



Quantifying behavior and collision risk of humpback whales surfacing near large ships: implications for detection and avoidance

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ABSTRACT: Lethal collisions between ships and whales ('ship strikes') are a pressing management issue across the globe, and recent work highlights the need for better information to support collision risk avoidance by mariners. Using a ship-based observer stationed on the bow, we recorded the behavior of humpback whales *Megaptera novaeangliae* surfacing around large cruise ships transiting Glacier Bay National Park, Alaska, one of the largest marine protected areas in North America. We documented surfacing bouts (i.e. series of surfacings when whales breathe between deeper foraging dives) over 460 h of observation from 65 cruises. We detected few surfacings per bout (mean = 2.9) and observed a moderate within-bout submergence time (median = 20.1 s), showing that whales are unavailable for detection during the majority of their time near the surface. We then used these data to parameterize a modified mark-recapture model to estimate the probability of a whale surfacing before and after first detection by mariners. The estimated probability that a whale surfaced prior to detection was moderate (0.54; 95% credible interval [CRI]: 0.52–0.57), indicating that often, the first detected cue (e.g. a blow or a visible fluke) was not the first cue produced (i.e. available to be detected). The probability that a whale remained near the surface following detection was high (median = 0.87; 95% CRI: 0.85–0.88). This indicates that whales likely remain at risk of collision following detection, enabling mariners to evaluate ship-speed-specific avoidance maneuvers based on initial sighting distances to decrease collision risk.

KEY WORDS: *Megaptera novaeangliae* · Humpback whale · Ship strike · Temporal symmetry model

1. INTRODUCTION

Lethal collisions between whales and ships ('ship strikes') are a recurring and significant source of mortality for many species of large whales (Thomas 2016). However, the true rates of ship strikes and other sources of anthropogenic mortality are difficult to quantify (Williams et al. 2011, Ransome et al. 2021). Even mortality rates based only on beach-cast carcasses or dead whales found at sea may exceed designated management thresholds for species including humpback whales *Megaptera novaeangliae*, blue whales *Balaenoptera musculus*, and fin whales

Balaenoptera physalus (Rockwood et al. 2017). In the case of North Atlantic right whales *Eubalaena glacialis*, minor mortality rate improvement could influence population viability (Fujiwara & Caswell 2001) due to the small population size and cumulative effects of ship strikes and entanglement on body condition and reproductive success (Christiansen et al. 2020, Moore et al. 2021). In response, management efforts primarily focus on shifting shipping lanes away from areas that support aggregations of whales (Vanderlaan et al. 2008) and/or mandating or incentivizing reductions in ship speed (Conn & Silber 2013, van der Hoop et al. 2015). However, shifts in

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feeding areas occupied by whales and non-compliance to speed reduction recommendations by mariners (e.g. McKenna et al. 2012, Guzman et al. 2020) highlight the need for additional and complementary approaches for reducing collision risk.

One such effort enables mariners to share whale locations in near-real-time, theoretically increasing their ability to enact risk-reducing operations. For example, acoustic arrays that detect certain calls of North Atlantic right whales were deployed around Stellwagen Bank to alert mariners nearby (www.listenforwhales.org). Likewise, mobile applications such as Whale Alert (www.whalealert.org/) and Repcet (www.repcet.com/en/home/) are intended to enable mariners to share whale sightings in order to increase situational awareness and thereby provide vessel operators a better chance to avoid whales. However, further work on whale behavior and detection is needed to develop 'active collision avoidance' protocols, whereby mariners make decisions about how to maneuver their vessels in order to avoid ship strikes. This is particularly important because to our knowledge, the effectiveness of these alert systems at reducing ship strikes has not been demonstrated in the field, even if the collected data may contribute to collaborative marine mammal protection decisions (Agardy et al. 2019).

In this context, understanding the behavior of whales surfacing around large vessels is critical because the type and frequency of observed surfacing behaviors ('cues,' Hiby & Ward 1986) represent the opportunities for mariners to detect whales nearby. This information guides decisions about whether, or to what degree, risk-reducing changes in vessel operations (e.g. a change in course or speed) are feasible and effective (Gende et al. 2019). Additionally, the quantity of cues (e.g. blows) coupled with submergence periods (the elapsed time a whale spends just below the surface between blows) indicate the total time a humpback whale spends at or near the surface between deeper foraging dives. Given that feeding whales are less likely to change their behavior around vessels than whales in other behavior states (Schuler et al. 2019), surfacing behavior can be used to assess the probability that humpback whales and other whales with similar surfacing patterns will still be at or near the surface by the time the ship covers the distance from its initial sighting location.

While a number of studies have quantified the surfacing behavior of whales, collecting unbiased information on the behavior of whales surfacing around ships for use in collision avoidance has proved difficult. For example, observations from shore-based

platforms that are used to quantify blow frequency, swim speeds, and submergence durations (Barendse et al. 2010, Kavanagh et al. 2017) do not take into account that whales may alter their surfacing behavior around vessels (Gulesserian et al. 2011). Additionally, diving patterns and other metrics vary according to behavior state, such as migration status (Kavanagh et al. 2017). Finally, while tagged whales can provide detailed records of dive duration, orientation, and movements near ships (e.g. McKenna et al. 2015), sample sizes are limited by constraints on tag deployment and the infrequent, brief periods when whales encounter ships. Although shipboard observers are limited in their ability to collect whale behavioral data prior to a whale surfacing, this method accounts for many of these other data collection challenges.

In this study, we used a ship-based observer to quantify the behavior of humpback whales surfacing in the proximity of large cruise ships in Alaska. This area is an important humpback whale feeding ground (Gabriele et al. 2017), where whales are primarily engaged in long feeding dives interspersed with intermittent surfacing dives (e.g. Dolphin 1987b). In our study area, cruise ships travel predetermined routes through this important habitat, and we conducted surveys from these repeated transits. Although there are no long-term statistics of ship strike rates in this region, at least one known whale mortality from a ship strike was detected in this area in 2001 (Gabriele et al. 2010). We designed our study from the perspective of mariners aiming to detect and actively avoid whales, and as such, we focused on collecting and using only the real-time information mariners have available for inferring whale behavior as it relates to collision risk. Ultimately, our study aims to contribute to the body of work quantifying the risk that whales face when surfacing around large ships by providing information that can help mariners make decisions about active collision avoidance strategies.

