

Planktivorous predation on copepods. Evaluation of mandible remains in predator guts as a quantitative estimate of predation

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ABSTRACT: Size and shape of mandibles from 8 common species of copepods in Norwegian coastal waters are described, with the aim of using gut contents of copepod mandibles as a precise technique of quantifying predation rates on copepods. The carapace length of 7 of the 8 copepod species could be closely predicted from a general linear regression equation of carapace length versus mandible width. The exception, *Temora longicornis*, had lower carapace length than expected from the equation. Similarly, the 6 copepodite stages of *Calanus finmarchicus* produced a highly significant species-specific linear regression equation between carapace length and mandible width, although adult males diverged somewhat by showing a lower carapace length than predicted. A correspondence analysis showed that it was impossible to separate all species and developmental stages from each other based on linear measurements of mandible structures alone, and the skill of a well-trained person is therefore needed. The relationship between individual dry weight and mandible width was well described by a regression equation, which hence could be used to calculate the biomass of consumed copepods, based on the contents of copepod mandibles in the predator's stomach. A comprehensive evaluation of the precision and accuracy in the estimates of prey mass is given, including effects of inter- and intra-specific variability and seasonal variation. By using a power function to regress body mass (mg dry weight) from mandible width (μm), the true prey biomass in the stomach content is estimated with a precision of $\pm 20\%$ or better, when based on more than a few mandibles. However, a considerable seasonal variation in the length/weight relationships of the prey copepods may cause considerable bias in the estimates if not compensated for

KEY WORDS: Planktivorous predation · Copepod mandibles · Gut contents · Predation measurements · Copepod prey · Predation-rate method

INTRODUCTION

The technique of analysing the stomach contents of a predator in order to define prey composition is widely used for marine animals, especially fish, seabirds and mammals. However, there are identification problems in cases where the predator tears the prey apart and when the identification is dependent upon the structure of soft tissues, which will gradually disintegrate in the stomach during the digestion process. Therefore prey identification will be most accurate if using an anatomical structure from the prey that is species-specific, highly inert to the digestion environment, and

small enough not to be broken apart during ingestion. For fish prey the otholith represents such a component, which consequently has been widely used for predators on fish. Copepods usually make up the main prey for invertebrate predators, and the prey is often torn apart during ingestion, making prey identification based on the size and shape of the whole body impossible. However, the copepod mandibles, which are composed of silica and chitin (Sullivan et al. 1975), are highly resistant. From stomach-content analyses of invertebrate predators it is known that the main part of copepod mandibles will withstand both the mechanical and chemical processes during feeding. Enumeration of such mandibles in predator stomach contents has therefore been used to quantify predation, especially for predation by krill (Stuart & Pillar 1990,

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Barange et al. 1991, Gibbons et al. 1991a, b), and chaetognaths (Øresland 1987, 1990, Falkenhaus 1991, Stuart & Verheye 1991, Gibbons 1992). Because the mandibles usually have a species-specific shape and size (Beklemishev 1959, Itoh 1970, Sullivan et al. 1975) it is also possible to identify the species. In this study we describe the mandibles of 8 common copepod species in Norwegian coastal waters, based on shape and size measurements. We also evaluate the method of estimating prey biomass from mandible occurrence in predator guts. Results from the method in practical use on krill species and an evaluation of some critical factors will be presented in a separate paper (Karlson & Båmstedt unpubl.).

MATERIAL AND METHODS

The copepods were collected in Raunefjorden (60° 16' N, 5° 11' E) south of Bergen, Norway. A conical net, 1 m diameter, 200 µm mesh size, equipped with a non-filtering cod end, was hauled vertically from 100 m to the surface. Samples were taken on 15 occasions in May, August, September and October 1992. The animals were kept alive in a 50 l tank and transported back to the laboratory within 2 h of collection. Copepods were sorted live under a stereo microscope (Wild M5) and only adult females from 8 of the most common species were used, except for *Calanus finmarchicus*, for which adult males and the 5 juvenile copepodite stages were also included. The carapace length was measured on fresh material, with 25 or 50× magnification, with a precision of 16 and 8 µm, respectively. The mandibles were then dissected free. Before microscopic slides were prepared, the mandibles were kept in glycerine/water (1/1) for 20 min and then dyed with methylene blue. Drawings of the mandibles were made by using a drawing tube connected to a Leitz, Dialux mod. 20, microscope. Mandible size was analysed using the Zeus Image Analysis System (ZIA, A/S Pixelwerks, Bergen; Estep & MacIntyre 1989). Four different morphometric measurements were made (Fig. 1). L_1 defines the total width of the toothed edge, whereas L_2 is the measured width at the base of the toothed edge. L_3 represent the height and L_4 the width of the ventral-most tooth, not including the tooth crown. Measurements were only made on the toothed edge of the mandible since mandibles in a predator's stomach are usually broken (pers. obs.). The siliceous tooth crowns (Beklemishev 1954) were not included in the measurements because they are worn down to varying degrees (Beklemishev 1959). All the morphometric data were used in a correspondence analysis (Braak 1986) in order to give a comprehensive overview. Tests on significant differences in the mor-

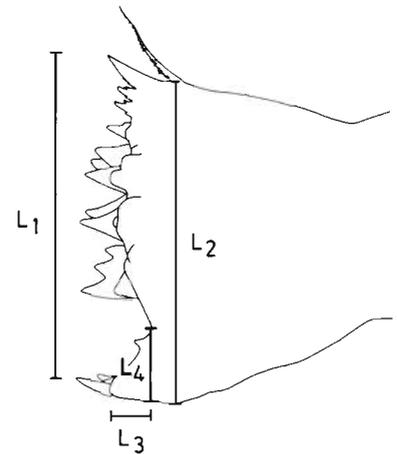


Fig. 1 Definition of the 4 length measurements (L_1 through L_4) performed on the copepod mandibles

phometric measurements were made by comparing the 95% confidence intervals of the means and defining significant difference as non-overlapping confidence intervals. In order to determine the relationship between individual dry weight and carapace length of *C. finmarchicus*, a group of 40 to 60 individuals of a given developmental stage was measured for individual carapace length, dried on a microscope slide for 2 h at 60°C and then weighed. Thus, individual variability in body size is given by the variance in carapace length, whereas individual dry weight is only given as a single value. The general relationship between individual dry weight and mandible width was calculated on the basis of all developmental stages of *C. finmarchicus* collected in August and 6 additional copepod species, ranging in dry weight from 28 to 278 µg. These were collected at the end of September and beginning of October, and between 9 (*Euchaeta norvegica*) and 71 (*Acartia* sp.) individuals were used in the single dry-weight measurement made on each species. A geometric mean functional regression (Ricker 1973) was used in addition to the standard regression in the size relationships calculated, but excluded in the presentations, as differences were minor.

