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Mortality and breeding failure of little penguins, *Eudyptula minor*, in Victoria, 1995–96, following a widespread mortality of pilchard, *Sardinops sagax*

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Abstract. In May 1995, numbers of little penguins, *Eudyptula minor*, coming ashore declined at Phillip Island and St Kilda concurrently with deaths of many penguins in western Victoria and a massive mortality of one of their food species (pilchard) throughout southern Australia. Among 1926 dead penguins reported were 131 banded birds recovered from Phillip Island (86% adults and 14% first-year birds), 26 from Rabbit Island and six from St Kilda. The number of banded penguins found dead per number of adult Phillip Island birds at risk was 2.3% in 1995 compared with an annual mean of 0.7% for 1970–93. Of 29 corpses autopsied, at least 26 died of starvation associated with mild–severe gastro-intestinal parasitism. Following the pilchard mortality, egg-laying by penguins in the subsequent breeding season (1995–96) was ~2 weeks later than the long-term mean and 0.3 chicks were fledged per pair compared with the long-term mean of 1.0. Unlike previous years, few penguins were recorded in Port Phillip Bay in September–October 1995, a period when pilchard schools were infrequently seen. It is concluded that the increase in penguin mortality in northern Bass Strait and the significant reduction in breeding success were associated with the widespread pilchard mortality.

Introduction

The little penguin, *Eudyptula minor*, breeds extensively around southern Australia and in New Zealand (Marchant and Higgins 1990). This species comes ashore at dusk and crosses beaches or rocky platforms to reach its breeding colonies. Colonies at Phillip Island represent ~30% of the population breeding in Victoria (Harris and Norman 1981). Although there is evidence that some previous colonies on Phillip Island have disappeared, those extant are apparently secure (Dann 1992, 1996). However, there was a marked decline in the numbers of penguins crossing Summerland Beach at the ‘Penguin Parade’ between 1977 and 1988, the number of birds breeding in the principal study area (on the eastern colony boundary) between 1968 and 1988, and the number of active burrows in the Penguin Parade area between 1980 and 1987. This decline was attributed to increased mortalities caused both by alien predators (particularly foxes, *Vulpes vulpes*, and stray dogs, *Canis familiaris*), by cars driving through the colony at night and, perhaps, factors operating at sea (Dann 1992). Between 1988 and early 1995, the local breeding population increased follow-

ing both reduction in the number of foxes and dogs and the management of vehicle access. Occasional die-offs (or ‘wrecks’) occur away from Phillip Island, involving relatively large numbers of little penguins. Such wrecks, which include birds from Phillip Island, occur predominantly off western Victoria in autumn and winter and generally affect young birds; other large-scale mortalities occur in Port Phillip Bay in winter and involve mostly adults (Dann *et al.* 1992; Norman *et al.* 1992).

At Phillip Island, the timing of breeding varies from year to year, although egg-laying usually peaks in September–October, chicks fledge about three months later and adults moult in February–March (Reilly and Cullen 1981, 1983). Pilchard (*Sardinops sagax*) and southern anchovy (*Engraulis australis*) make up much of the food of Phillip Island penguins and there is some suggestion that an early onset to laying is triggered by the abundance of pilchards in their diet (Cullen *et al.* 1992). The massive and widespread mortality of pilchards that occurred around southern Australia from March to May 1995 (Griffin *et al.* 1997; Whittington *et al.* 1997) may therefore have affected penguin populations.

Some deaths, of predominantly first-year little penguins, were reported in western Victoria in mid April 1995, and substantially more in late June and July. In May 1995, nightly totals of little penguins at Phillip Island decreased markedly, with numbers showing large declines from long-term means. This paper considers changes in the numbers of penguins coming ashore each evening at Phillip Island, the timing and extent of penguin mortalities around the Victorian coast and the low breeding success in Victoria in 1995–96. It also compares data available from some other penguin colonies in Victoria, and examines information pertaining to populations of penguins at Phillip Island.

