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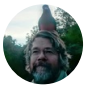

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RESEARCH ARTICLE

Pre-human New Zealand sea lion (*Phocarctos hookeri*) rookeries on mainland New Zealand

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Holocene New Zealand sea lion (*Phocarctos hookeri*) bones collected from the north of New Zealand's South Island strengthen existing evidence for the former Holocene presence of breeding colonies of *P. hookeri* on mainland New Zealand. The taxonomic identity of *Phocarctos* bones is confirmed using both morphology and ancient DNA analysis. Five radiocarbon dates on four adult and one pup bone from Creighton's Cave near Paturau, northwest Nelson, ranged from 1290 ± 30 yr BP to 5430 ± 30 yr BP. Three radiocarbon dates on pup bones spanning 200 ^{14}C yr (1550 ± 30 yr BP to 1390 ± 30 yr BP) reveal that a prehistoric breeding rookery was present at Delaware Bay, Nelson, until shortly before the time of human arrival c. AD 1280 (670 yr BP). The Delaware Bay site in particular provides a valuable 'snapshot' of coastal New Zealand faunas shortly before human arrival, one that has potential to enhance our understanding of changes in the endemic coastal fauna associated with human colonisation.

Keywords: ancient DNA; Delaware Bay; Creighton's Cave; extinction; Polynesian colonisation; New Zealand sea lion; *Phocarctos hookeri*

Introduction

Palaeontological data can provide important insights into the composition of endemic biotas prior to human colonisation, and the subsequent ecosystem changes associated with human arrival (Holdaway 1989; Smith 2013). Such data have been applied to studies of biological change associated with human arrival in recently colonised regions of the globe such as Madagascar, New Zealand and numerous Pacific Islands (Worthy & Holdaway 2002; Burney et al. 2004; Steadman 2006). New Zealand's Quaternary fossil record is particularly rich and Worthy & Holdaway (2002) describe it as 'one of the best Late Quaternary (less than 50,000 years) fossil records in the world' (p. xxx). Numerous prehistoric coastal taxa are well represented in deposits throughout coastal New Zealand (Anderson 1982; Worthy 1992, 1994; Smith 2013). Given the excellent preservation of pre-human faunal remains, it might seem surprising that relatively few studies have described and dated pre-human coastal assemblages in natural deposits (see Worthy 1998a).

Prehistoric New Zealand sea lion *Phocarctos hookeri* (Gray 1844) remains have been recorded along the length of mainland New Zealand's coastline (Fig. 1; Appendix 1) and on offshore islands including Stewart Island, the Chatham Islands

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and Enderby Island (Auckland Islands) (Smith 1985; McFadgen 1994; Childerhouse & Gales 1998; Anderson 2005). These widespread remains indicate that the pre-human geographic range of this species was much broader than otherwise suggested by the predominantly high-latitude (largely sub-Antarctic) range of the species today (Smith 1985; Childerhouse & Gales 1998). The majority of *P. hookeri* remains from mainland sites have been excavated from archaeological middens that cover the period of early Polynesian settlement approximately 600–700 years ago (Smith 1985). Smaller numbers of naturally deposited (pre-human) *P. hookeri* specimens have also been recorded from sand dunes (Worthy 1994; Gill 1998) and caves (Worthy 1992) on mainland New Zealand from the late Holocene.

A lack of pup and juvenile *P. hookeri* bones in natural deposits and archaeological sites has, in the past, contributed to uncertainty as to whether breeding populations of *P. hookeri* existed on mainland New Zealand at the time of human arrival. Cawthorn (1993) described the distribution of archaeological *P. hookeri* material as 'consistent with the current distribution and range of Hooker's sea lion' (p. 1), suggesting that 'no historical evidence of breeding rookeries (i.e. pup remains) has yet been found in mainland New Zealand'. However, Worthy (1994) suggested that small, porous pup bones were likely to be under-represented in natural dune deposits due to their relatively poor preservation potential. This phenomenon was discussed in relation to *P. hookeri* remains collected from the North Cape, where Gill (1998, p. 56) noted that the pup bones 'survived less well owing to their fragility' in comparison with adult bones from the same location.

The northern and northwestern regions of the South Island are of particular significance in terms of understanding prehistoric *P. hookeri* and their pre-human breeding distribution. Worthy (1994) provided the first evidence for a *P. hookeri* pup on mainland New Zealand from this region (Delaware Bay, Nelson), suggesting that this species was indeed breeding on the mainland during the Holocene. Worthy (1994) also re-examined *P. hookeri* material collected from caves at Paturau (northwest Nelson), including Creighton's Cave (Fig. 1) (Worthy 1992) and identified further pup bones. Holocene-aged remains of 'young' *P. hookeri* were previously identified from Hawkes Bay (Berry & King 1970; Weston et al. 1973), however it is not certain whether these bones were from pups or juveniles sufficiently young to definitively indicate breeding at this site.

Following the discovery of *P. hookeri* pup remains at Delaware Bay and Paturau (Fig. 1), additional observations of *P. hookeri* pup bones have been made from New Zealand's North Island. Gill (1998) observed the remains of both adult and juvenile *P. hookeri* from Tom Bowling Bay and Waikuku Beach in Northland. These Northland pup remains were found in Holocene-aged sand dunes and are thought to predate human settlement (Gill 1998). A pup bone has also been recorded from a likely breeding colony on D'Urville Island (Museum of New Zealand Te Papa Tongarewa [NMNZ] collection database). Additionally, juvenile *P. hookeri* remains have been identified from sand dunes on the Chatham Islands (McFadgen 1994), providing further evidence for a formerly widespread distribution of breeding *P. hookeri* prior to human arrival.

