Vol. 178: 295-305, 1999 | MARINE ECOLOGY PROGRESS SERIES Mar Ecol Prog Ser | Published March 17

Influence of phylogeny, diet, moult schedule and sex on heavy metal concentrations in New Zealand Procellariiformes

Fiona M. Stewart[1,*], Richard A. Phillips[2,], J. Alexander Bartle[3], John Craig[1], David Shooter[1]**

[1]School of Environmental and Marine Science, Tamaki campus, University of Auckland, Private Bag 92019, Auckland, New Zealand

[2]Dept of Biological Sciences, South Road, University of Durham, Durham DH1 3LE, United Kingdom

[3]Museum of New Zealand Te Papa Tongarewa, PO Box 467, Wellington, New Zealand

ABSTRACT: Mercury, cadmium, zinc and copper concentrations were analysed in the liver and kidney tissues of 14 species of albatross and petrel. These birds were obtained as by-catch of the long-line tuna fishing industry in New Zealand waters, and provided a unique opportunity to compare heavy metal accumulation in a group of closely related species. Mercury levels in the liver of the wandering and royal albatrosses were among the highest recorded for free-living birds. In multiple regression analyses, much of the inter-specific variation in cadmium and mercury levels was related to the importance of Crustacea in the diet, to phylogeny, or to the duration of the moult cycle. Species in which crustacea constituted >33% of the diet had significantly lower cadmium concentrations in liver tissues, and mercury concentrations in both liver and kidney tissues, than those in which birds consumed mainly or entirely squid and fish. This accords reasonably well with information on relative mercury and cadmium content of prey species. After accounting for dietary variation, Procellariidae (petrels, shearwaters and prions) and Hydrobatidae (storm petrels) still exhibited higher cadmium concentrations in the liver than Diomedeidae (albatrosses). In addition, albatrosses which took more than a year to moult accumulated higher mercury concentrations in their livers, probably because of a restricted ability to excrete mercury into growing feathers.

KEY WORDS: Diet · Moult · Seabirds · Pollution · Petrel · Albatross

INTRODUCTION

Heavy metal concentrations have been measured in numerous Northern Hemisphere seabirds at many locations, but studies on Southern Hemisphere species are rare. This is perhaps linked to a perception of the southern oceans as being less polluted and generally remaining a cleaner environment. Consequently, seabirds breeding at high southerly latitudes are not generally thought to be at risk from pollution nor are there any current plans to develop their role as biomonitors of toxins in that area. However, recent research has shown some alarming trends in the behaviour of pollutants whereby toxic chemicals released in the tropics or temperate zones are transported through the atmosphere to polar regions, where they accumulate in the ecosystem, cycling in food webs for many years (Mackay et al. 1995, Wania & Mackay 1995). Baseline studies of pollutant concentrations in biota are therefore essential, especially since atmospheric transfer of pollutants from developing countries is expected to continue well beyond cessation of output (Nriagu & Pacyna 1988, Mackay et al. 1995, Wania & Mackay 1995).

*Present address: Dept of Biological Sciences, South Road, University of Durham, Durham DH1 3LE, United Kingdom
**Addressee for correspondence.
E-mail: r.a.phillips@durham.ac.uk

Two potential pollutants of particular concern are the heavy metals, mercury and cadmium (Furness 1993). Currently, anthropogenic inputs are considered more important than natural sources in the biogeochemical cycle of mercury (Nriagu & Pacyna 1988, Slemr & Langer 1992). Moreover, it was estimated recently that mercury levels increased by more than 1% yr^{-1} in the South Atlantic Ocean from 1977 to 1990 (Slemr & Langer 1992). Previous studies have shown that many seabirds, particularly Procellariiformes (albatrosses and petrels), accumulate high levels of both mercury and cadmium (Muirhead & Furness 1988, Walsh 1990, Thompson et al. 1993). This is considered to be a consequence primarily of the natural cycling of these elements in the marine ecosystem, and their ability to bioaccumulate in food webs. Long-lived predatory species, which are at the apex of the food chain, are therefore prime end-point accumulators of potentially toxic pollutants.

Research on Northern Hemisphere species suggests that accumulation patterns are markedly species-specific (Walsh 1990, Becker et al. 1994, Stewart et al. 1997, Monteiro et al. 1998). Much of this inter-specific variation may be attributable to phylogeny as well as reflecting differences in physiology or ecology, yet few studies have attempted to identify which of these are the most important factors in a large number of species from within the same taxonomic order. This study records the cadmium, mercury, zinc and copper levels in individuals of 14 species of Procellariiformes obtained as fisheries by-catch in New Zealand waters in 1995 and 1996. This provided a unique opportunity to investigate heavy metal dynamics in a large number of closely related species, and to assess the importance of phylogeny, sex, diet and moult schedule on metal levels.

MATERIALS AND METHODS

The seabirds in this study were obtained as by-catch of the long-line tuna fishing industry around New Zealand in 1995 and 1996. These were: wandering albatross *Diomedia exulans antipodensis* and *D. exulans gibsoni*, southern royal albatross *D. epomophora epomophora*, northern royal albatross *D. epomophora sanfordi*, shy albatross *D. cauta steadi*, black-browed albatross *D. melanophris impavida*, southern Buller's albatross *D. bulleri bulleri*, southern giant petrel *Macronectes giganteus*, sooty shearwater *Puffinus griseus*, white-chinned petrel *Procellaria aequinoctialis*, black or Parkinson's petrel *Procellaria parkinsoni*, grey petrel *Procellaria cinerea*, cape petrel *Daption capense*, fairy prion *Pachyptila turtur*, grey-faced petrel *Pterodroma macroptera gouldi* and black-bellied storm petrel *Fregetta tropica*.

Birds were tagged and recorded by observers when landed on board fishing vessels, flash-frozen and later transferred still frozen to the Natural History Unit of the Museum of New Zealand, Wellington. They were then defrosted overnight before dissection using stainless steel instruments. All birds were sexed, and samples of liver and kidney removed. Liver and kidney tissues were refrozen and transported to the University of Auckland for analysis. Prior to analysis, tissues were dried to constant mass at 50°C.

