



Scales of Blue and Fin Whale Feeding Behavior off California, USA, With Implications for Prey Patchiness

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Intermediate-duration archival tags were attached to eight blue whales (*Balaenoptera musculus*; four females, three males, one of unknown sex), and five fin whales (*B. physalus*; two females, one male, two of unknown sex) off southern California, USA, in summer 2014 and 2015. Tags logged 1-Hz data from tri-axial accelerometers, magnetometers, and a depth sensor, while acquiring Fastloc GPS locations. Tag attachment duration ranged from 18.3 to 28.9 d for blue whales and 4.9–16.0 d for fin whales, recording 1,030–4,603 dives and 95–3,338 GPS locations per whale across both species. Feeding lunges (identified from accelerometer data) were used to characterize “feeding bouts” (i.e., sequences of feeding dives with <60 min of consecutive non-feeding dives), within-bout behavior, and to examine the spatial distribution of feeding effort. Whales fed near the tagging locations (Point Mugu and San Miguel Island) for up to 7 d before dispersing as far south as Ensenada, Mexico, and north to Cape Mendocino, California. Dispersal within southern California waters differed by sex in both species with males undertaking offshore, circuitous excursions, while females remained more coastal, suggesting that movement patterns on the feeding grounds may not be exclusively related to energy gain. Feeding bout characteristics were similar for both species, with the median bout having 24 dives and lasting 3.3 h for blue whales ($n = 242$), and 19 dives while lasting 2.7 h for fin whales ($n = 59$). Bout duration was positively correlated with the number of feeding lunges per dive within a bout for both species, suggesting whales left poor-quality prey patches quickly but fed intensively for up to 34.9 h when prey was abundant. Feeding bouts occurred further apart as the distance from shore increased, but there was no corresponding difference in the number of feeding lunges per dive, suggesting the whales were feeding at the same rate throughout their range, but that prey was more dispersed in offshore waters. This may be evidence of two feeding strategies, with spatially aggregated foraging around highly localized, topographically forced upwelling centers nearshore, and more dispersed foraging in larger areas of elevated, but patchy, productivity offshore.

Keywords: data loggers, accelerometers, GPS tracking, blue whale, fin whale, feeding behavior, sexual segregation

INTRODUCTION

Blue (*Balaenoptera musculus*) and fin (*B. physalus*) whales are the two largest species of cetaceans and both occur off the west coast of the United States (USA). Blue whales arrive seasonally beginning in the late spring-early summer and feed on aggregations of krill (*Thysanoessa spinifera* and *Euphausia pacifica*; Fiedler et al., 1998; Croll et al., 2005; Nickels et al., 2018) until the late fall-early winter when they migrate south to breeding areas off Baja California, Mexico, in the Gulf of California, and near an offshore oceanographic feature called the Costa Rica Dome (Mate et al., 1999; Bailey et al., 2010; Irvine et al., 2014). Although the seasonal movements of fin whales are less well-understood, they occur year-round off southern California (Stafford et al., 2009; Sirovic et al., 2015; Scales et al., 2017) suggesting they do not follow the typical baleen whale pattern of migrating to lower latitudes during the winter to breed and calve (see also Edwards et al., 2015; Geijer et al., 2016; Jiménez López et al., 2019). Fin whales primarily feed on the same species of krill as blue whales, but can also feed on small fish and squid (Pauly et al., 1998). Both species are listed in the USA as “Endangered” under the Endangered Species Act and consequently are labeled as “Depleted” and “Strategic” stocks under the Marine Mammal Protection Act. Additionally, blue whales are considered “Endangered” and fin whales “Vulnerable” according to the IUCN Red List of Threatened Species (Cooke, 2018a,b).

As with other rorquals, blue and fin whales feed by engulfing large volumes of water and schooling prey, then expelling the water through fibrous baleen plates to retain the prey (Goldbogen et al., 2017). This engulfment, termed “lunge feeding,” occurs during a rapid acceleration through/into a school of prey and can happen multiple times per dive. The evolution of this feeding behavior is closely tied with the animal’s large size, as it allows them to efficiently exploit highly concentrated prey patches (Goldbogen et al., 2011, 2012; Goldbogen and Madsen, 2018). In blue whales this feeding behavior has been shown to vary based on local prey concentrations, indicating they are able to adapt foraging strategies to maximize prey capture (Goldbogen et al., 2015) and energetic efficiency (Hazen et al., 2015).

While sexual differences in distribution and behavior are well-documented in toothed whales (Bigg et al., 1990; Whitehead, 2003; Parsons et al., 2009), such dynamics are less well-understood for rorqual whales, which are largely non-sexually dimorphic, but are known to occur (e.g., Laidre et al., 2009). Sex-based differences in acoustic behavior have been documented for both blue and fin whales, with most of the more complex vocal repertoire of each species being produced exclusively by males and believed to be related to reproduction, while singular calls are produced by both sexes in the context of foraging (Croll et al., 2002; Oleson et al., 2007; Stimpert et al., 2015; Lewis et al., 2018). Further, spatial variability in the type and rate of calling has been documented in blue whales off southern California, suggesting there may be spatial separation of behavioral activities (Lewis and Sirovic, 2018), although a lack of direct observation makes the underlying process unclear, as both feeding and reproductive calls are recorded throughout the feeding season in

southern California (Lewis and Sirovic, 2018). Considering that animals in southern California waters are exposed to a variety of regional stressors like ship strikes (Berman-Kowalewski et al., 2010; Redfern et al., 2013) and anthropogenic sound (Goldbogen et al., 2013; DeRuiter et al., 2017), a potential spatial segregation arising from behavioral differences between sexes could lead to disproportionate impacts (Sprogis et al., 2016) over short temporal scales (Pirootta et al., 2018) or on long-term population fitness (Pirootta et al., 2019).

To understand broad-scale ecological patterns arising from observed species distributions, including interactions among sympatric species, it is often relevant to understand how fine-scale behavior influences the larger trend (Evans, 2012). The movements and distribution of blue and fin whales at the scale of the eastern North Pacific Ocean have been described using satellite telemetry (Bailey et al., 2010; Irvine et al., 2014; Scales et al., 2017), ship based surveys (Redfern et al., 2013), and acoustic data (Burtenshaw et al., 2004; Sirovic et al., 2015). However, there is little data to explain how the broad-scale distributions of these animals are influenced by variations in behavior at more local scales. Here we used intermediate-duration data-logging tags to examine the fine-scale movements and diving behavior of blue and fin whales off southern and central California over periods of multiple weeks. Our primary goal was to characterize how feeding behavior varies across this region, including potential differences between the sexes and between the two species, which occur in sympatry in this region. Our results indicate a strong spatial and temporal heterogeneity in blue and fin whale foraging behavior, with implications for prey patchiness and quality. As such, this study provides new insights into the underlying drivers of broad-scale movement and occurrence during the feeding season for two of earth’s largest predators.

MATERIALS AND METHODS

Tag Configuration and Deployment

This study used Advanced Dive Behavior (ADB) tags, a configuration of the Wildlife Computers (Seattle, WA, USA) MK-10 time-depth recorder platform, which can record depth, temperature, and tri-axial accelerometer, and magnetometer data at 1-Hz resolution for multiple weeks before releasing from the whale for recovery (Mate et al., 2017). A Fastloc[®] GPS receiver and patch antenna were included in each tag to acquire GPS-quality locations (Bryant, 2007), along with an Argos Platform Terminal Transmitter for sending GPS location and summarized dive data messages via the satellite-based Argos Data Collection and Location System. Complete details of ADB tag construction and design configuration are provided in Mate et al. (2017).

