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GHOTI

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A widespread, consistent, and perplexing biphasic pattern in log catch-at-age data from a widely harvested family of tropical reef fishes

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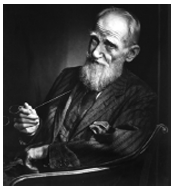
Abstract

Patterns of cohort decline are key demographic traits that provide a unique temporal perspective vital to understanding population dynamics. The discovery of multi-decadal lifespans in tropical surgeonfishes in the 1990s created a paradigm shift to the notion that they are highly vulnerable species with low population recovery rates; however, research into the mortality patterns of surgeonfishes (Acanthuridae) has been sparse until recently. Recent studies on this family have demonstrated an unusual (possibly unique), two-phase pattern of adult catch-at-age, whereby there is a population-level shift from higher-than-expected rates of decline early in life to lower-than-expected decline rates for the remainder of the lifespan. To examine the geographic and phylogenetic ubiquity of this pattern, we compiled age-based information from demographic samples of 70 populations of 25 tropical species spanning the Indo-Central Pacific and Central-Western Atlantic. Overall, we found that 79% of populations exhibited strong biphasic patterns, including 88% of populations across the Indo-Central Pacific. By accounting for empirical relationships instead of using linear catch curves or classical assumptions of natural population decay based on lifespan, we demonstrate that surgeonfishes have turnover times that are two to four times faster than previously believed. Faster turnover times may suggest a higher level of sustainability for surgeonfish fisheries throughout the global tropics than previously estimated.

KEYWORDS
Acanthuridae, circumtropical, life history, surgeonfish, survivorship, turnover time



Ghoti papers: Ghoti aims to serve as a forum for stimulating and pertinent ideas. Ghoti publishes succinct commentary and opinion that addresses important areas in fish and fisheries science. Ghoti contributions will be innovative and have a perspective that may lead to fresh and productive insight of concepts, issues and research agendas. All Ghoti contributions will be selected by the editors and peer reviewed.

Etymology of Ghoti: George Bernard Shaw (1856–1950), polymath, playwright, Nobel Prize winner, and the most prolific letter writer in history, was an advocate of English spelling reform. He was reportedly fond of pointing out its absurdities by proving that 'fish' could be spelt 'ghoti'. That is: 'gh' as in 'rough', 'o' as in 'women' and 'ti' as in palatial.

1 | INTRODUCTION

Understanding the principles of mortality schedules of ectotherms is necessary for unravelling the complexities of their population dynamics and life-history strategies. Ectotherms exhibit a natural decay with advancing age classes, characterized by an exponential decline in survivors that can be linearized to facilitate quantitative analyses and parameter estimation (Hilborn & Walters, 1992; see Figure 1), forming the foundation for age-structured population models. While this general pattern provides a fundamental framework, exceptions exist, notably in instances where extreme environmental variability (e.g., extreme climatic events) or interannual variability in recruitment affects annual survivorship (Forrester, 1995). Ectothermic species, through the course of evolution, have developed adaptive life-history traits to enhance survival. Understanding the interplay between inherent mortality schedules and the adaptive strategies that emerge is central to understanding the mechanisms of resilience and persistence within populations.

The study of age structures in fisheries science reveals key aspects of population dynamics (Hilborn & Walters, 1992). Age information, often derived from otoliths, provides a unique temporal perspective essential for understanding the life histories of fish species (Fowler, 2009). Otoliths, calcified structures within the inner ear of fish, serve as natural chronicles of growth, with increments representing discrete annuals periods of life. The ease and precision with which ages can be determined through otolith analysis offer a distinct empirical advantage for teleost fish species over methodologies applied to many other wild animals that humans attempt to manage or conserve (Fowler, 2009). This capability not only aids in the accurate estimation of age-specific mortality rates, recruitment patterns, and growth rates but also contributes to the formulation of effective fisheries management strategies (Hilborn & Walters, 1992).

Surgeonfishes (Acanthuridae) represent a common and diverse family circumtropically present on coral reefs and associated habitats. They are among the most studied reef-associated fish species because they are regarded as both ecologically important, given the diversity of feeding habits across the family, and a valuable resource as prime fishery targets for local economies (Dalzell et al., 1996). Given their high relative abundance and diversity, surgeonfishes were thought to be short-lived, fast-turnover species (DeMartini, 1993; Roberts, 1997) until the mid-1990s when the first age-based research demonstrated multidecadal lifespans for both small and large-bodied members of the family (Choat & Axe, 1996; Hart & Russ, 1996). Based on the principles of natural decay in marine ectotherms, such extended longevity suggested that natural mortality rates of surgeonfishes are very low (Choat & Axe, 1996; Choat & Robertson, 2002), implying a heightened sensitivity to fisheries extraction and a bet-hedging life-history strategy whereby reproduction is spread across many years because successful recruitment can be highly episodic (Longhurst, 2002). Episodic recruitment is certainly apparent in many species of surgeonfish (e.g., Doherty et al., 2004; Robertson, 1988; Trip et al., 2014). However, empirical evidence describing mortality patterns or fishery vulnerability among surgeonfishes has been rare. The earliest age-based catch curves showed considerable geographic variability within species across reefs of the Great Barrier Reef (GBR) (Hart & Russ, 1996) or among islands scattered throughout the Central- and West Atlantic (Robertson, Ackerman, et al., 2005), and often exhibited poor linear fits, possibly related to interannual recruitment variability or to complex mortality profiles. Catches of surgeonfishes dominate coastal fisheries throughout many regions of the Indo-Pacific (Taylor, 2019) and yet have shown a surprising resilience to fishing pressure (Ford et al., 2016; Houk et al., 2018). A better understanding of these dynamics is warranted to understand how schedules of cohort decline rectify the observed counterintuitive dynamics of surgeonfish populations across their vast distribution.

