



# Within-region differences in growth responses of an herbivorous coral reef fish to local and regional climatic processes

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**Abstract** Understanding how environmental stressors impact fisheries is imperative for the sustainable management of our marine resources. Synchrony in inter-annual growth patterns among individuals and populations has been identified across large spatial scales, both within and among species. This synchrony indicates a detectable sensitivity to changes in climatic or environmental conditions. We explored within-region effects of environmental and climatic variability using inter-annual otolith growth rates (increments) in a tropical coral reef fish, *Naso unicornis*. Dendrochronology techniques were applied to remove age-specific growth effects and extract a high-frequency variability signal indicative of short-term environmental change. Using linear mixed-effects models, we identified best predictors of the variation in growth at two adjacent latitude subsets in the Commonwealth of the Northern Mariana Islands. We found different latitude subset growth responses for the years 2000–2013 and 2005–2017, indicating independent fluctuations in growth across latitude however, synchrony

was present among individuals within a latitude range. Local environmental processes were more important than regional climatic processes for explaining *N. unicornis* growth in the north, but in the central islands, neither process had a clear effect. Otolith growth in fish inhabiting the north had a positive response to increased annual average sea surface temperature (SST). In adjacent central islands, otolith growth responded negatively to warmer winter SST. Baseline information for most fisheries on the direct impact of external forcings on fish, especially in tropical coral reef fisheries, remains sparse. We provide information on how climate and environment have impacted past growth with implications for future fisheries productivity monitoring.

**Keywords** Biochronology · Coral reef fishes · El Niño · Growth · Climate variability

## Introduction

Sustainability of marine resources is endangered by a globally changing climate. An understanding of how environmental stressors impact fisheries is imperative (Rowland et al. 2011), but this information remains elusive for many commercially important species (Wilson et al. 2009). Fish growth is a key element of population dynamics and is an important driver of productivity and catch yield of fish populations (Lorenzen 2016; Morais et al. 2023). Inter-annual variability in fish growth occurs in response to changes in the environment that affect food availability and temperature; such complex interactions may be more deeply linked to broad climatic forcing such as El Niño Southern Oscillation (ENSO) events. If fish respond similarly to external conditions, growth patterns can show synchrony—the simultaneous fluctuation of growth patterns through time

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(Liebhold et al. 2004). Synchrony can occur across temporal and spatial scales; for example, synchrony is often found in growth patterns of individuals within a population if individuals respond similarly to local conditions (Black et al. 2005). However, growth synchrony has also been identified across large spatial scales, both within and among species in the same region, indicating a detectable and common sensitivity to changes in climatic conditions or environment (Black et al. 2009; Ong et al. 2017, 2018). Favorable external drivers (i.e., increased productivity or increased SST under thermal maxima) could increase growth rates, and therefore, availability of fish to the associated fishery (Erisman et al. 2021). Alternatively, these impacts could act as additional stressors to a population, threatening collapse when environmental conditions are unfavorable for prolonged periods of time (Taylor et al. 2020). Therefore, mechanistic links between environmental or climatic interactions and the scale of synchrony in fish growth may be valuable information for fisheries management, industry, and local communities who are invested in the longevity of these resources.

Temperature is a key environmental factor affecting the metabolic rates and consequently the growth of marine ectotherms, including tropical fishes (Munday et al. 2008; Neuheimer et al. 2011). Changes of only a few degrees Celsius can influence an ectotherm's physiological condition, rate of development, swimming ability, and aspects of reproduction in addition to growth rate (Jobling 1997). The productivity of populations is indirectly influenced by the effect of temperature on the timing of growth and reproduction (Pörtner and Peck 2010). For species operating within their normal range or "thermal window," a small gradual increase in temperature would yield increases in individual growth because it elicits greater energy availability through metabolic processes, provided adequate food is available (Jobling 1997; Pörtner and Farrell 2008). For populations that are at the warm temperature extremes of their range, metabolic costs are higher and result in less availability of energy for growth and reproduction (Neuheimer et al. 2011).

A primary driver of inter-annual variability in the tropical Pacific Ocean's sea surface temperature (SST) is the El Niño Southern Oscillation (ENSO) (Bertrand et al. 2020). Impacts from ENSO events can have a wide range of physical, ecological and biological (growth, mortality, and reproduction) changes throughout the Pacific Ocean basin with the strongest effects in the eastern Pacific (Bertrand et al. 2020; Lehodey et al. 2020). The impacts on Pacific Ocean fisheries are varied with regional distinctions. More recently, accounting for the type of ENSO event (eastern or central Pacific) has been identified as important due to their differing spatial characterizations and intensities (Bertrand et al. 2020; Lehodey et al. 2020). El Niño Modoki is a type of El Niño event, also known as the Warm Pool or central Pacific El Niño, which has increased in frequency since

the 1980s and is attributed to changes in the central and western Pacific, although it is less intense than an eastern Pacific El Niño (Lehodey et al. 2020). In recent decades, El Niño Modoki events have been linked to steep declines in squid fisheries (Robinson et al. 2016), changes to marine food-webs that affect seabirds (Schmidt et al. 2014), and negative effects on fish populations or individuals due to sustained increased temperatures (Yen et al. 2017; McCoy et al. 2017). However, documented effects are mainly from temperate environments with the majority of ENSO effects attributed to eastern Pacific El Niño's. Regardless of type, the impact of ENSO events on the growth rate of marine ectotherms in the tropical Pacific broadly supports linkages between regional biological processes and large-scale climatic variability (Ong et al. 2017, 2018; Taylor et al. 2020).

Biological chronologies derived from fish otoliths allow us to reconstruct past time series of growth information, but also evoke pertinent links to the physical environment (Black et al. 2009). Intrinsic, or age-related, growth is well understood (Weatherley and Gill 1987), but extrinsic factors impacting growth are poorly understood in a fisheries management context (Lorenzen 2016). Currently, our ability to determine the interactions between a changing climate and population dynamics of marine fishes is limited by historical data on growth patterns (Morrongiello et al. 2012; Ong et al. 2018). Annual increments in fish otoliths have been well validated for decades and are widely used in fisheries research as a result of their reliability for somatic growth (Campana and Thorrold 2001). Otolith increment widths can be used to reconstruct not only past growth histories, but also past climate time series, and chronologies have also proven useful as an indicator of past climate effects in a marine environment (Black et al. 2005; Morrongiello et al. 2012). The extent to which a species has retained a climate signal consequently provides a window into ecosystem vulnerability to climate change (Ong et al. 2018).

Currently, there remain gaps in our knowledge of how climate change will affect tropical marine fishes and their fisheries. Climate change directly impacts climate variability, which operates on an inter-annual (ENSO) or decadal (Pacific Decadal Oscillation (PDO)) timescale. Focusing mainly on temperate regions (Black et al. 2009; Morrongiello et al. 2012), biochronologies have recently been used to explore how the growth of tropical marine fishes responds to extrinsic factors such as ENSO, PDO, sea level, the strength of a boundary current, chlorophyll-a, and SST (Ong et al. 2017, 2018; Taylor et al. 2020). However, to date, no biochronology-based research has explored within-species temporal growth synchrony at adjacent latitudes within a region. Such information may provide clues for potential local adaptation to climate change, which has been suggested for herbivorous acanthurid coral-reef fishes that have short generation times and/or for species with geographical ranges

spanning wide temperature gradients (Munday et al. 2008). Alternatively, extrinsic factors affecting growth of commercially important species can be used as environmental indicators for management entities to help aid the response of coastal communities who rely on their coral reef ecosystems for crucial sources of protein (Pratchett et al. 2011).

