

Stable-isotope and electron-microscopic evidence that cyamids (Crustacea: Amphipoda) feed on whale skin

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Abstract: Cyamids (Crustacea: Amphipoda) are found only on whales. Observational evidence and the morphology of the mouthparts have indicated that whale skin is the primary food for these organisms. It has also been suggested, however, that the cyamids may be feeding on epidermal diatoms and meiofauna associated with the skin or using the whales as transport to regions of high zooplankton densities, where small pelagic organisms are captured while the whales feed. Here we report electron-microscopic and isotopic evidence that whale skin was ingested and assimilated by cyamids. Stable carbon and nitrogen isotope ratios of cyamids and whale skin from six species of whales were compared with those of zooplankton from the regions through which the whales migrate, to infer the most likely food sources. In all cases, cyamid isotope ratios closely matched those of the whale skin and not those of the zooplankton, again indicating that whale skin was the predominant food source. Unlike most other carnivorous organisms, cyamids do not show a trophic enrichment of $\delta^{15}\text{N}$, a trait also found in other species of Amphipoda.

Résumé : Les cyamidés (Crustacea: Amphipoda) ne vivent que sur les baleines. Des observations et l'examen de la morphologie des pièces buccales indiquent que la peau des baleines est la principale source de nourriture de ces organismes. Il a cependant été suggéré que les cyamidés se nourrissent peut-être de diatomées épidermiques et de la meiofaune associée à la peau ou qu'ils utilisent les baleines pour leur transport vers des zones riches en zooplancton où les petits organismes pélagiques sont capturés pendant que les baleines se nourrissent. Nous présentons ici des illustrations au microscope électronique et des preuves par les isotopes que la peau des baleines est bel et bien consommée et assimilée par les cyamidés. Les rapports entre les isotopes stables de carbone et d'azote des cyamidés et de la peau de six espèces de baleine ont été comparés avec le zooplancton des régions situées le long des routes de migration des baleines pour repérer les sources de nourriture les plus probables. Dans tous les cas, les rapports entre les isotopes chez les cyamidés sont semblables à ceux de la peau de baleine, mais pas à ceux du zooplancton, confirmant que la peau de baleine est la principale source de nourriture. Contrairement à ce qui prévaut chez la plupart des carnivores, on ne trouve pas chez les cyamidés l'enrichissement trophique de $\delta^{15}\text{N}$ que l'on rencontre parfois chez d'autres espèces d'amphipodes.

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Introduction

Cyamids (Crustacea: Amphipoda) live only on whales, and there is morphological and observational evidence that cyamids feed primarily on the whales' skin tissue (Leung 1976; Samaras and Durham 1985; Sokolov and Evgen'eva 1988; Rowntree 1996). There was a close correlation between the color of the intestinal contents of fresh specimens of whale lice, *Cyamus boopis*, from a stranded humpback whale and that of the patch of whale skin (black or white) from which the cyamids were collected (Rowntree 1996).

Similarly, live specimens of the right whale cyamid, *Cyamus ovalis*, maintained in an aquarium were observed to feed on right whale skin by sweeping the maxilliped palps of the mouth back and forth across the surface. Also, their intestinal contents were observed to pass through the gut at the rate of one body segment per hour. However, there is a close taxonomic relationship between cyamids and caprellids, and cyamids, like caprellids, often assume an upright stance with the anterior portion of their body held vertically and their hind legs clasping the substrate. This suggests that cyamids, like caprellids, might also feed on diatoms, protozoans, and crustaceans and that they might even join their right whale hosts when they feed on dense aggregations of zooplankton (Rowntree 1996). E.A. Caine (quoted in Rowntree 1996) has argued that the structure of cyamid mouthparts precludes feeding on free-living organisms and suggests that cyamids are obligate ectoparasites. Nevertheless, if a whale was feeding in dense aggregations of copepods or other zooplankton prey, it might be possible for cyamids to feed opportunistically and supplement their diet even though they were not primarily adapted for that mode of feeding.

