

Directional and non-directional movements of bat rays, *Myliobatis californica*, in Tomales Bay, California

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Synopsis

The goal of this project was to determine if bat rays, *Myliobatis californica*, display oriented movements and are thus a viable model species for the further study of geomagnetic topotaxis in elasmobranchs. We tracked one male and three female rays during September 1998 and August and September 2001 in Tomales Bay, California. The rays exhibited two modes of travel: (1) rapid and highly directional movements in a straight line along the length of the bay and (2) slow and non-directional movements within small areas. Directional movements were defined as point-to-point vectors in the paths of the bat rays that were oriented in similar directions, and the distribution of these was clustered rather than dispersed and uniform. Mean rates of movement during directional swimming approached 0.5 m s^{-1} . In contrast, vectors in the path of bat rays were at times oriented in varying directions, and a distribution of these was widely dispersed as we would expect if the rays were moving randomly. These were defined as non-directional movements. Oriented straight-line swimming is consistent with the species either being able to orient to the bathymetry of the bay or possessing a compass and (or) piloting sense.

Introduction

Many species of sharks are capable of swimming highly directionally in the open ocean (for review, see Klimley et al. 2002). These movements are often attributed to a compass sense because the individual swims at a constant angle to either the direction of a distant object such as the sun (Gruber et al. 1988) or the axis of the earth's dipolar magnetic field (Carey & Scharold 1990; Klimley 1993). This mode of travel resembles the mariner maintaining a course by steering the boat toward a heading relative to the compass needle. Alternately, individuals may swim highly directionally, but along winding paths, which coincide with a fixed geographic feature in the environment, as a mariner sails between two ports

by keeping a constant distance between the boat and the curving shoreline – a navigational technique called 'piloting'.

Previous studies suggest that sharks may utilize both a compass and pilot sense to direct their movements. Kalmijn (1982, 1984) argued that sharks have a compass sense and are sensitive to the earth's dipolar field. Additionally, one of the present authors (Klimley 1993) argued that scalloped hammerhead sharks, *Sphyrna lewini*, possess a piloting sense derived from their electrosensitive acoustico-lateralis system. He demonstrated that sharks swim to and from a seamount in the Gulf of California with great directionality, yet along convoluted paths. These sharks traveled along maxima and minima in the geomagnetic field as

they moved between the seamount and distant foraging grounds. In contrast, the shark's movements when at locations far from the seamount were clustered and non-directional, consistent with foraging for the cephalopods present in these areas (Klimley 1987). He termed the shark's ability to orient to the local magnetic field and actively track ridges and valleys based on geomagnetic intensities as magnetic 'topotaxis'. With electro-receptors widely distributed over the underside of expanded pectoral fins resembling the broad distribution on the expanded head of the hammerhead shark, one might anticipate that bat rays, *Myliobatis californica*, may also utilize geomagnetic cues for orientation during long-distance migrations. Here we investigate whether bat rays exhibit directional movements consistent with possessing either a compass or a piloting sense. Bat rays were tracked during 1998 and 2001 to assess the directionality of movements of this species.

Methods

We tracked bat rays in Tomales Bay, California, located in Marin County north of San Francisco (Figure 1). Tomales Bay is a narrow bay, approximately 1.5 km in width and 24 km in length, formed by the differential movement of two crustal plates along the San Andreas fault. The bay is shallow with a maximum depth of approximately 20 m though the majority of it is considerably shallower, ranging between 1 and 4 m.

Bat rays were captured by hook and line and brought to the side of the boat. An ultrasonic beacon (Vemco Ltd., V32-8H, or Sonotronics, Acoustic) was externally affixed to each ray by means of a stainless steel dart head inserted into musculature on the ray's dorsum, half way between the snout and anterior margin of the pectoral fin. The beacons were cylindrical, having diameters of 24–32 mm and lengths of 60–70 mm, and emitted pulsing signals of 30–40 kHz. The rays were tracked using the "ground zero" method described by Nelson (1987). Briefly, rays were followed in a small skiff using a directional hydrophone and an ultrasonic receiver (Vemco Ltd. VR-60 or DuKane Corp. N30ASB). The receiver provided a direction to the beacon, and the boat was positioned above the ray by moving to a

position where the signal intensity did not vary with direction when the hydrophone was rotated from side to side and increased when the hydrophone was pointed downward. The range of reception was approximately 1000 m, depending on sea surface conditions and ambient noise. The Vemco receiver was linked to a laptop computer, which was interfaced with a differential-corrected global positioning system (GPS) [Magellan, NAV5000 DLX], providing latitude and longitude positions (± 5 m) for the boat at 10 s intervals.

