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Shine, R., Shine, T.G., Brown, G.P. et al. (2020) Life history traits of the sea snake *Emydocephalus annulatus*, based on a 17-yr study. *Coral Reefs*, vol. 39, pp. 1407–1414. <https://doi.org/10.1007/s00338-020-01974-y>

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1 **Life history traits of the sea snake *Emydocephalus***
2 ***annulatus*, based on a 17-year study**

3
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15 **Keywords** Aipysurine · Demography · Elapidae · Hydrophiidae · Hydrophiinae

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20 Manuscript for consideration as a Report in *Coral Reefs*

21 2 April 2020

22

23 **Abstract** Although sea snakes are important predators in coral reef ecosystems, and have
24 undergone substantial population declines in some areas, we have little robust information on
25 life-histories of these animals. Based on a 17-year mark-recapture study of Turtle-headed Sea
26 Snakes (*Emydocephalus annulatus*) in New Caledonia (> 1200 individuals marked), we can
27 confidently allocate ages to 539 individuals (1 to 11 years of age). Using data for those
28 snakes, we describe patterns of growth and reproduction. Using the entire data set, we also
29 estimate annual rates of survival. One to three large offspring (300 mm snout-vent length) are
30 born after a prolonged (8-month) gestation. The young snakes grow rapidly until they are
31 about two years old (500 mm SVL), after which growth slows, especially in males. Most
32 females begin reproducing at three years of age, and they produce a litter (typically of two
33 offspring) in about two out of every three or four years thereafter. Annual survival rates are
34 around 70% but some individuals live for more than a decade. Overall, the life-history of this
35 species involves rapid growth and early maturation, followed by low but sustained
36 reproductive output. Despite their relatively recent evolutionary origin, hydrophiine sea
37 snakes are remarkably diverse in life-histories as well as in morphologies and diets. Hence,
38 even closely-related taxa may differ substantially in their vulnerability to threatening
39 processes.

40

41 **Keywords** Aipysurine · Demography · Elapidae · Hydrophiidae · Hydrophiinae

42

43 **Introduction**

44

45 Diverse and abundant in coral reefs of the IndoPacific, sea snakes play important ecological
46 roles as mesopredators (Reed et al. 2002; Ineich et al. 2007). Thus, rapid declines of
47 populations of sea snakes have raised widespread concern about the conservation status of
48 this group, and the trophic consequences of their extirpation (Udyawer et al. 2018).
49 Puzzlingly, some of those declines have occurred in areas protected from overt anthropogenic
50 impacts (e.g. Goiran and Shine 2013; Lukoschek et al. 2013). The uncertain causation for
51 population decline suggests that we urgently need to understand more about the life-histories
52 of sea snakes. For example, traits such as slow growth, delayed maturation and infrequent
53 reproduction can render a population more vulnerable to threatening processes (e.g. Reed and
54 Shine 2002; Webb et al. 2002). Unfortunately, robust information on this topic is rare for sea
55 snakes, because of the logistical challenges involved (Udyawer et al. 2018).

56 Some life-history traits (such as mean adult body sizes, mean litter sizes, proportion of
57 adult females that are reproductive when sampled) can be determined from “snapshots” – for
58 example, by dissecting snakes that are taken as bycatch by commercial trawlers (e.g. Ward
59 1996; but see Fry et al. 2001 for a discussion of possible biases due to non-random
60 catchability). Much of what we know about the ecology (especially, diets) of sea snakes has
61 been gathered in this way (e.g. Glodek and Voris 1982; Voris and Voris 1983). However, we
62 cannot truly understand the life-history (especially, traits such as age at maturation, longevity
63 and frequency of reproduction) without knowing ages as well as sizes of the animals that we
64 study. Such information can be obtained by examining growth zones in bones or otoliths, but
65 the extensive validation studies required for this method are unlikely to be feasible in free-
66 ranging sea snakes (e.g. Ward 2001).

