Title

A Length-Based Approach to Estimating Age Among Tropical Reef Fish Populations

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A Length-Based Approach to Estimating Age Among Tropical Reef Fish Populations

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Marine Biology

by

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This thesis of Ram Iyer is approved, and it is acceptable in quality and form for publication and on microfilm and electronically.

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DEDICATION

This thesis is dedicated to several people. My parents, Ram and Sharon, have always driven me to pursue my passions and make a career of it. They instilled that ingenuity goes hand in hand with education and that belief led me to this field where my passions could flourish with creative thinking. My wife Amy has been a constant source of love, support and encouragement through the confusing and stressful moments of my education, and I can say I wouldn’t be where I am today without those gifts. My grandmother Meena who passed many years ago was always my biggest supporter with my education and she instilled a true reverence for it in me growing up. I will always be grateful to her for that. My sister, Asha, has always been my lifeline to remember to not take things too seriously. She is always there to remind me that the world is beautiful if you only take the time to look. Lastly, this is dedicated to my son, Bodhi. You changed my world the moment you were born. Thank you. I love you all.

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ABSTRACT OF THE THESIS

A Length-Based Approach to Estimating Age Among Tropical Reef Fish Populations

by

Ram Iyer

Master of Science in Marine Biology

University of California San Diego 2022

Professor Stuart A. Sandin, Chair

Time and energy are finite resources in any environment, and how and when organisms use their available resources to survive and reproduce is the crux of life history theory (Gadgil and Bossert 1970; Balon 1975; Stearns 1976). The different survival strategies used by animals are often shaped by their environment in addition to their biology (Winemiller and Rose 1992), which allows for exploration into biological variability when

environmental factors are known. For this reason, the Line Islands in the Central Pacific provide an ideal location to perform observational studies due to their unique productivity gradient and fish assemblage structures across the island chain (Sandin et al. 2008; DeMartini et al. 2008; Fox et al. 2018; Zgliczynski et al. 2019). Many of the world's coral reefs are in remote regions that lack monitoring programs or even local populations, so conducting ecological surveys on fish communities in these regions can require extensive amounts of time, energy, resources and people. The inherent variability an environment exerts on the many factors that contribute to growth over a lifetime make it difficult to generate a directly proportional formula that calculates age. A novel age estimation method was developed that utilizes *in-situ* visual census data to estimate the age of fishes, and as a case study, several fish were chosen as representative species to explore its capabilities. Through this process, new ecological information and insight can be gained about the age structures of fish populations both between and throughout the Line Islands.

Introduction

Growth, maintenance, reproduction and mortality are the base aspects of life that are studied to understand how populations adapt to their environment. These aspects are part of the life history theory framework that resource allocation drives a species' strategy for survival (Winemiller and Rose 1992). One dimension of these survival strategies is time and how it relates to different life history traits like age at maturity or the maximum age of the species. Collecting age data for marine species in remote locations is traditionally a resource-heavy endeavor, and the amount of effort currently required to process and analyze them on a community level is prohibitive for most noncommercial organizations (Campana 2001; Green and Bellwood 2009; Green et al. 2009). Conducting underwater visual surveys of fish populations in complex ecosystems like coral reefs can provide ample amounts of descriptive data with relatively low effort (Brock 1954; Green and Bellwood 2009), however, these methods lack the ability to generate the temporal information crucial for generating age-structures of populations. For this reason, a novel method was developed that utilizes length data to generate estimated ages of fish populations, and it is presented alongside a case study of seven reef associated species throughout the Line Islands.

Time and energy are finite resources in any environment, and how and when organisms use their available resources to survive and reproduce is the crux of life history theory (Gadgil and Bossert 1970; Balon 1975; Stearns 1976). The tradeoffs an organism makes in resource allocation can be measured within this framework through traits that encompass the optimal survival strategy given its environment (Stearns 1976; Winemiller and Rose 1992). As organisms progress through life, they reach certain biological milestones, and the age at which they reach those milestones can provide insightful information both on a population and its environment (Winemiller and Rose 1992; Lambert 2008; DeMartini et al. 2018). For example, older fish have higher quality eggs and larvae than similarly sized younger fish (Marteinsdottir and and Steinarsson 1998; Lambert 2008; Berkeley et al. 2016), so populations with older age classes that are disproportionately selected by pressures like fishing produce young with lower survivorship. This is an example of how environmental factors can indirectly affect entire populations over generations. The age ranges regional populations encompass can exhibit variance from one another based on the differences of each ecosystem (Helser and Lai 2004), so being able to quantify differences in regional mean ages generates a more complete view of the community and populations being studied. When contrasted alongside environmental gradients, population-level mean ages can provide insight into the trajectory of a species and the factors affecting them.

Roughly 1,000 miles south of the Hawaiian Archipelago in the Central Pacific, the Line Islands are a chain of atolls and islands that have several environmental gradients including productivity (Fox et al. 2018; Zgliczynski et al. 2019) and fishing (DeMartini et al. 2008; Sandin et al. 2008) that provide an ideal setting to explore large-scale population dynamics. Previous expeditions have garnered robust ecological data sets from both the Northern and Southern Line Islands. This data has shown significant variability in spatial population demographics of fish assemblages across the island chain (Sandin et al. 2008; Williams et al. 2011; Edwards et al. 2013; Zgliczynski 2015), however, age-based studies have been conducted on a select few species (Zgliczynski 2015) from these expeditions due to the logistical limitations of processing biological data.

As a case study, seven representative species were chosen to explore the capabilities of an age estimation method. Initial concepts were tested on a narrow range of herbivorous fishes in order to contrast the productivity gradient present throughout the Line Islands while attempting to limit trophic interactions associated with higher level consumers. Herbivores play a crucial role on coral reefs, not only as a primary consumer in the food web, but also as a key feeding guild to maintain reef health and diversity (Lewis 1986; Hughes et al. 2007; Burkepile and Hay 2006, Burkepile and Hay 2010; Bellwood et al. 2012). For these reasons herbivores can be organized into functional groups based on how and what they eat that allows for them to be treated as indicators of general reef health (Green and Bellwood 2009). These seven species represent several of the dominant herbivorous families of fishes on tropical coral reefs (Williams et al. 2011) which allows for a subsampling of the greater reef fish community at the Line Islands.

Many of the world's coral reefs are in remote regions that lack monitoring programs or even local populations, so conducting ecological surveys on fish communities in these regions can require extensive amounts of time, energy, resources, and people. Measurements like length or quantity are descriptive population metrics that are used to calculate how much of a species is in an environment, while temporal measurements like length-at-age data can help describe the quality of that population. Underwater visual surveys are currently the best ways to collect census data, however collecting temporal data on fish populations either requires iterative sampling or extractive sampling. Both of these methods are often constrained by the funding, time and the energy required to process biological age data for community-wide assessments. These data are bound by the time and region in which they were collected as environmental variability affects the very growth metrics being calculated. For this reason, age-related census data currently has limitations to its application outside of its spatiotemporal range and the resolution it provides is limited by resources. Having access to age data of reef fish populations that can be used outside of their temporal constraints would allow for a more holistic approach in ecological assessments, and provide a simple, albeit constrained, workaround to an otherwise complex problem.

The inherent variability an environment exerts on the many factors that contribute to growth over a lifetime make it difficult to generate a directly proportional formula that calculates age. Many species of reef fishes have ontogenetic growth patterns that further confuse general estimations of age. One of the best approximations of this is the Von Bertalanffy Growth Function, or VBGF. The Beverton-Holt model of the VBGF is a three-parameter nonlinear equation that considers much of the ecological and biological variability that affects growth (Beverton 1954; Beverton and Holt 1957). This equation models the growth of a species over time, and due to the variability of that growth, must be parameterized for each species and its growth strategies. The utility of this equation is generally bound by the same constraints as the data that is used to generate it, so it often provides a narrow view of any populations being studied.

This study is meant to validate the creation of a novel method to approximate the relative age differences of fish populations with *in situ* visual census data. Archived age data, that traditionally would exclude it from being used to estimate ages in current ecological surveys, was used concurrently with a set of functions that allowed for the estimation of relative ages. These functions permitted the generation of population-level age data for interpretation. This process is bound by several assumptions that restrict the scope of how the data may be utilized, however, employing this age estimation method along with current methods of quantifying spatial metrics will establish a more holistic approach to ecological monitoring and allow for a level of resolution of age data that is generally not possible.