RESULTS

Adult females from 8 species of copepods

The shape and size of the mandibles showed specific features in all species (Fig. 2, *Calanus finmarchicus* in Fig. 3). *Metridia longa* and *Metridia lucens* had very similar mandibular shapes but differed in size, as would be expected from their different body sizes. The mandibular width (L_1) of *M. longa* was on average 32% greater than that of *M. lucens*, parallel to a

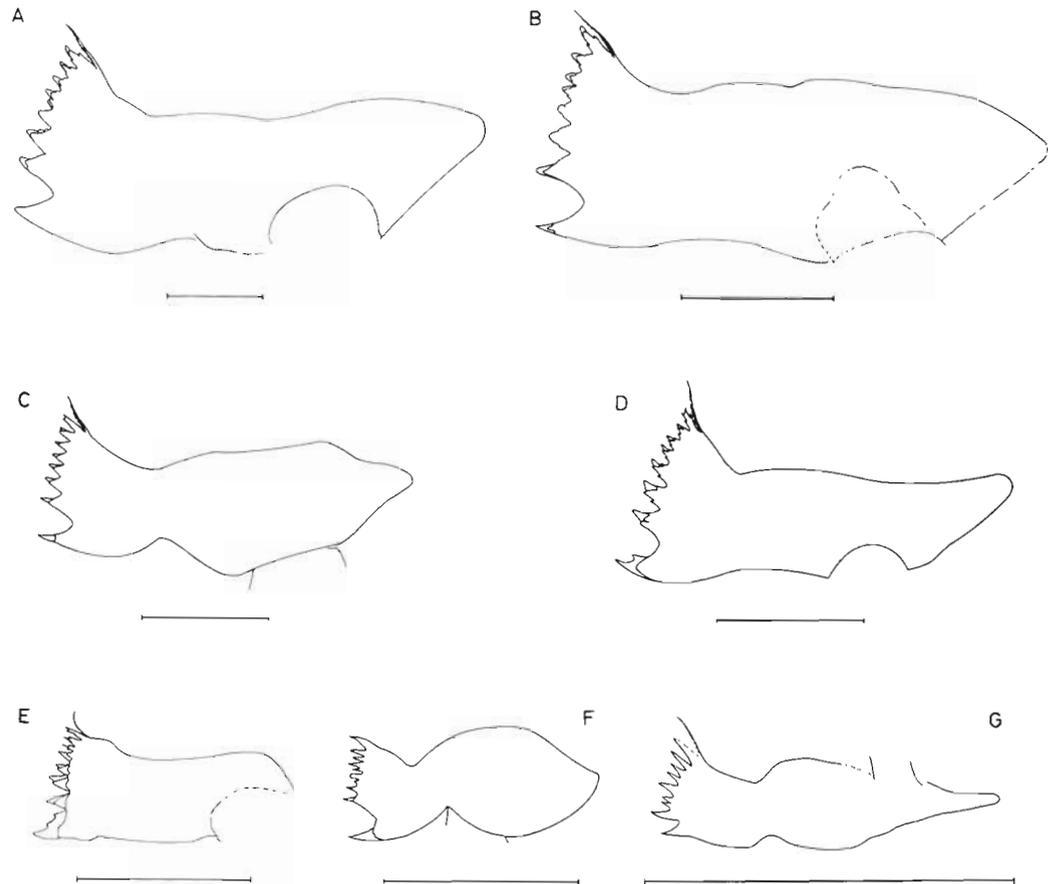


Fig. 2. Schematic drawings of the mandibles of 7 copepod species (adult females only), dissected from fresh specimens. Details shown only for the toothed edge. Scale bars = 100 μm . A = *Metridia longa*, B = *Metridia lucens*, C = *Centropages typicus*, D = *Temora longicornis*, E = *Pseudocalanus minutus*, F = *Acartia* sp., G = *Oithona* sp.

54% greater carapace length. The mandibular shape of *Temora longicornis* and *Centropages typicus* was somewhat similar to the 2 *Metridia* species, but the toothed edge (Fig. 2) and average size of the mandibles (Table 1) differed clearly. *Oithona* sp. was characteristic by its mandibular shape and small mandibular width (Fig. 2, Table 1). The 8 species were significantly different in their average mandibular width, in spite of similar carapace lengths for *T. longicornis*, *Pseudocalanus minutus* and *Acartia* sp. (Table 1). The correspondence analysis gave a full separation of *Pseudocalanus minutus* and *Oithona* sp. from the other species, partial separation by *T. longicornis* and *Acartia* sp., and complete mixing of the other 4 species. We therefore conclude that a correct species identification cannot be made from the 4 length measurements alone, but must be based also on the specific shapes (Figs. 2 & 3).

The average values for the 4 mandibular size measurements (L_1 through L_4) of the 8 copepod species were used as independent variables in estimating copepod carapace length from mandible size. All 4 variables were closely correlated with carapace length and a linear regression equation gave a coefficient of

determination varying between 0.843 and 0.853. By excluding *Temora longicornis* the regression was improved considerably, giving a coefficient of determination between 0.964 and 0.966. The mandibular width (L_1) was selected as the independent variable for further analysis, because it gave the best regression fit ($r^2 = 0.966$), was well defined in all species, and showed a relatively low variance within a species and significantly different average value for all the 8 species (Table 1). The linear equation describing this relationship, based on the mean values for the 7 species (excluding *T. longicornis*) was (Fig. 4):

$$Y = 0.0431 + 0.0112 X \quad r^2 = 0.966 \quad (1)$$

where Y = carapace length (mm); X = mandible width (μm).

