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RESEARCH ARTICLE



# CSI – Cuttlefish Sepion Investigation: overview of cuttlebones found on Aotearoa New Zealand shores and analysis of predation and scavenging marks

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## ABSTRACT

Despite the absence of cuttlefish in Aotearoa New Zealand waters, cuttlebones and cuttlebone fragments have been reported and collected in the country since the early twentieth century. Not all could be reliably identified. As such, here we review all cuttlebone material collected from New Zealand shores available in natural history collections, as well as literature and online records. Species were identified, through morphological features and, for the first time, DNA barcoding, as: the Australian endemic *Sepia apama* Gray, 1849 (and possibly *S. grahami* A. Reid, 2001) and the widely distributed Indo-Pacific *S. latimanus* Quoy & Gaimard, 1832. In addition, the predation/scavenging marks (praedichnia) left on the cuttlebones by other organisms are assigned to four major types and attributed to albatrosses, sharks, and dolphins. The successful extraction of DNA from cuttlebones has potential future applications, including the examination of type specimens, since species were described based only on cuttlebones.

## ARTICLE HISTORY

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Ancient DNA; cephalopoda; ichnology; praedichnia; sepiidae; cuttlebones

## Introduction

Cuttlefishes are cephalopod molluscs belonging to the family Sepiidae, characterised by a unique internalised calcareous shell called a sepion or cuttlebone. Cuttlebones are derived from secondary mineralisation of a chitinous gladius and act as tissue support and as a complex buoyancy device (Birchall and Thomas 1983; Doyle et al. 1994; Bonnaud et al. 2006). They are arranged in two distinct sections: a rigid dorsal shield and a ventral chambered portion consisting of calcium carbonate (aragonite) pillars and chambers (Birchall and Thomas 1983; Checa et al. 2015; Le Pabic et al. 2017). Both sections contain some organic matter ( $\beta$ -chitin and proteins; Checa et al. 2015; Le Pabic et al. 2017).

Sepiids inhabit tropical and warm temperate waters, primarily along the continental shelf, the upper portions of the continental slope and near oceanic islands (Khromov

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1998). They can be found throughout Europe, Africa, Asia and Oceania, but in the Pacific they only occur in the western portion, including Australia and Japan (Khromov 1998; Okutani 2005). They are absent from the whole extension of the Pacific from Aotearoa New Zealand to the Americas, as well as from the Atlantic coast of the Americas (Voss 1974). Given that cuttlefish are coastal animals with benthic young, they are unable to cross the deep waters of the Tasman Sea that separate Australia from New Zealand or to cross the Atlantic (Voss 1974). There are potential Paleogene fossils from North America that may belong either in Sepiidae or in the related (and extinct) Belosepiidae (Doyle 1993; Khromov 1998; Yancey et al. 2010).

Even though no living Sepiidae has ever been found in New Zealand waters, cuttlebones are often found on beaches, especially on the North Island (Powell 1979), which have drifted from elsewhere. After the animal dies, it floats to the surface where the flesh may be eaten by birds and other animals (Battam et al. 2010). After the flesh is gone, the cuttlebones, due to their natural buoyancy, can be carried great distances by currents (Reid 2016b), sometimes washing ashore far from their point of origin (e.g. across the Atlantic; Voss 1974). Drifting cuttlebones may be used as substrate for encrusting organisms, such as barnacles, and may bear marks of damage left by predators/scavengers (Cadée 1997a, 1997b, 2002; Jongbloed et al. 2016).

In New Zealand, cuttlebones or their fragments, have been reported since the early twentieth century from several regions of the country, and have usually been tentatively identified as the Australian giant cuttlefish *Sepia apama* Gray 1849 and/or the mourning cuttlefish *Sepia plangon* Gray 1849 (e.g. Suter 1913; Powell 1940, 1979; Dell 1952). The most recent checklist of New Zealand molluscs (Spencer et al. 2009) abstained from offering a species identification, presenting the entry simply as *Sepia* sp. A previous checklist (Spencer and Willan 1995) correctly excluded cuttlefish, given that they do not naturally inhabit the country's Exclusive Economic Zone. Cuttlebones are simply a part of general beach washed flotsam, so their inclusion in faunal lists is misleading.

Given the previous uncertainty regarding their identity, in the present work we review all cuttlebone material collected from New Zealand shores available in natural history collections, as well as further literature and online records. We present a taxonomic discussion based on morphological features and, for the first time, DNA barcoding, a tool that can be used to identify cuttlebone fragments that are lacking the morphological features needed for species identification. We discuss their possible origin, and figure all available specimens. Furthermore, we conduct an ichnologic study to extract further ecological data from the specimens, analysing in detail the predation/scavenging marks left on the cuttlebones by other organisms. The methods developed here may prove invaluable to examine historic type specimens, given that many species were originally described from beach washed cuttlebones alone, without the animals' soft parts.

## Material and methods

### Specimens

We analysed museum specimens of cuttlebones from the following collections in New Zealand: Auckland War Memorial Museum (AWMM, Auckland); Canterbury Museum (CM, Christchurch); GNS Science (GNS, Lower Hutt); Museum of New

Zealand Te Papa Tongarewa (NMNZ, Wellington); Otago Museum (OM, Dunedin); Southland Museum and Art Gallery (SMAG, Invercargill). Further records were extracted from the online database iNaturalist (<https://www.inaturalist.org>), a citizen science natural history platform. See Supplementary Material 1 for the full list of studied specimens and Supplementary Material 2 for photographs of all specimens in collections.

We constructed a distribution map of places in New Zealand where cuttlebones (or their fragments) have washed ashore based on the locality data of the studied specimens, as well as the information retrieved from the literature and iNaturalist. See Supplementary Material 1 for more details.

## Identification

Species identification was achieved by morphological analysis of cuttlebone specimens based on specialised literature (Lu 1998a; Okutani 2005; Reid et al. 2005; Reid 2016a), comparison with specimens from the collection of the Australian Museum (AM, Sydney, Australia; see Supplementary Material 2 for examples), and DNA barcoding.

Given that cuttlebones contain organic matter and that DNA has been successfully extracted from historical and archaeological marine gastropod and bivalve material (Der Sarkissian et al. 2017), as well as from the internal shell of the cephalopod *Spirula spirula* (Linnaeus, 1758) (Strugnell et al. 2006), we attempted to extract DNA from the dorsal shield of selected cuttlebone specimens in the ancient DNA laboratory of the NMNZ (n = 23, plus one trial sample extracted from the carbonate; from the collections of AWMM, GNS and NMNZ). The protocol can be seen in Supplementary Material 1.