Methods

Study Sites

The Line Islands were selected due to robust fish surveys conducted as part of the 100 Island Challenge effort from Scripps Institution of Oceanography. This island chain straddles the equator and is regionally divided into the Northern and Southern Line Islands. The Northern Line Islands (NLI) exhibit fishing and productivity gradients that lead to distinct fish biomass and trophic distributions through the archipelago (Sandin et al. 2008; DeMartini et al. 2008; Zgliczynski et al. 2019). Three of the NLI- Tabuaeran, Teraina and Kiritimati- are populated and display many of the common signs of fishing pressure being exerted on local fish populations like lower mean fish biomass and a reduced apex predator biomass compared to nonfished islands in the chain (Sandin et al. 2008; DeMartini et al. 2008). These three islands also fall into the higher ranges of the latitudinal productivity gradient present through the Line Islands (Fox et al. 2018; Zgliczynski et al. 2019). Palmyra and Kingman, which fall into the intermediate ranges of productivity (Zgliczynski et al. 2019), lack populations and any fishing that does occur there is negligible and unlikely to elicit signs of systemic fishing pressure. These unfished islands have the highest predator biomass and abundance throughout the NLI, but a lower abundance of herbivores relative to fished islands in the chain (Zgliczynski and Sandin 2017). The Southern Line Islands (SLI) exhibit a latitudinal gradient in pelagic primary productivity that almost doubles in productivity from south to north (Fox et al. 2018). None of the SLI have standing human populations that would contribute to noticeable amounts of fishing pressure. This leads to similar pattern of high apex predator and low herbivore abundance and biomass as unfished islands in the Northern Line Islands (Zgliczynski and Sandin 2017).

Study Species

Herbivores were the focus of this study due to the vital role they play in suppressing algal growth (Burkepile and Hay 2006, Burkepile and Hay 2010; Hixon 2015) and to omit any additional trophic interactions higher level consumers may experience which could mask signals across productivity gradients. Seven species were selected based on abundance, sampling consistency across the islands, diversity of feeding strategies and diversity of diet: *A. nigricans*, *C. marginatus*, *C. striatus*, *C. sordidus*, *S. frenatus*, *S. rubroviolaceus*, and *S. aureus*. Fishes in the family *Acanthuridae* generally follow a growth strategy of attaining their maximum size within a few years and then maintaining that size for the remainder of their lives, which may be 40+ years (Choat and Robertson 2002). *Scaridae*, or parrotfishes, have diverse growth strategies, reaching their maximum size in as short as 5 years or as long as 25 to 30 years (Choat and Robertson 2002). All six species of *Acanthuridae* and *Scaridae* in this study are considered roving grazers, however their diets and feeding strategies vary among them (Bellwood and Choat 1990; Purcell and Bellwood 1993; Choat and Clements 1998; Choat et al. 2002; Hamilton et al. 2014). *A. nigricans*, *C. marginatus* and *C. striatus* are algivore/detritovores that cover wide areas of reef as they feed (Choat and Clements 1998; Hamilton et al. 2014; Zgliczynski 2015). *C. sordidus*, *S. frenatus*, and *S. rubroviolaceus* are primarily roving grazer scraper/excavators that feed on algae, and detritus but in doing so leave barren substrate in their wake (Bellwood and Choat 1990; Choat and Clements 1998; Hamilton et al. 2014). *Stegastes aureus*, the lone *Pomacentridae* in this study, is included as a representative territorial herbivore with a gradual growth rate over its life that limits asymptotic growth after maturation (Zgliczynski 2015). *S. aureus* was included to increase the diversity of feeding strategies in this study. *S. aureus* is a territorial herbivore that feeds mainly on algae and invertebrates from a narrow home range (Miller et al. 2019). Species and trophic classification data followed the functional groupings described in Green & Bellwood 2009. Note that not all species were found on all islands, and island-specific analyses were omitted if there were insufficient data.

Data Acquisition and Parameter Generation

A database was created using Microsoft Excel (V16.60) to centralize the primary life history parameters that describe size-at-age and length-weight relationships of herbivorous tropical reef fishes. Allometric length-weight parameters, VBGF parameters and additional key values related to fish growth and longevity were included in the database. All data were standardized, sourced and verified manually to ensure accuracy. Values were obtained through literature searches, professional correspondence, digital data extraction, and samples collected from previous surveys conducted in part by the Sandin Lab (Zgliczynski 2015). A final parameter, the estimated variance around the VBGF, was collected, though it is not typically reported in standard databases. Estimating this value requires the raw length-age data used to generate the three VBGF parameters. These data were not available in an accessible format for every species in the study, so the web application Web Plot Digitizer (Rohatgi 2021) was used to extract data points from figures in published studies that represented raw data. These figures (Choat et al. 1996; Trip et al. 2008; DeMartini et al. 2018) contain the necessary raw length-age data needed to generate the variance of the VBGF curves. Parameters generated through this method differed by a maximum of 0.084%, therefore the variance generated by this method should have negligible differences from the true raw data. This method provided an alternative way of generating critical values that are traditionally generated from raw data when all other options had been exhausted.

Fish census data used in this study were obtained by the Sandin Lab and partners during expeditions to the NLI in 2005 and the SLI in 2009. Belt transect survey methods were utilized as described in DeMartini et al. (2008) and Friedlander et al. (2010). Briefly, paired SCUBA divers would survey a 25 m transect with an 8 m wide swim ‘out’ to survey fish > 20 cm and a 4 m wide swim ‘back’ to survey fish ≤ 20 cm. Fish were counted, identified to species level, and lengths were visually estimated to the nearest 5 cm. Three of the seven species had raw length-age data that had been previously collected by the Sandin Lab (Zgliczynski 2015). This raw length-age data was generated manually through the removal and reading of otoliths as described in Green et al. 2009.

Once known data sources were exhausted in creating the database, the most robust and complete data sets were selected for further scrutiny. Components of each potentially viable data set including sample size, region of study, accessibility to associated raw data and completeness of all required parameters were then considered. In analysis of size-at-age relationships, location-specific parameters provide additional accuracy that can minimize environmental variability, because these values embody that variability through biological growth rates (Von Bertalanffy 1938; Schnute and Fournier 1980). As will be detailed, there was room for focus to be kept on quality data in similar regions instead of solely for the region-specific studies, which allowed for less stringent data requirements. This is based on an assumption of our estimator that all ages are relative to each other instead of quantitative estimates of absolute age. The flexibility of this assumption was beneficial because in many cases data-poor tropical species only have a single usable data set if any.

To generate four of the five parameters needed for the age estimator from both lab-provided data sets and extracted data sets, the R packages FSA (Ogle et al. 2022) and nlstools

(Baty et al. 2015) were used. These packages allow for rapid assessment and generation of VBGF parameters given individual size-at-age data. In addition to the K, t_0 and L_{inf} parameters generated by the packages (see below), variance of the model was also calculated with outputs from the packages. The fifth parameter needed for our age estimation function is the maximum age a species can attain. These values were gathered from current literature or contrasted from data sets against current literature.

Age Estimation Function

Based on some simplifying assumptions, the size-at age relationship can be used to estimate the age of an individual fish based upon an estimation of body length. This age estimator utilizes the Beverton-Holt model (Beverton 1954; Beverton and Holt 1957) of the VBGF:

$$L_t = L_{inf}\,(1\text{-}e^{-K(t-t0)})$$

which requires three parameters and either a given age or length. The VBGF parameterizes asymptotic mean length (L_{inf}) of a fish population which is where the rate of growth is zero, a growth rate coefficient (K) that describes the rate at which that asymptotic length is reached, and the extrapolated age at which the length equals zero (t_0). Maximum age (t_{max}) and the variance of a fitted nonlinear least-squared regression along the VBGF fitted curve are used with the three known parameters to produce the environment necessary to estimate age (Fig. 1B).

