

1 **Marine mammals and sea turtles listed under the U.S. Endangered Species Act are**
2 **recovering**

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4 Abel Valdivia^{1,*}, Shaye Wolf¹, Kieran Suckling²

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6 ¹Center for Biological Diversity, 1212 Broadway Suite 800, Oakland, CA 94612

7 ²Center for Biological Diversity, P.O. Box 710, Tucson, AZ 85702

8

9 *Corresponding author

10 Email: avaldivia@biologicaldiversity.org

11 **ABSTRACT**

12 The U.S. Endangered Species Act (ESA) is the world's strongest environmental law protecting
13 imperiled plants and animals, and a growing number of marine species have been protected
14 under this law as extinction risk in the oceans has increased. Marine mammals and sea turtles
15 comprise 36% of the 161 ESA-listed marine species, yet analyses of recovery trends after listing
16 are lacking. Here we gather the best available annual population estimates for all marine
17 mammals (n=33) and sea turtles (n=29) listed under the ESA as species. Of these, we
18 quantitatively analyze population trends, magnitude of population change, and recovery status
19 for representative populations of 23 marine mammals and 9 sea turtles, which were listed for
20 more than five years, occur in U.S. waters, and have data of sufficient quality and span of time
21 for trend analyses. Using generalized linear and non-linear models, we found that 78% of marine
22 mammals (n=18) and 78% of sea turtles (n=7) significantly increased after listing; 13% of
23 marine mammals (n=3) and 22% of sea turtles (n=2) showed non-significant changes; while 9%
24 of marine mammals (n=2), but no sea turtles declined after ESA protection. Overall, species with
25 populations that increased in abundance were listed for 20 years or more (e.g., large whales,
26 manatees, and sea turtles). Conservation measures triggered by ESA listing such as ending
27 exploitation, tailored species management, and fishery regulations, among others, appear to have
28 been largely successful in promoting species recovery, leading to the delisting of some species
29 and to increases in most. These findings underscore the capacity of marine mammals and sea
30 turtles to recover from substantial population declines when conservation actions under the ESA
31 are implemented in a timely and effective manner.

32

33 **Keywords:** Endangered Species Act, marine mammals, sea turtles, population trends, population
34 recovery, marine conservation, endangered, threatened, management actions, fishery regulations

35

36 **INTRODUCTION**

37 Extinction risk for many marine species is increasing as the world's ocean ecosystems are
38 degraded by pervasive and increasing anthropogenic stressors [1,2] including over-fishing [3],
39 habitat loss and degradation [4], pollution [5], and climate change [6,7]. Recent assessments
40 have identified elevated levels of extinction risk in specific marine taxonomic groups: 14% of
41 seagrasses [8], 16% of mangroves [9], 33% of reef-building corals [10], at least 25% of sharks
42 and rays [11], and 11% of billfish and scombrids (e.g., tunas, bonitos, mackerels) [12]. Although
43 considerably fewer extinctions of marine than terrestrial species have been recorded [1], marine
44 species have a comparably high extinction risk as terrestrial species [13].

45

46 The Endangered Species Act (ESA) of the United States is the world's strongest environmental
47 law expressly designed to prevent extinction and promote recovery of imperiled species [14].

48 The strength of the ESA lies in its requirement to base decisions on the best available scientific
49 information and its enforceable tools to reduce threats, protect habitat, and restore the abundance
50 and geographic representation of listed species [15]. ESA's tools include critical habitat
51 designation, recovery planning with concrete and measurable goals, a science-based consultation
52 process for federal agencies to prevent jeopardizing listed species or adversely modifying their
53 critical habitat, and a prohibition on killing or harming listed species (16 U.S.C. § 1531 et seq.).
54 Species protected under the ESA generally receive tailored federal and state conservation efforts
55 with increased funding for management [16] and thus have better chances for recovery.

56

57 Evaluations of the ESA's efficacy in preventing extinction and fostering recovery have become
58 more imperative as extinction risks increase [1], available resources for conservation are often
59 limited and mostly insufficient [17], and attacks on the ESA's effectiveness by political
60 opponents are escalating, with baseless critiques of the law [18]. Analyses to date of the ESA's
61 performance have consistently concluded that the ESA is highly effective in preventing species
62 extinction [19]. After more than 45 years since the law was enacted in 1973, the ESA has
63 shielded more than 99.5% of the species under its care from extinction [20]. Without the ESA's
64 protection, an estimated 227 species would have disappeared by 2006 [21].

65

66 The ultimate goal of the ESA is to promote the recovery of imperiled species. Numerous
67 analyses have found that species status improves with time since listing, i.e., the longer a species
68 is listed the more likely it is to increase in population abundance [22–24]. Species listed as
69 threatened tend to respond faster to protection than endangered species because they generally
70 have higher numbers at the time of listing, requiring relatively shorter time to recover [23,25].
71 Not surprisingly, species recovery is also associated with effectively implementation of the
72 ESA's tools, including funding for recovery actions [16,22,24,26,27]; presence of a dedicated
73 recovery plan [23,28,29]; progress toward completing recovery goals (Abbitt & Scott 2001;
74 Kerkvliet & Langpap 2007); and designation of critical habitat [23,but see 22,30,24].

75

76 Despite the increasing number of threatened and endangered marine species listed under the ESA
77 [31], evaluations of the ESA's track record in protecting marine species are lacking. This is
78 especially evident for marine mammals and sea turtles that comprise a 36% of currently listed

79 marine taxa [31]. Most studies of species recovery under the ESA are broad analyses of
80 thousands of species [23,32–34] or are tailored to specific terrestrial-related taxa, such as plants
81 [29], anadromous fish [35,36], amphibians [37], or birds [16,25,38,39]. Recent assessments of
82 the status of marine mammal stocks in U.S. waters and global analyses of sea turtles categorize
83 species by current population status, but do not analyze recovery trends since ESA listing
84 [40,41].

85

86 The objective of our study was to assess how listed marine mammal and sea turtle species are
87 faring under ESA protections, particularly for species occurring under U.S. jurisdiction where
88 conservation actions promoted by the law are more robust. Thus, we gather the best available
89 annual population estimates for all 33 marine mammals and 29 sea turtles listed under the ESA
90 as species. Of these, we analyze recovery progress of 23 marine mammals and 9 sea turtles,
91 which were listed for more than five years, reproduce or occur in U.S. waters, and had enough
92 quality data to assess population trends during ESA protection. We hypothesize that marine
93 mammals and sea turtles listed for several decades would be more likely to be recovering than
94 recently listed species. To assess how ESA listing influenced population trends we followed
95 three steps. First, we selected one representative population for each marine mammal and sea
96 turtle species. Second, using generalized linear and non-linear models, we calculated species-
97 specific population-level trends (significantly increased, no significant change, or significantly
98 decreased) and magnitude of population change for each species after ESA protection. Third, we
99 discuss conservation actions promoted by ESA listing that may contribute to species recovery,
100 and illustrate this through three case-study species: the humpback whale in Hawaii and Alaska,
101 Western Steller sea lion, and the North Atlantic green sea turtle.

102

103 **METHODS**

104 *ESA listed marine mammal and sea turtle species selection*

105 We reviewed the NMFS and USFWS’s endangered and threatened species database and selected
106 all marine mammals (n=33) and sea turtles (n=29) currently listed or delisted as “species” under
107 the ESA (Table 1, and S1 Table). We followed the ESA’s definition of “species”, which includes
108 both species and subspecies that “interbreed when mature,” as well as distinct population
109 segments (DPSs) (16 U.S.C. § 1532(16)). A DPS is defined as a vertebrate fish or wildlife
110 population or a group of populations that is discrete from other populations of the species and is
111 considered significant in relation to the entire species (61 FR 4722). For example, the humpback
112 whale (*Megaptera novaeangliae*) is a biologically defined species, but it is currently divided in
113 14 DPSs under the ESA (81 FR 62259) that are considered different ESA-listed species.

