



Growth patterns of specialized reef fishes distributed across the Red Sea to Gulf of Aden

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Abstract Determining how growth rates and body size vary spatially and among reef fish species is important to understanding functional traits and demographic trade-offs. Variability in reef fish growth trajectories may be influenced by intrinsic (e.g., biological, phylogenetic) and extrinsic factors (e.g., environmental), as well as their interaction via

ecological processes. To assess interspecific variation in these traits, we estimated age and growth for a guild of butterflyfishes sampled from reefs spanning ~10° degrees of latitude in the Red Sea to the adjacent Gulf of Aden. This study region was chosen because it spans environmental gradients known to influence fish life history traits and allowed for comparisons between regional versus more widespread butterflyfish species. Across the 10 study species, we found significant interspecific differences in growth.

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This finding contrasted with almost no intraspecific differences between populations across the study region. Moreover, we found that maximum body size was significantly correlated with the phylogenetic placement of the butterflyfish species. These patterns suggest that intrinsic factors and a high degree of ecological specialization may elicit spatially conservative demographic profiles, even when faced with considerable environmental variation across a region.

Keywords Butterflyfish · Coral reef · Demographic · Growth rate · Life history · Phylogenetic constraint

Introduction

Growth and body size of individuals are fundamental life history traits that influence rates of population turnover. These traits are mediated by intrinsic (e.g., biological, phylogenetic) and extrinsic factors (e.g., environmental), as well as their interaction via ecological processes, which may even reflect trade-offs with each other through growth-type dependent mortality (Metcalf and Monaghan 2003). Age-based demographic research on coral reef fishes has been slow to emerge, but recent work has highlighted two generalities. First, despite living in high-diversity ecosystems in warm regions, many coral reef fish taxa possess long life spans (i.e., multiple decades; Trip et al. 2008; Ogino et al. 2019; Taylor et al. 2021) with highly asymptotic growth trajectories, whereby life spans greatly exceed expectations based on presumed high population turnover (Sale 1980). Second, growth rates can be highly variable between populations at small spatial scales, a feature that often reflects the extreme variability in habitat and oceanographic forces in coral reef ecosystems (Gust et al. 2002; Kingsford et al. 2019; D'Agostino et al. 2021). Hence, understanding the scale at which growth and body size vary spatially and among species is imperative to modeling population processes in coral reef communities.

The reefs of the Red Sea and adjacent Gulf of Aden present an excellent arena for exploring spatial and taxonomic variability in reef fish growth trajectories. In contrast to the reef systems of the central Indo-West Pacific, these peripheral reefs occupy one of the most geologically and oceanographically

complex regions in our tropical oceans (DiBattista et al. 2015, 2016a,b; Xu et al. 2015), and are defined by two distinct features: (1) a sharp increase in primary productivity and turbidity in the Southern Red Sea (Raitsos et al. 2013), and (2) the narrow (29 km), shallow (137 m) Strait of Bab al Mandab that constitutes the only connection between the Red Sea and Indian Ocean. In the first instance, the Gulf of Aden and waters of Djibouti have a high and relatively stable temperature regime with extensive limestone reefs and high coral cover (Wilkinson 2008). In contrast, the Red Sea is characterized by a distinct habitat shift marked by steep reefs and clear, oligotrophic waters in the Northern and Central Red Sea and shallow banks with turbid, nutrient-rich waters in the south. Absolute Chlorophyll-*a* values in the Southern Red Sea, which is an accepted proxy for phytoplankton biomass, appear to be several orders of magnitude higher compared to the Northern Red Sea (Raitsos et al. 2013). The turbid water region south of 19–20° N in the Red Sea may also limit successful larval dispersal owing to a reduction in coral reef habitat and persistent meso-scale eddies that form at this boundary (Raitsos et al. 2013), a hypothesis supported by the disjunct distribution of some reef fish species (Roberts et al. 1992). This nutrient gradient is accompanied by gradients in both salinity and temperature across the Red Sea and adjacent Gulf of Aden (Raitsos et al. 2013). For example, the Red Sea is characterized by an average winter low sea surface temperature (SST) of ~22 °C to an average summer high of 29–30 °C in the north, versus an average winter low SST of <26 °C to an average summer high of >31 °C in the south and adjacent Gulf of Aden (Berumen et al. 2019). Salinity, on the other hand, shows the inverse pattern, with higher salinities in the Northern Red Sea (>40 parts per thousand) and the lowest salinities in the south (36 parts per thousand; Berumen et al. 2019). In the second instance, historical water exchange between the Red Sea and Indian Ocean (i.e., Gulf of Aden) was repeatedly restricted during Pleistocene glacial cycles and thus periods of lowered sea level (for review, see DiBattista et al. 2016b).