We targeted the barcoding fragment (ca. 650 bp) of the mitochondrial COI gene, using primers LCO and HCO (Folmer et al. 1994) alongside the internal primers Ill\_B\_F and Ill\_C\_R (Shokralla et al. 2015). PCR products (see Supplementary Material 1 for PCR protocol) were Sanger sequenced at Massey Genome Service (Massey University, Palmerston North, New Zealand). Sequences were assembled in Geneious Prime (v. 2020.2.2, Biomatters Ltd.), quality-proofed, and uploaded to NCBI GenBank (see Supplementary Material 1 for registration numbers).

Ethanol-preserved tissue samples from whole-animal specimens of *S. apama* and *S. latimanus* Quoy & Gaimard, 1832 were obtained from the AM collection for comparison (Supplementary Material 1). These two species were targeted following preliminary examination of the New Zealand cuttlebone samples. For these, only the primers LCO and HCO were used.

Further sequences were obtained from GenBank (see Supplementary Material 1) for a phylogenetic analysis, belonging to the following species of interest: *S. apama*, *S. latimanus*, *S. officinalis* Linnaeus, 1758, and *S. pharaonis* Ehrenberg, 1831. Sequences belonging to other South Pacific species of interest (*S. grahami* A. Reid, 2001, *S. plangon*, and *S. smithi* Hoyle 1885) were not available. A sequence from *Octopus vulgaris* Cuvier, 1797 was used as outgroup. Sequences were aligned, contained no insertion/deletion events (indels), and submitted to three phylogenetic analyses: maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI). See Supplementary Material 1 for details.

## ***Praedichnia***

We investigated the damage marks present on the cuttlebones using the methodology of the field known as ichnology, the study of trace fossils (Seilacher 1953; Bromley 1996; Hasiotis et al. 2006). This field takes into account what is known of the biology of the studied animals and is also informed by taphonomy (or, more specifically, its subfield biostratinomy), which studies the events that take place from the death of the animal to fossilisation (Martin 1999). We used the damage marks on the cuttlebones discovered on New Zealand shores to hypothesise their causes.

The damage marks consisted of holes, furrows and scratches, of different sizes and shapes, that were caused by other animals, either predators or scavengers. We use the term ‘praedichnia’ (Ruggiero 1991) to refer to the predation/scavenging marks herein. Praedichnia were measured with a digital calliper (accuracy  $\pm 0.02$  mm), described and allocated to different categories, which we delineate further below.

We compared each type of praedichnia present on the cuttlebones with skulls of species of sharks, teleost fishes, birds and mammals that inhabit the Australian coast and the Tasman Sea available in the NMNZ vertebrate collection. We took into account bill shape, size and position of teeth, and the gape and biting force of each animal. We also used the skulls to create artificial praedichnia for comparison using the synthetic mouldable rubber compound Blu Tack (Bostik) as substrate.

## ***Associated biota***

Some cuttlebone specimens recently collected on beaches in the Wellington region possessed an associated biota of encrusting organisms (barnacles and hydroids). These have been preserved in ethanol 80% and housed in the NMNZ collection (see Supplementary Material 1). The specimens were identified using specialised literature and consultation with experts (see Acknowledgements).

## **Results**

### ***Identification***

In total, we analysed 45 cuttlebone specimens gathered from seven collections in New Zealand. To that, another 12 records from iNaturalist and three from the literature were added (see Supplementary Material 1).

Despite intraspecific and ontological variation in cuttlebones, these structures can be used to assist with species identification (Lu 1998b; Neige 2016). However, definitive species identifications often require examination of both the animals’ soft and hard parts, and while reliance on the cuttlebone alone has been used historically as an identification tool, whole-animal morphology can sometimes reveal a more complex story (e.g. Reid 2000). It is also recognised that some cryptic species have seemingly identical cuttlebones (e.g. the *S. pharaonis* species-complex; Anderson et al. 2011).

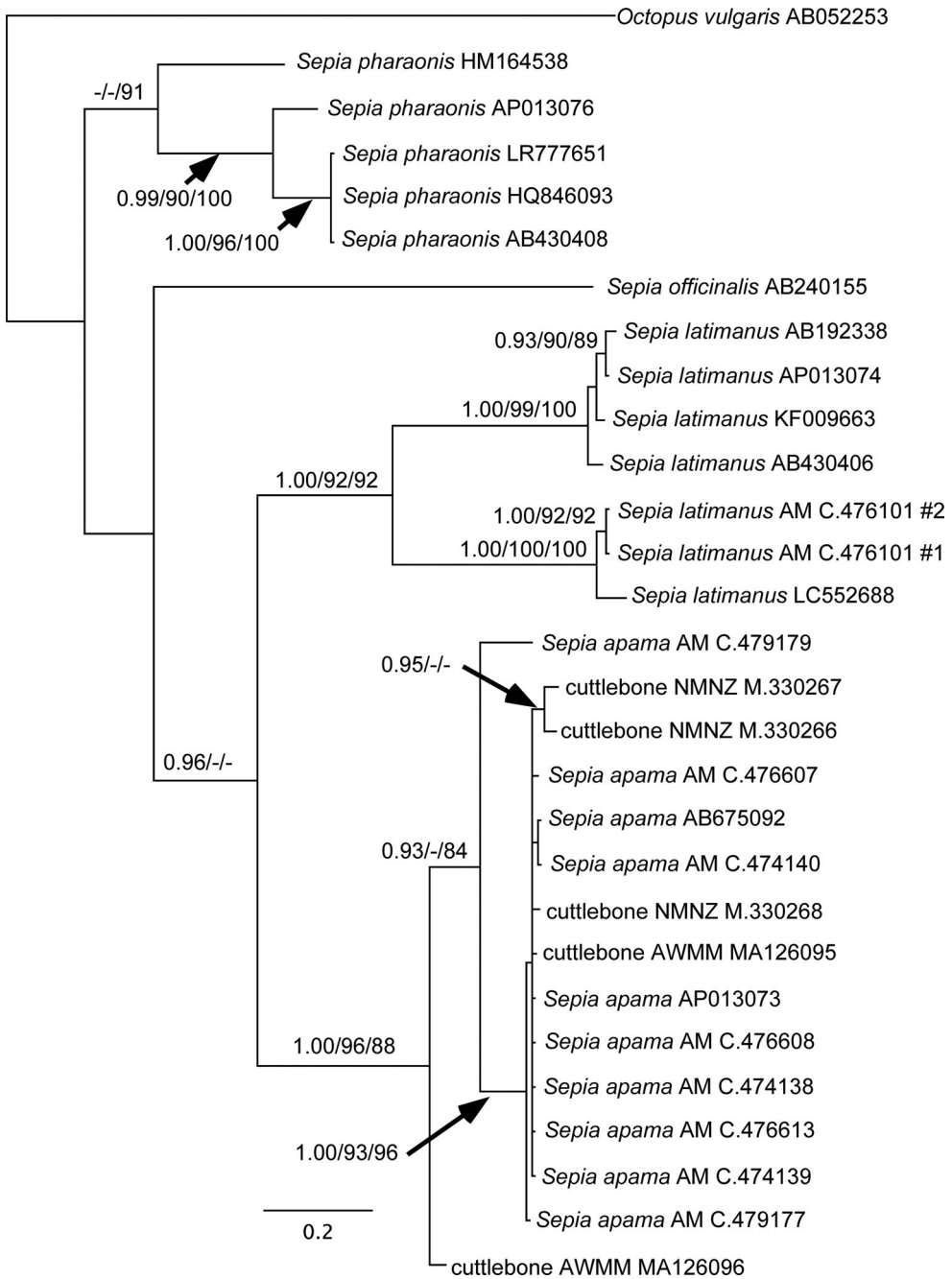
The preservation of most specimens studied here was too poor to allow definitive identification, with most of the diagnostic characters, in particular the posterior-ventral inner and outer cone, broken off (Supplementary Material 2). As such, the species names assigned here are in most cases tentative (Supplementary Material 1).

