

Modeling the population dynamics of lemon sharks

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Abstract

Long-lived marine megavertebrates (e.g. sharks, turtles, mammals, and seabirds) are inherently vulnerable to anthropogenic mortality. Although some mathematical models have been applied successfully to manage these animals, more detailed treatments are often needed to assess potential drivers of population dynamics. In particular, factors such as age-structure, density-dependent feedbacks on reproduction, and demographic stochasticity are important for understanding population trends, but are often difficult to assess. Lemon sharks (*Negaprion brevirostris*) have a pelagic adult phase that makes them logistically difficult to study. However, juveniles use coastal nursery areas where their densities can be high. Thus, we use a stage-structured, Markov-chain stochastic model to describe lemon shark population dynamics from a 17-year longitudinal dataset at a coastal nursery area at Bimini, Bahamas. We found that the interaction between delayed breeding and demographic stochasticity accounts for 33 to 49% of the variance. Demographic stochasticity contributed all random effects in this model, suggesting that the existence of unmodeled environmental factors may be driving the majority of interannual population fluctuations. In addition, we are able

26 to use our model to estimate the natural mortality rate of older age classes of lemon
27 sharks that are difficult to study. Further, we use our model to examine what effect
28 the length of a time series plays on deciphering ecological patterns. We find that—
29 even with a relatively long time series—our sampling still misses important rare events.
30 Our approach can be used more broadly to infer population dynamics of other large
31 vertebrates in which age structure and demographic stochasticity are important.

32 1 Introduction

33 Many large marine megavertebrates (e.g. sharks, turtles, mammals, seabirds) are particu-
34 larly vulnerable to anthropogenic mortality due to their complex life history characteristics,
35 including long lifespans, delayed maturity, low fecundity, and extended migrations (Fujiwara
36 and Caswell 2001; Baum et al. 2003; Lewison et al. 2004; Ward-Paige et al. 2012; Senko
37 et al. 2014). These animals often act as ecological keystones, and their removal can lead to
38 considerable ecosystem changes such as cascading ecological effects on lower trophic levels
39 (Lewison et al. 2004; Myers et al. 2007; Heithaus et al. 2008; Wirsing et al. 2008; Baum and
40 Worm 2009; Ferretti et al. 2010; Heithaus et al. 2010). For example, as predators, sharks not
41 only regulate their own prey populations but also those of species deeper in the food web
42 (Myers et al. 2007; Baum and Worm 2009; Ferretti et al. 2010; Heithaus et al. 2010) and see
43 recent review by (Heupel et al. 2014). Given their importance to ecosystem stability and
44 the multiple anthropogenic threats they face (Kyne et al. 2012; Worm et al. 2013), it is im-
45 perative that we develop a better understanding of shark population dynamics, particularly
46 to identify primary drivers of annual population variation.

47 Physiologically structured population models (Crouse et al. 1987; Caswell 2001; Mor-
48 ris and Doak 2002; Brauer and Castillo-Chávez 2012) that incorporate delayed breeding
49 (Gourley and Kuang 2004; Wang et al. 2009), density-dependent mechanisms (Neubert and
50 Caswell 2000; Caswell 2001), demographic stochasticity (Morris and Doak 2002; Ovaskainen
51 and Meerson 2010; Jenouvrier et al. 2012; Mills 2012; McCarthy and Possingham 2012), or
52 some combination of these processes, have been applied to many ecological systems to an-
53 swer questions related to population dynamics, conservation, and management. In examining

54 shark populations, physiologically structured discrete demographic models have been used
55 to study overfishing and population viability, calculate specific demographic parameters, and
56 predict population dynamics (Hoenig and Gruber 1990; Cortés 1998; Gallucci et al. 2006;
57 Gedamke et al. 2007; Mollet and Cailliet 2002; Knip et al. 2010; Cortés 2002; Beerkircher
58 et al. 2002; Booth et al. 2011; Tsai et al. 2010; Forrest and Walters 2009; Dulvy and Forrest
59 2010), also see review (Cortés 2007). Although these demographic models are useful, they
60 typically have three key shortcomings (Cortés 2007): (1) they typically include assumptions
61 that are biologically unrealistic, including density independent, deterministic mechanisms,
62 which makes application of model outputs to real data difficult to accept; (2) given that
63 these models are deterministic, they cannot capture demographic stochastic events, which
64 are likely to be important drivers of interannual population fluctuations; and (3) parame-
65 terization and validation of such models from data are often logistically difficult and require
66 long-term field operations (Lewison et al. 2004; McCauley et al. 2012).

67 The third challenge has been met by a longitudinal field study of lemon sharks (*Negaprion*
68 *brevirostris*) at Bimini, Bahamas. Data from this study includes an annual population census
69 of juvenile lemon sharks (ages 0-2 years) from 1996 to the present. The number of juveniles in
70 our study population (see Methods) typically fluctuates between 50 and 100 sharks, although
71 the complete range is estimated to be between about 35 and 150 (Fig. 1), which illustrates
72 the significance of annual fluctuations in the juvenile age class of this lemon shark population.
73 Also, fecundity and mortality rates have been estimated precisely using mark-recapture and
74 genetic methods (Gruber et al. 2001; Feldheim et al. 2002 2004).

