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Stomach contents and diel diving behavior of melon-headed whales (*Peponocephala electra*) in Hawaiian waters

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Knowledge of the diet and diving behavior of a species is crucial for understanding its behavior and ecology, and also has relevance to assessing the impact of potential changes in behavior or spatial use. Assessing diet for many species of cetaceans is difficult, given that most foraging occurs far below the surface and that stomach contents of stranded animals are rarely available. Very little information on food habits or the diving behavior of melon-headed whales (*Peponocephala electra*) is available from any region of the world.

Although there is a paucity of knowledge on melon-headed whales, more is known about them in Hawaiian waters than anywhere else in the world (Aschettino *et al*. 2012, Woodworth *et al*. 2012, Baird 2016). In Hawai'i, two populations of melon-headed whales are recognized, a Hawaiian Islands population estimated to be close to 5,000 individuals that travels offshore and among the islands, and a smaller, inshore population estimated to be about 450 individuals that is found off Hawai'i Island and known as the Kohala resident population (Aschettino 2010, Aschettino *et al*. 2012, Woodworth *et al*. 2012, Carretta *et al*. 2014, Martien *et al*. 2017). Melon-headed whales have been satellite tagged in Hawaiian waters and in the Commonwealth of the Mariana Islands in an effort to describe movement patterns (Woodworth *et al*. 2012, Baird 2016). However, dive depth data has not previously been reported from tagged individuals.

Despite their distribution throughout the tropics and subtropics world-wide, there are no published studies dedicated to the dietary habits of this species. All that is known about the melon-headed whale diet comes from the stomach contents

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of individual specimens in Hawai'i and South Africa and from a mass stranding in Brazil (Barros, unpublished data; Best and Shaughnessy 1981; Sekiguchi *et al.* 1992; Clarke and Young 1998). An examination of the dietary habits of melon-headed whales from any region of the world would be a valuable contribution to further understand the foraging behavior of this species.

The aims of this study were to investigate habitat use and foraging activity of melon-headed whales at depth by: (1) describing the diet composition of melon-headed whales from the stomach content analysis of 11 stranded specimens in Hawai'i and (2) examining the diving behavior of three melon-headed whales from dive depth data collected from deployment of depth-transmitting satellite tags in Hawaiian waters.

Stomach contents were collected from 11 stranded melon-headed whales from the main Hawaiian Islands, 10 that stranded between 2009 and 2017 and one from 1985. In most cases, melon-headed whales were identified to species based on body length, coloration, head shape, and pectoral fin shape. One individual, found dead in 2013 at Kaupoa, Moloka'i, had genetic analyses performed by the Southwest Fisheries Science Center in order to confirm the species identification. It was not possible to determine the sex of this individual due to tissue degradation.

For the stomach contents from the 1985 individual, the otoliths were removed and stored dry in gel caps and the cephalopod and fish bones were fixed in formalin. Stomach contents were initially frozen for the 10 individuals that stranded between 2009 and 2017. Frozen contents were later thawed and each sample was then rinsed through a progression of sieves with decreasing mesh sizes of 1.4 mm, 0.94 mm, and 0.50 mm. After sorting, cephalopod beaks and fish bones were preserved in 70% ethanol. Fish otoliths were stored dry in gelatin capsules. All remains were identified to the lowest possible taxon using the private reference collection of WAW and the fish bone, otolith, and cephalopod beak reference collections housed at the Marine Mammal Laboratory (MML), Seattle, Washington. A voucher series of selected beaks and otoliths representing each prey taxon were removed from the individual stomach samples and incorporated into the MML reference collections. The remainder of the individual stomach samples were stored in alcohol at MML.

The number of lower beaks present was used to estimate the total number of cephalopod species. The total number of each fish species was estimated based on the greater number of left or right otoliths. In a few instances the number of fish prey was estimated based on the greater number of left or right paired cranial bones. Dorsal mantle length and total weights were estimated by measuring lower beak rostral length for the cephalopod decapods and lower beak hood length for the cephalopod octopods and then applying the appropriate regression equations. Cephalopod beaks were measured to the nearest 0.1 mm with either an optical micrometer or, in the case of large beaks, Vernier calipers. In most cases, regression equations from the literature were used to estimate prey size and mass for the cephalopod species present (Clarke 1962, 1980, 1986; Wolff 1982*a, b*). Regressions for similarly sized *Abraliopsis felis* (Wolff 1982*a*) were used to estimate sizes of *Lycotheuthis* sp., *Abralia trigonura*, and *Pyroteuthis addolux*. Prey sizes were estimated using data from individuals of near equivalent beak size housed in the MML reference collection for the genus *Enoploteuthis* and for the species *Ocythoe tuberculata*. Fish otoliths and diagnostic bones were measured to the nearest 0.1 mm using an optical micrometer. In most cases, fish prey standard lengths and weights were estimated using regression equations from the literature (Ohizumi *et al.* 2001, Spear *et al.* 2007, Sinclair *et al.* 2015), or from regressions developed for similar, closely related species at the MML.

