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Prey of Auckland Island shags (*Leucocarbo colensoi*) in winter

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Abstract Diagnostic prey remains of Auckland Island shags (*Leucocarbo colensoi*) were analysed from 23 regurgitated pellets collected in August 2010 at Enderby Island, Auckland Islands. Allometric equations from a reference collection were applied to prey remains to provide estimates of prey length and wet mass. A minimum total of 1058 prey items from 7 genera were represented in pellets, with an estimated total wet mass of 13.2 kg. The mean number of prey items per pellet was 46 (range 7-90), with mean total prey mass per pellet of 589 g (range 86–1037 g). Small octopus (*Octopus* sp.) was by far the most important prey item and was present in all regurgitated pellets. It accounted for 57% of prey by number and 68% of prey by wet mass. Only 2 other genera contributed ≥ 5% towards the total mass of prey—red cod (*Pseudophycis bachus*) and triplefin (*Forsterygion* sp.) The overwhelming importance of octopus in the diet is unprecedented among shags for which diet composition is known.

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Keywords Auckland Island shag; *Leucocarbo colensoi*; diet composition; *Octopus*; *Pseudophycis*; *Forsterygion*

INTRODUCTION

New Zealand's endemic Auckland Island shag (*Leucocarbo colensoi)* is restricted to the Auckland Is in the New Zealand subantarctic where it has an estimated total population of less than 1000 breeding pairs, with about half at Enderby I at the northern tip of Auckland Is (Taylor 1988, 2000; Moore & McClelland 1990). Due to its small population size and restricted distribution the species is classified as 'nationally vulnerable' (Miskelly *et al.* 2008) under the New Zealand Department of Conservation Threat Classification System and 'vulnerable' by the IUCN (2011). Little is known of its ecology (Taylor 2000).

The Auckland Island shag is 1 of 6 species of 'blue-eyed shag' in New Zealand designated to the genus *Leucocarbo* (Gill *et al*. 2010), each with small population sizes and restricted distributions. The other 5 species are New Zealand king shag (*L. carunculatus*), Stewart Island shag (*L. chalconotus*), Chatham Island shag (*L. onslowi*), Bounty Island shag (*L. ranfurlyi*), and Campbell Island shag (*L. campbelli*). Blue-eyed shags are a circumpolar genus of marine shags found in temperate and polar regions of the southern hemisphere, with 13 species worldwide (Siegel-Causey 1988; Marchant &

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Higgins 1990; Cook *et al*. 2008). Blue-eyed shags dive both deeper and longer than other shags (Croxall *et al.* 1991; Quintana *et al.* 2007; Cook *et al*. 2008), with dives routinely deeper than 20 m (maximum 145 m recorded for Crozet Island shags *L. melanogenis* by Tremblay *et al*. 2005), and durations longer than 2 minutes (maximum 6 minutes recorded for imperial shags *L. atriceps* by Wanless *et al*. 1992).

Shags usually regurgitate 1 pellet per day of indigestible prey remains encapsulated in a mucous sac which represents the food intake from the previous day (*e.g*., Duffy & Laurenson 1983; Johnstone *et al*. 1990; Zijlstra & van Eerden 1995). These pellets can be easily identified and collected at sites where shags roost overnight. The analysis of regurgitated pellets to investigate diet has become widely accepted as a non-invasive research technique (*e.g*., Favero *et al*. 1998), a particularly important aspect for a threatened species such as Auckland Island shags. A significant constraint to pellet collection has been identified for imperial shags where all pellets regurgitated outside of the breeding season were scavenged by lesser sheathbills (*Chionis minor*) (Espitalier-Noel *et al*. 1988). Auckland Island shags regurgitate pellets in the morning before departing to forage, however Marchant & Higgins (1990) report that these are usually eaten by red-billed gulls (*Larus novaehollandiae*), suggesting that scavenging may also limit access to pellets for diet analysis in this species.

Analyses of diet from regurgitated pellets can produce biased results: prey that lack indigestible remains are under-represented and digestive erosion of otoliths can result in underestimates of the numbers and sizes of fish prey for *Phalacrocorax* species of shags (Duffy & Laurenson 1983; Jobling & Breiby 1986; Barrett *et al.* 1990; Johnstone *et al*. 1990; Zijlstra & van Eerden 1995). In contrast to eroded otoliths from the pellets of some *Phalacrocorax* species, many otoliths from regurgitated pellets of blue-eyed shags show little erosion from digestion (e.g., Casaux & Barrera-Oro 1993; Lalas & Brown 1998).