Heavy metal analysis. For mercury analysis, samples of 0.05 to 0.10 g of dried liver and kidney tissue were acid-digested according to the method of Furness et al. (1986). Total mercury in the samples was determined by cold vapour analysis using a GBC Atomic Absorption Spectrophotometer. For cadmium, zinc and copper determination, 0.05 to 0.5 g of tissue was digested in 10 ml concentrated nitric acid on a hot plate by first pre-soaking for 2 h and then boiling until the sample had completely digested. Samples were then diluted with deionised water and analysed by flame atomic absorption spectrophotometry.

Accuracy and reproducibility of methods for mercury, cadmium, zinc and copper determination were tested by using NRC DOLT-2 (National Research Council, Canada), and NIST Bovine Liver (National Institute of Standards and Technology, U.S. Dept of Commerce, No. 1577b) reference standards. All samples were run in duplicate and reference material, standards and blanks were analysed along with each set of samples.

Statistical analysis. Levels of copper, zinc, cadmium and mercury in liver and kidney were compared among species using 1-way ANOVAs. Metal levels in the 2 sexes were compared within species with sufficiently large sample sizes. Multiple regressions were carried out to investigate the influence of phylogeny, diet and moult schedule on heavy metal levels. The mean (or single) measurement for each species was included as the dependent variable. Independent variables were coded as dummy variables with 1 of 2 possible values. To look at phylogenetic differences, Diomedeidae (albatrosses) were coded as 1, and Procellariidae (petrels, shearwaters and prions) and Hydrobatidae (storm petrel) coded as 0. An extensive review of published studies of diet during the breeding season was compiled. Reliance on each of 3 main prey categories (fish, cephalopods and Crustacea) was included as a separate variable in the regressions. If over 33% of the diet by percentage occurrence or percentage wet mass was made up by a particular type of prey at any site (see Table 2), that prey was considered to be of major importance and the representative variable in the regression was coded as 1. If the prey category was of minor importance or absent from the diet, the variable was coded as 0. Data on moult duration was patchy (see Marchant & Higgins 1990 for details), but it was clear that in wandering albatross, royal albatross and black-browed albatross, feathers routinely take more than 1 yr to replace. Consequently, the variable representing moult duration was coded as 1 in these 3 species. In the absence of information to the contrary, all other species were assumed to replace their feathers annually and were coded as 0.

Several of the birds had been partially eaten by predators while they had been immersed on the long-line and as a result were missing liver or kidney tissue. Consequently, sample sizes vary slightly depending on the analysis. The southern giant petrel had been ringed as a chick on Elephant Seal Island, South Shetland Islands in 1992, and was only 3 yr old when caught. Therefore, although the values for heavy metal concentrations are presented in the tables, this individual was excluded from statistical analyses. Sub-species of wandering and royal albatrosses were grouped for analysis. Metal concentrations are presented in the results as means ± 1 SD in µg g^{-1} on a dry mass basis.

RESULTS

Inter-tissue comparisons

Mercury, cadmium, zinc and copper concentrations in liver and kidney tissues of the 14 species are presented in Table 1. In all species, with the exception of grey-faced petrel, mercury levels were higher in liver than in kidney tissue, and cadmium concentrations were higher in kidney than in liver tissue. By contrast, inter-specific variation in levels of the essential metals, zinc and copper, did not follow a consistent pattern, some species having higher levels of these metals in the liver and others in the kidney. A low

Table 1. Concentrations of cadmium, mercury, zinc and copper in liver and kidney tissues of Procellariiformes in 1995 and 1996. Mean values (µg g^{-1} dry mass) are presented ± 1 SD, with coefficient of variation (CV) below. Sample sizes (n) shown in parentheses in the first column unless indicated otherwise for particular metals in subsequent columns. **$p < 0.01$, ****$p < 0.0001$

Species (n)	Cadmium		Mercury		Zinc		Copper	
	Liver	Kidney	Liver	Kidney	Liver	Kidney	Liver	Kidney
Diomedea exulans (9)	27.2 ± 21.5	125.4 ± 62.5	360.0 ± 183.0	23.7 ± 16.3	303.5 ± 131.1	224.2 ± 91.6	38.9 ± 28.1	15.9 ± 5.8
	79	50	51 (8)	69 (7)	43	41	72	37 (8)
Diomedea epomophora (4)	11.5 ± 5.6	132.2 ± 84.9	449.3 ± 490.1	12.9 ± 8.7	240.3 ± 99.7	149.2 ± 47.6	31.1 ± 14.7	16.6 ± 4.6
	49	64	109 (3)	68	42	32	47	28
Diomedea cauta (42)	7.7 ± 4.1	74.2 ± 23.9	35.0 ± 17.6	5.1 ± 5.1	127.6 ± 28.9	150.3 ± 32.8	21.9 ± 7.2	12.9 ± 2.1
	53 (40)	32	50 (29)	99 (30)	23 (40)	22	33 (40)	16
Diomedea bulleri (26)	13.4 ± 5.3	120.5 ± 41.3	22.2 ± 13.4	4.8 ± 4.6	145.5 ± 53.9	151.1 ± 27.6	14.1 ± 2.9	11.2 ± 2.5
	39 (25)	34	61 (24)	98 (25)	37 (25)	18	20 (25)	22
Diomedea melanophris (6)	19.4 ± 7.9	85.7 ± 33.8	124.6 ± 74.6	7.6 ± 11.5	148.1 ± 25.8	144.3 ± 30.9	16.3 ± 2.2	9.8 ± 1.7
	41 (5)	40	60 (5)	152 (5)	17 (5)	21	14 (5)	18
Puffinus griseus (7)	28.2 ± 15.3	151.1 ± 64.8	2.5 ± 1.8	1.7 ± 1.1	91.3 ± 17.3	143.8 ± 25.8	16.7 ± 3.8	19.0 ± 2.0
	54	43 (6)	71	66 (6)	19	8 (6)	23	11 (6)
Procellaria aequinoctialis (27)	20.7 ± 9.3	87.5 ± 33.8	79.4 ± 62.9	12.6 ± 18.6	122.2 ± 36.3	160.0 ± 37.5	22.1 ± 5.5	16.7 ± 4.4
	45	39	79 (25)	148 (25)	30	23	25	26
Procellaria cinerea (6)	44.9 ± 19.0	190.0 ± 87.7	142.8 ± 146.8	18.9 ± 18.1	146.1 ± 42.8	169.1 ± 50.5	16.2 ± 4.4	23.8 ± 6.6
	42	46	103 (4)	96 (5)	29	30	27	28
Procellaria parkinsoni (2)	35.6 ± 13.6	93.4 ± 23.0	130.0 ± 9.0	52.1 ± 8.6	183.7 ± 30.4	97.1 ± 59.5	12.9 ± 0.3	15.6 ± 0.8
Pachyptila turtur (2)	24.0 ± 1.4	75.9 ± 9.2	2.6 ± 0.8	2.5 ± 0.8	130.4 ± 24.1	132.5 ± 0.7	19.1 ± 4.4	18.3 ± 1.8
Macronectes giganteus (1)	9.4	30.6	96.6	32.3	136.1	143.4	11.9	11.0
Pterodroma macroptera (1)	39.8	130.1	21.3	28.3	247.2	140.7	12.9	15.2
Daption capense (1)	15.7	98.9	3.0	1.9	90.4	122.9	10.6	29.82
Fregatta tropica (1)	18.1	99.1	–	–	119.5	155.1	18.7	–
ANOVA result	$F_{12,129} = 10.7$ ****	$F_{12,132} = 5.6$ ****	$F_{11,110} = 12.6$ ****	$F_{11,112} = 5.4$ ****	$F_{12,129} = 10.0$ ****	$F_{12,132} = 2.9$ **	$F_{12,129} = 5.0$ ****	$F_{11,130} = 12.4$ ****

