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Bounding the number of calling animals with passive acoustics and reliable locations

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ABSTRACT:

When n animal calls are passively detected at n different times, the number of animals producing the sounds is anywhere between one and n unless more information is available. When extremely reliable confidence intervals of location are also available for each call, the upper bound is still n , but a lower bound can be derived. The lower bound exceeds one when it is physically impossible for an animal to travel quickly enough to go from one reliable location to another within the temporal call interval. When many calls are detected, it may be too complicated or numerically prohibitive to determine the minimum number of animals responsible for the calls in space and time by inspection or brute force methods. Instead, it is advantageous to use graph theory. The lower bound for the number of calling animals can be derived using 100% confidence intervals of each call's location. Mathematical theorems guarantee the lower bound is correct: a lesser value is impossible to obtain. Guaranteed bounds for the abundance of calling animals are useful for conservation in the presence of environmental stress and studying behavior.

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I. INTRODUCTION

If we hear n animal calls, we only know we heard 1 to n animals unless other information is available. For example, suppose we listen to recordings from an omnidirectional hydrophone, where non-overlapping calls from five bearded seals are heard. If we know nothing about the source level of seal calls or their rate of calling, we know the number of seals detected is from one to five. The problem we solve, perhaps for the first time, is how to derive a certifiably correct lower bound for the calling abundance (number of calling animals) when each call is reliably located. The guarantee is provided via mathematical theorems. To this end, we ask if two calls come from the same animal. If the animal can travel quickly enough to go the minimum distance between the two localizations during the calling interval, we know we could have heard one or two animals; otherwise, we know we heard two. It is, therefore, of critical importance to have an extremely reliable 100% confidence

interval of location (CIL). With 100% CIL, the minimum distance between two call locations and minimum speed needed to traverse this distance can be computed with the corresponding temporal interval between calls.

One method for locating animal sounds is to plot a point at some location without error bounds (Swartz *et al.*, 2003). Using this process, the probability that the animal's location actually intersects this point is small. Using the methods described by Spiesberger (2003, 2012, 2005, 2020a,b), we will use 100% CIL, and the animal is guaranteed to be within the CIL. It is important to note the methods developed and described in this paper reveal nothing about the upper bound of calling abundance because there could have always been n calling animals if no other information is available. We are not advocating a single value of calling abundance because any single number has a low probability of being correct. However, the range between lower and upper bounds is mathematically guaranteed to contain the true calling abundance. This guarantee is valid only when using 100% CIL for the location. Population abundance is always equal to or greater than the calling abundance because some animals may be silent. Translating calling

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abundance to population abundance is outside the scope of our current thinking, although others consider it, e.g., Marques *et al.* (2013) and Thomas and Marques (2012).

The advantages of passively monitoring animal sounds in the ocean and atmosphere for the purposes of conservation and understanding their behavior have long been known (Archer *et al.*, 2020; Davis *et al.*, 2017; Hannay *et al.*, 2013; Marques *et al.*, 2013; Moore *et al.*, 2006; Opzeeland and Hillebrand, 2020; Parijs *et al.*, 2001; Stafford *et al.*, 2013; Thomas and Marques, 2012). The ocean is particularly well suited for sound monitoring because calls at a few hundred Hertz can be detected at tens to hundreds of kilometers, and it is often difficult and expensive to observe animals by other means. Reliable bounds of calling abundance are useful for monitoring the population size and changes in location with time in the presence of environmental or anthropogenic stressors. These bounds can also influence national and international policies regarding endangered and protected species. For example, there are an estimated 30 right whales remaining in the eastern North Pacific (Wade *et al.*, 2010). Suppose the mathematically guaranteed lower bound yields 60. This might further impact policy protection and monitoring.

Estimating the abundance of calling animals is the subject of hundreds of articles and books (e.g., see Marques *et al.*, 2013; Thomas and Marques, 2012, for a review); no attempt is made here to summarize all of the important contributions. Distance sampling is a method wherein estimated distances to calling animals are related to the probability of detection, and assumptions are employed to estimate the abundance (Buckland *et al.*, 1993; Marques *et al.*, 2013). The probability of detection generally decreases with distance as the received signal becomes weaker. Distance can be estimated in several ways, including crossing of directional data from two or more receivers (Thode *et al.*, 2012) and matched-field processing (Wiggins *et al.*, 2004). The mark-recapture method can be used to estimate density when individuals can be recognized from their calls and even when they are not recognizable from their calls (Marques *et al.*, 2012). In the latter case, calls are detected (captured) on one receiver and also detected (captured) on another receiver. The history of captures provides information on the abundance without locating or recognizing individuals.

If the location of a call is computed by any means, the abundance can be estimated with the spatially explicit capture-recapture method. The abundance is sometimes computed by multiplying detection counts by empirical factors (McDonald, 2006; Mellinger, 2014). These factors may include the relationship between the number of calling versus non-calling animals, false detections, cue-counting, and cue-rate. The calling abundance has been estimated with measurements of the acoustic bearing angles, received signal-to-noise ratio, source levels, models of acoustic propagation, and calling rates (Harris *et al.*, 2018).

