Sea temperature variations mediate annual changes in the diet of Australian fur seals in Bass Strait

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ABSTRACT: Using a 9-yr data set, we investigated annual fluctuations in the diet of an apex predator, the Australian fur seal *Arctocephalus pusillus doriferus*. At Seal Rocks (northern Bass Strait), home to 25% of the entire species population, we assessed diet through collections (1997 to 2006) of scat and regurgitate samples. We identified prey remains of 42 fish taxa and 7 cephalopod taxa. Only crustaceans that were fish parasites or fish prey (amphipods and isopods) were found; no birds were identified in the samples. Six species represented 80% (as frequency of occurrence) of the fish prey, and the arrow squid *Nototodarus gouldi* represented 70% of cephalopod prey. There was significant annual variability in the diet. Principal component analysis indicated this was variability due to the presence of redbait *Emmelichthys nitidus* in some years, and its near absence and replacement in other years by increased proportions of barracouta *Thyrsites atun*, red cod *Pseudophycis bachus* and leatherjackets (Family Triglidae). Generalised Linear Models indicated the annual variation was related to mean sea surface temperatures in western Bass Strait where the seals foraged. Redbait proliferated in cooler years and were less abundant in warmer years. No corresponding annual correlation was evident between the prey assemblages and either annual fisheries catch-per-unit-effort or the annual mean Southern Oscillation Index. The propensity for diet regimes to persist for several years, then change suggests that oceanographic fluctuations probably influence previously unrecognised multi-year cyclic fluctuations of prey and of Bass Strait ecosystems.

KEY WORDS: *Arctocephalus* · Fur seal diet · Sea temperature · Bass strait · *Emmelicthys nitidus*

INTRODUCTION

Although large-scale climatic features such as the El Niño Southern Oscillation (ENSO) are known to influence the marine environment, the nature of the ecological linkages that lead up the food chain to marine mammals is less well understood. In part, this is due to the lack of long-term data sets that span a sufficient range of climatic variations. The structure of marine ecosystems changes at various temporal scales through seasonal, annual and decadal fluctuations (Hawkins et al. 2003, Evans et al. 2005), and in response to catastrophic events that may alter food chains (Trillmich & Ono 1991, Ward et al. 2001). A means of detecting subtle ecosystem changes is through monitoring foraging parameters of apex predators, such as pinnipeds (Hindell et al. 2003). Pinniped diet, for example, varies

temporally in relation to differences in prey distribution and abundance (Lea et al. 2002, Reid et al. 2006). In South America, oceanographic variations related to ENSO events can cause dramatic changes in local fish assemblages, influencing the diet and breeding success of pinnipeds (Trillmich & Ono 1991). Monitoring of pinniped diet in conjunction with oceanographic variables can provide insights into causes and effects of fluctuations in marine communities.

Between 1998 and 2006, we monitored the diet of an apex marine predator in southeastern Australia shelf waters (the Australian fur seal *Arctocephalus pusillus doriferus*) at Seal Rocks in northern Bass Strait. Australian fur seals breed mainly in Bass Strait, between Tasmania and the Australian mainland, and forage throughout southeastern Australian shelf waters (Warneke & Shaughnessy 1985, Kirkwood et al. 2005, 2006,

Arnould & Kirkwood 2008). Like other fur seals, such as the New Zealand fur seal *A. forsteri* (Harcourt et al. 2002), Australian fur seals are generalist predators and consume a range of benthic and pelagic prey; they exhibit some spatial and temporal variations in diet. During the 1920s and 1940s, their diet at breeding colonies in northern Bass Strait was determined by inspection of stomach contents in several shot animals, and comprised mainly barracouta (also known as snoek *Thyrsites atun*), cephalopods, and southern rock lobster *Jasus novaehollandiae* (Lewis 1930, McNally & Lynch 1954). In the 1980s and 1990s, the diet, determined from prey hard parts in scats and regurgitates at sites in southern Bass Strait and south of Tasmania, comprised mainly redbait *Emmelichthys nitidus*, jack mackerel *Trachurus declivis*, leatherjackets (Family Monocanthidae) and arrow squid *Nototodarus gouldi* (Gales et al. 1993, Gales & Pemberton 1994, Hume et al. 2004). Between 1997 and 2001 in northeastern Bass Strait, the same prey, plus red cod *Pseudophycis bachus* were the key species (Littnan 2003, Littnan et al. 2007); during 2001/2002 in South Australian waters, redbait was the dominant prey of adult male Australian fur seals (Page et al. 2005). Although variation is evident in the diets, factors influencing the variation are unclear, partly because sampling has been opportunistic and/or short term.

Bass Strait is a shallow (<100 m maximum depth) marine basin at 39° S on the continental shelf between mainland Australia and Tasmania. It is well mixed vertically, but characterized by a limited nutrient regime (Gibbs et al. 1986). The central basin is quite stagnant, with weak currents and long flushing times (>160 d, Sandery & Kämpf 2004). Subtle changes in surrounding water bodies may influence the flow rates and water quality within Bass Strait (Evans & Middleton 1998). Water bodies that may enter the strait are the Subantarctic Surface Water (SASW) from the south, South Australian Current (SAC) from the northwest and East Australian Current (EAC) from the northeast (Newell 1961). Most current flow is eastward and enhanced by the predominantly westerly winds across southern Australia (Blackman et al. 1987, Middleton & Bye 2007).

Inter-annual variability in Bass Strait water temperature and productivity may be influenced by broad-scale events, including the ENSO in the western Pacific Ocean (Kidson & Renwick 2002, Middleton & Bye 2007, Middleton et al. 2007). ENSO cycles influence the relative strength of the Leeuwin Current, causing variability in ocean productivity and species' movements (Pearce & Phillips 1988, Wilson et al. 2001). The Leeuwin Current moves southwards along the coast of Western Australia and feeds into the SAC (Kidson & Renwick 2002). Sea temperature anomalies in Bass Strait may also be influenced by the Antarctic Circumpolar Wave (ACW) (which pulses colder then warmer waters northwards from the Southern Ocean in a 4 to 5 yr cycle, White & Peterson 1996), or by meteorological influences (Blackman et al. 1987).

In this study we aimed to (1) quantify the interannual changes in Australian fur seal diet at the Seal Rocks colony in northern Bass Strait through a 9 yr program of scat sampling, (2) relate the variations in prey assemblages to broad scale oceanographic variables, and (3) assess the ecological implications of these relationships for variability in southeastern Australian marine ecosystems.

