

# **Carbon and nitrogen contents of mesopelagic organisms: Results from Sagami Bay, Japan**

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Received 21 November 2002

**Keywords :** midwater, carbon, nitrogen, fishes, shrimps, copepods

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## Abstract:

The elemental compositions (carbon, nitrogen and water content) of midwater organisms were described. Groups analysed included fishes, shrimps, euphausiids, cladocerans, ostracods, copepods and cephalopods. Data for enigmatic organisms such as the megamouth shark, roundhead grenadier and vampire squid are included. Trends were clearer when expressed in terms of wet weight and it is recommended that in future studies the water contents of the tissues involved should be determined before analysis. The analysis of elemental compositions for both whole organisms and the muscle tissue fraction only is encouraged, as the information so gained may illuminate different aspects of the organism's ecology.

## Introduction

It is difficult to describe the influences of variable environmental factors on marine communities, but an even greater challenge is to describe how life in the sea interacts with the ocean and atmosphere to influence global climatic and biogeochemical cycles. Large-scale biological-physical feedbacks exist and therefore must be quantified to predict changes in global climate, but at this time one can predict neither the magnitude nor the direction of many key interactions.

Many pelagic marine organisms migrate to exploit gradients in resources (light, nutrients, oxygen), thereby transporting important chemicals independently of the surrounding medium. This capacity produces a need to understand more rigorously the biogeochemical consequences of mass movement of organisms in the pelagic environment in a manner that includes quantitative information on biogeochemical fluxes. Mass movements include, for example, diel and ontogenetic migrations by zooplankton, micronekton and larger, highly mobile species such as fishes and squids. Elemental composition (as carbon and nitrogen) has long been used as an index of an organism's caloric content (phytoplankton, Parsons *et al.*, 1961; zooplankton, Platt *et al.*, 1969), and the stoichiometry of this relationship has been defined quantitatively (Gnaiger and Bitterlich, 1984). Data presented here provides quantitative information on the elemental composition of major midwater species for incorporation into such biogeochemical models.

## Materials and Methods

Samples were collected on 14 May 1994 on the R/V Tansei Maru cruise KT94-6 by an IKMT (2×2mm mesh) tow, and from 23 to 28 May 1995 at fixed station P (34°35'N, 139°20'E) in Sagami Bay using an Isaacs-Kidd Midwater Trawl (IKMT) (2×2mm mesh), MTD multilayer closing nets (0.8m mouth diameter, 0.33mm mesh) (Motoda 1971) and an ORI conical plankton net (1.6m mouth diameter, 0.69mm mesh). Submersible observations were made using the crewed submersible *Shinkai 2000*. Species and size classes were separated into surface, vertically migrating and non-migratory groups. The non-migratory group was further split into groups with abundance maximums between 300-500m, 500-700m and below 700m, termed the "upper mesopelagic", "mid mesopelagic" and "lower mesopelagic" groups, respectively. All samples were frozen in sealable polyvinyl bags at -80°C until ready for analysis. Samples were rinsed quickly with distilled water and their lengths measured. When fishes or shrimps were analysed whole, the gut contents were dissected out. Wet weight was determined using a microbalance. Elemental analyses of muscle tissues were also carried out for various organisms other than copepods that were collected from 23 to 28 May 1995.

Organisms were desiccated in a dry oven at 60°C until dry weight stabilized and were then ground to a fine powder. The solvent-extractable lipid fraction was removed from subsamples of organisms collected on 25 May 1995 by regrinding with a mixture of chloroform:methanol (2:1), filtration onto a Whatman GF/C glass fibre filter, rinsing with the chloroform/methanol solution several times and subsequent redrying at 60°C overnight. Samples were converted to CO<sub>2</sub> and N<sub>2</sub> gas by the quartz combustion method of Minagawa *et al.* (1984). These gases were cryogenically separated and the C:N ratios of the samples determined volumetrically using a mercury manometer. Percentages of sample dry weight composed of carbon and nitrogen were computed based on the weight of the powdered sample placed into the combustion tube.

## Results

### Distributions and biometrics

Three bristlemouths of the genus *Cyclothone* occur in large numbers in Sagami Bay and their habitats were

segregated vertically according to species (Fig.1); *C. alba* being shallowest with an abundance maximum between 300 and 500m, *C. pseudopallida* between 500 and 700m and with *C. atraria* occurring at the greatest depths (500-700m for smaller, and below 700m for larger individuals). There was a trend for the larger fish of each species to live deeper than the smaller individuals of that species (unpublished data, Miya and Nemoto 1991). No evidence of extensive diel vertical migrations was found. Physical dimensions of migratory and non-migratory shrimps are outlined in Figures 2 and 3 respectively.

### Elemental Compositions

The elemental compositions of organisms collected on 14 May 1994 and 25 May 1995 are outlined in Tables 1 and 2, respectively. Values from the literature are outlined in Table 3 for comparison. The percentage of dry weight composed of nitrogen was higher for muscle tissue than for total organic matter in all species while the percentage composed of carbon was approximately equal for both. Higher C+N content was observed for highly mobile species than for others.

### Discussion

The chemical makeup of organisms is usually expressed as the elemental composition, that is the percentage of an organism's dry weight that is composed of

various elements, usually carbon, nitrogen and hydrogen. For the purposes of this study, the term "elemental composition" refers to that of carbon and/or nitrogen. Overall the amount of variation in the elemental composition of muscle tissues, as measured in this study, is lower than that found for whole organisms in previous studies (Tables 1, 2, 3). This is to be expected, as in different organisms, the proportion of body mass allocated to tissues such as muscle, bone, chitin and internal organs, varies.

This is illustrated well in the macrouroidid, *Squalogadus modificatus*. The head of *S. modificatus* is extremely large in comparison to body size and the cavity of the specimen examined was filled with a fatty liquid, of presumably low density. Submersible observations (unpublished data) prove *S. modificatus* to swim in a near horizontal attitude, something which would only be possible if the density of the bulbous head were lower than ambient seawater. The C/N ratio of muscle tissue from *S. modificatus* was not affected by the defatting process (Table 2), signifying a low level of lipid present in the muscle tissue. If the elemental composition of the whole animal were determined, undoubtedly this result would have differed. The nitrogen content of muscle tissue was high (Table 2), although the reason for this is not clear. Perhaps ammonium or some other low density nitrogenous substance is present in this tissue.

