Prof. S. Nishizawa, Faculty of Fisheries, Hokkaido

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University, for their critical reading of the manuscript.

### Methods and materials

*Animals:* Sampling of animals and experiments were carried out on board the "Oshoro Maru" during Cruise 30 to the Tropical Pacific Ocean and the Gulf of Carpentaria, November 1968-January 1969 (tropical species), Cruise 32 to the Bering Sea, June-August 1969 (boreal species), Cruise 33 to the Southeast of

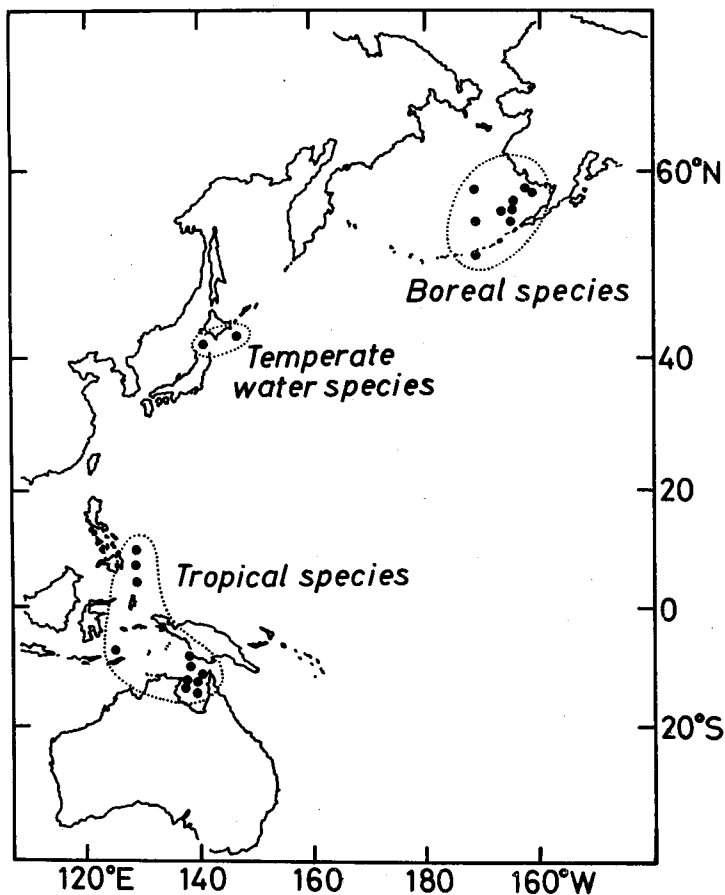


Fig. 1. Map showing locations where the experimental animals were collected. The stations were occupied on the following cruises;

*Boreal species:* "Oshoro Maru" Cruise 32 to the Bering Sea (June-Aug. 1969).

*Temperate water species:* "Oshoro Maru" Cruise 33 to the Southeast of Hokkaido (Sept. 1969) and "Tansei Maru" Cruise KT-69-17 to Mutsu Bay (Oct. 1969).

*Tropical species:* "Oshoro Maru" Cruise 30 to the Tropical Pacific Ocean and the Gulf of Carpentaria (Nov. 1968-Jan. 1969)

Hokkaido, September 1969 (temperate water species). An additional work was done on Cruise KT-69-17 of the "Tansei Maru" to Mutsu Bay, October 1969 (temperate water species) (Fig. 1).

The animals were collected with a specially designed tow net (Ikeda, 1970). The net was gently towed for a few minutes in the surface layer (about 0-10 m) by the slow wind shift of the drifting ship so as to avoid doing damage to the animals caught. The samples were sorted in the ship's laboratory through the use of a large bore pipette (0.8 mm in dia.), and transferred to 1 l glass bottles filled with surface sea water. The glass bottles were put in a wooden water tank and the animals were maintained in darkness. Fresh surface sea water was continuously circulating through the tank. After 1-2 days, the animals were subjected to the measurements described below. A total of 77 species for all four cruises, covering almost all systematic marine zooplankton groups, were used for experimentation (Table 1).

Table 1. Systematic list of the plankton animals experimented

Boreal species (23 species)	Brachyuran zoea larva
Coelenterata	Chaetognatha
* <i>Sarsia mirabilis</i> L. AGASSIZ	* <i>Sagitta elegans</i> VERRILL
<i>Aglantha digitale</i> (MÜLLER)	Pisces
Otenophora	* <i>Eumicrotremus orbis orbis</i>
* <i>Hormiphora palmata</i> CHUN	(GÜNTHER), juv.
Pteropoda	Temperate water species (13 species)
* <i>Clione limacina limacina</i> (PHIPPS)	Cephalopoda
<i>Limacina helicina helicina</i> (PHIPPS)	* <i>Idiosepius (Idiosepius)</i>
Polychaeta	<i>pygmaeus paradoxus</i> (ORTMANN)
* <i>Tomopteris (Tomopteris) septentrionalis</i>	Copepoda
STEENSTRUP	<i>Calanus pacificus</i> BRODSKY, ♂
Copepoda	Mysidacea
<i>Calanus cristatus</i> KRÖYER, V	<i>Hypererythrops</i> sp.
<i>Calanus plumchrus</i> MARUKAWA, V	Cumacea
<i>Calanus glacialis</i> YASHNOV, IV V	<i>Diastylis</i> sp., ♀
<i>Eucalanus bungii bungii</i> JOHNSON, ♀	Isopoda
<i>Pseudocalanus elongatus</i> (BOECK), ♀ ♂	<i>Aega</i> sp.
* <i>Pareuchaeta japonica</i> (MARUKAWA), ♀	Amphipoda
* <i>Candacia columbiae</i> CAMPBELL, ♀	* <i>Hyperia</i> sp., ♀ ♂
* <i>Tortanus discandatus</i>	* <i>Hyperia</i> sp., juv.
(THOMPSON & SCOTT), ♀ ♂	Euphausiacea
Amphipoda	<i>Euphausia pacifica</i> HANSEN, ♀ ♂
* <i>Hyperia galba</i> (MONTAGU), ♀ ♂	Decapoda
* <i>Hyperia</i> sp., ♀	* <i>Lucifer typus</i> H. MILNE EDWARDS,
* <i>Eutheimisto libellula</i> (MANDT), ♀ ♂	♀ ♂
Euphausiacea	* <i>Leptochela gracilis</i> STIMPSON, juv.
<i>Thysanoessa raschii</i> (M. SARS)	* <i>Crangon affinis</i> DE HAAN, juv.
HANSEN, ♀ ♂	Brachyuran megalopa larva
<i>Thysanoessa inermis</i> (KRÖYER)	Brachyuran zoea larva
HANSEN, juv., ♀	Tropical species (41 species)
Decapoda	Heteropoda
* <i>Penaeus</i> sp.	* <i>Firiloida desmaresti</i> LESUEUR

