Ontogenetic diet shift in the euphausiid *Euphausia pacifica* quantified using stable isotope analysis

Jeong-In Park[1], Chang-Keun Kang[2], Hae-Lip Suh[1],*

[1]Department of Oceanography, Chonnam National University, Gwangju 500-757, South Korea
[2]School of Environmental Science and Engineering, Pohang University of Science and Technology, Pohang 790-784, South Korea

ABSTRACT: The euphausiid *Euphausia pacifica* is an omnivorous species of plankton that has been implicated in important food web processes such as the lengthening of food chains and the restructuring of community dynamics and energy transfer. We used carbon and nitrogen stable isotopes (δ^{13}C and δ^{15}N) to quantify the ontogenetic diet shift in *E. pacifica* in the East Sea (Japan Sea or Sea of Japan). Analyses revealed that δ^{15}N values of adults (4.17 ± 0.10‰) were significantly lower than those of juveniles (5.40 ± 0.30‰), reflecting a shift in the diet of *E. pacifica* adults towards copepod *Neocalanus cristatus* carcasses, which have been suggested to drift throughout the year in the epipelagic layer of the East Sea. This suggests a trend toward increasing detritivory with maturity, which is not consistent with the results of previous conventional approaches to diet analysis in *E. pacifica*. Our results should be useful to modelers concerned with quantifying the effects of *E. pacifica* on energy transfer in marine food chains.

KEY WORDS: *Euphausia pacifica* · Ontogenetic diet shift · Stable isotope analysis · East Sea · Sea of Japan · Trophic level · Copepod carcass · *Neocalanus cristatus*

INTRODUCTION

Euphausiids are among the most common groups of marine zooplankton. In the East Sea, also known as Japan Sea or Sea of Japan, 4 species of euphausiids have been reported: *Euphausia pacifica* (Hansen), *Thysanoessa inermis* (Krøyer), *T. longipes* (Brandt) and *T. raschii* (M. Sars). Of these, *E. pacifica* is widely distributed and is also one of the most dominant zooplankton (Ponomareva 1963, Suh et al. 1998). Thus, *E. pacifica* occupies a key role in the East Sea ecosystem, both as a pelagic grazer and as prey for vertebrates. This species performs extensive diel vertical migrations (Iguchi 1995, Yoon et al. 2000, Lu et al. 2003) and seems to be capable of using a wide range of diet items as well as suspended organic matter or detritus (Ponomareva, 1963, Dilling et al. 1998, Nakagawa et al. 2001, 2004). Copepod carcasses are a major component of suspended organic matter, and *Neocalanus cristatus* carcasses (NCCs) have been reported to drift for more than a year in the epipelagic layer of the East

Sea (Terazaki & Wada 1988). *E. pacifica* is a major prey for many of the commercially harvested fishes in the East Sea, including pink salmon *Oncorhynchus gorbuscha* (Fukataki 1967) and walleye pollock *Theragra chalcogramma* (Kooka et al. 1998), as well as seabirds and baleen whales (Mauchline 1980).

Euphausia pacifica is broadly omnivorous (Ponomareva 1963) and this trophic flexibility has contributed to difficulty in predicting their trophic linkages. Previous studies based on rearing experiments (Ohman 1984, Dilling et al. 1998, Nakagawa et al. 2004), stomach contents analyses (Nakagawa et al. 2001, Taki et al. 2002), gut pigment analyses (Nakagawa et al. 2002) and molecular gut content analyses (Theilacker et al. 1986, Bailey et al. 1993) have shown that *E. pacifica* can feed on nanoplankton but generally become more zooplanktivorous as they mature, which suggests that body size is a good predictor of diet composition. However, data on functional morphology of *E. pacifica* have indicated that the fine mesh size of its feeding basket is nearly consistent

from juveniles to adults, suggesting that there is competition between the 2 stages for food (Suh & Choi 1998).