The bluespine unicornfish, *Naso unicornis* (Family: Acanthuridae), is one of the most commercially valued reef-associated species caught in coral reef fisheries in the Indo-Pacific (Taylor 2019; Taylor et al. 2019). It has a wide geographic range throughout the Indo-Pacific and no recorded gene flow barriers between the Indian and Pacific Ocean (Horne et al. 2008; Taylor et al. 2019). This species is widely regarded to be of ecological importance in coral reef environments because it feeds on macroalgae which has been a proposed mechanism to support coral reef resilience in the face of habitat phase-shifts (Puk et al. 2016; Hoey and Bellwood 2009). The *N. unicornis* in particular has a unique set of life-history characteristics for a reef fish, which includes a relatively long-life span and reaching a large maximum size (> 60 cm in length), both of which may increase this species' vulnerability to overexploitation (Andrews et al. 2016; Taylor et al. 2019). The age, longevity, reproduction, and growth of *N. unicornis* have been described reasonably well across regions, indicating a comprehensive foundation as to the life history of this species and how it varies spatially (Taylor et al. 2014, 2019, 2024; DeMartini et al. 2014). Its longevity ranges from ~ 16 years in Pohnpei (Taylor et al. 2014) to the oldest fish recorded, ~ 50+ years in Hawai'i (Andrews et al. 2016). In the Northern Mariana Islands, this species reaches moderate longevity of ~ 33–37 years (Taylor et al. 2019). The abundance of life history knowledge on this species, the relatively long lifespan, and its ecological and commercial importance makes *N. unicornis* an attractive candidate for biochronology studies in the tropics where time series data are scarce.

In this study, we explored signals of environmental and climatic variability through the use of inter-annual otolith growth increments in the tropical coral reef fish, *N. unicornis*. We constructed two geographically distinct otolith biochronologies for *N. unicornis* in the Commonwealth of the Northern Mariana Islands (CNMI). The time series are used to assess intraspecific growth responses separated by two degrees in latitude in the same island archipelago. Previously, synchrony in growth responses among different populations of the same species in the same ocean basin have been found for this species (Taylor et al. 2019) and other reef fish (Ong et al. 2017, 2018); here we explore smaller-scale connections across a thermal (latitudinal) gradient. We hypothesized that there would be synchrony in growth across a relatively small latitudinal range due to many studies having found evidence of large-scale synchrony driven by regional or broad-scale climate indices in fish species

(e.g., Black et al. 2009; Morrongiello et al. 2012; Ong et al. 2018). Using dendrochronology detrended growth data, we first explored the degree of synchrony in growth responses in two latitude subsets of *N. unicornis* in the CNMI. We then used linear mixed-effects models to evaluate the influence of high-frequency (inter-annual) climate and environmental variability on growth. We tested three hypotheses for predictors of growth rate of the shallow water herbivorous reef fish, *N. unicornis*, in the two latitude adjacent regions. Specifically, to address our hypotheses, we (1) tested the influence of local scale processes (temperature and productivity); (2) tested the influence of regional scale processes (broad-scale climate indices) on adult fish growth rate in each region; and (3) assessed the relative importance of local vs. regional scale environmental variation in driving fish growth at each latitudinal subset. We expected that due to minimal or no fishing pressure, increased temperatures would lead to an association with increased growth rate, particularly during El Niño conditions.

## Methods

### Study region and sample collection

The Mariana Archipelago is a group of coral limestone and volcanic islands that includes the CNMI and the Territory of Guam which are under the jurisdiction of the United States Affiliated Pacific Islands (USAPI) (Heron et al. 2016). The CNMI is a part of the USAPI including the Territory of Guam, Republic of Palau, Republic of the Marshall Islands, Federated States of Micronesia, and American Samoa. The Mariana Archipelago is located in the western Pacific Ocean along the Mariana Trench subduction zone and is uniquely positioned, running from north to south across a ~7–8°N latitudinal gradient. CNMI spans 14 islands from 14 to 20°N latitude. Nine of these islands are emergent volcanic islands that do not have permanent human populations (Heron et al. 2016). Five islands to the south are composed of limestone and are geologically older. Three of these limestone islands are inhabited (Saipan, Tinian, and Rota) (Heron et al. 2016). The islands north of Saipan span ~6° of latitude and experience little to no reef-associated fishing pressure. The annual ranges in SST experienced can vary from 2.5 °C in the southern islands to 3.8 °C in the northern islands (Gove et al. 2013). Specifically, the annual temperature range experienced in the north is generally wider and more variable (Urucus 20.6°N: 25.1–28.9 °C) compared to the uninhabited and more southern islands like Sarigan (16.7°N) which has recorded thermal limits from 26.4 to 28.9 °C, (Gove et al. 2013).

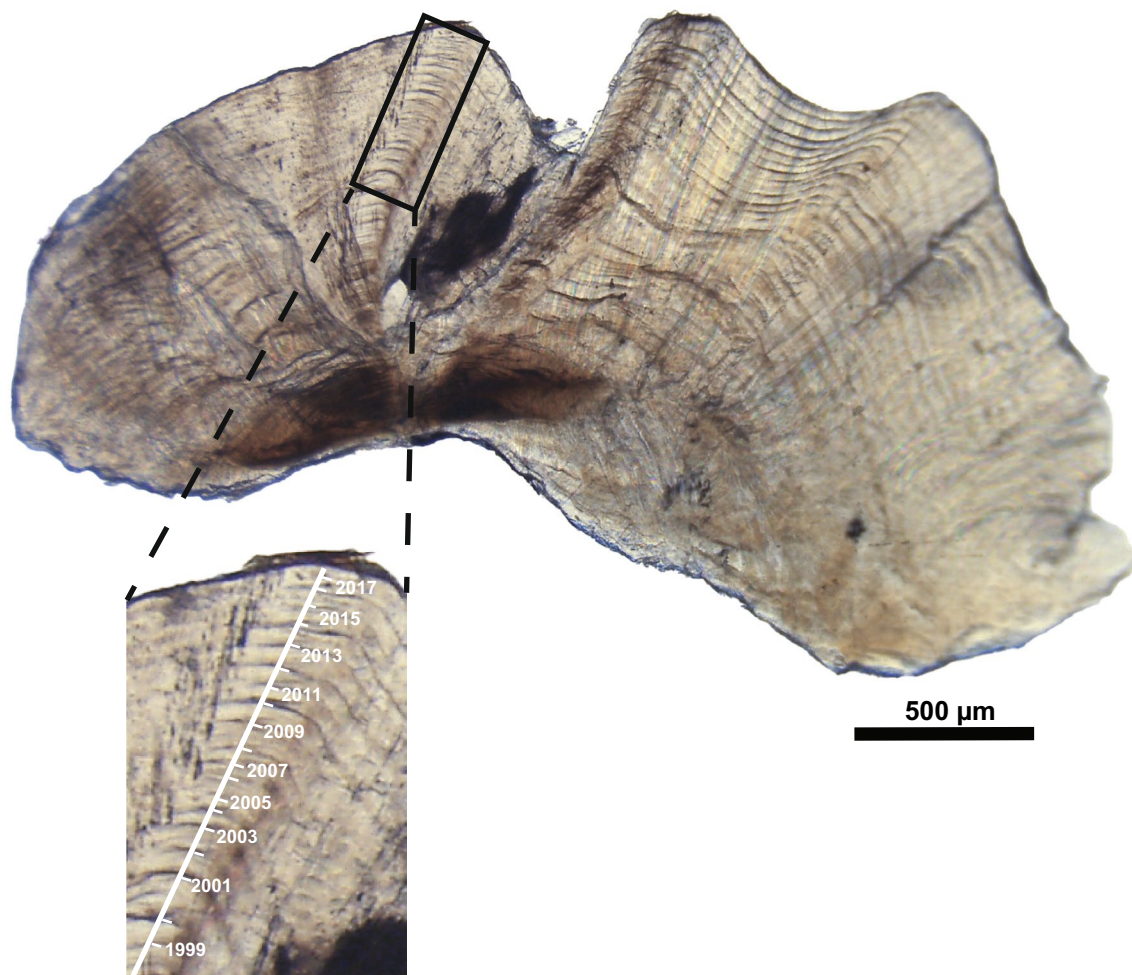
Bluespine unicornfish (*Naso unicornis*) were collected from seven northern uninhabited islands of the CNMI

