

Fishes: Trophic modelling of the Ross Sea

M.H. Pinkerton¹, S.M. Hanchet², J. Bradford-Grieve¹

¹ 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

² National Institute of Water and Atmospheric Research Ltd (NIWA), PO Box 893, Port Nelson 7010, Nelson, New Zealand

1 Introduction

More than 100 species of fishes have been recorded from the Ross Sea shelf and slope (e.g. Chernova & Eastman 2001; Eastman & Hubold 1999; Stewart & Roberts 2001) (Table 1). Fishes are an important part of the trophic modelling because a number of species are amongst the most likely components of the system to be impacted indirectly by the fishing of Antarctic toothfish in the region. Unfortunately, little is known of the biomass of many of the fish species. The fish fauna can be divided into a coastal (shelf) fauna dominated (probably >90% biomass) by the endemic perciform suborder Notothenioidei, including *P. antarcticum* adults (La Mesa et al. 2004b), and a continental slope fauna dominated by macrourids, rajiids, and deeper water notothenioids. Sampling on the shelf out to a depth of about 500 m has been carried out locally from the shore based stations in McMurdo Sound and Terra Nova Bay using a variety of gear including vertical drop lines, traps, trammel nets, gill nets etc. Sampling further offshore has been sporadic (e.g., Iwami & Abe 1981; Eastman & Hubold 1999; Mitchell & Clark 2004; Donnelly et al. 2004). Sampling has mainly been focused on the collection of specimens (Eastman & Hubold 1999; Donnelly et al. 2004) and defining biodiversity (Mitchell & Clark 2004). Two recent New Zealand surveys, “BioRoss” in 2004 (Mitchell & Clark 2004) and “CAML-IPY” 2008 (Hanchet et al. 2008 b) have considerably improved our knowledge of fishes over large parts of the Ross Sea. The CAML-IPY (2007/8 International Polar Year – Census of Antarctic Marine Life) voyage was carried out using the Research Vessel *Tangaroa*. Multi-frequency acoustics combined with midwater trawling and bottom trawling were used in a stratified design covering the western Ross Sea shelf and northern slope areas of Cape Adare although not all these data are available yet.

Table 1. List of fishes from the Ross Sea as defined in this report (after Bradford-Grieve & Fenwick 2002).

Species	Life-style ¹	Comp ²	Depth ³ (m)	Diet ⁴	Occ ⁵	Catch ⁶ (t)
ARTEDIDRACONIDAE (barbeled plunderfishes)	B	MD	0–1700	70M,30K	O	0.124
<i>Artedidraco glareobarbatus</i>	B	SD				
<i>Artedidraco loennbergi</i>	B	SD				
<i>Artedidraco orianae</i>	B	SD				
<i>Artedidraco shackletoni</i>	B	SD				
<i>Artedidraco skottsbergi</i>	B	SD				
<i>Dolloidraco longedorsalis</i>	B	SD			C	
<i>Histiodraco velifer</i>	B	SD				
<i>Pogonophryne albipinna</i>	B	SD				
<i>Pogonophryne barsukovi</i> Andriashev	B	SD				
<i>Pogonophryne cerebropogon</i>	B	SD				
<i>Pogonophryne lanceobarbata</i>	B	SD				
<i>Pogonophryne macropogon</i>	B	SD				
<i>Pogonophryne marmorata</i>	B	SD				
<i>Pogonophryne mentella</i>	B	SD				
<i>Pogonophryne permitini</i>	B	SD				
<i>Pogonophryne scotti</i>	B	SD				
BATHYDRACONIDAE (Antarctic)	B/BP	SD	0–3000	40K,40D,20B	O	0

dragonfishes)							
<i>Acanthodraco dewitti</i>		SD					
<i>Akarotaxis nudiceps</i>		SD					
<i>Bathyraco macrolepis</i>	B	SD					
<i>Bathyraco marri</i>	B	SD		60Z,40K	C		
<i>Bathyraco scotiae</i>	B	SD					
<i>Cygnodraco mawsoni</i>	B/BP	SD	100–300	60D,20C,20K	O		
<i>Gerlachea australis</i>	BP	SD			O		
<i>Gymnodraco acuticeps</i>	BP	SD	0–550	50B,30K,20C	O		
<i>Prionodraco evansii</i>		SD					
<i>Racovitzia glacialis</i>		SD					
<i>Vomeridens infuscipinnis</i>		SD					
BATHYLAGIDAE (deepsea smelts)							
<i>Bathylagus antarcticus</i>	MP/BY	SD	500–1000	60K,40M	C		0
CETOMIMIDAE (flabby whalefishes)							
<i>Gyrinomimus grahami</i>	MP/BY	SD	500–2000	??	R		0
CHANNICHTHYIDAE (crocodile icefishes)							
<i>Chionobathyscus dewitti</i>	P/EB	SD	5–2000	70B,30K	C		20.8
<i>Chionodraco hamatus</i>	EB	SD	4–600	50K,50B	C		Y
<i>Chionodraco myersi</i>	P	SD	200–800	50K,50B	C		Y
<i>Chaenodraco wilsoni</i>	P	SD	200–800	50K,50B	C		
<i>Cryodraco antarcticus</i>	EB	SD	250–800	100B	C		Y
<i>Cryodraco atkinsoni</i>	EB	SD			R		
<i>Dacodraco hunteri</i>	P	SD	300–800	100B	R		
<i>Neopagetopsis ionah</i>	P	SD	20–900	100B	C		
<i>Pagetopsis macropterus</i>	EB	SD	5–700	50K,50B	O		
<i>Pagetopsis maculatus</i>	EB	SD	200–800	50K,50B	C		
GEMPYLIDAE (snake mackerels)							
<i>Paradiplospinus gracilis</i>	MP/BY	SD	200–3000	70K,30B	R		0
GONOSTOMATIDAE (bristlemouths)							
<i>Cyclothone kobayashi</i>	MP/BY	SD	500–3000	100Z	O		
<i>Cyclothone microdon</i>	MP/BY	SD	500–3000	100Z	C		
<i>Cyclothone pseudopallida</i>	MP/BY	SD	400–1000	100Z	R		
LIPARIDAE (snailfishes)							
<i>Careproctus ampliceps</i>	B/BP	SD	0–3000	70K,20M,10Z	R		0
<i>Careproctus catherinae</i>					R		
<i>Careproctus inflexidens</i>					R		
<i>Careproctus polarsterni</i>					R		
<i>Careproctus pseudoprofundicola</i>					R		
<i>Careproctus vladibeckeri</i>					R		
<i>Edentoliparis terraenovae</i>					R		
<i>Paraliparis andriashevi</i>					R		
<i>Paraliparis antarcticus</i>					R		
<i>Paraliparis devriesi</i>					R		
<i>Paraliparis fuscilingua</i>					R		
<i>Paraliparis macrocephalus</i>					R		
<i>Paraliparis rossi</i>					R		
MACROURIDAE (grenadiers, rattails)							
<i>Coryphaenoides armatus</i>	BP/BY	SD/MD	500–3000	30B,30K,30M,10S	A		705.3
<i>Coryphaenoides ferrieri</i>	B/BP	MD	>2000	?60B,40S	R		0.2
<i>Coryphaenoides lecointei</i>	B/BP	MD	>2000	?60B,40S	R		0
<i>Cynomacrurus piriei</i>	B/BP	MD	1000–2000	?	O		0
<i>Macrourus whitsoni</i>	B/BP	MD	500–1500	30B,30K,30M,10S	A		705
MELANOCETIDAE (black seadevils)							
			500–2500				

<i>Melanocetus rossi</i>	MP/BY	SD	500+	50B,50Z?	R	0
MORIDAE (deepsea cods)						31.8
<i>Antimora rostrata</i>	B/BP	SD/MD	800–1800	70K,30S??	O	31.7
<i>Lepidion</i> sp.	B/BP	SD/MD	?	?		0.1
MURAENOLEPIDIDAE (eel cods)				70K,30B??		29.0
<i>Muraenolepis marmoratus</i>	B/BP	SD	20–1600	?	O	Y
<i>Muraenolepis microps</i>	B/BP	SD	10–2000	?	O	Y
<i>Muraenolepis orangiensis</i>	B/BP	SD	140–600	?	O	Y?
MYCTOPHIDAE (lanternfishes)	MP/BY		0–800	80K,20Z	A	0
<i>Electrona antarctica</i>	MP	P		100K	C	
<i>Gymnoscopelus braueri</i>	MP	P		80K,20Z	C	
<i>Gymnoscopelus nicholsi</i>	MP	P		80K,20Z	C	
<i>Gymnoscopelus opisthopterus</i>	MP	P		?	C	
<i>Krefflichthys anderssoni</i>	MP	P		60K,40Z		
<i>Nannobranchium achirus</i>	MP	P		?		
<i>Protomyctophum bolini</i>	MP	P		80Z,20K		
NOTOTHENIIDAE (cod icefishes, nototheniids)						
<i>Aethotaxis mitopteryx</i>	P	P	50–400	100K	R	Y
<i>Dissostichus mawsoni</i>	P/BP	MD/LD	400–2000	80D,13S,6B,	A	7344
<i>Dissostichus eleginoides</i>	P/BP	MD/LD	400–2000	80D,10B,10S	R	97.3
<i>Gvozdarus svetovidovi</i>	P	MD/LD	500?	80D,10B,10S	R	
<i>Lepidonotothen larseni</i>	B	SD	30–550	100K	R	
<i>Lepidonotothen squamifrons (= kempi)</i>	B/BP	SD	5–900	80K,20B	O	
<i>Notothenia coriiceps</i>	B	SD	0–550	50M,50K	O	
<i>Pagothenia borchgrevinkii</i>	C	SD	0–30	70Z,20K,10B	O	
<i>Pagothenia brachysoma</i>	C	SD	0–30	70Z,20K,10B	R	Y
<i>Paranotothenia dewitti</i>	B	SD	0–255?	?	R	
<i>Pleuragramma antarcticum</i>	P	P/SD	0–700	70K,30Z	A	
<i>Trematomus bernacchii</i>	B	SD	0–700	90M,10K	A	
<i>Trematomus eulepidotus</i>	EB	SD	70–550	60K,40B	C	
<i>Trematomus hansonii</i>	B	SD	5–550	80M,10K,10Z	C	
<i>Trematomus lepidorhinus</i>	EB	SD	200–800	100K	C	Y
<i>Trematomus loennbergii</i>	EB	SD	300–1000	70K,20B,10Z	C	Y
<i>Trematomus newnesi</i>	C	SD	0–400	70K,20K,10B	C	
<i>Trematomus nicolai</i>	B	SD	30–400	40K,30M,30Z	O	
<i>Trematomus pennellii</i>	B	SD	0–730	80M,10K,10Z	C	Y?
<i>Trematomus scotti</i>	B	SD	20–800	50M,50K	C	
<i>Trematomus tokarevi</i>	B?	SD	300–700	?	O	
Unidentified nototheniids						0.6
ONEIRODIDAE (dreamers)						0
<i>Oneirodes notius</i>	MP/BY	SD	700–2000	?50B,50K	R	
PARALEPIDIDAE (barracudinas)						0
<i>Anotopterus pharao</i>	EP	MD	>1000	100B	O	?
<i>Notolepis coatsi</i>	MP	P	0–1000	100K	C	
RAJIDAE (skates)					C	250*
<i>Bathyraja cf. eatonii</i>	B	SD/MD	30–1200	100M	O	
<i>Bathyraja maccaini</i>	B	SD/MD	30–1200	100M	O	
<i>Bathyraja</i> sp.	B	SD/MD	30–1200	100M	O	
<i>Amblyraja georgiana</i>	B	SD/MD	20–1200	100M	C	
ZOARCIDAE (eelpouts)				100M	O	0
<i>Dieidolycus leptodermatus</i>	B	SD		100M		
<i>Lycodichthys dearborni</i>	B	SD	500–600	100M	O	
<i>Ophthalmolycus amberensis</i>	B	SD	140–900	100M	O	
<i>Ophthalmolycus bothriocephalus</i>	B	SD	140–900	100M	O	

<i>Pachycara brachycephalum</i>	B	SD	200–2000	100M	O	
<i>Seleniolytus laevifasciatus</i>	B	SD	800–1000	100M	R	

Notes to Table 1.

- ¹ Lifestyle following La Mesa et al. (2004b) or Gon & Heemstra (1990): B, benthic; BP, benthopelagic; BY, bathypelagic; CP, cryopelagic; EB, epibenthic; EP, epipelagic; MP, mesopelagic; P, pelagic.
- ² “Comp” indicates compartment in model, where: P=pelagic fishes; SD=small demersal fishes; MD=medium demersal fishes; LD=large demersal fishes. Note that some species belong to more than one group at different stages of their life.
- ³ Depth mainly from Gon & Heemstra (1990). The vertical distribution in the water column of demersal fish species in the Antarctic has been the subject of much debate (e.g. La Mesa et al. 2004b). Many of the species (and some whole families) listed within this group are strictly benthic (Table 1). However, many of the other species may be termed pelagic to varying degrees. Of all the families, Artedidraconidae is probably the most strictly benthic, others are predominantly benthic with some benthopelagic species, whereas other families (e.g., Channichthyidae) are generally more pelagic with several epipelagic and/or epibenthic species.
- ⁴ Diet mainly from La Mesa et al. (2004b) for most notothenioids and Gon & Heemstra (1990) for most remaining species. Symbols refer to model compartments, where A–D are defined above. K, krill and macrozooplankton; M, macrobenthos; S, squids; Z, mesozooplankton.
- ⁵ Occ. Qualitative measure of abundance in area based on trawl surveys and fishery data, where R, rare; O, occasional; C, common; A, abundant.
- ⁶ Catch indicates catch (metric tonnes) in bottom longline fishery from 1997–98 to 2004–05 (Stevenson et al. 2008). *, estimate taken from Table 11 of Dunn et al. (2007c), which includes landed skates as well as an estimate of released skates which subsequently die.
- ⁷ Species names checked using Eschmeyer & Fricke (2009), family names according to Nelson (2006).

1.1 Wet weight-carbon conversion factors

In order to convert between wet weight and carbon we used reported values of 1gC ~ 10–12 kcal (Ikeda 1996). For fish, 0.95–1.35 kcal/gWW is reported (Steimle & Terranova 1985; Croxall et al. 1985; van Franeker et al. 1997; Parsons et al. 1977). These imply 1 gWW is equivalent to approximately 0.095–0.11 gC. More recently, Bury et al. (2008) measured carbon content of dry samples of fishes from the Ross Sea as 43.6% (10th–90th percentile range of 41.9–45.6%). A number of common Ross Sea species were sampled including Antarctic toothfish (*Dissostichus mawsoni*), icefish (*Chionobathyscus dewitti*) and Whitson’s grenadier (*Macrourus whitsoni*) with a total sample size of 402. A dry:wet weight ratio of 20–30% (e.g. Hartman & Brandt 1995; Holmes & Donaldson 1969) implies a range of 0.09–0.12 gC gWW⁻¹. Vinogradov (1953) gave an oft-used conversion factor of 0.1 gC gWW⁻¹ for fish which we will use for all conversions here.

