

DEMOGRAPHIC PATTERNS IN THE PEACOCK GROUPE *Cephalopholis argus*,
AN INTRODUCED HAWAIIAN REEF FISH

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ABSTRACT

This study utilizes a unique opportunity to collect large sample sizes of a coral reef fish species across a range of physical and biological features of the Hawaiian Archipelago in order to investigate variability in the demography of an invasive predatory coral reef fish, *Cephalopholis argus* (Family: Serranidae). Age-based demographic analyses were conducted at 10 locations on four islands in the main Hawaiian Islands. Estimates of weight-at-length, size-at-age and longevity were compared among locations. Each metric differed among locations, although patterns were not consistent. Length-weight relationships for *C. argus* differed among locations and individuals weighed less at a given length at Hilo, the southernmost location studied. Longevity differed among and within islands being greater at locations on Maui and Hawaii compared to the more northern locations on Oahu and Kauai. Within- island growth patterns differed at Kauai, Oahu, and Hawaii. This work provides a case study of fundamental life history information from distant and/or spatially limited locations that are needed for developing robust fishery models. The differences observed both among and within islands indicate that variability may be driven by cross-scale mechanisms that need to be considered in fisheries stock assessments and ecosystem-based management.

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CHAPTER 1:

General Introduction

Levin (1992) stated that “the problem of pattern and scale is the central problem in ecology,” acknowledging that processes in ecology operate at different scales than they are typically measured. Identifying the proper scale to measure ecological mechanisms can be difficult, and a series of recent studies have begun to evaluate this problem (Gust et al. 2001, Chittaro 2004, Kritzer & Sale 2004, Pittman et al. 2004, White et al. 2010, La Mesa et al. 2011). Likewise, Sale (2002) identified that the largest gap in coral reef fish ecology was the lack of a definition of the spatial scales on which populations operate. Sale therefore concluded that the best solution for providing insight into the generality of patterns and processes of coral reef ecology was to design multi-scale studies (Sale 1998). The need for a better understanding of scale in coral reef ecology is heightened by the increasing trend towards ecosystem-based management (Christensen et al. 1996, Browman et al. 2004) and the recent scaling-up of ecological studies (Forrester & Steele 2004, Steele & Forrester 2005).

Understanding the spatial and temporal scales at which populations operate is becoming increasingly important in fisheries management (Bellwood & Hughes 2001, Palumbi 2004, Hughes et al. 2005, Mangel & Levin 2005). Biological reference points are based on definitions of what defines a stock and the models are for closed-populations. This assumes homogenous life-history characteristics when predicting sustainable yields (Beverton & Holt 1957, Begg et al. 1999). But, the stock definition underlying this assumption is often a source of uncertainty in fisheries management as life history information is difficult to obtain and can vary temporally and spatially (Rahikainen & Stephenson 2004).

The ability to conduct robust evaluations of coral reef fisheries in particular is hindered by inadequate data. Recent mandates to establish catch-limits for coral reef fishes in the United States have created pressure for more information on these stocks. Thus, there is a compelling reason for using available data to create generic measures for multiple species

and across multiple locations. Doing this should be done with caution because recent studies have found large differences among species and locations in the life histories of coral reef fishes (Adams et al. 2000, Gust et al. 2002, Kritzer 2002, Choat et al. 2003, Williams et al. 2003, Robertson et al. 2005a, Trip et al. 2008).

Demographic variability

Recent work has revealed spatial variation in the life-history of reef fishes is related to a combination of geographic and environmental factors (Gust et al. 2002, Robertson et al. 2005a, Taylor & McIlwain 2010). The extent of geographic variation in reef fish life histories has been investigated across environmental conditions, ecological processes, genetic variation, and anthropogenic impacts (Gust et al. 2002, Choat et al. 2003, Williams et al. 2003, Robertson et al. 2005a).

The effects of environmental factors on the life histories of coral reef fishes have largely been addressed by assessing patterns along latitudinal gradients (Yamahira & Conover 2002, DeMartini et al. 2005, Robertson et al. 2005a, Ruttenberg et al. 2005, Trip et al. 2008). Robertson *et al.* (2005a, 2005b) found strong relationships between variations in growth, size and temperature along a latitudinal gradient in the Caribbean Sea. Further investigation into this pattern revealed that growth and size were subject to local environmental factors rather than latitude, but longevity was likely influenced by both of these factors (Trip et al. 2008).

The effect that ecological processes can have on the life history of coral reef fish was investigated by Gust *et al.* (2002) where age and growth of four species were compared across the outer reef crest and inner shelf of the Great Barrier Reef (GBR). They found that fishes were growing slower and had shortened longevity on the outer-shelf reefs and suggested that differences in life history parameters at the spatial scale of reef zones were the result of density-dependence and that post-settlement processes, resource limitation, and predation effects mediated these differences. Cross-shelf comparisons such as this have provided insight, but a lack of direct testing has left uncertainty about the mechanisms driving the observed patterns (Kingsford & Hughes 2005).

Demographic variation has also been well studied in the context of fishing. Selective fishing practices influence demography and life history strategies, as demonstrated in several species of marine fishes (Rijnsdorp & Vanleeuwen 1992, Buxton 1993, Choat et al. 2003, Williams et al. 2003, Berkeley et al. 2004, Hamilton et al. 2007, Taylor & McIlwain 2010, Caselle 2011). Differences in growth of the parrotfish *Sparisoma viride* in the tropical Atlantic were found to vary with fishing pressure (Choat et al. 2003). Fishing selectivity was also found to play a role in regional differences in growth of the red throat emperor (*Lethrinus miniatus*) at multiple spatial scales on the GBR (Williams et al. 2003).

Given the large body of research conducted on geographic variation in the life history parameters of coral reef fish, few studies have focused on genetic variation within populations. Yet it is essential to differentiate between life history differences that reflect phenotypic plasticity in dispersing larvae, versus local adaptation post settlement. (Warner & Swearer 1991, Dudgeon et al. 2000). One study found high levels of gene flow in the GBR precluded genetic variation as a factor influencing different growth rates, indicating that post-settlement processes elicited the observed differences (Dudgeon et al. 2000).

Coral reef fishes appear to exist as meta-populations with plastic traits that vary geographically (Kritzer & Davies 2005). In order to determine whether fish populations are resilient to external stressors such as fishing and climate change it is necessary to understand the spatial variability in coral reef fish demographics (Wilson et al. 2010). If spatial structure significantly influences coral reef fish population productivity, stocks should be managed on a location-specific basis within a species' range.

Study species

The peacock grouper *Cephalopholis argus* (family Serranidae, subfamily Epinephelidae; known in Hawaii by its Tahitian name “roi”), is an introduced species that has become well established in Hawaiian waters. *C. argus* was introduced to the Hawaiian Islands from the South Pacific during the 1950s as part of a program attempting to enhance nearshore fisheries by supplementing the depauperate native Hawaiian grouper and snapper fauna (Randall 1987). A total of 2,385 individuals of *C. argus* were introduced at two locations, one in Kaneohe Bay on Oahu and along the Kona Coast in 1956 and 1961, respectively. Populations have proliferated in many parts of the Main Hawaiian Islands (MHI), and *C. argus* has become the dominant shallow reef predator on many Hawaiian reefs (Dierking et al. 2009). Despite hopes of creating a new fishery, *C. argus* has not become a preferred target species in Hawaii, because of concern about ciguatera fish poisoning. In Hawaii and elsewhere, *C. argus* is known to prey on small fishes, including the recently settled and older juveniles of many species; consequently there are concerns that the current abundance of *C. argus* may have had detrimental impacts on local reef fish assemblages (Dierking et al. 2009). In Hawaii, the diet of *C. argus* is composed of fishes across a wide range of taxa, including acanthurids, holocentrids, and chaetodontids among many others (Dierking et al. 2009). A study found that length, weight, and body condition were significantly greater for *C. argus* in Hawaii than in a native South Pacific population, indicating competitive release (Meyer & Dierking 2011).

Knowledge of the biology of *C. argus* is limited, but available information includes demographics, movement and population genetics. Investigators studied *C. argus* demographics in the GBR and Seychelles found that longevity and average age were lower at high densities possibly in response to density-dependence (Pears 2005). Movement studies of *C. argus* found that this species shows high site fidelity, spending the majority of its time in core-use areas with a home range size of approximately 1200 m² (Shpigel & Fishelson 1989, Meyer 2008). Further, ongoing work on the population structure of *C. argus* has found that *C. argus* is panmictic across the Hawaiian archipelago indicating high gene flow and thus little evidence for phenotypic differences pre-settlement (M.R. Gaither, unpublished).