We used electron microscopy of cyamid digestive tracts and the stable-isotope ratios ($^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$, expressed

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as $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively) of cyamids and their associated whale hosts to indicate whether the cyamids were eating whale skin or zooplankton. Stable-isotope ratios can be used to trace dietary carbon and nitrogen and indicate trophic relationships (Fry and Sherr 1984; Wada et al. 1987). Since many marine environments contain isotope-ratio gradients across water-mass boundaries and currents, the isotope ratios can also provide information on migratory movements of mobile species (Saupe et al. 1989; Best and Schell 1996; Schell et al. 1998). The accession of cyamids singularly associated with six species of whales (bowhead whale, *Balaena mysticetus*; northern right whale, *Eubalaena glacialis*; southern right whale, *Eubalaena australis*; narwhal, *Monodon monoceros*; humpback whale, *Megaptera novaeangliae*; and gray whale, *Eschrichtius robustus*), along with pieces of skin, provided an opportunity to use stable-isotope ratios of carbon and nitrogen as indicators of direct feeding on the host versus use of the host as transportation to regions of high potential prey density.

The carbon-isotope ratio of a consumer closely matches that of its diet. When dietary carbon is consumed and incorporated into tissues, the isotope ratio of the tissue is generally conservatively within 0.5–1.0‰ of the diet (DeNiro and Epstein 1978; Fry and Sherr 1984). The assimilated nitrogen incorporated into consumer tissues also reflects the initial isotope ratio ($\delta^{15}\text{N}$) of the food source, but subsequent protein metabolism results in fractionation and the preferential loss of the lighter isotope during excretion. When the dietary nitrogen of the consumer is in excess of requirement, tissues are typically enriched in the heavy isotope by 3–5‰ relative to the diet (Minagawa and Wada 1984; Wada et al. 1987; Michener and Schell 1994). Thus, for most marine herbivores and carnivores, carbon-isotope ratios closely match those of the diet, while nitrogen-isotope ratios are enriched relative to the diet and can indicate the trophic level at which the consumer is feeding (Yoshioka and Wada 1994). If cyamids are eating whale skin, their carbon-isotope ratios should be similar to that of their host's skin and their nitrogen-isotope ratios should be enriched relative to their host's skin, if protein is the primary energy source.

Some marine amphipods do not conform to this model and may be enriched or depleted in the heavier isotope relative to their food source. Macko et al. (1982) reported the isotope ratios of two species of herbivorous amphipods collected from natural settings and from specimens raised on macrophytic algae under laboratory conditions. Specimens of *Amphithoe valida* were slightly depleted (<1‰) in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ relative to their diet, whereas *Paryhale hawaiiensis* had 2.3‰ enrichment in $\delta^{15}\text{N}$ and were lower in $\delta^{13}\text{C}$ by approximately 1‰. Also, Schell (1992) reported that *Parathemisto libellula* and *Parathemisto pacifica* from Alaskan waters were similar in $\delta^{13}\text{C}$ to calanoid copepods but typically 3‰ lower in $\delta^{15}\text{N}$ than chaetognath predators of the copepods at the same sites. *Parathemisto* spp. are known to be carnivorous and would be expected to show a higher $\delta^{15}\text{N}$ than herbivorous copepods. Hobson and Welch (1992) collected food-web components from Barrow Strait – Lancaster Sound in the Canadian Arctic and reported a typical trophic enrichment in $\delta^{15}\text{N}$ of nearly 3‰ for the carnivorous amphipod *Stegocephalus inflatus*, but did not find similar enrichment in *Onisimus* spp., which are also omnivorous.

Onisimus spp. had $\delta^{15}\text{N}$ values about 2 and 1‰ higher than calanoid copepods and mysids, respectively, whereas calanoid copepods were 4‰ enriched relative to particulate organic matter (presumably phytoplankton) collected from the water column.

The close correlation of amphipod isotope ratios with those of their food source leads us to hypothesize that if the cyamids are feeding solely or primarily on whale skin, their carbon- and nitrogen-isotope ratios should consistently match those of the skin or be at a constant offset. Since all the species of whales maintaining cyamids that were examined, with the possible exception of *M. monoceros*, migrate across large gradients in isotope ratios in their marine environments (e.g., Rau et al. 1991a; Best and Schell 1996; Schell et al. 1998), feeding by the cyamids on a significant amount of zooplankton should result in wide deviations from the isotope ratios of whale skin. The cyamids would also be expected to show a tendency to match the zooplankton in the location where they were collected. The whales feed seasonally in habitats of high zooplankton abundance, typically at the higher latitudes of their range. The isotope ratios of the skin would reflect an integration of the predominant food sources.

