

1 Risky business for a juvenile marine predator? Testing the influence of foraging
2 strategies on size and growth rate under natural conditions
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32 **ABSTRACT**

33 Mechanisms driving selection of body size and growth rate in wild marine vertebrates are
34 poorly understood, thus limiting knowledge of their fitness costs at ecological,
35 physiological and genetic scales. Here, we indirectly tested whether selection for size
36 related traits of juvenile sharks that inhabit a nursery hosting two dichotomous habitats,
37 protected mangroves (low predation risk) and exposed seagrass beds (high predation risk),
38 is influenced by their foraging behaviour. Juvenile sharks displayed a continuum of
39 foraging strategies between mangrove and seagrass areas, with some individuals
40 preferentially feeding in one habitat over another. Foraging habitat was correlated with
41 growth rate, whereby slower growing, smaller individuals fed predominantly in sheltered
42 mangroves, whereas larger, faster growing animals fed over exposed seagrass.
43 Concomitantly, tracked juveniles undertook variable movement behaviours across both the
44 low and high predation risk habitat. These data provide supporting evidence for the
45 hypothesis that directional selection favouring smaller size and slower growth rate, both
46 heritable traits in this shark population, may be driven by variability in foraging behaviour
47 and predation risk. Such evolutionary pathways may be critical to adaptation within
48 predator-driven marine ecosystems.

49

50 **KEYWORDS**

51 Elasmobranch, food web, lemon shark, life-history, natural selection, predation risk, stable
52 isotopes

53

54

55 **BACKGROUND**

56 Spatial plasticity in selection is known to occur as a consequence of the biotic and abiotic
57 conditions that shape the sea or landscape [1]. This dynamicity naturally leads to
58 population divergence through localized adaptation, whereby traits in one population are
59 favoured based on local conditions, irrespective of the fitness consequences or adaptive
60 value of those traits among other populations [2], or even at later life stages (e.g. DiBattista
61 et al. [3]). Nonetheless, selection for large size and fast growth has long been considered a
62 central force that dictates population fitness and evolutionary success [4,5]. Larger size
63 allows organisms to mature earlier [6], consume a wider size spectrum of prey to maximize
64 growth and fitness [7], improves maneuverability to locate prey and evade predators [8],
65 increases survival potential during extreme conditions [9] and when exposed to disease
66 [10], as well as improves reproductive output in terms of both the number and size of young
67 [11]. Indeed, larger individuals within a cohort have reduced predation risk relative to
68 conspecifics within that same age class (the “bigger is better” hypothesis [12]). Faster
69 growth is similarly thought to increase survival because organisms require less time to
70 transit through juvenile phases when they are most vulnerable to predators (the “stage-
71 duration” hypothesis [13]).

72 More recent data, however, is questioning the benefits of larger size and faster growth.
73 Instead, negative fitness consequences have been shown as a direct result of increased risk
74 behaviours to facilitate larger size and faster growth [14,15]. For example, heightened
75 locomotory performance associated with larger size can drive foraging activity over larger
76 spatial scales, which in turn requires a threshold of consumed prey to balance the energetic
77 cost of those movements. Expansion of home ranges also increases encounter probabilities

78 with predators, heightening the potential for reduced fitness through both unprofitable
79 foraging excursions and stress related non-consumptive predator interactions [16]. This is
80 further exacerbated at early life stages when individuals are still naïve and developing
81 foraging skills [17].

82 The direction of selection for body size and growth rate, i.e. larger vs. smaller body
83 size and faster vs. slower growth rate, is likely more plastic than originally thought and an
84 important component of adaptation within any predator-driven marine ecosystem. Yet our
85 understanding of the mechanisms that drive selection for size remains limited. Typically,
86 to examine the mechanisms of selection, one of four approaches is used: experimental
87 studies (e.g. size-selective predation), selection or other genetic experiments under
88 laboratory conditions, quantitative selection analysis and correlational approaches using
89 field data [5]. Most adopt experimental and laboratory based studies where parameters can
90 easily be controlled and manipulated, but how these results transfer to natural conditions
91 is unclear. For aquatic organisms, specifically large marine vertebrates, field studies
92 provide the only viable option to determine the mechanisms of selection but these are
93 typically hindered by logistical challenges.

94 An exhaustively sampled population of juvenile lemon sharks, *Negaprion brevirostris*
95 (Poey, 1868) at Bimini, Bahamas presents a unique model to overcome these limitations
96 and allow examination of the mechanisms underpinning selection and adaptation in a large
97 bodied marine vertebrate. Lemon sharks are born and remain within the Bimini nursery for
98 a minimum of three years [18], with mature females known to be philopatric to natal sites
99 for parturition [19]. The nursery habitat consists of seagrass beds fringed by dense
100 mangroves along the shoreline that provide abundant prey resources for developing

101 juveniles during their residency phase (Fig. 1). Using quantitative selection analysis,
102 DiBattista et al. [3] examined ~700 individuals over a four-year period, encompassing
103 >99% of the total juveniles born in the Bimini nursery. The authors demonstrated that
104 smaller, slower growing lemon sharks were selected for, facilitating an evolutionary
105 trajectory that may be offset by selection for faster growth and larger size during later life
106 stages or at other nursery sites [20,21]. A subsequent genetic analysis and pedigree
107 reconstruction of this population confirmed heritability of these size-related traits [22]. The
108 mechanism proposed for driving selection of slower growth and smaller size in these sharks
109 was preferential foraging within protected fringing mangroves, where predator encounter
110 rates are much lower compared with risky foraging behaviour over exposed seagrass beds
111 [3]. Indeed, sub-adult and adult lemon sharks are the main predators of juveniles on the
112 exposed seagrass beds in the nursery [23,24,25].

