
Volume 78, issue 4
November 2009
ISSN 0924-7963
ELSEVIER
Special Issue
Revisiting the Role of Zooplankton in Pelagic Ecosystems
Edited by
Jean-Henri Hecq and Anne Goffart
JOURNAL OF
MARINE
SYSTEMS

Journal of Marine Systems 78 (2009) 518–524

Contents lists available at ScienceDirect

Journal of Marine Systems

journal homepage: www.elsevier.com/locate/jmarsys

Elemental composition, biochemical composition and caloric value of Antarctic krill. Implications in Energetics and carbon balances

Jaime Färber-Lorda [a,*], Raymond Gaudy [b], P. Mayzaud [c]

[a] Centro de Investigación Cientifica y de Educación Superior de Ensenada.Carr. Tijuana, Ensenada, Km. 107, Ensenada, B. C. México
[b] Station Marine d'Endoume, Chemin de la Batterie del Lions, Marseille 13007, France
[c] Obervatoire Océanologique, B. P. 28, Villefranche sur Mer, 06230, France

ARTICLE INFO

Article history:
Received 7 November 2006
Received in revised form 8 May 2008
Accepted 16 December 2008
Available online 21 February 2009

Keywords:
Krill
Calorimetry
Elemental composition
Biochemical composition
Energetic balance

ABSTRACT

Samples of Antarctic krill were analyzed for elemental composition, biochemical composition, weight and caloric content. Sexes and maturity stages were separated. Mature females showed the highest caloric values (Joules) and juveniles the lowest in a per animal basis. On unit of wet weight per animal basis, spent females showed the lowest caloric values. For the caloric values by animal, a significant difference was found between males, mature females, spent females and juveniles, either on a per animal basis or in the basis of 1 g of wet weight, showing a real difference between the groups, regardless of their individual size. Significant differences were found for carbon, nitrogen and lipids, but not for proteins, analyzed in % of dry weight. Carbon was lowest for spent females and highest for mature females. On the contrary, nitrogen values were lowest for mature females and highest for males. Mature females had the highest lipid content and males the lowest. All variables were significantly correlated. For the linear regression analysis, the best correlation found was between Joules and carbon, followed by carbon vs. dry weight and Joules vs. dry weight. In an analysis with two independent variables, the best correlation was found for Joules vs. lipids and dry weight, followed by Joules vs. carbon and nitrogen, and Joules vs. lipids and proteins. The results obtained were used to make an analysis of the energy and carbon fluxes through the food chain in the sampled area, showing higher energetic and carbon "densities" in frontal areas, the POM calorific values showed an opposite pattern than that of krill.

1. Introduction

Much work has been dedicated to the study of the biology and ecology of Antarctic krill, its biochemical composition, (Clarke, 1980, 1983; Färber-Lorda, 1986, 1991; Pond et al., 1995; Mayzaud et al., 1998); its biology, and physiology (Kils, 1979, 1981; Hirche, 1983). We now know that this species plays a central role in the Antarctic Ecosystem, however, we lack certain basic information. Considering the preponderant role of this species, it is important to know more about its energetic balance. The calorific value of Antarctic krill has always been calculated from its biochemical composition, and its caloric values given in literature, but never through real calorimetry. In trophic studies, this information is very useful. Carbon values of Antarctic krill have been obtained on different size groups (Ikeda and Bruce, 1986; Ikeda and Kirkwood, 1989; Ikeda and Mitchell, 1982; Ikeda, 1984; Huntley et al., 1994) however, sexes were never separated. Considering this, differences believed to be related to seasonal differences in metabolism, could be more due more to the male/female composition of the samples, giving higher values when gravid females are dominant. Biochemical composition differs among males, females and juveniles (Clarke, 1980, 1983; Färber-Lorda, 1986, 1991). Significant differences were found among these groups. Also, a significant difference in lipid content was found between two morphologically differing male groups (Färber-Lorda, 1986, 1990, 1991; Färber-Lorda et al. 2009-this volume). The possible consequences of these differences for energetic balance were discussed by Färber-Lorda (1991), and Färber-Lorda et al. (2009-this volume) in relation to biochemical composition; it was shown that morphometric differences are related to biochemical composition differences, and, thus, could be also related to energetic balance. In this paper we analyze the calorific value of Antarctic krill, Euphausia superba, in relation to elemental and biochemical composition, and in relation to sex and maturity stage.

Some simple models with one or two independent variables for evaluating the calorific value or carbon content of Antarctic krill were obtained, and, are used for comparisons between geographic areas and different trophic levels, with the purpose to better understand trophic relationships and carbon fluxes in Antarctic krill.

2. Material and methods

Samples were obtained as described in Färber-Lorda (1986, 1990). Frozen samples at −70 °C were utilized. Samples were thawed and

---

[*] Corresponding author.
E-mail address: jfarber@cicese.mx (J. Färber-Lorda).

0924-7963/$ – see front matter © 2009 Elsevier B.V. All rights reserved.
doi:10.1016/j.jmarsys.2008.12.021

measured under a stereo microscope, sex was determined, and each animal was weighed. Samples were freeze-dried and placed in desiccators for 24 h. Each individual was weighed, then, sub-samples were obtained from each homogenized animal. One sub-sample, each sub-sample was used for calorimetry, lipid and protein, and for elemental analysis determinations. Thus all information was obtained for each animal, and multiple correlations were possible.

For calorimetry, we used the Phillipson (1964) microcalorimeter. Benzoic acid was used as standard. Calorific values were obtained from the peaks obtained on a plotter, and corrected from the cooling slope, as described in the manual.