67 The most reliable way to document age-related life-history traits in a biological
68 population is to conduct long-term mark-recapture studies, whereby the attributes and fates of
69 known individuals can be tracked through time – preferably, for at least as long as mean
70 longevity of individuals within the population (e.g. Tinkle et al. 1993). With most species of
71 sea snakes, this would require prolonged time on boats, in remote areas, working with mobile
72 and deadly animals. As a result, most long-term mark-recapture studies on marine snakes
73 have been performed on amphibious species (laticaudine sea kraits and homalopsine mud
74 snakes) where the investigators can gather data on land (e.g. Shine and Shetty 2001;
75 Brischoux and Bonnet 2009; Chim and Diong 2013). To our knowledge, there have only been
76 two published mark-recapture programs on fully aquatic (hydrophiine) sea snakes, and both
77 have relied on relatively small sample sizes (43 recaptures more than a month apart in Burns
78 and Heatwole’s (2000) study of *Aipysurus laevis*; 38 recaptures more than 300 days apart in
79 Masunaga and Ota’s (2003) study of *Emydocephalus ijimae*). The authors of those studies
80 used growth rates to estimate ages at maturation, because they did not know the ages of
81 individual snakes (apart from young-of-the-year).

82 We have taken advantage of a logistically favourable study system to conduct a long-
83 term (to date, 17-year) mark-recapture study on Turtle-headed Sea Snakes (*Emydocephalus*
84 *annulatus*) in small bays beside the city of Noumea, in New Caledonia (e.g. see Shine et al.
85 2012; Goiran et al. 2013). First, the coral-reef sites where this species lives are readily
86 accessible from shore, eliminating the need for boats. Second, accommodation and laboratory
87 facilities are available < 100 m from the study sites. Third, the water is clear and shallow,
88 facilitating snorkelling rather than requiring scuba diving. Fourth, the snake species is
89 harmless (unlike virtually all other hydrophiine species); the fangs and venom apparatus are
90 greatly reduced due to the snakes’ reliance on small fish eggs as their sole prey (e.g. Goiran et
91 al. 2013). Fifth, these snakes are remarkably philopatric (Lukoschek and Shine 2012; Shine et

92 al. 2012), and have small home ranges such that a marked snake is likely to be recaptured
93 year after year throughout its life. Reflecting those advantages, we have accumulated data on
94 more than 1200 snakes (total of > 2500 capture events) over the 17 years of our study. The
95 present analysis is based primarily on data from 539 snakes that we captured and marked in
96 their first year of life, of which 271 were recaptured in subsequent years (up to 11 years later).
97 Thus, we can confidently assign ages to these recaptured individuals. That dataset allows us
98 to quantify life-history traits in more detail than has been possible with most previous
99 research on snakes.

100

101

102 **Methods**

103

104 **Study species and area**

105 The Turtle-headed Sea Snake (*Emydocephalus annulatus*) is a relatively small (to 800 mm
106 snout-vent length [SVL], in our study population) heavy-bodied hydrophiine elapid snake
107 (Fig. 1). The species occurs in coral-reef habitats in the Timor Sea and the Coral Sea
108 (Nankivell et al. 2020) and feeds entirely on the eggs of small demersal-spawning blennies,
109 gobies and damselfish (Goiran et al. 2013). Foraging snakes use chemical cues to locate nests
110 (Shine et al. 2004) and often must overcome defence from nest-guarding fish (Goiran and
111 Shine 2015, 2020). Male snakes > 500 mm SVL focus on mate-searching and courtship
112 during winter months (Shine 2005a); female snakes > 500 mm SVL are gravid over the
113 austral summer and produce offspring in May (see below).

114 Our studies were centred on two small shallow bays (Baie des Citrons [2 sites: north and
115 south] and Anse Vata: 22°16'S, 166°26'E) beside the city of Noumea, in the Pacific
116 archipelago of New Caledonia. Water depth ranges from 1–4 m at high tide, with an average

117 tidal range of around 1.5 m (Goiran et al. 2020). The substrate consists of a mosaic of live
118 coral, coral rubble, and sand (Goiran et al. 2020). Detailed analyses have revealed few if any
119 associations between an individual snake's phenotype (size, sex, colour morph) and the
120 habitats with which it is associated (Shine et al. 2003; Goiran et al. 2020). Although our three
121 study sites are separated by < 1.5 km, individuals rarely move between sites (Lukoschek and
122 Shine 2013; Shine et al. 2012). For the present analyses, we combine data from all three sites
123 in order to maximise sample sizes.