The ratios between L_1 , L_2 , L_3 and L_4 showed some species-specific characters. *Pseudocalanus minutus* could be clearly defined by its exceptionally high L_1/L_3 and L_2/L_3 ratios, as well as its low L_3/L_4 ratio. In contrast, *Oithona* sp. was defined by its low L_1/L_3 and L_2/L_3 ratios, and high L_3/L_4 ratio. *Acartia* sp. was similar to *Temora longicornis*, but differed by showing somewhat lower L_1/L_4 , L_2/L_4 and L_3/L_4 ratios. *Metridia longa*,

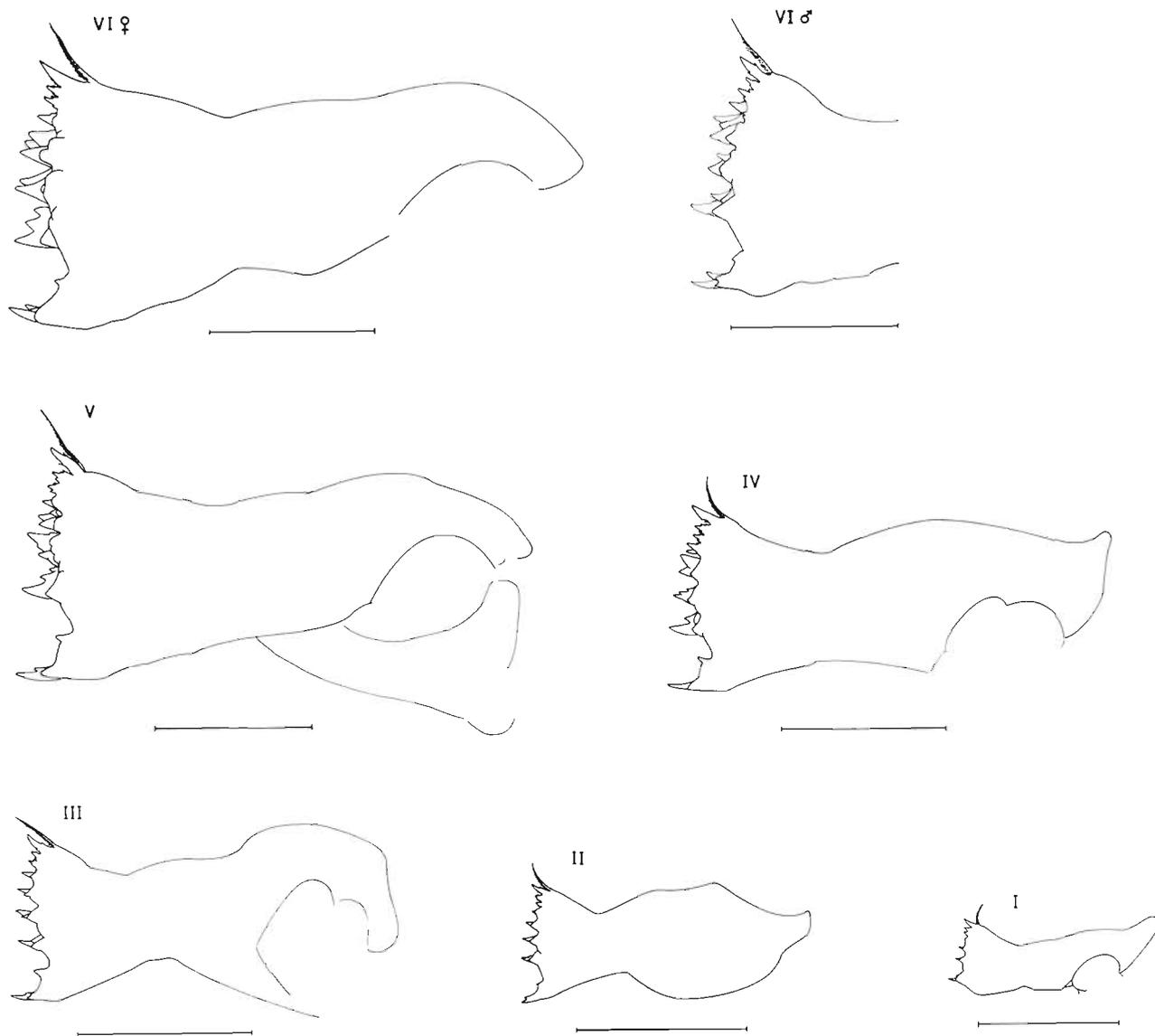


Fig. 3. *Calanus finmarchicus*. Schematic drawings of the mandibles of copepodite stages I to VI, with the adult sexes shown separately. Details shown only for the toothed edge. Scale bars = 100 μ m

M. lucens, *Calanus finmarchicus* and *Centropages typicus* could not be easily identified from any of the ratios given, but the absolute sizes of L_1 through L_4 (Table 1) as well as the general visual appearance (Fig. 2) gave enough criteria for a proper identification.

Copepodite stages of *Calanus finmarchicus*

From copepodite stage II through adulthood the shape of the mandibles of *Calanus finmarchicus* was relatively uniform, although the toothed edge became

more complex with age (Fig. 3). In copepodite stage I, a significantly smaller number of teeth had developed and the ventral-most tooth was less pronounced. All size parameters, L_1 through L_4 , showed significantly different mean values for copepodite stage I through IV and adult females, whereas adult males and stage V copepodites were not fully separated by these length measurements (Table 1). In a correspondence analysis, using the variables L_1 through L_4 , especially the younger copepodite stages occurred as separate clusters, whereas stage IV copepodites and older stages increasingly overlapped.

Table 1. Carapace length and defined mandible size characters (L₁ to L₄, see text) of adult females (ad. fem.) of 8 copepod species, and adult males (ad. male) and different developmental stages of *Calanus finmarchicus*. Average values, 95% confidence intervals and number of measurements are given