Previous studies indicate that teleost fish generally make up the largest portion of the diet of blue-eyed shags, supplemented by cephalopods, polychaete worms and crustaceans (Brothers 1985; Espitalier-Noel *et al.* 1988; Favero *et al.* 1998; Barrett *et al.* 1990, Green *et al*. 1990; Coria *et al.* 1995). In New Zealand, quantitative investigations of blue-eyed shags have only been conducted for Stewart Island shags (Lalas 1983, summarised in Marchant & Higgins 1990) and New Zealand king shags (Lalas & Brown 1998) with both species designated as solitary benthic foragers. King shags in Pelorus Sound fed primarily on benthic fish, and Stewart Island shags feeding in Otago Harbour took a variety of teleost fish, crustaceans and cephalopods, the proportion of which changed seasonally with fish being most important in spring, and least important in winter (Lalas 1983). Auckland Island shags have been described as both solitary and gregarious foragers (Marchant & Higgins 1990). Current knowledge of their diet is limited to 2 anecdotal accounts which indicate that their diet includes lobster krill (*Munida gregaria*) and small fish (Oliver 1955; Marchant & Higgins 1990).

A thorough understanding of the ecology, including the diet of threatened seabirds, is important in facilitating effective conservation management strategies. However, to date no systematic research has been conducted on the diet of the Auckland Island shag. The aim of this study was to document the prey species of this threatened endemic New Zealand marine shag during winter at Enderby I.

MATERIALS AND METHODS

Regurgitated pellets from Auckland Island shags were collected in Aug 2010 at a cliff-top roost site at North East Cape (50°30′S, 166°19′E), Enderby I, Auckland Is, during a Department of Marine Science, University of Otago, research expedition aboard RV *Polaris II*. Following collection, each pellet was teased apart under water and then soaked for 1 hour in 95% ethanol to satisfy New Zealand biosecurity protocol for the sterilisation of animal specimens. Pellet contents were then sorted, dried and stored in ziplock plastic bags. Diagnostic prey remains were identified by comparisons against a reference collection compiled by CL aboard fishing vessels in southern New Zealand waters from 1981 to 1997. Fishes were identified from otoliths, cephalopods from beaks (keratinous jaws), crustaceans from claws and carapaces, polychaete worms from keratinous jaws and salps from tests. Species names presented here follow Gill *et al*. (2010) for birds, Paulin *et al*. (1989) for fishes, and O'Shea (1999) for octopuses. Beaks were indistinguishable between *Octopus campbelli* and *O. huttoni*, the 2 species of small octopus that frequent the continental shelf around Auckland Is (depicted in O'Shea 1999). Otoliths found in the Auckland Island shag pellets were readily identified to genus (Fig. 1). Triplefins of the genus *Forsterygion* cannot be differentiated reliably by otolith shape (Lalas & Brown 1998). Only 1 species, deepwater triplefin (*F. bathytaton*), was represented in the reference collection from around Auckland Is and so they were taken as representative of the genus. Two notothenid cod are present at Auckland Is—smallscaled cod (*Paranotothenia microlepidota*), and Maori chief (*P. angustata*) (Kingsford *et al*. 1989). The otoliths of these 2 species could not be differentiated