Some studies estimate the calling abundance with acoustic and visual data. In one study, bowhead whales were

censused in the Arctic from visual observations and acoustic arrays (Raftery and Zeh, 1998). They did not attempt to create a census from acoustic data only. Acoustically derived locations were shown as points and they stated “In some cases it is impossible to know whether different locations correspond to different whales.” Resolving this ambiguity is the principal motivation for our research.

There are many ways of locating sounds. The examples in this paper generate 100% CIL using a call’s time-difference-of-arrivals (TDOA) from a plurality of widely separated receivers using a technique called sequential bound estimation (SBE; Spiesberger, 2005, 2020a,b, 2003, 2012). The problem of finding a lower bound from calls is complicated when there are many 100% CIL, and the goal is to determine the minimum number of animals responsible for these CILs in space and time (Spiesberger *et al.*, 2019, 2020c). As explained in this paper, 100% CIL makes it possible to yield a mathematically guaranteed lower bound for the number of calling animals. This CIL can be computed in many ways, including via SBE. We briefly summarize why it is possible to obtain a 100% CIL that is finite and sometimes small.

The 100% CILs are computed with SBE from measurements of the TDOA between pairs of receivers. The finiteness of the CIL is possible because all prior probability distributions for error have finite bounds. Probability distributions with infinite tails are mathematical concepts created to yield analytically convenient solutions to problems; their infinite tails are unreal. For example, the location of a receiver cannot be anywhere: it is always possible to know it is in a finite region of space with 100% confidence. SBE imposes finite bounds for all prior probabilities of variables contributing to the error of location, and the 100% CIL can be small compared with the size of the receiving array (Spiesberger, 2005). The novel aspects in this paper are unrelated to SBE. The novelty stems from a means to estimate the certified lower bound for the calling abundance using 100% CIL.

Section II discusses the mathematical problem of estimating a lower bound. The solution is derived using theorems from graph theory. It is not possible to explain the derivations of the theorems within the confines of a single journal paper. Consequently, we make no such attempt and instead list the approaches and provide references so readers know where to look to seek understanding. A few concepts are presented to provide an introduction for how the problems are approached. Section III presents simulations based on graph theory. The approach is then applied to marine mammal calls recorded in the Chukchi Sea in Sec. IV, followed by a discussion in Sec. V.

II. LOWER BOUND FOR NUMBER OF CALLING ANIMALS

Suppose n calls occur at times t_i , $i = 1, 2, 3, \dots, n$ and their 100% CIL, l_i , are derived from each. Set $t_1 = 0$, so the t_i are the elapsed times. The minimum distance between l_i and l_j is d_{ij} . The minimum speed needed for an animal to

travel between l_i and l_j is $v_{ij} = d_{ij}/|t_i - t_j|$. Let \hat{v} be the maximum speed of an animal. The only possible call-pairs belonging to the same animal obey

$$v_{ij} \leq \hat{v}; \quad i \neq j. \quad (1)$$

In the parlance of graph theory, a pair of call numbers is “comparable” if they obey Eq. (1). Because of the triangle inequality (Euclid *et al.*, 2002), if (i,j) and (j,k) are comparable, then (i,k) is comparable. In the context of this paper, the triangle inequality states the sum of the lengths of any two sides of a triangle exceeds the length of the third side.

Let A be the set of all call numbers, $1, 2, 3, \dots, n$. Let C denote the set of all call numbers from comparable pairs, and assume the values in C are unique. Let C' denote the call numbers from A not in C , and let there be n_c elements in C' . Each of the n_c calls must have come from different animals. These are easy to identify. However, the minimum number of animals responsible for the calls in C is not as easy to identify.

This problem’s difficulty is made apparent by analyzing the number of possible ways to find a minimum number through an exhaustive calculation. Suppose 100 calls are emitted at different times. It is possible to estimate which calls are comparable with others. Imagine the location of the first call is comparable with 20 other call locations, the second call is comparable with 42 other call locations, the third call is comparable with 30 other call locations, a fourth call is comparable with 19 other call locations, and so forth. A brute force method might start with the hypothesis that there is only one animal, but we can easily exclude its possibility when at least two calls are incomparable. In our example, the first call location is incomparable with 80% of the 100 call locations, therefore, one animal could not have produced all of the sounds. Next, the brute force method hypothesizes there are two animals and attempts to determine if there is a starting location where each of the two animals could travel fast enough to reach (between them) each of the 100 locations. The two-animal hypothesis is not as easy to check as the one-animal hypothesis. We know the first call is associated with one of the animals, but we do not know the earliest call associated with the second animal. If calls from two animals have other call numbers in common, we must try all of the possible ways to share these other calls between two animals and see if all of the 100 calls can be explained by any assignment among comparable pairs so all 100 locations can be reached exactly once by exactly one animal. Even if we refute the two-animal hypothesis, we must proceed to hypothesizing three animals, then four, and so on until we find the minimum number of animals and their associated tracks wherein the locations corresponding to each of the 100 calls are visited by exactly one of those animals. Moreover, just because the first four calls, in our example, are comparable with more than 100 locations collectively does not mean it is possible to initiate a disjoint path from each and still cover all 100 locations at the times specified. The number of checks required to implement a

brute force technique is a problem whose number of possibilities is $n!$ (n -factorial). Hence, for example, with 100 call locations, we are dealing with a problem with $100!$ possibilities or 9×10^{157} . The brute force method, therefore, is not feasible with any computer except in cases with a very small number of calls or in other idealized cases.

