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## Morphological Comparison of Feeding Appendages of *Calanus* and *Neocalanus* Copepods

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### Abstract

Morphological comparison of feeding appendages was made for copepods dominating in some regions in world oceans; including *Calanus finmarchicus* (C6 females) and *C. hyperboreus* (C6 females) in the subarctic Atlantic, *C. marshallae* (C5), *C. pacificus* (C6 females), *Neocalanus plumchrus* (C1–C5) and *N. flemingeri* (C2–C5), and *N. cristatus* (C1–C5) in the subarctic Pacific, and *N. tonsus* (C5 and C6 females) in the subantarctic Pacific. Cluster analysis based on the length measurements of 11 parts of the appendages revealed admixture of four distinct groups (Group A to D). Of the four groups, the two (Groups A and C) are for *Calanus* spp. and the other two (B and D) are for *Neocalanus* spp. The two groups of each genus are characterized by smaller (Groups A and B) and larger (C and D) appendages relative to the prosome length. Possible functional relationships between the relative size of appendages and feeding activity, growth rate and generation length are discussed.

**Key words:** Feeding appendages, Copepods, Calanidae, *Calanus*, *Neocalanus*

### Introduction

Copepods belonging to the genera *Calanus* and *Neocalanus* (Calanoida: Calanidae) include large-sized species and are the dominant component of zooplankton biomass in high latitude seas. For example, *Calanus finmarchicus* alone occupy 40–80% of copepod biomass at OWS I in the North Atlantic (Williams and Conway, 1988), *Neocalanus* spp. together with *Eucalanus bungii* make up 70–80% of the zooplankton biomass in summer of the Bering Sea (Heinrich, 1962). Because of such the high abundance and large body size, Calanidae copepods are considered to exert a significant impact on the structure of food webs through their grazing on microplankton (Harris, 1996), predation by animals at higher trophic levels (Beamish et al., 1999), and mediating vertical fluxes of biogenic particulate and dissolved materials (cf. Morales, 1999; Bradford-Grieve et al., 2001).

Calanidae copepods have been known as omnivores, and feed on a wide size-spectrum of organisms occurring in nature (Gifford, 1993; Harris, 1996). Morphology of feeding appendages of Calanidae is considered to be evolved to suit capturing small particles (Anraku and Omori, 1963; Arashkevich, 1969; Minoda, 1971). Functional relationships between mouth part morphology and feeding patterns have been studied on sympatric *Calanus* (*C. tenuicornis* and *C. lighti*; Mullin, 1969)

and *Neocalanus* species (*N. robustior* and *N. gracilis*; Mullin and Evans, 1976). Since the feeding mechanism of the species within the family Calanidae appears to be more or less similar, the size of mouthparts might bear a more direct relationship to their preference for foods, i.e., larger mouthparts being necessary to feed on larger particles (Mullin, 1969; Mullin and Evans, 1976). On this basis, we compared mouthpart morphology of a total of 20 copepodid stages of 8 Calanidae copepods: e.g., *Calanus finmarchicus* (Gunnerus) and *C. hyperboreus* Krøyer from the North Atlantic; and *Calanus pacificus* Brodsky, *C. marshallae* Frost, *Neocalanus plumchrus* (Marukawa), *N. flemingeri* Miller, and *N. cristatus* (Krøyer) from the subarctic Pacific and *Neocalanus tonsus* (Brady) from the subantarctic Pacific. While morphological differences between the genera *Calanus* and *Neocalanus* are subtle (Bradford and Jillett, 1974) the validity of the separation has been supported by the recent nucleotide sequence data of nuclear 18S rDNA and mitochondrial 16S rDNA genes (Taniguchi et al., unpublished data).

### Materials and Methods

Details about samplings of the specimens of 4 *Calanus* spp. and 4 *Neocalanus* spp. are given in Table 1. The specimens were preserved with 5% borax-buffered formalin. A total of 20 copepodid stages of 8

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Table 1 Sampling data of copepods analyzed. Abbreviations of species (Abb.) are shown in the parentheses. Observed copepodid stages are indicated by open circles.

