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Demographic patterns in coral reef fishes: Biogeographic trends and fishing effects

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For the degree of

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In
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◆

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I dedicate this dissertation to my parents from whom I inherited my passion for nature.

JAMES COOK UNIVERSITY

Demographic patterns in coral reef fishes: Biogeographic trends and fishing effects

ABSTRACT

The present study is a multi-scale study which investigates the demographic plasticity within and between geographically distinct reef fishes of the families Lutjanidae (Snappers), Serranidae (groupers) and Labridae (hogfish). This also investigates how fishing alters fish demography and demographic shifts associated with introduction to new habitats. These were determined by analyzing age-based demographic parameters, biological and ecological information as a basis for management and conservation. Demographic characteristics such as size, age, longevity, mortality rates and broad-scale spatial patterns in growth were described in this comparative study. Present study will provide unique contribution to general life history theory by focusing on number of species and large scale environmental gradients extending latitudinally and longitudinally across and within Caribbean, Pacific and Indian oceans.

The potential shifts in demography of *Lutjanus griseus* (gray snapper) was examined across a geographic gradient. Samples were obtained from locations spanning from low latitude Los Roques (11° N), and Belize (17° N) to high latitude Bermuda (32° N) in the Caribbean. Results revealed substantial plasticity in demography across latitudinal gradient within and among species. Maximum longevity for *L. griseus* varied from 6 yr in Belize, 12 yr in Los Roques to 34 in Bermuda. Longevity showed almost 5-fold difference in Bermuda compared to its Belize counterpart. Maximum age of 34 yr determined in this study is the oldest age recorded for *L. griseus*, anywhere in the world. Maximum size also showed great degree of variation among location. Largest maximum size of 770 mm for *L. griseus* was found in Bermuda where as smallest maximum size was 440 mm in Belize. This large body size and extended lifespan of Bermuda population presumed to be latitudinal effect rather than fishing effect. Maximum longevity showed a strong negative relationship with sea surface temperature. This support the idea that there are fundamental differences in ecology, biology and population dynamics of reef fish assemblages over bio-geographic scales.

Present study also investigated the age-specific growth and life-history characteristics of hogfish, *Lachnolaimus maximus*, a large reef fish belongs to the family Labridae (wrasses). Fishing pressure on hogfish has reduced many populations of hogfish to critically low levels and the species has identified as vulnerable to extinction and included in IUCN Red List. *L. maximus* examined from four geographic locations in the Caribbean subjected to varying levels of fishing pressure. Hogfish from Margarita and Belize, locations with high fishing pressure, had a smaller FL (mean FL of 239 and 278 mm, respectively). Los Roques, where the reefs are protected from fishing has the largest mean FL (459 mm). Maximum longevity observed for *L. maximus* was 16 yr from Bermuda and 10 yr in Los Roques. Margarita and Belize populations were relatively short-lived with the oldest fish estimated were 5 yr and 7 yr, respectively. The results also demonstrated that hogfish collected from Bermuda and Los Roques attained a larger size-at-age than those fish sampled from Belize and Margarita. Growth curves indicated that *L. maximus* from Belize and Margarita were slower growing compared to two other populations making them more vulnerable to exploitation. Estimates of the instantaneous rate of total mortality for hogfish showed lower values in Los Roques (0.45) and Bermuda (0.53), in contrast, intensively fished populations showed significantly higher total mortality rates [Belize (0.81) and Margarita (0.71)].

Lutjanus apodus from Belize and Los Roques, and *Cephalopholis cruentatus* from Belize, Los Roques, Las Aves, Curacao and Barbados, locations from the same latitude but subjected to varying levels of fishing, were studied for possible demographic signatures of fishing. Growth curves of *L. apodus* showed significant differences among two locations indicating different growth trajectories. Both Belize and Los Roques populations had similar growth up to 6 years and noticeable shifts in L_∞ in Los Roques thereafter. 95% Confidence regions around K and L_∞ showed no overlapping between Belize and Los Roques which confirmed the existence of different growth trajectories. Among *L. apodus* populations, mean maximum sizes achieved were higher in Los Roques compared to Belize (510 and 381 mm, respectively). Belize population of *L. apodus* had higher instantaneous mortality rate (0.17) compared to Los Roques (0.08). Both Belize and Los Roques locations lie within the same latitude minimizing any latitudinal effects. Therefore differential growth trajectories presumed to be associated with different exploitation rates exert on the two populations. The smaller size-at-age observed in Belize could be a result of high fishing pressure and therefore, removal of older age classes. The maximum age achieved for *L. apodus* in present study was 31 years from a protected reef environment (Los Roques) while maximum age recorded from a location subjected to fishing (Belize) was 24 years. Maximum longevity observed in present study for *L. apodus* (31 yr) is the highest recorded from anywhere in the world. It was evident that *L. apodus* has remarkably greater longevity than previously reported. Six populations of Graysby (*Cephalopholis cruentatus*) subjected to three levels of fishing, (high fishing - Belize and Curacao, moderate fishing - Las Aves and Barbados and low fishing - Los Roques) were also evaluated for their resilience to fishing. These populations were found along same latitude. Graysby population from Los Roques, where fishing is not allowed, had extended lifespan (22 yr). Populations from Las Aves and Barbados had moderate level of fishing intensity and also moderate maximum lifespan, whereas in Belize and Curacao with highest fishing intensity, therefore, highest mortality rates (0.5 and 0.6), had very short maximum lifespans (8 yr in both locations). Belize and Curacao showed no obvious asymptote although all the other populations did so. The Curacao and Belize populations exhibited a pattern of exponential decline in age distribution without marked peaks thereafter, while other populations had multi-mode age distributions. Both Belize and Curacao populations showed slow growth making them more vulnerable to intense fishing. It seems that high fishing pressure influences age structure, resulting in shorter lived fish.

The demographic shift associated with introduction to new environments was investigated as the final part of this study. The Hawaiian Archipelago is known for its relatively less-represented nearshore marine fish fauna. The most striking feature is the absence of native shallow-water snappers and groupers, two most common taxa found in shallow reefs elsewhere in tropics. The blacktail snapper, *Lutjanus fulvus* has been introduced to Hawaii from their native habitats of Moorea and Marquesas Islands, where they become established in Hawaiian Archipelago. These introductions have implications for conservation biology because, in spite of the fact that only a few individuals transfer their characteristics to subsequent generations, no significant change in genetic diversity can be observed. As *L. fulvus* was introduced into the Hawaii reefs with no native snappers or groupers, it was expected that they would have a rapid growth rate compared to Moorea. However, the Marquesas is a high productivity environment due to upwelling which may result in very rapid growth. Results revealed that *L. fulvus* in Hawaii did not attain ages as great as none of their native populations in Marquesas or Moorea. Longest-lived *L. fulvus* were found from Marquesas 10 yr and Moorea (7 yr), and shortest-lived was the Hawaii population (6 yr). von Bertalanffy growth curves revealed that Hawaiian population grew faster than their native populations and attained a larger maximum size. Relative absence of competitors in Hawaii would be the reason for this larger body size and faster growth. These Pacific populations were also compared with *L. fulvus* from Cocos (Keeling) (Indian Ocean). The 95% confidence ellipse revealed that the demographic characteristic of Hawaiian population of *L. fulvus* was more similar to Cocos (Keeling) than their ancestral populations in Marquesas or Moorea.

Based on the studies I conclude that there are obvious biogeographical scale patterns in demographics and the differing patterns among and within species indicate complex spatial variability in demographics. Reduced maximum size with corresponding reduction in average age and longevity may be a result of latitudinal effect or fishing effect. Exploitation influences community structure directly through preferential removal of larger-bodied fishes or indirectly as, larger-bodied fishes may exert top-down control upon other community members. Some of the species concerned shared some characteristics associated with high vulnerability to fishing, e.g. relatively slow growth and moderate to long lifespans, demography and body size. Estimates of mortality and survival rates for the selected species indicate the present status of exploited populations and also give insight on how long this fishery could be sustain under present fishing pressure. This study also provides the opportunity to examine species that have recently invaded areas from which they were naturally absent. This will contribute significantly to the knowledge of the effects of introductions into the marine tropical water and improve the basis for management of such actions.

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Parameter	**Definition**
K	Parameter of the VBGF, expressing the rate at which the asymptotic length (or weight) is approached.
L_∞	Asymptotic length in mm, parameter of the VBGF expressing the mean length that the fish would reach if they were to grow indefinitely.
$\mathrm{L_{max}}$	Mean maximum length of the largest individual reported for a locality, in mm.
S	Number of survivors at age t.
T	Annual mean surface water temperature in °C for the locality where growth study was conducted.
t_0	Parameter of the VBGF expressing the theoretical age in years the fish would have at length zero, if they had always grown as described by the VBGF.
$\mathrm{t_{max}}$	Mean maximum age of the oldest individuals in a population, in years.
VBGF	Von Bertalanffy Growth Function, used to describe the growth in length or weight.

CHAPTER 1

GENERAL INTRODUCTION

1.1 Reef fish life-histories

Coral reef fishes demonstrate a high degree of flexibility in growth and life history patterns (Newman et al. 1996b, Gust et al. 2002 Robertson et al. 2005). This flexibility provides a powerful tool for the investigation of how reef fish respond to environmental changes. This includes both temporal and spatial variation in environmental parameters and increasingly, the impact of human activity on fish populations. This diversity of life history features seen in reef fishes reflects both demographic plasticity within an individual species and the underlying taxonomic and ecological diversity among the whole fauna. The recent growth in demographic studies of coral reef fishes is largely due to the realization that sectioned otoliths of tropical reef fishes provide reliable and accurate estimates of age (Fowler et al. 1995), and thus a key to obtaining estimates of demographic rates. The increasing need to obtain demographic information reflects the increasing exploitation of fishes of tropical reef systems (Munro 1996).

The analysis of reef fish demography and life history features can be approached in two ways. Age-based data provide a mean of assessing response of reef fish populations to natural and anthropogenic changes over relatively short time scales. Central to this is the assessment of fishing effects. The diversity of life history patterns also reflects the action of evolutionary processes. Natural selection favors individuals that make the greatest contribution to future generations. A perfect organism would mature early at a large size and produce a number of large offspring over a long reproductive lifespan. However, in reality, when an individual allocates resources to improve one aspect of fitness there will be a cost elsewhere as resources are limited. There are numerous ways that life histories can maximize fitness depending on costs and benefits set by the environment (Malausa et al. 2005). The focus of this study is on ecological aspects of variation in reef fish demography including the impacts of fishing. The main study region is the tropical Atlantic which has been subjected to major impacts by reef fisheries. In addition, examples have been drawn from the Indo-Pacific, primarily to take advantage of a unique experiment involving the introduction of reef fishes from rich to ecologically impoverished environments.

1.2 Age-based approaches to reef fish studies

Many early studies on tropical reef fish were size-based (i.e. Hughes 1984, Kirkpatrick 1984, Sauer and Slade 1987). Although size-based studies have provided some valuable insights into reef fish biology, there are problems associated with using size exclusively. Reef fish occur in a wide range of sizes, however, large may not correlate with longevity. Fishes stop growing early in their lives but may have extended life spans, and many species have very different growth patterns depending on sexual identity (Kritzer 2004). Reef fishes display variable growth rates and strong phylogenetic patterns in life-history data, especially longevity (Ackerman 2004, Choat and Robertson 2002, Robertson and Kaufmann 1998). For these reasons, it is unwise to predict life history features based on body size alone. Size is sometimes misleading, as the same species may vary in growth patterns under different environmental conditions. Therefore, size-based studies provide limited information on demographic properties of coral reef fishes (Choat et al. 2003). Increasing evidence suggests extended life spans and decoupling of size and age for reef fishes (e.g. Hart and Russ 1996).

There are a number of reasons for advocating a more comprehensive understanding of the age-based demography of coral reef fishes, including: 1) the primary reason relates to the increasing exploitation of coral reef fishes by both artisanal and commercial fisheries; 2) to provide a better basis for reef fish conservation and management; 3) to make predictions on the resilience of reef fish under different management scenarios; and 4) to facilitate generalization of life histories.

The otolith: Nature's chronometer

The chronological properties of otoliths are well understood, allowing precise estimates of age and growth at both daily and yearly scales. Thus, otolith applications have revolutionized our understanding of the integrity of fish populations and the management of fish stocks (Campana 2001). Unlike scales, otoliths grow by deposition rather than ossification. There is no evidence for their resorption during the periods of poor growth or stress, making them ideal for ageing. The choice of sagittal otoliths follows from the demonstration that they continue to accrete calcareous material in a linear fashion throughout the life of the fish, regardless of the pattern of somatic growth (Secor et al. 1995). The number of increments in sectioned otoliths is one of the most robust and reliable estimators of fish age in tropical reef fish (Cappo et al. 2000, Choat and Axe 1996, Hart and Russ 1996).

The physiological basis for the formation of distinct zones in calcified structures of tropical species has not been established conclusively (Ferreira and Russ 1994). The formation of such zones has been associated with both biotic and abiotic factors (Beckman and Wilson 1995), such as regular seasonal variances in water temperature (e.g. Panella 1980), photoperiod, feeding, reproduction, and spawning periods (Morales Nin and Ralston 1990). In general, denser layers of material are formed during periods of fast growth, and less dense layers during periods of slow growth (Wilson 1988). The different densities of these concentric zones form a series of light and dark rings when viewed under a microscope. An emerging picture of otolith-based demography of reef fishes has shown that many reef fishes are relatively long-lived (Munro and Polunin 1996), they have highly distinctive patterns of growth and age-based demographic features (e.g. Choat and Axe 1996, Newman et al. 1996a), and they also display strong phylogenetic structure (Choat and Axe 1996).

1.3 Fish growth

Growth is the increase in body size as a function of age. Organisms grow because larger body size confers a number of advantages that can ultimately result in higher lifetime reproductive output (Shine 1988). Larger individuals are subjected to lower predation mortality, and the faster they grow the more rapidly this mortality decreases (Arendt 1997). Larger individuals can store more energy (Murphy 1985), so they are less susceptible to fluctuations in food supply, and they also show increased tolerance to environmental extremes (Young and Cech 1996). Fecundity (Roff 1986) and the ability to compete (Huntingford et al. 1990) for mates and resources also increase with size. Large size can be attained by hatching at a large size (Hutchings 1991), growing fast or growing for a long time. Delaying the age at maturity provides more energy for growth. Most fish species have *indeterminate growth* (Charnov and Berrigan 1991, Sebens 1987), and begin reproduction before attaining maximum body size. It is worth investing spare energy in growth as long as this increases expected future reproductive output. From a fisheries point of view, growth same as recruitment influences the sustainable catch weight that can be taken from a stock (King 1995) .

1.4 Spatial scales in reef fish demography

Processes affecting population dynamics operate at a number of spatial and temporal scales (Levin 1992), and can result in subpopulations with distinct demographics. Differences in demography between populations may suggest geographic or reproductive isolation, and as such have been used in stock identification for fisheries assessment and management purposes (Begg et al. 1999). Knowledge of spatial structure within a unit stock is important because potential yields may vary spatially within a population (Caddy 1975). This knowledge is also important for conservation, in order to maintain intra-specific diversity. Hence, it is imperative to estimate demographic parameters over a range of temporal and spatial scales to determine the scales at which the parameters vary significantly (Caley et al. 1996) and therefore, to infer which scales are of greatest importance for assessment and management purposes (Sale 1998). Biologists and ecologists working on coral reef fish have often been criticized for working at too small spatial scale. However, broad understanding of spatial patterns will require considering variety of species on a variety of scales (Choat 1998).

There are an increasing number of studies examining spatial variation in life history traits of reef fishes (Ackerman 2004, Choat et al. 2003, Gust et al. 2001, Gust et al. 2002, Kritzer 2002, Lou et al. 2005, Meekan et al. 2001, Murdoch and Aronson 1999, Newman et al. 1996b, Robertson 2005, Robertson et al. 2005a, Sale and Kritzer 2003). However, the majority of otolith studies of coral reef fishes have focused on a very limited range of latitudes (Meekan et al. 2001). Multi-scale studies that examine a variety of aspects of population biology are rare for large reef fish, but are needed to identify which traits are likely to exhibit variation on which spatial scale (Kritzer 2002). Variation in geographical latitude typically affects the growth rates and growth patterns of fish (Conover et al. 1997). Generally, polar species grow slower (Johnston and Clarke 1990) and have a more regular pattern than faster growing equatorial species. In addition, sedentary species tend to display more geographical variation in growth patterns than migratory species (Meiri and Dayan 2003).

One way to examine any trade-off between growth, maturity and longevity is to use intra-specific variation in life history traits between geographically distinct populations (Charlesworth 1980). However, there is still little information on the spatial variation in the demographic structure of reef fish populations (Palumbi 2003) or on the degree of concordance between demographic and genetic characteristics.

Theoretical models imply that spatial scale derives its greatest importance through spatial variation in population densities (Chapman and Kramer 1999, Knouft 2002, Rijnsdorp and Van Leeuwen 1992, Sale and Tolimieri 2000, Zeller et al. 2003) and environmental variables (Atkinson and Sibly 1997, Bakun and Broad 2003, Bortone and Williams 1986, Elsdon and Gillanders 2002, Fey 2006, Kokita 2003, Roff 1980, Wilson and Meekan 2001, Young and Cech 1996). Such interactions cause population dynamics on large spatial scales to differ in many important ways from predictions based on measurements of population dynamics at smaller scales, a phenomenon called 'scale transition' (Chesson 1996). These differences can account for large-scale population stability and species co-existence.

Various processes taking place in reef-fish systems have recognizable spatial scales (Chesson 1998). The size of an individual's home range or the extents of its daily foraging activities may also set a scale limiting food resources. Variation in food density on a smaller scale may not affect individuals, while changes on the same or large scale would (Chesson 1998). The scale of predation or disease is likely to be much larger than these scales.

Estimates of age structure and growth rates of tropical demersal fishes are biased towards particular taxa, particularly lutjanids and serranids (Buesa 1987). These large carnivores are relatively easy to sample and have been traditional targets for coral reef fisheries (Alcala and Russ 1990). However, they represent only a limited range of the taxa that make up reef fish assemblages. Emphasis on these groups only will produce a selective picture of growth and life history patterns in coral reef fishes.

1.5 Demographic plasticity

Size-at-age has often been shown to vary over large geographic ranges involving a latitudinal or longitudinal gradient (Atkinson 1994). Temperature is likely to be a particularly important factor influencing life histories, especially for those animals that rely on external sources for body heat (Sebens 1987). Temperature is known to have a significant effect on metabolic rate, growth and overall size of ectotherms (Rilling and Houde 1998). It has long been realized that with an increased rearing temperature, the resultant body size of a poikilotherm decreased (Ray 1960).

Similarly, mean body size of ectotherms should increase with decreasing temperature and therefore, at higher latitude body size is often larger than that at lower latitude (Conover and Present 1990).

Smaller cod live in excess of 40 years, whilst the larger coral trout rarely live beyond 15 years. This is contrary to the positive relationship predicted by traditional life history theory. Furthermore, reef fish have been found to vary in age-based demography across relatively small spatial scales (Gust et al. 2002). However, we have no understanding of how these demographics vary over large spatial scale, (i.e. latitude). Life history theory predicts that at higher latitudes (lower temperatures) coral reef fish would exhibit larger final body sizes but smaller size at ages (i.e. slower growth). With slower growth there is likely to be a trend towards later maturation, but greater longevity (Stearns and Koella 1986). With later maturation (at larger size), reproductive effort is obviously delayed and therefore potentially decreased. However, there is a potential for greater fecundity (assuming fecundity increases with body size), yet these fundamental theories remain to be tested in coral reef fishes. Within localized areas, a species will occur in a variety of habitats. Growth and life history patterns of reef fishes can be expected to vary at geographic, latitudinal and habitat scale.

1.6 Vulnerability to fishing

Tropical reef fisheries is particularly difficult to manage because it involves multi-species with a diverse range of life histories and complex patterns of spatial distribution (Jennings et al. 1998, Sale et al. 1994). Healthy populations of reef fish also important in maintaining ecological processes in diverse tropical marine environments (Bellwood et al. 2004).

Fishing is known to influence fish demography (i.e. Chiappone et al. 2000, Jackson et al. 2001, Munro 1983, Roberts 1995, Rogers and Beets 2002) and abundance (Pears 2005) strongly. Intrinsic vulnerability of some reef fishes to over-fishing and increasing fishing pressure underpin the need for more effective management of reef fisheries (Russ and Alcala 1989, Sadovy et al. 2003). Populations of reef fishes which do display extended lifespans, and with individuals accumulating in older age classes, will be especially vulnerable to exploitation. Chesson (1985) suggests that under conditions such as fluctuating recruitment rates extended lifespans may be expected.

Spatial variation in demographic and life history characteristics may give populations varying resilience to disturbances such as fishing (Pears 2005). Such spatial structure may necessitate different management regimes over a species' range or a generally precautionary approach to avoid over-fishing of more vulnerable components of the population (Williams et al. 2003).