Currently, *C. argus* is gaining notoriety among some elements of the public as a harmful invasive species, and community-based efforts to control these populations are occurring at the local level. This effort is largely driven by the public, where individuals in the community are organizing spear-fishing tournaments around the state in an attempt to control the species. Further information on the population dynamics will allow for more accurate evaluations of the outcomes of removal efforts. In particular, information that would provide insight into the demographics of this invasive would enable population modeling and therefore predictive power for appropriate levels of removal or control.

CHAPTER 2

Demographic variability in an introduced Hawaiian reef fish

Introduction

Understanding scale in reef fish studies is important for a thorough understanding of population dynamics (Caselle & Warner 1996, Sale 2002, Palumbi 2004, Cowen et al. 2006). In general, coral reef fishes exist as meta-populations of relatively sedentary adults connected by larval dispersal; spatially segregated populations thus are subject to varying physical and biological conditions (Sale 1998). Previous studies have demonstrated that the biology of coral reef fishes can be highly variable in space (Caselle & Warner 1996, Meekan et al. 2001, Friedlander & DeMartini 2002, DeMartini et al. 2008, Pittman & Brown 2011), due to several mechanisms related to the dynamic, patchy environment of coral reef systems. For example, variability in the demography of coral reef fishes has been documented in several studies from the Caribbean and Great Barrier Reef (GBR) at multiple spatial scales (Gust et al. 2002, Choat et al. 2003, Williams et al. 2003, Robertson et al. 2005a). These studies describe the possible extent of geographic variation in reef fish population dynamics and highlight the need for understanding mechanisms driving the variability.

A range of factors related to variation in demography of both temperate and tropical fishes have been investigated including environmental conditions (Robertson et al. 2005a, Ruttenberg et al. 2005, Trip et al. 2008), ecological processes (Gust et al. 2002, Williams et al. 2003, Pears 2005), and anthropogenic impacts such as fishing (Trip et al. 2008, Taylor & McIlwain 2010, Caselle 2011). Together, these observations indicate that coral reef fishes exist as spatial populations with geographically varying phenotypic traits. Measuring demographic patterns at multiple spatial scales is therefore relevant and needed in order to understand how coral reef fish populations are structured and how they should be properly managed (Williams et al. 2003, Kritzer & Davies 2005).

Evidence that growth parameters of fishes vary by location has implications for both fisheries management and marine spatial planning. First, the application of stock assessment models needs to be grounded in a better understanding of what comprises a stock, and depends on the ability to distinguish between stocks. Most stock assessment methods assume fish populations are closed and homogeneous in life history characteristics (Beverton & Holt 1957). These assumptions are inappropriate given the growing body of research on the spatial variation in species life history parameters. Secondly, predicting a species response to protection and the appropriate tools for management will be dependent on the spatial scale at which variability in the life history of the species is considered. This is particularly true if differences in demography indicate the isolation of populations in question. Spatially varying population dynamics also violate assumptions of meta-population theory which are the basis of many spatial management practices (Kritzer & Davies 2005).

Sound management requires a better understanding of habitat requirements in the life histories of reef fishes, and the extent to which the relationship influences population dynamics at broader spatial scales (Friedlander et al. 2007). In Hawaii, diverse geological and oceanographic conditions exist to form distinct habitats along coastlines among and within islands (Grigg 1998). Habitat diversity, quality and extent are important determinants of fish assemblage structure on coral reefs in Hawaii (Friedlander & Parrish 1998, Friedlander et al. 2003). Studying variability in growth of fishes across the Hawaiian archipelago therefore provides an opportunity to assess the physical and biological process shaping fish populations.

The peacock grouper *Cephalopholis argus* (known in Hawaii by its Tahitian name “roi”) family Serranidae, is an introduced fish that has become well established in Hawaiian waters. *C. argus* was introduced to Oahu and Hawaii island in the Hawaiian Archipelago from the South Pacific during the 1950s as part of a program to enhance nearshore fisheries by supplementing the depauperate native Hawaiian grouper and snapper fauna (Randall 1987). (Dierking et al. 2009). Despite hopes of creating a new fishery, *C. argus* has not become a preferred target species in Hawaii, because of concern about ciguatera

fish poisoning. In recent years, *C. argus* gained notoriety among some elements of the public as a harmful invasive species, and community-based efforts to control these populations are occurring at the local level.

The community-based removal of this species provided a rare opportunity to comprehensively collect a coral reef fish across and within an archipelago. Not only is this an opportunity to provide insight into the population dynamics of an invasive species, but also provides for analysis, in a more general context, that will inform population models for coral reef fishes. The magnitude of collections enables comparisons across various spatial scales and allowed investigations into the relative status of populations across the state.

In this study we investigate the life history traits of this introduced grouper at 10 distinct locations in the Hawaiian archipelago. A spatially explicit sampling design was used in order to address the magnitude of variation among and within locations. We conduct an age-based demographic analysis and describe patterns of size and age, longevity, and growth at multiple locations. This study evaluates the importance of variability in demographic parameters in a coral reef fish for stock assessments. Further, this is a step towards understanding the variation of demographic parameters that occurs at multiple spatial scales and how this relates to the ecological role of a predatory fish species.

Methods

Study organism and study area

Cephalopholis argus were collected opportunistically throughout the main Hawaiian Islands from March 2008 to December 2011. Frozen specimens were donated to the University of Hawaii by community members, along with information on the location and date of capture. Ten locations across the Hawaiian Islands were chosen for comparison based on a minimum available sample size of 30, with additional consideration that the size range of the respective population was represented (Figure 1, Table 1). Three locations were selected on the island of Hawaii, one on the windward

coast in and around Hilo Bay, and two on the Kona coast. Sampling was concentrated at one location on Maui (Olowalu) where the most intensive sampling has occurred. On Oahu, samples were pooled along each of the four major coastlines. Two locations were sampled on Kauai, one on the north coast in and around Hanalei Bay, and one on the south coast near Poipu (Figure 1).

Dissections and otolith preparation

Each frozen specimen was thawed, blotted dry, and weighed to the nearest gram. Total length (TL), standard length (SL), gape (width between the widest two points of the mouth) and height (distance from the base of the dorsal fin to the base of the pectoral girdle) were measured to the nearest millimeter. Sagittal otoliths were extracted by removing the top of the cranium of each specimen with a bone saw. Otoliths were carefully removed, cleaned in water, rinsed in 95% ethanol, and air dried.

Once dry, otoliths were weighed (to 0.01). Damaged otoliths were not used for further analysis. Both the right and the left otolith were measured along the longest axis (0.1 mm) using digital calipers.

Otolith processing followed methods described by Choat *et. al.* (2003). The left otolith was used for ageing, unless missing or damaged. The sagitta was mounted in thermoplastic glue (CrystalBond) on the edge of a glass microscopy slide and ground down to the core with 800-1200 grit sandpaper on a rotary grinder. The thermoplastic glue was then reheated and the otolith was remounted flush on the slide on the ground side. The opposite side of the otolith was then ground until a suitable thickness was reached. The resultant thin slice was polished by hand with 30-3 micron polishing paper and viewed with a transmitted light microscope under 10-100x magnification.

One pair of sequential light and dark bands was assumed to form once-yearly; these were counted by one observer on three different occasions. In the case where counts were <10% different, either the median or younger age was consistently used for analysis. In the case of a disputed age (>10%), the annuli were recounted, and if consensus was not

made, the otolith was excluded from analysis. Otolith weight was regressed with age, and any extreme outliers (>4 S.E.) were given further attention. Otoliths from individuals with estimated age 1 year were re-analyzed for daily rings to validate the yearly increments and provide age estimates in portions of years. Pears (2005) conducted initial age validation experiments for *C. argus* by marking wild-caught individuals with oxytetracycline, recapturing 4 fish that had been at liberty for 6 months and subsequently examining the width of marginal material deposited on the outer edge since marking. She found that the marking was generally consistent with annual period formation and there was a strong correlation between otolith weight and number of increments, indicating that otoliths accrete calcium carbonate throughout the life of the fish (Choat & Axe 1996, Fowler 2009).