Recently, in an Indo-Pacific-wide study of the most harvested surgeonfish *Naso unicornis*, a consistent and novel two-phase pattern of cohort decline was discovered across adult age classes, whereby populations shift from lower-than-expected (based on observed longevity) survival rates earlier in life (but well past maturity) to greater-than-expected survival rates for the remainder

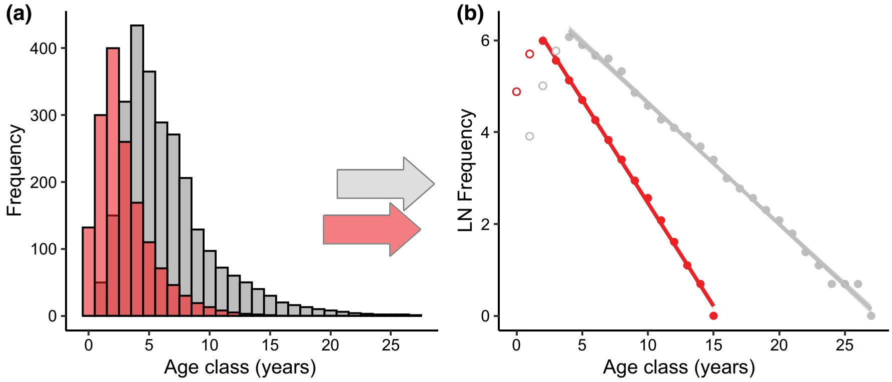


FIGURE 1 (a) Simulated age frequency distributions ('age structures') of fish populations with 80% and 65% annual survival rates with sampling selectivity in the first few years of life and very little interannual variability in recruitment. The decay in numbers per age class can be linearized through a log-transformation (b) to estimate the instantaneous total mortality rate (Z; the slope of the linear fit). This practice has drawbacks based on the underlying assumptions but should almost always result in a linear fit past the age at full recruitment in a representative sample of an ectothermic population.

of the lifespan (Taylor et al., 2019). This was summarized in a segmented, two-part linear catch curve that the authors termed 'biphasic mortality' (Figure 2). This pattern has been repeatedly identified in studies of surgeonfishes since (Pardee et al., 2020, 2022; Taylor et al., 2024; Figure 2); however, it is unclear how ubiquitous this pattern is across species or geography. Consistent patterns of variation in otolith increment sizes imply that fast-growing fish die young and that slower-growing fish become the oldest fishes, thereby linking this pattern to growth-type dependent mortality (Mulligan & Leaman, 1992; Taylor et al., 2019). The biphasic pattern, however, challenges traditional models of mortality in marine organisms. Such observations may reveal a nuanced interplay between intrinsic biological factors and extrinsic environmental pressures. This pattern holds implications for our understanding of population dynamics, as it influences demographic structure and resilience to fishery harvest and environmental change. Unravelling the underlying mechanisms is paramount for informing conservation and management strategies in a dynamic future.

The objective of this study was to determine the prevalence and geographic distribution of biphasic patterns in age-based catch curves for surgeonfishes. To do so, we compiled published and unpublished age demographic data from surgeonfish populations spanning ~90% of their global range and compared the fit of linear versus biphasic catch curves, examined the influence of sample size bias on our outcomes, and explored the implications of biphasic mortality on cohort depletion times. We then reviewed the potential biases in our data and the evidence for mechanisms underlying biphasic catch-at-age as well as the implications for the ecology and management of this important tropical reef-fish family.

2 | METHODS

The pantropical family Acanthuridae includes 85 currently recognized species in six genera: *Acanthurus* (42 species), *Ctenochaetus* (nine species), *Naso* (20 species), *Paracanthurus* (one species),