Stable isotope methodology is extensively used to estimate ecosystem characteristics as a complementary method of dietary analysis and to provide real time, integrated information of trophic relationships and energy flows from primary producers to higher trophic levels (Cabana & Rasmussen 1994). To better predict the effects of *Euphausia pacifica* on food web processes, we used both carbon and nitrogen stable isotopes ($\delta^{13}C$ and $\delta^{15}N$, respectively) to quantify ontogenetic diet shifts in this species in its natural environment (McConnaughey & McRoy 1979, Fry & Sherr 1984, Frazer et al. 1997, Matthews & Mazumder 2008).

The objectives of our study were to (1) evaluate the fractionation of $\delta^{13}C$ and $\delta^{15}N$ ratios for juveniles and adults of *Euphausia pacifica* as well as coexisting sources of organic matter and (2) test for trophic level variation or ontogenetic diet change in a natural population of this omnivore.

MATERIALS AND METHODS

Sampling and sorting. From 12 to 14 May 2007, samples were collected at the 4 stations in the East Sea (Japan Sea) indicated in Fig. 1 and Table 1, as a part of the Korean EAST-1 program (EAST-1; www.east-1.snu.ac.kr). Zooplankton were collected with a twin bongo net (0.6 m diameter openings, 150 and 300 µm mesh sizes) equipped with a calibrated flow meter. Oblique hauls were conducted from approximately 280 m depth to the surface. All samples were immediately fixed in 95% ethanol (30% final concentration). The euphausiid *Euphausia pacifica*, the dominant copepod *Metridia pacifica* and NCCs were removed from the bulk zooplankton samples. NCCs, including the antennae and thoracic legs without body contents, remained in good condition. The body length (BL) of *E. pacifica* was determined as the distance from the anterior margin of the eye to the tip of the telson. *E. pacifica* were sorted into 2 length groups as small (5 mm < BL < 10 mm) and large (15 mm < BL < 20 mm). Because the minimum adult sizes are 11 to 12 mm BL, the small and large groups corresponded well to juveniles and adults, respectively (Iguchi et al. 1993).

Microplankton for stable isotope analyses were sampled from 30 m to the surface with vertical hauls of a standard net (0.5 m diameter opening, 20 µm mesh size) and then collected on

prewashed and precombusted (450°C for 4 h) GF/F filters (Whatman) (0.70 µm pore size). Nano- and picoplankton were collected on prewashed and precombusted GF/F filters by filtering a known volume (~20 l) of surface water, which was prefiltered through 200 µm and 20 µm sieves consecutively to remove microplankton and zooplankton. The filters were immediately frozen at –20°C and stored until isotope determination.

Stable isotope analyses and trophic level measurement. Zooplankton and NCC samples were treated with 10% HCl to remove bicarbonate before isotope measurements as carbonates present higher $\delta^{13}C$ values than organic carbon (DeNiro & Epstein
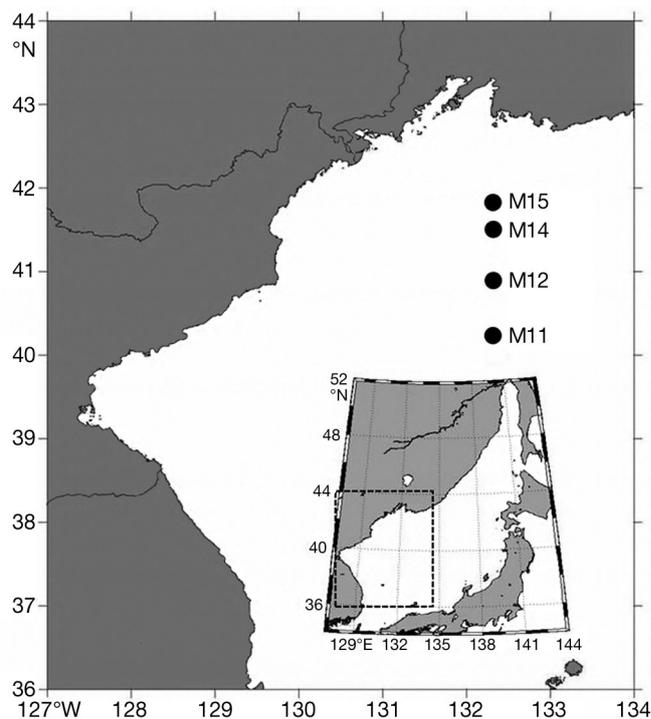