| Calanus/<br>Neocalanus | Abb. | Date         | Location       | Position          | Depth (m) | Net      | Copepodid stage |    |    |    |    |     |     |
|------------------------|------|--------------|----------------|-------------------|-----------|----------|-----------------|----|----|----|----|-----|-----|
|                        |      |              |                |                   |           |          | C1              | C2 | C3 | C4 | C5 | C6F | C6M |
| <i>C. finmarchicus</i> | (Cf) | 24 Sep/ 2000 | Barents Sea    | 76°26'N, 22°00'E  | 0-235     | WP2      |                 |    |    |    |    |     | ○   |
| <i>C. hyperboreus</i>  | (Ch) | 23 Sep/ 2000 | Barents Sea    | 76°52'N, 20°00'E  | 0-150     | WP2      |                 |    |    |    |    |     | ○   |
| <i>C. marshallae</i>   | (Cm) | 11 Jul/ 1995 | Gulf of Alaska | 58°40'N, 145°00'W | 0-150     | NORPAC   |                 |    |    |    |    |     | ○   |
| <i>C. pacificus</i>    | (Cp) | 30 Oct/ 1995 | NW Pacific     | 42°00'N, 141°30'E | 0-450     | NORPAC   |                 |    |    |    |    |     | ○   |
| <i>N. cristatus</i>    | (Nc) | 4 Jun/ 1997  | NW Pacific     | 41°30'N, 145°47'E | 0-500     | PCP      | ○               | ○  | ○  | ○  | ○  |     |     |
| <i>N. flemingeri</i>   | (Nf) | 4 Jun/ 1997  | NW Pacific     | 41°30'N, 145°47'E | 0-500     | PCP      |                 | ○  | ○  | ○  | ○  |     |     |
| <i>N. plumchrus</i>    | (Np) | 4 Jun/ 1997  | NW Pacific     | 41°30'N, 145°47'E | 0-500     | PCP      | ○               | ○  | ○  | ○  | ○  |     |     |
| <i>N. tonsus</i>       | (Nt) | 17 Oct/ 1996 | SW Pacific     | 45°46'N, 171°02'E | 0-80      | 1 m ring |                 |    |    |    | ○  | ○   |     |

