Seals: Trophic modelling of the Ross Sea

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1 Biomass, natural history and diets

Seals are the most common marine mammals in the Ross Sea (Ainley 1985). Given that some species of seal are known to predate on and/or compete with toothfish, it is possible that they will be affected significantly by the toothfish fishery (e.g. Ponganis & Stockard 2007). Five species of seal have been recorded in the Ross Sea, (in order of abundance): crabeater seal (*Lobodon carcinophagus*), Weddell seal (*Leptonychotes weddelli*), leopard seal (*Hydrurga leptonyx*), Ross seal (*Ommatophoca rossi*), and southern elephant seal (*Mirounga leonina*). All seals in the Ross Sea are phocids, or true seals/earless seals. The distribution of seals in the Ross Sea varies seasonally in response to the annual cycle of sea ice formation and melting. Nevertheless, seal breeding and foraging locations vary with species: e.g., the Weddell seal breeds on fast ice near the coast, whereas the crabeater and leopard seals are more common in unconsolidated pack ice.

Seal abundance is estimated from the data of Ainley (1985) for an area bounded by the continental slope which more or less corresponds with our model area although there are more recent estimates for more limited areas (e.g. Cameron & Siniff 2004). Abundances are converted to wet weights using information on body size, and thence to organic carbon using measurements of the body composition of Antarctic seals (e.g. Arnould et al. 1996). This work, conducted on Antarctic fur seals, shows that ash-free dry weight is approximately 35% of wet-weight. If ash-free dry weight were composed of material in approximately carbohydrate proportions ($C_6H_{12}O_6$), we would expect 0.15 gC/gww. This should be compared to 0.10 gC/gww for fish (Vinogradov 1953). Throughout this chapter, we assume that the carbon:wet weight ratio for seals in the Ross Sea is 0.15 gC/gww. Data for each species is summarised in Table 1.

Annual average biomass for each seal species were calculated from estimates of summer numbers, adjusted by the period of time over which the populations are present in the Ross Sea per year. Where not described in the text, much of the information regarding marine mammals comes from systematic counts of animals at sea (e.g., Bassett & Wilson 1983; Ainley 1985) and demographic studies at specific breeding areas (e.g., Siniff et al. 1980; Testa & Siniff 1987; Schreer & Testa 1992). A basic review of mammalian species in the Ross Sea was taken from Bradford-Grieve & Fenwick (2001).

1.1 Crabeater seals

Crabeater seals (*Lobodon carcinophagus*) almost exclusively occur in Antarctic pack ice south of 79°S, although a very few reach subantarctic islands as far north as New Zealand and the southern coasts of Africa, Australia, and South America (Kooyman 1981a). In the Ross Sea, they can be found as far south as McMurdo Sound and along the coast during summer (Oritsland 1970), but are more frequently found within heavy, unconsolidated pack ice, particularly over the Antarctic Slope Front in the northern Ross Sea (Ainley 1985). Crabeater seals are considered to be the most abundant seal species and one of the most numerous large mammals on earth. The recent Ross Sea crabeater population is estimated to be about 204 000 individuals, estimated indirectly from ship-board observations (Ainley 1985, Table 4), and reside in the study area for about 3 months of the year over the summer. Adults reach 2.6 m in length and the mean weight is estimated to be 295 (180–410) kg (Trites & Pauly 1998). Females are slightly larger than males (Shirihai 2002; Laws et al. 2003). Crabeater seal neonates are at least 1.1 m and about 36 (20–40) kg in weight.

Because of their shy behaviour and difficult habitat, relatively little is known of their biology (Kooyman 1981a). Mating and birth are likely to occur at sea or on unconsolidated pack ice (Shirihai 2002). Breeding occurs around January. Pupping occurs in September–October. Mortality is high in the first year and may reach 80%. Much of this mortality is attributed to leopard seal predation as most crabeaters that survive through their first year have injuries and scars from leopard seal attacks. Leopard seal attacks appear to fall off dramatically after crabeaters reach one year of age. Sexual maturity is reached in 2.5-6 years, with females reaching maturity before males. Approximately 80% of the female population are thought to breed annually (Shirihai 2002).

The crabeater seal dives to 20–30 m typically at night (Shirihai 2002) although in winter, at 67°S along the western Antarctic Peninsula, they foraged between 6 and 713 m (Burns et al. 2004). Crabeaters are specialist krill eaters (Oritsland 1977; Laws 1984; Ainley & DeMaster 1990). The main cusps of the upper and lower teeth fit together to sieve invertebrates from the water. In the Ross Sea, krill (*Euphausia crystallorophias* and *E. superba*) are likely to be consumed almost exclusively (>95%) with small amounts of fish and squid making up the remainder. Given that most crabeater seals in the Ross Sea are found over the continental slope (Ainley 1985), their consumption is likely to be mainly *E. superba* with some *E. crystallorophias*. Stable isotope work in the Ross Sea (Zhao et al. 2004) suggests that crabeater seals forage predominantly on the same prey type (*Euphausia sp.*) but in various locations around the Ross Sea. Here, we initially assume crabeater seal diet of: 35% *E. crystallorophias*; 45% *E. superba*; and 20% other macrozooplankton.

1.2 Weddell seal

Weddell seals (*Leptonychotes weddelli*) are widespread through the Southern Ocean and occur in large numbers on fast ice, right up to the Antarctic continent, and offshore in the pack ice zone north to the Antarctic Convergence (Kooyman 1981c). Weddell seals occur throughout the Ross Sea and breed along the coast of Victoria Land and Ross Island (Ainley 1985; Testa & Siniff 1987). Weddell seals in McMurdo Sound have been studied for over 30 years (e.g. Stirling 1969; Burns et al. 1998, 1999; Testa & Siniff 1987; Stewart et al. 2003). A relatively stable population of about 1500 animals occurs on the eastern side of McMurdo Sound (Testa & Siniff 1987), with about a further 500 animals on the western side of McMurdo Sound, mostly near the Strand Moraines and Blue Glacier (Ross et al. 1982). Weddell seals are the second-most common seal in the Ross Sea, with estimates ranging from 32,000 to 50,000 individuals (Stirling 1969; Ainley 1985; Stewart et al. 2003). These figures may underestimate the actual total because Stirling's (1969) estimate did not include animals that may occur in the vicinity of the King Edward VII Peninsula. Ainley (1985) conducted systematic censuses of marine mammals and birds during five cruises in the Ross Sea and estimated 0.054 individuals per km^2, implying 32,000 individuals in the Ross Sea area. Based on maps of the distribution of seals in Ainley (1985) we estimate that about 85% of this number will be feeding inside the study area in summer. Adult seals reach 2.6–3.0 m (males) and 2.6–3.3 m (females) in length, and weigh 300–600 kg (Harcourt 2001; Shirihai 2002). An average Weddell seal weight was estimated to be 160 kg by Trites & Pauly (1998) which seems low. Here, we use an average weight of 375 kg. Newborns are about 1.5 m long and average 24 (22–29) kg (Tedman & Green 1987; Shirihai 2002).