Table 1. Continued

Pteropoda	<i>Iphinoe</i> sp., ♀
<i>Creseis acicula clava</i> RANG	<i>Iphinoe</i> sp., juv.
* <i>Hydromyles globulosa</i> (RANG)	Amphipoda
* <i>Cliome</i> sp.	* <i>Orchomene</i> sp.
Cephalopoda	* <i>Synopia ultramarina</i> DANA, ♀ (?)
* <i>Octopus</i>	* <i>Phronima</i> sp.
Polychaeta	* <i>Brachyscelus latipes</i> STEBBING, ♀
* <i>Lepidasthenia grimaldi</i> (MARENZELLER)	Euphausiacea
Trochophora larva	* <i>Euphausia mutica</i> HANSEN, ♂
Ostracoda	Decapoda
<i>Cypridina hilgendorfi</i> G. W. MÜLLER	* <i>Lysemata</i> sp.
<i>Pyrocypris</i> sp.	Macruran post mysis larva
Copepoda	Macruran mysis larva
<i>Calanus gracilis</i> (DANA), ♀	Brachyuran megalopa larva
<i>Calanus vulgaris</i> (DANA), ♀	Brachyuran zoea larva
<i>Eucalanus crassus</i> GIESBRECHT, ♀	Chaetognatha
<i>Eucalanus monachus</i> GIESBRECHT, ♀	* <i>Sagitta inflata</i> GRASSI
<i>Eucalanus mucronatus</i> GIESBRECHT, ♀	* <i>Sagitta robusta</i> DONCASTER
* <i>Euchirella amoena</i> GIESBRECHT, ♀	Thaliacea
* <i>Euchaeta marina</i> (PRESTANDREA), ♀	<i>Thalia democratica</i> (FORSKAL),
* <i>Euchaeta plana</i> MORI, ♂	solitary salpa
* <i>Candacia aethiopica</i> DANA, ♀	<i>Thalia democratica</i> (FORSKAL),
* <i>Labidocera acuta</i> (DANA), ♀ ♂	chain salpa
* <i>Labidocera detrunata</i> (DANA), ♀	Pisces
* <i>Labidocera</i> sp., ♀	* <i>Trachurus japonicus</i> (TEMMINCK &
<i>Acartia spinicauda</i> GIESBRECHT, ♀	SCHLEGEL), juv.
* <i>Sapphirina gemma</i> DANA, ♂	* <i>Upeneus</i> sp., juv.
Cumacea	* <i>Chelidonichthys</i> sp., juv.

\* regarded as carnivores indicated by preceding authors or by direct observation of feeding by the present author

*Respiration rate*: The procedure of the water bottle method was the same as the one used by Ikeda (1970). On small animals several individuals closely matching in size were used in a single bottle. Cannibalism was frequently observed on some tropical carnivorous species when placed in a crowded *entourage*. To prevent this, the number of animals in an experimental bottle was kept small and when cannibalism occurred during the incubation the results were discarded.

It is known that the respiration of marine animals is markedly lowered if the oxygen concentration in the medium water decreases below a certain level. Critical concentration is higher in active animals than in inert animals. Data on marine animals indicate that critical oxygen concentration is about 50% saturation, though it differs with species fairly (Hall, 1929; Marshall *et al.*, 1935; Weymouth *et al.*, 1944; Zeuthen, 1947; Fry, 1957; Nicol, 1960; Wolvekamp & Waterman, 1960; Prosser, 1961a; Miyauchi & Irie, 1966; Nimura & Inoue, 1969). In the present experiments the duration of incubation was adjusted so as the oxygen concentration at the end of incubation was kept above 70% saturation. Usually 24 hours' incubation for boreal species and 12 hours' incubation for temperate and tropical species with adequate density of animals were chosen.

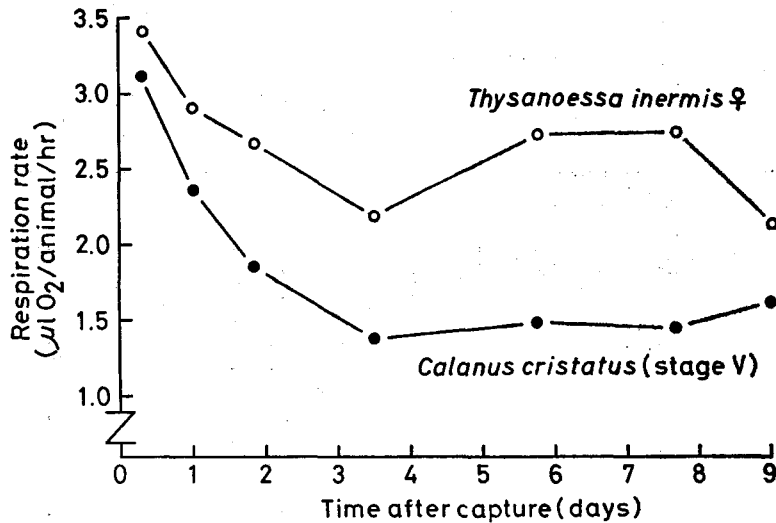


Fig. 2. Changes in respiration rate of *Calanus cristatus* (stage V) and *Thysanoessa inermis* (female) in experimental jars at temperatures of 9.7–12.2°C during 9 days after capture from the sea. The animals were collected at 55°01'N 165°28'W, July 22, 1969

It is a common experience among workers that animals show an abnormally high respiration rate just after capture from the sea (Marshall *et al.*, 1935; Conover, 1956; Berner, 1962). Fig. 2 shows observed variations in respiration rate in *Calanus cristatus* (stage V) and *Thysanoessa inermis* (female) during the course from just after the capture till the end of a 9-day culture period. The rates obtained by incubation immediately after capture were nearly two times as high as those obtained after several days of successive incubation. In the present experiments the respiration rate was measured on the animals kept in darkness for 1–2 days after their capture.

The effect of nutritional conditions on the respiration rate in various plankton animals is little known. An experiment on *C. cristatus* (Ikeda, 1970) showed that the rate was not lowered by starving the animals for at least one week.