1.2 Transfers between groups due to growth

Because one of the principal methods of dividing fishes into trophic groups in this model is by size, there will be an annual transfer of biomass from a smaller group to a larger group where parts of the population a given species occur in both. This growth transfer is described by the T^g parameter for

each group, which is defined as the fraction of the annual production of a group that is transferred to a larger group due to growth of individuals. We estimate four growth transfers in the model: (1) for medium toothfish to large toothfish; (2) for small demersal fishes to medium demersal fishes; (3) pelagic fishes to small demersal fishes due to juveniles recruiting into the adult populations. We estimated these growth transfer fractions from simple age-structured population models. We do not estimate a growth transfer from juvenile silverfish to adult silverfish as this is within the same trophic group in the model.

1.3 Ecotrophic efficiency

Ecotrophic efficiencies (E) are not known for fishes in the Ross Sea and is assumed to be 0.95 for all groups on the basis that the vast majority of fish mortality is likely to be due to direct predation rather than other causes such as starvation, disease or excessive parasite loading.

1.4 Unassimilated consumption

Unassimilated consumption factors are not known for fishes in the Ross Sea and were assumed to be $U=0.27$ for all fish groups in the model as for carnivorous fish (Brett & Groves 1979).

2 Trophic groups in the model

The aim of grouping fishes into trophic compartments in the model is to have a reasonably small number of groups (<10) where the biota in a given group have a “similar” set of energetic parameters and trophic roles, and where there is enough reliable information on each group to drive the modelling. Given the large variety of fishes in the Ross Sea, and the poor basic information on the basic ecology and trophic role of most of these, this is a considerable challenge. There are many alternative ways to group fishes in mass-balance models. Models have been constructed where fishes have been grouped by a variety of measures (Table 2).

Table 2. Methods of grouping fishes in mass-balance models.

Method of grouping	Example	Rationale
Single species	<i>Dissostichus mawsoni</i> , <i>P. antarctica</i> etc	Information and management is usually by species. But, too many species and too limited information on rarer species to be feasible for all fishes
Taxonomic groups	Toothfish, macrourids, rajiids etc	Information and management is usually by species. But, taxonomic similarity does not imply similarity of ecosystem role (e.g. <i>Trematomus</i> sp. occupy widely varying niches)
Size-based	Small, medium, large	Energetics and potential prey are closely linked to size. But, there is some degree of niche separation between fishes of similar size
Lifestyle	Demersal, benthopelagic, pelagic, cryopelagic etc.	Trophic role (prey, predators) is often linked to lifestyle. But, different sizes of fish with the same lifestyle have very different energetics.
Functional role (predominant prey)	Piscivores, planktivores, scavengers etc.	Most fishes will have a diet that varies with season and age. Diet is often poorly known.

None of these methods of grouping fishes into trophic groups is completely objective or ideal. A grouping based on a mixture of factors will be used here. We choose to group species with: (1) similar energetic parameters (hence a size-based grouping); (2) (very broadly) similar trophic connections,

which is taken to depend to some extent on the typical position occupied in the water column; and (3) species, where one species is particularly important in the system (i.e. *Pleuragramma antarcticum*). The total number of fish groups is limited to a small number (five) because of the paucity of robust information on: (1) their abundance in the study area; and (2) trophic connections (proportions of various fish species in the diets of major predators; predator-prey linkages between fish groups; diets of fishes in the Ross Sea). The number of groups and grouping criteria used for fishes in the model can be changed in the future as data and understanding of their trophic roles becomes available. In the current model, the fishes of the Ross Sea are here partitioned into:

1. Large demersal fishes: demersal fishes >100 cm maximum length and/or >50 kg maximum weight. Almost exclusively Antarctic toothfish *Dissostichus mawsoni*).
2. Medium demersal fishes: medium sized (40–100 cm length and/or 1–50 kg weight) fishes, including macrourids, rajiids, deepsea and eel cods, large icefishes, large notothenids, and pre-recruit toothfish.
3. Small demersal fishes: small demersal notothenioids (including *Trematomus* sp.), and cryopelagic fish (e.g. *Pagothenia borchgrevinki*): 10–40 cm length and/or <1 kg weight. This group will be referred to henceforth as “small demersal fishes” for convenience, but we note that the various fish in this compartment occupy diverse locations in the water column which change with a number of factors (age, latitude, depth etc). *Pleuragramma antarcticum* (silverfish) is excluded from this group although a proportion of the adult silverfish population is known to be demersal in some areas.
4. *Pleuragramma antarcticum* (Antarctic silverfish): all post-larval, juvenile and adult silverfish are included together in this group. This species is treated separately as it occupies a unique position in the Ross Sea food web.
5. Pelagic species which includes all juvenile and postlarval fishes between 20 and 100 mm in length (larval fishes <20 mm in length are included in the macrozooplankton compartment), and adult mesopelagic fishes over the slope and deeper waters to the north of the Ross Sea proper. Juvenile and adult *P. antarcticum* found in the water column are excluded from this group. This group is distinguished from “small demersals” by size as well as nominal position in the water column. Early life stages of a large number of fishes in the Ross Sea, especially notothenioids, may spend one or two years in the water column before becoming demersal (Kock 1992; Kellerman 1986, 1990b; Slosarczyk 1987). Larval fishes in the Ross Sea are dominated by the juveniles of *P. antarcticum* over the continental shelf which are excluded from this group. Mesopelagic/pelagic fish are dominated by myctophids seaward of the continental shelf.

3 Large demersal fishes (large toothfish)

3.1 Species and general distribution

This group includes the adults (sexually mature) of three toothfish species: Antarctic toothfish (*Dissostichus mawsoni*), Patagonian toothfish (*Dissostichus eleginoides*) and the rare *Gvozdarus svetovidovi*, of which the former is by far the most abundant species in the study area. Antarctic toothfish is distributed throughout the study area from 78°S in the south to 69°S in the north and from 165°E to 160°W (Hanchet 2006; Hanchet et al. 2007) and has been caught on virtually every longline set. In contrast, Patagonian toothfish has a much more northern distribution, and within the study area is only caught on 1% of the lines set and contributes to less than 0.1% of the toothfish catch (Hanchet et al. 2003). *G. svetovidovi* is a very rare species only known from two specimens, one of which was caught in the Ross Sea, and this species is not considered further.

3.2 Life cycle of Antarctic toothfish

The life cycle of Antarctic toothfish in the Ross Sea is not well understood. A summary of our current understanding of the life cycle is given in Hanchet (2006) and Hanchet et al. (2007, 2008a). From eggs to adults, Antarctic toothfish are present in a number of groups in the trophic model.

Antarctic toothfish are believed to spawn on the banks, ridges, and seamounts to the north of the Ross Sea (north of 70°S) during the winter months (Hanchet 2006, Fenaughty et al. 2008, Hanchet et al. 2007, 2008a, Mormede et al. 2008). However, the exact timing and location of spawning is unknown because much of this area is covered by ice during the winter months and virtually no fishing has been carried out there after May. Antarctic toothfish eggs and larvae are probably pelagic like those of the closely related Patagonian toothfish (Kellermann, 1990a). Antarctic toothfish eggs and larvae would be included as a small component of the mesozooplankton and macrozooplankton groups. Postlarval fish are probably also pelagic, which is supported by the fact that juvenile fish <15 cm have been caught in large numbers by Russian vessels using midwater trawls targeting krill and *P. antarcticum* at 0–100 m over bottom depths of 400–2000 m (Roshchin 1997). At this stage they are probably feeding on early life stages of krill and other meso and macrozooplankton. At a size of 5–15 cm, these postlarvae and fingerlings are part of the pelagic trophic group. However, their contribution to the biomass of this group is likely to be small and they are not considered explicitly in the model.

At a length of about 15 cm, toothfish are thought to descend to the bottom and assume a more benthic lifestyle (Hanchet et al. 2008a). Between lengths of 15–40 cm, juvenile toothfish are included in the “small demersal fish” group in the model. The biomass (and indeed presence) of these small juveniles in the Ross Sea is unknown. Despite a variety of fishing methods including bottom longlines, bottom and midwater trawls, traps, gill nets, and trammel nets, employed in coastal and off-shore areas in the southwestern part of the study area, small juvenile toothfish (<50 cm in length) have never been caught (Reseck, 1961; DeWitt 1970; Iwami and Abe, 1981; Testa et al., 1985; Eastman and Hubold, 1999; Vacchi et al., 1999). The smallest toothfish caught in the Ross Sea region were three individuals measuring 32–46 cm SL from research bottom trawls at the Balleny Islands in 2004 (O’Driscoll et al. 2004), whilst the smallest toothfish caught in the fishery was 45 cm also from the Balleny Islands (Hanchet, pers. comm.). Fish do not appear in the fishery on the Ross Sea shelf until they are 60–80 cm long and 5–7 years old. Elsewhere, juvenile toothfish (15–75 cm long) have been caught by Russian vessels using midwater and bottom trawls in depths of 200–2000 m (Roshchin 1997) so it may be that juvenile toothfish occur somewhere in the shallow waters of the Ross Sea, but this is looking increasingly unlikely.

At lengths of 40–100 cm, Antarctic toothfish are included in the “medium-sized demersal fish” group. This includes the larger juveniles (40–75 cm) and sub-adult toothfish (“pre-recruits”) 75–100 cm. For the purposes of this study we have used a length cut-off of 100 cm to define adult Antarctic toothfish. Although maturity is assumed to occur at a length of 100 cm (± 15 cm) corresponding to age 9 (± 2 years) in the assessment model (Dunn et al. 2005a), recent work indicates that females mature at larger sizes (Livingston & Grimes 2005; Mormede et al. 2008). Large numbers of sub-adults (70–90 cm fish) have been caught in the longline fishery in 600–800 m in the southern Ross Sea, and they are also caught at similar depths on the upper continental slope. As toothfish grow they typically move deeper, and there is a positive relationship between toothfish length and depth (Hanchet et al. 2003). However, substantial catches of 50–80 cm long fish were also made in 1000–1500 m depth in SSRU 88.2F in 2006 (Stevenson et al. 2008), so the depth distribution can be quite variable and it can, at times, occupy the entire water column. At McMurdo Sound it was recorded using video at mean depths of 168 m and 93 m (minimum 17 m) during day and night respectively over a bottom depth of 570 m (Fuiman et al. 2002). Movement over deepwater between seamounts to the north of the Ross Sea region (Hanchet et al. 2003), and presence in sperm whales stomachs caught over deep water (Yukhov 1971) further confirm its semi-pelagic lifestyle.

Adult toothfish (>100 cm) are mainly found on the continental slope and are most abundant in depths of 800–1500 m. However, large adult fish have been caught in depths shallower than 500 m at McMurdo and Terra Nova Bay and deeper than 2000 m in the fishery. Large adult toothfish form a continuous distribution on seamounts, banks, and ridges to the north of the study area (to 60°S). The origin of these fish has not been proven, but it is suspected that they originate from the Ross Sea region, and thus represent a net emigration of fish from the study area. Two tagging experiments have provided some indication of movements; whilst most toothfish have been recaptured close to where

they were tagged there have been some spectacular long-distance migrations. Five adult toothfish (131–144 cm long) originally tagged and released at McMurdo Sound have been recaptured in the fishery. One was recaptured 800 km to the north off Cape Adare after 3.3 years at liberty, three were recaptured more than 1000 m to the north in SSRU 88.1C, whilst a fifth was recaptured 2300 km north-east out of the Ross Sea altogether after 18 years at liberty (Dunn et al. 2007d). Of the six large-scale movements of fish tagged and recaptured in the fishery, all were fish <100 cm long which had migrated from the continental slope onto the south-western part of the Ross Sea shelf. Clearly, the movements and migrations remain largely unknown, and the importance of the latitudinal and inshore-offshore migrations in the life cycle of the species have still to be clarified. Gaining a better understanding of the spawning dynamics and, in particular its relationship to the extent of the seasonal sea ice could be one of the most important research topics to be developed in the future, in order to assess the impact of climate change on this primary Antarctic fishing resource.

3.3 Biomass

Estimates of spawning stock biomass of Antarctic toothfish for the Ross Sea stock are presented in Dunn et al. (2007a). The biomass estimates are based on the results of a tagging study initiated by New Zealand vessels in 2001. The best estimate of unfished equilibrium mid-season spawning stock biomass is 71 200 t (95% confidence intervals 59 570–87 900 t). Biomass as of September 2007 is believed to be about 82% of the virgin level, but we base our estimates of biomass on the unfished stock as the model seeks to represent the system before fishing began. These estimates apply to the entire toothfish population in CCAMLR Subareas 88.1, 88.2A and 88.2B, which extends north to 60°S west of 170°W. Based on relative fish densities (CPUE) and seabed areas, it has been estimated that about 15% of the population migrates north of the study area once they reach adult size (Hanchet, pers. com.), so that biomass of toothfish in the study area is estimated to be 85% of the modelled biomass given by Dunn et al. (2007a). We also estimated this proportion from fishery data as follows. For the fishing seasons 1997/98–2007/08 using the CCAMLR C2 observer data we calculated an average age-frequency in the catch for 3 regions: the shelf (SSRUs 88.1J, 88.1L), slope (SSRUs 88.1H, 88.1I, 88.1K, 88.2A, 88.2B) and northern regions (SSRUs 88.1A, 88.1B, 88.1C, 88.1E, 88.1F, 88.1G). We did this for male and female fish separately. Length-frequencies from different years were combined according to catch in the region in each year. Ages were converted to lengths and thence weights of fish using von Bertalanffy coefficients for the population as a whole (Dunn & Hanchet 2007a), and length-weight relationships specific to male and female fish in the three regions (shelf, slope, northern) (Dunn & Hanchet 2007b). Age-frequencies in the catch between regions were then calculated by scaling to the actual catch in those regions. We converted age-frequencies in the catch to age-frequencies in the population using selectivities fitted by the assessment model (Dunn & Hanchet 2007a). Using the model described by (Dunn & Hanchet 2007a) we estimated the number fish of age year 1–4 not caught in the fishery; these were added to the shelf region. Age-frequencies in the population were finally converted to lengths and weights as (Dunn & Hanchet 2007a,b) and summed by region and length group (<40 cm, 40–100 cm, >100 cm). This analysis suggests that 85.6% of the total biomass (all ages) of toothfish in the Ross Sea stock resides in the shelf and slope areas that make up the study area.

Assuming fish >100 cm are sexually mature as Dunn & Hanchet (2007a), our analysis predicts that 87.7% of the Ross Sea stock are within the spawning stock biomass assessed in the model. We hence estimate a spawning stock toothfish biomass in the Ross Sea study region of 81 160 t (71 200/0.877), and a total biomass of Antarctic toothfish in the study region of 69 500 tWW (81 160*0.856). Within the portion of the fish in the study area, large fish (>100 cm) comprise 86.6% of the biomass (60 200 t), medium sized fish (40–100 cm) comprise 13.2% (9170 t), and small fish (<40 cm) 0.2% of the biomass (140 t).

