

 Open access • Journal Article • DOI:10.1111/1365-2656.13095

Demographic plasticity facilitates ecological and economic resilience in a commercially important reef fish — [Source link](#)

Brett M. Taylor, Brett M. Taylor, John Howard Choat, Edward E. DeMartini ...+5 more authors

Institutions: Joint Institute for Marine and Atmospheric Research, Australian Institute of Marine Science, James Cook University, University of Hawaii ...+2 more institutions

Published on: 01 Dec 2019 - Journal of Animal Ecology (Wiley-Blackwell)

Topics: Population and Population model

Related papers:

- [Latitudinal variation in lifespan within species is explained by the metabolic theory of ecology](#)
- [Temperature and Organism Size—A Biological Law for Ectotherms?](#)
- [Temperature-related variation in growth rate, size, maturation and life span in a marine herbivorous fish over a latitudinal gradient](#)
- [Inter-oceanic analysis of demographic variation in a widely distributed Indo-Pacific coral reef fish](#)
- [Environmental and fishery-induced effects on life histories and assemblages of parrotfishes](#)

Share this paper:    

View more about this paper here: <https://typeset.io/papers/demographic-plasticity-facilitates-ecological-and-economic-3mjzhws50u>

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29

DR BRETT M TAYLOR (Orcid ID : 0000-0002-4746-7228)

Article type : Research Article

Demographic plasticity facilitates ecological and economic resilience in a commercially important reef fish

Brett M. Taylor^{1,2*}, J. Howard Choat³, Edward E. DeMartini⁴, Andrew S. Hoey⁵, Alyssa Marshall⁶, Mark A. Priest⁷, Kevin L. Rhodes⁸ Mark G. Meekan¹

¹Australian Institute of Marine Science, Crawley, Western Australia, Australia

²Joint Institute for Marine and Atmospheric Research, University of Hawaii and NOAA Pacific Islands Fisheries Science Center, Honolulu, Hawaii, USA

³College of Science and Engineering, James Cook University, Townsville, QLD, Australia

⁴Hawaii Institute of Marine Biology, University of Hawaii, Kaneohe, HI, USA

⁵ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD, Australia

⁶Department of Marine Science and Fisheries, College of Agricultural and Marine Science, Sultan Qaboos University, Muscat, Oman

⁷School of Biological Sciences, University of Queensland, Brisbane, QLD, Australia

⁸MarAlliance, Grass Valley, CA, USA

*Corresponding author: b.taylor@aims.gov.au

Running title: Demographic plasticity in a coral reef fish

Abstract

This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the [Version of Record](#). Please cite this article as [doi: 10.1111/1365-2656.13095](https://doi.org/10.1111/1365-2656.13095)

This article is protected by copyright. All rights reserved

30 **1.** Variation in life-history characteristics is evident within and across animal populations.
31 Such variation is mediated by environmental gradients and reflects metabolic constraints or
32 trade-offs that enhance reproductive outputs. While generalizations of life-history
33 relationships across species provide a framework for predicting vulnerability to
34 overexploitation, deciphering patterns of intraspecific variation may also enable recognition
35 of peculiar features of populations that facilitate ecological resilience.

36 **2.** This study combines age-based biological data from geographically disparate populations
37 of bluespine unicornfish (*Naso unicornis*)—the most commercially-valuable reef-associated
38 species in the insular Indo-Pacific—to explore the magnitude and drivers of variation in life
39 span and examine the mechanisms enabling peculiar mortality schedules.

40 **3.** Longevity and mortality schedules were investigated across eleven locations encompassing
41 a range of latitudes and exploitation levels. The presence of different growth types was
42 examined using back-calculated growth histories from otoliths. Growth-type dependent
43 mortality (mortality rates associated with particular growth trajectories) was corroborated
44 using population models that incorporated size-dependent competition.

45 **4.** We found a threefold geographic variation in life span that was strongly linked to
46 temperature, but not to anthropogenic pressure or ocean productivity. All populations
47 consistently displayed a two-phase mortality schedule, with higher than expected natural
48 mortality rates in earlier stages of post-settlement life. Reconstructed growth histories and
49 population models demonstrated that variable growth types within populations can yield this
50 peculiar biphasic mortality schedule, where fast growers enjoy early reproductive outputs at
51 the expense of greater mortality, and benefits for slow growers derive from extended
52 reproductive outputs over a greater number of annual cycles. This promotes population
53 resilience because individuals can take advantage of cycles of environmental change
54 operating at both short and long-term scales.

55 **5.** Our results highlight a prevailing, fundamental misperception when comparing the life
56 histories of long-lived tropical ectotherms: the seemingly incongruent combination of
57 extended life spans with high mortality rates was enabled by coexistence of variable growth
58 types in a population. Thus a demographic profile incorporating contrasting growth and
59 mortality strategies obscures the demographic effects of harvest across space or time in *N.*
60 *unicornis* and possibly other ectotherms with the combination of longevity and asymptotic
61 growth.

62

63 **Key-words:** Acanthuridae, coral-reef fish, ectotherm, life span, mortality, unicornfish,
64 biogeography, growth plasticity, *Naso unicornis*

65

66

67 **Introduction**

68 Variation in life-history traits among individuals within a population is prevalent in
69 common, widespread species as it offers flexibility to adapt to a range of environmental
70 conditions (Bradshaw, 1965). In ectotherms, life span often increases with latitude because
71 metabolism slows at lower temperatures (i.e., oxygen consumption, protein synthesis and
72 energy flow are reduced; Clarke & Johnston, 2002). This relationship can be explained by the
73 metabolic theory of ecology (Brown, Gillooly, Allen, Savage, & West 2004; Munch &
74 Salinas, 2009), and reflects the longer-term thermodynamic costs of growth (Clarke, 2017).
75 However, variation in traits such as growth performance, reproductive output, and life span
76 also occurs within a population due to differences in temperature, resource availability, and
77 competition experienced by individuals. This variation is constrained by trade-offs that
78 optimize lifetime reproductive outputs for individuals and, collectively, for populations
79 (Stearns, 1976; Trip, Clements, Raubenheimer, & Choat, 2014).

80 The growth and condition of individuals within ectothermic populations is largely
81 mediated by the environmental and social conditions to which they are exposed. Fast growth,
82 and hence larger body size, generally facilitates a greater competitive advantage and lower
83 predation risk to individuals compared with smaller members of a cohort, thereby reducing
84 the overall risk of mortality (Sogard, 1997), but is often associated with reduced life span
85 (Metcalf & Monaghan, 2003). This somewhat counterintuitive pattern highlights the trade-
86 offs that occur among demographic traits (Arendt, 1997). For example, garter snake
87 populations have been shown to support demographic variants that include both fast- and
88 slow-growing individuals (Bronikowski & Arnold, 1999; Bronikowski & Vleck, 2010). In
89 these populations, fast-growing individuals had higher rates of mass-specific resting
90 metabolism and mortality, as well as larger body size, earlier maturation, and a high
91 reproductive output. Slow-growing individuals showed the opposite trends of smaller body
92 size, late maturation, and low reproductive output, along with increased longevity. Such
93 variation in traits is also evident in coral reef fishes exposed to marked environmental
94 variation across relatively small spatial scales (10s of km; Gust, Choat, & Ackerman, 2002;
95 Taylor et al., 2018).

96 Under intense natural selection, particular phenotypes will be favoured for survival
97 (Kingsolver & Pfennig, 2007). For traits under disruptive selection, whereby individuals with
98 extreme trait values have the greatest fitness, a wide range of phenotypes will evolve. If the
99 selective forces acting on fast and slow growth stabilize one another (by producing equal
100 lifetime reproductive values, similar to alternative reproductive strategies within
101 populations), then multiple growth types can be retained through high phenotypic variation
102 (e.g., Rios-Cardenas, Bono, & Morris, 2018; Weinstein et al., 2019). Additionally, for long-
103 lived species, trade-offs between growth, mortality, and longevity described above (growth-
104 type dependent mortality) may favour a range of phenotypes when environmental conditions
105 affecting juvenile recruitment and survival vary over time (Warner & Chesson, 1985).

106 Growth-type dependent mortality within populations can result in highly asymptotic
107 length-at-age relationships of populations, with the oldest individuals often having a smaller
108 mean length (slower growth) than younger individuals that are approaching maximum body
109 size more rapidly (Mulligan & Leaman, 1992). This pattern reflects changes in the
110 demographic composition of cohorts across ages and the delayed senescence of slow-growing
111 individuals, rather than a true picture of average growth trajectories. Such a bias may also be
112 evident through instantaneous measures of cohort survivorship, which can yield unusual
113 patterns of mortality across adult age classes (e.g., Meekan, Ackerman, & Wellington, 2001;
114 Robertson, Ackerman, Choat, Posada, & Pitt, 2005). For such species, an understanding of
115 patterns of growth and mortality within populations is essential for appropriate management,
116 particularly where the species are the target of commercial harvest (e.g., fisheries).
117 Furthermore, such studies also facilitate a greater understanding of processes leading to
118 evolutionary persistence (Mulligan & Leaman, 1992).

119 The bluespine unicornfish *Naso unicornis* is a coral reef-associated species
120 preferentially targeted by fishing across the insular Pacific (Hoey & Bellwood, 2009; Taylor,
121 2019). Several studies and formal stock assessments based on inferred life-history traits have
122 characterized *N. unicornis* as among the most vulnerable species to overexploitation in
123 multispecies fisheries in the western Pacific (e.g., Houk et al., 2012; Bejarano, Golbuu,
124 Sapolu, & Mumby, 2013; Nadon, Ault, Williams, Smith, & DiNardo, 2015). However,
125 despite the dominance of this species in regional fisheries, there is very limited spatial or
126 temporal evidence of demographic shifts (e.g., decreases in harvested length or proportion of
127 fishery catch) that might result from overfishing (Ford, Bejarano, Marshall, & Mumby, 2016;
128 Houk, Cuetos-Bueno, Tibbatts, & Gutierrez, 2018; Rhodes et al., 2018). Earlier life-history
129 studies of *N. unicornis* identified an unusual pattern of mortality in both exploited (Taylor,

130 Rhodes, Marshall, & McIlwain, 2014; Andrews et al., 2016) and unexploited populations
131 (Choat & Axe, 1996) whereby initial adult-stage mortality was high, but then abruptly
132 decreased, resulting in a two-phase mortality profile across age classes that results in the
133 atypical combination of high mortality and long life span. The spatial ubiquity of this pattern,
134 as well as its potential drivers, are unknown.

