



Notes

MARINE MAMMAL SCIENCE, **(*) : ***-*** (** 2017)
© 2017 Society for Marine Mammalogy
DOI: 10.1111/mms.12420

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

NAHIID STEPHENS,¹ College of Veterinary Medicine, School of Veterinary and Life Sciences, Murdoch University, Perth, Western Australia 6105, Australia; PÁDRAIG DUIGNAN, 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; CARLYSLE 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 preying 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)³ 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.

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

⁴Personal 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.⁵

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

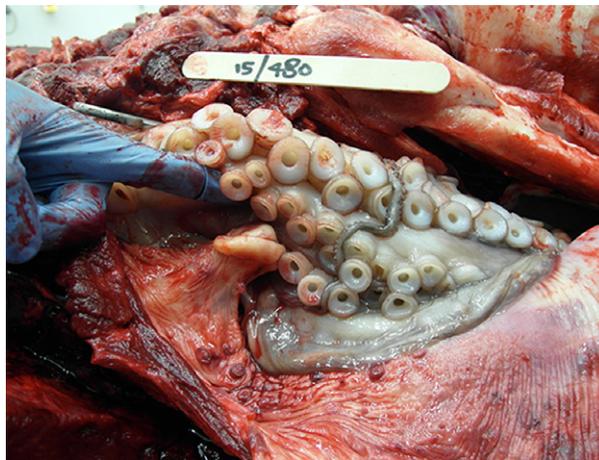


Figure 2. Octopus *in situ* within the dolphin's opened caudal pharynx and proximal esophagus; several suckers have been detached in order to lift the arms that were surrounding and covering the now revealed larynx. For scale, the wooden case identification marker measures 15 × 1.7 cm.

⁵Personal communication from Kate Sprogis, Murdoch University Cetacean Research Unit, Western Australia, September 2015.

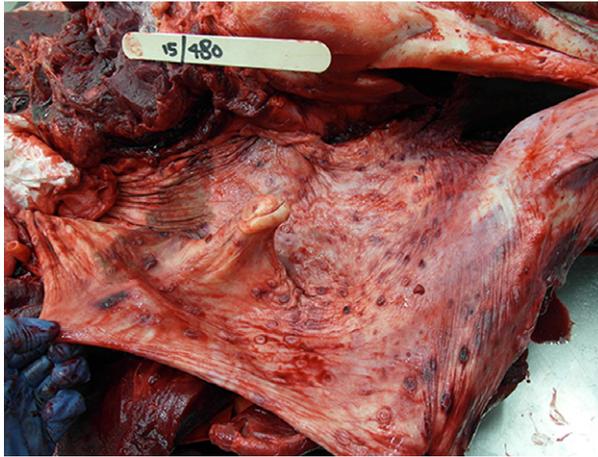


Figure 3. Umbilicated sucker marks (hyperemia and acute hemorrhage) ranging from 5 to 17 mm diameter affecting the mucosa of the caudal pharynx, larynx, and proximal esophagus. For scale, the wooden case identification marker measures 15 × 1.7 cm.

exhale). 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. Loporati and K. Sprogis⁶) (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

⁶Personal communications from Stephen Loporati, Department of Fisheries, Western Australia, October 2015 and Kate Sprogis, Murdoch University Cetacean Research Unit, Western Australia, October 2015.

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 *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 *et al.* 2015; Cozzi *et al.* 2017*a, b*), centrally located between the wide lateral channels of the pharynx, which lead to the esophagus lying dorsally to the trachea (Pabst *et al.* 1999, Cozzi *et al.* 2017*c*). 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 *et al.* 1999; Brzica *et al.* 2015; Cozzi *et al.* 2017*a, b*). The lateral channels of the pharynx communicate dorsally; food passes through them either side of the larynx when swallowed (Pabst *et al.* 1999, Cozzi *et al.* 2017*c*). 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 *et al.* 2013, IJsseldijk *et al.* 2015, Cozzi *et al.* 2017*a*). 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 faecal isthmus (Cozzi *et al.* 2017*c*). One study of stomach contents in *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 *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 *et al.* (2017). Globally, marine mammals of various species have been reported in

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

⁸Personal 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 predated 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.

ACKNOWLEDGMENTS

We thank the following for their invaluable support and assistance: Douglas Coughran AM and the Department of Parks and Wildlife, Murdoch University Cetacean Research Unit (MUCRU) team member Delphine Chabanne and Murdoch University technician James Poynton for their assistance with the postmortem examination, MUCRU member Dr. Kate Sprogis and Dr. Stephen Leporati for octopus species identification and discussion, Michael Slaven and Gerard Spoelstra for their histology expertise. As the relevant governmental regulatory body, Department of Parks and Wildlife granted permission for access to and use of this cadaver for research purposes, this research was conducted under the Department of Parks and Wildlife Animal Ethics Committee approvals DEC AEC 2005/01 and 2008/08 and Scientific Purposes Licenses SF000007, SC000619, SC000941, and SC001255. The postmortem examination was carried out under Murdoch University’s scientific license to use animal cadavers for research purposes (Animal Ethics Committee, Murdoch University). The authors state they have no conflicts of interest to declare.

