RESEARCH ARTICLE

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

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Abstract

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

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

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

4. We found a threefold geographic variation in life span that was strongly linked to temperature, but not to anthropogenic pressure or ocean productivity. All populations consistently displayed a two-phase mortality schedule, with higher than expected natural mortality rates in earlier stages of post-settlement life. Reconstructed growth histories and population models demonstrated that variable growth types within populations can yield this peculiar biphasic mortality schedule, where fast growers enjoy early reproductive outputs at the expense of greater mortality, and benefits for slow growers derive from extended reproductive outputs over a greater number of annual cycles. This promotes population

resilience because individuals can take advantage of cycles of environmental change operating at both short- and long-term scales.

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

1 | INTRODUCTION

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

The growth and condition of individuals within ectothermic populations are largely mediated by the environmental and social conditions to which they are exposed. Fast growth, and hence larger body size, generally facilitates a greater competitive advantage and lower predation risk to individuals compared with smaller members of a cohort, thereby reducing the overall risk of mortality (Sogard, 1997), but is often associated with reduced life span (Metcalfe & Monaghan, 2003). This somewhat counterintuitive pattern highlights the trade-offs that occur among demographic traits (Arendt, 1997). For example, garter snake populations have been shown to support demographic variants that include both fast- and slow-growing individuals (Bronikowski & Arnold, 1999; Bronikowski & Vleck, 2010). In these populations, fast-growing individuals had higher rates of mass-specific resting metabolism and mortality, as well as larger body size, earlier maturation and a high reproductive output. Slow-growing individuals showed the opposite trends of smaller body size, late maturation and low reproductive output, along with increased longevity. Such variation in traits is also evident in coral reef fishes

exposed to marked environmental variation across relatively small spatial scales (10 s of km; Gust, Choat, & Ackerman, 2002; Taylor, Brandl, et al., 2018).

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

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

The bluespine unicornfish *Naso unicornis* is a coral reef-associated species preferentially targeted by fishing across the insular

Pacific (Hoey & Bellwood, 2009; Taylor, 2019). Several studies and formal stock assessments based on inferred life-history traits have characterized *N. unicornis* as among the most vulnerable species to overexploitation in multispecies fisheries in the western Pacific (e.g. Bejarano, Golbuu, Sapolu, & Mumby, 2013; Houk et al., 2012; Nadon, Ault, Williams, Smith, & DiNardo, 2015). However, despite the dominance of this species in regional fisheries, there is very limited spatial or temporal evidence of demographic shifts (e.g. decreases in harvested length or proportion of fishery catch) that might result from overfishing (Ford, Bejarano, Marshell, & Mumby, 2016; Houk, Cuetos-Bueno, Tibbatts, & Gutierrez, 2018; Rhodes et al., 2018). Earlier life-history studies of *N. unicornis* identified an unusual pattern of mortality in both exploited (Andrews et al., 2016; Taylor, Rhodes, Marshell, & McIlwain, 2014) and unexploited populations (Choat & Axe, 1996) whereby initial adult-stage mortality was high, but then abruptly decreased, resulting in a two-phase mortality profile across age classes that results in the atypical combination of high mortality and long life span. The spatial ubiquity of this pattern, as well as its potential drivers, is unknown.

Here, we compiled a large dataset of published and previously unpublished age-based demographic information for *N. unicornis* from 20 islands and atolls across the Western, Central, and South Pacific and Central Indian Oceans. Our study had two major objectives. The first objective examined the influence of anthropogenic pressure and environmental differences among locations on variability in life span of the species. Prevailing metabolic theory posits that increasing temperature will negatively influence life span (Munch & Salinas, 2009). However, fishery exploitation may have an overarching effect, whereby any relationship between temperature and life span is obscured by variability in human extraction, given the capacity for fishery-induced age truncation in taxa that are long-lived and harvested heavily (e.g. Beamish, McFarlane, & Benson, 2006). The second objective explored patterns of adult mortality among locations that ranged across a large gradient of human population densities. We examined the intrinsic biological characteristics (e.g.

growth-type-dependent mortality) that facilitated population-level longevity, variable mortality profiles across age classes and the evolutionary implications of variable life-history strategies within populations. To achieve this goal, we used an analysis of patterns of otolith increment width (a proxy for somatic growth) to test the hypothesis that fast growers died young, whereas the slowest growing individuals attained the oldest ages in a population (Metcalfe & Monaghan, 2003; Mulligan & Leaman, 1992). We followed this with a population model that examined the potential contribution of size-dependent mortality towards population-level biphasic mortality profiles. Finally, we evaluated the results in the context of multispecies fisheries management and the ecological significance of variable life-history traits within species.

