PATTERNS OF HABITAT USE BY HARBOR PORPOISE (*PHOCOENA PHOCOENA*) IN CENTRAL SAN FRANCISCO BAY

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by

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San Francisco, California

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CERTIFICATION OF APPROVAL

I certify that I have read *Patterns of habitat use by Harbor Porpoise (*Phocoena phocoena*) in Central San Francisco Bay* by Laura Margaret Duffy, and that in my opinion this work meets the criteria for approving a thesis submitted in partial fulfillment of the requirement for the degree Master of Science in Biology: Marine Biology at San Francisco State University.

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PATTERNS OF HABITAT USE BY HARBOR PORPOSE (*PHOCOENA PHOCOENA*) IN CENTRAL SAN FRANCISCO BAY

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This research takes an innovative approach to modeling distribution of a marine predator explicitly in the temporal domain. Harbor porpoise (*Phocoena phocoena*) are a small cetacean seen in San Francisco Bay year round. Porpoise presence at the entrance of the Bay varies from zero sightings to over 100 in an hour. The solitary social and foraging behavior of this non-migratory species makes it an especially useful indicator of habitat patchiness along the west coast and of tide-dependent ecological processes in central Bay. Bathymetry data of the Golden Gate channel show steep shelf breaks and complex outcroppings that effect water flow and create spatially stable areas where tidal fronts occur. Oceanographic features associated with tidal fronts are recognized by marine predators as areas in which prey biomass accumulates. Sighting frequencies were hypothesized to vary according to changes in the same spatially consistent, but temporally variable, tidal factors that correlate to lower trophic level congregating mechanisms. Circular statistics were used to describe sightings data over a 24 hour tidal period. Sightings were fit to circular models based on tidal segments that correlated to tidal state: ebb or flood, and changes in current velocity. One year of data show a greater number of porpoises are present during a flood tide, but there are more sightings during an ebb tide. Porpoise sighting frequency showed multimodal distribution and best fit a model with a specific mean direction at the 95% confidence interval with [$F=0.34$, $p = 0.001$]. Most sightings occurred within three hours after maximum inflow current velocity on the north side of the channel. The time at which the most sightings occurred over a 24 hour tidal period correlated to the time at which the most defined shear zones occur in central Bay with a circular correlation coefficient of -0.15 (p=0.0006). A three tiered, nested ANOVA found significant variation in porpoise foraging behavior correlated to tidal phase or tidal front presence. Foraging behavior varied significantly according to tidal state with [$F=9.96$, $p = 9.38 \times 10^{-08}$]. The data show that it is the patch in tidal progression, rather than geographic space, which is significant to variations in porpoise sightings and foraging behavior in the Golden Gate. The results produce a temporal habitat model for a federally protected, upper trophic level predator in the Bay. Models like this are an efficient way to inform management in a highly anthropogenic influenced area.

I certify that the Abstract is a correct representation of the content of this thesis.

Chair, Thesis Committee

12/2/2015

Date

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INTRODUCTION

HARBOR PORPOISE

Biological Description

Harbor porpoises are small, toothed cetaceans. A complete taxonomic classification is shown in Figure 1. The family Phocinidae dates back to the late Miocene period and evolved allopatrically in both hemispheres, separated by the tropics (Berta et al. 2006). The most common of four species in the genus *Phocoena* is the harbor porpoise (*Phocoena phocoena*), which was first described by Linnaeus in 1758 (Reeves et al. 2002). Four subspecies are recognized between ocean basins, with *P.p. vomerina* occurring in the eastern North Pacific. There is an unnamed subspecies in the western Pacific (Allen et al. 2011, Anderson 2014). Six different genetic units of *P.p. vomerina* have been defined along the coast of California, Oregon, Washington, and Alaska (Chivers et al. 2002, Carretta et al. 2013, Forney et al. 2014). There are limited data on population structure and gene flow between these units.

The harbor porpoise (referred to as 'porpoise' from here on) has small pectoral flippers, no prominent rostrum, and a small triangular dorsal fin (Figure 2). Females are slightly larger than males, with body sizes varying from 1.5 to two meters in length and weights ranging from 50 to 70 kg (Dorfman 1990, Reeves et al. 2002). It is usually a mottled gray and white body color with distinctive patterns per individual. The lifespan of a porpoise is approximately 10 years, reaching sexual maturity at approximately three to four years of age (Read & Hohn 1995, Reeves et al. 2002; Allen et al. 2011). Common to all cetaceans, females reproduce one calf per ovulation cycle. Females off the coast of California are estimated to calf every other year with a breeding and calving cycle that is highly synchronized with late spring to early summer (Read & Hohn 1995). It is the smallest cetacean in North Pacific waters.

Distribution

Porpoises are found in temperate and higher-latitude waters of all oceans in the northern hemisphere. In the northeast Pacific, range extends from temperate waters of coastal central California to the subarctic Chukchi and Bering Seas (Calambokidis et al. 1990, Reeves et al. 2002, Hammond et al. 2008, Carretta et al. 2009). Sightings usually occur in areas such as bays, estuaries, and fjords, or in coastal waters less than 300 meters in depth (Calambokidis et al. 1990, Reeves et al. 2002, Carretta et al. 2009, Allen et al. 2011).. Above-water surveys have recorded porpoises within the 90m isobaths off California with some sightings between the 100m and 200m isobaths off Washington and Oregon (Carretta et al. 2009). Porpoises are commonly seen in the Greater Farallones National Marine Sanctuary (GF) off the coast of San Francisco, Marin, and Sonoma counties in depths less than 40 meters (Szczepaniak 1988, Calambokidis et al. 1990, Carretta et al. 2013). The boundaries of the GF are shown in Figure 3, noting the exclusion of San Francisco Bay inside the Golden Gate Straight, the channel that connects estuarine waters with the Pacific Ocean.

California population estimates are based on aerial and vessel surveys. Abundance provides a base model for porpoise density as a function of water depth, and vessel surveys additionally examine the effect of environmental conditions on porpoise sightings (Barlow 1988). NMFS has conducted marine mammal abundance surveys on research cruises along the continental shelf since 1984 (Barlow 1988). Aerial zig-zag transects extend to the 200m isobaths and have been done in 2-5 year intervals since 1991 from point Conception, CA to the CA/OR border (Forney et al. 2014). Population abundance is estimated from both vessel and aerial surveys, density is estimated from boat-based line transects.

Porpoise distribution is discontinuous between continents, with preferential habitat hugging the coastline or shallow waters of the continental shelf, shown in Figure 4. Bio-contaminant and genetic studies on porpoise stocks along the west coast of North

America additionally show limited movements between provincial coastal areas (Calambokidis & Barlow 1991, Barlow & Hanan 1995, Chivers et al. 2002, Carretta et al. 2009, Carretta et al. 2013).Tissue samples from stranded animals, or those caught as bycatch, have helped discern porpoise stocks within the northeast Pacific population. Lipophilic pollutants in the water such as PCB (polychlorinated biphenyls, industrial chemical), DDT (pesticide), and HCB (hexachlorobenzene, fungicide used in agriculture) build up in cetacean blubber in different ratios depending on where the animals forage and are regionally bound (Calambokidis & Barlow 1991). The time it takes for porpoises to accumulate contaminant ratios characteristic to a specific area is close to their lifetime. Analysis of Molecular Variance (AMOVA) studies also show genetic distinction among geographically distinct coastal zones (Chivers et al. 2002). These distinctions are likely the result of disparate foraging areas and separate mating areas withlittle interchange over the span of generations. There are no known barriers or obstructions along the west coast that would limit animal movement and therefore gene flow (Barlow et al. 1988, Calambokidis & Barlow 1991). Instead, these discrete stocks alternatively support little to no evidence of migratory behavior in this species.

The National Marine Fisheries Service (NMFS) federally protects porpoises under the Marine Mammal Protection Act (MMPA). There are eight stocks within the Northeast Pacific population that have been defined geographically (COSEWIC 2007, Barlow 1988). Along the United States and Canadian coastlines, six stocks are regulated independently based on genetic distinction and local management concerns (Barlow & Hanan 1995, Hammond et al. 2008, Allen et al. 2011; Forney et al. 2014, Carretta et al. 2013). The San Francisco – Russian River stock (SF stock), for example, was specifically designated as a separate management unit due to bycatch levels in the west coast gillnet fishery (Barlow & Hanan 1995). Eastern North Pacific stock boundaries along the United States are shown in Figure 5.

The most recent abundance estimate of the SF stock, based on 2007 – 2012 aerial line-transect surveys within 200 meter depth and 15 nautical miles from shore, is 9,886 (CV=0.51) porpoises (Forney et al. 2014). The GF population was estimated at approximately 2,000 porpoises in the 1990's and is thought to be a subset of the SF stock. Based on four study areas in the GF, porpoise density was estimated at 0-1.9 porpoise per squared kilometer offshore of San Francisco Bay (SF Bay), with most sightings occurring just outside the Golden Gate channel outside of designated shipping lanes (Szczepaniak 1988). Porpoises were seen year-round in this area.

Sightings data record environmental conditions, group size, and distance from shore. Based on preliminary survey data, efforts have been focused within the 50-fm isobath off California since the late 1980s (Carretta et al. 2009). Opportunistic sightings data have also been collected on Oceanic Society nature trips in the GF (majority of effort between 1983 to 1987) and by the Point Reyes Bird Observatory travel time to and from the Farallone Islands (effort between 1971 to 1979) (Calambokidis et al. 1990). These data provided abundance and density estimates for what may be the same population travelling through the channel at the mouth of SF Bay.

Food and foraging

A relatively small body size and thick blubber layer require porpoises to feed often, and restrict long distance travel and habitat range according to a constant search for prey. Porpoises feed at a daily rate of ten percent of their body weight, and movements likely rely on patches of prey aggregations (Dorfman 1990, Calambokidis & Barlow 1991, Read & Hohn 1995, Johnston et al. 2005, Allen et al. 2011, Santora et al. 2012, Sveegaard et al. 2012). Smaller schooling fishes such as herring, anchovy, and sardines are the main source of prey; juvenile rockfish and small squid are also dietary components to west coast populations (Smith & Gaskin 1974, Recchia & Read 1989, Dorfman 1990, Allen et al. 2011, Anderson 2014). Lipophilic contaminants ratios in blubber samples imply porpoises feed locally on prey with distinctive pollutant patterns, compared to migratory species of porpoise elsewhere in the world which show homogenous pollutant ratios (Calabokidis & Barlow 1991). Most knowledge of feeding activity is sourced indirectly from fatty acid analysis and stomach contents from animals that were stranded or caught as bycatch. Animals stranded or caught closer to shore seem to feed across broader trophic levels than those in deeper waters (Recchia & Read 1989). This may be evidence of opportunistic feeding in areas where prey biomass accumulates and with access to more variety.

Social & Surfacing Behavior

Porpoises are most often sighted alone or in small groups, and are not often seen travelling or socializing in pods. They are sometimes seen in larger aggregations that are thought to be associated with mating and calving seasons or with a localized abundance of prey (Reeves et al. 2002; Allen et al. 2011; Keener 2011). A study which tagged porpoises to record underwater activity showed they travel at about 1.5 m/s and commonly stay within the upper 10m of the water column (Otani et al. 2000; Allen et al. 2011). Porpoises surface quickly by rolling to the surface and exposing their small dorsal fin above the water for only a few seconds before making the next dive (Reeves et al. 2002; Allen et al. 2011). A short time at the surface with one to two breaths in rapid succession, the animals' small size, and frequent changes in swimming direction can make them difficult to see in varying sea state or weather. Additionally, they tend to shy away from boats and human activity (Barlow 1988, Carretta et al. 2009, Allen et al. 2011: Anderson 2014). Solitary and somewhat cryptic social behavior has provided limited opportunity to observe free-swimming porpoises for more than a few surfacings. Much of what is known of porpoises is inferred from a brief glimpse of the animal while at the surface.

Conservation Status

Harbor porpoise are one of the most commonly sighted cetaceans in the world. Global abundance of porpoises is estimated at about 700,000 individuals (Hammond et al. 2008). Based on this number, they are listed as a "Least Threatened" species on the IUCN Red List. Despite a sustainable global population estimate, there is not enough data to define conservation status on a smaller biogeographic scale. Porpoises in North America were listed as a species of concern under the Endangered Species Act (ESA) in the early 1990's, based on economic and scientific review of fisheries bycatch rates (NMFS 2001). Post-mortem data provides limited information on feeding behavior, carrying capacity, and population recovery rates (Hammond et al. 2008, Bisack & Magnusson 2014). Insufficient data has led to continuous review on porpoises, now listed with an undefined status under the ESA and MMPA, and as a species of Special Concern in Canada (COSEWIC 2007, NOAA Fisheries Office of Protected Resources 2014). Reviews of west coast population management continue in North America based on biological characteristics and according to identified threats in geographic regions.

Threats

Porpoise coastal distribution leaves them highly susceptible to human interaction. The most significant threat comes from incidental catches in fishing gear, primarily gill nets, and competition with commercial fishing industry for food (Calambokidis et al. 1990, Read & Hohn 1995, NMFS 2001, Hammond et al. 2008, Marubini et al. 2009, Reeves et al. 2013). Substantial takes were documented in tens to hundreds per year in the 1980s and 1990s off the coast of central California (Barlow and Hanan 1995, NMFS 2002). CA Fish and Game successfully moved the fishery to waters deeper than approximately 100 meters in 1994 under Proposition 132, then banned gillnet fishing completely in SF Bay and Monterey Bay in 2000 (Martin 2000). Most gill nets were banned within porpoise range off central CA in 2002 (Forney et al. 2014). Despite this success, there is a need for more realistic, species-specific values to improve stock analysis related to coastal fisheries.

Fishing quotas are based on a potential biological removal estimate, the number of porpoises that the population can afford to lose in a fishing season and still maintain sustainable levels. This estimate is currently based upon a generalized productivity rate use for all cetaceans and an assumed recovery factor for species with an unknown status (Hammond et al. 2008, Bisack & Magnusson 2014, Forney et al. 2014). The same standard recovery factor numbers have been in use since the earliest years of sampling, and restrictions based on multispecies analysis have been in use since 1994 (NMFS 2001, Carretta et al. 2009). The default use of these numbers leads to variations of uncertainty from 30% to 97%, depending input variables, and concluded abundance estimates in need of verification. (Calambokidis et al. 1990, Carretta et al. 2009). Surveying this species when and where the opportunity arises improves census data so that conservation regulations are more accurate and effective. .