124

125 **Methods for capturing and processing snakes**

126 Every January from 2004 to 2020 ($n = 17$ years), we have conducted mark-recapture surveys
127 of these populations by snorkelling in shallow water during daylight hours. Each site is
128 sampled about six times per annum, for 45–60 min per survey session. Teams consist of 2 to
129 14 people (but typically, around 4 to 6 people) who search for both active and inactive snakes.
130 The animals are captured by hand, and are retained in floating cages before being taken to a
131 nearby laboratory to be measured (snout-vent length), weighed, and (if not already carrying a
132 tag) individually marked by insertion of a PIT tag on the posterior lateral surface. We
133 classified snakes > 500 mm SVL as adults, based upon extensive datasets for males during the
134 courtship season (i.e., males > 500 mm SVL exhibited courtship, whereas males below this
135 size did not: e.g., Shine 2005a) and our palpations of females (i.e., almost all records of
136 gravid snakes came from animals > 500 mm SVL). Adult males can be distinguished from
137 females by a male's longer tail, more rugose skin, and rostral spine (e.g., Avolio et al. 2006;
138 Shine et al. 2012). PIT tags have been used for two of the populations (Anse Vata and Baie
139 des Citrons south) from 2004, but tags have only been used in the third site (Baie des Citrons
140 north) since 2016. Female snakes are palpated to detect and count oviductal embryos. The
141 snakes are then released at their site of capture, usually < 90 min after they were first

142 encountered. We clip a scale on the tail when a snake is processed, and do not recapture these
143 tail-marked snakes for the remainder of the trip. Thus, each snake is only captured and
144 handled once per year, to minimise stress.

145

146 **Statistical analyses**

147 Examination of size-frequency distributions of the captured snakes revealed a distinctive
148 cohort of small animals, undoubtedly young-of-the year (< 460 mm SVL: see Fig. 2). Birth
149 occurs in May (see below), so these animals are in their first year of life (on average, 8
150 months old during the January census). We assigned an age of 1 year to all animals within
151 this size range. We then allocated an age class to those snakes when we captured them in
152 subsequent years, giving us a total of 539 records for body sizes of known-age snakes, and 94
153 records for reproductive state and litter size in known-aged adult female snakes. To examine
154 how these parameters shifted with age, we plotted body sizes, reproductive frequencies
155 (proportions of gravid animals) and litter sizes against known ages.

156 We used ANOVA in JMP 13.0 to ask if the age-related variation in reproductive
157 frequency and litter size was greater than expected under the null hypothesis. To estimate
158 annual survival rate, we used the program MARK 8.2 (White and Burnham 1999) to estimate
159 survival of sea snakes based on individual mark-recapture histories, including all snakes
160 rather than only the known-age specimens. We fitted a full set of 16 Cormack-Jolly-Seber
161 (CJS) models in which survival (ϕ) and recapture rates (p) were either held constant, varied
162 between sexes, varied over time, or varied over time in a different manner for each sex. We
163 assessed the fits of the 16 CJS models by comparing their Akaike information criterion
164 (AICc) values.

165

166

167 **Results**

168

169 **Seasonal timing of gestation**

170 Many of the adult females palpated in January contained large oviductal embryos. Based on
171 dissection of occasional mortalities, we infer that ovulation occurs around September-
172 October. Parturition occurs around May, based on the appearance of neonates in the
173 population at this time (see below). Thus, gestation extends for around eight months.

174

175 **Sexual size dimorphism**

176 Both sexes attain sexual maturity at around 500 mm SVL, but adult females grow larger than
177 adult males (Fig. 2).

178

179 **Offspring size**

180 Neonates average around 300 mm SVL and 30 g in mass ($N = 12$ snakes captured 26 April to
181 30 May, mean SVL = 309.6 mm, SE = 0.47, range 290–335 mm; mean mass = 30.3 g, SE =
182 1.19, range 23–36 g).

183

184 **Growth rate**

185 Based on body lengths of known-age snakes, growth in length is rapid in both sexes until they
186 are about two years old (i.e. around 500 mm SVL). From that point on, growth is faster in
187 females than in males. Older snakes continue to increase in size for at least ten years (Fig. 3).

188

189 **Reproductive frequency in females**

190 Only one two-year-old female produced a litter (3% of the sample), but that proportion rose to
191 at least 50% in all subsequent age classes (Fig. 3b). The proportion of adult females that were
192 gravid in January averaged 68% (62 of 91 females that were at least 3 years old when
193 assessed). Excluding the single 2-year-old animal that was gravid, the proportion of
194 reproductive animals among adult females did not differ significantly among snakes of
195 different ages ($F_{6,84} = 1.26$, $P = 0.28$). In the larger data set (including snakes for which ages
196 were unknown), the proportion of adult-size females that were reproductive was 56.3% (564
197 of 1002 records).

