AN ABSTRACT OF THE DISSERTATION OF

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Abstract approved:

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Green sea turtles, *Chelonia mydas*, have endangered and threatened populations globally, but several populations show signs of population recovery. In Hawaii, nesting female green turtles have increased 5.7% year^{-1} since 1973, but wide fluctuations in census counts of nesting females make recovery diagnosis difficult. For effective management planning, it is critical to have the best information possible on vital rates, and to determine the best tools and practices for incorporating vital rate information, particularly variability, into population models to assess population size and status. Process and observation errors, compounded by late maturity, obscure the relationship between trends on the nesting beach and the entire population. Using sea turtle nesting beach surveys as a population index for assessment is problematic, yet often pragmatic because this is the only population index that is easily accessible. It is advantageous to use a modelling approach that estimates interannual variability in life history traits, accounts for uncertainty from individual-level variability, and allows for population dynamics to emerge from individual behaviors. To this end, I analyzed a long-term data set of marked green sea turtles to determine the degree of temporal variability in key life history traits. From this analysis, I built an agent-based model (ABM) to form the basis of a new assessment tool – Monitoring Strategy Evaluation.

In Chapter 2, I evaluated annual changes in demographic indicators (DIs) of 3,677 nesting green turtles from a 38-year tagging program in the Hawaiian Islands to determine if key life history traits are changing over time and in response to nester density. I used linear mixed models and multistate open robust design models to estimate several DIs and correlated them with nesting female counts. Mean nester carapace length and breeding probability were highly variable over time, suggesting shifts in age structure that could be due to recruitment. The top-ranked model predicted constant female survival over time. A significant positive relationship between the nesting population and breeding probability was evident, and breeding probability shows promise as an indicator of population recovery. This work contributes to a growing set of studies evaluating sea turtle demography for temporal variability and is the first for Hawaiian green turtles.

In Chapter 3, I develop the Green Sea Turtle Agent-Based Model (GSTABM) to evaluate how recovery processes differ across disturbance types. The GSTABM incorporates individually variable age-at-maturity, clutch frequency and clutch size, annually variable breeding probability, environmental stochasticity and density dependence in hatchling production. The GSTABM simulates the process of population impact and recovery and the monitoring process, with observation error, on the nesting beach. The GSTABM captures the emergent patterns of interannual nesting variation, nester recruitment, and realistic population growth rates. Changes in survival rates of the nearshore age-stage classes directly affected adult and nester

abundance, population growth rate and nester recruitment more than any of the other input parameters. In simulating 100 years of recovery, experimentally disturbed populations began to increase but did not fully return to pre-disturbance levels in adult and nester abundance, population growth or nester recruitment. In simulations with different levels of monitoring effort, adult abundance was poorly estimated, was influenced by population trajectory and disturbance type, and showed marginal improvements in accuracy with increased detection probability. Estimating recruitment showed improvements with increasing detection levels. In the GSTABM, variability in the nesting beach does not mirror variability in adult abundance. The GSTABM is an important tool to determine relationships with monitoring, population assessment, and the underlying biological processes driving changes in the population, and especially, changes on the nesting beach.

In Chapter 4, I develop a new simulation-based tool: Monitoring Strategy Evaluation (MoSE) to determine which data source yields the most useful information for population assessments. The MoSE has three main components: the simulated “true” operating, observation, and estimation models. To explore this first use of MoSE, I apply different treatments of disturbance, sampling, and detection to the virtual “true” population, and then sample the nests or nesters, with observation error, to test if the observation “data” accurately diagnose population status indicators. Based on the observed data, I estimated adult abundance, nester recruitment, and population trend and compare them to the known values. I tested the accuracy of the estimated abundance when annually varying inputs of breeding probability, detection and clutch frequency were used instead of constants. I also explored the improvement of trend accuracy with increased study duration. Disturbance type and severity can have important and persistent effects on the accuracy of population assessments drawn from monitoring rookeries. Accuracy in abundance estimates may be most improved by avoiding clutch frequency bias in sampling and including annually varying inputs in the estimation model. Accuracy of nester recruitment may be most improved by increasing detection level and avoiding age-bias in sampling. The accuracy of estimating population trend is most influenced by the underlying population trajectory, disturbance type and disturbance severity. At least 10 years of monitoring data are necessary to accurately estimate population trend, and longer if juvenile age classes were disturbed and trend estimates occur during the recovery phase. The MoSE is an important tool for sea turtle biologists and conservation managers and allows biologists to make informed decisions regarding the best monitoring strategies to employ for sea turtles.

This modeling framework is designed to provide an evaluation of monitoring program effectiveness to assist in planning future programs for sea turtles. Altogether, my research suggests certain life history traits of green sea turtles have important temporal variation that should be accounted for in population models, understanding the relationships between nesting and the total population is essential, and basing population assessments from nesting beach data alone is likely to result in incorrect or biased estimates of status indicators. The quantitative tools employed here can be applied to other sea turtle populations and will improve monitoring, and result in better estimates of current population trends and enhance conservation for all species of sea turtles.

Quantitative Tools for Monitoring Strategy Evaluation and Assessment of Sea Turtle Populations

by
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I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Susan E. H. Piacenza, Author

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While much of my research here is forward thinking – how to improve sea turtle monitoring to enhance population assessments – I think conservation biology is indelibly historical. Conservation biologists want to know historical abundances to inform recovery targets, the nature and degree of historical impacts, and how to restore species to their former functional roles – all historical questions. I read *The Unnatural History of the Sea*, by Callum Roberts, mid-way through my PhD and it had a profound influence on me. I personally think the first commandment of population modelling should be "know your species' history." I open my dissertation with a quote that is both, I think, pragmatic and optimistic:

"We can restore the life and habitats of the sea because it is in everyone's interest that we do so. The same large-scale networks of marine reserves, complemented by other measures of fish and habitat protection, best serve the interests of both commerce and conservation. You can have exploitation with protection, because reserves help sustain catches in surrounding fishing grounds. But you cannot have exploitation without protection, not in the long term."

- Callum Roberts, *The Unnatural History of the Sea*

CONTRIBUTION OF AUTHORS

Mr. George Balazs and Ms. Stacy Hargrove provided data used for the analysis in Chapter 2, provided background on long-term monitoring of green sea turtles in Hawaii and provided editorial comments on Chapter 2. Dr. Paul Richards assisted with the development, testing, and analysis of the green sea turtle agent-based model and the Monitoring Strategy Evaluation presented in Chapters 3 and 4. Dr. Richards was involved with the writing of Chapters 2 – 4. Dr. Selina Heppell was involved with the development, design, analysis and writing of Chapters 2 – 4.

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1 - General Introduction

Biodiversity is declining at an unprecedented rate (Pimm et al. 1995). Efforts to protect species from extinction, such as the US Endangered Species Act, are beginning to achieve species recoveries (Taylor et al. 2005, Lotze et al. 2011, Suckling et al. 2012, Magera et al. 2013, Roman et al. 2015). Examples of recovering populations complement the many examples of declining populations in studying resilience. Perturbed populations, in general, exhibit unusual behavior that can be attributed to transient dynamics (Mills 2013). Transient dynamics in structured populations occur because of impacts to specific demographic classes and time lags in the recovery as those classes “fill in” (Hastings 2004, Koons et al. 2005, Ezard et al. 2010, White et al. 2013, Gamelon et al. 2014). For example, even after a disturbance has been ameliorated, populations can continue to decline or can exhibit dampening oscillations (Crowder et al. 1994, Hastings 2004, Koons et al. 2005, Gamelon et al. 2014).

Transient dynamics in populations have important implications for monitoring and management. First, in long-lived, migratory species, in which monitoring can only occur on particular demographic classes for short periods of time, population indices may give a false signal of abundance and population trend during unstable periods (Maxwell & Jennings 2005, Singh & Milner-Gulland 2011, Lynch et al. 2012). Second, if monitoring yields inaccurate data and the subsequent population assessments make false interpretations of trends, management errors can ensue. There are two main kinds of conservation errors: to conclude a population is threatened when in fact it is not and to conclude a population is not threatened when in fact it is; both kinds of error have biological, economic and societal consequences (Taylor & Gerrodette 1993, Snover & Heppell 2009). While population recovery is welcome, unexpected complications in management can occur; for example, recovering species may be viewed as "nuisances", scapegoats, or competitors with humans for natural resources (Roman et al. 2015). This would be especially troubling if biologists conclude a population is recovered, and the public perceives recovery but considers it a nuisance and reacts negatively, when in fact the species is still endangered. Biologists and managers need to exercise caution when interpreting population indices from monitoring. In this dissertation, I develop an analytical approach and simulation-based tools to clarify relationships between observed and true population abundance and trends.

Sea turtles are globally threatened taxa, and many populations of sea turtles are recovering, while some continue to decline despite intensive conservation measures (Chaloupka et al. 2008, Wallace et al. 2011, IUCN 2015). The life history of these species complicates monitoring and consequently conservation efforts. Sea turtles are long-lived, with late maturity, have long distance migrations, and are mostly pelagic. With late maturity comes temporal lags in recovery that depend on which age classes are disturbed and how conservation impacts survival of those age classes; this can have important implications for monitoring and assessment (Crowder et al. 1994, Heppell et al. 1996, Koons et al. 2005, White et al. 2013). Most sea turtle monitoring is conducted at nesting beaches, where nests are counted and/or individual female nesters are tagged and counted (Schroeder & Murphy 1999, Kendall & Nichols 2002). But, females are skip-nesters and do not breed annually, and adults are thought to be vastly outnumbered by juveniles (Heppell et al. 2003). Thus, just a fraction of the total population is monitored and monitoring provides a narrow view into the population. A great deal of inter-annual fluctuation in the numbers of nesters and nests exists and makes it difficult to determine population trends (Chaloupka et al. 2008, Bjorndal et al. 2010, NOAA & USFWS 2015). It is uncertain how accurately rookery survey methods estimate abundance, recruitment and population trend. In addition, considering that most sea turtles populations are in flux, either declining or recovering, transient dynamics may further obscure true population dynamics when monitoring only observes reproductive classes, i.e. nesters and nests (Hastings 2001, 2004, White et al. 2013). However, beach surveys are often the only way biologists can encounter sea turtles and measure abundance, and in-water surveys can be cost prohibitive and often have very low encounter rates. This leads to a critical question: how can we optimize monitoring from the nesting beach to give the most accurate estimates of population size, recruitment and trends over time?

In this dissertation, my research culminates in the development of the Monitoring Strategy Evaluation tool which was motivated by Management Strategy Evaluation (MSE) and its potential to benefit conservation of sea turtles. MSE is a simulation-based framework developed by fisheries scientists to evaluate trade-offs in alternate management schemes and to assess the consequences of biological and management uncertainty for achieving management goals (Smith et al. 1999, Punt et al. 2014). MSE simultaneously considers three main aspects of the biological-management cycle: the biological system (operating model), the observation process, and population assessment and management (Sainsbury et al. 2000, Bunnefeld et al. 2011). Bunnefeld et al. (2011) first suggested that MSEs may be applied to species of conservation concern and suggest several case studies of where MSEs have the potential to benefit endangered species management. More recently, MSEs have been applied to species of conservation concern. For example, MSEs have been used to set sustainable quotas for trophy hunting of African lions, despite a paucity in abundance time-series (Edwards et al. 2014), to set biological limit reference points for bycatch of pacific leatherback sea turtles in the US West Coast Exclusive Economic Zone (Curtis et al. 2015), and to evaluate trade-offs of the conflicting objectives of biodiversity protection, benthic impacts from trawling, ecosystem function, and economics with the use of spatial closures in the Gulf of Carpentaria, Australia (Dichmont et al. 2013). For endangered species, harvest options are not as pertinent (but levels of allowed take or bycatch may be evaluated), but the role of analyzing the observation model can be of the upmost importance. Endangered species are often considered data-poor or have low encounter rates with monitoring programs (Colyvan et al. 1999, Akçakaya et al. 2000) and understanding relationships between the little data available and true biological trends is critical. In Monitoring Strategy Evaluation (MoSE), I hold management constant, as the objective is often to increase population size and population growth from one year to the next. Instead, the accuracy of population status indicators is compared for different monitoring strategies, rather like a power analysis used to estimate the ability to detect a decline in a population (Taylor & Gerrodette 1993). Evaluating the accuracy of monitoring, and determining which data streams, and how long of a time-series is necessary to detect changes in population trend, will ultimately benefit sea turtles, and endangered species in general, and the MoSE is an important tool toward this goal.

My research used long-term monitoring data on individual green sea turtles tagged on the primary nesting beach in Hawaii to determine the degree of temporal variability in nester body length, breeding probability, adult survival and size-at maturity (Chapter 2). I asked three questions: Do the demographic indicators (annual survival rate, annual breeding probability, nester carapace length, and size-at-maturity) show temporal trends and fluctuations? And if so, are the DIs correlated with nester abundance? And finally, which of these measures could serve as a good indicator of population size and status (i.e. increasing, decreasing or stable over time)? In this analysis, I developed an approach to evaluate temporal changes in life history traits and to evaluate them for density-dependence, and temporally variable life history traits may serve as indicators of population change.

Using estimates of the demographic indicators from Chapter 2, I built an agent-based model of green sea turtles (GSTABM; Chapter 3). I created the GSTABM to simulate green sea turtle population dynamics, population disturbance and recovery, and to simulate the processes of monitoring and population assessment. Ultimately, I wanted to contrast the recovery dynamics of populations subjected to different kinds of disturbance histories to answer three main research questions: (1) Can the GSTABM adequately reproduce the population dynamics of green sea turtle populations? (2) How do the recovery dynamics differ when the disturbance occurs to different demographic groups (e.g., older turtles and eggs), and 3) what predictions can we make from the GSTABM regarding recovery dynamics of green sea turtles?

The GSTABM is the operating model used to develop a new assessment tool – Monitoring Strategy Evaluation (MoSE; Chapter 4). The MoSE approach is novel in that it specifically experiments with monitoring strategies to determine how observation errors propagate to population assessment errors, such as inaccurate estimates of adult abundance, recruitment and population trend. My primary goal is to provide advice on how to optimize monitoring actions on nesting beaches used to assess populations of sea turtles. I asked four main questions: Given each biological (process variability) and observation (measurement variability) scenario, can we accurately estimate population size, recruitment, and population trend? How long of a time-series is necessary to accurately estimate population trend? What are the probabilities of false positive and false negative trend diagnoses? Does the population structure and harvest legacy influence which monitoring strategy is best?

Declining and recovering species exhibit transient dynamics and this has important implications for accurately assessing population size and trend. Green sea turtles are currently undergoing recovery in many populations and have a complex life history and most monitoring focuses on a narrow portion of the life cycle: female breeders and their nests. The recovery provides an important opportunity to improve our knowledge of the dynamics of species recovery and the relationship with monitoring and population assessment. My modeling framework presented here is designed to provide an evaluation of monitoring program effectiveness to assist in planning future programs for sea turtles. Ultimately this research could be applied to other endangered species, particularly those where monitoring is limited or challenging. The quantitative tools employed here can be applied to other sea turtle populations, and endangered species, and will improve monitoring, and result in better estimates of current population trends and enhance conservation for all species of sea turtles.

2 - Trends and variability in demographic indicators of a recovering population of green sea turtles (*Chelonia mydas*)

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Endangered Species Research
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ABSTRACT

Several populations of green sea turtles show signs of population recovery. In Hawaii, green turtles have increased 5.4% year^{-1} since 1973, but wide fluctuations in census counts of nesting females make recovery diagnosis difficult. Evaluating demographic rates for temporal change and in relation to population density, and indicators of recruitment to sea turtle nesting populations will ultimately improve population assessments. Using linear mixed and multistate open robust design models, we estimated the demographic indicators (DIs) of size-at-maturity, nester carapace length, breeding probability, and adult female survival rate using 3,677 tagged nesting green turtles from 1973 - 2010 in Hawaii. To evaluate changes with density, we correlated the DIs with nesting female counts. We estimated size-at-maturity, assuming newly tagged nesters are tagged on their first nesting migration, and first-time nesters have statistically significant smaller carapace length than recaptures, but the difference in size was only ~0.5 cm year^{-1}. Mean nester carapace length (range: 89.21 - 91.69 cm) and breeding probability (range: 0.0766 - 0.444 year^{-1}) showed directional changes over time, suggesting shifts in age structure that could be due to recruitment. The top-ranked model predicted constant female survival over time (S = 0.929 year^{-1}, 95% CI: 0.924 – 0.933, model likelihood = 1.00). Counter to our hypothesis based on density-dependence, breeding probability increases with increasing nester abundance; this suggests that breeding probability is probably more driven by environmental influences than population densities, at least within the range of observed nester abundances. This work contributes to a growing set of studies evaluating sea turtle demography for temporal variability and is the first for Hawaiian green turtles. Our study demonstrates that some easily monitored demographic variables may serve as indicators of population change.

2.1 INTRODUCTION

Some populations of green sea turtles (*Chelonia mydas*) have experienced remarkable recovery from over-exploitation in the last decades, but with a great deal of interannual fluctuation in the numbers of nesters and nests, the primary demographics monitored by biologists (Chaloupka et al. 2008, NOAA & USFWS 2015). Populations undergoing recovery often display wide fluctuations in abundance and population growth rates. These fluctuations could be the result of demographic stochasticity, particularly early on in the recovery process, inter- and intra-specific interactions or environmental variation (Saether et al. 2004, Shelton & Mangel 2011). Regardless of the cause, interannual variability in abundance makes it difficult to determine population trends to quantify the rate of recovery and to make predictions.

Variation in life history traits occurs across species, populations, and individuals (Gotthard & Nylin 1995, Cam et al. 2002, Bjorkvoll et al. 2012). Crucially, in the case of overexploited or endangered species, population perturbations may have important and persistent effects on demographic rates, which may affect a species' resilience. Research suggests a degree of plasticity in vital rates that may be a function of environmental factors, population density, and age structure; these factors may be particularly important in populations that are recovering from perturbations, in which population density and age structure are changing rapidly (Gotthard & Nylin 1995, Kuparinen & Merila 2007). In turn, population-level changes in demographic rates may affect the ability of species to recover. For example, in several populations of Atlantic cod (*Gadus morhua)*, fisheries-induced changes to mean size- and age-at-maturity have likely decreased the ability of this species to recover from overfishing (Hutchings 1996, 2000, Hutchings & Reynolds 2004). Conversely, as abundance increases and age structure is restored, demographic rates may return to pre-disturbance levels (Conover et al. 2009). Studies of demographic rate changes in the context of population depletion or recovery suggest that shifts in mean growth, survival, or reproduction are important to consider in modeling exercises to evaluate future trends and response to management (Rochet 2000a, b, Gerber & Heppell 2004, Thorson et al. 2015).

We hypothesize that once populations are in the process of recovery, changes in demographic rates or life history traits can also give an indication of the status of the population, hereafter referred to as demographic indicators (DIs). However, we must first understand how DIs and their variability are linked to abundance. If a DI displays a trend in response to decline or recovery, then the DI can be linked to population density (Bjorndal et al. 2000, Sæther & Bakke 2000, Caut et al. 2006, Hutchings, Myers, et al. 2012). Conversely, if a DI has high interannual variability but no significant trend, the variability itself could affect population growth, abundance, and recovery rates (Mazaris & Matsinos 2006, Bjorndal et al. 2010). Further, the timeframe in which DIs are estimated in relation to the status of the species (e.g., prior to exploitation, during, or post-exploitation) can have important ramifications for population assessments, especially if temporal variability is not accounted for in the estimation process. For long-lived species with long generation times, it is also important to account for time lags in changes to DIs. For example, in a study of Kemp's ridley sea turtles (*Lepidochelys kempi*), Heppell et al. (1996) found that recovery times depend on age at maturity, as newly protected age classes recruit into the adult population. Population models often must rely on estimates of DIs from the literature, which often come from historic references, taken at times that no longer directly pertain to the current population. This imprecision of DI estimates can have important implications on accurately estimating abundance and population growth, and forecasting short-term and long-term trends, even though temporal variability in DIs is rarely measured in sea turtle studies (Bjorndal et al. 2010, Richards et al. 2011).

To understand how DIs vary over time and in relation to abundance of a long-lived species, we examined a well-studied population of green sea turtles in Hawaii. A recent National Research Council (NRC) report emphasized that monitoring the numbers of nesters or nests is insufficient to diagnose changes in population size (Bjorndal et al. 2010). Rather than focusing on indices of abundance, the NRC report emphasized research toward quantifying changes and variability in key DIs to better understand the relationship with DIs and population abundance and population growth. Looking to the future, many sea turtle monitoring programs may not be able to continue indefinitely or may not be able to supply the work force to keep pace with the size of recovering populations (and maintain sufficient detection probabilities). Examining DIs may be one solution and could complement monitoring index nesting beaches, especially as changes in DIs may give important context to observed changes in abundance on nesting beaches.

Green sea turtles are listed as an endangered species throughout most of the USA and are a threatened species in Hawaii (NOAA & USFWS 2015). However, the population has experienced remarkable recovery in the last two decades with an estimated 5.4% year^{-1} increase in the nesting population in the Hawaiian Islands since 1973 (Fig. 2.1; Chaloupka et al. 2008, Balazs et al. 2015). Population recovery is primarily attributed to elimination of hunting pressure for juvenile and adult sea turtles in the Hawaiian Islands (Balazs & Chaloupka 2004b). Intensive monitoring of this recovering population and its relative geographic isolation make it an excellent case study for examination of temporal variability in demographic indicators.

Because of fisheries management and conservation measures, it is also likely that vital rates of green turtles in Hawaii have changed over time, in the absence of hunting pressure and in response to changes in population density (Gotthard & Nylin 1995, Hutchings 1996, 2000, Hutchings & Reynolds 2004, Conover et al. 2009). Existing estimates of the number of years females spend between nesting (remigration interval) and mean body size of Hawaiian green sea turtles do not account for changes in the vital rates, even though data collection began in the 1970s, when harvest was still permitted (Balazs 1980, Balazs et al. 2015). In addition, some of these estimates were taken from short-term field studies, with relatively small sample sizes of females (Balazs 1980, Van Buskirk & Crowder 1994). Adult female annual survival rate for Hawaiian green turtles was recently estimated using matrix projection models and Monte Carlo techniques for optimization, but survival rate was not evaluated for temporal variability, nor was uncertainty estimated (Van Houtan et al. 2014).

We hypothesize that DIs will be different today than when the population was at very low density. Protection of the neritic, or near-shore, life stages from harvest should result in high annual survival and strong recruitment of new nesters each year (Campbell & Lagueux 2005, Troeng & Chaloupka 2007). As the population grows and approaches carrying capacity, remigration interval would increase as greater intraspecific competition for resources makes it harder for females to build up physiological stores for egg-laying (Miller 1997, Troeng & Chaloupka 2007). During recovery, as age structure is restored, it is likely that mean nester size and size-at-maturity will decrease as new cohorts recruit into the adult population (Crowder et al. 1994).

To address the issue of temporal variability in DIs and their relationship with abundance and population recovery, we asked three questions: Do the demographic indicators (annual survival rate, annual breeding probability, nester carapace length, and size-at-maturity) show temporal trends and fluctuations? And if so, are the DIs correlated with nester abundance? And finally, which of these measures could serve as a good indicator of population size and status (i.e. increasing, decreasing or stable over time), given that we have strong evidence that this population is recovering? Using a 38 year mark-recapture data set from the principle nesting ground, we evaluated these questions for a population that has grown more than an order of magnitude, from about 35 nesting females to a peak of nearly 600.

2.2 MATERIALS AND METHODS

Study population - Hawaiian green sea turtles

Green sea turtles in Hawaii were recently categorized as a distinct population segment based on mitochondrial DNA, anatomical features, and migratory patterns (Dutton et al. 2008, NOAA & USFWS 2015). There is little gene flow between Hawaii and other populations throughout the Pacific Ocean. The vast majority of nesting takes place in the Northwestern Hawaiian Islands (NWHI) and the largest rookery is at East Island, French Frigate Shoals, where approximately 50% of Hawaiian nesting occurs, and where continuous monitoring has occurred since 1973 (Balazs 1980, Balazs & Chaloupka 2004b). East Island is a small sandy atoll, ~0.036 km^2, surrounded by a shallow lagoon on the western side and a fairly steep shelf on the eastern side. Generally, nesting site fidelity at French Frigate Shoals is high (~ > 95%; Balazs 1980, Dizon & Balazs 1982, Bowen et al. 1992). Females generally will not nest in the year immediately following a nesting year (i.e. obligate skip-nesting), and vary in the number of years between nesting migrations. The length of the remigration interval depends on energetics, physiology, and environmental conditions (Chaloupka & Limpus 1996, Miller 1997, Limpus & Chaloupka 1997, Solow et al. 2002). Within a nesting season, Hawaiian green turtles will return several times to lay an average of four clutches at approximately 2 week intervals (Balazs 1980, Tiwari et al. 2010), so the probability of sighting an individual turtle at least once during a season in which she breeds is high.

Historically, green sea turtles were abundant and nested throughout the entire Hawaiian Islands chain (Kittinger et al. 2013). Nesting contracted to the NWHI sometime in recent history, but prior to modern scientific records (as late as the early 1950s), and was most likely due initially to subsistence harvest of sea turtles and then later by more intensive commercial harvest (Balazs 1980, Witzell 1994, Kittinger et al. 2013). Generally, nesting in the NWHI was naturally protected by its remoteness from permanent human settlements, however, intermittent harvest from ships passing through the area and by the military probably occurred and egg harvest was extremely limited before protection, unlike many other sea turtle rookeries globally (Balazs 1980, Mast et al. 2011). Sea turtle harvest was tightly regulated by the “kapu” system of native Hawaiians, but after European colonization, around 1819, this system began to erode (Balazs 1980). In the 20th century, numbers of green sea turtles dropped precipitously as harvest intensified and became more commercialized in the Hawaiian Islands (Balazs 1980, Witzell 1994, Van Houtan & Kittinger 2014). Fishermen often selected juveniles, sub-adults and smaller adults for harvest, and shifted towards larger animals and fish trips moved offshore towards the end of the fishery (Balazs 1980, Witzell 1994, Kittinger et al. 2013, Van Houtan & Kittinger 2014). In 1978, green sea turtles were placed on the endangered species list and harvest was prohibited (NOAA Office of Protected Resources 2014).

Data description

Globally, the Hawaiian green sea turtle nesting population experienced one of the most continuous and consistent monitoring efforts. We used data from the NOAA Pacific Islands

Fisheries Science Center Turtle Research Program (TRP). Nesting at East Island was monitored annually, during the summer months, since 1973, first by G. Balazs and the Hawaii Institute of Marine Biology and then by NOAA Fisheries and the US Fish and Wildlife Service from 1981 onward (Nurzia Humburg & Balazs 2014). Data collection was conducted under proper approved State of Hawaii and US Federal permits. Survey effort and duration varied annually depending on a number of logistical factors (Balazs & Chaloupka 2004b), ranging from nine (1977) to 143 (1989) nights. Females that emerged to nest were individually marked with flipper tags, etched with an electric drill, and painted for easy re-identification at a distance during the rest of the nesting season. Double-tagging with passively integrated transponder (PIT) tags was instituted in 1996 to improve individual turtle identification, as flipper tags can be lost. When encountered, turtles were checked for existing tags, carapace length was measured, and nesting behavior was noted (e.g., body pit excavation, egg laying, covering nest burial). The TRP maintains a tag database of all turtles encountered on the nesting beach. Previous evaluation of the nesting beach data during a period of extended intensive survey (1988-1992) suggests that 56-66% of nesting females identified each year were newly tagged (Nurzia Humburg & Balazs 2014). However, in years where sampling did not cover the entire nesting season, it is possible that some nesters, particularly those females who started nesting early or late in the season (since sampling strives to cover the mid-point of the nesting season), were not captured during their first nesting season and would not be tagged until a return nesting migration.

Temporal analysis of demographic indicators

Size-at-maturity – Carapace length distributions of newly tagged and veteran nesters

Newly tagged turtles likely represent neophyte (first season) nesters, and size at first tagging likely represents the minimum size-at-maturity for those animals (Richardson et al.

2006), given the history of nesting season surveys. In using this approach, we assume that these newly tagged (nominal neophytes) nesters have not nested in previous seasons or on other unmonitored islands in Hawaii. We used 1981 as our first year of analysis, because it was the first year in which the percentage of newly tagged turtles stopped increasing, following a high percentage in the early years when the monitoring program first started, after this initial tagging effort (Nurzia Humburg & Balazs 2014). We plotted the straight carapace length (SCL; cm) of newly tagged turtles (i.e. nominal neophytes) and veteran turtles (turtles with tags or tag scars) across years to determine if there were differences in carapace lengths between the two groups. If an individual was measured multiple times within a season, we took the average of the measurements, as it is unlikely adult sea turtles would grow appreciably within a nesting season. We tested the fit of the residual SCLs to a normal distribution and found no significant departure from that distribution. We then statistically tested for differences using linear mixed models (LMM) with a restricted maximum likelihood estimator, and accounted for the temporal autocorrelation within individuals, and across years, using a specified covariance structure (e.g., AR(1), Toeplitz, compound symmetry, etc.), in SAS 9.3. Linear mixed models are advantageous compared to other statistical methods in that they can take advantage of repeated measurements across individuals, account for the intrinsic autocorrelation of repeated measures, and correctly characterize the variance associated with the estimated parameters (Littell et al. 1998, Bolker et al. 2009). The candidate model set included an intercept-only null model, a categorical year effect, a tagging effect (tagged or untagged), or year and tagging effects. We tested various covariance structures for temporal autocorrelation of individual turtles, and compound symmetry had the best model fit.

Carapace length-distributions – Linear Mixed Models

To test for differences in carapace length over time, we estimated the mean SCL of nesters each year using LMM with a restricted maximum likelihood estimator, in SAS 9.3. We followed the same modeling routine as with size-at-maturity. We tested various covariance structures for temporal autocorrelation of individual turtles, and compound symmetry had the best model fit. The candidate model set included an intercept-only null model, and a categorical year effect, along with the tested covariance structures.

Survival and reproduction vital rates – Mark and recapture-based models

We used a multi-state open robust design model (MSORD), with an unobservable state, to estimate the transition probabilities of moving from nesting to foraging states and from foraging (unobservable) to nesting ($\psi_{N\rightarrow F}$ and $\psi_{F\rightarrow N}$, respectively), detection probability (p), probability of entering the nesting state (p_{ent}), and the probability of remaining in the nesting state (φ), using maximum likelihood in Program Mark, version 7.1 (Pollock 1982, Kendall & Bjorkland 2001, Kendall & Nichols 2002, Cooch & White 2013, Kendall 2013). The MSORD model accounts for sampling error and confounding between mortality and non-detection (Kendall & Nichols 2002, Kendall 2013). The robust design provides secondary within season information, which improves parameter estimation and precision (Kendall & Nichols 2002). Open robust design models permit the relaxation of two assumptions of closed populations: the population is closed to additions and deletions within a primary season, and each member of the population has an equal probability of being available for detection in a given time period (Kendall & Bjorkland 2001). Following the approach of Kendall and Bjorkland (2001), we divided the nesting survey season into 14 day periods, because the average inter-nesting interval for green sea turtles in Hawaii is 13.4 days (range: 11 – 18 days) and this was the optimal period after preliminary iterative testing of the interval length (Balazs 1980, Kendall & Bjorkland

2001). The total number of within-season survey periods varied annually depending on the total number of survey nights in a primary season. The parameters were modeled as time-varying or constant for each primary (year) and secondary (14-day) period. Survival for nester and non-nesters was assumed to be equal. For the unobservable state (skip-nesting), p_{ent}, φ, and p are set = 0. For models with full time-dependence in detection probability (p_{tt}), it is necessary to set the final year equal to the previous year (i.e., $p_{2008}=p_{2009}$) to avoid issues with parameter estimation (Kendall 2013). We modeled within season temporal effects on p_{ent} as a multinomial distribution so that within secondary periods, p_{ent} summed to one. We were only able to run these models for 1981-2009, as 1973-1980 and 2010 did not have large enough sample sizes or long enough primary seasons for the models to converge.

The transition probability $\psi_{F\rightarrow N}$ may be used as an estimate of annual breeding probability, as only females observed on the nesting beach in the process of nesting (e.g., egg laying, nest burial, complete crawls up to nest and back to the water, etc.) were included in the dataset (Kendall & Bjorkland 2001). Since many turtles bask on East Island, and potentially could give a false positive of nesting, and ultimately yield a biased estimate of breeding probability, we only included confirmed nesting events in the dataset. With this model structure, we were also able to test for random transition probabilities, where the probability of transitioning from a nester to skip-nester equaled the probability of transitioning from skip-nester to nester ($\psi_{N\rightarrow F} = \psi_{F\rightarrow N}$), and Markovian transition probabilities, where the probability of transitioning from nester to skip-nester does not equal the probability of transitioning from skip-nester to nester ($\psi_{N\rightarrow F} \neq \psi_{F\rightarrow N}$), and this ultimately tests the occurrence of obligate skip-nesting (Kendall & Bjorkland 2001, Kendall 2013). Typically, breeding frequency for sea turtles is calculated as (remigration interval)$^{-1}$ (Bjorndal et al. 2010). We back-calculated remigration interval as 1+ $\psi_{F\rightarrow N}^{-1}$. If annual breeding probability is the probability of becoming a nester when an individual was a skip nester in year t-1, then it is necessary to add one year to $\psi_{F\rightarrow N}^{-1}$ to account for the additional year it would take to go from nester to skip-nester (as green sea turtles are obligate skip nesters).

It is also possible to derive clutch frequency from the tagging data using the MSORD model, based on the residence time of sea turtles in the nesting state. However, we did not include it here because of a strong bias with the number of secondary sampling periods, where years with fewer secondary periods had a lower estimate of clutch frequency (see Appendix A for more information).

We tested the hypothesis that temporal variation was important in the estimation of the DIs by determining if a model containing temporal effects on survival and breeding probability was top-ranked based on Akaike Information Criterion correction for small sample sizes (AICc). First, we tested a variety of models with temporal effects within and across seasons for the parameters p, p_{ent}, and φ, and assumed temporal effects across and within seasons for adult annual survival (S), the probabilities of transitioning from nester to skip-nester, and skip-nester to nester ($\psi_{N\rightarrow F}$, and $\psi_{F\rightarrow N}$, respectively). Using the best-fitting model, we then tested for temporal effects of S and ψ, and whether $\psi_{N\rightarrow F} = \psi_{F\rightarrow N}$. In addition, we explored different parameterizations of ψ, using the initial second ranked model as well.

Currently, no standardized goodness-of-fit test exists for MSORD models, although some experimental methods have been tested. As an alternative, we ran a median $\hat{c}$ test (Cooch & White 2013) on a simplified multistate fully time-dependent model (with nesters and unobservable skip-nesters, but no robust design), and found that $\hat{c}$ = 1.489 (1.466 – 1.513 95%

CI). Previous research indicates $\hat{c} \leq 3.0$ is acceptable and suggests a reasonable fit of the model to the data (Lebreton et al. 1992).

Model Selection procedures

For all analyses, we compared models with and without a year effect to test for temporal trends in DIs. Model selection was based on AICc and the information-theoretic approach to select the most parsimonious model of the candidate model set (Burnham & Anderson 2002). In the information-theoretic approach, candidate models represent biological hypotheses, and are tested via the degree of quantitative support, i.e. model likelihoods and AICc (Burnham & Anderson 2002, Johnson & Omland 2004). Model selection is preferred to traditional null hypothesis testing for observational data, where no explicit experimental framework is imposed or when multiple models have the potential for similar levels of support (Anderson et al. 2000, Burnham & Anderson 2002, Johnson & Omland 2004). We compared the top model to an intercept-only model that represented the null model, and used evidence ratios to assess the strength of evidence for the top-ranked model (Anderson et al. 2000). Evidence ratios (ρ) are calculated by dividing the AICc weight of the model containing the term under consideration (w_i) by the AICc weight of the model when the term is removed (w_j). The greater ρ, the more important the explanatory variable of interest is as a predictor in the model.

Nester abundance estimation

We used estimates of nester abundance derived from a model by Wetherall et al. (1998) in our analysis (Fig. 2.1). Wetherall et al. (1998) developed a method using an Horvitz-Thompson type estimator to estimate the number of nesters based on the number of survey nights in a given season, and using the covariates of arrival time, nesting frequency, nesting duration, and inter-nesting interval (see also (Balazs & Chaloupka 2004b). Their sighting probability function was calibrated using the entire nesting season census derived from nightly emergence probabilities during a five year period of saturation tagging (1988-1992; Wetherall et al. 1998). Confidence intervals were derived using an empirical bootstrap approach for each annual estimate. We used this approach as it was an independent method to estimate nester abundance, rather than the abundance estimates derived from the MSORD approach, which uses the estimates of $\psi_{F \to N}$ (i.e. breeding probability) in the calculation.

Demographic indicators and nester abundance

If the top-ranked model included a temporal effect on a DI, we tested for a relationship between the annual estimate of the demographic indicator and the estimated nester abundance for the given year. We used generalized linear models (GLMs) to test for relationships between *ln*(Nester Abundance) and the DIs in R (version 3.0.1) with the packages *car, MASS, gvlma,* and *MuMIn*. We modeled SCL with a Gaussian distribution, and all assumptions of a linear model were met based on tests of skewness, kurtosis, and heteroscedasticity. Breeding probability was best fit by using a gamma distribution. We compared the models with and without *ln(*Nester Abundance), i.e. intercept-only, using evidence ratios, to test our hypothesis that nester abundance and the DIs are related (Burnham & Anderson 2002).

2.3 RESULTS

Size-at-maturity – Carapace length distributions of newly tagged and veteran nesters

A total of 3,277 individual turtles were examined for differences in the mean carapace length of nominal neophyte and veteran nesters, with 6,773 total observations (with repeated measurements on turtles across years). Substantial overlap existed in the size distributions for the two groups for all years (Fig. 2.2). However, we found that the model, which included the tagging effect and a categorical year effect, along with a compound symmetry covariance structure to account for temporal autocorrelation within individual turtles, was orders of magnitude more likely than the null model (Table 2.2). While the top ranked model included tagging status as a predictor (i.e., newly tagged or veteran nester), the magnitude of the difference was small: the estimated range of the yearly means of SCL for newly tagged turtles was 89.3 cm (95% CI: 88.4 – 90.2) to 91.2 cm (95% CI: 90.7 – 91.7) and the range for veteran turtles was 89.8 cm (95% CI: 88.9 – 90.3) to 91.7 (95% CI: 91.3 – 92.2) (Fig. 2.3; Table S1). This amounts to roughly 0.5 cm difference in carapace length between newly tagged and veteran nesters each year, which falls within measurement error. As such a small difference in carapace length between nominal neophyte and veteran nesters, we did not distinguish neophytes and veterans for the rest of the analysis.

Temporal analysis of carapace length

Year was an important predictor of carapace length, based on the top ranked model, which included annual estimates of carapace length, and a compound symmetry covariance structure to account for temporal autocorrelation within individual turtles. A total of 3,677 individual turtles were included, with 7,348 total observations (with repeated measurements on individual turtles across years). Carapace length experienced temporal variability from 1973 to 2010, and the estimates of SCL ranged from 89.21 (95% CI: 88.97 - 89.46) in 1988 to 91.69 (95% CI: 91.50 - 91.8) in 2008 (Table 2.1 and Fig. 2.4). While the top ranked model included year as an important predictor of SCL, there was not a strong directional trend in the estimates of SCL over the entire time-series, but short-term trends of increasing SCL over several years followed by steep declines in SCL were apparent (Fig. 2.4). Moreover, more general longer term trends (~ 10 years) were apparent; after a period of declining SCL (1977-1989), turtle lengths began to increase.

Mark-recapture modeling of demographic indicators (DIs)

Temporal variation figured prominently in the top-ranking MSORD model used to estimate annual survival rate, breeding probability, probability of entering the nesting state, probability of remaining in nesting state, and detection probability. The top-ranking model included a full model weight of 0.999 and model likelihood of 1 (Table 2.3). A total of 3,405 individual turtles were included in the encounter histories and 2,678 turtles were recaptured at least once. The top-ranking model did not include temporal variation in annual adult female survival (S= 0.929 year^{-1}, 95% CI: 0.924 – 0.933; Table 2.1).

Breeding probability, or the probability of transitioning from a foraging to nesting, was estimated annually in the top-ranking model. Annual breeding probability ranged from 0.0766 (95% CI: 0.0574 - 0.102) in 1998 to 0.444 (95% CI: 0.398 – 0.490) in 1997 (Table 2.1 and Fig. 2.4). If these probabilities were constant for individuals, they would correspond to remigration intervals of 3.25 – 14.1 years. The top ranked model included year as an important predictor of breeding probability, but there was not a strong linear trend over the whole time series, though there were short-term trends of increasing breeding probabilities, followed by steep drop-offs (Fig. 2.4). The strong cyclic pattern appears to dampen in later years of the time series, but additional years of data are needed to verify this.

The top-ranking model also included a constant estimate of transition probability of nesters moving to skip-nesting, 0.989 (95% CI: 0.925 – 0.998). This result corroborates a wide body of previous research that nearly all individual females will not nest the year immediately following nesting, and take at least two years to return to the nesting beach, and likely much longer on average (Miller 1997, and references therein).

For detection probability, the top-ranking model included temporal estimates for both within season and across season effects (Table 2.3). The range of estimates for detection probability was 0 (95% CI: 0- 1) – 1(95% CI: 0-1), e.g., $p = 0$ in the third secondary sampling period in 1982, and $p = 1$ in the first secondary sampling period of 1984 (Table 2.1). Notably, the MSORD models can have difficulty in estimating parameters and the uncertainty of those estimates when estimates are close to their boundaries of zero or one (Kendall 2013). In general, detection also varied across secondary periods within primary periods (years). For example, in 2008, detection ranged from $p_{2008,4} = 0.147$ (95% CI: 0.118 – 0.0183) to $p_{2008,2} = 0.970$ (95% CI: 0.947 – 0.983), where subscripts indicate the year and two-week within-season secondary periods. During the years of saturation tagging, 1988 – 1992, detection probabilities were higher, and ranged from 0.59 (95% CI: 0.39 – 0.76) to 1.00 (95% CI: 0 – 1).

Demographic indicators as a function of nester abundance

We did not find a strong relationship between mean SCL and nester abundance (Fig 4). The intercept-only model was selected over the models with temporal variation of SCL (Table 2.4). We did not evaluate annual survival because the top-ranking model did not include temporal estimates of survival.

Nester abundance was a good predictor of breeding probability – the probability of breeding increased with an increasing nester population (Fig. 2.5). Model selection of the regression between nester abundance and the breeding probability ranked the model with temporal estimates of breeding probability over an intercept-only model (no difference across years). The model with annual estimates of breeding probability was 11 times more likely than the intercept-only model, based on evidence ratios (Table 2.4). To put this in terms of remigration interval, as the nester abundance increases, the remigration interval (the number of years between nesting events) decreases, which is counter to our original hypothesis regarding density dependence.

2.4 DISCUSSION

Overall, we found considerable variability in demographic indicators for Hawaiian green turtles, but little evidence of directional trends through time. This is the first analysis of temporal trends in survival rates for green sea turtles in Hawaii, and survival was estimated to be constant since 1981 (S = 0.929 year^{-1}, 95% CI: 0.924 – 0.933). During the period of population recovery that we evaluated, the estimates of mean body length and annual breeding probability had important annual fluctuations, and this annual variability was supported by the model selection process. Neophyte nesters were statistically smaller than veteran nesters. However, as the difference was ~0.5 cm, on average, the practicality of applying the distinction of tagging status to determine size at sexual maturity is nonexistent for these data. We hypothesized that breeding probability and body size would decrease with increasing nester abundance, because of intraspecific competition. However, we found no relationship with body size and nester abundance and breeding probability appears to *increase* with greater nester abundance. But, as breeding probability has a relationship with nester abundance, it has potential to indicate population recovery. In all, our work contributes to a small but growing set of studies that evaluate changes in vital rates and life history traits over time for sea turtles, and ours is the first to do so for Hawaiian green sea turtles (Kendall & Bjorkland 2001, Troeng & Chaloupka 2007, Pfaller et al. 2013, Phillips et al. 2014, Garcia-Cruz et al. 2015).