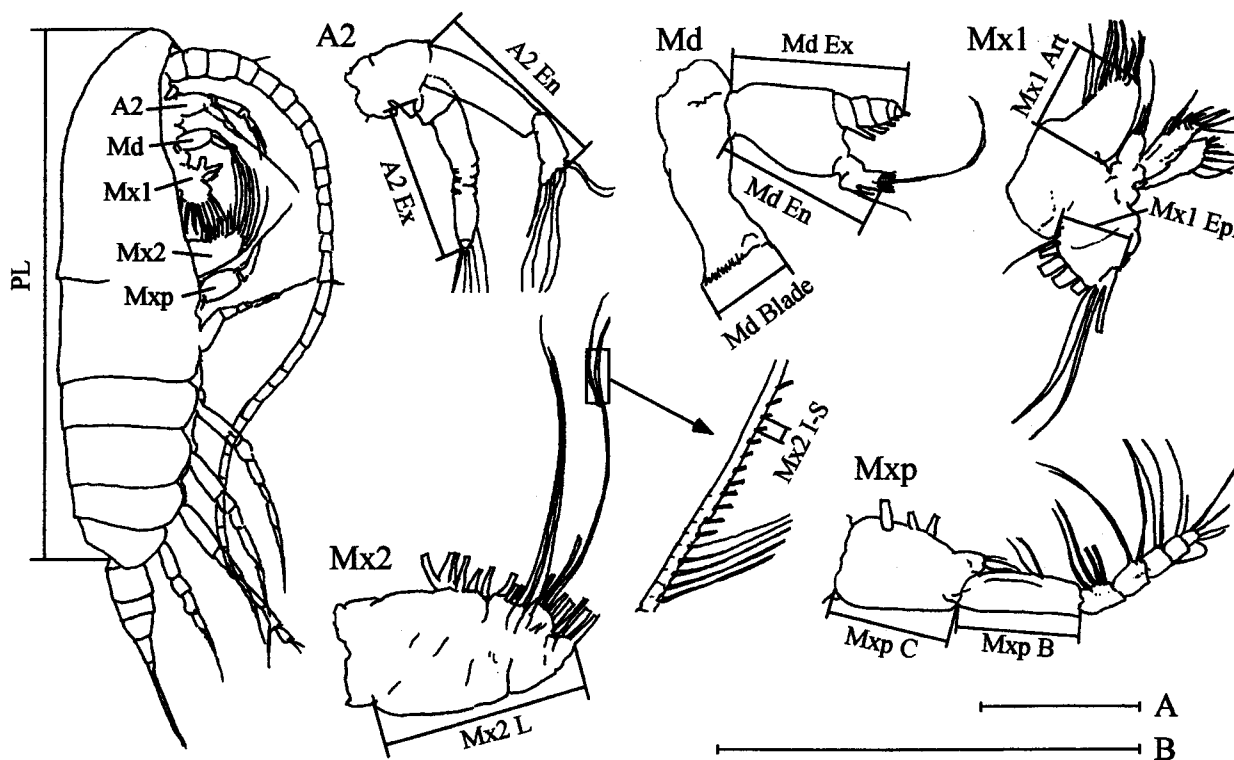


Fig. 1. Diagrams showing the prosome length (PL) and 11 parts of feeding appendages measured for interspecific comparisons (abbreviations are shown in the parentheses): A2 endopods (A2 En), A2 exopods (A2 Ex), Md cutting blade (Md Blade), Md endopods (Md En), Md exopods (Md Ex), Mx1 arthrite (Mx1 Art), Mx1 epipodite (Mx1 Epi), length of Mx2 (Mx2 L), inter-seta spacing of near the tip of strong spine on Mx2 basis (Mx2 I-S), Mxp coxa (Mxp C), and Mxp basis (Mxp B). Scale bar (both in 1 mm) A is for whole body (*Neocalanus plumchrus* C5) and B for feeding appendages (except for strong spine on Mx2 basis).

species (*Calanus finmarchicus*, *C. hyperboreus*, *C. marshallae*, *C. pacificus*, *Neocalanus cristatus*, *N. flemingeri*, *N. plumchrus*, and *N. tonsus*) were selected for this study (Table 1). For *Calanus* species and *N. tonsus* only C5 or C6 females were observed because of insufficient numbers of the other stages. For the North Pacific sympatric *Neocalanus* spp. (*N. flemingeri*, *N. plumchrus*, and *N. cristatus*) C1 to C5 specimens were examined. It is noted that C6F and C6M stages of these three species have reduced feeding appendages (cf. Miller, 1988) thereby no observation was made for these

stages. C1 of *N. plumchrus* could not be distinguished from that of *N. flemingeri* morphologically (Tsuda et al., 1999).

Five specimens for each copepodid stage were selected arbitrary, and their prosome lengths (PL) were measured under a dissecting microscope with eye-piece micrometer to the nearest 50  $\mu$ m, then their Antenna (A2), Mandible (Md), Maxillule (Mx1), Maxilla (Mx2), and Maxilliped (Mxp) were dissected off (Fig. 1). Each feeding appendage was mounted on slides in gum-chloral. Under a light microscope, the linear dimension of

11 parts of the feeding appendages (Fig. 1) was read using a digital microscopic software "Mac Scope" (Mitani Corporation Co. Ltd) with a precision of 0.24 to 2.4  $\mu\text{m}$  (depend on the magnification between 40x and 400x). Terminology used in this study is followed that

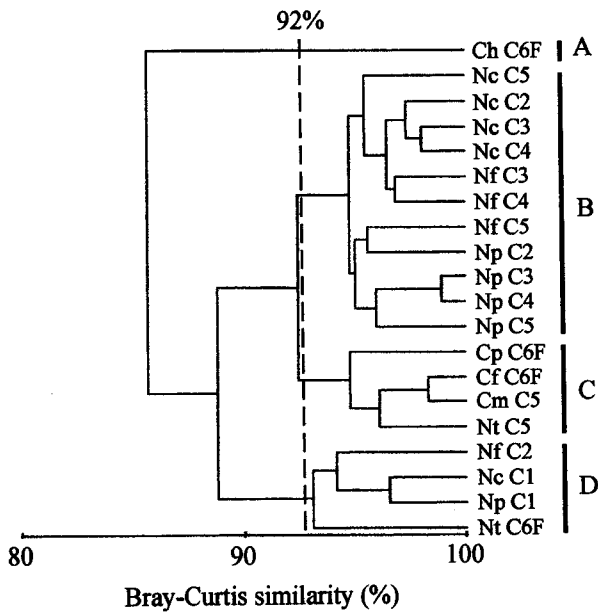


Fig. 2. Results of cluster analyses based on Bray-Curtis similarity indices (%) of feeding appendages of *Calanus* and *Neocalanus* copepods. Four Groups (A, B, C, and D) are identified at the similarity of 92%. For species abbreviation, see Table 1.

of Mauchline (1998), and the measured 11 parts of the appendages include (abbreviations in the parentheses): A2 endopods (A2 En), A2 exopods (A2 Ex), Md cutting blade (Md Blade), Md endopods (Md En), Md exopods (Md Ex), Mx1 arthrite (Mx1 Art), Mx1 epipodite (Mx1 Epi), length of Mx2 (Mx2 L), inter-seta spacing of near the tip of strong spine on Mx2 basis (Mx2 I-S), Mxp coxa (Mxp C), and Mxp basis (Mxp B) (Fig. 1).