MATERIALS AND METHODS

Study area and sample collection. This study was based in northern Bass Strait at Seal Rocks, a colony of 20 000 to 25 000 Australian fur seals (about 25 % of the species' population, Kirkwood et al. 2005). Scats deposited on Seal Rocks derive from prey eaten within 200 km, assuming Australian fur seals can travel about 100 km d^{-1} (Kirkwood et al. 2006, Arnould & Kirkwood 2008), and the mean passage rate of prey through the digestive system of fur seals is about 2 d (derived from captive Antarctic fur seals *Arctocephalus gazella*, Staniland 2002). Seals tracked from Seal Rocks tended to forage within western Bass Strait (Kirkwood et al. 2006, Arnould & Kirkwood 2008).

Fresh scat and regurgitate samples were collected between 1998 and 2006 at Seal Rocks (38°30′S, 145°10′E; Fig. 1, Table 1). We aimed to make monthly sample collections, but this was not always possible for logistical reasons. Like other otariids, Australian fur seals routinely regurgitate stomach contents that are difficult to digest and too large to pass from the stomach into the intestine. Actual diets of the seals may be assessed from a combination of the scats and regurgitates, but the ratio of one to the other is difficult to determine due to differences in passage and production rates (Gales et al. 1993). Also, at Seal Rocks, gulls (*Larus dominicanus* and *L. novaehollandiae*) readily consume seal regurgitates, which reduces the number available for collection (R. Kirkwood pers. obs.). Accordingly, we focus on interannual variation in scat data, although regurgitate data are presented for comparison.

Samples were placed in separate plastic bags and stored frozen until analysis. In the laboratory, samples were soaked in warm water, then washed through a series of sieves (from 1 to 0.2 mm). Diagnostic remains of fish (otoliths, mouthparts, body plates, spines, etc.), cephalopods (beaks) and crustaceans (exoskeletons and carapace fragments) were collected.

Saggital otoliths were identified by comparison with reference collections and an atlas (Furlani et al. 2007). Fish prey were identified mostly to species and genus, although identification was possible only to family for Monocanthidae (leatherjackets), Triglidae (gurnard), Macrouridae (whiptail), Ostracontidae (cowfish), Myctophidae (Myctophid) and Bothidae (flounder). Also, scorpion fish other than common gurnard perch *Neosebastes scorpaenoides* and reef ocean perch *Helicolenus percoides* were assigned to the Order Scorpaeniformes. *Pseudophycis* spp. (red cod *P. bacchus* and bearded rock cod *P. barbata*) could not be distinguished using a microscope, but were separable by microchemical analysis. Laser ablation techniques showed that the core region of bearded rock cod otoliths have significantly higher lithium enrichment than red cod otoliths (J. Kemp unpubl. data). Only red cod otoliths were identified in the diet samples. All identifiable Gempylidae otoliths were from abundant barracouta *Thyrsites atun*, so eroded Gempylid otoliths were assumed to be of this species rather than the less common gemfish *Rexea solandri*. Likewise, eroded *Trachurus* spp. otoliths were assumed to be from the abundant jack mackerel *T. declivis*, although some may have been from yellowtail *T. novaezelandiae*. Very eroded otoliths of *Trachurus* spp. and redbait *Emmelichthys nitidus* are similar, and where species could not be positively identified, they were assigned to species based on proportional occurrence of the identified otoliths of these species in the collection
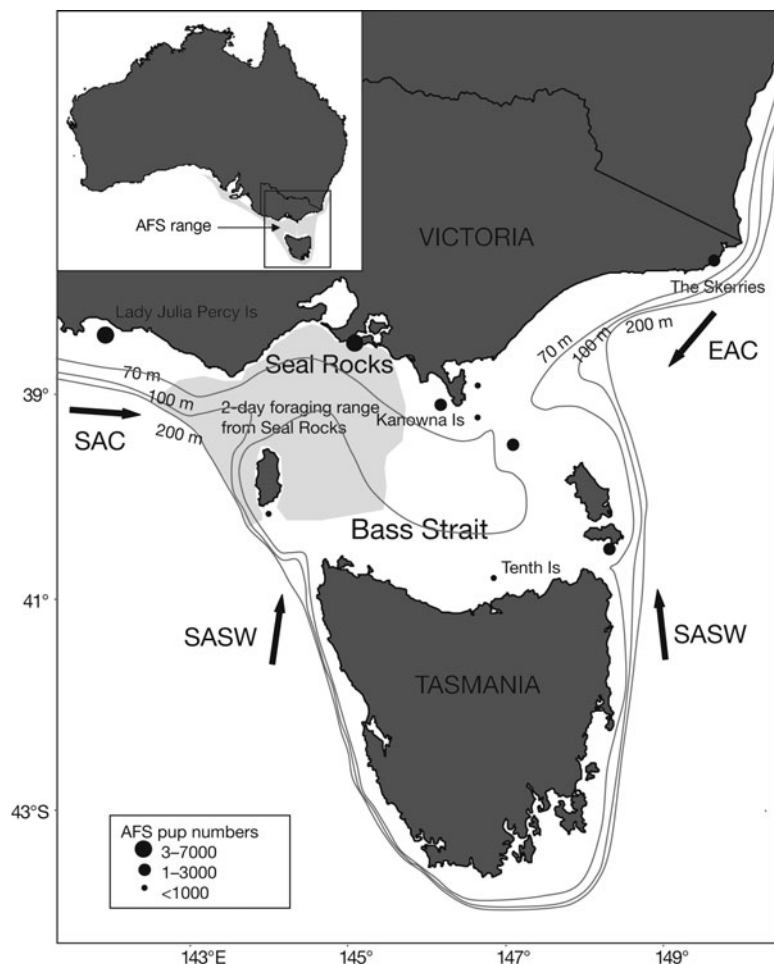

Fig. 1. *Arctocephalus pusillus doriferus*. Location of Seal Rocks and other colonies of Australian fur seals (AFS) and water currents that may enter Bass Strait (SAC: South Australia Current; EAC: East Australia Current; SASW: Subantarctic Surface Water). The estimated 2 d foraging range of seals from Seal Rocks is indicated by light grey shading. Bottom depth contours are shown

Table 1. *Arctocephalus pusillus doriferus*. Seal diet samples collected at Seal Rocks. Within table cells (month × year), the 1st value gives numbers of scats, the 2nd value in italics gives numbers of scats with identifiable fish remains that were incorporated in frequency of occurrence estimates, and the 3rd value in parentheses gives number of regurgitates

