Ecography 36: 001–005, 2013
doi: 10.1111/j.1600-0587.2013.00245.x

Subject Editor: Eric Post. Accepted 30 January 2013

Forum

Using historical data to assess the biogeography of population recovery

John N. Kittinger, Kyle S. Van Houtan, Loren E. McClenachan and Amanda L. Lawrence

J. N. Kittinger, Dept of Geography, Univ. of Hawai'i at Mānoa, 445 Saunders, 2424 Maile Way, Honolulu, HI 96822, USA, and Center for Ocean Solutions, Stanford Univ., 99 Pacific Street, Suite 555E, Monterey, CA 93940, USA. – K. S. Van Houtan (kyle.vanhoutan@noaa.gov) and A. L. Lawrence, NOAA Fisheries, Pacific Islands Fisheries Science Center, 1601 Kapiolani Blvd, Suite 1000, Honolulu, HI 96822, USA. KSVH also at: Nicholas School of the Environment and Earth Sciences, Box 90328, Duke Univ., Durham, NC 27708, USA. – L. E. McClenachan, Environmental Studies Program, Colby College, 5351 Mayflower Hill, Waterville, ME 04901-8853, USA.

Historical ecology research is valuable for assessing long-term baselines, and is increasingly applicable to conservation and management. In this study, we describe how historical range data can inform key aspects of protected species management, including evaluating conservation status and recovery, and determining practical management units. We examine contemporary (1973–2012) and historical (1250–1950) data on nesting beach distributions for green sea turtles *Chelonia mydas* in the Hawaiian Islands. Green turtle populations in Hawai'i declined until federal and international protections began in the 1970s, but over the past four decades one index population has shown encouraging increases and broader recovery has been inferred. We find that 80% of historically major nesting populations are extirpated, or have heavily reduced nesting abundances in comparison with current estimates. Furthermore, historical nesting areas were not geographically isolated, but distributed across the archipelago. In comparison, today more than 90% of green turtle nesting in Hawai'i occurs at a single site that is vulnerable to sea level rise. This research suggests that assessing recovery without historical data on spatial patterns may overlook important ecological dynamics at the population or ecosystem level, which can result in improper or inadequate conservation assessments and recovery targets.

Establishing historical baselines is critical for understanding long-term ecological changes (Jackson et al. 2001, Lotze et al. 2011, McClenachan et al. 2012). Though historical data are often limited in their precision, they can provide scientifically meaningful information when ecological survey data are lacking (Jackson et al. 2001, Pandolfi et al. 2003, Lotze et al. 2006). Historical baselines have much potential to inform conservation planning efforts (McClenachan et al. 2012, Ban et al. 2013), including establishing benchmarks of success for assessing population recovery.

In marine systems, most historical ecology research has focused on megafauna abundance (Ferretti et al. 2008, Lotze et al. 2011) and ecosystem-level trends (Pandolfi et al. 2003, Kittinger et al. 2011). Historical data have also proven instrumental in assessing spatial patterns, including loss of breeding habitat (McClenachan et al. 2006, Van Houtan et al. 2012), patterns of species extinctions (McClenachan and Cooper 2008) and species' range contractions in response to exploitation (Smith 2005, Josephson et al. 2008). Understanding biogeographic shifts is an important aspect of endangered species management and specified in both the U.S. Endangered Species Act (ESA) and in the IUCN Red List (USFWS 1973, IUCN 2001).

Population recovery has followed conservation protections among many historically overexploited marine taxa worldwide (Chaloupka et al. 2008, Lotze et al. 2011), but assessing when such protections are no longer necessary is difficult. Historical data can aid in such assessments by helping define viable recovery targets that are referenced to ecological baselines. Green sea turtles, in particular, provide an ideal case study to evaluate recovery success as they have been historically exploited, and some populations have experienced recent increases that have been interpreted as population recovery (Balazs and Chaloupka 2004, Chaloupka et al. 2008).

