Inferring surface time of Minke whales from inter-surfacing interval data using a hidden Markov model

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ABSTRACT

Surfacing rate data of Minke whales is an important factor used in the abundance estimates of Minke whale (*Balaenoptera acutorostrata*) stocks, both in aerial and vessel based surveys. Today, most abundance estimates of Minke whales rely on VHF-transmitters data rather than visual data. Visual data collected from land has the advantage of being relatively cheap to collect, which allows data to be collected from a larger number of individuals while causing no effect on the surfacing rates of the animals being studied, hence limiting biases. In this study, individual follows of Minke whales were conducted from a land-based station in Faxaflói bay, Iceland, and data on inter-breath intervals (IBI) were collected. Two distinct dive types were present within the surfacing data, which we defined as regular dives and deep dives. Those emerged from two different biological processes: whales spending time at the surface and whales engaging in foraging activities. A hidden Markov model was used to identify and define the density distribution of IBI as the observation state of these two hidden diving processes. Regular dives had a mean surfacing interval of 43 seconds (SD=44.8) and deep dives had a mean surfacing interval of 155 seconds (SD=115.1). The transition probabilities between the two dive types were estimated, from which the relative proportion spent in each dive type could be inferred. Minke whales perform regular dives during 62% and deep dives during 38% of their time. The relative proportions spent in each dive type can be used as estimates of how much time a whale will be typically at the surface available to be detected during cue counting surveys and to estimate the odds that a whale is in a long dive and therefore unlikely to be detected.

Data was also collected from commercial whalewatching boats in the same bay, and were analysed together with the land based data to measure the effect of whalewatching boat interaction on Minke whale surface intervals. The proportion of time spent in deep dives decreased from 38% to 14% during interactions with whalewatching boats, while regular dives increased from 62% to 86%.

The inter-surfacing interval used in abundance estimates of Minke whales in the North Atlantic today is derived from VHF-transmitter data and is about 77 seconds. Our mean values of surface intervals lies below and above this mean, which raises the question if a single mean value of surfacing interval can be used to make reliable abundance estimates of Minke whales, as both the dive type and the presence of vessels is likely to affect this value.

INTRODUCTION

Dive time data plays an important role in whale abundance and density estimations. Traditional sampling techniques rely on cue counting, the detection of a whale surfacing, and therefore estimates need to be inflated for whales that could not be detected because they were underwater. Inter-breath interval data is needed to assess how long a whale will typically spend at the surface available to be detected. The total abundance estimates of Minke whales (*Balaenoptera acutorostrata*) in the North Atlantic (Schweder et al. 1997; Skaug et al. 2004; Bøthun, Skaug & Øien 2009) relies on this inflation factor and in turn is used directly in the management program of the North Atlantic Marine Mammal Commission (NAMMCO) and the International Whaling Commission (IWC) to determine sustainable catch quotas. The abundance estimates of Minke whales are based on shipboard survey data and the collection of Minke whale surfacing data has been part of these surveys. The value that is currently used in the abundance estimates of Minke whales in the North Atlantic is 48.56 blows per hour (BPH), or a mean inter-breath interval (IBI) of 77.22 seconds (Øien, Bøthun & Kleivane 2009). This estimate is based on data collected from 20 VHF tagged Minke whales between 2001 and 2008 (Øien, Bøthun & Kleivane 2009).

The use of dive time data obtained from VHF transmitters has been criticised for causing a positive bias in the abundance estimate of Minke whales, as the VHF method detects more surfacing than what would normally be visible for the observers conducting the sighting surveys. This results in the data collected in the sighting surveys to be subject to human measurement errors (which gives higher surface rates and lower inter-breath intervals), which therefore cannot be directly compared to the VHF data (IWC 2008; Skaug, Bøthun & Øien 2009). Further, VHF transmitters can also produce false surfacing indications even if the whale doesn't surface when the tag antenna is close to the surface. VHF based dive time data are also relatively expensive to collect, so the surface rate estimates are all based on relatively few replicates in terms of animals. Because of this, individual variations in surfacing patterns are going to have a large influence on these estimates (Stern 1992), which is also one of the conclusions drawn from these studies (Øien, Bøthun & Kleivane 2009). Few individual replicates will also limit the data collection time period, which can result in bias due to seasonal variations in Minke whale surfacing patterns (Stockin et al. 2001).