135 Here, we compiled a large data set of published and previously unpublished age-based
136 demographic information for *N. unicornis* from 20 islands and atolls across the Western,
137 Central, and South Pacific and Central Indian Oceans. Our study had two major objectives.
138 The first examined the influence of anthropogenic pressure and environmental differences
139 among locations on variability in life span of the species. Prevailing metabolic theory posits
140 that increasing temperature will negatively influence life span (Munch & Salinas, 2009).
141 However, fishery exploitation may have an over-arching effect, whereby any relationship
142 between temperature and life span is obscured by variability in human extraction, given the
143 capacity for fishery-induced age truncation in taxa that are long-lived and harvested heavily
144 (e.g., Beamish, McFarlane, & Benson, 2006). The second objective explored patterns of adult
145 mortality among locations that ranged across a large gradient of human population densities.
146 We examined the intrinsic biological characteristics (e.g., growth-type dependent mortality)
147 that facilitated population-level longevity, variable mortality profiles across age classes, and
148 the evolutionary implications of variable life-history strategies within populations. To
149 achieve this goal, we used an analysis of patterns of otolith increment-width (a proxy for
150 somatic growth) to test the hypothesis that fast growers died young, whereas the slowest-
151 growing individuals attained the oldest ages in a population (Mulligan & Leaman, 1992;
152 Metcalfe & Monaghan, 2003). We followed this with a population model that examined the
153 potential contribution of size-dependent mortality towards population-level biphasic mortality
154 profiles. Finally, we evaluated the results in the context of multispecies fisheries management
155 and the ecological significance of variable life-history traits within species.

156

157 **Materials and methods**

158 To assess the generality of life-history characteristics and geographic variation in age-
159 based demography, we collated age-based biological data (i.e., annualized fish ages and
160 associated body length measurements) derived from sectioned otoliths (ear stones) for *N.*
161 *unicornis* from 20 islands and atolls, geographically summarized into 11 locations across the
162 Indo-Pacific region (Fig. 1). Specimens were collected using fishery-dependent or -

163 independent sampling protocols (Table 1; expanded sampling methods are provided in the
164 Supporting Information).

165

166 PREDICTORS OF LIFE SPAN

167 We estimated the life span *N. unicornis* at each location using the maximum age
168 derived from sectioned otoliths. Maximum derived age was validated by bomb radiocarbon
169 analysis of micro-milled cores of otoliths of Oahu specimens (Andrews et al., 2016). This
170 method provides a defensible estimate of life span when derived from large sample sizes
171 (Kritzer, Davies, & Mapstone, 2001; Hoenig, 2017). Here, we used age data from 2603
172 individuals from the eleven locations, with a range of 61-533 samples per location (mean 229
173 ± 153 S.D.). On average, this level of sampling yielded 9.2 specimen samples per age class
174 across locations, which falls within the acceptable level of precision (7-10 per age class)
175 proposed by Kritzer, Davies, and Mapstone (2001). We note that sample sizes for four
176 locations (Chagos Archipelago, Mariana Trench Marine National Monument, Northern
177 Mariana Islands, and Yap) fall below this proposed sample level (2.4-4.5 samples per age
178 class. However, these four locations are either unfished or had the lowest human density
179 among populated locations (Yap); thus, sampling efforts at these locations, where fishing
180 pressure is low to nonexistent, have an inherently higher likelihood of capturing the oldest
181 age classes. Ultimately, this method was used to approximate rather than directly measure life
182 span. Techniques for sectioning and interpreting otoliths not documented in the literature
183 followed Taylor, Rhodes, Marshall, & McIlwain (2014). All otoliths from published studies
184 (Choat & Axe, 1996; Taylor, Rhodes, Marshall, & McIlwain, 2014; Andrews et al., 2016)
185 were re-examined by the lead author for consistency in reading across locations.

186 Measures of environmental variables sea surface temperature (SST; °C) and
187 chlorophyll-a productivity (Chl-*a*; g C m³) for each location were derived from remotely
188 sensed data. For SST, we calculated the average annual temperature (SST_A), the average
189 temperature from the coldest month of the year (SST_L), and the average temperature from the
190 warmest month of the year (SST_H) using the Global High Resolution Blended SST database
191 from the NOAA ERDDAP website (1-day composite; 0.0879° resolution) from Jan 2006 to
192 May 2011. For Chl-*a*, we used the Aqua MODIS Global 4 km database to derive the mean
193 Chl-*a* value across the period Jan 2006 to Jul 2018. Finally, we calculated human density for
194 each location by dividing the 2010 census population by total coral reef area <30 m deep
195 (km²). We then examined the relationships between explanatory variables and life span
196 estimates using linear models, fitted to raw data across locations using least squares

197 estimation. We used single predictor models given the limited number of data points and
198 compared these models using Akaike's Information Criterion (AIC).

199

200 POPULATION DYNAMICS AND DEMOGRAPHIC STRUCTURE

201 We explored mortality schedules (patterns of instantaneous mortality across age
202 classes) by fitting age-based catch curves to the natural-log-transformed frequencies of age
203 classes for each location (Ricker, 1975). This standard technique linearizes the exponential
204 decay of survivors across age classes, so that the slope of a linear model fitted to the
205 descending limb of the curve estimates the instantaneous mortality rate. Age classes with no
206 sampled individuals or those considered not fully recruited to the fishery or scientific
207 sampling (i.e., age classes younger than the peak in the age-frequency distribution) were
208 omitted from the analysis. We interpreted the slope of the linear fit as representing the
209 instantaneous total annual mortality rate (Z). Initial inspection of catch curves revealed non-
210 linear mortality schedules at all locations, with residuals conforming to a U-shaped pattern
211 across ages, suggesting a two-phase mortality schedule (Figure S1, Supporting information).
212 Consequently, we used a breakpoint analysis (Zeileis, Leisch, Hornik, & Kleiber, 2002) to
213 establish the optimal breakpoint (i.e., age at which mortality schedules shift) for data from
214 each location followed by analysis of covariance to test whether the slopes before and after
215 the breakpoint were significantly different. This analysis fitted two independent lines on
216 either side of the optimal breakpoint; therefore, we also modeled mortality using a segmented
217 analysis (Muggeo, 2008) that generates a continuous two-phase model joined at the
218 breakpoint. We note that linear catch curve analysis is based on the assumption of constant
219 annual recruitment. Species of the genus *Naso* can experience episodes of mass recruitment
220 (e.g., Doherty et al., 2004) which may bias estimates of mortality rates considerably.
221 However, our analysis does not focus on mortality rate values, but rather on mortality profiles
222 across the life span of a population. We further expect our results to be buffered by long life
223 spans (ranging 20-50 years among locations) and multiyear collections for seven of the
224 eleven locations (Supporting Information).

225 A two-phase mortality schedule that does not delineate major life phases (e.g.,
226 metamorphosis from pelagic phase or onset of sexual maturation) could reflect either a biased
227 sampling protocol or an intrinsic biological phenomenon. Our sampling protocols varied
228 between fishery-dependent (stratified random market sampling) and fishery-independent
229 (spearfishing during research cruises) among populations, and we have no reason to suspect
230 that an aspect of all the sample collections would facilitate a consistent bias. Hence, we set

231 out to test the hypothesis that initial growth trajectories within populations yielded different
232 life span potentials that resulted in a distinct change in natural mortality rates across age
233 classes. Specifically, we hypothesized that fast-growing fish had shorter life spans than slow-
234 growing fish (mechanisms reviewed in Metcalfe & Monaghan, 2003), such that the oldest
235 fish in a population were exclusively derived from slow-growing individuals. Individual
236 growth histories and life spans cannot be determined from length-at-age data alone (Mulligan
237 & Leaman, 1992). Therefore, to test this hypothesis and its feasibility in relation to
238 population dynamics, we (1) examined annual increment width profiles in four of the five
239 longest-lived populations (Oahu, Marianas Trench Marine National Monument [MTMNM],
240 Northern Mariana Islands [NMI], and Chagos Archipelago) as a proxy for somatic growth
241 histories of fish (Campana, 1990) and (2) constructed simple population models exploring the
242 effects of variable growth profiles on population dynamics. For the first objective, we
243 selected fish specimens from the smaller (slow grower) and larger (fast grower) ends of the
244 age-specific length distribution, as well as old fish (representatives from the oldest age
245 classes with appropriate otolith clarity for high-resolution measurements) for increment-
246 width analysis. Slow and fast growers were taken from age classes displaying a high adult
247 growth trajectory, implying that fish could only reach those length-age combinations through
248 slower or faster initial growth compared with the rest of the population. Pre-settlement
249 growth (pelagic phase from hatching to reef settlement) and the first ten years of post-
250 settlement otolith growth were measured and summarized by growth type for each location
251 separately. Our hypothesis posits that slow-growing and old fish would have invariant
252 increment-width profiles across stages in their early life history, whereas increment widths of
253 fast-growing fish would differ across some stage in their early life history. This hypothesis
254 stems from studies that show that early growth rate is the best predictor of adult mortality,
255 with slow growth being associated with the longest life expectancy (Metcalfe & Monaghan,
256 2003). Age-specific analysis of variance tests were used to explore differences in increment
257 widths among growth types.

258 For the population model, we interpreted life-history traits based on the upper and
259 lower limits of the growth curve distribution (fast versus slow growers) separately for the
260 Oahu sample and the combined Mariana Archipelago samples (MTMNM and NMI were
261 pooled to provide adequate sample sizes of growth and reproductive output data). Doing so
262 effectively splits the populations into two growth types with associated errors (Table S1,
263 Supporting information), with growth modelled using the von Bertalanffy growth function:

264
$$L_t = L_\infty[1 - e^{-k(t - t_0)}],$$

265 eqn1

266 where L_t is the predicted length at age t (years), L_∞ represents the asymptotic length, k is the
 267 growth coefficient, and t_0 is the hypothetical age at which length is equal to zero. These
 268 growth types had considerable overlap in length-at-age profiles, thereby reflecting the
 269 continuum of growth rates and the natural variation observed in the populations on which our
 270 models were based. Life-history theory suggests that variable growth types can be maintained
 271 within a population if reproductive output is approximately the same among the growth types.
 272 Our model assumed that only slow-growers reached the oldest age classes and we chose a
 273 maximum age for fast growers informed from the breakpoint analysis from mortality profiles
 274 and overall life span (average breakpoint at ~40% of lifespan). Natural mortality rates (M) for
 275 both growth types were estimated based on established relationships with life span (Then,
 276 Hoenig, Hall, & Hewitt, 2014; $M = 4.899[\text{maximum life span}]^{-0.916}$), presuming maximum
 277 ages of 50 years (Oahu, slow growers), 20 years (Oahu, fast growers), 40 years (Mariana
 278 Archipelago, slow growers), and 15 years (Mariana Archipelago, fast growers). Population
 279 decay across age classes was calculated using the standard exponential decay equation:

280
$$N_{t+1} = N_t e^{-M}$$

281 eqn2

282 where N represents population size, t represents age class, and M represents the instantaneous
 283 natural mortality rate. To estimate reproductive output, we then modelled the relationship
 284 between fork length and female ovary weight (OW ; Supporting Information) and multiplied
 285 the length-specific OW by cohort survivorship (the relationship between OW and fork length
 286 did not differ between growth types based on empirical data). The ovary weight \times
 287 survivorship values were summed across age classes from the age at maturity (t_{mat}) to the
 288 maximum age (t_{max}) and considered a proxy for total reproductive output (RO) of a cohort:

289
$$RO = \sum_{t=t_{mat}}^{t_{max}} N_t OW_t$$

290 eqn3

291 In this scenario, we therefore used total mass of propagules through a cohort's existence to
 292 represent reproductive output. We acknowledge that changes in egg size or spawning
 293 frequency across different body sizes may affect actual reproductive value, but this
 294 information was not available for any population in this study. The model assumed an equal
 295 number of fast- and slow-growing recruits in a cohort. Finally, we included an additional

296 mortality factor (percentage relative to M) for slow-growing recruits during the age classes
297 that overlapped with the life span of fast growers, to represent increased mortality from
298 competition with faster-growing individuals and increased predation risk. We used an
299 optimization procedure on this additional mortality factor to find the scenario that yielded
300 equal lifetime reproductive output estimates from fast-growing and slow-growing
301 components of a cohort across their respective life spans.

