Pitman Robert (Orcid ID: 0000-0002-8713-1219)

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Long in the tooth: Biological observations from at-sea sightings of strap-toothed beaked whales (*Mesoplodon layardii*)

Robert L. Pitman,[1] Antarctic Ecosystem Research Division, Southwest Fisheries Science Center, National Marine Fisheries Service, NOAA, 8901 La Jolla Shores Drive, La Jolla, California 92037, U.S.A.; **John Totterdell**, CETREC (Cetacean Research), PO Box 140, Exmouth, Western Australia 6707, Australia; **Rebecca Wellard**, Centre for Marine Science & Technology and Project O.R.C.A (Orca Research and Conservation Australia), Curtin University, GPO Box U1987, Perth, Western Australia 6845, Australia; **Pierce Cullen**, Project O.R.C.A (Orca Research and Conservation Australia), Curtin University, GPO Box U1987, Perth, Western Australia 6845, Australia; **Marijke de Boer**, Seven Seas Marine Consultancy, PO Box 11422, Amsterdam, The Netherlands.

Among the 15 currently recognized species of mesoplodont beaked whales (Ziphiidae, *Mesoplodon* spp.), only adult males have functional teeth, and these have been reduced to a single, enlarged tooth emerging from each side of the lower jaw. It has long been inferred that males use their teeth as tusks to aggressively vie for access to breeding females because only adult males acquire extensive tooth-rake marks on their bodies (Kellogg 1940, McCann 1974, Heyning 1984, MacLeod 1998).

This repurposing of mesoplodont teeth has led to some remarkable, species-specific variations in tooth size, shape, and placement. For example, with the possible exception of the spiraled tusk of the narwhal (*Monodon monoceros*), the strap-toothed beaked whale (*Mesoplodon layardii*) has perhaps the most bizarre teeth in the animal kingdom. As the males mature, a single, strap-like tooth emerges from the middle of each lower jaw, and, as it grows, it curves up and back at a *ca*. 45° angle, over the top of the rostrum. Full-grown teeth measure up to 34 cm in length (Best 2007) and often meet or overlap on top of the rostrum (Fig. 1a). Despite being by far the largest tooth of any beaked whale, only the small, up-turned denticle at the tip of the tooth (Fig. 1b) makes contact with opponents.

It would seem unavoidable that tooth development in male *M. layardii* would restrict jaw movement and impair feeding. However, Sekiguchi *et al.* (1996) reported that although an adult female and an immature male *M. layardii* could both open their mouths 6.5 cm at the tip, two adult males could open their mouths only 3.2 and 4.0 cm, respectively, but both appeared to have been feeding normally prior to stranding. Beaked whales suck in their prey, and a reduced aperture at the tip should allow them to be more forceful and directed with their suction feeding (Heyning and Mead 1996). Thus, male *M. layardii* may not be as handicapped in their foraging as they might otherwise appear to be.

M. layardii is also unique among mesoplodonts (and perhaps all cetaceans) in having a definitive adult color pattern that is entirely different from its juvenile coloration (*cf*. Fig. 2, 3). Although tooth eruption in male mesoplodonts generally coincides with the onset of adulthood (Mead 1989), teeth in *M. layardii* begin to erupt while males are still in their juvenile coloration (see below). Therefore, for the purposes of this note, we will refer to the different color pattern stages of *M. layardii* as “juvenile” (largely uniform gray), “adult” (definitive black and white pattern), or “subadult” (transitioning between juvenile and adult). These terms are only meant to be descriptive, with no implications about the physical, social, or sexual maturity of the individuals. Further study with fresh-stranded animals will be necessary to determine how maturity correlates with the tooth and color pattern development in this species.

