CALORIFIC CONTENT OF SQUID (MOLLUSCA : CEPHALOPODA)

By J. P. CROXALL *and* P. A. PRINCE

ABSTRACT. Published information appears to be lacking on the chemical composition and calorific content of Southern Ocean squid, which are important prey of sperm whales and many seabirds. Data for 17 species of squid (all but one from the Northern Hemisphere) are reviewed. It is concluded that they have calorific contents distinctly lower than those of Antarctic fish and krill, mainly because of lower lipid content. Because of the importance of such information to studies of energy transfer between trophic levels, it is recommended that data on the chemical composition and calorific content of Antarctic squid should be rapidly obtained.

IN the course of research into the relationships between diet and the rate of growth of chicks of grey-headed albatrosses (*Diomedea chrysostoma*) and black-browed albatrosses (*D. melanophris*) at South Georgia (Prince, 1980*a*; Prince and Ricketts, in press) and into estimation of the impact of seabirds on Antarctic marine resources (Croxall and Prince, 1980*a*, in press), a recurrent problem has been the apparent scarcity of information on the calorific content and chemical composition of squid. The only value usually quoted (Voss, 1973; Clarke and Prince, 1980) is that of Leung and others (1952), where the species analysed is cited as not recorded but is in fact *Todarodes pacificus* (synonym *Ommastrephes sloani;* Akimushkin, 1965).

Because squid are an important item in the diet of albatrosses (Clarke and Prince, 1981; Clarke and others, 1981) and many other seabirds (Imber and Berruti, 1981), we have recently undertaken a search of available literature to locate additional information on the chemical composition or calorific content of squid. The results of this survey are presented here.

METHODS

In addition to conventional bibliographic searches, a computer search was made of all entries contained in the *BIOSIS Previews* and *Oceanic Abstracts* data bases.

It appears, however, that information on the chemical composition of squid is prone to appear in literature of rather restricted circulation and it is likely that we may have overlooked some relevant information, particularly in commercial fishery reports and similar sources.

RESULTS

Our main interest is in the calorific content of squid. Several studies, however, only report data on chemical composition. To convert these, we have assumed that the calorific contents of fat and protein are, respectively, 39.7 and 16.7 kJ g^{-1} (Petrusewicz and Macfadyen, 1970). Fat and protein, however, are not the only constituents of squid and, to assess the error introduced by making this assumption, we compared these estimates with actual calorific contents for eight species for which this was recorded (Table I). The overall conclusion is that calorific contents estimated as above are 98% of experimental determinations. This correction factor was subsequently applied to all estimated values.

The basic composition and calorific value for 17 species of squid are summarized in Table II. The average value for all 21 studies is 3.47 kJ g^{-1} (SD $\pm$ 0.45) wet weight, with a range from 2.88 kJ g^{-1} (*Eledone moschata*) to 4.50 kJ g^{-1} (*Loligo reynaudi*). The values reported by Cooper (1979) for *L. reynaudi* and *Todaropsis eblanae* are considerably greater than those for all other species, except one value for *Todarodes pacificus*. If these three records are excluded, the average value is then only 3.29 kJ g^{-1}.

Lipid content (fresh weight) is available for three additional species, *Ommastrephes bartrami* (1.5%), *Nototodarus sloani* (0.7%) and *Illex illecebrosus* (0.4%) (Hayashi and Takagi, 1979) but no values for protein and content are given. A calorific content equivalent to 4.05 kJ g^{-1} is mentioned in Montevecchi and Porter (1980) but the lipid content (3.0%) is very high and the species analysed is not recorded.

TABLE I. RELATIONSHIP BETWEEN ESTIMATED AND EXPERIMENTALLY DETERMINED CALORIFIC VALUES OF SQUID

Species	Calorific value* (kJ g^{-1})		Ratio E/D (%)	Reference
	Estimated (E)†	Determined (D)†		
Loliginidae				
Doryteuthis (Loligo) bleekeri	3.37	3.36	100.3	Sato, 1975
Loligo vulgaris	3.56	3.62	98.3	Gouveia and Gouveia, 1951
Sepioteuthis lessoniana	3.72	3.71	100.3	Sato, 1975
Ommastrephidae				
Todarodes pacificus	3.10	3.26	95.1	Leung and others, 1952
T. pacificus	3.89	4.19	92.8	Sato, 1975
Sepiidae				
Sepia madokai	3.16	3.32	95.1	Sato, 1975
Sepia sp.	3.51	3.50	100.3	Sato, 1975
Sepiella japonica	3.02	3.01	100.3	Sato, 1975

* Wet weight.
† Mean value for mantle and head plus arms combined.