coefficient of variation (CV = 100 × SD/mean) is usually taken to be an indication that a particular metal is regulated within internal tissues (Walsh 1990). CVs were generally highest for mercury, lower for cadmium, and lower still for copper and zinc levels.

Inter-specific variation in metal levels

There were highly significant differences among species in concentrations of cadmium, mercury, zinc and copper in liver and kidney tissue (Table 1).

Cadmium

Multiple Tukey ranges tests indicated that cadmium concentrations in the kidney of shy albatross, Buller's albatross, black-browed albatross and white-chinned petrel were significantly lower than in grey petrel, and those in shy albatross were also lower than in Buller's albatross and sooty shearwater. Mean cadmium concentrations in liver tissue exhibited a much lower overall range. Mean concentrations in shy albatross, wandering albatross, royal albatross, Buller's albatross, black-browed albatross and white-chinned petrel were lower than in grey petrel, those in shy albatross were also lower than in wandering albatross, white-chinned petrel, sooty shearwater and black petrel, and, in addition, those in Buller's albatross were lower than in wandering albatross and sooty shearwater.

Mercury

Mercury levels in the liver of royal albatross were significantly higher than in all other species apart from wandering albatross. Levels in wandering albatross were also significantly higher than all other species, with the exception of royal albatross, grey-faced petrel and black petrel. Variation in mercury levels in kidney tissue were less pronounced. Black petrel had significantly higher levels than all other species apart from wandering albatross and grey-faced petrel, and, in addition, wandering albatross had significantly higher levels than shy albatross, Buller's albatross and sooty shearwater.

Zinc

Inter-specific variation in zinc concentration was generally less marked (Table 1). Zinc levels in the kidney of shy albatross, Buller's albatross, black-browed albatross, white-chinned petrel, sooty shearwater and black petrel were significantly lower than in wandering albatross. Similarly, in the liver, zinc concentrations were significantly lower in shy albatross, Buller's albatross, black-browed albatross, white-chinned petrel, sooty shearwater, cape petrel, grey petrel and fairy prion than in wandering albatross, and those in shy albatross, white-chinned petrel and sooty shearwater were also lower than in royal albatross.

Copper

Variation in copper levels in the kidney was more pronounced. Mean concentration in shy albatross, Buller's albatross, black-browed albatross, wandering albatross, royal albatross, black petrel and white-chinned petrel were lower than in black-bellied storm petrel, and in all these species, with the exception of royal albatross and black petrel, levels were also lower than in grey petrel. In addition, levels in shy albatross, Buller's albatross and black-browed albatross were significantly lower than in white-chinned petrel, grey petrel and sooty shearwater. In contrast, in the liver, copper concentrations of wandering albatross were significantly higher than in shy albatross, Buller's albatross, black-browed albatross, white-chinned petrel, sooty shearwater, grey petrel and black petrel.

Influence of phylogeny, diet and moult duration on metal levels

Cadmium

In the stepwise multiple regression, inter-specific variation in cadmium concentration in the liver was related to crustacea consumption ($F_{1,11} = 6.3$, $p < 0.05$, $r^2 = 0.36$), with family (Diomedeidae vs Procellariidae and Hydrobatidae) explaining a further 34% of the variation ($F_{2,10} = 11.7$, $p < 0.005$, $r^2 = 0.70$). The association between consumption of crustacea and cadmium levels was negative, and, in addition, Procellariidae and Hydrobatidae had higher cadmium concentrations than Diomedeidae. If the variable representing family was unavailable, none of the remaining variables entered the regression after crustacea. In contrast to these results for liver, none of the independent variables had a significant effect on cadmium concentrations in the kidney.

Mercury

In the stepwise multiple regression, inter-specific variation in mercury concentration in the liver was related to moult duration ($F_{1,10} = 19.2$, $p < 0.005$, $r^2 =$

0.66), with crustacea consumption explaining a further 18% of the variation ($F_{2,9}$ = 22.9, p < 0.001, overall r^2 = 0.84). Species that took more than a year to replace their feathers had higher mercury levels, and those that ate substantial amounts of crustacea had lower mercury levels. By comparison, in the regression, crustacea consumption ($F_{1,10}$ = 14.2, p < 0.005, r^2 = 0.59), but not moult, had a significant effect on mercury concentration in the kidney. Again, those species that consumed lots of crustacea had lower mercury levels.

Zinc

In the stepwise multiple regression, inter-specific variation in zinc concentration in the liver was related to crustacea consumption ($F_{1,11}$ = 19.6, p < 0.001, r^2 = 0.64), and family explained a further 15% of the variation ($F_{2,10}$ = 18.5, p < 0.0005, r^2 = 0.79). There was a negative association between consumption of crustacea and zinc levels. In contrast to cadmium levels, zinc concentrations in the liver of Diomedeidae were higher than in Procellariidae and Hydrobatidae. With family unavailable, moult entered the regression equation after crustacea consumption, and explained only slightly less (14%) of the additional variation in zinc levels (overall $F_{2,10}$ = 17.9, p < 0.001, r^2 = 0.78). Species that took more than a year to replace their plumage had higher zinc levels. As with cadmium, zinc levels in the kidney were unaffected by any of the independent variables.