302

303 **Results**

304 We found a remarkably strong relationship between SST and life span, with the
305 average temperature of the coldest month (SST_L) being the predictor that explained the most
306 variation (Fig. 2). Although life span estimates ranged widely from 16 to 52 years, SST_L
307 explained 83% of the variation across locations ($F_{1,9} = 44.82$, $P < 0.0001$, $AIC = 68.52$). All
308 locations were oceanic island systems except for Lizard Island, Great Barrier Reef, which
309 was a high island on a continental shelf. Sampling at Lizard Island provided an outlier in the
310 data set, and removal of this point improved the correlation to 93% of variance explained
311 ($F_{1,8} = 111.34$, $P < 0.0001$, $AIC = 54.56$). Human density (a proxy for anthropogenic
312 pressure) had no relationship with life span ($F_{1,9} = 3.88$, $P = 0.0804$, $AIC = 84.26$). Chl-*a*
313 (natural log-transformed) also did not correlate with life span ($F_{1,9} = 0.44$, $P = 0.5234$, $AIC =$
314 87.67).

315 Despite the variability in life span, we observed two-phase mortality schedules of
316 varying intensity in all populations, whereby a breakpoint occurred somewhere between 7 to
317 20 years (Fig. 3). The change in slope before and after the optimal breakpoint was significant
318 at all of the locations (Table S2, Supporting information), with the exception of the Northern
319 Mariana Islands. The instantaneous mortality rate prior to the breakpoint ranged from 1.5 to
320 24.8 times higher than the later part of the life span across locations (comparing disjunct fits
321 here as they are not constrained by one another). The difference in slopes between parts of
322 the mortality schedule was not significantly related to temperature (linear model; $F_{1,10} = 2.05$,
323 $P = 0.19$), anthropogenic pressure ($F_{1,10} = 0.06$, $P = 0.82$), or Chl-*a* ($F_{1,10} = 0.45$, $P = 0.52$).

324 Increment-widths (Fig. 4a) were derived for slow-growing, fast-growing, and old fish
325 (Fig. 4b) across the first ten years of life. For the four populations examined, increment-width
326 profiles were very similar during pre-settlement growth and across the first ten years for
327 slow-growing and old fish, but growth during year 1 was significantly greater for fast-
328 growing fish (Fig. 4c). Although fast-growing fish also had significantly larger increment
329 widths for other age classes at Oahu and the Northern Mariana Islands, the large and

330 consistent disparity at year 1 across populations confirms that fast-growing fish attained the
331 majority of their growth advantage in the first year after settlement (i.e., growth potential is
332 not predetermined during the pelagic phase). Further, the comparisons of increment-width
333 profiles between growth types and old fish provide strong support for the hypothesis that the
334 oldest fish are represented by survivors among the slowest-growing individuals, thus that
335 fast-growing fish die young.

336 Our population models independently integrated two growth extremes based on
337 empirical data from Oahu and the Mariana Archipelago. Fig. 5a displays the simulated
338 length-at-age information for each growth type for the Oahu population. By integrating the
339 relationship between ovary weight and fork length (Fig. 5b) across natural population decay,
340 we determined that fast-growing and slow-growing cohorts can reach the same lifetime
341 reproductive value when intraspecific competition and predation increase natural mortality of
342 the slow growers by approximately 60% at Oahu and 35% in the Mariana Archipelago. This
343 scenario results in a two-phase mortality schedule similar to the low end observed from
344 empirical data, whereby natural mortality of all growth types combined is nearly doubled
345 during the life span of the fast-growing fish (Fig. 5a; Fig. S2, Supporting information).
346 Because fast-growing fish mature earlier and reach larger sizes faster, their reproductive
347 output is much greater than slow-growing fish in the first ten years (Fig. 5c; Fig. S2,
348 Supporting information).

349

350 **4 | Discussion**

351 Contemporary tropical fisheries assessments are often data-poor and based on
352 assumed geographically invariable values for life-history traits. Here, we showed two
353 phenomena that influenced the life history of the commercially-important bluespine
354 unicornfish, *N. unicornis*, that challenge such assumptions. We found a significant and strong
355 relationship between sea surface temperature and life span, whereby warmer water yielded
356 shorter-lived populations. This is predicted by metabolic theory and supports previous
357 evidence demonstrating high variability in longevity strongly linked to ambient temperature
358 in other acanthurid reef fishes and more generally in ectotherms (Robertson, Ackerman,
359 Choat, Posada, & Pitt 2005, Munch & Salinas, 2009). Failing to account for this relationship
360 in fishery models results in gross over- or under-estimates of exploitation, mortality, and
361 yield. The second phenomenon was the presence of a two-phase mortality schedule, common
362 across all locations examined. This suggests that metabolic trade-offs between growth rates
363 and life spans are conserved within populations irrespective of geographic location.

364 The wide variation in life span recorded across a latitudinal gradient is consistent with
365 the metabolic theory of ecology (Brown, Gillooly, Allen, Savage, & West, 2004; Munch &
366 Salinas, 2009), and is reflective of trade-offs between thermally-enhanced growth and
367 reproductive life span (Trip, Clements, Raubenheimer, & Choat, 2014). Other studies have
368 found a similar threefold change in life span of primary consumers that is tightly correlated
369 with temperature (Robertson, Ackerman, Choat, Posada, & Pitt, 2005; Taylor, Trip, & Choat,
370 2018). For the ocean surgeonfish *Acanthurus bahianus*, temperature had a much stronger
371 influence on life span than it did on either growth rate or body size, but all three were
372 inversely related to temperature (Robertson, Ackerman, Choat, Posada, & Pitt, 2005). These
373 authors also highlighted trade-offs with reproduction, whereby frequency of spawning
374 activity generally decreased with declining temperature. Despite the broad geographic
375 patterns documenting decreased life span with increased environmental temperature in both
376 ectotherms and endotherms, the proximal mechanism underlying variation in life span is still
377 debated (Speakman, 2005). Analysis of ectothermic species, however, consistently indicates a
378 complex integration of thermal constraints on growth in which higher temperatures at low
379 latitudes elicit faster growth through more efficient protein synthesis (Clarke, 2017) despite
380 the physiological costs of higher metabolic demands on life span (Metcalf & Monaghan,
381 2003).

382 Our results support the hypothesis that intraspecific variation in growth rates within
383 cohorts of *N. unicornis* drives observed patterns of biphasic mortality. Differential growth
384 rates in the pre-maturational and early reproductive phases of the benthic life cycle – as
385 observed through otolith increment width patterns – were clearly linked to variation in
386 mortality rates and maximum life spans in the sampled populations. Individuals with slower
387 initial growth rates lived longer than those with faster initial growth rates. Differential growth
388 rates within a cohort will have impacts on reproductive demography, as fast growth is
389 associated with earlier maturation and greater reproductive outputs compared with slow
390 growth in a cohort. Moreover, enhanced growth rate and the associated increases in size
391 would confer advantages in terms of intra-specific competition and reduced predation risk
392 compared with other members of a cohort. However, fast growth and the resulting large body
393 size require greater metabolic demands (i.e., energy expenditure), and although these features
394 generally yield greater reproductive output and a competitive advantage, greater metabolic
395 demands eventually bring a growth cost resulting in early senescence (Speakman, 2005).
396 Ultimately, when selection pressures yield benefits for different growth types, a wide variety

397 of phenotypes can be retained within populations. This concept in population demography is
398 analogous to portfolio effects in ecological systems.

399 Our population model implies that a species will only evolve biphasic mortality
400 schedules if slow-growing fish are subjected to a factor that induces additional mortality
401 during the period when they co-occur with shorter-lived fast growers. This additional factor is
402 on the order of a 30-60% greater mortality rate (relative to natural mortality predicted from
403 life span) and presumably stems from lower capacity for successful competition and greater
404 predation risk among smaller-bodied individuals. Empirical field tests support this range as a
405 realistic estimate. For instance, demography of newly settled fairy basslets (*Gramma loreto*)
406 on patch reefs was heavily influenced by the density of older/larger individuals (Webster,
407 2004). Greater abundance of larger conspecifics both reduced feeding rates (by up to 60%)
408 and increased predation risk of juveniles, with mortality doubling in the presence of high
409 adult densities (Webster & Hixon, 2000; Webster, 2004). Hixon & Jones (2005), in a multi-
410 year study, found that intraspecific competition was the primary driver of density-dependent
411 mortality. Within a cohort, density-dependent effects were lagged across time, only emerging
412 once body-size distributions widened because of variability in individual growth profiles,
413 suggesting size-based competitive advantages. Overall, patterns of mortality dependent on
414 body size appear to be common among marine fishes, with extreme examples demonstrating
415 greater survival of larger-bodied conspecifics by factors up to nearly 40 (Sogard, 1997).

416 The demographic benefits for fast-growing individuals of earlier maturation and
417 greater competitive abilities within the cohort are properties that might be beneficial if
418 sequential cohorts are confronted by a habitat characterised by a high degree of patchiness on
419 a local scale. Under these circumstances, individuals could exploit patches of high quality
420 food resources, with rapid growth and early maturation leading to enhanced reproductive
421 outputs. Empirical measurements of larval dispersal show high levels of larval retention
422 regardless of a species' early life-history characteristics (Jones, 2015). Such retention would
423 ensure that successful offspring would be able to take advantage of the conditions that
424 provided for increased reproductive output in the parental generation, whereas the long larval
425 pelagic duration of *N. unicornis* (~71-75 d; Doherty et al., 2004; Andrews et al. 2016) affords
426 the potential to exploit new and distant habitats (Horne, van Herwerden, Abellana, &
427 McIlwain, 2013). However, the oceanic and near reef conditions that strongly influence the
428 success of larval cohorts may vary considerably on decadal scales, and are implicated in
429 generating highly successful year classes (Bergenius, McCormick, Meekan, & Robertson,
430 2005). This is supported in reef fishes of the genus *Naso* that are characterised by episodes of

431 mass recruitment (Doherty et al., 2004). Longevity at the scale observed in acanthurid fishes
432 (3-4 decades post maturation) provides the opportunity for some offspring to experience the
433 oceanic conditions that are outstandingly favourable to larval success that occur at decadal
434 time scales. This represents a variant of the storage effect (Warner & Chesson, 1985) in
435 which slow-growing but long-lived individuals may secure the benefits of favourable
436 conditions for larval settlement and recruitment that occur only episodically. The argument
437 predicts a trade-off between rapid initial growth and maturation versus slower growth with an
438 extended life span that provides opportunity to contribute to numerous annual spawning
439 episodes (Metcalfé & Monaghan, 2003), with both variants retained within discrete
440 geographic populations.

