TIDAL INFLUENCE ON DIEL MOVEMENT OF NORTH ATLANTIC RIGHT WHALES (*Eubalaena glacialis*) IN THE BAY OF FUNDY

by

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ABSTRACT

The endangered North Atlantic right whale (*Eubalaena glacialis*), is known to aggregate in the Bay of Fundy, between New Brunswick and Nova Scotia, Canada to feed during summer. The Bay of Fundy is famous for its extreme tidal range of up to 15 meters, but the effect of these tides on the distribution of whales has not been thoroughly investigated. I hypothesized that the distribution of movements of the whales is influenced by tidal currents, which can average from two to three knots at mid–tide. To test this hypothesis, I queried the North Atlantic Right Whale Catalog of photographically identified individuals and compiled sighting records of animals seen more than once a day in the Bay of Fundy. Paired sightings for each animal were analyzed for time, distance and tidal stage changes between each set of sightings. These results were compared to the hypothetical movement of a passive particle using Canada’s Department of Fisheries and Ocean WebDrogue model. My results indicate that right whales are displaced by the tides. The likelihood that they have remained with a discrete prey patch was correlated with the overall displacement of the whale and the amount of time elapsed. There was a significant correlation between the tidal current direction and the short–term movements of right whales in this habitat area. Understanding how right whales utilize this important habitat area will help inform more effective management decisions.
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INTRODUCTION

The Bay of Fundy, Canada is a primary summer and autumn habitat for the endangered North Atlantic right whale, *Eubalaena glacialis*. As many as two-thirds of the small population of 325 animals (IWC, 2001) utilize this habitat yearly as a feeding, nursery and socializing area from July to October (Murison and Gaskin, 1989; Woodley and Gaskin, 1996; Baumgartner *et al.*, 2003a). The Bay is widely known for its extreme tidal ranges, resulting in tidal currents which affect the distribution and concentration of many organisms, including the preferred prey species of right whales, *Calanus* spp. (Murison and Gaskin, 1989; Woodley and Gaskin, 1996; Baumgartner *et al.*, 2003a). Right whales aggregate in Grand Manan Basin, east of Grand Manan in the lower Bay of Fundy. Tidal currents in the Grand Manan Basin have a central gyre (Davis, 1984) that promotes the accumulation of *C. finmarchicus* and other zooplankton in the area (Fish & Johnson, 1937; Murison, 1986). The currents in this area advect passive particles in an elliptical pattern (Baumgartner *et al.*, 2003b). The relationship between these currents and the distribution and movement of right whales, however, is still relatively unclear.

Right whales in the Bay of Fundy are able to move quickly across long distances, do not remain in discrete areas for well-defined periods of time and prefer the deepest parts of the Bay (Mate *et al.*, 1997; Slay and Kraus, 1998). Woodley (1992) found right whales associated with warm sea surface temperature, but attributed this correlation to chance, as most of the temperatures throughout the study area were within the range known to be utilized by right whales throughout their range (10-15.4 °C, Winn *et al.*, 1986). Murison and Gaskin (1989) discovered that most right whales were found in stratified waters and that they were observed feeding along tidal convergent fronts in the lower Bay of Fundy. However, their work on tidal currents and copepods concentrated primarily on large-scale movements over the course of days and weeks. Murison (1986) observed right whales travelling in the direction of tidal currents, but her sample size was small, precluding any statistical analyses. Woodley (1992) later suggested that it might be energetically efficient for whales to passively travel with the tidal currents.
The effects of tidal phase and currents have been examined for other marine mammal species. For example, increased densities of fin whales (*Balaenoptera physalus*), minke whales (*Balaenoptera acutorostrata*), and harbor porpoise (*Phocoena phocoena*) north of Grand Manan Island in the Bay of Fundy occur during flood tides due to the aggregation of prey in the wake of the island (Johnston *et al.*, 2005a; Johnston *et al.*, 2005b). Several studies have identified correlations between foraging behavior, movement and distribution of bottlenose dolphins (*Tursiops truncatus*) with tidal stage (Lockyer and Morris, 1986; Harzen, 1998; Gregory and Rowden, 2001). These studies suggest that there are correlations between the distribution and movement of animals and their prey, which are in turn strongly correlated with tidal stage. However, these studies primarily address near-shore situations where small-scale tidal fronts are presumed to be concentrating prey and attracting the dolphins (Mendes *et al.*, 2002).