Considerable work has examined reef fish ecology over the last few decades, widening our understanding of patterns and processes that shape reef fish communities (Sale 2002). Understanding of reef fish ecology, population dynamics and responses to fishing is therefore fundamental to achieving a better management approach (Sale et al. 1994). Therefore, incorporation of multiple spatial scales into sampling designs for studies of reef fish biology will help answer ecological questions related to the scales at which most variation in biological attributes occur. This will ensure results are widely applicable and provide useful data at scales applicable to fisheries and conservation (Gust et al. 2001, Sale 1998).

Life history features (such as mean size, longevity and growth rate) are known to vary over latitudinal environmental gradients. In addition, fishing also influences the same life history traits. Therefore, it is important to distinguish natural from human induced variation. One of the possibilities, as a first approach to differentiate these variations, is by comparing relatively unfished populations in Marine Protected Areas (MPA) or remote areas with highly fished populations.

However, before we can evaluate the ways by which life histories could maximize fitness we require a more comprehensive database on variation in the patterns of life histories. The primary purpose of this dissertation is to describe demographic patterns in large commercially important coral reef fishes. This is an important step in the development of predictions about how life histories will vary under specified conditions. Here, I specifically test two major sources of variation, habitat structure along latitudinal and longitudinal gradients, and fishing gradient on reef fish life histories.

1.7 Aims of the study

The primary aim of the study was to investigate the patterns of demographic response of reef fishes to environmental variation at different locations within their distributional ranges. The study was designed to investigate; i) variation along significant latitudinal gradients; ii) variation across a longitudinal gradient within a single latitudinal; and iii) response to different levels of fishing pressure. Geography, patterns of reef distribution and the distribution of human activity prevent the development of a properly balanced design in this or similar studies. There was however, sufficient balance to allow detection of fishing impacts. In order to focus on the impact of fishing, the study locations were primarily on Caribbean reefs where there is a long, well-documented history of human activity. The species selected - a serranid, lutjanids and a large labrid - are subjected to different levels of fishing over much of their range. An additional case history reflecting the impacts of environmental variation on lutjanid life history was also selected, one representative of an increasing phenomenon in reef fish ecology - the artificial introduction of fish into novel reef habitats. The most appropriate example was provided by the deliberate introduction of a lutjanid from the western Pacific into the relatively impoverished reef environment of Hawaii.

Therefore, three major issues have been addressed in this study;

1. Natural (latitudinal) demographic variation in population in areas protected from fishing at two different latitudes.
2. Demographic variation within single latitude over a fishing gradient.
3. Demographic changes associated with introduction to new habitats.

1.8 Dissertation structure

Following the introductory first chapter, description to materials and methods used in the study has given in Chapter 2.

In Chapter 3, the demographic patterns of *Lutjanus griseus* (gray snapper) and *Lachnolaimus maximus* (hogfish) were compared among latitudinally and longitudinally distinct locations that differed in terms of fishing pressure. *L. griseus* were collected from two largely unfished locations, Bermuda and Los Roques, spanning 22 degrees of latitude. *L. griseus* were also collected from Belize, at similar latitude as Los Roques, but subject to heavy fishing. *L. maximus* were compared among four locations, Belize, Los Roques, Margarita and Bermuda.

In Chapter 4, to follow up the previous study, I further looked at *Cephalopholis cruentatus* (graysby) from Belize, Los Roques, Curacao, Las Aves and Barbados; and at *Lutjanus apodus* (schoolmaster snapper) from Los Roques and Belize. These locations lie within the same latitude and are subjected to varying levels of fishing ranging from marine protected areas, remote areas to highly fished areas.

Chapter 5 examines the demographic changes associated with introduction to a new environment. The blacktail snapper, *Lutjanus fulvus* was introduced to Hawaii and became established there from its native habitats of Moorea and Marquesas Islands. A number of species have shown the capacity to invade new marine environments as a consequence of deliberate introduction, but the demographic responses to colonization episodes are poorly understood.

The final chapter is the general discussion which ties all the studies together and summarizes key findings, limitations, and implications.

The overall sampling design is shown in Figure 1.1. Three of the data chapters in this study are based on following core elements;

- Natural (latitudinal) variation of demography in areas protected from fishing (figure 1-1A, see chapter 3).
- Demographic variations in populations within same latitude, subject to different degrees of fishing (figure 1-1B, see chapter 4).
- Demographic responses of fish introduced into new habitats (chapter 5).

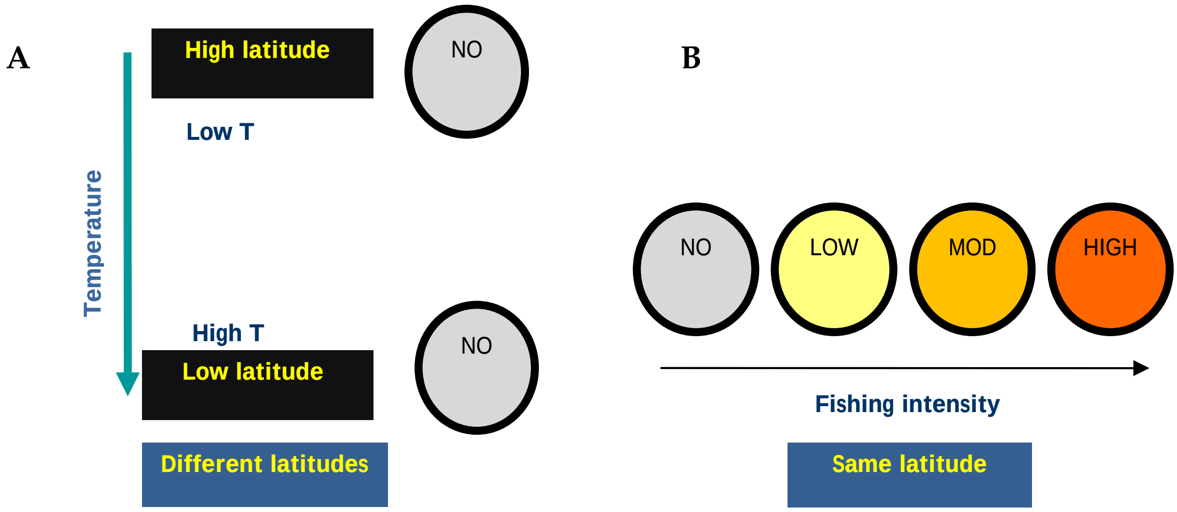


Figure 1-1. Sampling design A) Locations from different latitudes but subjected to same levels of fishing pressure. B) Locations from the same latitude but subjected to different levels of fishing pressure. (NO = no fishing, LOW = low fishing, MOD = moderate fishing, HIGH = high fishing).

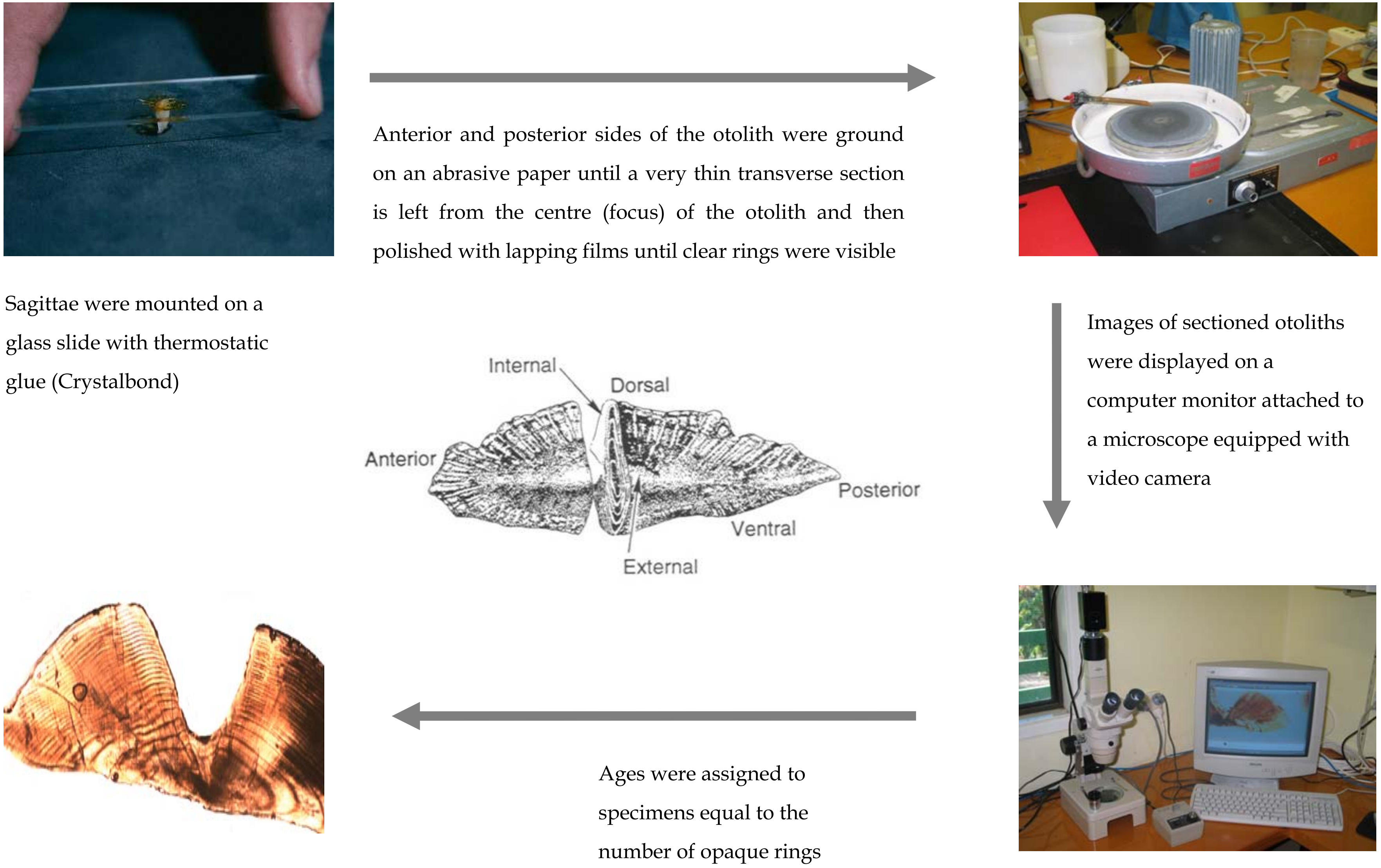
CHAPTER 2

Material and methods

2.1 Sample collection

Analysis of demographic variation at multiple spatial scales requires age-based data derived from otoliths sampled over a variety of geographic locations. In this study I sampled across latitudes (therefore, a range of sea temperatures), across longitudinal zones within a given latitude subject to different levels of fishing pressure, and across ocean basins. Care was taken to sample similar depth ranges, and similar habitats across the regions. Some samples were obtained from institutes such as Smithsonian Tropical Research Institute and Sultan Qaboos University, Oman and some people such as Dr. Ross Robertson as a part of cooperative investigations. However, most of the samples were obtained with spear fishing. Fish were targeted as sighted in order to collect representative samples both juveniles (aiming to include the smallest available) and a representative sample of the adult size range to provide information on the size and age structure of the population. Commercial fishery data, if unbiased, will give an accurate picture of the mortality inflicted on a stock. However, commercial fishing will only target financially rewarding fish and hence not give an accurate idea of stock levels. (Gulland 1988).

The fork length (FL) of each fish was recorded to the nearest mm. Sagittal otoliths were removed, cleaned in fresh water and stored dry. Individual otoliths were weighed to the nearest 0.0001 g on a Mettler® AE240 balance.



Sagittae were mounted on a glass slide with thermostatic glue (Crystalbond)

Anterior and posterior sides of the otolith were ground on an abrasive paper until a very thin transverse section is left from the centre (focus) of the otolith and then polished with lapping films until clear rings were visible

Images of sectioned otoliths were displayed on a computer monitor attached to a microscope equipped with video camera

Ages were assigned to specimens equal to the number of opaque rings

Figure 2-1. Laboratory procedure of otolith thin sectioning, image processing, and age interpretation (following Choat and Axe 1996).

2.2 Otolith preparation and age determination

Otoliths were prepared following the procedure in Choat and Axe (1996). The left otolith from each pair was chosen for ageing; however, the right otolith was used if the left was not available or not suitable for ageing. A transverse section was obtained from the core area of the otolith (fig. 2-1) and the section was mounted on a microscope slide with thermoplastic mounting media (crystalbond™). Each preparation was then hand polished using appropriate abrasive paper (grade ranging from 400 to 1200). Optimum thickness for reading was determined by frequent examination of the section until the annuli were clearly defined. Sectioned otoliths were viewed using a dissecting microscope with transmitted light which was equipped with a Nikon® video camera and computer monitor, a personal computer with an Image grabber® and Uthsla Image tool® image analysis software.

Otolith sections were sorted by 50mm FL intervals and read in ascending order as an aid in determining size at first annulus formation. Transmitted light revealed alternating opaque and translucent rings. Opaque rings were presumed to be annuli (Fowler et al. 1995) and ages (in years) equal to the number of opaque rings were assigned to specimens. Counts were taken along the *sulcus acousticus* from the core to the edge of the otolith. In order to establish the level of confidence placed in the interpretation of the otolith structure, the precision of counts from the sectioned otoliths was assessed. Each otolith was examined on three separate occasions without knowing the previous counts. For those fish in which first two counts differed, the third count was used as final count under the assumption that additional experience had been gained and interpretation of annuli had improved. If all the three counts were differed fourth count was obtained after discussing with an experienced reader (Dr. William Robins). Indeterminate increments (false bands) were found in many otoliths. They were distinguished from increments formed at regular intervals based on the consistency and by comparing to otoliths with well defined bands.

2.3 Sagittal weight versus age relationship

The sagittal weight and age relationship is very important to understand how fish otoliths grow throughout their lifespan and also as a measure of consistency in reading age from otoliths. The correlation between otolith weight and the number of increments has been considered an indirect method of age validation (Choat and Axe 1996). A strong correlation would be expected if otoliths accrete calcium carbonate throughout the life of fish. The relationship between otolith weight and annulus number was examined by least-squares regression analysis with sagittal weight as the independent variable. Analysis of covariance (ANCOVA) (Zar 1996) was used to compare slopes and intercepts among sampling locations. Pairwise comparisons using the Bonferroni method (SPSS 12.0) was performed to discern the most important sources of strong differences detected by ANCOVA.

2.4 Age structure distribution

The percentage of fish in each age class was plotted against corresponding age to obtain the age distributions.

2.5 The von Bertalanffy Growth Function (VBGF)

Von Bertalanffy derived an equation that could be used to predict the length of an organism as a function of its age, the equation commonly referred to as the Von Bertalanffy Growth Function (VBGF). When fitted with least-squares residuals this represents the average growth of the members in the population. VBGF has been widely accepted to describe indeterminate growth in length of fish, particularly after its incorporation into fisheries yield equations (Beverton and Holt 1957). This function has been used not only to describe fish growth, but also to compare growth between sexes (Choat et al. 2003), populations (Gust et al. 2002), and species (Meekan et al. 2001). The VBGF is a useful growth model (Schnute 1981), and if used carefully, can be a valuable tool (Essington et al. 2001). In addition, the VBGF can also be used as a common ground for comparative analysis of fish growth (Roff 1980), since there are many compilations of parameters over a long period of time. The von Bertalanffy growth function, in its mathematical expression, has the form of;

$L_t = L_\infty \{1\text{-exp}^{-k(t-to)}\}$

where L_t is the total length at age t, L_∞ is the asymptotic length (the length at which growth rate is theoretically zero), k (the Brody growth coefficient) is the curvature parameter which defines the rate at which the fish grows towards L_∞, and t_0 is the hypothetical age at which the fish would have zero length if it had always grown in a manner described by the equation (Figure 2-2). k is correctly defined as the rate at which the increase in size decreases with unit of time but, is often misinterpreted as growth rate.

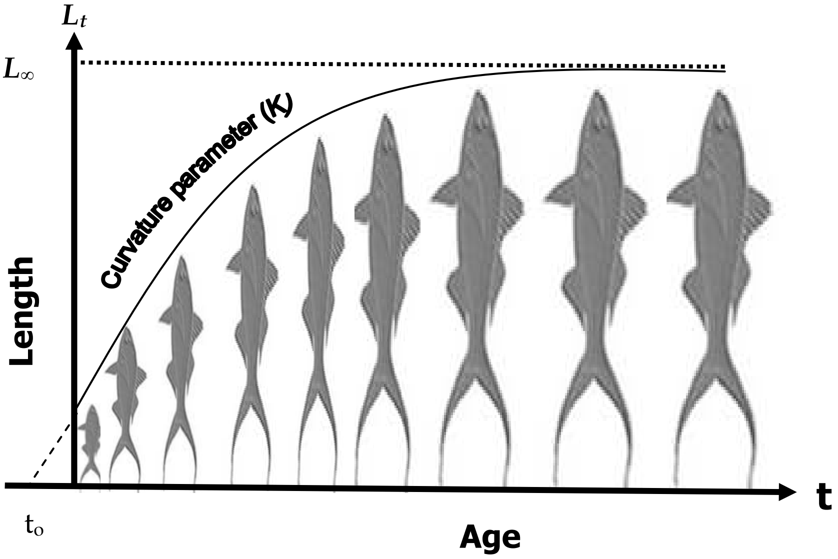


Figure 2-2. Graphical representation of the Von Bertalanffy Growth Function (VBGF). The asymptote is illustrated by the dashed horizontal line. Some data points may lie above this line because, L_∞ is interpreted as the average length of the maximum age class.

In general, high k is associated with low age- and size-at-maturity, high reproductive output, short lifespans and low asymptotic length. Conversely, species with low k have greater age and size-at-maturity, lower reproductive output, longer lifespans and greater asymptotic length. However, there can be a great deal of variation around k estimates particularly for fish that show very fast initial growth and asymptote for the majority of the lifespan (Choat and Robertson

2002). Therefore, use of this parameter in interpreting other VBGF parameters has limitations, especially if used as a growth rate (Ackerman 2004).

There are other limitations associated with the use of VBGF. Usually there are fewer data points for the younger and older age classes, and most data occur where the curve is turning. This under representation of the younger and older ages can distort resulting parameter estimates. Since the fastest growing individuals tend to mature first, the mean size is increasingly biased by the slower growing animals (King 1995). As a result, the mean curve is asymptotic even though not many individual follow this trajectory. In most length-frequency data, therefore, the smallest fish has a length well above zero and the largest fish often has a length well below L_∞. Values of L_∞ and t_0 which relate to the extreme ends of the growth curve, often represent large extrapolations beyond the range of sample data (King 1995). Estimation of VBGF parameters can also be sensitive to exclusion of younger and smaller fish. This can be eliminated by choosing a common t_0 value estimated by analysis of early growth of the fish (Kritzer 2001). Knight (1969) argued that L_∞ estimated through extrapolation, would have no biological meaning. The estimation of L_∞ is a problem especially for fish that do not exhibit an asymptotic maximum size. It is a common practice to fit growth curves even with little data available for younger and older individuals, even if the sampled population is fished and has a legal maximum size. In these cases, the data are not fully representative and care must be taken with the generality of the resulting curves and comparison with other populations.

In this study, growth curves were generated from size-at-age data obtained from the analysis of sagittal otoliths. Lifetime growth parameters were estimated through fitting the VBGF using nonlinear least squared estimation procedure. The intercepts of the curves were constrained to the approximate size at settlement (Kritzer et al. 2001) in order to facilitate comparisons among the species or regions, since VBGF parameter estimates can be sensitive to the range of ages and sizes used (Craig et al. 1999, Ferreira and Russ 1994). Common approximate size at settlement of 20 mm was used for all the species in this study.

2.6 Comparison of growth

There are number of ways that growth patterns can be compared. However, individual parameters in the VBGF growth model should not be compared as some are strongly correlated. The standard ANCOVA test is not appropriate because of non-linear nature of the growth regressions. Moulton et al. (1992) recommended the re-parameterized VBGF of Francis (1988) and then using the likelihood ratio for comparison. In this study, growth patterns at different locations and between sexes were assessed using one or more of the options outlined below:

1. 95% confidence regions of k and L_∞ (Kimura 1980, Meekan et al. 2001, Choat et al. 2003)
2. Maximum likelihood ratio test (Kimura 1980)
3. Comparing sizes at 3 arbitrary ages using re-parameterized von Bertalanffy growth function (Francis 1990).

2.6.1 95% confidence ellipse

Growth estimates were compared by plotting 95% confidence regions around the parameters K and L_∞ (Kimura 1980, Meekan et al. 2001), then examining the degree of overlapping. A Microsoft Excel macro was used to calculate 95% confidence regions.

2.6.2 Kimura's Maximum Likelihood Ratio Test

A maximum likelihood ratio test (Kimura 1980) was used to test for growth differences between sexes. Pairwise comparisons were made if more than two entities were to be compared. A Microsoft Excel macro was used to compute maximum likelihoods. This is considered to be the most reliable procedure for such comparisons (Cerrato 1990). Following Haddon (2001), a common age range was used for each comparison.