Methods

Reports of dead (including banded) penguins

Between 1968 and mid 1995, ~11 300 adult and ~23 400 fledging penguins were banded (flipper tag) in and around colonies at Phillip Island (38°31'S, 145°08'E) in Victoria (Fig. 1). In this study, we examined recoveries of banded little penguins found dead in Victoria from January 1995 and reported to the Australian Bird and Bat Banding Scheme to the end of 1995, in relation to the following: (i) the numbers involved, the timing and their distribution along the southern coast of Australia; (ii) the numbers considered to be at risk of dying within a fixed period following fledging (i.e. young banded within six weeks of fledging, or adults estimated as being at risk within the particular calendar year assuming a stable population and using mean mortality data presented by Dann and Cullen (1990)); (iii) the age and sex of birds involved; and (iv) the timing of recoveries within selected periods (separated into age cohorts whenever possible).

The reports of dead penguins along the Victorian coast throughout 1995 were accumulated but it was not possible to standardize search effort. Samples of dead penguins found along the coast at about the time of the peak mortalities were collected and frozen until later autopsy when causes of death were determined.

Measurement of colony characteristics

Penguins making the evening crossing of one of the beaches at Phillip Island (at the Penguin Parade) within a standard period (50 min from the time of first arrival) have been counted each night since 1982. These totals provide an index of attendance ashore and reflect activities within the colonies. For the present study, nightly totals were averaged for each month during 1982–94 and compared with data obtained in 1995. Particular attention was paid to individual daily totals in 1995 in months when counts were below long-term averages.

Little penguins breed at the westernmost point of Phillip Island (Dann 1992) and data on breeding success have been collected at sites there from 1968 to the present. These areas, each containing 20–50 pairs of penguins, were visited during the day at two-week intervals during the breeding seasons and infrequently at other times. Breeding success here is considered as the number of chicks fledged per breeding pair. Body masses of adults ashore on Phillip Island were measured (day and night) each month to the nearest 25 g on Pesola 2 kg spring balances. Information regarding adults ashore, breeding events and body mass was also obtained at night for the small colony of little penguins breeding at the St Kilda breakwater in Port Phillip Bay. Recovery rates were also obtained from long-term studies at Rabbit Island (~150 km east of Phillip Island) and at Port Campbell (200 km west of Phillip Island, Fig. 1)

Surveys of pilchard distribution and abundance

Aerial surveys were conducted in early daylight along fixed transects in northern central Bass Strait from the shore south to 15 nautical miles

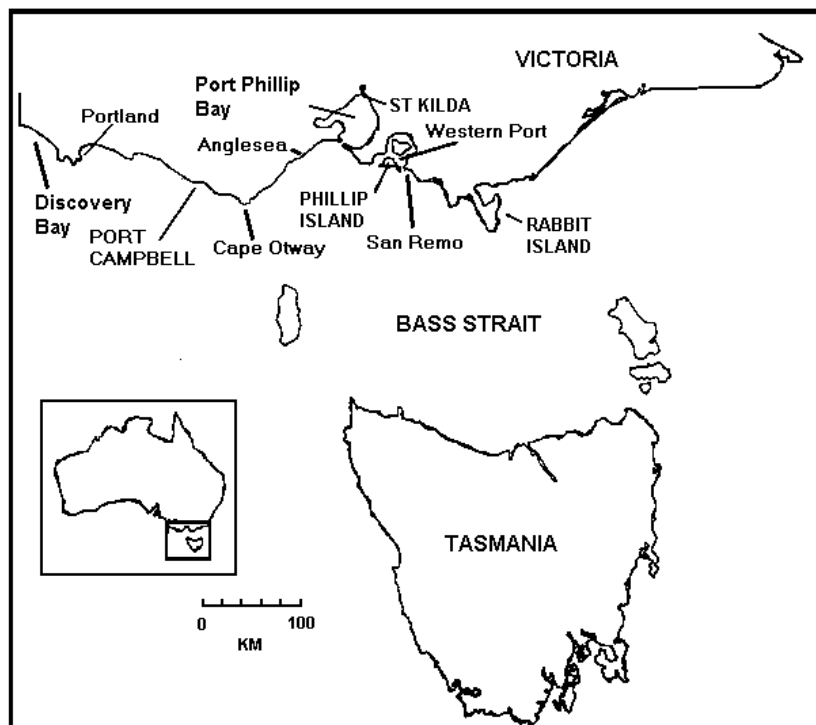


Fig. 1. Locations and colonies of little penguins, *Eudyptula minor*, in Victoria specifically mentioned in the text.