The files of ray positions at 6 min intervals were imported into a geographic information system (ESRI, Arc View 3.2) where they were layered with a 5 m grid digital elevation model of the bathymetry of Tomales Bay prepared by the California Department of Fish and Game, Information Technology Division, GIS Service Center, Sacramento, California.

In order to assess the directionality of each track we calculated a measure of the angular directionality to the vectors in each section of a track, termed the Rayleigh's concentration coefficient (r). This value ranges from '0', when the headings are uniformly distributed, to '1', when all of the headings are in the same direction.

The observed movements of the bat rays were compared against correlated random walks to further assess the degree of orientation. Using the Site Fidelity Test in the Animal Movement 2.0 extension for ArcView (Hooge and Eichenlaub 2000)¹, 100 iterations of random headings were generated for known distances between sequential position determinations from a directional and non-directional section of the track of BR1.

Results

We tracked four bat rays in Tomales Bay, California (Table 1). Bat Ray (BR) 1, a female with a disk width (DW) of 100 cm, was tracked for 28:25 h 26–27 September 1998. BR2 and BR4, females with 43.2 cm and 45.7 cm DWs, were

¹ Hooge P. N. & B. Eichenlaub. 2000. Animal Movement Extension to Arcview. ver. 2.0. Alaska Science Center – Biological Science Office, U.S. Geological Survey, Anchorage, AK, USA.

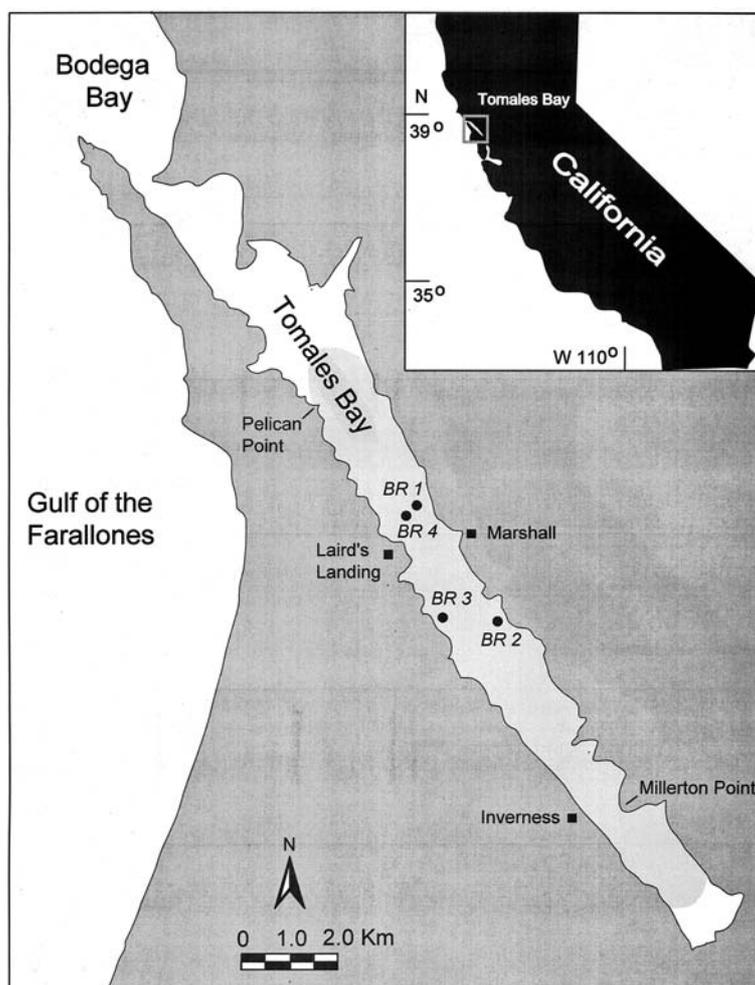


Figure 1. Map of Tomales Bay where four bat rays (BR1–BR4), tagged with ultrasonic beacons, were tracked for periods from 28.4 to 75.6 h during Sep 1998 and Aug and Sep 2001. Solid circles indicate locations where bat rays were tagged; fine stippling denotes extent of the movements by the bat rays. Inset shows location of Tomales Bay on map of California.

tracked for 31:13 and 72:46 h on 17–19 August and 6–8 September 2001, respectively. BR3, a male with a 53.3 cm DW, was tracked for 75:39 h on

23–25 August 2001. The four rays stayed within the inner two thirds of the bay (see light stippling, Figure 1).

