Carbon sources and trophic position of two abyssal species of Anomura, *Munidopsis alvisca* (Galatheidae) and *Neolithodes diomedeae* (Lithodidae)

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ABSTRACT.- The carbon sources and trophic position of the abyssal species *Munidopsis alvisca* and *Neolithodes diomedeae* are described on the basis of stable carbon and nitrogen isotopes. These two species occur in large abundance at the hydrothermal vents in the central Gulf of California. As dominant components in the crustacean assemblage they define the use of resources and export of vent materials to the abyssal ecosystem. The $\delta^{13}C$ and $\delta^{15}N$ values of the squat lobster *Munidopsis alvisca* suggest a mixed diet based on sediment surfur bacteria and metazoans associated with bacterial mats. The anomuran crab *Neolithodes diomedeae* is a scavenger feeding on infauna of the abyssal plain where photoautotrophic sources play the major role in the diet. The influence of the vents on the organic matter composition of sediments is limited to the immediate venting area and is not recorded in sediments at distance from the active vent structures.

Key words: deep-sea, megafauna, stable isotopes, trophic structure.

Palabras clave: mar profundo, megafauna, isótopos estables, estructura trófica.

Introduction

Exogenous carbon sources affect the distribution and composition of benthic fauna (Grassle 1986). The presence of hydrothermal vents has a large influence on patterns of the deep sea fauna, providing food sources and spatial complexity (by the gradient in water temperature and water chemistry) to the abyssal plain (Johnson et al. 1986). A clear zonation closely related to the microhabitats is determined by these gradients (Hessler & Smithey 1983).

Substantial information regarding the source and transfer of both carbon and nitrogen to and within the deep sea lies in the isotopic composition of organic matter (Macko 1992). The signature of the stable isotopic composition of the tissues of higher trophic level animals and their potential prey items allows us to track the transfer of organic carbon and nitrogen in the food web. It offers a powerful tool to delineate the utilization of carbon compounds, the source of nitrogen, and food web interactions (Harrigan et al. 1989). These interactions are understood by assessing the isotope enrichment during trophic transfer in which 3‰ enrichment in ^{15}N occurs with each trophic level transfer (Voss 1991). Carbon isotopes exhibit an increase of approximately 1‰ per trophic level (Macko 1992).

A dual tracer approach with elemental carbon and nitrogen and $\delta^{13}C$ and $\delta^{15}N$ stable isotopes was analyzed in the abyssal species *Munidopsis alvisca* and *Neolithodes diomedea* and in sediment from the abyssal plain obtained in the central Gulf of California. These two species have been reported dominant components in the crustacean assemblage both in the abyssal plain and the hydrothermal vent ecosystem. By their dominant condition these species determine the biological control of resources originated in the vent. These two species were chosen to define the use of resources originated in the vents and evaluate the potential export of vent material to the abyssal ecosystem in the central Gulf of California.

Materials and Methods

Specimens of the two species and sediments were collected in dives on the DSV NAUTILE from two venting sites in the central Gulf of California (27°00.94'N, 111°24.66W, 2022 m) during the French Mexican expedition GUAY-NAUT.

The area of study is a hydrothermally active, sediment covered sea-floor spreading segment (Lonsdale et al. 1980), 20 km in length and 5 km in width (Peter & Scott 1991). It is characterized by a high sedimentation rate (1-2 m /1000 yrs; Peter et al. 1991) of hemipelagic muds and turbidites (Tunnicliffe 1991). The adjacent abyssal sediment is pelagic in origin (Baba et al. 1991), composed primarily of diatoms that contribute 3 to 4% of the total organic carbon in the sediments (Calvert 1966). Chimneys are characteristic of the morphology of the deposits; sediments are generally saturated with high molecular weight hydrocarbons that appear to be derived from hydrothermal alteration of recent organic material (Peter et al. 1991).

Sediment was obtained from cores 10 cm in diameter off the venting structures along a 50 m transect, starting at the base of an active vent, and at distances of 5, 20, and 50 m. Sediment samples were frozen upon collection. Onboard samples were thawed and oven dried at 60ºC to later determine both the C and N elemental and stable isotope composition.

NAUTILE's mechanical arm and tweezers were employed to capture living organisms within the 50 m radius of active vent structures. All specimens in both species were dissected, and the muscle tissue was extracted. The gills of the lithodid crab *N. diomedeae* were analyzed separately, rinsed with distilled water, and oven dried onboard at 60º. Due to the reduced size of the squat lobsters, analysis were carried out in a mixture that included both muscle and gills. In the laboratory both the tissues and sediment were finely ground and acidified with 0.1N HCl, to remove carbonates. Later the materials were washed with de-ionized water, oven dried at 60ºC and finely ground. The dried material was weighted on a Mettler ME22 microbalance. Three milligram tissue and 500 mg sediment were used for multiple stable isotope analysis, and 2-3 mg tissue and 10-15 mg sediment were used for carbon and nitrogen elemental analysis. Analysis of the proportions of carbon and nitrogen were run in triplicate on a Carlo Erba Elemental Analyzer Model 1106.