In instances where appropriate weight regressions were unavailable, weight was estimated by comparison with other closely related species of similar size.

As part of a multispecies investigation of odontocetes in Hawai'i (Baird *et al.* 2013, Baird 2016), melon-headed whale groups were approached and studied off the island of Hawai'i. Data presented here are from tags deployed between 2011 and 2014. Individuals in each group encountered were photographed, and photos of distinctive individuals were later compared to a photo-identification catalog to determine population identity (Aschettino *et al.* 2012). Because no mixing of individuals between populations has been documented, photographic matches to known individuals from one or the other population were used to confirm population identity.

Depth transmitting satellite tags (Wildlife Computers SPLASH10-A in the LIMPET configuration) were deployed with a pneumatic projector and attached with two 4.4 cm titanium darts with backward facing petals (Andrews *et al.* 2008). Tags were programmed to transmit 17 h/d with a maximum of 800 transmissions/d, giving an estimated battery life of approximately 22 d. Tags were set to record dive start and end time and maximum depth and duration for any dives greater than or equal to 30 m in depth. For two of the tags, the start and end of a dive was determined by the wet/dry sensor (surface), for the last tag deployed, a depth reading of 3 m was used to determine the start and end of dives. Given typical odontocete descent and ascent rates of 1–2 m/s, dive duration recorded are likely 3–6 s shorter than actual dive durations for the third tag. The duration of periods of "surface" time, where the individual remained shallower than 30 m, were also recorded. Given data throughput limitations in the Argos system, there are gaps in the periods of dive and surfacing data obtained during a tag deployment, thus the number of hours of data obtained varied. Tags were deployed during three encounters with melon-headed whales, on two individuals from the Kohala resident population (one in October 2011 and one in August 2012) and one individual from the Hawaiian Islands population (in July 2014).

Data obtained from the Argos System were processed through the Wildlife Computers DAP Processor v. 3.0 to obtain diving and surfacing data from the tags. Location data from tags were processed through the Douglas Argos-filter to remove unrealistic locations, using the same methods/settings used by Woodworth *et al.* (2012). Depths at tagged animal locations were determined using ArcGIS, using the 50 m resolution multibeam data set available at http://www.soest.hawaii.edu/HMRG/Multibeam/index.php. Using tag location data in the R package *maptools* (Bivand and Lewin-Koh 2016), solar angles were determined to delineate day, night, and the two twilight periods (dawn and dusk). Periods with a solar angle $>6^\circ$ were considered daytime, those $<-6^\circ$ were considered nighttime, and those between -6° and $+6^\circ$ were classified as twilight (either dawn or dusk depending on time of day). Each dive or surfacing segment was then assigned to one of these four periods based on the solar angle at the start of the dive or surfacing segment.

Information on date of stranding, body length, and specific location is provided in Table S1. Photos of the dorsal fin of one individual (stranded at Waiehu, Maui, in 2011) were matched to the Cascadia Research Collective (CRC) photo-identification catalog as HIPe0603, an individual from the Hawaiian Islands population first documented in 2004. Based on stranding locations, all other individuals were also likely members of the Hawaiian Islands population (Aschettino *et al.* 2012, Carretta *et al.* 2014).

Together, the eleven stomachs contained 783 food items ranging from 1 to 205 items per stomach. Six contained only cephalopods and five contained both cephalopods and fish. Relative frequency by number indicated that fish comprised 22.7% of the diet by number. Cephalopods were found in 100% of the stomachs examined and contributed 77.3% of the diet by number. However, when estimating prey contribution by mass, 86.2% is comprised of cephalopods and only 13.8% of fish (Table 1).