113 Stable isotopes can provide a method to systematically track energy flow within
114 marine ecosystems, allowing differentiation of the proportional importance of distinct
115 baseline producers (or habitats) to consumer diets [26]. For example, when an animal
116 consumes prey, preferential loss of the lighter carbon isotope, ^{12}C , compared to the heavier
117 isotope, ^{13}C occurs at each hierarchical level of consumption in a food web [27].
118 Consequently, if carbon isotope values ($\delta^{13}\text{C}$) of prey that reside in distinct habitats within
119 an ecosystem can be readily distinguished, isotope values of predators that consume that
120 prey can then be used to retrospectively track their foraging locations [28]. Serial sampling
121 of individual predators, through capture and recapture, can then be used to examine inter-
122 and intra-individual variation in foraging behaviours over time. An additional isotopic
123 tracer, sulphur ($\delta^{34}\text{S}$), which exhibits minimal fractionation between consumer and prey,

124 can also provide a novel proxy to identify individual variation in consumer foraging
125 locations, thus complementing the more traditional $\delta^{13}\text{C}$ approach [29].

126 A combined stable isotope ($\delta^{13}\text{C}$ and $\delta^{34}\text{S}$), field sampling and telemetry approach was
127 adopted to test the proposed hypothesis of localised selection within the juvenile lemon
128 shark population at Bimini. Carbon stable isotope values of both juvenile lemon sharks and
129 their most common teleost prey group (family Gerreidae) were measured. This prey group
130 was targeted in both mangrove and seagrass habitats given their dominance in the diet of
131 juvenile lemon sharks [30], the known distinct $\delta^{13}\text{C}$ values of these two habitats [31] and
132 previous work discriminating $\delta^{13}\text{C}$ values of Gerreidae fishes sampled in mangrove and
133 seagrass [32]. Carbon isotope data for predator and prey were then incorporated into an
134 individual-level hierarchical Bayesian mixing model to quantify inter-individual variation
135 in foraging locations. A subset of juvenile sharks were; (i) analysed for $\delta^{34}\text{S}$ to provide a
136 second (complementary) tracer, and (ii) sampled at two time points one year apart to
137 examine uniformity in $\delta^{13}\text{C}$ isotope values as a measure of consistent foraging behaviour.
138 Growth rates derived from field morphometric data on recaptured individuals were used to
139 test if slow and fast growth were correlated with foraging in mangrove and seagrass
140 habitats, respectively. Finally, acoustic telemetry tracking of juvenile sharks was used to
141 examine variation in habitat use relative to the predation risk associated with the occurrence
142 of sub-adult sharks. Specifically, we tested whether juvenile lemon sharks show variable
143 growth rates and foraging strategies along the mangrove-seagrass isotopic continuum,
144 which would be consistent with the hypothesis that the trade-off between foraging
145 behaviour and predation risk drives known selection for small juvenile size in this
146 population.

147

148 **METHODS**

149 *Study site*

150 The subtropical Bimini Islands are located on the western edge of the Great Bahama Bank
151 (25°44 N, 79°16 W; Fig. 1). The two main islands are separated by a shallow central lagoon
152 and are predominantly fringed by red mangroves (*Rhizophora mangle*). This study focused
153 on the north island's inner shoreline, the North Sound and Shark Land, both previously
154 identified as an interconnected lemon shark nursery [19] (Fig. 1). This area is characterised
155 by two distinct habitats, the mangrove fringed shoreline and shallow seagrass beds
156 dominated by turtle grass (*Thalassia testudinum*) and to a lesser extent (*Halodule wrightii*),
157 interspersed with areas of exposed sand substrate.

158

159 *Sample collection and preparation*

160 Juvenile lemon sharks were captured using monofilament gillnets and biological data was
161 recorded (supplementary material S1). During processing, a fin clip was taken from the
162 trailing edge of the anal fin and stored in 20% DMSO. Sharks were then placed in a holding
163 pen for recovery and released back into the nursery. This annual population census of
164 juvenile lemon sharks has been ongoing for the past 21 years, but for the purposes of this
165 study, capture and morphometric data (size, sex and umbilical scar) were used from
166 individuals sampled between 2005 and 2010. For the stable isotope component of the
167 analysis, we used fin clips taken from individuals captured in 2009 and 2010, including
168 multiple animals that were recaptured following periods at liberty. The healing of the

169 umbilical connection ranked from open wound (newborn-neonate) to healed (≥ 1 year old
170 juvenile) and was used to assign age class.

171 To define the carbon/sulphur source endpoints, seagrass blades ($n = 3$) and mangrove
172 leaves ($n = 3$) from exposed seagrass beds in the central area of the nursery and from
173 fringing habitats, respectively, were sampled. To sample the principle prey species of
174 juvenile lemon sharks, mojarra (*Eucinostomus* spp.) [30], a hand pulled seine net (75 m
175 length, 2 m depth and 1 cm stretched mesh size) was closed in a parallel direction to the
176 shoreline and pursed. Captured fish were retained, tissue sampled and biological data
177 recorded (supplementary material S2). All samples were processed and then analysed for
178 carbon ($\delta^{13}\text{C}$) and a subset of samples for sulphur ($\delta^{34}\text{S}$) using an elemental analyser
179 (Costech 410) interfaced to a Thermo Finnigan Delta^{PLUS} mass spectrometer
180 (supplementary material S3). Nitrogen isotope data ($\delta^{15}\text{N}$) were also measured for all
181 samples to allow presentation of sharks and primary prey in isotopic space (Fig. 2).