(nm) between September and December 1995. This area (~900 nm²), between Anglesea (85 km west of Phillip Island) and San Remo, was divided into a grid of 45 blocks. Surveys were also conducted within Port Phillip Bay (20 nm², 28 blocks of 5' by 5') and Western Port (4 blocks). During these surveys (flown at 2000 feet, at 120 knots), the area and location of near-surface pilchard schools were determined. Identification of schools was based on physical characteristics and behaviour, and size of each school was assessed on the basis of horizontal shape and area of the school (Squire 1972).

Details of pilchard catches from commercial purse-seiners within Port Phillip Bay, and associated catch-and-effort data, were also obtained for the study period and compared with data available from 1985/1986 to 1994/1995 (Neira *et al.* 1999). The locations and timing of reports of dead pilchards were obtained from CSIRO Marine Research (R. Bradford, personal communication).

Surveys of little penguin distribution at sea

Two census runs were made in Port Phillip Bay in 1995 (15 September and 4 October) along the same transects covered in previous penguin studies and following the methods used by Norman (1992a). Little penguins and other piscivores within 500 m of the boat were counted and their positions estimated by dead reckoning. Data were compared with those available for runs made on similar dates in earlier surveys (Norman 1992a).

Results

Distribution and origin of dead penguins

Apart from 50 dead birds in the second week of April 1995, only small numbers of dead birds were recorded along the Victorian coast in the first half of 1995. However, between June and September 1995, 1926 little penguins were reported dead along the Victorian and South Australian coastline. Most corpses (80%) were recorded west of Cape Otway (Table 1), particularly in Discovery Bay where at least 855 were found (B. Jarrett, personal communication). Among the corpses along the Victorian coastline, 131 were penguins that had been banded at Phillip Island; 26 had been banded at Rabbit Island and six at the St Kilda colony. Apart from the high number involved, their distribution differed significantly ($\chi^2 = 33.7$, df 5, $P < 0.001$) from that of recoveries of previous years (Table 1), with more penguins being found west of Cape Otway and fewer around Phillip Island and between Port Phillip Heads and Anglesea. Recoveries from Phillip Island included only 14% of birds in their first year.

Chronology of penguin deaths

Although a small number of dead penguins were recorded in April, known deaths along the Victorian coast in 1995 were mainly from late June to late August (Fig. 2). The peak reported in late July was due primarily to 855 found in Discovery Bay (Fig. 1). Recoveries of banded adult and first-year penguins (i.e. fledged in early 1995) showed a similar temporal pattern (Fig. 3), with most being found in July and, to a lesser extent, August and September. Between 1980 and 1995, most recoveries of first-year birds (75.3%) occurred between January and April, whereas deaths of banded adults occurred throughout the year with small increases being reported in April, July, September and October. In 1995, adult, but not first-year, recoveries were substantially higher than normal. The concentration of adult recoveries from July to September skewed previous trends (see Dann *et al.* 1992).

In 1995, the average rate of band recovery (from dead adults) per number of adult birds estimated to be at risk (2.3%) was the highest recorded and similar to the rate reported in 1984, when adult mortality was widespread (Norman *et al.* 1992). In 1996, the rate was not significantly different to the mean of previous years (Table 2). For first-year birds, the average rate was 2.6% between 1970 and 1993, and in 1995 the rate was identical; however, it was much higher (6.2%) in 1996 ($\chi^2 = 25.6$, df 1, $P < 0.001$).

For Phillip Island birds, the band recovery rate from dead adults was 0.7% between 1970 and 1993 (Table 3). At Rabbit Island and Port Campbell, the band recovery rate from dead adults was also three to five times higher in 1995 than in previous years ($\chi^2 = 39.9$, df 1, $P < 0.05$, Table 3). In contrast, the band recovery rate from dead adults from the St Kilda colony did not differ in 1995 from previous years. There were insufficient data to make similar comparisons between first-year birds at these sites.