2. MATERIALS AND METHODS

2.1. Study site

Glacier Bay National Park (GLBA) in southeastern Alaska serves as an important summer feeding area for the Hawai'i Distinct Population Segment of humpback whales (Neilson & Gabriele 2007, Bettridge et al. 2015) and is one of the largest marine protected areas in North America. The number of

whales utilizing Glacier Bay increased by $5.1\% \text{ yr}^{-1}$ between 1985 and 2013 (Saracco et al. 2013), but more recently, population numbers declined, possibly as a result of the marine heat wave in the North Pacific (Neilson and Gabriele 2021). Glacier Bay is also a coveted destination for large cruise ships, where more than 250 ship visits occur annually (Webb & Gende 2015). The National Park Service (NPS) is mandated to both protect its resources for future generations and to enable the public to use and enjoy the park. As such, it is important to quantify and ultimately mitigate the risk to humpback whales posed by ships to ensure that the whale population is adequately protected while still providing access to visitors.

2.2. Data collection

Surveys of humpback whales surfacing around large cruise ships (\bar{x} length = 263 m; \bar{x} height above water at bow = 15.5 m; mean draft = 7.5 m) were conducted on 79 d in GLBA from late May through mid-August in 2016 ($n = 41$ d) and 2017 ($n = 38$ d). On each survey day, a single observer boarded a designated cruise ship just inside the mouth of Glacier Bay via a transfer vessel that departed from the NPS headquarters in Bartlett Cove (Fig. 1). Shortly after boarding, the observer set up a station on the bow of the ship (as opposed to inside the navigational bridge alongside the captain and pilot, which is higher above the water and behind windows) and surveyed continuously throughout each morning as the ship transited northbound to Tarr Inlet (Fig. 1). After a multi-hour break while the ship remained at the head of the fjord for glacier viewing, where whales are rarely seen (Gende et al. 2011), surveys were reinstated as each ship roughly retraced its path south through the bay where the observer disembarked onto an NPS transfer vessel just outside of Bartlett Cove. The same observer conducted all surveys. Surveys were typically conducted on days when sea states did not exceed Beaufort 2. Surveys yielded a mean of 5.9 h of effort during each cruise (SD: ± 0.6 h). Owing to navigational constraints and park regulations, all ship transits followed similar tracks across the season at comparable speeds. Due to speed limits in the park, ships typically traveled at speeds of around 13 knots (speed over ground) in the lower parts of the bay, around 16–19 knots in the middle of the bay, and less than 10 knots approaching the tidewater glacier areas.

During each cruise, the observer scanned for whales using a combination of hand-held binoculars (Swarovski 10 × 42), tripod-mounted Leica laser rangefinder binoculars (Viper II, magnification: 7 × 42, accuracy: +1 m at 1 km, Leica), and the naked eye. Distances to whales were successfully obtained at 1000 m or more, although the success depended upon the surfacing behavior and sea surface conditions. Surveys covered the water's full extent from near the ship to the limit of the optics (approximately 12 km in excellent visibility conditions) and the 180° range from abeam (a bearing of 90° to the side of the ship) of the port side to abeam starboard. When an observer detected a whale, the ship's location was recorded using a handheld Global Positioning System (GPS) unit (Garmin 76Cx), and the distance between the observer and the whale was measured using the rangefinder binoculars. The whale's bearing was estimated by the observer. If a surfacing event (any set of behaviors that result in a whale breaking the surface of the water) was too brief or too far away to make contact using the rangefinder, the observer estimated the ship-to-whale distance based on the relative distances between the whale, ship, and other landmarks like shore and islands (~ 1000 to $\sim 15\,000$ m, where shore could be reliably measured with the rangefind-

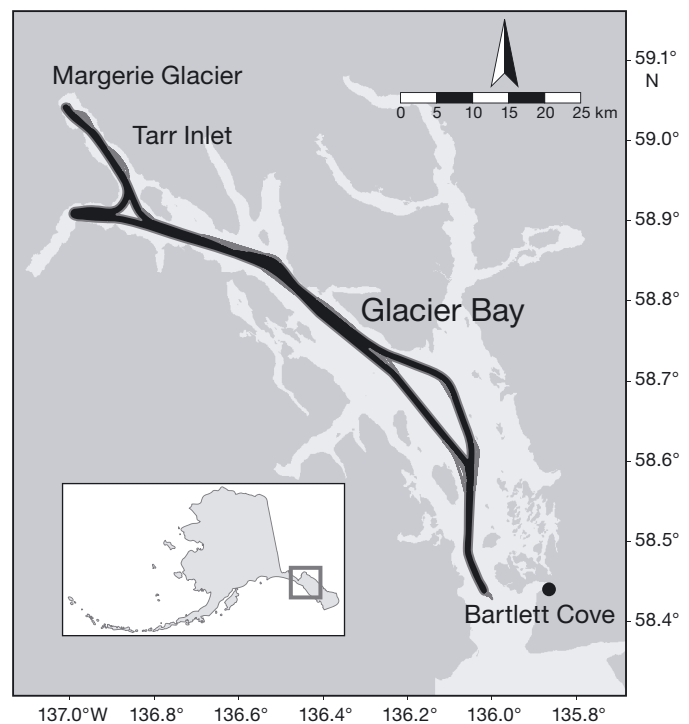


Fig. 1. Glacier Bay National Park with a sampling of cruise ship tracks during the study (dark line). Collection of ship track data and whale surfacing behavior began once the observer boarded the ship just outside of Bartlett Cove

ers to around 6000 m). To test for bias in distance estimates, the observer intermittently recorded estimated and rangefinder-measured distances to various inanimate objects such as icebergs (out to ~1000 m), islands (out to ~6000 m), and shore (out to ~6000 m). Accuracy of distance estimation decreased slightly as distance increased but exhibited no bias ($R^2 = 0.946$).

Using a modified individual-follow approach (Mann 1999), we recorded observations using a digital voice recorder (Olympus Imaging America Inc.; VN-702PC) and field notebooks. Once a cue was detected, the observer focused search efforts on that area and recorded data on the same whale until either a terminal (i.e. fluke-up) dive was observed, the whale was abeam, or the ship passed the area where the whale was last detected before it resurfaced. For each surfacing bout, the observer spoke the observations into the audio recorder in real-time. For example, if a whale blow was detected, the observer would speak 'blow' into the audio recorder and then 'blow gone' when it completely dissipated. The voice-recorded data from each transit were saved as an .mp4 file and transcribed using Audacity® recording and editing software (Audacity Team 2018) immediately after the survey, at which time the timestamp of each cue was linked to the observation to enable calculation of cue durations and timing. Sampling effort totaled 464.8 h of observation over the 2 summer seasons. We excluded the first 3 cruises of 2016 due to observer training and excluded 11 other cruises due to data transcription difficulty. We excluded 2 southbound surveys in 2017 due to gear malfunctions, yielding a total of 65 cruises over 2 yr used for this analysis.