Much is still unknown about porpoise life history, which also informs conservation management. Aside from fisheries bycatch mortality, habitat degradation, contaminant pathology, and incidental mortality from recreational and industrial vessels are among some of the other threats that harbor porpoises face off the west coast (NMFS 2001). It is necessary to obtain greater knowledge on porpoise habitat preference and activity, especially close to shore where the likelihood of human interaction is greater. Land-based surveys, with alternative methods and parameters to boat-based surveys offshore may create an opportunity to ground-truth estimates numerical and close gaps in surface-based data-sets (Barlow 1988, Calambokidis et al. 1990, Forney et al. 2014). Viewing this species at close range from shore in SF Bay is an opportunity that may decrease uncertainty in abundance and density estimates as well as increase knowledge on population structure. In this study area specifically, , detailed behavioral data may additionally be observed from the stationary, aerial perspective of the Golden Gate Bridge.

History of Presence in San Francisco Bay

While porpoises have been documented consistently in the GF, there is a substantial gap in recorded porpoise sightings inside SF Bay from the 1940s to early 2000s. Porpoises were present inside the Bay in the 19^{th} and 20^{th} century, with evidence from fossil remains in Bay area Native American ruins, captains' ship logs, and local resident sightings prior to World War II (Calambokidis et al. 1990, Keener 2011). There was much more human activity in the Bay during WWII and after with rapid industrial development. San Francisco experienced the highest period of development post-war and its greatest population increase of approximately five million people in the mid-20^{th} century (Cloern & Jassby 2012, Barnard et al. 2013). The installation of a submarine and torpedo net at the entrance of the Bay would have inhibited larger marine animals to travel in and out of the estuary. Increased vessel traffic, unregulated run-off consisting of raw waste-water and other pollutants, as well as development of underwater urban infrastructure are all anthropogenic influences that would have likely made the Bay relatively less desirable habitat during the time of zero sightings.

Efforts to document sightings began in 2008 and continue as part of the creation of a photo-ID catalogue by the local non-profit research organization, Golden Gate Cetacean Research (GGCR). Sightings are believed to be greater in California coastal areas since the 1970s, after a gap in sightings and in research effort during the World War II era (Camphuysen 2004, Thomsen et al. 2006, Keener 2011, Anderson 2014, Sheldon et al. 2015). In association with GGCR, this research effort is among the first to document, quantify, and investigate porpoise activity inside SF Bay.

PREDATOR-PREY DISTRIBUTION IN THE MARINE ENVIRONMENT

Habitat Use

Predator distribution in the marine environment is strongly associated with its prey. Timing and the degree of correlation is scale dependent (Charnov 1974, Haury 1978, Levin 1992, Stern 1998). Environmental variability directly affects prey species, and the availability of prey across varying spatial scales determines predator habitat selection and foraging site-fidelity (Charnov 1974, Mendes et al. 2002, Zamon 2003, Johnston et al. 2005, Torres et al. 2008, Scott et al. 2010, Sveegaard et al. 2012, Booth et al. 2013, de Boer et al. 2014). Habitat use exists as the dynamics of foraging probability, a trade-off between the metabolic cost of searching for prey in a patch of dwindling resources, and the potential benefit of resources in the destination patch (Charnov 1974, Bull et al. 1996, Johnston et al. 2005). Predictability of local density and spatial aggregations may be perceived as habitat quality, as variability in prey density determines predator foraging efficiency (Benoit-Bird et al. 2013). It is additionally important to note that it is not just where the biomass occurs, but also when it accumulates that creates predictability in a heterogeneous environment.

Physical – Biological Coupling

Biological processes require interactions between physical and chemical factors, each with its own temporal and spatial scale (Haury et al. 1978). Physical-biological coupling links patterns between ecological variables and animal distribution (Marubini et al. 2009, Dransfield et al. 2014, Becker et al. 2014). The convergence of bay and ocean water at the coastal interface of SF Bay creates boundaries where significantly different water masses meet. Some differences may be detected visibly above the surface. Surface slicks are calm patches of water visible associated with horizontal convergences due to wind stress or water flow (Dorfman 1990). Eddies may also be visible as swirled rotations that occur as currents along shear zones flow past each other or past underwater obstructions

(Anderson 2014). Langmuir circulation cells form just below the surface as an interaction between wind and water energy, creating a convergent frontal zone that forces planktivorous organism congregations (Barstow 1983, Alpine & Cloern 1988). Turbidity-forced subsurface congregations of plankton are called the entrapment zone, and these areas of elevated biomass attract mobile grazers and predators (Largier 1993, Chadwick & Largier 1999, Kimmerer 2004, Santora 2012, de Boer et al. 2014). The association of a predator with a patch of prey is an emergent pattern in the environment which is a result of biological, physical, and chemical processes along with primary production, prey movement, and predator movement.

Phytoplankton, zooplankton, and small fishes are directly and physiologically constrained by physical factors in the environment. In contrast, larger, more mobile predators such as porpoises may move through and between favorable areas of space. Due to their high feeding rates, porpoises have been used to model predator presence as a result of the same physical conditions which accumulate prey. Zamon (2003) found porpoise presence was significantly correlated to prey abundance and availability altered by tidal currents. Johnton et al. (2005) also found porpoise core-use areas and fine-scale movement focus around oceanographic features that aggregate prey. Porpoise distribution in the Baltic Sea was successfully modeled according to the same environmental factors that serve as proxies for schooling fish (Sveegaard et al. 2012). The efficiency of habitat models of small cetaceans in Florida Bay were improved when prey density estimates were not incorporated, and rather predicted predator habitat selection directly from environmental data (Torres et al. 2008). Any physical feature that causes eddies or fronts may be recognized by predators as features that concentrate prey (Mendes et al. 2002, Johnston et al. 2005, Santora 2012, de Boer et al. 2014, Becker et al. 2014). If predator foraging habitat tracks environmental variability which determines prey distribution and accumulation, then the same physical environmental proxies may be used to predict predator presence.

Tide – Dependent Ecosystems

Mixing bodies of water, salt, and sediment within central Bay develop physical patterns that affect biological processes at multiple trophic levels. The tide-dependent ecosystem changes over periods of stability and disturbance within the community or in the physical environment (Cloern & Jassby 2012). Estuarine fronts are the meeting of two bodies of water of dissimilar densities, delineated by neap-spring variation and bottom topography (Largier 1993, Barnard et al. 2013). As tidal exchange occurs, gravity circulation pulls relatively dense ocean water below bay water at the same time as tidal currents force lateral movement (Geyer & MacCready 2014). Tidal forcing affects fronts in central bay more than salinity stratification, gravitational circulation, or wave energy (Barnard et al. 2013). The effect of tidal flow on nutrient and plankton accumulation, and behavioral responses of grazers and predators exceeds net flow and river flow in the area (Kimmerer 2004, Barnard et al. 2013). Tidal features are spatially consistent in central Bay, but they form, dissipate, and reform over the course of a full flood and ebb tide.

In such a dynamic coastal ecosystem, time is an important variable to consider as a predictive, stable environmental factor. Cyclic, repeated tidal flow is useful in observing and understanding ecological variability in central Bay. The temporal scale at which tidal fronts vary may be used as a measurement of habitat patchiness (Largier 1993, Zamon 2003, Gibson 2003, Kimmerer 2004). In relatively shorter timescales of the tidal exchange, hourly physical effects dominate environmental heterogeneity and drive biological processes (Kimmerer 2004, Cloern & Jassby 2012). Additionally, it may not just be variables, but derivatives in magnitude, direction, and acceleration that create favorable foraging zones (Torres and Urban 2008). Studying temporal changes in physical patterns along with varying accumulation of an upper-level trophic predator may provide valuable information on the interconnectivity of biotic and abiotic parts of the ecosystem.

In the case of harbor porpoises, which can move easily and quickly between frontal regions, spatial extent of fronts becomes trivial when observing predator movements with possible foraging activity. When incorporated into habitat models in the Bay of Fundy, the Baltic Sea, and off the coast of northwest Scotland, tidal phase has successfully predicted porpoise density and social behavior, with more sightings close to high tide and faster current speeds (Johnston et al. 2005,Marubini et al. 2009, Sveegaard 2012). Tidal l featuresform and dissipate over time rather than space. Signification variations in prey congregations and predator presence are likelypatterns based upon time, when patches of foraging effort overlap with patches of prey. While tide strength varies, there is predictability in how the environment will change over the fixed amount of time it takes for a tide to transpire.

RESEARCH OBJECTIVES

This research modeled porpoise habitat use in a spatially explicit and temporally fine-scale domain. Long-term data sets that consider seasonal or inter-annual variability as the temporal scale are limited by gaps in effort, different methodology, multiple observers, or modes of survey (Marubini et al. 2009, Forney et al. 2014). Porpoise distribution is assumed nonrandom relative to prey patches (Dorfman 1990, Calambokidis & Barlow 1991, Read & Hohn 1995, Zamon 2003, Johnston et al. 2005, Allen et al. 2011, Santora et al. 2012, Sveegaard et al. 2012). Surveying porpoises in accordance to the tides is a way to standardize long-term data sets and closely examine snapshots in biophysical coupling in the ecosystem.

The hypothesis stated that variation in porpoise presence in central SF Bay is associated with preferential foraging opportunities that increase and decrease over time along with tidal features. . By predicting variations in porpoise abundance based cyclic, repetitive tidal mechanisms, this temporal model may be used to quantitatively describe habitat use inside the Bay. .The first research question to address the hypothesis asked, does porpoise sighting frequency change at the Golden Gate in association to tidal state and tidal current velocity? The second asked, does porpoise surfacing activity differ depending upon visible surface turbulence associated with tidal fronts? Porpoise sightings through the Golden Gate were predicted to vary in a cyclic periodic manner along with environmental variables which change according to the progression of a tide. A spatial cross-check of the datahypothesized sightings to be more frequent in areas where the bathymetry and Bay currents create predictable tide-dependent features that may optimize foraging efforts of these mobile predators below the surface. The results created a temporal approach to predict porpoise abundance and distribution in fine-scale, spatially explicit area.

METHODS

STUDY AREA

Central San Francisco Bay

San Francisco Bay is a highly geologically, biologically, and economically active estuary. It is the largest and most complex estuary on the west coast of the United States. As a major global force in industry, agriculture, trade and commerce, approximately 95% of the Bay has been physically modified for human purposes, making it one of the most altered estuaries in the world (Cloern & Jassby 2012, Barnard et al. 2013). Anthropogenic influence in the Bay creates a high demand for environmental monitoring to quantify impact on the ecosystem.

The Bay is made of four very different components. The four sub-embayments are located in a tectonically-active basin that was created in the late Cenozoic era (Barnard et al. 2013). The coastal littoral cell extends from Point Reyes to Point San Pedro; the ebb-tidal bar acts as the entrance to the estuary, the submerged river bed that is the Golden

Gate channel wraps around the northwest edge, and the Bay-Delta extends north and south. Central SF Bay incorporates the Golden Gate straight and ebb-tidal entry with an area of approximately 175 km^2 and an average depth of 17 m (Barnard et al. 2013). The Gate is an ancient, submerged river bed made of bedrock that is just under three kilometers wide with depths ranging from less than 10m to 113m deep (Barnard et al. 2013, Green et al. 2013). Central Bay is highly influenced by seasonal upwelling and tidal exchange. Geomorphology, bathymetry, and the exchange of bay and coastal waters create important dynamic energy flows through central Bay (Cloern & Jassby 2012). It is an ideal field laboratory for what? because it is a spatially explicit area where ecological variability may be observed and assessed in the temporal domain, and it is the region of focus in this study.

Complex bathymetry at the estuary-coastal interface strongly influences the biological community in central Bay at all trophic levels. Strong tidal currents create periods of significant turbulent mixing and stratification that prevent bottom water from becoming hypoxic and surface water that promote short-term plankton blooms (Cloern & Jassby 2012). Rippled sediments and complex rock outcrops along the sides of the channel create primary habitat for multiple species of fishes and crustaceans (Greene et al. 2013). Steep shelf breaks and swift currents create areas of biological richness that are characteristic of cetacean foraging habitat (Marubini et al. 2009). While porpoise habitat is generally considered to be broad shelf within the 100m isobaths, the greatest number of sightings in the GF occur near the sharp, bathymetric contrast at the entrance of SF Bay (Barlow 1988, Szczepaniak 1988). Porpoise diving capacity would enable them to utilize the entire range of depth in the channel and central Bay for both benthic and water column foraging.

Tidal Exchange

San Francisco Bay is a time-dependent, salt-wedge estuary. Partially stratified and well-mixed waters alternate states along a mixed, semi-diurnal tide. Two high tides and two low tides of different heights occur every 24 hour period. The vertical rise and fall of the tides creates a six hour period of incoming and outgoing currents through the Golden Gate with a maximum height difference of 1.78m and tidal currents that vary from less than 1m/s to almost 3m/s (Barnard et al. 2013). Tidal currents enter the Bay as a standing wave, meaning the maximum flow velocity occurs midway between high tide and low tide (NOAA 2013). The Bay is classified as a strain-induced periodic stratification estuary, meaning tidal forcing and gravitational circulation alternate as dominating factors in the water column (Geyer & MacCready 2014). There is a six hour difference between peak high water and low water, and between maximum inflow and outflow current velocity. Approximately three hours after peak inflow or outflow is when slack high water or slack low water occurs. This temporal delay in tidal current velocity and tide height is shown in Figure 6.

PLATFORMS OF OPPORTUNITY

Land-based surveys were performed from two areas: the pedestrian lane of the Golden Gate Bridge and a rocky bluff on the northeast side of the Golden Gate channel. These areas had consistent human presence. Observer presence on natural shoreline and on permanent man-made structures in central Bay guaranteed zero effect of observers on porpoise behavior. The total observation area between the two areas encompassed the entire width of the Golden Gate straight and approximately two square kilometers of the entrance to SF Bay. Porpoise sightings were combined with tide and current data from the National Oceanic and Atmospheric Administration (NOAA). Tide height was recorded by the moored buoy station, San Francisco #9414290, located just off Chrissy

Field. Time and velocity of maximum and slack tide currents were taken from moored buoy station, San Francisco #6246, located approximately 1000 meters from the bridge in the Golden Gate. The location of each platform as well as moored buoys which provided tidal data are shown in Figure 7.

Golden Gate Bridge

The pedestrian lane of the Golden Gate Bridge is on the eastern side, 91 meters above mean high water. Until recent decades, when tagging technology came into use, most activity of porpoises was hidden below the surface of the water. The novel opportunity of using the bridge as an observation platform in the Bay created new, sustainable, and virtually free methods to study this species in detail from a stationary, aerial perspective. Depending on water conditions, observers were able to view the animals for extended periods of time under water, which allowed for notes on social structure and behavior in addition to quick dorsal fin counts.