One practical way to solve this problem is to use graph theory (Cormen *et al.*, 2009; Wilson, 1986; Erickson, 2019). This mathematical subject deals with issues of combinatorics. The origin of this mathematics is interesting. In 1741, Euler visited Königsberg, Prussia. This city had seven bridges connecting the city across waterways. Residents used to make a game of seeing if it was possible to leave their home, cross each bridge exactly once, and then return home. No one succeeded, and Euler developed a mathematical approach proving its impossibility (Euler, 1741). His approach involved the invention of graph theory. Considerable progress has been made in this field since 1741; new theorems are published every year. In this subsection, we summarize how modern results from graph theory may be used to estimate the lower bound for the calling abundance. Detailed explanations of the pertinent theorems are provided in the references.

We explained how two calls are either comparable or incomparable. In graph theory, this information is summarized in an adjacency matrix (Cormen *et al.*, 2009). It is used for simple and complicated cases and sometimes displayed when it is small. If n calls are detected, the adjacency matrix has n rows and n columns. In our adjacency matrix, the elements in row i and column j are shown as i,j if the calls are comparable. If incomparable, a dash is placed at this row and column. We only show values in the upper-triangular half because the matrix is symmetric, and there are no values on the diagonal. The symmetry of the matrix is due to the fact that it only contains information about the comparability of two calls: if calls 1 and 2 are comparable, then calls 2 and 1 are comparable. Comparability does not contain information about time-ordering. Figure 1 is an adjacency matrix derived from the calls of two animals whose simulated call times and locations are based on the simulation discussed below in Sec. III A. There are $N = 12$ calls, and all of the call numbers appear in the matrix, hence, C' is empty. In our example, the animal can swim fast enough to go from the location of call 1 to the location of call 3 but not fast enough to go from the location of call 1 to the location of call 4 (Fig. 1).

Under ideal conditions, the calls naturally establish a temporal ordering, so we know if calls one and two are heard ten minutes apart, and if they are comparable, then the animal could have swum from the CIL of 1 to 2 but not vice versa. In graph theory, the times of the calls and their associated locations can be thought of as a partially ordered set (POSET; Cormen *et al.*, 2009).

The Hasse diagram is another tool from graph theory whose presentation can make it easier to visually determine the desired lower bound when there are not many calls. The Hasse diagram displays the POSET: it contains the comparability information from the adjacency matrix plus the

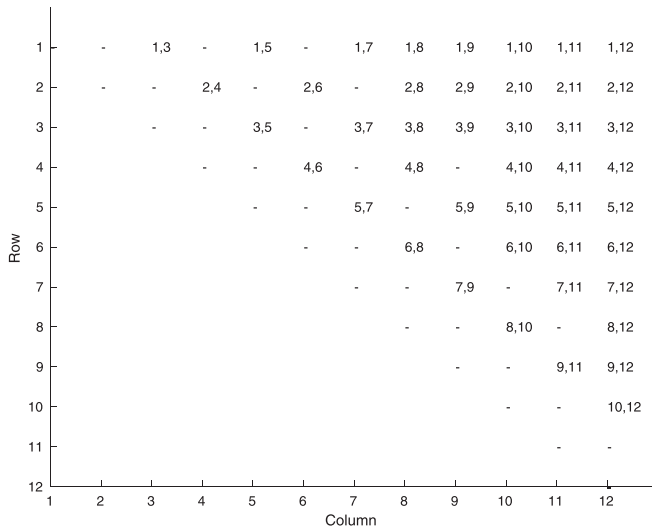


FIG. 1. Adjacency matrix derived from 2 animals calling at 12 locations [Fig. 3(A)] at times described in the text. The upper-triangular elements are filled if the animal can swim fast enough to go between two CILs. For example, the element 1,3 means that the locations of calls one and three are close enough. Comparability is determined using a maximum swimming speed of 10 m/s. The adjacency matrix is symmetric because it tabulates comparability. If calls 1 and 2 are comparable, then calls 2 and 1 are comparable.

time-ordering between comparable calls. For the two-animal simulation (Fig. 1), the Hasse diagram plots the locations of the calls as “vertices” and paths connect the comparable vertices with time flowing up along the paths connecting the comparable vertices (Fig. 2). Arrows show the directions of these so-called directed paths. The diagram conveys the temporal call ordering between comparable vertices by placing vertices associated with earlier call times at lesser values on the vertical axis. The vertical positions of the incomparable vertices are somewhat arbitrary. For example, vertices 1 and 2 are incomparable and could be plotted with the same vertical coordinate, as shown, or different vertical coordinates (e.g., 1 above 2 or 2 above 1), but vertices 1 and 2 must