2.6.3 Re-parameterized VBGF (rVBGF)

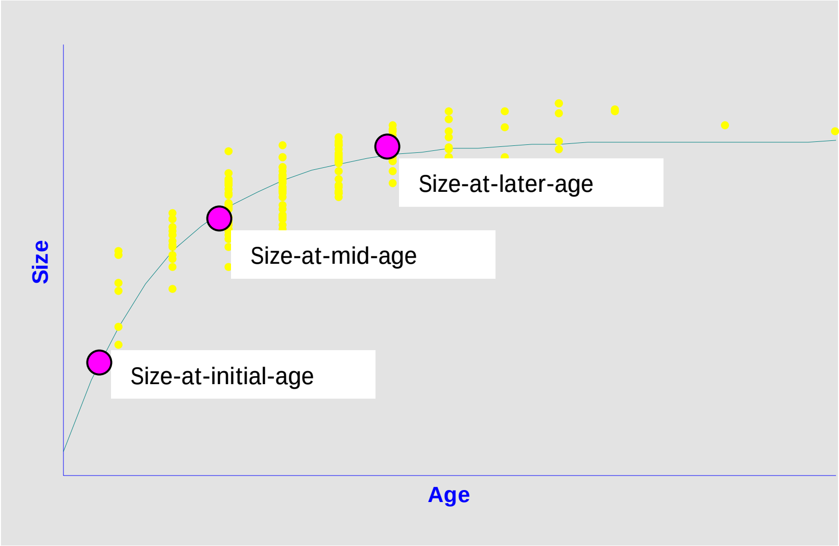


Figure 2-3. Re-parameterized VBGF, three arbitrary ages were chosen to compare growth.

Size at a particular age is a directly observable proxy of growth that can be used to compare growth rates among populations from different locations. Three arbitrary ages were chosen: 1) an age group corresponding to the initial steeper part of the growth trajectory (referred to as L_τ, size-at-initial age); 2) one corresponding to the flatter part of the growth trajectory L_ν (Size-at-later age); and 3) a group consisting of the mean of the above ages (L_ω size-at-mid age) (Fig. 2-3). A Microsoft Excel macro was used to generate bootstrap estimates of the rVBGF growth parameters L_τ, L_ω and L_ν (re-parameterized VBGF model, Francis 1990) to: 1) determine confidence intervals around the estimates, and 2) estimate the variance around the parameters for statistical comparisons among samples. The use of the rVBGF model allows comparing expected mean size at the aforesaid 3 arbitrary ages.

2.7 Length-weight models

The relationship between fork length (FL) and body weight (W) can be described by the power function:

$W = a\ L^b$,

where W is total weight (g), L is fork length (mm), a (proportionality constant or intercept) and b (exponent). The relationship between length and weight was fitted to log-transformed data.

2.8 Mean Maximum size and age

The mean maximum age, T_{max} and the mean maximum size, L_{max} were calculated using the oldest and the largest individuals of the sample. Size-at-age data were sorted in ascending order and the mean age or size is calculated for n individuals, which correspond to the oldest and largest 10% of the total sample size (Laman-Trip 2004). However, the percentage was adjusted according to the sample size, i.e., if sample size is reduced the number of individuals on which the means were calculated may be increased to higher percentage of the population.

This approach of estimating T_{max} and L_{max}, is considered preferable over using observed maximum sizes or maximum ages, particularly for small sample sizes, since estimates do not rely on a single individual that may unduly influence results (Ackerman 2006, Gust et al. 2002, Laman Trip 2004).

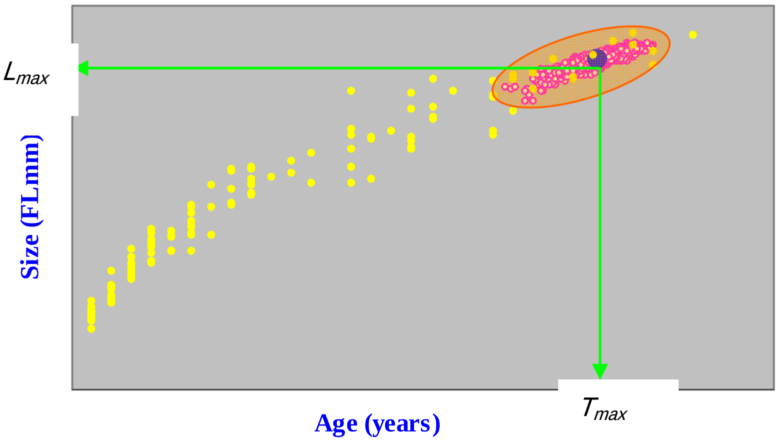


Figure 2-4. Diagram depicting mean maximum size (L_{max}) and mean maximum age (T_{max}). Light circles are the actual size-at-age data. Dark circles are the re-sampled data using bootstrapping procedure and the large circle within the oval is the estimated L_{max} and T_{max}.

A Microsoft Excel macro (recorded by Elizabeth Laman Trip) was used to calculate T_{max} and L_{max}. Confidence intervals around mean T_{max} and mean L_{max} were generated by randomly re-sampling the original data set (1000 iterations) using a bootstrapping procedure. The bootstrap values generated are pseudo-replicates and therefore, they are not true estimates of the variance as if the re-samples or replicates had been taken from the field.

2.9 Estimation of longevity

Maximum longevity was obtained directly from maximum increment counts on transverse sections of sagittal otoliths. Longevity estimates were used in analyzing the age-structure of the population. Natural longevity is a crucial statistic for fisheries management. The proportion of the population that can be safely harvested in any year depends on the period that it has taken to produce that population (Nicol 1990). Populations with long lifespans could replace itself by producing a good year class only once in every 10-15 years (Secor 2000). Hence, longevity serves to increase the probability of individual replacement and population persistence. Apparently, longevity as a life history tactic provides a degree of resilience to long-term recruitment failure regardless of the cause of depressed or absent year classes (Secor 2000).

2.10 Estimation of mortality

The mortality rate is the rate at which fish die in a population. It is usually expressed as an average annual value. It can be converted into a survival rate to demonstrate how many fish survive in a given year. Mortality and survival rates are used to indicate the status of exploited populations. In general, there are fewer larger and older individuals in a population than smaller and younger ones because the larger and older individuals expose to fishing or natural mortality for a longer period of time. The instantaneous total mortality rate, Z, is the sum of natural mortality (M) and fishing mortality (F).

In this study, instantaneous total mortality rate, Z, was estimated by age-based catch curve method of Beverton and Holt (1957) and Ricker (1975). The natural logarithm of the number of fish in each age class was plotted against their corresponding age (*t*). A linear regression was applied to the descending arm of the age-frequency distribution, with the absolute value of the regression slope equaling the instantaneous total mortality rate. This technique assumes constant declines across the older age classes due to mortality. Initial ascending points representing fish that were not fully recruited to the fishery were excluded from the analyses (Ferreira and Russ 1992). Data points after two consecutive zeros were also excluded from mortality estimates (Kritzer 2002). Survival rate (*S*) of each species was estimated as $S = \exp^{-Z}$ (Ricker 1975). Annual percentage survivorship, S, was then estimated for each location as: $S = 100 \times \exp^{-Z}$.

Comparisons of mortality rates between locations were made using ANCOVA, where the assumption of heterogeneity of slopes was tested according to Zar (1999). Pairwise comparisons using the Bonferroni method (SPSS 12.0) were performed to discern the sources of differences detected by ANCOVA. Total mortality rate is the life history parameter with the lowest precision. However, this can be improved with sample size, requiring nearly 300 samples to reach a precision of 10%, but reaching 15% precision between 100 and 150 samples (Kritzer et al. 2001). However, a sample size of 100 would be the cost effective minimum sample size for each location.

2.11 Fishing effects

Effects of fishing on demographic and life history traits including maximum and asymptotic sizes, size-at-age relationships, growth rates and lifetime growth trajectories, longevity and adult survivorships were concerned in this study. Comparisons were made between locations ranging from a large, well-protected marine reserve to areas with dense human populations and intensive fisheries. It was hard to quantify relative differences in fishing pressure among locations.

Three types of environments were defined low, moderate and high fishing pressure - based on historic fishing data (Robertson et al. 2005b). The presumed gradient in fishing intensity was defined for broad regions based on best available knowledge of past and current fishing pressure (Jennings et al. 1995, Jennings and Polunin 1996).

Effects on longevity and survivorship

The relationships of longevity and survivorship with sea surface temperature (SST) were investigated using linear regressions (Robertson et al. 2005a). Any linear decline in longevity and or survivorship with latitude would be due to latitudinal or fishing effects. To test this hypothesis, longevity and survivorship were compared against sea surface temperature (SST) in the most intensely fished areas with locations where there was low or no fishing.

Effects on body size

Maximum and mean maximum fork lengths were compared among location to see any fishing effect. Maximum size which is a good proxy for asymptotic size, was also compared with SST. But, one has to be cautious as low abundance of larger individuals may also result reduced size (Faunce et al. 2002).

2.12 Statistical analyses

All the statistical analyses were performed using Statistica® version 7 and SPSS® version 12.0. All null hypotheses were accepted if they fell within 95% confidence intervals.

Principal Component Analysis

A Principal Component Analysis (PCA) was performed to test the relationship between life history parameters and fishing intensity using the factor procedure in SPSS. Life-history variables without missing data were used to estimate variable loadings and generate principal component scores for each species. The interpretation was based on Eigen values of the correlation matrix that were greater than or equal to 1.0 (Grossman et al. 1991).

Spatial variation in demographic parameters

Following the PCA, ANOVA was used to explore spatial variation in size, age and growth parameters of each species among area and broad regions. Two factor ANOVA was used with the factors; area (fixed) and region nested in Area (random). Parameters examined were mean size, mean age, mean maximum size, 10% longevity, mortality rates and the three measures of size-at-age. Normal probability plots and residual plots were used to examine the assumptions of normality and homogeneity of variances for all data prior to analysis. The origins of significant patterns suggested by the ANOVAs were identified by Tukey's tests (Day and Quinn 1989).

2.13 Study areas and fishing levels

Barbados: Densely populated island (637 people /km^2 land), <100 km^2 of shallow reef area, has an extensive trap-fishery for reef-fishes (Robertson et al. 2005a).

Belize: Lower human population density (11 people /km^2 land) and large area of reefs (1330 km^2). Moderately intense fishing targeting predatory fish and large scarids and fishing is unregulated in many areas (Koslow 1994).

Bermuda: Dense human population (1226 people /km^2 land) and only 370 km^2 of reefs. A high-intensity trap-fishery was banned in 1990 and this ban has been well enforced since then. Current level of line fishing is not adequate to even meet the needs for local consumption (Luckhurst 2002, as cited in Robertson et al. 2005b). Herbivorous fishes are not targeted since the trap-fishery ended.

Curacao: Moderately populated area (455 people /km^2 of land), approximately 50 km^2 of reef. Predatory reef fishes are uncommon due to a long history of over fishing. There has been virtually no trap-fishing for the last two decades.

Las Aves archipelago: Solitude and completely deserted islands. No controls on fishing. Although Las Aves (~100 km^2 reef) is uninhabited, there is some fishing for reef-fishes, mainly by fishers from the nearby Venezuela mainland.

Los Roques Archipelago: Small human population (4 people/km^2 of reef). This is a well protected reserve with restricted fishing and the sampling area in Los Roques was a part of the reserve where historically no fishing was allowed.

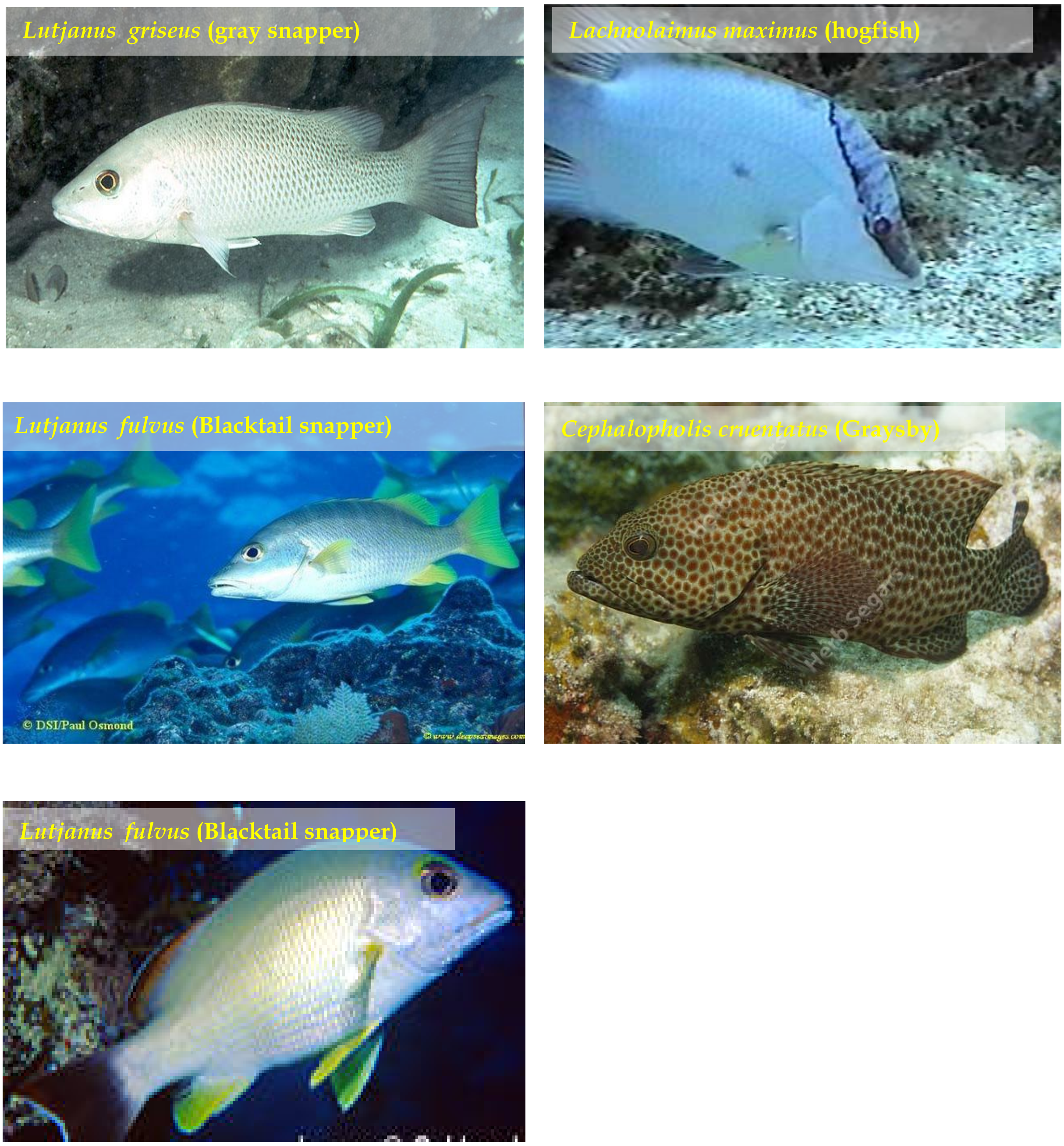
Margarita: Is the largest island of the Nueva Esparta state in Venezuela, situated in the Caribbean Sea. Moderately populated country with 412 people /km^2. Fishing plays an important role in Margaritas' gross domestic production.

The other 4 study areas; Cocos (Keeling) Islands, Marquesas, Moorea and Hawaiian Islands, are described in the materials and methods section of Chapter 5.

Table 2. Sampling locations, latitude and estimates of fishing intensity.

Location	Latitude	Ranking based on Fishing intensity*
Barbados	13° 10′N	High
Belize	17^{o} 15’ N	High
Bermuda	32 10^{o} N	Moderate
Curacao	12^{o} 10′N	High
Las Aves	15° 40′ N	Very low
Los Roques	11^{o} 51′ N	Very low
Margarita	10° 52'N	High

* Based on historic fishing data and population density (Robertson et al. 2005b)



Lutjanus griseus (gray snapper)

Lachnolaimus maximus (hogfish)

Lutjanus fulvus (Blacktail snapper)

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Cephalopholis cruentatus (Graysby)

Lutjanus fulvus (Blacktail snapper)

Figure 2-5. The study species.

CHAPTER 3

Demographic plasticity of *Lutjanus griseus* and *Lachnolaimus maximus*: Latitudinal and fishing effects.

3.1 Introduction

Large-scale environmental gradients are common in nature and may influence life history patterns (Cowen 1990). A number of fish species are known to show phenotypic variation in association with environmental gradients of temperature and seasonality (Robertson et al. 2005, Conover et al. 2006). Studies of the geography of phenotypic variation have been used to identify population structure (Swain and Foote 1999). Temperature is likely to be one of the most important factors influencing life histories, especially for ectotherms (Sebens 1987). Temperature has a significant effect on metabolic rate, growth and overall size of ectotherms (Rilling and Houde 1998). Therefore, as poikilotherms, growth and life history patterns of reef fishes can be expected to vary at geographic or latitudinal scales as well as with environmental gradients (Atkinson 1994).

The spatial scales of phenotypic and genotypic variation in marine systems are important in understanding the ecological and evolutionary processes (Conover et al. 2006). Species distributed across broad geographic ranges provide an opportunity to study intra-specific changes and co-variation in life history in response to environmental gradients. Studies from a wide variety of organisms have linked general trends in life history parameters to latitudinal gradients and include traits such as morphology (Floeter et al. 2004), growth (Brown et al. 1998, Conover et al. 1997, Conover and Present 1990, Denit and Sponaugle 2004, Murray 2000, Present and Conover 1992, Yamahira and Conover 2002, and mortality (Conover 1990, Ebert et al. 1999, Schultz and Conover 1997). Similar patterns of life history variation have evolved independently in geographically isolated populations, and it is suggested that consistent patterns of phenotypic variation may be adaptive (Endler 1986).

3.1.1 Geographic variation in body size, growth and longevity

Life histories reveal complex patterns often associated with particular environments. Plasticity in any demographic trait is suggested to be due to environmental variation (Rochet 2000). One prediction is a trend towards larger body size at higher latitudes, which is usually attained with slower, prolonged growth over a longer lifespan (Atkinson 1994, Mangel and Stamps 2001). The observation that organisms tend to grow bigger in colder environments is known as Bergmann's rule (Bergmann 1847). Recently, Bergmann's rule has been more generally applied to describe an increase in body size at higher latitude or when ambient temperature decreases (i.e. Meiri and Dayan 2003, Murphy 1985). The initial explanation suggested was that this is for heat conservation (Ashton et al. 2000, Bergmann 1847). However, current evidence proves that Bergmann's rule can be extended to ectotherms (Ashton and Feldman 2003, Morrison and Hero 2003). This is primarily mediated by season length rather than temperature (Mousseau 1997). Although there are some exemptions, changes in body size consistent with Bergmann's rule is common in literature (i.e. Meiri and Dayan 2003, Murphy 1985, Ray 1960).

In a number of cases, species distributed over latitudinal gradients show little phenotypic change despite major shifts in temperature. This has been identified as countergradient variation (CnGV) (Conover et al. 1997). Phenotypic traits are distributed in nature so that they counteract environmental influences across an ecological gradient (Conover and Schultz 1995). CnGV is known to generate phenotypic similarity. In some cases, specimens from the wild may appear identical, and therefore underlying genetic variation is hidden (Conover et al. 2006). If the plasticty can be accounted for by environmental differences among locations, then evidence of CnGV can be observed from field studies (Conover et al. 2006). However, the genetic component of CnGV can only be disentangled through common garden experiments (Conover and Schultz 1995).

Although it is not an universal phenominon (Conover et al. 2006), within the last decade, 26 species have displayed evidence of CnGV. Most of these involve physiological traits that are compensatory in nature, such as genotypes with elevated growth rates found in enviroments where the growing season is short (Conover and Present 1990).

If reef fishes really do follow CnGV at higher latitudes (lower temperatures), they would exhibit larger final body sizes but smaller size at age (i.e. slower growth). With slower growth there is likely to be a trend towards later maturation, but greater longevity (Stearns and Koella 1986). With later maturation reproductive effort is obviously delayed and therefore potentially decreased (Bell et al. 1992).

There is now increasing evidence that size of reef fishes varying along latitudinal gradients (Abookire and Macewicz 2003, Adams et al. 2000, Choat et al. 2003, Fowler et al. 2000, Gust et al. 2002, Jensen et al. 2000, L'Abee-Lund et al. 1989, Kritzer and Davies 2005, Robertson et al. 2005a). This is linked to the finding that demographic variation among populations of reef fishes may be more common than once believed (Choat et al. 2003, Choat and Robertson 2002, Gust et al. 2001, Meekan et al. 2001).