Species/stage	Carapace length (mm)		L ₁		L ₂		L ₃		L ₄		n
	Mean	95% CI	Mean	95% CI	Mean	95% CI	Mean	95% CI	Mean	95% CI	
<i>Metridia longa</i>	2.05	1.99–2.10	174.2	171.3–177.0	166.5	163.9–169.0	31.22	30.02–32.42	34.63	33.72–35.54	28
<i>Metridia lucens</i>	1.33	1.29–1.37	132.1	129.1–135.2	126.5	123.6–129.4	24.54	23.50–25.49	26.74	25.80–27.68	21
<i>Centropages typicus</i>	1.07	1.04–1.10	97.51	95.50–99.52	91.50	89.91–93.09	15.50	14.50–16.46	18.55	17.96–19.14	21
<i>Pseudocalanus minutus</i>	0.71	0.68–0.73	62.68	60.24–65.12	58.06	56.11–60.01	2.37	1.63–3.12	12.22	14.17–16.26	15
<i>Temora longicornis</i>	0.69	0.66–0.73	112.5	108.9–116.0	104.0	99.91–108.0	13.09	11.84–14.34	23.23	21.57–24.89	19
<i>Acartia</i> sp.	0.67	0.65–0.70	51.97	49.62–54.33	47.08	44.65–49.51	5.47	5.16–5.77	12.29	11.70–12.88	17
<i>Oithona</i> sp.	0.41	0.39–0.44	26.74	25.80–27.67	22.07	21.30–22.80	7.11	6.40–7.77	4.62	4.35–4.88	18
<i>C. finmarchicus</i> ad. fem.	1.96	1.91–2.01	158.0	153.1–162.9	148.5	144.6–152.4	26.57	25.32–27.82	34.18	32.90–35.45	27
<i>C. finmarchicus</i> ad. male	1.84	1.78–1.91	138.4	135.3–141.4	129.4	126.9–131.9	24.05	23.30–24.81	29.43	28.79–30.07	36
<i>C. finmarchicus</i> C-V	1.76	1.71–1.81	145.1	142.1–148.1	134.2	131.1–137.2	26.34	24.89–27.80	29.73	28.89–30.58	23
<i>C. finmarchicus</i> C-IV	1.35	1.30–1.40	112.7	108.2–117.2	105.1	100.6–109.6	20.78	19.23–22.34	23.17	21.70–24.64	24
<i>C. finmarchicus</i> C-III	1.08	1.06–1.10	96.04	94.23–97.84	88.78	86.61–90.95	16.32	15.23–17.41	18.95	18.30–19.59	19
<i>C. finmarchicus</i> C-II	0.76	0.73–0.79	70.08	67.90–72.26	65.85	63.34–68.37	12.78	11.48–14.08	13.59	13.04–14.15	17
<i>C. finmarchicus</i> C-I	0.57	0.54–0.59	44.44	41.77–47.10	42.30	39.95–44.65	6.41	5.94–6.88	7.84	7.41–8.26	21

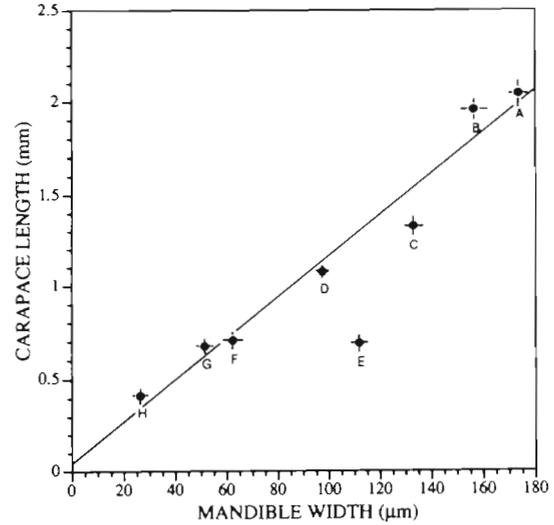


Fig. 4. Relationship between average carapace length (mm) and average mandible width (µm) of 8 copepod species (adult females only), sampled at the end of August. Vertical and horizontal bars denote 95% confidence interval of the carapace length and the mandible width, respectively. A = *Metridia longa*, B = *Calanus finmarchicus*, C = *Metridia lucens*, D = *Centropages typicus*, E = *Temora longicornis* (not included in regression), F = *Pseudocalanus minutus*, G = *Acartia* sp., H = *Oithona* sp.

The relationship between stage-specific mandible width (X, in µm) and carapace length (Y, in mm) for *Calanus finmarchicus* (Fig. 5) was well described by the linear regression equation:

$$Y = -0.0690 + 0.0126X \quad r^2 = 0.991 \quad (2)$$

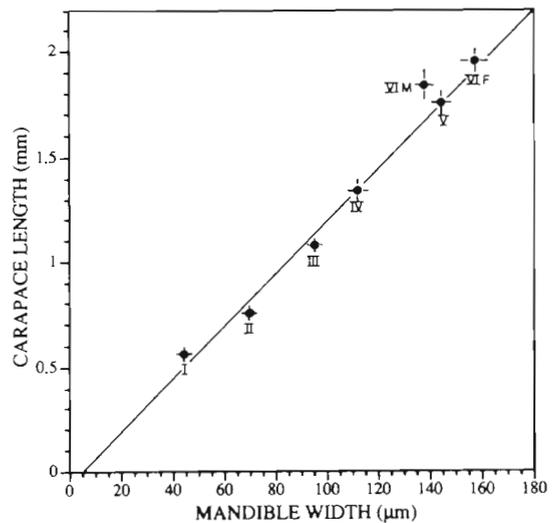


Fig. 5. *Calanus finmarchicus*. Relationship between average carapace length (mm) and average mandible width (µm) of copepodite stages I to VI (excluding adult males). Vertical and horizontal bars denote 95% confidence interval of the carapace length and the mandible width, respectively

The somewhat diverging position of adult males from the general trend is clear in Fig. 5. Adult males only occur in high numbers in connection with the mating period during very restricted periods of the year (Marshall & Orr 1972, Tande 1982), and they were therefore not included in the regression fit here.

Copepod length/weight relationships

Interspecific relationships

The mathematical relationship between length and weight of an organism is usually expressed as a power function, due to the general growth principle of organisms and the mathematical relationship between length and volume of a body. We therefore also express the length/weight relationships of the copepods by using this formulation, even though an exponential equation generally turned out to have a higher coefficient of determination.

In order to define a wide-range interspecific relationship between copepod carapace length (X , in mm) and dry weight (Y , in μg) we used average values from the same sampling occasion for stage V copepodites *Calanus finmarchicus*, together with 5 other species, in a regression equation. The individuals represented a range in dry weight from 28 to 278 μg , and a carapace

