INTRASPECIFIC VARIABILITY IN THE LIFE HISTORY OF ENDEMIC CORAL REEF FISHES BETWEEN PHOTIC AND MESOPHOTIC DEPTHS IN THE CENTRAL NORTH PACIFIC OCEAN

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ABSTRACT

For many coral reef-associated organisms, mesophotic coral ecosystems (MCEs) represent the lowest depth distribution inhabited by their species. Research on fishes associated with MCEs is sparse, so there is a critical lack of knowledge of how reef fish found at mesophotic depths may vary from their shallow reef conspecifics. We investigated intraspecific variability in body condition and growth of three Hawaiian endemic fish species collected from shallow, photic reefs (5-33 m deep) and MCEs (40-75 m) throughout the Hawaiian Archipelago and Johnston Atoll: the planktivorous threespot chromis *Chromis verater* and Hawaiian dascyllus *Dascyllus albisella*, and the detritivorous goldring surgeonfish *Ctenochaetus strigosus*. Estimates of body condition, weight-at-length, and size-at-age varied between shallow and mesophotic depths, and among the locations sampled within the central North Pacific Ocean. All three species exhibited lower body condition and weight-at-length in pooled mesophotic sites compared to shallow reef sites. However, there was no difference in parameter values of age-based growth curves between pooled shallow and mesophotic sites for all species. Body condition and maximum body size were lowest in samples collected from shallow and mesophotic Johnston Atoll sites, with no difference occurring between depths. Samples from the Northwestern Hawaiian Islands tended to have the highest body condition and reached the largest body sizes, with differences between shallow and mesophotic sites found to be highly variable between species. The findings of this study are first to demonstrate intraspecific variability in the life history of coral reef fish species whose distributions span shallow and mesophotic reefs. This information suggests that the application of conservation and fisheries management tools developed from studies of shallow reef fishes should be applied with caution to conspecific populations in mesophotic coral environments.
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CHAPTER 1. INTRODUCTION: REEF FISH OF MESOPHOTIC CORAL ECOSYSTEMS

Compared to shallow reefs, mesophotic coral ecosystems (MCEs) have been largely understudied (Menza et al. 2008; Kahng et al. 2010) and the majority of our understanding of MCE structure and assemblage is guided by studies from the Caribbean (see Kahng et al., 2010; Kahng et al. 2014). The limited scope of existing knowledge on MCEs is largely a result of the inherent logistical restraints and safety concerns associated with reaching mesophotic depths (Menza et al. 2008; Pyle 1996), given these systems span depths from 30m down to 150m or deeper, depending on local environmental factors, such as temperature and light irradiance (Hinderstein et al. 2010). While ROVs and submersibles have been used in the past to study MCEs, recent advances in technical diving now allow for divers using closed circuit rebreathers with mixed gas (i.e. TRIMIX) to dive beyond the normal limits of conventional SCUBA diving (Pyle 2000). When compared to open circuit SCUBA, rebreather diving not only allows for a longer bottom time at greater depths, but the lack of bubbles produced, which would normally frighten away organisms, facilitates enhanced observational strength and aids in specimen collections (Pyle et al. 2008).

Studies characterizing the benthic, habitat-building taxa and mobile invertebrate and reef fish communities are prominent within a nascent body of literature on MCEs, and have showed similar patterns across oceanic regions. MCEs are characterized by light-dependent coral reef communities composed of a variety of corals, algae, and sponges, which provide structure to support mobile invertebrates and reef fishes (Hinderstein et al. 2010). Though the upper 30m of mesophotic reefs are often still inhabited by common shallow coral reef species, a significant shift in the species assemblages have been observed at greater depths of 60-70m within MCEs in
both the Caribbean (Bejarano et al. 2014) and the Indo-Pacific (Bridge et al. 2011b; Rooney et al. 2010; Thresher and Colin 1986).

While the benthic habitat of shallow coral reefs is often characterized by highly complex coral colonies growing in various three-dimensional shapes, the abundance of branching corals decreases with depth as scleractinian corals in MCEs often adopt a plate-like morphology (Bejarano et al. 2014). By adopting flatter morphologies with increasing depth, phototrophic scleractinian corals can maximize light capture (Kühlmann 1983, Wallace 1978, Jaubert 1977). *Leptoseris* corals, known as ‘MCE specialists’ (Fricke et al. 1987), often dominate MCEs and form large, flattened colonies with thin walls to reduce self-shading (Rooney et al. 2010). Some phototrophic corals may adapt to low nutrient and light levels through heterotrophic feeding (Anthony and Fabricius 2000; Leichter and Genovese 2006). Depth-generalist *Montipora* corals are capable of sustaining their energetic demands entirely through heterotrophic feeding (Grottoli et al. 2006); which may enable their ability to persist within MCEs (Bridge et al. 2011b; Rooney et al. 2010). It has also been documented that certain coral species with broad depth distributions exhibit symbiont zonation (Bongaerts et al. 2015), which aids these species in adapting to both shallow and mesophotic environments (Frade et al. 2008).

Scleractinians are conspicuous components of mesophotic ecosystems but these benthic communities are often dominated by algae. Algal assemblages can persevere in mesophotic depths and some species have even been found at depths of up to 260m (Littler et al. 1985). Coralline algae, adapted to low-light conditions (Runcie et al. 2008), has been observed to dominate deep algal assemblages in MCEs (Sherman et al. 2010). Non-calcareous algae in MCEs often demonstrate morphological transformations, such as lateral spreading and flattening, which allows these species to enhance light capture by increasing their surface area (Hanisak and
Blair 1988; Aponte and Ballantine 2001). While algal assemblages in MCEs are often less diverse (Gilmartin 1960) and may grow more slowly than those found in shallow coral reefs (Markager and Sand-Jensen 1992), these species of algae can actually maintain relatively high abundances (Sherman et al. 2010), in part from low grazing pressure from herbivores (Brokovich et al. 2010) and in some locations due to nutrient input from deeper water (Lesser et al. 2009).

Although adopting a flattened morphology in mesophotic depths can increase the productivity of photosynthetic autotrophs in conditions where light irradiance decreases and changes in spectral qualities occur (Aponte and Ballantine 2001; Liddell and Ohlhorst 1988), this adaptation can still prove costly for these organisms. While MCEs are generally characterized by clear waters (Kahng et al. 2010), the process of sediment down-welling has been shown to affect the growth and community composition of benthic taxa in some of these environments (Colin et al. 1986, van Woesik and Done 1997; Fabricius 2005; Bridge et al. 2011b). Moreover, it has been documented that platting *Montipora* corals are especially susceptible to the burying effects of sedimentation given their limited ability to remove sediment (Stafford-Smith and Ormond 1992) and that total reef accretion overall decreases with increasing depth (Grigg 2006).

Reef fish community composition shifts with increasing depth, as herbivores have commonly been documented to be scarce in MCEs but are dominant components of shallow reef communities (Gilmartin 1960; Van den Hoek and Breeman 1978; Liddell and Ohlhorst 1988; Garcia-Sais 2010; Brokovich et al. 2010; Bejarano et al. 2014). Changes in grazing intensity along the depth gradient may contribute to the distribution of algae (Bejarano et al. 2014); however, the community structure and productivity of the algae that persists in mesophotic reefs may alternatively be affecting the distribution of herbivorous fishes (Nemeth and Appeldoorn 2009). While differences in the nutritional value of algae in MCEs versus shallow reefs is still
unclear (Clements et al. 2009), studies have shown that several species of abundant, deep-water algae are less palatable to herbivorous fishes, despite still being edible (Duffy and Hay 1990; Lesser et al. 2009). The potentially low algal productivity demonstrated in some MCEs due to slow growth and turnover (Brokovich et al. 2010) likely cannot support as high an abundance of grazing herbivores as in shallow coral reefs (Bejarano et al. 2014). Those herbivorous fish that do persist at mesophotic depths have been reported to be small-bodied; thus, these individuals may have found an ecological niche where their energetic needs can still be met (Bejarano et al. 2014). Small-bodied herbivores in mesophotic reefs are also likely to face less competition from larger herbivorous fish, given large grazers congregate in areas with high algal productivity (Russ 2003).