Fig. 1. Study area and sampling stations in the East Sea (Japan Sea). Inset shows general location of study area

Table 1. Data on plankton samplings in the East Sea (Japan Sea). See Fig. 1 for location of sampling stations

	Station	Towing method	Sampling layer (m)
Nano+picoplankton	M11, M12, M15	Water sample	Surface
Microplankton	M11, M12, M14	Vertical	0–30
Neocalanus cristatus carcasses	M14, M15	Oblique	0–280
Metridia pacifica	M14, M15	Oblique	0–280
Euphausia pacifica			
Juvenile	M11, M15	Oblique	0–280
Adult	M11, M14	Oblique	0–280

1978). Lipids were extracted with a 2:1 (wt%) chloroform:methanol mixture (Folch et al. 1957). The samples were then rinsed with deionized distilled water. All samples to be processed were dried in an oven at 60°C and powdered samples were kept frozen (–70°C) until the isotope analyses. Carbon and nitrogen isotope ratios were determined with continuous-flow isotope mass spectrometry. Dried subsamples (0.5 to 1.5 mg) were packaged into pressed tin capsules (Eurovector, 6 × 4 mm) designed for elemental isotope analysis. Samples wrapped in a tin capsule were oxidized at high temperature (1030°C) in a elemental analyzer (EA, Eurovector 3000 series), and the resultant CO_2 and N_2 were analyzed for stable isotope ratios with a continuous-flow isotope-ratio mass spectrometer (CF-IRMS, Micromass Isoprime). Stable isotope data were expressed as the relative difference between ratios of the sample and conventional standard gases (Vienna Pee Dee Belemnite for carbon and atmospheric N_2 for nitrogen). Delta (δ) notation is defined as the parts per thousand (‰) deviation from a standard material:

$$\delta^{13}C \text{ or } \delta^{15}N = [(R_{sample}/R_{standard}) - 1] \times 10^3$$

where $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$. A secondary standard of known relation to the international standard was used as a reference material. Measurement precision was approximately 0.1 and 0.2‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively.

The trophic (TL) level of consumers relative to primary producers (baseline) was estimated with the formula:

$$TL_{consumer} = [(\delta^{15}N_{consumer} - 3.86) / 3.4] + 2$$

where 3.86 is the $\delta^{15}N$ baseline value of primary producers (nano+picoplankton) because *Euphausia pacifica* can potentially consume food particles 2 μm in size based on morphological observation (Suh & Choi 1998). The +2 term is added because the trophic position is being estimated relative to primary consumers rather than to primary producers. An increase in $\delta^{15}N$ by about 3.4‰ per trophic level occurs as nitrogen is transferred (Minagawa & Wada 1984). We used this method to estimate the trophic level of each group of specimens of *E. pacifica*, *Metridia pacifica* and NCC. Vander Zanden & Rasmussen (2001) reported lower and more variable ${}^{15}N$ enrichment for herbivores (2.5 ± 2.5‰) than for carnivores (3.2 ± 0.4‰). Owing to this trophic level effect, $\delta^{15}N$ in the marine ecosystem can be interpreted as a function of both food sources and trophic level.

To complement our isotopic analysis, we also estimated trophic level with morphological and ecological data previously reported by Ponomareva (1963) and Suh & Choi (1998).

