DIET AND FORAGING BEHAVIOUR OF THE PROVIDENCE PETREL *PTERODROMA SOLANDRI*

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SUMMARY

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Studies of seabird diet and foraging behaviour contribute to identifying potential threats, particularly interactions between seabirds and fisheries. Diet and foraging behaviour of the Providence Petrel *Pterodroma solandri* on Lord Howe Island, Australia, were investigated during three consecutive breeding seasons. Diet consisted largely of squid (predominantly Cranchiidae, Onychoteuthidae, Spirulidae and Histioteuthidae) and fish (principally Myctophidae), with crustaceans (mainly Decapoda and Isopoda) being somewhat less important. The presence of mainly temperate, sub-tropical and tropical species in the diet indicates that Providence Petrels forage in warm water. Birds were recorded diving to 5.2 m, suggesting that some food items are captured by diving. The presence of large squid and bird remains in stomach samples, together with observations of kleptoparasitic behaviour, provide evidence of scavenging. Fishing line and metal traces in many stomachs suggest that Providence Petrels are taking discards from fishing boats, although diurnal observations near Lord Howe Island recorded few instances of birds following boats. Plastic was also found in some stomach samples. Further studies are required to determine the level of threat posed to the Providence Petrel by fishing activities and plastic ingestion.

Key words: Providence Petrel, *Pterodroma solandri*, diet, foraging behaviour

INTRODUCTION

The inadvertent and unsustainable catch (or bycatch) of non-target marine species in commercial fisheries is one of the principal threats to seabirds (Baker *et al*. 2002) as well as many other marine vertebrates (Lewison *et al*. 2004). Studies of seabird diet and foraging behaviour can help identify potential interactions between seabirds and fisheries (e.g. Freeman 1998, Bunce 2001). Analysis of stomach contents can also reveal other threats, such as the ingestion of plastics (Hutton *et al*. 2008). Additionally, dietary and foraging studies of seabirds can provide information on the dynamics of marine systems (Croxall *et al*. 1984) which, in turn, can be used to assess the health of marine environments (Cherel & Weimerskirch 1995).

The diets of gadfly petrels (*Pterodroma*) are poorly known compared with knowledge of diets in other genera within the Procellariiformes (e.g. albatrosses and shearwaters). Dietary data from the South Pacific are particularly scant; Grey-faced Petrel *Pterodroma gouldi* (Imber 1973) and Cook's Petrel *P. cookii* (Imber 1996) are among the few South Pacific species whose diet has been studied comprehensively. From the limited data available, it appears that the prey taken by *Pterodroma* varies both between species and between populations. Most species feed largely on squid, with fish and crustaceans being of secondary importance. The diet of the Providence Petrel *Pterodroma solandri* has never been investigated in any detail, but anecdotal observations indicate it includes fish, squid, crustaceans and fish offal (Gibson & Sefton 1956, King 1967).

The diet of seabirds can be assessed from stomach contents obtained using the water-offloading technique of Wilson (1984). This is a non-lethal, humane technique (Robertson *et al*. 1994) that can procure the entire contents of the stomach by undertaking multiple flushings (Gales 1987). In Procellariiformes, prey collected by this method is generally highly digested, although hard material such as cephalopod beaks and fish otoliths are often present because of their resistance to digestion (Shealer 2002). The exoskeletons of decapods, isopods and amphipods are also present in many stomach samples (Imber 1973). Such intact cephalopod beaks, fish otoliths and crustacean exoskeletons can usually be identified to genera or species level, and can sometimes even be used to estimate the age and size of individuals (Frost & Lowry 1981, Clarke 1986, Gales 1988).

The major limitation in determining dietary composition from stomach contents is the bias caused by different rates of digestion of prey items (Jackson & Ryan 1986). Although flesh can be completely digested within a few hours, otoliths may remain intact for several days (Wilson *et al*. 1985), and hard, indigestible material such as squid beaks can remain in the stomach for up to seven weeks (Furness *et al*. 1984). Thus, to avoid any bias, the relative frequency of prey in the diet is best estimated from fresh, undigested material only.

Knowledge of foraging behaviour and diving depth is a useful adjunct to dietary studies, particularly for species that either utilise fishing discards or are killed or injured in fishing operations. Procellariiformes use a number of foraging techniques to catch their prey. Some species also scavenge for dead or moribund prey on the sea surface (Warham 1990). The characteristic foraging techniques utilised by the *Pterodroma* are "dipping" and "surface seizing," although the Mottled Petrel *P. inexpectata* has been observed to "surface-plunge" and "pursuit-plunge" (Ainley *et al*. 1984, Prince and Morgan 1987). The diving depths of many Procellariiformes have been determined using depth gauges (e.g. Bocher *et al*. 2000, Mougin & Mougin 2000) although, to our knowledge, the diving depth of *Pterodroma* has not yet been studied.

