



A hierarchical Bayes approach to capture-recapture abundance estimation
by Tomoharu Eguchi

A dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of
Philosophy in Biological Sciences
Montana State University
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Abstract:

A reanalysis of stranding data for bottlenose dolphins along the Atlantic coast of the United States during the 1987-1988 epizootic indicated that the widely used mortality rate during the die-off of 53% was an overestimate. Using the same dataset, I computed the mortality during the epizootic to be less than 46%. Continuous and consistent effort in collecting stranding data and estimation of life history parameters were shown to be important in using stranding data to find die-off of a population. To make inferences on abundance of bottlenose dolphins in estuaries along the Atlantic coast of the United States, a hierarchical Bayes approach for capture-mark-recapture data was proposed. The performance of the proposed method was comparable to the maximum likelihood method. When sample sizes were small, however, the proposed method performed better than the maximum likelihood method. Simulation analyses indicated a frequent sampling and high capture probabilities increased the precision of posterior distributions. The proposed method was applied to the existing photographic identification datasets from eight locations along the coast. Opportunistically collected data were useful in obtaining the joint prior distribution of the hyperparameters of sighting probabilities. Although posterior distributions of abundance were computed for these datasets, potential violations of the underlying assumptions and differences in the sampling protocols among studies made impossible to compile all results. To obtain abundance estimations from capture-mark-recapture data, the existing sampling protocols should be modified so that the assumptions of capture-recapture analyses are satisfied.

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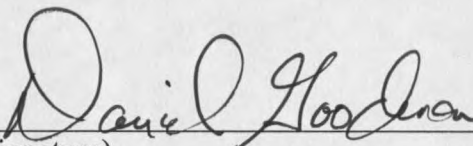
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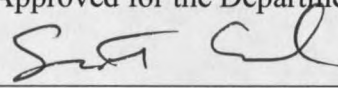
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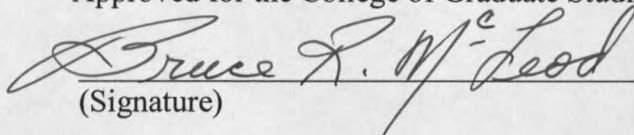
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ABSTRACT

A reanalysis of stranding data for bottlenose dolphins along the Atlantic coast of the United States during the 1987-1988 epizootic indicated that the widely used mortality rate during the die-off of 53% was an overestimate. Using the same dataset, I computed the mortality during the epizootic to be less than 46%. Continuous and consistent effort in collecting stranding data and estimation of life history parameters were shown to be important in using stranding data to find die-off of a population. To make inferences on abundance of bottlenose dolphins in estuaries along the Atlantic coast of the United States, a hierarchical Bayes approach for capture-mark-recapture data was proposed. The performance of the proposed method was comparable to the maximum likelihood method. When sample sizes were small, however, the proposed method performed better than the maximum likelihood method. Simulation analyses indicated a frequent sampling and high capture probabilities increased the precision of posterior distributions. The proposed method was applied to the existing photographic identification datasets from eight locations along the coast. Opportunistically collected data were useful in obtaining the joint prior distribution of the hyperparameters of sighting probabilities. Although posterior distributions of abundance were computed for these datasets, potential violations of the underlying assumptions and differences in the sampling protocols among studies made impossible to compile all results. To obtain abundance estimations from capture-mark-recapture data, the existing sampling protocols should be modified so that the assumptions of capture-recapture analyses are satisfied.

INTRODUCTION

Growing human activities around the globe have increased interactions between wildlife and humans. Many researchers have provided evidence that habitat degradation can cause population decline (Caley et al. 2001, Warren et al. 2001). Direct harvesting also has impacted many species (e.g., Steller's sea cows *Hydrodamalis gigas*, many baleen whales Balaenopteridae, northern elephant seals *Mirounga angustirostris*). In other situations, however, human activities unintentionally increase the mortality of a wildlife population, sometimes endangering the population. Studies have indicated that human activities, such as military activities, automobile and ship traffic, introduction of new species, and recreational beach activities, impact survival of wildlife (Gerrodette and Gilmartin 1990, Kraus 1990, Kenney and Kraus 1993, Doak et al. 1994, Marmontel et al. 1997, Burney et al. 2001).

In marine ecosystems, several kinds of fishing operations are known to catch untargeted species, such as marine mammals, sea birds, turtles, and fishes (National Research Council 1990, Mangel 1993, Crowder et al. 1994, Trippel et al. 1996, Bravington and Bisack 1996, Weimerskirch et al. 1997, Vinther 1999, Belda and Sánchez 2001, Romanov 2002). Because of the severity of incidental mortalities in some situations, various mitigation measures have been proposed to reduce accidental catches of non-target species in fisheries (e.g., acoustic deterrent devices, turtle-exclusion devices, streamer lines, and change in the timing of fishing; Crowder et al. 1994, Trippel et al. 1996, Melvin et al. 1999, Belda, and Sánchez 2001, Løkkeborg and Robertson 2002, Ryan and Watkins 2002). The effectiveness of these measures and compliance by fishers, however, often depend on regional and international regulations, cultural understandings, and enforcement (Crowder et al. 1994, Robertson 1998, Ryan and Boix

1998, Gilman 2001). In many instances, legal protection and enforcement are necessary for protecting wildlife from various human activities.

To protect marine mammals from anthropogenic mortality and disturbance, the United States enacted the Marine Mammal Protection Act in 1972 (MMPA, most recently amended 1994). The 1994 amendment explicitly incorporates a method of computing the number of individuals that can be killed incidentally for each marine mammal stock in U.S. waters. A "stock" of a marine mammal species is defined in the act as:

... a group of marine mammals of the same species or smaller taxa in a common spatial arrangement, that interbreed when mature.

The number of individuals of a stock that can be killed incidentally is called potential biological removal (PBR) and defined as the following:

... the maximum number of animals, not including natural mortalities, that may be removed from a marine mammal stock while allowing that stock to reach or maintain its optimum sustainable population. The potential biological removal level is the product of the following factors:

(A) The minimum population estimate of the stock.

(B) One-half the maximum theoretical or estimated net productivity rate of the stock at a small population size.

(C) A recovery factor of between 0.1 and 1.0.

The PBR of a stock, therefore, can be computed as:

$$PBR = N_{\min} \frac{R_{\max}}{2} F_R, \quad (1.1)$$

where $N_{\min}$ = the minimum population estimate of the stock, $R_{\max}$ = the maximum theoretical or estimated net productivity rate of the stock at a small population size, and F_R = a recovery factor between 0.1 and 1.0. The goal of the PBR is to allow each stock to reach or maintain its optimum sustainable population (OSP):

The term "optimum sustainable population" means, with respect to any population stock, the number of animals which will result in the maximum productivity of the population or the species, keeping in mind the carrying capacity of the habitat and the health of the ecosystem of which they form a constituent element.

Because the act lacked a practical method for computing these quantities, Wade (1998) provided quantitative definitions for the three components in equation (1.1) such that one can evaluate the impact of known levels of anthropogenic mortality of marine mammals. Because of the relatively small variability in the life history parameters of marine mammals, default values of $R_{\max}$ and F_R may be determined theoretically. Consequently, the minimum abundance of a stock is the only necessary information for computing the PBR when data are limited. Although simple, the method provides a means to offer robust management plans that can prevent the depletion of marine mammal populations from known anthropogenic mortality (Wade 1998).

To estimate abundance of marine mammal populations, line-transect and capture-mark-recapture methods often are used. For line-transect and other distance methods, distances from the transect line or point are used to adjust the encounter rate for estimating the density of animals (Buckland et al. 1993). Distance methods provide an estimate of abundance of a closed population in a short time period. In some situations, however, the line-transect method is impractical or inappropriate. For example, in the North Atlantic Ocean, two types of bottlenose dolphins exist: offshore and inshore ecotypes. These two ecotypes are indistinguishable from the distance. Consequently, to estimate the abundance of either population, one needs to identify the species of each individual. Capture-mark-recapture (CMR) techniques use marking or identification of individuals for estimating abundance and other population parameters, such as birth, death, immigration, and emigration rates.

The CMR method is a widely used technique for estimating abundance and other vital rates of a population. Mark-recapture abundance estimation procedures are based on the following concept: if one marks a portion of a population of animals, allows them to mix with unmarked animals, and takes a random sample from the population, then the sample should contain approximately the same proportion of marked animals as the proportion of marked animals in the entire population. In an algebraic expression:

$$\frac{M}{N} \approx \frac{m}{n} \quad (1.2)$$

where N = the total population size, M = the number of individuals with marks (i.e., the number of individuals in the first sample), n = the number of individuals in the second sample, and m = the number of individuals with marks in the second sample, i.e., recaptures.

In the last 50 years, many models have been proposed for analyzing mark-recapture data (Schwarz and Seber 1999). Recent developments in mark-recapture analyses have focused on multi-parameter models, in which survival, immigration and emigration, and movement rates are incorporated. Because the multi-parameter models are complex, the estimation procedure requires sophisticated mathematics or, more often, intense numerical approximations using advanced algorithms.

Although statisticians have built many complex models to deal with a variety of situations in CMR studies, successful applications of these models require a large amount of data from well-designed long-term studies. For many biologists, collecting enough data and finding an appropriate model for estimating a parameter of interest are difficult tasks. As Dhondt (2002) lamented, "... at the moment the statisticians are ahead of the biologists. They have developed the tools, but we have not often collected sufficient good quality data over a long enough time period to take full advantage of the tools."

Biologists have been relying on readily available software, such as CAPTURE, MARK, and POPAN, for analyzing mark-recapture data, sometimes without understanding the underlying assumptions and limitations of models (Dhondt 2002).

The existing CMR models can be separated into two broad categories: closed and open population models. These categories are based on the underlying assumptions about the population of interest. Closed models are based on the assumption that the population size is not affected by immigration, emigration, birth, and death, whereas open models lack this restriction (Seber 1982, Williams et al. 2001). Consequently, the number of parameters for open models is greater than for closed models. The main parameter in closed models often is the population size. Because the precision of estimates generally decreases as the number of parameters in a model increases, given the same amount of data, closed models provide better estimates of abundance than open models if assumptions are met.

Pollock (1982) introduced the "robust design," a sampling design that combined closed and open population models. This design is based on the assumption that the population of interest is closed over short time intervals (primary period), in which multiple samples are collected, but it is open when viewed from a long-term perspective across multiple primary periods (Figure 1.1). The abundance during each primary period is estimated from a closed model, whereas survival, immigration, and emigration rates are estimated between closed primary periods (Pollock 1982). The hierarchical assumption of the robust design is attractive for long-term studies because the approach allows one to obtain precise estimates of quantities in a simple sampling design.

The robust design has been used as an *ad hoc* approach and a likelihood-based approach. In an *ad hoc* approach, a combination of existing closed and open models is used. A closed model is used for estimating the abundance of a primary period, whereas

an open model is used for survival rates between primary periods. For the likelihood-based approach, the full likelihood function is constructed as a product of closed and open components of data. Several models have been proposed for estimating parameters using the hierarchical assumption (Kendall et al. 1995, Schwarz and Stobo 1997, Lindberg et al. 2001, Kendall and Bjorkland 2001).

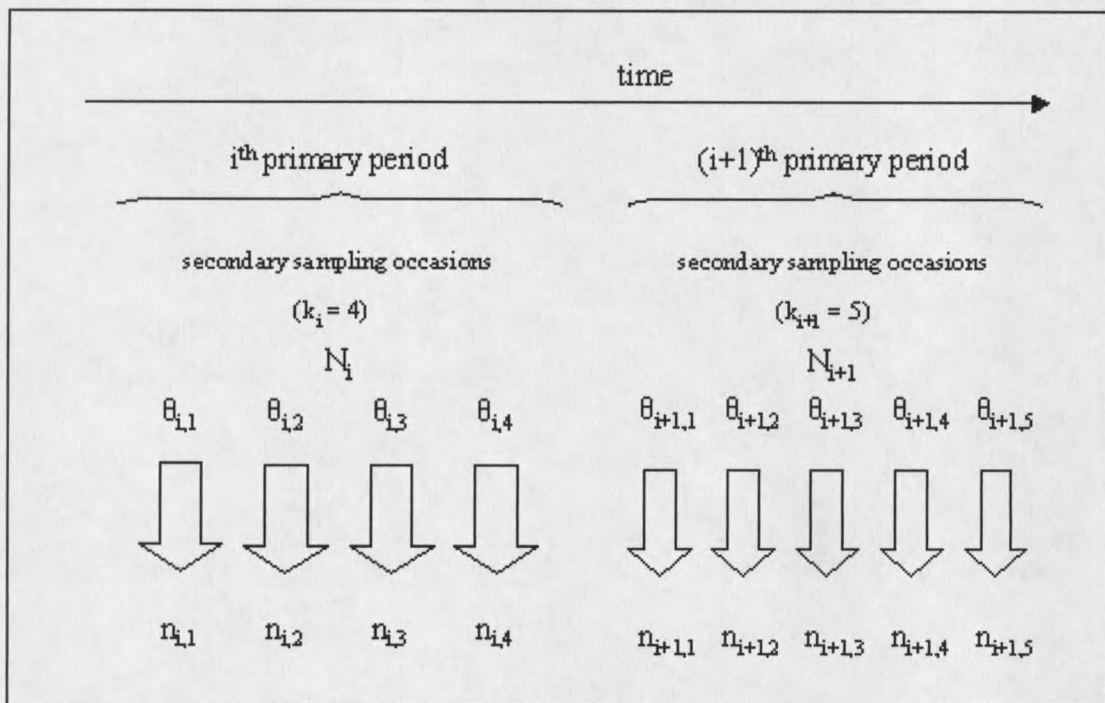


Figure 1.1. A schematic diagram of Pollock's robust design. Within each primary period, multiple samples are collected during secondary occasions with occasion-specific capture probabilities.

Kendall et al. (1995) first described a modeling framework and provided likelihood functions for a series of models for the robust design. The estimation procedure was conducted numerically. The models included capture probabilities and survival rates but the abundance was treated as a function of other parameters. Schwarz and Stobo (1997) and Kendall and Bjorkland (2001) extended the robust design so that

each primary period was considered open. In these models, the entire likelihood was considered a product of primary and secondary components. Parameters were estimated by sequentially maximizing the two parts. Lindberg et al. (2001) combined the robust design and band recovery for modeling the dispersal of Canvasback ducks (*Aythya valisineria*). Their model included temporary and permanent emigrations. Because the abundance was not a parameter of interest, it was not included in the model. In all these hierarchical models for the robust design, parameters were estimated using the maximum likelihood methods, most often via a numerical maximization of a likelihood function.

Many statisticians advocate maximum likelihood methods because of the statistically attractive properties of maximum likelihood estimators, e.g., minimum variance and being asymptotically unbiased. Because these desirable properties are based on large sample sizes, however, application of the method may be inappropriate when data are scarce. Uncertainties about a maximum likelihood estimate are expressed by a confidence interval, which is the long-run inclusion frequency of the parameter. It has been stressed that a confidence interval does not provide the probability of the estimate (Ellison 1996). A C% confidence interval includes the true value in C% of an infinite number of repeated samples from the population. Problems with using maximum likelihood estimates and confidence intervals in ecology, conservation biology, and management of small populations have been discussed (Ellison 1996, Ludwig 1996, Wade 2001, Goodman 2002). These authors suggest Bayesian statistics as an alternative approach.

Bayesian statistics is based on the same probability axioms as traditional statistics, which often is called frequentist statistics. The inference procedure in a Bayesian analysis, however, is based only on a probability model, observed data, and existing information on the parameters of interest. Assumptions about long-run sampling are not

used in the Bayesian inference procedure. The end result of an analysis is the probability distribution of parameters, conditional on the model and observed data. Although controversial, Bayesian methods have been recommended for ecological studies and conservation and management issues (Reckhow 1990, Ellison 1996, Ludwig 1996, Hilborn et al. 1994, Johnson 1999, Wade 2000). In a Bayesian analysis, previous knowledge about the parameters (prior distribution on parameters) is incorporated mathematically into the analysis via Bayes's theorem. Thorough discussions of philosophical and applied Bayesian analyses can be found elsewhere (Berger 1985, Robert 1994, Gelman et al. 1995, Lee 1997, Carlin and Louis 2000).

Although Bayesian analyses of mark-recapture models have been proposed previously (Freeman 1972, Gaskel and George 1972, Casteldine 1981), computational difficulties limited the applications. Recent developments in computer technologies, however, enabled the implementation of Bayesian methods in mark-recapture analyses (Gazey and Staley 1986, Zucchini and Channing 1986, Best and Underhill 1990, Kinas and Bethlem 1998, King and Brooks 2001). To my knowledge, however, no Bayesian method has been proposed for making inferences on abundance of a population with data from the robust design. In this dissertation, I propose a Bayesian approach for estimating the abundance of a closed population with the robust design. The proposed method is applied to previously collected data for bottlenose dolphins along the Atlantic coast of the United States.

Because of the die-off of 1987-1988, coastal stocks of bottlenose dolphins (*Tursiops truncatus*) along the Atlantic coast of the United States were listed as depleted under the MMPA (Waring et al. 2002). Although methods were not reported, Scott et al. (1988) stated that approximately 53% of bottlenose dolphins of the presumed coastal migratory stock died during the epizootic. The value has been used widely in literature

and management plans without verification of the method (Geraci et al. 1999, Waring et al. 2001). In an attempt to verify this estimate, I reanalyzed the same dataset using a different method and found that the mortality during the epizootic may have been significantly less than previously reported (Eguchi 2002).

Recent genetic and stable isotope studies have indicated that the presumed coastal stock may consist of several regional and migratory groups of bottlenose dolphins (Waring et al. 2002, A. Hohn, P. Rosel, K. Urian, pers. comm.). The most recent stock assessment report from the National Marine Fisheries Service (NMFS) lists seven management units for summer: northern migratory, northern North Carolina, southern North Carolina, South Carolina, Georgia, northern Florida, and central Florida (Waring et al. 2002; Figure 1.2). During winter, the northern migratory, northern NC, and southern NC units overlap geographically.

The management of these stocks depends largely on minimizing the number of by-catches in coastal fishing activities. Entanglements in fishing gear of coastal fishing activities may kill a significant number of bottlenose dolphins in some areas (Waring et al. 2001, 2002). For example, Palka and Rossman (2001) reported 146 bottlenose dolphins were killed by interactions with fishing operations off North Carolina and Virginia during winter 2000. Waring et al. (2002) reported that more than 50% of stranded carcasses of bottlenose dolphins in the coastal water of North Carolina exhibited signs of human interactions. Consequently, management actions are necessary to reduce human-induced mortality of bottlenose dolphins along the Atlantic coast of the United States. Proper management, however, requires an estimate of abundance for each management unit.

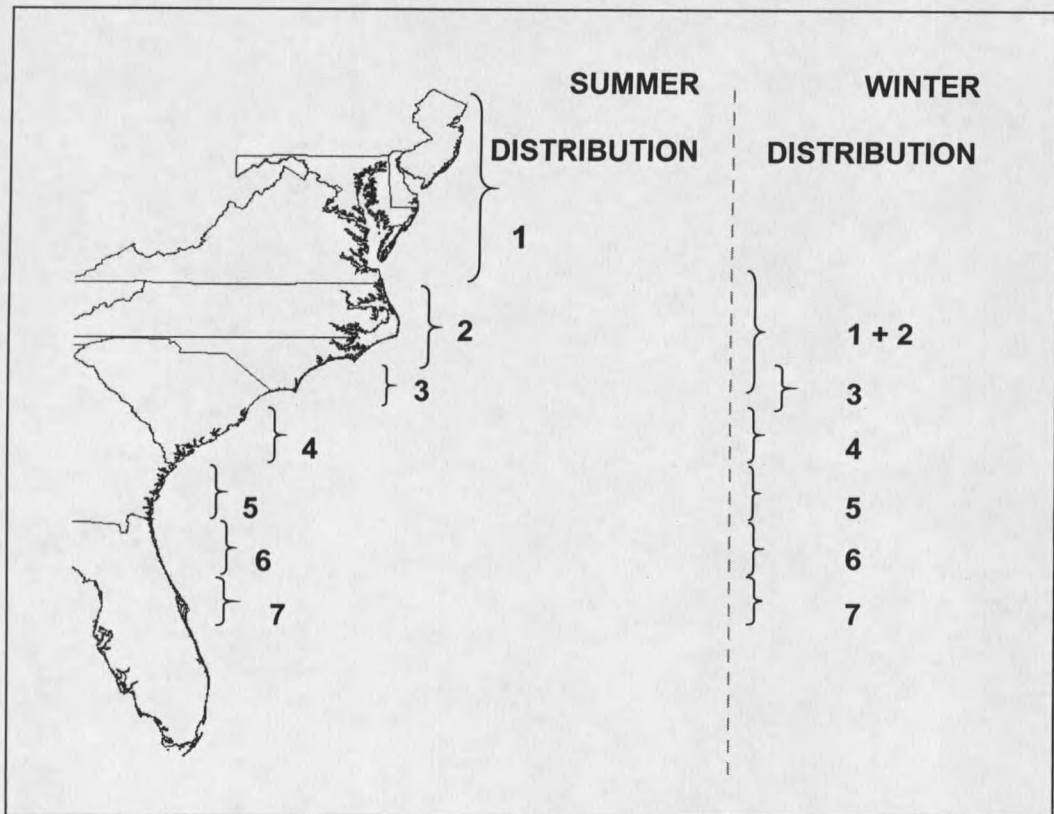


Figure 1.2. A schematic diagram of proposed management units of the coastal bottlenose dolphins along the Atlantic coast of the United States as defined from recent results of genetic, stable isotope ratio, photographic identification, and telemetry studies (from Waring et al. 2002). 1: Northern migratory unit, 2: northern NC unit, 3: southern NC unit, 4: SC unit, 5: GA unit, 6: northern FL unit, and 7: central FL unit.

The majority of existing information on the abundance of the presumed coastal stock of bottlenose dolphins comes from aerial line-transect surveys (Blaylock and Hoggard 1994, Blaylock 1995, Waring et al. 2002; Table 1.1). Only one survey has been conducted to estimate abundance of bottlenose dolphins in estuaries in North Carolina (Read et al. 2003). Waring et al. (2002) discussed potential sources of biases for these estimates: the aerial survey estimates were not corrected for the probability of detecting a group of bottlenose dolphins on the track line ($g(0)$), the relatively small herd sizes south of Cape Hatteras during winter likely introduced a negative bias, an unknown proportion

of offshore bottlenose dolphins, which belong to separate stocks, may have been included in a survey, and there was incomplete coverage of some seasonal management units.

Consequently, more comprehensive surveys and analyses are necessary for estimating abundances of management units, especially for bottlenose dolphins in bays, sounds, and estuaries. The low visibility in estuary waters and shallow waters in bays, sounds, and estuaries prohibit the use of aerial and ship-board line-transect surveys in these waters.

The mark-recapture approach is an alternative method for estimating abundance of these management units.

Table 1.1. Estimates of abundance and associated coefficient of variation (CV) for each management unit of coastal bottlenose dolphins (from Waring et al. 2002). The numbers for management units correspond to those in Figure 1.2.

Management units	Estimate ($\hat{N}$)	CV(N)
Summer (May – October)		
1	5,681	24.4
2 (oceanic)	3,383	41.8
2 (estuary)	919	12.5
3 (oceanic)	1,157	50.0
3 (estuary)	141	15.2
Winter (November – April)		
1+2+3	6,474	39.7
4	3,513	47.0
5	767	78.4
6	354	56.0
7	10,652	45.8

Although few studies have been conducted to estimate abundance of bottlenose dolphins in bays, sounds, and estuaries along the coast, researchers have conducted various studies on these local groups of bottlenose dolphins. These studies include

seasonal occurrences, home-range analyses, association patterns, residence patterns, and local relative abundances (Barco et al. 1999, Caldwell et al. 2001, Gubbins 2002a, 2002b, Zolman 2002). In these studies, researchers used photographic identifications of naturally identifiable bottlenose dolphins.

The dorsal fins of many bottlenose dolphins exhibit nicks, notches, and deformations. These 'markings' result from intra- and inter-specific interactions and possibly from collisions with watercrafts. These marks persist and can be used to photographically 'capture' individuals, enabling researchers to track individuals longitudinally.

The method of photographic identification of natural marks (dorsal fins and pigmentation patterns) has become one of the most common methods of cetacean abundance and survival estimation. The method has been used to provide information on movements (Cerchio 1998, Calambokidis et al. 2001), abundance (Williams et al. 1993, Cerchio et al. 1998, Wilson et al. 1999, Read et al. 2003), reproduction (Steiger and Calambokidis 2000), survival (Slooten et al. 1992, Cameron et al. 1999, Gabriele et al. 2001), and association among individuals (Slooten et al. 1993, Gubbins 2002b). Advantages of using natural marks in cetacean studies include the lack of direct handling of animals by researchers. Consequently, mortality from handling and the changes in behavior due to marking and handling do not arise. Further, the number of individuals that can be 'marked' in a study is greater than if artificial marks are used. Although these advantages outweigh potential disadvantages in using natural marks, the limitations should be considered.

Hammond (1986) listed potential problems and limitations of using photographic identification of natural marks: marks need to be constant throughout the study, marks need to be distinct so that individuals are identified uniquely, and not all individuals may

possess uniquely identifiable marks. The third problem is especially important when photographic identification is used to make an inference on the entire population. If a portion of the population does not possess identifiable markings, the inference from the identifiable individuals needs to be adjusted for the entire population. Consequently, when photographic identification is used to estimate the size of an entire population using a CMR method, the proportion of identifiable individuals in the population needs to be estimated.

In the following five chapters, I will discuss the bottlenose dolphin populations along the Atlantic coast of the United States and a method for estimating the abundance of the populations with CMR methods. In the first chapter, I review the species in general, emphasizing information on the population along the Atlantic coast of the United States. In the second chapter, I review and reevaluate the analysis conducted by Scott et al. (1988), whose conclusion was used to decide bottlenose dolphins along the coast were depleted under the MMPA. In the third chapter, I propose statistical models and procedures that can be used for making statistical inferences on the abundance of a closed population from longitudinal capture-mark-recapture data. Although the proposed method is motivated by the analysis of existing photographic identification data for bottlenose dolphins along the Atlantic coast of the U.S., they are applicable for longitudinal mark-recapture data in general. In the fourth chapter, I apply the proposed method to photographic identification datasets for bottlenose dolphins along the Atlantic coast of the United States. I also discuss possible modifications to the current sampling design and protocol, so that more precise abundance estimates could be obtained from the application of CMR methods to photographic identification data in the future. Finally, in the fifth chapter, I end the dissertation with concluding remarks.

THE BOTTLENOSE DOLPHIN (*TURSIOPS TRUNCATUS*)

Taxonomy and Systematics

The bottlenose dolphin (*Tursiops truncatus*) belongs to the Order Cetacea, Family Delphinidae, and Genus *Tursiops*. The genus *Tursiops* is polymorphic and at least 20 species have been described (Mead and Potter 1990). Because systematic studies have been conducted on relatively small sample sizes and restricted geographic areas, however, there is no general consensus on the validity of these species (Mead and Potter 1990, Ross and Cockcroft 1990, Rice 1998). A recent phylogenetic analysis of the mtDNA indicated that bottlenose dolphins of the tropical Indian Ocean are genetically closer to several species of *Stenella* than to *T. truncatus* (Curry et al. 1995, Curry 1997, Curry and Smith 1998). Consequently, for the interim it is treated as a separate species (*T. aduncus*; Rice 1998).

Distribution and Movements

The bottlenose dolphin is a cosmopolitan species and found in almost all oceans except at very high latitudes. This species is found in coastal waters of all continents, around most oceanic islands and atolls, and over shallow offshore banks and shoals (Rice 1998). In the Pacific, the species ranges along the both sides of the ocean from northern Japan and central California southward to Australia and Chile (Leatherwood and Reeves

1983, Wells et al 1990). In the Atlantic, bottlenose dolphins range from Nova Scotia and Norway southward to Patagonia and the tip of South Africa (Leatherwood and Reeves 1983). Bottlenose dolphins also are common in the Mediterranean Sea and the Indian Ocean (Leatherwood and Reeves 1983). Although the species is most common in the nearshore waters, pelagic populations have been reported for the Gulf Stream of the northwestern Atlantic and in the tropical eastern Pacific (Rice 1998).

Throughout the range of the species, researchers have found two morphological types among adult bottlenose dolphins, which often are referred to as ecotypes (Perrin 1984, Van Waerebeek et al. 1990). Bottlenose dolphins often exhibit offshore-inshore separation. Inshore, or coastal, bottlenose dolphins usually are found shoreward of the 18-m contour and often enter harbors, inlets, bays, lagoons, estuaries, and rivers (Leatherwood and Reeves 1983). Several studies have indicated that these coastal bottlenose dolphins have limited home ranges (Connor and Smolker 1985, Scott et al. 1990, Hammond and Thompson 1991, Caldwell et al. 2001, Gubbins 2002b, Zolman 2002). The offshore ecotype, however, is less restricted in its range and movements (Leatherwood and Reeves 1983, Leatherwood et al. 1988, Scott and Chivers 1990).

Kenney (1990) reported a distinct pattern in the distribution of bottlenose dolphins off the coast of the northeastern United States. Inshore sightings were located in the coastal waters (< 20 m) from Cape Lookout to Delaware Bay, whereas the offshore sightings were distributed between the 200 and 2000 m bottom contours, from Cape Hatteras to the eastern end of Georges Bank (Kenney 1990). The mean depth of the inshore sightings was 10.3 m, whereas that of the offshore sightings was 845.6 m

(Kenney 1990). The inshore-offshore distribution pattern, however, was less distinct south of Cape Hatteras (Scott et al. 1988) and no distinctive offshore groups of bottlenose dolphins have been described south of Cape Hatteras.

The offshore ecotype of bottlenose dolphins in the western Atlantic mainly exists in the oceanic waters (Duffield et al. 1983, Hersh and Duffield 1990, Mead and Potter 1995, Curry and Smith 1997). There are hematological, morphological, and genetic differences between these two ecotypes (Duffield et al. 1983, Hersh and Duffield 1990, P. Rosel, pers. comm.). The exact spatial distributions of these ecotypes, however, are unknown. These two ecotypes cannot be distinguished with certainty during visual observations from airplanes and large ships (Waring et al. 2001).

Some coastal bottlenose dolphins, north and south of Cape Hatteras, exhibit north-south seasonal migration. Researchers have hypothesized that coastal bottlenose dolphins migrate latitudinally in response to the seasonal change in the ocean temperature (Mead and Potter 1990). Because water temperature offshore is not influenced by the incursion of the Labrador Current during winter, offshore bottlenose dolphins may not migrate seasonally (Mead and Potter 1990). During summer, coastal bottlenose dolphins are distributed as far north as Long Island, New York. The main concentration of coastal bottlenose dolphins during summer, however, is along the coast of North Carolina to New Jersey (Scott et al. 1988).

During winter, only a few bottlenose dolphins are found in the coastal water north of Cape Hatteras (Kenney 1990, Blaylock and Hoggard 1994, Wiley et al. 1994). The coastal ecotype is found along the coast of North Carolina to Florida. The winter

destinations of bottlenose dolphins that are found north of Cape Hatteras during summer are unknown. It is suspected that they inhabit along the coast of North Carolina during winter.

Seasonal movements, extent of offshore distributions, and inshore-offshore movements of the offshore ecotype have not been determined because sampling has been limited to areas within 200 km of shore and no studies have been conducted to determine the movements (Wang et al. 1994).

The coastal bottlenose dolphins also are found throughout the year in some estuaries, inlets, and rivers south of Cape Hatteras (North Carolina to Florida; Scott et al. 1988, Hohn 1997, Caldwell et al. 2001, Gubbins 2002a, Zolman 2002, A. Hohn and L. Hansen, pers. comm.). Results of photographic identification studies indicate that there is a difference in the extent of residency among dolphins: residents throughout the year, seasonal residents (returning to the same area during one season every year but not present during other seasons), migrants or transients, and possible groups with large home ranges (Hohn 1997, Caldwell et al. 2001). Resident bottlenose dolphins have been reported from North Carolina to Florida (Sayigh et al. 1997, Hohn 1997, Caldwell et al. 2001, Gubbins 2002a, Zolman 2002). Researchers have reported sympatric occurrences of residents, seasonal residents, and transients at various locations (Odell and Asper 1990, Hohn 1997, Caldwell et al. 2001).

Movements and home ranges of bottlenose dolphins have been studied using radio telemetry, tagging, satellite telemetry, and photographic identification of natural marks. Extensive studies on home ranges of bottlenose dolphins come from the Sarasota

Bay area, Florida, in which some marked bottlenose dolphins have maintained fidelity to the area for over 17 years (Scott et al. 1990). In the Sarasota Bay area, home ranges of males are larger than females. Adult females create several relatively discrete spatial groups, with each group occupying different and relatively limited core areas that broadly overlap, and adult males travel from one female group to another (Scott et al. 1990).

Odell and Asper (1990) caught and freeze-branded 133 bottlenose dolphins in Indian River, Florida, between March 1977 and October 1981. Marked dolphins were searched for actively and opportunistically after branding from September 1979 through March 1982. Eight branded individuals were never identified following their release. Of 81 freeze-branded individuals with sighting records, 60 were sighted exclusively within Indian River (mean linear range = 32.8 km, SD = 18.0 km) whereas the others were seen in both Indian and Banana rivers (mean linear range = 55.6 km, SD = 20.5 km).

Gubbins (2002a) studied home ranges of 20 resident bottlenose dolphins in a South Carolina estuary using the photographic identification technique. The computed home ranges were 14.7 to 98.9 km², depending on the method of computations. She found that the resident bottlenose dolphins exclusively used the estuary. Caldwell et al. (2001) studied home ranges of bottlenose dolphins for Jacksonville, FL. They found three behaviorally and genetically distinct groups in their study area, two of which were year-round residents. One resident group was found in the coastal waters and the other in the Intracoastal Waterway (ICW). The third group was found only during summer in the St. John's River. The mean home range for the year-round residents in the ICW was 22.3 (SD = 7.5) km², whereas that for the summer residents in the St. John's River was 8.2

(SD = 4.2) km². They reported that the home range of the coastal dolphins was larger than the study area.

Continuous movements of bottlenose dolphins have been estimated using satellite telemetry. Mate et al. (1995) deployed a satellite transmitter on a bottlenose dolphin in Tampa Bay, Florida, and found that the dolphin traveled at least 581 km during 25 days, and the longest distance traveled in a day was 50.2 km. Similar results have been reported for resident bottlenose dolphins in Sarasota Bay, Florida (< 30 km/day; Irvine et al. 1981), and a satellite-tagged bottlenose dolphin off Japan (604 km/18 days; Tanaka 1987). Two rehabilitated adult bottlenose dolphins, both of which were believed to be the offshore ecotype, were tagged and tracked via satellite-linked transmitters (Wells et al. 1999). One was released in the Gulf of Mexico but moved around Florida peninsula and northward to off Cape Hatteras, NC, covering 2,050 km in 43 days. The other was released off Cape Canaveral, FL, and moved offshore covering 4,200 km in 47 days.

Morphology, Hematology, and Growth

Male bottlenose dolphins are larger than females. Tolley et al. (1995) reported the sexual dimorphism in bottlenose dolphins in waters near Sarasota Bay, Florida. Males were larger than females in 20 out of 29 measurements. For seven skull measurements, however, only one (rostral girth) indicated a sexual dimorphism, in which males had greater girths than females. Males also were proportionally more robust and

possessed larger appendages than females. Sexual dimorphism of offshore dolphins in the Atlantic has not been investigated.

Although bottlenose dolphins are the most studied cetacean species, few studies have been conducted to estimate the growth and reproduction of the species. The majority of the information comes from dolphins in the Gulf of Mexico and around Florida, especially near Sarasota. For bottlenose dolphins in Sarasota Bay and its vicinity, virtually all individuals in the community have been examined at least once since 1970 (Scott et al. 1990). Read et al. (1993) used the longitudinal data set from around Sarasota Bay to estimate growth of bottlenose dolphins (47 males and 49 females) in the community. Ages of captured bottlenose dolphins were either known from field observations or estimated by the method described by Hohn (1980, 1990). Male dolphins showed greater asymptotic values in length (266.4 ± 2.86 SE vs. 249.2 ± 1.30 SE (cm)), girth (154.0 ± 5.67 SE vs. 141.7 ± 1.36 SE (cm)), and mass (259.0 ± 14.6 SE vs. 194.4 ± 4.72 SE (kg)) than females (Read et al. 1993). During the first six years of life, however, most females were larger in length and mass than males of the same age (Read et al. 1993). Males grow continuously for several years, especially in mass and girth, after the age at which females reach their asymptotic body size (Read et al. 1993).

Fernandez and Hohn (1998) aged 195 stranded carcasses of bottlenose dolphins (78 males, 81 females, and 36 unknown sex) along the Texas coastline. The asymptotic lengths for these bottlenose dolphins using the Gompertz model were 263.5 cm for males and 244.7 cm for females, indicating no significant differences from the estimates for bottlenose dolphins near Sarasota, Florida (Read et al. 1993, Fernandez and Hohn 1998).

Data from the Cape Hatteras area, however, indicated no sexual dimorphism and the asymptotic length of 240 cm (44 females and 38 males; Mead and Potter 1990). Stolen et al. (2002) examined 199 stranded carcasses of bottlenose dolphins from the Indian River Lagoon system in Florida. They found an asymptotic length for males was 255 cm, whereas that for females was 246 cm.

In Florida, female bottlenose dolphins reach sexual maturity at 5 to 12 years of age and a length of 220 to 235 cm, whereas males mature at 10 to 13 years and 245 to 260 cm (Odell 1975). Mean length at birth for a sample of both sexes was estimated to be 109.4 cm ($SD = 8.5$, $n = 42$; Fernandez and Hohn 1998), which was comparable to another estimate from the Cape Hatteras area ($\bar{x} = 114.3$, $SD = 7.8$, $n = 26$; Mead and Potter 1990). Predicted birth lengths for bottlenose dolphins from the Indian River Lagoon system for males was 124 cm, whereas that for females was 114 cm (Stolen et al. 2002).

The number of stranded neonates has been used as an indicator of calving in the region. In the Cape Hatteras area, 20 out of 32 stranded neonates were found during March and April, indicating a prolonged calving season with a peak during the spring (Mead 1975, Mead and Potter 1990). In waters around Florida and Texas coast lines, however, calving appeared to occur almost throughout the year and varied among locations (Urian 1996, Fernandez and Hohn 1998). No information is available for the growth, calving seasons, and the sexual dimorphism of the offshore ecotype.

Morphological and hematological differences exist between the coastal and offshore ecotypes (Leatherwood and Reeves 1983, Duffield et al. 1983, Hersh and

Duffield 1990). Duffield et al. (1983) compared hematological variables of 70 Atlantic and 35 Pacific bottlenose dolphins, which were maintained at Sea World facilities in San Diego and Florida. Although no offshore ecotype bottlenose dolphins from the Atlantic were included in the sample, distinctive differences were found in hemoglobin concentration, packed cell volume, and red blood cell counts between coastal and offshore types from the Pacific (Duffield et al. 1983). Hersh and Duffield (1990) compared hemoglobin profiles and morphometrics among fresh carcasses of stranded bottlenose dolphins along the east coast of Florida and found distinctive differences. Four carcasses that were found in the area close to the deep water exhibited electrophoretically different hemoglobins from the carcasses found in areas with no immediate deep water access. They also found significant differences in skull measurements between the two groups. In general, offshore bottlenose dolphins had longer body lengths with a proportionately shorter snout and proportionately smaller flippers and wider skulls and rostrums than coastal bottlenose dolphins (Hersh and Duffield 1990).

Diet

Because bottlenose dolphins are found nearshore and often interact with fishing activities, their diet has been described by several researchers. Bottlenose dolphins are often described as opportunistic foragers and they feed on a wide variety of fish and invertebrates. Stomach samples ($n = 76$) from stranded carcasses of bottlenose dolphins

in the southeastern United States indicated that the main prey items of bottlenose dolphins included silver perch (*Bairdiella chrysoura*), Atlantic croaker (*Micropogonias undulatus*), mullet (*Mugil* spp.), brief squid (*Lolliguncula brevis*), and spot (*Leiostomus xanthurus*), all occurring in 20% or more of the stomachs (Barros and Odell 1990).

Although most prey were benthic species (e.g., drums, croakers, seatrouts, toadfishes, and midshipman), pelagic (e.g., jacks, bluefish, and cutlass fish) and surface (e.g., mullets and clupeids) fishes also were included in their diet. Main prey items of bottlenose dolphins differed among locations, reflecting the abundance of local fish species (Barros and Odell 1990). To compare prey items found in stranded carcasses of bottlenose dolphins and that of free ranging bottlenose dolphins, Mead and Potter (1990) compared the stomach samples of stranded carcasses and those of bottlenose dolphins that were incidentally killed in fishing operations. No differences in prey items were found between these two groups (Mead and Potter 1990).

Although few studies have been conducted to describe food habits of the offshore type bottlenose dolphins, Barros and Odell (1990) reported that ommastephid squids (*Illex* sp. and *Ornithoteuthis antillarum*) were the primary prey items in one offshore bottlenose dolphin. Another stomach sample of an offshore type bottlenose dolphin contained 150 beaks from the shortfin squid (*Illex illecebrosus*), three octopodid squids, and an unidentified fish otolith (Mercer 1973).

Anecdotal reports indicate that bottlenose dolphins steal several fish species from fishing lines of fishermen, including king mackerel (*Scomberomorus cavall*), Spanish mackerel (*S. maculatus*), kingfish (*S. regalis*), tarpon (*Megalops (Tarpon) atlanticus*),

sailfish (*Istiophorus americanus*), hammerhead shark (*Sphyrna zygaena*), speckled trout (*Cynoscion nebulosus*), roballo (*Centropomus undecimalis*), spotted eagle-ray (*Aetobatus (Stoasodon) narinari*), mullet (*Mugil* sp.), sea catfish (*Aris (Galeichthys) felis*), sheephead (*Archosargus probatocephalus*), and flounder (*Paralichthys* sp.; Gunter 1942, Odell 1975). Gunter (1942) also examined stomach samples collected from 34 bottlenose dolphins killed in a small-scale harpoon fishery in Aransas County, Texas, and found striped mullet (*Mugil cephalus*), gizzard shad (*Dorosoma cepedianum*), spot (*Leiostomus xanthurus*), croaker (*Micropogon undulatus*), sand trout (*Cynoscion arenarius*), puffer (*Sphoeroides marmoratus*), sheephead, needle gar (*Strongylura marina*), black drum (*Pogonias cromis*), spotted trout (*Cynoscion nebulosus*), and flounder (*Paralichthys lethostigmus*).

Abundance

To estimate the abundance of bottlenose dolphins along the Atlantic coast of the United States, aerial surveys have been conducted. In the areas north of Cape Hatteras, Kenney (1990) used data from the surveys conducted by the Cetacean and Turtle Assessment Program (CETAP) between 1978 and 1983. Data were collected from the shoreline to 5 nautical miles seaward of the 1,600 m isobath, using random line-transect procedures (Kenney 1990). This study defined the inshore as all bottlenose dolphins found in waters less than 32 m, whereas all bottlenose dolphins found in waters deeper than 32 m were considered the offshore form. No bottlenose dolphins were observed in

inshore waters during winter. The greatest number of bottlenose dolphins was found in the coastal water during summer, with estimates ranging from 400 to 700. In the offshore water, the number of bottlenose dolphins was least during winter (1,500 to 2,300) and greatest during summer (9,700 to 12,800; Kenney 1990).

From 1992 through 1994, several aerial surveys were conducted along the Atlantic coast of the United States between Cape Hatteras and southeast Florida (Blaylock and Haggard 1994, Blaylock 1995). The abundance of bottlenose dolphins during the winter of 1992 was estimated to be 12,435 (95% CI = 9,684 - 15,967) between Cape Hatteras and southeast Florida using the line-transect method (Blaylock and Haggard 1994). During the summer of 1994, two types of aerial surveys were conducted. One type was a direct count of bottlenose dolphins within approximately 1 km of shore, and the other was the simple-random line transect method (Blaylock 1995). Direct count surveys indicated the minimum of 2,482 dolphins along the shore. The estimated abundance of dolphins from the line-transect survey was 25,841 (95% CI = 13,010 - 51,329; Blaylock 1995). During these surveys, however, offshore-inshore types were not distinguished.

All aerial surveys targeted bottlenose dolphins in the oceanic waters. Until recently, no study had been conducted to estimate abundance of bottlenose dolphins in inshore waters, including bays, sounds, and estuaries. To estimate abundance of bottlenose dolphins in bays and sounds of North Carolina, Read et al. (2003) conducted a mark-recapture study during summer 2000. Using a closed model that allows variable

capture probabilities over time and among individuals, the abundance of bottlenose dolphins was estimated to be 1,154 (95% CI = 996 – 1,370).

From June 1987 to March 1988, an epizootic of morbilliviruses caused mass die-off of bottlenose dolphins along the Atlantic coast of the United States from New Jersey to Florida (Scott et al. 1988, Lipscomb et al. 1994, Duignan et al. 1996). Between June 1987 and April 1988, a total of 742 dolphins were found dead from New Jersey to Florida, which was 10 times greater than the previous 3-year historical level of carcass detection (mean = 73 dolphins; Wang et al. 1994). Although the exact number of deaths was unknown, Scott et al. (1988) estimated greater than 50% of the coastal migratory stock between New Jersey and Florida died during this epizootic. The method of the estimation, however, was not described in the report. Consequently, on 6 April 1996, the National Marine Fisheries Service (NMFS) listed the migratory stock of Atlantic coastal bottlenose dolphins as depleted under the Marine Mammal Protection Act (MMPA 1972, amended 1994; Wang et al. 1994).

Human Interactions

Increasing human activities in nearshore waters and fishing activities have added another source of mortality for bottlenose dolphins. From 1991 through 1995, an average of 81.8 (CV = 0.27) offshore type bottlenose dolphins were killed annually by commercial fisheries (Waring et al. 1997). Pelagic pair trawl fisheries killed the greatest number of bottlenose dolphins (44.8/yr, CV = 0.28) compared with other fisheries

(Pelagic drift gillnet (18.8/yr, CV = 0.06), bottom trawl (18.2/yr, CV = 0.97), and coastal sink gillnet; Waring et al. 1997). Because of the differences in the methods used to estimate the number of incidental kills among fisheries and among years, these numbers may not indicate the actual number of bottlenose dolphins killed during their operations.

Stranded bottlenose dolphins along the Atlantic coast of the United States often show signs of interactions with fishing activities: entanglement, net marks, and missing appendages. During 1993, 22% of stranded bottlenose dolphins in North Carolina indicated interactions with fisheries (Waring et al. 1997). During 1994, 192 bottlenose dolphins stranded along the coast between Florida and North Carolina, of which 24 (12%) indicated signs of human interaction and 14 (7%) had evidence of entanglement with fishing gear. During 1995, 23 (12%) out of 196 stranded dolphins indicated human interactions and 12 (6%) had evidence of entanglement with fishing gear. From 1988 to 1995, the annual average of 22 stranded bottlenose dolphins indicated signs of human interaction (Waring et al. 1997). Palka and Rossman (2001) reported that the highest incidental mortality of bottlenose dolphins in the coastal gillnet fisheries for the Atlantic coast of the U.S. was found along the coast of North Carolina and Virginia during winter. They estimated that an average of 181 (SD = 46.7) bottlenose dolphins were killed annually by the coastal gillnet fisheries off NC and VA from 1996 to 2000.

Other causes of human-induced mortality in bottlenose dolphins may include contamination of the environment, habitat degradation, boat strikes, and gunshots (Waring et al. 1997). Gorzelany (1998) reported deaths of two previously identified bottlenose dolphins in the Sarasota area by ingestion of fishing gear. McFee and

Hopkins-Murphy (2002) reported that 23.1% of all stranded bottlenose dolphins (n=153; 1992 to 1996) along the coast of South Carolina were killed by interactions with human activities.

An immediate management action is necessary for the bottlenose dolphin along the Atlantic coast of the U.S. Recent studies have indicated that there are many small genetically distinct subgroups of bottlenose dolphins may exist in inshore waters, which may require separate stock status. Without a sound management plan, the reported high anthropogenic mortality may extirpate one or more of these small stocks. To establish a management goal for a stock, abundance of the stock needs to be estimated. As Read et al. (2003) demonstrated, CMR methods are viable alternatives to distance-based methods for these waters.

A REANALYSIS OF THE CHANGE IN THE ABUNDANCE OF THE COASTAL MIGRATORY STOCK OF THE BOTTLENOSE DOLPHIN DURING THE 1987-1988 EPIZOOTIC

Introduction

From the 1970s through 1990s, the number of die-offs among marine mammals increased (Geraci et al. 1999). Causes of these die-offs included viral infections, parasitic infections, brevetoxin poisoning, oil spills, and environmental changes (such as El Niño). Although no populations were extirpated by these die-offs, the reported total mortality by population ranged from a few percent to greater than 50% (Geraci et al. 1999). Because the total population sizes often were unknown in these species, however, only the number of detected carcasses was reported for many of these die-offs. Long-term consequences of these die-offs, therefore, were difficult to evaluate.

The existing management regulations for marine mammals in the U.S. waters depend on the abundance of a population relative to its optimum sustainable population (OSP; Marine Mammal Protection Act, 1972, amended 1994). A population of a marine mammal species is defined "depleted" if the population is either "(i) ... below its optimum sustainable population or (ii) listed as an endangered or threatened species under the Endangered Species Act of 1973 (MMPA)." Consequently, if a die-off reduces a population below its OSP, the population should be declared as depleted. Without the knowledge of the abundance of the population before a die-off, however, the estimation of the population size after the die-off relative to its OSP is difficult.

An indicator of many die-offs is the increased number of carcasses found on beaches. In many U.S. coastal areas, stranded carcasses of marine mammals are reported to a regional stranding network. Each reported carcass is recorded in a stranding

database, which allows longitudinal records of the number of stranded carcasses in the region. By using these longitudinal stranding records, a die-off may be detected.

In this study, the stranding process of marine mammal carcasses was modeled for calculating the mortality rate during a die-off by using a longitudinal stranding database. The epizootic event during 1987 and 1988 of the coastal bottlenose dolphin (*Tursiops truncatus*) along the Atlantic coast of the United States was used as a numerical example.

Methods

The mortality during a die-off of a marine mammal population was calculated by modeling the stranding process of a carcass. The estimation was based on the number of carcasses found and reported to a stranding network. I defined relationships among the following parameters and variables: natural mortality, human-induced mortality, additional mortality during the die-off, probability of a carcass being stranded and reported, numbers of carcasses stranded and reported before, during, and after the die-off, abundance of the population, and the duration of the die-off (Table 3.1). In defining these relationships, I made the following assumptions:

- (1) The duration of the die-off was < 1 yr,
- (2) The additional instantaneous per capita mortality rate owing to the die-off was constant throughout the die-off,
- (3) The instantaneous per capita birth rate remained constant before, during, and after the die-off period (i.e., no density dependence on the birth rate was incorporated into the calculation) and the die-off had no direct effects on reproduction,
- (4) The instantaneous birth rate (yr^{-1}) equaled the sum of the natural mortality rate, exclusive of the die-off mortality, and human induced mortality rates (yr^{-1}),

- (5) The per capita instantaneous human induced mortality rate remained constant before, during, and after the die-off,
- (6) The instantaneous per capita natural mortality rate, exclusive of deaths due to the die-off, remained constant before, during, and after the die-off,
- (7) The population was at equilibrium before the die-off, and
- (8) No immigration or emigration occurred to the population.

