# Quantifying impacts of plastic debris on marine wildlife identifies ecological breakpoints

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Quantifying sub-lethal effects of plastics ingestion on marine wildlife 1 is difficult, but key to understanding the ontogeny and population dy-2 namics of affected species. We developed a method that overcomes 3 the difficulties by modelling individual ontogeny under reduced en-4 ergy intake and expenditure caused by debris ingestion. The pre-5 dicted ontogeny is combined with a population dynamics model to 6 identify ecological breakpoints: cessation of reproduction or neg-7 ative population growth. Exemplifying this approach on loggerhead 8 turtles, we find that between 3 % and 25 % of plastics in digestive con-9 tents causes a 2.5 % to 20 % reduction in perceived food abundance 10 and total available energy, resulting in a 10% to 15% lower condi-11 tion index and 10% to 88% lower total seasonal reproductive output 12 compared to unaffected turtles. The reported plastics ingestion is in-13 sufficient to impede sexual maturation, but population declines are 14 possible. The method is readily applicable to other species impacted 15 by debris ingestion. 16

Physiological energetics | Conservation | Sea turtles | Stressors | Debris ingestion

lastic debris in marine environments represents a global anthropogenic pressure that, despite heightened aware-2 ness and preventive regulations (Thompson et al., 2009), is 3 likely to keep increasing for the foreseeable future (Moore, 4 2008; Jambeck et al., 2015). Annually, between 4-12 million 5 tons of plastic waste from land (Jambeck et al., 2015) and 1-2 6 million tons from rivers (Lebreton et al., 2017) find their way into the sea, making plastic items and microplastic particles 8 omnipresent in global oceans (Derraik, 2002; Moore, 2008; 9 Barnes et al., 2009; Cozar et al., 2014; Eriksen et al., 2014). 10

Negative effects of plastic debris on over 700 marine species 11 have already been documented, and sea turtles are among 12 the top three wildlife groups impacted by plastics (Gall and 13 Thompson, 2015). Namely, all seven species of sea turtles in all 14 major oceans have been found to ingest plastic debris (Schuyler 15 et al., 2014a; Nelms et al., 2016; Lynch, 2018), with as many 16 as 52% of all sea turtle individuals ingesting plastics sometime 17 during their lifetime (Schuyler et al., 2016). Plastic debris 18 has therefore been identified as one of the global research and 19 conservation challenges for sea turtles (Hamann et al., 2010; 20 Wallace et al., 2011). 21

Plastics ingestion occurs when sea turtles encounter and 22 ingest debris accidentally (i.e., opportunistically) or mistake 23 debris for prey and ingest it actively (Schuyler et al., 2012; 24 Narazaki et al., 2013; Schuyler et al., 2014b). Data suggest that 25 oceanic turtles are less selective and more likely to encounter 26 floating debris while feeding on pelagic organisms (Schuyler 27 et al., 2012), which makes them vulnerable to opportunistic 28 plastics ingestion (Schuyler et al., 2014a; Nelms et al., 2016; 29 Schuyler et al., 2016). This is in contrast to neritic sea turtles 30

who are more selective and encounter fewer floating items 31 while feeding on benthic organisms, which in turn results in 32 predominantly active plastics ingestion (Schuyler et al., 2012). 33 During feeding, turtles may also indirectly ingest plastics 34 already consumed by their prey (Thompson et al., 2004; Barnes 35 et al., 2009; Rochman et al., 2015). Indirect ingestion, in 36 addition to environmental debris prevalence and turtle feeding 37 ecology, partly depends on prey behaviour. Furthermore, 38 indirectly ingested plastics are likely to be fragmented into 39 small, hard-to-detect pieces termed microplastics that exert 40 both physical and biochemical effects on individuals (Rezania 41 et al., 2018). Biochemical effects intensify, whereas physical 42 subside, inversely to particle size (Batel et al., 2016), implying 43 that larger macroscopic debris causes mostly physical effects. 44

The physical effects of plastics ingestion cause a range of 45 lethal and sub-lethal consequences. Ingested debris blocks, 46 damages, or reduces the volume of a turtle's digestive system 47 (Gramentz, 1988; Stahelin et al., 2012; Schuyler et al., 2014a), 48 thus decreasing the caloric intake at best, and fatally harm-49 ing the turtle at worst (Mascarenhas et al., 2004; Lazar and 50 Gračan, 2011; Casale et al., 2016). Sub-lethal consequences 51 of plastics ingestion, observed in other species (Connors and 52 Smith, 1982; Ryan, 1988; Yamashita et al., 2011) and sea tur-53 tles alike (McCauley and Bjorndal, 1999; Mascarenhas et al., 54 2004; Stahelin et al., 2012), include slower weight gain, de-55 creased fat deposits, less feeding activity, longer gut residence 56 times of ingested material, and inflammation. Ingested plastics 57 therefore has the potential to substantially reduce the physio-58 logical condition of individuals, thereby lowering their chances 59 of survival or reproduction and, in turn, lowering the popula-60 tion growth rate. Our goal here is to lay the methodological 61 foundation for quantifying these effects. 62

Quantifying sub-lethal effects of plastics ingestion is challenging. Studies of controlled plastics ingestion involving sea turtles are rare and limited to short periods of time (Lutz, 1990; Narazaki et al., 2013; Fukuoka et al., 2016) or a single life stage (McCauley and Bjorndal, 1999). The most elaborate efforts to date have produced a quantitative link between the number of ingested items and mortality (Santos et al., 2015; Wilcox et al., 2018), whereas sub-lethal effects have only been mentioned as "an area of considerable uncertainty and concern" for sea turtles (Gall and Thompson, 2015). Studies on quantitative, let alone mechanistic, links between plastics

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NM designed the research with guidance from MJ and TK, and feedback from SALMK. NM performed individual-level and MJ population-level simulations. NM and MJ performed analyses. NM drafted the manuscript, subsequently modified by NM and MJ, and revised by all authors.

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Fig. 1. Presence of plastic debris reduces effective food abundance experienced by sea turtles. As the prevalence of plastics in the environment increases relative to food, animals are more likely to ingest plastics. A direct consequence is that sea turtles experience less food abundance (top black curve) than they would in a pristine ocean (yellow star). The effect is compounded if, in addition, plastic debris has a longer residence time than food (black curves indexed by relative residence times from  $1.25 \times to 10 \times$ ). The horizontal dashed lines mark 3% and 25% of debris in digestive contents, which corresponds to mean and maximum reported values for percentage of debris in stomach contents (Frick et al., 2009).

ingestion and sub-lethal physiological or life-history effects on 74 sea turtles are thus hard to come by. Nevertheless, there is still 75 a lot of information on sea turtles that could be assimilated 76 by mechanistic modelling approaches. Loggerhead turtles 77 (Caretta caretta) are of prime interest because of the extensive 78 information on this species from field studies, strong concerns 79 about the damaging effects of plastics ingestion (Schuyler 80 et al., 2014a; Nelms et al., 2016; Schuyler et al., 2016; Lynch, 81 2018), and the status as a potential bio-indicator for moni-82 toring plastics ingestion in the Mediterranean (Fossi et al., 83 2018). Serious effects of plastics ingestion have been docu-84 mented for post-hatchlings (McCauley and Bjorndal, 1999; 85 Rvan et al., 2016), oceanic-stage juveniles (Pham et al., 2017), 86 and juveniles and adults (Lazar and Gračan, 2011; Campani 87 et al., 2013; Schuyler et al., 2014a), with some authors quoting 88 loggerhead turtles as being "specially prone to debris inges-89 tion" (Tomás et al., 2002). Recent reports put the incidence 90 of plastics ingestion at an average of 49%, based on 42 studies 91 that examined three or more animals (Lynch, 2018). The on-92 togeny of loggerhead turtles has been characterized from the 93 perspective of physiological energetics and successfully linked 94 to environmental forcings such as food and temperature, to 95 96 capture the observed variability among individuals within and between populations (Marn et al., 2017b,a, 2019). Here, we 97 further extend the already validated mechanistic model of the 98 ontogeny by accounting for plastics ingestion. 99

