

A method for unbiased estimation of population abundance along curvy margins

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Estimating species abundance via transects and quadrats has the advantage over other methods (such as mark-recapture) that they can be less expensive and do not require handling the animals. Transect–quadrat sampling along habitat boundaries with complex geometry often leads to uneven selection probability over the sampling region. These uneven selection probabilities must be properly taken into account in constructing unbiased estimates of abundance. This requires that the selection probabilities be known by design or be computable. We discuss the implications of this requirement on sampling design and introduce a computational method based on a cubic-spline approximation to the habitat margin for estimating the selection probabilities. We present the method in the context of a study of Pacific herring (*Clupea pallasii*) egg abundance along coastal southeast Alaska, and show that an unbiased estimate constructed based on the computed selection probabilities (the Horvitz–Thompson (H-T) estimator) corrects for a potential bias in the estimate for egg abundance relative to the unweighted sample mean estimate. The sampling strategy used in the herring study, together with our method for computing the sampling probabilities, provides an economical and effective way to study species abundance along curvy habitat boundaries. Copyright © 2010 John Wiley & Sons, Ltd.

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INTRODUCTION

Accurately estimating the abundance of species is a key component of ecological studies. For species that are somewhat sedentary, sampling via placing quadrats in the survey region is common and estimation procedures can be found in foundational works (Seber, 1973; Burnham *et al.*, 1980; ; Buckland *et al.*, 2001 Borchers *et al.*, 2002). Quadrat sampling is often inexpensive and avoids handling the animals, in contrast with methods such as mark-recapture. An economical and efficient way to obtain quadrat samples is to collect them in batches or clusters by using transects. Fisheries scientists and marine biologists have relied on transect sampling regimes to estimate abundances for a wide variety of organisms including invertebrates (Pfister and Bradbury, 1996; Hart *et al.*, 1997; McGarvey *et al.*, 2008), seaweeds (Davis *et al.*, 1997), and fish (e.g., Fort *et al.*, 2008, http://www.pac.dfo-mpo.gc.ca/sci/herring/pages/herring_e.htm).

One common scenario faced in abundance studies is that the species' habitat lies along a boundary with complex geometry. Some examples include surveys conducted along coastlines, rivers, lake shores, and elevation contours. Many transect–quadrat sampling designs in this setting give rise to uneven selection probabilities over the survey regions. This non-uniformity in sampling coverage must be properly accounted for in the estimation procedure to avoid introducing bias into the abundance estimate. Horvitz and Thompson (1952) provided a simple solution to this, namely by weighting each data point (quadrat in the current context) using the inverse of the corresponding selection probability.

A prerequisite for adopting the Horvitz–Thompson (H-T) method is that the selection probabilities of the sampled quadrats must either be known by design or be computable. In this paper, we discuss the implications of this requirement on sampling design and

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introduce a method for computing the selection probabilities using a spline approximation to the habitat boundary. Our presentation will evolve in the context of a study conducted by the Alaska Department of Fish and Game (ADF&G) for estimating the abundance of herring (*Clupea pallasii*) eggs along a convoluted coastline in southeast Alaska. We show that in this study the H-T estimator, constructed using the selection probabilities estimated by our method, corrects for an overestimation of egg abundance by the sample mean estimate in an example year of herring survey data. In addition, we discuss other design issues such as measuring the size of the survey area in relation to transect–quadrat sampling in general and to the herring study in particular.

SAMPLING IN ABUNDANCE STUDIES ALONG CURVY MARGINS

Alaskan herring spawning study—a motivating example

Along the west coast of North America, Pacific herring (*Clupea pallasii*) spawn annually in shallow coastal areas vegetated with marine algae (e.g., the kelps, Order Laminariales) and seagrasses (e.g., *Zostera* spp.). Surveys of herring eggs deposited in spawning grounds provide an economical method to assess abundance of this ecologically important and commercially exploited species. Egg abundance is a critical component for determining population size and setting fisheries catch limits. Spawn deposition occurs in March, April, or May in southeast Alaska. Egg densities can be extraordinary, reaching 10^8 eggs/m² in places. Herring egg abundance estimates are derived from SCUBA surveys conducted at herring spawning grounds by the ADF&G. Herring surveys must be conducted very quickly before eggs begin to hatch and incorporate sampling sites that are spread across enormous areas. As a result, transect–quadrat sampling becomes a natural choice of study design.

Annually since 1992, ADF&G divers have measured herring egg abundances at herring spawning sites by initiating a transect from a randomly selected point along the coast known to have received herring spawn and conducting a transect perpendicular to the coastline. Within a given transect, the abundance of herring eggs attached to the substrate within a 0.1 m² quadrat is visually estimated every 5 m. The location of the first quadrat is random—the divers close their eyes and toss the square within the first 5 m of eggs to initiate the transect. The divers end a transect when they reach areas with no spawn or the water becomes too deep for typical herring spawn. Thus the length of each transect depends upon the extent of herring spawn and local bathymetry.

Transect–quadrat sampling along curvy habitat margins

Generally, in designing transect–quadrat sampling strategies, one must make four decisions in regard to the placement of the transects and quadrats—(i) the starting locations of the transects, (ii) the orientation of each transect, (iii) how quadrats should be placed along the transects, and (iv) the lengths of the transects.