(Uracus, Maug, Asuncion, Pagan, Guguan, Sarigan and Anatahan). Collections were completed on research cruises aboard the NOAA Ship *Oscar Elton Sette* during 2014 and 2018. From this collection of several hundred fish, samples were chosen if they satisfied a criterion of long lived (10+ years) and ring clarity for appropriate application of dendrochronology methods. The CNMI groupings according to latitude will be referred to as “North” for the latitude 21–19° (Uracus, Maug and Asunción) (n = 15 fish) and “Central” for the latitude 19–16° (Pagan, Guguan, Sarigan and Anatahan) (n = 14 fish) (Fig. S1; Table S1). Specimens were collected from uninhabited islands during research cruises (n = 26) by spearfishing with snorkel from small boats. A small portion of samples (n = 3) was collected from the islands Sarigan and Pagan through the Saipan fish markets in 2013 by the US Territorial Biosampling Program. Sarigan and Pagan are inhabited islands but have a small residency. After collection, fish were processed fresh onboard

the research vessel. Date and location of capture, fork length (0.1 cm), whole body weight (0.01 kg), macroscopic sex, and gonad weight were recorded for each individual. The sagittal otoliths were removed via dissection, cleaned, dried, and stored for future age analysis.

### Specimen processing

One sagittal otolith from each pair was sectioned transversely, photographed, and annuli were counted to quantify fish age (see Online Resource for complete otolith processing details). Annual increment widths were measured to create a time series of otolith growth rate; measurements were taken along a transect line running perpendicular from the otolith core to the distal edge of the section on the ventral side (Fig. 1). To develop a chronology of adult growth, we removed any growth occurring before year 4, i.e., the age at maturation (Taylor et al. 2014), prior to



**Fig. 1** Transverse section of a sagittal otolith of *Naso unicornis* from the Commonwealth of the Northern Mariana Islands (CNMI). Transect line in the image subset demonstrates the axis of measurement

perpendicular to annual growth bands as indicated by tick marks and years the growth occurred

analysis. Additionally, animals < 10 years of age are difficult for crossdating application techniques because there are too few degrees of freedom to accurately detect the synchronous growth signal (Smoliński et al. 2020). Therefore, to address extrinsic impacts to growth within our study region and to have a statistically robust number of samples to conduct analyses, we grouped the three northernmost islands (Uracus, Maug, and Asuncion) as one latitude subset (North) and (Pagan, Guguan, Sarigan, and Anatahan) as a second latitude subset (Central). There is approximately 1° latitude between these island subsets that makes for a natural separation point.

### Growth chronology development

Fish otoliths grow nonlinearly in relation to a fish's body size over time and thus are good proxies for somatic growth (Campana 1990). The principle of crossdating was used to assist in the correct assignment of all increments to the years each increment is formed. Crossdating methods, both visual and statistical, were developed for tree-ring analysis (dendrochronology) to evaluate increment series in a detrended capacity for the purpose of identifying synchronous growth patterns (Black et al. 2005). This technique is based on the concept that environmental drivers affect annual growth in a synchronous way that translates to a shared signal captured across individuals within a species and location (Black et al. 2005; Moyano et al. 2021). By using dendrochronology techniques on fish otoliths to create biochronologies, the influence of early growth effects can be removed and high frequency variability (i.e., short-term environmental signals on a year to year basis) preserved (Black et al. 2005; Morrongiello et al. 2012). Therefore, the synchrony in growth among individuals extracted with dendrochronology techniques is representative of a population-wide signal rather than individual variability in growth rate (Black et al. 2005, 2009). We used visual crossdating to assess narrow and wide increments common across samples in a location (Black et al. 2005).

Statistical crossdating was used to check the assignment of growth increments to a calendar year in an individual using the program COFECHA (Grissino-Mayer 2001). This program correlates the annual variability in growth widths in one individual to the rest of the individuals being analyzed. We loaded raw increment measurements of individual adult growth into COFECHA and detrended each individual series with a spline curve which has been shown to enhance inter-annual variability and increase strength of dating (Speer 2010). Spline rigidity parameter of 21 years was optimized for the species based on an iterative assessment and optimization of the interseries correlation as described in Taylor et al. (2020). Potential errors in the placement of increment boundaries were inspected visually and corrections were made when appropriate.

Each of the two chronologies, one per latitude subset, was constructed using the double detrending method to verify if there was a temporally synchronous growth response among individuals at each latitude subset (Rountrey et al. 2014). Crossdated increments were first detrended in R (R Core Team 2020) v. 4.0.2 with package dpIR (Bunn 2010), using a negative exponential function and subsequently a spline curve of rigidity parameters of 21 years for both the independent chronologies (Fig. S2). The negative exponential function removes the rapid decline in ontogenetic growth effects that occur in the early life history of a fish, also known as age-related growth effects (Black et al. 2005). The application of a spline removes departures from the negative exponential fit and miscellaneous low frequency variation (decadal) patterns that affect model fit (Rountrey et al. 2014). A mean index chronology from the average of all detrended increment series for all individuals for each calendar year was developed using Tukey's biweight robust mean (Bunn 2010). Calendar years with a sample depth less than nine individual measurements were excluded from the analysis (Fig. S2). The quality of the detrended increment series (chronology) was assessed using the population-level signal strength (common variance among individuals), mean of pairwise series correlations ( $\bar{r}$ ), the expressed population signal (EPS) – a measure of how well the chronology represents the theoretical population chronology – and the interseries correlation, which is a measure of synchrony among individuals (Speer 2010). Only periods  $\bar{r} > 0$  and  $\text{EPS} > 0.50$  were used to construct the master growth chronology for each region; these thresholds have been used for other tropical species to detect the strength of a growth response common among individuals in a population (Ong et al. 2018). The timespan for the two chronologies covered 17 years, from 2000 to 2017, with an overlap of nine years 2005–2013.

