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Behavior and inter-island movements of satellite-tagged humpback whales in Hawaiʹi, USA

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ABSTRACT: Humpback whales *Megaptera novaeangliae* encountered off the island of Kauaʹi, Hawaiʹi, USA, in 2017, 2018, and 2019 were photo-identified, and 19 whales were equipped with satellite telemetry tags to track their inter-island movements and use their movement behavior to estimate when and where the whales changed their behavior from breeding to migration. Fluke photographs were matched in the online photo-ID repository HappyWhale to track individual observation histories and movement records within the islands and on their way to their feeding grounds. Tag attachment periods were relatively short, with transmissions lasting 1.6–12.5 d. Movement behavior models were developed using hidden Markov models; whales in proximity to land were found to remain in area-restricted search or an intermediate behavior state, while whales that moved between islands or offshore tended to transition into directed travel behavior. Movement patterns and routes were similar between animals and across years, particularly when they transited between Kauaʹi and Oʹahu and began migrating from Niʹihau to the first seamounts of the northwestern Hawaiian Islands. Dive data were also analyzed in association with the movement behavior. Whales that transited between Kauaʹi and Oʹahu as well as those in offshore waters conducted repeated series of deep (>100 m) dives only at night, whereas whales that remained in nearshore waters conducted less frequent and less deep dives day or night. These results provide insight into the inter-island movements and behavior of humpback whales while on the Hawaiian breeding grounds as well as where and how their behavior transitioned into migration.

KEY WORDS: Humpback whales · Satellite tagging · Movement behavior · Dive behavior · Hawaiʹi

1. INTRODUCTION

Due to long-term efforts to study global humpback whale *Megaptera novaeangliae* populations (e.g. Smith et al. 1999, Calambokidis et al. 2001, Allen et al. 2020), this species has been a conservation success story, with 9 of 14 distinct population segments delisted from the US Endangered Species Act in 2016 (NOAA 2016), including the Hawaiian population. However, these populations are still highly susceptible to anthropogenic impacts such as fishing gear (Mazzuca et al. 1998, Johnson et al. 2005) and navy sonar (Sivle et al. 2016) as well as climate fluctuations (Cartwright et al. 2019, Kügler et al. 2020). When these events coincide, results can be catastrophic, such as in the case of the North Pacific marine heatwave driving humpback whales closer to shore where they entangled in fishing gear in record numbers (Santora et al. 2020). Therefore, continued work is needed to fill in the gaps in our knowledge of

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humpback whale behavior, particularly during the dynamic period when whales transition from breeding to migratory behavior, as new insights are changing our understanding of humpback whale behavior during this period (e.g. Derville et al. 2020).

The behavior of eastern North Pacific humpback whales on their Hawaiian breeding grounds has been well documented, particularly in the waters off Maui, where the highest abundance of whales occurs (Baker & Herman 1981). However, whether they transition into their migration from a specific area on their breeding grounds and how their behavior might change during that transition is less well understood. As in other global humpback whale populations, these whales migrate long distances between winter breeding grounds at lower latitudes (Darling & McSweeney 1985, Baker et al. 1986, Craig & Herman 1997, Calambokidis et al. 2001) and summer feeding grounds at higher latitudes (Calambokidis et al. 2001, Stevick et al. 2003, Rasmussen et al. 2007, Burns et al. 2014). Females without calves or juveniles are the first to arrive and first to leave, followed by males and then females with calves (Dawbin 1966, Craig et al. 2003). Individual whales may only stay on their breeding grounds for a few weeks (e.g. Herman et al. 2011), with females with calves staying the longest (up to 5 wk; Mobley & Herman 1985, Craig & Herman 1997). Palacios et al. (2019) found a minimum residence time (from tagging to departure) of individuals in the main Hawaiian Islands of 14.8 d, similar to the 12.9 d found by Mate et al. (2019), 13.6 d found by Lagerquist et al. (2008), and 11 d for males found by Herman et al. (2011). Humpback whales are present in the waters off all the main Hawaiian Islands; sightings and acoustic detections have also occurred in the northwestern Hawaiian Islands, suggesting that region may also be a part of the wintering grounds (Johnston et al. 2007, Lammers et al. 2011).

While the same humpback whales return to the Hawaiian Islands year after year, their movements between islands within and across years have not been well established. Some movement of individuals has been observed between the main Hawaiian Islands within a breeding season (Craig & Herman 1997, Cerchio 1998, Cerchio et al. 1998, Mate et al. 1998, Calambokidis et al. 2001), although Calambokidis et al. (2001) hypothesized that humpback whales were more likely to be observed off different islands in different years rather than within a season. However, some site fidelity to specific island regions across years has also been observed (Cerchio et al. 1998). Further, Craig & Herman (2000) found more females with calves off Maui than Hawai'i Island, indicating reproductive status may also play a role as to where whales may occur. While Cerchio et al. (1998) found animals to move in either direction within the main islands with equal probability, Baker & Herman (1981) suggested whales might be taking advantage of a clockwise gyre current north of O'ahu and Kaua'i, moving northwesterly through the islands to save energy. A general northwestern movement has also been observed in more recent tagging work (Mate et al. 2019, Palacios et al. 2019), although one male did travel east. Furthermore, 2 whales tagged in Alaskan waters both entered the Hawaiian breeding grounds at the island of Hawai'i, the most southeasterly island of the archipelago, and then moved northwest through the islands (Palacios et al. 2019), also supporting a northwesterly trend.

Similarly, although humpback whale behavior on breeding and foraging grounds has been well documented, their migratory movements are less established. Several studies have tracked migrating humpback whales along migratory routes between their feeding and breeding grounds through telemetry tags and have found animal movement when leaving the breeding grounds to be highly directed (Abileah et al. 1996, Mate et al. 1998, Norris et al. 1999, Lagerquist et al. 2008, Gales et al. 2009, Horton et al. 2011, 2017, Kennedy et al. 2014). However, there may be some transition in behavior before humpback whales begin their migration. For example, studies off New Caledonia have found several humpback whales spending time at shallow seamounts near the breeding ground before beginning directed travel (Garrigue et al. 2010, Derville et al. 2020), and another found humpback whales from the Revillagigedo Archipelago breeding ground visited other wintering areas in Mexico before heading northwest (Lagerquist et al. 2008). Similarly, Kennedy et al. (2014) found some humpback whales visited seamounts along their migration route in the Atlantic.

Some telemetry studies have also documented diving behavior, although many of these have been focused on foraging behavior (e.g. Goldbogen et al. 2008, Friedlaender et al. 2009, Calambokidis et al. 2019). Derville et al. (2020) found shallow (<80 m), long-duration dives to be square-shaped, while deep dives were U-shaped and occurred in series. Baird et al. (2000) found dives deeper than 100 m to occur at least once an hour, and more often in deeper water, while whales diving between 10 and 30 m spent some time motionless and therefore may have been singing. Movement behavior on breeding grounds and over seamounts is most often classified as area-restricted search (ARS), with slower swimming speeds and localized movements (Garrigue et al. 2010, Kennedy et al. 2014, Trudelle et al. 2016, Henderson et al. 2019). Once whales move offshore into deeper water, swim speeds increase and movement becomes more directed, classified as transit or travel (Kennedy et al. 2014, Trudelle et al. 2016, Palacios et al. 2019). Palacios et al. (2019) defined a 50 km buffer around the main Hawaiian Islands and found that once humpback whales moved offshore of that buffer they were generally engaged in directed travel, committed to their migration to the feeding grounds.

The recent development of an online repository and automated fluke photograph matching algorithm (HappyWhale, www.happywhale.com; Cheeseman et al. 2021) has enabled humpback whale researchers to upload and compare fluke photographs. This information can supplement telemetry data when investigating where humpback whales migrate within and across years. This analysis can include both the broad scales of the feeding and breeding grounds to which the whales travel as well as the finer spatial scale of where the animals may visit within those grounds.