Month	1998	1999	2000	2001	2002	2003	2004	2005	2006
J	16 *14* (2)							28 *23* (2)	11 *9* (0)
F	28 *17* (3)	22 *18* (0)			19 *16* (6)				25 *20* (1)
M	20 *12* (0)						23 *22* (0)		25 *20* (1)
A		25 *6* (3)	23 *17* (0)		19 *11* (1)	21 *17* (0)		27 *24* (2)	31 *25* (0)
M	24 *17* (2)	16 *10* (0)		11 *7* (1)	23 *17* (2)		27 23 (0)		29 *22* (0)
J	24 *21* (3)	26 *24* (0)			25 *22* (0)			28 *23* (0)	
J	28 *26* (0)	24 *23* (2)	31 *24* (0)			21 *19* (0)	28 *19* (1)	29 *22* (0)	24 *21* (0)
A	14 *10* (2)			25 *18* (1)	25 *21* (0)	32 *26* (0)	24 *24* (0)	31 *27* (0)	
S			28 *15* (0)	25 *17* (1)	24 *22* (0)		23 *20* (1)	34 *28* (0)	24 *21* (0)
O	17 *13* (1)	28 *23* (1)				25 *10* (0)	29 *25* (0)	28 *22* (0)	32 *25* (0)
N		12 *12* (0)							
D		17 *11* (0)							
Total	171 *130* (13)	170 *127* (6)	82 *56* (0)	61 *42* (3)	135 *109* (9)	99 *72* (0)	154 *133* (2)	205 *169* (4)	176 *143* (1)
Months	8	8	3	3	6	4	6	7	7

from that month. Similarly, lapillus and astericus otoliths of redbait, jack mackerel or barracouta (which could not be attributed to species) were occasionally present without saggital otoliths. In these cases, they were assumed to be in ratios at which identifiable otoliths occured for these species in the month's sample. Otoliths that could not be identified to taxonomic group, usually due to severe erosion, were recorded as unidentified.

Counts of paired left and right otoliths provided estimates of the minimum numbers of fish present in each sample. In addition to otoliths, the mouthparts, spines and distinctive vertebral growths of leatherjacket species, and mouthparts of wrasse species and barracouta indicated the presence of these fish taxa. The presence of cowfish (Family Ostracontidae) was indicated by characteristic hexagonal body plates.

Cephalopod beaks were identified by comparing lower beaks with reference collections and an atlas (Lu & Ickeringill 2002). The number of lower cephalopod beaks identified was recorded to provide a minimum number of cephalopods in a sample. As recognised previously (Hume et al. 2004), *Octopus berrima* and *O. pallidus* could not be distinguished, and so were recorded as *O. berrima/O. pallidus*.

Analyses. Separate scat and regurgitate profiles and separate fish and cephalopod profiles were prepared and compared for overall diet characterisation (Gales et al. 1993, Gales & Pemberton 1994, Fea et al. 1999). The prevalence of each prey group was quantified firstly using percentage numerical abundance (NA) across all samples, then proportional frequency of occurrence (PFO) based on the proportion of samples that contained identified prey remains of each taxon. A second frequency of occurrence (mean PFO) was determined by averaging PFO across the months sampled within each year, then averaging across years. This ensured that, despite sample size variation between months and sampling frequency variation between years, each month sampled contributed equally to annual diet estimates and each year contributed equally to the overall estimate. Finally, contributions by mass were determined. Otoliths and beaks were scored according to their level of erosion and those scored as pristine or near pristine were measured digitally under a binocular microscope. Prey lengths and masses were derived from otolith and beak (lower rostral) lengths using published equations (Gales & Pemberton 1990, Lu & Ickeringill 2002). Based on the mean masses and both NA and PFO of prey, we estimated prey contributions by mass to the diet. There are numerous biases associated with predicting marine mammal diet based on the recovery of partially digested prey hard-parts (Tollit et al. 1997, Staniland 2002). Accordingly, although our estimates signal im-

portant prey species and age classes, they only approximate the actual diet and some important prey may be under-represented.

Multivariate data analyses. Multivariate analysis focused on scat data only, as these comprised by far the largest data set (981 samples with identifiable prey spread across all sampling dates, Table 1). As the scats contained 41 species from 52 sampling occasions (Tables 1 & 2), we used a multivariate approach to minimise the number of dimensions for subsequent analyses. Only species that occurred in at least 3 scats in 3 monthly samples were included to eliminate the influence of rare species, and this reduced the number of species to 13 (Table 2). We used the PFO data for all of these analyses. A principal component analysis (PCA) was performed on the complete data set (i.e. all 51 PFO values for the 13 species), and the resulting principal components (PCs) with the greatest explanatory power were used as variables in further analyses. The relative importance of each species in each PC was assessed by examination of the individual loadings in that principal component. Each PC was therefore a single variable that contained information on the relative importance of each prey species for each of the 52 samples. These vectors are orthogonal to each other, ensuring they can be treated as independent variables.

Generalised linear models. Following PCA, we then used a series of Generalised Linear Models (GLMs) to examine the importance of several covariates in the dietary data summarised in the PCs. Our covariates were 'month', 'year' and the mean annual Southern Oscillation Index (SOI). We used the Troup SOI, which is the standardised anomaly of the mean sea level pressure difference between Tahiti and Darwin (available from Bureau of Meteorology, Australia: www.bom.gov.au/climate/). Other factors included were the mean annual sea surface temperature (MSST) for western Bass Strait, interpolated from monthly mean SST data for western Bass Strait (39°S, 144°E to 40°S, 145°E) obtained from the National Centre for Atmospheric Research (NCAR) Comprehensive Oceanic-Atmospheric Data Set (COADS available at: nomads.ncdc.noaa.gov/), and the mean annual catch per unit effort (CPUE) data for the area within 200 km of Seal Rocks, the presumed range across which seals forage and return to deposit scat at Seal Rocks, obtained from the database of the Australian Fisheries Management Authority (AFMA), Canberra.

Model selection was based on Akaike's information criterion corrected for small samples (AIC$_c$, Burnham & Anderson 2002). The information-theoretic weight of evidence ($w+_i$) for each predictor (month, year, etc.) was calculated by summing the model AIC$_c$ weights

Table 2. *Arctocephalus pusillus doriferus*. Percentage numerical abundance (NA), overall proportional frequency of occurrence (PFO) and mean monthly frequency of occurrence (xPFO, see 'Materials and methods — Analyses' for description) of prey in seal scat samples collected at Seal Rocks between 1998 and 2006