Copper

Copper levels in the liver were also influenced by moult duration ($F_{1,11}$ = 9.5, p < 0.02, r^2 = 0.46), again with higher levels in species that took longer to regrow their feathers. In the kidney, variation in copper levels was related to family ($F_{1,10}$ = 6.1, p < 0.05, r^2 = 0.38), with the Procellariidae and Hydrobatidae exhibiting higher levels than Diomedeidae. With family unavailable for entry, levels of copper were related to squid consumption ($F_{1,10}$ = 5.6, p < 0.05, r^2 = 0.36), with lower levels in species that consumed substantial amounts of squid.

Influence of sex

Samples of shy albatross, Buller's albatross and white-chinned petrel were large enough to test for the influence of sex on metal levels. *t*-tests revealed no differences between the sexes in cadmium or mercury concentrations in either organ (results not presented). However, zinc concentration was greater in the liver of females than males in both shy albatross (males, n = 20, mean = 118.0 ± 25.8 µg g^{-1}; females, n = 20, mean = 136.8 ± 29.4 µg g^{-1}; t_{38} = 2.1, p < 0.05) and Buller's albatross (males, n = 15, mean = 126.9 ± 41.6 µg g^{-1}; females, n = 10, mean = 173.2 ± 60.2 µg g^{-1}; t_{23} = 2.3, p < 0.05). Zinc concentration in the kidney was also higher in female than male Buller's albatross (males, n = 15, mean = 139.0 ± 21.5 µg g^{-1}; females, n = 11, mean = 167.5 ± 27.2 µg g^{-1}; t_{24} = 3.0, p < 0.01).

DISCUSSION

Mercury and cadmium concentrations: comparison with other studies

In terms of inter-specific variation in mercury and cadmium concentrations, the most interesting tissues to consider are, respectively, liver and kidney, as these are the principal sites for long-term storage (Walsh 1990). The wandering and royal albatrosses analysed in this study had among the highest concentrations (dry mass) of mercury in the liver of any free-living bird (wandering albatross, mean = 360 ± 183 µg g^{-1}; royal albatross, mean = 449 ± 490 µg g^{-1}), far in excess of those which would cause severe renal dysfunction and toxic effects in terrestrial birds (Scheuhammer 1987). Mercury concentrations in the liver of the black-browed albatross were also relatively high (mean = 125 ± 75 µg g^{-1}), particularly in comparison with the similarly-sized shy albatross (mean = 35 ± 18 µg g^{-1}) and Buller's albatross (mean = 22 ± 13 µg g^{-1}). Several of the petrels analysed, including grey petrel, black petrel and white-chinned petrel, had also accumulated considerably higher mercury concentrations (means of 143 ± 147, 130 ± 9, and 79 ± 63 µg g^{-1}, respectively) than shy and Buller's albatrosses.

Part of the reason why levels in Procellariiformes, in wandering and royal albatrosses in particular, are so high without the birds apparently experiencing any toxic effects is that they may be able to demethylate mercury from its more toxic methyl form to the less toxic inorganic form (Thompson & Furness 1989a, Honda et al. 1990). The inorganic mercury can then be stored, possibly bound up in a selenium complex, where it may accumulate perhaps even over the lifetime of the bird (Thompson & Furness 1989a). Thompson & Furness (1989a) found for 12 species of seabird (penguin, albatross, petrel, prion, shearwater and skua) that, as the total amount of mercury in the liver increased, the percentage of methyl mercury decreased, suggesting that many, if not all, species could demethylate mercury to a greater or lesser extent. Any remaining methyl mercury can be transferred into the

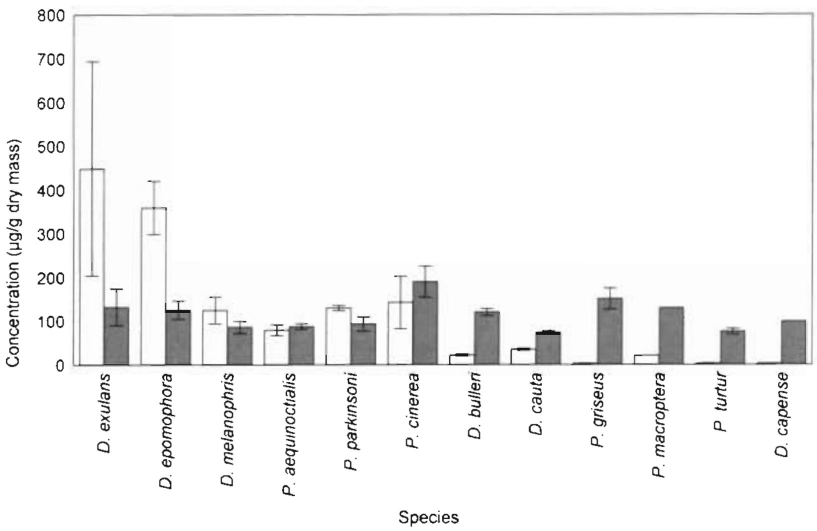

Fig. 1. Inter-specific differences in the pattern of accumulation of mercury in the kidney and cadmium in the liver of New Zealand Procellariiformes. Cadmium concentrations are indicated by shaded columns, mercury by open columns. Error bars are ±1 SE

plumage during moult, since it cannot be excreted in the inorganic form.

In contrast to mercury, the pattern of accumulation of cadmium in the kidney was entirely different, showing no correspondence with inter-specific variation in mercury levels; the greatest concentrations were recorded not in the large albatrosses, but in grey petrels and sooty shearwaters (means of 190 ± 88 and 151 ± 65 µg g^{-1}, respectively, see Table 1 and Fig. 1). Although cadmium concentrations were high, they did not reach the level of 100 to 200 µg g^{-1} wet mass thought to cause toxic effects (Scheuhammer 1987).