While humpback whales have been well studied in the Maui Nui region of Hawai'i (the 4-island region of Maui, Kaho'olawe, Lana'i, and Moloka'i), only a few studies have been conducted on humpback whales off Kaua'i and Ni'ihau. The availability of Mote receivers on 3 Hawaiian Islands and the use of FastLoc GPS tags enable the detection of finer-scale location data within the main islands than has been previously obtained with Argos satellite tracking technology. This has facilitated the examination of movement and dive behavior of satellite-tagged humpback whales encountered off Kaua'i. In addition, this study investigated what movement and dive behavior can tell us about habitat use and the inter-island movements of whales as well as their behavior as they move beyond the breeding grounds. These results provide valuable information on humpback whale behavior as they transition to migration, with insights that could not be observed through traditional visual observation-based studies.

2. MATERIALS AND METHODS

Vessel-based photo-identification and satellite tagging of humpback whales *Megaptera novaeangliae* were conducted on 17–24 March 2017, 4–12 February 2018, and 21–26 March 2019 in the waters off Kaua'i and Ni'ihau (see Fig. 1). Nonsystematic surveys were conducted in a 6.7 m rigid-hulled inflatable boat. Data on the location and time of each sighting, whale behavior, individual reproductive roles, presumed sex based on behavior, and group size were collected along with environmental data (e.g. Beaufort sea state, wind speed and direction, swell size, cloud cover). Individual reproductive roles included singletons (that may or may not also be singing), members of a dyad, or members of a competitive pod, including the female or nuclear animal, the primary escort, and secondary escorts (e.g. Tyack & Whitehead 1983). In addition, identification photos of the left- and right-side dorsal fin and tail fluke were taken when possible. Photos were taken using one of 3 types of digital SLR cameras (Canon 50D, 7D, or 7D Mark II) with a 100–400 mm zoom lens. Additional details on field methods, focal follows, and tagging approaches can be found in Henderson et al. (2019). Fluke photographs were uploaded to the online repository at HappyWhale (Cheeseman et al. 2021).

Satellite-monitored, location–dive tags (Wildlife Computers; SPLASH10-292 and SPLASH10 F-333) in the 'low-impact minimally percutaneous external-electronics tag' (LIMPET) configuration were used for tagging. The 2017 tags were Argos satellite-only (SPLASH10-292), while the tags used in 2018 and 2019 were enhanced with Fastloc-GPS (SPLASH10-F-333) to improve location accuracy and frequency, particularly when the whales were within line-of-sight of one of 3 Wildlife Computers Mote receivers (e.g. Jeanniard-du-Dot et al. 2017) installed on Kaua'i, Ni'ihau, and O'ahu. Tags were attached externally to the skin (see Andrews et al. 2019) on or near the whale's dorsal fin with two 6.8 cm sterilized surgical-grade titanium sub-dermal darts with 6 backward-facing petals, deployed with a DanInject JM25 pneumatic projector (DanInject). Tags were programmed to transmit 18 to 21 h d^{-1} (based on satellite availability in the area each year) with up to 750 transmissions d^{-1}. The tag's series function was used to record data on depth using a sampling interval of 75 s. This sampling interval creates unintended variability in actual maximum depth and duration. Dive thresholds were set to deeper than 5 m and longer than 30 s. Data gaps in both location and dive data were expected due to multiple factors affecting message transmittal and reception.

2.1. Satellite tag data analysis

Track positions were estimated using the Argos Data Collection and Location System with a Kalman filtering algorithm and were further screened using the Douglas-Argos Filter version 8.50 (Douglas et al. 2012) available in Movebank (https://www.movebank.org). Additional manual filtering was conducted to remove erroneous locations appearing on land. GPS locations were removed if they had residual deviance greater than 35 or greater than 10 min time errors. Both Argos and GPS positions were used when available. GPS location errors were assumed to be 500 m if 4 satellites reported and 50 m if 5 or more satellites reported (e.g. Hazel 2009, Dujon et al. 2014), while Argos location errors could be greater than 10 km (Costa et al. 2010). Therefore, during a final manual inspection of the data, some Argos positions were discarded if they were an unrealistic distance (i.e. requiring >15 km h^{-1} travel speed; based on maximum travel speeds observed by Noad & Cato 2007) from an adjacent GPS location occurring within 5 min.

The filtered locations were fitted with a correlated random walk to produce interpolated tracks at 1 position h^{-1} using the package 'crawl' (Johnson 2013, Johnson & London 2018) in R v.4.1.0 (R Core Team 2019). Tracks were also interpolated in 10 min increments in order to estimate the water depth along the track based on the ETOPO1 1-arc global relief data (https://www.ngdc.noaa.gov/mgg/global), gridded using the R package 'sp' (Pebesma & Bivand 2005, Bivand et al. 2013), and mapped along the track using the R package 'adehabitatLT' (Calenge 2006). The track movement behavior was determined using a discrete-time hidden Markov model (HMM) based on a Gamma distribution of the mean and standard deviation of step length (Euclidean distance between successive locations, in m) and the concentration (i.e. an indication of how concentrated the angle values are around the mean) of the wrapped Cauchy distribution of the turning angle (the change in bearing between locations) between interpolated hourly locations using the package 'momentuHMM' (McClintock & Michelot 2018). The HMM included 3 behavioral states: ARS (which typically indicates milling or foraging but may also be indicative of social behavior); an intermediate or transition behavior; and directed travel or transit (Henderson et al. 2019). The Viterbi algorithm was used to compute the most likely sequence of those 3 underlying states for each track (Zucchini et al. 2016, McClintock & Michelot 2018). In addition, other covariates in the state transition probabilities were tested for inclusion in the HMM: the cosinor function (used to incorporate cyclical behavior) of the hour of the day, water depth, and a binary factor indicating whether animals were outside the 50 km buffer established by Palacios et al. (2019). Furthermore, each variable was tested in a design matrix that indicated how each parameter influenced the state-dependent distribution of steps (McClintock & Michelot 2018). The final model chosen had the lowest Akaike information criterion (AIC) score. It should be noted that the increased resolution of GPS locations in 2018 and 2019 when the animals were in proximity to the Mote receivers could lead to improved classification of the ARS state in those areas and could create a nearshore bias in ARS classification.

Dive behavior was analyzed using the R package 'diveMove' (Luque 2007, Luque & Fried 2011), which determines the number of dives and dive depths (median, mean, and maximum), and categorizes the start of the descent, end of the descent/start of bottom time, end of bottom time/start of ascent, and total dive duration. From those data, the times and distances of descent and ascent periods can be extracted and descent and ascent rates can be calculated. Note that since dive time series data are only recorded every 75 s, these values are not exact and only represent the phase of the dive at each 75 s interval. Dives were also sorted by shape into square-, V-, or U-shaped dives based on the definitions given by Wildlife Computers (Square-shaped dives had bottom times of greater than 50% total dive time, V-shaped dives had bottom times less than 20% of total dive time, and U-shaped dives had bottom times between 20 and 50% of total dive time; e.g. Derville et al. 2020) and by depth category, with shallow dives <50 m and deep dives >100 m.

Generalized estimating equations (GEEs) were fit to the dive data using the R package 'geepack' (Højsgaard et al. 2006, 2022), with a Gamma distribution with a log link and an AR1 correlation structure. Residuals were checked for normality using a density plot. GEEs were used to account for the spatiotemporal correlation among the dive variables as well as inter-individual and inter-annual variability. Maximum dive depth was chosen as the response variable, while dive duration, descent rate, ascent rate, water depth, and start hour were included as continuous explanatory variables and dive shape (U, V, or square), diel period (daytime vs. nighttime), and whether the animal was further than 50 km offshore included as categorical explanatory variables; animal ID was used as the blocking unit. A sequential ANOVA was run on the GEE model output to facilitate model selection by determining which variables were statistically significant.