The linear dimension data of each part of feeding appendages were expressed as the proportion to the PL (each length [ $\mu\text{m}$ ]/PL [mm]) of the same specimens (Mullin, 1969; Mullin and Evans, 1976). Since the differences between the readings of left and right appendages of the same specimens were not significant ( $p > 0.05$ , paired  $t$ -test), a total of 10 data (= left and right parts of 5 specimens) were pooled for each stage of a given species to calculate a mean. Using the mean values thus derived, intra- and inter-specific differences were examined by cluster analysis in conjunction with the Bray-Curtis similarity index (Field et al., 1982). In these analyses, log transformation [ $\log_{10}(X+1)$ ] of variable ( $X$ ) is a common practice to reduce the bias due to extremely abundant species and to eliminate zero values. However, no transformation was made in this study since the variances of the data were relatively stable.

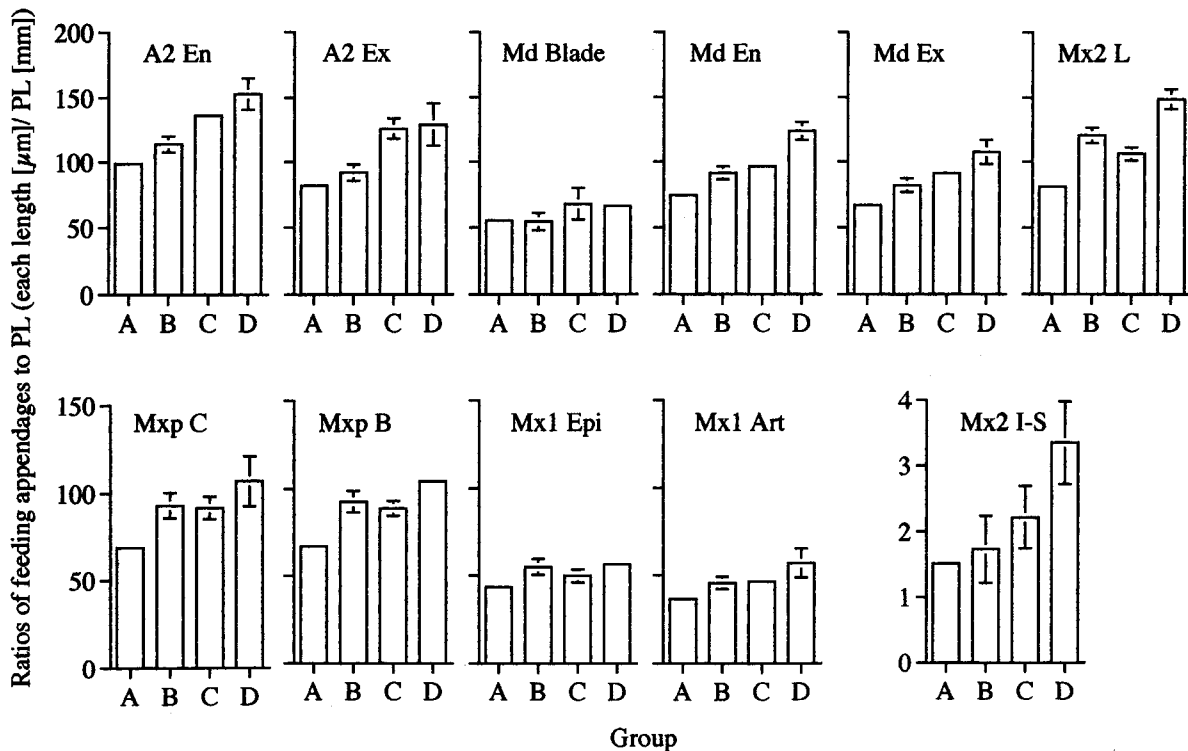


Fig. 3. Ratios of feeding appendage length to prosome length in each cluster group. Bars indicate 1 standard deviations. Abbreviations of feeding appendages are shown in Fig. 1.

## Results

The prosome length of various copepodid stages of 4 *Calanus* and 4 *Neocalanus* spp. ranged from 0.70 mm (*N. plumchrus* C1) to 7.02 mm (*N. cristatus* C5) (data not shown). The linear dimension of each appendage part relative to the PL (each length [ $\mu\text{m}$ ]/PL [mm]) ranged from 98.7 to 167.9 for A2 En, 81.9 to 156.5 for A2 Ex, 47.4 to 87.0 for Md Blade, 74.3 to 132.8 for Md En, 67.0 to 121.2 for Md Ex, 36.5 to 66.0 for Mx1 Art, 43.6 to 61.9 for Mx1 Epi, 81.2 to 160.8 for Mx2 L, 0.84–4.00 for Mx2 I-S, 68.9 to 122.2 for Mxp C, and 67.0 to 106.6 for Mxp B. Thus the variability of the linear dimension relative to the PL was the greatest for Mxp I-S (variations in 4.8 times) among the other parts (1.4–2.0 times).

