

Cephalopods: Trophic modelling of the Ross Sea

M.H. Pinkerton, J. Bradford-Grieve, D. Thompson

National Institute of Water and Atmospheric Research Ltd (NIWA), Private Bag 14901,
Wellington 6021, New Zealand.

Email: m.pinkerton@niwa.co.nz; Tel.: +64 4 386 0369; Fax: +64 4 386 2153

1 Introduction

In this study, because of the lack of data on cephalopod abundance and ecology in the Ross Sea, we have grouped all the cephalopods into one compartment. Lack of adequate biomass, growth and feeding parameter data at the moment for cephalopods leads us to treat this compartment as being mainly squid and it is their parameter estimates that are included in the model initially.

Information on cephalopod species occurring in the Ross Sea sector (which includes both the Ross Sea and the deeper, northern waters to 60°S) was advanced during three recent studies. First, studies of the diets of Antarctic toothfish (*Dissostichus mawsoni*) caught by the longline fishery in the Ross Sea region yielded cephalopod beaks which could often be identified to genus and sometimes species level (Stevens 2004, 2005, Thompson et al. 2008) (Table 1). Cephalopods were identified from characteristics of their beaks with the assistance of Dr Yves Cherel of the Centre d'Etudes Biologique de Chize, France. Second, cephalopod beaks, often with associated buccal muscle, retrieved from the stomachs of Antarctic toothfish, were analysed by mass spectrometry for the isotopic composition of carbon (^{12}C , ^{13}C) and nitrogen (^{14}N , ^{15}N) giving an insight into trophic position (Thompson et al. 2008). Finally, the January-March 2008 IPY-CAML (International Polar Year-Census of Antarctic Marine Life) voyage to the Ross Sea on the RV *Tangaroa* captured a number of cephalopods during trawl surveys which are, as yet, incompletely analysed. These data will increase the number of cephalopod species known to occur in the Ross Sea by at least a further four squid, six octopod species, and possibly a number of undescribed taxa.

The most diverse squid fauna appears to be found over the outer northwestern Ross Sea continental shelf with few squids penetrating into the southwestern corner of the Ross Sea where octopods dominated. This agrees with Ainley et al. (1984) who showed the prevalence of squid in seabird diets over the deep ocean north of the Ross Sea and slope but lower cephalopod consumption by seabirds over the Ross Sea shelf. It appears that only juveniles of the local squid population are found over the Ross Sea shelf and that the adult population occurs mainly over the continental slope. The octopus fauna is not yet well known but it appears that benthopelagic *Cirroctopus* may dominate by weight in the 2008 samples. *Gonatus antarcticus* is also likely to be significant in the Ross Sea as this squid species has been identified from beaks in the stomachs of emperor penguins (Cherel & Kooyman 1998). The maximum mantle length for this species is 35 cm (Okutani 1995).

The data available to date from the 2008 IPY-CAML Ross Sea voyage suggests that the squid fauna in the Ross Sea is similar to that of the Prydz Bay area at 68°S 75°E (Lu & Williams 1994). Lu & Williams (1994) found that the most common species encountered in the Prydz Bay area (in terms of numbers, not biomass) were: 53% *Psychroteuthis glacialis*; 28% *Galitheuthis glacialis*; 9% *Alluroteuthis antarcticus*; 8% *Mastigoteuthis psychrophila*; 1% *Brachioteuthis* sp; 1% *Bathyteuthis abyssicola*; <1% *Mesonychoteuthis hamiltoni*; <1% *Kondakovia longimana*. We summarise information on three common cephalopod groups below.

Table 1. Species of cephalopods from Antarctic toothfish stomachs from 2005/06 and 2006/07 fishing seasons from CCAMLR subarea 88.1 (Thompson et al. 2008).