LITERATURE CITED

- Altman, J. S. 1971. Control of accept and reject reflexes in the Octopus. *Nature* 229:204–206.
- Brzica, H., K. Špiranec, I. Zečević, H. Lucić, T. Gomerčić and M. Đuras. 2015. New aspects on the laryngeal anatomy of the bottlenose dolphin (*Tursiops truncatus*). *Veterinarski Arhiv* 85:211–226.
- Byard, R. W., J. D. Gilbert, S. E. Gibbs and C. M. Kemper. 2003. Cetacean café coronary. *Journal of Clinical Forensic Medicine* 10:85–88.
- Byard, R. W., I. Tomo, C. M. Kemper, S. E. Gibbs, M. Bossley, A. Machado and M. Hill. 2010. Unusual causes of fatal upper aerodigestive tract obstruction in wild bottlenose dolphins (*Tursiops aduncus*). *Forensic Science, Medicine, and Pathology* 6:207–210.
- Clark, M. R. 1996. Cephalopods as prey. III. Cetaceans. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences* 351:1053–1065.
- Cockcroft, V. G., and J. B. Ross. 1990. Food and feeding of the Indian Ocean bottlenose dolphin off Southern Natal, South Africa. Pages 295–308 *in* S. Leatherwood and R. R. Reeves, eds. *The bottlenose dolphin*. Academic Press, London, U.K.

- Corkeron, P. J., M. M. Bryden and K. E. Hedstrom. 1990. Feeding by bottlenose dolphins in association with trawling operations in Moreton Bay, Australia. Pages 329–336 in S. Leatherwood and R. R. Reeves, eds. The bottlenose dolphin. Academic Press, London, U.K.
- Cozzi, B., S. Huggenberger and H. Oelschläger. 2017a. Diving: Breathing, respiration, and the circulatory system. Pages 91–127 in B. Cozzi, S. Huggenberger and H. Oelschläger. Anatomy of dolphins. Academic Press, London, U.K.
- Cozzi, B., S. Huggenberger and H. Oelschläger. 2017b. Head and senses. Pages 159–1193 in B. Cozzi, S. Huggenberger and H. Oelschläger. Anatomy of dolphins. Academic Press, London, U.K.
- Cozzi, B., S. Huggenberger and H. Oelschläger. 2017c. Feeding and the digestive system. Pages 339–367 in B. Cozzi, S. Huggenberger and H. Oelschläger. Anatomy of dolphins. Academic Press, London, U.K.
- dos Santos, M. E., and M. Lacerda. 1987. Preliminary observations of the bottlenose dolphin (*Tursiops truncatus*) in the Sado Estuary (Portugal). Aquatic Mammals 13:65–80.
- dos Santos, M. E., C. Coniglione and S. Louro. 2007. Feeding behaviour of the bottlenose dolphin, *Tursiops truncatus* (Montagu, 1821) in the Sado Estuary, Portugal, and a review of its prey species. Zoociências 9:31–39.
- Doubleday, Z. A., T. A. A. Prowse, A. Arkhiphin, *et al.* 2016. Global proliferation of cephalopods. Current Biology 26:R387–R407.
- Finn, J., T. Tregenza and M. Norman. 2009. Preparing the perfect cuttlefish meal: Complex prey handling by dolphins. PLoS ONE 4(1):e4217.
- Geraci, J. R., and V. J. Lounsbury. 1993. Marine mammals ashore: A field guide for strandings. Texas A&M University Sea Grant Publication TAMU-SG-93-601.
- Hague, T., M. Florini and P. L. R. Andrews. 2013. Preliminary in vitro functional evidence for reflex responses to noxious stimuli in the arms of *Octopus vulgaris*. Journal of Experimental Marine Biology and Ecology 447:100–105.
- Hochner, B. 2012. An embodied view of octopus neurobiology. Current Biology 22:R887–892.
- Hocking, D. P., E. M. G. Fitzgerald, M. Salverson and A. R. Evans. 2016. Prey capture and processing behaviors vary with prey size and shape in Australian and subantarctic fur seals. Marine Mammal Science 32:568–587.
- Hult, R., S. E. Dupey and R. W. Badley. 1980. Mortalities associated with prey ingestion by small cetaceans. Cetology 38:1–2.
- Ijsseldijk, L. L., M. F. Leopold, E. L. Bravo, *et al.* 2015. Fatal asphyxiation in two long-finned pilot whales (*Globicephala melas*) caused by common soles (*Solea solea*). PLoS ONE 10(11): e0141951.
- Lalas, C. 2009. Estimates of size for the large octopus *Macroctopus maorum* from measures of beaks in prey remains. New Zealand Journal of Marine and Freshwater Research 43:635–642.
- Marshall, C. D. 2009. Feeding morphology. Page 406–413 in W. F. Perrin, B. Würsig, J. G. M. Thewissen, eds. Encyclopedia of marine mammals. Second edition. Academic Press, New York, NY.
- McCluskey, S. M., L. Bejder and N. R. Loneragan. 2016. Dolphin prey availability and calorific value in an estuarine and coastal environment. Frontiers in Marine Science 3. 30 pp.
- McEwen, B. J. 2016. Nondrowning asphyxia in veterinary forensic pathology: Suffocation, strangulation, and mechanical asphyxia. Veterinary Pathology 53:1037–1048.
- McLellan, W. A., V. G. Thayer and D. A. Pabst. 1996. Stingray spine mortality in a bottlenose dolphin, *Tursiops truncatus*, from North Carolina waters. Journal of the Elisha Mitchell Scientific Society 112(2):98–101.
- Mignucci-Giannoni, A. A., R. J. Rosario-Delestre, M. M. Alsina-Guerrero, *et al.* 2009. Asphyxiation in a bottlenose dolphin (*Tursiops truncatus*) from Puerto Rico due to choking on a black margate (*Anisotremus surinamensis*). Aquatic Mammals 35:48–54.