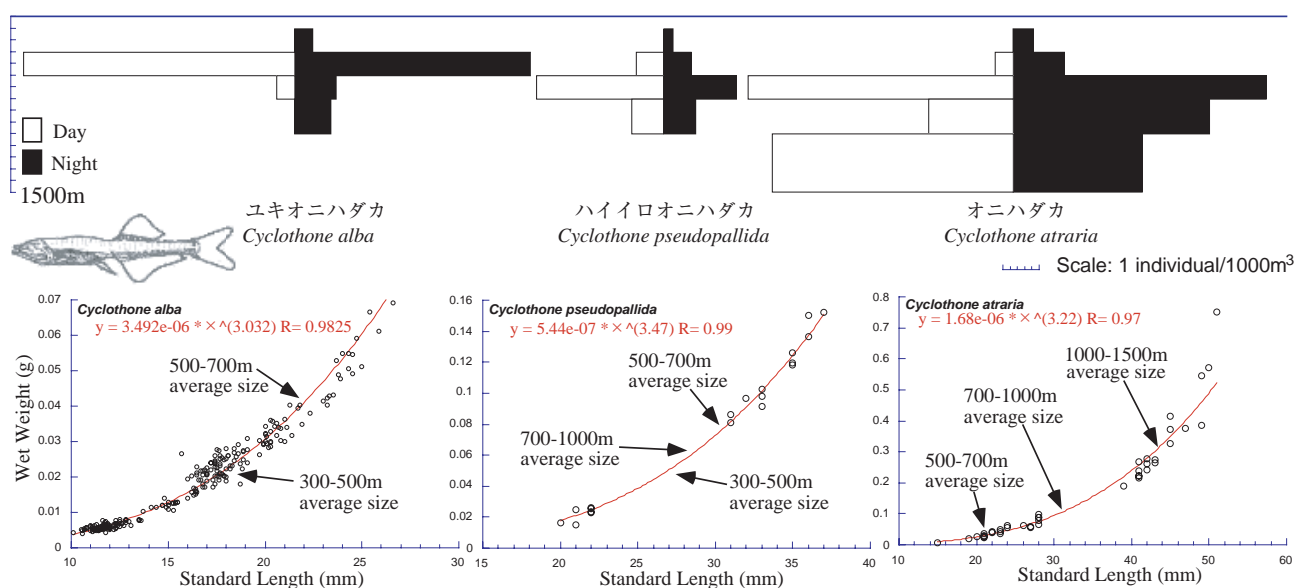


fig. 1 The vertical distributions and sizes of fishes of the genus *Cyclothone* at Station P, Sagami Bay, Central Japan.

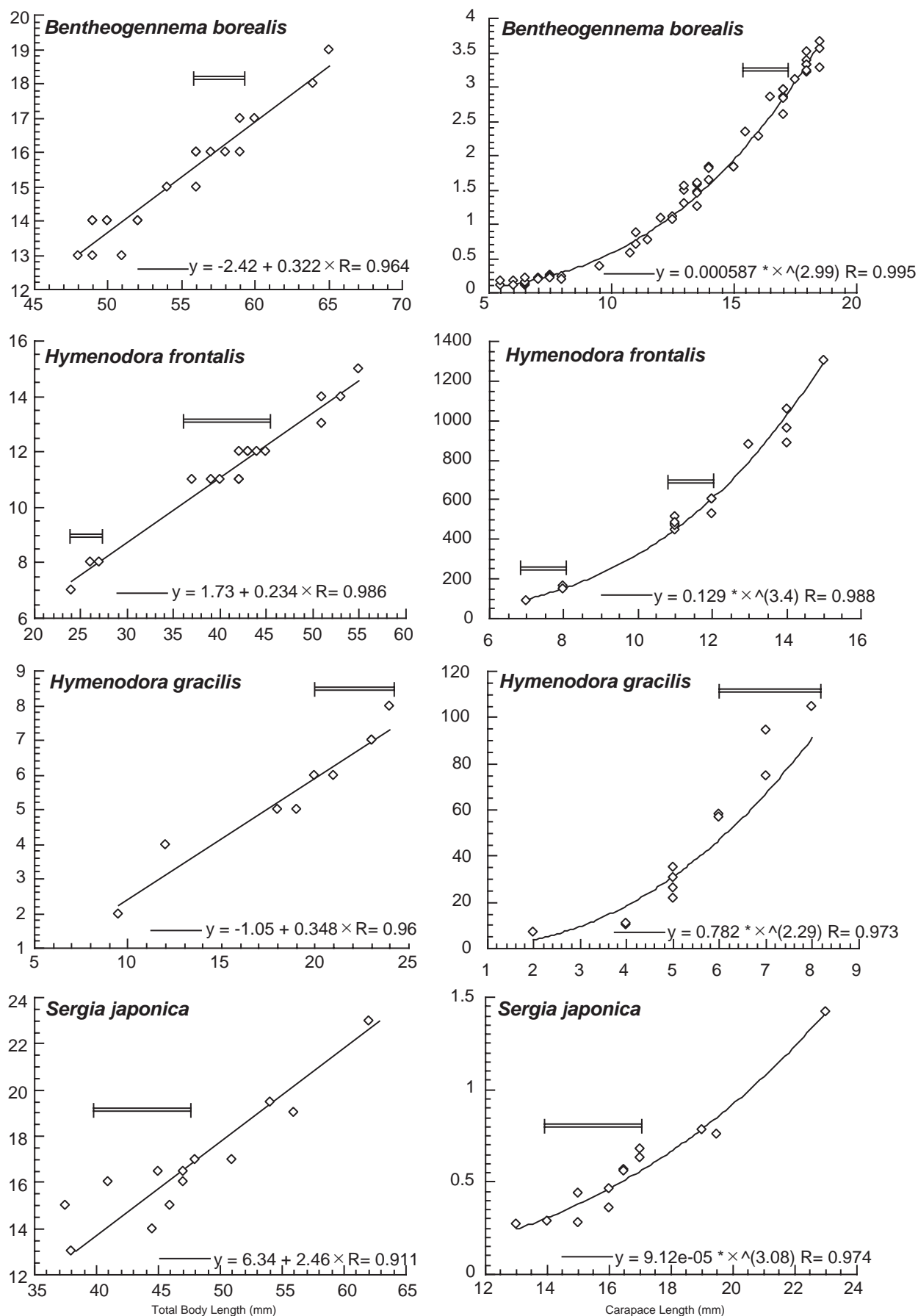


fig. 2 The physical dimensions of non-migratory shrimps taken at Station P, Sagami Bay.