Tags were deployed on blue and fin whales in southern California waters during August 2014 and July 2015. Field work was supported by the 25.6-m research vessel R/V *Pacific Storm*. Tags were mounted in a semi-implantable stainless steel housing and deployed at close range (2–4 m) from a 6.7-m rigid-hulled inflatable boat using the Air Rocket Transmitter System, a modified compressed-air line-throwing gun (Heide-Jorgensen et al., 2001; Mate et al., 2007). Tags were deployed 1–4.5 m

forward of the dorsal fin of the whale and no more than 20 cm down from the mid-line, following the protocol described in Mate et al. (2007). Tags were programmed to release from their housing for recovery 21 d after the start of field operations or if the tag recorded no change in depth for 24 h, indicating the housing had been shed from the whale and sunk to the bottom with the tag still attached. Following release, tags were located and recovered using an uplink receiver that was capable of acquiring, decoding, and solving Argos-transmitted Fastloc GPS location messages sent by the tags in real time, along with information on the tag's general location and the rate and direction of drift. A discussion of factors affecting attachment duration and tag recovery is presented in Mate et al. (2017).

Whenever possible, skin and blubber samples were collected simultaneously to tagging (on the same surfacing) using a crossbow. Crossbow bolts were fitted with circular cutting tips 4 cm in length and 8 mm in diameter, which removed a plug of skin and blubber from the whale. Sex determination was made from skin samples by amplification of regions on the X and Y chromosomes (Aasen and Medrano, 1990; Gilson et al., 1998).

Data Collection and Transmission

Tags were programmed to collect data from the various sensors (depth, accelerometer, magnetometer, and temperature) at 1 Hz for the duration of the deployment. While deployed, acquisition of a Fastloc GPS location was attempted every 7 min or the next time the whale surfaced after this time had elapsed. All data were stored in an onboard archive for download after tag recovery. The dive summary data from the Argos transmissions were not used in this study, although locations estimated from Argos transmissions (Argos, 2016) were used to examine movements of whales whose tags were not recovered. Further details about ADB tag dive summary messages are described in Mate et al. (2017).

Data Analysis

Maps were made using ArcGIS® software ArcMap™ 10.3 by Esri and the ArcGIS Online Ocean Basemap. Data manipulation and analysis for this study was conducted using Matlab (The Mathworks Inc, 2015) and R (R Core Team, 2018). The same suite of analyses were used for both blue and fin whales, except as noted for cases when data for one species were too limited for complete analyses. To detect feeding lunges, the change in the acceleration vector ("Jerk") was calculated from the accelerometer data as the norm of the difference between consecutive acceleration values (Simon et al., 2012; Allen et al., 2016). The Jerk is thus a measure of rapid changes in acceleration and orientation of the tagged whale. Lunge-feeding events in rorquals are characterized by a peak in Jerk with a coincident increase in the roll angle for multiple seconds, as the whale typically accelerates and rolls when opening its mouth to engulf prey (Goldbogen et al., 2006; Simon et al., 2012; Allen et al., 2016). A subsequent minimum in the Jerk value, as the whale ceases most movement to expel the water and filter out prey, signals the end of the lunge. Together, these three criteria (Jerk maximum, increase in roll, and subsequent Jerk minimum) were used to identify feeding lunges in the data records based on the lunge detection methodology described by Allen et al. (2016), but modified to use

a more conservative Jerk peak threshold and without the use of acoustic data. The large number of dives recorded by tags during their deployment periods precluded direct confirmation of each feeding lunge identified by the lunge detection algorithm for the entire data record. Instead, we implemented a validation protocol by randomly selecting 10% of dives from each track and visually reviewing them to estimate the percentage of correctly detected lunges (true positives), falsely detected lunges (false positives), and correctly identified feeding dives (dives with at least one true positive). Validation statistics were summarized for each tag and are presented briefly in the Results section, with a more detailed description in the **Supplementary Material**.

Dive summaries were generated for each track by isolating any submergence >10 m in depth (hereafter a "dive") from the tag's depth record and calculating maximum dive depth, dive duration, and the number of lunges that occurred during the dive. The dive end times were then matched to the nearest GPS location recorded by the tag, as locations were generally collected as the whale surfaced from a dive. If there was not a location within 10 min of a dive, a location was estimated by linear interpolation between the temporally closest GPS locations before and after the dive using the dive time to determine where on the line the location should fall. For tracks with less frequent GPS locations this resulted in linear segments of interpolated dive locations that do not represent the exact movement of the whale.

In order to distinguish between series of related feeding dives, a log-survivorship analysis (Holford, 1980; Gentry and Kooyman, 1986) was conducted on the time between feeding dives (i.e., dives with at least one detected lunge) for each tag record. In this case, the log-survivorship analysis graphically showed the number of feeding dive sequences (on a log scale) as a function of the time between them, and the goal was to identify a point along the curve where the number of feeding dive sequences stabilized as time between feeding dives continued to increase, suggesting a natural break in the data. Sequences of dives defined by this criterion were isolated and labeled "feeding bouts." To assess the horizontal extent of each feeding bout and the overall spatial scale of foraging effort, minimum convex polygons were created using the corresponding dive locations for bouts with at least three GPS locations (i.e., not including bouts with interpolated dive locations; see **Supplementary Figure 1**). We report feeding bout summary statistics including bout duration, time, and distance between consecutive bouts, and distance to the closest bout from the entire track. We also report summaries of dives within each feeding bout, including number of dives per bout, mean maximum dive depth and duration, mean number of lunges per dive, and the number of dives without a lunge. The univariate distributions of feeding bout metrics were assessed graphically using probability density plots, while inter-species comparisons of the distributions were made using Bhattacharyya's similarity coefficient (Bhattacharyya, 1943; Guillerme and Cooper, 2016). When Bhattacharyya's similarity coefficient between two distributions is <0.05, the distributions are significantly different, and when the coefficient is >0.95, the distributions are significantly similar. Values between these two thresholds can be used to indicate the probability of overlap between the distributions but cannot be

used to determine if they are significantly different or similar (Guillermé and Cooper, 2016).

Trends among these metrics were formally assessed using generalized linear mixed models (GLMMs), with the tag number as a random-effect grouping variable to account for differences between individuals, a fixed-effect “species” indicator variable, and an interaction term between the predictor of interest and the species indicator variable when inter-species comparisons were desired (Bolker et al., 2009; Harrison et al., 2018). Variables were log-transformed as needed based on graphical assessment of the data. Models were implemented in R using the lme4 package (Bates et al., 2015) or GLMMadaptive (Rizopoulos, 2019) using a two part/hurdle model if it was necessary to account for zero inflated data (GLMMzi). *P*-values were derived using the lmerTest package (Kuznetsova et al., 2017). We report and discuss *p*-values from these GLMMs in the context of levels of support for the outcome (rather than as a binary threshold of significance), with *p*-values <0.01 offering strong support, *p*-values between 0.01 and 0.1 offering suggestive, but inconclusive support, and *p*-values >0.1 offering no support (Gerrodette, 2011; Greenland et al., 2016; Wasserstein and Lazar, 2016).

To further examine fine-scale differences in feeding behavior between individuals, we isolated sections of tracks where two whales were in proximity to each other. Whales were considered to be in proximity when locations from one track were no more than 1 km away from another whale within 30 min from the time of the location. We present a representative map of these track sections and also report dive summary statistics for each section of track in close proximity to another whale for comparison between individuals.

RESULTS

During this study, eight blue whales were tracked for a median of 22.4 d (range = 18.3–28.9 d; **Table 1**) and five fin whales were tracked for a median of 14.2 d (range = 4.9–16.0 d; **Table 1**). Tags were deployed near Point Mugu in 2014 and off the west end of San Miguel Island in 2015 with the exception of blue Whale # 2015_838, which was deployed near Point Mugu in 2015 (**Figure 1**). All eight blue whale tags and three of five fin whale tags were recovered. In two cases the tags were found on the shore several years after having been thought to be lost.