Demographic parameter estimation

Weight-length: The relationship between length and weight for *C. argus* was estimated using non-linear regression for each location. Data were fit to an allometric length-weight function:

$$W = aL^b \tag{1}$$

where W is total weight, L is total length, b is the Allometric growth parameter and a is a scaling constant. Analysis of covariance (ANCOVA) was used to compare the relationship between location, with $\log_{10}(W)$ as a response variable and $\log_{10}(TL)$ as a covariate (Jennings et al. 2001).

Growth: Growth curves were generated using size-at-age data generated from the otoliths at each location using three candidate growth models. Traditionally, the von Bertalanffy growth function (VBGF) is used to describe growth in fishes (Ricker 1975).

$$L(t) = L_{\infty}(1 - e^{(-K(t-t_0)}) \tag{2}$$

where $L(t)$ is length at age t , L_∞ is mean asymptotic length, K is the rate of decline in growth rate with increasing size, t is the age in years, and t_0 is a theoretical age at which length is 0.

While VBGF parameters have been used extensively in fisheries, recent work has suggested that the interpretations of these parameters are inappropriate for statistical comparison, and thus the re-parameterized VBGF (rVBGF) has been proposed (Francis 1988, Trip et al. 2008). The re-parameterized equation is as follows:

$$L(t) = L(\tau) + \frac{(L(\mu) - L(\tau)) \left[1 - r^2 \frac{t - \tau}{\mu - \tau} \right]}{1 - r^2} \quad (3)$$

where, $r = \frac{L(\mu) - L(\omega)}{L(\omega) - L(\tau)}$ and $L(t)$ is the average size-at age t to be predicted by the model, provided that $L(\tau) < L(\omega) < L(\mu)$ and $(L(\mu) - L(\omega)) \neq (L(\omega) - L(\tau))$. Parameters $L(\tau)$, $L(\omega)$, and $L(\mu)$ are estimated from the average body size at three arbitrary ages τ , ω , and μ . Values for τ and μ were chosen to represent points during the slower growth phase and the early rapid phase, in this case $\tau=12$ years and $\mu=1$ year.

An important consideration when modeling growth is the inclusion of small-young individuals in order to accurately represent the initial rapid growth phase of the curve. Several species of fishes require curves that accommodate two phases of growth due to an ontogenetic shift from juvenile to adult habitat (Larkin 2011). To explore this possibility for *C. argus*, a double von Bertalanffy model was fit to data from West Maui. West Maui was chosen because it had the greatest overall sample size, and greatest range of small individuals. The model, which accounts for rapid growth at early ages while also describing slowing growth at older ages, jointly fits two curves and combines them at a transition age (t_x) defined as:

$$L(t) = \begin{cases} L_{\infty}(1 - e^{(-K_1(t-t_{01}))}) & \text{if } t < t_x \\ L_{\infty}(1 - e^{(-K_2(t-t_{02}))}) & \text{if } t > t_x \end{cases}$$

$$t_x = (K_2 t_{02} - K_1 t_{01}) / (K_2 - K_1) \quad (4)$$

Growth model parameters were fit by minimizing the negative log-likelihood given a probability density function with a normal distribution for the traditional model, and a Poisson distribution for the reparameterized model (Kimura 1980, Bolker 2008, Trip et al. 2008). Akaike's Information Criterion (AIC) (Akaike 1981) were calculated for both models where the model with the smallest AIC value was selected as the best among those tested.

Longevity: Longevity (t_{max}) was calculated as the mean age of the oldest 20% of individuals for each location (Gust et al. 2002). Differences in longevity across locations were evaluated with a one-way ANOVA with location as a factor. The average maximum length was calculated as the mean total length of the oldest 20% of individuals.

Comparison of demographic parameters

To compare growth curves among locations data were truncated to include only those ages after the transition age (t_x) found in equation [4]. Thus, the curve comparisons represent freely-fitted models of post-juvenile growth. Likelihood ratio tests were used to compare growth curves and parameter estimates between each of the locations (Kimura 1980). Additionally, 95% confidence regions around maximum likelihood estimates of L_{∞} and K were constructed following Kimura (1980). All analyses were conducted using R v.2.13 (R Development Core Team 2009).

Results

A total of 1,136 *C. argus* were collected across the main Hawaiian Islands, of which 592 were included in size at age analyses. Individuals ranged in size from 14.4 cm to 49.6 cm

TL (total length) and in age from 228 days to 26 years (Table 1). Sampling effort varied across locations, with the greatest effort at West Maui. Despite this, distributions of fish length for each sampling unit were similar, with minimum sizes by location ranging between 14.4 cm and 22.4 cm. The largest individual captured was 49.6 cm, 10 cm smaller than the reported maximum length (Randall 1996).

A strong weight-at-length relationship was observed, with no difference in slopes among locations (1-way ANCOVA, $F_{1,19} = 985.2$, $p = 0.13$; Table 2); intercepts differed ($p < 0.001$), however. This indicates that the shape of the relationship is the same but the weight of an individual at a given length differs among locations. At Hilo, the southernmost site, fish weighed less at a given length than at any other location ($p < 0.001$). Weight-at-length relationships for locations on Oahu did not differ (Table 2). Allometric weight-at-length relationships for fish from each location and all locations pooled are provided in Table 2 and Figure 2.

Otolith analysis satisfied Fowler's (2009) criteria for providing estimates of fish age in years: (1) otolith displayed internal structure of increments, (2) increments were regular and on a determined time scale and (3) otoliths grew throughout the life of the fish (following validation by Pears (2005)). Otolith weight was a good predictor of age ($r^2 = 0.83$, $F_{1,365} = 1786.1$, $p < 0.001$) with slopes of this relationship varying by location ($F_{10,337} = 192.1$, $p < 0.001$). The relationship between age and length was consistent across locations with fast initial growth followed by continued slowed growth.

Results from West Maui support the observation of fast initial growth in this species, but data from the first year was lacking at from other locations (Figure 4). The double-von Bertalanffy model was fit to West Maui data and the transition age was estimated to be 0.95 years with K equal to 0.70 and 0.12 before and after the transition age, respectively. *C. argus* juveniles are therefore growing very rapidly during their first months of life and after year 1 growth is more gradual (Figure 4). Given these results, comparisons among locations included individuals at least 1 year and older to account for variable sampling

of small, young fishes. The parameters of the growth functions therefore represent the growth trajectory of post-juvenile fishes.

Variation in the relationship between size and age was apparent across locations (Table 1, Figures 3-5). These differences were reflected in measures of longevity as well as traditional and reparameterized von Bertalanffy parameters. Longevity (mean age of oldest 20% of fish) differed among islands and locations within islands (Table 3). This pattern was also reflected in analysis of size data from individuals in the top 20% age groups for each location (“average maximum length”, Table 3). Longevity and maximum age were greatest at West Maui (Table 1,3). Additionally, longevity was greater for individuals at West Maui, North Kona and Hilo compared to locations on Oahu and Kauai (ANOVA, $F_{9,117}=5.89$, $p<0.001$).

Several combinations of location specific differences were observed. West Maui and North Kona separated from all other locations, reaching a smaller asymptotic length at a faster rate (Figure 3, 5), at were larger at 5 years of age $L(\omega)$ (rVBGF; Figure 7). Truncated age distributions were observed at locations on Kauai and Oahu, with disproportionately fewer individuals older than 15 years of age compared to Maui and Hawaii resulting in large confidence intervals on estimates for L_{∞} for these locations (Figures 5,6).

VBGF and rVBGF varied within islands. All three Hawaii Island locations differed from one another, with the locations on the north-leeward coast (North Kona) having the largest estimates of K and a similar estimate of L_{∞} as South Kona. Hilo, off the windward side of Hawaii Island differed from those at both other locations and had the largest L_{∞} estimate, indicating that fish are attaining a greater length on the windward coast. Four locations were sampled within Oahu with North Oahu statistically differing from other Oahu locations (Table 4, Figure 3,5). Confidence intervals for South Oahu were large because of small sample sizes and larger variance than other locations; parameter estimates for this location may not reflect the biology of fish in this location. West and East Oahu did not differ statistically from each other. Two locations (north, south) were

sampled within Kauai; estimates of L_{∞} were greater for South Kauai and confidence intervals did not overlap (Figure 3,5).