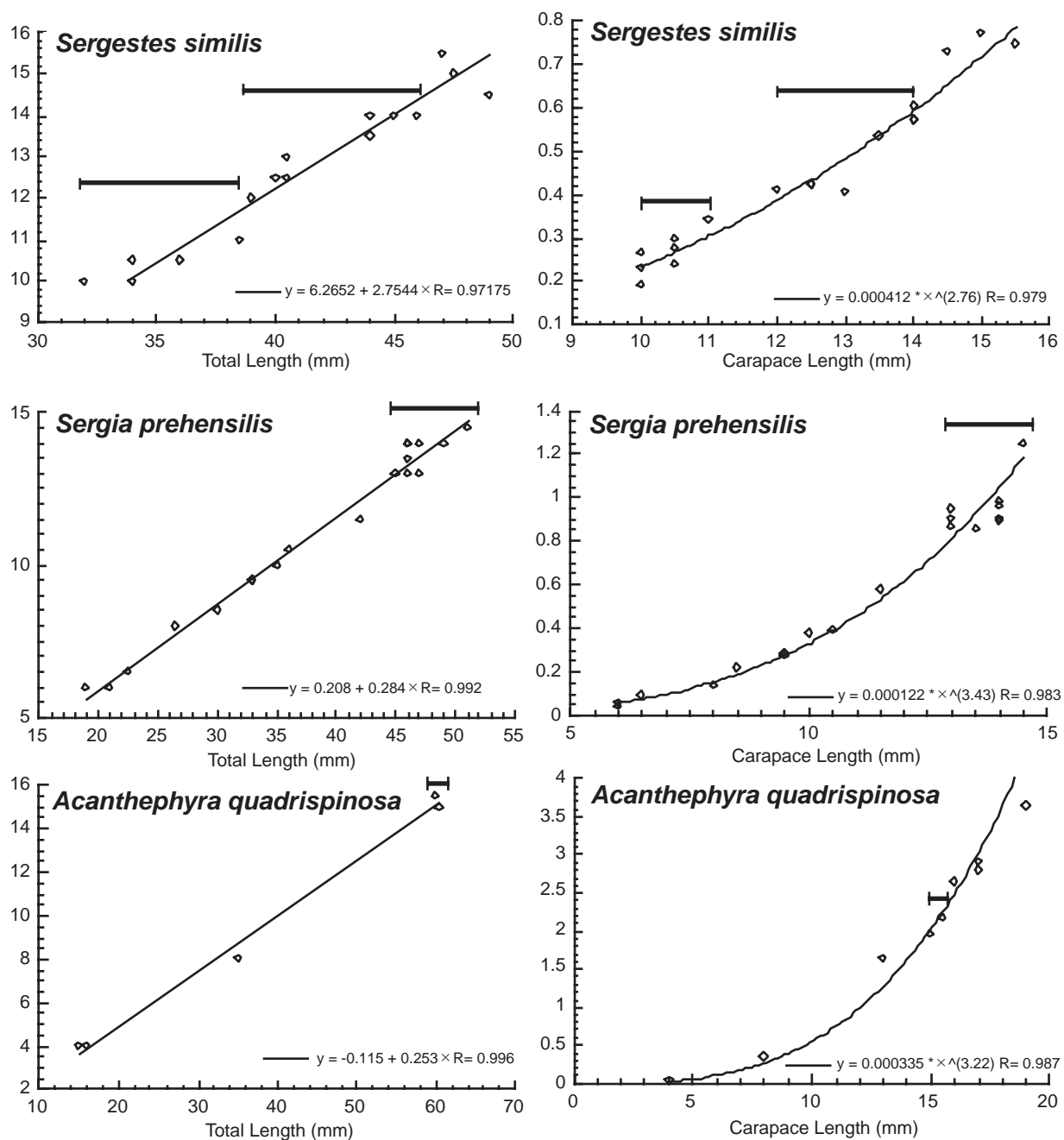


fig. 3 The physical dimensions of migratory shrimps taken at Station P, Sagami Bay.

Table 1 Elemental (carbon and nitrogen) compositions of micronekton and plankton from Sagami Bay, Central Japan on 14th May 1994. Water content is expressed as percent of wet weight. C and N compositions are expressed as percent of dry weight. nd: no data C:N was calculated according to the formula  $C:N = (C/N) \times (14/12)$ .  
Samples from June 1996 were reported by Okumura (personal communication)

Species	n	Size	Water	C/N Ratio	Nitrogen	Carbon
<b>Whole animal</b>						
<b>Fish</b>						
<i>Cyclothone alba</i>	9	15-18mm SL	nd	4.45	9.11	34.81
<i>C. pseudopallida</i>	1	31mm SL	nd	4.61	8.31	32.87
<i>C. atraria</i>	2	26mm SL	nd	6.72	7.92	45.61
<i>C. atraria</i>	1	37mm SL	nd	4.90	9.33	39.24
<i>Gonostoma gracile</i>	3	24-31mm SL	nd	4.29	9.08	33.41
<i>Maurolicus muelleri</i>	4	11-13mm SL	nd	4.58	10.21	40.12
<b>Shrimps</b>						
<i>Acanthephyra quadrispinosa</i>	1	51mg dry weight	nd	6.43	9.36	51.63
<i>Gennadas</i> sp.	1	510mg dry weight	nd	4.15	10.68	38.00
<i>Bentheogennema borealis</i>	1	553mg dry weight	nd	9.27	6.95	55.24
<i>Hymenodora frontalis</i>	1	68mg dry weight	nd	11.34	5.17	50.24
<b>Euphausiids</b>						
<i>Euphausia similis</i>	1	5.0mg dry weight	nd	4.41	11.65	44.02
<i>Euphausia similis</i>	1	3.9mg dry weight	nd	4.63	12.29	48.78
<i>Euphausia similis</i>	1	2.7mg dry weight	nd	4.55	14.16	55.21
<i>Euphausia similis</i>	3	4.7mg dry weight	nd	4.55	11.82	46.14
<i>Euphausia similis</i>	3	7.0mg dry weight	nd	4.53	9.69	37.62
<b>Ostrocods</b>						
? <i>Conchoecia</i> sp.	3	2.5-2.9mm TL	nd	5.73	8.98	44.18
? <i>Conchoecia</i> sp.	4	2.9-3.1mm TL	nd	7.01	6.95	41.80
? <i>Conchoecia</i> sp.	7	3.0-3.2mm TL	nd	6.84	7.82	45.85
<b>Copepods</b>						
<i>Neocalanus cristatus</i>	1	6.9-7.8mm PL	nd	7.91	7.89	53.53
<i>N. cristatus</i>	1	6.9-7.8mm PL	nd	8.07	7.97	55.19
<i>N. cristatus</i>	1	6.9-7.8mm PL	nd	10.16	6.95	60.48
<i>N. cristatus</i>	2	7.7mm PL	nd	9.06	5.24	40.75
<i>Pleuromamma</i> sp.	2	3.2, 4.0 mm PL	nd	4.54	13.61	52.99
<i>Pleuromamma</i> sp.	2	3.3, 3.4mm PL	nd	4.51	11.22	43.35
<i>Paraeuchaeta sarsi</i>	1	5.4mm PL	nd	9.61	7.24	59.62
<b>June 1996*</b>						
<b>Shrimps</b>						
<i>Acanthephyra quadrispinosa</i>	7	avg. 14.9mm CL	78.67(±1.28)	5.57(±0.60)	9.50(±0.59)	45.36(±2.61)
<i>Sergia prehensilis</i>	6	avg. 13.0mm CL	78.22(±1.31)	4.51(±0.36)	10.96(±0.52)	42.34(±2.55)
<i>Bentheogennema borealis</i>	6	avg. 15.4mm CL	71.89(±1.91)	10.25(±0.80)	6.62(±0.36)	58.14(±2.51)

Table 2 Elemental (carbon and nitrogen) compositions of micronekton and plankton from Sagami Bay, Central Japan sampled on 25th May 1995. Water content is expressed as percent of wet weight. Nitrogen and Carbon compositions are expressed as percent of dry weight. Mean values ( $\pm$  SD); nd: no data. Asterisk indicates samples where a portion of the information is suspect. C:N was calculated according to the formula  $C:N = (C/N) \times (14/12)$ .