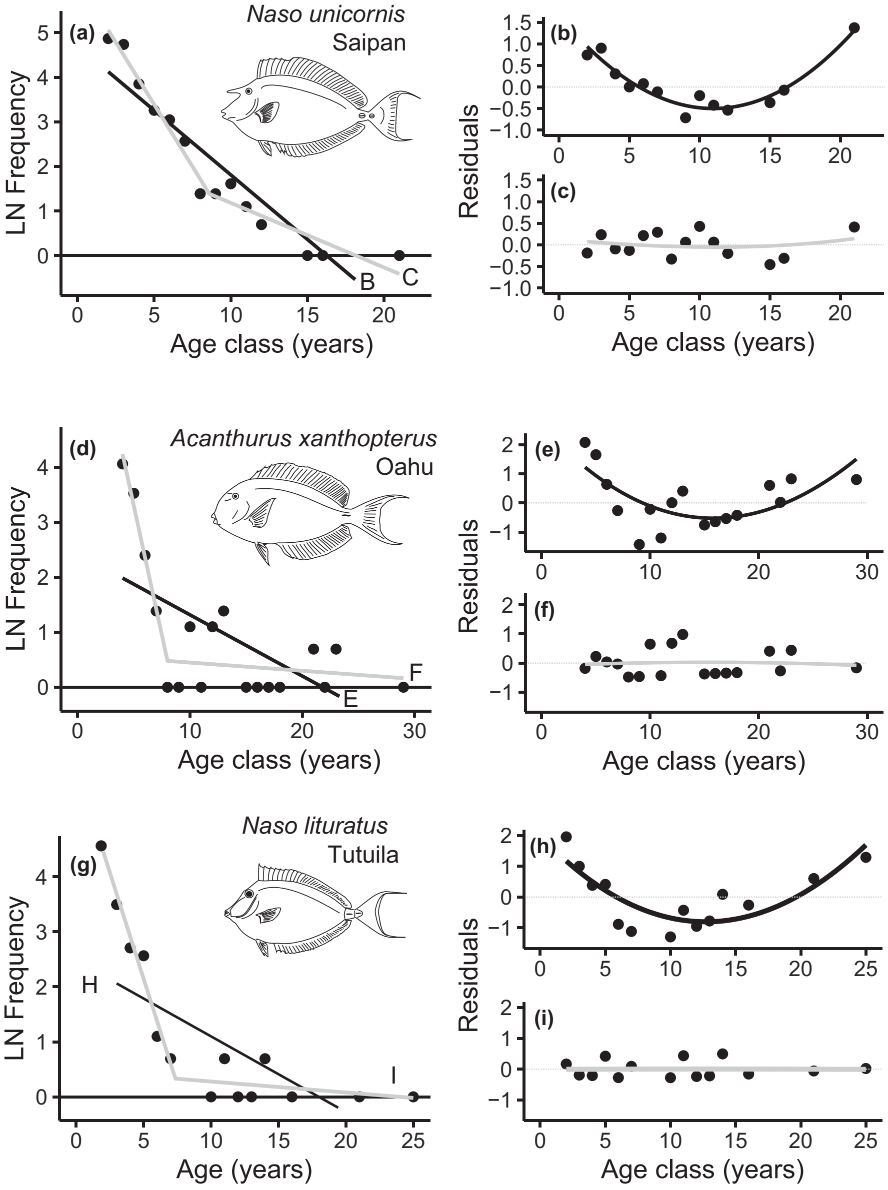


FIGURE 2 Populations of Pacific surgeonfishes commonly exhibit a segmented (grey) rather than linear (black) schedule of age-based catch curves (a, d, g). These examples demonstrate a U-shaped residual structure across age classes (b, e and h) with the linear fit, indicative of a distinct population-level shift from higher average rates of mortality earlier in life (but well past maturation) to lower average rates throughout the remainder of life. This residual fit is corrected with a simple two phase linear model (c, f, i). Examples from Taylor et al. (2019) and Pardee et al. (2020, 2022).

Prionurus (six species), and *Zebrasoma* (seven species). To investigate the prevalence and geographic distribution of biphasic catch curves across surgeonfishes globally, we compiled published and unpublished age-frequency data of surgeonfish populations across their distribution from the Indo-Central Pacific (hereafter ICP) and the Central-Western Atlantic (hereafter CWA). Authors from this study were involved in all sample collection efforts and aging standardization and validation has been highly consistent across this collective research group. Samples were collected through fishery-independent and fishery-dependent techniques, consistent within each study and detailed in the Supplemental material. Catch-curve analysis is sensitive to the accuracy of sample representation, which requires adequate sample sizes as well as encapsulating the breadth of age classes. Further, the likelihood of analytically identifying a segmented versus linear model fit inherently increases with the number of age classes. Hence, we filtered demographic datasets by threshold criteria to promote representation: (1) modal age (i.e., the age considered to be fully recruited to the sampling) must be below 10 years (surgeonfishes reach asymptote before 10 years [Choat & Robertson, 2002] thus an excessively old modal age suggests underrepresentation of younger age classes, perhaps through biased targeting of the largest fish); (2) sample size >30 specimens of post-modal age classes; (3) the number of age classes spanned beyond the mode should be ≥10 (surgeonfish populations have maximum ages greater than a decade); and (4) the number of age classes incorporated beyond the mode should be ≥10. We removed datasets ($n=8$) if two or more of the above criteria were violated. We explored the potential impacts of sample sizes through a bootstrap resampling procedure (see Appendix S1) and by considering stricter sample size criteria on our contributed data sets.