In the southern Ross Sea, Weddell seals form large colonies (several hundred animals) from late September, with pups born around October. Pups dive and swim within 2 weeks, and are weaned at 6 weeks. Mating occur around November–December. During this period (October to December), breeding adults and nursing pups remain inshore, and foraging effort is low (Testa et al 1985; Hill 1987; Burns & Kooyman 2001). Pups born in McMurdo Sound leave their natal areas by the end of February, moving north along the Antarctic continent coastline (Burns et al. 1999). It is unclear to what extent Weddell seals are migratory between breeding seasons. Some individuals remain in residence year round in the fast ice at latitudes as high as 78°S in McMurdo Sound, whereas others, particularly newly weaned and subadult animals, spend the winter in the pack ice to the north of the Ross Sea (Stewart et al. 2003). Satellite tracking of adult females from breeding colonies in McMurdo Sound showed that most remained in the northern part of the Sound during winter, although some travelled as far as 500 km north beyond the Sound (Testa 1994). All adult seals tracked from McMurdo Sound by Stewart et al. (2000) moved north after moulting and then spent the autumn, winter and early spring foraging in open-ocean and pack ice habitats over the broad continental shelf of the western Ross Sea. Although ice conditions, the availability of prey, and the abundance of predators such as leopard seals and killer whales, appear to determine where adults and young go when they disperse from the breeding colonies (Testa 1994), it seems likely that most Weddell seals breeding in the southern Ross Sea remain in the study area year round. Tagging experiments show that some pups born in McMurdo Sound return there within a year, while others stay more than 400 km distant for a number of years (Burns et al. 1999). After a number of years, fewer than 25% of pups born in Erebus Bay (in McMurdo Sound) have been observed recruiting into the breeding population there (Testa 1987; Hastings 1996). The low return rate may be because pups suffer high mortalities in their first few years of life, because pups tend to recruit into other colonies, or because studies are not long enough to observe pups returning to their natal areas (Burns et al 1999). Here, we assume that Weddell seals are present in the study region for 3 months of the year over the ice-free period around the summer.

There is a considerable literature on the feeding of Weddell seals, with a concentration of studies in McMurdo Sound (e.g. Ross et al. 1982; Laws 1984; Green & Burton 1987; Plotz et al. 1991; Testa 1994; Burns et al. 1998, 1999; Davis et al. 1999; Casaux et al. 2006). Weddell seals forage mainly in shelf waters, usually below ice. When ice cover is continuous, seals often congregate round breathing holes. Adult Weddell seals are reported to dive to depths up to 750 m, but <350 m is more common (Burns & Kooyman 2001). Pups have been measured diving to >400 m, but most dives are less than 80 m deep, with diving patterns indicating they are actively hunting prey which has a diel vertical migration (Burns et al. 1999). Almost all studies of Weddell seal diets throughout Antarctica suggest a dominance of fish in the diet (>90% by mass). Many studies report a preference for feeding on *P. antarcticum*, other pelagic nototheniids, and icefish (Channichthyidae), over demersal fishes, and fishes of the Myctophidae and Paralepididae families (e.g. Casaux et al. 2006). Feeding studies in the Ross Sea have identified the following prey items: (1) bentho-pelagic fish (mainly *Pleuragramma antarcticum*); (2) benthic fish (including *Trematomus* spp.); (3) Antarctic toothfish (*Dissostichus mawsoni*); (4) cryopelagic fish (*Pagothenia borchgrevinki*) (5) squid (*Histioteuthiid* sp., *Kondakovia longimana*, *Mastigoteuthiid* sp.); (6) crustacea (mainly decapods, Antarctic shrimps).

It is likely that the diet of Weddell seals in the Ross Sea is almost entirely fish, taken in the midwater over deeper bathymetry or near the bottom in shallower areas. There has been conflicting results from studies as the predominant species of fish in the diet of Weddell seals, and this may be due to the fact that the proportions of different fish will vary according to prey availability. Prey availability will depend on the individual seal (adult, juvenile, pup), season and location. There are relatively few direct measurements of Weddell seal diet in the winter or away from McMurdo Sound.

In McMurdo Sound, it is known that Antarctic silverfish (*Pleuragramma antarcticum*) often make up a significant proportion of the diet of Weddell seals (Castellini et al. 1992; Burns et al. 1998, 1999). Kooyman (1981c) reports that the diet of Weddell seals in McMurdo Sound is "almost entirely" fish, and especially *Dissostichus mawsoni*. However, using video cameras mounted on Weddell seals in McMurdo Sound, Fuiman et al. (2002) noted that seals always attacked schools of *P. antarcticum*, but only occasionally attacked *D. mawsoni*. There is evidence that yearling Weddell seals in McMurdo Sound are divided into two groups: those that feed close to the bottom in shallower water, and those that dive in the deep-water pelagic zone (Burns et al. 1998). Ross et al (1982) suggested that the significant increase in toothfish numbers in the McMurdo Sound area from October to mid-November may be the reason why so many Weddell seal breeding colonies are established there. However, Burns et al. (1999 and references therein) suggested that the significance of toothfish in the diet may have been overestimated, and concluded that pups in McMurdo Sound are likely to feed predominantly on *P. antarcticum* and small squid. Stable isotope analysis of blood samples show that Weddell seals occupy the highest trophic level of seals from the Ross Sea, and, interestingly, pups and juveniles tended to have slightly higher trophic levels than adults (Zhao et al. 2004), suggesting that the diet is not entirely *P. antarcticum*.

