Local and migratory movements of Hawaiian humpback whales tracked by satellite telemetry

Bruce R. Mate, Robert Gisiner, and Joseph Mobley

Abstract: We examined inter-island movements and offshore migrations of six humpback whales (*Megaptera novaeangliae*) tagged during March and April 1995 with satellite-monitored radio tags off Kaua'i, Hawai'i. The tags transmitted 0.5–17 days ($x = 8.5 \pm 2.7$ days) and produced 1–66 edited locations. Total travel distances per individual ranged from 30 to 1860 km. After editing, satellite-acquired locations ranged from 1.8 to 3.9/day for individuals (group average 2.7/day). One adult traveled 250 km to Oahu in 4 days. Another visited Penguin Banks and five islands (820 km) in 10 days, suggesting faster inter-island movement than had been previously thought. Three whales traveled independent, parallel courses toward the upper Gulf of Alaska on north-northeast headings. A female with a calf was the fastest: 670 km in 4.5 days (150 km/day). Another adult traveled 1610 km in 14.7 days (110 km/day). The average speeds on the two longest tracks were identical (4.5 km/h). A 4200-km migration to the upper Gulf of Alaska at that speed would take 39 days. If the fastest whale's speed was maintained on a straight course, the entire migration could be accomplished in as little time as 28 days. Based on the two longest tracks, the first third of the migration route is within 1° of magnetic north. These data represent the first route and travel speeds for humpbacks migrating from Hawai'i toward Alaska.

Résumé : La radiotélémétrie par satellite nous a permis d'étudier les déplacement entre les îles et les mouvements migratoires le long de la côte chez six Rorquals à bosse (*Megaptera novaeangliae*) marqués en mars et avril 1995, au large de Kaua'i, Hawai'i. Les marqueurs ont fonctionné 0,5–17 jours ($x = 8{,}5 \pm 2{,}7$ jours) et, après un tri, 1–66 repérages ont été gardés pour analyse. Les distances totales parcourues par les individus se situaient entre 30 et 1860 km. Après le tri, les repérages acquis par satellite allaient de 1,8 à 3,9/jour (moyenne du groupe, 2,7 repérages/jour). Un adulte s'est déplacé sur une distance de 250 km jusqu'à Oahu en 4 jours. Un autre a visité Penguin Banks et cinq îles (820 km) en 10 jours, ce qui représente des déplacements entre îles plus rapides qu'on ne l'avait cru à ce jour. Trois rorquals ont suivi des par cours parallèles et indépendants vers la partie supérieure du golfe d'Alaska en direction nord-nord-est. C'est une femelle avec un petit qui a fait le parcours le plus rapide : 670 km en 4,5 jours (150 km/jour). Un autre adulte a voyagé 1610 km en 14,7 jours (110 km/jour). Les vitesses moyennes des deux parcours les plus longs se sont avérées identiques (94,5 km/h). À cette vitesse, la migration de 4200 km jusqu'à la partie supérieure du golfe d'Alaska prendrait 39 jours. Si le rythme de croisière du rorqual le plus rapide était maintenu sur un parcours en ligne droite, la migration pourrait ne prendre que 28 jours. D'après les deux parcours les plus longs enregistrés, le premier tiers de la route de migration est à moins de 1° du nord magnétique. Ce sont là les premiers résultats jamais obtenus sur le trajet migratoire et la vitesse de nage de Rorquals à bosse en migration de l'archipel d'Hawai'i vers l'Alaska.
[Traduit par la Rédaction]