3.4 Diet

Dissostichus mawsoni appears to be an opportunistic feeder, with quite different dietary composition depending on location and habitat. An analysis of 58 adult toothfish (82–148 cm SL) caught in McMurdo Sound found that they fed primarily on fishes and mysids, with 90% and 10% dry weight proportionally (Eastman 1985). Of the fishes, 63% were *P. antarcticum*, 22% were demersal (mainly icefishes), and 5% were cryopelagic by frequency occurrence. In a more recent study Stevens (2006) analysed stomach contents of 190 sub-adult (51–100 cm TL) toothfish caught from the continental slope of the Ross Sea. Toothfish diet comprised 78% fish and 21% cephalopods by weight. The fish comprised icefish (33%), macrourids (16%), nototheniids (13%) and eel cods (5%). This is taken to be representative of the diet of medium-sized toothfish (40–100 cm) which occur over the shelf and slope of the Ross Sea. No sizes of macrourids are given, but the vast majority consumed by toothfish <100 cm in length are presumed to be <40 cm in length. The diet of medium toothfish is hence taken to be; 45% small demersal fish; 20% silverfish; 10% pelagic fish; 20% squid; 5% other (i.e. non-krill) macrozooplankton.

The vast majority of the biomass of large toothfish (>100 cm) is thought to reside in the slope area (Hanchet 2006, and see above). Adult toothfish caught from the continental slope in the toothfish fishery fed primarily on demersal fishes (86%) and cephalopods (13%) by weight (Stevens 2004) consistent with the less detailed information on toothfish diet from Petrov & Filippova (2007). The fishes were 38% grenadiers (*Macrourus whitsoni*), 26% icefishes (mainly *Chionobathyscus dewitti*), and 11% eel cods (*Muraenolepis* spp. – probably *Muraenolepis microps*). The remaining prey species comprised a variety of small mainly benthic fishes (e.g., *Trematomus* spp., eel pouts, dragonfishes, snailfishes, and plunderfishes), together with small invertebrates (prawns). Fenaughty et al. (2003) also report on the diet of Antarctic toothfish mainly taken from the Ross Sea slope, which was dominated by fishes (c. 80% in terms of occurrence), with smaller proportions of cephalopods, and crustaceans (decapods, amphipods). The fish species identified by Fenaughty et al. (2003) were 54% icefish, 37% *Macrourus whitsoni*, 7% *Muraenolepis microps*, and 5% *Antimora rostrata*. *Pleuragramma antarcticum* are likely to make up <1% by weight of the diet of large toothfish. *Macrourus whitsoni* and *Antimora rostrata* are split between the medium (40–100 cm) and small (<40 cm) demersal fish compartments, and, in the absence of information on the sizes of individuals of these species as prey, we assume consumption of these species by Antarctic toothfish is split 50-50 between “medium” and “small” individuals. The majority of the other piscine prey of Antarctic toothfish are in the small demersal fish compartment in the model. The diet of large toothfish is hence taken as: 15% medium demersal fish; 70% small demersal fish; 1% silverfish; 13% cephalopods; 1% carcasses.

3.5 Production

Production by medium (40–100 cm) and large (>100 cm) toothfish is estimated in two ways. First, we use a simple model of the population growth. The von Bertalanffy growth parameters of *D. mawsoni* are given as $K=0.0985 \text{ y}^{-1}$, $L_{\infty}=177.4 \text{ cm}$ and $t_0=0.405$ (Hanchet et al. 2003). The length/weight relationship for *D. mawsoni* is given as $W=aL^b$ where W is the fish weight in g, L is the fish length in cm, and the coefficients for toothfish are: $a=0.008015 \text{ g}$, and $b=3.0859$ (Hanchet et al. 2003). Natural mortality for *D. mawsoni* in the Ross Sea is taken as constant with age and equal to 0.13 y^{-1} (Dunn et al. 2007a). The model estimates $P/B=0.23 \text{ y}^{-1}$ (medium toothfish) and $P/B=0.08 \text{ y}^{-1}$ (large toothfish). For the medium-sized fish, this is similar to production values estimated for fish in subantarctic waters of New Zealand (e.g., $P/B=0.3 \text{ y}^{-1}$: Bradford-Grieve et al. 2003). Annual P/B ratios for fish were calculated to be: $0.36\text{--}0.74 \text{ y}^{-1}$ for hoki; 0.52 y^{-1} for ling; 0.41 y^{-1} for hake; and 0.32 y^{-1} for southern blue whiting. Orange roughy P/B ratio has been calculated to be 0.15 y^{-1} (Pankhurst & Conroy, 1987).

An alternative method of estimating production is to use the allometric equations of Banse & Mosher (1980), or Haedrich & Merrett (1992). The equations lead to $P/B=0.29 \text{ y}^{-1}$ (medium toothfish) and $P/B=0.17 \text{ y}^{-1}$ (large toothfish). These relationships give an indication of production rates of demersal

fish generally, but may overestimate production rates in the Antarctic. We take our best estimate as the average of the two methods giving $P/B=0.26 \text{ y}^{-1}$ (medium) and $P/B=0.12 \text{ y}^{-1}$ (large).

We also use the model to estimate the transfer of biomass between groups per year, as fish become too large for one category and move to the next. We express this as the ratio of transfer to production of the donating group (i.e. the small fish). The model estimates $T^e=0.58$ (export from medium to large toothfish category).

3.6 Consumption

A method of calculating fish consumption/biomass is given by Palomares & Pauly (1989, 1998) based on the fish asymptotic weight, water temperature, diet (carnivore, herbivore, omnivore), and aspect ratio of the caudal fin ($= h^2/s$ where h is height of tail and s is surface area of tail). *D. mawsoni* have an aspect ratio of the caudal fin of 1.7, for *D. eleginoides* it is 1.9 (calculated from photographs in Fishbase: Froese & Pauly 2009). The water temperature is approximately 2°C. We hence estimate a consumption rate for toothfish of the Ross Sea to be $Q/B=2.0 \text{ y}^{-1}$ (medium toothfish) and $Q/B=1.3 \text{ y}^{-1}$ (large toothfish). These values imply a growth efficiency, $P/Q=0.17$ (medium toothfish) and $P/Q=0.09$ (large toothfish) which are reasonable.

3.7 Export

There is an export from the study area due to large toothfish spawning migration. As yet, the net export (as a proportion of annual production) of large toothfish within the study area is not known. The spatial toothfish model currently under development (Dunn & Rasmussen 2008) may allow us to estimate this parameter in the future, but for now, we assume a value of $X=0.2$.

4 Medium demersal fishes

4.1 Species and general distribution

This group contains a range of fish species (see Table 1) with lengths of 40–100 cm, and weights of approximately 1–50 kgWW. Note that although a proportion of the skates are >100 cm, they have been included in this group because they will have similar energetic and trophic parameters to smaller skates. The species listed within this demersal group cover a broad range of lifestyles including demersal, benthic, benthopelagic, epibenthic, and epipelagic. We assume that these species, although highly variable in biological and ecological adaptations, form a group with comparable energetic and trophic parameters. As part of the BioRoss voyage in February–March 2004, the New Zealand research vessel *Tangaroa* carried out 52 bottom trawls in depths of 123–1165 m along five transects in the northwestern Ross Sea (70°–72°S and 170°–173°E) between Cape Adare and Cape Hallett (Mitchell & Clark 2004; BioRoss 2006). The BioRoss voyage used a rough bottom orange roughy otter trawl with 28 m mouth opening, 5 m headline height, and 40 mm codend. The catch was dominated (by weight) by the following medium and small demersal fishes: Whitson's grenadier (*M. whitsoni*) (72%); skate *Bathyraja* cf. *eatonii* (10.9%); icefishes (6.7%) mainly *C. hamatus* and *C. antarcticus*, and notheniids (9.6%) mainly *D. mawsoni* (3.9%), with some *P. antarcticum* (3.1%) and *T. lepidorhinus*.

4.2 Biomass

There are few quantitative estimates of biomass of medium-sized demersal fish biomass over large areas of the Ross Sea. Data from the BioRoss voyage is only available for the SSRU 88.1H and extrapolation to the larger area was not attempted. Instead, we used estimates of the biomass of Whitson's grenadier (*M. whitsoni*) from the New Zealand IPY-CAML survey in February and March 2008 (voyage code TAN0802: Hanchet et al. 2008c, b, d) to scale measurements of bycatch from the commercial toothfish fishery to the study area.

The IPY-CAML voyage used a very similar rough bottom orange roughly trawl to BioRoss (Mitchell & Clark 2004), and this was towed for about 20 minutes at 3 knts at each station. This trawl had a mouth width of 25 m, headline of 6 m, and a nominal codend mesh of 60 mm. It was fitted with a 40 mm codend liner to catch smaller fish. Due to persistent sea ice over the eastern and northern slope areas of the Ross Sea, fewer stations in these slope strata than planned could be carried out. Nevertheless, this voyage carried out 17 bottom tows over the Ross Sea shelf (10 stations) and slope areas (7 stations). The most abundant fish caught by number was the Antarctic silverfish, closely followed by Whitson's grenadier. Few other medium-sized (>40 cm) demersal fish were caught. As on the BioRoss voyage, and also seen in the commercial fishery bycatch data, macrourids were found to be common over the slope area, but rare elsewhere in the Ross Sea. Macrourid CPUE (kg/hook) was 2–3 times greater in SSRU 881I and K, than in SSRU 881H where the BioRoss and IPY-CAML surveys took place (Hanchet et al. 2004, 2008b). Plots of macrourid CPUE by depth suggests that fish density peaks at 1000 m and drops to around zero at less than 500 m and greater than 1800 m depth (NIWA, unpublished data). Data from the CAML-IPY voyage were used to estimate biomass of demersal fish for the entire study area according to methods explained in Hanchet et al. (2008d), and adjusted assuming a catchability coefficient of 0.4 for macrourids (Hanchet pers. com.). Individual trawl catches were used to estimate total biomass via six strata on the shelf and slope using two methods: (1) the NIWA TrawlSurvey Analysis program; (2) the CCAMLR TRAWLCI program. The results of these were averaged here. High and low bounds corresponding to +/- the estimate coefficients of variation were applied and also combined by averaging these two methods. The densities of Whitson's grenadier in the CAML-IPY strata were extrapolated to the study area to estimate an indicative biomass by Hanchet et al. (2008b) using two alternative assumptions: (1) that *M. whitsoni* densities were constant across the entire slope; (2) that *M. whitsoni* densities were proportional to the CPUE of macrourid in the longline fishery. The final unadjusted estimate of biomass for the study area were 26 892 t (cv= 29%) to 41 823 t (cv=28%). The middle value was 34,360 tWW. Hanchet et al. (2008b) stress that the estimates of *M. whitsoni* biomass are tentative given the relatively few trawls that could be carried out on the Ross Sea slope during the CAML-IPY voyage.

We assume a catchability coefficient of less than unity for macrourids in the Ross Sea for two reasons: (1) fish may be able to avoid the net by swimming; (2) a proportion of the biomass of macrourids may reside off the sea bed and not be caught in a bottom trawl as this species has a benthopelagic lifestyle rather than being truly benthic. Demersal trawl surveys in New Zealand subantarctic waters of similar-sized fish (700–900 mm) at similar depths (hoki, *Macruronus novaezealandiae*) have a catchability of about 0.4 (Hanchet pers. com.). Given the effect of low temperature on reducing swimming speeds, the amount of avoidance of the net by fish, either by sideways or upwards movement, in the Antarctic is likely to be less than in subantarctic waters, though this is not proven. Assuming half the escapement in the Ross Sea, we use a catchability coefficient of 0.7. Applying this factor gives an estimate of macrourid biomass for the study area of 49 100 tWW.

We implemented a simple age-length-weight model of an unfished population of *M. whitsoni* to estimate the proportions of fish at sizes <40 cm (“small demersal fish” compartment) and >40 cm (“medium demersal fish” compartment). Basic biological parameters for this species were taken from Marriott et al. (2003). This species has a maximum average total length of 84 cm and maximum average fish weight of 5.1 kg. The mean length and weight for fish in the fishery is about 70 cm (TL) and 2.2 kg respectively. The length-weight relationship is $a=1.609 \cdot 10^{-5}$, $b=2.8603$, where $W=aL^b$, W (weight, g), and L (total length, cm). Von Bertalanffy parameters for *M. whitsoni* are $L_{inf}=76.12$, $K=0.065$ and $t_0=-0.159$ for males and $L_{inf}=92.03$, $K=0.055$ and $t_0=0.159$ for females. Natural mortality is not known and is here assumed to be 0.1. The model estimates that *M. whitsoni* (>40 cm) make up 81% of the stock biomass. We hence estimate a biomass of *M. whitsoni* in the medium demersal compartment of 39 600 tWW.

Both the BioRoss and CAML-IPY voyages showed that the majority of the medium sized demersal fish biomass is located on the continental slope in SSRUs 881H, 881I, and 881K. No macrourids have been caught south of 76°S, and few skates (Hanchet et al. 2003). This is confirmed by analysis of the

commercial catch data by SSRU (Hanchet et al. 2004; Stevenson et al. 2008). Here we use data on bycatch of medium sized fish from the Ross Sea toothfish fishery to make a first attempt at a biomass estimate for all fish, based on the biomass estimate for *M. whitsoni* described above. If we make the assumption that the catchability of medium sized (40–100 cm) fish in the Ross Sea (except Antarctic toothfish which are targeted by the fishery) is similar to that of *M. whitsoni*, we can pro-rata the proportions of each species group in the bycatch by our estimate of the biomass of *M. whitsoni* to estimate biomasses of the other “medium-sized” demersal species (Equation 1). Here, B_x is our estimate of medium-sized biomass of species X in the study area, B_{WGR} is the biomass of *M. whitsoni* in the study area (estimated as explained above), and C_x and C_{WGR} are the total bycatch of species X and *M. whitsoni* respectively by the toothfish fishery up to and including 2006. For skates, the value of C includes released fish from Table 11 of Dunn et al. (2007c). The results are given in Table 3.

$$B_x = \frac{C_x}{C_{WGR}} B_{WGR} \quad (\text{Equation 1})$$

This method leads to an estimate of the total biomass of “medium demersal fish” in the study area of 52 000 tWW, with *M. whitsoni* and other macrourids making up 76% of the biomass. This method should be considered very preliminary and wide bounds of uncertainty will be used.

Table 3. Major medium size fishes in the Ross Sea study region. Species are grouped because the bycatch identification by observers, onboard the fishing vessels, is unconfirmed. * data from Dunn et al. (2007c) used instead of CCAMLR (C2) data to include non-landed bycatch of skates.