However, a few specimens in which the entire cuttlebone was intact, or the diagnostic inner and outer cone regions of the cuttlebone were present, could be identified following comparison with cuttlebones obtained from whole, intact animals. Most were identified as *Sepia apama* Gray 1849. One specimen could be identified as Ken's Cuttlefish *Sepia grahami* A. Reid, 2001; it lacks collection details, but is presumed to be from New Zealand. A single specimen showed some similarities to the broadclub cuttlefish *Sepia latimanus* Quoy & Gaimard, 1832, although we were unable to confirm this.

*Sepia apama* cuttlebones differ from those of all relatively large species in lacking a pointed spine on the distal posterior tip of the cuttlebone in adults, although it is seen as a short spike in sub-mature and juvenile animals less than ca. 20 cm in length (e.g. specimen SMAG 8366; Supplementary Material 2). This ontogenetic change has been documented with illustrations in Lu (1998b), which also shows the cuttlebone having a broad oval shape in juveniles to a more elongate oval in adults. The cuttlebone outer cone in *S. apama* is very broad and extends posteriorly well beyond the V-shaped inner cone (clearly seen in specimen AWMM MA126096; Supplementary Material 2). In addition, in cuttlebones exceeding ca. 10 cm in total length there is a rough callus on the anterior margin of the inner cone (in the middle of the V-shaped inner cone). The dorsal side of the cuttlebone has an indistinct median ridge that is bordered laterally by shallow grooves; these grooves are narrow and indistinct posteriorly and broaden anteriorly (see *S. apama* comparative material from Australia in Supplementary Material 1 and the abraded partial cuttlebone in Figure 4A). *Sepia grahami* differs in having a prominent posterior spine and, in contrast to the V-shaped inner cone seen in *S. apama*, the inner cone broadens posteriorly and has a U-shaped outline. The outer cone of *S. grahami* does not extend posteriorly beyond the inner cone as in mature *S. apama*, and the adult body and cuttlebone length in *S. grahami* does not exceed ca. 8 cm in length. A cuttlebone spine is also present in *Sepia latimanus*, and the outer cone does not extend far beyond the inner cone. The inner cone comprises a narrow V-shaped ridge that is approximately uniform in width along its length. The dorsal side of the cuttlebone does not bear indistinct ridges as in *S. apama* but is roughly granulose.

We managed to extract DNA from only five of the 23 dorsal shield samples, with other specimens either failing to amplify or producing sequences from a non-target organism such as algae or bacteria. The trial with the carbonate fraction of the sepiion failed. The full-length COI sequence was not able to be amplified from any of the five cuttlebones with the HCOI and LCOI primers, indicating that the DNA from these specimens was degraded. Amplifications of the shorter DNA fragments using the internal primers were more successful, and the resulting partial sequences were sufficient for species identification. To our knowledge, this was the first time DNA has been extracted and sequenced from cuttlebones.

Of the 658 characters in the COI alignment 178 were parsimony informative. Maximum parsimony analysis recovered 116 most parsimonious trees of length 469. The three tree-building analyses produced similar topologies with only small differences in the weakly-supported parts of the trees. All of the sequenced cuttlebone specimens grouped with *S. apama* with strong support (Figure 1), thus validating our morphology-based identifications. The two basal branches in the *S. apama* clade (Figure 1), however, could represent a distinct



**Figure 1.** Phylogram from the Bayesian phylogenetic analysis of the COI sequences showing the placement of the cuttlebone specimens. Other ethanol-preserved tissue samples sequenced here can be identified by their Australian Museum register number that starts with 'AM C.' Further sequences were extracted from GenBank (see also Supplementary Material 1). Support values for branches are shown in the following order: Bayesian inference posterior probability (PP)/ maximum likelihood bootstrap support (BS)/ maximum parsimony BS. Only values >0.90 PP and >70% BS are shown. Scale bar represents substitutions per site.



population or even a still unidentified related species. Notably, the reference specimen AM C.479179 was caught outside the known range of *S. apama* (Supplementary Material 1) and its morphological identification was not conclusive.

Our findings corroborate most previous statements that cuttlebone of *Sepia apama* is the most common species cast ashore on New Zealand beaches. Furthermore, we have found evidence of the potential presence of *S. grahami* and *S. latimanus* cuttlebones, which had not been previously detected in New Zealand. We could not find evidence of *S. plangon*, which has been suggested in the literature to be present. Likewise, photographic records of *S. smithi* and *S. pharaonis* are problematic and could not be corroborated (see details in Supplementary Material 1).