Methods

Sample collection

Cyamids and host-skin samples (Table 1) were collected from six species of whales: humpback whale, gray whale, northern right whale, southern right whale, narwhal, and bowhead whale. In most cases, whale-skin samples came from the cyamids' claws and were collected fortuitously when the cyamids were removed from stranded whales. All cyamids and skin were collected from stranded whales, with the exception of *Cyamus scammoni* (February 1982) collected from "friendly" gray whales and *Cyamus monodontis* from narwhal and *Cyamus ceti* from bowhead whales taken during hunts. Cyamids and skin samples associated with them were placed in 70% ethanol for long-term storage, except for the bowhead whale samples, which were collected fresh and frozen. Some samples were placed in 10% formalin at the collection site and later transferred to 70% ethanol and further treated as noted below. The narwhal cyamid was initially preserved in Scotch whiskey and later transferred to 70% ethanol. The $\delta^{13}\text{C}$ values of the formalin-preserved samples may have been altered by carbon from reacted formaldehyde, but no significant difference was noted when comparisons were made with samples that had been stored in alcohol or were frozen (bowhead whale cyamids).

Electron microscopy

Cyamus boopis were collected from a humpback whale and initially preserved in 70% ethanol. They were subsequently postfixed in 5% glutaraldehyde – 4.4% formaldehyde – 2.75% picric acid in 0.05 M sodium cacodylate buffer at pH 7.4 (Pfeiffer and Lowe 1989). Skin was also collected from the head of a southern right whale and fixed initially in the above glutaraldehyde fixative.

The proximal digestive tract of the fixed cyamid, which can be readily observed in the intact specimen under a dissecting microscope, was removed for electron microscopy. The fixed cyamid foregut and whale skin were postfixed in 1% osmium tetroxide in 0.1 M cacodylate buffer for 1 h, washed in buffer again, and dehydrated in an ethanol series for transmission electron microscopy (TEM). Semithin sections (1 μm) were cut from specimens embedded in Poly/bed 812 (Polysciences) for preliminary study and orientation by light microscopy. Thin sections for TEM were doubly

Table 1. Carbon- and nitrogen-isotope ratios of whale skin and associated cyamids.

	Collection date	Associated cyamids	Collection date	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
Humpback whale	1984			-20.3	15.5
		<i>C. boopis</i>		-18.3	13.7
	31 December 1987			-19.2	13.6
		<i>C. boopis</i>		-18.8	10.5
	31 August 1988			-19.2	13.3
		<i>C. boopis</i>		-18.3	11.7
	1987			-19.5	10.9
		<i>C. boopis</i>		-20.0	12.8
	6 November 1982			-17.9	15.3
		<i>C. boopis</i>		-16.9	14.3
Gray whale	10 December 1987			-20.4	12.9
	20 February 1982			-16.2	14.1
		<i>C. scammoni</i>		-15.3	11.8
	14 February 1982			-15.1	13.8
		<i>C. scammoni</i>		-13.7	13.8
	8 February 1982			-15.8	13.6
		<i>C. scammoni</i>		-13.7	13.8
	22 March 1986			-16.9	15.3
		<i>C. ceti</i> *		-16.5	15.3
		<i>C. scammoni</i> *	22 March 1986	-16.9	15.3
	<i>C. scammoni</i> *		-16.4	14.7	
Northern right whale	13 March 1991			-20.6	12.8
		<i>C. ovalis</i> *		-19.3	12.8
	10 January 1993			-21.4	10.7
		<i>C. ovalis</i>		-19.4	11.3
	24 February 1983			-18.6	11.9
		<i>C. ovalis</i>		-18.4	11.5
		<i>C. gracilis</i>		-16.0	12.4
Southern right whale	17 July 1995			-23.3	10.9
		<i>C. ovalis</i> *		-20.6	11.9
	October 1995			-22.4	6.8
		<i>C. erraticus</i>		-19.9	6.8
	25 October 1993			-22.4	7.5
	<i>C. ovalis</i>		-21.4	7.5	
	<i>C. erraticus</i>		-22.4	8.9	
Narwhal	4 July 1983			-16.9	17.1
		<i>C. monodontis</i>		-16.8	16.3
Bowhead whale	95B13 (black skin)			-19.7	14.0
		<i>C. ceti</i> (specimen 1)		-18.2	14.3
		<i>C. ceti</i> (specimen 2)		-18.6	14.8
		<i>C. ceti</i> (specimen 3)		-18.3	14.9
	95B16 (black skin)			-20.5	13.7
	95B16 (white skin)			-20.6	13.6
		<i>C. ceti</i>		-22.4	13.8

*Fixed initially in formaldehyde solution and stored in 70% ethanol.

stained with lead citrate and uranyl acetate and studied with a JEOL 100 CX-II transmission electron microscope operating at 80 kV.