We mechanistically describe how plastics ingestion affects the ontogeny of loggerhead turtles, seeking answers to two primary questions. First, is the reported plastics ingestion sufficient to impede sexual maturation or egg production of these turtles? Second, even if individual turtles successfully mature and reproduce, can the population as a whole maintain positive growth? In doing so, we identify two ecologically critical events of interest: one is the cessation of reproduc-107 tion, which we define as an *individual*-level breakpoint; the 108 other is non-positive population growth which we define as 109 a population-level breakpoint. We investigate the extent of 110 plastics ingestion required to reach either breakpoint, and how 111 this relates to plastic loads currently experienced by sea tur-112 tles in the wild. Further methodological details are available 113 in the Methods section and Supplementary Information (SI) 114 Appendix. 115

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#### Results

Ingesting plastic debris has the effect of reducing effective food 117 abundance experienced by sea turtles (Fig. 1). We quantify 118 food abundance as a fraction of the maximum that healthy sea 119 turtles could ingest during the same time given unrestricted 120 continuous access to food. The reduction in effective food 121 abundance occurs because of competition between food and 122 debris for the limited digestive capacity of gastrointestinal 123 tract, where the amount of debris compared to food in digestive 124 contents at any given time is determined by two quantities. 125 First, a debris-to-food ratio estimates how likely it is for a 126 turtle to ingest debris instead of food; more debris in the 127 environment results in proportionately more ingested debris 128 (Schuyler et al., 2016). Second, the relative debris residence 129 time estimates how much longer than food ingested debris 130 remains inside gastrointestinal tract (Lutz, 1990; Mascarenhas 131 et al., 2004; Valente et al., 2008). (See also SI Appendix, 132 Fig. S1). As a baseline, our previous analysis has shown that 133 free-ranging loggerhead turtles experience, on average, food 134 abundance of 0.81 (Marn et al., 2017b,a). The effect of said 135 competition between food and debris for the limited digestive 136 capacity is nearly negligible when there is 3% of debris in 137 digestive contents, but when there is 25% of debris in digestive 138 contents, effective food abundance is as low as 0.64. As will 139 be shown shortly, a drop in food abundance from 0.81 to 0.64 140 is already enough to considerably affect the life history of sea 141 turtles. 142

Ingested debris reduces the energetic scope for growth, mat-



Fig. 2. Ingested debris reduces the energetic scope for growth, reproduction, and reserve accumulation of sea turtles. The decrease happens both in absolute and relative terms. Shown is the total energy budget size and the energy usage of loggerhead turtles at the moment of sexual maturation. **A**, The decrease in effective food abundance from 0.81 for unexposed loggerheads (Marn et al., 2017b) to 0.64 for loggerheads exposed to 25% plastics is digestive contents would mean a 24% reduction in the total energy budget size. Also plotted for reference is the energy budget size at the maximum theoretical food abundance of 1.00. **B**, Beside reducing the total energy budget size, lower effective food abundance leaves a smaller fraction of the energy budget available for growth, reproduction, and energy accumulation. This is because maintenance demands are largely size-driven, and loggerhead turtles mature at approximately the same size (albeit possibly at very different age) as long as food abundance is sufficient for reaching sexual maturation.



Fig. 3. Ontogenetic development of loggerhead turtles is negatively affected by higher ingestion and longer residence of plastic debris. Ingested debris competes with food for a limited digestive capacity as shown in Fig. 1, thus lowering the effective food abundance below  $\approx 80\%$  of the maximum that loggerhead turtles normally experience in the wild. This negatively affects ontogeny. **A**, Body size can decrease from  $\approx 100$  cm straight carapace length under normal conditions to  $\approx 80\%$  cm, when also sexual maturation becomes delayed. **B**, The corresponding reduction in body mass is even more striking, falling from as much as 160 kg to as little as 60 kg. Periodic mass fluctuations are due to allocation to reproduction in adults, culminating in nesting that takes place roughly biannually in loggerhead turtles. **C**, The reduction in, typically biannual, fecundity is the most striking of all as the number of eggs declines from several hundreds to less than a hundred in a nesting season. Despite the large magnitude of the described negative effects, the effects may be difficult to recognize in the field due to imprecise age determination and natural variation between individuals.

uration or reproduction, and reserve accumulation (Fig. 2). 144 For example, a turtle with an average plastics load of 3% in 145 digestive contents, which is close to the mean reported values 146 for loggerhead turtles (Frick et al., 2009; Clukey et al., 2017), 147 experiences  $\approx 2.5$  % reduction in perceived food abundance and 148 total available energy, causing  $\approx 10\%$  lower condition index 149 and total seasonal reproductive output. With plastics loads in 150 excess of 25 %, which is the reported maximum (Frick et al., 151 2009), a fully grown turtle experiences  $\approx 20\%$  reduction in 152 available energy, causing  $\approx 15\%$  lower condition index and 153  $\approx 88\%$  lower total seasonal reproductive output compared to 154 unaffected turtles. This reduction is due to a smaller energy 155 budget in absolute terms (Fig. 2A), but also a larger contribu-156 tion of maintenance to the budget in relative terms (Fig. 2B). 157 At the moment of sexual maturation, for example, the decrease 158 in effective food abundance from 0.81 for unexposed individu-159 als to 0.64 for individuals exposed to 25% plastics in digestive 160 contents corresponds to a 24% reduction in the total energy 161 budget size. Meanwhile, in unexposed turtles, maintenance 162 costs comprise 78% of the energy budget, whereas in exposed 163 ones, as much as 96% of the energy budget. With only 4%164 of the daily energy budget left for growth, reproduction, and 165 reserve accumulation, exposed turtles potentially experience 166 difficulties allocating energy to egg production simply because 167 less energy is available for reproduction once maintenance 168 demands are satisfied. 169

A particular energy budget gives rise to a particular on-170 togeny. For simplicity, the presented simulations describe 171 North Atlantic loggerhead turtles experiencing a typical con-172 stant environment from hatching onward (Marn et al., 2017b); 173 174 the percentage of plastics in digestive contents is the only differing factor between simulations. The ultimate body sizes 175 of adults, expressed in terms of straight carapace length, range 176 between 80 cm and 100 cm (Fig. 3A). The corresponding range 177 of body masses is more dramatic, extending from as little as 178 60 kg for turtles exposed to plastics to as much as 160 kg for un-179 exposed turtles (Fig. 3B). Consistent with observations under 180 favourable conditions in the wild (Zug et al., 1986; Tiwari and 181 Bjorndal, 2000; Tucker, 2010; Hawkes et al., 2005), unexposed 182

turtles under simulated conditions mature already at the age 183 of 14, and are at maximum size capable of producing up to 640 184 eggs in one nesting season (Fig. 3C). The sexual maturation 185 age of exposed turtles may be substantially prolonged, followed 186 by reduced egg production. For example, turtles that start to 187 mature at the age of 26 years produce at maximum size only 188 75 eggs over a nesting season. When plastics occupies >30%189 of digestive contents, effective food abundance drops below 190 0.61, and turtles never mature or reproduce. 191