Temporal variability of demographic indicators

The estimates of temporal variability for our demographic indicators give insight into how this population may have changed over a 38 year time period. Although the data did not support a linear trend in the time series, short-term (3-4 years) and decadal cycling were evident in both mean nester body length and breeding probability. The amount of variability estimated for these DIs of sea turtles is not unprecedented (Limpus et al. 2003, Troeng & Chaloupka 2007, Limpus 2008, Phillips et al. 2014). Probably several drivers exist for observed short-term trends and the degree of temporal variability. Possibly, new cohorts of neophyte nesters that recruit into the adult reproductive population contribute to variation to the DIs. However, environmental or climate fluctuations could also be driving the temporal patterns (Carr & Carr 1970, Broderick et al. 2001, Solow et al. 2002, Chaloupka & Limpus 2005). Patterns in the DIs could be related to population density, because this population is increasing, based on multiple lines of evidence of trends in both adults and juveniles (Balazs & Chaloupka 2004a, Chaloupka & Balazs 2007, Chaloupka et al. 2008). However, our data suggest environmental stochasticity may be the dominant driver of annual variation in that the DI estimates vary annually and are not negatively correlated with nester abundance.

We found decreasing turtle carapace lengths and breeding probability fairly early in the time series. Strong year classes recruiting into the adult reproductive population following harvest protection may be driving down the average size in years with high recruitment. Size-selective harvest of sub-adults and smaller adults prior to ESA protection may have driven this population’s response to conservation measures (Van Houtan & Kittinger 2014). Egg harvest was extremely limited in the extant nesting beaches in the uninhabited NWHI, unlike many other sea turtle rookeries globally (Mast et al. 2011). In addition, fishermen selectively harvested smaller individuals (Balazs 1980, Witzell 1994, Kittinger et al. 2013, Van Houtan & Kittinger 2014). In an historical analysis, Van Houtan & Kittinger (2014) found that from 1948 – 1974, fishermen preferentially selected juvenile turtles (mean size= 30.5 kg, ~63.8 cm SCL), but towards the end of the fishery average sizes of landed turtles dramatically increased. According to skeletochronology, the mean size of turtles harvested corresponds to an estimated age of roughly 20 years (Zug et al. 2002). If age at maturity is 20 – 40 years (Balazs 1980, Zug et al. 2002, Hargrove & Balazs 2012, Van Houtan et al. 2014), then we would expect to see sizeable changes in the adult population and in the age structure within the first 20 years after harvest was prohibited, as younger age classes experienced improved survivorship to maturity (Crowder et al. 1994). If eggs had also been harvested, recovery would likely have taken much longer, as has been observed in the Florida green turtle population (Chaloupka et al. 2008, NOAA & USFWS 2015). Ultimately, examining changes in juvenile size distributions over time may be a better indicator of population-level changes than sizes of adults, as juvenile size distributions could give an early indication of changes in age structure as cohorts “fill in” the gaps caused by exploitation (White et al. 2013).

Long-term datasets are necessary to capture the full range of variability for breeding probability and its inverse, remigration interval. Our estimates of breeding probability and body length suggest significant variability, but are in line with some recent estimates. Balazs et al. (2015) estimated remigration interval of Hawaiian green turtles, summing data from 1973 – 2013, to be 4 years (breeding probability = 0.25), in contrast to an earlier estimate of 2.47 years (breeding probability = 0.404; Table 2.1; Balazs 1980). Balazs et al. (2015) also found the mean body length for adult females in Hawaii to be 90.7 cm SCL, reduced from the original 1980 estimate of 92.2 cm SCL (Table 2.1; (Balazs 1980, Van Buskirk & Crowder 1994, Balazs et al.

2015). We also found smaller mean carapace lengths of nesters than those reported for green sea turtle populations elsewhere. For example, the mean size of nesters in Tortuguero, Costa Rica was estimated to be 100.2 cm SCL, and in Heron Island, Australia was estimated at 102.4 cm SCL compared to 89.2 – 91.7 cm for this study (Table 2.1; Van Buskirk & Crowder 1994). The smaller average size of nesters may be due to the influx of younger animals into the Hawaiian population during the recovery period. Overall, our model selection procedures suggest that annual estimates of both breeding probability and body length are the more accurate than constant estimates and that significant interannual variability exists.

Given that the top-ranked model for mean nester carapace length estimated a large range of mean sizes annually, suggesting potential cohort effects, it is surprising to see so little difference in the estimated sizes of newly tagged turtles, i.e. nominal neophytes, and veteran nesters (~0.5 cm difference year^{-1}). In contrast, in the southern Great Barrier Reef, veteran turtles are on average 3 cm larger than neophyte nesters (Limpus 2008). There are at least two possible explanations for our result. First, newly mature green turtles may not all be tagged upon their first reproductive year, leading to inflated length estimates of nominal neophytes. Given the amount of effort on the nesting beach, it is unlikely that neophyte nesters are consistently missed by nest surveyors if those turtles are coming to East Island exclusively. But detectability could be lower for neophytes if those females have low nest site fidelity as they recruit into the adult population, i.e., some neophytes nest at other rookeries in the Hawaiian Islands, and then nest at East Island subsequently (Limpus et al. 2003, Tucker 2010). At least 95 individuals are recorded as nesting at East Island and other outlying islands in the NWHI at some time, corresponding to a 3% rate of “infidelity” (unpublished reports, PIFSC). However, surveys at the other nesting rookeries in the NWHI are infrequent and opportunistic, so it is hard to quantify survey effort outside of East Island. A second explanation for the size distribution overlap between newly tagged and veteran nesters is variable growth and size at maturation. Growth rates vary widely among individual turtles, with little or no growth following maturation (Balazs & Chaloupka 2004a, Goshe et al. 2010, Avens et al. 2012, 2013). In captive-reared green sea turtles that were monitored from birth to past sexual maturity, wide variations in both age and size-at-maturity were observed (Bjorndal et al. 2013). This variability is likely to obscure distinctions between sizes of neophytes and veteran nesters. Further investigations of site fidelity and size at maturation, as well as development of physiological methods to identify newly mature turtles are needed to fully understand the implications of shifts in nester size during population recovery.

We did not find evidence that survival rates varied over time from 1980-2009. Following ESA protection, survival rates were expected to increase, especially as adults were targeted for harvest towards the end of the fishery. However, survival rates had likely already increased by 1980 (the first year included in the MSORD model), as there had been a campaign to protect green sea turtles in Hawaii in the 1970s; the state of Hawaii passed regulations restricting harvest starting in 1974 (Balazs 1980), and ESA protection formally occurred in 1978. Our results are comparable to the findings of Van Houtan et al. (2014), who used matrix models to deterministically estimate survival rates (Table 2.1). Our study is apparently the first to test whether the survival rate for Hawaiian adult females has changed since harvest was prohibited; however, a constant estimate was supported by model selection. In population models, it may be simplest to use a time-invariant constant estimate of survival, albeit with consideration of uncertainty, unless there is strong evidence for a change in adult survival over time. Mark-recapture analysis is a valuable tool for detecting such changes, which could have profound effects on population productivity (Bjorndal et al. 2010).

Demographic indicators as a function of nester abundance

We did not see a decrease in breeding probability as the Hawaiian green turtle population recovered, as might be predicted by density-dependence. This result suggests that either density-independent factors are driving remigration (e.g., climate), or that the population is still below carrying capacity and not yet regulated by population density. In that case, the result also suggests that the Hawaiian population is still in the process of recovery and the population has not yet reached equilibrium. Because of the observed positive relationship of breeding probability, or its inverse remigration interval, with nester abundance, breeding probability shows promise as an indicator of nester abundance during periods of population recovery. Hays (2000) found in his theoretical models that when variability in forage quality was included, remigration interval was variable, drove interannual variation in nesting numbers, and interannual variation remained constant regardless of population size. Understanding the relationship between demographic indicators and population size is valuable for sea turtle populations that can only be monitored over a small proportion of their geographic range. Our results also highlight the importance of carefully interpreting raw counts of increased nester abundance, as a positive trend could be attributable to increased nesting frequency – a greater breeding probability – and not necessarily a true increase in population abundance (Bjorndal et al. 2010). If breeding probability increases with nester abundance, as we report, estimated recovery rates may be inflated if only raw counts of nests or nesters (rather than the identities of nesters) are monitored across seasons (Pfaller et al. 2013). In the future, our results could be compared to other recovering populations of green sea turtles to determine if these are general trends.

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Table 2.1. Published estimates of demographic indicators and estimates from this analysis for Hawaiian green sea turtles (*Chelonia mydas*). P_{ent} = probability of entering nesting state, φ = probability of remaining in nesting state, and p = detection probability. See Appendix A for discussion of clutch frequency analysis.

Demographic indicator	**Estimate or Range of Estimates in this analysis (95% CI)**	**Published value**	**Reference**
Size-at-maturity (cm)	89.3 cm (88.4 – 90.2) – 91.2 cm (90.7 – 91.7)	89.7 (SD = 3.9), 80	Van Houtan et al. 2014, Balazs and Chaloupka 2004a
Nester Straight Carapace Length (cm)	89.21 (88.97 – 89.46) – 91.69 (91.50 – 91.88)	90.7, 92.2	Balazs 1980, Van Buskirk and Crowder 1994, Balazs et al. 2015
Annual Breeding Probability, ψ (year^{-1})	0.0766 (0.0574 –0.102) – 0.444 (0.398 – 0.490)	0.25 (= 4^{-1} remigration interval), 0.404 (=2.47^{-1} remigration interval)	Balazs 1980, Van - Buskirk and Crowder 1994, Balazs et al. 2015
Adult Female Survival Rate (year^{-1})	0.929 (0.924 – 0.933)	0.930	Van Houtan et al. 2014
p_{ent}	0.000 (0 – 0) – 1.000 (0 – 1)	N/A	
φ	0 ($-1\cdot10^{-6}$ – 0.000001) – 1 (0 – 1)	N/A	
p	0 (0 – 1) – 1.000 (1 – 1)	N/A	
Clutch Frequency (nests/season)	1.39 (1.18 – 1.60) – 4.96 (-30.7 – 40.6)*	4, 1.8	Tiwari et al. 2010, Balazs 1980, Van Buskirk and Crowder 1994, Balazs et al. 2015

* Estimates restricted to years with ≥ 5 secondary sampling periods

Table 2.2. Evidence ratio (ρ) for straight carapace length (SCL) during the years 1981-2010 as a function of tagging status (newly tagged or veteran nester) and year compared to an estimate without tagging status. Evidence ratios are calculated as the ratio of the Akaike Information Criterion correction (AICc) of the best model with and without the variable of interest.

	SCL 1981-2010
AICc weight for best model with Tagging Status Effects, w_i	1.000
AICc weight for best model without Tagging Status Effect, w_j	$2.12 \cdot 10^{-233}$
Evidence Ratio, ρ (w_i/w_j)	$4.713 \cdot 10^{232}$

Table 2.3. Akaike Information Criterion correction (AICc) for five highest ranking models fit to capture-recapture data collected from breeding green sea turtles (*Chelonia mydas*) at East Island, French Frigate Shoals, Hawaii, 1980-2009. S=survival rate, ψ = transition probabilities between the two states, nester and skip-nester (N and F, respectively), p_{ent} = probability of entering the nesting population, φ = probability of remaining in nesting population during a secondary sampling period, p=detection probability, and L = likelihood. Survival for nesters and skip-nesters is assumed to be equal. For the unobservable state (skip-nesting), p_{ent}, φ and p are set = 0. Constant = constant estimate over time, Time = separate estimate for each time period, 1^0 = single estimate per primary period, and 2^0 = single estimate per secondary period. AICc weight indicates the relative support and fit of each model.

Model	S	$\psi_{N\ to\ F}$	$\psi_{F\ to\ N}$	p_{ent}	φ	p	**# Par**	**Δ AICc**	**AICc Weight**	**Model L**
1	Constant	Constant	Time	Time	Time	Time	309	0	0.99999	1
2	Constant	Time	Time	Time	Time	Time	335	23.8029	0.00001	0
3	Time	Time	Time	Time	2^0	Time	311	69.9503	0	0
4	Constant	Constant	Time	1^0	Time	Time	231	129.0565	0	0
5	Constant	Time	Time	1^0	Time	Time	259	182.9021	0	0

Table 2.4. Evidence ratios (ρ) calculated separately for two demographic indicators (mean SCL and breeding probability) as a function of nester abundance compared to a simple model without temporal variation. Evidence ratios are calculated as the ratio of the Akaike Information Criterion correction (AICc) of the best model with and without the variable of interest.

	Demographic Indicator	
	Mean SCL	Breeding Probability ($\psi_{F\ to\ N}$)
AICc weight for best model with temporal effect of DI, w_i	0.562	0.910
AICc weight for best model without temporal effect of DI, w_j	0.817	0.0808
Evidence Ratio, ρ (w_i/w_j)	0.688	11.26

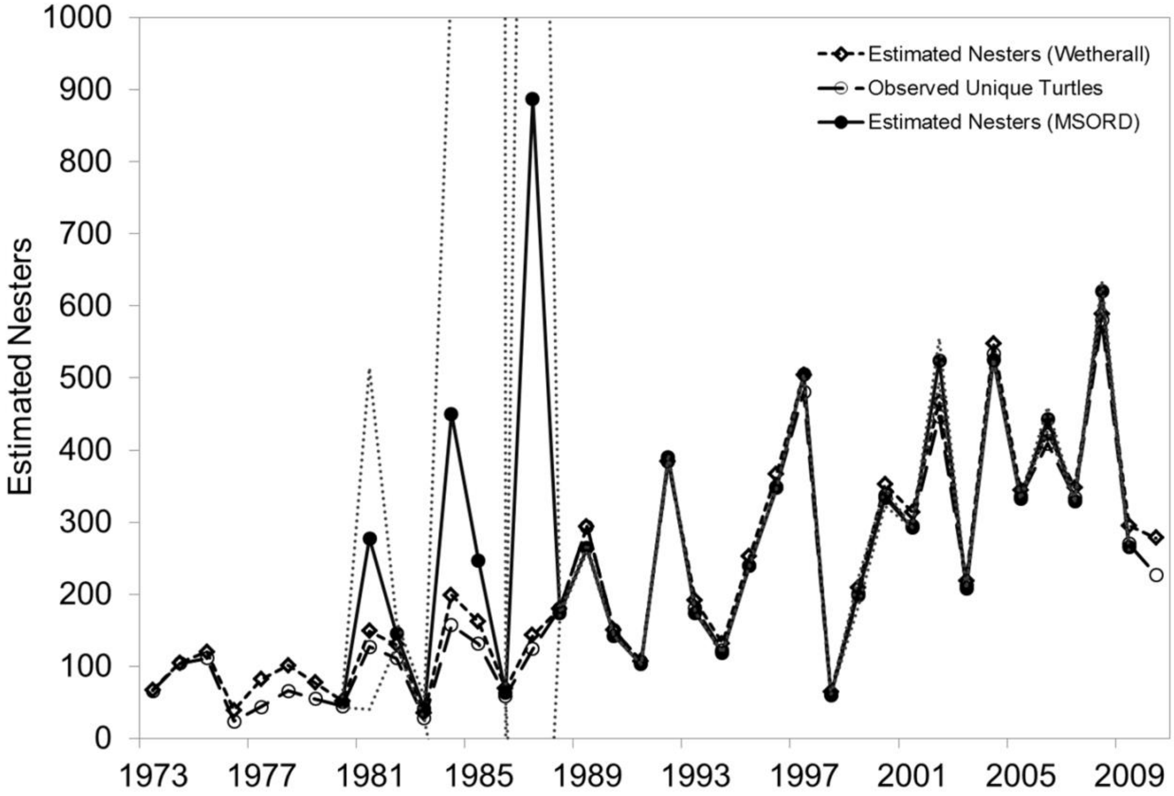

Figure 2.1. Abundance of nesting green sea turtles, *Chelonia mydas*, at East Island, Hawaii based on counts of observed individual turtles, the estimated number of nesters (using the method of Wetherall et al. 1998), and the estimated number of nesters using the top-ranked multistate open robust design model (MSORB) at East Island, French Frigate Shoals, Hawaii 1973-2010. Dotted lines indicate 95% confidence intervals around the estimated number of nesters. Extreme values for the 95% confidence intervals in some years were left off for better visualization of the data.

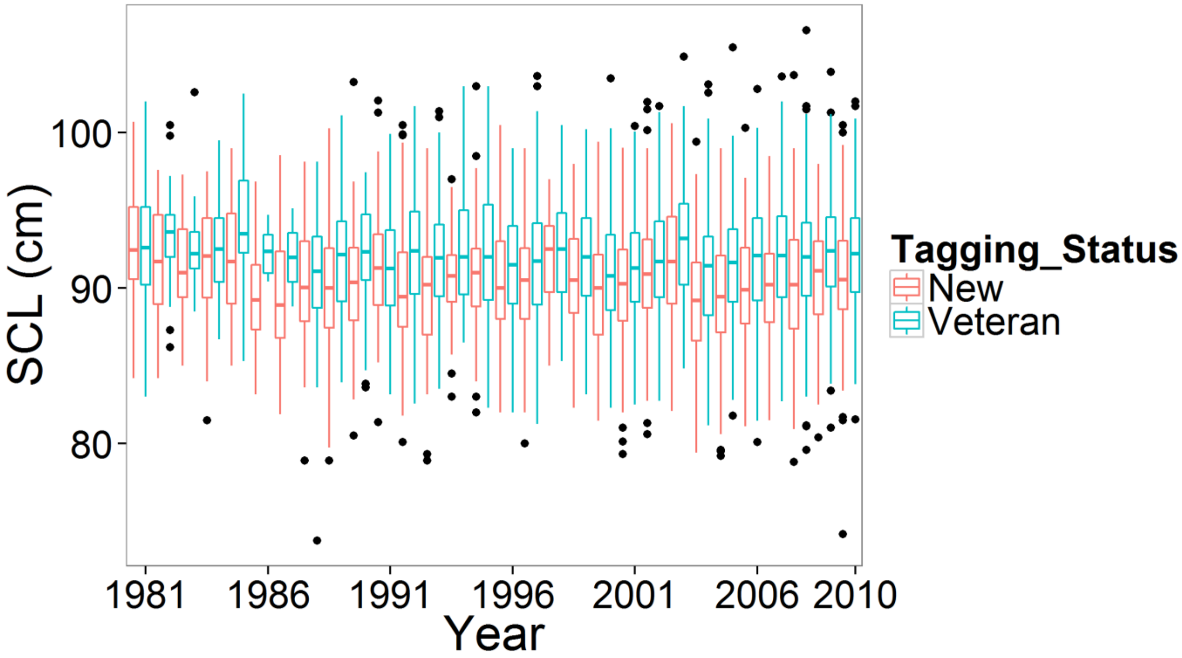

Figure 2.2. Box-and-whisker plot of straight carapace length (cm) of newly tagged and veteran nesters from 1981 to 2010 at East Island, French Frigate Shoals. 1973-1980 were excluded to account for untagged veteran nesters. Black dots indicate outliers.

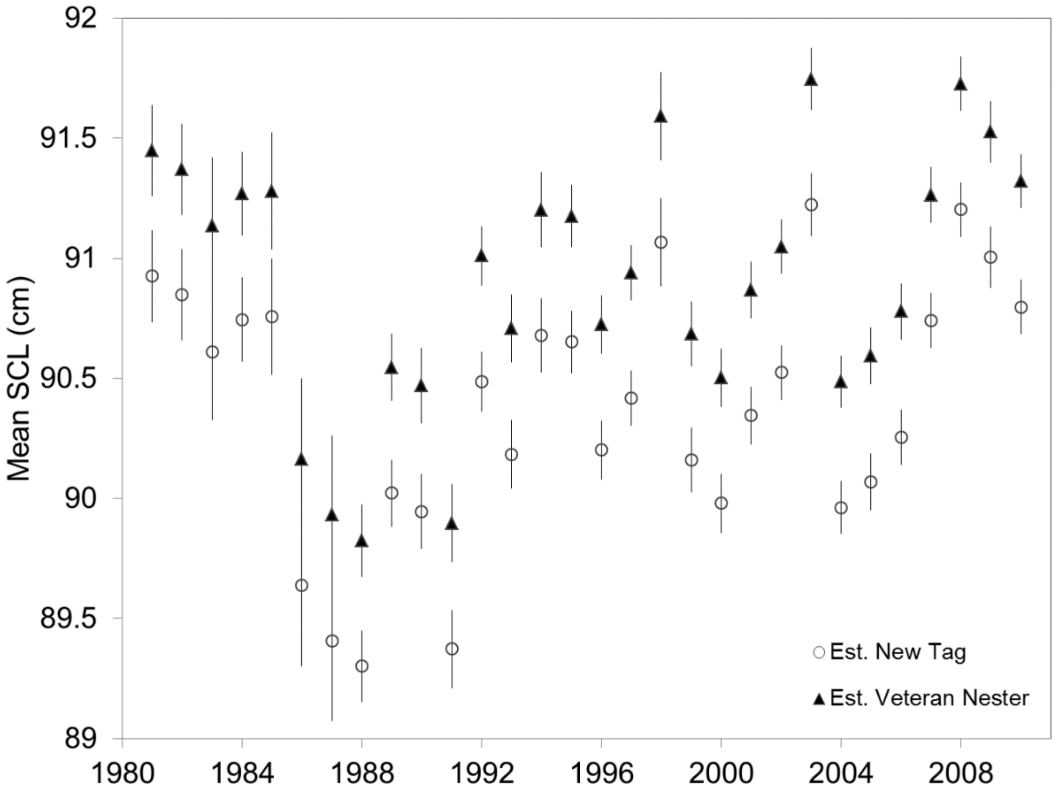

Figure 2.3. Linear mixed model estimates of mean straight carapace length (cm) of newly tagged and veteran nesters (± standard error) at East Island, 1981-2010. 1973-1980 were excluded to account for untagged veteran nesters.

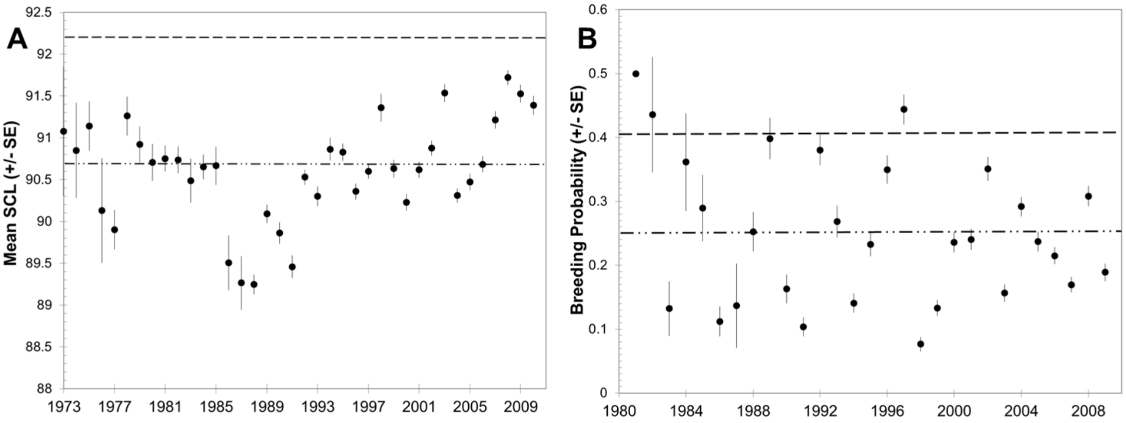

Figure 2.4. Annual estimates of demographic indicators (± standard error): mean straight carapace length of nesters (cm) based on linear mixed models (LMM) from 1973-2010 (A), and mean breeding probability (year^{-1}) based on multistate open robust design models (MSORD) from 1980-2009 (B). Remigration interval (years between nesting seasons) equals breeding probability^{-1} +1 (see Methods: Survival and reproduction vital rates). Dashed lines refer to the published estimates and the dot-dash line represents the recent constant estimates of Balazs et al. (2015) of the demographic indicators.

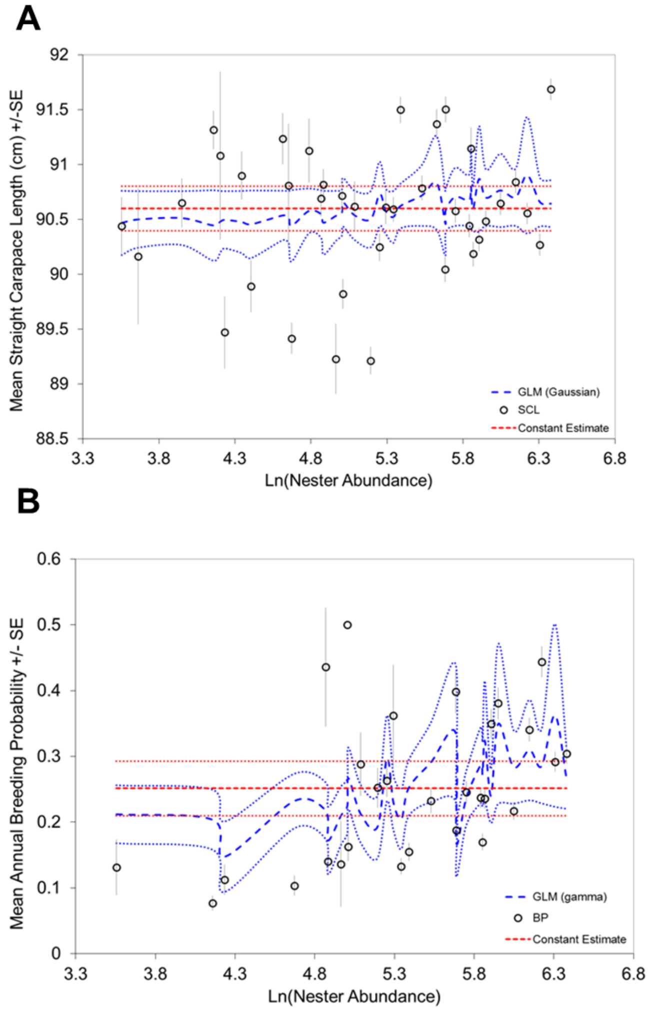

Figure 2.5. Relationships between ln-transformed estimates of nester abundance (based on an estimation model developed by Wetherall et al. 1998) and two demographic indicators, mean straight carapace length (SCL, ± SE) (A) and breeding probability (± SE) (B). The predicted values of SCL are based on a generalized linear model (blue dashed line) with a Gaussian distribution and 95% confidence interval (CI; blue dotted line), and breeding probability is based on a generalized linear model with a gamma distribution and 95% CI. The red dashed line indicates the regression line for an intercept-only model (which represents the null model where there is no relationship between the demographic indicator and nester abundance) and 95% CI (red dotted line).

3 - The mirror cracked: An agent-based model to simulate recovery dynamics and monitoring strategies for green sea turtles

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ABSTRACT

Green sea turtles are threatened globally, as some populations continue to decline while others are recovering. Recovery efforts may be confounded by complex life history and reproductive behavior, with individual variation in reproductive output of adult females. Most monitoring efforts encounter sea turtles on rookeries and census nesters, nests, or both. Because of skip-breeding and inter-annual variability in nesting, monitoring rookeries provides an imperfect mirror of true population level changes in abundance. We used demographic parameters estimated from the Hawaiian green turtle population to develop and implement the green sea turtle agent-based model (GSTABM) to simulate population dynamics, population disturbance and recovery, and to simulate the processes of monitoring and population assessment. The GSTABM simulates individual variability in age-at-maturity, clutch size, clutch frequency, and skip-breeding behavior. We added biological complexity to the GSTABM to simulate an annually changing breeding probability based roughly on climate anomalies and individually-variable breeding intervals. Inter-annual variability in nester abundance emerges as output in the model. To explore the model behavior and outputs, we subjected the virtual populations to sub-adult, adult, and nest disturbances and simulated the monitoring process of observing nesters and nests with error. We found that the GSTABM simulates population-level processes of nester abundance, and nester recruitment over time are within the bounds of observed values from Hawaii. The GSTABM outputs are most sensitive to changes in nearshore juveniles, sub-adult and adult survival rates. In simulating 100 years of recovery, populations began to increase but did not fully return to pre-disturbance levels in adult and nester abundance, population growth or nester recruitment. In simulated monitoring trials, adult abundance was poorly estimated, was influenced by population trajectory and impacts, and showed marginal

improvements with increased detection. Estimating recruitment showed improvements with increasing detection levels, and accuracy depended on the impact legacy. In the GSTABM, variability in the nest and nester counts did not always reflect variability in adult abundance, which translated into measurable uncertainty in assessing population size and trends from nesting beaches. The GSTABM is an important tool to determine relationships with monitoring, population assessment, and the underlying biological processes driving changes in the population, and especially, changes on the nesting beach. The ultimate purpose of the GSTABM is to be an operating model with which to evaluate optimal monitoring strategies for nesting beach surveys that will enhance accuracy of population assessments.

3.1 INTRODUCTION

The green sea turtle (*Chelonia mydas*) is a globally threatened species due primarily to over-exploitation, habitat loss and degradation, and disease (Seminoff 2011). Effective management depends on reliable monitoring of abundance indices and an understanding of the species' population dynamics. For long-lived and highly migratory species like sea turtles, monitoring is usually only possible for discrete demographic groups over short spans of time when life stages are accessible and observation is possible, such as nesting females or nests during the breeding season. It is unclear how well indices based on beach surveys mirror the entire population. And, perhaps, our assessment of the status of these populations is flawed. Some populations of sea turtles are recovering, while many are not, despite intensive conservation measures (Wallace et al. 2011, NOAA & USFWS 2015). For example, counts of nesting females in the Hawaiian population of green sea turtles is estimated to be increasing at 5.7% year^{-1}, but the nest counts of the recovering Kemp's ridley sea turtle (*Lepidochelys kempii*) have experienced a recent rapid decline at the primary rookery in Mexico (Chaloupka et al. 2008, Caillouet 2014). When a change in the trend of an index of abundance occurs, particularly for a long-lived species, it can be difficult to ascertain the cause of the change or whether it reflects a change in unobservable components of the population (Heppell et al. 2003, Bjorndal et al. 2010).

Cases of endangered species recovery are relatively rare and present a valuable opportunity to improve our understanding of the transient dynamics of increasing populations. Importantly, as a population recovers it is possible that the underlying relationships between the monitored demographic group and the rest of the population could be changing. For example, breeding probabilities can change as a function of the population size (Piacenza et al. *In press*). But if only certain demographic indicators or life stages are monitored, biologists may have no way to know that the underlying relationships are changing. Observer error, limited sampling windows, and nesting site ranges larger than the typical stretch of beach monitored insure that most sea turtle monitoring programs produce indices rather than true censuses (Gerrodette et al. 1999, Jackson et al. 2008, Tucker 2010, Pfaller et al. 2013, Hart et al. 2013, Whiting et al. 2013). In addition, because we do not generally have population indices from other demographic groups in the population from which to compare or to confirm with nesting beach indices, biologists and managers are often ignorant of how misleading population trends based on nesting beach indices may be (Bjorndal et al. 2010).

Population models are a critical tool in the effort to understand population dynamics and can give insight into unmonitored demographic groups and their status (Morris & Doak 2002). Demographic models for sea turtles typically make simplifying assumptions that females reach sexual maturity at the same age, breeding probability is constant for all individuals in a size/age class, and productivity is density independent. But, our understanding of sea turtle population dynamics is complicated by intermittent breeding, a long lifespan, density-dependence and long demographic time lags (Parmenter & Limpus 1995, Bjorndal et al. 2000, Girondot et al. 2002, Heppell et al. 2003, Caut et al. 2006). For example, if green sea turtles mature at 40 years of age, as has been estimated (Balazs & Chaloupka 2004a), then any research following hatchlings to maturity transcends the length of most field studies. Although the range of many demographic variables has been estimated, only recently have biologists regularly attempted to incorporate that variability into population models (e.g., Chaloupka, 2002; Chaloupka and Balazs, 2007; Mazaris and Matsinos, 2006; Mazaris et al., 2006, 2005; Warden et al., 2015; Whiting et al., 2013). Worse yet, some parameters may be trend coefficients rather than moments of simple distributions (Solow et al. 2002). Female green sea turtles are obligate skip-nesters (i.e. take at least two years to breed again; Miller 1997) and breeding probability may be highly variable (Piacenza et al. *In press*). Breeding probability, which is often calculated as "remigration interval" based on the number of years between sightings of tagged individuals, has been tied to environmental conditions for green turtles (Solow et al. 2002), leatherbacks (Rivalan et al. 2005, Saba et al. 2007), and loggerheads (Broderick et al. 2001, 2003). Differences in physiology and the influence of the environment result in individual variability in remigration intervals (Chaloupka & Limpus 1996, Miller 1997, Limpus & Chaloupka 1997, Solow et al. 2002, Broderick et al. 2003, Stokes et al. 2014). By accounting for individual variability in life history traits, deviations in population dynamics emerge which are in contrast to results produced by traditional modelling approaches (DeAngelis & Mooij 2005). In addition, individual variability, can be especially important during disturbance and recovery, as outliers (e.g., highly fecund individuals) can be important to population resilience and recovery. Accounting for individual variability in life histories in our models could improve our assessment of overall population variability, improve the accuracy of status determinations, and result in more realistic for population recovery times.

One way to address these variation-related issues is through the use of agent-based models (ABMs; also referred to as Individual Based Models, IBMs; Railsback and Grimm, 2012). ABMs have the flexibility to incorporate more complex mechanisms, such as individual variability in life history traits and density dependence. ABMs can simulate individual behaviors and therefore operate at the scale by which population dynamics are based and at which monitoring occurs (Lomnicki 1988, Letcher et al. 1998, DeAngelis & Mooij 2005). ABMs have previously been applied to sea turtles to examine the influence of temporal variability and age-dependent mortality on population dynamics, to measure population viability and to test different monitoring schemes for within season sampling (Mazaris et al. 2005, 2006, Mazaris and Matsinos 2006, Whiting et al. 2013). In addition, ABMs provide a platform with which to perform disturbance experiments and to simulate the process of population monitoring. As ABMs use a bottom up modeling approach, rather than aggregate-level equations, population dynamics emerge due to events and behaviors of the individuals (Grimm & Railsback 2005, Semeniuk et al. 2012). By addressing these issues, ABMs can give more biologically realistic predictions and better estimates of variability and uncertainty, and allow biologists to enhance understanding of the dynamics of population recovery and the relationships between population indices and the entire population (Semeniuk et al. 2011).

We created our green sea turtle ABM (GSTABM) to simulate green sea turtle population dynamics, population disturbance and recovery, and to simulate the processes of monitoring and population assessment. Our primary goal in creating the GSTABM was to let our questions and the basic principles of green sea turtle life history dictate the model design. Specifically, we wanted to allow individual variability in life history traits, i.e. breeding periodicity, age-at-maturity, clutch frequency, and clutch size, and to create mechanisms for density-dependence and the influence of environmental variability on reproduction. We simulate anthropogenic disturbance to populations and observe the associated transient dynamics as they affect multiple indices of abundance. Ultimately, we wanted to contrast the recovery dynamics of populations subjected to different kinds of disturbance histories. We had three main research questions: (1) Can the GSTABM adequately reproduce the dynamics of green sea turtle populations? (2) How do the recovery dynamics differ when the disturbance occurs to different demographic groups (e.g., older turtles and eggs), and 3) What predictions can we make from the GSTABM regarding recovery dynamics of green sea turtles?

1.1 Biological Background

The model is parameterized to simulate the Hawaiian population of green sea turtles, where long-term data have been collected (Piacenza et al. *In review,* Balazs and Chaloupka, 2004; Balazs, 1980; Balazs et al., 2015; Dizon and Balazs, 1982; Niethammer et al., 1997; Nurzia Humburg and Balazs, 2014; Tiwari et al., 2010; Van Houtan et al., 2014), but could easily be modified to represent other sea turtle populations and species, and other endangered and recovering species. In the archipelago, the vast majority of nesting takes place in the Northwestern Hawaiian Islands (NWHI) and the largest rookery is at East Island, French Frigate Shoals, a small atoll (~0.036 km^2), where approximately 50% of Hawaiian nesting occurs (Balazs 1980, Balazs & Chaloupka 2004a). Females generally will not nest in the year immediately following a nesting year (i.e. obligate skip-nesting) and vary in the number of years between nesting seasons (Piacenza et al. *In review*, Broderick et al., 2003; Stokes et al., 2014).

Energetics, physiology, and environmental conditions all appear to influence the length of the breeding, or remigration, interval (Chaloupka & Limpus 1996, Miller 1997, Limpus & Chaloupka 1997, Solow et al. 2002). Within a nesting season, green turtles will return several times to lay an average of four clutches at approximately 2 week intervals (Tiwari et al. 2010, Piacenza et al. *In review*).

Historically, green sea turtles were abundant and nested throughout the entire Hawaiian Islands chain (Kittinger et al. 2013). In recent history, harvest occurred on larger juveniles, sub-adults and adults, with progressively more pressure on larger individuals as the fishery developed, and there was little to no egg harvest (although episodic egg harvest in the NWHI may have occurred; Balazs, 1980; Kittinger et al., 2013; Van Houtan and Kittinger, 2014). Prior to European colonization in the early 1800s, green sea turtle populations are thought to have been minimally disturbed in the Hawaiian archipelago due to a variety of factors, as harvest was tightly regulated by the “kapu” system of native Hawaiians (Balazs 1980). In the 20th century, numbers of green sea turtles dropped precipitously as harvest intensified and became more commercialized in the Hawaiian Islands (Balazs 1980, Witzell 1994, Van Houtan & Kittinger 2014). In 1978, green sea turtles were placed on the endangered species list and harvest was prohibited (NOAA Office of Protected Resources 2014).

3.2 METHODS AND MODEL DESCRIPTION

The model description follows the ODD (overview, design concepts, details) format for describing agent-based models (Grimm et al. 2006, 2010). We implemented the model in NetLogo 5.1.0 (Wilensky 1999) and the program code is available in Appendix B. We simulated the population dynamics of green sea turtles in Hawaii based on known life history information.

Purpose

The GSTABM was developed to evaluate the influence of observation error (e.g., in monitoring) on perceived population status and ultimately on status determinations based on monitoring of nesting females and nests. The model was designed to simulate the dynamics of sea turtle populations that are (1) at equilibrium (e.g., stable, unperturbed state), (2) undergoing decline due to increased loss of individuals via anthropogenic and natural impacts, e.g., harvest, bycatch, environmental change, or (3) are recovering from such impacts so that populations are increasing (Fig. 3.1). As such, one of the main goals was to capture the transient dynamics of green sea turtle populations following perturbation. In addition, this model was developed as an operating model to be used in a modified Management Strategy Evaluation framework (Smith et al., 1999, Piacenza et al. *In prep.*).

Entities, state variables and scales

The model entities are individual female green sea turtles of different age classes (hatchlings (year 1), pelagic juveniles (years 2-3), neritic juveniles (years 4-11), sub-adults (years 12 to age-at-maturity), neophytes (year of age-at-maturity), adults (post maturity)). The state variables are age, demographic stage, age-at-maturity, clutch frequency, clutch size, reproductive status (nester or non-nester), hatchling production, remigration interval, and lifetime nesting migrations (Table 1). The life history traits of age-at-maturity, clutch frequency and clutch size vary across individuals, are assigned at birth, stochastic, and based on empirical data (Table 2). We assume a 50/50 sex ratio for each clutch (Balazs 1980, Niethammer et al. 1997). Breeding probability is stochastic and varies annually (Fig. 3.2B). Age-at-maturity is variable across individuals, so that stage lengths for sub-adults vary individually (Fig. 3.2A).

Realized hatchling production (HP) is density-dependent and is based on a Ricker type function (Fig. 3.2C; Jennings et al., 2001).

The temporal scale of the model progresses with annual time steps. The model incorporates environmental variation by including a climate variable that influences breeding probability (Fig. 3.2D; Solow et al., 2002). The model includes several agent-sets: age classes, reproductive state (nester or non-nester), monitored nesters, and monitored nests.

Process overview and scheduling

With each time step, individual turtles grow older, survive, are exposed to risk of environmental/anthropogenic impacts (at certain time periods), reproduce, and may be monitored when nesting (Fig. 3.1). Model entities are processed in a randomized order and changes in state variables are updated immediately. The number of nesters is updated after nesting takes place and before the monitoring sub-model proceeds.

Update age class

Sea turtles age and proceed to the next age class if they survive. Age class designates which life stage each individual is part of for the year, i.e., hatchling, pelagic juvenile, neritic juvenile, sub-adult, neophyte, or adult (Mazaris et al. 2005, Van Houtan et al. 2014).

Survival

Survival is dependent on the age class of the individual (Table 3.2).

Update removal status – nests and older individuals

Additional mortality from anthropogenic or natural impacts can occur through random removals of individuals. This step determines which individuals (sub-adults and adults or eggs) are removed from the population in addition to natural mortality.

Choose nesters

This step determines if an adult is a non-nester or nester for the time step.

Hatchling production

The function calculates the number of hatchlings produced by a nester, based on the individual’s clutch size and clutch frequency and current population density.

Produce Hatchlings

This step produces the new offspring for each individual and includes all eggs produced across clutches.

Monitoring nesters and nests

This step determines which nesters and nests are sampled during nesting beach monitoring and become part of the Monitored Nesters and Monitored Nests agent-sets.

Design concepts

Basic Principles

How populations recover and the variability associated with reproduction, both at the individual and population levels, along with the influence of the environment, is of fundamental importance to understanding the trajectories towards recovery and the time spans involved (Lotze et al. 2011, Kuparinen & Hutchings 2012, Hutchings, Butchart, et al. 2012, Kuparinen et al. 2014). We used a bottom up modeling approach based on the first principles of life history (Grimm et al. 2005, Wilensky & Rand 2015). One goal was to keep the model simple enough that we could minimize the number of unknown parameters that would require internal calibration (Grimm et al. 2005).

Emergence

The annual population size, abundance of nesters, population growth rate ($\lambda = N_{t+1}/ N_t$, where N_{t+1} is the population size at time $t+1$), age distribution, and nester recruitment (defined as the proportion of first-time breeders, i.e. neophytes, in the nester population) emerge from demographic processes. While individual demographic traits are dictated by the distributions of the input parameters, the population level mean demographic rates (e.g., remigration interval, clutch frequency, clutch size, age-at-maturity, and hatchling production) are emergent variables as well.

Stochasticity

We incorporate stochasticity into many model elements to represent natural variability (Table 3.2). Individual turtle survival is randomly assigned each year from life stage-dependent distributions. Age-at-maturity, clutch frequency, and clutch size, is drawn randomly from a Poisson distribution (Table 3.2). The threshold for breeding probability varies annually and is drawn randomly from a truncated gamma distribution (range 0-1; Fig. 3.2B). In addition, a climate condition parameter simulates poor climate conditions that reduce breeding probability, such as in an extreme *El Nino* year. Poor climate conditions in the GSTABM occur ~10 years on average and reduce breeding probability by 25% (Fig. 3.2D). For adults eligible to nest in a given year (not immediately following a nesting year), nester status is selected based on a random number draw (between 0 – 1) against the breeding probability threshold. During the time periods where anthropogenic mortality is in effect, turtles are randomly chosen to be removed from the population. Detection probability is randomly drawn from a logit-normal distribution. Nesters and nests are randomly selected to be part of the monitoring agent-set.

Observation

The model automatically collects data on individuals and population-level parameters by year. The data include population size, age structure, number of nesters, number of nests, number of turtles removed due to anthropogenic/natural impacts, nester recruitment, and annual breeding probability. In addition, population level means and standard deviations of hatchlings produced female^{-1}, remigration interval, age-at-maturity, clutch frequency, clutch size, and total number of lifetime nesting seasons for each time-step are collected.