182 Telemetry tracking

183 To track the movements of newborn/juvenile (< 100 cm PCL) and sub-adult (> 100 cm
184 PCL) lemon sharks, individuals were captured using either monofilament gill nets (as
185 described above) or rod and line. On capture, an acoustic transmitter (Sonotronics –
186 individually coded continuous signal tag; 68-78 KHz) was surgically implanted into each
187 shark or externally attached and standard morphometric measurements recorded.
188 Following release, sharks were actively tracked using a hydrophone (Sonotronics, DH4)
189 and receiver (Sonotronics, USR-96) mounted on a small flat-bottomed skiff for periods up
190 to 48 hrs. Locations were recorded every 5 – 15 mins with a hand-held GPS (Garmin 72H)

191 along with a compass bearing and the distance to the shark estimated (to nearest 5m based
192 on audible signal intensity) (see [25] for details).

193

194 *Analyses*

195 Previous work has shown distinct $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ isotopic differences between mangrove
196 versus seagrass food webs [31, 33] and distinct $\delta^{13}\text{C}$ isotope profiles for individual
197 *Eucinostomus* spp. sampled within those respective habitats [32]. We first examine if $\delta^{13}\text{C}$
198 and $\delta^{34}\text{S}$ values of mangrove and seagrass in Bimini are distinct and if juvenile sharks show
199 a large range in $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ values that are highly correlated, as would be predicted. We
200 then assume that the $\delta^{13}\text{C}$ values of *Eucinostomus* spp. sampled at Bimini are representative
201 of the distinct carbon source habitats (mangrove versus seagrass) where they occur.
202 ANCOVA was used to test for differences in $\delta^{13}\text{C}$ values of *Eucinostomus* spp. between
203 habitats while accounting for individual size using *lme* in R (R Development Core Team
204 2014).

205 A hierarchical Bayesian mixing model was constructed to examine individual
206 variation in the foraging locations of one to three year old sharks within the nursery based
207 on consumption of *Eucinostomus* spp. Specifically, the model quantified the percentage
208 contributions of mangrove- and seagrass-origin *Eucinostomus* spp. compared to the $\delta^{13}\text{C}$
209 values of individual sharks (i.e. sharks feeding exclusively on prey in seagrass, mangrove
210 or some combination of the two habitats). Bayesian mixing models allow for propagation
211 of uncertainty into estimates of posterior probability distributions of contributions to
212 isotopic mixtures [34; for further model details see supplementary material S4]. All priors
213 were set to be flat or diffuse with source proportions assigned a Dirichlet prior ($\alpha=1$), which

214 is a multivariate extension of the beta distribution (uniform on the compositional simplex).
215 Posterior probability distributions of parameters were quantified using Markov chain
216 Monte Carlo (MCMC) sampling implemented in JAGS in R [35]. Three parallel chains,
217 each with 150,000 iterations and a burn-in phase of 100,000 iterations were used, retaining
218 every other sample. All MCMC chains showed visual evidence of convergence, exhibited
219 low levels of auto-correlation and Gelman and Rubin diagnostics were all less than 1.05.

220 To determine if one to two year old lemon sharks consistently foraged in the same
221 habitat over time, $\delta^{13}\text{C}$ values of sharks captured in the nursery ground in 2009 and
222 recaptured in 2010 following a year at liberty ($n = 19$) were determined. To measure
223 individual foraging uniformity over the one year period, the difference of the mean ($\mu_1 -$
224 μ_2) and standard deviation ($\sigma_1 - \sigma_2$) parameters between years and the normality of the data
225 within groups (v) were simultaneously estimated using a Bayesian t-test approach, BEST
226 in R [36]. A non-committal prior was used that has minimal impact on the posterior
227 distribution and the shape of the data in each group described by a t-distribution [36]. The
228 posterior distribution of differences (mean and standard deviation) and effect size were
229 estimated, and the 95% high density intervals (HDIs) were used to describe the credibility
230 interval for each. If the 95% HDI is significantly above zero, the parameter estimates are
231 credibly different.

232 Growth rates of one and two year old recaptured sharks were then calculated from the
233 difference in length (PCL, cm) and mass (kg) between capture and recapture, and
234 multiplied by the total number of days at liberty, where 365 days = 1. We used one year
235 old sharks that were born in 2008 (sampling time points 2008 and 2009; isotopic data from
236 2009; $n = 9$) and 2009 (sampling time points 2009 and 2010; isotopic data from 2010; $n =$

237 43) and two year old sharks born in 2007 (sampling time periods 2008 and 2009, isotopic
238 data 2009; n = 6) and 2008 (sampling time periods 2009 and 2010, isotopic data 2010; n =
239 10). This included nine individuals with growth data for both years one and two in the
240 nursery ground. To examine if the isotopic values of these sharks were related to growth
241 rate, the relationship between $\delta^{13}\text{C}$ values for each individual and the covariates of growth
242 rate, age and sex were examined using a mixed effects model fit with maximum likelihood
243 in the *lme* package in R. Growth rate, sex and age were included as fixed effects and birth
244 year as a random effect. An ANOVA was used to compare models with progressively
245 simplified fixed effects. Linear regression was used to determine the relationship between
246 $\delta^{13}\text{C}$ values of the sharks (i.e. depleted ^{13}C values, foraging in mangroves or enriched ^{13}C
247 values, foraging in seagrass) and growth rate (i.e. slow vs. fast). Only sharks that were ≥ 1
248 year and < 3 years old were included in these analyses given (i) maternal effects on isotopic
249 signatures of < 1 year old sharks and (ii) three year old animals start to make broader scale
250 movements within the nursery and lagoon areas. We focus solely on $\delta^{13}\text{C}$ for the latter
251 analyses given the correlation between $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ values.

