



An agent-based model to evaluate recovery times and monitoring strategies to increase accuracy of sea turtle population assessments



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ABSTRACT

Green sea turtles are threatened globally, and some populations continue to decline while others are recovering. Assessing recovery status largely depends on monitoring efforts that encounter sea turtles on nesting beaches and sample nesters, nests, or both. Monitoring nesting beaches provides an imperfect index of true population level changes in abundance due to demographic time lags and inter-annual variability in nesting. But, it is still unclear how much and in which direction nesting beach indices diverge from true population status. To address this concern, 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 stable and transient population dynamics, monitoring and population assessment. We subjected the virtual populations to sub-adult, adult, and nest disturbances and simulated the monitoring process of observing nesters and nests with error. The GSTABM simulates population-level processes of nester abundance and corresponds with observed data from Hawaii. 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. The accuracy of estimated adult abundance was influenced by population trajectory and impacts, and was not sensitive to increasing detection probability. The accuracy of estimated recruitment improved with increasing detection levels, but depended on the impact legacy. The GSTABM is an important tool to determine relationships with monitoring, population assessment, and the underlying biological processes that drive changes in the population. 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, allowing agencies to invest in the most cost-effective monitoring efforts.

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1. Introduction

The green sea turtle (*Chelonia mydas*) is a globally threatened species primarily due 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 reflect the entire popula-

tion. Thus, the assessment of the status of these populations may be flawed. Some populations of sea turtles are recovering, while many are not, despite intensive conservation measures (NOAA and USFWS, 2015; Wallace et al., 2011). 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 nest counts of Mediterranean green turtles remain critically low with high levels of direct take and bycatch (Balazs et al., 2015; Broderick et al., 2002; Casale and Heppell, 2016). 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 (Bjorndal et al., 2010; Heppell et al., 2003).

While sea turtle recovery is a welcome event, it also presents a valuable opportunity to improve our understanding of the transient dynamics of increasing populations. Importantly, as a popula-

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tion recovers, 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., 2016). However, 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; Hart et al., 2013; Jackson et al., 2008; Pfaller et al., 2013; Tucker, 2010; 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 with nesting beach indices, biologists and managers are often ignorant of how misleading population trends based on nesting beach indices may be (Bjørndal et al., 2010).

Population models are a critical tool in the effort to understand population dynamics and provide insight into unmonitored demographic groups and their status (Morris and 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 (Bjørndal et al., 2010). But, our understanding of sea turtle population dynamics is complicated by intermittent breeding, a long lifespan, density-dependence, and long demographic time lags (Bjørndal et al., 2000; Caut et al., 2006; Girondot et al., 2002; Heppell et al., 2003; Parmenter and Limpus, 1995; Girondot et al., 2002; Heppell et al., 2003; Parmenter and Limpus, 1995). For example, if green sea turtles mature at 40 years of age, as has been estimated (Balazs and Chaloupka, 2004), then any research following hatchlings to maturity would transcend the length of most field studies. Although the ranges of many demographic variables have 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 in actuality be trend coefficients but are modelled as 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, and breeding probability may be highly variable (Miller, 1997; Piacenza et al., 2016). Further, breeding probability 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). By accounting for individual variability in life history traits, deviations in population dynamics emerge which are in contrast to results produced by traditional modeling approaches (DeAngelis and 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 population recovery times.

One way to address these variation-related issues is through the use of agent-based models (ABMs; Railsback and Grimm, 2012; Wilensky and Rand, 2015). ABMs have the flexibility to also incorporate complex mechanisms, such as individual variability in life history traits as well as aggregate individuals into classes of “agents” that have a class level of variation (e.g., an individual-oriented model (IOM), Wolff, 1994). ABMs operate at the scale by which population dynamics are based and at which monitoring occurs (DeAngelis and Mooij, 2005; Letcher et al., 1998; Lomnicki, 1988). ABMs have previously been applied to sea turtles to examine the influence of temporal variability and age-dependent mortal-

ity 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, and yield more biologically realistic predictions and better estimates of variability and uncertainty (Grimm and Railsback, 2005; Semeniuk et al., 2011). Thus, ABMs allow biologists to enhance understanding of population recovery dynamics and the relationships between population indices and the entire population.

We created our green sea turtle ABM (GSTABM) to simulate green sea turtle population dynamics, population disturbance and recovery, as well as the processes of monitoring and population assessment, based on data from Hawaii. We designed the GSTABM to incorporate individual variability in life history traits (i.e. breeding periodicity, age-at-maturity, clutch frequency, and clutch size), the influence of environmental variability on reproduction, and include mechanisms for density-dependence. We simulated specific scenarios reflecting population disturbance and observed the associated transient dynamics as they affected multiple indices of abundance. We had three main research questions: (1) How do the recovery dynamics differ when the disturbance occurs to different demographic groups (e.g., older turtles and eggs), (2) What predictions can we make from the GSTABM regarding recovery dynamics of green sea turtles, and (3) What is the accuracy of population indicators based on nesting beach data? Ultimately, we wanted to contrast the recovery dynamics of populations subjected to different kinds of disturbance histories, and the influence of those dynamics on assessment accuracy.

1.1. Biological background

In the Hawaiian archipelago, the vast majority of green sea turtle nesting takes place in the Northwestern Hawaiian Islands (NWHI) and the largest nesting beach is at East Island, French Frigate Shoals, where about 50% of all nesting occurs (Balazs and Chaloupka, 2004; Balazs, 1980). Females vary in the number of years between nesting seasons, and energetics, physiology, and environmental conditions all appear to influence the length of the breeding, or remigration, interval (Broderick et al., 2003; Chaloupka and Limpus, 1996; Limpus and Chaloupka, 1997; Miller, 1997; Piacenza et al., 2016; Solow et al., 2002; Stokes et al., 2014). Within a nesting season, green turtles will return several times to lay an average of four clutches at approximately 2 week intervals (Piacenza et al., 2016; Tiwari et al., 2010).

Historically, green sea turtles were abundant and nested throughout the entire Hawaiian Islands chain (Kittinger et al., 2013). Prior to European colonization in the early 1800s, green sea turtle populations are thought to have been minimally disturbed in the Hawaiian archipelago as harvest was tightly regulated by the “kapu” system of native Hawaiians (Balazs, 1980). In the 20th century, harvest initially occurred on large 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). Numbers of green sea turtles dropped precipitously as harvest intensified and became more commercialized in the Hawaiian Islands after World War II (Balazs, 1980; Van Houtan and Kittinger, 2014; Witzell, 1994). In 1978, green sea turtles were placed on the endangered species list and harvest was prohibited (NOAA Office of Protected Resources, 2014). Thus, intensive harvest was relatively short-lived compared to other green turtle populations (Balazs, 1980; Jackson et al., 2001; Kittinger et al., 2013; Witzell, 1994).

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