### Environmental and climate datasets

Extrinsic predictors of growth rate were derived from remotely sensed datasets of approximately 4° latitude subsets between 22 and 16° and longitude 146–144° from the NOAA ERRDAP portal (<https://oceanwatch.pifsc.noaa.gov>). Coral Reef Watch CoralTemp-Monthly composite SST °C data with a 5-km resolution was extracted. SST was derived into an annual, three-month high average (*SST<sub>hi</sub>*), and a three-month low average (*SST<sub>low</sub>*) for each of the two latitudinal subsets explored, calculated from the three highest (*SST<sub>hi</sub>*) or lowest (*SST<sub>low</sub>*) months of average SST for each year (Fig. S3). Chlorophyll-a concentration (mg C m<sup>3</sup>) data was extracted from ESA OC CCI (European Space Agency Ocean Color Climate Change Initiative). Monthly composite v5.0 with a 4-km resolution was used as a measure of ocean productivity. Chlorophyll-a data were only derived

as an annual composite due to the lack of seasonal variation seen during exploration of the data in each latitude subset.

Monthly averages for all climate indices were averaged into an annual grand mean corresponding to a year of growth. Climate teleconnections span wide spatial and global scales; therefore, the climate indices used were not derived on a spatial scale specific to this study. ENSO events have a known impact in our study region (Chowdry et al. 2019; Houk et al. 2020). We used the multivariate ENSO index (MEI) as an indicator of eastern Pacific Ocean driven ENSO events. MEI is defined as the leading principal component of sea-level pressure, zonal and meridional components of the surface wind, sea surface temperature, surface air temperature, and cloudiness in the tropical Pacific (Wolter and Timlin 2011). Since the 1970s the central-western Pacific Ocean originating ENSO events have increased in frequency which is predicted to have an increased frequency in years to come (Liang et al. 2021). To evaluate the impact that this type of ENSO event has on fish in our study area we used the El Niño Modoki index (EMI) from the APEC Climate Center (<https://www.jamstec.go.jp/virtualearth/>). The EMI represents the unique tripolar Sea Surface Temperature Anomaly (SSTA) averaged over three areas in the central Pacific (165°E–140°W, 10°S–10°N), (110°W–70°W, 15°S–5°N), and (125°E–145°E, 10°S–20°N) (Ashok et al. 2007). Positive values indicate the warm phase, or El Niño Modoki events, and negative values indicate the cold phase, or La Niña Modoki events (Ashok et al. 2007). Lastly, we used an annual average of the Pacific Decadal Oscillation Index (PDO) to explore any possible decadal signals in growth rate extracted from <https://www.ncei.noaa.gov/access/monitoring/pdo/>. For all three climate indices, warm phases are indicated by positive numbers and cold phases by negative.

## Data analysis

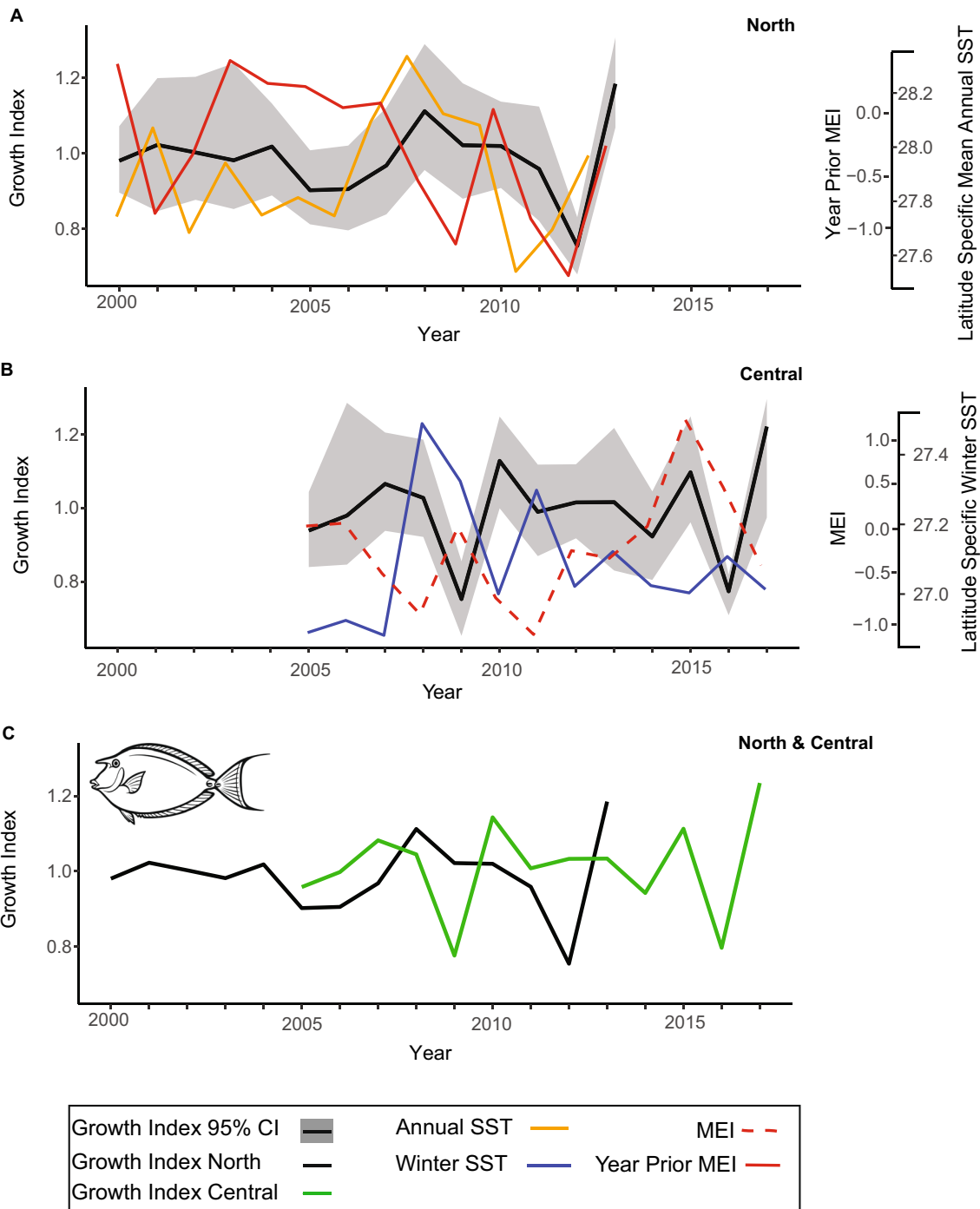
Following detrending, we first examined growth chronologies (indices) for between region level synchrony using the Gross synchrony metric (Gross et al. 2014). The North and Central growth indices were tested using the *codyn* package (Hallett et al. 2016) in R which in this case, compares the average correlation in growth within each location with the aggregated growth data. This synchrony metric can be interpreted as a standardized scale where -1 is perfect asynchrony, 1 is perfect synchrony, and 0 is when individuals fluctuate independently (Hallett et al. 2016).