441 It remains unclear if the proximal driver of growth variation among *N. unicornis*
442 populations is inherently genetic, reflects the environmental variability to which individuals
443 are exposed, or represents both factors to some spatially or temporally variable extent. At
444 present the information that would allow us to determine if the different demographic modes
445 represent historical divergences due to adaptation are elusive. However, the increasing
446 evidence of fine-scale demographic variation in other fishes and the possibility that this may
447 reflect ecological speciation (Roney, Oomen, Knutsen, Olsen, & Hutchings, 2018) shows that
448 the mechanisms underlying intra-population diversification of life histories in reef fishes
449 deserve further investigation.

450 Life-history traits have proven to be powerful predictors of vulnerability to
451 overexploitation in a wide variety of harvested fishes (Jennings, Greenstreet, & Reynolds,
452 1999; Abesamis, Green, Russ, & Jadloc, 2014; Taylor, Houk, Russ, & Choat, 2014). This
453 pattern reflects the highly correlated relationships between various traits across closely-
454 related species (Roff, 1984) and is based largely on fundamental principles concerning
455 population replenishment and turnover time. However, initial age-based summaries of
456 surgeonfishes demonstrate a surprising lack of consistent patterns among demographic traits
457 across species (Choat & Robertson, 2002). Surgeonfishes of all genera are long-lived (>30
458 years) and most display 'square' growth profiles (long life span with rapid initial growth that
459 quickly reaches an asymptotic size; Trip, Craig, Green, & Choat, 2014). Given this pattern
460 and the relative paucity of empirical derivations of mortality for surgeonfishes, we suspect
461 that the two-phase mortality schedule and demographic characteristics yielding it are not
462 unique to *N. unicornis*, but are presently unappreciated and much more general across
463 acanthurids and possibly other lineages displaying 'square' growth trajectories and extensive
464 longevity. We further postulate that this characteristic facilitates greater species-specific

465 resilience to fishery exploitation than previously presumed, given that empirical derivations
466 of natural mortality based on observations of maximum life span will overestimate population
467 turnover time. Hence, while life-history traits are often useful predictors of vulnerability to
468 overexploitation, we predict that interspecific relationships in traits will ultimately be poor
469 predictors of yield in fisheries for the acanthurids and other demographically similar species.

470 Although demographic resilience is certainly a positive feature, we highlight that
471 growing human populations, increases in fishing efficiency resulting from constant
472 advancements in technology, and documented declines in other harvested taxa are causing
473 unicornfishes and other surgeonfishes to be harvested at greater rates than ever before
474 (Rhodes et al., 2018). This justifies legitimate concerns regarding both regional and broad-
475 scale sustainability. Based on contemporary data sets, the bluespine unicornfish appears to
476 remain a large component of fishery harvests rather than diminishing over time from high
477 fishing pressure, but that does not mean populations are not impacted in other ways. More
478 elusive concerns are the ‘Darwinian’ effects of sustained fishing pressure (Conover, 2000),
479 whereby strong selection pressure on particular traits (for example, overrepresentation of fast
480 growers in fishery harvests) by human harvesting systematically removes genotypes from the
481 gene pool or might impair recovery by indirectly inflating rates of natural mortality on the
482 smaller survivors of fishery extraction (Meekan, McCormick, Simpson, Chivers, & Ferrari,
483 2018). As this effect would require many generations to materialize and consistent surveying
484 to identify, we are at present generally unable to observe the direct or indirect consequences
485 of fishery-induced evolution in the context of coral reef fisheries or ecosystems (Kuparinen &
486 Merilä, 2007).

487 Non-extractive anthropogenic impacts such as warming water temperatures resulting
488 from climate change loom in the future for species like bluespine unicornfish whose life
489 histories are strongly influenced by temperature. Numerous studies have demonstrated the
490 diverse physiological, ecological, and interactive responses of fishes and other ectotherms to
491 increases in water temperature within the scope of global warming (Munday, Warner, Monro,
492 Pandolfi, & Marshall, 2013; Morrongiello, Sweetman, & Thresher, 2019). Body sizes will
493 generally decrease due to ocean warming and reduced oxygen levels (Cheung et al., 2013),
494 but one cannot predict the effect of generally higher temperatures and lower oxygen on
495 biphasic growth, for example, across populations of this or any other species. Changes in
496 vital rates associated with body size, in addition to those resulting from increased human
497 extraction, will however almost certainly occur in the oceans of the future.

498

499

500 **ACKNOWLEDGEMENTS**

501 We thank M. Chinkin, E. Cruz, T. Flores, J. Gourley, S. Lindfield, C. Pardee and many others
502 for assistance in fieldwork or labwork. Discussions with P. Houk, J. O'Malley, S. Newman,
503 M. Trianni, and C. Wakefield assisted in the development of the manuscript. Unpublished
504 data sets from American Samoa and the Commonwealth of the Northern Mariana Islands
505 were funded by the Commercial Fisheries Biosampling Program from the Pacific Islands
506 Fisheries Science Center, through Joint Institute for Marine and Atmospheric Research grant
507 6105137. We would like to thank the United Kingdom Foreign and Commonwealth Office
508 and the British Indian Ocean Territory Administration for granting us permission to
509 undertake research in the Chagos Archipelago. The project was funded in part by the
510 Bertarelli Foundation and contributed to the Bertarelli Program in Marine Science. We thank
511 two anonymous reviewers for their comments on the manuscript.

512

513 **AUTHORS' CONTRIBUTIONS**

514 B.M.T. and J.H.C. conceived the idea for the study; B.M.T., J.H.C., E.E.D., A.S.H., K.L.R.,
515 and M.G.M. secured funding for field collections; all authors collected field data; B.M.T.
516 conducted laboratory and data analysis; B.M.T. led the writing of the manuscript and all
517 authors contributed critically to drafts and gave final approval for publication.

518

519 **DATA ACCESSIBILITY**

520 Data available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.v2g567n>
521 (Taylor et al., 2019).

522

523 **REFERENCES**

524 Abesamis, R.A., Green, A.L., Russ, G.R., & Jadloc, C.R.L. (2014). The intrinsic vulnerability
525 to fishing of coral reef fishes and their differential recovery in fishery closures. *Reviews*
526 *in Fish Biology and Fisheries*, 24, 1033-1063. doi:10.1007/s11160-014-9362-x
527 Andrews, A.H., DeMartini, E.E., Eble, J.A., Taylor, B.M., Lou, D.C. and Humphreys, R.L.
528 (2016). Age and growth of bluespine unicornfish (*Naso unicornis*): a half-century life-
529 span for a keystone browser, with a novel approach to bomb radiocarbon dating in the

530 Hawaiian Islands. *Canadian Journal of Fisheries and Aquatic Sciences* 73, 1575-1586.
531 doi:10.1139/cjfas-2016-0019

532 Arendt, J.D. (1997). Adaptive intrinsic growth rates: an integration across taxa. *The*
533 *Quarterly Review of Biology*, 72, 149-177.

534 Beamish, R.J., McFarlane, G.A., & Benson, A. (2006). Longevity overfishing. *Progress in*
535 *Oceanography* 68, 289-302. doi:10.1016/j.pocean.2006.02.005

536 Bejarano, S., Golbuu, Y., Sapolu, T., & Mumby, P.J. (2013). Ecological risk and the
537 exploitation of herbivorous reef fish across Micronesia. *Marine Ecology Progress*
538 *Series* 482, 197-215. doi:10.3354/meps10270

539 Bergenius, M.A.J., McCormick, M.I., Meekan, M.G., & Robertson, D.R. (2005).
540 Environmental influences on larval duration, growth and magnitude of settlement of a
541 coral reef fish. *Marine Biology* 147, 291-300. doi:10.1007/s00227-005-1575-z

542 Bradshaw, A.D. (1965). Evolutionary significance of phenotypic plasticity in plants.
543 *Advances in Genetics* 13, 115-155.

544 Bronikowski, A.M., & Arnold, S.J. (1999). The evolutionary ecology of life history variation
545 in the garter snake *Thamnophis elegans*. *Ecology* 80, 2314-2325. doi:10.1890/0012-
546 9658(1999)080[2314:TEEOLH]2.0.CO;2

547 Bronikowski, A., & Vleck, D. (2010). Metabolism, body size and life span: a case study in
548 evolutionary divergent populations of the garter snake (*Thamnophis elegans*).
549 *Integrative and Comparative Biology* 50, 880-887. doi:10.1093/icb/icq132

550 Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., & West, G.B. (2004). Toward a
551 metabolic theory of ecology. *Ecology* 85, 1771-1789. doi:10.1890/03-9000

552 Campana, S.E. (1990). How reliable are growth back-calculations based on otoliths?
553 *Canadian Journal of Fisheries and Aquatic Sciences* 47, 2219-2227. doi:10.1139/f90-
554 246

555 Cheung, W.W.L., Sarmiento, J.L., Dunne, J., Frölicher, T.L., Lam, V.W.Y., Palomares,
556 M.L.D., Watson, R. & Pauly D. (2013). Shrinking of fishes exacerbates impacts of
557 global ocean changes on marine ecosystems. *Nature Climate Change*, 3, 254–258.
558 DOI:10.1038/NCLIMATE1671

559 Choat, J.H., & Axe, L.M. (1996). Growth and longevity in acanthurid fishes; an analysis of
560 otolith increments. *Marine Ecology Progress Series* 134, 15-26.
561 doi:10.3354/meps134015