Table 2. Experiments on the effect of an antibiotic (dihydrostreptomycin sulfate, 50 mg/l) on the respiration rate of *Calanus plumchrus* at 9.7–10.5°C. The animals were collected at 56°13'N 162°35'W, July 25, 1969

	No. and stage	µl O <sub>2</sub> /animal/hr	µl O <sub>2</sub> /mg dry wt./hr
No antibiotic added	6, stage V	0.74	0.87
	6, stage V	0.66	0.91
Antibiotic added	6, stage V	0.65	0.69
	6, stage V	0.56	0.66

Table 3. Summary of experimental data on body weight and respiration rate of wet weight in each

Animals	No.	Experimental temp. (°C)	Total respiration rate ( $\mu\text{l O}_2/\text{animal/hr}$ )
<b>Boreal species (23 species)</b>			
<b>Coelenterata</b>			
<i>Sarsia mirabilis</i>	2	5.1- 7.5	6.28
<i>Aglantha digitale</i>	2	7.7- 7.9	2.96
	3	7.7- 7.9	2.57
<b>Ctenophora</b>			
<i>Hormiphora palmata</i>	1	6.6-6.8	11.28
	1	5.1-7.5	9.64
<b>Pteropoda</b>			
<i>Clione limacina limacina</i>	2	7.7- 7.9	3.94
<i>Limacina helicina helicina</i>	4	5.5- 6.0	0.863
	1	7.7- 7.9	0.750
<b>Polychaeta</b>			
<i>Tomopteris (Tomopteris) septentrionalis</i>	2	7.7- 7.9	8.62
<b>Copepoda</b>			
<i>Calanus cristatus</i> (stage V)	5	12.1-12.2	1.01
	5	10.9-12.0	1.899
	3	7.7- 7.9	1.96
<i>Pareuchaeta japonica</i> ♀	3	6.6- 6.8	1.12
<i>Eucalanus bungii bungii</i> ♀	8	5.1- 7.5	0.749
	8	5.5- 6.0	0.853
<i>Candacia columbiae</i> ♀	1	5.1- 7.5	0.130
	1	6.6- 6.8	0.310
<i>Calanus plumchrus</i> (stage V)	6	9.7-10.5	0.740
	8	6.6- 6.8	0.600
	6	9.7-10.5	0.657
	7	5.5- 6.0	0.409
<i>Calanus glacialis</i> (stage IV, V)	10	5.5- 6.0	0.289
	20	5.5- 6.0	0.277
<i>Tortanus discaudatus</i> ♀ ♂	21 (♀ 18 ♂ 3)	10.7-11.6	0.229
<i>Pseudocalanus elongatus</i> ♀ ♂	88 (♀ 80 ♂ 8)	10.7-11.6	0.0465
<b>Amphipoda</b>			
<i>Hyperia galba</i> ♀	1	6.9- 9.0	17.35
	1	12.1-12.2	7.60
<i>Hyperia</i> sp. ♀	2	6.6- 6.8	1.37
<i>Euthemisto libellula</i> ♀ ♂	3 (♀ 2 ♂ 1)	5.5- 6.0	1.77
	4 (♀ 2 ♂ 2)	6.6- 6.8	2.62
<b>Euphausiacea</b>			
<i>Thysanoessa raschii</i> ♀	1	5.3- 8.2	20.99
	1	5.3- 8.2	19.89
	1	6.6- 6.8	10.79
<i>Thysanoessa inermis</i> ♀	4	10.9-12.0	3.323
(juv.)	4	10.7-11.6	1.39
<b>Decapoda</b>			
<i>Penaeus</i> sp.	1	12.1-12.2	22.92
Brachyuran zoea larva	8	12.1-12.2	0.720
	17	5.3- 8.2	0.179
<b>Chaetognatha</b>			
<i>Sagitta elegans</i>	3	7.7- 7.9	5.70
	2	5.3- 8.2	0.930

plankton animals. The animals are arranged in the order of their magnitude of specific group

Body weight (mg/animal)			Weight specific respiration rate		
Wet wt.	Dry. wt.	Ash free dry wt.	$\mu\text{l O}_2/\text{mg wet wt./hr}$	$\mu\text{l O}_2/\text{mg dry wt./hr}$	$\mu\text{l O}_2/\text{mg ash free dry wt./hr}$
372.98	18.18	6.08	0.017	0.346	1.033
95.62	5.81	3.095	0.031	0.509	0.955
95.30	6.18	3.370	0.027	0.416	0.763
425.04	27.59	15.10	0.027	0.409	0.747
261.86	18.94	11.06	0.037	0.509	0.872
31.13	5.100	4.135	0.126	0.772	0.952
5.21	1.00	0.68	0.166	0.860	1.268
2.87	0.55	0.39	0.261	1.364	1.923
43.28	5.61	4.27	0.200	1.538	2.019
18.29	1.50	0.972	0.055	0.672	1.039
18.27	3.22	2.716	0.104	0.589	0.699
16.76	1.79	1.283	0.117	1.099	1.530
9.30	2.01	1.730	0.121	0.558	0.648
8.22	0.93	0.676	0.091	0.809	1.107
8.07	0.81	0.554	0.106	1.051	1.540
3.67	0.42	0.30	0.035	0.310	0.433
3.12	0.60	0.48	0.098	0.516	0.646
3.95	0.85	0.74	0.188	0.867	1.000
3.21	0.570	0.476	0.187	1.057	1.257
3.20	0.720	0.632	0.205	0.910	1.040
2.66	0.420	0.339	0.154	0.969	1.207
2.15	0.710	0.648	0.134	0.406	0.446
1.83	0.530	0.475	0.152	0.524	0.583
0.20	0.050	0.0391	1.132	4.670	5.866
0.04	0.012	0.00966	1.186	3.858	4.812
252.74	28.62	20.21	0.069	0.606	0.858
49.72	6.16	4.50	0.153	1.234	1.689
9.27	1.20	0.880	0.147	1.138	1.551
7.91	1.53	1.290	0.224	1.157	1.375
4.55	0.80	0.653	0.560	3.271	4.010
107.57	17.53	14.05	0.195	1.197	1.494
107.17	18.54	15.32	0.186	1.073	1.298
46.63	8.00	6.57	0.232	1.349	1.642
8.01	1.19	0.928	0.415	2.798	3.582
3.89	0.640	0.495	0.357	2.164	2.798
102.95	15.58	12.25	0.223	1.471	1.871
3.12	0.51	0.398	0.231	1.401	1.811
0.85	0.12	0.0835	0.212	1.441	2.141
53.64	4.83	3.33	0.106	1.180	1.713
11.20	1.13	0.80	0.083	0.827	1.163

Table 3.