Introduction

Our current knowledge of the seasonal distribution and movements of humpback whales (*Megaptera novaeangliae*) in the North Pacific Ocean has been pieced together from whaling data, photo-identification studies (Baker et al. 1986; Darling and Jurasz 1983), and DNA analysis (Baker et al. 1990). The calving and breeding population that overwinters around the Hawaiian Islands (Herman and Antinoja 1977; Herman et al. 1980) has been linked primarily to southeast Alaska during the spring/summer/fall feeding season (Baker et al. 1985; Darling and McSweeney 1985). However, a few identification photographs match animals identified in Hawai'i to animals at California summer feeding sites (Baker et al. 1986) and also to animals at a Mexican winter breeding area 800 km south of the tip of Baja California Sur, Mexico (Darling and McSweeney 1985). Despite efforts to relocate humpback whales at sea during the migration, few have been observed and the actual migration route(s) is (are) unknown (Baker et al. 1985). Several investigators have used photo-identification of individual whales to study inter-island movements and identify where whales migrate, but coverage areas are large and the relative proportion of identified individuals is low. As a consequence, analyses of resightings provide conservative estimates of travel speed. Obtaining accurate speed estimates on migration routes requires considerable survey effort at many sites to detect departure and arrival times.

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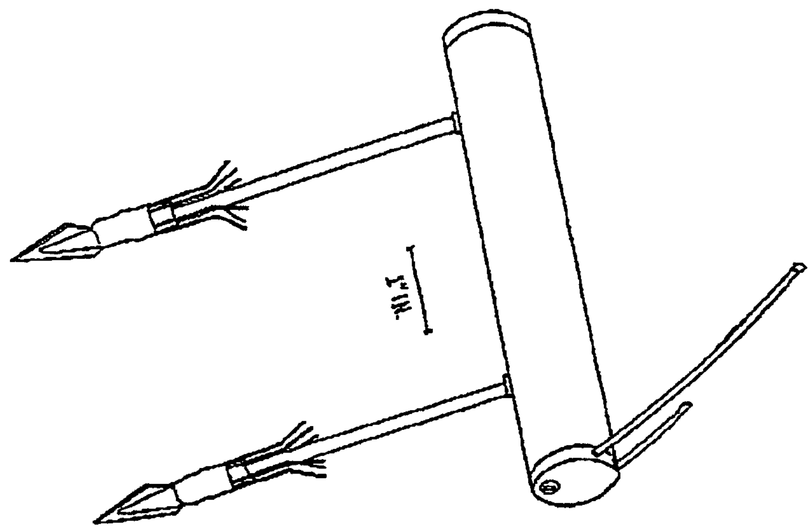
Fig. 1. Housing and attachment of a satellite-monitored radio transmitter used to tag humpback whales in March and April 1995 off Kaua'i, Hawai'i.



This study is the first to examine the details of inter-island movements and the early migration route of Hawaiian humpback whales by means of satellite-monitored radiotelemetry. Radiotelemetry requires no additional field effort after tagging to obtain the frequent "resightings" (locations) that provide detailed migratory and local movement data.

Materials and methods

Between 26 March and 2 April 1995, we tagged six humpback whales off the southwest coast of Kaua'i with Argos satellite-monitored ultra high frequency (UHF) radio tags. The Argos Data Collection and Location Service uses receivers on National Oceanographic and Atmospheric Administration television infrared observational satellite (TIROS-N) weather satellites in sun-synchronous polar orbits (Fancy et al. 1988). Locations are calculated from the Doppler shift of received messages resulting from the movement of the satellite. Location accuracy is dependent on the number of messages received and on their spacing during satellite passage over the transmitter (average duration 10 min, maximum duration 16 min). Each of three active satellites provided 3–4 orbits/day passing over Hawai'i. We refer to such orbits as passes.

Each tag (Fig. 1) consisted of a Telonics ST-10 transmitter housed in a stainless-steel cylinder (2.5 cm diameter × 17 cm; 495 g) with two Saft7 lithium C-cell batteries. We estimated the tag's operational life at 220 days. An antenna (3 mm × 17 cm) of stainless-steel cable covered with shrink wrap was mounted in an endcap. Next to the antenna, a 5-cm piece of cable with its lower half shrink-wrapped acted as a conductivity sensor to prevent the tag from transmitting while underwater, thus prolonging battery life. Two stainless-steel subdermal anchors (6 mm × 15 cm) were silver-soldered to the housing. Each anchor had a cutting blade and 10 stainless-steel wires (0.2 mm × 3 cm) attached to the distal end. Each wire was bent to promote lateral displacement (and therefore hold better) if the tag started to back out. Tag transmissions lasted 320 ms and consisted of an identification code and a 64-bit message relating cumulative time spent at the surface. Transmissions occurred during 6 of every 12 h coinciding with good satellite coverage and an average of six possible passes per day. Argos requirements limited transmission to no more than once every 20 s.