Here we undertake field sampling, radiocarbon-dating and ancient DNA analysis of Holocene *P. hookeri* bones to shed light on the history of sea lions on mainland New Zealand. This research provides further evidence for the former presence of breeding colonies of *P. hookeri* on mainland New Zealand during the Holocene until just prior to human arrival using radiocarbon dating of newly excavated bones and ancient DNA analysis to confirm the taxonomic identity of these bones.

Methods

Sampling

Phocarctos hookeri bones were collected from Delaware Bay and Creighton's Cave (Fig. 1) on

Figure 1 A, Geographic distribution of New Zealand sea lion based on presence in archaeological and natural deposits (see also Appendix 1). The late Holocene natural sites of Delaware Bay and Creighton's Cave are marked on the map in bold type. Sites with solid black circles indicate the presence of pup or juvenile remains. Geographic distribution data have been sourced from Smith (1985), Worthy (1992, 1994) and collection records of the Canterbury Museum, Museum of New Zealand Te Papa Tongarewa and Auckland Museum. Sites with superscript numbers represent multiple localities within the same geographic locale: [1] Cape Maria van Diemen, Te Werahi Beach and Spirits Bay; [2] Waikuku and Whareana Beach; [3] Tokerau Beach/Doubtless Bay, Matai Bay and Karikari Beach; [4] Ohawe and Te Rangatapu; [5] Creighton's Cave, Wet Neck Cave and Baby Grand Cave; [6] Redcliffs Flat, Sumner, Moa Bone Point Cave; [7] Hooper's Inlet and Papanui Beach; [8] Saint Clair and Otoika Mouth; [9] Pounawea, New Haven, Cannibal Bay and False Islet; [10] Ruapuke Island containing the sites West Point, Lee Island and Parangiaio; and [11] Port Pegasus and Cook Settlement. **B** and **C**, Regional maps showing the location of the late Holocene natural sites Delaware Bay and Creighton's Cave respectively. Grids are 1 km^2.

1 and 2 December 2011. Bones were collected and stored in plastic ziplock bags until required for analysis.

Delaware Bay

Delaware Bay is a sand dune site, approximately 15 km northeast of Nelson, where Worthy (1994) first recorded *P. hookeri* pup remains on mainland New Zealand. We sampled the south-facing edge of the sand dune, described by Worthy (1994), covering an area of c. 500 m^2. Bones observed on the surface were collected, as well as additional bones of an individual found to be present beneath the surface (up to a depth of c. 200 mm). There is evidence of early Māori occupation near this site; umu (Māori ovens) are visible at the western end of the sand dune and middens are present in the upper levels of the nearby sand dune (Worthy 1994). However, the *P. hookeri* bones collected from Delaware Bay were all from natural deposits stratigraphically below the Polynesian middens (Worthy 1994). Bones of a number of different vertebrate taxa including various coastal bird species were also collected during this sampling trip, including the Waitaha penguin *Megadyptes waitaha* Boessenkool et al. 2009, Caspian tern *Hydroprogne caspia* (Pallas 1770) and fluttering shearwater *Puffinus gavia* (J.R. Forster 1844) (Appendix 2). These specimens are housed in the NMNZ and Canterbury Museum (CM).

Creighton's Cave

There are numerous limestone caves throughout the Paturau region of the northwest South Island, and Holocene terrestrial and coastal vertebrate assemblages have been observed in several of these sites (Worthy 1992). In many cases, openings in the roofs of these caves have created 'pitfall traps' that have facilitated accumulation of terrestrial fauna over time. Creighton's Cave is a large cave located 500 m from the present shoreline, and is currently surrounded by farmland. The cave is entered via its resurgence entrance and a little over 1 km of passages are known upstream of this point. The bones derive from gravels in the current stream bed 100–200 m upstream of the entrance in a passage that is about 10 m wide and 25 m high (Worthy et al. 1992). As there is one main entrance to the cave, Worthy (1992) suggested it is likely that Holocene bones in Creighton's Cave have fallen through 'sinkhole' openings from the valley floor into the cave. Pre-European faunal remains that we collected from Creighton's Cave included extinct and locally extinct taxa such as moa (Aves: Dinornithiformes), South Island snipe *Coenocorypha iredalei* (Rothschild 1921) (Appendix 3) and *P. hookeri*. These specimens are also housed in NMNZ.

Phocarctos hookeri bones have also been recorded from nearby caves in the Paturau region (Worthy 1992). Sea lion bones from Wet Neck and Turimawiwi Caves have been dated to 3690–2380 yr BP and 12,036–10,882 yr BP, respectively (Worthy 1992).

Morphological and genetic analyses

Phocarctos hookeri remains from Delaware Bay and Creighton's Cave were identified morphologically following Worthy (1992, 1994). Avifaunal remains were identified morphologically using collections at NMNZ and CM and their classification follows Gill et al. (2010). To confirm morphological identifications of sea lion bones, a short (189 base pairs), highly variable region of the mitochondrial control region was amplified and sequenced from one individual from each of Delaware Bay and Creighton's Cave. No specimens from previous collections (Worthy 1992, 1994) were sampled for ancient DNA (aDNA) analysis. All aDNA extractions and polymerase chain reaction (PCR) set up were carried out in a purpose built ancient DNA laboratory at the University of Otago. The lab is physically isolated from any other molecular laboratories (Knapp et al. 2012) and we followed strict ancient DNA procedures to minimise contamination of samples with exogenous DNA (Cooper & Poinar 2000).