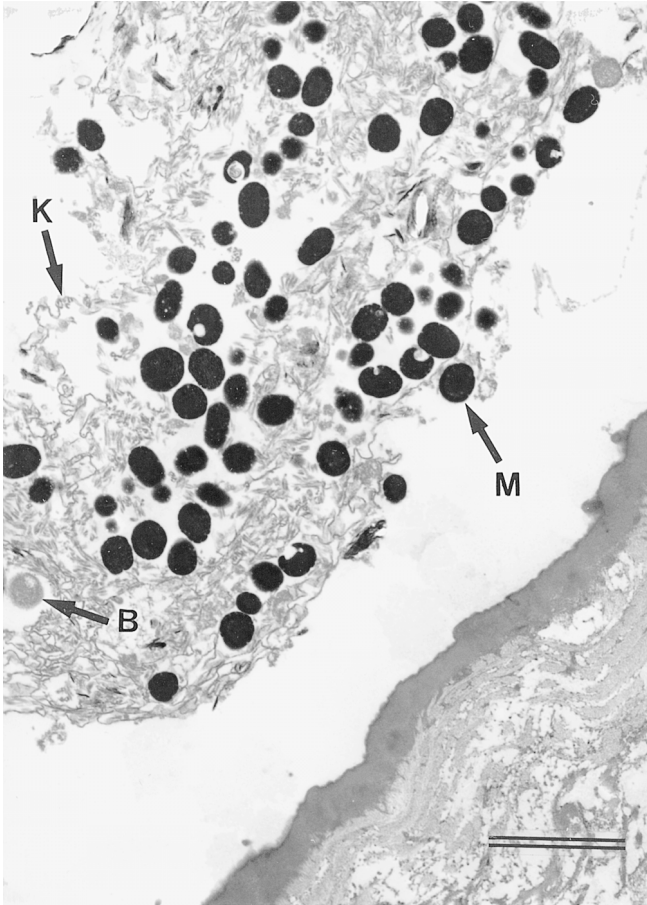
Stable-isotope ratios

Samples of whale skin were dried and powdered and a 1-mg subsample was analyzed for stable-isotope ratios. No attempts were made to remove lipids, and the analyses represent "whole-skin" composition. Cyamid and skin samples, having been stored in alcohol, may have had some of the lipids extracted, but the isotope ratios of the frozen bowhead whale tissues were assumed to

be unchanged by preservation. Lipids, being more depleted in ^{13}C , can offset isotope ratios if they comprise a large fraction of the sample. We did not note such offsets when comparing frozen and preserved samples.

Samples of cyamid legs were acidified to remove any carbonate in the exoskeleton, dried, and ground to a fine powder; subsamples (~1 mg) were analyzed for carbon- and nitrogen-isotope ratios on a Europa ANCA automated mass spectrometry system. This system burns the sample to carbon dioxide and nitrogen gases, separates the gases by gas chromatography, and then determines the isotope ratios on the eluted gases sequentially. Replicability for the entire

Fig. 1. Partially digested epidermal cetacean keratinocyte in the gut lumen of *C. boopis*. Cuticle-lined epithelium of the proximal aspect of the cyamid foregut can be seen at the lower right. Note the numerous electron-dense melanosomes (M), keratin fibers (K), and lighter inclusion bodies (B) that resemble lipid in the skin cell. Scale bar = 2 μm . $\times 9100$.



procedure and machine precision was $\pm 0.15\%$ for both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. Working standards were a peptone and powdered bowhead whale baleen.