114

115 To determine the influence of ESA conservation measures on species recovery, we selected
116 extant marine mammal and sea turtle species, listed or delisted, that meet five criteria: (1) ESA-
117 listed for more than five years (pre-2012) to provide a minimum of post-listing population data
118 time for conservation measures to be applied; (2) occurrence and reproduction in U.S. waters,
119 i.e., excluding species that only occur in foreign waters where the ESA provides fewer
120 protections [42]; (3) with enough reliable abundance data to determine population-level trends,
121 i.e., at least three data points within 10 years, which is generally recommended for determining
122 population change in ESA endangered and threatened species (82 FR 24944) and has been used
123 for marine mammals [43] and sea turtles [44]; (4) with population data covering at least 40% of
124 the ESA listing period, which we considered adequate for determining population trends after

125 ESA listing; and (5) with a population that numerically represents over 50% of the abundance of
126 the listed species (e.g., most green sea turtles of the North Atlantic DPS nest in Florida and thus
127 Florida nest counts were used to represent this DPS). To delimit a population in our study, we
128 used abundance data consistently collected over time in geographically defined areas such as
129 stocks under the Marine Mammal Protection Act (MMPA), recovery units and DPSs as managed
130 under the ESA, and other geographically restricted population units (e.g., ocean basins). As a
131 result, population trend calculations are likely representative of the status of the entire ESA-listed
132 species, even though an ESA-listed species may be comprised of several smaller populations.
133 We identified 32 species that met our selection criteria, totaling 23 marine mammals and nine sea
134 turtles (Tables 1 and S1). Of the 26 marine mammal and sea turtle species that did not meet our
135 selection criteria, most (74%) do not occur in U.S. waters.

136
137 We also evaluated changes in species protection status. Species can be listed under the ESA as
138 endangered or threatened. The ESA defines an endangered species as “in danger of extinction
139 throughout all or significant portion of its range” while threatened species are “likely to become
140 endangered in the foreseeable future throughout all or significant portion of its range” (16 U.S.C.
141 § 1532(6) and (20)). For several species, the protection status (i.e., endangered or threatened)
142 changed since the species was first listed at the global population level, and a few species were
143 divided into DPSs (Table 1 and S1 Table). For the purpose of our study, we used the most
144 current ESA protection status but the original year that the species was protected (Table 1).

145

146 *Data compilation and availability*

147 We collected information and population-level abundance estimates for ESA-listed marine
148 mammals and sea turtles from published papers and government reports. Main data sources
149 included NMFS and USFWS technical memorandum and administrative reports, U.S. marine
150 mammal stock assessment reports, species recovery plans, five-year status reviews, and primary
151 sources from peer-reviewed scientific journals (see data in supporting information). When
152 possible, we collected abundance data up to 2017 or to the most recently available population-
153 level estimate. For populations that occur and reproduce in both U.S. and foreign waters, we
154 used datasets from surveys that occurred, at least in part, in waters under U.S. jurisdiction.

155
156 Population abundance estimates came from a variety of survey methodologies (aerial, land, and
157 ship-based surveys), mark-recapture population modeling, extrapolated data based on sex ratios,
158 and photo-identification models (see data in supporting information). For marine mammals,
159 population abundance comprised the total number of individuals including adults, juveniles, and
160 pups or calves. For sea turtles, we used number of nests on nesting beaches, number of nesting
161 females, or number of individuals to determine population trends. The number of nesting females
162 and number of nests are common metrics for monitoring and evaluating population status of sea
163 turtles [44].

164
165 Estimate bias and errors in population abundance obtained from data sources were variable
166 among species and even within the same species over time. For example, survey effort and
167 methodologies changed over time and population estimates have been calculated using different
168 approaches over the years for the same population (e.g., traditional population abundance
169 models, Bayesian population models, or habitat-based density models). Thus, where available,

170 each data point was accompanied with information on data collection methodology, error
171 information (e.g., coefficient of variation), and data estimation reliability (see data in supporting
172 information). Time-series of population abundance for each species were carefully constructed to
173 ensure all annual data points were derived from adequate and quantitative methodologies.

174

175 ***Population trends and magnitude of change***

176 For each marine mammal and sea turtle species, we calculated the population trend (as
177 percentage change per year) and the magnitude of population change (as percentage change)
178 after ESA listing based on the predicted distributions from the best and final fitted generalized
179 linear and non-linear models (Table 2 and S2 Table). Population trajectories were classified as
180 significantly increasing, non-significant change (non-significant slope), or significantly
181 decreasing as in Magera et al. [43]. Recovering populations were defined as those that
182 significantly increased in abundance after ESA listing, independently of whether or not they
183 were on track to meet the recovery criteria for downlisting or delisting found in recovery plans.
184 Populations with non-significant trends were not classified as “stable” as in other studies [see
185 40]. This was because determining population stability overtime requires further assessment of
186 the accuracy of annual population estimates (e.g., the confidence intervals), which were often not
187 available. Analysis of the magnitude of population recovery from estimated historical baselines
188 was also not performed because this has been described elsewhere [43,45,46].

189

190 ***Data analysis: Population trajectories and model selection***

191 To explore population trajectories after listing we used several models including linear models
192 (*lm*), generalized linear models (*glm*), generalized least square models (*gls*), or generalized
193 additive models (*gam*) in which population abundance estimates were modeled by running time
194 in years (S2 Table). Because population trends were species specific, we used several family
195 distributions and error links for each of the population-level models (S2 Table). For each
196 population, we performed a comprehensive exploratory analysis using all models and possible
197 combinations of families and links with and without a log transformation of the abundance
198 estimates. In several *gls* models we added correlation and variance structures to account for
199 potential temporal autocorrelation among years and variation in the data (S2 Table).
200 Improvement in model fit was evaluated through theoretical model inference based on Akaike's
201 Information Criterion (AIC) [47], and comparing adjusted regression (r-squared) parameters
202 when available [48]. Final model selection was based on a multi-model inference approach using
203 AICc corrected for small samples [49]. See supporting information for final model details (S2
204 Table). All calculations and graphing were performed in R version 3.3 [50] using the packages
205 *nlme v.3.1-131* for generalized least squared models [51]; *gam v.1.14-4* for generalized additive
206 models [52]; *MuMIn v.1.15.6* for multi-model inference [53]; and *ggplot2 v.2.2.1* for data
207 visualizations [54]. The dataset with specific data sources and references, and the R code of the
208 analysis are provided in supporting information.

209

210 **RESULTS**

211

212 *Status of ESA-listed marine mammal and sea turtle species in U.S. waters*

213

214 Protection status for 10 out of the 32 species analyzed in our study changed since they were first
215 listed, with eight of the 10 improving in status. Four species were downlisted from endangered to
216 threatened: the Mexico DPS of humpback whale in 2016; the Florida manatee (*Trichechus*
217 *manatus latirostris*) and the Antillean manatee (*Trichechus manatus manatus*) subspecies in
218 2017; and the North Atlantic DPS of green sea turtle in 2016 (Table 1). Four species were
219 delisted from the ESA because NMFS determined they have recovered: the Eastern North Pacific
220 Stock of gray whale (*Eschrichtius robustus*) in 1994, two DPSs of humpback whales (Hawaii
221 and West Indies) in 2016, and the Eastern Pacific DPS of Steller sea lion in 2013 (Table 1). Two
222 species were uplisted from threatened to endangered: the Western Pacific DPS of Steller sea lion
223 (*Eumetopias jubatus*) in 1997, and the Central West Pacific DPS of green sea turtle in 2016
224 (Table 1).