Recently, Pinkerton et al. (2008) and Ainley & Siniff (2008) summarised the available evidence on the Weddell seal-Antarctic toothfish trophic connections in the McMurdo Sound region. Pinkerton et al. (2008) concluded that:

- There is evidence that Antarctic toothfish have lower densities near to seal breeding colonies in McMurdo Sound than further away (Testa et al. 1985).
- Direct information on diet of the Weddell seals, including diver observations, animal-mounted camera information, and observations from field scientists in the McMurdo Sound region suggest that toothfish are a significant prey item for Weddell seals.
- In contrast, research using seal stomach contents, vomit and scats provides no evidence that Weddell seals consume toothfish at all. Diver observations suggest that seals may feed selectively on only parts of toothfish so that otoliths and vertebrae may be under-represented in remains.
- Indirect information using stable isotopes of carbon and nitrogen, even including recent analyses that have not been previously reported, remains inconclusive. Further research using stable isotope analysis of blood samples from seals not at the breeding colonies, and samples of muscle or other slower-turnover tissue of seals at the breeding colonies may be conclusive.
- Information from fatty acids or other biomarkers could potentially be used to investigate the importance of toothfish as a prey item for seals, but no results are available.
- Pinkerton et al. (2008) compared mortality of Antarctic toothfish in McMurdo Sound to consumption by Weddell seals. The estimates, although preliminary and subject to uncertainty, indicate that it is possible that toothfish comprise a substantial proportion of the diet of seals in McMurdo Sound between October and January.

Pinkerton et al. (2008) conclude that while there is strong evidence that toothfish are a prey item for Weddell seals in McMurdo Sound between October and January, it is plausible but unproven that they are an important prey item. Here, we assume a Weddell seal diet of 7% large demersal fishes; 2% medium demersal fishes; 25% small demersal fishes; 50% silverfish; 5% pelagic fishes; 9% cephalopods; 2% megabenthos.

1.3 Leopard seal

Leopard seals (*Hydrurga leptonyx*) are widely-distributed in Antarctic and Subantarctic waters of the Southern Hemisphere, from the coast of the continent north throughout the pack ice and at most Subantarctic islands (Kooyman 1981b). An estimated 8000 leopard seals inhabit the Ross Sea, with most occurring within pack- ice in frontal areas (Ainley 1985: Table 4). Most sightings made by Ainley (1985) were in the western Ross Sea, which supports the densest concentrations of Adélie penguins, a frequent prey species of the seals. Adult leopard seals are c. 3.3–3.8 m in length (Trites & Pauly 1998). Males weigh up to 400 kg. Adult females weigh 260 to upwards of 500 kg. Trites & Pauly (1998) give 460 kg as a mean weight which we use here. Pups weigh 30–35 kg at birth (Shirihai 2002).

Breeding is confined to pack ice areas in the spring, with pupping occurring in October–November on pack ice. Mating is believed to occur around December (Shirihai 2002), but has not been observed. Males become sexually mature at 3–6 years, and females at 2–7 years. Leopard seals are considered to be seasonal residents of Ross Sea pack ice (Stewart et al. 2003), leaving the study region for islands to the north of the study area in winter (Oritsland 1970). There was high interannual variability in the numbers of leopard seals seen ashore in the Ross Sea. Most of the leopard seals hauling out at Bird Island were not sexually mature (<4 years old; Walker et al. 1998). Gilbert & Erickson (1977) suggested that northward dispersal of non-breeding leopard seals in winter may occur in relation to food availability related to the northward encroachment of sea ice. Rogers & Bryden (1997) suggested that competition for space could influence the dispersion. In this study, we assume that half of the Ross Sea population of leopard seals is resident in the study region year round (mature adults). The remainder, which includes the majority of younger seals, are assumed to remain in the study region for 3 months of the year, and disperse northwards outside the summer.

The diet of leopard seals is varied and changes with season and location (Knox 2007, and references therein). Leopard seals are thought to forage relatively shallowly (<100 m), and consume krill, fish, squid, penguins (especially Adelie penguins), a variety of other types of seabirds, and seals, including crabeater seals, (small) southern elephant seals, and fur seals where present (Penney & Lowry 1967; Siniff & Stone 1985; Knox 2007; Walker et al. 1998; Hall-Aspland & Rogers 2004, 2007). In Prydz Bay, leopard seals preyed on penguins, fish and seals in late spring, mainly Adelie penguins in summer (>85% by frequency of occurrence in scats), and fish during winter (Hall-Aspland & Rogers 2004 and references therein). Leopard seals may dive too shallowly to take substantial quantities of krill in the winter (Kuhn et al. 2006). Leopard seals will also occasionally scavenge from carcasses of whales. Fish in the diets off Prydz Bay were largely unidentified, but tended to be small (<100g) benthic, inshore species including *Pagothenia borchgrevinki* and *Trematomus hansoni* (Hall-Aspland & Rogers 2004). Researchers from New Zealand have also observed a leopard seal catch and consume a large Weddell seal off Bird Island in the Ross Sea (Ainley pers. com.) but this probably unusual. Hairs found in scats of leopard seals suggest that crabeater seals were the most common seal prey taken (Hall-Aspland & Rogers 2007). It is interesting that only a portion of seals (skin and blubber), and no bones, were found in scats (Hall-Aspland & Rogers 2004).

Here, we propose to use a starting diet of leopard seals in the model of: 1% Emperor penguins, 5% Adélie penguins, 5% crabeater seals; 16% medium demersal fishes; 15% small demersal fishes; 22% silverfish; 5% pelagic fishes; 5% cephalopods; 3% *E. crystallorophias*, 5% *E. superba*; 3% other macrozooplankton; 5% megabenthos; and 10% carcasses.

1.4 Ross seal

The Ross seal (*Ommatophoca rossi*) is the smallest, least frequently sighted and least known of the Antarctic pinnipeds (Ray 1981; Southwell 2005). Ross seals are exclusively Antarctic species, being rarely reported north of the Antarctic Circle (Shirihai 2002). They have a circumpolar distribution and are usually found in dense consolidated pack ice, but can also be found on smooth ice floes in more open areas. Ainley (1985) concluded that Ross seals are irregularly distributed with high concentrations in localised areas, and that the Ross Sea is apparently not an area where this species concentrates. An estimated 5000 Ross seals occur in the Ross Sea (Ainley 1985: Table 4). Ross seals appear to occur in very low densities throughout the loose pack ice of the outer Ross Sea (Ainley 1985), with tagging efforts revealing that they migrate north out of the pack ice zone into open water for extended periods of time to forage. We assume the Ross Sea population is resident in the study region for 3 months a year.