75 The causes of annual variation in population size remain unclear for many species, and
76 we are unaware of any previous studies that have assessed these causes in detail for lemon
77 sharks. Furthermore, little is known regarding mortality rates of both the larger juveniles
78 (ages 3-11), who leave the nursery site around age three, and the adults (ages 12+) who
79 mature at approximately 12 years of age (Brown and Gruber 1988; Kessel 2010).

80 Here we present a mathematical model detailing annual fluctuations in a juvenile lemon
81 shark population at Bimini, Bahamas. The model is physiologically structured, with age class
82 as the (discrete) structuring variable. Hoenig and Gruber (1990) also used a physiologically
83 structured model in the form of a Leslie matrix. Unlike our model, their work only deals

84 with deterministic models. We make births and deaths stochastic, but fix environmental
85 parameters. We parameterize the model using estimates of fecundity and juvenile mortality
86 rate estimates obtained from the field study described above and apply inverse pattern-
87 oriented techniques to fit the model to data (Wiegand et al. 2003; Grimm et al. 2005; Hartig
88 et al. 2011; Anadón et al. 2012).

89 We show that demographic stochasticity in the model predicts only 33% to 49% of the
90 observed variance. Therefore, we predict that another source of stochasticity, probably
91 environmental, accounts for at least half of the variance observed in annual population
92 fluctuations in this population of lemon sharks. In addition, our use of inverse pattern-
93 oriented modeling allows us to estimate the unknown mortality rates of subadults and adults,
94 which illustrates the utility of this type of modeling. Further, such modeling can be used to
95 study how sample size (length of the time series) affects estimated population parameters
96 and dynamics. We find that time series with 15 consecutive years may be too short to
97 capture critical, but rare, stochastic events.

98 **2 Methods**

99 **2.1 Study Site and Field Data**

100 This study builds on field work conducted in Bimini Lagoon, Bimini, Bahamas (25°44N,
101 79°16W). The Biminis are located approximately 86 km east of Miami, Florida and provide
102 habitat for numerous species of fish, arthropods, birds, and mollusks (Jennings et al. 2012).
103 Of the three lemon shark nursery sites (as defined by (Heupel et al. 2007)) in Bimini, our
104 study focuses on the most northerly one, known as the North Sound. Between 1996 and
105 2012, standardized gillnet methods were used to capture juvenile lemon sharks within 45
106 days of parturition (Fig. 1). For a more detailed treatment of the gillnetting protocols and
107 yearly censuses, see (Manire and Gruber 1993; Gruber et al. 2001; Feldheim et al. 2004);
108 and (DiBattista et al. 2011).

109 In addition to population censuses, genetic analyses from tissue samples were used to
110 reconstruct family pedigrees (Feldheim et al. 2002 2004; DiBattista et al. 2011) from which

111 we estimate per-female annual fecundity in the Bimini population (Fig. 2). Reproductive-
112 age female lemon sharks (ages 12+) show strong philopatry to their natal nursery sites, with
113 about 45% returning to a given nursery area to reproduce every other year (Feldheim et al.
114 2002). Newborn and juvenile sharks (ages 0-2 years old) stay in these protected, mangrove
115 fringed nursery areas (Morrissey and Gruber 1993). In addition, there appears to be very
116 little dispersal among nursery sites in this region, so the population of juvenile lemon sharks
117 in the North Sound is essentially closed (Gruber et al. 2001). At about age 3, lemon sharks
118 enter their subadult phase (ages 3-11), begin to leave the lagoon area and move to deeper
119 waters (Morrissey and Gruber 1993; Franks 2007; Newman et al. 2010).

120 Our model is constructed to capture this natural history in such a way that key model
121 parameters, such as mortality rates of different age groups, can be estimated from field
122 data. This allows us to use inverse pattern-oriented methods to estimate other life history
123 parameters that are otherwise difficult or presently impossible to measure directly.

124 2.2 Model

125 We model the Bimini lemon shark population as an age-structured, Markov-chain stochastic
126 process. We choose this formalism due to the complexity of the lemon shark's life cycle—
127 in particular the delay in breeding to the 12th year—and because breeding populations at
128 nursery sites in any given year appear to be too small to be buffered from fluctuations due
129 to demographic stochasticity. Since the maximum age for lemon sharks is thought to be 25
130 years (Cortés 1998; Gedamke et al. 2007), we assume a maximum of 26 age classes (including
131 the 0th age class).

132 Let $\mathbf{x}(n)$ be the shark population vector at census time n ; that is, its elements, $x_a(n)$, $a \in$
133 $\{0, 1, \dots, 25\}$, $n \in \{0, 1, 2, \dots\}$, represent the number of lemon sharks of age a in the North
134 Sound population, including all animals born to and breeding in the North Sound nursery,
135 whether they are in the nursery or open ocean at census n . Age class 0 represents sharks
136 born the year of the census. To match the timing of the actual Bimini census, we assume
137 that this census occurs just after reproduction (i.e., pups are born April/early May and are
138 sampled late May/June).