Cluster analysis based on the relative dimensions of 11 parts of these feeding appendages revealed a high similarity within a total of 20 copepodid stages of 8 species (87% similarity, Fig. 2), confirming that the feeding pattern of the species of Calanidae is similar as a whole (cf. Marshall, 1973). However, they could be separated into four species/stage groups at the similarity level of 92% (dashed line, Fig. 2). The species designated to Group A was *Calanus hyperboreus* C6F whose feeding appendages are all small (Fig. 3). Group B was composed of *Neocalanus cristatus* C2–C5, *N. flemingeri* C3–C5, and *N. plumchrus* C2–C5 whose feeding appendages are medium size. Group C contained *C. pacificus* C6F, *C. finmarchicus* C6F, *C. marshallae* C5, and *N. tonsus* C5, all of which are featured by having larger A2, Md and Mx2 I-S (Fig. 3). Group D was consisted of C1 and C2 stages of *Neocalanus* spp. and *N. tonsus* C6F; all of them equipped with the largest feeding appendages (Fig. 3).

The proportion of Mx2 I-S to PL was consistently greater in early copepodid stage in a given species (Figs. 2 and 3). This indicates that the smaller developmental changes in Mx2 I-S relative to that in the PL. Since the intersetule distance of maxillary setae is indicative of the size of particles that can be removed from the water (Marshall, 1973; Frost et al., 1983), the absolute dimension ( $\mu\text{m}$ ) of Mx2 I-S of each stage of *Calanus* or *Neocalanus* spp. were presented as Fig. 4. It is noted that the inter-setae distance of Mx2 increased progressively with development within the species, with an exception for C5 of *Neocalanus cristatus* (Fig. 4). Sympatric pairs (*Calanus finmarchicus* and *C. hyperboreus* in the North Atlantic, and *N. cristatus*, *N. flemingeri* and *N. plumchrus* in the North Pacific) showed some differences in Mx2 I-S. In the North Pacific species, Mx2 I-S was the smallest for *N. plumchrus* and largest for *N. cristatus* with *N. flemingeri* being between the two. The inter-setae distances of *C.*

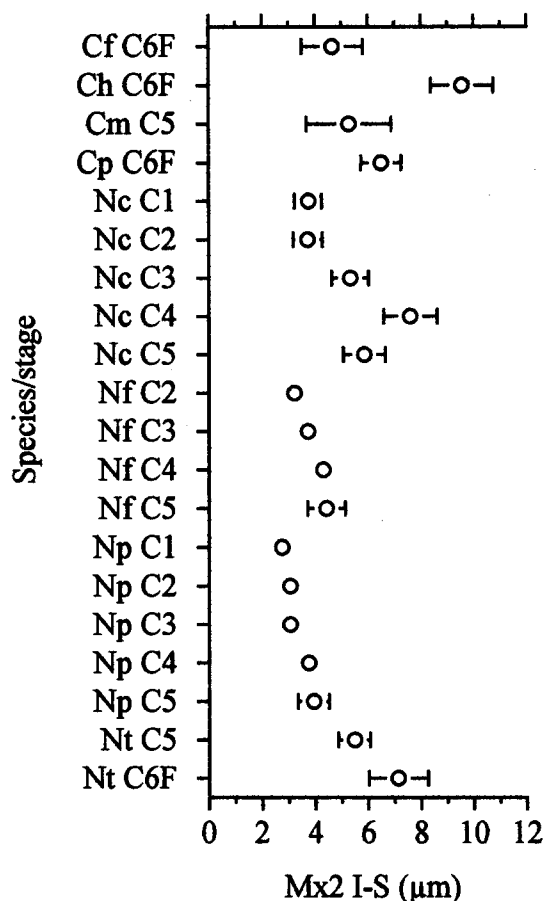


Fig. 4. Between species/stages comparison of inter-seta spacing at near the tip of strong spine on Mx2 basis (Mx2 I-S). Circles and horizontal bars denote means and 1 standard deviations. For species abbreviation, see Table 1.