Stable isotope samples were placed in pre-combusted quartz tubes containing purified cupric oxide beads and high purity granular copper. The tubes were evacuated and sealed. The combustion processed followed included heating for an hour at 900C, and then cooled to 700ºC at a rate of 4ºC min^{-1}, and finally from 700 to 500ºC at a rate of 0.6ºC min^{-1} to ensure that any oxides of nitrogen were converted to N_2. The CO_2 and N_2 gases were isolated cryogenically from other combustion products and analyzed separately on a Finnigan 251 CNOS and a Nuclide 3-60 isotope ratio mass spectrometers, respectively, and expressed as ‰ differences from a standard. The standard reference used for ^{15}N was atmospheric nitrogen and the standard reference for carbon was the PeeDee belemenite limestone with an assigned value of 0.0‰. On the basis of replicate analysis of samples, the reproductibility in combustion and measurement was within ±0.2‰. Data were presented as:

$$\delta X=[(R_{sample}/R_{standard})-1]x\ 10^3\ (‰)\ (1)$$

with: X= stable isotope elements ^{13}C or ^{15}N

R= ratios $^{13}C/^{12}C$ or $^{15}N/^{14}N$

The resulting isotopic ratios were compared with those of several hydrothermal vent sites in the Eastern Pacific.

Results and Discussion

Sediments.- The sediment organic carbon and nitrogen values ranged from 2.7 to 16.2% and 0.1 to 3.3%, respectively of the dry weight. Sediment obtained at the base of vents had the highest content of both carbon (mean 15.1%) and nitrogen (mean 3.1%). Organic carbon and nitrogen values at 50 m from the vents had impoverished (1-2%) deep-sea values (Fig. 1).

The lowest sediment C/N ratio was recorded at the base of the vent, among large amounts of tubeworm debris (4.9), indicating the presence of large bacterial activity. The C/N ratios increased 4 to 6 times in the most distant samples from the vent (13.1 to 20.6) and characterize the abyssal sediment. The carbon stable isotope values recorded in the sediment, along the vent to abyss transect ranged from -32.2 to -18.0‰. A $\delta^{13}C$ significant enrichment of the sediment organic matter was recorded with distance from the active vent. The carbon value recorded at the vent base (-32.2‰) was impoverished by -14.0‰. In contrast, the sediment collected at distances 5, 10 and 50 m showed values that were enriched. These results suggest sulfur-based sediment at the base of the active vent site ($\delta^{13}C$-32.2‰) and the input of organic matter of pelagic photoautotrophic origin for samples from distances 5, 20, and 50 m (mean of $\delta^{13}C$ -18.1±0.5‰).

The nitrogen isotopic composition values in sediment ranged from $\delta^{15}N$ +3.4 to +11.1‰. The stable isotope composition of sediments progressively increased away from the active hydrothermal sites. The lowest sediment value (+3.4‰) was recorded at the base of the vent. This sediment consisted mostly of tubeworm debris and was covered by a thin bacterial mat. From the $d^{15}N$ perspective, the values resemble those recorded for the tubeworm collagen analysed. The elemental carbon content in sediment changes at the same rate as does the $\delta^{13}C$ with distance from the vent site (r^2= 0.95).

The influence of endogenous organic carbon was restricted to the vent site. Sediment collected in the proximity of the vent was 13C depleted, suggesting the presence of sulfur bacteria in the sediment (Rau 1981). The 13C enrichment insediment observed with increasing distance from the vent reflects the change in the source of the organic matter; the endogenous organic carbon is being replaced by particulate organic carbon (POC) of pelagic origin (Peters et al. 1978). The carbon value at greatest distance from the vent approaches values for POC recorded in