As the prevalence of herbivorous fishes decreases with depth, zooplanktivores dominate fish assemblages in MCEs (Bejarano et al. 2014; Thresher and Colin 1986; Feitoza et al. 2005; García-Sais 2010). This abundance of zooplanktivores has been linked to upwelling and internal waves, which import nutrients and particulate matter from very deep waters to mesophotic depths (Leichter et al. 1996; Leichter and Genovese 2006). Upwelling can fuel rich plankton communities, which are considered to be the main energy source for fishes in MCEs (Lesser 2006; Kahng et al. 2010) and therefore replace benthic primary producers within the food chain (Bejarano et al. 2014; García-Sais 2010).

While changes in light intensity and nutrient upwelling are strongly linked to differences in species assemblages and community structure between shallow coral reefs and MCEs, other environmental factors may contribute to this variability. The topography of MCEs can range from steeply sloping walls (Bridge et al. 2011a) to flat tops of submerged banks (Parrish and Boland 2004). Coral reefs with both high coral cover and topographic complexity are correlated
with fish abundance and diversity (Luckhurst and Luckhurst 1978; Bell and Galzin 1984; Sano et al. 1984; Gratwicke and Speight 2005; Komyakova et al. 2013), which can reduce the risk of predation by increasing refuge space for reef fishes (Murdoch and Oaten 1975; Holt 1985; Hixon and Menge 1991). Increased vulnerability of reef fishes in certain mesophotic environments with limited shelter availability may influence fish abundance and diversity in MCEs.

While thermal gradients and isotherm depths vary regionally, it has been observed that seawater temperatures are frequently cooler in MCEs than shallow coral reefs (Feitoza et al. 2005; Rooney et al. 2010; Kane et al. 2014). Exposure to low temperatures not only inhibits reef growth (Rooney et al. 2010), but can result in chronic and acute stress and mortality of sessile flora and fauna unable to relocate to warmer waters (Coles and Fadlallah 1991).

Shallow coral reefs are declining globally due to the effects of climate change (i.e. increasing seawater temperatures and ocean acidification) and other anthropogenic impacts (e.g., overfishing and pollution) (Kleypas et al. 1999; Hoegh-Guldberg et al. 2007; Cooper et al. 2008; De’ath et al. 2009). Approximately 19% of coral reefs are estimated to have already been lost, and an additional 35% are projected to vanish in the next 40 years (Wilkinson 2004). This decline in reef condition has largely been documented in shallow reefs, and given most studies have focused on the shallowest 20% of coral reef environments (see Kane et al. 2014), this has resulted in a biased understanding of how to manage and conserve these coral reef ecosystems across their depth range (Kane et al. 2014). In light of the suite of stressors threatening coral reefs, MCEs have been suggested by scientists and ocean resource managers as potential refugia for corals driven out of degraded shallow environments (Loya et al. 2016).

The presence of shallow coral reef species at mesophotic depths postulates a level of biological and physical connectivity between these two ecosystems (Hinderstein et al. 2010).
Research has shown that genetic connectivity exists between shallow and mesophotic reef fish populations (Tenggardjaja et al. 2014). Mesophotic coral larvae have the capacity and are highly likely to settle in shallow coral reefs (Holstein 2013). Therefore, understanding how shallow and mesophotic systems are linked has become increasingly important given MCEs hold the potential to be serve as refuge and a source of replenishment for shallow coral reef species (Lesser et al. 2009; Bongaerts et al. 2010; Kahng et al. 2014; Loya et al. 2016). The ‘deep-reef refugia hypothesis’, first introduced by Glynn (1996), encompasses these ideas and suggests that MCEs are more stable environments than shallow coral reefs and may become vital for the continued survival of tropical coral reef species (Riegl and Piller 2003; Bongaerts et al. 2010).

The depth and relative isolation of MCEs is thought to offer a buffer from biotic and physical disturbances, serving as a haven for threatened populations (Bak et al. 2005; Graham et al. 2007; Lesser et al. 2009). Deeper reefs are substantially less vulnerable to the direct destructive effects of hurricanes (Aronson et al. 1994, Bak et al. 2005; Woodley et al. 1981), such as storm-induced waves (Bongaerts et al. 2010). For example, even in relatively shallow depths of 12m, storm-driven waves and currents capable of dislodging corals are rare enough that these species can persist for 50+ years. Lower instances of disease outbreaks have been documented in mesophotic reefs (Smith et al. 2008), which may be tied to lower stress from anthropogenic influences (Bongaerts et al. 2010). The release of large quantities of nutrients and toxins from populated areas into the marine environment, which can increase stress and lower resistance to disease, has been documented to reach an acceptable concentration by mesophotic depths (Lapointe 1997; Nowlis et al. 1997). MCEs may also be less susceptible to overfishing, given fishing intensity is typically highest in shallow waters (Polunin and Roberts 1993; Bongaerts et al. 2010).
Vertical connectivity between coral reefs at shallow and mesophotic depths suggests the possibility for MCEs to supply recruits to shallow reef areas, thereby aiding in recovery (Hughes and Tanner 2000; Lesser et al. 2009; Bongaerts et al. 2010). Colonists from intact subpopulations may rescue or resurrect other suffering subpopulations (den Boer 1968). Although the distance to shallow coral reefs from MCEs varies, this is likely inconsequential given that when long-distance dispersal events occur, they can still often deliver large larval quantities (Siegel et al. 2008). Given the recovery of shallow coral reefs in the wake of natural and anthropogenic stressors may be assisted by MCEs, implementing pertinent management regimes to conserve mesophotic populations is of high importance. However, the current need to address knowledge gaps on many of the processes that occur within MCEs precludes the development of pertinent management and conservation tools.

Coral reef fish are integral in maintaining the resilience of coral reef ecosystems, holding a critical role transferring and cycling nutrients, energy and matter within both shallow coral reefs and MCEs. Species with broad depth ranges found in both shallow and deep reef ecosystems are innately exposed to different environmental conditions throughout their distributions. However, research on fishes associated with MCEs is sparse (Bejarano et al. 2014), and the most recent studies investigating how environmental variability between shallow coral reefs and MCEs affects reef fish populations have largely focused on community structure (Bejarano et al. 2014; Lindfield et al. 2015; Pinheiro et al. 2015; Rosa et al. 2016) and genetic connectivity (Tenggardjaja et al. 2014). While copious life history information exists for shallow coral reef fishes, practically no research has been done examining the life history traits of reef fishes in MCEs. There is a current need to address this disparity, as knowledge of life history traits is necessary to understand population dynamics in MCEs (Kahng et al. 2010).
Biotic and abiotic factors including seawater temperature, habitat availability, prey availability, diet composition, and predation intensity can influence variability in the life history traits of many species (Gust et al. 2002; Caselle et al. 2011; Hamilton et al. 2011; Donovan et al. 2013; Ruttenberg et al. 2005). Those populations inhabiting both shallow coral reefs and MCEs may potentially exhibit intraspecific variability in their life history strategies in order to acclimate or adapt to inherently different environments. Understanding the life history strategies of mesophotic fishes and how they may vary from their shallow water conspecifics is necessary to understand the dynamics of and effectively manage MCE populations, since the establishment of accurate demographic parameters is essential to inform sound decision-making by marine resource and fisheries managers. As shallow coral reef conditions continue to decline, the sustainable management of MCE fish communities provides an important component to maintaining local and regional biodiversity and sustainable marine resources in coral reef ecosystems (Riegl and Piller 2003).