Table 1. Bat rays tracked in Tomales Bay, California (DL = disk length; DW = disk width; M = male; F = female; * = estimated size).

Ray no.	DL (cm)	DW (cm)	Sex (M/F)	Tracking		
				Date	Start (h)	Duration (h: min)
1	–	100.0*	F	26 Sep 1998	1117	28:25
2	76.2	43.2	F	17 Aug 2001	2106	31:13
3	76.2	53.3	M	23 Aug 2001	1622	75:39
4	78.7	45.7	F	6 Sep 2001	1642	72:46

Spatial resolution of tracking

Due to the wind and tide, as well as the movements of the boat and the rays, it was impossible to keep the boat directly over the ray at all times. This, plus the accuracy limitations of GPS, introduced error into the position determinations and set limits on the spatial resolution of our tracking efforts. If one were to simply plot every position recorded, the compounded error would imply a

great deal more movement than was actually taking place (Figure 2 inset), whereas spatial resolution would be lost if one were to use too long a time interval between points. To address this and determine the spatial resolution of our method, we selected two portions of the track of BR1 (Figure 2): (1) a non-directional movement (1137–1754 h, 26 September 1998) in which the ray stayed in a confined area, and (2) a highly directional movement (0111–0512 h, 27 September

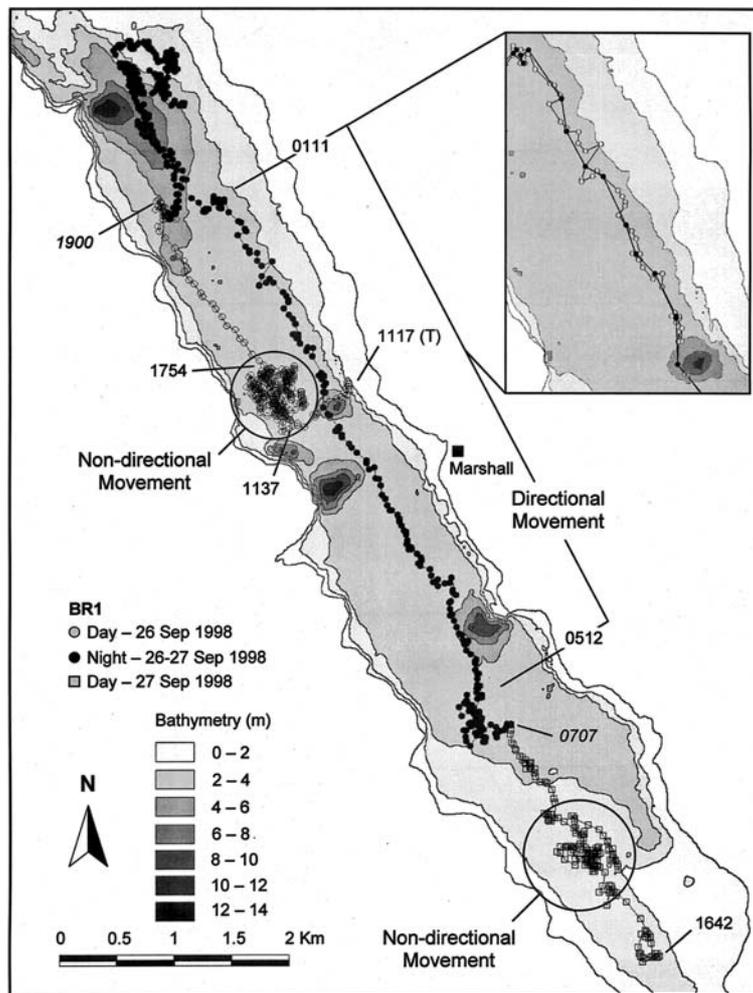


Figure 2. Track of Bat Ray 1 (BR1) in Tomales Bay, tagged (T) at 1117 on 26 Sep 1998 and tracked for 28.4 h until 27 Sep 1998. Clear symbols designate daytime positions determined at 1 min intervals, solid symbols indicate nighttime positions, times for dawn and dusk are in italics. Note the clusters of closely spaced positions indicating non-directional swimming, contrasting with the more widely spaced, linearly oriented positions indicative of directional swimming. Inset shows expanded view of directional movement between 0111 h and 0226 h 27 Sep 1998. Clear circles designate 1 min intervals, solid circles indicate 6 min intervals. Note that the 1 min vectors display significant variability in heading; however, this includes the movement of the boat due to wind and current as well as movement while following the fish. Filtering the positions to 6 min intervals removes much of this variability and gives a more accurate indication of the actual movement of the ray.