	Scientific name	Common name	Maximum mantle length
Squids	<i>Mesonychoteuthis hamiltoni</i>	Colossal squid	
	<i>Kondakovia longimana</i>	No common name	
	<i>Psychroteuthis glacialis</i>	Glacial squid	44 cm (Roper et al. 1984)
	<i>Galiteuthis glacialis</i>	No common name	50 cm (Roper et al. 1988)
	<i>Moroteuthis knipovitchi</i>	Smooth hooked squid	
Octopods	<i>Stauroteuthis gilchristi</i>	No common name	
	<i>Cirroctopus glacialis</i>	No common name	
	<i>Cirrata</i> sp. A		
	Octopodid sp. 1		
	Octopodid sp. 2		

***Psychroteuthis glacialis*.** Lu & Williams (1994) caught *Psychroteuthis glacialis* in Prydz Bay in three clusters: (1) 4–18 mm mantle length (ML) - immature; (2) 95–201 mm ML – immature; (3) >200 mm mature class which was poorly sampled. The two size classes of paralarvae are possibly two year classes (Lu & Williams 1994) although they could also represent more than one spawning time in a year (see Cherel & Weimerskirch 1999; Arkhipkin 2004), or a males and females may have significant sexual dimorphism in growth patterns (Dr Uwe Piatkowski, Universität Kiel, pers. comm.). Small individuals were mostly pelagic whilst larger specimens (>95 mm) were only captured in bottom trawls on the shelf. The data suggest strong ontogenetic descent that for this species, with small individuals at shallow depths and subadults living on or near the bottom close to the edge of the continental shelf.

***Galiteuthis glacialis*:** At least two size classes of *Galiteuthis glacialis* were also caught in Prydz Bay, but these were not distinct Lu & Williams (1994). Small individuals were captured both on the shelf and in the open ocean whereas most large individuals were caught in the open ocean. The data suggest that ontogenetic descent takes place and adults live in deep water. One lone night trawl suggests some adults or subadults come up to shallow depths to feed at night.

Cirroctopodidae: Little is known about the Cirroctopodidae (containing a single genus *Cirroctopus*) which is a Southern Hemisphere family (Collins & Villanueva 2006). The life history of cirrate octopods is known mainly from *Opisthoteuthis*. Breeding seems to extend over a long period while the animal continues to grow with eggs maturing and being released one or two at a time. The numbers of eggs produced are known only for a few species. It is thought that eggs are not brooded but are released directly onto the sea floor. The duration of embryonic development is unknown but as egg size and temperature are primary determinants of the duration of embryonic developments in cephalopods it is expected that development time will be long. Nesis (1999) estimated the development time, from models, of *Cirroctopus glacialis* to be 2.5 y at 0.5°C in the Antarctic. It is thought that the post hatching life is also probably several years.

2 Carbon content of cephalopod tissue

Work by Vlieg (1988) found arrow squid dry weight to be 22.5% of wet weight, and ash to be 6.2% of dry weight. Vinogradov (1953) gives similar data for dry weight of Cephalopoda ranging from 13–30% of wet weight and a value for ash proportion of 0.9–2.4% of wet weight equivalent to c. 7.7% dry weight. If ash-free dry material is made of material in carbohydrate proportions ($C_6H_{12}O_6$) then carbon is likely to make up ~40% dry weight or 8.4% wet weight.

3 Cephalopods diet

Lu & Williams (1994) report that stomachs of *Psychroteuthis glacialis* caught in Prydz Bay contained *Euphausia superba* (46% by weight), *Pleuragramma antarcticum* (23% by weight), other fish (28% by weight), other *P. glacialis* (0.23%) and rest composed of other crustacean and unidentified material. Larger individual squid were found to take larger krill, though the diet of larger squid is generally poorly studied because they are difficult to catch. Stomach contents of *Galiteuthis glacialis* were *E. superba* (95% by weight), and unidentified fish (5% by weight) according to Lu & Williams (1994). We note that *Euphausia crystallorophias* was not found in Prydz Bay by the study of squid by Lu & Williams (1994), and so it is not surprising this species does not occur in the diet of squid found there. We speculate that squid of the Ross Sea are opportunistic feeders, and their diet is likely to reflect the abundance of different prey items of a suitable size. Squid of the shelf region of the Ross Sea are likely to feed on *Euphausia superba* and *E. crystallorophias*, along with other macrozooplankton, *P. antarcticum*, and other small, water-column fish. Fishers on board longliners in the Ross Sea have reported squid feeding on Antarctic toothfish caught on the longlines, and a very large colossal squid was caught and retained by a longline vessel in 2003. Some Antarctic toothfish have been documented as having been subjected to significant depredation by squid while caught on longlines in the Ross Sea. Whether squid feed on free-swimming toothfish is unknown.