Proteins were analyzed according to Färber-Lorda (1986, 1991), and Mayzaud et al. (1985), adapted from the Biuret method, as described by Raymont et al. (1964, 1971), using an *Euphausia superba* protein standard. The values obtained were extrapolated for the entire animal.

For lipids, an extraction was first performed with the Bligh and Dyer (1959) method on the sample, and later a colorimetric determination was performed, according to Pande et al. (1963), as described in Färber-Lorda (1986). Tripalmitin was used as standard.

For carbon and nitrogen analysis, we used a CHN Perkin–Elmer 240 Elemental Analyzer, using acetanilide as a standard, samples were weighed in a Perkin–Elmer AD2Z microbalance. All values, for calorimetry, were calculated on an ash-free dry weight (AFDW) basis. Calorific values were corrected for nitrogen content as suggested by Kersting (1972), so values with and without nitrogen correction were obtained, but given the low nitrogen content of the samples it was not considered useful. According to Schroeder (1977) acidic corrections were considered negligible (<3%).

Different ANOVAS were performed on the data, as also linear regression analysis, and multiple linear regressions with two independent variables, to obtain predicting models for different parameters. The Mathlab program was utilized to perform some of the figures.

3. Results

As expected, the highest calorific values were those of matured females, and the lowest for juveniles. Four main groups were separated, juveniles, males, mature females, and spent females (see Table 1). An ANOVA on the calorific values of these groups, shows a significant difference among the ($F_3^{38}=7.83$, $P<0.001$). This, of course, also reflects size differences. To avoid size related differences, we calculated the calorific values on a gram of wet weight basis, another ANOVA was performed. There is also a significant difference ($F_3^{38}=10.23$, $P<0.001$), but in this case, the lowest calorific value was that of spent females, and the highest again for mature females, juveniles and males showing an intermediate value.

In Table 1 we can see the biochemical and elemental composition results in percentage of the dry weight. For all percentage data a previous arcsine transformation was performed. An ANOVA was performed on the transformed biochemical data, for protein there is no significant difference among the groups ($F_3^{38}=1.99$), the highest value was that of the spawned females and the lowest that of mature females. Lipids did show a significant difference among the different sex groups ($F_3^{38}=15.69$, $P<0.001$) mature females showing the highest values, and males the lowest. For carbon, in percentage, we also performed an ANOVA, and found a significant difference ($F_3^{41}=10.46$, $P<0.001$), with the lowest mean being that of spent females, and the highest, for mature females. Nitrogen also showed a significant difference ($F_3^{38}=7.01$, $P<0.001$) the highest mean being that of spawned females, and the lowest that of mature females. The C/N ratio, showed the highest values for mature females and the lowest again for spent females, however, variability was higher for mature females. Regression analysis was performed for all the data, nine variables were studied for each animal.

All variables are significantly correlated (see Table 2); the best correlation was found between carbon and Joules, with an $r^2=0.957$ as shown in Table 3 and Fig. 1. Dry weight also showed a very good correlation with Joules ($r^2=0.923$) (see Table 3 and Fig. 2), the regressions for lipids ($r^2=0.770$), and proteins ($r^2=0.747$) were not as good. The regression between dry weight and carbon is also shown (Fig. 3), and gives a good regression index.

Linear regressions were obtained for all the possible combinations among the variables (see Table 2). In the equations with two dependent variables, the best correlation was found between Joules and lipids and dry weight ($r^2=0.967$, Fig. 4), followed by the Joules vs. carbon and nitrogen ($r^2=0.957$, Fig. 5), and the Joules vs. protein and lipid equation ($r^2=0.949$, Fig. 6). A good correlation was obtained between dry weight, and carbon and nitrogen ($r=0.987$, Fig. 7). In Fig. 8 we can see the good regression obtained between carbon and protein and lipids, which were used in our carbon flux calculations. Different prediction equations were obtained, on a per animal basis, but valid for different sexes or development stages. The regressions obtained are in Tables 3 and 4.

Table 2
Regression indexes between each of the studied variables of *Euphausia superba*, calculated with uncorrected values.

							Weight	
	Joules	Carbon	Nitrogen	Lipids	Protein	Length	Wet	Dry
Joules	1.000							
Carbon	0.957	1.000						
Nitrogen	0.721	0.766	1.000					
Lipids	0.770	0.867	0.477	1.000				
Protein	0.747	0.893	0.893	0.608	1.000			
Length	0.675	0.725	0.869	0.474	0.835	1.000		
Wet weight	0.803	0.842	0.911	0.585	0.913	0.919	1.000	
Dry weight	0.923	0.949	0.874	0.782	0.901	0.837	0.930	1.000

Table 3
Linear regressions obtained for the variables analyzed $Y=a+bX$.

Y	*a*	*b*	*X*	R^2
Joules corr.	−142	46.7	Carbon	0.950
Joules corr.	−256.4	24.1	Dry weight	0.897
Joules corr.	1850	79.2	Lipids	0.797
Joules corr.	620.3	33.2	Protein	0.771
Joules	−32.7	49.8	Carbon	0.957
Joules	−205.2	25.9	Dry weight	0.923
Joules	2142.4	82.7	Lipids	0.770
Joules	699.8	36.2	Protein	0.747
Carbon	−2.65	0.516	Dry weight	0.949
Protein	−6.07	0.613	Dry weight	0.901
Nitrogen	2.07	0.0767	Dry weight	0.757

Table 1
Elemental, biochemical in %, and calorific mean values for each of the studied groups of *Euphausia superba*.