2.3. Statistical methods

We analyzed the surfacing data using the Temporal Symmetry Model (TSM; Pradel 1996), a mark-recapture model originally designed to estimate population abundance and demographic parameters. In the typical application of the TSM, a population of interest is defined, such as a colony of breeding birds (e.g. Tenan et al. 2014). Then, parameters of interest, which can include seniority (the probability of being previously in the population; Pradel 1996) and survival, are estimated using sighting histories generated when animals are marked and recaptured or resighted during pre-defined encounter periods (Pradel 1996, Dreitz et al. 2002, Tenan et al. 2014). In our application, we defined the population of interest as whales at or near the surface, or in the 'strike zone,' which we

defined as a depth equal to the draft of the ship, which we assumed would encompass all of the surfacing dives within a surfacing bout between feeding bouts. Thus, whales regularly enter into, persist for short periods in, and then exit from this population as part of their regular foraging dive cycles. By extension, 'seniority' in our model is the probability that a whale was already present in the population (i.e. near the surface) prior to detection, and 'survival' is analogous to the probability that it remains at or near the surface in future encounter periods before exiting the population via a deep foraging dive. Thus, the first detected surfacing event represents the 'marking' occasion, and blows or other cues sighted during subsequent surfacing events during that same surfacing bout (i.e. series of surfacings when whales breathe between deeper foraging dives) constitute 'recaptures' (Fig. 2).

The TSM is particularly well-suited to meet our objectives because model estimates can be either back-casted or run forward in time. Back-casting model estimates allows for an unbiased estimate that a whale was present in the strike zone during the encounter period prior to detection (i.e. the analog to seniority), assuming that whales are behaving similarly near and far from ships, since intermittent ship noise is common in this area. While mariners cannot initiate active collision avoidance maneuvers based on a whale that was present but went undetected, estimating the probability that a whale is present at or near the surface prior to detection does provide a measure of improvement for detecting whales and thus the value of adding personnel to increase detection probability. Forecasting also had benefits inasmuch that it allowed us to estimate the probability that a whale will still be at the surface across future encounter periods (i.e. the analog to survival). This metric is particularly applicable in the context of ship strikes because it identifies how long whales typically remain at or near the surface (in the strike zone) following detection, a key factor in collision risk. Below, we detail the model adjustments, data structuring, and assumptions that enabled the application of this model to whale surfacing behavior.

First, to enable the application of this discrete-time mark-recapture model, we divided the maximum duration of a 1-way transit through Glacier Bay (3:55:51) into 20 s encounter periods (Fig. 2) because data points (whale observations) could be collected at any point in time owing to continuous scans. The 20 s duration corresponded to the median submergence time, defined as the duration between surfacing events, calculated from our data. These short

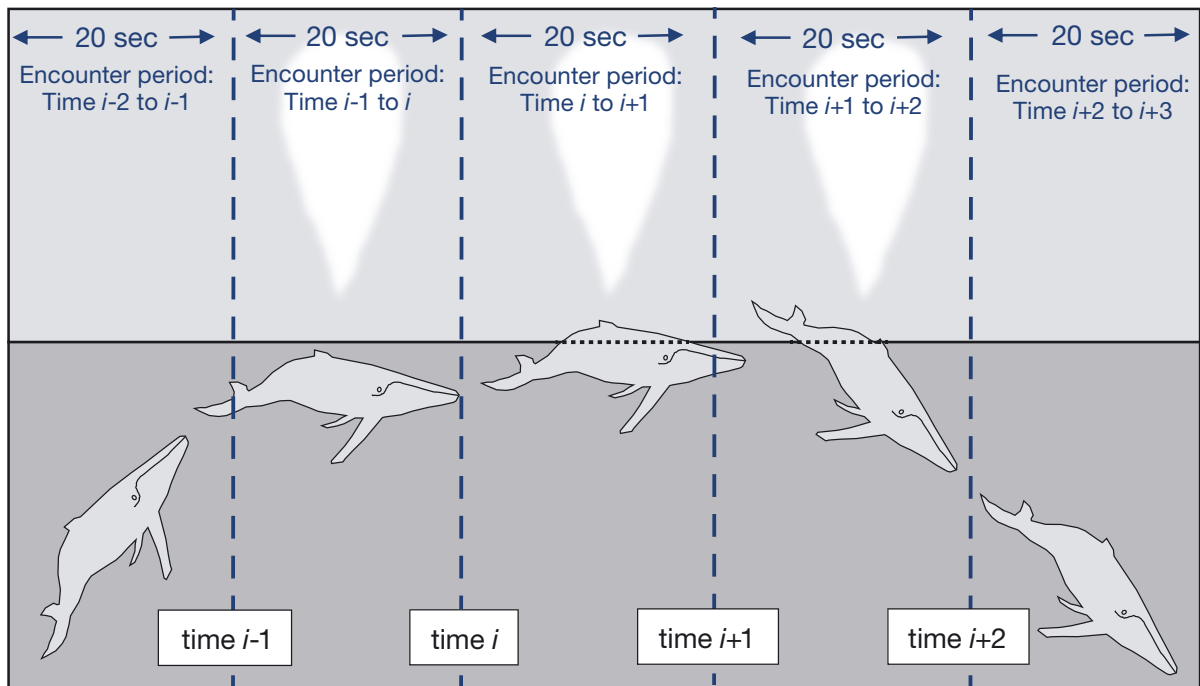


Fig. 2. Diagram displaying the relationship between encounter periods and whale surfacing behavior. Each cruise ship track was divided into 20 s encounter periods starting with the onset of survey effort. The encounter period in which a whale was detected was defined as time i to $i+1$. In this scenario, the whale entered the population of whales at risk of collision in period $i-2$ to $i-1$ and displays its first cue (a blow) during period $i-1$ to i . Model parameters are estimated across encounter periods

encounter periods allowed whales to be resighted in encounter periods following detection, producing a sighting history for the whale from which we generated parameter estimates (Fig. 2).

Second, we truncated the parameter estimation window for each sighted whale to the maximum observed surfacing bout duration (645 s). The estimation window was ended if a whale exhibited a fluke-up dive, as we assumed based on long-term observation of whale behavior in our study area that this indicated that the whale was ‘exiting’ the population of whales at risk of collision by diving vertically to depths greater than the ship’s average draft, following Dolphin (2017b). For surfacing bouts where a fluke-up dive was not observed, the estimation window was centered on the midpoint of the encounter history because we did not have any information about when the whale dove to depth. This was primarily due to the ship passing abeam ($n = 396$) while the whale was still engaged in the series of surfacing events and submergences.

We developed a hierarchical Bayesian implementation of the TSM to estimate 3 parameters across each 20 s encounter period that are relevant to ship-whale collision risk including (1) the probability that a whale was present at or near the surface prior to

the encounter period of detection (probability of a prior surfacing event; PSE), the probability that a whale remained present at or near the surface following the period it was initially detected (probability of remaining present; PRP), and the probability that a whale could feasibly be observed by mariners stationed on the bow (probability of availability for detection, PAD) (Table 1). Our implementation was similar to a hierarchical implementation of the Cormack-Jolly-Seber (CJS) model (e.g. Kery & Schaub 2012). We used R 3.4.3 (R Core Team 2017) and package ‘R2jags’ (Su & Yajima 2015) to implement the model in JAGS (Plummer 2003).