DISCUSSION

Intraspecific variation

With the exceptions noted above, average calorific contents are very similar for all species but the range of values indicates appreciable variation, which is probably mainly attributable to seasonal changes, particularly those associated with reproductive status, condition and age.

For only four species, however, are data available on seasonable variation. Gouveia and Gouveia (1951) sampled 29 *Loligo vulgaris* from Portugal between November and March and 26 in July and August. The July sample had a protein content 10% higher than any winter value and a lipid content higher than all winter values except January. Individuals sampled in August had 10% less protein and 90% less fat than July specimens and were presumably post-spawning individuals. However, in data for the same species from the Adriatic (Coppini, 1972), analysed on a monthly basis, there is no clear seasonal pattern in calorific or protein content. Lipid values are high from May to December, lower between January and March, and very low in April. Similarly, for *Eledone moschata* and *Sepia officinalis* (Coppini, 1972), protein and calorific contents show no seasonal variation although lipid contents are lower in April in the former and from June to August in the latter.

In *Sepiella japonica* from Japan, Sato's (1975) data show a substantial difference in calorific value between pre-spawning young individuals in April (3.24 kJ g^{-1}) and post-spawning young individuals in June (2.90 kJ g^{-1}). Old individuals before spawning also have low values (2.90 kJ g^{-1}). Changes in protein, as well as lipid, composition seem to be involved. There is no clear difference between the sexes in any category.

Comparison with other marine organisms

It is not the purpose of this note to make any general comparisons between the calorific content of squid and other marine organisms. It is relevant, however, to our interest in the energy value of squid prey to its predators, briefly to compare squid values with those of representatives of the two other main groups, fish and krill (*Euphausia superba*), that form the main prey of Antarctic seabirds.

A. Clarke (1980) emphasized that the lipid content and calorific value of krill are strongly correlated with the state of sexual maturity. Gravid females contain 6.3% lipid and have calori-

TABLE II. COMPOSITION AND CALORIFIC VALUE OF SQUID

Species	*Composition* (% of wet weight)						*Calorific value* (kJ g^{-1})		*Reference*
	Water		*Protein*		*Lipid*				
	Mean	*Range*	*Mean*	*Range*	*Mean*	*Range*	*Mean*	*Range*	
Gonatidae									
Gonatopsis borealis									
Loliginidae	81.4		16.8		0.29		2.99†		Sasaki, 1975
Doryteuthis	79.1		17.8		1.00		3.37*		Sato, 1975
bleekeri	80.9		15.7		0.86		3.09†		Ferreyra *in* Pandit and Magar, 1972
Loligo gahi									
Loligo reynaudi	76.3	74.0–77.0	—		—		4.50*	4.21–4.72	Cooper, 1979
Loligo vulgaris	—		17.3	14.9–19.2	1.08	0.19–1.95	3.62*	3.02–4.02	Gouveia and Gouveia, 1951
L. vulgaris	79.6	75.7–83.9	16.4	13.0–17.9	1.12	0.53–1.23	3.32†	3.12–3.60	Coppini, 1972
L. vulgaris	79.7		16.5		0.81		3.21†		Pandit and Magar, 1972
Sepioteuthis lessoniana	78.0		19.1		1.32		3.71*		Sato, 1975
Octopodidae									
Eledone moschata	80.7	79.5–83.7	15.3	13.7–16.6	0.52	0.19–0.64	2.88†	2.47–3.13	Coppini, 1972
Octopus vulgaris	80.0		17.9		0.75		3.42†		Saavedra, 1949
Ommastrephidae									
Ommastrephes bartrami	79.8		17.6		0.34		3.13†		Sasaki, 1975
Todarodes pacificus	—		16.4		0.90		3.26*		Leung and others, 1952
T. pacificus	76.6		20.6		0.96		4.19*		Sato, 1975
T. pacificus	76.9		19.0		0.72		3.53†		Sasaki, 1975
Todaropsis eblanae	77.6		—		—		4.46*		Cooper, 1979
Onychoteuthidae									
Onychoteuthis boreali-japonica	79.1		18.2		0.72		3.41†		Sasaki,1975
Sepiidae									
Sepia officinalis	79.6		16.6		0.70		3.18†		Coppini, 1972
Sepia madokai	79.7		17.0		0.81		3.32*		Sato, 1975
Sepia sp.	78.5		19.0		0.82		3.50*		Sato, 1975
Sepiella japonica	81.6		16.2		0.78		3.01*		Sato, 1975

* Experimentally determined.
† Calculated.

fic values of 5.45 kJ g^{-1}, which is 42% greater than the value for mature males (2.4% lipid; 3.84 kJ g^{-1}). An average value for krill is probably about 4.2–4.5 kJ g^{-1} (Clarke and Prince, 1980).

