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Variation in assimilation efficiencies of dominant *Neocalanus* and *Eucalanus* copepods in the subarctic Pacific: Consequences for population structure models

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ABSTRACT

The assimilation efficiency of zooplankton is an essential parameter required to estimate energy transfer to higher trophic levels in marine ecosystems. However, little information is available for large oceanic copepods, especially the *Neocalanus* and *Eucalanus* species dominant in the subarctic Pacific. In this study, the assimilation efficiencies of the C5 stages of *Neocalanus cristatus*, *Neocalanus flemingeri* and *Eucalanus bungii* were evaluated using eight phytoplankton species as food. The average assimilation efficiencies of *N. cristatus*, *N. flemingeri* and *E. bungii* ranged between 45 and 66%, 44 and 66% and 34 and 65%, respectively. The assimilation efficiency was highly variable depending on the food phytoplankton species. In all species, the assimilation efficiency showed a significant negative relationship with the ash content of the phytoplankton ($r^2 = 0.79–0.87$, $p < 0.001$). The assimilation efficiency of large-body sized *N. cristatus* for large-sized diatoms was higher than for the other copepod species. In population models of *N. cristatus*, changes in assimilation efficiency affect the growth and survival rates of the population. The Lagrangian ensemble model (LEM) for *N. cristatus* showed that, for assimilation efficiencies less than 57%, the population could not be maintained. Because variations in assimilation efficiency may have significant effects on the copepod population, their variability should be incorporated into marine ecosystem models in the future.

1. Introduction

In marine ecosystems, copepods feed on phyto- and micro-zooplankton and are preyed upon by pelagic fishes, sea birds and whales; thus, they play an important role in energy transfers to higher trophic organisms (Beamish et al., 1999; Hunt et al., 1998; Ikeda et al., 2008; Nemoto, 1963). In the summer zooplankton community of the subarctic Pacific, large oceanic copepods, *Neocalanus* and *Eucalanus* species, are predominant and form 85–90% of the total zooplankton biomass (Vinogradov, 1970). Because *Neocalanus* and *Eucalanus* species egest large faecal pellets and perform seasonal vertical migrations, they play an important role in transporting organic material from the surface layer to the deep sea, called the "biological pump" (Kobari et al., 2003, 2008).

Among the various copepod parameters that affect the material flux, the assimilation efficiency is an essential parameter required to estimate the energy transfer to higher trophic levels in marine ecosystems (Conover, 1966a,b). From the 1960s to the present, many studies have been performed on the assimilation efficiencies of copepods. Through these studies, much information has been accumulated, e.g., assimilation efficiency varies with the ash content of the food (Conover, 1966a,b), and the carbon assimilation efficiency is correlated with the concentrations of soluble carbohydrates in diets (Head, 1992). However, our knowledge about assimilation efficiency has mainly come from coastal species (cf. Berggreen et al., 1988; Besiktepe and Dam, 2002; Gottfried and Roman, 1983; Katechakis et al., 2004), and little information is available for large oceanic copepods, especially the *Neocalanus* and *Eucalanus* species that are dominant in the subarctic Pacific. Even in marine ecosystem models such as NEMURO, a constant value (70%) is applied for the copepod assimilation efficiency (Kishi et al., 2007; Terui and Kishi, 2008; Terui et al., 2012). As mentioned above, a few large oceanic copepods (*Neocalanus* and *Eucalanus* species) are dominant in the zooplankton biomass of the subarctic Pacific; therefore, information on their assimilation efficiency is very important for increasing the accuracy of ecosystem models (e.g., NEMURO) in this region.

