Death by octopus (Macroctopus maorum): Laryngeal luxation and asphyxiation in an Indo-Pacific bottlenose dolphin (Tursiops aduncus)

NAHJID STEPHENS,1 College of Veterinary Medicine, School of Veterinary and Life Sciences, Murdoch University, Perth, Western Australia 6105, Australia; PÁDRAIG DUGNAN, The Marine Mammal Center, 2000 Bunker Road, Fort Cronkhite, Sausalito, California 94965, U.S.A.; JOHN SYMONS, Cetacean Research Unit, Environmental and Conservation Sciences, School of Veterinary and Life Sciences, Murdoch University, Perth, Western Australia 6105, Australia; CARLYSE HOLYOAKE,2 College of Veterinary Medicine, School of Veterinary and Life Sciences, Murdoch University, Perth, Western Australia 6105, Australia; LARS BEJDER, Cetacean Research Unit, Environmental and Conservation Sciences, School of Veterinary and Life Sciences, Murdoch University, Perth, Western Australia 6105, Australia; KRISTIN WARREN, College of Veterinary Medicine, School of Veterinary and Life Sciences, Murdoch University, Perth, Western Australia 6105, Australia.

There are numerous reported cases of nondrowning asphyxiation due to laryngeal displacement and resultant suffocation caused by an intended prey item in various cetacean species, most involving fish species either too large to be swallowed, or whose strong dorsal spines caused them to become lodged in place, rarely with concurrent involvement of fishing gear (Hult et al. 1980, Byard et al. 2003, Watson and Gee 2005, Mignucci-Giannoni et al. 2009, Byard et al. 2010, Stolen et al. 2013, Ryan and Bolin 2014, IJsseldijk et al. 2015). A notable exception is that of two long-finned pilot whales (Globicephala melas) that asphyxiated due to the presence of fish in their nasal cavities (IJsseldijk et al. 2015). The present case report is, to the authors’ knowledge, the first cetacean asphyxiation reported involving a cephalopod, namely an octopus; this report outlines relevant postmortem findings, and discusses the risky, but potentially rewarding, practice of predating upon octopodes.

The temperate waters off the coast of the busy port city of Bunbury (33°32’S, 115°63’E), Western Australia, are home to a population of coastal Indo-Pacific bottlenose dolphins (Tursiops aduncus). Year-round boat-based photo-identification

1Corresponding author (e-mail: n.stephens@murdoch.edu.au).
2nee Palmer.
surveys conducted along systematic transects (2007–2013) found that dolphin abundance estimates were seasonally dependent, with high abundance during summer, and lower abundance in the winter; indeed, population size approximately doubled in summer vs. winter (Smith et al. 2013, Sprogis et al. 2016). The work of Smith et al. (2013, 2016) and Sprogis et al. (2016) and the resultant evolving photo-identification catalog suggests there to be a year-round “resident” population of approximately 60 animals (unpublished data) consisting mainly of juveniles of both sexes, as well as adult females and their dependent calves. Similar to bottlenose dolphins globally, the Bunbury dolphins consume a wide variety of prey species (with fish and cephalopods predominating), and are therefore generalist or opportunistic feeders (McCluskey et al. 2016), although if faced with choice, they are likely to display food selectivity, as documented in common bottlenose dolphins (Tursiops truncatus) elsewhere in Australia (Corkeron et al. 1990). Individuals from Bunbury have been observed on numerous occasions feeding on octopus (Sprogis et al. 2017); such observations concur with anecdotes from elsewhere in Western Australia. 4

An adult male Indo-Pacific bottlenose dolphin (Tursiops aduncus) was found dead at Stratham Beach, Western Australia (33°21′7″S, 115°34′30″E) on 30 August 2015; octopus arms were protruding from its mouth (Fig. 1). Based upon comparison to the photo-identification catalog images, the dolphin was definitively identified as a known male named “Gilligan.” It was first sighted as an adult in July 2007, and was therefore estimated to be in excess of 20 yr of age; it had been sighted 25 times since surveys began mid-2007 (i.e., 8 yr prior to death), and was documented to be in an alliance with two other adult male individuals. Interestingly, this case occurred on

Figure 1. Adult male *Tursiops aduncus* (“Gilligan”) as found on the beach.