- 562 Choat, J.H., & Robertson, D.R. (2002). Age-based studies. In P.F. Sale (Ed.), *Coral reef*
563 *fishes: dynamics and diversity in a complex ecosystem* (pp. 57-80). San Diego, CA:
564 Academic Press.
- 565 Clarke, A. (2017). *Principles of Thermal Ecology: Temperature, Energy and Life*. Oxford
566 University Press, New York.
- 567 Clarke, A., & Johnston, N.M. (2002). Scaling of metabolic rate with body mass and
568 temperature in teleost fish. *Journal of Animal Ecology* 68, 893-905. doi:10.1046/j.1365-
569 2656.1999.00337.x
- 570 Conover, D.O. (2000). Darwinian fishery science. *Marine Ecology Progress Series* 208, 303-
571 307.
- 572 DeMartini, E.E., Langston, R.C., & Eble, J.A. (2014). Spawning seasonality and body sizes
573 at sexual maturity in the bluespine unicornfish, *Naso unicornis* (Acanthuridae).
574 *Ichthyological Research* 61, 243-251. doi:10.1007/s10228-014-0393-z
- 575 Doherty, P.J., Dufour, V., Galzin, R., Hixon, M.A., Meekan, M.G., & Planes, S. (2004). High
576 mortality during settlement is a population bottleneck for a tropical surgeonfish.
577 *Ecology* 85, 2422-2428. doi:10.1890/04-0366
- 578 Ford, A.K., Bejarano, S., Marshall, A., & Mumby, P.J. (2016). Linking the biology and
579 ecology of key herbivorous unicornfish to fisheries management in the Pacific. *Aquatic*
580 *Conservation: Marine and Freshwater Research* 26, 790-805. doi:10.1002/aqc.2623
- 581 Gust, N., Choat, J.H., & Ackerman, J.L. (2002). Demographic plasticity in tropical reef
582 fishes. *Marine Biology*, 140, 1039-1051. doi:10.1007/s00227-001-0773-6
- 583 Hixon, M.A., & Jones, G.P. (2005). Competition, predation, and density-dependent mortality
584 in demersal marine fishes. *Ecology*, 86, 2847-2859.
- 585 Hoenig, J.M. (2017). Should natural mortality estimators based on maximum age also
586 consider sample size? *Transactions of the American Fisheries Society*, 146, 136-146.
587 doi:10.1080/00028487.2016.1249291
- 588 Horne, J.B., van Herwerden, L., Abellana, S., & McIlwain, J.L. (2013). Observations of
589 migrant exchange and mixing in a coral reef fish metapopulation link scales of marine
590 population connectivity. *Journal of Heredity*, 104, 532-546. doi:10.1093/jhered/est021
- 591 Houk, P., Rhodes, K., Cuetos-Bueno, J., Lindfield, S., Fread, V., & McIlwain, J.L. (2012).
592 Commercial coral-reef fisheries across Micronesia: A need for improving management.
593 *Coral Reefs*, 31, 13-26. doi:10.1007/s00338-011-0826-3

- 594 Houk, P., Cuetos-Bueno, J., Tibbatts, B., & Gutierrez, J. (2018). Variable density dependence
595 and the restructuring of coral-reef fisheries across 25 years of exploitation. *Scientific*
596 *Reports*, 8, 5725. doi:10.1038/s41598-018-23971-6
- 597 Jennings, S., Greenstreet, S.P.R., & Reynolds, J.D. (1999). Structural change in an exploited
598 fish community: a consequence of differential fishing effects on species with
599 contrasting life histories. *Journal of Animal Ecology*, 68, 617-627. doi:10.1046/j.1365-
600 2656.1999.00312.x
- 601 Jones, G.P. (2015). Mission impossible: unlocking the secrets of coral reef fish dispersal. In
602 C. Mora (Ed.), *Ecology of fishes on coral reefs: the functioning of an ecosystem in a*
603 *changing world* (pp. 16-27). Cambridge, Massachusetts: University of Cambridge
604 Press.
- 605 Kingsford, M.J., Welch, D., & O'Callaghan, M. (2019). Latitudinal and cross-shelf patterns
606 of size, age, growth, and mortality of a tropical damselfish *Acanthochromis*
607 *polyacanthus* on the Great Barrier Reef. *Diversity*, 11, 67. doi:10.3390/d11050067
- 608 Kingsolver, J.G. & Pfennig, D.W. (2007). Patterns and power of phenotypic selection in
609 nature. *BioScience*, 57, 561-572. doi:10.1641/B570706
- 610 Kritzer, J.P., Davies, C.R., & Mapstone, B.D. (2001). Characterizing fish populations: effects
611 of sample size and population structure on the precision of demographic parameter
612 estimates. *Canadian Journal of Fisheries and Aquatic Sciences*, 58, 1557-1568.
613 doi:10.1139/f01-098
- 614 Kuparinen, A., & Merilä, J. (2007). Detecting and managing fisheries induced evolution.
615 *TRENDS in Ecology and Evolution*, 22, 652-659. doi:10.1016/j.tree.2007.08.011
- 616 Meekan, M.G., Ackerman, J.L., & Wellington, G.M. (2001). Demography and age structures
617 of coral reef damselfishes in the tropical eastern Pacific Ocean. *Marine Ecology*
618 *Progress Series*, 212, 223-232.
- 619 Meekan, M.G., McCormick, M.I., Simpson, S.D., Chivers, D.P., & Ferrari, M.C.O. (2018).
620 Never off the hook—how fishing subverts predator-prey relationships in marine
621 teleosts. *Frontiers in Ecology and Evolution*, 6, 157. doi: 10.3389/fevo.2018.00157
- 622 Metcalfe, N.B., & Monaghan, P. (2003). Growth versus lifespan: perspectives from
623 evolutionary ecology. *Experimental Gerontology*, 38, 935-940. doi:10.1016/S0531-
624 5565(03)00159-1
- 625 Morrongiello, J.R., Sweetman, P.C., & Thresher, R.E. (2019). Fishing constrains phenotypic
626 responses of marine fish to climate variability. *Journal of Animal Ecology*. doi:
627 10.1111/1365-2656.12999

628 Muggeo, V.M.R. (2008). segmented: an R package to fit regression models with broken-line
629 relationships. *R News*, 8, 20-25.

630 Mulligan, T.J., & Leaman, B.M. (1992). Length-at-age analysis: can you get what you see?
631 *Canadian Journal of Fisheries and Aquatic Sciences*, 49, 632-643. doi:10.1139/f92-072

632 Munch, S.B., & Salinas, S. (2009). Latitudinal variation in lifespan within species is
633 explained by the metabolic theory of ecology. *Proceedings of the National Academy of*
634 *Sciences*, 106, 13860-13864. doi:10.1073/pnas.0900300106

635 Munday, P.L., Warner, R.R., Monro, K., Pandolfi, J.M., & Marshall, D.J. (2013). Predicting
636 the evolutionary responses to climate change in the sea. *Ecology Letters*, 16, 1488-
637 1500. doi: 10.1111/ele.12185

638 Nadon, M.O., & Ault, J.S. (2016). A stepwise stochastic simulation approach to estimate life
639 history parameters for data-poor fisheries. *Canadian Journal of Fisheries and Aquatic*
640 *Sciences*, 73, 1874-1884. doi:10.1139/cjfas-2015-0303

641 Nadon, M.O., Ault, J.S., Williams, I.D., Smith, S.G., & DiNardo, G.T. (2015). Length-based
642 assessment of coral reef fish populations in the Main and Northwestern Hawaiian
643 Islands. *PLoS ONE*, 10, e133960. doi:10.1371/journal.pone.0133960

644 Prince, J., Hordyk, A., Valencia, S.R., Loneragan, N., & Sainsbury, K. (2014). Revisiting the
645 concept of Beverton-Holt life-history invariants with the aim of informing data-poor
646 fisheries assessment. *ICES Journal of Marine Science*, 72, 194-203.
647 doi:10.1093/icesjms/fsu011

648 Rhodes, K.L., Hernandez, D.X., Cuetos-Bueno, J., Ioanis, M., Washington, W., & Ladore, R.
649 (2018). A 10-year comparison of the Pohnpei, Micronesia, commercial inshore fishery
650 reveals an increasingly unsustainable fishery. *Fisheries Research*, 204, 156-164.
651 doi:10.1016/j.fishres.2018.02.017

652 Ricker, E.E. (1975). Computation and interpretation of biological statistics of fish
653 populations. *Bulletin of the Fisheries Research Board of Canada*, 191, 1-382.

654 Rios-Cardenas, O., Bono, L., Morris, M.R. (2018). Negative frequency-dependent selection
655 and fluctuations around an equilibrium for alternative reproductive tactics in a
656 swordtail. *Animal Behaviour*, 140, 19-28. doi:10.1016/j.anbehav.2018.03.018

657 Robertson, D.R., Ackerman, J.L., Choat, J.H., Posada, J.M., & Pitt, J. (2005). Ocean
658 surgeonfish *Acanthurus bahianus*. I. The geography of demography. *Marine Ecology*
659 *Progress Series*, 295, 229-244. doi:10.3354/meps295229

660 Roff, D.A. (1984). The evolution of life history parameters in teleosts. *Canadian Journal of*
661 *Fisheries and Aquatic Sciences*, 41, 989-1000.

- 662 Roney, N.E., Oomen, R.A., Knutsen, H., Olsen, E.M., & Hutchings, J.A. (2018). Fine-scale
663 population differences in Atlantic cod reproductive success: a potential mechanism for
664 ecological speciation in a marine fish. *Ecology and Evolution*, 8, 11634-11644.
665 doi:10.1002/ece3.4615
- 666 Sogard, S.M. (1997). Size-selective mortality in the juvenile stage of teleost fishes: a review.
667 *Bulletin of Marine Science*, 60, 1129-1157.
- 668 Speakman, J.R. (2005). Body size, energy metabolism and lifespan. *The Journal of*
669 *Experimental Biology*, 208, 1717-1730. doi:10.1242/jeb.01556
- 670 Stearns, S.C. (1976). Life-history tactics: a review of the ideas. *The Quarterly Review of*
671 *Biology*, 51, 3-47.
- 672 Sundberg, M., Humphreys, R., Lowe, M.K., Cruz, E., Gourley, J., & Ochavillo, D. (2015).
673 Status of life history sampling conducted through the commercial fisheries bio-
674 sampling programs in the Western Pacific Territories of American Samoa and Guam
675 and in the commonwealth of the Northern Mariana Islands. *NOAA Administrative*
676 *Report H-15-08*, 56 pp. [httpS://pifsc-
677 www.irc.noaa.gov/library/pubs/admin/PIFSC_Admin_Report_15-08.pdf](httpS://pifsc-
677 www.irc.noaa.gov/library/pubs/admin/PIFSC_Admin_Report_15-08.pdf).
- 678 Taylor, B.M. (2019). Standing out in a big crowd: high cultural and economic value of *Naso*
679 *unicornis* in the insular Pacific. *Fishes*, 4, 40. doi:10.3390/fishes4030040
- 680 Taylor, B.M., Houk, P., Russ, G.R., & Choat, J.H. (2014). Life histories predict vulnerability
681 to overexploitation in parrotfishes. *Coral Reefs*, 33, 869-878. doi:10.1007/s00338-014-
682 1187-5
- 683 Taylor, B.M., Rhodes, K.L., Marshall, A., & McIlwain, J.L. (2014). Age-based demographic
684 and reproductive assessment of orangespine *Naso lituratus* and bluespine *N. unicornis*
685 unicornfishes. *Journal of Fish Biology*, 85, 901-916. doi:10.1111/jfb.12479
- 686 Taylor, B.M., Brandl, S.J., Kapur, M., Robbins, W.D., Johnson, G., Huveneers, C., Renaud,
687 P., & Choat, J.H. (2018). Bottom-up processes mediated by social systems drive
688 demographic traits of coral-reef fishes. *Ecology*, 99, 642-651. doi:10.1002.ecy.2127
- 689 Taylor, B.M., Trip, E.L., & Choat, J.H. (2018). Dynamic demography: investigations of life-
690 history variation in the parrotfishes. In A.S. Hoey & R.M. Bonaldo (Eds.), *Biology of*
691 *Parrotfishes* (pp. 69-98). Boca Raton, FL: CRC Press.
- 692 Taylor, B.M., Choat, J.H., DeMartini, E.E., Hoey, A.S., Marshall, A., Priest, M.A., Rhodes,
693 K.L., & Meekan, M.G. (2019). Data from: Demographic plasticity facilitates ecological
694 and economic resilience in a commercially important reef fish. *Dryad Digital*
695 *Repository*. <https://doi.org/10.5061/dryad.v2g567n>