In the Bay of Fundy, Baumgartner *et al.* (2003b) observed right whales diving to deeper than 100m to feed on resting stage five *Calanus* (C5). These authors suggested that the energetic benefits of feeding on these less active and energy rich (due to larger oil sacs) prey was greater than feeding on the younger *Calanus* in shallower waters, because the latter have less oil stores and are more active. The presence of diapausing *C. finmarchicus* in the depths of 90-140m has been correlated strongly to the presence of right whales in Grand Manan Basin (Baumgartner *et al.*, 2003b). This study also noted that the movement of mid-water *C. finmarchicus* and right whales was related to tidal phase, leading to the hypothesis that the right whales may remain with a single patch of copepods for as long as a day and over spatial scales of several kilometres, as it is advected by tidal currents. However, Baumgartner *et al.* (2003b) did not identify individual right whales so it is still unclear whether the same animals were remaining with the prey patch.

The purpose of the present study was several-fold. First, I tested the hypothesis that individual right whales were being displaced by the tidal currents. Second, I looked at whether right whale movement could be directly correlated with the tidally induced movements of their prey. I queried the North Atlantic Right Whale Catalog (Right Whale Consortium, 2007) for
sightings of individual animals over daily time frames and compared the movements of these animals to the simultaneous movement of modeled particles using the Canadian Department of Fisheries and Oceans WebDrogue model. I compared different tide stages for changes in correlation between whale movement and modeled prey movement.

METHODS

Study Area

The Bay of Fundy is located in southeast Canada between New Brunswick and Nova Scotia, with the southwest end open to the Gulf of Maine. The prevailing tidal currents in the lower Bay of Fundy occur in a northeasterly direction with an incoming, or flood tide, and in a southwesterly direction with an outgoing, or ebb tide (Nobeltec, 1996). In the lower Bay of Fundy this results in an elliptical tidal circulation in a counterclockwise direction (Sankaranarayanan and McCay, 2003) (Figure 1). The Bay of Fundy tides are semidiurnal, with high and low tides occurring approximately twice a day (Kelley and Kelley, 1995). The Gulf of Maine system has a natural period of “oscillation,” of a little over 13 hours (Cutnell and Johnson, 1995), which coincides approximately with the 12.4 hour period of lunar tide coming in from the North Atlantic, resulting in exaggerated tide ranges of up to 15 meters at the head of the Bay of Fundy (Kelley and Kelley, 1995). The speed of the tidal currents in the Bay of Fundy average between 2-3 knots (3.7-5.5 km/hr) at mid–tide (Nobeltec, 1996).

Photographic Identification

Right whales can be photographically identified by the patterns of cornified epidermis, or callosity, found on their upper jaw, or rostrum (Kraus et al. 1986; Payne et al. 1983). The callosity is formed by the eruption of cornified skin in areas on the whale that are comparable to the places that humans grow hair. Callosities are found on the rostrum, chin, behind the blowholes and above the eyes. The callosity itself is black in color, but is inhabited by vast numbers of tiny cyamids,
Cyamus ovalis. The cyamids are white in color and cause the callosity pattern to appear white. Each right whale has a unique pattern along the rostrum visible when the whale comes to the surface. This information, combined with other unique features that the whale may acquire throughout its life, such as scars, is used to identify individual animals using photographs taken from both vessel and aerial research platforms (Payne et al., 1983; Kraus et al., 1986).

Right Whale Database

The North Atlantic Right Whale Catalog, curated by the New England Aquarium, contains over 200,000 images representing over 20,000 sightings of 410 whales. The Catalog is a compilation of the efforts of many individuals, whale watch groups and research organizations along the east coast of North America. Each sighting is entered into a MS Access database, which includes the corresponding time, date and location.