Pisces			
<i>Eumicrotremus orbis orbis</i> (juv.)	1	5.1- 7.5	4.67
Temperate water species (13 species)			
Cephalopoda			
<i>Idiosepius</i> ( <i>Idiosepiion</i> )	2	17.0	8.887
<i>pygmaeus paradoxus</i>	1	17.0	6.347
Copepoda			
<i>Calanus pacificus</i> ♂	10	17.0	0.441
Mysidacea			
<i>Hypererythrops</i> sp.	6	17.0	0.871
Cumacea			
<i>Diastylis</i> sp. ♀	1	17.0	0.310
Isopoda			
<i>Aega</i> sp.	1	17.0	12.160
Amphipoda			
<i>Hyperia</i> sp. ♀ ♂	6 (♀ 1 ♂ 5)	17.0	0.719
<i>Hyperia</i> sp. (juv.)	5	17.0	0.300
Euphausiacea			
<i>Euphausia pacifica</i> ♀ ♂	4	17.2	8.440
Decapoda			
<i>Crangon affinis</i> (juv.)	1	17.0	7.258
<i>Leptochela gracilis</i> (juv.)	1	17.0	4.390
Brachyuran megalopa larva	1	17.0	1.614
Brachyuran zoea larva	2	17.0	0.803
<i>Lucifer typus</i> ♀ ♂	5 (♀ 3 ♂ 2)	17.0	0.526
Tropical species (41 species)			
Heteropoda			
<i>Firoloida desmaresti</i>	1	30.2	6.20
	1	29.4-30.3	14.46
Pteropoda			
<i>Creseis acicula clava</i>	1	30.0	7.42
<i>Hydromyles globulosa</i>	10	28.3-29.2	0.578
<i>Clione</i> sp.	1	29.4-30.3	3.36
Cephalopoda			
Octopus	1	29.4-30.3	17.62
Polychaeta			
<i>Lepidasthenia grimaldi</i>	1	30.2	6.21
Trochophora larva	2	29.4-30.3	5.21
Ostracoda			
<i>Cypridina hilgendorfi</i>	3	30.0	4.85
<i>Pyrocypris</i> sp.	3	30.0	1.02
Copepoda			
<i>Euchirella amoena</i> ♀	1	27.9-28.0	5.41
<i>Calanus gracilis</i> ♀	3	28.0	2.92
<i>Eucalanus crassus</i> ♀	1	30.2	5.77
<i>Eucalanus monachus</i> ♀	2	30.2	6.29
<i>Euchaeta marina</i> ♀	5	28.0	2.69
♀	16	28.3-29.2	2.24
<i>Calanus vulgaris</i> ♀	3	30.0	4.52
<i>Sapphirina gemma</i> ♂	4	29.0	1.28
♂	1	30.0	7.63
<i>Labidocera acuta</i> ♀ ♂	3 (♀ 2 ♂ 1)	30.0	2.87
<i>Euchaeta plana</i> ♂	5	28.0	2.62
<i>Labidocera detruncata</i> ♀	1	27.9-28.0	1.16

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Continued

34.79	5.38	4.18	0.134	0.868	1.117
40.83	6.84	5.695	0.218	1.299	1.560
34.11	5.90	4.91	0.186	1.076	1.293
0.513	0.090	0.078	0.860	4.904	5.659
1.11	0.542	0.508	0.785	1.608	1.713
0.60	0.18	0.10	0.517	1.722	3.100
25.95	6.64	4.95	0.469	1.832	2.457
1.31	0.19	0.15	0.549	3.783	4.792
0.428	0.072	0.052	0.702	4.172	5.777
17.70	3.300	2.748	0.477	2.559	3.074
50.63	10.92	9.07	0.143	0.665	0.800
10.90	1.93	1.59	0.403	2.275	2.761
2.12	0.23	0.19	0.761	7.017	8.495
1.315	0.20	0.11	0.611	4.015	7.300
0.466	0.068	0.062	1.128	7.732	8.481
13.08	1.08	0.53	0.47	5.74	11.70
10.45	0.81	0.40	1.38	17.85	36.15
3.36	1.07	0.22	2.21	6.93	33.73
3.11	0.398	0.294	0.186	1.45	1.97
2.58	0.28	0.16	1.30	12.00	21.00
6.84	1.28	1.04	2.58	13.77	16.94
5.51	0.98	0.57	1.13	6.34	10.89
1.36	0.24	0.16	3.85	22.17	32.56
1.98	0.35	0.21	2.45	13.73	23.47
0.45	0.080	0.027	2.25	13.30	38.25
2.66	0.56	0.51	2.03	9.66	10.61
2.12	0.39	0.30	1.38	7.48	9.62
2.07	0.36	0.22	2.79	16.03	26.23
1.45	0.19	0.11	4.34	34.00	57.18
1.43	0.234	0.218	1.88	11.49	12.33
0.822	0.119	0.097	2.73	18.77	23.14
1.06	0.22	0.17	4.25	20.86	27.12
0.71	0.070	0.035	1.80	19.00	36.64
1.00	0.08	0.04	7.63	95.38	190.75
0.99	0.17	0.10	2.89	16.90	29.72
0.95	0.158	0.130	2.74	16.57	20.14
0.93	0.15	0.13	1.25	7.73	8.92

Table 3.

<i>Labidocera</i> sp. ♀	3	30.0	2.68
<i>Eucalanus mucronatus</i> ♀	2	30.0	0.695
<i>Candacia aethiopica</i> ♀	10	28.3-29.2	1.76
<i>Acartia spinicauda</i> ♀	8	30.0	2.44
Cumacea			
<i>Iphinoe</i> sp. ♀	1	29.0	1.19
<i>Iphinoe</i> sp. (juv.)	5	30.0	0.346
Amphipoda			
<i>Phronima</i> sp.	1	28.3-29.2	38.42
<i>Orchomene</i> sp.	1	29.4-30.3	14.33
<i>Brachyscelus latipes</i> ♀	1	29.0	4.64
<i>Synopia ultramarina</i> ♀ (?)	1	30.2	14.56
Euphausiacea			
<i>Euphausia mutica</i> ♂	3	28.3-29.2	11.05
Decapoda			
Brachyuran megalopa larva	1	27.9-28.0	8.11
<i>Lysmata</i> sp.	2	30.0	14.04
Macruran post mysis larva	1	30.2	12.49
	1	29.0	11.23
Macruran mysis larva	4	28.0	2.93
Brachyuran zoea larva	1	28.0	4.22
	3	30.0	0.777
Chaetognatha			
<i>Sagitta enflata</i>	3	30.0	5.20
	3	29.4-30.3	7.55
<i>Sagitta robusta</i>	1	29.0	7.09
Thaliacea			
<i>Thalia democratica</i> (solitary salpa)	3	30.0	4.01
<i>Thalia democratica</i> (chain salpa)	3	29.0	1.90
Pisces			
<i>Trachurus japonicus</i> (juv.)	1	27.9-28.0	40.50
<i>Upeneus</i> sp. (juv.)	1	30.0	12.67
<i>Chelidonichthys</i> sp. (juv.)	1	30.0	13.49

In the present experiments the culture of animals preceding the respiration measurement was made in the natural surface sea water without supplying any special food.

Antibiotics have been used in the respiration experiments on plankton animals by several workers to reduce the effect of oxygen consumption by bacteria (Marshall & Orr, 1958a, b; Berner, 1962; Zeiss, 1963; Anraku, 1964; Marshall & Orr, 1966; Paranjape, 1967). Table 2 shows the result of the respiration rate in *C. plumchrus* when an antibiotic (dihydrostreptomycin sulfate, 50 mg per 1 l) was added. The addition of antibiotic seemed to depress the rate slightly compared with the control. Because the difference between the experimental and the control was small, no antibiotic was used in later experiments.