Reef fish species distributed across the Red Sea through to the Gulf of Aden (including Djibouti and Yemen) show abrupt changes in demographic features over relatively small spatial scales and moderate environmental variation (Taylor et al. 2015, 2018).

The butterflyfish family (Chaetodontidae) are an ideal group to identify patterns and generalities for this region given their small home ranges, territoriality, variable social structure, different feeding modalities ranging from obligate corallivores to generalists, and variable range distributions (Pratchett et al. 2013; Nowicki et al. 2018). Indeed, this specialization with respect to food sources and habitat association means that we should expect that variability in local conditions will impact on their demographic features.

In terms of species distributions for range-restricted endemics, *Chaetodon austriacus* and *Chaetodon paucifasciatus* are found in the Northern and Central Red Sea but, for the most part, no further south, and so they may have adapted to the oligotrophic conditions experienced there (see Fig. 1). On the other hand, *Chaetodon larvatus* is found in the Central Red Sea, Southern Red Sea, and Gulf of Aden (Djibouti and Yemen) but for the most part, no further north, and so they may have adapted to the eutrophic conditions experienced there. *Chaetodon pictus* and *Chaetodon melapterus* are Gulf of Aden to Arabian Gulf regional endemics. *Chaetodon semilarvatus* and *Chaetodon fasciatus* are Red Sea endemics but distributed from the northern

reaches of the Red Sea outside to the Gulf of Aden, and therefore may be able to tolerate a greater range of conditions. The widespread species (*Chaetodon auriga* and *Chaetodon trifascialis*) are both distributed across the Indo-West Pacific, but *C. trifascialis* is an *Acropora* coral-feeding specialist whereas *C. auriga* is a generalist feeder not normally found in the “eutrophic zone” within the Red Sea. Finally, *Chaetodon trifasciatus* is another widespread species distributed across protected coral-rich lagoons and exposed reefs in the Indian Ocean.

The main aim of our study was therefore to compare growth rates and body size between multiple species of butterflyfish sampled to establish general patterns across this region (Central Red Sea to Gulf of Aden). We also test whether differences in these life history traits are associated with phylogenetic age and topological position given that life history traits can be influenced by both intrinsic (phylogenetic) and extrinsic (environmental) factors. Indeed, previous research has shown that many life history traits, including body size, are often related to shared ancestry in fishes (Floeter et al. 2018; Siqueira et al. 2019, 2020).

