Nitrogen and carbon stable isotopic ecology in the ocean: The transportation of organic materials through the food web

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Abstract—Organic matter originally synthesized by primary producers is transported through food webs to higher trophic level animals. The transportation mechanism of organic matter through the food web has been investigated by various means. Direct observations of feeding behavior or gut contents have been traditionally used but this gives information only on temporal food habits. Long-term food habits of organisms may be deduced from the natural abundance of stable isotope ratios of carbon ($^{13}$C/$^{12}$C) and nitrogen ($^{15}$N/$^{14}$N) of organisms. Since isotopic fractionation occurs in the biochemical process, heavy isotopes are enriched in the bodies of predatory organisms. The enrichment in $^{15}$N is large whilst that of $^{13}$C is less marked. The nitrogen isotope ratio is therefore useful as an indicator of the trophic level of an organism, whilst the carbon isotope ratio is affected by the food source.

In the sea, primary production from the surface water is also transported vertically as food webs contain many macrozooplankton and micronekton that are vertical migrants. Therefore, marine food webs expand not only horizontally but also vertically and their predator-prey relationships significantly contribute to the vertical transportation of organic matter. Therefore, the stable isotope ratios are useful to examine the importance of downward pathways of organic matter through the food web. We will briefly show results which indicate that the vertical migrations of macrozooplankton and micronekton play a role of quick vertical transporters of organic materials in the western North Pacific.

INTRODUCTION

Marine food webs are very complex three dimensional systems which range from the sea surface to the sea bed. They have longer trophic steps and more species in each trophic compartment than terrestrial food webs (COHEN, 1994). Therefore, marine food webs have rarely been described accurately. Direct observations of gut contents and feeding behavior are important methods of analyzing food webs (e.g. HOPKINS, 1985, 1987; BRODEUR and PEARCY, 1992). These methods are qualitative and reflect the temporal feeding habits of organisms to a species level, but these methods are limited in quantitative analyses. By contrast, some natural chemical tracers such as fatty acids (e.g. SARGENT and FALK-PETERSEN, 1981; REINHARDT and VAN VLEET, 1986; FALK-PETERSEN et al., 1987), pigments (e.g. ABELE-OESCHGER et al., 1992),

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heavy metals (e.g. HAMANAKA and TSUJI, 1981; MACDONALD and SPRAGUE, 1988; RAINBOW, 1989), and radioactive isotope ratios (e.g. HEYRAUD and CHERRY, 1979; HEYRAUD et al., 1988) have been used more quantitatively and indicate the long-term feeding trends.

Since the late 1970’s, the stable isotope ratios of carbon and nitrogen in organisms have been used as tracers in studies of organism’s feeding habits. The usefulness of these isotope ratios in the study of marine food webs is briefly reviewed in this article.

HISTORICAL REVIEW

An early study by DE NIRO and EPSTEIN (1978b) showed the differences of prey types between two hyrax species using carbon isotope ratios. FRY et al. (1978) measured $^{13}$C/$^{12}$C ratios of many species in a sand dune and deduced the structure of the food web. MCCONNAUGHY and McROY (1979) applied the isotope method to the study of marine food webs. The stable isotope ratios for carbon and nitrogen are expressed as,

$$\delta^{13}C(\%) = \left( \frac{^{13}C/^{12}C}_{sample} \right) \cdot 1000,$$

$$\delta^{15}N(\%) = \left( \frac{^{15}N/^{14}N}_{sample} \right) \cdot 1000$$

where PDB represents the Pee Dee Belemnite standard.

Both $\delta^{13}$C and $\delta^{15}$N of metazoans reflect the stable isotope ratios of their diet (MIYAKE and WADA, 1967; DE NIRO and EPSTEIN, 1978a). Organic nitrogen and carbon are oxidized and utilized in the body and excreted as a byproduct of metabolism. Since the reaction velocity of the oxidation of lighter isotopes are faster than that of heavier ones, fractionation occurs in the biochemical process. Therefore, light isotopes are excreted from the body of organisms faster than heavy ones, and heavy isotopes are enriched in the body of organisms (CHECKLEY and MILLER, 1989). A small enrichment (less than 2%) in $\delta^{13}$C has been observed during the feeding process of many species (DE NIRO and EPSTEIN, 1978a; FRY and SHERR, 1984; WADA et al., 1987a). MONTEIRO et al. (1991) measured $\delta^{13}$C in many organisms and traced the food web from phytoplankton to fish by examining the $\delta^{13}$C enrichment. However, it is difficult to utilize the carbon isotope ratio as a tracer of the trophic level, because fractionation of carbon occurs in various organs and organic compounds of animal body (DE NIRO and EPSTEIN, 1978a; YONEYAMA et al., 1983; SHOLTON-SMITH et al., 1991). For example, the $^{13}$C content of lipid is considerably lower than those of other compounds e.g. proteins etc. (McCONNAUGHY and McROY,
The fractionation of \( \delta^{13}C \) values in various organs is larger than that occurs in the feeding process.