Species	Size	Water	C/N Ratio	C/N (post-defat.)	Nitrogen	Carbon
<b>Muscle tissue</b>						
<b>Fish</b>						
<i>Cyclothone alba</i>	20-22mm SL	nd	4.07	3.75	11.03	38.44
<i>C. pseudopallida</i>	20-22mm SL	nd	3.93	3.74	11.14	37.55
<i>C. pseudopallida</i>	31-36mm SL	nd	4.14	3.64	12.89	45.76
<i>C. pallida</i>	31-37mm SL	77.6	4.02	3.45	12.28	42.30
<i>C. atraria</i>	20-22mm SL	nd	4.36	3.70	11.65	43.57
<i>C. atraria</i>	27-28mm SL	nd	4.81	3.69	11.08	45.70
<i>C. atraria</i>	41-42mm SL	nd	4.48	3.64	11.45	43.95
<i>Lampanyctus jordani</i>	100-120mm SL	nd	4.58	3.65	12.64	49.59
<i>Stenobrachius nannochir</i>	71-88mm SL	74.1	6.58	3.66	10.40	58.65
<i>Engraulis japonicus</i>	24-25mm SL	nd	4.12	3.54	12.23	43.16
<i>Maurolicus muelleri</i>	23-25mm SL	71.5	3.90	nd	13.66	45.68
<i>D. garmani</i>	32-38mm SL	nd	4.79	3.76	11.70	48.00
<i>Diaphus kuroshio</i>	21-27mm SL	72.0	3.49*	3.73	13.86*	41.45*
<i>D. kuroshio</i>	40-49mm SL	nd	3.99	3.68	13.54	46.33
<i>D. kuroshio</i>	63-65mm SL	nd	4.48	3.63	12.80	49.10
<i>D. kuroshio</i>	66-68mm SL	nd	4.51	3.67	12.39	47.90
<i>D. suborbitalis</i>	46-56mm SL	nd	4.17	3.70	12.94	46.29
<i>Ceratoscopelus warmingii</i>	73mm SL	76.0	4.75	3.75	12.40	50.53
<i>Borodindula (Avocettina) infans</i>	450mm SL	nd	4.88	3.64	11.92	49.88
<i>Chauliodus sloani</i>	125mm SL	85.1	3.73	3.69	13.24	42.38
<i>C. sloani</i>	137mm SL	85.8	3.77	3.67	13.69	44.26
<i>Stomias affinis</i>	90mm SL	79.7	4.10	3.89	11.80	41.49
<i>Squalogadus modificatus</i>	280mm SL	nd	3.63	3.58	14.75	45.94
<i>Leptoderma lubricum</i>	211-222mm SL	89.6	3.79	3.61	13.65	44.34
<i>Serrivomer sector</i>	215mm SL	nd	3.75	3.70	12.66	40.67
<i>Megacasma pelagios</i>	nd	nd	2.37	nd	19.42	39.42
<i>Rhincodon typus</i>	nd	nd	2.70	nd	17.31	40.01
<b>Shrimps</b>						
<i>Bentheogennema borealis</i>	15-17mm CL	nd	3.78	3.52	14.81	47.93
<i>Hymenodora frontalis</i>	7-8mm CL	nd	4.08	3.61	13.39	46.84
<i>H. frontalis</i>	11-12mm CL	nd	3.78	3.54	14.43	46.78
<i>H. gracilis</i>	6-7mm CL	nd	4.26	3.67	13.78	50.33
<i>Sergia japonica</i>	15-17mm CL	81.2	3.88	3.31	12.09	40.23
<i>S. prehensilis</i>	13-14.5mm CL	nd	3.65	3.48	14.62	45.76
<i>Acantheephyra quadrispinosa</i>	15mm CL	75.3	3.79	3.57	13.79	44.83
<i>A. quadrispinosa</i>	15.5mm CL	78.1	3.72	3.47	12.98	41.39
<i>Sergestes similis</i>	10-11mm CL	72.6	3.58	3.49	13.37	40.99
<i>S. similis</i>	12-14mm CL	75.8	3.64	3.44	12.25	38.21
<b>Euphausiids</b>						
<i>Euphausia similis</i>	15-17mm TL	nd	3.90	3.72	12.42	41.56
<b>Copepods</b>						
<i>Eucloteuthis luminosa</i>	192-208mm DML	nd	3.65	3.50	14.40	45.09
<i>Vampyroteuthis infernalis</i>	110mm DML, 24.5g	nd	3.98	3.57	9.64	32.88
<b>Whole animal</b>						
<b>Fish</b>						
<i>Cyclothone alba</i> (n=8)	21-23mm SL	78.4 (0.9)*	4.40 (0.29)	nd	10.00 (0.88)	37.71 (1.82)
<i>C. pseudopallida</i> (n=7)	20-23mm SL	77.3 (1.5)	4.24 (0.18)	nd	10.30 (0.77)	37.46 (3.02)
<i>C. atraria</i> (n=8)	23-24mm SL	80.5 (2.4)	4.75 (0.37)	nd	10.59 (0.70)	43.10 (1.89)
<i>Maurolicus muelleri</i> (n=7)	20-23mm SL	75.5 (0.8)	4.15 (0.13)	nd	12.45 (0.27)	44.33 (0.74)
<b>Cladocerans</b>						
<i>Evadne tergestina</i>	nd	nd	5.14	nd	9.58	42.20
<b>Copepods</b>						
<i>Arietellus simplex</i>	nd	nd	7.95	3.73	8.92	60.82
<i>Bathycalanus richardi</i>	nd	nd	8.42	nd	7.26	52.39
<i>Cornucalanus indicus</i>	nd	nd	7.90	3.95	7.08	47.99
<i>Lucicutia wolfendeni</i>	nd	nd	7.81	4.24	6.91	46.28
<i>Paraeuchaeta rubra</i>	nd	nd	6.92	nd	10.28	60.99
<i>P. sarsi</i>	nd	nd	7.79	nd	7.65	51.07
<i>Calanus sinicus</i>	nd	nd	5.30	4.12	8.89	40.42
<i>Neocalanus cristatus</i>	nd	nd	5.40	3.66	9.51	44.01
<i>N. cristatus</i>	nd	nd	5.82	4.01	8.35	41.69

Table 3 Elemental (carbon and nitrogen) compositions of micronekton and plankton reported in the literature.

Water content is expressed as percent of wet weight. C and N compositions are expressed as percent of dry weight. nd: no data C:N was calculated according to the formula  $C:N = (C/N) \times (14/12)$ .