Taxon		NA (%)	PFO (%)	xPFO (%)
Fishes				
Redbait[a]	*Emmelichthys nitidus*	52.9	16.9	19.9
Leatherjacket[a]	Family Monocanthidae	6.4	14.7	17.7
Jack mackerel[a]	*Trachurus declivis*	11.4	9.4	12.8
Barracouta[a]	*Thyrsites atun*	4.2	9.1	11.5
Red cod[a]	*Pseudophycis bachus*	8.0	8.3	9.5
Gurnard[a]	Family Triglidae	5.4	6.7	6.9
Silverbelly[a]	*Parequula melbournesis*	0.9	1.8	2.2
Unknown sp1[a]		1.3	1.9	2.1
Silver trevally[a]	*Pseudocaranx dentex*	0.9	1.3	1.8
Silver dory	*Cyttus australis*	0.5	1.1	1.7
Tiger flathead	*Neoplatycephalus richardsoni*	0.6	1.1	1.7
Western red mullet[a]	*Upeneichthys vlamingii*	0.7	1.4	1.4
Sand flathead	*Platycephalus bassensis*	0.9	1.1	1.4
Silverside[a]	*Argentina australiae*	0.7	1.2	1.1
Anchovy	*Engraulis australis*	1.3	0.8	1.1
Pink ling	*Genypterus blacodes*	0.5	1.0	1.0
Reef ocean perch	*Helicolenus percoides*	0.4	0.7	0.9
Apogonidae	Family Apogonidae	1.1	0.6	0.7
Wrasse	Family Labridae	0.1	0.3	0.5
Blue warehou	*Seriolella brama*	0.1	0.2	0.4
Ocean perch	*Helicolenus* sp.	0.2	0.3	0.4
Stargazer	Family Uranoscopidae	0.1	0.2	0.4
Spotted warehou	*Seriolella punctata*	0.1	0.1	0.4
Scorpionfish	Order Scorpaeniformes	0.1	0.2	0.3
Redfish	*Centroberyx affinis*	0.1	0.2	0.3
Warehou	*Serioella* spp.	0.1	0.2	0.3
Flounder	Family Bothidae	0.2	0.3	0.3
Pilchard	*Sardinops neopilchardus*	0.2	0.2	0.2
Morwong	*Nemadactylus* spp.	<0.1	0.1	0.2
White cardinalfish	*Epigonis denticularis*	0.1	0.2	0.2
Yellow eyed mullet	*Aldrichetta forsteri*	0.3	0.1	0.1
Eastern school whiting	*Sillago flindersii*	0.1	0.2	0.1
Snapper	*Pagrus auratus*	0.1	0.0	0.1
Common gurnard perch	*Neosebastes scorpaenoides*	<0.1	0.0	0.1
Bastard trumpeter	*Latridopsis forsteri*	<0.1	0.0	0.1
Hardyhead	*Atherinidae* spp.	<0.1	0.0	0.1
Whiptail	Family Macouridae	<0.1	0.0	0.1
Marblefish	*Dactylosargus arctidens*	<0.1	0.0	<0.1
Hapuku	*Polyprion oxygeneios*	<0.1	0.0	<0.1
Slimy (blue) mackerel	*Scomber australasicus*	<0.1	<0.1	<0.1
Cowfish	Family Ostracionthidae	<0.1	<0.1	<0.1

Total (n): Unidentified/eroded otoliths = 318; identified fish = 5139; samples with identifiable fish remains = 981

Cephalopods				
Arrow squid[a]	*Nototodarus gouldi*	74.1	73.0	
Calamari squid	*Sepioteuthis australis*	10.5	11.1	
Pale/keeled octopus	*Octopus pallidus/O. berrima*	6.0	8.7	
Maori octopus	*Octopus maorum*	1.9	4.0	
Southern argonaut	*Argonauta nodosa*	4.9	1.6	
Giant cuttlefish	*Sepia apama*	2.3	1.6	
New Holland cuttlefish	*Sepia novaehollandiae*	0.4	0.8	

Total (n): Unidentified/eroded cephalopods = 183; identified cephalopods = 266; samples with identifiable cephalopods = 118

Crustaceans   Samples with crustaceans = 59

[a]Species included in the multivariate analyses (i.e. occurred in at least 3 scats mo^{-1} in at least 3 monthly samples)

(w_i) over all models in which each term appeared. However, the $w+_i$ values are relative, not absolute, because they will be >0 even if the predictor has no contextual explanatory importance (Burnham & Anderson 2002). To judge which predictors were most relevant, a baseline for comparing relative $w+_i$ across predictors was required, so we randomized the data for each predictor separately, re-calculated $w+_i$, and repeated this procedure 100 times for each predictor. The median of this new randomized $w+_i$ distribution for each predictor was taken as the baseline (null) value ($w+_0$). For each term, the absolute weight of evidence ($\Delta w+$) was obtained by subtracting $w+_0$ from $w+_i$, and predictors with $\Delta w+$ of ≤ 0 have essentially no explanatory power (Burnham & Anderson 2002). Specific model comparisons were based on the information-theoretic evidence ratio (ER) which is equivalent to the AIC_c weight (w) of the full model divided by the w of the null model (Burnham & Anderson 2002). Higher ER values indicate higher likelihoods of the tested model relative to the null. We also calculated the percent deviance explained (%DE) by each model constructed as a measure of model goodness-of-fit. All statistical analyses were done using the R Package (Ver. 2.4.1; R Development Core Team 2004, available at: www.r-project.org/).

RESULTS

Overall diet

Across the 52 sample dates, we collected 1253 scats and 38 regurgitates from which we identified diagnostic remains of a minimum of 5211 fish from 42 different taxa and 389 cephalopods from 7 taxa (Tables 2 & 3). No samples contained bird remains. Crustaceans, exclusively amphipod and isopod exoskeletons, were recognised in 55 scats and 2 regurgitates, and were probably derived from either external parasites or stomach contents of the prey.

Based on scat samples, the most numerically important fish species (contributing >5%) were redbait (58%), red cod (8.5%), jack mackerel (8.0%) and leatherjackets (6.3%). Using frequency of occurrence, the same species, plus barracouta and gurnard were recognised as principal prey. Numerically important cephalopods were arrow squid (74.0% of cephalopods), calamari squid (10.4%) and pale/keeled octopus (6.4%). Based on regurgitates, the most important fish species were red cod (54.2%), leatherjackets (9.7%), wrasse (9.7%) gurnard (6.9%) and eastern school whiting (5.6%), while important cephalopods were arrow squid (82.1%) and calamari squid (9.8%).

Sufficient pristine otoliths (most from scats) and beaks (most from regurgitates) were recovered to estimate the sizes of key prey. Modal fork lengths for fish and mantle lengths for cephalopods indicated that most prey were between 100 and 300 mm body length (Table 4). The seals preyed on mature fish of most species; however, juveniles accounted for 95% of red cod, 90% of redbait and jack mackerel, and 50% of barracouta.