3 Unpublished data from Kate Sprogis and Lars Bejder, Murdoch University Cetacean Research Unit, Western Australia.

4 Personal communications from Douglas Coughran AM, Department of Parks and Wildlife, Western Australia, September 2015; Melissa Evans, Department of Parks and Wildlife, Western Australia, September 2015; and Krista Nicholson, Murdoch University Cetacean Research Unit, Western Australia; February 2016.
the cusp of the austral winter transitioning to spring when most instances of octopus predation by Bunbury individuals have been observed, possibly because semelparous senescence may render octopus more vulnerable at this time of year (Sprogis et al. 2017). This dolphin was an adult, as were the majority of Bunbury individuals observed preying upon octopus, suggesting a learned behavior (Sprogis et al. 2017). The majority (60%) of Bunbury dolphins known to prey on octopus are female (Sprogis et al. 2017), and this male had not been observed in the previous study feeding on this prey species. The dolphin carcass was fresh (code 2, per Geraci and Lounsbury 1993) with no evidence of significant external injuries; it was transported on ice to Murdoch University. It was 242.3 cm standard length and was in excellent body condition, with blubber depth thicknesses of 44 mm dorsally, 23 mm laterally, and 27 mm ventrally (measured just rostral to the dorsal fin). Significant diffuse dental attrition confirmed Gilligan’s estimated advanced age. The octopus was still in situ with some arms protruding from the mouth and the remainder obstructing the pharynx, larynx and esophagus. The dolphin’s arytenoepiglottic tube (“goosebeak” larynx) was displaced from its normal intranarial position, compressed ventrally, obstructed, and unable to communicate with the nasal passage (Fig. 2). The octopus’ suckers were firmly adhered to the adjacent mucosa of the dolphin’s caudal tongue, faucal isthmus, lateral channels of the pharynx, the esophagus, and the lateral aspects of the larynx from which they had to be detached, revealing innumerable circular (5–17 mm diameter) umbilicated lesions, many of which were discolored red-purple (hyperemia and acute hemorrhage were confirmed on histopathological examination) (Fig. 3). The dolphin’s lungs were hyperinflated with marked rib impressions, an enhanced lobular pattern, and diffuse interstitial emphysema (alveolar over-inflation due to inability to

Figure 2. Octopus in situ within the dolphin’s opened caudal pharynx and proximal esophagus; several suckers have been detached in order to lift the arms that were surrounding and covering the now revealed larynx. For scale, the wooden case identification marker measures 15 × 1.7 cm.

5Personal communication from Kate Sprogis, Murdoch University Cetacean Research Unit, Western Australia, September 2015.
When the laryngeal obstruction was removed, the lungs self-deflated. One of the octopus’ arms extended aborally within the dolphin’s esophagus to the entrance of its first gastric compartment (C1); the octopus’ mantle (including eyes and brain) was completely detached and within the first compartment leaving the “crown” of arms intact. The entire octopus weighed 2.1 kg; its widest arm span was 130 cm. The dolphin’s first gastric compartment (C1) also contained a copious amount of varied prey items: a portion of an unidentifiable fish, numerous otoliths, numerous squid beaks, cuttlefish, and fragments of crayfish antennae and walking legs. The remaining gastric compartments (C2, C3) were empty apart from a small volume of fluid. There was no evidence of underlying disease or internal injury which could have caused or contributed to death (e.g., extrinsic or intrinsic lesions causing airway/esophageal compression and/or stenosis). The findings were consistent with the cause of death being due to nondrowning asphyxiation, specifically suffocation, caused by choking (McEwen 2016). The octopus was identified as a benthic inshore Maori octopus (Macroctopus maorum, synonyms: Octopus maorum, Pinnoctopus cordiformis; (S. Leporati and K. Sprogis) (Sprogis et al. 2017). A robust and muscular species, it is the largest octopod in Australasia and the third largest in the world, weighing up to 12 kg with a total length of up to 2 m and an arm span in excess of 3 m (Norman and Reid 2000, Lalas 2009, Sprogis et al. 2017).