For each population, we fit a linear regression to the natural log of the frequency of individuals per age class starting from the modal (i.e., first fully recruited) age. We then fit a segmented model to the same data points using the package *segmented* (Muggeo, 2008) in R, which assigns an optimal breakpoint based on the data structure. The segmented model reflects a non-linear decline in log-transformed age-class frequency, specifically two distinct slopes at different phases. Analytically, this could be interpreted as two distinct mortality trajectories across age classes. However, biologically this likely reflects more complex underlying processes, notably growth-type dependent mortality among segments of a population with high variability in individual growth. We then used analysis of variance to test whether the segmented model provided a significantly better model fit compared with the standard linear model. Since most regressions were based on a low number of data points (mean = 16.2 age classes), we extended our significance threshold to P-values up to 0.10. Note that catch-curve analysis assumes full selectivity for all ages past the modal age class as well as invariable recruitment through time. Given that surgeonfishes exhibit asymptotic growth and were targeted primarily by spearfishing, the first assumption is likely valid. However, interannual variability in recruitment is a known feature of surgeonfishes, and can certainly bias the fitting of catch curves. Fortunately, this bias may be reduced with longer-lived species as the influence of variability is dampened across more age classes; nevertheless, we expect that past recruitment variability negatively influences our ability to identify and differentiate between catch-curve trajectories.

We examined the differential effects of accounting for biphasic catch-curve patterns on population processes versus effects using standard linear catch curves or lifespan-based mortality estimators by modelling population depletion under different mortality schedules. To avoid the influence of fishing mortality and to presume that empirical estimates of cohort decay reflect natural mortality (M), we identified 20 ‘pristine’ populations of 15 species in either remote protected locations (Central and Northern Mariana Islands, Northwest Hawaiian Islands, Chagos Archipelago) or in locations where surgeonfishes are not fishery targets (GBR, St. Helena, and Bermuda; Robertson, Choat, et al., 2005). For each population, we used the linear and segmented catch-curve analysis described above to infer different schedules of M. We also derived estimates of M using the Hamel and Cope (2022) estimator based on maximum observed lifespan ($t_{\max}$; Table S1). For each population, we developed a population model that tracked a cohort through time, based on the three empirically derived estimates of M. We then estimated the number of years for the cohort to naturally deplete to 20% of its original abundance (analogous to population turnover time) and compared the segmented with other natural mortality regimes through ratios.

3 | RESULTS

In total, we collated a dataset that represented age distributions of 78 populations of 26 species of surgeonfish across the tropics, representing all genera except *Paracanthurus* and *Prionurus*. Most of these samples were obtained from prior or ongoing research programs led by the authors (Choat & Axe, 1996; Choat & Robertson, 2002; Pardee et al., 2020, 2022; Robertson, Ackerman, et al., 2005; Taylor et al., 2014, 2019, 2024; Winston et al., 2017), with most contributions stemming from the Mariana Islands, GBR, Hawaiian Islands, and CWA. The sourced samples were almost circumtropical, reflecting the global breadth of latitudes and longitudes where surgeonfishes occur. After filtering, our final dataset contained 70 populations of 25 species (8929 specimens, mean = 127.6 population^{-1}), including 50 populations of 21 species from the ICP and 20 populations of four species from the CWA (Figure 3).

In total, we found that 78.6% (55/70) of surgeonfish populations displayed significant biphasic patterns (Figure 3). This pattern varied geographically, whereby 88.0% (44/50) of populations from the ICP were significantly biphasic and 55.0% (11/20) of populations from the CWA were significantly biphasic. Considering those at $p < 0.05$, the proportions change to 69% total, 78% for ICP, and 45% for CWA. The mean lifespan (i.e., observed maximum age) in the ICP was 26.4 years and was 19.6 years in the CWA. Of note, six of seven populations from higher latitude or colder Atlantic locations (Bermuda, Ascension Is., St. Helena, and Cabo Frio; mean lifespan = 26.9; Figure 3) showed biphasic catch curves, whereas