225

226

227 **Table 1 Status of marine mammals and sea turtle species protected under the ESA included in the analysis.** These species are
 228 listed for more than five years (before 2012), are found exclusively within United States (US) or within both US and foreign (US/F)
 229 waters, have adequate population data that cover at least 40% of the listing period, and the population represents over 50% of the
 230 listed species. Distinct population segment (DPS); listing year; ESA status as endangered (E), threatened (T), delisted (D), or status
 231 change (e.g., T→E); and number of years listed are shown. Year of ESA status change due to down-listing (dl) and up-listing (ul); and
 232 reason for delisting such as recovered (re) are presented. Several species were listed before 1973 under the Endangered Species
 233 Preservation Act of 1966 and the Endangered Species Conservation Act of 1969, which were later replaced by the more
 234 comprehensive Endangered Species Act of 1973. See S1 Table for marine mammals and sea turtle ESA species excluded from the
 235 analyses. Data as of July 2017 [31].

236

Common Name	Scientific Name	DPS/Stock/Population	Water	Listed year	ESA status	Years listed	Status change
Mammal: Cetacea							
Beluga whale	<i>Delphinapterus leucas</i>	Cook Inlet, Alaska DPS	US	2008	E	9	–
Blue whale	<i>Balaenoptera musculus</i>	Eastern North Pacific Stock	US/F	1970	E	47	–
Bowhead whale	<i>Balaena mysticetus</i>	Western Artic Stock	US/F	1970	E	47	–
Fin whale	<i>Balaenoptera physalus</i>	California/Oregon/Washington Stock	US/F	1970	E	47	–
		Western North Atlantic Stock	US/F	1970	E	47	–
Gray whale	<i>Eschrichtius robustus</i>	Eastern North Pacific Stock	US/F	1970	E→D	24	1994 –re
		Western North Pacific Stock	US/F	1970	E	47	–
Humpback whale	<i>Megaptera novaeangliae</i>	Central America DPS	US/F	1970	E	47	–
		Hawaii DPS	US	1970	E→D	46	2016 –re
		Mexico DPS	US/F	1970	E→T	47	2016 –dl
		West Indies DPS	US/F	1970	E→D	46	2016 –re

Killer whale	<i>Orcinus orca</i>	Southern Resident DPS	US	2005	E	12	–
N. Atlantic right whale	<i>Eubalaena glacialis</i>	North Atlantic Population	US/F	1970	E	47	–
Sei whale	<i>Balaenoptera borealis</i>	Eastern North Pacific Stock	US/F	1970	E	47	–
		Nova Scotia Stock	US/F	1970	E	47	–
Mammal: Carnivora							
Guadalupe fur seal	<i>Arctocephalus townsendi</i>	Guadalupe Island Population	US/F	1985	T	32	–
Hawaiian monk seal	<i>Neomonachus schauinslandi</i>	NW Hawaiian Islands Index Population	US	1976	E	41	–
Northern sea otter	<i>Enhydra lutris kenyoni</i>	Southwest Alaska DPS	US	2005	T	12	–
Southern sea otter	<i>Enhydra lutris nereis</i>	California Population	US	1977	T	40	–
Steller sea lion	<i>Eumetopias jubatus</i>	Western DPS	US/F	1990	T→E	27	1997 –ul
		Eastern DPS	US/F	1990	E→D	23	2013 –re
Mammal: Sirenia							
Florida manatee	<i>Trichechus manatus latirostris</i>	Florida Population (subsp.)	US	1967	E→T	50	2017 –dl
Antillean manatee	<i>Trichechus manatus manatus</i>	Puerto Rico Population (subsp.)	US/F	1970	E→T	47	2017 –dl
Reptile: Sea Turtles							
Green turtle	<i>Chelonia mydas</i>	Central North Pacific DPS	US/F	1978	T	39	–
		Central West Pacific DPS	US/F	1978	T→E	39	2016 –ul
		North Atlantic DPS	US/F	1978	E→T	39	2016 –dl
		South Atlantic DPS	US/F	1978	T	39	–
Hawksbill turtle	<i>Eretmochelys imbricata</i>	Atlantic Population	US/F	1970	E	47	–
		Pacific Population	US/F	1970	E	47	–
Kemp's ridley turtle	<i>Lepidochelys kempii</i>	Texas Population	US/F	1970	E	47	–
Leatherback turtle ^b	<i>Dermochelys coriacea</i>	Atlantic DPS	US/F	1970	E	47	–
Loggerhead turtle	<i>Caretta caretta</i>	Northwest Atlantic Ocean DPS	US/F	1978	T	39	–

237 ^aThe leatherback sea turtle is managed independently in the Atlantic and Pacific Oceans as DPSs. Only Atlantic leatherback sea turtles nest on U.S. beaches,

238 Pacific leatherback were excluded from the analysis.

239

240

241 ***Population trends and magnitude of change***

242 Overall, approximately 78% of marine mammals (18 out of 23) and 78% of sea turtles (7 out of
243 9) analyzed that met our selection criteria significantly increased in abundance after ESA listing
244 (Fig 1A). Representative populations of three marine mammals (~13%) and two sea turtles
245 (~22%) experienced non-significant change. Only two marine mammals (~9%), but no sea
246 turtles significantly declined after ESA protection (Fig 1A). Marine mammals and sea turtles
247 with populations that significantly increased were listed between two to five decades and
248 increasing population trends was positively associated with time since listing. In contrast, there
249 was no association with listing time for populations that showed non-significant trend or that
250 declined in abundance (Fig 1B; Table 2). Out of the 25 species with populations that
251 significantly increased, 52% were listed as endangered, 32% as threatened, and 16% were
252 delisted, indicating that population increases occurred independent of whether a species was
253 classified as threatened or endangered (Tables 1 and 2).

254

255 **Fig 1. Number and percentage of marine mammal and sea turtle species protected under**
256 **the ESA** with population trends that significantly increased (inc), non-significant change (nsc),
257 and significantly decreased (dec) after listing. **(A)** Calculations were based on representative
258 populations of 23 marine mammal and 9 sea turtle ESA listed species that met our selection
259 criteria. **(B)** Relationship between population trend and time since listing for marine mammals
260 (blue circles) and sea turtles (green circles) species. Black line is the median and grey circle the
261 mean.

262

263

264 **Table 2. Linear model and ANOVA results of the relationship between time since ESA**
265 **listing and population trends (increasing, non-significant, decreasing) for marine mammal**
266 **and sea turtle species.** The decreasing trend was used as reference for the linear model.
267 Significant codes are ‘***’ 0.01 and ‘*’ 0.05.

268

Linear model	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	26.500	7.327	3.617	0.00112 **
Non-significant trend	2.700	8.669	0.311	0.75769
Increasing trend	16.020	7.614	2.104	0.04417 *
ANOVA	DF	Mean Sq	F value	Pr(>F)
Trend	2	548.17	5.1057	0.01260 *
Residuals	29	107.36		

269

270 Most marine mammals that significantly increased after ESA listing had substantial population
271 growth (Figs. 2 and 3; Table 3). Several populations of large whale species increased in numbers
272 from ~3% to ~43% per year, often doubling to quadrupling their initial population estimates
273 (Table 3). For example, all four DPSs of humpback whales analyzed in our study showed
274 substantial population increases (Fig 2; Table 3). In fact, the Hawaiian DPS of humpback whale
275 reached over 10,100 individuals in 2005 from only 800 individuals estimated in 1979 (Fig 2;
276 Table 3). NMFS subsequently delisted it from the ESA in 2016 (Table 1). While most large
277 whale populations trended toward recovery, the critically endangered population of the North
278 Atlantic right whale (*Eubalaena glacialis*) increased at 4.2% per year from 270 to 481 whales
279 between 1990 and 2010 , but declined to an estimated 451 whales between 2010 to 2016 (Fig 2;
280 Table 3 and S2 Table). At least 17 individuals died in 2017, representing nearly 4% of the entire
281 population (Table 3 and S2 Table).