Tagged animals of both species dispersed as far north as Cape Mendocino in northern California, and as far south as Ensenada, Baja California, Mexico, during their tracking periods (**Figures 2, 3** and **Supplementary Figure 4**). However, most of the tracks, and the majority of feeding dives (89%) occurred within southern California waters. Two blue whales (Whale # 2014_5650 and Whale # 2015_4177) and one fin whale (Whale # 2014_5685) made a clockwise loop across a large portion of southern California waters. All three of these whales were male, while females remained closer to shore until leaving southern California waters (**Figures 2, 3**).

The eight blue whale ADB tags recorded a median of 126 dives > 10 m in depth per day (range = 73–207 dives/d; **Table 1**), whereas the three recovered fin whale tags recorded a

median of 106 dives/d (range = 84–210 dives/d; **Table 1**). The number of Fastloc GPS locations recorded by the tags varied widely, with recovered blue whale tags recording a median of 72 locations per day (range = 10–139; **Table 1**) and recovered fin whale tags recording a median of 46.5 locations per day (range = 1–99; **Table 1**). Some variability in the number of locations was likely due to different hardware configurations within the tags, as all tags using newer Fastloc v. 3 technology recorded at least 54 locations per day while only one tag using Fastloc v. 1 recorded more than 47 locations per day (**Table 1**; see also Mate et al., 2017).

Validation of the feeding lunge detection algorithm indicated a mean true positive rate of 70.5% (sd = 20.1%) and a mean false positive rate of 13.6% (sd = 10.0%). The mean percentage of correctly identified feeding dives (dives with at least one lunge) was 85.3% (sd = 16.8%), suggesting mis-classified lunges (both false positive or false negative) often occurred during dives with other correctly identified lunges. Additional details of the validation methodology and results are presented in the **Supplementary Materials**.

Tagged whales of both species generally made deeper dives during the daytime than at night (**Supplementary Figures 2, 3** and **Supplementary Table 1**), although there was high variability within and between individuals, and daytime surface feeding was recorded on multiple occasions both visually while in the field and in the data record. Daytime dive depths were deepest near San Miguel Island where maximum dive depths reached 362 m for blue whales and 365 m for fin whales. Dive durations were as long as 30.7 min for blue whales and 23.1 min for fin whales (**Supplementary Figures 2, 3** and **Supplementary Table 1**). Almost no feeding lunges were recorded during dives >20 min in duration for either species. Feeding activity (as measured by lunge-feeding events) generally took place during daylight hours, although nighttime lunges were recorded on some occasions for both species (**Supplementary Figures 2, 3** and **Supplementary Table 1**). Most blue whale feeding effort was concentrated near the tagging areas, with additional areas of elevated feeding effort southwest of San Miguel Island and offshore of central California (**Figure 2** and **Supplementary Figure 4**). Whales tagged near Point Mugu also heavily used the nearshore waters extending south to San Diego. Tagged fin whales showed a similar trend (**Figure 3** and **Supplementary Figure 4**).

Log-survivorship curves for all tags stabilized at 60 min or less (**Supplementary Figure 5**), so a criterion of at least 60 min with no feeding dives was used to differentiate between feeding bouts. A total of 242 blue whale feeding bouts and 59 fin whale feeding bouts were identified in the tag records (**Tables 2, 3**). For blue whales, the median number of feeding bouts made per whale was higher in 2014 (median = 35, range = 22–38, 4 tags) compared to 2015 (median = 23, range = 17–45, 4 tags), despite tags remaining attached for a median of over 7 d longer in 2015 (**Table 1**). The number of fin whale feeding bouts was more similar across years (range = 13–25 bouts, 3 tags), although the more limited number and duration of tracks was too small for inter-annual comparisons. Across both years, feeding bouts were separated by a median of 5.7 h (range = 1–231.9 h) for

TABLE 1 | Deployment summary for ADB tags attached to eight blue and five fin whales in southern California waters during August 2014 and July 2015.

Species	Year	Tag ID	Sex	Tag generation	Recovered?	Duration (d)	# Dives	# GPS locations	Dives/d	GPS Locs/d	Total Distance (km)
Blue	2014	2014_5644	Female	G3	Yes	19	1,392	185	73	10	1,454
Blue	2014	2014_5650	Male	G4	Yes	20	3,004	2,297	150	115	1,708
Blue	2014	2014_5655	Female	G3	Yes	19.8	4,089	799	207	40	1,563
Blue	2014	2014_5803	Female	G4	Yes	18.3	2,789	2,539	152	139	2,033
Blue	2015	2015_838	Female	G4	Yes	25.9	4,603	3,338	178	129	2,137
Blue	2015	2015_840	Unknown	G3	Yes	24.8	2,252	1,558	91	63	1,610
Blue	2015	2015_4177	Male	G4	Yes	27.5	2,824	1,480	103	54	2,545
Blue	2015	2015_5650	Male	G4	Yes	28.9	2,298	2,337	80	81	2,509
					Median	22.4	2,807	1,928	126	72	1,871
Fin	2014	2014_5685	Male	G3	Yes	14.2	1,188	95	72	6	1,037
Fin	2014	2014_5790	Female	G3	No*	13.3	279	14	21	1	426
Fin	2014	2014_5838	Female	G3	Yes	4.9	1,030	228	210	47	133
Fin	2015	2015_5644	Unknown	G4	No*	15.4	406	12	26	1	1,517
Fin	2015	2015_5654	Unknown	G4	Yes	16	1,695	1,591	106	99	1,370
					Median	14.4	1,030	95	72	6	1,037
					Median (recovered tags)	10.5	1,188	228	106	47	1,037

*Data were transmitted through Service Argos, Inc.

Some tags were not recovered due to poor weather and the tag's distance to shore after release (>160 km in some cases) limiting recovery opportunities. See Mate et al. (2017) for additional details.

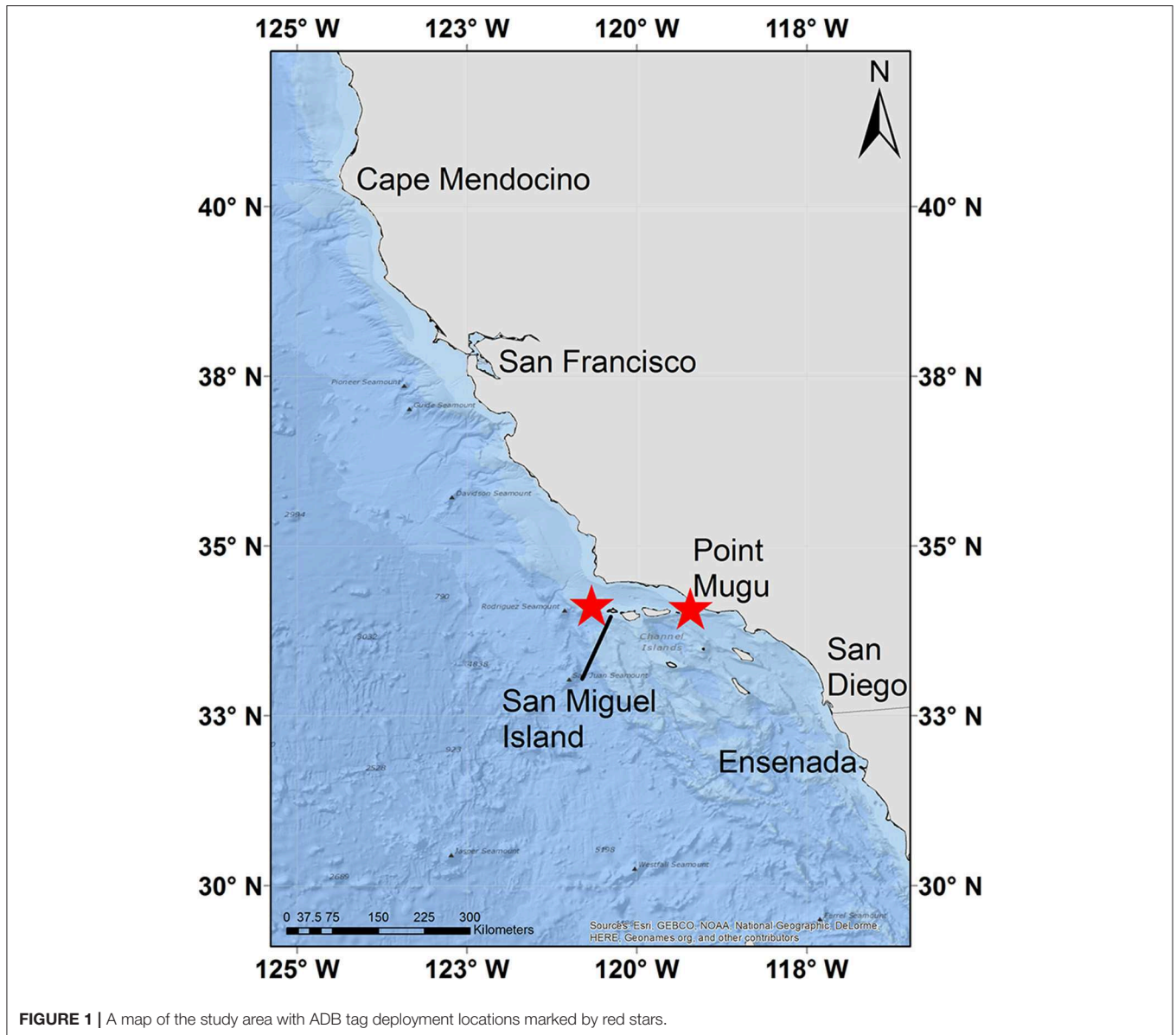
blue whales and a median of 3.1 h (range = 1–227.6 h) for fin whales, and were generally small in area (median = 5.6 km², range = 0.003–546.5 km² for blue whales; and median = 7.6 km², range = 0.001–317.1 km² for fin whales). The median blue whale feeding bout contained 23.5 feeding dives over 3.3 h (range = 4–360 feeding dives and 0.2–34.9 h, respectively), while the median fin whale feeding bout contained 19 feeding dives and lasted 2.7 h (range = 4–142 feeding dives and 0.3–19.6 h, respectively; **Tables 2, 3**).