Initialization

The initial conditions for abundance and population structure were based on the stable age distribution generated from an age-structured projection matrix model using parameters in Table 3.1. Initial abundance of stage classes is presented in Table 3.3. To decrease model run times and the amount of time to reach quasi-stability, the abundance of hatchlings and pelagic juveniles are modelled as super-individuals by the use a scaling factor (Table 3.2). The scaling factor was calculated by dividing the number of female eggs produced per capita by the survivorship to the first year of the neritic juvenile age class (Scheffer et al. 1995). Turtles are initialized with their randomly drawn life history traits (age-at-maturity, clutch frequency, and clutch size). We set the initial carrying capacity for the nesting beach based on preliminary model runs that suggested the best accordance of the model output to observed data from the Hawaiian green turtle population. The nester carrying capacity parameter is only used in the function to calculate the hatchling production per nester in a nesting season.

Input data

The current version of the model does not include input data.

Sub-models

Update age class

Each time step the age of individual sea turtles is advanced by one year and the individual may proceed to the next age class. Ages included in each life stage were based on those in Van Houtan et al. (2014; Table 3.2). To set age-at-maturity, we used the median age-at-maturity from multiple studies of Hawaiian turtles as the mean age-at-maturity in the GSTABM (Table 3.1; Balazs and Chaloupka, 2004; Van Houtan et al., 2014; Zug et al., 2002).

Survival

Survival is dependent on the age class of the individual. The adult female survival rate is based on a mark-recapture analysis, which used 29 years of tagging data (Piacenza et al. *In review*). For the other age classes (hatchling – sub-adult), we use survival rates estimated in Van Houtan et al. (2014), which are based on a deterministic projection matrix model fit to observed data. We model the survival rates as having a constant mean within each life stage (Table 3.2). Individual survival is based on random draws against the survival threshold for each age class and results in demographic stochasticity. We set the maximum age to be 85 years old, based on estimates of age-at-maturity and reproductive longevity (Zug et al. 2002, Chaloupka et al. 2004, Nurzia Humburg & Balazs 2014, Van Houtan et al. 2014).

Removals

During the period in which anthropogenic impacts can occur (50 years after the model reached equilibrium), sub-adults and adults are randomly removed from the population to simulate a population decline:

$$TR_t = SA_t + A_t \cdot F \tag{2.1}$$

where TR_t = total removed t, SA_t = sub-adults and A_t = adults in a given time step t, and F = removal rate. After the impact period is over, the removals sub-model no longer removes turtles from the population. A similar function is used to remove nests, except the total number of hatchlings produced is used in the numerator ($Hatchlings_t$). To remove separate age classes, separate calculations were made, with specific impact rates for both Nests and Age 11+ individuals. In the base removal setting, 6.67% of sub-adults and adults were removed annually for 50 years (Table 3.2). For the nest removals, 50% of nests were removed annually for 50 years. For nest and Age 11+ (sub-adults and adults), 25% of nests and 3.33% of Age 11+ were removed.

Choose nesters

This step calculates if the individual sea turtle is eligible to breed in the current year, based on if she bred the year before. If the individual did not breed the previous year, she is eligible in the current time step. Breeding is based on a random draw (0 – 1) against the breeding probability threshold. If the random draw is < Breeding Probability, then the individual is a nester that year.

Hatchling production – super-individuals

Hatchling production is represented as a function of an individual's assigned clutch size and clutch frequency, and a density-dependent term (based on a Ricker type density dependent equation):

$$HP_t = (CS \bullet CF)e^{(r(1-(\frac{Nesters_t}{K_{nesters}}))} \tag{2.2}$$

where HP_t= hatchling production at time t, CS = clutch size, CF = clutch frequency, r = intrinsic rate of increase, $Nesters_t$ = total number of nesters in the current time step, and $K_{nesters}$ = the carrying capacity for hatchling production based on the number of nesters present in a year (Fig. 3.2C). We used a Ricker type function because studies have shown decreased numbers of viable nests and hatchlings with high numbers of nesters or nests (Girondot et al. 2002, Caut et al. 2006). As no empirical data on the form of density dependence of hatchling production exists, the intrinsic rate of increase, r, was fit internally to the model so as to achieve an asymptotic relationship of hatchling production for green sea turtles (Fig. 3.2C). Empirical evidence supports density dependence in egg and hatchling production, and it can be exerted through several different mechanisms, including intraspecific nest destruction, intraspecific competition for food influencing a female's fecundity, yolk stores, egg viability, and increased egg and hatchling predation (Girondot et al. 2002, Tiwari et al. 2006, 2010, Caut et al. 2006, Ocana et al. 2012).

We represent the hatchlings produced as super-individuals to reduce model run times (Scheffer et al. 1995). A super-individual encompasses a portion of a female's hatchling production, and a female produces, on average, 8 super-individual hatchlings season^{-1} equivalent to ~ 64 female hatchlings. We scaled super-individuals to the number of hatchlings that would survive to the neritic juvenile stage (age 4) based on life table analysis (Scheffer et al. 1995).

Monitoring

We developed a monitoring sub-model to simulate population monitoring on the nesting beach. The detection probability, p, is a random variable drawn from a logit-normal distribution. We scale the standard deviation of detection so that it is proportional to the mean input value. We based the standard deviation on the coefficient of variation (CV = 0.2) of observed detection probabilities in a long-term mark-recapture study of Hawaiian green turtles (Fig. 3.3; Piacenza et al. *In review*). We experimented with 3 different mean detection levels: 0.1, 0.5, and 0.9. The detection probabilities represent the proportion of all nesters in a population that are being monitored, and not at a single rookery. After nesting has occurred, the number of nesters is summed and the total number of monitored nesters is $p \cdot Nesters_t$ (Fig. 3.1). The monitored nesters agent-set is a random selection of all nesters in a given time step. Since nesters lay more than one clutch of eggs per season, a similar routine was followed to conduct monitoring on nests. The GSTABM collects data from the monitored-nesters agent-set similar to output data collected on the population as a whole, including: observed nester abundance, observed nest abundance, observed nester recruitment, as well as data on the observed population level means and standard deviations of hatchlings produced female^{-1}, remigration interval, age-at-maturity, clutch frequency, clutch size, and total number of lifetime nesting seasons.

Population assessment

To simulate population assessment, we estimate the total number of adults from observed nesters, while assuming constant breeding probability and detection probability, such that:

$$\hat{A}_{t,obs.nesters} = \frac{Obs.Nesters_t}{BP \bullet p} \tag{2.3}$$

where $\hat{A}_{t,\,obs.\,nesters}$= estimated number of adults at time t based on the observed nesters, BP = breeding probability and p = detection probability. We followed a similar routine to estimate the total number of adults from observed nests, while assuming constant breeding probability, clutch frequency and detection probability:

$$\hat{A}_{t,obs.nests} = \frac{Obs.Nests_t}{BP \bullet CF \bullet p} \tag{2.4}$$

where $\hat{A}_{t,\,obs.\,nests}$= estimated number of adults at time t based on the observed nests, and CF = clutch frequency. For the purposes of population assessment, we assume that BP, p, and CF could be estimate accurately from field data. The assumed constant estimates were BP = 0.25 and CF = 4, and the p = mean detection treatment level (p= 0.1, 0.5, or 0.9). The estimated number of adults from observed nesters or observed nests was compared to the true number of adults to determine the level of accuracy associated with the varying detection probabilities. To maintain equal sample sizes for the three impact phases, we randomly selected 25 time-steps (within each replicate model run) from the impact and recovery phases (which both included >25 years), and the stable phase was composed of the first 25 years post-model initialization.

Model analysis and simulations

To determine the adequate sample size for analysis of the baseline model and each input parameter setting, we used an approach that employs the cumulative coefficient of variation (CV) over a running number of replicates to determine when adequate sampling is achieved (Cowled et al. 2012). We analyzed the CV for the four main response variables of adult abundance, nester abundance, the discrete population growth rate, and nester recruitment. The model was allowed to reach equilibrium at 175 time steps (before which all output data are discarded), and the model was allowed to run to 350 time steps. The model has three main population trajectory phases: stable population (years 175 – 199), impact phase (years 200 – 250), and the recovery phase (251 – 350).

The age structure of the five age classes (hatchling, pelagic juvenile, neritic juvenile, sub-adult and adult and neophyte) was examined to determine if the proportion of individuals in each age class was realistic, given previous age-structured models for sea turtles (Crouse et al. 1987, Crowder et al. 1994, Heppell et al. 1996, 2000, Casale & Heppell 2016). We included four main emergent output parameters to focus our analysis on: adult abundance, nester abundance, discrete annual population growth, and nester recruitment. These parameters were not controlled for in the input parameters for individuals or model coding, and thus should emerge on a higher (population) level of organization as a result of the interactions of individual female green sea turtles (Breckling et al. 2005). We compared the means and 95% confidence intervals (95% CI) of nester abundance and nester recruitment to empirical data from the Hawaiian population of green sea turtles as a way to “ground truth” the model performance (Grimm et al. 2005). All model outputs were evaluated including the four main emergent variables, and the population-level life history traits (i.e. hatchlings produced per female, remigration interval, age-at-maturity, clutch frequency, clutch size, hatchling production, and total number of lifetime nesting seasons).

Sensitivity analysis

We conducted a local one-at-a-time sensitivity analysis of 12 input parameters (Table 3.2) on the main response variables: adult abundance, nester abundance, discrete annual population growth, and nester recruitment (Table 3.1). Since ABMs are stochastic, and outputs vary with each simulation run, we assessed model sensitivity using an approach that incorporates the shape of the distribution of the output response variables, which is based on the t-statistic (Bar Massada & Carmel 2008). Sensitivity (S_t) was calculated as:

$$S_t = \frac{|\bar{Y}_{alt} - \bar{Y}_{ref}|}{(p_{alt-}p_{ref})\sqrt{(s_{alt}^2 + s_{ref}^2)/n}} \bullet p_{ref} \qquad (2.5)$$

where $\bar{Y}_{alt}$ is the mean of the response variable generated with an alternate input parameter and $\bar{Y}_{ref}$ is the mean of the response variable generated from the baseline input parameter, p_{alt} and p_{ref} are the alternant and reference parameter values, respectively, and s^2_{alt} and s^2_{ref} are the standard deviations of the two distributions. For constant input parameters, we varied the mean input by +/- 5%. For stochastic input parameters, we varied the mean input by +/- 5% (for values that were integers, we selected the next value below and above), and the biological extremes of the parameters, based on reports in the literature (Table 3.2).

3.3 RESULTS

Model stabilization

The CV decreased and stabilized after 30 replicate runs, at the most, for the four primary response variables (i.e. adult abundance, nester abundance, discrete population growth, and nester recruitment; Fig. 3.4). We conducted 50 replicate runs per simulation for baseline simulations and the sensitivity analysis to capture the range of model outputs.

We discarded the first 175 years of each model run, during which the GSTABM initialized. Most runs generally became quasi-stable after ~85 years, but we included roughly one extra generation time to buffer against potential delays in equilibration. We compared output variables across 175 years (post-model initialization), during which populations were subjected to a 50 year impact, where 6.67% of sub-adults and adults, 50% of nests, or 3.33% of sub-adults and adults and 25% of nests were removed annually, simulating anthropogenic disturbance of green sea turtle populations (i.e. harvest, bycatch, physical injuries), and the subsequent recovery phase post-impact.

Life history traits

At time-step 350, the average number of female eggs produced for each clutch was 43.2 (SD = 15.3), transformed back from the scaled super-individuals (see *Hatchling production – super-individuals*), and the average clutch frequency was 4.0 (SD = 2.00; Fig. 3.5A and B). The average remigration interval was 3.4 (SD = 2.72; Fig. 3.5D). The average total number of female hatchlings produced (across clutches laid in a season) was 92.9 (SD = 64.1), transformed back from the scaled super-individuals. The average age-at-maturity was 28.6 (SD = 3.1; Fig. 3.5C). All of the stochastic input parameters for reproduction correspond to the empirical data on green sea turtle reproduction (Table 3.2). As these inputs were imposed in the model structure, this is not surprising, yet is also a good check that the model was performing as intended. The average annual breeding probability was 0.234 (SD = 0.1087), and the realized breeding probability (calculated as the ratio of nesters and adults) was 0.239 (SD = 0.0768). As the model automatically does not allow turtles to re-nest the year following nesting (since green sea turtles are obligate one year non-nesters), the realized breeding probability tends to be slightly greater, albeit within the range of the standard deviations. The average number of breeding remigrations in an adult female turtle’s reproductive lifetime was 3.2 (SD = 2. 3), and the maximum lifetime nesting migrations of any individual across all replicate model runs was 32.

Population size, nesting abundance and age structure

The mean population size at time-step 350 across 50 replicate runs was 375,437 (SD = 8,602). The pelagic juveniles (ages 1 – 3) were the most abundant stage class (back-transformed from super-individuals) and adults were the least abundant stage class (Fig. 3.6). The average adult population was 9,912 females (SD = 311), and the average number of nesters was 2,370 (SD = 756) at time-step 350. Variability in the abundance of age classes was greatest for the youngest age classes (pelagic juveniles SD = 22,614, hatchlings SD = 14,343) and least for adults (SD = 311). Populations tended to be stable, and did not go extinct, over the entire model run if the removals sub-model was turned off.

Adult abundance showed little variability during the stable population periods, declined during the impact phase and began to recover after the impact ceased (Fig. 3.7A), with a time lag. While no data exist on the total adult population size for Hawaiian green turtles, we compared the estimated number of females nesting to the simulated nester abundance (Fig. 3.7B). We assumed 50% of nesting in Hawaii occurs at the primary rookery at East Island, French Frigate Shoals (Balazs 1980, Nurzia Humburg & Balazs 2014). In Hawaii, nester monitoring began in 1973, and green sea turtles were listed as an endangered species and harvest was prohibited in 1978 (NOAA Office of Protected Resources 2014). We scaled the Hawaii time-series to 5 years prior to the cessation of harvest in the model (e.g., 1973 = Year 245 in the GSTABM). With an impact rate of 6.67% of sub-adults and adults, the model predicts a slightly higher mean nester population at the beginning of the impact phase (Year 250) and then subsequently lower mean population sizes during the recovery phase. However, individual model run variability is in accordance with the observed inter-annual nester variability in Hawaii (Figure 7B). Indeed, most of the Hawaii nester time-series falls within the bounds of the 95% confidence interval of the GSTABM, and suggests a good model fit to the observed data.

Population growth rate

After the initialization stage, the discrete annual population growth rate (λ) was close to $\lambda = 1.00$ (SD = 0.0037) (Fig. 3.7C). During the harvest phase, population growth initially decreased to $\lambda = 0.94$ (SD = 0.013), and then increased slightly and appeared to reach dynamic stability at $\lambda = 0.97$ (SD = 0.012). During the recovery phase, λ initially increased to $\lambda = 1.046$ (SD = 0.013), and displayed dampening oscillations with a mean of $\lambda = 1.017$ (SD = 0.011) towards the end of the model runs.

Nester recruitment – proportion of neophytes

During the initial stable phase of the model runs, nester recruitment (proportion of neophytes, females nesting for the first time) stabilized at about 0.331 (SD = 0.110) each year (Fig. 3.7D). During the impact phase, nester recruitment displayed a lag in a response after 10-15 years of the impact, and reached a mean maximum of 0.437 (SD = 0.117), in Years 226 -250. Recruitment began to decrease during the later years of the impact phase, and reached a mean local minimum of 0.429 (SD =0.116), in years 240 – 249, and then increased again during the initial recovery phase. Oscillations in nester recruitment continue during the recovery phase, and appeared to approach the undisturbed recruitment rate towards the end of the model runs.

While no data on nester recruitment exists *per se* for green sea turtles in Hawaii, there is an estimate of the percent of newly tagged turtles out of total nesters (mean = 49%, standard deviation = 14; Nurzia Humburg and Balazs, 2014). Assuming tagging saturation of adult females, newly tagged turtles may be used as a proxy for proportion of neophytes. However, evidence suggests that the assumption of saturation tagging is specious (Piacenza et al. *In review*), and should be treated with caution. The observed estimate of Hawaiian nester recruitment falls within the bounds of the 95% CI for the GSTABM and suggests a good model fit to the observed data (Fig. 3.7D).

Population impact and recovery

During years 200 – 250, we simulated a harvest impact in which sub-adults and adults, nests, or nests, sub-adults, and adults were removed from the population, in addition to the natural mortality. For sub-adult and adult impacts during the impact phase, the adult population decreased to an average minimum of 3,760 (SD = 2,686) adults and 950 (SD = 745) nesters (Fig. 3.8A & B). In the last ten years of the recovery phase, the average adult population was 9,637 (SD = 402), and the average number of nesters was 2,407 (SD = 806). Oscillations in the adult population are apparent during the recovery phase (Figs. 3.6 and 3.7A). Nesting is naturally more variable than the adult population because of the innate breeding periodicity of green sea turtles. However, similar oscillatory patterns during recovery are apparent in the nester abundance time-series (Fig. 3.7B). In general, the output variables did not achieve complete recovery to pre-impact levels in the 100 years of recovery after the cessation of the 50 year impact phase.

In general, when nests were disturbed, either alone or in conjunction with sub-adult and adult impacts, the response variables showed different patterns during the impact and recovery phases when compared to the sub-adult and adult harvest scenario. When 50% of nests were harvested, there was a delayed response in the four main response variables (Fig. 3.8). The mean number of nesters during the 50 year impact phase was higher (mean nesters = 2,303 and SD = 1153), and during the first 100 years of the recovery the average number of nesters was lower than during the impact phase (mean nesters = 1,551 and SD = 811). There were substantial time lags in the recovery phase, where the four main emergent variables did not show signs of recovery for at least the first 25 years of the recovery phase (Fig. 3.8).

When nests, sub-adults, and adults were disturbed, simulating nest and Age 11+ harvest, the recovery rate was slower and nester abundance during the impact phase was larger and had greater variability (mean nesters = 1,435, SD = 841) compared to sub-adult and adult only impacts, which was not unexpected considering that a larger proportion of the population was disturbed (Fig. 3.9). However, the pattern of the discrete population growth rate and nester recruitment showed interesting changes. When hatchlings, sub-adults and adults were disturbed, the population growth rate had a muted response during the impact phase, neither dipping as low nor showing as large of an increase, relative to the other impact types, and the height of the oscillations was smaller during the recovery phase (Fig. 3.9C). For nester recruitment, there was a much longer lag, and did not show as big of an increase during the impact phase, and the height of the oscillations during the recovery phase was lower (Fig. 3.9D). For all cases of impacts, none of the four response variables indicated a complete recovery to pre-impact levels in the 100 years following the end of the impact phase.

Population monitoring

Estimating adult population from observed nesters and nests

We compared population level indices from the known adults and observed nesters or observed nests. Estimates of adult abundance drawn from observed nesters and nests differed substantially from the true total number of adults, and the accuracy of the estimate did not greatly increase with detection probability (Fig. 3.10). The accuracy improved marginally with increasing detection probability, but was rarely a precise estimate. In general, there were more incidences of over-estimates than under-estimates, except during the stable population trajectory. The accuracy in the population estimate also depended on the underlying population trajectory (i.e. stable, impact or recovery phases), and the largest under-estimates occurred during the stable phase.

The impact legacy, in which certain age classes were disturbed, had an influence on the accuracy and bias of the adult abundance estimation (Figs. 3.10, 3.11, 3.12). For example, there was a greater chance of underestimating the adult population size if the impact legacy only included nests (Fig. 3.11) compared to disturbances to nests, sub-adults and adults (Fig. 3.12).

Estimating Nester Recruitment from Observed Nesters

Estimating the nester recruitment (proportion of neophytes) from observed nesters showed improved accuracy with increasing detection probability (Fig. 3.13 A-C), and the gains in accuracy where greater compared to estimating adult abundance. When only sub-adults and adults were disturbed, the overall variability in estimated nester recruitment slightly greater, compared to nest impacts and nest, sub-adult and adult impacts. The worst errors in estimated proportion of neophytes tend to occur during the recovery and impact population trajectories.

Sensitivity Analysis

The GSTABM response variables were most sensitive to neritic juvenile, sub-adult and adult survival rates (Table S1). Given the wealth of study of sea turtle survival rates in projection matrix models, this result was not surprising (Crouse et al. 1987, Crowder et al. 1994, Heppell et al. 2000). Adult abundance was most sensitive to a 5 % increase in adult survival rate, followed by a 5% decrease in sub-adult survival rate. Nester abundance was most sensitive to 5% decrease and 5% increase in the sub-adult survival rate. Nester recruitment was most sensitive to a 5% decrease in adult survival rate, followed but a 5% increase in adult survival rate. The discrete population growth rate was most sensitive to a 5% decrease in adult survival rate and neritic juvenile survival. Interestingly, there were some unsymmetrical results across the perturbation range. For example, discrete population growth rate was most sensitive to a 5% increase in adult survival rate, but only had a moderate sensitivity to a 5% decrease in the adult survival rate. Stochastic input variables were also subjected to a sensitivity analysis across the biological extremes, but none of these had as big of an impact on the output variables as the survival rates.

3.4 DISCUSSION

The GSTABM was developed to address management concerns of recovery dynamics, monitoring strategies and population assessments. In this model, we introduced a novel way to represent breeding periodicity in ABMs, which is stochastic and varies annually, and allows for more biological realism in representing green sea turtle breeding dynamics. In addition, breeding is influenced by climate anomalies (i.e. extreme *El Nino* events). This climate parameter could be adapted for sequential change over time to simulate the influence of climate change (e.g., where increasing frequency of harsh climatic conditions decrease breeding probability). Age-at-maturity, clutch frequency and clutch size were also variable across individuals. Based on comparisons to empirical data, our model matches observed patterns of population dynamics, in particular inter-annual variability in nester abundance and nester recruitment. The model can be modified for other sea turtle species and serve as an underlying “operating model” for simulation analyses to evaluate management and monitoring strategies (Piacenza et al. *in prep* and *Chapter 4*).

Our GSTABM builds on of previous sea turtle ABMs. Mazaris et al. (2005) introduced an ABM for Mediterranean loggerhead sea turtles that uses “super-individuals” throughout all life stages to improve model run times. Later ABM versions included a parameterization for green sea turtles, and examined the influence of environmental variability and age-dependent mortality, respectively (Mazaris & Matsinos 2006, Mazaris et al. 2006). Similar to those authors, we employed super-individuals to represent the earliest pelagic life stages. Interestingly, Mazaris et al. (2005) found that the probability of persistence (i.e. extinction risk) depends most on fecundity and survival rate of the youngest life stages, which is counter to many other sea turtle demographic studies (Crouse et al. 1987, Crowder et al. 1994, Heppell et al. 1996, Heppell 1998). The authors suggest that stochastic events and individual variability in their ABM could explain this difference in results. Mazaris and Matsinos (2006) included density dependence, where the high abundance of immature and mature turtles results in a reduction in somatic growth and reproduction. This form of density dependence increased extinction risk in their simulation experiments. While the work of Crouse et al. (1987), Crowder et al. (1994) and Heppell et al. (1996,1998) suggested that changes in survival rates of large juvenile and sub-adult sea turtles would have the biggest proportional effect on population growth, and indeed the GSTABM is most sensitive to those survival rates, our model shows that when nest impacts occur, either alone or in conjunction with adult removals, important time lags occur in abundance and nester recruitment which can obscure the accuracy of population assessments. Overall, ABMs for sea turtles reveal unexpected patterns and relationships that may be obscured in other modeling frameworks.

It is clear from our results that variability at the nesting beach does not reflect variability in adult populations of green sea turtles, and even less so the total population variability. Our finding is supported by suggestions from sea turtle working groups and statisticians that have evaluated nesting beach trends (Magnuson et al. 1990, Gerrodette et al. 1999, Bjorndal et al. 1999, 2010, Hays 2000, Chaloupka 2001, 2002, Solow et al. 2002, Heppell et al. 2003, Turtle Expert Working Group 2007, 2009, Chaloupka & Balazs 2007). Nester abundance tends to mirror the adult trends during the impact and recovery phases, but the magnitude of variability is much greater, which translates into much greater uncertainty in assessing population size and trends. Population estimates drawn from observed nesters and nests may obscure true population trends and uncertainty in the estimates could yield either overly pessimistic (higher extinction risk) or optimistic (recovery targets met prematurely) conclusions, particularly when nesting frequency is stochastic or cyclical. Surprisingly, increasing detection from 10% to 90% of nesters did little to improve accuracy of estimated adults. As monitoring nesting beaches is an imperfect mirror of the true adult trend, increasing detection only results in modest gains in accuracy when using nesting beach data to estimate adult abundance. Nester recruitment, on the other hand, did show improvements in accuracy with increasing detection. The worst conservation error is to conclude that a population is faring well, when in fact is it declining (Taylor & Gerrodette 1993); however, under-estimating population size can cause undue restrictions on stakeholders, such as overly restrictive bycatch limits. Care should be exercised when using data from sea turtle nesting monitoring programs to assess adult abundance, without any other population indicators, such as nester recruitment, breeding probability changes, and size-distributions over time.

In our GSTABM, the accuracy of estimating nester recruitment depends on the underlying impact history (and subsequent alterations in age structure). This is concerning, given the importance of this vital rate in providing context to changes in nester and nest abundance, such as lending support to hypotheses that an increase in nester abundance is due to increased recruitment to the rookery, changes in breeding periodicity, or an increase in the adult population (Bjorndal et al. 2010). In addition, nester recruitment has long lag times during the impact and recovery phases, and, potentially even direct monitoring of nester recruitment from the nesting beach, could lead to spurious conclusions towards that overall status of the population. To accurately assess patterns in nester recruitment by monitoring nesters, direct measures of recruitment (e.g.,, physical or physiological indicators, Hamann et al., 2003) and/or a longer time series are necessary, and should be viewed in the context of short-term and long-term impacts to the population that may be influential.

The GSTABM predicts that a population subjected to 50 years of a relatively low impact, ~7% of sub-adults and adults removed annually, would take over 100 years to reach a full recovery back towards quasi-stable level prior to the impact. When hatchlings are disturbed (either alone or in conjunction with sub-adults and adults), the recovery time line is even longer, because of demographic time lags. As green sea turtles can take ~ 30 years to reach sexual maturity (Zug et al. 2002, Balazs & Chaloupka 2004a, Van Houtan et al. 2014), it is not surprising that recovery would be prolonged. However, such a long recovery period is unexpected and suggests at least 4 generations are needed to reach ecological recovery. In addition, because of delayed maturity, it would take the age structure a long time to “fill in” and recover after a sustained impact phase (White et al. 2013). Green sea turtles were listed on the endangered species list in 1978 (NOAA Office of Protected Resources 2011), more than 30 years ago, but this suggests that green turtles are still in the initial phase of recovery. While no estimates of green sea turtle abundance prior to commercial harvest exist, they were likely quite abundant (Balazs 1980, Kittinger et al. 2013, Van Houtan & Kittinger 2014). Prior to commercialization, sea turtle harvest in the Hawaiian Islands was regulated by native Hawaiian social laws, but European colonialists were known to harvest more intensively, and the Hawaiian social restrictions on sea turtle harvest began to erode in the 1800s (Balazs 1980, Witzell 1994). In a historical reconstruction of green sea turtle exploitation in Hawaii in the 20th century, the commercial fishery was small-scale with limited production and had a localized market, but even with relatively low exploitation, fisheries dependent data suggest serial progression, spatial expansion and shifts in fishing gears to meet demand – all signs of over-harvest (Van Houtan & Kittinger 2014). Our model mirrors this as a relatively small impact rate to sub-adults and adults results in a dramatic decline and recovery pattern that fell in line with nesting data from Hawaii. If Hawaiian green sea turtles are allowed to continue on the current recovery trajectory, with no other major impacts to population growth, it is plausible that population size will continue to increase for quite some time.

We present a simple analysis of annually varying levels of detection probability that clearly illustrates the chasm between data collected on the nesting beach and the true number adults. We made the simplifying assumption that average detection probabilities were constant over time and independent of other variables. Yet, this is a simplification of how sea turtle monitoring occurs. Detection probabilities often show trends over time (Pfaller et al., 2013), and can vary within seasons (Piacenza et al. *In review*) or could potentially be dependent on the size of the nester population (i.e. observer saturation). In addition, in the GSTABM the monitoring sub-model randomly samples, with error, all available nesters each year. However, most sea turtle monitoring occurs on discrete stretches of beaches, i.e. index beaches, and does not randomly sample from all possible nesters; as sea turtles have a measure of nest site fidelity not all nesters are equally prone to monitoring (Tucker, 2010). These facets of sea turtle monitoring further occlude the relationship between the estimated and true population size. In reality, the relationships of estimated adult population from observed nesters or nests are probably much more complex. Additionally, we made the simplifying assumptions that vital rates (breeding probability and clutch frequency) and detection probabilities could be accurately estimated from field data and were constant over time. This is not a trivial assumption, as most sea turtle monitoring programs, especially those that monitor only nests, cannot accurately estimate breeding probability and clutch frequency. This assumption further simplifies the relationship between true and estimated adult abundance, and in reality estimating adults from observed nesters and nests is probably much more inaccurate. Further work, using the GSTABM as an operating model with realistic monitoring functions, to assess which monitoring strategies provide the most accurate population assessments should help to clarify these concerns.

Conclusions

In summary, the similarity of our predictions from the GSTABM with observed patterns suggests that the model is a faithful representation of green sea turtle population dynamics and that it can be a used as a tool for sea turtle biologists and managers. Additionally, because the GSTABM simulates population impact and monitoring processes, it is an important tool to determine relationships with monitoring, population assessment, and changes in the underlying biological processes driving changes in the population, and especially, changes on the nesting beach. Future work will examine in detail how changes in biological processes can influence population assessments drawn from data collected from nesting beaches.

Finally, in simulating population dynamics, population modelers typically use many replicates to represent the variability and uncertainty in outcomes. However, in reality most biologists and managers are focused on one single population, and are thus are only working with one single population trajectory, with a particular harvest legacy and demographic time lags dependent on how the age structure was disturbed. Without knowing the underlying biological processes driving changes in observed nesters or nests, it is impossible to determine where a population falls in the schema of monitored data to true population size (i.e. Fig. 3.10), in other words we cannot know if a population is being over- or under-estimated. However, important clues can be gleaned by understanding differential impacts to age classes and subsequent recovery, and monitoring vital rates, such as breeding probability, clutch frequency, and age-at-maturity.

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Table 3.1 Summary of state variables in the agent-based model of green sea turtle population dynamics.

Variable Name	**Description**	**Mean (Range) or States**	**Units**	**Statistical Distribution**
Age	Age in years	(0-85)	years	-
Age Class	Development stage	Hatchling, Pelagic Juvenile, Neritic Juvenile, Sub-adult, Neophyte, Adult	-	-
Age-at-maturity	Age individual reaches sexual maturity	30 (17 – 41)	years	Poisson
Clutch Frequency	Nests laid during reproductive season	4 (1 – 8)	nests	Poisson
Clutch Size	Potential number of eggs laid per nest	43 (5 – 87) (8; 1 - 16 super-individuals)	eggs	Poisson
Reproductive Status	Indicates if individual nested at given time step	nester / non-nester	-	-
Hatchlings Produced	Realized number of eggs laid across all clutches in a given reproductive season, based on Ricker density dependent type function	103 (0 – 187) (19; 0 – 34.7 super-individuals)	eggs	-
Remigrations	Number of years between nesting seasons	2.4 (2 - 17)	years	-
Times-nested	Total number of nesting migrations in lifetime	3.2 (0 – 32)	nesting seasons	-

Table 3.2. Summary of parameter information used in the agent-based model of green sea turtle population dynamics. SD = standard deviation, CV = coefficient of variation.

Parameters	Value	Reference	Notes
Age Classes			
Hatchling	Ages 0 - 1	Balazs and Chaloupka, 2004; Bjorndal et al., 2013; Van Houtan et al., 2014; Zug et al., 2002	
Pelagic Juvenile	Ages 2 -3		
Neritic Juvenile	Ages 4 - 10		
Sub-adult	Age 11 - < Age Maturity		
Neophyte	Age Maturity		
Adult	> Age Maturity – Age 85		
Annual Survival			
Hatchling	0.350	Van Houtan et al., 2014, Piacenza et al. *In Review*	based on long-term MSORD mark-recapture analysis
Pelagic Juvenile	0.800		
Neritic Juvenile	0.824		
Sub-adult	0.876		
Neophyte	0.929		
Adult	0.929		
Breeding Probability	0.2519 (SD = 0.0127), gamma distribution (α=4.80124, β=19.06008)	Piacenza et al. *In Review*	based on long-term MSORD mark-recapture analysis
Scale factor	5.4		scaling factor used to reduce the raw number of hatchlings and pelagic individuals into super-individual groups, fit based on lifetable analysis
Clutch Frequency	4 (SD = 4)	(Tiwari et al., 2010; Piacenza et al. *In review*	
Clutch Size	8 (SD = 8)	(Niethammer et al. 1997)	values for super-individual groups
Intrinsic rate of increase (*r*)	0.15		intrinsic rate of increase for Ricker function for hatchling production, calibrated internally

Table 3.2 (Continued). Summary of parameter information used in the agent-based model of green sea turtle population dynamics. SD = standard deviation, CV = coefficient of variation.

Parameters	**Value**	**Reference**	**Notes**
Hatchling production carrying capacity ($K_{nesters}$)	500		Carrying capacity for nesting beaches, calibrated internally
Hatchlings Produced	$HP_t = (CS \bullet CF)e^{(r(1-(\frac{Nesters_t}{K_{nesters}}))}$	(Niethammer et al. 1997)	density-dependent function
Removal function	$TR_t = SA_t + A_t \cdot F$		
Removal rate (F)	Age 11+: 6.67% Nests: 50% Nests:25%, Age 11+: 3.33%		occurs for 50 years, calibrated internally
Detection probability (p)	0.1, 0.5, 0.90 (CV=2),	Pfaller et al., 2013; Phillips et al., 2014, Piacenza et al. *In review*	

Table 3.3. Initial conditions for green sea turtle age structure.

Age Class	**Ages**	**Initial Abundance**
Hatchlings	0 - 1	499,311 / scale-factor
Pelagic Juveniles	2 - 3	508,129 / scale-factor
Neritic Juveniles	4 - 11	161,297
Sub-adults	12 - Age-at-maturity	73,388
Neophytes	Age-at-maturity	1,416
Adults	> Age-at-maturity	18,909

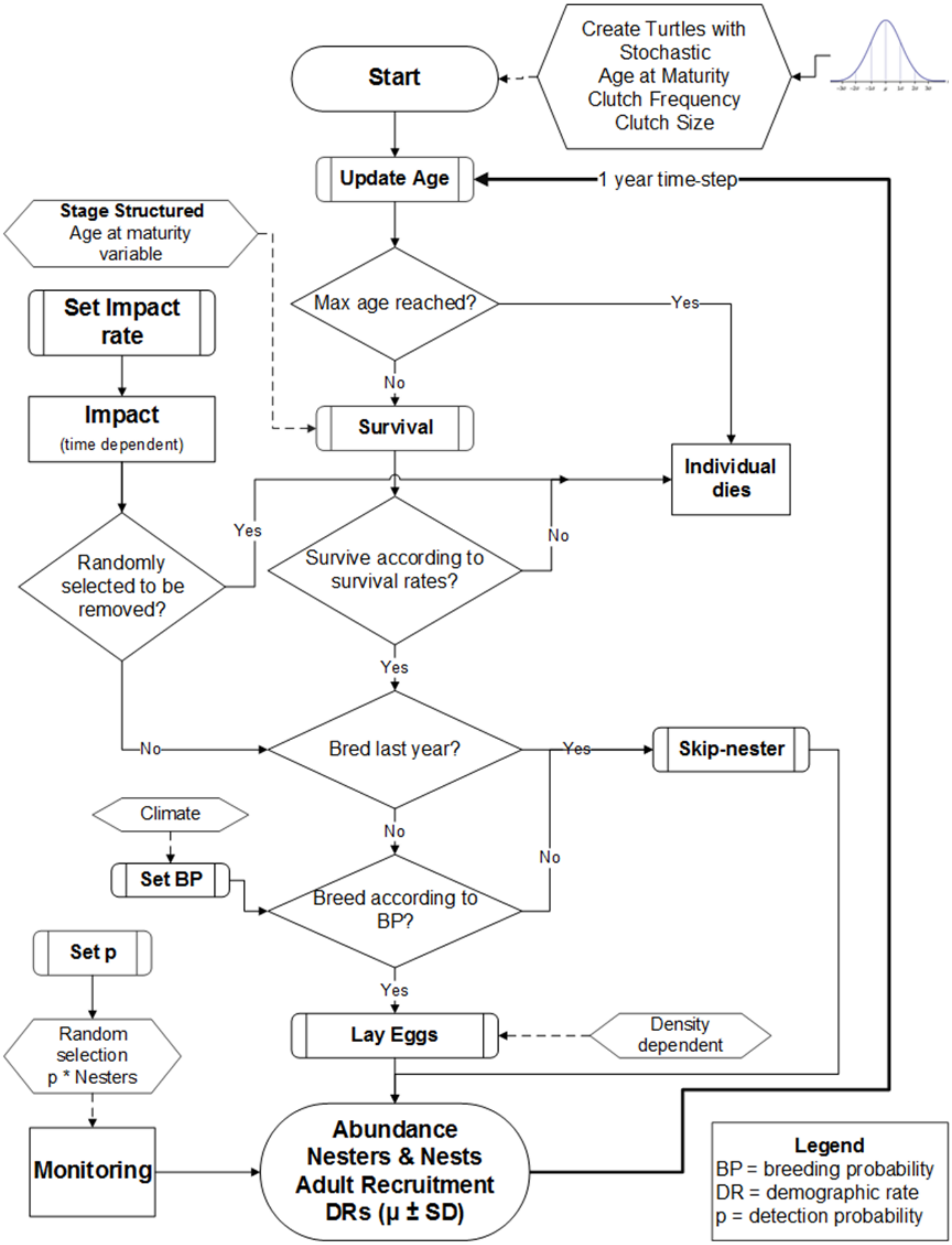

Figure 3.1. Conceptual diagram of model processes for the agent-based model of green sea turtle population dynamics.

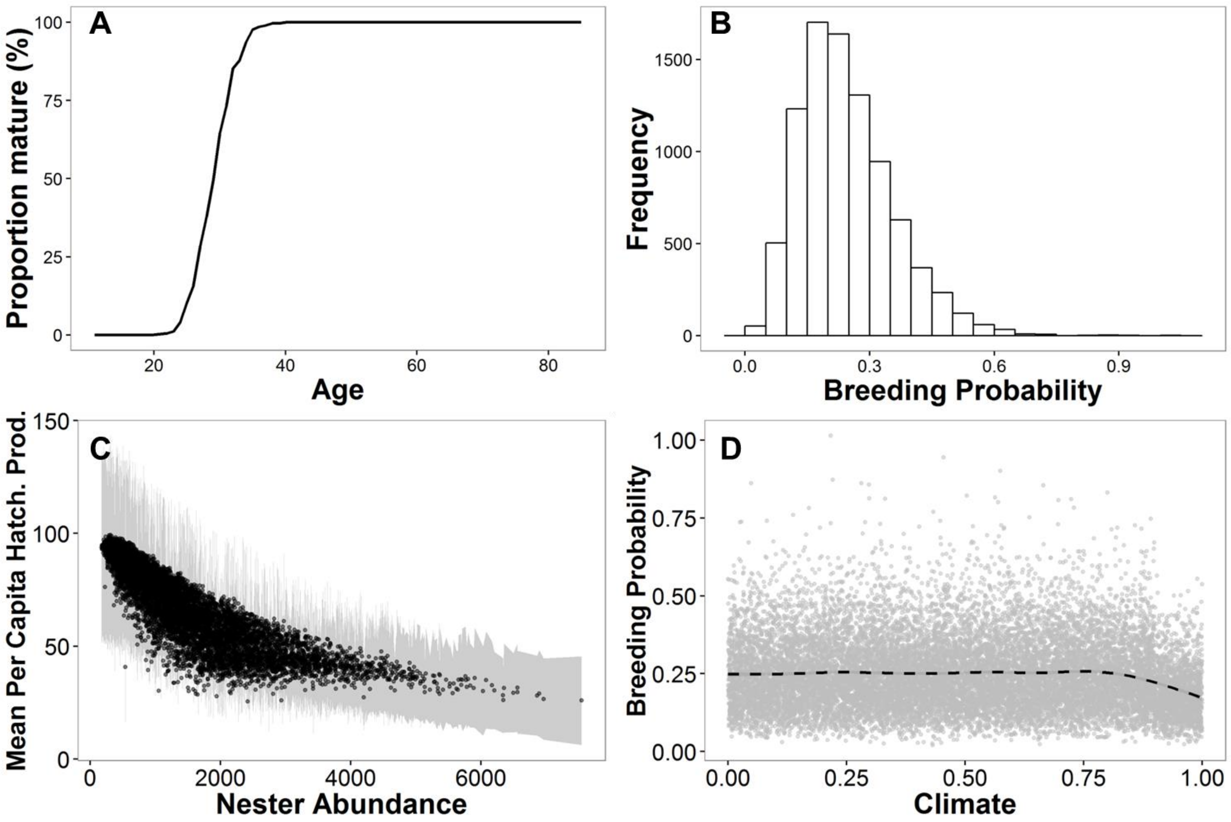

Figure 3.2. Green sea turtle agent-based model sub-processes. (A) Cumulative frequency of mature sea turtles as a function of age, (B) frequency of annual breeding probability as drawn from a truncated gamma distribution, (C) hatchling density-dependent production by nester abundance (the black points are the mean hatchling production at each time-step across 50 model replicates and the shaded area is the 95% confidence interval and (D) Influence of the climate parameter on breeding probability (gray points are raw data and the dashed line indicates mean breeding probability as a loess function of climate). Output is for all model runs time-steps 175-350.

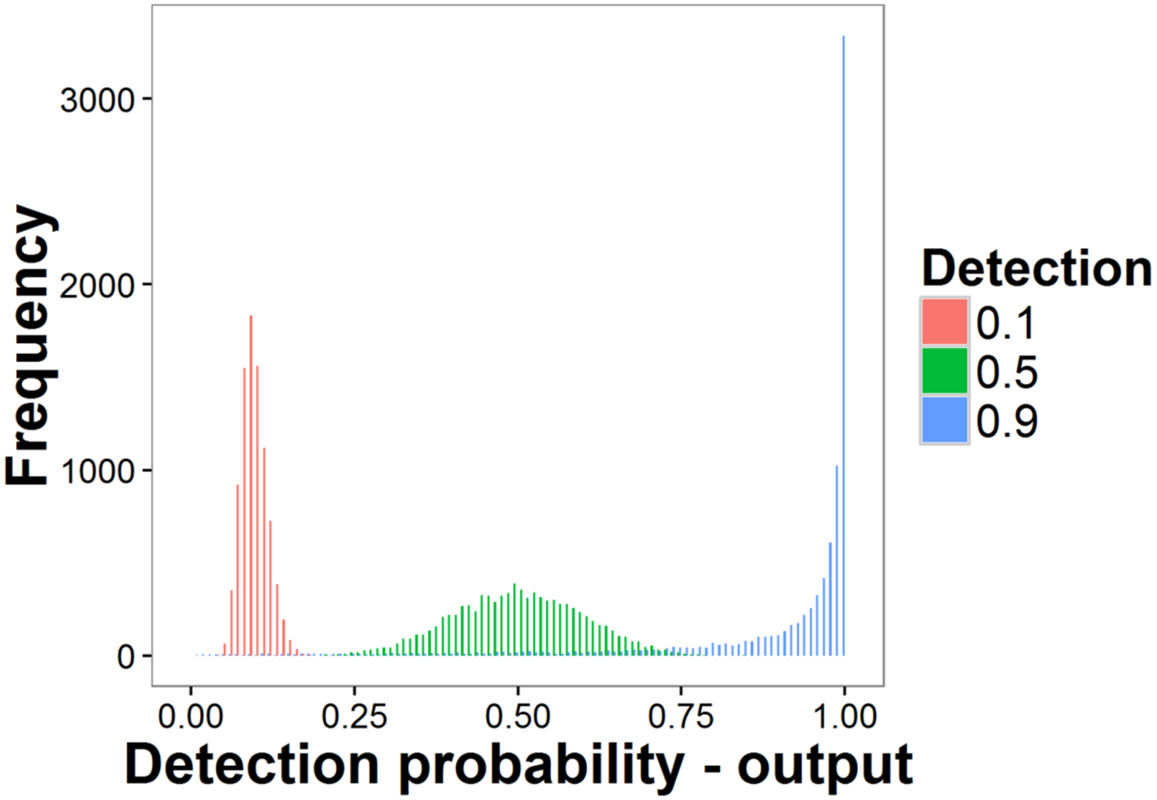

Figure 3.3. Realized detection probabilities for the three experimental mean inputs (*p* = 0.1, 0.5, and 0.90). Detection is a stochastic parameter with a logit-normal distribution. Standard deviation of the three mean inputs was scaled based on coefficient of variation (CV = 0.2). Output is for all model runs time-steps 175-350.