3.1.2 Fishing effects

Theoretical and empirical studies demonstrate that life history parameter values will change in response to fishing (Fromentin and Fonteneau 2001, Jennings et al. 1999a, Jennings et al. 1999b, Robertson et al. 2005b, Rochet et al. 2000, Rowell 1993). These changes may be a result of phenotypic plasticity, but in the longer term, the selective fishing pressure may lead to genetic changes (Rowell 1993). Sadovy et al. (2003) identified adverse impacts of fishing on Humphead Wrass, *Cheilinus undulatus*.

The existence of fishing effects on life history traits is well documented (e.g. Nelson et al. 1987, Trippel 1995, Trippel et al. 1997). However, fishing effects are difficult to measure because they are often confounded with other environmental changes (e.g. changes in temperature or predation) and cannot be separated in a single-species, single-location time series (Hempel 1978, Pitt 1975, Rijnsdorp et al. 1991, Rijnsdorp and Van Leeuwen 1992). Therefore, a comparative approach involving many populations seems appropriate. An understanding of the links between life histories and responses to exploitation could provide the basis for predicting shifts in community structure by identifying susceptible species and linking life history tactics with population dynamics (Jennings et al. 1999b). However, possible linkages between life history and changes in community structure are not yet been comprehensively understood due to a lack of data for exploited fishes. Information on geographic variation in the body size, population densities, longevity, survivorship, and growth rates can provide evidence of possible fishing effects (Robertson et al. 2005b).

The present study provides an opportunity to determine if effects of fishing can be readily separated from natural variation in reef fish demography. In order to achieve this, longevity, adult survivorship, size and abundance for sets of geographically dispersed reef fish, exposed to varying level of fishing pressure were examined (Choat et al. 2003, Dulvy et al. 2004b, Hawkins and Roberts 2003, Jennings and Polunin 1996, and Williamson et al. 2004).

3.1.3 The study species

Gray snapper (*Lutjanus griseus*)

Lutjanus griseus, commonly referred to as mangrove or gray snapper, is a tropical and subtropical reef fish found along the southeastern Atlantic coast of the United States from North Carolina to Bermuda, throughout the Gulf of Mexico, and south to Brazil (Allman and Grimes 2002). As one of the top predators in the seagrass beds and on coral reefs, gray snapper have an important ecological role in marine ecosystems (Denit and Sponaugle 2004). They can tolerate and grow over a wide range of temperatures and salinities (Wuenschel et al. 2004). Gray snappers are associated with coral reefs, shipwrecks, rocky outcroppings, mangroves, and other natural live-bottom areas, usually as large aggregations (Claro and Lindeman 2003). Spawning occurs in offshore waters around reefs, wrecks, and other bottom structures (Domeier and Colin 1997). Gray snapper undergo ontogenic habitat shifts (Allman and Grimes 2002). Juveniles are common in inshore waters and adults are found in areas of moderate to high relief on the continental shelf (FLMNH 2006). Settlement occurs at ~14mm SL (Wuenschel et al. 2004). At a size of approximately 80 mm they move into shallow rocky areas and the coastal reefs where they are commonly found as adults (FLMNH 2006). Sexual maturity occurs at about 190 mm SL (Wuenschel et al. 2004), which is probably the size when some gray snapper reach an age of 1 or 2 years (Allman and Grimes 2002).

There are several studies examining age and growth of *L. griseus*. Fischer et al. (2005) studied the age, growth and mortality of *L. griseus* from Louisiana using thin sagittal sections; Denit and Sponaugle (2004) studied the growth variation across a latitudinal gradient; Allman and Grimes (2002) studied temporal and spatial variations in settlement and growth of gray snapper from the west Florida shelf. Burton (2001) looked at the age, growth and mortality of the *L. griseus* from the east coast of Florida and validated periodicity of opaque zone formation using marginal increment analysis. There are few others who studied the age and growth of gray snapper (i.e. Ahrenholz 2000, Faunce et al. 2002, and Rutherford et al. 1989). Early 1990's harvest and seasonal restrictions on established red snapper fisheries (*Lutjanus campechanus*) coincided with a rapid expansion of the gray snapper fisheries in many regions (Fischer et al. 2005). Recreational anglers in some areas target gray snapper once they have reached their bag limit of red snapper. Currently there is a 305 mm (12 inches) minimum size and a recreational bag limit of 10 fish/person/day for gray snapper has enforced in the Gulf of Mexico (Fischer et al. 2005)

Snappers are subject to substantial fishing mortality from commercial and recreational fisheries (Goodyear 1995). Life history characteristics such as longer lifespan (i.e., red snapper, *Lutjanus campechanus,* 53 years, Wilson and Nieland 2001), slow growth and late reproduction in some regions, as well as behavioral patterns associated with aggregation formation and site fidelity make them particularly vulnerable to exploitation (Coleman et al. 2000). According to the limited information available, many snapper species in the Atlantic are considered over fished (Musick 1999, Sadovy and Eklund 1999), for example *Lutjanus campechanus* (Wilson and Nieland 2001)

The Lutjanidae is an ideal group to identify some of the patterns involved with latitudinal variation due to their abundance and distribution. They share many of the life history traits, such as potentially longer life spans typical of larger mobile reef fish (Meekan et al. 2001). Large variations in body size within the family provide a good opportunity to investigate the correlation between body size and other life history traits (Kamukuru et al. 2005). In addition, the widespread dispersal of pelagic larvae avoids the need to separate ancestral effects from genetic responses as this reduces the opportunity for local genetic differentiation (Schultz and Warner 1991)., Variations in life history parameters between populations therefore, are likely to be a response to environmental conditions or fishing effects.

Hogfish (*Lachnolaimus maximus*)

The hogfish, *Lachnolaimus maximus* is a monotypic member of the family Labridae (wrasses). Hogfish have a recorded range in the warm subtropical and tropical waters from Nova Scotia, Canada, to northern South America, to Bermuda, the Caribbean Sea and Gulf of Mexico (Ault et al. 2003). Ontogenetic migrations occur between the shallow coastal lagoons that serve as nursery areas for juveniles and the offshore coral reef and hard-bottom habitats used by the adults (Ault et al.

2003). As a predator, hogfish play an essential ecological role within the larger multi-species reef fish community.

Hogfish are protogynous hermaphrodites, i.e., they begin life as females then change to males and also exhibit sexual dimorphism (Davis 1977). The extensively synthesized population dynamic database of hogfish demographic parameter estimates was considered to be at a level sufficient to conduct a comprehensive stock assessment and fishery risk assessment (Ault et al. 2003).

L. maximus is an esteemed food fish and supports valuable commercial and recreational fisheries. They are also a popular target of spear fishing. There is some concern that the species may be growth or recruitment overfished in Florida waters. Anecdotal information indicates that average hogfish size has decreased in recent years (DeMaria 1996). Life-history parameters such as size-at-maturity have also changed relative to previous reports of hogfish life-history (McBride 2001). A tendency to remain in the vicinity of diver activity makes hogfish particularly vulnerable to spear fishing. Concerns about the sustainability of the hogfish fisheries have prompted a more in depth look at the status of the stock in Florida (Ault et al. 2003). Fishing pressure on hogfish has reduced many populations to critically low levels such that the species has been identified as vulnerable to extinction (IUCN 2000).

The smaller maximum size of hogfish in south Florida compared to the eastern Gulf of Mexico suggests higher levels of fishing mortality in the former (Ault et al. 2003). A minimum size limit of 305mm FL (12 inches FL) was instituted in 1994, largely in response to observations of decreasing availability of large hogfish in the Florida Keys (DeMaria 1996). McBride (2001) reported, however, that the size at 50% sexual transformation was considerably larger: 389 mm (15.3 inches) FL. Because a single male controls a harems of as many as 15 females (Colin 1982), harvesting mature males could disrupt reproductive output from an entire harem.

There is no extensive literature on demography of hogfish; however, Ault et al. (2003) documented a stock assessment of the Florida hogfish fishery. McBride (2001) has also studied the age, growth and reproduction of hogfish. Annual periodicity of check-marks observed in sagittal otoliths has been validated by McBride (2001) for *L. maximus*.

Labrids are both highly characteristic of coral reefs and increasingly targeted in localized reef-based fisheries (DeMartini 1993, Russ 1991). However, labrids have a characteristically dynamic demography, where rapid growth rates, especially in males, are linked to relatively high mortality rates and reduced life spans (Choat et al. 1996, Choat et al. 2003, Choat and Robertson 2002). The extent to which these features vary with increase in body size is a matter of considerable interest.

3.1.4 Objectives of the study

The aims of this chapter were to demonstrate demographic variability across 1) large latitudinal gradient, and 2) under different fishing regimes of two species of exploited reef fishes, *L. griseus* and *L. maximus,* in the Caribbean. Specific objectives were to describe age-based demographics, growth patterns, longevity, age-structures and mortality of the population.

3.2 Materials and methods

Samples of *L. griseus* were collected from 3 locations in the Atlantic, namely, Los Roques (11.8° N), Belize (16.8° N) and Bermuda (32.3° N), whereas, *L. maximus* were collected from Los Roques, Belize, Bermuda and Margarita (10.9° N) (table 3.1). Locations were spanning over 20° of latitude for both species, allowing effective latitudinal comparisons (Fig. 3-1). Samples were obtained from both fishery dependent (commercial fishing) and independent (research spear fishing) methods. A total of 194 *L griseus* and 357 *L. maximus* were examined in this study.

Chapter 2 details all experimental and analytical procedures adopted in the study and also a brief description of each locality.

Figure 3-1. Map showing sampling locations (circled); 1. Belize, 2. Bermuda, 3. Los Roques, and 4. Margarita in the Atlantic.

3.3 Results

3.3.1 Otolith interpretation and age determination

The sagittal otoliths of *L. griseus* and *L. maximus* are fusiform in shape, laterally compressed, with a concave distal surface, and a slightly pointed rostrum and post-rostrum. Sectioned otoliths had a highly characteristic appearance, the depth of the sulcal groove increases with increasing age. *L. maximus* has slightly deeper sulcal groove compared to *L. griseus.* Annuli were counted in the region from the primodium to the proximal surface along the ventral margin of the sulcus acousticus. Annuli in this region were well defined and more readily interpreted.

Dorsal view ventral view

Source: http://www.sefscpanamalab.noaa.gov/OtolithGuide

Figure 3-2. *L. griseus* (top) and *L. maximus* (bottom) whole otolith pairs: ventral and dorsal views.

The left and right otoliths were tested for differences in otolith weights using a paired *t*-test. There was no significant difference (t=0.914, df=5, p>0.05) between the weights of the left and right otoliths and therefore, left sagittae was chosen for further analysis in order to maintain consistency. However, right sagittae were selected whenever left sagittae was not available or not suitable for ageing.

Table 3-1. Sampling locations, mean sea surface temperatures and sampling years

Locality	Latitude	Mean SST (°C)	Sampling years
Belize	16.8° N	28.1	*L. griseus* – 2002
			L. maximus – 2002
Bermuda	32.3° N	22.9	*L. griseus* – 2002
			L. maximus – 2001/2002
Los Roques	11.8° N	27.1	*L. griseus* – 2002 and 2004
			L. maximus – 2002 and 2004
Margarita	10.9° N	27.0	*L. maximus* – 2005

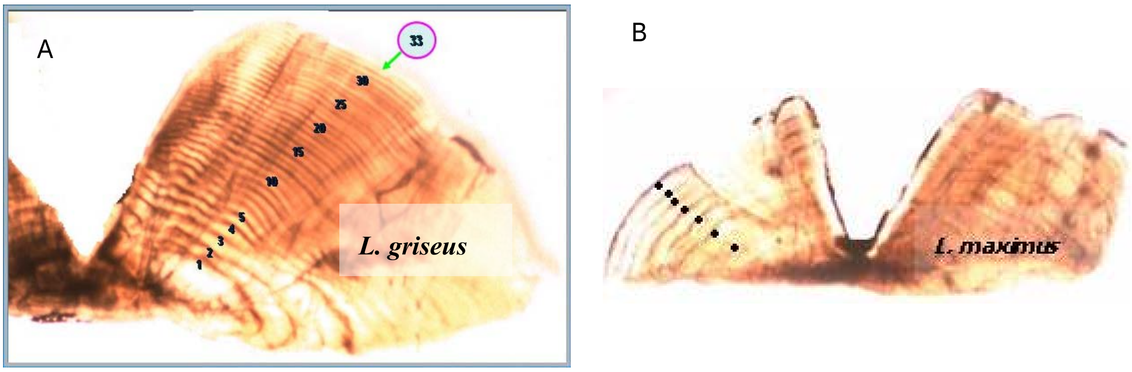


Figure 3-3. Sagittal sections showing alternating opaque and translucent bands. A) *L. griseus* (from Bermuda, age= 33 yr, FL= 770 mm) B) *L. maximus* (From Los Roques, age=7 yr, FL=680 mm)

Sagittal otoliths of both *L. griseus* and *L. maximus* were found to have a distinct pattern of alternating translucent and opaque bands (annuli). The first few annuli were somewhat broad and diffuse with subsequent annuli becoming progressively more compact towards the edge of the otolith. Growth increments were clearly visible as opaque bands in the matrix of the sectioned otolith when viewed under transmitted light and they were readily interpretable for ageing.

Table 3-2. Demographic information for *L. griseus and* L. *maximus*. T_{max} is the mean age of the oldest 10% of the population and L_{max} is the mean size of the largest 10%.

Species	Locality	L_∞	*k*	t_o	Age range (yr)	T_{max} (yr)	Size range (FL, mm)	L_{max} mm	n
L. griseus	Belize	459	0.406	-0.110	1-6	5	198-440	398	40
	Bermuda	523	0.257	-0.106	1-34	27.7	102-770	634	58
	Los Roques	378	0.479	-0.079	1-12	9.5	90-466	373	96
L. maximus	Belize	896	0.104	-0.272	1-7	5.9	101-554	427	109
	Bermuda	483	0.315	-0.169	1-16	14.8	82-659	555	53
	Los Roques	835	0.122	-0.249	1-10	8.9	202-687	603	99
	Margarita	427	0.253	-0.190	1-5	4.8	125-353	314	96

A total of 194 *L. griseus* otoliths from 3 locations- Belize, Bermuda and Los Roques - were examined, 357 as were those from individuals of *L. maximus* from 4 locations- Belize, Bermuda, Los Roques, and Margarita (table 3.2). Ages could not be determined for 8 *L. maximus* and they were excluded from further analysis. There was no apparent relationship between readability and size, age or location, except for Bermudian samples, which showed clearer bands. Table (3.2) summarizes the von Bertalanffy growth parameters for *L. griseus* and *L. maximus*.

3.3.2 Sagittal weight and age relationship

Otolith weight was linearly correlated with estimated fish age for both species and all the locations (r^2 values: *L. griseus* - Belize 0.84, Bermuda 0.96, Los Roques 0.88; *L. maximus* - 0.87, 0.93, 0.82, and 0.77 for Belize, Bermuda, Los Roques and Margarita, respectively) (Figure 3.4 and 3.5). This suggests the otoliths continue to grow in mass even if the fish has reached its maximum size. Because the otoliths grow throughout the life of the fish and have regularly formed growth increments, otolith weight can be a very good proxy for fish age. Otolith weight explained 84% of the variability in *L. griseus* age, and 77% in *L. maximus*. ANCOVA results showed sagittal mass and age relationship was strongly significant for *L. griseus* (F=38.3, p=0.000, df=2), and pairwise comparisons suggested this relationship differed significantly among all three locations. . Similarly, ANCOVA revealed significantly different sagittal weight–age relationships among locations for *L. maximus* (p=0.000, F=150.02, df=3). Pairwise comparisons for *L. maximus* demonstrated significant differences for all pairs except Belize and Bermuda.

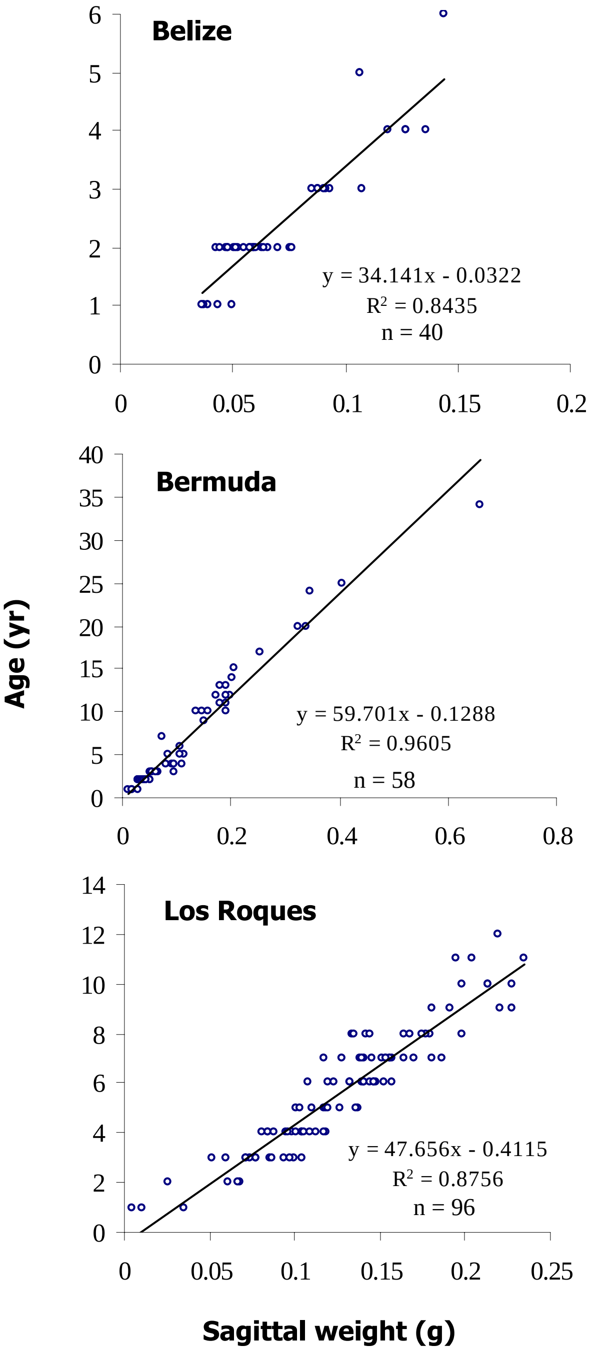


Figure 3-4. Regressions of sagittal weight on age for *Lutjanus griseus* by region.

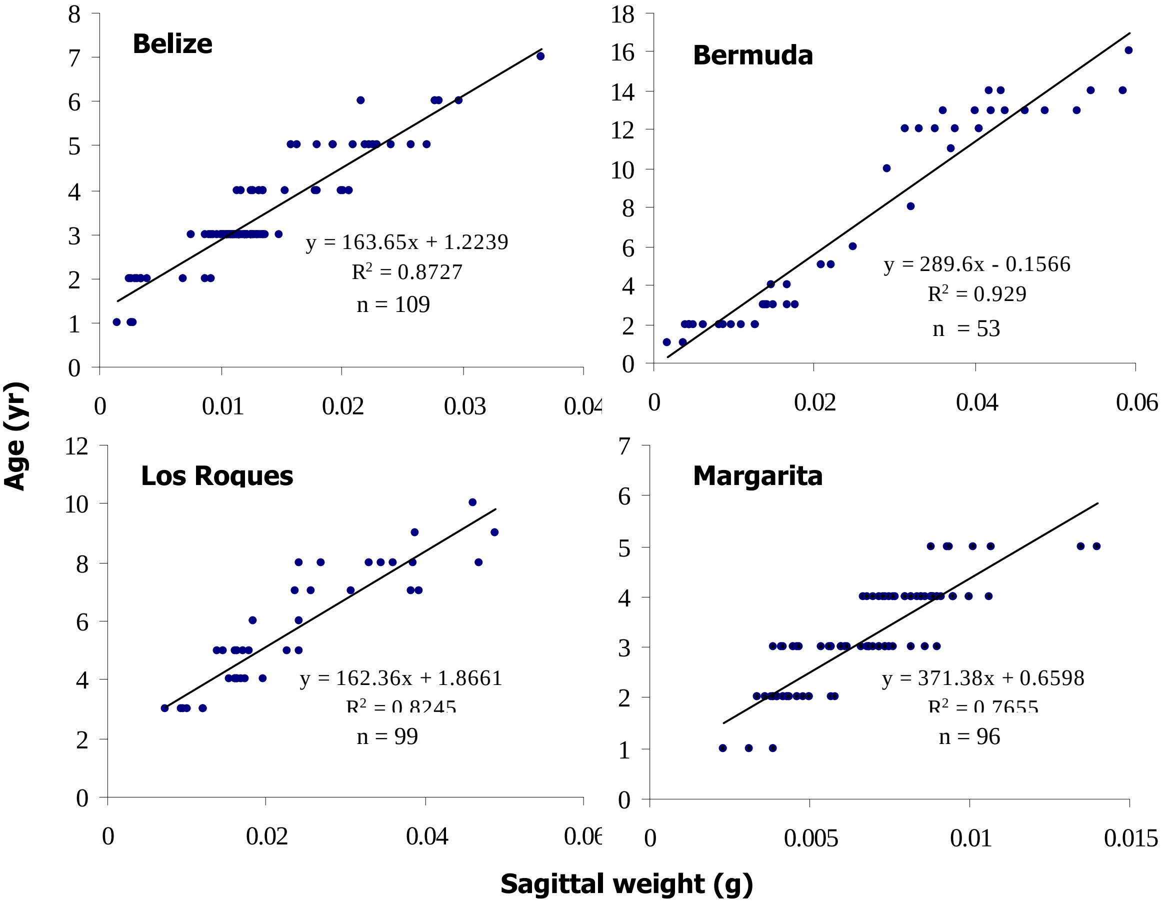


Figure 3-5. Regressions of sagittal weight on age for *Lachnolaimus maximus* by region.