Median bout duration for the four female blue whale tags (3.9 h) was twice that of males (1.8 h) although median bout duration of Whale # 2014_5644 (a female) was = 1.9 h. Female feeding bouts had a lower proportion of non-feeding dives than those of males (0.26 vs. 0.38; **Table 2**). The distribution of feeding bout duration was similar for both blue and fin whales (Bhattacharyya's similarity coefficient = 0.934), with a strong peak near 2 h and a secondary peak at 14–15 h (**Figure 4**). Mean feeding lunges per dive within bouts varied substantially for both blue and fin whales, but feeding bout duration increased with increasing mean lunges per dive (GLMM, p -value <0.001), with no significant difference between blue and fin whales (GLMM, interaction p -value = 0.84; **Figure 5**). The median bout duration for one blue whale (Whale # 2015_840, of unknown sex) was 12.2 h, suggesting it fed almost continuously during daylight hours on many days. Another blue whale (# 2015_838) fed continuously for almost 1.5 days (**Table 2** and **Figure 2**).

Comparison of the distributions for closest feeding bout and for the distance to shore of a feeding bout between blue and

fin whales (**Figure 4**) using Bhattacharyya's similarity coefficient was inconclusive in terms of providing support for similarity or difference between them, although the probability of overlap was relatively high in both cases (Bhattacharyya's similarity coefficient = 0.840 and 0.833, respectively). Investigation of the distance between closest feeding bouts required accounting for zero-inflated data, as 44% of bouts overlapped spatially with at least one other bout from the same track, resulting in many zero distances. As the distance to shore of a feeding bout increased, the distance between closest feeding bouts also increased (GLMMzi, p -value <0.005), indicating that feeding bouts were more dispersed further offshore (**Figure 5**). However, there was no significant difference in the average number of lunges per dive made within bouts as a function of the distance from shore (GLMM, p -value = 0.77), suggesting the whales were feeding at the same rate throughout the study area. There was suggestive but inconclusive evidence that bouts were more dispersed for fin whales compared to blue whales after accounting for the distance to shore (GLMMzi p -value = 0.093), but there were no inter-species differences in the effect of distance to shore on both the distance to the closest bout (GLMMzi interaction p -value = 0.80) or the number of lunges per dive (GLMM interaction p -value = 0.96).

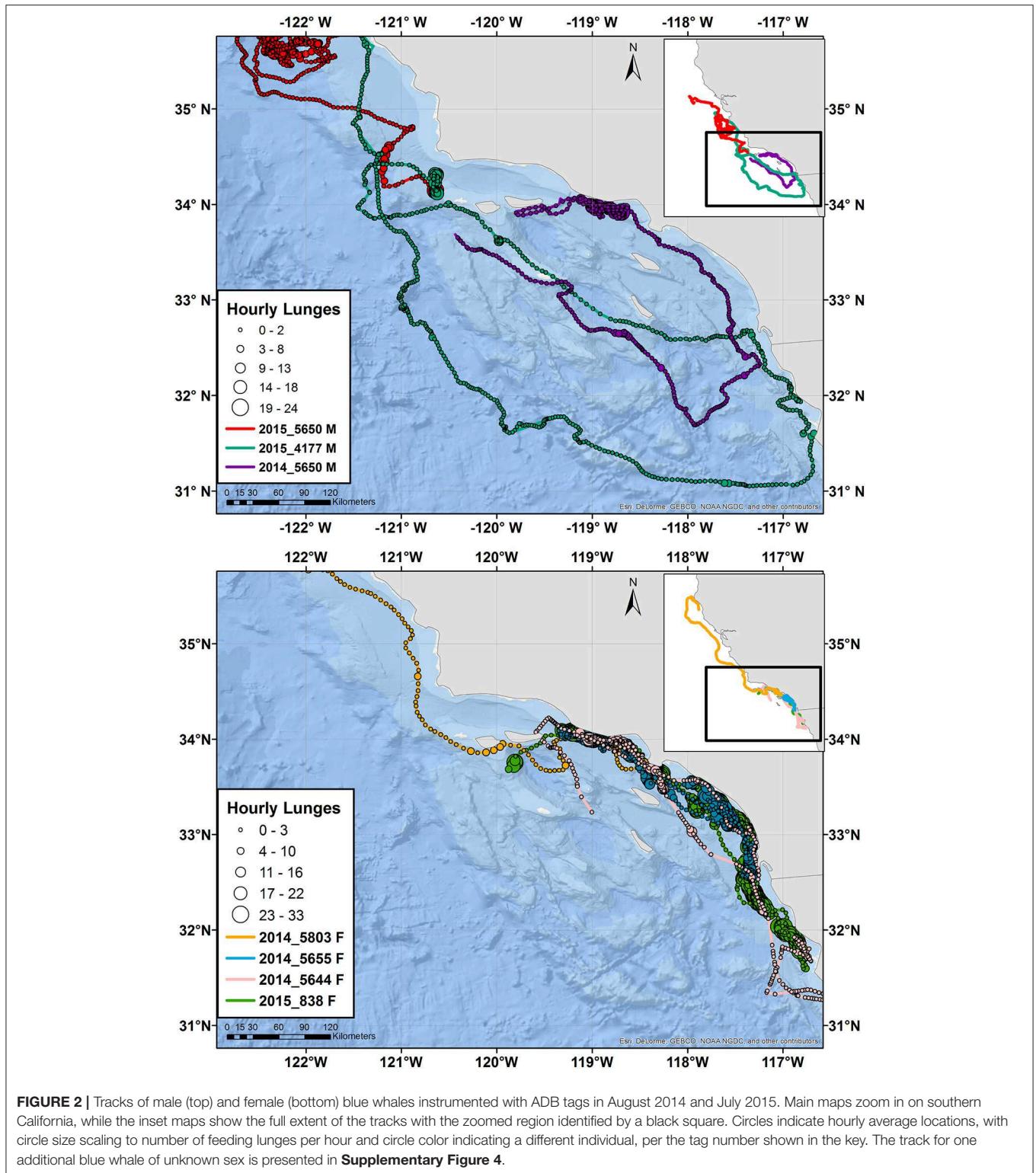
In two cases, a tagged whale passed through an area without stopping, where another tagged whale of the same species was feeding. Blue Whale # 2015_4177 (a male) passed through an area 1 day after Whale # 2015_840 (of unknown sex) had fed nearly continuously during daylight hours in the same location and more broadly for 12 d (**Supplementary Figure 6**). Similarly, fin



Whale # 2014_5685 (a male) passed through a different area <1 day before Whale # 2014_5838 (a female) spent 4 d feeding there (not shown). Both whales passing through were male and their movements were part of a larger circuit of southern California waters (Figures 2, 3). The males' dive records were visually reviewed to ensure no feeding lunges had been missed by the lunge detection algorithm during this period of time.