Code(s)	Species	Common name	Average weight of individual bycatch (kg)	Estimated biomass (tWW)	Prop'n (%)
ANT	<i>Antimora rostrata</i>	Violet cod	1.5	1389	2.7
BAM	<i>Bathyraja maccaini</i>	Maccain's skate	5.8	5	
BEA, BMU, BYR	<i>Bathyraja eatonii</i>	Eatons skate	8.2	286	
BHY	<i>Bathyraja spp</i>	Dwarf prickly skate	7.5	153	
SRR, RAJ, RFA, SRX	<i>Raja georgiana</i>	Antarctic starry skate	7.1	5196	
All skates*			6.9	8322	16.0
TOP	<i>Dissostichus eleginoides</i>	Patagonia toothfish	12.3	2618	5.0
WGR, CEH, CVY, GRV, MCC	<i>Macrourus whitsoni</i>	Whitsons grenadier	1.2	39 636	76.3
Total				51 965	100

We note that other methods for monitoring and estimating biomass of rattails and skates are currently being explored, including the use of tag-retrievals for skates (O’Driscoll et al. 2005; Dunn et al. 2007c). Dunn et al. (2007c) carried out a very preliminary stock assessment of skates in this area based on tag-recapture data and estimated a virgin biomass of 5700 t, which is the same order of magnitude but about 32% lower than the estimate provided in Table 5 (8322 t). A large scale tagging program carried out by CCAMLR in 2008/09 may lead to an improved estimate of skate biomass in the near future.

To the medium size estimate for all by-catch species we must add the biomass of Antarctic toothfish in this size range (40–100 cm). The estimated biomass of toothfish in this size range from the stock model is 9170 tWW. This gives an overall estimate of medium demersal fish of 61 100 tWW. Of this, 67.1% is potential prey for Antarctic toothfish; there is no evidence of Antarctic toothfish consuming skates, rays, Patagonian or Antarctic toothfish.

4.3 Diet

We base the diet of this component on that of Whitson's grenadier, the Antarctic starry skate (*Amblyraja georgiana*) and 40–100 cm long Antarctic toothfish. The diets of the first two species have not been studied in detail in the Ross Sea. Some preliminary examination of *M. whitsoni* stomachs indicated that they had been feeding on krill and other macrozooplankton, benthic invertebrates, and demersal fish (University of Otago, pers. comm.). More recent detailed work on stomach contents from Whitson's grenadier collected on the IPY-CAML voyage (Hanchet et al. 2008d) shows a diet of amphipods and isopods (34%; mainly *Eurethenes gryllus*, 26% and *Eusirus* sp., 5%), Lanternfish (*Gymnoscopelus opisthopterus*) 23%, *P. antarcticum* (21%) and *E. superba* (15%) (Forman, unpublished data). Although the size of *P. antarcticum* were not measured, they are likely to be mainly adults at the depth that Whitson's grenadier are feeding on the slope. Sizes of other prey fishes were not routinely measured and we assume they are all likely to be <40 cm in length and hence in the small demersal fishes compartment of the model. The key amphipods are epibenthic and will largely be included in the macrobenthic compartment in the model, rather than in the macrozooplankton. Elsewhere, macrourids typically feed on benthic and epibenthic organisms including small fishes, cephalopods, natant decapods, and isopods and also macrozooplankton including salps and krill (e.g. Laptikhovsky 2005). Large mature *Amblyraja georgiana* feed mainly on fishes, whilst small immature skates (which make up the majority of skate consumption in this group) feed on polychaetes, gammarids, mysids, decapods, and krill (Permitin 1970). Based on published diets we hence estimate a diet for the (non-toothfish) medium-sized demersal fishes of: 21% small demersal fishes; 15% silverfish; 5% pelagic fishes; 5% cephalopods; 22% macrozooplankton (5% *E. crystallorophias*; 12% *E. superba*; 5% other macrozooplankton), 7% megabenthos; 25% macrobenthos. The diet of 40–100 cm Antarctic toothfish was given in Section 3.4.

4.4 Production

Production estimates for the medium sized demersal fish assemblage will be based on values for Whitson's grenadier the most abundant macrourid in the Ross Sea. The simple population model described previously for an unfished population of *M. whitsoni* estimates a production of $P/B=0.072 \text{ y}^{-1}$ for fish >40 cm length. Annual production/biomass ratios for fish of different sizes can be calculated from the equations given by Banse & Mosher (1980), or Haedrich & Merrett (1992). These methods generally differ by only a few percent. Production for a typical medium size of *M. whitsoni* (total length 62 cm, weight 1.2 kg) is estimated to be $P/B=0.39 \text{ y}^{-1}$. This does not take the low temperatures of the Ross Sea into account, and seems high. Fishbase (Froese & Pauly 2009) states that production rates for *M. whitsoni* are likely to be low, with a minimum population doubling time of more than 14 years in the Antarctic, implying a P/B nearer 0.1 y^{-1} . We propose using an average of the former estimates above $P/B=0.23 \text{ y}^{-1}$ for the non-toothfish Ross Sea demersal fish assemblage. For comparison, annual production/biomass ratios for orange roughy in subantarctic waters has been calculated to be $P/B=0.15 \text{ y}^{-1}$ (Pankhurst & Conroy, 1987).

Using the population model for *M. whitsoni* we estimate that the transfer of biomass from the small to medium demersal fish group due to aging of the medium sized species (especially *M. whitsoni*) is estimated to be equivalent to 0.58 of the annual production of the small *M. whitsoni* individuals.

4.5 Consumption

Consumption estimates for the demersal fish compartment will be based on values for *Macrourus whitsoni*. *Notothenia neglecta* from the South Orkney Islands consumed 7–9% of its weight for one meal (Johnston & Battram 1993). We do not know how often they need to fill their stomachs to cover their basic metabolic requirements and growth. The method of Palomares & Pauly (1989, 1998) is not easily applicable to *Macrourus whitsoni* because we cannot calculate an aspect ratio for the caudal fin. However, assuming a nominal value of 1.0 gives an estimate of $P/B=1.9 \text{ y}^{-1}$. Bradford-Grieve et al. (2003) used a ratio of consumption to biomass, $Q/B=2.6 \text{ y}^{-1}$ for demersal fish in New Zealand

subantarctic waters. It is likely that consumption rates of fish in the Antarctic will be lower than those for temperate and subantarctic waters. The values give P/Q=0.10.

5 Small demersal fish

5.1 Small true demersal fish

5.1.1 Species and general distribution

This compartment includes many small (<40 cm maximum length and/or <1 kg maximum weight) notothenids (especially *Trematomus* sp.), icefish, deepsea cods, eel cods, and macrourids, with diverse life histories and trophic roles (La Mesa et al. 2004b). All Antarctic silverfish (*P. antarcticum*) are excluded from this group. Small notothenids found in the Ross Sea include *Trematomus bernacchii*, *T. eulepidotus*, *T. hansonii*, *T. lepidorhinus*, *T. loennbergii*, *T. pennellii*, and *T. scotti*. In addition, dragonfishes (especially *Bathydraco marri*) and a number of small icefishes (especially *Chinobathyscus dewitti*) are present. None of these fish except Whitsons grenadier (*Macrourus whitsoni*) generally reaches more than 1 kg in weight (Table 4).

Table 4. Small demersal fishes in the Ross Sea. Data of non-silverfish small demersal fishes from the bycatch of the toothfish fishery in the Ross Sea region and from the CAML-IPY bottom trawl survey (Hanchet et al. 2008d). These data are used to show average weights and maximum weights for species. Note that some of these identifications are by observers at sea and are unverified.

Code	Species	Common name	Average weight of individual bycatch (kg)	Max weight in CAML-IPY trawl survey (kg)
AZT	<i>Artedidraco mirus</i>	Dragonfish	0.82	
ART	<i>Artedidraco spp</i>	Barbelled plunderfishes	0.49	
PLF	<i>Artedidraconidae</i>	Barbelled plunderfishes	0.39	
SSI	<i>Chaenocephalus aceratus</i>	Blackfin icefish	0.41	
AJH	<i>Champscephalus gunnari</i>	Mackerel icefish	0.49	
ICX	<i>Channichthyidae</i>	Unidentified icefish	0.41	
CHW	<i>Chionobathyscus dewitti</i>	Icefish	0.37	0.83
MIC	<i>Chionodraco myersi</i>	Crocodile icefish	0.53	
TIC	<i>Cryodraco hamatus</i>	Icefish	1.00	0.73
CMY	<i>Cryodraco myersi</i>	Crocodile icefish	not caught as bycatch	0.61
YDB	<i>Cryodraco spp</i>	Unidentified icefish	0.68	
WGR	<i>Macrourus whitsoni</i>	Whitsons grenadier	1.24	4.49
MVC	<i>Muraenolepis marmoratus</i>	Moray (eel) cod	0.53	
MWS	<i>Muraenolepis microcephalus</i>	Moray (eel) cod	0.65	
MOY	<i>Muraenolepis microps</i>	Moray (eel) cod	0.78	
MWO	<i>Muraenolepis orangiensis</i>	Moray (eel) cod	0.86	
MRL	<i>Muraenolepis spp</i>	Unidentified eel cods	0.63	
JIC	<i>Neopagetopsis ionah</i>	Crocodile icefish	not caught as bycatch	1.88
NOK	<i>Notothenia kempii</i> *	Notothen	0.31	
NOS	<i>Notothenia squamifrons</i>	Notothen	0.27	
PMA	<i>Pagetopsis macropterus</i>	Crocodile icefish	0.50	
PGR	<i>Pogonophryne permitini</i>	Barbelled plunderfishes	0.49	
POG	<i>Pogonophryne spp</i>	Barbelled plunderfishes	0.43	
TEP	<i>Trematomus eulepidotus</i>	Blunt scalyhead	not caught as bycatch	0.49
TRD	<i>Trematomus lepidorhinus</i>	Slender scalyhead	not caught as bycatch	0.38

* Probably a synonym of *Lepidonotothen squamifrons*

5.1.2 Biomass

A number of demersal fish surveys of the Ross Sea are available. A summary of sampling for demersal fish in the Ross Sea is given below.

- (1) Several Soviet research vessels carried out exploratory trawling in the Ross Sea during the 1970s (e.g., Balushkin & Fedorov 1981; Balushkin 1989). They caught mainly *P. antarcticum* and *T. newnesi*, with smaller catches of *T. bernacchii*, *T. pennellii*, and *T. eulepidotus* and various species of icefishes including *C. hamatus*. Biomass estimates for demersal fish could potentially be obtained from these data were they to be made available.
- (2) Four bottom trawls were made from the vessel *Daini Banshu Maru* at depths of 280–600 m in the western Ross Sea between 72 and 77° S (Iwami & Abe 1981). Notothenioids were the most common species, with *P. antarcticum* and *C. myersi* dominating the catch by number.
- (3) About 20 bottom trawls were made by the R.V. *Nathaniel B. Palmer* in 1996 and 1997 in the south-western Ross Sea (south of 73°S and west of 177°E) covering a depth range of 107–1191 m (Eastman & Hubold 1999). Notothenioids were the most abundant species with *T. scotti* (29.7%), *B. marri* (10.4%), *T. eulepidotus* (8.7%) and *D. longedorsalis* (6.1%) dominating the catch. Demersal fish densities of 438 kg/km² and 90 kg/km² were calculated for two stations at 310 m and 910 m depth respectively.
- (4) A total of six bottom trawls carried out by R.V. *Nathaniel B. Palmer* at depths of 238–517 m were made between 160°W and 128°W (Donnelly et al. 2004). This sampling was in the extreme eastern Ross Sea, and as such are mainly east of the current study area. Notothenioids were again the most abundant species with *T. eulepidotus* (36.5%), *T. scotti* (32%), *P. evansii* (4.9%), *T. loennbergii* (4.7%), and *C. wilsoni* (4.3%) dominating the catch. A fish density of 1650 kg/km² was calculated for all stations combined. The authors noted that the fish fauna was generally similar to that recorded in the western Ross Sea by Eastman & Hubold (1999).
- (5) Donnelly et al. (2004) present data from 6 bottom trawls on the eastern Ross Sea shelf from which we can estimate total demersal fish biomass assuming that data from the eastern area are applicable to the Ross Sea in general. No silverfish were caught demersally. Most specimens caught were <30 cm in length, implying that these are in the “small demersal fish” category. The range of density of small demersal fish found at depths of 238–517 m were 0.67–3.5 gWW m⁻², with an average of 1.7 gWW m⁻². Data are summarised by region in Table 5.
- (6) Densities of small demersal fishes were taken from the papers by Eastman & Hubold (1999) based on two trawl stations from the R.V. *Nathaniel B. Palmer* in January 1997 (Table 5). An 9.1 m long Marinovich Gulf Coast style flat trawl (type of otter trawl) was used. The effective width of the trawl opening was 7.6 m and the towing speed was 2–3 kts. The main mesh used was 70-mm size but this was fitted with a liner of 13-mm mesh. Non-silverfish were 83–96% of the total demersal fish biomass.
- (7) Mean standardised catch rates for the main small demersal fish species are available from the BioRoss survey (Mitchell & Clark 2004; BioRoss 2006). There was large variations between tows. We calculated catch rates separately for two depth ranges (130–560 m) and (630–870 m) (Table 5).
- (8) The New Zealand IPY-CAML survey in February and March 2008 (voyage code TAN0802) aimed to measure the abundance of demersal fish in the Ross Sea shelf and slope (Hanchet et al. 2008c, b, d). The IPY-CAML survey carried out seventeen bottom trawls over the Ross Sea shelf (10 trawls) and slope areas (7 trawls) using a rough bottom (orange roughy) trawl towed for about 20 minutes at 3 knots. This trawl has a mouth width of 25 m, headline of 6 m, and a nominal codend mesh of 60 mm. It was fitted with a 40 mm codend liner to catch smaller fish. Data presented in Hanchet et al. (2008d) are used to estimate biomass of demersal fish for the study area (Table 5). Individual trawl catches were used to estimate biomass via six strata on the shelf and slope using two methods: (1) TrawlSurvey Analysis program; (2) TRAWLCI program. The results of these were averaged. High and low bounds corresponding to +/- the estimated coefficients of variation were applied and also combined by

averaging these two methods. The biomass is made up of (in descending order): *P. antarcticum* 42%, *Cryodraco myersi* 6.3%, *Macrourus whitsoni* 5.0%, *Trematomus eulepidotus* 4.1%, *Chionodraco hamatus* 3.5%, *Trematomus lepidorhinus* 2.4%, *Chionobathyscus dewitti* 0.6%. More details are given in Hanchet et al. (2008d). We removed the fish >40 cm or >1 kg from the IPY-CAML data to estimate a biomass for the small demersal fish component. The only two species of substantial biomass caught in the survey outside the small demersal fish size and depth range are Whitson's grenadier (*Macrourus whitsoni*) and the crocodile icefish (*Neopagetopsis ionah*). The length-frequency and length-weight relationships given by Hanchet et al. (2008d) allow us to estimate the proportion of the total demersal biomass given to remove. This corresponds to about 34% of the biomass of *Macrourus whitsoni* and all of the biomass of *Neopagetopsis ionah*. Non-silverfish made up 46–100% of the total small demersal fish biomass depending on stratum.