139 **2.2.1 Fecundity**

140 We assume an equal sex ratio and that females only reproduce every other year after their
 141 11th year of life (Feldheim et al. 2002). Let R be a random variable taking on values
 142 in $\{0, 1, 2, \dots\}$ with probability density $\{p_0, p_1, p_2, \dots\}$. We interpret R as the number of
 143 offspring born to a particular breeding female, and p_i as the probability that a female gives
 144 birth to i pups. Let the number of breeding females in year n be denoted b_n ; that is,

$$b_n := \frac{1}{4} \sum_{a=12}^{25} x_a(n); \tag{1}$$

145 the coefficient of $1/4$ follows from the assumptions of equal sex ratio and biennial breeding
 146 with the further assumption that, for each age class, the proportions of females breeding
 147 in even and odd numbered years are equal. We assume that all breeding females have the
 148 same reproductive potential regardless of age class, time or population density. Therefore,
 149 the set $\{R_i; i \in \{1, 2, \dots, b_n\}\}$ is a collection of independent, identically distributed random
 150 variables, and R_i is the reproductive output of the i th female in year n . Therefore,

$$B(n) = \sum_{i=1}^{b_n} R_i \tag{2}$$

151 is the total reproductive output of the population in year n . Note that the dependence of B
 152 on n comes only through the number of breeding females in year n , not through R .

153 The probability density, $\{p_0, p_1, p_2, \dots\}$, for R can be obtained from a variety of assump-
 154 tions. We consider two possibilities. In some simulations, we obtain this density from data;
 155 in particular, each p_i is set to the observed frequency of females producing i pups (Fig. 2),
 156 with the convention that $p_j = 0$ for all $j > 18$. In the second case, we assume that all R_i s
 157 are Poisson-distributed with fixed mean λ . In this case, the probability density for the total
 158 population fecundity in year n becomes

$$\Pr(\{B(n) = j\}) = e^{-b_n \lambda} \frac{(b_n \lambda)^j}{j!} \text{ for all } j \in \{0, 1, 2, \dots\}. \tag{3}$$

159 A Poisson distribution is often assumed to be a good fit for a birth process. We explicitly

160 test that assumption here.

161 2.2.2 Mortality

162 We assume that the probability of mortality is evenly distributed across all individuals in a
163 given age class; therefore, within an age class the number of sharks that die between censuses
164 is distributed binomially. Generally speaking, the parameter of that distribution—the prob-
165 ability that a given shark dies—could potentially depend on population size. However, in
166 the case of lemon sharks, we only have evidence for density-dependent mortality in the first
167 age class (Gruber et al. 2001; Gedamke et al. 2007). There is insufficient evidence to support
168 either density-dependent or -independent mortality assumptions in other age classes; indeed,
169 very little is known about lemon sharks once they leave their nursery area. Therefore, as
170 a first approximation we chose density-independent mortality for all age-classes above the
171 first.

172 In this first age class, the probability that a shark pup dies between birth (age class 0)
173 and its second census (i.e. dies in age class 1) is a generally increasing function of the size of
174 its cohort ($x_0(n)$) in the lagoon in that year (Gruber et al. 2001; Gedamke et al. 2007). This
175 type of density-dependent mortality may be a result of reduced prey resources (although the
176 population does not appear to be prey-limited in any way), predation from large barracudas,
177 predation from other shark species, or cannibalism, which has been documented for this
178 population (Morrissey and Gruber 1993; Guttridge et al. 2012). We model this cohort-density
179 dependence with a generalized Michaelis-Menten function (equivalent to a Hill function):

$$\hat{\mu}(x_0(n)) = \frac{x_0(n)^h}{k^h + x_0(n)^h}, \quad (4)$$

180 with (constant) Hill and shape parameters $h \geq 1$ and $k > 0$, respectively. Let $M_0(n)$ be a
181 random variable representing the number of sharks born in year n that die between their
182 first and second censuses. Then $M_0(n)$ has probability distribution

$$\Pr(\{M_0(n) = m\}) = \binom{x_0(n)}{m} \hat{\mu}^m (1 - \hat{\mu})^{x_0(n) - m}, \quad m \in \{0, 1, \dots, x_0(n)\}, \quad (5)$$

183 where we suppress the dependence of $\hat{\mu}$ on $x_0(n)$ for clarity.

184 As a first approximation, we assume that no age classes except the first have density
185 dependent mortality. We further assume that the probability of mortality for any shark in
186 age classes 1 or higher is invariant across individuals regardless of age (this assumption could
187 be relaxed with our model structure). We denote this constant probability as μ and define
188 $M_a(n)$ to be a random variable representing number of deaths in age class $a \in \{1, 2, \dots, 25\}$.
189 Then

$$\Pr(\{M_a(n) = m\}) = \binom{x_a(n)}{m} \mu^m (1 - \mu)^{x_a - m}, \quad m \in \{0, 1, \dots, x_a(n)\}. \quad (6)$$

190 It is important to note that many of these assumptions can be relaxed without altering
191 the form of our model (see below). For example, here we assume no fishing mortality because
192 there is no shark fishery in Bimini. One could easily incorporate such an assumption into μ ,
193 and even make μ age-class- and (or) density-dependent with fairly obvious alterations to the
194 probability distribution for mortality equation (6) which have no effect on the overall model
195 form.

196 2.2.3 Model Form and Parameterization

197 The development above generates a model with the following form:

$$\begin{cases} x_0(n+1) = B(n), \\ x_a(n+1) = 1 - M_{a-1}(n), \quad a \in \{1, 2, \dots, 25\}, \\ \mathbf{x}(0) = \mathbf{x}_0, \\ n \in \{0, 1, \dots\}, \end{cases} \quad (7)$$

198 where \mathbf{x}_0 is the initial age distribution.