2 | MATERIALS AND METHODS

To assess the generality of life-history characteristics and geographic variation in age-based demography, we collated age-based biological data (i.e. annualized fish ages and associated body length measurements) derived from sectioned otoliths (ear stones) for *N. unicornis* from 20 islands and atolls, geographically summarized into 11 locations across the Indo-Pacific region (Figure 1). Specimens were collected using fishery-dependent or fishery-independent sampling protocols (Table 1; expanded sampling methods are provided in Appendix S1).

2.1 | Predictors of life span

We estimated the life span of *N. unicornis* at each location using the maximum age derived from sectioned otoliths. Maximum derived age was validated by bomb radiocarbon analysis of micro-milled cores of otoliths of Oahu specimens (Andrews et al., 2016). This method provides a defensible estimate of life span when derived from large sample sizes (Hoenig, 2017; Kritzer, Davies, & Mapstone, 2001). Here, we
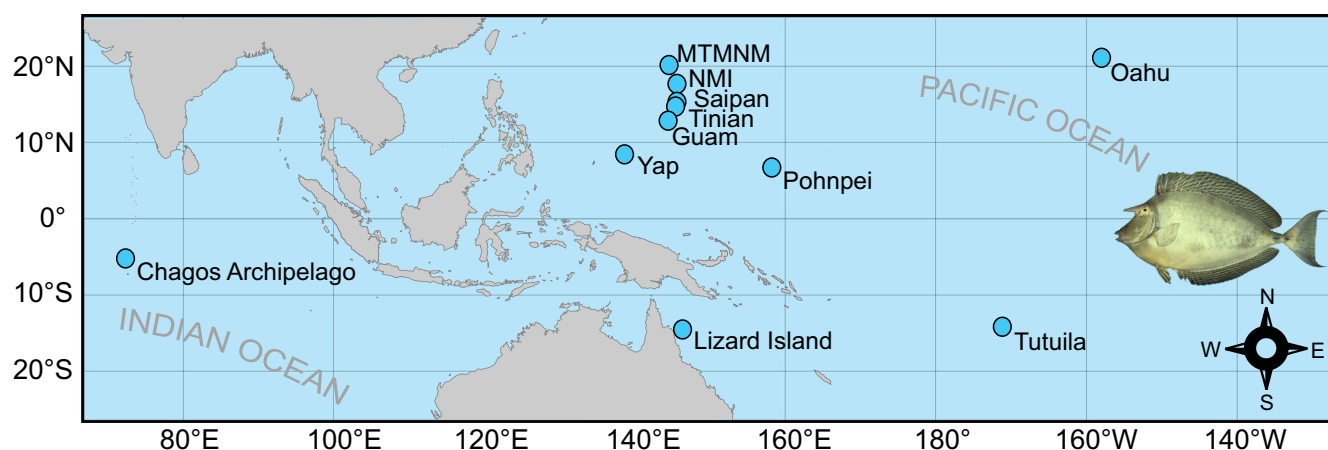

FIGURE 1 Indian and Pacific Ocean study sites where demographic samples of bluespine unicornfish *Naso unicornis* were collected. MTMNM = Mariana Trench Marine National Monument (comprises islands of Farallon de Pajaros [Urracas], Maug and Asuncion); NMI = Northern Mariana Islands (comprises sampled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

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

Location	$n^{\dagger}$	FL range (mm)	Age range (years)	Collection method	Winter SST	Productivity (g C m³)	Human density (ppl/km² 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	1,163	Taylor, Rhodes, et al. (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, et al. (2014)
Oahu, Hawaii	533	67–596	0–52	Fishery-dependent, market biosampling	23.726	0.081	2,923	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	1,118	Sundberg et al. (2015) [method]

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

[†]Sample size of individuals with age estimates.

[‡]Islands of Urracas, Maug and Asuncion.

[§]Islands of Alamagan, Pagan, Guguan, Sarigan and Anatahan.

used age data from 2,515 individuals from the eleven locations, with a range of 61–533 samples per location (mean 229 ± 153 *SD*). On average, this level of sampling yielded 9.2 specimen samples per age class across locations, which falls within the acceptable level of precision (7–10 per age class) proposed by Kritzer et al. (2001). We note that sample sizes for four locations (Chagos Archipelago, Mariana Trench Marine National Monument, Northern Mariana Islands and Yap) fall below this proposed sample level (2.4–4.5 samples per age class). However, these four locations are either unfished or had the lowest human density among populated locations (Yap); thus, sampling efforts at these locations, where fishing pressure is low to nonexistent, have an inherently higher likelihood of capturing the oldest age

classes. Ultimately, this method was used to approximate rather than directly measure life span. Techniques for sectioning and interpreting otoliths not documented in the literature followed Taylor, Rhodes, et al. (2014). All otoliths from published studies (Andrews et al., 2016; Choat & Axe, 1996; Taylor, Rhodes, et al., 2014) were re-examined by the lead author for consistency in reading across locations.