All density and biomass estimates provided in these studies are based on using the distance between the wings (wingspread) as the area swept by the trawl net. In the present study we assume a catchability coefficient of less than unity for small demersal fishes caught by demersal trawls in the Ross Sea for two reasons: (1) fish may be able to avoid the net by swimming; (2) a proportion of the biomass of these small demersals may reside off the sea bed and not be caught in a bottom trawl; (3) the main mesh size used in the trawl surveys used here were larger than the girth of many small demersal fish, so there will probably be a reasonably large non-retained proportion of fishes. Catchability of small demersal fishes by bottom trawls in the Ross Sea is not known. For hoki (*Macruronus novaezealandiae*) in New Zealand subantarctic waters, comparison between demersal trawl surveys and stock models suggest a catchability of about 0.4 (Hanchet pers. com.). The low water temperature, and smaller size of Antarctic small demersals compared to hoki is likely to reduce swimming speeds and hence active net avoidance, but there is likely to be greater loss due to fish passing through the coarse mesh. Here, we will use a catchability coefficient of 0.5. We applying this factor to all trawl survey data used here (namely: from BioRoss, Mitchell & Clark 2004; IPY-CAML survey; Donnelly et al. 2004; Eastman & Hubold 1999).

There are considerable differences in densities of small demersal fish caught between regions, depths and voyages (Figure 1). Each estimate of fish density was assigned to a region based on their depth and location. The estimates of fish density for each region were obtained by averaging fish densities across all trawls made in that region (Table 5). The final catch rates used as density estimates representing the three regions are given in the table. There are no density estimates of fish shallower than 200 m (region 1) over large areas, so we assume this density is the same as in the 200–400 m shelf area (region 2). There are no density estimates of fish deeper than 2000 m (region 7), but fish densities in deepwater are generally considered low and so we assume a very low mean density of 50 kg/km². These are combined according to the area of each region as shown in Table 6.

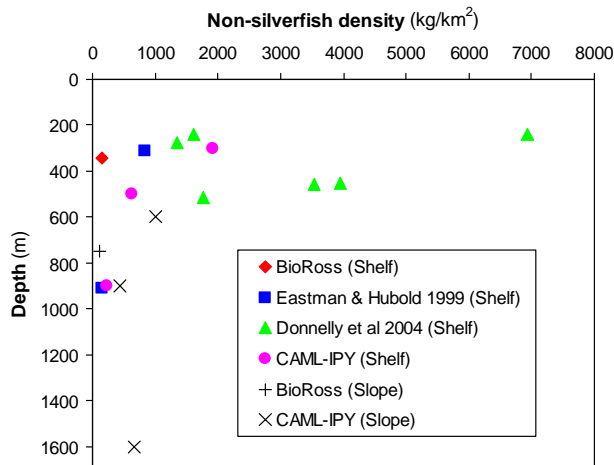


Figure 1. Small demersal fish density (excluding silverfish) in the Ross Sea as measured by trawl surveys, and adjusted for assumed catchability. See text for more details.

Table 5. Catch rates of small demersal fish (excluding silverfish) in bottom trawls during various surveys of the Ross Sea by 7 strata. N is the number of trawls, except where marked *. Actual numbers of trawls from the BioRoss survey were 24 (region 2) and 6 (region 5) but these have been downweighted relative to the CMLR-IPY voyage data. Donnelly et al. (2004) data have also been downweighted relative to IPY-CAML data as they are on the extreme eastern edge of the study area and less likely to be applicable to the majority of the study area. Figures in bold are used in Table 6. Catch figures from the literature have been adjusted by the assumed trawl catchability for small Antarctic demersal fishes (see text).

Region	Region (depth)	Mean density (gWW m ⁻²)	Wgt	Source
1	Shelf (0-200 m)	1580	0	No data, same as shelf 200-400 m
2	Shelf (200-400 m)	1921	3	IPY-CAML (shelf 200-400)
		1354	0.5	Donnelly et al. (2004)
		6938	0.5	Donnelly et al. (2004)
		1621	0.5	Donnelly et al. (2004)
		840	1	Eastman & Hubold (1999)
		148	2*	BioRoss
		1580	7.5	Mean
3	Shelf (400-600 m)	634	3	IPY-CAML (shelf 400-600)
		1759	0.5	Donnelly et al. (2004)
		3961	0.5	Donnelly et al. (2004)
		3526	0.5	Donnelly et al. (2004)
		1450	4.5	Mean
4	Shelf (600-1200 m)	232	4	IPY-CAML (shelf 600-1200)
		149	1	Eastman & Hubold (1999)
		215	5	Mean
5	Slope (400-1200 m)	1002	1	IPY-CAML (slope 400-600)
		442	3	IPY-CAML (slope 600-1200)
		110	2*	BioRoss
		510	6	Mean
6	Slope (1200-2000 m)	668	3	IPY-CAML (slope 1200-2000)
7	Slope (>2000 m)	50	0	No data, nominal

Table 6. Estimates of mean density, area and biomass of small demersal fish for the 7 regions. * indicates assumed data (see text and Table 5 for details). These figures have all been adjusted by the assumed trawl catchability for small Antarctic demersal fishes (see text).

Region	Region (depth)	Mean density (gWW m ⁻²)	Area (km ²)	Biomass (t)
1	Shelf (0–200 m)	1580	8276	13 080
2	Shelf (200–400 m)	1580	73 364	115 951
3	Shelf (400–600 m)	1450	241 796	350 627
4	Shelf (>600 m)	215	98 461	21 210
5	Slope (400–1200 m)	510	35 818	18 254
6	Slope (1200–2000 m)	668	57 699	38 533
7	Deep (>2000 m)	50	121 584	6079
Total		885	636 998	563 734

The data suggests a total small demersal fish biomass for the study area of 564 000 tWW. The overall mean density estimate of 885 kg/km² is lower but a comparable order of magnitude to that of 920 kg/km² recorded for similar depths in the Vestkapp region of the Weddell Sea (Ekau 1990). The data shown here suggests that the vast majority (89%) of the small demersal fish biomass is on the shelf (66% of total area), with a small proportion (10%) on the slope (15% of the area), with an estimated 1% of the total biomass in deep water (19% area).

5.1.3 Production

Annual production/biomass ratios (P/B) for small demersal fish are estimated from the equations given by Banse & Mosher (1980). Applied to the median sizes of species found in the IPY-CAML survey (Hanchet et al 2008d) gives estimates of P/B between 0.48–1.0 y⁻¹. The lower value in this range is most likely to be applicable for small fish in the Antarctic, P/B=0.48 m⁻¹ and will be used here. This is comparable with the production value previously estimated for adult *P. antarcticum* of P/B=0.63 y⁻¹.

5.1.4 Consumption

The method of Palomares & Pauly (1989, 1998) is used to estimate Q/B for the major species of small demersal fish identified by Hanchet et al. 2008d). An average aspect ratio of the caudal fin of 2.5 as for *P. antarcticum* calculated from the photographs given by Fishbase: Froese & Pauly (2009) is used. Assuming a water temperature at depth of approximately 2°C we estimate a Q/B for small demersal fish in the Ross Sea of Q/B=3.0–5.3 y⁻¹, with an average value of 4.2 y⁻¹ which is very close to that for adult *P. antarcticum* estimated previously (3.8 y⁻¹) and which we use here. Together with the estimate of P/B, this suggests P/Q=0.11.

5.1.5 Diet

As a consequence of their broad range of lifestyles, the diet of the small demersal fish group is particularly diverse ranging from strictly benthic, to almost completely pelagic, with some species having both benthic and pelagic components (La Mesa et al. 2004b). Furthermore, many species are opportunistic feeders, capable of feeding on both benthic and pelagic organisms, and with diets that can vary with prey abundance according to location, depth, and season. The diet of many of the notothenioid species found in the southern Ross Sea was reviewed by La Mesa et al. (2004b).

Some information on diet is available for small demersal fish in the Ross Sea e.g. La Mesa et al. (2004b) and Gon & Heemstra (1990), as summarised in Table 1. Pakhomov (1997) and Pakhomov & Tseytlin (1992) give more information from other Antarctic regions on the diet of juveniles and adults of several species of fishes. Pakhomov & Tseytlin (1992) show that key prey items of several species of small Antarctic demersal fish species include krill (*E. superba*), fishes (nototheniids, myctophids),

and various mesozooplankton (especially amphipods, and polychaetes), while cephalopods are only a minor component (<4%).

The nototheniids (Nototheniidae) can be divided into epibenthic and benthic feeders (La Mesa et al. 2004b). The latter feed on a wide variety of species including polychaetes, molluscs, pteropods, gammarids, hyperiids, mysids, and decapods, whilst the epibenthic species feed to a greater extent on *E. crystallorophias* and fish (*P. antarcticum*). Sutton et al. (2006) summarise data showing *Trematomus bernacchii* is a generalised benthic feeder (La Mesa et al. 2004b) and organisms were represented in its diet include polychaetes 15%, bivalves 45%, gastropods 10%, amphipods 3%, isopods 3%, fishes 12% with minor amounts of krill, mysids, decapods, pycnogonids and echinoderms. The plunderfishes (Arteidraconidae) feed mainly on benthic or epibenthic organisms including polychaetes, gastropods, gammarids, isopods, mysids, and decapods. The larger dragonfishes (Bathydraconidae) are benthopelagic predators on fishes such as *P. antarcticum* and *P. borchgrevinki*, whilst the smaller species feed mainly on benthic or epibenthic crustaceans. *Bathyraco marri* from 330–340 m depth fed exclusively on crustaceans (La Mesa et al. 2007). Smaller fishes fed on mesozooplankton and larger species fed on benthopelagic prey from the macrozooplankton. Overall percentage (by number) of prey were mysids 37%, amphipods 30%, copepods 27%. The icefishes (Channichthyidae) and especially *Chionobathyscus dewitti*, is likely to feed almost exclusively on pelagic species such as *E. crystallorophias*, small pelagic fish (*P. antarcticum*), and ichthyoplankton (mainly fish eggs), with minor components of crustaceans, and squid or squid remains (probably *Kondakovia longimana*). Based on their diet, and on the relative proportions of the various species as well as adult *P. antarcticum* in this compartment, we assume a diet for the demersal fish assemblage of: 7% small demersal fish; 7% silverfish; 2% pelagic fish; 5% cephalopods; 2% *E. crystallorophias*; 2% *E. superba*; 4% other macrozooplankton; 16% mesozooplankton (mainly copepods); 25% megabenthos; 30% macrobenthos.

5.2 Cryopelagic fish

5.2.1 Species and general distribution

This group represents species of fish that are usually associated with the under-surface of the ice. There are three cryopelagic fish species occurring in the Ross Sea: *Pagothenia borchgrevinki*, *P. brachysoma*, and *Trematomus newnesi* (Andriashev 1970). The three main species are known mainly from inshore specimens collected from under sea ice and from around the shores of the Ross Sea in McMurdo Sound and Terra Nova Bay. Their occurrence offshore in the Ross Sea is not well known. In addition, juveniles of other *Trematomus* species (e.g., *T. nicolai*) have also been reported to be associated with the underside of the ice (Andriashev 1970; La Mesa et al. 2000).

P. borchgrevinki appears to be the most common cryopelagic fish in the Ross Sea. It is usually collected by jigging with lines through holes drilled in fast ice in McMurdo Sound over depths ranging from 310 to 640 m (Eastman & de Vries 1985; Foster et al. 1987; Janssen et al. 1992; Foster & Montgomery 1993). These holes are up to 5 km from land and 15–20 km from the edge of the annual ice. However, *P. borchgrevinki* also appear common close to shore in shallow water. They have been reported in traps set in 7 m in McMurdo Sound by Eastman & de Vries (1985), and in Prydz Bay were caught only in depths of less than 20 m, with 80% of fish collected immediately under sea ice, and the remaining 20% from within 5 m of the bottom (Williams 1988). Occasional specimens have been reported from bottom trawls in deeper water (e.g., in 550 m depth off Cape Adare: Iwami & Abe (1981); and in 646 m depth in the Weddell Sea: Ekau 1990), however, it is not known for certain that these fish were caught on the bottom. Andriashev (1970) noted that in the Davis Sea, *P. borchgrevinki* occurred under the ice near the coast (Mirny) and far out in the open sea (Novolazorevskaya), but the actual distances and water depths are not given. Postlarvae (24–30 mm SL) were reported from stomachs of *T. newnesi* caught in 92 m depth in Terra Nova Bay (Vacchi & La Mesa 1995), whilst small juvenile (4–6 cm SL) fish were recorded from krill swarms down to 70 m near the Antarctic

Peninsula (Kellerman & Kock 1988), and 4–12 cm SL fish were recorded from under the ice shelf at about 80 m depth in the southeastern Weddell Sea (Gutt 2002).

T. newnesi appears to have a similar distribution to *P. borchgrevinki*, being commonly caught in very shallow coastal waters of less than 20 m depth (Williams 1988; Eastman & de Vries (1997), and also through holes in the ice over deeper water (Andriashev 1970; La Mesa et al. 2000). However, *T. newnesi* also appear to occur somewhat deeper than *P. borchgrevinki*, being caught by trammel nets in Terra Nova Bay on the bottom at depths of 130 m (La Mesa et al. 2000). This species is also the only cryopelagic species to be caught in bottom trawls in the Ross Sea, with 15 fish caught in a single bottom trawl in 238 m in the eastern Ross Sea (Donnelly et al. 2004) and 12 fish caught in five trawls during the BioRoss survey (NIWA, unpublished data). *P. brachysoma* has been rarely reported from the Ross Sea and so it is probably uncommon there. The maximum lengths of *P. borchgrevinki*, *P. brachysoma*, and *T. newnesi* are given as 28, 17, and 20 cm total length respectively (Eastman & de Vries 1997; FishBase: Froese & Pauly 2009).

As energetic parameters of cryopelagic fish (see below) are similar to those estimated for adult *P. antarcticum* in the Ross Sea, and lower than for smaller mesopelagic fish in subantarctic and temperate waters and juvenile fish, so it is appropriate to group these cryopelagic fish with small demersal fish rather than pelagic fish.

5.2.2 Biomass

There are very few data on the density or biomass of cryopelagic species in the Antarctic. Montgomery et al. (1989) considered that *P. borchgrevinki* occurs in loose ill-defined schools, and were able to catch 62–84 fish in 1–1.5 hours fishing when fishing through the ice in McMurdo Sound. Janssen et al. (1992) note that *P. borchgrevinki* is an abundant schooling fish commonly seen swimming by ice holes in schools of up to 100 fish, whilst Andriashev (1970) mentions the occurrence of *P. borchgrevinki* and *T. newnesi* in large winter sub-ice swarmings in the Davis Sea. The only estimates we could find of actual fish densities of *P. borchgrevinki* were from observations made by remotely operated vehicle in the southeastern Weddell Sea (Gutt 2002). He recorded juvenile fish (4–12 cm long) at densities of 7 fish per 10 m² under the ice shelf, and adult fish densities of 0.5 fish per 10 m² under the sea ice (fast ice). However, he noted that the small spatial extent of the study and the low number of fish observed under the sea ice made the results very uncertain.

The benthic biomass of *T. newnesi* could be estimated from the trawl surveys, but this would be a gross underestimate, and probably of little value. In the absence of better information we speculate that the cryopelagic species could have a combined density of 10 fish per 100 m². We have further assumed for this analysis that cryopelagic species occur only in regions with a bottom depth of less than 100 m - although in some areas (e.g., McMurdo Sound) fish clearly do occur at times over deeper water. Length, *L* (mm) vs *W*, weight (g) relationship for *T. newnesi* is given as $W=3.17 \times 10^{-6}(\text{SL})^{3.34}$ (Eastman & de Vries 1997). For fish of length 20 cm, this implies a maximum weight of 154 g. We assume that average weight is about 50% maximum weight. Based on an area less than 100 m deep of c. 0.6% of the study area (see Physical section), this suggests a biomass density within the study area of 0.0051 gC m⁻².