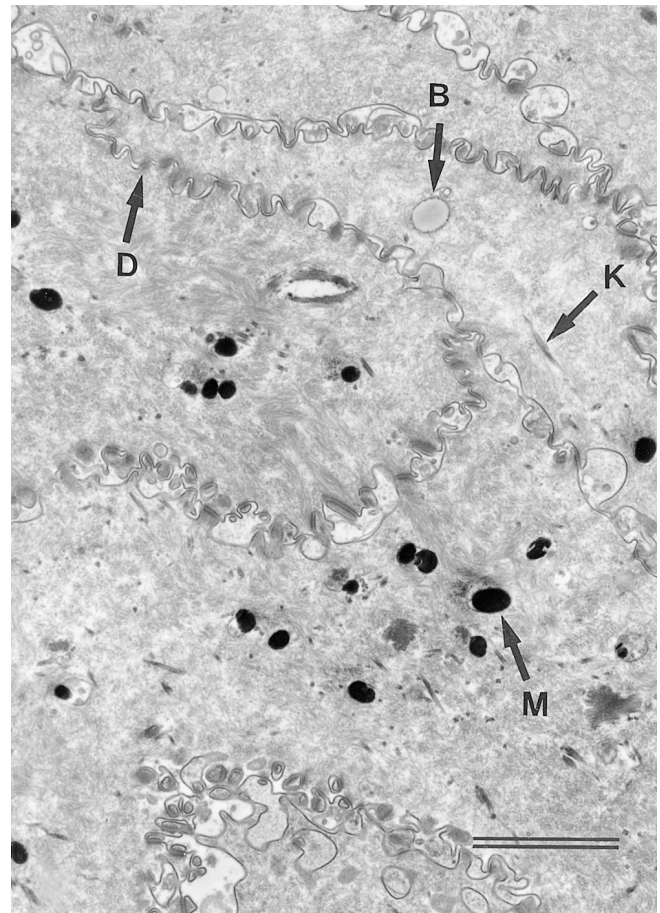
Zooplankton data were obtained primarily from literature sources, but six stations were sampled on the continental shelf and at the shelf break along the Patagonian coastline. All samples were collected and dried prior to analysis and no preservatives were used. Copepods from four stations and euphausiids from two stations were run for isotope ratios as described above. Copepods and euphausiids from northern right whale feeding grounds were collected from continental shelf waters off Cape Cod, Mass., as part of a right whale feeding study.

Results and discussion

Electron microscopy

Partially digested and fragmented cetacean epidermal cells were observed (Fig. 1) within the lumen of the cyamid foregut. Fully intact electron-dense melanosomes, fragments of cytoplasmic keratin, and occasional cytoplasmic bodies of only moderate electron density that resembled lipid bodies were observed in the foregut lumen. These partially digested epidermal cells (keratinocytes) closely resembled normal intact cetacean epidermal cells such as those shown in Fig. 2

Fig. 2. Normal, intact epidermal keratinocytes sampled from a southern right whale (head region), showing a few melanosomes (M), keratin fibers (K), lipid inclusion bodies (B), and numerous desmosomes (D). Scale bar = 3 μm . $\times 6400$.

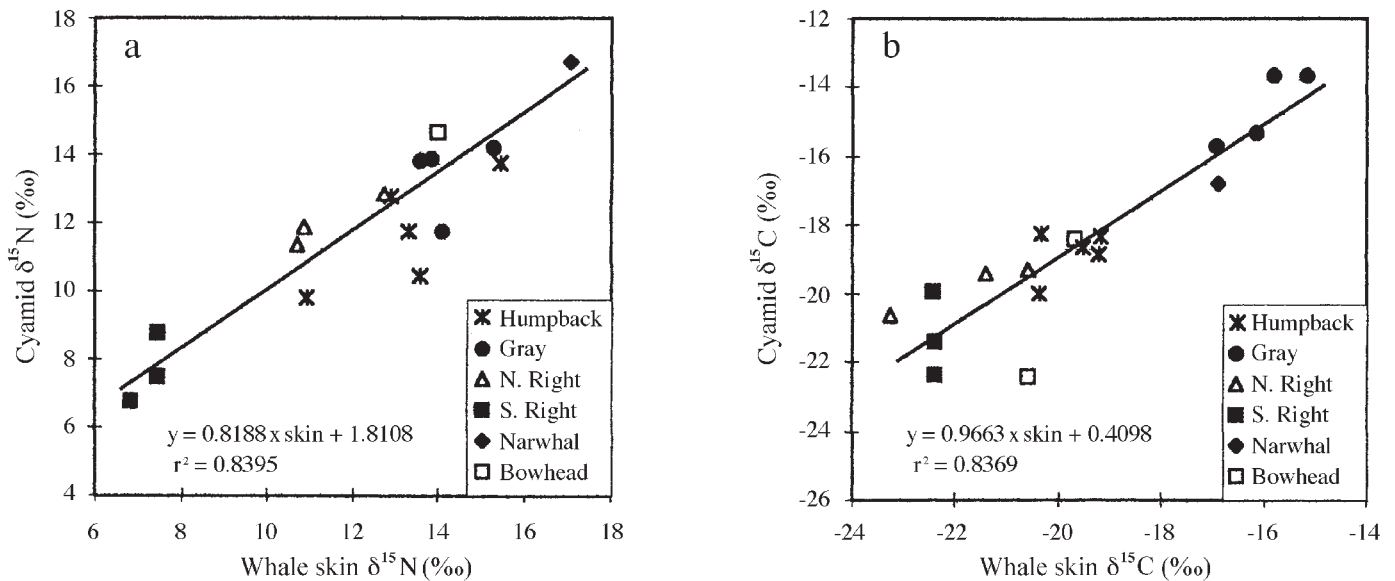


that contain the same organelles. The innermost lining of the cyamid foregut consisted of cuticle (Fig. 1) in this region, indicating that it was close to the oral–esophageal zone. Deeper musculature (not shown) was also seen nearby. Non-epidermal luminal detritus was not seen.