Since whale detection probability depends on whale-to-ship distance and visibility (Williams et al. 2016), we incorporated an informative prior distribution on the initial detection probability (z). We used a hazard rate function with a visibility covariate incorporated via a scale parameter, which was developed in the same study system using whale sighting data collected from cruise ships during previous years (Williams et al. 2016). This adjusted the initial detection probability such that whales were more likely to be initially detected at close distances and in excellent visibility conditions than at far distances or in poor visibility conditions (Williams et al. 2016).

Table 1. Parameter definitions from application of the Temporal Symmetry Model (TSM) to whale surfacing behavior around ships

Parameter name	Definition
Initial detection probability	Distance-specific probability of detecting a single whale based on excellent sighting conditions (from equations in Williams et al. 2016)
Probability of availability for detection (PAD)	Probability that a whale presents at least one cue during a 20 s encounter period (interval) after it is initially detected given the whale remains near the surface. This is the probability that a whale can be detected during a 20 s interval
Probability of a prior surfacing event (PSE)	Probability that a whale entered into the population of whales at risk of collision (into the strike zone) and presented a cue that went undetected in the 20 s encounter period (interval time $i-1$ to i) prior to the encounter period in which it was initially detected (interval i to $i+1$)
Probability of remaining present (PRP)	Probability that a whale remains in the strike zone and presents at least one cue during the 20 s encounter period (interval time $i+1$ to $i+2$) immediately following the interval the whale was initially detected (time i to time $i+1$)

We also made a key assumption that the initial detection probability of a whale cue is lower than the detection probability of other cues in the same surfacing bout. This assumption is based on work with ship operators who, once a whale is detected, focus their search efforts on the small area where the whale may resurface following initial detection rather than continuing to scan the entire area forward of the ship. Analytically, this equates to a perception probability = 1 for all surfacing events following detection. If the probability of initial detection is known and the probability of perception equals 1, then we can use the TSM to obtain unbiased parameter estimates.

Finally, we assumed that (1) the data reflected successive independent binomial trials, (2) there was no temporary emigration (except possibly random), and (3) all whales were identical, uniquely identifiable, and had independent fates. We ensured that the assumptions of unique identifiability and independent fates were met by exclusively using data from whales traveling alone to ensure that consecutive observations were from the same individual and that cow-calf pairs—whose behaviors might not be independent—were excluded. We note that in 2016 and 2017, over 90% of whales sighted in GLBA were singletons. In the application of the model to our study, we felt that each of these assumptions was reasonable.

3. RESULTS

During 65 cruises in 2016 and 2017, we observed an average of 17 surfacing bouts per cruise (SD = 11.0). The location of whales upon first detection varied across the 180° arc forward of the ship (Fig. 3), ranging from 150 to 15 000 m away, although for our analysis (see Section 2) we truncated initial sighting distances to a maximum of 6000 m (Fig. 4). Surfacing bouts varied from 1 to 33 surfacing events (\bar{x} surfacing events per bout = 2.9; SD = 2.7). The inter-surfacing intervals, measured from the beginning of a surfacing event to the beginning of the next surfacing event, averaged 20 s (SD = 42.5 s, Fig. 5) although the

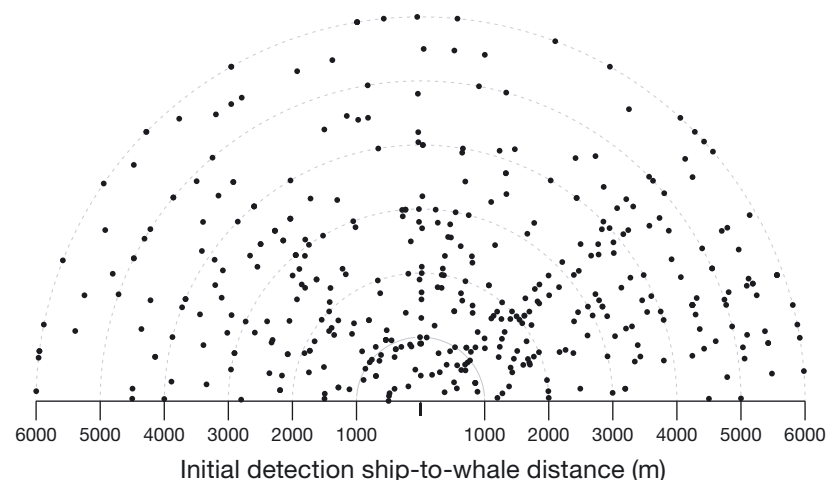


Fig. 3. Aggregate distribution of whale surfacing events upon initial detection (black dots) in the 180° arc forward of the ship. Small rectangle at the center of the x-axis (short thick black line) is to scale representing the average-sized cruise ship (length = 263 m, draft = 7.5 m) boarded during this study

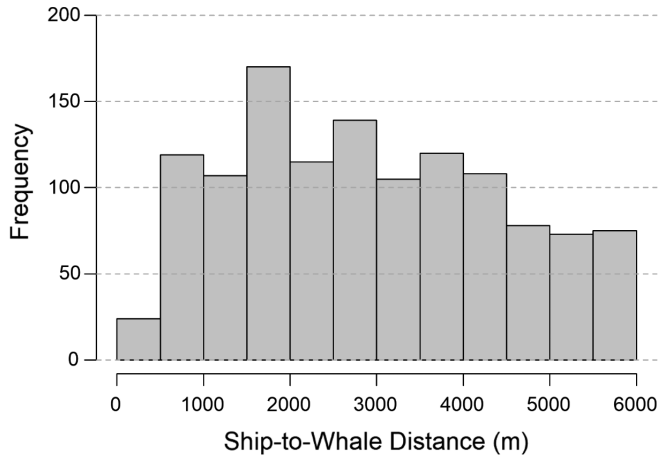


Fig. 4. Histogram of distances for surfacing whales initially sighted by an observer stationed at the bow of cruise ships ($n = 1095$). For analyses, the dataset was truncated at 6000 m due to concerns about model assumption violations

data were highly skewed with infrequent lengthy submergence periods.