One pair of blue whales each from 2014 to 2015 were recorded feeding in the same geographic space, in one case showing strong differences in dive behavior and in the other showing strong similarities. Whale # 2014_5650 (a male) and Whale # 2014_5803 (a female), tagged off Point Mugu, were in close proximity 13 times across an 8-d period, including times with both feeding and non-feeding behavior (Supplementary Table 2). While the characteristics of close-proximity periods were highly

variable, Whale # 2014_5803 generally dove more deeply and recorded more feeding lunges than Whale # 2014_5650. On two occasions it dove to over twice the depth as Whale # 2014_5650, and in one instance, was foraging when Whale # 2014_5650 was not (Supplementary Table 2). During one of the longer periods of close proximity, both whales appeared to have been behaving similarly after passing closer than 0.5 km from each other (Supplementary Figures 7, 8), with both whales making foraging dives to a similar depth. An hour later, Whale # 2014_5803 was feeding at almost twice the depth as Whale # 2014_5650 (Supplementary Figures 7, 8) while in the same geographic space. In contrast, in 2015, Whale # 2015_4177 (a male) and Whale # 2015_5650 (also a male), tagged off San Miguel Island, fed in close proximity for 4.5 h on 8 July (the day they were tagged). These whales fed at approximately



the same depth (mean maximum dive depth = 273 and 212 m, respectively; **Supplementary Figure 9**) and shifted their feeding depth shallower during and after sunset with remarkable synchrony. Three other close-proximity events were recorded

in 2015 but all were very limited in duration and number of dives recorded, so will not be presented. Other tagged whales from 2014 may have been in close proximity but the smaller number of Fastloc GPS locations collected by those tags did not

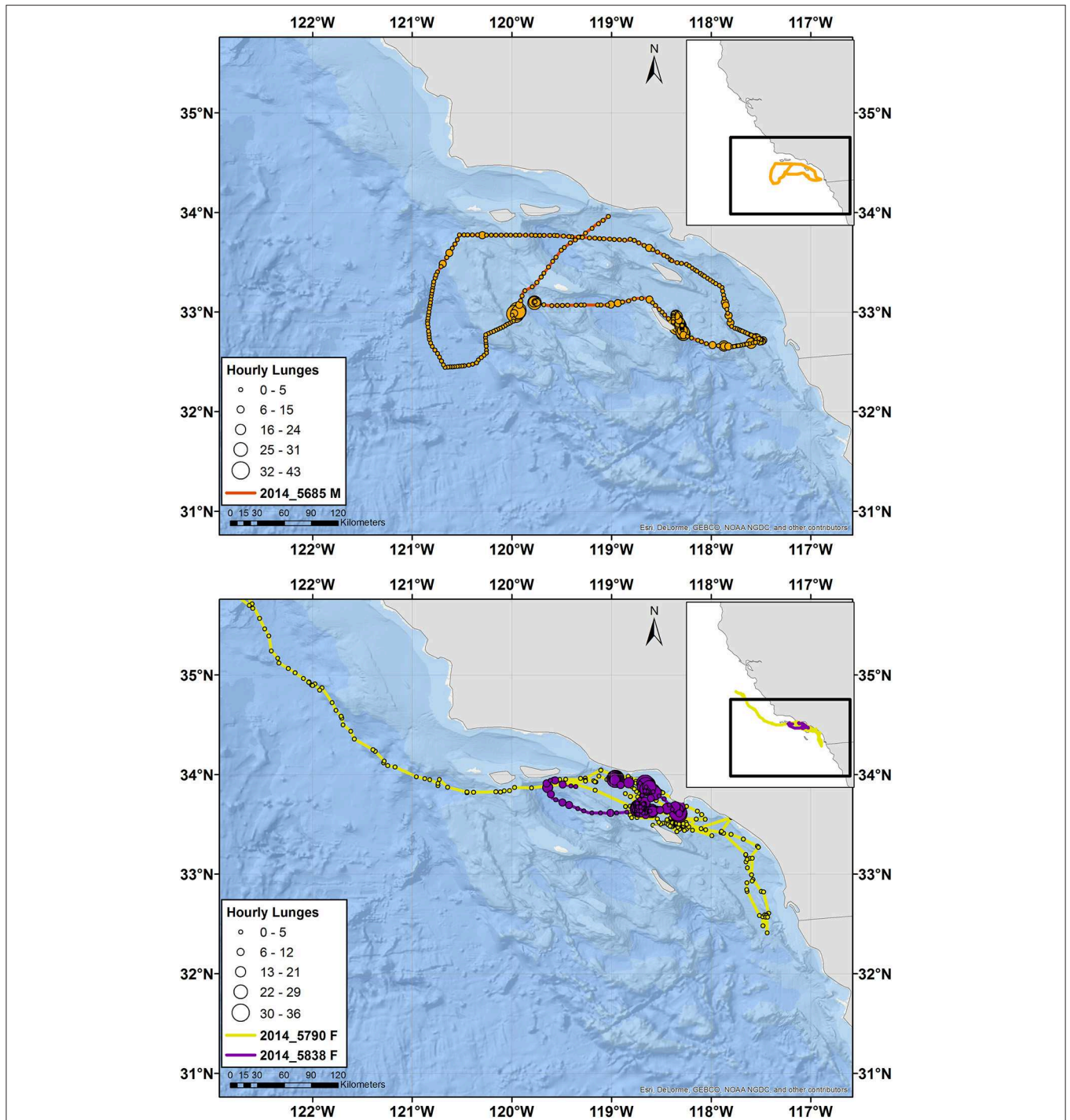


FIGURE 3 | Tracks of male (top) and female (bottom) fin whales instrumented with ADB tags off southern California in August 2014. Main maps zoom in on southern California, while the inset maps show the full extent of the tracks with the zoomed region identified by a black square. Circles indicate hourly average locations, with circle size scaling to number of feeding lunges per hour and circle color indicating a different individual, per the tag number shown in the key. Note that the tag for Whale # 2014_5790 was not recovered and therefore no feeding data are available, but locations received through Argos are shown. The tracks for two additional fin whales of unknown sex are presented in **Supplementary Figure 4**.

allow for fine-scale resolution of their movements. In contrast to blue whales, there were no instances of close proximity between tagged fin whales, or between blue and fin whales, despite both

being tagged in the same areas; in one case on the same day (e.g., blue Whale # 2014_5655 and fin Whale # 2014_5685), and in two cases of fin whales (Whale #s 2014_5790 and 2014_5838) being

TABLE 2 | Summary of dives occurring during feeding bouts made by eight blue whales instrumented with ADB tags off southern California in August 2014 and July 2015.