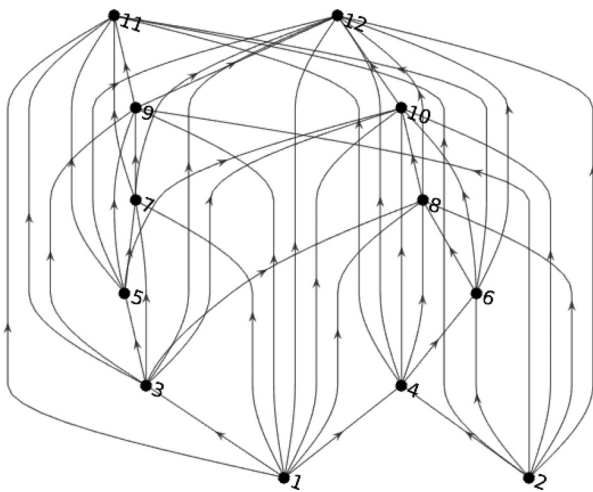


FIG. 2. The Hasse diagram corresponding to the adjacency matrix in Fig. 1. Call numbers are in chronological order with arrows indicating increasing chronological time.

both be below vertex 4 because vertices 1 and 4 are comparable and vertices 2 and 4 are comparable and vertex 4 occurs later than both vertices 1 and 2. All vertices comparable with vertex 2 have time flowing up, and all vertices comparable with vertex 1 have time flowing up.

An animal can travel along many different possible paths. For example, from vertices 3 to 8 and then to vertex 10, which is written as 3, 8, 10. Another directed path is 7, 9, and 12. We see there is no path from vertices 3 to 4 because we cannot go backward in time through call 1, so calls 3 and 4 are incomparable. This case is simple enough to see one animal cannot explain all 12 calls because if we start at call 1, there is no way to get to call 2 and vice versa. However, we see all 12 vertices can be covered by two animals. One way to do this is 1, 3, 5, 7, 9, and 11. The other path is 2, 4, 6, 8, 10, and 12. These two tracks touch each vertex exactly once. The minimum number of animals needed to explain all 12 calls is 2. When there are many more calls, it is usually impossible to determine the minimum number by eye.

Graph theory provides efficient methods to estimate the minimum number of paths needed to cover each vertex exactly once. The number of these so-called vertex-disjoint paths equals the number of vertices, V , in the graph minus the size of the so-called “maximum-matching”, m , of the associated bipartite graph (p. 361 of Erickson, 2019). In our problem, this theorem proves the impossibility of explaining the data with fewer than $V - m$ animals where V is the number of located calls. The vertex-disjoint paths are called tracks in bioacoustics. The approach we chose to obtain the lower bound of calling animals is as follows. The adjacency matrix is transformed into a bipartite graph to find all its maximum matchings. For each maximum matching, we construct its associated chain partition. Each chain partition is a subset of vertices, any pair of which are comparable. The vertices in each chain comprise a vertex-disjoint path and represent the time-ordered set of calls for a possible track of a single animal. Each so-called ‘isolated vertex’ of the bipartite graph is also a chain partition consisting of one call. The maximum-matching is not necessarily unique. Enumeration of all the maximum matchings is done using the method described by Takeaki (1997).

A. Call-time ambiguity

In reality, there is uncertainty in the call time of an animal, and this should be accounted for to get the minimum calling abundance. The measured arrival times of calls a , b , and c could be 0, 1, and 2 s, respectively, but this does not mean the emitted call order is a , b , and c . For this case, suppose that the calls are emitted at distances of 10, 2000, and 6000 m from the receiver and the speed of sound is 1500 m/s. The emitted time of call a is $0-10/1500 = -0.0067$ s. Similarly, the emitted times of calls b and c are $1-2000/1500 = -0.033$ s and $2-6000/1500 = -2.0$ s, respectively. Therefore, the emitted calling order is c, b, a while the measured arrival order is $a,$

b, c. The emitted call order can be determined from the CILs and possible speeds of sound.

Suppose the measured arrival time of a call is τ and the minimum and maximum distances between the receiver and its 100% CIL are \check{D} and \hat{D} , respectively. Then, the bounds for the call's emission times are

$$\check{t} = \tau - \hat{D}/\check{c}, \tag{2}$$

$$\hat{t} = \tau - \check{D}/\hat{c}, \tag{3}$$

where \check{c} and \hat{c} are the minimum and maximum speeds of sound, respectively.

Comparability of calls *i* and *j* can be determined from the minimum distance, d_{ij} , between their 100% CILs, the maximum interval of time, \hat{T}_{ij} , between these calls' emission times, and the maximum speed, \hat{v} , of the animal. Calls *i* and *j* are comparable when $d_{ij} \leq \hat{v}\hat{T}_{ij}$ or, equivalently, when $d_{ij}/\hat{T}_{ij} \leq \hat{v}$. Both the temporal and spatial uncertainties of the calls are needed to compute comparability.

Call-time ambiguity affects the tracks; if two calls, 1 and 2, have overlapping temporal bounds and are comparable, then one track would have the animal going from the CIL of call 1 to call 2, and the other track would go from call 2 to call 1. If the bounds of *m* calls mutually overlap in time, the number of all orderings equals $m!$. For $m = 10$, $m! \sim 3.6 \times 10^6$. Call-time ambiguity potentially leads to a large number of possible tracks. One scenario yielding ten overlapping call times occurs if the calls are received from eight calling dolphins near each other and the 100% CILs are rather large.