Light poles and support towers along the pedestrian lane of the bridge are labeled with a series of ordered, progressing, odd numbers, similar to street addresses along a road. Latitude and longitude coordinates of each numbered station were recorded on the handheld mapping device with a datum and spheroid classification WGS84, accurate to two meters. Each labeled pole was considered a sighting station along straight-line transects on the bridge. The end points for bridge transects were determined to be the last labelled bridge pole on either end at which an observer could look out over the water for wildlife without substantial land obstructions. The total distance between start and end points was 2,790 meters.

Yellow Bluff

Yellow Bluff sits on the coastline above Fort Baker, on the northeast side of the Golden Gate as the channel curves north (Figure 8). A flat, dirt area on the edge of the bluff served as the observation platform, 19 meters above mean high water. It overlooks SF Bay with unobstructed views north to estuarine? Marin waterways, east toward Angel Island and Alcatraz, and south to San Francisco's city's northern edge. The area just off of Yellow Bluff is an area where the bathymetry highly influences Bay currents (Green et al. 2013). Water enters through the Golden Gate and is obstructed by a rock structure called Cavalo Spire, shown in Figure 8. The obstruction causes fine-scale upwelling west of the spire on an incoming tide, and eddy wake on an outgoing tide. The flow of water through the channel forms a persistent front along the edge of Fort Baker on a flood and ebb tide. Upwelling sites are areas of preferred foraging habitat for marine mammals, essential in determining marine mammal distribution and activity (Learmonth et al. 2006). This site provided quality assurance data with a theodolite to show consistency in the spatial domain of this research.

FIELD METHODS

Theodolite Surveys

Theodolites are a form of survey equipment thatplace an object of interest in a two-dimensional space based on (1) horizontal angle from magnetic north and (2) vertical angle from observer zenith (Figure 9). Theodolite surveys have been used in cetacean tracking studies since the 1970's in land-based surveys as a noninvasive way to track the animals with minimal effect on behavior (Wursig et al. 1991, Gailey & Ortega-Ortiz 2000, Harzen 2002, Anderson 2014). In this observing method, the latitude and longitude of the observer is recorded. Height above the water's surface is recorded with an accuracy to 10cm unless the fixed point is within 500m (Wursig et al. 1991). Distance of a fixed point to the observer is calculated from the vertical angle and height above mean sea level. Using geometric angles of the station, distance to point, and horizontal bearing, the x/y coordinates may be projected on a map with an accuracy to a few meters (Wursig et al. 1991, Gailey & Ortega-Ortiz 2000, Harzen 2002, Anderson 2014). Theodolite surveys were performed from Yellow Bluff opportunistically based upon field conditions and tidal cycles. The geographic location of tidal fronts were recorded to support data that show how bathymetry affects Bay currents and front formations.

Bridge Transects

Point-count surveys of porpoises were conducted during straight-line transects across the Golden Gate Bridge. The end points of each survey were set between two support towers in which an observer view of the channel would not be obstructed by land masses. Data collection began in December, 2013 and continued for one year to December, 2014. Observers were allotted two hours on the bridge, and exact start and end times were recordedto account for each individual survey effort, which varied according to sighting activity, visibility, or weather conditions. . Observers walked along the eastern side of the bridge looking over the water with a visual range estimated at approximately 300 meters. Any porpoise surfacing or visible underwater activity was recorded as sighting.

Time, location, porpoise group size, dispersion, behavior, and porpoise position relative to surface turbulence (if present) were described for each sighting. The time of each sighting was later matched to a time segment in tidal progression. Location was associated with the closest, last passed bridge pole (regarded as a station number). Behavioral categories were defined as travel (a single surfacing or multiple surfacings in a single direction), forage (multiple surfacings in the same location or close circling of the same area by porpoise groups), or confirmed feeds (visible prey with the porpoise at or near the surface). Position to surface turbulence was categorized as inside (porpoise activity between the observer and the front), outside (porpoise activity beyond the tide front), or directly over surface turbidity.

Observer walking pace was not standardized.Instead, time on effort was standardized into "units of effort," calculated by dividing the total number of minutes spent on a survey by 30 minute increments. The 30 minute time segment was chosen to match the methods by which tidal progression was divided in the temporal analysis of this research. Porpoise group estimates in each sighting were then converted into a frequency value by dividing the count data by the units of effort calculated for that survey. Standardized porpoise frequency value,defined as the number of porpoise sighting per unit effort, was used instatistical analysis.

DATA ANALYSIS

Tidal Progression Defined

The timing of tides and porpoise sightings was divided into segments of tidal progression. The hour and minute of each sighting were derived to standardized tidal units consistent to any sampling day over a 24 hour tidal period. Here are terms we have developed to describe tidal progressions for the methods used in this research.

<u>Tidal Progression</u>: the evolution of a tide cycle, divided into 30 minute segments.

<u>Tidal State</u>: an increase of water volume inside the bay during an incoming, flood tide, and a decrease in volume during an outgoing, ebb tide; considered to be six hours, or twelve 30 minute tidal segments.

<u>Current Progression</u>: the increase and decrease of tidal current velocity; considered to occur every three hours, or six 30 minute tidal segments.

The time of maximum and minimum tide height was recorded from NOAA tide tables and considered to be the time of slack high and slack low water. The time and velocity of the maximum tidal current was also recorded for each ebb (-) and flood (+) tide. The time of each porpoise sighting was classified within a 30 minute tidal segment after slack high water and maximum tidal current velocity (Figure 10). Timing of porpoise sightings, slack water, and maximum current velocities were entered into an Excel document and then analyzed in the statistical software R. Porpoise sightings, according to tidal progression, were analyzed using circular statistics with tidal state and current progression.

Circular Distribution Models

Tide-dependent variables, like hours on a clock, cycle on a regular basis. Periodic increases and decreases in tidal currents and volume are predictable based on tidal phase. Although there are alternating periods of tidal strain and relatively stabilized water column conditions, density gradients and stratification in tide-forced estuarine circulation is highly nonlinear (Geyer & MacCready 2014). Proxies that do not have a linear effect on the data introduce biased effects of autocorrelation, risk over-smoothing with explicitly placed kernel functions, and do not account for cyclic affects (Marubini et al. 2009, Cloern & Jassby 2012). Alternatively, circular methods can be applied to ecological data that are nonparametric and multimodal where linear regression analysis may not be appropriate to observe environmental change (Batschelet 1981, Oliveira et al. 2012, 2013). When data are considered on a circular scale, those effects are minimized. Porpoise sightings were analyzed with circular statistics along a 24 hour "clock" representing the time it takes for a full mixed, semi-diurnal tide regime to take place.

In circular statistics, a wrapping estimator tests data against a distribution model similar to?goodness of fit models in linear analysis. A bandwidth value replaces a kernel function, calculated from the concentration parameter for spherical data rather than a smoothing parameter that is used in linear methods (Hall et al. 1987, Taylor 2008).

Parameter estimation is done by Akaike Information Criteria (AIC) and selects models from skewedness and peakedness of the data around a model circle (Oliveira 2012). Bandwidths are validated using the data-driven cross validation rule for circular regression estimation which decreases density parameter error caused by multimodality (Oliveira et al. 2012, 2013). The translation of linear to circular terms used in this research is shown in Table 1.

Data were first grouped three ways corresponding to tidal proxies. Group (a) used 24, one-hour tidal segments which represented data distributed around an entire tidal progression. Group (b) used eight, three-hour tidal segments that represented data with a distribution concentrated by the increase or decrease in tidal current velocity. Group (c) placed the data into four, six-hour time bins, representing data concentrated in respect to tidal state: flood or ebb.

Three models were fit to grouped data. The first used a von Mises distribution, which assumes a symmetrical concentration across all angles on a circle and displays a normal distribution (Taylor 2008, Pewsey 2013). This model served as the null hypothesis that sightings were not significantly affected by cycling tidal parameters. If tidal proxies did not have an effect on porpoise sightings, then the number of sightings would not vary throughout a 24 hour tidal progression. Two high tides and two low tides of different heights occur in SF Bay's mixed, semi-diurnal tide regime, which may lead to multimodal distribution. The second model, Wrapped Cauchy, best fits data with reflective symmetry. If only tidal state, the direction of water flow in or out of the Bay, had a significant effect on porpoise sightings, then this model would best fit the data. The third model, Wrapped-Skew, accounts for data concentrated around a specific mean direction. If differing tide heights and current strengths among two high and two low tides in a mixed, semi-diurnal tide regime have a significant effect on porpoise sightings, then this model would significantly fit the data. A representation of these three models with simulated data in R is shown in Figure 11.

Asymmetrical Tiered Analysis of Variance (ANOVA)

Behavioral states were observed as a way to investigate habitat utilization based on environmental conditions. Dynamic state modeling for foraging decisions have been used to observe the impact of temporal and spatial scales on relative foraging effort in fishes, birds, and marine mammals (Clark & Ekman 1995, Underwood et al. 1993, Bull et al. 1996, de Boer et al. 2014). In the case of porpoises, species-habitat relationships have been found to be highly scale-dependent as covariates change with resolution (Marubini et al. 2009). In a time sequential model, the study period, foraging time period, and decision period need to be defined in order to optimize variable relationships within the model (Underwood 1993). The study period for this research was one year. The foraging time period was considered over a 24 hour tide regime. In corroboration with other literature with these methods, the foraging decision period was considered within one hour or less by dividing sighting times and tidal progression into 30 minute segments.

A three-way, nested Analysis of Variance (ANOVA) was designed after to describe asymmetrical analyses of variance similar to a BACI (Before/After, Control/Impact) model. This type of ANOVA is useful when considering impacts of specific factors at various temporal scales and at multiple sampling stations (Underwood 1993). Factors 'before' & 'after' were translated to 'flood' & 'ebb' tidal state; factors 'disturbed' vs. 'control' sites were translated to 'front' vs. 'no front' present; response variables at each 'location' were translated to behavior states in each 'sighting.' The classic BACI model and porpoise ANOVA are shown in Figure 12. In this way, sightings were considered samples and the model accounts for patterns of abundance at multiple temporal phases.

RESULTS

Bridge transects were conducted from December 2013 through December 2014. A total of 495 porpoise sightings were recorded in 943.4 hours on effort. A total number of 239 sightings were recorded during a flood tide, with a mean sighting frequency of 0.80 porpoises per unit effort. The total number of sightings during an ebb tide was 256 sightings, with a mean sighting frequency of 0.67 porpoises per unit effort. The average group estimate for both tidal states was two porpoises. Figure 13 summarizes porpoise sightings and sighting frequency for each 30 minute tidal segment. The tidal segment in which the most sightings occur is not the same tidal segment in which porpoises are seen in the largest numbers within sightings. Figure 14 summarizes sighting frequency according to sighting location. Sightings were concentrated on the northern side of the channel.

TEMPORAL ANALYSIS

Porpoise sightings were analyzed with circular methods for nonparametric data with possible multimodal distribution. Angular variance and angular deviation calculated the concentration parameter, which in turn defines the fit of a model to the data. A summary of these for the three wrapped estimate models (von Mises, Wrapped Cauchy, Wrapped Skew) are shown in Table 2. AIC parameter selection was done automatically in R. Bootstrap analysis with 9,999 replicates was performed in place of the absence autocorrelation residual test with Monte Carlo randomization to test the data against uniformity.

A Rayleigh test for departure from uniformity performed with 9999 replicates for each wrapped estimate model and per each group of data: (a) uniform, (b) divided by tidal velocity increase and decrease, and (c) divided to represent tidal state. Groups (a) and (c) showed significant departure from uniform distribution of the von Mises model in the 95% confidence interval with [$p = 0.001$] and [$p = 0.0009$], respectively. No group of data showed significant departure from uniformity to show reflective symmetry of the Wrapped Cauchy model. Ungrouped data showed a significant departure from uniformity with a concentration in a specific mean direction reflective of the Wrapped Skew model with [$p = 1.61 \times 10^{-56}$]. These results are summarized in Table 3.

Wrapped estimators from each model and ? were fit to the data. Data are displayed as different density distribution curves around the 24-hour tidal progression circle in Figure 15. The model which showed the best fit for the data was the Wrapped Skew model, with a concentration parameter 0.83, angular variance of 0.17, and angular deviation 0.61. The Rao's Spacing test was additionally performed on ungrouped data. A Rao's Spacing tests data for multimodal departures for uniformity and can account for reflective symmetry or a specified mean direction in time or geographic space (Batschelet 1981, Jamalamadaka & SenGupta 2001, Pewsey et al. 2013). The results showed significant multimodal distribution and a specific mean direction at the 95% confidence level with [$F=0.34$, $p=0.001$].

Circular correlation coefficients were additionally calculated for porpoise sighting frequencies in each divided category of tidal progression. Analysis employed the Jammalamadaka-Sarma correlation coefficient, which adapts the Pearson's product moment correlation to circular data (Jammaladaka & SenGupta 2001, Pewsey et al. 2013). Four tidal states associated with water volume entering and exiting the Bay were considered as High-High to High-Low (ebb1), High-Low to Low-High (flood1), Low-High to High-Low (ebb2), and Low-Low to High-High (flood2). When flood and ebb sightings were considered together ($n = 496$), sightings showed significant negative correlation with sighting frequency [$r = -0.16$; $p = 0.0007$]. An increase and decrease of tidal velocity occurred in each of the four categories, creating eight tidal velocity states. Porpoise sighting frequency was considered significantly correlated to tidal phase at the

95% confidence level with p-values ≤ 0.05. Increasing tidal velocity on an incoming (flood) tide showed significant negative correlation to sighting frequency [$r = -0.93$, $p = 0.01$] and [$r = -0.41$, $p = 0.01$] (Table 4).

SPATIAL VERSUS TEMPORAL TIDE COMPONENTS

Variation in porpoise sighting frequencies was hypothesized to depend on tidal features that may optimize foraging efforts. To analyze the effect of tidal state and tidal front presence on porpoise behavior, a nested ANOVA was performed. Three behavioral states were assigned to porpoise sightings: travel, forage, and feed. A summary of the number of sightings per predictor variable is shown in Table 5. Each sighting was considered a separate sample, behavioral state the response variable.

The adapted BACI ANOVA model was run in a hierarchical manner to demonstrate temporal trends that may be caused by short-term fluctuations in the environment. First, an independent ANOVA test was performed for each tidal variable (state, front, behavior) to test for significant effect on porpoise sighting frequency (Table 6). Tidal state had a significant effect on sighting frequency at the 95% confidence ($p<0.05$) with [$F = 5.48$, $p = 0.02$]. Behavioral state had a significant effect as well with [$F = 19.69$, $p = 5.95 \times 10^{-08}$]. Next, each variable (state, front, behavior) was tested for interaction. No significant interaction was found (Table 7). Third, as a result of no significant interaction among variables, a nested ANOVA test was performed on behavioral state (impact) within tidal state (time) and tidal front presence (space). These results are displayed in Table 8. Behavior produced a significant result when nested within tidal state with [$F = 9.96$, $p = 9.38\ 10^{-08}$], but not within tidal front presence.