Measures of environmental variables sea surface temperature (SST; °C) and chlorophyll-a productivity (Chl-*a*; g C m³) for each location were derived from remotely sensed data. For SST, we calculated the average annual temperature (SST_A), the average temperature from the coldest month of the year (SST_L) and the average temperature from the warmest month of the year (SST_H) using the Global

High Resolution Blended SST database from the NOAA ERDDAP website (1-day composite; 0.0879° resolution) from January 2006 to May 2011. For Chl-*a*, we used the Aqua MODIS Global 4 km database to derive the mean Chl-*a* value across the period from January 2006 to July 2018. Finally, we calculated human density for each location by dividing the 2010 census population by total coral reef area <30 m deep (km^2). We then examined the relationships between explanatory variables and life span estimates using linear models, fitted to raw data across locations using least squares estimation. We used single predictor models given the limited number of data points and compared these models using Akaike's information criterion (AIC).

2.2 | Population dynamics and demographic structure

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

A two-phase mortality schedule that does not delineate major life phases (e.g. metamorphosis from pelagic phase or onset of sexual maturation) could reflect either a biased sampling protocol or an intrinsic biological phenomenon. Our sampling protocols varied between fishery-dependent (stratified random market sampling) and fishery-independent (spearfishing during research cruises) among populations, and we have no reason to suspect that an aspect of all the sample collections would facilitate a consistent bias. Hence, we set out to test the hypothesis that initial growth trajectories within populations yielded different life span potentials that resulted in a distinct change in natural mortality rates across age classes. Specifically, we hypothesized that fast-growing fish had shorter life spans than slow-growing fish (mechanisms reviewed in Metcalfe & Monaghan, 2003), such that the oldest fish in a population were exclusively derived from slow-growing individuals. Individual growth histories and life spans cannot be determined from length-at-age data alone (Mulligan & Leaman, 1992). Therefore, to test this hypothesis and its feasibility in relation to population dynamics, we (a) examined annual increment-width profiles in four of the five longest lived populations (Oahu, Marianas Trench Marine National Monument [MTMNM], Northern Mariana Islands [NMI] and Chagos Archipelago) as a proxy for somatic growth histories of fish (Campana, 1990) and (b) constructed simple population models exploring the effects of variable growth profiles on population dynamics. For the first objective, we selected fish specimens from the smaller (slow grower) and larger (fast grower) ends of the age-specific length distribution, as well as old fish (representatives from the oldest age classes with appropriate otolith clarity for high-resolution measurements) for increment-width analysis. Slow and fast growers were taken from age classes displaying a high adult growth trajectory, implying that fish could only reach those length–age combinations through slower or faster initial growth compared with the rest of the population. Pre-settlement growth (pelagic phase from hatching to reef settlement) and the first ten years of post-settlement otolith growth were measured and summarized by growth type for each location separately. Our hypothesis posits that slow-growing and old fish would have invariant increment-width profiles across stages in their early life history, whereas increment widths of fast-growing fish would differ across some stage in their early life history. This hypothesis stems from studies that show that early growth rate is the best predictor of adult mortality, with slow growth being associated with the longest life expectancy (Metcalfe & Monaghan, 2003). Age-specific analysis-of-variance tests were used to explore differences in increment widths among growth types.

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

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

where L_t is the predicted length at age t (years), L_∞ represents the asymptotic length, k is the growth coefficient, and t_0 is the hypothetical age at which length is equal to zero. These growth types had considerable overlap in length-at-age profiles, thereby reflecting the continuum of growth rates and the natural variation observed in the populations on which our models were based. Life-history theory suggests that variable growth types can be

maintained within a population if reproductive output is approximately the same among the growth types. Our model assumed that only slow growers reached the oldest age classes and we chose a maximum age for fast growers informed from the breakpoint analysis from mortality profiles and overall life span (average breakpoint at ~40% of lifespan). Natural mortality rates (M) for both growth types were estimated based on established relationships with life span (Then, Hoenig, Hall, & Hewitt, 2014; $M = 4.899[\text{maximum life span}]^{-0.916}$), presuming maximum ages of 50 years (Oahu, slow growers), 20 years (Oahu, fast growers), 40 years (Mariana Archipelago, slow growers) and 15 years (Mariana Archipelago, fast growers). Population decay across age classes was calculated using the standard exponential decay equation:

$$N_{t+1} = N_t e^{-M} \tag{2}$$

where N represents population size, t represents age class, and M represents the instantaneous natural mortality rate. To estimate reproductive output, we then modelled the relationship between fork length and female ovary weight (OW; Appendix S1) and multiplied the length-specific OW by cohort survivorship (the relationship between OW and fork length did not differ between growth types based on empirical data). The ovary weight × survivorship values were summed across age classes from the age at maturity (t_{mat}) to the maximum age (t_{max}) and considered a proxy for total reproductive output (RO) of a cohort:

$$RO = \sum_{t=t_{mat}}^{t_{max}} N_t OW_t \tag{3}$$

In this scenario, we therefore used total mass of propagules through a cohort's existence to represent reproductive output. We acknowledge that changes in egg size or spawning frequency across different body sizes may affect actual reproductive value, but this information was not available for any population in this study. The model assumed an equal number of fast- and slow-growing recruits in a cohort. Finally, we included an additional mortality factor (percentage relative to M) for slow-growing recruits during the age classes that overlapped with the life span of fast growers, to represent increased mortality from competition with faster-growing individuals and increased predation risk. We used an optimization procedure on this additional mortality factor to find the scenario that yielded equal lifetime reproductive output estimates from fast-growing and slow-growing components of a cohort across their respective life spans.

3 | RESULTS

We found a remarkably strong relationship between SST and life span, with the average temperature of the coldest month (SST_L) being the predictor that explained the most variation (Figure 2). Although life span estimates ranged widely from 16 to 52 years, SST_L explained 83% of the variation across locations ($F_{1,9} = 44.82$, $p < .0001$, AIC = 68.52). All locations were oceanic island systems except for Lizard Island,
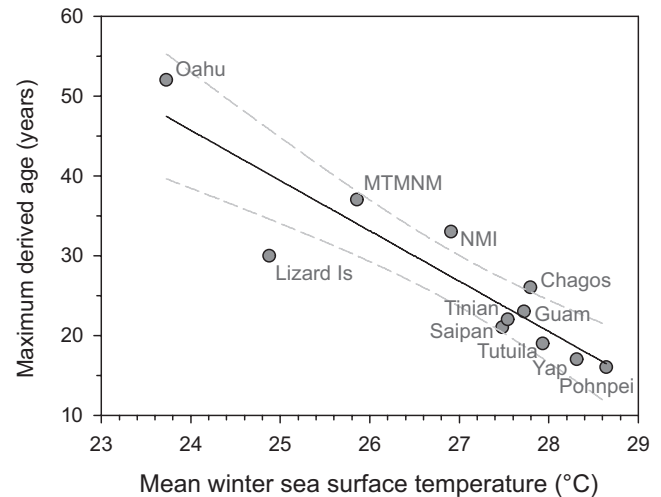

FIGURE 2 Relationship between maximum derived age (life span) of *Naso unicornis* and mean winter sea surface temperature (SST_L). Temperature was calculated as the mean SST of the coldest month for each location, based on remotely sensed satellite data from 2006 to 2011. The relationship ($R^2 = .83$) is described by *Maximum derived age* = −6.30*(SST_L) + 197.01 and is displayed with 95% confidence bands

Great Barrier Reef, which was a high island on a continental shelf. Sampling at Lizard Island provided an outlier in the dataset, and removal of this point improved the correlation to 93% of variance explained ($F_{1,8} = 111.34$, $p < .0001$, AIC = 54.56). Human density (a proxy for anthropogenic pressure) had no relationship with life span ($F_{1,9} = 3.88$, $p = .0804$, AIC = 84.26). Chl-*a* (natural log-transformed) also did not correlate with life span ($F_{1,9} = 0.44$, $p = .5234$, AIC = 87.67).

Despite the variability in life span, we observed two-phase mortality schedules of varying intensity in all populations, whereby a breakpoint occurred somewhere between 7 and 20 years (Figure 3). The change in slope before and after the optimal breakpoint was significant at all of the locations (Table S2), with the exception of the Northern Mariana Islands. The instantaneous mortality rate prior to the breakpoint ranged from 1.5 to 24.8 times higher than the later part of the life span across locations (comparing disjunct fits here as they are not constrained by one another). The difference in slopes between parts of the mortality schedule was not significantly related to temperature (linear model; $F_{1,10} = 2.05$, $p = .19$), anthropogenic pressure ($F_{1,10} = 0.06$, $p = .82$) or Chl-*a* ($F_{1,10} = 0.45$, $p = .52$).