	Proteins	Lipids	N	C	C/N	Joules (J.ind.-1)	Joules (J.P.Hum gr. -1)
Juveniles	56.67 ± 4.63 (10)	13.02 ± 3.50 (10)	8.60 ± 0.93 (10)	49.89 ± 2.50(10)	5.88 ± 0.89 (10)	3153 ± 858(10)	5588 ± 764(10)
Males	59.55 ± 8.05 (10)	10.23 ± 4.32 (10)	9.62 ± 0.87 (10)	47.56 ± 2.66 (10)	4.99 ± 0.70 (10)	4210 ± 1066 (10)	4758 ± 964 (10)
Mature females	55.42 ± 4.93 (15)	20.11 ± 2.52 (15)	8.13 ± 0.92 (15)	52.99 ± 2.97 (15)	6.70 ± 1.01 (15)	5477 ± 1721 (15)	6312 ± 879 (15)
Spent females	60.61 ± 3.50 (7)	13.19 ± 2.33 (7)	9.76 ± 1.10 (7)	47.52 ± 2.67 (7)	4.95 ± 0.92 (7)	4661 ± 1007 (7)	4879 ± 778 (7)

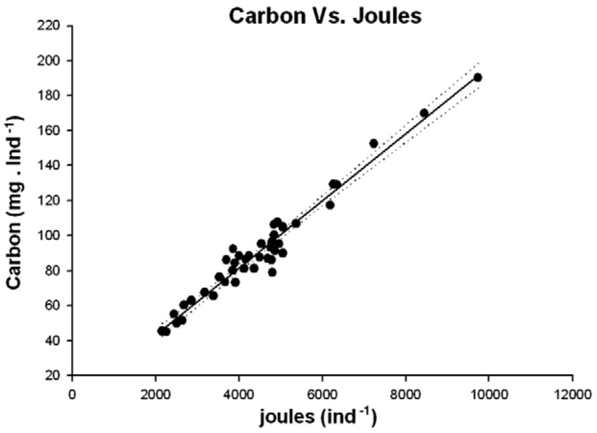

Fig. 1. a Linear regression between C and Joules for *Euphausia superba*.

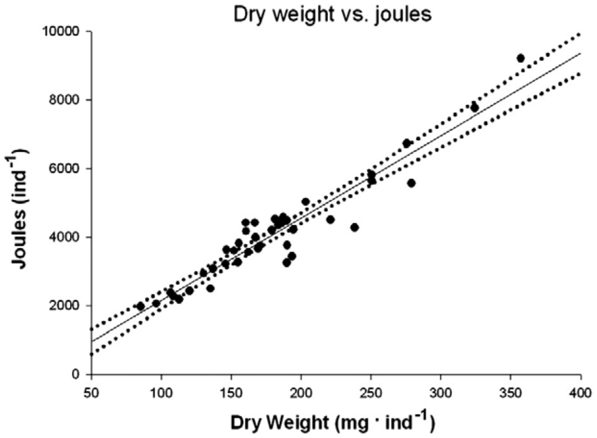

Fig. 2. Linear regression between C and Dry weight for *Euphausia superba*.

3.1. Energy fluxes in the southern part of the Indian Ocean

Assuming that our sampling was representative of the populations in the area, caloric "densities" of Antarctic krill were evaluated using our equation relating protein and lipids to Joules (without correction for nitrogen, because nitrogen in general showed low concentrations), and the echosounding results from the same cruise (Masson, 1989). Thus results are per 1000 m^3, biochemical composition for *Thysanoessa macrura*, was obtained for some stations, the same equation was utilized considering that calorific value is dependent of the protein and lipids content of the samples, which is also the case for Particulate Organic Matter (POM) results. For the POM results obtained simultaneously during the cruise (Mayzaud et al., 1985) at a standard depth of 15 m, were utilized. POM values are a rough estimation of the euphotic zone average values, they are calculated by adding all the studied fractions (protein, carbohydrates, lipids, for carbohydrates, the equivalence from literature was used from Lehninger, 1985, and added to the value obtained with the equation) obtained per liter, and extrapolated to 1000 m^3. Results are shown with the isotherms at 50 m, which correspond approximately to the depth of the thermocline (from Färber-Lorda et al., 2009-this volume), frontal areas corresponding to higher productivity areas, except where krill concentrations were found (Fig. 9). Lower values of particulate organic matter caloric values were found at the stations where krill concentrations were encountered, suggesting active grazing by krill. "Calorific Density" is also shown in Fig. 10, in areas where we have high values of POM calorific value, we have the opposite situation in krill "Caloric Density".

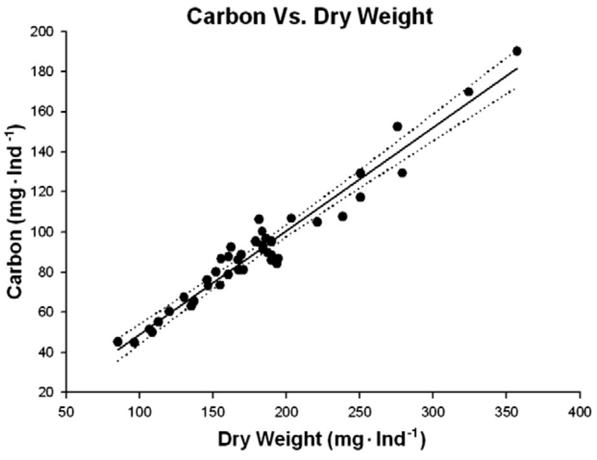

Fig. 3. Linear regression between C and dry weight for *E. superba*.