The combination of a distinctive, black and white adult color pattern and the unique dentition of males make adult *M. Layardii* perhaps the most readily identifiable of the 22 known species of beaked whales (Best 2007, see Jefferson *et al.* 2015). Furthermore, *M. layardii* appears to be common within its circumpolar range in the cold/temperate waters of the Southern Hemisphere—it has been cited as the most commonly stranded mesoplodont worldwide (Mead 1989), including in South Africa (Best 2007) and Australia (Bannister *et al*. 1996). However, despite being distinctively patterned and relatively common, *M. layardii* has seldom been identified alive in the wild. This may be due, in part, to the fact that juveniles are mostly uniform gray and superficially similar to several other mesoplodont species—their distinguishing field marks have not been adequately described. In addition, for well over a century, the type specimen of the recently resurrected spade-tooth beaked whale (*M. traversii*) was misidentified as *M. layardii* due to similarities in tooth and skull morphology. There are no descriptions of fresh specimens of *M. traversii*, alive or dead, and it could resemble *M. layardii* (van Helden *et al.* 2002, Best 2007).

Herein we describe ontogenetic stages in *M. layardii* color patterning and tooth development based on a series of photographs from two recent observations at sea (Fig. 3–10). These descriptions should prove useful for distinguishing *M. layardii* from other, similar-looking mesoplodonts in the field, especially if no adult *M. layardii* are observed. We also discuss group size and social structure in this species based on these observations.

Sightings

Sighting #1 was observed by MdB on 12 April 2017, just north of Tristan da Cunha Island in the South Atlantic Ocean—the location was 33.39ºS, 11.07ºW; the water temperature was 22ºC. Three animals were present, and they were traveling slowly, abreast, about 10 m apart. Two of the animals showed different stages of subadult color pattern (Fig. 7, 9), and a third individual was not photographed well enough to document its color patterning. It was not possible to tell if any had erupted teeth, and their sex was determined.

Sighting #2 occurred on 19 March 2018. The first four authors were conducting killer whale (*Orcinus orca*) research off Western Australia when a group of *M. layardii* surfaced several times in front of their transiting vessel. The sighting location was 34.99ºS, 119.28ºE, approximately 64 km due south of Bremer Bay, Western Australia, over Cheyne Canyon. The water depth was 2,200–2,400 m, and the sea surface temperature was 20ºC–21ºC. Two individuals surfaced initially, and the rest of the group appeared several seconds later. Individuals were spread out over an estimated 30 × 30 m area and seemed to coalesce during the course of the observation. After all of the whales had surfaced 3–4 times, the entire group sounded almost simultaneously. At the surface, they all seemed hurried and somewhat agitated perhaps due to the presence of our vessel, which was heading in their direction and did not alter course or change speed during the sighting. Less than 20 min prior to the sighting, we had observed killer whales, which are known to prey upon *M. layardii* in the waters offshore of Bremer Bay (Wellard *et al*. 2016), and this also could have contributed to their apparent skittish behavior at the surface.

When the whales first surfaced, three of the authors had DSLR cameras in hand, each with motor-drives and 100–400 mm lenses. Although, based on photograph metadata, the total observation period spanned only 25 s (16:10:51–16:11:16 LMT), 199 still images were recorded as the whales surfaced approximately 200–300 m ahead of the vessel. Although at the time each of the authors independently estimated that there were approximately 10 animals present, only seven separate individuals were identified from the images, including four males and three unsexed juveniles. Males were identified by the presence of erupted teeth; individuals without erupted teeth were classified as unsexed. Six of the identified animals appeared to be swimming in pairs, which may have been random given the brevity of the encounter. Pairs included two unsexed juveniles (Fig. 3, 4); a juvenile male (Fig. 5) with a subadult male (Fig. 8); and another juvenile male (Fig. 6) with another, unsexed juvenile (not shown). The remaining individual in the group was an adult male (Fig. 10), which appeared to be swimming alone, approximately 15 m apart from the subadult and juvenile male pair. We did not identify any females, *i.e.*, individuals either having an adult or subadult color pattern but without erupted teeth (see below) or with dependent calves.