DNA was extracted from bone from one Delaware Bay pup (330890, CM Ma4105, right humerus, 204 mg) and one Creighton's Cave pup (333719, NMNZ S.45732, right humerus, 140 mg), following Rohland et al. (2010). Two primer pairs (NZSLCR1f 5′ ATGTATATCGT GCATTAGTGGTTTG 3′/NZSLCR1r 5′ TTG TGGGCTAGGTGAATTA 3′ and NZSLCR2f 5′ AACTACTTCAAGCACTATAAAGTTCC 3′/NZSLCR2r 5′ AGTCTAGCTACCCCCGT T 3′) were designed, based on published whole mitochondrial genome sequences of *P. hookeri* (GenBank accession number AM181019.1) to amplify short, overlapping regions of the control region, resulting overall in a 189 base pair fragment (excluding primers). Each PCR was replicated twice. PCR products (from independent amplifications) were sequenced bi-directionally and blasted against existing modern *P. hookeri* control region sequences available on GenBank. This methodology allowed robust species identification of the bones collected.

A Maximum Likelihood analysis was performed in PAUP* (Swofford 2003), including sequences from the Delaware Bay and Creighton's Cave individuals, modern *P. hookeri* (GenBank accession number AM181019.1) and pinniped outgroups (Australian sea lion *Neophoca cinerea* [Peron 1816] AM181020.1, Australian fur seal *Arctocephalus pusillus* [Schreber 1775] NC_008417, New Zealand fur seal *Arctocephalus forsteri* Lesson 1828 NC_004023, southern elephant seal *Mirounga leonina* [Linnaeus 1758] NC_008422.1, Leopard seal *Hydrurga leptonyx* [Blainville 1820] NC_008425.1). Sequences were aligned using the Clustal W algorithm and checked by eye. The most appropriate model of evolution, as determined by MODELTEST (Posada & Crandall 1998) under the Akaike information criterion, was K81uf + I. A maximum likelihood analysis was performed in PAUP* (Swofford 2003) using the full heuristic search option. Parameters for the K81uf + I model were then re-estimated from the data and node support was calculated with 10,000 bootstrap replicates.

Radiocarbon dating of bones

Eight *P. hookeri* bones were radiocarbon dated (Table 2) at Beta Analytic Inc (USA). Three pup bones from Delaware Bay, and four adult and one pup bone from Creighton's Cave were included in radiocarbon dating analyses. Dates are reported as radiocarbon ages, based on Libby $T^{1/2} = 5568$ years, uncorrected for calendar variation, in years before present (present is AD 1950). Radiocarbon ages were calibrated using OxCal v4.2 (Bronk Ramsey 2009) and the Marine09 calibration curve (Reimer et al. 2009). A local (Ligar Bay, -35 ± 46) ΔR value (Petchey et al. 2008) was applied to the calibrations of radiocarbon dates. The large geographic ranges of many pinnipeds in their adult stage can make it difficult to select appropriate ΔR values for such taxa (Yoneda et al. 2001; de Bruyn et al. 2009). To account for this issue we also applied minimum and maximum New Zealand ΔR values (Petchey et al. 2008) to the adult bones radiocarbon-dated. Minimum and maximum ΔR values were not necessary for the calibration of radiocarbon dates associated with pup bones, as sea lion pups do not move great distances during the early stages of their life (Wilkinson et al. 2003; Chilvers & Wilkinson 2008). As applying the minimum or maximum ΔR values did not substantially alter the calibrated ages (results not shown), the Ligar Bay ΔR value of -35 ± 46 was used hereafter for all radiocarbon dates yielded from *P. hookeri* bones. Calibrated ages are reported as 95.4% confidence calibrated ages in years BP. Calibrated ages were compared with published radiocarbon dates from Wairau Bar (moa eggshell) and rat-gnawed seeds as proxies for human presence in the northern South Island and New Zealand, respectively (Higham 1994; Wilmshurst & Higham 2004; Wilmshurst et al. 2008). Moa eggshell and rat-gnawed seed dates were calibrated using OxCal v4.2 (Bronk Ramsey 2009) and the ShCal04 calibration curve (McCormac et al. 2004).

Table 1 *Phocarctos hookeri* bones collected from Delaware Bay (DEB) and Creighton's Cave (CRC). Bones were identified to element and age, following the methodology of Worthy (1992, 1994). Delaware Bay samples not consumed in analyses will be stored at the Canterbury Museum and Creighton's Cave samples will be stored at the Museum of New Zealand Te Papa Tongarewa.

Site	Accession number	^{14}C lab. no. (Beta)	Element	Age
Delaware Bay	CM Ma4104	330889	Complete (or near complete) skeleton	Pup
Delaware Bay	CM Ma4105	330890	Partial skeleton	Pup
Delaware Bay	CM Ma4106	330888	Partial skeleton	Pup
Delaware Bay	CM Ma4107		Tooth (canine)	Adult
Delaware Bay	CM Ma4108		Tooth	Adult
Delaware Bay	CM Ma4109		Partial skeleton	Pup
Delaware Bay	CM Ma4110		Partial skeleton	Pup
Delaware Bay	CM Ma4111		Vertebra	Adult
Delaware Bay	CM Ma4112		Ulna	Sub-adult
Delaware Bay	CM Ma4113		Cervical vertebra	Adult
Delaware Bay	CM Ma4114		Bulla	Juvenile
Delaware Bay	CM Ma4115		Bulla	Juvenile
Delaware Bay	CM Ma4116		Bulla	Sub-adult
Creighton's Cave	NMNZ S.45731		Vertebra	Adult
Creighton's Cave	NMNZ S.45732	333719	Humerus	Pup
Creighton's Cave	NMNZ S.45733	330892	Tibia	Sub-adult
Creighton's Cave	NMNZ S.45734		Tibia	Adult
Creighton's Cave	NMNZ S.45735		Tibia	Adult
Creighton's Cave	NMNZ S.45736	330891	Ulna	Adult
Creighton's Cave	NMNZ S.45737	333721	Pelvis	Sub-adult
Creighton's Cave	NMNZ S.45738	333720	Vertebra	Adult

