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Use of a hydrodynamic model to examine behavioral response of broadnose sevengill sharks (*Notorynchus cepedianus*) to estuarine tidal flow

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Abstract Innovative telemetry and biologging technology has increased the amount of available movement data on aquatic species. However, real-time information on the environmental factors influencing animal movements can be logistically challenging to obtain, particularly in habitats where tides and currents vary locally. Hydrodynamic models are capable of simulating complex tidal flow, and may thus offer an alternative method of contextualizing animal movement in coastal habitats. Here we use this tool to examine the influence of tide on the movement of broadnose sevengill sharks (*Notorynchus cepedianus*) in the San Francisco Bay estuary. Three sharks were actively tracked using acoustic transmitters for 3 to 4 days. We then generated a hydrodynamic model of the estuary and calculated current vectors along each track. We hypothesized that the sharks would adjust their swimming speed and direction depending on current strength when passing through the channel underneath the Golden Gate Bridge. Our results indicate that sharks did tend to follow the current flow in the channel, but their overall displacement did not significantly correlate with tidal amplitude. We conclude that the sharks may respond to environmental factors other than tidal flow, altering their movement at a finer scale than initially considered. Overall, this suggests that hydrodynamic simulation models can be used to visualize and quantify environmental factors that may affect movement patterns in aquatic organisms. We recommend future studies combine these models with other biologging techniques to measure energy expenditure at a finer spatial scale.

Keywords Active tracking · Estuary · Movement ecology · Environmental data

Introduction

Animal movement is affected by a variety of factors, including the animal's internal state, navigation and motion capacity, and the surrounding biotic and abiotic environment (Nathan et al. 2008). Among these, there has been increasing recognition that external constraints in particular may play a larger role in shaping an organism's movement path than previously considered (Wilson et al. 2012; Shepard et al. 2013;

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Brownscombe et al. 2017; Gallagher et al. 2017). In estuarine habitats, one such external force is the seasonal and daily hydrological variance, which is generated by complex bathymetry and water flux from various inshore and offshore sources (Brodersen et al. 2008; Anderson and Beer 2009; Forsythe et al. 2012; Kelly and Klimley 2012). Due to the presence and variability of these currents, it is likely that different species that reside in or transit through estuaries will exhibit plasticity in their movement in response to the currents. In some cases, currents may induce little to no active response from aquatic organisms, while in others they can be an impediment to the organism by deflecting the animal off course (Chapman et al. 2011; Kelly and Klimley 2012). Currents can also be beneficial by reducing an individual's travel time and energetic expenditure (e.g., Bernatchez and Dodson 1987; Kelly and Klimley 2012) or by increasing foraging opportunities (e.g., in upwelling areas; Benjamins et al. 2015).

Assessing the nature of behavioral response requires an understanding of how the animal moves in the context of the major environmental constraint in question. There has been recent attention to this area of research due to interest in dynamic management approaches, which require repeated assessment or measurement of biological and environmental data to update management recommendations. These tools rely on environmental datasets obtained via remote sensing to predict animal location on a daily, regional scale (e.g., EcoCast; Hazen et al. 2018; Welch et al. 2019). However, real-time measurements of the more fine-scale environmental variables affecting organism movement patterns, such as current flow, can be logistically challenging to obtain via remote sensing or direct field measurement (Benjamins et al. 2015). Thus, complementary methods may be necessary to contextualize animal movement data and forecast species distribution at a local scale.

Multi-dimensional hydrodynamic models are typically used to investigate water movement, sediment transport, and water quality for estuarine and coastal environments (Elias et al. 2001). These models can also provide information on localized currents in dynamic aquatic habitats. In cases where empirical data from buoys or remote sensors are missing, this tool could therefore be utilized to quantify the environment through which marine organisms move, offering greater insight into the impact of environmental constraints.

Here we explore the use of hydrodynamic models in examining the influence of tide on broadnose sevengill shark (*Notorynchus cepedianus*) movements in the San Francisco Bay estuary. We combine tidal current simulations generated at a ~50 m resolution with active tracking data from three sharks. In the estuary, sevengill sharks show a preference for high-flow areas, such as the channel underneath the Golden Gate Bridge (Ketchum et al. 2017). We first hypothesized that sevengill sharks would minimize energy expenditure by consistently moving in the direction of tidal flows to travel within the high-flow channel. Second, because the San Francisco Bay experiences a mixed semi-diurnal tide, we predicted that this response would vary by current strength; specifically, that I) in slow currents generated by weak tides, sharks would swim more actively in the direction of the current flow in order to move through the channel. In this case, the total displacement of the shark during that tidal segment would be greater than that of the current along the shark's movement path; and ii) in faster currents resulting from stronger tides, sharks would move passively within the water mass while being transported through the channel in the direction of the tide. The total displacement of the shark would then be equal to or less than that of the current. Our ultimate goal was to explore the use of hydrodynamic models to determine the frequency with which the sharks moved in and out of the estuary with the tide, and whether the environmental tidal conditions altered their mode of transport.