1998) during which the ray was observed to move in a straight and continuous path. The raw data points, recorded at 10 s intervals, were filtered at time intervals of between 1 and 15 min. Rayleigh's r coefficients were calculated for each time interval and the results plotted (Figure 3). The r value for the non-directional movement is low and does not increase significantly as the time interval between position determinations lengthens (e.g., $r_{1\text{min}} = 0.06$, $r_{6\text{min}} = 0.04$, $r_{15\text{min}} = 0.15$, Figure 3a). In contrast, the r value of the directional movement increased as the time interval lengthened (Figure 3b). After an interval of 6 min ($r = 0.75$), the rate of increase diminished and the line became asymptotic. The mean rate of increase between intervals of 1 and 6 min is $0.056 r \text{ min}^{-1}$;

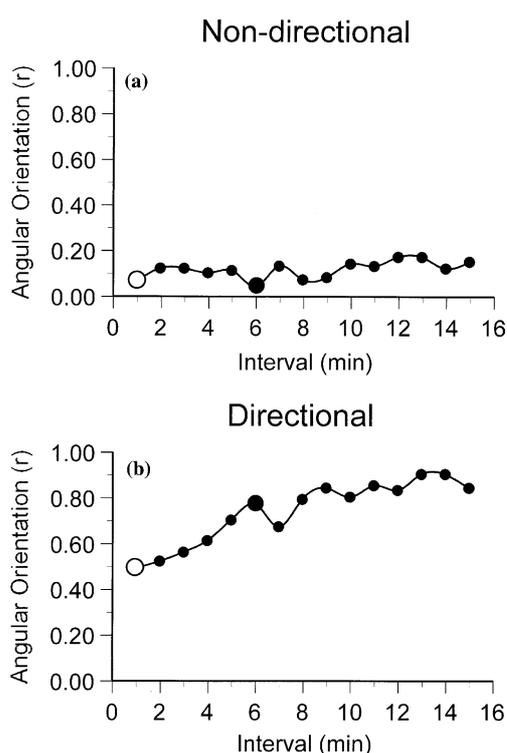


Figure 3. Rayleigh coefficients of angular concentration (r) for vectors determined between positions for BR1 after increasing intervals of time: (a) example of non-directional movement. Note that the coefficient r does not increase with increasing time intervals between position determinations; (b) example of highly oriented movement. The coefficient r for the shortest time interval (1 min, large clear circle) is significantly higher than that of the non-directional movement, and increases as the time interval lengthens, reaching an asymptote at an interval of 6 min (large solid circle).

the rate for intervals 7–15 min is $0.014 r \text{ min}^{-1}$. Based on this analysis, an interval of 6 min was selected as optimum tracking resolution in this instance and used in all subsequent analyses.

We observed two types of travel, directional and non-directional, by bat rays in Tomales Bay. Both of these movement patterns are apparent in the track of BR1 during 26–27 September 1998 (Figure 2). Comparison of these two modes of movement with randomly generated tracks indicates that the directional and non-directional movements of the ray were different than we would expect if the ray was simply moving randomly.

Directional movement

BR1 performed a highly directional movement in Tomales Bay from 0111–0512 h on 27 September 1998 (Figure 4a) covering a linear distance of 6 km. The ray's track followed a roughly straight line, consisting of 39 vectors each with its own heading and distance. The ray moved in a mean southeasterly direction with 36% of the headings in the $121\text{--}150^\circ$ angular class and 41% in the $151\text{--}180^\circ$ class. The mean direction of movement of BR1 was 121° (southeast) and the angular dispersion of its headings was 58° . The r value of this movement was 0.75, which is significantly different than a uniform distribution ($p < 0.01$, Rayleigh Test). In comparison, the distribution of vectors for the 100 random walks generated from this movement were highly dispersed (e.g. dotted line, Figure 4a, $r = 0.06$).