3. RESULTS

In total, 23 d of effort were conducted across 3 yr. During that time, 209 groups of humpback whales *Megaptera novaeangliae* were encountered, with average group sizes of 2.3, 1.8, and 2.0 in 2017, 2018, and 2019, respectively, highlighting the prevalence of dyads off Kaua'i. A total of 259 unique dorsal fins were photographed, along with 188 unique flukes (with some overlap between those 2 categories). Within each field season, 2 to 12 whales were resighted, but no animals were resighted across years; 88 individuals were matched in HappyWhale to previous fluke photographs. The majority of these animals were found to forage in the Alaskan feeding grounds, with fluke matches from the Aleutian Islands, Gulf of Alaska, SE Alaska, and British Columbia (Fig. 1). However, 12 flukes were matched to Russian feeding grounds (11 from the Kamchatka peninsula and one from the Bering Sea), and 3 flukes were matched to Baja Sur Mexico. Eight of the Russian matches occurred in 2017, along with the matches to Mexico, while the remaining 4 matches to Russian occurred in 2018. There were no matches made to the Russian or Mexican feeding grounds in 2019. Within the Hawaiian Islands, most matches from other islands occurred across different years (e.g. sighted at another island, most frequently Maui, one year and sighted at Kaua'i in a different year). However, 5 animals were photographed within the same year. Four of these animals were photographed first at Kaua'i, then at either O'ahu (5 d later) or Maui (6 d and 33 d later), while one animal was photographed at Maui then at Kaua'i 21 d later.

A total of 19 whales were satellite tagged, the majority of which were suspected to be males based on their behavior in competitive pods or confirmed as males due to the absence of a hemispheric lobe from underwater video taken with a GoPro camera on a pole. The tagged female (presumed female based on her position as nuclear animal and behavior in a competitive pod; e.g. Tyack & Whitehead 1983, Pallsbøll et al. 1992) was confirmed to be a female from a genetic sample obtained by Whale Trust (Jones 2010, Henderson et al. 2021). Sixteen of the tagged animals were estimated to be adults based on their size; the other 3 appeared to be sub-adults. Nine animals were encountered in competitive pods, 5 were in presumed male–female dyads (e.g. Corkeron & Brown 1995) while 4 dyads were likely sub-adult or adult males based on behavior, and one was encountered alone. The tags lasted from 1.6 to 12.5 d, with individual tags lasting the longest in 2017 and the shortest in 2019. One tag only transmitted 3 times and was not included in subsequent analyses. Individual tag information is included in Table 1. Three of the tagged animals from 2017, 2 from 2018, and 4 from 2019 had resight information based on fluke matches in HappyWhale. Two of the 2017 whales (tag IDs 158569 and 164792) were observed on the Russian feeding grounds, with resights going back as far as 2010 and 2013, respectively. The third whale from 2017 was observed off Maui in 2004. One tagged whale (173784) with resight information from 2018 was observed on feeding grounds in the Gulf of Alaska 3 times starting in 2002. The other whale from 2018 (173786) was first sighted off Maui in 2008. The female (173791) from the competitive pod tagged in 2019 had been sighted in the Gulf of Alaska as early as 2005 and was also observed off Maui in that year. She was photographed off O'ahu 5 d after being tagged, along with the primary escort from that group, which is consistent with their tag track (Henderson et al. 2021). Two of the secondary escorts from the same competitive pod also had resight data; one (179029) was observed off Maui in 1998 and on SE Alaskan feeding grounds in 2019, while the other secondary escort (179030) had been seen off Maui multiple years since 2013 (the latest being 2020).

Three tagged whales traveled east to O'ahu (Fig. 2). Of these, 2 were a confirmed male and female

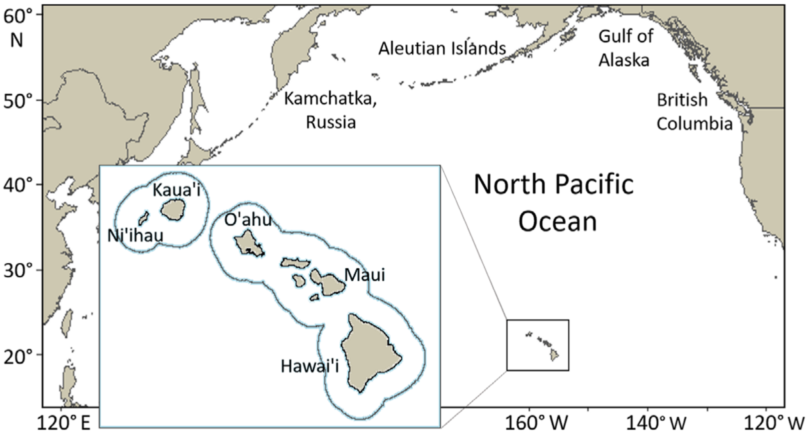

Fig. 1. North Pacific Ocean, with an inset map of the main Hawaiian Islands outlined with the 50 km buffer (the blue line around the Hawaiian Islands; this is a distance at which humpback whales are most likely to be on their migration to or from the feeding grounds). The feeding grounds of the North Pacific humpback whale population are labeled

Table 1. PTT ID and tagging, group, and individual information for all 19 tagged humpback whales. Travel direction and next island visited (NI: Ni'ihau; OH: O'ahu; KA: Kaua'i) are also included, along with any photo-ID match locations from Happy-Whale and the earliest year they were observed at that location. Date given as mo/d/yr; Time is Hawai'i standard time (HST); GoA: Gulf of Alaska. DY: dyad; CG: competitive group; SE: singleton/singer, secondary escort; PE: primary escort; FE: female/nuclear animal; na: not applicable

Tag ID	Time deployed		Last transmission		No. of days trans-mitted	Age class	Group information	Role (sex if known)	Travel direction	Photo-ID match location and earliest obs.
	Date	Time	Date	Time						
158569	3/19/17	10:45	3/21/17	16:00	2.3	Adult	DY	DY	West (NI)	Russia 2010[a] Maui 2017[b]
158570	3/20/17	09:29	3/26/17	10:32	6.0	Sub-adult	DY sub-adult males	DY	West (NI)	
158571	3/22/17	09:02	3/30/17	11:36	8.1	Sub-adult	Single animal	Singleton	West (NI)	
164790	3/22/17	15:47	3/25/17	14:35	3.0	Adult	CG of 5 animals	SE (male)	West (NI)	
164791	3/21/17	11:26	4/2/17	21:41	12.5	Sub-adult	DY sub-adult males	DY	West (NI)	Maui 2004[c]
164792	3/22/17	16:41	3/24/17	23:11	2.3	Adult	CG of 5 animals	SE (male)	West (NI)	Russia 2010[a]
164793	3/24/17	08:27	3/25/17	22:50	1.6	Adult	DY adult males, joined CG	DY/SE (male)	West (NI)	
173784	2/7/18	08:28	2/15/18	23:23	8.6	Sub-adult sub-adult males	DY	DY	West (NI)	GoA 2002[d]
173785	2/6/18	14:03	2/8/18	09:30	1.8	Adult	DY	DY	West (NI)	
173786	2/10/18	12:15	2/18/18	11:07	8.0	Adult	DY	DY	West (NI)	Maui 2008[c]
173787	2/11/18	11:49	2/13/18	22:14	2.5	Adult	DY	DY	West (NI)	
173788	2/12/18	11:37	2/18/18	06:25	5.8	Adult	CG of 5 animals	PE (male)	East (OH)	
173789	2/12/18	12:12	2/18/18	11:09	6.0	Adult	CG of 9 animals	SE (male)	West (NI)	
173790	3/21/19	09:49	3/24/19	23:21	4.4	Adult	CG of 6 animals	PE (male)	West (NI)	
173791	3/25/19	10:13	3/29/19	10:02	4.0	Adult	CG of 7 animals	FE (female)	East (OH)	SE Alaska 2005[e] Maui 2005[c] O'ahu 2019[f]
179027	3/24/19	09:52	3/26/19	02:40	1.7	Adult	DY	DY	na (KA)	
179028	3/25/19	10:31	4/1/19	20:48	7.4	Adult	CG of 7 animals	PE (male)	East (OH)	O'ahu 2019[f]
179029	3/25/19	11:57	4/1/19	11:07	7.0	Adult	CG of 7 animals	SE (male)	West (NI)	Maui 1998[g] SE Alaska 2019[h]
179030	3/25/19	11:26	3/28/19	15:58	4.2	Adult	CG of 7 animals	SE (male)	na (KA)	Maui 2013[g] Maui 2020[g]