Published data on mercury and cadmium concentrations for a number of southern ocean albatross and petrel species from Gough Island are presented in Muirhead & Furness (1988), for others from the New Zealand region in Lock et al. (1992) and for sooty shearwaters collected in the North Pacific in Honda et al. (1990). Unfortunately, in these studies, all tissues were analysed on a wet mass basis and are not directly comparable. Water content of tissues can vary greatly both within and between species (Furness et al. 1994, Stewart unpubl. data), and analysis of dried samples is clearly preferable given the error involved in any conversion to dry mass equivalents. In addition, sample sizes in both Muirhead & Furness (1988) and Lock et al. (1992) were small for many species, and, in view of the high level of individual variation in metal concentrations, the mean values should be viewed with caution. Furthermore, many of the specimens analysed by Lock et al. (1992) were beached birds, and in many cases would have starved to death. Atrophy of internal tissues associated with starvation is likely to have altered both water content and metal levels. However, in keeping with the pattern from this study (see Fig. 1), Honda et al. (1990) did find that sooty shearwaters accumulated very low levels of mercury in the liver, but high concentrations of cadmium in the kidney.

Inter-specific variation in zinc and copper concentrations

There was a fair degree of variation in zinc and copper levels in the albatrosses and petrels analysed in this study (Table 1). Zinc and copper are essential metals, and, as such, their concentrations in the body are regulated (Walsh 1990). Consequently, both intra- and inter-specific variations are expected to be generally quite low (Walsh 1990). However, concentrations in internal tissues will fluctuate depending upon requirements, and, replacement of moulted feathers, changes in nutritional requirements during breeding, and seasonal changes in diet may all have an influence (Stewart et al. 1994). Changes in zinc and copper levels may also result from co-accumulation with cadmium, as all 3 bind onto the same low molecular weight protein, metallothionein (Stewart et al. 1996). Metallothionein is thought to have a protective influence which ameliorates the potential toxic effects of cadmium, as well as being involved in storage of both zinc and copper. Zinc and copper were correlated with cadmium concentrations in most of the albatross and petrel species in this study (Stewart unpubl. data), which could account for some of the inter-specific variation. It is as yet unclear whether increases in zinc and copper levels per se offer some protection from the toxic effects of cadmium, or whether they are an incidental consequence of cadmium-mediated metallothionein induction.

Patterns of accumulation of mercury and cadmium

The pattern of accumulation of mercury in the liver and cadmium in the kidney in the different species appears to fall into 3 broad categories (see Fig. 1): extremely high mercury and high cadmium levels (wandering and royal albatross), moderately high mercury and high cadmium levels (black-browed albatross, white-chinned petrel, black petrel and grey petrel) and low or very low mercury but high cadmium levels (Buller's albatross, shy albatross, sooty shearwater, grey-faced petrel, cape petrel and fairy prion). There was no relationship between mercury and cadmium burdens, but this is unsurprising given the distinctive biochemistry of the 2 metals (Scheuhammer 1987, Walsh 1990, Stewart et al. 1996).

Factors determining intra- and inter-specific variation in mercury and cadmium levels

Diet

Diet is often considered the most important factor in determining metal levels (Hutton 1981, Becker et al. 1994, Monteiro et al. 1998). In this study on a number of closely related seabirds, differences in diet were responsible for a considerable amount of the inter-specific variation in levels of some metals. Species that included appreciable amounts of crustacea in their diet (>33%; see 'Materials and methods') had lower cadmium concentrations in liver tissue, and lower mercury concentrations in both liver and kidney tissue, than those that tended to rely predominantly on squid and fish alone.

Although there are many published values for heavy metal concentrations in seabirds, there is a paucity of data on total metal content of their prey. Analysis of fish, squid and crustacea tends to be conducted in order to assess the threat of contamination to humans after consumption and often only muscle tissues are analysed. Since metals are concentrated mainly in liver, kidney, or digestive gland (cephalopods) tissue, and these are not only the largest sources of metals but are probably also consumed preferentially by scavenging species, many studies are of limited value in determining heavy metal exposure to seabirds.

Cephalopod digestive glands do contain high concentrations of cadmium: 19 to 110 $\mu g\ g^{-1}$ dry mass in *Notodarus gouldi* (Smith et al. 1984), 71 to 694 $\mu g\ g^{-1}$ in *Ommastrephes bartrami*, 42 to 1106 $\mu g\ g^{-1}$ in *Symplectoteuthis oulananiensis* and 33 to 233 $\mu g\ g^{-1}$ in *Loligo opalescens*, all dry mass (Martin & Flegal 1975), and 31 to 146 $\mu g\ g^{-1}$ wet mass in arrow squid *Notodarus sloani* (Fenaughty et al. 1988). Muscle tissue of cephalopods contains comparatively low levels of mercury, with mean values of less than 5 $\mu g\ g^{-1}$ dry mass (Rossi et al. 1993) and 0.15 $\mu g\ g^{-1}$ wet mass (Monteiro et al. 1992) recorded. As indicated above, however, most mercury is likely to be in the digestive gland, but unfortunately no data are available.

In fish, in general, both cadmium and mercury levels in muscle tissue are usually low (<1 $\mu g\ g^{-1}$ wet mass), with those in kidney and liver tissue somewhat greater (Thompson 1990). However, mesopelagic species, as well as some other groups, exhibit very high mercury concentrations (Thompson 1990, Monteiro et al. 1996). Cadmium concentrations of crustacea are variable, with values (wet mass) of 0.1 to 0.7 $\mu g\ g^{-1}$ in copepods, 7 to 9 $\mu g\ g^{-1}$ in decapods and as high as 24 to 34 $\mu g\ g^{-1}$ in amphipods (Ritterhoff & Zauke 1997) recorded. In contrast, mercury levels in crustacea are generally very low, at 0.1 to 0.7 $\mu g\ g^{-1}$ wet mass (Dietz et al. 1996, Ritterhoff & Zauke 1997).

The overall pattern seems to be that cadmium concentrations are higher in cephalopods and some crustacea than in fish, and mercury concentrations are far greater in fish and cephalopods than in crustacea. Inter-specific variation in mercury and cadmium concentrations in tissues of the procellariiform seabirds in this study therefore accords reasonably well with that in their principal prey. However, dietary variation provided only part of the explanation for the patterns of metal accumulation. Several species with somewhat similar diets had quite different metal burdens. For example, both wandering and royal albatrosses show much higher mercury concentrations than Buller's albatross, grey-faced petrel, white-chinned petrel and sooty shearwater, even though all share the characteristic of a diet, at least during the breeding season, which includes considerable quantities of cephalopods (Table 2). High mercury levels, particularly in wandering and royal albatrosses, may be partly attributable to greater longevity, as birds retain a proportion of ingested mercury from one year to the next.