Below, we present photographs and descriptions of ontogenetic color pattern changes and tooth development in *M. layardii* based on these two sightings; the figures are presented in order of what we infer to be the youngest to the oldest individuals.

Young juveniles (Fig. 3, 4), sighting #2—These were almost uniform pale gray with long beaks and moderately prominent melons; they were identified as “young” juveniles because they had a noticeably pale melon (Fig. 3). At the trailing edge of the pale melon, immediately behind the blowhole, was a slightly darkened area, which formed an indistinct stripe on the side of the neck ("neck-stripe") that traveled down toward each eye (Fig. 3a; see also Jefferson *et al*. 2008, p. 141, bottom right photo; Jefferson *et al*. 2015, p. 160, bottom right photo). The visible body posterior to the neck-stripe was also pale gray but lighter than the neck-stripe and slightly darker than the melon. The dorsal fin was low, triangular, slightly falcate, and set far back on the body (Fig. 3b). The near animal in Figure 3b has a slightly whitish tip to the dorsal fin (see also this same animal in Fig. 4c) and the far animal does not, although they seem to be of similar age. The distant animal in Figure 3a appears to have a longer beak than the animal in the foreground, which could signify an older animal, a female (females of at least some species of beaked whales have longer beaks than males; von Haast 1876, Besharse 1971, Thompson *et al.* 2014), or, possibly, individual variation. There was no visible blow when the animals surfaced.

Figure 4 shows details of the animal in the foreground of Figure 3. It has a long, uniformly pale gray beak, and the gape is largely straight, with a slight downward turn toward the rear. It has a moderately sloping forehead and the beak protruded at a 30º–45º angle when it surfaced (Fig. 4a). The paler melon and darker neck-stripe is evident in Figure 4b; the orange area at side of the melon is a diatom patch. Figure 4c shows the unmarked, pale gray back and flanks, a dorsal fin that is starting to acquire a white tip, and another diatom patch at the base of the fin.

Juvenile males (Fig. 5, 6), sighting #2—Figure 5 is a roll sequence of one individual animal; Figure 6 is a different individual. Both were identified as juvenile males by their all gray coloration and the presence of a tooth just starting to emerge from the lower jaw. As in all age classes, the long beak jutted high up out of the water at a 30º–45º angle when the animals surfaced. The tooth is just beginning to erupt and the beak is still entirely gray (Fig. 5a, b). The forehead is moderately sloped, and the pale melon and dark neck-stripe appear to be absent at this stage (Fig. 5a–c, 6). The body color is slightly darker gray compared to the younger juveniles in Figures 3 and 4, but there is still no hint of black on the head, no whitening of the beak, and the dorsal cape has not begun to develop (Fig. 5b–d). Pale mottling on the back (Fig. 5c, d) appears to be due to scarring (including healed bites from cookiecutter sharks, Dilatiidae, *Isistius* spp.; see below) and, perhaps, skin molt. The dorsal fin is uniformly dark with no evidence of white tip (Fig. 5d), and comparing Figure 4c with Figure 5d, it is clear that some animals acquire a white tip to the dorsal fin later than others do.

Figure 6 shows a different juvenile male, also with a single tooth erupting from each side of the lower jaw. The head, back and rostrum are still uniform gray, but the lower lip in front of the right tooth is just starting to turn white, perhaps the first sign of transition into the subadult color pattern. This male appears to be slightly older than the one in Figure 5 due to this whitening of the lower lips and the somewhat longer teeth.