Little is known about the biology of the species, apart from observations made from ships and the examination of dead animals. Females are reported as being slightly larger than males. Based on a small sample of measured animals, Ross seals reach at least 2.4 m and have an estimated population weight of 150 kg (Trites & Pauly 1998) or 180 kg (Shirihai 2002), and we use the latter. It is estimated that pups are about 1 m and 16 kg at birth. Pupping occurs in November–December, with mating in late December–early January on pack ice, and moulting in February (Blix & Nordøy 2007). Ross seals are thought to reach sexual maturity at age 3 years.

The diet of the Ross seal is poorly known (Knox 2007). The Ross seal may be a relatively deep diver, with dives of 80–300 m (typically about 100 m) (Bengtson & Stewart 1997; Blix & Nordøy 2007). Mid-water squid (mainly *Psychoteuthis glacialis* and *Alluroteuthis antarcticus*), and mid-water fish (*Pleuragramma antarcticum*) appear to be the main part of their diet (Oritsland 1977; Skinner & Klages 1994; Knox 2007; Bengsten & Stewart 1997), but they may also take krill. Patterns of diving suggest that Ross seals pursue vertically migrating prey (Bengsten & Stewart 1997). Based on data given by Knox (2007), we assume the diet of Ross seals in the Ross Sea is 2% medium demersal fishes; 5% small demersal fishes; 10% silverfish; 13% pelagic fishes; 35% cephalopods; 10% *E. crystallorophias*; 15% *E. superba*; 10% other macrozooplankton.

1.5 Southern elephant seal

Southern elephant seals (*Mirounga leonina*) have a nearly circumpolar distribution in the Southern Hemisphere it enters the Ross Sea only in the summer from breeding and feeding grounds further to the north. The southern elephant seal is consequently the least common seal in the Ross Sea. It is estimated that there are 40 animals present in the study area for the three summer months (Brownell & Ainley 1976; Ainley 1985: Table 4) and no southern elephant seals in the Ross Sea outside the summer period. This is too small to be considered further in this trophic model.

2 Estimation of parameters for the trophic model

2.1 Consumption and diet

We estimated food consumption requirements for each species of seal were estimated by three methods, using an average of all three methods as our best estimate.

Method 1. Nagy (1987) estimated daily dry weight food consumption for eutherian mammals (with placenta) according to body weight as Q_d=0.235$W^{0.822}$, where Q_d is the daily consumption in g dry weight; *W* is the animal weight (g). An estimate of oxygen consumption of a southern elephant seal by Hindell & Lea (1998) suggested that Nagy's (1994) equation may overestimate field metabolic rate. However, this result is still uncertain, and so we retain this method as a valid estimate.

Method 2. In the second method we used the relation between animal weight and daily consumption developed by Innes et al. (1987). For toothed whales: $Q=0.258 \cdot W^{0.69}$, where Q is daily consumption kg/d or WW prey, and *W* is the animal wet weight in kg. For "other marine mammals", which we apply to seals, $Q=0.123 \cdot W^{0.80}$ (symbols as above). These relationships give mean consumption rates and were based on a compilation of published data for captive and wild marine mammals. There is conflicting evidence on whether the food requirements of Antarctic mammals is significantly greater than that of terrestrial mammals of a similar size (e.g., Riedman 1990, and references therein). Some studies have shown metabolic rates for polar mammals to be 1.5–3 times higher than terrestrial mammals in more temperate regions (e.g., Costa et al. 1986). Other work found that metabolic rates of polar mammals were only slightly higher (1.1–1.2 times) than those of a terrestrial mammal of similar size (see Riedman 1990). The relationships of Innes et al. (1987) give values similar to consumption rates for terrestrial mammals of the same size so we increase the values given by the relationship of Innes et al. (1987) by a factor 2 for Antarctic pinnipeds.

Method 3. Here, we use an estimate of standard (or basal) metabolic rate from Lockyer (1981a): SMR=$70.5 \cdot W^{0.7325}$, where SMR is the resting or basal rate of animals (kcal/d) and *W* the animal weight (kgWW). This results in basal metabolic rates 11–19% lower than those given by SMR=$70 \cdot W^{0.75}$ (Kleiber 1975; Lavigne et al. 1986). The average daily energy expenditure of animals will be higher than the SMR, especially if the animals are undergoing exertion such as swimming long distances (Lockyer 1981a). The active metabolism is estimated to be about 2–5 times SMR (Kenney et al. 1997 and references therein), and we use an average of these of 3.5. We use assimilation efficiencies for pinnipeds of 80% (Bradford-Grieve et al. 2003).

Conversion factors between energy, carbon, dry- and wet-weights vary between studies and with species. For fish, 0.95–1.3 kcal/gWW is reported (Steimle & Terranova 1985; Croxall et al. 1985; van Franeker et al. 1997). For crustaceans, 0.93–1.1 kcal/gWW is reported (Lockyer 1981a; Croxall et al. 1985). We used weight conversion factors of 0.108 gC/gWW (fish: Schneider & Hunt 1982) and 0.030–0.055 gC/gWW (zooplankton: Weibe 1988; Ikeda & Kirkwood 1989). We use these to estimate 10.2 kcal/gC (fish) and 18.3 kcal/gC (crustaceans). These were combined according to the estimated diets of the individual species of seal. Dry weight of prey items was converted to carbon using a ratio of 0.4 gC/gWW (Vinogradov 1953; Curl 1962).

These three methods differed by 24% on average, with method 1 giving the highest estimate of consumption, and method 3 the lowest. An average of these three estimates gave values of Q/B between 23.4–33.1 y^{-1} for the 4 species of pinnipeds. Values are given in Table 1. For comparison, other work reports daily food intake for captive seals as 10% of body weight (Laws 1984), and 3.3% for harp seals (Nordoy et al. 1995). These imply Q/B values of between 12–37 y^{-1}, assuming seals and their prey have approximately the same carbon to wet weight ratio which is reasonable for fish-eaters. Jarre-Tiechmann et al. (1998) estimate that Cape fur seals have a Q/B ratio of 19 y^{-1}. Pinniped energetics have been reviewed by Lavigne et al. (1982, 1986), and a summary is given by Knox (2007). For an adult crabeater seal, they estimate an annual average Q/B of 28 y^{-1}, compared to our estimate of 23.4 y^{-1} using an average of the three methods described above. Bradford-Grieve et al. (2003) used Q/B=46 y^{-1} for New Zealand fur seals which may be high.

