

1658

# Cephalopods in the diet of wandering albatrosses and sea-surface temperatures at the Sub-Antarctic Front

P. G. RODHOUSE

Marine Life Sciences Division, British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, U.K.

**SUMMARY:** Cephalopod beaks in the regurgitations of wandering albatross chicks from the breeding colony at Bird Island, South Georgia were collected throughout the austral winters of 1983 and 1984. There were large changes in relative frequency of species between the two years. In 1984 there were fewer Antarctic species in the bird's diet and more species which are known to occur to the north of the Sub-Antarctic Front. Notably, the proportion of an *Illex* sp. increased from 11 % to 33 % by number. *Illex* sp. was absent from a collection of cephalopod beaks from wandering albatross chick regurgitations made in 1976-77. The nearest known stock of this genus is *Illex argentinus*, which occurs over the Patagonian shelf. The data indicate that in 1984 the wandering albatrosses were exploiting a warmer water cephalopod community. Either their foraging range was extended further to the north and west in that year or there was a south easterly incursion of water from the South Atlantic which carried warmer water cephalopods closer to Bird Island. Sea-surface temperature records (NOAA, Climate Analysis Center) show no evidence of an incursion of warm water in 1984. On the contrary, in 1984 sea surface temperatures were cooler than in 1983. It is proposed that the collapse of the krill population in the vicinity of South Georgia, reported in the literature for the 1983 austral winter, resulted in sufficient disruption of the food web in the region to cause the wandering albatrosses to extend their foraging range in the austral winter of 1984.

*Key words:* Cephalopods, albatrosses, avian diets, Sub-Antarctic Front.

## INTRODUCTION

Cephalopods are an important component of the diet of the wandering albatross, *Diomedea exulans* (MATTHEWS, 1929; IMBER & RUSS, 1975; CLARKE *et al.*, 1981). The indigestible beaks of squid and octopods accumulate in the stomachs of the adults and chicks and can be sampled by inducing the birds to regurgitate. The beaks can be assigned to family, and often to species, level and there is strong correlation between beak size and cephalopod body mass. The biomass represented by the beaks of different species of cephalopod in the bird's stomachs can therefore be estimated (CLARKE, 1986).

Collections of cephalopod beaks were taken from the regurgitations of wandering albatross chicks on the breeding colony at Bird Island, South Georgia in the breeding seasons of 1983 and 1984. Important differences were found, between the two years, in the relative numbers of different species of squid fed to

the chicks by the parent birds (RODHOUSE *et al.*, 1987). In 1983, thirty five cephalopod species were present and this increased to 45 in 1984. Of the ten species which were present in 1984 but not 1983, nine are not considered to be Antarctic in origin and are presumed to have been caught by the parent birds to the north of the Sub-Antarctic Front (SAF). One of these, an *Illex* sp., was probably taken over the Patagonian Shelf; two other species, *Egea inermis* and *Megalocranchia* sp., have sub-tropical or tropical distributions (VOSS, 1974, 1980). *Illex* sp. did not occur in the regurgitations of wandering albatross chicks collected in 1976-77.

These observations suggest that in 1984, cephalopods from warmer water were available to the wandering albatrosses, either because of an incursion of water from the South Atlantic or because their foraging range was extended. In this paper these alternative hypotheses are examined by reference to blended sea-surface temperature data.

## MATERIALS AND METHODS

Wandering albatross chicks at the breeding colony on Bird Island, South Georgia were sampled at approximately monthly intervals between May and September 1983 and 1984. Methods for the collection and treatment of cephalopod beaks are described by RODHOUSE *et al.* (1987). Species were designated Antarctic or non-Antarctic according to their distributions given by OKUTANI & CLARKE (1985) and ROPER *et al.* in FISCHER & HUREAU (1985).