DISCUSSION

POTENTIAL BIAS

Vessel Interactions

There were a few instances where fishing boats, sailing and personal recreational vessels, as well as the Bay ferry fleet came within 10 meters or less to porpoises. Observers from the pedestrian lane of the bridge noted that some porpoises changed their behavior in reaction to the ferry. There were also instances where the ferry slowed or changed course to avoid porpoises. In contrast, sailing vessels were observed very close to porpoises while underway; there were no instances where porpoise behavior changed due to a sailing vessel. Kayakers were also able to get very close to porpoises off of Yellow Bluff. Neither? Travel direction nor milling behavior stopped when kayakers passed within a few meters. Idle fishing vessels and porpoises even utilized the same persistent tide fronts off of Yellow Bluff in some sightings. It is likely that porpoises here are habituated to high levels of boat traffic and human activity. Because porpoise behavior most often did not change in occurrence with vessel activity, boat traffic and incidental interactions were not considered a variable to create bias in sighting results.

Visibility due to Fog

Visibility greatly varied from both platforms of opportunity depending upon weather conditions that create fog clouds in central Bay. On a clear day, the distance an observer would be able to see along the water in clear conditions was estimated 300 meters. Alternatively, some surveys made no observations because the surface was not visible at all from either platform of opportunity. Complex topography and a wide range of temperatures at the coastal-sea interface near San Francisco produce micro-climates that are difficult to forecast (Koracin et al. 2005, SFMX 2010). However, a mixture of coastal upwelling, persistent north-west winds, and a stable low pressure system over inland valleys in Spring and Summer create relatively foggier conditions at the Golden Gate than Fall or Winter (SFMX 2010). Fog was recorded in 34% of bridge transects, with a 32% increase during summer months (June through August). Fog prevented a total of seven surveys to be completed: three in winter months, one in fall, two in spring, and one in summer.

Citizen science

Citizen science is a tool that may be used in ecological studies to expand monitoring efforts and obtain larger data sets (Dickinson et al. 2010). In this research, a volunteer program was created through the SF Bay Chapter of the American Cetacean Society and Golden Gate Cetacean Research to place observers on the Golden Gate Bridge for most hours of daylight for the data collection period. Volunteers were trained in the field and were given printed, step-by-step instructions to follow on bridge transects. Walking pace was addressed as a possible area of bias by standardizing time on effort and by using porpoise sighting frequency data rather than raw count data from surveys. Areas of bias that were not addressed are as follows. Shifts were assigned on a volunteer basis. This lead to some volunteers accounting for more surveys than others, and bridge coverage varied on a monthly basis which may introduce seasonal gaps in the data. In addition to weather, there were five surveys that were called off for personal reasons including sickness or lack of parking. Comment in general on how the results might be changed by these issues. If you deem them not to have a significant effect at least anecdotally, then say so.To improve this situation, all observers would need to be committed to an equal number of shifts, and attendance would need to be guaranteed over an annual term of surveys.

SUMMARY OF RESULTS

Temporal

The null hypothesis stated that if tidal variables had no effect on porpoise sightings, then the data would have a uniform distribution around a 24 hour tidal progression period. If the null hypothesis was not rejected, the von Mises distribution model best fit the data. The null hypothesis was rejected, as the results show significant departure from uniformity for ungrouped and grouped data, as well as a concentration of data in a specific mean direction. The Rao's Spacing test also produced a numerical significant result of multimodal distribution in a specific mean direction. The Wrapped Skew model best fit the data, reflecting tidal segments 0.5 to 2.5 which contained the most porpoise sightings. These segments represent the space in time 30 minutes to 2.5 hours after High-High water occurs in central Bay on an increasing ebb tidal velocity.

The Jammaladaka-Sarma correlation coefficient found porpoise sighting frequency to be negatively correlated with an increasing tidal velocity on a flood tide. This is reflected in the number of sightings as well. An increasing flood tidal velocity shows the lowest sample sightings of any of the tidal categories. More sightings occur at the end of a flood tide, and the most sightings occur in the beginning of an ebb tide. At the turn of a flood to ebb tide is also when the most defined shear zones are observed in central Bay, when tidal forcing overtakes gravitational circulation (Green et al. 2011; Geyer & MacCready 2014). The water column is stratified by density at this time, while current velocity and eddy viscosity are at a minimum in surface waters (Figure 16). This stage in tidal progression may create optimum conditions for prey concentrations to occur in near-surface waters.

Spatial versus Temporal Tide Components

The tiered ANOVA produced significant results to relate space and time to variations in porpoise abundance and space-use in central Bay. A visual map of the results as produced through the three-step analysis are shown in Figure 17. Behavioral categories were made to denote information on the functional mechanisms for habitat use. Repeated dives, circling, and observed feedings in contrast to travel show focused interest in certain areas that may relate to foraging. Difference in abundance and in space-use did vary depending on tidal variables, but the point was not to show differences in behavior dependent on specific areas of use. The fine spatial scale of the study area is not significant to analyze such a highly mobile animal. It is unlikely that changes in porpoise sightings were due to movement of the animals in and out of such a small area. Rather, it was likely due to the greater mechanism affecting the entire area as a whole (tidal flow) to influence porpoise behavior and therefore likelihood to be seen at the surface.

In the first step of analysis, the independent ANOVA analyzed all the data and tested for significant effects of environmental fluctuations on sample abundance. The results showed tidal state and behavioral state had a significant effect on porpoise sighting frequency, but tidal front presence did not. This shows that the temporal, not spatial, tidal fluctuations affected the number of porpoise sightings per unit effort. No significant results in the test for interaction meant that short-term fluctuations were not significant. This meant the response variable, behavioral state, could be analyzed nested within environmental variables. According to this analysis, behavioral states vary significantly according to tidal state rather than tidal front presence. This means that significant results when 'behavior' is nested within 'tide state,' then variability is most likely due to site variability over short periods of time.

ENVIRONMENTAL IMPLICATIONS

Studying foraging habitat of an upper-level trophic predator gives a top-down perspective of water quality and productivity of an ecosystem. Primary productivity has increased in SF Bay from 1978 to 2010 and is ecologically significant through all trophic levels (Cloern & Jassby 2012). Marine Protected Areas (MPA) within the Bay, which regulate human activity and resource takes, have helped fish stocks improve since 1999 according to CA Department of Fish and Wildlife (NMFS 2001, Gleason et al. 2010, Jassby & Cloern 2012). High-use areas of porpoises also indicate a reliable place to find prey, and predator conservation is also closely related to fish populations. While there has been extensive work to study sea grass, invertebrate, and fish, it is also important to give attention to energy flow at higher trophic levels in SF Bay. Spatio-temporal trends in multi-trophic level interactions are important to grasp for ecosystem management.

While some MPAs are designated within the Bay, the estuary is currently excluded from the Marine Life Protection Act (MLPA) and the GF. The area is under review for a possible expansion to include the urban waters inside the Golden Gate. A portion of the review investigates sufficient justification for an expansion based upon conservation, ecological, recreational, historical, cultural, and educational values (Batha et al. 2013). In addition to gathering habitat use details on a federally protected species, this research extended ecological study to the local community. The citizen-science program opened up recreational and educational opportunities, and promoted conservation awareness to the public. Therefore, it was not just scientifically insightful for harbor porpoise research, but it was also considerably important for influencing public education and outreach for interactions of human society with the estuarine community.

One theory for the high level of porpoise activity in central Bay is thought to be historically linked to the areas advances in conservation efforts. Increased attention on environmental health post-WWII may be responsible for an improving ecosystem. Central Bay and the mouth the estuary experienced a net loss of sediment from 1947 to

2005 (a combined 143 million m^3) which may have reduced the amount of settled pollutant materials (Barnard et al. 2013). The Clean Water Act (CWA) Amendments of 1977 and 1987 that raw sewage and toxic waste water was prohibited to be dumped into the estuary (EPA 2011). Restricted run-off and dumping to Bay water would gradually change the chemical and biological composition of the estuary closer to natural conditions and decreased pollutants would theoretically improve water quality.

Porpoise habitat range is closely linked to the physical and chemical characteristics of the water column which create reliable foraging areas. SF Bay has already been studied as a primary example of how physical variability in coastal oceans drives biological variability in bays and estuaries at lower trophic levels (Cloern & Jassby 2012). San Francisco Bay is not the only place where porpoise sightings have increased close to the coast. Shore-based sightings were rare or nonexistent in the last several decades, but are now increasing in areas of the Pacific and Atlantic Oceans (Camphuysen 2004, Thomsen et al. 2006, Anderson 2014, Sheldon 2015). It may be a trend that is shared among ocean basins. Whether the increase is due to ecological regime shifts linked to ocean dynamics, or simply increased efforts by researchers, relating water quality components between distinct geographic areas increased porpoise sightings may be important to analyze trends of marine predator critical habitat.

Climate change could also be playing a role, as it alters water masses and current boundaries which determine prey accumulation and predator range. Seasonal abundance may change for marine mammals that migrate, and dispersal mechanisms may change to create new areas or periodic residence for more provincial species, such as the harbor porpoise (Learmonth et al. 2006). Surveys in Monterey Bay in 1989 to 1990 found porpoise sightings were positively correlated with average surface temperature (Dorfman 1990). The largest observed El Nino/La Nina event occurred in 1997 to 1999, which created abrupt ecosystem changes measured regionally off the coast of SF Bay by surface temperature and upwelling indexes (Cloern & Jassby 2012). It may be that this ecological regime shift in SF Bay was a positive thing for harbor porpoise populations in the GF. Monitoring population changes is an important way to increase understanding the trophic cascade by which El Nino/La Nina, North Pacific Gyre Oscillation, and climate change may effect biological communities in the estuary (Cloern & Jassby 2012). Conducting further research on marine mammals in SF Bay and GF is important to consider along with the rest of the ecosystem.

Greater Trends in Time and Space

Data analyzed in the temporal, rather than spatial, domain provided a relatively stable method of predicting porpoise presence in a habitat that drastically changes with tidal exchange. Adding temporal analysis to habitat modeling may be extrapolated to larger timescales that are associated with physical patterns and biological processes (Figure 18). In a time-state variability model, time provides an explanatory variable that does not decrease resolution or increase noise as geographic scale is increased. Patch dynamics may therefore be thought of as spaces in time, rather than geographic location. Concrete segments of time, rather than variable conditions in space, could be isolated to analyze ecological trends.

A dynamic state variable model described fine-scale distribution patterns of harbor porpoise that may be used to better understand habitat use in central SF Bay. Predicting when porpoises are seen in highest abundance in this area will create more efficient methods for spatial-species conservation related to anthropogenic threats. It will also provide more efficient survey methods for future observations related to improving knowledge of life history details. Identifying spatial-temporal trends of marine mammal occurrence may also relate to analysis of prey population dynamics, to monitoring water quality, and serve as an ecological link between local, fine-scale and regional, long-term patterns of the ecosystem.

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TABLES

Table 1: Translation of Linear Statistical Terms to Circular Methods.

Function	Linear Term	Circular Term
Model	Goodness of Fit	Wrapped Estimate
Manipulates the Fit	Kernel Estimator	Bandwidth Value
Defines the Fit	Smoothing Parameter	Concentration Parameter
Calculates the Parameter	Variance Standard Deviation	Angular Variance Angular Deviation
Validates the Model	Maximum Likelihood with Monte Carlo Simulation	Cross-validation Integral with Bootstrap Analysis

Table 2: Summary of Circular Statistics Calculated for each Distribution Model. These values were calculated in R and used to define parameters which fit circular models to the data.

n = 495	von Mises	Wrapped Cauchy	Wrapped Skew
Angular Deviation	1.92	0.64	0.61
Angular Variance	0.84	0.33	0.17
Concentration Parameter	0.16	0.67	0.83

Table 3: Results of the Rao's Spacing Test for Multimodal Departures from Uniformity. Grouped data were each tested against the null, uniform distribution. An asterisk next to a p-value ≤ 0.05 shows a significant departure with multimodal distribution in the 95% confidence level.

Model	**Group**	**p**
von Mises (uniform distribution)	a. Ungrouped b. Tidal Velocity c. Tidal State	0.001*** 0.82 0.0009***
Wrapped Cauchy (reflective symmetry)	a. Ungrouped b. Tidal Velocity c. Tidal State	0.16 0.56 0.93
Wrapped Skew (Specific Mean Direction)	a. Ungrouped b. Tidal Velocity c. Tidal State	1.61×10^{-56}*** 0.89 0.63

Table 4: Correlation between Porpoise Sighting Frequency and Tidal Phase Segments. Data were divided into groups according to (a) tidal progression (24, 30 minute segments), (b) tidal velocity (8, 3 hour segments), and (c) tidal state (4, 6 hour segments). Correlation coefficients were calculated in R with the Jammalamadaka-Sarma caluclations for comparing circular to circular data. P-values were returned with a Bootstrap analysis with 9999 replications and were considered significant at the 95% confidence level with $p \leq 0.05$.

(b) Tidal Velocity	**HH to HL**		**HL to LH**		**LH to LL**		**LL to HH**	
Inc / Dec	**↑ebb 1**	**↓ebb 1**	**↑flood 1**	**↓flood 1**	**↑ebb 2**	**↓ebb 2**	**↑flood 2**	**↓flood 2**
# Sightings	154	28	6	71	91	32	38	76
Mean Sighting Freq.	0.99	0.85	1.08	1.21	1.08	1.42	1.38	1.30
Correlation Coefficient	-0.13	-0.10	-0.93	-0.80	-0.05	-0.19	-0.41	-0.06
p-value	0.11	0.65	0.01**	0.51	0.64	0.30	0.01**	0.62

(c) Tidal State					
	ALL (a)	**HH to HL**	**HL to LH**	**LH to LL**	**LL to HH**
# Sightings	496	182	77	123	114
Mean Sighting Freq.	1.14	0.97	1.20	1.17	1.32
Correlation Coefficient	-0.16	-0.13	-0.08	0.09	-0.11
p-value	0.0007***	0.28	0.81	0.63	0.61

Table 5: Summary of Porpoise Sightings Used in ANOVA Tests.

n = 495	Front Present		Front Absent	
Tidal State	**# Sightings**	**Mean Sighting Frequency**	**# Sightings**	**Mean Sighting Frequency**
Flood Tide				
travel	93	0.98	13	0.94
forage	112	1.50	4	1.86
feed	15	0.99	1	0.52
Ebb Tide				
travel	101	0.7	18	0.79
forage	103	1.3	26	1.21
feed	7	1.2	2	0.71

Table 6: Step 1 in BACI ANOVA Model: Independent ANOVA. Variables each tested against porpoise sighting frequency to show if short-term environmental fluctuations have a significant effect on sighting frequency. Values with an asterisk represent a p-value ≤ 0.05 and show significance at the 95% confidence level.