The life history traits for fish species with depth distributions encompassing both shallow and mesophotic coral reefs have been typically based on studies occurring only in shallow waters. Neglecting to factor in the potential for intraspecific variability can introduce uncertainty into the ecological modeling and fishery assessment of fish populations (Alonzo and Mangel 2005, Hamilton et al. 2011). The goal of this study was to investigate intraspecific variability by comparing growth and condition of coral reef fishes between euphotic and mesophotic populations. This study examined three species of coral reef fishes with varying diet, behavior, and life histories: Chromis verater, Ctenochaetus strigosus, and Dascyllus albisella. Specimens of the three endemic reef fish species for this study were collected across the extent of their geographic range in the Hawaiian Archipelago and Johnston Atoll within the central north
Pacific Ocean. A better understanding of reef fish life history trait variability could directly inform the appropriateness of applying conservation and fisheries management strategies developed from studies of shallow reef fishes to conspecific fish populations in mesophotic coral environments.
CHAPTER 2. INTRASPECIFIC VARIABILITY IN THE LIFE HISTORY
OF ENDEMIC CORAL REEF FISHES BETWEEN PHOTIC AND
MESOPHOTIC POPULATIONS IN THE CENTRAL PACIFIC OCEAN

(MANUSCRIPT FOR SUBMISSION TO CORAL REEFS)

INTRODUCTION

Coral reef research has been historically focused on the organisms and processes occurring within shallow water habitats accessible to snorkelers and SCUBA divers. Beyond the depths of shallow coral reefs, mesophotic coral ecosystems (MCEs) are prevalent in tropical and subtropical waters worldwide, ranging from 30m to 150m or deeper (Hinderstein et al. 2010). These light-dependent coral reef communities are composed of a variety of corals, algae, and sponges that provide benthic communities supporting reef fishes and mobile invertebrates (Hinderstein et al. 2010). Compared to shallow coral reefs, MCEs experience lower light availability, seawater temperature, and wave stress (Bak et al. 2005; Lesser et al. 2009; Kahng et al. 2010; Rooney et al. 2010; Franklin et al. 2013; Lindfield et al. 2015). Despite the differences of environmental conditions between shallow and mesophotic reefs, the flora and fauna that characterize shallow reefs are also found inhabiting the upper reaches of MCEs (Thresher and Colin 1986; Rooney et al. 2010; Bridge et al. 2011b; Bejarano et al. 2014; Wagner et al. 2014).

While the species composition from shallow reefs to MCEs has been characterized for several locations globally (Baker et al. 2016), there has been no prior examination of intraspecific traits that might contribute to species persistence to the range of environmental conditions experienced across this depth gradient.
As shallow coral reefs continue to decline globally due to the effects of climate change (i.e., increasing seawater temperatures and ocean acidification) and other anthropogenic activities (e.g., overfishing and pollution) (Kleypas et al. 1999; Hoegh-Guldberg et al. 2007; Cooper et al. 2008; De’ath et al. 2009), a better understanding of the similarities and differences in ecological structure and function between MCEs and shallow coral reefs has become increasingly important. The ‘deep-reef refugia hypothesis’, first introduced by Glynn (1996), suggests that MCEs are more stable environments than shallow coral reefs and may become vital refuges from environmental stressors as well as sources of replenishment for shallow coral reef species (Riegl and Piller 2003; Bongaerts et al. 2010; Smith et al. 2014). Due to the presence of shallow coral reef species at mesophotic depths, a level of biological and physical connectivity between these two ecosystems can be postulated (Hinderstein et al. 2010) but it is unclear whether or how individual species may differ biologically between shallow and mesophotic reefs. Increasing the understanding of population ecology within MCEs by studying the life history traits of organisms that inhabit these remote environments has been emphasized as a research priority (Puglise et al. 2009; Kahng et al. 2010).

Across depths, fishes play an integral ecological role transferring and cycling nutrients, energy, and matter in coral reef ecosystems. The extent of the vast majority of studies focusing on MCE-dwelling reef fishes has been to characterize patterns in ecological community structure (see Baker et al. 2016). Similar species of fishes have been found inhabiting shallow coral reefs and MCEs (Baker et al. 2016), though there is a clear shift in the reef fish community with depth. As the prevalence of herbivorous fishes decreases with depth (Gilmartin 1960; Van den Hoek and Breeman 1978; Liddell and Ohlhorst 1988; Garcia-Sais 2010; Brokovitch et al. 2010;

For species with broad depth distributions, prior life history work based upon samples collected from shallow coral reefs has typically neglected to address intraspecific variability across depths. Factors such as temperature, habitat, prey availability, and predation intensity can influence intraspecific variability in the life history strategies of many fishes (Gust et al. 2002; Ruttenberg et al. 2005; Caselle et al. 2011; Hamilton et al. 2011; Donovan et al. 2013). Therefore, fish populations inhabiting both shallow coral reefs and MCEs may potentially exhibit intraspecific variability in their life history, thereby acclimating and/or adapting to inherently different environments. Likewise, species with varying diets may exhibit diverse responses to depth based upon differences in food availability and prey behavior.

This study investigates intraspecific variability in the life history traits of three species of coral reef fishes that are endemic to the Hawaiian Archipelago and Johnston Atoll, all three with broad depth distributions and varying diets: *Ctenochaetus strigosus*, *Chromis verater* and *Dascyllus albisella*. While *C. strigosus* grazes on benthic detritus, diatoms, and bacteria (Jones 1968) and is commonly found in shallow reef areas, this species has also been observed at a depth of 113 m (Randall and Clements 2001). The damselfishes *C. verater* and *D. albisella* are found in both shallow coral reefs and deeper mesophotic habitats (≥ 55 m deep) (Stevenson 1963; Mundy 2005). *C. verater* and *D. albisella* are both planktivorous species, feeding primarily on copepods (Stevenson 1963; Swerdloff 1970; Hoover 2007). In this study, we compare age-based life-history traits and estimates of body condition of the three reef fish species between shallow and mesophotic depths across the extent of their geographic range.
MATERIALS & METHODS

Study site and sample collections

A total of 169 *Chromis verater* (Jordan and Metz, 1912), 282 *Ctenochaetus strigosus* (Bennett, 1828), and 162 *Dascyllus albisella* (Gill, 1862) were collected on research cruises throughout the Northwestern Hawaiian Islands (NWHI), Main Hawaiian Islands (MHI), and Johnston Atoll from September 2012 to November 2015 (Fig. 1). Shallow and mesophotic (hereafter referred to as “deep”) samples were collected by divers using pole spears or hand nets. Divers collecting in shallow sites (< 40m deep) used open-circuit systems, while divers collecting in deep sites (≥ 40m deep) used closed-circuit rebreather trimix systems. Sampling effort was considerably higher within shallow sites than deep sites, due the logistical limitations of rebreather diving that restrict bottom time. To reduce bias in the collection, divers endeavored to collect representative samples across the observed size range of each species. The length of *C. verater* specimens ranged from 68 mm to 156 mm SL in shallow locations and 41 mm to 152 mm SL in deep locations (Table 1). *C. strigosus* specimens ranged from 65 mm to 176 mm in shallow locations and 60 mm to 165 mm in deep locations (Table 1). *D. albisella* specimens ranged from 39 mm to 98mm in shallow locations and 14 mm to 101 mm in deep locations (Table 1). All fish were stored frozen until dissections were performed.

Dissections and otolith preparation

Specimens damaged by spearing or with broken otoliths were not used for analysis; thus, morphometric measures were made for 158, 275, and 155 specimens of *C. verater, C. strigosus, and D. albisella*, respectively, which were then dissected and aged (Table 1). Standard lengths (SL) and total lengths (TL) were measured to the nearest millimeter and whole body weights
were recorded to the nearest gram of each thawed specimen. Sagittal otoliths were removed, cleaned of residual material, rinsed in 95% ethanol, and air-dried. Once dry, otoliths were weighed (to 0.1 mg), photographed, and stored dry for ageing later.