The \( \delta^{15}N \) value of a predator is ubiquitously 3–4\% higher than that of the prey (Minagawa and Wada, 1984; Fry, 1988), suggesting that it is more suitable as an index of trophic level than the \( \delta^{13}C \) value. The stepwise increase of the nitrogen isotope ratio with increasing trophic levels has been documented. Minagawa and Wada (1984) measured \( \delta^{15}N \) of marine and freshwater animals from various seas and lakes, and concluded that the \( \delta^{15}N \) values can be used to deduce the trophic level of animals in various ecosystems. Wada et al. (1987a) found that \( \delta^{15}N \) is enriched by 3.3\% per one trophic level and revealed quantitatively the food web from phytoplankton to fish in the Arctic Ocean. Rau et al. (1992) and Hobson and Welch (1992) also investigated the Antarctic and Arctic food webs with the same method. In these papers, trophic distances between various organisms were illustrated in the diagrams. From Hobson and Welch (1992), \( \delta^{15}N \) was least enriched for POM (particulate organic matter), most enriched for polar bears, and there were 5 trophic levels between them. The advantages of nitrogen isotope are: it can be adopted ubiquitously for species of metazoans, and it is a parametric indicator of the trophic distance between each species.

The \( \delta^{13}C \) values of the organisms are similar to that of the primary producer when the food web has a single carbon source. In ecosystems which have two carbon sources, the contribution of each source can be estimated from following equation:

\[
\frac{f_A}{\text{\%}} = \frac{\delta^{13}C_{\text{source A}} - \delta^{13}C_{\text{sample}}}{\delta^{13}C_{\text{source A}} - \delta^{13}C_{\text{source B}}} \cdot 100
\]

where \( f_A \) represents the percentage contribution of carbon source A. Wada et al. (1987b) estimated the percentage contribution of land-derived organic materials in estuarine and bay sediments. Kojima and Ohta (1989) analyzed the carbon supply of planktonic and terrestrial components for a benthic ecosystem. These studies are good examples of the usefulness of carbon isotope ratio for deducing the carbon sources of a food web. Thus, the \( \delta^{13}C \) values are affected by the carbon source rather than by fractionation through the food web in natural ecosystems.

For studying the pathway of a food web, the simultaneous use of \( \delta^{13}C \) as an indicator of the food source and \( \delta^{15}N \) as an indicator of trophic level is most effective. Welch and Parsons (1993) found a positive correlation between \( \delta^{15}N \) and \( \delta^{13}C \) values of various salmon species with the only exception being the carbon isotope data of chum salmon which did not fit the general trend. They concluded that chum salmon and other salmon species belong to different branches of the food web.

It should be noted here the following constraint for the stable isotopic method. Because these isotopic values do not have any species specificity, they cannot reveal any predator-prey relationship between individual species. Even when the trophic level of species A is one step higher than species B, we cannot categorically say that species A is a predator of species B. For example, Hobson and Welch (1992) found the trophic level of a small carnivorous crustacean was higher than walrus. It is
obvious that a small crustacean cannot predate on walrus. Thus, food webs cannot be deduced from only the stable isotope ratios. Direct observations of gut contents and/or feeding behavior is also required to be carried out simultaneously to validate any suggested trophic relationships.