Fish remains represented nine families and 25 species. Myctophid lanternfish were the most abundant making up 16.3% of the total prey by number but only 6.6% by mass (Table 1). Of these, the most abundant species were *Lampadena urophaos* (7.5%) with lengths ranging between 105 and 151 mm, *Lampanyctus nobilis* (2.7%) with lengths varying between 133 and 143 mm, and *Diaphus fragilis* (1.8%) with lengths between 99 and 122 mm (Table 1, Fig. 1). By number, the fish family Stomiidae represented 2.7% of the prey, with a contribution by mass of 4.9%. The family Stomiidae was primarily represented by the species *Chauliodus macouni*, which accounted for 2.4% of the prey by number and 4.2% by mass (Table 1, Fig. 1).

A total of 605 lower beaks were identified, representing 15 families and at least 26 species of cephalopods. The highest contribution of cephalopod prey by weight was represented by the Enoploteuthidae family (28.2%). Enoploteuthid squid were present in nine of the eleven stomachs examined and represented 35.5% of the prey contribution by number. Within this family, *Enoploteuthis* sp. *cf. E. jonesi* adults with estimated dorsal mantle lengths ranging between 86 and 156 mm represented 16.3% of the contribution by mass and 5.9% by number (Fig. 2). *Abralia trigonura* specimens with estimated dorsal mantle lengths between 95 and 164 mm contributed 7.8% by number and 5.9% by mass and *Abraliopsis* sp. with dorsal mantle lengths between 38 and 83 mm contributed 19.5% by number and 2.3% by mass to diet (Fig. 2). The Cranchiidae family was represented in 4 of the 11 stomachs examined. Cranchiidae accounted for 11.4% of the prey contribution by number and 8.0% by mass, where *Megalocranchia* sp. *cf. M. fisheri* with estimated dorsal mantle lengths of 52–365 mm contributed the most by number (10.6%) and by mass (5.3%) (Fig. 2). The Cycloteuthidae family represented 13.5% of the prey contribution by mass and 6.6% by number and was represented in 6 of the 11 stomachs examined. Thirty-one *Cycloteuthis sirventi* juveniles were present among four of the stomachs, accounting for 9.8% of the mass contribution in this family. A single diamond squid, *Thysanoteuthis rhombus*, with an estimated dorsal mantle length of 429 mm and weight of 2,249 g was found in one of the melon-headed whale stomachs and accounted for 5.7% of the total prey mass. An unknown species of onychoteuthid, *Onychoteuthis sp.*, was present in 9 of the 11 stomachs examined but contributed only 4.5% by mass and 4.5% by number. With the exception of the Enoplotheuthidae, Onychoteuthidae, and Cycloteuthidae families, no other cephalopod families were represented in more than half of the stomachs examined.

A total of 519.1 h of dive and surfacing data were obtained from three melon-headed whales (Table 2). The tagged Kohala resident animals had been documented on multiple occasions prior to and posttagging. PeTag014, identified as HIPe1496 in the CRC photo-identification catalog, was first identified in 2006 and has been documented 10 times since, including when it was tagged in October 2011, and most recently in 2012. PeTag017, identified as HIPc1495 in the catalog, was first identified in 2005 and has been documented on 11 occasions since, including when it was tagged in 2012 and most recently in 2015. This individual had been previously biopsied and was genetically identified as a male. The Hawaiian Island individual (PeTag021) was not distinctive and had not been previously documented.

Table 1. Melon-headed whale *Peponocephala electra* prey species identified from stomach contents of 11 individuals examined in the Hawaiian Islands

	Minimum number of prey represented	Frequency by number	Occurrence	Estimated mean prey length (mm)[a]	Estimated mean prey weight (g)	Estimated contribution by mass (g)	Estimated contribution by mass (%)
Totals	783	100	11			39,170.9	100
Fish	178	22.7	5			5,411.1	13.8
Microstomatidae							
Nansenia sp.	1	0.1	1	84.4	5.2	5.2	<0.1
Gonostomatidae							
Gonostoma elongatum	7	0.9	1	145.5	7.9	55.3	0.1
Phosichthyidae							
Woodsia nonsuchae	5	0.6	2	76.0	8.0	40.0	0.1
Stomiidae	21	2.7	2			1,904.3	4.9
Chauliodus macouni	19	2.4	2	163.6	86.6	1,645.4	4.2
Astronesthes sp. *cf. A. indica*	1	0.1	1	123.0	158.4	158.4	0.4
Borostomias sp.	1	0.1	1	145.0	100.5	100.5	0.3
Scopelarchidae							
Scopelarchus sp.	3	0.4	1	269.0	147.8	443.4	1.1
Myctophidae	128	16.3	4			2,587.85	6.6
Ceratoscopelus warmingii	5	0.6	1	70.0	6.1	30.5	<0.1
Diaphus garmani	5	0.6	3	42.0	0.85	4.25	<0.1
Diaphus fragilis	14	1.8	1	113.7	26.6	372.4	1.0
Diaphus bertelseni	5	0.6	1	84.4	10.0	50.0	<0.1
Diaphus chrysorhynchus	2	0.3	1	67.4	4.9	9.8	<0.1
Diaphus brachycephalus	1	0.1	1	59.4	3.1	3.1	<0.1
Diaphus sp. (eroded)	2	0.3	2		4.9	9.8	<0.1
Hygophum proximum	1	0.1	1	41.8	2.0	2.0	<0.1
Lampadena urophaos	59	7.5	4	134.4	17.3	1,020.7	2.6
Lampadena yaquinae	1	0.1	1	128.6	14.3	14.3	<0.1