Species	Size	Water	C/N Ratio	Nitrogen	Carbon
<b>Whole animal</b>					
<b>Fish</b>					
<i>Cyclothone alba</i> <sup>1</sup>	>10mm SL	85	nd	nd	nd
<i>C. signata</i> <sup>2</sup>	28-36mm SL	81.5-85.0	nd	nd	nd
<i>C. braueri</i> <sup>3</sup>	nd	nd	5.83	8.00	40.00
<i>C. pseudopallida</i> <sup>1</sup>	>10mm SL	84.1	nd	nd	nd
<i>C. acclinidens</i> <sup>4</sup>	0.07-0.6g	79.4	nd	<9.7	<52.6
<i>C. acclinidens</i> <sup>2</sup>	27.4-60.0mm SL	76.0-83.7	nd	nd	nd
<i>C. microdon</i> <sup>5</sup>	57-64mm SL	67	nd	nd	nd
<i>C. microdon</i> <sup>5</sup>	51-67mm SL	66.9	nd	nd	nd
<i>C. pygmaea</i> <sup>3</sup>	nd	nd	4.54	8.90	34.60
<i>C. pallida</i> <sup>6</sup>	nd	81.6	4.23	10.21	37.07
<i>C. pallida</i> <sup>1</sup>	>10mm SL	85.9	nd	nd	nd
<i>Gonostoma elongatum</i> <sup>6</sup>	nd	85.9	4.00	10.25	35.11
<i>G. elongatum</i> <sup>1</sup>	69-160mm SL	89.4	nd	nd	nd
<i>G. ebelingi</i> <sup>1</sup>	100-126mm SL	85.8	nd	nd	nd
<i>G. atlanticum</i> <sup>1</sup>	39-52mm SL	76.5	nd	nd	nd
<i>Lampanyctus lineatus</i> <sup>6</sup>	nd	88.3	4.12	9.83	34.70
<i>L. niger</i> <sup>b</sup> <sup>1</sup>	71-92mm SL	86.1	nd	nd	nd
<i>L. nobilis</i> <sup>1</sup>	83-94mm SL	79.9	nd	nd	nd
<i>L. steinbecki</i> <sup>1</sup>	40-52mm SL	76.9	nd	nd	nd
<i>L. tenuiformis</i> <sup>1</sup>	130mm SL	79	4.24	11.00	40.00
<i>L. ritteri</i> <sup>4</sup>	2-5g	70.6	nd	<8.2	<58.7
<i>L. ritteri</i> <sup>2</sup>	39.2-105.1mm SL	68.2-76.3	8.36	7.40	53.01
<i>L. regalis</i> <sup>4</sup>	2-64g	86.3	5.96	8.76	44.74
<i>L. regalis</i> <sup>7</sup>	>50mm SL	86.7	nd	nd	nd
<i>L. regalis</i> <sup>2</sup>	36.7-117.8mm SL	79.1-81.9	nd	nd	nd
<i>Stenobrachius nannochir</i> <sup>7</sup>	>85mm SL	66.7	nd	nd	nd
<i>S. leucopsaurus</i> <sup>4</sup>	1-1.5g	66.8	nd	<6.8	<61.5
<i>Engraulis japonicus</i> <sup>8</sup>	9.1mm SL	nd	4.35	11.60	43.30
<i>E. japonicus</i> <sup>8</sup>	6.6mm SL	nd	4.30	11.70	43.10
<i>E. mordax</i> <sup>4</sup>	12-17g	66.7	nd	nd	nd
<i>Diaphus brachycephalus</i> <sup>1</sup>	42-51mm SL	77.5	nd	nd	nd
<i>D. mollis</i> <sup>a</sup> <sup>1</sup>	23-35mm SL	77.2	nd	nd	nd
<i>D. schmidtii</i> <sup>1</sup>	30-32mm SL	76	nd	nd	nd
<i>D. theta</i> <sup>4</sup>	1.6g	66.1	10.31	5.92	52.33
<i>D. theta</i> <sup>7</sup>	>35mm SL	75.3	nd	nd	nd
<i>Ceratoscopelus townsendi</i> <sup>2</sup>	22.9-71.6mm SL	65.6-78.3	nd	nd	nd
<i>C. warmingii</i> <sup>1</sup>	33-50mm SL	80.0	nd	nd	nd
<i>Avocettina</i> sp. <sup>4</sup>	11.9g	80.7	4.85	9.95	41.35
<i>Avocettinops infans</i> <sup>1</sup>	21.0g	87.3	4.26	11.00	40.20
<i>Chauliodus sloani</i> <sup>1</sup>	185mm SL	88.3	4.13	11.10	39.30
<i>C. macouni</i> <sup>4</sup>	21g	78.3	nd	nd	nd
<i>C. spp.</i> <sup>2</sup>	31.7-210mm SL	74.0-85.4	nd	nd	nd
<i>Stomias atriventer</i> <sup>4</sup>	5-20g	80.9	7.73	7.07	46.86
<i>S. boa</i> <sup>3</sup>	nd	nd	4.14	9.70	34.40
<i>Serrivomer beanii</i> <sup>9</sup>	ca. 234mm SL	87.49	4.61	11.42	45.09
<b>Shrimps</b>					
<i>Sergia fillicum</i> <sup>10</sup>	nd	63.8	4.92	8.59	36.19
<i>S. grandis</i> <sup>10</sup>	nd	74.5	4.25	10.28	37.45
<i>S. robustus</i> <sup>10</sup>	nd	75.5	4.42	9.71	36.82
<i>S. robustus</i> <sup>3</sup>	nd	nd	4.80	9.30	38.30
<i>S. splendens</i> <sup>10</sup>	nd	71.6	4.22	13.38	48.43
<i>Sergestes similis</i> <sup>11</sup>	nd	76.6	4.51	10.98	42.44
<i>S. similis</i> <sup>12</sup>	178mg dry weight/ind.	nd	5.62	9.80	47.20
<i>S. lucens</i> (juv.) <sup>12</sup>	7.4mg dry weight/ind.	nd	4.52	11.10	43.00
<i>S. lucens</i> <sup>12</sup>	133mg dry weight/ind.	nd	4.70	10.50	42.30
<i>S. prehensilis</i> <sup>12</sup>	228mg dry weight/ind.	nd	4.33	11.30	41.90
<i>S. japonicus</i> (juv.) <sup>12</sup>	33mg dry weight/ind.	nd	4.15	11.30	40.20
<i>S. japonicus</i> <sup>12</sup>	158mg dry weight/ind.	nd	5.27	10.20	46.10
<i>S. arcticus</i> <sup>13</sup>	48mm TL	83.63	6.53	8.27	46.29
<i>S. arcticus</i> <sup>3</sup>	nd	nd	4.61	11.70	46.20
<i>S. phorcus</i> <sup>11</sup>	nd	77.5	4.82	10.36	42.76
<i>S. henseni</i> <sup>10</sup>	nd	75.5	4.07	10.57	36.86
<i>S. paraseminudus</i> <sup>10</sup>	nd	67.0	4.01	11.00	37.79
<i>S. corniculatum</i> <sup>3</sup>	nd	nd	4.86	9.60	40.00
<i>Acanthephyra pelagica</i> <sup>3</sup>	nd	nd	4.31	9.20	34.00
<i>A. quadrispinosa</i> (juv.) <sup>12</sup>	114mg dry weight/ind.	nd	4.85	10.80	44.90
<i>A. quadrispinosa</i> <sup>12</sup>	469mg dry weight/ind.	nd	5.46	9.70	45.40
<i>Gennadas parvus</i> (juv.) <sup>3</sup>	4.7mg dry weight/ind.	nd	4.73	10.60	43.00



Table 3 Elemental (carbon and nitrogen) compositions of micronekton and plankton reported in the literature.