Unsexed subadult (Fig. 7), sighting #1—This individual is transitioning from the juvenile to the adult color pattern. It is mostly dark gray (Fig. 7a), with a dark shoulder patch and eye-patch (Fig. 7b); the distal portion of the beak is white (Fig. 7a), and the melon is becoming black (Fig. 7a, b). It was not possible to determine from the available photographs if it had erupted teeth. The cape is just beginning to develop, and it appears to be formed by two separate processes. At this stage, the most prominent part of the cape is a broad, pale, transverse band immediately behind the black on the melon. This white "neckband" extends rearward only a short distance behind the blowhole and terminates in a straight line, perpendicular to the back, which drops down between the shoulder patch and eye-patch (Fig. 7a, b; see also Fig. 9a, b). Another pale area is also developing, low, mid-body, on the side (Fig. 7b), which will form the lower, trailing edge of the cape. Presumably, as the cape develops, this second pale area will radiate dorsally and forward, eventually joining over the back and merging with the neckband. Another photograph of *M. layardii* with a pale neckband and an incompletely formed cape is shown in Jefferson *et al.* (2015, p. 160, bottom left photograph).

Subadult male (Fig. 8), sighting #2—The beak juts up at a *ca*. 45° angle when surfacing (Fig. 8a). The tooth is longer than that of the juvenile males in Figures 5 and 6, but it still does not extend above the top of the rostrum. (A suggested feature for distinguishing *M. layardii* from *M. traversii* is that the leading and trailing edge of *layardii* tooth is tapered toward the tip, while on the shorter, *traversii* tooth, the edges are parallel [van Helden *et al*. 2002, Best 2007]; however, this may not apply to *M. layardii* with partially grown teeth; Fig. 8b). The distal portion of the beak is white on top and bottom, but the white does not extend as far toward the base of the beak as in older adults (*cf*. Fig. 8b with Fig. 2a, 10a). The black on the rostrum extends farthest forward on the mid-dorsal line and mid-ventral line. The head and base of the beak are black, extending almost as far back as the blowhole (Fig. 8b). The cape on this animal is more developed compared to that in Figure 7; it extends from the trailing edge of the black melon, just in front of the blowhole, to two-thirds of the way back to the dorsal fin, and reaches furthest back on the mid-dorsal line (Fig. 8c). The trailing edge of the cape has joined over the back, and the lower leading edge has merged with the neckband on the side of the head (Fig. 8c). Embedded in the cape, behind the blowhole, on the mid-line of the back, is a large dark patch, which is the last area of the cape to develop. It is roughly triangular in shape, with the apex pointed toward the rear, and the base is formed by the neckband (Fig. 8c; see also Fig. 9, and Jefferson *et al*. 2008, p. 141, middle photograph, right side). The cape of this animal appears muted, more grayish, compared to the lighter cape of the older adult in Figure 10; it also lacks the contrasting, fluted border at the trailing edge along the flanks (*cf.* Fig. 8c with Fig. 10c). The dorsal fin has a pale gray tip, which is also not as conspicuous as in the older adult in Figure 10c. There are several patches of orange diatoms visible on lighter areas of this animal (Fig. 8b, c).

Unsexed adult (Fig. 9), sighting #1—This animal appears quite pale because its cape is nearly completely developed, and only the upper, forepart of the body is exposed. Again, due to water splashes partly obscuring the base of the beak, it was not possible to positively determine from the available photographs if it had erupted teeth. The distal portion of the beak is extensively white (Fig. 9a); the melon, shoulder patch and eye-patch are all blackish (Fig. 9b); and there is only a remnant of the dark triangle behind the blowhole (*cf*. Fig. 8c). The noticeably paler neckband is still evident, although the expanding cape has begun to merge with it. The dark spot near the waterline toward the rear of the cape is probably a recent cookiecutter shark bite (see below).