The Cirroctopodidae have very large eyes compared with other octopods but it is not known how important these are for feeding. The prey of cirrate octopods is small individuals with slow swimming speeds: gammarid amphipods and polychaetes may be the major prey items as well as other small crustaceans. Bathypelagic and demersal cephalopods (e.g., *Bathyteuthis abyssicola*) may also take benthic macro- and mega-fauna from the Ross Sea shelf region. There is also some cannibalism amongst Southern Ocean cephalopods: 0.23% by weight of the stomach contents of *P. glacialis* was found to be material from *P. glacialis* (Lu & Williams 1994). The rates of cannibalistic consumption are not known.

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We suggest a possible diet for cephalopods of the Ross Sea is: 5% small demersal fishes; 5% silverfish; 5% pelagic fishes; 5% cephalopods (cannibalism); 10% *E. crystallorophias*; 15% *E. superba*; 10% other macrozooplankton; 30% mesozooplankton; 5% megabenthos; 10% macrobenthos.

4 Production

We have not found any research on growth rates of cephalopods specifically in the Ross Sea, but here estimate a production rate for *Psychroteuthis glacialis* which is taken as a “typical” Ross Sea cephalopod.

We first briefly summarise cephalopod life history in Antarctic waters. It is likely that Southern Ocean cephalopods lay eggs in masses, but we don't know if benthic or pelagic egg masses are laid, or when in the year they are laid. Both of these factors are likely to vary between species and possibly between locations of the Southern Ocean. Botelzky (1994) suggests that typical ingredients of cold-water cephalopod life cycles in waters colder than 5°C may be an embryonic phase covering 3–12 months or more. This protracted embryonic phase may be the reason why some Antarctic cephalopods seem to have longer lifespans than species in temperate waters (c. 2 years) compared to <1 year (Jackson & O'Dor 2001). Also, the fact that Antarctic cephalopods may have more protracted individual spawning activity over several months than warmer water species (Botelzky 1994) may necessitate a longer lifespan. Unfortunately, to the authors' knowledge there are no aging studies of Antarctic cephalopods using observations of statolith increments as Jackson & O'Dor (2001) summarised for squids in temperate waters.

Grist & Jackson (2004) provide a physiologically based model for two-phase growth in cephalopods, first described by Forsythe (1993). Cephalopod larvae typically display rapid, exponential growth until adulthood, when growth becomes slower and is often described by a power law. The model is based on the well-known observation that P/B is approximately proportional to $B^{-0.25}$ for a given species (Grist & Jackson 2004). This leads to a growth curve of the form $B(t) = K \cdot (t - t_0)^{4.0}$, where t is time (days). Such a power law gives high P/B values for small cephalopods such that the growth appears almost exponential, decreasing as the cephalopods age. To estimate K and t_0 we use two estimates of size at age for *Psychroteuthis glacialis*. First, we consider the smallest samples of this species taken. Paralarvae taken in Prydz Bay in Nov/Dec were 4–13.9 mm mantle length (ML) whereas paralarvae taken in Jan/Feb (Lu & Williams 1994) were generally found in two size classes 4–15.9 mm and 90–179 mm ML. We assume that the paralarvae taken in the period Nov/Dec and the smaller paralarvae found in Jan/Feb were relatively recently hatched (Lu & Williams 1994). Lu & Williams (1994) give a relationship between mantle length (ML, mm) and weight (W g wet weight) for large specimens of *Psychroteuthis glacialis* (it is not clear if these are fresh or preserved): $\log W = 2.55 \times \log ML - 3.664$ ($n = 75$, $r = 0.84$) although we note that this relationship may not be accurate for very small specimens. If we assume the relationship holds for small specimens, then the weight of the paralarvae is about 0.036 g.

Next, we apply the length-weight relationship for *Psychroteuthis glacialis* of Lu & Williams (1994) to a maximum mantle length of 44 cm (Roper et al. 1984) gives a maximum weight of 1190 gWW. The time to reach this size is not known for *Psychroteuthis glacialis* and here we use an estimate of 1.5 years. These values allow us to estimate a weight-at-age for this species of cephalopod, and hence a production rate for all ages of squid in the population.