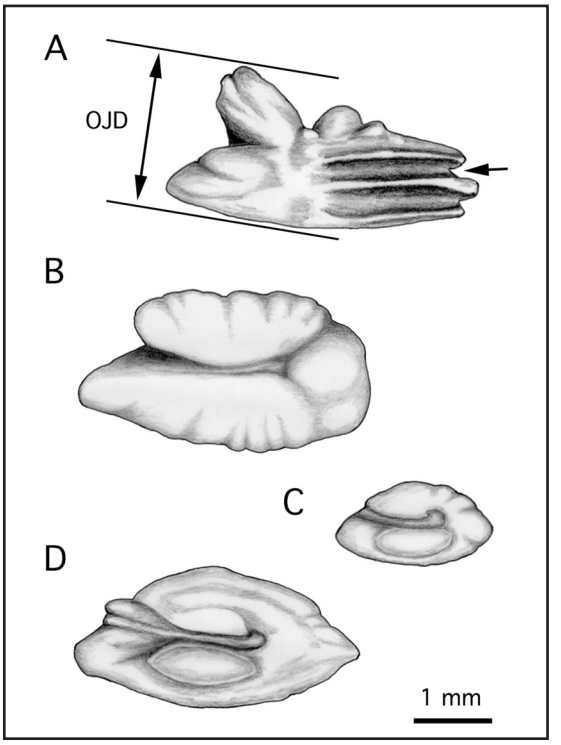

Fig. 1. Diagrams of the mesial surface of right otoliths of fishes found in this study; orientated with anterior to the left and dorsal up. **A.** Red cod (*Pseudophycis bachus*) fish total length (TL) = 8.3 cm; OJD = otolith jammed depth; arrow indicates posterio-dorsal notch = posterior end of otolith length measure ONL. **B.** Smallscaled cod (*Paranotothenia microlepidota*) TL = 24.2 cm. **C.** Deepwater triplefin (*Forsterygion bathytaton*) TL = 5.3 cm. **D.** Deepwater triplefin TL = 8.8 cm.

in regurgitated pellets, and so were designated as 'notothenid cod'.

Diagnostic prey remains were measured to the nearest 0.01 mm with vernier callipers. For octopuses, diagnostic beak measures were upper hood length (UHL) and lower hood length (LHL), as depicted in Lalas (2009). For fishes, otolith measures differed among species and were restricted to uneroded otoliths. For species other than red cod (*Pseudophycis bachus*), otolith maximum length (horizontal distance between anterior and posterior tips) was measured on intact otoliths and otolith maximum depth (perpendicular to length) was measured on broken otoliths. These measures were inappropriate for red cod otoliths because they have fragile posterior tips that make otolith maximum length measures unreliable and measures of otolith maximum depth are inconsistent. The length measure for red cod otoliths was taken from the anterior tip to the posterior-dorsal notch (otolith notch length) and the depth measure was taken from the anterior end with callipers tight against dorsal and ventral surfaces (otolith jammed depth) (Fig. 1).

Length and wet mass for all prey were estimated with allometric equations derived from measures of diagnostic remains from reference specimens (Table 1). Left and right fish otoliths, upper and lower cephalopod beaks and left and right polychaete jaws were each measured separately; species-specific equations were then applied to each element (Table 1). Within individual pellets, opposite elements were designated as pairs belonging to the same prey item based on similarity (within 5%) of estimated prey length. The exception was red cod where otoliths were sufficiently large to show individual variation and pairings were made based on both shape and length.

The relationship between the total wet mass of prey items (M_i) and the number of prey items per regurgitated pellet (N_i) was assessed with a logistic growth curve fitted in SPSS® Version 17.0, SPSS Inc., 2008, with the equation:

$$M_i = M_\infty/(1 + e^{-k(N_i - y_0)})$$

where M_∞ = asymptote for total wet mass of prey items per pellet, k = exponential rate of increase and y_0 = point of inflexion of the curve.

Incidental observations of foraging Auckland Island shags were made from the University of Otago Research Vessel *Polaris II* anchored in Erebus Cove (50°32'S, 166°13'E) in Ross Harbour, Auckland I, and elsewhere in Ross Harbour from small boats or from land. In total we estimate that these observations accounted for ~10 hours.

RESULTS

Analysis of regurgitated pellets

A total of 23 regurgitated pellets were collected from Auckland Island shags at North East Cape, Enderby I: 7 on 7 Aug, 9 on 9 Aug and 7 on 14 Aug 2010. All pellets were collected early afternoon (1230 – 1400 h) with 10-20 shags and 3–5 red-billed gulls present. No birds flew off during sampling. Most, if not all, pellets were incomplete and typically lacked a mucous sac. Pellet remains were spherical or ovoid in shape with a diameter of 1-1.5 cm. All pellets contained fish otoliths, fish bones and octopus beaks. None contained rocks, but most contained several small gastropod shells (0.5-1.0 cm), but lack of operculae indicated that they were not taken as prey. Additional contents not attributed to prey remains were 2 parasitic isopods (1.2 and 1.3 cm TL), parasites that inhabit the gills of teleost fish, and one unidentified krill. No digestive erosion was apparent for any fish otoliths recovered. However, cephalopod beaks and fish otoliths in pellets were typically found broken. A total of 627 otoliths were

Table 1. Equations used to estimate the length and mass of prey items from diagnostic remains in regurgitated pellets of Auckland Island shags. Origin of specimens in the New Zealand region: AI = Auckland Is (50-51°S), SP = Southern Plateau (50-53°S), SI = Stewart I and southern South I (44-47°S). Measures on diagnostic remains (mm): JL = jaw length, UHL = upper beak hood length, LHL = lower beak hood length, ONL = otolith length from anterior tip to posterio-dorsal notch (Fig. 1), OJD = otolith jammed depth (Fig.1), OML = otolith maximum length, OMD = otolith maximum depth; Measures for length (cm): ML = ventral mantle length, TL = total length, CW = carapace width.