(Continued)

Table 1. *(Continued)*

	Minimum number of prey represented	Frequency by number	Occurrence	Estimated mean prey length (mm)[a]	Estimated mean prey weight (g)	Estimated contribution by mass (g)	Estimated contribution by mass (%)
Lampanyctus nobilis	21	2.7	2	137.1	43.7	917.7	2.3
Nannobrachium hawaiiensis	1	0.1	1	136.8	24.8	24.8	<0.1
Myctophum lychnobium	1	0.1	1	90.0	14.8	14.8	<0.1
Myctophum brachygnathum	1	0.1	1	74.8	7.7	7.7	<0.1
Notoscopelas resplendens	2	0.3	2	66.0	3.4	6.8	<0.1
Nannobrachium sp.	4	0.5	2	136.8	24.8	99.2	0.3
unident. Myctophidae	7	0.9	4				
Neoscopelidae							
Neoscopelus macrolepidotus	1	0.1	1	77.0	9.5	9.5	<0.1
Paralepididae							
Sudis atrox	2	0.3	1	196.0	127.0	254.0	0.7
Melamphaidae							
Scopelogadus mizolepis	5	0.6	1	104.3	22.3	111.5	0.3
unidentified teleost	1	0.1	1				
Cephalopods	605	77.3	11			33,759.8	86.2
Lycoteuthidae							
Lycoteuthis sp.	12	1.5	2	139.2	46.3	555.6	1.4
Pyroteuthidae							
Pyroteuthis addolux	13	1.7	4	45.7	3.9	50.7	0.1
Enoploteuthidae	278	35.5	9			11,043.7	28.2
Enoploteuthis sp. *cf E. jonesi*	46	5.9	7	123.5	138.8	6,384.8	16.3
Enoploteuthis sp.	18	2.3	4	101.4	83.8	1,508.4	3.9
Abralia trigonura	61	7.8	3	118.6	37.1	2,263.1	5.8
Abraliopsis sp.	153	19.5	6	55.3	5.8	887.4	2.3

(Continued)

Table 1. *(Continued)*

	Minimum number of prey represented	Frequency by number	Occurrence	Estimated mean prey length (mm)[a]	Estimated mean prey weight (g)	Estimated contribution by mass (g)	Estimated contribution by mass (%)
Octopoteuthidae	19	2.4	5			2,253.4	5.8
Octopoteuthis nielseni	17	2.2	4	120.8	126.6	2,152.2	5.5
Taningia danae	2	0.3	1	87.1	50.6	1,01.2	0.3
Pholidoteuthidae							
Pholidoteuthis massyae	7	0.9	3	154.4	167.2	1,170.4	3.0
Onychoteuthidae	41	5.2	9			3,197.5	8.2
Callimachus youngorum	1	0.1	1	110.9	50.3	50.3	0.1
Onychoteuthis sp.	35	4.5	9	110.9	50.3	1,760.5	4.5
Onychoteuthis sp. *cf. O. banksii*	2	0.3	1	270.0	660.5	1,321.0	3.4
Onykia sp.	3	0.4	1	4.7	21.9	65.7	0.2
Chtenopterygidae							
Chtenopteryx sicula	5	0.6	3	60.3	23.7	118.5	0.3
Histioteuthidae	30	3.8	4			1,636.0	4.2
Stigmatoteuthis hoylei	10	1.3	4	61.9	101.3	1,013.0	2.6
Histioteuthis oceani	5	0.6	2	49.4	39.1	195.5	0.5
Histioteuthis sp.	15	1.9	4	27.4	28.5	427.5	1.1
Ommastrephidae	6	0.8	4			1,365.0	3.5
Nototodarus hawaiiensis	2	0.3	1	156.4	180.3	360.6	0.9
Sthenoteuthis oualaniensis	4	0.5	3	146.3	251.1	1,004.4	2.6
Thysanoteuthidae							
Thysanoteuthis rhombus	1	0.1	1	429.0	2248.6	2,248.6	5.7
Cycloteuthidae	52	6.6	6			5,304.8	13.5
Cycloteuthis sirventi(juveniles)	31	4.0	4	135.0	123.5	3,828.5	9.8