Variable	F-stat	p-value
Tidal State	5.48	0.02 *
Tidal Front Presence	0.16	0.68
Behavior	19.69	5.95×10^{-08} ***

Table 7: Step 2 in BACI ANOVA Model: Test for Interaction. No significant results were found at the 95% confidence level with p-values ≤ 0.05.

Variable	F-stat	p-value
Tidal State : Behavior	0.42	0.66
Tidal Front : Behavior	0.28	0.76
Tidal State : Front	0.10	0.75

Table 8: Step 3 in BACI ANOVA Model: Nested ANOVA. In this step, behavioral state is tested as the impact response variable within tidal parameters for short-term variations in space (front presence) or longer-term environmental fluctuations in time (tidal state). Behavioral state showed significant change at the 95% confidence level with a p-value $\leq$ 0.05 when nested within tidal state, but not tidal front presence, as shown by the values with asterisks.

Variable	F-stat	p-value
Tidal State x Behavior	5.48	0.02*
Tidal Front x Behavior	0.16	0.68

FIGURES

Taxonomic Classification	
Order:	Cetacea
Suborder:	Odontoceti
Superfamily	Delphinoidea
Family:	Phocoenidae
Genus:	*Phocoena*
Species:	*Phocoena phocoena*

Figure 1: Taxonomic Classification of the harbor porpoise, *Phocoena phocoena.* Copyright Berta et al. (2006).

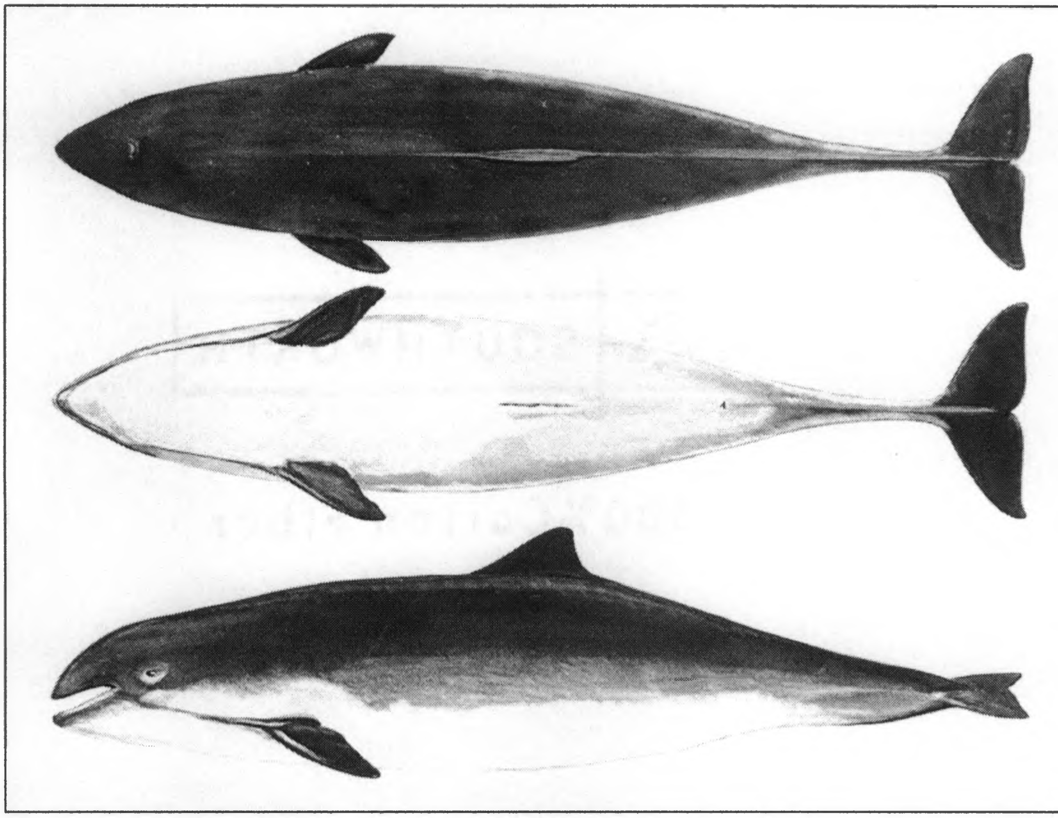


Figure 2: Dorsal, Ventral, and Lateral Illustration of a Harbor Porpoise. Illustration by Wilde Whales BC Cetaceans Sightings Network. http://wildwhales.org/harbor-porpoise

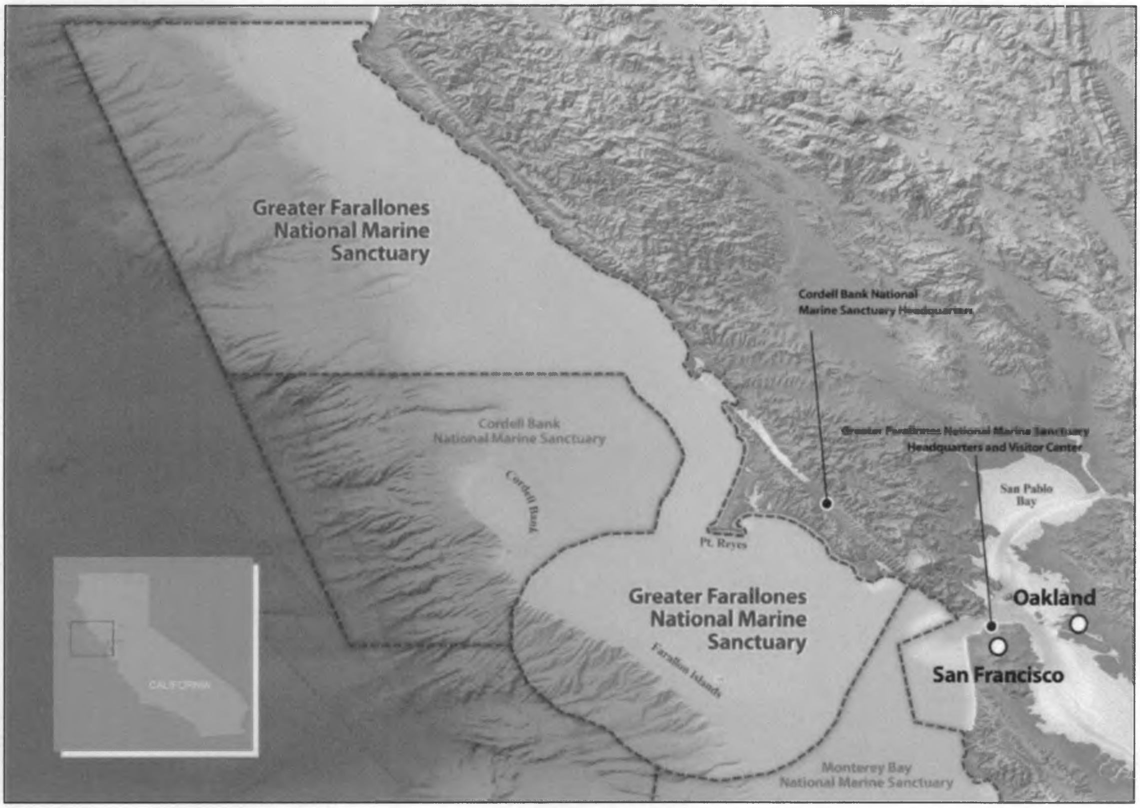


Figure 3: The Greater Farallones National Marine Sanctuary. http://farallones.noaa.gov/

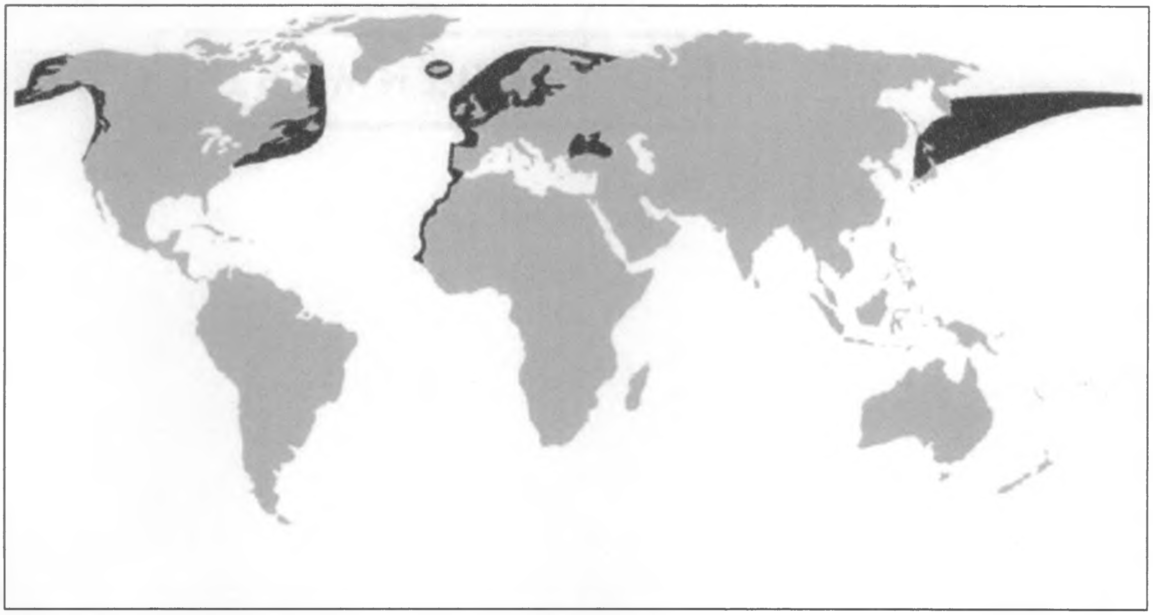


Figure 4: Worldwide Harbor Porpoise Distribution. Copyright BY-SA 3.0 http://commons.wikimedia.org/wiki/File:Cetacea_range_map_harbour_porpoise.PNG

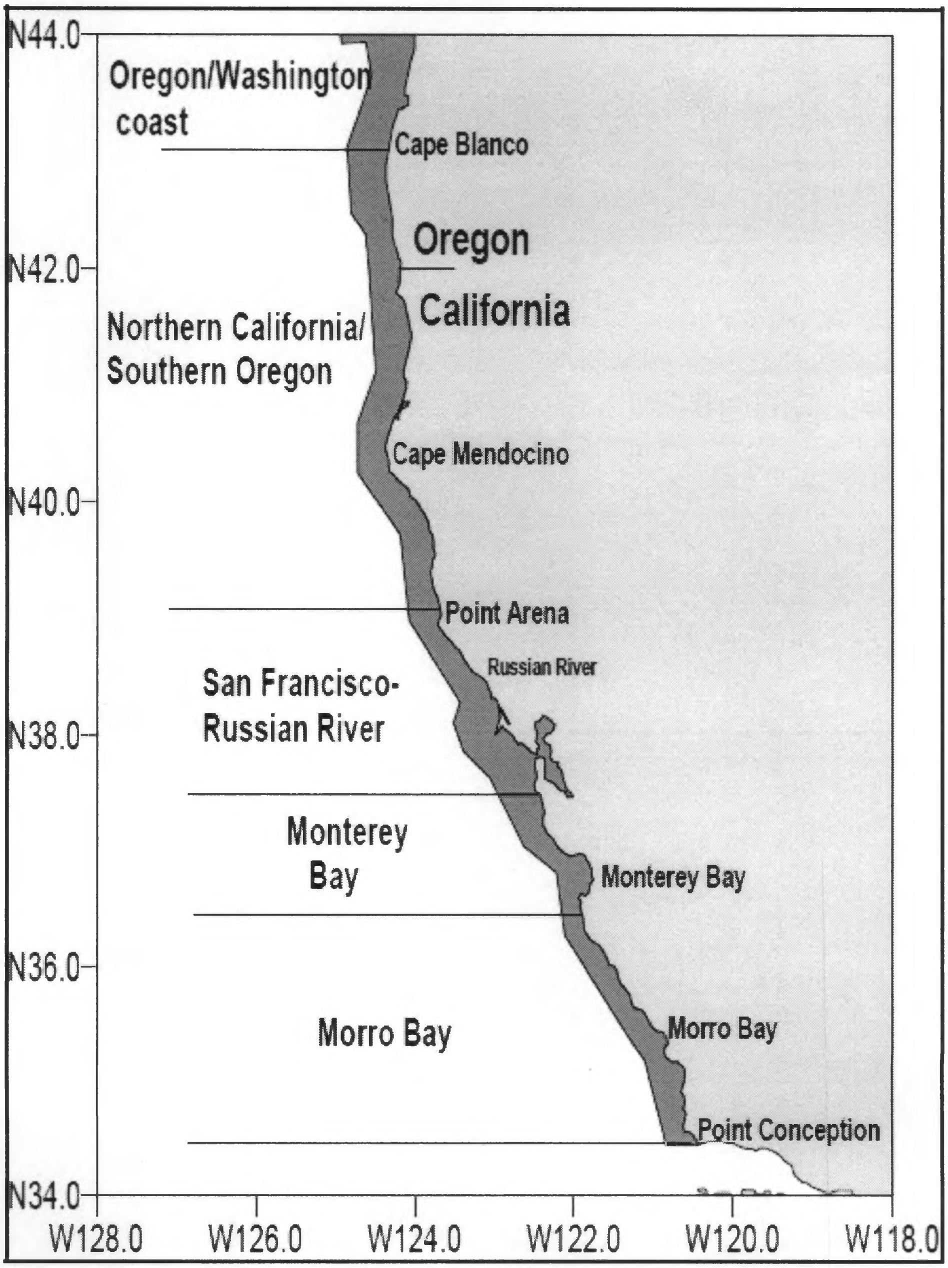


Figure 5: Substock Boundaries of the N. American Pacific Population of Harbor Porpoise, Designated by the National Marine Fisheries Service (Carretta et al. 2013).