Estimates for $L(\omega)$ increased by location from north to south, indicating that the inflection point at which growth slows decreased with latitude (Figure 7). Estimates of $L(\tau)$, which represents the theoretical size at which fish are 12 years old, were larger at the southern locations, with the exception of South Kona, but this might be an artifact of a small sample size.

Discussion

This study assessed spatial differences in several life history characteristics of an invasive reef fish across a range of locations in the Hawaiian Archipelago. We were able to sample across a broad geographic area due to a community-based effort to remove an invasive species. The extent of the sampling may have captured an interaction between cross-scale mechanisms as growth of *C. argus* varied by location both within and among islands. Longevity estimates were greater at locations on the southern two islands versus the northern islands. Similarly, individuals were smaller at a given age and the point at which growth slowed was later for the northern vs. southern sites.

Our findings provide data of fundamental importance that are necessary for illustrating that robust fishery models must incorporate life history data taken from distant and/or spatially limited locations. This means that typical stock production models that rely on life history information would not be accounting for this variability if only a single location were to be used. Although several north to south patterns existed, there were no indications of a simple linear latitudinal gradient in our results. Thus, mechanisms driving spatial variability in growth rates may not be simply related to factors correlated with latitude, but instead may be a combination of drivers occurring across spatial scales. Questions can therefore be raised about the mechanisms driving spatial variability in

growth rates such as environmental conditions, ecological processes, and anthropogenic impacts.

Other studies have examined variation in demography of coral reef fishes and attributed patterns to large scale temperature differences (Choat et al. 2003, Trip et al. 2008). While temperature was not explicitly tested here, it could be a factor contributing to the observed differences in growth among locations. Trip *et. al.* (2008) found a negative relationship between longevity and mean sea surface temperature in an analysis of surgeonfish age and growth across the Pacific Basin. Our observations of shorter lived *C. argus* at the northernmost locations and islands, where mean annual sea surface temperatures are lowest (Friedlander et al. 2008) are inconsistent with those of Trip *et al.* (2008). However, *C. argus* were smaller at a given age and the point at which growth slowed occurred later for fish from northern versus southern sites. The latter pattern might suggest a latitudinal effect, but could also be explained by factors operating at finer spatial scales (e.g. within individual reefs).

Evidence for within-ocean basin variability provides only one end of the scale spectrum. In fact, the same study where longevity differences were found concluded that patterns in growth varied at the scale of sampling locations within an overall ocean basin (Trip et al. 2008). Further, a study on the Great Barrier Reef investigated differences in growth among samples from tens-of-kilometers apart and found large differences. The conclusion was that small scale variability in resource availability and exposure to wind and waves may have driven the differences (Gust et al. 2002). Here, locations were compared at an intermediate spatial scale with locations representing reefs within an island separated by 30-80 km, and locations between islands separated by one to several hundred kilometers. Therefore, the extent of sampling in this study may be capturing an interaction between cross-scale mechanisms. Each location sampled is unique due to the complex physiography of the Hawaiian Islands which are geographically isolated and exposed to large scale ocean winds and currents combining to form unique flow patterns and habitats along each of the coasts (Friedlander et al. 2008).

Differences in habitat composition and complexity may influence the patterns of growth in fishes through several mechanisms. *C. argus* is an ambush predator, meaning that in order to feed this species utilizes complex physical structures to conceal itself while waiting for prey to come within attack distance. This behavior requires suitable habitat as the availability of prey resources have been shown to increase with both habitat composition and complexity (Ruttenberg et al. 2005, Shibuno et al. 2008). Therefore, it is not surprising that *C. argus* is typically found in coral rich habitats and feeds primarily on small, reef-associated fishes (Meyer & Dierking 2011). By extension it is expected that fishes will be more robust, grow to larger sizes, and live to greater ages when there are more resources and/or preferable habitats. Patterns observed in this study may be a reflection of this mechanism, which was not tested directly, but may explain variation from the predictions based on latitude alone.

Evidence from fisheries independent surveys suggest that populations of *C. argus* were not well established in Hawaii before the late 1980's. Populations started to increase on Hawaii Island and Maui by 1990 (*B. Walsh, I. Williams unpublished data*). Oahu and Kauai on the other hand did not see this increase until the mid-1990s. The collections for this study occurred from 2008-2012, suggesting that the oldest fish observed on Oahu and Kauai may represent some of the first successful year classes at these islands. This observation is supported by data from collections from Oahu in 2003, in which no fish older than 15 years of age were encountered (*J. Dierking, unpublished data*). This change in the demographic profile could lead to differences in how the northern populations are structured versus the southern populations which were established earlier.

Density dependent factors may be playing a stronger role on all cohorts in the southern locations, whereas the cohorts that initially colonized the northern locations may have been free from competition. Density dependent factors have been shown to influence differences *C. argus* demographics among and within locations in the GBR and Seychelles (Pears 2005). Areas with higher densities were associated with decreased maximum size and longevity compared to areas with low densities. Detailed fisheries

independent surveys stratified by habitat are needed to properly address whether density-dependent factors are important in Hawaii.

In coral reef fishes diverse patterns of life history have been recognized and there are several important considerations when modeling growth (Choat & Robertson 2002). Specifically, the form of the growth curve, and importance of adequately describing the early stages of the curve are important considerations (Berumen 2005). Low sampling of juveniles or a distinct form of growth for juveniles can lead to greater variability in the parameter estimations (Kritzer et al. 2001). Thus, many studies of reef fishes have constrained the intercept of the curve to limit the potential range of values for the other parameters and provide additional data that are missing from the samples (Kritzer et al. 2001). But, this approach assumes that this constraint, by improving the fit, will accurately describe all portions of the curve. Depending on the shape of the growth curve for a given species constraints on the intercept may not lead to biologically meaningful parameter estimates. For *C. argus* in the Hawaiian Islands, although the most rapid growth is in the first year and growth slows appreciably during the subsequent few years, growth does not continue to decelerate markedly thereafter. These factors create problems for parameterizing the von Bertalanffy curve as the two major parameters, L_{∞} and K , are correlated. Constraining the intercept therefore results in an underestimation of size-at-age for the older ages. For these reasons a biphasic growth curve was explored for West Maui. Results from the biphasic model suggest that growth during the first year needs to be modeled differently than the latter portion of the curve. With this as evidence, models outcomes for the other locations represent only the second portion of the growth curve and can be interpreted as patterns of growth for the post-juvenile phase.

The lack of individuals less than one year of age for most of the study locations could be a consequence of sampling bias, but more likely due to the rapid growth of this species in the first months of life. Sampling occurred year round, but sporadically. All sampling was done by spear-fishermen in habitats ranging from shore to depths limited by free-diving. Whereas fisheries-dependent sampling is usually biased towards large individuals, this was not the case here. The goal of the fishing effort was for removal of an invasive

species, and therefore any individual seen was generally targeted in the catch. If a fishing event did not occur within a short period of time after settlement small individuals may not have been encountered. The recruitment period of this species is unknown, but is thought to occur in the first half of the calendar year. Increased sampling during this period might provide samples of the smallest size class.

Alternatively, the lack of individuals in our collection less than 15 cm could be explained by an ontogenetic habitat shift. Theory suggests that energy is primarily allocated towards growth initially to achieve a large enough size to avoid predation (Hixon 1991, Dahlgren & Eggleston 2000). Once an optimal size is reached energy can be re-allocated to fat storage and reproduction, whereby slowing of growth would coincide with the onset of maturity. Several studies have documented rapid initial growth of groupers and have found that this phase usually occurs prior to an ontogenetic shift in habitat (Beets & Hixon 1994, Ross & Moser 1995, Manickchand-Heileman & Phillip 2000). For gag (*Mycteroperca microlepis*) in the Atlantic Ocean, juveniles settle to seagrass beds in the spring and reach a mean size of 13.2 cm by September of the same year. Subsequent to the rapid initial growth, juveniles move to hard bottom reefs during mid-late autumn (Ross & Moser 1995). A similar pattern may be occurring with *C. argus* in Hawaii as anecdotal evidence suggests that this species recruits to intertidal habitats. Recruitment surveys would provide a greater understanding of the timing and contribution of recruitment patterns to the population dynamics of this species in Hawaii.