Sea-surface temperatures (SST) and sea surface temperature anomalies (SSTA), at intervals of 2° of longitude, along a latitudinal transect between South Georgia and the Patagonian shelf in the vicinity of the Falkland Islands (53°S 39°W to 53°S 59°W), for the period January to September 1983 and 1984, were extracted from blended SST data (NOAA Climate Analysis Center; REYNOLDS, 1988). This transect is probably the shortest distance between the wandering albatross nesting colony at Bird Island and known stocks of *Illex* sp. which is the most important warm water cephalopod species in the diet of these birds (RODHOUSE *et al.*, 1987). The area of the Patagonian shelf in the vicinity of the Falkland Islands is within the foraging range of wandering albatrosses at South Georgia (CROXALL *et al.*, 1984) and so this is the most likely source of *Illex* sp. (*Illex argentinus*). The transect crosses the SAF which lies between the Patagonian shelf and South Georgia (Fig. 1).

The SST data are a hybrid between satellite and ship observations averaged monthly on a two-degree grid. Ship observations are scarce in the South Atlantic by comparison with other geographical areas so there are fewer 'sea-truth' temperature values. However, satellite coverage in the region is sufficient to

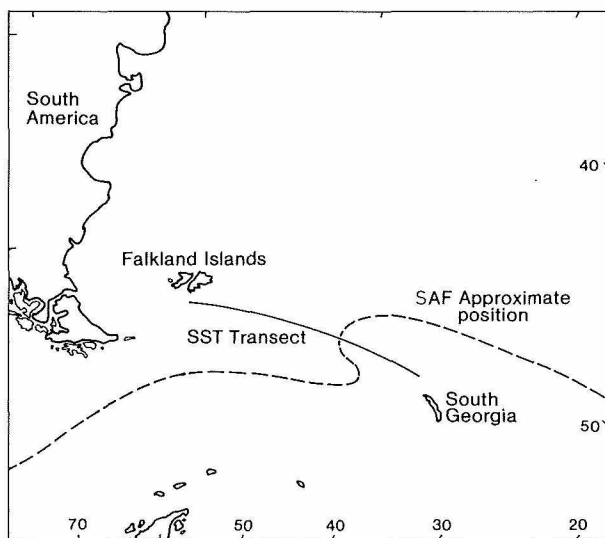


FIG. 1. — Chart of the Atlantic sector of the Southern Ocean showing approximate position of the Sub-Antarctic Front and sea surface temperature transect.

allow useful inter-year comparison of trends in SST. Similarly, SSTA is based on limited climatic data for the region so that magnitude of the anomaly is of less relevance than the inter-year comparison in the context of this study.

## RESULTS AND DISCUSSION

A summary of data from RODHOUSE *et al.* (1987) on the number of beaks of Antarctic and non-Antarctic cephalopods in the regurgitations of wandering albatross chicks on Bird Island, South Georgia, in 1983 and 1984 is given in figure 2. Estimated wet weight biomass of each cephalopod species represented by these beaks is also shown. Number of Antarctic species decreased from 54 % in 1983 to 42 % in 1984 and this was reflected in a decrease in biomass of Antarctic species from 81 % to 69 % in the respective years. The ratio of number of Antarctic species to warm-water species was significantly different ( $X^2 = 143.98$ ;  $P < 0.001$ ) between the two years. The major influence in this trend is a reduction in the numbers and biomass of the two Antarctic onychoteuthids, *Kondakovia longimana* and *Moroteuthis knipovitchi* in 1984 and a concomitant increase in the numbers and biomass of the ommastrephid, *Illex* sp. in 1984 (RODHOUSE *et al.*, 1987). The ratio of number of *Kondakovia longimana* to *Illex* sp. was significantly different ( $X^2 = 54.40$ ;  $P < 0.001$ ) between the two years. Although the ommastrephid, *Martialia hyadesi*, increased in 1984 this species is known to occur both north and south of the SAF (ROPER *et al.* in FISCHER & HUREAU, 1985).

Sea surface temperatures and sea surface temperature anomalies along the transect 53° 59'W to 53° S 39' W for the period January to September, 1983 and 1984, are shown plotted in figures 3 and 4. Between April and July 1983, SST was consistently higher by up to 1.6 °C along the entire length of the transect between the Patagonian Shelf and South Georgia (Fig. 3). The data illustrated in figure 4 suggest that between May and July anomalously high SST occurred along the transect in both years but that these anomalies were consistently greater in 1983.