Multiple-source mixing model and statistical analyses. We used the IsoSource model to determine the potential contribution of phytoplankton (nano+picoplankton and microplankton), *Metridia pacifica* and NCCs to the main diets of *Euphausia pacifica* by the combination of $\delta^{13}C$ and $\delta^{15}N$ values. Essentially, the model iteratively creates all possible combinations of source proportions with each combination equaling 100% at preset increments (1% in this study) to create a set of predicted mixtures of sources, and a tolerance is initially set at 0.1‰ (see Phillips & Gregg 2003). The statistical analyses were performed with SPSS 14.0 software.

RESULTS

$\delta^{13}C$ and $\delta^{15}N$ of particulate organic matters and consumers

Both $\delta^{13}C$ and $\delta^{15}N$ values of the different sources of particulate organic matter and consumers are presented in Table 2. Mean $\delta^{13}C$ of the sources exhibited a large range of values (from –26.11 to –21.79‰) compared with $\delta^{15}N$ (from 2.11 to 5.42‰). Significant differences were observed among the sources for $\delta^{13}C$ (Kruskal-Wallis test: df = 5, p = 0.001) and for $\delta^{15}N$ (Kruskal-Wallis test: df = 5, p = 0.002), as shown in Fig. 2. However, post hoc comparisons showed indistinguishable $\delta^{13}C$ values between NCCs and *Euphausia pacifica* adults (p > 0.1), and between *E. pacifica* juveniles and microplankton (p > 0.4). For $\delta^{15}N$, post hoc comparisons revealed no significant differences between *Metridia pacifica* and *E. pacifica* juveniles (p > 0.4) and microplankton (p > 0.5). However, NCCs exhibited significantly depleted $\delta^{15}N$ (2.11‰) compared with the other sources (p < 0.001). There was no difference between adults and juveniles of *E. pacifica* in $\delta^{13}C$ (p > 0.2), whereas there was a sig-

Table 2. $\delta^{13}C$ and $\delta^{15}N$ values (mean ± SE) of food sources and consumers in the East Sea (Japan Sea). n: number of samples; TL: trophic level

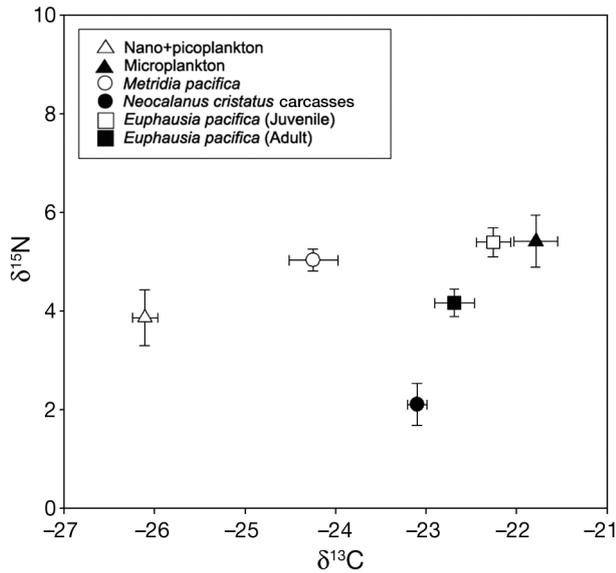|	$\delta^{13}C$ (‰)	n	$\delta^{15}N$ (‰)	n	TL
Nano+picoplankton	–26.11 ± 0.14	4	3.87 ± 0.57	4	
Microplankton	–21.79 ± 0.24	3	5.42 ± 0.53	3	
Neocalanus cristatus carcasses	–23.10 ± 0.11	6	2.11 ± 0.43	5	
Metridia pacifica	–24.25 ± 0.27	4	5.04 ± 0.22	3	2.3
Euphausia pacifica					
Juvenile	–22.26 ± 0.19	6	5.40 ± 0.30	6	2.5
Adult	–22.69 ± 0.29	5	4.17 ± 0.10	5	2.1

Fig. 2. Mean (± SE) $\delta^{13}C$ (‰) versus $\delta^{15}N$ (‰) values of food sources and consumers in the East Sea (Japan Sea)

nificant difference in $\delta^{15}N$ (p < 0.01). Differences between nano+picoplankton and microplankton were not distinguishable for $\delta^{15}N$ (p > 0.07), but significant for $\delta^{13}C$ (p < 0.05). Because the different organic matter sources had distinct $\delta^{13}C$ versus $\delta^{15}N$ values, it was possible to infer their role as trophic base for the associated fauna.