The estimated probability of a PSE was moderate (median = 0.54; 95% credible interval [CRI] = 0.52, 0.57; Table 2, Fig. 6), suggesting that around half the time that whales ascended from depth, they surfaced to breathe but went undetected in the 20 s encounter period prior to the encounter period in which they were detected. This estimate was largely consistent across initial sighting distances in part owing to the visibility-based correction factor applied to the initial detection probability (Williams et al. 2016). The estimated probability of a whale remaining present (PRP)

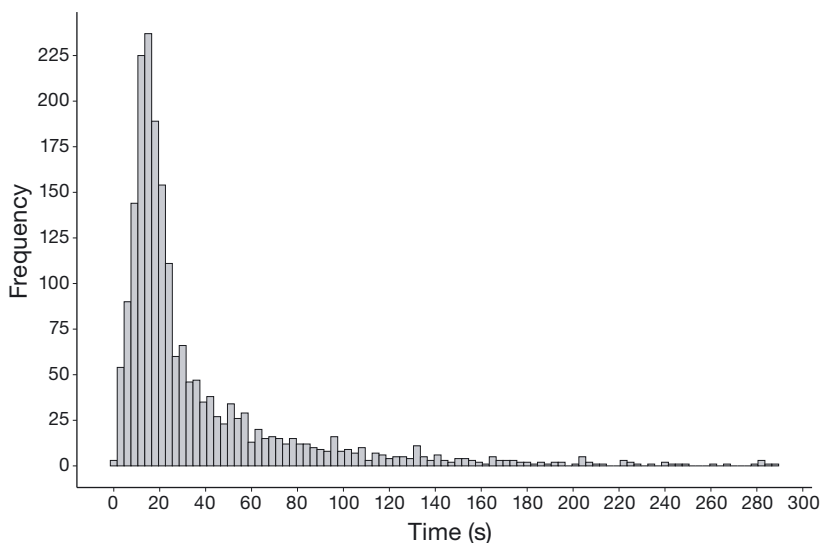


Fig. 5. Distribution of within-bout submergence durations, defined as the elapsed time between the last cue detected during a whale's surfacing event and the first cue detected during its next surfacing event ($n = 6804$)

Table 2. Parameter estimates for the probability of availability for detection (PAD), the probability of a prior surfacing event (PSE), and the probability of remaining present (PRP)

Parameter	Estimate	95 % CI	\hat{R}
PAD	0.319	(0.303, 0.336)	1.001
PSE	0.540	(0.515, 0.566)	1.001
PRP	0.865	(0.854, 0.877)	1.001

at the surface after initial detection was high (median = 0.87; 95% CRI = 0.85–0.88, Table 2, Fig. 6), indicating that, following detection, whales remained in the top of the water column for a period of time before initiating a fluke-up dive or the ship passed abeam ($n = 505$ fluke-up, $n = 396$ passed abeam). The median probability of being available for detection (PAD) was 0.32 (95% CRI = 0.30–0.34, Table 2, Fig. 6), showing that in a given 20 s period, the whale was only visible to an observer stationed at the bow about one-third of the time that it was present.

Exponentiating the PRP estimates by the number of future 20 s encounter periods produced probabilities that the whale would still be at the surface by the time a ship covered the ship-to-whale distance after initial detection. For example, a whale that was first detected 1000 m directly in front of a ship had a ~50% chance of still being at or near the surface and at risk of a collision by the time a ship traveling 20 knots (10.3 m s^{-1}) covered that distance. This risk is reduced by nearly half (probability = 0.34) for a ship travelling 13 knots (6.7 m s^{-1}). For a whale first detected at 2000 m ahead of the ship, there was a 25% chance that it would still be at risk by the time a 20 knot ship reached it, as opposed to an 11% chance for a 13 knot ship (Fig. 7).

4. DISCUSSION

We estimated components of whale surfacing behavior around transiting cruise ships to better understand the opportunities and constraints for whale detection and avoidance by ship operators. Detection followed by active avoidance maneuvers represents a complementary approach to regulatory mechanisms such as shifts in shipping lanes and/or mandated reductions in ship speed, because even mariners within new shipping lanes encounter

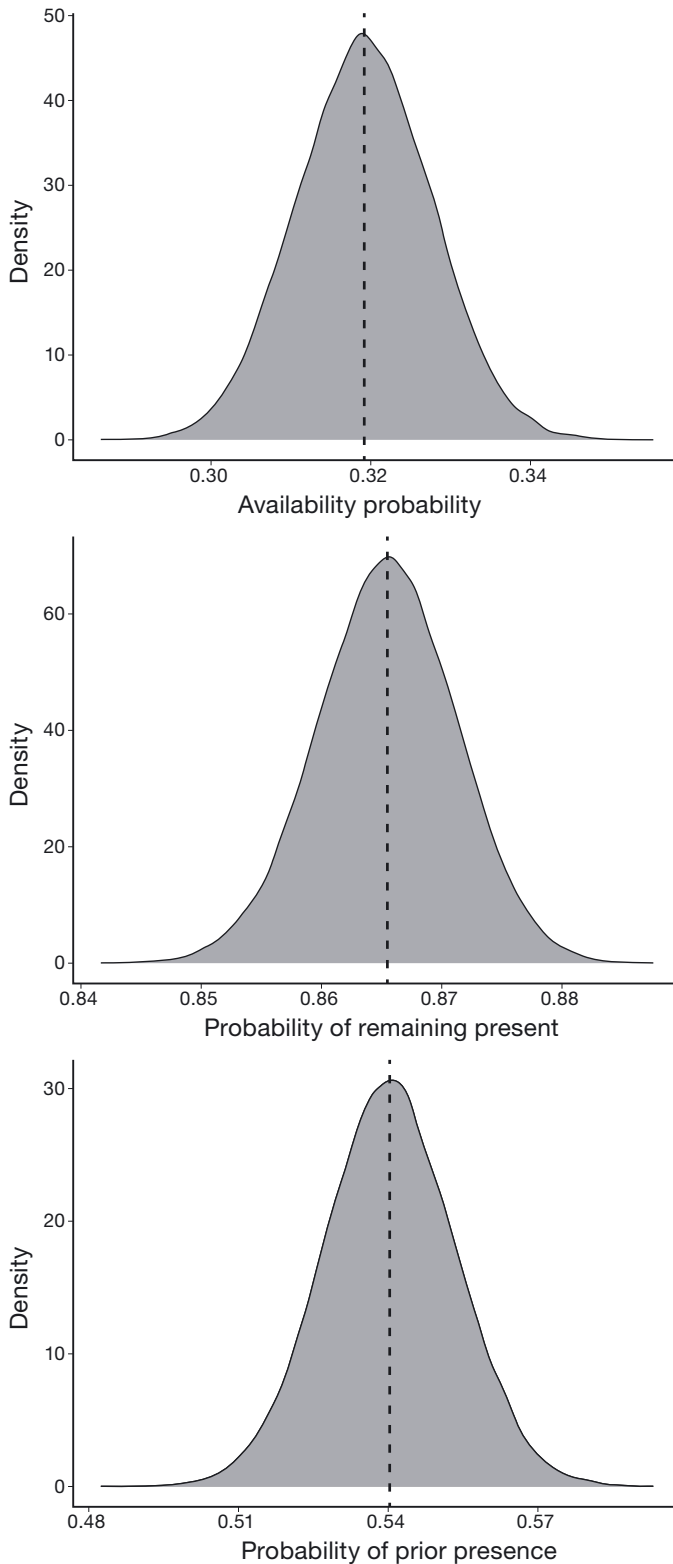


Fig. 6. Posterior distributions of parameter estimates of the availability probability (probability of availability for detection, PAD), the probability of remaining present following detection (PRP), and the probability of a prior surfacing event (PSE)