Water content is expressed as percent of wet weight. C and N compositions are expressed as percent of dry weight. nd: no data C:N was calculated according to the formula  $C:N = (C/N) \times (14/12)$ .

Species	Size	Water	C/N Ratio	Nitrogen	Carbon
<i>G. elegans</i> <sup>3</sup>	nd	nd	4.89	9.20	38.60
<i>Bentheogennema borealis</i> <sup>12</sup>	931mg dry weight/ind.	nd	12.50	6.00	64.30
<b>Euphausiids</b>					
<i>Euphausia krohnii</i> <sup>3</sup>	nd	nd	3.63	10.00	31.10
<i>E. pacifica</i> <sup>14</sup>	12 to <16mm TL	79.2	4.26	12.00	43.80
<i>E. pacifica</i> <sup>14</sup>	16 to <19mm TL	78.7	4.23	11.70	42.40
<i>E. superba</i> <sup>15</sup>	7-26mg (dry wt.)	nd	4.13-5.60	9.9-11.6	41.1-47.5
<i>E. triacantha</i> <sup>15</sup>	15mg (dry wt.)	nd	4.14	11.60	41.20
<b>Cephalopods</b>					
<i>Vampyroteuthis infernalis</i> <sup>16</sup>	nd	94.03	nd	nd	nd
<b>Ostracods</b>					
<i>Conchoecia pseudodiscophora</i> VII <sup>17</sup>	nd	nd	9.72	5.70	47.50
<i>C. pseudodiscophora</i> VIII <sup>17</sup>	nd	75.9	6.38	7.30	39.90
<b>Cladocerans</b>					
<i>Evadne</i> spp. <sup>18</sup>	nd	nd	4.93	9.87	41.69
<b>Copepods</b>					
<i>Lucicutia</i> sp. <sup>19</sup>	nd	nd	6.08	8.31	43.28
<i>L. auerita</i> <sup>19</sup>	nd	nd	5.61	9.4	45.18
<i>Bathycalanus princeps</i> <sup>11</sup>	nd	81.5	6.20	8.65	45.95
<i>Paraeuchaeta elongata</i> V <sup>17</sup>	nd	74.5	7.82	8.4	56.3
<i>P. elongata</i> VI <sup>17</sup>	nd	77.3	7.26	8.5	52.9
<i>Calanus sinicus</i> <sup>8</sup>	nd	nd	4.18	12	43
<i>C. sinicus</i> <sup>18</sup>	nd	nd	4.58	12.09	47.43
<i>C. sinicus</i> <sup>20</sup>	nd	nd	9.61-10.22	7.1-7.3	60.1-62.2
<i>Neocalanus cristatus</i> V <sup>17</sup>	nd	82	6.77	8.7	50.5
<i>N. cristatus</i> V <sup>19</sup>	nd	nd	3.0-9.6	5.9-15.6	32.1-64.8
<i>N. plumchrus</i> V,VI <sup>17</sup>	nd	82.2	9.57	6.9	56.6
<i>Pleuromamma xiphias</i> <sup>19</sup>	nd	nd	4.63	11.2	44.4
<i>P. xiphias</i> <sup>19</sup>	nd	nd	4.5	8.9	34.3
<i>P. xiphias</i> <sup>19</sup>	nd	nd	4.83	9.4	38.9

Sources, 1: Childress et al. (1990); 2: Bailey and Robison (1986); 3: Gorsky et al. (1988); 4: Childress and Nygaard (1973); 5: Donnelly et al. (1990); 6: Stickney (1987); 7: Butler and Percy (1972); 8: Uye (1982); 9: Bailey et al. (1995); 10: Donnelly et al. (1993); 11: Childress and Nygaard (1974); 12: Omori (1978); 13: Bailey et al. (1994); 14: Iguchi and Ikeda (1998); 15: Ikeda and Mitchell (1982); 16: Robison (1989); 17: Ikeda and Hirakawa (1998); 18: Hirota (1981); 19: Oh (1992); 20: Omori (1969)

Generally speaking, the carbon and nitrogen contents of myctophid muscle tissue were high, both for migratory and non-migratory species. The C+N content per unit dry weight of the muscle tissue of members of the genus *Cyclothone* were lower than those of both migratory and non-migratory myctophids (Fig.4). Submersible observations (Hunt and Lindsay, unpublished data) have found individuals of the genus *Cyclothone* to be relatively immobile in the water column, fluttering weakly upon collision with the submersible's bow wake. In contrast, the myctophid species that have been observed showed high levels of swimming activity. This correlates well with the observed elemental compositions of their muscle tissues. The lower C+N content per unit dry weight in the shallower dwelling *C. alba* and *C. pseudopallida*

of 20-24mm SL than in the deeper-dwelling congeners may be a reflection of a lower availability of food in the 300-500m layer than in the layers below 500m.

Apart from *Vampyroteuthis infernalis*, the lowest percentages of C+N per unit dry weight were found in surface-dwelling planktonic crustaceans (Fig.5). Energy in such organisms is channelled into reproduction and growth rather than being stored as food reserves to cope with an intermittent food supply, as in the deeper living copepods. The high C+N content of most of the deep-living shrimps may also be a reflection of this energy storing strategy (Fig.5). *Neocalanus cristatus*, previously a surface-dwelling copepod, is in diapause and seems to have used up a considerable proportion of its energy reserves (Fig.5).