The sagittal otoliths were prepared following the methodology of Choat et al. (2003). Unless missing or damaged, the left otolith of each specimen was processed. Each otolith was mounted on the edge of a glass microscopy slide with thermoplastic glue (CrystalBond) and ground to the nucleus with a 1200 grit diamond lap on a CrystalMaster 8 grinding wheel. The otolith was then remounted so that the ground side of the otolith was flush with the slide, and the other side of the otolith was ground down until a thin transverse section was attained. The resulting section was finally hand-polished using 3-9µm grit aluminum oxide lapping film and coated with a layer of CrystalBond for improved clarity of growth increments.

Each sectioned otolith was examined under transmitted light with a low-power dissecting microscope (10-40x magnification). Growth increments have been shown to be deposited annually for several tropical pomacentrids (e.g. Meekan et al. 1999) as well as acanthurids (e.g. Choat and Axe 1996), so they were assumed to be deposited annually for C. verater, C. strigosus, and D. albisella. Pairs of dark opaque and light translucent bands assumed to be the annual growth increments were counted along a consistent axis by two independent observers (MW and BT). If the two counts varied, then each observer independently recounted until an exact agreement was made. If the observers could not reach a consensus after each conducting three counts, then the otolith was excluded from analysis. Otoliths of individuals found to be less than 1 year of age were subsequently reground until daily growth increments were visible, and reanalyzed to estimate daily ages. Daily ages were converted into fractions of a year to be incorporated into growth curves.
As an evaluation of aging estimates, the otolith weight was regressed on estimated age using an ordinary linear regression, given that a positive relationship would indicate continual growth of otoliths through the accretion of calcium carbonate during a fish’s lifespan (Fowler and Doherty 1992; Choat and Axe 1996).

**Analysis of life history traits**

In order to investigate intraspecific differences in life history traits across depths, fish from all regions were compared between pooled shallow and deep populations for each species. Fish were also compared among six “locations” (shallow Johnston Atoll, deep Johnston Atoll, shallow MHI, deep MHI, shallow NWHI, and deep NWHI) to examine variability at a finer depth scale and across a latitudinal gradient. However, due to the low sample size of *C. strigosus* and *D. albisella* (two and seven specimens, respectively) from the deep MHI, these samples were omitted from the comparative analysis. For each location, we compared Fulton’s body condition index, parameters from length-weight relationships, and the asymptotic length and growth coefficient from the von-Bertalanffy growth function for all three species.

**Body condition**

Fulton’s body condition index (also known as Fulton’s *K*) was calculated for individual samples using the following equation:

\[
K = \frac{W}{L^3}
\]

where *W* is total weight (g) and *L* is standard length (mm). Fulton’s *K* provides a morphometric index of fish “bulk”, or body condition. Student’s t tests were used to determine whether body condition varied between shallow and deep populations for each species. The body condition of
each species was also analyzed using a one-way analysis of variance (ANOVA) to determine whether condition varied among locations. Assumptions of ANOVAs were evaluated for each test using standard diagnostic practices. ANOVAs were followed by multiple comparison tests (each pair, student’s t) were used to examine specific differences in body condition between each of the locations. All data manipulation and statistical analyses described in the following sections were conducted using R v3.1.1 (R Development Core Team 2009).

Length-weight
The weight at length data for each species by location were fit to the following allometric length-weight equation:

\[ W = aL^b \]  

where \( W \) is total weight (g), \( L \) is standard length (mm), \( b \) is an allometric growth parameter, and \( a \) is a scaling constant. For each species, an analysis of covariance (ANCOVA) with \( \log_{10}(W) \) as the response variable and \( \log_{10}(L) \) as the covariate was used to determine whether the parameters of the linearized \( \log(\text{length}) \) vs. \( \log(\text{weight}) \) relationship differed significantly between shallow and deep populations, and among populations from each of the six locations. To examine specific differences in the length vs. weight relationship between the locations, these ANCOVAs were followed by multiple comparison tests.

Growth
The von Bertalanffy growth function (VBGF), a conventional method of describing growth in fishes (Ricker 1975), was fit to size at age data for each species by pooled shallow and deep samples and by location using least squares techniques:
\[ L(t) = L_\infty \left( 1 - e^{-k(t-t_0)} \right) \]  

where \( L(t) \) is length (mm) at age \( t \) (years), \( L_\infty \) is the mean asymptotic length (mm), \( k \) is the growth coefficient, and \( t_0 \) is the theoretical age at length zero. Growth curves were fit by constraining the \( y \)-intercept (i.e., \( L_0 \)) to a common length of settlement for each species in order to increase the accuracy of VBGF parameter estimates (Kritzer et al. 2001). Length at settlement of \( C. \) strigosus and \( D. \) albisella were obtained from existing literature and set as 28mm (Randall 1955; Sancho et al. 1997) and 10mm (Booth 1992), respectively. Settlement size for \( C. \) verater has not been published; therefore, the length at settlement for the congeneric \( Chromis \) multilineata of 19mm (Wellington and Robertson 2001) was used, given these two species attain a similar maximum length. Estimates of the VBGF parameters obtained from the best-fit models were used to generate growth curves for each species. To visually compare parameter estimates, 95% confidence ellipses were constructed around maximum likelihood estimates of \( L_\infty \) and \( k \) following methods of Kimura (1980).
RESULTS

Body Condition

Body condition (Fulton’s $K$) differed significantly between depths for *Chromis verater* ($t_{100} = 2.5$, $p < 0.05$), *Ctenochaetus strigosus* ($t_{42} = 2.7$, $p < 0.05$), and *Dascyllus albisella* ($t_{145} = 2.8$, $p < 0.01$). For each species, body condition was significantly higher for samples collected in shallow sites than in deep sites (Fig. 2).

Body condition also differed significantly between locations for *C. verater* ($F_{5, 152} = 8.6$, $p < 0.001$), *C. strigosus* ($F_{4, 238} = 5.9$, $p < 0.001$), and *D. albisella* ($F_{4, 143} = 6.9$, $p < 0.001$), yet different trends emerged between species. In fishes collected from shallow locations, the body condition of each species generally appeared to be lowest at Johnston Atoll and highest in either the NWHI or MHI. Body condition in fishes from deep locations was variable between species, with no clear emerging trend (Fig. 2).

*C. verater* from the shallow MHI had significantly higher body condition than their conspecifics collected from deep Johnston Atoll (Fig. 2a). Body condition was significantly higher in fishes from both the shallow and deep NWHI than in fishes from both shallow and deep Johnston Atoll sites, and in fishes collected from the deep MHI. Body condition did not differ significantly between depths at each region.

The body condition of *C. strigosus* was highest in fishes from the shallow NWHI, and differed significantly from the body condition of both shallow and deep fishes from Johnston Atoll (Fig. 2b). Body condition was also significantly higher in fishes from the shallow NWHI than in fishes from the deep NWHI, but there was no difference in body condition between fishes from shallow and deep sites at Johnston Atoll. The low sample size of *C. strigosus* from the deep MHI did not allow for comparisons to be made using this location for this species.
D. albisella from the shallow MHI had significantly higher body condition than their conspecifics from both shallow and deep sites in Johnston Atoll, and from the deep NWHI (Fig. 2c). Body condition did not differ between fishes from shallow and deep sites within any of the regions, but the low sample size of D. albisella from the deep MHI did not permit this location to be incorporated into the comparisons.

Summary statistics for the ANOVA and Tukey HSD comparisons for the body condition analyses are included in the Appendix (Tables A.1., A.2).

Length-weight

The weight-at-length relationship differed significantly between depths for C. verater (F1, 151 = 6.7, p < 0.05), C. strigosus (F1, 242 = 18.04, p < 0.001), and D. albisella (F1, 149 = 10.6, p < 0.005) (Table 3). For all species, weight was higher at a given length for fishes collected from shallow sites than deep sites.