Causes of mortality

Twenty-nine corpses collected between 21 June and 10 August 1995 from Port Phillip Bay (6), Phillip Island (4), and along the western Victorian coast from Anglesea to Portland (19) were autopsied. Twenty-six of these died as a

Table 1. Numbers of first-year and adult little penguins, *Eudyptula minor*, banded at Phillip Island, Victoria and recovered along sections of the Victorian and South Australian coastlines in 1995 ($n = 199$) and from 1968 to 1994 ($n = 1019$), compared with totals of unbanded dead penguins recovered in 1995 ($n = 1926$)

Longitude	Section	1995 (% of recoveries)	1968–94 (% of recoveries)	No. carcasses
137–140°W	South Australia	18	10	240
141–143°W	Cape Otway to Portland	25	30	1307
144°W	Port Phillip Heads to Anglesea	11	17	74
144°30'W	Port Phillip Bay	25	13	197
145°W	Phillip Island to Wilsons Promontory	17	28	74
146–149°W	Wilsons Promontory and eastwards	3	3	34
Total		199	1019	1926

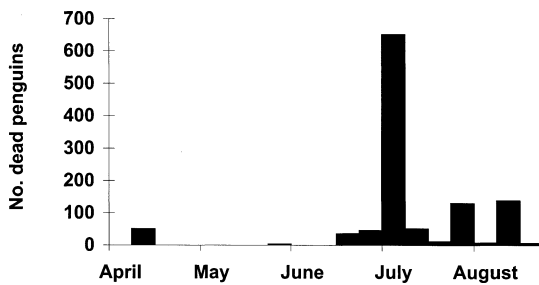


Fig. 2. Numbers of dead little penguins, *Eudyptula minor*, recorded each week along the Victorian coast between April and August 1995.

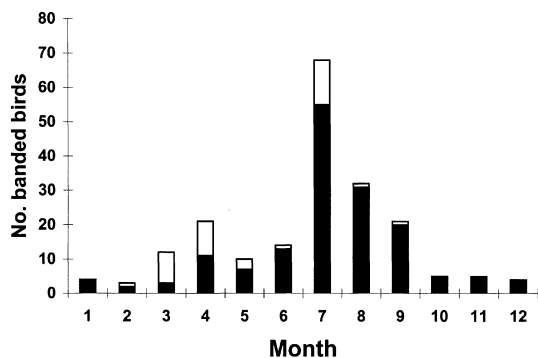


Fig. 3. Numbers of adult and first-year little penguins, *Eudyptula minor*, banded at Phillip Island, and recovered in each month along the Victorian coast in 1995. Black bars, adults; white bars, first-year birds.

Table 2. Recovery rates of bands from dead adult and first-year little penguins, *Eudyptula minor*, banded at Phillip Island, Victoria, between 1980 and December 1996

Rates expressed as number of penguins in the cohort known to have died in each calendar year as a percent of the total number estimated to be at risk. Numbers of birds at risk of dying were calculated for chicks within the six weeks following fledging or, for adults, calculated within the calendar year, assuming a stable population and using mean mortality data presented by Dann and Cullen (1990)

Year	Adults	First-year birds
1980	0.67	2.70
1981	0.22	1.49
1982	1.28	2.70
1983	0.45	1.37
1984	2.24	6.45
1985	0.89	2.10
1986	0.61	4.27
1987	0.58	3.04
1988	1.00	3.09
1989	0.44	2.64
1990	0.51	2.11
1991	1.06	2.03
1992	0.77	1.33
1993	0.59	1.72
1994	0.77	5.08
1995	2.30	2.64
1996	0.61	6.15

Table 3. Comparison of recovery rates of adult little penguins, *Eudyptula minor*, banded at Phillip and Rabbit Islands, Port Campbell and St Kilda between January 1970 and December 1996

In parenthesis, no. birds estimated to be at risk. See Table 2 for details of calculation of recovery rates