Methods

Study system

The San Francisco Bay is the most geographically expansive estuary along the California coastline, with a surface area of 1240 km^2 (Conomos et al. 1985). Tides are mixed and semidiurnal (i.e., two unequal high and low tides per day), with a high-flow channel where currents reach peak velocities (approximately 2.0 m/s; Bennett et al. 2002) through the narrow passage underneath the Golden Gate Bridge (Conomos et al. 1985; Ketchum et al. 2017). The mean tidal range is approximately 1.7 m (NOAA, National Ocean Service 2019), and during the study period, tidal amplitude ranged from 1.5–4.0 m. The mean depth of the entire estuary is less than 10 m, but the central channels (such as that beneath the Golden Gate Bridge) can reach depths of over 100 m (US Geological Survey 2014). The estuary also holds several small islands. Relevant to this study, Alcatraz Island (.09 km^2) is located approximately 2.9 km east of the Golden Gate Bridge, while Angel Island (3.1 km^2) is approximately 4 km northeast (Fig. 1). It is also important to note that the estuary is highly urbanized and impacted by numerous anthropogenic activities including channel dredging, freshwater diversions, watershed modifications, urban run-off, and ship traffic (Barnard et al. 2013). Due to the complex shape and bathymetry caused by the influence of both these anthropogenic and natural factors, the San Francisco Bay estuary is an area in which tidal influence is not only highly variable but also heterogeneously distributed. It is thus an ideal location to examine how organisms respond to dynamic current flow.

During the spring and summer, the San Francisco Bay estuary serves as a foraging and pupping ground for one such species, the sevengill shark (*Notorynchus cepedianus*; Ebert 1989; Barnett et al. 2010a, 2012; Ketchum et al. 2017). Classified as data deficient by the International Union for Conservation of Nature (Compagno 2009), sevengill sharks are widely distributed in temperate coastal regions, and diet studies have shown that they may play a significant ecological role through regulation of mesopredator populations in these habitats (Barnett et al. 2010b). This species tends to occupy bays and estuaries throughout its range, moving seasonally between inshore and offshore waters (Ebert 2003; Last and Stevens 2009; Barnett et al. 2010a, 2012; Ebert and Compagno 2012). Sevengill sharks also show a preference for high-flow areas (Ketchum et al. 2017), like many other mobile marine predators such as cetaceans, pinnipeds, and seabirds that exploit tidally energetic environments for foraging opportunities (Benjamins et al. 2015; Lieber et al. 2018). It is therefore likely that their movements are affected by the prevailing tidal flow in the deep narrow channel underneath the Golden Gate Bridge.

Active tracking

Three sharks were collected on a flood tide near a small reef northwest of Alcatraz Island on 29 July, 9 September and 14 October 2008. Each was caught using a baited hook and netted to bring aboard the vessel. The shark was then placed in a tank filled with flowing seawater, was sexed and measured for total length (TL, meters), standard length (SL), and girth behind the pectoral fins. The shark was then rotated onto its back to induce tonic immobility. An ultrasonic transmitter (V22TP, 50 kHz, 22 mm length, Vemco Ltd., Nova Scotia) was inserted into its body cavity through a 2–3 cm incision made off of the midline behind the pelvic fins. The transmitter was sanitized in a 10‰ solution of chlorhexidine gluconate (Nolvasan) and washed in a bath of deionized water prior to insertion. We also injected a liquid antibiotic into the body cavity following transmitter insertion. The incision was closed with 4–5 absorbable sutures. The shark was then rotated back to an upright position and placed in a stretcher to be lowered into the water, allowing the shark to depart volitionally. Handling time was kept under seven minutes.