Because the duration of the die-off was assumed to be short (< 1 yr) relative to life cycles of marine mammals, effects of density dependence were ignored in the model.

Table 3.1. List of notations.

Notation	Definition
b	Instantaneous per capita birth rate of the population (yr^{-1}), which was assumed to be equal to $\mu_0 + h$
f_0	The probability of a stranded carcass being sighted and reported before the die-off ($0 < f_0 < 1$)
f_1	The probability of a stranded carcass being sighted and reported during the die-off ($0 < f_1 < 1$)
f_2	The probability of a stranded carcass being sighted and reported after the die-off ($0 < f_2 < 1$)
μ_0	Instantaneous per capita base mortality rate of the population before the die-off (yr^{-1} ; $0 < \mu_0 < 1$)
μ_1	Additional instantaneous per capita mortality rate of the population caused by the die-off (yr^{-1} ; $0 < \mu_1 < 1$),
h	Instantaneous per capita human-induced mortality rate of the population (yr^{-1} ; $0 \leq h < 1$)
N_0	The constant abundance of the population before the die-off ($0 < N_0$)
N_t	The abundance of the population during the die-off at time = t , which was measured as time since the beginning of the die-off in years ($0 < N_t$; $0 \leq t \leq T$)
T	Duration of the die-off (yr; $0 < T < 1$),

The following three equations were written based on these assumptions. The total number of observed stranded carcasses per year before the die-off (D_0) was:

$$\begin{aligned} D_0 &= \int_0^1 N_0 (\mu_0 + h) f_0 dt \\ &= N_0 (\mu_0 + h) f_0 \end{aligned} \quad (3.1)$$

The total number of stranded carcasses during the die-off (D_1) was:

$$\begin{aligned} D_1 &= \int_0^T N_t (\mu_0 + h + \mu_1) f_1 dt \\ &= \int_0^T N_0 e^{(b - \mu_0 - h - \mu_1)t} (\mu_0 + h + \mu_1) f_1 dt \\ &= N_0 (\mu_0 + h + \mu_1) f_1 \int_0^T e^{-\mu_1 t} dt \\ D_1 &= \frac{N_0 (\mu_0 + h + \mu_1) f_1 (1 - e^{-\mu_1 T})}{\mu_1} \end{aligned} \quad (3.2)$$

Finally, the total number of stranded dead animals during the first year after the die-off (D_2) was:

$$\begin{aligned} D_2 &= \int_0^1 N_0 e^{-\mu_1 T} (\mu_0 + h) f_2 dt \\ &= N_0 e^{-\mu_1 T} (\mu_0 + h) f_2 \end{aligned} \quad (3.3)$$

Calculating the mortality during the die-off

In these three equations, information often is available on T , D_0 , D_1 , and D_2 , whereas N_0 , f_0 , f_1 , f_2 and μ_1 are usually unknown. To simplify the algebra, the detection

probability after the die-off (f_2) is expressed as a simple function of the detection probability during the die-off (f_1):

$$f_2 = \alpha f_1, \quad (3.4)$$

where $0 < \alpha$. The multiplier α indicates the amount by which the detection probability changed from during the die-off to after the die-off. Equation (3), therefore, becomes:

$$D_2 = N_0 e^{-\mu_1 T} (\mu_0 + h) \alpha f_1. \quad (3.5)$$

Equations (3.2) and (3.5) involved 4 unknowns: α , f_1 , N_0 , and μ_1 . In these two equations, however, N_0 and f_1 only appeared as a product in both equations.

Consequently, this product was treated as a single unknown variable ($C = N_0 f_1$), allowing me to compute a solution for μ_1 . Solving equation (3.2) for C :

$$C = N_0 f_1 = \frac{D_1 \mu_1}{(\mu_0 + h + \mu_1)(1 - e^{-\mu_1 T})}. \quad (3.6)$$

Substituting equation (3.6) into equation (3.5):

$$\begin{aligned} D_2 &= N_0 e^{-\mu_1 T} (\mu_0 + h) \alpha f_1 = \alpha C e^{-\mu_1 T} (\mu_0 + h) \\ &= \frac{\alpha e^{-\mu_1 T} (\mu_0 + h) D_1 \mu_1}{(\mu_0 + h + \mu_1)(1 - e^{-\mu_1 T})} \end{aligned} \quad (3.7)$$

In equation (3.7), μ_1 and α were the only unknown parameters. Equation (3.7) was considered to be a function of μ_1 and rewritten as:

$$f(\mu_1) = D_2 - \frac{\alpha e^{-\mu_1 T} (\mu_0 + h) D_1 \mu_1}{(\mu_0 + h + \mu_1)(1 - e^{-\mu_1 T})} = 0. \quad (3.8)$$

Equation (3.8), then, was solved numerically for μ_1 . Because α was a positive value, equation (3.8) was a non-decreasing function with respect to μ_1 for all values of $(\mu_0 + h)$.

Only one root (μ_1), therefore, was possible for a value of $\mu_0 + h$.

Calculating the change in abundance and detection probabilities

Under my assumptions, the population size changed without density dependence during the die-off. Consequently, the change in abundance during the die-off can be expressed as:

$$\frac{N_T}{N_0} = e^{-\mu_1 T} \quad (3.9)$$

Equation (3.3) involved 2 unknowns ($N_0 \times f_2$ and μ_1), whereas, the product of N_0 and f_0 was the only unknown variable in equation (3.1). Therefore, the system can be solved for the ratio of detection probabilities before and after the die-off (f_2/f_0) as a function of μ_1 . To calculate the ratio of detection probabilities, equation (3.1) was solved for f_0 :

$$f_0 = \frac{D_0}{N_0(\mu_0 + h)} \quad (3.10)$$

Equation (3.3) was solved for N_0 :

$$N_0 = \frac{D_2}{e^{-\mu_1 T}(\mu_0 + h)f_2} \quad (3.11)$$

Equation (3.11), then, was substituted into (3.10) and was rearranged:

$$f_0 = \frac{D_0}{\left(\frac{D_2(\mu_0 + h)}{e^{-\mu_1 T}(\mu_0 + h)f_2} \right)} = \frac{D_0 e^{-\mu_1 T} f_2}{D_2} \quad (3.12)$$

$$\frac{f_2}{f_0} = \frac{D_2}{D_0 e^{-\mu_1 T}} \quad (3.13)$$

Equation (3.13) calculates the amount by which the survey effort changed before and after the die-off.

Numerical example

A large number of bottlenose dolphins were found dead on beaches along the Atlantic coast of the United States during 1987 and 1988 (Scott et al. 1988). Later analyses on carcasses indicated that infection by morbilliviruses was the main cause of the mass mortality event (Scott et al. 1988, Lipscomb et al. 1994, Duignan et al. 1996). Assuming there was one coastal migratory stock of the species, Scott et al. (1988) reported more than 50% of the entire stock was killed by this epizootic.

To apply the model to the epizootic, I examined stranding records of bottlenose dolphins along the Atlantic coast of the United States between 1987 and 1997 (courtesy of Blair Mase¹ and Charles Potter²). I grouped all stranding records of bottlenose dolphins along the Atlantic coast by 30-day periods, starting from 1 January 1987 (Table 3.2). I defined the duration of the epizootic to be the number of 30-day periods between 1 June 1987 and 30 April 1988 (Scott et al. 1988), in which the number of stranded bottlenose dolphins was greater than the 95 percentile for the entire time series.

I calculated the additional instantaneous mortality rate during the epizootic (μ_1) by inserting numerical values for instantaneous mortality rates ($\mu_0 + h$), the multiplicative factor for the change in detection probability of a carcass (α), and the three known variables (T , D_1 , and D_2) into equation (3.8) and solving the equation. I considered a range of the sum of natural and anthropogenic mortality rates between 0.04 and 0.10,

¹ National Marine Fisheries Service, Southeast Fisheries Science Center, 75 Virginia Beach Dr., Miami, FL 33149

² Smithsonian Museum of Natural History 10th St. and Constitution Ave., NW Washington D.C. 20560

which was within the plausible mortality for dolphin populations (Reily and Barlow 1986). I considered a range of α between 0.1 and 2.0.

Table 3.2. The number of stranded bottlenose dolphins per 30 days along the Atlantic coast of the United States. The duration of the epizootic was defined as the time period in which the number of stranded carcasses was greater than the 95 percentile between 1/1/1987 and 12/03/1997 and indicated by bold face.

Start Date	End Date	Number per 30 days
19870101	19870130	0
19870131	19870301	0
19870302	19870331	1
19870401	19870430	2
19870501	19870530	6
19870531	19870629	19
19870630	19870729	83
19870730	19870828	234
19870829	19870927	110
19870928	19871027	48
19871028	19871126	38
19871127	19871226	58
19871227	19880125	69
19880126	19880224	62
19880225	19880325	21
19880326	19880424	30
19880425	19880524	23
19880525	19880623	11
19880624	19880723	15
19880724	19880822	19
19880823	19880921	11
19880922	19881021	15
19881022	19881120	12
19881121	19881220	7
19881221	19890119	16
19890120	19890218	19
19890219	19890320	17
19890321	19890419	16
...	...	...
19971104	19971203	23
Mean		24.6
SD		25.5
95%-ile		58

To estimate effects of errors in the estimated parameter ($\mu_0 + h$) and measured variables (D_1 and D_2) on the additional mortality (μ_1), sensitivity analyses were conducted. I calculated additional mortality (μ_1) as a function of the sum of natural and human-induced mortality rates ($\mu_0 + h$). To estimate effects of the number of undetected stranded carcasses on the computed additional mortality rates (μ_1), I considered errors in detecting stranded carcasses. The additional mortality rate (μ_1) was calculated when D_1 and D_2 in equation (3.8) was varied from 101% to 125% of the reported value. I also estimated the sensitivity of the solutions for (N_T/N_0) to uncertainties in estimates for ($\mu_0 + h$), D_1 , and D_2 . Equation (3.9) was evaluated under ranges of ($\mu_0 + h$), D_1 , and D_2 .

Results

During eight 30-day periods between 30 June 1987 and 24 February 1988 along the U. S. Atlantic coast, a total of 702 carcasses of bottlenose dolphins were reported to the stranding network (D_1 ; Table 3.2). Although there were two months during which the number of stranded carcasses was less than the 95 percentile, the duration of the epizootic was defined as 240 days, or eight months ($T = 8/12$). A total of 199 (D_2) carcasses were reported during the 1-yr period after the epizootic. An average of 73.3 ($D_0=73$) bottlenose dolphins was reported to the stranding network every year during the 3-yr period before the epizootic (Scott et al. 1988).

Under my assumptions, the computed additional mortality rate during the 8-mo epizootic ranged approximately from 0.16 to 0.37 (Table 3.3). By incorporating uncertainty in variables and parameters in the model, however, significant variability was found in the calculated additional mortality rate. There was a positive relationship between the sum of natural and anthropogenic mortality rates ($\mu_0 + h$) and computed

additional mortality rate during the epizootic (μ_1 ; Table 3.3). The calculated change in the population size ranged from 10% to >20% if the detection and reporting probability was the same during and after the epizootic (i.e., $\alpha = 1.0$; Table 3.3).

Table 3.3. Calculated instantaneous additional mortality rate (μ_1) during the epizootic, calculated change in the abundance of the stock (N_T/N_0), and calculated change in detection probabilities before and after the epizootic (f_2/f_0) as a function of the sum of natural and human-induced mortality rates ($\mu_0 + h$). The duration of the epizootic was assumed to be 8 mo. Equation (3.8) was used to calculate the additional mortality rate during the epizootic. Change in the abundance was calculated by using equation (3.9). Change in detection probability (f_2/f_0) was calculated by using equation (3.13). The probability of detecting and reporting a carcass during and after the epizootic was assumed to be the same (i.e., $\alpha = 1.0$).

	Natural and human-induced mortality ($\mu_0 + h$; yr ⁻¹)						
	0.04	0.05	0.06	0.07	0.08	0.09	0.10
μ_1	0.161	0.198	0.233	0.268	0.302	0.335	0.367
N_T/N_0	0.899	0.877	0.856	0.836	0.818	0.800	0.783
f_2/f_0	3.03	3.11	3.19	3.26	3.33	3.41	3.48

The sensitivity analysis indicated positive relationships between the proportion of undetected stranded carcasses during the epizootic (D_1) and the computed additional mortality rates during the epizootic (μ_1 ; Figure 3.1). The proportion of undetected stranded carcasses during the first year after the epizootic (D_2), however, indicated negative relationships with calculated additional mortality rates during the epizootic (μ_1 ; Figure 3.1). The proportion of undetected stranded carcasses had less effect on computed additional mortality rates during the epizootic (μ_1 ; Figure 3.1) than the uncertainty in natural and anthropogenic mortality rates.

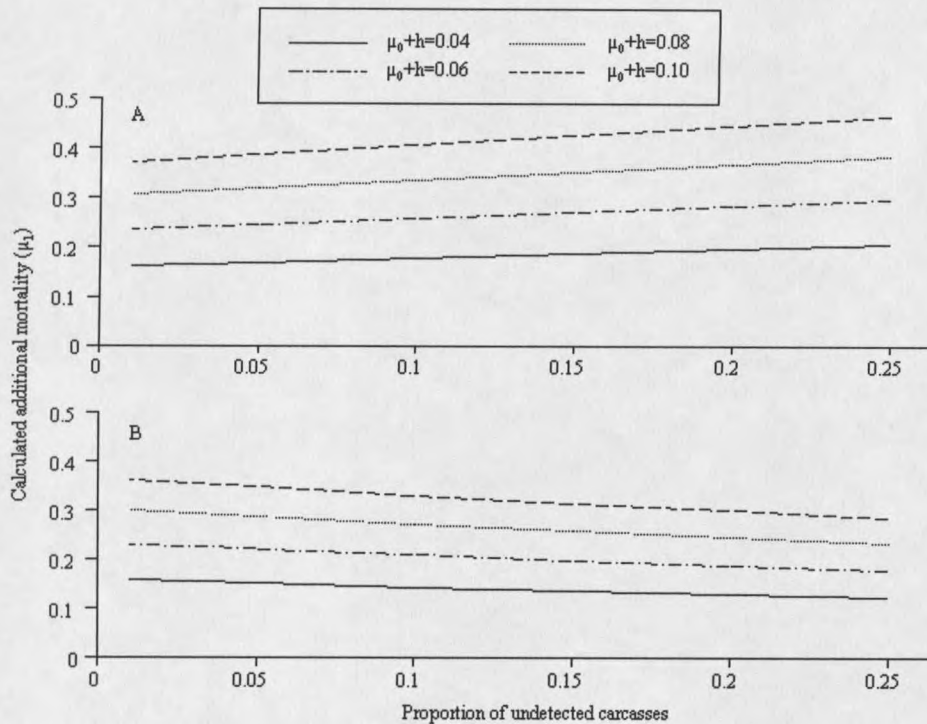


Figure 3.1. Effects of uncertainty in the proportion of undetected stranded carcasses and natural and human-induced mortality rates ($\mu_0 + h$) on calculated additional mortality rate (μ_1). The abscissa of the upper figure (A) indicates the proportion of undetected carcasses during the epizootic (D_1), whereas that of the lower figure (B) indicates the proportion of undetected carcasses during 1 yr after the epizootic (D_2). The duration of the epizootic (T) was assumed to be 8 mo ($T = 8/12$), the number of reported carcasses during the epizootic (D_1) was 702, and the number of stranded carcasses during 1 yr after the epizootic (D_2) was 199. Additional mortality rate (μ_1) was calculated as the solution for equation (3.8). The probability of detecting and reporting a carcass during and after the epizootic was assumed to be the same (i.e., $\alpha = 1.0$).

The sensitivity analysis also indicated positive relationships between the proportion of undetected stranded carcasses during the epizootic (D_1) and the change in the population size during the epizootic (μ_1 ; Figure 3.2). Negative relationships were found between the proportion of undetected stranded carcasses during the first year after the epizootic (D_2) and change in the population size during the epizootic (μ_1 ; Figure 3.2).

Uncertainty in D_1 and D_2 had less effect on the calculated rate of change in abundance during the epizootic (N_T/N_0) than the uncertainty in natural and anthropogenic mortality rates (Figure 3.2).

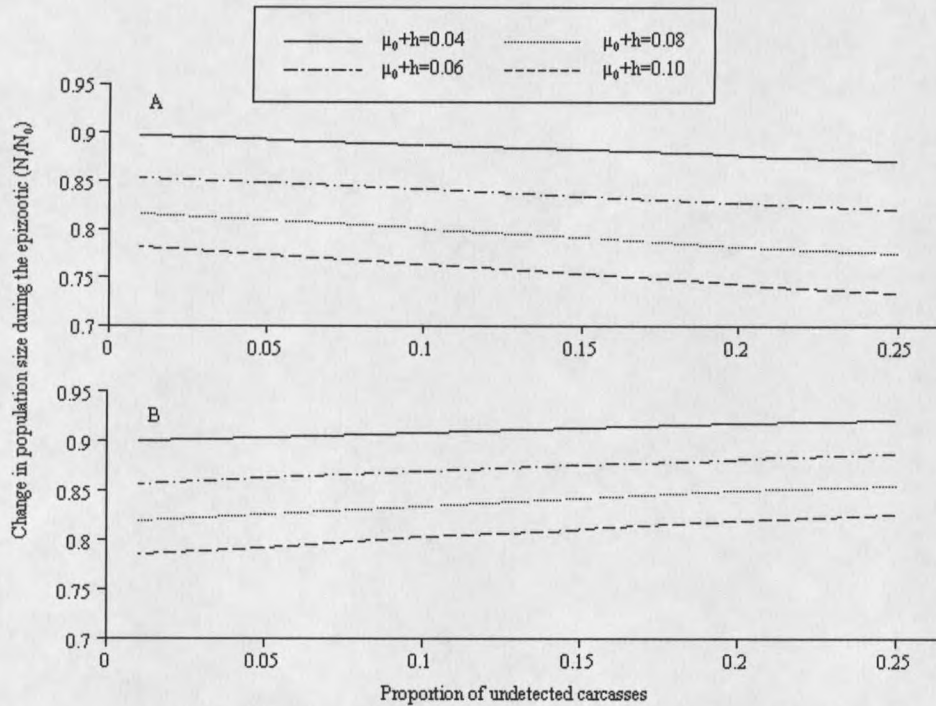


Figure 3.2. Effects of uncertainty in the proportion of undetected stranded carcasses on the calculated change in the abundance (N_T/N_0). The abscissa of the upper figure (A) indicates the proportion of undetected carcasses during the epizootic (D_1), whereas that of the lower figure (B) indicates the proportion of undetected carcasses during 1 yr after the epizootic (D_2). The duration of the epizootic (T) was assumed to be 8 mo ($T = 8/12$), the number of reported carcasses during the epizootic (D_1) was 702, and the number of reported carcasses during 1 yr after the epizootic (D_2) was 199. Change in abundance (N_T/N_0) was calculated by using equation (3.9). The probability of detecting and reporting a carcass during and after the epizootic was assumed to be the same (i.e., $\alpha = 1.0$).

For the range of natural and human-induced mortality rates under consideration, the calculated detection probability of carcasses was approximately 3 times greater after

the epizootic than before the epizootic ($f_2/f_0 \approx 3.0$; Table 3.3). The calculated additional mortality rate (μ_1) during the epizootic was greater if the detection probability of a carcass increased after the end of the epizootic (α ; Table 3.4). If the effort increased during the epizootic and the same effort continued after the epizootic (i.e., $\alpha \approx 1$), then the computed additional mortality rate during the epizootic ranged from approximately 0.17 to 0.4 (Table 3.4). If, however, the majority of increased effort was after the epizootic (i.e., $\alpha > 1$), the calculated additional mortality rates were much greater (Table 3.4).

Table 3.4. Effects of change in detection probabilities (α) between during and after the epizootic on calculated additional mortality rate during the epizootic (μ_1). Duration of the epizootic was assumed to be 8 mo ($T = 8/12$), the number of reported carcasses during the epizootic (D_1) was 702, and the number of reported carcasses during 1 yr after the epizootic (D_2) was 199. Additional mortality rate (μ_1) was calculated as the solution for equation (3.8).

Mortality ($\mu_0 + h$)	Rate of change in detection probability (α)					
	0.5	0.8	1.1	1.4	1.7	2.0
Additional mortality during the epizootic (μ_1)						
0.04	0.064	0.123	0.179	0.234	0.287	0.338
0.06	0.094	0.179	0.260	0.337	0.409	0.479
0.08	0.123	0.233	0.336	0.432	0.522	0.607
0.10	0.151	0.284	0.407	0.520	0.625	0.724

Discussion

The deterministic model of stranding and reporting process was shown to be useful in calculating additional mortality during a die-off from longitudinal stranding records. The model incorporated the stranding and reporting process, enabling sensitivity analyses on unknown parameters and variables. The result of using this model for estimating additional mortality during a die-off, however, depended on precision of other parameters and variables.

Sensitivity analyses indicated that uncertainty in natural and anthropogenic mortality rates had significant effects on calculated additional mortality rates during the epizootic of bottlenose dolphins during 1987-1988. The proportion of undetected stranded carcasses during and after the epizootic also had significant effects on calculated additional mortality rates during the epizootic (Figure 3.1). I have shown that by varying the proportion of undetected carcasses from 1% to 25% of the reported number of carcasses, the calculated additional mortality during the epizootic ranged from 0.12 to 0.46 (Figure 3.1). Consequently, the calculated decline in the abundance of the coastal migratory stock during the epizootic ranged approximately from 10% to 27% (Figure 3.2). These sensitivity analyses indicated that uncertainty in the proportion of undetected carcasses should be incorporated when the stranding record was used in estimating the mortality rate. The proportion of undetected carcasses may be estimated indirectly by recording the longitudinal effort dedicated to detecting stranded carcasses.

The computed detection and reporting probability of carcasses increased by approximately a factor of three over the period of the epizootic. Without the information on how search and reporting effort changed over the duration of the epizootic, it is impossible to attribute when the change occurred. A great variability was found in

calculated additional mortality rates as a function of the rate of change in detection probability. This sensitivity analysis indicated that survey effort should be estimated for stranding data if these data are to be used for estimating the mortality during a die-off.

To obtain reliable mortality rates during a die-off, precise estimations of life history parameters, such as birth rate, natural mortality rate, and anthropogenic mortality rate, are critical. Without information on natural mortality and human-induced mortality rates, the calculated additional mortality rate during the die-off could be either insignificant to the population or significant enough to nearly exterminate the population. These results were not directly useful in making a decision for successful management of the population. The following information on the population should be collected prior to the onset of the die-off: (1) natural mortality rate, (2) anthropogenic mortality rate, (3) birth rate, and (4) trend of the population size.

Stranding data should be collected in a consistent manner and effort for establishing the baseline data. Survey areas should be predetermined and defined. Trained observers should collect stranding data periodically within these defined survey areas. These data should include but not be limited to: species, the number of animals, and location of stranding. Effort data (e.g., hours of survey) for each survey area should be recorded for non-die-off periods. Collected data, then, should be added to a database, which will enable a data analyst to detect the unusual number of stranded carcasses of a species if a die-off occurs. If a die-off is suspected, the survey effort should be continued but not necessarily increased. If more funding or volunteer workers are available, the change in survey effort should be measured. Data collection should continue after the die-off. These data will enable a reliable estimate of mortality rate during the die-off.

In conclusion, a mathematical modeling of stranding processes was shown to be useful for calculating the mortality during a die-off. For these analyses to be satisfactory,

however, baseline data should be collected on several factors prior to a potential die-off and continue after the die-off. In particular, search effort must be quantified.

A STATISTICAL METHOD FOR ESTIMATING THE ABUNDANCE OF A POPULATION WITH CAPTURE-MARK-RECAPTURE DATA AND A HIERARCHICAL BAYES APPROACH

Introduction

Estimating the abundance of a population is important in understanding biological processes and successful management of the population. Numerous methods have been developed for estimating the abundance of a population (Seber 1982, Schwarz and Seber 1999, Williams et al. 2001). Depending on the sampling process and underlying model, these methods can be grouped into one of three broad categories: counts, distance-based, and capture-mark-recapture (Williams et al. 2001). In this chapter, I develop a Bayesian method for estimating the abundance of a closed population using capture-mark-recapture (CMR) data. Discussion on other methods can be found elsewhere (e.g., Buckland et al. 1993, Williams et al. 2001).

In CMR methods, animals are caught in a series of samples. Animals in the first sample are marked individually and released into the population. In subsequent samples, new animals are marked individually and released, whereas recaptured animals are recorded and released. Consequently, capture histories of individual animals are available at the completion of a study. Marks on animals may be either artificial or natural. When feasible, natural marks are preferable to artificial marks and tags because the marking procedure does not affect the behavior of animals, the mortality due to direct handling of animals is absent, and loss of marks is usually less of an issue.

Existing methods for estimating the abundance of a population via CMR experiments require large numbers of recaptures to obtain precise results. In the user manual for their population analysis software, Arnason et al. (1998) stressed the

importance of a carefully designed study and the use of prior knowledge of the population:

"Failure to use every scrap of prior information about the population of interest, or to carry out a proper sampling program that fully exploits this information, can have disastrous consequences. More often than not, a poor experiment, even if it has deployed prodigious amounts of equipment and man-hours, can lead to data that are difficult or impossible to analyse, and estimates that are vague, misleading, or even absurdly biased (Arnason et al. 1998; Chapter 6.2)."

In many statistical models for capture-mark-recapture analyses, abundance is not incorporated in these models explicitly. The abundance during a period, however, is estimated by using the following relationship:

$$E[N_t] = \frac{n_t}{\hat{p}_t}, \quad (4.1)$$

where n_t is the number of animals caught during the t^{th} primary period and $\hat{p}_t$ is the estimated capture probability for the t^{th} primary period from a model. In these models, other population parameters, such as survival, immigration, emigration, and birth rates, also are incorporated. Using the maximum likelihood approach, estimation procedures involve maximizing a multidimensional surface with multiple parameters, which may not exhibit prominent peaks. Consequently, capture probabilities sometimes are estimated imprecisely, resulting in imprecise estimates of abundance.

In this chapter, a statistical method is proposed for making an inference on the abundance of a closed population using data from a CMR study with the robust design (Pollock 1982). In this method, the entire experiment is divided into a series of short time periods (primary periods). The population is assumed closed to additions and

deletions within a primary period. Within each primary period, individuals are caught during multiple secondary occasions (Figure 4.1).

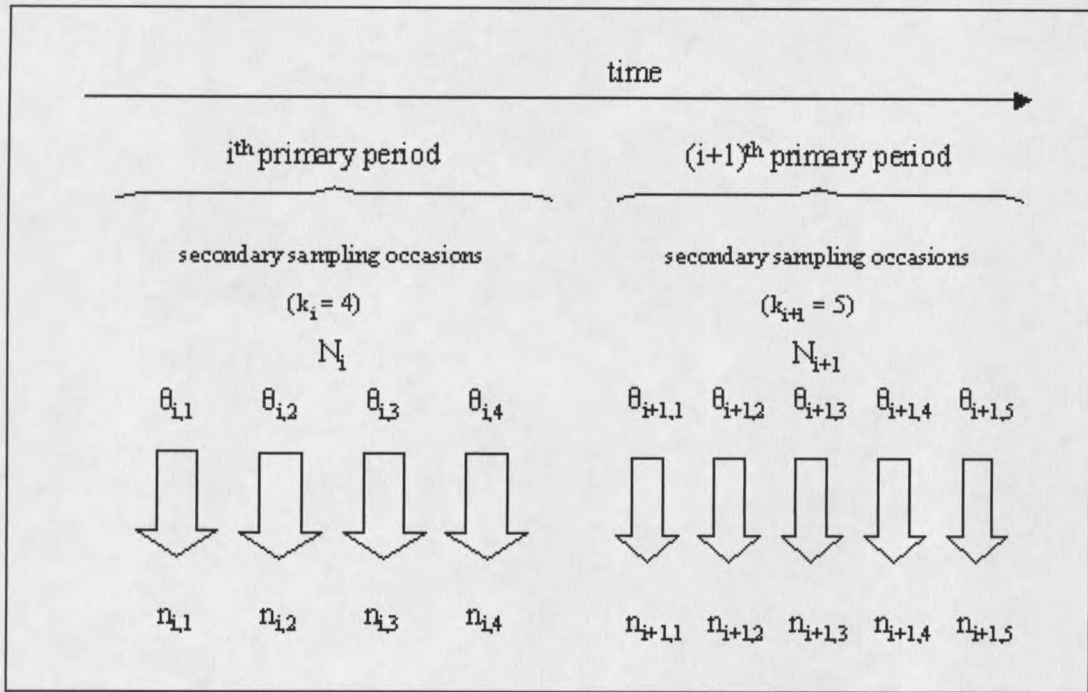


Figure 4.1. A schematic diagram of Pollock's robust design. Within each primary period, multiple samples are collected during secondary occasions with occasion-specific capture probability ($\theta_{i,j}$)

In many ecological studies and management situations, the inference on abundance for one primary period is desired. In the proposed method, a data set is divided into two groups: one primary period for which the abundance is inferred and all other primary periods from which supporting information on the capture probabilities is obtained. The assumption under this approach is that capture probabilities may vary between secondary occasions, but they are similar for the duration of the study. Consequently, the use of data from all other primary periods provides information on capture probabilities for the primary period of interest. Capture probabilities at a

sampling location are considered random samples from a beta distribution, defined by two hyperparameters. The joint distribution of these hyperparameters is found by using all primary periods except for the primary period of interest. The inference on abundance for the primary period is made by using the distribution of the hyperparameters, observed data for the primary period, and a probabilistic model. I consider beta-binomial and multinomial models. Although methods for estimating mortality, immigration and emigration rates, and movement rates have been proposed for analyzing data from the robust design (Kendall et al. 1995, Schwarz and Stobo 1997, Lindberg et al. 2001, Kendall and Bjorkland 2001), I only consider the inference for the abundance.

I use the hierarchical approach for the following two reasons: (1) capture probabilities are affected by factors independent of target animals, e.g., weather, personnel, and geographic features, and (2) capture histories and the number of individuals caught during a sampling occasion are affected by capture probabilities and the total number of available individuals. By using the hierarchical approach, I can indirectly incorporate the factors independent of target animals into the analysis. Inference for the abundance is made by using the relationship among the numbers of individuals caught, capture probabilities, and the total number of individuals available for capture.

In this chapter, I first derive the model and computational procedure. To test the performance of the proposed method, I use simulated data. I also compare the results to maximum likelihood estimates from freely available software (MARK; White and Burnham 1999).

Methods

The proposed inference procedure contains two steps. In the first step, I use the capture-recapture data for all but one primary period to make inference on the hyperparameters of capture probabilities. The posterior distribution of these hyperparameters is used to determine whether or not the data provide enough information about capture probabilities. If the posterior distribution is informative, i.e., if it is not diffuse over the parameter space, the posterior distribution is used in the second step, in which the posterior distribution of abundance in the primary period of interest is computed. If the posterior distribution from the first step is diffuse, a uniform distribution on the hyperparameters of capture probabilities is used in the second step, because no useful information on capture probabilities can be obtained from other primary periods. For making the inference on the abundance, I consider two likelihood functions, beta-binomial and multinomial. The former is appropriate when few animals are recaptured, whereas the latter is applicable when a large number of animals are recaptured. Performances of these two models are compared.

The posterior distribution of abundance is computed for a primary period, whereas the data for other primary periods are used for computing the posterior distribution of hyperparameters for capture probabilities. Although the primary period of interest, i.e., the primary period for which the posterior distribution of abundance is computed, can be any primary period, often the abundance estimate is required for the most recent primary period. Consequently, in the following analyses I make inferences on the abundance for the last primary period, whereas the data for all other primary periods are used for the inference on the hyperparameters of capture probabilities.

Assumptions

I made the following assumptions for building capture-recapture models for making the inference for the abundance of a population.

- (1) The population is assumed closed to immigration, emigration, births, and deaths during each primary period, which is a short time period, e.g., 15 days, 30 days, etc. Consequently, the population size (N_t) remains constant during the t^{th} primary period ($t = 1, 2, \dots, T$). Individuals in the population are caught and recaptured on secondary occasions ($j = 1, \dots, k_t$) within a primary period (Figure 4.1). Captured individuals are marked, and recaptured individuals are identified and released into the population. No animals are killed in the process. All previously marked individuals are identified without errors.
- (2) All individuals in the population have equal capture probability (θ_{tj}) during the j^{th} sampling occasion of the t^{th} primary period regardless of their capture history.
- (3) Captures are mutually independent events. Let $c_{t,j,l}$ = event that an individual l is caught during the j^{th} secondary occasion of the t^{th} primary period. I assume that $\{c_{t,j,l}\}$ are mutually independent for all t, j , and l .
- (4) At least two sampling occasions exist for each primary period ($\min(k_t) > 1$).
- (5) Capture probabilities (θ_{tj}) are exchangeable among all sampling occasions for the entire experiment (Figure 4.2). In other words, the joint density of capture probabilities is not dependent of the order of captures.
- (6) Capture probabilities during the j^{th} secondary occasion of the t^{th} primary period (θ_{tj}) are mutually independent for all t and j .

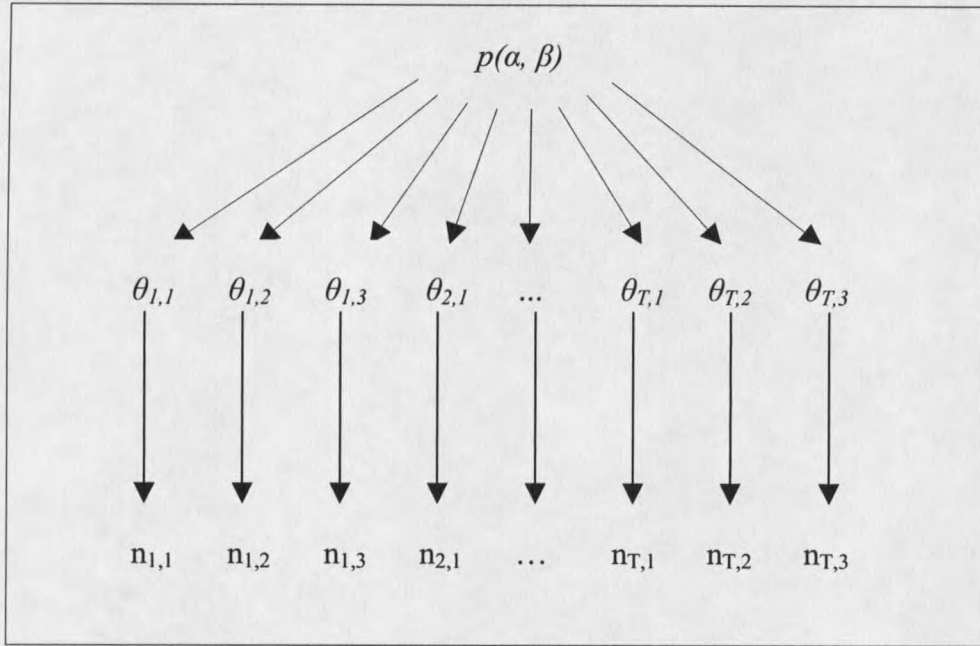


Figure 4.2. The structure of the hierarchical model for the capture-recapture model.

Models

Notation

N_t = population size during the t^{th} primary period ($t = 1, \dots, T$),

$\theta_{t,j}$ = capture probability during the j^{th} secondary occasion of the t^{th} primary period
 $(j = 1, \dots, k_t, t = 1, 2, \dots, T)$,

$U_{t,j}$ = set of all individuals in the t^{th} primary period ($t = 1, 2, \dots, T$) that are caught
for the first time on the j^{th} secondary occasion ($j = 1, \dots, k_t$),

$u_{t,j}$ = the number of individuals in $U_{t,j}$,

$n_{\omega}^{(t)}$ = the number of individuals with a particular capture history ω during the t^{th}
primary period, where ω is a non-empty subset of 0's and 1's of length k_t
that indicates recapture histories for the t^{th} primary period. $\omega \in \Omega^{(k_t)}$,

where $\Omega^{(k_t)}$ is a non-empty set of 0's and 1's that indicates all possible recapture histories of length k_t .

$n_{t,j}$ = the total number of individuals caught during the j^{th} secondary occasion of the t^{th} primary period.

For all equations I use a bold face font for vectors and regular font for scalars.

Likelihood function for capture probabilities

Recapture processes can be modeled by describing recaptures as a function of capture probabilities conditional on the first capture. First, I present an example with three secondary occasions ($k = 3$). Because I assume that capture probabilities for secondary occasions are independent of each other (assumption 7) and abundances are independent among primary periods (assumption 1), I describe a model for a primary period and omit the subscript for primary periods. The general likelihood function for $k \geq 2$ is presented in the subsequent section.

With three secondary occasions, there are six possible recapture histories: $\Omega^{(3)} = \{111, 110, 101, 100, 011, 010\}$, where $\{001, 000\}$ are omitted because individuals that belong to these capture histories have not been recaptured. The individuals that belong to the first four capture histories in $\Omega^{(3)}$, i.e., $\{111, 110, 101, 100\}$, are elements of U_1 , whereas those that belong to the last two, i.e., $\{011, 010\}$, are elements of U_2 . The likelihood function for the numbers of individuals that belong to the first four capture histories ($\mathbf{n}_{1..} = [n_{111}, n_{110}, n_{101}, n_{100}]$), conditional on the individuals caught for the first time in the first occasion (u_1) and recapture probabilities for occasions 2 and 3 (θ_2 and θ_3), is:

$$l(\mathbf{n}_{1..} | u_1, \theta_2, \theta_3) = \frac{u_1!}{n_{111}! n_{110}! n_{101}! n_{100}!} \times (\theta_2 \theta_3)^{n_{111}} [\theta_2 (1 - \theta_3)]^{n_{110}} [(1 - \theta_2) \theta_3]^{n_{101}} [(1 - \theta_2)(1 - \theta_3)]^{n_{100}}. \quad (4.2)$$

The likelihood function for the numbers of individuals that belong to the last two capture histories ($\mathbf{n}_{01.} = [n_{011}, n_{010}]$), conditional on the individuals caught for the first time in the second occasion (u_2) and the recapture probability for the third occasion (θ_3), is:

$$l(\mathbf{n}_{01.} | u_2, \theta_3) = \frac{u_2!}{n_{011}! n_{010}!} (\theta_3)^{n_{011}} (1 - \theta_3)^{n_{010}}. \quad (4.3)$$

Because captures are independent events (assumption 4), the likelihood function for these three secondary occasions is a product of the two likelihood functions:

$$\begin{aligned} l_1(\mathbf{n}_{\omega \in \Omega^{(3)}} | u_1, u_2, \theta_2, \theta_3) &= l(\mathbf{n}_{1..} | u_1, \theta_2, \theta_3) \times l(\mathbf{n}_{01.} | u_2, \theta_3) \\ &= \frac{u_1! u_2!}{\left(\prod_{\omega \in \Omega^{(3)}} n_{\omega}! \right)} \times \theta_2^{n_{111} + n_{110}} (1 - \theta_2)^{n_{101} + n_{100}} \theta_3^{n_{011} + n_{010}} (1 - \theta_3)^{n_{010}}. \end{aligned} \quad (4.4)$$

Equation (4.4) is proportional to a product of two binomial probability mass functions and can be rewritten as:

$$\begin{aligned} l_1(\mathbf{n}_{\omega \in \Omega^{(3)}} | u_1, u_2, \theta_2, \theta_3) &= \frac{u_1! u_2!}{\left(\prod_{\omega \in \Omega^{(3)}} n_{\omega}! \right)} \theta_2^{n_{11.}} (1 - \theta_2)^{u_1 - n_{11.}} \theta_3^{n_{01.}} (1 - \theta_3)^{u_2 - n_{01.}} \\ &= \frac{\prod_{j=1}^2 u_j!}{\left(\prod_{\omega \in \Omega^{(3)}} n_{\omega}! \right)} \prod_{i=2}^3 \theta_i^{n_{\omega, i}} (1 - \theta_i)^{\sum_{j=1}^i u_j - n_{\omega, i}}, \end{aligned} \quad (4.5)$$

where $\omega_{j,i}$ represents the capture history with ones in digits j and i ($j < i$) and $\omega_{j,i} \in \Omega^{(k)}$.

For example, $\omega_{1,2}$ represents {111 and 110} whereas $\omega_{,3}$ represents {111, 101, 011}.

$n_{\omega_{j,i}}$ represents the observed number of individuals that belong to the capture history $\omega_{j,i}$.

The general likelihood for $k \geq 2$ can be constructed in a similar fashion.

Recapture data are summarized into a vector of recapture histories ($\mathbf{n}_\omega$) and a vector of u_j 's ($\mathbf{u}$). The likelihood function for k secondary occasions is a product of $(k-1)$ multinomial probability mass functions with capture probabilities $\boldsymbol{\theta}$, the numbers of individuals sighted for the first time ($\mathbf{u}$), and the number of individuals that belong to capture histories $\omega_{j,i}$, similar to equation (4.5):

$$l_1(\mathbf{n}_{\omega \in \Omega^{(k)}} | \mathbf{u}, \boldsymbol{\theta}) = \prod_{j=1}^{k-1} \text{Mult}(\mathbf{n}_{\omega_j \in \Omega^{(k)}} | \mathbf{u}, \boldsymbol{\theta}), \quad (4.6)$$

where n_{ω_j} = the number of individuals that belong to $\omega_{,j}$. This likelihood, however, is proportional to a product of binomial probability mass functions as is shown in the example with $k = 3$:

$$l_1(\mathbf{n}_{\omega \in \Omega^{(k)}} | \mathbf{u}, \boldsymbol{\theta}) = \frac{\prod_{i=1}^{k-1} u_i!}{\prod_{\omega \in \Omega^{(k)}} n_\omega!} \prod_{i=2}^k \theta_i^{n_{\omega_{,i}}} (1 - \theta_i)^{\sum_{j=1}^{i-1} u_j - n_{\omega_{,i}}}. \quad (4.7)$$

With an assumption that all primary periods are independent of each other, the likelihood function for the entire experiment with T primary periods is a product of l_1 (4.7) for all primary periods:

$$l\left(\left\{\mathbf{n}_{\omega \in \Omega^{(k_t)}}\right\}_{t=1}^T \mid \left\{\mathbf{u}^{(t)}\right\}_{t=1}^T, \left\{\boldsymbol{\theta}^{(t)}\right\}_{t=1}^T\right) = \prod_{t=1}^T \left[\frac{\prod_{i=1}^{k_t-1} u_i^{(t)}!}{\prod_{\omega \in \Omega^{(k_t)}} n_\omega^{(t)}!} \prod_{i=2}^{k_t} \theta_{t,i}^{n_{\omega_{,i}}^{(t)}} (1 - \theta_{t,i})^{\sum_{j=1}^{i-1} u_j^{(t)} - n_{\omega_{,i}}^{(t)}} \right], \quad (4.8)$$

where superscript and subscript (t) index primary periods. To increase the legibility of equations, I omit braces and Ω 's in the subsequent equations. It is assumed that all ω 's for each primary occasion are appropriate subsets of the corresponding $\Omega^{(k_t)}$'s and vectors contain all primary periods and secondary occasions.

I construct a hierarchical model for the capture probabilities. In this approach, I create a population of capture probabilities from which each capture probability is drawn randomly (Figure 4.2). Capture probabilities are independently and identically distributed (i.i.d.) according to a distribution. For computational convenience, I use a beta distribution:

$$\theta_{t,i} \stackrel{i.i.d.}{\sim} \text{Beta}(\alpha, \beta), \quad (4.9)$$

where the subscript t indexes primary periods and the subscript i indexes secondary occasions. The two parameters for the beta distribution (α and β) are hyperparameters of the model that describe the distribution of $\theta_{t,i}$.

The joint posterior distribution of parameters and hyperparameters conditional on the observed data, $p(\boldsymbol{\theta}, \alpha, \beta | \mathbf{n}_\omega, \mathbf{u})$, is:

$$\begin{aligned} p(\boldsymbol{\theta}, \alpha, \beta | \mathbf{n}_\omega, \mathbf{u}) &= \frac{p(\boldsymbol{\theta}, \alpha, \beta, \mathbf{n}_\omega | \mathbf{u})}{p(\mathbf{n}_\omega | \mathbf{u})} \\ &= \frac{p(\alpha, \beta) p(\boldsymbol{\theta} | \alpha, \beta) p(\mathbf{n}_\omega | \mathbf{u}, \boldsymbol{\theta})}{p(\mathbf{n}_\omega | \mathbf{u})}, \end{aligned} \quad (4.10)$$

where $p(\alpha, \beta)$ is the unconditional joint probability density function of (α, β) , $p(\boldsymbol{\theta} | \alpha, \beta)$ is the probability density function of $\boldsymbol{\theta}$ conditional on α and β , which is a product of independent beta distributions:

$$p(\boldsymbol{\theta} | \alpha, \beta) = \prod_{t=1}^T \prod_{i=2}^{k_t} \frac{\Gamma(\alpha + \beta)}{\Gamma(\alpha)\Gamma(\beta)} \theta_{t,i}^{\alpha-1} (1 - \theta_{t,i})^{\beta-1}, \quad (4.11)$$

$p(\mathbf{n}_\omega | \mathbf{u}, \boldsymbol{\theta})$ is the probability mass function of $\mathbf{n}_\omega$ conditional on $\mathbf{u}$ and $\boldsymbol{\theta}$ (4.8), and

$$p(\mathbf{n}_\omega | \mathbf{u}) = \int \dots \int p(\boldsymbol{\theta}, \alpha, \beta, \mathbf{n}_\omega | \mathbf{u}) d\boldsymbol{\theta} d\alpha d\beta. \quad (4.12)$$

Using the product of beta distributions (4.11) and the likelihood function (4.8), the joint conditional posterior distribution of $(\boldsymbol{\theta}, \alpha, \beta)$ is:

$$p(\boldsymbol{\theta}, \alpha, \beta | \mathbf{n}_\omega, \mathbf{u}) = \frac{p(\alpha, \beta) \prod_{t=1}^T \left[\prod_{i=2}^{k_t} \left[\frac{\Gamma(\alpha + \beta)}{\Gamma(\alpha)\Gamma(\beta)} \theta_{t,i}^{\alpha-1} (1 - \theta_{t,i})^{\beta-1} \right] \left[\frac{\prod_{l=1}^{k_t} u_l^{(t)}!}{\prod_{\omega^{(t)}} n_{\omega^{(t)}}^{(t)}!} \prod_{i=2}^{k_t} \left[\theta_{t,i}^{n_{\omega,i}^{(t)}} (1 - \theta_{t,i})^{\sum_{j=1}^{i-1} u_j^{(t)} - n_{\omega,i}^{(t)}} \right] \right] \right]}{p(\mathbf{n}_\omega | \mathbf{u})}. \quad (4.13)$$

Rearranging θ 's:

$$p(\boldsymbol{\theta}, \alpha, \beta | \mathbf{n}_\omega, \mathbf{u}) = \frac{p(\alpha, \beta) \prod_{t=1}^T \left[\left[\frac{\prod_{l=1}^{k_t} u_l^{(t)}!}{\prod_{\omega^{(t)}} n_{\omega^{(t)}}^{(t)}!} \right] \prod_{i=2}^{k_t} \left[\frac{\Gamma(\alpha + \beta)}{\Gamma(\alpha)\Gamma(\beta)} \theta_{t,i}^{\alpha + n_{\omega,i}^{(t)} - 1} (1 - \theta_{t,i})^{\beta + \sum_{j=1}^{i-1} u_j^{(t)} - n_{\omega,i}^{(t)} - 1} \right] \right]}{p(\mathbf{n}_\omega | \mathbf{u})}. \quad (4.14)$$

Equation (4.14) can be simplified by multiplying the kernel of the numerator by

$$\frac{\Gamma(\alpha + \beta + \sum_{j=1}^{i-1} u_j^{(t)})}{\Gamma(\alpha + n_{\omega,i}^{(t)})\Gamma(\beta + \sum_{j=1}^{i-1} u_j^{(t)} - n_{\omega,i}^{(t)})} \frac{\Gamma(\alpha + n_{\omega,i}^{(t)})\Gamma(\beta + \sum_{j=1}^{i-1} u_j^{(t)} - n_{\omega,i}^{(t)})}{\Gamma(\alpha + \beta + \sum_{j=1}^{i-1} u_j^{(t)})} = 1. \quad (4.15)$$

The numerator becomes:

$$\begin{aligned}
p(\boldsymbol{\theta}, \alpha, \beta, \mathbf{n}_\omega | \mathbf{u}) &= p(\alpha, \beta) \times \\
&\prod_{t=1}^T \left[\frac{\prod_{l=1}^{k_t} u_l^{(t)}!}{\prod_{\omega} n_{\omega}^{(t)}!} \prod_{i=2}^{k_t} \left[\frac{\Gamma(\alpha + \beta)}{\Gamma(\alpha)\Gamma(\beta)} \frac{\Gamma(\alpha + n_{\omega,i}^{(t)})\Gamma(\beta + \sum_{j=1}^{i-1} u_j^{(t)} - n_{\omega,i}^{(t)})}{\Gamma(\alpha + \beta + \sum_{j=1}^{i-1} u_j^{(t)})} \right] \right] \times \\
&\prod_{t=1}^T \prod_{i=2}^{k_t} \left[\text{Beta}(\alpha + n_{\omega,i}^{(t)}, \beta + \sum_{j=1}^{i-1} u_j^{(t)} - n_{\omega,i}^{(t)}) \right].
\end{aligned} \tag{4.16}$$

Consequently, the joint posterior distribution of $(\boldsymbol{\theta}, \alpha, \beta)$ conditional on $\mathbf{n}_\omega$ and $\mathbf{u}$ is

$$\begin{aligned}
p(\boldsymbol{\theta}, \alpha, \beta | \mathbf{n}_\omega, \mathbf{u}) &= cp(\alpha, \beta) \times \\
&\prod_{t=1}^T \left[\prod_{i=2}^{k_t} \frac{\Gamma(\alpha + \beta)}{\Gamma(\alpha)\Gamma(\beta)} \frac{\Gamma(\alpha + n_{\omega,i}^{(t)})\Gamma(\beta + \sum_{j=1}^{i-1} u_j^{(t)} - n_{\omega,i}^{(t)})}{\Gamma(\alpha + \beta + \sum_{j=1}^{i-1} u_j^{(t)})} \text{Beta}(\alpha + n_{\omega,i}^{(t)}, \beta + \sum_{j=1}^{i-1} u_j^{(t)} - n_{\omega,i}^{(t)}) \right],
\end{aligned} \tag{4.17}$$

where

$$\frac{1}{c} = \int_0^\infty \int_0^\infty p(\alpha, \beta) \prod_{t=1}^T \prod_{i=2}^{k_t} \left[\frac{\Gamma(\alpha + \beta)}{\Gamma(\alpha)\Gamma(\beta)} \frac{\Gamma(\alpha + n_{\omega,i}^{(t)})\Gamma(\beta + \sum_{j=1}^{i-1} u_j^{(t)} - n_{\omega,i}^{(t)})}{\Gamma(\alpha + \beta + \sum_{j=1}^{i-1} u_j^{(t)})} \right] d\alpha d\beta. \tag{4.18}$$

To compute the joint posterior distribution of (α, β) , θ 's are integrated over the entire support:

$$p(\alpha, \beta | \mathbf{n}_\omega, \mathbf{u}) = \int_0^1 \int_0^1 \cdots \int_0^1 p(\boldsymbol{\theta}, \alpha, \beta | \mathbf{n}_\omega, \mathbf{u}) d\theta_{1,1} d\theta_{1,2} \cdots d\theta_{T,k_t} \tag{4.19}$$

Because θ 's in equation (4.17) appear only in the beta distributions and all θ 's are assumed independent, the product of the integrals is 1:

$$p(\alpha, \beta | \mathbf{n}_\omega, \mathbf{u}) = cp(\alpha, \beta) \prod_{t=1}^T \left[\prod_{i=2}^{k_t} \frac{\Gamma(\alpha + \beta)}{\Gamma(\alpha)\Gamma(\beta)} \frac{\Gamma(\alpha + n_{\omega,i}^{(t)})\Gamma(\beta + \sum_{j=1}^{i-1} u_j^{(t)} - n_{\omega,i}^{(t)})}{\Gamma(\alpha + \beta + \sum_{j=1}^{i-1} u_j^{(t)})} \right]. \quad (4.20)$$

To compute the conditional probability distributions of parameters and hyperparameters, however, the prior distribution on hyperparameters (i.e., $p(\alpha, \beta)$) needs to be defined. One could construct a probability distribution for the hyperparameters from available information, outside the dataset ($\mathbf{n}_\omega$ and $\mathbf{u}$). In this report, however, I assume that there is no such available information on the capture probabilities. A diffuse non-informative prior distribution, therefore, is defined for the hyperparameters. I follow the method of Gelman et al. (1995).