Year	Phillip I.	Rabbit I.	Port Campbell	St Kilda
1970–93	0.71 (48866)	0.42 (4492)	0.66 (2418)	2.52 (634)
1994	0.77 (5702)	0.17 (1202)	0.53 (187)	1.86 (161)
1995	2.30 (6622)	2.15 (1535)	2.17 (184)	3.17 (189)
1996	0.61 (6713)	1.15 (1563)	0 (198)	0.56 (180)

consequence of starvation, associated with mild to severe gastro-intestinal parasitism (19 cases; where identified, the nematode *Contracaecum eudyptulae* and the cestode *Tetrabothrius lutzi* were reported), oedemas and air sac problems. In two instances, some infective agents were noted. In another, a garfish, *Hyporhamphus melanochir*, had occluded the pharynx causing pulmonary oedema associated with asphyxiation. Fat deposits were generally absent from autopsied birds and in some instances autolysis was recorded (K. Harrigan and R. Norman, personal communication). Of the 27 corpses sexed at autopsy, 16 were males. Body mass of 11 adult males that died following starvation averaged 728.5 g (± 95.25 s.e., range 644–896 g.); for four adult females, body mass averaged 663.5 g (± 31.7 , 630–706 g). By comparison, adult male penguins coming ashore at Phillip Island in June 1995 had a mean mass of 1215 g (± 13 , $n = 84$) and females 1039 g (± 21 , $n = 46$). The body mass of males in 1995 was similar to the average for 1984–94, whereas females weighed considerably less from July to August 1995 than the previous means for those months (Fig. 4).

Counts and colony events

In 1995, monthly means of nightly counts of little penguins at the Penguin Parade were above long-term means from January to April but then dropped below average between May and August (Fig. 5); numbers in June and July were lower than recorded in any previous monthly minima, but they increased from September and exceeded previous maxima by December 1995. Nightly counts between May and August (Fig. 6) declined substantially about 12 May and numbers arriving ashore were lower than average for the rest of the month, being the lowest recorded during 15–19 May and again during 23–25 May. Throughout May, June and July, nightly counts were well below average, usually below previous minimum counts, with both low numbers and extended minima, continuing until 25 August when counts again began to resemble long-term averages (Fig. 5). Counts at the St Kilda colony were markedly reduced in May and remained so until October, when there was an increase in attendance (Cullen, unpublished).

In 1995–96, not only was egg-laying delayed on Phillip Island (~2 weeks later than the long-term mean of 2 October

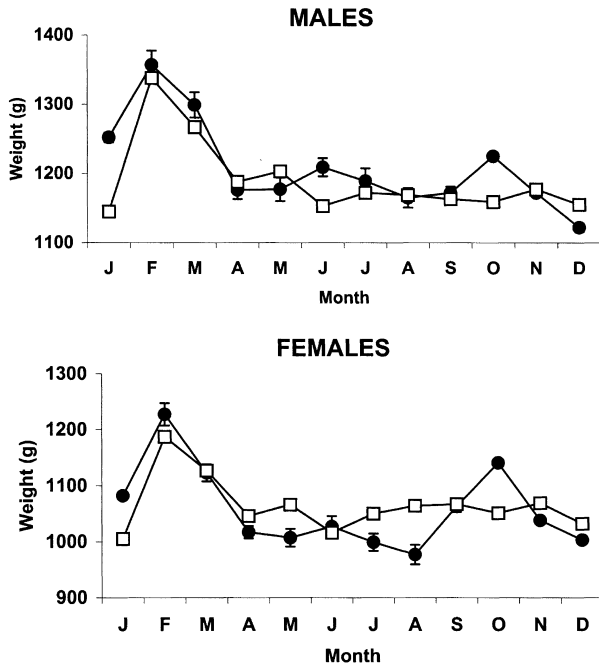


Fig. 4. Monthly weights (mean \pm s.e.) of male and female little penguins, *Eudyptula minor*, in 1995 (●) compared with mean values for 1984–94 (□).