The model gives an average P/B for *Psychroteuthis glacialis* less than 60 days old of 5.9%. This growth rate is very reasonable compared to other studies. For example, *Illex illecebrosus* is able to grow at rates up to 5% of wet weight per day depending on the food intake as a percentage of body weight with highest growth rates achieved at food intake of about 10% per day (see Wells & Clarke 1996 and references therein). Pecl et al. (2004) uses squid growth rates of 4–9% body weight per day. The growth rate of young squid paralarvae probably depends on the breeding success of copepods and prey of *P. glacialis* that depend on sea ice retreat at high latitudes (Schnack-Shiel & Hagen 1995). We note that anomalies in monthly ice extent in the Prydz Bay area were zero to negative in 1991 (Comiso 2003, fig 4.6) when many large squid paralarvae

were taken and zero to positive in 1985 when only small paralarvae were taken. This may reflect the effect of sea ice on the abundance of food for cephalopods in Prydz Bay. High interannual variability in cephalopod growth rates in the Ross Sea is hence likely.

The annual-average production rate of the whole squid population depends on the mortality of squid which is unknown. It was estimated that 946 out of every 1000 *Todarodes pacificus* (Japanese flying squid) die during the first two weeks of life (Gibson 1995), implying a daily mortality rate of 0.21 d^{-1} . Assuming a lower mortality rate for longer-lived Antarctic squid of 0.02 d^{-1} leads to an estimate of annual production of $P/B=7.3 \text{ y}^{-1}$. This is equivalent to an annual survival rate of less than 0.07%.

This estimate compares reasonably well with other estimates from polar and subantarctic regions around the world. Work in subantarctic waters around New Zealand on the most common species of squid found there, arrow squid (*Nototodarus sloani*), suggests that the animals live for around one year, with rapid length growth of more than 3 cm per month (Gibson 1995). The von Bertalanffy growth parameters, and natural mortality of 0.99 y^{-1} for *Nototodarus sloani* lead to P/B value for adult arrow squid ($>10 \text{ cm ML}$) of 3.1 y^{-1} . The von Bertalanffy growth parameters and length-weight relationship for arrow squid in Mattlin et al. (1985) suggest P/B of 26 y^{-1} for small squid ($\text{ML}<10 \text{ cm}$). For the whole squid population, these values may be combined to give an annual average P/B of 10.5 y^{-1} . Bradford-Grieve et al. (2003) suggest $P/B=8.0 \text{ y}^{-1}$ may be appropriate for subantarctic squid off New Zealand. Annual production-to-biomass ratios for gonatid squid in the Bering Sea are estimated to be $P/B=6.7 \text{ y}^{-1}$ (Radchenko 1992) and for captive *Illex illecebrosus* measured to be 2.9–9.1 at 7°C (Hirtle et al. 1981). Work by O’Dor et al. (1980) points out that growth rates of *I. illecebrosus* from field data are well below those for captive animals, indicating that food supply of the natural population can be an important limiting factor. We propose to initially use production values estimated for non-captive squid in polar waters from Radchenko (1992) of $P/B=6.7 \text{ y}^{-1}$.

5 Consumption

The daily ration of *Loligo pealei* ranges from 3.2–5.8% of body weight per day (Vinogradov & Noskov, 1979) which represents an annual Q/B of 12–21 y^{-1} . The mean daily ration of *Illex illecebrosus* is 5.2% (Hirtle et al. 1981) or a Q/B of 19 y^{-1} . In the absence of data for squid in the Ross Sea, we may initially assume that Q/B is an average of these values, i.e. 17 y^{-1} . In the future, it may be possible to use work on cephalopod metabolism by Seibel et al. (1997) to estimate metabolic requirements of squid, and the implications for food consumption in the Ross Sea.

Taking Q/B as 17 y^{-1} and P/B as 6.7 y^{-1} gives an annual average gross efficiency, P/Q of 39%. This is consistent with Boucaud-Camou & Boucher-Rodoni (1983) who quotes a value of 25–70% for the incorporation of food into body tissue for octopus. The cephalopod growth model of Grist & Jackson (2004) leads to P/Q of 28% for the cuttlefish *Sepia apama*. Such P/Q values are unusually high for animals of this size, and are attributable to the special ecophysiological characteristics of cephalopods which allow rapid growth (Jackson & O’Dor 2001).