Lord Howe Island and Phillip Island (a small island in the Norfolk Island Group) support the only known breeding populations of the Providence Petrel; consequently, the species is listed as vulnerable under both the *IUCN Red List of Threatened Animals* (Criteria D2) and the *New South Wales Threatened Species Conservation Act 1995*. Approximately 32 000 breeding pairs of Providence Petrels nest on Lord Howe Island (Bester 2003), predominantly on the two southern mountains—Mount Gower (875 m) and Mount Lidgbird (777 m). The population breeding on Phillip Island is probably less than 20 pairs (D.P., pers. obs.). These two colonies are the last remaining vestige of a much larger population that once occurred within the Norfolk Island and Lord Howe Island Group. Between 1790 and 1793 about 1 million Providence Petrels were harvested on Norfolk Island itself (Medway 2002). Continued harvesting, together with the depredations of introduced pigs (which by 1796 numbered 15 000) saw petrels extirpated from Norfolk Island by about 1800 (Schodde *et al*. 1983).

This study investigated the diet and foraging behaviour of the Providence Petrel on Lord Howe Island during three consecutive breeding seasons. Knowledge of any potential interaction with fisheries or other threats at sea is of prime importance for the informed management of this species.

METHODS

Study area

Lord Howe Island (31°33'S, 159°05'E) is located in the South Pacific Ocean, 780 km northeast of Sydney, New South Wales, Australia, and 1570 km northwest of Auckland, New Zealand. The study site for collection of stomach samples was located near the summit of Mount Gower. Foraging behaviour was observed from boats within 20 km of Lord Howe Island. Although the Providence Petrel (~500 g body mass) is frequently observed close to Lord Howe Island, the area surveyed encompassed only a very small part of the known foraging range of this species (Bester 2003). Waters around the island are a mixture of tropical (Coral Sea) and temperate (Tasman Sea) waters, commonly referred to as the Tasman Front (Baird *et al*. 2008). Water depth within 5–10 km of Lord Howe Island is generally less than 200 m deep; beyond this distance, depths drop steeply to 2000 m (Commonwealth of Australia 2002).

Stomach contents

Sixty-one samples of stomach contents were collected from Providence Petrel chicks over the three years of study: nine between 23 August and 4 October 1999; 22 between 30 July and 4 October 2000; and 30 between 31 August and 15 October 2001. In addition, 48 samples were collected from breeding adults, all between 3 September and 4 October 2000. All adults sampled were caught while in or entering their nest burrow, and all were known to have a chick. All birds were weighed, measured and banded before samples were taken.

Stomach samples were collected using the water-offloading procedure described by Wilson (1984). The equipment included a garden pressure sprayer connected to a 40 cm catheter (internal diameter: 3 mm; external diameter: 5 mm). Flushing was repeated three times, or until the water ejected from the bird contained no food material.

Freeman (1998) reported that collecting stomach samples at night overestimates the importance of prey species captured during the day, because prey eaten the night before would be more digested. This limitation was reduced by collecting samples from birds returning to the colony between 18h00 and 23h00. After each stomach sample was taken, the captured bird was returned to its burrow. No more than one sample was taken from any individual bird. Each sample was sieved through a fine mesh strainer to remove the liquid. Any oil was separated from the water and its volume measured to ± 0.1 mL. The solid material was then placed into a sterilised container containing 70% ethanol, which was then labelled and stored for later analysis.

Diet analysis

Each sample of stomach contents was sorted, and fresh prey items (those that contained flesh) were separated from the hard accumulated items (predominantly squid beaks and fish otoliths) that did not have any flesh attached. Non-food items, such as stones, plastic or fishing gear, were also separated and recorded. All fresh items were examined to identify, as far as possible, the species of prey and the number of individuals consumed. Most fresh items were partially digested; consequently, very few could be measured accurately or identified from their external appearance. Cephalopods were identified from lower beaks using Clarke (1962, 1986) and Imber (1978, 1992), and by Mike Imber (Department of Conservation, New Zealand, retired) using reference collections. Fish were identified from otoliths using reference collections together with the advice and assistance of Dianne Furlani (Commonwealth Scientific and Industrial Research Organisation, Australia). Crustaceans were identified from descriptions in Jones & Morgan (2002) and advice and assistance from Shane Ahyong (National Institute of Water and Atmospheric Research, New Zealand).

To aid identification and to estimate the number of individuals, cephalopod prey remains were reconstructed if possible. In addition, the relationship between size of the lower beaks and body length was calculated using data collected from intact prey. For decapod cephalopods, body length was taken as the length of the lower rostrum, measured to ± 0.1 mm using dial calipers. For octopods, body length was taken as the length of the lower hood (Clarke 1986). Estimates of cephalopod mass based on body length vary greatly among studies because different allometric equations are used. In this study, the mass of cephalopods was estimated from length/mass regression analyses in Clarke (1962, 1986). If regression equations were not available for a particular species, equations for the genus or family were used.