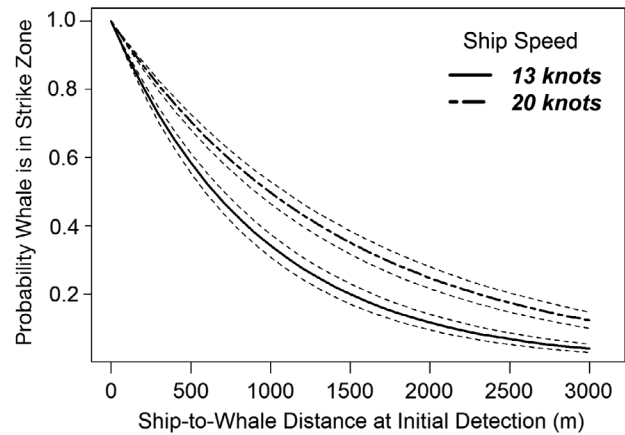


Fig. 7. Probability that a whale will still be at or near the surface, and thus susceptible to a collision (in the strike zone), after the elapsed time it takes for a ship to cover the distance to the whale following initial detection. Probabilities and credible intervals are based on median parameter estimates across all initial detection distances. Thick lines represent medians for a ship travelling 13 knots (6.7 m s^{-1}) vs. 20 knots (10.3 m s^{-1})

whales, slow ships can be involved in lethal collisions (Kelley et al. 2021), and adherence to different regulatory efforts is variable (Ebdon et al. 2020). Additionally, cruise ship operators demonstrate willingness and ability to change operational state to avoid detected whales (Gende et al. 2019). Our work builds on other studies that use data on whale surfacing behavior to quantify risk of ship strikes whereby the time at or near the surface equates to their availability to be struck (Calambokidis et al. 2019, Keen et al. 2019, Rockwood et al. 2021).

Humpback whales in Glacier Bay surfaced an average of 2.9 times during a typical surfacing bout, which is slightly lower, but consistent with, results that estimated an average of 3.2 blows per surfacing bout by humpback whales in Frederick Sound, Alaska (Dolphin 1987b). Our results also mirrored Dolphin (1987b) inasmuch that the number of surfacing events per bout and submergence durations, together constituting the total time at the surface at risk of collision, were highly skewed with whales surfacing in proximity of an approaching cruise ship on 4 or more occasions during a surfacing bout, with several exceeding 20 surfacing events (Fig. 5). Dolphin (1987a) attributed this variation in surfacing to dive duration, with longer dives positively correlated to more blows per surfacing interval or longer surface times and to the behavioral state of the whale at the time of sighting, with certain behaviors, such as ‘resting,’ producing longer surfacing bouts. In the context of our observations being conducted from

cruise ships, it is possible that some of this variation could be attributed to changes in respiration by whales around ships, although whale-to-ship distances were typically large and changes in respiration were not obvious. Additionally, feeding whales tend not to change their behavior in the presence of vessels (Schuler et al. 2019).

While our study was not designed to explain the underlying biological mechanisms driving the variation in surfacing duration, large skewness in surfacing time is relevant for whale avoidance. Our data demonstrate that prudent mariners who detect whales surfacing within the 'cone of concern,' or the area forward of a ship where whales are at risk of being struck based on whale swimming and ship transit speeds (Gende et al. 2019), should not assume that whales will safely dive out of the strike zone before the ship reaches the general area where it was first detected, particularly for whales surfacing closer to the ship where hydrodynamic forces could make it more difficult for whales to move out of the way (Silber et al. 2010). We observed many instances when whales submerged for extended periods of time without initiating a fluke-up dive and resurfaced later, forward of the ship. These long submergences, while potentially deep-feeding dives, could have actually been short, shallow dives. Thus, it is a tenuous assumption that whales first detected forward of the ship have left the strike zone if a fluke-up dive is not detected.

Ironically, these longer surfacing bouts, which were often characterized by a higher-than-average number of surfacings, could contribute to the ability of ships to avoid whales. In general, the quality of information available to mariners is often a measure of their willingness to act (Gende et al. 2019). Because surfacing cues generally persist for only a second or two, mariners will often be uncertain in identifying the precise location or swim direction of a detected whale, particularly at larger ship-to-whale distances or when environmental conditions such as strong winds are present (Williams et al. 2016). More detected surfacings may contribute to higher confidence in the whale's location and behavior, potentially increasing both the willingness of mariners to act upon that information and the chance that mariners choose the 'correct' risk-reducing change in operational state, should one exist, such as turning behind a whale that is swimming in a crossing pattern. A whale that spends more time on the surface may thus result in a reduction in the ability of the whale to avoid the ship but potentially increases the opportunities for the ship to avoid the whale.

Our parameter estimates for PSE were consistent with previous studies demonstrating imperfect detection of available surfacing cues. In general, the opportunities to make an avoidance maneuver are maximized when the first detected surfacing event is also the first surfacing event available to be detected. When this happens, there is an increase in ship-to-whale distance and the time available for mariners to command, and then achieve, a new risk-reducing operational state, such as a slight change in heading or speed (Gende et al. 2019). Our results demonstrate a moderate chance that whales initially surface without immediate detection. These results likely serve as a minimum estimate of this probability, as our data were collected in lower sea states; heavier seas would make it more difficult to detect the first available cue (Barlow 2015). While we accounted for some of this variation using an initial detection function derived from the same study area (Williams et al. 2016), any method that improves detection probability, such as adding a designated 'watch,' can improve the opportunities for avoiding whales. We highlight that while cruise ships transiting GLBA are required to have a dedicated watch on the bridge, this is not a requirement in many waters.

Our model was parameterized to estimate probability of remaining at the surface with the key assumption that all surfacing events of a whale were associated with the same surfacing bout, i.e. we made no attempt to use survival analyses or other methods (Crance et al. 2017) to statistically differentiate between submergences and foraging dives. The result was that the reduction in collision risk persisted with increasing initial detection distances. In reality, the relationship between collision risk and initial detection distance is more likely to be U-shaped. At relatively close distances, whales, on average, will complete their surfacing bout and dive to depth with the ship safely passing overhead. This relationship is likely to invert at comparatively larger initial detection distances because the whale will have enough time to complete a dive and re-surface much closer to the ship. For example, a ship traveling 20 knots (10.3 m s^{-1}) will travel over 1700 m during the time it takes for a humpback whale to complete an average foraging dive in this area (170 s; Dolphin 1987a). Thus, a whale that completes a surfacing bout and dives at 1000 m forward of the ship will remain safely at depth long after the ship passes overhead. In contrast, a whale that embarks on the same dive duration at 2000 m forward of the ship would resurface before the ship passed overhead, dramatically increasing collision risk.