252 To examine whether habitat use of juvenile lemon sharks was biased towards
253 mangrove or exposed seagrass habitat as a measure of predation risk, the mean (\pm SD)
254 distance from shore was calculated for each shark from all GPS locations recorded per
255 month. For individuals tracked at > 1 month intervals, size was re-estimated based on
256 growth rate (or from recaptures) and a new mean distance-to-shoreline value was
257 calculated for that individual. Shark-shoreline distances were calculated using the Animal
258 Movement extension in ArcGIS (ESRI). For sub-adult sharks, location data were divided
259 by tidal cycle (low versus high; data from the National Oceanic and Atmospheric

260 Administration) and data for all individuals presented to show their overall distribution
261 around the Bimini Islands.

262

263 **RESULTS**

264 *Ecosystem isotopic variation*

265 The $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ values for mangrove leaves and seagrass blades, the source endpoints in
266 the nursery ground, were markedly different ($\delta^{13}\text{C} = -23.8 \pm 0.3\text{‰}$ and $-7.1 \pm 0.6\text{‰}$ and
267 $\delta^{34}\text{S} = -16.9$ and 12.0 ; mangrove and seagrass, respectively) in agreement with previous
268 findings [31]. *Eucinostomus* spp. sampled in mangrove (mean \pm SD: $-17.3\text{‰} \pm 0.8$) and
269 seagrass habitats ($-13.4\text{‰} \pm 1.2$) had significantly different $\delta^{13}\text{C}$ values that scaled
270 accordingly between the carbon source endpoints ($F_{2,29} = 42.77$, $p < 0.0001$; Fig. 2). There
271 was no effect of size on $\delta^{13}\text{C}$ values of *Eucinostomus* spp. For juvenile lemon sharks
272 sampled within the nursery in 2010 ($N = 62$), $\delta^{13}\text{C}$ were highly variable with a minimum
273 and maximum value of -12.6‰ and -8.4‰ (range 4.2‰ ; Fig. 2). Equally, large variation
274 in $\delta^{34}\text{S}$ values was observed for the subset of sharks analysed ($n = 15$), ranging from a
275 minimum of -0.4‰ to a maximum of 5.7‰ (range = 6.1‰). As predicted, the $\delta^{13}\text{C}$ and
276 $\delta^{34}\text{S}$ values of sharks were highly correlated further supporting foraging across the
277 mangrove-seagrass continuum (supplementary material Fig. S1). Juvenile sharks ranged in
278 size from 49.5 to 74.5 cm PCL (mean \pm SD = 55.7 ± 5.5 cm) and 1.1 to 5.5 kg (1.9 ± 0.8
279 kg).

280

281 *Individual foraging behaviour*

282 Our hierarchical Bayesian stable isotope-mixing model found that individual sharks
283 adopted variable foraging strategies. The median proportional contribution of mangrove-
284 derived *Eucinostomus* spp. to the 62 individual sharks ranged from 73.9% to 7.4% (Fig. 4).
285 The median shark was estimated to feed on approximately 26.9% of mangrove-derived
286 *Eucinostomus* spp. As expected, the estimation of posterior probabilities for individual
287 sharks had some level of uncertainty (Fig. 3). This uncertainty could be reduced by treating
288 individuals as random effects (rather than fixed effects as implemented here), but we were
289 primarily interested in estimating where individuals fell on the gradient between mangrove
290 and seagrass habitats. These data identify that some sharks forage predominantly on
291 *Eucinostomus* spp. in mangrove habitat, others mostly on *Eucinostomus* spp. in seagrass
292 habitat, with the remaining shark foraging locations scaling between the two habitats (Fig.
293 3).

294

295 ***Temporal uniformity in foraging behaviour***

296 For one and two year old sharks that were sampled both in 2009 and 2010 ($n = 18$),
297 $\delta^{13}\text{C}$ values were consistent between the two sampling periods (mean central tendency [CT]
298 = 0.06; 95% HDI -0.69, 0.80 $t_{17} = 0.55$; $p = 0.59$), with only minor variation (SD CT =
299 0.11; 95% HDI -0.48, 0.73: 0.03 – 0.80) and effect size (effect CT = 0.01; 95% HDI -0.64,
300 0.72; Fig. 4). This suggests that juvenile lemon sharks undertake systematic individual
301 level foraging behaviour in mangrove, seagrass or combined mangrove-seagrass habitats
302 over an annual cycle during their first three years in the nursery habitat.