199 Application of model (7) to the lemon shark population requires field estimates of fecun-
200 dity and mortality. Starting with the former, as noted above we can estimate the probability
201 distribution directly from data (Fig. 2), or we can assume that per-female reproductive
202 output is Poisson-distributed with mean λ . Data from Bimini over the last 20 years suggests
203 that $\lambda \approx 6.1$ pups per female (Feldheim et al. 2002), although this value is somewhat lower
204 than that used in previous modeling studies (perhaps because of the high mortality of pups

205 between birth and our sampling season; in this case the 6.1 pups per female simply repre-
206 sents the number of sharks that make it past that interim period) (Hoenig and Gruber 1990;
207 Gedamke et al. 2007).

208 Less is known about mortality in this species. The first-year mortality function, equation
209 (4), requires two parameters: the Hill parameter (h) and the shape parameter (k), whereas
210 non-first-year mortality only requires an estimate of mean per-shark probability of mortality,
211 μ . Because of the lack of data, we compare model output to population data from the Bimini
212 study to define a range of potential values for these parameters using a sensitivity analysis
213 similar to that in (Hartig et al. 2011). We describe this method in the next section.

214 2.3 Simulations and analysis

215 For clarity of exposition we will refer to sharks from ages 0 to 2 as juveniles, from ages 3 to 11
216 as subadults and above age 12 as adults. We partition the traditionally-defined juvenile class
217 into two groups to make connections with the Bimini study—“juveniles” as defined above
218 are the animals actually caught each year in the Bimini nursery census. In particular, we
219 evaluate the model by comparing its behavior to the Bimini nursery census data. Model (7)
220 was implemented and all analyses were conducted using the open-source computing language
221 R (R Development Core Team 2011).

222 We used an inverse pattern-oriented technique to quantitatively compare simulations and
223 data (Wiegand et al. 2003; Grimm et al. 2005; Hartig et al. 2011; Anadón et al. 2012). In
224 this approach, one compares actual means and variances from data with the distribution of
225 means and variances predicted by model simulations. We explored 9000 distinct parameter
226 combinations (λ : range 1-15; k : range 0-200; μ : range 0-0.35; h fixed at 1). Note that,
227 although λ is known from Fig. 2, it is still of interest to examine a range of values for λ to
228 evaluate the type of compensatory responses generated by variations in λ . We fixed $h = 1$
229 in equation (4) because this gave the best fit (least sum of a squares) to the relationship be-
230 tween mortality and density obtained by (Gedamke et al. 2007). Likewise, we also limited k
231 below 200 because larger values produce a linear mortality rate that greatly underestimates
232 that measured by (Gedamke et al. 2007) and (Gruber et al. 2001). For each of the 9000
233 combinations, model simulations were repeated 100 times with the same initial conditions.

234 Simulations were run for 300 time steps (in “years”) or until the population went extinct.
235 Among-year mean and variance for juveniles were recorded for each of the 100 simulations,
236 which provided an estimate of parametric distributions of simulation means and variances.
237 To assess how well any given parameter combination represented the field data, we deter-
238 mined if both the mean and variance of the field data set fell within the middle 95 percent
239 of the distribution of means and variances generated from the simulations of a particular
240 parameter combination. The fit between model and data was deemed “good” if (i) mean size
241 of the juvenile population size from the data fell within the middle 95% of the distribution of
242 mean juvenile population sizes from the simulations; (ii) variance in juvenile population size
243 from the data fell within the middle 95% of its distribution from the simulations; and (iii)
244 the population remained extant after 300 years in each of the 100 runs. By eliminating pa-
245 rameter combinations that fail to satisfy any of these three criteria, we effectively constrain
246 possible values for the unknown parameters (see Fig. 3).

247 **2.3.1 Testing the effect of sampling length**

248 We generated the mean and variance distributions by drawing random 17-year-long samples
249 out of each of the 100 trials; that is, we sampled a randomly-chosen sequence of 17 con-
250 secutive years—after initial transient dynamics have settled down—from each simulation as
251 an analogue to the 17 consecutive years of field data at hand. However, a question arises
252 regarding how well a 17 year data set represents centuries of ecological dynamics. To assess
253 this, we compare data to various sized samples from simulations, including complete (300
254 year) simulations, and find that interannual variance in population size is strongly affected
255 by the duration of sample run.

256 **3 Results**

257 The Bimini nursery data suggest that on average about 77 juvenile sharks inhabit the lagoon
258 at census time, on average, with interannual variance, s^2 , of 498 (Fig. 1). With default
259 parameters ($\lambda = 6.1$, $\mu = 0.15$, $k = 100$) we can match mean juvenile population sizes from
260 the simulation to the actual mean; however, at default the mean of variances from simulation

261 runs, denoted s_{sim}^2 , is 176 ($n = 100$ trials), which represents only 35 percent of s^2 in the
262 actual data set.

263 We compared field estimates of annual mean and variance of population size to annual
264 mean and variance of simulated population sizes generated by each of the 9000 parame-
265 ter combinations. By the methods described in the simulations and analysis section, we
266 determined that most of the 9000 parameter combinations were a poor fit to actual data.
267 Therefore, the volume of the possible parameter space that admits dynamics having any
268 chance of representing the actual Bimini population is greatly constrained (Fig. 3), even
269 when λ is allowed to vary from 1-15. Note that in Fig. 3, lemon shark births were Poisson
270 distributed according to equation (3). Using the observed distribution of births per female
271 (Fig. 2) further tightens our constraints on k and μ (Fig. 4).