There are some natural and simple choices in making these decisions when the sampling occurs along a curvy habitat margin as in our herring example. First, the habitat boundary itself provides a repeatable location at which to initiate transects, and drawing the transect starting positions along these boundaries from a linear, uniform distribution is natural. Second, because species composition and abundance often change along elevation or distance gradients that surround the habitat boundary (Didham *et al.*, 1998; Burns, 2004; Power *et al.*, 2004), the perpendicular to the boundary tangent is a logical direction in which to extend sampling transects. As for (iii), along each transect, the quadrats should be placed in such a way that the survey covers all parts of the region of interest. An equidistant design such as the one used in the herring study is the simplest to meet this criteria (given that the starting position of the first quadrat along each transect is random). Finally for (iv), one can let the length of the transects to be either fixed, such as 50 m per transect, or random, such as the one that depends on the result of the measurement as in the herring study. As we will see shortly, this last seemingly innocuous decision has important implications on both the computation of sampling probabilities and the estimation of survey area.

UNBIASED ESTIMATION OF POPULATION ABUNDANCE

Non-uniform sampling coverage and weighted estimation

Most habitat boundaries in nature are irregular or convoluted, and a transect–quadrat sampling scheme such as the one used in the herring study typically leads to non-uniform sampling coverage over the survey area. In the herring study, for instance, the chance for a given point in the survey region to be sampled is determined by the length of the boundary from which this point can be reached. (We say that a point is reachable from a transect origin if a potential quadrat on the corresponding transect covers that point.) As an illustration, in Figure 1, Point 1 is much more likely to be sampled than Point 2.

Due to the non-uniform sampling coverage, simply taking the average of the population density in the sampled quadrats will produce a biased estimate of the true average density if the population's distribution is related in some way to the habitat's boundary geometry. For example, if the population of interest tends to occur in regions closer to the boundary, and if points closer to the boundary are overall more likely to be selected than points farther away, then this simple estimator will overestimate the true average density in the region. Therefore, to obtain unbiased estimates of abundance, one must properly take into account the uneven sampling coverage. Horvitz and Thompson [1952] proposed a simple way to achieve this, namely by weighting the sampled points inversely proportional to their sampling probabilities.

Next we will present the specific form of the H-T estimator for the transect–quadrat sampling design used in the herring study. First, we need to introduce some basic notation. For simplicity, from now on we will refer to the q th quadrat placed along the t th transect as $Q(t, q)$. Let Q_t denote the total number of quadrats placed along the t th sampled transect, T the total number of transects sampled,

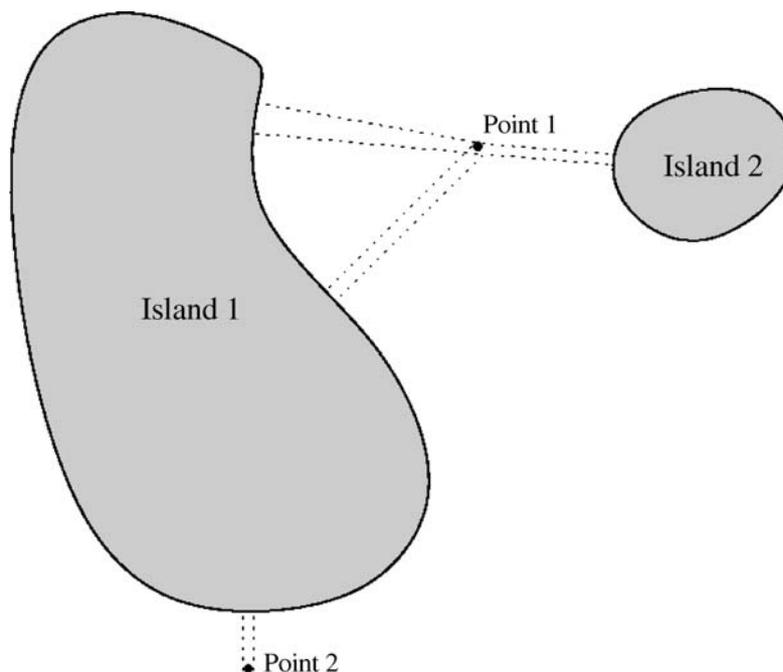


Figure 1. Unequal sampling probabilities. Point 1 is much more likely to be sampled than Point 2

d the distance between two adjacent quadrats on each transect, π_{tq} the sampling probability of the central point of $Q(t, q)$, and finally X_{tq} the measured population density in $Q(t, q)$.

Under the assumption that sampling probabilities vary little for points within the same quadrat, which is typically true when the quadrats are small compared to the scale of the transects, the H-T estimator for average population density in the survey region is

$$\hat{\mu} = \frac{\sum_{t=1}^T \sum_{q=1}^{Q_t} (1/\pi_{tq}) X_{tq}}{\sum_{t=1}^T \sum_{q=1}^{Q_t} 1/\pi_{tq}} = \frac{\sum_{t=1}^T Y_t}{\sum_{t=1}^T Z_t} \tag{1}$$

where $Y_t = \sum_{q=1}^{Q_t} (1/\pi_{tq}) X_{tq}$ and $Z_t = \sum_{q=1}^{Q_t} 1/\pi_{tq}$. The Y_t s, Z_t s and thus $\hat{\mu}$ can all be calculated by computing π_{tq} for all sampled quadrats. (See detailed derivation in Appendix A1.)