(Continued)

Table 1. *(Continued)*

	Minimum number of prey represented	Frequency by number	Occurrence	Estimated mean prey length (mm)[a]	Estimated mean prey weight (g)	Estimated contribution by mass (g)	Estimated contribution by mass (%)
Discoteuthis laciniosa	21	2.7	3	100.2	70.3	1,476.3	3.8
Chiroteuthidae	36	4.6	4			1,028.4	2.6
Chiroteuthis picteti	32	4.1	4	99.6	31.8	1,017.6	2.6
Grimalditeuthis bonplandi	4	0.5	1	26.0	2.7	10.8	<0.1
Mastigoteuthidae	8	1.0	3			669.5	1.7
Magnoteuthis pyrodes	5	0.6	2	122.5	79.0	395.0	1.0
Magnoteuthis microlucens	3	0.4	1	124.7	91.5	274.5	0.7
Cranchiidae	89	11.4	4			3,116.5	8.0
Megalocranchia sp. *cf. M. fisheri*	83	10.6	4	147.7	25.1	2,083.3	5.3
Cranchia scabra	6	0.8	1	63.5	172.2	1,033.2	2.6
Ocythoidae							
Ocythoe tuberculata (juvenile)	1	0.1	1	14.9	1.2	1.2	<0.1
Unidentifiable lower beak	7	0.9	1	9.1			

[a]Prey length measurements are standard length for fish and dorsal mantle length for cephalopods.

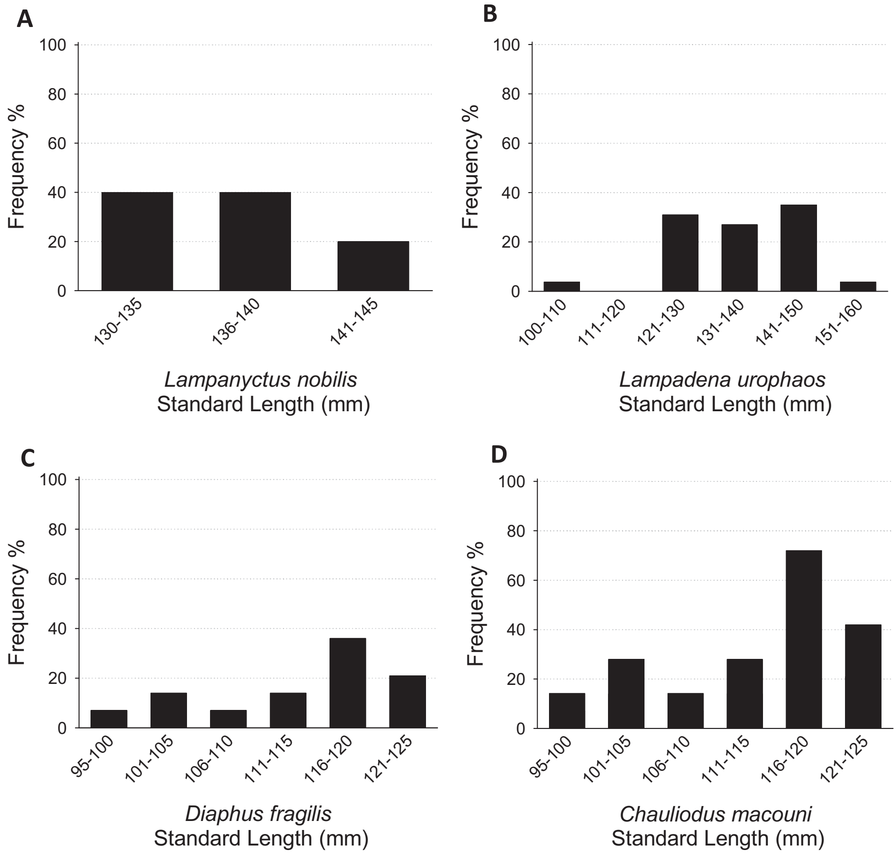

Figure 1. Frequency distribution of estimated standard length of (A) *Lampanyctus nobilis*, (B) *Lampadena urophaos*, (C) *Diaphus fragilis*, and (D) *Chauliodus macouni* combined for the five melon-headed whales where fish remains were present among the stomach contents.