6 Biomass

There is an almost complete lack of direct information on squid and octopus biomass in the Ross Sea. In the absence of direct measurements, cephalopod biomass in previous studies has been estimated based on predator consumption (e.g. Klages 1996; Polito et al. 2002; Xavier et al. 2002; Fenaughty et al. 2003; Kooyman et al. 2004). Clarke (1983) estimates that 34 million tonnes of cephalopods are consumed by birds, seals and whales in the Southern Ocean each year. This

result is not directly scalable to the Ross Sea because most of the research on cephalopods in the Southern Ocean, used by Clarke (1983), was from locations close to the shelf break, or from deep ocean waters. The Ross Sea is predominantly composed of shelf waters where diets of predators may be different. For example, using seabirds as a sampling tool, the paper by Ainley et al. (1984) shows high prevalence of squid in seabird diets over the deep ocean north of the Ross Sea and over the Ross Sea slope, but dramatically lower prevalence over the shelf.

Here, we make an initial estimate the total consumption of cephalopods in the Ross Sea from predator consumption, using biomass, diet and food consumption information found in the other sections on these predators (see Table 2). The biomass of cephalopods is then calculated as equation 1.

$$B = \frac{\sum Q}{\left(\frac{P}{B} - \frac{Q}{B} - D_{cannibalism}\right)} \quad \text{[Equation 1]}$$

Where $\sum Q$ is the consumption of cephalopods by all predators except cephalopods themselves, P/B is the annual production rate of cephalopods (see below), Q/B is the annual consumption rate of cephalopods (see above) and $D_{cannibalism}$ is the (relatively small) consumption of cephalopods by cephalopods. This method allows us to estimate a total biomass of cephalopods in the Ross Sea, (assuming that all squid biomass, apart from their eggs, is used in the food web) of approximately 31 700 tonnes wet weight, equivalent to a carbon density of 4.9 mgC m⁻² for the Ross Sea.

Table 2. Estimate of the total biomass of cephalopods eaten by predators in the Ross Sea. “Biomass” has been adjusted to account for the proportion of the year the predator is in the Ross Sea i.e. annual equivalent biomass. The final column gives the proportion of the total annual cephalopod production estimated to be consumed by each predator.

Predator	Biomass	Q/B	Cephalopods in diet	Cephalopods consumed	% Cephalopods consumed
	t WW	y ⁻¹	%	t WW y ⁻¹	%
Emperor penguins	3130	44	4.0	6591	2.6
Adelie penguins	7942	81	1.0	7671	3
Flying birds	860	115	9	10623	4.3
Weddell seals	2550	28	9.0	7785	3.1
Leopard seals	928	23	5.0	1295	0.5
Ross seals	224	33	35	3095	1.2
Other baleen whales	2979	8	1.5	447	0.18
Orca	3017	11	10	4002	1.6
Sperm whale	2315	6	75	13429	5
Other toothed whales	157	14	61	1554	0.6
Large demersal fishes	60199	1.13	13	10568	4.2
Medium demersal fishes	61138	1.9	7	9673	3.9
Small demersal fishes	596421	4	4.6	141247	57
Cephalopods	37262	17	5	31672	12.7
Total				249653	100

* Calculated from the sum of the other consumptions as Equation 1.

These estimates of cephalopod consumption should be regarded as highly uncertain because much of the work on the importance of cephalopods to predators to date in the Southern Ocean is based on cephalopods beaks retrieved from the guts of predators. Cephalopods beaks are known to be retained in the guts of predators for many weeks making it difficult to know where the cephalopods were consumed or how many of them were taken. Also, the estimates of predator numbers in the Ross Sea and their consumption rates are subject to high uncertainty.

7 Unassimilated consumption

In the present study, we use $U=0.2$ as the proportion of unassimilated food for all cetacean groups (Bradford-Grieve et al, 2003). Unassimilated consumption is channelled to water column detritus in the model.

8 Ecotrophic efficiency

Ecotrophic efficiencies (E) are not known for cephalopods in the Ross Sea and are assumed to be 0.95 on the basis that the vast majority of cephalopods are predated.

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