Next, we explored the best predictors of growth through linear mixed-effects models (LME) where the response variable in all models was the detrended growth increment data. Due to small sample sizes, we used growth increment data instead of the master chronologies to increase the sample size and to better facilitate detection of variation among data

points. To investigate local drivers of growth rate (Table S2), environmental predictors for SST and chlorophyll-a were mean centered. Climate indices were left in their original standardized form to investigate regional drivers of growth rate (Table S2). One-year lags for climate indices and environmental variables were also tested to investigate any relationships with conditions during the year prior to growth (Table S2). The North final chronology spanned the years 2000–2013 and the Central spanned the years 2005–2017 for all data analyzed. We followed the methods from Taylor et al. (2020) for the use of dendrochronology detrending and linear mixed-effects models (LME) for our two independent latitude subsets; however, our analysis differed in that we used detrended otolith increment data instead of the master chronologies due to our short time series. Prior to analysis, we assessed the degree of correlation among extrinsic variables using correlation matrices for each latitude subset (Fig. S4). We used LME with a Gaussian error structure and identity link fit to detrended growth data across individuals and years of growth using the *lmer* package in R (Bates et al. 2015). We tested all extrinsic predictors described above for each latitude subset as fixed effects. We accounted for individual fish variation in growth for each individual fish by including the identifier FishID as a random intercept in each model tested. The *MuMIn* package in R was used for model selection using multi-model averaging (Bartoń 2015) through minimization of the corrected Akaike's information criteria (AICc) for small data sets. All models were fitted using restricted maximum likelihood estimation (REML). Models within 2 AICc of the lowest model were considered the best models and subsequently validated with a plot of standardized residuals vs. fitted values. For each model, we calculated the marginal  $R^2$  (the proportion of variance explained by the fixed effects) and the conditional  $R^2$  (the proportion of variance explained by the fixed and random effects) (Nakagawa and Schielzeth 2013).

## Results

Fish specimens used ranged from 10 years of age to 33 (Table S1). The age range of fish from the North was 12–33 years; the oldest fish was ten years older than the oldest Central fish (Central fish ages ranged from 10 to 23 years) (Table S1). Otolith growth chronologies constructed from detrended series yielded partially overlapping time periods of growth, 2000–2013 for *N. unicornis* North and 2005–2017 for *N. unicornis* Central (Fig. 2). These chronologies had similar levels of synchrony in a population-level response as indicated by the interseries correlations of 0.219 and 0.232, respectively (Fig. 2, Table 1), with  $\bar{r}$  (relative magnitude of common variance among individuals) values of 0.138 (95% CI 0.326– -0.050;



**Fig. 2** Otolith growth-increment chronologies within a latitudinal gradient in the Northern Mariana Islands. **A** The North chronology for *Naso unicornis* caught from the northernmost islands (Uracus, Maug, and Asuncion) is plotted against the most influential environmental time series for this region, mean annual SST, and the year prior mean annual MEI. **B** The Central chronology for *Naso unicornis* caught in the central islands (Pagan, Guguan, Sarigan, and North) and 0.308 (95% CI 0.599- 0.017; Central). However, the North  $\bar{r}$  was about half of the signal strength of the Central  $\bar{r}$ , indicating less signal strength in common

Anatahan) is plotted with the winter SST and the mean annual MEI of the same year. **C** Growth chronologies for each latitude subset illustrate the independence of the north and central islands, Gross synchrony=0.0387. SST refers to the mean annual sea surface temperature for the latitude subset, winter SST refers the coldest three-month period average, and MEI is the mean annual multivariate ENSO index of the same year or the year prior

variance among individuals at ~2° latitude higher. We found no evidence of synchrony in growth between the North and Central latitude subsets (Gross = 0.0387;

**Table 1** Descriptive statistics for the *N. unicornis* chronology from the northern most islands of CNMI with a sample depth > 9

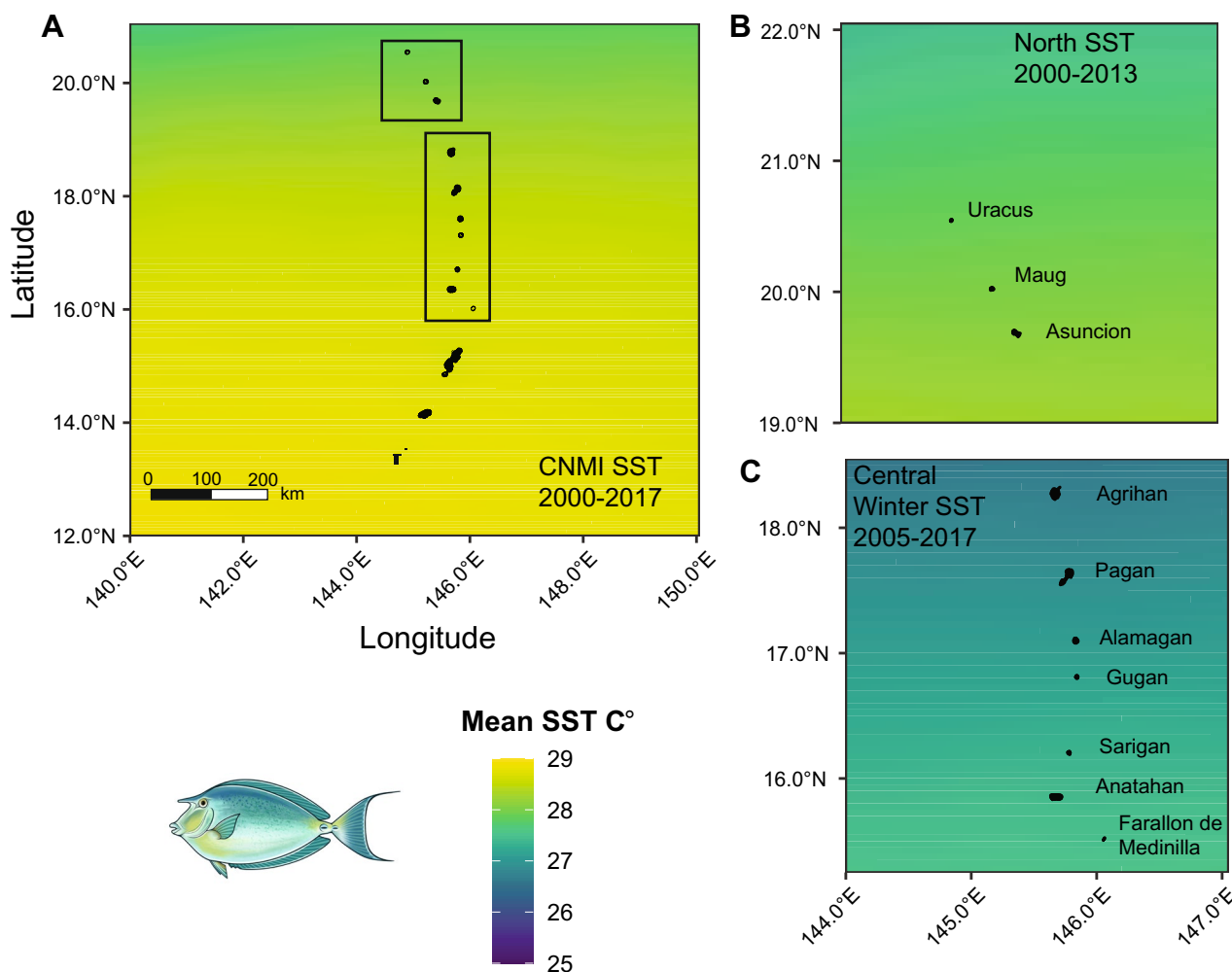
<i>N. unicornis</i> biochronology	North	Central
Latitude	22–19°	19–16°
No. series	15	14
Timespan	2000–2013	2005–2017
Interseries correlation	0.219	0.232
Mean $\bar{r}$ (95% CI)	0.138(0.326- -0.05)	0.308(0.599–0.017)
EPS	0.690	0.834