- 696 Then, A.Y., Hoenig, J.M., Hall, N.G., & Hewitt, D.A. (2014). Evaluating the predictive
697 performance of empirical estimators of natural mortality rate using information on over
698 200 fish species. *ICES Journal of Marine Science*, 72, 82-92.
699 doi:10.1093/icesjms/fsu136
- 700 Trip, E.D.L., Clements, K.D., Raubenheimer, D., & Choat, J.H. (2014). Temperature-related
701 variation in growth rate, size, maturation and life span in a marine herbivorous fish over
702 a latitudinal gradient. *Journal of Animal Ecology*, 83, 866-875. doi:10.1111/1365-
703 2656.12183
- 704 Trip, E.D.L., Craig, P., Green, A., & Choat, J.H. (2014). Recruitment dynamics and first year
705 growth of the coral reef surgeonfish *Ctenochaetus striatus*, with implications for
706 acanthurid growth models. *Coral Reefs*, 33, 879-889. doi:10.1007/s00338-014-1182-x
- 707 Warner, R.R., & Chesson, P.L. (1985). Coexistence mediated by recruitment fluctuations: a
708 field guide to the storage effect. *The American Naturalist*, 125, 769-787.
- 709 Webster, M.S. (2004). Density dependence via intercohort competition in a coral-reef fish.
710 *Ecology*, 85, 986-994.
- 711 Webster, M.S., & Hixon, M.A. (2000). Mechanisms and individual consequences of
712 intraspecific competition in a coral-reef fish. *Marine Ecology Progress Series*, 196,
713 187-194.
- 714 Weinstein, M., Liotta, M.N., Solitt, A., Hunt, A., Abbott, J.K., Rios-Cardenas, O., & Morris,
715 M.R. (2019). Selection on growth rates via a trade-off between survival to sexual
716 maturity and longevity in the swordtail fish *Xiphophorus multilineatus*. *Evolutionary
717 Ecology*, in press. doi:10.1007/s10682-019-09989-w
- 718 Zeileis, A., Leisch, F., Hornik, K., & Kleiber, C. (2002). strucchange: an R package for
719 testing for structural change in linear regression models. *Journal of Statistical Software*,
720 7, 1-38.

721 **Table 1.** Summary of demographic samples for *Naso unicornis* and associated explanatory factors from eleven locations across the Indo-Pacific
 722 region.

Location	n†	FL range (mm)	Age range (years)	Collection method	Winter SST	Productivity (g C m ³)	Human density (ppl/km ² reef)	Previous references
Chagos Archipelago	61	235 - 544	2 - 26	Fishery-independent, research cruise collections	27.792	0.111	0	-
Mariana Trench Marine National Monument‡	96	165 - 520	1 - 37	Fishery-independent, research cruise collections	25.855	0.053	0	-
Northern Mariana Islands§	141	192 - 524	1 - 33	Fishery-independent, research cruise collections	26.905	0.051	0	-
Saipan, CNMI	447	108 - 532	1 - 21	Fishery-dependent, market biosampling	27.478	0.055	524	Sundberg et al. (2015) [method]
Tinian, CNMI	144	222 - 488	2 - 22	Fishery-dependent, market biosampling	27.541	0.055	165	Sundberg et al. (2015) [method]
Guam	248	114 - 520	0 - 23	Fishery-dependent, market biosampling	27.722	0.048	1163	Taylor, Rhodes, Marshall, and McIlwain (2014)
Yap, FSM	76	136 - 514	1 - 17	Fishery-independent, research sampling	28.313	0.059	70	-
Lizard Island, Great Barrier Reef	209	60 - 542	0 - 30	Fishery-independent, research sampling	24.876	0.288	0	Choat and Axe (1996), Choat and Robertson (2002)
Pohnpei, FSM	232	207 - 496	1 - 16	Fishery-dependent, market biosampling	28.640	0.064	230	Taylor, Rhodes, Marshall, and McIlwain (2014)

Oahu, Hawaii	533	67 - 596	0 - 52	Fishery-dependent, market biosampling	23.726	0.081	2923	Andrews et al. (2016), DeMartini, Langston, and Eble (2014)
Tutuila, American Samoa	328	124 - 535	1 - 19	Fishery-dependent, market biosampling	27.930	0.050	1118	Sundberg et al. (2015) [method]

723

724 FL, fork length; SST, sea surface temperature; FSM, Federated States of Micronesia; CNMI, Commonwealth of the Northern Mariana Islands

725 †Sample size of individuals with age estimates

726 ‡Islands of Uracas, Maug, and Asuncion

727 §Islands of Alamagan, Pagan, Guguan, Sarigan, Anatahan

Author Manuscript

728 **Figure Legends**

729 **Figure 1.** Indian and Pacific Ocean study sites where demographic samples of bluespine
730 unicornfish *Naso unicornis* were collected. MTMNM = Mariana Trench Marine National
731 Monument (comprises islands of Farallon de Pajaros [Uracas], Maug, and Asuncion); NMI =
732 Northern Mariana Islands (comprises sampled islands of Pagan, Alamagan, Guguan, Sarigan,
733 and Anatahan).

734
735 **Figure 2.** Relationship between maximum derived age (life span) of *Naso unicornis* and
736 mean winter sea surface temperature (SST_L). Temperature was calculated as the mean SST of
737 the coldest month for each location, based on remotely-sensed satellite data from 2006-2011.
738 The relationship ($R^2 = 0.83$) is described by *Maximum derived age* = $-6.30 * (SST_L) + 197.01$
739 and is displayed with 95% confidence bands.

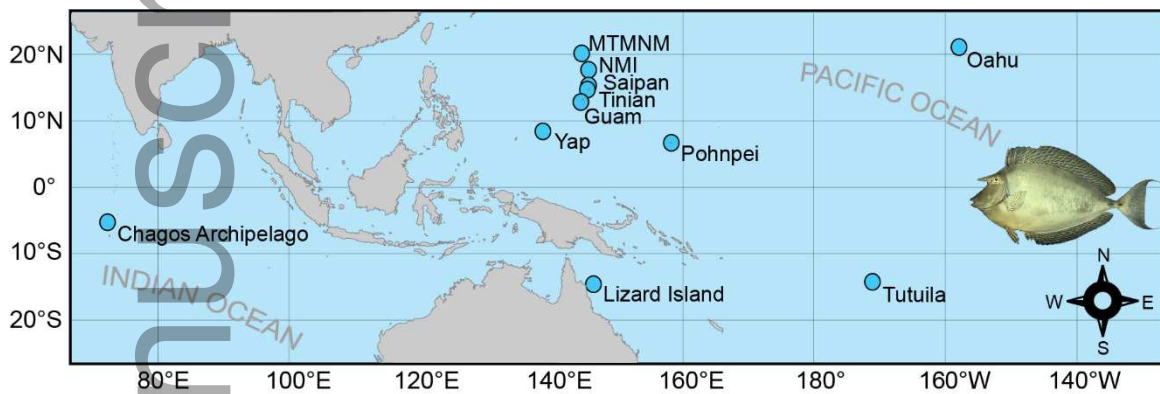
740
741 **Figure 3.** Age-based catch curves for *Naso unicornis* from all study locations, demonstrating
742 a ubiquitous two-phase mortality schedule punctuated by a breakpoint. White circles
743 represent estimates for age classes not fully recruited to the sampling strategy, black circles
744 represent estimates across the first stage of the mortality schedule, grey circles represent
745 those for the second stage of the mortality schedule. Optimal breakpoints were computed
746 using a structural change function. Black lines are continuous segmented fits, grey lines are
747 disjunct fits.

748
749 **Figure 4.** (A) Annual increment widths follow measurements along transverse sections of
750 otoliths in *Naso unicornis* from Oahu, Hawaii (with inset showing the annotated transverse
751 section of a fish estimated as 9-yr old), two locations from the Mariana Archipelago (inset
752 map), and the Chagos Archipelago. (B) Increment widths were measured from subsampled
753 'fast-growing', 'slow-growing', and 'old' fish based on length-at-age growth plots. (C)
754 Increment width profiles showing divergence among growth types and 'old' fish across the
755 first ten age classes. 0 = from hatching to reef settlement (pelagic phase), 1 = first year of
756 growth (from settlement to first ring deposition), 2 = second year of growth, 3 = third year of
757 growth, etc. *represents significant differences between growth types (F = fast growers, S =
758 slow growers, O = old fish).

759
760 **Figure 5.** (A) Simulated growth profiles (with associated von Bertalanffy growth curves) and
761 life spans of 'fast-growing' and 'slow-growing' *Naso unicornis* based on the Oahu sample.