Sexual maturation and reproduction are not a guarantee 192 of population viability. Long-term viability of a population is 193 secured only if reproduction makes up for mortality, thereby 194 preventing population declines (see Methods). Our simula-195 tions show that the loggerhead turtle population growth, just 196 like sexual-maturation age, strongly depends on effective food 197 abundance driven by both the debris-to-food ratio and relative 198 residence times (Fig. 4). The lowest ratios and residence times 199 result in the fastest population growth and the youngest sexual-200 maturation age. As long as effective food abundance permits 201 sea turtles to mature by the age of  $\approx 22$  years, the population 202 remains viable; longer maturation times cause the population 203 to decline even though individuals can mature (Fig. 4). Ac-204 cordingly, the population-level ecological breakpoint at which 205 population transits from growth to decline is breached before 206 the individual-level breakpoint at which individuals stop sex-207 ually maturing. Ecological monitoring may thus show that 208 a population has many reproducing individuals when in fact 209 their reproductive output is insufficient to offset various causes 210 of mortality, and the population is headed towards extinction. 211

### Discussion

Sub-lethal effects of marine debris, though much discussed 213 (Ryan, 1988; McCauley and Bjorndal, 1999; Barnes et al., 214 2009; Mato et al., 2001; Yamashita et al., 2011), have so far 215 been deemed "particularly difficult to quantify" (Gall and 216 Thompson, 2015). We have overcome this difficulty by de-217 veloping a mechanistic modeling framework that links levels 218 of biological organisation to quantify the effects of plastics 219 ingestion on ontogeny and population growth of endangered 220

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Fig. 4. Reported debris ingestion is unlikely to impede sexual maturation of sea turtles, but population declines are possible. Population growth (colormap) is overlaid with sexual maturation age (contours) as functions of (i) the environmental debris-to-food ratio (y-axis) and (ii) gastrointestinal debris residence times relative to food (x-axis), which determine the percentage of plastics in the digestive contents and consequently the effective food abundance (see Fig. 1). White and grav isocurves respectively delineate zones of population decline (population-level breakpoint) and permanent sexual immaturity (individual-level breakpoint). The two breakpoints are separated by a 25% difference in the debris-to-food ratio or relative residence time Plastics in turtles is known to equal  $\approx$ 3% of digestive contents on average, but has been observed to exceed 25% (Frick et al., 2009). In the former case, loggerhead turtles in our simulations mature at the age of 14 years, which is well within the safe zone of positive population growth. In the latter case, however, turtles sexually mature only at the age of 25 years; if this became the norm, the population growth would land in the danger zone delineated by a white isocurve in the figure, and the population would be headed to extinction despite the reproducing individuals.

loggerhead turtles. The results show that amounts of plastics 221 observed in the digestive contents of sea turtles are insufficient 222 to prevent sexual maturation, but population declines as a 223 consequence of plastics cannot be ruled out. Considering indef-224 inite sexual maturation and population decline as individual-225 and population-level ecological breakpoints, we see that while 226 the former is far from being breached, the latter may have 227 already been breached. A population could therefore be in 228 distress despite a seemingly favorable physiological state of 229 individuals. 230

231 Pinpointing indicators of physiological state that are sensi-232 tive to plastics ingestion may help identify negatively affected individuals, the prevalence of such individuals in a popula-233 tion, and thereby the population's state. Our framework, for 234 example, predicts that turtles exposed to plastics have a re-235 duced scope for growth, maturation, reproduction, and reserve 236 accumulation. To test this prediction we looked at Fulton's 237 condition factor (Nash et al., 2006) whose values are expected 238 239 to be lower for exposed individuals due to less reserve accumulation. We used a limited dataset on loggerhead turtles from 240 the Adriatic Sea (SI Appendix, Result 1). Exposed turtles 241 indeed appear to have a lower condition factor than those 242 unaffected by plastics (SI Appendix, Fig. S4), but more data 243 is needed for a decisive conclusion. Ultimately, however, the 244 model suggests that other indicators linked to ontogeny may 245 be more sensitive to the long-term sub-lethal effects of plastics than the condition factor, with the added benefit of also being 247

less sensitive to short-term fluctuations. The ontogeny of ex-248 posed turtles can be greatly delayed, causing major life-history 249 milestones to be reached at a later age. Accordingly, if mea-250 surements of body size and fecundity were supplemented with 251 the age of sea turtles, every individual could be positioned 252 in one or more plots in Fig. 3, and compared against expec-253 tations calculated for that population, taking into account 254 the average food abundance and temperature experienced by 255 the turtles. Individuals whose position was closer to the blue 256 (resp., yellow) side of the spectrum of expected ontogenies 257 would then be deemed affected (resp., unaffected) by plastics. 258 Due to inter-individual variability present even after account-259 ing for population-specific characteristics (Marn et al., 2017a, 260 2019), the results would have to be interpreted in a statistical 261 sense, i.e., based on samples of sufficient size that are currently 262 unavailable. 263

Gaps in current field data , and by extension knowledge, 264 prompted us to limit simulations to continuous average sub-265 lethal exposure to plastics. The limitation, however, is not 266 methodological; if high-resolution field data is leveraged with 267 the present methodology, insights into multiple ecological 268 scenarios become possible. To illustrate, we have considered 269 one such scenario: the potentially damaging effects of short-270 term spikes in plastics ingestion on ontogeny and reproductive 271 output of loggerheads. In these additional simulations we 272 mimic reality by making debris ingestion stochastic, with the 273 mean and the maximum percentage of plastics in digestive 274 contents corresponding to the observed values of 3% and 25%, 275 respectively (SI Appendix, Result 2). The periods of favorable 276 feeding conditions allow sea turtles to grow almost as large as 277 if there was no exposure to plastics (SI Appendix, Fig. S5C), 278 yet the periods of occasional starvation decrease condition and 279 thus reproductive output (SI Appendix, Fig. S5D, E). This 280 is worrying because body size in terms of carapace length 281 is the easiest to measure in practice, and thus much more 282 often reported than body mass and fecundity, although a 283 combination of at least two of these quantities would be a 284 better indicator of the true state in the field. 285

Ecologically important difference in plastics ingestion be-286 tween pelagic-feeding juveniles and benthic-feeding adults 287 could also be explored with presented methodology and addi-288 tional data. Debris ingestion is likely to change over a lifetime 289 (Nelms et al., 2016; Schuyler et al., 2014b, 2016), thus raising 290 questions about the realistic exposure in each life stage, and 291 about identifying which life stage is then a bottleneck in the 292 population growth of loggerhead turtles. Similarly, not all 293 species of sea turtles are equally affected by environmental 294 prevalence or ingestion of debris (Nelms et al., 2016; Schuyler 295 et al., 2016; Lynch, 2018). Species with a highly specialized or 296 generally nutritionally poor diet may be at a higher risk by ad-297 ditional energy limitations imposed by plastics ingestion than, 298 e.g., carnivorous loggerheads. Again, answers are method-299 ologically within our reach (Mazaris et al., 2006; Schuyler 300 et al., 2016; Ijima et al., 2019; Stubbs et al., 2020), but remain 30 speculative until high-fidelity field data become available. 302

Plastics can have ecological consequences extending beyond energy limitation caused by reduction in digestive capacity of individuals. These are most likely to arise from ingested microplastics (Rezania et al., 2018), and manifest as feedbacks between energy allocation and the bioconcentration of leached toxins (Klanjscek et al., 2007). Incorporating ecotoxicology into the ontogenetic model presented here is conceptually
straightforward (Jager et al., 2006; Jager and Zimmer, 2012),
but uncovering the true nature of such dynamics is not. The
process is, in fact, extremely data-intensive, implying that
biochemical effects on metabolism of plastics ingestion are
probably going to be quantified last.