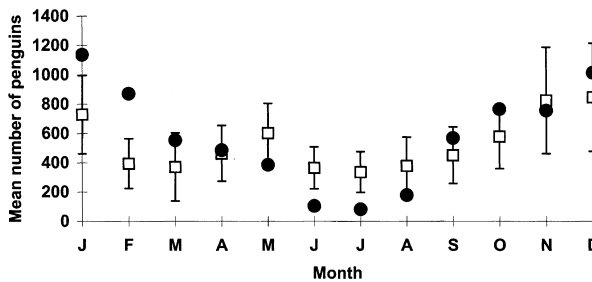


Fig. 5. Monthly means (\pm s.e.) of nightly counts of little penguins, *Eudyptula minor*, coming ashore at Summerland Beach, Phillip Island, Victoria, in 1995 (●) compared with long-term means 1982–94 (□).

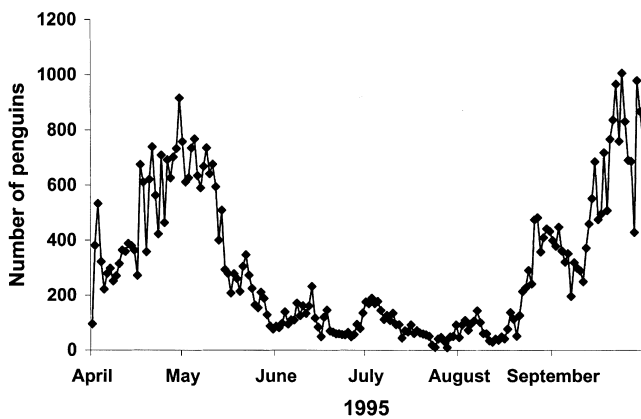


Fig. 6. Nightly counts of little penguins, *Eudyptula minor*, coming ashore at Summerland Beach, Phillip Island, Victoria, between April and October 1995.

± 4.52 days) (Fig. 7), but the subsequent breeding success in the 1995–96 season was poor (0.3 chicks fledged per pair) compared with all but one of the previous 28 years, and substantially less than the long-term mean of 1.0 ± 0.4 chicks fledged per pair ($n = 28$, Fig. 8).

Pilchard distribution and abundance

Aerial surveys conducted during this study in northern central Bass Strait between September and December 1995 revealed few schools of pilchards, and even those found were small. In Port Phillip Bay, no schools were recorded during four aerial surveys in September and October 1995. Two schools were seen twice offshore in September (2 September off Anglesea; 16 September off Anglesea and Phillip Island) and none in October. Between June and November 1995, no pilchards were caught in Port Phillip Bay by commercial fishers despite some searching effort at that time (Neira *et al.* 1999).

Penguin (and other seabird) distribution and abundance in Port Phillip Bay

Penguin numbers in the two boat surveys conducted in Port Phillip Bay in September and October 1995 were low (10 and 0), although similar results were obtained along identical routes in September 1988 (Table 4). Other piscivorous species also showed considerable variation in previous surveys. Totals of individual birds (of species other than penguins) were at their lowest in September 1995 (97), and at a maximum at about

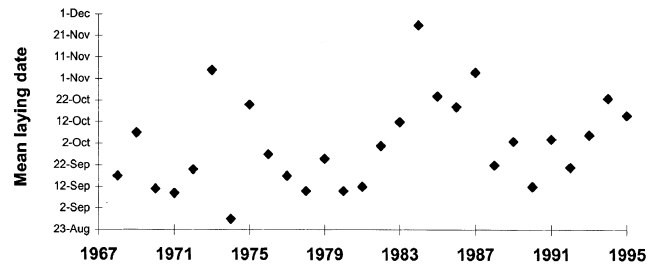


Fig. 7. Mean laying dates of little penguins, *Eudyptula minor*, breeding at Phillip Island, Victoria, between 1968 and 1996.

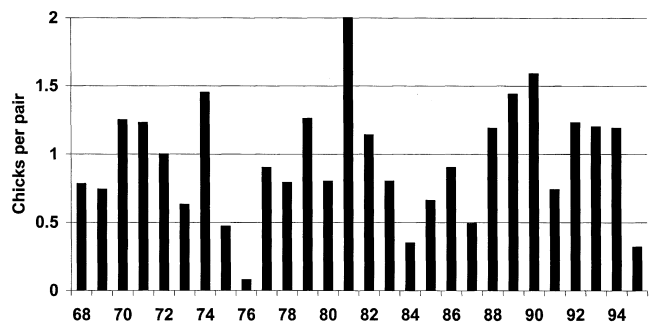


Fig. 8. Number of chicks fledged per breeding pair of little penguins, *Eudyptula minor*, at Phillip Island, Victoria, between 1968 and 1996.