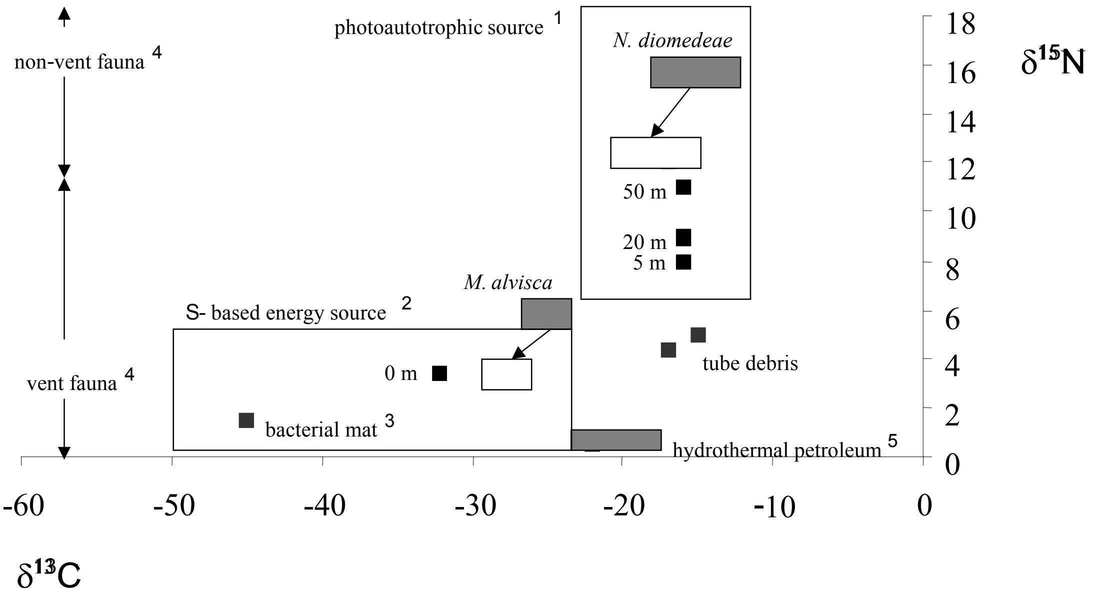

Fig. 1. Stable isotope composition of sediment samples and the abyssal species *Munidopsis alvisca* and *Neolithodes diomedeae* (large black boxes). White boxes depict the resulting $\delta^{13}C$ 1‰ and $\delta^{15}N$ 3.4‰ decrease to define potential food sources (arrow in direction of potential food source). Boxes of energy sources delimited according to (1) Brooks et al. (1987), Kennicutt et al. (1992); (2) MacDonald et al. (1990); (3) Rau (1981), van Dover & Fry (1994), (4) Fisher et al. (1994); (5) Schoell et al. (1990).

the northeastern Pacific Rise (-21‰) and resembles other sediment values in the area (Peters et al. 1978).

The ^{15}N enrichment recorded with distance from the hydrothermal flow suggests a rather pelagic-sedimentary origin, related to signatures of particulate organic nitrogen (PON) exported to the deep-sea (Saino & Hattori 1987) that will determine the ^{15}N enriched diets of abyssal species (van Dover & Fry 1989). Similar enriched nitrogen values (9.2 ‰) are suggested to derive from phytoplankton export in the region (e.g., diatoms, Peters et al. 1978).

Fauna.- The crustacean elemental values ranged from 33.1 to 43%C and 8 to 12.1%N of the dry weight. The C/N ratio ranged from 3.6 to 4.1. The elemental values of both carbon and nitrogen were lower in *M. alvisca* (muscle: 33.7±0.4%C, 8.2±0.1%N) than in *N. diomedeae* (muscle 41.1±0.3%C, 11.7±0.2%N, gills 9.8±0.04%C, 38.0±0.1%N). Both species have a C/N ratio close to 4 (range 3.6 to 4.1), which is similar to values identified for grazers, omnivores, and scavengers in which enrichment in both %C and %N correlates with higher trophic position, structural complexity of tissues, and increasing size of the organisms. Few studies have described the ecology of the abyssal fauna in the Gulf of California (Grassle 1986). The organic carbon and nitrogen values appear to be more enriched than values previously recorded in similar fauna by Fisher et al. (1988) in the Galapagos. These are as well attributed to the sedimentary condition of the basin.

The δ^{13}C values ranged from -26.4 to 13.8‰. The δ^{13}C values of species *M. alvisca* (-26.4‰) suggest a mixed diet based on sulfurbased energy sources, probably bacteria that obtain their energy sources from sulfur-based activity in the sediment and photoautotrophic organic debris exported (Rau 1981) (Fig.1). The δ^{15}N value recorded in *M. alvisca* was significantly lower (5.5‰). *M. alvisca* uses more than one energy source, feeding on deep-sea materials, vent debris and free-living sulfurbased bacteria, suggesting the farming of microbes to supplement the nutrition.