5.2.3 Diet

The diet of *Pagothenia borchgrevinki* has been the subject of several studies – but all have been based exclusively on specimens captured through the sea ice in McMurdo Sound (e.g., Eastman 1985; Eastman & de Vries 1985; Foster & Montgomery 1993; Foster et al. 1987; Montgomery et al. 1989; La Mesa et al. 2000). This species is planktivorous, feeding in the platelet ice, in the water immediately beneath the ice, and in the water column when ice has melted, mainly on amphipods (*Orchomene plebs*), pteropods (*Limacina helicina*), small copepods (e.g., *Calanus* spp.), and hyperiid amphipods. Secondary food consists of euphausiids, mysids, chaetognaths, pelagic polychaetes, and fish (*P. antarcticum*). Janssen et al. (1992) recorded juvenile *P. antarcticum* from almost 50% of

stomachs but considered that the high incidence of *P. antarcticum* in that study may have been due to the samples being collected further from shore over depths of 640 m. Stomach evacuation rates for adult *P. borchgrevinki* were quantified by Montgomery et al. 1989). Small *P. borchgrevinki* (65–75 mm TL) fed on small copepods in McMurdo Sound (Eastman & de Vries 1985), whilst elsewhere fry eat *Paralabidocera antarctica* (Hoshiai et al. 1989, 1991).

Feeding data on *T. newnesi* are available from McMurdo Sound and Terra Nova Bay (Vacchi & La Mesa 1995; Eastman & de Vries 1997; La Mesa et al. 2000). Diet varies spatially and temporally, but like *P. borchgrevinki* they are primarily planktivores. In spring, when the area is covered by sea ice it feeds mainly on krill (*E. crystallorophias*) and mesozooplankton (small pteropods, copepods, hyperiid amphipods). In summer, when the ice cover disappears the prey become more diverse, including the above species as well as decapods (*Chorismus antarcticus* and *Notocrangon antarcticus*) and fish larvae (*P. antarcticum*, *P. borchgrevinki*, *Chionodraco* sp., *Pagetopsis* sp., *Gymnodraco acuticeps*, *Trematomus* spp.) (La Mesa et al. 2000), and there is at times a high incidence of cannibalism on small (24–33 mm) *T. newnesi* post-larvae (Vacchi & La Mesa 1995). No feeding data are available for *Pagothenia brachysoma* in the Ross Sea, but elsewhere they feed on copepods and euphausiids (Gon & Heemstra 1990).

In this initial study, the diet of this trophic compartment will be assumed to be: 35% *E. crystallorophias*; 15% *E. superba*; 10% other macrozooplankton; 15% ice metazoa; 15% mesozooplankton; 5% pelagic fishes; 5% silverfish (mainly juvenile *P. antarcticum*).

5.2.4 Production

In McMurdo Sound during October and November 1987 fish are estimated to be about 2–7 years old (Pankhurst 1989). Growth in length is reported as being linear (Pankhurst 1990) (implying a high natural mortality) and $L = 20.08A + 60.1$, where L = length in mm and A = age in years. Weight was related to age: $W = 1.96A^2 - 4.33A + 9.42$, where W = weight (gWW). Growth rate of *Pagothenia borchgrevinki* were measured in laboratory-reared fish (Sakakibara et al. 1989). An approximate annual P/B is estimated by dividing the growth increment over 4 years of 4 fish and relating it to the median weight of each fish for each year. P/B of the youngest fish ranged from 0.54–0.97 and for the oldest fish from 0.14–0.32. The overall mean is $P/B = 0.53 \text{ y}^{-1}$.

Alternatively, annual production/biomass ratios for fish of different sizes can be calculated from the equations given by Banse & Mosher (1980), or Haedrich & Merrett (1992). These give P/B for the three species of cryopelagic fish (*Pagothenia borchgrevinki*, *P. brachysoma*, *Trematomus newnesi*) of 0.8–1.4 y^{-1} with a mean of 1.1 y^{-1} . As these equations were not developed for Antarctic fish, it is likely that they are too high, and an average of the two values of 0.82 y^{-1} will be used.

5.2.5 Consumption

Gut evacuation rates of *P. borchgreviniki* were determined by Montgomery et al. (1989). The decline in gut contents is related to time: $\log_e y = 0.29 - 0.03x$, where y = gut contents as a percentage of body weight and x = time in h. It is therefore possible that fish do not fill their guts every day.

Two methods were used to estimate consumption. First, the methods of Palomares & Pauly (1989, 1998) were used to estimate Q/B based on the fish asymptotic weight, water temperature, diet (carnivore, herbivore, omnivore), and aspect ratio of the caudal fin. *Pagothenia borchgrevinki* and *P. brachysoma* have aspect ratios of the caudal fin of 1.8 and 1.7 respectively (calculated from the photographs given by Fishbase: Froese & Pauly 2009). The water temperature is approximately 0°C. We hence estimate a Q/B for adult cryopelagic fish of the Ross Sea of 3.9–5.7 y^{-1} , with a mean of 4.9 y^{-1} . Second, we used measurements of respiration rate to estimate Q/B based on P/B estimate previously. The oxygen consumption normalised to body mass for *P. borchgreviniki* has measured at 189 $\text{mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$ (Lowe & Davison 2006) at 0°C. This implies a respiration:biomass ratio of $R/B = 4.8 \text{ y}^{-1}$. We assume an unassimilated consumption for cryopelagic fish in the Ross Sea as for

carnivorous fish of $U=0.27$ (Brett & Groves 1979). If $P/B=0.82 \text{ y}^{-1}$, we estimate $Q/B=7.7 \text{ y}^{-1}$. Here, we use an average of these methods of 6.3 y^{-1} . These imply $P/Q=0.13$ which is reasonable.

6 Antarctic silverfish

6.1 General distribution

Antarctic silverfish (*P. antarcticum*) has a circumpolar distribution in high Antarctic waters at depths down to 700 m (see Outram & Loeb 1995). They are a prime example of the complexity of adaptations necessary for an animal to thrive in the realm of Antarctic shelf waters, a niche largely unoccupied by other fish species. For example, unlike myctophids, silverfish do not have a swim bladder but use lipid stores to control buoyancy. It is the most abundant fish species in the water column above the Antarctic continental shelf and its dominance is well documented especially in the Ross and Weddell Seas where it constitutes, both in abundance and in biomass, 90% of the local fish populations (DeWitt 1970; Granata et al. 2002; Hubold & Ekau 1987). It acts as a key link between plankton and the community of top predators in the shelf waters of the Ross Sea (Williams 1985; Ainley & DeMaster 1990; La Mesa et al. 2004b).

6.2 Life history

In this section information is given relating to the life cycle of Antarctic silverfish because this is such an important species. Age groups are defined according to Hubold (1985) and described below.

Eggs (2.2–2.5 mm in diameter) (Vacchi et al. 2004) are spawned in areas along the continental ice shelves during late winter/early spring (Woehrmann et al. 1997; Faleyeva & Gerasimchuk 1990). Vacchi et al. (2004b) observed eggs and newly hatched larvae under the sea ice among the platelets and eggs hatched in mid November and onwards in Terra Nova Bay. Kellerman (1986) observed larvae (6–9 mm in length) hatching by November and December in colder, near shore areas. The northern part of Terra Nova Bay seems to be a nursery ground for silverfish (Guglielmo et al. 1998; Vacchi et al. 2004c). Highest densities of silverfish post-larvae and juveniles were associated with the westward flowing current of the limb of the Antarctic coastal current and southern limb of the Ross Sea Gyre (Guglielmo et al. 1998). The permanent polynya there could provide favourable food conditions for the development of the first life stages and suggests a tight relationship between reproduction events and the seasonal dynamics of the pack-ice zone (Vacchi et al. 2004c).

In the Weddell Sea, it is thought that vertical and horizontal segregation of post-larvae, juveniles and adults prevents cannibalism (Hubold 1984, 1985). Faleyeva & Gerasimchuk (1990) found that spawning success is related to the developmental dynamics of stationary polynyas based on the observation that a proportion of the silverfish females with mature gonads do not spawn. There is a strong correlation between fecundity and fish body size (Gerasimchuk 1987). The average fecundity of females is 7500 eggs per female (Gerasimchuk 1987), although Woehrmann et al. (1997) give 1300 eggs and FishBase (Froese & Pauly 2009) give 4000 per female.

Larvae (which have the yolk sac still attached) are less than about 8 mm standard length (SL, assumed henceforth when referring to length of silverfish). Larvae will not be considered explicitly in the model, and are implicitly included in the macrozooplankton component. Post-larval fish, 8–30 mm SL (Guglielmo et al. 1998) are known to occur in large numbers in the Ross Sea (e.g. Granata et al. 2002). Granata et al. (2002) show that, in the Ross Sea, early post-larval silverfish may be distributed in the water column down to at least 700 m while later post-larvae inhabit progressively more superficial depths, mostly in the surface 100 m, and concentrated in Terra Nova Bay (Granata et al. 2002; White & Piatkowski 1993).

During their second summer, silverfish start to accumulate large lipid deposits (mainly triacylglycerols) (Woehrmann et al. 1997). These low-density compounds provide this species with hydrostatic lift, an important factor for a fish without a swim bladder. Lipid stores may also serve as a food reserve for metamorphosis. The onset of metamorphosis of postlarvae to juvenile stages occurs at 20–30 mm SL and is completed at a length of about 30–40 mm (Woehrmann et al. 1997). Juveniles are defined as 30–60 mm SL. The transition from post-larval stage to juvenile is accompanied by a move to occupying the deeper water column, though juveniles are still largely pelagic or benthopelagic (Kock 1992; Kellerman 1986, 1990b; Slosarczyk 1987). During the 2008 IPY-CAML survey juvenile silverfish (40–80 mm) were entirely pelagic, being mainly found in the upper 150 m of the water column over bottom depths of 200–500 m (R. O’Driscoll, pers. comm.). They were found throughout the Ross Sea shelf region, and were particularly abundant over the Pennell Bank, but were absent over the slope and northern seamounts. However, in the south-eastern Ross Sea Donnelly et al. (2004) occasionally recorded them in oblique tows over depths of 500–2000 m along the continental slope.

We define adults as being fish over 60 mm SL following Hubold (1985) who found that specimens larger than this appeared to occupy a deeper (more benthopelagic) habitat to that of post-larvae and juveniles. During the IPY-CAML survey, adult silverfish were found in depths of 150–450 m over bottom depths of 200–500 m, and were generally 50–150 m above the seabed (O’Driscoll, pers. comm.) They were seen acoustically and consistently caught in midwater and bottom trawls throughout the Ross Sea shelf and upper slope from Ross Island in the south to Cape Adare in the north, but were absent from stations on the lower slope and northern seamounts. Adults have also been recorded in the vicinity of the Ross Ice Shelf and in McMurdo Sound, where they are predated by Weddell seals and Antarctic toothfish (Eastman 1985, Granata et al. 2000). In the eastern Ross Sea adults were generally found in greatest concentrations over the continental slope and shelf (Donnelly 2004). Silverfish appear to show an ontogenetic migration into deeper water as they get older (O’Driscoll, pers. comm.). They reach sexual maturity at age 6–7 years (Faleyeva & Gerasimchuk 1990) at a size usually >130 mm. Silverfish are known to spawn at Terra Nova Bay during late winter/early spring (Vacchi et al. 2004). We therefore hypothesise that during late winter adults migrate to Terra Nova Bay, and possibly other inshore areas, to spawn near shore under the ice. The maximum length of this species is 250–320 mm (Froese & Pauly 2009).

6.3 Biomass

6.3.1 Acoustic estimate

The New Zealand IPY-CAML survey in February and March 2008 (voyage code TAN0802) aimed to measure the abundance of Antarctic silverfish in the Ross Sea shelf and slope using multifrequency acoustics combined with target strength measurements of specimens obtained by midwater and demersal trawling (Hanchet et al. 2008d). The survey carried out 28 acoustic transects in the Ross Sea (11 shelf, 7 slope, and 10 abyss) with a total transect length of 1641 n. miles, using four frequencies: 12, 38, 70, 120 kHz. Target strength will be calculated from samples collected at 11 midwater trawls, 19 oblique midwater trawls, and 23 demersal trawls. Final data are not yet available and here we present preliminary data courtesy of Richard O’Driscoll (pers. com.). We caution that these data are of unvalidated accuracy and are liable to change. In particular, target strength measurements for silverfish from the IPY-CAML survey are not yet available, and in the interim, data based on previous research have been used which are of unknown validity in this area. Acoustic data from IPY-CAML show that juvenile and adult silverfish have different occurrences with depth, which will allow a separate estimate of biomass for each to be obtained. Juvenile silverfish (30–80 mm) were found between the surface and c. 200 m. Adult silverfish (60–190 mm) were found at depths of c. 200–400 m, both pelagically and demersally. The average weight of Antarctic silverfish in the IPY-CAML survey was 0.19 kg. Preliminary estimates of biomass from the New Zealand IPY-CAML survey are of the order of 92,700 tWW (juvenile silverfish) and 200,000 tWW (adult silverfish).

6.3.2 Adult biomass from trawls

Given that a large proportion (perhaps the majority) the population of adult silverfish in the Ross Sea live in the water column, an estimate of biomass based on trawling is not appropriate. Instead, the preliminary acoustic estimate of biomass will be used, despite issues regarding the target strength of silverfish in the Ross Sea discussed above.

6.3.3 Juvenile biomass from trawls

The estimate of biomass of juvenile silverfish from the acoustic survey of the New Zealand IPY-CAML survey is almost certainly an underestimate of the true biomass because of uncertain target identification and low signal-to-noise ratios in the acoustic return data (O'Driscoll pers. com). Consequently, biomass estimates for post-larval and juvenile fish in the water column over the Ross Sea shelf, slope and deep water were assembled from a number of midwater sampling voyages to the region. Granata et al. (2002) found that the number of larval and juvenile fish taken in shelf waters was much greater than in the open ocean and suggested that the Ross Sea is a nursery for young fish. Given the high variability in fish density with water depth and region, data on fish densities were combined by strata using log-averages (Table 7).