During the period of tag attachments the two Kohala resident individuals remained close to where they were tagged (median distances of 13.1 and 14.8 km for PeTag014 and PeTag017, respectively), in shallow water off the northwest coast of Hawai‘i Island. The median depths at tagged animal locations were 621 m (PeTag014, n = 157 locations) and 437 m (PeTag017, n = 276 locations). The individual from the Hawaiian Islands population (PeTag021) ranged more broadly off the west and south side of the island (median distance from tagging location of 47.7 km), and median depth at tagged animal locations was 3,397 m (n = 166 locations).

All three individuals had similar diving patterns, with few dives >30 m during the day, more frequent dives >30 m at night, and longer median and maximum dive durations and deeper median and maximum depths at night than during the day (Table 2, Fig. 3, S1). Median depths of dives >30 m during the day ranged from 33 m to 34.5 m, while during the night they ranged from 219.5 m to 247.5 m.

Based on our data, the prey of Hawaiian melon-headed whales consists of at least 51 different species that represent a wide diversity of cephalopods and fish. When considering prey by number or mass, the cephalopod contribution to diet was greater than that

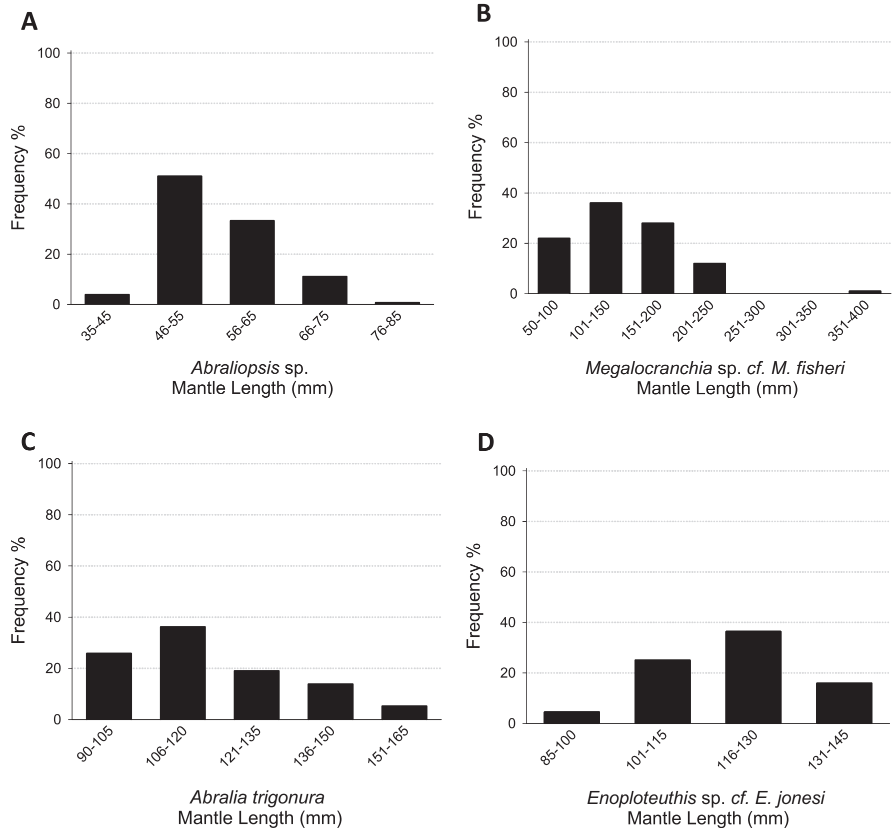

Figure 2. Frequency distribution of estimated mantle length of (A) *Abraliopsis* sp., (B) *Megalocrancia* sp. *cf. M. fisheri*, (C) *Abralia trigonura* and (D) *Enoploteuthis* sp. *cf. E. jonesi* combined for the 11 melon-headed whales examined.

of fish. Of the 11 stomachs examined, only 5 contained fish, while all 11 contained cephalopods. When comparing prey contribution by number and mass, fish comprised a greater proportion of the diet by number (22.7%) as compared to 13.8% by mass, which suggests that when melon-headed whales forage on fish, the fish are of a large number but small size. For example the most abundant species of fish, *L. urophaos*, ranged only 100–150 mm in size. A minimum of 59 individuals were found in only four of the whale stomachs, accounting for a greater contribution by number compared to mass.