\*CNMI Northernmost islands (North) and CNMI central islands (Central)

The latitude ranges each chronology covers, the number of series (individuals) included in the chronology, the timespan the chronology covers, interseries correlation with standard deviation, the mean  $\bar{r}$  with 95% CI, and the expressed population signal (EPS)

Fig. 2). A Gross synchrony value near zero suggests the two latitude subset's growth responses are fluctuating independently of each other.

The temperature ranges documented in our analysis consistently showed the north CNMI experienced cooler temperatures than the central CNMI directly south. North annual SST during years 2000–2013 ranged from 27.6 to 28.3 °C, with a grand mean temperature of 27.9 °C, while winter (annual average three month low) temperatures ranged from 25.4 to 26.4 °C, and the grand mean temperature experienced was 25.9 °C (Fig. 3; Fig. S3). In contrast, the annual average SST experienced in the central during years 2005–2017 ranged from 28.3 to 28.9 °C, and the grand mean temperature experienced was 28.6 °C, while winter temperature range experienced was 26.9–27.5 °C with a grand mean temperature of 27.1 °C (Fig. 3; Fig. S3). The annual grand



**Fig. 3** Spatial average maps of sea surface temperature (SST) across a latitudinal gradient of the Mariana Archipelago and associated sampling sites. **A** The change in annual SST from north (Uracus) to south (Guam) across the years of growth examined in this study. **B** The change in annual average SST for the northern most islands of

the Commonwealth of the Northern Mariana Islands (CNMI), Uracus Maug, and Asuncion for the chronology 2000–2013. **C** The change in the coldest three-month period average in SST indicating winter (SST-low) for the central islands of Pagan, Guguan, Sarigan, and Anatahan during the period of the chronology 2005–2017

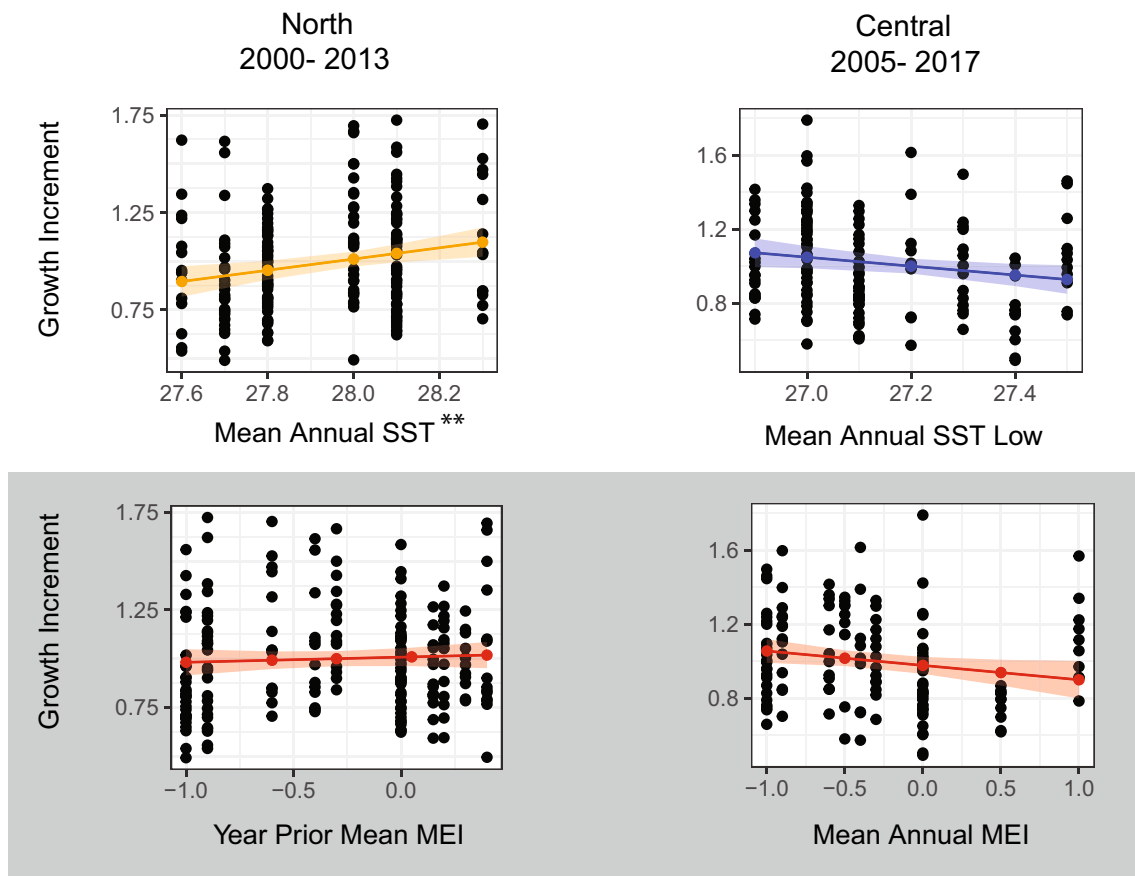


mean temperature in the Central was 0.7 °C hotter than the North, and in the winter, the North was approximately 1.2 °C cooler than Central during the time periods studied.

The best LME model for explaining *N. unicornis* otolith growth at the Northern latitude subset, North, was the model with the current year's *SST* as the sole explanatory variable (Fig. 4; Table 2; Fig. S5A). Mean annual *SST* had a positive relationship with *N. unicornis* growth, where an increase in *SST* at this latitude range was correlated with increased growth rate during the years of growth 2000–2013, and *SST* explained 3.8% variation in growth, (marginal  $R^2=0.038$ ,  $p=0.006$ ; Fig. 4; Table 2). The model containing both *SST* and *chlorophyll-a* received similar support, with a  $\Delta AICc < 2$  (Fig. S5A; Table. S3A). The relationship with *chlorophyll-a* was also positive, indicating that increased productivity during the year explained additional variation in growth, though only 0.6% (marginal  $R^2=0.044$ ,  $p=0.305$ ). The optimal LME model for regional processes contained *MEI* of the year prior as the explanatory variable,

however all other models had  $\Delta AICc < 2$ , suggesting similar support, or lack thereof, for all climate indices as drivers of *N. unicornis* growth in the North. The fixed factor year prior mean *MEI* was retained in the best regional model and explained only 0.7% variation in growth (marginal  $R^2=0.007$ ,  $p=0.239$ ; Table S3A). When the two best models were compared to determine the relative importance of local- vs. regional-scale processes for fish growth in the north, the best fit model indicated local processes (*SST*) were most important (Fig. 4; Table S3A).