2.2 Production

We estimated production rates of Antarctic seals as the average of two methods given below.

Method 1

In this method, we use estimates of survival rates to give production. It is assumed that the weight and number of seals populations does not change significantly from year to year. In this case, the annual production (the biomass that is available for transfer out of the trophic compartment) may be estimated to be made up of two parts: (1) seal pups surviving to adulthood that replace loss due to adult mortality; (2) pups dying before reaching adulthood. The average weight of a pup dying before reaching adult size is taken as the geometric average of the birth weight and adult weight. This implicitly assumes a constant mortality rate with age and a linear growth rate. A declining mortality rate with age, and a decreasing growth rate with age, will tend to act to cancel each other out, so that this assumption is reasonable as a first approximation. We estimate values of 60% seals breed each year, one young per pair per year, and a pup survival rate to adulthood of 0.2. This leads to P/B values of 0.12–0.15 y^{-1}.

Method 2

The second method followed Banse & Mosher (1980) who related production to animal biomass as: $P/B=12.9 \cdot M_s^{-0.33}$ where M_s is the animal weight expressed as an energy equivalent (kcal), and P/B is the annual value (y^{-1}). Mammals are likely to have a higher energy content than fish (c. 1 kcal/gWW: Schindler et al. 1993) as a result of their fat-rich blubber. Although the biochemical analysis of blubber of mammals varies, 60% lipid is likely (Koopman 2007) implying an energy content of about 9 kcal/g. Assuming such high-lipid tissues make up about 40% of the seals's body weight, we estimate a total energy density for whales of 4.2 kcal/g. This method gives P/B values between 0.11–0.15 y^{-1}, about 8% on average different from values by the first method.

Here, we an average of the P/B values estimated by the two methods. For comparison, P/B values for Antarctic seals is given as 0.22 y^{-1} (Laws 1984, Table VIII) assuming mortality equals production in a stable population. Jarre-Tiechmann et al. (1998) estimated that Cape fur seals had a P/B ratio of 0.95 y^{-1} although this seems high.

2.3 Export

Given that all four species of seal discussed are likely to breed in the Ross Sea study area, and that a large proportion of the juveniles and adults will probably move out of the region after breeding to areas of less consolidated sea ice, there will be an export of biomass from the study region each year at the end of the breeding season. This export will be offset by the breeding adults moving back into the study area to breed the following year. Breeders entering the study area are likely to be heavier on average than those leaving the study area after breeding, suggesting a net import of biomass over a year. However, high mortality of juveniles between leaving the study region for the first time and re-entry as a breeding adult tends to lead to a net export of biomass. The required data is generally not available to estimate the net import/export of biomass for seals on a species by species basis and here we estimate it to be 25% of annual production.

2.4 Ecotrophic efficiency

Ecotrophic efficiencies (*E*) are not known for seals in the Ross Sea. Where seals are known to suffer direct predators in the study area (crabeater seals, Weddell seals), ecotrophic efficiencies are set so that a nominal half the mortality is due to direct predation and half due to non-predation mortality (starvation, disease etc). Where little direct predation in the study area is likely or it is not known whether this occurs, (leopard seals, Ross seals), all mortality is assumed to be non-predation and ecotrophic efficiency calculated accordingly. Biomass associated with non-predation mortality is channeled to the carcass group in the model.

2.5 Unassimilated consumption

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

3 Summary of model parameters for seals

A summary of the parameters used by the model for seals is given in Table 1 and Table 2.

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Table 1. Summary of trophic information on mammals in the Ross Sea.

Compartment	Scientific name	Weight (kg)	No. in summer in Ross Sea	Time (months)	B (tonnes)	B (gC m^{-2})	P/B (y^{-1})	Q/B (y^{-1})
Crabeater seal	*Lobodon carcinophagus*	295	204,000	3	15045	2.36E-03	0.13	23.4
Weddell seal	*Leptonychotes weddelli*	375	27,200	3	2550	4.00E-04	0.12	28.5
Leopard seal	*Hydrurga leptonyx*	464	8000	3	928	1.46E-04	0.11	23.4
Ross seal	*Ommatophoca rossi*	180	5000	3	224	3.52E-05	0.15	33.1

Table 2. Summary of diet information seals in the Ross Sea.

	Predators (proportion in diet)			
Prey	**Crabeater seal**	**Weddell seal**	**Leopard seal**	**Ross seal**
Emperor penguins			0.01	
Adelie penguins			0.05	
Crabeater seals			0.05	
Large demersal fishes		0.07		
Medium demersal fishes		0.02	0.16	0.02
Small demersal fishes		0.25	0.15	0.05
Antarctic silverfish		0.50	0.22	0.10
Pelagic fishes		0.05	0.05	0.13
Cephalopods		0.09	0.05	0.35
Euphausia crystallorophias	0.35		0.03	0.10
Euphausia superba	0.45		0.05	0.15
Other macrozooplankton	0.20		0.03	0.10
Megabenthos		0.02	0.05	
Carcasses			0.10	
Total	1	1	1	1

5 References

Ainley, D.G. 1985. Biomass of birds and mammals in the Ross Sea. *In*: Siegfried, W.R.; Condy, P.R.; Laws, R.M. (eds) *Antarctic nutrient cycles and food webs.* Berlin, Springer-Verlag. Pp. 498-515.

Ainley, D.G.; DeMaster, D.P. 1990. The upper trophic levels in polar marine ecosystems. *In*: Smith W.O. (ed.) Polar oceanography, Part B, chemistry, biology, and geology. Academic, San Diego, pp. 599-630.

Ainley, D.; Siniff, D. 2008. Addressing uncertainty over the importance of Antarctic toothfish as prey of seals and whales in the southern Ross Sea: a review. *CCAMLR document WG-EMM-08/22*, CCAMLR, Hobart, Australia.

Ainley, D.; Siniff, D.; Garrott, R.; Wilson, P. 2007. Protocol for censusing of Weddell seals as a EMM protocol. Unpublished CCAMLR document, WG-EMM 07/13, 5pp.