Differences in size or trophic status of squid prey might account for some of the variation in metal levels. However, although there is a slight tendency for wandering and royal albatrosses to consume larger cephalopods on average than the smaller albatrosses and petrels, size selection of squid by procellariiforms is not particularly pronounced (Ridoux 1994, Croxall & Prince 1996). Part of the explanation may instead lie in the relative importance in the diet of mercury-rich mesopelagic prey (both fish and squid), particularly in light of recent suggestions that consumption of mesopelagic prey is a crucial determinant of mercury burdens in North Atlantic seabirds (Monteiro et al. 1998, Thompson et al. 1998).

Moult

One factor that did account for some of the inter-specific variation in the level of certain metals was moult duration (see 'Results'). Mercury can be eliminated from internal tissues in its methyl form by transportation from storage in the liver into growing feathers during the moult cycle (Furness et al. 1986, Thompson &

Table 2. Diet of albatrosses and petrels during the breeding season. PWM: percentage of wet mass; PO: percentage of samples containing a particular item; PDM: percentage of dry mass

Species	Location	Type	Fish	Cephalopod	Crustacea	Carrion	Tunicate	Other	Source
Diomedea exulans	Bird Island, South Georgia	PWM	42	40	<1	19	–	–	Prince & Morgan (1987)
	Crozet Islands	PWM	15	77	<1	8	–	–	Ridoux (1994)
	Marion Island	PWM	37	59	<1	5	–	–	Cooper et al. (1992)
Diomedea epomophora	Campbell Island, NZ	PWM	21	75	3	–	1	–	Marchant & Higgins (1990)
	Chatham Islands, NZ	PWM	14	85	–	–	1	–	Marchant & Higgins (1990)
	Taiaroa Head, NZ	PWM	15	80	3	–	2	–	Marchant & Higgins (1990)
Diomedea cauta	Albatross Island, Tasmania	PO	59	53	35	–	32	–	Green (1973) cited in West & Imber (1986)
Diomedea bulleri	Snares Islands, NZ	PO	64	79	43	–	29	21	West & Imber (1986)
	Chatham Islands, NZ	PO	31	92	46	–	23	15	West & Imber (1986)
Diomedea melanophris	Bird Island, South Georgia	PWM	38	21	40	–	–	2	Prince (1980)
	Falkland Islands	PWM	47	47	3	–	–	3	Thompson (1992)
	Kerguelen Islands	PWM	87	7	3	3	–		Weimerskirch et al. (1988)
	Crozet Islands	PO	58	42	–	42	–	–	Weimerskirch et al. (1986)
Macronectes giganteus	Bird Island, South Georgia	PWM	1	1	21	77	–	1	Hunter (1985)
	Signy Island	PWM[a]	1	4	27	68	–	1	Hunter (1985)
	Terre Adélie, Antarctica	PWM[a]	5	1	10	83	–	1	Hunter (1985)
	Macquarie Island	PWM[a]	2	6	6	87	–	1	Hunter (1985)
	Crozet Islands	PWM	6	5	–	89	–	–	Ridoux (1994)
Puffinus griseus	Putauhinu Island, NZ	PO	73	55	88	–	–	–	de Cruz (unpubl. data)
Procellaria aequinoctialis	Bird Island, South Georgia	PWM	33	19	48	–	<1	–	Croxall et al. (1995)
	Possession Island	PO	14	91	19	–	–	–	Mougin (1970)
	Crozet Islands	PWM	55	25	16	–	1	3	Ridoux (1994)
Procellaria parkinsoni	Little Barrier Island, NZ	PO	25	96	3	–	4	1	Imber (1976)
Procellaria cinerea	Crozet Islands	PWM	28	70	<1	–	–	1	Ridoux (1994)
Pterodroma macroptera	Whale Island, NZ	PWM	28	58	12	–	2		Imber (1973)
	Marion Island	PWM	4	90	6	–	–	–	Schramm (1986)
	Crozet Islands	PWM	4	64	32	–	–	–	Ridoux (1994)
Daption capense	Rauer Islands, Antarctica	PWM	14	<1	86	–	–	<1	Arnould & Whitehead (1991)
	Prydz Bay Islands, Antarctica	PWM	23	–	77	–	–	–	Green (1986)
	Terre Adélie, Antarctica	PWM	29	<1	64	–	–	7	Ridoux & Offredo (1989)
Pachyptila turtur	Poor Knights Islands, NZ	PWM	4	–	96	–	–	–	Prince & Morgan (1987)
	Bird Island, South Georgia	PWM	3	1	96				Prince & Copestake (1990)
Fregatta tropica	Crozet Islands	PWM	21	6	33	–	–	39[c]	Ridoux (1994)
	South Shetland Islands	PO[b]	40	1	39	–	–	46[c]	Hahn (1998)

[a]Data from other studies converted from percentage occurrence to percentage biomass by Hunter (1985); [b]Data from regurgitates and stomach flushings combined; [c]Unidentified organic particles

Furness 1989b). Work on Bonaparte's gull *Larus philadelphia* demonstrated that up to 93% of the accumulated body burden of mercury could be excreted during moult (Braune & Gaskin 1987). Three species of albatross (wandering albatross, royal albatross and black-browed albatross) do not routinely moult and regrow feathers on an annual basis. These may have a restricted ability to excrete mercury, which presumably contributes to higher concentrations of this metal, especially in the liver. There was no effect of moult duration on cadmium concentrations, which was expected as this is not an excretion pathway for this metal (Stewart unpubl. data).

Sex

By excreting a substantial amount of what is a potentially toxic material into the egg, breeding females have the potential to reduce their body pool of mercury between moults (Braune & Gaskin 1987, Lewis et al. 1993). However, there was no evidence that this resulted in consistent long-term differences between the sexes in cadmium or mercury levels in Buller's albatross, black-browed albatross or white-chinned petrels in this study. It might also be anticipated that sexual size dimorphism or differences in diet between males and females could play a role in determining cadmium or mercury concentrations, particularly as many albatrosses and petrels appear to have sex-specific foraging strategies (Bartle 1990, Prince et al. 1992). However, the similarity in mean concentration of these metals in males and females suggests that any dietary segregation between the sexes is likely to be minor.