An almost identical case involving another adult T. aduncus is recorded in the Department of Parks and Wildlife (DPaW) database (record 702). The dolphin (an unidentified individual) was found stranded dead on 11 April 2009 within the Shoalwater Bay Islands Marine Park, Western Australia (32°20’S, 115°42’E), approximately 162 km from where this case was found. Once again, octopus arms protruded from its mouth, and while a postmortem examination was not carried out and the...
octopus species not identified, its cause of death was recorded as being due to nondrowning asphyxiation.\(^7\) DPaW rangers on Penguin Island, Western Australia (32°18'19"S, 115°41'28"E) and staff of the nearby ecotourism company Rockingham Wild Encounters have anecdotally reported similar octopus-related deaths in the past in both dolphins and Australian sea lions (Neophoca cinerea) and recounted stories of having seen, in some instances when dolphins were observed holding an octopus in their mouths, the apparently live octopus reaching up towards the dolphin’s blowhole.\(^8\)

Most mammals process their food via mastication to facilitate safe consumption. Dolphins possess monophyodont and simple homodont dentition, and are thus unable to shear and chew their prey into smaller pieces; instead, they usually swallow their prey whole or tear fragments off following its capture using ram and raptorial feeding techniques (Marshall 2009). This poses a problem when swallowing large, bulky prey. In terrestrial mammals, the epiglottis in its intranarial breathing position separates the respiratory and digestive tracts; as the animal swallows, the larynx rises and the epiglottis protects the entrance to the trachea so the food bolus is diverted into the esophagus (Pabst \textit{et al.} 1999). In odontocetes, the epiglottis and paired cuneiform processes of the arytenoid cartilages form, respectively, the ventral and dorsal elements of a rigid elongated arytenoepiglottic tube referred to as the “goosebeak” larynx (Reidenberg and Laitman 1987; Brzica \textit{et al.} 2015; Cozzi \textit{et al.} 2017a, b), centrally located between the wide lateral channels of the pharynx, which lead to the esophagus lying dorsally to the trachea (Pabst \textit{et al.} 1999, Cozzi \textit{et al.} 2017c). The rostral tip of the larynx is permanently seated within the internal nares (choanae) by the palatopharyngeal sphincter muscle, therefore separating the respiratory and digestive tracts to a greater extent than in other mammals (Reidenberg and Laitman 1987; Pabst \textit{et al.} 1999; Brzica \textit{et al.} 2015; Cozzi \textit{et al.} 2017a, b). The lateral channels of the pharynx communicate dorsally; food passes through them either side of the larynx when swallowed (Pabst \textit{et al.} 1999, Cozzi \textit{et al.} 2017c). Therefore, under normal circumstances, the respiratory and digestive tracts of odontocetes do not communicate, a useful adaptation for ingesting prey underwater; however, dolphins can voluntarily displace their larynx from the choanae in order to swallow large, bulky prey (Reidenberg and Laitman 1987, Stolen \textit{et al.} 2013, IJsseldijk \textit{et al.} 2015, Cozzi \textit{et al.} 2017a). As their esophagus is highly distensible, the limiting factor for prey size is the diameter of the dorsally communicating lateral channels of the pharynx, as well as that of the faucal isthmus (Cozzi \textit{et al.} 2017c). One study of stomach contents in \textit{Tursiops} sp. found the prey length to be less than 37 cm and generally between 6 and 20 cm (Cockcroft and Ross 1990), significantly smaller than the octopus in this report. Voluntarily displacing their larynx in order to ingest large prey as a behavioral adaptation carries a high degree of risk, given water and/or prey may potentially enter the internal nares and/or the trachea (IJsseldijk \textit{et al.} 2015). It is especially risky given such prey items may still be alive when swallowed, and, presumably, actively fighting becoming a meal.

To minimize risk, the Bunbury dolphins utilize complex prey handling techniques to process octopus prior to swallowing, the “shake” and “toss,” as described in Sprogis \textit{et al.} (2017). Globally, marine mammals of various species have been reported in

\(^7\)Personal communication from Douglas Coughran AM, Department of Parks and Wildlife, Western Australia, September 2015.