Species	Origin	Size range (cm)	Length (cm)	*n*	r^2	Mass (g)	*n*	r^2
Polychaete worm (*Perinereis* sp.)	SI	10-31	$0.19JL^{2.20}$	10	0.89	$0.037JL^{2.02}$	10	0.95
Octopus (*Octopus campbelli)*	AI	7.0-21.0	$6.38UHL^{1.00}$ $9.39LHL^{0.98}$	21 21	0.71 0.55	$1.98ML^{1.83}$	21	0.83
Red cod (*Pseudophycis bachus)*	SP	8.3-73.5	$0.86ONL^{1.61}$ $1.51OJD^{2.15}$	73 73	0.98 0.97	$0.009TL^{3.04}$	73	0.99
Deepwater triplefin (*Forsterygion bathytaton)*	SI & AI	4.0-11.4	$3.89OML^{0.96}$ $5.05OMD^{1.16}$	101	0.96 0.93	$0.005TL^{3.35}$	80	0.99
Smallscaled cod (*Paranotothenia microlepidota)*	AI	23.2-60.5	$4.39OML^{1.35}$ $10.83OMD^{1.31}$	51	0.81 0.80	$0.014TL^{3.00}$	51	0.97
Swimming crab (*Nectocarcinus bennetti)*	AI	3.9-8.4	-	-	-	$0.55CW^{2.64}$	30	0.98
Salp (*Iasis zonaria)*	SI	1.4-7.3	-	-	-	$0.11TL^{1.39}$	9	0.96

Table 2. Composition of prey represented in 23 regurgitated pellets collected from Auckland Island shags in Aug 2010.

Prey	Frequency	Minimum number	Total mass (g)
Octopus	23 (100%)	602 (57%)	8980 (68%)
Red cod	21 (91%)	54 (5%)	2537 (19%)
Triplefin	21 (91%)	348 (33%)	1221 (9%)
Notothenid cod	5 (22%)	6 (<1%)	349 (3%)
Polychaete worm	13 (57%)	24 (2%)	47 (<1%)
Swimming crab	3 (13%)	3 (<1%)	33 (<1%)
Salp	3 (13%)	21 (2%)	11 (<1%)
Total		1058	13179

recovered from pellets, of which 613 (98%) were measured. Of these, 488 (80%) were broken and could not be measured for otolith length; instead they were represented by otolith depth.

The 23 regurgitated pellets analysed contained remains of a minimum of 1058 prey items with an estimated total original wet mass of 13.2 kg (Table 2). Octopus and fish were represented in all pellets. Three taxa contributed at least 5% towards the total mass of prey. The most important prey was *Octopus* spp. accounting for 57% of prey items and 68% of total prey mass, followed by 2 taxa of fish each occurring in 90% of the regurgitated pellets: red cod (5% by number and 19% by mass) and triplefin (33% by number and 9% by mass) (Table 2). The remainder of prey items—notothenid cod, polychaete worms, swimming crab (*Nectocarcinus bennetti*) and salp (*Iasis zonaria*) —together accounted for only 5% of prey items and 4% of total prey mass. Prey size range varied from 2 cm for salp to 28 cm for red cod (Table 3, Fig. 2).

The mean number of prey items per pellet was 46.0 (*sd* = 25.3, range 7-90), with mean total prey mass of 589 g per pellet (*sd* = 262, range 86-1037 g). These results should be regarded as minima for 2 reasons: breakage or loss of diagnostic prey remains and incomplete pellets. Evidence for undercounting attributable to breakage or loss was indicated by many prey items being designated only by a single element from paired elements. This was exemplified by the 2 most numerous prey species. For the 602 octopus remains, 469 (78%) were derived from measures of paired beaks, 24 (4%) from unpaired upper beaks and 109 (18%) from unpaired lower beaks. Similarly for the 348 triplefin, 205 (59%) remains were derived from measures of paired otoliths, 77 (22%) from unpaired left otoliths and 66 (19%) from unpaired right otoliths. To assess the integrity of pellets a logistic curve was fitted to the relationship between total mass and number of prey items, $y = 876/(1+e^{-0.06(x-27.7)})$ ($r^2 = 0.649$, $n = 23$) (Fig. 3). Here the asymptote for total mass (876 g) had 95% confidence limits of 672-1080 g. The lower confidence limit was matched or exceeded by 6 of

Table 3. Size of prey represented in 23 regurgitated pellets collected from Auckland Island shags in Aug 2010. * Length measure = carapace width.