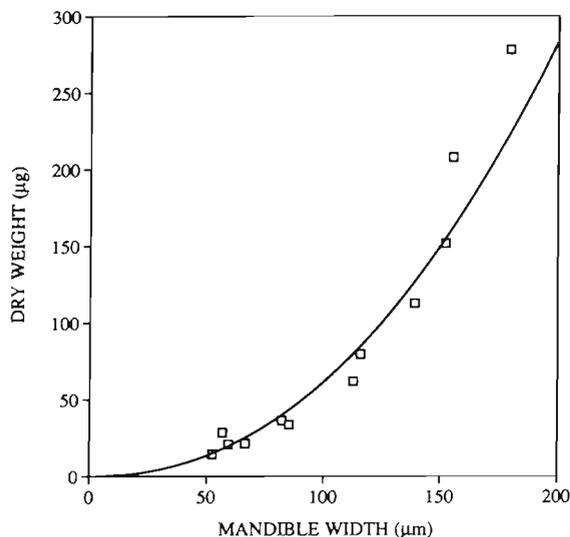


Fig. 6. Relationship between average dry weight (μg) and average mandible width (μm) of *Calanus finmarchicus* (all copepodite stages as separate points) and 5 other copepod species. The graph includes copepodite stage IV of *Euchaeta norvegica*, and adult females of *Metridia lucens*, *Centropages typicus*, *Pseudocalanus minutus*, and *Acartia* sp.; points represent the average value of between 9 and 71 measurements

length from 0.7 to 2.1 mm. The relationship was best described by the equation:

$$Y = 49.700 X^{2.267} \quad r^2 = 0.962 \quad (3)$$

By combining these data with the general relationship between carapace length and mandible width (Eq. 1) a regression equation describing the relationship between the mandible width (X , in μm) and the individual dry weight (Y , in μg) can be defined:

$$Y = 0.00310 X^{2.176} \quad r^2 = 0.960 \quad (4)$$

By also including data for the other copepodite stages of *Calanus finmarchicus*, a regression equation applicable to most copepods is given (Fig. 6):

$$Y = 0.00235 X^{2.208} \quad r^2 = 0.950 \quad (5)$$

Intraspecific relationships for *Calanus finmarchicus*

The relation between average carapace length (X , in mm) and average individual dry weight (Y , in μg) of *Calanus finmarchicus*, from August (Fig. 7A), was described by the equation:

$$Y = 37.978 X^{2.134} \quad r^2 = 0.983 \quad (6)$$

By using the average mandible width of each developmental stage, the mathematical relationship between individual dry weight (Y , in μg) and mandible width (X , in μm) could be calculated (Fig. 7B, excluding adult males):

$$Y = 0.00200 X^{2.215} \quad r^2 = 0.987 \quad (7)$$

Our material on *Calanus finmarchicus* (Fig. 7A) showed that the average dry weight of stage V copepodites differed by a factor of 1.85 from the beginning of August to the end of September. This partly reflected a parallel change in carapace length, but nevertheless, this result indicates that seasonal variation is important. Unfortunately, we cannot distinguish whether biological or physical factors (different populations sampled) produced this variation in our results.

Individual variability

Individual variability was evaluated by looking at the intraspecific relationship between carapace length and mandible width of each given species and developmental stage from a single sample (Table 2). The results showed that between 2 and 81% (average 43%, $n = 14$) of the individual variation in carapace length of a given species/stage could be explained by a corresponding variation in mandible width. This, in turn, means that between 19 and 98% (average 57%)

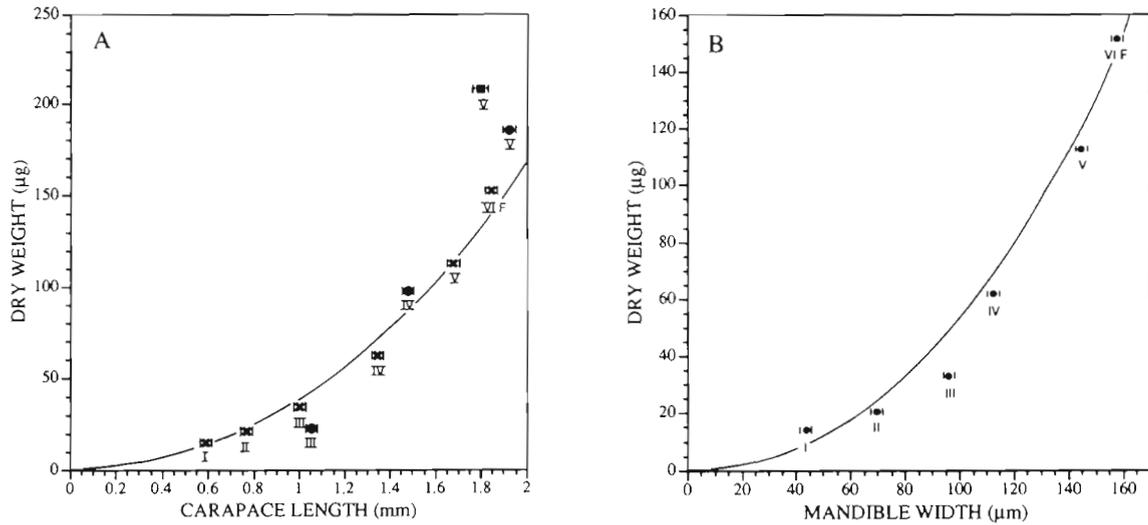


Fig. 7. *Calanus finmarchicus*. (A) Relationship between average dry weight (μg) and average carapace length (mm) of the 6 copepodite stages, excluding adult males. All stages were represented in August (\times) whereas May (\bullet) and September (\blacksquare) only included one or a few developmental stages. Regression line calculated for August data only. Horizontal bars denote 95 % confidence interval. (B) Relationship between average individual dry weight (μg) and average mandible width (μm) in August

of the individual variation in carapace length of animals of a given species and developmental stage was not reflected in a corresponding variation in the mandible width.

DISCUSSION

Identification

One of the main problems in using mandible analysis as a technique to estimate predation is certainly the limitations involved in identifying species and developmental stages. In some previous investigations on

krill predation, only the width of the mandibles was measured (Stuart & Pillar 1990, Barange et al. 1991, Gibbons et al. 1991a) and not related to taxonomic group or body weight of the prey. Falkenhaug (1991), studying chaetognath predation in the Barents Sea, identified the copepod prey from mandibles in chaetognath guts, but used only standard values of the body mass of different species. Stuart & Verheye (1991) estimated prey prosome length from the width of copepod mandibles in the gut contents of chaetognaths, without identification of the species. The method was utilised most completely in 2 previous papers, one on chaetognath predation (Gibbons 1992), and particularly the one on krill predation by Gibbons et al. (1991b), where

Table 2. Relationship between mandible width (X , in μm) and carapace length (Y , in mm), as given by linear regression equations, $Y = a + bX$, of copepods in Raunefjorden, sampled at times given