Note that because the transects are chosen independently, $(Y_1, Z_1), (Y_2, Z_2), \dots, (Y_T, Z_T)$ are independent even though the quadrats sampled within the same transect are not. (By grouping quadrat level measurements into transect level measurements, we are essentially treating each transect as the sampling unit.) Thus, the variance of the estimator in Equation (1) can be estimated by (Cochran, 1977, p. 155)

$$\widehat{\text{Var}}(\hat{\mu}) = \frac{1}{T} \left(\frac{\bar{Y}}{\bar{Z}} \right)^2 \left(\frac{s_Y^2}{\bar{Y}^2} + \frac{s_Z^2}{\bar{Z}^2} - \frac{2s_{YZ}}{\bar{Y} \cdot \bar{Z}} \right) \tag{2}$$

where $\bar{Y} = \frac{1}{T} \sum_{t=1}^T Y_t$, $\bar{Z} = \frac{1}{T} \sum_{t=1}^T Z_t$, $s_Y^2 = \frac{1}{T-1} \sum_{t=1}^T (Y_t - \bar{Y})^2$, $s_Z^2 = \frac{1}{T-1} \sum_{t=1}^T (Z_t - \bar{Z})^2$, and $s_{YZ} = \frac{1}{T-1} \sum_{t=1}^T (Y_t - \bar{Y})(Z_t - \bar{Z})$. Also note that the unweighted estimator $\hat{\mu}^0$ coincides with the H-T estimator $\hat{\mu}$ when all of the π_{tq} s are equal. Hence we can use Equation (2) to estimate the variance of $\hat{\mu}^0$ as well.

Estimating the sampling probabilities

Dependence on the sampling design

The key to constructing the H-T estimator and its variance estimate is to find the sampling probability, π_{tq} , for the center of each sampled quadrat. Depending on the sampling design, this may or may not be possible to accomplish. In the herring study design, for instance, the sampling probability for each quadrat center depends on several factors among which the most important are (i) the coastline geometry, in particular, the length of the coastal segments from which a transect may potentially have a quadrat covering the point and (ii) the actual distribution of the herring spawn, because the divers only go so far as they think there is no more spawn further along the transect. Because the actual distribution of the spawn is unknown, in principle there is no way to determine for certain whether a quadrat center can be reached even when it does lie along a transect. In other words, the sampling probabilities are random quantities that can neither be known *a priori* nor computed *a posteriori*. In contrast, had the lengths of the transects been fixed and known, calculating the sampling probabilities would boil down to measuring the length of the boundary segments from which the

quadrat centers can be reached. (We will discuss methods for doing this in the following subsection.) This illustrates the important point that when designing sampling strategies that can lead to uneven selection probabilities, one should take into consideration the feasibility of computing the sampling probabilities.

Is the sampling scheme used in the herring study doomed then? Fortunately, no. This is because it can be “embedded” into another design that does use fixed transect length. To see this, first note that if the divers had not stopped at the point they did, (that is, where they believed no more spawning could be further along the transect), but rather had kept going, they would have sampled quadrats with no spawning. (Here we assume they were reasonably experienced and had good judgment.) In other words, the transects could be extended beyond the actual recorded lengths, with the added quadrats all having zero spawning reading. How much should the transects be extended? One simple choice is a fixed length D for which the survey region—the habitat region within distance D to the boundary—covers (almost) the entire population. In the herring study, for example, since we know herring rarely spawn more than 400 m away from the shore, one can choose $D = 400$ m. One can then treat the data as if they were collected in this extended scheme. (Occasionally, some of the sampled transects may fall into narrow channels in the habitat. Extending such transects too far may cause them to reach areas close to the other side of the channel—e.g., the opposite side of a river—where the population is present. A simple way to resolve this problem is to “cap” those transects at the middle of the channel.)

As we extend the transects, the corresponding survey region is also expanded. Accordingly, the population density estimate given in Equation (1) decreases because it estimates the density *in the survey region*. The increase in the size of the survey region and the decrease in the density estimate balance each other, and the product of the two gives an unbiased estimate of the total population size,

$$\hat{N} = \hat{\mu}A_E = \frac{\sum_{t=1}^T Y_t}{\sum_{t=1}^T Z_t} \cdot A_E \tag{3}$$

where A_E denotes the size of the extended survey region (ESR). An estimate of the variance of \hat{N} is given by

$$\widehat{\text{Var}}(\hat{N}) = A_E^2 \widehat{\text{Var}}(\hat{\mu}) \tag{4}$$

Note that this formula relies on the fact that the size of the ESR, A_E , is non-random and hence uncorrelated with $\hat{\mu}$. This is a nice feature of a design with fixed transect length.