An alternative to the VHF transmitters for collecting Minke whale dive time data is visual observations (Stern 1992; Stockin et al. 2001; Curnier 2005). Data from visual observations benefit from being relatively cheap to collect, especially if a land based research platform is used, so data from many individuals can be collected. Another benefit is that the dive time data can be directly compared to the data obtained from sighting surveys, since both include the same kind of measurement errors. However, the fact that a visual observer might miss surfacing, or mistakenly combine surfacing from several animals in the same area, will make the dive time data less accurate from a biological point of view (Øien, Bøthun & Kleivane 2009). The measurement errors are likely to be larger for longer follows, since the probability of missing surfacing increases with increased follow length. Even though visual follows of Minke whales are generally quite short in length in comparison to VHF follows, which can obtain data from the same animal for periods of a few hours up to several days in length, short follows can also induce bias in the measurement estimates, due to selection bias (Williams, Trites & Bain 2002b; Øien, Bøthun & Kleivane 2009).

This study presents an approach for estimating not only reliable Minke whale surfacing rates from dive time data obtained from visual observations, but more importantly the ratio of time a whale will spend unavailable for detection. By using a hidden markov model, which estimates the transition probability between different dive types, identified from the dive time data, the length of the follow becomes less important. Thus, large sample sizes can be collected from many individual whales. We demonstrate the use of this method on Minke whale dive time data collected from a land based research platform in Faxaflói bay Iceland.

The land based data is also compared to dive time data collected from commercial whalewatching boats, to measure the effect of boat presence on Minke whale surfacing rates. This is a factor that is currently not taken into consideration in sighting surveys even though studies show that the surfacing rates of cetaceans, including mysticetes, can be affected by boat presence, by causing either an increase (Nowacek, Wells & Solow 2001a; Lusseau 2003; Schaffar et al. 2009) or decrease (Stone et al. 1992) in inter-breath intervals. A potential effect of the survey vessel on the surfacing rate of Minke whales could cause a bias in the estimate of the detection probability of Minke whales, which could result in a bias the abundance estimates.

METHODS

Data on Minke whale surfacing time was collected from land and sea between June and September 2010 in Faxaflói bay, Iceland. Continuous individual focal follows (Altmann 1974) of Minke whales were conducted both from a land based research platform and from commercial whalewatching boats, constituting time series of control and impact data respectively. On land, observations were carried out from a 27 meter tall lighthouse (64°04’56’’N, 22°41’24’’W) located in Garður on the northern tip of the Keflavik peninsula. One researcher was tracking the whale, using either binoculars or a theodolite (Wild T16), and recording the time of every surfacing. These surfacing times were entered into a computer in real time by another researcher. Focal animals were chosen randomly and if another whale was in close proximity of the focal animal the follow was terminated to avoid measurement errors from sampling several whales.

From the surfacing times, Minke whale inter-breath intervals (IBI) were estimated as the time elapsed between two consecutive surfacing. A multi-state model was used to analyse the time series data. A multi-state model describes how an individual moves between a series of states in continuous time. The movement between states is represented by a transition probability matrix, which can be effected by both internal and external covariates (W). In a hidden Markov model (HMM), the states (S) are not observable, and the transition probability between the states must instead be inferred from time series of observed behavioural data (B) (Fig. 1). The observed data is linked to the hidden states by their density distributions being conditional on the hidden states. The time series of observed behaviours, along with the covariates, are used for model inference and parameter estimation.

A HMM was fitted to the Minke whale inter-breath data using the msm package in R 2.12 (R Development Core Team 2010), which allows Markov models to be fitted to processes which are continuously observed. Inter-breath intervals were fitted as a function of time (the time elapsed from the beginning of the follow in seconds), conditional on Follow, so that each individual follow was treated as an independent time series. Follows needed to be of a minimum length of two dive intervals to constitute a time series. For Minke whale dive behaviour in Iceland, the process model of interest is not the observable time series of inter-breath intervals (B), but the transition probability between the hidden dive types (S) and the effect of whalewatching boats (W) on this probability (Fig. 1). The msm package requires initial values for the number of hidden states in the data, as well as the density distribution around these states. The number of states and their initial density distributions (mean and SD) were given from visual inspection of density histograms of the inter-breath interval data. Given that there are several dive types within the diving pattern of Minke whales, we assumed no restrictions in transferring between these different states. Thus we set all the initial transition probabilities to 1. We assumed the IBI to be the mixture of two normal distributions. The maximum likelihood of the density distribution of the two states (dive types) and the transition probability matrix was estimated from the observed data, starting from the initial values obtained from data exploration. The maximum likelihood is the product of probabilities of transition between the hidden states, over all the follows and observation times.