Increment widths (Figure 4a) were derived for slow-growing, fast-growing and old fish (Figure 4b) across the first 10 years of life. For the four populations examined, increment-width profiles were very similar during pre-settlement growth and across the first 10 years for slow-growing and old fish, but growth during year 1 was significantly greater for fast-growing fish (Figure 4c). Although fast-growing fish also had significantly larger increment widths for other age classes at Oahu and the Northern Mariana Islands, the large and consistent disparity at year 1 across populations confirms that fast-growing fish attained the majority of their growth advantage in the first year after settlement (i.e. growth potential is not predetermined during the
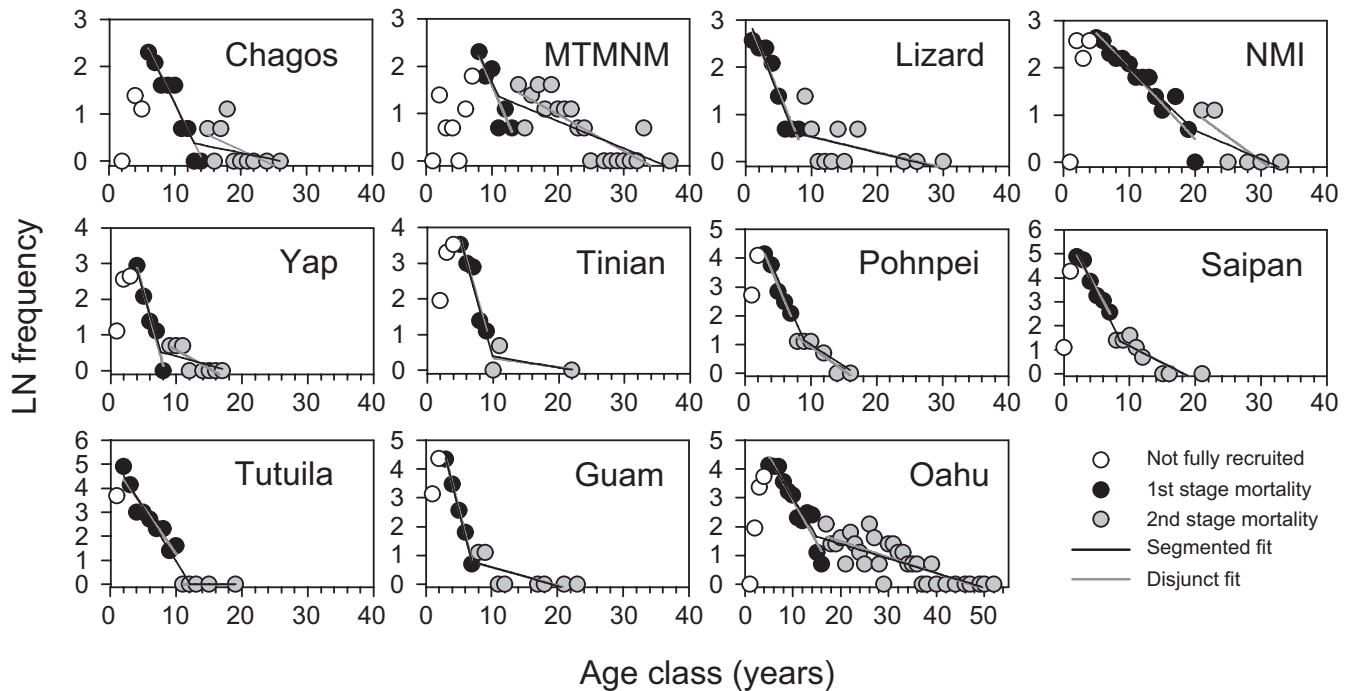
FIGURE 3 Age-based catch curves for *Naso unicornis* from all study locations, demonstrating a ubiquitous two-phase mortality schedule punctuated by a breakpoint. White circles represent estimates for age classes not fully recruited to the sampling strategy, black circles represent estimates across the first stage of the mortality schedule, and grey circles represent those for the second stage of the mortality schedule. Optimal breakpoints were computed using a structural change function. Black lines are continuous segmented fits, and grey lines are disjunct fits

pelagic phase). Further, the comparisons of increment-width profiles between growth types and old fish provide strong support for the hypothesis that the oldest fish are represented by survivors among the slowest growing individuals and thus that fast-growing fish die young.

Our population models independently integrated two growth extremes based on empirical data from Oahu and the Mariana Archipelago. Figure 5a displays the simulated length-at-age information for each growth type for the Oahu population. By integrating the relationship between ovary weight and fork length (Figure 5b) across natural population decay, we determined that fast-growing and slow-growing cohorts can reach the same lifetime reproductive value when intraspecific competition and predation increase natural mortality of the slow growers by approximately 60% at Oahu and 35% in the Mariana Archipelago. This scenario results in a two-phase mortality schedule similar to the low end observed from empirical data, whereby natural mortality of all growth types combined is nearly doubled during the life span of the fast-growing fish (Figure 5a; Figure S2). Because fast-growing fish mature earlier and reach larger sizes faster, their reproductive output is much greater than slow-growing fish in the first 10 years (Figure 5c; Figure S2).