The mass of individual prey was estimated for cephalopods only. Estimating the mass of individual fish and crustaceans was not possible because there were too few whole specimens of these taxa in the stomach samples to determine the necessary regression equations. Some studies have used otolith erosion categories to estimate the size of fish (Berrow & Croxall 1999), but such calculations are subject to high error (Gales 1988), so they were not used in this study.

To estimate the number of fish represented by the otoliths present in the fresh component of each sample, each otolith was placed into one of eight size categories based on its diameter (1 mm to 8 mm). For each sample, the total number of otoliths in each size category was halved and rounded up to the nearest integer. The number of fish within each size class was then tallied, and added to the counts of whole fish (presumed to have retained otoliths) in the samples. Semi-digested fish were not added to the tally, as it was assumed that some of the otoliths in the sample belonged to these semi-digested specimens.

The contribution of each species to the overall diet was quantified by scoring: (i) the proportion of stomachs in which a particular prey species was present, hereafter referred to as the frequency of occurrence (FOO) following Ashmole and Ashmole (1967); and (ii) the number of individuals of a species as a percentage of the total number of prey collected, hereafter referred to as the relative occurrence (RO) following O'Sullivan and Cullen (1983). For each of the three main prey groups (cephalopods, fish and crustacea) the relative occurrence of each species within the group was calculated, hereafter referred to as the prey group relative occurrence (PGRO) following Montague and Cullen (1988). The FOO and RO of major prey items were compared between Providence Petrel chicks and adults using χ^2 analyses.

Accumulated (i.e. non-fresh items) were also examined and, where possible, identified to determine whether they contained species not present in the fresh material. Because of marked differences in digestibility of the accumulated items, no attempt was made to determine the relative occurrence of prey species based on these items.

Foraging behaviour

To investigate the local foraging behaviour of the Providence Petrel, a total of 1980 1 min scans were made at sea during 14 local commercial fishing charters undertaken between 8 August 2001 and 12 April 2002. Observations were also made to determine whether Providence Petrels followed boats, took fish offal, or attempted to take bait from fishing lines. In addition, 32 birds were observed continuously for 3 min each. All observations were made between 09h00 and 17h00.

The maximum depths of dives by Providence Petrels were determined for 28 breeding adults. Two transparent plastic capillary tubes were glued to feathers on the back of the bird using *Loctite 401*. These tubes, approximately 10 cm in length and 0.8 mm internal diameter, were blocked at one end and dusted on the inside with icing sugar. Each tube weighed less than 1 g and, when attached to the bird, did not appear to annoy, hinder or restrain the bird; nor was any bird observed attempting to remove the tubes. Dive depths were computed from the distance that water penetrated into the tube, following Burger and Wilson (1988). Data were discarded if the difference between the two tubes of a pair was >10%.

RESULTS

Diet composition

Of the 109 birds sampled, 98 yielded stomach samples that contained fresh or accumulated food items. Eleven adults regurgitated only water, each having offloaded their stomach contents to their offspring shortly before being captured, as evidenced by the associated increase in weight of the chick. Of the 98 stomach samples that contained food items, nine contained no fresh material. In all, the 61 chick samples contained a total of 378 fresh prey items and 499 accumulated items. The 37 adult samples contained a total of 165 fresh prey items and 59 accumulated items.

Analysis of the number of fresh items in the stomach samples taken from chicks and adults (Table 1) indicated, not surprisingly, that there was no significant difference in either the FOO ($\chi^2 = 4.16$, $P = 0.125$) or RO ($\chi^2 = 4.36$, $P = 0.113$) of the major prey groups (cephalopods, fish and crustaceans). Therefore, data were combined for further analyses. Overall, 78.7% of fresh samples contained cephalopods, 62.9% contained fish and 43.8% contained crustaceans (Table 2). Gastropods were present in 2.2% of stomachs and bird remains in 1.1%. Overall, of the 543 fresh items collected, 47.9% were cephalopods, 34.8% were fish and 16.6% were crustaceans. Gastropods and bird remains each represented less than 1% of prey items (Table 2).

Cephalopoda

We found 774 pairs of squid beaks (260 fresh, 514 accumulated): 81.4% of fresh items, but only 10.1% of accumulated items could be identified. From the fresh material, the families Cranchiidae (PGRO = 26.9%), Onychoteuthidae (13.4%), Spirulidae (11.2%) and Histioteuthidae (10.7%) were the most common cephalopods identified (Table 2). The dominant species were *Leachia* spp. (PGRO = 12.7%), *Spirula spirula* (11.2%), *Onychoteuthis* sp. B (9.6%), *Taonius* sp. C (6.5%), *Octopoteuthis* sp. (5.8%) and *Histioteuthis meleagroteuthis* (5.8%). The only species in the accumulated samples that did not occur in the fresh samples was *Ancistrocheirus lesueurii* (n = 1).