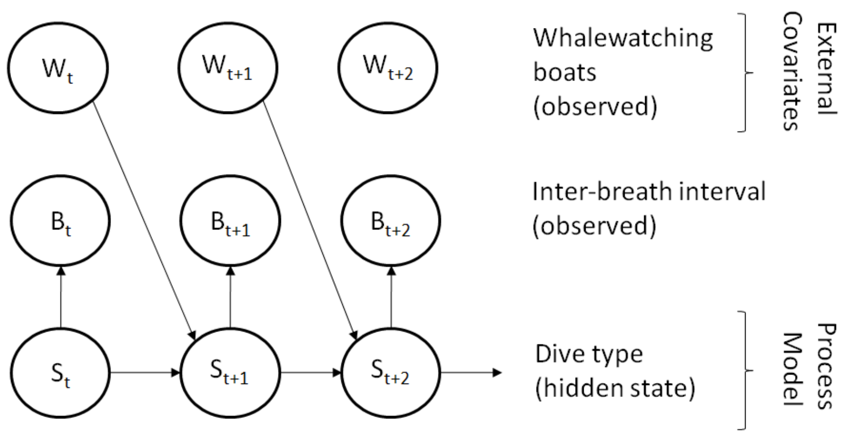

Fig. 1. *The structure of the hidden markov model developed for Minke whales.*

From the transition probability matrix of the fitted model it was possible to estimate the expected total length of stay in each state (dive type), from which the relative proportions that Minke whales spend in each dive type could be calculated. To avoid extrapolation, the time periods used in these estimates were the maximum follow lengths for the control and impact follows respectively. The effect of vessel presence on Minke whales dive types was investigated by including vessel presence as a covariate in the HMM and then comparing the relative proportions of the two dive types for the control and impact data.

RESULTS

A total of 88 hours of Minke whale respiration data was collected during 67 days between May 29 and August 28 2010, in Faxaflói bay, Iceland. 5574 surfacing times of Minke whales were recorded (1828 control, 3746 impact) from 545 follows (227 control, 318 impact), from which 4943 inter-breath intervals could be calculated (1576 control, 3367 impact). 61 follows had to be excluded from the analysis as these only included one estimate of inter-breath interval, which was not enough to constitute a time series. The effective sample size used in the analysis were 4882 inter-breath intervals (1518 control, 3364 impact) from 484 follows (169 control, 315 impact), which gives an average of ten inter-breath intervals per follow (SD=9.5).

Visual inspection of the density distribution of inter-breath intervals and logged inter-breath intervals of Minke whales revealed two distinct dive types for Minke whales in Faxaflói bay (Fig. 2). The first state had a mean around 20 seconds (SD~40), and was referred to as regular dives. The second state has a mean around 150 seconds (SD~70), and was referred to as deep dives. The visually inferred density distributions of the two states were used as initial state values in the HMM.