The best LME model for explaining *N. unicornis* otolith growth at the Central latitude subset, was the model with *SSTlow* as the sole explanatory variable (Fig. 4; Table 2; Fig. S5B); however, the amount of variation explained by the winter temperatures was relatively small (2.3%), and the growth response ranged from essentially no response (0.02 increase in growth/1° increase in *SSTlow*) to a negative response (−0.41 decrease in growth/1° increase in *SSTlow*; Table 2). The model containing *SSTlow* from the previous



**Fig. 4** Fixed effects plots for optimal linear mixed-effects models of *Naso unicornis* growth measurements local versus regional best predictors for both north and central latitude subsets. North growth measurements for the years of the final chronology with fixed effects mean annual *SST* and mean annual *MEI* of the prior year. Central growth measurements for the years of the final chronology 2005–

2017 with fixed effects for winter *SST*, the mean annual *MEI* of the current year. *SST* is the orange line, winter *SST* is blue, both *MEI* of the prior year and *MEI* of the current year in red. Note, y-axes for growth indices differ due to different ranges of growth for each latitude subset. \*\* indicates statistical significance, and grey shading indicates regional predictors only

**Table 2** Linear mixed-effects model results for best models testing local versus regional influence

A)				B)		
Predictors	Estimates	<i>p</i>	<i>F</i>	Estimates	<i>p</i>	<i>F</i>
(Intercept)	0.9997 (0.96–1.04)	< 0.001***		1.0007 (0.96–1.04)	< 0.001***	
SST	0.25 (0.07–0.42)	<b>0.006**</b>	<b>7.7284**</b>			
SST <sub>low</sub>				–0.20 (–0.41–0.02)	0.068	3.3777
<b>Random effects</b>						
$\sigma^2$	0.07			0.06		
$\tau_{00}$	0.00 <sub>FishID</sub>			0.00 <sub>FishID</sub>		
N	15 <sub>FishID</sub>			14 <sub>FishID</sub>		
Observations	195			146		
Marginal R <sup>2</sup> / Conditional R <sup>2</sup>	0.038/0.038			0.023/0.023		

A) CNMI North (North) best explanatory variable is the mean annual SST or SST. B) CNMI Central (Central) best explanatory variable is the three-month average low of SST or the winter SST<sub>low</sub>. Estimates include 95% confidence intervals.  $\sigma^2$  is the standard deviation within a group squared and  $\tau$  is the standard deviations between groups. \**p* < 0.05; \*\**p* < 0.01; \*\*\**p* < 0.001

year, and the model containing *chlorophyll-a* also had similar support with  $\Delta\text{AICc} < 2$  (Fig. 4; Fig. S5B; Table S3B). The optimal LME model for regional processes contained *MEI* of the current year as the variable, explaining 1.7% of variation in *N. unicornis* growth (marginal  $R^2 = 0.017$ ,  $p = 0.033$ ; Table S3B). *MEI* was negatively correlated with the growth index, indicating a negative growth response to warming El Niño conditions as predicted by the *MEI* (Fig. 4; Fig. S5B). However, all other models had  $\Delta\text{AICc} < 2$  suggesting similar support for all climate indices as drivers of *N. unicornis* otolith growth in the Central latitude subset (Fig. S5B; Table S3B). When the two best models were compared to determine the relative importance of local- vs. regional-scale processes for fish growth in the Central latitude, the model containing SST<sub>low</sub> was the strongest; however, the models indicated a high level of similarity ( $\Delta\text{AICc} < 2$ ), suggesting that neither local nor regional processes were more important in this region (Fig. S5B; Table S3B). In addition, we tested the effect of latitude on growth for our latitude subsets spanning  $\sim 6^\circ$  in latitude and found no relationship.

## Discussion

Interestingly, despite synchrony in growth patterns having previously been identified between fish populations across large spatial scales, suggesting a common sensitivity in numerous fish species to changes in climatic conditions (e.g., Black et al. 2009; Ong et al. 2017, 2018), we did not find any evidence of synchrony in growth patterns between our two latitudinal subsets of *N. unicornis*. We did, however, find synchrony in the growth response among individuals of the same latitude subset, indicating a local response to a common external forcing. For both

latitudinal subsets, the importance of local-scale environmental processes vs. regional-scale climatic processes for explaining *N. unicornis* growth differed, with the strongest effect of local-scale environmental processes on growth in the north and no clear greater importance of either effect on growth in the central CNMI.

In the uninhabited islands of CNMI, inter-annual variation in temperature had the strongest effect on *N. unicornis* otolith growth across a  $\sim 6^\circ$  latitudinal gradient, however the variability explained by our best models was relatively low. We found local environmental conditions indicated by SST to be the main predictor of variation in otolith growth in both latitude subsets, although the temporal scale of the significant temperature predictor differed (annual vs. seasonal). The differences in response to temperature among individuals of the same species could be a result of intraspecific variation in thermal tolerance, where a higher thermal tolerance to increased temperatures reflects a population response to local thermal regimes (McKenzie et al. 2021). It may be that fish in the north have a higher thermal tolerance because they experience more temperature variability in their environment, particularly in recent winters (Fig. 3; Fig. S3). However, regardless of mechanism, the critical result from our study is that we found differences in *N. unicornis* responses to local environmental conditions, even over a relatively small latitudinal gradient. This work is the first to provide evidence of local predictors of intraspecific otolith growth responses across a latitudinal gradient in this region. As the variability explained by our models was relatively low overall, the addition of other annual and seasonal location-specific extrinsic predictors in the future will provide a more comprehensive picture as to the drivers impacting coral reef fish growth rate in this uninhabited environment. Nevertheless, this work highlights the need for intraspecific

variability to be considered when assessing the vulnerability of this species to a changing climate.

Increases in annual SST during the period of past otolith growth studied (2000–2013) were associated with increases in *N. unicornis* otolith growth in the northernmost islands. An increase in growth during rising temperature conditions is only likely to occur if the fish are experiencing temperatures that are physiologically favorable for feeding (Jobling 1997; Neuheimer et al. 2011), and the food availability is adequate to accommodate increased metabolic demands resulting in increased growth (Jobling 1997; Erisman et al. 2021). Our finding suggests *N. unicornis* is experiencing favorable environmental conditions in the north islands, where annual temperatures range from 25.1 to 28.9 °C. However, if food availability is limited or temperature increases beyond what is physiologically favorable, then growth rate has the capacity to fall below average (Pörtner and Farrell 2008).