Individual cephalopods ranged in mass from 1 g (*Spirula spirula* and *Sepia* sp.) to 267 g (*Histioteuthis hoylei*). The *Leachia* spp. present in the stomach samples were all small (<15 g), but most size categories were present (Fig. 1), with the size distribution of prey probably reflecting that of the population. In contrast, Providence Petrels fed mainly on sub-adult *Chiroteuthis capensis* and *Taonius* sp. C. The size distribution of *Teuthowenia pellucida* was bimodal, with small and large individuals being taken, but none of the intervening size classes (Fig. 1). This, however, may be a reflection of the small sample size (n = 14). Other prey species with

TABLE 1
Frequency of occurrence (FOO) and relative occurrence (RO) of fresh prey items in the stomach contents of Providence Petrel chicks (n = 55) and breeding adults (n = 34) on Lord Howe Island during 1999–2001

	Chicks				Adults			
	FOO (n)	FOO (%)	RO (n)	RO (%)	FOO (n)	FOO (%)	RO (n)	RO (%)
Cephalopoda	43	78.2	190	50.3	27	79.4	70	42.4
Fish	29	52.7	121	32.0	27	79.4	68	41.2
Crustacea	24	43.6	64	16.9	15	44.1	26	15.8
Other			3	0.8			1	0.6
Total			**378**	**100**			**165**	**100**

TABLE 2
Frequency of occurrence (FOO), relative occurrence (RO) and prey group relative occurrence (PGRO) of fresh prey items in the stomach contents of Providence Petrels (n = 89) on Lord Howe Island during 1999–2001

	FOO		Number (n)	RO (%)	PGRO (%)	Body mass (g)	
	(n)	(%)				Range	Mean
Cephalopods	70	78.7	260	47.9	100	1.1–267.4	41.5
Spirulidae							
Spirula spirula	18	20.2	29	5.3	11.2	1.1–48.8	9.0
Sepiidae							
Sepia sp.	7	7.9	14	2.6	5.4	1.1–26.5	14.4
Octopoteuthidae							
Octopoteuthis sp.	11	12.4	15	2.8	5.8	112.9–235.5	178.6
Onychoteuthidae							
Onychoteuthis sp. B	13	14.6	25	4.6	9.6	8.7–90.1	27.2
Onychoteuthis banksi	8	9	10	1.8	3.8	1.8–204.3	101.0
Brachioteuthidae							
Brachioteuthis sp.	2	2.2	2	0.4	0.8	1.5–2.0	1.5
Histioteuthidae							
Histioteuthis atlantica	4	4.5	4	0.7	1.5	72.3–175.7	139.5
Histioteuthis bonnellii	1	1.1	1	0.2	0.4		37.2
Histioteuthis miranda	3	3.4	4	0.7	1.5	18.7–61.2	30.8
Histioteuthis hoylei	2	2.2	4	0.7	1.5	43.2–267.4	121.3
Histioteuthis meleagroteuthis	15	16.9	15	2.8	5.8	7.5–88.9	34.2
Ommastrephidae							
Nototodarus gouldi	3	3.4	4	0.7	1.5	1.3–17.7	7.2
Chiroteuthidae							
Chiroteuthis capensis	11	12.4	13	2.4	5.0	2.3–74.6	29.5
Mastigoteuthidae							
Mastigoteuthis sp. A	1	1.1	1	0.2	0.4		91.4
Mastigoteuthis sp. New#	1	1.1	1	0.2	0.4		34.3
Mastigoteuthis sp. 2	5	5.6	5	0.9	1.9	5.5–18.0	9.6
Mastigoteuthis cf. *Dentata*	10	11.2	10	1.8	3.8	15.0–75.0	41.8
Cranchiidae							
Cranchia scabra	2	2.2	2	0.4	0.8	6.9–19.4	13.1
Leachia spp.	25	28.1	33	6.1	12.7	2.6–14.1	6.2
Taonius sp. C	17	19.1	17	3.1	6.5	30.0–98.2	72.0
Teuthowenia pellucida	10	11.2	13	2.4	5.0	1.7–65.1	34.1
Galiteuthis sp. 3	5	5.6	5	0.9	1.9	21.2–177.8	86.2
Amphitretidae							
Amphitretus pelagicus	1	1.1	1	0.2	0.4		
Unidentified cephalopods A	18	20.2	32	5.9	12.3		
Fish	56	62.9	189	34.8	100		
Sternoptychidae							
Polyipnus indicus	1	1.1	1	0.2	0.5		
Myctophidae							
Metelectrona ventralis	35	39.3	110	20.3	58.2		
Electrona subaspera	1	1.1	1	0.2	0.5		
Diaphus sp.	5	5.6	6	1.1	3.2		
Symbolophorus barnardi	1	1.1	1	0.2	0.5		
Unidentified myctophidae	8	9.0	30	5.5	15.9		
Carangidae							
Carangidae sp.	1	1.1	1	0.2	0.5		
Scorpaenidae							
Helicolenus sp.	1	1.1	1	0.2	0.5		
Unidentified fish	28	31.5	38	7.0	20.1		
Crustaceans	39	43.8	90	16.6	100		
Mysidacea							
Gnathophausia ingens	4	4.5	5	0.9	5.6		
Amphipoda							
Paraleucothoe novaehollandiae	1	1.1	1	0.2	1.1		
Isopoda							
Anilocra nemipteri	2	2.2	2	0.4	2.2		
Cirolana sp.	3	3.4	21	3.9	23.3		
Unidentified isopoda	1	1.1	1	0.2	1.1		
Euphausiacea							
Nyctiphanes australis	6	6.7	10	1.8	11.1		
Decapoda							
Oplophorus spinosus	1	1.1	1	0.2	1.1		
Systellaspis debilis	1	1.1	1	0.2	1.1		
Pasiphaea sp.	8	9.0	12	2.2	13.3		
Unidentified decapoda	19	21.3	27	5.0	30		
Unidentified crustaceans	8	9.0	9	1.7	10		
Gastropods	2	2.2	3	0.6			
Unidentified gastropods	2	2.2	3	0.6			
Bird	1	1.1	1	0.2			
Chalcites sp.	1	1.1	1	0.2			
Total			**543**	**100**			