198

199 **Litter size**

200 Palpation revealed a mean litter size of 2.01 (SE = 0.08, range = 1–3). The most common
201 litter sizes were 2 ($N = 41$, = 64% of all records) followed by 3 ($N = 12$) and 1 ($N = 11$). Litter
202 size did not change significantly with maternal age ($F_{7,56} = 1.06$, $P = 0.40$) but increased with
203 increasing maternal SVL ($N = 64$, $r^2 = 0.12$, $P < 0.003$; Fig. 3c). In the larger data set (566
204 records), litter size averaged 2.06 (SE = 0.03, range 1–4).

205

206 **Rate of annual survival**

207 Table 1 ranks the fit of the top five CJS models. The best model was one in which both
208 annual rate of survival and probability of recapture were allowed to vary among years. This
209 model fit the data overwhelmingly better than any others (all $\Delta\text{AICc} > 6$). The next three best-
210 fitting models also had the annual probability of survival modelled as time-dependant (i.e.
211 $\Phi(t)$). The sexes exhibited similar annual rates of survival: the best model that incorporated
212 separate estimates for males and females was #5 (based on ΔAICc this model was 21.98x
213 worse fit than the top model). Annual survival estimates from the top model ranged from 42

214 to 94% among years (Table 2), with a mean of 68.8% (SE = 3.3). Annual recapture
215 probabilities ranged from 42 to 69% (Table 2), with a mean of 67.0% (SE = 2.1).

216

217

218 **Discussion**

219

220 At our study sites in New Caledonia, Turtle-headed Sea Snakes exhibit seasonal patterns of
221 reproduction and hence, of parturition. Neonates grow rapidly, and typically attain sexual
222 maturity at two years of age (males) and three years of age (females). Thereafter, an adult
223 female produces litters (usually of two large offspring) in about two out of three years.
224 Females grow larger than males not because of higher survival rates, but because of higher
225 rates of growth after maturation. Broadly, these traits (size at birth, gestation period, litter
226 size, age at maturity, reproductive frequency, sexual size dimorphism) resemble those
227 reported for a congeneric species from Japan (*E. ijimae*) (Masunaga and Ota 2003; Masunaga
228 et al. 2003) but differ considerably from some other hydrophiine species. For example, Burns
229 and Heatwole (2000) inferred a later age at maturation in *Aipysurus laevis* (4 to 5 years in
230 females) and high longevity (to > 15 years). At the other extreme, some sea snakes mature
231 early and have short lifespans (*Enhydrina schistosa* [*Hydrophis schistosus*] maturation 18
232 months, lifespan to 4 years: Voris and Jayne 1979; *H. hardwickii* and *H. elegans* maturation 2
233 years, lifespan 4–5 years: Ward 2001).

234 Mean offspring size in *E. annulatus* (300 mm SVL) is similar to that in *E. ijimae* (315
235 mm SVL: Masunaga et al. 2003), as is litter size (means of 2.74 in *E. ijimae*, 2.01 in *E.*
236 *annulatus*). Using the metric of Lemen and Voris (1981), relative reproductive effort per
237 embryo in *Emydocephalus* thus is among the highest reported for any hydrophiines (around
238 10.3% for *E. ijimae*). That result fits well with extensive datasets on the allometry of

239 reproductive output in terrestrial snakes: relative to larger taxa, smaller species tend to
240 produce fewer offspring, that are larger relative to maternal body size (Shine 2005b). Adult
241 females of both *Emydocephalus* species are among the smallest sea snakes, and hence would
242 be expected to produce small litters of large offspring.

243 Previous studies have pointed out that the adaptive radiation of hydrophiine sea snakes,
244 although relatively recent, encompasses a substantial diversity in morphology (e.g. Sherratt et
245 al. 2018) and ecology (notably, diets: Voris and Voris 1983; Heatwole 1999). The examples
246 reviewed in the above paragraph suggest that the same is true of life-histories. Selective
247 forces imposed by the marine environment have favoured a constellation of traits rarely seen
248 in terrestrial snakes (notably, the infrequent production of small litters of large offspring:
249 Lemen and Voris 1981; Ward 2001) and a reduced overall investment into reproduction by
250 females (Shine 1988). Despite those pressures for convergence, however, hydrophiine species
251 vary considerably in traits such as ages at maturation, reproductive frequency, and offspring
252 sizes (see above) as well as relative clutch mass (Lemen and Voris 1981) and sexual size
253 dimorphism (Shine 1994).