The weight-at-length relationship also differed significantly between locations for C. verater (F5, 151 = 9.9, p < 0.001), C. strigosus (F4, 237 = 10.2, p < 0.001), and D. albisella (F4, 139 = 9.4, p < 0.001) (Table 3). For C. verater at a given length, weight-at-length was highest for this species in fishes from the deep NWHI and lowest in fishes from deep Johnston Atoll sites. The length-at-weight relationship for C. verater did not differ between depths in the NWHI and Johnston Atoll. C. strigosus from the shallow NWHI reached the highest weight at a given length for this species, while fishes from the deep NWHI sites reached the lowest weight at length. The length-at-weight relationship did not differ between C. strigosus from deep locations, or between shallow and deep sites at Johnston Atoll. D. albisella had the highest weight-at-length from the shallow MHI and the lowest weight-at-length from deep Johnston Atoll sites. The length-at-
weight relationship of *D. albisella* did not differ between fishes from deep locations, or between shallow and deep sites at Johnston Atoll.

For each of the three fish species, the parameters of the total length-standard length parameters of the ordinary linear regression, \( TL = a + bSL \), where TL is total length (in mm), SL is standard length (in mm) and \( a, b \) are model parameters, are available in the Appendix (Table A.3.).

**Growth**

The growth curves for all three species were asymptotic, with initial rapid growth followed by slower growth, typical of fishes. As a validation of age estimates, otolith weight was a good predictor of age for *C. verater* (\( r^2 = 0.70, F_{1,150} = 341.1, p < 0.001 \)), *C. strigosus* (\( r^2 = 0.76, F_{1,237} = 750.9, p < 0.001 \)), and *D. albisella* (\( r^2 = 0.79, F_{1,144} = 538.4, p < 0.001 \)) (Fig. 3). The otolith weight-age parameters for the ordinary linear regression are available in the Appendix (Table A.4). *C. strigosus* was the longest lived species documented during this study; the oldest individual found to be 39 years old surpassed previous age estimations for this species (Langston et al. 2009). Length-at-age relationships were highly variable due to the observed variability in growth amid individuals at each location (Table 2, Fig. 4-6). Intraspecific variability in growth, with trends unique to each species, occurred between locations.

*C. verater* from shallow locations had an age range of 1 year to 22 years (Table 1, 2). Specimens of *C. verater* from deep locations encompassed a narrower age range from 144 days to 15 years. On average, deep fishes exhibited faster initial growth while attaining a smaller asymptotic maximum length than shallow fishes (Fig. 4a; 5a,d). However, the overlapping 95%
confidence ellipses surrounding the VBGF parameters $L_\infty$ and $k$ for shallow and deep fishes showed that the growth curves were not significantly different between depths (Fig. 6a).

*C. verater* from shallow habitats at Johnston Atoll had faster juvenile growth and reached a smaller asymptotic length than individuals from deep habitats at Johnston Atoll, but a similar pattern was not observed in the Hawaiian Archipelago (Fig. 4b,c,d). The largest asymptotic length of *C. verater* was estimated for fishes from the shallow NWHI (Fig. 5a). *C. verater* sampled in the MHI and NWHI from deep sites grew more quickly at younger ages than their conspecifics sampled from shallow sites (Fig. 4b,c,d). However, the growth model for the shallow MHI fishes may not accurately represent this population because of the lack of young individuals (<3 years old) collected here. The 95% confidence ellipses surrounding the VBGF parameters $L_\infty$ and $k$ did not overlap between estimates obtained for the shallow and deep NWHI fishes, which suggests growth patterns in the NWHI differed significantly between shallow and deep populations (Fig. 5a,d; Fig. 6d). While the confidence ellipses for the shallow and deep Johnston Atoll fishes overlapped, these ellipses were separate from all others constructed for the NWHI and MHI fishes (Fig. 6d). Thus both shallow and deep *C. verater* from Johnston Atoll reached a significantly smaller asymptotic length at a generally faster rate than most fishes from the Hawaiian Archipelago.

*C. strigosus* from shallow locations reached the oldest age of all three species, with an age range of 1 year to 39 years. *C. strigosus* from deep locations were aged from 1 year to 19 years (Table 1). In general, *C. strigosus* from shallow populations grew at a similar rate as conspecifics from deep populations, yet reached a larger asymptotic length (Fig. 4e; Fig. 5b, e). However, the overlapping 95% confidence ellipses surrounding the VBGF parameters $L_\infty$ and $k$
for the pooled shallow and deep samples showed that the growth curves were not significantly different between depths (Fig. 6b).

Deep *C. strigosus* from the NWHI obtained the largest asymptotic length (Fig. 5b), yet individuals greater than 10 years of age were rare at this location. The smallest asymptotic length estimated for *C. strigosus* was from shallow Johnston Atoll sites (Fig 5b). The non-overlapping 95% confidence ellipses surrounding $L_\infty$ and $k$ for shallow and deep NWHI fishes demonstrated a significant difference in their growth patterns (Fig. 6e). The confidence ellipses constructed for fishes from shallow sites did not overlap, revealing that fish from the MHI reached the largest asymptotic length while fish from Johnston Atoll reached the smallest. The confidence ellipses of shallow and deep *C. strigosus* from Johnston Atoll did overlap, largely due to their similarity in $L_\infty$, but these growth patterns were distinct from the rest of the Hawaiian Archipelago fishes.

The oldest recorded ages of *D. albisella* were similar to those of *C. verater*, with fishes from shallow locations ranging in age from 1 year to 21 years, and fishes from deep locations ranging from 55 days to 16 years (Table 1). *D. albisella* from shallow populations exhibited slightly faster initial growth and reached a marginally larger asymptotic length than conspecifics from deep populations (Fig. 4i; Fig. 5c, f). The overlapping 95% confidence ellipses surrounding the VBGF parameters $L_\infty$ and $k$ for pooled shallow and deep samples showed that the growth curves were not significantly different between depths (Fig. 6c).

There were no significant differences in the growth patterns of *D. albisella* sampled from shallow and deep sites at Johnston Atoll (Fig. 4j; Fig. 5c,f; Fig. 6f). *D. albisella* from the shallow NWHI had more rapid juvenile growth and reached a larger asymptotic length than those from the deep NWHI (Fig. 4l; 5c,f), and the non-overlapping confidence ellipses provided evidence that these growth patterns were distinct (Fig. 6f). Unlike for *C. verater* and *C. strigosus*, the
growth patterns of *D. albisella* from Johnston Atoll were not distinct from those collected from the Hawaiian Archipelago. The largest mean asymptotic sizes were found for individuals of *D. albisella* from the shallow locations at the NWHI and Johnston Atoll (Fig 5c). While the smallest size was found for *D. albisella* from the shallow MHI, all of the fishes from this location were found to reach an age of five years of less.
DISCUSSION

Prior studies have investigated intraspecific variability in the demographic traits of coral reef fishes, but they primarily examined differences across spatial scales at shallow depths (Gust et al. 2002; Ruttenberg et al. 2005; Caselle et al. 2011; Hamilton et al. 2011; Donovan et al. 2013). The present study not only presents patterns of intraspecific variability in the growth and condition of *C. strigosus, C. verater, and D. albisella* across the extent of their geographic ranges, but also demonstrates previously undocumented differences between populations inhabiting shallow coral reefs and mesophotic coral ecosystems. This study shows significant differences in patterns of life history among species, so caution should be applied in generalizing these patterns amongst other reef fishes with broad depth ranges. These results emphasize the need to further investigate variability in the life history of fishes whose distributions span shallow coral reefs and MCEs.