282

283

284 **Table 3. Population trends and magnitude of population change of selected marine mammal and sea turtle species protected**
 285 **under the ESA.** Population (Pop.) trends (significantly increased↑, non-significant change →, significantly decreased↓) are based on
 286 species-specific models and time periods are shown. Current population trends (% per year) and magnitude of population change (%)
 287 were calculated based on available data after listing. First and last population abundance estimates for the time period are shown for
 288 reference.

289

ESA Species (DPS/Stock/Location)	Time period (years)	Pop. trend (sign)	Pop. trend (% yr ⁻¹)	Pop. change (%)	First pop. estimate (No.)	Last pop. estimate (No.)
Cetacean						
Beluga whale (Cook Inlet DPS)	08-14	→	-0.44	-8.8	375	340
Blue whale (Eastern North Pacific Stock)	79-14	↑	+4.99	+174.5	705	2,000
Bowhead whale (Western Arctic Stock)	78-11	↑	+8.34	+273.1	4,765	16,892
Fin whale (California, Oregon, Washington Stock)	91-14	↑	+13.34	+306.9	1,744	9,892
Fin whale (Western North Atlantic Stock)	92-11	→	-0.75	-14.2	2,700	1,618
Gray whale (Eastern North Pacific Stock)	70-11	↑	+1.28	+52.6	14,553	20,990
Gray whale (Western North Pacific Stock)	94-12	↑	+6.22	+111.9	66	140
Humpback whale (Central America DPS, California + Oregon)	85-14	↑	+15.18	+440.2	300	1,403
Humpback whale (Hawaii DPS, Hawaii winter)	79-05	↑	+42.86	+1,114.3	800	10,103
Humpback whale (Mexico DPS, Southeast Alaska to Alaska Peninsula)	86-11	↑	+13.40	+334.4	393	1,115
Humpback whale (West Indies DPS)	79-05	↑	+3.00	+78.0	7,260	12,312
Killer whale (Southern Resident DPS)	05-17	↓	-0.93	-11.2	88	76
North Atlantic right whale (North Atlantic)	90-10	↑	+4.20	+84.0	270	481
	10-16	↓	-1.05	-6.3	481	451
Sei whale (Eastern North Pacific Stock)	96-14	↑	+33.09	+595.6	150	864
Sei whale (Nova Scotia Stock)	70-11	↑	+1.98	+81.4	93	357
Carnivora						

Guadalupe fur seal (Guadalupe Island, Mexico)	85-15	↑	+ 14.84	+ 905.4	2,017	20,000
Hawaiian monk seal (NW Hawaiian Islands)	85-13	↓	- 2.04	- 57.0	1,997	789
(NW Hawaiian Islands)	13-16	↑	+ 5.72	+ 22.9	789	968
Northern sea otter (Southwest Alaska DPS, Attu, Amchitaka, Adak, Kiska Islands)	05-11	→	+ 5.06	+ 30.3	687	863
Southern sea otter (California)	79-17	↑	+ 3.02	+ 114.7	1,443	2,688
Steller sea lion (Eastern DPS, California to Southeast Alaska)	90-13	↑	+ 5.79	+ 133.2	19,103	59,968
Steller sea lion (Western DPS, Alaska)	90-03	↓	- 3.04	- 39.4	64,761	39,963
	03-15	↑	+ 2.34	+ 28.1	39,963	52,009
Sirenia						
Florida manatee (Florida)	74-17	↑	+ 17.14	+ 737.3	800	6,620
Antillean manatee (Puerto Rico)	76-13	↑	+ 4.75	+ 175.8	51	142
Sea Turtles						
Green turtle (Central North Pacific DPS, East Island, French Frigate Shoals, HI) ¹	78-16	↑	+ 12.66	+ 480.9	101	88
Green turtle (Central West Pacific DPS, Guam waters) ²	78-10	→	+ 7.46	+ 238.6	92	299
Green turtle (North Atlantic DPS, Florida index beaches) ³	89-16	↑	+ 75.71	+ 2,044.2	464	2,978
Green turtle (South Atlantic DPS, Buck Reef NWR + Sandy Point NWR + Jack, Isaac, and East End Bays, VI) ³	82-15	↑	+ 104.2	+ 3,439.1	31	931
Hawksbill turtle (Atlantic DPS, Mona Island, Puerto Rico) ³	74-15	↑	+ 22.64	+ 928.5	177	1,328
Hawksbill turtle (Pacific DPS, Island of Hawaii) ¹	91-15	↑	+ 13.91	+ 333.9	4	25
Kemp's ridley turtle (Texas) ³	79-17	↑	+ 284.2	+ 11,083.8	1	353
Leatherback turtle (Atlantic DPS, Florida +Puerto Rico + Sandy Point NWR, VI) ³	84-16	↑	+ 32.25	+ 1,032.2	368	3,625
Loggerhead turtle (NW Atlantic DPS, Peninsular FL index beaches) ³	89-16	→	+ 1.16	+ 31.4	39,083	65,807

290 ¹ Number of nesting females

291 ² Number of individuals

292 ³ Number of nests

293 **Fig 2. Population trends of cetacean marine mammals listed under the ESA.** Trend lines
294 (gray area: 95% confidence interval) are loess curves with span of 0.5 to aid in visual
295 representation. Grey dots are estimated number of individuals. Panels are organized by
296 decreasing length of time listed and then in alphabetical order based on species names. Dashed
297 vertical red lines indicate the year of ESA listing. For species selection criteria see methods; for
298 protection status see Table 1; and for results of fitting models see S2 Table. Abbreviations are
299 CA/OR/WA: California/Oregon/Washington; E.N.: Eastern North; and W.N.: Western North.

300
301 Non-cetacean marine mammals also significantly increased in abundance at relatively high
302 population growth rates since ESA protection. Notably, the Guadalupe fur seal (*Arctocephalus*
303 *townsendi*) increased about nine times at ~15% per year since listing in 1985 (Fig 3; Table 3).
304 The California population of the Southern sea otter (*Enhydra lutris nereis*) approximately
305 doubled in numbers and it is likely to reach the demographic recovery criteria in the coming
306 years (Fig 3; Table 3). The Eastern DPS of Steller sea lion (*Eumetopias jubatus*) tripled its
307 population at ~6% per year since 1990, reaching its recovery criteria of ~60,000 individuals in
308 2013, and was subsequently delisted from the ESA (Fig 3; Table 3). Also, both the Florida and
309 Antillean manatee subspecies increased approximately eight and three times (~17% and ~5% per
310 year), respectively, for the past 40 years (Fig 3; Table 3); and the USFWS downlisted them from
311 endangered to threatened in 2017 (Table 1).

312
313 **Fig 3. Population trends of non-cetacean marine mammals listed under the ESA.** Trend
314 lines (gray area: 95% confidence interval) are loess curves with span of 0.5 to aid in visual
315 representation. Grey dots are estimated number of individuals. Panels are organized by

316 decreasing length of time listed. Dashed vertical red lines indicate the year of ESA listing. For
317 species selection criteria see methods; for protection status see Table 1; and for results of fitting
318 models see S2 Table. Abbreviations are DPS: Distinct Population Segment; Pop.: Population;
319 N.W. North Western; and S.W: Southwest.