254 Our study is the first to report rates of survival in any sea snake population. The annual
255 survival rate in our study population (70%) is similar to that of terrestrial snakes that mature
256 at the same age as does *E. annulatus* (i.e. 3 years; annual adult survival rates 62–80%, from a
257 1987 review by Parker and Plummer). More recent studies support this pattern: for example,
258 average annual survival rates of adult snakes were estimated as 82% for the elapid
259 *Hoplocephalus bungaroides* and 74% for the elapid *Cryptophis nigrescens* (Webb et al.
260 2002), around 70% for the viper *Vipera aspis* (Altwegg et al. 2005), and around 80% for the
261 colubrid *Drymarchon couperi* (Hyslop et al. 2012).

262 Unfortunately, comparisons across phylogenetic lineages are hampered by high levels of
263 variation within a single population. An extensive literature on the ecology of snakes has

264 documented very high flexibility in critical life history traits. For example, weather-driven
265 shifts in prey availability can massively modify not only rates of survival, but also of growth
266 and reproduction, and age at maturation (e.g. Madsen and Shine 2000; Brown and Shine
267 2007; Ujvari et al. 2010). Strong temporal shifts (declines) in the abundance of sea snakes
268 (e.g. Lukoschek et al. 2013) suggest that rates of survival are similarly variable in marine
269 reptiles. In keeping with that inference, annual rates of survival estimated from our own study
270 varied strongly among years (42–94%: see Table 2). That high level of variation of survival
271 rates through space and time means that current data on survival (and perhaps other life-
272 history traits) do not allow robust overall comparisons between terrestrial and marine snakes.

273 Nonetheless, the high levels of variation in survival rates through space and time, as well
274 as substantial interspecific (and in some cases, intraspecific: Lemen and Voris 1981) variation
275 in traits such as fecundity and frequency of reproduction, are likely to engender corresponding
276 variation in the vulnerability of sea snake populations to threatening processes such as
277 pollution, predation, overexploitation and coral bleaching. As a result, managers have only
278 limited ability to predict which taxa are most likely to be at risk. The recent expansion of
279 fundamental research into the biology of sea snakes is encouraging, but major knowledge
280 gaps remain (see Udyawer et al. 2018). Until we know far more about these mysterious
281 marine organisms, we are poorly-placed to predict and mitigate the impacts of anthropogenic
282 modifications to oceanic environments.

283

284 **Acknowledgements** Our studies were funded by the Australian Research Council (grant
285 FL120100074 to RS). We thank the many volunteers who have helped us to catch snakes over
286 the years, notably Terri, Mac and Ben Shine, Heather Zimmerman, Mariella Dunaj, Francois
287 Brischoux, Troy and Teresa Baird, David Pike, Betsy Roznick, Reid Tingley, Cassey
288 Flanagan, Vinay Udyawer, Tyffen Read, Rafael Valente-Teixeira, Marine Marziac, Fabien

289 Sraui, and Grégoire Maniel. We also thank Pierre Laboute, Richard Farman and all the staff
290 of Aquarium des Lagons, and the Fantastic Grandmothers Citizen Science group for
291 assistance and support over the course of our research.

292

293 **Compliance with ethical standards**

294 All procedures with live animals conformed to international guidelines for animal welfare,
295 and were approved by the University of Sydney Animal Care and Ethics Committee (approval
296 # L04/6-2005/3/4111). Our research was also approved by the relevant wildlife management
297 authority in the Southern Province of New Caledonia (permit 34756-2019-3REP/DENV).

298

299 **Conflict of interest**

300 All authors declare no competing interests.

301

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411 **Figure legends**

412

413 **Fig. 1** Turtle-headed Sea Snake (*Emydocephalus annulatus*). Photograph by C. Goiran

414

415 **Fig. 2** Frequency distributions of body size (snout-vent length) in Turtle-headed Sea Snakes

416 (*Emydocephalus annulatus*). **a** Body sizes of all snakes combined ($N = 2406$), **b** Body sizes of

417 adult females ($N = 1005$), and **c** body sizes of adult males ($N = 945$). The number on the X-

418 axis represents the lower limit of each size category (e.g., “300” shows data for snakes

419 between 300 and 320 mm SVL)

420

421 **Fig. 3** Effects of age on **a** mean body size, **b** reproductive frequency in adult females, and **c**

422 mean litter size in known-age (individually marked) Turtle-headed Sea Snakes

423 (*Emydocephalus annulatus*). Vertical bars show standard errors

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