Multiple-source mixing model

In Fig. 3, IsoSource modeling values for *Euphausia pacifica* juveniles indicated that microplankton (83%) was the major food source, followed by *Metridia pacifica* (14.6%), nano+picoplankton (2.1%) and NCCs (0.3%). In the case of *E. pacifica* adults, however, the food sources consisted of microplankton (51.3%), NCCs (34%), *M. pacifica* (9.2%) and nano+picoplankton (5.5%). Contribution of microplankton to the food sources decreased from 83 to 51.3%, but that of NCCs increased remarkably from 0.3 to 34% with maturity of *E. pacifica*.
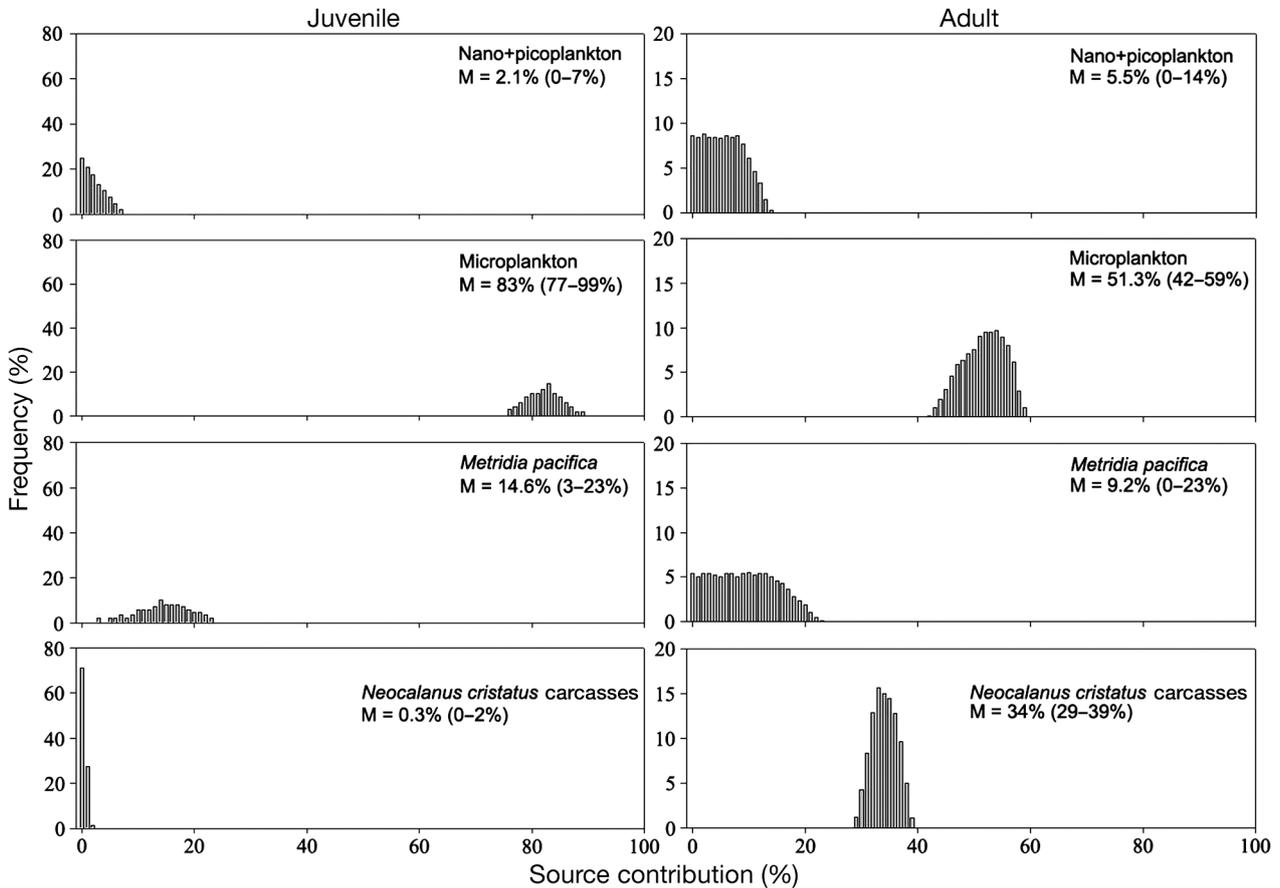