On the procedure of dissolved oxygen analysis (Winkler method, Strickland & Parsons, 1965) the consumption of iodine by excreta of the experimental animals was examined. A given amount of iodate solution was added to sample water which had been taken in the same manner as that of the respiration experi-

Continued

0.82	0.18	0.12	3.28	14.87	21.70
0.72	0.140	0.075	0.97	5.15	9.27
0.46	0.065	0.057	3.83	27.06	30.86
0.06	0.020	0.014	43.31	139.21	177.18
6.64	1.09	0.82	0.18	1.09	1.45
0.62	0.100	0.048	0.56	3.53	7.21
144.94	8.17	3.57	0.265	4.70	10.76
3.62	0.91	0.61	3.96	15.75	23.49
1.28	0.19	0.10	3.63	24.42	46.40
0.70	0.09	0.07	20.80	161.78	208.00
3.26	0.42	—	3.39	26.32	—
20.32	1.52	0.94	0.399	5.34	8.63
10.92	1.47	1.32	1.29	9.58	10.63
8.53	1.37	1.01	1.46	9.12	12.37
0.98	0.13	0.10	11.46	86.38	112.30
3.23	0.630	0.503	0.91	4.65	5.83
1.96	0.30	0.21	2.15	14.07	20.10
0.60	0.070	0.037	1.30	11.10	21.18
21.33	1.24	0.54	0.24	4.20	9.62
16.41	1.17	0.62	0.46	6.43	12.24
9.78	1.23	0.91	0.72	5.76	7.79
21.52	1.10	0.38	0.19	3.64	10.54
5.14	0.25	0.07	0.37	7.51	27.19
22.64	4.21	3.20	1.79	9.62	12.66
8.67	1.98	1.47	1.46	6.40	8.62
7.37	1.60	1.17	1.83	8.43	11.53

ment. After 24 hours, titration by thiosulfate was made to examine whether there occurred any consumption in iodine content. The result indicated that the consumption was insignificant at least for 24 hours at room temperature (20°C). From this, titration by thiosulfate solution for dissolved oxygen analysis was carried out within 24 hours after manganous sulfate reagent and alkaline iodide solution were added to the sample water.

*Wet, dry and ash free dry weight:* At the end of the respiration measurement, the animals were preserved in 10% formalin-sea water. The weighing of the animals was done at the land laboratory after returning from the cruise. The wet weight was measured by removing the excess of water on the surface of the animal; the dry weight was obtained by drying the animal at room temperature in a reduced pressure desiccator until a constant weight was obtained; the ash free dry weight was determined by burning the animal in a muffle furnace at 450°C until a constant weight was obtained. The dry weight of the body minus the ash weight gives an ash free dry weight. A Mettler balance was used for weighing.

Table 4. Regression equations and correlation coefficients ( $r$ ) of log total respiration rate ( $\mu\text{l O}_2/\text{animal/hr}$ ) ( $R$ ) and log body weight of animal (wet, dry and ash free dry weight in  $\text{mg}/\text{animal}$ ) ( $W$ )

	Body weight		
	Wet wt.	Dry wt.	Ash free dry wt.
Boreal species	$R=0.687W-0.523$ ( $r=0.897$ )	$R=0.830W+0.024$ ( $r=0.929$ )	$R=0.865W+0.131$ ( $r=0.934$ )
Temperate water species	$R=0.722W-0.159$ ( $r=0.974$ )	$R=0.691W+0.357$ ( $r=0.953$ )	$R=0.679W+0.428$ ( $r=0.957$ )
Tropical species	$R=0.446W+0.455$ ( $r=0.594$ )	$R=0.538W+0.874$ ( $r=0.639$ )	$R=0.542W+0.981$ ( $r=0.657$ )

For statistical treatment reference was made to Snedecor (1946).

### Results

All the results obtained in the present experiments are shown in Table 3. Because of the general trend that metabolism is a power function of body weight\*, the values in the table were converted to the logarithm. Then, the regression equations and the correlation coefficients ( $r$ ) between log total respiration rate ( $\mu\text{l O}_2/\text{animal/hr}$ ) and log body weight (each for wet, dry and ash free dry weight in  $\text{mg}/\text{animal}$ ) were calculated for each animal group (Table 4). The correlation is highly significant for boreal and temperate species. The correlation coefficients for the tropical species are low compared with those of the temperate and boreal species. The coefficient of  $W$  and the correlation coefficient ( $r$ ) tend to increase in this order: wet weight, dry weight and ash free dry weight, suggesting that the metabolism is related more closely to the mass of organic matter (ash free dry weight) than to water and ash content in the organism. The correlation diagram of log total respiration rate-log dry weight for all the results obtained is shown in Fig. 3. The patterns of correlation for the other two expressions of body weight (wet and ash free dry weight) are substantially the same. For same size (weight) animals the respiration rate increases with habitat temperature. The slopes of three regression lines (coefficient of  $W$  in the Table 4) significantly differ from one another, tending to become smaller with the increase of habitat temperature. The analysis of covariance proved that there is significant difference among the

\* This relation is expressed as

$$R = a \cdot W^b$$

or

$$\log R = \log a + b \cdot \log W$$

where  $R$  is the rate of respiration in terms of total respiration rate ( $\mu\text{l O}_2/\text{animal/hr}$ ) or weight specific respiration rate ( $\mu\text{l O}_2/\text{mg body weight/hr}$ ) and  $W$  is body weight of animals in terms of wet, dry and ash free dry weight ( $\text{mg}/\text{animal}$ ) in the present case.  $b$  is an exponential constant and  $a$  a constant of proportionality.