## Mapping

Cuttlebones have been found along virtually the entire coast of New Zealand (Figure 2). The majority of available specimens come from the southern North Island, but this is a collection artefact due to one of us (AJDT) finding and collecting an unusual number of specimens in 2020 after a period of onshore winds that cast ashore these and many other pelagic invertebrates (e.g. *Physalia physalis* (Linnaeus, 1758), *Velella velella* (Linnaeus, 1758), and *Janthina* spp).

The *Sepia* cuttlebones found in New Zealand do not indicate that they originated from animals living in local waters. In spite of decades of benthic marine specimen collection and diver observations, no intact animals have ever been collected or observed. *Sepia apama* lives in coastal waters from south-eastern to south-western Australia and the northern coast of Tasmania (Reid 2016a). *Sepia grahami* is largely restricted to the coast of New South Wales, in eastern Australia (Reid 2016a). *Sepia latimanus* is found throughout the Indo-Pacific, from as far west as Mozambique through to southern Japan, north-eastern Australia, New Caledonia and Fiji (Reid 2016a).

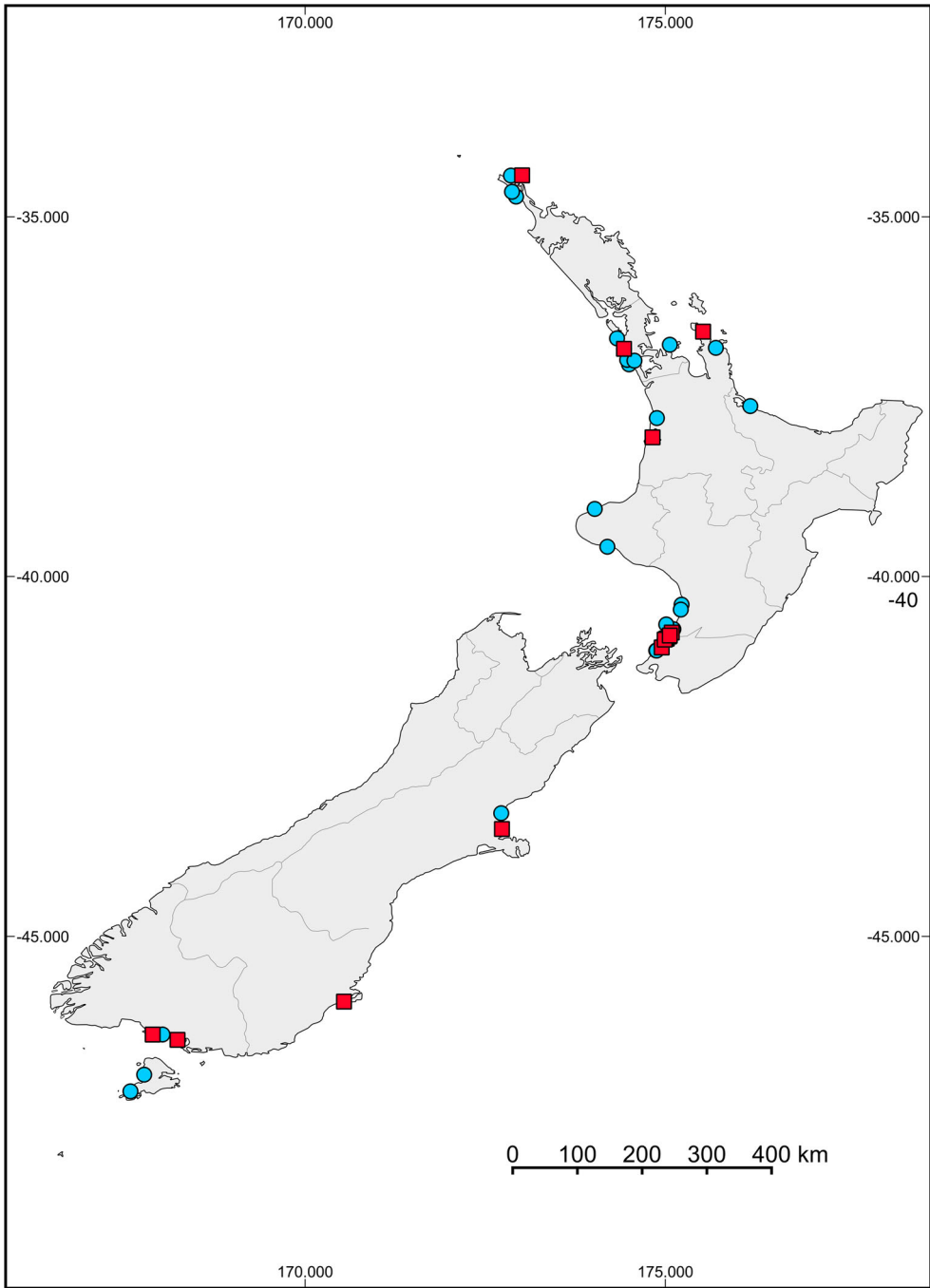
## Praedichnia

Predation/scavenging marks were found in almost all of the studied specimens. Praedichnia are more typically seen on the soft calcareous ventral side of the sepiion, with only a few well-preserved specimens also having marks on the dorsal shield (e.g. specimens NMNZ M.330089 and M.330090). This is in line with what is observed from fresh cuttlebones beached in Australia, where most marks are on the soft ventral side rather than the robust dorsal shield (AR, pers. obs.)

After analysing all the specimens side by side, we could allocate all praedichnia into four well-circumscribed categories (Table 1): (1) triangular holes; (2) thin linear furrows; (3) row of elongated holes; (4) row of circular holes.

**Type 1:** The triangular holes (Figure 3B, C) have rounded vertices, with the two basal vertices being rather elongated in a manner that the hole resembles a stylised letter A. The shape is better defined when present on the dorsal shield; marks on the ventral carbonate surface often have the edges eroded, to an extreme where they look like a simple circular-conical hole. As such, we restricted our measurements to the dorsal surface: the marks are ca. 3.9–4.2 mm in width, although a single large example (NMNZ M.330089) measures 5.2 mm across.





**Figure 2.** Map showing where specimens of *Sepia apama* (squares) and undetermined *Sepia* sp. (circles) have been found in New Zealand, according to museum vouchers, literature records, and iNaturalist observations.