Prey	Number quantified		Total length (cm)			Mass (g)		
			mean	*sd*	range	mean	*sd*	range
Octopus	602	100%	13.8	2.3	5.1-21.9	14.9	6.2	1.3-44.5
Red cod	43	80%	15.5	5.3	6.1-28.1	46.4	42.7	1.9-209
Triplefin	348	100%	6.5	1.7	2.9-11.4	3.5	3.0	0.2-18.3
Notothenid cod	6	100%	13.9	6.2	7.9-24.0	58.1	72.6	7.0-194
Polychaete worm	24	100%	6.2	2.1	3.0-10.1	1.8	1.2	0.4-4.3
Swimming crab*	1	33%	3.1	-	-	10.5	-	-
Salp	12	57%	3.0	1.1	1.6-5.1	0.6	0.4	0.1-1.5

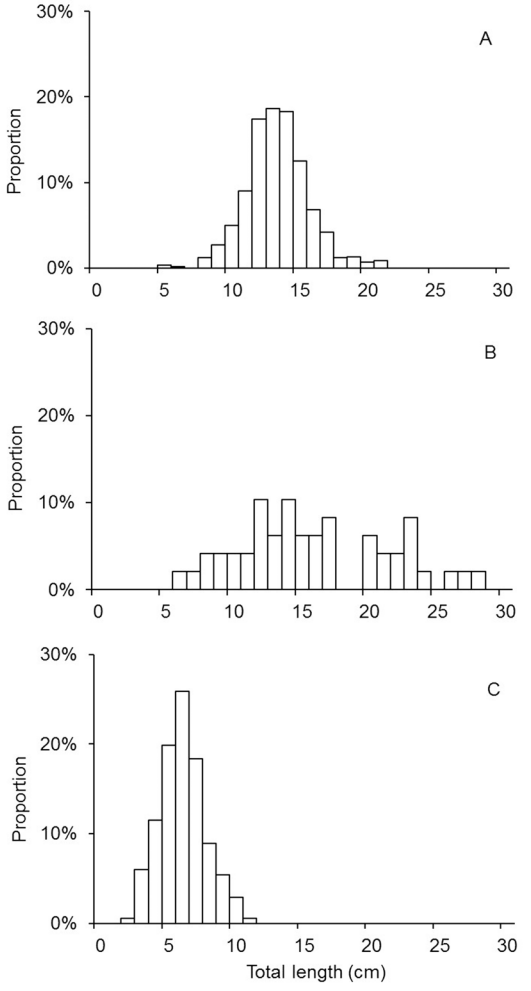

Fig. 2. Length frequency distributions of the 3 most important prey species recorded in regurgitated pellets from Auckland Island shags in Aug 2010. **A.** 602 octopus (*Octopus* sp.). **B.** 43 red cod (*Pseudophycis bachus*). **C.** 348 triplefin (*Forsterygion* sp.).

the 7 pellets with >60 prey items but only by 2 of the 16 pellets with <60 prey items. This outcome indicated that pellets with <60 prey items may have been incomplete.

Observations of shag behaviour

Auckland Island shags encountered in Ross Harbour (2-40 m) typically foraged alone several hundred metres apart. These observations were numerous, but unquantified. A total of 3 foraging groups were observed incidentally in Erebus Cove (2-20 m): a group of 4 shags on 5 Aug, a group of 22 on 9 Aug, and a group of 5 shags on 11 Aug 2010. The latter group foraged among a group of about 35 yellow-eyed penguins (*Megadyptes antipodes*). Group foraging was preceded by shags flying to a site (either single birds that were foraging elsewhere, or groups of birds that were roosting ashore together) and congregating at the surface. The pattern of foraging was observed for the 2 small groups: individuals dived asynchronously for about 30 minutes and then groups disbanded as shags flew off. Our observations were too distant to discern prey species caught. The only potential prey we saw swimming at or near the surface were small red cod (10-20 cm estimated TL) and lobster krill.

No nesting activity was observed on the first 2 pellet collection dates, 7 and 9 Aug 2010. However, nest building by Auckland Island shags was observed on a cliff ledge at North East Cape on 14 Aug 2010, indicating the beginning of the breeding season.