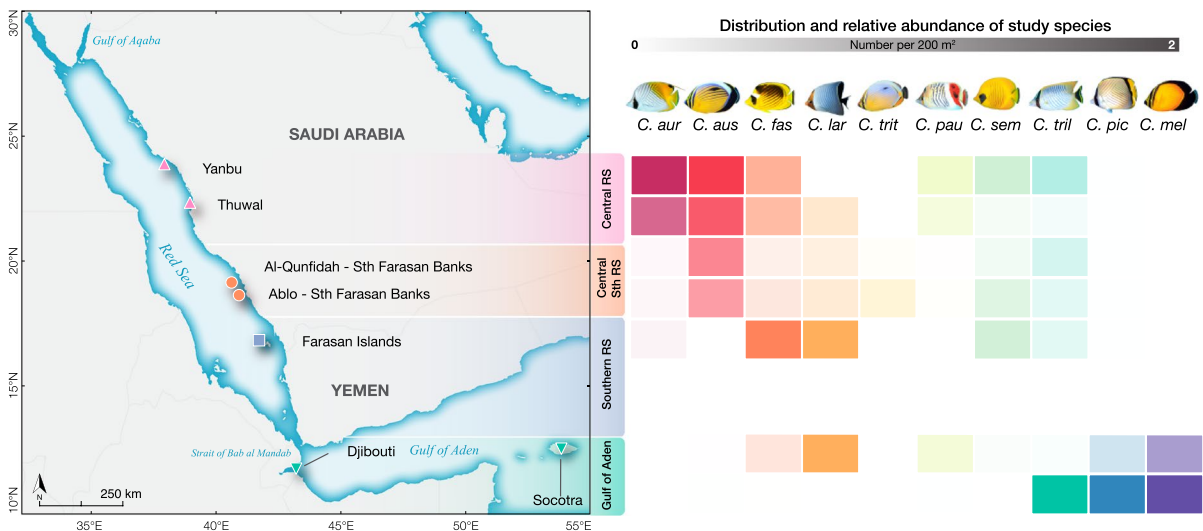


Fig. 1 Butterflyfish species distributions within the study region (right panel) based on standardized abundance data (individuals per 200 m²) extracted from visual surveys reported by Roberts et al. (2016) and Hobbs (unpublished data) at the sites listed on the left panel. Darker colour shading indicates greater abundance at that location for that species.

Abbreviations are as follows: *C. aur*, *Chaetodon auriga*; *C. aus*, *Chaetodon austriacus*; *C. fas*, *Chaetodon fasciatus*; *C. lar*, *Chaetodon larvatus*; *C. mel*, *Chaetodon melapterus*; *C. pau*, *Chaetodon paucifasciatus*; *C. pic*, *Chaetodon pictus*; *C. sem*, *Chaetodon semilarvatus*; *C. tril*, *Chaetodon trifascialis*; *C. trit*, *Chaetodon trifasciatus*

Methods

Sampling sites

We sampled 10 butterflyfish species opportunistically at 13 sites from the Central Red Sea to sites just outside of the Red Sea in the adjacent Gulf of Aden in the south while SCUBA diving or snorkeling between 2012 and 2015 (Fig. 1). Cases of low (or no) samples for a species from a site reflect rarity or complete absence in those locations, presumably owing to the heterogeneous nature of habitat and the variable distribution of each species (Table 1). To increase sample size per species, we grouped sites into the following regions: (1) Central Red Sea (sites: Yanbu and Thuwal), (2) Central-South Red Sea transition zone (site: South Farasan Banks), (3) Southern Red Sea (site: Farasan Islands), and (4) Gulf of Aden (sites: Djibouti and Socotra). The Northern Red Sea was excluded owing to low sample sizes from this region. This research was carried out under the general auspices of King Abdullah University of Science and Technology's (KAUST) arrangements for marine research with the Saudi Arabian Coast Guard and the Presidency of Meteorology and Environment.

The animal use protocol was approved by KAUST's Biosafety and Ethics Committee (KAUST did not provide specific approval numbers at the time of sampling).

Derivation of age and growth profiles

We derived age information from individual butterflyfish specimens based on annual increments in transverse sections of sagittal otoliths. Each sagittal otolith was weighed to the nearest 0.0001 g and mounted on the edge of a glass slide using a thermoplastic glue (Crystalbond 509[®]) with the primordium situated just inside the slide edge and the sulcal groove approximately perpendicular to the slide edge. The otolith material was sanded away using a 600-grit diamond lap on a GEMMASTA lapping machine with constant water flow.

The slide was then heated (200 °C) and remounted with the newly sectioned surface affixed flat against the surface of the glass slide, and the remaining bulk of material was ground away until a thin transverse cross section (~150 µm) remained. Finally, the section was covered with thermoplastic glue to improve

Table 1 Summary of life history trait estimates for 10 species of butterflyfish sampled from the Central Red Sea to the Gulf of Aden. These fish include sexually immature and undifferentiated fish in growth or length–weight models. SS , sum of squares; L_{∞} , asymptotic TL; k (year^{-1}), the coefficient used to describe the curvature of fish growth toward L_{∞} ; t_0 (year), the hypothetical age at which TL is equal to zero, as described by k ; n , the sample size for each species at each location