While these examples are overly simplistic, they highlight that a mariner who detects a whale at a larger distance from the ship could expect the whale to resurface again much closer, enforcing the need to consider risk-reducing measures when whales are seen in the cone of concern across all ship-to-whale distances. In fact, some of the closest encounters we observed were not whales that were first encountered in a longer series of blows/submergences but instead were whales that surfaced suddenly. To that end, more studies on variation in dive behavior, and factors that influence it, would help to further refine risk models such that they can more accurately represent the relationship between risk and initial sighting distance.

Another caveat of our modeling approach, and estimates of risk, is that our ship-to-whale encounter distances were mostly concentrated at intermediate to large distances; only 2 of the 300+ surfacing bouts were first detected within 200 m of the ship's bow. We assumed that whale behavior at large ship-to-whale distances was similar to behavior for whales surfacing very close to the ship. In fact, the only times we have witnessed 'flight' behavior, whereby the whale rapidly changed direction of travel or very rapidly initiated a fluke up dive (often turning sideways in the process) were when surfacing events occurred within 200 m of the bow and directly forward of the ship. In these instances, our parameters overestimate the length of time at the surface because whales would 'exit' the strike zone faster than model predictions if they initiated such a flight response.

Our results contribute to the holistic understanding of opportunities for active whale avoidance by ship operators. Previous work found that instantaneous detection probability is largely influenced by distance (Williams et al. 2016), although the cumulative probability of detecting any of the series of cues provided by whales during their surfacing bout is larger because whales provide multiple cues per surfacing bout (Gende et al. 2019). Studies also demonstrated that detection probability is likely to increase at similar distances if mariners focus on the 'cone of concern,' which is the area forward of the ship where theoretically whales could swim into the path of the ship (Gende et al. 2019). While increasing detection probability may not lead to active avoidance maneuvers by ships due to the challenges associated with implementing these actions, maximizing early detection of whales gives mariners the best chance to act. Although we recognize that stakeholder buy-in may be required to implement a dedicated watch on all

ships (Vanderlaan & Taggart 2009), and that voluntary (Wiley et al. 2008) and even mandatory regulations may not lead to compliance (Silber et al. 2014, Ebdon et al. 2020), this new evidence that even dedicated observers don't see all whales suggests that implementing watches on ships should be prioritized, and we hope that the shipping industry heeds this advice. Our current results reinforce that opportunities for detection improvement exist and begins to clarify risk as a function of detection distance. Integrating studies of detailed dive behavior of whales around ships with double-observer studies comparing observations from inside the navigational bridge with observations from the bow would further advance our understanding of the opportunities for large ship operators to avoid whales.

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LITERATURE CITED

- ✦ Agardy T, Cody M, Hastings S, Hoyt E, Nelson A, Tetley M, Notarbartolo di Sciarra G (2019) Looking beyond the horizon: an early warning system to keep marine mammal information relevant for conservation. *Aquat Conserv* 29: 71–83
- ✦ Audacity Team (2018) Audacity (R) v2.1.2: Free Audio Editor and Recorder, copyright 1999. audacityteam.org
- ✦ Barendse J, Best PB, Thornton M, Pomilla C, Carvalho I, Rosenbaum HC (2010) Migration redefined? Seasonality, movements and group composition of humpback whales *Megaptera novaeangliae* off the west coast of South Africa. *Afr J Mar Sci* 32:1–22
- ✦ Barlow J (2015) Inferring trackline detection probabilities, $g(0)$, for cetaceans from apparent densities in different survey conditions. *Mar Mamm Sci* 31:923–943
- ✦ Bettridge S, Baker CS, Barlow J, Clapham PJ and others (2015) Status review of the humpback whale (*Megaptera novaeangliae*) under the Endangered Species Act. NOAA technical memorandum NMFS-SWFSC-540
- ✦ Calambokidis J, Fahlbusch JA, Szesciorka AR, Southall BL, Cade DE, Friedlaender AS, Goldbogen JA (2019) Differential vulnerability to ship strikes between day and night for blue, fin, and humpback whales based on dive and movement data from medium duration archival tags. *Front Mar Sci* 6:1–11