The VBGF, as parameterized, offers a relationship that predicts the length of a fish based upon the age of the individual. The VBGF provides the best-guess estimate of size at age, and a variance term describes the probability of each potential length given that age. If an assumption is made that all ages are equally likely to be found in a population, this VBGF can be used reciprocally, estimating the age of an individual given a length. The approach can be considered by visualizing the VBGF in three dimensions, with age, length, and probability (Fig. 1B, 1C). With the simplifying assumption that all ages are equally probable, the relative probability of each age given a length is simply a trace of the three-dimensional VBGF for that particular length, thus describing relative probability as a function of age (for the specific length) (Fig. 1C). This function of relative probability can be standardized to a probability density function by dividing by the integral across all ages (from 0 to the maximum age). This probability density function can be used to provide estimates of age given known length. For each input length, a focal length is selected at random based on uniform distribution within that bin (Fig. 1B). A weighted probability density function for length-specific estimation is generated in several steps. A weighted probability distribution is created at the focal length with a mean of the VGBF curve and homoscedastic error. A function that integrates itself over the entire age range is used to standardize the probability density function as a uniform distribution.

There are several assumptions that were taken in order for this estimator to provide meaningful interpretable results. It is assumed that all error is homoscedastic across the entire age range, which means it is assumed that the lengths of fishes are normally distributed with the same variance around the VBGF curve throughout all stages of life. It is also assumed that fish are evenly distributed across all age classes of the entire age range due to the difficulty of aging fish with determinate growth strategies. Many reef fishes have growth patterns that result in static length for many years through the end of life, which hampers the ability to visually estimate a population with widely varying ages (Choat and Robertson 2002; Helser and Lai 2004). This assumption does not account for variability in yearly recruitment or large recruitment pulses which are more accurate of what is occurring in nature. A third assumption being presented is that all fish surveyed are binned in 5 cm intervals to reduce the variability in surveying. This assumption will detract from the accuracy of 1:1 length-to-age estimations but will reduce any surveying biases as this is standard operating procedure for underwater visual census operations (DeMartini et al. 2008; Friedlander et al. 2010). The final assumption is that results should be interpreted as relative differences in age instead of absolute ages. Accurately ageing fish requires location-specific VBGF parameters; therefore, by treating our parameters as cosmopolitan, we assume relative age instead of absolute age estimates. Relative ages should also be used as there is no way to visually infer differences in age of fish that exhibit determinate growth accurately.

Productivity

Productivity data was collected and analyzed in the manner presented in Gove et al. 2013. This data is used as both a proxy for phytoplankton concentration (chl-*a* mg m^{-3}) and for benthic productivity at the study islands. Data used in this study is the data provided from Fox et al. 2018 and Zgliczynski et al. 2019.

Data Analysis

All data manipulation and statistical analysis was performed in R (http://CRAN.R-project.org). Standard regression analysis was performed on mean lengths at each island and output mean ages for each island to determine initial relationships and a connection between length, which was verifiable and observed in nature, and age, which is our estimation. Regression analyses were then performed between mean length and mean productivity, mean length and mean density, mean age and mean productivity, and mean age and mean density by island to determine significant relationships, direction and magnitude.

Results

To properly interpret these results, the aforementioned assumptions must be followed so that inferences are not made beyond the limitations of the data or the methods that use them. The ages that are estimated should be interpreted as relative differences in magnitude because the parameters used to generate them may not be spatiotemporally linked to the population. Thus, any differences in ages between two locations can be interpreted as a conservative estimate of the actual difference in age structure between the two populations.

All results of regression analysis

Productivity

Productivity data are provided to add context to island means of the population data analyzed (Fig. 2A, Fig. 3A, Fig. 4A). Mean chl-*a* productivity presented a negative relationship with latitude ($F_{1,8}$ = 85.6, p = <0.001, Slope = -0.009, Intercept = 0.0191) culminating at a peak value of 0.18 mg m^{-3} at Kiritimati in the Northern Line Islands. This relationship between productivity and latitude creates a gradient along the length of the Line Islands, Southward, from a low at Flint to high at Kiritimati and back to low at Kingman.

Acanthurus nigricans

A. nigricans was present on all islands surveyed but was not present in large enough sample sizes on Teraina to provide reliable results. A significant positive relationship was observed between length and age (Fig. 5A). Significant positive linear relationships were observed between mean length and productivity ($F_{1,7}$ = 101.1, p <0.001, Slope = 99.387) (Table 1, Fig. 6A) and mean age and productivity ($F_{1,7}$ = 60.46, p = <0.001, Slope = 111.525) (Table 2, Fig. 7A), however no relationships were observed between length or age and density. The mean ages throughout the Line Islands for *A. nigricans* increased over sixfold between the lowest and highest mean ages (1.99 yrs on Flint and 12.84 yrs on Kiritimati) (Fig. 2B). Of note, the highest mean ages and size were observed at Kiritimati, which had nearly the lowest population density (Fig. 2 B,E,H).

Ctenochaetus marginatus

C. marginatus was present in large enough quantities for adequate sampling on all islands except for Teraina, Malden, Starbuck and Flint. A significant positive relationship was observed between length and age (Fig. 5B). A significant negative relationship was observed between mean length and productivity across the remaining islands ($F_{1,4} = 13.38$, $p = 0.022$, Slope = -116.39) (Table 1, Fig. 6B), however the similarly distributed mean ages were not significant. The mean ages (3.73 yrs on Kiritimati and 9.92 yrs on Starbuck) differed by more than a magnitude of 2.5 across the islands (Fig. 2C).

Ctenochaetus striatus

C. striatus was present in large enough quantities for reliable sampling results at five of the ten islands surveyed. Teraina, Malden, Starbuck, Vostok and Flint were excluded. Two-thirds of the 1,613 fish surveyed were from Tabuaeran alone. A significant positive relationship was observed between length and age (Fig. 5C). Positive relationships were observed between mean length and productivity ($F_{1,3} = 43.65$, $p = 0.007$, Slope = 22.015) (Table 1, Fig. 6C), and mean age and productivity ($F_{1,3} = 75.37$, $p = 0.003$, Slope = 56.037) (Table 2, Fig. 7C). Estimated mean ages doubled between the lowest age (4.22 yrs on Millennium) and the highest age (8.42 yrs on Kiritimati) (Fig. 2D). Mean densities were fairly similar across the islands except at Tabuaeran, which exhibited a density five times higher than the next island (Fig. 2J). This may be due to the presence of a wreck at some of the transect sites at this island, which can cause aggregating behavior among reef fishes.

Chlorurus sordidus

C. sordidus was present in large enough quantities for reliable sampling results at five of the ten islands surveyed. Teraina, Malden, Starbuck, Vostok and Flint were excluded. A significant positive relationship was observed between length and age (Fig. 5D). Positive relationships were observed between mean length and productivity ($F_{1,3} = 14.55$, $p = 0.032$, Slope = 50.699) (Table 1 Fig. 6D) and mean age and productivity ($F_{1,3} = 9.42$, $p = 0.055$, Slope = 17.019) (Table 2, Fig. 7D) despite a relatively narrow mean estimated age range across the Line Islands (5.46 ± 0.55 yrs) (3B).

Scarus frenatus

Kingman, Palmyra, Tabuaeran and Kiritimati were the only islands to have sufficient sample sizes of *S. frenatus* to provide confident results, and almost half were found at Tabuaeran. A significant positive relationship was observed between length and age (Fig. 5E). There were no significant relationships between length and age with productivity and density, however there was a threefold increase in age among the islands (2.97 yrs at Tabuaeran to 9.66 yrs on Kiritimati) (Fig. 3C). Densities of *S. frenatus* were high (0.023 fish m^{-2}) on Tabuaeran relative to the other three islands surveyed (0.005 - 0.007 fish m^{-2}) and may be a result of the same wreck described earlier (Fig. 3I).

Scarus rubroviolaceus

Teraina, Millennium, Vostok and Flint were excluded due to insufficient sample sizes, however the remaining six islands produced 694 surveyed samples of *S. rubroviolaceus* with two-thirds being from the SLI. A significant positive relationship was observed between length and age (Fig. 5F). A significant positive relationship was observed between mean age and productivity ($F_{1,4} = 11.2$, $p = 0.029$, Slope = 19.753) (Table 2, Fig. 7F) even with relatively low age variability across the islands (3.42 ± 0.50 yrs) (Fig 3D).