There was a significant change in the sizes of arrow squid (Fig. 2). Up to April 2002, lower-rostral lengths (± SD) of arrow squid beaks averaged 7.3 ± 1.5 mm (n = 92, mantle length 288 ± 51 mm, mass 707 ± 286 g) and from April 2002 to October 2005 they averaged 3.6 ± 1.4 mm (n = 71, mantle length 166 ± 49 mm, mass 130 ± 156 g; z = 15.65, p < 0.01).

Reconstructing the diet based on prey mass altered the apparent order of importance of the main prey (Table 5). The reconstruction emphasised the value of larger bodied prey, such as barracouta, arrow squid and tiger flathead, and reduced that of smaller prey, such as leatherjackets and anchovy.

Multivariate analysis

The first three PCs accounted for 77.8% of the total variance (Table 6). Principal Component 1 (PC1) explained 46.4%, PC2 18.8% and PC3 12.6%. All remaining PCs explained less than 10% of the total variance and were not used in subsequent analyses. PC1 was dominated by the presence of redbait (Table 6). Leatherjacket, barracouta and bearded/red cod were at the other end of the vector. The other species were unimportant (Fig. 3). PC2 was dominated by jack mackerel, bearded/red cod and gurnard. PC3 had leather-

jacket, gurnard, redbait and jack mackerel as its primary species.

Diet by month and year

The most parsimonious GLM testing for the effect of month and year on PC1 included only year (Table 7). This model provided the best fit and explained 31.0% of the deviance. The very large evidence ratio (ER = 19 124) indicates very strong support for this model, and, hence, that PC1 varied among years. The year-month model had a similar AIC_c value, but explained only an additional 0.3% of the deviance, indicating that month had negligible influence.

The GLM testing for the effect of month and year on PC2 indicated the month+year model was the most parsimonious. However, this model explained only 5.3% more of the deviance than the month only model (which itself explained 23.8%), suggesting that PC2 was strongly influenced by month. There was strong support for this model (ER = 2320).

PC3 varied mainly by year, and month had little influence (Table 7). As our study is primarily concerned with inter-annual variation in diet, we have chosen to focus the remainder of the analysis on PC1, the most important of the components, and the one that varied among years.

Table 3. *Arctocephalus pusillus doriferus*. Percentage numerical abundance (NA) and overall proportional frequency of occurrence (PFO) of prey in seal regurgitate samples collected at Seal Rocks between 1998 and 2006

		NA (%)	PFO (%)
Fishes			
Red cod	*Pseudophycis bachus*	54.2	26.7
Leatherjacket	Family Monocanthidae	9.7	23.3
Wrasse	Family Labridae	9.7	20.0
Gurnard	Family Triglidae	6.9	3.3
Eastern school whiting	*Sillago flindersii*	5.6	3.3
Alfonsin	*Beryx splendens*	4.2	3.3
Pink ling	*Genypterus blacodes*	2.8	3.3
Redbait	*Emmelichthyis nitidus*	1.4	3.3
Scorpionfish	Order Scorpaeniformes	1.4	3.3
Barracouta	*Thyristes atun*	1.4	3.3
Marblefish	*Dactylosargus arctidens*	1.4	3.3
Tiger flathead	*Neoplatycephalus richardsoni*	1.4	3.3

Total (n): Unidentified/eroded otoliths = 8; identified fish = 72; samples with identifiable fish remains = 21

Cephalopods			
Arrow squid	*Nototodarus gouldi*	82.1	52.0
Pale/Keeled octopus	*Octopus pallidus/O. berrima*	4.9	20.0
Calamari squid	*Sepioteuthis australis*	9.8	16.0
Giant cuttlefish	*Sepia apama*	2.4	8.0
Maori octopus	*Octopus maorum*	0.8	4.0

Total (n): Unidentified/eroded cephalopods = 11; samples with identified cephalopods = 28; identifiable cephalopods = 123

Table 4. *Arctocephalus pusillus doriferus*. Modal fork lengths of fish and mantle lengths of cephalopods that were prey of seals, based on sizes of pristine otoliths and beaks found in diet samples, plus lengths and ages at maturity, and % of prey that were mature (maturity data from Kailola et al. 1993, Marshall et al. 1993, Horn 2002, Jackson et al. 2003, Welsford & Lyle 2003). For taxonomic species names see Tables 2 & 3

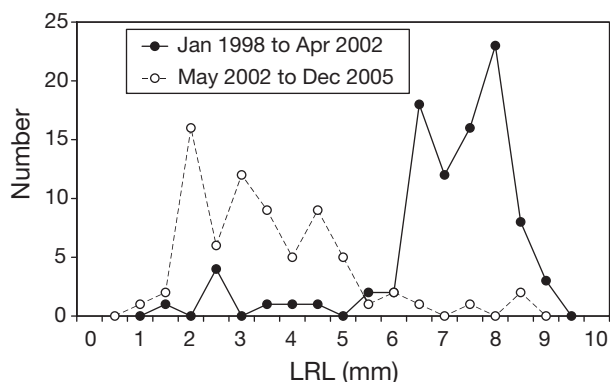| Prey	n	Modal length (mm)	Range (mm)	Length at maturity (mm)	Age at maturity (yr)	Mature prey (%)
Pale octopus	18	54	17–90	50	?	–
Anchovy	69	86	65–110	60	1	100
Leatherjacket	26	110	50–260	?	–	–
Redbait	1242	140	80–260	245	2	10
Red cod	202	170	30–470	320	1	5
Jack mackerel	395	110, 190	65–370	300	3–4	10
Calamari squid	26	206	50–430	160	1	60
Gurnard	158	220	150–300	?	–	–
Silver trevally	46	270	200–435	280	?	–
Arrow squid	170	160, 300	90–360	150	0.5	87
Barracouta	10	600	220–800	450–600	2–4	50

Fig. 2. *Nototodarus gouldi.* Frequency of lower-rostral lengths (LRL) of near-pristine beaks from arrow squid recovered from Australian fur seal scats. Data are separated temporally to emphasise a size change that occurred after April 2002

Diet by MSST, CPUE and SOI

The most parsimonious model when testing for the effect of MSST, CPUE and SOI on PC1 (redbait, leatherjacket, barracouta and bearded/red cod) was the MSST model (Table 8). There was very strong support for this model (ER = 1.27×10^7, % deviance = 44.3), indicating that as MSST increased, less redbait were in the diet (Fig. 4a). The next best model was MSST+ SOI, but it had a weighted Akaike's information criterion ($_w$AIC) of 0.36 compared to 0.42 for the MSST model, and explained only a further 2.3% of the deviance. Given that redbait was such a dominant aspect of this component we also modelled it separately. Again the best model was MSST alone, with ER lending very strong support (ER = 1.89×10^6, % deviance = 46.2) for this model, indicating that as MSST declines, the

amount of redbait in the diet increases (Fig. 4b).