\(^8\)Personal communication from Melissa Evans, Department of Parks and Wildlife, Western Australia, September 2015.
various locations, exhibiting diverse specialized foraging and prey handling techniques; Australian fur seals (*Arctocephalus pusillus doriferus*) also shake and toss cephalopods (and large fish) before swallowing (Hocking *et al*. 2016), and common bottlenose dolphins repeatedly hit common cuttlefish (*Sepia officinalis*) on the water’s surface before consumption (dos Santos and Lacerda 1987). Complex prey handling techniques have been reported in bottlenose dolphins predating upon cephalopods, specifically giant cuttlefish, *Sepia apama* (Finn *et al*. 2009, Smith and Sprogis 2016) and common cuttlefish (dos Santos and Lacerda 1987, dos Santos *et al*. 2007); unfortunately unlike some of the cuttlefish reports, the Bunbury octopus prey handling report is limited to above water boat-based observations (Sprogis *et al*. 2017) so it is not known if there are also underwater techniques that may be part of the sequence. Presumably, the Bunbury dolphins shake and toss the octopus to both stun/kill it, as well as break it up into smaller pieces, in order to render it safer and more manageable for consumption (Sprogis *et al*. 2017).

However, this is still a risky practice. Due to the unique organization of the octopus nervous system, most processing of motor and sensory information is performed in the peripheral nervous system and the optic lobes, with the central brain acting predominantly as a coordination and decision-making control center. Indeed, central representation of the arms is lacking in octopus, and much of the arm function occurs without central involvement (Hochner 2012). Octopus arm nociceptors and defensive withdrawal reflexes (following noxious stimulation of the arm tip) have been documented to remain functional in chilled gassed seawater for up to one hour following the octopus’ death and subsequent detachment of the crown of arms from the body (Hague *et al*. 2013). Similarly, both the “accept” and “reject” reflexes (in which an object is presented to stimulate the mid-arm suckers, resulting in a series of combined arm and sucker movements designed to either pass the object proximally towards the mouth or distally towards the arm tip to push it away, respectively) remain intact following individual arm and entire crown amputation, suggesting both reflexes are organized by the arm nerve cord. Indeed, the “reject” reflex is less easily elicited than the “accept” reflex, with research suggesting that specific lobes of the octopus’ central nervous system (often detached with crown amputation) are essential for the control of rejection (Altman 1971). More recent work confirms that amputated octopus arms are not only viable, but are highly active for >1 h following detachment, with the arms exhibiting movements similar to those seen in intact individuals, and the suckers capable of grasping, attaching, and holding various objects (Nesher *et al*. 2014). Therefore, even though the octopus’ mantle, including its brain, was detached from the crown of arms in this report, the suckers and arms remained functional, as indicated by the presence of fastened, sealed suckers as well as hyperemia and acute hemorrhage (both antemortem processes) in the dolphin’s affected mucosa. It is presumed this dolphin simply did not process the crown sufficiently to break it up into individual arms or arm fragments, such that during the pharyngeal stage of swallowing the crown lodged around and over (*i.e.*, the dolphin had voluntarily displaced its larynx in order to consume its large meal) the larynx and subsequently the suckers fastened themselves to apposing surfaces. The majority of the arms and suckers were then unable to be dislodged neither by the combined movements of the genioglossus, hyoglossus, and styloglossus muscles nor by the larynx, although esophageal peristaltic waves appear to have resulted in one arm tip reaching the stomach.