4 | DISCUSSION

Contemporary tropical fisheries assessments are often data-poor and based on assumed geographically invariable values for

life-history traits. Here, we showed two phenomena that influenced the life history of the commercially important bluespine unicornfish, *N. unicornis*, that challenge such assumptions. We found a significant and strong relationship between sea surface temperature and life span, whereby warmer water yielded shorter-lived populations. This is predicted by metabolic theory and supports previous evidence demonstrating high variability in longevity strongly linked to ambient temperature in other acanthurid reef fishes and more generally in ectotherms (Munch & Salinas, 2009; Robertson et al., 2005). Failing to account for this relationship in fishery models results in gross over- or underestimates of exploitation, mortality and yield. The second phenomenon was the presence of a two-phase mortality schedule, common across all locations examined. This suggests that metabolic trade-offs between growth rates and life spans are conserved within populations irrespective of geographic location.

The wide variation in life span recorded across a latitudinal gradient is consistent with the metabolic theory of ecology (Brown et al., 2004; Munch & Salinas, 2009) and is reflective of trade-offs between thermally enhanced growth and reproductive life span (Trip, Clements, et al., 2014). Other studies have found a similar threefold change in life span of primary consumers that is tightly correlated with temperature (Robertson et al., 2005; Taylor, Trip, & Choat, 2018). For the ocean surgeonfish *Acanthurus bahianus*, temperature had a much stronger influence on life span than it did on either growth rate or body size, but all three were inversely related to
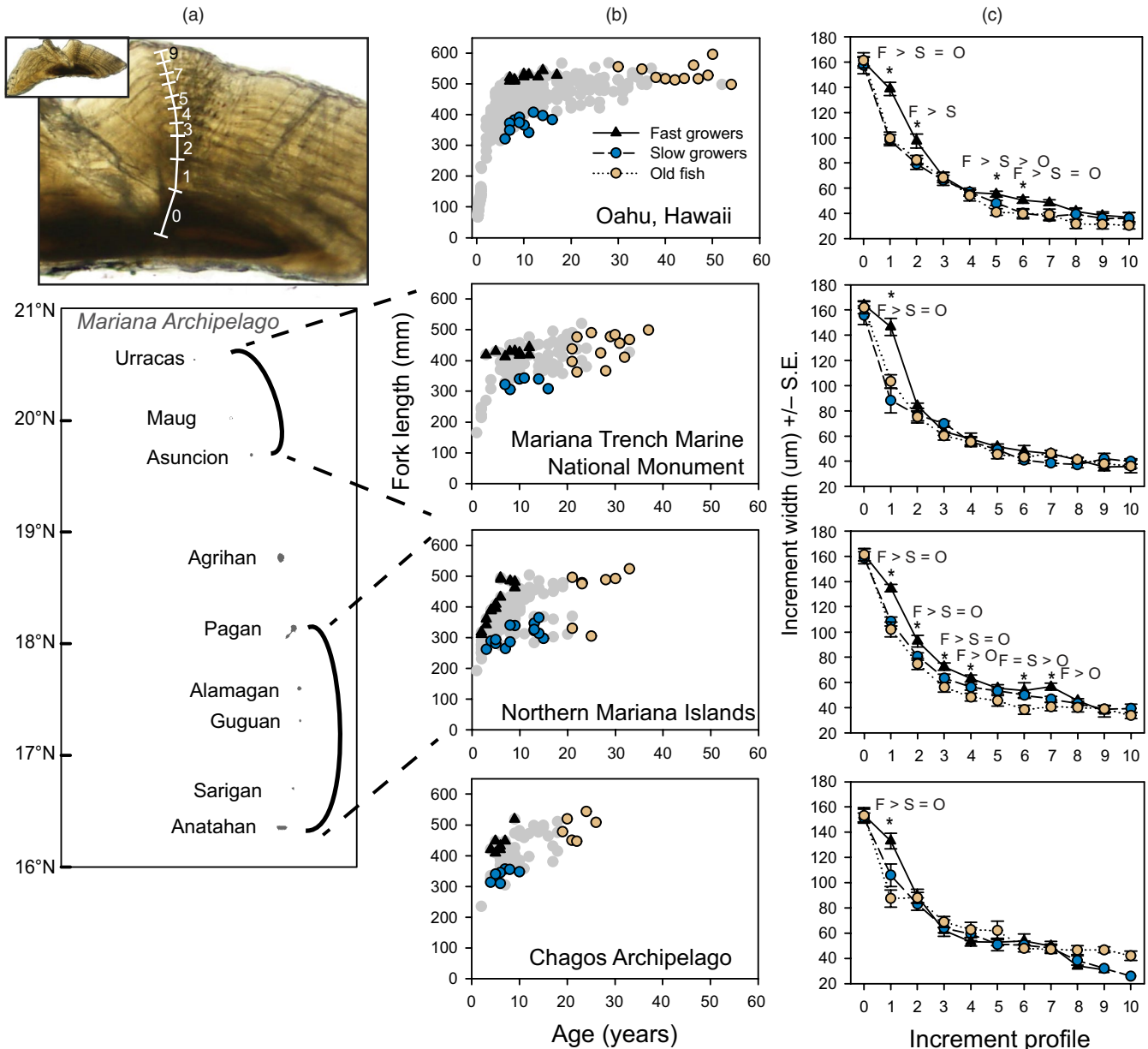
FIGURE 4 (a) Annual increment widths follow measurements along transverse sections of otoliths in *Naso unicornis* from Oahu, Hawaii (with inset showing the annotated transverse section of a fish estimated as 9 years old), two locations from the Mariana Archipelago (inset map) and the Chagos Archipelago. (b) Increment widths were measured from subsampled 'fast-growing', 'slow-growing' and 'old' fish based on length-at-age growth plots. (c) Increment-width profiles showing divergence among growth types and 'old' fish across the first ten age classes. 0 = from hatching to reef settlement (pelagic phase), 1 = first year of growth (from settlement to first ring deposition), 2 = second year of growth, 3 = third year of growth, etc. *Represents significant differences between growth types (F = fast growers, S = slow growers, O = old fish)