Monthly temperatures in redbait years versus other years

Mean monthly SSTs were compared between years when redbait represented >30% of prey (based on PFO), termed 'redbait' years (1998 to 2001), and <10% of the prey, or 'other' years (2002 to 2005). The greatest monthly differences occurred in January to March, when water temperatures during 'other' years averaged 17.7 to 18.0°C, as opposed to an average of 16.6 to 17.3°C in 'redbait' years; the mean difference between 'redbait' and 'other' years was 1.1°C. Monthly temperatures over the rest of the year were on average 0.3°C (range –0.1 to 0.5°C) warmer during 'other' years than during 'redbait' years.

Table 5. *Arctocephalus pusillus doriferus*. Reconstructed diet based on mass and occurrence of principal prey identified in scat remains of seals at Seal Rocks (see Table 2). When there were insufficient near-pristine otoliths to measure ([a]), mean prey masses were taken from Littnan (2003), or were based on standard fish sizes in Furlani et al. (2007). In the absence of other data, we adopted a substitute value of 100 g. Representative gurnard and leatherjackets were *Lepidotrigla* spp. and common bridled leatherjacket *Acanthaluteres spilomelanurus*, respectively. NA: numerical abundance, PFO: proportional frequency of occurrence. For taxonomic species names see Tables 2 & 3

Prey	Mass (g)	Diet based on NA (%)	Diet based on PFO (%)
Barracouta	826	30.4	48.3
Redbait	47	22.1	5.1
Arrow squid	458	8.5	8.2
Jack mackerel	77	7.8	4.7
Gurnard	150[a]	7.1	6.5
Bearded/Red cod	96	6.8	5.1
Tiger flathead	1169[a]	6.6	8.4
Silver trevally	270	2.1	2.2
Calamari squid	691	1.8	1.9
Leatherjacket	28	1.6	2.6
Pink ling	356[a]	1.6	2.2
Unknown sp.1	100[a]	1.2	1.3
Western red mullet	148[a]	0.9	1.3
Silver dory	100[a]	0.4	0.7
Maori octopus	362	0.2	0.4
Pale/keeled octopus	101	0.2	0.2
Sand flathead	30[a]	0.2	0.2
Silverside	30[a]	0.2	0.2
Silverbelly	18	0.1	0.2
Anchovy	6	0.1	0.0

Table 6. *Arctocephalus pusillus doriferus.* Principal components analysis on 12 species of seal prey from 51 samples showing the loadings (eigenvectors) for each species on the first 3 principal components (PCs). Blank cells indicate small but not zero values; any values between –0.1 and 0.1 have been excluded for ease of interpretation. Values for Unknown sp.1, silverbelly, western red mullet, silver trevally, silverside and arrow squid were all between –0.1 and 0.1, so these species have been excluded from the table

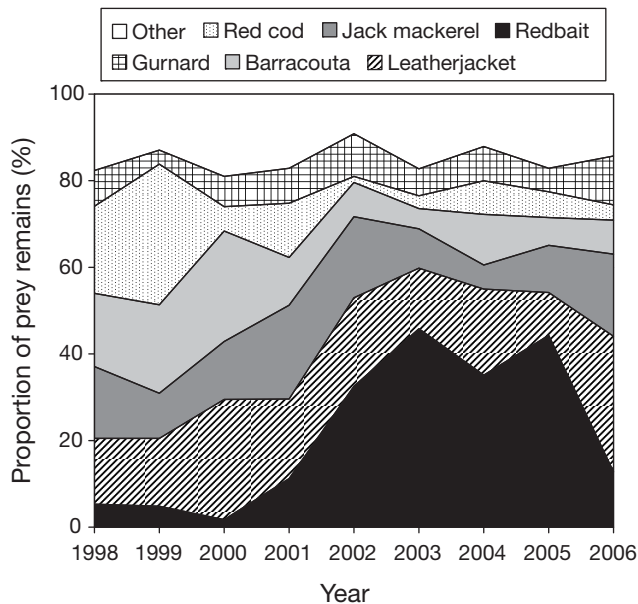|	PC1	PC2	PC3
Cumulative variance (%)	46.4	65.2	77.8
Species loadings			
Redbait	0.935		0.164
Leatherjacket	–0.167		0.875
Jack mackerel		0.935	0.136
Barracouta	–0.210		
Bearded/Red cod	–0.216	–0.255	
Gurnard		–0.170	0.400

Fig. 3. *Arctocephalus pusillus doriferus.* Summary of the diet of seals at Seal Rocks, based on the proportional frequency of occurrence of prey remains in scats collected at a nearly bi-monthly frequency. See Table 1 for species list

DISCUSSION

Prey of Australian fur seals

The diet of Australian fur seals at Seal Rocks was similar to those reported at other locations in recent years (Gales et al. 1993, Gales & Pemberton 1994, Hume et al. 2004, Page et al. 2005, Littnan et al. 2007). Across their range, Australian fur seals prey on 60 to 70 species of fishes and cephalopods. The importance of particular prey varies geographically, but the principal species consumed remain the same, and include redbait, jack mackerel, barracouta, arrow squid, leatherjackets (Monocanthidae), gurnards (Triglidae), red cod and flathead species. Some inter-annual changes in diet have been reported previously, based on sampling over 2 or 3 yr at several sites (Hume et al. 2004, Littnan et al. 2007); the present study of over 9 yr of routine sampling, however, is by far the longest time series of data available for this species, and one of the longest for any pinniped species.

Our sampling spanned an initial 4 yr of redbait scarcity in the seals' diet (<10% of prey in 1998 to 2001), then 4 yr of redbait prevalence in the diet (>30% in 2002 to 2005) and a final year of redbait scarcity (in 2006). In years of redbait scarcity, they were replaced in the seal diet by increases in barracouta, leatherjackets and/or bearded cod. Other prey, such as jack mackerel and arrow squid, were prevalent throughout the study. The extended time scale of the variation, i.e. 4 yr on one diet, then 4 yr on another, suggests an enduring multi-year influence on the seals' foraging environment (which contemporary satellite tracking studies indicate is western Bass Strait; Kirkwood et al. 2006, Arnould & Kirkwood 2008). Oceanographic fluctuations may trigger such a cycling in this environment.

Oceanographic influences

In years with cooler SSTs in western Bass Strait, redbait were more prevalent in the diet of Australian fur seals visiting Seal Rocks (>30% of PFO). Differences in SSTs between 'redbait' and 'other' years were greatest in January to March, suggesting oceanic conditions at this time of year might influence the relative availabilities of prey.