Adult male (Fig. 10), sighting #2—This adult male has a long beak that is snowy white on the distal half; the base of beak and head are black (Fig. 10a, b). The tooth erupts at the boundary between the white and black on the side of the beak, and it angles back, over the top of the rostrum; the blow is faint and angled forward (Fig. 10a). The teeth of adult males are sometimes cream-colored and easy to discern (Fig. 10a), but more often they are darkened by greenish-brown diatoms and can be difficult to detect (Best 2007, RLP, personal observation). There is a sharp boundary between the black head and the white or pale gray of the cape (Fig. 10b). The cape is uniformly pale; it has completely merged with the neckband, in this case obscuring it, and the gray triangle behind the blowhole is no longer visible (Fig. 10b). Although the neckband on this animal is no longer discernible, Shirihai (2007, p. 389, top right) shows an *M. layardii* with a fully formed cape and a still-evident neckband. The cape extends from the black on the melon, just in front of the blowhole, to approximately two-thirds of the way back to the dorsal fin (Fig. 10c); it extends farthest back on the mid-dorsal line and has a distinctive, fluted border along the trailing edge on the flanks (Fig. 10c). The remainder of the back is black, and the dorsal fin is black but with a conspicuous white tip (Fig. 10c). Although not evident from our photos, *M. layardii* also has white fluke tips, which, like the dorsal fin tip, also appear to become lighter with age (Fig. S1a, b).

The adult male in Figure 10 shows none of the obvious linear scarring often found on adult male mesoplodonts and attributable to tooth rake marks from aggressive interactions with male conspecifics (Heyning 1984, MacLeod 1998). Although it could be that this animal has not yet had contact with other adult males, we suggest that the lack of visible scarring is due to two other factors. First, unlike some species of *Mesoplodon*, superficial flesh wounds on *M. layardii* heal the same color as the adjacent skin, making these scars nearly invisible (see MacLeod 1998). As evidence for this, cookiecutter sharks are small, oceanic sharks (to 54 cm, Compagno 1984) that sometimes feed by excising a round or oval plug out of the flesh of larger animals, including cetaceans (Jones 1971, Best and Photopoulou 2016). These bite wounds typically leave small (5–7 cm across long axis, Shirai and Nakaya 1992), round or oval scars, which on some species of *Mesoplodon* heal conspicuously white (*i.e.*, unpigmented). On *M. layardii*, however, cookiecutter shark bites heal the same color as the surrounding skin, so that the scars are nearly invisible (Fig. S2a, b), and this would presumably apply to any tooth rake marks that this species might acquire from conspecifics, also. A second factor contributing to a lack of conspicuous rake-mark scarring on *M. layardii* is that, although the teeth of adult males are very large, as mentioned previously, the actual cutting point is a tiny, up-turned denticle on the top, leading edge of the tooth (Fig. 1b; MacLeod 2000). These denticles leave relatively superficial scratches on conspecifics, which are much less conspicuous than the deep furrows left by mesoplodonts with larger “tusks” (see below).

Currently, there are two recognized species of cookiecutter sharks, *I.brasiliensis* and *I. plutodus* (de Figueiredo Petean and R. de Carvalho 2018), and because *Isistius* bite wounds and scars tend to be either oval or round, it has been suggested that these shapes could be indicative of the biting species (*e.g.*, Williams and Bunkley Williams 1996, Pérez-Zayas *et al*. 2002). However, the adult *M. layardii* male in Fig. 10c-d has a conspicuous rectangular bite wound low on the mid-body. Although less common than the round or oval shapes, rectangular wounds and scars have been observed on various species of oceanic cetaceans in low latitudes (Baird 2016; RLP, personal observation) and could be evidence for another species of shark of similar size and feeding habits, but with, perhaps, a different jaw structure (*e.g.*, Grace *et al.* 2015).