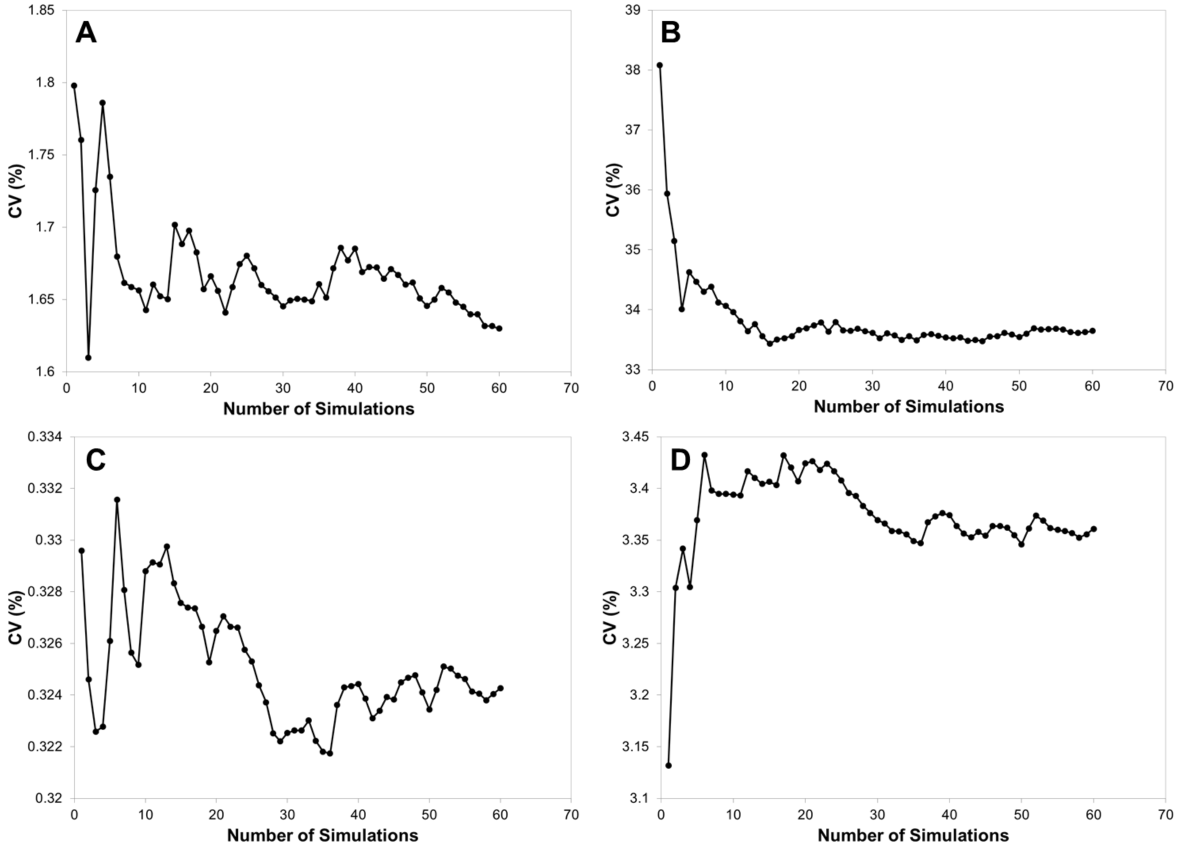

Figure 3.4. Number of simulations needed to reach quasi-stabilization in the percent coefficient of variation (CV) of (A) adult abundance, (B) nester abundance, (C) discrete population growth rate, and (D) nester recruitment. Approximate consistency (the initial drop in CV after in the CV was achieved after ~ 30 simulations across all four output variables.

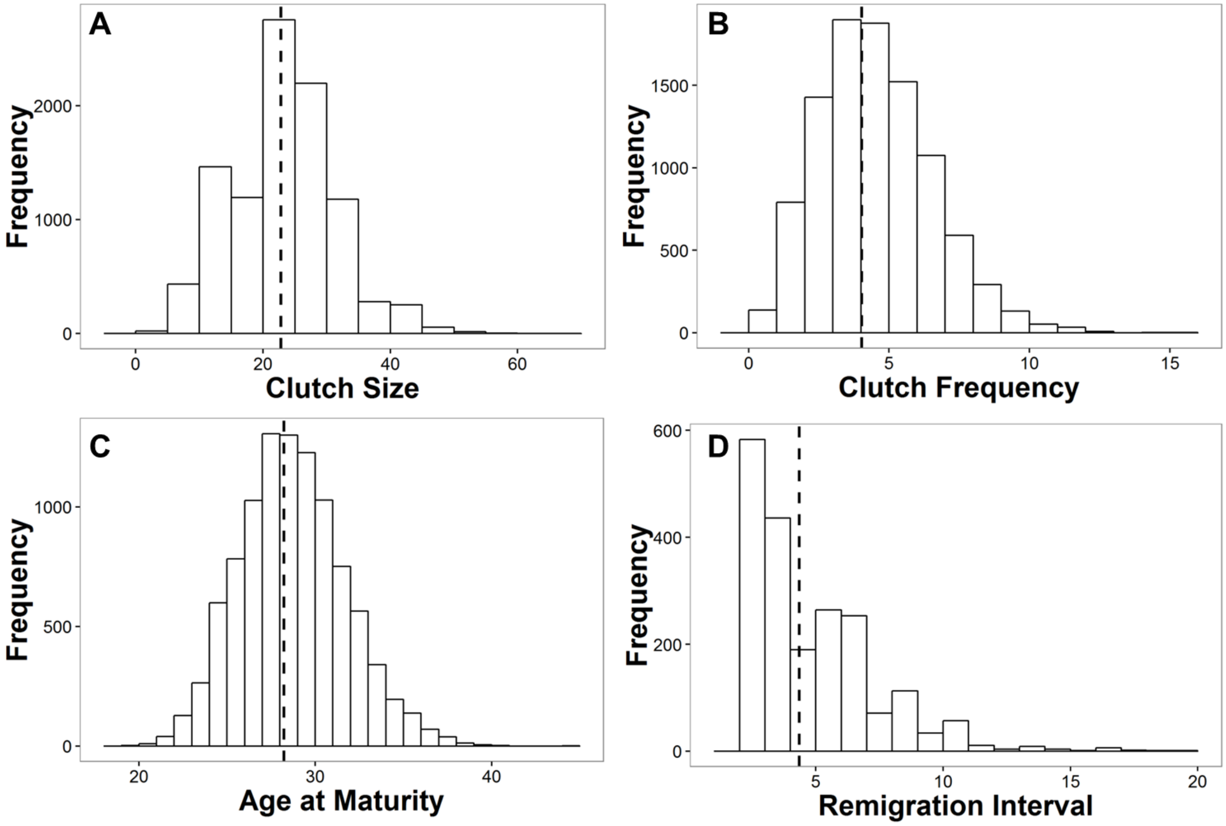

Figure 3.5. Realized frequency distributions of the four main individually variable life history traits. (A) Clutch Size, (B) Clutch Frequency, (C) Age-at-Maturity, and (D) Remigration Interval. The vertical dashed lines indicate the mean value. Clutch size, clutch frequency, and age-at-maturity are stochastic variables drawn from a Poisson distribution. Remigration interval emerges based on the annual breeding probability and non-nester behavior. Individual-based data are for all individual adults from time-step 350 for 1 model run. Remigration interval was analyzed from individual veteran nesters.

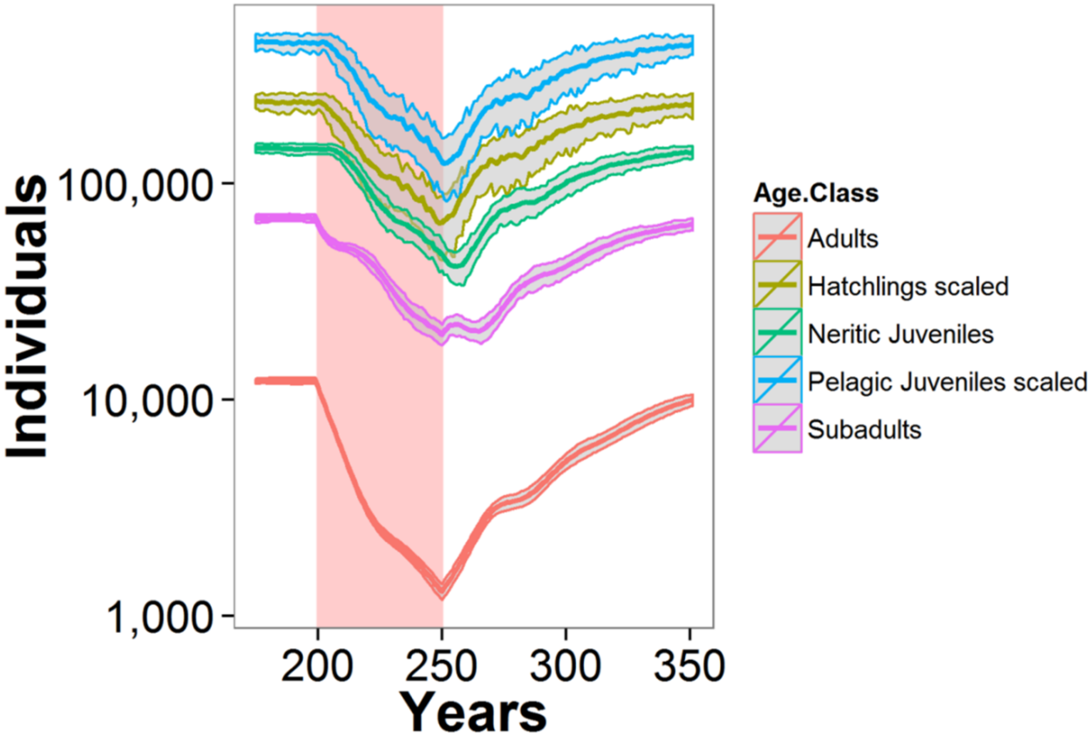

Figure 3.6. Female green sea turtle population size and structure simulated for 175 years and replicated 50 times. Colored lines indicate the mean size of the age classes and shaded areas indicate the 95% confidence intervals. The pink shaded area indicates the 50 year removal period of sub-adults and adults, simulating intensified harvest of green sea turtles in Hawaii in the 20th Century.

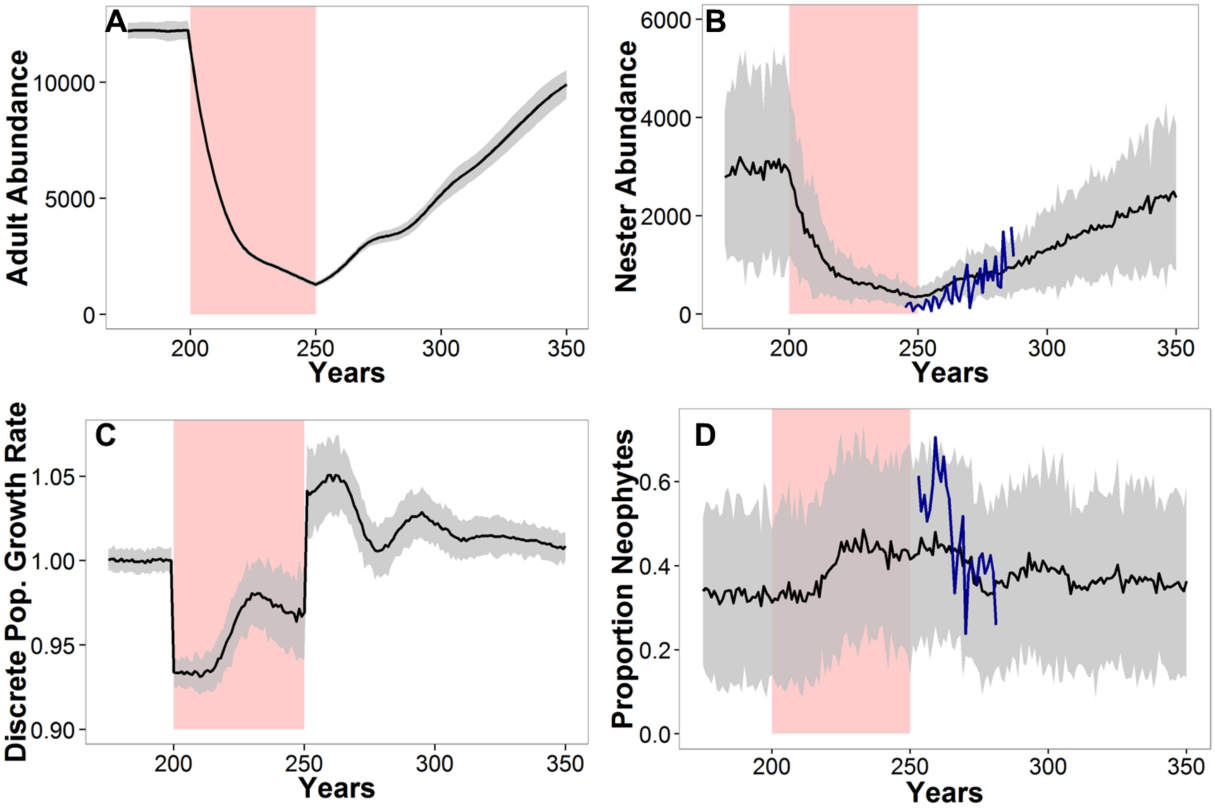

Figure 3.7. Emergent population level processes were evaluated over 175 years, with three distinct phases. (A) Adult abundance, (B) nester abundance, (C) discrete population growth rate, and (D) nester recruitment. Population trajectories are: Stable (years 175-199), Impact (years 200-250; 6.67% sub-adults and adults removed year^{-1}), and Recovery (years 251 – 350). Black lines show the mean value with confidence limits (95%) in gray, the pink shaded area indicates the 50 year impact phase. In (B), the blue line indicates the observed nester abundance in the Hawaiian Islands, assuming 50% of nesting occurs at the main rookery in East Island. In (D), the blue line represents the observed proportion of neophytes (assumed from newly tagged individuals) in Hawaii.

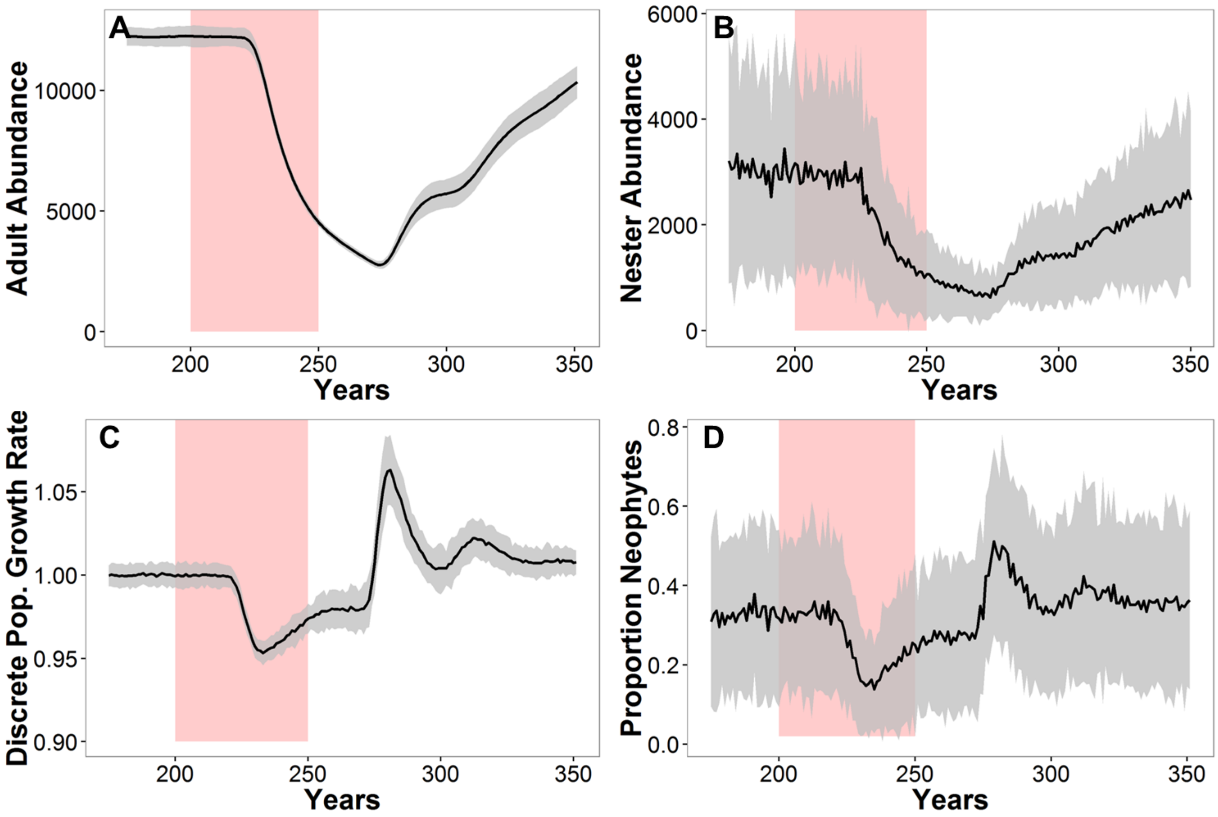

Figure 3.8. Emergent population level processes when nests are disturbed (50% removed year-1 for 50 years). (A) Adult abundance, (B) nester abundance, (C) discrete population growth rate, and (D) nester recruitment. Emergent processes were evaluated over 175 years, with three distinct phases: Stable (years 175-199), Impact (years 200-250), and Recovery (years 251 – 350). Black lines show the mean value with confidence limits (95%) in gray, the pink shaded area indicates the 50 year impact phase.

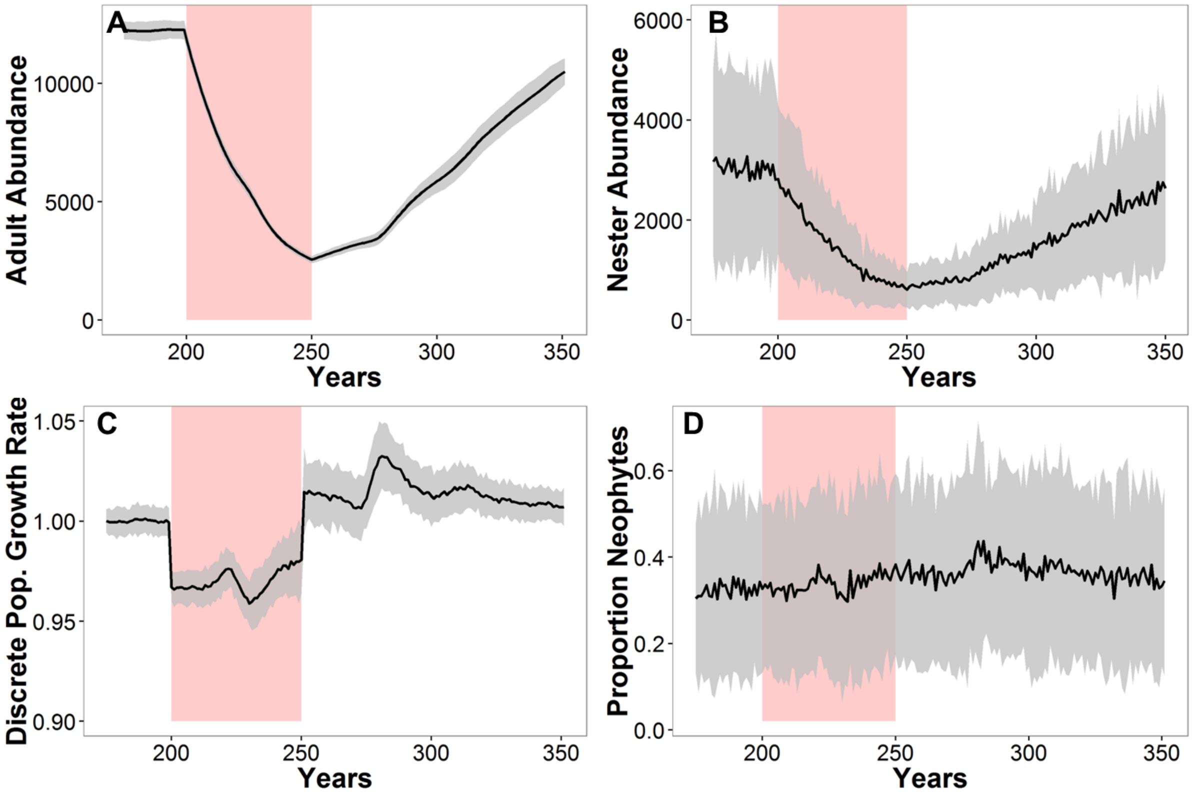

Figure 3.9. Emergent population level processes when nests, sub-adults, and adults disturbed (25% nests and 3.33% sub-adults and adults removed year-1 for 50 years). (A) Adult abundance, (B) nester abundance, (C) discrete population growth rate, and (D) nester recruitment. Emergent processes were evaluated over 175 years, with three distinct phases: Stable (years 175-199), Impact (years 200-250), and Recovery (years 251 – 350). Black lines show the mean value with confidence limits (95%) in gray, the pink shaded area indicates the 50 year impact phase.

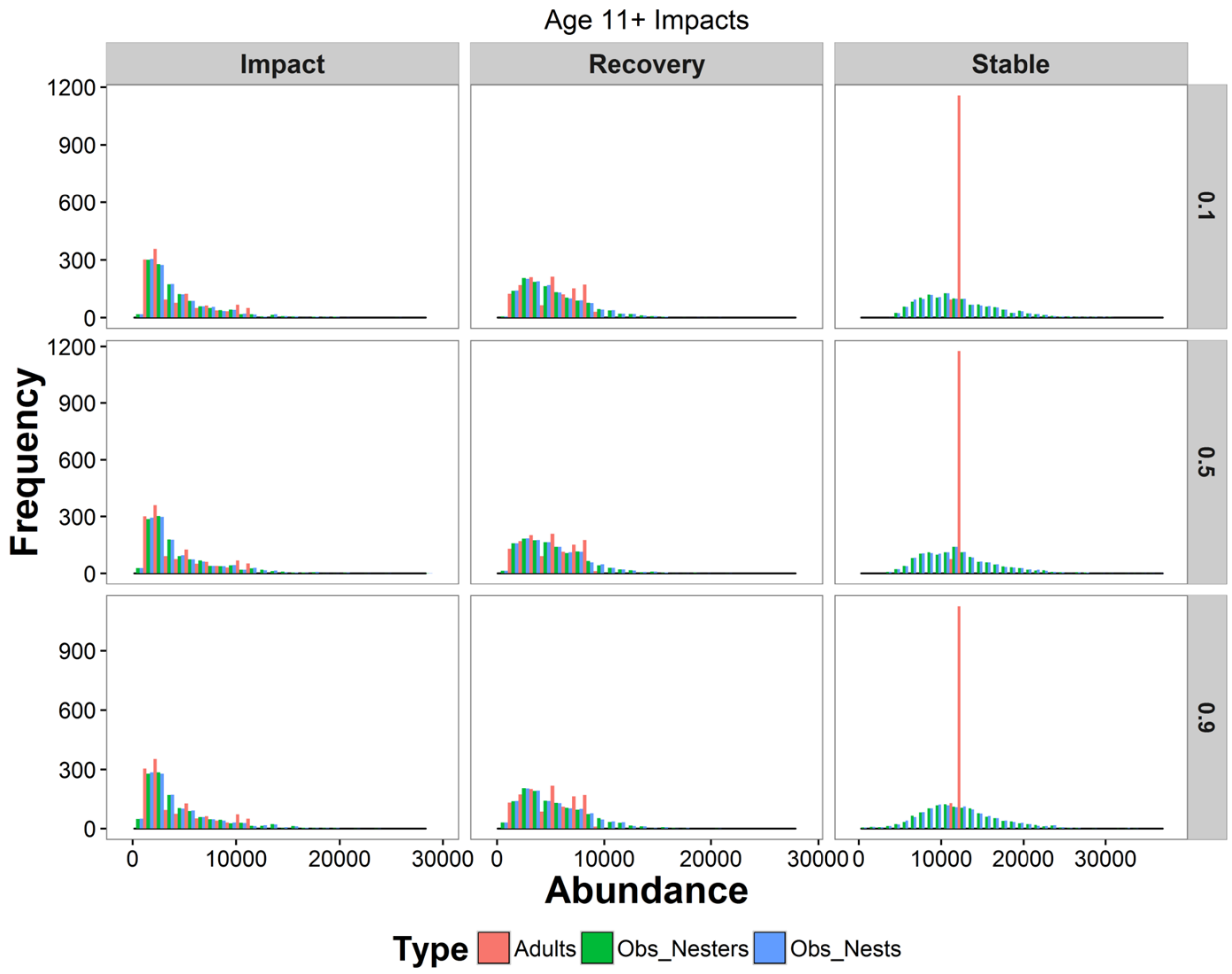

Figure 3.10. Frequency distributions for true and estimated adult abundance with sub-adult and adult impacts. 6.67% of sub-adults and adults were removed annually for 50 years. Detection levels varied with a mean of 0.1, 0.5, and 0.9. The axes were allowed to change between figures to improve visualization.

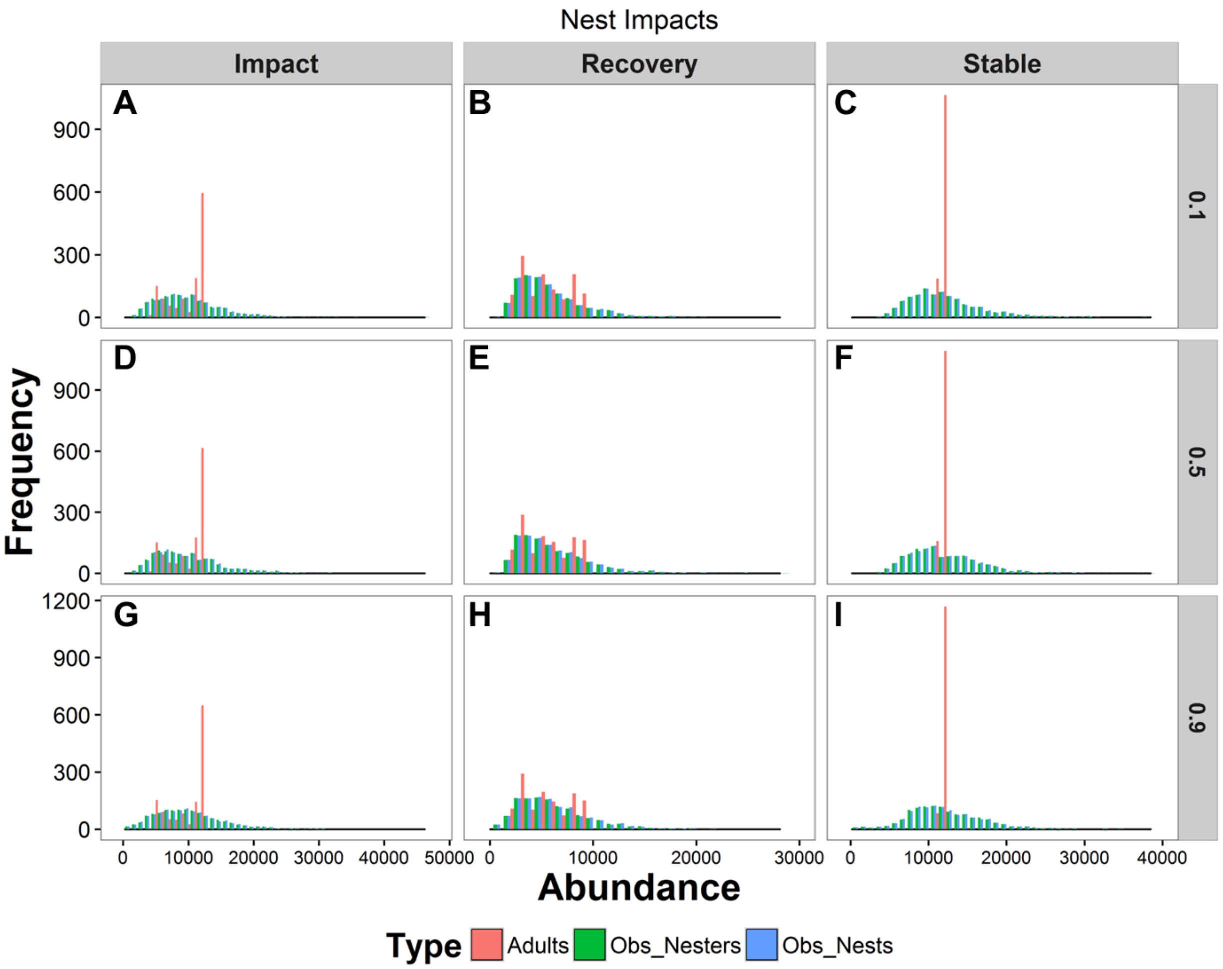

Figure 3.11. Frequency distributions for true and estimated adult abundance with nest impacts. 50% of nests were removed annually for 50 years. Detection levels varied with a mean of 0.1, 0.5, and 0.9. The axes were allowed to change between figures to improve visualization.

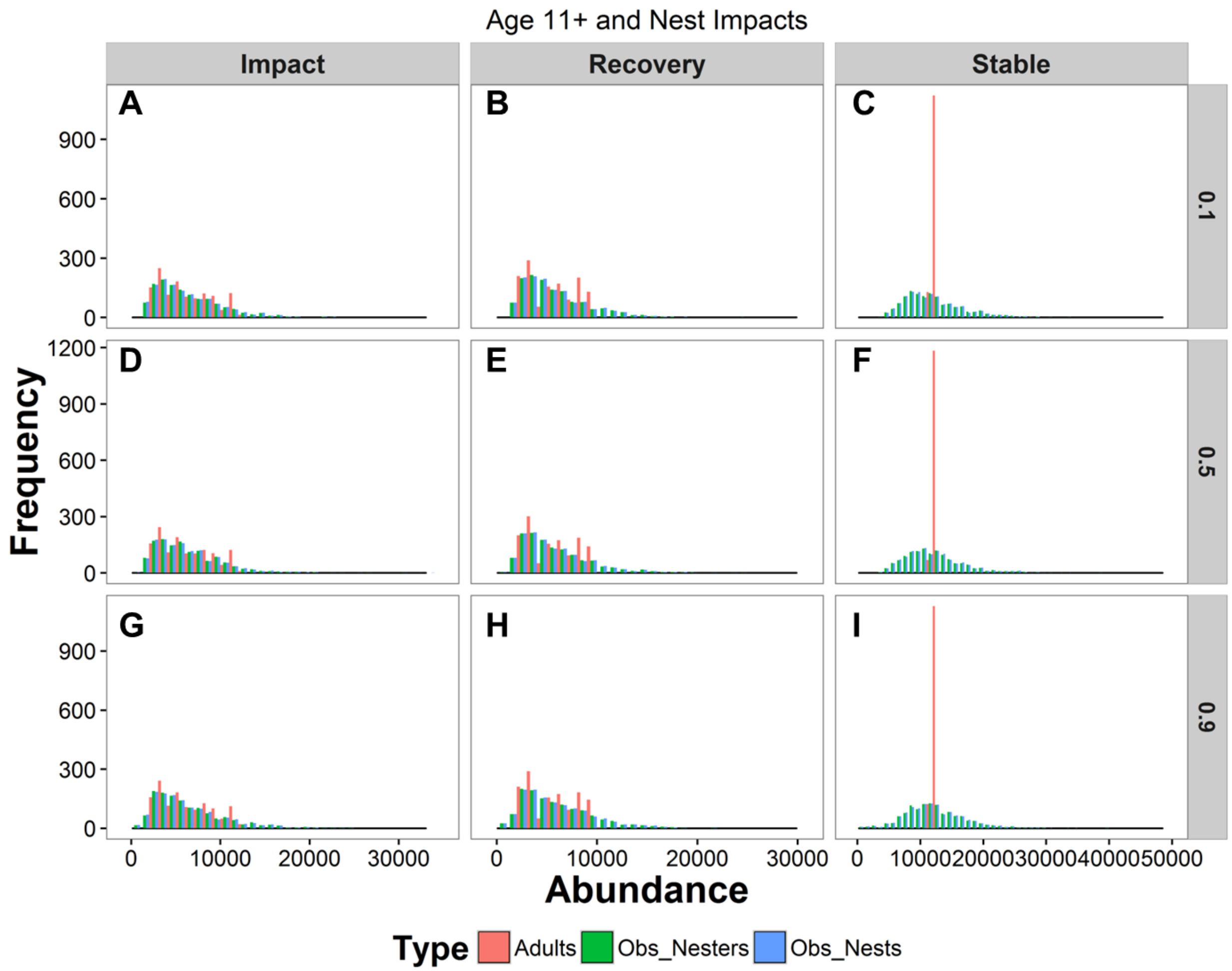

Figure 3.12. Frequency distributions for true and estimated adult abundance with nest and Age 11+ impacts. 3.33% of sub-adults and adults and 25% of nests were removed annually for 50 years. Detection levels varied with a mean of 0.1, 0.5, and 0.9. The axes were allowed to change between figures to improve visualization.

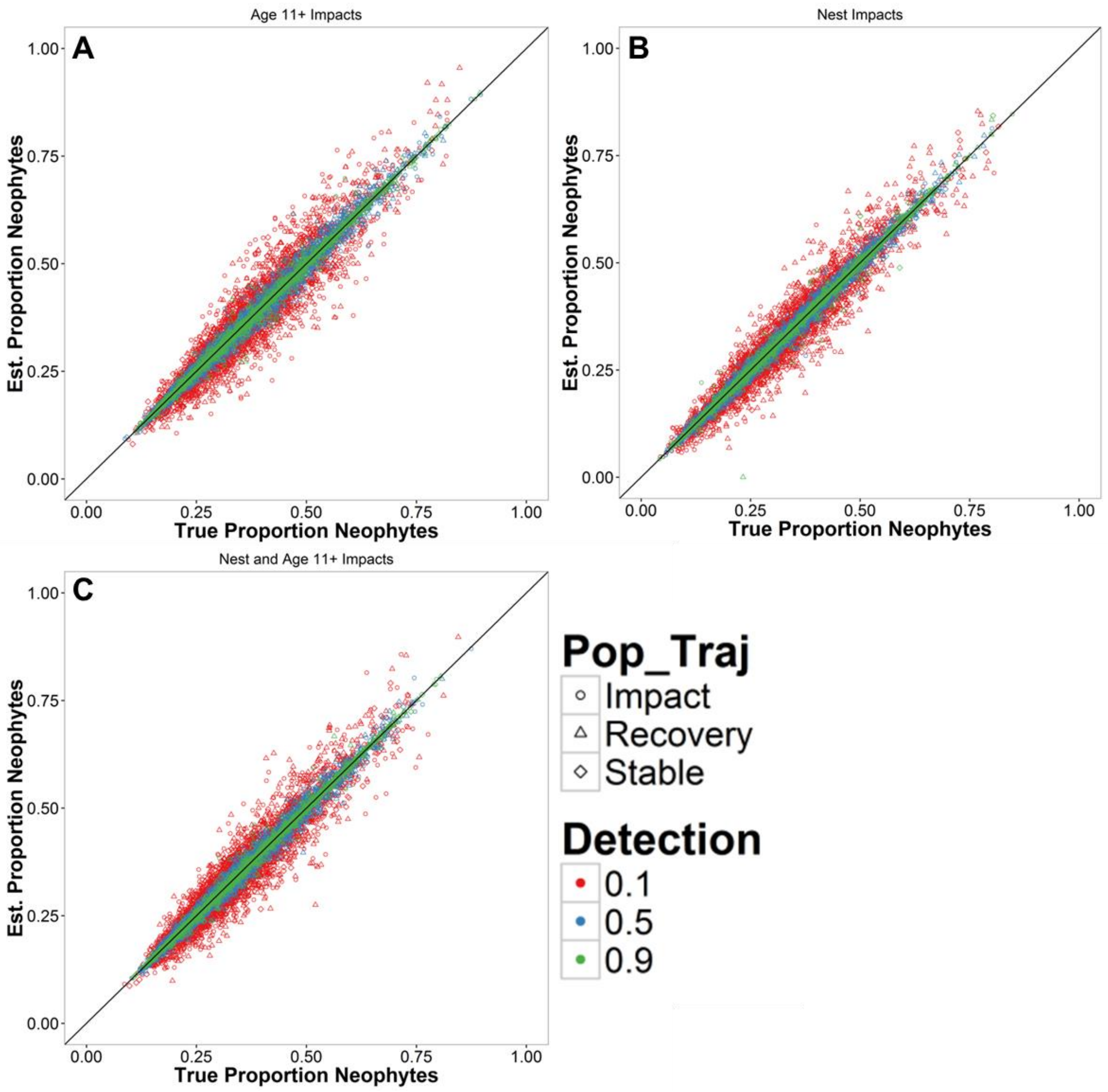

Figure 3.13. Estimates of nester recruitment drawn from observed nesters, with varying levels of detection probability, and different impact scenarios. (A), Age 11+ were removed (6.67% year^{-1} for 50 years), (B) nests were removed (50% year^{-1}), and (C) nests (25% year^{-1}) and Age 11+ (3.33% year^{-1}) were removed. The black line represents the 1:1 line between the true and the estimated nester recruitment. For improved visualization and to maintain equal sampling, 25 years were randomly selected from both the impact and recovery phases.

4 - Fathoming Baselines: A Monitoring Strategy Evaluation for Status Determination of Sea Turtles Populations

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In preparation for submission to Ecological Applications

ABSTRACT

Population monitoring must be accurate and reliable to correctly classify populations as endangered or recovering. Green sea turtles, *Chelonia mydas*, have endangered and threatened populations globally, but several nesting beaches have shown substantial increases in the number of nests or nesting females. Using sea turtle nesting beach surveys as a population index for assessment is problematic, yet pragmatic because they are often the only population indices that are easily accessible. Process and observation errors, compounded by delayed maturity, obscure the relationship between trends on the nesting beach and the population as a whole. We present a new simulation-based tool, Monitoring Strategy Evaluation (MoSE), to explore the relationships between monitoring data and assessment accuracy. Like its predecessor, Management Strategy Evaluation, MoSE has three main components: the simulated "true" operating model (an agent-based virtual population of sea turtles), an observation model, and an estimation model. To explore this first use of MoSE, we apply different treatments of population impacts, sampling, and detection of the virtual "true" population, and then sample the nests or nesters, with observation error, to test if the observation "data" accurately diagnose population status indicators. Based on the observed data, we estimate adult abundance, nester recruitment, and population trend and compare these indices to the known values from the operating model. We ran a series of scenarios with different process and measurement errors, including harvest impacts, cyclical breeding probability, and sampling biases, to see how these realistic factors impact accuracy in estimating status indicators that are based on constant demographic parameters or parameters that are measured annually. We also explored the necessary duration of monitoring for accurate trend estimation. Disturbance type and severity can have important and persistent effects on the accuracy of population assessments drawn from monitoring rookeries.

Accuracy in abundance estimates may be most improved by avoiding clutch frequency bias in sampling and including annually varying (versus constant) breeding probability, detection probability, and clutch frequency in the estimation model. Accuracy of proportion of neophytes may be most improved by increasing detection level and avoiding age-bias in sampling. The accuracy of estimating population trend is influenced by the underlying population trajectory, age classes disturbed and disturbance severity. At least 10 years of monitoring data are necessary to accurately estimate population trend, and longer if juvenile age classes were disturbed and trend estimates occur during the recovery phase. The MoSE is an important tool for sea turtle biologists and conservation managers because it allows biologists to make informed decisions regarding the best monitoring strategies to employ for sea turtles

4.1 INTRODUCTION

Population monitoring must be accurate and reliable for biologists and conservation managers to correctly classify populations as endangered or in recovery. In addition, monitoring data is an important indicator of whether management actions are effective, but the data must be reliable. Many endangered species are often considered data-poor or have low encounter rates with monitoring programs that may obscure true population trends (Colyvan et al. 1999, Akçakaya et al. 2000). In long-lived, migratory species, where monitoring can only occur on particular demographic classes for short periods of time, monitoring may only give a narrow view into population, and indices may give a false signal of abundance and population trend, especially during unstable periods (Maxwell & Jennings 2005, Taylor et al. 2007, Singh & Milner-Gulland 2011, Lynch et al. 2012). If monitoring yields inaccurate data and the subsequent population assessments make false interpretations of population size and trends, conservation errors may ensue. There are two main kinds of conservation errors: to conclude a population is threatened when in fact it is not and to conclude a population is not threatened when in fact it is; both kinds of error have biological, economic and societal consequences (Taylor & Gerrodette 1993, Snover & Heppell 2009). In all, biologists and managers need to exercise caution when interpreting population indices from monitoring, particularly when those interpretations have strong management implications. Certain analytical tools may help to clarify relationships between observed and true population abundance, recruitment and trends.

Sea turtles are globally threatened taxa, with some populations in recovery from overexploitation while others continue to decline (Chaloupka et al. 2008, Wallace et al. 2011, IUCN 2015). The life history of these species complicates monitoring. Sea turtles are long-lived, late-maturing, highly migratory, and spend most of their life offshore. With late maturity comes temporal lags in recovery, and the length of those time lags depend on the age classes disturbed and how conservation benefits survival of those age classes. The duration of the time lags ultimately may have important implications for monitoring and assessment (Crowder et al. 1994, Heppell et al. 1996, Koons et al. 2005, White et al. 2013). Most sea turtle monitoring is conducted at nesting beaches, where nests or individual female nesters are counted. But, females do not breed annually and may be decades old at first nesting, so just a tiny fraction of the total population is monitored (Crouse et al. 1987). Nesting abundance typically displays large fluctuations inter-annually, likely due to variability in breeding frequency and environmental conditions, but these fluctuations do not necessarily reflect true changes in the adult population (Piacenza et al. *In review,* Hays 2000, Solow et al. 2002). It is uncertain how accurate the extrapolations from nesting beach indices are for estimating population abundance, recruitment, and population trends (Hays 2000, Bjorndal et al. 2010, Richards et al. 2011). Considering that most sea turtle populations are in demographic flux, and transient behaviors in structured populations can have opposing responses for some demographic classes during the impact and recovery phases, it seems likely that population assessments are inaccurate when based on monitoring from beach surveys (Crowder et al. 1994, Hastings 2001, 2004, Koons et al. 2005, White et al. 2013). True population dynamics may further be obscured when monitoring only observes reproductive classes, i.e. nesters and nests.

Beach surveys, however, are often the only way biologists can encounter sea turtles to measure abundance, as in-water surveys can be cost prohibitive and often have very low encounter rates. Can we optimize monitoring on the nesting beach to give the most accurate data on population size, recruitment and trends over time? In a recent report of the National Research Council (NRC), the authors recommended a tiered approach to nesting female abundance counts on beaches spanning a spectrum of data scope and monitoring (Bjorndal et al. 2010). But are these recommendations too expensive and too time consuming for government agencies, academics, and non-profit monitoring groups to implement? Given the effort and time spans involved in monitoring sea turtles, prognostic evaluation of monitoring options is important so that research groups can decide in advance how to optimize monitoring efforts on nesting beaches (*sensu* Heppell and Crowder 1998).