*marshallae*, *C. pacificus* and *N. tonsus* were relatively large (5–8  $\mu\text{m}$ ) as compared with those of large-sized *N. flemingeri* and *N. plumchrus* ( $\leq 5 \mu\text{m}$ )

## Discussion

The present cluster analysis based on the linear dimensions of 11 parts of the feeding appendages identified successfully four distinct groups (Fig. 2). All copepodids of *Calanus* spp. were classified into Groups A and C, and those of *Neocalanus* spp. were into Groups B and D (as only exception *N. tonsus* C5 was designated as Group C). Group C, to which three *Calanus* species *C. pacificus* C6F, *C. finmarchicus* C6F, and *C. marshallae* C5 classified, is characterized by relatively large feeding appendages and large inter-setae of Maxilla (Fig. 3). These *Calanus* species and *Neocalanus tonsus* are known to have relatively shorter generation time; 2–3 generations per year for *C. pacificus* (depending geographical locations, cf. Osgood and Frost, 1994), 1–4 generations per year for *C. finmarchicus* (Conover,

Table 2 Results of statistical tests (one-way ANOVA and Fisher's PLSD) between groups. Any two groups not underscored by the same line are significantly different. Significant levels: \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ ; ns, non-significant.

| Feeding appendages | F of one-way ANOVA | Multiple comparisons by Fisher's PLSD* |   |   |   |
|--------------------|--------------------|--|---|---|---|
| A2 En              | 28.33***           | A                                      | B | C | D |
| A2 Ex              | 20.66***           | A                                      | B | C | D |
| Md Blade           | 3.73*              | B                                      | A | D | C |
| Md En              | 38.85***           | A                                      | B | C | D |
| Md Ex              | 17.66***           | A                                      | B | C | D |
| Mx1 Art            | 6.68**             | A                                      | B | C | D |
| Mx1 Epi            | 3.94*              | A                                      | C | B | D |
| Mx2 L              | 9.50***            | A                                      | C | B | D |
| Mx2 I-S            | 8.07**             | A                                      | B | C | D |
| Mxp C              | 4.64*              | A                                      | C | B | D |
| Mxp B              | 13.14***           | A                                      | C | B | D |

1988), 1–3 generations per year for *C. marshallae* (Osgood and Frost, 1994), and 2 generations per year for *N. tonsus* (Jillett, 1968). To maintain multi-generations per year, relatively large feeding appendages seen in these copepods in this study are apparent advantage to secure efficient food intake. The egg production of *C. finmarchicus* takes place in females after their upward ontogenetic migration, and is generally fueled by freshly ingested food (cf. Hirche, 1996). However, some females are known to have potential to produce eggs using stored energy as in *N. tonsus*, e.g. overwintered females are able to spawn without feeding (Ohman et al., 1989). Feeding near the surface layer is known to be an essential event to initiate reproduction of *C. marshallae* and *C. pacificus* (Osgood and Frost, 1994).

Group D, in which only *Neocalanus* spp. are included, is characterized by stage/species with largest feeding appendages (Table 2). Since the feeding appendages are significantly larger than those of other stages/species compared, extremely high feeding potentials may be the case for these stages. This is not surprising since the specific rates of growth, metabolism, and then feeding across all copepodid stages are often highest at C1 for marine pelagic copepods (cf. Mauchline, 1998). From this view point, C6F of *N. tonsus* in Group D is of special interest. *N. tonsus* C6 females from the subantarctic ocean are an active suspension feeder (Ohman, 1987), contrast to cease-feeding of C6 females of the three *Neocalanus* (*N. plumchrus*, *N. flemingeri*, and *N. cristatus*) from the subarctic Pacific. Ohman

(1987) noted that there are inter-specific differences in morphology of feeding appendages: upon molting to the C6F the Md, Mx1, Mx2, and Mxp of *N. tonsus* all enlarge, in association with elongation of the setae on it. The mandibular blade of *N. tonsus* females also enlarges retaining crisp dentition (Tanaka, 1956; Vervoort, 1957). These phenomena were also confirmed in the present study (Table 2). As a marked contrast, the terminal molt to C6F of *Neocalanus* in subarctic species is accompanied by the reduction in size and setation of the Mx1, Mx2, and Mxp and a complete loss of the cutting blade of the Md (Campbell, 1934; Tanaka, 1956), and their C6F do not feed (Fulton, 1973).

As only species classified to Group A, the response of spawning *Calanus hyperboreus* to feeding is somewhat similar to that reported for *Neocalanus tonsus*. *C. hyperboreus* females could release eggs in the absence of particulate food, but the highest egg viability is achieved in the presence of food (Conover 1967). However, the present cluster analysis resulted *C. hyperboreus* being distant group from *N. tonsus* (Fig. 2). *C. hyperboreus* C6F is featured by significantly smaller feeding appendages (Fig. 3). Since the species repeating multi-generation per year equip with relatively large feeding appendages, the smaller feeding appendages of *C. hyperboreus* may be related with their long generation time (2–4 years; Hirche, 1997). Their slower growth rates may be reflected by the small feeding appendages of this species or vice versa.

