Quantifying multiple threats to endangered species: an example from loggerhead sea turtles

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The effectiveness of recovery plans for threatened and endangered species has been questioned in academic and political domains. A comprehensive assessment of species recovery plans concluded that quantification and prioritization of threats have received insufficient attention, which contributes to the failure of some plans. On the basis of this assessment, we developed and implemented a detailed analysis of threats in the *Recovery Plan for the Northwest Atlantic Population of the Loggerhead Sea Turtle (Caretta caretta)*, produced by the National Marine Fisheries Service and US Fish and Wildlife Service. The analytical approach that we designed and summarize here provides an objective process for quantifying known threats and prioritizing recovery actions in terms of their relative impact on population growth rate (λ) of the loggerhead sea turtle. Although this process was developed for loggerhead sea turtles, it can be applied to other species.

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The US Endangered Species Act requires that a recovery plan be developed for each species listed as threatened or endangered with extinction, with the aim of helping the species to recover so it can eventually be removed from Federal listing (ie delisting). Tremendous effort and considerable funds have been invested in the development of species recovery plans. However, the effectiveness of these plans has "come under increased scrutiny in both political and academic arenas as species are continually added to the endangered species list but few are removed" (Hoekstra *et al.*

In a nutshell:

- Endangered species face multiple threats
- To ensure a greater chance for success, recovery plans must prioritize threats according to the risk posed to a species' population growth rate (λ), but, to date, have generally failed to do so
- We present an analytical approach to quantify multiple threats by the relative impact of each threat on λ , so that recovery actions may be prioritized
- Our threats analysis is transparent, easy to update as new information becomes available, and applicable to many different species

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Loggerhead sea turtles have complex life histories (Figure 1), are highly migratory, and can be found in temperate and tropical regions of the Atlantic, Pacific, and Indian oceans (Bolten and Witherington 2003). Most loggerhead nesting occurs on beaches located along the western rims of the Atlantic and Indian ocean basins, with nesting aggregations in Florida and Oman accounting for the majority of nesting worldwide (Baldwin et al. 2003; Ehrhart et al. 2003). However, observed nesting activity in Florida has declined by 43% over the past decade (Witherington et al. 2009), highlighting the need for identifying and quantifying the threats to loggerhead sea turtles so that conservation actions can be prioritized relative to their impact on population growth rate (λ). A quantified threats analysis supports objective development of management priorities.

Here, we describe the process we used to identify, categorize, and quantify threats to the Northwest Atlantic



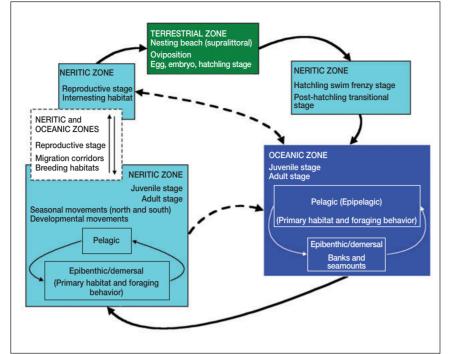


Figure 1. Basic life cycle of loggerhead sea turtles (modified from Bolten 2003) used in the threats analysis. Solid arrows represent the most common pattern; dashed arrows represent recent discoveries of an oceanic adult stage (Hatase et al. 2002; Hawkes et al. 2006) and return of some large juveniles from the neritic zone to the oceanic zone (Eckert and Martins 1989; McClellan and Read 2007).

population of the loggerhead sea turtle. An interactive version of the threats analysis is available online (www.nmfs.noaa.gov/pr/recovery/threats_tables-final.xls). The analytical approach we developed provides an objective process for quantifying threats and prioritizing recovery actions in terms of their relative impact on λ . Although developed for loggerhead sea turtles, the procedure can be applied to other species for which mortality data exist for several threats. Our approach is dynamic and transparent, and the threats analysis can be easily updated as new information becomes available.

Threats analysis process

Identification of life stages and ecosystems inhabited

Threats that affect species are often specific to particular life stages. For the threats analysis, we identified and evaluated eight life stages for loggerhead sea turtles (Figures 1 and 2; Table 1): egg, hatchling terrestrial, hatchling swim frenzy and transitional, juvenile oceanic, juvenile neritic (see definition below), adult oceanic, adult neritic, and nesting female. Individual turtles may not go through every stage; for example, not all adults have an adult oceanic stage.