The detritus in the lumen of the cyamid foregut was sufficiently intact to clearly indicate the presence of cetacean epidermal cells. Such cells, although they may contain variable numbers of melanosomes, depending on skin coloration, cetacean species, etc., are ultrastructurally similar in diverse cetacean species (Haldiman et al. 1985; Peiffer and Rowntree 1996). Both morphological as well as physiological details of the digestive tract remain to be elucidated. It is not yet known precisely where the absorptive cells first appear. The cuticle of the foregut near the oral region appears to be similar to that on the external surface of the cyamid (Peiffer and Viers 1998).

Cyamid and cetacean isotope ratios

Table 1 lists the isotope ratios for each whale and its associated cyamids. Figure 3 shows the carbon- and nitrogen-isotope ratios of the cyamids plotted against those of whale skin with a standard regression line. The slope for $\delta^{13}\text{C}$ was 0.9663 and $r^2 = 0.83$. The data were tested to determine whether the slope of the line was equal to 1 (i.e., constant

Fig. 3. Nitrogen (a) and carbon (b) stable-isotope ratios of cyamids and the skin of their hosts.**Table 2.** Average carbon- and nitrogen-isotope ratios of zooplankton and particulate organic matter from known feeding areas of whales in the study.

Feeding area of the:	Sample	n	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	
Humpback and northern right whales (northwest Atlantic Ocean)	Calanoid copepods	28	-24.7	7.3	
	Euphausiids	2	-23.5	7.1	
Southern right whale (Patagonia – Drake Passage)	Calanoid copepods (Patagonia)	4	-20.7	10.6	
	Euphausiids (Patagonia)	2	-18.0	11.4	
	Particulate organic matter (Drake Passage)	23	-25.5 to -30.3		Rau et al. 1991a, 1991b
Gray whale (northern Bering Sea – southern Chukchi Sea)	Euphausiids (Drake Passage – Scotia Sea)	6	-28.0	2.6	Rau et al. 1991a, 1991b
	Ampeliscid amphipods	23	-19.9	8.4	Schell 1992
Bowhead whale (northern Bering Sea – Chukchi Sea)	Calanoid copepods	32	-21.6	9.9	Schell 1992
	Euphausiids	11	-20.2	9.4	Schell 1992
Bowhead whale (Beaufort Sea)	Calanoid copepods	30	-25.6	10.4	Schell 1992
	Euphausiids	18	-23.7	9.5	Schell 1992
Narwhal (Lancaster Sound, Baffin Bay)	Calanoid copepods	6	-20.4	9.2	Hobson 1992
	Particulate organic matter	5	-23.5	5.4	Hobson 1992

fractionation) by using a reduced model approach. In this analysis, the regression slope (β_1) is considered to be a constant under the null hypothesis (Neter et al. 1990). The results indicated that the slope was not significantly different from 1 ($p = 0.7558$) and, thus, that the ^{13}C fractionation of the whale skin was nearly constant for all species of whales and all cyamids tested. Using this approach, the slope = 1 line indicates that the fractionation factor averages 1.03‰ by comparing the average cyamid with whale skin. This value is slightly greater than the typical enrichment for carbon fractionation moving up one trophic level, but that may be due to some contribution by carbon derived from formaldehyde. Since the samples were from several sources and

the $\delta^{13}\text{C}$ values of the formaldehyde used are unknown, no better estimate can be made. The *C. ceti* samples contained no formaldehyde and were in the same range. The close correlation between species is also strong evidence that the whale skin is the primary source of food.

Results for the ^{15}N fractionation were similar, with a slope of 0.82 and $r^2 = 0.84$. Applying the test above showed that this slope, also, does not differ from 1 ($p = 0.07$), indicating similar isotopic fractionation for all species of whales and cyamids. The average fractionation factor of -0.17% (cyamid–diet) for nitrogen, however, is not typical of trophic transfers (Minagawa and Wada 1984; Michener and Schell 1994) and matches more closely the value of -0.3% found

by Macko et al. (1982) for *A. valida* on a diet of macroalgae. Although the cause of this slight depletion is not certain, it could result from a high C:N ratio in the diet if the cyamid cannot digest the keratin fibers in the skin cells. Pfeiffer and Rowntree (1996) note that right whale calf skin cells contain small lipid droplets and, if this is the primary food obtained by the cyamid, the low nitrogen content may require nitrogen conservation by the cyamid, resulting in reduced fractionation. Alternatively, the nitrogen-isotope ratios in the individual amino acids composing the skin cells may be such that selective incorporation by the cyamid leads to a body isotope ratio close to the overall skin ratio.