Cooler waters in western Bass Strait generally result from a greater inflow of SASW and/or upwelling of Antarctic Surface Waters (Evans & Middleton 1998, Middleton et al. 2007, Middleton & Bye 2007). Conversely, warmer waters may result from weak current flow through the strait (leading to a long seawater residence time) and/or from increased warmer current inflows, notably from the SAC.

Little is known of oceanographic variations and their influences on productivity across southern Australia, including Bass Strait (Middleton et al. 2007). There are 2 known SOI-related variations, which, despite their absence in our models, might influence sea temperature in Bass Strait. Firstly, the onset of El Niño conditions tends to reduce winter-time circulation along Australia's southern shelf region without there being a compensatory increase in summer currents during El Niño summers (Middleton et al. 2007, Middleton & Bye 2007). The reduced circulation appears to enhance

Table 7. *Arctocephalus pusillus doriferus*. Results of 3 Generalised Linear Models examining effects of month and/or year on diet of seals expressed as the first 3 PCs of a PCA. The models related the PC scores for each sample to the month and year in which that sample was collected. The models are ranked in order of weighted Akaike information criterion, corrected for small samples ($_w$AIC$_c$). Log(L): maximized log-likelihood of the model; AIC$_c$: selection criteria; ΔAIC$_c$: difference between the model's AIC$_c$ value and the minimum AIC$_c$ value; %DE: percent deviance explained by model

	Log(L)	AIC$_c$	ΔAIC$_c$	$_w$AIC$_c$	%DE
PC1					
Year	−169.766	346.043	0.000	0.741	30.996
Month+year	−169.639	348.148	2.104	0.259	31.339
Month	−179.201	364.912	18.869	0.000	0.102
Null+null2	−178.446	365.761	19.717	0.000	3.017
PC2					
Month+year	−147.119	303.107	0.000	0.659	29.196
Month	−148.962	304.434	1.327	0.339	23.889
Year	−154.230	314.971	11.864	0.002	6.422
Null+null2	−155.532	319.933	16.826	0.000	1.522
PC3					
Year	−141.895	290.300	0.000	0.681	20.052
Month+year	−141.488	291.846	1.546	0.314	21.317
Month	−147.142	300.794	10.494	0.004	1.787
Null+null2	−147.027	302.924	12.624	0.001	2.227

Table 8. *Arctocephalus pusillus doriferus*. Results of the Generalised Linear Models examining the effect of the Southern Oscillation Index (SOI), fisheries catch per unit effort (CPUE) within 200 km of Seal Rocks and the annual mean sea surface temperature (MSST) in western Bass Strait on diet of seals, expressed as the first 3 PCs. The models are ranked in order of Akaike weights ($_w$AIC$_c$). Log(L): maximized log-likelihood of the model; AIC$_c$: selection criteria; ΔAIC$_c$: difference between the model's AIC$_c$ value and the minimum AIC$_c$ value; %DE: percent deviance explained by model

	Log(L)	AIC$_c$	ΔAIC$_c$	$_w$AIC$_c$	%DE
MSST	−160.386	327.295	0.000	0.402	46.222
SOI+MSST	−159.301	327.491	0.196	0.364	48.507
MSST+CPUE	−160.377	329.643	2.349	0.124	46.242
MSST+CPUE+SOI	−159.301	329.965	2.670	0.106	48.507
SOI+CPUE	−164.518	337.926	10.631	0.002	36.557
SOI	−166.043	338.607	11.313	0.001	32.568
CPUE	−170.307	347.136	19.841	0.000	20.027
Null3	−175.585	357.691	30.397	0.000	1.229
Null5	−175.846	358.213	30.919	0.000	0.193
Null4	−175.881	358.283	30.989	0.000	0.053
Null3+null4	−175.562	360.013	32.719	0.000	1.318
Null3+null5	−175.584	360.056	32.762	0.000	1.233
Null4+null5	−175.833	360.554	33.259	0.000	0.245
Null3+null4+null5	−175.561	362.486	35.192	0.000	1.322

upwelling along the southern Australian coast (Middleton et al. 2007), providing cold water that may enter Bass Strait. Secondly, the warm EAC is enhanced in La Niña years and extends past Bass Strait to the east Tasmanian coast (Harris et al. 1991), and this current may partially block westward flow through the strait, thus causing it to warm. That we found no direct link between seal diet and the SOI may indicate that

one does not exist, or the temporal scales we used were not sufficiently predictive. There may be a delay between cause and effect, or a confounding influence, for example redbait drawn into Bass Strait by a single event may remain there for several years.

Other meteorological conditions can influence annual differences in Bass Strait water temperatures. In some years, single storm events may draw lenses of cold water into western Bass Strait (Blackman et al. 1987). On a longer time scale, the ACW pulses colder than average, then warmer than average Antarctic waters in a northerly direction in a 4 to 5 yr cycle (White & Peterson 1996). Also, the ACW influences a near-decadal cycle in zonal (westerly) and meridional (southerly) winds, and this cycle has been linked to variability in fish recruitment patterns (Thresher 1994) and cetacean stranding periodicity in southeastern Australia (Evans et al. 2005). Further oceanographic investigations in the Bass Strait region are required to help clarify the way in which currents and meteorological conditions may influence sea temperatures.

Inter-annual patterns in the prey

Redbait and jack mackerel are species that commonly school together in south-eastern Australian waters (Williams & Pullen 1993), and annual variability in their surface schooling on the east coast of Tasmania has been related to sea temperature and ENSO cycles (Young et al. 1993). Sea temperatures along the east coast of Tasmania are influenced by changes in the extent of the East Australia Current and the position of its convergence with SASW (Harris et al. 1991). In La Niña years, the East Australia Current is stronger than average and extends further down the Tasmanian east coast, preventing SASW from dominating shelf waters. Having this warmer, nutrient poor water on the shelf reduces primary productivity (Harris et al. 1991), which in turn reduces the abundance of a key zooplankton species, the krill *Nyctiphanes australis*, which is an important prey of redbait and jack mack-
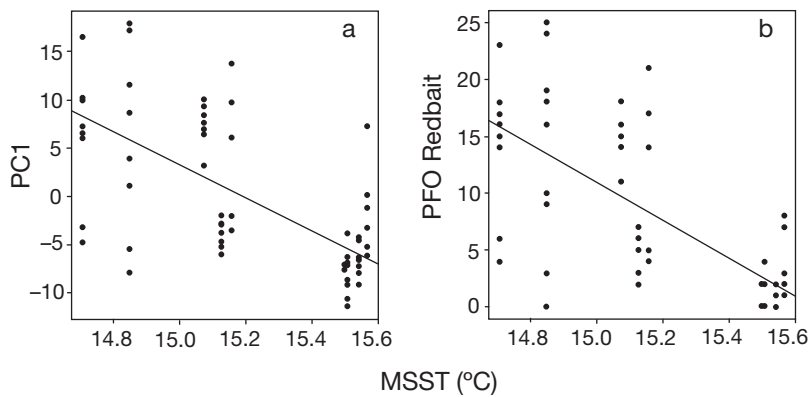
Fig. 4. *Arctocephalus pusillus doriferus.* Graphical representation of the main models identified by the GLM. (a) PC1 in relation to mean sea surface temperature (MSST): PC1 = 260.44 – MSST × 17.15. (b) Proportional frequency of occurrence (PFO) of redbait in seal diet in relation to MSST: PFO Redbait = 260.488 – MSST × 16.635