Beyond general fisheries management, this project is focused on the biology of an introduced coral reef fish species and has the potential to inform its management. The increasing involvement of fisherman in *C. argus* removal from local reefs underpins the importance of this issue to the local community. The close involvement of scientists and fishers in this process could lead to stronger and more successful management actions because the fisherman will be able to have more confidence in the results. This project is not only strengthened by this, but is possible due to the large scale efforts to remove this fish from the reefs of Hawaii.

Understanding the level and life history variation of this species is only a first step. Future work should focus on mechanisms driving this demographic variability. The Hawaiian Archipelago is an ideal place to conduct such a study owing to its unique physical environment and clear biogeographic gradients (Friedlander et al. 2010). In addition to the growth variation characterized in this study, future work is needed on recruitment, reproduction, and mortality to make predictions about population dynamics of *C. argus* in the Hawaiian Islands. These additional metrics will allow for calculation of population turnover and reproductive output which will be the key to minimizing invasive populations in the Main Hawaiian Islands and preventing invasion of the Northwestern Hawaiian Islands.

Table 2.1. Sample locations and demographic parameter estimates for *Cephalopholis argus* in the main Hawaiian Islands sampled across four islands and 10 locations. Collected sample size (total available), aged sample size (subset used in age analysis), size range of total length (TL) in cm, von Bertalanffy (VBGF) parameters (\pm S.E.), reparameterized (rVBGF) parameters, longevity and model selection results are presented and summarized for all samples combined. T_{\max} is the mean of the oldest 20% of individuals. AIC is the Aikake Information Criterion for each model.

Location		n		Size range (TL, cm)	VBGF parameters			rVBGF parameters			Longevity		AIC VBGF	AIC rVBGF
Island	Location	Collected	Aged		L_{∞}	K	t_0	L(2)	L(8)	L(14)	Tmax (yr)	Max age (yr)		
Kauai	North Kauai	52	51	18.5 - 46.0	52.4 (9.2)	0.055 (0.03)	-9.3	24.1	32.6	38.0	16.1	22	252.1	502.7
	South Kauai	60	54	20.2 - 48.1	67.8 (20.2)	0.035 (0.02)	-10.5	24.2	32.7	39.4	15.2	24	264.9	534.6
Oahu	North Oahu	113	54	20.7 - 46.7	68.9 (21.4)	0.035 (0.02)	-10.8	25.1	33.5	40.3	13.3	21	250.67	510.3
	West Oahu	156	62	22.3 - 45.0	53.1 (6.9)	0.066 (0.02)	-7.3	24.4	33.7	40.0	14.8	21	296.5	596.6
	East Oahu	75	66	21.8 - 49.0	48.7 (3.8)	0.085 (0.02)	-6.0	23.8	33.9	39.7	16.5	22	304.6	608.4
	South Oahu	34	30	17.5 - 41.1	43.1 (12.2)	0.113 (0.12)	-6.1	25.6	34.4	38.0	10.2	13	174.1	381.3
Maui	West Maui	349	107	14.4 - 48.7	45.5 (1.1)	0.122 (0.01)	-4.6	23.1	35.1	40.5	19.2	25	506.7	1024.4
Hawaii	North Kona	204	78	15.8 - 49.0	47.9 (9.2)	0.118 (0.02)	-3.4	22.5	35.5	41.8	17.4	24	427.0	907.1
	South Kona	51	47	18.0 - 44.5	50.5 (11.0)	0.061 (0.04)	-8.4	23.3	32.1	37.6	15.2	20	242.9	487.9
	Hilo	42	41	23.4 - 49.6	72.0 (23.2)	0.038 (0.03)	-8.5	24.1	33.8	41.7	17.8	22	205.0	404.2
	Total	1136	590	14.4 - 49.6	50.6 (1.6)	0.075 (0.01)	-6.5	23.9	33.8	39.9	16.7	25	2972.1	6127.2

Table 2.2. Allometric length-weight relationship by location and for all samples combined including size range in grams for each sample. Letter groups are from pos-hoc student's t-test of ANCOVA results on the log-log relationship with contrasting letters indicating significantly different intercepts.

Island	Location	<i>a</i>	<i>b</i>	Min-Max W (g)	ANCOVA group
Kauai	North Kauai	0.006	3.335	107 - 1983	C D
	South Kauai	0.012	3.134	137 - 2354	C
Oahu	North Oahu	0.017	3.032	126.1 - 1865.2	C D
	West Oahu	0.02	2.991	194.6 - 1865.7	D
	East Oahu	0.022	2.973	165.9 - 2239.9	D
	South Oahu	0.011	3.168	283.2 - 1411.7	C D
Maui	West Maui	0.027	2.903	48.54 - 3500.2	C
Hawaii	North Kona	0.017	3.015	68 - 2069.5	B
	South Kona	0.001	3.808	127.5 - 1492	D
	Hilo	0.014	3.026	160 - 1940	A
Total		0.02 (0.00)	2.99 (0.05)	48.5 - 3500.2	

Effect	SS	MS	df	F	p
Location	2.99	13.23	9	24.76	<0.0001
logTL	130.61		1	9726.87	<0.0001
Location*logTL	0.19		9	1.533	0.1317
Residual	11.37	0.0134	847		

Table 2.3. Results of nested ANOVA comparing longevity and average maximum length based on age and size data from the oldest 20% of individuals.

Variable	Effect	SS	MS	df	F	p
Avg. max Length	Intercept	561.93	62.44	9	5.89	<0.001
	Island	223.78		3	7.04	<0.001
	Location[Island]	364.57		6	5.74	<0.001
	Residual	1143.94	10.59	108		
Longevity	Intercept	595.44	66.16	9	5.75	<0.001
	Island	452.96		3	13.14	<0.001
	Location[Island]	216.25		6	216.25	0.007
	Residual	1241.11	11.49	108		

Table 2.4. Results of likelihood ratio tests comparing estimates of VBGF by location.

Comparison	df	chi 2	p	
West Maui vs. South Kona	3	32.53	0.000	*
North Kona vs. South Kona	3	26.11	0.000	*
North Kauai vs. West Maui	3	23.87	0.000	*
North Kauai vs. North Kona	3	21.37	0.000	*
Hilo vs. North Kauai	3	18.88	0.000	*
Hilo vs. South Kona	3	18.42	0.000	*
West Maui vs. South Kauai	3	16.79	0.001	*
Hilo vs. West Maui	3	16.74	0.001	*
North Kona vs. South Kauai	3	13.89	0.003	*
North Oahu vs. West Maui	3	12.25	0.007	*
North Oahu vs. South Kona	3	10.63	0.014	*
South Kona vs. West Oahu	3	10.60	0.014	*
North Kona vs. North Oahu	3	9.81	0.020	*
East Oahu vs. Hilo	3	9.61	0.022	*
East Oahu vs. South Kona	3	8.99	0.029	*
North Kauai vs. North Oahu	3	8.95	0.030	*
North Kauai vs. West Oahu	3	7.62	0.055	
Hilo vs. South Kauai	3	7.12	0.068	
North Kona vs. West Oahu	3	7.05	0.070	
East Oahu vs. North Kona	3	6.99	0.072	
East Oahu vs. North Kauai	3	6.16	0.104	
West Maui vs. West Oahu	3	6.10	0.107	
South Kona vs. South Oahu	3	5.99	0.112	
Hilo vs. North Kona	3	5.89	0.117	
North Kauai vs. South Oahu	3	5.82	0.121	
South Kauai vs. South Oahu	3	5.65	0.130	
West Maui vs. South Oahu	3	5.49	0.139	
North Kona vs. South Oahu	3	5.30	0.151	
Hilo vs. West Oahu	3	5.11	0.164	
North Kona vs. West Maui	3	4.78	0.189	
South Kauai vs. South Kona	3	4.16	0.245	
East Oahu vs. West Maui	3	4.00	0.261	
East Oahu vs. South Oahu	3	3.38	0.337	
East Oahu vs. South Kauai	3	3.33	0.343	
North Kauai vs. South Kauai	3	3.27	0.352	
North Oahu vs. South Kauai	3	3.06	0.382	
South Oahu vs. West Oahu	3	2.95	0.399	
Hilo vs. South Oahu	3	2.94	0.401	
East Oahu vs. North Oahu	3	2.90	0.407	
Hilo vs. North Oahu	3	2.90	0.407	
South Kauai vs. West Oahu	3	2.87	0.412	
North Oahu vs. South Oahu	3	2.26	0.520	
North Oahu vs. West Oahu	3	1.11	0.775	
East Oahu vs. West Oahu	3	0.47	0.925	
North Kauai vs. South Kona	3	0.34	0.952	