The wide range in values for the cyamid-whale pairs reflects the similar ranges of isotope ratios found in the oceanic environments in which the whales feed. Southern Ocean right whales have the lowest average $\delta^{13}\text{C}$ values and these are consistent with feeding at or south of the subtropical convergence in the Southern Ocean. Both carbon- and nitrogen-isotope ratios drop sharply below the convergence, and the low $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in the whales indicate that most of their feeding is done in the southern reaches of their range (Altabet et al. 1994; Francois et al. 1993). The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values are consistent with the conclusion that the right whales which calve off South Africa (Best and Schell 1996) feed south of the subtropical convergence. The copepods and euphausiids collected off Patagonia had $\delta^{13}\text{C}$ values ranging from -23.0 to -18.0‰ and $\delta^{15}\text{N}$ values between 8.4 and 14.6‰; these values are much higher than those found in the samples of whale skin, so it is unlikely that significant annual feeding by the whales occurs in Patagonian waters. Also, cyamids consuming zooplankton from Patagonian waters would be expected to have much higher isotope ratios than were found in the samples from whales collected at Peninsula Valdes, Argentina (Table 1).

The isotope ratios in northern right whales are also low, reflecting their entirely zooplanktivorous diets and the low isotope ratios in zooplankton off Cape Cod and in Massachusetts Bay, where the animals are observed to feed (Table 2). In contrast, humpback whales from the same region feed on forage fishes and larger zooplankton, primarily euphausiids, and have higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. The highest $\delta^{13}\text{C}$ values are evident in the gray whales and the single narwhal. The values in the gray whale reflect their feeding on amphipods in the northern Bering Sea and other benthos. The higher isotope ratios found in the carnivorous narwhal also match its diet, which is derived from piscivory and benthic feeding.

The isotope ratios of both whales and cyamids are consistent with scenarios for regions where the feeding observations are abundant, and give insight about feeding habitats in areas where data are sparse, such as the Southern Ocean. The close match that exists between the isotope ratios in the whale skin and the associated cyamids also implies that the typical fractionation of nitrogen isotopes seen in carnivores does not occur during assimilation of whale skin by cyamids.

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References

- Altabet, M.A., and Francois, R. 1994. Sedimentary nitrogen isotope ratio as a recorder for surface ocean nitrate utilization. *Global Biogeochem. Cycles*, **8**: 103–116.
- Best, P.B., and Schell, D.M. 1996. Stable isotopes in southern right whale (*Eubalaena australis*) baleen as indicators of seasonal movements, feeding and growth. *Mar. Biol. (Berl.)*, **124**: 483–494.
- DeNiro, M.J., and Epstein, S. 1978. Influence of diet on the distribution of carbon isotopes in animals. *Geochim. Cosmochim. Acta*, **42**: 495–506.
- Francois, R., Altabet, M.A., Goericke, R., McCorkle, D.C., Brunet, C., and Poisson, A. 1993. Changes in the $\delta^{13}\text{C}$ of surface water particulate matter across the subtropical convergence in the S.W. Indian Ocean. *Global Biogeochem. Cycles*, **7**: 627–644.
- Fry, B., and Sherr, E.B. 1984. $\delta^{13}\text{C}$ measurements as indicators of carbon flow in marine and freshwater ecosystems. *Contrib. Mar. Sci.* **27**: 13–47.
- Haldiman, J.T., Henk, W.G., Henry, R.W., Albert, T.F., Abdelbaki, Y.Z., and Duffield, D.W. 1985. Epidermal and papillary dermal characteristics of the bowhead whale (*Balaena mysticetus*). *Anat. Rec.* **211**: 391–402.
- Hobson, K.A., and Welch, H.E. 1992. Determination of trophic relationships within High Arctic marine food webs using stable isotope analysis. *Mar. Ecol. Prog. Ser.* **84**: 9–18.
- Leung, Y.M. 1976. Life cycle of *Cyamus scammoni* (Amphipoda: Cyamidae), ectoparasite of the gray whale, with a remark on the associate species. *Sci. Rep. Whales Res. Inst. (Tokyo)*, **28**: 153–160.
- Macko, S.A., Lee, W.Y., and Parker, P.L. 1982. Nitrogen and carbon isotope fractionation by two species of marine amphipods: laboratory and field studies. *J. Exp. Mar. Biol. Ecol.* No. 72. pp. 243–249.
- Michener, R.H., and Schell, D.M. 1994. The use of stable isotopes in tracing marine aquatic food webs. *In* Stable isotopes in ecology and environmental science. *Edited by* K. Lajtha and R. Michener. Blackwell Scientific Publications, London. pp. 138–157.
- Minagawa, M., and Wada, E. 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between $\delta^{15}\text{N}$ and animal age. *Geochim. Cosmochim. Acta*, **48**: 1135–1140.
- Neter, J., Wasserman, W., and Kutner, M.H. 1990. Applied linear statistical models: regression, analysis of variance and experimental design. 3rd ed. Irwin, Homewood, Ill.
- Pfeiffer, C.J., and Jones, F.M. 1993. Epidermal lipid in several cetacean species: ultrastructural observations. *Anat. Embryol.* **188**: 209–218.
- Pfeiffer, C.J., and Lowe, K.J. 1989. Cirral structure of the pedunculated marine barnacle *Lepas anatifera* L. (Crustacea,