272 Our model also places tight constraints on adult mortality ($\mu = 0.14 - 0.17$). Values for
273 μ greater than 0.17 drive the population to extinction. This range for μ also tends to agree
274 with the indirect methods for estimating mortality given by (Pauly 1980; Hoenig 1983) and
275 (Jensen 1996) and summarized in Table 2. These indirect methods place the mortality rate
276 between 0.086-0.179. Interestingly, the half-saturation value (k) is much less constrained;
277 good fits can be obtained for any $k > 100$ (Fig. 4).

278 It is important to note that even for parameter combinations that qualified as good fits,
279 all greatly underestimated annual variance observed in the actual data.

280 In general, our model dynamics were robust with respect to the two assumed distribu-
281 tions of per-female fecundity. Specifically, both produced very similar regions of parameter
282 combinations that matched Bimini (Fig. 4), with the nuanced exceptions noted above. In ad-
283 dition, however, the actual distribution of litter sizes consistently generated a higher variance
284 in annual population size than did the Poisson distribution. Therefore, although the Poisson
285 distribution is a reasonable choice to use when the actual distribution is not available, one
286 needs to be aware that it tends to underestimate variance.

287 To test the effect of sample size on characterization of population dynamics from real
288 data, we compared sequences of years of various lengths as described in the methods (Fig.
289 5). We find that variance is a generally increasing function of sample length and appears
290 to approach an asymptote which represents our estimate of the parametric variance. This

291 asymptote is considerably higher than the variance typically obtained using 17-year sample
292 runs (vertical red line in Fig. 5). Nevertheless, this estimated parametric variance is still
293 well below the observed variance of 498 sharks² (horizontal green line in Fig. 5).

294 4 Discussion

295 Lemon sharks have complex life histories—they delay breeding for over a decade, mature
296 in an environment (nursery lagoons at the Bimini site) vastly different from their adult
297 habitat (open ocean) and when mature breed every other year. Also, nursery populations are
298 typically not large enough (order 10² at most) to buffer demographic stochasticity; indeed,
299 demographic stochasticity can dominate dynamics in patchy systems with sizes orders of
300 magnitude larger than this one (McKane and Newman 2004 2005; McKane et al. 2007).

301 Therefore, generalized, deterministic population models can hope to elucidate only the
302 broadest outlines of lemon shark population dynamics and should be interpreted only in
303 the “ensemble average” sense (McKane and Newman 2004; van Kampen 1992). That is,
304 deterministic models at best provide an expectation or mean behavior for an infinite number
305 of Bimini’s lemon shark populations. Although this abstract notion of an ensemble mean
306 is sensible and provides some insight about expected behavior of the population, under a
307 suitable definition of “expected,” that insight is limited because such models provide no
308 measure of the fluctuations about this ensemble average one can expect to see in any real
309 instance (Ovaskainen and Meerson 2010)).

310 We addressed this shortcoming by developing a model of the lemon shark population at
311 Bimini incorporating both demographic stochasticity and age structure. Despite the added
312 realism, the model remains relatively simple. Parameters requiring estimates include the
313 probability distribution for the number of pups born to breeding females in a give year, or just
314 the mean number of pups per female if one assumes a Poisson distribution, two parameters
315 characterizing density-dependent mortality in the first age class, and the probability(-ies) of
316 mortality for all individuals in all other age classes, which here we assume to be invariant
317 across individuals. We obtain the reproductive parameters directly from a field study of the
318 Bimini lemon shark nursery (Fig. 2), and we use an exhaustive parameter search to obtain

319 bounds on the other parameters.

320 **4.1 Fecundity assumptions**

321 As far as we know, this is the first elasmobranch study to use actual litter sizes derived
322 from genetic data to parameterize a mathematical or computational model's birth function.
323 Typically such studies rely on an assumed distribution, of which Poisson is usually thought
324 to be a good first estimate. Since we have a data-driven, realistic estimate of the distribution
325 of litter sizes, we can explore the consequences of making the Poisson assumption, and we
326 find that, in this instance, the Poisson assumption appears reasonable. If researchers only
327 have mean number of pups per female, which is often the case without genetic maternity
328 data, the Poisson distribution approximates the actual distribution remarkably well (Fig.
329 2). Also, the regions of viability within the parameter space for both actual and Poisson
330 distributions are comparable (Fig. 4). However, the simulations we ran using the Poisson
331 assumption consistently exhibited lower interannual variance than did simulations using the
332 actual reproductive data. Therefore, although the Poisson assumption generates estimates
333 of adult mortality that are essentially identical to those produced using the data, it should
334 be used with care when modeling to assess population viability and fluctuations.

335 **4.2 Mortality assumptions**

336 In the present study we model density-dependent mortality in the first age class as a non-
337 stationary Bernoulli process; that is, the probability of mortality is a generally increasing
338 function of the number of sharks in this age class. This assumption is justified based on
339 field data (Gruber et al. 2001; Gedamke et al. 2007). We represented this density-dependent
340 mortality using a Hill function (equivalently a Michaelis-Menten form) from phenomenologi-
341 cal considerations only—we hypothesize a monotonically increasing function, which the Hill
342 function exhibits, with the added benefits of relative simplicity and plasticity. Nevertheless,
343 the parameters of this function have biological meaning. In particular, the shape parameter,
344 k , measures how sensitive sharks are to competition from same-age conspecifics. As such,
345 although it quantifies an important biological response, in general it will be very difficult to

346 estimate accurately in the field. Importantly, this model demonstrates that practical esti-
347 mates need not be very precise. The model matches data for a wide range of this parameter's
348 values; in fact, for $k > 100$ or so, the model fit is largely unaffected (Fig. 4). Therefore, this
349 model is robust for parameterizations of k .