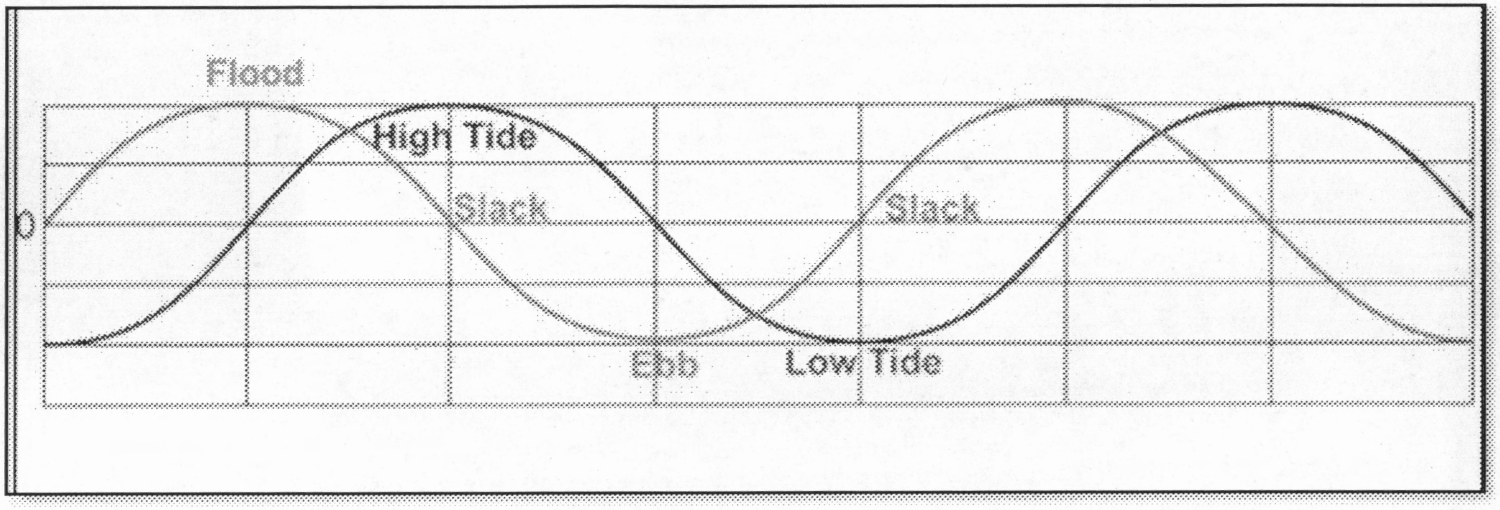


Figure 6: The Standing Wave. The red line represents tidal current velocity and the black line represents tidal height, or the volume of water inside the Bay. There is a six hour difference between peak high water and low water, and between maximum inflow and outflow velocity. Copyright NOAA (2013).

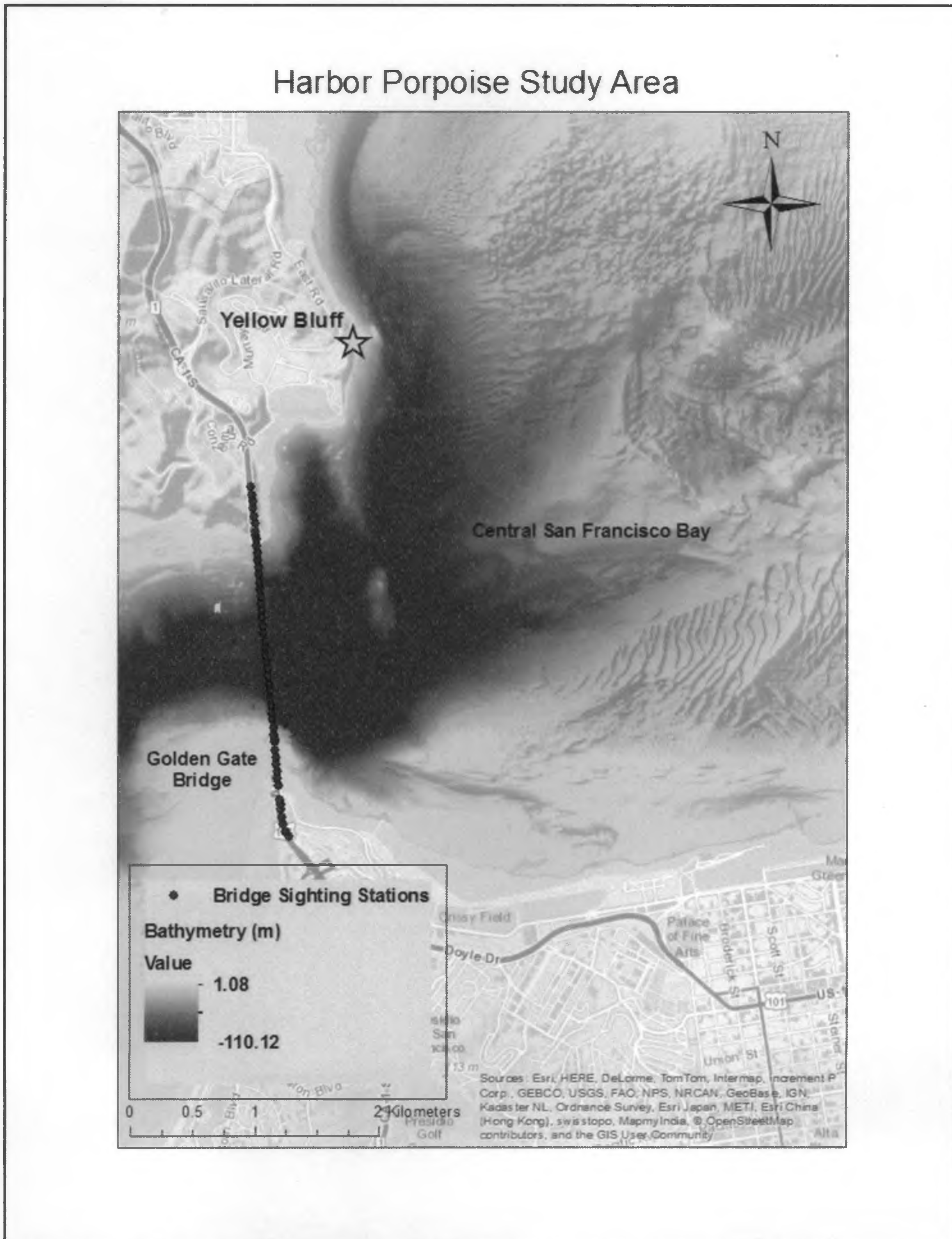


Figure 7: Platforms of opportunity. *Data used in this study were acquired, processed, archived, and distributed by the Seafloor Mapping Lab of California State University Monterey Bay.* The pedestrian lane of the Golden Gate Bridge overlooks the eastern side, providing an aerial view of the entire width of the straight. Yellow Bluff, on the north side of the Golden Gate, is an area where tidal fronts form and provides an additional view of the entrance to the estuary from the north side of the channel.

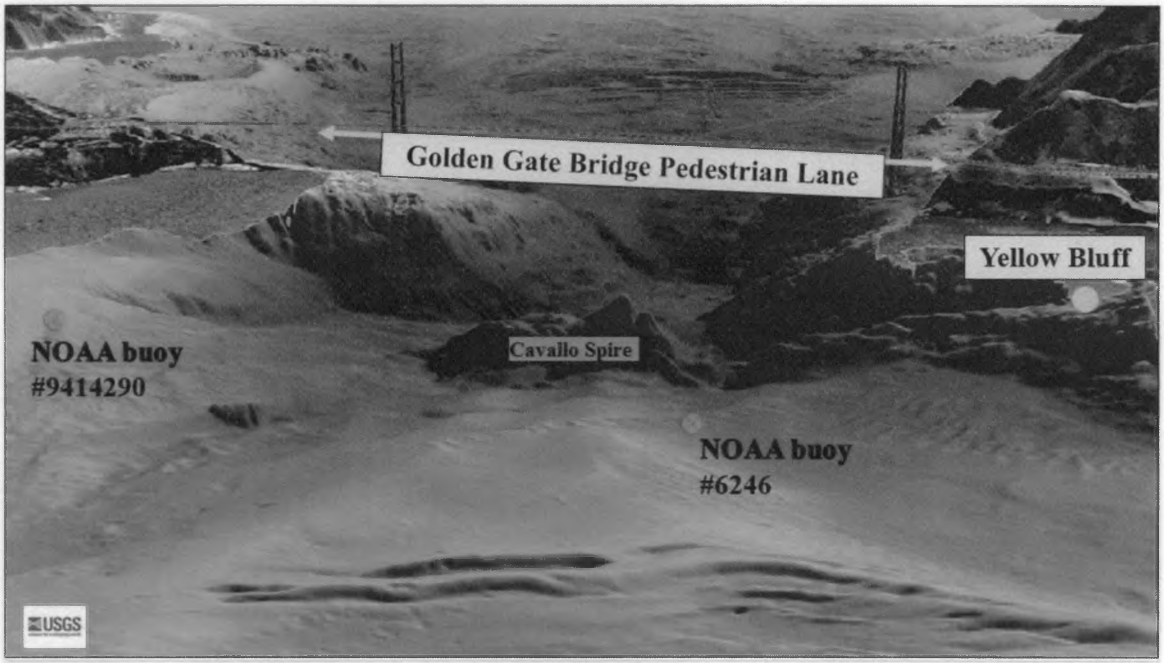


Figure 8: Central San Francisco Bay, Looking West. Bathymetric data from US Geological Survey. Channel bathymetry causes fine-scale upwelling west of Cavallo Spire on an incoming tide, and eddy wake on an outgoing tide. The flow of water through the channel forms a persistent front along the edge of Fort Baker on a flood and ebb tide. The Golden Gate Bridge Pedestrian Lane and Yellow Bluff, above Fort Baker, were chosen as platforms of opportunity to observe tidal exchange and porpoise sightings.

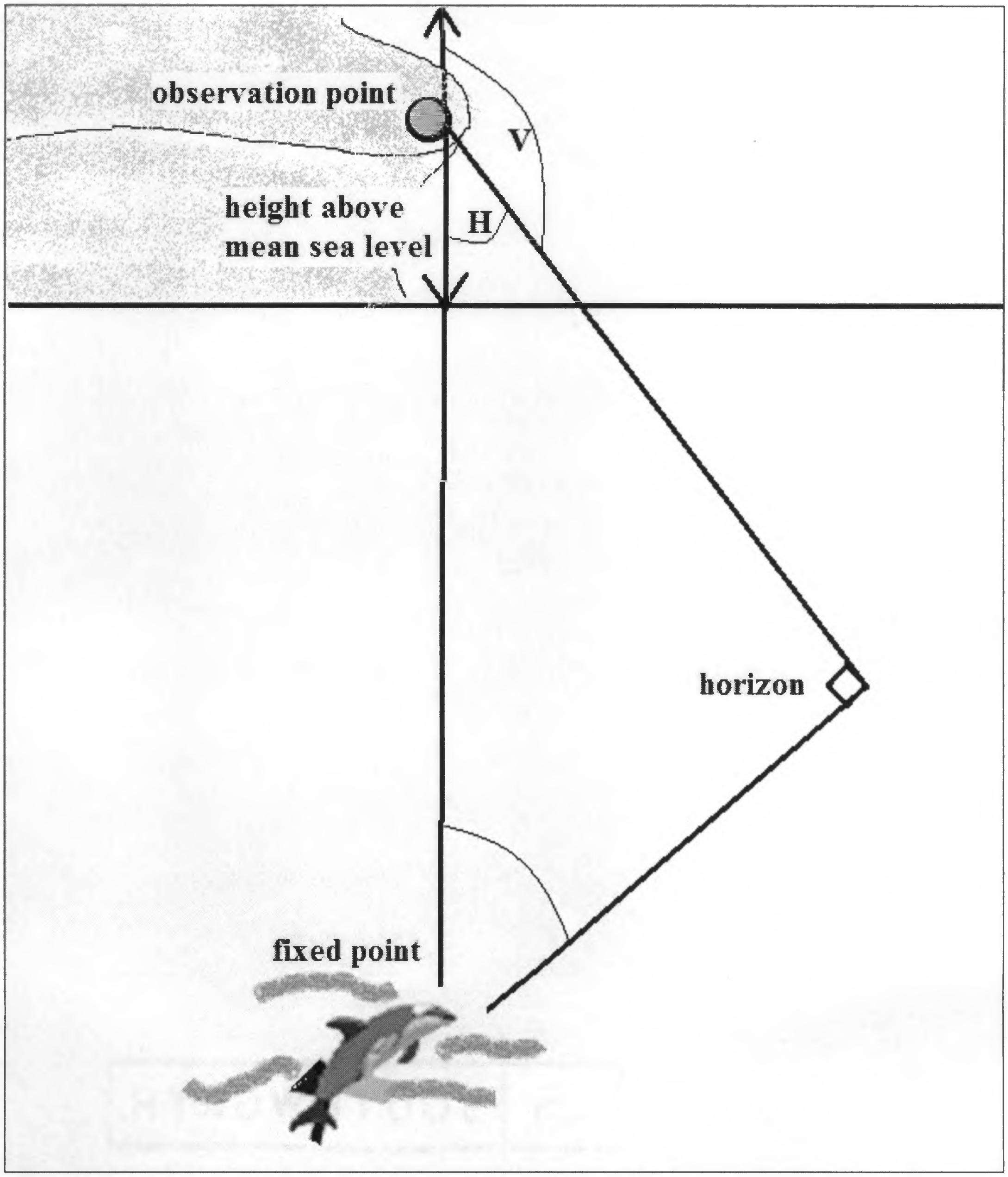


Figure 9: Trigonometry of Theodolite Surveys. Adapted from Gailey & Ortega-Ortiz (2000) & Harzen (2002). Vertical (V) and Horizontal (H) bearings are taken from the observation point, from which distance geometric angles may be calculated to find the geographic coordinates of a fixed point.