**Table 1.** Summary of praedichnia types found on New Zealand cuttlebones.

Praedichnia	Description	Figures	Causative organisms	Examples
Type 1	Triangular hole with rounded vertices	Fig. 3B, C	Procellariform birds	<i>Thalassarche cauta</i> , <i>Macronectes</i> spp.
Type 2	Pair of thin converging linear furrows	Fig. 3A	Procellariform birds	<i>Thalassarche cauta</i> , <i>Macronectes</i> spp.
Type 3	Row of narrow elongated deep marks, either straight or arched	Fig. 4A, 4B	Sharks	<i>Prionace glauca</i> , <i>Carcharhinus brachyurus</i> , <i>Galeorhinus galeus</i>
Type 4	Straight row of roughly equally-spaced circular punctures	Fig. 4C	Dolphins	<i>Delphinus delphis</i>

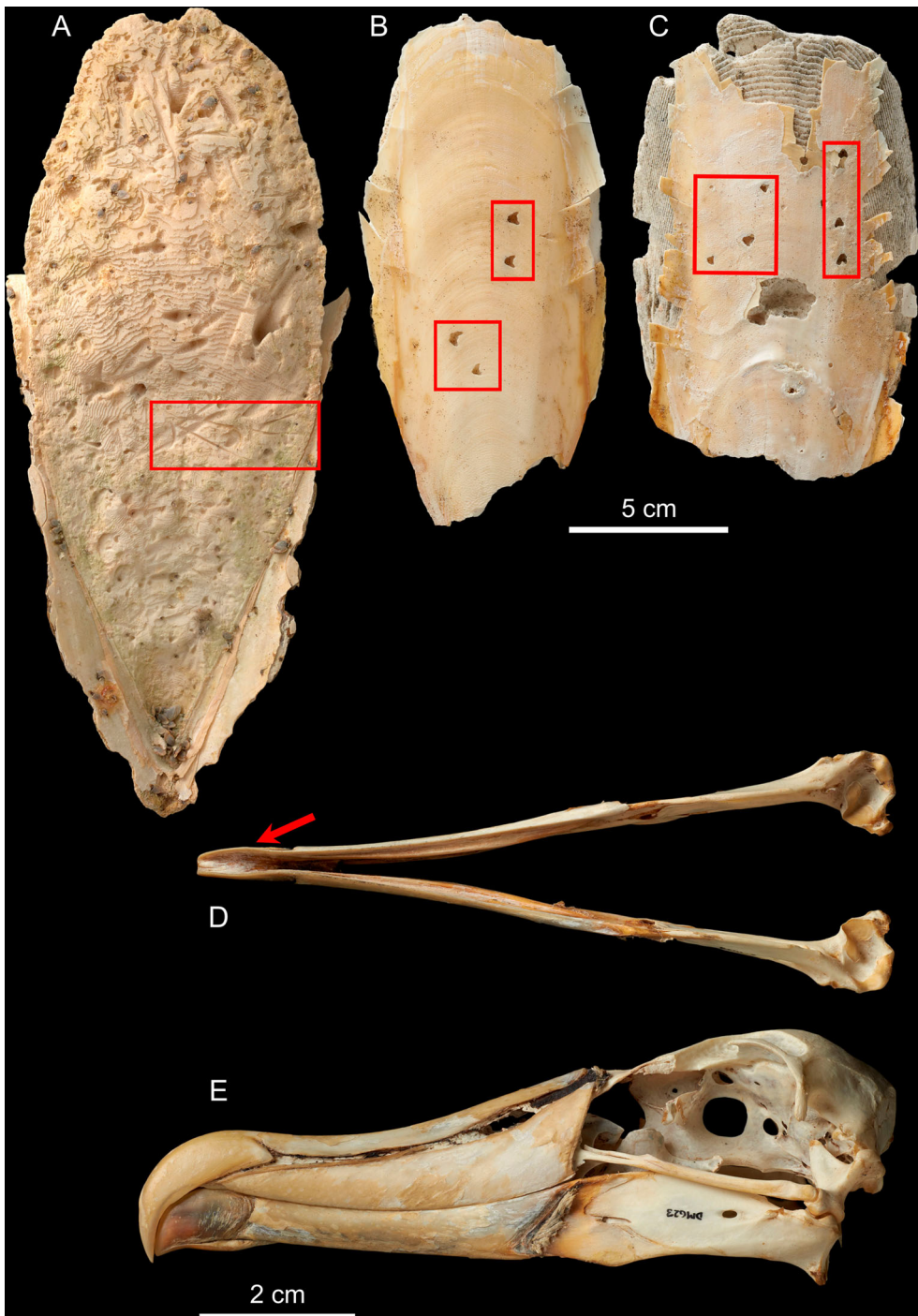
We compared these triangular holes with the upper mandible tip of the bill (with the rhamphotheca preserved) of sea birds, and with the artificial bite marks we produced. The bill of the white-capped albatross *Thalassarche cauta* (Gould, 1841) (Procellariiformes: Diomedidae; [Figure 3E](#)) leaves an impression that is virtually a perfect match to these praedichnia and thus, this or a closely related species is the most likely ‘culprit’. The giant petrels *Macronectes* spp. leave a broader mark, so it is possible that they could be responsible for some of the praedichnia observed (like the 5.2 mm one mentioned above).

On the ventral surface of some cuttlebone specimens (e.g. NMNZ M.330087; see Supplementary Material), there are triangular praedichnia that present a long and deep furrow of the same width as the initial triangular hole. This probably results from when a bird bites down and tears backwards, taking a portion of the soft calcium carbonate with it.