[a]Russian Cetacean Habitat Project; [b]Ultimate Whale Watch; [c]M. Jones, Whale Trust (Jones 2010); [d]Rainbow Tours; [e]O. von Ziegesar, Winged Whale Research; [f]Atlantis Cruises; [g]J. Currie, Pacific Whale Foundation; [h]D. Rogers, Alaska Sea Adventures

(the female was confirmed with genetics, the male was confirmed by an underwater video) from 2019 that were tagged together in a competitive group and remained together for at least 4 d (Henderson et al. 2021). The third was a male from 2018 that had been a primary escort in another competitive pod. The tag duration of 2 additonal whales was too short to capture their movements beyond Kaua'i, although one male (a secondary escort, 173730) did circumnavigate the entire island before his tag stopped transmitting. The remainder of the whales traveled west to Ni'ihau. Among these, one began migrating northward from Ni'ihau, and the rest with tags still transmitting con-

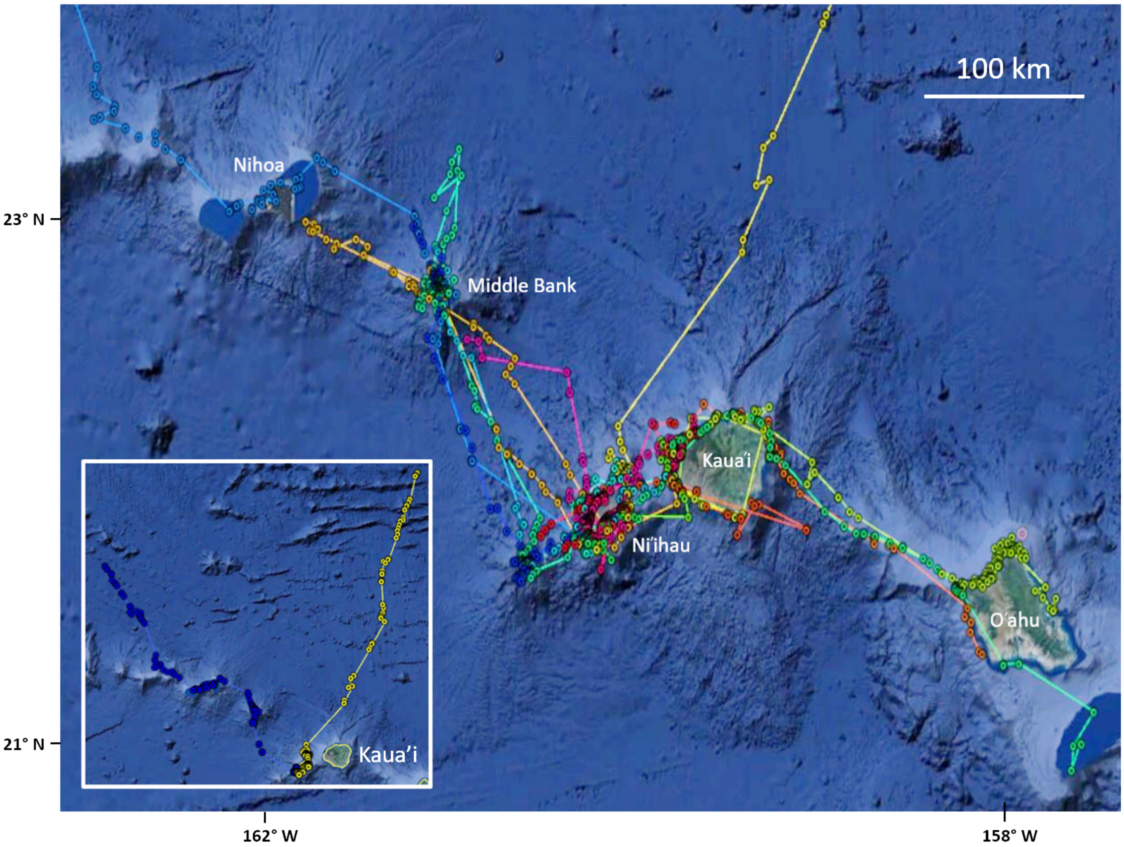

Fig. 2. All 19 satellite-tracked humpback whales, with an inset map of the 2 tracks that extend beyond the main Hawaiian Islands. Points are the raw, filtered Argos and GPS locations, connected by straight lines. Nihoa is a small island surrounded by reef; Middle Bank is a seamount

tinued traveling northwest from Ni'ihau moving between islands, surfacing reefs, and seamounts of the northwestern archipelago (Fig. 2). Only 5 whales moved outside of the 50 km buffer into offshore waters; their minimum residency time after tagging within the buffer was 1.21 to 8.42 d.

3.1. Movement behavior

The results of the HMMs for the 3 behavioral states based on step length and turning angle are as follows. The best fit HMM of the movement behavior that minimized the AIC score (Table S1 in the Supplement at www.int-res.com/articles/suppl/m685p197_supp.pdf) included habitat type (inshore vs. offshore) and time of day; both variables were also included in the design matrix of the state transition probabilities for step length (Fig. S1). As would be expected, mean step length and speeds were lowest for ARS and highest for directed travel (Table 2). Similarly, mean turning angles were largest for ARS and smallest (closest to zero) for directed travel. The step length for all 3 behavioral states was longer when the animals were offshore than when inshore, although the

Table 2. Counts (number of locations in interpolated tracks) of each behavioral state of humpback whales from all combined tag data, along with mean (±SD) values for step length, speed, and turning angle, and the percent of time within and outside the 50 km buffer spent in each state. ARS: area-restricted search

State	Count	Step length (m)	Speed (km h^{-1})	Turning angle	% Time nearshore	% Time offshore
ARS	624	689.6 ± 360.7	0.7 ± 0.4	−0.075 ± 1	29.5	25.0
Intermediate	918	2095.0 ± 891.7	2.1 ± 0.9	−0.017 ± 0.8	48.3	19.3
Directed travel	643	5754.2 ± 2166.8	5.8 ± 2.2	0.008 ± 0.6	22.1	55.7