a disjunct size distribution included *Onychoteuthis* sp. B (n = 25) and *O. banksi* (n = 10). There were no significant differences in the size of each cephalopod among years, or throughout the year (five half–month blocks), except for *Taonius* sp. C (one-way ANOVA, $F = 2.83$, $P < 0.044$). Significantly more adults of this species were found in samples collected in October.

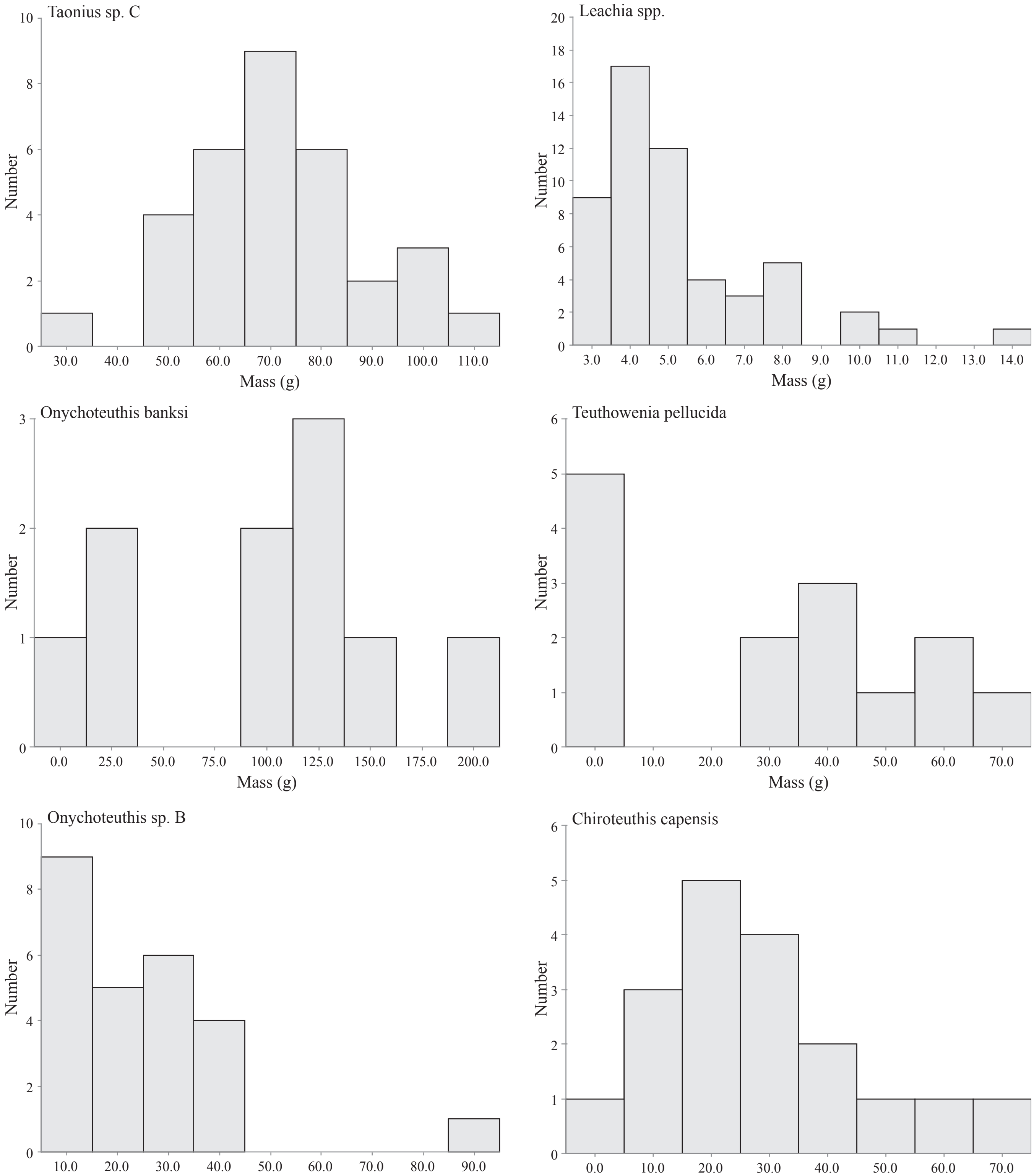

Fig. 1. Mass of individual cephalopod prey (fresh and accumulated) in the stomach contents of Providence Petrels on Lord Howe Island during 1999–2001.

Fish

Out of 226 pairs of fish otoliths (189 fresh, 37 accumulated), identification was possible for 79.9% of fresh items and 40.5% of accumulated items. The most common species present in the fresh material (Table 2) was *Metelectrona ventralis* (PGRO = 58.2%) and an unidentified species also of the family Myctophidae (15.9%). We were able to measure 43 *Metelectrona ventralis* (mean ± standard deviation 3.2 ± 2.0 cm) and one *Symbolophorus barnardi* (12.0 cm). All species identified in the accumulated material were also present in the fresh material.

Crustacea

A total of 97 food items of crustacean origin (90 fresh, 7 accumulated) were collected, of which 90% of fresh items could be identified, but none of the accumulated items. Decapods (PGRO = 45.5%), isopods (26.6%), euphausiids (11.1%), mysids (5.6%) and amphipods (1.1%) were present (Table 2), with the dominant species being *Cirolana* sp. (PGRO = 23.3%), *Pasiphaea* sp. (13.3%), *Nyctiphanes australis* (11.1%) and *Gnathophausia ingens* (5.6%). Unidentified decapods also comprised a substantial proportion of the samples (PGRO = 30.0%). *Cirolana* sp. were probably the prey of larger crustaceans or squid found in the samples (Jones & Morgan 2002).

Other items

Proventricular oil was present in 32 samples, with most (81%) of these samples obtained near the end of chick-rearing (October). Approximately half the oil samples were deep red, while the others were light orange in colour. Mesogastropods were present in two samples in low abundance (n = 3). Two bird feet and feathers were collected from the stomach contents of an adult Providence Petrel on 3 October 2000. These body parts were identified by W. Boles (Australian Museum) as belonging to either a Shining Bronze-cuckoo *Chalcites lucidus*, or possibly a Horsfield's Bronze-cuckoo *C. basalis*.