The hyperparameters (α, β) are re-parameterized in terms of $\text{logit}(\alpha/(\alpha+\beta)) = \ln(\alpha/\beta)$, which is the logit of the mean, and $\ln(\alpha+\beta)$, which is the natural logarithm of the ‘sample size’ in the beta distribution for θ (Gelman et al. 1995; p. 130). I use a bivariate uniform prior distribution on $(\alpha/(\alpha+\beta), 1/\sqrt{\alpha+\beta})$, which yields a proper posterior distribution (Gelman et al. 1995; p. 131). By multiplying by the appropriate Jacobian (Appendix A), this hyperprior distribution on the original scale is:

$$p(\alpha, \beta) \propto (\alpha + \beta)^{-\frac{5}{2}}, \quad (4.21)$$

and on the natural logarithm scale (Appendix B):

$$p\left(\ln\left(\frac{\alpha}{\beta}\right), \ln(\alpha + \beta)\right) \propto \alpha\beta(\alpha + \beta)^{-\frac{5}{2}}, \quad (4.22)$$

or

$$p(A, B) \propto \frac{e^{\frac{A-B}{2}}}{(1+e^A)^2}, \quad (4.23)$$

where $A = \ln(\alpha/\beta)$ and $B = \ln(\alpha + \beta)$.

The joint posterior distribution of $(A, B) = (\ln(\alpha/\beta), \ln(\alpha + \beta))$ is obtained numerically via the Metropolis algorithm (Metropolis et al. 1953, Hastings 1970). The Metropolis algorithm is a Markov chain simulation, which creates samples from a specified target distribution (Gelman et al. 1995). For each data set, I use a minimum of four independent chains with 15,000 steps within each chain. The starting point for each chain is a random point in the range $-3 < A < -1$ and $1 < B < 4$. The jumping distribution for the first chain is $\text{Unif}(-0.1, 0.1)$. To eliminate the initial sojourn steps, I discard the first 7,500 steps from each chain. The ratio between the two parameters of the jumping distribution for the next sequence is proportional to the covariance structure of the remaining 7,500 samples for A and B .

The scale reduction factor ($\sqrt{\hat{R}}$) of Gelman et al. (1995) is used to determine the convergence of a posterior distribution from a total of 30,000 pairs of A and B (7,500 times four chains). The scale reduction factor is the square root of the ratio between the marginal posterior variance and within-sequence variance:

$$\sqrt{\hat{R}} = \sqrt{\frac{\widehat{\text{var}}^+(\psi | y)}{W}} \quad (4.24)$$

where

$$\widehat{\text{var}}^+(\psi | y) = \frac{n-1}{n} W + \frac{1}{n} B, \quad (4.25)$$

$$W = \frac{1}{J} \sum_{j=1}^J \left[\frac{1}{n-1} \sum_{i=1}^n (\psi_{i,j} - \bar{\psi}_{\cdot,j})^2 \right], \quad (4.26)$$

$$B = \frac{n}{J-1} \sum_{j=1}^J (\bar{\psi}_{\cdot,j} - \bar{\psi}_{\cdot\cdot})^2, \quad (4.27)$$

$$\bar{\psi}_{.,j} = \frac{1}{n} \sum_{i=1}^n \psi_{i,j}, \text{ and} \quad (4.28)$$

$$\bar{\psi}_{..} = \frac{1}{J} \sum_{j=1}^J \bar{\psi}_{.,j}. \quad (4.29)$$

The numerator in the square root of (4.24) is the estimated marginal posterior variance, which overestimates the marginal posterior variance under the assumption that the starting distribution is appropriately overdispersed but unbiased as $n \rightarrow \infty$. For any finite n , however, the within-sequence variance W should be an underestimate of $\text{var}(\psi | y)$ because the individual sequences have not had time to range over all of the target distribution. Consequently, $\sqrt{\hat{R}}$ declines to 1 as $n \rightarrow \infty$ (Gelman et al. 1995; p. 331).

If the maximum scale reduction factor is less than or equal to 1.2, the posterior samples are retained (Gelman et al. 1995). If the convergence statistic is greater than 1.2, another sequence of four chains is computed. A maximum of four independent sequences (i.e., 16 independent chains) are computed. To avoid the serial correlation among posterior samples, a total of 7,500 random samples with replacement are drawn from these retained posterior samples and used in the inference for the abundance. These 7,500 posterior samples are transformed back into the original scale (α, β) . If the posterior distribution does not converge after four independent sequences, the uniform prior distribution is used for the hyperdistribution, i.e., $(\alpha, \beta) = (1, 1)$.

To obtain the joint probability distribution of hyperparameters for the capture probabilities during the t^{th} primary period, all data except for the t^{th} primary period are used. The prior distribution of hyperparameters for the t^{th} primary period is denoted by $p(\alpha^{(-t)}, \beta^{(-t)})$, emphasizing the deletion of data for the t^{th} primary period. These

hyperparameters, then, are used in the following analysis for modeling the abundance for the t^{th} primary period.

To make an inference on the abundance, the relationship among the abundance within the t^{th} primary period, capture probabilities, and the number of animals caught during each secondary occasion needs to be modeled. I consider two models: beta-multinomial and beta-binomial. Although both models are based on the same set of assumptions, the beta-binomial model does not use the information from recaptures. The beta-multinomial model does use the information from the number of individuals that are recaptured.

Beta-multinomial model

The observed numbers of individuals that belong to unique capture histories during the t^{th} primary period ($\mathbf{n}_{\omega \in \Omega}^{(t)}$) are modeled with a multinomial likelihood function: $\mathbf{n}_{\omega \in \Omega}^{(t)} \sim \text{mult}(N^{(t)}, \boldsymbol{\theta}^{(t)})$, where $N^{(t)}$ is the total number of catchable individuals in the population during the t^{th} primary period and $\boldsymbol{\theta}^{(t)}$ is a vector of capture probabilities with length k_t , where k_t is the number of secondary occasions within the t^{th} primary period. The full likelihood function is:

$$p(\mathbf{n}_{\omega \in \Omega}^{(t)} | N^{(t)}, \boldsymbol{\theta}^{(t)}) = \frac{N^{(t)}!}{\prod_{\omega \in \Omega} n_{\omega}^{(t)}!} \prod_{\omega \in \Omega} \theta_{\omega}^{n_{\omega}} \quad (4.30)$$

where θ_{ω} is the appropriate product of capture probabilities for the capture history ω .

For example, for $k_t = 3$, $\Omega = \{111, 110, 101, 100, 011, 010, 001, 000\}$ and $n_{000} = N -$

$(n_{111} + n_{110} + n_{101} + n_{100} + n_{011} + n_{010} + n_{001}) = N - n^{(t)}$, indicating the total number of individuals caught during the t^{th} primary period. The likelihood function for $k_t = 3$ is:

$$\begin{aligned}
p(\mathbf{n}_{\omega \in \Omega}^{(t)} | N^{(t)}, \boldsymbol{\theta}^{(t)}) = & \frac{N^{(t)}!}{n_{111}!n_{110}!n_{101}!n_{100}!n_{011}!n_{010}!n_{001}!(N^{(t)} - n^{(t)})!} \times \\
& (\theta_1\theta_2\theta_3)^{n_{111}} (\theta_1\theta_2(1-\theta_3))^{n_{110}} (\theta_1(1-\theta_2)\theta_3)^{n_{101}} \times \\
& (\theta_1(1-\theta_2)(1-\theta_3))^{n_{100}} ((1-\theta_1)\theta_2\theta_3)^{n_{011}} \times \\
& ((1-\theta_1)\theta_2(1-\theta_3))^{n_{010}} ((1-\theta_1)(1-\theta_2)\theta_3)^{n_{001}} \times \\
& ((1-\theta_1)(1-\theta_2)(1-\theta_3))^{N^{(t)} - n^{(t)}}
\end{aligned} \tag{4.31}$$

Rearranging θ 's results in the following form:

$$\begin{aligned}
p(\mathbf{n}_{\omega \in \Omega}^{(t)} | N^{(t)}, \boldsymbol{\theta}^{(t)}) = & \frac{N^{(t)}!}{n_{111}!n_{110}!n_{101}!n_{100}!n_{011}!n_{010}!n_{001}!(N^{(t)} - n^{(t)})!} \times \\
& (\theta_1)^{n_{(1)}} (\theta_2)^{n_{(2)}} (\theta_3)^{n_{(3)}} \times \\
& (1-\theta_1)^{N^{(t)} - n_{(1)}} \times (1-\theta_2)^{N^{(t)} - n_{(2)}} (1-\theta_3)^{N^{(t)} - n_{(3)}}
\end{aligned} \tag{4.32}$$

where $n_{(j)}$ is the sum of the number of individuals that belong to capture histories with 1 in the j^{th} digit. For example, $n_{(2)} = n_{111} + n_{110} + n_{011} + n_{010}$. In general, the likelihood function for a primary period with k secondary occasions can be expressed as

$$p(\mathbf{n}_{\omega \in \Omega}^{(t)} | N^{(t)}, \underline{\theta}^{(t)}) = c \frac{N^{(t)}!}{(N^{(t)} - n^{(t)})!} \prod_{j=1}^k (\theta_j)^{n_{(j)}} (1-\theta_j)^{N^{(t)} - n_{(j)}}, \tag{4.33}$$

where $c = 1/n_{111}!n_{110}!n_{101}!n_{100}!n_{011}!n_{010}!n_{001}!$, which does not depend on $N^{(t)}$ and $\boldsymbol{\theta}^{(t)}$.

Under the assumption of independent capture probabilities among capture occasions, the joint distribution of capture probabilities during the t^{th} primary period is the product of beta distributions:

$$p(\boldsymbol{\theta}^{(t)} | \boldsymbol{\alpha}^{(t)}, \boldsymbol{\beta}^{(t)}) = \prod_{j=1}^{k_t} \frac{\Gamma(\alpha_j^{(t)} + \beta_j^{(t)})}{\Gamma(\alpha_j^{(t)})\Gamma(\beta_j^{(t)})} (\theta_j^{(t)})^{\alpha_j^{(t)} - 1} (1 - \theta_j^{(t)})^{\beta_j^{(t)} - 1} \tag{4.34}$$

The joint posterior probability distribution of the abundance, capture probabilities, and the hyperparameters conditional on the recapture data during the t^{th} primary period is proportional to the following:

$$p(N^{(t)}, \theta^{(t)}, \alpha^{(t)}, \beta^{(t)} | \mathbf{n}_\omega^{(t)}) \propto p(N^{(t)}) p(\alpha^{(t)}, \beta^{(t)}) p(\theta^{(t)} | \alpha^{(t)}, \beta^{(t)}) p(\mathbf{n}_\omega^{(t)} | N^{(t)}, \theta^{(t)}) \quad (4.35)$$

Assuming that there is no prior information on the abundance, I consider the uniform distribution for the prior distribution of the abundance. If there is information on abundance, however, it should be used to construct a probability distribution for the abundance. The joint prior distribution of the hyperparameters is computed numerically during the first stage, where recapture data for all primary periods except for the t^{th} primary period are used for computing the joint distribution, which I denote

$p_{\alpha^{(-t)}, \beta^{(-t)}}(\alpha, \beta | \mathbf{n}_\omega^{(-t)}, \mathbf{u}^{(-t)})$. I use this joint distribution for the hyperparameters for all capture probabilities within the primary period:

$$p(\alpha_j, \beta_j) = p_{\alpha^{(-t)}, \beta^{(-t)}}(\alpha_j, \beta_j | \mathbf{n}_\omega^{(-t)}, \mathbf{u}^{(-t)}) \quad (4.36)$$

for all $j = 1, \dots, k_t$. The joint prior distribution for the hyperparameters of capture probabilities is the product of (4.36):

$$\begin{aligned} p(\alpha^{(t)}, \beta^{(t)}) &= p(\alpha_1^{(t)}, \beta_1^{(t)}) p(\alpha_2^{(t)}, \beta_2^{(t)}) \cdots p(\alpha_{k_t}^{(t)}, \beta_{k_t}^{(t)}) \\ &= \prod_{j=1}^{k_t} p_{\alpha^{(-t)}, \beta^{(-t)}}(\alpha_j^{(t)}, \beta_j^{(t)} | \mathbf{n}_\omega^{(-t)}, \mathbf{u}^{(-t)}) \end{aligned} \quad (4.37)$$

Consequently, using the equation (4.34):

$$p(\alpha^{(t)}, \beta^{(t)}) p(\theta | \alpha^{(t)}, \beta^{(t)}) = \prod_{j=1}^{k_t} p_{\alpha^{(-t)}, \beta^{(-t)}}(\alpha_j^{(t)}, \beta_j^{(t)} | \mathbf{n}_\omega^{(-t)}, \mathbf{u}^{(-t)}) \prod_{j=1}^{k_t} p(\theta_j^{(t)} | \alpha_j^{(t)}, \beta_j^{(t)}) \quad (4.38)$$

Substituting (4.33), (4.34), and (4.38) into (4.35):

$$\begin{aligned}
p(N^{(t)}, \boldsymbol{\theta}^{(t)}, \boldsymbol{\alpha}^{(t)}, \boldsymbol{\beta}^{(t)} | \mathbf{n}_\omega^{(t)}) &\propto p(N^{(t)}) \prod_{j=1}^{k_t} p_{\alpha^{(-t)}, \beta^{(-t)}}(\alpha_j^{(t)}, \beta_j^{(t)} | \mathbf{n}_\omega^{(-t)}, \mathbf{u}^{(-t)}) \times \\
&\left[\prod_{j=1}^{k_t} \frac{\Gamma(\alpha_j^{(t)} + \beta_j^{(t)})}{\Gamma(\alpha_j^{(t)}) \Gamma(\beta_j^{(t)})} (\theta_j^{(t)})^{\alpha_j^{(t)}-1} (1 - \theta_j^{(t)})^{\beta_j^{(t)}-1} \right] \times \\
&\left[\frac{c \Gamma(N^{(t)} + 1)}{\Gamma(N^{(t)} - n^{(t)} + 1)} \prod_{j=1}^{k_t} (\theta_j^{(t)})^{n_{(j)}^{(t)}} (1 - \theta_j^{(t)})^{N^{(t)} - n_{(j)}^{(t)}} \right]
\end{aligned} \tag{4.39}$$

Rearranging terms results in the following:

$$\begin{aligned}
p(N^{(t)}, \boldsymbol{\theta}^{(t)}, \boldsymbol{\alpha}^{(t)}, \boldsymbol{\beta}^{(t)} | \mathbf{n}_\omega^{(t)}) &\propto \frac{c p(N^{(t)}) \Gamma(N^{(t)} + 1)}{\Gamma(N^{(t)} - n^{(t)} + 1)} \times \prod_{j=1}^{k_t} p_{\alpha^{(-t)}, \beta^{(-t)}}(\alpha_j^{(t)}, \beta_j^{(t)} | \mathbf{n}_\omega^{(-t)}, \mathbf{u}^{(-t)}) \\
&\prod_{j=1}^{k_t} \frac{\Gamma(\alpha_j^{(t)} + \beta_j^{(t)})}{\Gamma(\alpha_j^{(t)}) \Gamma(\beta_j^{(t)})} (\theta_j^{(t)})^{n_{(j)}^{(t)} + \alpha_j^{(t)} - 1} (1 - \theta_j^{(t)})^{N^{(t)} - n_{(j)}^{(t)} + \beta_j^{(t)} - 1}
\end{aligned} \tag{4.40}$$

The posterior distribution of the abundance ($N^{(t)}$) is computed by integrating over $\boldsymbol{\alpha}$, $\boldsymbol{\beta}$, and $\boldsymbol{\theta}$. Using the following relationship,

$$\int_0^1 \theta_j^{n_j + \alpha_j^{(t)} + 1} (1 - \theta_j)^{N^{(t)} - n_j + \beta_j^{(t)} + 1} d\theta_j = \frac{\Gamma(n_j + \alpha_j^{(t)}) \Gamma(N^{(t)} - n_j + \beta_j^{(t)})}{\Gamma(N^{(t)} + \alpha_j^{(t)} + \beta_j^{(t)})}, \tag{4.41}$$

capture probabilities ($\boldsymbol{\theta}$) are integrated out from (4.40). To improve the legibility of the equation, I omit the superscripts on $\boldsymbol{\alpha}$ and $\boldsymbol{\beta}$:

$$\begin{aligned}
p(N^{(t)}, \boldsymbol{\alpha}, \boldsymbol{\beta} | \mathbf{n}_\omega) &\propto \frac{c p(N^{(t)}) \Gamma(N^{(t)} + 1)}{\Gamma(N^{(t)} - n^{(t)} + 1)} \prod_{j=1}^{k_t} p_{\alpha^{(-t)}, \beta^{(-t)}}(\alpha_j^{(t)}, \beta_j^{(t)} | \mathbf{n}_\omega^{(-t)}, \mathbf{u}^{(-t)}) \times \\
&\prod_{j=1}^{k_t} \frac{\Gamma(n_j + \alpha_j) \Gamma(N^{(t)} - n_j + \beta_j) \Gamma(\alpha_j + \beta_j)}{\Gamma(N^{(t)} + \alpha_j + \beta_j) \Gamma(\alpha_j) \Gamma(\beta_j)}
\end{aligned} \tag{4.42}$$

Integrating out α and β results in the posterior distribution of the abundance:

$$p(N^{(t)} | \mathbf{n}_\omega) \propto \int_0^\infty \cdots \int_0^\infty p(N^{(t)}, \alpha_j, \beta_j | \mathbf{n}_\omega) d\alpha_1 \cdots d\alpha_{k_t} d\beta_1 \cdots d\beta_{k_t} \quad (4.43)$$

Beta-binomial model

The number of captured animals during the j^{th} secondary occasion is modeled with an independent beta-binomial likelihood function: $n_j^{(t)} \stackrel{i.i.d}{\sim} \text{Beta} - \text{Bin}(N^{(t)}, \alpha_j^{(t)}, \beta_j^{(t)})$ for $j = 1, 2, \dots, k_t$. In other words, the number of animals caught during the j^{th} occasion is a binomial random variable with parameters $N^{(t)}$ and $\theta_j^{(t)}$; $n_j^{(t)} \sim \text{Bin}(N^{(t)}, \theta_j^{(t)})$, whereas the capture probability during the j^{th} occasion is a beta random variable with parameters $\alpha_j^{(t)}$ and $\beta_j^{(t)}$; $\theta_j^{(t)} \sim \text{Beta}(\alpha_j^{(t)}, \beta_j^{(t)})$. The combination of these distributions result in the beta-binomial distribution; $n_j^{(t)} \sim \text{Beta} - \text{Bin}(N^{(t)}, \alpha_j^{(t)}, \beta_j^{(t)})$.

The likelihood function for the t^{th} primary period with k_t secondary occasions, therefore, is a product of k_t independent beta-binomial probability mass functions:

$$p(\mathbf{n}_t | N^{(t)}, \alpha^{(t)}, \beta^{(t)}) = \prod_{j=1}^{k_t} \frac{\Gamma(N^{(t)} + 1) \Gamma(\alpha_j^{(t)} + n_j^{(t)}) \Gamma(N^{(t)} + \beta_j^{(t)} - n_j^{(t)}) \Gamma(\alpha_j^{(t)} + \beta_j^{(t)})}{\Gamma(n_j^{(t)} + 1) \Gamma(N_j^{(t)} - n_j^{(t)} + 1) \Gamma(\alpha_j^{(t)} + \beta_j^{(t)} + N^{(t)}) \Gamma(\alpha_j^{(t)}) \Gamma(\beta_j^{(t)})}, \quad (4.44)$$

where $\mathbf{n}^{(t)} = (n_1^{(t)}, \dots, n_{k_t}^{(t)})$, $\alpha^{(t)} = (\alpha_1^{(t)}, \dots, \alpha_{k_t}^{(t)})$, and $\beta^{(t)} = (\beta_1^{(t)}, \dots, \beta_{k_t}^{(t)})$. The inference on the abundance during the t^{th} primary period, $N^{(t)}$, is made by using the beta-binomial model (4.44), prior distributions for $(\alpha^{(t)}, \beta^{(t)})$ and $N^{(t)}$, and the observed data $(\mathbf{n}^{(t)} = (n_1^{(t)}, \dots, n_{k_t}^{(t)}))$ via a Bayesian procedure.

The joint posterior probability distribution of $N^{(t)}$, $\alpha^{(t)}$ and $\beta^{(t)}$ can be expressed by:

$$p(N^{(t)}, \alpha^{(t)}, \beta^{(t)} | \mathbf{n}^{(t)}) \propto p(N^{(t)}) \prod_{j=1}^{k_t} p(\alpha_j^{(t)}, \beta_j^{(t)}) p(n_j^{(t)} | N^{(t)}, \alpha_j^{(t)}, \beta_j^{(t)}). \quad (4.45)$$

The posterior distribution of the abundance is computed by integrating out α 's and β 's over the entire parameter space:

$$p(N^{(t)} | \mathbf{n}^{(t)}) \propto \int_0^\infty \cdots \int_0^\infty p(N^{(t)}, \alpha_j^{(t)}, \beta_j^{(t)} | \mathbf{n}^{(t)}) d\alpha_1^{(t)} \cdots d\alpha_{k_t}^{(t)} d\beta_1^{(t)} \cdots d\beta_{k_t}^{(t)} \quad (4.46)$$

Computation of the posterior distribution

To compute the posterior marginal distribution of the abundance from either model ((4.43) or (4.46)), I use a uniform prior distribution for $N^{(t)}$ under the assumption that no information is available, i.e., $p(N^{(t)}) \sim UNIF(N_{\min}^{(t)}, N_{\max}^{(t)})$, where $N_{\min}^{(t)}$ and $N_{\max}^{(t)}$ are positive integers, where $N_{\min}^{(t)} < N_{\max}^{(t)}$, and denote possible minimum and maximum population sizes. For the prior distribution of the hyperparameters, the posterior distribution from the previous analysis, i.e., $p(\alpha^{(-t)}, \beta^{(-t)})$, is used. The posterior probability distribution of $N^{(t)}$ conditional on data can be computed by numerically integrating the hyperparameters $(\alpha^{(t)}, \beta^{(t)})$ from the joint posterior distribution.

Because no algebraic solution is available for (4.43) or (4.46), I compute the posterior distribution directly using the following steps:

- (1) Compute $n_j^{(t)}$ for $j = 1, 2, \dots, k_t$, i.e., the number of individuals caught per secondary occasion within the t^{th} primary period.
- (2) For the primary period t , find the joint prior distribution for $(\alpha_j^{(t)}, \beta_j^{(t)})$ by using equation (4.20) from the previous section, i.e., $p(\alpha^{(-t)}, \beta^{(-t)} | \mathbf{n}_\omega, \mathbf{u})$.
- (3) For each possible $N^{(t)}$ between $N_{\min}^{(t)}$ and $N_{\max}^{(t)}$:
 - a. For each pair of (α, β) from the posterior distribution $p(\alpha^{(-t)}, \beta^{(-t)} | \mathbf{n}_\omega, \mathbf{u})$ compute the natural logarithm of unnormalized posterior density by using the natural logarithm of the likelihood function (4.44) for each secondary occasion and sum over all secondary occasions ($j = 1, 2, \dots, k_t$).

- b. Transform the unnormalized log-posterior to anti-log scale.
 - c. Numerically integrate over all (α, β) pairs for computing $cp(N_i | \mathbf{n}_i)$, where c is a constant.
 - d. Repeat the previous steps (a) through (c) for all possible $N^{(i)}$ values.
- (4) Normalize the posterior by setting the total probability $p(N^{(i)} | \mathbf{n}^{(i)})$ under the curve to be one.

If information on abundance is available and a probability distribution can be assigned to the abundance, it can be used in step (3). I use a common prior distribution for capture probabilities for all secondary occasions within the primary period of interest because there is no information, outside the data for this period, to distinguish them.

To summarize the inference on the abundance for the t^{th} primary period, the mode, median, and mean of the posterior distribution are reported along with the quantiles of interest. To conduct the analyses, computer programs were written in Matlab® (MathWorks).

Simulations

To evaluate the validity of the proposed method and effects of changes in the temporal sampling design and the underlying parameters on posterior distributions, I conducted a series of Monte Carlo simulations. A total of seven combinations of parameters were tested (Table 1). The true hyperparameters that created simulated data are denoted (α_0, β_0) , whereas the hyperparameters in the models are denoted with either no subscripts or subscripts other than 0.

Table 4.1. Combinations of temporal sampling design and true hyperparameters for Monte Carlo simulations. T = the number of primary periods, k = the number of secondary occasions within each primary period, (α_0, β_0) = set of the true hyperparameters for capture probabilities.

Case	T	k	(α_0, β_0)
A	3	4	(20, 2)
B	3	4	(2, 20)
C	3	4	(3, 3)
D	6	4	(2, 20)
E	12	4	(2, 20)
F	3	6	(2, 20)
G	3	8	(2, 20)

Simulation case A was used for validating the inference procedures. With consistently high capture probabilities, posterior distributions should center on the true abundance and their widths should be narrow.

To determine the effectiveness of using the two-step approach, I analyzed datasets for simulation cases A, B, and C with the two-step approach and when the hyperparameters in the analyses were set at constants ($(\alpha, \beta) = (1, 1)$). The latter approach is equal to assigning a non-informative prior distribution on capture probabilities. If the two-step approach is not useful, posterior distributions from both approaches should be the same.

To determine the effects of true capture probabilities on posterior distributions of abundance, datasets for simulation cases A, B, and C were analyzed using the two models with the two-step approach. Sampling distributions of true capture probabilities in these simulation cases corresponded to consistently high (case A), consistently low (case B), and variable (case C) capture probabilities. Corresponding beta distributions are shown in Figure 4.3. The numbers of primary periods and secondary occasions were held constant for these simulation cases.

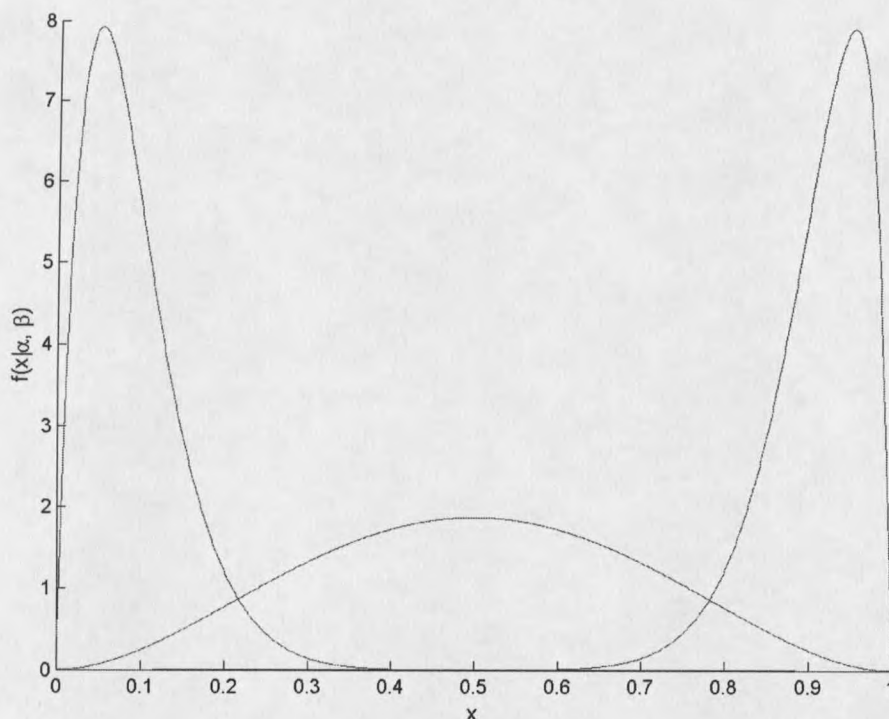


Figure 4.3. Probability density functions for three beta distributions; (mode from left to right) Beta(2, 20), Beta(3, 3), and Beta(20, 2).

To determine effects of temporal sampling designs on posterior distributions of abundance, the numbers of primary periods and secondary occasions were changed systematically, while keeping the true hyperparameters constant. Effects of the number of primary periods on posterior distributions were determined by comparing posterior distributions from three simulation cases. For these simulations, the number of primary periods was increased from three (case B) to six (case D) and twelve (case E), while the number of secondary sampling occasions per primary period and the true hyperparameters were held constant (Table 4.1).

Effects of the number of secondary sampling occasions on posterior distributions were determined by comparing posterior distributions from three simulation cases. For

these simulations, the number of secondary occasions for each primary period was increased from four (case B) to six (case F) and eight (case G), while the number of primary periods and the true hyperparameters were held constant (Table 4.1).

To create a simulated dataset, the number of individuals in a population for a primary period was drawn from a uniform distribution with the minimum 50 and maximum 500; $N^{(t)} \sim \text{UNIF}(50, 500)$. The capture probability for a sampling occasion was drawn from a beta distribution with the appropriate hyperparameters for the simulation case ($\theta_j^{(t)} \sim \text{Beta}(\alpha_0, \beta_0)$; Table 4.1). For each sampling occasion, each individual in the population was caught with the true capture probability ($\theta_j^{(t)}$) for the sampling occasion (i.e., a capture of an individual during a sampling occasion is a Bernoulli event with probability $\theta_j^{(t)}$). This process resulted in sequences of zeros and ones for all individuals in the population. These sequences, then, were summarized into the sufficient statistics for the models; the number of individuals caught for each sampling occasion, the number of recaptured individuals for each sampling occasion, and the number of new individuals captured for each sampling occasion. For each simulation case, 500 independent datasets were simulated.

These simulated datasets were analyzed using the proposed method. I used $\text{UNIF}(10, 1500)$ for the prior distribution of the abundance. By defining the prior distribution, an implicit assumption of the maximum possible population size was made for each analysis. The implication of the violation of the assumption is discussed in the discussion section.

Posterior distributions were summarized in the following statistics: widths of 95% posterior intervals, the proportion of 95% posterior intervals that included the true abundance, point estimators (mode $\hat{N}_{\text{mode}}$, mean $\hat{N}_{\text{mean}}$, and median $\hat{N}_{\text{med}}$ of the posterior distribution), differences between point estimates and true abundances ($\Delta = \hat{N} - N$), and

the ratio between the width of the 95% posterior intervals (97.5 percentile – 2.5 percentile) and the mode. The ratio is analogous to the coefficient of variation, in which variability is expressed in the same scale regardless of the size of a point estimate. I hereafter call this ratio the relative precision.

These summary statistics provided several criteria for finding a better model (beta-binomial vs. beta-multinomial) and approach (i.e., two-step vs. fixed hyperparameters). A model or approach is considered better than the other when widths of posterior intervals are narrow, point estimates are close to the true abundances, the relative precision is consistently small and unaffected by the true abundance, and the posterior intervals include the true abundance with claimed probability.

To quantify the variability of point estimators, I report the slope, intercept, and coefficient of determination (R^2) of a simple linear regression between the true abundance and a point estimator. If the point estimator provides accurate estimates for a case of simulated datasets, the regression line should have a slope of one, an intercept of zero, and a coefficient of determination (R^2) = 1.0. The slope and intercept of a regression line indicate the discrepancy between point estimates and the true abundance. An imprecise point estimator would result in a smaller value of the coefficient of determination.

To compare the performance of the proposed method to the maximum likelihood, I analyzed the same simulated datasets using software MARK (White and Burnham 1999). In MARK, ‘Closed Captures’ (CC) and ‘Huggins Closed Captures’ (HCC) models were used for the analysis. I used these models to compute the abundance estimate for the last (t^{th}) primary period of each dataset. The difference between these models is whether the abundance (N) is treated as an explicit parameter (CC) or as a derived parameter (HCC). Consequently, the number of parameters was greater for the

CC model than for the HCC model. For example, for a period with four capture occasions, the CC model contains five parameters (four capture/recapture probabilities and abundance), whereas the HCC model contains four parameters (four capture/recapture probabilities), where I set capture probabilities and recapture probabilities equal. Outputs of MARK were summarized in the point estimates (MLE) of the abundance and the 95% confidence intervals. To compute a comparable statistic to the relative precision defined previously, I computed the ratio between the width of 95% confidence interval and maximum likelihood estimate for each dataset. It is called the relative precision of MLE in this chapter.

Results

Effectiveness of the two-step approach

To determine the effectiveness of the two-step approach, three simulation sets (A, B, and C) were analyzed using two approaches: the two-step and when hyperparameters were held constant ($\alpha = 1$, $\beta = 1$). For this analysis, I only consider the beta-multinomial model because the beta-binomial likelihood function is independent of data when $\alpha = 1$ and $\beta = 1$. For simulation case A, point estimates from the two approaches indicated no apparent differences (Figure 4.4).

When the hyperparameters were fixed, point estimators did not overestimate the true abundance ($-2 \leq \Delta_{\text{mode}} \leq 0$, $-2 \leq \Delta_{\text{median}} \leq 0$, $-2 \leq \Delta_{\text{mean}} \leq 0$). For all estimators, point estimates were less than the true abundance for 36% (180/500) of the simulations. For the remainder, point estimates equaled the true abundance. Widths of 95% posterior intervals were one or two. Only 65% (325/500) of the posterior intervals included true

abundance. For all estimators, the estimated intercepts of the regression lines were 0.48, slopes were 1.00, and coefficients of determinations were 1.0 (Table 4.2).

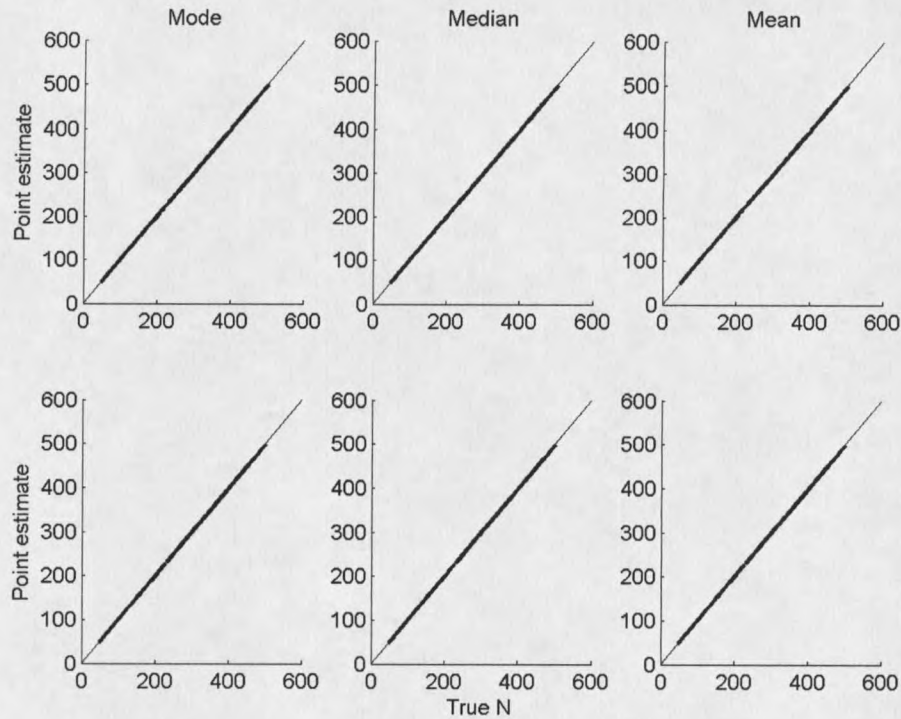


Figure 4.4. Relationships between point estimates from the beta-multinomial model and the true abundance for simulation case A. The upper three figures are results for the constant hyperparameters (1, 1), whereas for the lower three figures are for the two-step approach.

For the two-step approach, point estimators did not overestimate the true abundance ($-3 \leq \Delta_{\text{mode}} \leq 0$, $-3 \leq \Delta_{\text{median}} \leq 0$, $-3 \leq \Delta_{\text{mean}} \leq 0$). Point estimates were less than the true abundance for approximately 50% (253/500) of the simulations. For the remainder, point estimates equaled the true abundance. Widths of 95% posterior intervals ranged from one to three. Only 54% (270/500) of the posterior intervals included true abundance. For all estimators, the estimated intercept of the regression

lines were 0.92, slopes were 0.99, and coefficients of determinations were 1.0 (Table 4.2).

Table 4.2. Estimated parameters for the linear regression analysis between the true abundance and point estimates for simulation case A for the beta-multinomial model.

Approach	Point estimates	Intercept	Slope	r^2
Fixed parameters	Mode	0.48	1.00	1.000
	Median	0.48	1.00	1.000
	Mean	0.48	1.00	1.000
Two-step	Mode	0.92	0.99	1.000
	Median	0.92	0.99	1.000
	Mean	0.92	0.99	1.000

Relative precisions were similar for the two approaches. The narrow posterior intervals caused the relative precision to be an inverse function of the true abundance ($1/N$, $2/N$, or $3/N$; Figure 4.5). When the hyperparameters were fixed, the relative precision ranged from 0.002 to 0.03 with the median of 0.004, whereas for the two-step approach, it ranged from 0.002 to 0.024 with a median of 0.004 (Figure 4.5).

For simulation case B, point estimators were less accurate than for simulation case A (Figure 4.6). When the hyperparameters were fixed, point estimators were variable around the true abundance ($-280 \leq \Delta_{\text{mode}} \leq 258$, $-253 \leq \Delta_{\text{median}} \leq 387$, $-235 \leq \Delta_{\text{mean}} \leq 414$). The majority of modes (453/500), medians (380/500), and means (342/500) were less than the true abundances. Consequently, the intercepts of least squares regression lines were negative (Table 4.3). Coefficient of determinations were approximately 0.80.

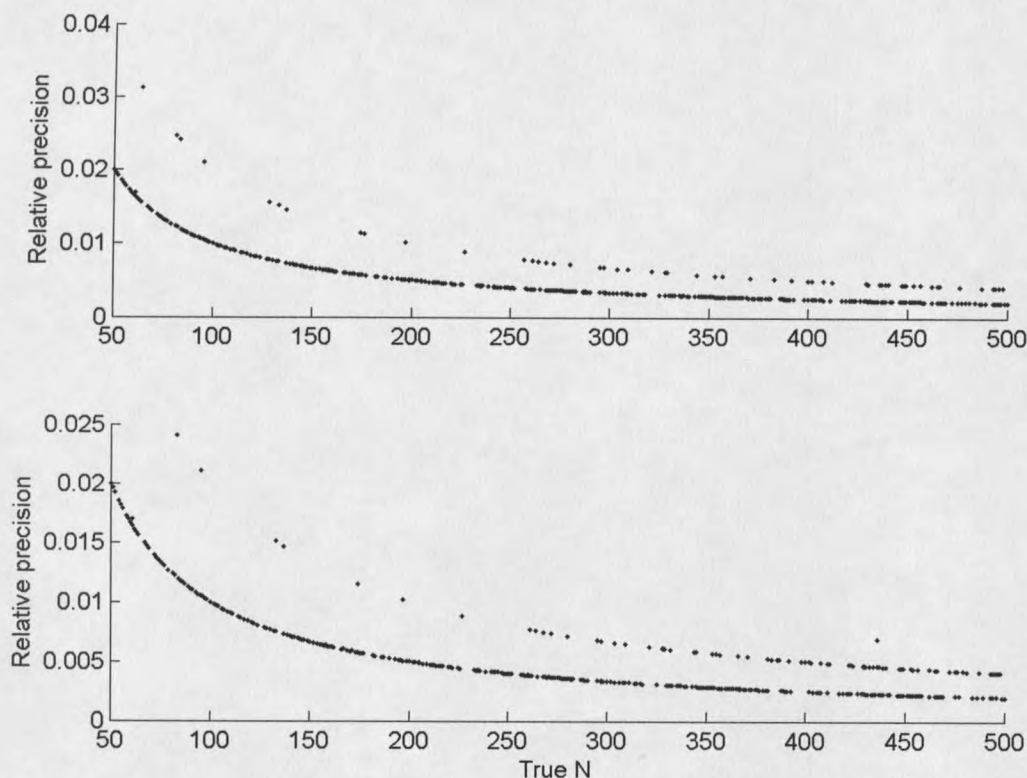


Figure 4.5. The relationships between the true abundance and relative precision for simulation case A when the beta-multinomial model was used. The upper figure is the result for the constant hyperparameters (1, 1), whereas for the lower figure is for the two-step approach.

When the same datasets were analyzed using the two-step approach, the variability in point estimators was similar to when the hyperparameters were fixed ($-264 \leq \Delta_{\text{mode}} \leq 346$, $-236 \leq \Delta_{\text{median}} \leq 479$, $-211 \leq \Delta_{\text{mean}} \leq 500$; Figure 4.6). Approximately 62% (310/500) of modes, 48% (244/500) of medians, and 40% (202/500) of means were less than the true abundances. The intercept of the regression line for the mode was negative, whereas they were positive for median and mean. Coefficient of determinations ranged between 0.70 and 0.78 (Table 4.3).

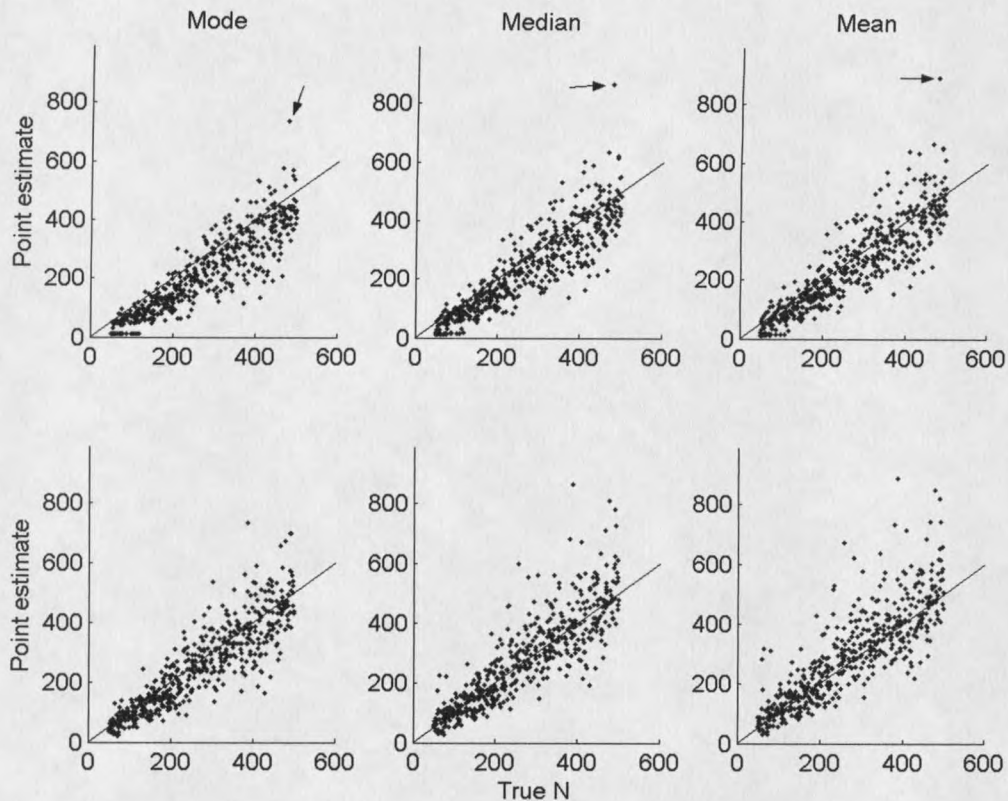


Figure 4.6. Relationships between point estimates and true abundance for simulation case B. The multinomial model was used for computing the posterior distributions. The top three panels are results for the fixed hyperparameters, whereas the bottom three panels are for the two-step approach. Solid lines indicate 45-degree lines. An arrow indicates one extreme value.

Table 4.3. Estimated parameters for the linear regression analysis between the true abundance and the point estimates for simulation case B when the beta-multinomial model was used.

Approach	Point estimates	Intercept	Slope	r^2
Fixed parameters	Mode	-35.1	0.93	0.803
	Median	-28.42	0.98	0.791
	Mean	-22.42	1.01	0.779
Two-step	Mode	-9.03	0.98	0.781
	Median	4.36	1.02	0.741
	Mean	17.05	1.03	0.707

Posterior intervals for simulation case B were wider than for simulation case A. When the hyperparameters were fixed, widths of 95% posterior intervals ranged from 11 to 1045, with the median of 215. True abundances were included in approximately 88% (438/500) of the posterior intervals. For the two-step approach, they ranged from 37 to 1208, with a median of 248, and approximately 94% (472/500) of the posterior intervals included the true abundances.

The relative precision for simulation case B was uncorrelated with the true abundance (Figure 4.7). When the hyperparameters were fixed, the relative precision ranged from 0.29 to 23.7, with the median of 1.2. Several extreme values were found for small population sizes. The relative precisions for the two-step approach ranged from 0.30 to 14.44 with the median of 1.1.

For simulation case B, the additional information from the past periods increased the proportion of posterior intervals that included the true abundance and the range of relative precision. Widths of posterior distributions, however, were comparable for both approaches.

For simulation case C, both approaches performed approximately the same (Figure 4.8). For the two-step approach, however, hyperparameters did not converge for 14 datasets. When the hyperparameters were fixed, the variability of point estimators was small ($-33 \leq \Delta_{\text{mode}} \leq 18$, $-31 \leq \Delta_{\text{median}} \leq 19$, $-30 \leq \Delta_{\text{mean}} \leq 20$; Figure 4.8). The two-step approach did not improve the variability of point estimators ($-35 \leq \Delta_{\text{mode}} \leq 17$, $-33 \leq \Delta_{\text{median}} \leq 18$, $-32 \leq \Delta_{\text{mean}} \leq 18$). Estimated regression parameters were comparable between the two approaches, where intercepts were approximately -1 , slopes were 1 , and coefficient of determinations were approximately 1.0 (Table 4.3).

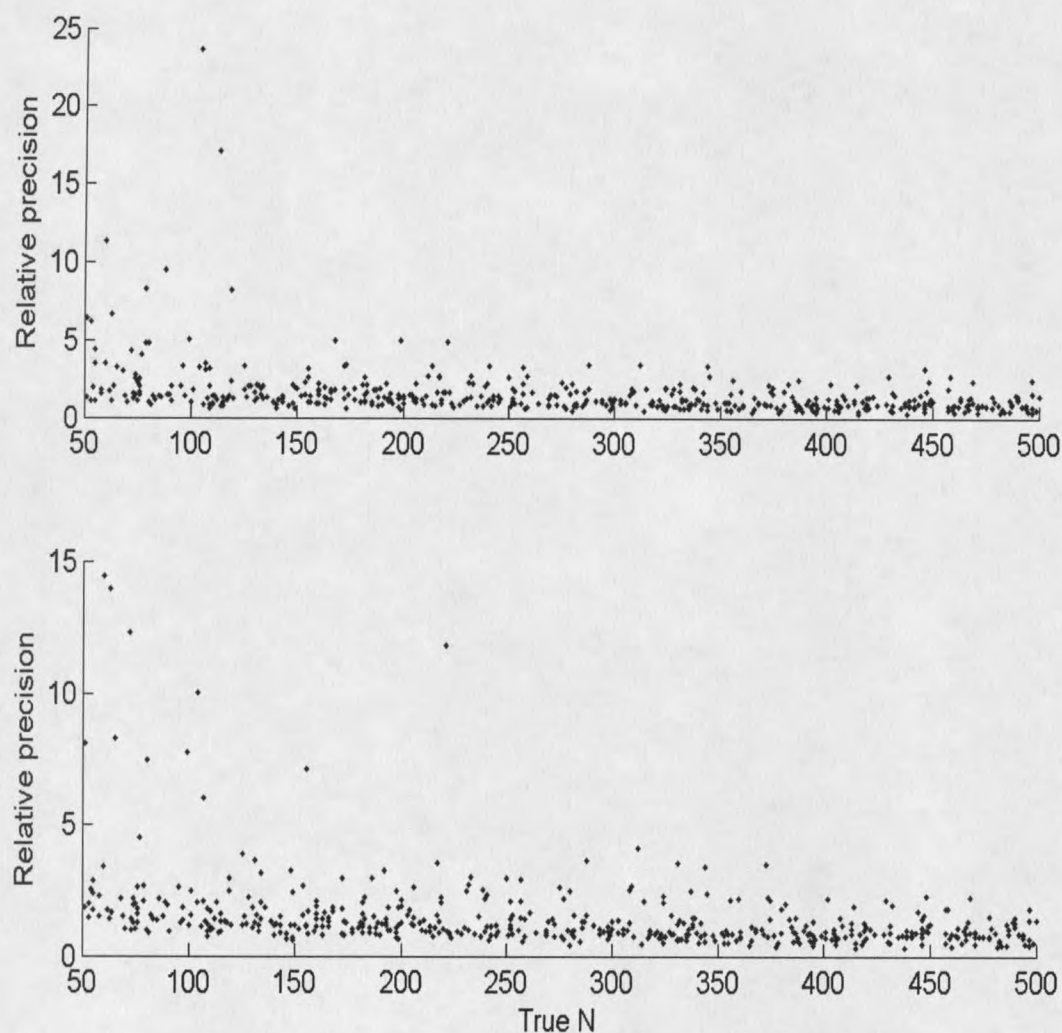


Figure 4.7. The relationships between the true abundance and relative precision for simulation case B, when the beta-multinomial model was used. The upper figure is the result for the constant hyperparameters (1, 1), whereas for the lower figure is for the two-step approach.