To address these issues, we developed a new tool to explore the effects of different kinds of monitoring data, and their realistic uncertainties, on population response predictions: Monitoring Strategy Evaluation (MoSE). We based this tool on Management Strategy Evaluation (MSE), a simulation-based framework developed in fisheries science (Smith et al. 1999). Management Strategy Evaluation was developed to evaluate trade-offs in alternate management schemes and to assess the consequences of uncertainty for achieving management goals (Punt et al. 2014). MSE simultaneously considers three main aspects of the biological-management cycle: the biological system (operating model), the observation process, and population assessment and management (Sainsbury et al. 2000, Bunnefeld et al. 2011). In the MoSE, we use the same general approach of creating a biologically realistic virtual population for sampling, and then apply various uncertainties to the "data" collected from the operating model to see how interpretations of population status are affected by what data are obtained. The general framework can also be used to simulate management actions and the ability to detect their effects, such as a simulation based power analysis to examine the importance of time series length and measurement error (Taylor and Gerodette 1993). Our MoSE approach is novel in that it specifically experiments with monitoring and data uncertainty to determine the effect of different monitoring strategies on population assessments and how observation errors propagate to population assessment errors, such as inaccurate estimates of adult abundance, recruitment and population trend.

Our primary goal is to illustrate how the MoSE approach can provide advice on how to improving monitoring plans used to assess populations of sea turtles, using an agent-based model for green sea turtles (Piacenza et al. *In Prep, Chapter 3)* as the operating model and a series of simulated population conditions. We asked four primary questions:

(1) Given each biological and observation scenario, can we accurately estimate population size, recruitment, and population trend?

(2) How does time-series length affect the accuracy of these population status indicators?

(3) What are the probabilities of false positive and false negative trend diagnoses?

(4) Does the population structure and harvest legacy influence which monitoring strategy is best?

4.2 METHODS

Monitoring Strategy Evaluation: A New Tool

Our Monitoring Strategy Evaluation (MoSE) tool builds on the Management Strategy Evaluation framework to address concerns regarding monitoring effectiveness of sea turtles. While management strategy evaluation focuses on the entire cycle of biological system, monitoring, stock assessment and management, we simplify the cycle to examine the biological system, monitoring and population assessment (Fig. 4.1). Here we are most interested in the discrepancies of the population status indicators (PS_0; estimated population size, recruitment and population trend) from the true values obtained from the operating model (PS^*), dependent on the biological and impact state and monitoring approach employed.

The Operating Model – Simulating green sea turtle populations

We developed our MoSE tool using an agent-based model (ABM) – the green sea turtle agent-based model (GSTABM: Piacenza et al. *in prep, Chapter 3*), where individual sea turtles, with individual level variation in reproduction, survival, and age at maturation, are simulated and the process of observing and collecting data from sea turtle nesters and nests is simulated (Table 4.1 and Fig. 4.2). Simulating biological and observation data is advantageous in this effort for several reasons. First, we "know" the "true" state of the population as the biological model is simulated and can compare that to the state of simulated observed data. ABMs are also useful because they allow for explicit modeling of two independent sources of variability in simulated data: process and observation errors. ABMs simulate individual behaviors and therefore operate at the scale by which population dynamics and monitoring occur (Letcher et al. 1998, DeAngelis & Mooij 2005). ABMs were previously used for MSEs to evaluate multiple uses of ocean resources off the western coast of Australia and recreational fishing in Australia (McDonald et al. 2008, Gao & Hailu 2013). ABMs have been applied to sea turtles to study population viability, the influence of temporal variability and age-dependent mortality on populations dynamics, and to test different monitoring schemes for within season sampling to optimize monitoring season timing and duration (Mazaris et al. 2005, 2006, Mazaris & Matsinos 2006, Whiting et al. 2013). ABMs are particularly useful when studying the coupling of biological and monitoring models, as biological and monitoring complexity can both be incorporated, such as density-dependence, environmental forcing, sampling biases, and interannual variability in sampling.

The GSTABM creates individuals with variable age-at-maturity, clutch frequency, and clutch size (Fig. 4.2). Hatchling production is density dependent, and regulated by the nester population in a given year. Because individuals vary in their age-at-maturity, stage lengths of sub-adults vary across individuals (range for sub-adults: 6 – 31 years). Environmental variability is imposed with a random climate effect that reduces breeding probability by 25% every 10 years on average. The GSTABM also simulates annually varying breeding probabilities, which is a more accurate representation for green turtles, as they are obligate 1-year skip nesters, than how breeding probability is typically modelled in matrix projection models, for example. In turn, interannual variability in nesting abundance, characteristically observed in nesting populations, emerges in the model (Piacenza et al. *In Review (Chapter 2)*, Carr et al. 1978, Hays 2000, Solow et al. 2002). After initialization (years 0-174), the model follows this general timeline: stable population (175-199 time steps), impact (200-249 time steps), and recovery (250 – 350 time steps). The initialization period is discarded as the population is reaching quasi-stabilization in the population structure. Henceforth, we refer to the three main phases, stable, impact and recovery as the population trajectories. The stable phase represents the "control" period in which no harvest and variability in abundance and nesting is due to demographic and environmental stochasticity. We implemented the model in NetLogo 5.1.0 (Wilensky 1999). For complete details on model overview, design and details see Piacenza et al. *In Prep. (Chapter 3).*

The Observation Model - Simulating Population Monitoring

Details of the base population monitoring sub-model of the GSTABM are included in Piacenza et al. *In prep. (Chapter 3).* The input detection probability (*p*) is a random variable with a logit-normal distribution (Fig. 4.2D). We assume that variability was constant and proportional to the mean. We scale the standard deviation to the mean so that the standard deviation would be proportional to the mean across the experimental detection levels, based on the coefficient of variation (CV = 0.2) from estimated detection probabilities from a 29 year study of mark-recapture analysis of green sea turtles in Hawaii (Piacenza et al. *In review, Chapter 2*). Detection of nesters and nests in MoSE pertains to detection of nesters and nests within an entire population, not a specific nesting beach. The GSTABM collects data from the monitored-nesters agent set similar to output data collected on the population as a whole, including: observed nester abundance, observed nest abundance, observed nester recruitment, as well as data on the population level means and standard deviations of hatchlings produced per female, remigration interval, age-at-maturity, clutch frequency, clutch size, hatchling production, and total number of lifetime nesting seasons.

The Estimation Model – Simulating Population Assessments

Estimating Adult Abundance

To simulate population assessment, we estimated the total number of adults from monitored nesters, while assuming constant breeding probability and detection probability, such that:

$$\hat{A}_{t,obs.nesters} = \frac{Obs.Nesters_t}{BP \bullet p} \tag{4.1}$$

where $\hat{A}_{t,\ obs.nesters}$= estimated number of adults at time t, BP = breeding probability and p = detection probability. We followed a similar routine to estimate the total number of adults from monitored nests, while assuming constant breeding probability, clutch frequency and detection probability:

$$\hat{A}_{t,obs.nests} = \frac{Obs.Nests_t}{BP \bullet CF \bullet p} \tag{4.2}$$

where $\hat{A}_{t,\ obs.nesters}$= estimated number of adults at time t, and CF = clutch frequency. We assume BP, CF, and p could be accurately estimated from field data, but would be estimated as constants, as it is typically performed for sea turtle population assessments (Table 4.2 and Fig. 4.2; Turtle Expert Working Group 2007, 2009, Bjorndal et al. 2010). We based the parameter estimates on the known mean values from the operating model (Table 4.2 and Fig. 4.2). To test the improvement in accuracy of incorporating annual estimates of the input parameters, we also conducted the same estimation procedure using the known annual values of breeding probability, detection probability, and clutch frequency of sampled nesters from the operating model. During analysis, to maintain equal sample sizes for the three population trajectories, we randomly selected 25 time-steps (across all model replicates) from the impact and recovery phases (which both included >25 years), and the stable phase was composed of the first 25 years post-model initialization.

Estimating Proportion of neophytes

We defined nester recruitment as the proportion of first-time nesters, i.e. neophytes, in the nester population:

$$PN_t = \frac{Neophytes_t}{Nesters_t} \tag{4.3}$$

where PN_t is the proportion of neophytes at time t ($Neophytes_t$) in the nester population ($Nesters_t$). For the purposes of estimating nester recruitment, we calculated the estimated proportion of neophytes, from monitoring nesters, as the observed number of neophytes divided by total number of observed nesters, as in Eqn. 4.3.

Estimating Population Trend

We calculated the trends in population growth based on the true and observed number of nesters and nests. We calculated the population trend (*r*) as the slope of an exponential regression across 5, 10 or 20 years. We randomly selected the starting points for each trend time-series within the three population trajectories for each of the 50 replicate runs of the experimental treatments.

Determining Trend Duration – Deviance from truth and error types

We measured the degree of deviance from the true population trend by subtracting the estimated trend (either from observed nesters or nests) from the true trend (either total population or adult population). Trend was measured from 5, 7, 10, 15, or 20 year time-series, and the starting points for the time series was randomly selected within the three population trajectories for each of the 50 model runs. We also measured the proportion of false negatives and false positives in error estimation. We calculated the proportion of false negatives the number of times the estimated trend was negative when the true trend was positive out of each of the 50 replicate runs, and calculated the proportion of false positives as the number of times the estimated trend was positive when the true trend was negative out of each of the 50 replicate runs. We included a ± 3% buffer about the trend estimate, so that trends $-0.03 \leq r \leq 0.03$ where regarded as stable.

For all three population assessment status indicators, population trend, adult abundance and proportion of neophytes, we compared the estimated values to the quantity simulated in the GSTABM operating model, heretofore referred to this as the simulated "true" value. Accuracy was defined as the degree of correctness of a quantity, and we practically defined it as the amount of deviation from the simulated "true" value (Flexner 1988). For all three population assessment status indicators, we ranked the factors by mean percent error across the 27 experimental treatments to determine which factors contribute the most towards improving estimation accuracy.

Biological Disturbance and Monitoring Experiments

To explore this first use of MoSE, we created a 3 x 3 x 3 factorial experiment (27 treatments) with three levels of detection probability, sampling type (random and two forms of non-random), and disturbance type (Fig. 4.1). Each treatment was replicated 50 times for 350 years. We modelled the mean detection with three levels: 10%, 50% and 90% of nesters and nests. We included a broad range of detection probabilities with which to sample the nesters and nests to provide an overview of the influence of detectability on sea turtle population assessments.

We included three experimental treatments for sampling error: random, age bias, and clutch frequency bias. The random sampling treatment represents a null model, in that sea turtle monitoring rarely implements beach monitoring by randomly sampling individuals. Rather, rookery monitoring is more comparable to large line-transects along stretches of known nesting beaches, and monitoring strives to encounter every single individual or nest on the nesting beach or at least the turtles or nests sequentially encountered while moving down the beach (Gerrodette et al. 1999, Schroeder & Murphy 1999, Bjorndal et al. 2010). In the random sampling treatment, observed nesters = $p \cdot N_{nesters}$, where monitored nesters are a random sample of the total number of nesters at each time step. In addition, we included two different model specifications to include non-random sampling of sea turtle nesters and nests: (1) age bias and (2) clutch frequency bias. In the non-random sampling treatments, the GSTABM sorts nesters by age or clutch frequency and selects the oldest or most fecund individuals, i.e. if $p = 50\%$, then the GSTABM selects the top 50% oldest turtles. The age bias sampling treatment strives to simulate bias towards encountering older individuals and their nests, who may have higher site fidelity to the nesting beach than newly recruited nesters or where fisheries bycatch impacts sub-adults and small adults so that recruitment to the nesting beach is limited (Mortimer & Carr 1987, Tucker & Frazer 1991, Van Houtan & Kittinger 2014). Clutch frequency-biased sampling simulates the bias towards more fecund individuals, and their nests, who return to the nesting beach more frequently during a nesting season and are more likely have a greater detection probability than lesser fecund individuals (Tucker 2010, Hart et al. 2013). While both these non-random sampling types may be simplifications of how sea turtle monitoring occurs, we argue that either form is more representative of how monitoring occurs than a random sampling type.

We included three disturbance treatments: (1) Cyclic Breeding Probability with sub-adult and adult impacts, (2) High Severity Neritic Juvenile Impacts, and (3) Low Severity Neritic Juvenile Impacts. The Cyclic Breeding Probability treatment represents oscillations in annual breeding probability that could be a result of large scale climatic events, such as *El Nino* Southern Oscillation. In this treatment, breeding probability oscillates as a sine function, with the form:

$$BP = 0.27 \cdot (\sin(50 \cdot year) + 0.3) \tag{4.4}$$

Where BP = breeding probability and BP fluctuates between 0.02 and 0.57 (Fig. 4.2B). The breeding probability cycle frequency in the GSTABM occurs every 8 years, which is intended to simulate about the same frequency as major El Nino events (Limpus & Chaloupka 1997, Saba et al. 2007, Trujillo & Thurman 2008). In the Cyclic Breeding Probability treatment, populations are also subjected to a disturbance where 7% of sub-adults and adults (ages ≥11) are removed from the population annually for 50 years. This treatment simulates the population disturbance of targeted sea turtle fishery (Witzell 1994, Van Houtan & Kittinger 2014). While this treatment confounds environmental forcing and anthropogenic impacts, it is intended to simulate real-life situations where both factors occur simultaneously, but population size and trends are still assessed. The Low and High Severity Neritic Juvenile Impacts treatments simulate disturbances where neritic juveniles (ages 4 – 10) are removed, such as by fisheries bycatch (Magnuson et al. 1990, Epperly et al. 2002). In the low severity treatment, 10% of the neritic juveniles removed annually for 50 years, and in the high severity treatment, 50% of neritic juveniles removed annually for 50 years.

We recognize that many other experimental biological, detection level and sampling treatments could have been conducted. However, our goal is to compare plausible scenarios in which to test the MoSE tool and to illustrate the potential drivers of error in population assessments of sea turtles.

4.3 RESULTS

Population response to disturbance

Fig. 4.3 illustrates the general population structure during the stable, disturbed and recovery phases of two of the experimental treatments: Cyclic Breeding Probability with sub-adult and adult harvest (Fig. 4.3A) and High Severity Neritic Juvenile Impacts (Fig. 4.3B). When the simulated green sea turtle populations were subjected to an 8-year Cyclic Breeding Probability and 50 year impacts to sub-adults and adults, the degree of process variance depended on the demographic group, e.g., adult population size tended to be more stable inter-annually than the nester population (Fig. 4.3A). During the 50 year population perturbation, all demographic groups declined and then post-disturbance the population began to recover. The adult, sub-adult and neritic juvenile age classes showed low amplitude oscillations during the recovery period. Fig. 4.3 also depicts the time-series for monitoring nesters and nests with 50% detection of nesters and nests randomly sampled to illustrate patterns of monitored demographic groups relative to the true population size. Observed nesters and nests were always less than the true total number of nesters and nests, respectively, and the degree of interannual variation did not mirror the adult population. The cycling of nesters, nests, observed nesters, and observed nests were in synchrony.

When the simulated populations were subjected to 50 years of neritic juvenile impacts, population level responses were more complex (Fig. 4.3B). As sea turtle populations tend to be very sensitive to changes in neritic juvenile survival, the responses of the age classes to the disturbance was, perhaps, not surprising (Crowder et al. 1994, Heppell 1998). Higher amplitude oscillations in abundance occurred for all demographic groups, but were the strongest for Sub-adults and Neritic Juveniles (Fig. 4.3B). After 100 years of recovery, the populations had not returned to pre-disturbance levels. The variance about the main age classes (adults, sub-adults, neritic juveniles) was less in comparison to nesters, nests, observed nesters and observed nests.

The variance about nesters and nests tended to increase during the latter stages of the impact and during the early stages of recovery. Consequently, variance about the observed nesters and nests also was increased during this period of the time-series.

Population assessment from simulated population monitoring

Estimating adult abundance

To illustrate how the MoSE tool works, Fig. 4.4 depicts a single model run for each detection level of the Low Severity Neritic Juvenile Impacts treatment. The estimated adult abundance from observed nests was greater than the estimated adult abundance from observed nesters, and this improved with detection level. The accuracy of estimated abundance improved considerably when the estimation procedure included annual estimates of detection, breeding probability, and clutch frequency (for observed nests only). The exception to this is in occasional low breeding frequency years, which give the appearance of sudden drops in adult abundance.

The accuracy and precision of estimating adult population size under the three disturbance treatments was influenced by the sampling scheme (random, age-biased, clutch frequency-biased), demographic group monitored (nesters or nests), and the population trajectory (Figs. 4.5 and 4.6, Table 4.3, and Appendix C). The abundance estimates tended to be under-estimates of the true adult abundance if observed nesters were used, but tended to be over-estimates if observed nests were used (Fig. 4.5 and Appendix C). The worst estimation errors occurred during the stable population trajectory. The worst correspondence in estimating adult abundance emerged from monitoring nests with a clutch frequency bias, and resulted in over-estimated adult abundance. In this case, increasing detection improved accuracy, but even when detection was at 90% over-estimation still tended to occur (Fig. 4.5). The severity of neritic juvenile impacts influenced the degree of variability about adult abundance and the estimated adult abundance from observed nesters and nests; during the recovery phase of the high severity treatment, the accuracy of the estimated abundance improved (Appendix C). If constant inputs for the estimation model were used, accuracy generally did not increase with increasing detection probability (Fig. 4.5). When the estimation model included annual values of the model inputs, accuracy greatly improved even when a clutch-frequency bias was present (Fig. 4.6). In general, the accuracy in abundance estimates was most improved by avoiding clutch frequency biases in sampling and including annually varying (versus constant) breeding probability, detection probability, and clutch frequency in the estimation model (Table 4.3).

Estimating proportion of neophyte nesters

Increased detection of nesters tended to result in increased accuracy of estimated proportion of neophytes in the nester population, regardless of sampling scheme (Figs. 4.7 and 4.8). When monitoring occurred with an age bias, estimates of the proportion of neophytes tended to be under-estimated and even with 90% detection of nesters, accuracy was worse than with random sampling or a clutch frequency-biased sampling (Fig. 4.7B, 4.8C, and 4.8D). When neritic juvenile impacts occurred, the accuracy of the estimates of proportion neophyte decreased with increasing impact severity (Fig. 4.8). In general, the accuracy of proportion of neophytes was most improved by increasing detection level and avoiding age-bias in sampling (Table 4.3).

Estimating population trend

Precision in the estimates of adult population trend drawn from observed nesters increased with the duration of the trend time-series and detection level across the biological treatments of Cyclic Breeding Probability and the Low and High Severity Neritic Juvenile Impacts (Fig. 4.9 and Appendix C). We also examined relationships between the true total population trend and estimated trend drawn from observed nesters and nests, and true adult population trend and estimated trend drawn from observed nests. Patterns across these groups tended to be similar to true and nester-estimated adult population trend presented here (see Appendix C). Precision of the trend also depended on the population trajectory; stable populations tended to result in more accurate estimates even with just five years of data. For the Cyclic Breeding Probability treatment, the impact phase tended to have the least precise estimates, but for the neritic juvenile impacts the recovery phase tended to have the least precise estimates. For neritic juvenile impacts, the more severe impact resulted in reduced accuracy of the trend estimate.

If only five years of monitoring data is available, a low severity impact to neritic juveniles resulted in the most accurate trend estimates, regardless of detection level and sampling scheme (Fig. 4.10). Among the three main biological treatments, a low impact to the neritic juvenile life stage resulted in the best degree of accuracy in trend estimates with just 5 years of data, albeit error in trend estimates were still present. In general, the accuracy of estimating population trend was most influenced by the underlying population trajectory, age classes disturbed and severity of impacts (Table 4.3).

Trend duration and accuracy – how long of a time series is necessary to accurately estimate population trend?

The trend deviance tended to reach an asymptote after 10 years, and variance about the deviance for less than 10 years of data was an order of magnitude larger than the mean deviance from the true adult population trend (Fig. 4.11). We do not show the detection levels as there were only modest differences in deviance (see Appendix C). Variance about the deviance in trend estimate tended to be greater for the Cyclic Breeding Probability treatment than both the Low and High Severity Neritic Juvenile Impacts treatments, but accuracy tended to improve after

15 years trend estimate duration. The bias in deviance alternated depending on the population trajectory and the biological treatment. For example, the deviance during the impact phase for Cyclic Breeding Probability treatment tended to be positive with 5 or 7 years trend duration and then approached 0 (Fig. 4.11A), but for the High Severity Neritic Juvenile Impact treatment, during the recovery phase, the deviance tended to be negative and remained so for 20 years trend duration (Fig. 4.11E).

The proportion of false negative and false positive trend estimates tended to decrease with trend duration, except for during the stable population trajectory (Fig. 4.12). False positive errors – concluding a population was increasing when in fact it was decreasing – occurred more frequently than false negative errors. But, with the 90% detection, false positive errors did not occur during the impact phase of the Cyclic Breeding Probability and false negative errors did not occur in the recovery phase of the High Severity Neritic Juvenile Impact treatment (Fig. 4.12A and H). False positive errors tended to decrease with trend duration during the impact and recovery phases, but increased during the stable phase, regardless of detection level. Both types of error were more frequent in the Low Severity Neritic Juvenile Impacts than the high severity neritic juvenile impact treatment.

4.4 DISCUSSION

The MoSE approach has great potential to help modify and design future monitoring programs for sea turtles, and illustrates the potential error and bias that can arise from population assessments based on nesting beach data alone. We also found that the history of population disturbance, and its severity, can have important and persistent effects on the accuracy of population assessments drawn from monitoring rookeries. Increasing detection levels generally results in improved accuracy in population assessments, however imprecision may remain even with 90% detection of nesters in a population because of unavoidable process and observation errors in monitoring rookeries and in extrapolating data from the nesting beach to the population at large.

The model suggests that improving the accuracy of population status indicators depends on which indicators are used in assessment. Accuracy in abundance estimates may be most improved by avoiding clutch frequency biases in sampling and including annually varying (versus constant) breeding probability, detection probability, and clutch frequency in the estimation model. Accuracy of proportion of neophytes may be most improved by increasing detection level and avoiding age-bias in sampling. The accuracy of estimating population trend is influenced by the underlying population trajectory, age classes disturbed and disturbance severity. At least 10 years of monitoring data are necessary to accurately estimate population trend, regardless of biological impact, underlying process errors, detection level, and population trajectory. Longer trend durations are necessary if juvenile age classes were disturbed and trend estimates occur during the recovery phase. Our model suggests that at least 10 years of monitoring data are necessary to accurately estimate population trend; this would be influenced by the duration of cycles in breeding probability (Solow et al. 2002, Saba et al. 2007, del Monte-Luna et al. 2012).

Our work builds on other studies working to optimize monitoring of sea turtle rookeries. Sims et al. (2008) found that by examining the statistical power of an intensive protocol versus those of shorter duration and later start dates, it is possible to optimize monitoring start date to later in the season and for a survey duration of just 10 weeks with a negligible loss of statistical power, and a cost savings, for Hawksbill sea turtles (*Eretmochelys imbricata*) in the Eastern

Caribbean. Jackson et al. (2008) examined how accurately different monitoring schemes estimated the total number of nests and the ability to detect a population decline based on monitoring nests for green and loggerhead (*Caretta caretta*) turtles in Cypress. Jackson et al. (2008) found that accurate nest abundance estimates could be derived from a bolus sampling, where monitoring occurs daily for at least 21 days during the peak of the nesting season. However, the monitoring schemes were relatively insensitive to small population declines (~1% year^{-1}), but on average could detect a 10% year^{-1} in 12 years for green turtles and 5 years for loggerheads. Whiting et al. (2013) compared within season monitoring schemes to determine the optimal scheme for sampling nests for populations with short and long nesting seasons, and found that the phenology of nesting (timing and duration of the nesting season) influenced the optimal sampling regime. Our work suggests that estimating population trend is relatively robust to detection level, sampling bias, and process errors, but may be sensitive to population trajectory and the type of biological impacts. Estimating adult abundance and proportion of neophytes is sensitive to sampling bias, detection levels and impact history, but less sensitive to underlying population trajectory. Altogether, these studies suggest that monitoring program managers could make critical decisions to optimize monitoring such that little statistical power is lost, but financial and manpower resources are conserved.

We present here a proof of concept of the MoSE approach. Future work could explore other complexities of sea turtle life history, such as within and across season variation in reproduction, and differences in reproductive output between neophytes and veteran nesters (Broderick et al. 2003, Stokes et al. 2014). We performed a simple base estimation model with constant detection, breeding probability, and clutch frequency. However, by including annual estimates of these parameters dramatically improved abundance estimates. In doing this we assumed that these parameters could be accurately estimated from field data. In reality, this is not a simple or cheap operation and future work could further explore the separate contributions of detection level, breeding probability, and clutch frequency to improving accuracy or could even explore alternative regimes for collecting these data (e.g., 2 or 5 year sampling cycles). In all, we advocate research towards improved ways to accurately measure breeding probability and proportion of neophytes. In addition, adding a spatial dimension to the GSTABM would enhance exploration of issues of nesting site fidelity, clutch frequency, and line-transect sampling of stretches of nesting beaches versus complete census or randomized sampling and their influence on the accuracy of population assessments.

We found that estimates of the proportion of neophytes is sensitive to detection level and sampling scheme (random vs. age-biased). Adult recruitment is an important indicator of population growth (Heppell et al. 2003, Richardson et al. 2006, Stokes et al. 2014), and provides context to trends observed on nesting beaches (Bjorndal et al. 2010). Integrating proportion of neophytes as a metric may enhance the accuracy of population assessments. However, monitoring programs would need to ensure high detection levels, and randomized sampling to ensure accuracy of recruitment estimates. In addition, improving estimates of the degree of "leakiness" to nesting site fidelity (Tucker 2010, Hart et al. 2013, Stokes et al. 2014), in particular in relation to neophyte and veteran nesters, or expanding survey areas to capture full nest site ranges, would improve adult recruitment estimates.

Our MoSE does not include a built in biological mechanism for non-random sampling (i.e. annual clutch frequency is independent of breeding periodicity, and fecundity is independent of age and breeder status, i.e., neophyte vs. veteran nester), so in some ways it is surprising that we found deviations for the biased sampling schemes. If we had included these more complex behaviors, we expect that the non-random sampling schemes would have produced even worse estimation errors than we report here. This suggests that there are pure mathematical relationships with estimating abundance and recruitment that can result in biased estimates, above and beyond biological behaviors that would yield biased estimates. In addition, we modeled a perfect bias; the oldest turtles and most fecund turtles, for age-bias and clutch frequency-biased schemes respectively, were sampled first. In reality, sampling biases are more mixed with a predilection towards a certain trait – monitoring *tends* to sample more fecund or older females – but our results suggest that including annual estimates of detection, breeding probability and clutch frequency in abundance estimates can greatly improve the accuracy, and can overcome unavoidable sampling biases. Our results also suggest that there is an interaction with sampling bias and detection (Table 4.3). If unavoidable biases in nesting beach sampling occur, then increasing detection to close to 90% of nesters may help to improve accuracy.

In the MoSE, detection levels were modelled as a stochastic variable with a logit-normal distribution. We made the simplifying assumption that the mean of the inputted detection probability parameter would be proportional to the standard deviation. However, variability may increase as detection decreases. In practice, if a monitoring program has a high detection level annually, there may be strong relationships with effort and quality control that would reduce inter-annual variability. On the other hand, if a monitoring program has low detection levels, effort may vary annually and quality control may be limited which would lead to higher inter-annually variability. It may often be the case that detection levels improve over time as monitoring programs become formalized and monitoring staff become more experienced (Pfaller et al. 2013). Alternatively, as a population recovers, it is also possible that nesting could flood observer efforts and detection could be inversely related to population size. These have important implications for how accurately we can estimate adult population from monitoring nesters. Indeed, if inter-annual variability increases with the long run mean detection probability for a monitoring program, then the confidence intervals for estimated adult abundance would become increasing large, and may result in estimates of abundance, adult recruitment and trends being completely uninformative. Monitoring programs should strive to have the highest detection levels possible, given financial and labor resources, but attention should also be paid towards limiting inter-annually variability in detection. In other words, it is better to be consistently mediocre in detection than inconsistently good over time.

Estimating adult abundance and population trend from observed nesters is marginally more accurate than when extrapolating from observed nests. We caution readers from interpreting this as there is no benefit from monitoring individual nesters, a more costly effort, over nests. There is an appreciable accuracy gap by using rookery data in general as a population index, and a much smaller difference between either source of rookery data – observed nesters and nests. The inaccuracy of monitoring nests versus nesters is minimal in comparison, but both population indices are problematic, and observed nests are only marginally worse than nesters. In addition, monitoring nesters includes value added to a monitoring program in that additional biological data can be collected from nesters: body length and size distribution changes, proportion of neophytes, size-at-maturity, breeding probability, clutch frequency, clutch size in relation to nester size and status (neophyte versus veteran) (Broderick et al. 2003, Stokes et al. 2014, Piacenza et al. *In review*). In addition, monitoring nests is a particularly spatial problem, in comparison to monitoring nesters (albeit spatial issues exist here as well, i.e. nest site fidelity), and had monitoring been modelled as spatially explicit, we may have seen more differences in the degree of accuracy from extrapolating abundance and trend from observed nesters and nests. Future work will included expanding the GSTABM to be spatially explicit.

While there are obvious problems with monitoring sea turtle rookeries, versus in-water studies, we recognize that monitoring rookeries remain the most accessible option for encountering individuals and collecting individual level data (Bjorndal et al. 2010, Hamann et al. 2010, Stokes et al. 2014). Our results suggest that a monitoring strategy may be best tailored based on the impact history, current population trajectory, and environmental drivers. For example, for a population that is currently recovering from intense impacts to neritic juveniles, every effort should be made to avoid an age bias to sampling, and 20 years or more are needed to accurately estimate population trend using nesting data, because of demographic lags and population momentum. Population assessors would need to acknowledge that estimates of adult abundance and trend, at least during the early recovery years, are likely to be under-estimated. Including annual estimates of detection, breeding probability and clutch frequency reduce estimation errors dramatically. On the other hand, for a population susceptible to environmental drivers on reproduction (i.e. a strong *El Nino* influence on reproduction), and with impacts to adults and sub-adults (i.e. a targeted fishery), estimates of trend may be inaccurate but are just as likely to be over-estimated as under-estimated, at least in the early years of recovery. For this kind of population, trend could be accurately estimated in 10 years. However, it may be difficult to have precise estimates of impact rate and history. It may be possible to qualitatively assign impact history, based on bycatch rates, or historical records, and categorically assign impact rate (i.e., low or high). To assist monitoring groups, The GSTABM, which includes the MoSE tool, will be made available to users at the NetLogo User Community Models (http://ccl.northwestern.edu/netlogo/models/community/index.cgi). The NetLogo program contains a guided user interface, where users can enter particular life history traits (clutch frequency, clutch size, age-at-maturity, etc.), impact rate, life stages disturbed, and detection levels, to obtain results for a particular sea turtle population and impact history. Ultimately, it is important to carefully consider the impact history, and specifically which age classes were disturbed, when developing a monitoring program and objectives for monitoring duration.

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Table 4.1. Parameter definition and inputted specifications for the green sea turtle operating model used in the Monitoring Strategy Evaluation. For more detailed information on parameterization of the Green Sea Turtle Agent-based Model see Piacenza et al. *In preparation (Chapter 3)*.

Parameter	**Description**	**Mean ± Std. Deviation or (Range)**	**Units**	**Statistical Distribution**
Age-at-maturity	Age individual reaches sexual maturity	30 (17-41)	years	Poisson
Clutch Frequency	Nests laid during reproductive season	4 ± 4	nests	Poisson
Clutch Size	Potential number of eggs laid per nest	43.2 ± 43.2	eggs	Poisson
Hatchlings Produced	Realized number of eggs laid across all clutches in a given reproductive season, based on Ricker-type density-dependent function	103 (0 - 187)	individuals	-
Remigration Interval	Number of years between nesting seasons	3.4 ± 2.72	years	-
Breeding Probability	Mean annual breeding probability	0.2519 ± 0.0127, (α=4.80124, β=19.06008)	$year^{-1}$	Gamma
Detection probability	Mean probability of detecting a nester	0.1 ± 0.020, 0.5 ± 0.099, 0.9 ± 0.18	$year^{-1}$	Logit-normal

Table 4.2. Estimation model parameter inputs. In the base estimation model, we assumed that parameters would be estimated as constant value, and not annually estimates, but could be correctly estimated from field data.

Parameter	**Assumed Value**
Breeding Probability	0.25
Clutch Frequency	4
Detection	0.1, 0.5, 0.9

Table 4.3. Mean percent error for the status indicators for the 27 treatments. Mean percent error of population trend is presented for 10 years trend duration. The lowest mean percent error for each of the three main status indicators is indicated in bolded italics. Mean percent error is based on estimated adult abundance calculated with constant detection levels, breeding probability, and clutch frequency. CBP = Cyclic Breeding Probability with 7% year^{-1} sub-adult and adult impacts, Low NJ = Low Severity (10% year^{-1}) Neritic Juvenile Impacts, and High NJ = High Severity (50% year^{-1}) Neritic Juvenile Impacts treatments.

Sampling Scheme	**Detection Probability**	**Disturbance Treatment**	**Status Indicator**				
			Abundance - Obs. Nesters	**Abundance -Obs. Nests**	**Proportion of neophytes**	**Trend - Obs. Nesters**	**Trend - Obs. Nests**
Random	0.1	CBP	39.3	39.4	9.0	2354.5	2208.9
		Low NJ	30.3	30.3	7.7	3888.5	3846.0
		High NJ	32.6	32.6	31.1	5099.3	5119.7
	0.5	CBP	40.1	40.1	3.1	2601.9	2597.6
		Low NJ	30.3	30.2	2.5	3296.6	3297.0
		High NJ	32.5	32.5	10.2	4165.6	4236.7
	0.9	CBP	42.1	42.1	0.9	1790.3	1823.6
		Low NJ	30.5	30.5	0.8	3885.3	3911.3
		High NJ	33.3	33.3	2.8	2970.1	3044.3
Age-biased	0.1	CBP	40.0	40.2	99.5	2709.9	3024.3
		Low NJ	33.2	33.5	98.7	55652.7	56172.4
		High NJ	30.1	30.2	100.0	7855.0	7787.8
	0.5	CBP	39.8	39.9	78.4	***1523.5***	1542.8
		Low NJ	33.3	33.4	85.6	5549.7	5296.7

Table 4.3 (Continued). Mean percent error for the status indicators for the 27 treatments. Mean percent error of population trend is presented for 10 years trend duration. The lowest mean percent error for each of the three main status indicators is indicated in bolded italics. Mean percent error is based on estimated adult abundance calculated with constant detection levels, breeding probability, and clutch frequency. CBP = Cyclic Breeding Probability with 7% year-1 sub-adult and adult impacts, Low NJ = Low Severity (10% year-1) Neritic Juvenile Impacts, and High NJ = High Severity (50% year-1) Neritic Juvenile Impacts treatments.

Sampling Scheme	**Detection Probability**	**Disturbance Treatment**	**Status Indicator**				
			Abundance - Obs. Nesters	**Abundance -Obs. Nests**	**Proportion of neophytes**	**Trend - Obs. Nesters**	**Trend - Obs. Nests**
Age-biased	0.5	High NJ	30.6	30.7	86.6	6097.4	6171.6
	0.9	CBP	41.7	41.7	16.4	3771.7	3841.9
		Low NJ	32.7	32.7	26.1	7299.7	7432.1
		High NJ	31.1	31.1	18.6	5947.1	5923.2
Clutch frequency-biased	0.1	CBP	39.4	118.7	9.4	4138.3	3687.1
		Low NJ	31.0	91.4	7.8	3428.4	3362.8
		High NJ	32.3	90.1	30.8	4400.6	4167.1
	0.5	CBP	39.4	65.3	3.1	64706.2	35684.9
		Low NJ	31.1	44.9	2.6	9619.9	9022.9
		High NJ	32.8	46.6	10.1	2569.5	2339.0
	0.9	CBP	41.9	42.8	1.0	3946.0	2872.1
		Low NJ	30.6	***29.6***	***0.7***	4388.4	3907.0
		High NJ	33.0	31.9	2.9	6659.8	5469.9

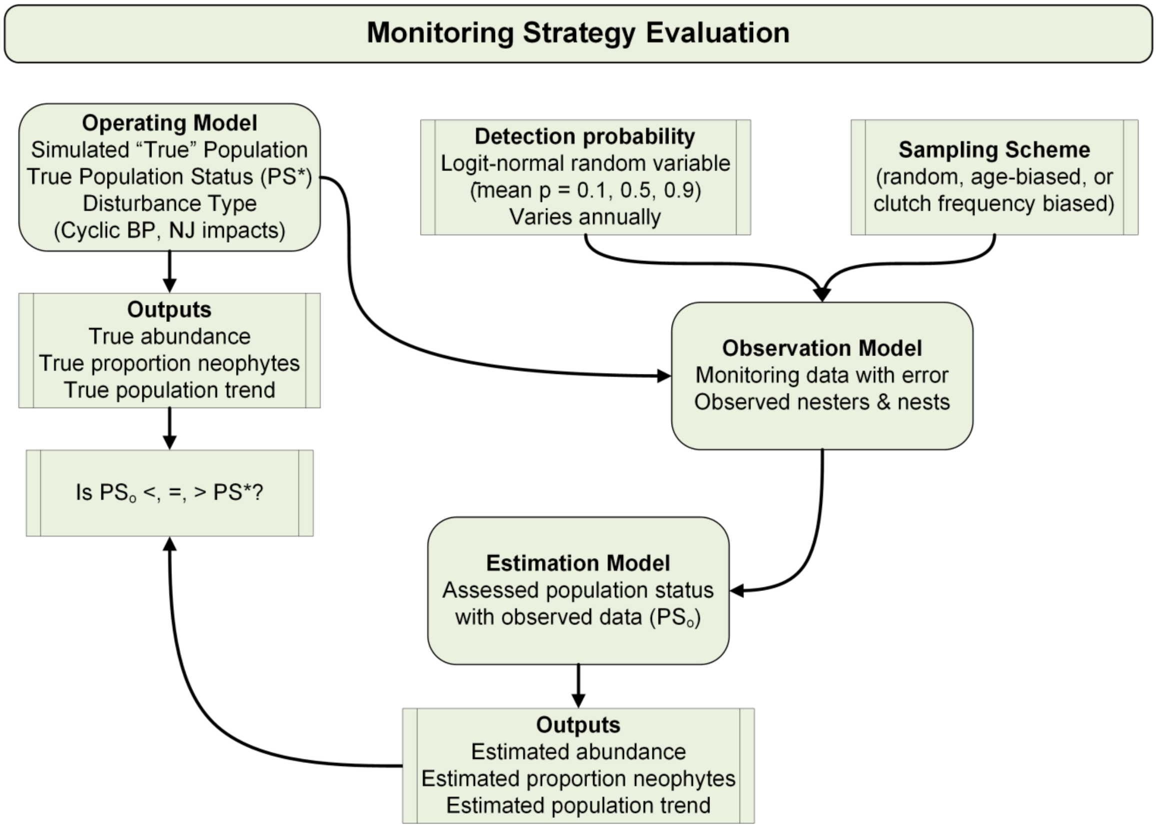

Figure 4.1. Flow chart for Monitoring Strategy Evaluation (MoSE). Green sea turtle populations are simulated in the operating model, using the Green Sea Turtle Agent-Based Model. Female green sea turtle population structure and monitoring simulated for 175 years and replicated 50 times. In each replicate run, the population was subjected to an experimental disturbance from time-steps 200-250. Disturbance is simulated with (1) Cyclic Breeding Probability (BP) and 7% of sub-adults and adults removed year^{-1} for 50 years, (2) Low Severity Neritic Juvenile (NJ) Impacts (10% removed year^{-1}), and (3) High Severity Neritic Juvenile Impacts (50% removed year^{-1}). The monitoring model samples nesters and nests, either randomly or with a type of bias, and with an annually variable detection probability randomly drawn from a logit-normal distribution. The estimation model uses the simulated monitoring data to estimate adult abundance, proportion of neophytes and population trend. Estimated abundance, proportion of neophytes, and population trend are compared to the simulated true values generated in the operating model.

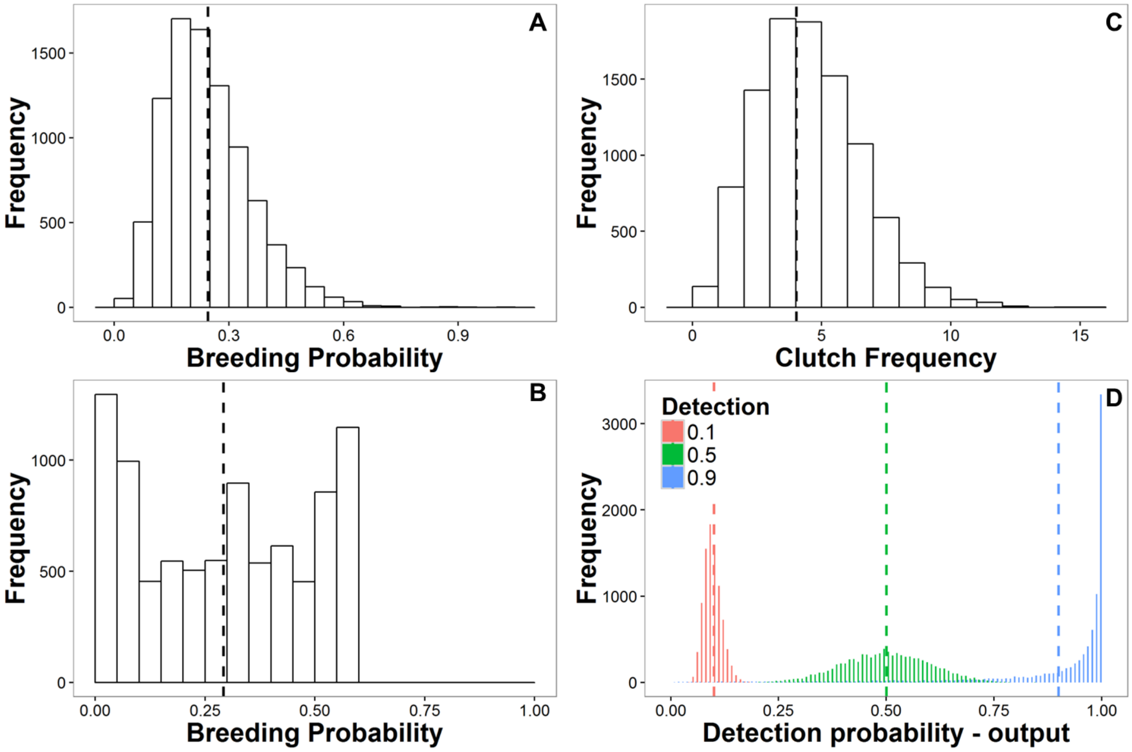

Figure 4.2. Green sea turtle agent-based model sub-processes. (A) Frequency distribution of annual breeding probability as drawn from a truncated gamma distribution, used in the Neritic Juvenile Impacts treatments, (B) frequency distribution of annual breeding probability as a sinusoidal function for the Cyclic Breeding Probability treatment, (C) frequency distribution of clutch frequency drawn from a Poisson distribution, and (D) frequency distribution of detection probabilities for the three experimental mean inputs (*p* = 0.1, 0.5, and 0.90). Clutch frequency is from individual-based data for all individual adults from time-step 350 for 1 model run; all others are for annual values from 50 model runs.