We tagged whales late in their Hawaiian Island occupancy to examine inter-island movements and their departure points for the spring migration to Alaska. All whales were tagged between Port Allen and the Napali Coast within 8 km of shore from a 5.5-m Boston whaler with twin 70-h.p. engines. We slowly approached individuals and groups of up to six animals to within 3–7 m for tagging. Tags were applied with a modified 68-kg Barnett compound crossbow. A C-shaped cup at the end of a pushrod held the tag and a trailing string recovered the pushrod after tag attachment.

Locations were edited from the data if the calculated speed between consecutive locations exceeded 12 km/h for periods >2 h or 16 km/h for periods <2 h (assuming a 5-km radial error around each location).

Results

Whales exhibited no observable overt reaction to tagging beyond that elicited by a close boat approach without tagging. We obtained data for 0.5–17 days ($\bar{x}$ = 8.5 ± 2.7 days) from all six whales (Table 1): a female with a calf, four adults of unknown sex, and a smaller whale of unknown sex that may have been immature. The number of locations varied from 1 to 66 per whale. The mean number of locations per day varied from 1.8 to 3.9 ($\bar{x}$ = 2.7 ± 0.03 locations/day) per individual and provided records of movements ranging from 30 to 1860 km, for a total of 5240 km ($\bar{x}$ = 870 ± 298 km).

Approximately 80% of all the animals we encountered during the 2-week field season moved from east to west along the southwest side of Kaua'i. Five of the tagged whales moved clockwise (starting with east to west movement) along the Kaua'i coast. Four of the six tagged whales were relocated exclusively near or north of Kaua'i. One whale (No. 4) was relocated only once, 32 km from the tag site, 11 h after tagging.

Inter-island movements

Two of the whales (Nos. 3 and 5) visited other islands (Fig. 2). Whale 3 nearly circumnavigated Kaua'i before traveling to the west coast of Oahu, a total of 250 km, in 3.9 days ($\bar{x}$ = 60 km/day). Whale 5 moved clockwise around Kaua'i to the

Table 1. Summary of tagging duration, edited locations, distances traveled, and average travel speeds (distance/time) of six humpback whales equipped with satellite-monitored radio tags in March and April 1995 off Kaua'i, Hawai'i.

Whale No.	Age	Tagging date	No. of edited locations	Time (days)	Distance (km)	Avg. speed (km/day)
1	Adult/calf	26 Mar.	12	4.5	670	150
2	Adult	27 Mar.	32	14.7	1610	110
3	Adult	27 Mar.	7	3.9	250	60
4	Adult	1 Apr.	1	0.5	30	60
5	Adult	1 Apr.	33	9.9	820	80
6	Juvenile?	2 Apr.	66	17.0	1860	110
Total			151	50.7	5240	
Unweighted mean ± SE				8.5±2.7	870±290	90±14

Fig. 2. Tagging locations and movements of three satellite-monitored humpback whales tagged in March and April 1995 off Kaua'i, Hawai'i. Whale 1 is a female with a calf and whales 3 and 5 are adults of unknown sex.