BR1 moved over ground at a mean rate of 0.45 m, when rates were calculated from the straight-line distance between points ($N = 39$) throughout the track. The highest percentages of rates of movement were in 0.30–0.39 to 0.50–0.59 m s^{-1} rate classes (Figure 5a), although half as many movements were split between the slower classes such as ≤ 0.09 or faster classes such as 0.90–0.99 m s^{-1} .

BR4 was tagged near the center of Tomales at 1943 h on 6 September 2001 (Figure 1). BR4 moved northwesterly toward the mouth of the bay until 2324 h, when it reversed its direction and began moving southeastward toward the base of the bay (Figure 6a). BR4 spent much of the first night and following day between three deep areas, two along the eastern coast and one along the

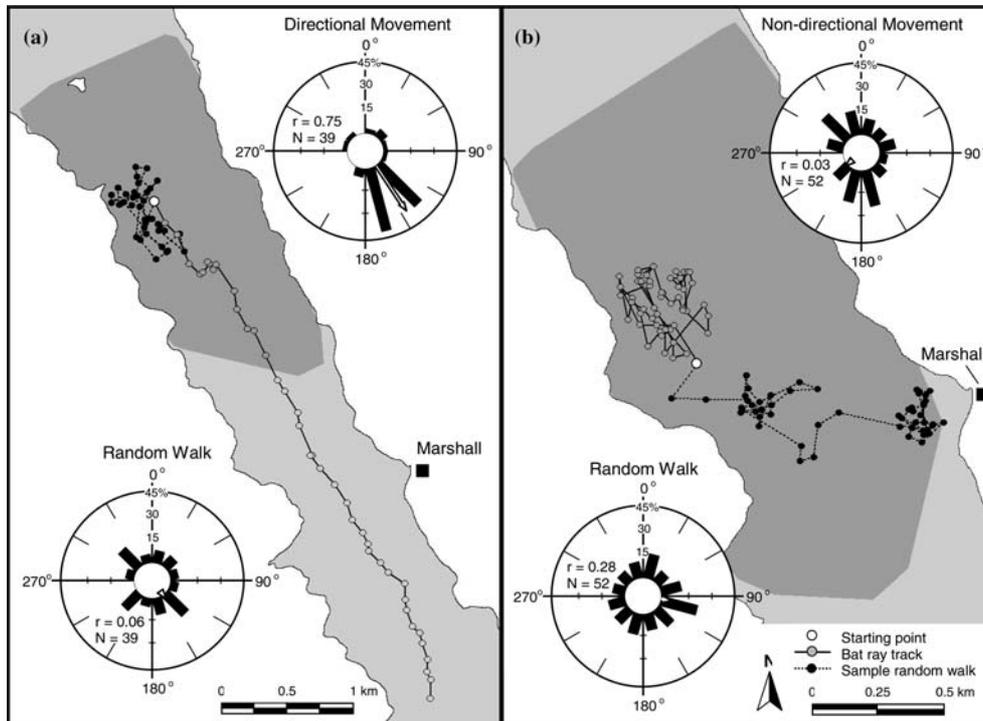


Figure 4. Comparison between random walks and observed movements of BR1 for a directional track segment (27 Sep 1998) (a) and non-directional track segment (26 Sep 1998) (b). Tracks are composed of vectors between points recorded at 6 min intervals. The dark stippling indicates the minimum convex polygon surrounding the area encompassed by 100 random walks. The solid line with clear circles indicates the actual track, whereas the dotted line with solid circles indicates an example random walk. The vector distributions for the directional movement (a) are highly concentrated ($r = 0.75$) while a sample corresponding random walk is dispersed ($r = 0.06$). In contrast, the vector distribution for the non-directional movement (b) is as dispersed ($r = 0.03$) as the sample corresponding random walk ($r = 0.28$).

western coast of the bay. During the night of 7 September 2001, BR4 moved northwestward along the same path taken during the prior night (Figure 6b). The bat ray passed the same locale at 2319 h as it had passed at 2339 on the prior night. BR4 also visited the same vicinity at 1338 h on 8 September 2001, the third day of the track (not shown). In total, during the period of 6–8 September, BR4 conducted 11 directional movements along the eastern shore of Tomales Bay (mean $r = 0.68$, ranging between 0.52 and 0.97, $p < 0.01$).