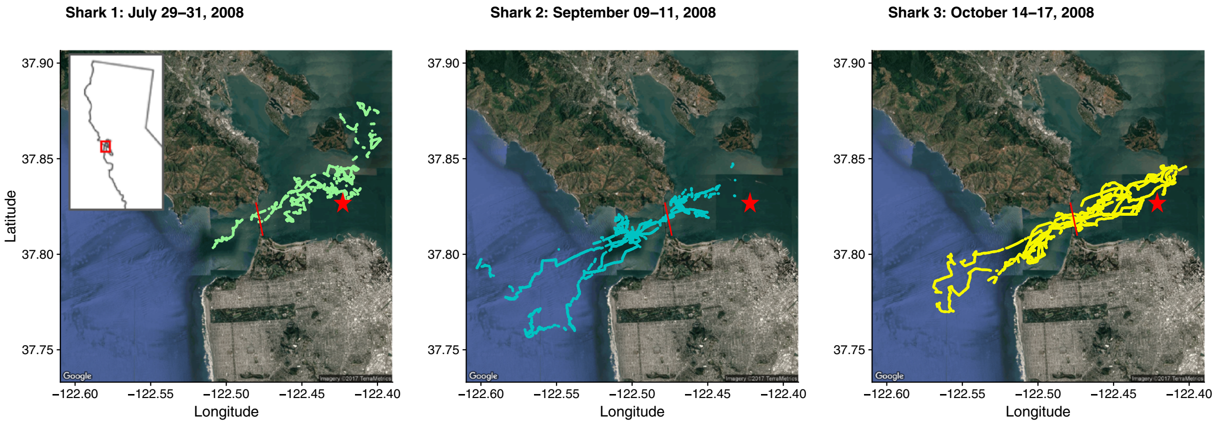


Fig. 1 Maps of San Francisco Bay Estuary, displaying relocation data for each acoustically tagged sevengill shark. Sharks were captured, tagged, and released northwest of Alcatraz Island (marked with a star), and tracked at three separate time periods in 2008. The red line overlays the Golden Gate Bridge, used in this study as a threshold to mark the transition (i.e., channel) between marine and estuarine habitats. The inset in the upper left shows the location of the study in California, USA

Once tagged, each shark was tracked using a portable ultrasonic receiver and directional hydrophone (VR100, Vemco Ltd., Nova Scotia), with boat operators navigating as close as possible to the ultrasonic signal. The electronic tag transmitted pulses at intervals varying from 1 to 2 s. Each transmission received ("fix") when the shark was within range of the receiver provided a timestamp and signal strength, which were stored along with the boat's geographic coordinates (latitude, longitude) determined by an external GPS. The boat track thus served as a proxy for the shark track. The tracking period for each shark lasted for 7–10 semidiurnal tidal cycles. The theoretical range of detectability of the transmitters can be estimated using output power, ambient noise at the transmitter frequency, and the loss of energy due to spherical spreading and absorption in the water (see Klimley et al. 1998; Pincock and Voegeli 2002). Given an output power of 156 dB measured at a distance of 1 m, we calculated the range of the transmitter to be approximately 1.0 km given the wave conditions (wave height = 0.33 m) commonly recorded in the study area. Because the depth of the water at the Golden Gate Bridge (approx. 100 m) should have allowed for near free-field propagation, the actual range of the transmitter was likely similar to theoretical range. This range of potential error was further supported by range tests conducted in similar habitats (80% detection at 300 m, Alexandra McInturf, unpublished data; 80% detection at 400 m, Eric Chapman, unpublished data).

Current simulation

We modelled tidal flow in the San Francisco Bay estuary by simulating current data for the tracking periods using the Delft3D-FLOW module in the Deltares Open Source Software v. 3.15, Delft3D (Elias et al. 2001; Lesser et al. 2004; Deltares Systems 2014). The Delft3D suite consists of various process modules that can interact to carry out simulations of flows, sediment transport, waves, water quality, and morphological developments. The hydrodynamic module, Delft3D-FLOW, calculates non-steady flow resulting from tidal and meteorological forcing on a curvilinear, boundary-fitted grid. In the vertical direction, the sigma coordinate system was adopted to represent water layers. Models generated by the Delft3D software have been previously validated by field studies in multiple locations including the San Francisco Bay (Elias and Hansen 2013), and have demonstrated accurate reproduction of hydrodynamic measurements even on standard parameter settings (Elias et al. 2001). To test the efficacy of this model in contextualizing movement data, we used the previously compiled and publicly available San Francisco Bay-Delta System Community Model to obtain the Delft3D curvilinear grid (Elias and Hansen 2013). Produced by environmental data collected by the United States Geological Survey, this DELFT3D-FLOW model consisted of six 2-way coupled curvilinear domains that constituted one 282 × 201 grid (Elias and Hansen 2013). Though DELFT3D-FLOW models can simulate three-dimensional current flow, we selected a depth-averaged simulation (Delft 2DH) because of the uncertainty in shark position. We thus obtained the estimated average velocities in the general location of the animal, rather than assuming inappropriate precision. Grid resolution varied over the selected habitat, but was finest in the vicinity of the Golden Gate Bridge (50 m × 50 m; Elias and Hansen 2013; US Geological Survey 2014). The software integrated bathymetry data from the San Francisco Bay (US Geological Survey 2014), and simulated tides with amplitudes and phases of 12 locally-dominant tidal constituents along the open ocean boundary (Elias and Hansen 2013). During the shark tracking dates, the simulation calculated current direction and strength at each node of the irregular grid (total = 28,958) covering the estuary. Historical predictions of tidal height (NOAA, National Ocean Service 2019) from the tracking dates were used to verify the patterns observed in the simulated tidal movements. The data generated by the Delft3D model were exported to R v. 3.4 (R Core Team 2017) using the ncdf4 package (Pierce 2017).