The variability in life history traits observed across space and depth is likely influenced by multiple environmental and ecological factors. Given reef fish exhibit significant intraspecific plasticity in demographic traits across scales ranging from 100s to 1,000s of km (Gust et al. 2002; Ruttenberg et al. 2005), conclusions drawn from the results of comparisons between pooled shallow and deep samples may not accurately represent the populations occurring at each sampling region. Quantifying the differences in life history traits between shallow and mesophotic reef fish populations based purely on the pooled results requires broad generalizations to be made, so examining the variability in life history at a finer scale is warranted. Moreover, unique differences in life history patterns were evident between species, indicative of an interaction of species-specific drivers (such as habitat preference, behavior, and morphology) with broad scale environmental factors.
Effects of latitude

Several trends in life history characteristics were suggestive of a latitudinal effect. Body condition generally increased with latitude, with the lowest body condition for all species found at Johnston Atoll and the highest body condition found in the NWHI (C. strigosus and C. verater) or MHI (D. albisella). Body condition, estimated using Fulton’s $K$, is defined as a measure of energy reserves relative to body size that represents a measure of overall well-being. Body condition can represent a proxy for how favorable the surrounding environment is for an organism. A habitat with low food availability, high competition for limiting resources, and/or high predation risk is innately unfavorable, thus, body condition is significantly related to these environmental factors (Bachman 1993; Relyea and Hoverman 2003; Page et al. 2007; Donelson et al. 2008; English et al. 2014). The observed increase in body condition with increasing latitude may be associated with the increase in productivity documented to occur along this gradient. Mean annual primary productivity, described by Williams et al. (2015) using surface chlorophyll-a concentrations as a proxy, was higher in the NWHI (average of 1.0 mgm$^{-2}$) than the MHI and Johnston Atoll (average of 0.08 mgm$^{-2}$ and 0.05 mgm$^{-2}$, respectively). Low levels of primary productivity directly influence feeding resources for many coral reef fish species, and food availability is positively related to body condition (Page et al. 2007; Donelson et al. 2008). Furthermore, under conditions with limited food, decreased body condition in females results largely from increased energy allocation towards reproduction (Donelson et al. 2008). Females under conditions with abundant food sources do not sacrifice their body condition during reproductive periods and also reproduce more frequently with larger and more numerous eggs.
that lead to larger juveniles on average. Moreover, juvenile fishes in better condition are reported
to have higher levels of survivorship on coral reefs (Booth and Hixon 1999; Booth and Alquezar
2002).

Maximum length increased with latitude for *C. strigosus* and *C. verater*, though no
consistent trends in growth rate emerged across this gradient. It has been well documented that
colder waters associated with increases in latitude often result in the increased body sizes of
tropical and subtropical reef fishes (e.g. Cowen 1990; Gilligan 1991; Luckhurst et al. 2000;
Choat and Robertson 2002). While sea surface temperatures can drop as low as 16°C at certain
locations in the NWHI (Kane et al. 2014), Johnston Atoll experiences sea surface temperatures
of 25-27 °C with little seasonal variability due to its location nearer to the equator (Ralston et al.
1986; Boehlert et al. 1992). For all species, growth patterns did not differ between fish collected
from shallow and deep sites at Johnston Atoll. This result may similarly be driven by
temperature; while the thermocline is found in waters 60m or shallower in certain locations in
the NWHI (Grigg et al. 2008), moving southward the thermocline becomes deeper, ranging from
100 to 400 m at Johnston Atoll (US Army Corps of Engineers 1983). At such a depth at Johnston
Atoll, MCEs are less likely to experience substantially lower temperatures than found in shallow
coral reefs here. Hence, the temperature difference between MCEs and shallow coral reefs at
Johnston Atoll may not be strong enough to drive variability in the growth rate of reef fishes
found at both depths.

While the maximum length of *C. strigosus* and *C. verater* increased along the latitudinal
gradient from Johnston Atoll to the NWHI, *D. albisella* exhibited a different trend in body size.
Shallow samples of *D. albisella* were found to obtain larger body sizes in Johnston Atoll and the
NWHI where the percentage of hard coral cover and substrate height is higher, than the MHI
(Williams et al. 2015). This trend may be associated with this species’ site-attached nature, with larger sizes being reached in locations with higher shelter availability. Juvenile *D. albisella* closely associate with sessile benthic organisms, such as branching coral heads, which serve as refuges from predation (Stevenson 1963; Booth 1991, 1992).

*Species-specific variability*

The NWHI was the only region examined in this study where significantly different life history characteristics were found between shallow and mesophotic populations. While intraspecific variability in growth and condition occurred between depths for *C. strigosus*, *C. verater*, and *D. albisella*, differences in life history traits were also evident among the three species.

*C. strigosus* attained larger body sizes at mesophotic depths in the NWHI, but these fish had slower growth and lower body condition than their conspecifics at shallow depths in the NWHI. It is unlikely that this variability is driven by competition for limited resources, given the low density of benthic grazers found in MCEs and potentially similar food availability between depths. In the NWHI, the density of benthic grazers has been found to peak at depths less than 10m (Fukunaga et al. 2016), resulting in fewer potential competitors of *C. strigosus* in deeper habitats. Despite the decrease in light irradiance with depth, upwelling of cold-nutrient rich waters to MCEs can support diverse and productive algae and phytoplankton communities at these depths (Jensen et al. 1985; Littler et al. 1986; Spalding 2012; Lesser 2006; Leichter and Genovese 2006), thereby enhancing primary productivity and increasing resource availability. Low competition for abundant resources, along with colder water temperatures, may facilitate
the growth of *C. strigosus* to larger maximum sizes in the MCEs of the NWHI. The substantially colder water temperatures found at mesophotic depths here may also affect the growth rate and body condition of *C. strigosus*. Decreasing temperatures have been documented to reduce growth rates (Atkinson 1994; Atkinson and Sibly 1997; Pauly 1998), and in these cold waters *C. strigosus* may be approaching their thermal tolerance limit, lowering their body condition.

Mesophotic samples of *D. albisella* grew more slowly and attained smaller body sizes than shallow samples in the NWHI, which may be driven by lower shelter availability and heightened predation intensity. In the NWHI, the abundance of scleractinian corals decreases with depth (Chang et al. 2015), while the density of piscivores peaks between 50 and 60 m deep (Fukunaga et al. 2016). Given *D. albisella* were also documented to reach smaller sizes in regions with lower coral cover, the difference between shallow and deep samples in the NWHI is consistent with the hypothesis that shelter availability is a principal driver of the life history of this site-attached species. *D. albisella* are more vulnerable to predation in mesophotic depths in the NWHI not only because there is less shelter available, but also due to the increase in the abundance of piscivores. Increased vigilance for predators has been shown to slow growth (Holbrook and Schmitt 1988; Werner et al. 1983), and decreased asymptotic size may be driven by the increased risk of mortality due to predation (Choat and Robertson 2002).

Unlike *C. strigosus* and *D. albisella*, shallow and deep *C. verater* samples from the NWHI attained similar maximum sizes, but deep samples exhibited more rapid initial growth than shallow samples. Though defined as depth-generalists, *C. verater* are typically sparse in shallow waters and are more abundant at depths > 18m (Swerdloff 1970; Randall 1998), dominating deep reefs in the north central Pacific (Brock and Chamberlain 1968; Wagner et al. 2014; Fukunaga et al. 2016). Moreover, it has been documented that species can adapt to colder
temperatures by increasing their growth rates (Conover and Present 1990). Given fast growth rates may enhance the survival of newly settled reef fishes, *C. verater* may be better adapted to life in the mesophotic zone than *C. strigosus* and *D. albisella*.

While *C. verater* and *D. albisella* both feed on zooplankton, their patterns of life history differ. Not only are *C. verater* more abundant in MCEs than *D. albisella* (which are most common at depths from 15 to 24m (Stevenson 1963)), these species have different morphologies that may influence their success at relative depths. Regardless of depth, both species feed in the water column, where there is a high flow rate of plankton. However, when swimming through the water column, fishes are exposed and vulnerable to predation. In the low light environment of MCEs where there are high densities of piscivores, *C. verater* may have an advantage over *D. albisella* due to their differing caudal fin morphologies. *C. verater* have a forked caudal tail with a higher aspect ratio, which facilitates rapid acceleration, while *D. albisella* possess a rounded caudal tail with a low aspect ratio, which serves to improve maneuverability (Bridge et al. 2016). *C. verater* are likely to be able to flee faster from predators, while *D. albisella* can better maneuver into tight refuge spaces. However, in certain mesophotic environments where shelter availability is lower, such as the NWHI, improved maneuverability may not serve *D. albisella* as beneficially as faster acceleration does for *C. verater*. Therefore, the variability in life history characteristics and preferred depth distributions of these planktivorous species may be related to differing morphological traits.