For species that move between habitat types, threats may also be specific to an ecosystem. The three ecosystems in which loggerheads live are: (1) the terrestrial zone – the nesting beach where oviposition, embryonic development, hatching, and hatchling transit to the sea occur; (2) the neritic zone – the nearshore marine environment (from the water surface to the sea floor), where water depths do not exceed 200

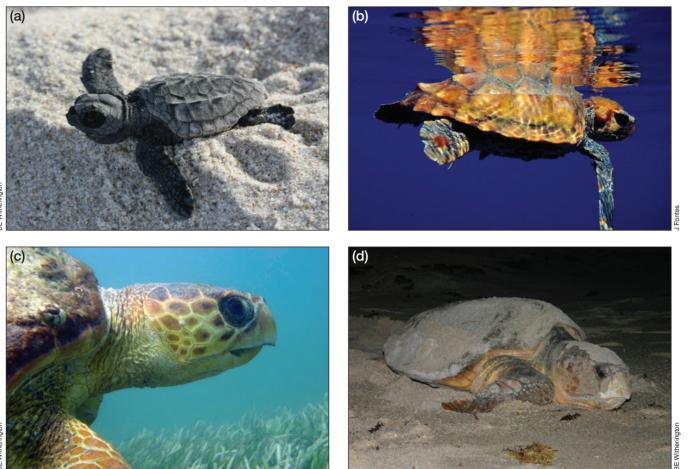
m; and (3) the oceanic zone – the vast open-ocean environment (from the water surface to the sea floor), where water depths are greater than 200 m. The neritic zone generally includes the water column above the continental shelf, but in areas where the continental shelf is very narrow or non-existent, the neritic zone conventionally includes areas where water depths are less than 200 m.

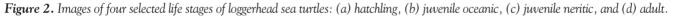
The three ecosystems inhabited by loggerheads (terrestrial, neritic, and oceanic) were linked with the life stages occurring in those ecosystems as the first step in developing the threats analysis matrix (Table 1, columns 1 and 2).

Table 1. Threat category: fisheries	bycatch - estimated annual mortality	ty for each type of fisheries bycatch

Life stage	Ecosystem	Trawl (bottom)	Trawl (top/mid water)	Dredge fisheries	Longline (pelagic)	Longline (demersal)		Gillnet (demersal, sm mesh)	Gillnet (drift)	Pound nets and weirs	Pot/trap fisheries	Haul seine	Channel net		Other hook and line (recreational)	Other hook and line (commercial)	Sum	RRV	Total adjust- ted annual mortality (1)
Nesting female	Terrestrial																0	1.000	0
Egg	Terrestrial																0	0.004	0
Hatchling	Terrestrial																0	0.004	0
Swim frenzy, transition	Neritic		I														I	0.004	0
Juvenile	Oceanic				30 000	I			Т								30 002	0.029	870
Adult	Oceanic				I				I								2	0.789	2
Juvenile	Neritic	30 000	I	300	I	3000	3000	300	30	30	30	Т	Т	Т	30	30	36 755	0.235	8637
Adult	Neritic	3000	I	30	I	300	300	30	3	3	30	I	I	Т	3	3	3707	0.789	2925
Total adjusted annual mortality (2)		9417	I	94	872	942	942	94	10	9	31	I	I	Т	9	9			

Notes: Total adjusted annual mortality (1) = total annual mortality for each life stage, summed for all types of fisheries and adjusted for relative reproductive values (RRV). Total adjusted annual mortality (2) = total annual mortality for each type of fishery, summed for all life stages and adjusted for RRV. Modified from NMFS and USFWS (2008). An interactive version is available online (www.nmfs.noaa.gov/pr/recovery/threats_tables-final.xls).