The δ^{13}C values of *N. diomedeae* (muscle -13.8±3.1‰; gills -18.2±1.2‰) indicated that the diet of the crab consists mainly of deep-sea organic matter of pelagic origin, the crab can be considered a non-vent scavenger (Fig.1). Differences larger than 3‰ in isotopic δ^{13}C composition in *N. diomedeae* were observed at different sites, indicating a variation in carbon composition among sites, which might be related to the variability in vent input into the abyssal sediment. The δ^{15}N values in *N. diomedeae* were higher (muscle δ^{15}N +15.4±0.5‰; gills δ^{15}N +15.3±1‰) than the values recorded for *M. alvisca*. The lithodid crab *N. diomedeae* can be considered a typical non-vent scavenger whose diet is based on deep-sea debris resulting in the enriched d^{15}N values recorded (Fig. 1).

Carbon and nitrogen stable isotope composition in the study site were in general more ^{13}C depleted and less ^{15}N enriched than values recorded at other hydrothermal vent sites in the Pacific (Table 1). In spite of the similarities shared among vent sites, the nature (quality and quantity) of outflows from the vent sulfide concentration in the water flow (Johnson et al. 1986), the bacteria, and other nutritious particles (Hessler et al. 1988) help to create a variety of microhabitats (Fisher et al. 1988).

The main carbon sources identified include a sulfurbased source produced by seeping through the soft sediments that is utilized by infauna and *M. alvisca* and a photoautotrophic source that supports the abyssal, non-vent crab *N. diomedeae* (van Dover & Fry, 1989). Its aggregated distribution pattern in the areas affected by the hydrothermal venting shows that the lithodid crab is an opportunstic species. Pogonophoran tubes and bacterial mats contribute to the organic matter and are potential substrates for bacteria and smaller invertebrates of the smaller benthic fauna that provide food to the abyssal Crustacea.

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Table 1. Selected ranges of $\delta^{13}C_{VPDB}$ and $\delta^{15}N_{Air}$ of energy sources and species composition.

Source/Species	max $\delta^{13}C$ ‰	min $\delta^{13}C$ ‰	max $\delta^{15}N$ ‰	min $\delta^{15}N$ ‰	Reported conditions or location	Reference
Chemosynthesis, bacteria						
	-16.8	-42	-7.5	-9.6	bacterial mat at Gorda vent system	van Dover & Fry 1994
	-10	-15	5	-13	bacterial populations at vent sites	van Dover & Fry 1994
Sulfur, bacteria						
	-30	-42	5	0	sulfur-based energy source	MacDonald et al. 1990
	-32.2		3.4		sediment at base of the active vent	This study
Photochemotrophic, marine						
	-24.6		4		sediment in the Gulf of California	Peters et al. 1978
	-15	-22	5	10	photoautotrophic organic matter settling	Kennicutt et al. 1992
	-17.6	-18.6	11.1	8	sediment at distance from the active vent	This study
Squat lobsters						
	-17.7		10.5		*Munidopsis*, North Atlantic	van Dover & Fry 1994
	-16.4		12.4		*Munidopsis subsquamosa*, Hanging Gardens	van Dover & Fry 1989
	-17.7		7.7		*Munidopsis subsquamosa*, Galapagos Rift	Fisher et al. 1994
	-23.7		6.6		*Munidopsis subsquamosa*, Galapagos Rift	Fisher et al. 1994
	-1	-3			*Munidopsis subsquamosa*, Rose Gardens	van Dover 1986
	-26.4		5.5		*Munidopsis alvisca*, Gulf of California	This study
Non vent fauna						
	-12	-22	5	13	marine organisms	Fisher et al. 1994
	-14	-20			heterotrophic deep-sea fauna	Brooks et al. 1987
	-19.4	-10.7	15.9	14.3	*Neolithodes diomedeae*, Gulf of California	This study

Resumen

Las fuentes de carbono y la posición trófica de las especies abisales *Munidopsis alvisca* y *Neolithodes diomedeae* se describen con base en isótopos estables de carbono y nitrógeno. Estas dos especies son abundantes en las ventilas hidrotermales del golfo de California central. Al ser componentes dominantes de las comunidades de crustáceos, éstas definen el uso de los recursos y de la exportación de materiales procedentes de las ventilas al ecosistema abisal. Los valores de $\delta^{13}C$ y $\delta^{15}N$ del galateido *Munidopsis alvisca* sugieren una dieta mixta basada en bacterias sulforreductoras del sedimento y metazoas asociados con los tapetes bacterianos. El cangrejo anomuro *Neolithodes diomedeae* es un carroñero que se alimenta de macrofauna de la planicie abisal donde el detrito de origen fotoautotrófico ocupa la dieta principal. La influencia de las ventilas sobre la composición de la materia orgánica de los sedimentos se limita al área inmediata a las ventilas y no ha sido observada en sedimentos que se encuentran a cierta distancia de las estructuras hidrotermales activas.

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