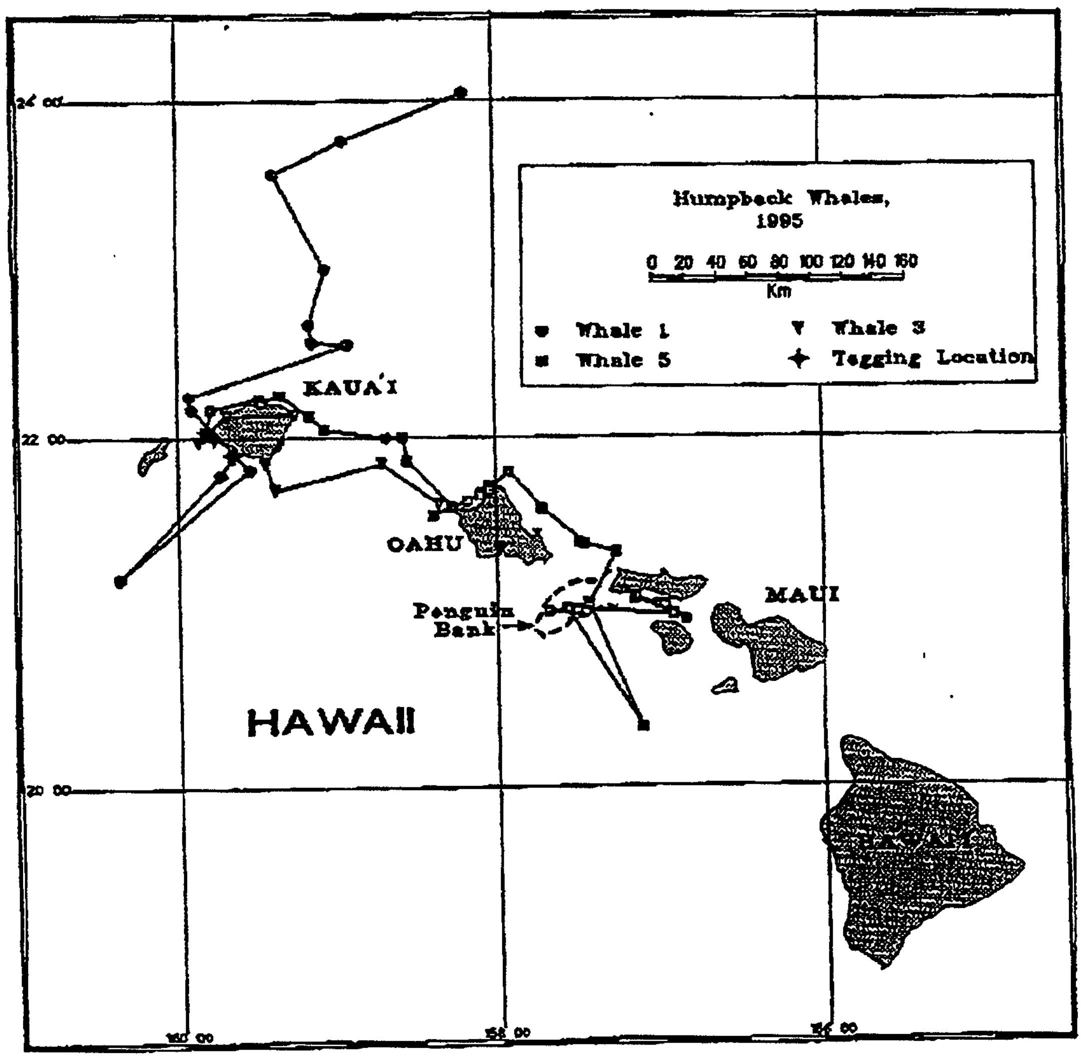
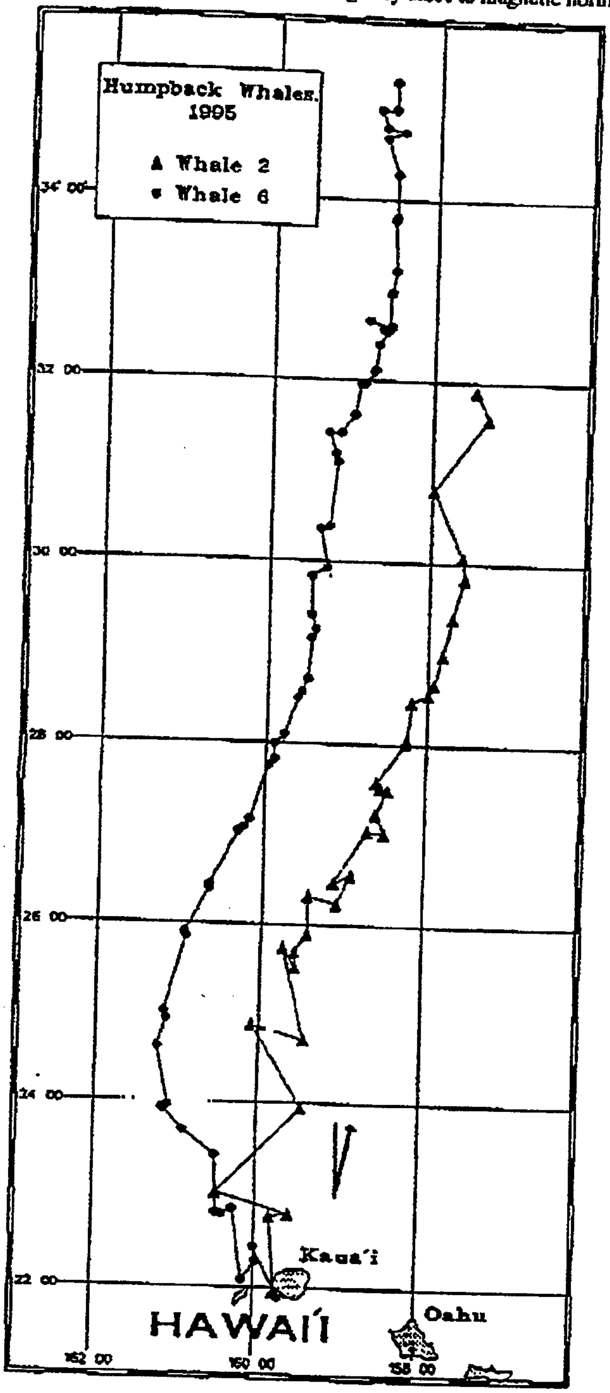