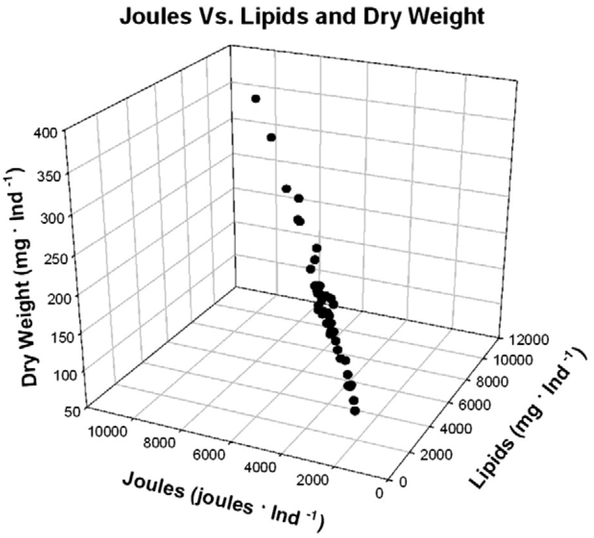

Fig. 4. Multiple linear regression between Joules, and lipids and dry weight for *E. superba*.

3.2. Carbon budget in the southern section of the Indian Ocean

With the equation involving protein and lipids with carbon, we determined the carbon content of the two trophic levels, krill and

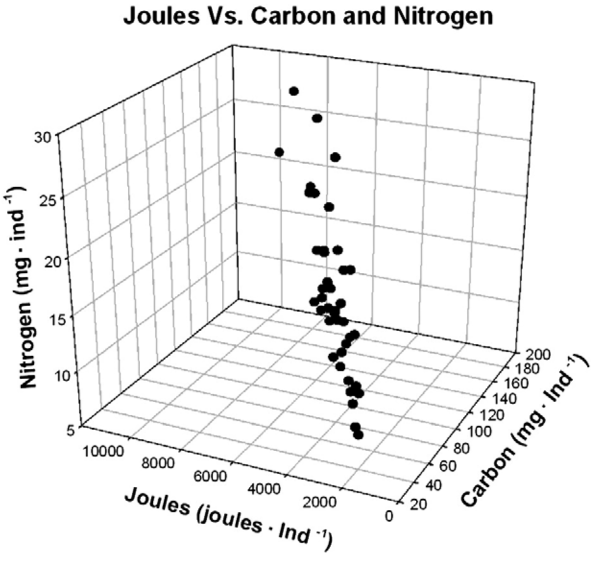

Fig. 5. Multiple linear regression between Joules, C and N.

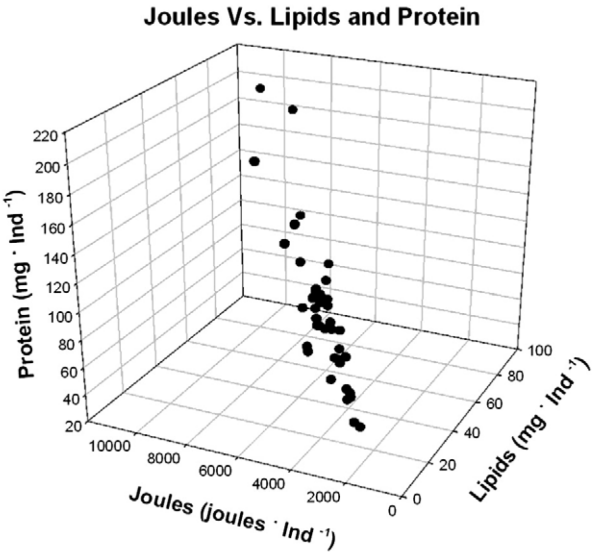

Fig. 6. Multiple linear regression between Joules and lipids and protein.

particulate matter. The C vs. dry weight equation was utilized to determine krill carbon. For the POM, we used the equation relating calorific value to carbon, and utilizing the formerly calculated calorific values of the particulate matter (POM) at each station, for 1000 m^3. Fig. 11 shows the carbon distribution over the isotherm for the area and Fig. 12 shows the distribution of carbon for the area, for POM and krill, showing the same distribution of Joules.

4. Discussion

For the first time calorific values, using direct calorimetry were obtained for Antarctic krill, we found a significant difference between sexes, either by animal or, by gram of wet weight. This support former evidence by Clarke (1980, 1983), Clarke and Morris (1983); Färber-Lorda (1986, 1991); Mayzaud et al. (1998) Pond et al. (1995); saying that lipid content is different in different sex groups, being higher in mature females and lower in spent females, which also reflect different calorific values. A significant difference was also found for C and for N, no significant differences were found for protein, however N was low in most animals. C values were slightly higher than those

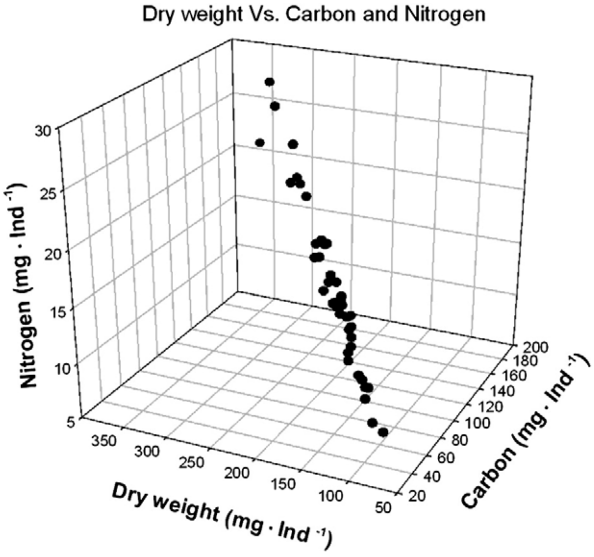

Fig. 7. Multiple linear regression between dry weight, C and N.