Stegastes aureus

S. aureus was present in large enough quantities for sampling at all but the three southernmost islands. The remaining islands provided 3,192 samples for surveying with almost one-third from Kiritimati. A significant positive relationship was observed between length and age (Fig. 5G). There were no significant relationships between length and age with productivity and density, however the differences in mean age differed by a magnitude of over 2.5 (Fig. 4B).

Discussion

This age estimator allowed, for the first time, the calculation of relative differences of age among reef fish populations across an island chain. The overarching goal was to create a simple age estimation method that permits the use of visual census data in a meaningful manner. By applying the assumptions described and following ecological theory, new inferences were made about populations from data that is over a decade old without the need for the quantitative values traditionally associated with age-based studies.

Among the ten islands and seven species surveyed and studied, Kiritimati presented a maximum mean age for five of the seven species (*A. nigricans, C. striatus, S. frenatus, S. rubroviolaceus, S. aureus*) , was second by 22 days for the sixth species (*C. sordidus*) and was notably the lowest mean age for the seventh (*C. marginatus*). Four of the seven populations experienced positive relationships between mean age and productivity, three experienced a positive and one a negative relationship between mean length and productivity. There was also a noted lack of any significant relationships between length or age and density across the island chain. All relationships between length and age were intrinsically significant as ages were generated from length; however, due to the nature of the age estimator's random sampling, variability in those length-age relationships is introduced.

Acanthuridae

Mean lengths and ages that *A. nigricans* and *C. striatus* exhibited across the Line Islands followed along the latitudinal productivity gradient and may be partially due to these species spending at least 80% of their grazing time on fleshy or turf algae (Dee et al. 2021). This could also be a contributing factor associating the oldest and thus most robust populations to Kiritimati, the region with highest productivity. The negative relationship observed between length and productivity of *C. marginatus* may at least partially be explained by its feeding habits, which tend to be split evenly between turf algae and crustose coralline algae (Dee et al. 2021). The increase in island-wide mean ages by a factor of six for *A. nigricans* and over two for both *C. marginatus* and *C. striatus* is a remarkable difference in age that warrants further investigation. The diets of these seeming herbivores tend to be complex and ascribing a proxy of chl-*a* only accounts for a portion of their dietary compositions. For example, gut content analysis in Choat et al. 2002 reveals that the large majority the diet of *A. nigricans* consists of red algae, and a recent study of gut content using DNA metabarcoding revealed a high level of diversity in diet (Nalley et al. 2022). This same study by Nalley showed a low dietary diversity for *C. striatus*, which shared similar age profiles across the Line Islands. This illustrates why a comprehensive and holistic approach is needed to better understand the intricacies that can be ascribed to a population profile.

Scaridae

C. sordidus and *S. rubroviolaceus* exhibited positive albeit weak relationships between mean age and productivity and *C. sordidus* displayed a positive relationship between length and productivity. These interactions may be at least partially due to low dietary diversity (Nalley et al. 2022; Hamilton et al. 2014), creating more robust populations in areas of higher productivity and simultaneously maintaining similar ages across the region with the assumption that their narrow dietary needs are met. All three Scarids shared mean ages at or near the maximum at Kiritimati; however, *S. frenatus* did not have a significant relationship between age and productivity. This similarly may be an artifact of robust populations in more productive regions. The inter-island differences in age for *S. frenatus* are especially stark with over a threefold increase in age between Tabuaeran and Kiritimati. When comparing density estimates along with age at these two islands it can be inferred that the high density-low age population at Tabuaeran is many young fish while the low density-high age population at Kiritimati is comprised of fewer older fish. This information creates new descriptors of regional populations that allow for new insights about those populations. Knowing the age/size at maturity will allow for understanding of these populations. In the case of *S. frenatus*, age at maturity is around 2 years old and 18 cm (Choat and Robertson 2002), while our population averages 2.97 years and 15 cm. This highlights that breeding populations of *S. frenatus* at Tabuaeran may be producing significantly less hardy offspring than at Kiritimati. Since we know relative differences, but not exact value differences of age we can assume there is a near enough value for functional ecological understanding since the size also falls within the maturity inflection range.

Pomacentridae

S. aureus was the only Pomacentrid and non-roving grazer in this study. Length and age of *S. aureus* did not have any significant relationships with either productivity or density throughout this study. An increase in mean age by a factor of more than 2.5 was observed between Kingman (2.06 yrs) and Kiritimati (5.44 years), which again produced the population with the highest mean ages. Gut content analysis reveals that *S. aureus* primarily has a diet of filamentous algae and invertebrates (Miller et al. 2019) and this influx of additional protein sources may account for noise among a signal from the productivity gradient. This is also the fifth and final species that had a maximum mean age for the population at Kiritimati.

Regional Interpretations

With six of the seven species' populations showing maximum or near maximum mean age at Kiritimati, it is possible that this could be an indication that there is a signal being observed between higher productivity and more robust populations among many reef fish species. As in any complex ecosystem, that signal will be masked by environmental noise. A distinct possibility for the variability on a population level for several species in this study is their home ranges and niches overlap. For example, niche width expansion has been observed across productivity gradients for several reef fish guilds and could be attributed to many environmental factors including inter-guild competition (Miller et al. 2019). Complex interactions due to predation and fishing may play a part in the variability noticed between islands such as Kiritimati and Palmyra, which have high differences in predator biomass as noted in DeMartini et al. 2008.

Conclusion

Traditional methods of aging fishes are time consuming and resource-heavy endeavors that do not lend themselves well to regional population-level studies (B. S. Green et al. 2009).

This age estimation method and case study has proven fruitful as a preliminary effort to add the additional dimension of time to marine monitoring efforts without increasing sampling efforts. The ability to further describe populations with relative differences in age adds to the toolbox of marine ecological monitoring and allows a more holistic approach to the process. Fishing pressure was not assessed in this study because none of these species are exceptionally targeted at the islands where fishing is occurring (DeMartini et al. 2008).

Expanding this study to include other trophic groups like predators and planktivores may yield additional information on groups of fishes that are affected by other environmental factors, such as fishing pressure, and broaden the knowledge base of the reef fish community at the Line Islands. It would prove interesting to further investigate any relationships on a functional group level to garner more insight into community-wide age differences across the islands. These methods of allocating species in studies have shown to be useful as indicators of reef health (A. L. Green and Bellwood 2009). By obtaining and integrating fish census data for Jarvis Island in the Southern Line Islands, we can include a data set that has higher productivity than Kiritimati and lacks fishing pressure. This would allow for the ability to detangle the relationship that Kiritimati has with fishing pressure and productivity.

Material from this thesis is currently being prepared for submission for publication. Iyer, Ram B.; Akiona, Anela A.; French, Beverly J.; Lubarsky, Katie; Zgliczynski, Brian J.; Sandin, Stuart A. The thesis author was the primary author of this material.