Arnould, J.P.Y.; Boyd, I.L.; Speakman, J.R. 1996. Measuring the body composition of Antarctic fur seals (*Arctocephalus gazella*): validation of hydrogen isotope dilution. *Physiological Zoology* 69: 93-116.

Banse, K.; Mosher, S. 1980. Adult body size and annual production/ biomass relationships of field populations. *Ecological Monographs* 50: 355-379.

Bassett, J.A.; Wilson, G.J. 1983. Birds and mammals observed from the M.V. Benjamin Bowring during the New Zealand-Ross Sea cruise January/February 1981. *Transglobe Expedition Scientific Report No. 3*.

Bengtson, J.L; Stewart, B.S. 1997. Diving patterns of a Ross seal (*Ommatophoca rossii*) near the eastern coast of the Antarctic Peninsula. *Polar Biology* 18: 214-218.

Blix, A.S.; Nordøy, E.S. 2007. Ross seal (*Ommatophoca rossii*) annual distribution, diving behaviour, breeding and moulting, off Queen Maud Land, Antarctica. *Polar Biology* 30: 1449-1458.

Bradford-Grieve, J.; Fenwick, G. 2001. *A review of the current knowledge describing the biodiversity of the Ross Sea*. Final research report for Ministry of Fisheries, Research Project ZBD2000/01 Objective 1 (in part). 93 pp.

Bradford-Grieve, J.M.; Probert, P.K.; Nodder, S.D.; Thompson, D.; Hall, J.; Hanchet, S.; Boyd, P.; Zeldis, J.; Baker, A.N.; Best, H.A.; Broekhuizen, N.; Childerhouse, S.; Clark, M.; Hadfield, M.; Safi, K.; Wilkinson, I. 2003. Pilot trophic model for subantarctic water over the Southern Plateau, New Zealand: a low biomass, high transfer efficiency system. *Journal of Experimental Marine Biology and Ecology* 289: 223-262.

Brownell, R.L. Jr.; Ainley, D.G. 1976. Southern elephant seals in the Ross Sea. *Antarctic Journal of the United States* 11: 189-190.

Burns, J.M.; Kooyman, G.L. 2001. Habitat use by Weddell seals and emperor penguins foraging in the Ross Sea, Antarctica. *American Zoologist* 41:90-98.

Burns, J.M.; Castellini, M.A.; Testa, J.W. 1999. Movements and diving behaviour of weaned Weddell seal (*Leptonychotes weddellii*) pups. *Polar Biology* 21: 23-36.

Burns, J.M.; Costa, D.P.; Fedak, M.A.; Hindell, M.A.; Bradshaw, C.J.A.; Gales, N.J.; McDonald, B.; Trumble, S.J.; Crocker, D.E. 2004. Winter habitat use and foraging behaviour of crabeater seals along the western Antarctic Peninsula. *Deep-Sea Research II* 51: 2279-2303.

Burns, J.M.; Trumble, S.J.; Castellini, M.A.; Testa, J.W. 1998. The diet of Weddell seals in McMurdo Sound, Antarctica as determined from scat collections and stable isotope analysis. *Polar Biology* 19(4): 264-282.

Cameron, M.F.; Siniff, D.B. 2004. Age-specific survival, abundance, and immigration rates of a Weddell seal (*Leptonychotes weddellii*) population in McMurdo Sound, Antarctica. *Canadian Journal of Zoology* 82: 601-615.

Casaux, R.; Baroni, A.; Ramon, A. 2006. The diet of Weddell sea *Leptonychotes weddelli* at the Danco Coast, Antarctic Peninsula. *Polar Biology* 29: 257-262.

Castellini, M.A.; Davis, R.W.; Kooyman, G.L. 1992. Annual cycles of diving behavior and ecology of the Weddell seal. *Bulletin of the Scripps Institution of Oceanography* 28: 1-54.

Costa, D.P; LeBoeuf, B.J.; Ortiz, C.I.; Huntley, D.C.A. 1986. Energetics of lactation in the northern elephant seal, *Mirounga angustirostris*. *Journal of Zoology* 209: 21–33.
Croxall, J.P. 1987. Seabirds: feeding ecology and role in marine ecosystems. Cambridge University Press, pp 408.
Croxall J.P.; Prince, P.A.; Ricketts, C. 1985. Relationships between prey life-cycles and the extent, nature and timing of seal and seabird predation in the Scotia Sea. In: Siegfried, W.R., Condy, P.R., Laws, R.M. (eds) Antarctic nutrient cycles and food webs. Springer, Berlin Heidelberg New York, pp 516-533.
Curl, H.S. 1962. Analyses of carbon in marine plankton organisms. *Journal of Marine Research* 20:181–188.
Davis, R.W.; Fuiman, L.A.; Williams, T.M.; Collier, S.O.; Hagey, W.P.; Kanatous, S.B.; Kohin, S.; Horning, M. 1999. Hunting behavior of a marine mammal beneath the Antarctic fast-ice. *Science* 283: 993-996.
Fuiman, L.A.; Davis, R.W.; Williams, T.M. 2002. Behavior of midwater fishes under the Antarctic ice: observations by a predator. *Marine Biology* 140: 815-822.
Gilbert, J.R.; Erickson, A.W. 1977. Distribution and abundance of seals in the pack ice of the Pacific sector of the Southern Ocean. In: Llano, G.A. (Ed.). Adaptations within Antarctic ecosystems. Houston: Gulf Publishers. pp. 703–740.
Green K.; Burton, H. 1987. Seasonal and geographical variation in the food of Weddell seals *Leptonychotes weddellii* in Antarctica. *Australian Wildlife Research* 14: 475-489.
Hall-Aspland, S.; Rogers, T. 2004. Summer diet of leopard seals (*Hydrurga leptonyx*) in Prydz Bay, Eastern Antarctica. *Polar Biology* 27: 729-734.
Hall-Aspland, S.; Rogers, T. 2007. Identification of hairs found in leopard seal (*Hydrurga leptonyx*) scats. *Polar Biology* 30: 581-585.
Harcourt, R.G. 2001. Advances in New Zealand mammalogy 1990-2000: pinnipeds. *Journal of the Royal Society of New Zealand* 31(1): 135-160.
Hastings, K.K. 1996. Juvenile survival and maternal strategies of Weddell seals in McMurdo Sound, Antarctica. M.S. Thesis. University of Alaska, Fairbanks.
Hill, S.E.B. 1987. Reproductive ecology of Weddell seals (*Leptonychotes weddelli*) in McMurdo Sound, Antarctica. Ph.D. Thesis. University of Minnesota, Minneapolis
Hindell, M.A.; Lea, M.-A. 1998. Heart rate, swimming speed, and estimated oxygen consumption of a free-ranging southern elephant seal. *Physiological Journal* 71: 74-84.
Ikeda, T.; Kirkwood, R. 1989. Metabolism and body composition of two euphausiids (*Euphausia superba* and *E. crystallorophias*) collected from under the pack-ice off Enderby Land, Antarctica. *Marine Biology* 100: 301-308.
Innes, S.; Lavigne, D.M.; Kovacs, K.M. 1987. Feeding rates of seals and whales. *Journal of Animal Ecology* 56: 115-130.
Innes, S.; Lavigne, D.M.; Earle, W.M.; Kovacs, K.M. 1986. Estimating feeding rates of marine mammals from heart mass to body mass ratios. *Marine Mammal Science* 2: 227-229.
Irving L. 1970. Morpho-physiological adaptations in marine mammals for life in polar areas. *In:* M.W. Holdgate (ed.), *Antactic Ecology. Vol. 1*. Academic Press, London, pp. 455–463.
Jarre-Teichmann, A.; Shannon, L.J.; Moloney, C.L.; Wickens, P.A. 1998. Comparing trophic flows in the southern Benguela to those in other upwelling ecosystems. *South African Journal of Marine Science* 19: 391-414.
Kenney, R.D., Scott, G.P., Thompson, T.J., Winn, H.E. 1997. Estimates of prey consumption and trophic impacts of cetaceans in the USA northeast continental shelf ecosystem. *Journal Northwest Atlantic Fisheries Sciences* 22: 155–171.
Kleiber, M. 1975. The Fire of Life: An Introduction to Animal Energetics. New York: Krieger Publishing.
Knox, G.A. 2007. Biology of the Southern Ocean. Boca Raton, CRC Press. 2nd edition, 621 pp.