- Christiansen F, Dawson SM, Durban JW, Fearnbach H and others (2020) Population comparison of right whale body condition reveals poor state of the North Atlantic right whale. *Mar Ecol Prog Ser* 640:1–16
- Conn PB, Silber GK (2013) Vessel speed restrictions reduce risk of collision-related mortality for North Atlantic right whales. *Ecosphere* 4:1–16
- Crance JL, Berchok CL, Keating JL (2017) Gunshot call production by the North Pacific right whale *Eubalaena japonica* in the southeastern Bering Sea. *Endang Species Res* 34:251–267
- Dolphin WF (1987a) Dive behavior and estimated energy expenditure of foraging humpback whales in southeast Alaska. *Can J Zool* 65:354–362
- Dolphin WF (1987b) Ventilation and dive patterns of humpback whales, *Megaptera novaeangliae*, on their Alaskan feeding grounds. *Can J Zool* 65:83–90
- Dreitz VJ, Nichols JD, Hines JE, Bennetts RE, Kitchens WM, DeAngelis DL (2002) The use of resighting data to estimate the rate of population growth of the snail kite in Florida. *J Appl Stat* 29:609–623
- Ebdon P, Riekkola L, Constantine R (2020) Testing the efficacy of ship strike mitigation for whales in the Hauraki Gulf, New Zealand. *Ocean Coast Manage* 184:105034
- Fujiwara M, Caswell H (2001) Demography of the endangered North Atlantic right whale. *Nature* 414:537–541
- Gabriele CM, Lockyer C, Straley JM, Jurasz CM, Kato H (2010) Sighting history of a naturally marked humpback whale (*Megaptera novaeangliae*) suggests ear plug growth layer groups are deposited annually. *Mar Mamm Sci* 26:443–450
- Gabriele CM, Neilson JL, Straley JM, Baker CS, Cedarleaf JA, Saracco JF (2017) Natural history, population dynamics, and habitat use of humpback whales over 30 years on an Alaska feeding ground. *Ecosphere* 8: e01641
- Gende SM, Hendrix AN, Harris KR, Eichenlaub B, Nielsen J, Pyare S (2011) A Bayesian approach for understanding the role of ship speed in whale-ship encounters. *Ecol Appl* 21:2232–2240
- Gende SM, Vose L, Baken J, Gabriele CM, Preston R, Hendrix AN (2019) Active whale avoidance by large ships: components and constraints of a complementary approach to reducing ship strike risk. *Front Mar Sci* 6:1–19
- Gulesserian M, Slip D, Heller G, Harcourt R (2011) Modelling the behavior state of humpback whales *Megaptera novaeangliae* in response to vessel presence off Sydney, Australia. *Endang Species Res* 15:255–264
- Guzman HM, Hinojosa N, Kaiser S (2020) Ship's compliance with a traffic separation scheme and speed limit in the Gulf of Panama and implications for the risk to humpback whales. *Mar Policy* 120:104113
- Hiby AR, Ward AJ (1986) Analysis of cue-counting and blow rate estimation experiments carried out during 1984/85 IDCR Minke whale assessment cruise. *Rep Int Whaling Comm* 36:473–475
- Kavanagh AS, Noad MJ, Blomberg SP, Goldizen AW, Kniest E, Cato DH, Dunlop RA (2017) Factors driving the variability in diving and movement behavior of migrating humpback whales (*Megaptera novaeangliae*): implications for anthropogenic disturbance studies. *Mar Mamm Sci* 33:413–439
- Keen EM, Scales KL, Rone BK, Hazen EL, Falcone EA, Schorr GS (2019) Night and day: diel differences in ship strike risk for fin whales (*Balaenoptera physalus*) in the California current system. *Front Mar Sci* 6:1–16
- Kelley DE, Vlastic JP, Brillant SW (2021) Assessing the lethality of ship strikes on whales using simple biophysical models. *Mar Mamm Sci* 37:251–267
- Kery M, Schaub M (2012) Bayesian population analysis using WinBUGS: a hierarchical perspective. Academic Press, Waltham, MA
- Mann J (1999) Behavioral sampling methods for cetaceans: a review and critique. *Mar Mamm Sci* 15:102–122
- McKenna MF, Katz SL, Condit C, Walbridge S (2012) Response of commercial ships to a voluntary speed reduction measure: Are voluntary strategies adequate for mitigating ship strike risk? *Coast Manage* 40:634–650
- McKenna MF, Calambokidis J, Oleson EM, Laist DW, Goldbogen JA (2015) Simultaneous tracking of blue whales and large ships demonstrates limited behavioral responses for avoiding collision. *Endang Species Res* 27:219–232
- Moore MJ, Schick RS, Sharp SM, Smith CR, Thomas L, van der Hoop JM, Ziccardi MH and others (2021) Assessing North Atlantic right whale health: threats, and development of tools critical for conservation of the species. *Dis Aquat Org* 143:205–226
- Neilson JL, Gabriele CM (2007) Results of humpback whale population monitoring in Glacier Bay and adjacent waters: 2007. National Park Service Resource Brief, Gustavus, AK
- Neilson JL, Gabriele CM (2021) Glacier Bay and Icy Strait humpback whale population monitoring: 2020 update. National Park Service Resource Brief, Gustavus, AK
- Plummer M (2003) JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. Proceedings of the 3rd International Workshop on Distributed Statistical Computing (DSC 2003), Vienna, 20–22 March 2003
- Pradel R (1996) Utilization of capture-mark-recapture for the study of recruitment and population growth rate. *Biometrics* 52:703–709
- R Core Team (2017) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Ransome N, Loneragan NR, Medrano-González L, Félix F, Smith JN (2021) Vessel strikes of large whales in the eastern tropical Pacific: a case study of regional under-reporting. *Front Mar Sci* 8:1–15
- Rockwood RC, Calambokidis J, Jahncke J (2017) High mortality of blue, humpback and fin whales from modeling of vessel collisions on the U.S. West Coast suggests population impacts and insufficient protection. *PLOS ONE* 12: e0201080
- Rockwood RC, Adams JD, Hastings S, Morten J, Jahncke J (2021) Modeling whale deaths from vessel strikes to reduce the risk of fatality to endangered whales. *Front Mar Sci* 8:1–20
- Saracco JF, Gabriele CM, Neilson JL (2013) Population dynamics and demography of humpback whales in Glacier Bay and Icy Strait, Alaska. *Northwest Nat* 94:187–197
- Schuler AR, Piwetz S, Clemente JD, Steckler D, Mueter F, Pearson HC (2019) Behavior response to whale-watching vessels in Juneau, AK. *Front Mar Sci* 6:710
- Silber GK, Slutsky J, Bettridge S (2010) Hydrodynamics of a ship/whale collision. *J Exp Mar Biol Ecol* 391:10–19

- ✦ Silber GK, Adams JD, Fonnesbeck CJ (2014) Compliance with vessel speed restrictions to protect North Atlantic right whales. *PeerJ* 2:e399
- ✦ Su YS, Yajima M (2015) R2jags: using R to Run 'JAGS'. <https://cran.r-project.org/web/packages/R2jags/R2jags.pdf>
- ✦ Tenan S, Pradel R, Tavecchia G, Igual JM, Sanz-Aguilar A, Genovart M, Oro D (2014) Hierarchical modelling of population growth rate from individual capture-recapture data. *Methods Ecol Evol* 5:606–614
- ✦ Thomas PO (2016) Status of the world's baleen whales. *Mar Mamm Sci* 32:682–734
- ✦ van der Hoop JM, Vanderlaan ASM, Cole TVN, Henry AG and others (2015) Vessel strikes to large whales before and after the 2008 ship strike rule. *Conserv Lett* 8:24–32
- ✦ Vanderlaan ASM, Taggart CT (2009) Efficacy of a voluntary area to be avoided to reduce risk of lethal vessel strikes to endangered whales. *Conserv Biol* 23:1467–1474
- ✦ Vanderlaan ASM, Taggart CT, Serdyńska AR, Kenney RD, Brown MW (2008) Reducing the risk of lethal encounters: vessels and right whales in the Bay of Fundy and on the Scotian shelf. *Endang Species Res* 4:283–297
- ✦ Webb KR, Gende SM (2015) Activity patterns and speeds of large cruise ships in southeast Alaska. *Coast Manage* 43: 67–83
- ✦ Wiley DN, Moller JC, Pace RM, Carlson C (2008) Effectiveness of voluntary conservation agreements: case study of endangered whales and commercial whale watching. *Conserv Biol* 22:450–457
- ✦ Williams R, Gero S, Bejder L, Calambokidis J and others (2011) Underestimating the damage: interpreting cetacean carcass recoveries in the context of the Deepwater Horizon/BP incident. *Conserv Lett* 4:228–233
- ✦ Williams SH, Gende SM, Lukacs PM, Webb K (2016) Factors affecting whale detection from large ships in Alaska with implications for whale avoidance. *Endang Species Res* 30:209–223

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