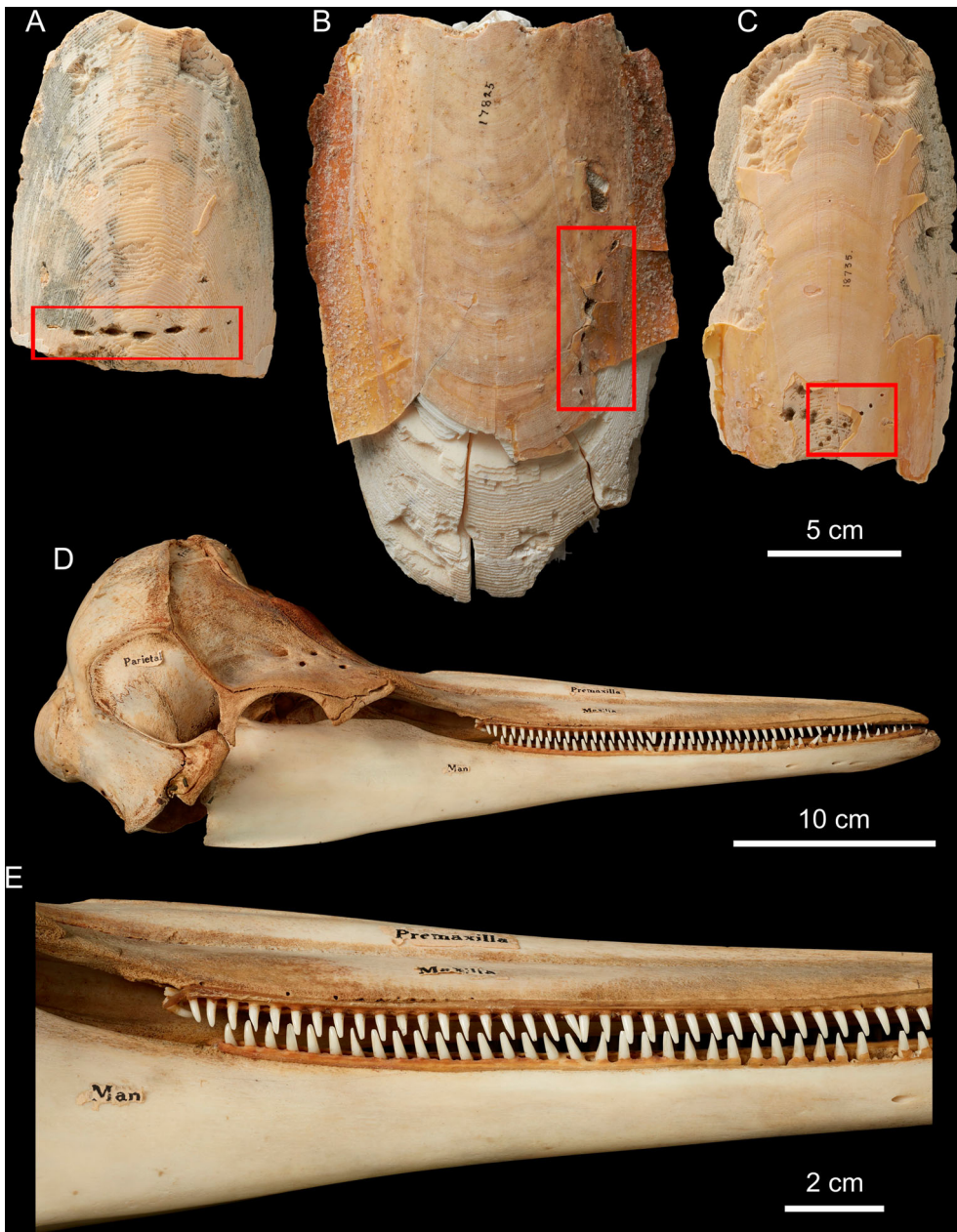
**Type 2:** The thin linear furrows ([Figure 3A](#)) are shallow straight lines, typically positioned in pairs where one line is the mirror image of the other, looking like they are converging towards one another. Such marks can only be seen in the soft carbonate ventral surface of the sepion. In the best-preserved examples, the pair of linear furrows were clearly positioned on the ventral surface of the sepion right below the triangular-hole praedichnia (type 1 above). Unsurprisingly, the very sharp edges of the central to distal portion of the mandible ([Figure 3D](#)) of the procellariiforms tested above perfectly match the shape of the furrows.

A single specimen (NMNZ M.016880) has a longer set of linear furrows immediately following the ‘regular’ set after a narrow unmarked section of cuttlebone separating them. These longer furrows are shallower and are still a perfect match to the bill of a large procellariform. Based on our tests, the unmarked interval is where a concave portion of the bill does not come into contact with the cuttlebone. In this example, the bird might have bitten the cuttlefish particularly hard.

**Type 3:** Four specimens (AWMM MA126095, NMNZ M.010926, NMNZ M.330096, SMAG 8358) present rows of narrow elongated deep marks on the dorsal portion of the sepion. The row on specimen NMNZ M.010926 is straight ([Figure 4A](#)) and those on specimens NMNZ M.330096 and SMAG 8358 are only slightly curved (see Supplementary Material); in both cases, the largest marks (in the centre of the row) are ca. 9 mm long. Specimen AWMM MA126095 shows an arched row of marks, with the largest punctures being only ca. 6.5 mm long ([Figure 4B](#)). The latter specimen also bears a matching set of marks on the ventral surface of the sepion, although heavily eroded.



**Figure 3.** **A**, Cuttlebone (NMNZ M.032420) in dorsal view, showing type 2 praedichnia (linear narrow furrows). **B**, Cuttlebone (NMNZ M.330089) in dorsal view, showing type 1 praedichnia (triangular hole). **C**, Cuttlebone (NMNZ M.330090) in ventral view, showing type 1 praedichnia (triangular hole). **D**, Dorsal view of lower mandible of *Thalassarche cauta* (NMNZ OR.000623), showing cutting edges of bill. **E**, Same specimen of *T. cauta*, complete skull in lateral view.



**Figure 4.** **A**, Cuttlebone (NMNZ M.010926) in dorsal view, showing type 3 praedichnia (row of elongated holes). **B**, Cuttlebone (AWMM MA126095) in dorsal view, showing type 3 praedichnia (row of elongated holes). **C**, Cuttlebone (NMNZ M.018735) in dorsal view, showing type 4 praedichnia (row of circular punctures). **D**, Skull of *Delphinus delphis* (NMNZ MM.000547) in lateral view. **E**, Same specimen of *D. delphis*, close-up of teeth.

These narrow arrow-like punctures were probably caused by sharks. We tested this using a variety of shark jaws present in the NMNZ collection and found that most larger species (from ca. 2 m long and larger) would be able to leave such marks.



Furthermore, the position at which the sharks bit the cuttlefish (e.g. using frontal or lateral teeth) could influence the shape of the praedichnia (i.e. straight versus a curved line). As such, it is difficult to suggest particular species as the cause. Nevertheless, the teeth of blue sharks *Prionace glauca* (Linnaeus, 1758) and copper sharks *Carcharhinus brachyurus* (Günther, 1870) (known as bronze whalers in New Zealand) (Carcharhini-formes: Carcharhinidae) produce a close match for the marks on specimen NMNZ M.010926. The teeth of school sharks *Galeorhinus galeus* (Linnaeus, 1758) (Carcharhini-formes: Triakidae) are a closer match to the marks on specimen AWMM MA126095, due to school shark teeth being more closely spaced than in other potential species.