![Graph showing isotopic values for different marine organisms in the North Pacific and Japan Sea.](image)

Fig. 1. $\delta^{15}N$ and $\delta^{13}C$ value distributions of macrozooplankton and micronekton.
CARBON AND NITROGEN ISOTOPES OF MACROZOOPLANKTON AND MICronekton AROUND JAPAN

We measured stable carbon and nitrogen isotopes of macrozooplankton and micronekton together with observations of their gut contents and vertical migration behaviors in the Japan Sea and the western North Pacific off Japan. Details of the study will be published elsewhere. In the Pacific Ocean, δ¹³C values of various organisms are relatively constant (Fig. 1(a)). This implies that the pelagic community originates from a single carbon source, e.g. the phytoplankton. On the other hand, δ¹³C values of organisms in Japan Sea are variable, ranging from −21 to −25‰ (Fig. 1(b)). Especially, the δ¹³C values of the abundant pelagic amphipod, *Themisto japonica*, varied widely. This suggests that there are several carbon sources for this amphipod. SUGISAKI et al. (1991) reported that *T. japonica* did not inhabit below 500 m depth in the Pacific Ocean, although they distribute from the surface to below 2000 m, even being found on the sea bottom in the Japan Sea (SATO, 1988). Since a variety of organisms were detected from the gut contents of *T. japonica* (SUGISAKI et al., 1990, 1991), they might fed on benthos which could have another carbon source, such as land derived carbon, other than phytoplankton. This may be the reason why the carbon isotope ratios of *T. japonica* in the Japan Sea show a broad variation of values. It is also likely that *T. japonica* provides a benthic carbon source to the pelagic community by its diel vertical migration in the Japan Sea.

From the δ¹⁵N data (Fig. 1), the difference of trophic structures of organisms between the Japan Sea and the Pacific Ocean can be seen. Many species in the Japan Sea are distributed to deeper layers compared to their conspecifics in the adjacent seas (VINOGRADOV, 1968; SUGISAKI et al., 1991; TERAZAKI, 1993). In the Pacific Ocean, many species of mesopelagic fish distribute below 500 m day and night. On the contrary, in the Japan Sea, the cold proper water (the Japan Sea Proper Water) does not allow most mesopelagic fish species to migrate through this temperature discontinuity. NISHIMURA (1968, 1969) hypothesized that some species which compete for food with mesopelagic fish can intrude into the mesopelagic layer and occupy their niche, because this niche is vacant in the Japan Sea. *T. japonica* in the Pacific Ocean showed δ¹⁵N values of <7.3‰ and its trophic level was lower than that of mesopelagic fish. In the Japan Sea, however, the δ¹⁵N values of *T. japonica* spread upward to 10‰, suggesting that *T. japonica* occupied the trophic level of plankton feeder instead of the mesopelagic fish. This gives substance to Nishimura’s hypothesis, and shows that stable isotope ratios are useful indicators of the trophic niche within an ecosystem.

VERTICAL TRANSPORT OF ORGANIC MATTER THROUGH THE FOOD WEB, DEDUCED FROM STABLE ISOTOPE RATIOS

Rapid transportation of materials from the surface to abyssal depths in the ocean have been shown by various radioactive tracers (e.g. HEYRAUD et al., 1976; PEARCY et al., 1977a). The downward flux is considered to be mediated by sinking particles as well as the vertical migration of organisms. In contrast to terrestrial ecosystems, organisms segregate their habitat vertically in marine ecosystems. Some species
inhabit above the pycnocline which can be a barrier to the sinking of particulate organic matter, some inhabit below the pycnocline, and others migrate vertically across the pycnocline. Distances of their diel vertical migrations vary from a few meters to more than a 100 m. It has been suggested that organic matter synthesized in euphotic zone are successively fed on by higher trophic animals and transported to progressively deeper depths by diel vertical migration of zooplankton and micronekton (RILEY, 1951; VINOGRADOV, 1962).

We have data from two cold water masses around Japan which show downward transport of organic matter taking place through the food web. Details of the observations will be published elsewhere. The vertical distribution of low trophic level zooplankton (grazers) as determined by the $\delta^{15}$N values are mirror images of those of high trophic level zooplankton (predators) almost throughout the day in both areas (Fig. 2). The grazers seemed to migrate vertically to avoid their predators.