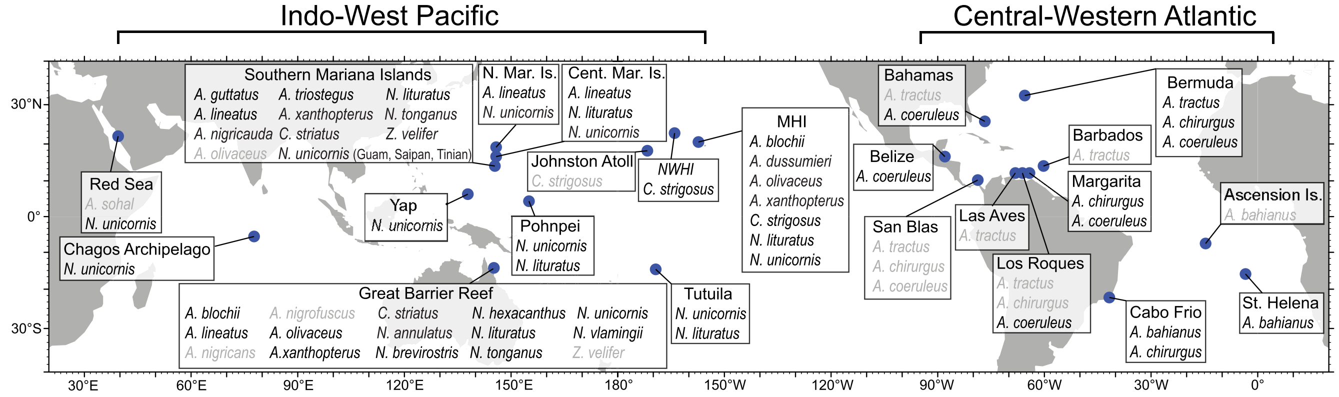


FIGURE 3 Across 70 populations of 25 surgeonfish species, biphasic catch-curve patterns were identified in 88% of populations in the Indo-Central Pacific and 55% of populations in the Central-Western Atlantic. Black species names indicate populations with a significantly better fit (*p*-value threshold of .10) using a segmented versus linear catch curve on age-based demographic sample data; grey species names indicate populations with non-significant differences between catch curves. In the tropical Atlantic, species are generally shorter-lived and biphasic patterns were more prevalent at colder, higher-latitude locations. Individual catch-curve plots for all populations are displayed in the Appendix S1.

five of the 13 populations from the warmer Caribbean region (mean lifespan = 15.6 years) were significantly biphasic. Our threshold of 30 specimens per population from the modal age class was liberal and used to retain as much information as practical. However, if increased to 50 specimens, despite losing 15 populations, the values for the CWA and ICP are consistent at 53% and 90%, respectively; at 100 specimens (retaining only 22 populations), the values increase to 75% and 100%, respectively. Catch-curve plots and criteria summary metrics for every population are presented in the Figure S1 and Table S2.

Segmented catch curves predicted cohort depletion times (i.e., time required for an unfished cohort to decay to 20% of original abundance) ranging from 2.1 to 13.0 years. These ranges were 8.6–72.3 and 7.5–13.1 years for the linear catch curve and the Hamel and Cope (2022) lifespan-based estimators, respectively. Note the generally poor fit of the linear model resulted in four depletion times that were unrealistic (37.0, 45.5, 52.6, and 72.3 years) compared with observed life spans, and otherwise ranged up to 32.7 years. Overall, segmented catch curves inferred cohort depletion times that were over twice as fast as standard predictors, with mean ratios that were 25% and 52% of the estimated depletion time of standard estimators (Figure 4).

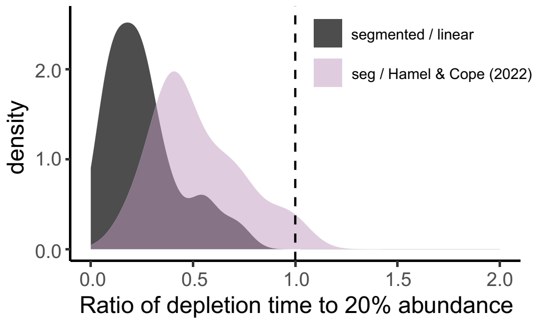


FIGURE 4 Population models based on life-history traits of 20 unfished surgeonfish populations representing 15 species demonstrated that the time it takes for a cohort to naturally deplete to 20% of its original abundance is more than twice as fast as that predicted by application of linear catch curves and lifespan-based estimators. Populations include *Acanthurus* ($n = 5$), *Ctenochaetus* ($n = 2$), and *Naso* ($n = 10$) from the Indo-West Pacific and *Acanthurus* ($n = 3$) from the Central-Western Atlantic.

4 | DISCUSSION

Given the comprehensive dataset comprising age distributions of surgeonfishes through all three major oceans, our analysis reveals a substantial prevalence of biphasic catch-curve patterns in this family. Remarkably, nearly 80% of surgeonfish populations globally exhibited significant biphasic patterns, with 88% observed across the ICP region. Geographic variation was evident, with only 53% of the CWA populations exhibiting biphasic patterns. Yet collectively this demonstrates the global pervasiveness of this pattern of cohort decline and spans all speciose genera across the surgeonfishes independent of diet, nutritional ecology, and foraging mode. These findings grow more robust when accounting for sample size limitations, whereby the prevalence of biphasic catch-at-age increased upon considering only populations with the highest sample sizes.

The biphasic log catch-at-age pattern suggests that natural mortality differs substantially between younger and older adult surgeonfish. However, we must first explore potential systematic biases that might elicit the observed pattern. Interannual changes in year-class strength, age-reading errors, and differences in catchability between younger and older fish might erroneously produce a biphasic catch curve where otherwise single linear catch curves are more representative. Regarding recruitment variability, surgeonfish recruitment has the potential to be highly variable across years (Robertson, 1988; Trip et al., 2014). In our compiled dataset, interannual recruitment variability can be observed in many populations through residuals to the segmented catch curve, yet this variability sometimes muddles the analytical imprint of biphasic catch curves where it otherwise may exist (e.g., Ascension Island *Acanthurus bahianus* and Red Sea *Acanthurus sohal*; Figure S1). While extremely successful recruitment years could potentially result in overrepresentation of some older age classes, this is unlikely given the density-dependent mortality observed in cohorts of large recruitment pulses (Doherty et al., 2004). Moreover, the recruitment variability observed in the initial descending arm of the biphasic catch curve is not of a magnitude that would 'bend' catch curves across additional decades. Second, regarding age-reading errors, surgeonfish annuli have been validated numerous times and are comparatively easy to interpret. Thus, we feel that potential age reading errors would have little effect on catch-curve patterns as the errors would need to be substantial (more than several years) to have such a systematic effect on analyses. Finally, catchability differences between younger and older surgeonfishes could produce nonlinear catch-at-age patterns, although it is unclear how or why this would manifest. Surgeonfishes display asymptotic growth, meaning young and old adults have similar mean sizes. To produce biphasic curves, older individuals would have to be selected at higher rates than younger individuals, yet across large demographic samples, older age classes are often either not sampled or represented by one or two individual specimens, implying they are notably rare in the wild.