3.3.3 Longevity and mean maximum age (T_{max})

Longevity for *L. griseus* varied from 6 years at Belize, to 12 years at Los Roques to 34 years at Bermuda (table 3.2). There was a 5-fold difference in longevity between Belize and Bermuda.

The maximum longevity observed in *L. maximus* was 16 years for Bermuda and 10 years for Los Roques. The margarita population was relatively short-lived, with the oldest fish estimated to be 5 years of age, while in Belize a few attained a maximum age of 7 years. Therefore, the maximum age in the Bermuda population was 3-fold higher than that in the Margarita population. Maximum longevity showed a strong negative relationship (r^2=0.99 and 0.78) with sea surface temperature for both *L. griseus* and *L. maximus* (fig. 3.6).

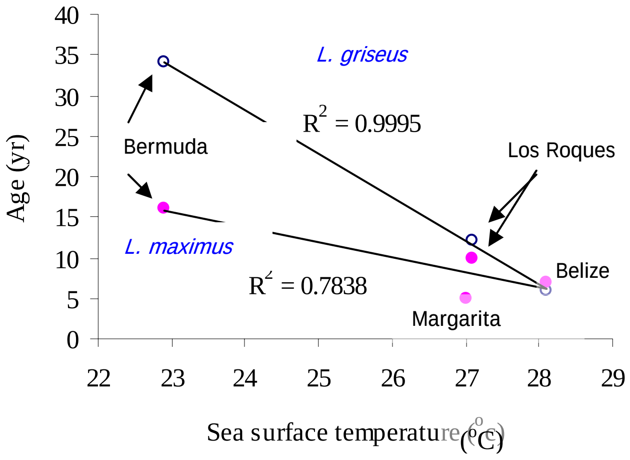


Figure 3-6. Relationship between Sea Surface Temperature and maximum longevity for *L. griseus* and *L. maximus*.

3.3.4 Lifetime growth trajectories

Figures 3-7 and 3-8A show the comparison of von Bertalanffy growth curves. Lifetime growth curves for *L. griseus* showed considerable differences among locations indicating they have different growth trajectories. *L. griseus* approached an asymptote at age 12 years in Bermuda compared to age 7 in Los Roques. However, the Belize population subjected to intense fishing, showed no obvious asymptote and displayed somewhat continuous growth.

L. maximus showed similar patterns among location. They approached asymptotic size at around age 9-10 years in Bermuda and Los Roques. Belize and Margarita populations subjected to intense fishing, showed continuous growth with no clear asymptote. L_∞ was unusually higher (895 mm) in Belize than other localities, although observed mean size was only 278 mm. Hogfish from Bermuda and Los Roques were larger at-age than those from Belize and Margarita (Fig. 3-9 and 3-10). Furthermore, Belize and Margarita populations had similar growth rates in their initial 2 years but diverged thereafter, with lower growth in the latter (Fig. 3-10). Patterns of growth varied among locations such that the 95% confidence regions around the least squares estimate of k and L_∞ for *L. griseus* showed no overlapping

(Fig 3.8 B). Similarly, 95% confidence regions (fig 3.11) showed no overlapping for *L. maximus* among locations indicating different growth trajectories.

3.3.5 Maximum size and mean maximum size

Maximum and asymptotic sizes showed a high degree of variation among location (table 3.2). The largest *L. griseus* (770 mm) was found in Bermuda. In contrast the largest gray snapper found in Belize was only 440 mm. The largest *L. maximus* measured 678 mm and was found in Los Roques. However, *L. maximus* from intense fishing locations were much smaller (Margarita, 353 mm and Belize, 553 mm).

Table 3.3 displays mean sizes for each population and re-parameterized von Bertalanffy growth parameters (L_τ, L_ω and L_ν, after Francis [1990]). Hogfish samples from Margarita and Belize, both subjected to high fishing pressure, had smaller mean lengths (239 mm and 278 mm, respectively). Similarly, gray snappers collected from Belize, with high fishing pressures had a smaller mean FL (281 mm). In Los Roques, where reefs were protected from fishing, mean lengths were much higher for both species.

Table 3-3. Mean size and size at three arbitrary ages (re-parameterized von Bertalanffy parameters [L_τ, L_ω and L_ν] after Francis [1990]).

Species	Locality	Mean size ± SD	L_τ ± CI	L_ω ± CI	L_ν ± CI
L. griseus	Belize	281 ± 69.0	215 ± 13.3	335 ± 20.7	356 ± 22.1
	Bermuda	345 ± 146.5	119 ± 7.4	290 ± 17.9	426 ± 26.4
	Los Roques	336 ± 55.7	160 ± 9.9	302 ± 18.7	356 ± 22.1
L maximus	Belize	278 ± 76.6	126 ± 7.8	271 ± 16.8	356 ± 22.0
	Bermuda	353 ± 130.3	158 ± 9.8	341 ± 21.1	445 ± 27.6
	Los Roques	459 ± 119.1	199 ± 12.4	381 ± 23.6	452 ± 28.0
	Margarita	239 ± 52.3	141 ± 8.7	264 ± 16.4	314 ± 19.5

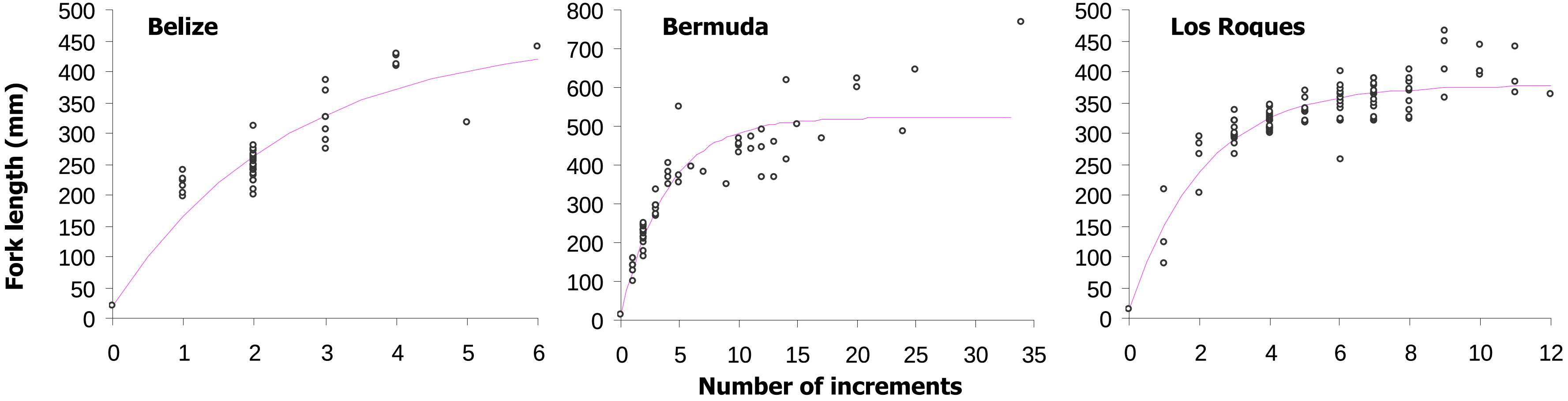


Figure 3-7. Size-at-age data with fitted VBGF for *L. griseus*, plotted by region. Curves have been constrained to 20 mm approximate size-at-settlement.

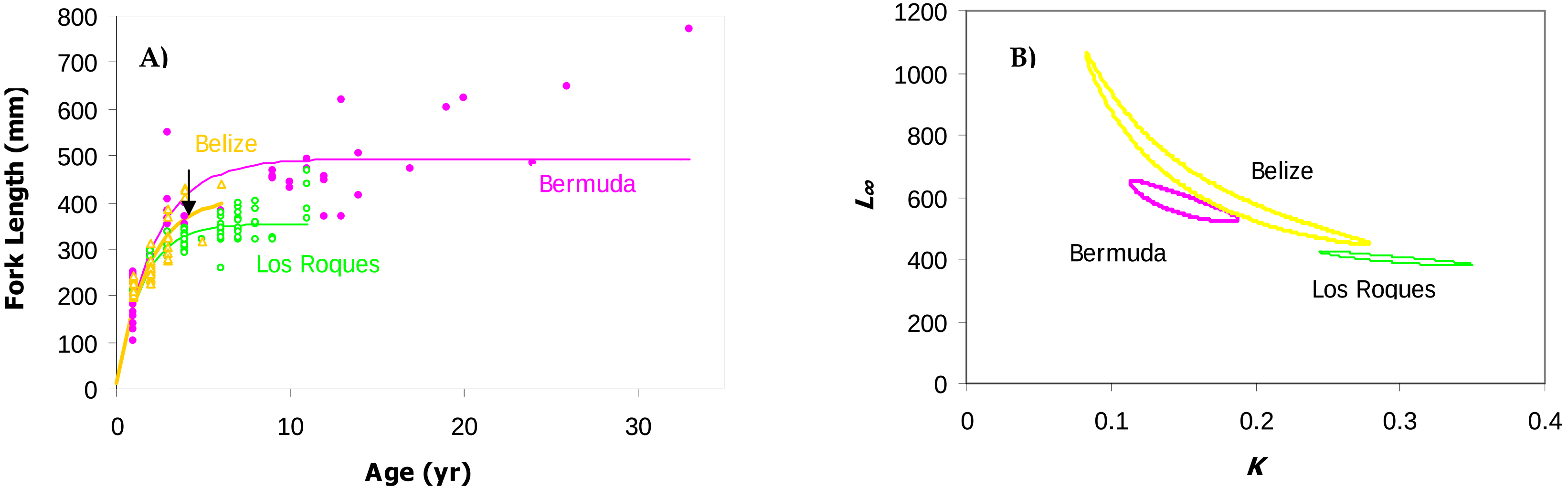


Figure 3-8. *L. griseus* A) Comparison of von Bertalanffy growth curves among 3 locations B) 95% confidence regions around least squares estimates of K and L_∞ are shown (after Kimura 1980).

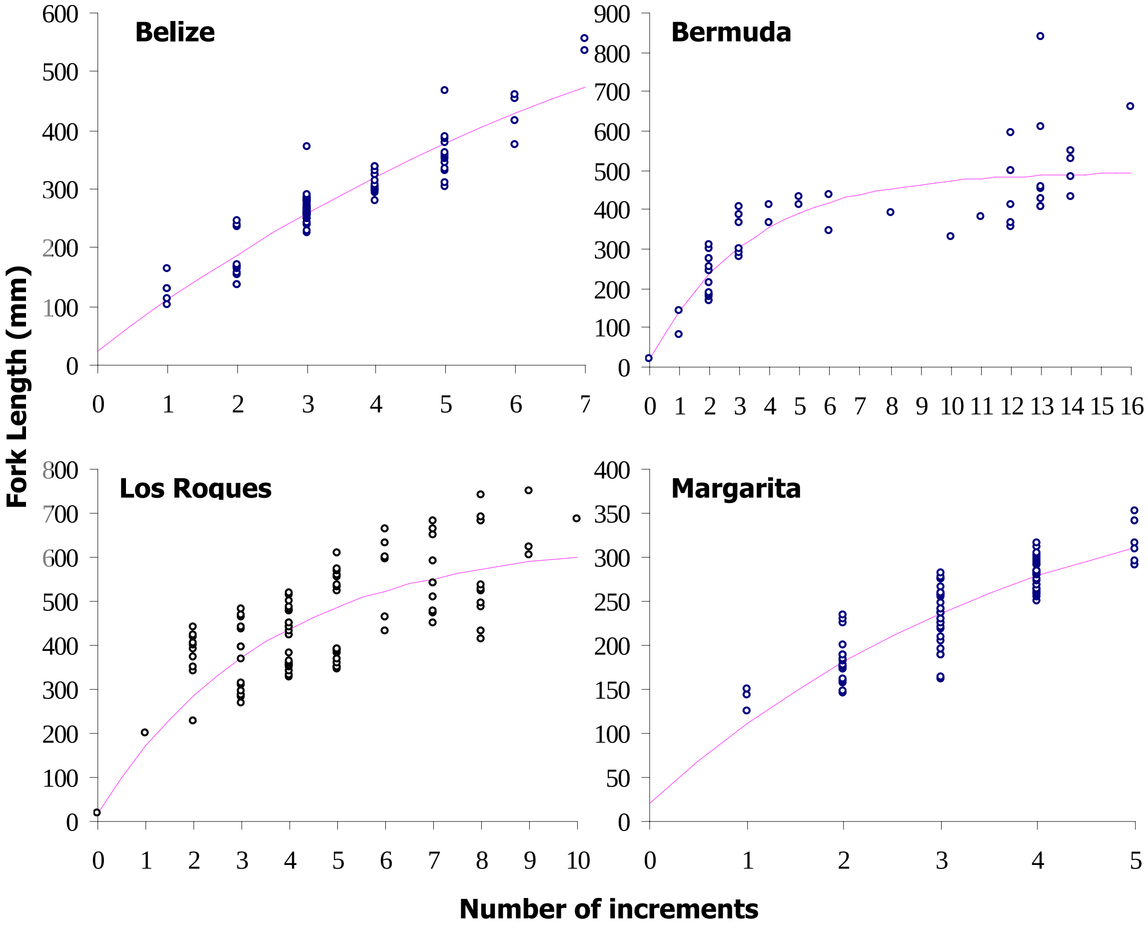


Figure 3-9. Size-at-age data with fitted VBGF curves for *Lachnolaimus maximus* by region. Curves have been constrained to 20 mm approximate size-at-settlement.

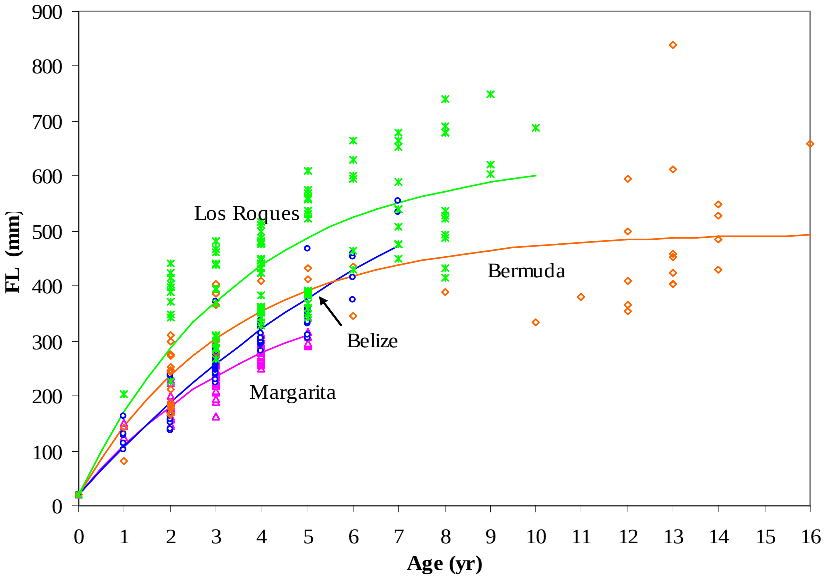


Figure 3-10. *Lachnolaimus maximus,* comparison of VBGF curves among location.

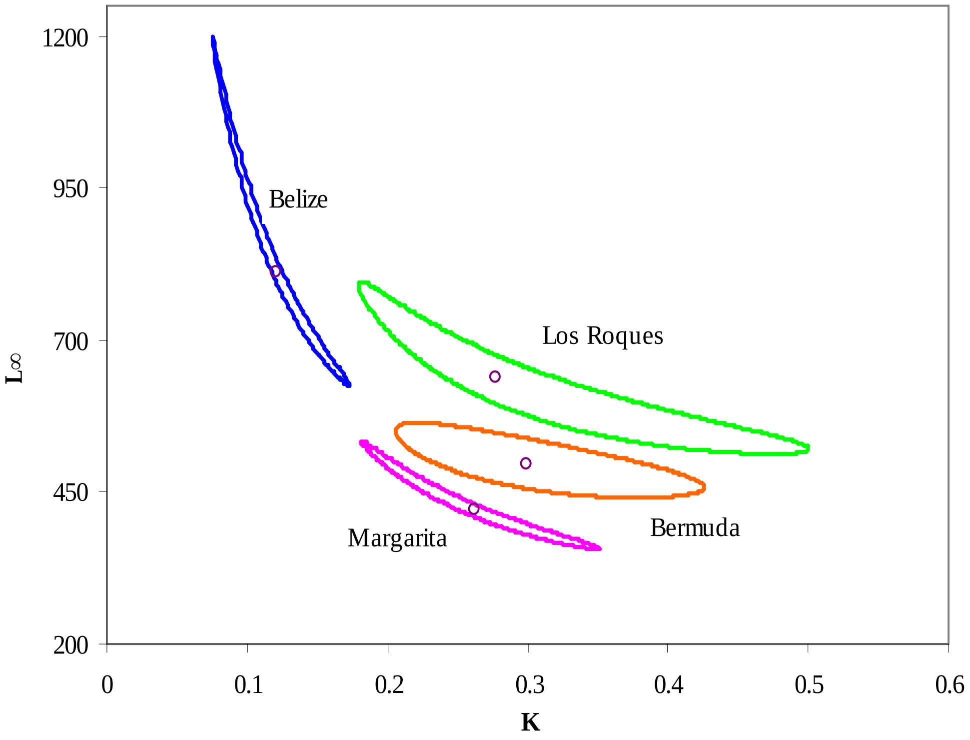


Figure 3-11. Plots of approximate 95% confidence regions around the parameter estimates *k* and L_∞ of VBGF curves for *L. maximus*.

3.3.6 Age structure and mortality estimates

Both Bermuda and Los Roques populations of *L. griseus* had multimodal age distributions (figure 3-12A). In Bermuda, strong age classes were observed at the age 2 and 10 years whereas in Los Roques modes at ages 4 and 7. The Belize population had a unimodal distribution with a strong mode at age 2.

L. maximus in Belize and Margarita displayed unimodal age distributions with strong modes at age 3 and 4 (Fig. 3-13A), whereas in both Bermuda and Los Roques they showed bimodal distributions. Strong age classes of 2 and 13 years were evident in Bermuda and 4 and 8 years in Los Roques.