All mid- and late copepodid of *Neocalanus* spp. (*N. cristatus*, *N. flemingeri*, and *N. plumchrus*) in the subarctic Pacific are classified to Group B. As a common life history trait, these *Neocalanus* spp. reduce mandibles at C6F and reproduce by utilizing stored lipids as the sole energy source (Conover, 1988). These *Neocalanus* spp. repeat one generation per year, thereby shorter than the species in Group A, but longer than those in Group C. Among these three *Neocalanus* spp. between-species differences can be seen for some parts of feeding appendages (Fig. 2); the proportion of Mx2 length of *N. plumchrus* is much larger than those of other *Neocalanus* spp. Miller (1988) mentioned that the difference in the mechanics of feeding between *N. flemingeri* and *N. plumchrus* is implied by the difference in the structure of their Mx2. Similar sized sympatric *N. flemingeri* and *N. plumchrus* are known to achieve niche separation by a difference in seasonal timing (Miller and Clemons, 1988). *N. flemingeri* passes through its late copepodid stages earlier in spring than does *N. plumchrus* with little overlap of the periods in which each species is predominantly in the largest, heavily feeding, and ecologically dominant C5 stage (Miller and Clemons, 1988; Tsuda et al., 1999). Large

*N. cristatus* are overlapped their developmental season with *N. flemingeri* and *N. plumchrus*. However, since the Mx2 I-S of *N. cristatus* is larger than them (Fig. 4), feeding niche separation may allow them to occur in the same season. Spatial separation in vertical distribution of these species is also has a function of relaxation of competition of these sympatric species (Mackas et al., 1993).

Compared with description-oriented studies on feeding appendages of copepods in the past (e.g. Anraku and Omori, 1963; Arashkevich, 1969; Minoda, 1971), the present results indicate clearly that cluster analysis based on Bray-Curtis similarity index is a powerful tool to differentiate copepodid stages of different copepod species into distinct groups. Four groups identified in this study could be interpreted by different magnitudes of feeding activity; all deduced from development stage-growth rate relationship, generation length, and feeding/spawning couplings of each copepod. The advantage of the present technique lies on the fact that information about feeding activity of a given copepodid stage can be obtained without feeding experiments. For example, greater feeding activities of *Neocalanus* C1 are expected than C2-C5 of the same species because of greater size of every feeding appendages of the former (Table 2). Possibly, feeding rates of copepods can be estimated by measuring feeding appendage indices if the relationship between feeding rates and feeding appendage indices is established in future study.