I queried the right whale catalog for multiple sightings of the same whale during a single day in the Bay of Fundy. Mothers with calves or animals seen in surface active groups (SAGs) (Kraus and Hatch, 2001) were excluded from the analysis, because their behavior over time may have been less influenced by foraging and more influenced by maternal care or social behavior. Some animals were seen three or more times in a day. In these cases, data points were combined so that the first and second sightings comprised one record, and the second and third sightings were paired to make a second record. I examined the records to determine the time elapsed between each pair of sightings. Sightings less than one hour apart were not used in the analysis because too little time had elapsed to reasonably expect the locations to differ as a result of the effect of current. The resulting dataset consisted of 1118 paired sightings of individual whales between 1982 and 2006.

Tide Data

I acquired predictions of local tidal currents from Tides & Currents for Windows v.3 software (Nobletec Software, 1996), based on U.S. National Oceanic and Atmospheric Administration and Canadian Hydrographic Service harmonic constants. The software uses recorded tide and current observations to tabulate and reduce them to a set of factors that model tide
and current trends at a given location, referred to as a “harmonic station.” “Secondary” station tide and current data are derived from the data recorded at harmonic stations. Thus there is no physical record of actual tide and current data at secondary stations, only an inferred set using data from a nearby harmonic station. In this case, tidal current data from secondary station Point Prim, Nova Scotia (44°45.0N, 66°15.0W) were used, which is approximately 11 nautical miles northeast of the center of the Bay of Fundy Right Whale Conservation Area (44°37.5N, 66°26.5W). The times of high tide, low tide, maximum flood currents and maximum ebb currents predicted by the software were verified during the 2001 study of oceanographic variables (Baumgartner et al., 2003b) using the NOAA Ship Albatross IV scientific depth sounder (Simrad EK-500), and found to be accurate.

Each sighting was coded for tidal stage, i.e. flood, ebb, or slack, using Tides & Currents Pro software version 3.3. Each whale sighting was rounded to the nearest 15 minute interval and joined to the corresponding 15 minute interval in the Tides and Currents output table for tide stage (flood, ebb, or slack) and the tidal current speed. Slack tide was defined as periods of current speed less than 0.1 knot with no flow direction. Slack tide was thus usually under 15 minutes in duration and not every switch between tides included a slack tide time. Flood tides were defined as current speeds of 0.2 knots or greater and a 40° direction of flow. Ebb tides were 0.2 knots or greater in a 235° flow direction. Average flood current speed for the sightings coded as flood was 1.28 knots while the average for ebb sightings was 0.8 knots. In addition, each pair of sightings was coded for overall tidal difference, resulting in codes of “same” if both sightings occurred in within the same flood or ebb tide, “switch” if the pair changed from one tide stage to the other, and “slack” if one of the two sightings occurred during a slack tide time.

**WebDrogue Model**

I used the Canadian Department of Fisheries and Oceans WebDrogue Drift Prediction Model (http://www.mar.dfo-po.gc.ca/science/ocean/coastal_hydrodynamics/WebDrogue/webdrogue.html) to predict the movements of passive “particles” from the same time and location as the first sighting in each right whale pair. The location of this “particle” at the same time as the
second sighting was recorded and compared to the actual location of the right whale after the same amount of time. (Figure 2) The WebDroge drift trajectory program was run using the five major tidal constituents in the Bay of Fundy (Sankaranarayanan and McCay, 2003).

The WebDroge predictions were all started at a depth of 100m, a vertical average of the 95-105m depth velocity fields. This depth corresponds to the average depth of 90-140m for Calanus patches and right whale feeding dives reported by Baumgartner et al. (2003b). In cases where the averaging interval in the WebDroge program intersected the bottom, the average over the bottom 10m was used.

Using ArcGIS 9.2 Hawth’s tools extension (Beyer, 2004), distances were calculated between the position of the modeled particle and the second sighting position for each record. To assess the hypothesis that individual whales were tracking patches of prey that were passively advected by tidal currents, I analyzed the probability of the second sighting being within a patch, assuming the modeled particle was in the center of a prey patch 530 ± 280m across with a range from 230 to 840 meters (Wishner et al., 1995). While there have been numerous studies on the vertical distribution of Calanus copepods (Baumgartner and Mate, 2003; Kenney et al., 1986), this is the only known estimate of horizontal patch size. I used a generalized linear model (GLM) to determine which variables (time between sightings of the whale; distance between whale sightings; and tide stages at each sighting) influenced the likelihood that the second sighting was within the modeled position of the prey patch. Models were compared using Akaike Information Criterion (AIC). Correlations between these variables were also determined for each tidal stage.