Non-directional movement

BR1 exhibited non-directional movements at 1137–1754 h on 26 September 1998 (Figure 4b). Its track was highly clustered and lay entirely within a circular area with a diameter of 500 m over a bottom depth of 4.1–6.0 m. The coefficient

of angular concentration was 0.03 ($N = 52$) which does not differ statistically from an even distribution in all directions ($p > 0.05$, Rayleigh Test). This is statistically equivalent to the random walks generated from these data ($r = 0.28$ in the example illustrated in Figure 4b). Note, though, that the recorded track was considerably more localized than those predicted by the random model, suggesting that the rays are actively remaining in a discreet area rather than simply moving haphazardly.

The distribution of the swimming headings during this section of the track was somewhat bi-modal with directional modes toward the northwest ($301\text{--}330^\circ$ and $331\text{--}360^\circ$ classes) and southeast ($151\text{--}180^\circ$ and $181\text{--}210^\circ$ classes). The ray moved back and forth in a small area along an axis oriented along the length of the bay. BR1's rate of movement during this period was much slower than during the directional portion of the track. BR1's

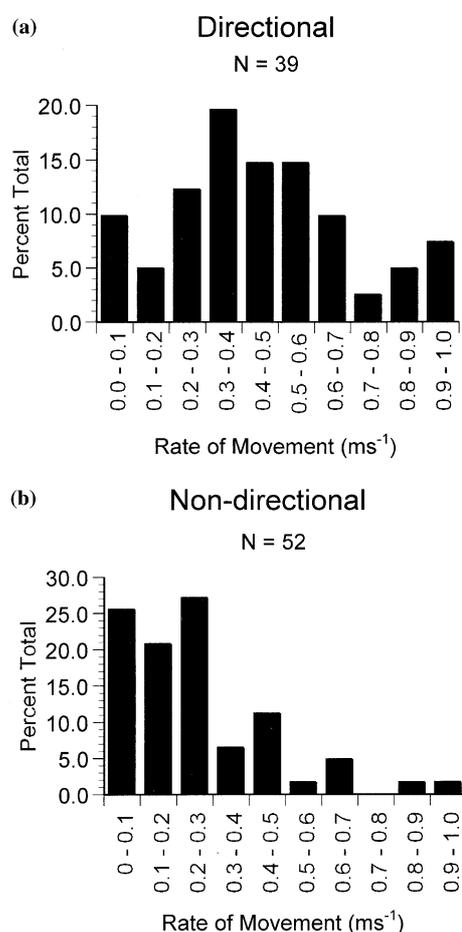


Figure 5. The rates of movement during directional (a) and non-directional (b) segments of track of BR1 during 26–27 Sep 1998. The highest percentages of rates during the directional movement were recorded in the three rate classes encompassing 0.2–0.6 m s⁻¹. The highest percentages of swimming speeds during the non-directional movement were slower, encompassing the 0–0.3 m s⁻¹ rate classes.

mean rate of movement was 0.24 m s⁻¹ and the majority of vectors ($N = 52$) were in the slowest three rate classes, 0–0.09 to 0.20–0.29 m s⁻¹ (Figure 5b).

BR2 was tagged at 2106 h on 17 August 2001 in a depth of 4.1–6.0 m, 1 km northwest of the northernmost of four aquaculture facilities along the eastern coast of Tomales Bay (Figure 7a), where oysters are grown in bags attached to rafts. This ray swam to the second northernmost of these facilities within 1.5 h, arriving at it at 2236 h, and spent the rest of the first night and much of the following morning making small, randomly

directed movements similar to those of BR1 ($r = 0.19$, $N = 84$, $p > 0.05$) within the confines of the facility (Figure 7a). BR2 left the facility at 1026 h and moved southeasterly toward the middle of the bay, where it stayed until we broke contact at 1717 h to refuel the boat. We eventually relocated BR2 within the aquaculture facility at 2026 h on 18 August, where it remained until we again broke contact at 0415 h the next morning, 19 August, for reasons of safety.

BR3 was tagged at 1622 h on 23 August 2001 at a location 1.5 km west of BR2 near the western coast of Tomales Bay (Figure 1). This male bat ray was tracked intermittently for a period of four days (Figure 7b). BR3 moved initially to the eastern side of the bay and then slowly moved northward before reversing its direction and moved along the eastern coast in a southeastern direction during Night 1. Contact was broken with BR3 at 0311 h, but the bat ray was relocated at 0800 h, 100 m southwest of the northernmost aquaculture facility. This bat ray spent most of one night and three days moving little within a small circular area with a diameter of 1 km toward the center of the bay. During this time period, BR3 swam slowly and non-directionally ($r = 0.07$, $N = 164$, $p > 0.05$). The ray left this area 1541 h on 26 August and moved slowly 1.5 km toward the southeast until contact was broken off with the individual at 2001 h.