Computing the sampling probabilities

If (either by design or by the embedding procedure discussed above) the transect length is non-random so the reachability of the sampled quadrats from the boundary points can be determined, the selection probabilities can be computed. In this subsection we introduce a method for achieving this and discuss some alternatives.

The sampling probability of each quadrat center depends on two geometric quantities of the boundary—(1) its local tangency and (2) the length of its segments. Local tangency determines the reachability and the length of the segments from which each quadrat center can be reached, in turn, determines the selection probability. Thus, the key is to numerically compute these two quantities. To this end, a (uniform) cubic B-spline approximation (Bartels *et al.*, 1987) to the boundary profile is attractive because it produces an analytical representation of the boundary with which both of the two quantities can be easily calculated.

A uniform cubic B-spline approximation to the boundary profile is a twice continuously differentiable curve whose x and y coordinates can, respectively, be parametrized as piecewise cubic polynomials. Each piece between two adjacent pixels is determined by the four adjacent boundary pixels around that segment, and the x and y coordinates of each piece are parametrized as cubic functions of a “speed” parameter $t \in [0, 1]$. (For more detail on cubic B-splines, see Bartels *et al.*, 1987.)

With an approximating B-spline, numerical computation of the sampling probabilities can proceed as follows. First, divide the approximating B-splines into tiny pieces—for example, we let each piece be 0.002 pixel-width long for the herring study. The choice of this “unit” length is arbitrary up to the extent that they must be small enough so that the boundary segments can be treated as points for numerical purposes. Within each of these tiny segments the edge is approximately straight, so the tangency of the boundary in each of these segments is well defined and can be attained from taking the ratio of the derivatives of the two coordinates with respect to the speed parameter. The tangency determines the direction of the corresponding transect. With this we can then algorithmically translate the reachability of any given quadrat center from a boundary segment into the following criteria: (1) the distance from the point to the transect is less than half of the side length of the quadrats and (2) there is no physical barrier (e.g., deep water) that would prevent the surveyors from sampling the entire transect. Summing up the length of all the tiny segments satisfying the above criteria gives the sampling probability of that quadrat center (up to a constant).

There are alternative ways to computing the sampling probabilities. One example is to use local linear regression. More specifically, one can find the local tangency of the boundary profile by fitting a simple regression line through a sliding window of boundary pixels. The appropriate window size needs to be very carefully chosen in that windows too wide cannot effectively capture local curvature while those too narrow are more prone to local variability.

One may also consider using simulation to estimate the selection probabilities—simply repeat the sampling procedure on a computer many times and see what fraction of times each quadrat center is sampled. Despite its conceptual simplicity, simulation is not easier to implement than methods such as splines and regression in this context. This is because in carrying out the simulation, one would still need to compute (1) the length of boundary segments in order to simulate the transect origins and (2) the local tangency of the

boundary profile at the simulated transect origins to determine the transect direction. Therefore, one would still need to implement some tools such as spline approximation at the core of the simulation procedure.

Moreover, in most studies, transects are typically sparsely located along the boundary. In our herring example, for instance, only 42 transects were sampled along a coastline of about 148 km. Hence, when doing simulation, one must sample transect origins conditional on the small fraction of boundary from which the sampled quadrats can potentially be reached, for otherwise few of the simulated data points will cover the actual sampled data. (As an analogy, imagine using simulation to estimate the relative chance of sampling a value in $[0.3122, 0.3125]$ versus one in $[0.5003, 0.5004]$ from a uniform $[0, 1]$ distribution.) However, determining what fraction of boundary is relevant to a degree that would conquer the sparsity problem would involve not much less programming effort than the spline approach. For these reasons, we believe simulation is not a particularly desirable way to compute selection probabilities for the sampling design under consideration.

Measuring the survey area

When the total population size is of interest, one also needs to estimate the size of the survey region. With fixed transect length, the survey region is fixed and known, and the size of this region can be measured by counting the corresponding pixels on a digital map. For the herring study, for instance, more than tens of thousands of pixels fall into the survey region, so the area can be estimated with very good accuracy. The ease of measuring the survey region is in fact a nice side product of using a fixed transect length (or using the "embedding" method introduced earlier).

In contrast, for designs with random transect length, the survey region is unknown and must be estimated. One common method is by constructing a polygon with the outer points of the sampled transects as vertices. However, in the context of sampling along a curvy boundary, this approach has some serious drawbacks. First, because the transects are typically sparse and the variance in the transect length is often large, the variability in the polygon area estimate can be tremendous. Second, the sparsity of the transects often makes constructing polygons impossible when the habitat boundary consists of small disconnected pieces. For example, in the herring study, a considerable portion of the coastline comes from small islands, almost none of which received more than two transects. Thus, it is impossible to construct polygons for those islands.

A simple alternative to the polygon approach is to estimate the survey area by taking the product of the boundary length and the average length of the sampled transects. In fact, ADF&G has used this approach in their analysis of the herring data in the past. However, depending on the convexity/concaveness of the boundary profile, this approach can introduce bias into the area estimate.