Non-prey items were present in 91 of the 98 stomach samples (Table 3). Plant material, found in 72.5% of samples, probably came from the stomach contents of prey such as fish and crustaceans. Nematodes were present in 57.1% of samples, and stones in 18.4%. Fishing line, but no hooks, was present in 13.3% of stomachs, and metal traces in 1.0%. This material was probably attached to fishing discards that the birds scavenged. Plastic was found in 11.2% of samples, and paper in 2.0%. The single parasitic bopyrid isopod (*Parathelges* sp.) in the samples had probably been attached to a larger prey item (Jones & Morgan 2002).

Foraging behaviour

Providence Petrels were observed on 12 of the 14 local commercial fishing expeditions at a mean (± standard deviation) of 54.5 ± 57.3 birds per trip (range 1–161; n = 1980 1 min surveys). There was no relationship between Providence Petrel numbers seen on each cruise (after adjusting for survey time) and wind speed ($r_s = 0.24$; n = 11; $P = 0.487$), swell ($r_s = -0.06$; n = 11; $P = 0.869$) or time of day ($r_s = 0.86$; n = 54; $P = 0.536$). Most Providence Petrels were observed on the wing, although on one occasion a bird was observed sitting on the water. During observations of more than 600 individuals at 54 locations, only once was a bird seen obtaining prey. On this occasion the bird caught a squid by "dipping." A number of conspecifics then unsuccessfully attempted to steal the squid from the bird. Although other species such as Wandering Albatross *Diomedea exulans*, Cape Petrel *Daption capense*, Flesh-footed Shearwater *Ardenna carneipes*, Common Noddy *Anous stolidus* and Masked Booby *Sula dactylatra* were frequently observed either following boats or taking bait off fishing lines, Providence Petrels rarely exhibited such behaviour. On one occasion a Providence Petrel appeared to be interested in fishing scraps, although none were taken. On two occasions Providence Petrels appeared to be following a rescue boat. Of the 32 individuals observed for 3 min each, none made any foraging attempt.