350 The bounds we found for subadult and adult mortality rates are remarkably narrow
351 (Figs. 3 & 4). In fact, a key prediction from this model is that the probability of mortality
352 for any individual in any age class, after the first, lies between 0.14 and 0.17. Indeed,
353 above 0.17, populations invariably die out very rapidly. These mortality estimates compare
354 favorably to estimates obtained using the techniques in Table 2. We emphasize that the
355 technique applied here, known as inverse pattern-orientated modeling, has seldom been used
356 to estimate parameters for any shark population. If subadult and adult mortality were to
357 increase by only a few percentage points, the model predicts rapid extinction. Therefore,
358 we suggest that any added fishing pressure (there is currently no fishing pressures for lemon
359 sharks at Bimini) to this population would threaten its sustainability. This result agrees with
360 others in suggesting that long-lived species with low fecundity, like lemon sharks, would not
361 be able to handle added fishing mortality in adult age classes (Ward-Paige et al. 2012).

362 One difficulty this model faces is a lack of information about mortality in subadults and
363 adults. As a first approximation, we assume a fixed probability of mortality in all age classes
364 after the first. However, we recognize the tentative nature of this assumption. In particular,
365 it is challenging to relate age to mortality rate of untagged adult sharks. (Peterson and
366 Wroblewski 1984) suggested that one method to overcome this problem is to construct a
367 function that maps shark mortality rate to mass. In this case age can then be related
368 to mass with conversion methods such as those used in (Beerkircher et al. 2002). This
369 method needs modifications in situations where mortality is density-dependent, and it relies
370 on assumptions of von Bertalanffy growth and reliable estimate of mass, length, and age from
371 catch data. However, where applicable, this technique may only be needed for the first few
372 age classes, or at least until the age at which individual sharks are large enough avoid being
373 preyed upon by natural predators (Cortés 1998). However, in this study such a technique
374 is unavailable because size data of adult sharks is limited to length only; length-to-weight
375 standards exist only for juvenile age classes (Gruber, unpublished data).

376 **4.3 Effect of sampling length**

377 As one might expect, we found that longer sampling lengths (i.e. longer time series or
378 more years sampled) from simulated populations represent the entire simulation better than
379 smaller samples do. The quality of the representation, as measured by a comparison of
380 sample variance to variance in the entire simulation, appears to approach some parametric
381 value asymptotically. In this study, that asymptotic approach requires samples measured
382 in units of centuries (Fig. 5). Apparently, random walks to exceptionally large or small
383 population sizes, caused only by demographic stochasticity, occur on time scales on the order
384 of hundreds of years. This observation further supports our prediction that environmental
385 stochasticity generates much of the variance observed in the 17-year dataset we study here. It
386 also calls into question the generality of conclusions about demographic stochasticity drawn
387 from samples even decades long. If such forces strongly influence population dynamics of
388 species with similar life histories, modeling will be required to correctly characterize the
389 dynamics; studies relying solely on statistical assessments of data at hand are likely to miss
390 significant dynamical processes.

391 **4.4 Environmental stochasticity**

392 Our primary method for comparing simulation output to data focuses on matching means
393 and variances. Within the portion of parameter space that admitted reasonable fits to the
394 data, our simulations consistently matched the mean population size in the Bimini nursery
395 (Fig. 1); however, simulations regularly generated variances distinctly lower than that seen
396 in the actual data set, even when data variance fell with the middle 95% of the distribution
397 of simulation variance. Specifically, simulations on average account for approximately 33-
398 49% of the data variance. The variance in our models is generated entirely by demographic
399 stochasticity and any instabilities caused by delayed breeding and age structure. What, then,
400 caused the missing variance? We postulate it may have been a combination of variations in
401 prey abundance, environmental stochasticity, including weather patterns and global climate
402 change, habitat loss, and effects of fishing.

403 Whatever this environmental stochasticity is, we predict that its effects are relatively

404 sparse, even though we underestimate the actual variance by a considerable amount. This
405 prediction follows from a close inspection of the data from North Sound (Fig. 1). It appears
406 that the high and low points in this time series (2005 and 2008, respectively) may be outliers.
407 Removing these points from the data set reduces s^2 to 164.12 but leaves the mean at 75.13,
408 both of which are in almost exact agreement with simulation mean and variance at default
409 parameter settings. Therefore, the discrepancy between our simulations and the data appear
410 to be driven by only two events in the 17-year data run.

411 The next step with this model is to incorporate environmental stochasticity so that more
412 accurate assessments of population viability can be made (Ovaskainen and Meerson 2010).
413 However, such modifications will be difficult because stochastic environmental effects include
414 an enormous array of possibilities. In addition, predator-prey dynamics, including juveniles
415 as prey for both conspecifics and other species, should be modeled. Cannibalism, which has
416 been documented in this species (Morrissey and Gruber 1993; Guttridge et al. 2012), needs
417 careful attention because it can have very drastic effects on population dynamics (Dennis
418 et al. 2001; Ziemba et al. 2000).