APPLICATION TO DATA

In this section, we apply our method to the ADF&G herring spawn survey data collected in Sitka Sound in southeastern Alaska. We used egg counts for 637 sampled quadrats along 42 transects randomly selected from 148 km of coastline that received herring spawn in 2004. The numbers of quadrats included in each of the 42 transects range from 3 to 65 with an average of 15 and a standard deviation of 13.5. The map available for this region is a NOAA nautical chart at an approximate scale of 1:25000. We applied the "embedding" method introduced earlier and extended the transects to have a common length $D = 400$ m. We then used the B-spline method to compute the selection probabilities, and in turn constructed the H-T estimator.

Results

The weights for the H-T estimator, $1/\pi_{tq}$, are presented in Figure 2. Note that they are rescaled so that 1 represents the weight for a quadrat if the coast were a straight line and the sampling on the spawning region were uniform. They range from 0.074 to 11.5, and most are smaller than 1. An intensity map of the selection probabilities shows the effect of spatial location in this instance (Figure 3): most quadrat centers close to the coast have significantly greater chances of being sampled than if the coastline were a straight line.

Table 1 presents the estimates of the egg density and the total number of eggs using four different methods: (1) unweighted estimation on the ESR, (2) H-T estimation on the ESR, (3) unweighted estimation on the (unextended) survey region (SR), and (4) H-T estimation on the SR. Note that because there is no way to attain the sampling probabilities for the original (unextended) survey, we used the corresponding weights from the extended survey for constructing the H-T estimator on the SR.

On both the ESR and the SR the unweighted estimator overestimates the population density. This bias due to ignoring the unequal sampling probabilities is substantial—it is about 85% of the root mean squared error (RMSE) on the ESR and about 48% of the RMSE on the SR. (The RMSEs are computed by treating the H-T estimates as the true values.) This is intuitive in that expanding the survey region increases the variability of the selection probabilities, and therefore, ignoring these unequal probabilities leads to larger bias on the ESR than the SR.

Another interesting observation is that both the H-T and the unweighted methods produce much higher estimates for the total egg count when applied to the SR. This is mainly because the estimate for the (unextended) survey area, which is attained by taking the product of the total coastal length and the average transect length, is probably much larger than the true survey area. This overestimation is likely due to both the bias in the way of estimating the area and the high variability in the random transect length.

One potential concern about the embedding procedure is its impact on the variance of the population estimate \hat{N} . In particular, in the absence of strong prior knowledge on how to choose the extended transect length, one may wonder whether a poor choice of this length could lead to inflated variability in the estimate. To check this, we constructed a sequence of ESRs by changing the maximum