The assimilation efficiency of copepods is measured by several methods; the Ratio method, the Radio tracer method and the Calculation method, based on ingestion rate, evacuation rate and faecal pellet volume (Besiktepe and Dam, 2002; Conover, 1966a; Sorokin, 1968). Among these methods, the Radio tracer method is mainly used for minimally metabolised materials, such as heavy metals. For common materials (e.g., carbon and phosphorus), the Radio tracer method cannot be applied because they are readily metabolised, which prevents

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accurate measurement (Båmstedt et al., 2000). The Calculation method requires the quantitative collection of faecal pellets, so this method is also difficult (Conover and Francis, 1973; Omori and Ikeda, 1984). The Ratio method by Conover (1966a) does not require quantitative collection of faecal pellets, is readily applicable to various animals and is an effective method, even though nearly half a century has passed since it was originally described (Azad et al., 2011; Enríquez-Ocaña et al., 2012; Nelson et al., 2012). Recently, most studies on assimilation efficiency of copepods have mainly concerned marine heavy metal pollution in coastal small copepods as evaluated using the Radio tracer method (Chang and Reinfelder, 2000; Fisher and Reinfelder, 1991; Hutchins et al., 1995; Stewart and Fisher, 2003; Wang and Fisher, 1998; Wang et al., 2007; Xu and Wang, 2001, 2002; Zheng et al., 2011). However, little information is available on the assimilation efficiencies of common materials (organic material, carbon and nitrogen) by large oceanic copepods.

In this study, the assimilation efficiencies of three large oceanic copepods (*N. cristatus, N. flemingeri* and *E. bungii*), which are dominant in the zooplankton biomass in the subarctic Pacific, were measured by applying the Ratio method considering eight phytoplankton species (diatoms, a dinoflagellate and a raphidophycean) as food. Phytoplankton cell size, colony formation, swimming ability and ash contents were also analysed as factors that may affect the assimilation efficiency of copepods. The effects of food carbon concentration on copepod assimilation efficiency were also evaluated. By applying the observed assimilation efficiency of one species of copepod (*N. cristatus*), the effects of changes in the assimilation efficiency on copepod population structure were evaluated using the LEM (Lagrangian ensemble model) population model.

2. Materials and methods

Live specimens of the C5 stages of *N. cristatus, N. flemingeri* and *E. bungii* were collected using vertical hauls of a 80-cm ring net from 0 to 30 or 0 to 150 m deep at several stations in the subarctic Pacific from March to July 2011 and May to August 2012. Because adult (C6) *Neocalanus* spp. degrade feeding appendages and cease feeding (Miller, 1988; Miller et al., 1984), we used the C5 stage as experimental specimens. Seawater was collected from 30 m deep using Niskin bottles, filtered through a GF/F filter and used in the subsequent experiments. Ten live specimens were transferred into a 1-L bottle filled with filtered seawater (FSW). Up to 100 specimens of each species were kept at 2 °C and then carried to the land laboratory.

To obtain sympatric phytoplankton species, 5 ml of unfiltered seawater was added to a flask containing 300 ml of modified SWM-3 medium (Chen et al., 1969; Imai et al., 1996), then incubated at 15 °C under illumination of 100 to 120 μmol photons $m^{-2}\ s^{-1}$ with a 14 h light and 10 h dark photocycle. Three diatoms (*Chaetoceros* sp., *Ditylum brightwellii* and *Thalassiosira nordenskioeldii*) were isolated from this treatment. Six diatoms (*Attheya septentrionalis*, *Chaetoceros* sp., *D. brightwellii*, *Pauliella taeniata*, *Skeletonema* sp. and *Th. nordenskioeldii*), one dinoflagellate (*Alexandrium tamarense*) and one raphidophycean (*Heterosigma akashiwo*) were incubated under the same conditions as food for the copepods. The carbon contents of *Chaetoceros* sp., *D. brightwellii* and *Skeletonema* sp. were estimated by multiplying 0.43 (for the former two species) or 0.51 (for the latter species) with the ash-free dry weight (AFDW) (Parsons et al., 1961). For *Th. nordenskioeldii* and *A. tamarense*, the carbon contents were obtained by multiplying 0.108 or 0.173 with the dry weight (DW), respectively (Liu and Wang, 2002). Information regarding cell size, carbon and ash contents, colony formation, swimming ability and initial cell density of each phytoplankton is summarised in Table 1.