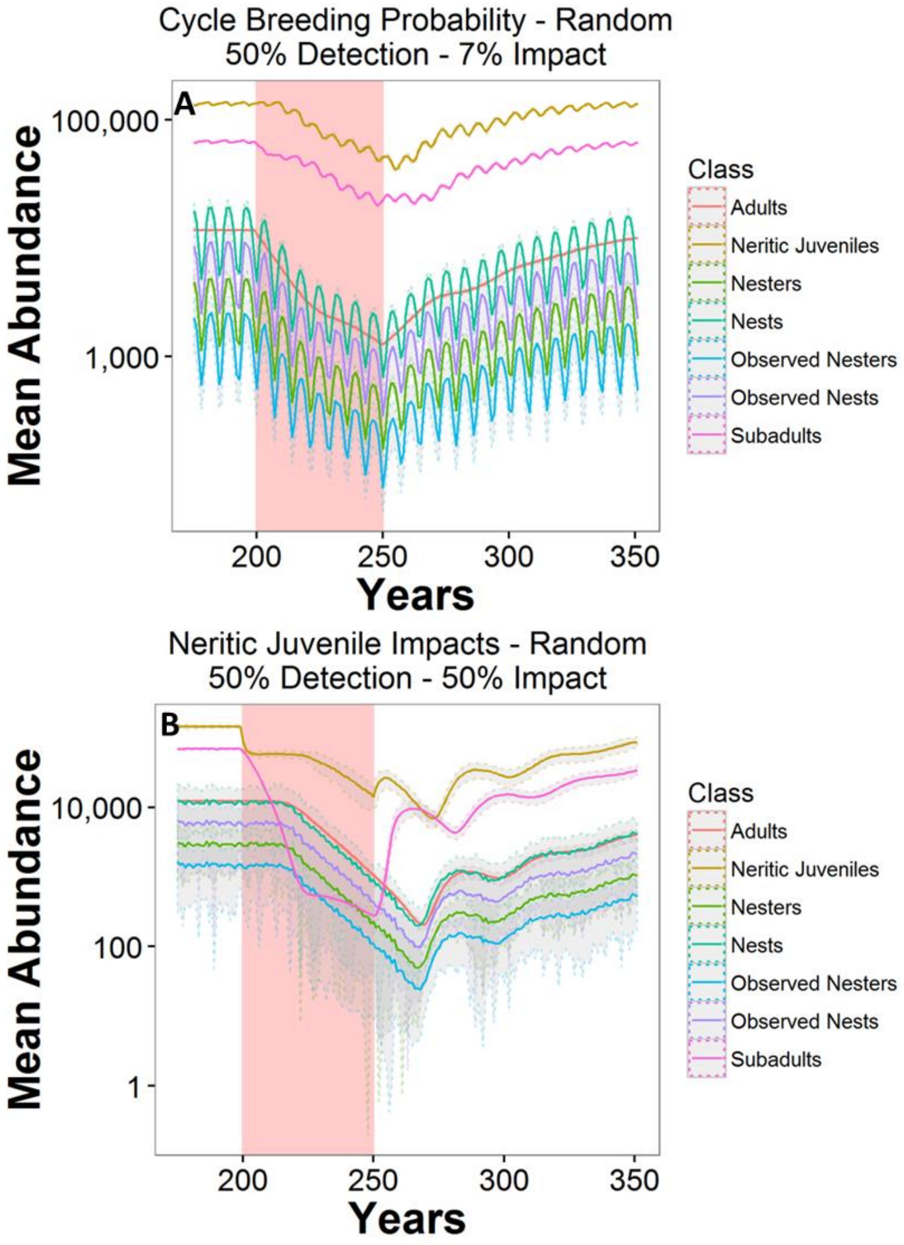

Figure 4.3. Female green sea turtle population structure and monitoring simulated for 175 years and replicated 50 times for two of the biological disturbance treatments: Cyclic Breeding Probability with a 7% of sub-adults and adults removed annually for 50 years (A) and High Severity Neritic Juvenile Impacts for 50 years (B). Both panels show monitoring results for detection probability with a mean of 50% for nesters and nests. Colored lines indicate the mean abundance of the demographic classes and shaded areas indicate the 95% confidence intervals. The pink shaded area indicates the 50 year impact period.

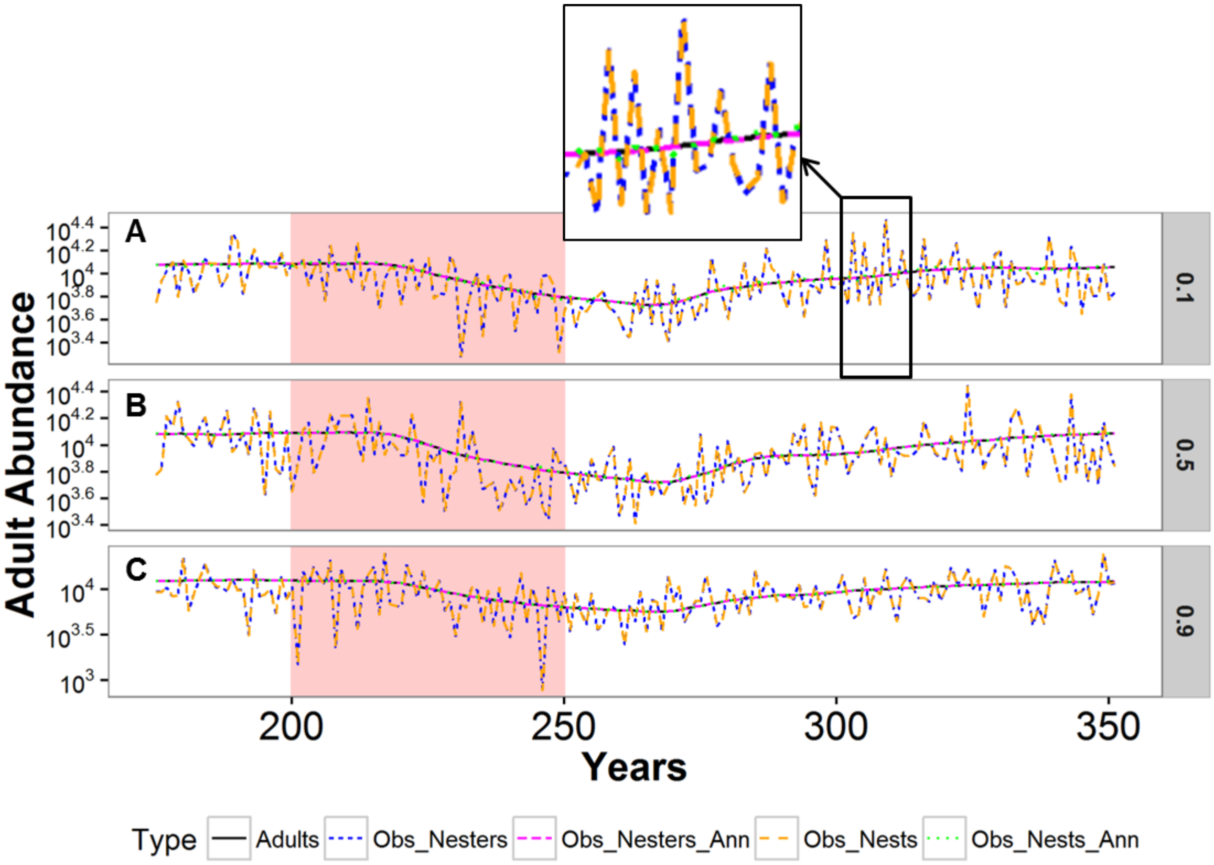

Figure 4.4. Example of MoSE for estimating adult abundance from 1 model run of the Low Severity Neritic Juvenile Impact treatment for the three detection levels. Constant parameter inputs for breeding probability, detection, and clutch frequency were used for Observed Nesters and Observed Nests. Annual inputs for breeding probability, detection, and clutch frequency were used for Observed Nesters Annual and Observed Nests Annual. Detection levels varied with a mean of 10% of nesters detected (A), 50% (B), and 90% (C).

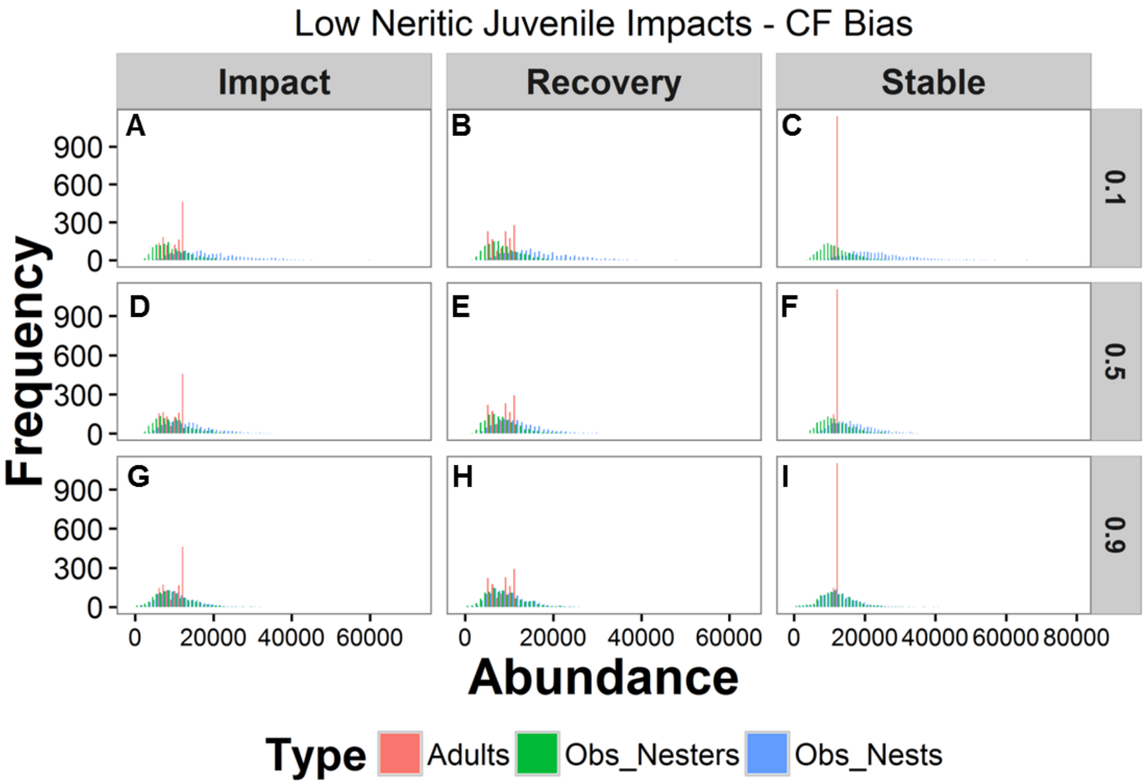

Figure 4.5. Frequency distributions for true and estimated adult abundance, using constant estimates of breeding probability, detection and clutch frequency, from the Low Severity Neritic Juvenile Impacts with clutch frequency-biased sampling treatment. Detection levels varied with a mean of 0.1, 0.5, and 0.9. The axes were allowed to change between figures to improve visualization.

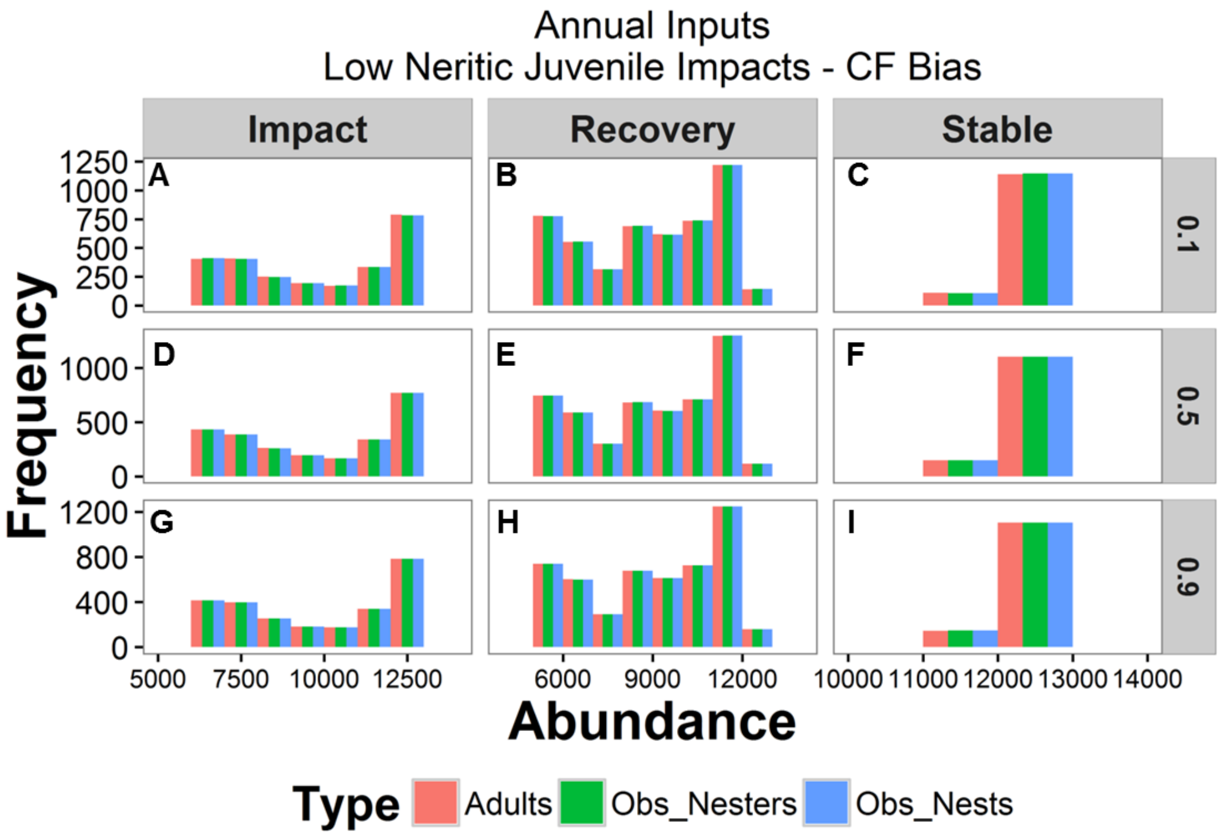

Figure 4.6. Frequency distributions for true and estimated adult abundance, using annual estimates of breeding probability, detection and clutch frequency, from the Low Severity Neritic Juvenile Impacts with clutch frequency-biased sampling treatment. Detection levels varied with a mean of 0.1, 0.5, and 0.9. The axes were allowed to change between figures to improve visualization.

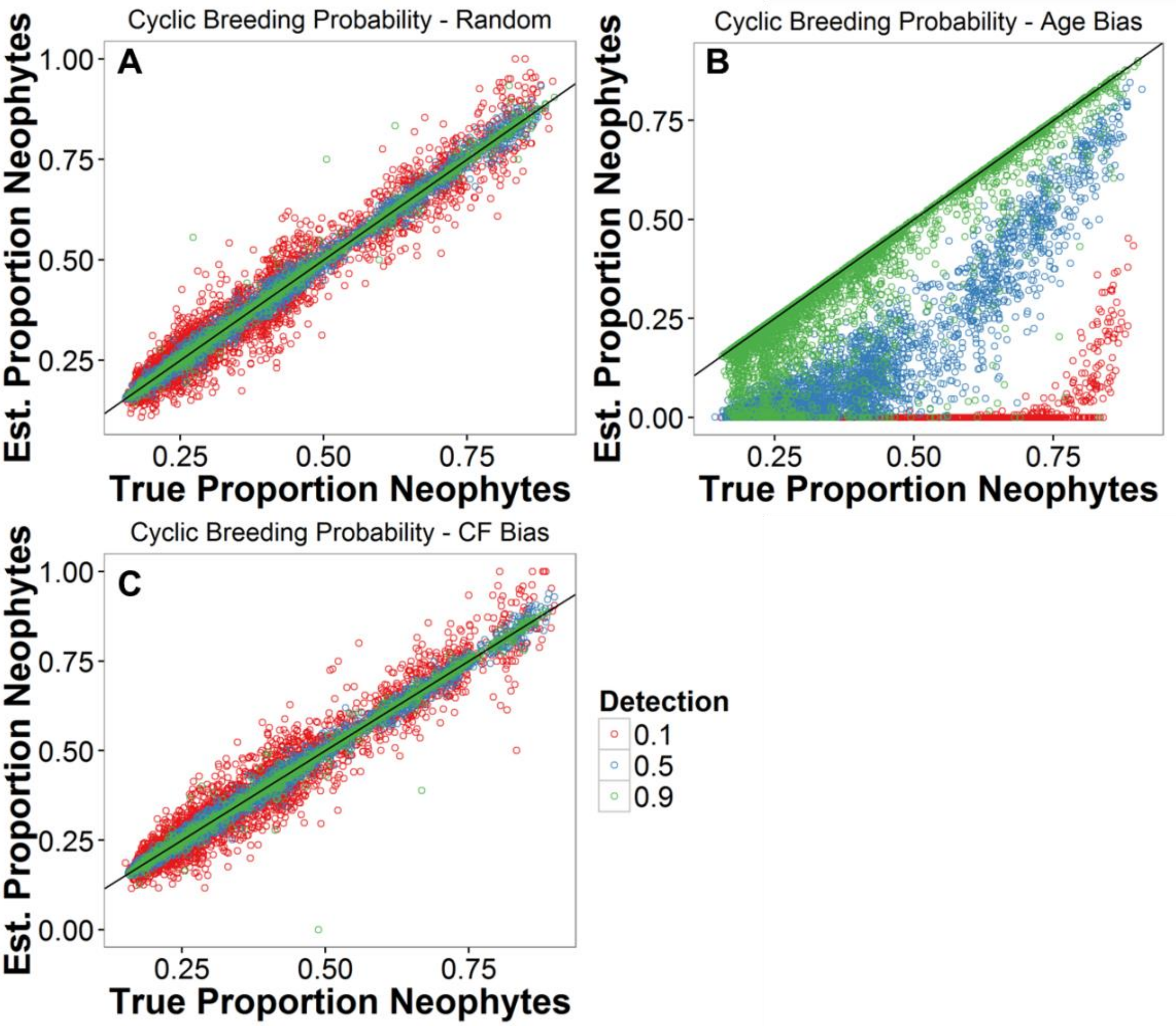

Figure 4.7. True and estimated proportion of neophytes from the nine treatments with Cyclic Breeding Probability. Proportion neophyte estimates were based on random (A), age-biased (B), and clutch frequency-biased (C) sampling. Detection levels varied with a mean of 0.1 (red), 0.5 (green), and 0.9 (blue). The diagonal line represents the 1:1 line between the true and estimated proportion of neophytes. The proportion of neophytes is calculated as the number of neophytes divided by the total number of nesters. Populations were disturbed with 7% of sub-adults and adults removed annually for 50 years.

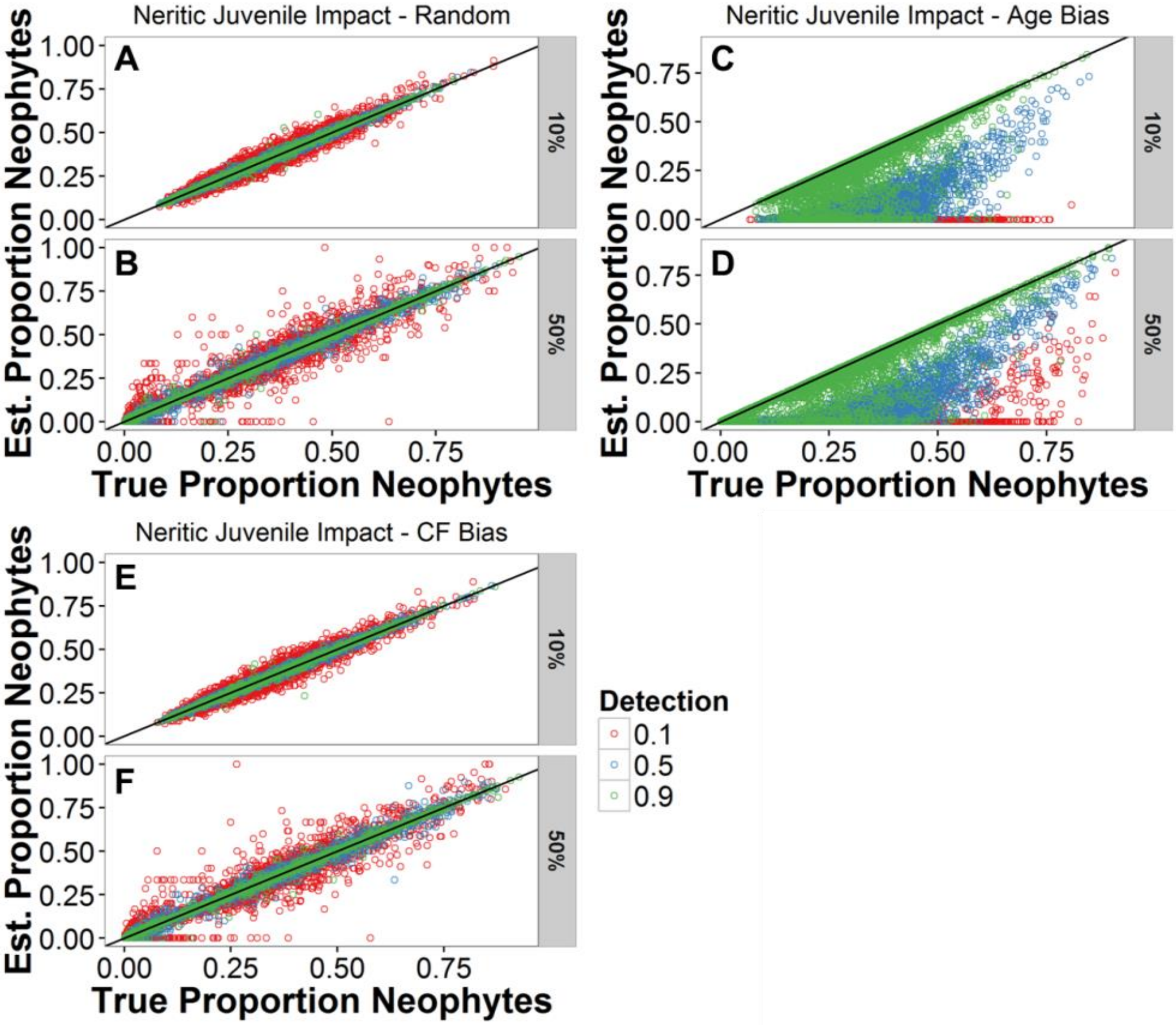

Figure 4.8. True and estimated proportion of neophytes from the treatments with High (9 treatments) and Low (9 treatments) Severity Neritic Juvenile Impacts. Proportion neophyte estimates were based on random (A and B), age-biased (C and D), and clutch frequency-biased (E and F) sampling. Detection levels varied with a mean of 0.1 (red), 0.5 (green), and 0.9 (blue). The diagonal line represents the 1:1 line between the true and estimated proportion of neophytes. The proportion of neophytes is calculated as the number of neophytes divided by the total number of nesters. 10% of neritic juveniles were removed (A, C, E) or 50% (B, D, F) were removed for 50 years.

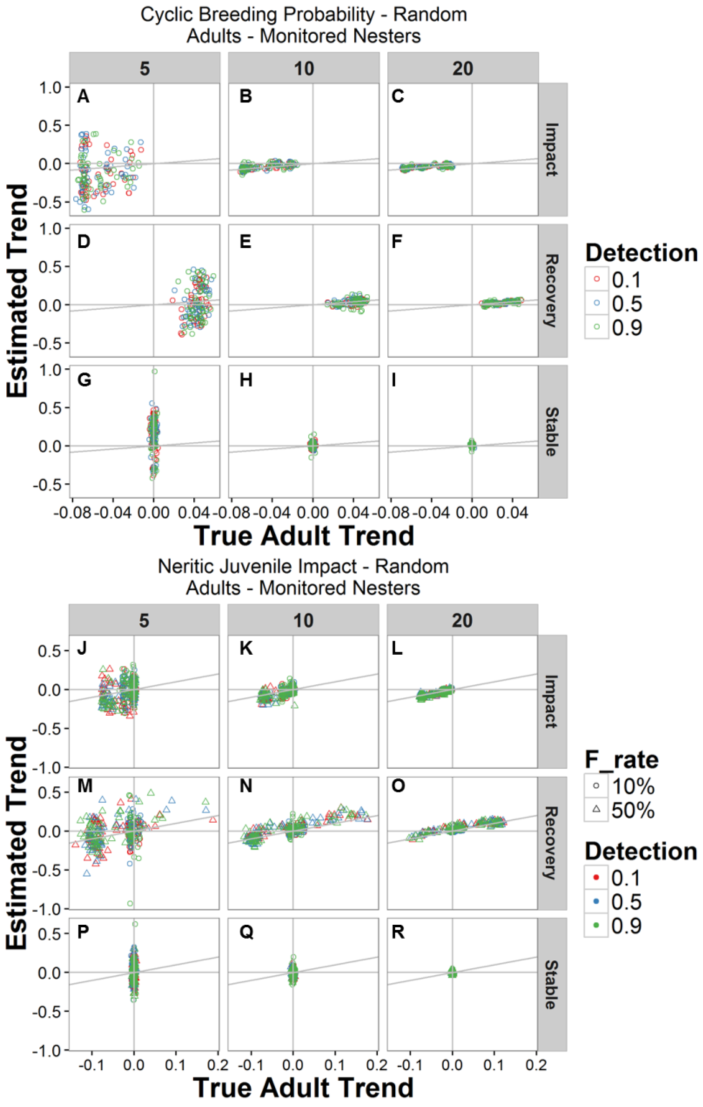

Figure 4.9. True and estimated adult population trend for populations with random sampling. Trend duration was 5 (A, D, G, J, M, and P), 10 (B, E, H, K, N, and Q) and 20 (C, F, I, L, O, and R) years of monitoring of the Cyclic Breeding Probability (A – I) and High and Low Severity Neritic Juvenile Impacts (J – R) treatments. Population trend is shown for the population trajectories: impact (A – C, and J – L), recovery (D – F, and M – O), and stable (G – I, and P – R). Neritic juvenile impacts were either 10% or 50% of neritic juveniles removed annually for 50 years (impact phase) and in the Cyclic Breeding Probability treatment 7% of sub-adults and adults were removed annually for 50 years. Detection levels varied with a mean of 0.1, 0.5, and 0.9. The diagonal line represents the 1:1 line between the true abundance and the estimated abundance. Axis ranges across plots were allowed to vary to enhance visualization of the points.

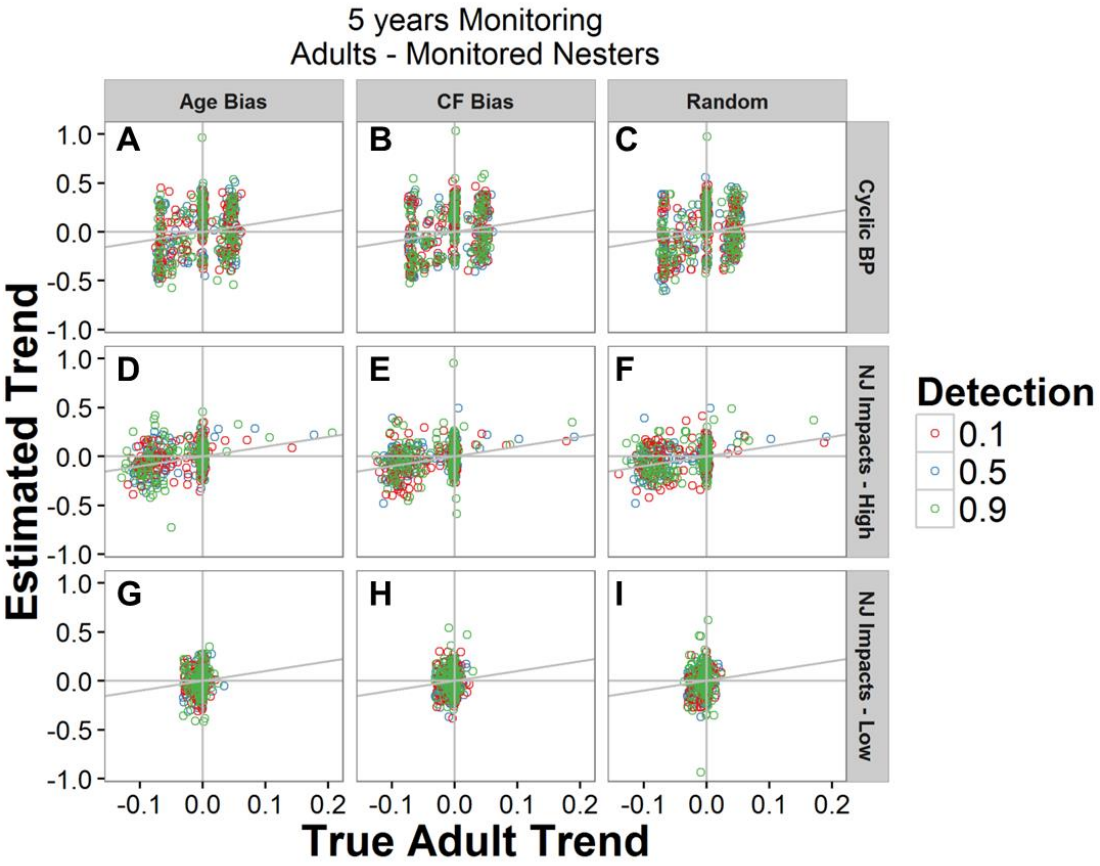

Figure 4.10. True and estimated population trend with 5 years of monitoring nesters across the three biological treatments. The biological treatments were Cyclic Breeding Probability (A – C), High Severity Neritic Juvenile Impacts (D – F), and Low Severity Neritic Juvenile Impacts (G – I). Nesters were monitored using age-biased (A, D, and G), clutch frequency-biased (B, E, and H) and random (C, F, and I) sampling. Detection levels varied with a mean of 0.1, 0.5, and 0.9. The diagonal line represents the 1:1 line between the true and estimated abundance.

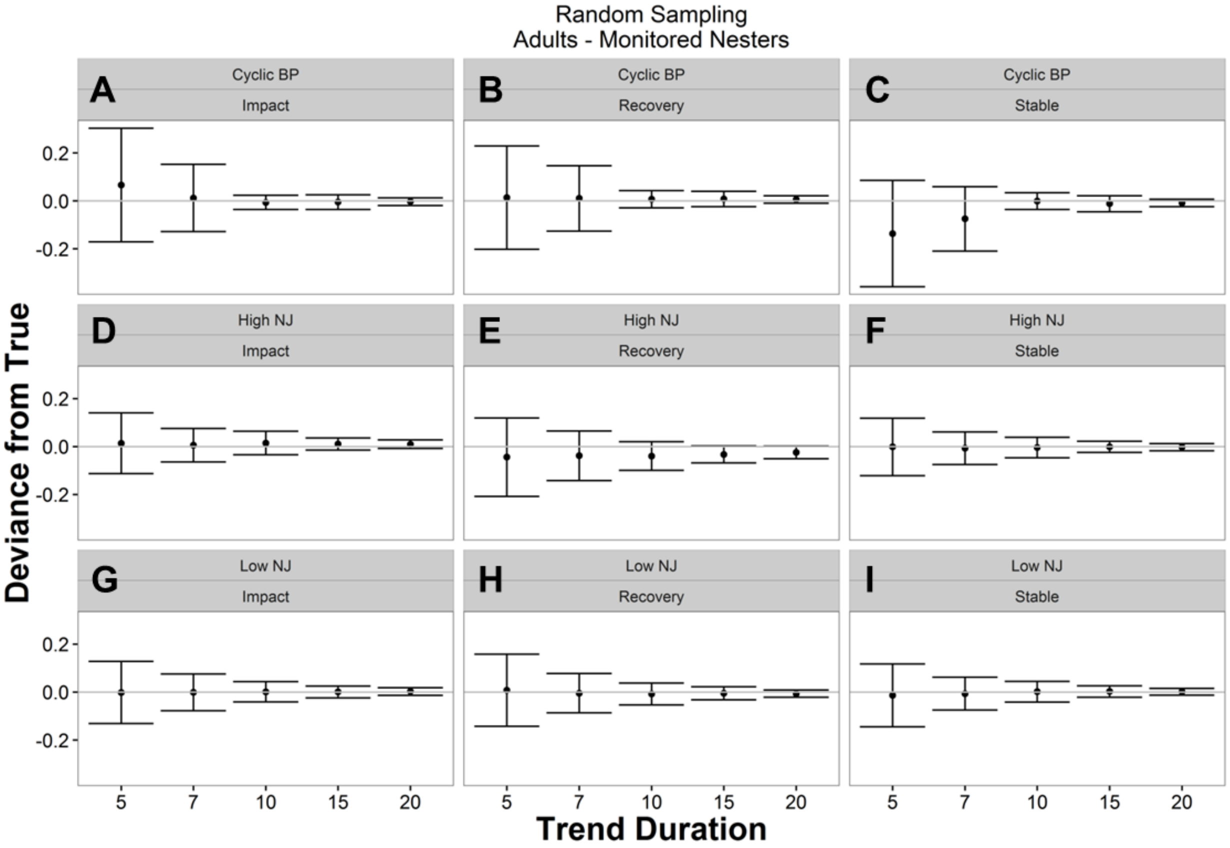

Figure 4.11. Adult population trend duration and the mean deviance from the true trend from randomly sampled nesters. The biological treatments were the Cyclic Breeding Probability (A – C), the Low Severity Neritic Juvenile Impacts (D – F), and the High Severity Neritic Juvenile Impacts (G – I) treatments. Deviance is calculated as the difference of the true population trend minus the estimated population trend. A deviance of 0 indicates no difference between the true and estimated population trend. Errors bars indicate the standard deviation about the mean deviance. True and estimated population trend were calculated across 5, 7, 10, 15, and 20 year durations. Axis ranges across plots were allowed to vary to enhance visualization of the points.

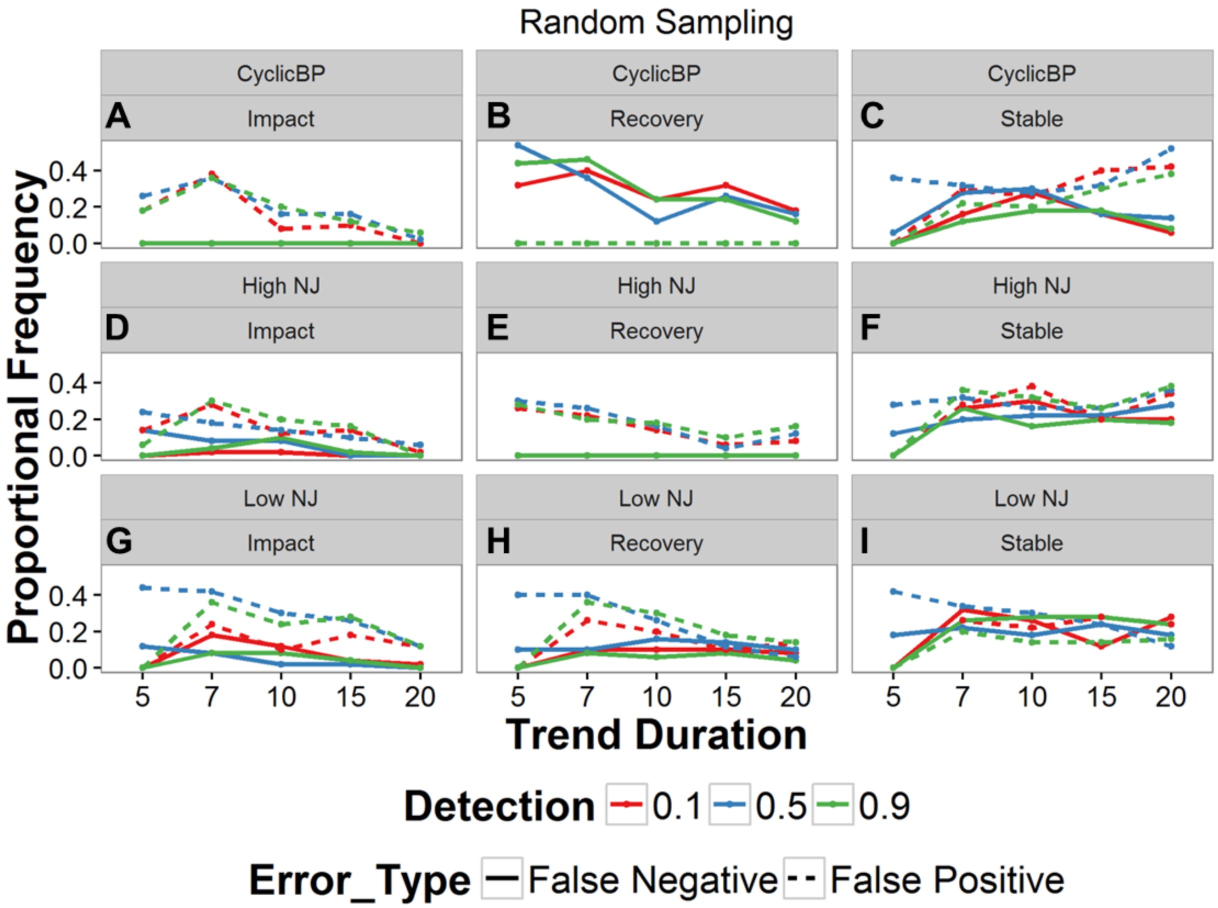

Figure 4.12. Proportion of false negative and false positive trend estimates from randomly sampled nesters. The biological treatments were the Cyclic Breeding Probability (A – C), the Low Severity Neritic Juvenile Impacts (D – F), and the High Severity Neritic Juvenile Impacts (G – I) treatments. False negative errors occur if the estimated trend < -0.03, but the true trend is > 0.03. False positive errors occur if the estimated trend > 0.03, but the true trend is < -0.3. Axis ranges across plots were allowed to vary to enhance visualization of the points.

5 - General Conclusions

In the field of conservation biology, research has focused necessarily on documenting species abundance and assessing extinction risk based on trends for both marine and terrestrial species (Morris & Doak 2002). However, formalized study of the ecological dynamics of recovering populations has been limited, partly due to the nascence of this phenomenon. Indeed, examining recovering marine species across taxa and habitats for general trends has been limited (but see Lotze et al. 2011, Magera et al. 2013). Multiple populations of green sea turtles are showing signs of recovery (Chaloupka et al. 2008). Indeed, green sea turtles in Florida and off the Pacific coast of Mexico were recently down-listed from endangered to threatened (National Marine Fisheries Service & U.S. Fish and Wildlife Service 2016). This welcome advancement brings novel complications and raises new questions to the management of this species (Roman et al. 2015). Can we safely transfer rehabilitated species from national control to state or local control? Can we relax bycatch limits or even allow harvest without threatening the hard-earned and still novel recovery? How resistant is recovery to additional and emergent stressors such as climate change? Can we divert limited conservation budgets from newly recovered populations to other populations without risking relapse? All of these questions are predicated on accurate and reliable assessments of population size and changes over time. Most population assessments of sea turtles heavily rely on population indices from rookeries (Schroeder & Murphy 1999, Bjorndal et al. 2013). My research presented here shows that population indices drawn from nesting beaches must be treated with caution and should be carefully interpreted in light of additional biological information, such as time-series of breeding probabilities, size-distributions, historical impacts, detection levels, and nester recruitment. Simple constant estimates, and even those robustly estimated with uncertainty, are useless without an evaluation of whether these vital rates are changing over time.

Agent-based modelling was a useful and flexible tool towards addressing my research questions regarding population perturbations and monitoring. From a population modeler's perspective, the type of software used for ABMs is not a trivial decision. I used the software NetLogo to program the GSTABM and MoSE. While there are many ABM software programs available, and ABMs can be created from scratch using generic statistical programs, such as R, NetLogo has many advantages. First, NetLogo was explicitly developed for ABMs and automatically accounts individuals, their traits, behaviors, choices, locations, and their ultimate fates. It is open access and uses a computer language, Logo, that was originally developed to teach children computer coding, and thus should be relatively intuitive (Wilensky & Rand 2015). The BehaviorSpace module facilitates sensitivity analysis and experiments by adjusting parameter inputs and exports output. NetLogo interfaces with R software, and can communicate to R to either run R programs or utilize packages (i.e. statistical packages), and NetLogo can be run from R completely and reports output directly to R (Thiele et al. 2014). Across disciplines, NetLogo is the most widely used, becoming more common in biology, and allows scientists a common platform with which to compare to and learn from other ABMs (Railsback & Grimm 2012, Wilensky & Rand 2015). For future students considering using ABMs in their research, NetLogo comes highly recommended from this student.

This dissertation presents a modeling framework designed to provide an evaluation of monitoring program effectiveness to assist in planning future programs for sea turtles. The analysis in Chapter 4 is meant to heuristically present the capabilities of Monitoring Strategy Evaluation (MoSE). In the future, more complex biological, observation, and management scenarios will be used to expand the generality of the results presented here. The analysis was developed based on data from Hawaiian green sea turtles, but there are many facets of the GSTABM and MoSE that make them applicable to other sea turtles and to endangered and recovering species in general. First, the MoSE and the GSTABM were developed with the idea that eventually the program could be used by any conservation organization to optimize their monitoring to meet specific assessment and management goals. Second, The GSTABM code is available in Appendix B and the program itself will be deposited in the NetLogo program library (https://ccl.northwestern.edu/netlogo/models/index.cgi) and is available for anyone to use. Third, the GSTABM can be easily modified to simulate any species or population of sea turtles as it includes a guided user interface (GUI) where users can adjust life history parameters, detection, and catch rates directly without have to change the internal code. Future work could focus on enhancing the GSTABM and MoSE so that is user-friendly and requires no internal coding to modify and run. The quantitative tools employed here can be applied to other sea turtle populations and will improve monitoring, and result in better estimates of current population trends and enhance conservation for all species of sea turtles.

My research was not without obstacles and some I decided to circumvent rather than surmount. One of my initial goals was to perform a similar analysis to the one I did in Chapter 2 using data on green sea turtles from the Archie Carr National Wildlife Refuge in Melbourne, FL. The estimates of the Florida life history parameters could then have been used to parameterize a Florida version of the GSTABM. However, while long-term data was available (the University of Central Florida has been monitoring nesters and nests for over 30 years), data proofing of individuals and their tagging IDs was not advanced enough to allow for an analysis similar to the Hawaii data. It is unfortunate that I was not able to complete this arm of the research as it would have been a valuable contribution to be able to compare the changes in the demographic indicators across two recovering populations. Hopefully, in the near future data-proofing and linking tag IDs to individuals across seasons will be completed and the analysis may be performed. In addition, during the MoSE analysis I included an additional biological treatment which I eventually discarded. I originally included a pulse impact were a large proportion (20 % or 50%) of all neritic juveniles were subjected to a single one-year impact. This treatment was meant to simulate an environmental disaster, such as an oil spill or red tide. The pulse treatment was intended to test if the estimated population trend detected a short-term impact but the results were uninformative. There are several reasons why this might be. The severity of the impact (20% and 50% of all neritic individuals in one year) may not have been extreme enough to influence the true population trend. In a long-lived species, a one-time impact may not cause a population level response (Heppell et al. 2005). Also, the pulse impact may have needed to be repeated multiple times over the course of the model runs (which were for 175 years), to be at the appropriate scale for the analysis. Third, the form of the trend estimate, an exponential regression, may have been inappropriate to detect pulse impacts. I decided to keep the assessment methodology simple, however, further analysis of trend estimation forms and the use of different types, such as general additive models, may be helpful here (Whiting et al. 2014). There has been much debate about the ability for short-term pulse impacts to influence population trends in sea turtles (Bjorndal et al. 2011, Caillouet 2014). It seems with further development of the proper impact scenario, scale and cycling of environmental catastrophes, and estimation model this would be an important research avenue to further explore. Finally, I initially made a mistake in the coding for detection probabilities early on; the standard deviation of detection was disproportionately large for the smaller detection levels. While the mistake was corrected, the preliminary results were interesting in that when variability in detection was large relative to the mean, quite different results were seen for estimates of population abundance, recruitment and population trend, and estimation biases were exacerbated. It would be interesting to experimentally control the variance about detection levels and approach the analysis similar to Chapter 4. As it is possible for variance in detection to be correlated with nester abundance, survey duration, observer experience, or monitoring technologies this would be another interesting area to further explore in the MoSE framework.