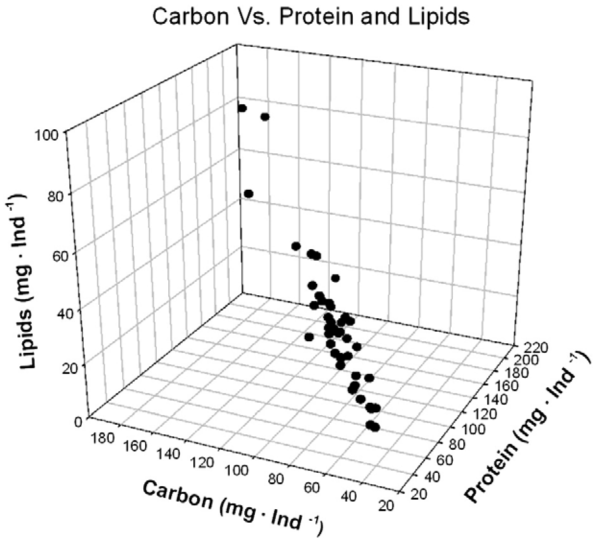

Fig. 8. Multiple linear regression between C, protein and lipids.

found by Ikeda and Bruce (1986), by Ikeda and Kirkwood (1989) and Huntley et al. (1994), this is probably related to the fact that we made individual analysis, thus enhancing sexual differences more related to the physiology and biology of the species.

The approach utilized enables us to obtain different equations, useful to study energetics in Antarctic krill, and in general in biological material, this is purpose of this work. It is also useful to calculate carbon budgets between primary and secondary producers.

The results on krill were more or less expected, but the lower calorific value of spent females was not predicted, this group showed lower values than males. Former evidence by Clarke (1980) showed: that females loose ~60% of their lipids with spawning, Färber-Lorda (1986) evaluated this to 56%, during the same cruise where these samples were obtained (Färber-Lorda et al., 2009-this volume). We now know that there is an important geographic variability, which is reflected in either weight or length–weight relationships, population composition and biochemical composition as shown by Färber-Lorda (1986, 1994), (Färber-Lorda et al., 2009-this volume); or the simultaneously studied differences, related to changing trophic conditions present during sampling (Mayzaud et al., 1985), which are more important than sex differences. The general equations in Tables 3 and 4, are per animal, they are useful to transform data per animal. For the one independent variable equations, the best correlation was that between Joules and carbon ($r^2 = 0.957$), Finlay and Uhlig (1981) also found a similar slope for protozoans, Salonen et al. (1976) also found a dependence of calorific values on carbon content. In this paper the dry weight–Joules ($r^2 = 0.923$) also give a high correlation. Comitta and Schindler (1963) obtained calorific values for different microcrustaceans; they found that copepods had the highest caloric content, and that copepod females had slightly

Table 4
Multiple linear regression $Y = a + bx + cz$.

Y	*a*	*b*	*c*	*X*	*Z*	R^2
Joules corr.	158.6	16.2	35.2	Dry weight	Lipids	0.960
Joules corr.	590	53.6	18.9	Lipids	Protein	0.946
Joules corr.	−72.3	48.7	−15.7	Carbon	Nitrogen	0.951
Joules	164.3	19	31.3	Dry weight	Lipids	0.967
Joules	669.9	52.9	22.1	Lipids	Protein	0.949
Joules	−72.3	48.7	8.96	Carbon	Nitrogen	0.957
Carbon	13.5	0.95	0.48	Lipids	Protein	0.964
Carbon	3.27	0.503	0.405	Lipids	Dry weight	0.978
Dry weight	−1.02	1.40	3.43	Carbon	Nitrogen	0.987
Lipids	−41.1	0.197	5.84	Dry weight	C/N ratio	0.762

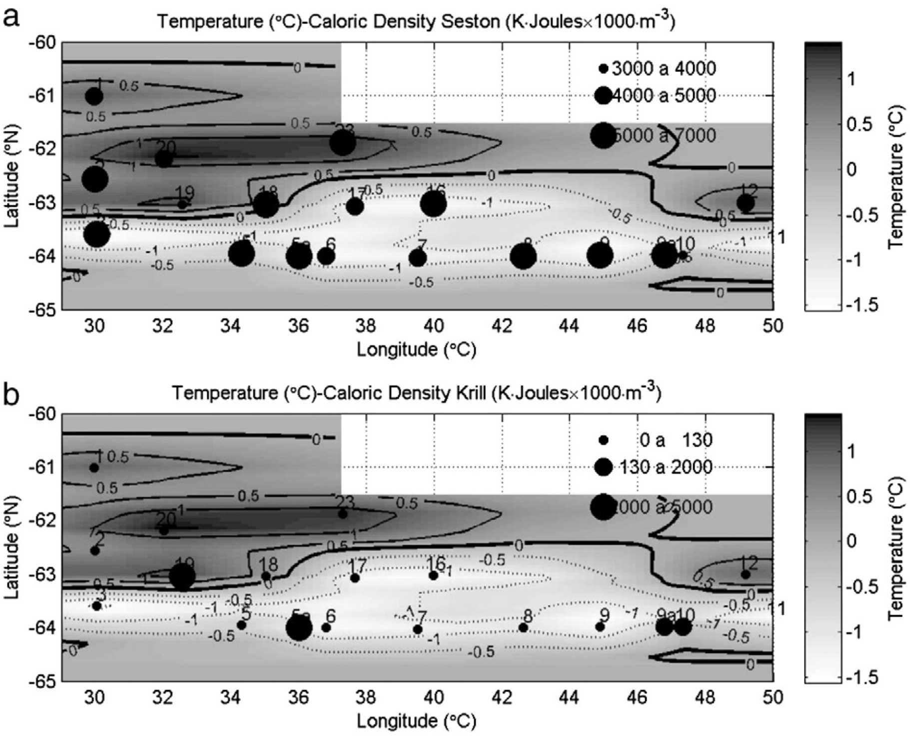

Fig. 9. Calorific values per station of seston (a) and krill (b) for the MD-25 FIBEX cruise, calculated with the results by Färber-Lorda (1986) and Mayzaud et al. (1985), per station, over the isotherms distribution.

higher values when they were mature. Comitta et al. (1966) followed the seasonal variation of copepods in relation to organic matter content, but they did it for *Calanus finmarchicus*, however their regression determination was similar to ours. A good correlation was found between C and dry weight ($r^2 = 0.949$). Only other study by Platt and Irwin (1973) relates the biochemical composition of phytoplankton with its calorific value. For the two independent variables equations, the best correlation was found between Joules and dry weight and lipids ($r^2 = 0.967$), followed by the Joules vs. C and N and closely followed by the Joules vs. lipids and proteins relationship, C vs. protein and lipids is very useful to balance budgets between different trophic levels.