Harvested for centuries and throughout their range, green turtle populations declined dramatically and their role in coastal ecosystems is greatly diminished (Bjorndal and Jackson 2002, McClenachan et al. 2006, Allen 2007). Though protected by international laws today, a number of anthropogenic threats (Magnuson et al. 1990) and life history traits challenge green turtle conservation. Like most sea turtles, green turtles exhibit: a) high juvenile mortality, b) late age of maturity, and c) high nesting beach fidelity (Avise and Bowen 1994). These traits have four problematic effects that differentiate turtles from other marine taxa. First, chronic harvest pressure can reduce or completely eradicate nesting populations in a few decades

(Bjorndal and Jackson 2002, McClenachan et al. 2006). Second, the effects of conservation may not be visible for decades (Musick 1999) thereby limiting adaptive management. Third, because the population memory of philopatry is lost, extirpated rookeries may not recover even after harvest pressures cease (McClenachan et al. 2006). Fourth, juvenile recruitment may be limited by persistent oceanographic conditions, unrelated to nesting abundance (Van Houtan and Halley 2011). Despite these significant challenges, significant increases of green turtle populations have followed conservation protections (Hays 2004, Chaloupka et al. 2008, Lotze et al. 2011).

In this study, we assess the spatial dynamics of population changes in Hawaiian green turtles, comparing contemporary (1973–2012) and historical (1250–1950) nesting records. Green turtles have been protected under the ESA and by Hawai'i State law since 1978. Monitoring at one remote atoll island (Fig. 1) shows a corresponding increasing trend since protections began (Balazs and Chaloupka 2004), providing compelling evidence of the effectiveness of legal protections. The IUCN, as a result, recently downgraded Hawaiian green turtles to 'least concern' (Pilcher et al. 2012) and the population is under ESA status review (NMFS 2012). Here, we consider recent trends at this single location in relation to historical data on nesting across the Hawaiian Archipelago. We show that conservation assessments that do not consider historical baselines of spatial biogeography can result in inaccurate status determinations and recovery targets, with important implications for endangered species management generally.

Material and methods

We searched archival holdings at: Univ. of Hawai'i at Mānoa Hamilton Library; the State of Hawai'i Historical Preservation Division Libraries; Bernice P. Bishop Museum; Hawai'i State Archives; Hawaiian Historical Society; Mission House Museum; Univ. of Hawai'i at Hilo Mo'okini Library; and NOAA PIFSC library. We also researched special collections including: Thrum's Hawaiian Almanac and Annual series, the Smithsonian Institution's Atoll Research Bulletin series, the eight volume American activities in the Pacific 1790–1870 (Ward 1966), Hawaiian language newspapers, and other archival sources and online repositories (sensu Van Houtan et al. 2012, Van Houtan and Kittinger unpubl.). A complete list of data sources and datasets used in this study are available as Supplementary material Appendix 1.

Our archival search targeted quantitative and qualitative information on nesting, observed densities, and human exploitation of Hawaiian green sea turtles. We developed spatially rectified databases on 1) nesting sites and abundances (Supplementary material Appendix 1, Table A1) and 2) archaeological deposits containing turtle bones in the Hawaiian Islands (Supplementary material Appendix 1, Table A2). We also drew on an interview dataset from a related project (Van Houtan and Kittinger unpubl.) with observations from key respondents knowledgeable about historical green turtle distributions to derive additional nesting data. Abundance estimates were derived from observational and interview data and classified into one of several ordinal categories: abundant, recorded (confirmed as present), or harvest (meaning enough were available as to have been harvested). Observations were excluded when positive evidence of nesting was equivocal (e.g. references to eggs could not be differentiated from nesting seabird populations). For archaeological data, all turtle bones recovered in midden deposits were considered to be *Chelonia mydas*, as the only other turtle species in Hawai'i (hawksbills *Eretmochelys imbricata*) is reportedly toxic and were not consumed (Van Houtan et al. 2012). Latitude and longitude positions for midden sites were determined by geo-referencing maps of excavation sites in published reports in Google Earth. Finally, we collected current green turtle nesting data from field monitoring programs of NOAA's Pacific Islands Fisheries Science Center (PIFSC) (Supplementary material Appendix 1, Table A3).