Perhaps one of the most important message from my research is the importance of evaluating breeding probability, size-at-maturity and age-at-maturity for inter-annual variability and temporal trends. These life history traits are not easy to monitor in sea turtles, especially size- and age-at-maturity, but the importance of these traits to population assessments and to accurately detecting changes in population abundance are paramount (Bjorndal et al. 2010). Breeding probability can be accurately estimated from mark-recapture efforts, albeit both labor-intensive and costly (Kendall & Bjorkland 2001). However, more accurate techniques to measure size- and age-at-maturity are needed, such as laparoscopic or genetic indicators of maturity (Limpus et al. 2003, Hamann et al. 2010). Concerted efforts to improve aging techniques of sea turtles are making advancements and should also aid in this effort (Goshe et al. 2010, Snover et al. 2011, Avens et al. 2013, 2015, Tomaszewicz et al. 2015).

Long-term data sets are necessary to adequately estimate changes in demographic indicators, and to assess population size, changes in nester recruitment, and population trends. Yet studies that result in appropriate datasets are becoming increasingly difficult to maintain. For example, the United States Fish and Wildlife Service recently reduced funding for monitoring Kemp’s ridley sea turtles (*Lepidochelys kempii*) in the Gulf of Mexico after 35 years, despite a substantial slowing of population growth since 2009 (Plotkin & Bernardo 2014). Many sea turtle populations are data-poor and occur in remote locations that make logistically-challenging nightly beach surveys impossible. Further, many existing monitoring programs have limited budgets, or are facing budget cuts, or lack infrastructure maintenance to sustain monitoring and ultimately make long-term monitoring infeasible. In Hawaii, after 40 years of monitoring nesting on East Island, a storm destroyed the primary field camp on Tern Island in December 2012, and lacking funding to rebuild the field camp, monitoring efforts on East Island have since been *ad hoc*; this storm effectively ended one of the longest running individual monitoring programs of sea turtles globally (Nurzia Humburg & Balazs 2014). Because of limited public and governmental support for long-term funding and logistical challenges to accessing rookeries, sea turtle biology needs a sea change in how populations are monitored. Monitoring programs, either out of choice or necessity, can start to optimize the program to enhance data accuracy and reliability, and should also consider within season adjustments to the survey timeframe (Jackson et al. 2008, Sims et al. 2008, Whiting et al. 2013). In Chapter 4, the results suggest that the historical legacy of impacts can influence the accuracy of monitoring data used to assess population trends and nester recruitment. Monitoring programs may take this information into consideration and tailor monitoring efforts so that survey duration, detection levels (and variability) can be suited to the particular population. This could optimize monitoring so that the most information can be gleaned from nesting beach surveys. Further, my research can provide justification for the need for at least 10 years of nesting surveys to adequately estimate population trend, and potentially longer when impacts to younger age classes have occurred.

Determining which data streams provide the most accurate estimates of population status, evaluating the effects of measurement error and environmental uncertainties on the accuracy of monitoring, and measuring the improvements in status assessment with increasing representativeness and time series length will ultimately benefit sea turtles, and endangered species in general, by allowing biologists and conservation managers to improve their monitoring programs. In all, it is essential to consider the goals of a monitoring plan and intended data stream before initiating a monitoring project. Our results suggest detection level, impact legacy, process error, sampling bias, and population trajectory can all influence the accuracy of population assessments when using data from nesting beaches. Important data from monitoring individual nesters and nests can give insight into the population status, but careful consideration of all of these factors is warranted. Notably, the biggest contributors towards increasing the accuracy of the three population status indicators evaluated here, abundance, recruitment and population trend, were different for each. Thus, if a monitoring program is striving to accurately estimate all three indicators it would be necessary to make improvements on multiple fronts; i.e. detection level, reducing sampling biases, and qualitatively assign population trajectory. In all, because of the life history of sea turtles, long-lived, late age-at-maturity, and highly migratory, monitoring over long time spans is useful for accurate population assessments. If most late maturing sea turtle populations follow the general patterns I found in my model based on Hawaiian green turtles, I would make the following recommendations:

1) *A priori* knowledge of general population trajectory (stable, disturbed, recovering), may assist with informed judgements regarding likely biases in trend estimates. Accurately estimating trend is particularly difficult during unstable phases such as during decline and recovery.

2) We suggest as least 10 years of monitoring data are necessary to calculate population trend. If impacts occurred to the younger life stages, and trend is being estimated during recovery

even longer time-series are required. Other research on sampling duration support this conclusion as well (Jackson et al. 2008, Sims et al. 2008).

3) Estimating adult abundance from observed nests is particularly sensitive to clutch frequency-biased sampling. Efforts to accurately estimate clutch frequency should be made. Pairing surveys of nests with focused individual study (i.e. satellite tags) may assist in rookery-specific estimates of clutch frequency (Tucker 2010, Hart et al. 2013).

4) Time-series of nester recruitment (proportion of neophytes) can be extremely useful for population assessments and provides context to population changes observed on nesting beaches (Bjorndal et al. 2010). Accurately determining proportion of neophytes from mark-recapture analysis can be problematic (Piacenza et al. *In press),* but development of physiological or genetic markers or tagging of juveniles in foraging grounds and recaptured at rookeries may help to enhance this (Hamann et al. 2003, Avens et al. 2009, Goshe et al. 2010). Estimates of proportion of neophytes from model outputs were sensitive to age-biased sampling and detection levels. In the field, efforts to expand survey areas beyond historically dense nesting beaches (which may have an older mean age of nesters) to novel nesting sites, presumably utilized by new nesters, may help to alleviate age-bias in sampling, and alternative forms of sampling such as aerial survey may assist in this effort (Witt et al. 2009). Understanding the phenology of neophyte nesting, versus veteran nesters, for example determining if neophytes nest less frequently and arrive at nesting beaches later in the season (Broderick et al. 2003, Stokes et al. 2014), may also decrease errors in estimating recruitment.

5) Nesting beach surveys should strive for the highest detection level possible and reduce interannual variation in detection. Variation in detection levels alone can give a false signal of population size (Pfaller et al. 2013). When detection levels are by necessity low, such as in

populations that are difficult or unsafe to access (Autar 1994, Witt et al. 2009, Whiting & Whiting 2011), the best course of action may be to focus on reducing interannual variation on detection levels, e.g., maintaining strict survey procedures across years, consistent field technician training, consistent length of survey periods over time, etc.

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Appendix A. Supplemental information for Chapter 2

Table A1. Estimates of straight carapace length (SCL) for newly tagged and veteran nesters at East Island, French Frigate Shoals, 1981 – 2010, derived from the top ranked linear mixed model.

Year	Estimated New Tag	New Tag SE	New Tag Lower 95% CI	New Tag Upper 95% CI	Estimated Veteran Nester	Veteran SE	Veteran Lower 95% CI	Veteran Upper 95% CI
1981	90.9253	0.1895	90.25572	91.59488	91.4488	0.1895	90.85864	92.038956
1982	90.8475	0.189	90.10564	91.58936	91.371	0.189	90.62914	91.960176
1983	90.6113	0.2837	89.68481	91.53779	91.1348	0.2837	90.20831	91.909588
1984	90.74532	0.1734	89.8494	91.64124	91.26882	0.1734	90.3729	91.82742
1985	90.75639	0.242	89.94221	91.57057	91.27989	0.242	90.46571	91.972946
1986	89.6385	0.337	88.50366	90.77334	90.162	0.337	89.02716	91.041256
1987	89.4076	0.3317	88.09695	90.71825	89.9311	0.3317	88.62045	90.799968
1988	89.3011	0.1492	88.35854	90.24366	89.8246	0.1492	88.88204	90.335768
1989	90.0224	0.1392	89.45714	90.58766	90.5459	0.1392	89.98064	91.037468
1990	89.9465	0.1551	89.36967	90.52333	90.47	0.1551	89.89317	90.992732
1991	89.3731	0.1613	88.75296	89.99324	89.8966	0.1613	89.27646	90.431484
1992	90.4865	0.1236	89.9281	91.0449	91.01	0.1236	90.4516	91.470992
1993	90.1847	0.1406	89.66687	90.70253	90.7082	0.1406	90.19037	91.202512
1994	90.6786	0.1536	90.10197	91.25523	91.2021	0.1536	90.62547	91.721892
1995	90.6514	0.1292	90.09711	91.20569	91.1749	0.1292	90.62061	91.646868
1996	90.2013	0.1217	89.70954	90.69306	90.7248	0.1217	90.23304	91.182068
1997	90.4168	0.1146	89.95365	90.87995	90.9403	0.1146	90.47715	91.383652
1998	91.0679	0.1827	90.48519	91.65061	91.5914	0.1827	91.00869	92.168228
1999	90.1615	0.1339	89.54096	90.78204	90.685	0.1339	90.06446	91.16618
2000	89.9799	0.1214	89.47951	90.48029	90.5034	0.1214	90.00301	90.96008
2001	90.3448	0.1183	89.87499	90.81461	90.8683	0.1183	90.39849	91.318904
2002	90.5251	0.1122	90.07332	90.97688	91.0486	0.1122	90.59682	91.487248
2003	91.2229	0.1296	90.74897	91.69683	91.7464	0.1296	91.27247	92.219152
2004	89.963	0.108	89.4973	90.4287	90.4865	0.108	90.0208	90.916916
2005	90.0706	0.1174	89.62882	90.51238	90.5941	0.1174	90.15232	91.04294
2006	90.2549	0.1154	89.79861	90.71119	90.7784	0.1154	90.32211	91.22332
2007	90.74062	0.115	90.28904	91.1922	91.26412	0.115	90.81254	91.708256
2008	91.2036	0.1127	90.75731	91.64989	91.7271	0.1127	91.28081	92.166728
2009	91.0038	0.1269	90.53418	91.47342	91.5273	0.1269	91.05768	91.99476
2010	90.7972	0.1116	90.54848	91.04592	91.3207	0.1116	91.07198	91.539436

Estimating Clutch Frequency using MSORD Models

In addition to the other demographic indicators estimated in this study, clutch frequency, or the number of nests laid in a season, is an important demographic indicator used in population models. Clutch frequency is used to estimate nester abundance from the total number of nests when only nests are monitored, egg production and cohort strength (National Research Council, 2010). Clutch frequency could be influenced by age structure of females or environmental conditions (Miller 1997).

In intensively monitored sea turtle populations, clutch frequency can be measured directly through re-sights of females within a nesting season, but the estimate will almost always be biased low due to missed nesting events. The MSORD model also calculates a derived parameter, residence time, or the average number of secondary survey periods that an individual spent in the study area during a primary period. This parameter could give an indication of clutch frequency. Residence time was modeled as a function of the time since arrival to the nesting beach (e.g., the probability a female lays a clutch is dependent on the number of clutches already laid), and as our data set only contains breeding females on the nesting beach, allowed for derivation of clutch frequency from the model output (Kendall, 2013).

Clutch frequency from MSORD displayed wide temporal fluctuations (Fig. A1). The top-ranked model included temporal effects on φ and p_{ent}, the parameters used to derive clutch frequency. The estimates of clutch frequency ranged from 1.05 (0.0367981 – 1.125 95% CI) to 4.96 (-30.7 – 40.6 95% CI). However, we found a strong relationship between the estimated clutch frequency and the number of secondary sampling periods (Fig. A2). A low number of secondary sampling periods biased the estimates of clutch frequency low. If the number of secondary survey periods is restricted to ≥ 5, then the estimate of clutch frequency ranged from

1.39 (1.18 – 1.60 95% CI) to 4.96 (-30.7 – 40.6 95% CI). In all, these estimates are still greater than previously published and show a wide range of variability across years (Table 2.1). Based on these results, it is important to carefully consider the length of the survey season when setting up a survey with the goal of estimating clutch frequency.

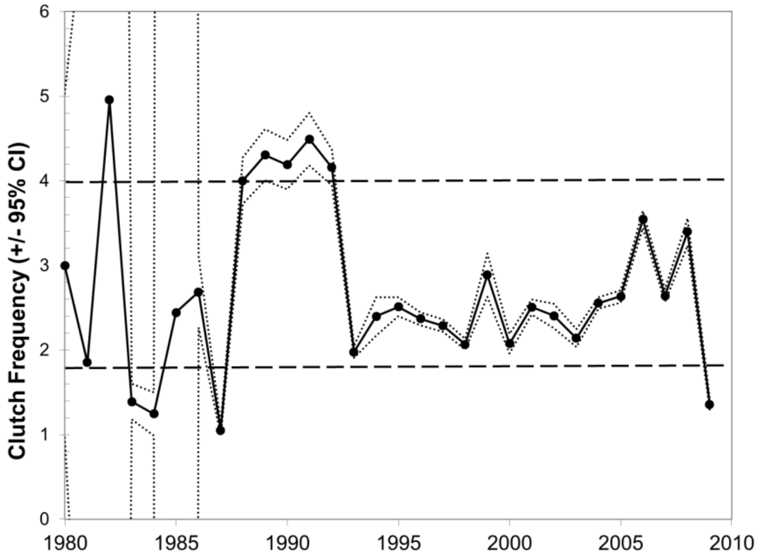

Figure A1. Annual estimates of clutch frequency (nests/year) with 95% confidence intervals based on multistate open robust design models (MSORD) from 1980-2009. Dashed lines refer to published estimates of clutch frequency.

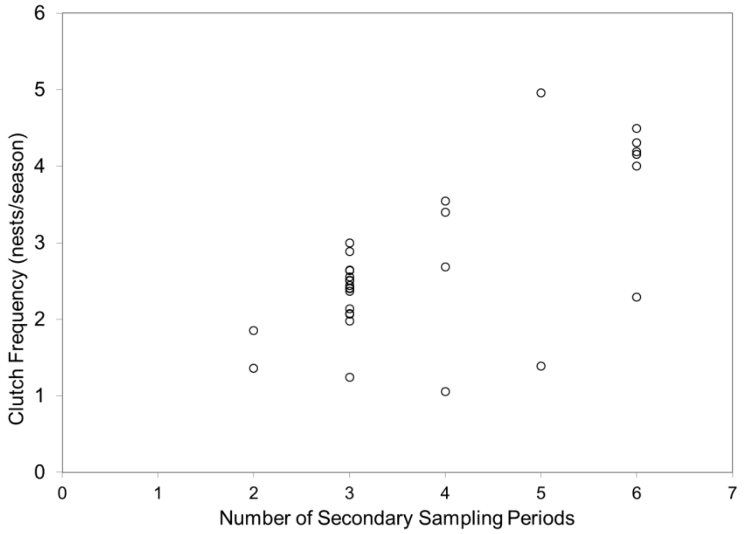

Figure A2. Estimates of clutch frequency as a function of the number of secondary survey periods.

Appendix B. Supplemental Information to Chapter 3

Table B1. Local sensitivity index values S_t of the four output parameters: adult abundance, nester abundance, discrete population growth rate, and nester recruitment.

Input Parameter (reference value)	**Min**	**Max**	**Output Parameter**	**Sensitivity (St)**			
				Biological Minimum	**95% of Baseline**	**105% of Baseline**	**Biological Maximum**
Adult survival rate (0.929)	0.88	0.98	Adult abundance		-2820.95	3754.66	
			Nester abundance		-285.69	207.10	
			Nester recruitment		116.44	-60.64	
			Population growth rate		49.01	-250.45	
Age-at-maturity (19+11, SD=11)	29 (19)	31 (45)	Adult abundance	139.06	548.90	-511.96	-113.51
			Nester abundance	15.32	40.76	-66.83	-10.623
			Nester recruitment	0.23	-11.84	18.013	-7.083
			Population growth rate	-10.54	-45.23	26.67	-4.32
Breeding probability (0.2519, SD = 0.114)	0.24 (0.077)	0.26 (0.5)	Adult abundance	-188.937	-97.27	108.20	40.61
			Nester abundance	-26.13	-42.52	43.071	9.25
			Nester recruitment	14.31	23.24	-29.66	-8.58
			Population growth rate	1.26	-2.93	-6.53	-10.19
Climate influence on breeding probability (0.75)	0.71	0.79	Adult abundance		-50.89	-33.43	
			Nester abundance		1.63	-19.29	
			Nester recruitment		14.73	9.68	
			Population growth rate		85.21	114.33	
Climate Threshold (0.90)	0.86	0.95	Adult abundance		-11.44	32.70	
			Nester abundance		6.87	9.53	
			Nester recruitment		3.56	0.77	
			Population growth rate		48.35	47.93	
Clutch frequency (4, SD=4)	3.8 (1.053)	4.2 (4.96)	Adult abundance	-246.56	-323.89	302.68	308.86
			Nester abundance	-27.31	-33.43	55.76	22.90
			Nester recruitment	-2.47	1.70	-35.87	-2.36
			Population growth rate	-0.037	39.67	-18.31	-23.10

Table B1 (Continued). Local sensitivity index values S_t of the four output parameters: adult abundance, nester abundance, discrete population growth rate, and nester recruitment.

Input Parameter (reference value)	**Min**	**Max**	**Output Parameter**	**Sensitivity (St)**			
				Biological Minimum	**95% of Baseline**	**105% of Baseline**	**Biological Maximum**
Clutch size (8, SD=8)	7.6 (6.92)	8.4 (10.06)	Adult abundance	-373.36	-397.04	413.07	394.33
			Nester abundance	-40.76	-40.89	17.76	27.48
			Nester recruitment	6.86	13.029	21.44	-6.26
			Population growth rate	27.62	20.35	-6.33	-27.95
Hatchling production carrying capacity (500)	475	525	Adult abundance		-159.75	138.98	
			Nester abundance		-31.22	3.82	
			Nester recruitment	-0.40	-6.69	7.87	-0.055
			Population growth rate		-14.90	12.81	
Hatchling production slope (0.15)	0.14	0.16	Adult abundance		90.11	-102.80	
			Nester abundance		-13.52	-38.06	
			Nester recruitment		21.73	11.66	
			Population growth rate		-22.14	-58.60	
Neritic juvenile survival rate (0.824)	0.78	0.87	Adult abundance		-2358.03	2544.16	
			Nester abundance		-281.12	143.91	
			Nester recruitment		13.02	-4.43	
			Population growth rate		27.56	-201.68	
Removals (15)	14	6	Adult abundance		-124.15	104.56	
			Nester abundance		-15.52	14.85	
			Nester recruitment		11.18	-1.28	
			Population growth rate		14.27	-26.84	
Sub-adult survival rate (0.876)	0.83	0.92	Adult abundance		-3994.03	1521.66	
			Nester abundance		-7607.63	2816.93	
			Nester recruitment		-1.24	-1.07	
			Population growth rate		-13.02	-131.36	

Green Sea Turtle Agent-Based Model NetLogo Code

```
;;; Green Sea Turtle ABM - The impact of individual variability in demographic rates on population recovery and
Monitoring Strategy Evaluation

;; Define global parameters
globals [
  year
  timesHere
  timesHere2
  timesGo
  timesAge
  maxTicks
  numberturtles
  numberHatchlings
  numberPelagicJuveniles
  numberNeriticJuveniles
  numberSubadults
  numberNeophytes
  numberAdults
  rh ; intrinsic rate of increase for Ricker function for hatchling production
  Climate ; Climate index to simulate good and poor environmental conditions annually
  q-norm ; normal random variable for logit-normal distribution for selecting detection stochastic variable
  q ; catchability coefficient for monitoring nesters
  q-std-dev ; Standard deviation used for setting q
  scale-factor ; scaling factor for Super Individual of hatchlings and pelagic juveniles for initialization of SAD
  SampleSize
  countNesters
  countNesters2
  Nesters
  Monitored-Nesters
  Catch ; number of turtles removed during harvest
  Catch_hatchlings
  BreedProb
  Nests
  Monitored-Nests
 ]

;; Define life history stages
breed [ Hatchlings Hatchling ] ; Hatchlings
breed [ PelagicJuveniles PelagicJuvenile ] ; Pelagic juveniles
breed [ NeriticJuveniles NeriticJuvenile ] ; neritic juveniles
breed [ Subadults Subadult ] ; subadults
breed [ Neophytes Neophyte ] ; Neophyte Nesters
breed [ Adults Adult ] ; adults
;; Define turtle specific parameters
turtles-own [ age AgeClass reprostatus reprostatus2 times-nested remigs remigs_old ClutchFrequency ClutchSize
newHatchlings AgeMaturity
  ] ; ; reprostatus = nester or skip-nester, newHatchlings = reproduce new hatchlings , times-nested = count how
many times in lifetime nested, remigs=how many years since last nesting, AgeClass = Hatchling, PelagicJuvenile
NeriticJuvenile Subadult Neophyte Adult

;; Initialization procedures
to setup
  clear-all
  ;set Monitored-Nesters no-turtles
```

```
 ifelse DetectA = 3.841832 [set q-std-dev 2.417518] [ifelse DetectA = -1.643709E-9 [set q-std-dev 0.41646]
   [ifelse DetectA = -2.216764 [set q-std-dev 0.221504] [set q-std-dev 0]]] ;ifelse DetectA >= 0.94 [set q-std-dev
0.025] [set q-std-dev (0.2165 * DetectA)]
 set q-norm random-normal DetectA q-std-dev ;while [(q <= 0) or (q > 1.0) ] [ set q random-normal DetectA q-std-
dev ]; random-normal 0.79 0.17 while [(q <= 0.3) or (q >= 1.0) ] [ set q random-normal 0.75 0.25 ]   ; Catchability
coefficient = p(t.) top ranked model MSORB Mark
 set q 1 / (1 + (exp (- q-norm)))
 set scale-factor 5.4 ; per life table
 set rh rhA ;0.15
 set numberHatchlings round (499311 / scale-factor) ; based on Stable age distribution from age structured Matrix
projection model and Hatchlings and Pel. Juveniles scaled for Super-Individuals
 set numberPelagicJuveniles round (508129 / scale-factor);
 set numberNeriticJuveniles 161297
 set numberSubadults 73388
 set numberNeophytes 1416
 set numberAdults 18909
 set maxTicks 352;601
 set year 0
 set timesHere 0
 set timesHere2 0
 set timesGo 0
 set timesAge 0
 set Climate random-float 1.0
 ifelse BreedProbVariability [set BreedProb random-gamma BPGammaShape 19.06008193] [set BreedProb
BreedProbA];[set BreedProb random-normal BreedProbA 0.114 while [(BreedProb < 0) or (BreedProb >= 1.01) ]
[ set BreedProb random-normal BreedProbA 0.114 ]] [set BreedProb BreedProbA]
 ;set breedprob random-normal BreedProbA 0.114 while [(breedprob < 0) or (breedprob >= 1.01)] [set breedprob
random-normal 0.251900417 0.114083441]


;; Initializing individuals for start of model run
 set-default-shape turtles "turtle"

create-Hatchlings numberHatchlings [ setxy random-xcor random-ycor
  set color magenta - 1
  set age 0
  set times-nested 0
  set remigs 0
  set remigs_old remigs
  ifelse AgeMatVariability [
  set AgeMaturity 19 + random-poisson AgeMatRand] [set AgeMaturity AgeMatA] ; 30 (median of 40 and 22) - 17
+ 1 = 14 Zug 2001 and Van Houtan et al. 2014
 ifelse ClutchFreqVariability [
  set ClutchFrequency random-poisson ClutchFreqA] [set ClutchFrequency ClutchFreqA] ; ; mean 4-1 = 3; mean =
3.37304065, SD=1.254475826 (MSORD Program Mark, with Sec Seasons >=4)
  ifelse ClutchSizeVariability [
  set ClutchSize random-poisson ClutchSizeA] [set ClutchSize ClutchSizeA]
  if age = AgeMaturity [set breed Neophytes ]
 if age > AgeMaturity  [set breed Adults]
 ifelse (breed = Adults) or (breed = Neophytes) [set reprostatus "nester"]
 [set reprostatus "skip-nester"]
 set reprostatus2 reprostatus
    ]

 create-PelagicJuveniles numberPelagicJuveniles [ setxy random-xcor random-ycor
  set color magenta - 1
```

```
  set age 2 + random 1
  set times-nested 0
  set remigs 0
  set remigs_old remigs
  ifelse AgeMatVariability [
  set AgeMaturity 19 + random-poisson AgeMatRand] [set AgeMaturity AgeMatA] ; 30 (median of 40 and 22) - 17 + 1 = 14 Zug 2001 and Van Houtan et al. 2014
  ifelse ClutchFreqVariability [
  set ClutchFrequency random-poisson ClutchFreqA] [set ClutchFrequency ClutchFreqA] ; ; mean 4-1 = 3; mean = 3.37304065, SD=1.254475826 (mark, with Sec Seasons >=4)
  ifelse ClutchSizeVariability [
  set ClutchSize random-poisson ClutchSizeA] [set ClutchSize ClutchSizeA]
 if age = AgeMaturity [set breed Neophytes ]
 if age > AgeMaturity  [set breed Adults]
 ifelse (breed = Adults) or (breed = Neophytes) [set reprostatus "nester"]
 [set reprostatus "skip-nester"]
 set reprostatus2 reprostatus
    ]

create-NeriticJuveniles numberNeriticJuveniles [ setxy random-xcor random-ycor
  set color magenta - 1
  set age 4 + random 7
  set times-nested 0
  set remigs 0
  set remigs_old remigs
  ifelse AgeMatVariability [
  set AgeMaturity 19 + random-poisson AgeMatRand] [set AgeMaturity AgeMatA] ; 30 (median of 40 and 22) - 17 + 1 = 14 Zug 2001 and Van Houtan et al. 2014
  ifelse ClutchFreqVariability [
  set ClutchFrequency random-poisson ClutchFreqA] [set ClutchFrequency ClutchFreqA] ; ; mean 4-1 = 3; mean = 3.37304065, SD=1.254475826 (mark, with Sec Seasons >=4)
  ifelse ClutchSizeVariability [
  set ClutchSize random-poisson ClutchSizeA] [set ClutchSize ClutchSizeA]   if age = AgeMaturity [set breed Neophytes ]
 if age > AgeMaturity  [set breed Adults]
 ifelse (breed = Adults) or (breed = Neophytes) [set reprostatus "nester"]
 [set reprostatus "skip-nester"]
 set reprostatus2 reprostatus
    ]

create-Subadults numberSubadults [ setxy random-xcor random-ycor
  set color magenta - 1
  ;set AgeClass "Adult"
  set age 11
  set times-nested 0
  set remigs 0
  set remigs_old remigs
  ifelse AgeMatVariability [
  set AgeMaturity 19 + random-poisson AgeMatRand] [set AgeMaturity AgeMatA] ; 30 (median of 40 and 22) - 17 + 1 = 14 Zug 2001 and Van Houtan et al. 2014
  ifelse ClutchFreqVariability [
  set ClutchFrequency random-poisson ClutchFreqA] [set ClutchFrequency ClutchFreqA] ; ; mean 4-1 = 3; mean = 3.37304065, SD=1.254475826 (mark, with Sec Seasons >=4)
  ifelse ClutchSizeVariability [
  set ClutchSize random-poisson ClutchSizeA] [set ClutchSize ClutchSizeA] ; mean 98 - 85 = 13 scaled to survivorship to neritic juvenile stage, avg survivorship = 8.5 see survival excel worksheet
```

```
  if age = AgeMaturity [set breed Neophytes ]
  if age > AgeMaturity  [set breed Adults]
  ifelse (breed = Adults) or (breed = Neophytes) [set reprostatus "nester"]
  [set reprostatus "skip-nester"]
  set reprostatus2 reprostatus
     ]

create-Neophytes numberNeophytes [ setxy random-xcor random-ycor
   set color black
   ;set AgeClass "Adult"
   ifelse AgeMatVariability [
   set AgeMaturity 19 + random-poisson AgeMatRand] [set AgeMaturity AgeMatA]
   set age AgeMaturity
   set times-nested 0
   set remigs 0
   set remigs_old remigs
   ifelse ClutchFreqVariability [
   set ClutchFrequency random-poisson ClutchFreqA] [set ClutchFrequency ClutchFreqA] ; ; mean 4-1 = 3; mean =
3.37304065, SD=1.254475826 (mark, with Sec Seasons >=4)
   ifelse ClutchSizeVariability [
  set ClutchSize random-poisson ClutchSizeA] [set ClutchSize ClutchSizeA] ; mean 98 - 85 = 13 scaled to
surivorship to neritic juvenile stage, avg survivorship = 8.5 see survival excel worksheet
  if age = AgeMaturity [set breed Neophytes ]
  if age > AgeMaturity  [set breed Adults]
  ifelse (breed = Adults) or (breed = Neophytes) [set reprostatus "nester"]
  [set reprostatus "skip-nester"]
  set reprostatus2 reprostatus
     ]


create-Adults numberAdults [ setxy random-xcor random-ycor
   set color magenta - 1
   ifelse AgeMatVariability [
   set AgeMaturity 19 + random-poisson AgeMatRand] [set AgeMaturity AgeMatA]
   set age 28 + random 57
   set times-nested random 10
   set remigs random 4
   set remigs_old remigs
   ifelse ClutchFreqVariability [
   set ClutchFrequency random-poisson ClutchFreqA] [set ClutchFrequency ClutchFreqA] ; ; mean 4-1 = 3; mean =
3.37304065, SD=1.254475826 (mark, with Sec Seasons >=4)
   ifelse ClutchSizeVariability [
   set ClutchSize random-poisson ClutchSizeA] [set ClutchSize ClutchSizeA]    if age = AgeMaturity [set breed
Neophytes ]
  if age > AgeMaturity  [set breed Adults]
  ifelse (breed = Adults) or (breed = Neophytes) [set reprostatus "nester"]
  [set reprostatus "skip-nester"]
  set reprostatus2 reprostatus
     ]

set countNesters2 count turtles with [ reprostatus = "nester"]
set SampleSize round(q * countNesters2)
set Monitored-Nesters no-turtles ;(n-of SampleSize turtles with [reprostatus = "nester"])

ask patches [ set pcolor cyan + 3 ]
```

```
reset-ticks

end

;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;; start procedures ;;;;;;;;;;;;;;;;;;;;;;;;;;

to go
tick
set year year + 1
if ticks >= maxTicks [stop]
if not any? turtles [ stop ]
 set q-norm random-normal DetectA q-std-dev ;while [(q <= 0) or (q > 1.0) ] [ set q random-normal DetectA q-std-dev ]; random-normal 0.79 0.17 while [(q <= 0.3) or (q >= 1.0) ] [ set q random-normal 0.75 0.25 ]   ; Catchability coefficient = p(t.) top ranked model MSORB Mark
  set q 1 / (1 + (exp (- q-norm)));set q random-normal DetectA q-std-dev while [(q <= 0) or (q > 1.0) ] [ set q random-normal DetectA q-std-dev ]; random-normal 0.79 0.17 while [(q <= 0.3) or (q >= 1.0) ] [ set q random-normal 0.75 0.25 ]   ; Catchability coefficient = p(t.) top ranked model MSORB Mark
; if ticks < 175 [set q random-normal DetectA 0.171 while [(q <= 0) or (q > 1.0) ] [ set q random-normal DetectA 0.25 ]] if (ticks >= 175)  [set q ((0.9428 * ln ticks) - 4.6572) while [(q <= 0) or (q > 1.0) ] [ set q ((0.9428 * ln ticks) - 4.6572)]] ;p increasing over time
;if ticks < 175 [set q random-normal DetectA 0.171 while [(q <= 0) or (q > 1.0) ] [ set q random-normal DetectA 0.25 ]] if (ticks >= 175)  [set q ((0.1309 * ln countNesters2) - 0.158) while [(q <= 0) or (q > 1.0) ] [ set q ((0.9428 * ln ticks) - 4.6572)] ]  ;p function of nester abundance
ifelse BreedProbVariability [set BreedProb random-gamma BPGammaShape 19.06008193] [set BreedProb BreedProbA] ;[set BreedProb random-normal BreedProbA 0.114 while [(BreedProb < 0) or (BreedProb >= 1.01) ] [ set BreedProb random-normal BreedProbA 0.114 ]] [set BreedProb BreedProbA]
;set breedprob random-normal BreedProbA 0.114 while [(breedprob <= 0) or (breedprob >= 1.01)] [set breedprob random-normal 0.251900417 0.114083441]
set Climate random-float 1.0
Climate_BP
Harvest
Harvest_Nests
ask turtles [
grow_old
set timesGo timesGo + 1
survive
     ]
ask Adults [Nesters?]
set Nesters (turtles with [reprostatus = "nester"])
set countNesters count Nesters ; used for Hatchling Production equation
ask Nesters [Hatchling_Production]
;ask Neophytes [Hatchling_Production]
;ask Nesters [Remig_DD_Climate]
;ask Neophytes [Remig_DD_Climate]
;ask Adults [Remig_2]
ask Nesters [reproduce]
;ask Neophytes [reproduceNeos]
Monitor
update-outputs
end

to Climate_BP
 ifelse ClimateBPVariability [ if Climate > ClimateThresh [
 set BreedProb BreedProb * BP-Climate-influence]] []
end
```

```
to grow_old
set timesAge timesAge + 1
set age age + 1
 if age > 85 [die]
 if age <= 1 [set breed Hatchlings]
 if (age > 1) and (age < 4) [set breed PelagicJuveniles]
 if (age >= 4) and (age < 11) [set breed NeriticJuveniles]
 if (age >= 11) and (age < AgeMaturity) [set breed Subadults]
 if (age = AgeMaturity) [set breed Neophytes set reprostatus "nester" set reprostatus2 "nester" set color black] ;and (times-nested < 1)
 if (age > AgeMaturity) [set breed Adults set color magenta - 1] ; and (times-nested >= 1)
end

to Harvest
ifelse Harvest_on
    [
if ticks < 200 []
if (ticks >= 200) and (ticks < 251) [ set Catch (round ((count turtles with [age >= 11]) / F)) (ask n-of Catch turtles with [age >= 11] [die] )
   ] ;set Catch_hatchlings (round (count hatchlings) / F_hatch) (ask n-of Catch_hatchlings hatchlings [die] )
if ticks >= 250 []
]
 []
end


to Harvest_Nests
ifelse Harvest_Nests_on
    [
if ticks < 200 []
if (ticks >= 200) and (ticks < 251) [ set Catch_hatchlings ((round (count hatchlings) / F_hatch)) (ask n-of Catch_hatchlings hatchlings [die])
   ] ;set Catch_hatchlings (round (count hatchlings) / F_hatch) (ask n-of Catch_hatchlings hatchlings [die] )
if ticks >= 250 []
]
 []
end

to survive
;ifelse (ticks > 100) and (Climate < 0.9) [
; set juvenile2Survival 0.824
; set subadultSurvival 0.876
; set adultSurvival 0.929]
; [set juvenile2Survival 0.7416 ; 0.9*0.824
; set subadultSurvival 0.7884 ; 0.9*0.876
; set adultSurvival 0.8361 ]; .9*0.929 ;  ]]
;if AgeClass = "Hatchling" [if random-float 1.0 > hatchlingSurvival[ die]]  ;;hatchling survival 0.786 (sd=19.2, Niethammer et al. 1997) (0.71 (Van Buskirk and Crowder 1994 FFS HI)
;if AgeClass = "PelagicJuvenile" [if random-float 1.0 > juvenile1Survival [ die]] ;;oceanic juvenile survival 0.8804 (0.835 - 0.927 95 % CI Chaloupka and Limpus 2005 S GBR)
if breed = NeriticJuveniles [if random-float 1.0 > juvenile2Survival [ die]] ;; neritic juvenile survival 0.8804 (0.835 - 0.927 95 % CI Chaloupka and Limpus 2005 S GBR, 5-18 yrs)
if breed = Subadults [if random-float 1.0 > subadultSurvival [ die]] ;; subadult and adult survival 0.8474, ( 0.79-0.91 95% CI, Chaloupka and Limpus 2005 S GBR, 18-35 years)
if breed =  Neophytes [set timesHere timesHere + 1 if random-float 1.0 > adultSurvival [die]]
if breed = Adults [set timesHere timesHere + 1 if random-float 1.0 > adultSurvival [die]]
```

```
stop
end

to Nesters?
ifelse remigs = 0 [
   set reprostatus "skip-nester"  set remigs remigs + 1]
[
ifelse random-float 1.0 < BreedProb [set reprostatus "nester"] [set reprostatus "skip-nester" set remigs remigs + 1]]
stop
end

to Hatchling_Production
set newHatchlings round(ClutchSize * ClutchFrequency) * exp (rh * ( 1 - (countNesters / K_nesters))) ;; Ricker
Function N(t+1) = (CS*CF) *exp(rh[1-(N(t)/K)])  Alt form of Logistic: X[t+1] = X[t] + r * X[t] * (1 – X[t] / K)
density dependence if number hatchlings produce per capita
   if newHatchlings < 0 [set newHatchlings 0]
end

to reproduce
; ifelse reprostatus = "skip-nester"
;   [ set remigs remigs + 1 stop ]
   ;[
     hatch-Hatchlings newHatchlings [ ; inherited by new
      set age 0
      set color blue - 1
      setxy random-xcor random-ycor
      set reprostatus "skip-nester"
      set reprostatus2 "skip-nester"
      set times-nested 0
      set remigs 0
      set remigs_old remigs
      ifelse AgeMatVariability [
      set AgeMaturity 19 + random-poisson AgeMatRand] [set AgeMaturity AgeMatA] ; 30 (median of 40 and 22) -
17 + 1 = 14 Zug 2001 and Van Houtan et al. 2014
      ifelse ClutchFreqVariability [
      set ClutchFrequency random-poisson ClutchFreqA] [set ClutchFrequency ClutchFreqA] ; ; mean 4-1 = 3; mean
= 3.37304065, SD=1.254475826 (mark, with Sec Seasons >=4)
      ifelse ClutchSizeVariability [
     set ClutchSize random-poisson ClutchSizeA] [set ClutchSize ClutchSizeA]
           ]
    set times-nested times-nested + 1
    set remigs_old remigs
    set remigs 0
    stop ;]
end

to reproduceNeos

;ifelse Climate > 0.9 [ ]
;[
;set reprostatus "nester"
      hatch-Hatchlings newHatchlings [
      set age 0
      set color green - 1
      setxy random-xcor random-ycor
      set reprostatus "skip-nester"
```

```
      set reprostatus2 "skip-nester"
      set times-nested 0
      set remigs 0
      set remigs_old remigs
      ifelse AgeMatVariability [
      set AgeMaturity 19 + random-poisson AgeMatRand] [set AgeMaturity AgeMatA]
      ifelse ClutchFreqVariability [
      set ClutchFrequency random-poisson ClutchFreqA] [set ClutchFrequency ClutchFreqA] ; ; mean 4-1 = 3; mean
= 3.37304065, SD=1.254475826 (mark, with Sec Seasons >=4)
      ifelse ClutchSizeVariability [
     set ClutchSize random-poisson ClutchSizeA] [set ClutchSize ClutchSizeA]
                 ]
    set times-nested times-nested + 1
    set remigs_old remigs
    set remigs 0
    stop
end


to Monitor
  set Monitored-Nesters no-turtles
  set countNesters2 count Nesters ;turtles with [ reprostatus = "nester"]
  set SampleSize round(q * countNesters2)
  set Monitored-Nesters (n-of SampleSize Nesters) ;turtles with [reprostatus = "nester"]
  ;set Monitored-Nesters (max-n-of SampleSize Nesters [ClutchFrequency]) ; Monitored-Nesters sampled based on
turtles with greatest clutch frequency (better chance of being observed on nesting beach
  ;set Monitored-Nesters (max-n-of SampleSize Nesters [Age]) ; Monitored-Nesters sampled based on oldest turtles
(older turtles have great site fidelity/larger (easier to spot) better chance of being observed on nesting beach
  set Nests sum [ClutchFrequency] of Nesters
  set Monitored-Nests round(q * Nests)
end
```

Appendix C. Supplemental Information to Chapter 4

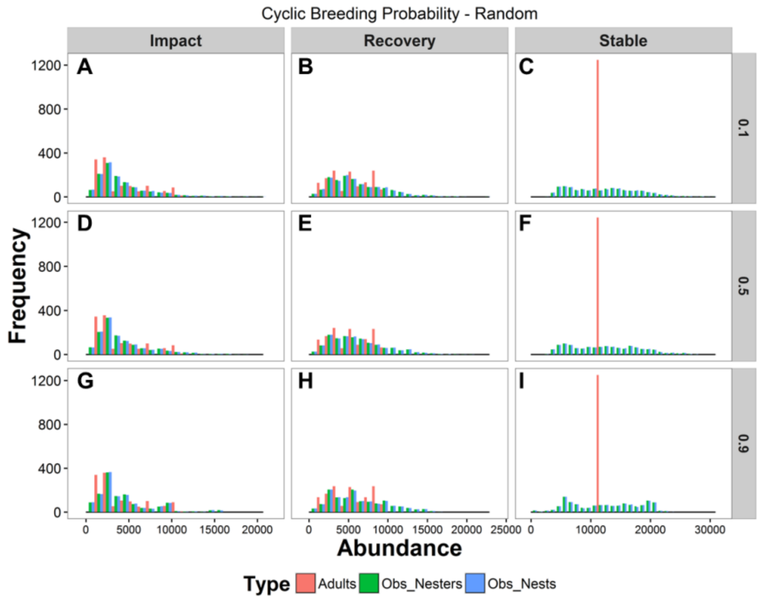

Figure C1. Frequency distributions for true and estimated adult abundance from the Cyclic Breeding Probability with random sampling treatment. Detection levels varied with a mean of 0.1 (red), 0.5 (blue), and 0.9 (green). The diagonal line represents the 1:1 line between the true and estimated abundance. The axes were allowed to change between figures to improve visualization.

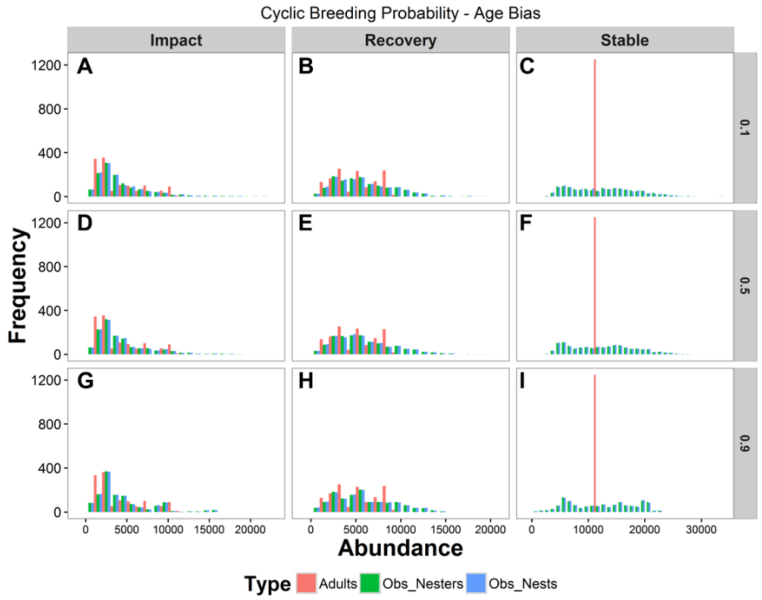

Figure C2. Frequency distributions for true and estimated adult abundance from the Cyclic Breeding Probability with age-biased sampling treatment. Detection levels varied with a mean of 0.1 (red), 0.5 (blue), and 0.9 (green). The diagonal line represents the 1:1 line between the true and estimated abundance. The axes were allowed to change between figures to improve visualization.