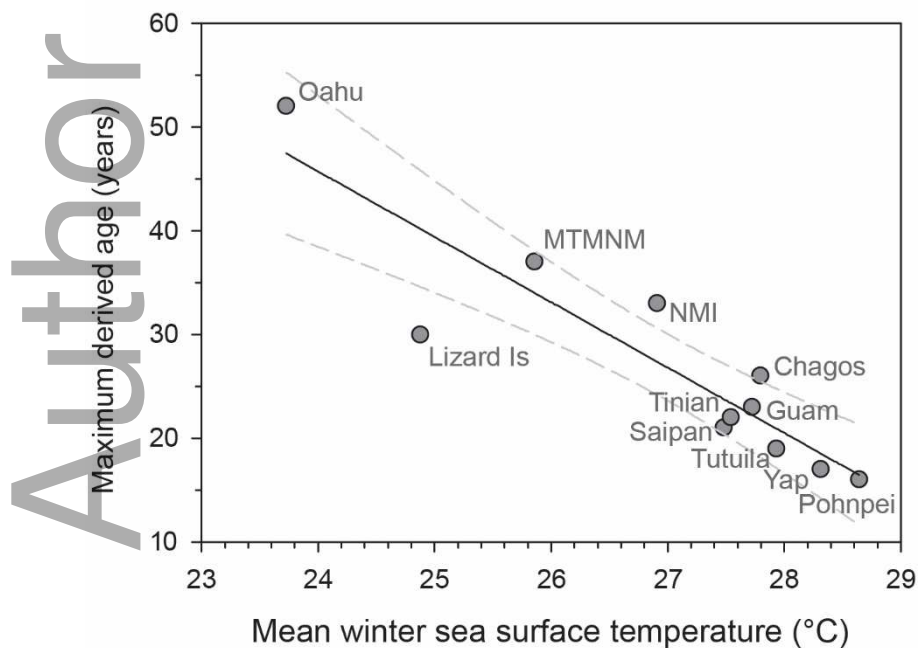
762 Bold lines represent the simulated two-phase mortality schedule (natural mortality rate [M] is
 763 nearly double in the first phase versus the second phase) from this population and relates to
 764 the y-axis. (B) Empirical relationship between ovary weight and fork length for female *N.*
 765 *unicornis* from Oahu. (C) Relative and cumulative reproductive value of ‘fast-growing’ and
 766 ‘slow-growing’ cohorts over their respective life spans.