Phylogeny

Although Procellariiformes clearly concentrate heavy metals, resulting in much higher metal burdens than many other seabirds (Walsh 1990), phylogeny explained comparatively little of the inter-specific variation within the order. There were no consistent differences in mercury levels in kidney or liver tissue, or in cadmium levels in kidney tissue between the 2 families. However, the Diomedeidae (albatrosses) generally had lower cadmium but higher zinc levels in the liver and lower copper concentrations in the kidney (see 'Results'). Higher zinc concentrations in the liver of albatrosses appeared to be related to their longer moult duration, whereas lower copper levels in the kidney seemed to be partly attributable to whether or not squid was an important component in the diet (see 'Results').

Conclusions

The albatrosses and petrels analysed in this study had particularly high cadmium burdens compared to many seabirds, probably attributable to a high level of squid consumption and presumably a slow rate of excretion of bound cadmium. The high mercury levels accumulated by most species can be explained by a combination of a diet of squid and fish, many of which are mesopelagic, a long life-span during which mercury may be demethylated and stored, and in the case of wandering, royal and black-browed albatrosses, slow moult cycles which restrict mercury excretion. The Procellariiformes seem therefore to have evolved a suite of physiological mechanisms which allows them to cope with high levels of these potentially very toxic metals in their prey. In particular, the manner by which wandering and royal albatrosses are able to de-toxify and store extraordinarily high quantities of mercury, even compared with other albatrosses, still remains very poorly understood, and deserves further study.

Acknowledgements. This work was supported by The Royal Society of London exchange Fellowship to New Zealand and a grant from the Auckland University Research Committee. Many thanks to Peter Keen and Willem Stroozenijer at SEMS and to Noel Hyde at the National Museum of New Zealand for help and support. We are also very grateful to Tina de Cruz at Otago University, who very kindly allowed us access to unpublished dietary data for sooty shearwaters. Thanks also to David Thompson and 4 anonymous referees for helpful comments on the manuscript.

LITERATURE CITED

Arnould JPY, Whitehead MD (1991) The diet of Antarctic petrels, cape petrels and southern fulmars rearing chicks in Prydz Bay. Antarct Sci 3:19–27

Bartle JA (1990) Sexual segregation of foraging zones in procellariiform birds: implications of accidental capture on commercial fishery longlines of grey petrels (*Procellaria cinerea*). Notornis 37:146–150

Becker PH, Henning D, Furness RW (1994) Differences in mercury contamination and elimination during feather development in gull and tern broods. Arch Environ Contam Toxicol 27:162–167

Braune BM, Gaskin DE (1987) A mercury budget for the Bonaparte's gull during autumn moult. Ornis Scand 18: 244–250

Cooper J, Henley SR, Klages NTW (1992) The diet of the wandering albatross *Diomedea exulans* at Subantarctic Marion Island. Polar Biol 12:477–484

Croxall JP, Prince PA (1996) Cephalopods as prey. I. Seabirds. Philos Trans R Soc Lond B Biol Sci 351:1023–1043

Croxall JP, Hall AJ, Hill HJ, North AW, Rodhouse PG (1995) The food and feeding ecology of the white-chinned petrel *Procellaria aequinoctialis* at South Georgia. J Zool Lond 237:133–150

Dietz R, Riget F, Johansen P (1996) Lead, cadmium, mercury and selenium in Greenland marine animals. Sci Total Environ 186:67–93