Of the two piscivorous stomiid fish species that were analyzed, *Stomias affinis* exhibited a low C+N content per unit dry weight, lower than that of the deep-dwelling *Cyclothone* species (Fig.5). The C+N contents per unit dry weight of *Chauliodus sloani* were higher than those of *Cyclothone* but lower than those of all myctophids. Both exhibited high water content in their muscle tissues and the low C+N content of the muscle tissue of these species is even more apparent when plotted against wet weight (Fig.6). The stomiid fishes that have been seen from submersibles in Japanese waters have invariably been in fishing position, immobile with the first dorsal ray extended over the mouth in *C. sloani* and immobile with the chin barbel waving before the mouth in *S. affinis*, only moving when disturbed by the submersible (Hunt and Lindsay, unpublished data). The high water contents and low nitrogen and carbon contents per unit wet weight (Table 2, Fig.6) of body muscle tissue correlate well with this "lie in wait" predation strategy as, although jaw and lure muscles would need to be highly developed, the ability to give chase over long distances would presumably be unnecessary. The

water content of *S. affinis* muscle tissue is lower than that of *C. sloani* (Table 2), as would be expected from the data on vertical distributions gained in this study. As *C. sloani* does not migrate, its muscle tissue need not be as highly developed as *S. affinis*, which has been found to migrate asynchronously (unpublished data, Sutton and Hopkins 1996). In contrast, the elemental composition of *Borodina infans* muscle tissue is high in both carbon and nitrogen (Fig.5) which suggests that rather than employing a "lie in wait" strategy, it chases its prey down actively. Rapid movement of *B. infans* upon disturbance has been observed from a submersible (unpublished data).

The total muscle tissue of the archaic cephalopod *Vampyroteuthis infernalis* has an extremely low C+N content, both in terms of dry and wet weights (Table 2, Figs.5, 6). This is probably due to a large proportion of "muscle tissue" wet weight being composed of a soft, gelatinous, non-muscular tissue, as reported by Young (1964). Low C+N content was also found in the arm muscle of *V. infernalis* by Robison (1989) and the

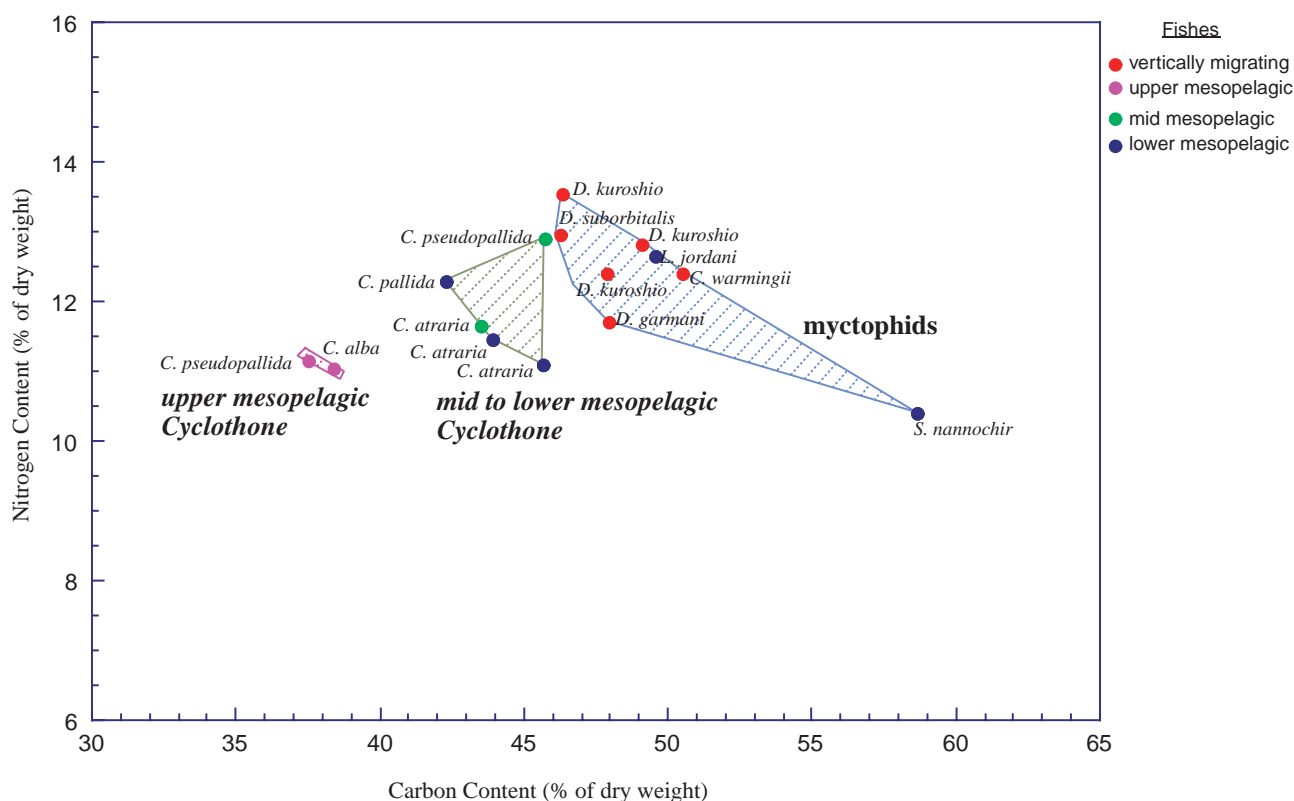


fig. 4 Comparison of nitrogen and carbon contents of muscle tissue from the bristlemouth fishes *Cyclothone* and myctophid fishes taken at Station P, Sagami Bay, on 25 May 1995.