Species/stage	Month	a	b	r^2	n
<i>Calanus finmarchicus</i> adult females	August	1.139	0.005	0.492	27
<i>Calanus finmarchicus</i> adult males	August	0.691	0.008	0.315	36
<i>Calanus finmarchicus</i> C-V	August	1.518	0.002	0.020	23
<i>Calanus finmarchicus</i> C-IV	August	0.551	0.007	0.719	24
<i>Calanus finmarchicus</i> C-III	August	0.609	0.005	0.389	18
<i>Calanus finmarchicus</i> C-II	August	0.171	0.008	0.728	17
<i>Calanus finmarchicus</i> C-I	August	0.445	0.003	0.187	21
<i>Metridia longa</i> adult females	October	0.580	0.008	0.411	28
<i>Metridia lucens</i> adult females	October	0.613	0.005	0.347	21
<i>Centropages typicus</i> adult females	October	0.951	0.001	0.022	17
<i>Temora longicornis</i> adult females	October	0.073	0.005	0.754	19
<i>Pseudocalanus minutus</i> adult females	October	0.304	0.006	0.550	15
<i>Acartia</i> sp. adult females	October	0.244	0.008	0.808	17
<i>Oithona</i> sp. adult females	October	0.125	0.011	0.333	18

both species/genus identification and prosome length and dry weight were calculated from the recovered mandibles.

We have presented complete data only for *Calanus finmarchicus*. However, this species is probably the most important prey organism in the Northeast Atlantic, and therefore especially important to describe. A proper identification of the juvenile stages of the 7 other species, as well as of more sparsely occurring species, requires further studies. The data for *Temora longicornis* indicate different regression parameters for this species, so it is therefore especially important to identify mandibles from this species correctly and to use a species-specific regression equation for them.

Although our descriptions of the different mandible shapes seem sufficient for a proper identification, some uncertainties remain. For example, the mandibular teeth are difficult to separate from cusps, especially for *Acartia* sp. and *Oithona* sp., when using a light microscope, since the mandible edge is 3-dimensional. Scanning electron microscopy (SEM) would be a preferable technique, and has been used to study the complex mandible edge on 11 species of copepods (Sullivan et al. 1975). However, applying SEM in routine analysis of a large volume of material is impractical. Accordingly, we must accept some doubtful identi-

fications in routine gut-content analyses, but usually this will not be critical.

Prey biomass estimations

The mandible-analysis technique, fully utilised, can provide a way of estimating the predation rate in terms of prey biomass. This is an important step when applying the method in studies on the energy budgets of predators and the energy flow in food webs. However, such calculated estimates have inherent errors that cause uncertainties in the accuracy and precision, which hitherto have been unknown when using this technique. We have therefore studied this problem with some care.

Any of the presented regression equations relating copepod body mass to mandible width could be used to estimate consumed prey biomass, but will all probably produce a more or less biased estimate. The ideal would be to use species- and season-specific regression equations on each occasion. In addition, a considerable geographical variation in body size (cf. Båmstedt & Ervik 1984) implies that a set of such equations for each region is needed. This is unrealistic and the gain in precision would probably not pay for the enormous work required. In spite of the shortcomings we recommend using a single equation for all mandibles found. In order to evaluate what effects the choice of equation will have upon the estimate, the regression lines are displayed together in Fig. 8A. If Eq. (5) is used as reference, the other equations give body-mass estimates that diverge from the reference. The relative deviation will be a function of the mandible size, as shown in Fig. 8B, but well below 20% deviation from the reference for typical sizes of mandibles. If the analysed material is dominated by *Calanus finmarchicus*, Eq. (7) should be used, but even if the more general equation (Eq. 5) is used for such material, this will only introduce an overestimation of less than 15% (cf. Eq. 7, Fig. 8B).

Individual variability

Invertebrate predators like krill, amphipods and chaetognaths commonly have only a few copepod mandibles in their stomachs. If individual variations in mandible width are high and unrelated to body size, the precision of the estimated prey biomass will be outside the suggested 20%. Our data indicate that this may be a main problem, since on average 57% of the variation in carapace length within a defined species and developmental stage was not related to a corresponding variation in mandible width (Table 2). Since

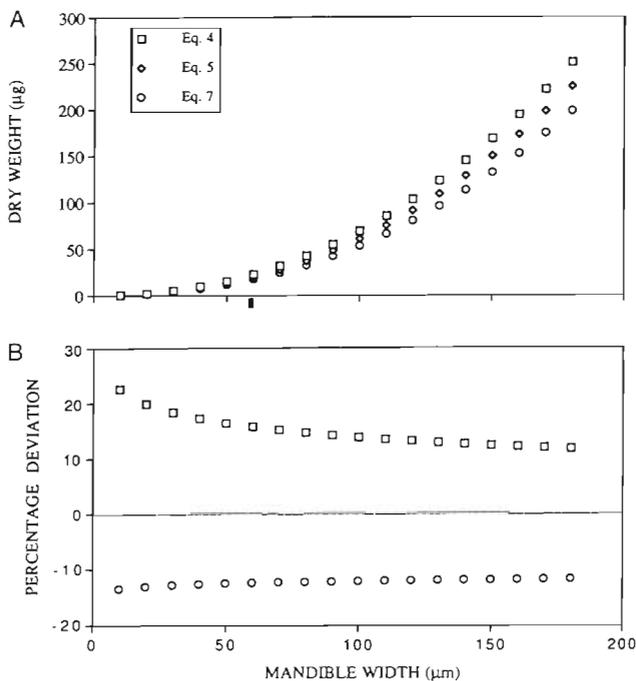


Fig. 8. Sensitivity analysis of predicted dry weights using Eqs. (4), (5) and (7). (A) Dry weight/mandible width relationships given by the 3 equations. (B) Eq. (5) used as a reference, showing the relative deviation from the reference for the other 2 equations