767
 768



769
 770
 771
 772

Fig. 1



773
 774

Fig. 2

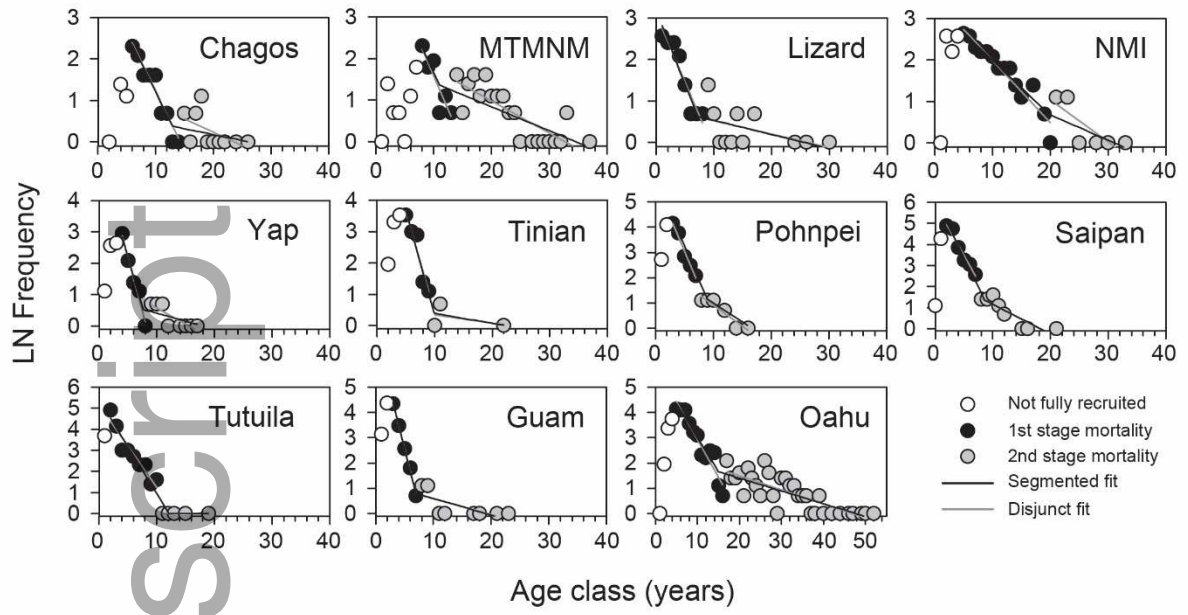


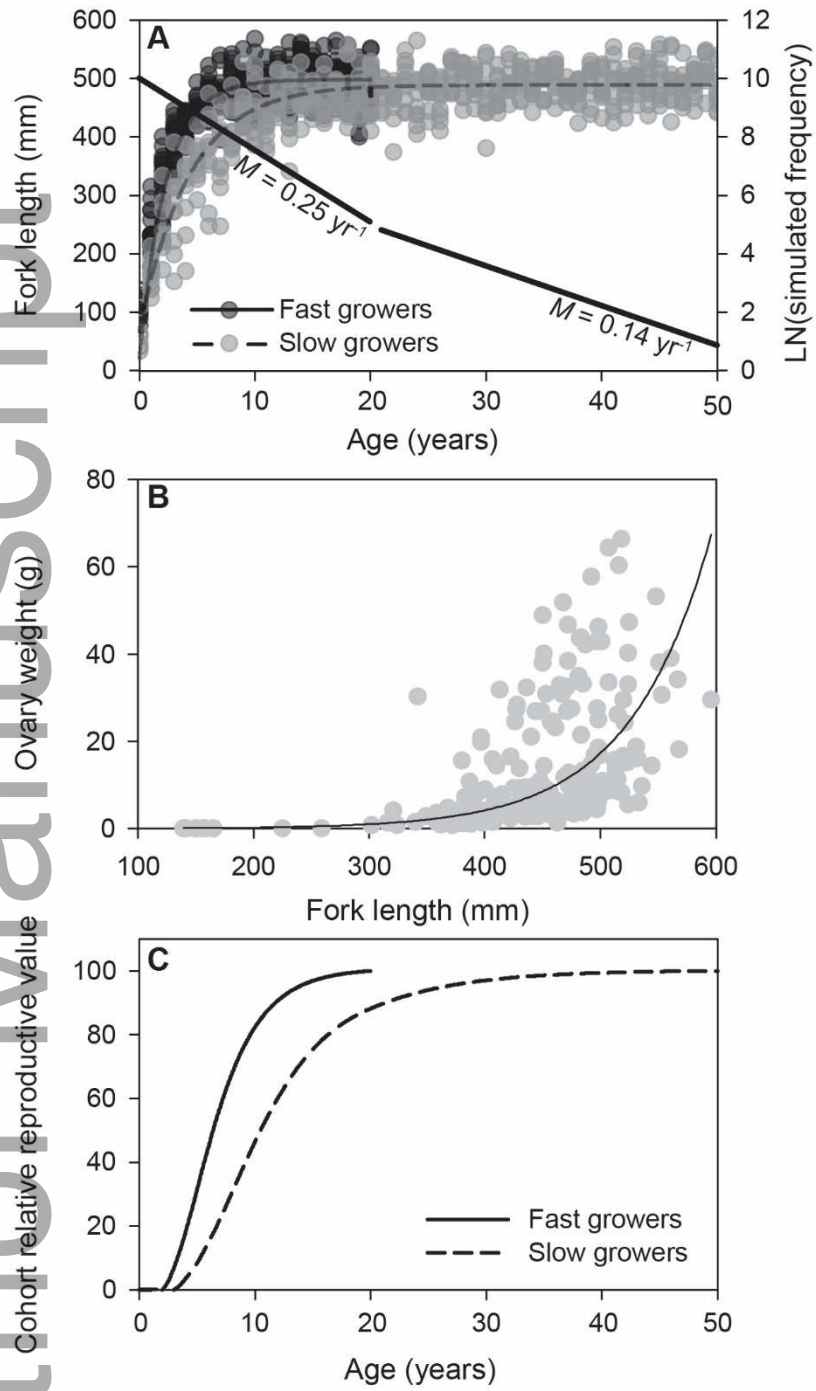
Fig. 3

775

776

777

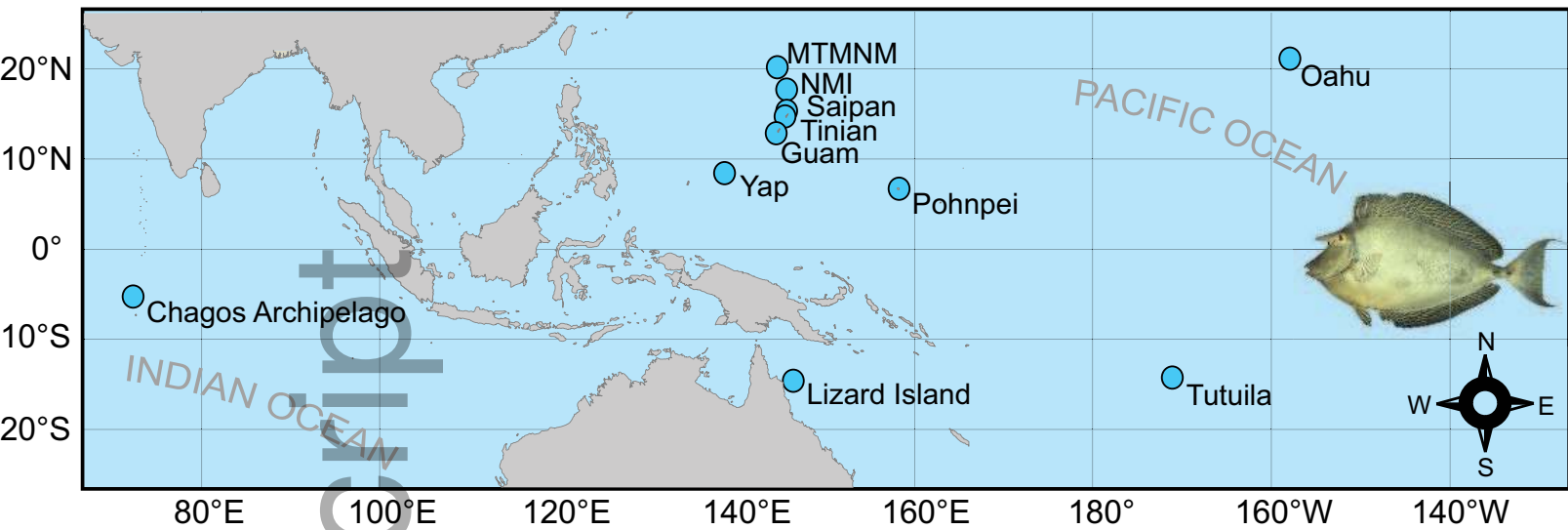
778



782

783

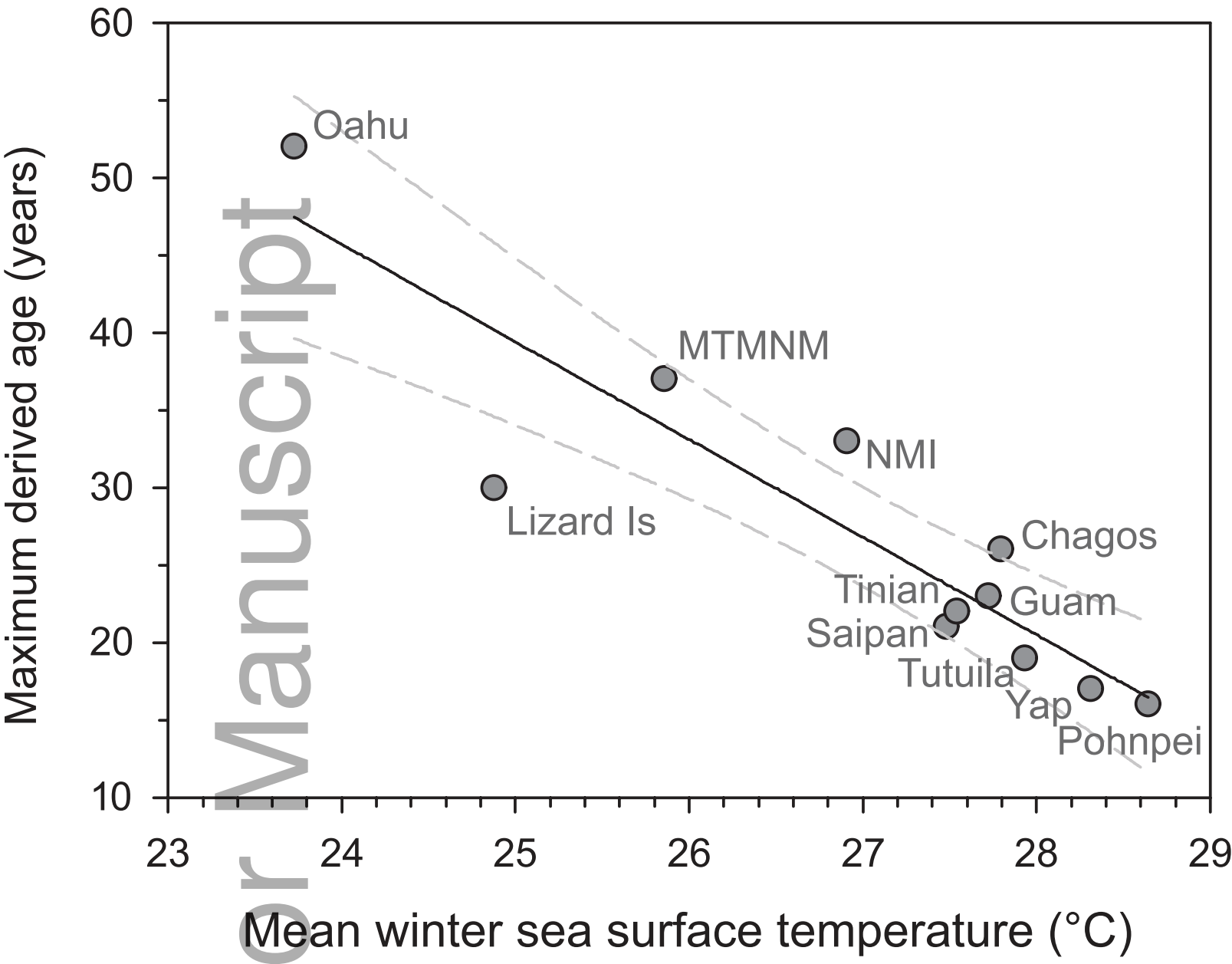
Fig. 5



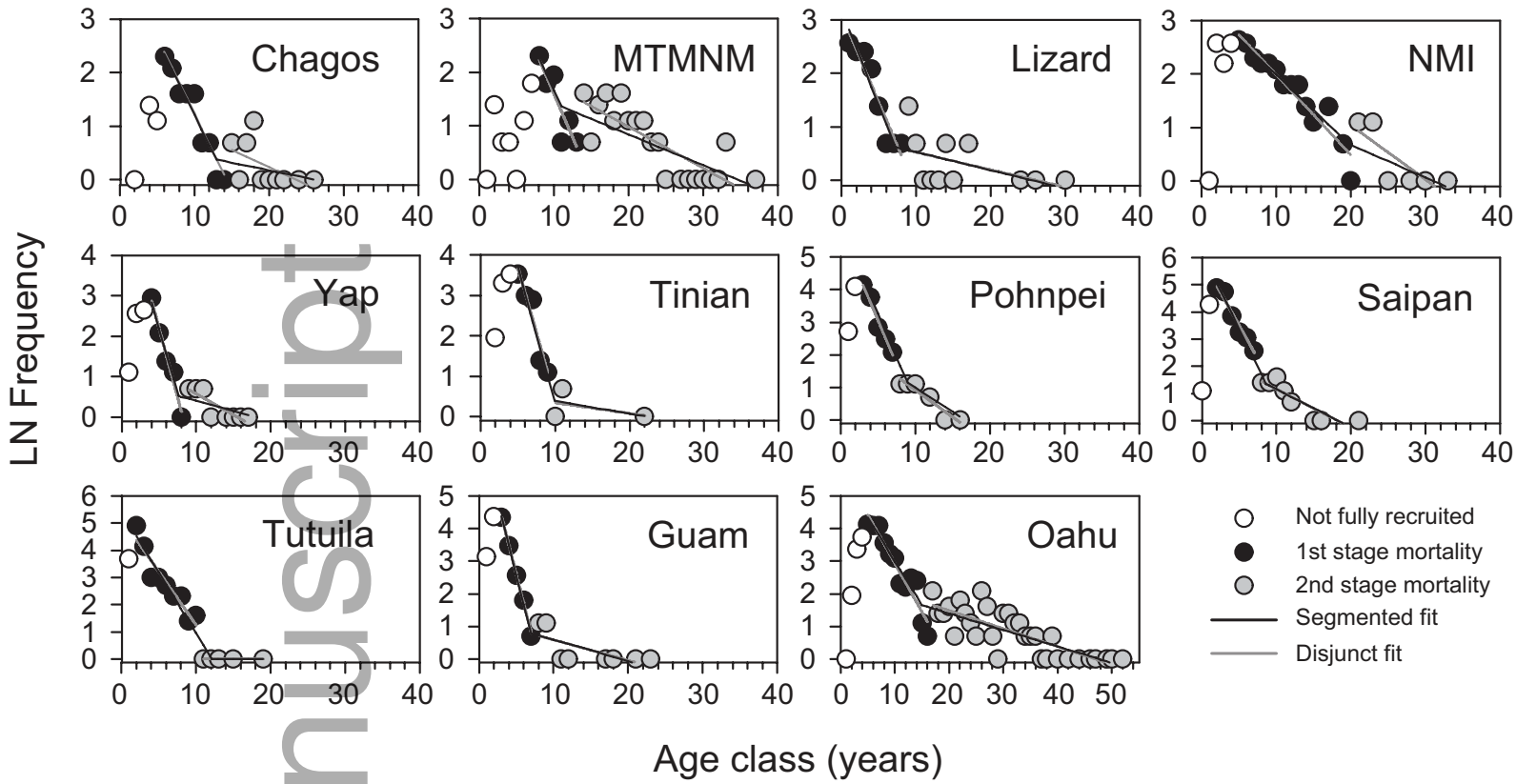
jane_13095_f1.eps

Author Manuscript

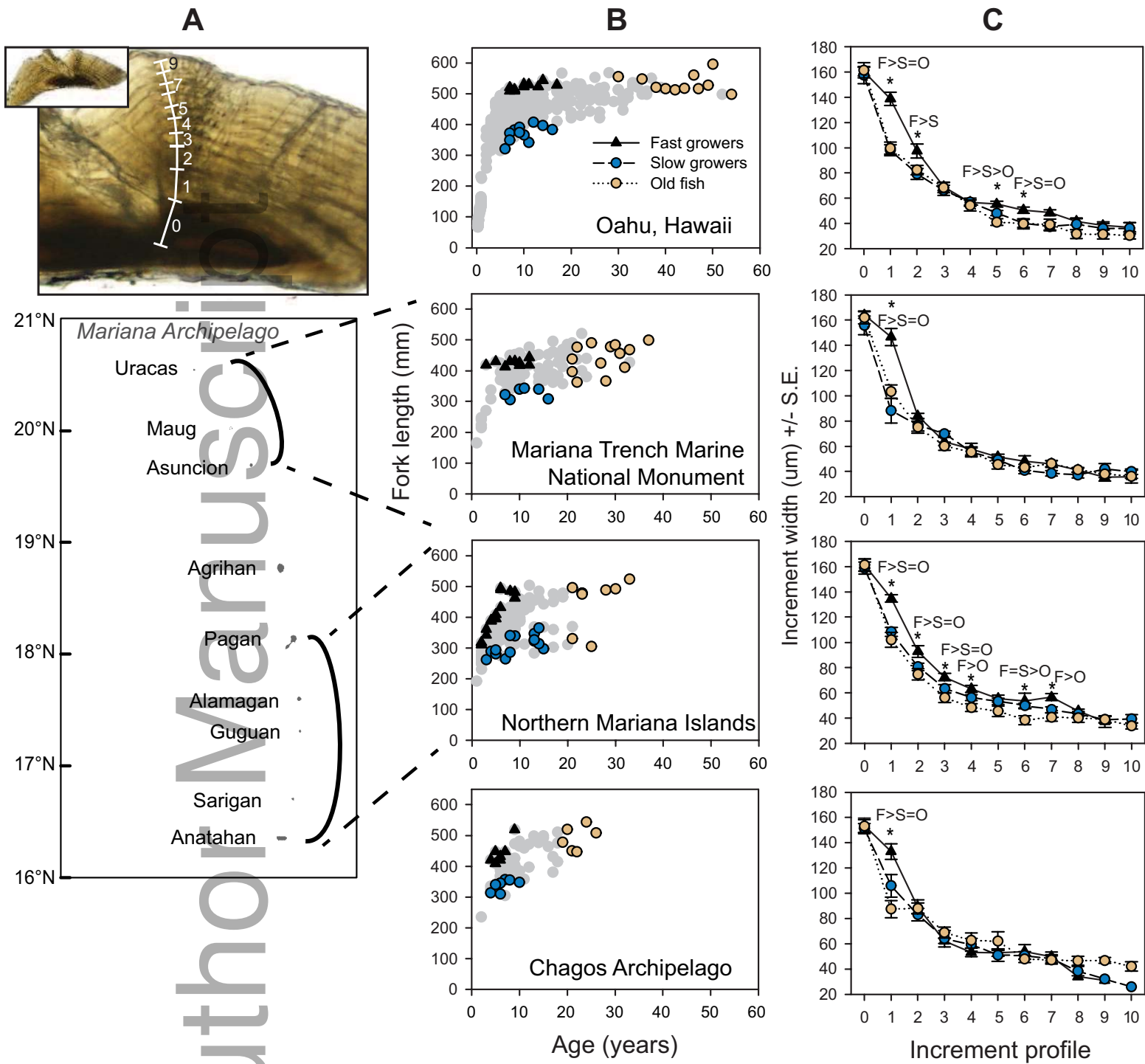
Author Manuscript



jane_13095_f2.eps



jane_13095_f3.eps



jane_13095_f4.eps