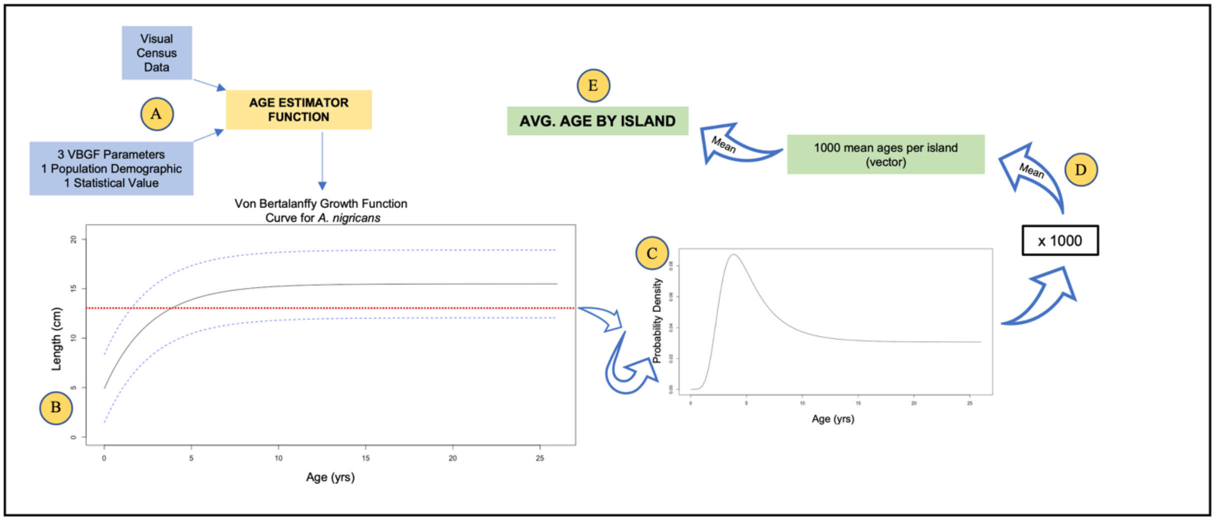


Figure 1: Conceptual diagram of age estimation method. **(A)** Vectorized and binned visual census data, three VBGF parameters (L_{inf}, K and t_o), the maximum age of the species (T_{max}), and one statistical value (variance of the VBGF) are input into the age estimation function as our defining values for each species. **(B)** The VBGF curve is plotted for the species with the three VBGF parameters and T_{max} (In this example *A. nigricans* was used). An input binned length from survey data is randomly assigned a length from within that bin (13 cm in this example). **(C)** A probability density function is generated and a guess is then made in this estimation space. **(D)** “B” and “C” are repeated for every length collected from the visual census and then replicated 1000 times to bootstrap the data. **(E)** The mean of the 1000 vectors of results are calculated and an island-wide mean is calculated from those results.

Figure 2: *Acanthuridae* case study results. **(A)** Scale of mean chlorophyll-*a* concentrations (mg m^{-3}) throughout the Line Islands. Kingman (KIN), Palmyra (PAL), Teraina (TER), Tabuaeran (TAB), Kiritimati (KIR), Malden (MAL), Starbuck (STA), Millennium (MIL), Vostok (VOS) and Flint (FLI) have their respective latitudes included with the first row. Subsequent rows include island and gradient colors to orient the graphs. *Acanthurus nigricans* (Top Row). *Ctenochaetus marginatus* (Middle Row). *Ctenochaetus striatus* (Bottom Row). **(B, C, D)** Boxplot of estimated mean age (yrs). The boxes represent the first and third quartile and the black line in the middle of the box represents the mean age of the population at each island. The whiskers represent the minimum and maximum values excluding outliers, which were omitted from the figure. **(E, F, G)** Boxplots of total length (cm). The boxes represent the first through third quartile. The circles represent the mean age at each island. The whiskers represent the minimum and maximum values excluding outliers, which were omitted from the figure. **(H, I, J)** Boxplots of density (# fish m^{-2}). The boxes represent the first and third quartile and the black line represents the median. The circle represents the mean density for each island. The whiskers represent the minimum and maximum values excluding outliers, which were omitted from the figure. (ND = "Not Determined"). Fish and island illustrations by Amy Iyer.

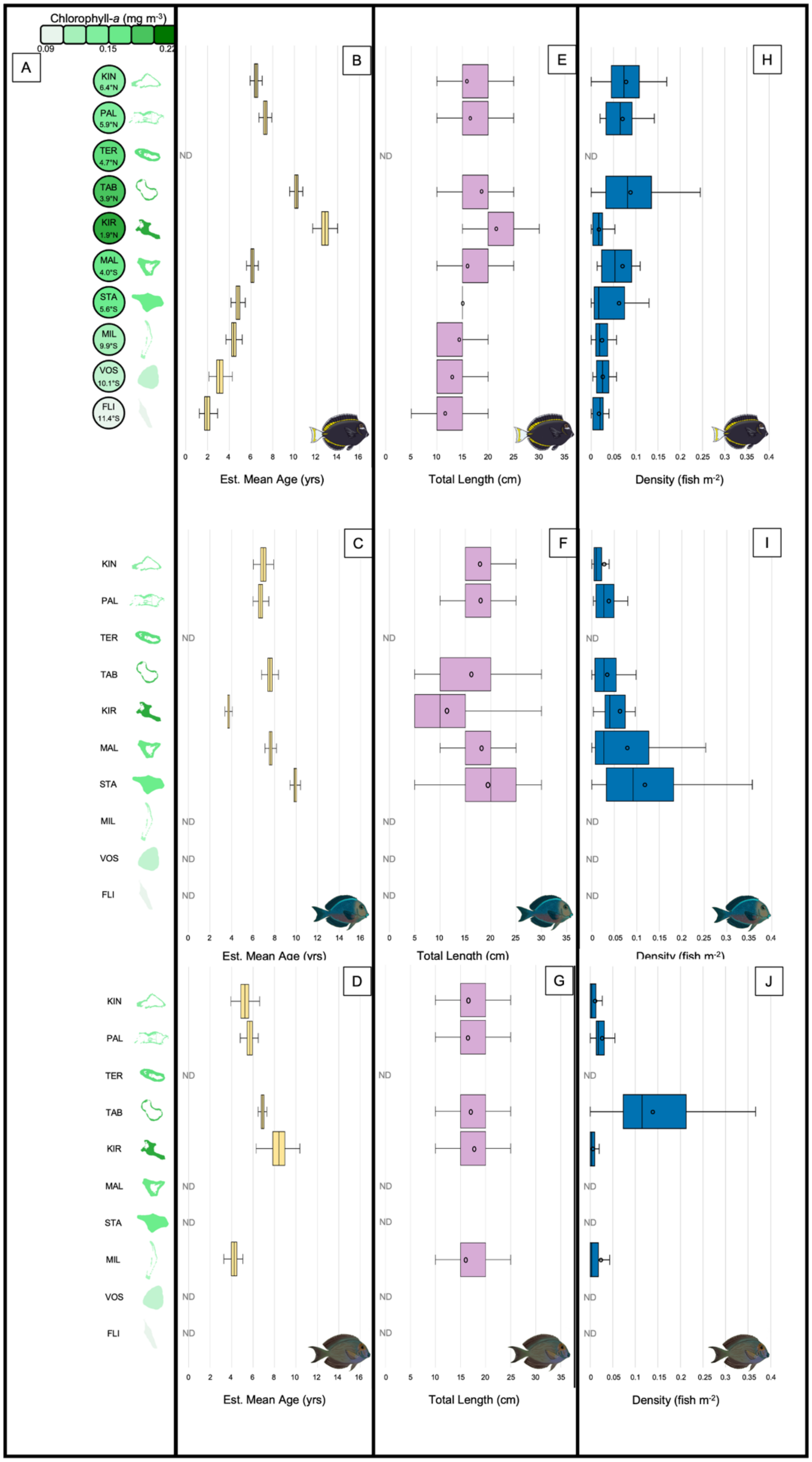
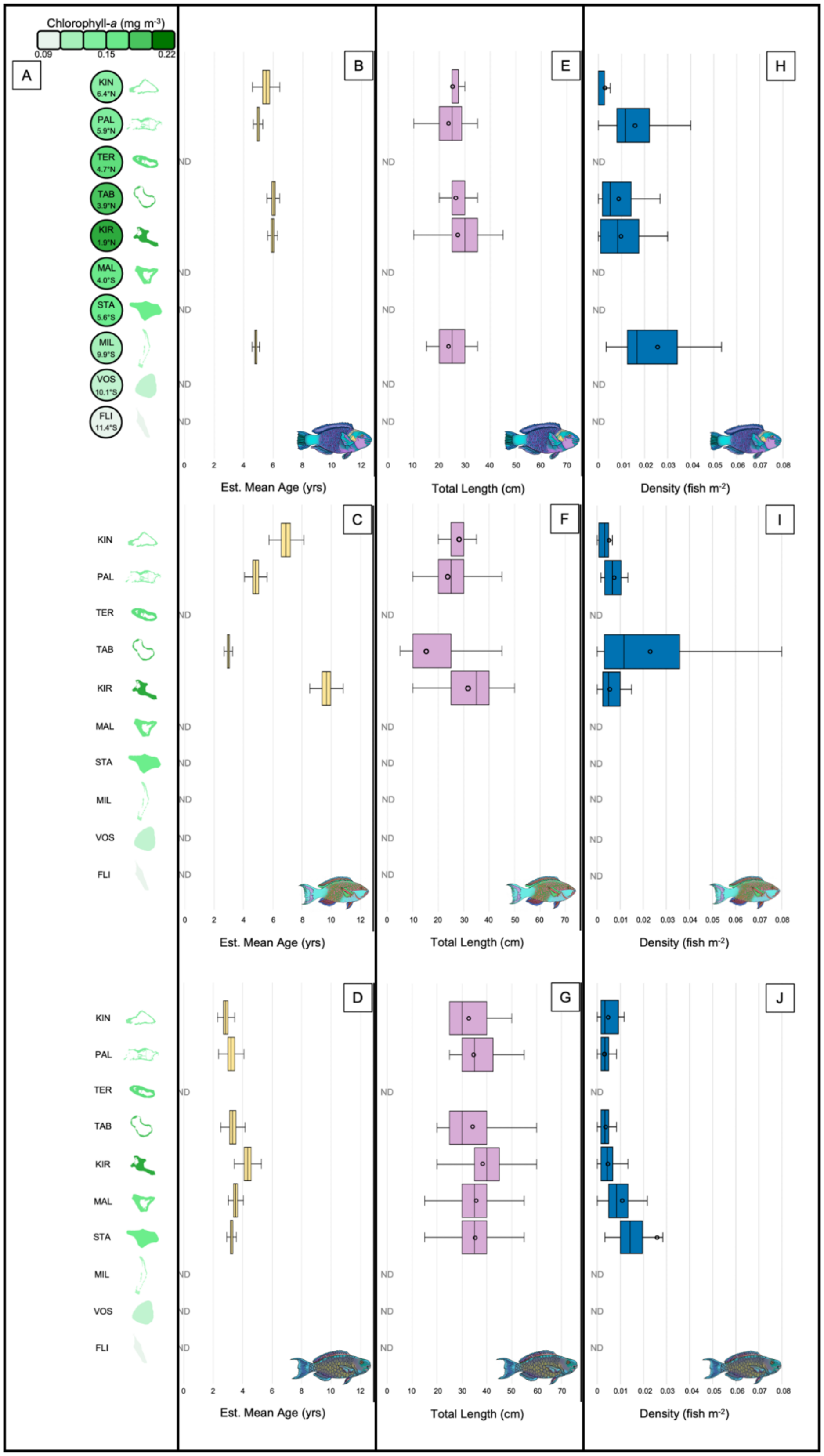