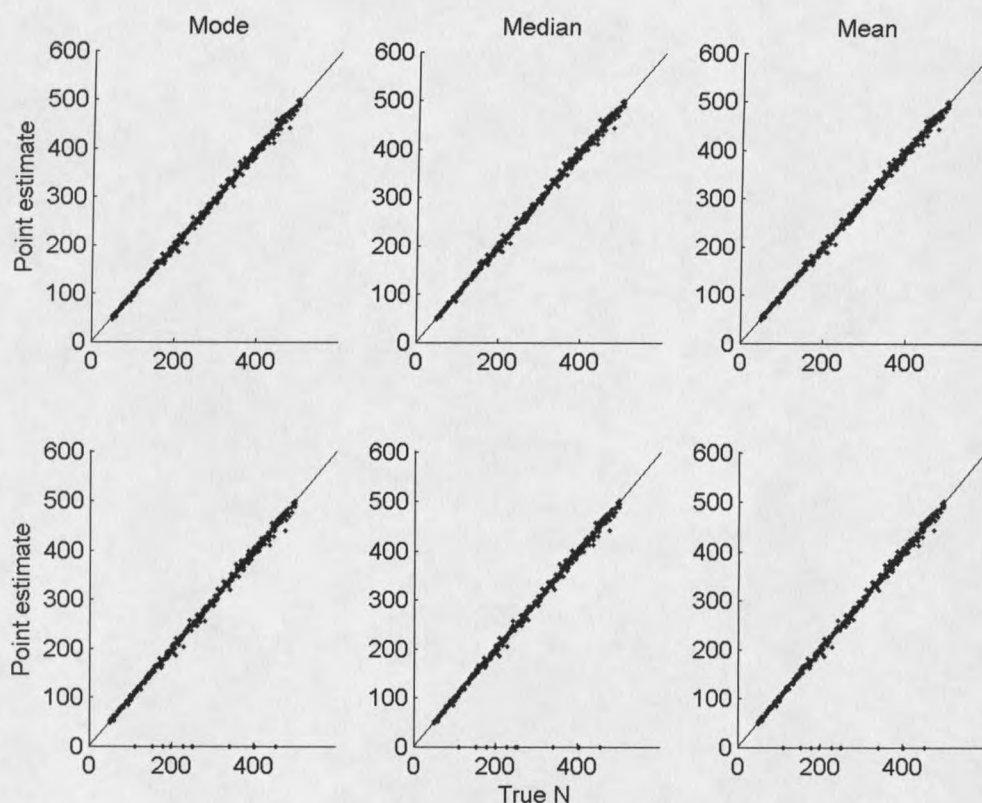


Figure 4.8. Relationships between point estimates and true abundance for simulation case C. The multinomial model was used for computing the posterior distributions. The top three panels are results for the fixed hyperparameters, whereas the bottom three panels are for the two-step approach.

Posterior intervals for simulation case C for both approaches were comparable. When the hyperparameters were fixed, widths of 95% posterior intervals ranged from 2 to 85, with the median of 16. Approximately 97% (483/500) of the posterior intervals included true abundances. For the two-step approach, they ranged from 3 to 76, with the median of 16. Approximately 96% (467/486) of the posterior intervals included true abundances.

Table 4.4. Estimated parameters for the linear regression analysis between the true abundance and the point estimates for simulation case C, using the beta-multinomial model. For intercept, slope, and r^2 , values in parentheses are for the analysis when the hyperparameters were fixed.

Model	Point estimates	Intercept	Slope	r^2
Beta-multinomial	Mode	(-1.46) -1.69	(1.00) 1.00	(0.998) 0.998
	Median	(-0.63) -1.10	(1.00) 1.00	(0.998) 0.998
	Mean	(-0.22) -0.65	(1.00) 1.00	(0.998) 0.998

The relative precisions for both approaches also were comparable (Figure 4.9). When the hyperparameters were fixed, relative precisions ranged from 0.008 to 0.389 with a median of 0.064. For the two-step approach, they ranged from 0.01 to 0.353 with the median of 0.068.

For simulation case C, results were similar when numerical convergence was reached in the two-step approach. When the convergence was not reached, the fixed-parameter approach performed better than the two-step approach.

The proposed two-step approach provided additional information for making the inference on abundance (Table 4.5). For simulation case B, approximately 95% posterior distributions included the true abundance for the two-step approach, whereas 88% included the true abundance for the fixed-parameter approach. For simulation cases A and C, no apparent differences were found between the two approaches. When the hyperparameters did not converge in simulation case C, however, the fixed-parameter approach performed better than the two-step approach.

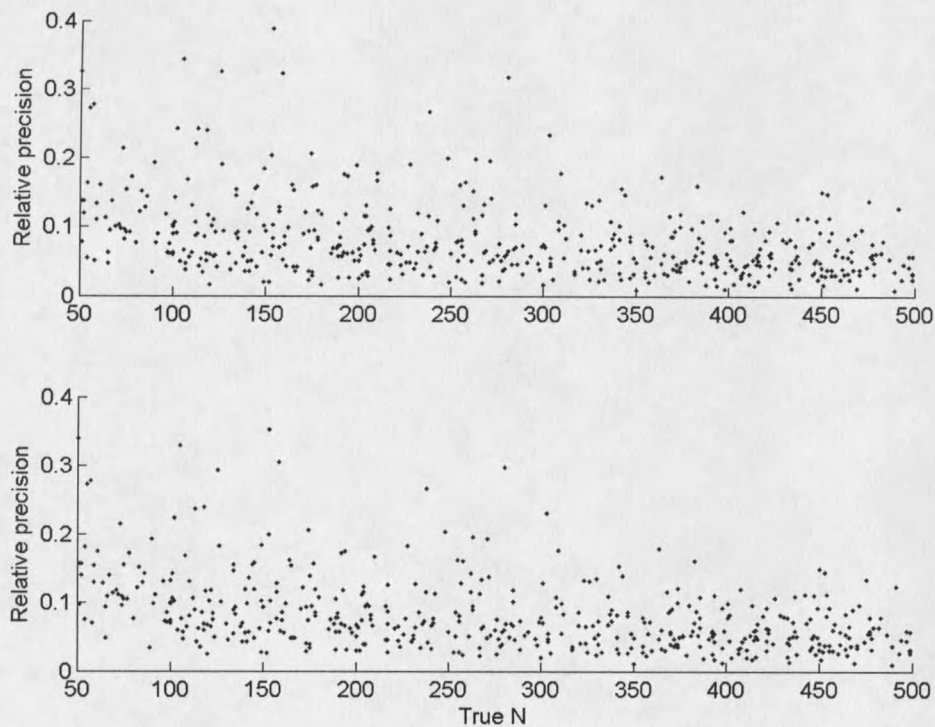


Figure 4.9. The relationships between the true abundance and relative precision for simulation case C when the beta-multinomial model was used. The upper figure is the result for the constant hyperparameters (1, 1), whereas for the lower figure is for the two-step approach.

Table 4.5. A summary of the comparison between the two-step and fixed-hyperparameter approaches. Values are minimum and maximum, whereas medians are in parentheses.

Simulation case	Fixed-hyperparameters	Two-step
A		
Widths of 95% PI	1 - 2	1 - 3
% true N captured	65%	54%
Relative precision	0.002 - 0.03 (0.004)	0.002 - 0.024 (0.004)
B		
Widths of 95% PI	11 - 1045 (215)	37 - 1208 (248)
% true N captured	88%	94%
Relative precision	0.29 - 23.7 (1.2)	0.30 - 14.44 (1.10)
C		
Widths of 95% PI	2 - 85 (16)	3 - 76 (16)
% true N captured	97%	96%
Relative precision	0.008 - 0.389 (0.064)	0.01 - 0.353 (0.068)

Effects of capture probabilities on the
posterior distribution of abundance

To assess the effects of true capture probabilities on posterior distributions of abundance, results from the two-step approach were compared among simulation cases A, B, and C. Posterior distributions of abundance from the proposed method also were compared to results from MARK.

With consistently high capture probabilities (case A), estimators from both models were precise (Figure 4.10). For the beta-binomial model, the variability of point estimators was small ($-50 \leq \Delta_{\text{mode}} \leq 33$, $-40 \leq \Delta_{\text{median}} \leq 35$, $-37 \leq \Delta_{\text{mean}} \leq 38$).

Approximately 20% (102/500) of modes, 46% (228/500) of medians, and 59% (294/500) of means were greater than the true abundance.

Slopes of the regression lines between point estimators and true abundance were approximately one and intercepts were near zero (Table 4.6). Widths of posterior intervals ranged from 4 to 130, with a median of 37. Approximately 98% (491/500) of posterior intervals included the true abundance.

Table 4.6. Estimated parameters for the linear regression analysis between the true abundance and the point estimates for simulation case A, using the two-step approach.

Model	Point estimates	Intercept	Slope	r^2
Beta-binomial	Mode	0.22	0.98	0.993
	Median	0.42	1.00	0.995
	Mean	0.75	1.00	0.995
Multinomial	Mode	0.92	0.99	0.999
	Median	0.92	0.99	0.999
	Mean	0.92	0.99	0.999
Closed capture	MLE	-0.53	1.00	1.000
Huggins closed	MLE	-0.53	1.00	1.000

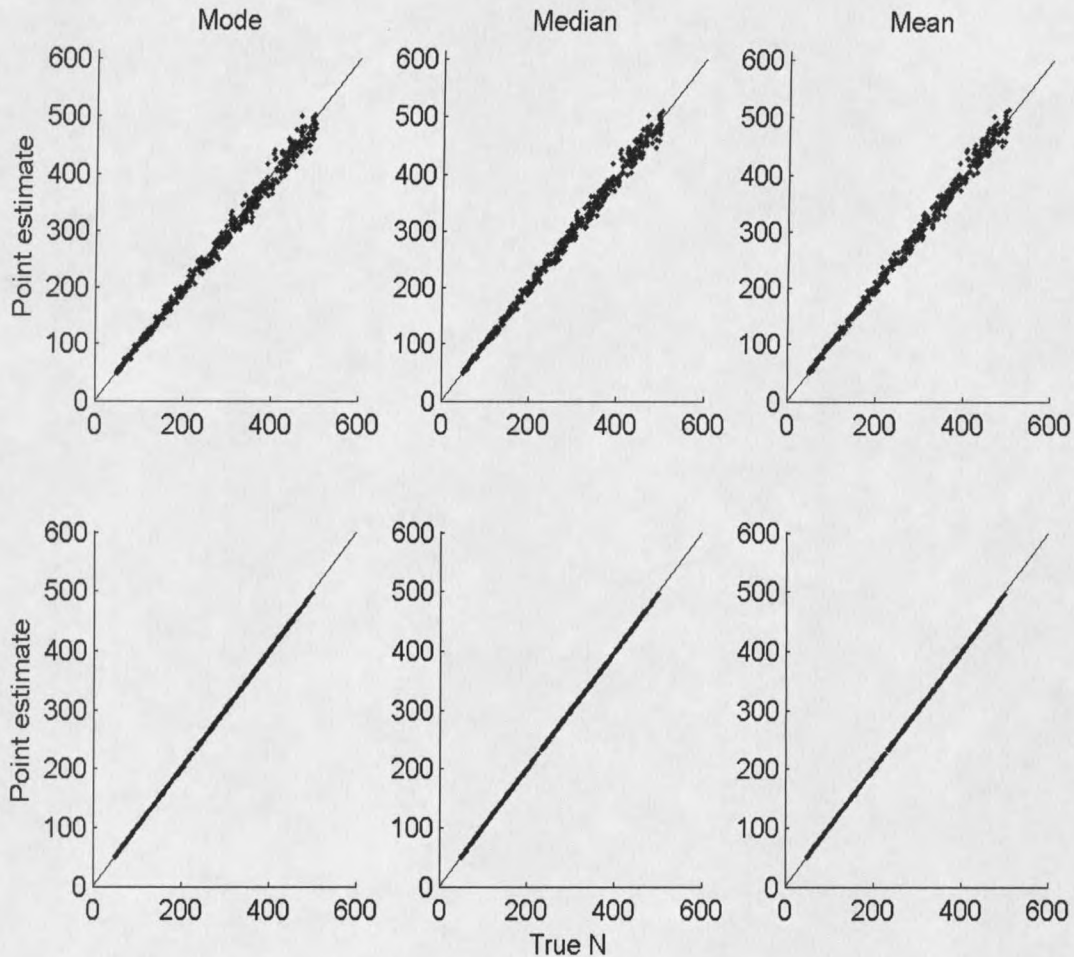


Figure 4.10. Relationships between three point estimates and the true population size for simulation case A. Solid lines indicate the 45-degree lines. The upper three panels are for the beta-binomial model whereas the lower three panels are for the multinomial model.

The relative precision was uncorrelated with the true abundance and ranged from 0.06 to 0.3 with the median of 0.14 (Figure 4.11). Results for the beta-multinomial model were discussed in the previous section.

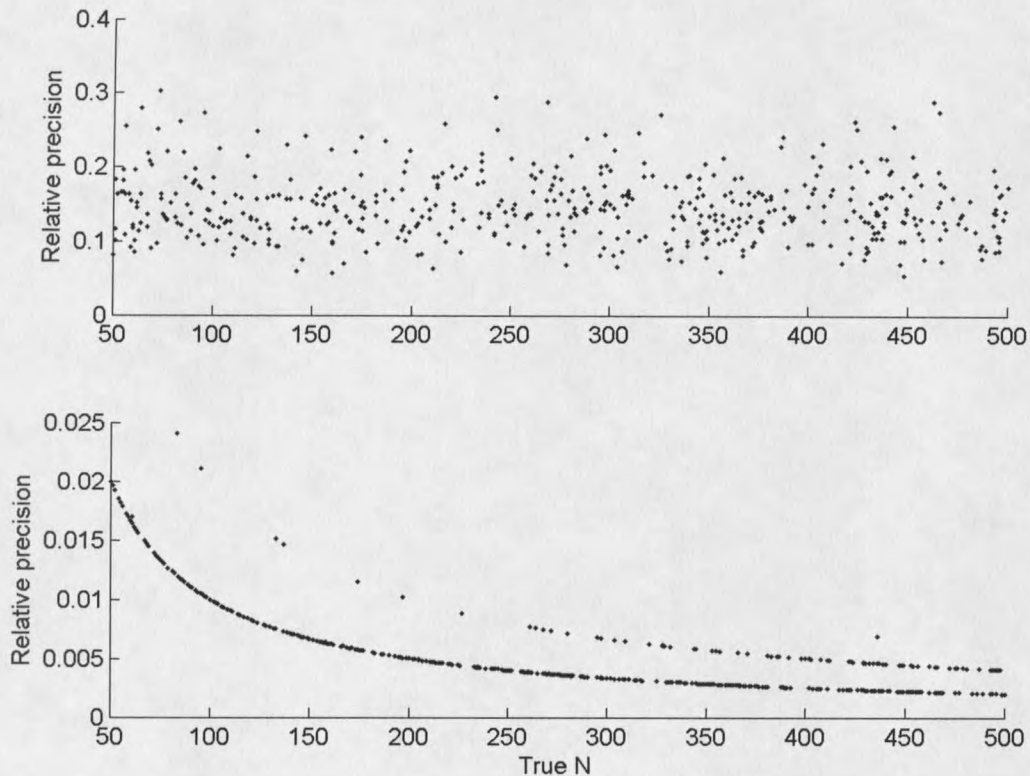


Figure 4.11. The relationship between the relative precision and the true population size for simulation case A. The upper panel is for the beta-binomial model whereas the lower panel is for the multinomial model.

When datasets for simulation case A were analyzed using MARK, MLE's underestimated the true abundance. For both models, all estimates were less than true abundances (Figure 4.12). Consequently, the intercepts of regression lines were negative (Table 4.6). For the closed capture model, widths of 95% confidence intervals ranged from 0 to 0.004, with the median of 0.00. None of the confidence intervals, however, included true abundances. Widths of confidence intervals were positively correlated with the true abundance. The relative precision of MLE was 0.00 for all results because of the extremely narrow confidence intervals. For the Huggins closed model, widths of 95%

confidence intervals ranged from 0 to 3.1, with a median of 0.002 (Figure 4.12). Only 12% (60/500) of confidence intervals included true abundances. The relative precision of MLE ranged from 0.00 to 0.027 with the median of 0.002.

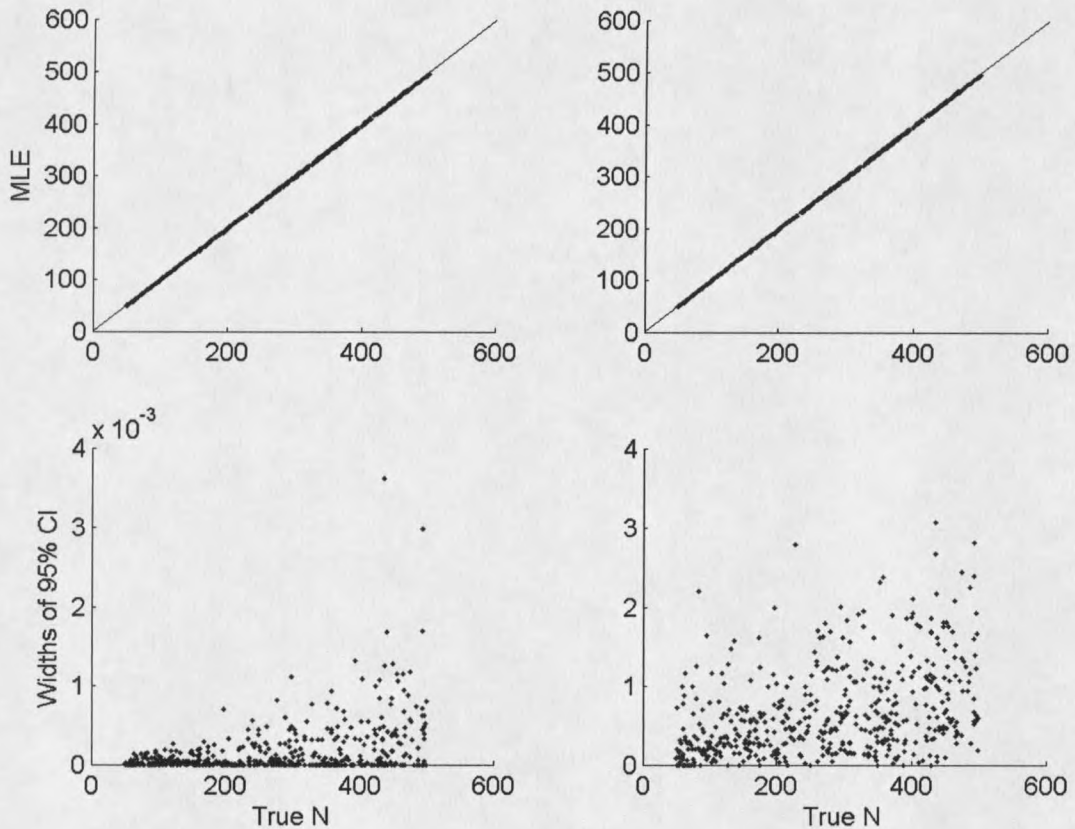


Figure 4.12. Relationships between the true abundance and maximum likelihood estimates (upper figures) and widths of 95% confidence intervals (lower figures) from MARK for simulation case A. The solid line indicates the 45-degree line. Left panels are for the closed capture model, whereas right panels are for the Huggins closed model.

When datasets for simulation case B were analyzed using the proposed method, point estimators were less precise than for simulation case A (Figure 4.13). For the beta-binomial model, point estimators were imprecise and inaccurate ($-422 \leq \Delta_{\text{mode}} \leq 1029$, -

$315 \leq \Delta_{\text{median}} \leq 751$, $-209 \leq \Delta_{\text{mean}} \leq 707$). Approximately 28% (138/500) of modes, 60% (299/500) of medians, and 74% (370/500) of means were greater than the true abundances. Consequently, the estimated intercepts of regression lines between true abundance and medians and means were positive.

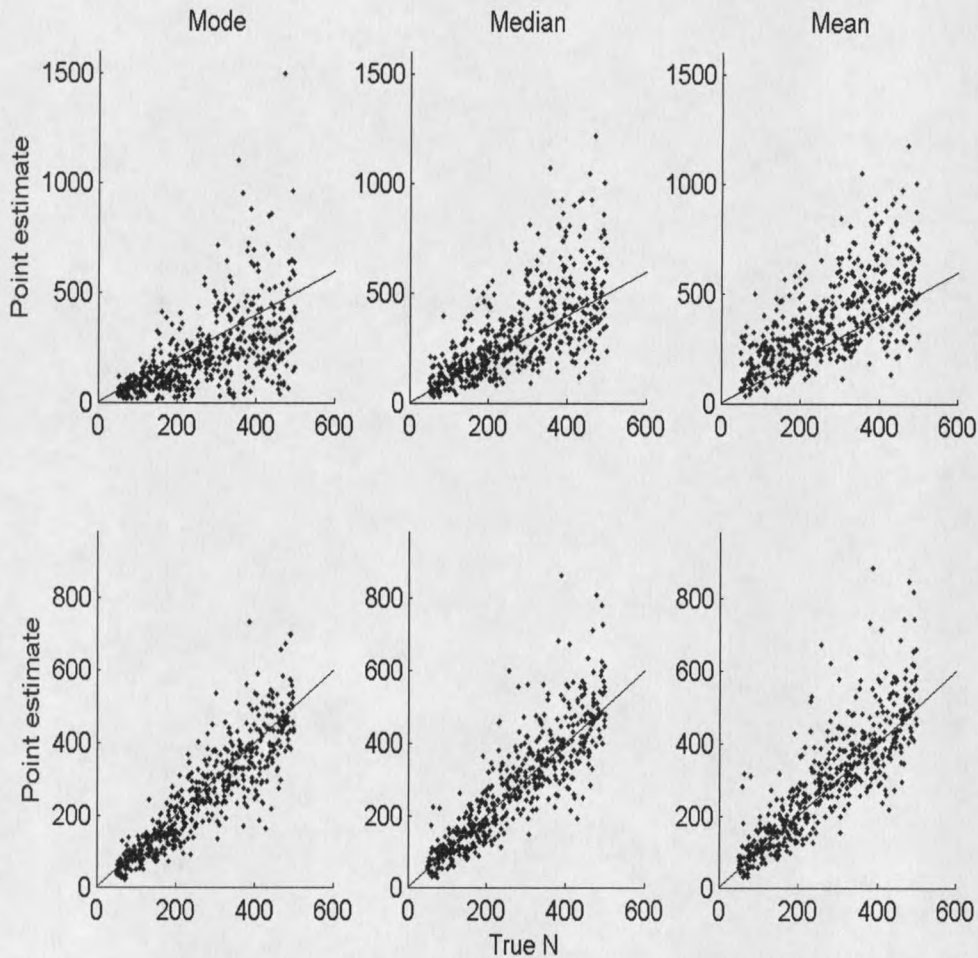


Figure 4.13. Relationships between three point estimates and the true population size for simulation case B. Solid lines indicate the 45-degree lines. Upper three panels represent the results for the beta-binomial model, whereas lower three panels represent the results for the multinomial model

Table 4.7. Estimated parameters for the linear regression analysis between the true abundance and the point estimates for simulation case B.

Model	Point estimates	Intercept	Slope	r^2
Beta-binomial	Mode	3.12	0.82	0.335
	Median	26.27	1.07	0.454
	Mean	90.73	1.06	0.457
Multinomial	Mode	-9.03	0.98	0.781
	Median	4.36	1.02	0.741
	Mean	17.05	1.03	0.707
Closed Captures	MLE	-14.63	1.17	0.404
Huggins Closed	MLE	3.37	1.10	0.518

The estimated slopes of the regression lines were approximately 1. Coefficient of determinations were approximately 0.4 (Table 4.7). Widths of the posterior intervals ranged from 54 to 1374, with the median of 1010. Approximately 99% (493/500) of the posterior intervals included the true abundance. The relative precision ranged from 0.6 to 90.1 with a median of 4.3 (Figure 4.14). The combination of low capture probabilities and few capture occasions resulted in the small number of recaptures within each primary period. Consequently, posterior distributions were imprecise. Results for the beta-multinomial model were discussed in the previous section.

When datasets for simulation case B were analyzed using MARK, unreasonable estimates were obtained for 11 datasets in the closed capture model and 12 datasets in the Huggins closed capture model. Maximum likelihood estimates for these datasets were greater than 10,000. These estimates, therefore, were deleted from the following analyses. For both models, maximum likelihood estimates were similar to those from the two-step multinomial model (Figure 4.15).

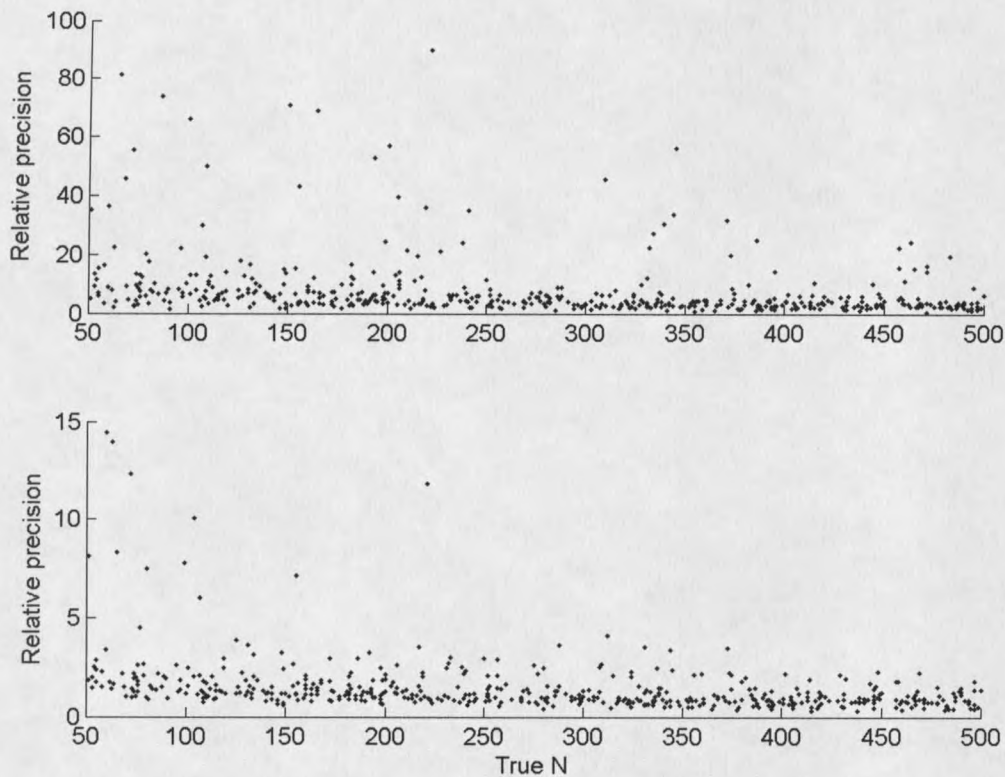


Figure 4.14. The relationship between relative precision and true population size for simulation case B. Upper panel is for the beta-binomial model, whereas the lower panel is for the multinomial model.

For the closed capture model, large estimates were found in several datasets ($191.1 < \Delta_{mle} < 2831.1$; Figure 4.15). Approximately 48% (235/489) of estimates were greater than true abundances. The estimated intercept of the regression line was -14.6 , the slope was approximately 1, and the coefficient of determination was approximately 0.4 (Table 4.7). Widths of 95% confidence intervals ranged from approximately 41 to 16146, with a median of 290 (Figure 4.15). True abundances were included in approximately 94% (463/489) of the confidence intervals. The relative precision of MLE ranged from 0.29 to 4.88 with the median of 1.16.

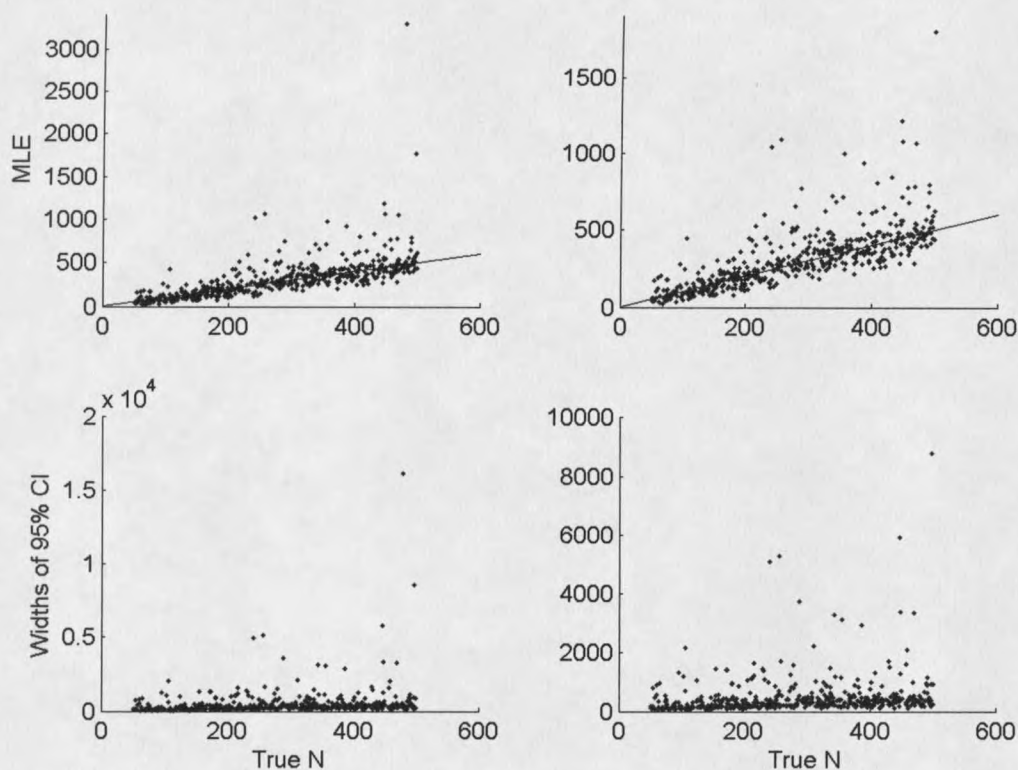


Figure 4.15. Relationships between true abundance and maximum likelihood estimates and widths of 95% confidence intervals from MARK for simulation case B. The solid line indicates the 45-degree line. Left panels are for closed capture model, whereas right panels are for Huggins closed capture model.

For the Huggins closed model, large estimates were found in several datasets ($-186.4 < \Delta_{mle} < 1315.3$; Figure 4.15). Approximately 53% (258/488) of MLE's were greater than the true abundance. The estimated intercept of the regression line was 3.4, the slope was 1.1, and the coefficient of determination was approximately 0.52 (Table 4.7). Widths of 95% confidence intervals ranged from approximately 43 to 8781, with a median of 296 (Figure 4.15). True abundances were included in approximately 95%

(465/488) of confidence intervals. The relative precision of the MLE's ranged from 0.29 to 4.85 with a median of 1.16.

For simulation case C, posterior distributions of the hyperparameters did not converge in 14 datasets. For these 14 datasets, no posterior distributions of abundances were computed. For the beta-binomial model, the point estimators were variable ($-452 \leq \Delta_{\text{mode}} \leq 254$, $-197 \leq \Delta_{\text{median}} \leq 323$, $-462 \leq \Delta_{\text{mean}} \leq 371$; Figure 4.16). The variability was positively correlated with the true abundance (Figure 4.16). Approximately 32% (156/486) of modes, 57% (278/486) of medians, and 71% (345/486) of means were greater than the true abundances.

Although the differences between the point estimates and true abundances were large, the slopes of regression lines were approximately 1.0 (Table 4.8). The coefficient of determinations ranged between 0.65 and 0.78 (Table 4.8). Widths of 95% posterior intervals ranged from 38 to 1066, with a median of 339. Approximately 97% (470/486) of the posterior intervals included the true abundance. Relative precision for the beta-binomial model was uncorrelated with the true abundance and ranged from 0.46 to 6.22 with the median of 1.42 (Figure 4.17). Results for the beta-multinomial model were discussed in the previous section.

Table 4.8. Estimated parameters for the linear regression analysis between the true abundance and the point estimates for simulation case C, using the hierarchical approach.

Model	Point estimates	Intercept	Slope	r^2
Beta-binomial	Mode	-4.36	0.91	0.654
	Median	-2.42	1.07	0.779
	Mean	0.68	1.12	0.693
Multinomial	Mode	2.75	0.98	0.964
	Median	3.36	0.98	0.964
	Mean	3.81	0.98	0.964
Closed captures	MLE	-1.33	1.00	0.998
Huggins closed	MLE	-0.62	1.00	0.998

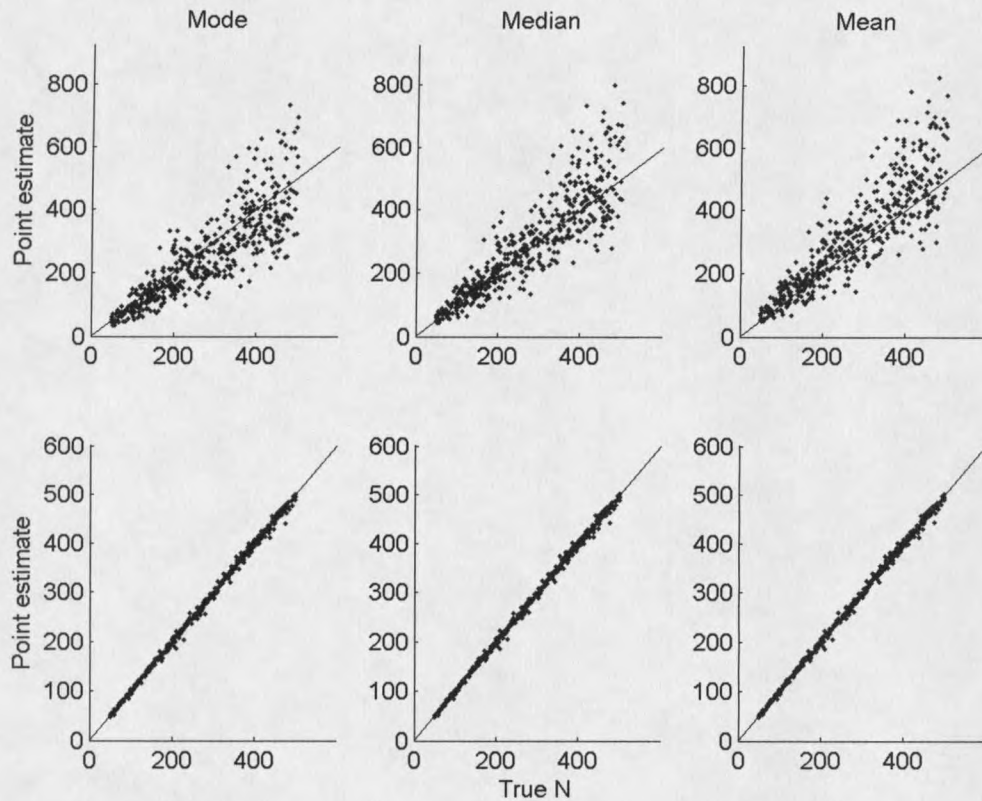


Figure 4.16. Relationships between true population size and three point estimates for simulation case C. The upper three panels are for the beta-binomial model, whereas the lower three panels are for the multinomial model. The solid lines indicate the 45-degree lines.

The numerical convergence of hyperparameters was critical for obtaining precise estimates for simulation case C. Because of the assumed broad distribution of the true hyperdistribution of capture probabilities, combined with infrequent sampling, not enough information was available for computing joint posterior distributions for the hyperparameters in some data sets. The diffuse prior distribution of the hyperparameters dominated the posterior distribution of the hyperparameters.

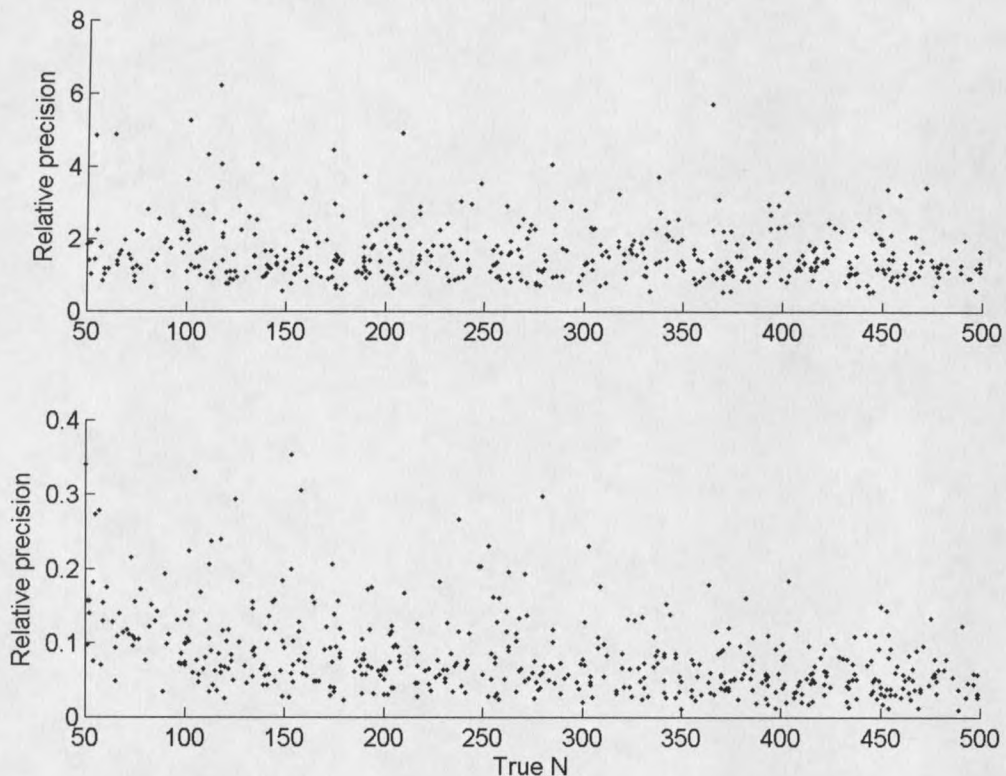


Figure 4.17. Relative precision as a function of true population size for simulation case C. Upper panel is for the beta-binomial model, whereas the lower panel is for the multinomial model.

When the same datasets for simulation case C were analyzed using MARK, maximum likelihood estimators were accurate for both models (Figure 4.18). For the closed capture model, variability of the estimator was similar to that of the multinomial model ($-31.2 \leq \Delta_{\text{mle}} \leq 18.68$). Approximately 33% (165/500) of estimates were greater than true population sizes. The estimated intercept of the regression was -1.0 , the slope was one, and the coefficient of determination was greater than 0.99 (Table 4.8). Widths of 95% confidence ranged from 0.0 to 86.7, with a median of 15.5, and 476 (95%)

included the true abundance. The relative precision of MLE ranged from 0.00 to 0.39 with the median of 0.07.

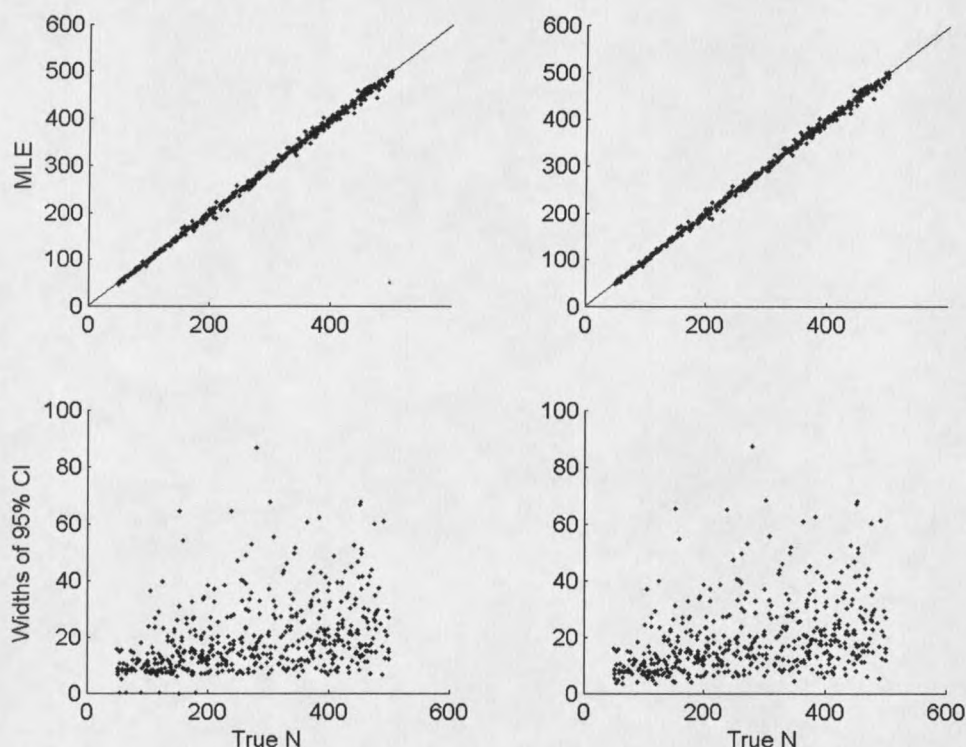


Figure 4.18. Relationships between true abundance and MLE and the widths of 95% confidence intervals for simulation set C. Left panels are for the closed capture model, whereas the right panels are for the Huggins closed model. The solid line indicates the 45-degree line.

For the Huggins closed model, the variability in the estimator was similar to that of the closed model and the multinomial model ($-30.2 \leq \Delta_{mle} \leq 19.6$). Approximately 39% (193/500) of estimates were greater than true abundances. The estimated intercept was -0.62 , the slope was one, and the coefficient of determination was greater than 0.99 (Table 4.8). Widths of 95% confidence intervals ranged from 3.3 to 87.4 with the median of 15.7. Approximately 96% (478/500) of confidence intervals included the true

abundance. The relative precision of MLE ranged from 0.01 to 0.39 with a median of 0.07.

Results for the three simulation cases (A, B, and C) indicated that greater capture probabilities resulted in more precise estimates of abundance. The comparison among these simulation cases indicated that the average capture probability affected the precision of posterior distributions more than the variance of capture probabilities for both models. When capture probabilities were variable, however, the joint posterior distributions of hyperparameters did not converge in some datasets.

In all simulation cases, results from the proposed method were comparable to those from MARK, except for simulation case A (Table 4.9). For simulation case A, posterior intervals of the Bayes hierarchical beta-multinomial model and confidence intervals of the two maximum likelihood methods were narrow (0 to 3). Consequently, true abundances were included only in a fraction of the confidence intervals (12% of HCC and 0 for CC) and the half (54%) of the posterior intervals from the Bayes hierarchical beta-multinomial model. For the Bayes hierarchical beta-binomial model, however, posterior intervals were wider (4 – 130) and true abundances were included in 98% of the posterior intervals. For simulation case B, the hierarchical beta-multinomial model resulted in the narrowest intervals around point estimates and the smallest relative precision. For simulation case C, widths of posterior and confidence intervals and the proportion of true abundances that were included in the intervals were similar for the maximum likelihood methods and the Bayes hierarchical beta-multinomial model. The Bayes approach, however, provided the most precise estimates (Table 4.9).

Table 4.9. A summary of the comparison among the hierarchical beta-binomial, the hierarchical beta-multinomial, closed captures, and Huggins closed captures models. Minimum, maximum, and median (in parentheses) are reported.

Simulation case	Beta-Binomial	Beta-Multinomial	Closed capture	Huggins closed capture
A				
Widths	4 – 130 (37)	1 – 3 (1)	0.0 – 0.004 (0.0)	0.0 – 3.1 (0.51)
% true N	98%	54%	0%	12%
Precision	0.06 – 0.3 (0.14)	0.002 – 0.024 (0.004)	0.00 – 0.00 (0.00)	0.00 – 0.27 (0.002)
B				
Widths	54 – 1,374 (1,010)	37 – 1,208 (248)	41 – 16,146 (290)	43 – 8,781 (296)
% true N	99%	94%	94%	95%
Precision	0.6 – 90.1 (4.3)	0.30 – 14.44 (1.10)	0.29 – 4.88 (1.16)	0.29 – 4.85 (1.16)
C				
Widths	38 – 1,066 (339)	3 – 76 (16)	0.0 – 86.7 (15.5)	3.3 – 87.4 (15.7)
% true N	97%	96%	95%	96%
Precision	0.46 – 6.22 (1.42)	0.01 – 0.353 (0.068)	0.29 – 4.88 (1.16)	0.29 – 4.85 (1.16)

Effects of the number of primary periods on the posterior distribution of abundance

To determine the effects of the number of primary periods on the precision of posterior distributions for abundance, posterior distributions for three simulation cases were compared. The number of primary periods was increased from three (case B), to six (case D) and twelve (case E), while keeping the number of secondary occasions and the true hyperparameters constant (Table 4.1). No analyses were conducted using MARK in this analysis because the number of primary periods did not affect the estimates for the

last primary period when the closed capture or the Huggins closed capture model was used.

For simulation case D, point estimators were similar to those for simulation case B (Figure 4.13 vs. Figure 4.19). For the beta-binomial model, the variability of point estimators was large ($-349 \leq \Delta_{\text{mode}} \leq 673$, $-327 \leq \Delta_{\text{median}} \leq 648$, $-298 \leq \Delta_{\text{mean}} \leq 632$) and increased with the true abundance (Figure 4.19). The variability, however, was less than that for simulation case B (Figure 4.13). Approximately 35% (348/500) of modes, 60% (301/500) of medians, and 74% (372/500) of means were greater than the true population sizes.

Estimated intercepts of the regression lines were positive, the slopes were approximately one, and coefficient of determinations were approximately 0.5 (Table 4.10). Widths of the 95% posterior intervals ranged from 43 to 1309, with a median of 836. True abundance was included in 96% (480/500) of posterior intervals. The relative precision ranged from 0.84 to 48.6 (median = 3.1; Figure 4.20).

Table 4.10. Estimated parameters for the linear regression analysis between the true abundance and the point estimates for simulation case D, using the hierarchical approach.

Model	Point estimates	Intercept	Slope	r^2
Beta-binomial	Mode	6.57	0.91	0.486
	Median	26.57	1.08	0.508
	Mean	65.49	1.12	0.510
Multinomial	Mode	-5.89	0.95	0.784
	Median	4.40	0.99	0.773
	Mean	12.77	1.00	0.758

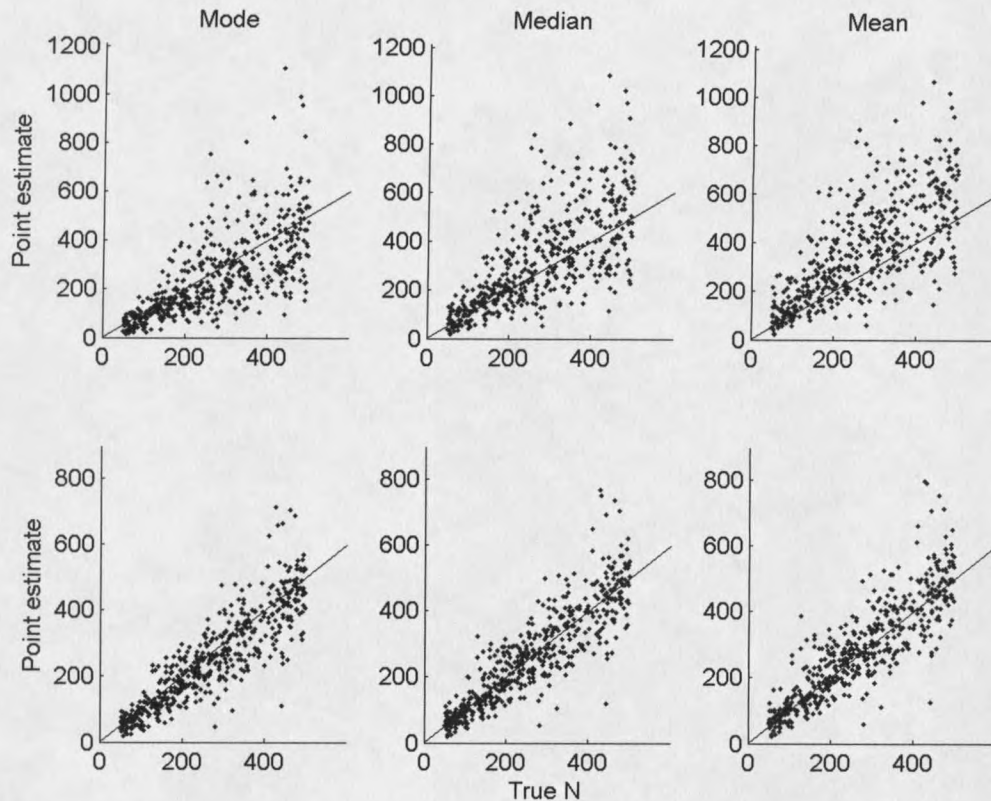


Figure 4.19. Relationships between true abundances and point estimates for simulation case D. The upper three panels are for the beta-binomial model whereas the lower three panels are for the multinomial model.

For the multinomial model, the variability in the point estimators was less than that for the beta-binomial model ($-331 \leq \Delta_{\text{mode}} \leq 286$, $-322 \leq \Delta_{\text{median}} \leq 342$, $-316 \leq \Delta_{\text{mean}} \leq 371$; Figure 4.19). The variability was less than that of simulation case B (Figure 4.13). Approximately 35% (173/500) of modes, 48% (240/500) of medians, and 55% (277/500) of means were greater than the true population sizes.

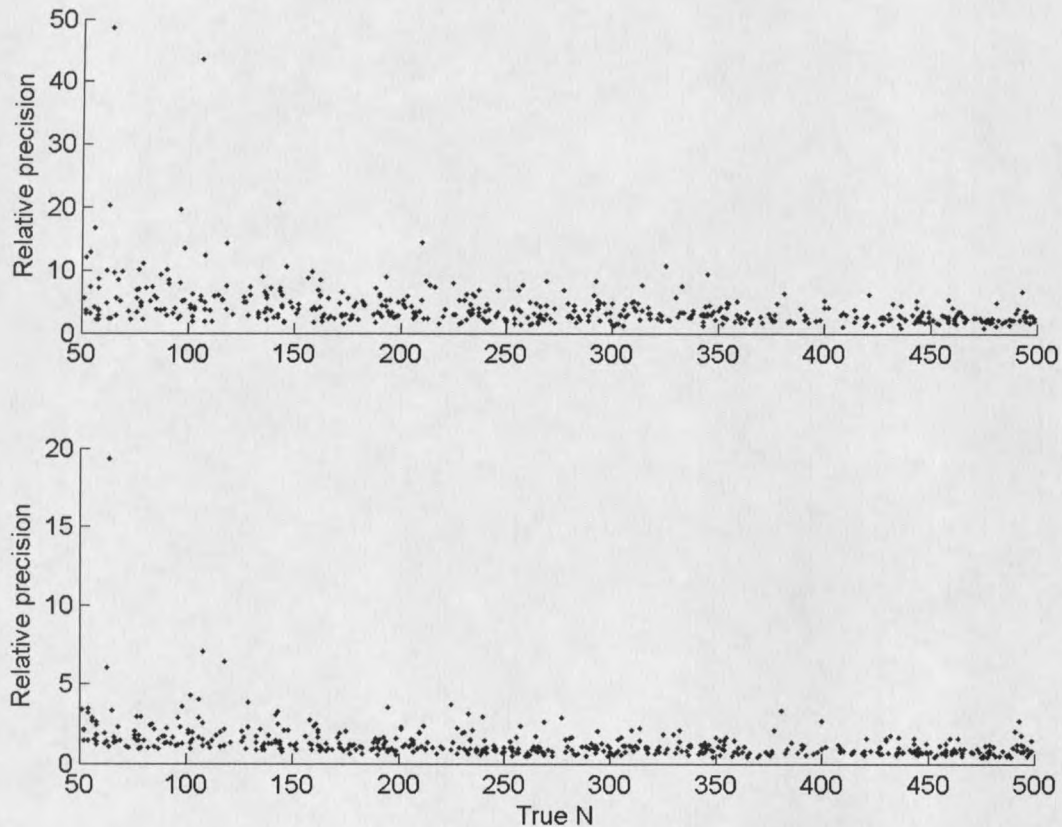


Figure 4.20. The relationship between relative precision and true abundance for simulation case D. The upper panel is for the beta-binomial model whereas the lower panel is for the multinomial model.