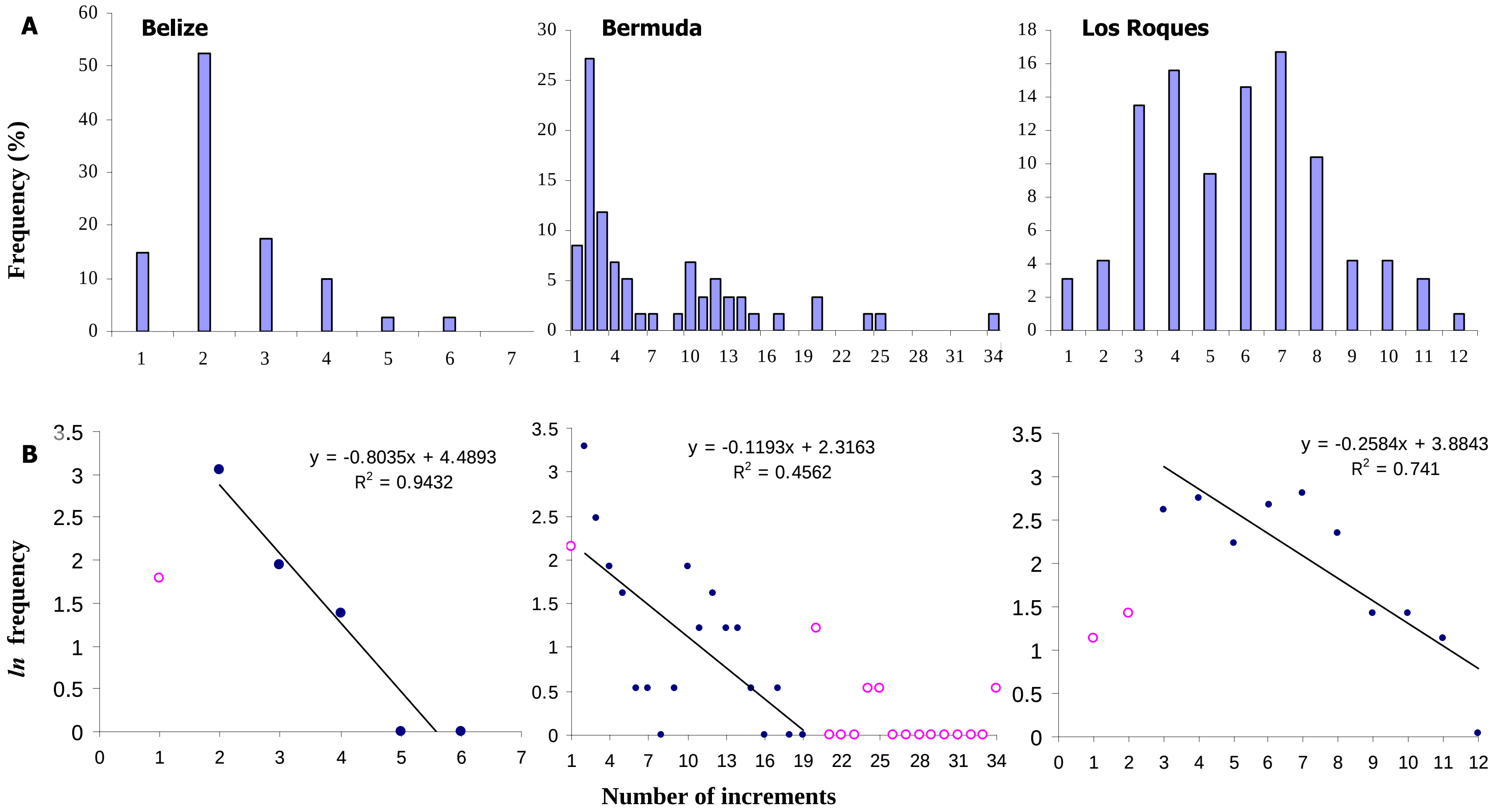


Figure 3-12. ***Lutjanus griseus*** **(A) Age-frequency (%) distribution (B) log-linear regression of abundance on age by location.**

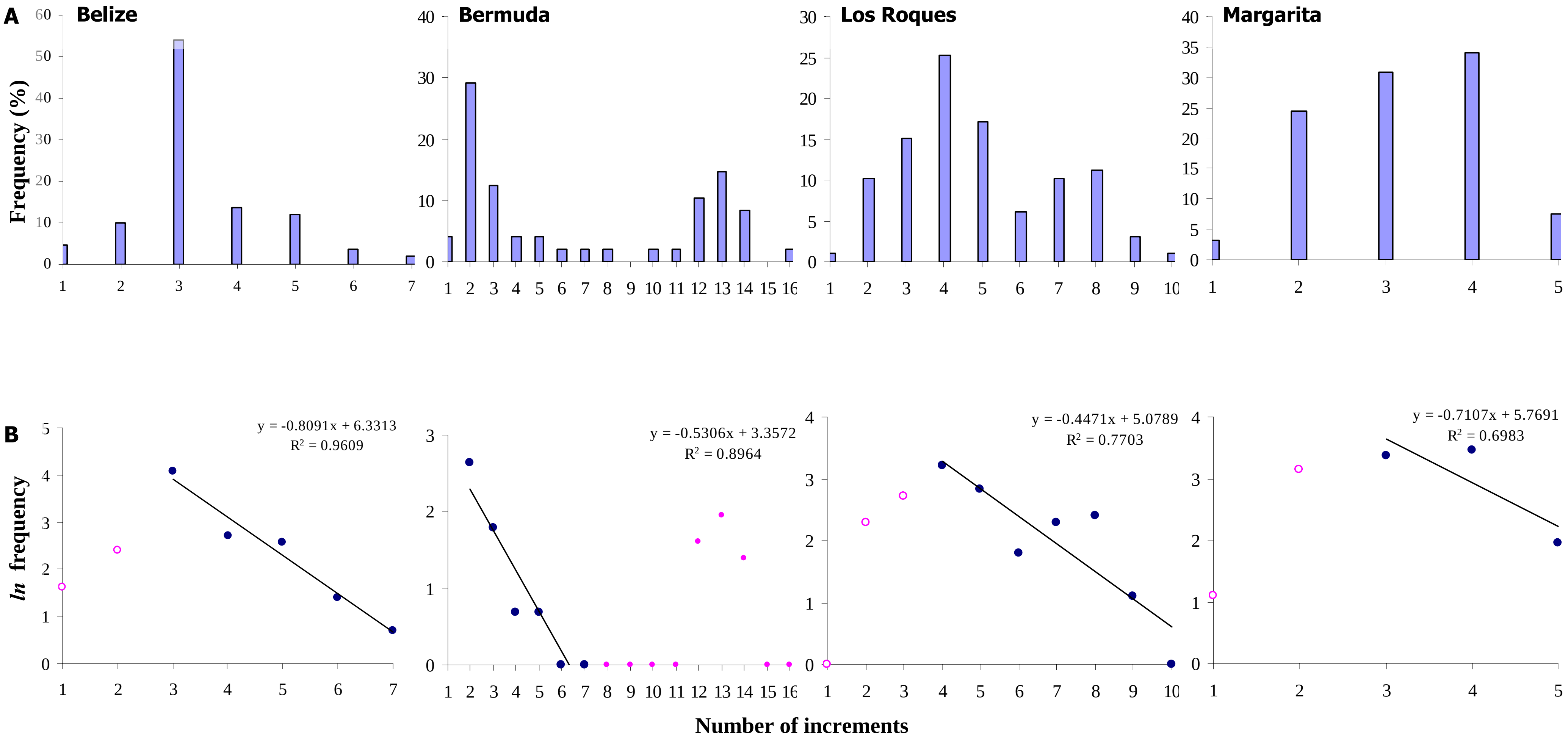


Figure 3-13. *Lachnolaimus maximus* (A) Age-frequency (%) distribution (B) log-linear regression of abundance on age by location.

Table 3-4. Instantaneous mortality rates, *Z*, and annual percentage survivorships (S) for *L. griseus* and *L. maximus*

	Location	Instantaneous mortality rate, Z	Survivorship S (%)
L. griseus	Belize	0.80	45
	Bermuda	0.12	89
	LR	0.26	77
L. maximus	Belize	0.80	45
	Bermuda	0.53	59
	LR	0.45	64
	Margarita	0.71	49

The total instantaneous mortality rate for *L. griseus* was highest in Belize (0.8), followed by Los Roques (0.26) and Bermuda (0.12) (Table 3-4). ANCOVA suggested the differences in mortality rates among location were significant. Pairwise comparisons showed that the values for Belize and Los Roques were significantly lower than that for Bermuda for *L. griseus* (P=0.025, F=4.09, df=2).

Fig. 3-13B shows the mortality patterns for *L. maximus* among localities. The Los Roques population had the lowest Z (0.45), followed by Bermuda (0.53). In contrast, Z was highest in Belize (0.81), followed by Margarita (0.71). ANCOVA demonstrated that mortality rates differed significantly among location (P=0.000, F=20.5, df=3), and pairwise comparisons suggested that the mortality rate in Bermuda differed significantly from the three other locations.

3.3.7 Length-weight relationship

A positive exponential relationship was observed for all the three locations where, weight-length data were available (fig. 3-14). Weight data were not available for Margarita population. When increase in weight is proportional to length (allometric growth), then the estimate for b equals 3. However, b was smaller than 3 in Bermuda and Los Roques populations, suggesting that the weight increases at a slower rate than length. Weight data were not available for *L. griseus.*

The body weight-FL relationships of *L. maximus* for are described in the following regressions:

Belize ln (W) = 2.98 ln (FL) - 10.6 (R^2= 0.98)

Bermuda ln (W) = 2.46 ln (FL) - 7.6 (R^2= 0.96)

Los Roques ln (W) = 2.64 ln (FL) - 8.6 (R^2= 0.95)

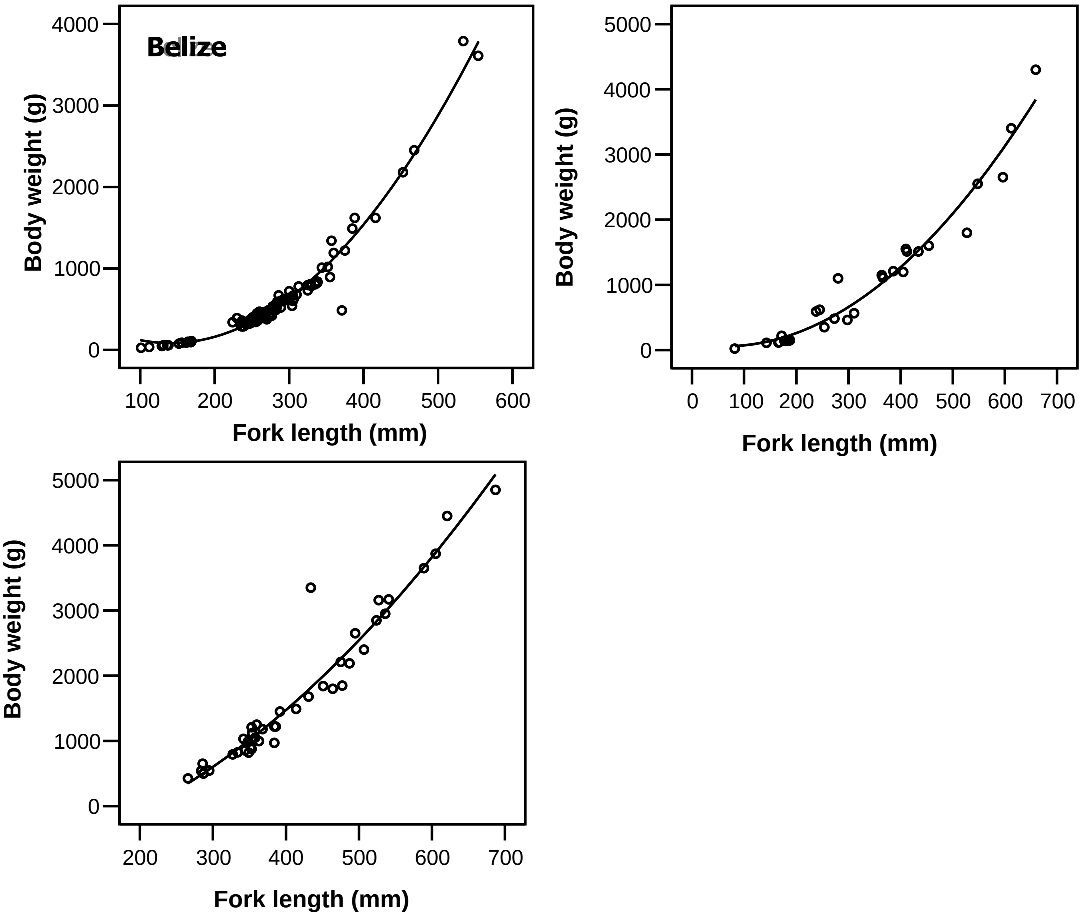


Figure 3-14. Scatter plots of the length-weight relationships of *Lachnolaimus maximus.*

3.4 Discussion

Otolith structure

Thin-sectioned sagittal otoliths gave reliable age estimates that satisfied the major criteria needed to validate the relationship between increment periodicity and age (Fowler 1990). The placement of the first annulus varied in distance from the core. Fischer et al. (2005) observed a similar pattern for gray snapper, while Wilson and Nieland (2001) did so for red snapper. They suggested that this variability may be a function of both a long spawning season, common to both species, and also a rapid growth rate as juveniles. This variability in first annulus location and difficulty in reading the outermost increment are the major reasons for reader variation in otolith interpretation (Fisher et al. 2003).

The positive linear relationship between number of increments and sagittal weight indicated that otoliths grow throughout the life, and therefore, the increment pattern can readily be interpreted as corresponding to an annual time scale. Since otoliths grow throughout a fish's life independent of the somatic growth, the otolith weight has been used as a predictive tool to determine age in a number of species (Cardinale and Arrhenius 2004, Lou et al. 2005, Pawson 1990, Pilling et al. 2003). However, other studies have found considerable variability in older age classes (i.e. Fisher et al. 2003), thus, preventing a precise age estimate based on otolith weight alone.

Growth variation

There were striking differences in the growth characteristics of the populations examined. Growth curves were asymptotic in many instances, however, *L. griseus* from Belize and *L. maximus* from Belize and Margarita (both locations subjected to heavy fishing pressure) showed no asymptote. Most of the growth occurred within the first third of the lifespan for the long-lived *L. griseus* population from Bermuda.

Both gray snapper and hogfish populations from Bermuda, which had extended lifespans and larger body sizes, showed smaller theoretical maximum sizes compared to mean maximum size. Johnson et al. (1994) noted that the presence of larger, older fish may result in the overall model coming to an asymptote at a smaller L_∞ and having a larger *k*. Knight (1969) noted an inverse relationship between *k* and L_∞; therefore, smaller *k*'s will result in higher L_∞ values. All the other populations exhibited L_∞ values greater than mean maximum sizes. Hogfish from Belize and Los Roques showed exceptionally high L_∞ values compared to mean maximum sizes. Significant differences in theoretical maximum size (L_∞) between locations were also observed. The maximum theoretical sizes for *L. griseus* estimated with von Bertalanffy growth model were 378 mm, 459 mm and 523 mm FL from Los Roques, Belize and Bermuda populations, respectively. Fischer et al. (2005) had reported a L_∞ of 656.4 SL for *L. griseus.* Burton (2001) and Johnson et al. (1994) observed similar results. However, theoretical maximum sizes estimated in present study were smaller for all the locations than those in previous studies.

Longevity and maximum size

Maximum size and longevity achieved were greater in Bermuda populations of both gray snapper and hogfish. Gray snapper ages ranged from 1 yr to maximum age of 34 yr. The oldest fish was sampled from Bermuda. Maximum age recorded in this study was the highest recorded for *L. griseus*. Previously recorded maximum age was 28 years from Louisiana (Fisher et al. 2003). Johnson et al. (1994) recorded 25 years, whereas Burton (2001) reported a non-sex-specific maximum age of 24 years. Samples for both Johnson et al. (1994) and Burton et al. (2001) studies were obtained from Florida where there is high fishing pressure on gray snapper which would shorten the maximum age. Bermudian gray snapper had an extended lifespan with five-fold difference with Belize population and almost 3 fold differences with Los Roques population. Bermuda population also attained larger body size compared to other counterparts. Larger adult body size and extended lifespan in Bermudian populations may be a result of adaptive response to lower average temperatures (due to its high latitude location) experienced during development (Atkinson 1994). Choat and Robertson (2002) have also noted that an increase in average annual temperature correlates negatively with maximum age in some fishes. Luckhurst et al. (2000) found a 5 fold difference in longevity of lane snapper (*Lutjanus synagris*) in Bermuda compared to other Caribbean counterparts. Long lifespan however acts as a buffer against occasional recruitment failures. It is also associated with greater vulnerability to fishing and lengthy recovery times after episodes of population depletions (Jennings et al. 1999a). Choat et al. (2003) also found an inverse relationship between growth and temperature for *Sparisoma viride* across a latitudinal gradient. Many other studies on tropical reef fishes also revealed similar patterns (e.g. Choat and Robertson 2002, Craig et al. 1999, Meekan et al. 2001). Countergradient growth represents a mechanism that compensates for shorter growing seasons provided by low temperatures in high latitudes (Conover 1990). Such compensatory growth may allow temperate species to cope with size-dependent winter mortality (Conover 1990, Schultz and Conover 1997). The inverse relationship between growth and temperature for *L. griseus* is consistent with countergradient growth. Latitudinal increases in size are common among ectotherms (Atkinson 1994, Atkinson and Sibly 1997), including tropical and subtropical reef fishes (Choat and Robertson 2003, Luckhurst et al. 2000). Similar patterns of latitudinal variations such as faster growth and larger terminal size at lower temperatures seem to occur in many taxa of reef fishes in the tropics.

Among all the *L. griseus* populations, the maximum size observed was 770 mm FL individual from Bermuda. Fischer et al. (2005) recorded 756 mm TL from Louisiana and Burton (2001) found an individual from the east coast of Florida recording a maximum size of 760 mm TL. However, maximum size observed from Belize population was only 440 mm FL. There were no representative samples with individuals below 198 mm FL from Belize. Samples were obtained through fishery dependent methods where minimum size limits apply for gray snapper and this could be the main factor influencing the minimum size.

McBride (2001) conducted an empirical study of lifetime growth of hogfish from the eastern Gulf of Mexico and estimated a maximum age of 23 years, whereas in Florida Keys they lived only up to 13 years. Ault et al. (2003) suggested that these differences are due to fishing pressure. Although Belize *L. maximus* population showed unusually high asymptotic size, it is not reflected in its mean size. This would be a result of error in the model estimation.

Age structure and mortality

Gray snapper exhibited multimodal distribution in age frequencies for both Bermuda and Los Roques populations (See Fig. 3-12A). Initial peak at the age class 2 in Bermuda and age class 4 in Los Roques would be when gray snapper started to recruit to the fishery. Successive peaks in age-class abundance were observed. Beckman et al. (1989) suggested year-class variability in these species might be due to environmental factors experienced during early life stages or biological controls on the population (e.g. competition). Although analysis showed these patterns, monthly samples with more representation across a range of age groups would give more realistic picture. However, relatively long lived and strongly multimodal age structure suggests strong fluctuations in recruitment.

Present study showed that fish from intensively fished areas had significantly higher total mortality rates than those in less intensively fished areas. The lowest estimate of instantaneous mortality rate, Z for *L. griseus* was for Bermuda population followed by Los Roques. This is clearly associated with the abundance of older, larger individuals in the sample. In Belize, gray snapper is heavily fished as evident from their high estimates of Z. Apparent age structure, historical landing data and personal observations indicate that gray snapper is lightly fished in both Bermuda and Los Roques. Fischer et al.(2005) estimated total mortality rate of 0.17 for *L. griseus* from Louisiana, however, estimates of Z ranged from 0.15 to 0.5 depending on the method employed (Fischer et al. 2005). In this study, an unusually high Z value (0.80) was observed for Belize population. Life history traits of low rates of mortality and relatively long lifespans observed in Bermuda and Los Roques populations were consistent with those of congeneric species in the area (Fischer et al. 2005). Similarly, highest mortality rates were observed in Belize for *L. maximus* while lowest mortality recorded in Los Roques.

Mortality rates estimated in this study should be treated with caution. Ideally, it would be calculated with repeated sampling through time. However, samples collected for this study had no regular temporal distribution and mortality rates were estimated using log-linear models (Pauly and Munro 1984). Results must also be analyzed carefully when sample size is very small. Errors or uncertainty in age analysis may smooth the distributions and this may obscure prominent year-classes.

Spatial variation in demography

There was strong evidence of regional-scale variation in the demographic patterns in the study species. Any differences in growth trajectories between geographic regions may be a result of genetic and environmental influences (Sebens 1987). It is unlikely that adaptation to such local conditions through genetic selection (Warner and Schultz 1992). Because reef fishes have a dispersive larval phase and reef systems considered to be genetically open (Sale 1991). Some genetic studies found no evidence of regional patterns in demography because of distinct genetic stocks (i.e. Bermingham 1995, Doherty et al. 1995, Dudgeon et al. 2000, Shulman and Williams 2003). Environmental factors that may influence growth patterns would be predation pressure, temperature, variation in resources (e.g. food), and water conditions. However, this study only investigated the plasticity of demographic patterns rather than examining the causes of such variation.

Studies have demonstrated significant differences in age structure, somatic growth, mortality, and otolith growth in lutjanids, acanthurids and pomacentrids over a range of spatial scales (Doherty and Fowler 1994, Hart and Russ 1996, Newman et al. 1996b). Kingsford and Hughes (2005) cautioned against pooling demographic parameters over broad spatial scales without considering local scale variation. The scale of variation in demography of a large, potentially more mobile fish population would be larger compared to smaller, site-attached reef fish (Williams et al. 2003). Consistency of demographic parameters among reefs or regions may be a result of movement between reefs (i.e. *L. miniatus*, Williams et al. 2003). This, however, does not fit with typical meta-population models for coral reef fish, in which adults are confined to a single reef and the larval stage is the only means of dispersal among reefs. Any observed regional variation in demography may be also a result of differences in post-settlement processes such as competition (Jones 1987), food and habitat availability (Hart and Russ 1996), population density (Doherty 1983), and water temperature (Conover 1992). Alternatively, regional variations in recruitment, density dependent processes and other factors that influence larval survival and settlement, might influence the regional variation in demography. Unfortunately, lack of or limited data for examining these processes restrict forming any conclusions on the causative factors driving observed regional patterns.

However, some studies have shown that there is no linear trend in demography with latitude. Factors such as temperature, which has a strong latitudinal gradient (Lough 1994) are unlikely to independently explain the observed differences as many other factors could influence simultaneously. Meekan et al. (2001) also showed temperature had no obvious effect on spatial differences in demography of damsel fishes in the east Pacific.