Twenty-eight pairs of tubes were retrieved from Providence Petrel adults. One of these pairs was discarded because no powder remained in the tubes. The difference between the two tubes for all other pairs was <10%, so none of these were discarded. The sampled birds dived to a maximum depth of 5.2 m. The average maximum depth (± standard deviation) was 2.9 ± 1.2 m. No correlation was found between length of deployment and maximum diving depth ($r_s = -0.02$; n = 27; $P = 0.921$).

DISCUSSION

This study provides the first detailed description of the diet and foraging behaviour of the Providence Petrel. It found that the Providence Petrel has a broad diet, consisting largely of squid, fish and crustaceans. Among the most prominent prey were Cranchiidae squid and Myctophidae fish, with the Flaccid Lanternfish *Metelectrona ventralis* being the most common species taken. Other *Pterodroma* that are known to feed heavily on Myctophidae include Cook's Petrel (Imber 1996) and, to a lesser extent, the Grey-faced Petrel (Imber 1973) and Galapagos Petrel *P. phaeopygia* (Imber 1992).

Among the cephalopods, the families Cranchiidae, Onychoteuthidae, Spirulidae, and Histioteuthidae were common in the diet of Providence Petrels. These families have been found to be important in the diet of other Procellariiformes (Schramm 1986, Imber *et al.* 1995, Freeman 1998, Imber 1999). Cranchiidae accounted for more

TABLE 3
Frequency of occurrence (FOO) and relative occurrence (RO) of non-prey items in the stomach contents of Providence Petrels (n = 98) on Lord Howe Island during 1999–2001

	FOO		Number	RO
	(n)	(%)	(n)	(%)
Plant material	71	72.5	343	21.1
Nematode	56	57.1	1168	72.0
Stone	18	18.4	65	4.0
Fishing line	13	13.3	14	0.9
Plastic	11	11.2	27	1.7
Paper	2	2.0	3	0.2
Metal trace	1	1.0	1	0.1
Parathelges sp.	1	1.0	1	0.1
Total			**1622**	**100**

than a quarter of the identified squid component of the diet, with *Leachia* spp. being the most common species. Cranchiidae also feature prominently in the diet of Grey-faced Petrels (Imber 1973, Imber 1978). The size of cephalopods taken by Providence Petrels was similar to that taken by species such as the Grey-faced Petrel (Imber 1973), Great-winged Petrel *Pterodroma macroptera*, Soft-plumaged Petrel *P. mollis* and Kerguelen Petrel *Lugensa brevirostris* (Schramm 1986). Cook's Petrel, a much smaller species (~175 g) takes mainly juvenile and immature squid (Imber 1996).

Most Procellariiformes, with the exception of shearwaters and diving-petrels, are not proficient divers (Bocher *et al*. 2000). It appears that Providence Petrels are capable of shallow dives, possibly "surface plunging" or "pursuit plunging" like the Mottled Petrel (Prince and Morgan 1987) and Kerguelen Petrel (Harper 1987). The 5 m diving depth attained by Providence Petrels contradicts a previous suggestion that the *Pterodroma* only "dip" and "surface seize" for their food (Warham 1990). By diving, the Providence Petrel may be able to broaden its dietary spectrum.

Low counts of diurnal foraging observed during this study, together with previous observations of nocturnal feeding (Marchant & Higgins 1990), suggest that Providence Petrels feed mainly at night. The presence of bioluminescent prey in the diet would seem to confirm this, as these organisms tend to migrate to the surface at night. However, data loggers placed on other Procellariiformes have revealed what appears to be a mismatch between prey biology and bird behaviour by showing that some species that feed on vertically migrating bioluminescent prey feed more during the day than at night (Phillips *et al*. 2008). Further insights into the foraging behaviour of the Providence Petrel may be obtained through the use of data loggers.

The large range in body sizes of cephalopod prey taken by Providence Petrels suggests that they not only prey on small cephalopods but also scavenge larger species. Scavenging by Procellariiformes is well-documented and has been recorded for several *Pterodroma* (Ashmole & Ashmole 1967, Harper 1987, Warham 1990, Imber *et al*. 1995). Many of the cephalopods taken as prey by Providence Petrels are deep-living species (e.g. *Sepia, Amphitretus* and adult *Teuthowenia pellucida*) that float after post-spawning mortality (Voss 1985, Clarke *et al*. 1985, Lipinski & Jackson 1989). Most *Spirula spirula* in the stomach samples were adults subject to post-breeding die-offs (Dell 1952), so they could have been scavenged from the surface. *Histioteuthis* also float after death (Lipinski & Jackson 1989). Given that some *H. hoylei* were half the weight of an adult Providence Petrel, these squid are more likely to be scavenged from the surface than caught at depth. This would also be the case for the larger *Octopoteuthis* sp. (maximum 236 g) and *Onychoteuthis banksi* (maximum 204 g). Some of these large cephalopods may have been fisheries bycatch (Imber 1999). Other evidence to support scavenging by the Providence Petrel includes the attempted kleptoparasitic behaviour observed at sea. Kleptoparasitism, although uncommon among Procellariiformes, has been observed in Waved Albatross *Phoebastria irrorata*, Murphy's Petrel *Pterodroma ultima*, Kermadec Petrel *P. neglecta* and Wedge-tailed Shearwater *Ardenna pacificus* (Spear & Ainley 1993, Warham 1996).