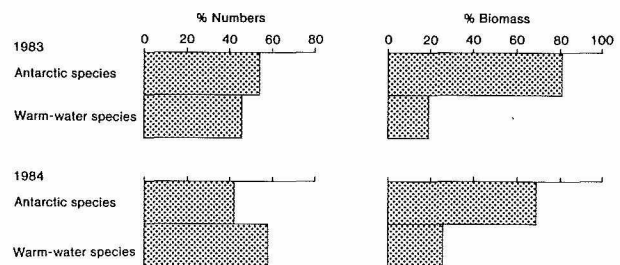


FIG. 2. — Percentage of beaks, and percentage of biomass represented by beaks, of Antarctic and warm-water cephalopods in the diet of wandering albatross chicks at Bird Island, South Georgia.

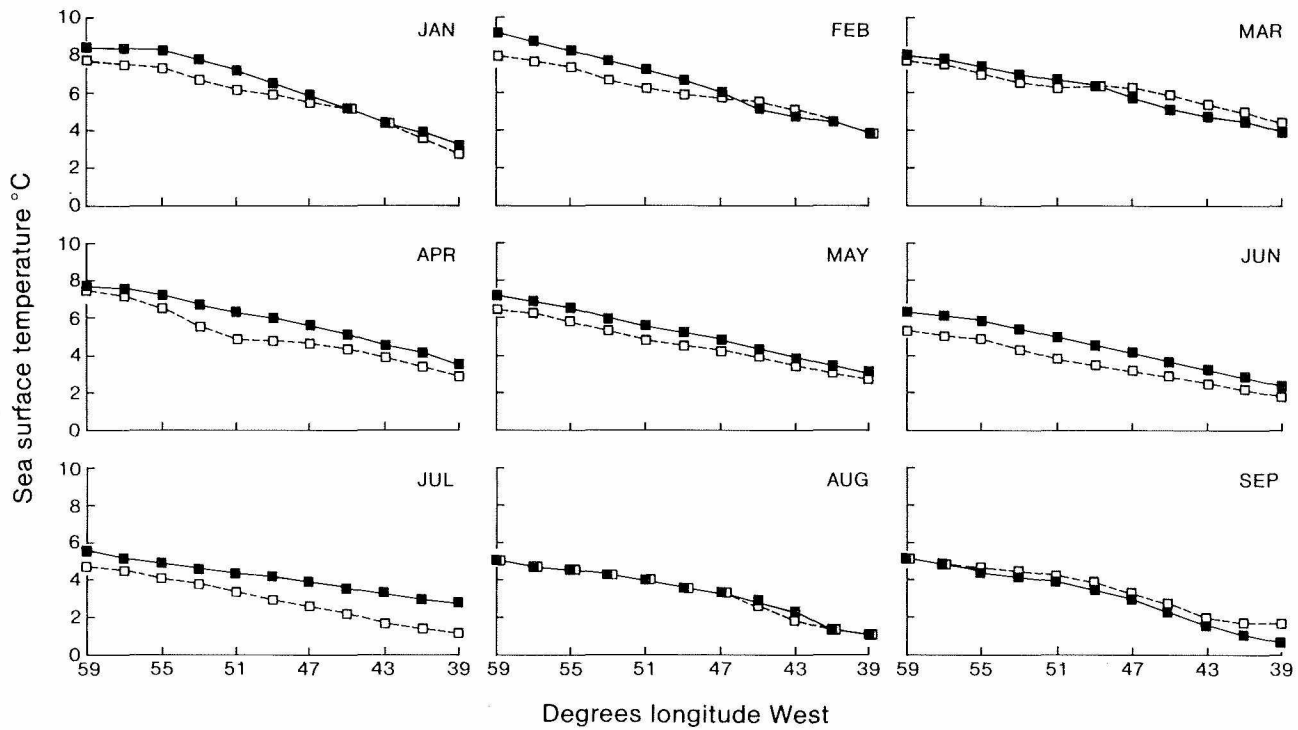


FIG. 3. — Sea surface temperatures along the transect 53°S 39°W to 53°S 59°W for the period January to September, 1983 and 1984. Closed squares: 1983; open squares: 1984.