DISCUSSION

The 68% contributed by octopus towards the total prey mass in the diet of Auckland Island shags is unprecedented among all species of shags. The largest contribution by octopus in the 8 other blue-eyed shag species for which diet has been quantified was 15% by mass for Stewart Island shags in winter (Lalas 1983). Octopus contributed a maximum of 6% towards the mass of diet in the other 7 species (Brothers 1985; Espitalier-Noel *et al.* 1988; Punta *et*

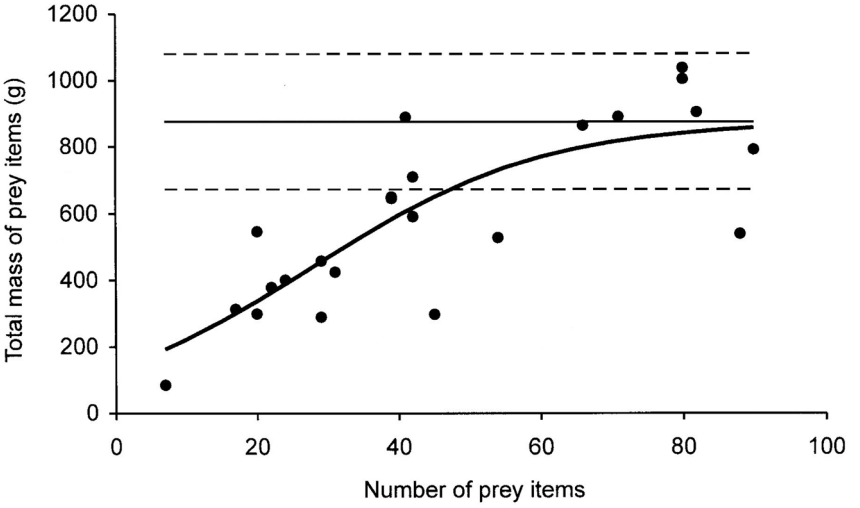

Fig. 3. Relationship between total mass and number of prey items represented in 23 regurgitated pellets from Auckland Island shags in Aug 2010. The curved line is the logistic curve of best fit; the horizontal lines show the asymptote of the logistic curve (solid) flanked by 95% confidence limits (dashed).

al. 1993; Ridoux 1994; Coria *et al.* 1995; Favero *et al.* 1998; Lalas & Brown 1998). All but one had diets dominated by fish—the exception was the Heard Island shag (*L. nivalis*) where polychaete worms were recorded in 99% of the 210 pellets analysed (Green & Williams 1997). The only other shag species for which a cephalopod reportedly plays a major part in the diet is the flightless cormorant (*Phalacrocorax harrisi*) of the Galapagos Is for which incidental reports indicate octopus is an important component of the diet (Johnsgard 1993; Nelson 2005).

Maximum prey length recorded for Auckland Island shags was 28 cm, midway through the range of maxima (20-36 cm) recorded from the 6 other blue-eyed shag species with comparable results (Lalas 1983; Espitalier-Noel *et al.* 1988; Ridoux 1994; Coria *et al.* 1995, Lalas & Brown 1998; Punta *et al.* 1993). The maximum lengths of the 3 major prey taxa fell into 2 categories: those representing the maximum recorded for the species, and those representing only young cohorts. Maxima for octopus (21.9 cm) and triplefin (11.4 cm) as prey matched the maximum lengths recorded for these species in our reference collection from the Auckland Is (21.0 and 11.4 cm, respectively). Consequently, all age classes of *Octopus* sp. and triplefin were subject to predation by Auckland Island shags. In contrast, the maximum length of red cod as prey (28.1 cm) was only 40% of the maximum length recorded for this species in our reference collection (70.5 cm). Red cod are a fast growing fish that grow to about 25 cm in their 1st year and achieve sexual maturity at 45-50 cm TL at age 2-3 years (Horn 1996). Consequently, only young red cod were subject to predation by Auckland Island shags, and the average length of red cod taken is therefore likely to vary seasonally.

Our opportunistic observations of Auckland Island shags using 2 different foraging strategies—gregarious foraging and solitary foraging—concur with previous observations by G.F. van Tets and E.R. Waite (summarised in Marchant & Higgins 1990). We suggest that shags foraged gregariously when targeting schooling pelagic prey such as juvenile red cod and foraged alone when targeting benthic prey such as octopus and triplefin. However, further studies are required to investigate and quantify the foraging behaviours used by Auckland Island shags and how they might differ from other species of blue-eyed shags.