temperature (Robertson et al., 2005). These authors also highlighted trade-offs with reproduction, whereby frequency of spawning activity generally decreased with declining temperature. Despite the broad geographic patterns documenting decreased life span with increased environmental temperature in both ectotherms and endotherms, the proximal mechanism underlying variation in life span is still debated (Speakman, 2005). Analysis of ectothermic species, however, consistently indicates a complex integration of thermal constraints on growth in which higher temperatures at low latitudes

elicit faster growth through more efficient protein synthesis (Clarke, 2017) despite the physiological costs of higher metabolic demands on life span (Metcalfe & Monaghan, 2003).

Our results support the hypothesis that intraspecific variation in growth rates within cohorts of *N. unicornis* drives observed patterns of biphasic mortality. Differential growth rates in the pre-maturational and early reproductive phases of the benthic life cycle—as observed through otolith increment-width patterns—were clearly linked to variation in mortality rates and maximum life spans in the
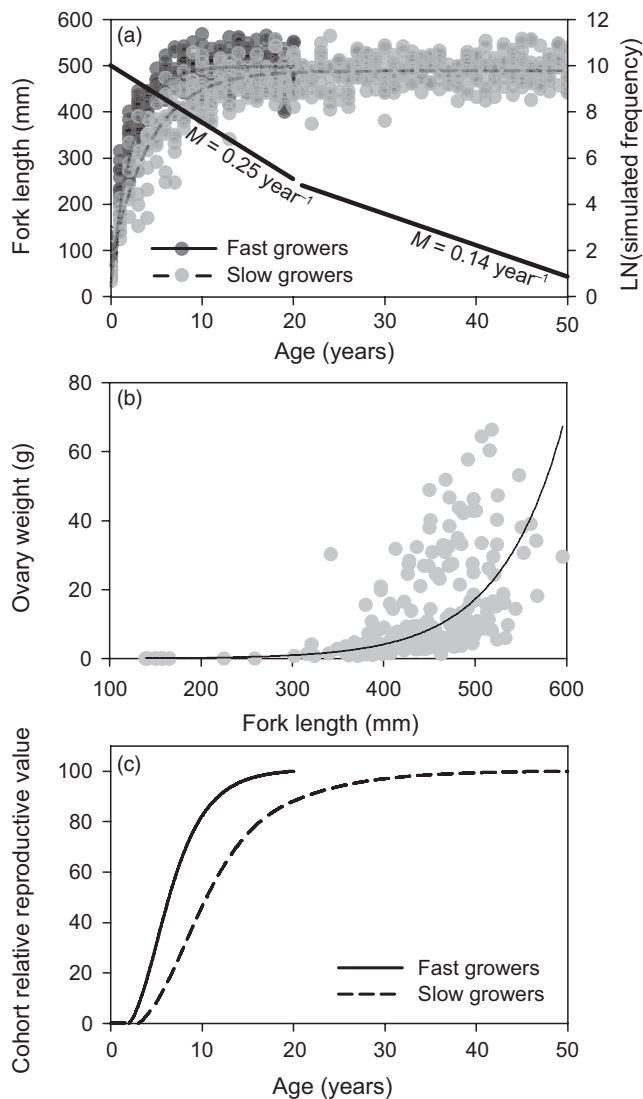
FIGURE 5 (a) Simulated growth profiles (with associated von Bertalanffy growth curves) and life spans of 'fast-growing' and 'slow-growing' *Naso unicornis* based on the Oahu sample. Bold lines represent the simulated two-phase mortality schedule (natural mortality rate [*M*] is nearly double in the first phase vs. the second phase) from this population and relates to the *y*-axis. (b) Empirical relationship between ovary weight and fork length for female *N. unicornis* from Oahu. (c) Relative and cumulative reproductive value of 'fast-growing' and 'slow-growing' cohorts over their respective life spans