Fig. 2. Relative abundance of low trophic level organisms (filter-feeding zooplankton level; solid line) and high trophic level organisms (carnivorous zooplankton level; broken line) which are grouped by averaged $\delta^{15}$N values.
However, at dawn, grazers in the surface layer migrated downward and encounter their potential predators (Fig. 2). Another example which had resolution to the species level, was obtained in western North Pacific during spring. The $\delta^{15}$N value of *Diaphus theta*, a myctophid fish, was low compared to other mesopelagic fishes (Fig. 3). This species ascends to the near surface layer and feeds on zooplankton at night and descends below 200 m depth in daytime (Pearcy *et al.*, 1977b). We observed that the gut contents of *D. theta* were mainly copepods, especially *Metridia*

![Graph](image)

Fig. 3. $\delta^{15}$N values of dominant species of crustacean macrozooplankton and mesopelagic fish in the western subarctic North Pacific.
*pacific*ca, one of the dominant copepod species in the shallow layer. GORDON et al. (1985) also examined the gut contents of many species of mesopelagic fish, and reported that the copepods *Metridia* spp. were important as food for *D. theta* and that they are eaten in the surface and near surface layers. *M. pacifica* is an active vertical migrant, and the trophic level of *M. pacifica* is low compared with those of other filter-feeding copepods (e.g. *Neocalanus* spp., Fig. 3). From the measurement of gut pigment, it is revealed that *M. pacifica* fed on phytoplankton, while other grazing copepods do not depend on phytoplankton for their main food source (Table 1). Other species of mesopelagic fish investigated in this study, *Lampanichthys jordani* and *Stenobrachius leucopsar*us, do not ascend to the surface and hence feed at deeper layers (PEARCY et al., 1979). From these results, *D. theta* fed on the low trophic level zooplankton which mainly fed on phytoplankton. A pathway from the phytoplankton to mesopelagic fish was thus traced. In conclusion, a part of the organic matter produced by phytoplankton is transported downward daily through the feeding process, and some mesopelagic organisms rely on this pathway to sustain their biomass.

ALTABET and SMALL (1990) reported that the δ¹⁵N of sinking particles and faecal pellets of macrozooplankton are similar. These faecal pellets were mainly produced above 150 m depth. SAINO and HATTORI (1987) reported that the δ¹⁵N values of sinking materials are constant below 300 m depth in the western Pacific. These results imply that sinking particles are produced in shallow layers and sink to the deep layers without any other feeding processes occurring. If deep-sea organisms mainly utilize these sinking particles as a food source, the δ¹⁵N value of organisms

<table>
<thead>
<tr>
<th>Species</th>
<th>Stage</th>
<th>Ingestion rate</th>
<th>Metabolic requirement</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Chl (ng cop⁻¹d⁻¹)</td>
<td>Carbon a (µg cop⁻¹d⁻¹)</td>
</tr>
<tr>
<td><em>Neocalanus cristatus</em></td>
<td>CV</td>
<td>208.61</td>
<td>3.26</td>
</tr>
<tr>
<td><em>N. flemingeri</em></td>
<td>CV</td>
<td>29.81</td>
<td>0.47</td>
</tr>
<tr>
<td></td>
<td>CV</td>
<td>11.18</td>
<td>0.17</td>
</tr>
<tr>
<td><em>Eucalanus bungii</em></td>
<td>female</td>
<td>13.81</td>
<td>0.22</td>
</tr>
<tr>
<td></td>
<td>CV</td>
<td>9.71</td>
<td>0.15</td>
</tr>
<tr>
<td></td>
<td>CV</td>
<td>6.64</td>
<td>0.10</td>
</tr>
<tr>
<td><em>Metridia pacifica</em></td>
<td>female</td>
<td>142.76</td>
<td>2.23</td>
</tr>
<tr>
<td><em>Pleuromammma scutullata</em></td>
<td>female</td>
<td>36.42</td>
<td>0.57</td>
</tr>
<tr>
<td><em>Gaetanus simplex</em></td>
<td>female</td>
<td>72.84</td>
<td>1.14</td>
</tr>
</tbody>
</table>

aEstimated using a C/chl ratio of 16 (Montani, personal communication).
bEstimated from IKEDA (1974).
should be constant below 300 m. On the contrary, if meso- and bathypelagic organisms eat living animals which are brought by diel and ontogenetic migrations rather than sinking particles, the $\delta^{15}N$ values of organisms should increase with the depth of their habitat. So far, information about the stable isotope ratios of meso- and bathypelagic organisms is limited. The downward transport of organic matter through the food web has not been quantitatively analyzed yet. However, Figs. 2 and 3 imply that the trophic level of organisms increases with depth. Moreover, VAN DOVER and FRY (1989) reported that $\delta^{15}N$ values of benthic organisms in deep-sea species (2600 m in depth) were relatively high. Then, it is plausible that deep-sea organisms depend on repeated feeding processes for their supply of organic materials. Thus, studies using stable isotopes will help to elucidate the importance of the downward pathways of organic matter in deep-sea ecology.

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