The perplexing pairing of low adult survival with multidecadal longevity in tropical surgeonfishes, as well as its prevalence in different genera and all three tropical oceans, suggests complex age-specific shifts in adult mortality and warrants exploration of potential mechanisms driving this phenomenon. Confusion over this pairing dates to the first age-based work on surgeonfishes (Craig et al., 1997). Most surgeonfishes exhibit rapid growth to asymptotic size relative to their lifespan (high growth coefficient values, K), producing what has been termed 'square' or 'flat-topped' growth curves (Choat & Robertson, 2002; Fowler, 2009). In theory, such fast-growing species should not exhibit low natural mortality or long lifespans (Craig, 1985), although many exceptions to this rule exist. A recent meta-analysis using longevity-based estimators of natural mortality (M) expressed confusion over the extreme departure from expected ratios of mortality to growth (M/K ratios) across the surgeonfishes (Nadon & Ault, 2016). However, our results demonstrate that linear or longevity-based predictors of mortality are not suitable for most surgeonfish species and that, if we consider the initial descending arm of the biphasic catch curve ('M1'), M/K ratios within unharvested surgeonfishes are much closer to that predicted by theory (mean = 0.86 ± 0.15 SE versus 0.3 ± 0.1 [Nadon & Ault, 2016]).

Despite the widespread application of static natural mortality rates in fish populations, evidence for within-population size-dependence in natural mortality is strong (Lorenzen et al., 2022). Surgeonfishes show high variability in individual growth early in life, a feature that can be visualized in simple size-at-age plots. Hence, the 'fast-growers die young' foundation can be rectified *within* surgeonfish populations by patterns of growth-type dependent mortality (Mulligan & Leaman, 1992), whereby a wide range of size-dependent mortality manifests across age classes exhibiting extreme variability in size-at-age. By relating growth profiles in otolith increments to body growth, a simplified binary view of populations (i.e., fast- versus slow-growers) has demonstrated that the oldest fish in multiple populations of *Naso unicornis* are comprised of 'slow-growers' (Taylor et al., 2019). That study demonstrated that if fast growers die young, but outcompete slow growers early on, a two-phase catch curve can reasonably manifest at the population level. Ultimately, the concept of slow growers becoming old fish was well-supported across locations with empirical data in that study. However, as a mechanism for mortality patterns, this conceptual model probably explains, at best, only a portion of what is happening in the population dynamics of species with naturally high variability in demographic phenotypes.

So, what might underly such high variability in individual growth and consequent mortality among the surgeonfishes? Three plausible explanations could be genetic differences, sex-specific variation, and the influence of different habitats. Genetic differences, though plausible, may be unlikely as a primary factor, given the aggregative reproductive behaviour observed among surgeonfishes and the low genetic structuring across Indo-Pacific basins for several species of *Naso* (Horne et al., 2008). Sex-specific differences were explored using our dataset, revealing that males and females within species exhibit similar patterns of age-specific mortality and longevity, with only subtle differences in growth for a minority of species (Pardee et al., 2022; Taylor et al., 2024). The role of habitats in influencing growth rates and mortality profiles is evident from studies in the GBR (Gust et al., 2002; Hart & Russ, 1996) and the tropical Atlantic (Robertson, Ackerman, et al., 2005). Although most collections in our compiled dataset were conducted at the general location scale, hindering habitat testing, datasets with habitat delineation demonstrated distinct growth and mortality profiles. The inherent habitat diversity and patchiness of coral reef ecosystems pose challenges to identifying proximal mechanisms but underscore the likely contribution of these factors to the perplexing population dynamics of surgeonfishes.

We suggest that surgeonfishes exhibit an atypical, complex pattern of natural mortality. Given their rapid growth and multidecadal lifespans, surgeonfish body-size distributions would be highly left-skewed with a pile up of individuals around the asymptotic length under expected schedules of cohort survivorship (Prince et al., 2015). However, this pattern of size distribution is exceedingly rare, even in remote, unfished surgeonfish populations (Choat & Axe, 1996; Taylor et al., 2019). Extended lifespans within populations are regarded as a bet-hedging strategy by prolonging the reproductive phase as a natural safeguard against potential recruitment during years marked by unfavourable recruitment conditions (Craig, 1985; Robertson, Ackerman, et al., 2005). However, we found that only a small portion of cohorts in unexploited populations reach extended ages, with 80% of a cohort having died by about 5 years of age. This consistent pattern reflects a population turnover rate that is much faster than predicted by the lifespan potential, thereby a possibly resilient life-history strategy to exploitation. Faster natural turnover rates may help explain the resilience to overexploitation observed in many, but not all, harvested surgeonfish populations across the Indo-Pacific.