Granata et al. (2002) give the results of four surveys of ichthyoplankton in different parts of the Ross Sea, sampled in 4 years and in different months, in numbers per 1000 m³. Details of collection data and specific data is found in Guglielmo et al. (1998) for the 1987/88 survey in Terra Nova Bay region; Granata et al. (2000) for the 1989/90 section through central west Ross Sea and stations to the north of the Ross Sea; Vacchi et al. (1999) for the 1994/95, section through central west Ross Sea and in the northern slope region; and Granata et al. (2002) for the 1995/96 section through eastern, southern and central Ross Sea. We omit data from the 1989/90 survey as this focussed on stations to the north of the study region. Accompanying the abundance data in Guglielmo et al. (1998), Granata et al. (2002) and Vacchi et al. (1999) are standard lengths of the most numerous fish in the four years; these were 13, 38 and 14 mm SL for the 87/88, 94/95, and 95/96 surveys respectively. We converted numbers of fish to weights using length-weight data for *P. antarcticum* from FishBase (Froese & Pauly 2009) and the recent CAML-IPY voyage to the Ross Sea (Hanchet et al. 2008d). Granata et al. (2002) sampled a small and variable proportion of the water column, usually sampling only the upper c. 200 m. Granata et al. (2002) show that this upper portion of the water column is likely to contain 96% of the post-larval/juvenile fish biomass. Notothenioid species were found to constitute 98% by number of the total midwater biomass of post-larval/juvenile fish (Granata et al. 2002). Among these post-larvae and juveniles, *P. antarcticum* constituted more than 96% by number on one survey (95/96: Granata et al. 2002), but only 26% on a previous survey (94/95: Vacchi et al. 1999).

In Terra Nova Bay, silverfish post-larvae and juveniles were particularly abundant (Guglielmo et al. 1998), so we take this region as a separate stratum. For the purposes of this estimation, the Terra Nova Bay area is defined as being constrained between 74.5°–75.5°S and 163.5°–165.5°E, with an area of 6500 km².

Data on midwater and demersal (fish) trawling in the eastern Ross Sea at the extreme edge of the study area are presented in Donnelly et al. (2004). Three types of gear were used over the 20 midwater trawls: (1) MOCNESS with 4 mm mesh nets and a 1 mm mesh cod-end; (2) Tucker trawl with 4 mm mesh nets and a 1 mm mesh cod-end; (3) balloon fish trawl with 10 cm, 5 cm, 3.8 cm mesh tapering nets and a 60 mm mesh cod-end liner. The data is divided into in 3 zones: offshore, slope, and shelf. Here, we use only their data from the slope regions to give densities of *P. antarcticum* in the water column and assume that data from the eastern area are applicable to the Ross Sea in general. Data from the shelf zone was not used to estimate densities because the sampling was different and did not have accompanying volume-filtered measurements (Donnelly et al. 2004). The study reports that *P. antarcticum* were taken midwater in depths 500 m deep, and also in subsequent bottom trawling. Donnelly et al. (2004) report that *P. antarcticum* was a very minor (<5%) part of the midwater catch over deep water (>900 m), which was dominated by *Electrona antarctica* and *Bathylagus antarcticus*.

Midwater *P. antarcticum* had sizes 49–78 mm, suggesting they are post-larval juveniles, with adults (80–180 mm) taken on the bottom. Data are included in Table 7. Data on fish abundances per stratum are combined in Table 8.

Table 7. Catch rates of post-larval/juvenile silverfish from midwater trawls during various surveys of the Ross Sea by 5 strata. N is the number of trawls. * Where no data was available for stratum 4, we used an average of those for strata 3 and 5. Log-means were used to calculate averages to prevent undue influence of high values.

Region	Region (depth)	Mean density (gWW m ⁻²)	N	Source
1	Terra Nova Bay	3.43	33	Gugliemo et al. 1998; Granata et al. 2002
2	Shelf (all depths)	0.0555	10	Vacchi et al. 1999
		0.909	24	Granata et al. 2002
		0.420	38	Mean
3	Slope (600-1200 m)	0.0250	8	Donnelly et al. 2004
		0.0330	8	Donnelly et al. 2004
		0.0290	16	Mean
4	Slope (1200-2000 m)	0.0158	0	No data, assumed*
5	Deep (>2000 m)	0.0025	7	Vacchi et al. 1999

Table 8. Estimates of mean density, area and biomass of post-larval/juvenile silverfish for the 5 strata. * indicates assumed data (see text and Table 7 for details).

Region	Region (depth)	Mean density (gWW m ⁻²)	Area (km ²)	Biomass (t)
1	Terra Nova Bay	3.43	6459	22 151
2	Shelf (all depths)	0.42	415 438	174 287
3	Slope (600-1200 m)	0.029	35 818	1038
4	Slope (1200-2000 m)*	0.016	57 699	909
5	Deep (>2000 m)	0.0025	121 584	308
	Total	0.31	636 998	198 693

In the absence of seasonal data on larval/post-larval/juvenile fish biomass, we assume that these assembled measurements represent the annual average. The biomass may actually be higher at other times of the year (e.g. due to spawning events of other fish, growth of larvae/post-larvae/juveniles) or could be smaller (e.g. due to mortality of ichthyoplankton, transfer of juveniles to another compartment in the model). The overall average annual biomass density for the Ross Sea is hence estimated to be 0.56 gWW m⁻² which corresponds to $B=56$ mgC m⁻² for this component of the model. We note that 23% of this is in Terra Nova Bay (3.8% of area) and 76% of the biomass is estimated to be on the rest of the shelf (62% of area).

As a check, the population model for *P. antarcticum* described previously can be used to estimate the relative biomass of adult (>60 mm) and post-larval/juvenile silverfish (8–60 mm SL). Since mortality is not known, we again use a range of plausible values which decrease from integrated annual mortality 0.5–0.9 y⁻¹ for silverfish aged 1 year to annual integrated mortality 0.2–0.5 y⁻¹ for fish aged 4 and older. This approach estimates that post-larval/juvenile silverfish may have a biomass between 0.16 and 8.2 times the adult biomass. Numbers of post-larvae/juveniles always dominate the adults (7–800 times) as expected. The biomass figure estimated here for post-larvae/juvenile biomass is 0.20 the value for adult small demersal fish, which is (just) within this wide range. The fact it is towards the lower limit considered here is consistent with lower mortality rates of adults and juvenile silverfish.

Finally we note the variability in surveys of the average abundances of post-larval/juvenile silverfish abundance on the Ross Sea shelf. The difference between the average shelf biomass measured on the 94/95 survey (Vacchi et al. 1999) and the 95/96 survey (Granata et al. 2002) was large: a factor of 16 higher in the later survey. Donnelly et al. (2004) shows that catch rates of *P. antarcticum* using the same gear and methodology in the same depth of water can vary by two orders of magnitude (stations

T3 and T6). This uncertainty in post-larval/juvenile fish biomass means that biomass estimates for this group should be given high uncertainty in the model.

6.4 Diet

Post-larvae/juveniles are opportunistic predators, well-adapted to feed on a wide range of zooplankton depending on seasonal availability, although copepods usually dominate (Hopkins 1987; Williams 1985; DeWitt et al. 1990; Hubold & Ekau 1990; Gröhsler 1994; Granata et al. 2008). Silverfish greater than 30 mm take a bigger proportion of larger planktonic crustacean as well as copepods (Williams 1985; DeWitt et al. 1990; Hubold & Ekau 1990) (e.g. *Euphausia crystallorophias*), benthic animals (molluscs, benthic crustacean including copepods) (Daniels 1982; DeWitt et al. 1990), and sometimes larval fishes (Williams 1985; DeWitt et al. 1990). In the Ross Sea, in summer, silverfish caught in bottom trawls have been feeding on the amphipod *Themisto gaudichaudii* (20%), *E. crystallorophias* (49%), copepods (27%), and general amphipods (3%) (Takahashi & Nemoto 1984). In the Weddell Sea, silverfish 40–60 mm feed on calytopsis stage of *E. crystallorophias* and calanoid copepods (65%).

Fish between 60–120 mm in length fed mostly on the copepods *Calanoides acutus*, *Metridia gerlachei* and *Calanoides propinquus* (70% by mass). Fishes over 120 mm ate *Euchaeta* spp., some gammarid amphipods 5–10 mm long and chaetognaths 20–30 mm long (Hubold & Ekau 1990). Cannibalism has also been reported from fish collected at McMurdo Sound (Eastman 1985). In Prydz Bay fish ate mesozooplankton 48%, macrozooplankton 31%, and juvenile fishes 21% (Williams 1985). Daniels (1982) records the diet of adult silverfish in the Antarctic Peninsula region as being composed of macrozooplankton 69%, fish larvae 3%, benthos 12% and mesozooplankton are presumed to make up the difference of 16%. Copepod eggs and chaetognaths were found in stomachs rarely.

For post-larval/juvenile *P. antarcticum* (10–60 mm SL), we use the diet proportions: *E. crystallorophias* 6%, other macrozooplankton 3%, mesozooplankton 90%, and ice metazoa 1%. For adult *P. antarcticum* >60 mm (demersal stage), we use the diet proportions: *E. crystallorophias* 40%, other macrozooplankton 12%, mesozooplankton 30%, Antarctic silverfish (juveniles) 9%, pelagic fish 1%, macrobenthos 5%, megabenthos 3%.

6.5 Production

Growth of juvenile and adult silverfish is amongst the slowest known in marine fish (Hubold & Tomo 1989). This slow growth appears to allow the fish to continue to feed on zooplankton and invest its metabolic energy into reproduction (see Woehrmann et al. 1997 for summary).

Production rates for adult silverfish were estimated in two ways. First, annual production/biomass ratios (P/B) can be calculated from the equations given by Banse & Mosher (1980): $P/B = a M_s^b$ where M_s is the energy-equivalent body weight in kcal, and $a=2.75$, $b=-0.26$. Haedrich & Merrett (1992) give a similar relationship, $P/B = a M^b$ where M is in g wet weight, $a=2.40$ and $b=-0.26$. These relationships differ by only a few percent. Applied to adult *P. antarcticum* of length 170 mm (weight 40 gWW) – the median length found on the recent Ross Sea voyage (Hanchet et al. 2008d) – these relationships estimate a $P/B=0.95 \text{ y}^{-1}$.

Second, P/B was estimated for adult fish from a simple population model of *P. antarcticum*. The von Bertalanffy growth parameters of *P. antarcticum* are given as $K=0.08$ and $L_\infty=314$ mm (FishBase: Froese & Pauly 2009). Assuming the onset of metamorphosis from larval to adult fish occurs at length of 25 mm at 2 years old (Woehrmann et al. 1997), gives $t_0=1.0$ y. In FishBase (Froese & Pauly 2009) the length/weight relationship for silverfish is given as $W=aL^b$ where W is the fish weight in g, L is the fish length in cm, and the coefficients for silverfish are: $a=0.0045$, and $b=3.25$. Note values for silverfish collected from the Ross Sea during the IPY survey were $a = 0.0026$, $b = 0.34$ (Hanchet et al. 2008d). Natural mortalities for silverfish of various ages in the Ross Sea are unknown, so we used a

range of natural mortalities of silverfish corresponding to integrated annual mortalities of between 0.2–0.5 for fish aged 4+ and between 0.5–0.9 for silverfish aged 1 year. A linear decline in mortality between 2 and 4 years of age was assumed. This gives population P/B values for adults of 0.20–0.40 y^{-1} , with a mean value of $P/B=0.31 y^{-1}$, equivalent to that for a length 140 mm, 8 years old fish. This is equivalent to an average growth rate for the population of 0.05 mm/d. We take an average of the two methods as our best estimate, to give P/B for adult *P. antarcticum* of 0.63 y^{-1} .

The same population model can be used to estimate a production rate for post-larval/juvenile fish of P/B between 0.77–0.82 y^{-1} . These seem low and correspond to a daily growth increment of 0.04 mm/d. The growth rate of silverfish larvae has been measured between December 1979 and February 1980 in the inner Weddell Sea over a six week period to be about 0.2 mm/d (Keller 1983). The average growth rate over a period of one year of juvenile silverfish (c. 13 mm SL) in Terra Nova Bay was measured as 0.08 mm/d (Guglielmo et al. 1998) suggesting $P/B=1.9 y^{-1}$. Guglielmo et al. (1998) report a mean daily increment of silverfish in the period 5 January to 2 February was about 0.15 mm/d though such fast growth rates are likely to be restricted to the period Nov–Mar (Hubold 1985 and references therein). Allometric equations from Banse & Mosher (1980) and Haedrich & Merrett (1992) suggest $P/B=3.5 y^{-1}$ for silverfish aged 3 years and 35 mm SL typical of the Ross Sea (Granata et al. 2002). Here, we propose to take an average of these three estimates, giving a value for post-larval/juvenile fish of $P/B=2.1 y^{-1}$.

Using the simple population model for *P. antarcticum* we estimate that the transfer of biomass from the juvenile stage to the adult stage at length of c. 60 mm is equivalent to an export of approximately 48% of the annual production of the post-larval/juvenile silverfish group.

6.6 Consumption

The method of Palomares & Pauly (1989, 1998) was used to estimate Q/B for adult silverfish, which have an aspect ratio of the caudal fin of 2.5 (calculated from the photographs given by Fishbase: Froese & Pauly 2009). Taking the water temperature at depth to be approximately 2°C, we hence estimate a Q/B for adult silverfish of the Ross Sea of 3.8 y^{-1} . This implies $P/Q=0.17$. For comparison, measurements by Olaso et al. (2004) of silverfish in the eastern Weddell Sea gave Q/B between 1.1–2.2 y^{-1} . The model of Dos Santos & Jobling (1992) applied to measurements in the work by Olaso et al. (2004) gave estimates of Q/B between 1.8–4.0 y^{-1} . The Q/B value used here for adult *P. antarcticum* is substantially lower than estimated for Antarctic mesopelagic fish (see below) which is likely to be due to the larger size of silverfish compared to mesopelagic fish, and perhaps also lower activity reflected in a smaller caudal fin aspect ratio.

The same method (Palomares & Pauly 1989, 1998) was used to estimate Q/B for post-larval/juvenile *P. antarcticum*. The consumption rate of a 3 year old post-larval/juvenile silverfish of length of 3.5 cm and weight of 0.26 gWW was estimated to be $Q/B=13.7 y^{-1}$. This figure suggests a $P/Q=0.15$ which is reasonable.

7 Pelagic fish

7.1 Post-larval and juvenile fish (non silverfish)

7.1.1 Species and general distribution

This compartment includes larval, post-larval and juvenile fish of length approximately 8–60 mm. The life histories and spawning behaviour of Ross Sea fish are poorly known. Most Antarctic larval/post-larval/juvenile fish appear to be pelagic (Loeb et al. 1993) although many species are not well represented in the literature on midwater sampling (e.g. Vacchi et al. 1999). Using midwater sampling, Granata et al. (2002) record 43 species of larval/post-larval/juvenile fish in the Ross Sea and the area to the north. The study identified post-larval and juvenile stages of *P. antarcticum*, as well as some

larval/post-larval/juveniles of *Macrourus whitsoni*, *Notolepis coatsi*, *N. annulata*, *Chionodraco rastrospinosus*, *Trematomus newnesi*, *T. lepidorhinus*, *T. eulepidotus*, *Dacodraco hunteri*, *Chionobathyscus dewitti*, *Bathylagus antarcticus*, *Notolepis* sp. (Vacchi et al. 1999, Granata et al. 2002). That the larvae of several species of demersal fishes known to be present in the Ross Sea were not taken in the larval sampling of Granata et al. (2002) can be explained in various ways: (1) the breeding seasons of some of these fishes may not overlap with the larval surveys; (2) pelagic development varies from a few months to a year or more (Kock 1985), but may be very short in some fish species; (3) fishes may spawn in specific locations that were not representatively sampled.