Fenaughty CM, Tracey DM, Lock JW (1988) Heavy metal and organochlorine concentrations in New Zealand aquatic fish, crustaceans and molluscs. NZ Fisheries Data Report 34, MAFFish, Wellington
Furness RW (1993) Birds as monitors of pollutants. In: Furness RW, Greenwood JJD (eds) Birds as monitors of environmental change. Chapman and Hall, London, p 86–143
Furness RW, Muirhead SJ, Woodburn M (1986) Using bird feathers to measure mercury in the environment: relationships between mercury content and moult. Mar Pollut Bull 17:27–30
Furness RW, Thompson DR, Harrison N (1994) Biometrics and seasonal changes in body composition of common guillemots *Uria aalge* from north-west Scotland. Seabird 16: 22–29
Green K (1986) Food of the cape pigeon (*Daption capense*) from Princess Elizabeth land, east Antarctica. Notornis 33: 151–154
Hahn S (1998) The food and chick feeding of black-bellied storm-petrel (*Fregatta tropica*) at King George Island, South Shetlands. Polar Biol 19:354–357
Honda K, Marcovecchio JE, Kan S, Tatsukawa R, Ogi H (1990) Metal concentrations in pelagic seabirds from the North Pacific Ocean. Arch Environ Contam Toxicol 19: 704–711
Hunter S (1985) The role of giant petrels in the Southern Ocean ecosystem. In: Siegfried WR, Condy PR, Laws RM (eds) Antarctic nutrient cycles and food webs. Springer-Verlag, Berlin, p 534–542
Hutton M (1981) Accumulation of heavy metals and selenium in three seabird species from the United Kingdom. Environ Pollut Ser A Ecol Biol 26:129–145
Imber MJ (1973) The food of grey-faced petrels (*Pterodroma macroptera gouldi* (Hutton)), with special reference to diurnal vertical migration of their prey. J Anim Ecol 42: 645–662
Imber MJ (1976) Comparison of prey of the black *Procellaria* petrels of New Zealand. NZ J Mar Freshw Res 10:119–130
Lewis SA, Becker PH, Furness RW (1993) Mercury levels in eggs, tissues, and feathers of herring gulls *Larus argentatus* from the German Wadden Sea coast. Environ Pollut 80: 293–299
Lock JW, Thompson DR, Furness RW, Bartle JA (1992) Metal concentrations in seabirds of the New Zealand region. Environ Pollut 75:289–300
Mackay D, Wania F, Schroeder WH (1995) Prospects for modeling the behaviour and fate of mercury, globally and in aquatic systems. Water Air Soil Pollut 80:941–950
Marchant S, Higgins PJ (1990) Handbook of Australian, New Zealand and Antarctic birds. Oxford University Press, Melbourne
Martin JH, Flegal AR (1975) High copper concentrations in squid livers in association with elevated levels of silver, cadmium and zinc. Mar Biol 30:51–55
Monteiro LR, Porteiro FM, Gonçalves JM (1992) Inter- and intra-specific variation of mercury levels in muscle of cephalopods from the Azores. Archipélago 10:13–22
Monteiro LR, Costa V, Furness RW, Santos RS (1996) Mercury concentrations in prey fish indicate enhanced bioaccumulation in mesopelagic environments. Mar Ecol Prog Ser 141:21–25
Monteiro LR, Granadeiro JP, Furness RW (1998) Relationship between mercury levels and diet in Azores seabirds. Mar Ecol Prog Ser 166:259–265
Mougin JL (1970) Le pétrel à menton blanc, *Procellaria aequinoctialis* de l'Île de la Possession (Archipel Crozet). Oiseau 40:62–96
Muirhead SJ, Furness RW (1988) Heavy metal concentration in the tissues of seabirds from Gough Island, South Atlantic Ocean. Mar Pollut Bull 19:278–283
Nriagu JO, Pacyna JM (1988) Quantitative assessment of worldwide contamination of air, water and soils by trace metals. Nature 333:134–139
Prince PA (1980) The food and feeding ecology of grey-headed albatross *Diomedea chryostoma* and black-browed albatross *D. melanophris*. Ibis 122:476–488
Prince PA, Copestake PG (1990) Diet and aspects of fairy prions breeding at South Georgia. Notornis 37:59–69
Prince PA, Morgan RA (1987) Diet and feeding ecology of Procellariiformes. In: Croxall JP (ed) Seabirds: feeding ecology and role in marine ecosystems. Cambridge University Press, Cambridge, p 135–171
Prince PA, Wood AG, Barton T, Croxall JP (1992) Satellite tracking of wandering albatrosses (*Diomedea exulans*) in the South Atlantic. Antarct Sci 4:31–36
Ridoux V (1994) The diets and dietary segregation of seabirds at the subantarctic Crozet Islands. Mar Ornithol 22:1–192
Ridoux V, Offredo C (1989) The diets of five summer breeding seabirds in Adélie Land, Antarctica. Polar Biol 9:137–145
Ritterhoff J, Zauke G (1997) Trace metals in field samples of zooplankton from the Fram Strait and the Greenland Sea. Sci Total Environ 199:255–270
Rossi A, Pellegrini D, Belcari P, Barghigiani C (1993) Mercury in *Eledone cirrhosa* from the northern Tyrrhenian Sea: contents and relations with life cycle. Mar Pollut Bull 26: 683–686
Scheuhammer AM (1987) The chronic toxicity of aluminium, cadmium, mercury, and lead in birds: a review. Environ Pollut 46:263–295
Schramm M (1986) The diet of chicks of greatwinged, Kerguelen and soft-plumaged petrels at the Prince Edward Islands. Ostrich 57:9–15
Slemr F, Langer E (1992) Increase in global atmospheric concentrations of mercury inferred from measurements over the Atlantic Ocean. Nature 355:434–436
Smith JD, Plues L, Heyraud M, Cherry RD (1984) Concentrations of the elements Ag, Al, Ca, Cd, Cu, Fe, Mg, Mn, Pb and Zn and the raionuclides ^{210}Pb and ^{210}Po in the digestive gland of the squid *Notodarus gouldi*. Mar Environ Res 13:55–68
Stewart FM, Thompson DR, Furness RW, Harrison N (1994) Seasonal variation in heavy metal levels in tissues of common guillemots, *Uria aalge* from northwest Scotland. Arch Environ Contam Toxicol 27:168–175
Stewart FM, Furness RW, Monteiro LR (1996) Relationships between heavy metal and metallothionein concentrations in lesser black-backed gulls, *Larus fuscus*, and Cory's shearwater, *Calonectris diomedea*. Arch Environ Contam Toxicol 30:299–305
Stewart FM, Phillips RA, Catry P, Furness RW (1997) Influence of species, age and diet on mercury concentrations in Shetland seabirds. Mar Ecol Prog Ser 151:237–244
Thompson DR (1990) Metal levels in marine vertebrates. In: Furness RW, Rainbow PS (eds) Heavy metals in the marine environment. CRC Press, Boca Raton, FL, p 143–182
Thompson DR, Furness RW (1989a) The chemical form of mercury stored in South Atlantic seabirds. Environ Pollut 60:305–317
Thompson DR, Furness RW (1989b) Comparison of the levels of total and organic mercury in seabird feathers. Mar Pollut Bull 20:577–579
Thompson DR, Furness RW, Lewis SA (1993) Temporal and spatial variation in mercury concentrations in some albatrosses and petrels from the South Atlantic. Polar Biol 13: 239–244

Thompson DR, Furness RW, Monteiro LR (1998) Seabirds as biomonitors of mercury inputs to epipelagic and mesopelagic marine food chains. Sci Total Environ 213:299–305
Thompson KR (1992) Quantitative analysis of the use of discards from squid trawlers by black-browed albatrosses *Diomedea melanophris* in the vicinity of the Falkland Islands. Ibis 134:11–21
Walsh PM (1990) The use of seabirds as monitors of heavy metals in the marine environment. In: Furness RW, Rainbow PS (eds) Heavy metals in the marine environment. CRC Press, Boca Raton, FL, p 183–205
Wania F, Mackay D (1995) A global distribution model for persistent organic chemicals. Sci Total Environ 161:211–232
Weimerskirch H, Jouventin P, Stahl JC (1986) Comparative ecology of the six albatross species breeding on the Crozet Islands. Ibis 128:195–213
Weimerskirch H, Bartle JA, Jouventin P, Stahl JC (1988) Foraging ranges and partitioning of feeding zones in three species of southern albatrosses. Condor 90:214–219
West JA, Imber MJ (1986) Some foods of Buller's mollymauk *Diomedea bulleri*. NZ J Zool 13:169–174

Editorial responsibility: Otto Kinne (Editor), Oldendorf/Luhe, Germany

Submitted: October 5, 1998; Accepted: November 18, 1998
Proofs received from author(s): March 1, 1999