419 **4.5 Implications of model**

420 Our modeling approach is applicable to other shark populations as well as other megaver-
421 tebrates. The age structure and stochastic birth and death rates can be easily altered to
422 fit a different population. This type of model is also useful when applied to species that
423 exhibit distinct stages in their lifecycle that can then be ordered into specific physiological
424 classes (Crouse et al. 1987; Caswell 2001). The lemon shark life cycle is naturally broken
425 into three primary stages, but this structuring can be relaxed to fit life cycles in many other
426 species. In addition, this model is ideally suited to study populations where basic data on
427 annual population size is available; all the technique requires are estimates from the data
428 of mean population size and interannual variance from at least some age class or classes.
429 However, even this requirement can be relaxed. Any measurement made in the field that
430 can be mapped to a variable in the model could be used to determine which combinations of
431 parameters are a good fit (Hartig et al. 2011). For example, if the only field data available
432 is an estimate of subadult mortality, researchers can match distributions of that variable to

433 the field data and thereby constrain the biologically relevant parameter space using the same
434 techniques we employ here. The ability of this technique to predict bounds for parameters
435 that are not easily estimated in the field has important implications for management and
436 conservation, generating as it does predictions about which parameters and life cycle stages
437 may be most sensitive to anthropogenic impacts such as overfishing or bycatch. For lemon
438 sharks at Bimini, we show it is essential to include density-dependent mortality in the first
439 age class and to incorporate delayed breeding to predict even basic population dynamics. We
440 also show that adult lemon sharks must have a mortality rate below 0.17 in order for the pop-
441 ulation to remain viable. Although we have a relatively long data set (17 consecutive years),
442 longer time series may be required to capture important, rare stochastic events. These types
443 of events, whether they be environmental or demographic, seem to be the primary factor in
444 driving the fluctuations in the population size of juvenile sharks in Bimini.

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Table 1. Notation and interpretations of model parameters, their default values, ranges and sources for the lemon shark (*Negaprion brevirostris*).

Parameter	Meaning	Default	Range	Source
λ	Pups born per female	6.1	1-18	(Feldheim et al. 2002 2004)
h	Juvenile mortality Hill parameter	1	NA	This paper
k	Juvenile mortality shape parameter	100	0-200	This paper
t_{max}	Maximum age for adult	25	20-35	(Cortés 2002; Hoenig and Gruber 1990)
x_m	Age at maturity	12	NA	(Cortés 2002; Hoenig and Gruber 1990)
μ	Mortality rate for all animals above age one	0.15	0.05-0.30	This paper

Table 2. Indirect methods used to calculate mortality rates. Here M and Z represent natural and total mortality, respectively. Similar analysis as (Heupel and Simpfendorfer 2002) and (Knip et al. 2012).

Method	Relationship	Value	
Hoenig (1983) (fish)	$\ln(Z) = 1.46 - 1.01 \ln(t_{max})$	0.167	
Hoenig (1983) (cetacean)	$\ln(Z) = 0.941 - 0.873 \ln(t_{max})$	0.154	
Hoenig (1983) (combined)	$\ln(Z) = 1.44 - 0.982 \ln(t_{max})$	0.179	
Pauly (1980)	$\log(M) = -0.0066 - 0.279 \log(L_{\infty}) + 0.6543 \log(K) + 0.4634 \log(T)$	0.140	Note:
Jensen (1996) (age)	$M = 1.65/x_m$	0.138	
Jensen (1996) (growth)	$M = 1.5 K$	0.086	
Jensen (1996) (Pauly)	$M = 1.6 K$	0.091	

Life history parameters are based on (Brown and Gruber 1988). K , body growth parameter (0.057); L_{∞} , maximum theoretical length (317.65 cm); x_m , age at maturity (12 years); t_{max} , maximum age (25); T , mean temperature (27.1 °C, (Newman et al. 2007))

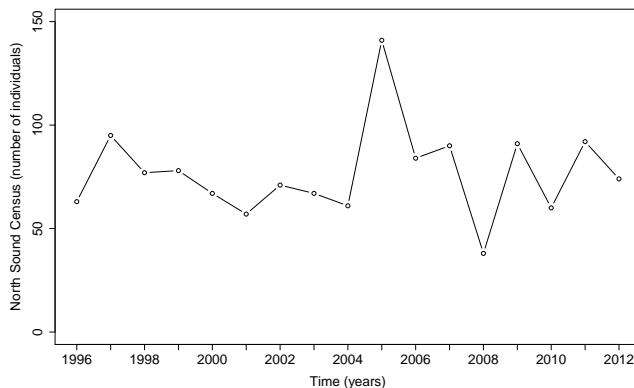


Figure 1: Juvenile population data from the past 17 censuses in the North Sound of Bimini.