Myctophid fish, which can be an important prey for some small petrels (e.g. blue petrel *Halobaena caerulea* (Prince, 1980*b*)), are well known to be lipid-rich (Butler and Pearcy, 1972; Childress and Nygaard, 1973) and calorific contents for two Antarctic species were 5.6 kJ g^{-1} and 8.0 kJ g^{-1}, with lipid contents of 8% and 14%, respectively (Clarke and Prince, 1980).

Nototheniid fish, which are an important prey of albatrosses (Prince, 1980*a*) and gentoo penguins (Croxall and Prince, 1980*b*), have much less lipid, only 2.3% in *Notothenia* sp. (Clarke and Prince, 1980), and 0.94% in *N. coriiceps* (Crawford, 1979). The calorific value of *N. coriiceps* was 4.1 kJ g^{-1} (Crawford, 1979).

In comparison with these results for krill and fish, the squid values summarized here suggest that as a group they have an appreciably lower calorific content and the main reason for this may be a lipid content which only averages 0.88%.

The squid data so far available represent only six families of the Cephalopoda, the members of all of which are characteristically denser than sea-water and none belongs to the families characterized by neutral buoyancy, achieved by high ammonium concentrations in certain tissues (Clarke and others, 1979). *Gonatus fabricii* and probably other species of the genus (e.g. *G. antarcticus*) maintain buoyancy by containing large amounts of low-density oil, particularly in the liver (Clarke and others, 1979; Kristenson and others, in preparation) and, being lipid-rich, are likely to have particularly high calorific contents. Furthermore, all but one of the species analysed are from the Northern Hemisphere, and only one species (*Todarodes pacificus*) was regarded as an oceanic species by Clarke (1966), although later (Clarke, M. R., 1980) several of the other species were noted to have been recorded from oceanic locations.

As it is oceanic species that are mainly taken by seabirds (and sperm whales, seals and other vertebrates), chemical and calorific analyses of Southern Hemisphere oceanic squids are urgently required if realistic assessments of energy transfer between trophic levels are to be made for Southern Ocean ecosystems.

Acknowledgements

We thank T. Kubodera and T. Okutani for providing and translating information on Japanese squid research and A. Clarke, M. R. Clarke and T. Kristenson for helpful comments on the manuscript.

MS received 27 May 1981; accepted in revised form 16 July 1981

REFERENCES

Akimushkin, I. I. 1965. *Cephalopods of the seas of the USSR*. Jerusalem, Israel Program for Scientific Translations.

Butler, J. L. *and* W. G. Pearcy. 1972. Swimbladder morphology and specific gravity of myctophids off Oregon. *Journal of the Fisheries Research Board of Canada*, **29**, 1145–50.

Childress, J. J. *and* M. H. Nygaard. 1973. The chemical composition of mid-water fishes as a function of depth of occurrence off Southern California. *Deep-Sea Research*, **20**, 1093–109.

Clarke, A. 1980. The biochemical composition of krill *Euphausia superba* from South Georgia. *Journal of Experimental Marine Biology and Ecology*, **43**, 221–36.

————. *and* P. A. Prince. 1980. Chemical composition and calorific value of food fed to mollymauk chicks *Diomedea melanophris* and *D. chrysostoma* at Bird Island, South Georgia. *Ibis*, **122**, 488–94.

Clarke, M. R. 1966. A review of the systematics and ecology of oceanic squids. *Advances in Marine Biology*, **4**, 91–300.

————. 1980. Cephalopods in the diet of sperm whales of the Southern Hemisphere and their bearing on sperm whale biology. *Discovery Reports*, **37**, 1–324.

————. *and* P. A. Prince. 1981. Cephalopod remains in regurgitations of black-browed and grey-headed albatross *Diomedea exulans L.* at South Georgia. *British Antarctic Survey Bulletin*, No. 54, 9–21.

————., Denton, E. J. *and* J. B. Gilpin-Brown. 1979. On the use of ammonium for buoyancy in squids. *Journal of the Marine Biological Association of the United Kingdom*, **59**, 259–76.