Additional observations

On 8 September 2001, we detected BR2 and BR3 moving with BR4 in a southeastern direction at 1628 h. The three bat rays were found together in a small area at 1642 h, and again 500 m away at 1657 h. We detected two or more of the rays near the base of the bay until dusk, between 1936–1940 h, when BR 4 separated from them and moved northeastward.

Discussion

The four bat rays which we tracked stayed for periods of 4–24 h within confined areas of Tomales Bay, where they exhibited both directional and non-directional movements. We believe that this limited movement is consistent with the

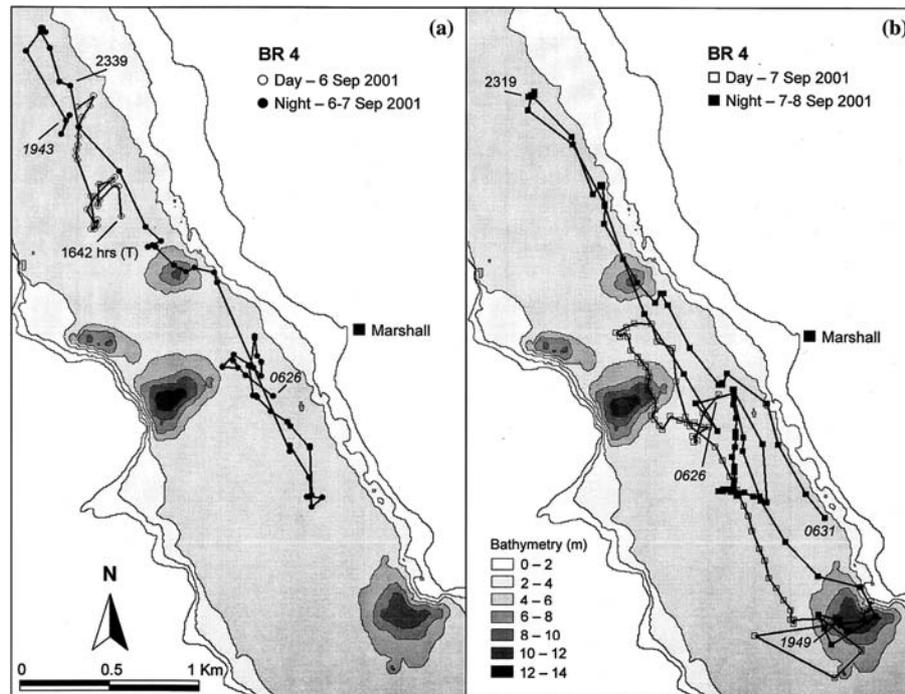


Figure 6. Tracks of Bat Ray 4, tagged (T) at 1642 h on 6 Sep 2001, from 6 to 7 Sep 2001 (a) and 7–8 Sep 2001 (b). Note that BR4 traveled over roughly the same path, close and parallel to the eastern shore of Tomales Bay, during both nights and passed the same geographical point at similar times, 2339 h the first night and 2319 h on night two. Times of dawn and dusk are in italics.

rays searching for prey buried in the sand flats where the species is known to feed (Karl & Obreski 1976).

Two of the four bat rays (BR1 & BR4) made highly oriented movements. The steady courses of these rays were consistent with the species being able to orient within the bay. Their movements were similar to the straight-line swimming observed in blue sharks, *Prionace glauca* (Landesman 1984; Carey & Scharold 1990), mako sharks, *Isurus oxyrinchus* (Klimley et al. 2002), scalloped hammerhead (Klimley 1993; Klimley & Nelson 1984), and a juvenile white shark *Carcharodon carcharius* (Klimley et al., 2002). BR4 swam repeatedly along the same 3 km path and along the eastern shore of Tomales Bay during three consecutive nights. The bat ray traveled through the same locale at times < 20 min apart on successive nights (2339 h on 6 September vs. 2319 on 7 September 2001). This travel strategy is more consistent with the possession of a piloting sense (e.g., geomagnetic topotaxis as described in Klimley 1993). It is also possible that the ray may

have been following visual landmarks or depth contours within the bay on both occasions.