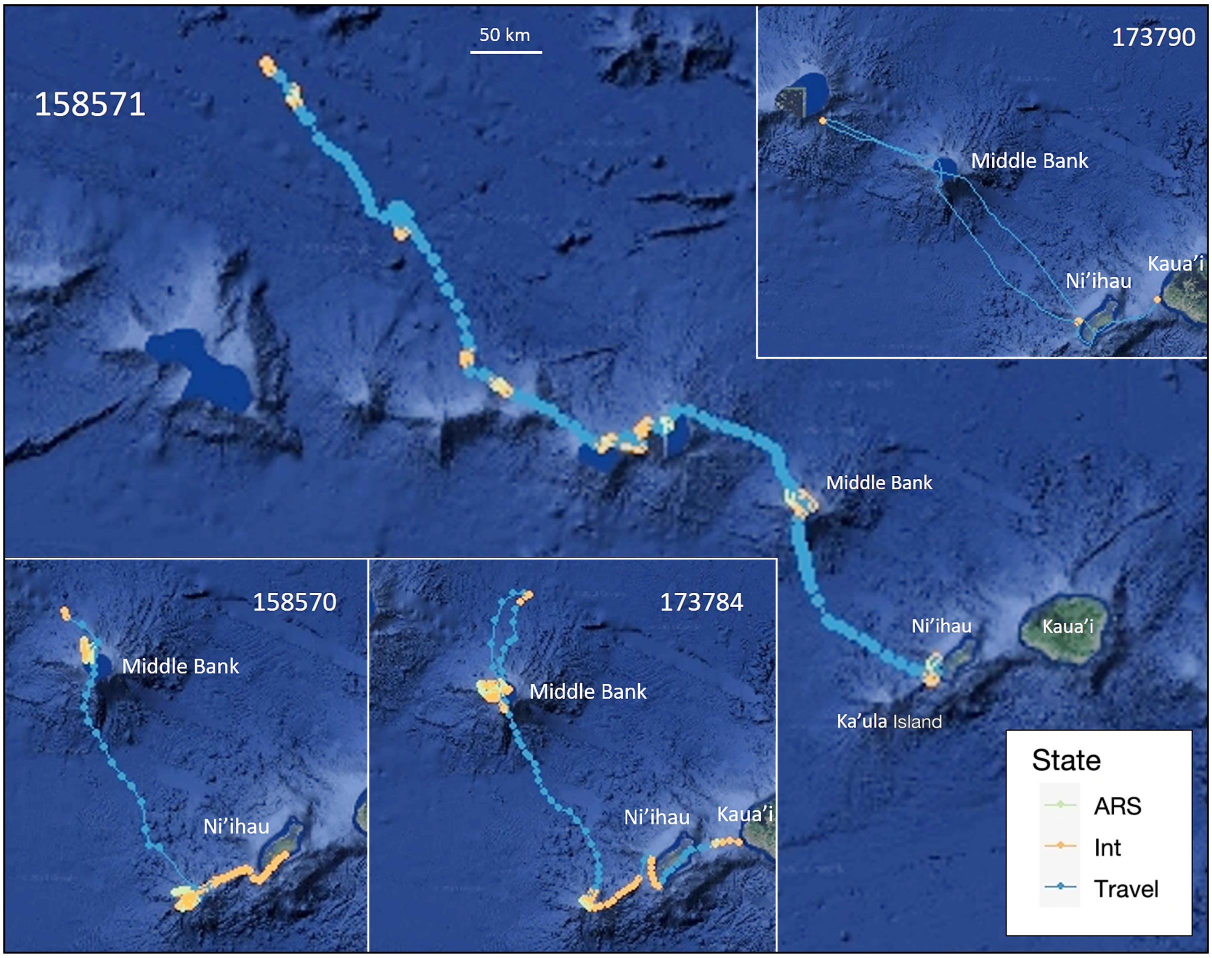

Fig. 3. Interpolated tracks (1 h) of humpback whales, fitted with the crawl model and movement behavior determined by hidden Markov models, demonstrating similarities in movement behavior and travel routes across individuals and years. Tracks for whales 158570 and 158571 are from 2017, 173784 is from 2018, and 173790 is from 2019. ARS: area-restricted search; Int: intermediate

difference was small in the intermediate behavior (Fig. S2). ARS and the intermediate behavior were the most common inshore behaviors, while directed travel was the dominant behavior offshore of 50 km. The intermediate behavior was the most common overall (Table 2). There was a low likelihood of transitioning from directed travel into ARS or vice versa; most transitions occurred via the intermediate state. The whales would transition from intermediate behavior into directed travel when moving between islands into deeper water, and from directed travel to intermediate when approaching shallower water near an island or seamount (Fig. S3). Movement behavior and travel routes were similar across all 3 years in humpback whales traveling northwest beyond Ni'ihau along seamounts (Fig. 3) as well as whales traveling east to O'ahu (Fig. 4).

3.2. Dive behavior

Dive data were similar across all 3 years, with mean dive durations of 8.7 min (range: 1.0–46.3 min), mean dive depths of 37.1 m (6.8–412.0 m), mean descent and ascent rates of 0.3 and 0.2 m s^{-1}, respectively (0.03–2.3 and 0.03–2.9 m s^{-1}), and mean bathymetric depths of 640.8 m (3.7–5152.0 m). Of the 7 animals tagged in 2017, 4 moved beyond the 50 km buffer into offshore waters, compared to only one animal each in 2018 and 2019. Animals crossing from Kaua'i to Ni'ihau or O'ahu were considered inshore since they were within the 50 km buffer. However, animals that crossed between islands did perform deeper dives as well, with the known female diving to a maximum of 412 m.

Most humpback whale dives were shallower than 50 m (82.2% of 5314 recorded dives), while only a

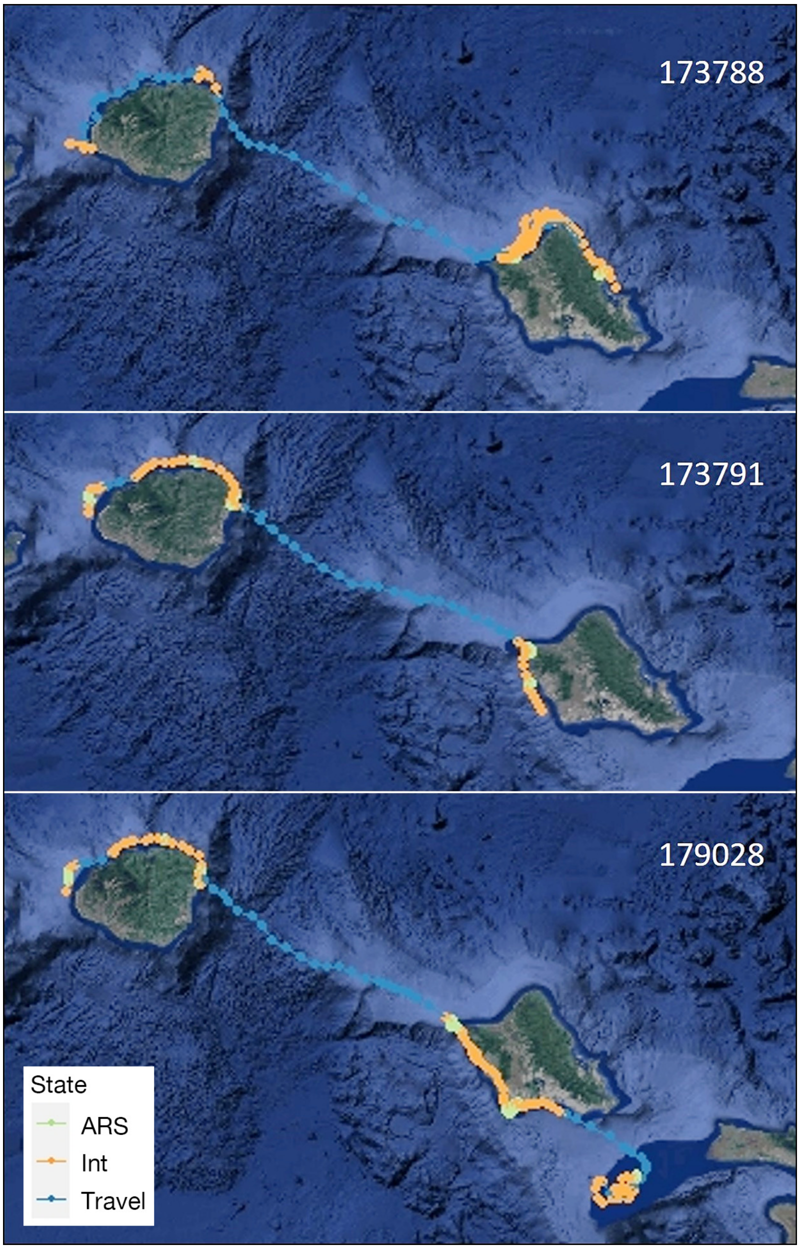

Fig. 4. Interpolated tracks (1 h) of humpback whales fitted with the crawl model and movement behavior determined by hidden Markov models, demonstrating the similarities in both movement behavior and route utilized by the 3 humpback whales that traveled east to O’ahu. Track for whale 173788 was from 2018, while 173791 and 179028 were both from 2019 and appear to have remained together for 4 d as they traveled to O’ahu (Henderson et al. 2021)

small percentage of dives were greater than 100 m (5.9%). However, dives deeper than 100 m occurred more frequently at night during directed travel in deeper water and occurred more frequently in offshore waters than shallow dives (Table 3). In contrast, square-shaped dives had the highest proportion during ARS and the lowest during travel, and a higher proportion of shallow dives occurred in ARS. These findings align with an examination of the dive series data from humpback whales transiting between islands or seamounts offshore of the 50 km buffer (and including whales crossing between Kaua’i and O’ahu; Fig. 5a), which conducted repeated series of long, deep dives (>100 m) only at night. In contrast, for whales remaining nearshore to Kaua’i or Ni’ihau or transiting between the 2 islands via the Kaulakahi Channel where the water depth remains relatively shallow (~1000 m), deep dives occurred day or night but not in repeated series as observed in deeper waters (Fig. 5b).