320

321 Representative populations of five marine mammals analyzed in our study did not increase in
322 abundance. Three marine mammals showed non-significant population change after listing:
323 Western North Atlantic fin whale (*Balaenoptera physalus*), Cook Inlet beluga whale
324 (*Delphinapterus leucas*) DPS (Fig 2; Table 3 and S2 Table), and Southwest Alaska DPS of the
325 northern sea otter (*Enhydra lutris kenyoni*) (Fig 3; Table 3 and S2 Table). In contrast, two marine
326 mammals significantly declined after ESA listing: the critically endangered Southern Resident
327 killer whale (*Orcinus orca*) and the Hawaiian monk seal (*Neomonachus schauinslandi*).
328 Southern Resident killer whales declined at -0.93% per year since listing in 2005, when the
329 population had 88 individuals (Fig 2, Table 3). This population suffered major declines after a
330 record high of 98 individuals in 1995, and the last population survey estimated 76 individuals in
331 September 2017, a 30-year low (Fig 2; Table 3). Total abundance of Hawaiian monk seals from
332 six index subpopulations in the Northwestern Hawaiian Islands significantly declined from 1,997
333 individuals in 1985 to 789 seals in 2013 at approximately -2% per year (Fig 3; Table 3).
334 However, the population has increased to 968 seals by 2016 (Table 3).

335

336 Nearly all sea turtle species analyzed in our study significantly increased after ESA listing (Fig
337 4; Table 3 and S2 Table). Estimates of the number of individuals, nesting females, and number
338 of nests in nesting beaches of representative populations of green, hawksbill, Kemp's ridley, and

339 Atlantic leatherback sea turtles showed that these species increased at considerably high growth
340 rates (~13% to ~284% per year) for several decades, depending on initial estimates (Fig 4; Table
341 3 and S2 Table). For example, the number of nesting females of green sea turtle at East Island of
342 the French Frigate Shoals in Hawaii (Central North Pacific DPS) increased at ~13% per year
343 from 101 individuals in 1978 to 492 nesting females in 2015 (Fig 4; Table 3). The number of
344 nests of green sea turtles across Florida statewide beaches (North Atlantic DPS) increased at
345 ~76% per year from 62 nests in 1979 to a record high of 37,341 nests in 2015 (Fig 4; Table 3).
346 Due the strong recovery of green sea turtles across Florida, NMFS and the USFWS downlisted
347 the entire North Atlantic DPS from endangered to threatened in 2016 (Table 1). Similarly, the
348 number of nests of the hawksbill turtle population at Mona Island in Puerto Rico (Atlantic DPS)
349 increased at over 22% per year from 177 in 1974 to a record high of 1,626 nests in 2014 (Fig 4;
350 Table 3). Notably, the Atlantic leatherback populations have also experienced a considerable
351 rebound, and the combined number of nests across Florida, Puerto Rico, and the Virgin Islands,
352 significantly increased after ESA listing (Fig 4; Table 3).

353

354 **Figure 4 Population trajectories of sea turtles listed under the ESA.** Trend lines (gray area:
355 95% confidence interval) are loess curves with span of 0.5 to aid in visual representation. Grey
356 dots are estimated number of nests, except for the hawksbill Pacific DPS and the green turtle
357 Central North Pacific DPS (number of nesting females), and green turtle Central West Pacific
358 DPS (number of individuals). Panels are organized by decreasing length of time listed. Dashed
359 vertical red lines indicate the year of ESA listing. For species selection criteria see methods; for
360 protection status see Table 1; and for results of fitting models see S2 Table. Abbreviations are

361 DPS: Distinct Population Segment; Pop.: Population; C.N.: Central North; C.W.: Central West;
362 and N.W: Northwest.

363

364 Among the sea turtles analyzed in this study, our models were not able to detect significant
365 population linear trends for the Central West Pacific DPS of the green turtle (Guam waters), and
366 the Northwest Atlantic DPS of the loggerhead turtle (*Caretta caretta*) across the Florida
367 peninsula (Fig 4; Table 3 and S2 Table). For example, the best models for the number of nests of
368 loggerhead turtles across index beaches of the Florida peninsula described a non-linear
369 relationship where the number of nests substantially fluctuated since 1989, with a record high of
370 65,807 in 2016 (Fig 4).

371

372

373 **DISCUSSION**

374 Most marine mammals and sea turtles listed under the ESA that met our selection criteria,
375 significantly increased after listing indicating strong population recoveries. Our analyses confirm
376 the hypothesis that ESA listed marine mammal and sea turtle species are more likely to be
377 recovering the longer they stay protected under the law, regardless of whether they are listed as
378 threatened or endangered. Previous studies support these findings for a variety of terrestrial taxa,
379 marine birds, and anadromous fishes [16,19,23,25,39,55]. Here we discuss how these findings
380 suggest that ESA protections and conservation measures are important for the recovery of
381 imperiled marine mammals and sea turtles, and illustrate specific examples through three case
382 studies.

383

384 The ESA's prohibitions on commercial exploitation paired with the implementation of
385 widespread conservation measures such as interagency consultation, recovery plans and critical
386 habitat designations have been crucial to mitigating threats that affect marine mammals and sea
387 turtles [34,56]. Strong population increases for most marine mammal and sea turtle species after
388 ESA protection demonstrate the capacity of these taxa to recover from drastic declines after
389 decades of exploitation, habitat degradation, and other threats. Between the 18th to early 20th
390 century these groups were substantially depleted [4,46,57,58], in a few cases to extinction such
391 as the Steller's sea cow [59] and the Caribbean monk seal [60,61]. Marine mammals and sea
392 turtles have greatly benefited from a major change from resource exploitation (e.g., whaling,
393 hunting, egg harvesting) to conservation measures that protect these species from direct and
394 indirect harm [62].

395
396 For the large whales, ESA protections facilitated the recovery of populations that were severely
397 depleted by commercial whaling by reducing key threats such as ship strikes, entanglement in
398 fishing gear, and pollution [56,63–67]. For example, ESA protection led to the establishment of
399 vessel speed limits and restrictions on approaching whales too closely to lower the likelihood of
400 death and injury from vessel strikes [68–70]. By triggering a depleted designation under the U.S.
401 Marine Mammal Protection Act (MMPA), ESA marine mammal listings have prompted the
402 implementation of take reduction plans to reduce injury and death from fisheries entanglement
403 that require gear modifications, time and area closures, and vessel observers [40,71]. ESA
404 regulations have also helped to limit acoustic harms to whales and other marine mammals by
405 restricting U.S. military use of sonar and explosions in biologically important habitat areas
406 around Hawaii Islands and Southern California [72].

407
408 For sea turtles, ESA protections have been instrumental in reducing primary threats from human
409 harvest, fishery bycatch, and habitat destruction. The ESA's prohibitions on harvesting sea
410 turtles and their eggs has virtually eliminated this key threat – historically the principal cause of
411 sea turtle population declines – in U.S. turtle nesting and foraging grounds [73,74]. ESA listing
412 prompted regulations that have reduced sea turtle bycatch mortality in commercial fisheries by
413 requiring gear modifications (e.g., turtle excluder devices in trawl fisheries, circle hooks in
414 longline fisheries, modifications to pound net leaders), time and area closures, bycatch limits,
415 changes to fishing practices, and monitoring programs [75–78]. ESA-prompted reductions in off-
416 road-vehicle use and night lighting on nesting beaches have improved nesting success [79,80], as
417 has protection of important turtle nesting beaches as National Wildlife Refuges (NWR) on the
418 Atlantic coast (e.g., Archie Carr NWR, Florida) and the U.S. Caribbean (e.g., Culebra NWR,
419 Puerto Rico; Sandy Point NWR, U.S. Virgin Islands) [73,74,81]. In addition, ESA protections
420 have facilitated federal and state agencies (e.g., National Park Service, Florida Fish and Wildlife
421 Conservation Commission) to contribute funding and supported conservation efforts including
422 species reintroductions, e.g., Kemp's ridley turtles in Texas [82], and volunteer monitoring and
423 scientific data collection on most sea turtle nesting beaches across the U.S. (e.g., Florida
424 Statewide and Index Nesting Beach Survey program).