Finally, modular structure and mechanistic underpinning of 315 the framework allow not only exploration of additional specific 316 ecological scenarios for the sea turtle related to plastics, but 317 also generalizations to other species and stressors. The module 318 for individual ontogeny can directly account for thousands of 319 species in a rapidly expanding Add-my-Pet database (Marques 320 et al., 2018), and can be augmented to include a number of al-321 ternative or coexistent stressors (Galic et al., 2018). Therefore, 322 in addition to elucidating consequences of exposure to plas-323 tics important for loggerhead turtle conservation, the present 324 study answers a long-standing call by ecotoxicologists (Kramer 325 et al., 2011) and conservationists (Cushman, 2006; Mazaris 326 et al., 2006) for a flexible framework relating environmental 327 pressures to both individual- and population-level indicators. 328 Probably the most important feature of the new framework 329 is the ability to assimilate and make best use of disparate 330 sources of knowledge ranging from molecular-level processes, 331 through individual-level data and time series, to environmental 332 and population-level indicators (Nisbet et al., 2000), taking 333 us a big step closer to understanding the general ecological 334 consequences of plastic pollution. 335

#### 336 Materials and Methods

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Herein, we showcase a general and flexible modeling Overview. 338 approach aiming to relate the individual-level effects of sub-lethal 339 exposure to a stressor and the population-level effects of such expo-340 sure in order to quantify ecological breaking points. The approach 341 342 is general in the sense of pertaining to any wildlife species and multiple types of stressors. Our focus was on sea turtles and plastic 343 debris, but we could have easily worked with another endangered or 344 otherwise-of-interest species whose energy budget is known (Mar-345 ques et al., 2018). Similarly, the stressor could have been an abiotic 346 factor such as temperature or salinity, or anthropogenic substances 347 such as pollutants or toxicants. The approach is modular: the 348 outputs of one module serve as the inputs for another module, 349 while each module's internal functioning is separate from others. 350 To describe an individual's ontogeny we thus used dynamic energy 351 budgets (Nisbet et al., 2000; Sousa et al., 2008, 2010; Jusup et al., 352 2017), although other approaches based on physiological energetics 353 would do (Nisbet et al., 2012). Similarly, population dynamics is 354 implementable in any number of ways, e.g., via the Euler-Lotka 355 equation (De Roos, 2008; Beekman et al., 2019), matrix population 356 models (Klanjscek et al., 2006; Ijima et al., 2019), physiologially 357 structured population models (De Roos and Persson, 2002; Diek-358 mann et al., 2003), integral projection models (Smallegange et al., 359 2017). Finally, we modeled the effects of debris ingestion in the 360 form of competition between food and plastics for available digestive 361 capacity. We assumed that ingested debris occupied a fraction of 362 digestive capacity, but delivered zero digestible energy. Below, each 363 module is conceptually introduced; mathematical derivations and 364 other details are in the SI Appendix, Methods. 365

We relied on physiological energetics to generate the Ontogeny. 366 ontogenetic development of individuals as a function of exposure to 367 external factors (food, temperature, stressors, etc.). Physiological 368 energetics contrasts energy sources and sinks, and thus determines 369 370 the proportion of ingested energy available for growth, maturation, and reproduction. We used the standard dynamic energy budget 371 model because of an existing and detailed adaptation to loggerhead 372 turtles (Marn et al., 2017b,a, 2019), and straightforward application 373

to more than 2000 other species<sup>\*</sup> (Marques et al., 2018).

The model expresses body size, L, as a function of age, a, via 375

$$\frac{\mathrm{d}L}{\mathrm{d}a} = \dot{G}\left(i\text{-state}, e\text{-state}\right), \qquad [1] \quad 376$$

where  $\dot{G} = \dot{G}$  (*i*-state, *e*-state) is a growth function dependent on the 377 individual's state, e.g., body size L (*i*-state variables), and the state 378 of the environment, e.g., the aforementioned abiotic factors and 379 anthropogenic substances (e-state variables). A concrete functional 380 form of G is decided by the animal's energy allocation scheme or 381 simply the energy budget, the side-product of which is also a fecun-382 dity function,  $\dot{F} = \dot{F}$  (*i*-state, *e*-state). The energy budget is only 383 indirectly inferable by specifying model assumptions and testing how 384 well the resulting model fits empirical data. The assumptions of the 385 standard dynamic energy budget model, as well as the consequent 386 energy budget, are detailed in the SI Appendix, Methods. The 387 model parameters for North Atlantic loggerhead turtles produce 388 realistic predictions with a good fit to observed data (See Marn 389 et al. (2017b,a) and the online Add-my-pet collection<sup>\*</sup> for more 390 information on model calibration and comparison to observations). 391 Ontogenies were simulated at the temperature of 21.8°C and a range 392 of effective food abundance (see Fig. 1). 393

**Population growth.** Key ingredients for determining the long-term population growth rate,  $\dot{r}$ , are fecundity  $\dot{F}$  and survival S as functions of age. This is most evident by writing the Euler-Lotka equation of population growth

$$1 = \int_0^\infty e^{-\dot{r}a} \dot{F}(a) S(a) \,\mathrm{d}a.$$
 [2] 398

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Generally, however, fecundity and survival depend on *i*-state and 399 e-state variables, with body size L often being the dominant vari-400 able that drives major ecological events (De Roos and Persson, 401 2002). To calculate the loggerhead population growth, we se-402 lected size as the dominant variable driving major ecological events, 403 and obtained the survival curves by integrating size-dependent 404 hazard rates found in the literature (Heppell et al., 2003; Sasso 405 et al., 2006) (SI Appendix, Fig. S6). The individual-level energy 406 budget gives access to environment-dependent fecundity function 407  $\dot{F} = \dot{F}(L, e\text{-state}) = \dot{F}(L)$ , and by means of Eq. (1), to age-length 408 relationship L = L(e-state; a) = L(a). The composition of func-409 tions  $\dot{F} = \dot{F} \left[ L \left( a \right) \right]$  is then directly insertable into Eq. (2) to yield a 410 population growth rate sensitive to the specifics of ontogenetic devel-411 opment. Analogous reasoning applies to composition S = S[L(a)]412 with the exception that survival is, at best, partly inferable from 413 the individual's energy budget in the form of aging-related hazard 414 (van Leeuwen et al., 2010) because natural (diseases and preda-415 tion) or anthropogenic (direct exploitation or collateral damage) 416 hazards almost always dominate. We reported population growth 417 in terms of  $\lambda = \exp(\dot{r}/\dot{r}_0)$ , where we set the reference growth rate 418 to  $\dot{r}_0 = 1 \, \mathrm{y}^{-1}$ . The population is thus growing if  $\lambda > 1$ , declining if 419  $\lambda < 1$ , and stagnating if  $\lambda = 1$ . 420