Results

Morphological and genetic analyses

Thirteen and nine *P. hookeri* individuals (minimum number of individuals, MNI, based on most common element and ontogenetic stage) were collected in 2011 from Delaware Bay and Creighton's Cave, respectively (Table 1). One pup bone from each locality was sequenced for the 189 base pair control region fragment. Both sequences exhibited phylogenetic similarity with modern *P. hookeri* (genetic divergence $<4\%$) and were highly genetically distinct from all other modern pinniped taxa (genetic divergence 10.9%–23.3% (Fig. 2).

Radiocarbon dating of Delaware Bay and Creighton's Cave bones

Three *P. hookeri* pups were radiocarbon dated from Delaware Bay. All three bones were of a similar age, covering a period of less than 200 ^{14}C yr (1264–1008 yr BP to 1122–852 yr BP; Table 2, Fig. 3). Bones from four adult and one pup *P. hookeri* were dated from Creighton's Cave. Radiocarbon dating of these bones revealed more variation between dates, with ages ranging from 5970–5701 yr BP to 978–730 yr BP (Table 2, Fig. 3). Comparison of the Delaware Bay and Creighton's Cave dates with previously published proxies for human arrival in New Zealand (Higham et al. 1999; Wilmshurst & Higham 2004; Wilmshurst et al. 2008) confirms the presence of breeding *P. hookeri* in the region prior to human colonisation (Fig. 3).

Discussion

Radiocarbon dating and genetic analyses of adult and juvenile *P. hookeri* remains from the northern South Island strengthen existing evidence for the presence of breeding *P. hookeri* on

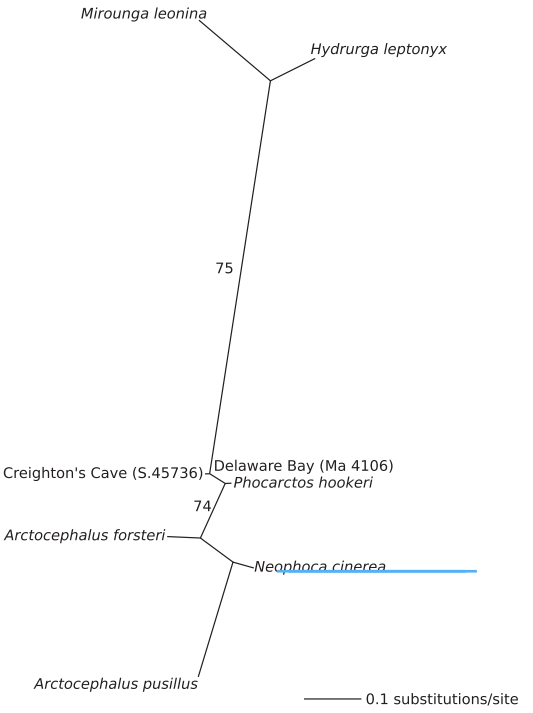

Figure 2 Maximum likelihood (ML) phylogeny supporting the combined monophyly of prehistoric specimens from Delaware Bay and Creighton's Cave, and modern *Phocarctos hookeri*. Numbers on branches indicate ML bootstrap support.

mainland New Zealand prior to the time of human arrival (Worthy 1994).

Polynesians colonised New Zealand c. AD 1280 (Higham et al. 1999; Wilmshurst & Higham 2004; Wilmshurst et al. 2008). The radiocarbon dating of the Delaware Bay *P. hookeri* bones suggests that this site represents a 'snapshot' of mainland New Zealand's coastal biota shortly prior to human settlement. Specifically, all radiocarbon dated bones from Delaware Bay yielded calibrated ages from AD 744–1080 (maximum to minimum 95.4% calibrated range; Table 2, Fig. 3). These data confirm that *P. hookeri* were breeding in the northern South Island during the Holocene and as recently as 200 years prior to human settlement. Remains of additional taxa were also recorded at Delaware Bay, including species that are now extinct or locally extirpated, such as the New Zealand coot *Fulica prisca*

Table 2 Radiocarbon dates on *Phocarctos hookeri* remains from Delaware Bay and Creighton's Cave. Dates were calibrated using the Marine09 calibration curve (Reimer et al. 2009) in OxCal v4.2 (Bronk Ramsey 2009) and a local (Ligar Bay) ΔR of -35 ± 46 (Petchey et al. 2008) was applied to all *P. hookeri* dates. Asterisks indicate pup bones.

Lab no. (Beta)	Museum accession number	Geographic location	Element dated	Conventional radiocarbon age (yr BP)	±	Bone used (g)	Cal. Age (yr BP) (95.4%)	Cal. Age (yr BC/AD, 95.4%)	$\delta^{13}C$ (o/oo)
330888	CM Ma4106*	Delaware Bay	Rib	1550	30	1.5	1264–1008	AD 744–940	−12.6
330889	CM Ma4104*	Delaware Bay	Humerus (right)	1520	30	1.5	1240–975	AD 786–974	−12.1
330890	CM Ma4105*	Delaware Bay	Humerus (right)	1390	30	1.6	1122–852	AD 914–1080	−14.1
330891	NMNZ S. 45736	Creighton's Cave	Ulna	5430	30	2.9	5970–5701	BC 3941–3770	−13.3
330892	NMNZ S.45733	Creighton's Cave	Tibia	1290	30	4.5	978–730	AD 1039–1199	−13.5
333719	NMNZ S.45732*	Creighton's Cave	Humerus	3070	30	1	3036–2748	BC 978–802	−14.0
333720	NMNZ S.45738	Creighton's Cave	Vertebra	3370	30	1	3414–3124	BC 1387–1196	−13.2
333721	NMNZ S.45737	Creighton's Cave	Pelvis	3020	30	1	2962–2718	BC 914–774	−14.5