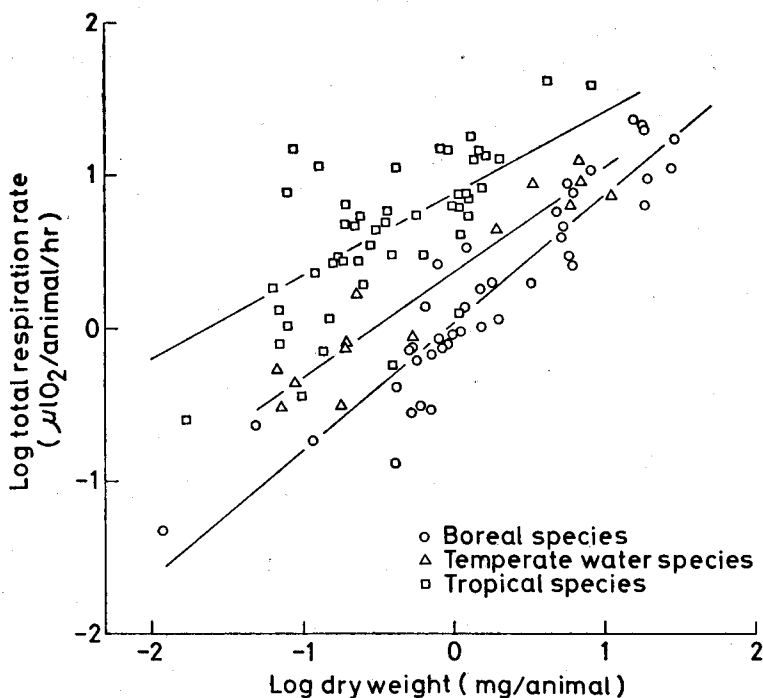


Fig. 3. Regression lines for the plankton animals from boreal, temperate and tropical waters, drawn for log total respiration rate ( $\mu\text{l O}_2/\text{animal/hr}$ ) plotted against log dry weight (mg/animal)

three regression lines and in the slopes of these lines. The case is the same when different bases of weight (wet weight and ash free dry weight) are used against total respiration rate. Table 5 shows the results of the significance test on the log total respiration rate versus the log dry weight relation.

The regression equations and the correlation coefficients ( $r$ ) between log weight specific respiration rate ( $\mu\text{l O}_2/\text{mg body weight/hr}$ ) and log body weight were calculated (Table 6). The weight specific respiration rate decreases as expected with the increasing of body weight for each animal group (Fig. 4). However, the correlation coefficients obtained are distinctively lower than the coefficients of log total respiration rate-log body weight. For this reason, total respiration rate and body weight represent two independent determinations, while weight specific respiration rate and body weight do not represent two independent determinations, since body weight has been already entered into weight specific respiration rate. As a result, the correlation is indicated even when total respiration rate and body weight are not correlated. This so-called "spurious correlation" is well known to statisticians (Weymouth *et al.*, 1944).

Table 5

## 1) Analysis of variance of the log total respiration rate

Null hypothesis; No difference in the mean log total respiration rate among the plankton animals inhabiting the boreal, temperate and tropical waters

Source of variation	Degrees of freedom	Mean square
Animals within lots	100	0.3187
Between different habitat temperatures	2	2.2447

Since  $F=2.2447/0.3187=7.04 > F_{0.01}[2,100]=4.82$ , reject null hypothesis

## 2) Analysis of covariance and test of significance of adjusted lot means

Null hypothesis; No difference in the log total respiration rate among the plankton animals inhabiting the boreal, temperate and tropical waters after removing effect of weight

Source of variation	Degrees of freedom	Sums of squares and products			Errors of estimate		
		$Sx^2$	$Sxy$	$Sy^2$	*Sum of squares	Degrees of freedom	Mean square
Total	102	54.0309	25.5692	36.3600	24.2598	101	
Between different habitat temperatures	2	9.5410	-6.0671	4.4894			
Within lots (error)	100	44.4899	31.6363	31.8706	9.3744	99	0.0947
For test of significance of adjusted means					14.8854	2	7.4427

\* $Sy^2 - \frac{(Sxy)^2}{Sx^2}$  Since  $F=7.4427/0.0947=78.59 > F_{0.01}[2,99]=4.82$ , reject null hypothesis

Where, x: log dry weight (mg/animal), y: log total respiration rate ( $\mu\text{l O}_2/\text{animal/hr}$ )

## 3) Analysis of errors of estimate from average regression within groups

Null hypothesis; No difference in the slopes of three regression lines between log total respiration rate and log body (dry) weight on boreal, temperate and tropical species

Source of variation	Degrees of freedom	Errors of estimate	
		Sum of squares	Mean square
Deviations from average (error) regression within lots	99	9.3744	
Deviations from individual lot regressions	97	8.6490	0.0892
Differences among lot regressions	2	0.7254	0.3627
Since $F=0.3627/0.0892=4.07 > F_{0.05}[2,97]=3.09$ , reject null hypothesis			

Table 6. Regression equations and correlation coefficients ( $r$ ) of log weight specific respiration rate ( $\mu\text{l O}_2/\text{mg}$  body weight/hr) ( $R$ ) and log body weight of animal (wet, dry and ash free dry weight in mg/animal) ( $W$ )

	Body weight		
	Wet wt.	Dry wt.	Ash free dry wt.
Boreal species	$R = -0.312W - 0.524$ ( $r = -0.679$ )	$R = -0.169W + 0.023$ ( $r = -0.454$ )	$R = -0.135W + 0.131$ ( $r = -0.377$ )
Temperate water species	$R = -0.278W - 0.159$ ( $r = -0.855$ )	$R = -0.309W + 0.357$ ( $r = -0.814$ )	$R = -0.321W + 0.428$ ( $r = -0.841$ )
Tropical species	$R = -0.556W + 0.456$ ( $r = -0.677$ )	$R = -0.464W + 0.874$ ( $r = -0.583$ )	$R = -0.459W + 0.981$ ( $r = -0.593$ )

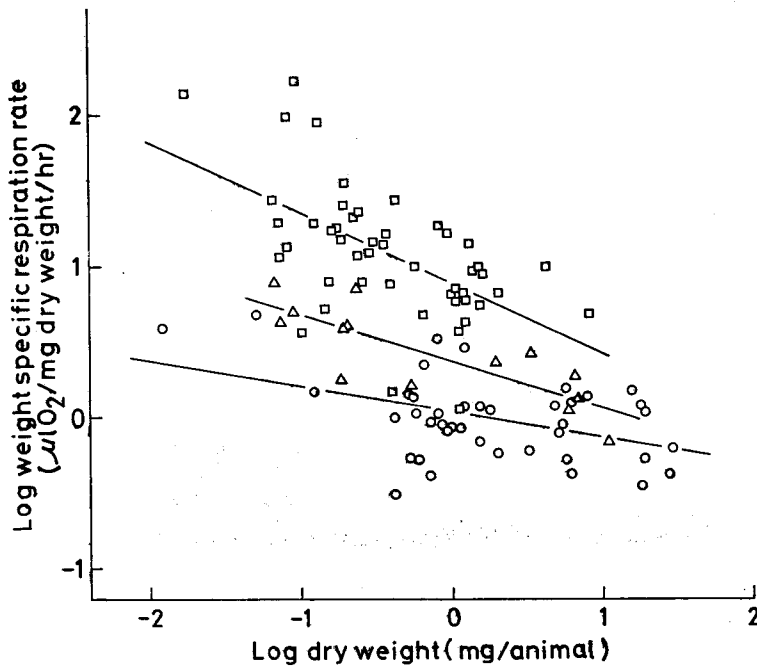


Fig. 4. Regression lines for the plankton animals from boreal, temperate and tropical waters, drawn for log weight specific respiration rate ( $\mu\text{l O}_2/\text{mg}$  dry weight/hr) plotted against log dry weight (mg/animal); symbols as in Fig. 3

Data presented by the preceding workers on the relationship between respiration rate and body size (weight) in plankton animals are tabulated in Table 7. Among them the experiments by Conover (1960) and Rajagopal (1962) are specially comparable with the present one on boreal and tropical species respectively in that the variety of species as well as the size range of animals used in these experiments overlaps with those of the present one. In addition, their experiments were carried out under the near habitat temperature of the animal.