Table 4. Comparison of numbers of little penguin, *Eudyptula minor*, and other piscivorous species during surveys of Port Phillip Bay, Victoria, 15 September and 4 October 1995

Data are also compared with those obtained on similar dates between 1986 and 1988 (Norman 1992a; Norman, unpublished)

Species	Survey dates				
	9.ix.86	17.ix.87	16.ix.88	15.ix.95	4.x.95
<i>Eudyptula minor</i> , little penguin	566	176 ^A	2	10	0
<i>Morus serrator</i> , Australasian gannet	40	17	47	14	57
<i>Phalacrocorax carbo</i> , great cormorant	3	5	3	4	2
<i>P. varius</i> , pied cormorant	340	184	167	70	48
<i>P. melanoleucos</i> , little pied cormorant,	32	11	3	0	11
<i>P. sulcirostris</i> , little black cormorant	4	0	0	4	0
<i>P. fuscescens</i> , black-faced shag	9	20	17	1	121
Cormorant species ^B	0	2	21	2	3
<i>Sterna bergii</i> , crested tern	33	12	18	2	5
Individuals minus penguins	461	251	276	97	247

^AOnly one on 21 October. ^BOccasional birds not identified to higher taxon.

the same time in September 1986 (461). In the more recent surveys, numbers of crested terns and pied cormorants were small compared with those in previous surveys.

Discussion

The decline in numbers and breeding success of penguins at Phillip Island described here was not associated with a concurrent increase in penguin numbers in Port Phillip Bay, whereas numbers in the bay (where foraging birds often visit, Weavers 1992; Collins *et al.* 1999) had previously been negatively associated with attendance at the Penguin Parade (Norman 1992a). Stomach samples of penguins obtained between September and December 1995 showed that returning adults had been feeding mainly on squid, krill and fish species other than pilchards (Chiaradia 1999). The diet in late 1995, and again in the 1996–97 breeding seasons showed a lower pilchard content than in previous studies (Montague and Cullen 1988; Cullen *et al.* 1992; Chiaradia 1999).

At about this time, and unusually, occasional individual penguins were seen swimming in shallow waters well inshore, perhaps searching for food (Clark 1995; Norman, personal observation). Following the decline of penguins at Phillip Island and at the breeding colony in St Kilda in Port Phillip Bay in May, there were no commercial landings of pilchard from Port Phillip Bay, and only a few of the 22 licensed pilchard fishers were searching for them. By comparison, in 1994–95, commercial pilchard fishers in Port Phillip Bay caught >1450 t (Neira *et al.* 1996). Pilchard catches in Port Phillip Bay are usually highest between March and May (Neira *et al.* 1999), but aerial surveys and (current) catch information suggested that pilchards were absent from northern Bass Strait at that time in 1995. In August and September 1995, large numbers of little penguins (probably >>2000) died off western Victoria and South Australia, including birds from Phillip Island. Deaths of birds in late June to August were primarily due to starvation, with

some birds holding intestinal parasites which, unlike the fluke *Mawsonotrema eudyptulae*, tend to pose supplementary problems rather than cause death (Harrigan 1992). In little penguins, starvation may result from a reduction in, or absence of, a food supply, or from a combination of food unavailability and inclement weather (Norman *et al.* 1992). Previously, such mortalities have involved essentially first-year birds (Harrigan 1992; Norman *et al.* 1992), but in 1995 the deaths included birds of all ages, with a predominance of adults. A relatively small but identifiable group of young little penguins (most a few months old) died in April 1995 and were washed up along Victorian beaches. This mortality of young penguins occurs to some degree each year, usually in autumn (Dann *et al.* 1992; Norman *et al.* 1992), and appears to be unrelated to the other mortality of both adults and young from April onwards since these birds had no influence on the numbers of birds coming ashore at Phillip Island.