The remains of a bronze-cuckoo in the stomach of one adult were a remarkable find. Such a peculiar item has never been recorded in the diet of any gadfly petrel. Even the larger giant petrels and albatrosses have been recorded preying only on seabirds and seal carcasses (Hunter 1983, Weimerskirch *et al*. 1986, Imber 1999). That only the feet were present suggests this material was scavenged rather than taken as live prey. It is possible that the remains were scavenged from the ground, as the Shining Bronze-cuckoo is present on Lord Howe Island from spring to late summer. However, it is more likely that these items were taken at sea as the migratory flight path of this species (Gill 1983) crosses the foraging grounds of the Providence Petrel (Binder 2009).

Proventricular oil, present in one-third of Providence Petrel stomach samples, has been recorded in many other Procellariiformes (Lewis 1969, Freeman 1998). For Great-winged Petrel, Kerguelen Petrel and Soft-plumaged Petrel, proventricular oil constituted 16–19% by mass of stomach samples (Schramm 1986). In Providence Petrels, oil made up 30% of the wet weight of samples that contained oil. The origin of this oil was not determined, although the rich red colour suggests it was from crustacea (Lewis 1969) and fish (Connan *et al*. 2005).

The presence of mainly temperate, sub-tropical to tropical prey species, and the absence of many sub-Antarctic species such as *Histioteuthis eltaninae* in the diet of the Providence Petrel indicate that this species feeds in warm waters, at least during the breeding season. This is consistent with data from satellite tracking and from geolocating archival tags, both of which indicate that, while breeding on Lord Howe Island, Providence Petrels forage in waters east of Australia as far north as the Solomon Islands and as far south as Tasmania (Bester 2003, Binder 2009). Sightings along the east coast of Australia suggest that Providence Petrels feed largely on continental slopes and shallow oceanic waters. Many of the species taken as prey by the Providence Petrel are predominantly associated with such habitats, including some Myctophidae (Hulley 2002), *Paraleucothoe novaehollandiae* (Lowry *et al*. 2000), *Nyctiphanes australis* (Blackburn 1980), *Anilocra nemipteri* (Lowry 2000), *Histioteuthis miranda* (Voss 1969, Voss *et al*. 1998), *H. atlantica* (Voss 1969), *Spirula spirula* (Bruun 1943) and *Sepia* (Imber 1992). Other prey species are exclusively oceanic or found only in mesopelagic and bathypelagic depths: *Histioteuthis hoylei* (Voss 1969), *Ancistrocheirus lesueurii* (Young *et al*. 1998), *Mastigoteuthis* spp. (Imber 1992, Salceds-Vargas & Young 1996) and *Amphitretus pelagicus* (Young *et al*. 1996). The presence of these animals in the diet suggests that the Providence Petrel also forages in pelagic waters.

Many non-food items were recorded in the stomachs of Providence Petrels. Most were probably taken from the sea surface or were present in the stomachs of larger prey items. Plastic was found in 11% of birds sampled. At least two-thirds of all Procellariiforme species are known to ingest plastic, and in many cases the proportion of the population that contains plastic exceeds 80% (Laist 1997). On Lord Howe Island, high levels of plastic ingestion have been reported in chicks of Flesh-footed Shearwater and Wedge-tailed Shearwater (79% and 43%, respectively) (Hutton *et al*. 2008). Plastics in high concentrations may adversely affect the health of marine birds (Fry *et al*. 1987), although no ill effects were apparent in this study.

Fishing material (line and metal traces) was not uncommon in the stomach samples of Providence Petrels. Most of the line appeared to have been cut by a sharp instrument, and we presume that the petrels picked up this material while scavenging fishing discards.

Discarded fish heads often retain hooks, fishing line and traces, but these scraps usually sink fairly rapidly, suggesting that the petrels that ingested this material were probably following boats at the time. Although no Providence Petrels were observed taking fishing scraps during this study, other studies have reported this species taking fish discards from boats (Kuroda 1955; S. Wilson pers. comm.). Judging from diet, sightings and tracking data, the Providence Petrel forages within waters where there is potential overlap with a number of fisheries including the longlining fleet of Australia's eastern tuna and billfish fishery. Although this study has identified a potential threat to Providence Petrels from fishing activities, more detailed studies are required to determine the degree and extent of this threat.

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