RESULTS

When I examined the overall direction of travel between paired sightings, I first determined in which tidal stage the movement occurred. For the purposes of this analysis, sightings coded as “same” were separated into ebb and flood codes. In pairs in which one of the individual sightings
was coded as slack, the pair was given the tidal code of the other sighting. For instance, if the whale was first sighted during a slack tide and next seen during the flood tide after the slack, the pair was coded as “flood.” I used a Chi square test to determine whether the displacement for each pair of sightings was different from that expected by chance. In each case the results were significantly different than chance (Figure 3), with 185 of 261 ebb pairs moving to the southwest, the prevailing direction of ebb tides in the Bay ($\chi^2 = 313.45, p < 0.0001$). Of the 482 flood pairs, 329 had an overall movement to the northeast, the prevailing direction of a flood tide in the Bay ($\chi^2 = 512.739, p < 0.0001$).

To determine if individual right whales remained within discrete patches of prey, the second sighting in each pair was compared to the prey position predicted by the WebDrogue model. A truncated normal distribution was assumed for these calculations with the Wishner et al. (1995) maximum and minimum estimated patch sizes (230 and 840m) as the endpoints.

The results were fitted to a generalized linear model (GLM) to determine the influence of the time between whale sightings, distance between sightings (or displacement), and the tidal stage. The predictor variables were analyzed for correlation using a Spearman ranked correlation. Time between sightings and whale displacement variables had a positive correlation ($r = 0.5068, p < 0.0001$). Perhaps it is to be expected that the longer the time lapse, the further the whale may have traveled. The best model (Figure 4) included the significance of the time elapsed between sightings ($p < 0.0001$) and amount of whale displacement ($p < 0.0001$). The model did not include any tide variables.

The ability of the time elapsed and displacement variables to predict the distance between the whale and the predicted location of its “prey” over time was tested using Spearman correlations. All pairs of whale sightings with elapsed times between sixty minutes and two and half hours were compared to sightings with elapsed times between four hours and six hours, times chosen arbitrarily, taking into account there were no sightings under one hour. There was a difference in the degree of correlation between the time elapsed and the distance from the modeled prey patch.
For the shorter time periods there was a significant positive correlation ($r = 0.4396, n = 685, p < 0.0001$) and for the longer time periods there was hardly any correlation at all ($r = 0.0779, n = 131, p = 0.3768$) and it was not significant.

The best fit GLM excluded tide variables, but when they were included, the “same” tide variable was significant ($p < 0.0001$). To more closely examine at the effects of tidal stage on the difference between whale displacement and modeled prey movement, I examined Spearman correlations. During ebb tides, the strongest correlation was between the amount of time elapsed and the whale displacement distance ($n = 263, r = 0.6145, p < 0.0001$). There was also some correlation between the time elapsed and distance from the predicted prey patch ($n = 263, r = 0.4366, p < 0.0001$). During flood tides, there was some correlation between whale displacement distances and distances from the prey patch ($n = 479, r = 0.5031, p < 0.0001$) as well as between the amount of time lapsed and the whale displacement ($n = 479, r = 0.5303, p < 0.0001$). Interestingly, the correlation between the time elapsed and the distance from the prey patch ($n = 479, r = 0.3337, p < 0.0001$) was weaker than between the other variables. Correlation between the whale displacement and the distance from the prey patch during “switch” tides was stronger ($n = 376, r = 0.5568, p < 0.0001$) than the correlations between the time lapse and distance from prey patch ($n = 376, r = 0.3368, p < 0.0001$) and between the time lapse and the overall whale displacement ($n = 376, r = 0.4391, p < 0.0001$).