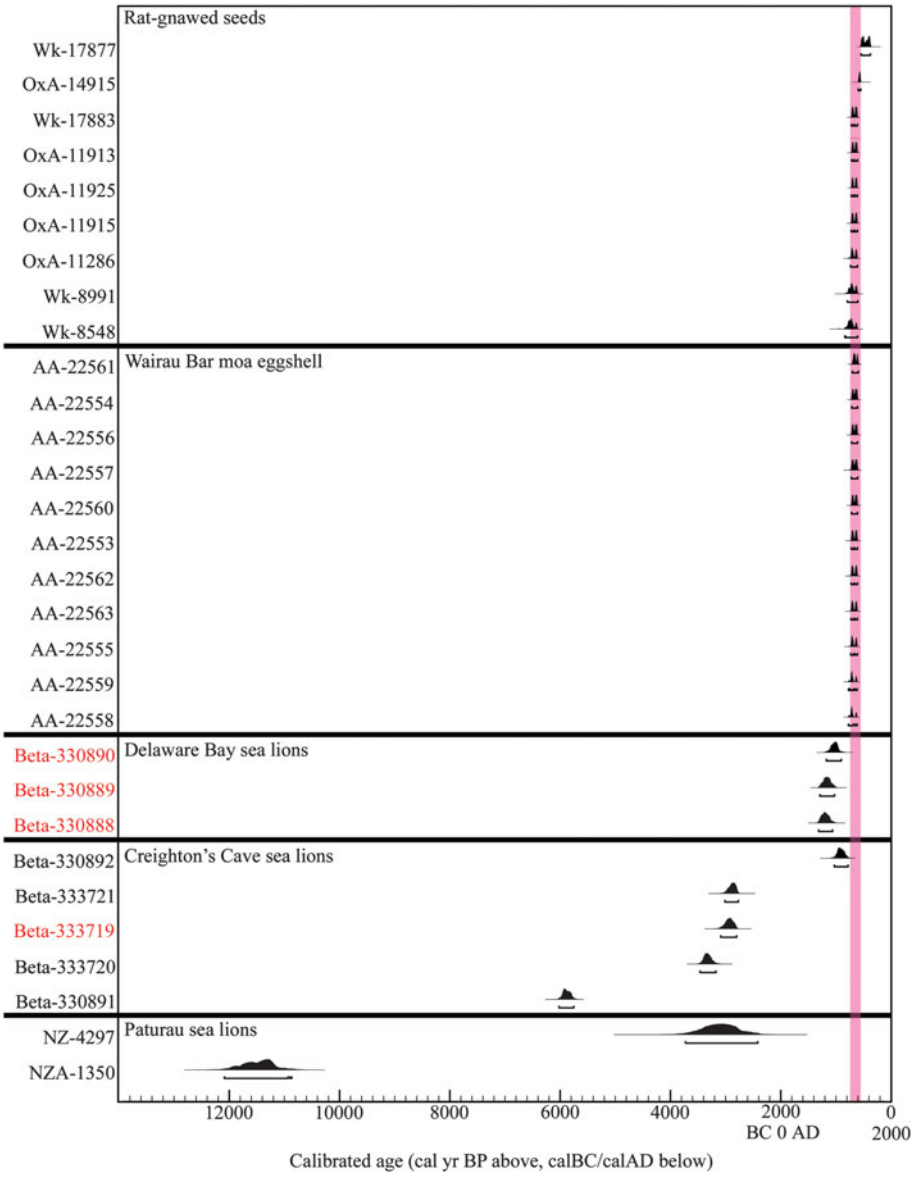

Figure 3 Probability distribution for calibrated ages of *Phocarctos hookeri* remains from Delaware Bay and Creighton's Cave, and previously published ages of *P. hookeri* from two nearby caves (Turimawiwi Cave and Wet Neck Cave, Worthy 1992). Dates were calibrated using the Marine09 calibration curve (Reimer et al. 2009) and a local (Ligar Bay) ΔR of -35 ± 46 (Petchey et al. 2008) and plotted in OxCal v4.2 (Bronk Ramsey 2009) with 95.4% confidence intervals underlined. Two proxies for human presence are also plotted: moa eggshell from burial sites at New Zealand's earliest archaeological site at Wairau Bar (Higham et al. 1999) and rat-gnawed seeds (Wilmshurst & Higham 2004; Wilmshurst et al. 2008). Dates on moa eggshell and rat-gnawed seeds were calibrated using the Southern Hemisphere calibration curve (McCormac et al. 2004). The period between Polynesian settlement (c. AD 1280) and c. AD 1450, during which New Zealand's mega-avifauna were hunted to extinction (purple bar; Tennyson & Martinson 2007; Rawlence & Cooper 2013) is also shown.

Hamilton, 1893, Fiordland crested penguin *Eudyptes pachyrhynchus* G.R. Gray, 1845, and *Megadyptes waitaha* (Appendix 2). The observation of a natural coastal site providing a temporal 'snapshot' of New Zealand biota, shortly prior to human arrival, has potential to enhance our understanding of human-mediated changes to the country's coastal fauna.