During these months SST and SSTA differences between the two years persist on both sides of the mean position of the Sub-Antarctic Front.

The data in figure 2 show that in 1984 a greater proportion of cephalopods fed to wandering albatross chicks were of warm-water origin than in 1983. Of the warm-water species in the diet, *Illex* sp. is the most common by numbers and biomass. *Illex* sp. was absent from the diet of wandering albatrosses in the 1976-77 season (CLARKE *et al.*, 1981). The nearest known population of this genus (*Illex argentinus*) is over the Patagonian shelf from 30°S to 50°S and the shelf around the Falkland Islands (ROPER *et al.*, 1984). The increased importance of *I. argentinus* in 1984, together with the increase in incidence of other non-Antarctic species, suggests that either there was an incursion of warm water from the South Atlantic towards South Georgia in 1984, which carried these species further into the bird's foraging range, or that the wandering albatrosses foraged further to the north and west in 1984 than in 1983.

The SST and SSTA data in figures 3 and 4 give no indication that there was an incursion of warm water towards South Georgia in 1984. On the contrary, SST along the entire transect between the Patagonian shelf and South Georgia was consistently lower in 1984 for most of the period, May to September, when the cephalopod diet of the wandering albatrosses was sampled. It therefore seems unlikely that warm water cephalopods were carried further into their foraging range in that year.

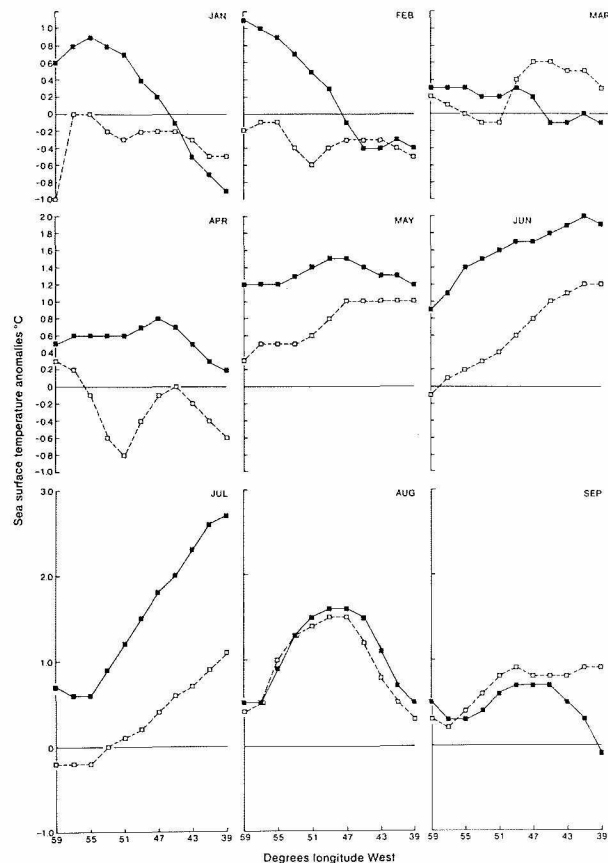


FIG. 4. — Sea surface temperature anomalies along the transect 53°S 39°W to 53°S 59°W for the period January to September, 1983 and 1984. Closed squares; 1983; open squares: 1984.

During the austral winter of 1983 there was a marked reduction in the concentration of krill, *Euphausia superba*, in the Scotia Sea (HEYWOOD *et al.*, 1985). This collapse of the krill population was linked with a reduction in the breeding success of summer breeding species of vertebrate predators; black-browed and grey-headed albatrosses (*Diomedea melanophrys* and *D. chrysostoma*), gentoo and macaroni penguins (*Pygoscelis papua* and *Eudyptes chrysolophus*) and Antarctic fur seals (*Arctocephalus gazella*), at South Georgia in the austral summer of 1983-84 (CROXALL *et al.*, 1988). Wandering albatrosses breed in the austral winter and feed their chicks on fish and cephalopods and there was a decrease in the proportion of cephalopods in their diet from 39.5 % in 1983 to 29.7 % in 1984 (CROXALL & PRINCE, pers. comm.). However, although there has been a gradual, but significant, decline in the wandering albatross population at Bird Island over the last decade, there was no reduction in breeding success in this species in the 1983 or 1984 breeding seasons, which could be linked, as for krill predators, to the krill population failure observed in the austral winter of 1983.