Debris ingestion. We described food abundance in terms of quan-421 tity  $0 \le f < 1$  representing a fraction of the maximum ingestion rate 422 for individuals of a given size. The value of f reflects food supply 423 in the environment because f = 0 when supply ceases, and  $f \rightarrow 1$ 424 when supply is unlimited. Assuming that individuals spend time 425 searching for and then clearing food (Jusup et al., 2017), the rela-426 tionship between f and food supply X becomes  $f = X/(X + K_X)$ , 427 where  $K_{\mathbf{x}}$  is known as the half-saturation constant for food. This 428 constant is a compound parameter containing information on how 429 aptly food is searched for and cleared by the animal. Therefore, 430 if plastic debris is mistaken for food, some of the searching and 431 clearing efforts are in vain, and the half-saturation constant should 432 increase in the presence of plastics. We modeled this by assuming 433 that a fraction of digestive capacity is occupied by ingested debris 434 (SI Appendix, Methods). Instead of f, turtles experience effective 435 food abundance  $f_{\text{eff}}$ , with  $K_X$  replaced by  $K_{\text{eff}} = K_X (1 + Y/K_Y)$ , 436 where Y is the supply of plastics in the environment, and  $K_Y$  is an 437 analogue of the half-saturation constant, but now for plastic debris 438 instead of food. Quantity  $f_{\rm eff}$  is related to food abundance f via 439

$$f_{\text{eff}} = \frac{f}{1 + fR\frac{Y}{X}},\tag{3}$$

\*https://www.bio.vu.nl/thb/deb/deblab/add\_my\_pet

where dimensionless R is the gastrointestinal residence time of 441 plastics relative to food, and Y/X is the environmental plastics-to-442 food ratio. Previous work (Marn et al., 2017b) shows that loggerhead 443 turtles in the wild experience food abundance f = 0.81. Ranges of 444 445 simulated R and Y/X were determined from passage time of plastics relative to food (Lutz, 1990; Mascarenhas et al., 2004; Valente et al., 446 447 2008), and environmental debris prevalence (Moore et al., 2001; Figueiredo and Vianna, 2018) (SI Appendix, Methods). The debris-448 to-food ratio implicitly assumes uniform mixing of plastic debris and 449 450 food in the ocean, and that the higher likelihood of debris ingestion due to higher debris occurrence (Schuyler et al., 2016) results in 451 more debris in the digestive system relative to food. 452

Ecological literature often expresses the influence of plastics on sea turtles in terms of the percentage of debris in digestive contents,  $%V_{dc}$ . Under the assumption that digestive capacity is indiscriminately occupied by both, we obtain the simplest relation between quantities R, X/Y, and  $%V_{dc}$ :

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 $\frac{\%V_{\rm dc}}{1-\%V_{\rm dc}} = R\frac{Y}{X}.$ 

[4]

The simple form is intuitively appealing because either Y/X = 0 or 459 R = 0 leads also to  $%V_{dc} = 0$ , whereas either  $Y/X \rightarrow \infty$  or  $R \rightarrow \infty$ 460 leads to  $\%V_{dc} = 1$ . In other words, debris in digestive contents 461 is negligible in a plastics-poor environment or if the clearance of 462 plastics is much faster than that of food. Conversely, debris over-463 whelms gastrointestinal tract in a plastics-rich environment or if the 464 clearance of plastics is relatively slow. By using the percentage of 465 debris in digestive contents as the target quantity for simulations, 466 we bypass the uncertainties linked to preferential plastics ingestion 467 of specific life stages, as well as different types of plastic debris hav-468 ing different residence times. The chances of debris ingestion and 469 variability of residence time by the plastics types does not matter as 470 long as relative abundance of ingested plastics remains reasonably 471 472 constant. The simulated percentages in stomach contents have been truth-grounded against necropsy data (Frick et al., 2009; Lynch, 473 2018); presently, the mean and the maximum value of  $%V_{dc}$  are 3% 474 and 25%, respectively (Frick et al., 2009). 475

476 Data Accessibility. The data associated with the paper has been
477 made available via HAL (hal-02880223) and associated code via
478 GitHub<sup>†</sup> and Add-my-Pet repository<sup>‡</sup>.

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<sup>&</sup>lt;sup>†</sup>https://github.com/ninamarn/marineDebrisTurtle

<sup>&</sup>lt;sup>‡</sup> http://www.bio.vu.nl/thb/deb/deblab/add\_my\_pet/entries\_web/Caretta\_caretta/Caretta\_caretta\_ res.html

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# **Supplementary Information for**

# Quantifying impacts of plastic debris on marine wildlife identifies ecological breakpoints

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- 8 Figs. S1 to S6
- <sup>9</sup> References for SI reference citations

### Supporting Methods

Model equations for ontogenetic development. To simulate realistic ontogenies of individual sea turtles, we relied on physiological energetics, and specifically the standard Dynamic Energy Budget (DEB) model (Sousa et al., 2008, 2010; Kooijman, 2010; Jusup et al., 2017) (Fig. S1). This model traces the individual's state—its size, life stage, and condition (*i*-state variables)—as a function of age, depending on physiological characteristics that are mirrored in the values of the model parameters. The environmental conditions, such as food abundance and temperature, act as

<sup>16</sup> forcing variables (*e*-state variables).

The rates of change of a sea turtle's *i*-state variables are given by a set of three differential equations. Eq. (1) for length L (in cm) tracks energy used for growth, Eq. (2) for life-stage indicator  $E_H$  (in J) tracks cumulative energy invested into maturation, and Eq. (3) for condition E (in J) tracks the amount of available energy reserve:

$$\frac{\mathrm{d}L}{\mathrm{d}t} = \frac{\dot{p}_G}{3L^2[E_G]},\tag{1}$$

$$\frac{\mathrm{d}E_H}{\mathrm{d}t} = \begin{cases} \dot{p}_R & \text{if } E_H < E_H^p \\ 0 & \text{otherwise} \end{cases}, \text{ and}$$
[2]

$$\frac{\mathrm{d}E}{\mathrm{d}t} = \dot{p}_A - \dot{p}_C,\tag{3}$$

where  $[E_G]$  (in J cm<sup>-3</sup>) is the volume-specific cost for growth, and  $E_H^p$  (in J) is threshold maturity for sexual

maturation. Length L is not a measurable quantity itself, but connects to often measured straight carapace length  $L_{SCL}$  via shape factor  $\delta_{SCL}$ , i.e.,  $L = L_{SCL}\delta_{SCL}$ . Below, we define energy flows  $\dot{p}_*$  (in J d<sup>-1</sup>) in terms of *i*-state variables. A sea turtle acquires energy through assimilation:

$$\dot{p}_A = \{\dot{p}_{Am}\}L^2 f,\tag{4}$$

<sup>24</sup> where the performance of the turtle's digestive system is reflected in the surface-specific maximum assimilation rate,

 $\{\dot{p}_{Am}\}\$  (in J d<sup>-1</sup> cm<sup>-2</sup>), while food abundance  $f, 0 \leq f < 1$ , is the ratio of the current ingestion rate to the maximum ingestion rate at unlimited food supply. Assimilated energy gets mobilized from reserve to power metabolic processes

<sup>27</sup> at a rate determined by the utilization energy flow:

$$\dot{p}_C = [E] \frac{\dot{v}[E_G]L^2 + [\dot{p}_M]L^3}{[E_G] + \kappa[E]},$$
[5]

where  $[E] = E/L^3$  is energy reserve density, parameter  $\dot{v}$  (in cm d<sup>-1</sup>) is energy conductance, and dimensionless parameter  $\kappa$ ,  $0 < \kappa < 1$ , is a fraction of utilization flow directed to somatic maintenance and growth. Finally, the sea turtle grows at a rate:

$$\dot{p}_G = [E_G] \frac{\kappa \dot{v}[E] L^2 - [\dot{p}_M] L^3}{[E_G] + \kappa [E]},$$
[6]

provided there is mobilized energy left after satisfying the somatic maintenance needs, i.e.,  $\kappa \dot{p}_C > [\dot{p}_M] L^3$ .