Identification of threats

All known threats to loggerheads were identified and characterized as part of the threats analysis process. We included both natural and anthropogenic threats, although it can sometimes be difficult to distinguish between the two. For example, predation on sea turtle eggs and hatchlings by raccoons (Procyon lotor) may be increased as a result of human activities that enhance raccoon populations by reducing natural predators and increasing food availability. We grouped all identified threats into seven functional categories: (1) fisheries bycatch (incidental capture of turtles in fisheries targeting other species); (2) resource use (non-fisheries), including legal and illegal harvest and numerous other human activities that cause turtle mortality, such as vessel strikes; (3) construction and development, including shoreline stabilization projects and coastal construction; (4) ecosystem alterations, including trophic changes caused by fishing and habitat alteration; (5) pollution, including artificial lighting, debris, and petroleum contamination; (6) species interactions, including diseases from and predation by both native and exotic species; and (7) other factors, including climate change and natural chronic or episodic events (eg hurricanes). See WebTable 1 for a complete list of all threats within each category.

To facilitate quantifying and presenting the threats, we combined the three elements (life stage, ecosystem, and specific categories of threats) into a spreadsheet. We developed a separate spreadsheet for each of the seven threat categories, with each specific threat within a category identified as a separate column. Table 1 presents the spreadsheet for the fisheries bycatch threats category.

Estimation of annual mortality

Depending on the quality of data available, the accuracy with which annual mortality can be estimated for each threat varies greatly among species. Because of this uncertainty, we estimated annual loggerhead mortality for each life stage/ecosystem, with respect to each specific threat, as a range of mortality using a color-coded log₁₀ scale (Table 2). For the spreadsheet calculations, we used the \log_{10} midpoint for each color-coded range as the estimate of annual mortality. The data were sufficient to allow us to assign most known mortalities into the appropriate log₁₀ bin, without relying on expert opinion. When quantitative data were not available, mortality was assigned into the appropriate log₁₀ bin based on best available information and expert opinion. Some of the problems associated with the use of expert opinion (Regan et al. 2002) were avoided by reaching consensus among the eight members of the

2	1		9	
1	۲	4	4	

Table 2. Key used to assign estimated annual mortality to each threat category

category		
Estimated annual mortality	Color code	Value
No evidence of mortality, based on best available information		
Sublethal effects occur at this stage and may result in reduced fitness (eg reduced somatic growth rates, reduced hatchling production, reduced prey abundance, reduced quality of nesting and/or foraging habitats)		
> 0 Mortality has been documented or is likely to occur; however, data are insufficient to estimate mortality		I
I – I0		3
11 – 100		30
101 – 1000		300
1001 – 10 000		3000
10 001 - 100 000		30 000
100 001 - 1 000 000		300 00

Notes: The value is the log_{10} midpoint of the range of estimated annual mortality. For those threats for which mortality is known but not quantified, the cell is shaded gray and assigned a value of 1 (= annual mortality of one individual in that category), so that these potentially important sources of mortality would appear in the summary tables (eg Tables 1, 3, and 4). From NMFS and USFWS (2008). An interactive version is available online (www.nmfs.noaa.gov/pr/recovery/threats_tables-final.xls).

Loggerhead Recovery Team (composed of biologists from universities and State and Federal resource management agencies responsible for writing the recovery plan; NMFS and USFWS 2008). We used the "comment" functionality of Microsoft Excel to document the data source, calculations, and justification for each estimate of mortality presented in each cell of the spreadsheet. These embedded comments can be seen in the online version by placing the cursor in a given cell (www.nmfs.noaa.gov/pr/recovery/ threats_tables-final.xls). This feature provides transparency for reviewers, policy makers, stakeholders, and researchers, and facilitates updating the threats spreadsheets as new data become available and new threats emerge.

We identified many threats for which mortality has been documented or is likely to occur, but for which data were insufficient to estimate the range of mortality on our log_{10} scale. For these threats, the associated cell is shaded gray and assigned a value of 1 (= annual mortality of one individual in that category), so that these potentially important sources of mortality would appear in the summary tables to illustrate that these threats occur at unknown levels (Tables 1, 3, and 4).