This reduction in krill concentration in the Scotia Sea appears to have had a considerable effect on those predators for which krill is a major food resource. There are few data on prey items of Southern Ocean cephalopods but there is some evidence that *Kondakovia longimana*, the major Antarctic squid taken by wandering albatrosses, is a krill predator (FILIPPOVA, 1972). If, as seems likely, krill is also a major food resource for other Antarctic cephalopods then it is likely that cephalopod, especially squid, populations may have been adversely influenced by the low krill densities observed in 1983. If the reproductive success of the cephalopods in the Scotia Sea was reduced during the austral summer of 1983-84, as a result of diminution of the food resource, this would explain the reduction in the proportion of squid, especially cold water species, fed by wandering albatrosses to their chicks during their 1984 breeding season. The increased incidence of warm water cephalopods in the wandering albatrosses diet in 1984 suggests that they extended their foraging range in order to meet their own and their chicks' food requirements, at a time when squid stocks in the Scotia Sea were reduced.

The possible causes of the disappearance of krill from the Scotia sea in 1983 were considered by PRIDDLE *et al.* (1988), who concluded that mesoscale, surface oceanographic events, forced by strong southward airflow, probably displaced the Antarctic Polar Frontal Zone southwards and disrupted the surface eddy structure in the Scotia sea. This, it is suggested, resulted in the krill population being released from the area to pass downcurrent in the West

Wind Drift (TCHERNIA, 1980). Such events are possibly associated with larger scale climatic phenomena; the events in 1983 coincided with a strong El Niño/Southern Oscillation (ENSO) event in the eastern Pacific basin (CANE, 1983). There is circumstantial evidence that ENSO years in the past have been associated with reduced breeding success in Antarctic vertebrate predators (CROXALL *et al.*, 1988) and with reduced whale catches (PRIDDLE *et al.*, 1988).

It is only possible to speculate on the medium and long-term consequences for cephalopods of such irregular, large scale disruptions of the food chain in the Scotia Sea. Cephalopod populations elsewhere appear to be food limited at certain times of the year and resort to cannibalism (O'DOR, 1983). Most cephalopods are fast growing and short lived (BOYLE, 1983) and it is generally recognised that such organisms recover quickly when populations collapse as a result of natural events or over exploitation (GULLAND, 1983). The reproductive tactics by cephalopods are apparently adapted to maximise population growth when utilising an intermittent or patchy food resource but the short life cycle and rapid growth will give rise to large fluctuations in numbers and biomass (O'DOR & WEBBER, 1986).

Cephalopods are generally opportunistic and it is suggested that they can rapidly increase population size to fill niches left unoccupied following the depletion of other groups (CADDY, 1983).

The long-term stability of the wandering albatrosses breeding success on Bird Island, by comparison with other vertebrate predators which feed on krill, may in part derive from their predation on a diverse and geographically widespread cephalopod community, the individual components of which may fluctuate dramatically, but probably recover relatively quickly from perturbations of the food web.

## ACKNOWLEDGEMENTS

I thank R. W. Reynolds for providing the SST data used in this paper and M. R. Clarke, J. P. Croxall, R. B. Heywood, A. W. A. Murray, J. Priddle and M. G. White for their advice and criticism.