Given octopus arms and suckers remain active and functional for over an hour (Nesher *et al*. 2014), they would far outlast the breath-holding capacity of any
dolphin. The respiratory frequency for an adult, 159 kg, female *Tursiops truncatus* engaged in slow swimming at rest at the water’s surface is 2.3 breaths/min (Mortola and Limoges 2006), although another study using an adult, 145 kg, female *Tursiops truncatus* found the resting respiratory rate to be as high as 5.9 breaths/min (Williams et al. 1993). Williams et al. found that heavy exercise (pushing against a load cell and open water swimming), comparable to struggling with an octopus, increased the respiratory rate as high as 12.5 breaths/min in the female dolphin; the adult, 145 kg, male *Tursiops truncatus* was much less affected by exercise, showing only a 60% increase in respiratory rate between rest (3.54 breaths/min) and exercise, with a mean respiratory rate at exercise of 5.9 ± 0.7 breaths/min. Certainly, *Tursiops* sp. are capable of considerable periods of breath-holding during diving sequences—typically, a foraging *Tursiops truncatus* breath holds for <5 min to dive shallowly to <20 m depth, however, the maximum duration recorded is 8 min, albeit at a maximum depth of 390 m; therefore it is possible that at the surface a longer period is achievable (Ponganis 2011), although the heavy exertion involved in struggling with an octopus may negate this. Despite this considerable ability, the dolphin would have been no match for the octopus’ tenacity, and it is unknown how long this individual might have struggled to free its larynx from choking before succumbing.

Death is presumed to have occurred either from pure hypoxia due to airway occlusion, or from neurogenic cardiac arrest secondary to the vasovagal reflex (causing reflex bradycardia and asystole), the latter ("café coronary syndrome," per Byard et al. 2003) possibly accelerated by excessive catecholamine release due to the fight-or-flight response, ultimately leading to irreversible cerebral ischemia (Byard et al. 2003, Saukko and Knight 2004, McEwen 2016). Byard et al. (2003) note that various heavy metal and industrial chemical intoxications in humans can cause neuropathy, encephalopathy, and dementia, all of which can lead to both misinterpretation of the appropriateness of food bolus size as well as impairment of the neurologic mechanisms of swallowing. Given Gilligan was in excellent body condition (i.e., capable of foraging for adequate intake) at postmortem examination and was both behaviorally and physiologically normal (i.e., with no clinical signs consistent with toxicity including: ataxia/abnormal swimming, inability to forage/hunt, seizures, muscle fasciculation, altered mentation) when last sighted and followed four and a half months prior to death during a boat-based survey, intoxication was considered unlikely and no postmortem toxicological testing was undertaken. Furthermore, histopathological examination of various tissues including brain was unremarkable, although it is noted that this does not necessarily preclude various toxicities.

So why do dolphins persist with making meals of large octopodes, given the danger imbued by both their arms and suckers remaining functional, and the need to disengage their larynx to consume them? It likely comes down to risk vs. reward—large muscular cephalopods are an excellent, concentrated source of high quality proteins, and most cephalopods tire rapidly following a period of fast swimming (Clark 1996). Semelparous senescence may render octopus sluggish and more vulnerable and therefore an attractive prospect (Sprogis et al. 2017). Another example of risky practice by *Tursiops* sp. is that of their predation upon various stingray species, often with fatal consequences (albeit not by asphyxiation, but rather due to the combined effects of penetrating wounds and venom) (Walsh et al. 1988, and McLellan et al. 1996), although postinjury survival is documented (Spanier et al. 2000). Given dolphins must constantly swim, their energy consumption is high; therefore when considering a prey item as fuel for this continual process, the balance between (1) the metabolic cost of capture and the risk involved in predating a particular item, vs. (2) the
“pay-off” of the quality of the meal and the quantity of energy gained, is important (Cozzi et al. 2017a). Additionally, prey abundance may influence dietary selectivity. A recently published global study by Doubleday et al. (2016) spanning 61 yr (1953–2013) confirmed that cephalopod populations, including octopodes, have increased globally over the past six decades, correlating with several regional studies that have found cephalopod numbers have increased in regions where fish abundance has declined due to overfishing. Doubleday et al. (2016) concluded that this increase was likely multifactorial, with contribution not only from factors associated with developing fisheries, but also likely from factors associated with anthropogenic climate change and ocean warming. While a specific time-series study on prey availability does not appear to have been undertaken in the Bunbury area, octopodes may be of importance as a food source for the Bunbury population when alternate, less risky prey, is unavailable or limited (Sprogis et al. 2017), particularly in years to come in the face of a changing ocean environment. Assuming an octopus carcass is sufficiently processed to render its arms into small enough fragments such that they and their suckers can be effectively and safely swallowed, their consumption must generally be a risk worth taking, although it did not play out well in this individual’s case.

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