This study indicated the diversity of prey and minimum daily intake by Auckland Island shags roosting at North East Cape, Enderby I, in Aug. The large proportion of broken prey remains (*e.g.*, 80% of measurable fish otoliths) and the potential inclusion of incomplete pellets, mean that our results nearly certainly underestimate the number of prey items. We suspect that incomplete pellets (*i.e.*, pellets lacking a mucous sac) could be attributed to scavenging by red-billed gulls as individuals of this species were consistently present at the roost site during sample collection. It is possible that the broken otoliths could be a direct result of this scavenging, as could loss of prey remains through secondary ingestion by the gulls. Because of the short duration of this study and the localised nature of the study site, we must limit our conclusions strictly to the prey of Auckland Island shags based at Enderby I in winter and recommend that further studies are undertaken on diet of Auckland Island shags to investigate potential spatial and temporal variations in prey species and size of prey. In addition, finding intact regurgitated pellets would enable estimates to be made for daily intake.

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LITERATURE CITED

Barrett, R.T.; Rov N.; Løen, J.; Montevecchi, W.A. 1990. Diets of shags *Phalacrocorax aristotelis* and cormorants *P. carbo* in Norway and possible implications for gadoid stock recruitment. *Marine Ecology Progress Series 66:* 205–218.

Brothers, N.P. 1985. Breeding biology, diving and morphometrics of the *Phalacrocorax albiventer purpurascens*, at Macquarie Island. *Australian Wildlife Research 12:* 81–94.

Casaux, R.J.; Barrera-Oro, E.R. 1993. The diet of the blue-eyed shag *Phalacrocorax atriceps bransfieldensis* feeding in the Bransfield Strait. *Antarctic Science 5*: 335–338.

Cook, T.R.; Lescroel, A.; Tremblay, Y.; Bost, C. 2008. To breathe or not to breathe? Optimal breathing, aerobic dive limit and oxygen stores in deep-diving blue-eyed shags. *Animal Behaviour 76:* 565–576.

Coria, N.; Casaux, R.; Favero, M.; Silva, P. 1995. Analysis of the stomach content of the blue-eyed shag *Phalacrocorax atriceps bransfieldensis* at Nelson Island, South Shetland Islands. *Polar Biology 15:* 349–352.

Croxall, J.P.; Naito, Y.; Kato, A.; Rothery, P.; Briggs, D.J. 1991. Diving patterns and performance in the Antarctic blue-eyed shag *Phalacrocorax atriceps*. *Journal of Zoology London 225*: 177–199.

Duffy, D.C.; Laurenson, L.J.B. 1983. Pellets of cape cormorants as indicators of diet. *Condor 85*: 305–307.

Espitalier-Noel, G.; Adams, N.J.; Klages, N.T. 1988. Diet of the imperial cormorant *Phalacrocorax atriceps* at sub-Antarctic Marion Island. *Emu 88:* 43–46.

Favero, M.; Casaux, R.; Silva, P.; Barrera-Oro, E.; Coria, N. 1998. The diet of the Antarctic shag during summer at Nelson Island, Antarctica. *Condor 100:* 112–118.

Gill, B.J.; Bell, B.D.; Chambers, G.K.; Medway, D.G.; Palma, R.L.; Scofield, R.P.; Tennyson, A.J.D.; Worthy, T.H. 2010. *Checklist of the birds of New Zealand, Norfolk and Macquarie Islands, and the Ross Dependency, Antarctica.* Fourth Edition. Wellington: Ornithological Society of New Zealand & Te Papa Press.

Green, K.; Williams, R.; Woehler, E.J.; Burton, H.R.; Gales N.J.; Jones, R.T. 1990. Diet of the Heard Island cormorant *Phalacrocorax (atriceps) nivalis*. *Antarctic Science 2*: 139–141.

Green, K.; Williams, R. 1997. Biology of the Heard Island shag *Phalacrocorax nivalis.* Part 3. Foraging, diet and diving behaviour. *Emu 97:* 76–83.

Horn, P.L. 1996. Age and growth of red cod (*Pseudophycis bachus*) off the south-east coast of South Island, New Zealand. *New Zealand Journal of Marine and Freshwater Research 30:*151–160.

IUCN 2011. *Phalacrocorax colensoi*. In: IUCN 2011. IUCN Red List of Threatened Species. Version 2011.1 www.iucnredlist.org. Downloaded on 16 June 2012.