An important question is whether call-time ambiguity affects the calculation for the minimum number of calling animals. If it does, then it might be necessary to estimate the minimum number by applying graph theory $m!$ times, once for each temporal ordering of calls. However, we provide a proof that the minimum number of calling animals is the same for all $m!$ cases. In other words, we prove the minimum number is independent of the ordering of calls whose call times are ambiguous. The minimum calling abundance can be determined from any one of the millions of cases—a desirable outcome.

Proof: Changing the temporal order of time-ambiguous calls does not change their comparability. In other words, if calls *j* and *k* are comparable, then calls *k* and *j* are comparable because switching the order does not change d_{jk}/\hat{T}_{jk} . Also, note, if calls *j* and *k* are incomparable, they are still incomparable after any time-ambiguous calls are switched because d_{jk}/\hat{T}_{jk} does not change. Thus, switching the order of time-ambiguous calls does not change the comparability or incomparability for all pairs of calls. Now recall the theorem that the minimum vertex-disjoint path cover equals $V - m$ [p. 361 (Erickson, 2019)]. Changing the temporal order does not change the number of calls, V , nor does it change the size of the maximum matching, m , since a change of time-ordering of time-ambiguous calls is nothing more than a relabeling of vertices with the same comparability and incomparability.

Therefore, the minimum number of animals is unchanged. Q.E.D. We do not know if this proof is novel.

To the best of our knowledge, estimating a lower bound of the calling abundance from a reliable CIL in space and time is a novel application of graph theory.

III. SIMULATIONS

We apply graph theory to demonstrate how a lower bound for calling abundance can be determined. The compilation of these approaches is called the lower bound estimator (LBE) in this paper. We used software from publicly available sites for much of our computations in graph theory (Freese *et al.*, 1995a,b). The software was written to automatically compute the minimum calling abundance and possible tracks from the output of the SBE (Spiesberger, 2003, 2012, 2005, 2020a,b). The SBE provides 100% CIL and has been independently tested with real data by the U.S. Navy with a multistatic sonar. Its 100% CIL contained the independently measured location of the target without tuning with data for every 1 of the 100 cases studied (Spiesberger, 2016).

We estimate a lower bound for the number of calling animals in an ideal situation in which the locations of each call are known to occur at points in the horizontal plane and times of each call are known perfectly. These simulations reveal how the LBE works in simple circumstances.

A. Two animals

The locations of two animals are simulated, assuming each has an initial swimming speed randomly chosen in the interval between 0 and 10 m/s. Their locations are constrained to a planar surface. The temporal evolutions of their locations are generated within specified minimum and maximum radial and azimuthal accelerations. An animal's speed is not allowed to exceed 10 m/s. For simplicity, we assume each animal calls six times at 200 s intervals [Fig. 3(A)]. The corresponding adjacency matrix and Hasse diagrams are shown in Figs. 1 and 2. The minimum distance between each call's location and the location of every other localized call is computed with the Pythagorean theorem. In this idealized case, locations are at exactly known points, therefore, the minimum distance is simple to compute. This adjacency matrix is inputted into the LBE, yielding two calling animals [Fig. 3(B)]. In this case, the LBE correctly determines that there are two calling animals and their tracks.

B. Four animals

Each of four animals calls six times at 200 s intervals with a swimming speed between 0 and 10 m/s [Fig. 4(A)]. The adjacency matrix is not shown because it is too large. This matrix is inputted into the LBE, and the LBE correctly determines four animals can explain the data. The LBE correctly recovers the tracks for two of the animals [Fig. 4(B), left two tracks]. Its reconstruction of the two other tracks is imperfect because it determines that there are more than two paths that the animals can take to explain the calls on the

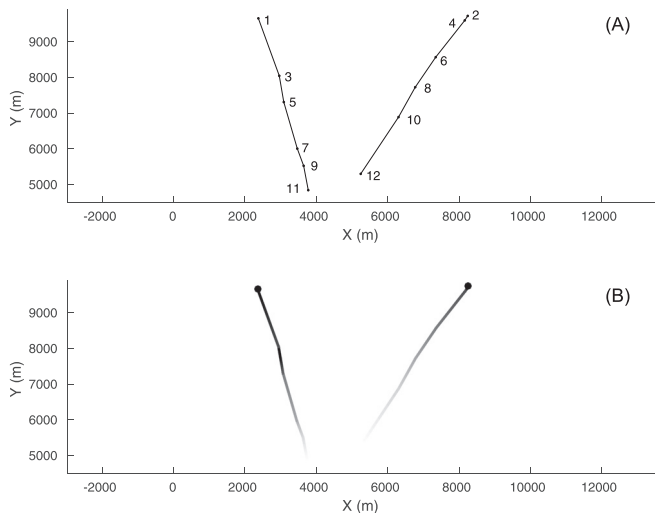


FIG. 3. (A) The true tracks of two animals (lines). Dots indicate the locations for each of 12 labeled calls. (B) The LBE determines that two is the lower bound for the number of calling animals where two dots indicate the starting locations for each animal.

right side of Fig. 4. Without further data, this is the maximum amount of information to be gleaned from the adjacency matrix.