With the purpose to better understand trophic conditions in the area, data were converted to energy "density". Using simultaneously obtained data from Mayzaud et al. (1985) and Färber-Lorda (1986),

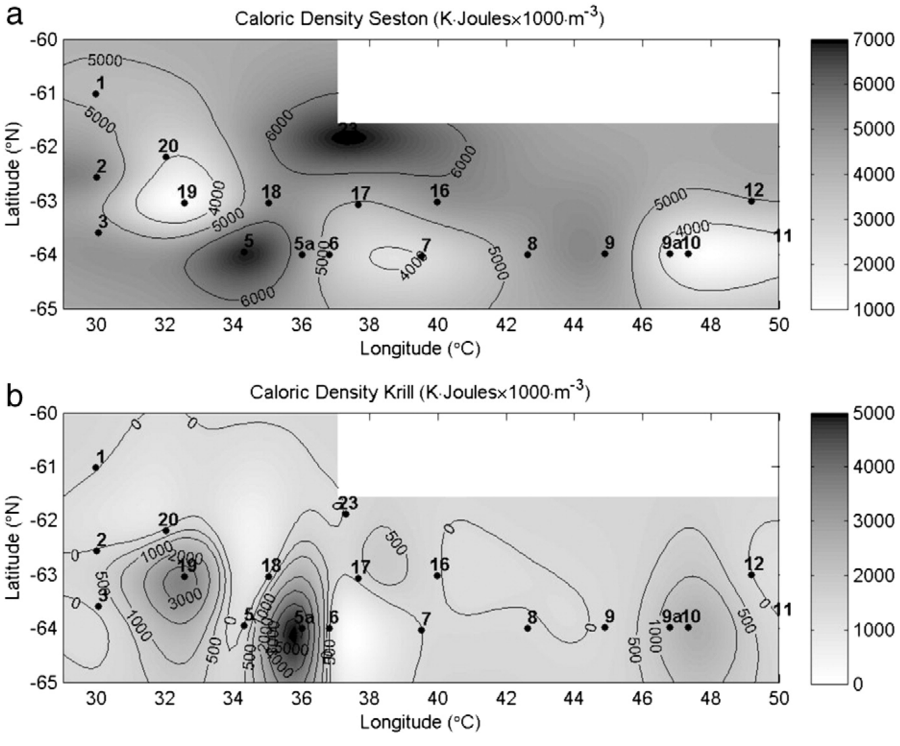

Fig. 10. Spatial distribution of the "Calorific Density" of seston (a) and krill (b) for the MD-25 FIBEX cruise.

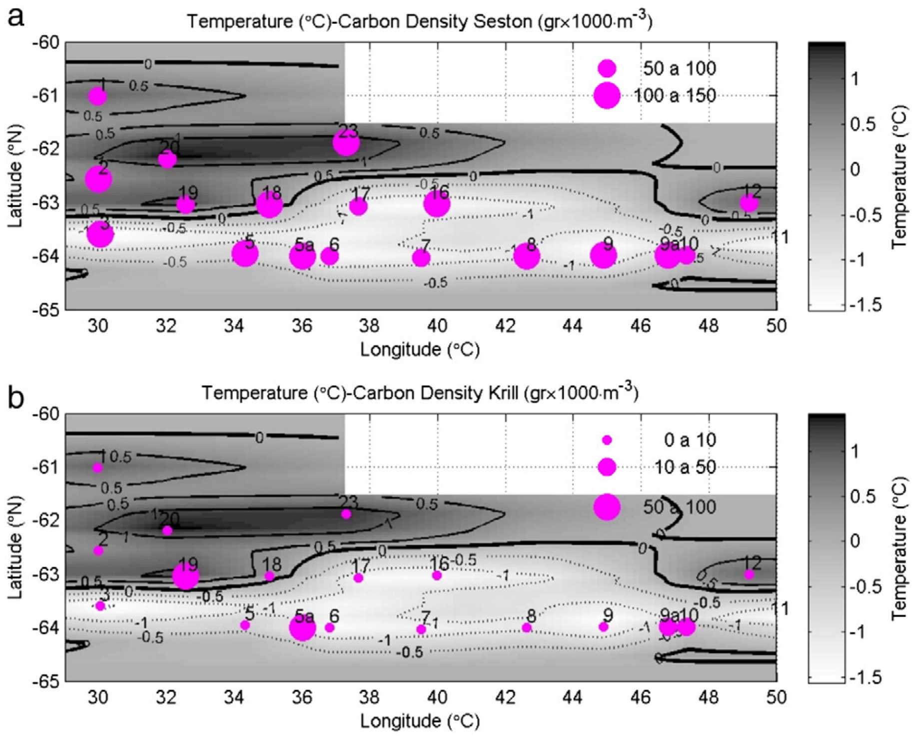

Fig. 11. C per station of seston (a) and krill (b) for the MD 25 cruise, during February, over the isotherms distribution.