## REFERENCES

- BOYLE, P. R. (Ed.) 1983. *Cephalopod life cycles*, 1. Academic Press. London.
- CADDY, J. F. 1983. The cephalopods: factors relevant to their population dynamics and to the assessment and management of stocks. In: *Advances in assessment of world cephalopod resources*. FAO Fisheries Tech. Pap. 231: 416-452.
- CANE, M. A. 1983. Oceanographic events during El Niño. *Science*, 222: 1189-1195.
- CLARKE, M. R. 1986. *A handbook for the identification of cephalopod beaks*. Clarendon Press. Oxford.
- CLARKE, M. R., CROXALL, J. P. & PRINCE, P. A. 1981. Cephalo-

- pod remains in the regurgitations of the wandering albatross *Diomedea exulans* L. at South Georgia. *British Antarctic Survey Bull.* 54: 9-21.
- CROXALL, J. P., MCCANN, T. S., PRINCE, P. A. & ROTHERY, P. 1988. Variation in reproductive performance of seabirds and seals at South Georgia 1976-1986 and its implication for Southern Ocean monitoring studies. In: *Antarctic Ocean and resources variability* (D. Sahrhage, ed.): 261-285. Springer. Berlin.
- CROXALL, J. P., RICKETS, C. & PRINCE, P. A. 1984. Impact of seabirds on marine resources, especially krill of South Georgia waters. In: *Seabird energetics* (G. Causey Whittow & Herman Rahn, eds.): 285-317. Plenum. New York.
- FILIPPOVA, J. A. 1972. New data on the squids (Cephalopoda: Oegopsida) from the Scotia Sea (Antarctic). *Malacologia*, 11: 391-406.
- FISHER, W. & J. C. HUREAU (Eds.). 1985. *FAO species identification sheets for fishery purposes. Southern Ocean (Fishing areas 48, 58 and 88) (CCAMLR Convention Area)*. Rome, FAO, 1.
- GULLAND, J. A. 1983. *Fish stock assessment: a manual of basic methods*. Wiley. Chichester.
- HEYWOOD, R. B., EVERSON, I. & PRIDDLE, J. 1985. The absence of krill from the South Georgia zone, winter 1983. *Deep-sea Res.*, 32: 369-378.
- IMBER, M. J. & RUSS, R. 1975. Some foods of the wandering albatross *Diomedea exulans*. *Notornis*, 22: 27-36.
- MATTHEWS, L. H. 1929. The birds of South Georgia. *Discovery Rep.*, 1: 561-592.
- O'DOR, R. K. 1983. *Illex illecebrosus*. In: *Cephalopod life cycles*, 1 (P. R. Boyle, ed.): 175-199. Academic Press. London.
- O'DOR, R. K. & WEBBER, D. M. 1986. The constraints on cephalopods: why squid aren't fish. *Can. J. Zoology*, 64: 1591-1605.
- OKUTANI, T. & CLARKE, M. R. 1985. *Identification key and species description for Antarctic squids*. Biomass Handbook, 21. U.S. NOAA Washington, D.C.
- PRIDDLE, J., CROXALL, J. P., EVERSON, I., HEYWOOD, R. B., MURPHY, E. J., PRINCE, P. A. & SEAR, C. B. 1988. Large-scale fluctuations in distribution and abundance of krill - a discussion of possible causes. In: *Antarctic Ocean and resources variability* (D. Sahrhage, ed.): 169-182. Springer. Berlin.
- REYNOLDS, R. W. 1988. A real-time sea surface temperature analysis. *J. Climate*, 1: 75-86.
- RODHOUSE, P. G., CLARKE, M. R. & MURRAY, A. W. A. 1987. Cephalopod prey of the wandering albatross *Diomedea exulans*. *Marine Biology*, 96: 1-10.
- ROPER, C. F. E., SWEENEY, M. J. & NAUEN, C. E. 1984. *Cephalopods of the world. An annotated and illustrated catalogue of species of interest to fisheries*. FAO Fisheries Synopsis, 125 (3).
- TCHERNIA, P. 1980. *Descriptive regional oceanography*. Pergamon. Oxford.
- VOSS, N. A. 1974. Studies on the cephalopod family Cranchiidae. A redescription of *Egea inermis* Joubin, 1933. *Bull. Mar. Sci.*, 24: 939-956.
- VOSS, N. A. 1980. A generic revision of the Cranchiidae (Cephalopoda: Oegopsida). *Bull. Mar. Sci.*, 30: 365-412.