Kooyman G.L. 1981a. Crabeater seal – *Lobodon carcinophagus*. *In*: Ridgway, S.H.; Harrison, R.J. (eds) *Handbook of Marine Mammals, Volume 2: seals.* Academic Press, London. Pp 221–236.

Kooyman G.L. 1981b. Leopard seal – *Hydrurga leptonyx*. *In*: Ridgway, S.H.; Harrison, R.J. (eds) *Handbook of Marine Mammals, Volume 2: seals.* Academic Press, London. Pp 261–274.

Kooyman G.L. 1981c. Weddell seal – *Leptonychotes weddelli*. *In*: Ridgway, S.H.; Harrison, R.J. (eds) *Handbook of Marine Mammals, Volume 2: seals.* Academic Press, London. Pp 275–296.

Kuhn, C.E.; McDonald, B.I.; Shaffer, S.A.; Barnes, J.; Crocker, D.E.; Burns, J.; Costa, D.P. 2006. Diving physiology and winter foraging behaviour of a juvenile leopard seal (*Hydrurga leptonyx*). *Polar Biology* 29: 303-307.

Lasiewski, R.C.; Dawson, W.R. 1967. A re-examination of the relation between standard metabolic rate and body weight in birds. *Condor* 69: 13-23.

Lavigne, D.M.; Barchard, W.; Innes, S.; Øritsland, N.A. 1982. Pinniped bioenergetics. FAO Advisory Committee on Marine Resources Research Working Party on Marine Mammals. *FAO Fisheries Series (5)* Vol. 4: pp. 191-235.

Lavigne, D.M.; Innes, S.; Worthy, G.A.J.; Kovacs, K.M.; Schmitz, O.J.; Hickie, J.P. 1986. Metabolic rates of seals and whales. *Canadian Journal of Zoology* 64: 279-284.

Laws, R.M. 1984. (Ed.) *Antarctic Ecology, Vol 2*. Academic Press, London, 850 pp.

Laws, R.M.; Baird, A.; Bryden, M.M. 2003. Size and growth of the crabeater seal *Lobodon carcinophagus* (Mammalia: Carnivora). *Journal of Zoology, London* 259: 103-108.

Lockyer, C., 1981a. Growth and energy budgets of large baleen whales from the Southern Hemisphere. In: Mammals in the Seas. Vol. III, General Papers and Large Cetaceans. *FAO Fisheries Series* 5, pp. 379–487.

Lockyer, C., 1981b. Estimation of the energy costs of growth, maintenance and reproduction in the female minke whale (*Balaenoptera acutorostrata*), from the Southern Hemisphere, south of 401S. *Report of the International Whaling Commission* 31: 337–343.

Nagy, K.A. 1987. Field metabolic rate and food requirement scaling in mammals and birds. *Ecological Monographs* 57: 111-128.

Nagy, K.A. 1994. Field bioenergetics of mammals: what determines field metabolic rate? *Australian Journal of Zoology* 42: 43-53.

Nagy, K.A. 2005. Field metabolic rate and body size. *Journal of Experimental Biology* 208: 1621-1625.

Nordoy, E.S.; Martensson, P.E.; Lager, A.R.; Folkow, L.P.; Blix, A.S. 1995. Food consumption of the northeast Atlantic stock of harp seals. In: Whales, seals, fish and man. Blix, A.S.; Walløe, L.; Ulltang, Ø. (eds.). Elsevier, Amsterdam. Pp 255-260.

Øritsland, T. 1970. Sealing and seal research in the southwest Atlantic pack ice, Sept-Oct 1964. In: Antarctic Ecology (Holdgate MW, ed.) pp. 367-376. Academic Press, London.

Øritsland, T. 1977. Food consumption of seals in the Antarctic pack ice. *In*: G. Llano (ed.) *Adaptation within Antarctic Ecosystems*. Washington, D.C., Smithsonian Institution, pp. 749-768.

Penney, R.L.; Lowry, G. 1967. Leopard seal predation on Adélie penguins. *Ecology 48*: 879-881.

Pinkerton M.H.; Dunn, A.; Hanchet, S.M. 2008. Trophic overlap of Weddell seals *(Leptonychotes weddelli*) and Antarctic toothfish (*Dissostichus mawsoni*) in the Ross Sea, Antarctica. Document WG-EMM-08/43, CCAMLR, Hobart, Australia.