Species/region	SS	L_{∞} (mm TL)	k (year^{-1})	t_0 (year)	n
<i>Chaetodon auriga</i> /Central	4594.94	144.97	0.63	−0.24	20
<i>Chaetodon auriga</i> /Central-South	3249.40	153.86	0.61	−0.23	17
<i>Chaetodon austriacus</i> /Central	2188.53	125.51	0.90	−0.19	20
<i>Chaetodon fasciatus</i> /Central	5012.29	150.93	1.03	−0.14	14
<i>Chaetodon fasciatus</i> /Central-South	2762.93	146.26	1.05	−0.14	19
<i>Chaetodon fasciatus</i> /Southern	1704.90	152.45	1.01	−0.14	11
<i>Chaetodon fasciatus</i> /Gulf of Aden	5100.60	180.79	0.76	−0.16	25
<i>Chaetodon larvatus</i> /Central	1043.60	123.46	0.79	−0.22	14
<i>Chaetodon larvatus</i> /Central-South	1290.70	119.45	0.66	−0.28	29
<i>Chaetodon larvatus</i> /Southern	3934.00	125.72	0.70	−0.25	43
<i>Chaetodon larvatus</i> /Gulf of Aden	5039.06	114.26	0.87	−0.22	32
<i>Chaetodon melapterus</i> /Gulf of Aden	2200.64	129.39	1.42	−0.12	26
<i>Chaetodon paucifasciatus</i> /Central-South	109.25	103.22	1.19	−0.18	12
<i>Chaetodon pictus</i> /Gulf of Aden	3397.22	153.62	0.82	−0.17	31
<i>Chaetodon semilarvatus</i> /Central	971.57	182.96	0.85	−0.14	19
<i>Chaetodon semilarvatus</i> /Gulf of Aden	3964.23	182.79	0.80	−0.14	30
<i>Chaetodon trifascialis</i> /Central	1115.89	131.76	1.36	−0.12	21
<i>Chaetodon trifascialis</i> /Central-South	2135.08	129.35	1.29	−0.13	22
<i>Chaetodon trifascialis</i> /Gulf of Aden	4221.64	137.72	1.33	−0.12	24
<i>Chaetodon trifasciatus</i> /Gulf of Aden	1310.31	110.99	1.42	−0.14	15

clarity and annual bands were enumerated using a stereo microscope with transmitted light. Annuli were counted on three separate occasions by a single reader using a stereo microscope for annual increments. Final age (in years) of fish with one or more annuli was derived when two or more readings matched, or when the three counts differed by no more than two annuli (e.g., 14, 12, and 13 would be scored 13). Pelagic larval duration (PLD) was estimated for three species only using sagittal otoliths from fishes collected in the Northern Red Sea (i.e., Gulf of Aqaba), Central Red Sea, Central-South Red Sea, and Southern Red Sea as previously defined to provide baseline data from these regions. This subset of species was chosen because they had the largest sample sizes and therefore provided the most robust data sets for this analysis. Sample sizes were as follows: *C. austriacus* (Northern, $N=13$; Central-South, $N=10$; Southern, $N=5$), *C. paucifasciatus* (Northern, $N=16$; Central, $N=13$; Southern, $N=4$), and *C. trifascialis* (Northern, $N=8$; Southern, $N=3$). Otoliths were processed following Wilson and McCormick (1999). Increments were assumed to represent daily rings and the settlement mark was determined by an abrupt decrease in increment width (Wilson and McCormick 1999).

Overall patterns of growth for each species were examined using length-at-age data (total length, TL) fitted with the von Bertalanffy growth function (VBGF), represented by:

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

where L_t is the predicted mean total length TL in mm at age t (years), L_∞ is the asymptotic TL, k is the coefficient used to describe the curvature of fish growth toward L_∞ , and t_0 is the hypothetical age at which TL is equal to zero, as described by k . Sex was not considered a factor in the analysis given that the sex of few individuals could be confirmed, but we do not expect any bias in sampling toward either male or females given that sexual size dimorphism has not been reported in these butterflyfishes. Approximate 95% ellipsoidal confidence regions around the parameter estimates k (coefficient of growth) and L_∞ were used to compare the growth functions among species and regions (Kimura 1980). Growth analyses were done in Microsoft Excel using non-linear least squares estimation.