Whale ID	Sex		# Dives/Bout	Mean max dive depth (m)	Mean dive duration (min)	Mean lunges per dive	Dives with no lunges	Bout duration (h)	Area of bout (km ²)	Time to next bout (h)	Dist. to next bout (km)
2014_5644 # bouts = 22	Female	Median	13	83.1	9.4	1	4.5	1.9	2.00E - 02	12.1	11.8
		Min	4	14.7	1.4	0.3	0	0.7	2.60E - 04	1.1	0
		Max	57	206.6	15.7	3.1	27	9.1	4.09E + 01	139.9	214.3
2014_5650 # bouts = 39	Male	Median	14	51.3	6.9	0.7	6	1.5	1.20E + 00	2.5	3.9
		Min	4	15	2.4	0.2	0	0.3	7.00E - 03	1.1	0
		Max	138	253.5	13.1	3.5	85	13.4	5.61E + 01	78.4	184.3
2014_5655 # bouts = 38	Female	Median	36.5	98.3	6.1	1.5	6	4.3	4.20E + 00	3.7	6.4
		Min	5	16.2	2.1	0.2	0	0.5	1.00E - 06	1.1	0
		Max	182	210	11.1	3.3	46	16.2	2.17E + 02	17.5	95
2014_5803 # bouts = 35	Female	Median	28	78.4	6.2	0.8	7	4.0	1.08E + 01	6.6	10.9
		Min	4	33.7	1.7	0.2	0	0.6	1.00E - 01	1.1	0
		Max	191	215.6	11.3	2.9	69	15.3	5.47E + 02	22.3	113.5
2015_838 # bouts = 45	Female	Median	59	108.0	6.2	1.8	14	6.7	1.71E + 01	3.5	6.1
		Min	4	14.9	1.5	0.2	0	0.7	8.75E - 04	1.0	0
		Max	360	170.9	11.2	3.6	95	35.0	1.74E + 02	14.9	85.0
2015_840 # bouts = 19	Unknown	Median	56	134.9	10.1	2.1	9	12.2	2.69E + 01	9	4.5
		Min	5	13	2.9	0.8	0	0.2	3.20E - 04	1.7	0
		Max	100	229.2	13.6	3.5	31	17.4	9.70E + 01	231.9	173.7
2015_4177 # bouts = 17	Male	Median	10	72	11.7	0.8	4	1.9	2.00E + 00	13.5	33.4
		Min	5	23.8	3.9	0.4	1	0.7	1.00E - 04	1.1	0
		Max	74	187.7	17.4	2.2	19	13.5	2.52E + 01	227.6	484
2015_5650 # bouts = 27	Male	Median	7	90.3	11.4	1	3	1.8	1.50E + 00	9.9	8
		Min	4	18.2	2	0.4	0	0.3	3.10E - 04	1.1	0
		Max	81	192.5	14.7	3	22	16.1	2.35E + 02	80.3	205.6

Total bouts = 242.

Feeding bouts are sequences of dives with no more than 60 min between dives with recorded feeding lunges. Unknown sex whales are cases where no biopsy sample was collected. Note that scientific notation is used for the area of bout column, as values spanned several orders of magnitude.

tagged on a day when a tagged blue whale (Whale # 2014_5655) was re-sighted nearby.

DISCUSSION

The data presented here constitute the longest continuous dive behavior records collected to date for blue and fin whales, which allowed us to examine fine-scale behavior over timescales that previously have not been possible. Both species were observed and tagged concurrently during this study and subsequently occupied generally similar areas during their tracking periods, allowing for a comparative analysis between these two species, which occur in sympatry off California. Our focus was on characterizing feeding effort and its scales of variability over periods of multiple weeks. Short- to intermediate-duration (<6h) feeding bouts were most numerous for both species and there was a positive correlation between bout duration and the number of feeding lunges made per dive within a bout. Blue whales have been shown to adjust their behavior and number of lunges made per dive based on the density of prey in the area (Goldbogen et al., 2015; Hazen et al., 2015), so the correlation between bout duration and number of lunges per

dive suggests that the whales tracked in this study left lower-density prey patches quickly, while staying longer, and foraging more intensely, in higher-density patches. Some of the observed short-duration bouts may also represent the whales exhausting a highly localized abundance of prey. These results suggest the whales were following the marginal value theorem (Charnov, 1976), a foundational model of ecological theory that postulates that animals feeding in a patchy environment make decisions about when to depart a patch based on their assessment of its value, with the main prediction being that animals should spend more time in patches of higher quality (McNair, 1982).

Feeding bouts were more dispersed further offshore, although the whales were able to feed at the same rate throughout southern California waters, as the number of lunges per dive within a feeding bout did not change as a function of distance to shore. While there was evidence of inter-species differences in relation to distance from shore, they may have been the result of the more extensive use of offshore waters or more limited sample size of fin whales. The greater distance between bouts offshore suggests there may be two feeding strategies, with whales concentrating on highly localized, physically forced upwelling centers nearshore, such as off San Miguel Island (Fiedler et al., 1998), and more dispersed areas of elevated productivity offshore,

TABLE 3 | Summary of dives occurring during feeding bouts made by three fin whales instrumented with ADB tags off southern California in August 2014 and July 2015.

Tag #	Sex		# Dives/Bout	Mean Max Dive Depth (m)	Mean Dive Duration (min)	Mean Lunges per Dive	Dives With No Lunges	Bout Duration (h)	Area Of Bout (km ²)	Time To Next Bout (h)	Dist. To Next Bout (km)
2014_5685 # bouts = 25	Male	Median	12	63.0	9.2	0.9	5.0	2.5	1.95E + 00	3.0	12.1
		Min	4	18.8	2.7	0.4	0.0	0.8	1.30E - 05	0.0	0.0
		Max	88	174.7	15.9	3.0	16.0	14.6	1.94E + 02	61.2	81.1
2014_5838 # bouts = 13	Female	Median	10	72.0	11.7	0.8	4.0	1.9	1.96E + 00	10.0	33.4
		Min	5	23.8	3.9	0.4	1.0	0.7	1.02E - 04	0.0	0.0
		Max	74	187.7	17.4	2.2	19.0	13.5	2.52E + 01	227.6	484.0
2015_5654 # bouts = 21	Unknown	Median	22	98.7	8.6	3.3	2.0	3.4	7.64E + 00	6.7	9.4
		Min	4	28.4	1.7	0.4	0.0	0.7	2.24E - 01	0.0	0.0
		Max	119	247.5	11.7	5.2	55.0	15.7	1.32E + 02	47.8	111.4

Total bouts = 59.

Feeding bouts are sequences of dives with no more than 60 min between dives with feeding lunges. Unknown sex whales are cases where no biopsy sample was collected. Note that scientific notation is used for the area of bout column, as values spanned several orders of magnitude.

likely driven by nearshore productivity that has been advected offshore, or by open-ocean Ekman pumping (Rykaczewski and Checkley, 2008). This has a range of implications for both habitat modeling and abundance estimation, as well as for managers trying to mitigate anthropogenic interactions, as the multiple scales of behavior and occurrence should be accounted for.

The spatial scale of feeding bouts was highly variable within and between individuals. The size of the feeding bout areas was likely an overestimate, as convex hulls are sensitive to irregular, concave shapes of the underlying points (Burgman and Fox, 2003; **Supplementary Figure 1**) and GPS locations were somewhat sparse in some cases, such that the number of locations may have been insufficient to define the true extent of the area being used for feeding. Despite this, median feeding bout size for fin and blue whales (5.6 and 7.6 km², respectively) appeared to correspond with the spatial scale of krill patches described off central California (1.8–7.4 km; Santora et al., 2011a). While some of the feeding bouts were significantly larger than the median values (>200 km²), krill patches up to 18 km in extent have been recorded in some years (Santora et al., 2011a), suggesting the larger feeding bouts may have been indicative of broad-scale areas of elevated krill abundance.