Before the experiments, no food was added for the copepod specimens for at least one day (24 h). For the experiments, each phytoplankton species was adjusted to a density of 5.0×10^2–2.0×10^4 cells ml^{-1} (110–2577 μg C L^{-1}) (Table 1). For each experiment, 15 individuals of *N. cristatus* or *E. bungii* or 20 individuals of *N. flemingeri* were added to each phytoplankton species in 1-L bottles and incubated for 24 h under dark conditions at 3 °C. Experiments were carried out in triplicate along with one control bottle with no added copepods. During the experiments, the bottles were rotated every 3 h to prevent the phytoplankton from sinking. After the 24-h experiment, the copepods were transferred to new bottles containing FSW. Faecal pellets were pipetted from the incubation bottles using sterile Pasteur pipettes, placed in Petri dishes filled with chilled FSW and rinsed 5–10 times by

Table 2
The volume of the faecal pellets of *Neocalanus cristatus*, *Neocalanus flemingeri* and *Eucalanus bungii* observed with various phytoplanktons as food. For comparison possible, faecal pellet volumes (*FPV* in μm^3) predicted by prosome length (PL in mm) (Log FPV = 2.474 log PL + 5.226, Mauchline, 1998) are shown in the bottom column. Values are mean ± 1 sd.

Taxa/Species	Faecal pellet volume ($10^6\ \mu m^3$)		
	Neocalanus cristatus	*Neocalanus flemingeri*	*Eucalanus bungii*
Diatoms			
Attheya septentrionalis	16.06 ± 14.60		
Chaetoceros sp.	17.16		21.52
Ditylum brightwellii	12.53 ± 4.44	5.95	10.33 ± 2.84
Pauliella taeniata	29.38		
Skeletonema sp.	12.23 ± 4.09		
Thalassiosira nordenskioeldii	49.67	5.20	13.24 ± 2.64
Dinoflagellates			
Alexandrium tamarense	16.94 ± 9.80	3.77	5.20 ± 1.94
Raphidophyceae			
Heterosigma akashiwo	20.98 ± 1.74		
FPV predicted by *PL*	38.88	5.64	16.06

Table 1
Data on phytoplankton (cell size, carbon, ash contents, colony formation and movement ability) used as food for copepods in the laboratory experiments. Owing to size, cell density of phytoplankton was changed for assimilation experiments. For carbon and ash contents, values are mean ± 1 sd.

Taxa/Species	Cell size (μm)	Carbon content (pg C $cell^{-1}$)	Ash content (pg ash $cell^{-1}$)	Colony formation	Movement ability	Concentration	
						(cells ml^{-1})	(μg C L^{-1})
Diatoms							
Attheya septentrionalis	5 – 10		190 ± 99	+		5.0×10^3 – 1.0×10^4	
Chaetoceros sp.	10 – 40	249 ± 3	754 ± 105	+		1.0×10^3	249
Ditylum brightwellii	25 – 100	2596 ± 1540	9400 ± 582	+		5.0×10^2	1298
Pauliella taeniata	25 – 30			+		5.0×10^2 – 1.0×10^4	
Skeletonema sp.	2 – 21	48 ± 16	105 ± 76	+		1.0×10^4 – 2.0×10^4	480 – 960
Thalassiosira nordenskioeldii	10 – 50	252 ± 62	1389 ± 540	+		1.0×10^3	252
Dinoflagellates							
Alexandrium tamarense	30 – 40	2577 ± 543	6796 ± 1747		+	5.0×10^2 – 1.0×10^3	1289–2577
Raphidophyceae							
Heterosigma akashiwo	10 – 20	100	528 ± 85		+	5.0×10^3	500