The estimated intercepts of the regression analyses were positive for medians and means, whereas it was negative for the mode. The slopes of regression lines were approximately one and the coefficients of determinations were between 0.76 and 0.78 (Table 4.10). Widths of 95% posterior intervals ranged from 32 to 959, with a median of 223. Approximately 92% (460/500) of the posterior intervals included the true abundance. The relative precision ranged from 0.39 to 19.3 (median = 1.0; Figure 4.20).

As the number of primary periods was increased to 12 (simulation case E), the variability in point estimators decreased from simulation cases B and D. For the beta-binomial model, the variability in point estimators increased with the true abundance ($-275 \leq \Delta_{\text{mode}} \leq 502$, $-238 \leq \Delta_{\text{median}} \leq 564$, $-233 \leq \Delta_{\text{mean}} \leq 573$; Figure 4.21). The variability, however, was less than for simulation case D (Figure 4.19). Approximately 42% (212/500) of modes, 67% (334/500) of medians, and 78% (390/500) of means were greater than the true population sizes.

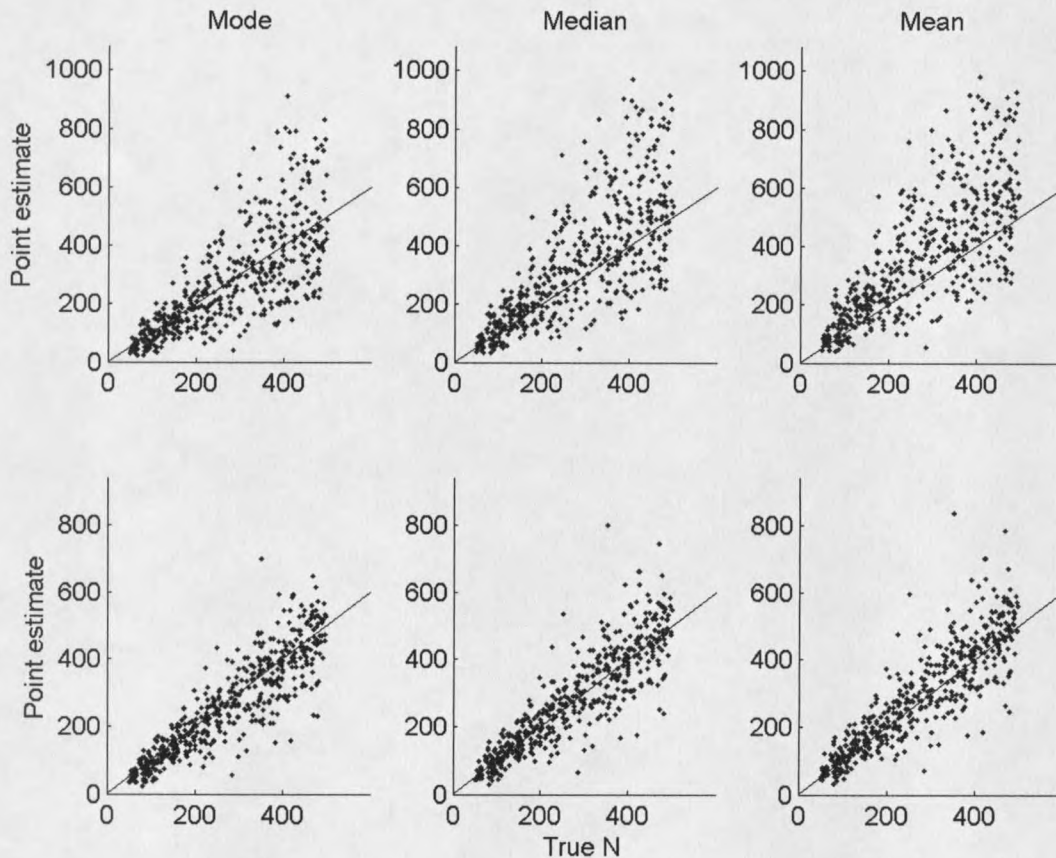


Figure 4.21. Relationships between the true population size and three point estimates for simulation case E. The upper three panels are for the beta-binomial model, whereas the lower three panels are for the multinomial model.

Estimated intercepts of the regression analyses were positive for medians and means, whereas it was negative for the mode. Estimated slopes of the regression lines were approximately one and coefficients of determinations were approximately 0.57 (Table 4.10). Widths of 95% posterior intervals ranged from 83 to 1236, with a median of 671. Approximately 95% (477/500) of the posterior intervals included the true abundance. The relative precision ranged from 1.05 to 27.9 (median = 2.5; Figure 4.22). The outlier in the relative precision (27.9) was the result of recapturing only one individual in the primary period when the true population was small ($N = 65$). The outlier was caused by the wide posterior interval for the dataset, when the mode was 27. For the remainder of datasets, the relative precision was less than 10.

For the multinomial model, the variability in point estimators for simulation case E was less than that for case D ($-260 \leq \Delta_{\text{mode}} \leq 347$, $-242 \leq \Delta_{\text{median}} \leq 447$, $-234 \leq \Delta_{\text{mean}} \leq 484$; Figure 4.21). Approximately 41% (205/500) of modes, 54% (272/500) of medians, and 59% (297/500) of means were greater than the true population size. Estimated intercepts of the regression analyses were positive for medians and means, whereas it was negative for the mode.

Table 4.11. Estimated parameters for the linear regression analysis between the true abundance and the point estimates for simulation case E, using the hierarchical approach.

Model	Point estimates	Intercept	Slope	r^2
Beta-binomial	Mode	-1.76	1.01	0.566
	Median	12.57	1.16	0.569
	Mean	36.51	1.22	0.576
Multinomial	Mode	-7.47	0.99	0.795
	Median	2.37	1.02	0.782
	Mean	9.32	1.03	0.771

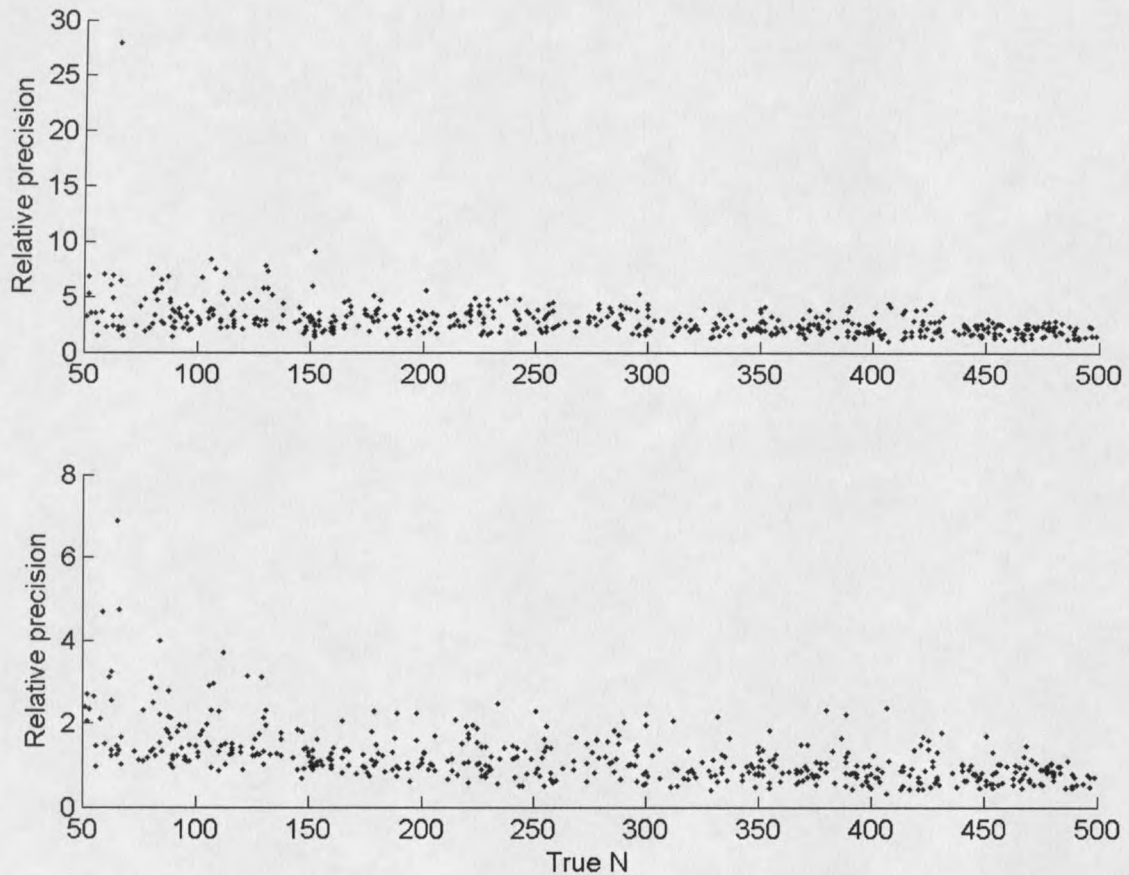


Figure 4.22. Relationships between the relative precision and the true abundance for simulation case E. The upper figure is for the beta-binomial model, whereas the lower figure is for the multinomial model.

Estimated slopes of the regression lines were approximately one and the coefficients of determinations were approximately 0.8 (Table 4.11). Widths of 95% posterior intervals ranged from 55 to 1035, with a median of 233. Approximately 93% (466/500) of the posterior intervals included the true abundance. The relative precision ranged from 0.33 to 6.88 (median = 1.01). Although the relative precision improved as the number of primary periods increased from three (Figure 4.14) to six and twelve

(Figure 4.20 and Figure 4.22), no prominent improvement in the precision of posterior distributions of abundance was found when the number of primary periods increased.

Table 4.12. A summary of the comparison among the hierarchical beta-binomial, the hierarchical beta-multinomial, closed captures, and Huggins closed captures models. Values are minimum and maximum, whereas medians are in parentheses.

Simulation case	Beta-Binomial	Beta-Multinomial
B		
Widths	54 – 1374 (1010)	37 – 1208 (248)
% true N	99%	94%
Precision	0.6 – 90.1 (4.3)	0.30 – 14.44 (1.10)
D		
Widths	43 – 1,309 (836)	32 – 959 (223)
% true N	96%	92%
Precision	0.84 – 48.6 (3.1)	0.39 – 19.3 (1.0)
E		
Widths	83 – 1,236 (671)	55 – 1,035 (233)
% true N	95%	93%
Precision	1305 – 27.9 (2.5)	0.33 – 6.88 (1.01)

Effects of the number of secondary occasions on the posterior distribution of abundance

To determine the effects of the number of secondary occasions on the precision of posterior distributions of abundance, posterior distributions from three simulation cases were compared. In these cases, the number of secondary occasions was increased from four (case B) to six (case F) and eight (case G), while keeping the number of primary

periods and the true hyperparameters constant (Table 4.1). These datasets also were analyzed using MARK.

For simulation case F, results from the beta-binomial model indicated the variability in the point estimators was large and increased with the true abundance ($-306 \leq \Delta_{\text{mode}} \leq 787$, $-291 \leq \Delta_{\text{median}} \leq 778$, $-281 \leq \Delta_{\text{mean}} \leq 766$; Figure 4.23). The variability, however, was less than for simulation case B (Figure 4.13). Approximately 35% (174/500) of modes, 56% (280/500) of medians, 70% (351/500) of means were greater than the true abundance.

Table 4.13. Estimated parameters for the linear regression analysis between the true abundance and the point estimates for simulation case F, using the hierarchical approach.

Model	Point estimates	Intercept	Slope	r^2
Beta-binomial	Mode	-3.17	0.96	0.542
	Median	6.71	1.11	0.558
	Mean	27.29	1.17	0.567
Multinomial	Mode	-1.32	0.97	0.904
	Median	5.65	0.98	0.900
	Mean	10.02	0.98	0.895
Closed capture	MLE	9.37	0.98	0.865
Huggins closed	MLE	12.53	0.98	0.861

The estimated intercepts of the regression lines were positive for medians and means, whereas it was negative for the mode (Table 4.13). Estimated slopes of the regression lines were approximately one and the coefficients of determinations were approximately 0.55. Widths of 95% posterior intervals ranged from 58 to 1272, with the median of 628. Approximately 97% (486/500) of the posterior intervals included the true abundance. The relative precision ranged from 0.76 to 17.16 with a median of 2.57.

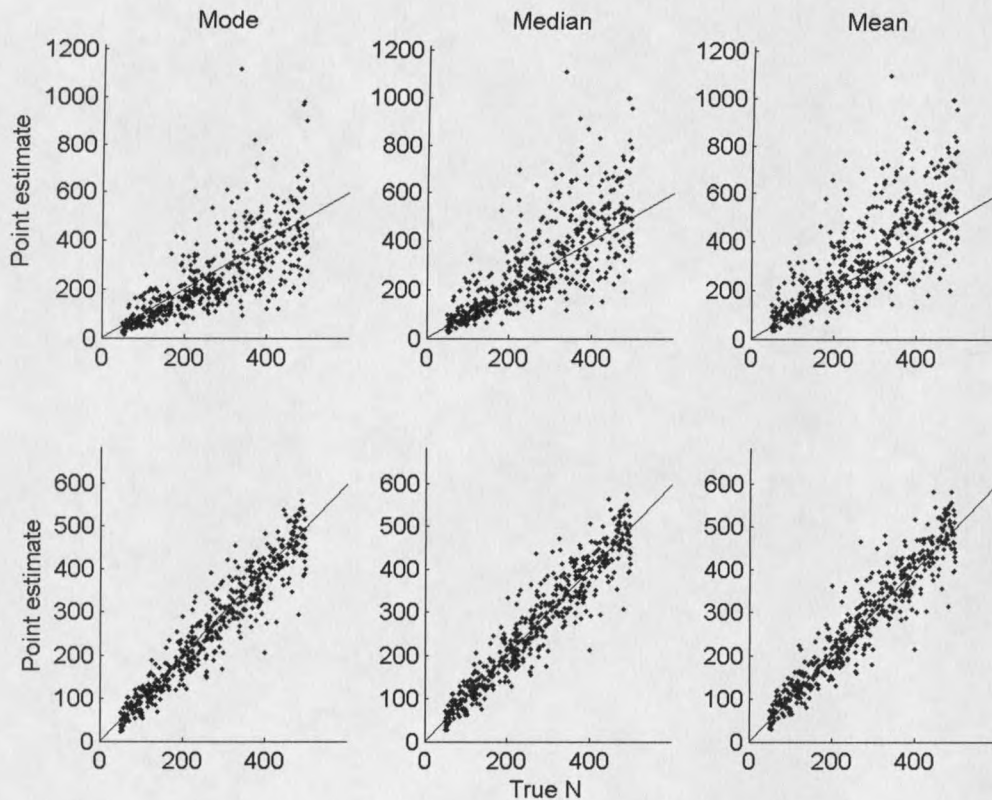


Figure 4.23. Relationships between the true abundance and three point estimates in simulation case F. The solid lines indicate 45-degree lines. Upper three panels were for the beta-binomial model, whereas the lower three panels were for the multinomial model.

For the beta-multinomial model, the variability in the point estimators was less than for the beta-binomial model ($-195 \leq \Delta_{\text{mode}} \leq 127$, $-189 \leq \Delta_{\text{median}} \leq 168$, $-186 \leq \Delta_{\text{mean}} \leq 196$; Figure 4.23). The variability, also, was less than for simulation case B (Figure 4.13). Approximately 41% (204/500) of modes, 50% (250/500) of medians, and 55% (276/500) of means were greater than true abundances.

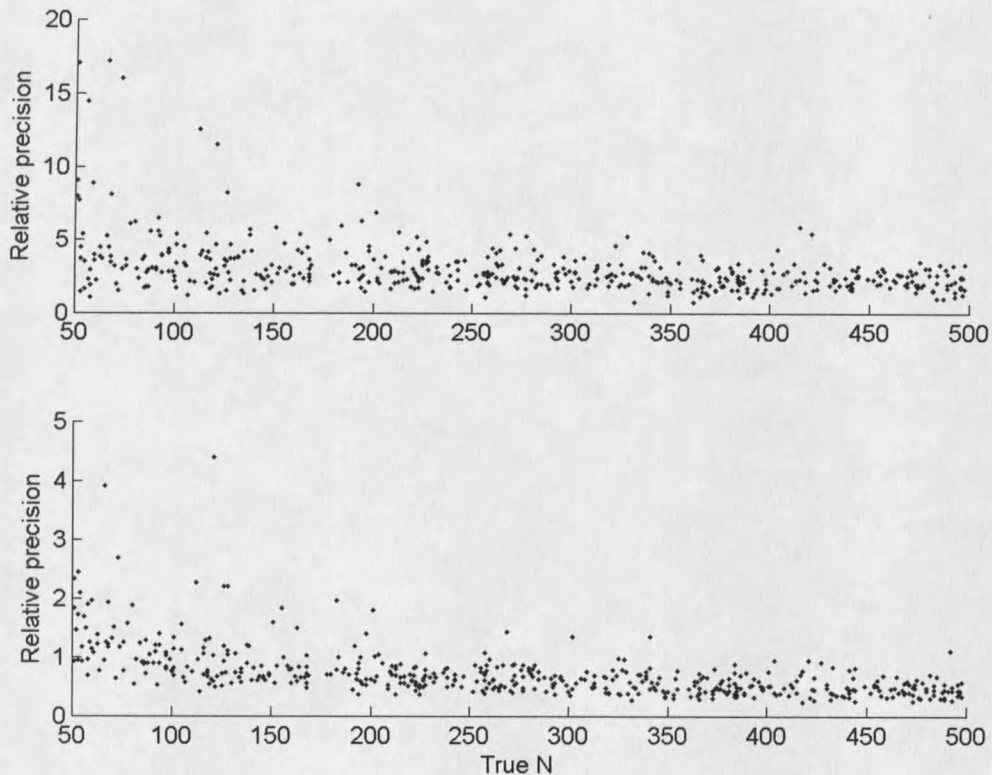


Figure 4.24. The relationship between the relative precision and the true abundance for simulation case F. The upper figure is for the beta-binomial model, whereas the lower figure is for the multinomial model.

The estimated intercepts of the regression lines were positive for the median and mean, whereas it was negative for the mode (Table 4.13). Estimated slopes of the regression lines were approximately one and the coefficients of determinations were 0.9 (Table 4.13). Widths of 95% posterior intervals ranged from 35 to 571, with a median of 146. Approximately 94% (470/500) of the posterior intervals included the true abundance. The relative precision ranged from 0.23 to 4.39 with the median of 0.62. For both models, large values of the relative precision were found for small population sizes (Figure 4.24).

When the same datasets for simulation case F were analyzed using MARK, the variability of maximum likelihood estimators were small for both models (Figure 4.25). Results from one dataset were discarded because these estimates (MLE's > 10,000) were unreasonable. For the closed capture model, the variability in the estimator was less than for simulation case B ($-135.0 < \Delta_{mle} < 311.2$; Figure 4.25). Approximately 52% (258/499) of estimates were greater than the true population sizes.

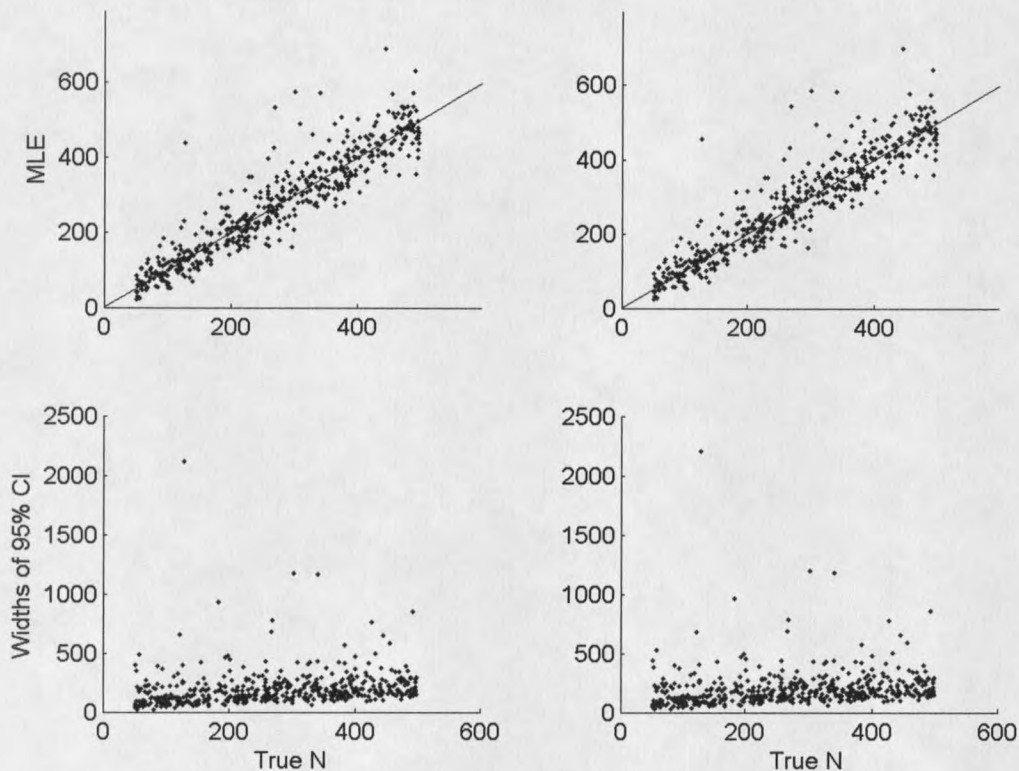


Figure 4.25. Relationships between true abundance and MLE and the widths of 95% confidence intervals for simulation set F. Left panels are for the closed capture model, whereas right panels are for the Huggins closed model. Solid lines indicate 45-degree lines.

The estimated intercept of the regression line was approximately 9, the slope was approximately one, and the coefficient of determination was 0.87 (Table 4.12). Widths of 95% confidence intervals ranged from 23.9 to 2118.4, with a median of 162.4. Approximately 93% (466/499) of confidence intervals included the true abundance. The relative precision of MLE ranged from 0.22 to 4.83 with the median of 0.65.

For the Huggins closed model, results were almost identical to those from the closed capture model. The variability of the estimator was less than for simulation case B ($-132.8 < \Delta_{\text{mle}} < 328.5$; Figure 4.25). Approximately 55% (275/499) of estimates were greater than true abundances.

The estimated intercept of the regression line was 13, the slope was approximately one, and the coefficient of determination was 0.86 (Table 4.12). Widths of 95% confidence intervals ranged from 24.5 to 2202.4, with a median of 164.5. Approximately 93% (466/499) confidence intervals included the true abundance. The relative precision of MLE ranged from 0.22 to 4.83 with a median of 0.65. When the number of secondary occasions within each primary period was increased to 8 (simulation case G), the variability of point estimators for the beta-multinomial model decreased. For the beta-binomial model, however, the variability of the estimators was less than for simulation case F ($-273 \leq \Delta_{\text{mode}} \leq 526$, $-243 \leq \Delta_{\text{median}} \leq 591$, $-220 \leq \Delta_{\text{mean}} \leq 598$; Figure 4.26). Approximately 42% (209/500) of modes, 57% (285/500) of medians, and 67% (335/500) of means were greater than the true abundance. The estimated intercept of the regression lines were positive, the slopes were approximately one, and the coefficients of determinations were approximately 0.6 (Table 4.14). Widths of 95% posterior intervals ranged from 32 to 1152, with a median of 448. The true abundances were included in 475 (95%) posterior intervals. The relative precision ranged from 0.84 to 7.20 (median = 1.9).

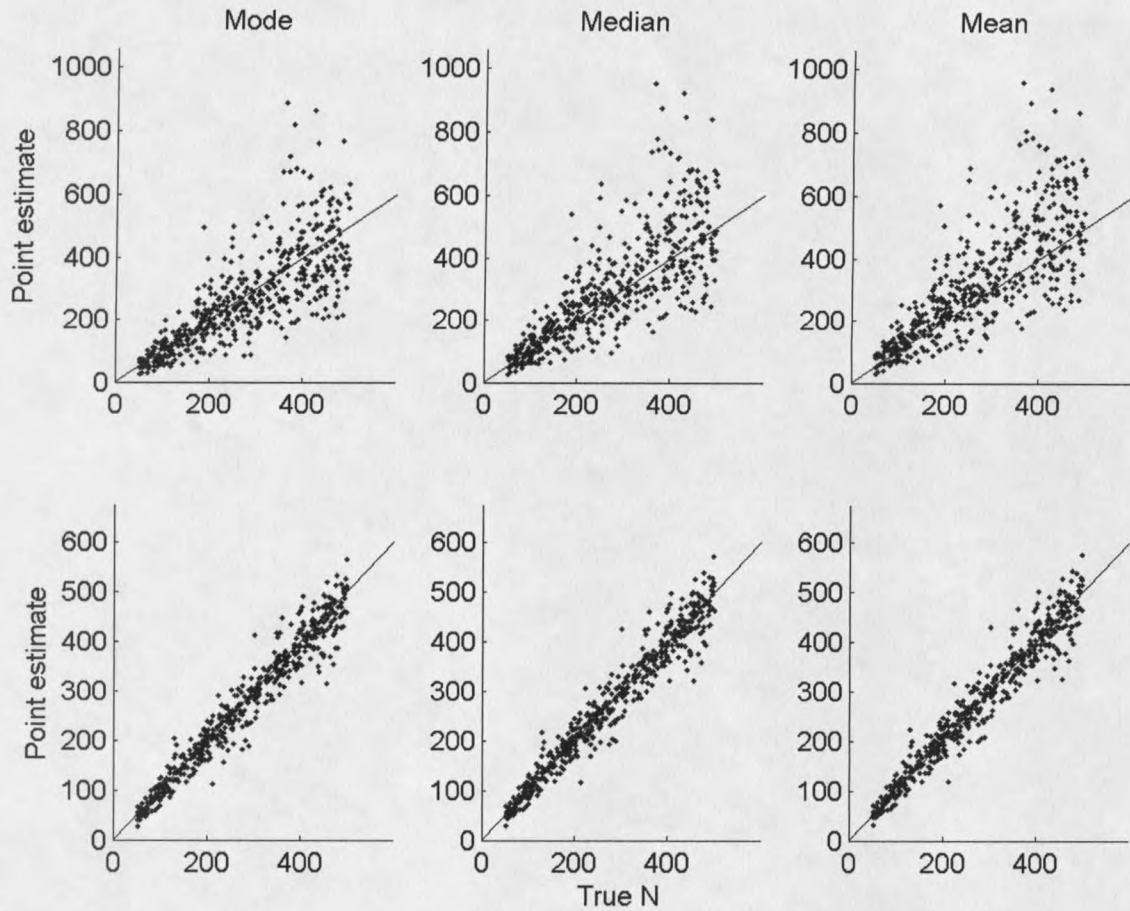


Figure 4.26. Relationships between true abundance and three point estimates in simulation case G. The solid lines indicate 45-degree lines. Upper three panels were for the beta-binomial model, whereas the lower three panels were for the multinomial model.

For the beta-multinomial model, the variability in point estimators was less than that for the beta-binomial model ($-141 \leq \Delta_{\text{mode}} \leq 111$, $-135 \leq \Delta_{\text{median}} \leq 124$, $-131 \leq \Delta_{\text{mean}} \leq 130$; Figure 4.26). The variability also was less than for simulation case F. Approximately 38% (191/500) of modes, 48% (239/500) of medians, and 51% (255/500) of means were greater than the true abundances.

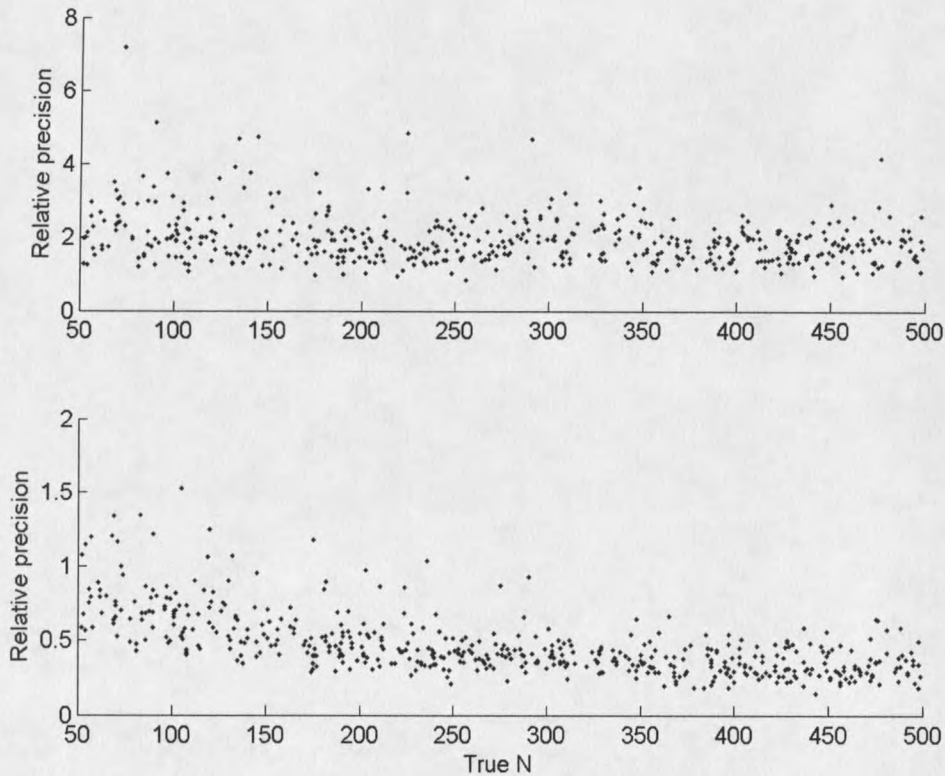


Figure 4.27. The relationship between relative precision and the true abundance for simulation case G. The upper figure is for the beta-binomial model, whereas the lower figure is for the multinomial model.

The estimated intercepts of the regression lines were positive for the median and mean, whereas it was approximately one for the mode. Estimated slopes of the regression lines were approximately one. Coefficient of determination was approximately 0.95 for all point estimators (Table 4.14). Widths of 95% posterior intervals ranged from 28 to 302, with the median of 103. Approximately 95% (476/500) of the posterior intervals included the true abundance. The relative precision ranged from 0.14 to 1.53 (median = 0.4; Figure 4.27).

When datasets for simulation case G were analyzed using MARK, the variability of point estimators from both models was similar. For the closed capture model, the variability in the point estimator was less than that for simulation case F ($-111.6 < \Delta_{mle} < 165.7$; Figure 4.28). Approximately 43% (216/500) of MLE's were greater than the true abundance. The estimated intercept of the regression line was 4.1, the slope was approximately one, and the coefficient of determination was 0.94 (Table 4.14). Widths of 95% confidence intervals ranged from 22.5 to 648.5 with a median of 107.0. Approximately 95% (476/500) of the confidence intervals included the true abundance. The relative precision of MLE ranged from 0.14 to 4.74 with a median of 0.44.

Table 4.14. Estimated parameters for the linear regression analysis between the true abundance and the point estimates for simulation case G, using the hierarchical approach.

Model	Point estimates	Intercept	Slope	r^2
Beta-binomial	Mode	9.04	0.94	0.602
	Median	13.28	1.06	0.610
	Mean	20.08	1.12	0.617
Multinomial	Mode	-0.14	0.97	0.949
	Median	3.54	0.98	0.948
	Mean	5.54	0.98	0.948
Closed captures	MLE	4.06	0.98	0.935
Huggins closed	MLE	6.02	0.98	0.934

For the Huggins closed model, the variability in the estimator was similar to that of the closed capture model ($-109.4 < \Delta_{mle} < 170.3$; Figure 4.28). Approximately 46% (229/500) of MLE's were greater than the true abundance. The estimated intercept of the regression lines was 6.02, the slope was approximately 1, and the coefficient of determination was 0.93 (Table 4.14). Widths of the 95% confidence intervals ranged from 23.1 to 695.6, with a median of 107.7. Approximately 95% (476/500) of the

confidence intervals included the true abundance. The relative precision of MLE ranged from 0.14 to 4.75 with a median of 0.44.

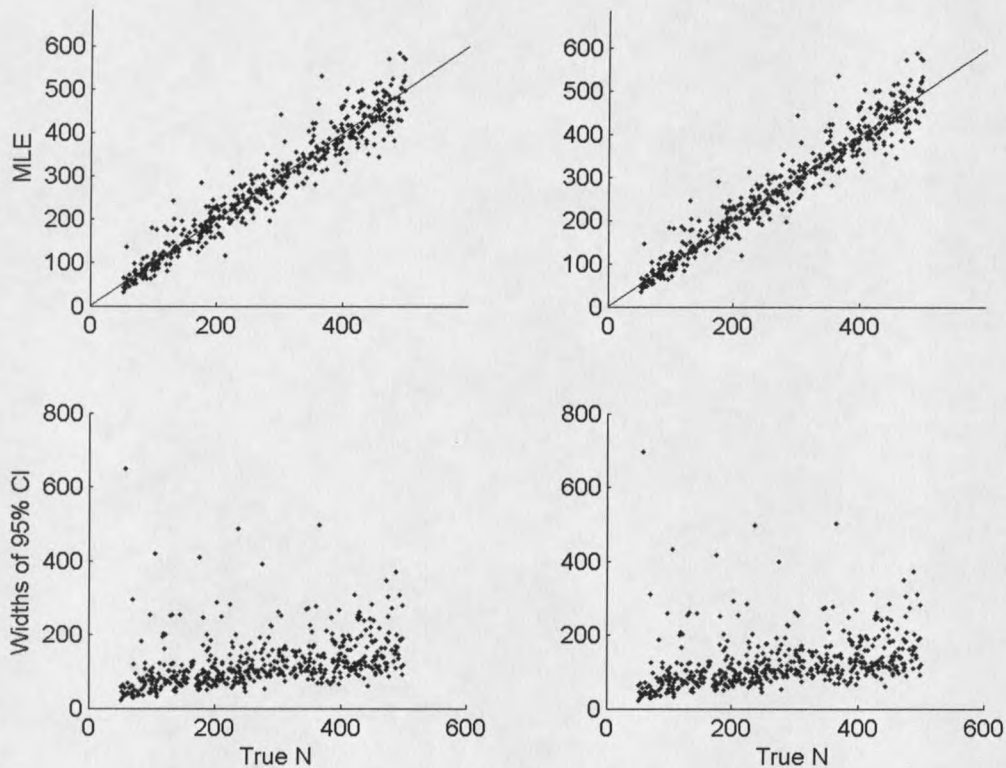


Figure 4.28. Relationships between the true abundance and MLE and widths of 95% confidence intervals for simulation case G. Left panels are for the closed capture model, whereas right panels are for the Huggins closed model. Solid lines indicate the 45-degree lines.

For all models that were considered in this analysis, precision of the posterior intervals of abundance improved as the number of secondary occasions increased (Table 4.15). Even with consistently low capture probabilities, precise posterior intervals were computed. In all cases, the beta-multinomial model performed better than the beta-binomial model, i.e., narrower posterior intervals and smaller relative precisions. The results from the hierarchical beta-multinomial model were comparable to those from the

two maximum likelihood models (Table 4.15). In the three simulation cases, 95% posterior intervals from the beta-multinomial model were narrower than 95% confidence intervals from the two maximum likelihood models.

Table 4.15. A summary of the comparison among the hierarchical beta-binomial, the hierarchical beta-multinomial, closed captures, and Huggins closed captures models. Values are minimum and maximum, whereas medians are in parentheses.

Simulation case	Beta-Binomial	Beta-Multinomial	Closed capture	Huggins closed capture
B				
Widths	54 – 1374 (1,010)	37 – 1,208 (248)	41 – 16,146 (290)	43 – 8,781 (296)
% true N	99%	94%	94%	95%
Precision	0.6 – 90.1 (4.3)	0.30 – 14.44 (1.10)	0.29 – 4.88 (1.16)	0.29 – 4.85 (1.16)
F				
Widths	58 – 1,272 (628)	35 – 571 (146)	23.9 – 2,118.4 (162.4)	24.5 – 2,202.4 (164.5)
% true N	97%	94%	93%	93%
Precision	0.76 – 17.16 (2.57)	0.23 – 4.39 (0.62)	0.22 – 4.82 (0.65)	0.22 – 4.83 (0.65)
G				
Widths	32 – 1,152 (448)	28 – 302 (103)	22.5 – 648.5 (107.0)	23.1 – 695.6 (107.7)
% true N	95%	95%	95%	95%
Precision	0.84 – 7.20 (1.9)	0.14 – 1.53 (0.4)	0.14 – 4.74 (0.44)	0.14 – 4.75 (0.44)

Through the comparison of posterior distributions among seven simulation cases, I have shown that capture probabilities affect the precision of posterior distributions of abundance more than sampling frequencies. For all models, including the maximum likelihood models, the number of primary periods is the least important factor in improving the precision of posterior distributions. The hierarchical beta-multinomial model performed comparable to or better than the two closed population models in MARK.

Discussion

Several researchers have discussed the use of Bayesian methods in estimating abundance with CMR data. Gaskel and George (1972) proposed a modification of the Lincoln index by using the Bayesian approach. Castledine (1981) considered prior information on capture probabilities for the mixture of hypergeometric and binomial likelihood functions. Gazey and Staley (1986) provided a sequential approach to negative binomial, binomial, and hypergeometric models. Zucchini and Channing (1986) used the hypergeometric model for estimating the abundance of small populations. Raftery (1988) used a hierarchical approach by defining the prior distributions on the mean number of captured animals and the capture probabilities. Smith (1991) compared the Bayesian method to empirical Bayes, and Bayes empirical Bayes methods for the mixture of binomial and hypergeometric likelihood functions. King and Brooks (2001) discussed the Bayesian model averaging techniques. The proposed method in this chapter, however, appears to be the first attempt to use CMR data from the robust design for making an inference on the abundance of a closed population in the Bayesian framework.

The proposed method provides a mathematical framework for incorporating available knowledge about capture probabilities in a particular study area into the current analysis for estimating the abundance. Data from previous studies from the same study area were used to quantify the hyperparameters of capture probabilities. These hyperparameters, then, were used for the inference on abundance. The proposed method also treats the abundance as an explicit parameter in the model rather than treating the abundance as a derived parameter.

Through simulations, I showed that the hierarchical approach was useful for computing a precise posterior distribution. If data were collected in a consistent manner, data from previous primary periods enhanced the precision of the posterior distribution of the abundance. A joint posterior distribution of the hyperparameters, however, sometimes lacked an apparent peak. If the likelihood function is flat, numerical algorithms may not find a peak in the joint posterior distribution of hyperparameters. In this situation, the hyperparameters may be fixed for computing the posterior distribution of abundance.

The proposed method provided reasonable posterior distributions for abundance of closed populations. Although the temporal sampling frequencies and capture probabilities in many simulations were unfavorable (e.g., only four secondary occasions within each primary period with the mean capture probability of 0.09 and the variance of 0.004), the 95% posterior intervals encompassed the true population sizes in approximately 95% of simulations, except for simulation case A. For simulation case A, only 54% of posterior intervals included the true abundances because of the widths of posterior intervals were narrow (≤ 3).

Analyses of various combinations of parameters in simulation data sets indicated that consistently high capture probabilities were the most effective factor in obtaining a precise posterior distribution. To increase capture probabilities, capture effort and capture efficiency should be maximized. Capture probabilities, however, often are not functions of elements that can be controlled by researchers, e.g., weather, behavior of target animals, and landscape. Analyses of simulated data indicate that the number of secondary occasions is more important than the number of primary periods in obtaining precise estimates. To obtain a precise abundance estimate for a closed population,

therefore, short-term frequent sampling is more effective than long-term infrequent sampling.

Comparisons of results of the proposed method and those from MARK indicated that the proposed method is comparable to maximum likelihood methods. When capture probabilities were consistently high or variable (case A and case C), results from the hierarchical beta-multinomial model and maximum likelihood models were almost identical. For simulations with consistently low capture probabilities (case B), the hierarchical beta-multinomial model provided better results than the maximum likelihood models. For the hierarchical beta-multinomial model, no extreme outliers were found in point estimates, whereas 11 MLE's were unreasonable. The variability of point estimators was less for the hierarchical beta-multinomial model than for the maximum likelihood models.

Although the proposed method performed better than MARK in some situations, I did not conduct a complete analysis in MARK for each dataset. The authors of MARK recommend the use of model averaging, where multiple candidate models are averaged (Cooch and White 2001, Burnham and Anderson 1998). To use MARK on several hundred datasets, I was unable to apply more than one model to each dataset. Results from MARK were used as a 'yardstick' to which performance of the hierarchical approach was compared. I have shown that the proposed method is comparable to the 'standard' in abundance estimation methods.

The proposed method should provide an alternative approach to abundance estimation with CMR data. The proposed method may be more suitable than MLE when opportunistic data are available for preliminary analyses. With a carefully designed and executed study with large sample sizes, both methods should provide a precise estimate.

For applied ecology, the proposed method has several attractive features in practice. First, the posterior distribution provides a probability distribution of abundance, conditional on data and the statistical model, so that the interpretation of the result is straightforward. Uncertainty in the abundance is described by a probability distribution rather than a 95% confidence interval. Results of the simulation analysis indicated that 95% posterior intervals contain the true abundance approximately 95% of the time, which can be interpreted as a probability statement. Consequently, interpretations of a posterior probability distribution are more direct than those of confidence intervals.

Second, the inference procedure works regardless of sample sizes. Even for the small number of captures and recaptures within a primary period, posterior distributions were computed for all datasets. With the MLE approach, however, unreasonable estimates were obtained in several occasions.

Third, the model is intuitive. Although several robust-design statistical models have been proposed (Kendall et al. 1995, 1997, Schwarz and Stobo 1997, Kendall and Bjorkland 2001, Lindberg et al. 2001), those models include several other parameters, making them complex. By reducing the number of parameters in the model, the proposed model is simple and intuitive, suited for making an inference only on abundance.

Fourth, the model can be applied to CMR data in two ways: ensemble or sequential. All analyses in this chapter were conducted using the ensemble method. The ensemble approach may be applicable when analyses are conducted on data from a completed study or using a completed study as the source of prior information for a new study. The sequential approach may be more appropriate if data for a longitudinal study are collected and analyzed concurrently. The posterior distribution of abundance from the previous periods can be used as the prior distribution for the next period.

Fifth, the sequential approach allows researchers to determine the sampling intensity according to the shape of the posterior distribution. For example, if a posterior distribution has a long tail, the sampling intensity may be increased for greater capture probabilities during a sampling, which would result in a more precise posterior distribution.

Sixth, integration of previous information is straightforward. For example, if the abundance at a study site is temporally correlated, the posterior distribution of a primary period may be used as the prior distribution for the abundance in the subsequent primary period. Samples can be drawn from a posterior distribution using the Metropolis algorithm (Metropolis et al. 1953, Hastings 1970), Gibbs sampler (Smith and Gelfand 1990), or other modifications to these methods (Carlin and Louis 2000, Martinez and Martinez 2002). Alternatively, a probability density function may be fitted to these data to create a prior probability distribution for abundance.

Seventh, the proposed method performs better than maximum likelihood method when data are insufficient for computing the MLE. This may be the case when an abundance estimate is necessary for an endangered species or a small population over wide spatial range and a long time period.

Last, the general method in this chapter can be expanded to additional parameters, such as survival, immigration, and emigration, if data are available and reasonable models can be constructed.

Although the proposed method is practical in many situations, there are a few drawbacks. The Metropolis algorithm is computationally intensive and there is no "canned" package. Each study requires programming and computations to obtain results. With the recent development of fast and inexpensive personal computers and readily available efficient interpreted programming languages, e.g., R, Matlab®, and

Mathematica®, however, programming and computations should not be major drawbacks in using the proposed method. Recent developments of freeware BUGS and WinBugs also facilitate the use of Bayesian methods.

Another potential problem may be that the proposed method is not efficient if there is no previous information. There are, however, many available models for estimating the abundance of a closed population without using prior information, e.g., Lincoln-Petersen model, Schnabel census, and their modifications. These methods have been discussed in detail elsewhere (Seber 1983, Kendall 1999, Williams et al. 2001). The recent development of abundance estimates based on sample coverage also seems to provide precise estimates of abundance (Hwang and Chao 1998).

Finally, the appropriateness of the proposed method to a particular study is contingent on the validity of the assumptions. If the violation of one or more assumptions is expected in a study, a new model should be constructed for the particular situation. For any Bayesian approach, the range of a posterior distribution is defined only over the range of the prior distribution with non-zero probability. Consequently, the prior distribution for abundance should be wide enough so that non-zero probability is assigned for all possible population sizes.

In conclusion, the proposed Bayesian approach provides an intuitive method for making an inference on the abundance from CMR data. The proposed method can be used for sparse data, which may not be analyzed successfully by other mark-recapture methods. Although some minor limitations exist, I think the advantages of the method outweigh the disadvantages.

ABUNDANCE ESTIMATES OF BOTTLENOSE DOLPHINS IN INSHORE WATERS ALONG THE ATLANTIC COAST OF THE UNITED STATES USING THE EXISTING PHOTO-IDENTIFICATION DATA

Introduction

Because of a mass die-off during 1987 and 1988 (Scott et al. 1988, Lipscomb et al. 1994, Duignan et al. 1996), the Western North Atlantic coastal stock of bottlenose dolphins (*Tursiops truncatus*) is considered to be depleted under the Marine Mammal Protection Act (MMPA 1972, most recently amended 1994). Consequently, there is a management need to estimate the abundance of bottlenose dolphins along the Atlantic coast of the U.S. Several factors, however, complicate the estimation of total abundance of the stock: mixing of the offshore ecotype, complex temporal and spatial structures of localized groups, and distribution of the species along the coast.

The National Marine Fisheries Service (NMFS) conducted five independent aerial surveys between 1992 and 1995 (Blaylock and Hoggard 1994, Blaylock 1995, NMFS 2001). These surveys, however, were conducted only over coastal waters and excluded bays, sounds, and estuaries. Consequently, all bottlenose dolphins in bays, sounds, and estuaries were excluded from the estimates. Abundance estimates, therefore, were necessary for bottlenose dolphins that inhabit in bays, sounds, and estuaries along the Atlantic coast of the United States.

Aerial surveys over waters in bays, sounds, and estuaries often are inappropriate because visibility of these waters is limited. Shipboard line-transect surveys also are difficult because the water is shallow and only small boats can enter these waters.

Distance sampling of these areas, therefore, is unfeasible. An alternative is to use capture-mark-recapture (CMR) methods. Capture-mark-recapture methods have been used successfully for estimating abundances of bottlenose dolphins (Wells and Scott 1990, Williams et al. 1993, Wilson et al. 1999, Read et al. 2003). Many bottlenose dolphins possess identifiable nicks on their dorsal fins, which remain identifiable for a long period of time (Wells and Scott 1990). By collecting photographs of these dorsal fins longitudinally, capture-mark-recapture data can be collected for bottlenose dolphins (Hammond 1986).

Along the Atlantic coast of the U.S., several researchers and a commercial dolphin watch company have been collecting photo-identification data of bottlenose dolphins. A majority of these photo-identification studies on bottlenose dolphins, however, are conducted to estimate seasonal occurrence, site fidelity, home-range analyses, and individual associations of bottlenose dolphins (Barco et al. 1999, Gubbins 2002a, 2002b, Zolman 2002). The sighting protocols at most of the study sites, therefore, are not ideal for using existing CMR methods. Further, sampling designs for these data did not provide enough spatial coverage to make inferences on abundance of bottlenose dolphins throughout the coastline. The objective of this chapter is to apply the proposed Bayesian method discussed in the previous chapter to the existing photo identification datasets.

Methods

Although sighting histories of bottlenose dolphins were obtained from 12 studies along the Atlantic coast of the United States, two locations (Chincoteague, VA and Virginia Beach, VA) were considered open coastline rather than bays, sounds, and estuaries, and one study did not contain enough data (Delaware Bay, DE). Consequently, nine datasets were analyzed for eight locations; Manteo, NC (R. Mallon-Day), Beaufort, NC (A. Read and K. Rittmaster), Wilmington, NC (L. Sayigh), Murrell's Inlet, SC (R. Young), Charleston, SC (E. Zolman), Hilton Head, SC (C. Gubbins), along the coast of Georgia (The Dolphin Project), and Jacksonville, FL (M. Caldwell). Sighting histories of individual bottlenose dolphins at each study site were treated as CMR data. The hierarchical Bayes method discussed in the previous chapter was used on these data to estimate abundance at each sampling area. For two studies at Beaufort, NC, two data sets were analyzed separately because of differences in sampling designs and sampling areas of the two studies.

To determine the rate of movements of bottlenose dolphins between sampling locations, I used the central catalog of photographed bottlenose dolphins for the coast. The central catalog was organized and maintained by Kim Urian. The central catalog was designed to include all previously photographed individuals from local catalogs and their sighting records among all sampling locations. Only individual bottlenose dolphins with high-quality photographs were accepted to the central catalog. For each dataset, I examined the sighting histories of only individual bottlenose dolphins that were accepted to the central catalog.

The central catalog also enabled me to determine the shortest duration during which a bottlenose dolphin was sighted at more than one sampling location. For each pair of sampling locations, the maximum time duration in which no bottlenose dolphin was sighted at the two locations was determined. The duration, then, was used as a crude estimate of the duration of a primary period.

Examinations of the central catalog indicated that bottlenose dolphins move freely among study sites within North Carolina, whereas no movements between North Carolina and southern states (South Carolina, Georgia, and Florida) had been reported (Urian et al. 1999). Consequently, two geographic groups were created for the datasets. The northern group included study sites within North Carolina, whereas the southern group included study sites from South Carolina, Georgia, and Florida. To compile the results for a geographic group, inferences on abundances were made for primary periods that were temporally close to each other.

For each dataset, I computed the cumulative number of individuals in the dataset. The rate of increase of the catalog size with respect to seasons and years was examined by plotting the number of individuals in the dataset against time from the beginning of the study. At the beginning of a study, a large number of new individuals were added to the dataset. If the population was closed and the study period was long enough, the rate of increase would slow down as the majority of individuals in the area were sighted. If a study area contained a large number of transient animals or the study period was not long enough relative to the size of the population, however, the rate of change would not decline. The rate of increase in the size of the dataset, therefore, should provide

information on the population closure and the measure of whether or not the study had been continued for a long enough time period.

The potential inclusion of transient animals to a dataset also was investigated by computing the number of days since the last time each individual was sighted. If an individual was a transient for a study area, the individual might not be sighted for a long time period. The median and maximum numbers of days since the last sighting of individuals for each study area were computed.

To qualitatively compare and contrast the sighting probabilities of bottlenose dolphins among study sites, two statistics for each study site were examined; efficiency and sighting rate. Efficiency was a measure of how many individual bottlenose dolphins were accepted to a dataset per sampling day. An efficient study would indicate a large number of individuals accepted to the dataset per sampling. The efficiency was a function of multiple factors, such as the number of hours spent per day, weather, sea state, geography, number of observers, skill of photographer, the height of the observing deck above the sea level, and the proportion of identifiable individuals in the area. To quantify the efficiency at a study site, I created a frequency histogram for the number of individuals accepted to the dataset per day. To assess the sighting rate, I created a frequency histogram of the number of times each individual was sighted. The sighting rate was a function of the efficiency, the size of the sampling area relative to the home range of individuals in the area, and the proportion of transient animals in the area. The sighting rate at a study site would be low if the efficiency was low, the sampling area was small relative to the home range of animals in the area, or many transients were in the

area. I used the median and maximum as the summary statistics for efficiency and sighting rate.