As indicated, fraction  $\kappa \dot{p}_C$  of mobilized energy is used for somatic maintenance and growth, while the remaining fraction,  $(1 - \kappa)\dot{p}_C$ , is allocated to maturation in embryo and juveniles, and to reproduction in adults:  $\dot{p}_R =$  $(1 - \kappa)\dot{p}_C - \dot{k}_J E_H$ , where  $\dot{k}_J$  (in d<sup>-1</sup>) is the maturity maintenance coefficient. Life-stage transitions from embryo to juvenile, and from juvenile to adult, occur at maturity thresholds  $E_H^b$  and  $E_H^p$ , respectively. Investment into reproduction starts after puberty ( $E_H^p$ ) and determines fecundity in adults:  $\dot{F} = \kappa_R \dot{p}_R / E_0$ , where dimensionless parameter  $\kappa_R$  is the efficiency of energy conversion from reserve to eggs, and  $E_0$  (in J) is the energetic value of an egg. Fig. S2 visualizes the energy allocation of a free-ranging loggerhead turtle experiencing food abundance f = 0.81.

In the described frameworks, body mass is not an *i*-state variable, but rather a function of length L, reserve E, and energy  $E_R$  stored for reproduction between two nesting seasons. Quantity  $E_R$  is calculated only for adult individuals using  $E_R = \int \dot{p}_R dt$ , where integration is performed over predominantly biannual remigration period (Hawkes et al., 2005). Body mass is calculated as:

$$W = d_V L^3 + \rho_E \left( E + E_R \right), \tag{7}$$

where  $d_V \approx 1 \,\mathrm{g \, cm^{-3}}$  is body density and  $\rho_E$  (in g J<sup>-1</sup>) is a mass-energy coupler for reserve. The second term in this equation indicates the animal's condition, which is best seen through the connection with Fulton's condition factor (Nash et al., 2006):

 $CF \propto \frac{W}{L_{SCL}^3} = d_V \delta_{SCL}^3 + \rho_E \frac{E + E_R}{L_{SCL}^3}.$ 

The proportionality constant is  $C_0 = 100 \text{ cm}^3 \text{ g}^{-1}$  if wet body mass is expressed in grams and straight carapace length in centimeters.

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[8]



Fig. S1. Schematic representation of the proposed modeling framework. More plastic debris in the environment or a longer ingested-plastics residence time result in more of the digestive capacity being occupied by plastics instead of food. This affects individual ontogeny by reducing the energy assimilated into reserve, and thereafter the energy available for growth and maturation (or reproduction) after all maintenance costs are paid. In response, individuals may grow smaller, their condition may decrease, they may lose the ability to reproduce, and they may even die under the most extreme circumstances. At the population level, moreover, reproducing individuals are no guarantee of positive growth because fecundity may be insufficient to compensate for mortality losses, in which case the population declines. Individual ontogeny depending on the state of the environment and the state of the individual is captured using the standard Dynamic Energy Budget model (box), but with parameter values adjusted to loggerhead turtles.

Model parameters and the generality of physiological energetics. The values of model parameters pertaining to the North Atlantic population of loggerhead turtles at the temperature of 21.8 °C are:  $[E_G] = 7322 \text{ J cm}^{-3}$ ,  $E_H^b = 2.535 \cdot 10^4 \text{ J}$ ,  $E_H^p = 9.875 \cdot 10^7 \text{ J}$ ,  $\{\dot{p}_{Am}\} = 868.11 \text{ J cm}^{-2}$ ,  $\dot{v} = 0.0791 \text{ cm} \text{ d}^{-1}$ ,  $[\dot{p}_M] = 13.01 \text{ J cm}^{-3}$ ,  $\dot{k}_J = 0.0013 \text{ d}^{-1}$ ,  $\kappa = 0.729$ ,  $\kappa_R = 0.95$ ,  $\delta_{\text{SCL}} = 0.39$ ,  $E_0 = 178.56 \text{ kJ}$ , and  $\rho_E = 1.552 \cdot 10^4 \text{ g J}^{-1}$  (Marn et al., 2017b). Data from all 49 50 51 life stages used to calibrate the model, as well as the potential updates to model parameters, are freely accessible in 52 the Add-my-Pet collection<sup>\*</sup> (Margues et al., 2018). A discussion on the model calibration and model predictions 53 in the context of the reported values for North Atlantic loggerhead turtles, including inter-individual variability in 54 growth, maturation, and reproduction due to experienced food abundance and temperature, are available in the 55 literature (Marn et al., 2017b,a). We deliberately decided to work with model parameters pertaining to the North 56 Atlantic population of loggerhead turtles, but other populations or species from the Add-my-Pet collection, e.g., the 57 Mediterranean population of loggerhead turtles (Marn et al., 2019), green turtles (Stubbs et al., 2019), or any other 58 species exposed to plastics ingestion would have been equally acceptable. Testifying to the generality of the approach 59

<sup>60</sup> is the fact that the Add-my-Pet collection currently contains over 2000 entries.

\*https://www.bio.vu.nl/thb/deb/deblab/add\_my\_pet



Fig. S2. Energy budget of a loggerhead turtle throughout its ontogeny. Shown is the allocation of assimilated energy to main ontogenetic processes: maintenance, growth, maturation or reproduction, and reserve buildup. Further emphasized is a snapshot of the energy budget at sexual maturation. Maintenance demands are sizedriven, leaving large turtles with less energy for growing and accumulating reserve. Investment into maturation halts when turtles sexually mature. Instead, investment into reproduction begins. Here, food abundance is set to f = 0.81, corresponding to what free-ranging loggerhead turtles experience in the wild

**Plastic ingestion and effective food abundance.** Food abundance f introduced in Eq. (4) depends on food density in the environment, X (in  $g dm^{-3}$ ), via the Holling type-II functional response (Holling, 1959): 62

$$f = \frac{X}{X + K_X}.$$
[9]

Here,  $K_X$  (in g dm<sup>-3</sup>) is the half-saturation constant for food. Relatively small  $K_X$  characterizes animals with low 63 ingestion demands and/or fast foraging rate, and such animals reach near-satiation at low food densities. The opposite 64

holds for relatively large  $K_X$ . 65

In the presence of debris in the environment, the animal's effective half-saturation constant  $K_{\rm eff}$  becomes larger 66 than  $K_X$ . Specifically, if Y (in g dm<sup>-3</sup>) denotes environmental debris density, then the relationship between  $K_{\text{eff}}$  and 67  $K_X$  is: 68

$$K_{\text{eff}} = K_X \left( 1 + \frac{Y}{K_Y} \right), \qquad [10]$$

where  $K_Y$  is a debris analogue of the half-saturation constant. The animal thus perceives food abundance  $f_{\text{eff}}$ 69  $X/(X+K_{\text{eff}})$  that is lower than f whenever Y > 0. Below, we derive Eq. (10) via the competition of food and 70 plastics for the limited digestive capacity of gastrointestinal tract. 71