Beyond factors such a diet, morphology, and behavior that influence differences in life history patterns between species, the myriad of varying environmental factors between shallow and mesophotic depths and along the latitudinal gradient are liable to have influenced intraspecific variability in the life history traits of the coral reef fishes examined in this study.
Given the confounding nature of many of these factors, future work should incorporate accurate measurements of reef productivity and examine the processes of competition and predation in mesophotic reefs. Moreover, this study presents the results of only three species of the many coral reef fishes that have broad depth distributions. Given the logistical difficulty of collecting fish at mesophotic depths, the study provides a preliminary examination of differences in life history traits between shallow and deep reef fish populations based on limited sample sizes. Further studies examining the life history of other coral reef fish species at the locations investigated in this study, and in MCEs worldwide, are warranted. Variability in reproduction between shallow and mesophotic reef fish populations should also be investigated in order to understand energetic trade-offs in life history traits.

This study provides life history information for three coral reef fish species endemic to the Hawaiian Archipelago and Johnston Atoll, which have been the subject of few age-based demographic studies. Not only do endemic species hold high cultural importance, they also serve an important function in the origin of biodiversity on coral reefs (Bird et al. 2011; Eble et al. 2011; Bowen et al. 2013). However, endemic species are also more susceptible to ill consequences that can arise from declines in habitat quality due to their restricted geographic ranges (Hawkins et al. 2000; Bonn et al. 2002). The vulnerability of endemic species emphasizes a need to properly understand the habitat occupied at all depths of their distributions. Reef fish assemblages in MCEs are dominated by endemic species (Kane et al. 2014), and recent surveys at mesophotic depths at Kure Atoll in the NWHI revealed that all fish observed were endemic (Kosaki et al. 2016). Hence, MCEs may act as hotspots for marine biodiversity that require special management and conservation consideration.
As the world’s shallow coral reefs continue to decline, generating information on mesophotic coral ecosystems is critical for conserving and managing these environments that may eventually serve as refugia for coral reef species and rejuvenate shallow systems. The sustainable management of MCE fish communities can contribute to maintaining healthy fisheries and local and regional biodiversity in coral reef ecosystems (Riegl and Piller 2003). Determining whether and how the life history strategies of mesophotic fishes vary from their shallow water conspecifics is critical in the effective assessment and management of MCE populations, because the establishment of accurate demographic parameters is essential for informing sound decision-making by fisheries managers. This study addresses a knowledge gap on understudied mesophotic environments by further understanding how life history parameters change with depth. The intraspecific variability observed between shallow and mesophotic coral reef fishes indicate that MCEs harbor organisms with distinct life history patterns from their shallow water complements, which must be considered in future management decisions to protect these valuable environments.
**TABLES**

**Table 1.** Collected sample size (total available), aged sample size (subset used in life history analysis), and range in standard length (SL, mm) for aged samples of *Chromis verater, Ctenochaetus strigosus, and Dascyllus albisella* from six locations across the Central Pacific.

<table>
<thead>
<tr>
<th>Location</th>
<th>Depth</th>
<th>Collected/Aged</th>
<th>Size range (SL, mm)</th>
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<tbody>
<tr>
<td></td>
<td></td>
<td><em>C. verater</em></td>
<td><em>C. strigosus</em></td>
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<tr>
<td>All Locations</td>
<td>Shallow</td>
<td>109/105</td>
<td>245/239</td>
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<td></td>
<td>Deep</td>
<td>60/53</td>
<td>37/36</td>
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<td></td>
<td>Deep</td>
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<tr>
<td>K</td>
<td>0.26</td>
<td>0.26</td>
<td>0.26</td>
</tr>
<tr>
<td>t₀</td>
<td>0.26</td>
<td>0.26</td>
<td>0.26</td>
</tr>
</tbody>
</table>

Table 2. Von Bertalanffy growth function (VBGF) parameters (± SE) and age range (years) for Chromis verater, Ctenochaetus strigosus, and Dascyllus albisella from six study locations.
**Table 3.** Allometric length-weight relationship and range in body weight (g) by species and location, with different letter groups denoting significantly different intercepts in ANCOVAs based upon post-hoc student’s t-tests using log-log data.

<table>
<thead>
<tr>
<th>Region</th>
<th>Depth</th>
<th>C. verater</th>
<th>Group</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>$a$</td>
<td>$b$</td>
</tr>
<tr>
<td>All Pooled</td>
<td>Shallow</td>
<td>5.40 x 10^{-05}</td>
<td>2.99</td>
</tr>
<tr>
<td></td>
<td>Deep</td>
<td>1.65 x 10^{-05}</td>
<td>3.22</td>
</tr>
<tr>
<td>Northwestern Hawaiian Islands</td>
<td>Shallow</td>
<td>1.83 x 10^{-04}</td>
<td>2.75</td>
</tr>
<tr>
<td></td>
<td>Deep</td>
<td>8.35 x 10^{-05}</td>
<td>2.91</td>
</tr>
<tr>
<td>Main Hawaiian Islands</td>
<td>Shallow</td>
<td>6.42 x 10^{-05}</td>
<td>2.96</td>
</tr>
<tr>
<td></td>
<td>Deep</td>
<td>7.69 x 10^{-05}</td>
<td>2.90</td>
</tr>
<tr>
<td>Johnston Atoll</td>
<td>Shallow</td>
<td>1.57 x 10^{-04}</td>
<td>2.74</td>
</tr>
<tr>
<td></td>
<td>Deep</td>
<td>8.24 x 10^{-05}</td>
<td>2.88</td>
</tr>
<tr>
<td></td>
<td></td>
<td>C. strigosus</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>$a$</td>
<td>$b$</td>
</tr>
<tr>
<td>All Pooled</td>
<td>Shallow</td>
<td>1.35 x 10^{-04}</td>
<td>2.82</td>
</tr>
<tr>
<td></td>
<td>Deep</td>
<td>1.61 x 10^{-04}</td>
<td>2.76</td>
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<tr>
<td>Northwestern Hawaiian Islands</td>
<td>Shallow</td>
<td>1.28 x 10^{-04}</td>
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<tr>
<td></td>
<td>Deep</td>
<td>2.26 x 10^{-04}</td>
<td>2.70</td>
</tr>
<tr>
<td>Main Hawaiian Islands</td>
<td>Shallow</td>
<td>1.49 x 10^{-04}</td>
<td>2.80</td>
</tr>
<tr>
<td></td>
<td>Deep</td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td>Johnston Atoll</td>
<td>Shallow</td>
<td>6.93 x 10^{-05}</td>
<td>2.94</td>
</tr>
<tr>
<td></td>
<td>Deep</td>
<td>1.83 x 10^{-04}</td>
<td>2.73</td>
</tr>
<tr>
<td></td>
<td></td>
<td>D. albisella</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>$a$</td>
<td>$b$</td>
</tr>
<tr>
<td>All Pooled</td>
<td>Shallow</td>
<td>2.83 x 10^{-04}</td>
<td>2.68</td>
</tr>
<tr>
<td></td>
<td>Deep</td>
<td>6.24 x 10^{-05}</td>
<td>3.00</td>
</tr>
<tr>
<td>Northwestern Hawaiian Islands</td>
<td>Shallow</td>
<td>4.06 x 10^{-04}</td>
<td>2.60</td>
</tr>
<tr>
<td></td>
<td>Deep</td>
<td>6.53 x 10^{-04}</td>
<td>2.45</td>
</tr>
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<td>Main Hawaiian Islands</td>
<td>Shallow</td>
<td>5.80 x 10^{-05}</td>
<td>3.07</td>
</tr>
<tr>
<td></td>
<td>Deep</td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td>Johnston Atoll</td>
<td>Shallow</td>
<td>9.12 x 10^{-05}</td>
<td>2.91</td>
</tr>
<tr>
<td></td>
<td>Deep</td>
<td>3.72 x 10^{-04}</td>
<td>2.58</td>
</tr>
</tbody>
</table>
Figure 1. Collection sites for *Chromis verater*, *Ctenochaetus strigosus*, and *Dascyllus albisella*.
Figure 2. Comparison of Fulton’s condition index ($K$, g m$^{-3}$) for *Chromis verater* (a), *Ctenochaetus strigosus* (b), and *Dascyllus albisella* (c) in shallow coral reefs and MCEs in three regions within the North-Central Pacific. Different letter groups indicate significant differences between locations based on post-hoc student’s t-tests.
Figure 3. The relationship between age and otolith weight (g) for *Chromis verater* (a), *Ctenochaetus strigosus* (b), and *Dascyllus albisella* (c) in the North-Central Pacific.
Figure 4. Von Bertalanffy growth functions fitted to *Chromis. verater* (a, b, c, d), *Ctenochaetus strigosus* (e, f, g, h), and *Dascyllus albisella* (i, j, k, l) size-at-age data for samples collected from pooled locations (a, c, i), Johnston Atoll (b, f, j), the Main Hawaiian Islands (MHI) (c, g, k), and the Northwestern Hawaiian Islands (NWHI) (d, h, l).
Figure 5. Parameter estimates ± S.E. for $L_\infty$ and $k$ by location for *Chromis verater* (a, d), *Ctenochaetus strigosus* (b, e), and *Dascyllus albisella* (c, f).
Figure 6. Plots of 95% confidence ellipses for parameters $L_\infty$ and $k$ by location for *Chromis verater* (a), *Ctenochaetus strigosus* (b), and *Dascyllus albissa* (c).
### Table A.1. ANOVA results comparing condition index (Fulton’s $K$) across locations by species, with entries in bold denoting significant differences.