425
426 Two marine mammal species with populations that did not significantly change were listed
427 relatively recently (< 15 years). For example, the Cook Inlet DPS of beluga whale in Alaska was
428 listed in 2008 and the Southwest Alaska DPS of the northern sea otter was listed in 2005.
429 Conservation measures for these two species were developed relatively recently and ongoing

430 threats have not been mitigated [83,84]. It is likely that these species will require more time
431 under ESA protection as well as the adoption of robust conservation measures. In contrast, one
432 marine mammal and two sea turtles listed for several decades had populations with non-
433 significant change. The lack of significant population changes in the Western North Atlantic
434 Stock of fin whale and the Central West Pacific DPS of green turtle may be related to lack of
435 statistical power to detect a trend in abundance as confidence intervals of population estimates
436 were relatively large (Figs. 2 and 4; S1 Table) [74,85]. Alternatively, the populations of these
437 species may be stable, but further population estimates are needed to determine stability [74,85].
438 Finally, fluctuations in the number of nests of the Northwest Atlantic DPS of loggerhead turtle
439 across Florida beaches have been strongly correlated with ocean conditions associated with long
440 term climate forcing such as the Atlantic Multidecadal Oscillation [86].

441
442 Endangered marine mammal species with relatively low population abundance that significantly
443 declined after listing (e.g., Southern Resident killer whale and Hawaiian monk seal) or showed
444 non-significant change (e.g., Cook Inlet beluga whale) require urgent conservation attention.
445 NMFS already recognizes these species among those most at-risk of extinction in the immediate
446 future and they are considered recovery priorities because of rapid population declines [87].
447 These species face several similar regional anthropogenic threats including prey reduction due to
448 fishing, habitat degradation, toxic pollutants, disturbance from boat traffic and marine noise,
449 fishery interactions, as well as global threats associated with climate change and ocean regime
450 shifts that affect food availability [88–92]. In particular, food limitation has been recognized as a
451 key driver of lower body condition, pregnancy failures, calf/pup and juvenile mortality, and lack
452 of population recovery [92–96]. Numerous conservation measures addressing anthropogenic

453 stressors have been developed for these species and are delineated in recovery plans [84,97,98].
454 For example, NMFS established regulations to protect killer whales in Washington waters from
455 vessel impacts in 2011 (76 FR 20870). For Hawaiian monk seals, entanglements in fishing gear,
456 fishery interactions, and other human-caused mortalities (e.g., intentional killing) have been
457 reduced since ESA listing, especially across the inhabited Main Hawaiian Islands [98,99]. In
458 fact, after more than 50 years of continued decline, the range-wide population seems to have
459 steadily increased in numbers since 2013 to approximately 1,400 seals in 2016 [100]. Recently,
460 stronger conservation measures have been developed in high-priority action plans that focus
461 efforts and resources to reduce threats and stabilize population declines [87]. The outcomes of
462 these conservation efforts will require time to be realized, although the compounding effects of
463 climate change stressors may compromise the ability of these endangered species to rebound.

464

465 ***Case studies illustrate the recovery benefits of ESA listing***

466 *Hawaii DPS of humpback whale*

467 The Hawaii DPS of humpback whale was delisted by NMFS in 2016 based on its strong
468 population growth and the mitigation of key threats (NMFS 2015). Whales in this population use
469 the waters surrounding the main Hawaiian Islands for mating and calving and migrate to feeding
470 in areas off Southeast Alaska and northern British Columbia. The size of the population in
471 Hawaiian waters increased from 800 individuals in 1979 to more than 10,000 individuals in
472 2005, with the recent population growth rate estimated around 6% (NMFS 2015). ESA listing in
473 1970 prompted conservation measures in Hawaii and Alaska to reduce key threats to recovery.
474 ESA regulations restricted vessels in Hawaiian and Alaskan waters from approaching whales
475 within 100 yards, prohibited disrupting normal behaviors, and required slower vessel speeds to
476 reduce the likelihood of ship strikes and minimize human disturbance (60 FR 3775, 66 FR

477 29502). ESA listing also prompted coordinated federal and state efforts to reduce whale
478 entanglements in fishing gear through the Hawaiian Islands Disentanglement Network and
479 Alaska Response Network. The threatened status of humpback whales also provided impetus for
480 the designation of the 1,400 square-mile Hawaiian Islands Humpback Whale National Marine
481 Sanctuary in 1992 to protect humpback whales and their habitat (60 FR 48000).

482

483

484 *Western DPSs of Steller sea lion*

485 Population abundance of the Western DPS of Steller sea lion, which ranges from Eastern Gulf of
486 Alaska to the Western Aleutian Islands and Bering Sea [101], significantly increased over the
487 past 13 years (Fig 3). This species has shown a tremendous population recovery despite years of
488 overexploitation (for their fur, meat, and oil), indiscriminate killing, and decades of habitat
489 degradation, ship strikes, and fishery interactions [102]. Subpopulations of the Western DPS
490 suffered major declines through 2003 when a substantial population rebound began to occur
491 [101]. Abundance estimates of the Western DPS declined from 140,000 to 110,000 individuals
492 between 1960 and 1979 in rookeries and haul-outs across Southwest Alaska [102]. Total counts
493 continued to decline at 15% per year in the late 1980s, prompting NMFS to list the Western DPS
494 as threatened throughout the entire range in 1990 (NMFS 2008) and to uplist it to endangered in
495 1997 because of continued declines during the 1990s [103]. Population abundance stabilized in
496 the early 2000s [104,105] with the lowest population estimate in 2003 [101]. Notably, population
497 abundance significantly increased at 2.34% per year from 2003 to 2015 (Fig 5).

498

499 Conservation efforts under both the ESA and the MMPA such as designation of protective zones,
500 critical habitat designation, fishery regulations for prey species, and local regulations around

501 major rookeries and haul-outs have likely contributed to the species recovery success [102].
502 NMFS implemented several fishery management measures (e.g., area closures, catch and harvest
503 limits, reduction of disturbance due to fishing) in the Alaska groundfish fisheries in 2003 (Bering
504 Sea and Gulf of Alaska) around major haul-outs and rookeries within the designated critical
505 habitat (68 FR 204). These regulations, designed to reduce competition for prey between
506 commercial fishing and Steller sea lions and increase prey availability, are thought to have
507 contributed to increased prey abundance and a rebound of the DPS [102,106]. In fact, counts
508 have increased at an average of 2.17% (juveniles and adults) and 1.76% (pups) per year from
509 2000 to 2015 [101,107], although geographical variation exists due to migration among
510 subpopulations (NMFS 2015).

511

512 *North Atlantic DPS of green sea turtle*

513 The North Atlantic DPS of the green sea turtle, which mostly nests across Florida beaches, is
514 another ESA conservation success. The species has been increasing exponentially and has
515 become one of the largest nesting aggregations in the western Atlantic in recent years [74].
516 Historically exploited across the Caribbean [46], this species has shown a high recovery potential
517 when nesting areas are strictly protected from human disturbance and development, and fishery
518 bycatch is substantially reduced [74]. The North Atlantic DPS of green turtles showed high
519 records of nest numbers in 2013 (36,169 nests) and 2015 (37,341 nests) across Florida nesting
520 beaches compared with only 62 nests estimated in 1979 (Fig 4). In 2016, NMFS and USFWS
521 reclassified green sea turtles into 11 DPSs of which the Florida population was downlisted from
522 endangered to threatened due to strong population growth and record numbers in nesting beaches
523 throughout the peninsula (81 FR 20057).