Digestive capacity. Inspired by the concept of Synthesizing Units (Kooijman, 1998, 2006), we modeled energy uptake 72 by assuming that ingested food and debris compete for the limited digestive capacity of the gastrointestinal tract. 73 Parts of the capacity are either: (i) occupied by food, (ii) occupied by plastics, or (iii) free (unoccupied), which we 74 respectively denote with fractions  $\theta_X$ ,  $\theta_Y$ , and  $\theta_-$ . By definition  $\theta_X + \theta_Y + \theta_- = 1$ . The dynamics of digestive capacity 75 is determined by a binding rate  $(\dot{b}_i \text{ in } dm^3 g^{-1} d^{-1})$ , and a release rate  $(\dot{k}_i \text{ in } d^{-1})$ , where i = X for food or i = Y for 76 debris. The ratio of the two rates gives the half-saturation constant:  $K_i = k_i/b_i$ . The dynamics of the three fractions 77 can then be written as a set of three ordinary differential equations (ODEs): 78

Dynamics	Eq.	Equilibrium densities	Eq.
$\frac{d\theta_X}{dt} = \dot{b}_X \theta \cdot X - \dot{k}_X \theta_X$	[d1]	$\theta_X^* = \theta_{-}^* \frac{X}{K_X}$	[e1]
$\frac{d\theta_Y}{dt} = \dot{b}_Y \theta Y - \dot{k}_Y \theta_Y$	[d2]	$\theta_Y^* = \theta_{-}^* \frac{Y}{K_Y}$	[e2]
$\frac{\mathrm{d}\theta_{-}}{\mathrm{d}t} = -\dot{b}_{X}\theta_{-}X + \dot{k}_{X}\theta_{X} - \dot{b}_{Y}\theta_{-}Y + \dot{k}_{Y}\theta_{Y}$	[d3]   6	$\frac{\partial^*}{\partial x} = \left(1 + \frac{X}{K_X} + \frac{Y}{K_Y}\right)^{-1}$	[e3]

79

The equilibrium digestive capacity fractions are marked with an asterisk. 80

Only the occupied part of the digestive capacity is responsible for energy assimilation. Analogously to Eq. (4), 81

we have:  $\dot{p}_{A} = \{\dot{p}_{Am}\}L^{2}(\theta_{X}^{*} + \kappa_{Y}\theta_{Y}^{*})$ , where  $\kappa_{Y}, 0 \leq \kappa_{Y} < 1$ , quantifies the energetic contribution of debris (Y)82 relative food (X). The effective food abundance is  $f_{\text{eff}} = \theta_X^* + \kappa_Y \theta_Y^*$ . Assuming debris has no energetic value,  $\kappa_Y = 0$ . 83

Inserting Eq. (e3) into Eq. (e1) finally yields: 84

$$f_{\text{eff}} = \theta_X^* = \frac{X}{X + K_X \left(1 + \frac{Y}{K_Y}\right)},$$
[11]

85

from where it becomes obvious that  $K_{\text{eff}} = K_X (1 + Y/K_Y)$  as specified in Eq. (10). Comparing Eq. (9) and Eq. (11) leads to  $f_{\text{eff}} = f/\left(1 + f\frac{K_X}{K_Y}\frac{Y}{X}\right)$ . Here, Y/X is an environmental debris-to-food ratio. The ratio of half-saturation constants,  $K_X/K_Y$ , is best understood as follows. Because digestive capacity is 86 87 indiscriminately occupied by food and debris, we have  $\dot{b}_X = \dot{b}_Y$ . We also have  $\dot{k}_X > \dot{k}_Y$  because plastics is more inert than food. Accordingly, quantity  $R = \frac{K_X}{K_Y} = \frac{\dot{k}_X}{\dot{k}_Y} > 1$  is a ratio of clearance rates for food and plastics that shows how much longer plastics occupy digestive capacity relative to food. Existing literature, in line with inequality R > 1, 88 89 90 posits that it takes more time to egest plastics than digested food (Lutz, 1990; Mascarenhas et al., 2004; Valente 91 et al., 2008). We finally arrive at an expression that relates food abundance f in the absence of plastics to effective 92 food abundance  $f_{\text{eff}}$  in the presence of plastics: 93

$$f_{\rm eff} = \frac{f}{1 + fR\frac{Y}{X}}.$$
[12]

**Plastics in digestive contents.** We have shown in Eq. (12) that effective food abundance in the presence of plastics 94 is critically determined by two dimensionless factors: (i) the environmental debris-to-food ratio, Y/X, and (ii) the 95 residence time of debris relative to food, R. The former factor quantifies the prevalence of debris in the environment, 96 while the latter factor quantifies how much longer debris stays in the gastrointestinal tract relative to food. Although 97 some indications of environmental debris prevalence and the relative debris residence time exist in the literature (Lutz, 98 1990; Moore et al., 2001; Mascarenhas et al., 2004; Valente et al., 2008; Barnes et al., 2009; Figueiredo and Vianna, 99 2018), field ecologists often measure the proportion of debris in digestive contents,  $V_{dc}$  (Frick et al., 2009; Clukey 100 et al., 2017; Lynch, 2018). To use available data in a consistent way, we need to establish a relationship between 101 quantities Y/X, R, and  $%V_{dc}$ , while satisfying several constraints. First, if  $Y \ll X$  then the presence of plastics is 102 negligible and  $%V_{dc} \rightarrow 0$ , whereas if  $Y \gg X$ , the presence of plastics is overwhelming and  $%V_{dc} \rightarrow 1$ . Similarly, if 103  $R \ll 1$  then plastics is quickly cleared from the gastrointestinal tract and  $V_{\rm dc} \rightarrow 0$ , whereas if  $R \gg 1$  then plastics 104 bioaccumulate in the gastrointestinal tract and  $V_{\rm dc} \rightarrow 1$ . The simplest relationship that satisfies these constraints is 105 (Fig. S3): 106

$$\frac{\% V_{\rm dc}}{1 - \% V_{\rm dc}} = R \frac{Y}{X}.$$
[13]

Based on the known residence times of food from 9 to 13 days (Valente et al., 2008), and of debris from several 107 weeks to several months (Lutz, 1990; Mascarenhas et al., 2004), we simulated relative debris residence times as 108 the ratio of debris and food residence times in the range between  $1 \le R \le 10$ . The values of the environmental 109 debris-to-food ratio are unknown at present for sea turtles, but in some areas more plastic particles than plankton 110 have been observed (Moore et al., 2001) implying Y/X > 1; in simulations we always varied Y/X sufficiently to reach 111 or even exceed the point at which individuals are unable to sexually mature. The different combinations of R and 112 Y/X result in a range of  $%V_{\rm dc}$  values (Fig. S3) and thus effective food abundances illustrated in Fig. 1 of the main 113 text. 114



Fig. S3. Environmental debris-to-food ratio and relative debris residence time control the proportion of debris in digestive contents. Shown is the percentage debris in digestive contents,  $\%V_{dc}$  (colormap), as a function of debris-to-food ratio in the environment, Y/X (y-axis), and the residence time of food relative to ingested debris, R (x-axis). The representative values of Y/X are currently unknown. We estimated the representative values of R,  $1.25 \le R \le 10$ , based on the known residence times of food and debris in gastrointestinal tract of loggerheads (Lutz, 1990; Mascarenhas et al., 2004; Valente et al., 2008). The displayed range of  $\%V_{dc}$  values between  $0 \le \%V_{dc} < 84\%$  is illustrative and exceeds the range used in simulations. Of note is that existing data on plastics loads are plagued by uncertainties. For North Atlantic loggerhead turtles, the mean and the maximum reported percentage of plastics in stomach contents equals 3.2% and 25.7%, respectively (Frick et al., 2009), yet the stomach is unlikely to be representative of the whole gastrointestinal tract in which ingested debris may bioaccumulate (Tomás et al., 2002; Campani et al., 2013). Measuring (i) debris in digestive contents and (ii) relative residence times, and then inverting the map shown here, may quantitatively constrain the presently unknown bio-availability of plastics to sea turtles.