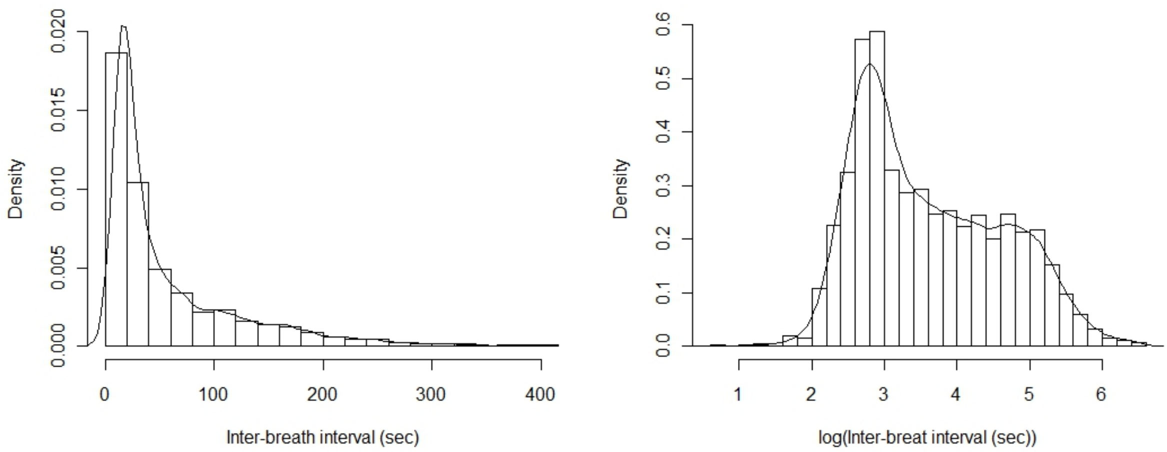

Fig. 2. *Density distribution of inter-breath interval and log(inter-breath interval) of Minke whales in Faxaflói Bay, Iceland.*

Given the observed data, the HMM estimated the most likely density distribution of regular dives to be slightly higher than the expected (initial) distribution, with a mean of 42.6 seconds (95%CI=40.93-44.23) and a standard deviation (SD) of 44.8 (95%CI=43.56-46.18). Deep dives had a density distribution with mean 154.59 seconds (95%CI=143.49-165.69) and standard deviation 115.13 (95%CI=108.77-121.87).

The relative proportions of time that Minke whales spend in the two dive types were estimated to 61.6% (95%CI=54.8-68.3) and 38.4% (95%CI=31.7-45.2), for regular dives and deep dives respectively (Fig. 3). Given that Minke whale surfacing patterns consists of several shorter dives followed by a single longer dive (Stern 1992), these proportions corresponds to a surfacing pattern of five to six regular dives followed by one deep dive, in the absence of boats.

The transition probability between dives types were significantly affected by the presence of whalewatching boats, which resulted in a change in relative proportions of the two dive types (Fig. 3). Minke whales spent less time performing deep dives in the presence of whalewatching boats (Chi-square two sample test, X^2=666.86, df=1, p<0.001), with deep dives decreasing in relative proportion to only 13.8% (95%CI=11.9-15.8), while regular dives increased significantly to 86.2% (95%CI=84.2-88.1) during interactions with whalewatching boats (Chi-square two sample test, X^2=666.86, df=1, p<0.001) (Fig. 3). This change in dive pattern corresponds to 23 regular dives followed by a single deep dive.

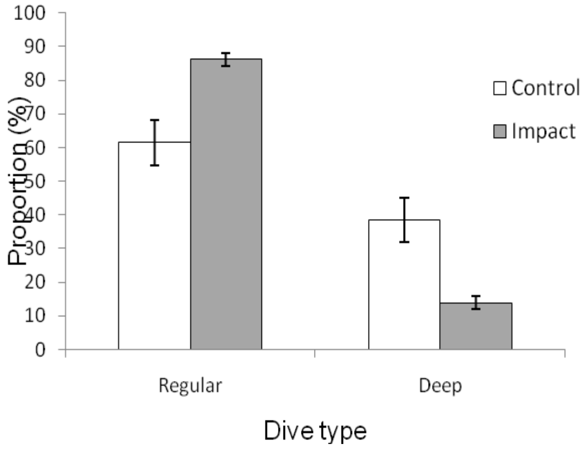

Fig. 3. *Relative proportions of time spent performing each dive type during control (no whalewatching boats present) and impact (whalewatching boats present) situations. Error bars represent 95% confidence intervals.*

DISCUSSION

The results of our HMM model shows that Minke whales in Faxaflói bay perform two types of dives, regular dives with a mean inter-breath interval of 43 seconds and deep dives with a mean inter-breath interval if 155 seconds. If we estimate the mean inter-breath interval straight form the dive time data, we get a mean of 76.9 and 57.3 seconds for control and impact situations respectively. If we calculate the mean based on the estimates of the hidden states and their relative proportion, we end up with a mean of 85.6 and 58.1 seconds, for control and impact situations respectively. Our HMM thus provide a higher estimate of the mean inter-breath interval during control situations than the raw data. The likely explanation for this is that the estimate from the raw data is sensitive to short follow durations, which will bias the estimate towards lower values, since it's a higher chance that the initial dive type measured in a follow will be a regular dive (Williams, Trites & Bain 2002b; Øien, Bøthun & Kleivane 2009). This bias can be avoided by using the dive time estimate from the HMM, since this is estimated from the transition probabilities derived from the time series (follows), and is thus not affected by the initial dive type of the animal.