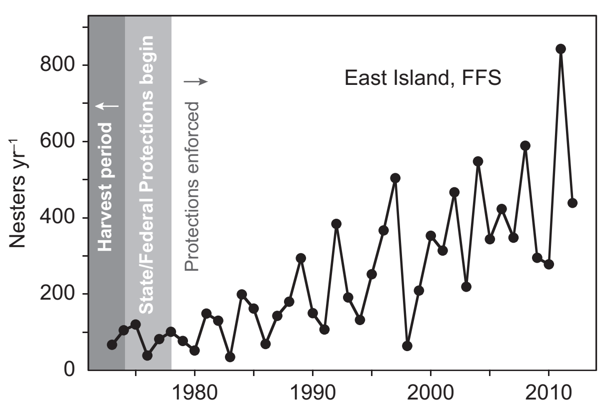

Figure 1. Nesting trends at East Island, French Frigate Shoals (FFS), Northwestern Hawaiian Islands. Shaded regions indicate different management regimes, including the: harvest period (when an active turtle fishery existed in the Hawaiian Islands), initiation of protections (listing of the species as threatened under the U.S. Endangered Species Act), and active enforcement of protections. Circles are the number of nesting female green turtles estimated annually.

Results

We uncovered evidence for 15 historical (1778–1950) green turtle nesting sites across the Hawaiian Islands (Supplementary material Appendix 1, Table A1) and 28 midden sites with turtle remains in the main Hawaiian Islands (MHI) (Supplementary material Appendix 1, Table A2). Of the 15 historical nesting sites, five areas (33%) were previously 'abundant' based on historical descriptions of these sites, including harvest data, explorer accounts of densities, or other evidence from archival records, and five sites (33%) were abundant enough to have been harvested. This historical magnitude of nesting suggests an evolutionary significance to the green turtle population in Hawai'i (Waples 1991, 2006), where one single nesting location might not (Lande and Barrowclough 1987).

Figure 2 plots these historical data against green turtle nesting surveys from 1973–2012 (Supplementary material Appendix 1, Table A3). Two major historical nesting sites