Data processing

To examine the extent and manner in which the sharks responded to tidal flow, we generated animations of each shark track overlaid on a map of coinciding current vectors in the San Francisco Bay (https://doi.org/10.6084/m9.figshare.5791503). While some studies (e.g., Whitney et al. 2017) suggest that it may be appropriate to remove the portion of the track immediately after capture and release to account for the behavioral effects of capture stress, we found that the number of times the sharks moved into and out of the bay in the first twenty hours of tracking ($n = 6$) proportionally reflected what we observed in the following twenty-four "or more"hours ($n = 9$). Thus, in order to maximize the movement data available to properly explore the use of hydrodynamic models in this context, we used the entirety of each shark track in the analysis.

To visualize shark movement parameters, the raw GPS tracks for each shark were filtered and smoothed. Missing points (including long periods when transmitter was not in range due to refueling or other instances) were approximated using simple linear interpolation. Because the raw tracks corresponded to the movement of the boat, they included sharp angles and intervals of unnaturally straight bearings. To account for this, we resampled and smoothed the resulting positions. We sampled one of every 10 points along the interpolated shark track, then used a cubic spline, fit with the "approxTrack" function from the "trajectories" R package (Pebesma et al. 2015), to smooth the trajectory. After smoothing, all interpolated points were removed from the analysis, and remaining points were spatially rediscretized to create intervals between shark positions of a consistent length (20 m), allowing us to evaluate trends in the track bearings (Turchin 1998). Large gaps in the track (>2 h) were excluded from the rediscretization process. Using these post-processed shark tracks, the speed and direction of the shark movements were calculated between sequential fixes and averaged to estimate an overall speed for each shark. The metrics of current corresponding to each post-processed shark location were extracted from the simulated current dataset.

Finally, we used our animations (https://doi.org/10.6084/m9.figshare.5791503) to count the number of times the sharks traveled in and out of the San Francisco Bay, marking the Golden Gate Bridge as the threshold between estuarine and deeper offshore water. With each crossing underneath the Golden Gate Bridge, we noted the timestamp and the approximate phase of the tide based on NOAA records. Each crossing where the shark locations were interpolated was classified as "unknown" and not included in this phase of our analysis.

Statistical analysis

To determine how current strength affected shark movement, we explored the relationship between shark movements underneath the Golden Gate Bridge and amplitude of the mixed semidiurnal tide. For each tidal cycle where sharks were observed to cross underneath the bridge and their tracks were relatively complete (missing data < half of tidal phase duration), we calculated the tidal amplitude and duration (Fig. 2). Within each tidal cycle, positional fixes for the shark as well as selected current vectors (i.e., current vectors at the shark's estimated location) were extracted. These vectors were used to calculate the displacement of the shark and the water mass within which it swam. Each shark displacement was defined as the distance between its location at the beginning and end of the cycle, while current displacement was determined by summing the lengths of the current vectors estimated along the shark's path during the tidal cycle (Table 1).

We used a linear mixed-effects model to evaluate our hypothesis that current strength would drive shark movement in response to tidal flow. Specifically, our model tested the relationship between shark and current displacement as a function of tidal amplitude, with the expectation that shark displacement would be greater than displacement of the water mass at smaller tidal amplitudes. This model included the difference between shark and current displacement as the response variable, the tidal amplitude and phase as fixed effects, and shark identity as a random effect (Table 2).

Data availability Videos generated from the hydrodynamic model and telemetered data can be found on the FigShare Data repository: DOI https://doi.org/10.6084/m9.figshare.5791503

Results

Three sharks were caught and tracked from either 29–31 July (Shark 1, tag ID: 8444), 9–12 September (Shark 2, tag ID: 8446), or 14–17 October 2008 (Shark 3, tag ID: 8448; Fig. 1). Shark 1 (S1) and shark 3 (S3) were both males of similar size with total lengths of 235 and 246 cm. Shark 2 (S2) was a smaller female with a total length of 135 cm. Between tracking periods, the range of the mixed semidiurnal tide in the estuary varied slightly. S1 tracking occurred during tides with amplitudes between 0.42–2.52 m (median: 1.52 m, range: 2.10), S2 tracking occurred during tides with amplitudes between 0.29–1.59 m (median: 0.72 m, range: 1.30), and S3 tracking occurred during tide with amplitudes between 0.68–2.28 m (median: 1.64 m, range = 1.60).