————., Denton, E. J. *and* J. B. Lilpin-Brown. 1979. On the use of ammonium for buoyancy in squids. *Journal of the Marine Biological Association of the United Kingdom*, **59**, 259–76.

Cooper, J. 1979. Length–mass relationships, water content and energy values for two species of squid *Loligo reynaudi* and *Todaropsis eblanae* off the south-western Cape. *Fisheries Bulletin of South Africa*, **11**, 43–45.

Coppini, R. 1972. Determinazione e comparazione del valore nutritivo e del valore commerciale di alcune specie di Molluschi eduli dell'Adriatico. *Ateneo Parmense Acta Naturalista*, **8**, 51–65.

Crawford, R. E. 1979. Effect of starvation and experimental feeding on the proximate composition and calorific content of an Antarctic teleost, *Notothenia coriiceps neglecta*. *Comparative Biochemistry and Physiology*, **62A**, 321–26.

Croxall, J. P. *and* P. A. Prince. 1980*a*. The food of gentoo penguins *Pygoscelis papua* and macaroni penguins *Eudyptes chrysolophus* at South Georgia. *Ibis*, **122**, 245–53.

————. *and* ————. 1980*b*. Food, feeding ecology and ecological segregation of seabirds at South Georgia. *Biological Journal of the Linnean Society*, **14**, 103–31.

————. *and* ————. In press. A preliminary assessment of the impact of seabirds on marine resources at South Georgia. *Comité National Français des Recherches Antarctiques*.

Gouveia, A. J. A. de *and* A. P. Gouveia. 1951. Contribuções para o estudo químico de moluscos da costa portuguesa. 1. Estudo analitico da espécie *Loligo vulgaris* Lamarck (Lula). *Revista da Faculdade de Ciencias Universidade de Coimbra*, **20**, 5–9.

Hayashi, K. *and* T. Takagi. 1979. Browning of dried-seasoned squid product. 1. On the chemical constituents for amino-acids and fatty acids of squid mantles. *Hokkaido Daigaku Suisangankabu Kenkyi Ito*, **30**, 288–93.

Imber, M. J. *and* A. Berruti. 1981. Procellariiform seabirds as squid predators. (*In* Cooper, J. E., *ed. Proceedings of the Symposium on Birds of the Sea and Shore, 1979*. Cape Town, African Seabird Group.)

Leung, W.-T. W., Pecot, R. K. *and* B. K. Watt. 1952. *Composition of food used in Far Eastern countries*. Washington, D.C., U.S. Department of Agriculture. [Agriculture Handbook, No. 34.]

Montevecchi, W. A. *and* J. M. Porter. 1980. Parental investment by seabirds at the breeding area with emphasis on northern gannets *Morus bassanus*. (*In* Burger, J., Olla, B. L. *and* H. E. Winn, *ed. Behaviour of marine animals. Vol. 4. Marine birds*. New York and London, Plenum Press, 323–65.)

Pandit, A. R. *and* N. G. Magar. 1972. Chemical composition of *Sepia orientalis* and *Loligo vulgaris*. *Fishery Technology*, **9**, 122–25.

Petrusewicz, K. *and* A. Macfadyen. 1970. *Productivity of terrestrial animals; principles and methods*. Oxford. Blackwell. [IBP Handbook 13.]

Prince, P. A. 1980*a*. The food and feeding ecology of grey-headed albatross *Diomedea chrysostoma* and black-browed albatross *D. melanophris*. *Ibis*, **122**, 476–88.

————. 1980*b*. The food and feeding ecology of the blue petrel *Halobaena caerulea* and dove prion *Pachyptila desolata*. *Journal of Zoology*, **190**, 59–76.

————. *and* C. Ricketts. In press. Relationships between food supply and growth in albatrosses: an interspecies fostering experiment. *Ornis Scandinavica*.

Saavedra, S. J. 1949. Análisis químico-bromatológico de la carne del *Octopus vulgaris*. *Revista de la Facultad de Farmacia y Bioquimica, Universidad Nacional, Lima*, **10**, 142–45.

Sasaki, M. 1975. On processing of squid fished off Kushiro, Hokkaido. *Kushiro Fisheries Experimental Station Newsletter*, **35**, 11–18.

Sato, T. 1975. Characteristics of squid flesh from the view of processing. (*In Development and utilization of world cephalopod resources*. Tokyo, Japanese Fisheries Agency, 201–13.)

Voss, G. L. 1973. Cephalopod resources of the world. *F.A.O. Fisheries Circular*, No. 149. [Rome. FAO/FIRM/C149.]