To make an inference on the abundance of bottlenose dolphins for a primary period at a sampling location, the hierarchical model discussed in the previous chapter was used. For the analyses in this chapter, however, I used 50,000 steps within each chain. To eliminate the initial sojourn steps, I discarded the first 7,500 steps from each chain. To quantify the convergence of the hyperparameters, the scale-reduction factor ($\sqrt{\hat{R}}$; Gelman et al. 1995, p. 3323) was computed for each hyperparameter. If the scale-reduction factor of either parameter was greater than 1.2 after four sequences of four independent chains, the hyperparameters were fixed at $\alpha = 1$ and $\beta = 1$. If the scale-reduction factors were less than 1.2, the joint posterior samples were used to compute a posterior distribution of the abundance. The multinomial model was used for the likelihood function if there was at least one recaptured individual during the primary period. If no individual was recaptured, I used the beta-binomial model for the likelihood function. For the prior distribution of abundance, I used UNIF(10, 1500). The posterior distribution of the abundance was summarized in point estimates (mode, median, and mean) and the 95% posterior interval.

Results

The examination of sighting records among study sites indicated that no bottlenose dolphin was sighted within 15 days at more than one location. Consequently, I used 15 days as the duration of a primary period for all locations.

For the northern group, inferences on abundances were made for August 1998. The posterior distribution of abundance was computed for the period between 8/12 and 8/26 for Manteo, between 8/14 and 8/28 for Beaufort (K. Rittmaster), between 8/18 and 9/2 for Beaufort (A. Read), and between 8/5 and 8/19 for Wilmington. For the southern group, inferences on abundances were made for September and October 1997. Posterior distributions of abundance were computed for the period between 10/25 and 11/8 for the Myrtle Beach area, SC, between 9/9 and 9/23 for Charleston, SC, between 9/13 and 9/27 for Hilton Head, SC, between 9/13 and 9/27 for Georgia, and between 9/5 and 9/19 for Jacksonville, FL.

Manteo, NC (R. Mallon-Day)

Sighting records of bottlenose dolphins near Manteo, NC, were collected on 280 capture occasions between 29 May 1998 and 28 October 2000. The study area was approximately 572 km² (Figure 5.1). Although bottlenose dolphins were sighted occasionally in the Atlantic Ocean, the majority of effort was dedicated within the inlet (Figure 5.1; R. Mallon-Day, pers. comm.). These data were collected as part of a commercial dolphin watch program during summer months (May through October) from a 40-foot pontoon boat carrying up to 36 passengers, one or two crew, and the captain. Each cruise was approximately 2 hours and one to three cruises were conducted daily. Data for all cruises per day were pooled in the following analyses.

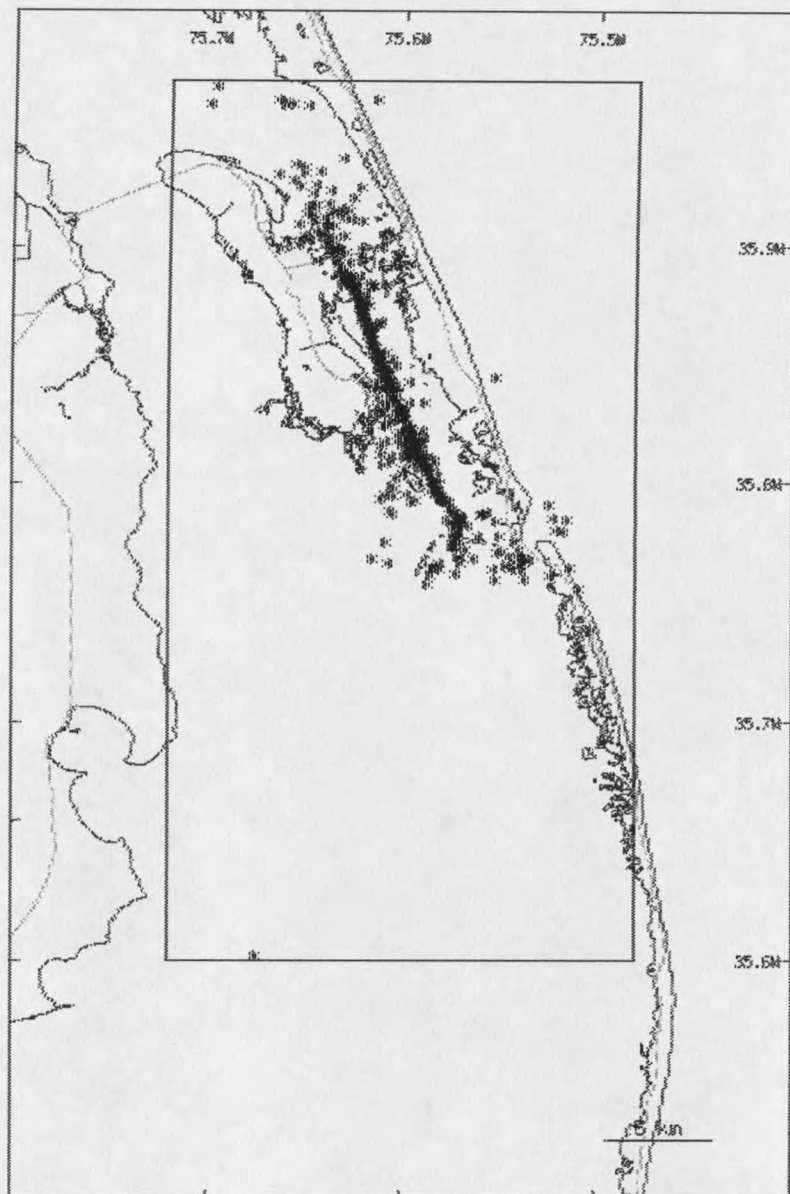


Figure 5.1. Sighting locations of identifiable bottlenose dolphins at the study site near Manteo, NC. Each * indicates one sighting of a bottlenose dolphin. The rectangle within the map indicates the approximate study area. Majority of effort was within the inlet.

The dataset contained sighting histories of 132 identifiable bottlenose dolphins. The number of bottlenose dolphins in the dataset increased during the first two years. The rate of increase was greater during the first few weeks of each summer than the rest

of the summer (Figure 5.2). During the second half of each summer, no new individuals were added to the dataset. No new individuals were added to the dataset during the third year. The median number of days since the last sighting was 116, whereas the maximum was 266.

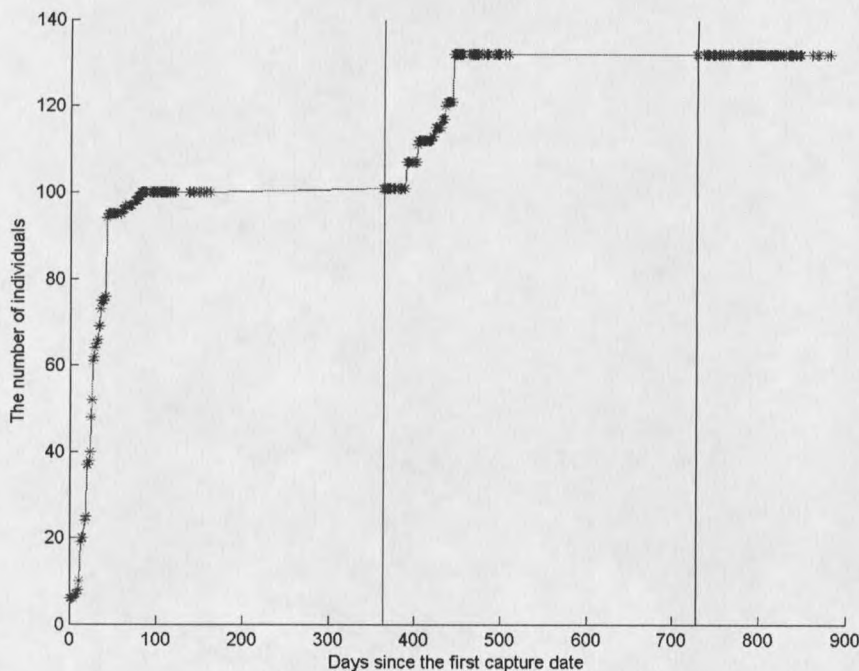


Figure 5.2. The cumulative number of bottlenose dolphins in the dataset for the photographic identification study near Manteo, NC. Day 0 corresponds to 29 May 1998. Vertical lines indicate 365-day periods.

The average number of sighting occasions per 15-day primary period was 9.3 (SE = 0.64, $n = 30$, range = 2-14). The number of bottlenose dolphins that were admitted to the dataset per day ranged from 1 to 25 (median = 4; Figure 5.3). Of the 132 individuals in the dataset, 89 were sighted more than once. The maximum number of sightings per individual was 106 (median = 3; Figure 5.4).

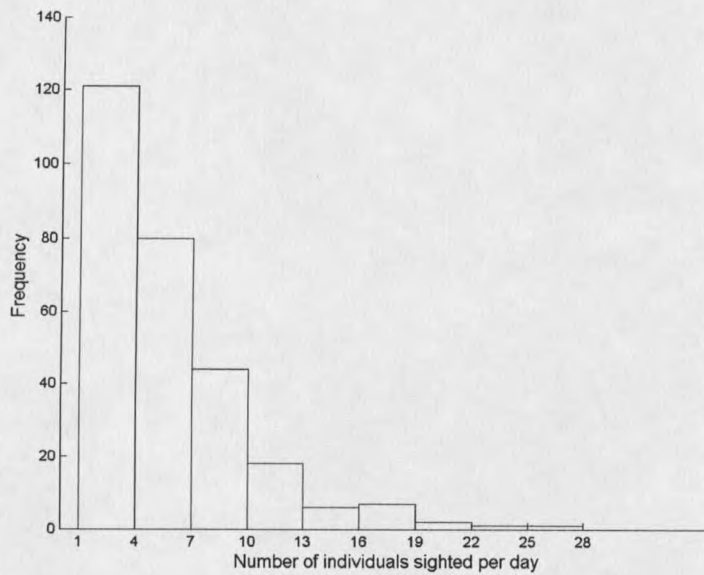


Figure 5.3. A histogram of the number of individuals admitted to the dataset per sampling day for the photographic identification study near Manteo, NC.

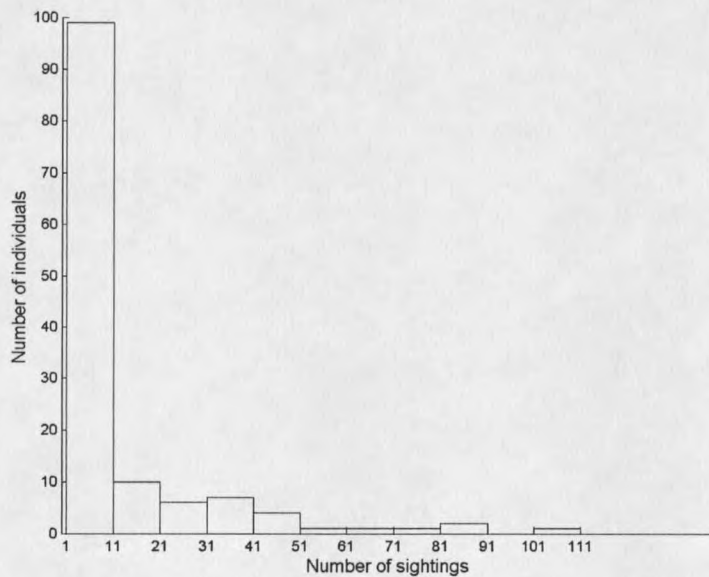


Figure 5.4. A histogram of the sighting frequency of each bottlenose dolphin in the dataset for the photographic identification study near Manteo, NC.

Sighting records from 29 primary periods were used to compute the joint distribution of the hyperparameters. The scale reduction factor was greater than 1.2 after four sequences. The hyperparameters, therefore, were fixed in the hierarchical model.

<figure>

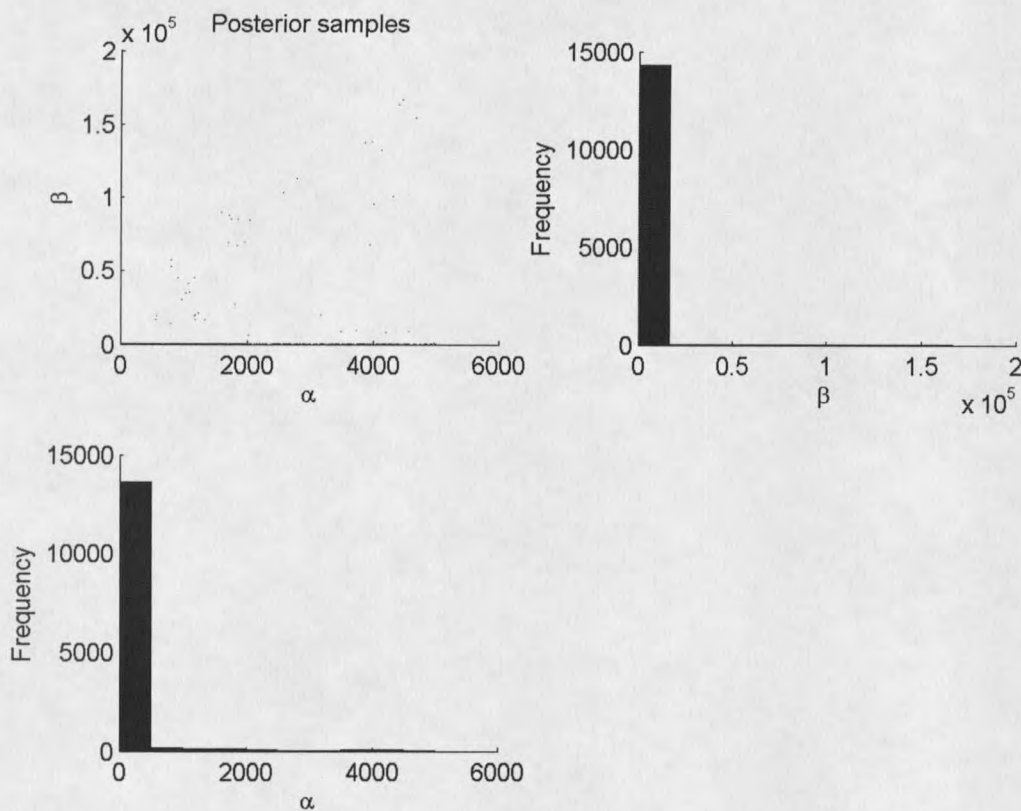


Figure 5.5. Posterior samples of the hyperparameters for sighting probabilities for the photographic identification study near Manteo, NC. Histograms are marginal distributions of hyperparameters.

A posterior distribution of abundance was computed for the 6th primary period, which included 14 secondary occasions. During the primary period, the number of individuals accepted to the dataset per day ranged from 2 to 11 (mean = 5.6, SD = 2.7). A total of 20 identifiable bottlenose dolphins were sighted, of which 15 were sighted

more than once. Consequently, the multinomial model was used for computing the posterior distribution. The mode, median, and mean of the posterior distribution of abundance were 20 (Figure 5.6). The approximate 95% posterior interval ranged from 19 to 21. Because abundance was a discrete parameter, the lower limit of the posterior interval was less than the number of individuals in the sample. The majority of probability mass of the posterior distribution was on 20. Consequently, the maximum abundance at which the cumulative probability was less than 0.025 (the lower limit) was 19, although the actual probability was zero.

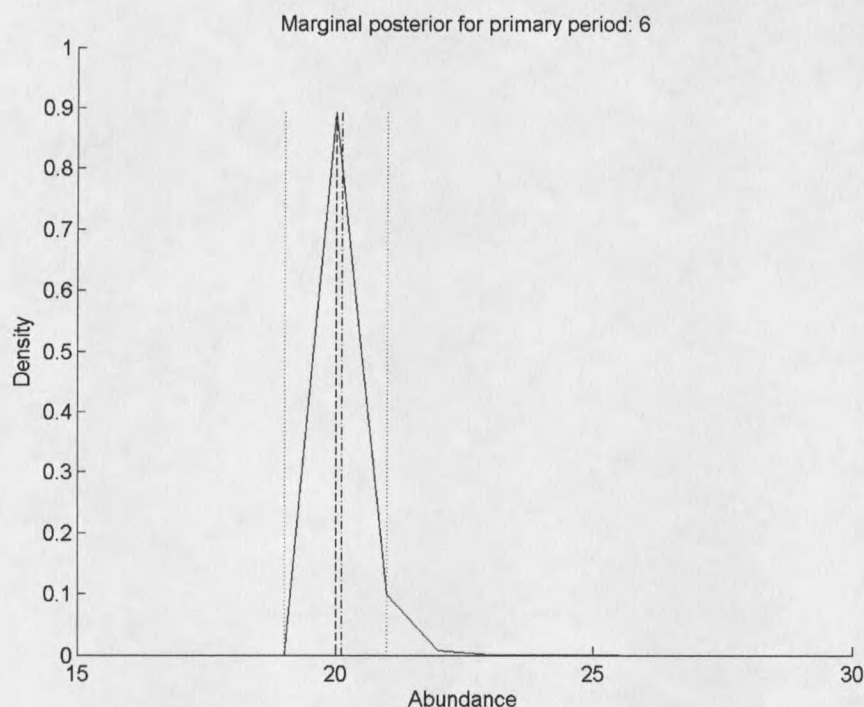


Figure 5.6. The posterior distribution of abundance for the 6th primary period at the photographic identification study site near Manteo, NC. The posterior distribution was computed with fixed hyperparameters ($\alpha = 1$, $\beta = 1$) and the multinomial model. The dashed line indicates the median, the dash-dotted line indicates the mean, and the dotted lines indicate lower and upper limits of the approximate 95% posterior interval.

Beaufort, NC (A. Read)

A research group at Duke Marine Laboratory in Beaufort, NC, collected sighting records of bottlenose dolphins on 87 sampling days from 10 July 1995 to 21 July 1999. The mean number of capture occasions per 15-day primary period was 3.75 (SE = 0.62, $n = 20$, range = 2 – 12). The study site included estuaries near Beaufort, NC, and the Neuse River (Figure 5.7). Although sighting data of bottlenose dolphins occasionally were collected outside of the outer banks, the majority of effort was concentrated for estuaries and the river in the region (Figure 5.7). The study area was approximately 650 km².

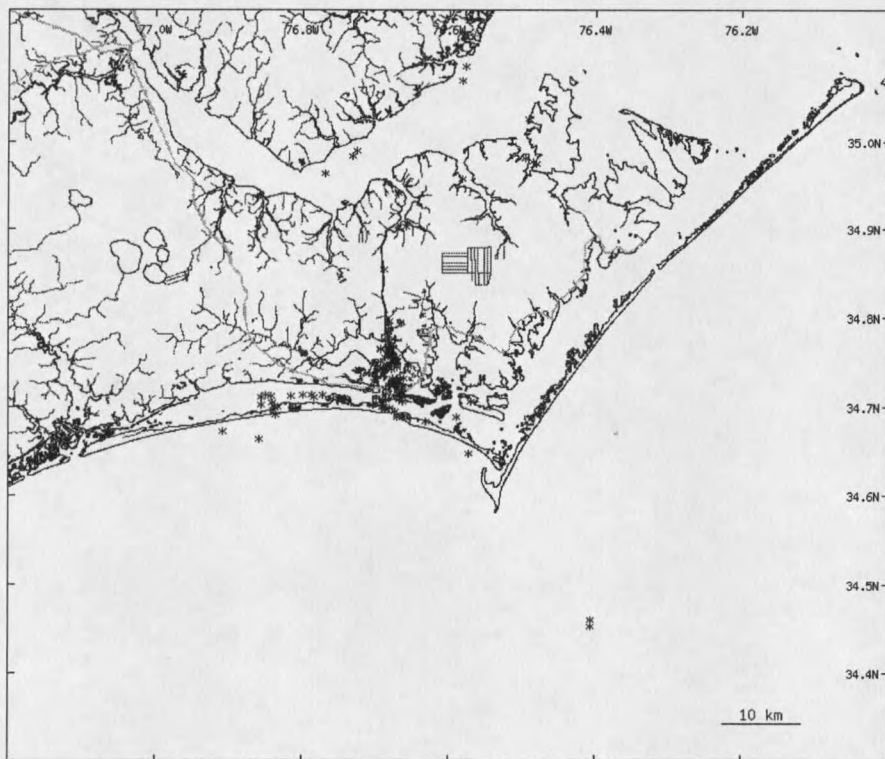


Figure 5.7. Sighting locations of bottlenose dolphins near Beaufort, NC. Data were from Duke Marine Laboratory. Each star indicates a sighting location of an identifiable bottlenose dolphin.

The cumulative number of bottlenose dolphins in the dataset indicated that the majority of new individuals were sighted during summer (Figure 5.8). During autumn and winter, a few new individuals were added to the dataset because of low effort. The rate of increase in the catalog size declined over the years. The median number of days since the last sighting was 25, whereas the maximum was 85.

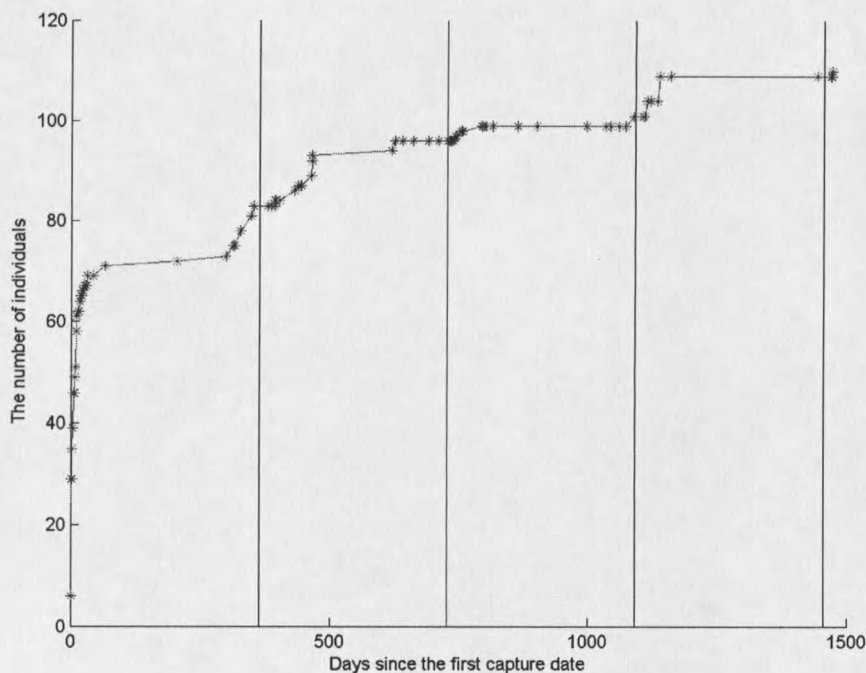


Figure 5.8. The cumulative number of bottlenose dolphins in the dataset for a photographic identification study near Beaufort, NC (A. Read). Day 0 corresponds to 10 July 1995. Vertical lines indicate 365-day intervals.

The maximum number of individuals accepted to the dataset per day was 24 (median = 6; Figure 5.9). Of 110 bottlenose dolphins in the dataset, 89 were sighted more than once (median = 3; Figure 5.10). The maximum number of sightings per individual was 29.

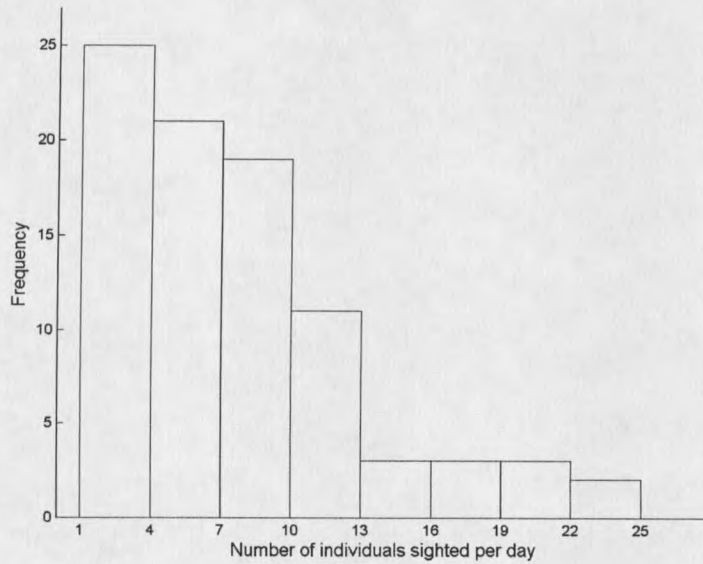


Figure 5.9. A histogram of the number of individuals admitted to the dataset per sampling day for a photographic identification study near Beaufort, NC (A. Read).

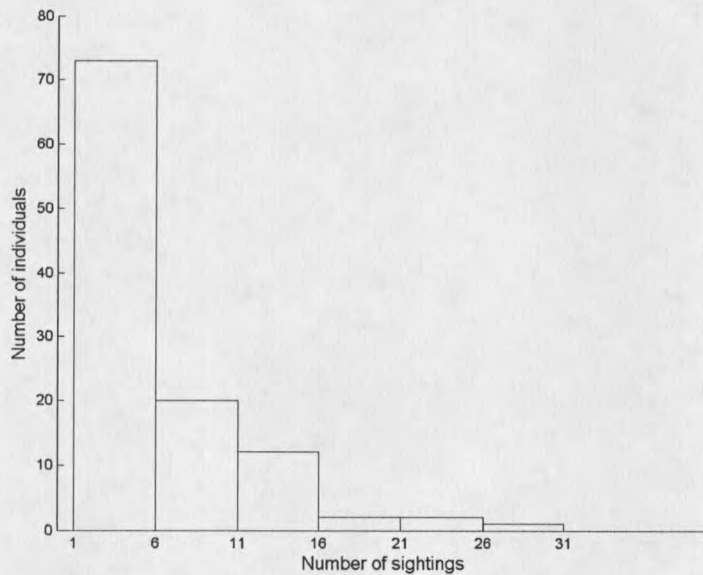


Figure 5.10. A histogram of the sighting frequency of each bottlenose dolphin in the dataset for the photographic identification study near Beaufort, NC (A. Read).

Sighting records from 19 primary periods were used to compute the joint distribution of the hyperparameters. The posterior samples of hyperparameters indicated a peak at approximately $\alpha = 1.8$ and $\beta = 5$ (Figure 5.11). Consequently, the posterior samples were used for computing the posterior distribution of abundance.

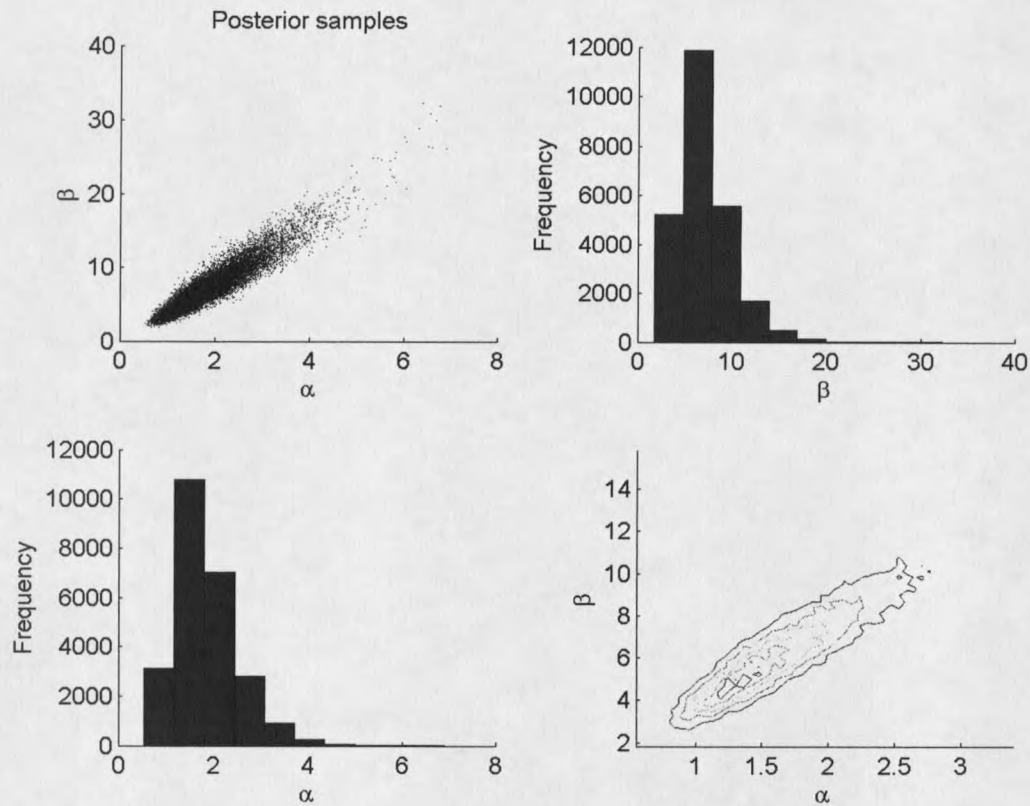


Figure 5.11. Posterior samples of hyperparameters for sighting probabilities for the photographic identification study near Beaufort, NC (A. Read). Histograms are marginal distributions of hyperparameters. The lower right figure is a contour plot of the density of posterior samples (upper left). Axes were truncated to emphasize the peak of the distribution.

A posterior distribution of abundance was computed for the 19th primary period (18 August 1998 to 2 September 1998), which contained two capture occasions. The number of individuals sighted per sampling day was five and six, none of which was

sighted more than once. Consequently, the beta-binomial model was used to compute the posterior distribution of the abundance. The mode of the posterior distribution was 23, the median was 39, and the mean was 66. The approximate 95% posterior interval ranged from 12 to 303 (Figure 5.12).

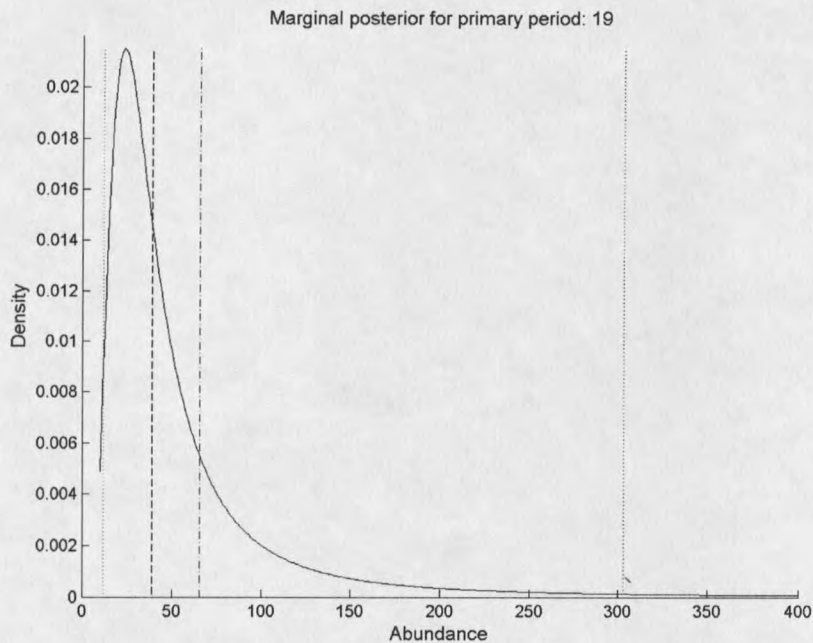


Figure 5.12. The posterior distribution of abundance of bottlenose dolphins for the 19th primary period at a photographic identification study site near Beaufort, NC (A. Read). The posterior distribution was computed using the beta-binomial model. The abscissa was truncated at 400. The dashed line indicates the median, the dash-dotted line indicates the mean, and the dotted lines indicate lower and upper limits of the approximate 95% posterior interval.

Beaufort, NC, (K. Rittmaster)

Another researcher (K. Rittmaster) collected sighting data of bottlenose dolphins near Beaufort, NC, during 543 sampling days from 1 July 1985 to 1 June 2000. The mean number of secondary occasions per 15-day primary period was 3.78 (SE = 0.13, n =

139, range = 2 – 13). The study site included inshore and offshore waters and was approximately 164 km² (Figure 5.13). Because of the time constraints, search effort was emphasized in three general areas within the study area where bottlenose dolphins frequented.

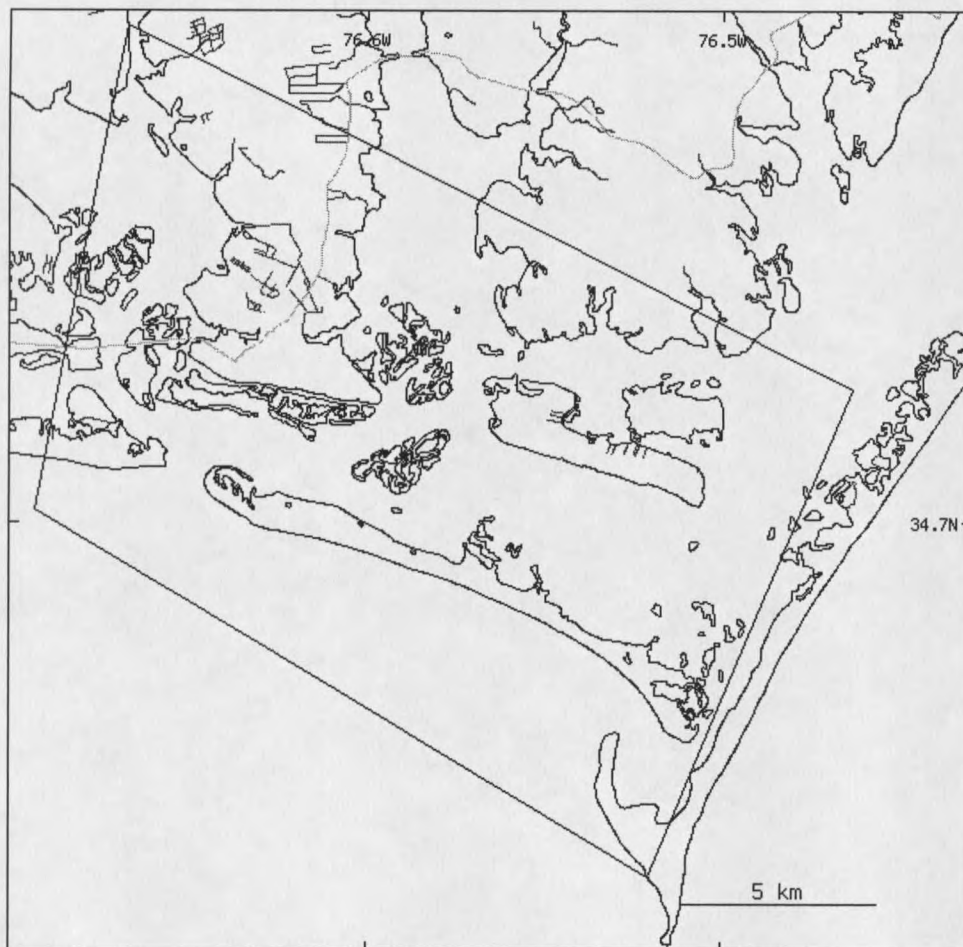


Figure 5.13. The photographic identification study site near Beaufort, NC, for K. Rittmaster. The solid line indicates the area that is covered by regular sampling. No sighting locations were available.

The cumulative number of individuals in the dataset increased continuously (Figure 5.14). The rate of increase, however, declined for the last two years. No

apparent seasonal difference was found in the rate of discovery of new individuals. During the last two years, no new individuals were added to the dataset. The median number of days since the last sighting was 92, whereas the maximum was 539.

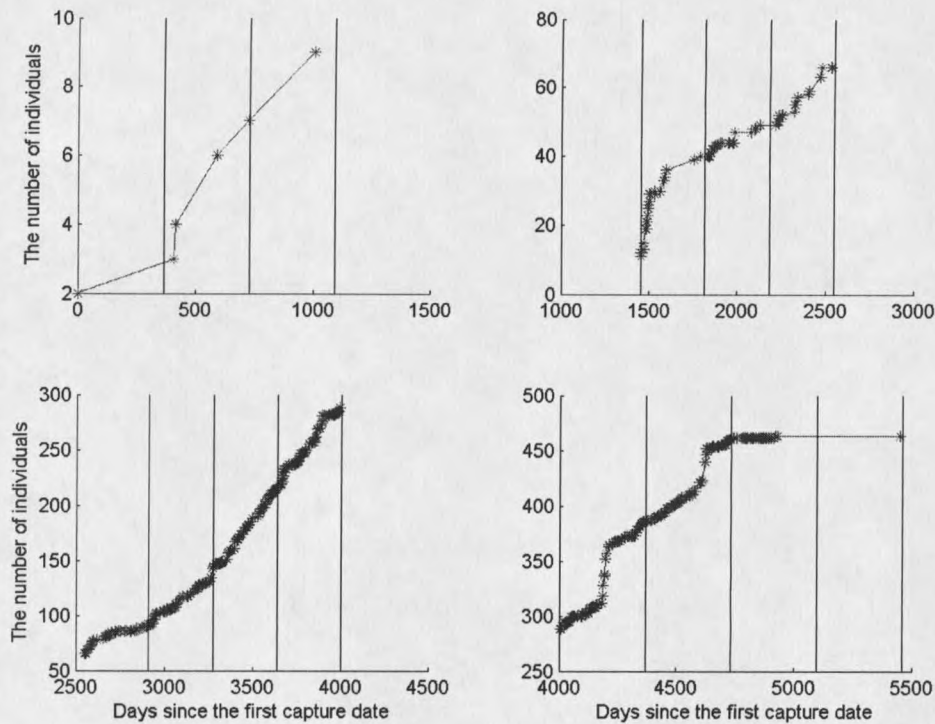


Figure 5.14. The cumulative number of individual bottlenose dolphins in the dataset for a photographic identification study near Beaufort, NC (K. Rittmaster). Vertical lines indicate 365-day periods from the beginning of the study, which was 1 July 1985.

The maximum number of individuals accepted to the dataset per sampling day was 41 (median = 4; Figure 5.15). Of 463 individuals in the dataset, 288 were sighted more than once. The maximum number of sightings per individual was 59 (median = 2; Figure 5.16).

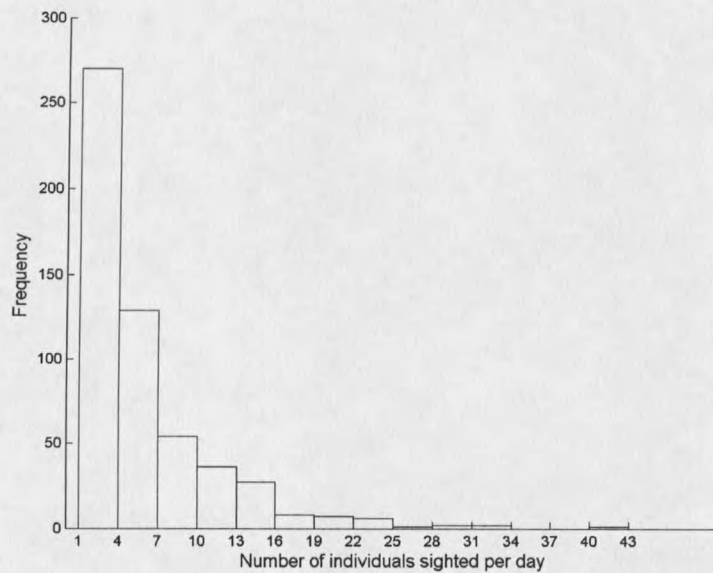


Figure 5.15. A histogram of the number of individuals accepted to the dataset per day for the photographic identification study near Beaufort, NC (K. Rittmaster).

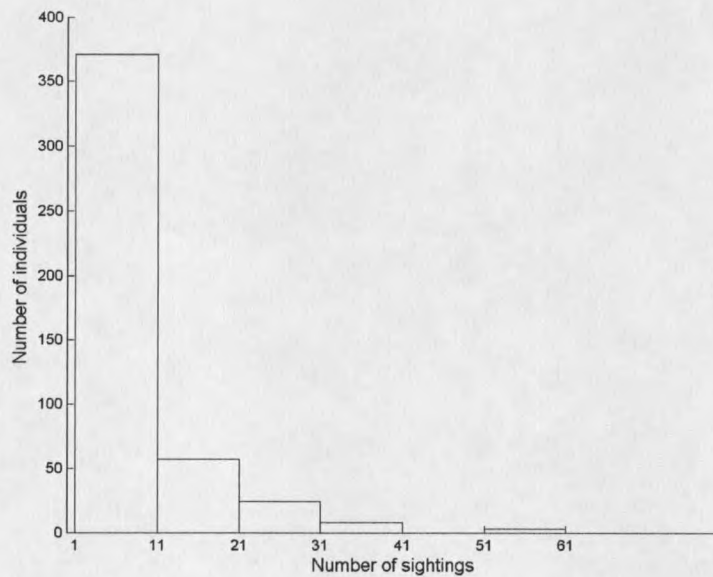


Figure 5.16. A frequency histogram of the sighting frequency of identifiable bottlenose dolphins in the dataset for a photographic identification study near Beaufort, NC (K. Rittmaster).

Sighting records from 138 primary periods were used to compute the joint distribution of the hyperparameters. The scale reduction factor was greater than 1.2 after four sequences. The hyperparameters, therefore, were fixed in the hierarchical model.

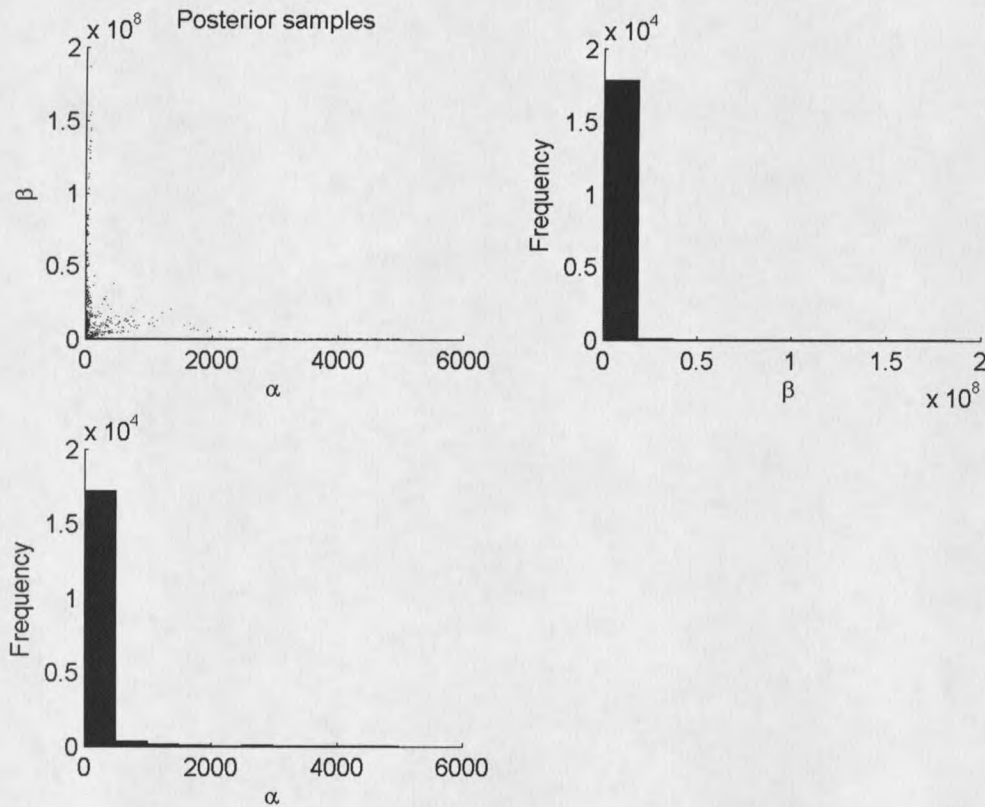


Figure 5.17. Posterior samples for the hyperparameters of sighting probabilities for a photographic identification study near Beaufort, NC (K. Rittmaster). Histograms are marginal distributions of hyperparameters.

A posterior distribution of abundance was computed for the 132nd primary period, which included four secondary occasions. A total of 28 individuals were photographed during the primary period (mean = 12, SD = 6.6). Fifteen individuals were sighted more than once during the primary period. The multinomial model, therefore, was used for computing the posterior distribution. The mode of the posterior distribution was 31, the

median was 32, and the mean was 33. The approximate 95% posterior interval ranged from 27 to 40 (Figure 5.18).

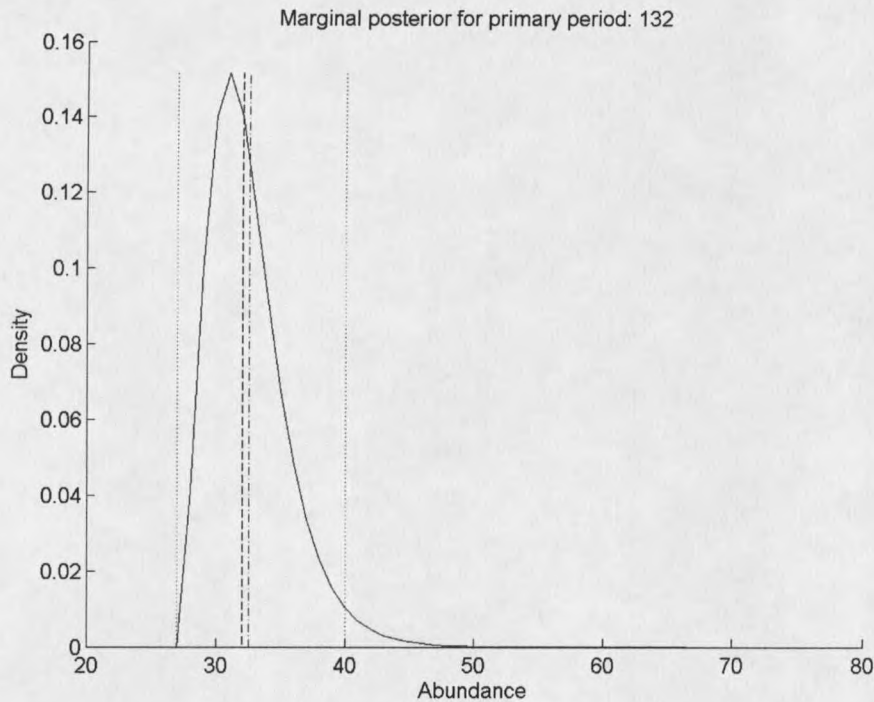


Figure 5.18. The posterior distribution of abundance for the 132nd primary period at a photographic identification study site near Beaufort, NC. The posterior distribution was computed using the multinomial model and fixed hyperparameters. The abscissa was truncated at 20 and 80. The dashed line indicates the median, the dash-dotted line indicates the mean, and the dotted lines indicate lower and upper limits of the approximate 95% posterior interval.

Wilmington, NC (L. Sayigh)

Sighting data of bottlenose dolphins for Wilmington, NC, were collected on 106 sampling days between 16 January 1996 and 22 November 1998. The mean number of secondary occasions per 15-day primary period was 3.42 (SE = 0.26, $n = 31$, range = 2-

7). The study site included estuaries and the Intracoastal Waterway. The study area was approximately 116 km² (Figure 5.19).

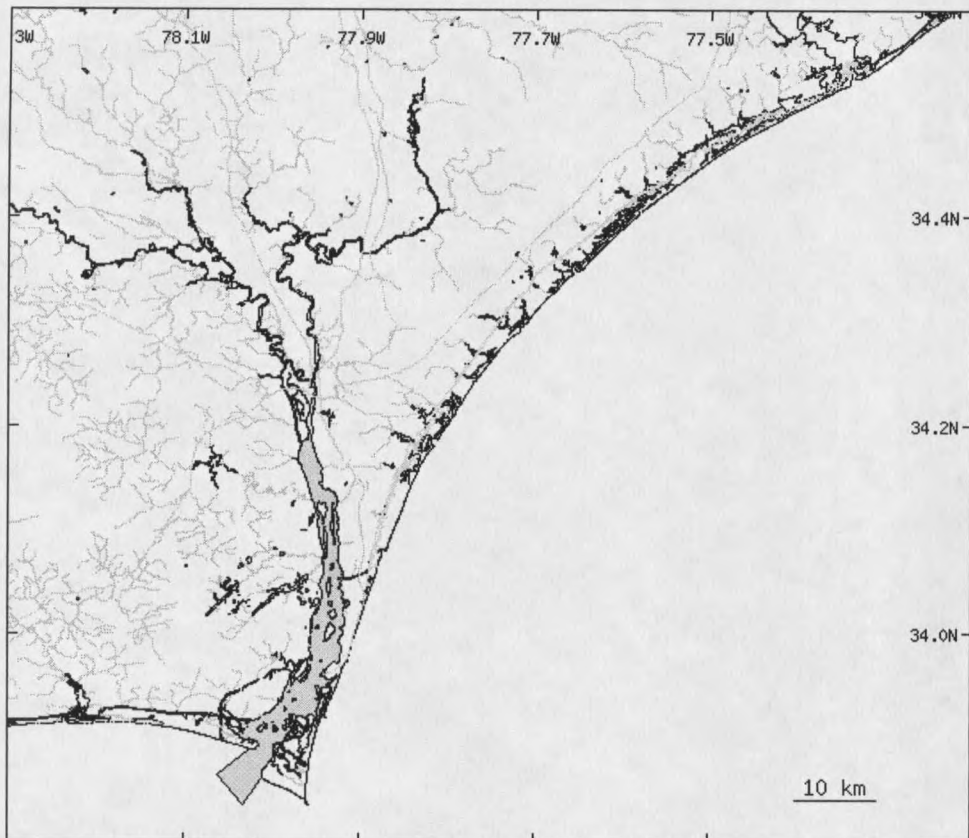


Figure 5.19. The photographic identification study area near Wilmington, NC. The study area includes part of the Intracoastal Waterway. No sighting locations were available.

The number of individuals in the dataset increased continuously (Figure 5.20). New individuals were added to the dataset throughout the year. There was a prominent increase in catalog size during summer 1998. The median number of days since the last sighting was 25, whereas the maximum was 112.