**Type 4:** Two specimens (NMNZ M.018735 and SMAG 8358) present a straight row of eight to nine small and approximately equally-spaced circular punctures on the dorsal portion of the sepion (Figure 4C). The larger punctures, close to the sepion's edge, measure ca. 1.7 mm in width, while the more distal ones are ca. 1.4–1.5 mm wide. Related marks were not observed on the eroded ventral surface of the sepion of specimen NMNZ M.018735, but specimen SMAG 8358 bears a matching set of marks, albeit very faint and eroded.

The punctures are too close together to be left by sharks and seem too deep and strongly incised to be caused by teleost fishes. Even large predatory fishes such as barracoutas (or snoeks) *Thyrstites atun* (Euphrasén, 1791) (Scombriformes: Gempylidae), have gapes that are too small and teeth that are too fragile to create this type of praedichnia. Fish praedichnia can only be seen on freshly collected cuttlebones of species with much smaller bodies (Bello and Paparella 2003).

The marks on the two New Zealand cuttlebones are a perfect match to the teeth of some dolphin species, which also have a larger, and thus more adequate, gape. The tooth arrangement of the short-beaked common dolphin *Delphinus delphis* Linnaeus, 1758 (Cetacea: Delphinidae) is a good match for these praedichnia (Figure 4D, E).

### **Associated biota**

Freshly collected specimens of cuttlebone had encrusting biota composed of goose barnacles (*Lepas anatifera* Linnaeus, 1758) and hydroids (*Obelia dichotoma* (Linnaeus, 1758)). See Supplementary Material 1 for details on their identification.

### **Discussion**

The cuttlefish species identified here (*Sepia apama*, *S. grahami*, and *S. latimanus*) are all of Australian or Indo-Pacific origin. These animals are not native to New Zealand, and the cuttlebones were evidently transported by sea. Given the known distribution of the species, presumably they floated from the Australian coast across the Tasman Sea.

### **Praedichnia**

There is little information in the literature about the praedichnia found on cuttlebones. Cadée (1997a, 1997b, 2002) studied two events of mass stranding of cuttlebones of the European common cuttlefish *Sepia officinalis* and one of the pink cuttlefish *S. orbignyana* Férussac, 1826 in Texel, The Netherlands. He reported that ca. 85% of

adults and 50% juveniles of *S. officinalis* had marks and that adults had a larger amount of marks, mostly on the soft ventral surface of the sepion (Cadée 1997a). Cadée (1997a, 2002) reported marks that match our praedichnia types 1 and 2.

Similarly, Jongbloed et al. (2016) reported a mass stranding of *S. officinalis* at Katwijk, The Netherlands. They described triangular pits (our type 1) on both sides of the cuttlebones (though more abundant on the ventral surface), as well as scratch marks (our type 2) and a single crescent-shaped pattern with impressions of teeth (our type 3).

Analogues of the fish praedichnia reported by Bello and Paparella (2003) from specimens of *S. orbignyana* were not found in the New Zealand material. That may be due to the fact that such delicate marks would be quickly obliterated by erosion of the cuttlebone surface. Furthermore, circular holes left by boring clionoid sponges described by Jongbloed et al. (2016) were not observed in the New Zealand specimens.

**Types 1 and 2:** Praedichnia type 1 is similar to the triangular holes that Cadée (1997a, 2002) assigned to northern fulmars, *Fulmarus glacialis* (Linnaeus, 1761). Although smaller birds, fulmars have similar scavenging habitats to albatrosses (Brooke 2004), backing both our conclusions about the source of the marks on the cuttlebones. Cadée concluded that the holes were made while the cuttlefish were still drifting in the open sea due to the mussels *Mytilus edulis* Linnaeus, 1758, found lodging in them. Cadée (2002) related the scratch marks (our type 2) to the margins of bird bills, although he did not make the connection that types 1 and 2 were marks left in tandem by the same individual bird. In fact, Cadée (2002) suggested that the scratch marks might have been left by gulls carrying the dead cuttlefish in their bills; that suggestion was made considering *S. orbignyana*, which is ca. 10 cm long and thus, not applicable to our specimens (mostly *S. apama*), which would generally be too large for gulls to carry.

Jongbloed et al. (2016) remarked that both the triangular holes and the scratch marks were caused by birds. They suggested that the triangular holes (our type 1) were made by gulls and plovers attacking floating cuttlebones (devoid of flesh) or already-beached cuttlebones to obtain calcium. That hypothesis is, however, not supported by observations or current understanding of the diets of such birds. Seabirds do not eat the cuttlebone per se (Battam et al. 2010), though they might end up ingesting bits scraped by their bills when tearing off the cuttlefish's flesh.

Similarly to Cadée (2002), Jongbloed et al. (2016) suggested the scratch marks (our type 2) were left by birds that picked up the cuttlebones in their bills, but assigned them to curlews, oystercatchers, and waders. Again, that is not supported by current understanding of shorebird biology. With the exception of a few species such as gulls and oystercatchers, the bills of most shorebirds are too fragile and not suitable to create punctures or even the deep scratch marks in the hard carbonate of cuttlebones, especially the punctures through the sepion. In any event, their bills are too small and narrow (with more parallel margins) to leave the twin V-shaped scratch marks observed on the New Zealand cuttlebones.

Due to the nature of praedichnia types 1 and 2, and the bird species that we have concluded made the marks, we believe that the cuttlefish were dead and buoyant on the sea surface and were scavenged (rather than predated) by birds. The presence of several triangular marks on both dorsal and ventral surfaces of the sepion means that the birds often — and possibly unintentionally — flipped the cuttlefish over while feeding (dead cuttlefishes tend to maintain a stable floating position with the mantle up and head down; Battam et al. 2010).

Battam et al. (2010) reported that albatrosses on the Australian coast (New South Wales) make use of the seasonal mass death of *Sepia apama* as a food source. While those authors did not identify the albatross species involved, *Thalassarche cauta* and black-browed albatrosses *T. melanophris* (Temminck, 1828) are certainly among the species that scavenge dead cuttlefish in southeast Australian waters (e.g. in Bass Strait, AJDT, pers. obs. 9 September 1995). While giant petrels and many species of albatross regularly feed in the Tasman Sea, the most abundant of these taxa in coastal southeastern Australian waters, and the only albatross to nest in that region, is *T. cauta* (Reid et al. 2002). It is, however, very likely that giant petrels and several other albatross taxa that are common in this region (Reid et al. 2002) regularly scavenge cuttlefish in coastal southeastern Australian waters.