The use of geomagnetic cues for orientation is an intriguing possibility in this region. The San Andreas Fault extends the length of Tomales Bay, separating a detached section of the North American plate on the western side of the fault from the main plate on the eastern side (J. S. McClain, University of California, Davis, Department of Geology, personal communication). The crust to the west is generally low in magnetic remanence, but the crust to the east is more magnetized because it is composed of basalt deposited during eruptions of an ancient seamount on the North American plate. Sections of these basalts contain tiny magnetic particles with a single polarity relative to the polarity of the earth's main field; other sections the opposite polarity, giving rise to magnetic maxima and minima. Thus, a magnetic valley or ridge may exist along the shore in the bay.

Matern et al. (2000) argued that the movements of bat rays in Tomales Bay result from behavioral

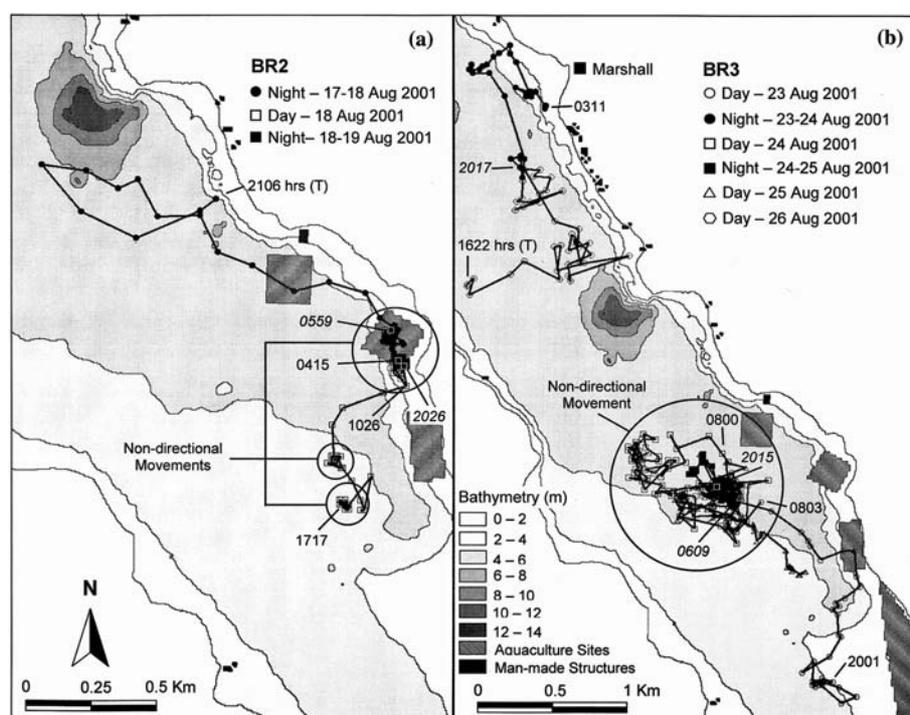


Figure 7. The tracks of Bat Rays 2 and 3 exhibiting non-directional movement, such as the movements of BR2 between 17–19 Aug 2001 (a) and the movements of BR3 during four days and two nights between 23 Aug and 26 Aug 2001 (b). Times of dawn and dusk are in italics.

thermoregulation. They found that the rays moved between the warmer and shallow inner bay and the cooler and deeper outer bay depending on water temperature conditions influenced by changes in tide and time of day. The highly directional movement of BR1 from 0111–0512 h on 26 September 1998 southeastward toward the base of the bay was consistent with the bat ray seeking warmer water. The oriented movements of BR4 toward the northwest after 2339 h on 6 September and 2319 h on 7 September 2001 were also consistent with its seeking out warmer water farther inside the bay. However, contrary to the thermoregulation hypothesis, BR2 lingered within a circular area < 1 km wide in order to feed during the night and day of 5 August 2001. BR 3 also stayed in a circular area < 1 km wide during the day of 25 August, night of 25–26 August, and day of 26 August 2001. There may be a cost-benefit element to this behavior of bat rays. The rays may tolerate lower temperatures at those times when foraging success is high in a particular region of the bay. Further work will need to be done in order to

determine the cues that bat rays use during directional as well as non-directional movements.

It is interesting to note that, of the multitude of bat rays residing in Tomales Bay, the three that were tagged within the same time period (BR2, 3, 4) all came into close contact with one another on several occasions. The probability of this being a chance occurrence seems exceedingly slim though difficult to quantify. While we may not assume a social context for this event without direct observations of the rays, this does suggest that bat rays may aggregate intermittently within the bay at specific locations. Aggregations at distinct locations would also provide support for a navigational ability.

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