## **115 Supplementary Results**

Supplementary Result 1. Turtles exposed to plastics are expected to have lower condition than comparably sized 116 unexposed turtles. Based on Eq. (8), for example, we predict a North Atlantic loggerhead juvenile of 40 cm straight 117 carapace length at effective food abundance of  $f_{\rm eff} = 0.64$  to have condition factor of CF $\approx$ 12. A similarly sized 118 juvenile at food abundance of f = 0.81 for unexposed loggerheads is expected to have a condition factor of CF $\approx$ 14. 119 This difference in condition factors corresponds to  $\approx 11\%$  less body mass for exposed turtles relative to unexposed 120 ones, which in turn corresponds to  $\approx 19\%$  less reserve because the difference in body mass is entirely due to less 121 accumulated reserve. Available data, albeit limited, seem to support the model's prediction (Fig. S4). Specifically, we 122 obtained from the Pula aquarium in Croatia sufficient information to estimate the condition factor of 77 loggerhead 123 turtles, of which 8 individuals have been found to have ingested plastics. The average condition of exposed turtles is 124 indeed lower by close to the predicted amount. However, more data is needed to establish statistical significance with 125 sufficient power; the small number of exposed turtles may cause type II error with a large probability. 126

<sup>127</sup> **Supplementary Result 2.** In the main text, we simplified simulations by assuming a constant exposure to plastics. A <sup>128</sup> more realistic scenario is that sea turtles experience a time-varying environment such that the periods of no exposure <sup>129</sup> interchange with the periods of potentially high exposure. To explore such a scenario, we performed additional <sup>130</sup> simulations in which the proportion of debris in digestive contents,  $%V_{dc}$ , is log-normally distributed with parameters <sup>131</sup>  $\mu = 0.6$  and  $\sigma = 1.0$  (Fig. S5A). This generates a realistic mean of  $%V_{dc} \approx 3\%$ , covers a realistic range of plastics <sup>132</sup> loads between zero and 30\%, and mostly the load is low to moderate, with only occasional spikes (Fig. S5B) just as <sup>133</sup> reported in the literature (Frick et al., 2009; Schuyler et al., 2014; Clukey et al., 2017; Lynch, 2018).

Based on the assumed distribution for the proportion of debris in digestive contents, we calculated new effective 134 food abundance experienced by sea turtles every 30 simulation days and performed smooth interpolation for days 135 in between. Spikes in plastics load were large enough to make effective food abundance occasionally insufficient to 136 satisfy the basic maintenance needs, i.e., the animal could enter starvation. The formal condition for starvation is 137  $\kappa \dot{p}_C < [\dot{p}_M] L^3$ , from which point the energy deficit is compensated for by draining the energy stored for reproduction 138 (*i*-state variable  $E_R$ ). If such energy is unavailable, the animal satisfies only the basic maintenance needs from reserve 139 (*i*-state variable E). In the latter case, Eq. (5) no longer holds, and instead  $\dot{p}_C = [\dot{p}_M] L^3 + \dot{k}_J E_H$ . We assumed 140 biannual reproduction (Hawkes et al., 2005) during which variable  $E_R$  is emptied until there is not enough energy to 141 produce a whole egg. The average energetic value of an egg calculated by the model equals 178.56 kJ, and is close to 142 that reported in literature (Hays and Speakman (1991)). The predicted reproductive output is expressed for the 143 whole season as, for example, 600 eggs—in reality this would correspond to between 4 and 5 clutches (Tucker, 2010) 144



**Fig. S4. Debris ingestion lowers condition.** The model predicts that similarly sized loggerhead turtles who have been exposed to plastics should have lower mass, and thus lower condition than unexposed turtles. Using data on 77 loggerhead turtles obtained from the Pula aquarium in Croatia, we found preliminary evidence favoring this model prediction. Specifically, the average condition factor of eight exposed turtles is significantly lower than the average condition factor of the remaining 69 turtles (one-sided t-test, test statistic 2.35, p-value p=0.011). The empirical difference in condition factors ( $\approx$ 2) is in line with the model-predicted difference. The inset shows the estimated condition factors, including the average values and the confidence intervals obtained with the dabest package (Ho et al., 2019). Also shown is the original data in a body-mass vs. body-size plot, where the red triangles depict eight exposed individuals, while the white circles depict 69 other individuals. These turtles have been found in the Adriatic Sea and thus belong to the Mediterranean population. For comparison, gray dots depict similarly sized North Atlantic turtles (Wabnitz and Pauly, 2008).

<sup>145</sup> of 120 to 150 eggs per clutch (Tiwari and Bjorndal, 2000; Hawkes et al., 2005).

Due to the stochasticity of plastics loads, the results vary between simulation runs. Here, we illustrate one typical 146 realization. The decrease in body size of turtles exposed to plastics, who experience effective food abundance  $f_{\text{eff}}$ , 147 compared to unexposed turtles, who experience food abundance f = 0.81, is small (Fig. S5C). The small decrease in 148 body size is explained by the average effective food abundance of  $f_{\rm eff} = 0.79$  being close to f = 0.81. Favorable feeding 149 periods allow sea turtles to grow relatively large. In contrast, intermittent periods of high plastics loads worsen the 150 condition of exposed turtles throughout their lifetime (Fig. S5D). With less energy available to accumulate reserve, 151 the reproductive output declines (Fig. S5E). These results are worrying because body size in terms of carapace length 152 is the easiest to measure in practice, and thus much more often reported than body mass and fecundity, although a 153 combination of at least two of these quantities would be better indicators of the true state in the field. 154



Fig. S5. Physiological response of loggerhead turtles to time-varying plastic exposure. A, We assumed that plastic load was log-normally distributed (PD - probability distribution) with parameters  $\mu = 0.6$  and  $\sigma = 1.0$ . This produced the mean of  $%V_{dc} \approx 3\%$ , with most values being relatively small, but occasional large spikes remained possible. B, As a consequence of the assumed probability distribution for  $%V_{dc}$ , the average effective food abundance in the shown simulation was  $f_{eff} = 0.79$ . This compares to f = 0.81 for turtles unexposed to plastics. C, Because the average effective food abundance for exposed turtles was close to that for unexposed turtles, the ultimate body size of 99.3 cm straight carapace length in the scenario with time-varying exposure is close to 100.8 cm straight carapace length in the scenario. D, As in the main text, plastic ingestion affects body mass and the corresponding condition factor more strongly than body size. The displayed difference in condition factor arises because turtles exposed to plastics accumulate less reserve. Oscillations in the adult stage are due to reserve accumulation for reproduction. During a nesting season this energy is converted into eggs. Nesting seasons dccur biannually Hawkes et al. (2005). E, Reproductive output of exposed turtles is also notably lower than that of unexposed turtles. The difference varies between any two nesting seasons depending on the realized plastic load.



Fig. S6. Survival curves for North Atlantic loggerhead turtles. The curves show the probability of survival from size at hatching to size indicated on the x-axis. We obtained the curves by integrating size-dependent hazard rates found in the literature (Heppell et al., 2003; Sasso et al., 2006). The yellow curve is for unexposed turtles at food abundance f = 0.81, whereas the blue curve is for turtles exposed to plastics at effective food abundance f = 0.64. We focus on North Atlantic loggerhead turtles, but survival estimates for Mediterranean loggerheads are also available (Casale and Heppell, 2016).

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