Fig. 3. *Euphausia pacifica*. Simulation of the distribution of feasible contributions of 4 sources to the diet of juveniles and adults. M = median value (ranges are 1 and 99 percentile values)

DISCUSSION

The foods of euphausiids are roughly divided into 3 categories: phytoplankton, zooplankton and detrital materials (Mauchline & Fisher 1969). Euphausiid omnivory depends on morphology of the feeding basket, foraging behaviour and prey availability. Species of *Euphausia* are thought to be omnivorous filter feeders (Ponomareva 1963, Ohman 1984, Suh & Choi 1998), and 6 pairs of thoracic legs function as a feeding basket to filter food particles (Hamner 1988). Thus, the mesh size in the feeding basket determines the range of particle sizes that euphausiids can filter and ingest, and is usually wider in carnivorous euphausiids than in herbivorous species (Suh & Choi 1998). However, morphology of the feeding apparatus alone does not predict trophic level of euphausiids in the marine ecosystem, because many herbivores are also opportunistic omnivores (Mauchline & Fisher 1969). Although some euphausiids can actively select their foods based on the size of the particles ingested, mechanoreception of prey movement or on chemosensory recognition of biochemical cues (Hamner et al. 1983), in others the quality of the ingested diet mirrors ambient phytoplankton communities (Mauchline 1980). The trophic level and feeding habits of euphausiids can be assessed by means of stomach content analysis (Hopkins & Torres 1989, Daly 2004, Meyer et al. 2009), rearing experiments (Meyer et al. 2002, Wickham & Berninger 2007) and molecular gut content analysis (e.g. immunoassay) (Theilacker et al. 1986, 1993, Bailey et al. 1993, Krautz et al. 2003). These methods are able to resolve the broad food web structure, but each has several limitations. For example, stomach content analysis provides a snapshot of information on food recently ingested in the field and a well-developed stomatogastric system makes it difficult to quantitatively and qualitatively analyze food items (Suh & Toda 1992). Rearing experiments are usually carried out under artificially controlled conditions (Schmidt et al. 2003). Moreover, molecular gut content analysis generally focuses on very few prey sources; and most such studies to date have been carried out under artificial rearing conditions (Mayfield et al. 2000). Additionally, the molecular technique requires the absence of cross-reactions that may arise from antibody affinity with proteins in nontargeted species (Krautz et al. 2003). Thus, the molecular method alone may result in misidentification of the realistic trophic position of an organism.