Possible effects of fishing

An important aspect of the relationship between fish stocks and fishing is the mortality imposed by fishing. Fishing, contributing to mortality may influence the dynamics of both the natural and the modeled population. In order to determine if a certain level of fishing is sustainable, we would ideally estimate the level of mortality induced by fishing. Attempts to assess the influence of fishing on tropical reef fishes (i.e. Chapman and Kramer 1999, Dulvy et al. 2004a, Fromentin and Fonteneau 2001, Graham et al. 2003, Hawkins and Roberts 2004, Jennings et al. 1999a, Polunin et al. 1996, Roberts 1995, Robertson et al. 2005b, Rochet et al. 2000, Rogers and Beets 2002, Russ 2002, Willis et al. 2003) have shown that increasing levels of fishing pressure can impact on target species. Stevens et al. (2000) and Mumby et al. (2006) have shown that depletion of apex predators can induce changes to the structure of marine communities as effects cascade through lower trophic levels. By comparing reefs along gradients of fishing intensity, Friedlander and DeMartini (2002) determined that the remote and lightly fished North Western Hawaii Islands support significantly more fish biomass than the heavily fished Main Hawaiian Islands, with apex predators comprising on average 54% of the total fish biomass in the NWHI, but only 3% in MHI.

This study provides strong evidence that gray snapper from Belize and hogfish from Belize and Margarita have truncated age distributions. Both species in these locations are subject to heavy fishing pressure, and this could explain the lack of older, larger age-classes in samples from these locations. Therefore fishing was obviously another plausible factor which could have influenced growth patterns. Gray snapper in Belize reach a smaller maximum size and younger maximum age. These biological features carry implications for overall population health, as fecundity usually relates to size and age. Increased pressure on younger fish could lead to growth overfishing, whereas easier access to mature adults may result in recruitment overfishing.

Table 3-5. Comparison of life history variables for *L. griseus* from the literature. (k, L_∞, L_0 are VBGF parameters, t_{max} and L_{max} are mean age and size of oldest and largest individuals in the sample, t_m is age at sexual maturity)

Location	Sex	K	t_0 years	L_∞ mm	L_{max} mm	t_{max} years	t_m years	Source
Florida	M ale	0.18	0.49	697	687	24	4	Burton 2001
Florida	Female	0.15	0.16	768	744	24	6	Burton 2001
NE Florida	Both sexes	0.17	-0.001	716	760	24	5	Burton 2001
S Florida	Both sexes	0.13	-1.33	625	618	15	3	Burton 2001
S Florida	Unsexed	0.14	-0.963	716	692	21	4.5	Rutherford et al. 1989
S Florida	Unsexed	0.13	-0.863	722	556	10	2	Ault et al. 1998

Table 3-6. Comparison of life history variables for *L. maximus* from the literature

	K	L_∞ (FL) mm	t_0 years	L_{max}	t_{max}	Source
Eastern GOM	0.080	913	-1.78	NA	23	McBride 2001
Florida Keys	0.240	438	-1.00	NA	13	McBride 2001
Southwest Cuba	0.098	850	-1.38	NA	NA	Claro et al. 2001

NA= not available, GOM = Gulf of Mexico

A preliminary stock assessment (reviewed in Ault et al. 2003) indicated that hogfish was severely overfished in Florida waters. McBride and Murphy (2001) examined the status of the hogfish fishery, especially in reference to the effect of the 1994 minimum-size regulation enforced on hogfish landings in Florida. They also explored cost benefit aspects of increasing the minimum legal fish size to increase the yield-per-recruit of hogfish. McBride and Murphy's (2001) study showed that until 2000, the sizes of most hogfish landed in Florida were very close to the 12-inch (305mm) FL size limit. Hogfish at this size are predicted to be approximately 3 years old. Hogfish can grow to 824 mm (32.4 inches) FL with an age of 25 years (Ault et al. 2003). The observed maximum size is lower in south Florida, where mortality is greatest, suggesting that growth overfishing is occurring in this region. The yield-per-recruit analysis conducted by McBride and Murphy (2001) indicted that maximum yield-per-recruit for hogfish would occur at a size larger than the current mean size of the fish harvested.

Commercial fishing for hogfish was unregulated in many Atlantic nations until 1994, when the state of Florida and South Atlantic Fishery Management Council (SAFMC) instituted a 12-inch (305 mm) FL minimum size limit. However, there is a concern that the 12 inches limit may be too small to allow females to change to males in heavily fished areas (Ault et al. 2003). Also, some argue that the protogynous species may be more susceptible to population collapse even at relatively low fishing mortality rates (Bannerot et al. 1987).

CHAPTER 4

Demographic signatures of fishing: Evidence from *Lutjanus apodus* (Walbaum, 1792) and *Cephalopholis cruentatus* (Lacepède, 1802).

4.1 Introduction

A growing literature on smaller non-commercial species (Gust et al. 2002, Jones 1990, Kingsford and Hughes 2005, Luckhurst et al. 2000, Meekan et al. 2001, Ruttenberg et al. 2005) document the range of demographic flexibility in reef fishes. In the face of such natural variation, is it possible to identify ecological and demographic evidence of fishing effects? Much of the evidence that has been accumulated on demographic variation concerns species subjected to localized fisheries (i.e. Belk 1995, Fischer et al. 2005, Newman and Williams 2001, Pears 2005, Rooker et al. 1999, Williams et al. 2003). The primary targets of these studies were surgeonfishes (Choat and Axe 1996, Munro et al. 2003, Robertson et al. 2005a, Robertson et al. 2005b) and parrotfishes (Bellwood 1995, Choat et al. 2003, Hawkins and Roberts 2004, Tuya et al. 2006, van Rooij and Videler 1997), which have been fished intensively in both Indo-Pacific and Caribbean.

Any attempt to describe variation in natural demographic patterns of reef fishes, and to differentiate this from the influences of fishing, study must be carried out over broad areas of their range, taking into account fishing activity levels. These should include localities protected by isolation or by legislation, and those in which only a small suite of species are targeted for fishing. For example, though surgeonfishes and parrotfishes are fished intensively in some locations (Hawkins and Roberts 2004, Tuya et al. 2006, van Rooij and Videler 1997), they may be only lightly fished over substantial areas of their range because effort is channeled into more commercially rewarding species such as groupers and snappers. Moreover, identification of areas where the study species is intensively fished helps to provide a benchmark for measuring the influence of human activity.

Given the fact that a substantial part of the fishing effort in reef systems is directed towards tropical snappers and groupers, the task of differentiating natural variation from fishing-associated demographic variation becomes more difficult. There are some locations where these groups are not fished or fishing is very limited due to remoteness (i.e. Las Aves in Venezuela) or marine protected status (i.e. Los Roques in Venezuela). These locations provide an opportunity for broad scale demographic work unconfounded by fishing effects. Although fishing will rapidly reduce the abundance of target species, establishing demographic effects of fishing has proven to be difficult (Lewison et al. 2004, Rochet et al. 2000). This is especially true with respect to reductions in life span. Even in intensively fished areas in which numbers were greatly reduced, there has been little evidence of reduction in life span that can be attributed directly to fishing (Choat et al. 2003, Huntsman and Schaaf 1994, Jennings et al. 1999a, Robertson et al. 2005b). Based on an empirical study of 58 populations, Dulvy et al. (2003) concluded that exploitation was an important primary cause of declines in 40 populations , although other effects such as habitat loss are not always readily separable. Russ and Alcala (1996) have shown that grouper and snapper numbers are reduced by fishing and that recovery times are slow.

The study species

Schoolmaster snapper *(Lutjanus apodus)*

Schoolmaster snapper, *L. apodus* occurs in shallow, clear, warm, coastal waters over coral reefs. Juveniles are encountered over sand bottoms often with seagrass (Thalassia) and over muddy bottoms of lagoons or mangrove areas (Froese and Pauly 2008). Young sometimes enter brackish waters. They may form resting aggregations during the day. *L. apodus* plays an important trophic role in tropical marine ecosystems (Raver 2005). The schoolmaster snapper is the most commonly encountered lutjanid on coral reefs in the Caribbean (Randall 1983). They are confined to reefs more than other snappers. However, it has also been reported that schoolmaster snapper is the predominant lutjanid in areas adjacent to or inside mangrove prop-root habitats (Rooker and Dennis 1991). They are highly esteemed food fish and an integral part of the commercial and sport fisheries in the areas of its geographic range, which extends from northern Brazil to Massachusetts (Allen 1985b). They are often a significant component of the landings from directed demersal fisheries as well as comprising a portion of the by-catch in the Caribbean.

Graysby *(Cephalopholis cruentatus)*

Graysby, *Cephalopholis cruentatus*, is a small tropical grouper (serranid) that occurs in the Western Central Atlantic and range from North Carolina, Bermuda, Gulf of Mexico, Bahamas, and Caribbean south to Brazil. Graysby is more closely associated with deepwater coral reefs (Nagelkerken 1981) and prefers coral reefs with small ledges and caves in depths to 170 m. They typically rest quietly on the bottom, blending with the surroundings. A maximum size of 42.6 cm TL, a maximum weight of 1130 g and a maximum longevity of 13 years have been recorded (Potts and Manooch 1999). They are also known to have a protogynous mode of reproduction (Potts and Manooch 1999). Limited recreational fishery data suggest that graysby is being landed with increasing frequency (Potts and Manooch 1999). Therefore, this is a good opportune time to study the long-term effects of fishing on the life history characteristics of this species.

This chapter adds information on demographic variation in commercially targeted species of *L. apodus* and *C. cruentatus*. Both families share characteristics such as extended lifespans, slow growth and a wide geographic distribution. Given the potential for confounding latitudinal effects on demography, study locations were chosen from within the same latitude in the Caribbean. The aim of this study was to examine possible demographic signatures of populations subject to extensive fishing pressure. Age-specific growth rate, growth patterns, theoretical and mean maximum size, rate at which asymptotic size is approached, longevity, mean maximum age, mortality rates and survivorship were investigated .

4.2 Materials and methods

L. apodus were collected from two geographically disperse locations, and *C. cruentatus* samples were collected from five distinct locations in the Caribbean (Table 4.1). All these locations were found between 11° and 17° North latitude; Belize (17° 15′ N, 88° 45′ W), Curacao (12° 10′ N, 68° 93′ W), Barbados (13° 10' N, 59° 35' W), Las Aves (15° 40′ N, 63° 36′ W) and Los Roques (11° 51′ N, 66° 45′ W) (see figure 4.1). A total of 241 *L. apodus* were collected from Belize and Los Roques, and 586 *C. cruentatus* were collected from Belize, Curacao, Las Aves, Los Roques and Barbados (Table 4.2). The selection of sample sites from the similar latitudes was very important to discern fishing effects eliminating confounding latitudinal effects.

Source : www. Worldatlas.com

Figure 4-1. Map showing sample locations (highlighted with open circles), 1. Belize, 2. Curacao, 3. Las Aves, 4. Los Roques, 5. Barbados; (part of the map (shaded small rectangle) have been enlarged and seen in large rectangle).

Samples were obtained using a mixture of fishery dependent (commercial fishing) and independent (research spear fishing) methods. Samples collected on different dates and months were pooled to obtain adequate sample sizes, assuming there were no temporal patterns in demographic characteristics over sampling dates.

Small fish were poorly represented or absent in the fishery dependant samples due to gear selectivity.

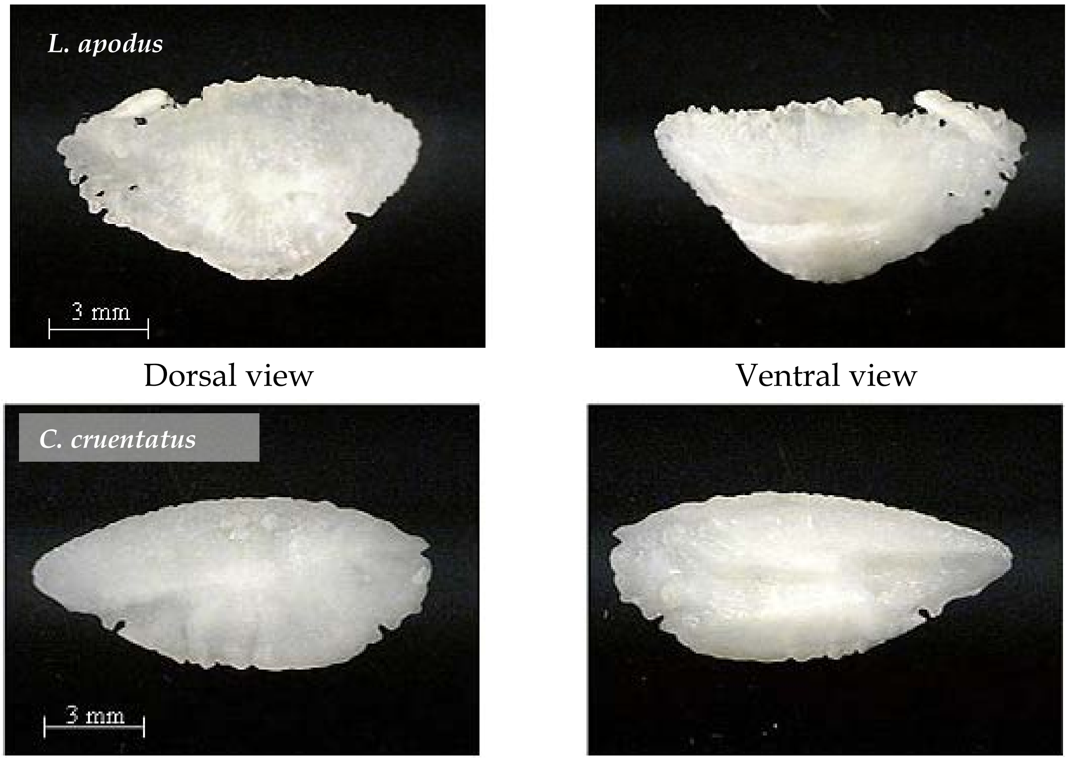
Table 4-1. Sampling locations, mean Sea Surface Temperature, and sampling years.

Locality	Latitude	Mean SST (°C)	Sampling years
Belize	17° 15' N	28.1	*L. apodus* – 2002 *C. cruentatus* – 2002
Curacao	12° 10′N	27.1	*C. cruentatus* – 2004/2005
Barbados	13°10′N	27.6	*C. cruentatus* – 2000
Las Aves	15° 40′ N	27.1	*C. cruentatus* – 2002
Los Roques	11° 51 N	27.1	*L. apodus* – 2002 and 2004 *C. cruentatus* – 2002

4.3 Results

Otolith morphology and interpretation

The sagittae of *L. apodus* are laterally compressed, with a very concave distal surface, and a slightly pointed rostrum and post-rostrum. Outer margin was heavily serrated. *C. cruentatus* otoliths are fusiform in shape and have more regular outer margin and they are not concave as *L. apodus* otoliths.



Source: www.sefscpanamalab.noaa.gov

Figure 4-2. Otolith morphology; dorsal and ventral views; Top: *L. apodus* Bottom: *C. cruentatus*.

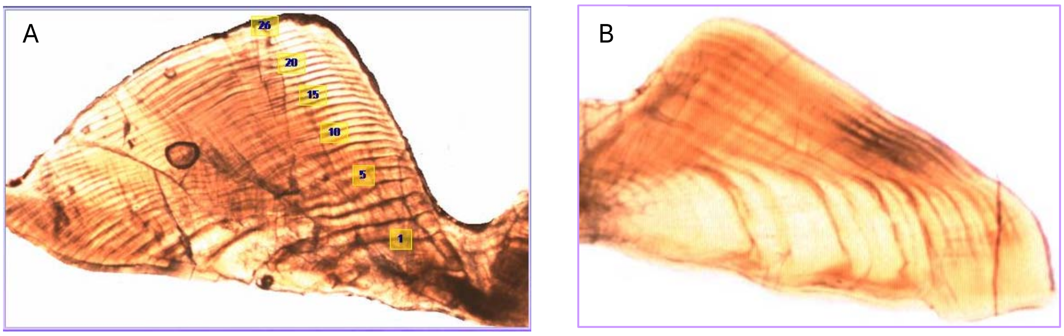


Figure 4-3. *L. apodus.* Sagittal sections showing alternating opaque and translucent bands A) from Los Roques, 26 yr, 523mm FL B) from Belize, 9 yr, 264 mm FL

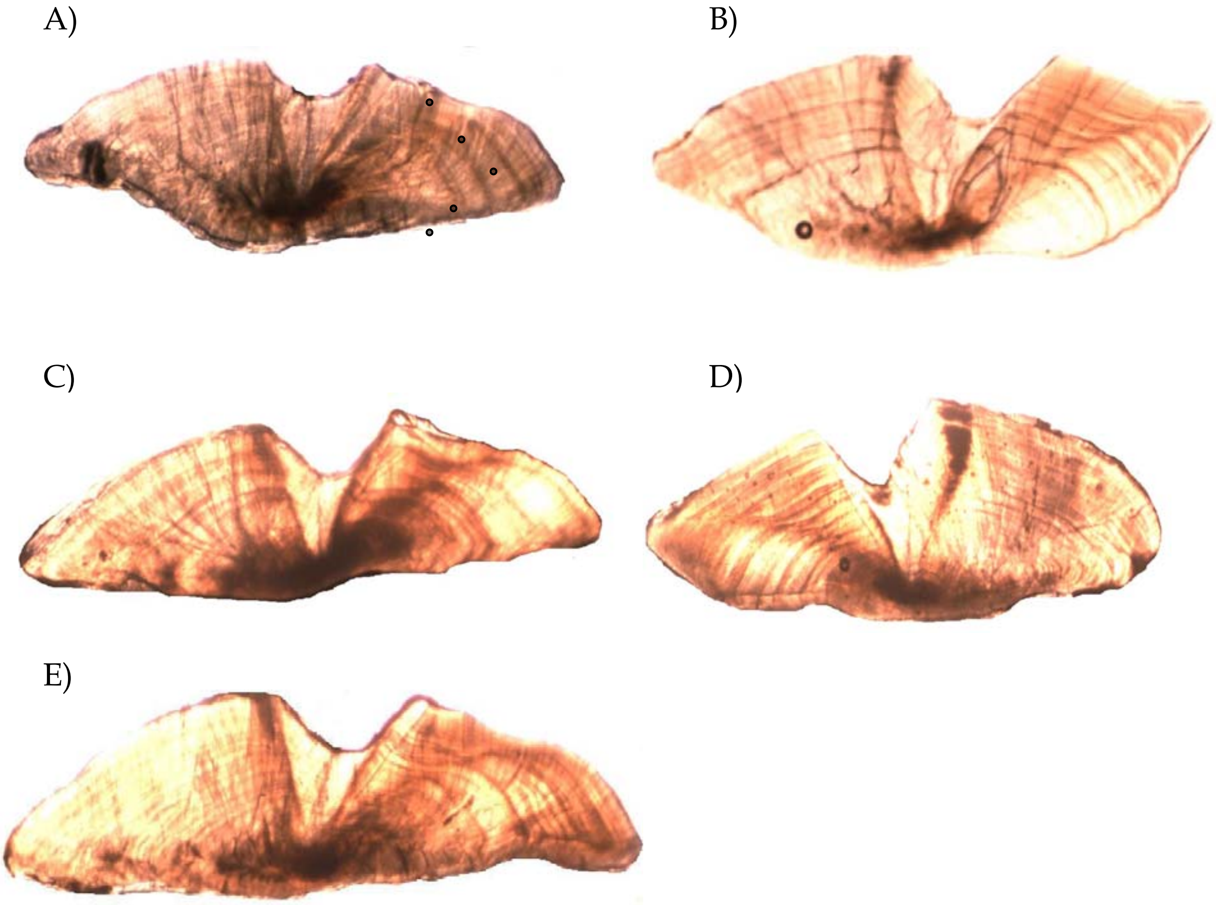


Figure 4-4. Representative sagittal sections of *C. cruentatus* from each location, showing alternating opaque and translucent bands (A) Curacao, 4 yr, 181mm FL (B) Belize, 4 yr, 178 mm FL (C) Barbados, 3 yr, 207 mm FL (D) Las Aves, 9 yr, 301 mm (E) Los Roques, 5 yr, 254 mm.

Sectioned sagittae of *L. apodus* and *C. cruentatus* revealed distinct patterns of alternating translucent and opaque bands (annuli) for all locations (Figures 4-3 and 4-4), and were readily interpretable with a high level of precision among replicate counts. The degree of readability varied by locality and among individuals. There was however no directly observable relationship between readability and size or age. Rather, in many instances, readability appeared to be a characteristic of the individual otolith. The first annulus in otolith sections was often faint and difficult to discern, a common phenomenon in many species (i.e. Ferreira and Russ 1994, Zhao et al. 1997).

Sagittal weight vs. age

Otolith weight was linearly correlated with estimated age (Figures 4-5 and 4-6). There was a strong relationship between sagittal weight and age for *L. apodus* with a r^2 of 0.93 for both Belize and Los Roques populations. Otolith weight and age of *C. cruentatus* were also linearly correlated with r^2's over 0.7 except for Los Roques, where r^2= 0.5. This suggests that the otoliths continue to grow in mass even if the fish has reached its asymptotic length. Since otoliths grow throughout the life of the fish and have regularly formed growth increments, otolith weight can be used as a proxy for age.