Fig. 3. Movements of an adult humpback whale (No. 2) and a smaller individual (possibly juvenile, No. 6) migrating from Kaua'i, Hawai'i, toward Alaska on a heading very close to magnetic north.



northeast coast, across the Kaua'i Channel to Oahu, along the north coast of Oahu, then across the Kaiwi Channel to the northwest tip of Molokai, south to Penquin Bank (southwest of Molokai), and into the Kalohi Channel between Molokai, Lanai, and Maui (Fig. 2). Thus, in 9.9 days the whale traveled at least 820 km ($\bar{x}$ = 80 km/day) through the coastal waters of five of the Hawaiian Islands. This movement across such a large portion of the winter range is more rapid than had been previously suspected.

Migration

Three tagged whales (Nos. 1, 2, and 6) moved offshore on what we believe was the beginning of the spring migration for each. A female with a calf (No. 1; Fig. 2) was the fastest whale, moving 670 km in 4.5 days ($\bar{x}$ = 149 km/day). She was last located 260 km north-northeast of the tagging site. An adult of unknown age and sex (No. 2; Fig. 3) traveled 1610 km between 32 locations in 14.7 days ($\bar{x}$ = 110 km/day), moving a net distance of 1127 km from the tagging site on an 11° heading. The longest movement was 1860 km in 17 days ($\bar{x}$ = 110 km/day) by a smaller animal (possibly a juvenile) of unknown sex (No. 6; Fig. 3) that was last located 1496 km on a 10° heading from the tagging site. Magnetic north is 10°31' east of true north at Kaua'i.

Speeds

Travel speeds of individual whales ranged from 60 to 150 km/day and the average speed of all animals was 90 ± 14 km/day (Table 1). The two whales traveling within the islands (Nos. 3 and 5) averaged 70 km/day (range 60–80 km/day) in comparison with the three traveling offshore (Nos. 1, 2, and 6), which averaged 120 km/day (range 110–150 km/day). The two longest ranging animals (Nos. 2 and 6) had identical average speeds (4.5 km/h). Not surprisingly, animals that moved in a more consistent direction probably traveled longer distances between locations and had higher average rates of movement than whales meandering among the islands. The extent to which whales meander may provide insight into some whale behaviors (searching for prey or mates versus migration) and can be expressed as a percentage of total distance traveled to achieve the "net" movement from the tagging site to the whale's last location. Thus, the female with a calf (No. 1) meandered more (39% net straight-line movement) than the longest ranging whale (81%). For the latter whale, its net rate of progress dropped from a travel speed of 4.5 km/h down to 4.0 km/h.