Chlorophyll-a (mg m-3)
0.09
0.15
0.22
A
KIN 6.4°N
PAL 5.9°N
TER 4.7°N
TAB 3.9°N
KIR 1.9°N
MAL 4.0°S
STA 5.6°S
MIL 9.9°S
VOS 10.1°S
FLI 11.4°S
B
C
D
E
F
G
H
I
J
ND
KIN
PAL
TER
TAB
KIR
MAL
STA
MIL
VOS
FLI
0 2 4 6 8 10 12 14 16
Est. Mean Age (yrs)
0 5 10 15 20 25 30 35
Total Length (cm)
0 0.05 0.1 0.15 0.2 0.25 0.3 0.35 0.4
Density (fish m-2)

Figure 3: *Scaridae* case study results. **(A)** Scale of mean chlorophyll-*a* concentrations (mg m^{-3}) throughout the Line Islands. Kingman (KIN), Palmyra (PAL), Teraina (TER), Tabuaeran (TAB), Kiritimati (KIR), Malden (MAL), Starbuck (STA), Millennium (MIL), Vostok (VOS) and Flint (FLI) have their respective latitudes included with the first row. Subsequent rows include island and gradient colors to orient the graphs. *Chlorurus sordidus* (Top Row). *Scarus frenatus* (Middle Row). *Scarus rubroviolaceus* (Bottom Row). **(B, C, D)** Boxplot of estimated mean age (yrs). The boxes represent the first and third quartile and the black line in the middle of the box represents the mean age of the population at each island. The whiskers represent the minimum and maximum values excluding outliers, which were omitted from the figure. **(E, F, G)** Boxplots of total length (cm). The boxes represent the first through third quartile. The circles represent the mean age at each island. The whiskers represent the minimum and maximum values excluding outliers, which were omitted from the figure. **(H, I, J)** Boxplots of density (# fish m^{-2}). The boxes represent the first and third quartile and the black line represents the median. The circle represents the mean density for each island. The whiskers represent the minimum and maximum values excluding outliers, which were omitted from the figure. (ND = "Not Determined"). Fish and island illustrations by Amy Iyer.


Chlorophyll-a (mg m-3)
0.09
0.15
0.22
A
KIN 6.4°N
PAL 5.9°N
TER 4.7°N
TAB 3.9°N
KIR 1.9°N
MAL 4.0°S
STA 5.6°S
MIL 9.9°S
VOS 10.1°S
FLI 11.4°S
B
C
D
E
F
G
H
I
J
ND
0 2 4 6 8 10 12
Est. Mean Age (yrs)
0 10 20 30 40 50 60 70
Total Length (cm)
0 0.01 0.02 0.03 0.04 0.05 0.06 0.07 0.08
Density (fish m-2)
KIN
PAL
TER
TAB
KIR
MAL
STA
MIL
VOS
FLI