A combination of nitrogen and carbon stable isotopes was useful for determining the differences in trophic position and dietary quality of *Euphausia pacifica* in the East Sea. The use of nitrogen stable isotopes to calculate trophic position is based on the fact that they display a constant level of enrichment (3.4 ± 1.1‰ per trophic level) with each trophic level (Minagawa & Wada 1984). Stable carbon isotopes do not display a significant enrichment between trophic levels and as such are useful for assessing the sources of carbon in food webs (McConnaughey & McRoy 1979). Therefore, carbon isotope composition is often used to determine the food source of different organisms (Fry & Sherr 1984) rather than to determine the trophic level. Although there are many advantages to stable isotope analysis, one disadvantage occurs when temporal changes in the trophic relationship occur. There is a time lag before the stable isotope value in the tissue reflects the change from one food source to the new source (Hesslein et al. 1993, Frazer et al. 1997, Mac-Avoy et al. 2001, Maruyama et al. 2001). The difference of isotopic turnover time between zooplankton and phytoplankton can cause an inversion of the nitrogen isotope signature, which can lead to a misunderstanding of the trophic relationship.

In *Euphausia pacifica*, the isotopic turnover rate is not yet known, but growth data are available. In the East Sea, Iguchi et al. (1993) measured the growth rates of juveniles and adults of *E. pacifica* as 0.102 mm d^{-1} and 0.076 mm d^{-1}, respectively. Daly (2004) revealed that the growth rates of *E. superba* juveniles were up to 0.036 mm d^{-1} in the Antarctic Peninsula. Frazer et al. (1997) reported that organisms with a high growth rate may have high rates of isotopic turnover. Moreover, from rearing experiments Schmidt et al. (2003) found that *E. superba* juveniles did not equilibrate with a new diet within 30 d, but juveniles had significantly increased their δ^{13}C and δ^{15}N ratios after 30 d. Because *E. pacifica* seems to have a higher growth rate than *E. superba*, the isotopic shifts for *E. pacifica* may occur on a time scale of a month. Therefore, the relative depletion of ^{15}N in *E. pacifica* adults sampled in spring suggests that this species had been feeding on an isotopically light component of the food items for an extended period of time.

Simulation data also showed that the proportions of microplankton in the diets of *Euphausia pacifica* were reduced from 83% for juveniles to 51.3% for adults (Fig. 3). The high contribution of microplankton supports the contention that *E. pacifica* juveniles are primarily herbivorous. Based on rearing experiments, Ohman (1984) observed that live copepods *Pseudocalanus* sp. may be attacked and injured by *E. pacifica* adults (19.56 ± 0.45 mm total length), but they are not an optimal prey item for this omnivore, suggesting incomplete consumption of calanoid copepods by *E. pacifica*. Ohman's (1984) observation is supported by our stable isotope data. As shown in Figs. 2 & 3, it is unlikely that *E. pacifica* adults can efficiently ingest the adult stage of the calanoid copepod *Metridia paci-*

fica. Terazaki & Wada (1988) found many NCCs in bulk zooplankton samples collected throughout the year in the epipelagic layer from the East Sea owing to their slow decomposition rates under the low temperature (<1°C). Those investigators also suggested that the drifting NCCs may become a good food source for carnivorous zooplankton and fishes. Since the heavy nitrogen isotope of NCCs is depleted relative to phytoplanktonic food sources (nano+picoplankton and microplankton), it is likely that detritivory by *E. pacifica* adults accounts for the observed pattern. Isotopic value of NCCs seems to be the primary determinant of isotopic composition in adults. Evidence of stable isotopes is consistent with a shift to a detritivorous mode of feeding as descent in trophic level is generally associated with a stepwise depletion in ^{15}N (Minagawa & Wada 1984). Consequently, consumption of NCCs may result in *E. pacifica* adults being descended by 0.4 trophic levels below juveniles (Table 2).

In the East Sea, there was some evidence for a significant difference in $\delta^{15}N$ between juveniles and adults of *Euphausia pacifica* sampled in spring, suggesting the ontogenetic diet shift of adults to detritivory. However, the extent to which seasonal and geographical differences might be represented was not known. Like other studies on diet (Werner & Gilliam 1984, Polis & Strong 1996), our results cast considerable doubt on the certainty of the assumption of classical food-chain models that species recognize single, discrete trophic niches in nature (Branstrator et al. 2000).

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