524
525 ESA tools have been crucial for the recovery of the North Atlantic DPS of green sea turtles. ESA
526 regulations have led to fishing gear modifications, major changes in fishing practices, time and
527 area closures, and the establishment of turtle excluder devices for shrimp trawlers [77,108]. In
528 particular, fishery regulations instituted because of ESA protection have been largely successful
529 in reducing green sea turtle bycatch from Atlantic pelagic longlines and gillnets, the Chesapeake
530 Bay pound net fishery, and the Gulf of Mexico's shrimp and flounder trawl fisheries [74]. Take
531 prohibitions (i.e., no killing of adults or egg harvesting) under the ESA have been a major
532 conservation tool that directly boosts population growth. In addition, several national wildlife
533 refuges were dedicated to protecting nesting areas on the Atlantic coast and Gulf of Mexico, with
534 nest watchers and patrolling during nesting seasons [74]. The Florida Statewide Nesting Beach
535 Survey program, initiated in 1979 (one year after listing) as a cooperative agreement between the
536 USFWS and the Florida Fish and Wildlife Conservation Commission, now monitors ~215
537 nesting beaches (~825 miles) across Florida, involving federal, state, and regional institutions as
538 well as several conservation organizations, university scientists, and private citizens [109].
539 Federal agencies (NMFS and USFWS) along with state agencies and other institutions have
540 worked together in implementing the management actions in the 1991 recovery plan, eliminating
541 or reducing threats in nesting and foraging areas [74].

542

543 **CONCLUSIONS**

544 Recovery is occurring for most marine mammals and sea turtles listed under the ESA and
545 analyzed in our study. Species listed for over 20 years were more likely to have populations that
546 significantly increased in numbers. In contrast, relatively recently listed species were more likely

547 to have populations with non-significant change or declining. Targeted conservation efforts
548 triggered by ESA listing have been largely successful in promoting species recovery leading to
549 the delisting of some species and to dramatic increases in most. The recovery of listed species
550 depends ultimately on the adequate implementation of the ESA's tools and conservation
551 measures. Studies have demonstrated that the government's failure to fully implement the ESA's
552 protections and adequately fund conservation actions have been major impediments to species
553 recovery [19]. In general, listed species with designated critical habitat, sufficient conservation
554 funding, and well-implemented species-specific recovery plans tend to recover relatively faster
555 [16,23,24]. Our analysis not only underscores the capacity of marine mammals and sea turtles to
556 rebound after decades of exploitation and habitat degradation, but also highlights the success of
557 marine species conservation through the ESA protection.

558

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563

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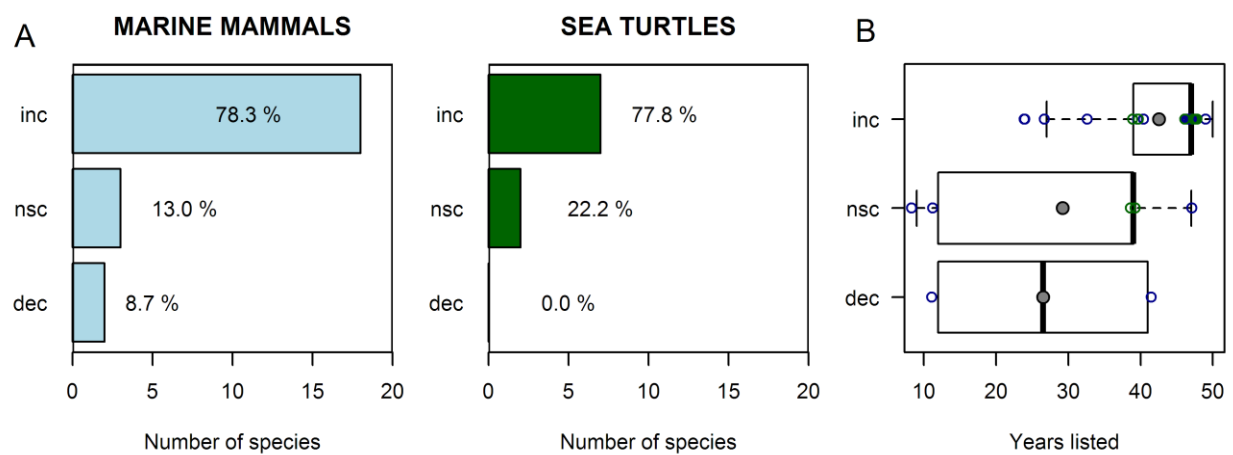
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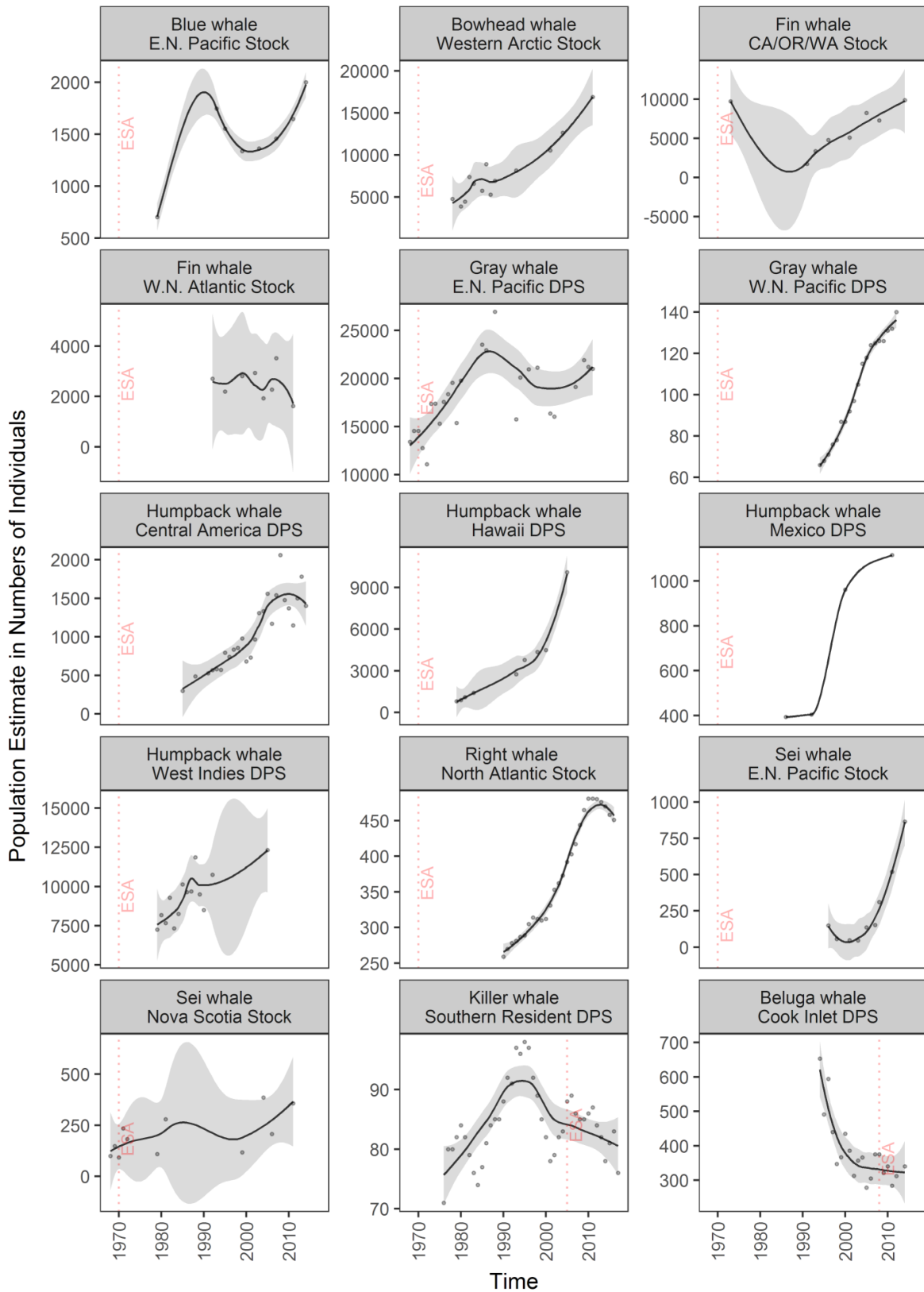
904 **Fig 1**