303

304 ***Foraging versus body size traits***

305 One, two and three year old sharks had variable $\delta^{13}\text{C}$ values that reflected the range of
306 the two distinct foraging habitats. For one year olds, a large proportion of individuals had
307 $\delta^{13}\text{C}$ values that were indicative of foraging in both seagrass and mangrove habitats but
308 predominantly on seagrass beds (Fig. 5). For two and three year old individuals, the spread
309 of $\delta^{13}\text{C}$ values was more even. Three years old sharks, with enriched ^{13}C values indicative
310 of foraging over seagrass beds, were also larger (mean $\delta^{13}\text{C}$ values of -9.9 ± 0.1 and PCL
311 of 71.2 ± 4.3 for three most enriched ^{13}C sharks vs. mean $\delta^{13}\text{C}$ values of -11.9 ± 0.3 and
312 PCL of 60.0 ± 5.0 cm for the three most depleted ^{13}C sharks; Fig. 5a). Growth rates for one
313 and two year old sharks ($N = 52$ and $N = 16$, respectively) ranged from 1.4 to 9.5 cm/yr
314 (PCL) and -0.4 to 1.7 kg/yr (mass). Only PCL growth rate data were modeled due to known
315 error in body mass field measurements and the confounding effect of recent feeding events,
316 contributing up to 5% of stomach mass to total body weight. The progressively simplified
317 mixed effect model found $\delta^{13}\text{C}$ values were significantly affected by growth rate, but sex,
318 age and birth year had no effect. While growth variability was observed, as would be
319 expected under natural conditions, there was a significant positive linear relationship
320 between growth rate and $\delta^{13}\text{C}$ values ($F_{1,66} = 11.97$, $p < 0.001$; $r^2 = 0.2$; Fig. 5b). Juvenile
321 lemon sharks foraging predominantly in mangrove habitats had significantly slower growth
322 rates than those foraging over seagrass beds, with growth rate increasing between the two
323 habitat end points.

324

325 *Variability in juvenile movements and predation risk*

326 Tracked juvenile lemon sharks ($n = 19$) displayed highly variable movements with some
327 individuals remaining predominantly close to the mangroves versus others that occupied

328 exposed seagrass habitat (Fig 6a). There was no effect of animal size on the observed
329 movement patterns (Fig 6a). A track of a newborn shark, measuring 44.3 cm PCL, ended
330 when it appeared to remain stationary for >10 mins over exposed seagrass beds. Upon
331 entering the water, remains of the dead shark were found documenting an active predation
332 event (Fig 6c). Tracking data for sub-adult sharks ($n = 67$) showed that they occupied both
333 inshore and offshore habitats throughout the Bimini Islands that was dependent on tidal
334 state, and thus suitable water depth to manoeuvre and forage (Fig 6b).

335

336 **DISCUSSION**

337 Resolving the underlying mechanisms driving selection processes in the wild, particularly
338 for large, long-lived and highly mobile marine organisms is complex and consequently is
339 often assumed rather than empirically tested [37]. Given known cannibalism and predation
340 on juvenile lemon sharks over exposed seagrass habitat by larger conspecifics [23,24; Fig
341 6c], we used the distinct isotopic baselines of mangrove versus seagrass to assess the
342 foraging locations of individual sharks. This facilitated an indirect test of the mechanism
343 for negative directional selection acting on size-related traits proposed by DiBattista et al.
344 [3]. Carbon and sulphur isotope values identified variable foraging strategies among
345 juvenile sharks, and hierarchical Bayesian mixing models revealed that some individuals
346 fed predominantly on prey from mangrove habitat while others fed predominantly on prey
347 from seagrass habitat. This was supported by variable movement among juveniles recorded
348 in the field via acoustic tracking. Foraging strategies were also correlated with growth rates,
349 whereby sharks that fed in sheltered mangrove habitats had slower growth rates than those
350 that fed over exposed seagrass beds. These cumulative findings support a continuum of

351 foraging strategies by juvenile lemon sharks between mangrove and seagrass habitat during
352 their first years' residency in the Bimini nursery. Concurrently, there was a notable shift
353 from one year old sharks feeding predominantly over seagrass to more evenly distributed
354 foraging over both habitats by age three. This provides evidence for a size range of
355 juveniles within the nursery where selection is free to act, favoring smaller size and slower
356 growth [3].

357 Our data provide compelling evidence that larger, faster growing individuals do occur
358 in the Bimini nursery habitat, but where do these individuals originate from to allow for
359 continuing selection for small size given the much larger individuals at age and faster
360 juvenile growth observed at other nurseries [21,22]? We suggest that male-mediated gene
361 flow and occasional stray pregnant females [38] at the adult stage maintains selection for
362 smaller size at Bimini through constrained local adaptation. Under this scenario,
363 maladaptive genes are continually introduced to Bimini, thus maintaining a body size
364 above the optimum and consequently promoting selection. The larger juvenile lemon
365 sharks seen at Marquesas Key, Florida for example are genetically similar to the Bimini
366 sharks, suggesting gene flow between these two populations [38]. Indeed, it would appear
367 that selection for slow growth and smaller size may be stronger at Bimini than other
368 neighbouring nursery grounds leading to a smaller equilibrium body size.

369 The appearance of distinct behavioural foraging strategies (over exposed seagrass vs.
370 in sheltered mangroves) among these juvenile sharks may be attributable to underlying
371 differences in personality. Juvenile lemon sharks (age 1 to 2 years) have been shown to
372 display persistent individual differences in the rate of movement within a novel open field
373 test at the Bimini nursery [39]. Importantly, the sharks showed habituation in movement

374 pattern over repeated trials, indicating that this was a reaction to novelty and not
375 representative of general activity. Recent research also suggests that personality variation
376 is determined by an individual's environment and age-related experience as well as a
377 heritable component [40] that may be under strong selection [41]. The mechanism driving
378 the proposed continual selection for smaller size and slower growth at Bimini may
379 therefore be an effect of introduced maladaptive genes from other populations that not only
380 include individuals of larger size and faster growth but also personality variation. As an
381 alternative, this dichotomy could relate to differences in habitat type among geographically
382 separate nursery habitat. For example, juvenile lemon sharks at Cape Canaveral, Florida
383 reside in an exposed coastal nursery habitat and undertake seasonal migrations of up to 190
384 km, which contrasts with the fidelity and small home-ranges of juveniles at Bimini [42].
385 Selection for larger size and bolder personality traits may support this exploratory
386 behaviour at Cape Canaveral, despite the potential for increased predation risk because of
387 a lack of available refuging habitat (i.e. sheltered mangrove). Moreover, evidence for gene
388 flow between these two geographically isolated populations (Cape Canaveral and Bimini)
389 has been shown [38].