We can compare our estimates of inter-breath intervals with those published from other studies (Table 1). The literature shows relatively little consistency between studies in estimates of Minke whale surfacing rates. Studies using visual observations to record surfacing rates show large variations between studies, even within the same geographical region. The VHF recorded data show less variation between studies, with the exception of one study carried out in Iceland (Joyce, Sigurjónsson & Vikingsson 1990) (Table 1). Since this estimate was based on only one individual, it is possible that individual variations in surface rates might be the cause of this discrepancy in estimates between Iceland and the Northeast Atlantic, which has been shown for Californian Minke whales (Stern 1992). Again, this highlights the problem of few replicates when using VHF transmitters to collect surface rate data. Californian Minke whales seem to have relatively longer inter-breath intervals than the Atlantic samples (Table 1). Whether or not this difference is due to geographical variations in surfacing rates of Minke whales (Stern 1992) or due to individual variations in seasonal changes in surfacing rates (Stockin et al. 2001) is hard to conclude. Minke whale surface rates if also affected by the activity of the animal, with foraging Minke whales having relatively shorter inter-breath intervals than travelling animals (Baumgartner 2008), especially when surface feeding (Curnier 2005) (Table 1). Blix and Folkow (1995) also showed that Minke whales had longer inter-breath intervals during resting compared to other activities. Foraging activity is likely to follow the diurnal and seasonal availability of prey species, which might explain why Minke whales show diurnally or seasonally changes in surfacing rates (Joyce 1982; Joyce, Sigurjónsson & Vikingsson 1990; Folkow & Blix 1993; Stockin et al. 2001) (Table 1). Surfacing rates during foraging is in turn likely to be affected by the animals foraging strategy, which is influenced by the prey preference of that particular area (Blix & Folkow 1995).

There is also the potential of the research vessel affecting the diving behaviour of Minke whales, which was shown to be the case in this study for the boat based research platform. Based on the assumption that animals perceive humans as predators and respond to human presence in the same way as in the presence of natural predators (Frid & Dill 2002), Minke whales should respond similarly to other types of boats (e.g. survey vessels). In the presence of whalewatching boats, the transition probability between dive types, and therefore their resulting relative proportions, changed which resulted in a decrease in mean inter-breath interval of Minke whales from 85.6 seconds to 58.1 seconds. All studies presented in this paper used boats to collect surfacing rates of Minke whales (Table 1). If the research platform itself affects the surfacing rate measurement, which was the case in this study, it is possible that all these estimates are in some extent biased towards lower estimates and that this is a factor in g(0) estimation.

Table 1. *Summary of Minke whale inter-breath interval (IBI) data, recorded from visual observation and VHF radio transmitters, from different geographical regions, and during different activities and times.*