As predicted, there was evidence of tidal flow influencing shark movement patterns in our animated model. Sharks displayed directional movements underneath the bridge that were consistent with

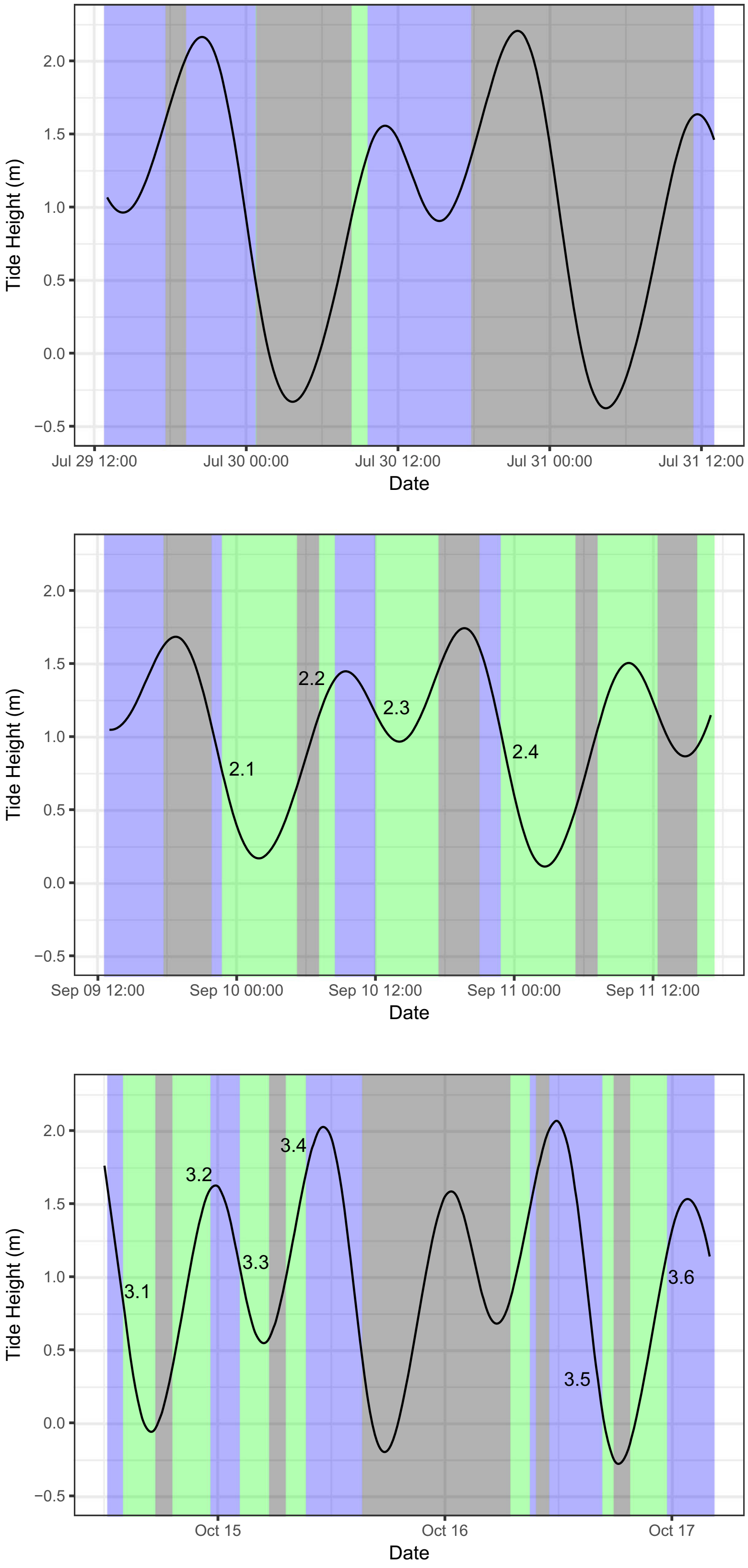


Fig. 2 Variations in tidal amplitude in the San Francisco Bay (data from NOAA buoy located at 37.807 N and 122.465 W) during the period of active tracking of each sevengill shark. Shading depicts location of the shark. Blue indicates the shark was in the estuary, green indicates the shark was in the coastal ocean, and grey indicates periods greater than one hour without a shark relocation (often due to refueling the vessel or exchanging crew). Tidal segments used in the statistical analysis are labelled with the tidal segment ID (Table 2 for reference)