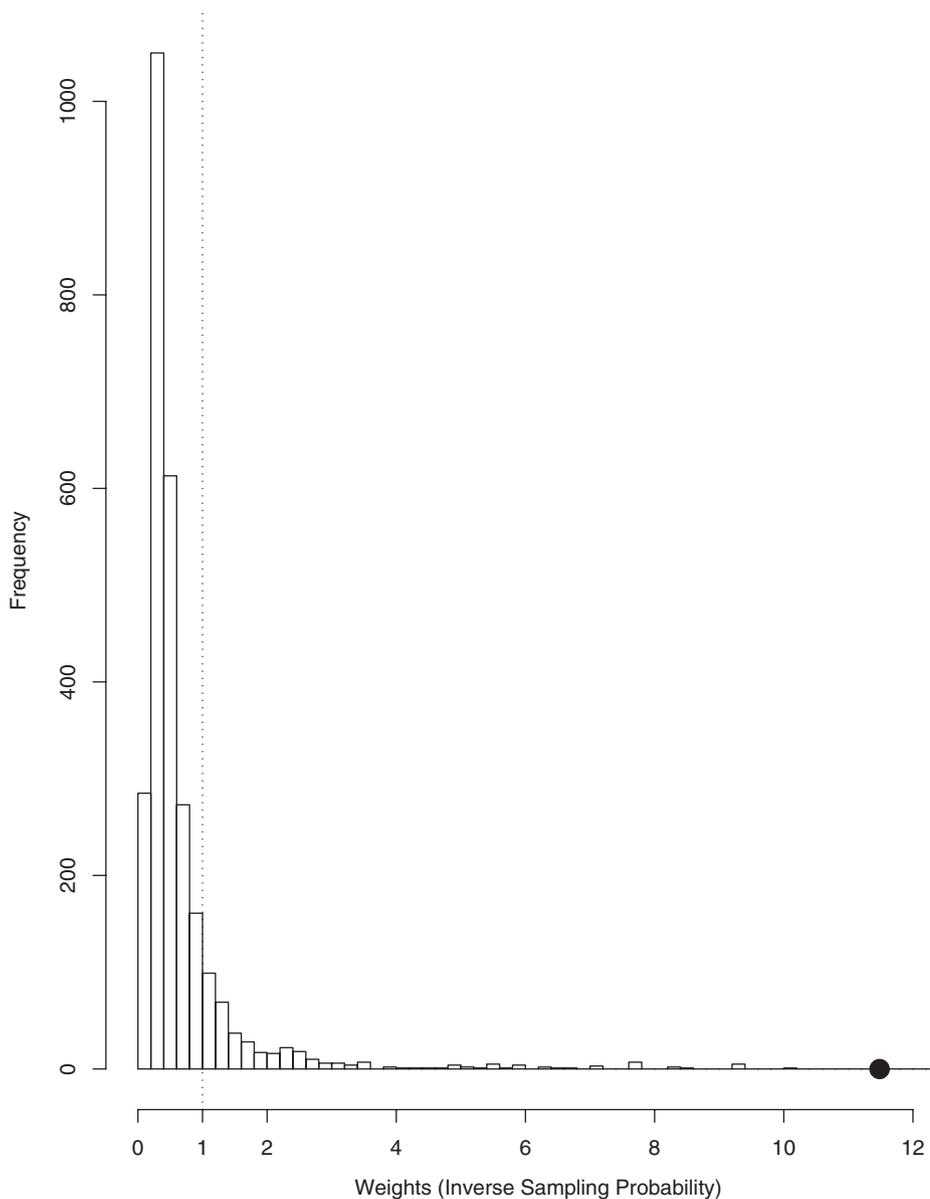


Figure 2. Histogram of the weights (inverse sampling probabilities of the central points) of quadrats from the 2004 herring spawning data set. The black dot represents the quadrat with the highest weight. Values to the left of the dashed line indicate those that had a higher sampling probability than a point along a straight coastline

transect length from 325 m (i.e., 65 quadrats), the observed length of the longest transect, up to 525 m (i.e., 105 quadrats), and found that the H-T estimate for the total egg count and its standard error were stable over this generous range of ESRs (Table 2).

DISCUSSIONS

The simple transect–quadrat sampling strategy used in the herring study, coupled with our methods for computing the selection probabilities and measuring the survey region, provides an effective, economical and general recipe for unbiased estimation of abundance along convoluted habitat boundaries. While our results indicate that ADF&G’s traditional herring survey estimation method can lead to biased estimates of the population size, this does not necessarily imply the fishery has been poorly managed as a consequence.

In many applications, the investigator may not be directly interested in the absolute size of the population, but rather in the comparison of multiple population estimates. For example, one may be interested in the change of population over time or trend estimate (temporal comparison), or in the difference across different habitats (spatial comparison). Because different habitats involve distinct boundary geometry, ignoring the unequal selection probabilities will lead to serious confounding in the comparison across