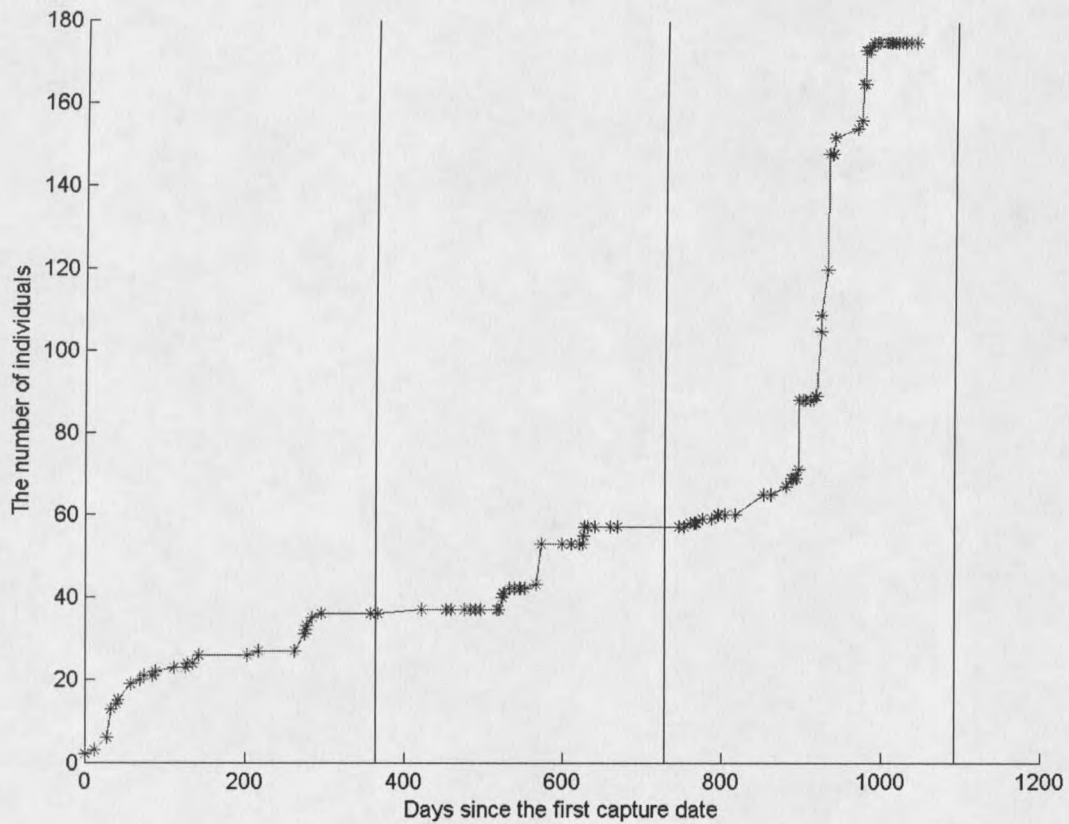


Figure 5.20. The cumulative number of individual bottlenose dolphins in the dataset for the photographic identification study site near Wilmington, NC. Vertical lines indicate intervals of 365 days. Day 0 corresponds to 16 January 1996.

The dataset consisted of sighting histories for 175 bottlenose dolphins from 106 capture occasions. The number of individuals accepted to the dataset per day ranged from 1 to 46 (median = 2; Figure 5.22). Of 175 individuals in the dataset, 89 were sighted more than once during the study. The maximum number of sightings per individual was 22 (median = 2; Figure 5.22).

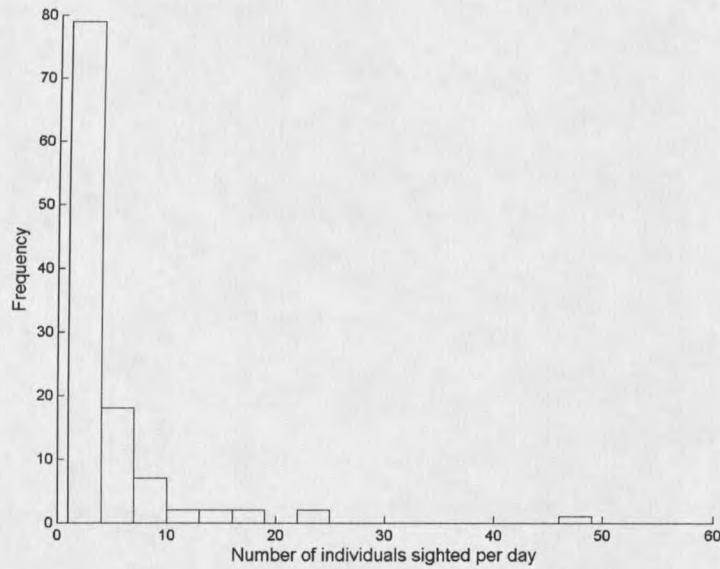


Figure 5.21. A histogram of the number of individuals accepted to the dataset per day for the photographic identification study near Wilmington, NC.

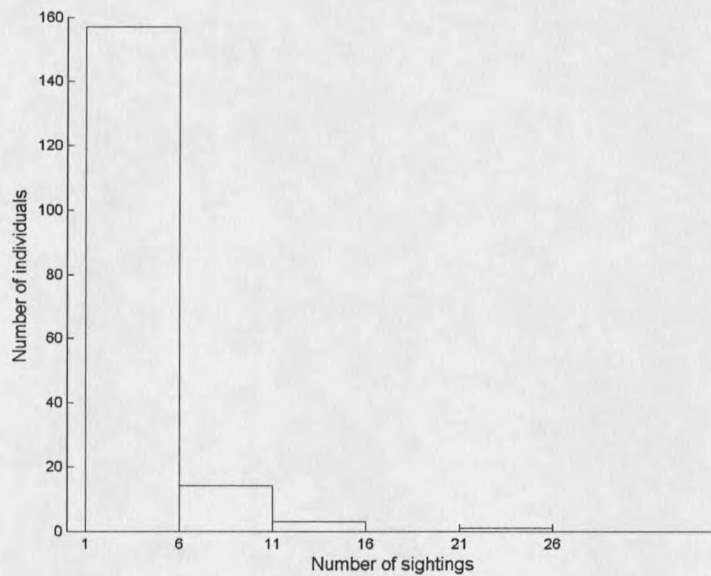


Figure 5.22. A histogram of the sighting frequency of individual bottlenose dolphins for the photographic identification study site near Wilmington, NC.

Sighting records from 30 primary periods were used to compute the joint distribution of the hyperparameters. Posterior samples for the hyperparameters indicated a peak at approximately $\alpha = 0.5$ and $\beta = 4.0$ (Figure 5.23). Consequently, the posterior samples were used for computing the posterior distribution of abundance.

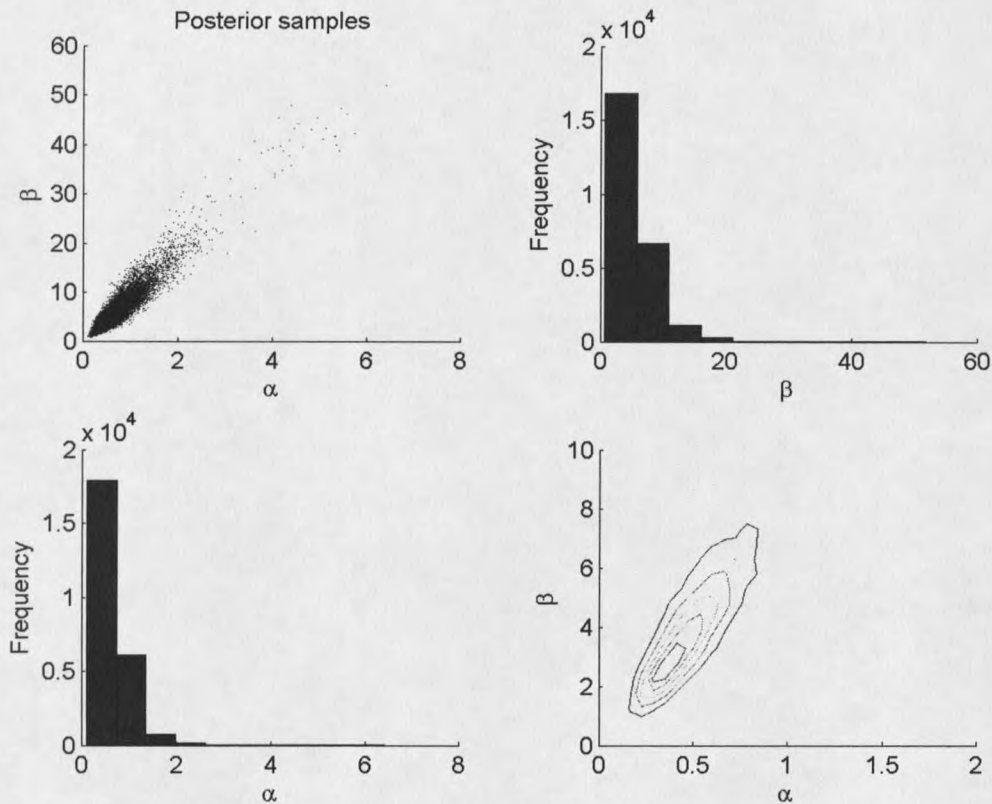


Figure 5.23. Posterior samples for the hyperparameters of sighting probabilities for Wilmington, NC, area. Histograms are marginal distributions of the hyperparameters. The lower right figure is a contour plot of the density of posterior samples (upper left figure). Axes for the contour plot were truncated to emphasize the peak of the distribution.

A posterior distribution of abundance was computed for the 27th primary period, which started on 5 August 1998. The primary period contained six secondary occasions.

During the primary period, the average number of sightings per secondary occasion was 13.2 (SD = 17.4). A total of 64 individuals were sighted, of which 13 were sighted more than once. The multinomial model, therefore, was used for computing the posterior distribution of abundance. The mode of the posterior distribution was 114, the median was 120, and the mean was 124 (Figure 5.24). The approximate 95% posterior interval ranged from 88 to 181.

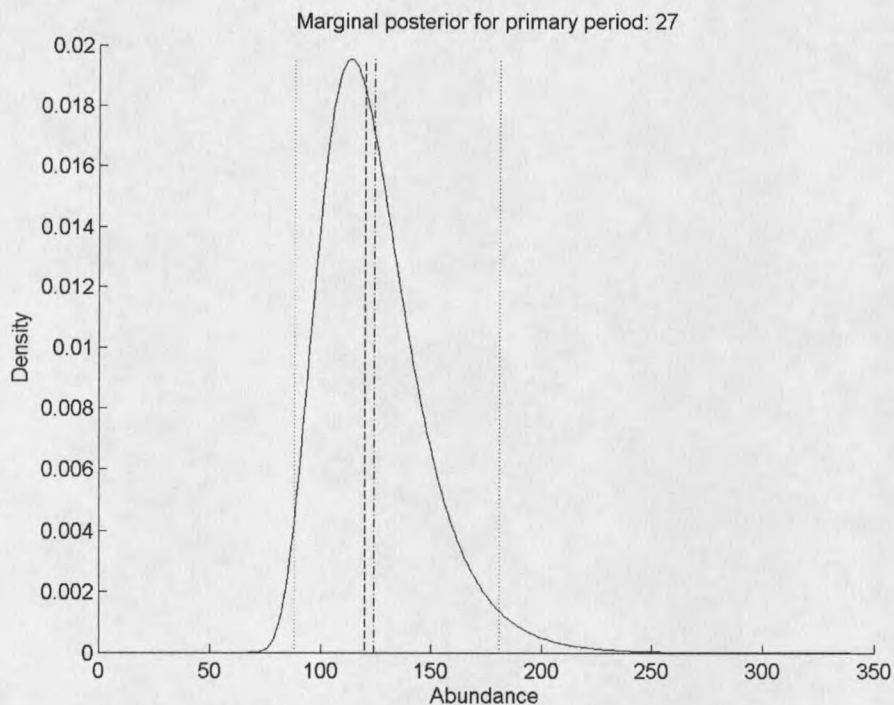


Figure 5.24. The posterior distribution of abundance for the 27th primary period for the photographic identification study site near Wilmington, NC. The posterior distribution was computed using the two-step approach and the multinomial model. The abscissa was truncated at 350. The dashed line indicates the median, the dash-dotted line indicates the mean, and the dotted lines indicate lower and upper limits of the approximate 95% posterior interval.

Murrell's Inlet and Winyah Bay, SC
(R. Young)

Sighting data for Murrell's Inlet and Winyah Bay, SC, were collected on 33 sampling days from 25 October 1997 to 13 November 1999. Five sampling days were excluded from the following analyses because they were the only secondary occasions within primary periods. The mean number of secondary occasions per 15-day primary period was 3.5 (SE = 0.63, $n = 8$, range = 2-6). Data were collected in estuaries and a bay along the coast of northern South Carolina (Figure 5.25 and Figure 5.26). The study area was approximately 166 km².

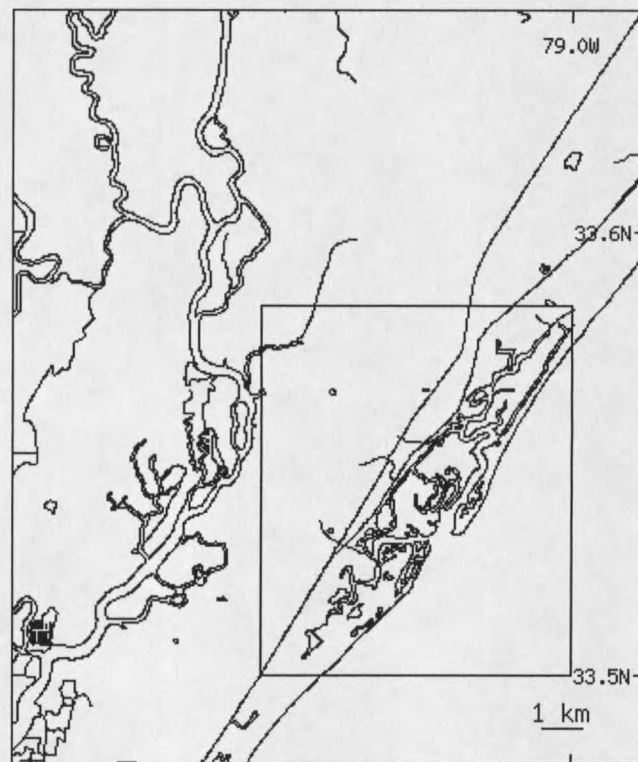


Figure 5.25. The photographic identification study site for Murrells Inlet, SC. The rectangle indicates an approximate study area. No sighting locations were available.

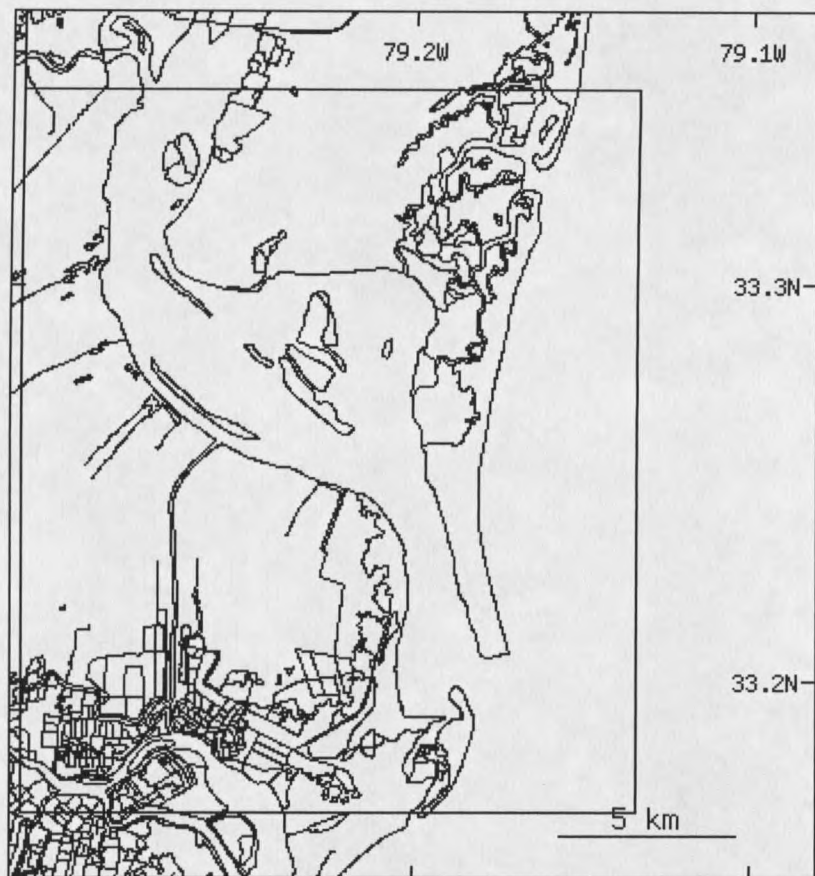


Figure 5.26. The photographic identification study area at Winyah Bay, SC. No sighting locations were available.

The cumulative number of individual bottlenose dolphins in the dataset increased continuously (Figure 5.27). The rate of increase was greater during autumn (September and October) than for the rest of the year. The median number of days since the last sighting was 7 and the maximum was 32.

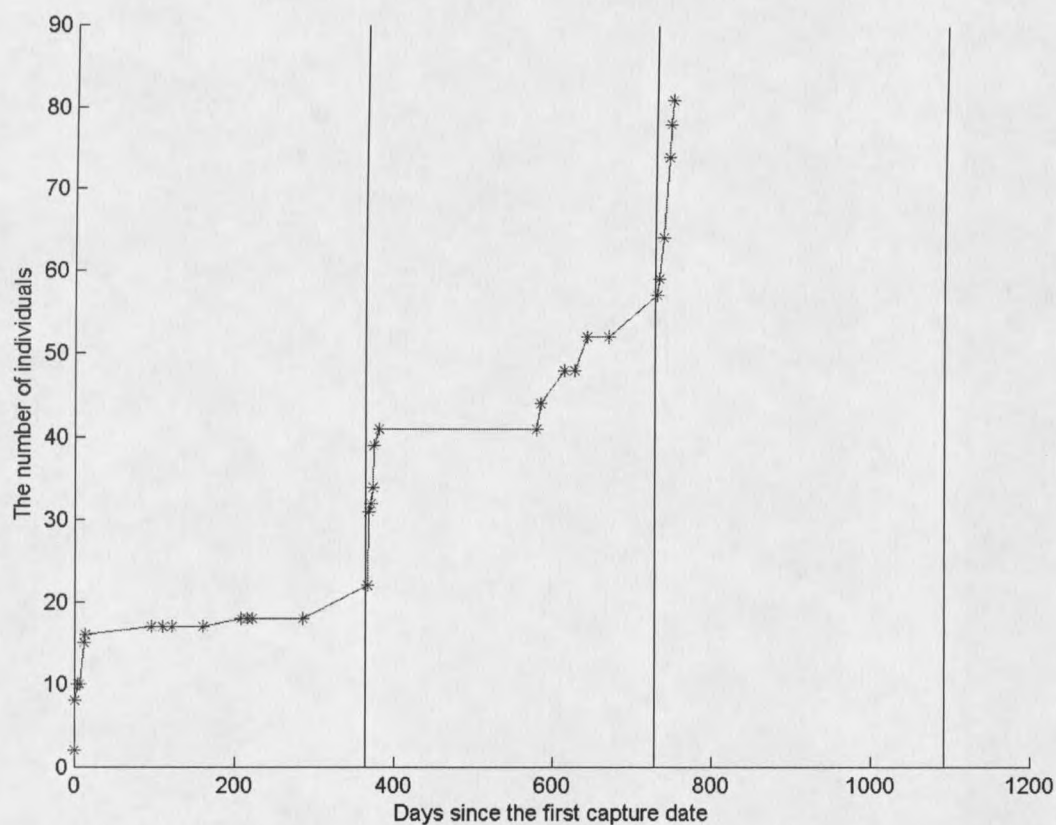


Figure 5.27. The cumulative number of individual bottlenose dolphins in the dataset for the photographic identification study near Myrtle Beach, SC. Vertical lines indicate 365-day intervals. Day 0 corresponds to 25 October 1997.

The dataset consisted of sighting histories of 81 individuals, of which 19 were sighted more than once. The number of individuals accepted to the dataset per sampling day ranged from 1 to 13 (median = 2; Figure 5.28). The maximum number of sightings per individual was 12 (median = 1; Figure 5.29).

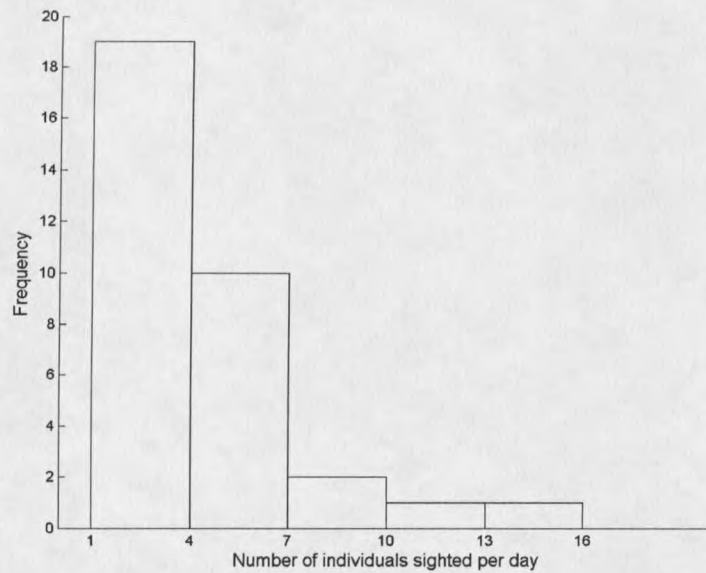


Figure 5.28. A histogram of the number of individuals accepted to the dataset per day for the photographic identification study near Myrtle Beach, SC.

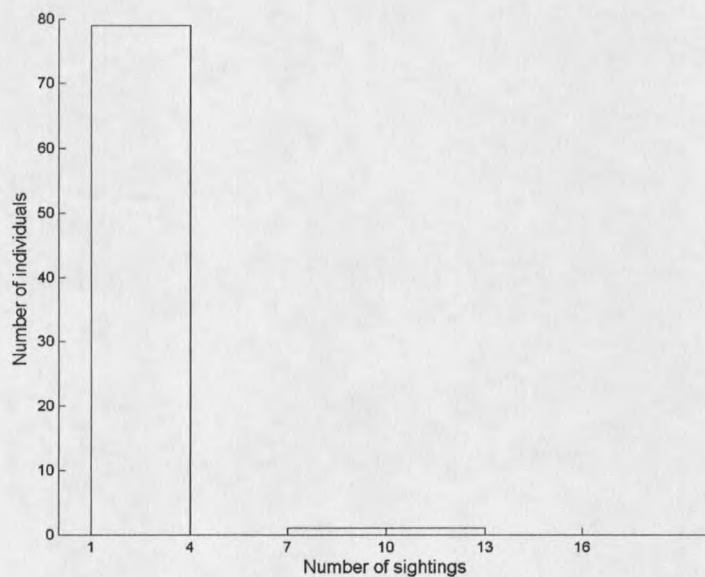


Figure 5.29. A frequency histogram of the sighting frequency of individuals in the dataset for the photographic identification study near Myrtle Beach, SC.

Sighting records from seven primary periods were used to compute the joint distribution of the hyperparameters. Because of the small number of primary periods for the study, the posterior samples of the hyperparameters were somewhat diffuse (Figure 5.30). The two-step approach, however, was used to compute a posterior distribution of abundance.

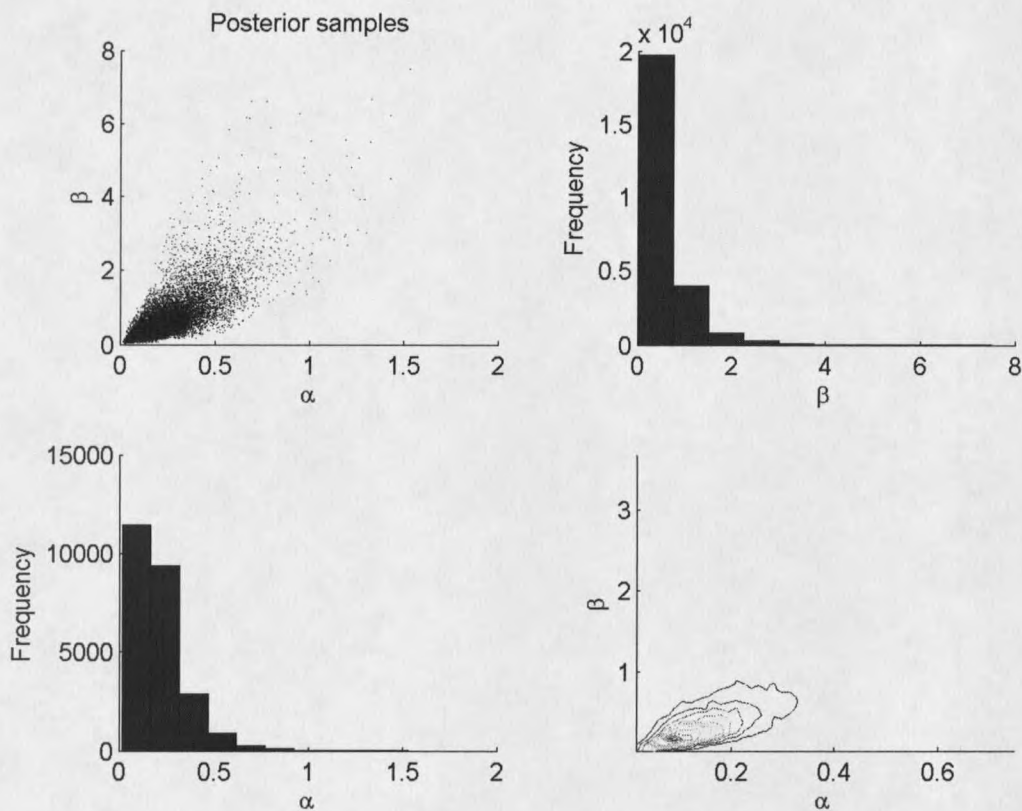


Figure 5.30. Posterior samples of the hyperparameters of sighting probabilities for the photographic identification study near Myrtle Beach, SC. Histograms are marginal distributions of the hyperparameters.

A posterior distribution was computed for the 1st primary period. The primary period contained six secondary occasions. The average number of individuals sighted per occasion was three (SD = 2.0). During the primary period, a total of 16 individuals were

sighted, of which two were sighted more than once. The multinomial model, therefore, was used to compute the posterior distribution of abundance. The mode of the posterior distribution was 39, the median was 61, and the mean was 88 (Figure 5.31). The approximate 95% posterior interval ranged from 24 to 324.

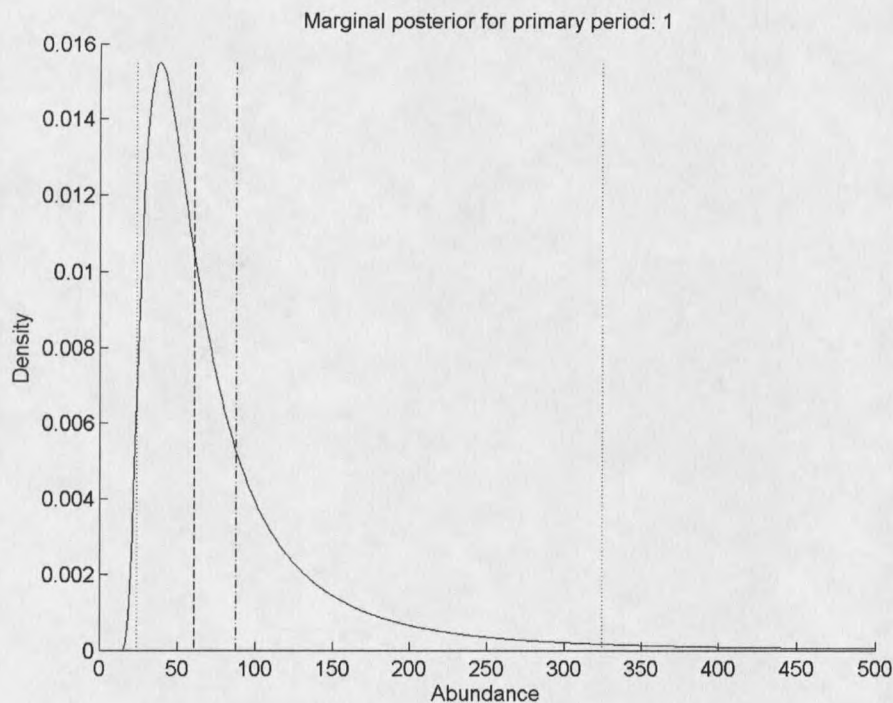


Figure 5.31. The posterior distribution for abundance of bottlenose dolphins for the 1st primary period at photographic identification study sites near Myrtle Beach, SC. The posterior distribution was computed using the hierarchical approach and the multinomial model. The abscissa was truncated at 500. The dashed line indicates the median, the dash-dotted line indicates the mean, and the dotted lines indicate lower and upper limits of the approximate 95% posterior interval.

Charleston, SC (E. Zolman),

Sighting data were collected on 152 sampling days from 14 February 1994 to 28 January 2000. The mean number of sampling occasions per 15-day primary period was

4.09 (SE = 0.3, n = 35, range = 2-10). Data were collected in rivers, estuaries, and open ocean near Charleston, SC. The study area was approximately 234 km² (Figure 5.32). Although data were collected in the open water, the majority of effort was concentrated for the waters in bays, rivers, and estuaries.



Figure 5.32. The study area near Charleston, SC. The solid line indicates the offshore boundary for the study area. Data were collected in the estuaries and rivers.

The cumulative number of individual bottlenose dolphins in the dataset increased steadily during the study (Figure 5.33). The rate of increase, however, decreased at the end of 1999. No apparent seasonal trend was found in the rate of increase. The median number of days since the last sighting was 54 and the maximum was 147.

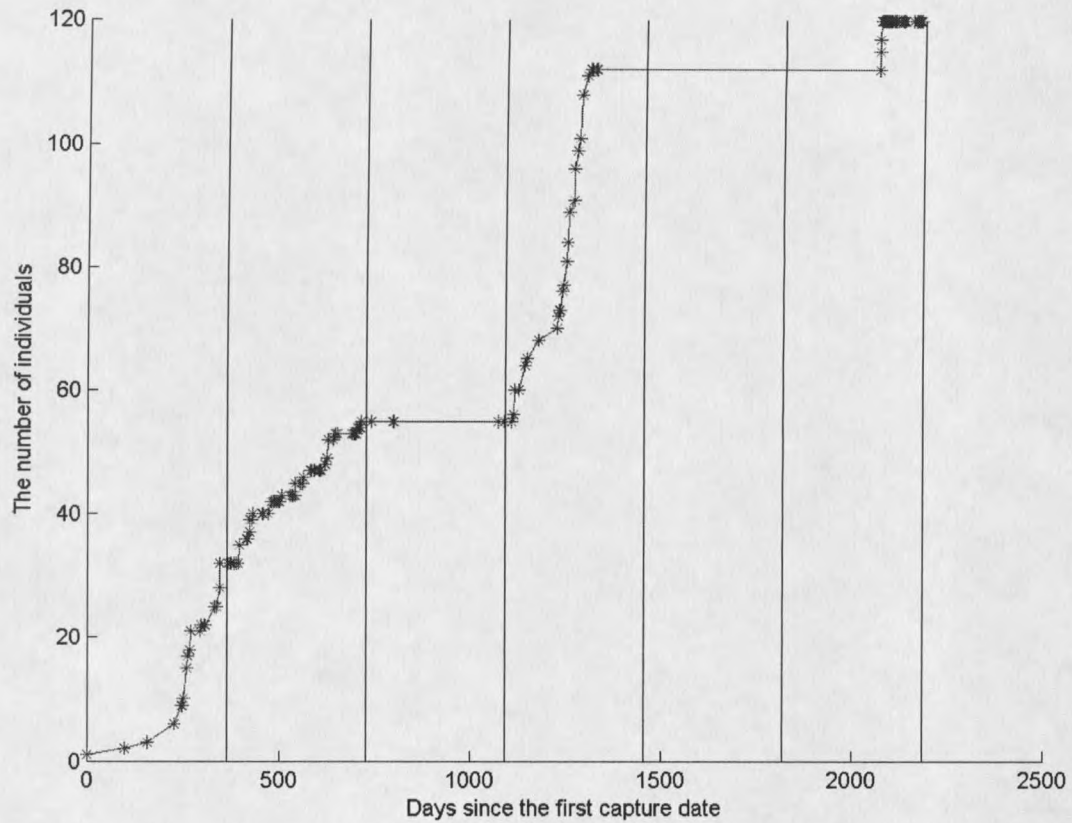


Figure 5.33. The cumulative number of individuals in the dataset for the photographic identification study near Charleston, SC. Vertical lines indicate 365-day periods. Day 0 corresponds to 14 February 1994.

The dataset consisted of capture histories of 121 individuals, of which 76 were sighted more than once. The number of individuals accepted to the dataset per secondary occasion ranged from 1 to 14 (median = 4; Figure 5.34). The maximum number of sightings per individual was 42 (median = 2; Figure 5.35).

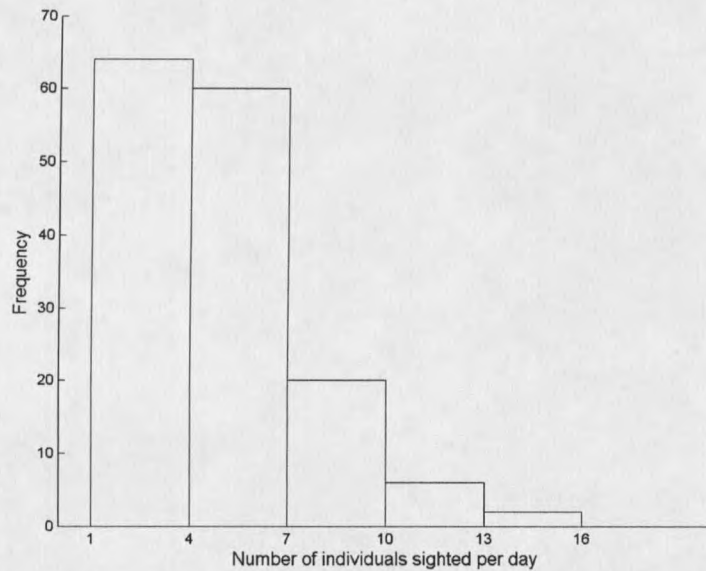


Figure 5.34. A frequency histogram of the number of individuals accepted to the dataset per day for the photographic identification study near Charleston, SC.

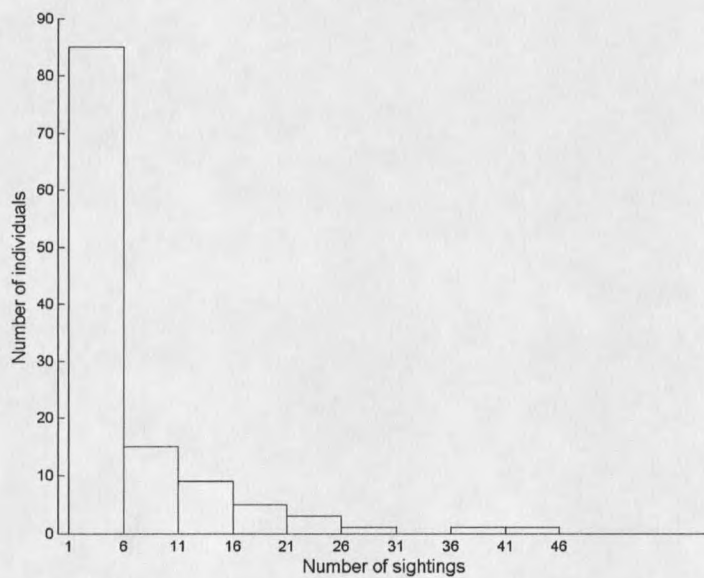


Figure 5.35. A frequency histogram of the sighting frequency of individual bottlenose dolphins in the dataset for the photographic identification study near Charleston, SC.

Sighting records from 34 primary periods were used to compute a joint distribution of the hyperparameters. Posterior samples of the hyperparameters indicated an apparent peak at approximately $\alpha = 0.8$ and $\beta = 2.2$ (Figure 5.36). Consequently, the posterior samples were used for computing the posterior distribution of abundance.

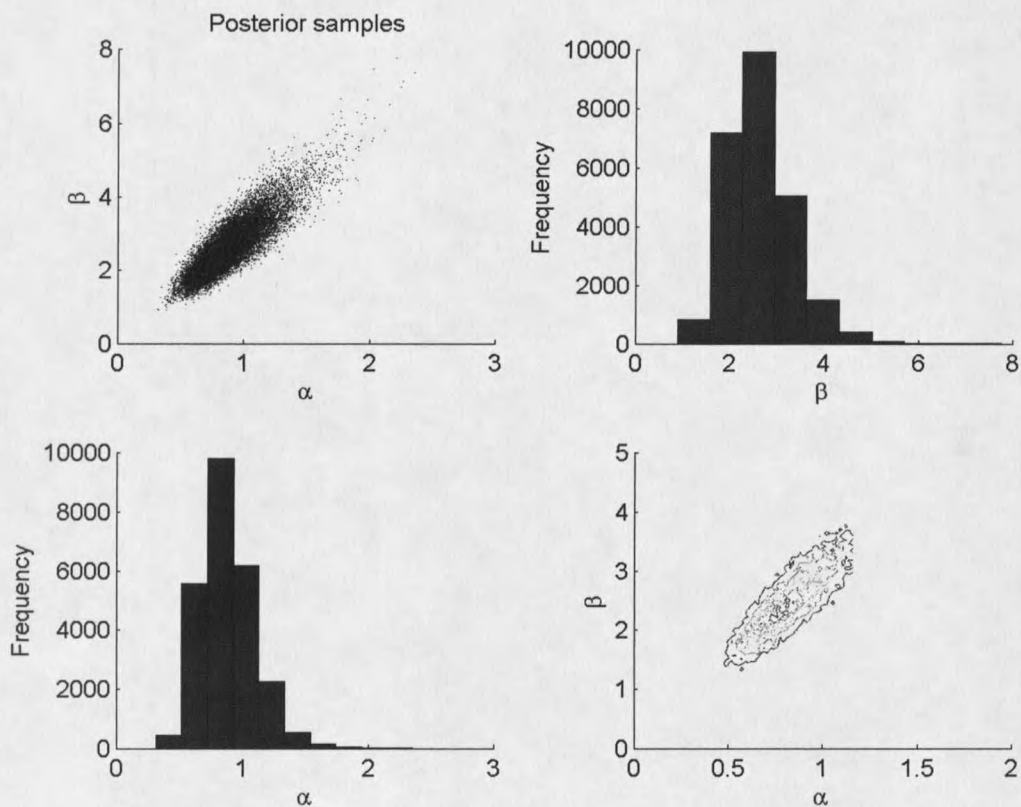


Figure 5.36. Posterior samples of the hyperparameters of capture probabilities for the photographic identification study near Charleston, SC. The lower right figure is a contour plot of the density of posterior samples (upper left figure). Axes for the contour plot were truncated to emphasize the peak of the distribution.

A posterior distribution of abundance was computed for the 27th primary period, which started on 9 September 1997. The primary period contained four sampling occasions. During the primary period, a total of 27 individuals were sighted, of which 4

were sighted more than once. Consequently, I used the multinomial model to compute a posterior distribution of abundance. The mode of the posterior distribution was 46, the median was 54, and the mean was 60. The approximate 95% posterior interval ranged from 31 to 122 (Figure 5.37).

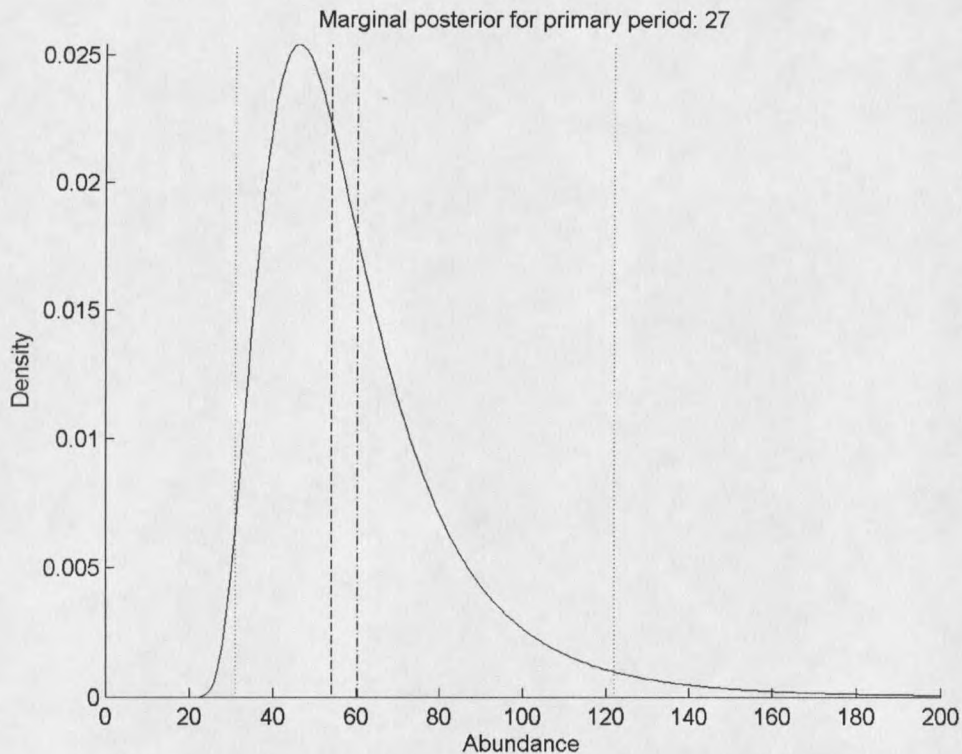


Figure 5.37. The posterior distribution of abundance for the 27th primary period for the photographic identification study near Charleston, SC. The posterior distribution was computed using the two-step hierarchical approach and the multinomial model. The abscissa was truncated at 200. The dashed line indicates the median, the dash-dotted line indicates the mean, and the dotted lines indicate lower and upper limits of the approximate 95% posterior interval.

Hilton Head, SC (C. Gubbins),

Sighting data for Hilton Head, SC, were collected on 189 sampling days from 29 October 1994 to 8 December 1998. The mean number of secondary occasions per 15-day primary period was 4.5 (SE = 0.37, $n = 42$, range = 2-13). Data were collected in estuaries and open water near Hilton Head, SC. The study area was approximately 324 km² (Figure 5.38).

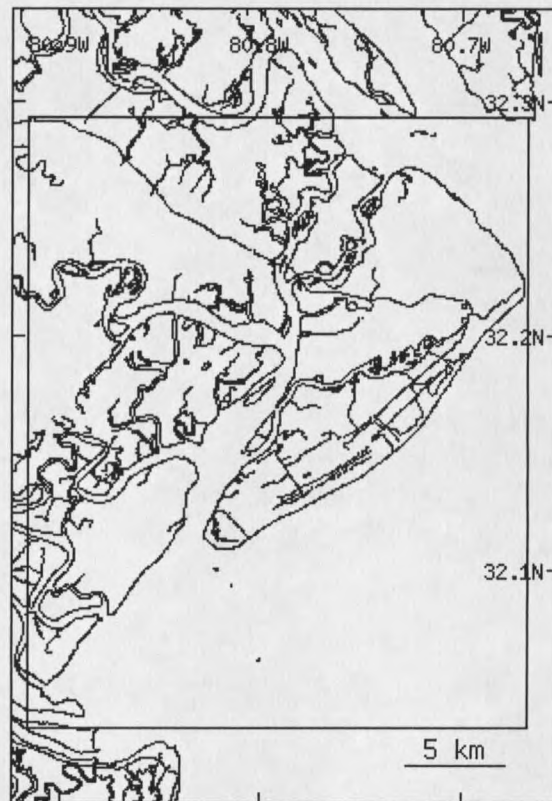


Figure 5.38. The photographic identification study site near Hilton Head, SC. Waters within the rectangle are the approximate study area. No sighting locations were available.

The cumulative number of individual bottlenose dolphins in the dataset increased continuously (Figure 5.39). For each year, the rate of increase was greater during spring

than during autumn and early winter. The median number of days since the last sighting was 44, whereas the maximum was 188.

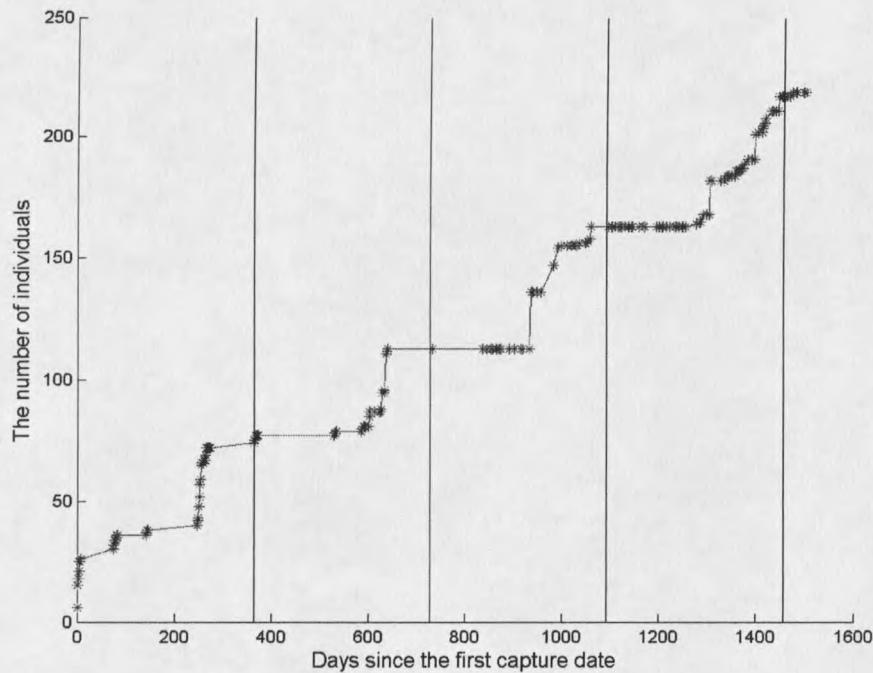


Figure 5.39. The cumulative number of individual bottlenose dolphins in the dataset for the photographic identification study near Hilton Head, SC. Vertical lines indicate 365-day intervals. Day 0 corresponds to 13 September 1997.

The dataset consisted of sighting histories for 219 bottlenose dolphins, of which 119 were sighted more than once. The number of individuals accepted to the dataset per day ranged from 1 to 33 (median = 5; Figure 5.41). The maximum number of sightings per individual was 95 (median = 2; Figure 5.40).

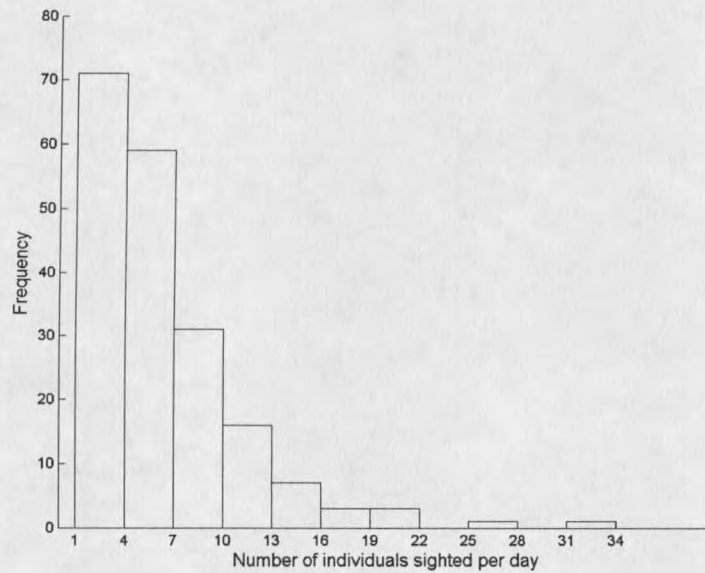


Figure 5.40. A frequency histogram of the number of individuals accepted to the dataset for the photographic identification study near Hilton Head, SC.

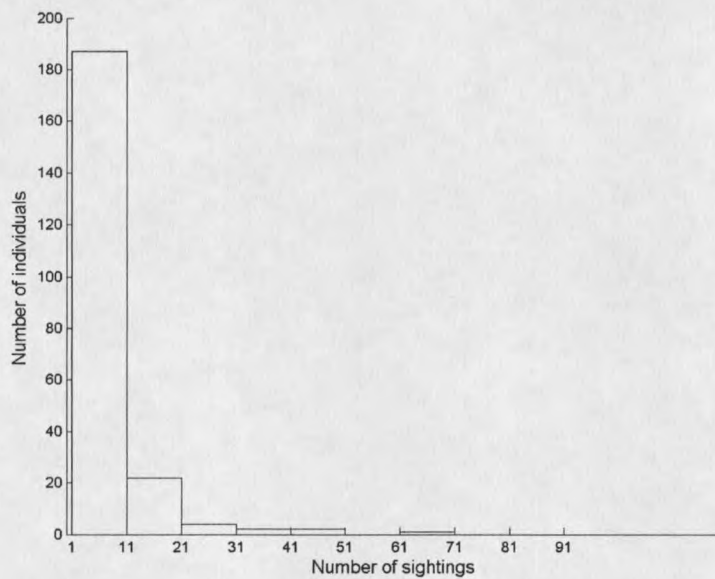


Figure 5.41. A frequency histogram of the sighting frequency of bottlenose dolphins in the dataset for the photographic identification study near Hilton Head, SC.

Sighting records from 41 primary periods were used to compute the joint distribution of the hyperparameters. Posterior samples of the hyperparameters indicated that the ratio between α and β was approximately 6, where α ranged between approximately 1 and 15 (Figure 5.42). A peak was found at approximately $\alpha = 3$, $\beta = 20$. Consequently, the posterior samples were used for computing the posterior distribution of abundance.

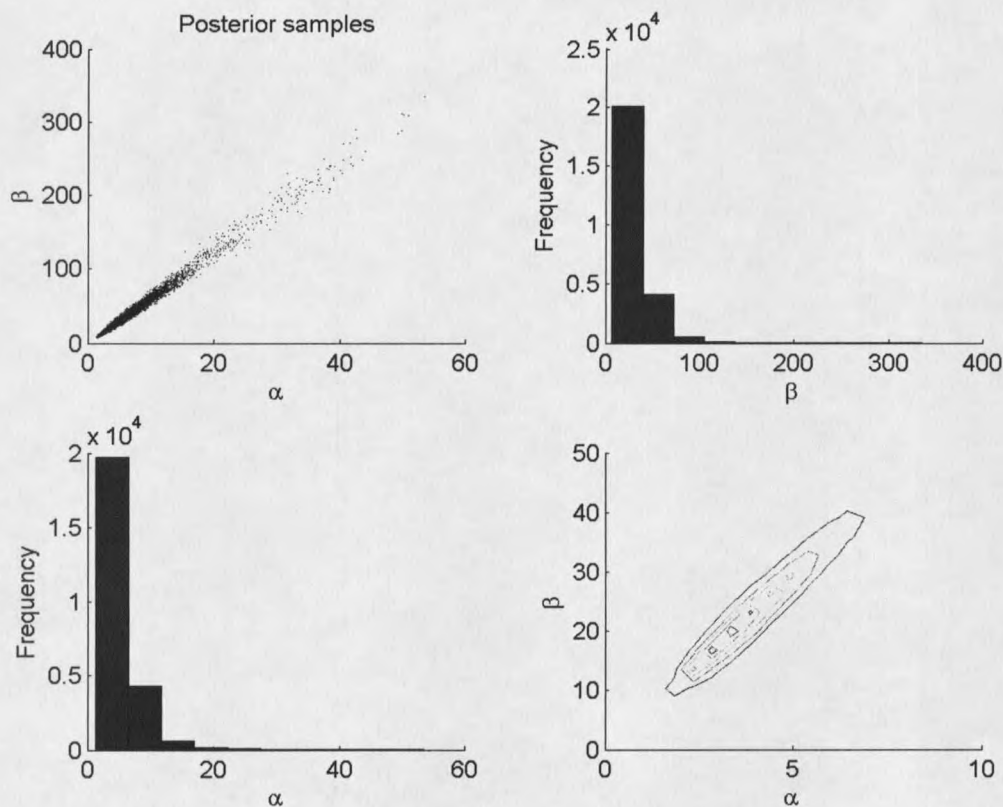


Figure 5.42. Posterior samples of the hyperparameters of capture probabilities for the photographic identification study near Hilton Head, SC. Histograms are marginal distributions of the hyperparameters. The lower right figure is a contour plot of the density of posterior samples (upper left figure). Axes for the contour plot were truncated to emphasize the peak of the distribution.