Phylogenetic body size analysis

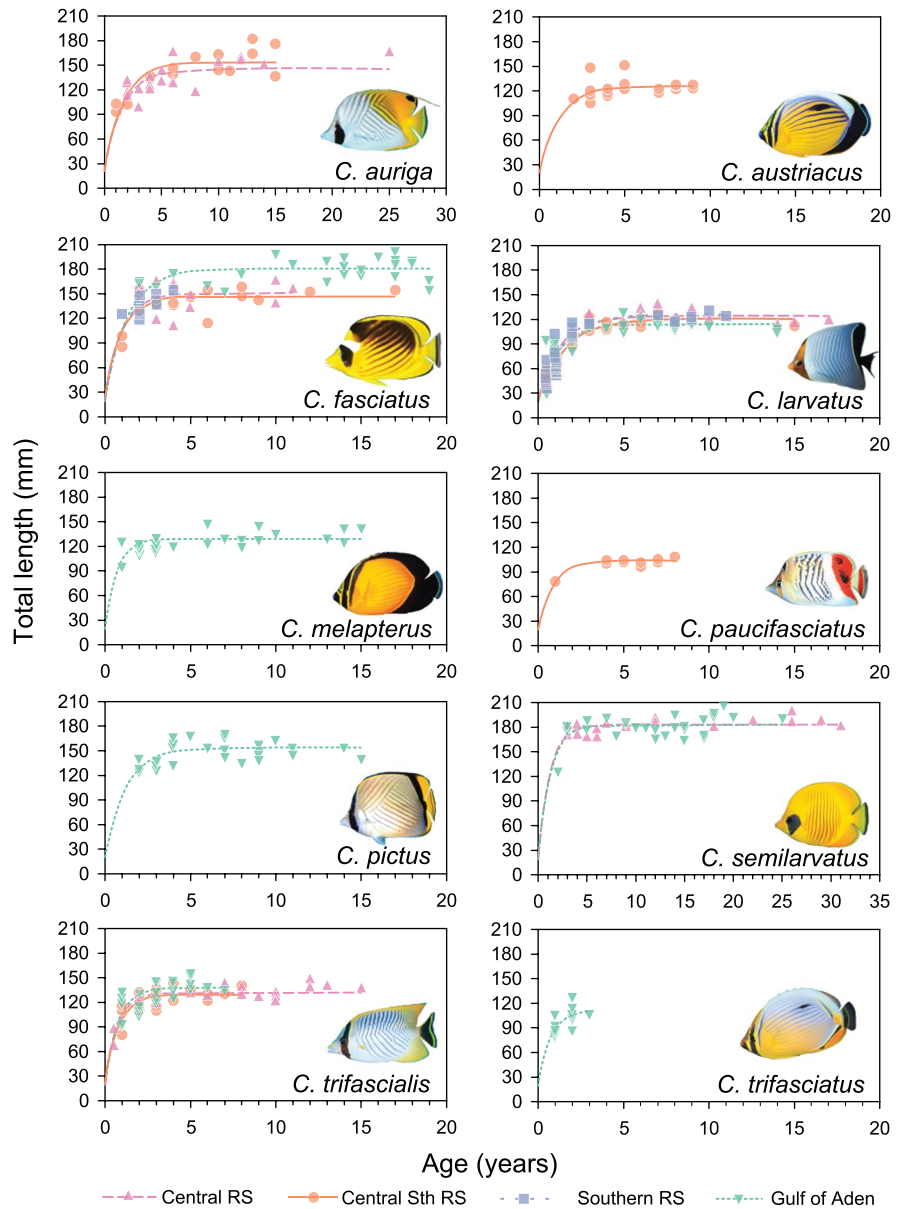
All 10 butterflyfish species sampled in this study were grouped according to three of the phylogenetic clades presented in DiBattista et al. (2018): Clade CH2 includes, *C. paucifasciatus*; Clade CH3 included *C. austriacus*, *C. larvatus*, *C. melapterus*, *C. trifascialis*, and *C. trifasciatus*; Clade CH4 included *C. auriga*, *C. fasciatus*, *C. pictus*, and *C. semilarvatus*. We used analysis of variance (ANOVA) with pairwise Holm-Sidak multiple comparisons to test whether reported maximum body size carried a phylogenetic signature among clades.

Results

There was little variation in intraspecific growth rates for multiple species of butterflyfish sampled across the Central Red Sea to the Gulf of Aden (Fig. 2 and Table 1). Indeed, all but one location for one species varied in asymptotic length by less than 6% from the median. The only exception was *C. fasciatus* sampled in the Gulf of Aden, which appeared to reach a larger asymptotic size (181 mm) relative to individuals sampled across the Red Sea (146–152 mm). All other butterflyfish species sampled across two or more regions showed similar length-at-age growth profiles (Fig. 2). For the subset of three species where PLD was estimated, which included two range-restricted species and one widespread species, we note a consistency in values among regions (Online Resource 1).