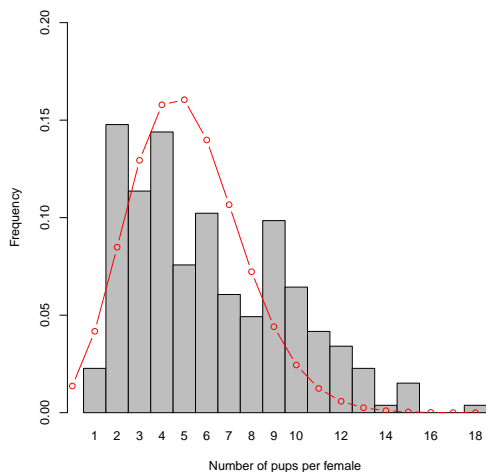


Figure 2: Distribution of litter size per female lemon shark in North Bimini. Grey bars: data from (Feldheim et al. 2002 2004), from 1996 to 2010 ($n=264$). Red curve: discrete Poisson distribution, $\Pr\{N = i\} = e^{-\lambda} \frac{\lambda^i}{i!}$, with λ equal to the mean of the litter size distribution depicted by the grey bars.

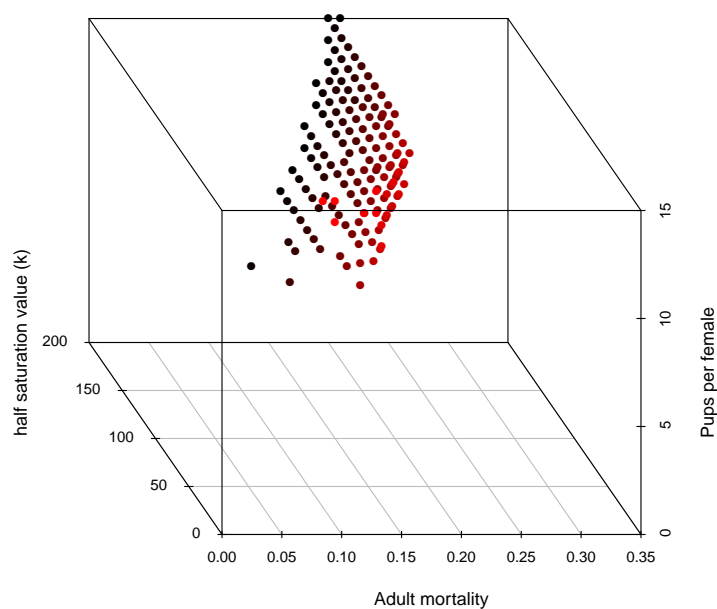


Figure 3: Region of parameter space in which simulations exhibited a “good” fit to the data of the lemon shark population based on criteria described in the main text. Each filled circle represents one of the 9000 parameter combinations that met the criteria of a good representation. The change in color represents degree of half saturation value, with red indicating smaller values of k .

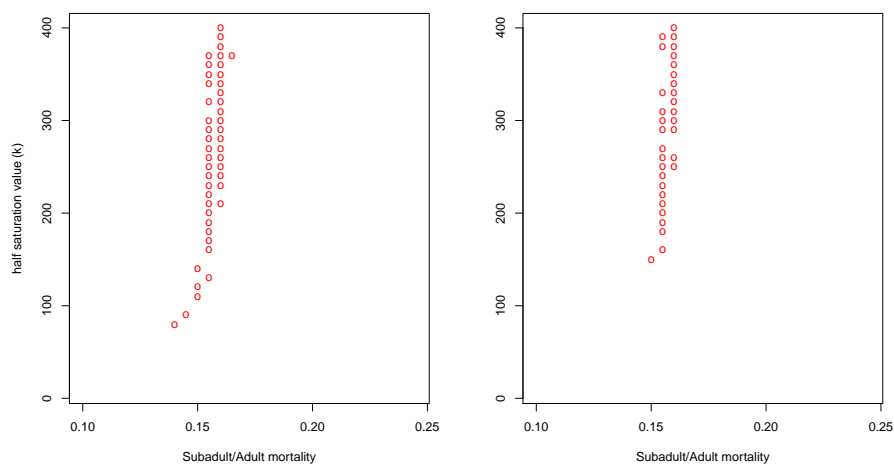


Figure 4: Left: Half-saturation value versus the mortality rate for subadults and adults for series of combinations utilizing the actual distribution of litter sizes for fecundity rate. Right: Same as left but uses a Poisson distribution for fecundity rates. Both pictures represent cases when λ was set at 6.1 for the Poisson distribution which is equivalent to the average of the actual distribution of litter sizes.

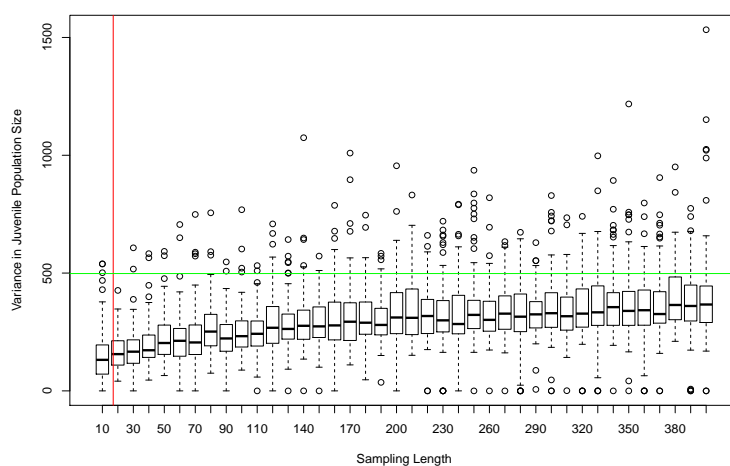


Figure 5: Simulation variance as a function of sample size. The sample at Bimini is a total of 17 years (indicated by the vertical red line). The green line represents the variance in the actual population size ($s^2=498$).