Group Size

Mesoplodonts generally occur in small groups (Mead 1989, MacLeod 2014)—the largest that we are aware of was a mass stranding of a purported 28 Gray's beaked whales (*M. grayi*, including holotype) from the Chatham Islands, New Zealand, in 1875 (von Haast 1876), but confirming details about that event are lacking. Loughlin *et al.* (1982) reported seven sightings of Stejneger's beaked whales (*M. stejnegeri*) from the Aleutian Islands, Alaska, and the two largest groups were an estimated 12 and 15 individuals, respectively. These are the largest reported group-size estimates for free-swimming mesoplodonts in the modern era that we are aware of (see also MacLeod and D’Amico 2006). However, body length estimates for these two sightings were “about 6 m,” and estimated body lengths for two other sightings were 5–8 and 6–8 m, respectively (Loughlin *et al.* 1982). These length estimates overlap the size range of a newly identified, but yet undescribed, diminutive form of *Berardius* sp. found in the North Pacific, including the Aleutian Islands (Kitamura *et al.* 2013, Morin *et al.* 2017). The maximum reported body length for *M. stejnegeri* is 5.7 m, and two adult males of the new dwarf *Berardius* measured 6.6 and 7.3 m, respectively, compared to a maximum of 11.0 m for Baird’s beaked whale (*Berardius bairdii*; MacLeod 2006, Morin *et al*. 2017). MacLeod and D’Amico (2006) suggested that beaked whales fall into two group-size categories: mesoplodonts were in the small group category (mean 2.9 individuals, *n* = 354, range 1–15; the “15" comes from the aforementioned Loughlin *et al*. 1982), and *Berardius* spp. was in the large category (mean 7.9 individuals, range 1–100, *n* = 335). Furthermore, Loughlin *et al.* (1982)

reported that the animals in at least some of their sightings "appeared to be traveling abreast, almost touching each other. They surfaced and submerged in unison." This shoulder-to-shoulder swimming behavior is commonly observed in *Berardius* spp. (including *B. arnuxii* in the Southern Ocean) and rarely, if ever, seen in mesoplodont groups (RLP, personal observation). Based on these comparisons of length, group size, and surface behaviors, it seems possible that at least some of the Loughlin *et al.* (1982) sightings could pertain to the recently identified *Berardius* sp., and that their group-size estimates may not be applicable to *Mesoplodon*.

The largest credible group-size estimates for free-ranging mesoplodonts that we are aware of come from Claridge (2013) and Baird (2016) who both reported maximums of 11 *M. densirostris* in the Bahamas and off Hawaii, respectively. A group of 8–10 Sowerby's beaked whales (*M. bidens*) was reported from the eastern North Atlantic by Øynes (1974; the same sighting was reported on by Benjaminsen *et al.* 1976 and Christensen 1977). Hooker and Baird (1999) also reported a group of 8-10 *M. bidens*, from the western North Atlantic, and Patel *et al.* (2016)

reported a mass-stranding of 10 *M. grayi* in the Chatham Islands, New Zealand. For *M. layardii*, Shirihai and Jarrett (2006), Groom *et al.* (2014), and MacLeod (2014) all reported group sizes of up to 5, while Best (2007) cited 2–6 individuals from at-sea sightings in the South African subregion. Our sighting of an estimated 10 individuals off Bremer Bay appears to be the largest group of strap-toothed beaked whales reported to date, and may be near the maximum for all mesoplodonts.

Social Structure

The Bremer Bay sighting (#2) offers some insight into the social structure of *M. layardii* and perhaps other mesoplodonts as well. Among the seven individuals identified in our photographs, at least four were males of various ages, and the other three were unsexed juveniles. No adult females or dependent calves were photographed or otherwise observed. Lien *et al.* (1990) reported six *M. bidens* swimming near shore off Newfoundland in 1986; three that eventually stranded were all mature males, and the authors speculated that *M. bidens* "may form all male social groups." Similarly, a group of 8–10 *M. bidens* observed by Hooker and Baird (1999) in the western North

Atlantic included at least four adult males; they also reported another group of three that was all adult males, and an aerial photograph in Jefferson *et al.* (2015, p. 151, top left) shows what appears to be four adult male *M. bidens* swimming together. Eight Stejneger's beaked whales (*M. stejnegeri*) that stranded at Adak Island, in the Aleutian Islands, Alaska, in August 2018, were adult females,[2] and 10 Baird's beaked whales that stranded on an island in the Gulf of California, Mexico, in 2006 were all mature males (Urbán *et al.* 2007). The prevalence and adaptive significance of sexual segregation among beaked whales is unknown, but it could be fairly common and widespread.