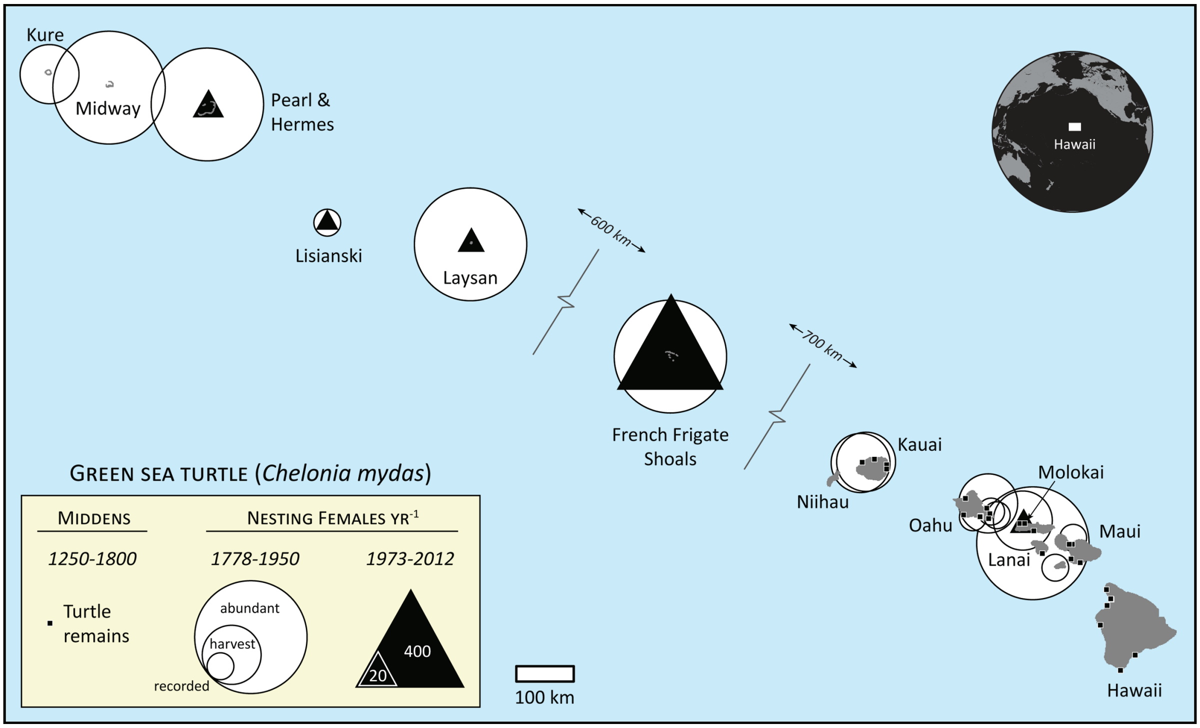

Figure 2. Historical and current nesting of green turtles in the Hawaiian Islands. Black triangles show modern (1973–2012) locations and nesting abundances, white circles are historical (1825–1960) nesting locations and their estimated abundances. Historical estimates were derived from descriptions in archival documents (Methods, Supplementary material Appendix 1, Table A1). Black squares are archaeological midden deposits with sea turtle remains, indicating harvests by Polynesian societies. The Hawaiian Archipelago is comprised of the inhabited high islands of the main Hawaiian Islands (from Kaua'i/Ni'ihau to Hawai'i Island) and the uninhabited reefs, banks, and atolls of the Northwestern Hawaiian Islands (NWHI). Breaks in the map are for display convenience, upper right inset map globally locates the Hawaiian Archipelago.

have been extirpated and two other sites have been substantially reduced. In the early 1900s, for example, Polihua beach on Lanai was a popular location to harvest nesting females (Balazs 1973) but today nesting there is nonexistent. Of the historically major nesting sites in the Northwestern Hawaiian Islands (NWHI), only the site at French Frigate Shoals remains, where several hundred turtles nest annually (Fig. 1). Although an 1859 nautical chart described 'an abundance' of green turtle nesting at Midway Atoll, only one female has nested there in the last 40 yr. Historical nesting at Laysan and Pearl and Hermes Atoll also appears to have been significant but recent observations suggests annual nesting never exceeds 10–15 females.

In the MHI there are no established green turtle nesting areas today. Scattered nesting at low levels has been observed since 2000. Genetic analyses suggest these females are closely related progeny from a decades-long captive breeding program on Oahu (Frey et al. 2012, Roden et al. in press). In contrast, we document turtle remains in archeological middens across the inhabited MHI, evidencing widespread historical harvest. As such midden remains are often linked to nesting sites (Allen 2007), these archeological data may evidence more widespread historical nesting areas in the MHI that were extirpated prior to European contact.

Our data suggest the current concentration of green turtle nesting on French Frigate Shoals is a historical anomaly. Nesting was once widely distributed across the Hawaiian archipelago, from the inhabited MHI throughout the remote atolls of NWHI. 80% of historically major nesting sites have been extirpated or are severely depleted (Fig. 2). While historical losses likely occurred before European contact, observation of nesting in the MHI in the late 19th and early 20th centuries (Supplementary material Appendix 1, Table A1), suggest significant nesting sites were extirpated since 1900. For example, green turtles nested on O'ahu in the early 1900s and on Kaua'i as late as the 1950s, but no records exist after this time.

Discussion

Compared to the current distribution and abundance, the historical declines of green turtle nesting in Hawai'i suggest a significant constriction in the spatial distribution of important reproduction sites, which presents a challenge to the population's future. At least four major historical nesting areas have been heavily reduced, and more locations that were abundant enough to have supported perennial harvesting have also disappeared (Fig. 2). Though the 40-yr trajectory for nesting at East Island, FFS is encouraging (Fig. 1) this location is the sole remnant of multiple nesting areas of major significance that were distributed more widely throughout the archipelago. Since extirpated nesting sites may not recover even after harvest pressures cease (McClenachan et al. 2006), these historical trends suggest green turtle population recovery is still limited compared to historical distributions.