As expected for a cave that has been present and potentially able to accumulate fossils for thousands of years (Worthy 1992, 1994), and given the period over which the cave has been similarly placed relative to the coastline, *P. hookeri* bones collected from Creighton's Cave yielded a wider age range than those obtained from Delaware Bay dune strata. The oldest Creighton's Cave bone in our sample was dated to 5970–5701 yr BP (Table 2, Fig. 3), whereas the youngest (978–730 yr BP; Table 2, Fig. 3) was similar in age to the Delaware Bay material. These new radiocarbon-dates extend the previously estimated age range of *P. hookeri* in the Paturau region (from 12,053–10,894 yr BP to 3690–2380 yr BP; Worthy 1992), indicating the presence of *P. hookeri* until closer to the time of human settlement. The older of these new Creighton's Cave dates are similar in age to radiocarbon-dated sea lion material from nearby Wet Neck Cave (Worthy 1992). The wide range of dates obtained from Creighton's Cave suggest a continuous Holocene presence of breeding colonies of *P. hookeri* on mainland New Zealand. The presence of an introduced bird species (common starling *Sturnus vulgaris* Linnaeus 1758) in these caves (Appendix 3) shows that they have continued to act as sites of bone preservation until the present day.

The differences between faunal assemblages from Delaware Bay and Creighton's Cave (Appendix 2 and 3) reflect the different depositional environments at these sites. Delaware Bay accumulated coastal species, whereas Creighton's Cave accumulated mainly species that were trapped by pit fall (e.g. flightless or ground-dwelling taxa, such as moa and kiwi *Apteryx* spp.) or taxa that sometimes lived in the cave, for example, laughing owl *Sceloglaux albifacies* (G.R. Gray 1844). At Delaware Bay, 36 vertebrate taxa were recorded, of which 12 (33%) are locally extinct and three (8%) are globally extinct, compared with Creighton's Cave, where 18 vertebrate taxa were recorded, of which five (28%) are locally extinct and seven (39%) are globally extinct. The higher proportion of globally extinct taxa detected at Creighton's Cave reflects that flightless and ground-dwelling taxa have been disproportionately affected by human arrival (Worthy & Holdaway 2002).

Conclusion

The presence of a number of bones from both adult and juvenile *P. hookeri* from up to 5430 yr BP (Table 2) across a wide geographic area (Fig. 1) strongly suggests that prior to the time of human arrival, mainland New Zealand possessed a substantial breeding population of *P. hookeri*. The likely rapid human-mediated extinction mirrors those previously inferred for more than a quarter of New Zealand's terrestrial avifaunal species, including moa (Tennyson & Martinson 2007; Rawlence & Cooper 2013; Rawlence et al. 2012), giant geese *Cnemiornis* spp. and Haast's eagle *Aquila moorei* (Haast 1872) (Tennyson & Martinson 2007). We hypothesise that the local extirpation of breeding colonies of *P. hookeri* from the northern and northwest South Island likely occurred over a timeframe comparable to New Zealand's avian megafauna c. AD 1280–1450 (Tennyson & Martinson 2007).

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Appendix 1

Appendix 1A Archaeological sites with sea lion bones.

Site	Site numbers	Repository	Accession numbers	Reference
Houhora	N03/59	UA; AIM		Smith 1985, Furey 2002
Henderson Bay	N03/9, 11, 13	UA		Smith 1985
Port Jackson	S09/53	AIM		Smith 1985
Sunde Site	N38/24	UA		Scott 1970, Smith 1985, Nichol 1988
Cross Creek Midden	T10/399	AIM		Smith 1985
Parker's Midden	T10/160	AIM		Smith 1985
Manukau South Head	Q11/344	UA		Smith 1985
Tairua	T11/62	AIM		Smith 1985
South Bay, Slipper Island	U12/9	AIM		Smith 1985
Wheritoa	T12/500	AIM		Smith 1985
Cooks Cove, Tolaga Bay	Z17/311	UO		Walter et al. 2011a
Onenui	Y20/30	unknown		Jeal 1987
Opua	P20/105	PA		Smith 1985
Hingaimotu	P20/120	PA		Smith 1985
Kaupokonui	P21/3	PA		Smith 1985
Ohawe	P21/75	unknown		Buist 1962
Te Rangatapu	Q21/76	unknown		Canavan 1960
Paremata	R26/122	NMNZ		Smith 1985
Washpool Midden	S28/49	NMNZ		Smith 1985
Pararaki North	S28/68	UO		Leach 1976
Rotokura	O27/1	NM		Smith 1985, NM collection database
Wairau Bar	P28/21	UO; CM	2008.1000	Smith 1985, Spinks n.d, CM collection database
Marfells Beach	P29/2	CM	2008.1104	Worthy 1998c
Kawatiri Site	K29/8	UO		Walter et al. 2011b
Sumner	M36/24(?)	CM	1915.25.9	CM collection database
Moa Bone Point Cave	M36/25	CM	Ma 664, 665	CM collection database
Redcliffs Flat	M36/24	CM	Ma666, Ma667, Ma668, Ma669	Trotter 1975
Wakanui	L37/8	CM	2008.1005	CM collection database
Tawhiroko Midden	J42/21	not collected		Anderson et al. 1978
Shag River Mouth	J43/2	UO		Anderson et al. 2006
Pleasant River Mouth	J43/1	UO		Teal 1975, Smith 1997
Long Beach	I44/23	UO		Smith 1985
Hoopers Inlet	I44/13	unknown		Davis 1980
Papanui Beach	J44/1	UO		Smith 1985
Otokia Mouth	I44/5			Anderson 1982, Smith 1985
Saint Clair	I44/121			Jacomb et al. 2010a
Southport 5, 10	B45/15, 20	SMAG		Coutts 1972
Cannibal Bay	H46/28	unknown		Hamel 1977
Pounawea	H47/1	OM		Hamel 1980, Smith 1985