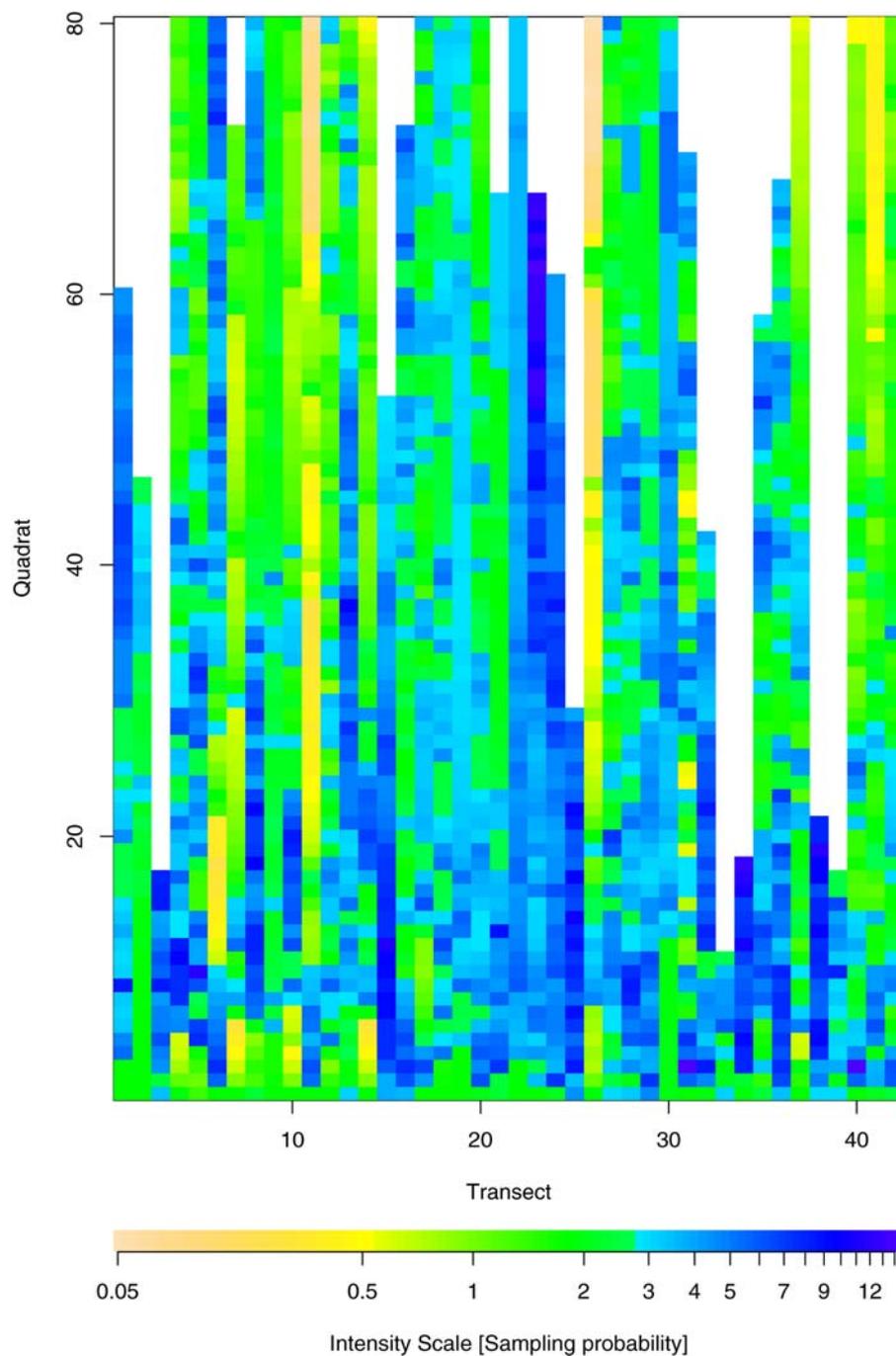


Figure 3. An intensity map of the sampling probabilities for quadrat centers. The probabilities have been rescaled so that “1” indicates the chance of being sampled if the coast were a straight line and the sampling over the survey region were spatially uniform. This figure is available in color online at www.interscience.wiley.com/journal/env

habitats. On the other hand, if the comparison is strictly temporal—sampling occurs along exactly the same boundary at different time points—the bias in the estimates is not of much concern provided that it stays *constant* (proportionally) over time. But in real applications, the distribution of the population is most likely changing over time, and therefore, constant bias is almost always too strong an assumption to make. For example, for the herring study, even along the same coastline, the actual spawn distribution over the region changes from year to year. Therefore, ignoring the unequal probabilities will introduce varying bias into the estimates across years, thereby confounding the trend estimate.

In temporal comparisons or trend estimation, the variability of the point estimates plays a very important role. Indeed, if this variance is large, the uncertainty in comparisons will be even larger, making all but the most significant difference or trend undetectable. This suggests that in such studies a fixed survey region design can be particularly favorable. With the survey region being fixed and identical

Table 1. Estimated egg density and total egg count by method (standard errors in parentheses)

	On the ESR		On the SR	
	Unweighted	H-T	Unweighted	H-T [†]
Egg density (1000/m ²)	131 (22)	95 (23)	570 (73)	530 (76)
Coast length (km)	146	146	146	146
Spawning area (km ²)	—	—	11.1*	11.1*
Extended spawning area (km ²)	40.8	40.8	—	—
Total egg count (10 ¹⁰)	534 (90)	390 (92)	633 (81) [‡]	588 (87) [‡]

* The true spawning area is unknown, and probably smaller than 11.1 km², which is the product of the total coastal length and the average transect length.

[†] The standard error for the estimated total egg count on the SR is computed assuming that the contribution to the variance of the estimated total egg count from the variance of the estimated spawning area is dominated by the uncertainty in the estimated egg density.

[‡] Because the actual spawning region is unknown, in theory there is no way to compute the appropriate weights for the H-T estimator on the SR. Here we use the weights computed from the ESR as an approximation.

Table 2. Estimated total egg count (/10¹⁰) using H-T estimation for different ESRs

Q _M *	65	70	75	80	85	90	95	100	105
Egg count	424	417	401	390	387	393	392	392	395
Standard error	99	95	92	92	91	92	93	94	95

* Q_M is the maximum number of quadrats in a transect, which defines our ESRs.

across the different time points, one can make the temporal comparison entirely based on the density estimates, eliminating the (often substantial) uncertainty that would have arisen from the survey area estimate.

Of course, a design with fixed transect length can be more expensive to implement. In the herring study, for example, costs would increase if the divers were asked to swim 400 m along each transect. In such cases, the embedding method demonstrated in this work can be adopted.

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Appendix A: Deriving the H-T estimator

We use a pair of coordinates (s, r) to represent a point in the sea, where s indexes the position of the corresponding transect origin on the coast and r the perpendicular distance of the point to that transect origin. Because a point in the sea could have more than one corresponding origin points on the coast (see Figure 1 in the paper), different pairs of coordinates could refer to the same spot. Next, we let $p(s, r)$ be the sampling probability for Point (s, r) and $X(s, r)$ the population density at Point (s, r) . Now if we let A_0 be the area of each quadrat, then under the assumption that sampling probabilities vary little within each quadrat, the Horvitz–Thompson estimator can be computed as

$$\begin{aligned} \hat{\mu} &= \frac{\sum_t \sum_q \int_{Q(t,q)} X(s,r) \cdot 1/p(s,r) dA}{\sum_t \sum_q \int_{Q(t,q)} 1/p(s,r) dA} \\ &\approx \frac{\sum_t \sum_q 1/\pi t q \int_{Q(t,q)} X(s,r) dA}{\sum_t \sum_q 1/\pi t q \int_{Q(t,q)} dA} \\ &= \frac{\sum_t \sum_q (1/\pi t q) X_{tq} A_0}{\sum_t \sum_q (1/\pi t q) A_0} = \frac{\sum_{t=1}^T \sum_{q=1}^{Q_t} (1/\pi t q) X_{tq}}{\sum_{t=1}^T \sum_{q=1}^{Q_t} 1/\pi t q} \end{aligned}$$

Appendix B: Extracting and thinning coastline

The first step to fitting a spline approximation to the coastline profile is to extract it from the map. Extracting the coastline would be a trivial matter if the map had a separate layer identifying the coast or it used a unique color to indicate coastal points. For the herring study, however, the map was a single digitized image of Southeast Alaska. Both the coastline and all the legends and comments are represented by black pixels in the image; land, shallow water, and deep water, on the other hand, are encoded as camel, blue and white pixels respectively. Also, in the map the coastline had a width of two to three pixels.