These general trends were further borne out in the GEE of dive depth. Predictor variables that were included in the final model were dive duration, descent and ascent rates, bathymetric depth, and whether it was day or night (Table 4, Fig. 6). Dive durations were longer with deeper dives, while descent and ascent rates increased with deeper dives, although there appears to be a secondary grouping of shallower dives to <125 m that had rapid descent and ascent rates (Fig. 6). Maximum dive depths were correlated with bathymetric depth, so that deeper dives were conducted in deeper waters and shallower dives in nearshore waters, with dives often extending close to the bottom. In addition, deeper dives tended to occur at night, but as described above, this only occurred in offshore waters during directed travel.

4. DISCUSSION

We tagged 19 humpback whales *Megaptera novaeangliae* off Kaua’i between 2017 and 2019; their dive and movement behaviors provide insight into how humpback whales behave when traveling between islands on the Hawaiian breeding grounds as well as how their behavior changes as they transition into migration. ARS and intermediate behaviors dominated while

Table 3. Humpback whale dive data statistics by dive shape and depth category (Shallow: <50 m; Deep: >100 m). The number of dives that occurred inshore or offshore, during the day or night, or by behavioral state are given as percentages of the total number of dives in that shape and depth category. ARS: area-restricted search; Int.: intermediate

Dive shape	Depth category	Totals	Offshore 50 km	Inshore 50 km	Nighttime (%)	Daytime (%)	ARS (%)	Int. (%)	Travel (%)	Mean dive depth (m)	Mean water depth (m)
Square	Shallow	1165	13.4	86.6	46.2	53.8	29.2	44.7	26.1	24.9	579.8
U	Shallow	1997	9.9	90.1	49.3	50.2	23.8	46.7	29.4	21.0	552.8
V	Shallow	1205	9.7	90.3	56.8	43.2	16.8	41.2	42.0	16.7	562.6
Square	Deep	144	18.1	81.9	66.7	33.3	8.3	31.9	59.7	185.7	1507.7
U	Deep	139	24.5	75.5	52.5	47.5	12.2	15.8	71.9	191.9	1774.4
V	Deep	34	32.4	67.6	55.9	44.1	8.8	17.6	73.5	185.9	1824.4

the animals were inshore, with predominantly shallow square-shaped dives and no diel patterns to the dives. However, once the animals moved offshore, either beyond the 50 km buffer that seems to be linked to migration (Palacios et al. 2019) or in the channel between Kaua'i and O'ahu, they switched to directed travel behavior and began conducting a series of deep dives (>100 m) at night. In addition, the whales transited along strikingly similar routes when traveling both east and west; when traveling west they extensively utilized islands, surfacing reefs, and seamounts along the northwestern Hawaiian archipelago.

Upon leaving the waters of Kaua'i, 3 whales transited eastwards to O'ahu while 14 traveled westward to Ni'ihau; 8 of the latter whales continued beyond Ni'ihau to the islands and seamounts of the northwestern archipelago. This predominantly northwestern movement mirrors what has been found for other satellite-tagged humpback whales in the Hawaiian Islands, with animals arriving at Hawai'i Island from their feeding grounds and most animals moving generally northwest through the main Hawaiian Islands, with some individuals traveling east (Mate et al. 2019, Palacios et al. 2019). In this study, the only tagged animals that traveled east were 2 primary escorts and a female, two of which traveled together for at least 4 d (Henderson et al. 2021). Two additional untagged animals were resighted off Maui after our encounters off Kaua'i (i.e. traveling east) based on fluke photographs in HappyWhale. In contrast, all tagged whales that were encountered as secondary escorts, in dyads, or as singletons traveled west. One animal was photo-identified off Maui 21 d prior to being tagged off Kaua'i (i.e. traveling west) in the Kaulakahi Channel and was observed in a dyad in Kaua'i. In this study, animals encountered further offshore or traveling west were more likely to continue moving westwards towards Ni'ihau and beyond. While more data are needed to confirm this hypothesis, it may be that animals in Kaua'i are more likely to be near the end of their residence time on the breeding grounds and are close to beginning their migration.

It is also possible that whales preferentially travel east or west depending on their feeding ground destination, such that whales heading to the western Aleutian Islands or Russia would depart from the westernmost islands of Hawai'i while whales heading to British Columbia or the Gulf of Alaska would move east to depart from Hawai'i Island. However, Palacios et al. (2019) and Mate et al. (2019) found whales migrating towards all feeding grounds regardless of which island they departed from, and flukes from whales encountered in this study were matched at all feeding grounds from Russia to Washington state. While the 2 tagged animals that had been observed on Russian feeding grounds departed from Ni'ihau, the tagged whales that were observed on the Gulf of Alaska and Southeast Alaska feeding grounds departed from both Ni'ihau and O'ahu. Therefore, there does not appear to be a relationship between the island that whales migrate from and their feeding ground destination. This may further support a general northwesterly movement through the islands during the breeding season, with whales departing from their westernmost point to their feeding grounds rather than departing from a specific island for a specific feeding ground.

Residence times between tagging and migration were far shorter in this study (mean: 5.42 d) than in other studies in the Hawaiian Islands (1.2–8.4 vs. 11–14.8 d in Lagerquist et al. 2008, Herman et al. 2011, Mate et al. 2019, Palacios et al. 2019), although tag retention time was also much shorter in this study compared to other studies. Additionally, fewer competitive groups were observed off Kaua'i than are known to occur in the Maui Nui region (e.g. Baker & Herman 1984, Helweg & Herman 1994); instead, dyads were the most commonly encountered group in this study, and mothers with calves were rarely