Appendix 1A (*Continued*)

Site	Site numbers	Repository	Accession numbers	Reference
Riverton	D46/35	UO		Leach & Leach 1980, Smith 1985
Papatowai	G47/50	UO		Hamel 1977, Anderson & Smith 1992
Tautuku Point	G47/64	unknown		Hamel 1977
Tiwai Point	E47/13	SMAG		Smith 1985
Hakapureirei (Sand Hill Point)	C46/31	SMAG, UO		Walter & Jacomb 2005, Jacomb et al. 2010b, Coutts 1970
Tokanui River Mouth	F47/53	SMAG, OM, UO		Jacomb et al. 2012
West Point, Ruapuke Is	E48/29	SMAG		Coutts & Jurisich 1972
Lee Island, Ruapuke Is	E48/36	SMAG		Coutts & Jurisich 1972
Parangaio, Ruapuke Is	E48/34	SMAG		Coutts & Jurisich 1972
Sealers Bay, Codfish Is	D48/5	UO		Bone 2012
Old Neck	E48/39	CM	Ma 670, 3036, 3039	Scarlett 1979, Worthy 1998b
Cook Settlement, Port Pegasus	D49/17	UO		Bone 2012

Appendix 1B Locations with non-archaeological sea lion bones.

Locality	Repository	Accession number	Reference
Tom Bowling Bay*	AIM	LM 869, 870, 868, 787, 776, 780, 789, 790, 800, 786, 791, 758, 759, 777, 782, 778, 788, 775, 774	AIM collection database, Scarlett 1979
Cape Maria van Diemen	AIM	LM 860, 861, 862, 908	AIM collection database
Te Werahi Beach	AIM	LM 753, 832	AIM collection database
Spirits Bay*	CM	Ma 113	Scarlett 1979, Worthy 1994
Waikuku Beach*	AIM	LM 864, 863, 866, 867, 865, 762, 760, 781, 761, 779, 785	AIM collection database, Smith 1985
Whareana Beach	AIM	LM 783	AIM collection database
Tokerau Beach	AIM; NMNZ	AIM LM 894, 981, 895, 979, 983, 984, 831; NMNZ MM.2151	Worthy 1994, NMNZ collection database
Doubtless Bay	AIM	LM 882, 884	AIM collection database
Matai Bay	AIM	LM 986	Worthy 1994
Karikari Beach	AIM; NMNZ	AIM LM 969, 970, 996, 997, 980, 982; NMNZ S.45537, 45543	AIM collection database, NMNZ collection database
Whangarei Heads	CM; AIM	CM Ma801; AIM LM 37	CM collection database; AIM collection database
Lady Alice Island	AIM	LM 783	AIM collection database
Kohimarama Beach	AIM	LM 679	AIM collection database
Raglan	CM	Ma 958, Ma 959	CM collections database

Appendix 1B (*Continued*)

Locality	Repository	Accession number	Reference
Whangara	AIM	LM 1486	AIM collection database
Cape Kidnappers	NMNZ	MM 532	Berry & King 1970
Ocean Beach (Hawkes Bay)	NMNZ	S.44795	NMNZ collection database
Mataikona	NMNZ	S.41837, 45460	NMNZ collection database
Uruti Point	NMNZ	S.39033, 39035	NMNZ collection database
D'Urville Island	NMNZ	S.45741	NMNZ collection database
Creighton's Cave	NMNZ	MM.2149, S.38683, 45713, 45731–45738	Worthy 1992, NMNZ collection database
Wet Neck Cave	NMNZ	MM.2146	Worthy 1992, NMNZ collection database
Baby Grand Cave	NMNZ	MM.2148	Worthy 1992, NMNZ collection database
Turimawiwi Cave	NMNZ	MM.2150	Worthy 1992, NMNZ collection database
Takaka	AIM	LM 147	Worthy 1992
Tarakohe	NMNZ	S.43851	NMNZ collection database
Delaware Bay*	NMNZ; CM	NMNZ MM.2147, S.38493, 38520, 38521, 38542, 38543, 38546, 38578–38582, 42143–42152, 42166–42175, 45500, 45510, 45513; CM Ma 4104–4116	Worthy 1994, NMNZ collection database
Oyster Island	NM?		Worthy 1994
Waima River	CM	Ma 802, 3973	CM collection database
New Haven	AIM	LM1003	AM collection database
False Islet	CM	Ma 1385	CM collection database
Port Pegasus	AIM	LM 505	AIM collection database

AIM = Auckland Museum; CM = Canterbury Museum; NM = Nelson Museum; NMNZ = Museum of New Zealand Te Papa Tongarewa; PA = Puke Ariki (Taranaki Museum); SMAG = Southland Museum and Art Gallery; UA = University of Auckland, Department of Anthropology; UO = University of Otago, Department of Anthropology & Archaeology. Locality names with asterisk are known to contain both archaeological and natural deposits.

Appendix 2

A list of Holocene vertebrate fossil remains found at Delaware Bay. Accession numbers are provided for specimens housed at the Museum of New Zealand Te Papa Tongarewa. Further unregistered specimens of several of these species are held in the Canterbury Museum.