Adjusting estimates of annual mortality through relative reproductive values

A key step in the threats analysis process was adjusting numerical mortality estimates within each life stage with the relative reproductive value (RRV) of that life stage. An individual's potential for contributing offspring to future generations is its reproductive value, which was calculated by a stage-based demographic model (see below; WebTable 2). We converted reproductive value to RRV by setting the reproductive value of a nesting female to 1 (column "RRV" in Table 1; WebTable 3). For each threat category, the total annual mortality for each life stage/ecosystem was then calculated with respect to all specific threats within that threat category by adding values across the row (column "Sum" in Table 1). To compare annual mortality among life stages for all specific threats within a threat category, we adjusted the summed annual mortality for each life stage by the RRV of that life stage (column "Total adjusted annual mortality" in Table 1). This adjustment is necessary because some individuals in a population are more "valuable" than others in terms of the number of offspring they are expected to produce.

The importance of adjusting the mortality for each life stage/ecosystem by RRV can be seen in Table 1. The summed mortality for the juvenile oceanic stage is an order of magnitude greater than that for the adult

neritic stage, but the former becomes an order of magnitude less than the latter after adjustment for the RRV of the two stages. Other examples can be seen in each of the spreadsheets in the online version of the threats analysis (www.nmfs.noaa.gov/pr/recovery/threats_tables-final.xls).

In calculating the RRV, we made several assumptions that need to be recognized when interpreting the results of this threats analysis. Results presented in WebTable 2 suggest that all loggerhead sea turtles shift from the juvenile oceanic stage to the juvenile neritic stage after age 7. In reality, this shift occurs over a range of ages from 7 to 12 years (Bjorndal *et al.* 2000, 2003). In addition, our analysis assumes that the juvenile neritic stage spans ages 8 through 33, which combines small and large juveniles into this single life stage and overestimates/underestimates adjusted mortality for threats affecting small/large juveniles, respectively, because of lower RRV of small juveniles.

The stage-based demographic model used to develop the reproductive values (WebTable 2) had the following parameters. We assumed age at first reproduction to be 34 years, and a total of 7 years in the juvenile oceanic stage (Bjorndal *et al.* 2000), which included the egg and hatchling stage. We used estimates from NMFS (2001) for adult (including both oceanic and neritic stages) annual survival rate (0.812), juvenile neritic annual survival rate (0.893), and juvenile oceanic annual survival rate adjusted to 0.725 to result in a λ equal to 0.98. The firstyear survival rate was the smallest value reported for

				Categorie	Categories of threats					
Life stage	Ecosystem	Fisheries bycatch	Resource use (non-fisheries)	Construction and development	Ecosystem alterations	Pollution	Species interactions	Other factors		
Nesting female	Terrestrial									
Egg	Terrestrial									
Hatchling	Terrestrial									
Swim frenzy, transition	Neritic									
Juvenile	Oceanic									
Adult	Oceanic									
Juvenile	Neritic									
Adult	Neritic									

Table 3. Annual mortality for each life stage/ecosystem, for each of the seven threat categories, adjusted by relative reproductive values (does not include sublethal effects)

Notes: Numeric values are not presented in this summary table, only ranges of annual estimates of mortality based on the color-coded log₁₀ scale (Table 2). Modified from NMFS and USFWS (2008) and from the online version (www.nmfs.noaa.gov/pr/recovery/threats_tables-final.xls).

potential oceanic annual survival rates (0.25) for small, similar-sized Kemp's ridley sea turtles (*Lepidochelys kempii*; Heppell *et al.* 2005). Fecundity values were 4.1 nests per year, 115 eggs per nest, and a 0.50 sex ratio (NMFS 2001). NMFS (2001) reported a nest survival rate of 0.675, which is the value from research conducted on Wassaw Island, Georgia. Given that this beach has been regularly monitored and protected for nesting sea turtles, we assumed a lower value would be more representative of the entire nesting region and so chose a value of 0.50. We also used an age-based matrix model that cycled adult females between breeding and non-breed-

Table 4. Annual mortality for each threat within a threat category, summed for all life stages/ecosystems and adjusted for relative reproductive values for each life stage/ecosystem (does not include sublethal effects; see individual threat spreadsheets [www.nmfs.noaa.gov/pr/recovery/threats_tables-final.xls])