The present regression equations for boreal and tropical species differ fairly from each comparable equations made by Conover (1960) and Rajagopal (1962) respectively. However, analyses of covariance indicate that there is no difference in each pair of data. That is, null hypothesis that there is no difference in the mean log weight specific respiration rate in each pair of data is accepted in each case at  $P=0.05$  (variance ratio  $F=0.13$ ;  $F_{0.05} [1,80]=3.96$  in the case of Conover's data versus the present one on boreal species, and  $F=1.85$ ;  $F_{0.05} [1,56]=4.02$  in the case of Rajagopal's data versus the present one on tropical species). The regression lines from different temperatures on a given species (e.g., Small, Hebard & McIntire, 1966; Haq, 1967; Paranjape, 1967; Comita, 1968; in the Table 7) cannot be compared easily with the present results, because in a given species the  $Q_{10}$  for respiration rate varies with body size and with the habitat temperature to which the animals are adapted (Rao & Bullock, 1954), and the speed of temperature change and the length of time spent at a new temperature affect the  $Q_{10}$  also (Bullock, 1955).

Preservation of the animals in formalin aqueous solution in the present experiments would have caused underestimation of body weight. However, the loss would be about 10% at most (Lovegrove, 1966; Hopkins, 1968).

### Discussion

It is generally accepted that the respiration rate in poikilotherms is dependent upon the temperature of their habitat. Fox (1936) first compared the rate of oxygen consumption of marine animals (echinoderms, annelids, crustaceans and lamellibranches) from cold water (5–7°C) with the same groups from warm waters (7–15°C). He found that the rate of warm water species was higher than that of the cold water species at the normal temperature of their habitats. Similar investigations have been carried out by several workers mainly for the purpose of obtaining knowledge on the mechanisms of metabolic compensation (adaptation) which permits the wide distribution of the organisms. They compared the MT (metabolism-temperature) curves from the organisms distributed in different latitudes (refer to Scholander *et al.*, 1953; Bullock, 1955; Prosser, 1955, 1961b). The results of Scholander *et al.* (1953) in particular showed on tropical (30°C) and arctic (0°C) aquatic poikilotherms (fishes and crustaceans) that the regression lines between log total respiration rate and log wet weight on fishes and crustaceans had the same slope (0.85) so that the two lines ran parallel with each other. The arctic forms showed a considerable metabolic adaptation in that their rates were only one fourth to one sixth of the rates of the tropical forms, resulting in the  $Q_{10}$  values of 1.6–1.8. In the present experiments, however, the  $Q_{10}$  varies with body weight, becoming smaller with the increasing body weight (Table 8). Rao &

Table 7. Data presented by the preceding workers on the relationship between respiration and body size (weight) in plankton animals

Author	Equation	Temperature (°C)	Size range (mg)	Species
Raymont & Gauld, 1951	<sup>1)</sup> R=0.73W+k R=0.77W+k	15.5-19		Copepods
Raymont, 1959	<sup>2)</sup> R=0.69W+k	15, 20		Copepods
Conover, 1959	R=0.856W-1.880	20±1	0.00176-0.01536	Copepods
Conover, 1960	<sup>3)</sup> R=0.745W-0.099	4-<10	0.0041-27.3	Copepods, Amphipods, Euphausiids
Rajagopal, 1962	<sup>4)</sup> R=0.273W+0.482	29±0.1	0.0025-5.75	Hydromedusa, Ctenophores, Copepods, Decapods, Tunicate
Small, Hebard & McIntire, 1966	R=0.962W-0.102	5	<sup>5)</sup> 2.2-14	<i>Euphausia pacifica</i> ,
	R=0.935W+0.152	10	2.0-40	<i>Thysanoessa</i>
	R=1.141W+0.083	15	4.0-12	<i>spinifera</i>
Haq, 1967	R=0.48W+k	4		<i>Metridia longa</i> , <i>M. lucens</i>
	R=0.48W+k	10		
	R=0.37W+k	14		
Small & Hebard, 1967	R=1.002W+0.103	10	<sup>6)</sup> 2.0-42.7	<i>Euphausia pacifica</i>
Paranjape, 1967	R=0.9848W-0.2865	5	0.976-8.018	<i>Euphausia pacifica</i>
	R=1.0084W-0.1057	10	0.868-6.146	
	R=0.9925W+0.0759	15	0.946-15.064	
	R=1.0521W-0.1726	20	2.070-7.056	
Comita, 1968	R=0.669W+2.820	5		Diaptomids
	R=0.721W+3.025	10		
	R=0.654W+3.133	15	<sup>7)</sup> 0.0032-0.3	
	R=0.626W+3.272	20		
	R=0.622W+3.444	25		
	R=0.658W+3.138	all		
Khmeleva & Yurkevich 1968	R=0.7W-0.4634	20	0.003-0.6	<i>Artemia salina</i>
	R=0.7W'-1.0605			
Pearcy <i>et al.</i> , 1969	<sup>9)</sup> (R=-0.19W <sup>2</sup> +1.9W)	10	<sup>8)</sup> 1.8-6.4	<i>Euphausia pacifica</i>

Where; R=log total respiration rate ( $\mu\text{l O}_2/\text{animal/hr}$ )

W=log dry weight (mg/animal)

(W'=log wet weight (mg/animal))

- 1) Calculated from  $\log R = 2.193 \log L - 0.9278$  and  $\log R = 2.302 \log L - 0.9901$  (L; cephalo-thorax length) assuming  $W \propto L^3$ .
- 2) Calculated from  $\log R = 2.08 \log L - 0.827$  assuming  $W \propto L^3$ .
- 3) Calculated by the present author including his data on *Pleuromamma robusta*.
- 4) Calculated by the present author from his Table 1 (Rajagopal, 1962).
- 5) Read from their Fig. 2 (Small, Hebard & McIntire, 1966).
- 6) Read from their Fig. 2 (Small & Hebard, 1967).
- 7) Minimum and maximum average body weight among 6 species of diaptomids experimented.
- 8) Read from their Fig. 2 (Pearcy *et al.*, 1969).
- 9) R and W are not the logarithm.