Jobling, M.; Breiby, A. 1986. The use and abuse of fish otoliths in studies of feeding habits of marine piscivores. *Sarsia 71*: 265–274.

Johnsgard, P.A. 1993. *Cormorants, darters and pelicans of the world*. Smithsonian Institution Press, Washington.

Johnstone, I.G.; Harris, M.P.; Wanless, S.; Graves, J.A. 1990. The usefulness of pellets for assessing the diet of adult shags *Phalacrocorax aristotelis. Bird Study 37*: 5–11.

Kingsford, M.J.; Schiel, D.R.; Battershill, C.N. 1989. Distribution and abundance of fish in a rocky reef environment at the Subantarctic Auckland Islands, New Zealand. *Polar Biology 9*: 179–186.

Lalas, C. 1983. Comparative feeding ecology of New Zealand marine shags (Phalacrocoracidae). Unpubl. PhD thesis, University of Otago, Dunedin, New Zealand.

Lalas, C.; Brown, D. 1998. Diet of New Zealand king shags (*Leucocarbo carunculatus*) in Pelorus Sound. *Notornis 45:* 129–139.

Lalas, C. 2009. Estimates of size for the large octopus *Macroptopus maorum* from measures of beaks in prey remains. *New Zealand Journal of Marine and Freshwater Research 43*: 635–642.

Marchant, S.; Higgins, P.J. (Eds) 1990. *Handbook of Australian, New Zealand and Antarctic birds*. Vol. 1, Pt. B. Oxford University Press, Melbourne.

Miskelly, C.M.; Dowding, J.E.; Elliott, G.P.; Hitchmough, R.A.; Powlesland, R.G.; Robertson, H.A.; Sagar, P.M.; Scofield, R.P.; Taylor, G.A. 2008. Conservation Status of New Zealand birds, 2008. *Notornis 55:* 117–135.

Moore, P.J.; McClelland, P.J. 1990. Notes on birds of the Auckland Islands, November – December 1989. *Science and Research Internal Report No. 93*, Department of Conservation, Wellington.

Nelson, J.B. 2005. *Pelicans, cormorants and their relatives: The Pelecaniformes*. Oxford University Press, New York.

Oliver, W.R.B. 1955. New Zealand birds. Second Edition. A.H. & A.W. Reed. Wellington, New Zealand.

O'Shea, S. 1999. The marine fauna of New Zealand: Octopoda (Mollusca: Cephalopoda). *NIWA Biodiversity Memoir 112*.

Paulin, C.; Stewart, A.; Roberts. C.; McMillan, P. 1989. New Zealand fish. A complete guide. *National Museum of New Zealand Miscellaneous Series No. 19.* Museum of New Zealand Te Papa Tongarewa, Wellington.

Punta, G.E.; Saravia, J.R.C.; Yorio, P.M. 1993. The diet and foraging behaviour of two Patagonian cormorants. *Marine Ornithology 21*: 27–36.

Quintana, F.; Wilson, R.P.; Yorio, P. 2007. Dive depth and plumage air in wettable birds: the extraordinary case of the imperial cormorant. *Marine Ecology Progress Series 334:* 299–310.

Ridoux, V. 1994. The diets and dietary segregation of seabirds at the subantarctic Crozet Islands. *Marine Ornithology 22:* 1–192.

Siegel-Causey, D. 1988. Phylogeny of the Phalacrocoracidae. *Condor 90*: 665–905.

Taylor, G.A. 1988. Report to the Department of Conservation on an expedition to the Auckland Islands National Reserve, February 1988. Unpublsihed Reprt, Department of Conservation, Invercargill.

Taylor, G.A. 2000. Action plan for seabird conservation in New Zealand. Part A: Threatened seabirds. *Threatened Species Occasional Publication No. 16*. Department of Conservation, Wellington.

Tremblay, Y.; Cook, T.R.; Cherel, Y. 2005. Time budget and diving behaviour of chick-rearing Crozet shags. *Canadian Journal of Zoology 83:* 971–982.

Wanless, S.; Harris, M.P.; Morris, J.A. 1992. Diving behaviour and diet of the blue-eyed shag at South Georgia. *Polar Biology 12:* 713–719.

Zijlstra, M.; van Eerden, M.R. 1995. Pellet production and the use of otoliths in determining the diet of cormorants *Phalacrocorax carbo sinensis*: trials with captive birds. *Ardea 83*: 123–131.