The majority of the Hawaiian melon-headed whale diet was comprised of a high diversity of cephalopods. Prey identification of 783 prey items from the eleven Hawaiian melon-headed whales was compared to the only prior published reports of melon-headed whales in Hawai'i and South Africa, with a maximum identification of six prey items from single individuals (Best and Shaughnessy 1981, Sekiguchi *et al*. 1992, Clarke and Young 1998). Only one squid from the family Ommastrephidae was common between our findings and those from one of the South African whales (Best and Shaughnessy 1981). From Hawai'i, the species *Bathyteuthis abyssicola* and a species of *Galiteuthis* (reported as *Teuthowenia* sp.) were not among the prey identified in the current study (Clarke and Young 1998) but we do not consider the absence of these two

Table 2. Details on diving behavior from depth-transmitting LIMPET satellite tags deployed on melon-headed whales in Hawaiian waters. Tags transmit a single maximum dive depth for each dive. Median values reported are of the maximum dive depths, while maximum value is the deepest dive recorded during the day- and night-time periods

Tag #	Stock[a]	# hours dive and surfacing data total	# hours day time	# hours night time	# dives day time ≥ 30 m	# dives night time ≥ 30 m	Median/ maximum depth day (m)	Median/ maximum depth night (m)	Median/ maximum duration day (min)	Median/ maximum duration night (min)
PeTag014	KR	196.8	49.9	147.1	16	468	33.0/79.5	219.5/391.5	4.18/6.92	8.25/10.65
PeTag017	KR	226.3	91.9	134.4	46	564	34.5/179.5	247.5/471.5	4.70/7.43	8.53/11.73
PeTag021	HI	96.0	22.8	73.2	55	220	33.0/73.5	227.5/407.5	4.60/6.93	7.58/10.00
Total		519.1								

[a]KR = Kohala resident stock, HI = Hawaiian Islands stock.

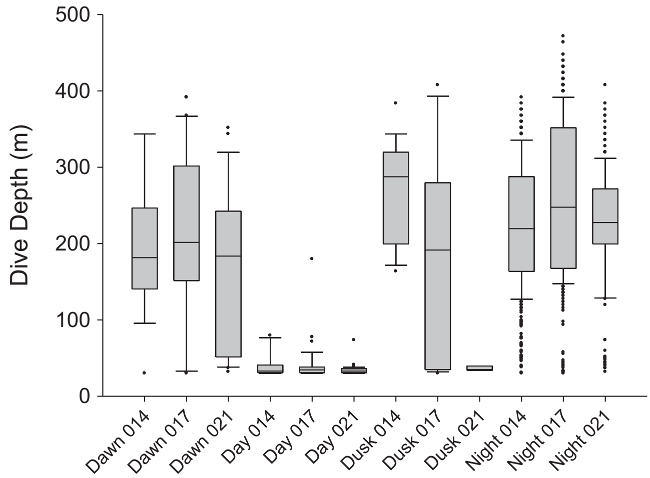

Figure 3. Dive depths for three individual melon-headed whales tagged with depth transmitting LIMPET satellite tags (Tag ID's: 014, 017 and 021), showing differences by day and night and during crepuscular periods. The horizontal lines within the boxes represent the median of the maximum depths for each dive, the bottom and top of the boxes represent the 25th and 75th percentiles, while the upper and lower lines represent the 10th and 90th percentile. Values below the 10th percentile and above the 90th percentile are represented by •.

species to be significant as they were represented by only single beaks obtained from a single stomach sample collected over 30 yr ago.