Table 8 The  $Q_{10}$  for respiration rate in plankton animals. The calculation is based on the experiments at different latitudes. The temperature in parenthesis indicates mean experimental temperature

	Body dry weight (mg)		
	0.1	1.0	10
Boreal species (8°C)	3.3	2.3	1.6
Temperate water species (17°C)	3.6	2.7	2.0
Tropical species (29°C)			

Bullock (1954) reviewed data from several sources, and concluded that the  $Q_{10}$  of various measures of activity commonly increases with increasing size (weight) over the range of ordinary physiological temperatures for animals, although there were several cases in which the trend was reversed. The result of the present experiment is a reversed case.

Existence of metabolic compensation (adaptation) in plankton animals living in cold waters is not certain. However, it seems probable that the animals inhabiting cold waters behave as actively as related animals in tropical waters.

Conover (1960), summarizing his experimental results in 1959 and 1960 (both cited in Table 7), first suggested the possible effect of the habitat temperature upon the relationship between body size and respiration in plankton animals. Then, he conducted an experiment with a single species, *Artemia salina*, and justified his thought\*. In the present experiments his thought was substantiated more precisely by the use of various plankton animals different in size and habitat temperature. An interesting finding by Conover (1960) shows that a carnivorous zooplankton group has a significantly higher respiration rate than a herbivorous group. In the science of nutrition of mammals this fact has been explained by a specific dynamic action due to the feeding of proteinous food substances. However, Conover's (1960) respiration experiment was carried out under almost starving condition of animals, so that the same line of explanation is not applicable to his results. His explanation is this: the body of carnivorous zooplankton is quite dense with hardened exoskeleton and this will require more energy to maintain the organism in the water against negative buoyancy, in contrast to high fat content with positive buoyancy which is common in herbivorous copepods. The predator has to move about actively in search of the prey using its greater physical strength and swiftness. On the other hand, herbivorous copepods can feed while they swim with a more or less continuous expenditure of a smaller amount of

\* He was inclined to discredit this experiment because both experimental temperatures were really outside the normal habitat temperature (Conover, 1968).

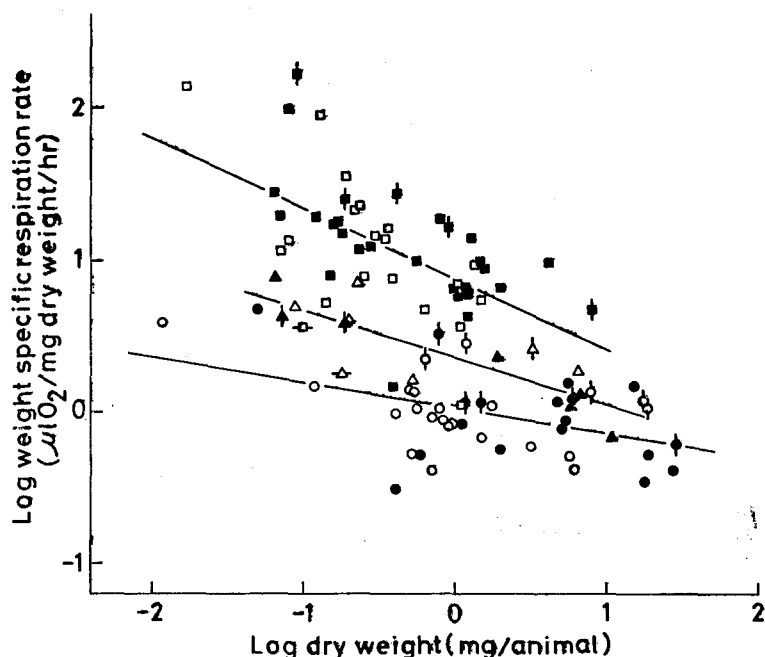


Fig. 5. Relationship between log weight specific respiration rate and log dry weight in plankton animals from boreal, temperate and tropical waters, reproduced from Fig. 4 with due regard to the difference in food habit (carnivores: solid symbols; non-carnivores: open symbols), swimming activity (agile animals such as amphipods and euphausiids: symbols with a vertical bar) and life habit (largely benthic forms such as cumaceans: symbols with a horizontal bar)

energy, since its food has at best extremely feeble power of escape.

Fig. 5 is reproduced from Fig. 4 with due regard to the difference in food habit, swimming activity and life habit of the animals experimented. Apparently there is no significant difference in the respiration rate between carnivores and non-carnivores (herbivores or filter feeders). However, data on active swimming animals such as amphipods and euphausiids tend to scatter above each regression line compared with those of other animals (Fig. 5). In contrast to this the rate of respiration in cumaceans is markedly low. This low value may be related to a largely benthic habit of this species. These trends remain unchanged even when the different bases of body weight (wet and ash free dry weight) are used against the rate of respiration.

A conclusion from the present experiments is that the respiration rate in plankton animals chiefly varies with their body size (weight) and habitat temperature. In a given size active animals seem to respire at a higher rate compared with inert ones irrespective of their feeding habit.

### Summary

(1) On 77 species of plankton animals, covering almost all systematic marine zooplankton species, inhabiting the boreal, temperate and tropical waters, the respiration rate was measured by the water bottle method at each habitat temperature.

(2) The regression equations of log total respiration rate ( $\mu\text{l O}_2/\text{animal/hr}$ ) against log body weight (each for wet, dry and ash free dry weight in mg/animal), and of log weight specific respiration rate ( $\mu\text{l O}_2/\text{mg body weight/hr}$ ) against log body weight were obtained on three animal groups: boreal species, temperate water species and tropical species.

(3) Total respiration rate generally increased and weight specific one decreased with increasing body weight. Statistical tests showed that the correlation coefficients were highly significant in each group.

(4) The remainder term also increased with increasing habitat temperature accompanied by a slight decrease (in the case of total respiration rate) or by a slight increase (in the case of weight specific respiration rate) in the inclination of the regression line. In other words, the respiration rate in terms of total respiration rate or weight specific respiration rate in a given size animal is higher in tropical species than in boreal species, and the rate in temperate water species is intermediate. The calculated  $Q_{10}$  for the respiration rate decreases with increasing body weight.

(5) Similar data by the preceding workers were tabulated and shortly discussed in comparison with the results of the present experiments. Although there was a fairly wide difference between the regression equations of the present experiments and the comparable tabulated one, the significance test showed little difference among those data which were used to calculate the regression equations.

(6) The effect due to the specific difference in feeding behavior, swimming activity and life habits of plankton animals on the respiration rate was briefly discussed; as far as the size range studied is concerned, no significant difference in the respiration rate was found due to the difference in feeding behavior. Visibly active animals such as euphausiids and amphipods seem to respire at some higher rate compared with the other inert animals studied. The rate is markedly low in largely benthic forms, such as cumaceans.

(7) The main source of difference in the respiration rate other than body size of animals seems to be the habitat temperature. The change in the respiration rate due to this source is highly significant at least for plankton animals that fall within the size range examined in the present experiments.

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