IV. CALLS FROM MARINE MAMMALS

As part of the Chukchi Sea Acoustics, Oceanography, and Zooplankton (CHAOZ) study, an integrated ecosystem project funded by an Interagency Agreement between the National Oceanic and Atmospheric Administration’s (NOAA’s) Alaska Fisheries Science Center and Pacific Marine Environmental Laboratory, three passive acoustic arrays were deployed around a cluster of biophysical moorings off Icy Cape, Alaska. Each array had a pentagonal arrangement of five subsurface passive acoustic recorder moorings that were deployed annually for two years

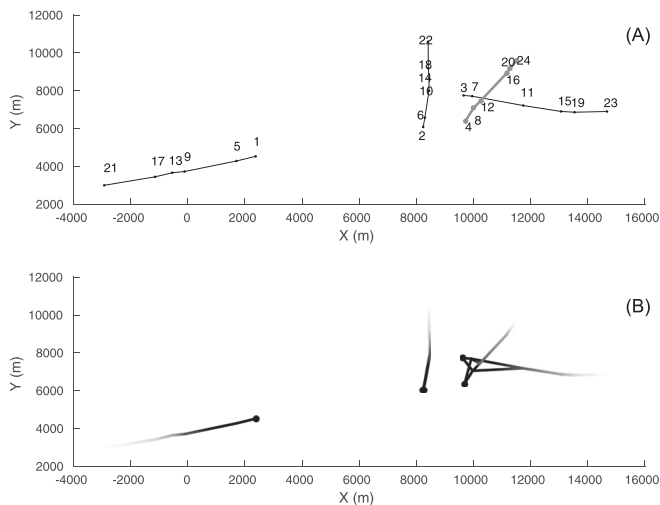


FIG. 4. (A) The same as in Fig. 3 except that there are four calling animals. (B) The LBE determines that 4 is the fewest number of animals responsible for the times and locations of the 12 calls. The four dots indicate the starting locations for each of the four animals.

(Mocklin and Friday, 2018). Here, we consider the data from the inshore array of recorders deployed from September 2011 through August 2012. Sounds were recorded on five receivers on the bottom at about 40 m depth in the Chukchi Sea in 2011 (Fig. 5). The receivers were oriented on the circumference of a circle of diameter about 6 km. Data were digitized at 16 384 Hz and stored on hard drives. The clocks for each receiver were unsynchronized and drifted up to about 0.2 s/day. They were synchronized using sounds from pingers mounted above each receiver. Extremely reliable 100% CILs were derived from measurements of the TDOA between one receiver and the other four (Spiesberger *et al.*, 2020b).

A. Bowhead whales

Ten bowhead whale calls are located with 100% CILs during a 31.057 min interval (Table I, Figs. 6–8). The maximum swimming speed of a bowhead is set to 10 m/s. This exceeds the maximum speed of 5.5 m/s that was observed by others (Mate and Krutzikowsky, 1995) but clearly illustrates the principles of estimating a certified lower bound with the data. Section V discusses how the lower bound depends on the maximum speed. All ten call numbers appear in the adjacency matrix (Fig. 6), thus, C' as defined in Sec. II is empty, but we cannot automatically deduce any of the calls are caused by only one animal because some pairs of calls are incomparable. The adjacency matrix is fed into the LBE, yielding two calling animals. The LBE determines that there are many groupings of calls consistent with two animals. In one grouping, the first bowhead is responsible for calls 1, 2, 7, 8, 9, and 10 (Fig. 8, top). The other is responsible for calls 3, 4, 5, and 6 (Fig. 8, bottom). These associations are evident in the corresponding Hasse diagram (Fig. 7). The supplementary material shows an animation of these ten 100% CILs.¹

V. DISCUSSION

We introduced the concept of estimating a reliable lower bound for the number of animals responsible for the

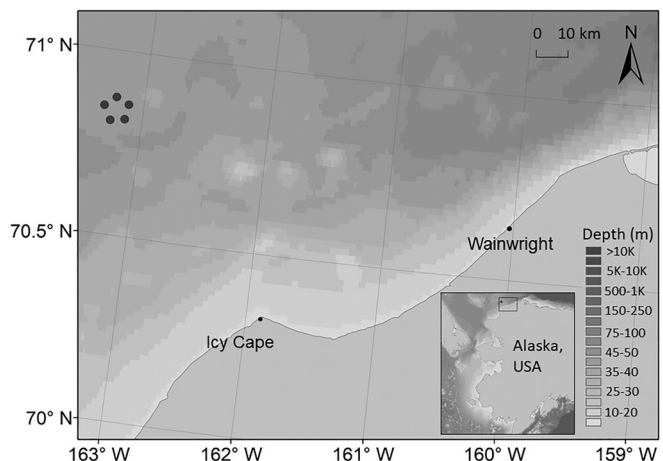


FIG. 5. The location of the receivers (five dots northwest of center) from the inshore array of the CHAOZ experiment (Mocklin and Friday, 2018).