Threat category	Speci	fic threat with	in a threat c	ategory											
Other factors	Climate change	Natural catastrophes	Cold water	Other (egg stage only)											
Species interactions	Predation by native species	Disease and parasites	Harmful algal blooms	Predation by exotic species	Exotic dune and beach vegetation										
Ecosystem alterations	Trophic changes from fishery harvest	Trophic changes from benthic habitat alteration	Beach erosion (washouts) and accretion	Aquaculture	Eutro- phication										
Pollution	Marine debris ingestion	Entangle- ment in derelict fishing gear	Entangle- ment in non-fishing gear	Beach debris	Oil pollution	Light pollution	Noise pollution	Thermal pollution	Chemical pollution						
Construction and development	Beach sand placement	Beach armoring	Other shoreline stabilization	Sand fences	Dredging	Stormwater outfalls	Coastal construction	Channel blasting	Bridge blasting						
Resource use (non-fisheries)	Legal harvest	lllegal harvest	Oil and gas activities	Vessel strikes	Beach cleaning	Human presence	Recreational beach equipment	Beach vehicular driving	Power plant entrainment	Conservation and research activities	Military activities	Salvage operations			
Fisheries bycatch	Trawl (bottom)	Trawl (top/ midwater)	Dredge fisheries	Longline (pelagic)	Longline (demersal)	Gillnet (demersal, Ig mesh)	Gillnet (demersal, sm mesh)	Gillnet (drift)	Pound nets and weirs	Pot/trap fisheries	Haul seine	Channel net	Purse seine	Other hook and line (recreational)	Other hook and line (commercial)

Notes: Numeric values are not presented in this summary table, only ranges of annual estimates of mortality based on the color-coded log₁₀ scale (Table 2). Modified from NMFS and USFWS (2008) and from the online version (www.nmfs.noaa.gov/pr/recovery/threats_tables-final.xls).

ing years (NMFS 2001; Heppell *et al.* 2003). Our matrix model differed slightly from those of NMFS (2001) and Heppell *et al.* (2003), in that first-year survival was not incorporated into the fecundity calculation (ie a post-breeding rather than a pre-breeding census model).

Summary tables

Two types of summary tables were created. The first summary table was developed by combining the row totals for all specific threats within a threat category, adjusted for RRV for each of the seven categories (Table 3). Values are not presented in this summary table, only ranges of annual estimates of mortality, based on the color-coded \log_{10} scale (Table 2). The relative importance of each threat category by life stage/ecosystem is summarized in Table 3.

We also developed a second summary table to present the annual mortality for each specific threat within a threat category summed for all life stages/ecosystems and adjusted for RRV for each life stage/ecosystem (Table 4). This summary table is a compilation of the bottom row for each threat category spreadsheet (see Table 1). The formulae used for the calculations of annual mortality can be observed by clicking on the appropriate cells in the online version of the threats spreadsheets (www.nmfs. noaa.gov/pr/recovery/threats_tables-final.xls).

Conclusions

We evaluated the relative importance of each threat at each life stage to λ by adjusting annual mortality by RRV. The summary tables allowed evaluation of the relative importance of each threat category by life stage/ecosystem (Table 3) and by specific threat within each category (Table 4). We used these summary tables to identify and prioritize recovery actions in the Recovery Narrative and Implementation Schedule within the Recovery Plan (NMFS and USFWS 2008). For example, on the basis of an overview of the summary (Table 3), fisheries bycatch is clearly a major threat. As a result, we developed numerous recovery actions to address this threat.

Another property that emerges from the summary tables is the number of threat cells that are shaded gray, indicating known but unquantified threats. These knowledge gaps suggest important areas for research, particularly for those life stages or threat categories that are associated with a large number of gray cells. Although we could not quantify these gray-shaded cells, they may represent substantial threats to recovery. For example, we believe that the "pollution" category, which includes chemical (including petroleum) pollution, light pollution, and marine debris, may result in very high mortality. However, mortality in this category is currently uncertain, resulting from the difficulty of observing these openocean threats and an inability to assign cause of death to many of the dead turtles that are observed.