What little is known about mesoplodont social structure suggests some interesting variability. Although more evidence is needed, the observations above suggest that at least some species occur in sexually segregated groups, or, at the very least, occur in groups with multiple males present, although some mesoplodont species clearly do not. For example, in *M. densirostris*, typically only one adult male associates with one or more females in what appears to be a harem arrangement (McSweeney *et al.* 2007, Claridge 2013, Dunn 2014), while *M.*

grayi (Patel *et al.* 2016), *M. bidens* (references above), and possibly *M. layardii* (this study) occur in groups with multiple males, including adults.

Heyning (1984) was perhaps the first to suggest a possible link between tooth development and social behavior among mesoplodonts, and we further propose that the degree of rostrum and tooth development among the different species might correlate not only with aggressiveness, but could also have implications for social structure and mating systems. For example, adult male *M. densirostris* have two massive tusks, each raised on a boney arch above the level of the head (think horns), and a stout, densely ossified rostrum that helps protect the beak against trauma when forcibly engaging opponents (Heyning 1984, MacLeod 2002). When *M. densirostris* males rake each other in combat, they leave “deep ruts” (MacLeod 2002; RLP, personal observation), which is presumably why there is almost never more than one adult male seen in a social group (MacLeod and D’Amico 2006, McSweeney *et al.* 2007, MacLeod 2014). On the other hand, adult males of species with longer, more delicate beaks and/or smaller, more fragile teeth (*e.g.*, *M. bidens*, *M.*

grayi, *M. layardii*) tend to leave relatively light scratches when they rake each other. The teeth of adult male ginkgo-toothed beaked whales (*M. ginkgodens*), for example, barely erupt above the gum line; as a result, adult males have almost no linear rake marks on their bodies, which Heyning (1984) interpreted as a sign of decreased aggressiveness. Reduced aggression among less well-armed mesoplodont species could allow for multiple males within groups and an altered social dynamic. Although *M. layardii* has the largest tooth of any beaked whale and might seem to be an exception to the rule, as mentioned above, its effective tooth size is actually very small because only the tiny, upturned denticle at the tip of the tooth is used for raking opponents (Fig. 1b; Best 2007).

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Supporting Information

The following supporting information is available for this article online at http://

Figure S1. (a) An aerial view of an adult *M. layardii* (an adult based on uniformly pale cape; see text) photographed at 60º28′S, 155º49′W, 6 January 2014, showing prominent white tips to the flukes. Photograph by E. Muirhead/Sea Shepherd; (b) top of the flukes of a female *M. layardii* that stranded in Golden Bay, New Zealand, 21 January 2007 (same animal as Fig. 2b). Compared to the animal on the left, it has less extensive white on its fluke tips, and it was presumably younger because it also had a gray triangular patch on the cape behind the blowhole (see Fig. 2b). It seems likely that, like the dorsal fin, fluke tips become whiter with age. Photo © Department of Conservation, New Zealand.

Figure S2. A female *M. layardii* stranded in Otago, New Zealand, 16 Sept 2008. Barely visible on its back are at least two dozen healed bite wounds from cookiecutter sharks, each *ca*. 4–7 cm across; (inset) an enlargement showing at least nine healed bite wounds, all of which have repigmented the same color as the adjacent skin. Photo © Department of Conservation, New Zealand.

Figure 1. (a) The skull of an adult male strap-toothed beaked whale (*Mesoplodon layardii*) showing how the single tooth from each lower jaw wraps up and back, over the rostrum, restricting the ability of the animal to open its mouth; the denticle on the top tooth has been worn off. (b) A small, sharp, up-turned denticle at the top of the tooth (arrow) is the only part of the tooth that makes contact with opponents. Photo courtesy Iziko South Africa Museum/Jofred Opperman.