Table 1 Summary table of tide, current, and shark movement patterns for selected tidal cycles when sharks were known to move into or out of the estuary, and shark tracks had minimal interpolated data. Amplitude is defined as the absolute value of the difference between the high and low tides for each tidal cycle. Tidal phase reflects the direction of the tide, while duration indicates the amount of time between high and low tides. Displacement differential refers to the difference in shark displacement versus current displacement during a given tide (i.e., positive values indicate greater displacement of the shark than that of the current)

Tidal segments	Amplitude (m)	Tidal phase	Duration (hh:mm)	Displacement differential (km)
2.1	1.53	Ebb	7:22	7.98
2.2	1.23	Flood	7:23	6.02
2.3	0.44	Ebb	4:37	−0.60
2.4	1.59	Ebb	7:03	4.93
3.1	1.94	Ebb	6:18	4.83
3.2	1.64	Flood	6:46	1.35
3.3	1.03	Ebb	4:58	−4.49
3.4	1.42	Flood	6:20	2.41
3.5	2.29	Ebb	6:46	−0.48
3.6	1.76	Flood	7:11	−3.82

the tidal flow for approximately 73% of observable tidal segments included in our analysis ($n = 19$; https://doi.org/10.6084/m9.figshare.5791503). S1 demonstrated this behavior the least, during half of all possible flood and ebb tides included in the analysis (two out of four tides, 50%). S2 did so in 62.5% of instances (five out of eight tides), while S3 tracked all tidal movements in and out of the estuary during the tracking period (seven out of seven tides, 100%; Fig. 2).

For those occasions when the sharks did move in or out of the estuary, we analyzed the relationship between their displacement and the current strength (Fig. 3). After removing tidal cycles where the shark's track while moving underneath the bridge was interpolated, We examined 10 tidal phases in total (Fig. 2, Table 1). Each lasted between approximately 4 and 7 h, with amplitudes ranging from 0.44 to 2.29 m. During a slim majority of these tidal segments (six out of 10), we observed shark movements where the shark moved over greater distances than the current displacement. In the remaining segments (four out of 10), sharks exhibited less displacement than that of the current (Fig. 3). However, while we did observe different movement responses to current flow as hypothesized, our linear mixed models found no significant effect of tidal amplitude on difference in displacement (Table 2).

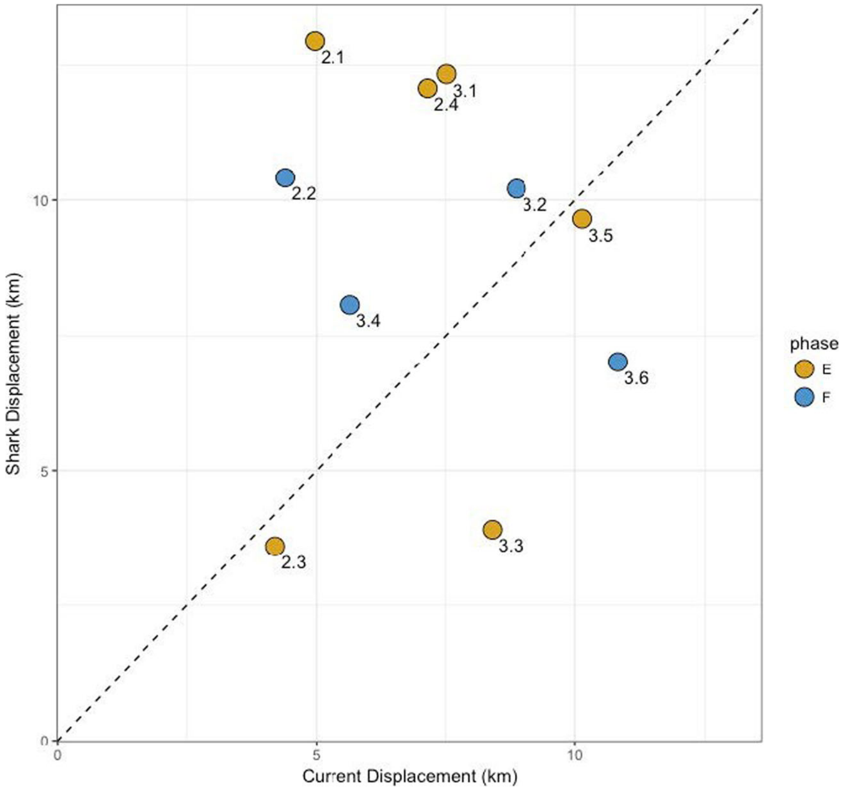
Table 2 Linear mixed-effects models examining the effect of tidal amplitude (in meters) on the differential between shark and current displacement. Shark identity was treated as a random-effects variable. β: coefficients of the linear predictor of the model. CI: 95% confidence interval of coefficients