To extract the coastline we distinguished the coastal pixels from all the other black pixels, and that required some definition of a “coastal pixel”. The appropriate definition depends on the specific properties of each map. For the herring study, the criteria we chose was that if the $5 \text{ pixel} \times 5 \text{ pixel}$ square centered at a black pixel included both land and water, then that black pixel in the middle was considered a coastal pixel. Picking out coastal pixels based on this rule produces a 2–3 pixel wide coastline. Figure 1A illustrates the effect of this algorithm on a typical portion of the map. Overall, this algorithm does a satisfactory job in identifying the coastal points.

After extracting the coastal pixels, the next step was to thin the coastline to one-pixel wide. There are standard 2D image processing algorithms for this particular purpose that preserve the Euler number of the coastline image (Pratt, 1991). Such algorithms are implemented in standard image processing packages such as the image processing toolbox in MATLAB, which we used. The result of

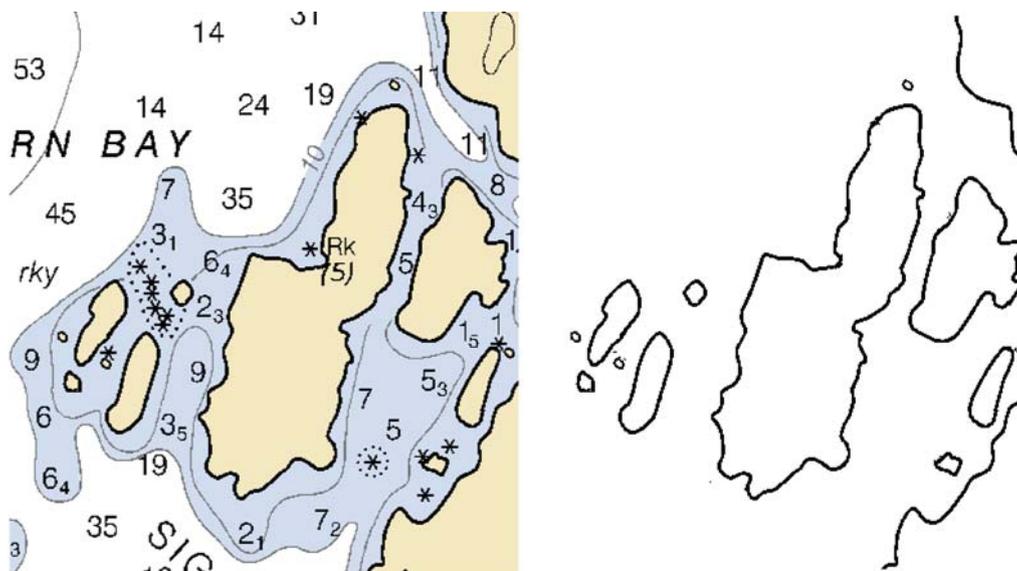


Figure A1. Coastline extraction of a portion of the map. This figure is available in color online at www.interscience.wiley.com/journal/env

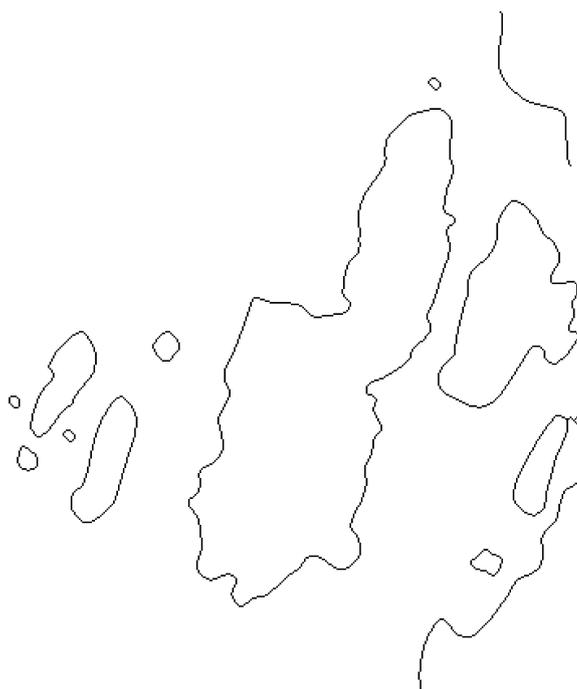


Figure A2. A thinned version of the coastline in Figure A1

the thinning procedure when applied to the coast segment in Figure A1 is presented in Figure A2. After obtaining a one-pixel wide coastline, we can then fit cubic uniform B-spline to it.

Reference for Appendices

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