A posterior distribution of abundance was computed for the 22nd primary period, which started on 13 September 1997. The period contained four secondary occasions. During the primary period, a total of 24 individuals were sighted, of which two were sighted more than once. Consequently, the multinomial model was used to compute the posterior distribution of abundance. The mode of the posterior distribution was 56, the median was 60, and the mean was 63. The approximate 95% posterior interval was from 38 to 102 (Figure 5.43).

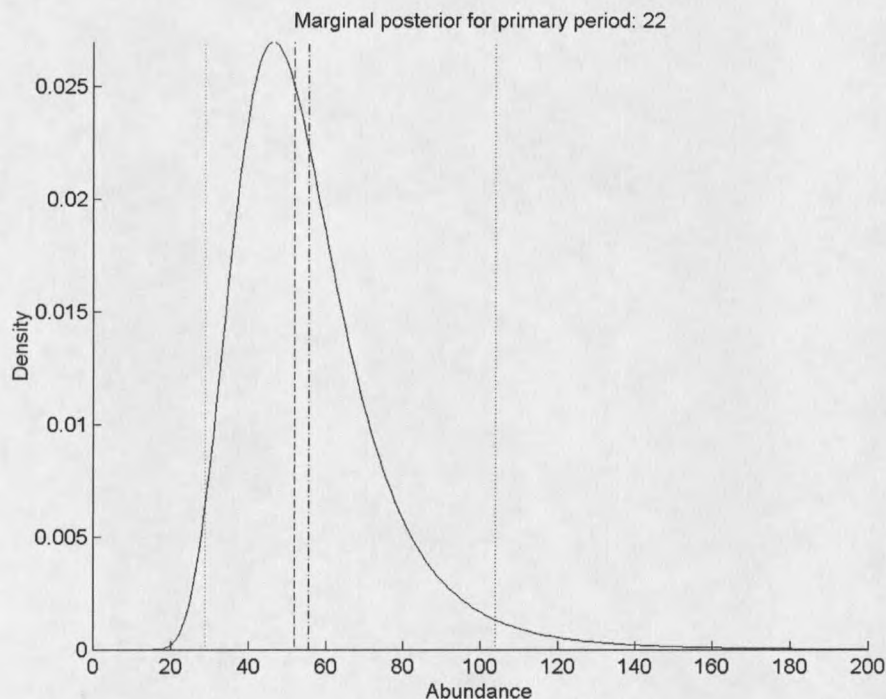


Figure 5.43. The posterior distribution of abundance for the 22nd primary period for the photographic identification study near Hilton Head, SC. The posterior distribution was computed using the two-step hierarchical approach and the multinomial model. The abscissa was truncated at 200. The dashed line indicates the median, the dash-dotted line indicates the mean, and the dotted lines indicate lower and upper limits of the approximate 95% posterior interval.

Georgia (The Dolphin Project)

Sighting data of bottlenose dolphins for Georgia were collected on 92 sampling days from 15 July 1989 to 11 March 2000. The mean number of secondary occasions per 15-day primary period was 2.1 (SE = 0.05, $n = 31$, range = 2-3). The coastline and estuaries along the coast of Georgia was divided into 56 regions and each region was surveyed twice monthly. Data for all regions were combined in this analysis.

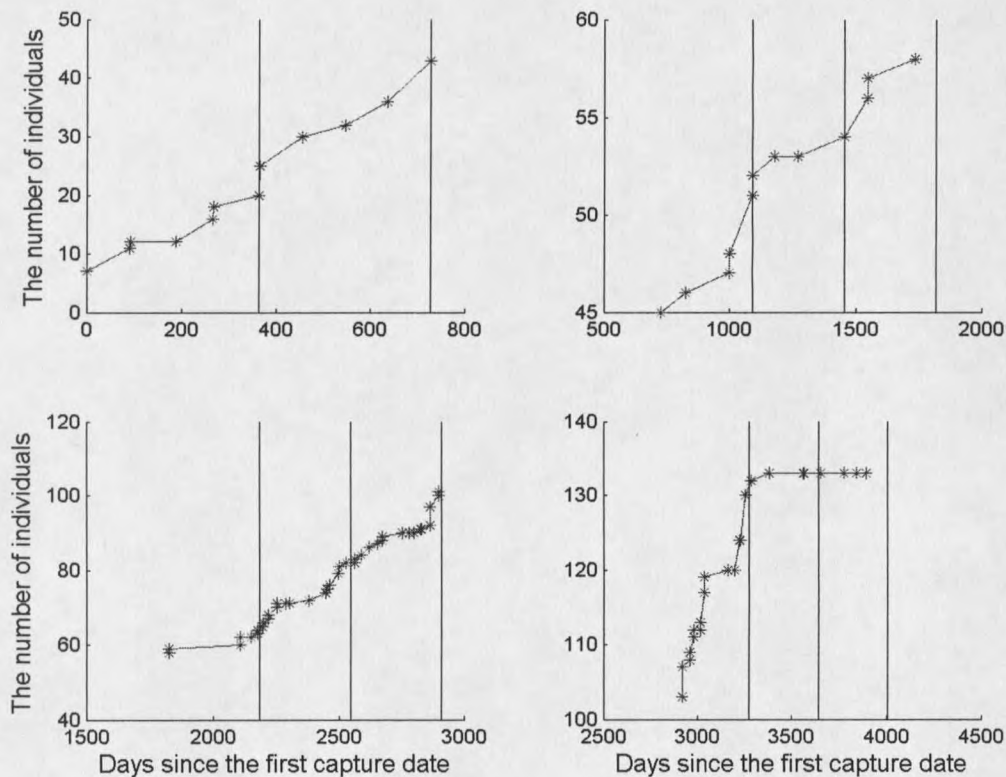


Figure 5.44. The cumulative number of individuals in the photographic identification dataset for Georgia. Vertical lines indicate 365-day periods. Day 0 corresponds to 15 July 1989.

The cumulative number of individual bottlenose dolphins in the dataset continuously increased for the first six years. For the last two years, however, only a few new individuals were added to the dataset (Figure 5.44). No apparent seasonal pattern in the addition of new individuals to the dataset was found. The median number of days since the last sighting was 38 and the maximum was 91.

The dataset consisted of sighting histories for 133 bottlenose dolphins, of which 47 were sighted more than once. The number of individuals that were accepted to the dataset per sampling occasion ranged from 1 to 11 (median = 2;). The maximum number of sightings per individual dolphin was 14 (median = 1; Figure 5.46).

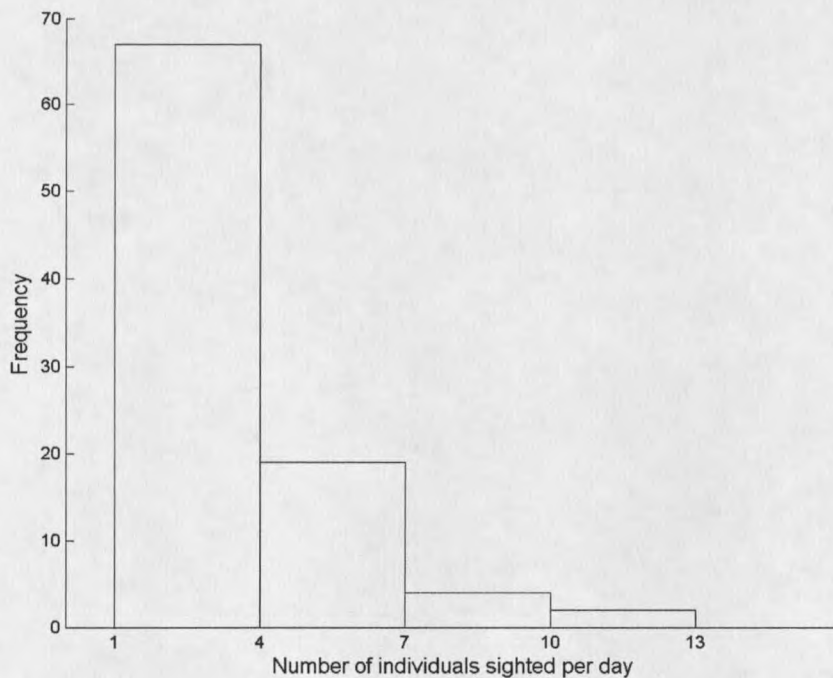


Figure 5.45. A frequency histogram of the number of individuals accepted to the dataset per day for the photographic identification study along the Georgia coast.

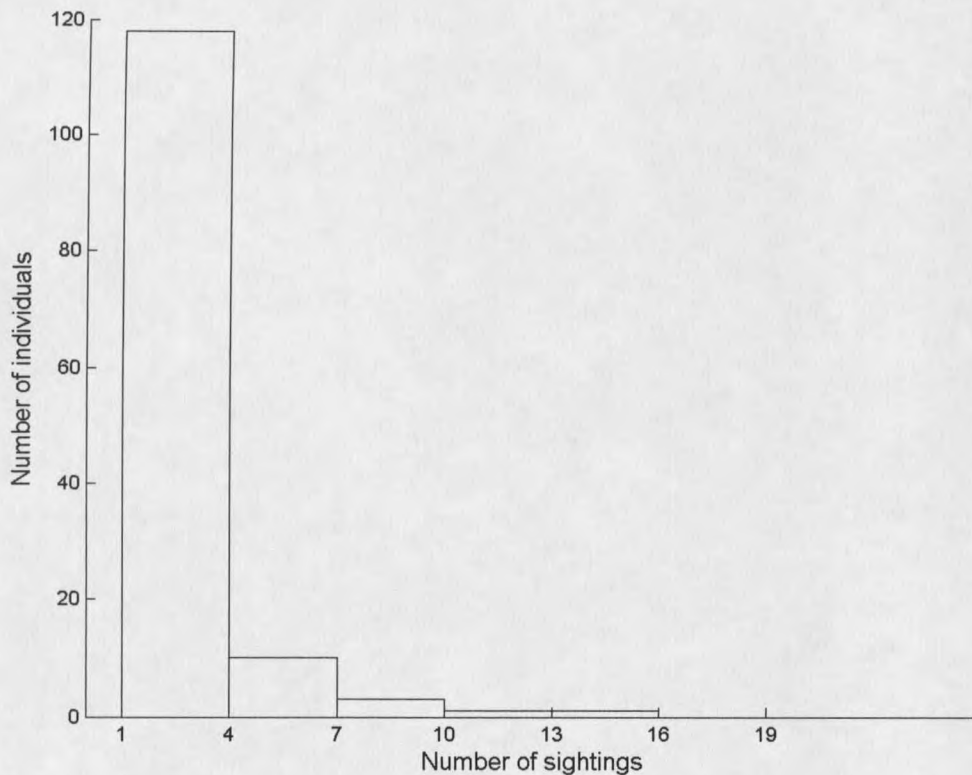


Figure 5.46. A frequency histogram of the sighting frequency of individuals in the dataset for the photographic identification study along the Georgia coast.

Sighting records from 30 primary periods were used to compute the joint distribution of the hyperparameters. Although posterior samples of the hyperparameters were diffuse (Figure 5.47), the scale-reduction factor was less than 1.2 for both hyperparameters. Consequently, the posterior samples were used for computing the posterior distribution of abundance. Because of the diffuse posterior distribution of the hyperparameters, no contour plot was created.

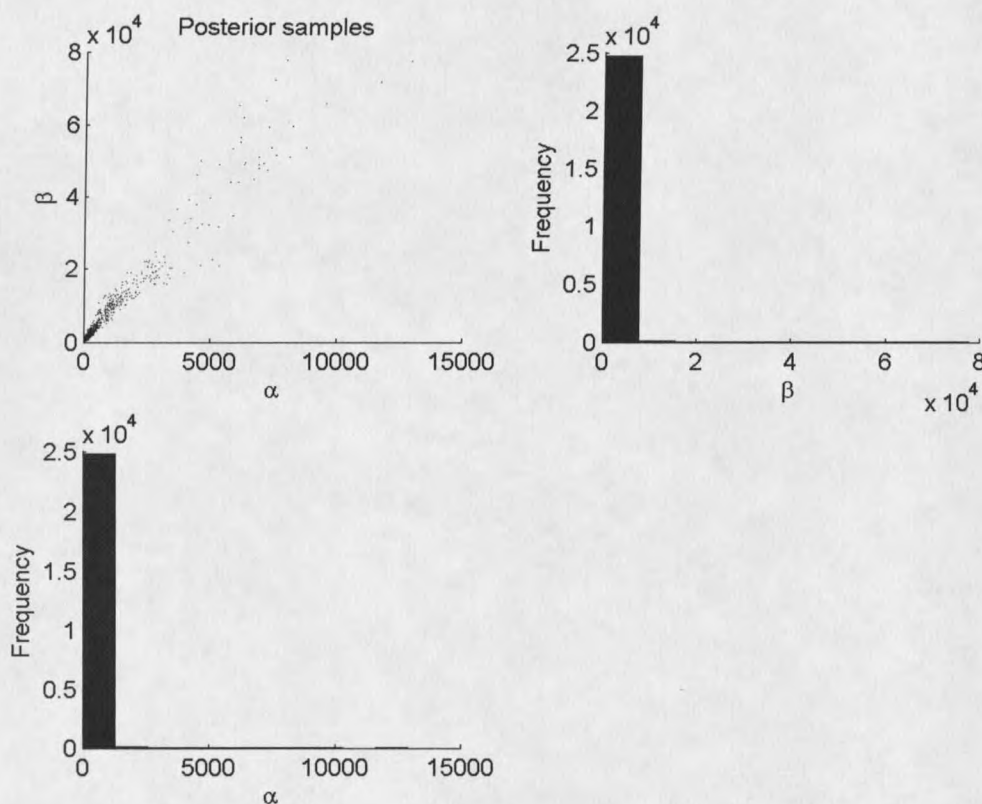


Figure 5.47. Posterior samples of the hyperparameters of capture probabilities for the photographic identification study in Georgia. Histograms are marginal distributions of the hyperparameters.

A posterior distribution of abundance was computed for the 26th primary period, which included two secondary occasions. During the primary period, a total of four individuals were sighted, of which none was sighted more than once. Consequently, I used the beta-binomial model to compute the posterior distribution of abundance. The mode of the posterior distribution was 18, the median was 43, and the mean was 185. The approximate 95% posterior interval ranged from 4 to 1,237 (Figure 5.48).

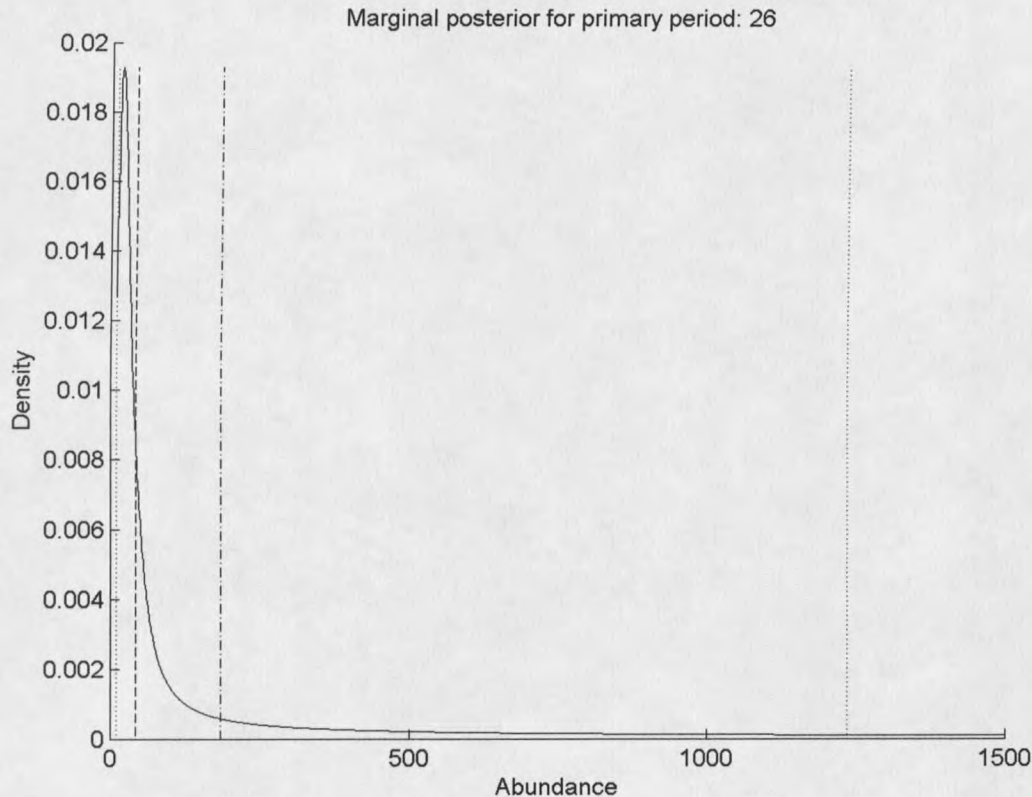


Figure 5.48. The posterior distribution of abundance for the 26th primary period for the photographic identification study in Georgia. The posterior distribution was computed using the non-hierarchical approach and the beta-binomial model. The abscissa was truncated at 400. The dashed line indicates the median, the dash-dotted line indicates the mean, and the dotted lines indicate lower and upper limits of the approximate 95% posterior interval.

Jacksonville, FL (M. Caldwell)

Sighting data of bottlenose dolphins for Jacksonville, FL, were collected on 176 sampling days from 28 December 1994 to 19 December 1997. The mean number of secondary occasions per 15-day primary period was 3.52 (SE = 0.16, $n = 50$, range = 2-6). Data were collected in estuaries and open ocean near Jacksonville, FL. The study area was approximately 774 km² (Figure 5.49).

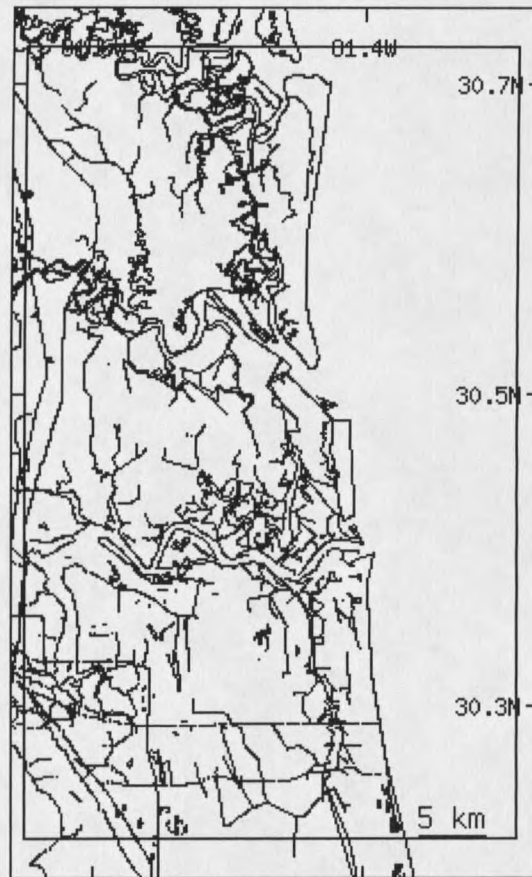


Figure 5.49. The photographic identification study site for Jacksonville, FL. No sighting locations were available.

The cumulative number of individuals in the dataset increased steadily for the first two years. For the last year, however, the rate of increase declined (Figure 5.50). No seasonal difference in the rate of increase was found. The median number of days since the last sighting was 79 and the maximum was 178.

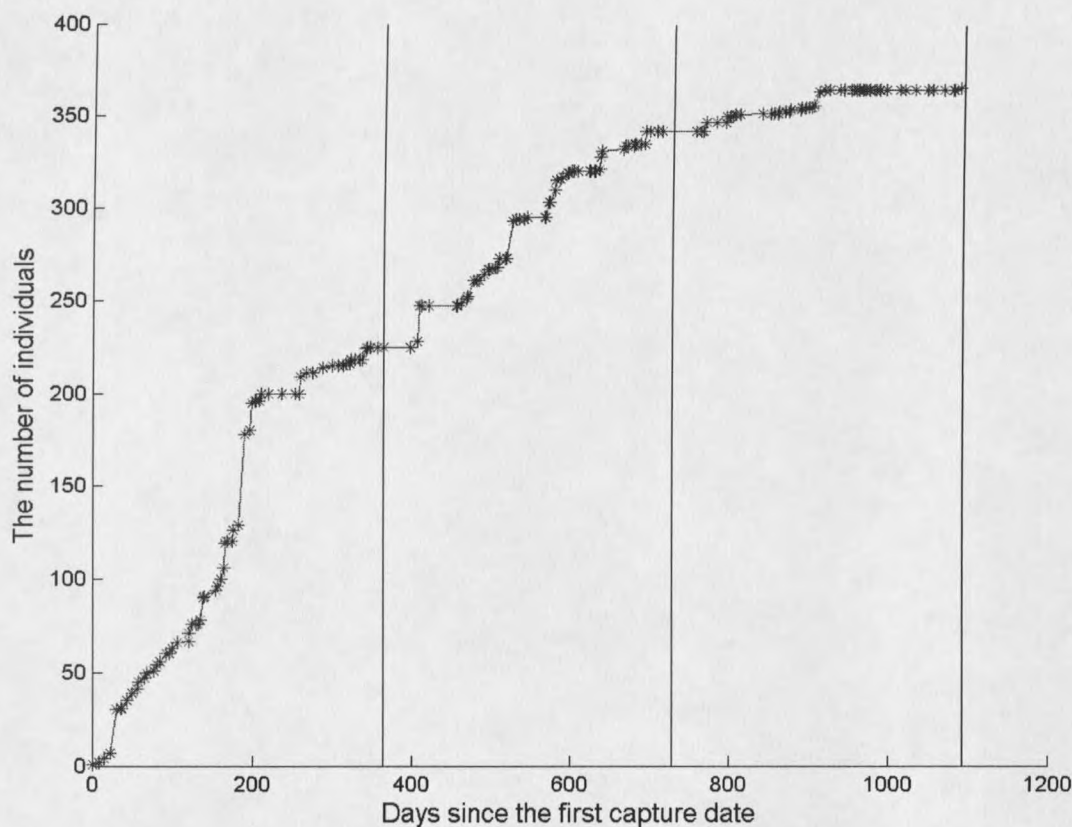


Figure 5.50. The cumulative number of individuals in the dataset for the photographic identification study near Jacksonville, FL. Vertical lines indicate 365-day periods. Day 0 corresponds to 28 December 1994.

The dataset consisted of sighting histories of 366 bottlenose dolphins, of which 209 were sighted more than once. The number of individuals accepted to the dataset per secondary occasion ranged from 1 to 50 (median = 9; Figure 5.51). The maximum number of sightings per individual bottlenose dolphin was 51 (median = 2; Figure 5.52).

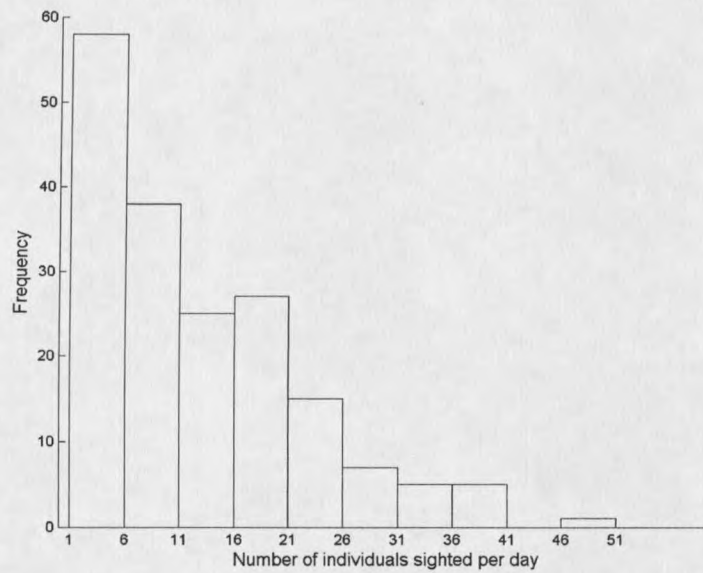


Figure 5.51. A frequency histogram of the number of individuals accepted to the dataset per day for the photographic identification study near Jacksonville, FL.

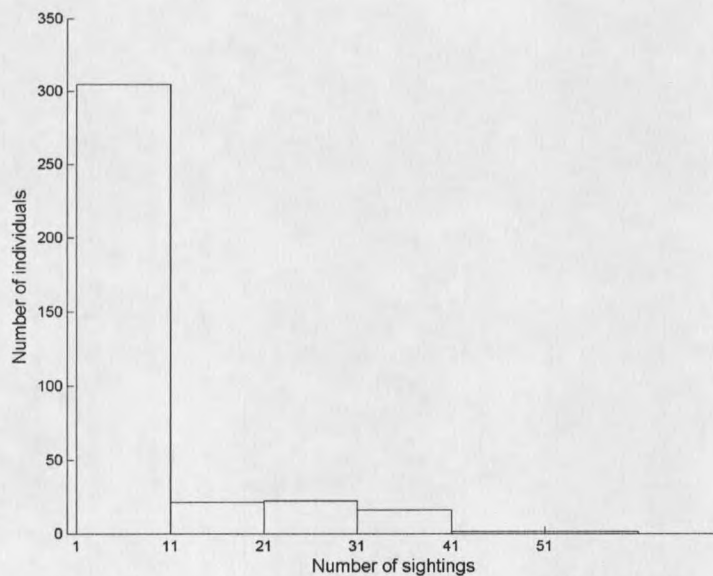


Figure 5.52. A frequency histogram of the sighting frequency of individual bottlenose dolphin in the dataset for the photographic identification study near Jacksonville, FL.

Sighting records from 49 primary periods were used to compute the joint distribution of the hyperparameters. Posterior samples for the hyperparameters indicated a peak at approximately $\alpha = 0.5$ and $\beta = 2.5$ (Figure 5.53). The ratio between α and β was approximately 5. Consequently, the hierarchical approach was used to compute a posterior distribution of abundance.

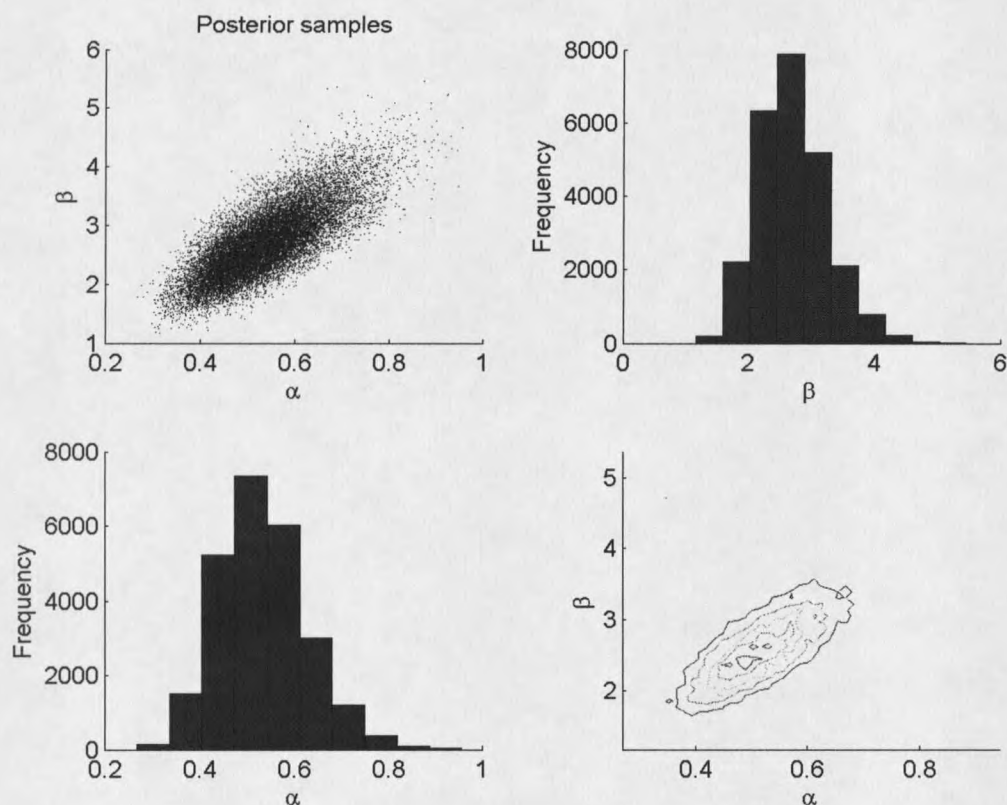


Figure 5.53. Posterior samples of the hyperparameters for sighting probabilities at Jacksonville, FL. Histograms are marginal distributions of the hyperparameters. The lower right figure is a contour plot of the density of posterior samples (upper left figure). Axes for the contour plot were truncated to emphasize the peak of the distribution.

A posterior distribution of abundance was computed for the 47th primary period, which contained four secondary occasions. During the primary period, a total of 27

individuals were sighted, of which two were sighted more than once. The multinomial model, therefore, was used to compute the posterior distribution of abundance. The mode of the posterior was 79, the median was 112, and the mean was 143. The approximate 95% posterior interval ranged from 48 to 434 (Figure 5.54).

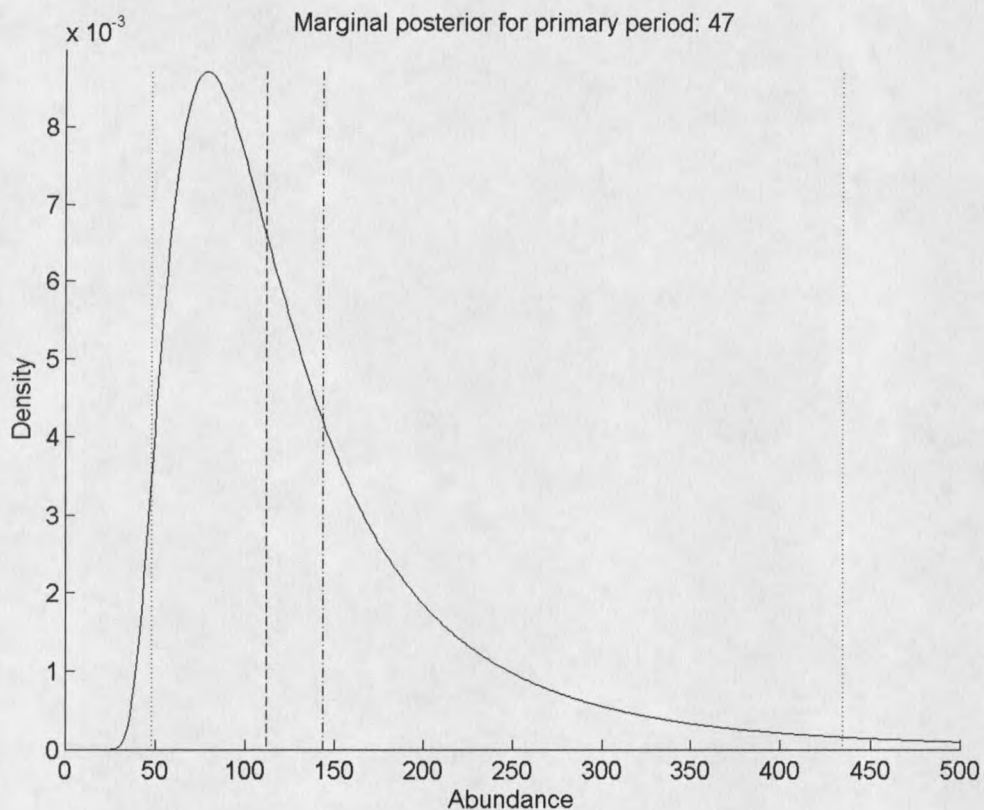


Figure 5.54. The posterior distribution of abundance for the 47th primary period for the photographic identification study site near Jacksonville, FL. The posterior distribution was computed using the two-step hierarchical approach and the multinomial model. The abscissa was truncated at 500. The dashed line indicates the median, the dash-dotted line indicates the mean, and the dotted lines indicate lower and upper limits of the approximate 95% posterior interval.

Northern group

Using results from Duke Marine Laboratory's data for the Beaufort area, the sum of the modes for the northern group was 157. The 95% posterior interval was between 120 and 505 (Table 5.1). A precise posterior distribution was obtained for Manteo because data were collected daily (Table 5.1). The imprecise posterior distribution for Beaufort (AR) was caused by the few secondary occasions within the primary period.

Table 5.1. The summary of posterior distributions of abundance of identifiable bottlenose dolphins for four northern sites. Lower and upper correspond to the lower and upper limits of 95% posterior intervals. The area of each study site is an approximate value. AR and KR for Beaufort, NC, indicate data for Andy Read and Keith Rittmaster, respectively. Catalog size is the total number of individuals in the dataset.

	Catalog size	Area (km ²)	Lower	Mode	Median	Mean	Upper
<u>August 1998</u>							
Manteo, NC	132	572	20	20	20	20	21
Beaufort, NC (AR)	110	650	12	23	39	66	303
Beaufort, NC (KR)	463	164	27	31	32	33	40
Wilmington, NC	175	116	88	114	120	124	181
Sum		1,502	147	188	211	243	545

Southern group

For the southern group, the sum of the modes of posterior distributions was 230. The 95% posterior distribution ranged between 145 and 1,311 (Table 5.2). The most precise posterior distribution was found for the dataset from Hilton Head, SC, where the relative precision (width of 95% posterior interval divided by mode) was 1.1. The imprecise posterior distribution for GA was caused by the few secondary occasions

within the primary period. Relative precisions were greater for study sites in the southern group than for the northern group.

Table 5.2. The summary of posterior distributions of the abundance of identifiable bottlenose dolphins for the southern group. Lower and upper correspond to the lower and upper limits of 95% posterior intervals. The area of each study site is an approximate value. Catalog size is the total number of individuals in the dataset.

	Catalog size	Area (km ²)	Lower	Mode	Median	Mean	Upper
<u>September 1997</u>							
Murrells Inlet + Winyah Bay, SC	81	166	24	39	61	88	324
Charleston, SC	120	234	31	46	54	60	122
Hilton Head, SC	219	324	38	56	60	63	102
Georgia	133	636	4	10	20	52	329
Jacksonville, FL	366	774	48	79	112	143	434
Sum		2,134	145	230	307	406	1,311

Discussion

Although precise posterior distributions were obtained for several datasets, interpretations of the analytical results were contingent on the validity of the underlying assumptions. These assumptions for each study area were: (1) The population was closed from immigration, emigration, births, and deaths during each 15-day primary period, (2) All individuals in the population were sighted with the equal sighting probability, (3) Sightings of individuals were mutually independent events, (4) At least two sampling occasions existed for each primary period, (5) Sighting probabilities were exchangeable among all sampling occasions for the entire experiment, and (6) Sighting probabilities were mutually independent for all secondary occasions and primary periods.

The first assumption of population closure during a primary period may have been violated in several study areas. Because of the longevity of the species, natural mortality probably was negligible for a 15-day period. Emigration and immigration of individuals, however, might have occurred within a primary period. Although no bottlenose dolphins were sighted at more than one location within a 15-day period, some individuals could have been outside of study areas when sampling was conducted. Intensive sampling on a larger spatial scale at each study site would have been necessary to determine population closure of a study area.

Williams et al. (2001) pointed out that equal capture probability among all individuals during a sampling period was seldom met in practice. This assumption may have been violated if data collection was limited to particular areas. If not all areas used by a population were searched, some individuals would have less probability of being photographed than others, creating heterogeneous sighting probabilities among individuals. Careful design of sampling protocols would minimize the variability in capture probabilities among individuals.

The third assumption may have been violated if individuals formed long-term groups. Gubbins (2002b) reported such associations of individuals within her study area near Hilton Head, SC. I did not analyze the association of individuals in each dataset. A likelihood function may be created to account for such associations among individuals, allowing variability in sighting probabilities among individuals.

The fourth assumption was met for all studies, and the fifth assumption was reasonable for all studies. The assumption of the independence of sighting probabilities among sampling occasions may have been violated within some study areas where data were collected intensely. Because sighting probabilities were affected by various physical and biological factors, including weather and behavior of dolphins, there may

have been temporal correlation among sighting probabilities when sampling was conducted in consecutive days.

Another limitation of the analyses was that the inference was made only for a subset of each group of bottlenose dolphins. Because not all bottlenose dolphins possess identifiable nicks on their dorsal fins, the estimated abundance needs to be adjusted for the 'unmarked' portion of the population. For example, Weigle (1990) reported 33% of 1,205 bottlenose dolphins photographed possessed recognizable natural marks in southern Tampa Bay, FL. In Doubtful Sound, New Zealand, approximately 65% of photographed bottlenose dolphins were identifiable by natural marks (Williams et al. 1993). Information was not available regarding the proportion of identifiable individuals in the current datasets. To use CMR methods to estimate the abundance of bottlenose dolphins in the future, the proportion of identifiable individuals in each study area should be determined.

Although possible violations of assumptions invalidate the compilation of results from many of the study areas, results from a few datasets may be more reliable because the majority of assumptions were satisfied in these studies. Bottlenose dolphins inhabiting areas near Charleston, SC, are genetically distinct from bottlenose dolphins from nearest study sites (Hilton Head and Myrtle Beach areas; P. Rosel, personal communication). Consequently, this group of bottlenose dolphins may be considered closed from immigration and emigration. Because of the longevity of the species, natural mortality during a 15-day period was negligible. Results from the current study augmented that these assumptions were satisfied. The median number of days since the last sighting of individuals in the dataset was 54 and the maximum was 147, indicating many individuals were sighted frequently. In addition, researchers at the study site used a sampling protocol that provided an equal probability of effort within the area.

A similar situation existed for the study near Jacksonville, FL. Genetic differences were reported for three sympatric groups of bottlenose dolphins in this area (Caldwell et al. 2001). Two of these groups were recognized as resident groups. The proposed CMR method probably was applicable for these groups of dolphins in the Jacksonville area. Because of the proprietary nature of the dataset, however, abundance could not be estimated for each group.

The examination of histograms of the number of individuals accepted per sampling day among all datasets indicated there were two groups of datasets; one group with a 'shoulder' in the histogram and the other without it. In the former group, which included Beaufort (AR; Figure 5.9), Charleston (Figure 5.34), Hilton Head (Figure 5.40), and Jacksonville (Figure 5.51), posterior samples of the hyperparameters exhibited apparent peaks, indicating a large amount of information on sighting probabilities in a dataset. With the exception of the Wilmington dataset, diffuse posterior distributions of the hyperparameters were found for the second group. A histogram of the number of individuals accepted per sampling day may provide a qualitative measure of the amount of information of capture probabilities contained in a dataset. No obvious pattern was found for the sighting frequency of individuals among study sites.

Marginal distributions of the hyperparameters indicated low sighting probabilities within study areas. For the five datasets for which non-diffuse joint distributions were obtained (Beaufort (AR; Figure 5.11), Wilmington (Figure 5.23), Charleston (Figure 5.36), Hilton Head (Figure 5.42), and Jacksonville (Figure 5.53)), the first parameter for the beta distribution (α) often was less than one, whereas the second parameter was greater than one. Beta distributions with such parameters exhibit exponentially decreasing probability function, where the mode is zero. As the simulation analyses of the previous chapter indicated, the posterior distributions from the proposed method were

most precise when sighting probabilities were high. The results for these study sites corresponded to the worst-case scenario for the simulation analysis. Consequently, the number of secondary occasions needed to be increased, without compromising other assumptions, to obtain a precise posterior distribution with the proposed method. With a large number of secondary occasions, the proposed method would provide precise and reliable estimates.

To use photographic identifications and CMR methods for estimating the abundance of bottlenose dolphins in bays, sounds, and estuaries along the Atlantic coast of the United States, the current sampling design and protocol should be modified slightly. The sampling design should ensure equal probability of sighting for all individual bottlenose dolphins. For example, an entire study area may be divided into contiguous cells, where each cell can be surveyed within a few hours. For each sampling day, a random starting point and the direction of survey should be selected. The sampling should continue to include as many cells as possible for the sampling day. If the study area is large, it may be stratified. Multiple boats may be used to sample all strata simultaneously.

When a survey boat encounters a group of bottlenose dolphins, photographs should be taken at all opportunities regardless of the number of times a particular individual has been photographed or the distinctiveness of a dorsal fin. This sampling protocol enables the researcher to use these photographs as CMR data for the group. By including photographs of all bottlenose dolphins sighted in a study area, including those without identifiable dorsal fins, the CMR data can be used to estimate the proportion of identifiable individuals in the study area.

The following method may be used to estimate the proportion of identifiable individuals in a study area. If we consider the process of obtaining a high-quality

photograph of an identifiable individual in the j^{th} group as an independent Bernoulli trial with probability p_j , the inference on p_j in the study area (p) can be made with a Bayesian approach. The prior distribution for p can be modeled with a Beta distribution, $p_j \sim \text{Beta}(\alpha, \beta)$. The posterior distribution of p is:

$$p(p | \mathbf{c}, \mathbf{T}) = \text{Beta}\left(\alpha + \sum_{j=1}^G c_j, \beta + \sum_{j=1}^G (T_j - c_j)\right) \quad (5.1)$$

where G is the total number of encountered groups during the study, c_j is the number of high-quality photographs with identifiable dorsal fins in the j^{th} group, and T_j is the total number of high-quality photographs for the j^{th} group. The p is a mixture of the proportion of identifiable individuals in the j^{th} group and the photographic capture process. If we consider the photographic capture process to be constant for all groups, the p should provide information on the proportion of identifiable individuals in the area. Although simplistic, the method may provide an alternative method to a crued conjecture from the field observations.

If abundance estimates are considered for these study sites in the near future, existing data can be used to compute the joint prior distribution of the hyperparameters. I have shown that even opportunistically collected data can be used to compute a joint probability distribution of the hyperparameters. Informative joint distributions of the hyperparameters are found for all but three study sites. This information greatly enhances the posterior distribution of abundance, as was shown in the previous chapter. Further, probability distributions for abundance also are available from this study. Although one may widen the posterior distributions of this study for including potential biases from the current analyses, these probability distributions can be used as prior distributions of abundances for future studies.

In conclusion, although abundance estimates were obtained for nine study sites, violations of assumptions invalidated the use of these estimates in computing the total abundance of bottlenose dolphins in bays, sounds, and estuaries along the Atlantic coast of the United States. To use photographic captures and CMR methods for estimating the abundance of bottlenose dolphins, sampling design and protocol should be modified in the future. A possible sampling design and protocol were proposed.

CONCLUSIONS

The widely used mortality rate estimated for the 1987-1988 epizootic of bottlenose dolphins along the Atlantic coast of the U.S. appeared to be an overestimate. Using the same stranding data as the previous analysis, a simple computation yielded the die-off mortality rate of <0.47 , which was less than the previously reported value (0.53). Although the analysis was based on the same set of assumptions as the previous study, these assumptions were neither testable nor persuasive. Further, recent studies indicated there was more than one stock of bottlenose dolphins along the coast, violating one of the main assumptions of the analysis. Consequently, the argument about the validity of these estimated mortality rates during the epizootic became meaningless. The process of estimating mortality during a die-off from stranding data, however, was shown to be useful as a methodology.

To compute mortality of a die-off from stranding data, estimation of vital rates of the species before the die-off is critical. The rate of recovery of a population from a mass die-off depends largely on anthropogenic mortality rates, birth rates, and natural mortality rates. Consequently, these parameters should be estimated before a mass die-off occurs in a population. Effort for collecting stranding data also should be measured because the recovery rate of carcasses generally increases during a die-off due to increased public awareness.

Regardless of the mortality rate during the epizootic of 1987-1988, management and conservation decisions are necessary for bottlenose dolphins along the coast. The most recent management decision for bottlenose dolphins along coast defines seven management units (Waring et al. 2002). Other studies have indicated this should be the minimum number of management units along the coast. The mortality due to human

interactions, such as by-catch from fishing operations, may be unacceptably high for some management units (Waring et al. 2002). If small genetically distinct stocks are combined together to form a large management unit, a computed PBR for the unit may be large enough to extirpate one or more of stocks within the unit. To estimate the abundance of bottlenose dolphin populations, capture-mark-recapture methods with photographic captures may be appropriate because of the existing photographic identification studies in many locations.

To successfully apply a CMR method to estimate the minimum abundance of a management unit, however, the existing sampling protocol for photographic identification studies needs to be refined. A sampling protocol for making inferences on abundance should include the randomization of sampling within a management unit so that all areas have the equal probability of being sampled. Further, a quantitative method should be used for estimating the proportion of identifiable individuals in each management unit.

Because the size of each management unit probably is small and the sighting probabilities are low, the maximum likelihood estimates may not provide precise estimates. The proposed Bayesian method provides an alternative approach. The proposed method enables a researcher or manager to use the existing photographic identification data for obtaining information on capture probabilities and abundance. The information, then, is updated via new data.

As Arnason (1998) pointed out, all available information should be used for designing and planning a CMR study. I have shown, through a simulation analysis and the analyses of real data, that incorporating prior information could enhance the precision of a posterior distribution of abundance via a Bayesian analysis. Even for opportunistically collected photographic sighting data in this study, considerable amount

of information was available for making inferences on sighting probabilities and abundance. The proposed Bayesian method is one way to incorporate the information into an analysis via a formal mathematical framework. The widely used maximum likelihood estimators, such as from MARK, are not capable of updating one's knowledge about capture probabilities or abundance. Bayesian methods should provide an alternative approach to the widely used frequentist methods, whose validity has been questioned by many statisticians.

Although Bayesian methods are useful in ecological sciences, the use of Bayesian methods has been criticized. I briefly justify the use of Bayesian methods in this study and ecological studies in general. More complete philosophical and theoretical discussion of Bayesian and non-Bayesian statistics can be found elsewhere (Berger 1985, Edwards 1992, Robert 1994, Royal 1997, Goodman 2002, Goodman 2003).

A strong criticism of the Bayesian philosophy in ecological science is found in Dennis (1986). Dennis (1996) condemned the use of Bayesian methods in ecology:

"...I would argue that the Bayesian philosophy of science is scientific relativism.

"To scientific relativists, truth is subjective. Scientific theories are socially 'warranted' constructs that do not necessarily make progress toward uncovering universal truths...."

He argued that Bayesian analyses were based on subjective beliefs of a researcher. In his paper, however, he implicitly assumed that all Bayesian analyses were based on subjective prior distributions. In many situations, however, prior distributions can be constructed from available data. These data may come from a similar species from the same area, the same species from other areas, the same population but from past studies, or a combination of these data. Hence, the belief of the investigator does not necessarily constitute the prior distribution. The state of current knowledge about the parameter,

which is described by the prior distribution, is updated via new data, a statistical model (i.e., likelihood function), and Bayes theorem. Bayesian analyses offer a formal mathematical method for incorporating existing knowledge about parameters into a current analysis. In this perspective, Bayesian methods are another set of tools for making inferences on unknown parameters, conditional on the model, data, and the prior information, which may be independent of the belief of a researcher.

Results of a scientific study often are not clear-cut, especially in ecological and conservation sciences, where a large variability exists in the system. Decisions have to be made at the conclusion of a study regarding interpretations of the results. A scientist would not make a decision independent of his/her knowledge about the system. Such a decision would be unproductive and ignores the progress of science. The Bayesian approach to a study requires that knowledge of the system be quantified; more specifically the knowledge needs to be expressed in a probability distribution. The probability distribution then is updated as more data are collected. I find this process to be a productive scientific process.

Several researchers have shown that Bayesian methods are valuable in conservation biology (Ludwig 1996, Taylor et al. 1996, Wade 2000) and assessment and management of populations (Best and Underhill 1990, Thompson 1992, Raftery et al. 1995, Punt and Butterworth 1997, Kinas and Bethlem 1998, Punt et al. 2000). As an ecologist, not as a professional statistician, I do not claim a complete knowledge of Bayesian statistics nor do I successfully defend Bayesian statistics from all criticisms. Rather, I think the Bayesian approach is a viable alternative (or at least addition) to the generally accepted hypothesis testing approach. I think my research has demonstrated a useful application of a Bayesian method in an ecological study.

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APPENDICES

APPENDIX A

COMPUTATION OF JACOBIAN OF THE HYPERPARAMETERS

Computation of Jacobian of $\left(\frac{\alpha}{\alpha+\beta}, (\alpha+\beta)^{-\frac{1}{2}}\right)$.

$$\begin{aligned}
 J &= \begin{vmatrix} \frac{\partial\left(\frac{\alpha}{\alpha+\beta}\right)}{\partial\alpha} & \frac{\partial\left(\frac{\alpha}{\alpha+\beta}\right)}{\partial\beta} \\ \frac{\partial(\alpha+\beta)^{-\frac{1}{2}}}{\partial\alpha} & \frac{\partial(\alpha+\beta)^{-\frac{1}{2}}}{\partial\beta} \end{vmatrix} \\
 &= \begin{vmatrix} \frac{\beta}{(\alpha+\beta)^2} & \frac{-\alpha}{(\alpha+\beta)^2} \\ -\frac{1}{2}(\alpha+\beta)^{-\frac{3}{2}} & -\frac{1}{2}(\alpha+\beta)^{-\frac{3}{2}} \end{vmatrix} \\
 &= -\frac{\beta}{2}(\alpha+\beta)^{-\frac{7}{2}} - \frac{\alpha}{2}(\alpha+\beta)^{-\frac{7}{2}} \\
 &= -\frac{1}{2}(\alpha+\beta)^{-\frac{5}{2}}
 \end{aligned}$$

APPENDIX B

TRANSFORMATION OF THE HYPERPARAMETERS

Transformation of $p(\alpha, \beta)$ to $p\left(\ln\left(\frac{\alpha}{\beta}\right), \ln(\alpha + \beta)\right)$, when $p(\alpha, \beta) \propto (\alpha + \beta)^{-\frac{5}{2}}$.

Let $y_1 = \ln\left(\frac{\alpha}{\beta}\right)$ and $y_2 = \ln(\alpha + \beta)$. Then the unique solutions for these equations are:

$$\alpha = \frac{e^{y_1} e^{y_2}}{1 + e^{y_1}}$$

$$\beta = \frac{e^{y_2}}{1 + e^{y_1}}$$

Then the Jacobian is:

$$\begin{aligned} J &= \begin{vmatrix} \frac{\partial \alpha}{\partial y_1} & \frac{\partial \alpha}{\partial y_2} \\ \frac{\partial \beta}{\partial y_1} & \frac{\partial \beta}{\partial y_2} \end{vmatrix} = \begin{vmatrix} \frac{e^{y_1} e^{y_2}}{(1 + e^{y_1})^2} & \frac{e^{y_1} e^{y_2}}{1 + e^{y_1}} \\ -e^{y_1} e^{y_2} & \frac{e^{y_2}}{1 + e^{y_1}} \end{vmatrix} \\ &= \frac{e^{y_1} e^{2y_2}}{(1 + e^{y_1})^2} = \alpha \beta \end{aligned}$$

Therefore, $p\left(\ln\left(\frac{\alpha}{\beta}\right), \ln(\alpha + \beta)\right) = p(\alpha, \beta) |J| \propto \alpha \beta (\alpha + \beta)^{-\frac{5}{2}}$.

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