	Displacement differential		
	β	CI	*p* value
Intercept	−4.21	−14.24 – 5.83	0.411
Tidal Amplitude	4.24	−3.52 – 5.20	0.706
Phase (flood)	0.84	−0.61 – 9.09	0.087
	$R^2 = 0.129$		

Discussion

Over the past century, numerical models of hydrodynamic and sediment processes have evolved from analytical single-dimensional models to multi-dimensional models able to predict more complex tidal flows (Lesser et al. 2004). Though they have been increasingly used for coastal management and engineering (Elias et al. 2001), hydrodynamic models can also be an invaluable tool in addressing the challenge of visualizing dynamic environments through which aquatic organisms move. Here we show that hydrodynamic models can also be used to examine the influence of tide on sevengill shark movement in estuarine systems, particularly in locations such as high-flow areas characterized by short-term variance due to both natural and anthropogenic factors.

Fig. 3 Relationship between shark and current displacement for each tidal cycle analyzed in the linear models. Color indicates tidal phase (ebb [E] or flood [F]), and labels correspond to the analyzed tidal segments. The dotted line indicates the 1:1 relationship between the shark and current displacement



The DELFT3D-FLOW module is powerful in this context because it integrates a large number of processes (e.g., wind shear, tidal and wave forces, density-driven flows, and stratification due to salinity and temperature gradients) to generate hydrodynamic models applicable to a wide range of coastal and estuarine situations (Deltares Systems 2014). These dynamic environments are often highly productive, supporting a large number of resident species. A unique challenge facing these organisms is the variable flow patterns that characterize these habitats. Species that are selective in habitat choice within these locations have likely evolved means of perceiving and responding to tidal patterns to achieve their movement goals in the most energy-efficient manner (Bernatchez and Dodson 1987; Kelly and Klimley 2012). In order to understand the behavioral responses of estuarine species, however, it is necessary to place their fine-scale movement patterns in an environmental context of similar scale, and a major obstacle in the field of movement ecology is the inability to consistently gather environmental data at the appropriate resolution for the corresponding animal tracks. This study thus presents a unique application of hydrodynamic modeling to contextualize animal movement patterns in a highly dynamic environment.

Many mobile marine predators are known to exhibit evidence of residency within high-flow areas (Benjamins et al. 2015). Among these, sevengill sharks in the San Francisco Bay often selectively occupy the channel underneath the Golden Gate Bridge (Ketchum et al. 2017). Consequently, we hypothesized that the sharks were able to adapt to such a high- energy environment by moving through the channel while adjusting their movement pattern according to the strength of the tidal flow. Our results supported our initial hypothesis that the direction of sevengill shark movements frequently corresponds with the current direction. Our hydrodynamic model revealed that sharks moved through the channel with the tide during a majority of observed tidal phases (14 out of 19). This was most evident in S3, which traveled through this area with every ebb and flood tide. This pattern may have been due to the fact that the shark was tracked during an equatorial tide when currents were strongest.

However, we did not detect an influence of tidal strength on sevengill shark movement, as initially hypothesized. This may have been because, while the hydrodynamic model demonstrated great potential for examining organism response to tidal flow, we applied this novel method to a fairly small sample size, although our dataset did record high-frequency positions over several days of behavior per individual. Additionally, the measurement error along the sharks' tracks was greater than the scale of the highest resolution grid area (50 × 50 m) located at the high-flow area near the Golden Gate Bridge. Because our hypotheses were formulated based on movement patterns at a larger spatial scale (i.e., movement through the channel over an entire tidal phase), this was unlikely to bias our results. However, we were not able to distinguish between the possible influence of the scale of data versus the model on our ability to infer movement responses in sevengill sharks in this study. Future studies should address this distinction by considering the use of more precise forms of biologging in addition to acoustic telemetry systems to address fine-scale behavioral questions more thoroughly. For instance, accelerometers are capable of both identifying complex behaviors and estimating their net energetic cost. When combined with the method presented here, this may offer an avenue for examining fine-scale movement patterns in response to tidal flow in an even greater capacity, such as through mapping energy landscapes to quantify the cost of transport in aquatic taxa.