- Mortola, J. P., and M-J Limoges. 2006. Resting breathing frequency in aquatic mammals: A comparative analysis with terrestrial species. *Respiratory Physiology and Neurobiology* 154:500–514.
- Nesher, N., G. Levy, F. W. Grasso and B. Hochner. 2014. Self-recognition mechanism between skin and suckers prevents octopus arms from interfering with each other. *Current Biology* 24:1271–1275.
- Norman, M. D., and A. Reid. 2000. Page 67 in *A guide to squid, cuttlefish and octopuses of Australasia*. CSIRO, Collingwood, Moorabbin, Australia.
- Pabst, D. A., S. A. Rommel and W. A. McLellan. 1999. The functional morphology of marine mammals. Page 15–72 in J. E. Reynolds III and S. A. Rommel, eds. *Biology of marine mammals*. Smithsonian Institution Press, Washington, DC.
- Ponganis, P. J. 2011. Diving mammals. *Comprehensive Physiology* 1:517–535.
- Reidenberg, J. S., and J. T. Laitman. 1987. Position of the larynx in Odontoceti (toothed whales). *The Anatomical Record* 218:98–106.
- Ryan, C., and V. Bolin. 2014. Stranded harbour porpoise (*Phocoena phocoena* (Grey)) with throat obstructed by a scad (*Trachurus trachurus* (L.)). *The Irish Naturalists' Journal* 33:155–156.
- Saukko, P., and B. Knight. 2004. Suffocation and asphyxia. Pages 352–367 in Knight's forensic pathology. 3rd edition. Arnold Publishers, London, U.K.
- Smith, H. C., and K. R. Sprogis. 2016. Seasonal feeding on giant cuttlefish (*Sepia apama*) by Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in south-western Australia. *Australian Journal of Zoology* 64:8–13.
- Smith, H. C., K. Pollock, K. Waples, S. Bradley and L. Bejder. 2013. Use of the Robust Design to estimate abundance and demographic parameters for a coastal bottlenose dolphin (*Tursiops aduncus*) population. *PLoS ONE* 8(10):e76574.
- Smith, H., C. Frere, H. Kobryn and L. Bejder. 2016. Dolphin sociality, distribution and calving as important behavioural patterns informing management. *Animal Conservation* 19:462–471.
- Spanier, E., O. Goffman, D. Kerem and K. Lavalli. 2000. Injury of an Indian Ocean bottlenose dolphin (*Tursiops aduncus*) in the Red Sea by a stingray spine. *Aquatic Mammals* 26:196–201.
- Sprogis, K., K. H. Pollock, H. R. Raudino, *et al.* 2016. Sex-specific patterns in abundance, temporary emigration and survival of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in coastal and estuarine waters. *Frontiers in Marine Science* 3. 12 pp.
- Sprogis, K. R., H. C. Raudino, D. Hocking and L. Bejder. 2017. Complex prey handling of octopus by bottlenose dolphins (*Tursiops aduncus*). *Marine Mammal Science* 33, DOI: 10.1111/mms.12405 [Epub ahead of Print].
- Stolen, M., J. St Ledger, W. N. Durden, T. Mazza and E. Nilson. 2013. Fatal asphyxiation in bottlenose dolphins (*Tursiops truncatus*) from the Indian River Lagoon. *PLoS ONE* 8(6): e66828.
- Walsh, M. T. D., G. D. Beusse, W. G. Young, D. K. Odell and G. W. Patton. 1988. Ray encounters as a mortality factor in Atlantic bottlenose dolphin, *Tursiops truncatus*. *Marine Mammal Science* 4:154–162.
- Watson, A., and L. E. Gee. 2005. Laryngeal displacement and asphyxiation by a beheaded sheepshead (*Archosargus probatocephalus*) in a bottlenose dolphin (*Tursiops truncatus*). *Aquatic Mammals* 31:447–452.
- Williams, T. M., W. A. Friedl and J. E. Haun. 1993. The physiology of bottlenose dolphins (*Tursiops truncatus*): Heart rate, metabolic rate and plasma lactate concentration during exercise. *Journal of Experimental Biology* 179:31–46.

Received: 27 January 2017

Accepted: 12 April 2017