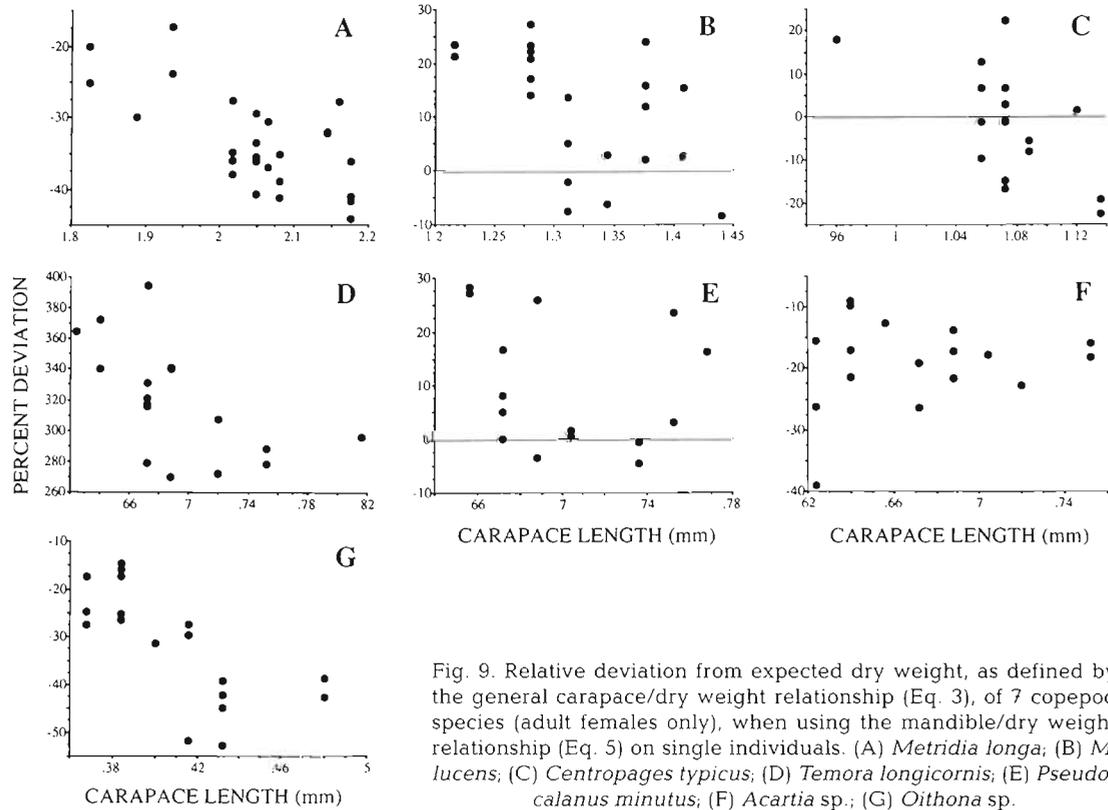


Fig. 9. Relative deviation from expected dry weight, as defined by the general carapace/dry weight relationship (Eq. 3), of 7 copepod species (adult females only), when using the mandible/dry weight relationship (Eq. 5) on single individuals. (A) *Metridia longa*; (B) *M. lucens*; (C) *Centropages typicus*; (D) *Temora longicornis*; (E) *Pseudocalanus minutus*; (F) *Acartia* sp.; (G) *Oithona* sp.

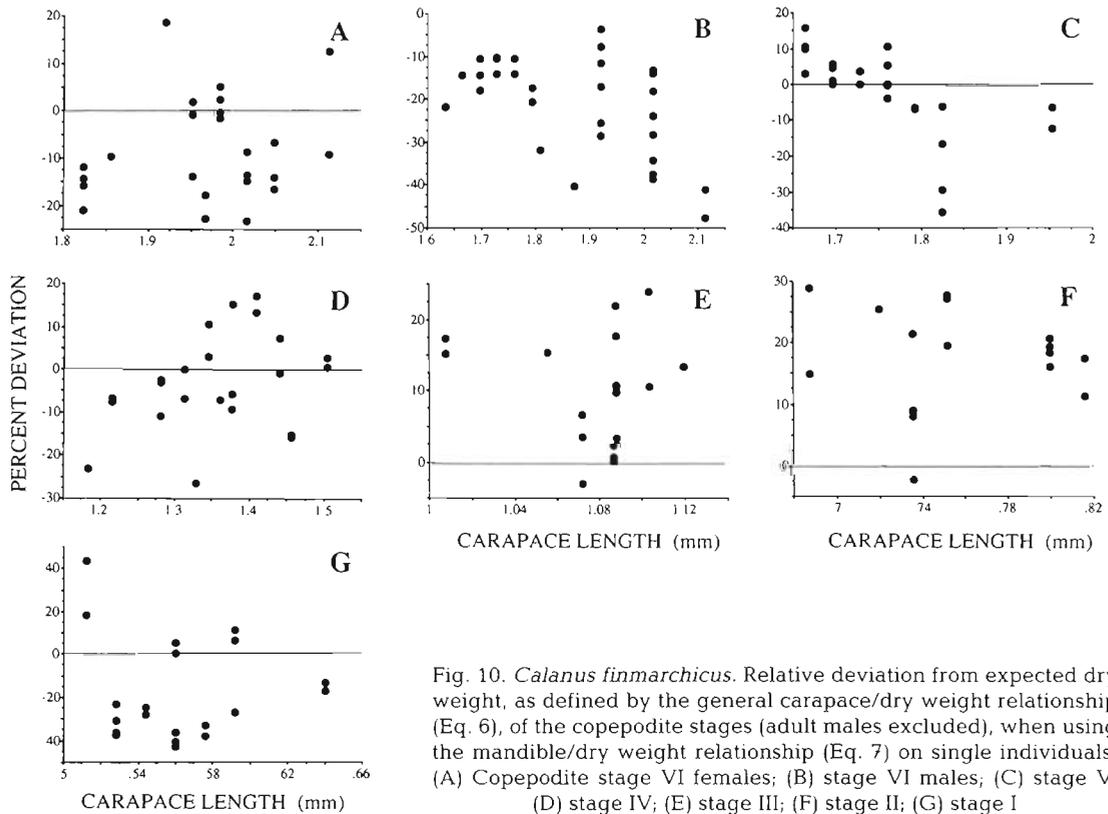


Fig. 10. *Calanus finmarchicus*. Relative deviation from expected dry weight, as defined by the general carapace/dry weight relationship (Eq. 6), of the copepodite stages (adult males excluded), when using the mandible/dry weight relationship (Eq. 7) on single individuals. (A) Copepodite stage VI females; (B) stage VI males; (C) stage V; (D) stage IV; (E) stage III; (F) stage II; (G) stage I

we do not have any direct measurements on the dry weight of single individuals, we are unable to compare the predicted dry weights with the actual ones. As an alternative we can compare the results obtained from Eqs. (5) & (7), based on the mandible measurements, with the results from carapace/weight relationships (Eqs. 3 & 6), that are commonly used in estimating individual dry weights. The results for the assemblage of copepod species, using Eq. (3) as reference (Fig. 9), indicates an underestimation of the dry weight of *Metridia longa*, *Acartia* sp. and *Oithona* sp., whereas the dry weight of *Temora longicornis* is heavily overestimated. There is a trend towards decreasing values with size within the species (except for *Acartia* sp.), indicating that the slope of a regression line within a species/stage is lower than that for the general regres-

sion line. The results for *Calanus finmarchicus* (Fig. 10) show that adult females and males, and copepodite stage I are usually underestimated by Eq. (7), whereas copepodite stage III and II are usually overestimated. For the mixture of species (excluding *T. longicornis*) the estimates vary from 28% higher to 53% lower than the reference, with ca 50% of the individual estimates within $\pm 20\%$ (Fig. 11A). For *C. finmarchicus* the predicted value varies from 48% lower to 44% higher than the reference, but ca 75% of the individual estimates were within $\pm 20\%$ (Fig. 11B).