Pilchard numbers were low during and after the decline in penguin numbers, and pilchards were still not being taken by returning birds sampled between September and December. Foraging adult penguins from Phillip Island were, at least in September and October 1995, dispersed considerably further afield than indicated in previous studies (Norman 1992a; Collins *et al.* 1999). The die-off of pilchards in southern Australia between late March and late June 1995 (Fletcher *et al.* 1997; Griffin *et al.* 1997) was of an unprecedented magnitude and commenced in the eastern Australian Bight, around Spencer Gulf (South Australia). It spread as far westwards and northwards as Geraldton in Western Australia (Fletcher *et al.* 1997) and eastwards and northwards to Noosa in Queensland (Griffin *et al.* 1997). Pilchard deaths began on or about mid March 1995, reached southern South Australia by 20–28 April, and were recorded in Bass Strait, off north-western Tasmania and eastern Victoria in early May. The spread of the die-off (estimated at 0.3–0.5 m s⁻¹, and appar-

ently not associated with surface water movements driven by anomalous winds or currents; Griffin *et al.* 1997), and the subsequent isolation of a possible viral agent (Whittington *et al.* 1997), suggest that the causative agent was transmitted by migrating fish – either the pilchards themselves or another intermediate host (Fletcher *et al.* 1997).

The coincidence of the decline in numbers of penguins at Phillip Island with the onset of pilchard mortality in the area, and the subsequent unseasonal and substantial mortality of adult penguins followed by a late and significantly unproductive breeding and the marked increase in first-year mortality, all suggest that several population parameters were closely linked to the pilchard mortality. We are unable to make more unequivocal connections between the pilchard mortality and penguin population parameters, because most pilchard data were collected after the penguin mortality became obvious. However, because other phenomena such as disease in local colonies were not apparent at the time, the pilchard mortality is the more parsimonious explanation for the food shortage and hence the death of penguins.

One anomaly apparent during the mortality was that only adult pilchards >10 cm fork length were reported as affected in the die-off (Fletcher *et al.* 1997; Griffin *et al.* 1997) and these are usually not taken by little penguins (Cullen *et al.* 1992). Fletcher *et al.* (1997) reported that pilchards affected in Western Australia had mean fork lengths of ~15–16 cm and did not include smaller size cohorts. However, most penguin prey items (mid-water schooling species) are <13 cm in length and adult pilchards, which represented ~23–24% of foods taken by penguins in Victoria, were 8.0 ± 1.9 (maximum 13) cm long (Cullen *et al.* 1992). Competition for small pilchards as prey by other species of birds, marine mammals and fish may have increased significantly after the larger cohort of pilchards died. Other seabirds also take pilchards routinely as a major or minor food component. For example, Norman and Menkhorst (1995) showed that Australasian gannets *Morus serrator*, a major contributor to the avian biomass in Port Phillip Bay (Norman 1992b), feed extensively on pilchards (58% of food mass) of an estimated length of 14 cm. Bunce and Norman (2000) have reported changes in the diet of *M. serrator* following a mortality of pilchards in 1998. There is also a suite of potential competitors for post-larval and juvenile or small adult pilchards. For example, crested terns (*Sterna bergii*) take prey of ~10 cm fork length, black-faced cormorants (*Phalacrocorax fuscescens*) take small fish, pied cormorants (*P. varius*) eat foods of ~14 cm (but up to 19 cm), and the most important biomass contributor off Phillip Island (Norman 1992), the short-tailed shearwater (*Puffinus tenuirostris*), takes fish of ~9 cm (Marchant and Higgins 1990; Higgins and Davies 1996). Additionally, some fish, e.g. barracouta (*Thyrstites atun*) and Australian salmon (*Arripis truttaceus* and *A. trutta*) also feed on post-larval to large adult pilchards and there is no relationship apparent between prey and predator sizes (Hoedt *et al.* 1995); marine

mammals also eat pilchards to a varying extent (Menkhorst 1995). The apparently unaffected juvenile cohort of pilchards remained, therefore, as the food for a suite of predators, and this may explain why obvious mortalities of pilchard-eating species other than penguins were not reported at the time but it does not explain why penguins seemed so affected.

Acknowledgments

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