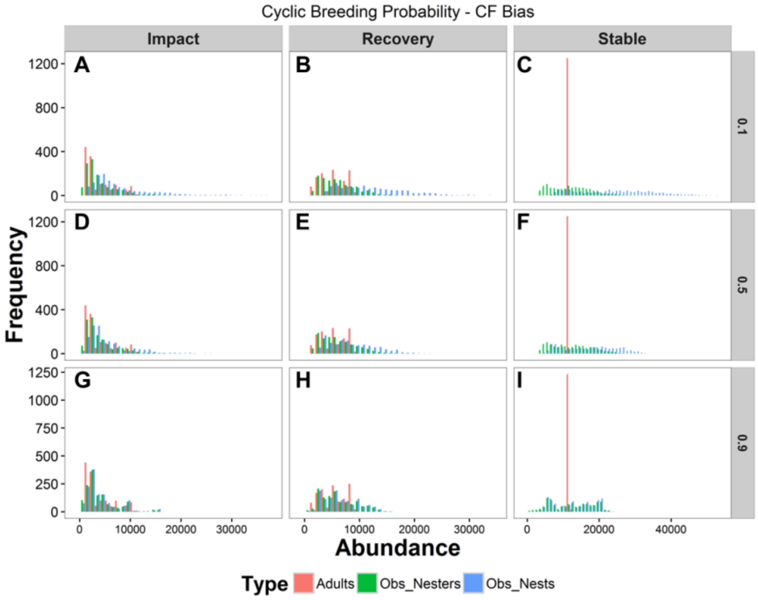

Figure C3. Frequency distributions for true and estimated adult abundance from the Cyclic Breeding Probability with clutch frequency-biased sampling treatment. Detection levels varied with a mean of 0.1 (red), 0.5 (blue), and 0.9 (green). The diagonal line represents the 1:1 line between the true and estimated abundance. The axes were allowed to change between figures to improve visualization.

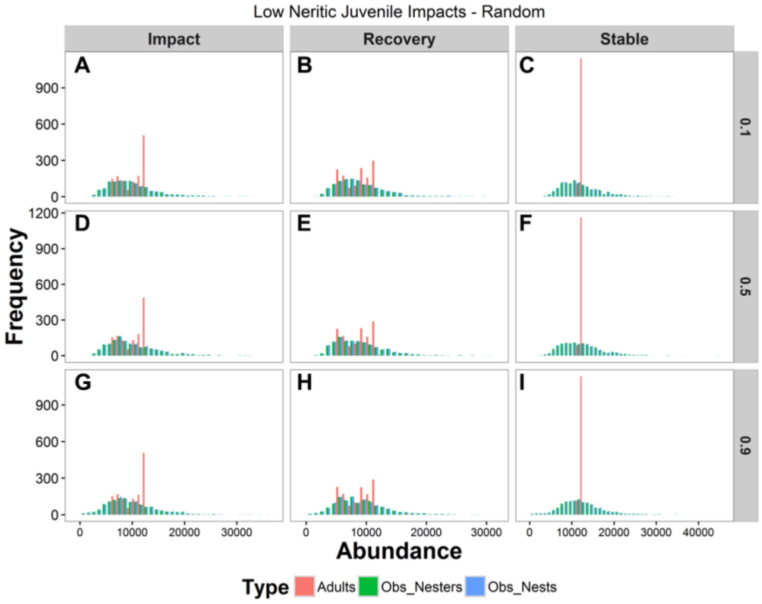

Figure C4. Frequency distributions for true and estimated adult abundance from the Low Severity Neritic Juvenile Impacts with random sampling treatment. Detection levels varied with a mean of 0.1 (red), 0.5 (blue), and 0.9 (green). The diagonal line represents the 1:1 line between the true and estimated abundance. The axes were allowed to change between figures to improve visualization.

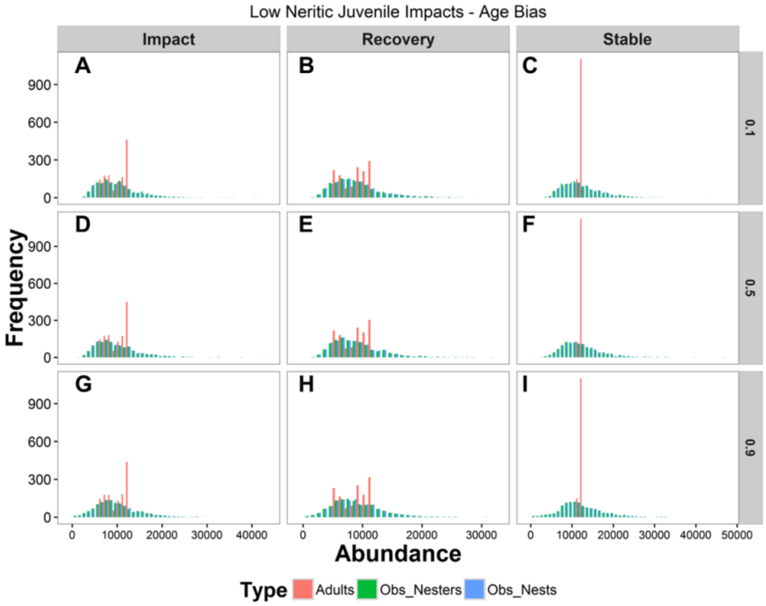

Figure C5. Frequency distributions for true and estimated adult abundance from the Low Severity Neritic Juvenile Impacts with age-biased sampling treatment. Detection levels varied with a mean of 0.1 (red), 0.5 (blue), and 0.9 (green). The diagonal line represents the 1:1 line between the true and estimated abundance. The axes were allowed to change between figures to improve visualization.

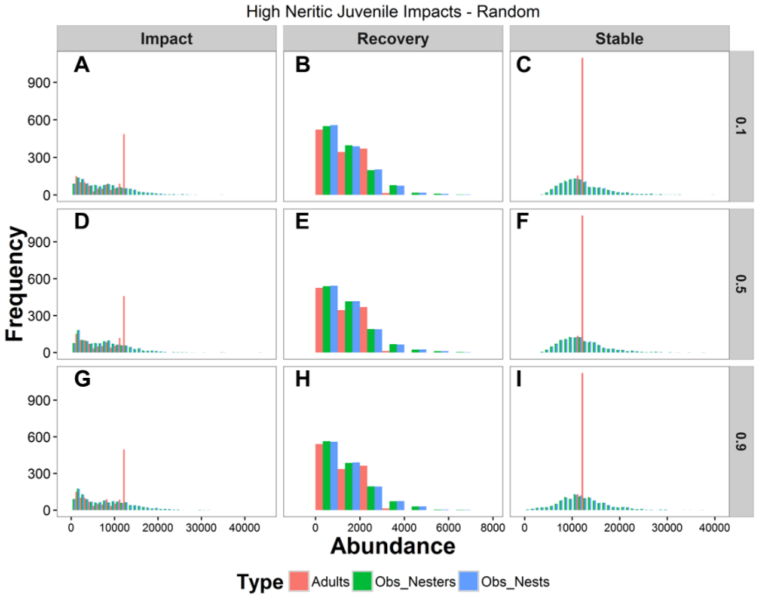

Figure C6. Frequency distributions for true and estimated adult abundance from the High Severity Neritic Juvenile Impacts with random sampling treatment. Detection levels varied with a mean of 0.1 (red), 0.5 (blue), and 0.9 (green). The diagonal line represents the 1:1 line between the true and estimated abundance. The axes were allowed to change between figures to improve visualization.

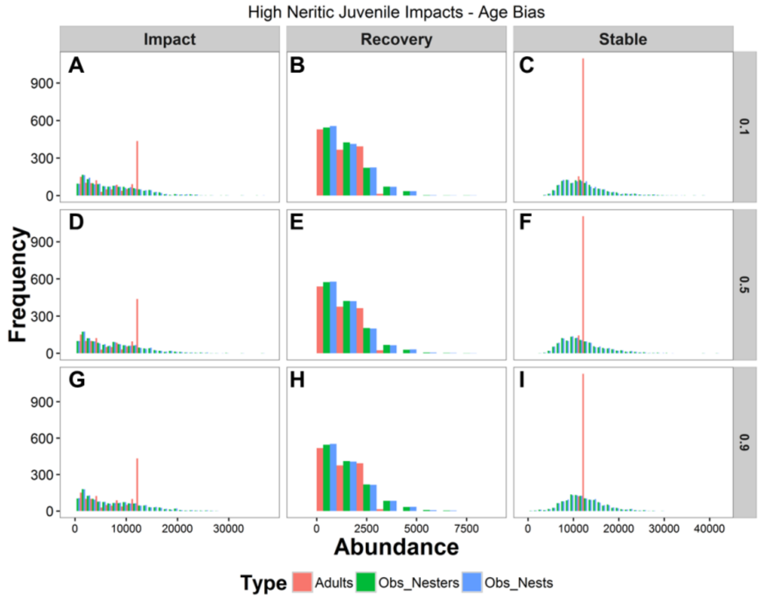

Figure C7. Frequency distributions for true and estimated adult abundance from the High Severity Neritic Juvenile Impacts with age-biased sampling treatment. Detection levels varied with a mean of 0.1 (red), 0.5 (blue), and 0.9 (green). The diagonal line represents the 1:1 line between the true and estimated abundance. The axes were allowed to change between figures to improve visualization.

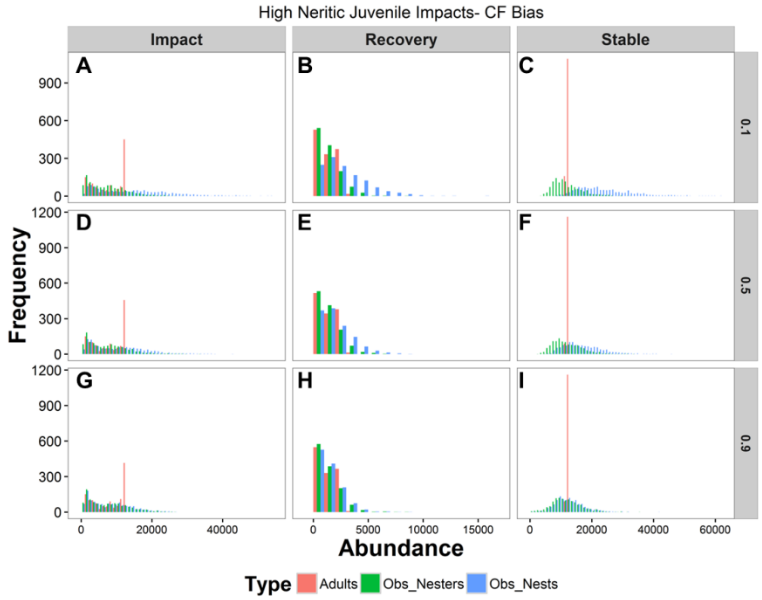

Figure C8. Frequency distributions for true and estimated adult abundance from the High Severity Neritic Juvenile Impacts with clutch frequency-biased sampling treatment. Detection levels varied with a mean of 0.1 (red), 0.5 (blue), and 0.9 (green). The diagonal line represents the 1:1 line between the true and estimated abundance. The axes were allowed to change between figures to improve visualization.

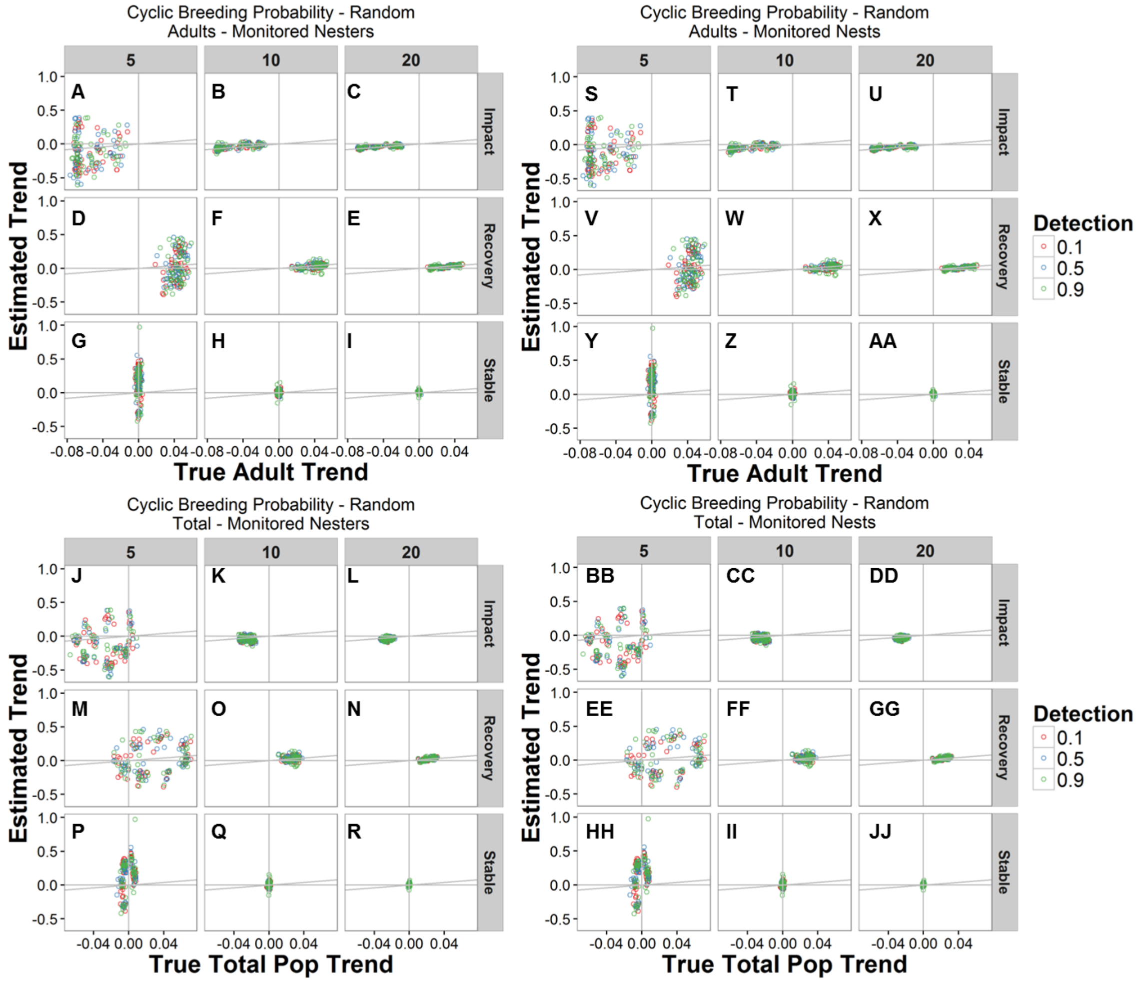

Figure C9. True and estimated adult and total population trend for Cyclic Breeding Probability treatments with random sampling. Estimated total population trend was drawn from observed nesters (J – R) or observed nests (BB – JJ). Population trend is shown for the population trajectories: impact (A – C, J – L, S – U, and BB – CC), recovery (D – F, M – O, V – X, EE – GG), and stable (G – I, P – R, Y – AA, HH – JJ). Trend duration was 5 (A,D, G, J, M, P, S, V, Y, BB, EE, and HH), 10 (B, E, H, K, N, Q, T, W, Z, CC, FF, and II) and 20 (C, E, I, L, N, R, U, X, AA, DD, GG, and JJ) years of monitoring. Estimated adult trend was drawn from observed nesters (A – I) or observed nests (S – AA). Detection levels varied with a mean of 0.1, 0.5, and 0.9. The diagonal line represents the 1:1 line between the true abundance and the estimated abundance. Axis ranges across plots were allowed to vary to enhance visualization of the points.

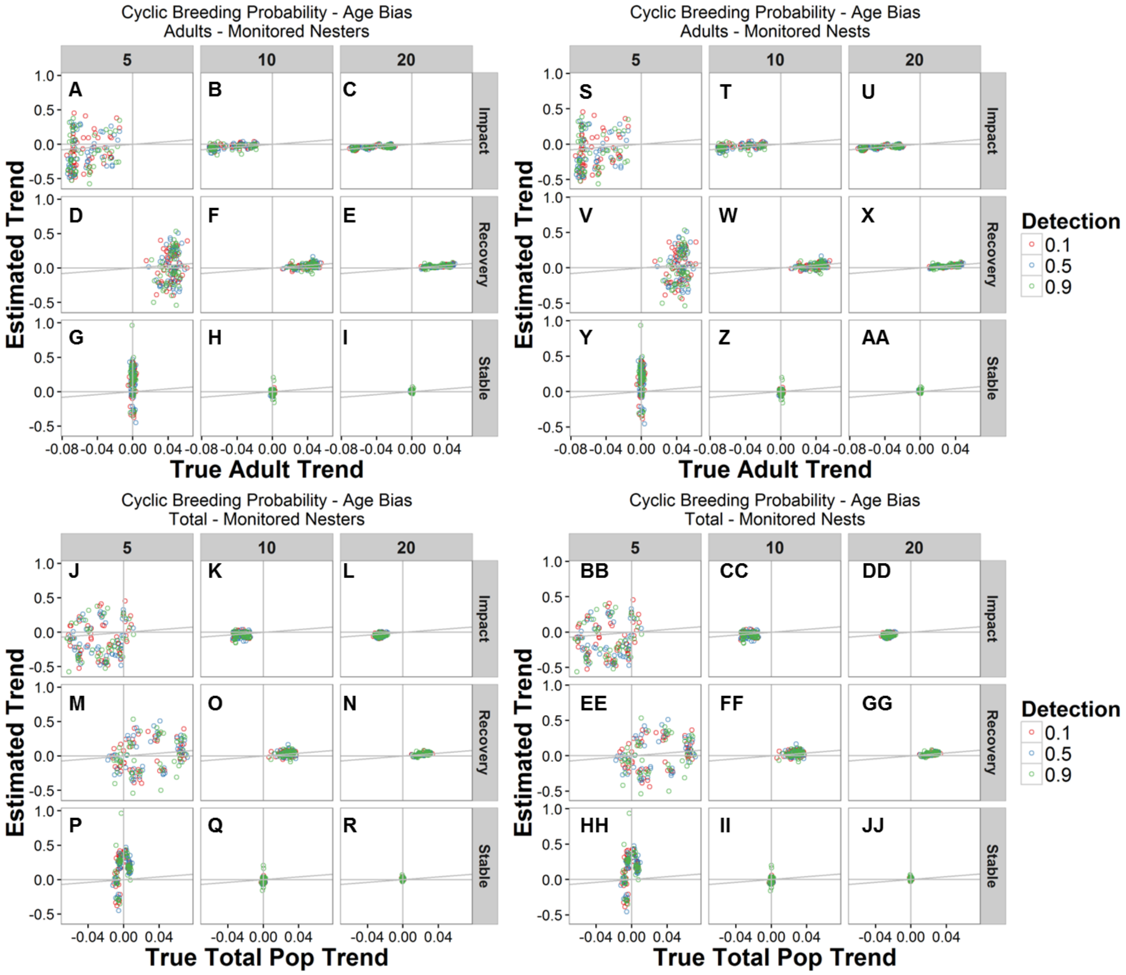

Figure C10. True and estimated adult and total population trend for Cyclic Breeding Probability treatments with age-biased sampling. Estimated total population trend was drawn from observed nesters (J – R) or observed nests (BB – JJ). Population trend is shown for the population trajectories: impact (A – C, J – L, S – U, and BB – CC), recovery (D – F, M – O, V – X, EE – GG), and stable (G – I, P – R, Y – AA, HH – JJ). Trend duration was 5 (A,D, G, J, M, P, S, V, Y, BB, EE, and HH), 10 (B, E, H, K, N, Q, T, W, Z, CC, FF, and II) and 20 (C, E, I, L, N, R, U, X, AA, DD, GG, and JJ) years of monitoring. Estimated adult trend was drawn from observed nesters (A – I) or observed nests (S – AA). Detection levels varied with a mean of 0.1, 0.5, and 0.9. The diagonal line represents the 1:1 line between the true abundance and the estimated abundance. Axis ranges across plots were allowed to vary to enhance visualization of the points.

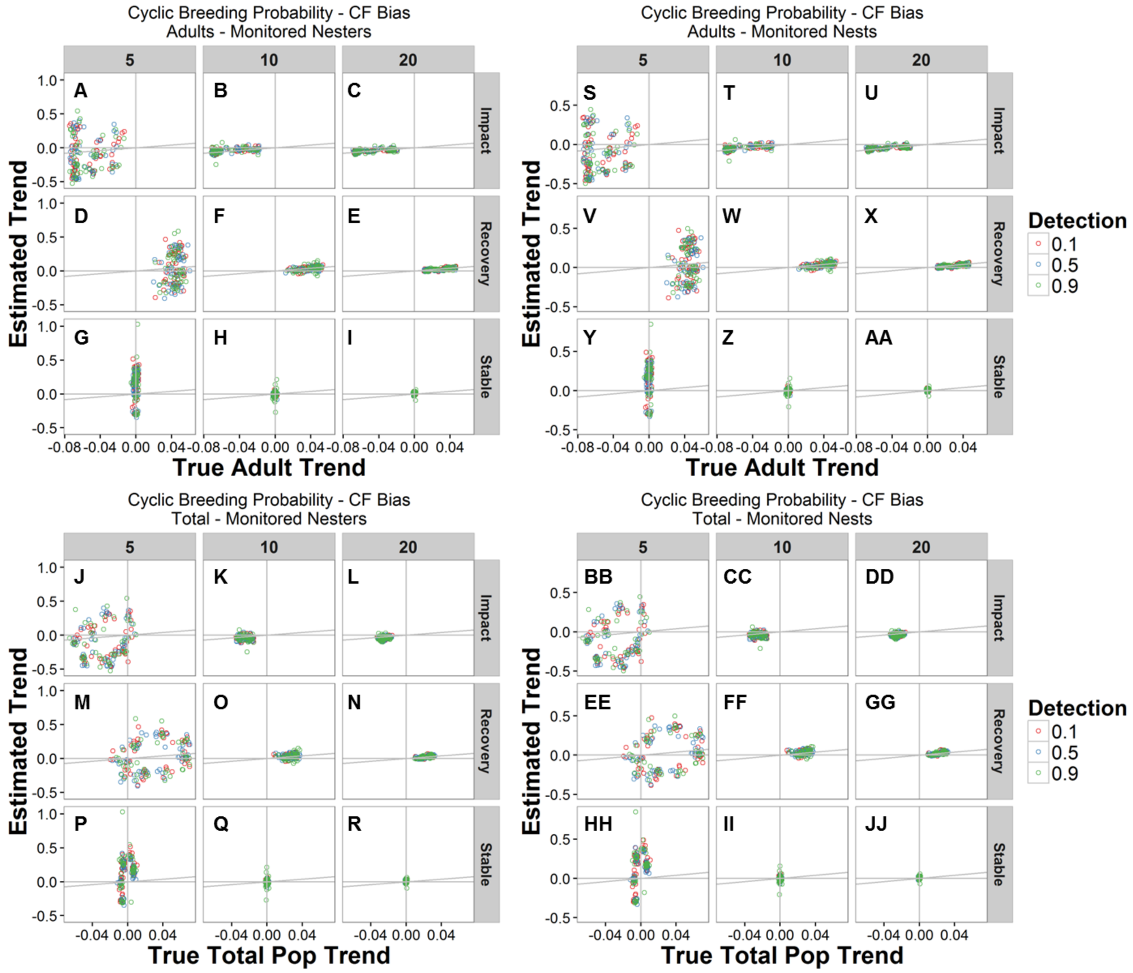

Figure C11. True and estimated adult and total population trend for Cyclic Breeding Probability treatments with clutch frequency-biased sampling. Estimated total population trend was drawn from observed nesters (J – R) or observed nests (BB – JJ). Population trend is shown for the population trajectories: impact (A – C, J – L, S – U, and BB – CC), recovery (D – F, M – O, V – X, EE – GG), and stable (G – I, P – R, Y – AA, HH – JJ). Trend duration was 5 (A,D, G, J, M, P, S, V, Y, BB, EE, and HH), 10 (B, E, H, K, N, Q, T, W, Z, CC, FF, and II) and 20 (C, E, I, L, N, R, U, X, AA, DD, GG, and JJ) years of monitoring. Estimated adult trend was drawn from observed nesters (A – I) or observed nests (S – AA). Detection levels varied with a mean of 0.1, 0.5, and 0.9. The diagonal line represents the 1:1 line between the true abundance and the estimated abundance. Axis ranges across plots were allowed to vary to enhance visualization of the points.

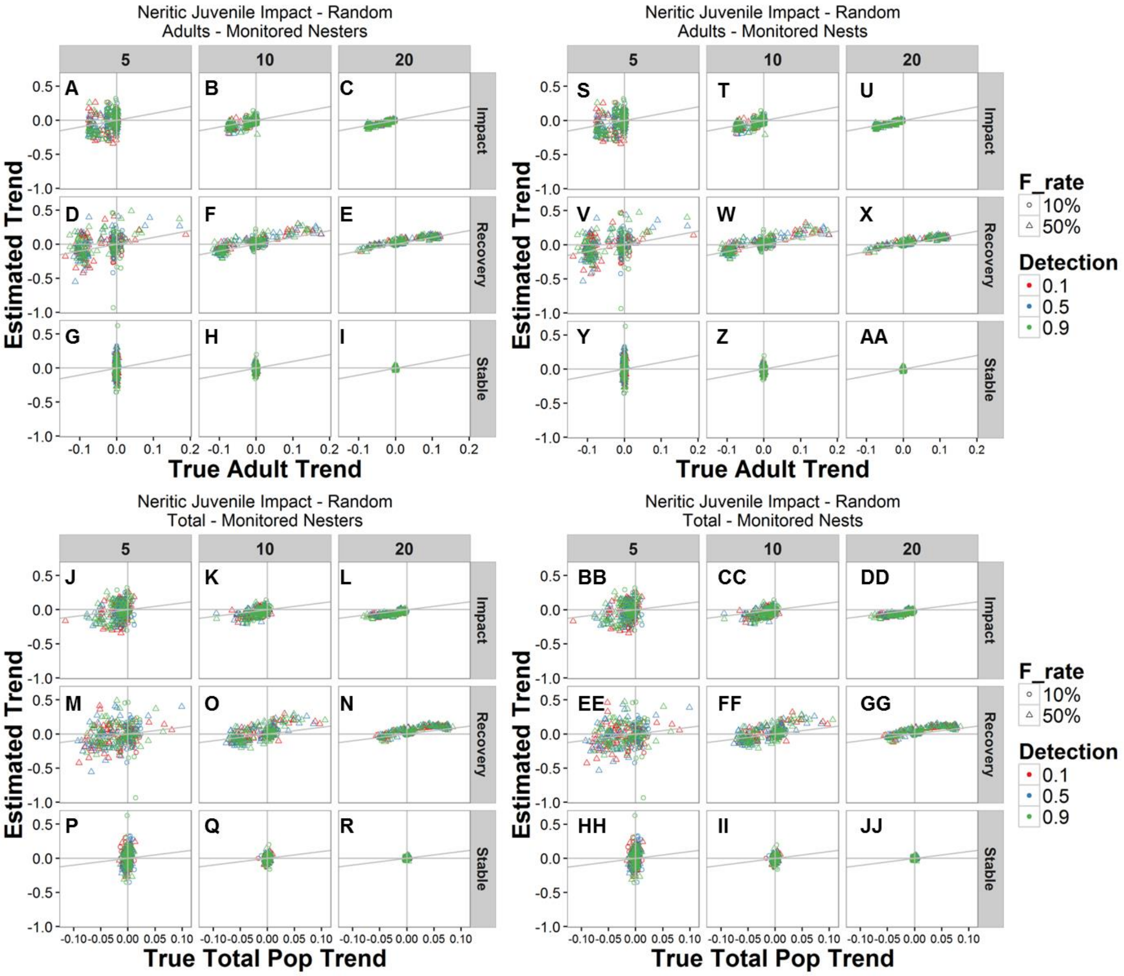

Figure C12. True and estimated adult and total population trend for the Low and High Severity Neritic Juvenile Impacts treatments with random sampling. Estimated total population trend was drawn from observed nesters (J – R) or observed nests (BB – JJ). Population trend is shown for the population trajectories: impact (A – C, J – L, S – U, and BB – CC), recovery (D – F, M – O, V – X, EE – GG), and stable (G – I, P – R, Y – AA, HH – JJ). Trend duration was 5 (A,D, G, J, M, P, S, V, Y, BB, EE, and HH), 10 (B, E, H, K, N, Q, T, W, Z, CC, FF, and II) and 20 (C, E, I, L, N, R, U, X, AA, DD, GG, and JJ) years of monitoring. Estimated adult trend was drawn from observed nesters (A – I) or observed nests (S – AA). Detection levels varied with a mean of 0.1, 0.5, and 0.9. The diagonal line represents the 1:1 line between the true abundance and the estimated abundance. Axis ranges across plots were allowed to vary to enhance visualization of the points.

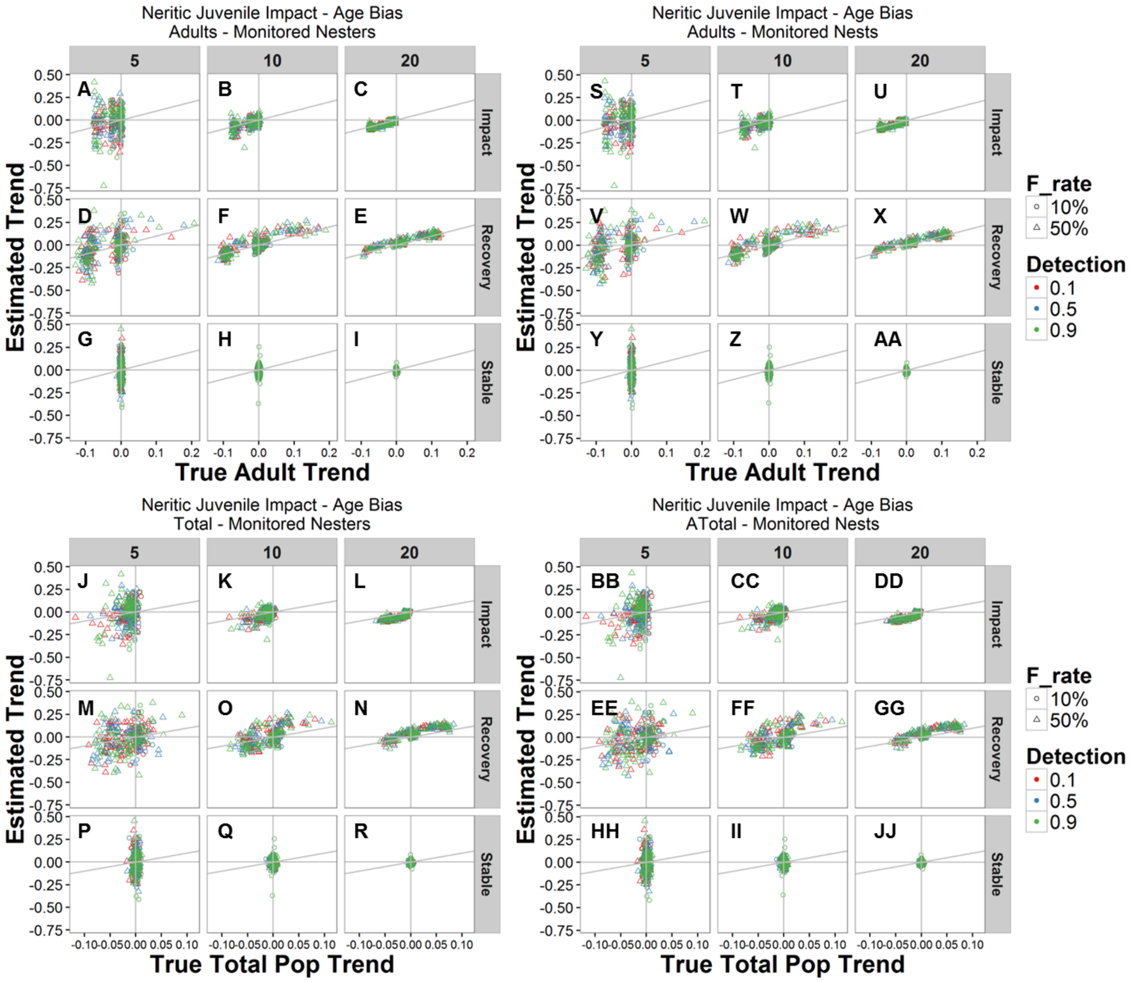

Figure C13. True and estimated adult and total population trend for the Low and High Severity Neritic Juvenile Impacts treatments with age-biased sampling. Estimated total population trend was drawn from observed nesters (J – R) or observed nests (BB – JJ). Population trend is shown for the population trajectories: impact (A – C, J – L, S – U, and BB – CC), recovery (D – F, M – O, V – X, EE – GG), and stable (G – I, P – R, Y – AA, HH – JJ). Trend duration was 5 (A,D, G, J, M, P, S, V, Y, BB, EE, and HH), 10 (B, E, H, K, N, Q, T, W, Z, CC, FF, and II) and 20 (C, E, I, L, N, R, U, X, AA, DD, GG, and JJ) years of monitoring. Estimated adult trend was drawn from observed nesters (A – I) or observed nests (S – AA). Detection levels varied with a mean of 0.1, 0.5, and 0.9. The diagonal line represents the 1:1 line between the true abundance and the estimated abundance. Axis ranges across plots were allowed to vary to enhance visualization of the points.

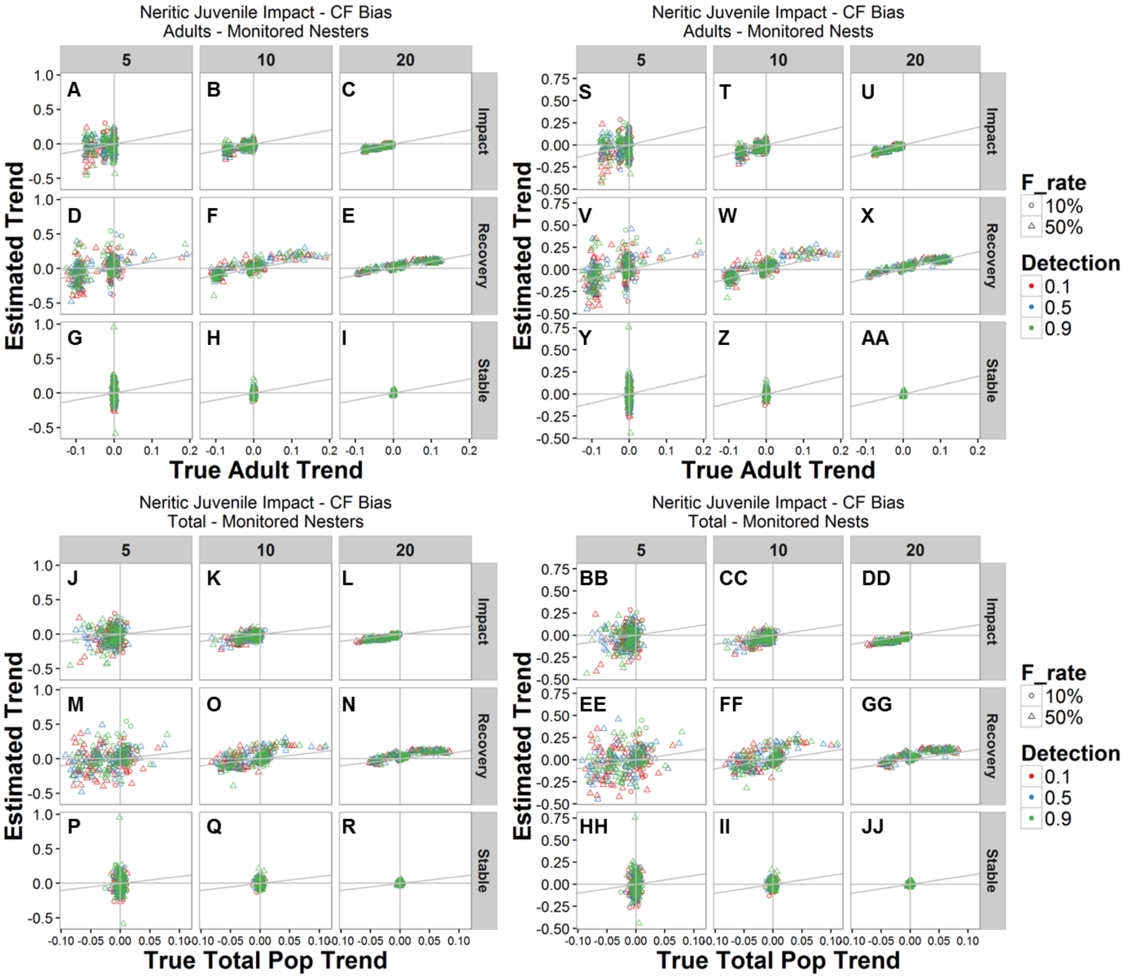

Figure C14. True and estimated adult and total population trend for the Low and High Severity Neritic Juvenile Impacts treatments with clutch frequency-biased sampling. Estimated total population trend was drawn from observed nesters (J – R) or observed nests (BB – JJ). Population trend is shown for the population trajectories: impact (A – C, J – L, S – U, and BB – CC), recovery (D – F, M – O, V – X, EE – GG), and stable (G – I, P – R, Y – AA, HH – JJ). Trend duration was 5 (A,D, G, J, M, P, S, V, Y, BB, EE, and HH), 10 (B, E, H, K, N, Q, T, W, Z, CC, FF, and II) and 20 (C, E, I, L, N, R, U, X, AA, DD, GG, and JJ) years of monitoring. Estimated adult trend was drawn from observed nesters (A – I) or observed nests (S – AA). Detection levels varied with a mean of 0.1, 0.5, and 0.9. The diagonal line represents the 1:1 line between the true abundance and the estimated abundance. Axis ranges across plots were allowed to vary to enhance visualization of the points.

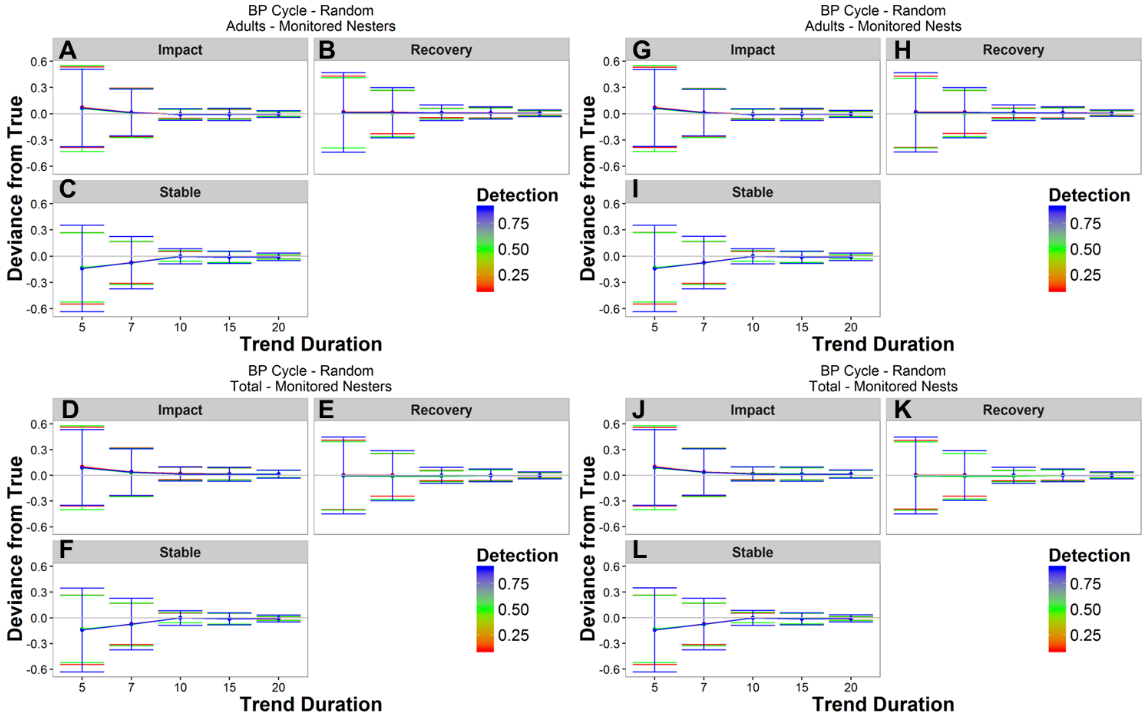

Figure C15. Adult population trend duration and the mean deviance from the true trend from randomly sampled nesters and nests in the Cyclic Breeding Probability treatments. The estimated adult trend was drawn from observed nesters (A – C) or observed nests (G – I). The estimated total population trend was drawn from observed nesters (D – F) or observed nests (J – L). Detection levels varied with a mean of 0.1, 0.5, and 0.9. Deviance is calculated as the difference of the true population trend minus the estimated population trend. A deviance of 0 indicates no difference between the true and estimated population trend. Errors bars indicate the standard deviation about the mean deviance. True and estimated population trend were calculated across 5, 7, 10, 15, and 20 year durations.

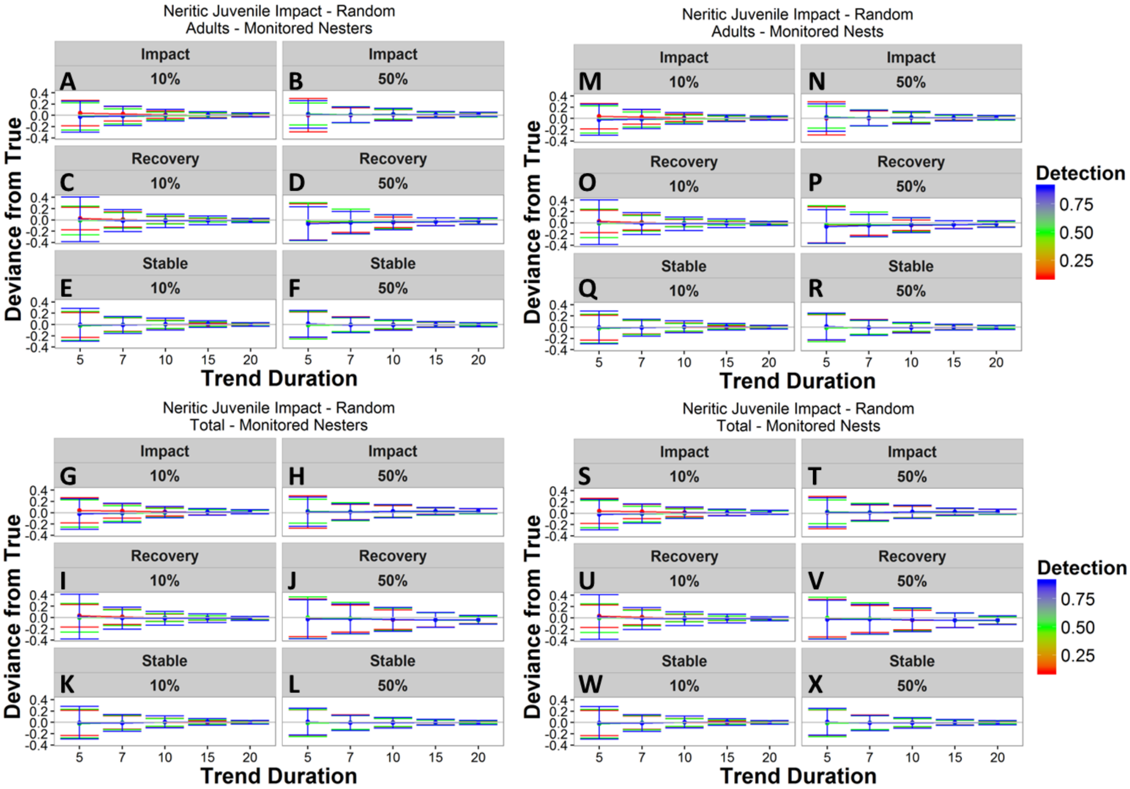

Figure C16. Adult population trend duration and the mean deviance from the true trend from randomly sampled nesters and nests in the Low and High Severity Neritic Juvenile Impacts treatments. The estimated adult trend was drawn from observed nesters (A – F) or observed nests (M – R). The estimated total population trend was drawn from observed nesters (G – L) or observed nests (S – X). Detection levels varied with a mean of 0.1, 0.5, and 0.9. Populations were subjected to a low severity treatment where 10% year^{-1} of neritic juveniles were removed, or a high severity treatment where 50% year^{-1} of neritic juveniles were removed. Deviance is calculated as the difference of the true population trend minus the estimated population trend. A deviance of 0 indicates no difference between the true and estimated population trend. Errors bars indicate the standard deviation about the mean deviance. True and estimated population trend were calculated across 5, 7, 10, 15, and 20 year durations.