7.1.2 Biomass

There is considerable variability in the proportions of different post-larvae and juvenile fish species in the water column over the Ross Sea shelf estimated using data from different surveys. Post-larvae and juveniles, *P. antarcticum* constituted more than 96% of all species by number on one survey (95/96: Granata et al. 2002), but only 26% on a previous survey (94/95: Vacchi et al. 1999). Taking into account average individual sizes on the two surveys (38 mm SL on the first, 14 mm on the second), the average contribution of silverfish to total post-larval/juvenile biomass in the study area may be about 38%. This would imply a non-silverfish post-larval/juvenile biomass in the study area of 62 000 t.

7.1.3 Food and feeding

Apart from post-larval/juvenile Antarctic silverfish (*P. antarcticum*), the diet of juvenile fish in the Ross Sea has not been well studied. Instead, we use measurements of the food of other juvenile fishes studied in the South Atlantic sector in the surface 200 m (Pakhomov et al. 1995). The study considered diet of juveniles of five species of *Trematomus* sp., *Lepidonotothen kempfi*, *Electrona antarctica*, *Dissostichus mawsoni*, and *Notolepis coatsi*. Mesozooplankton (especially copepods) dominated the diet (>95% interms of numbers), with some evidence of feeding on euphausiids, and other macrozooplankton. It is noted that 12 juveniles of *Dissostichus mawsoni*, 43–45 mm length, were feeding mainly on copepods and some hydromedusae. Here, we assume a diet for non-silverfish juvenile fish of: Mesozooplankton 91%, *E. crystallorophias* 3%, *E. superba* 2%, other macrozooplankton 2%, ice metazoa 2%.

7.1.4 Production

We use the same production value for non-silverfish post-larval/juvenile fish as for those of *P. antarcticum* as described previously, i.e. $P/B=2.1 \text{ y}^{-1}$.

7.1.5 Consumption

We used the method of Palomares & Pauly (1989, 1998) to estimate Q/B for a typical post-larval/juvenile fish as for silverfish, giving a value of $Q/B=13.7 \text{ y}^{-1}$, and hence $P/Q=0.15$.

7.2 Mesopelagic fish

7.2.1 Species and general distribution

No truly mesopelagic fish have been found over the Ross Sea continental shelf. However, north of the shelf over the continental slope, there are numbers of fish of the family Myctophidae. Other fish found in the water column in the Ross Sea include the deep-sea smelt (*Bathylagus antarcticus*) and the baracutta *Notolepis coatsi* (see also Table 1). Myctophidae in the north of the study region over the continental shelf includes many of the species most commonly found in the South Atlantic sector of the Antarctic (e.g. Piatkowski et al. 1994; Pusch et al. 2004). In the absence of biomass and other data

from the Ross Sea, we use South Atlantic biomass data and the production and food parameters from the most common species *Electrona antarctica*.

7.2.2 Individual size

Maximum lengths of several species of myctophids caught in the Ross Sea region during the IPY-CAML survey were: *Electrona antarctica* 10.9 cm, *Electrona carlsbergi* 10.4, *Gymnoscopelus braueri* 23.5 cm, *Gymnoscopelus nicholsi* 17.3 cm, *Gymnoscopelus opisthopterus* 21.7 cm, *Krefflichthys anderssoni* 7.2cm, and *Nannobrachium achirus* 16.3 cm (S. Hanchet, pers. comm.). The maximum length of *E. antarctica* is close to the mean maximum lengths for these species (12.1 cm). Length-at-age and weight-at-length for *E. antarctica* are given by Greely et al. (1999). The maximum length, weight and age of *E. antarctica* is reported as 101 mm, 14.9 gWW and 4.1 years respectively. Average values for the population are given as 69 mm, 4.2 gWW and 2.6 years. The average weight in the population is hence estimated to be about 27% of the maximum weight.

7.2.3 Biomass

Biomass is estimated from concentrations of *Electrona antarctica* found in several locations outside the Ross Sea sector, including in the South Shetland Islands at about 62°S and Scotia Sea at about 53°S and 57°S (Piatkowski et al. 1994; Pusch et al. 2004, respectively) although we note that these area are at a considerably lower latitudes than the study region. Piatkowski et al. (1994) record myctophids in concentrations of 1.9–2.1 gWW m⁻² integrated over 1000 m. Further north in the Scotia Sea biomass myctophid was 2.9 gWW m⁻² (Collins et al. 2008). In the Lazarev Sea the three most abundant species (*Bathylagus antarcticus*, *Electrona antarctica*, *Gymnoscopelus braueri*) had a collective biomass of 0.35 gWW m⁻² in the surface 200 m (Flores et al. 2008); this is probably a small proportion of the biomass as many mesopelagic fish are likely to be concentrated below 200 m (Pusch et al. 2004). Donnelly et al. (2004) found concentrations of adult mesopelagic fish (excluding *P. antarcticum* which are considered elsewhere) in the extreme eastern Ross Sea over water depths of >1000 m of 0.22–0.70 gWW m⁻². Donnelly et al. (2004) only found silverfish in the water column over water depths <900 m. A value in the middle of this range (1.0 gWW m⁻²) will be assumed for the area over the continental slope and deeper water (>1000 m) as mesopelagic fish biomass may be assumed to reduce towards the southern extent of their range. Adult mesopelagic fish are assumed to occur only in areas of the study region deeper than 1000 m, which comprise 30.2% of the study region. This leads to an estimate of biomass for the study region of 0.030 gC m⁻². It is possible that acoustic data from the 2008 IPY-CAML voyage to the Ross Sea may lead to improved estimate of this biomass density for the study region (O’Driscoll, pers. com.).

7.2.4 Food and feeding

Pusch et al. (2004) record the following proportions of prey in the diet of mesopelagic fish near the South Shetland Islands (Table 9). We assume that the spatial mismatch between myctophids and *Euphausia crystallorophias* in the study region is complete so that this not a possible prey item and is not shown. An estimate of the average proportions of diet items are weighed by the relative proportions of each species in the environment to give: mesozooplankton 18%, *E. superba* 69%, other macrozooplankton 12%, other pelagic fish 0.5% (which is assumed to be negligible).

Table 9. Diet composition of four common mesopelagic species (% by weight)

Food compartment	<i>Electrona antarctica</i>	<i>Gymnoscopelus braueri</i>	<i>Gymnoscopelus nicholsi</i>	<i>Protomyctophum bolini</i>
Number fish sampled	9931	2253	647	3212
Mesozooplankton (% W)	1	1	5	87
<i>E. superba</i> (% W)	85	75	79.9	13

Other macrozooplankton (%W)	14	24	1	0
Other pelagic fish (%W)	0	0	14	0

7.2.5 Production

Production was estimated in three ways. First, data for *Electrona antarctica* given by Greely et al. (1999) are consistent with a mortality rate of about 0.65 y^{-1} for the population which is not unreasonable. Such a population has an average production (growth) equivalent to 1.14 y^{-1} . Second and third, annual production/biomass ratios for fish of different sizes can be calculated from the equations given by Banse & Mosher (1980), or Haedrich & Merrett (1992). These give P/B for myctophids of 1.7 y^{-1} and 1.6 y^{-1} . As these equations were not developed for Antarctic fish, it is likely that they are too high, and the value of 1.1 y^{-1} will be used. For comparison, this is consistent with P/B values for other myctophids (e.g. P/B=1.15 for *Maurollicus muelleri*, Ikeda (1994); P/B between 0.87–1.38 for mesopelagic fishes, Childress et al. 1980).

7.2.6 Consumption

We estimate consumption in three ways. First, a typical unassimilated consumption for carnivorous fish of 0.27 (Brett & Groves 1979) was suggested as being appropriate for *E. antarctica* (Greely et al. 1999). Greely et al. (1999) estimate an annual metabolic energy expenditure of 7.69 kcal/y for an *E. antarctica* of length 68 mm. They suggest also using a heat increment (specific dynamic effect) value of 4.64 kcal/y to account for energy used during digestion and metabolic transformation of foodstuffs. Assuming a fish energy density of 0.95 kcal/gWW (Croxall et al. 1985), this suggests a respiration ratio of $R/B=3.2 \text{ y}^{-1}$. For comparison, oxygen consumption normalised to wet weight is known for a number of mesopelagic fish (Torres & Somero 1988) and ranges from $0.16\text{--}0.42 \mu\text{l O}_2 \text{ mg}^{-1} \text{ WW h}^{-1}$. These are equivalent to R/B of $5.8\text{--}15.3 \text{ y}^{-1}$ assuming a respiration quotient of 0.85. We use an average of the mean value from Torres & Somero (1988) and that based on Greely et al. (1999) to give an R/B values of 6.9 y^{-1} . This allows us to estimate a consumption rate of $Q/B=11.0 \text{ y}^{-1}$ based on P/B values above. Second, if we assume a daily ration of 2.4–2.5% body mass per day (Pusch et al. 2004; Greely et al. 1999; Brett & Groves 1979) then annual consumption rate might be $Q/B=9.0 \text{ y}^{-1}$. Third, the methods of Palomares & Pauly (1989, 1998) were used to estimate fish consumption/biomass based on the fish asymptotic weight, water temperature, diet (carnivore, herbivore, omnivore), and aspect ratio of the caudal fin. Aspect ratios of the caudal fin for a number of species of myctophids were calculated from the photographs given by Fishbase (Froese & Pauly 2009): 2.2 *Electrona antarctica*, 2.2 *Gymnoscopelus braueri*, 2.6 *Gymnoscopelus nicholsi*, 2.0 *Gymnoscopelus opisthopterus*, 2.2 *Krefflichthys anderssoni*, 3.7 *Nannobranchium achirus*, and 2.0 *Protomyctophum bolini*. The value for *Electrona antarctica* is close the average of these (2.2 compared to 2.4). We assume a subsurface water temperature of approximately 2°C . These values lead to estimates of Q/B of $6.2\text{--}7.9 \text{ y}^{-1}$. We use here an average value for consumption by myctophids on the Ross Sea slope of these three methods 9.0 y^{-1} .

For comparison, Bradford-Grieve et al. (2003) suggests $Q/B=16 \text{ y}^{-1}$ for subantarctic mesopelagic fish. Q/B values have been estimated to be $10.6\text{--}16.7 \text{ y}^{-1}$ for *Maurollicus muelleri*. Pakhomov et al. (1996) estimated similar Q/B for subantarctic myctophid species. The calculated low value of Q/B calculated here compared to these mesopelagic fish may be due a combination of low water temperatures in the Ross Sea and short primary production season compared to lower latitude waters. Our estimates of P/B and Q/B lead to $P/Q=0.13$.

8 Summary of parameters for fish

Summaries of the parameters used in the model are given in Table 10 and Table 11. Values of diets of individual groups were combined in proportion to estimated consumptions (based on total consumption $Q=B.[Q/B]$) to give diets for the model compartments (Table 12).

Table 10. Summary for model parameters for fish groups. “All” indicates the parameters used for the entire trophic compartment, obtained by combining the data from the constituent groups in proportion to biomass. * This group is used to calculate transfers (T^g) between groups, and is not used to obtain total biomass or other parameters for the small demersal fish group. NA=not estimated.

Compartment	Group	B (gC m ⁻²)	P/B (y ⁻¹)	Q/B (y ⁻¹)	P/Q	U	T^g	Biomass tWW	Indiv'l weight gWW
Large demersal fish	All	0.0095	0.12	1.1	0.11	0.27	0	60 199	29 400
Medium demersal fish	Medium demersal	0.0082	0.23	1.9	0.12	0.27	0	519 65	1163
	Medium toothfish	0.0014	0.26	1.7	0.15	0.27	0.58	9174	3800
	All	0.0096	0.24	1.9	0.13	0.27	0.10	61 138	1559
Small demersal fish	Small true demersal	0.0885	0.48	4.2	0.11	0.27	0	563 734	105
	Cryopelagic	0.0051	0.82	6.3	0.13	0.27	0	32 687	34
	Small "Medium demersal"*	0.0019	0.33	3.1	0.10	0.27	0.58	12 384	100
	All	0.0936	0.50	4.3	0.12	0.27	0.01	596 421	101
Antarctic silverfish	Adult silverfish	0.0314	0.63	3.8	0.17	0.27	0	200 000	22
	Juvenile silverfish	0.0312	2.1	13.7	0.15	0.27	NA	198 693	0.3
	All silverfish	0.0626	1.4	8.7	0.15	0.27	0	398 693	11
Pelagic fish	Myctophids	0.0302	1.1	9.0	0.13	0.27	0	192 558	4.0
	Juvenile non-silverfish	0.0098	2.1	13.7	0.15	0.27	0.58	62 352	0.3
	All	0.0400	1.4	10.1	0.14	0.27	0.22	254 910	3.1

Table 11. Diets of the fish groups as described in the text. Q/Q_{total} is the proportion of the overall consumption of the model group due to the individual groups of species considered in the text. These are combined to give diets given in Table 12.

		Predators							
Predator group		Pelagic		Silverfish		Small demersal fishes		Medium demersal fishes	
Prey		Mycto-phids	Juvenile non-silverfish	Juvenile silverfish	Adult silverfish	Small demersal	Cryopelagic fishes	Medium demersal fishes	Medium toothfish
	Q/Q_{total} (%)	67.0	33.0	78.1	21.9	92.0	8.0	86.3	13.7
14	Small demersal fish					0.07		0.21	0.44
15	Antarctic silverfish				0.09	0.07	0.05	0.15	0.20
16	Pelagic fishes				0.01	0.02	0.05	0.05	0.10
17	Cephalopods					0.05		0.05	0.20
18	<i>E. crystallophias</i>		0.03	0.06	0.40	0.02	0.35	0.05	
19	<i>E. superba</i>	0.69	0.02			0.02	0.15	0.12	
20	Other macrozoo	0.12	0.02	0.03	0.12	0.04	0.10	0.05	0.05
21	Mesozooplankton	0.18	0.91	0.90	0.30	0.16	0.15		
25	Ice metazoa		0.02	0.01			0.15		
28	Megabenthos				0.03	0.25		0.07	
29	Macrobenthos				0.05	0.28		0.23	
30	Carcasses					0.02		0.02	0.01

TOTAL	1	1	1	1	1	1	1	1
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Table 12. Diets of the fish groups as described in the text.

	Prey	Predators				
		Large demersal fishes	Medium demersal fishes	Small demersal fishes	Antarctic silverfish	Pelagic fishes
14	Medium demersal fish	0.15				
15	Small demersal fish	0.70	0.24	0.06		
16	Antarctic silverfish		0.16	0.07	0.02	
17	Pelagic fishes	0.01	0.06	0.02	0.00	
18	Cephalopods	0.13	0.07	0.05		
19	<i>E. crystallorophias</i>		0.04	0.05	0.13	0.01
20	<i>E. superba</i>		0.10	0.03		0.47
21	Other macrozoo		0.05	0.04	0.05	0.09
22	Mesozooplankton			0.16	0.77	0.42
26	Ice metazoa			0.01	0.008	0.01
29	Megabenthos		0.06	0.23	0.01	
30	Macrobenthos		0.20	0.26	0.01	
35	Carcasses	0.01	0.02	0.02		
	TOTAL	1	1	1	1	1

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