Also apparent from the summary tables is that all life

first sumtotals for sheets. An example of this is seen under the threats category "Ecosystem alterations", where the only mortality

each threat category.

gory "Ecosystem alterations", where the only mortality noted in the spreadsheet is for the egg stage (see the online threats spreadsheets; www.nmfs.noaa.gov/pr/ recovery/threats_tables-final.xls). However, we know that there has been substantial degradation of benthic foraging habitats (eg seagrass beds) as a result of fisheries operations (eg bottom trawling), dredging, and salvage activities. Although no direct mortality results from these habitat and ecosystem alterations, sublethal effects may affect individual fitness by reducing, for example, somatic growth, egg production, and hatchling production.

stages are subject to major threats. The tables allow visual

assessment of how these mortalities accumulate through-

out both the life stages and ecosystems, as well as within

Summary tables (Tables 3 and 4) only represent annual

mortality. However, sublethal effects can have considerable impacts on the species. We identified sublethal

effects for certain threats and life stages and coded them

In their response to the broad assessment of recovery plans, the US Fish and Wildlife Service emphasized the need for "more data, clearer standards, pragmatic models, and other aids to the practice of recovery" (Crouse et al. 2002). Our threats analysis is a pragmatic model that allows for quantitative, transparent, and dynamic assessment of threats and prioritization of management actions and research needs. Our process can be easily adapted for a wide range of species. The Kemp's Ridley Recovery Team has used this approach in the revision of the Binational Recovery Plan for the Kemp's Ridley Sea Turtle (Lepidochelys kempii) (E Possardt pers comm). Our methods did not formally involve the Delphic approach (a structured process for reaching decisions based on expert opinions; Dalkey and Helmer 1963) to assign magnitudes to threats, but this would provide an option for a similar threats analysis where mortality data are lacking.

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AB Bolten et al. - Supplemental information_

Category	Threat	Description			
Fisheries bycatch	Bottom trawl	Includes bottom trawl fisheries for blue crab, flounder, general finfish, scallop, shrimp, whelk, and the North Carolina flynet fishery for weakfish			
	Top/mid-water trawl	Includes trawls for sargassum and cannonball jellyfish			
	Dredge	Includes dredge fisheries for scallops and whelks			
	Pelagic longline	Includes longline fisheries for shark, swordfish, tuna, and wahoo			
	Demersal longline	Includes longline fisheries for black scabbard and shark			
	Demersal, large mesh gillnet	Includes gillnet fisheries for black drum, dogfish, monkfish, shark and southern flounder			
	Demersal, small mesh gillnet	Includes gillnet fisheries for general finfish			
	Drift gillnet	Includes drift-gillnet fisheries for shark, swordfish, and tuna			
	Pound nets and weirs				
	Pot/trap fisheries	Includes pot fisheries for blue crab, lobster, stone crab, and whelk			
	Haul seine				
	Channel net				
	Purse seine	Includes purse seines for menhaden and tuna			
	Other hook and line (recreational)				
	Other hook and line (commercial)	Includes commercial hook and line fisheries for snapper/ grouper, Gulf reef fish, king and Spanish mackerel, and sharks			
Resource use	Logal harvost				
(non-fisheries)	Legal harvest Illegal harvest				
	-				
	Oil and gas activities Vessel strikes				
	Beach cleaning				
	Human presence				
	Recreational beach equipment				
	Beach vehicular driving				
	Power-generating activities				
	Conservation/research activities	Includes harassment of nesting females and hatchlings, handling of eggs, etc			
	Military activities				
	Salvage operations				
Construction and development (although light pollution is	Beach-sand placement	Includes beach nourishment, beach restoration, and inlet san bypassing			
associated with construction and development, that threat is captured under the "Pollution"	Beach armoring	Includes bulkheads, seawalls, soil-retaining walls, rock revet- ments, sandbags, and geotextile tubes			
category)	Other shoreline stabilizations	Includes groins, jetties, mesh groins (nets), and offshore break- waters			
	Sand fences				
	Dredging				
	Stormwater outfalls				
	Coastal construction	Refers to buildings on the coast			

WebTable 1. Seven threat categories with specific threats and descriptions (modified from NMFS and USFWS 2008)