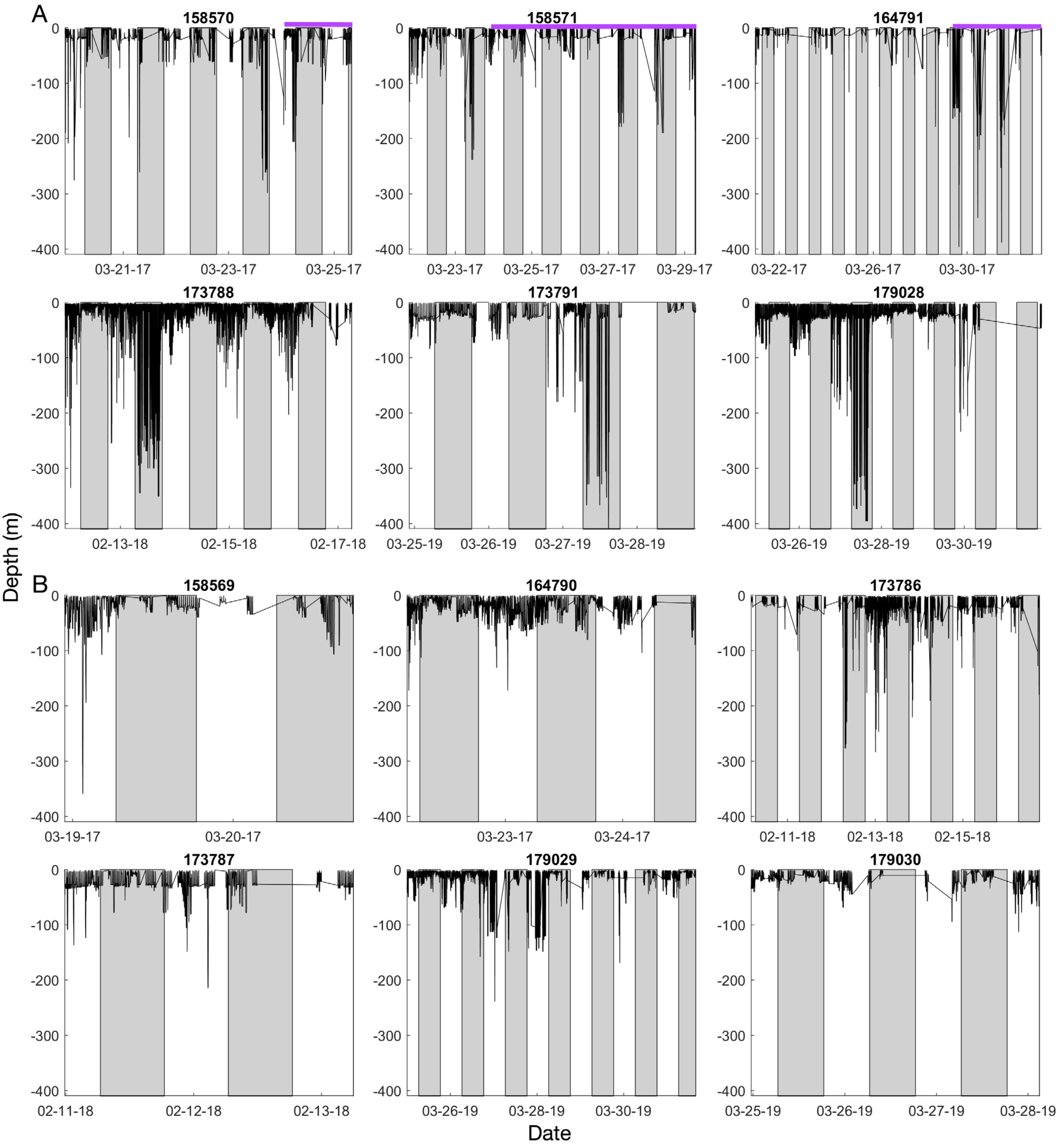

Fig. 5. Dive time series (black lines) from tagged humpback whales across 3 years; grey bars: nighttime hours; horizontal or diagonal lines connecting dives: periods of missing data. (A) Individuals that moved outside the 50 km buffer and likely began their migration (top 3; purple lines: offshore period) or crossed from Kaua'i to O'ahu within the buffer (bottom 3); all of these animals conducted a series of long, deep dives exclusively at night when in deep water. (B) Individuals that remained in the 50 km buffer near Kaua'i and Ni'ihau. Dates are given as mo-d-yr

encountered. However, the hypothesis that humpback whales off Kaua'i may be closer to the onset of their migration than whales at other islands is based on a small sample size, so more tagging and fluke matching between islands across the breeding season is needed to provide additional support.

Most studies modeling baleen whale movement behavior have focused on the 2 ends of the behav-

Table 4. Dive behavior generalized estimating equation model coefficients along with their estimates, test statistics, and p-values

	Estimate	SE	Wald	Pr(>|W|)
Intercept	1.88	0.04	2006.22	<0.001
Dive duration	0.07	0.004	335.53	<0.001
Descent rate	1.26	0.09	202.96	<0.001
Ascent rate	0.84	0.06	172.16	<0.001
Water depth	0.00006	0.00001	21.92	<0.001
Daytime	0.17	0.04	19.73	<0.001

ioral spectrum, ARS and travel, and have chosen not to classify the intermediate behavior (e.g. Bailey et al. 2009, Kennedy et al. 2014, Palacios et al. 2019). However, there may be information encoded in that intermediate behavior that warrants examination. In this study, humpback whales rarely transitioned directly between ARS and directed travel, and almost always moved into the intermediate state first. This was the dominant state in nearshore waters (48.3%), with both moderate swim speeds and turning angles, and may represent a transitional behavior as whales move between deep and shallow waters. Directed travel was also observed in nearshore waters, but was the dominant offshore behavior (55.7%), while the intermediate behavior became less prevalent and was only observed offshore when whales were approaching or departing from islands or seamounts.

Movement behavior on breeding grounds has often been categorized as ARS, with slower swimming speeds and non-directed movement. In this study, while the whales were in inshore waters and actively engaging in breeding behavior such as competitive pods and presumed male–female dyads, ARS and the intermediate behavior state were dominant, with mean travel speeds of 0.7 and 2.1 km h^{-1}, respectively. Kennedy et al. (2014) found mean swimming speeds on the Atlantic breeding ground to be 1.7 km h^{-1}, similar to the 1.31 km h^{-1} found during ARS by Palacios et al. (2019) in Hawai'i, 1.2 km h^{-1} speed on Mexican breeding grounds by Lagerquist et al. (2008), and 0.85–0.9 m s^{-1} (3.1 km h^{-1}) during localized movements in the coastal waters of Madagascar by Trudelle et al. (2016). Interestingly, Trudelle et al. (2016) found more ARS-type movements by males in coastal waters than by females, although females performed ARS in shallower, nearshore waters more than males. Swim speeds in the present study increased to an average of 5.8 km h^{-1} during directed travel. Trudelle et al. (2016) also found that directed travel increased as whales moved into deep waters, occurring in 79% of oceanic movements, with swim speeds increasing to 1.15 m s^{-1} (4.2 km h^{-1}). Similarly, Palacios et al. (2019) found swim speeds increased to 4.4 km h^{-1} and transit became the dominant behavior as humpback whales passed the 50 km buffer, and migrating whales in the Atlantic increased swim speeds to 4.3 km h^{-1} (Kennedy et al. 2014).

However, prior to shifting into directed travel and presumably their migration, several studies have