- Cirripedia) I. Ultrastructure of the neuromuscular apparatus. *Acta Zool. (Stockh.)*, **70**: 243–252.
- Pfeiffer, C.J., and Rowntree, V.J. 1996. Epidermal ultrastructure of the southern right whale calf (*Eubalaena australis*). *J. Submicrosc. Cytol. Pathol.* **28**: 277–286.
- Pfeiffer, C.J., and Viers, V. 1998. Microanatomy of the marsupium, juveniles, eggs and cuticle of cyamid ectoparasites (Crustacea, Amphipoda) of whales. *Aquat. Mamm.* **24**: 83–91.
- Rau, G.H., Hopkins, T.L., and Torres, J.J. 1991a. $^{15}\text{N}/^{14}\text{N}$ and $^{13}\text{C}/^{12}\text{C}$ in Weddell Sea invertebrates: implications for feeding diversity. *Mar. Chem.* **35**: 355–369.
- Rau, G.H., Takahashi, T., DesMarais, D.J., and Sullivan, C.W. 1991b. Particulate organic matter $\delta^{13}\text{C}$ variations across the Drake Passage. *J. Geophys. Res.* **96C**: 15 131 – 15 135.
- Rowntree, V.J. 1996. Feeding, distribution, and reproductive behavior of cyamids (Crustacea: Amphipoda) living on humpback and right whales. *Can. J. Zool.* **74**: 103–109.
- Samaras, W.F., and Durham, F.E. 1985. Feeding relationship of two species of epizoic amphipods and the gray whale, *Eschrichtius robustus*. *Bull. South. Calif. Acad. Sci.* **84**: 113–126.
- Saupe, S.M., Schell, D.M., and Griffiths, W. 1989. Carbon isotope ratio gradients in western arctic zooplankton. *Mar. Biol. (Berl.)*, **103**: 427–432.
- Schell, D.M. 1992. Stable isotope analysis of 1987–1991 zooplankton samples and bowhead whale tissues. Final report to U.S. Minerals Management Service. Report MMS 92-0020. Available from National Technical Information Service, Springfield, VA 22161, as PB93-135879.
- Schell, D.M., Barnett, B.A., and Vinette, K. 1998. Carbon and nitrogen isotope ratios in zooplankton of the Bering, Chukchi and Beaufort Seas. *Mar. Ecol. Prog. Ser.* **162**: 11–23.
- Sokolov, V.E., and Evgen'eva, T.P. 1988. Reaction of skin in epidermis of grey whale (*Eschrichtius gibbosus*) to parasitic crustaceans. *Dokl. Biol. Sci. (Engl. Transl. Dokl. Akad. Nauk SSSR)*, **303**: 730–733.
- Wada, E., Terazaki, M., Kabaya, Y., and Nemoto, T. 1987. ^{15}N and ^{13}C abundances in the Antarctic Ocean with emphasis on the biogeochemical structure of the food web. *Deep-Sea Res.* **34**: 829–841.
- Yoshioka, T., and Wada, E. 1994. A stable isotope study on seasonal food web dynamics in a eutrophic lake. *Ecology*, **75**: 835–846.