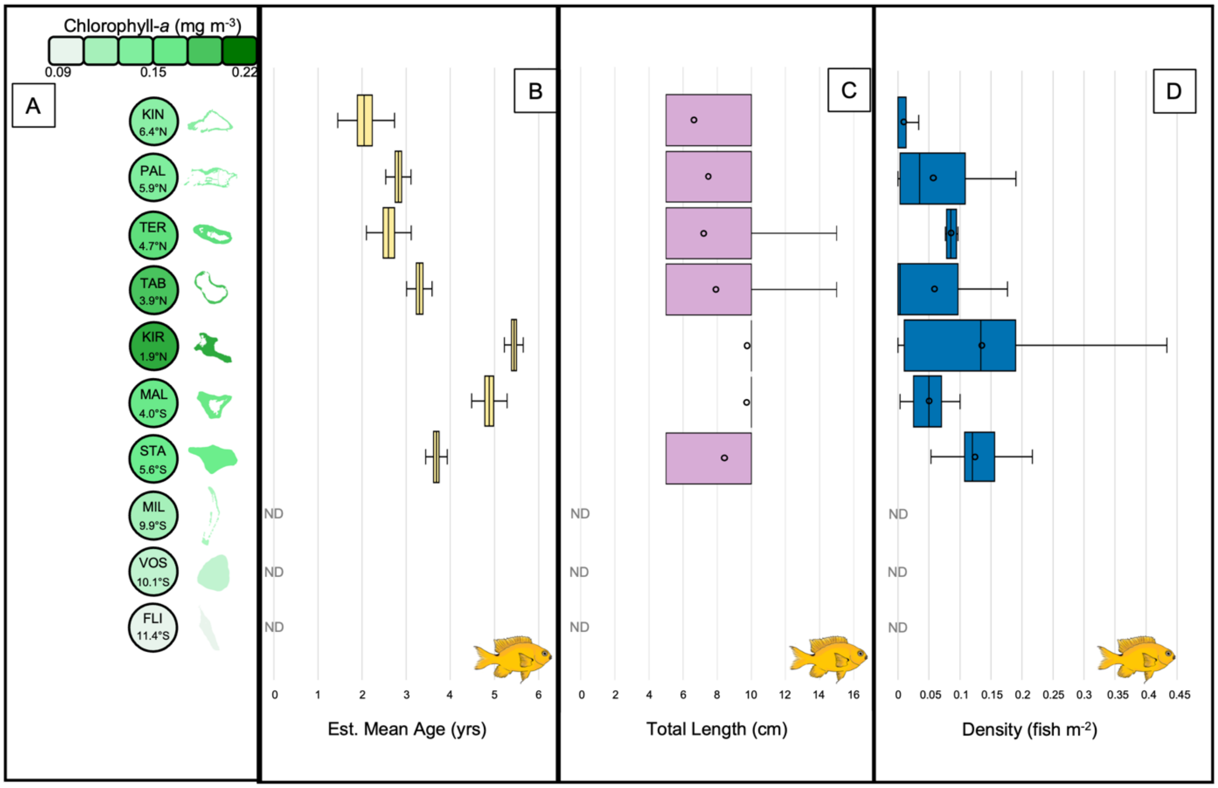


Figure 4: *Pomacentridae* case study results. **(A)** Scale of mean chlorophyll-*a* concentrations (mg m^{-3}) throughout the Line Islands. Kingman (KIN), Palmyra (PAL), Teraina (TER), Tabuaeran (TAB), Kiritimati (KIR), Malden (MAL), Starbuck (STA), Millennium (MIL), Vostok (VOS) and Flint (FLI) have their respective latitudes included with the first row. Subsequent rows include island and gradient colors to orient the graphs. *Stegastes aureus* **(B)** Boxplot of estimated mean age (yrs). The boxes represent the first and third quartile and the black line in the middle of the box represents the mean age of the population at each island. The whiskers represent the minimum and maximum values excluding outliers, which were omitted from the figure. **(C)** Boxplots of total length (cm). The boxes represent the first through third quartile. The circles represent the mean age at each island. The whiskers represent the minimum and maximum values excluding outliers, which were omitted from the figure. **(D)** Boxplots of density (fish m^{-2}). The boxes represent the first and third quartile and the black represents the median. The circle represents the mean density for each island. The whiskers represent the minimum and maximum values excluding outliers, which were omitted from the figure. (ND = "Not Determined"). Fish and island illustrations by Amy Iyer.

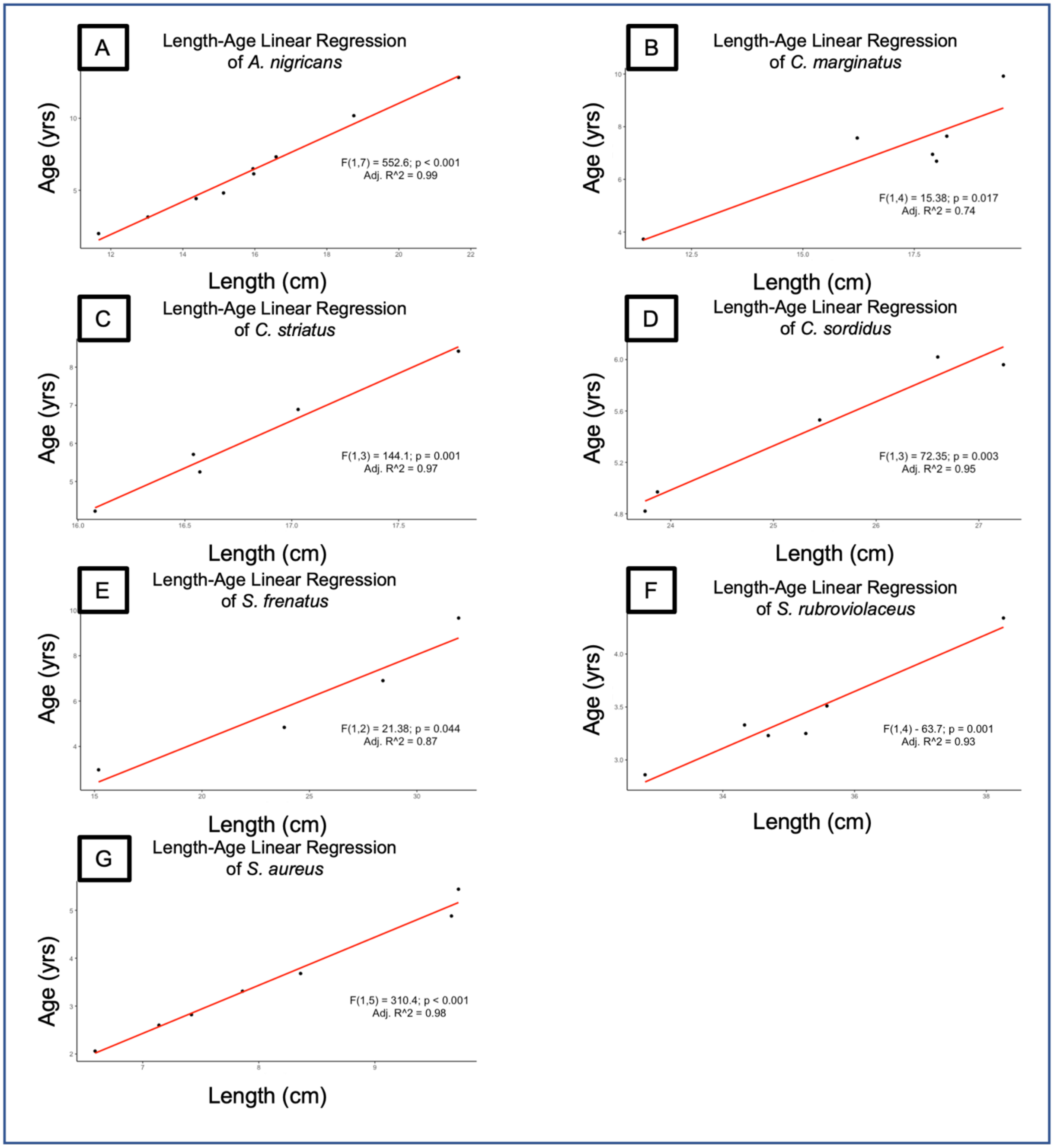


Figure 5: Linear regression relationships of length and age. **(A)** *A. nigricans* **(B)** *C. marginatus* **(C)** *C. striatus* **(D)** *C. sordidus* **(E)** *S. frenatus* **(F)** *S. rubroviolaceus* **(G)** *S. aureus*.

Table 1: Linear regression analysis for length of target species to determine relationships with chlorophyll-*a* and density. Slope and intercept are included for direction and magnitude of relationship.

		Length							
		Chlorophyll a				**Density**			
Species	N	F	p	Slope	Intercept	F	p	Slope	Intercept
AC.NIGR	3374	**101.1**	**<0.001**	**99.387**	**2.521**	0.546	0.484	28.201	14.466
CT.MARG	2798	**13.38**	**0.022**	**-116.39**	**34.28**	0.2708	0.63	20.64	15.67
CT.STRI	1613	**43.65**	**0.007**	**22.015**	**13.584**	0.018	0.901	0.902	16.763
CH.SORD	757	**14.55**	**0.032**	**50.699**	**17.975**	2.486	0.213	-127.15	26.98
SC.FREN	461	0.002	0.966	9.137	23.445	9.559	0.091	-771.314	32.751
SC.RUBR	694	5.262	0.083	62.624	25.793	0.027	0.878	16.76	35.01
ST.AURE	3192	2.442	0.179	35.179	2.841	2.214	0.197	15.128	6.981