[+]Brown teal *Anas chlorotis* (NMNZ S.38518)

[+]Fiordland crested penguin *Eudyptes pachyrhynchus* (NMNZ S.38566)

[++]Waitaha penguin *Megadyptes waitaha* (NMNZ S.38489, 38513, 38325, 38530, 38564, 42156)

Little penguin *Eudyptula minor* (NMNZ S.38475, 38482, 38490, 38515, 38526, 385331, 38563, 38565, 42137, 42157, 45498)

[+]Grey-faced petrel *Pterodroma* cf. *macroptera* (NMNZ S.38560)

[+]Mottled petrel *Pterodroma inexpectata* (NMNZ S.42158)

Fairy prion *Pachyptila turtur* (NMNZ S.38511, 38536, 38559)

Broad-billed prion *Pachyptila vittata* (NMNZ S.38512, 38537, 38561, 42138)

Sooty shearwater *Puffinus griseus* (NMNZ S.38523)

Fluttering shearwater *Puffinus gavia* (NMNZ S.38479, 38509, 38524, 38548, 38558, 42159, 45499)
Common diving petrel *Pelecanoides urinatrix* (NMNZ S.38480, 38510)
Pied shag *Phalacrocorax varius* (NMNZ S.38567, 42139, 42160)
$^{+}$New Zealand king shag *Leucocarbo carunculatus* (NMNZ S.38476, 38532)
Spotted shag *Stictocarbo punctatus* (NMNZ S.38477, 38483, 38491, 38517, 38527, 38568, 42161)
$^{\#}$Swamp harrier *Circus approximans* (NMNZ S.38538)
Weka *Gallirallus australis* (NMNZ S.38484, 38519, 38552, 38569, 42162)
$^{+}$South Island takahe *Porphyrio hochstetteri* (NMNZ S.38570)
$^{++}$New Zealand coot *Fulica prisca* (NMNZ S.42140)
Bar-tailed godwit *Limosa lapponica* (NMNZ S.38486, 38571)
Variable oystercatcher *Haematopus unicolor* (NMNZ S.38487, 38534, 42163)
$^{+}$New Zealand dotterel *Charadrius obscurus* (NMNZ S.38551)
Southern black-backed gull *Larus dominicanus* (NMNZ S.38478, 38516, 38528, 38535, 38554, 38573)
Caspian tern *Hydroprogne caspia* (NMNZ S.45497)
Black-fronted tern *Chlidonias albostriatus* (NMNZ S.38550, 38572)
White-fronted tern *Sterna striata* (NMNZ S.42141)
$^{+}$Kakapo *Strigops habroptilus* (NMNZ S.38485)
$^{+}$Kaka *Nestor meridionalis* (NMNZ S.38574)
$^{+}$Parakeet *Cyanoramphus* spp. (NMNZ S.38553, 38555)
Morepork *Ninox novaeseelandiae* (NMNZ S.38529)
$^{++}$New Zealand raven *Corvus antipodum* (NMNZ S.38488, 38492, 38575, 42164)
$^{\#}$Eurasian blackbird *Turdus merula* (NMNZ S.38539)
$^{+}$Tuatara *Sphenodon punctatus* (NMNZ S.42165)
Gecko *Hoplodactylus* sp. (NMNZ S.42142)
$^{\#}$Dog *Canis lupus* (NMNZ S.38474, 38540, 38577)
$^{+\#}$Pacific rat *Rattus exulans* (NMNZ S.38576)
$^{+}$New Zealand sea lion *Phocarctos hookeri* (NMNZ S.38493, 38520-3, 38546, 38578-38582, 42143-42152, 42166-42175, 45500, 45510, 45513; CM Ma 4104-4116)

$^{++}$globally extinct, $^{+}$locally extinct (excludes seabird species which still commonly wash up dead on local beaches) (see Robertson et al. 2007), $^{\#}$ post-human arrival

Appendix 3

A list of Holocene vertebrate fossil remains found at Creighton's Cave. These collections are housed at the Museum of New Zealand Te Papa Tongarewa.
$^{++}$Upland moa *Megalapteryx didinus* (NMNZ S.45711)
$^{++}$Little bush moa *Anomalopteryx didiformis* (NMNZ S.35128, 38682, 45715, 45716, 45727)
$^{++}$South Island Giant Moa *Dinornis robustus* (NMNZ S.45724)
$^{++}$Crested moa *Pachyornis australis* (NMNZ S.35129)
Great spotted kiwi *Apteryx haastii* (NMNZ S.35166)
$^{+}$Brown teal *Anas chlorotis* (NMNZ S.35173)
Little penguin *Eudyptula minor* (NMNZ S.34167)
$^{+}$Cook's petrel *Pterodroma cookii* (NMNZ S.35172)
Weka *Gallirallus australis* (NMNZ S.35168, 35185, 45718, 46729)
$^{++}$South Island snipe *Coenocorypha iredalei* (NMNZ S.45721)
Southern black-backed gull *Larus dominicanus* (NMNZ S.35183)
$^{+}$Kakapo *Strigops habroptilus* (NMNZ S.35169, 35184, 38681, 45719)
Kaka *Nestor meridionalis* (NMNZ S.45720)
$^{++}$Laughing owl *Sceloglaux albifacies* (NMNZ S.35171)
$^{++}$South Island stout-legged wren *Pachyplichas yaldwyni* (NMNZ S.35170)
$^{++}$South Island kokako *Callaeas cinerea* (NMNZ S.45722)
$^{\#}$Common starling *Sturnus vulgaris* (NMNZ S.45723)
$^{+}$Tuatara *Sphenodon punctatus* (NMNZ S.35174)
$^{+}$New Zealand sea lion *Phocarctos hookeri* (NMNZ S.38683, 45713, 45731-45738)
$^{\#}$Sheep cf. *Ovis* (NMNZ 45714)
$^{++}$globally extinct, $^{+}$locally extinct, $^{\#}$post-human arrival