erel (Young et al. 1993). Surface schooling behaviours of these fish appear linked to krill availability (Young et al. 1993). A purse-seine fishery that targeted surface schools of jack mackerel and redbait during the 1980s and 1990s caught up to 40 000 t in some years and <5000 t in others, with the variation being largely dependant on whether or not the fish surface schooled (Williams & Pullen 1993, Welsford & Lyle 2003).

The known behavioural response of redbait and jack mackerel to water temperature on the east coast of Tasmania may explain variations in the prevalence of these species in western Bass Strait. If cooler surface waters over the shelf to the west of Bass Strait were to bring redbait and jack mackerel up from deeper outer shelf waters toward the surface, currents would be more likely to flush them into the Bass Strait basin, making them available to the fur seals foraging from Seal Rocks. This scenario, however, suggests that redbait and jack mackerel behave similarly, so that their availabilities to the seals should correlate; however, only redbait prevalence fluctuated dramatically in the seals' diet. The reason for this could be that the seals ate mainly juveniles of these species, and the distributions of the juveniles may differ.

Although schooling together when co-occurring, redbait may be a more oceanic species than jack mackerel. Redbait has a broader distribution than jack mackerel, living over isolated sea mounts and in association with continental shelves of all Southern Hemisphere continents (except Antarctica), while jack mackerel inhabits just southern Australian and New Zealand shelf waters (Kailola et al. 1993, Welsford & Lyle 2003). Jack mackerel juveniles occur across the shelf and in sheltered coastlines and bays (Kailola et al. 1993, Williams & Pullen 1993, Welsford & Lyle 2003). Redbait juveniles, in con-

trast, appear to be most abundant offshore and can occur at depths of up to 500 m (Roschin 1985). Moreover, although purse-seine and mid-water trawl fisheries off the Tasmanian east coast have taken largely adult jack mackerel (Jordan et al. 1995), the redbait catch was dominated by juveniles (Welsford & Lyle 2003). Thus, within Bass Strait, the coastal jack mackerel juveniles may be more consistently available to seals foraging from Seal Rocks than the outer-shelf redbait juveniles, which may require inflows of cooler waters from the outer shelf to bring them into the seals' range. More data are needed on the biology of these fishes (particularly in shelf waters west of Bass Strait) to better explain variations in their availabilities to the seals.

Patterns in the sizes of arrow squid eaten by Australian fur seals may also be related to sea temperatures in different years. Smaller squid were caught by Australian fur seals in years of cooler SST in western Bass Strait (i.e. 2002 to 2005, Fig. 2). Cohorts of arrow squid may hatch in all months of the year (Jackson et al. 2005), unlike most fish species which spawn during a single period of the year (e.g. spring-time), and each squid cohort lives for 1 yr. Generally, squid grow faster and to a larger size in warm waters than in cool waters (Jackson et al. 2003). This pattern accords with the Australian fur seals predation on larger arrow squid between 1998 and early 2002, when Bass Strait surface waters were warmer than average, and smaller squid between late 2002 and 2005, when the waters were cooler.

Long-term trends

While 9 yr may represent a long sampling period relative to previous diet studies, it spans the diets of only several generations of Australian fur seals, which mature at 3 to 6 yr (longevity is about 20 yr) (Warneke & Shaughnessy 1985); 9 yr does not encompass long duration climatic cycles. The diet needs to placed into perspective by recognising longer term influences on the seal foraging environment. For example, the benthic foraging Australian fur seal probably originates from an Indian Ocean migration made by the pelagic foraging Cape fur seal *Arctocephalus pusillus pusillus* of southern Africa (Wynen et al. 2001). The benthic foraging behaviour of Bass Strait seals is likely to be an adaptation to prey assemblages available in southeastern Australian waters.

Over the past 200 yr, anthropogenic changes to coastal environments have modified the prey available to Australian fur seals. Firstly, the seals were harvested to near extinction between 1798 and the 1820s (Warneke & Shaughnessy 1985). Since the 1970s, though, Australian fur seal numbers have almost doubled in what appears to be a recovery from the earlier exploitation (Kirkwood et al. 2005). Secondly, commercial fisheries commenced in the late 1800s, initially targeting coastal, then shelf and, in the 1970s, off-shelf species (Kailola et al. 1993, Tilzey & Rowling 2001). Catch statistics have recorded subsequent declines of >50% in most major fisheries (Edgar et al. 2005). Thirdly, in 1995 and 1998, a herpes virus originating from fish-farms in South Australia caused the largest monospecific fish kill ever recorded, that of the local pilchard *Sardinops sagax neopilchardus* (Ward et al. 2001). Pilchards had been the primary prey of many marine species, including seabirds (Bunce & Norman 2000, Chiaradia et al. 2003). The removal of the seals and their recent recoveries, fisheries impacts and the catastrophic loss of pilchards have undoubtedly altered marine trophic structures along the southern Australian continental shelf.

Into the future, anthropogenic effects and oceanographic trends are likely to continue to influence ecosystem structure, prey availability and population trends of Australian fur seals. Climate change is resulting in an overall increase in mean SST (Poloczanska et al. 2007). On the east coast of Tasmania, for example, an increase of >1°C has been recorded since the 1940s (Crawford et al. 2000). Future increases are likely to reduce surface water productivity and have additive effects through the food chain to the seals.

Through routine monitoring of seal diet, we recorded ecosystem fluctuations that have not been previously recognised in Bass Strait. At South Georgia, in the south Atlantic Ocean, inter-annual variability in the fish diet of Antarctic fur seals *Arctocephalus gazelle* has also been related to changes in sea-surface temperature and its influence on the availability of an important prey, Antarctic krill *Euphausia superba* (Reid et al. 2006). Elsewhere, inter-annual variability in otariid diet has been linked to catastrophic changes in whole prey assemblages caused by strong El Niño events (Trillmich & Ono 1991), or the causes of fluctuations have been unclear, either due to complicated ecosystem links or short durations of study. Clearly, long-term data sets are the key to describing inter-annual variability in otariid diet, and their causes and consequences.

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