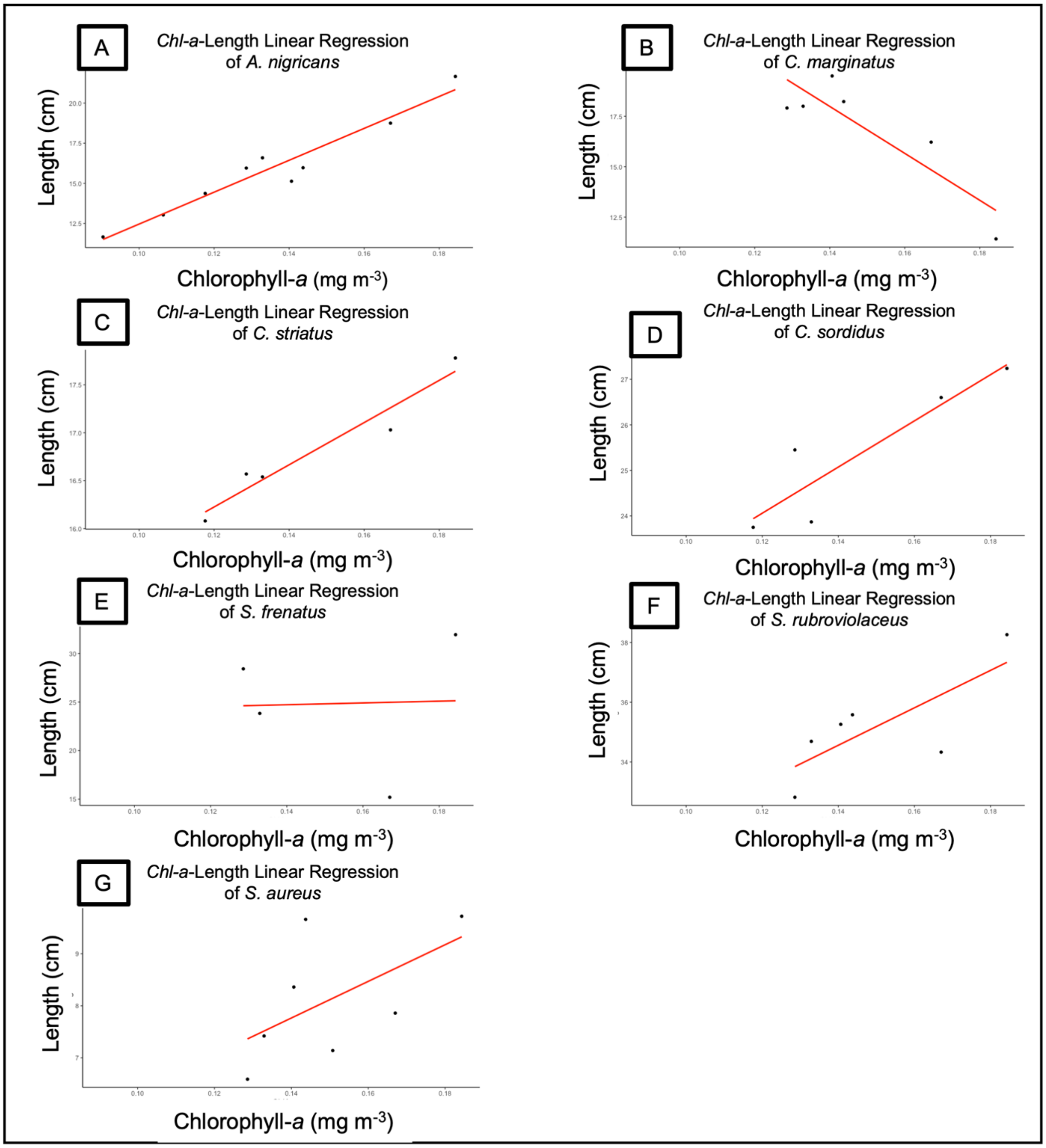


Figure 6: Linear regression relationships of chlorophyll-*a* concentrations and length. **(A)** *A. nigricans* **(B)** *C. marginatus* **(C)** *C. striatus* **(D)** *C. sordidus* **(E)** *S. frenatus* **(F)** *S. rubroviolaceus* **(G)** *S. aureus*.

Table 2: Linear regression analysis age of target species to determine relationships with chlorophyll a and density. Slope and intercept are included for direction and magnitude of relationship.

		Age							
		Chlorophyll a				**Density**			
Species	N	F	p	Slope	Intercept	F	p	Slope	Intercept
AC.NIGR	3374	**60.46**	**<0.001**	**111.525**	**-8.644**	0.565	0.477	32.843	4.699
CT.MARG	2798	2.11	0.22	-54.294	15.202	1.269	0.323	28.02	5.439
CT.STRI	1613	**75.37**	**0.003**	**56.037**	**-2.089**	0.085	0.79	4.843	5.898
CH.SORD	757	**9.421**	**0.055**	**17.019**	**2.974**	3.621	0.153	-49.026	6.078
SC.FREN	461	0.223	0.684	33.706	0.929	2.575	0.2498	-252.08	8.676
SC.RUBR	694	**11.2**	**0.029**	**19.753**	**0.467**	0.055	0.825	-6.632	3.48
ST.AURE	3192	3.663	0.114	40.436	-2.512	2.702	0.161	16.378	2.322

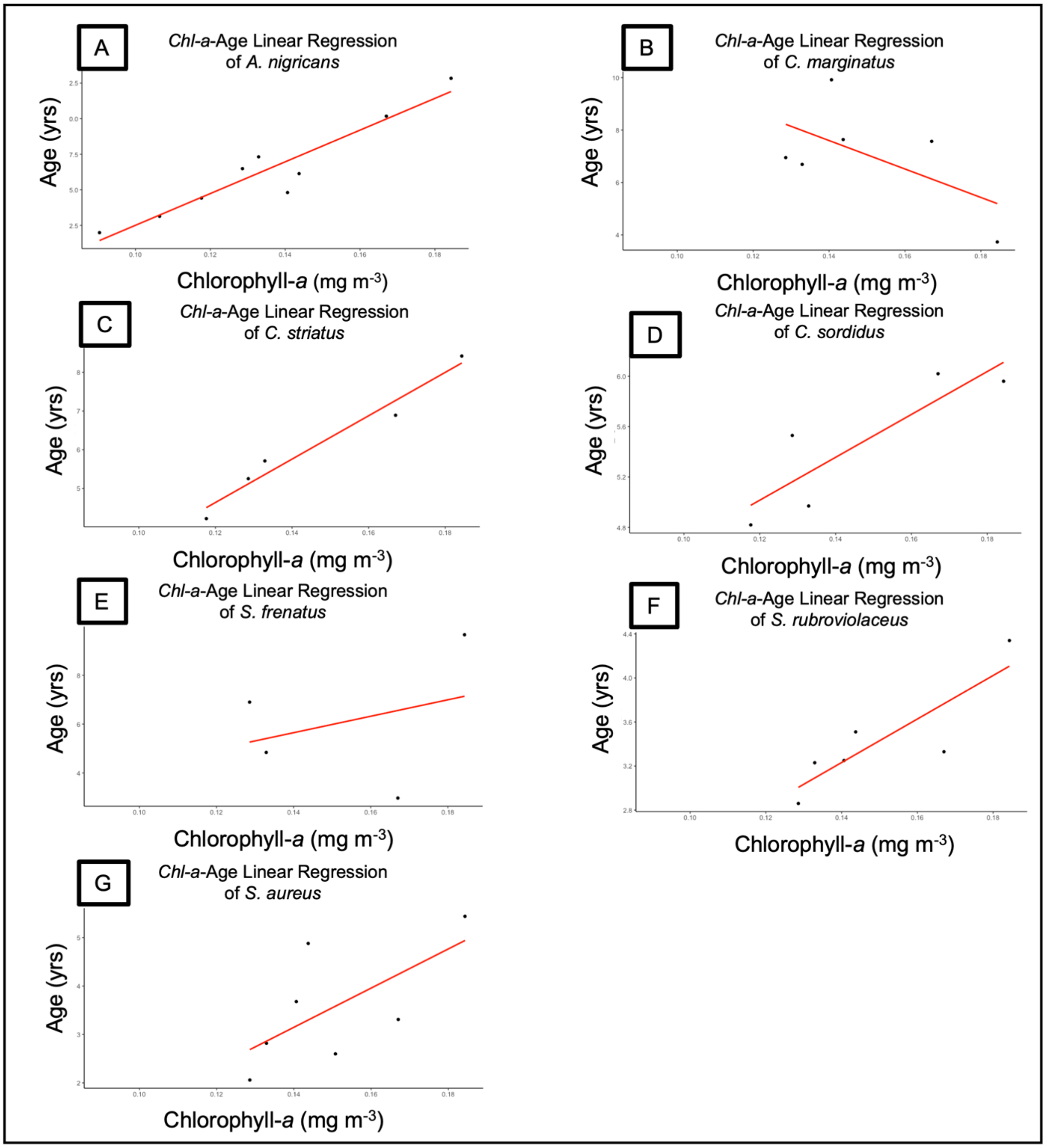


Figure 7: Linear regression relationships of chlorophyll-*a* concentrations and age. **(A)** *A. nigricans* **(B)** *C. marginatus* **(C)** *C. striatus* **(D)** *C. sordidus* **(E)** *S. frenatus* **(F)** *S. rubroviolaceus* **(G)** *S. aureus*.

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