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>SS</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>Sig</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>C. verater</strong></td>
<td>Location</td>
<td>1.087 x 10^{-09}</td>
<td>5</td>
<td>2.174 x 10^{-10}</td>
<td>8.647</td>
</tr>
<tr>
<td></td>
<td>Residual</td>
<td>3.821 x 10^{-09}</td>
<td>152</td>
<td>2.524 x 10^{-11}</td>
<td></td>
</tr>
<tr>
<td><strong>C. strigosus</strong></td>
<td>Location</td>
<td>8.807 x 10^{-10}</td>
<td>4</td>
<td>8.807 x 10^{-10}</td>
<td>5.8674</td>
</tr>
<tr>
<td></td>
<td>Residual</td>
<td>8.931 x 10^{-09}</td>
<td>238</td>
<td>3.753 x 10^{-11}</td>
<td></td>
</tr>
<tr>
<td><strong>D. albisella</strong></td>
<td>Location</td>
<td>5.507 x 10^{-09}</td>
<td>4</td>
<td>1.377 x 10^{-09}</td>
<td>6.867</td>
</tr>
<tr>
<td></td>
<td>Residual</td>
<td>2.867 x 10^{-08}</td>
<td>143</td>
<td>2.005 x 10^{-10}</td>
<td></td>
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</tbody>
</table>
Table A.2. Approximate probabilities of Tukey’s Honestly Significant Difference (HSD) comparisons between locations by species for Fulton’s condition index. Significant results (p < 0.05) are shown in bold.

<table>
<thead>
<tr>
<th>Chromis verater</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Region</td>
<td>Depth</td>
<td>Johnston Atoll</td>
<td>MHI</td>
<td>NWHI</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Shallow</td>
<td>Shallow</td>
<td>Shallow</td>
<td>Shallow</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Deep</td>
<td>Deep</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Johnston Atoll</td>
<td>Deep</td>
<td>0.92952</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MHI</td>
<td>Shallow</td>
<td>0.16749</td>
<td><strong>0.04059</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Deep</td>
<td>1.00000</td>
<td>0.94650</td>
<td>0.10963</td>
<td></td>
</tr>
<tr>
<td>NWHI</td>
<td>Shallow</td>
<td>&lt; <strong>0.001</strong></td>
<td>&lt; <strong>0.001</strong></td>
<td>0.64231</td>
<td>&lt; <strong>0.001</strong></td>
</tr>
<tr>
<td></td>
<td>Deep</td>
<td><strong>0.00809</strong></td>
<td><strong>0.00195</strong></td>
<td>0.66126</td>
<td><strong>0.00444</strong></td>
</tr>
</tbody>
</table>

| Ctenochaetus strigosus    |                |                |                |                |                |
|                          | Johnston Atoll | Deep           |                |                |                |
|                          | MHI            | Shallow        | 0.13080        | 0.16727        |                |
|                          | NWHI           | Shallow        | **0.00564**    | **0.00998**    | 0.37512        |
|                          | Deep           | 0.96397        | 0.97066        | 0.13336        | **0.01659**    |

| Dascyllus albisella       |                |                |                |                |                |
|                          | Johnston Atoll | Deep           |                |                |                |
|                          | MHI            | Shallow        | **0.00236**    | **0.00352**    |                |
|                          | NWHI           | Shallow        | 0.25511        | 0.18904        | 0.27272        |
|                          | Deep           | 0.99478        | 0.99979        | < **0.001**    | 0.07792        |
Table A.3. Total length-standard length parameters of the linear equation, \( TL = a + bSL \), by species.

<table>
<thead>
<tr>
<th>Species</th>
<th>( a )</th>
<th>( b )</th>
<th>( R^2 )</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Chromis verater</em></td>
<td>-5.05973</td>
<td>0.78376</td>
<td>0.9609</td>
</tr>
<tr>
<td><em>Ctenochaetus strigosus</em></td>
<td>7.41347</td>
<td>0.70172</td>
<td>0.9519</td>
</tr>
<tr>
<td><em>Dascyllus albisella</em></td>
<td>4.3432</td>
<td>0.7335</td>
<td>0.968</td>
</tr>
</tbody>
</table>
Table A.4. Otolith weight-age parameters of the linear equation, \( OW = a + bA \), by species.

<table>
<thead>
<tr>
<th>Species</th>
<th>( a )</th>
<th>( b )</th>
<th>( R^2 )</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Chromis verater</em></td>
<td>0.0177921</td>
<td>0.0023006</td>
<td>0.6946</td>
</tr>
<tr>
<td><em>Ctenochaetus strigosus</em></td>
<td>( 1.010 \times 10^{-02} )</td>
<td>( 1.347 \times 10^{-03} )</td>
<td>0.7601</td>
</tr>
<tr>
<td><em>Dascyllus albisella</em></td>
<td>( 2.941 \times 10^{-03} )</td>
<td>( 6.515 \times 10^{-04} )</td>
<td>0.789</td>
</tr>
</tbody>
</table>
Figure A.1. Size frequency distributions of *Chromis verater* (a, b, c, d), *Ctenochaetus strigosus* (e, f, g, h), and *Dascyllus albisella* (i, j, k, l) collected from all sites (a, e, i), Johnston Atoll (b, f, j), the MHI (c, g, k), and the NWHI (d, h, l).
Figure A.2. Age frequency distributions of *Chromis verater* (a, b, c, d), *Ctenochaetus strigosus* (e, f, g, h), and *Dascyllus albisella* (i, j, k, l) collected from all sites (a, e, i), Johnston Atoll (b, f, j), the MHI (c, g, k), and the NWHI (d, h, l).
Figure A.3. Standard length vs. total length relationship of *Chromis verater* (a), *Ctenochaetus strigosus* (b), and *Dascyllus albisella* (c) collected across the Central Pacific.
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