In the CNMI central islands where winter temperatures were warmer than in north islands, seasonal (winter) temperature was the best predictor of otolith growth variation rather than the variability in annual SST. This resulted in an inverse relationship with warming winters and growth rate, indicating warmer-than-average winters are possibly less favorable conditions for growth during the years 2005–2017. Though we did not specifically investigate food availability in this study, warmer-than-average winters could have negative effects on food availability for *N. unicornis* in this region. *Naso unicornis* is an herbivore that feeds primarily on large thallate brown algae, often the genera *Turbinaria* and *Dictyota* (Choat et al. 2002; Puk et al. 2016). Changes in ocean temperature and chemistry may alter palatability of algae (Borell et al. 2013) and/or increase feeding requirements for herbivores during the winter season when biomass of brown algae is known to decrease and epiphyte loads increase, thus decreasing the rate of algal removal by herbivores (Lefèvre and Bellwood 2010; Puk et al. 2016). Combined with the senescence of macroalgae commonly found in winter months in the Indo-Pacific (Puk et al. 2016), an increase in competition for food resources could have contributed to the inverse relationship we found between *N. unicornis* growth and warmer winter temperatures in the central islands. Alternatively, warmer winters could have led to increased competition for food in a different capacity, where structure and palatability of the algae is higher than expected and larger *N. unicornis* migrate to the better localized conditions while residents stay in place (Welsh and Bellwood 2015). While we did not find a significant relationship with chlorophyll-a for primary production, chlorophyll-a did explain additional variation when added to the best models for each latitude subset. Interestingly, the amount of variation explained by the environmental fixed-effects

retained in the best models remained small in both areas. This suggests that in addition to temperature, other important local factors not available for testing (e.g., freshwater input, location specific food availability) may contribute more to variation in growth of *N. unicornis* in the CNMI central islands.

The MEI was identified as a weak driver of adult growth in *N. unicornis* from the CNMI central islands but did not account for any variation in the north. Our results suggest that of the annual extrinsic variables tested, local drivers predominate in the central CNMI. ENSO effects have been documented as having an impact on otolith growth in a wide variety of fishes from rockfish (Black 2009), croakers (Erisman et al. 2021), to demersal pelagic (Moyano et al. 2021), and a variety of tropical fishes (Ong et al. 2017, 2018). We found an inverse relationship with otolith growth rate and warming winters likely associated with moderate to strong El Niño events over the period of 2005–2017. Our Central chronology only covered a time span of 13 years, which is considered short in the dendrochronology field, but this time series covered two strong El Niño events in recent decades. These events in 2009/2010 (El Niño Modoki) and 2015/2016 (eastern Pacific El Niño) were some of the strongest on record, similar to that of 1997/1998 eastern Pacific El Niño (Liang et al. 2021; Chowdhury et al. 2022). During the 2014/2016 El Niño, the USAPI experienced drought, persistent above-average SST, massive coral bleaching, as well as an increase in duration and frequency of tropical storms causing a massive disruption to marine ecosystems including in the CNMI (Rupic et al. 2018; Chowdry et al. 2022). It may be that a multi-decadal biochronology time-series capturing multiple moderate to strong events could indicate a stronger relationship with ENSO events in the central CNMI.

The North chronology had a different growth response to temperature and climate variability, which may reflect that it did not cover a time span of multiple strong events as the Central chronology did. It is possible that strength and duration of the event(s) are needed in combination to initiate an observable growth response. Alternatively, the annual average temperature range at the north latitudes is ~ 1 °C cooler than the central latitudes which could be enough of a refuge from increasing temperatures to maintain adult growth rate during significant disturbances associated with high temperature increases over extended periods of time. Additionally, it has been reported that due to the North Pacific subtropical gyre, the impacts of El Niño events vary spatially in the central North Pacific (Lehodey et al. 2020). The southern portion of the gyre below 15°N latitude experiences typical equatorial ENSO impacts vs. the northern portion (above 25°N) which experiences midlatitude teleconnections that result in southward westerly winds and productive subtropical fronts during El Niño conditions (Lehodey et al. 2020).

These documented spatial differences in the influence of ENSO events in this region may have also contributed to the two different growth responses according to latitude.

Climate variability has a wide variety of documented impacts on marine species, but sea water temperature continues to be an important driver of change in marine environments for both populations and individuals. Temperature is a primary component of many climate variability indices like the MEI (Wolter and Timlin 2011), and the impacts of rising temperatures are also a main result of anthropogenically induced climate change (Pörtner and Peck 2010; Asch et al. 2018). We found that local drivers in the form of latitude-specific SST were the best predictors of *N. unicornis* growth rate in this region, rather than broader regional drivers as often reported in the literature (Black et al. 2009; Morrongiello et al. 2012; Ong et al. 2018). Even though we found that MEI did account for a small amount of variation in growth rate in the central islands, interestingly all climate indices tested produced strikingly similar fits to the data (all within three AICc), suggesting that the teleconnection tested was insignificant. These results also indicated that the variability in impact to growth rate within the region occurred in the warm phase of all the climate indices tested. Future monitoring of increased SST impacts on fish growth rate in this region may continue to be important given future climate change predictions believed to impact the duration and frequency of ENSO events.

We faced several challenges in this study that limited the scope of predictor variables available for model inclusion and resulted in a focus on temperature and climate variables. Additional environmental predictors, such as food availability (i.e., abundance of targeted macroalgae) and freshwater inputs, were either not available for the study sites, or not available on the annual time scales during the years of growth formation of our final chronologies. The biochronology timeseries itself was limited in length and sample size due to the difficulty in obtaining *N. unicornis* older than 10 years of age in this region. While a more comprehensive picture of the possible extrinsic drivers of *N. unicornis* growth rate would be ideal to account for more of the unexplained variation in growth rates, our results begin to fill a knowledge gap on one of the most common and well-documented drivers of fish growth – temperature. Furthermore, this study highlights the need for long-term data collection efforts in remote regions of the world, which are difficult and costly to access, but are often among the most vulnerable to impacts of climate change. Changing environmental conditions associated with anthropogenically induced climate change are predicted to have negative impacts on reef-associated fishes and fisheries in localized coastal areas of the western tropical Pacific (Asch et al. 2018). As the frequency of extreme El Niño events is expected to double under the current

Paris target of 1.5 °C (Guojian et al. 2017), future ENSO events are the primary concern in the USAPI (Chowdhury et al. 2022).

We show that both SST and El Niño climatic events as predicted by MEI can have both positive and negative impacts on the growth rate of an herbivorous coral reef fish. The value of aquatic biochronologies lies in providing the necessary biological context of reconstructed past events to help climate change models predict future biological impacts to our fish and fisheries. Our results showed the usefulness of even shorter time series (13–14 years) in filling knowledge gaps as to how temperature and climate variability have influenced the variation in past biological responses to such changes in areas with little to no fishing pressure. We highlight independent growth responses in *N. unicornis* within a latitudinal gradient and how even within a species, the response to drivers like temperature and El Niño events can vary. This study also highlights the need for long-term environmental data sets from often remote tropical regions to fully understand drivers of ecological change in marine environments that are among the most vulnerable to climate change, and to obtain a greater understanding of the population-level response within and among coral reef fish species to climate or environmental drivers. Furthermore, we recommend studies exploring climate effects in the western tropical Pacific examine local-scale effects on fish and their fisheries in addition to regional effects of climate teleconnections according to the predicted increase in SST and persistence of strong El Niño events in the future.

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**Data availability** The data sets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: NOAA PIFSC Life history program estimates repository. Available: <https://inport.nmfs.noaa.gov/inport/item/59002>.

**Declarations**

**Conflict of interest** The authors have no conflict of interest to declare.

**Ethics approval** The animal study was reviewed and approved by the University of Hawai'i Animal Care & Use Committee (IACUC # 13–1696-7).

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