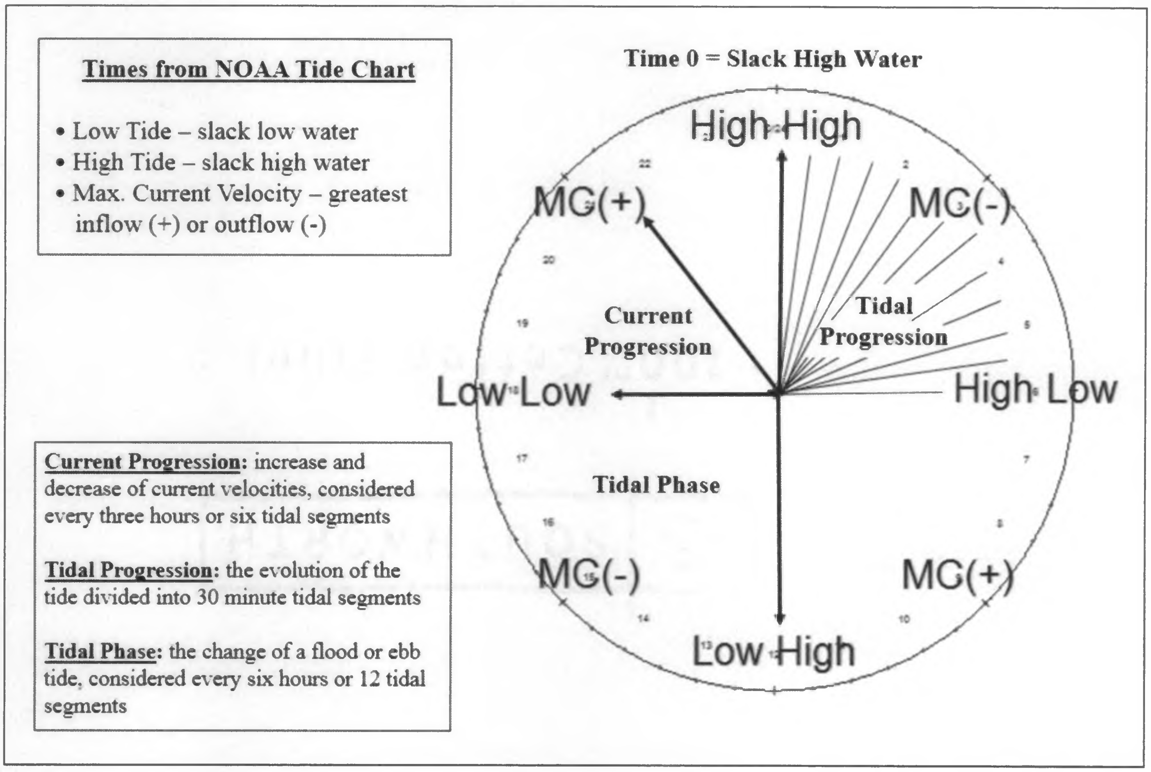


Figure 10: Temporal Analysis of Tidal Variables and Porpoise Sightings.

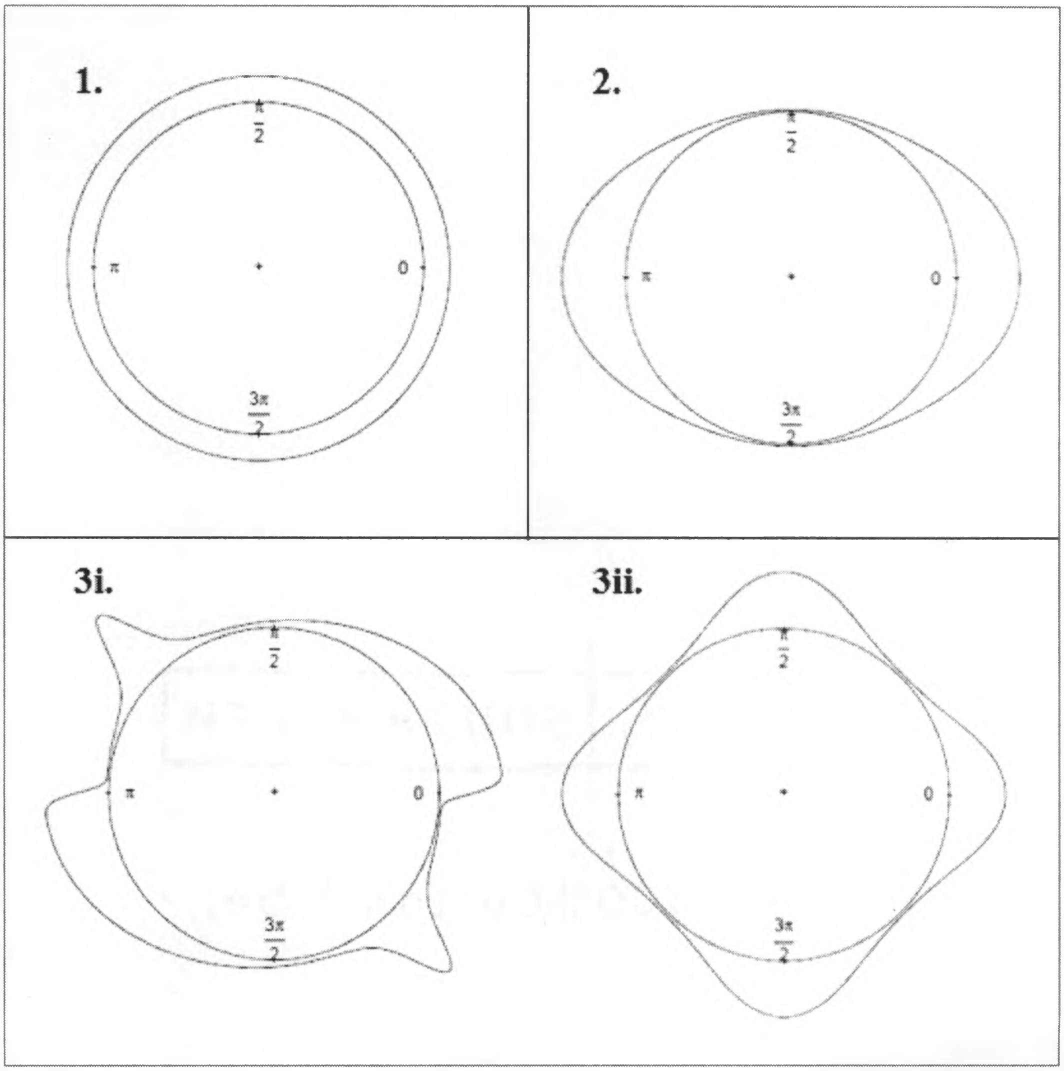


Figure 11: Distribution Models with Circular Statistics. 1. Von Mises Distribution: represents circular data that has an even concentration around the graph; analogous to a normal distribution in linear methods. 2. Wrapped Cauchy: represents data with anti-podal distribution or reflective symmetry. 3. Wrapped-Skew: represents data with multimodal distribution; skewed means may or may not be symmetrical. 3i shows a possible distribution with polarized effects, and 3ii shows symmetrical multimodal data Circular data analysis methods from Oliveira et al. (2012) and Pewsey et al. (2013).

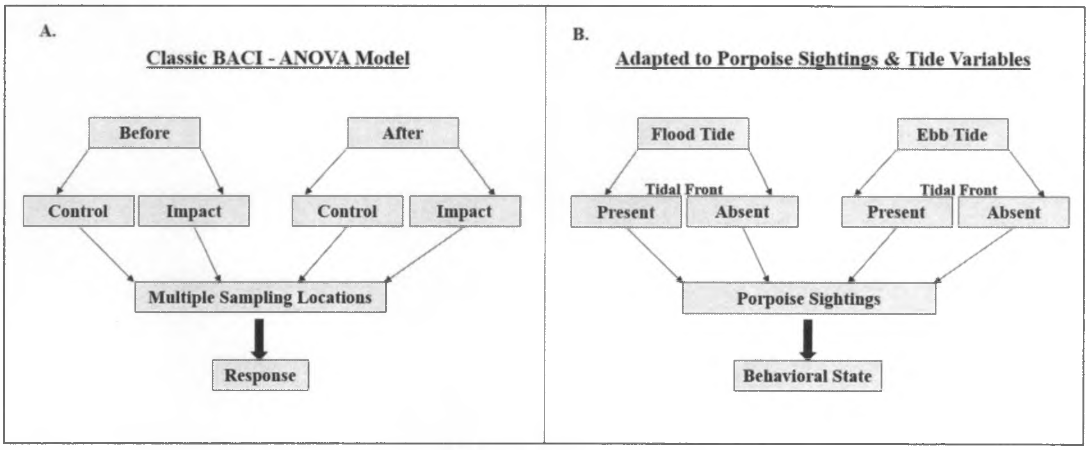


Figure 12: Dynamic State Modeling Analysis of Variance (ANOVA). A. shows the classic BACI (Before/After, Control/Impact) Model which compares statistical interactions from before and after an environmental disturbance and the difference in abundance at sampling sites. This was adapted to variations in porpoise sighting frequency and the effect on foraging behavior, shown in B.

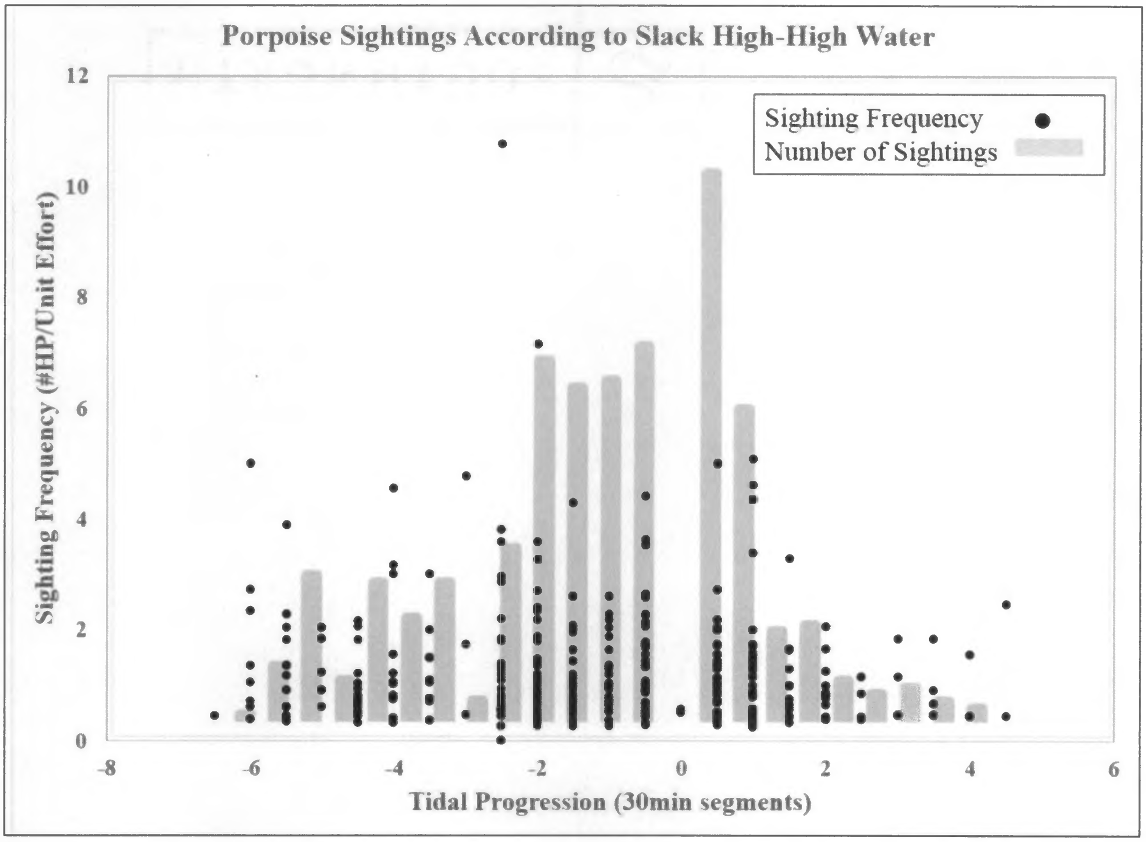
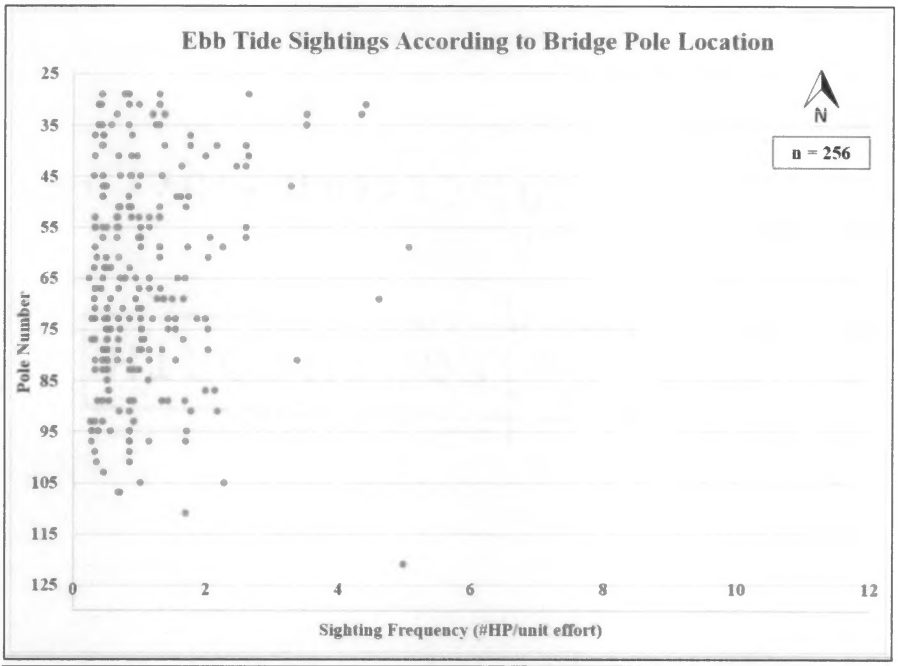


Figure 13: Porpoise Sightings and Sighting Frequency According to Slack High-High Water. Sightings were categorized into 30min tidal segments before (-) or after (+) the time of High-High water. Time zero equals the time High-High Water was recorded in NOAA tide charts for each tidal cycle. The maximum sighting frequency (10.78 porpoises per unit effort) occurred in segment -2.5, 2.5 hours before slack high water. The maximum number of sightings (79) occurred in segment 0.5, 30 minutes after slack high water.