and echosounding results from Masson (1989), it was possible to make a gross balance between the first trophic levels. The striking aspects of these results are, the great differences in krill energetic and carbon “density” between the swarming stations and the non-swarming stations, and the opposed situation found for POM and krill, which suggest that, krill is actively grazing down particulate matter. However, these results also show that krill had enough food in the area, thus food is not a restriction factor, at least in the area. For particulate matter, only one depth (15 m) was sampled, representing the euphotic zone, however, considering that krill is a vertical migrator, it is logic to suppose that POM is representative of the potential food supply for krill. Isotherms at 50 m show that frontal areas correspond to higher productivity (POM) and in some cases also to krill concentrations (Färber-Lorda, this volume). For lipid content in krill, higher concentration of lipids in krill were found near frontal areas; probably related to increased filtration by krill. Farber-Lorda et al.

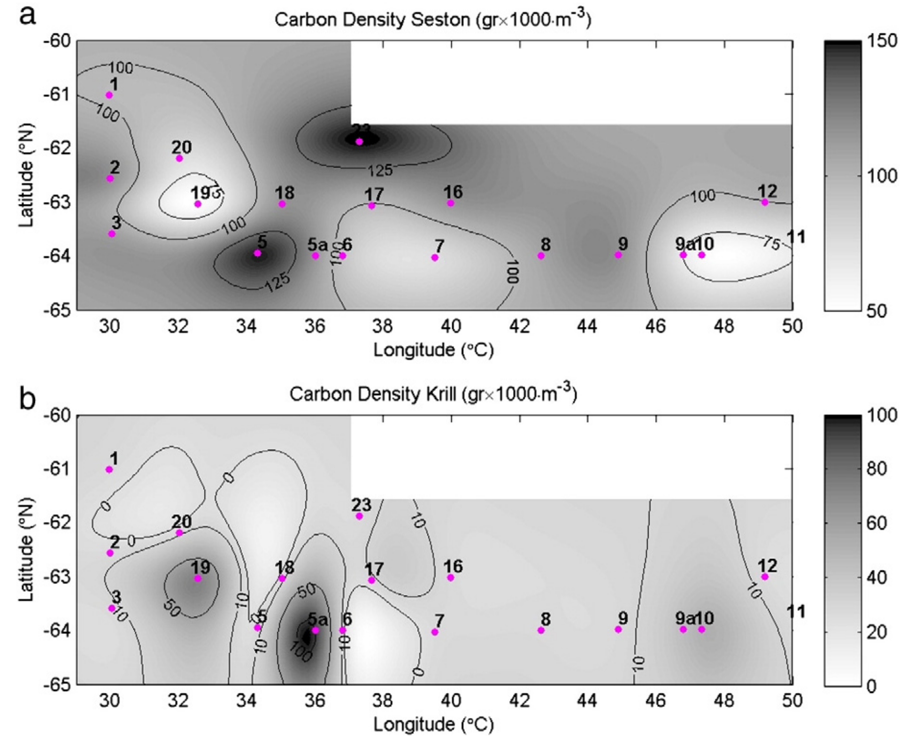

Fig. 12. Spatial distribution of seston carbon (a) and krill carbon (b) as calculated by our equations, and extrapolated for the entire area.

(this volume) show that there are two gyres in the area, one in the west and another in the east, and they correspond to higher productivity areas, for both POM and krill, at these stations krill had higher lipid content and were more differentiated morphologically. But also, populations had a dominance of females at these stations (except at station 5A), this shows that stage and sex composition of the populations are very important factors that must be considered when utilizing this approach (Färber-Lorda et al. 2009-this volume). This study concerns only post larval stages, thus, part of the information is lacking, however, if larval and juveniles biomass is known, the same equations could be apply, since they are based on the organic content, either on carbon and/or nitrogen or on protein and lipids. This is a useful way to make a global balance of the energy fluxes in the lower trophic levels of krill's food chain.

5. Conclusions

Useful and important equations were obtain, which will help in future studies, equations are also useful for calculations of energetic or carbon budget between different trophic levels, as shown for the studied area. Given the fact that the information obtained was the elemental and biochemical composition, which is the constituent of all living things. The importance of this paper reside in the fact that models are good enough to be able to predict many important variables. Our multiple linear regression combining protein and lipids were good and gave good results for both carbon and Joules. It was shown that at least for the area where samples were obtained, krill will have enough food if we consider that the POM sampled was its food supply. Results also show that krill is exerting a strong feeding pressure, since POM had an opposite trend for krill and POM in the spatial distribution, in both carbon and Joules. Higher productivity areas correspond to two gyres present in the area as shown by Färber-Lorda et al. (2009-this volume) with the dynamic geostrophy.

References

Bligh, E.G., Dyer, W.J., 1959. A rapid method for total lipid extraction and purification. Can. J. Biochem. Physiol. 37, 911–917.

Clarke, A., 1980. The biochemical composition of krill, *Euphausia superba* Dana, from South Georgia. J. Exp. Mar. Biol. Ecol. 43, 221–236.

Clarke, A., 1983. Biochemistry of *Euphausia superba*. Berich. Polarforsch. Sonderheft 4, 121–124.

Clarke, A., Morris, D.J., 1983. Towards an energy budget for krill: the physiology and biochemistry of *Euphausia superba* Dana. Polar Biol. 2, 69–86.

Comitta, G.W., Schindler, D.W., 1963. Calorific values of micro-crustacea. Science 140, 1394–1396.

Comitta, G.W., Marshall, F.R.S., Orr, A.P., 1966. On the biology of *Calanus finmarchicus*. XIII. Seasonal change in weight, calorific value and organic matter. J. Mar. Biol. Assoc. U. K. 46, 1–17.