Considerable geographic differences exist in the prevalence of biphasic catch curves. It is unclear whether these differences reflect evolutionary divergence within or across genera or are an artefact of sampling geography within ocean basins. Only the genus *Acanthurus* exists in the Atlantic, but confining comparisons to this genus alone does not explain the differences because 79% of the ICP *Acanthurus* populations were significantly biphasic. Surgeonfish longevity increases starkly along latitudinal gradients of decreasing winter ocean temperature (Robertson, Ackerman, et al., 2005; Taylor et al., 2019, 2024) and the analytical power for detecting a significant segmented model fit increases with the number of age classes incorporated. When corrected for temperature, surgeonfishes in the CWA are approximately 7–10 years shorter lived than those in the ICP (Figure S2). All but one population from colder regions of the CWA (mean lifespan >26 years) displayed biphasic catch curves, whereas only 38% of the Caribbean populations (mean lifespan of 16 years) were significantly biphasic. Differences in the relationships between temperature, body size, and lifespan for both surgeonfishes and parrotfishes (Choat & Robertson, 2002; Taylor et al., 2018) have been attributed to evolutionary divergence possibly related to ocean basin size and disturbance histories over geological time scales. Whether the geographic disparity observed here reflects evolutionary divergence, an artefact of analytical power, or some combination of both is unclear.

The identification of consistent and ubiquitous trends in empirical datasets, particularly those contrary to preconceived assumptions such as demonstrated here, serves as a catalyst for paradigm shifts in scientific understanding and may foster a more accurate and nuanced portrayal of the natural world. This study on surgeonfishes has scrutinized empirical evidence demonstrating a unique age-based catch curve exhibiting two possibly distinct phases. Although catch curves are generally indicative of patterns of mortality, our biphasic linear application is not an adequate mortality model for application in population assessments. In most instances, while the initial arm of the descending curve fit the data well, the second descending arm was almost always fit to too few data points and across many zero, one, and two count values per age class. We recommend further work to identify the mechanistic age-specific mortality models for surgeonfishes for better application in population models.

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DATA AVAILABILITY STATEMENT

Raw data and code are available from https://github.com/brettmtaylor/biphasicmortality.

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REFERENCES

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

Choat, J. H., & Robertson, D. R. (2002). Age-based studies on coral reef fishes. In P. F. Sale (Ed.), *Coral reef fishes: Dynamics and diversity in a complex ecosystem* (pp. 57–80). Academic Press.

Craig, J. F. (1985). Aging in fish. *Canadian Journal of Zoology*, *63*, 1–8. https://doi.org/10.1139/z85-001

Craig, P. C., Choat, J. H., Axe, L. M., & Saucerman, S. (1997). Population biology and harvest of the coral reef surgeonfish *Acanthurus lineatus* in American Samoa. *Fishery Bulletin*, *95*, 680–693.

Dalzell, P., Adams, T. J. H., & Polunin, N. V. C. (1996). Coastal fisheries in the Pacific Islands. *Oceanography and Marine Biology: An Annual Review*, *34*, 395–531. https://doi.org/10.1201/9780367805074

DeMartini, E. E. (1993). Modeling the potential of fishery reserves for managing Pacific coral reef fishes. *Fishery Bulletin*, *91*, 414–427.

Doherty, P., Dufour, V., Galzin, R., Hixon, M., Meekan, M., & Planes, S. (2004). High mortality during settlement is a population bottleneck for a tropical surgeonfish. *Ecology*, *85*, 2422–2428. https://doi.org/10.1890/04-0366

Ford, A. K., Bejarano, S., Marshell, A., & Mumby, P. J. (2016). Linking the biology and ecology of key herbivorous unicornfish to fisheries management in the Pacific. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *26*, 790–805. https://doi.org/10.1002/aqc.2623

Forrester, G. E. (1995). Strong density-dependent survival and recruitment regulate the abundance of a coral reef fish. *Oecologia*, *103*, 275–282. https://doi.org/10.1007/BF00328615

Fowler, A. J. (2009). Age in ears from otoliths of adult tropical fish. In B. S. Green, B. D. Mapstone, G. Carlos, & G. A. Begg (Eds.), *Tropical fish otoliths: Information for assessment, management and ecology* (pp. 55–92). Springer.

Gust, N., Choat, J. H., & Ackerman, J. L. (2002). Demographic plasticity in tropical reef fishes. *Marine Biology*, *140*, 1039–1051. https://doi.org/10.1007/s00227-001-0773-6

Hamel, O. S., & Cope, J. M. (2022). Development and considerations for application of a longevity-based prior for the natural mortality rate. *Fisheries Research*, *256*, 106477. https://doi.org/10.1016/j.fishres.2022.106477

Hart, A. M., & Russ, G. R. (1996). Response of herbivorous fishes to crown-of-thorns starfish *Acanthurus planci* outbreaks. III. Age, growth, mortality and maturity indices of *Acanthurus nigrofuscus*. *Marine Ecology Progress Series*, *136*, 25–35. https://doi.org/10.3354/meps136025

Hilborn, R., & Walters, C. (1992). *Quantitative fisheries stock assessment: Choice, dynamics and uncertainty* (p. 570). Springer.