TABLE I. The elapsed times of ten bowhead whale calls arriving at receiver one of the inshore array (second column). The arrival time of call 1 is 1 Nov 2011 at 14:11:6.7 GMT. The third column is bounds of call emission times derived from 100% CILs and bounds for the speed of sound. The adjacency matrix is shown in Fig. 6.

Call number	Received elapsed time (min)	Derived elapsed call time bounds (min)
1	0	[-0.283,-0.226]
2	0.075	[-0.464,-0.406]
3	3.981	[3.724,3.775]
4	5.543	[5.282,5.333]
5	8.161	[7.710,7.764]
6	20.238	[19.957,20.013]
7	20.997	[20.680,20.736]
8	21.095	[20.760,20.819]
9	21.172	[20.715,20.770]
10	31.057	[30.701,30.762]

recorded calls when their reliable locations are available. Without reliable locations and other information, we would only know that the number of animals responsible for n detected calls is any integer from one to n . Reliable locations introduce more information because it may be impossible for an animal to travel quickly enough to go from one reliable CIL to another during the associated call interval. The simplest invocation of our approach involves adopting one constraint: the maximum speed of the animal's travel. The maximum speed is almost always known, but any uncertainty in the maximum speed is resolved by increasing its value until reaching a unanimous consensus. In this sense, the approach does not depend on quantities that may or may not be well known such as the calling rate or calling source level. In the absence of reliable prior probability distributions for animal acoustic behaviors, such as calling rates and source levels, our approach offers a robust method

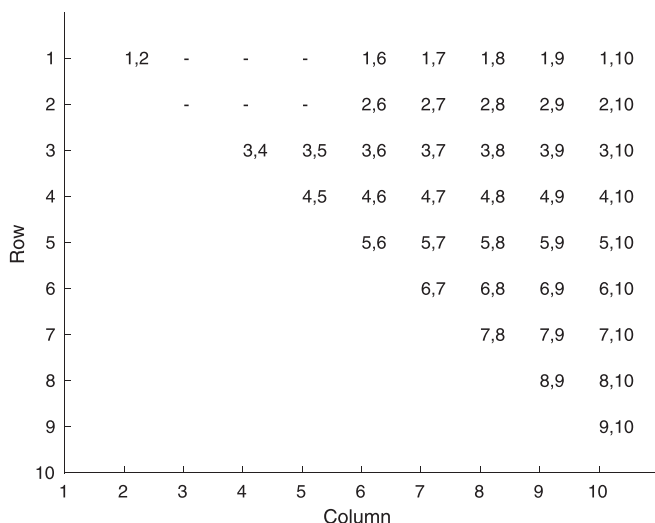


FIG. 6. The adjacency matrix for ten bowhead whale calls whose 100% CILs and elapsed calling times are shown in Fig. 8 and Table I, respectively.

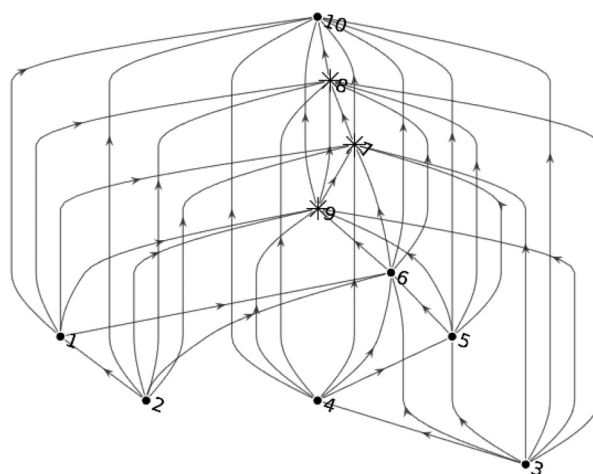


FIG. 7. The Hasse diagram for ten bowhead whale calls tabulated in Table I. Time-ambiguous calls are calls 7, 8, and 9, which are marked with an asterisk.

for estimating the fewest number of calling animals using only the knowledge of its maximum speed of travel. When the lower bound is derived with 100% CIL, graph theory provides a proof that the lower bound is correct: fewer calling animals are incapable of causing the observations.

Other variations exist for using an animal's traveling speed to derive a lower bound of calling abundance. One approach is to let the maximum speed be a function of the temporal interval between emitted calls. An animal might travel at a faster speed for a short duration. This information can be used when computing the adjacency matrix. The lower bound of the calling abundance must stay the same or increase as the swimming speed decreases because locations reachable at faster speeds may be unreachable at slower speeds.

Another approach uses a probability distribution of swim-speed to derive a probability distribution of the lower bound of the calling abundance. For example, suppose the upper bound of the swim-speed is assigned a uniform distribution on the interval from 5 to 6 m/s. The interval is subdivided at increments of 0.25 m/s, yielding five hypothesized maximum swim-speeds: 5, 5.25, 5.5, 5.75, and 6 m/s, each assigned a probability of 0.2. For each, a lower bound is derived for the calling abundance, yielding 13, 13, 12, 9, and 8 animals, respectively. Because 13 animals occur for both 5.0 and 5.25 m/s, its probability is $0.2 + 0.2 = 0.4$. The remaining lower bounds of the calling abundance are associated with a probability of 0.2 as 12, 9, and 8 occur once.