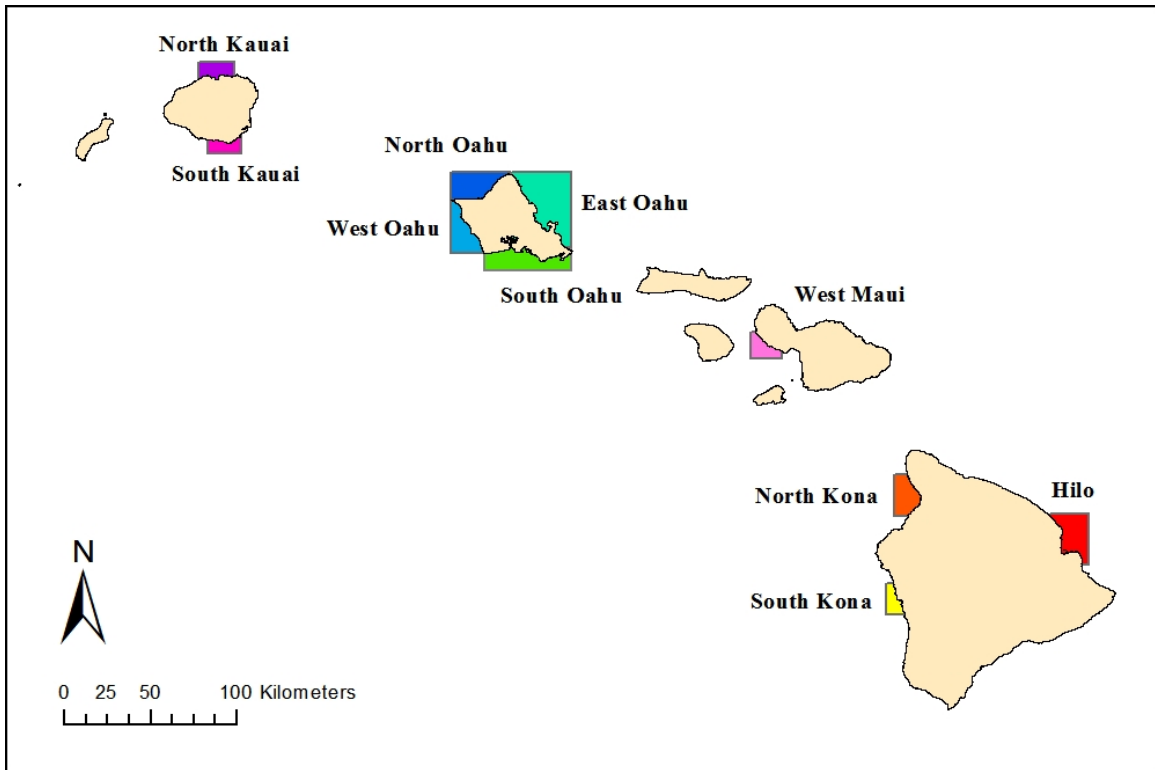


Figure 2.1. Map of sampling locations, boxes indicate general sampling areas but collections occurred nearshore to depths limited by free-diving.

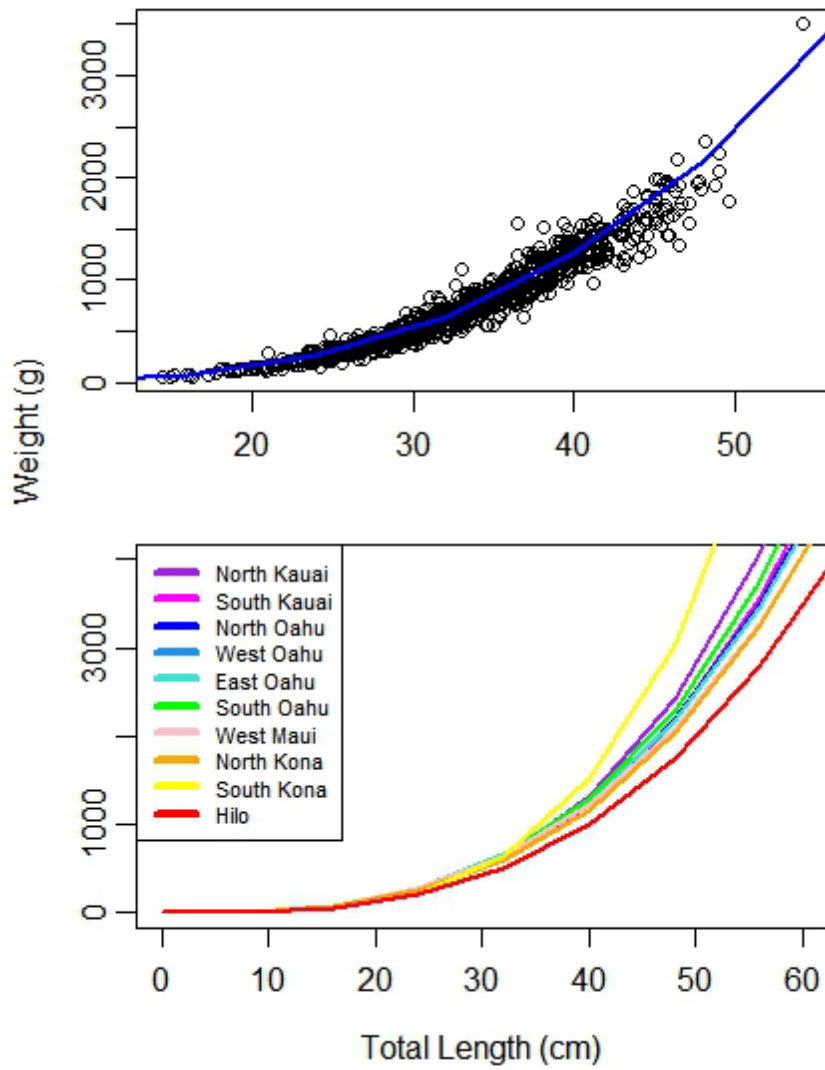


Figure 2.2. Allometric weight-length relationships for (a) all samples combined, and (b) by location