Horne, J. B., van Herwerden, L., Choat, J. H., & Robertson, D. R. (2008). High population connectivity across the indo-Pacific: Congruent lack of phylogeographic structure in three reef fish congeners. *Molecular Phylogenetics and Evolution*, *49*, 629–638. https://doi.org/10.1016/j.ympev.2008.08.023

Houk, P., Cuetos-Bueno, J., Tibbatts, B., & Gutierrez, J. (2018). Variable density-dependence and the structuring of coral-reef fisheries across 25 years of exploitation. *Scientific Reports*, *8*, 5725. https://doi.org/10.1038/s41598-018-23971-6

Longhurst, A. (2002). Murphy's law revisited: Longevity as a factor in recruitment to fish populations. *Fisheries Research*, *56*, 125–131. https://doi.org/10.1016/S0165-7836(01)00351-4

Lorenzen, K., Camp, E. V., & Garlock, T. M. (2022). Natural mortality and body size in fish populations. *Fisheries Research*, *252*, 106327. https://doi.org/10.1016/j.fishres.2022.106327

Muggeo, V. M. R. (2008). Segmented: An R package to fit regression models with broken-line relationships. *R News*, *8*, 20–25.

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

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

Pardee, C., Taylor, B. M., Felise, S., Ochavillo, D., & Cuetos-Bueno, J. (2020). Growth and maturation of three commercially important coral reef species from American Samoa. *Fisheries Science*, *86*, 985–993. https://doi.org/10.1007/s12562-020-01471-9

Pardee, C., Wiley, J., Schemmel, E., Fendrick, T., & Giglio, J. (2022). Comparative demography of four large-bodied surgeonfish. *Environmental Biology of Fishes*, *105*, 231–245. https://doi.org/10.1007/s10641-022-01216-w

Prince, J., Hordyk, A., Valencia, S. R., Loneragan, N., & Sansbury, K. (2015). Revisiting the concept of Beverton-Holt life-history invariants with the aim of informing data-poor fisheries assessment. *ICES Journal of Marine Science*, *72*, 194–203. https://doi.org/10.1093/icesjms/fsu011

Roberts, C. M. (1997). Ecological advice for the global fisher crisis. *Trends in Ecology & Evolution*, *12*, 35–38. https://doi.org/10.1016/S0169-5347(96)20109-0

Robertson, D. R. (1988). Abundances of surgeonfishes on patch-reefs in Caribbean Panama: Due to settlement, or post-settlement events? *Marine Biology*, *97*, 495–501.

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

Robertson, D. R., Choat, J. H., Posada, J. M., Pitt, J., & Ackerman, J. L. (2005). Ocean surgeonfish *Acanthurus bahianus*. II. Fishing effects on longevity, size and abundance? *Marine Ecology Progress Series*, *295*, 245–256. https://doi.org/10.3354/meps295245

Taylor, B. M. (2019). Standing out in a big crowd: High cultural and economic value of *Naso unicornis* in the insular Pacific. *Fishes*, *4*, 40. https://doi.org/10.3390/fishes4030040

Taylor, B. M., Choat, J., DeMartini, E., Hoey, A., Marshell, A., Priest, M. A., Rhodes, K. L., & Meekan, M. G. (2019). Demographic plasticity facilitates ecological and economic resilience in a commercially important reef fish. *Journal of Animal Ecology*, *88*, 1888–1900. https://doi.org/10.1111/1365-2656.13095

Taylor, B. M., McInnis, A. J. K., Deinhart, M., Kawahigashi, K., & Gourley, J. (2024). Comparative demography of surgeonfishes from the tropical western Pacific. *Reviews in Fish Biology and Fisheries*, *34*, 353–370. https://doi.org/10.1007/s11160-023-09816-0

Taylor, B. M., Rhodes, K. L., Marshell, A., & McIlwain, J. L. (2014). Age-based demographic and reproductive assessment of the orangespine *Naso lituratus* and bluespine *Naso unicornis* unicornfishes. *Journal of Fish Biology*, *85*, 901–916. https://doi.org/10.1111/jfb.12479

Taylor, B. M., Trip, E. D. L., & Choat, J. H. (2018). Dynamic demography: Investigations of life-history variation in the parrotfishes. In A. S. Hoey & R. M. Bonaldo (Eds.), *Biology of parrotfishes* (pp. 69–98). CRC Press.

Trip, E. D. L., Craig, P., Green, A., & Choat, J. H. (2014). Recruitment dynamics and first year growth of the coral reef surgeonfish *Ctenochaetus striatus*, with implications for acanthurid growth models. *Coral Reefs*, *33*, 879–889. https://doi.org/10.1007/s00338-014-1182-x

Winston, M. S., Taylor, B. M., & Franklin, E. C. (2017). Intraspecific variability in the life histories of endemic coral-reef fishes between photic and mesophotic depths across the Central Pacific Ocean. *Coral Reefs*, *36*, 663–674. https://doi.org/10.1007/s00338-017-1559-8

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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