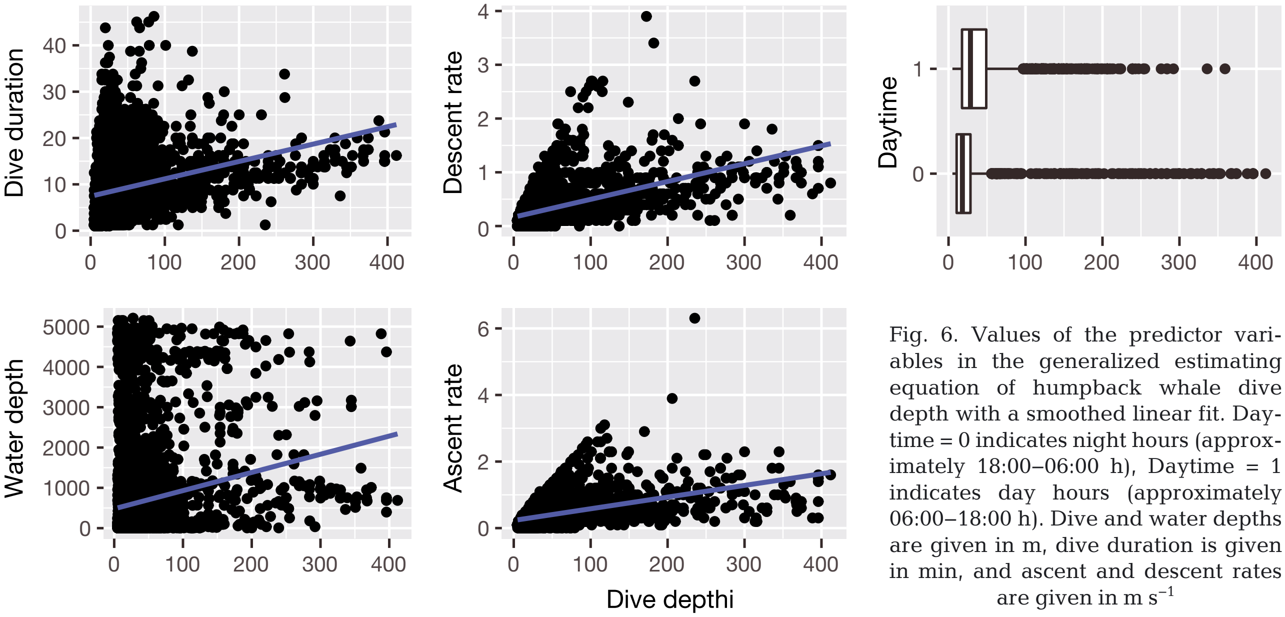

Fig. 6. Values of the predictor variables in the generalized estimating equation of humpback whale dive depth with a smoothed linear fit. Daytime = 0 indicates night hours (approximately 18:00–06:00 h), Daytime = 1 indicates day hours (approximately 06:00–18:00 h). Dive and water depths are given in m, dive duration is given in min, and ascent and descent rates are given in m s^{-1}

found that humpback whales first spend time over seamounts that are close to their breeding grounds with a return to ARS behavior, as was observed in this study. In New Caledonia, whales tagged on the inshore breeding grounds traveled to or between offshore seamounts and spent at least 1 to 14 d in the area (Garrigue et al. 2010). Whales moved extensively between different seamounts and shallow areas within this system before beginning their migration (Derville et al. 2020). Similar transits to seamounts before commencing migration have been observed in Madagascar (Trudelle et al. 2016) and Mexico (Lagerquist et al. 2008). This localized movement at seamounts could represent a continuation of breeding behavior but has also been hypothesized to indicate opportunistic foraging (Derville et al. 2020). Trudelle et al. (2016) found higher levels of chlorophyll *a* at the seamount visited by their tagged humpback whales than were measured in the surrounding waters, indicating a potential hotspot of productivity. Another study found evidence of feeding while on or near breeding grounds off Mexico (Gendron & Urban 1993), and whales have also been observed stopping over seamounts or in shallow water regions along other migratory routes (Mate et al. 1998, Stockin & Burgess 2005, Félix & Guzmán 2014), suggesting that this could be opportunistic foraging. In the present study, humpback whales traveling west visited islands, seamounts, and surfacing reefs and spent time in ARS behavior conducting shallow dives. More work should be done comparing the dive movement and behavior of both breeding and foraging humpback whales to what is recorded at seamounts to investigate this further. In particular, the use of fine-motion and acoustic recording tags such as DTAGs (Johnson & Tyack 2003) would be ideal, where lunges or other indications of foraging behavior could be captured along with foraging vocalizations.

Derville et al. (2020) reported humpback whales performing a series of deep, U-shaped dives in the offshore waters of New Caledonia during the day, similar to the nighttime dive series found in the present study. The authors hypothesized that the dives may also represent opportunistic foraging behavior on the deep scattering layer, comparing the U-shaped dives to foraging dives observed in humpbacks and other baleen whales (e.g. Croll et al. 2001, Goldbogen et al. 2008). While the dive series in the present study only took place at night rather than during the day, and in offshore, likely oligotrophic waters, the humpback whales in Hawai'i could still be diving to the rising scattering layer as has been observed in pelagic odontocetes (e.g. Abecassis et al. 2018, Copeland et al. 2019). However, defecation is rarely seen in Hawaiian waters, which would be expected if opportunistic foraging occurred. These deep dives could also be used for navigation, bringing animals closer to magnetic gradients (e.g. Klimley et al. 2002, Horton et al. 2017), which could facilitate navigation when crossing deep water between islands or migrating.

Individual humpback whales have previously demonstrated high fidelity to long-distance migration routes across years (Horton et al. 2011, 2017, Kennedy et al. 2014). Route fidelity has been found for migrating whales with a spatial accuracy of less than 150 km even across multiple years (Horton et al. 2017, 2020). These movements have also been linked to geophysical forces, suggesting that these forces (magnetism, gravity) may be used in navigation along with lunar illumination. However, even within the breeding grounds in this study, the observed movement behavior and travel patterns were similar across animals and years. Different whales transiting west from Ni'ihau followed similar paths in all 3 years, moving to Ka'ula Island and Middle Bank, similarly changing movement behavior from travel to intermediate behavior and then to ARS when over seamounts. The 3 animals transiting east to O'ahu also followed almost identical paths upon leaving Kaua'i and transitioned into intermediate behavior in almost the same location upon reaching O'ahu. These patterns are similar even compared to humpback whale movements in other studies. For example, the transit paths between O'ahu and Kaua'i and between Ni' ihau, Ka'ula Island, and Middle Bank in this study overlap with the paths used by tagged whales in Mate et al. (1998, 2019), and Palacios et al. (2019). While other studies have examined movements between islands or seamounts on other breeding grounds as previously discussed (e.g. Kennedy et al. 2014, Derville et al. 2020), no other studies have looked at the fidelity of these movements across animals or years. The proximity of the tracks to a shallow ridge between Kaua'i and O'ahu (Fig. 5), along with the occurrence of the deep nighttime dives when the animals were in that location, supports the idea that the deep nighttime dives may facilitate navigation. In the same way, the repeated use of the same path along seamounts could indicate that the seamounts and other seafloor features may aid in navigation, and may also be areas of increased geomagnetism that further facilitate orientation along migration routes (e.g. Horton et al. 2017). However, these same findings could also support the hypothesis of foraging, since the bathymetric features also serve to affect nutrient flow and aggregate prey. Further work focused on the fidelity of routes both within and beyond breeding grounds may provide additional insight into the mechanisms and drivers of movement and dive patterns by migrating humpback whales.

This study has provided new information on the inter-island movements of humpback whales on the Hawaiian breeding ground, including route fidelity when traveling both eastward and westward from Kaua'i. Most animals traveled west to the island of Ni'ihau and the seamounts of the northwestern archipelago, and then beyond to waters past the 50 km buffer that seems to be linked to the onset of migration. This finding may indicate that many of the whales encountered off Kaua'i are nearing the end of their time on the breeding grounds and are close to the onset of migration; however, some animals did travel east and continued apparent breeding behavior. Therefore, more work on inter-island movements and the onset timing of migration is needed to determine what (if any) relationship exists between location on the breeding ground and the onset of migration. When in nearshore waters, humpback whales preferentially engaged in ARS and intermediate behavior, with shallow, square-shaped dives. When in offshore waters or transiting between islands and seamounts, movement behavior switched to directed travel, with a return to intermediate or ARS behavior when approaching shallow water. Dive behavior in nearshore waters was highly variable, but when moving offshore, humpback whales engaged in repeated series of deep dives at night. These dives may be used for navigation or may indicate opportunistic foraging on the scattering layer. Higher resolution tags could be used to investigate these dives further in addition to the activity that takes place over seamounts, as these findings could shift the existing paradigm of humpback whale behavior on the breeding grounds.

Improved knowledge of the linkages between breeding and feeding grounds along with augmented information on migratory behavior could help support conservation efforts for animals facing a number of stressors across regions. Climate change could impact opportunistic foraging along the migration route, which could further negatively affect whales already stressed by increased water temperatures and reduced prey on traditional feeding grounds. Similarly, whales that have been injured or entangled in fishing gear on feeding grounds may be more susceptible to stressors on breeding grounds, such as mid-frequency active sonar in Hawai'i. Understanding the likelihood of these kinds of multiple stressors based on breeding and feeding ground locations or migratory routes is vital to the continued protection of this species.

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