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#### Literature cited

- Anraku, M. and Omori, M. (1963) Preliminary survey of the relationship between the feeding habit and the structure of the mouth-parts of marine copepods. *Limnol. Oceanogr.*, **8**, 116-126.
- Arashkevich, Ye.G. (1969) The food and feeding of copepods in the northwestern Pacific. *Oceanology*, **9**, 695-709.
- Beamish, R.J., Leask, K.D., Ivanov, O.A., Balanov, A.A., Orlov, A.M. and Sinclair, B. (1999) The ecology, distribution, and abundance of midwater fishes of the subarctic Pacific gyres. *Prog. Oceanog.*, **43**, 399-442.
- Bradford, J.M. and Jillett, J.B. (1974) A revision of the generic definitions in the Calanidae (Copepoda, Calanoida). *Crustaceana*, **27**, 5-16.
- Bradford-Grieve, J.M., Nodder, S.D., Jillett, J.B., Currie, K. and Lassey, K.R. (2001) Potential contribution that the copepod *Neocalanus tonsus* makes to downward carbon flux in the Southern Ocean. *J. Plankton Res.*, **23**, 963-975.
- Campbell, M.H. (1934) The life history and postembryonic development of the copepods *Calanus tonsus* Brady and *Euchaeta japonica* Marukawa. *J. Biol. Res. Bd. Can.*, **1**, 1-65.
- Conover, R.J. (1967) Reproductive cycle, early development, and fecundity in laboratory populations of the copepod *Calanus hyperboreus*. *Crustaceana*, **13**, 61-72.
- Conover, R.J. (1988) Comparative life histories in the genera *Calanus* and *Neocalanus* in high latitudes of the northern hemisphere. *Hydrobiologia*, **167/168**, 127-142.
- Field, J.G., Clarke, K.R. and Warwick, R.M. (1982) A practical strategy for analyzing multispecies distribution patterns. *Mar. Ecol. Prog. Ser.*, **8**, 37-52.
- Frost, B.W., Landry, M.R. and Hassett, R.P. (1983) Feeding behavior of large calanoid copepods *Neocalanus cristatus* and *Neocalanus plumchrus* from the subarctic Pacific Ocean. *Deep-Sea Res.*, **30A**, 1-13.
- Fulton, J. (1973) Some aspects of the life history of *Calanus plumchrus* in the Strait of Georgia. *J. Fish. Res. Bd. Can.*, **30**, 811-815.
- Gifford, D.J. (1993) Protozoa in the diet of *Neocalanus* spp. in the oceanic subarctic Pacific Ocean. *Prog. Oceanog.*, **32**, 223-237.
- Harris, R.P. (1996) Feeding ecology of *Calanus*. *Ophelia* **44**: 85-109.
- Heinrich, A.K. (1962) On the production of copepods in the Bering Sea. *Int. Revue ges. Hydrobiol.*, **47**, 465-469.
- Hirche, H.-J. (1996) The reproductive biology of the marine copepod, *Calanus finmarchicus*- A review. *Ophelia*, **44**, 111-128.
- Hirche, H.-J. (1997) Life cycle of the copepod *Calanus hyperboreus* in the Greenland Sea. *Mar. Biol.*, **128**, 607-618.
- Jillett, J.B. (1968) *Calanus tonsus* (Copepoda, Calanoida) in southern New Zealand waters with notes on the male. *Aust. J. Mar. Freshwat. Res.*, **19**, 19-30.
- Mackas, D.L., Sefton, H., Miller, C.B. and Raich, A. (1993) Vertical habitat partitioning by large calanoid copepods in the oceanic subarctic Pacific during spring. *Prog. Oceanog.*, **32**, 259-294.
- Marshall, S.M. (1973) Respiration and feeding in copepods. *Adv. Mar. Biol.* **11**, 57-120.
- Mauchline, J. (1998) The biology of calanoid copepods. *Adv. Mar. Biol.*, **33**, 1-710.
- Miller, C.B. (1988) *Neocalanus flemingeri*, a new species of Calanidae (Copepoda: Calanoida) from the subarctic Pacific Ocean, with a comparative redescription of *Neocalanus plumchrus* (Marukawa) 1921. *Prog. Oceanogr.*, **20**, 223-273.
- Miller, C.B. and Clemons, M.J. (1988) Revised life history analysis for large grazing copepods in the subarctic Pacific Ocean. *Prog. Oceanog.*, **20**, 293-313.
- Minoda, T. (1971) Pelagic copepoda in the Bering Sea and the northwestern North Pacific with special reference to their vertical distribution. *Mem. Fac. Fish., Hokkaido Univ.*, **18**, 1-74.
- Morales, C.E. (1999) Carbon and nitrogen fluxes in the oceans: the contribution by zooplankton migrants to active transport in the North Atlantic during the Joint

- Global Ocean Flux Study. *J. Plankton Res.*, **21**, 1799-1808.
- Mullin, M.M. (1969) Distribution, morphometry, and seasonal biology of the planktonic copepods, *Calanus tenuicornis* and *C. lighti* in the Pacific Ocean. *Pac. Sci.*, **23**, 438-446.
- Mullin, M.M. and Evans, P.M. (1976) Distribution, morphometry, and seasonal biology of the planktonic copepods *Neocalanus robustior* and *Neocalanus gracilis* in the Pacific Ocean. *Pac. Sci.*, **30**, 119-130.
- Ohman, M.D. (1987) Energy sources for recruitment of the subantarctic copepod *Neocalanus tonsus*. *Limnol. Oceanogr.*, **32**, 1317-1330.
- Ohman, M.D., Bradford, J.M. and Jillett, J.B. (1989) Seasonal growth and lipid storage of the circumpolar, subantarctic copepod, *Neocalanus tonsus* (Brady). *Deep-Sea Res.*, **36A**, 1309-1326.
- Osgood, K.E. and Frost, B.W. (1994) Comparative life histories of three species of planktonic calanoid copepods in Dabob Bay, Washington. *Mar. Biol.*, **118**, 627-636.
- Tanaka, O. (1956) Further note on *Calanus tonsus* Brady, in Japanese waters. *J. Oceanogr. Soc. Japan*, **12**, 49-52.
- Tsuda, A., Saito, H. and Kasai, H. (1999) Life histories of *Neocalanus flemingeri* and *Neocalanus plumchrus* (Calanoida : Copepoda) in the western subarctic Pacific. *Mar. Biol.*, **135**, 533-544.
- Vervoort, W. (1957) Copepods from Antarctic and Subantarctic plankton samples. *B.A.N.Z. Antarct. Res. Exped. 1929-31. Rep. Ser. B (Zool. and Bot.)*, **3**, 1-160.
- Williams, R. and Conway, D.V.P. (1988) Vertical distribution and seasonal numerical abundances of the Calanidae in oceanic waters to the south-west of the British Isles. *Hydrobiologia*, **167/168**, 151-159.