Plotz, J.; Ekau, W.; Reijnders, P.J.H. 1991. Diet of Weddell seals *Leptonychotes Weddellii* at Vestkapp, Eastern Weddell Sea (Antarctica) in relation to local food supply. *Marine Mammal Science* 7(2): 136-144.

Ponganis, P.J.; Stockard, T.K. 2007. The Antarctic toothfish: how common a prey for Weddell seals? WG-EMM-07/P4.

Ray, G.C. 1981. Ross seal – *Ommatophoca rossi*. *In*: Ridgway, S.H.; Harrison, R.J. (eds) *Handbook of Marine Mammals, Volume 2: seals.* Academic Press, London. Pp 237–260.

Riedman, M. 1990. Pinnipeds: Seals, Sea Lions, and Walruses. University Of California Press: Berkeley, pp 1–149.

Rogers, T.L.; Bryden, M.M. 1997. Density and haul-out behaviour of leopard seals (*Hydrurga leptonyx*) in Prydz Bay, Antarctica. *Marine Mammal Science* 13: 293–302.

Ross, J.; Testa, J.W.; Winter, J.D.; Kuechle, L.; Reichle, R. 1982. Weddell seal population dynamics and Antarctic cod movement patterns in McMurdo Sound. *Antarctic Journal of the United States* 18: 188-189.

Schneider, D.; Hunt, G.L. 1982. Carbon flux to seabirds in waters with different mixing regimes in the southeastern Bering Sea. *Marine Biology* 67: 337-344.

Schreer, J.F.; Testa, J.W. 1992. Population ecology of Weddell seals in McMurdo Sound. *Antarctic Journal of the United States* 27(5): 152.

Shirihai, H. 2002. *The Complete Guide to Antarctic Wildlife: Birds and Marine Mammals of the Antarctic Continent and the Southern Ocean*. Alula Press Oy, Finland.

Siniff, D.; Stone, S. 1985. The role of the Leopard seal *Hydrurga leptonyx* in the tropho-dynamics of the Antarctic Marine Ecosystems. *In*: Seigfried, W.; Condy, P.; Laws, R. (eds) *Antarctic Nutrient Cycles and Food Webs*. Berlin: Springer-Verlag, Pp 555-560.

Skinner, J.D.; Klages, N.T.W. 1994. On some aspects of the biology of the Ross seal *Ommatophoca rossii* from King Haakon VII Sea, Antarctica. *Polar biology* 14(7): 467-472.

Southwell, C. 2005. Diving behaviour of two Ross seals off east Antarctica. *Wildlife Research* 32(1): 63-65.

Steimle, F.W. Jr.; Terranova, R.J. 1985. Energy equivalents of marine organisms from the continental shelf of the temperate Northwest Atlantic. *Journal of the Northwest Atlantic Fisheries Science* 6: 117–124.

Stewart B.S.; Yochem P.K.; Gellat T.S.; Siniff D.B. 2000. First-year movements of Weddell seal pups in the Western Ross Sea, Antarctica. *In*: Davison, W., Howard-Williams, C., Broady, P. (eds) Antarctic Ecosystems: Models for Wider Ecological Understanding. Caxton, Christchurch, pp 71–76

Stewart, B.S.; Yochem, P.K.; Gelatt, T.S.; Siniff, D.B. 2003. The pack ice niche of Weddell seals in the western Ross Sea. *In*: Huiskies, A.; W.W. Gieskes; J.Rozema; R.M.L. Schornu; S.M. van der Vies; W.J.Wolff (eds). Antarctic Biology in a Global Context. Leiden: Backhuys Publishers: 224–229.

Stirling, I. 1969. Ecology of the Weddell seal in McMurdo Sound, Antarctica. *Ecology* 50: 533–544.

Tedman, R.; Green, B. 1987. Water and sodium fluxes and lactational energetics in suckling pups of Weddell seals (*Leptonychotes weddellii*). *Journal of Zoology 212*: 29-42.

Testa, J.W. 1987. Juvenile survival and recruitment in a population of Weddell seals (*Leptonychotes weddellii*) in McMurdo Sound, Antarctica. *Canadian Journal of Zoology* 65: 2993-2997

Testa, J.W. 1994. Over-winter movements and diving behavior of female Weddell seals (*Leptonychotes weddellii*) in the south-western Ross Sea, Antarctica. *Canadian Journal of Zoology* 72: 1700-1710

Testa, J.W.; Siniff, D.B. 1987. Population dynamics of Weddell seals (*Leptonychotes weddelli*) in McMurdo Sound, Antarctica. *Ecological Monographs* 57(2): 149-165.

Testa, J.W.; Siniff, D.B.; Ross, M.J.; Winter, J.D. 1985. Weddell Seal -Antarctic Cod interactions in McMurdo Sound, Antarctica. *In*: Siegfried, W.R., Condy, P.R & Laws, R.M. (eds). Antarctic Nutrient Cycles and Food Webs. Berlin: Springer Verlag. Pp. 561-565.

Trites, A.W.; Pauly, D. 1998. Estimating mean body masses of marine mammals from maximum body lengths. *Canadian Journal of Zoology* 76: 886-896.

Van Franeker, J.A.; Bathmann, U.V.; Mathot, S. 1997. Carbon fluxes to Antarctic top predators. *Deep Sea Research II* 44(1/2): 435-455.

Vinogradov, A.P. 1953. The elementary chemical composition of marine organisms. Memoir of the Sears Foundation for Marine Research, Yale University, New Haven II, 647 pp.

Walker, T.R.; Boyd, I.L.; McCafferty, D.J.; Huin, N.; Taylor, R.; Reid, K. 1998. Seasonal occurrence of leopard seals (*Hydrurga leptonyx*) at Bird Island, South Georgia. *Antarctic Science* 10(1): 75-81.

Waterhouse, E.J. (*ed.*) 2001. *Ross Sea region 2001: A state of the environment report for the Ross Sea region of Antarctic*. New Zealand Antarctic Institute, Christchurch New Zealand. 265 pp.

Weibe, P.H. 1988. Functional regression equations for zooplankton displacement volume, wet weight, dry weight, and carbon: a correction. *Fishery Bulletin* 86(4): 833-835.

Zhao, L.; Castellini, M.A.; Mau, T.; Trumble, S.J. 2004. Trophic interactions of Antarctic seals as determined by stable isotope signatures. *Polar Biology 27*: 368-373.