390 Both carbon and sulphur isotopes and growth data unequivocally show that juvenile
391 sharks at Bimini adopt variable foraging strategies with effects on growth rate and size, but
392 data are not available to directly quantify intra-specific predation rates. Substantial
393 evidence within this exhaustively studied system, however, supports predation on juvenile
394 lemon sharks within the nursery [23,24]. For example, telemetry tracking data in this study
395 and that reported previously found that the sub-adult lemon shark population at Bimini
396 have larger home-ranges and predominantly use exposed seagrass and sand flats within the

397 lagoon [43], a likely result of habitat structure (mangrove roots) and shallow water depths
398 restricting the size of sharks that can manoeuvre through the fringing mangroves. Recently,
399 Guttridge et al. [25] demonstrated that the movements of juvenile lemon sharks in an
400 adjacent nursery area at Bimini (Bonefish Hole) were influenced by the presence of sub-
401 adult sharks in the area as it related to tidal changes in water depth. These data suggested
402 that juveniles make fine-scale habitat selection decisions in response to intra-specific
403 predation risk. Moreover, observations of juveniles feeding on prey in the field were rare,
404 which may also suggest a trade-off between foraging and refuging [25], with impacts for
405 both size and growth rate. Refuging and anti-predator avoidance has been reported for
406 several shark species and is considered fundamental behaviours associated with coastal or
407 estuarine nursery habitats [44]. The predominant use of sheltered, shallow habitats by
408 juvenile lemon sharks is also documented at two more nurseries in the Atlantic Ocean
409 (Cape Eleuthera in the Bahamas and Atol das Rocas in Brazil) that have similar habitat
410 structure to Bimini [45,46]. As a result, the likelihood of predation in shallow waters areas
411 (particularly mangroves) is minimised both by habitat type, water depth and known
412 movements of the sub-adult lemon shark population. In contrast, several shark predation
413 events have been reported while tracking juvenile lemon sharks along the exposed nursery
414 shoreline [24] including one of the individuals tracked in this study (Fig. 6c). This includes
415 transmitted juveniles suddenly changing behavior or being detected in unexpected habitats,
416 rapidly increasing swimming speeds to unrealistic levels or as we report here, an acoustic
417 signal abruptly ending and the discovery of the remains of the predated juvenile (Fig 6c).
418 Importantly, our data and previous juvenile tracking data reveal a range of behaviours, with
419 some juvenile sharks predominantly moving in the mangroves or remaining very close to

420 the mangrove edge, while similar-sized individuals favour exposed seagrass habitats
421 hundreds of meters from shore [24,46; Fig 6a], where large sharks occur (Fig 6b; Guttridge
422 unpub. data).

423

424 **CONCLUSION**

425 Through a combination of isotopically distinct habitats and prey that reside in those habitats
426 and careful consideration of pragmatic assumptions (supplementary material S5), fine scale
427 tracking of the foraging behaviour of juvenile sharks within their nursery ground was
428 possible. Although several studies have tracked spatial movements of animals using stable
429 isotopes [47], this study represents one of few that were able to elucidate foraging patterns
430 over a fine spatial scale. When combined with field sampling and telemetry tracking, this
431 allowed novel insights into body size selection in a marine vertebrate. Identifying the
432 mechanism driving selection for slower growth and smaller size supports a growing body
433 of work showing that bigger is not always better and that size selection is more plastic than
434 originally thought. While an alternate explanation for the observed variable growth rates
435 could result from competition among conspecifics, the nursery ground is not resource
436 limited [48], aggression between juveniles has not previously been reported over extensive
437 monitoring periods [49] and population density does not appear to be correlated with the
438 strength of selection acting on these size-related traits [3]. Equally, while faster or slower
439 growth rates may represent a form of adaptive phenotypic plasticity, whereby individuals
440 for example have lower growth rates in response to poorer quality mangrove habitat, we
441 favor evolutionary change given the evidence of selection for smaller body size and
442 heritability of these traits in this population [3,22]. It is likely that predator dominated

443 systems may influence size selection and that the interplay of predator abundance,
444 personality and sociality, as well as available habitat types (exposed vs. refuges) at
445 localised scales influenced by broader scale variance in adaptation of mobile marine
446 species, shape the direction of selection.

447

448 **ETHICS**

449 All handling of juvenile lemon sharks and sampling of prey items was undertaken under a
450 permit issued from the Department of Fisheries of the Commonwealth of the Bahamas.

451

452 **COMPETING INTERESTS**

453 We have no competing interests

454

455 **AUTHORS CONTRIBUTIONS**

456 NEH, DDC and JDD conceived of the study, designed the study and coordinated the study;
457 NEH, ATF and OC undertook laboratory work; NEH, JWM and EJW carried out the
458 statistical analyses; STK, KAF, TLG, JDD and SHG collected field data; NEH wrote the
459 manuscript with support from JDD and input from all authors. All authors gave final
460 approval for publication.

461

462 **ACKNOWLEDGEMENTS**

463 The authors would like to thank the numerous volunteers at the Bimini Biological Field
464 Station who have participated in the annual sampling of lemon sharks as part of this long-
465 term population census. This study was financially supported by the Bimini Biological

466 Field Station and grants from the Canadian Research Chair Program to ATF. NEH was
467 supported by the Ocean Tracking Network and the Government of Nunavut.