Färber-Lorda, J., 1986 Etudes biologiques, energétiques et biochimiques du krill antarctique *Euphausia superba* et *Thysanoessa macrura* recolté au cours de la campagne FIBEX. Thése de doctorat. Ph. D. thesis, Université d'Aix-Marseille II, Marseille, France, Microfilm, Institut d'Ethnologie, Museum National d'Historie Naturelle 214 pp.

Färber-Lorda, J., 1990. Somatic length relationships and ontogenetic morphometric differentiation of *Euphausia superba* and *Thysanoessa macrura* of the southwest Indian Ocean during summer (February 1981). Deep-Sea Res. 37, 1135–1143.

Färber-Lorda, J., 1991. Multivariate approach to the morphological and biochemical differentiation of Antarctic krill (*Euphausia superba* and *Thysanoessa macrura*). Deep-Sea Res. 38, 771–779.

Färber-Lorda, J., 1994. Length vs. weight relationships and coefficient of condition of *Euphausia superba* and *Thysanoessa macrura* of the SW Indian Ocean during summer. Mar. Biol. 118 (4), 645–650.

Färber-Lorda, J., Beier, E., Mayzaud, P., 2009. Morphological and biochemical differentiation in Antarctic krill. J. Mar. Sys. 78, 525–535 (this volume).

Finlay, B.J., Uhlig, G., 1981. Calorific and carbon values of marine and freshwater Protozoa. Helgoländer Meeresunters. 34, 401–412.

Hirche, H.J., 1983. Excretion and respiration of the Antarctic krill *Euphausia superba*. Polar Biol. 1, 205–209.

Huntley, M., Nordhausen, W., Lopez, M.D.G., 1994. Elemental composition, metabolic activity and growth of Antarctic krill *Euphausia superba* during winter. Mar. Ecol. Prog. Ser. 107, 23–40.

Ikeda, T., 1984. Sequences in metabolic rates and elemental composition (C, N, P) during the development of *Euphausia superba* Dana and estimated food requirements during its life span. J. Crust. Biol. 4, 273–284.

Ikeda, T., Bruce, B., 1986. Metabolic activity and elemental composition of krill and other zooplankton from Prydz Bay, Antarctica, during early summer (November–December). Mar. Biol. 92, 545–555.

Ikeda, T., Kirkwood, R., 1989. Metabolism and body composition of two euphausiids (*Eupahusia superba* and *E. crystallorophias*) collected from under the pack-ice off Enderby Land, Antarctica. Mar. Biol. 100, 301–308.

Ikeda, T., Mitchell, A.W., 1982. Oxygen uptake, ammonia excretion and phosphate excretion in krill and other Antarctic zooplankton in relation to their body size and chemical composition. Mar. Biol. 71, 283–298.

Kersting, K., 1972. A nitrogen correction for calorific values. Limnol. Oceanogr. 17, 643–644.

Kils, U., 1979. Performance of Antarctic krill *Euphausia superba*, at different levels of oxygen saturation. Meeresforsch. 27, 35–48.

Kils, U., 1981. The swimming behavior swimming performance and energy balance of Antarctic krill *Euphausia superba*. BIOMASS Sci. Ser. 3, 1–121.

Lehninger, A.L., 1985. Biochemistry. Worth Publishers, Inc. 1104 pp.

Masson, M., 1989. Contribution to Antarctic krill acoustic studies—results of the NO *Marion Dufresne* MD25/FIBEX cruise. Polar Biol. 10, 101–106.

Mayzaud, P., Färber-Lorda, J., Corre, M.C., 1985. Aspects of the nutritional metabolism of two Antarctic euphausiids: *Euphausia superba* and *Thysanoessa macrura*. In: Siegfried, W.R., Condy, P.R., Lwas, R.M. (Eds.), Antarctic nutrient cycles and food webs. Springer-Verlag, Berlin, pp. 330–338. Heildelberg, New York, Tokyo.

Mayzaud, P., Albessard, E., Cuzin-Roudy, J., 1998. Changes in lipid composition of the Antarctic krill *Euphausia superba* in the Indian sector of the Antarctic Ocean: influence of geographical location, sexual maturity stage and distribution among organs. Mar. Ecol. Prog. Ser. 173, 149–162.

Pande, S.V., Parvin Khan, R., Venkitasubramanian, T.A., 1963. Microdetermination of lipids and serum total fatty acids. Anal. Biochem. 6, 415–423.

Phillipson, J., 1964. A miniature bomb calorimeter for small biological samples. OIkos 15, 130–139.

Platt, T., Irwin, B., 1973. Caloric content of phytoplankton. Limnol. Oceanogr. 18, 306–310.

Pond, D., Watkins, J., Priddle, J., Sargent, J., 1995. Variation in the lipid content and composition of Antarctic krill *Euphausia superba* at South Georgia. Mar. Ecol. Prog. Ser. 117, 49–57.

Raymont, J.E.G., Austin, J., Linford, E., 1964. Biochemical studies in marine zooplankton. I. The biochemical composition of *Neomysis integer*. J. Cons. Perm. Int. Explor. Mer. 28, 354–363.

Raymont, J.E.G., Srinivasagam, R.T., Raymont, J.K.B., 1971. Biochemical studies on marine zooplankton. IX. The biochemical composition of *Euphausia superba*. J. Mar. Biol. Assoc. U. K. 51, 581–588.

Salonen, K., Sarvala, J., Hakala, I., Viljanen, M.L., 1976. The relation of energy to organic carbon in aquatic invertebrates. Limnol. Oceanogr. 21, 724–730.

Schroeder, L.A., 1977. Caloric equivalent of some plant and animal material. Oecologia 28, 261–267.