Animals moving about in the Hawaiian Islands likely traveled greater distances than is indicated by the straight-line distance between only a few locations per day. The female with a calf (No. 1) had only an average number of locations per day (2.7), so her high average speed (149 km/day) was not biased upward by the fact that she had more locations per day than other whales.

Because we did not follow tagged whales, we do not know for sure why we stopped receiving messages. However, when we made follow-up observations of 11 of 12 tagged right whales (*Eubalaena glacialis*) (Mate et al. 1997), there were no signs of any serious injury or mortalities. We believe that transmissions stopped when the tags' attachments worked loose and the tags were lost.

Discussion

The distances between just a few Argos-determined locations each day result in conservative estimates of distance traveled and speed. The speeds reported here are close to those observed for satellite-monitored right whales traveling comparable distances at 3.5–3.7 km/h (Mate and Nieukirk 1997) and for a northbound migrant gray whale (*Eschrichtius robustus*) at 4–5.1 km/h monitored by conventional telemetry (Mate and Harvey 1984).

The trend of tagged whales to move in a similar direction around Kaua'i and the high degree of mobility they demonstrated within the Hawaiian Islands suggest that at times, animals' movements may not be random. Thus, if whales sometimes move in a consistent direction, surveys to estimate the population need to be carried out in a short period of time to avoid counting animals more than once. Baker and Herman (1981) suggested that whales move into Hawai'i at the southeast end of the island chain at the beginning of the winter season and depart from Kaua'i, the most northwesterly island. The three departures we documented from Kaua'i support the latter part of their hypothesis, but indicate that movement through the islands is not unidirectional.

With the exception of Penquin Bank, which is a shallow area of known humpback whale concentration, travel between islands appeared to be reasonably direct. This suggests that humpback whales in Hawai'i have a stronger preference for shallower coastal waters than for deeper inter-island channels. The movement of the female (No. 1) with a calf could be an exception. Females with calves are frequently among the last whales to leave the islands. If the tagged female with a calf (No. 1) had not actually left the islands to migrate, its meandering route is more understandable and may represent offshore milling behavior as the calf's strength develops.

The cues humpback whales use to navigate during migration are unknown. The consistent direction and speed of whales 2 (large) and 6 (smaller) moving away from Kaua'i toward Alaska suggest similar migratory corridors for animals of different ages, which are within 1° of magnetic north (10°31') (Fig. 3). Although these data are consistent with the hypothesis that whales use magnetic orientation as a means of navigation (Walker et al. 1985; Bauer et al. 1985), it may be a coincidence that their destination happens to be on that bearing.

The direction of travel for whales 2 and 6, if continued, would lead to a destination in the Gulf of Alaska up to 4200 km from Kaua'i. The currents north of Kaua'i tend to be negligible in March and probably did not influence the overall trajectory of the tagged animals. Humpback whales appear at several widely separated Alaskan locations at the start of summer, including the Gulf, the eastern Aleutian Chain, and southeast Alaska (Baker et al. 1985). The latter two locations are within a few hundred kilometres of the projected straight-line track that we observed. The course and speed of humpback whales may change as they near their destination. Gray whales increase their speed as they move farther north from their breeding/calving area (Mate and Harvey 1984), perhaps in part because of progressively less breeding activity en route.

The whale with the longest track (No. 6; Fig. 3) covered approximately 35% of the distance to the Gulf. With a net speed of 4 km/h, the entire migration would be accomplished in 44 days. However, if a calculated average speed of 5 or 6 km/h was efficiently maintained "on course," the migration could take as little as 35 or 29 days, respectively. Proof that such average speeds are sustainable comes from one photo-identified humpback whale observed in Hawai'i 37 days after its sighting in southeast Alaska (Gabriele et al. 1996).

These satellite-monitored radio-tag data are the first to describe the route and initial rate of travel for the spring migration of humpback whales from Hawai'i. Tagging earlier in the winter season and with longer duration tags will produce more information about inter-island movements. Tagging at different islands will generate more information about migration departure points. Longer duration tags will better describe the migration routes and rates.

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