468

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589

590 **FIGURE LEGENDS:**

591 **Figure 1.** The interconnected nursery habitat at Bimini Islands in the Bahamas where
592 juvenile lemon sharks (*Negaprion brevirostris*) remain resident for up to three years. The
593 red line indicates the mangrove fringed shoreline of the nursery region. The aerial
594 photograph depicts seagrass beds in the lagoon areas.

595

596 **Figure 2.** Stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopic biplot of the principal
597 ecosystem components in the nursery ground: (i) the average baseline carbon sources,
598 mangrove leaves (red diamond in circle) vs. seagrass blades (green diamond in circle), (ii)
599 the principal prey group in the diet of juvenile lemon sharks, mojarra spp. (*Eucinostomus*
600 spp.) sampled in both fringing sheltered mangroves (red dots) vs. exposed seagrass beds
601 (green dots) and 1 to 3 year old juvenile lemon sharks (blue dots) corrected for isotopic
602 discrimination (see Methods). Isotope data for individual prey and sharks and mean (± 1
603 SD) are presented. The $\delta^{15}\text{N}$ value of mangrove and seagrass is set to 7‰ for ease of
604 interpretation. Actual mean $\delta^{15}\text{N}$ values for mangrove and seagrass are -8.9‰ and -2.7‰,
605 respectively. The $\delta^{34}\text{S}$ values for mangrove and seagrass are not shown but are -16.9‰ and
606 12.0‰, respectively.

607

608 **Figure 3.** Individual variation in foraging locations of juvenile lemon sharks (*Negaprion*
609 *brevirostris*) within the nursery habitat, quantified through a Bayesian hierarchical mixing
610 model incorporating carbon stable isotopes ($\delta^{13}\text{C}$) of prey (*Eucinostomus* spp.) sampled in
611 fringing sheltered mangroves and on exposed seagrass beds and predators sampled
612 throughout the nursery. Each point shows the estimated proportional contribution of
613 mangrove-derived prey to each of the 62 individual sharks, with lines representing ± 1 SD.
614 Individual sharks were stacked based on ranked carbon stable isotope proportions.

615

616 **Figure 4.** Uniformity in foraging location by lemon sharks (*Negaprion brevirostris*) within
617 the nursery over a one-year period. Carbon isotope data ($\delta^{13}\text{C}$) are for two sampling points

618 per individual shark (June 2009 and 2010) and location is inferred based on significant
619 differences in carbon isotope values of the main prey sampled in mangrove vs. seagrass
620 beds. The continuous black line depicts the linear regression between isotopic sample
621 points per individual for each sampling time point and the dashed line represents the one
622 to one relationship for these data. Histograms show posterior distribution of differences
623 and effects size; 'HDI' denotes highest density interval.

624

625 **Figure 5.** (a) Body size distribution versus carbon stable isotope values of individual sharks
626 born in 2007, 2008 and 2009 and sampled in 2010 (1 to 3 years old; dark to light blue
627 circles, respectively) and; (b) the relationship between growth rate of individual lemon
628 sharks (*Negaprion brevirostris*; 1 and 2 year olds) calculated from field derived
629 measurements and the mean carbon isotope values ($\delta^{13}\text{C}$) of fin tissue sampled from each
630 shark at two time points approximately one year apart. The $\delta^{13}\text{C}$ values range over a
631 continuum from sharks feeding predominantly on prey in fringing sheltered mangroves to
632 those feeding on prey over exposed seagrass beds. The continuous line depicts the fitted
633 regression line for growth vs. $\delta^{13}\text{C}$ values of sharks and the dashed line the 95% confidence
634 intervals.

635

636 **Figure 6.** (a) Variation in proximity of juvenile lemon sharks (*Negaprion brevirostris*) to
637 the shoreline of the nursery habitat (distance in metres \pm 1 SD) as a measure of low (near
638 mangrove) versus high (over exposed seagrass bed) predation risk. Data are presented for
639 19 sharks, with multiple data points per individual if tracked over consecutive months (see
640 Methods); (b) tracks of sub-adult lemon sharks (n = 67) detected throughout the Bimini
641 Islands with each dot representing derived location estimates. Red and blue dots represent
642 high and low tide, respectively; and (c) remains of a newborn lemon shark that was
643 consumed during an active acoustic track over exposed seagrass beds within the nursery.