VBGF in contrast differed significantly among species (Fig. 3 and Online Resource 2), with *C. paucifasciatus* and *C. trifasciatus* representing the smallest species (100–120 mm TL) and *C. semilarvatus* and *C. fasciatus* representing the largest species (160–185 mm TL; Fig. 3). All species showed rapid initial growth whereby most of their mean asymptotic body size was achieved within their first 2 years. Life span appeared to reflect body size in terms of patterns of variation across species, although this was not the case within species (Fig. 2). Asymptotic length for each species was a significant linear predictor of the maximum observed age across species ($F_{1,9}=19.48$, $P=0.002$, $R^2=0.71$). Even though all species reached asymptotic size within the first 2 to 5 years of life, some of the butterflyfish species sampled

Fig. 2 Growth curves for all 10 butterflyfish species for each region. Growth curves were not plotted in regions where a species does not occur or there were insufficient samples

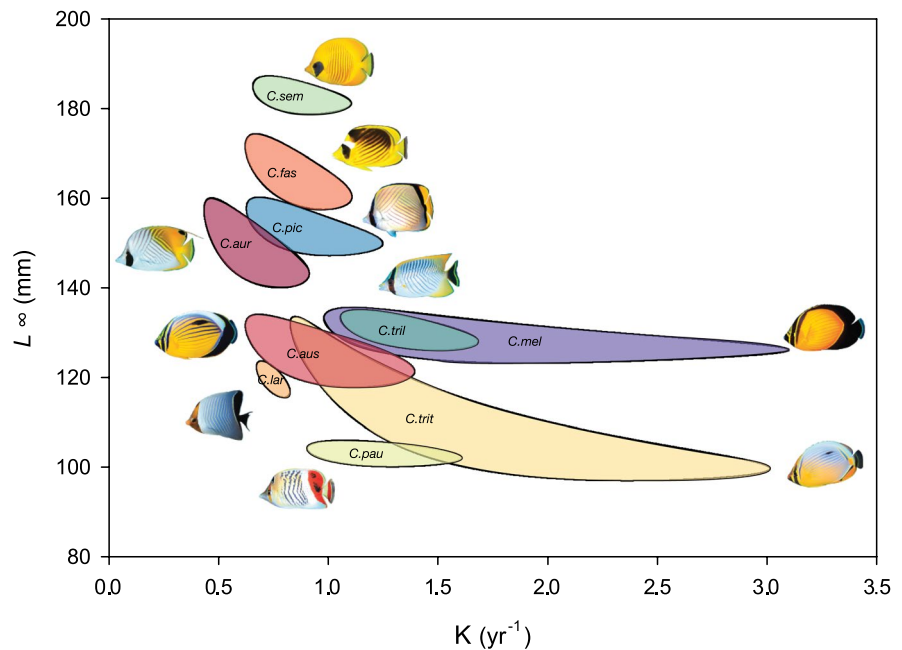


in our study were remarkably long-lived. One such example is *C. semilarvatus*, which reached a maximum size at 2 to 3 years of age but lived up to 31 years. The shortest life span of just three years was recorded for *C. trifasciatus*, although this value may reflect the low sample size ($n=15$) of individuals collected from a single island in the Gulf of Aden (i.e., Socotra). Despite these notable observations, sample sizes are too small overall to obtain robust insights into the age structure and longevity of the studied populations. For the subset of three species where PLD was estimated, we report mean values

among species ranging from 24.3 days (*C. trifasciatus*) to 29.2 days (*C. paucifasciatus*) (Online Resource 1).

We found evidence for potential phylogenetic constraints on growth rate based on: (1) overlapping growth ellipses for the three most closely related species that group together in the subgenus *Corallochaetodon* (*C. austriacus*, *C. melapterus*, and *C. trifasciatus*; Fig. 3), and (2) maximum length values ranging widely across species but correlating strongly with the reported maximum body size for each species (sourced from <https://www.fishbase.se/>; Linear

Fig. 3 Composite of ellipses representing approximate 95% confidence regions around the parameter estimates k (coefficient of growth) and L_∞ (mean asymptotic total length) of von Bertalanffy growth curves for all 10 butterflyfish species across all sampling regions. Abbreviations are as per Fig. 1



regression: $F_{1,9}=21.43$, $P=0.002$, $R^2=0.73$). Based on the ANOVA with pairwise Holm-Sidak multiple comparisons, we found that maximum body size varied significantly among clades ($F_{2,39}=14.815$, $P<0.001$), whereby species within clade CH4 were larger, on average, than clades CH2 and CH3 (Fig. 4).