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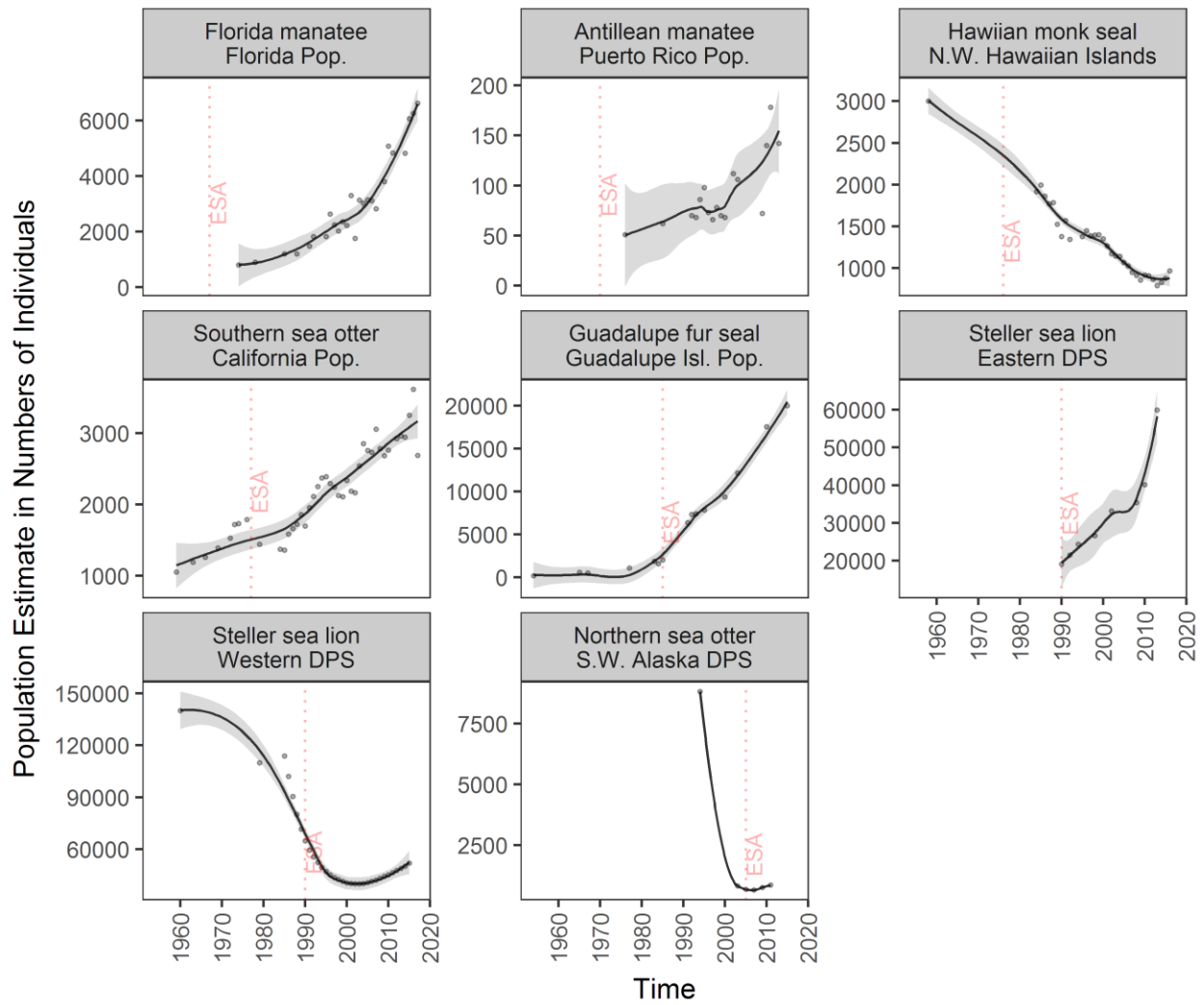
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907 **Fig 2**



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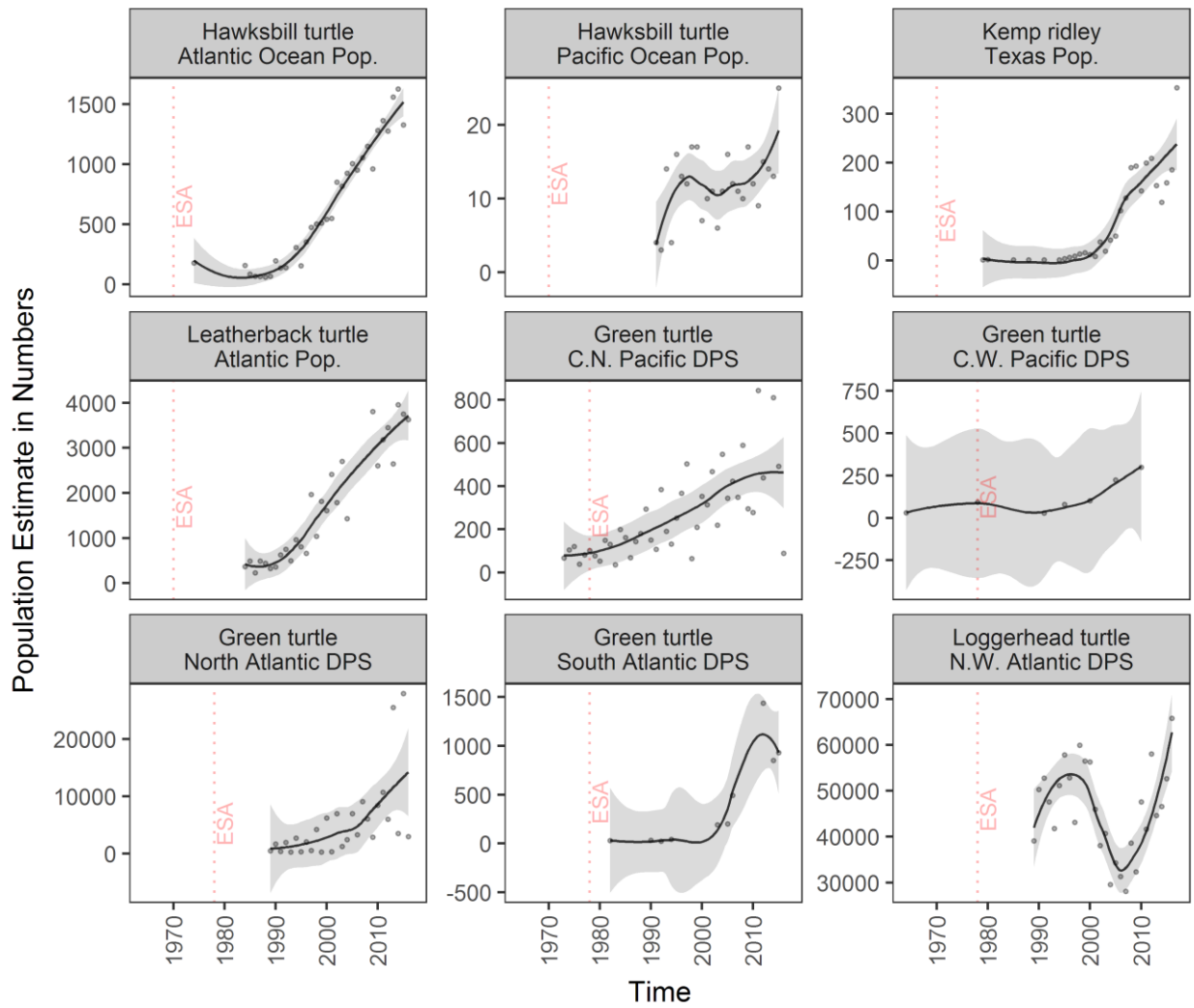
909 **Fig 3**



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912 **Fig 4**



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