Logistics and expense limit direct study of key prey resources such as krill to fine-scales, from which broader-scale predictions are made and sometimes compared to the distribution of predatory species for validation (Santora et al., 2011a,b, 2014, 2017). Modeled krill distributions have also been used to better understand spatial and temporal aspects of their patchiness (Dorman et al., 2015; Messie and Chavez, 2017). The feeding data for tagged blue and fin whales presented here can offer further insight into the distribution and scale of prey patches across southern and central California waters, similar to how seabird foraging tracks have been used to infer prey availability and patch quality in other areas (Chimienti et al., 2017). Since direct observations of prey abundance were not available for this study, linking blue and fin whale feeding bouts to modeled krill distribution could be an additional step to both validate krill

models and tie the overserved whale behavior more directly to prey abundance.

Tagged whale feeding behavior characteristics (like maximum dive depth or lunges per dive) fit into broadly similar ranges across individuals, although there was also evidence of fine-scale variability among individuals within those ranges, exemplified by the instances where two tagged blue whales (Whale # 2014_5803 and Whale # 2014_5650) were feeding in close proximity to one another but at different depths. Without knowing the structure of the prey field, it is difficult to be sure if these differences were related to the individual or the composition of prey being exploited. The observed differences may be a reflection of different individuals having different energetic requirements, allowing some whales to forage less intensively on lower prey concentrations (e.g., less dense prey at shallower depths), different age classes, or different prey species. However, across their entire tracks, Whale # 2014_5803 fed at deeper depths than Whale # 2014_5650, and this trend continued when the two occupied the same geographic space, suggesting the observed variability in dive behavior between individuals was likely due to different foraging strategies. It is not unusual for individuals to use a subset of their population's ecological niche due to variations of intrinsic traits or trade-offs that restrict an individual's ability to generalize (Bolnick et al., 2003). Further work is needed to better understand individual differences in rorqual behavior.

Previous work has found evidence of broad-scale spatial segregation between blue and fin whales off southern California (Fiedler et al., 1998; Irvine et al., 2014; Sirovic et al., 2015; Scales et al., 2017). However, our results showed that feeding behavior of tagged blue and fin whales was similar over a broad scale, with feeding occurring in relatively localized areas (median bout duration = 3.3 and 2.7 h, respectively; median bout area = 5.6 and 7.6 km², respectively) and with similar non-feeding periods in between (median time between bouts = 5.7 and 3.1 h, respectively). At finer scales, the characteristics of individual feeding bouts were also similar between the two species, with the

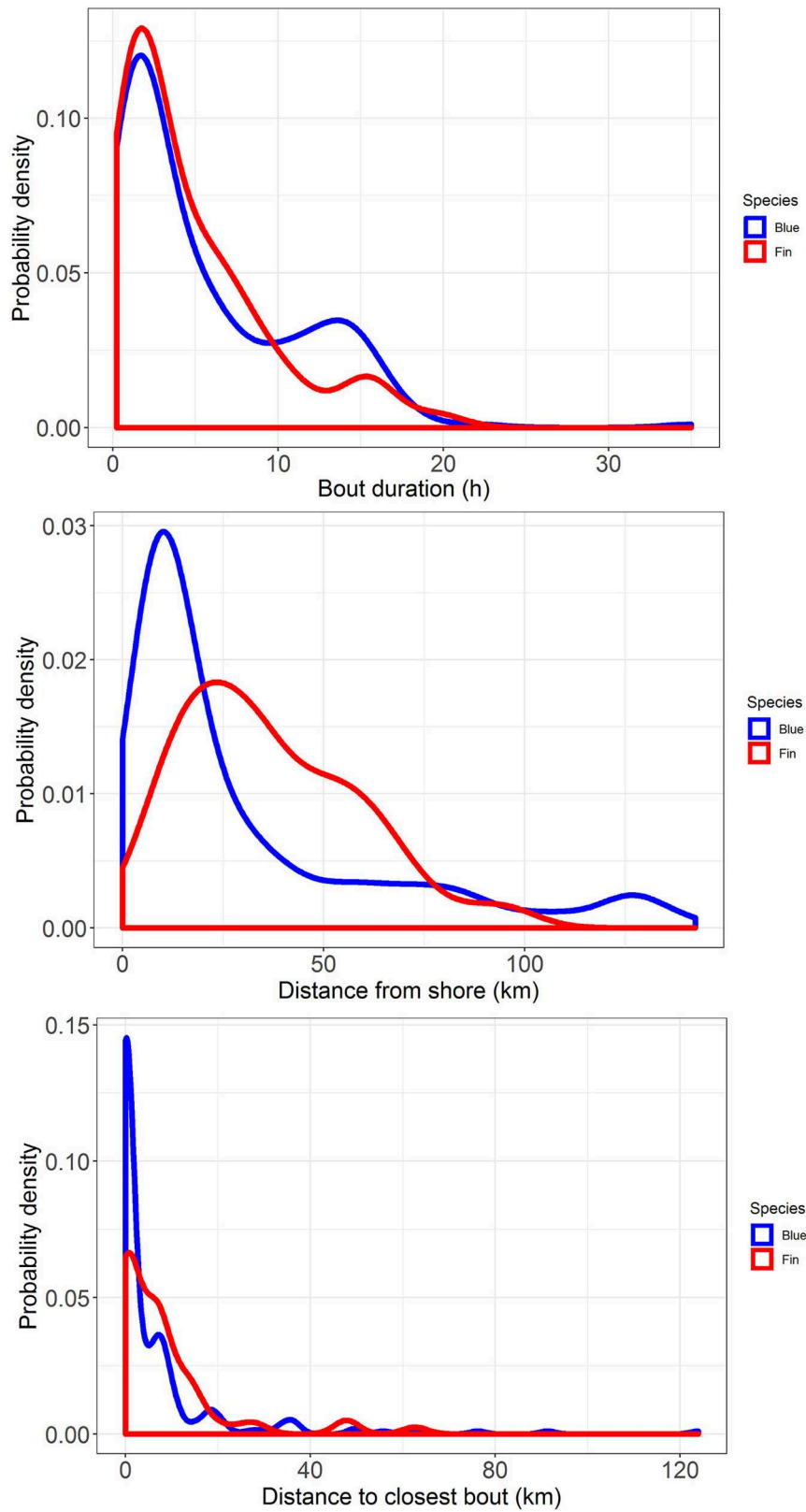
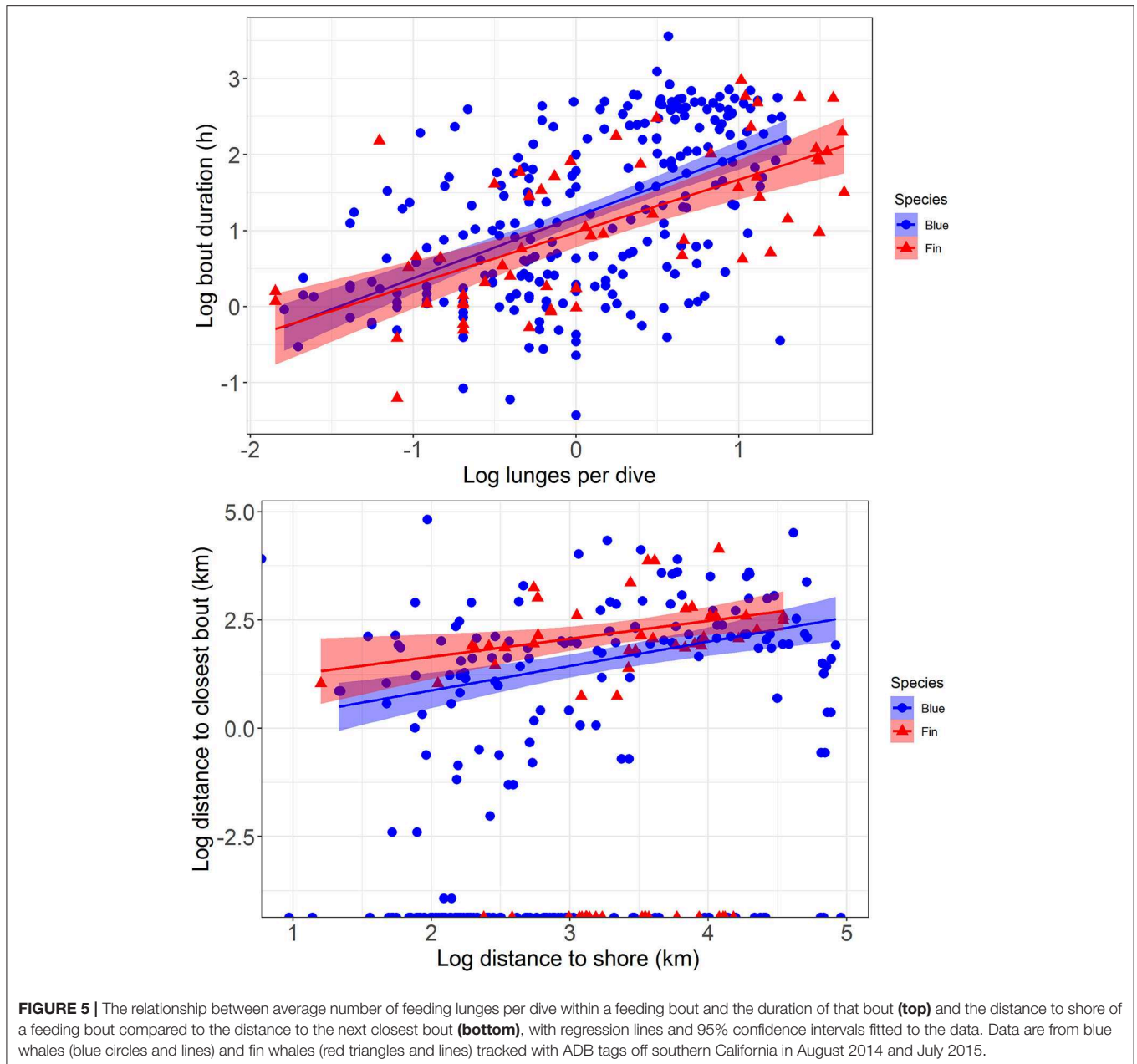