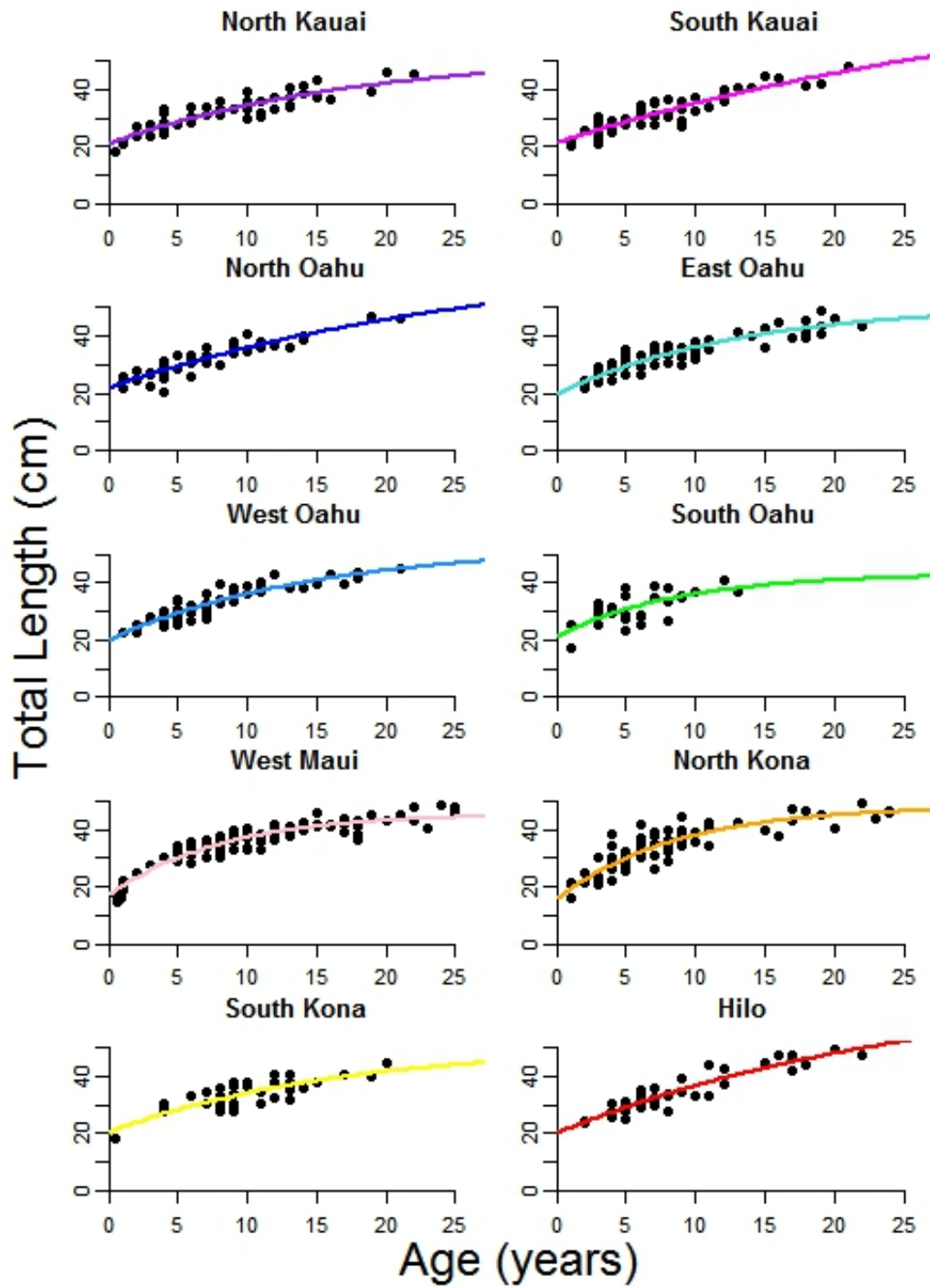


Figure 2.3. Size-at-age data for *C. argus* at 10 locations in Hawaii with best-fit curves for von Bertalanffy model with unconstrained parameters.

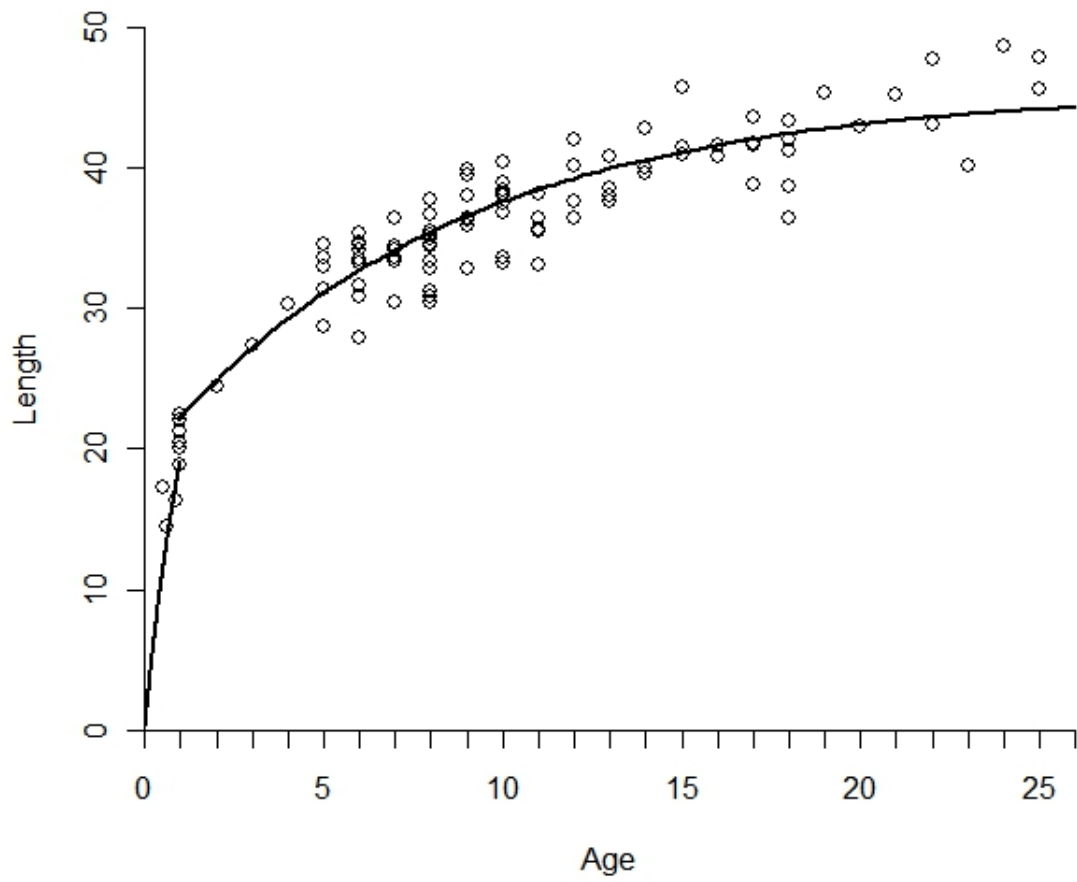


Figure 2.4. Double von Bertalanffy model for *C. argus* at West Maui. Point where lines do not connect represents transition age (t_p).

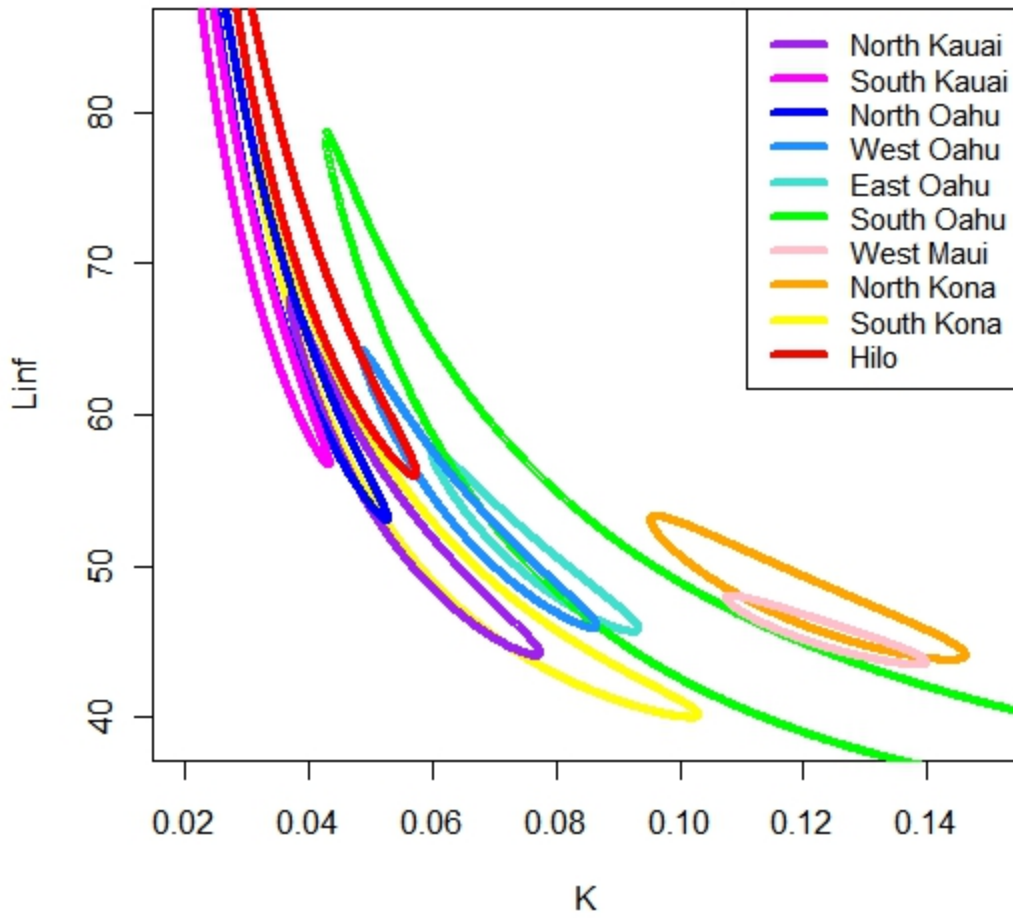


Figure 2.5. Plots of 95% confidence ellipses for parameters L_∞ and k by location.