A reader may be puzzled if there are many calls and the lower bound is one. An implausible picture of a single animal may come to mind where it zigzags from point-to-point. The paradox is solved by realizing that locations cannot be points but are 100% CIL (Fig. 8). With a lower bound of one, these CILs are usually large and often overlap, and a lower bound of one makes sense. The lower bound for the calling abundance stays the same or increases toward the true calling abundance as the 100% CIL decreases. CILs can

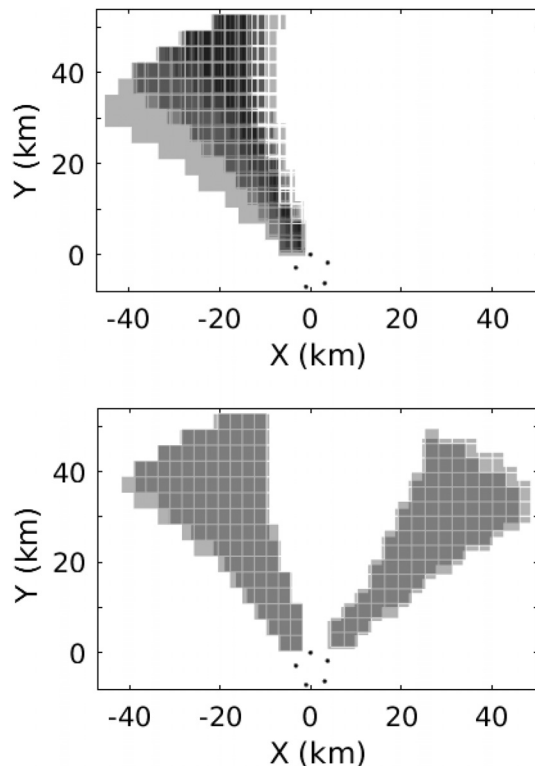


FIG. 8. The ten 100% CILs corresponding to the ten bowhead whale calls listed in Table 1 are shown. Two is the minimum number of animals responsible for the calls in space and time. The decomposition of the call number associated with each of the two animals is not unique. One decomposition has the first animal calling six times during a 27.0 min interval, shown on the left side of the region (top), and the second animal was calling four times during a 21.2 min interval, shown on both the left and right sides (bottom). The supplementary material provides an animation and still images displaying each animal's CIL in space and time (footnote 1). The 100% CIL corresponding to each call is translucent so when more CIL overlap, the corresponding intersection becomes blacker. The white grid lines have the following meaning. Each 100% CIL is produced by SBE where space is divided into rectangles. The union of all rectangular regions expresses the 100% CIL for each call. The data are from the inshore array of receivers (Fig. 5).

be made to decrease by adding acoustic receivers or improving the accuracy of the associated acoustic measurements.

It is usually impractical to determine the minimum number of animals responsible for the calls by checking all possibilities even with a supercomputer. The Hasse diagram provides a good way to visualize the lower bound when there are few enough calls (Fig. 2). We show how graph theory offers a computationally practical approach for deriving a lower bound for the calling abundance when their locations are reliably located in space and time (Cormen *et al.*, 2009; Erickson, 2019).

We create reliable CILs from passive measurements of the TDOA among at least three receivers (Spiesberger, 2003, 2012, 2005, 2020a,b). Reliable CILs could be made by other means, including intersecting acoustic beams and estimating lower and upper bounds of distances from single receivers.

The analysis provided in this paper uses 100% CIL. Analysis could be done with a lesser confidence interval, but

this would remove the mathematical certainty of the lower bound. There is, perhaps, a subtle reason for not wishing to use a lesser CIL. The derivation of this lesser value, e.g., 90%, is only meaningful if it is the correct 90% CIL. In the perspective of Bayesian analysis, the derived CIL depends on the prior distribution of variables affecting the location. For example, the practitioner is required to impose a prior probability for the error in a receiver's location. This is almost never known, therefore, when the Bayesian approach requires its use, an error is introduced into the analysis right from the start. The only way a Bayesian approach can correct this self-imposed error is to have enough data to overcome the error with data-adaptive methods. For most bioacoustic experiments, there are often insufficient data to overcome the errors in the priors. The most important motivation for the invention of the SBE is its insensitivity to errors in prior distributions (Spiesberger, 2003, 2012, 2005). Instead, the SBE depends only on the prior bounds of the error, and these prior bounds can always be made large enough to be true with a confidence of 100%. The experiment described in this paper is an excellent example in which the prior probabilities of error are unknowable. Thus, little credence can be assigned to CILs less than 100%.

In the future, these apparently new techniques could be used to estimate bounds for the calling abundance from large data sets. The findings in this paper and related topics are the subject of a U.S. patent (Spiesberger, 2021a,b).

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¹See supplementary material at <https://www.scitation.org/doi/suppl/10.1121/10.0004994> for video and still frames corresponding to Fig. 8.

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