Our results were also likely affected by behavioral or ecological processes. We assumed that shark movements would be consistent throughout an entire ebb or flood tide and would depend on the amplitude of the tide. However, even during the shortest tidal segment examined (segment ID 2.3; Fig. 2, Table 1), the current displacement (1.23 km) would have been sufficient to transport the shark through the channel. It is therefore likely that the shark response was more nuanced or may have occurred at a finer temporal scale. For instance, through the generated animations (https://doi.org/10.6084/m9.figshare.5791503), we found that some sharks displayed multiple movement patterns within a single tide. In one example, S3 was east of Alcatraz Island at the beginning of the tide (segment ID 3.6), where it was sheltered from strong ebb tides. This animal was only transported through the channel when it swam into currents that were both strong and oriented in that direction later in the tidal phase. Additionally, due to our use of a depth-averaged model, we were unable to account for the potential variation in shark movement due to their position in the water column. It is possible that the sharks experienced changes in the strength of current flow in this dimension, depending on their depth. For instance, sharks swimming near the bottom, where the current is reduced, may not have been exposed to the full strength of the tidal flow.

From an ecological perspective, we focused on the hypothesis that shark response to the variation in tidal current would reduce transport costs. However, it is likely that the sharks respond to other environmental factors as well, specifically those that may offset the cost of moving in a less energetically efficient manner (i.e., energy acquisition; Wilson et al. 2012; Shepard et al. 2013). Some predators, such as those that feed on anadromous fish (e.g., large teleosts, gulls, pinnipeds), have been known to occupy transitional habitats at estuarine or riverine mouths to take advantage of prey moving with the prevailing current flow (Roffe and Mate 1984; Wright et al. 2007 and others). However, because the diet of sevengill sharks includes several actively swimming species of fish and marine mammals (Ebert 1991), it is possible that sharks would exhibit different movement patterns by either tracking prey items as they are transported in the current through the channel or roaming widely to forage outside of the high-flow area. In either case, the motivations for behavioral flexibility may not be mutually exclusive; because sevengill sharks can perceive and respond to changes in tidal flow, they likely take advantage of local currents in addition to the overall tidal flow to forage. If feeding, rather than energy efficient transport, was the primary movement goal, this may have also led to deviations from the expected response to the prevailing tidal movement.

While it is beyond the scope of our study to examine the other factors that may affect the movement of these individuals in particular, the patterns documented using our hydrodynamic model suggest that sharks vary in their responses to dynamic and localized environmental conditions. To determine the extent to which this behavioral flexibility is adaptive will require future work to identify possible benefits of moving with the tides in high-flow areas, including the assessment of foraging opportunities available in different regions of the estuary and under different tidal conditions. Combining the methods used in this study with data from with accelerometers and biologgers could help elucidate the influence of different external factors on fine-scale movement among a variety of taxa within the San Francisco Bay and in other estuaries. This information would provide valuable insight into the effect of local environmental conditions on the distribution and behavior of marine organisms, which could be used to predict how these animals may respond to the multiple anthropogenic threats present in estuarine habitats. For instance, marine renewable energy infrastructure is often concentrated where coastal geometry helps enhance flows, and is thus predicted to alter flow patterns in these locations (Borthwick 2016). Consequently, there is a need to improve our understanding of key behaviors and fine-scale movement strategies of animals like sevengill sharks that selectively occupy high-flow regions. Establishing an effective method of doing so, such as through the use of the presented model, is an important step towards this goal.

In this study, we have shown how hydrodynamic models can be used to contextualize aquatic animal movement patterns in response to tidal flow. We believe this method can be powerful in exploring how predatory elasmobranchs and other nektonic organisms in tidal systems respond to current flow that varies locally in space and time (Stasko 1975; Chapman et al. 2011). We encourage future studies to expand the use of hydrodynamic models to predict fine-scale species distribution and space use, particularly in areas highly impacted by anthropogenic activities.

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Author contributions AGM wrote the manuscript, created the hydrodynamic model and performed statistical analyses. AES assisted in writing the manuscript, performing statistical analyses and prepared figures. MLB led the tagging and active tracking of sevengill sharks and contributed to the writing of the manuscript. PTS participated in shipboard tracking and reviewed the manuscript. CJS provided funding, assisted in data collection, and reviewed the manuscript. NF assisted in writing and reviewing the manuscript. APK conceived of the project, secured funding, assisted in data collection, and reviewed the manuscript. DC conceived of and supervised statistical analyses, generated the hydrodynamic model, and assisted in writing and reviewing the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Compliance with ethical standards

Ethical approval The methods pertaining to shark capture, tagging, and release in this study followed a protocol approved by the University of California, Davis Institutional Animal Care and Use Committee (Protocol 06–12,892). Sharks were collected under a California Department of Fish and Wildlife Scientific Collecting Permit (SC-3224). Transmitters were inserted by researchers practiced in the appropriate surgical technique, animal stress was monitored throughout the procedure, and handling time from capture to release was minimized.

Competing interests The authors declare no competing interests.

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