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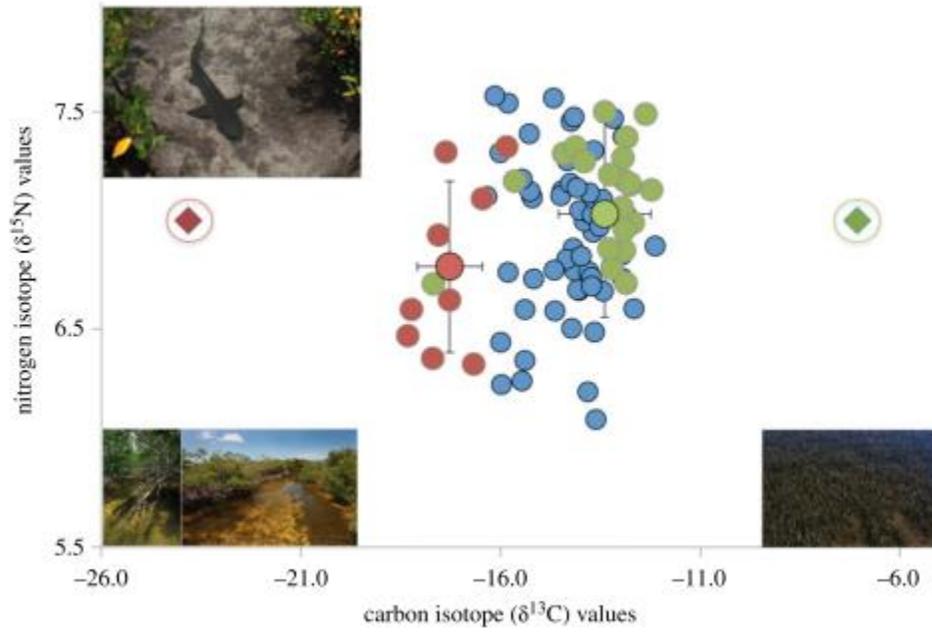
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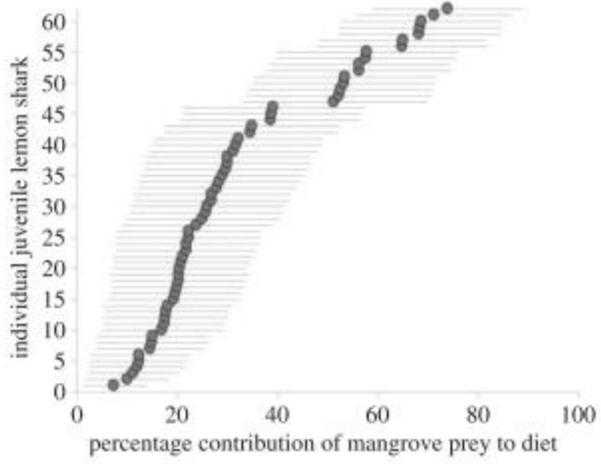
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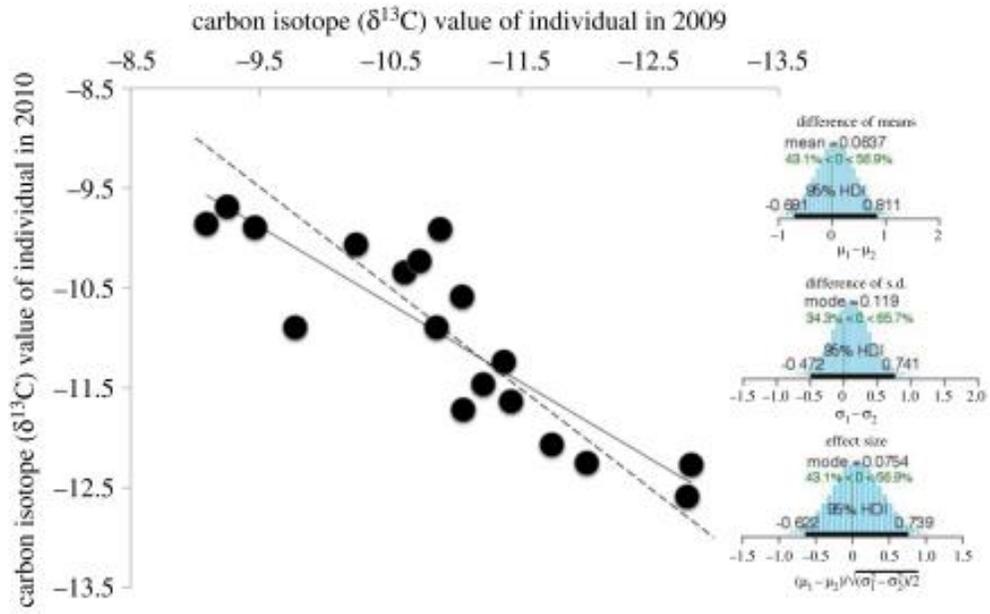
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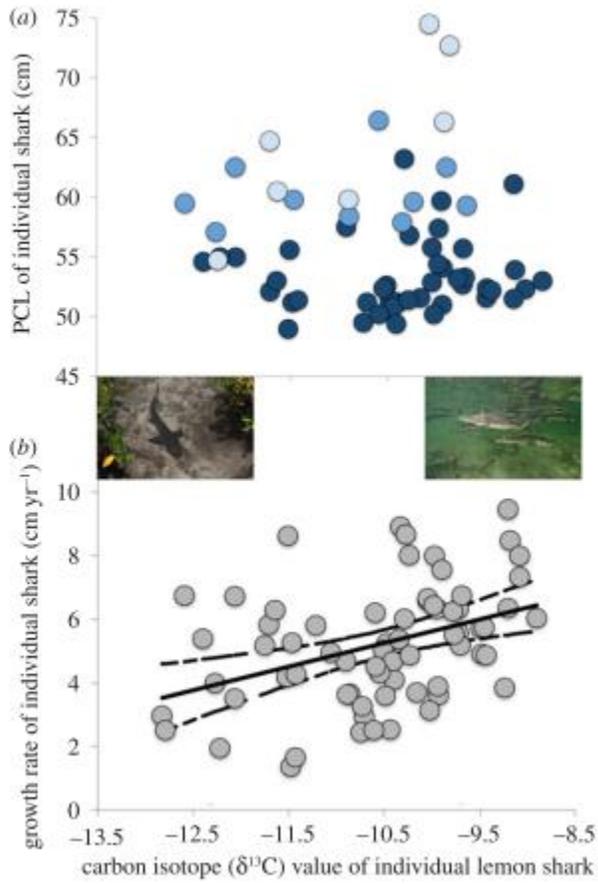
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