Discussion

In this study, we estimated age and growth for 10 species of butterflyfish sampled from reefs in the Central Red Sea to the Gulf of Aden. We found that despite significant interspecific differences in life span and growth, there was almost no intraspecific differences between fish populations across the study region. For example, *C. fasciatus* and *C. larvatus* were sampled across the geographic breadth of the study regions, but only one population (*C. fasciatus* in the Gulf of Aden) displayed a unique growth profile punctuated by a large terminal body size in this highly productive area. This spatially invariable growth pattern within most species was unexpected given the strong environmental gradients across the study region. Our estimated growth rate values were congruent with a previous study that focused on a single species of butterflyfish in a single region of the Red Sea (*C. larvatus* in the

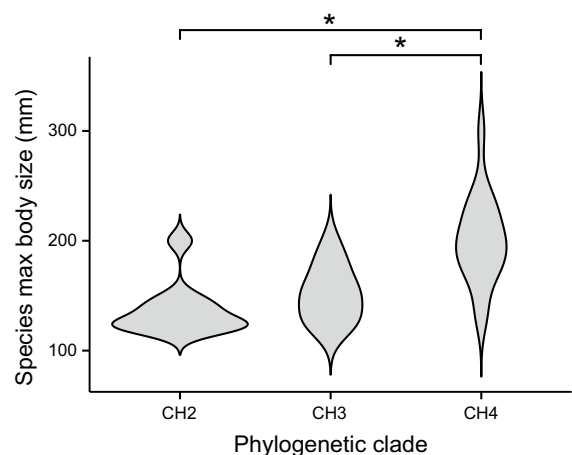


Fig. 4 Violin plots of maximum body size (TL in mm) for all 10 butterflyfish species sampled in this study grouped according to three of the phylogenetic clades presented in DiBattista et al. (2018) (CH2, *Chaetodon paucifasciatus*; CH3, *Chaetodon austriacus*, *Chaetodon larvatus*, *Chaetodon melapterus*, *Chaetodon trifascialis*, *Chaetodon trifasciatus*; CH4, *Chaetodon auriga*, *Chaetodon fasciatus*, *Chaetodon pictus*, *Chaetodon semilarvatus*). Asterisks indicate significant differences in maximum body size between clades ($P<0.001$)

Southern Red Sea; Zekeria et al. 2006). However, more samples are required to confirm the paucity of intraspecific variation in growth for butterflyfishes distributed across this region.

In this study, butterflyfishes were characterized by growth profiles that rapidly attained asymptotic size, along with moderately long lifespans. This generality is conserved despite a strong latitudinal gradient in environmental conditions across our study region. For example, mean summer and winter SST differ by 2 °C and 3 °C, respectively, between the northern and Southernmost locations (based on the HadISST global data base, 1990–2020; available at <https://coastwatch.pfeg.noaa.gov/erddap/index.html>). This level of temperature variation in the tropics is sufficient to elicit substantial physiological changes in marine ectotherms (Johansen and Jones 2011). Indeed, marine fishes along latitudinal gradients generally conform to the temperature-size rule (Atkinson 1994), whereby the mean maximum body size increases with latitude and decreasing water temperature. This growth pattern is driven by the influence of temperature on metabolic rates in ectotherms and is evident in studies spanning large latitudinal gradients (Robertson et al. 2005; Trip et al. 2014; Taylor and Pardee 2017; Taylor et al. 2019, 2021).

Marine fishes across a range of feeding modes and trophic positions should show demographic responses of enhanced growth resulting in larger body sizes in response to higher ocean productivity. This pattern emerges because their growth is limited by the quality and quantity of nutritional resources (Bowen et al. 1995), both factors that are universally affected by the underlying primary productivity. The Red Sea and Gulf of Aden represent a dynamic region with high levels of oceanic productivity that follow a spatial gradient counter to that of ocean temperatures (Raitsois et al. 2013). For example, the Gulf of Aden and Southern Red Sea have mean chlorophyll-*a* concentrations that are five times higher (0.79 versus 0.16 mg m⁻³) than those in the Northern Red Sea (Aqua MODIS Global database, monthly composite, 2003–2020; available at <https://coastwatch.pfeg.noaa.gov/erddap/index.html>). Surprisingly, these strong environmental gradients did not cause intraspecific variation in growth rates across the study region.