Due to the individual variability, an estimate of prey biomass based on only one or a few mandibles and using the recommended equation for a mixture of copepods will therefore probably introduce an additional variability of up to ca 50%, but usually considerably less (Fig. 11A). When using the *Calanus finmarchicus* equation on *C. finmarchicus* material, the individual variability will usually add less than 20% (Fig. 11B) to the other sources of variability in the prey biomass estimate.

Seasonal variation

Copepods from high latitudes show a considerable variation in body size, mainly as an adaptation to a seasonally variable food environment (Marshall & Orr 1972, Durbin & Durbin 1978, Vidal 1980, Båmstedt & Ervik 1984, Buchholz & Prado-Fiedler 1987). Therefore, seasonal corrections may be necessary in order to predict unbiased body weights from length measurements. If the length and weight of a copepod vary as described by the given relationships (Eqs. 3 & 6) the seasonal variation will not introduce any bias in the estimated body weight, but in situations where the animal builds up a body reserve or where the body reserve is heavily utilised, it is reasonable to suggest that the biomass estimate will be biased. As an example, we have looked at the data from the overwintering population of stage V copepodites *Calanus finmarchicus*, from a fjord in northern Norway (Tande 1982) and used our Eq. (6) to estimate the individual body dry weight. The original data shows that the mean dry weight varies by a factor of 3 over the year, whereas the predicted dry weight (from Eq. 6) varies over an annual cycle by a factor 1.5 (Fig. 12). As suspected, the main differences in the seasonal trend are found at the end of the overwintering and starving period (winter) and during summer/autumn, when there is a heavy load-

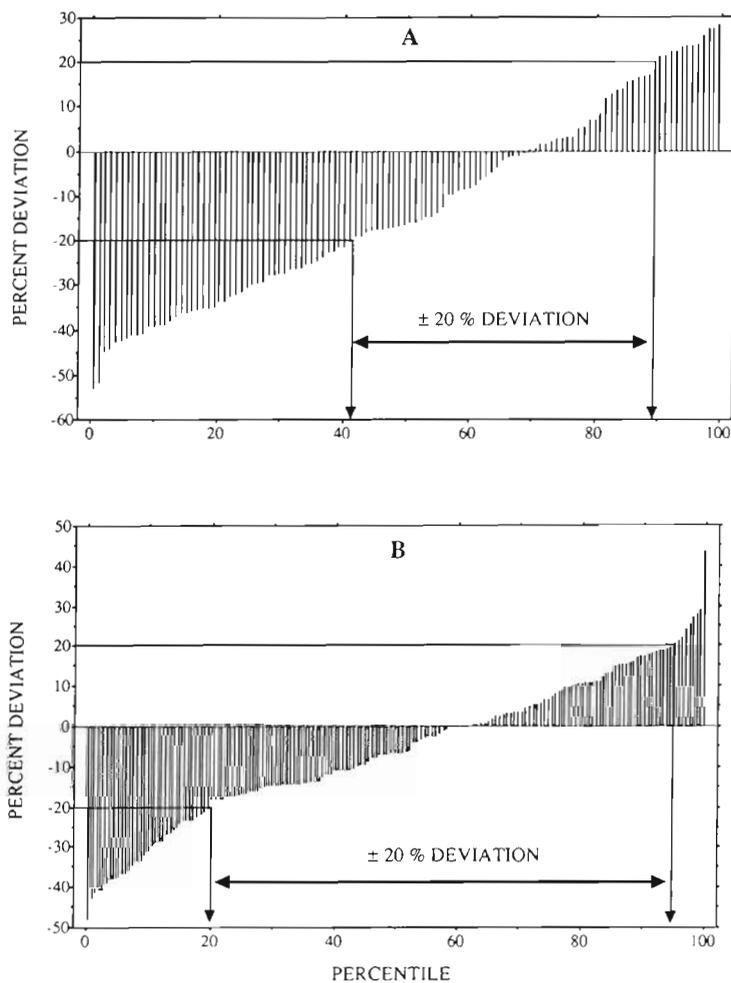


Fig. 11 Relative deviation from the 'reference' individual dry weight in a copepod population, when estimating the dry weight from the mandible width. (A) Adult females of 6 copepod species, calculated by Eq. (5). (B) *Calanus finmarchicus* (all copepodite stages) calculated by Eq. (7). Reference weight for the copepod assemblage (A) defined by Eq. (3), that of *C. finmarchicus* (B) by Eq. (6)

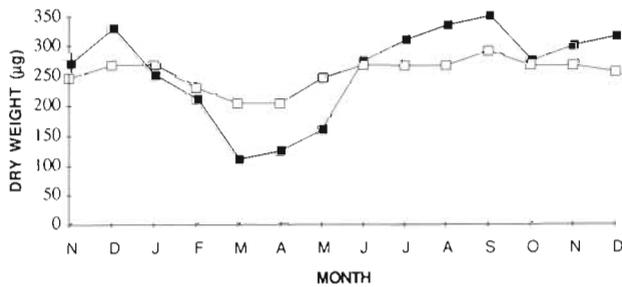


Fig. 12. *Calanus finmarchicus*, stage V copepodites. Example of a seasonally varying length/weight relationship of a copepod species. (■) Original data from Tande (1982). (□) Predicted dry weights calculated by using the original data on carapace length (Tande 1982) and our Eq. (6)

ing of body reserves as a preparation for overwintering. In March the predicted dry weight overestimates the true one by ca 90%, whereas in August, September and December the true weight is underestimated by 20% (Fig. 12). This source of bias is therefore assumed to be more serious when estimating the dry weight from length/weight relationships of copepod species without any seasonal correction, but the degree of error is certainly species dependent and probably directly related to the seasonal variation in stored energy of the species.

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