The spatial limitation of nesting sites further increases the threats of climate change to this species. The only current major nesting site (FFS, Fig. 2) is a low-lying atoll that is highly vulnerable to sea level rise. A recent analysis shows that anticipated sea level rise will reduce future nesting habitat at FFS by 50% or more, and will also expose future nests to increased flooding (Baker et al. 2006). Field monitoring confirms such shifts have already begun. Whale-Skate Island, which once hosted a significant proportion of FFS nesting, disappeared around 2000 (Balazs and Chaloupka 2004, Baker et al. 2006). (The loss of Whale-Skate Island, and the subsequent redistribution of nesting activity to other FFS islands, may also contribute to the increase in East Island nesting [Fig. 1] as well.)

As historical reconstructions are based on incomplete data records, our study may underestimate the historical distribution of green turtle nesting sites in Hawai'i (Pandolfi et al. 2003, McClenachan et al. 2006, Van Houtan et al. 2012). Several historical references to abundant historical turtle populations did not specify a geographic location or were equivocal in their evidence for nesting (Supplementary material Appendix 1, Table A1). A June 1867 newspaper article, for example, described a Honolulu market selling turtle eggs harvested from an unspecified NWHI location. An 1886 account noted that turtle soup was ubiquitous in Honolulu restaurants and a 1912 record said: 'Honolulu is indulging in an unwonted orgie [sic] of turtle soup… steaks, and cutlets' (Supplementary material Appendix 1, Table A1). However, the locations of these harvests are unknown.

In addition to vague records, many nesting sites may have been eliminated before most written historical records were archived. Archaeological deposits with turtle remains in Hawai'i document a long history of exploitation (Fig. 2). Pre-contact pressures included exploitation by Polynesian societies and nest depredation by introduced rats, pigs, and dogs, which likely impacted nesting sites prior to the advent of historical records (Kittinger et al. 2011). Recovered remains are often attributed to local turtle populations (Dye and Steadman 1990, Frazier 2004, Allen 2007), but may also represent harvests from further afield (Friedlander et al. 2013). However, the presence of nesting sites in the inhabited MHI as late as the 19th and 20th centuries indicates that Polynesian societies were able to sustainably co-exist with these nesting aggregations for several centuries.

These findings have important implications for endangered species management and recovery planning. First, historical data on abundance and biogeographic distribution can inform the process of listing and delisting species as endangered or threatened. Though processes vary, most assessment criteria include both temporal data on abundance change and spatial data on biogeographic distributions (USFWS 1973, IUCN 2001). Our data suggest that assessing recovery through recent trends at a single nesting beach site may overlook important spatial and temporal dynamics that bear on long-term population viability. Such approaches can result in improper conservation targets that are based solely on abundance change (Sáenz-Arroyo et al. 2006, McClenachan et al. 2012). Second, historical data can inform the process of assessment or biological status review. As we show, conservation assessments that include analyses comparing current distributions to historical biogeographic ranges can help define more accurate recovery targets based on ecological baselines. Such approaches can help determine rates and extent of species recovery as a benchmark for evaluating management success. Third, historical distribution data can shed light on population structure and significance at evolutionary time scales, which is useful for determining distinct management units today (Waples 1991, 2006).

In conclusion, conservation protections under the ESA have enabled a multi-decadal recovery trend for green turtles in the Hawaiian Islands. While this trajectory is positive, in comparison to historical baselines the spatial distribution of nesting sites is highly constricted, making the species highly vulnerable. Small aggregations of nesters are found elsewhere in the archipelago, but recovery of these emerging nesting locations to former abundances can require decades (McClenachan et al. 2006). Conservation planning should take into account these historical dynamics in assessing population status and developing historically-referenced recovery targets.

Acknowledgements – This is the second paper from the NOAA Pacific Sea Turtle Historical Ecology Working Group. S. Hargrove, B. Becker, and G. Balazs provided sea turtle abundance data. S. Pimm, J. Jackson, S. Pooley, F. Parrish, P. Opay, and T. Jones provided comments on an earlier version of this manuscript. JNK was supported by an NSF IGERT Graduate Fellowship (no. 0549514), a DDRI grant (no. 0926768), and a NOAA contract (PIFSC no. JJ133F10SE2956). KSVH was supported by a Presidential Early Career Award for Scientist and Engineers. ALL was supported by a NOAA PIFSC Internship.

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Supplementary material (Appendix ECOG-00245 at <www.oikosoffice.lu.se/appendix>). Appendix 1.