**Type 3:** Even though several shark species would be able to leave such marks, we concluded that three species common in Australasian waters (Gomon et al. 2008; Last and Stevens 2009) had teeth that were a close match for the marks on the New Zealand cuttlebone specimens: *Galeorhinus galeus*, *Carcharhinus brachyurus* and *Prionace glauca* (all are known to feed on cephalopods; Gomon et al. 2008; Last and Stevens 2009). The type 3 praedichnia could be caused either during a predation attempt (successful or otherwise) or by scavenging of dead cuttlefish floating on the surface.

The crescent-shaped praedichnia with impressions of teeth described by Jongbloed et al. (2016) compares well to our type 3, although the mark they observed was more deeply impressed. They attributed it to a small shark such as the nursehound *Scyliorhinus stellaris* (Linnaeus, 1758) or the small-spotted catshark *Scyliorhinus canicula* (Linnaeus, 1758) (Carcharhiniformes: Scyliorhinidae).

**Type 4:** This praedichnia is a particularly good match for the teeth of *Delphinus delphis*. This dolphin species is common in Australasian waters where it usually feeds on live squid and fish (Evans 1994; Guerra 2006), suggesting that the bite marks on the cuttlebone found in New Zealand were made when the cuttlefish were alive.

### **Taphonomy**

Cuttlebones are naturally buoyant, so the New Zealand specimens studied here (all native to coastal Australia) have presumably been transported across the Tasman Sea. That is not surprising, given that cuttlebones are known to be transported through large stretches of open ocean, such as across the Atlantic (Voss 1974).

Reid (2016b) reported the distances which cuttlebones can be transported (along the Australian coast) away from their source population: a maximum of ca. 380 km for *S. apama*, 770 km for *S. grahami*, and 1,500 km for *S. latimanus*. Given the live distribution of those species (Reid 2016a), the specimens found in New Zealand were probably transported from between 2,000 and 4,000 km. While approximately twenty species of cuttlefish occur in eastern Australian waters, the predominance of *S. apama* cuttlebones in New Zealand is likely due to it being the largest and most robust species. Thus, *S. apama* cuttlebones are more likely than other species to be carried across the Tasman.

The cuttlebones are likely to have reached New Zealand first via the East Australian Current (the western boundary of the South Pacific Gyre), which travels from north to south along the eastern Australian coastline and then veers eastward where it breaks into a series of eddies (Ridgeway and Hill 2009). Considering what is known about the



circulation of surface waters around New Zealand (Heath 1985; de Lange et al. 2003; Chiswell et al. 2015; Stevens et al. 2019), the cuttlebones were then in all likelihood transported along the Tasman Front to northern and central New Zealand. However, that does not explain cuttlebones found along the southern half of the South Island, where further transport by coastal currents on the Subtropical Front were likely involved.

The cuttlebones, upon arrival in New Zealand, are devoid of flesh and are typically worn and abraded (no cuttlefish tissue has been found so far). That, together with the presence of encrusting barnacles and hydrozoans, indicates a reasonable period in the ocean. Both encrusting species have cosmopolitan distributions and are known to occur in the Tasman Sea (Foster 1978; Fernandez and Marques 2018), although the complicated taxonomy of the hydrozoan *Obelia dichotoma* may account for its supposed widespread distribution (see discussion in Supplementary Material 1).

In the much shorter floating distances involved in a study in the Netherlands, Cadée (1997a) found a good variety of encrusting animals, including bivalves. That author identified two species of barnacles (*Semibalanus balanoides* (Linnaeus, 1767) and *Austrominius modestus* (Darwin, 1854)), the mussel *Mytilus edulis*, the hydrozoan *Obelia geniculata*, and undetermined algae. Similarly, Jongbloed et al. (2016) reported one barnacle species (*Balanus* cf. *improvisus* Darwin, 1854) and undetermined algae. In specimens freshly collected in New Zealand during 2019–2020, we observed that small barnacles often attach themselves inside the triangular praedichnia (type 1), similar to what was observed by Cadée (1997a).

Cadée (1997a, 2002) proposed that the cuttlebone specimens that he studied had been floating for two months before they were beached, while Jongbloed et al. (2016) proposed a range from some months to two or more years until a storm carried them to the shore. The encrusting organisms found on our specimens can be fully grown in a few weeks depending on water temperature (Russell 1953; MacIntyre 1966; Cornelius 1982; Anderson 1994; Whitehead et al. 2011). Reports of *Lepas anatifera* from Australia and New Zealand give a range of 17–50 days for the organisms to complete a life cycle (MacIntyre 1966). As such, Cadée's (1997a, 2002) hypothesis of two months is adequate to explain the accumulation of the various organisms recorded growing on cuttlebone. However, this does not negate the idea that cuttlebones can presumably remain afloat for much longer than two months.

## Conclusion

To date, the cuttlebones of one to three species of cuttlefish have reached New Zealand shores. According to evidence from morphological characters and DNA barcoding, nearly all confirmed records are of *Sepia apama*. However, *S. grahamsi* was also confirmed (although the specimen lacks collection details), and a possible example of *S. latimanus* was identified. This was the first time DNA has been extracted and sequenced from cuttlebones, so our technique has potential to work on other material, including historical type specimens.

The specimens are all of Australian or Indo-Pacific species and, in all cases, the cuttlebone appears to have floated to New Zealand (there are no records of live *Sepia* spp. from New Zealand waters). The three species reported here will also serve as a baseline of the past century: as the East Australian Current is affected by climate change (e.g.

Oliver and Holbrook 2014), it is expected that cuttlebones of further species will arrive on New Zealand shores.

Our ichnologic analysis revealed that most of the cuttlebones have marks indicative of scavenging, particularly by albatrosses. We also found tooth marks that we ascribed to predation and/or scavenging by sharks and dolphins. The cuttlebones were probably floating at sea for weeks or months before beaching in New Zealand, during which time many specimens were colonised by pelagic invertebrates, particularly hydrozoans and barnacles. We hope that this analysis will be of use to future researchers working on similar material in other regions of the globe.

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## Data availability statement

The authors confirm that the data supporting the findings of this study are available within the article and its supplementary materials.

## Disclosure statement

No potential conflict of interest was reported by the author(s).

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