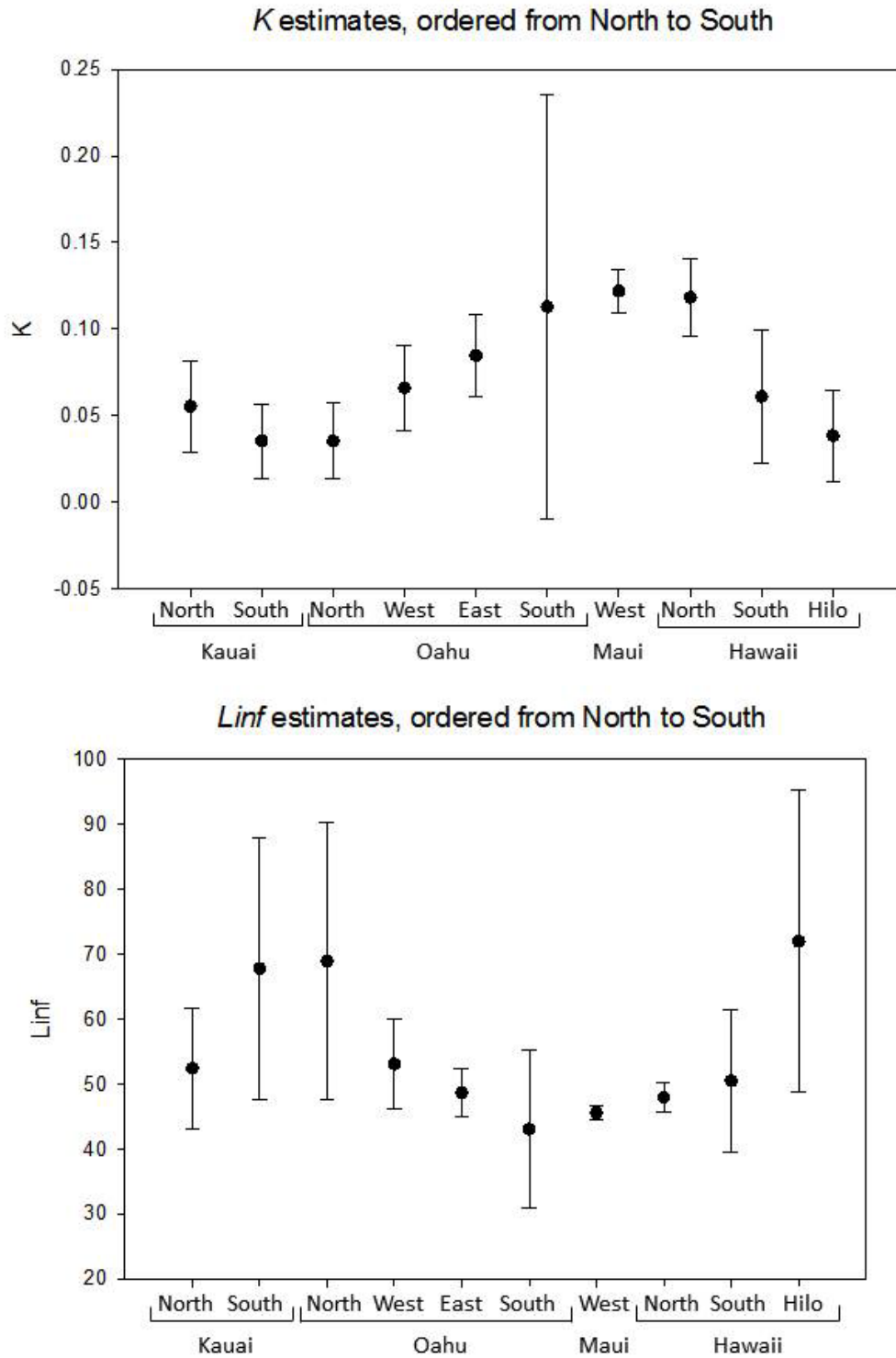


Figure 2.6. Parameter estimates \pm S.E. for L_∞ and k by location with locations ordered from north to south.

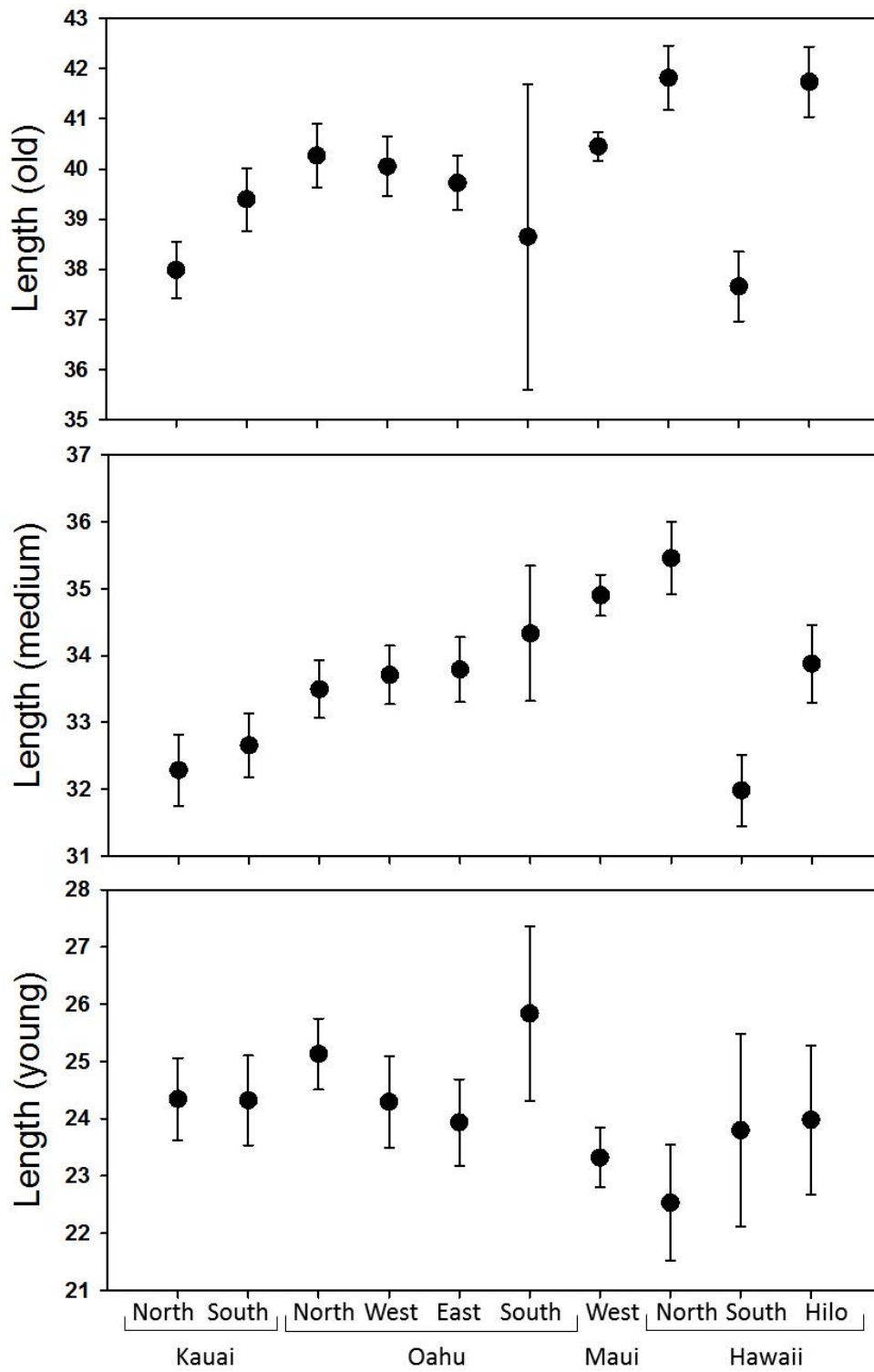


Figure 2.7. Parameter estimates \pm S.E. for τ [length(old)], ω [length(medium)] and μ [length(young)] by location with locations ordered from north to south.

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