We did not examine stomach content remains from any melon-headed whales from the Kohala resident population (although two of the tagged individuals were from that population), and although we cannot directly address whether the two populations have differing diets, the diel diving behavior among the three tagged individuals was similar. The only exception was shallower diving at dusk in the Hawaiian Islands individual but this may be an artifact of a much smaller sample of dive depths obtained at dusk from this individual. The similarity in dive data obtained from the two tagged Kohala resident animals and the tagged individual representing the Hawaiian Islands population suggests that while they have known differences in preferred habitat, how they are using the water column in the slope and offshore habitats may be similar. Based on sighting data, the Kohala resident population inhabits significantly shallower depths (median depth 381 m) compared to the Hawaiian Islands population (median depth 1,662 m) (Aschettino *et al*. 2012). This is consistent with considerably shallower tag locations for the Kohala resident animals with median depths near 500 m compared to a median depth of tag locations exceeding 3,000 m in the Hawaiian Islands individual. While the dive behavior data does not suggest niche partitioning between the two populations, a mesopelagic boundary community comprised of a distinct species composition that is found between 400 and 700 m around the Hawaiian Islands (Reid *et al*. 1991) that is important to spinner dolphin (*Stenella longirostris)* foraging (Benoit-Bird and Au 2003, Benoit-Bird 2004, Au and Benoit-Bird 2008) may also contribute to the diet of the Kohala resident population. The main Hawaiian Islands population forages almost exclusively on the oceanic mesopelagic community as only 3% of the prey contribution by mass in this study was represented by species of fish and squid described for the Hawaiian mesopelagic boundary community (Reid *et al*. 1991). An opportunity to examine stomach content remains from Kohala resident animals is needed to clarify the diet composition in this population, given the differences in sighting depths and home range.

The tag data demonstrated that melon-headed whales use near-surface waters primarily during daylight hours and deeper waters during the night. Dive rates for the two Kohala resident individuals increased at dusk, and all three individuals had high diving rates throughout the night and at dawn, with average dive depths more than four times deeper at night than during the day. We explored the relationship between dive depth and moon illumination fraction but found that time of day is the driving factor behind dive depths. Melon-headed whale diving follows a strong diel pattern (Fig. 3), with deep dives occurring when prey has vertically migrated to within the upper 400 m of the water column. These findings are consistent with behavioral and acoustic data from melon-headed whales inhabiting oceanic islands that have previously suggested a concentration of foraging activity at night (Brownell *et al*. 2009, Baumann-Pickering *et al*. 2015).

The diving behavior results are consistent with the stomach content analyses. Fish presence among the stomachs was dominated by various species of lanternfish. They were documented in four of the five stomachs that had fish remains with 15 different species represented. Lanternfish typically undergo diel vertical migrations and are found at greater depths during the day than at night. Hawaiian trawl data indicates significantly deeper daytime depths for the three most abundant species of lanternfish present in the stomachs. In the Hawaiian Islands, *Diaphus fragilis* is found at depths of 520–600 m during the day but in only 15–125 m at night (Mundy 2005). *Lampadena urophaos* is found in waters as shallow as 95 m at night but at a minimum depth of 500 m during the day (Clark 1973, Reid *et al*. 1991) and *L. nobilis* has been found to range in depths from 150 m to 500 m at night compared to daytime depths only near the deep end of this range (Mundy 2005). It is unknown at what depth melon-headed whales are ingesting lanternfish prey, but the dive depth data obtained from the three individuals suggests that foraging by melon-headed whales occurs during the dawn, dusk, or nighttime hours at the relatively shallower depths. The daytime depths, where several of the most common lanternfish identified from the stomach contents are found, are deeper than the maximum dive depths recorded for the whales during the day (Clark 1973, Reid *et al*. 1991, Mundy 2005). Similar to the most abundant fish prey among the stomach content remains, prey depth is deeper during the day for the families of cephalopods that were most frequent by number in our sample. The Enoploteuthidae and Cycloteuthidae families are typically found between 300 and 600 m during the day and in the upper 200 m at night (Roper and Young 1975).

Combined our findings demonstrate that melon-headed whales concentrate foraging activity at night while eating a diverse diet of both cephalopods and fish associated with the deep scattering layer. This indicates that the epipelagic and mesopelagic zones are important foraging grounds for Hawaiian melon-headed whales and signifies an important milestone in understanding habitat utilization by this relatively understudied whale.

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Supporting Information

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Table S1. Melon-headed whales stranded in the Hawaiian Islands between 1985 and 2017 where stomach contents were examined.

Figure S1. Example dive profiles showing dives greater than 30 m for the tagged Kohala resident individuals; (A) Pe014 and (B) Pe017. Periods with dives shallower than 30 m are indicated as a line at 0 m, and periods with missing data indicated with a broken line.