FIGURE 4 | Probability density plots of feeding bout duration (**top**), distance from shore (middle), and distance to the closest bout (**bottom**) for blue whales (blue lines), and fin whales (red lines) tracked off southern California with ADB tags in August 2014 and July 2015.



exception that fin whales recorded a higher maximum number of lunges per dive than blue whales (5.2 vs. 3.6, on average), consistent with previously observed species-specific differences in feeding rates (Friedlaender et al., 2015).

The observed similarities in feeding behaviors between the two species are likely a result of the highly specialized nature of lunge-feeding behavior (Goldbogen et al., 2006, 2011, 2017; Cade et al., 2016) and suggests the whales were feeding on krill given their highly stereotyped behavior (Cade et al., 2016). This further suggests the two species may potentially compete for a similar prey resource. Variations in the target prey species (Fossette et al., 2017), and even life stage of the same krill species (Santora et al., 2010), have also been shown to affect

the spatial distribution of sympatric whale species. There was suggestive evidence that fin whale feeding bouts were more dispersed compared to blue whales, so it is possible that fine scale differences in the timing or location of feeding between the two species may be the underlying driver of the previously observed broad-scale differences in spatial distribution (Fiedler et al., 1998; Irvine et al., 2014; Sirovic et al., 2015; Scales et al., 2017). However, without an understanding of the underlying distribution and demographics of the local prey resources, it is difficult to attribute a reason to any inter-species differences in the spatial distribution of fine-scale feeding we observed.

Three tagged whales (two blue and one fin; all males) made clockwise circuits of southern California waters with only limited

feeding effort, despite passing through areas where other tagged whales were feeding. Blue whales have been shown to adjust their dive behavior based on the density of prey in the area (Goldbogen et al., 2015; Hazen et al., 2015), so it is possible they encountered prey in insufficient concentrations for them to feed upon. More broadly, males and females of central-place foragers are known to have different sex-based foraging strategies arising from different energetic requirements during reproduction and resulting in differential exploitation of the offshore and coastal environment (Breed et al., 2006; Austin et al., 2019). A similar process could be driving the observed differences between male blue and fin whales. Alternatively, blue whales are known to engage in social behavior while in southern California (Lomac-MacNair and Smultea, 2016). Visual inspection of the tag records revealed that many dives made by individuals of both species during the circuits of offshore waters had the characteristics of dives made while whales are vocalizing (shallow, flat-bottomed, minimal acceleration; see Calambokidis et al., 2007; Oleson et al., 2007; Stimpert et al., 2015). Additionally, it has been suggested that the better acoustic propagation properties of offshore waters (Sirovic et al., 2015) make them advantageous for reproductive calls (Lewis and Sirovic, 2018). Thus, we speculate these circuits in southern California waters by males of both species were related to reproduction, although we caution that this is based on a rather small number of individuals. Little is known about blue and fin whale breeding behavior, but our interpretation implies that courtship, or at least advertising and searching for a potential mate, may begin while on the feeding grounds.

The potential difference in movement and areas occupied by males and females has the added implication of possible sex-based differences in exposure to regional stressors like anthropogenic sound (Goldbogen et al., 2013; DeRuiter et al., 2017) or ship strikes (Berman-Kowalewski et al., 2010; Redfern et al., 2013), which are of particular concern in the Southern California Bight. Differing levels of exposure to anthropogenic stressors arising from sexual segregation is a common situation for wildlife (Sprogis et al., 2016), and is especially problematic if it occurs to a species where one sex may be more susceptible to such impacts (Symons et al., 2014; Baird et al., 2015). If further studies confirm our observations about sex-specific differences in habitat use (at least within southern California), managers may need to consider mitigation strategies that explicitly address differential impacts based on sex.

The movements of whales on the feeding grounds are generally assumed to be driven by the search for prey, such that fine-scale behavior can be directly linked to broad-scale ecological patterns like distribution. The results presented here support this idea, showing whales of both species quickly left presumably poor-quality prey patches, with the implication that variable prey density drives local whale movements, while the existence of multiple, persistent hotspots of krill aggregation along the west coast of the USA drive the broad-scale seasonal movement pattern (Abrahms et al., 2019; Palacios et al., 2019). However, sex also appeared to influence movement patterns and habitat use, at least within southern California waters. While this result is based on a relatively limited number

of individuals, it constitutes a substantial refinement to our understanding of blue and fin whale behavior on the feeding grounds. Continuing to link fine-scale behavior to broader-scale movement is an important area of research, which was aided by the comparatively long data records generated by the tags used in this study. Developing a better understanding of the underlying mechanisms driving broad-scale behavior is critical to better assist the recovery of these endangered whales.

DATA AVAILABILITY

The data used in this study are published as a Movebank Data Repository under a Creative Commons Zero license (Irvine et al., 2019).

ETHICS STATEMENT

Tagging was conducted under the authorization of National Marine Fisheries Service Marine Mammal Protection Act/Endangered Species Act Research/Enhancement Permit No. 14856 and Oregon State University Institutional Animal Care and Use Committee Permit No. 4495.

AUTHOR CONTRIBUTIONS

LI conceived the study, led field work, conducted the data analysis, and drafted the manuscript. DP helped secure funding for the project, helped conceive the study, participated in the field work, consulted on analysis methodologies, and critically reviewed the manuscript. BL participated in the field work, assisted with data analysis, and critically reviewed the manuscript. BM secured funding for the project and critically reviewed the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2019.00338/full#supplementary-material>

- Goldbogen, J. A., Cade, D. E., Calambokidis, J., Friedlaender, A. S., Potvin, J., Segre, P. S., et al. (2017). How baleen whales feed: the biomechanics of engulfment and filtration. *Ann. Rev. Mar. Sci.* 9, 367–386. doi: 10.1146/annurev-marine-122414-033905
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