Method	Location	Time	Activity	IBI(sec)	Source
Visual	Iceland	Daytime	Feeding	68.3	(Gunnlaugsson 1989)
Visual	Northeast Atlantic	Daytime	N/A	68.7	(Joyce et al. 1989)
Visual	Northeast Atlantic	Daytime	N/A	85.7	(Øien, Folkow & Lydersen 1990)
Visual	Northeast Atlantic	Daytime	N/A	78.9	(Folkow & Blix 1992)
Visual	Northeast Atlantic	Daytime	N/A	46.3	(Skaug & Bøthun 2003)
Visual	Northeast Atlantic	Daytime	N/A	47.8	(Skaug, Bøthun & Øien 2009)
Visual	West Greenland	Daytime	N/A	78.1	(Heide-Jørgensen & Simon 2007)
Visual	Northwest Scotland	Daytime	N/A	66.1	(Stockin et al. 2001)
Visual	Northeast Scotland	Daytime	All	69.9	(Baumgartner 2008)
Visual	Northeast Scotland	Daytime	Feeding	62.1	(Baumgartner 2008)
Visual	Northeast Scotland	Daytime	Foraging	69.0	(Baumgartner 2008)
Visual	Northeast Scotland	Daytime	Travelling	83.7	(Baumgartner 2008)
Visual	California	Daytime	N/A	93.3	(Stern 1992)
Visual	California	Morning	N/A	98.4	(Stern 1992)
Visual	California	Afternoon	N/A	90.9	(Stern 1992)
Visual	St Lawrence, Canada	Daytime	All	54.8	(Curnier 2005)
Visual	St Lawrence, Canada	Daytime	Near-surface feeding	52.0	(Curnier 2005)
Visual	St Lawrence, Canada	Daytime	Deep feeding	52.5	(Curnier 2005)
Visual	St Lawrence, Canada	Daytime	Travelling	71.2	(Curnier 2005)
Visual	St Lawrence, Canada	Daytime	Surface feeding	43.5	(Curnier 2005)
Visual	Antarctica	Daytime	N/A	75.0	(Ward 1988)
Visual	Antarctica	Morning	N/A	83.3	(Joyce 1982)
Visual	Antarctica	Midday	N/A	113.2	(Joyce 1982)
Visual	Antarctica	Afternoon	N/A	90.9	(Joyce 1982)
VHF	Iceland	All	N/A	54.1	(Joyce, Sigurjónsson & Vikingsson 1990)
VHF	Iceland	Daytime	N/A	59.0	(Joyce, Sigurjónsson & Vikingsson 1990)
VHF	Iceland	Night time	N/A	48.1	(Joyce, Sigurjónsson & Vikingsson 1990)
VHF	Northeast Atlantic	Daytime	N/A	74.6	(Folkow & Blix 1993)
VHF	Northeast Atlantic	Night time	N/A	89.4	(Folkow & Blix 1993)
VHF	Northeast Atlantic	Daytime	All	76.9	(Blix & Folkow 1995)
VHF	Northeast Atlantic	Daytime	Feeding	70.6	(Blix & Folkow 1995)
VHF	Northeast Atlantic	Daytime	Travelling	82.2	(Blix & Folkow 1995)
VHF	Northeast Atlantic	Daytime	Resting	101.7	(Blix & Folkow 1995)
VHF	Northeast Atlantic	Daytime	N/A	77.2	(Øien, Bøthun & Kleivane 2009)

The large variations in surfacing rates between studies show that the diving behaviour of Minke whales is highly dynamic. Thus, it is unlikely that the diving behaviour of Minke whales can be captured by a single mean of the surfacing rates. Since diving behaviour is a process reflecting both internal (e.g. activity) and external (e.g. boat presence) covariates, this needs to be incorporated into the inference of inflation factors. The HMM captures this process and can be further extended to include more covariates, such as activity, diurnal and seasonal changes, foraging strategy, etc. The HMM approach is robust against both missed surfacing and potential biases derived from short or long follow durations, respectively, which has been the main criticisms against using visual observations to estimate surfacing rates (Øien, Bøthun & Kleivane 2009). The HMM approach therefore provide a way forward to understanding the diving behaviour of Minke whales, and other species, to provide more accurate estimates of surfacing rates. This study presents a relatively cheap alternative to VHF transmitters for collecting large samples of accurate data on Minke whale surfacing rates from land and sea. The land based method further benefits from the fact that the observer is unlikely to affect the measured behaviour of the study animal (Bejder & Samuels 2003), which can give accurate estimates of Minke whale surfacing rates in an undisturbed environment.

Surfacing rates plays an important role in the pre-implementation assessment for the Revised Management Procedure (RMP) of the IWC (Schweder et al. 1997; Skaug et al. 2004; Bøthun, Skaug & Øien 2009). This study shows that Minke whale surfacing rates can not be considered constant, and that apart from a number of possible internal factors, the survey vessel itself can have an effect on diving behaviour. Based on the results of this study, regular dives will become more frequent at closer proximities to the survey vessel, which will result in more surfacing close to the vessel. This means that the actual number of observations are inflated, resulting in a positive bias in the abundance estimate of Minke whales.

We suggest that given the risk of positive bias in the abundance estimates of Minke whales, a more conservative estimate for surfacing rates should be used, preferably one based on data collected from land or some other research platform that doesn’t affect the diving behaviour itself. Another solution would be to quantify the effect of the survey vessel on surfacing rates of Minke whales at different distances from the vessel and incorporate this into the abundance estimate analysis.

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