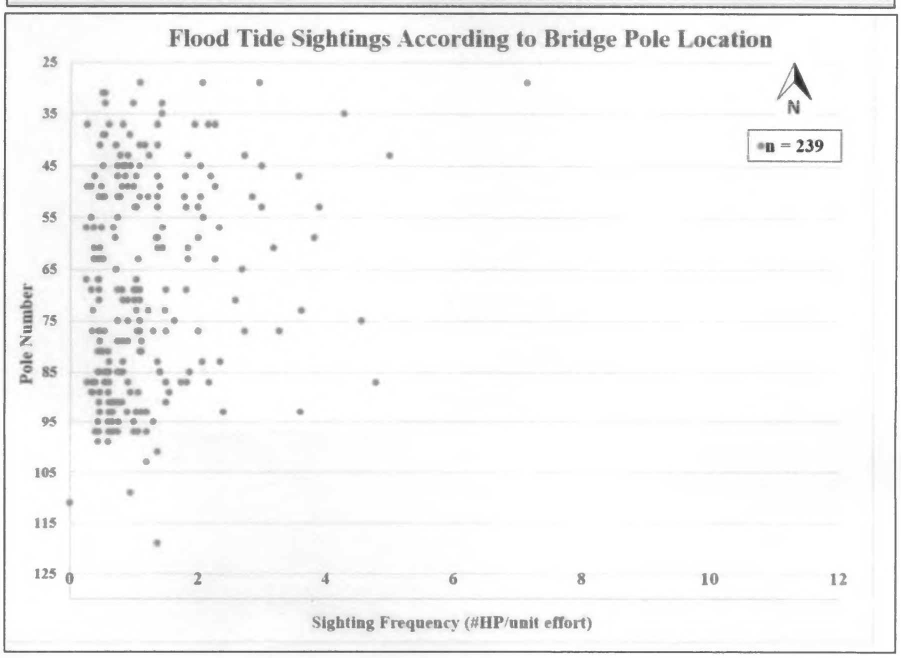


Figure 14: Porpoise Sightings According to Bridge Pole Locations. Each marking represents an individual sighting. Values along the x-axis are sighting frequencies, representative of the number of porpoises observed in each sighting per unit effort of that bridge transect. Sightings were concentrated to the center and north side of the Golden Gate Channel. There were more porpoise sightings during an ebb tide, but higher frequency values during a flood tide.

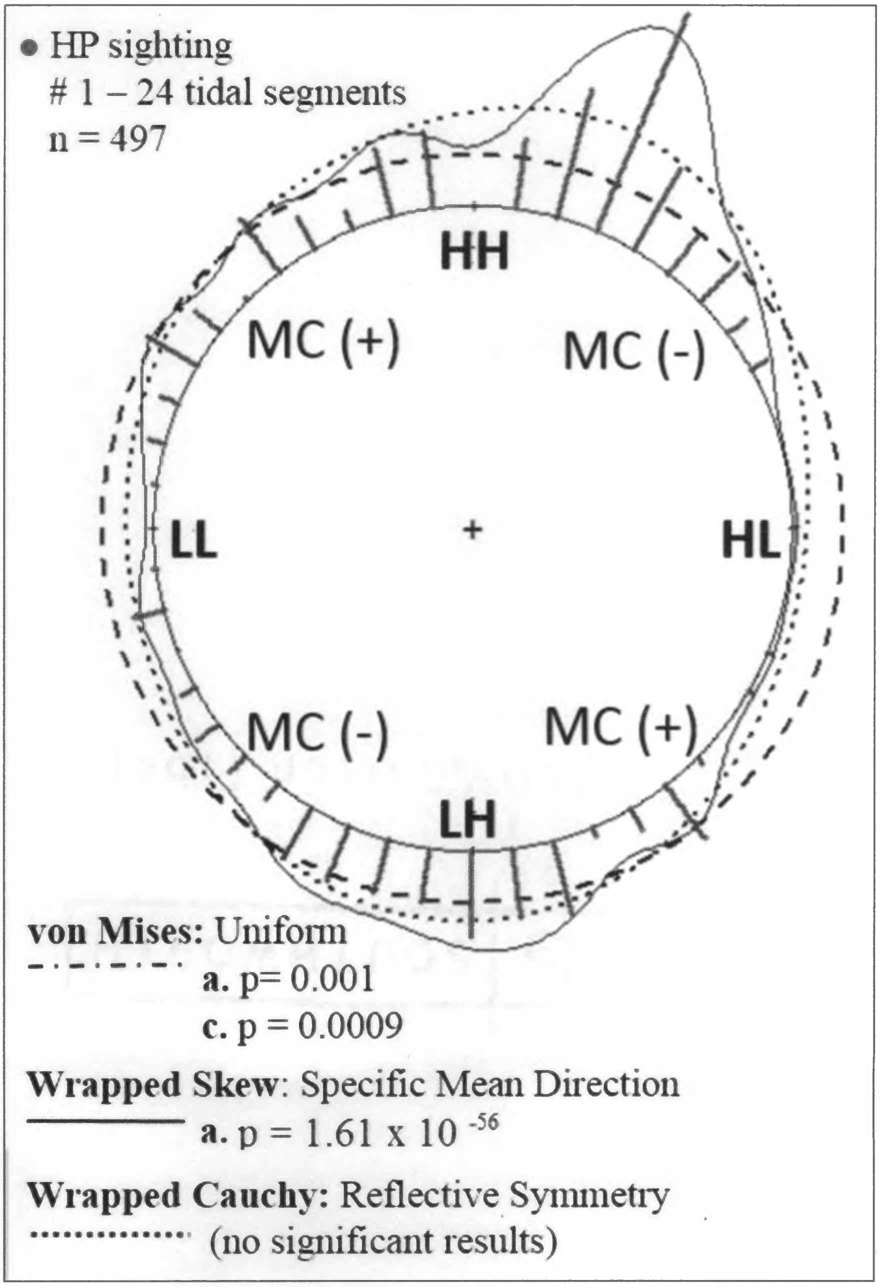


Figure 15: Fitting Circular Models to Porpoise Data. Sightings are shown around the circle as a condensed group of blue dots at each 30 minute tidal segment. The Wrapped Skew model shows the best fit to the data. The Rao's Spacing Test, used to show departure from uniformity in data with underlying multimodal distribution in a possible specific mean direction showed porpoise sightings are significantly multimodal in a specific mean direction with [F=0.34, p=0.001].

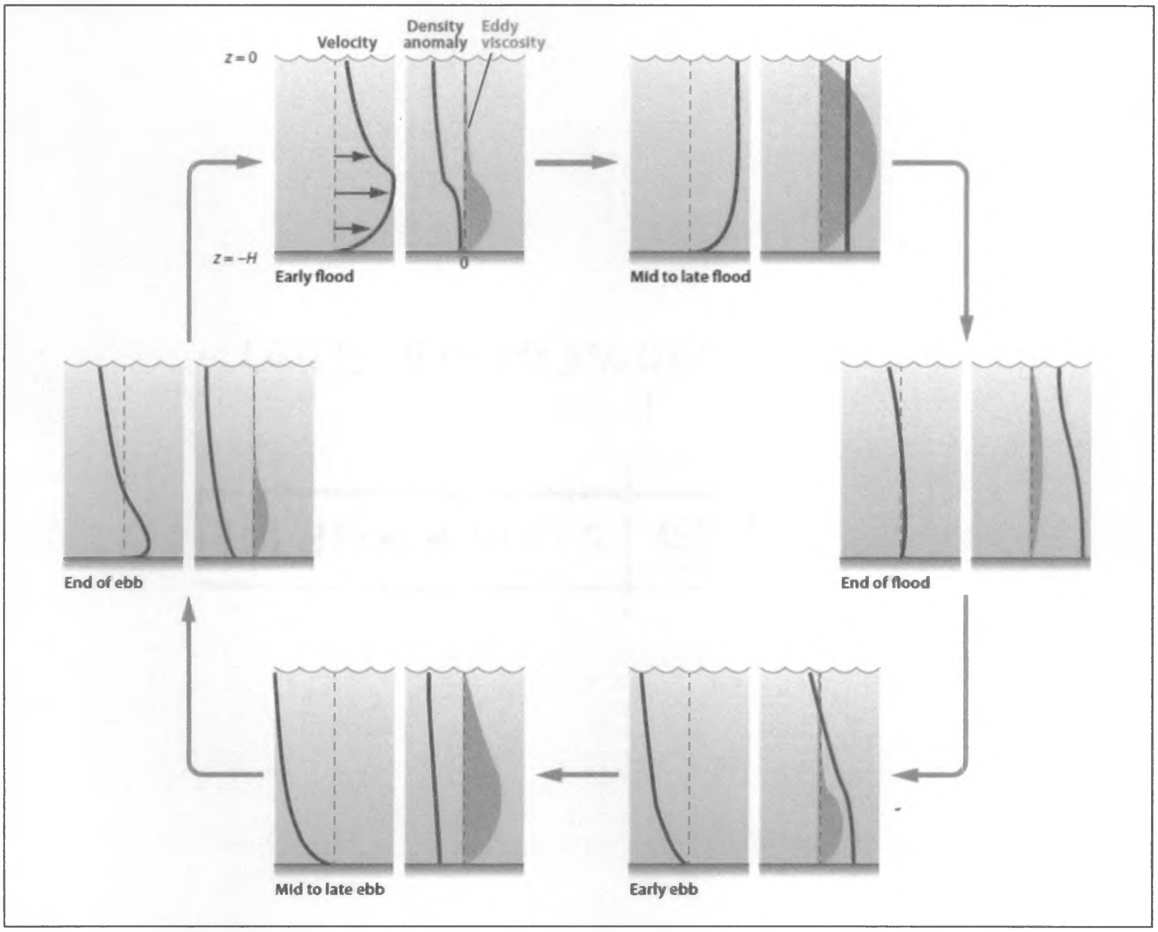


Figure 16: Phases of Tidal Progression in a Strain-Induced Periodic Stratification Estuary. Copyright Geyer & MacCready (2014). At the turn of a tide is when current velocities are at a minimum. Eddy viscosity is also at a minimum in surface waters. Tidal forcing overtakes gravitational circulation and creates a horizontal density gradient. Porpoise sighting frequency was found to be negatively correlated with the increase of a flood tide [$r = -0.93$, $p = 0.01$]; [$r = -0.41$, $p = 0.01$]. More porpoise sightings occurred at the beginning of an ebb tide ($n = 154$; $n = 91$) than any other category of tidal progression.

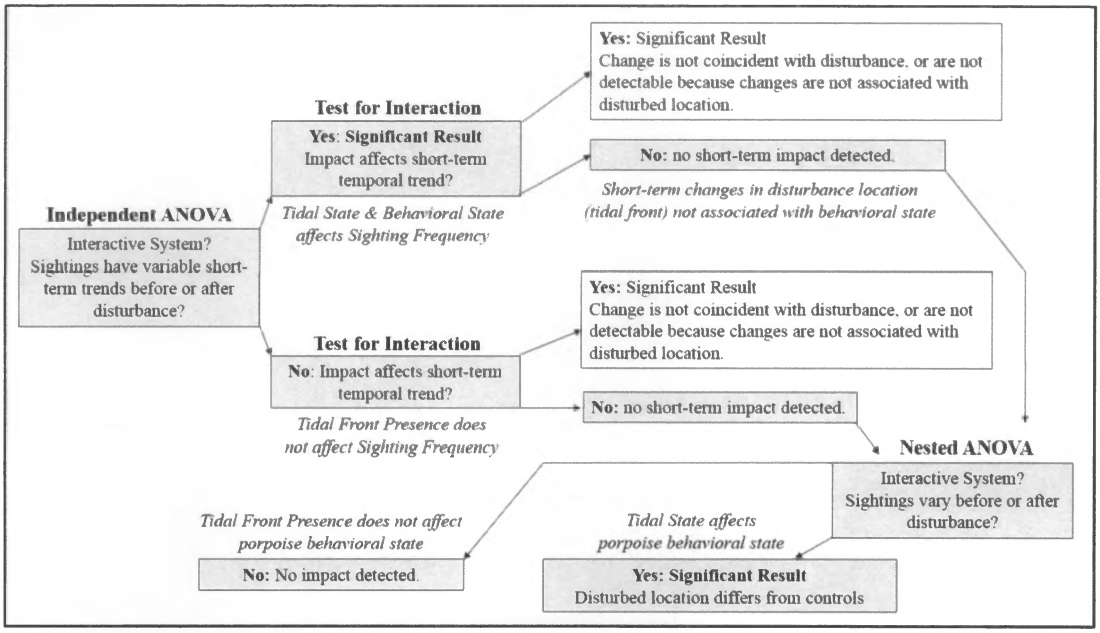


Figure 17: Sequence of Tests Performed in the Analysis of Variance (ANOVA). This three-step process, as described in Underwood (1993), detects environmental impact in asymmetrical design. The first test, an independent ANOVA, detects variations in abundance based on temporal and spatial fluctuations in the environment. The second, a test for interaction, analyzes disturbance effect on a response variable. The third, a nested ANOVA, shows significant results of disturbance on a controlled sample. Shaded boxes represent the results produced from porpoise data. Italicized text gives an applied explanation for the statistical language.

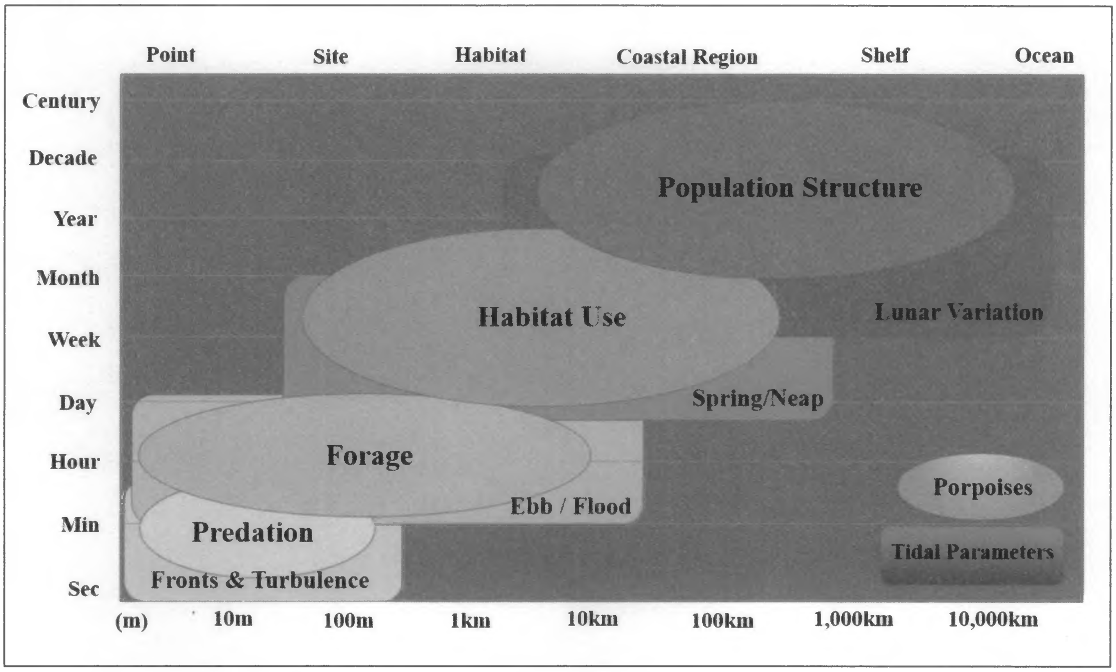


Figure 18: Theoretic Scale Variation in Temporal and Spatial Domains. Adapted from Haury et al. (1978), Blanton et al. (1987), and Levin (1992), this diagram indicates possible scale correlation between porpoise population dynamics and tide-related oceanographic patterns.