Figure 2. (a) A breaching *M. layardii* (sex undetermined) shows the distinctive and unique adult color pattern of this species, including the prominent cape, largely white beak, and white-tipped dorsal fin and flukes; 18 March 2005, 57º24'S 39º46'W; photo by S. Howell; (b) An adult female *M. layardii* stranded in Golden Bay, New Zealand, 21 January 2007; a pale neckband extends from behind the black on the melon, to behind the blowhole, and forms the base of a darker gray triangle on the back behind the blowhole (see text). Photo © Department of Conservation, New Zealand.

Figure 3. (Sighting #2). (a) A pair of young *M. layardii* in juvenile coloration surfaces off Bremer Bay, Western Australia;

species identification was based on the presence of adult and subadult males photographed in the same group (see Fig. 8, 10). Notice the long beak, paler melon with a slightly darkened “neck-stripe” just behind the blowhole, and (b) otherwise nearly uniformly gray body.

Figure 4. (Sighting #2). A roll sequence of the same juvenile *M. layardii* shown in foreground of Figure 3 showing (a) a relatively straight gape with a slight downturn toward the rear, (b) slightly paler melon and darker neck-stripe, and (c) the dorsal fin is starting to show a white tip; the orange patches on the head and below the dorsal fin are diatoms.

Figure 5. (Sighting #2). A male *M. layardii* in juvenile coloration off Bremer Bay, Western Australia, March 2018; (a, b) its tooth is just starting to erupt from the lower jaw; (a, c) it has lost its pale melon and darker neck-stripe, but has not yet begun to transition into the adult color pattern; (d) its dorsal fin does not have a white tip yet. Its traveling companion in the lower right (b, c) is shown in Figure 8.

Figure 6. (Sighting #2). A young male *M. layardii* sighted off Bremer Bay, Western Australia, in March 2018; the slightly

longer teeth and whitening lips of the lower jaw suggest that it is a bit older than the male in Figure 5, although it is still retains the juvenile coloration.

Figure 7. (Sighting #1). Two views of the same *M. layardii* of unknown sex from a group of three photographed in April 2017 north of Tristan da Cunha Island, in the South Atlantic Ocean. This animal is transitioning into the adult color pattern: (a) the distal portion of the beak is white; (a, b) the white neckband has formed, and (b) the shoulder patch, eye-patch and melon are darkening, and the rear, lower portion of the cape is starting to develop. Photo by S. Steadman.

Figure 8. (Sighting #2). A roll sequence of a subadult male *M. layardii* off Bremer Bay, Western Australia, in March 2018. (a, b) Although the teeth are still only partially grown, it has acquired much of the adult color pattern - the head is black and the beak bicolored, although not as white as a full adult (see Fig. 10); (c, d) the dorsal cape, although well developed, is still somewhat muted; (c) there is a dark gray, triangular patch on the dorsal mid-line, forward on the cape; (d) the dorsal fin has a white tip and orange diatom patches are evident in several

places.

Figure 9. (Sighting #1). Associated with the animal in Figure 7, this animal was a bit older. (a, b) it has a white-tipped beak, blackish shoulder- and eye-patches; the white of the cape has advanced dorsally and forward and has become continuous with the white neckband. A dark gray triangle is still evident behind the neckband.

Figure 10. (Sighting #2). A roll sequence of an adult male *M. layardii* sighted off Bremer Bay, Australia, in March 2018. (a) The distal half of the beak is snowy white, and the cream-colored tooth curves up and back, over the top of the rostrum; (b, c) the dorsal cape is fully developed; it has completely merged with the neckband and the gray triangle behind the blowhole is no longer visible; there is a distinctive, fluted border on the trailing edge trailing edge, and (c) the dorsal fin has a conspicuous white tip. (b, c) Two dark spots on the cape are recent bite wounds from cookiecutter sharks (*Isistius* spp.); (d) the wound near the water line, mid-flank, is enlarged in to show its rectangular shape (see text).

[1] Corresponding author (e-mail: robert.pitman@noaa.gov).

[2] Personal communication from Marc Webber, U.S. Fish and Wildlife Service, Homer, AK, September 2018.