DISCUSSION

The results of the present analysis demonstrate a correlation between the short–term movements of right whales and tidal currents in the Bay of Fundy. Whales were more likely to be displaced to the southwest in an ebb tide and to the northeast during a flood tide. Photographic images of individuals confirm that individual animals were displaced by tidal currents, as hypothesized by Baumgartner et al. (2003b).
The likelihood that a whale will remain in the same area as a potential prey patch can be predicted by the overall displacement of the whale and the time elapsed. Baumgartner et al. (2003b) suggested that whales may remain with a prey patch for up to a day and over spatial scales of several kilometers. I demonstrated a positive correlation between both the time elapsed and whale displacement variables and the ultimate distance between the whale and the modeled prey patch. Whales may remain with a discrete prey patch for a period, as the time elapsed increases or the distance the whale is displaced increases, so does the distance between the whale and the modeled prey patch. When I examined the correlation between time and distance from “prey” for periods of time less than two and a half hours there was a much stronger correlation than for time differences between four and six hours where there was no significant correlation. Whales may remain with discrete patches of prey over short periods of time, but my analysis suggests that this association does not last more than a few hours.

When the observations were compared between different tidal stages there was little difference in the amount of correlation between the elapsed times and distance from the “prey.” However, the correlation between the time elapsed and whale displacement during the same tidal stages was stronger than when the tides switched suggesting that animals tend to move further with the running tide than they do when the time includes a slack tide. My results suggest that this is due to the fact that the whales are displaced by tidal currents.

During time periods when the tides switched the correlation between whale displacement and distance from the “prey” was stronger than within the same tidal stage. Whales that traveled farther during a tide switch were less likely to be near the “prey,” than whales that traveled farther during running tides. This could support the hypothesis that right whales in the Bay rest during slack tide, perhaps because running tides aggregate their prey and the patches disperse during slack tide. Following this period of rest, right whales resume search behavior and forage new prey patches. Previous studies have shown that the currents in the lower Bay of Fundy advect passive particles in an elliptical pattern, retaining them in the area and the WebDrogue model simulated this
pattern repeatedly (see Figure 2). If copepods are retained in the area, then whales which travel too far may leave the area of aggregated prey.

Future research should better describe the distribution and behaviour of prey patches. A more accurate estimate of horizontal patch size could help refine the analysis of distances from “prey.” Prey distribution and behavior during slack tides also warrants further research to examine the hypothesis that the running tides aggregate the prey and slack tides disaggregate them.

As one of five identified critical habitats for the North Atlantic right whale (Kraus and Kenney, 1991; Kraus and Brown, 1992; Russell et al., 2001), the Bay of Fundy has been designated as a conservation area by the Canadian government (Brown et al., 1995). The Bay of Fundy is transected by shipping lanes that pass to the east of conservation area. These lanes were moved four miles to the east in 2003, drastically reducing the likelihood of an interaction between a right whale and a ship by 80% (Vanderlaan et al., 2008). It was made possible by years of research that showed an overlap in right whale habitat and the shipping lanes. The Bay of Fundy often experiences thick fog, strong winds and rough sea conditions that make vessel surveys impractical. Understanding how right whales utilize their habitat areas will help researchers and managers create more effective protection measures for this critically endangered species.

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LITERATURE CITED


Noble tec Software. 1996. Tides and Currents Pro, v. 3.3.


Figure 1. Tidal currents in the lower Bay of Fundy illustrating the northeast and southeast movement and the resulting elliptical pattern in Grand Manan Basin.
Figure 2. Examples of the WebDrogue output of modeled prey, with the starting point (●) of the model (and the first sighting of the whale) and the final position of the modeled “prey” (●) compared to the second sighting of the whale (○).
Figure 3. Whale displacement direction by tidal stage showing the significant displacement of whales to the southwest during an ebb tide ($X^2 = 313.45$, $P < 0.0001$) and to the northeast during a flood tide ($X^2 = 512.739$, $P < 0.0001$).
Figure 4. Generalized Linear Model (GLM) for predicting whale distance from modeled results showing the significance of the elapsed time and whale displacement variables in predicting overall distance between the whale and the predicted movement of their prey.

|                  | Estimate  | Std. Error | t value | Pr(>|t|)  |
|------------------|-----------|------------|---------|-----------|
| Intercept        | -6.434e+00| 2.217e-01  | -29.017 | < 2e-16   |
| Time Elapsed     | -5.029e-03| 1.356e-03  | -3.709  | 0.000218  |
| Whale Displacement| -1.304e-04| 3.318e-05  | -3.931  | 0.00009   |