sampled populations. Individuals with slower initial growth rates lived longer than those with faster initial growth rates. Differential growth rates within a cohort will have impacts on reproductive demography, as fast growth is associated with earlier maturation and greater reproductive outputs compared with slow growth in a cohort. Moreover, enhanced growth rate and the associated increases in size would confer advantages in terms of intraspecific competition and reduced predation risk compared with other members of a cohort. However, fast growth and the resulting large body size require greater metabolic demands (i.e. energy expenditure), and although these features generally yield greater reproductive output

and a competitive advantage, greater metabolic demands eventually bring a growth cost resulting in early senescence (Speakman, 2005). Ultimately, when selection pressures yield benefits for different growth types, a wide variety of phenotypes can be retained within populations. This concept in population demography is analogous to portfolio effects in ecological systems.

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

The demographic benefits for fast-growing individuals of earlier maturation and greater competitive abilities within the cohort are properties that might be beneficial if sequential cohorts are confronted by a habitat characterized by a high degree of patchiness on a local scale. Under these circumstances, individuals could exploit patches of high-quality food resources, with rapid growth and early maturation leading to enhanced reproductive outputs. Empirical measurements of larval dispersal show high levels of larval retention regardless of a species' early life-history characteristics (Jones, 2015). Such retention would ensure that successful offspring would be able to take advantage of the conditions that provided for increased reproductive output in the parental generation, whereas the long larval pelagic duration of *N. unicornis* (~71–75 days; Andrews et al., 2016; Doherty et al., 2004) affords the potential to exploit new and distant habitats (Horne, van Herwerden, Abellana, & McIlwain, 2013). However, the oceanic and near reef conditions that strongly influence the success of larval cohorts may vary considerably on decadal scales and are implicated in generating highly successful year classes (Bergenius, McCormick, Meekan, & Robertson, 2005). This is supported in reef fishes of the genus *Naso* that are characterized by episodes of mass recruitment (Doherty et al., 2004). Longevity at the scale observed in acanthurid fishes (3–4 decades post-maturation) provides the opportunity for some offspring to experience the oceanic

conditions that are outstandingly favourable to larval success that occurs at decadal time-scales. This represents a variant of the storage effect (Warner & Chesson, 1985) in which slow-growing but long-lived individuals may secure the benefits of favourable conditions for larval settlement and recruitment that occurs only episodically. The argument predicts a trade-off between rapid initial growth and maturation versus slower growth with an extended life span that provides opportunity to contribute to numerous annual spawning episodes (Metcalfe & Monaghan, 2003), with both variants retained within discrete geographic populations.

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

Life-history traits have proven to be powerful predictors of vulnerability to overexploitation in a wide variety of harvested fishes (Abesamis, Green, Russ, & Jadloc, 2014; Jennings, Greenstreet, & Reynolds, 1999; Taylor, Houk, Russ, & Choat, 2014). This pattern reflects the highly correlated relationships between various traits across closely related species (Roff, 1984) and is based largely on fundamental principles concerning population replenishment and turnover time. However, initial age-based summaries of surgeonfishes demonstrate a surprising lack of consistent patterns among demographic traits across species (Choat & Robertson, 2002). Surgeonfishes of all genera are long-lived (>30 years), and most display 'square' growth profiles (long life span with rapid initial growth that quickly reaches an asymptotic size; Trip, Craig, Green, & Choat, 2014). Given this pattern and the relative paucity of empirical derivations of mortality for surgeonfishes, we suspect that the two-phase mortality schedule and demographic characteristics yielding it are not unique to *N. unicornis*, but are presently unappreciated and much more general across acanthurids and possibly other lineages displaying 'square' growth trajectories and extensive longevity. We further postulate that this characteristic facilitates greater species-specific resilience to fishery exploitation than previously presumed, given that empirical derivations of natural mortality based on observations of maximum life span will overestimate population turnover time. Hence, while life-history traits are often useful predictors of vulnerability to overexploitation, we predict that interspecific relationships in traits will ultimately be poor predictors of yield in fisheries for the acanthurids and other demographically similar species.

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

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

AUTHORS' CONTRIBUTIONS

DATA AVAILABILITY STATEMENT

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