Given that lower temperatures and higher productivity produce larger body sizes in marine ectotherms, the contrasting gradients of these environmental influences along the Red Sea and Gulf of Aden may explain the lack of intraspecific variation in growth across a considerable latitudinal gradient for butterflyfishes. Northern populations are subject to low concentrations of nutrients and

lower water temperatures necessitating low metabolic demands, whereas Southern populations at warmer water temperatures can easily meet higher metabolic demands in a nutrient-rich environment. This scenario is plausible yet does not conform with patterns shown in other reef fish taxa from the region. Acanthurids (surgeonfishes, tangs, and unicornfishes), scarine labrids (parrotfishes), pomacentrids (damselfishes), and epinepheline groupers, for example, conform more noticeably to a combination of temperature-size and somatic responses to increased nutrition through high productivity (J.H. Choat unpublished data). This trend persists despite significant differences in modes of feeding and assimilation of nutrients (e.g., Clements and Choat 2018).

An alternative hypothesis is that the high level of ecological specialization in butterflyfishes limits their capacity for demographic variation. Most butterflyfish species have very specific nutritional resource requirements (Pratchett et al. 2013) and strict social dynamics. A multi-species study in the same region suggests that territoriality and partitioning of food resources may maintain specialization in butterflyfishes (Zekeria et al. 2002). A more broader review highlights low variation in body size for all chaetodontids relative to other reef fishes, with 80% of all species having an average size between 100 and 200 cm, which the authors suggest relates to their dependency on coral reefs for food and shelter (Floeter et al. 2018). As a comparative example, parrotfishes, another ubiquitous and conspicuous group of coral reef fishes, display environmentally mediated nutritional and social dynamics that manifest in highly variable biological characteristics (e.g., growth, maturation, and sex change), even across small spatial scales (Gust et al. 2002; Taylor et al. 2018). A similar study comparing butterflyfish growth between two locations with drastically different temperature regimes but similar productivity demonstrated changes more aligned with temperature-size predictions (Berumen et al. 2012). That said, intraspecific patterns of growth were still largely invariable compared with that observed in other taxa (Berumen et al. 2012). It is most likely that a combination of nutritional resource requirements, social dynamics, habitat dependency, and regional temperature variation contributes to the patterns we observe for butterflyfishes in the Red Sea and Gulf of Aden, although more samples at more sites are needed to confirm this generality.

Despite a lack of intraspecific variation in these butterflyfish species, we found striking differences in the growth and life span of individuals between

widespread and range-restricted butterflyfishes. Indeed, the Northern-Central regional endemics (*C. austriacus* and *C. paucifasciatus*) tended to be smaller and shorter lived than the rest of the species. This variation could be split into two types: large-bodied (*C. semilarvatus*, *C. fasciatus*, *C. pictus*, and *C. auriga*) and small-bodied (*C. trifascialis*, *C. melapterus*, *C. austriacus*, *C. larvatus*, *C. trifasciatus*, and *C. paucifasciatus*) species, diverging across a L_{∞} value of ~140 mm.

The observed variation between species may also reflect phylogenetic placement, whereby species of clade CH4 were significantly larger, on average, than clades CH2 and CH3 based on our analysis. We suggest that clade CH3 may have exploited the emerging acroporid assemblage in the region (Renema et al. 2016), whereby smaller size ensures shelter in reef interstices for younger individuals and with coral feeding that allowed linkage between shelter and food resources. Indeed, CH3 is a clade of small, shallow water obligate coral feeders with several regional endemics. In contrast, clade CH4 is comprised of larger species that tend to have larger home ranges, allowing them to occupy a wider range of habitats including deeper waters. The level to which within-family phylogenetic structure influences demographic traits is generally quite small, given the need for morphologically similar species to occupy different niches to avoid competition (e.g., Taylor and Choat 2014). The butterflyfishes appear to be unique in this regard, however, given their high level of diversity within a comparatively small niche breadth.

This study demonstrates considerable interspecific variation and low intraspecific variation in life histories among the butterflyfishes. The spatially conserved demographic profiles across a biogeographic region with considerable gradients of temperature, salinity, and oceanic productivity was unexpected, but may reflect a pattern unique to the ecologically specialized Chaetodontidae family. Such growth information may be used to parameterize models predicting community dynamics or biomass production.

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Declarations

Competing interests The authors declare no competing interests.

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