WebTable 1. – <i>continued</i>	1	
Category	Threat	Description
	Channel blasting	
	Bridge blasting	
Ecosystem alterations	Trophic changes from fishing	Refers to trophic changes from fishing-related activities (eg bottom trawling)
	Trophic changes from benthic habitat alteration	
	Beach erosion (washouts) and accre	etion
	Aquaculture	
	Eutrophication	
Pollution	Marine debris ingestion	
	Marine debris entanglement in derelict fishing gear	
	Marine debris entanglement in non-fishing gear	
	Beach debris	Includes large items that can impede or trap hatchlings and/or nesting females
	Oil pollution	Includes all types of petroleum contamination
	Light pollution	
	Noise pollution	
	Thermal pollution	Includes thermal pollution from power plants
	Chemical pollution	
Species interactions	Predation by native species	
	Diseases and parasites	
	Harmful algal blooms	
	Predation by exotic species	
	Exotic dune and beach vegetation	
Other factors	Climate change	
	Natural catastrophes	
	Cold water	
	Other (egg stage only)	Includes root damage, disease events, infertile eggs, relocation mortality, and inundation

NMFS and USFWS (National Marine Fisheries Service and US Fish and Wildlife Service). 2008. Recovery plan for the Northwest Atlantic population of the loggerhead sea turtle (*Caretta caretta*), 2nd rev. Silver Spring, MD: NMFS. www. nmfs.noaa.gov/pr/pdfs/recovery/turtle_loggerhead_atlantic. pdf. Viewed 15 Jan 2010.

WebTable 2. Results of the stage-based demographic model for the calculation of reproductive values (see text for the model parameters; modified from NMFS and USFWS 2008)

Life stage	Age (yr)	Stable age distribution	Stable age distribution, eliminating eggs/hatchlings stage	Reproductive values (RV)	Weighted mean of RV for each stage
Eggs/hatchlings	I	0.439		1	I.
Oceanic juveniles	2	0.112	0.199207793	3.915	7.3287694
	3	0.083	0.147627204	5.294	
	4	0.061	0.108497102	7.16	
	5	0.045	0.080038846	9.683	
	6	0.034	0.060473794	13.095	
	7	0.025	0.044466025	17.71	
Neritic juveniles	8	0.018	0.032015538	23.95	59.565532
	9	0.017	0.030236897	26.223	
	10	0.015	0.026679615	28.712	
	11	0.014	0.024900974	31.438	
	12	0.013	0.023122333	34.422	
	13	0.012	0.021343692	37.689	
	14	0.011	0.019565051	41.267	
	15	0.009709	0.017268826	45.184	
	16	0.008868	0.015772988	49.473	
	17	0.008099	0.014405214	54.169	
	18	0.007397	0.013156608	59.311	
	19	0.006756	0.012016499	64.941	
	20	0.00617	0.010974215	71.105	
	21	0.005635	0.010022642	77.854	
	22	0.005146	0.009152887	85.244	
	23	0.0047	0.008359613	93.336	
	24	0.004293	0.007635706	102.195	
	25	0.003921	0.006974051	111.896	
	26	0.003581	0.006369313	122.517	
	27	0.00327	0.005816156	134.146	
	28	0.002987	0.005312801	146.88	
	29	0.002728	0.004852133	160.822	
	30	0.002491	0.004430595	176.087	
	31	0.002275	0.004046408	192.801	
	32	0.002078	0.003696016	211.102	
	33	0.001898	0.003375861	231.14	
Breeding adults	34	0.00385 I	0.006849547	253.081	253.081
Non-breeding adults	35	0.006374	0.011337058	167.563	167.563
Adults					199.771

Life stage	Ecosystem	Reproductive values	Relative reproductive values
Nesting female	Terrestrial	253.1	1.000
Egg	Terrestrial	I	0.004
Hatchling	Terrestrial	I	0.004
Swim frenzy, transition	Neritic	I	0.004
Juvenile	Oceanic	7.3	0.029
Adult	Oceanic	199.8	0.789
Juvenile	Neritic	59.6	0.235
Adult	Neritic	199.8	0.789

WebTable 3. Reproductive values and relative reproductive values

Notes: We calculated the reproductive values using a stage-based demographic model (see text) for the Northwest Atlantic loggerhead sea turtle population (WebTable 2). The reproductive values were converted to "relative reproductive values" by setting the reproductive value of a nesting female to 1. Modified from NMFS and USFWS (2008).