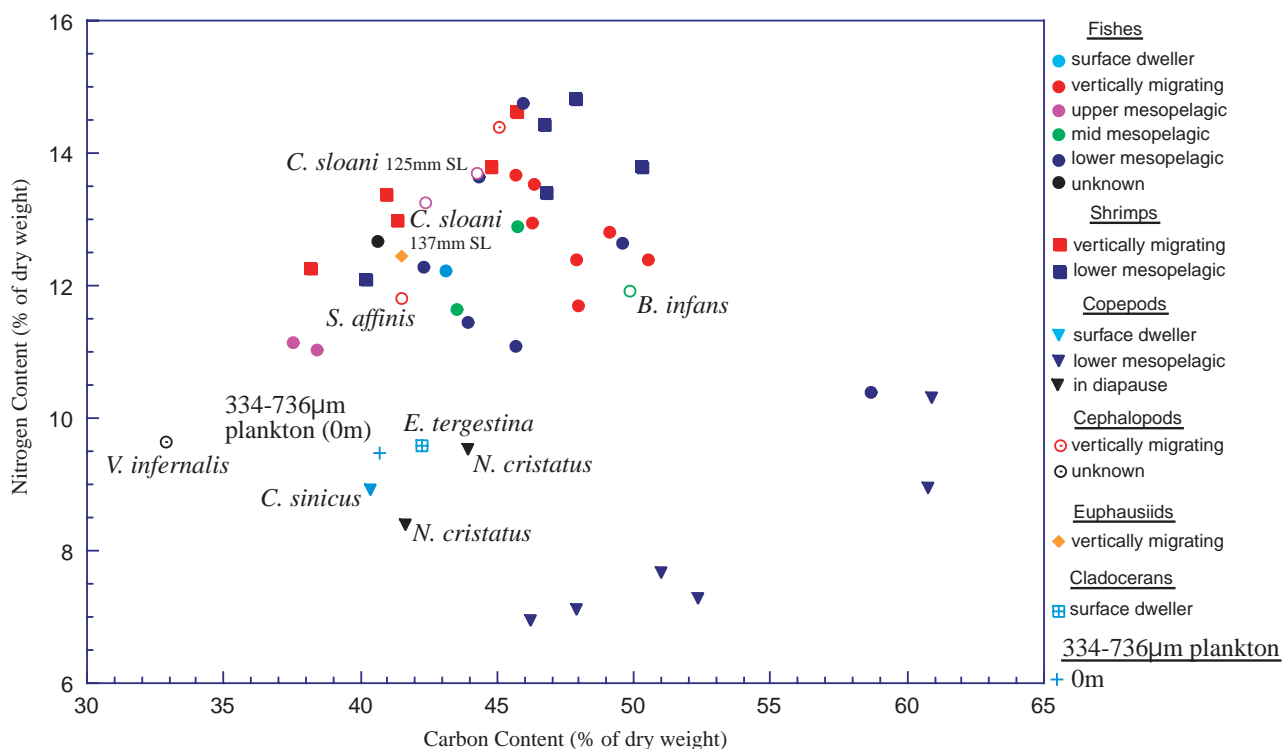


fig. 5 Comparison of the nitrogen and carbon contents of zooplankton (analyzed whole) and micronekton (muscle tissue) taken at Station P, Sagami Bay, on 25 May 1995.

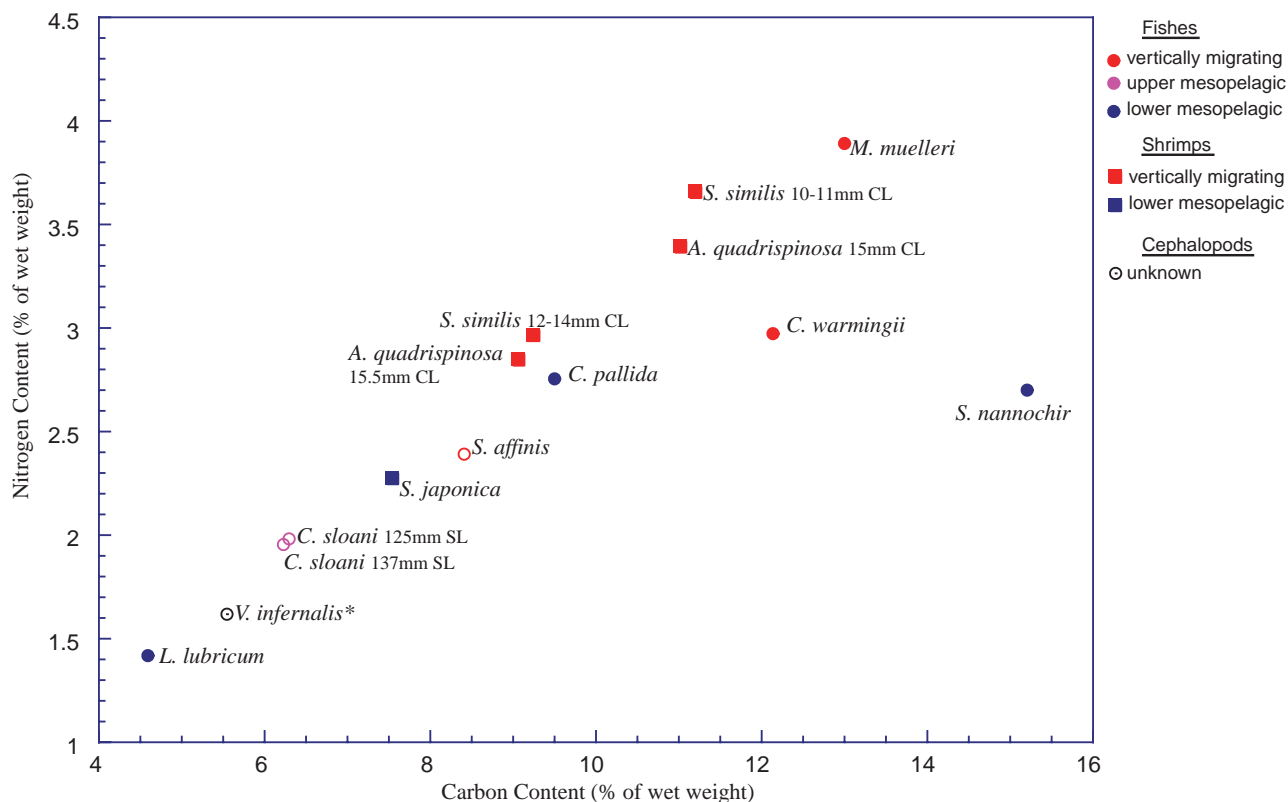


fig. 6 Comparison of the nitrogen and carbon contents of muscle tissue from micronekton taken at Station P, Sagami Bay, on 25 May 1995. Values are expressed as percentage of wet weight. Unfilled circles denote that the vertical distribution pattern is proposed but not certain. Asterisk indicates that the %H<sub>2</sub>O value was taken from Robison (1989).

results of the present study show that his data probably also hold for the total muscle tissue mass. The most common items in the guts of *V. infernalis* are copepods (Young 1964) and Hunt (1996) has reported that it uses its luminescent arm-tip organs and possibly a luminescent, mucoidal ejecta, to feed on small crustaceans. It also drags one of two sensory filaments behind it and, upon sensing a prey item, slowly circles and envelops it (Hunt 1996). The most common type of defence behaviour in *V. infernalis* that includes locomotion involves swimming at a relatively quick pace and turning the body sharply, with an arm tip flash just before the turn (Hunt 1996). Neither this escape behaviour nor the feeding behaviour described above requires a high degree of muscle activity and the low C+N and high water contents in the muscle tissues of this cephalopod confirm this. Furthermore, this species inhabits the oxygen minimum layer (Hunt 1996), where a low C+N content of muscle tissue would be metabolically advantageous. It is also not thought to undertake a diel vertical migration (Hunt, personal communication), which is a muscularly demanding undertaking for an organism without a swim bladder or large lipid deposits. Ecological observations and elemental composition data therefore show a high degree of consistency.

## Conclusions

Trends in the elemental compositions of midwater organisms were clearer when expressed in terms of wet weight (Fig.6) and it is therefore recommended that in future studies the water contents of the tissues involved should be determined before analysis. The analysis of elemental compositions for both whole organisms and the muscle tissue alone is encouraged, as the information so gained may illuminate different aspects of the organism's ecology.

## Acknowledgements

We thank Drs. Koh Kawaguchi and Shuhei Nishida from the Ocean Research Institute, University of Tokyo, for their support. We sincerely thank the captain and crew of the R/V *TanseiMaru* and R/V *Natsushima* as well as the operations team of the *Shinkai 2000* for their dedicated efforts.

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(Manuscript received 22 November 2002)