ANCOVA revealed that for *L. apodus* the slopes of the sagittal weight and age regressions did not significantly differ among locations (F=0.622, p=0.431, df=1). However, ANCOVA for *C. cruentatus* was significant (F=59.7, P=0.000, df=4). Pairwise comparisons using the Bonferroni method further revealed that these significant differences were evident in *C. cruentatus* for all location pairs other than Belize-Curacao and Los Roques-Barbados.

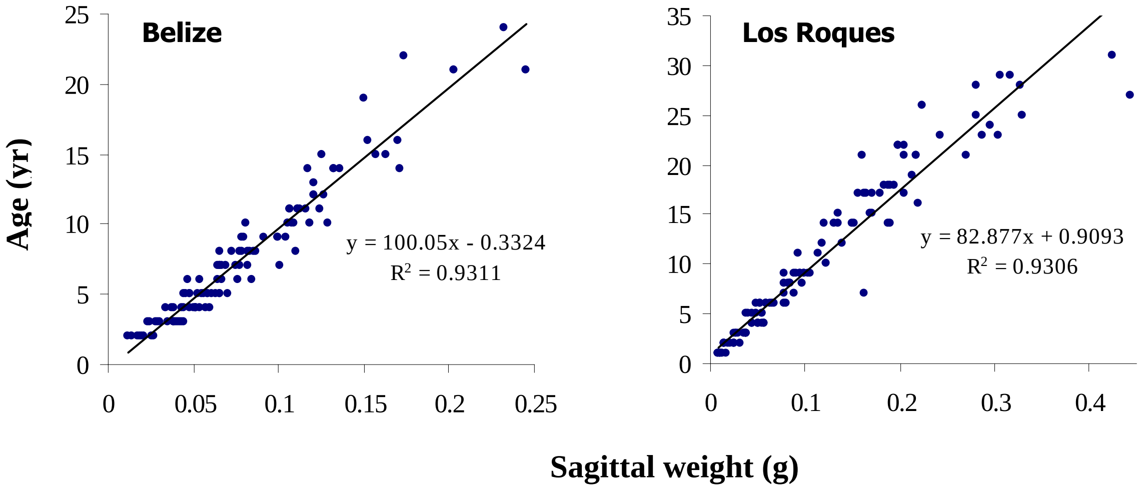


Figure 4-5. Least squares linear regression of sagittal weight on estimated age for *L. apodus* by region.

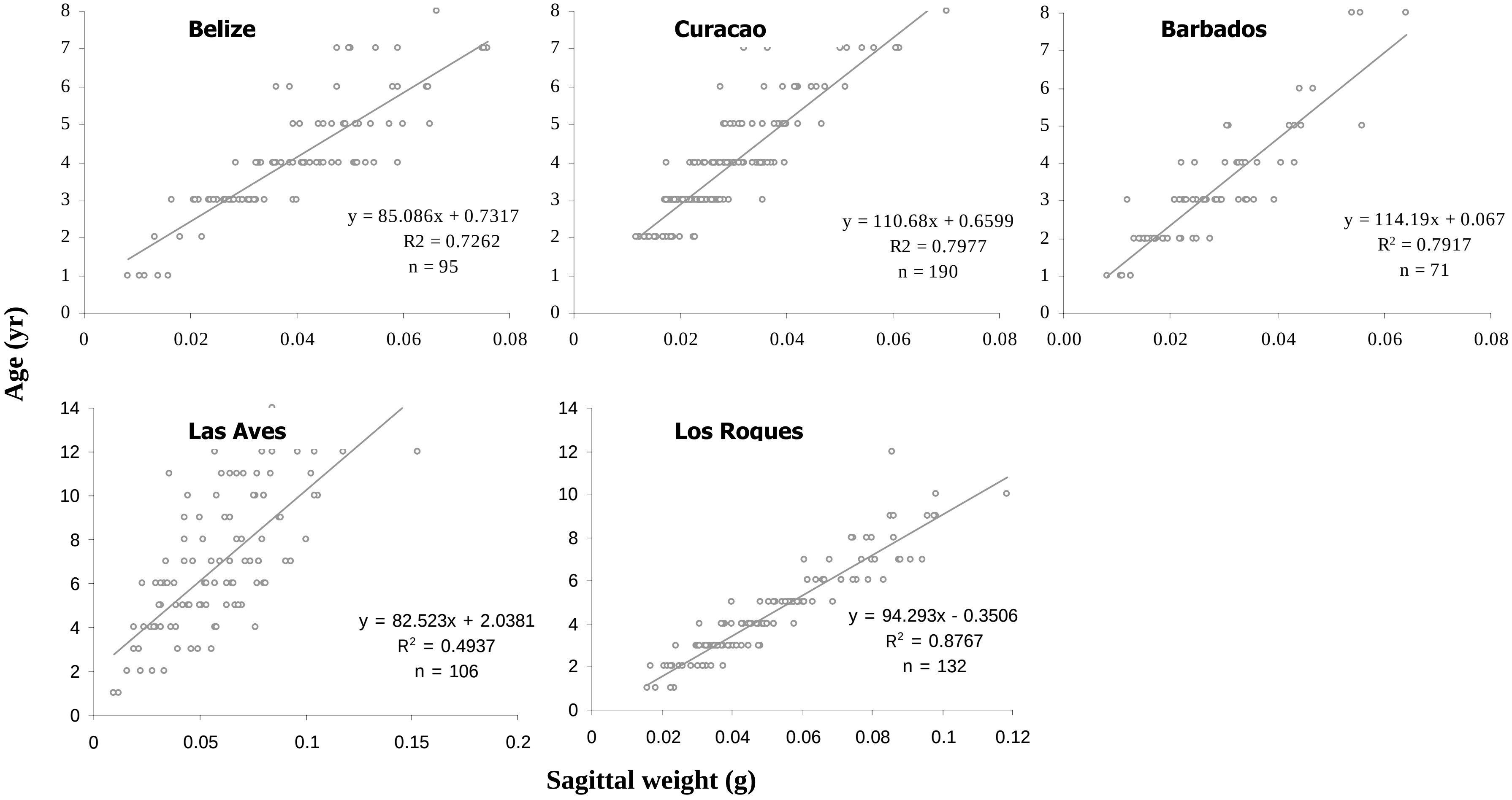


Figure 4-6. Least squares linear regression of sagittal weight on age for *C. cruentatus* plotted by region.

Maximum size and age

There was no clear relationship between maximum longevity and mean sea surface temperature for *C. cruentatus* (Fig. 4-7). Thus, minor variations in latitude (therefore, sea surface temperature) seems to have no significant impact on longevity of *C. cruentatus*.

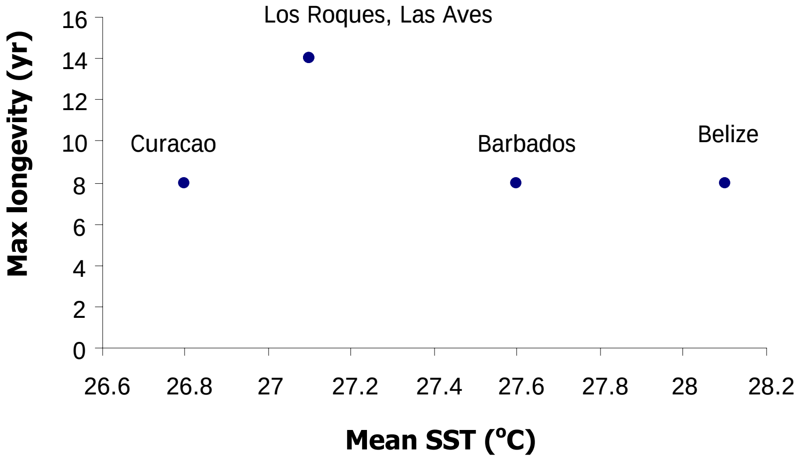


Figure 4-7. Relationship of mean SST and maximum longevity for *C. cruentatus* among localities.

Table 4-2 shows the mean size (FL) for each population and re-parameterized von Bertalanffy growth parameters. *L. apodus* and *C. cruentatus* from locations subjected to intense fishing (Belize, Curacao and Barbados) have lower mean FL's. In contrast, for both species from a protected area (Los Roques) and lower fishing intensity area (Las Aves) has higher mean FL's. This reveals that fishing has truncated to size structure of both study species.

Table 4-2. Mean sizes and size at three ages, 2, 4 and 6 (re-parameterized von Bertalanffy parameters (L_τ, L_ω and L_v) after Francis 1990).

Species	Locality	Mean FL ± SD	L_T ± CI	L_ω ± CI	L_V ± CI
L. apodus	Belize	263 ± 66.2	159.8 ± 9.3	219.0 ± 13.6	255.4 ± 15.8
	Los Roques	298 ± 127	168.0 ± 10.4	232.7 ± 14.4	260.1 ± 16.1
C. cruentatus	Belize	196 ± 34.9	150.8 ± 9.3	213.4 ± 13.2	243.3 ± 15.1
	Curacao	185 ± 32.5	149.5 ± 9.3	209.2 ± 12.9	236.6 ± 14.7
	Barbados	188 ± 36.0	182.6 ± 11.3	231.7 ± 14.4	246.0 ± 15.2
	Las Aves	235 ± 34.1	172.5 ± 10.7	239.5 ± 14.8	268.1 ± 16.6
	Los Roques	245 ± 50.3	159.2 ± 9.9	216.7 ± 13.4	239.8 ± 14.9

L. apodus lived upto 24 yr in Belize and 31 yr in Los Roques (table 4-3). *L. apodus* is not a target species in Belize and they are lightly fished there. Los Roques (a national park) and Las Aves (a remote Island with no inhabitants, only seasonal fishing from neighboring countries) populations of *C. cruentatus* achieved the greatest longevity (14 yr), whereas those in Belize, Curacao, and Barbados, with high fishing rates showed reduced longevity (8 yr).

Mean maximum sizes of *L. apodus* were higher in Los Roques than in Belize (510 and 381 mm, respectively). Similarly, *C. cruentatus* in Las Aves and Los Roques attained higher mean maximum sizes (275 and 281 mm) compared to the three other study locations. *L. apodus* showed a high degree of variation in asymptotic sizes among locations. The largest asymptotic size (492 mm) was observed in Los Roques while the minimum (363mm) was observed in Belize . However, *C. cruentatus* showed no large variations in asymptotic sizes among locations.

Table 4-3. Summary of the VBGF and other demographic parameters derived from observed length-at-age data for *L. apodus* and *C. cruentatus* over the range of localities sampled. Intercepts were constrained to approximate size at settlement.

Species	Locality	L_∞	k	t_0	Age range (yr)	Mean max age (yr)	Size range (FL mm)	Mean max size (mm)	N
L. apodus	Los Roques	492	0.126	-0.229	1-31	26.3	93-556	510	131
	Belize	363	0.206	-0.190	1-24	19.2	111-406	381	110
C. cruentatus	Belize	242	0.43	-0.199	1-8	7.2	93-266	227	95
	Curacao	242	0.38	-0.227	2-8	6.4	126-273	238	190
	Barbados	252	0.47	-0.222	1-8	6.9	109-268	237	71
	Las Aves	272	0.52	-0.147	1-14	9.8	149-302	275	132
	Los Roques	278	0.37	-0.253	1-14	11.7	94-322	281	106

Somatic growth

Overall shapes of the growth curves were not consistent among location for both species (Figures 4-8 and 4-11). However, they coincide with the general growth patterns observed for many lutjanids. VBGF growth curves for *L. apodus* (Fig 4-8) differed considerably between locations, indicating they have different growth trajectories. Belize and Los Roques populations had similar growth upto 6 yr, but, Los Roques population diverged thereafter (Fig 4-9). The 95% confidence regions of *K* and L_∞ (Fig 4-10) for *L. apodus* in Belize and Los Roques did not overlap, confirming the existence of different growth trajectories in the two locations.

Comparison of VBGF curves for *C. cruentatus* (Fig. 4-12) revealed strikingly similar growth trajectories for Belize, Curacao, Barbados, Las Aves and Los Roques populations. The 95% confidence regions of *K* and L_∞ displayed considerable uncertainty (Fig. 4-13) and only those of Los Roques and Barbados overlapped. There was clear differentiation among other locations, indicating different growth trajectories, although growth parameters and growth curves showed closely related. The upward shift in confidence plots of Las Aves and Los Roques reflect greater sizes-at-age in these two populations.

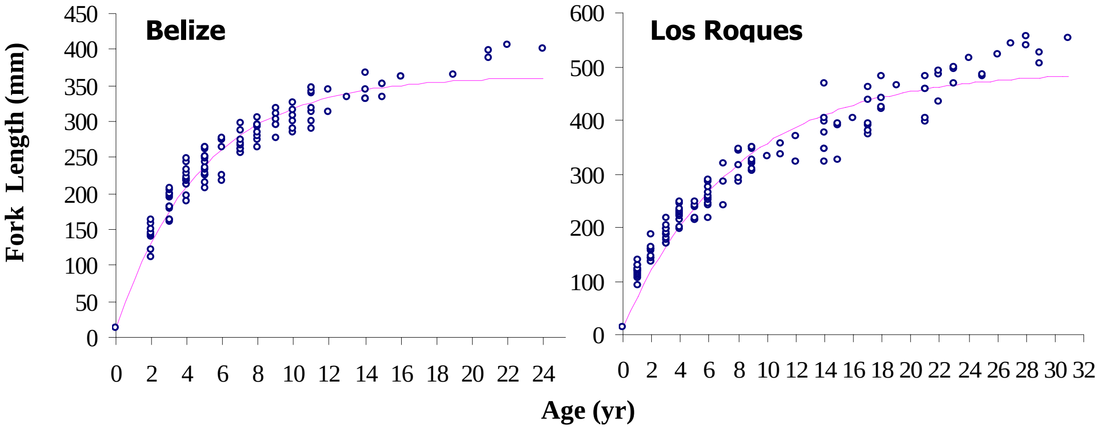


Figure 4-8. *L. apodus,* Von Bertalanffy growth curves fitted to size-at-age data plotted by region; t_0 has constrained to approximate size-at-settlement (20 mm).

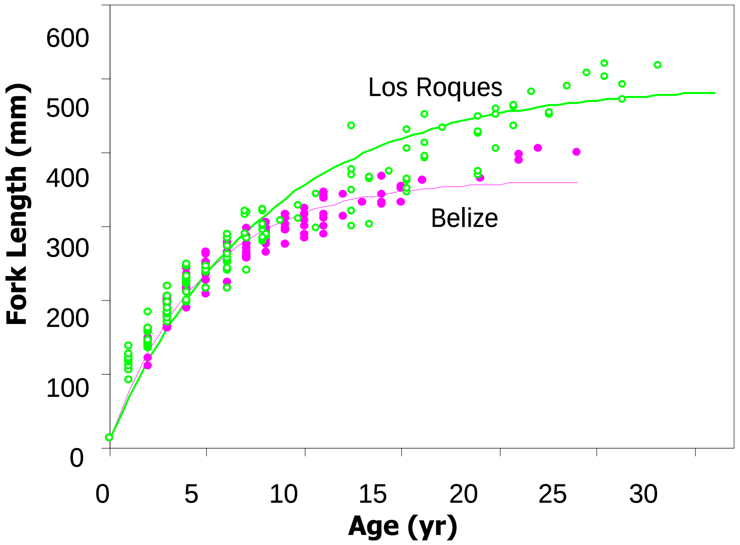


Figure 4-9. ***L. apodus,*** **comparison of VBGF growth curves among location.**

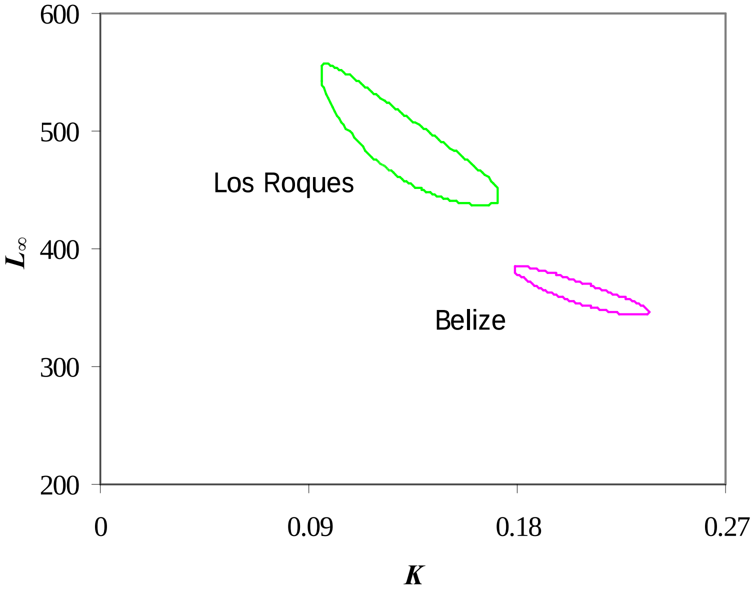


Figure 4-10. ***L. apodus*****, 95% confidence regions around least squares estimates of** ***K*** **and** L_∞ **(after Kimura 1980).**

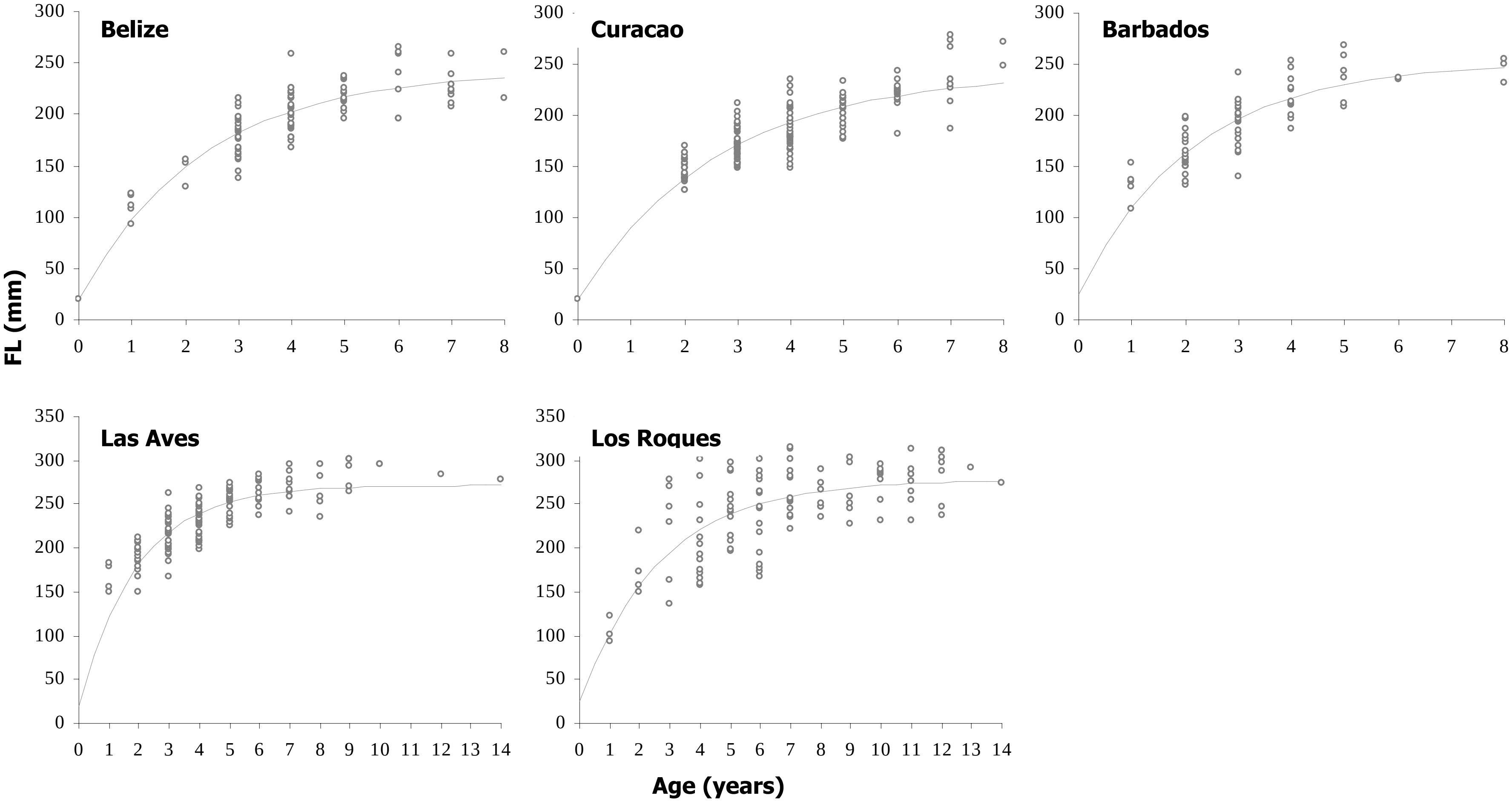


Figure 4-11. *C. cruentatus*. VBGF curves fitted to size-at-age data plotted by region; the t_o has constrained to approximate size-at-settlement (20 mm).

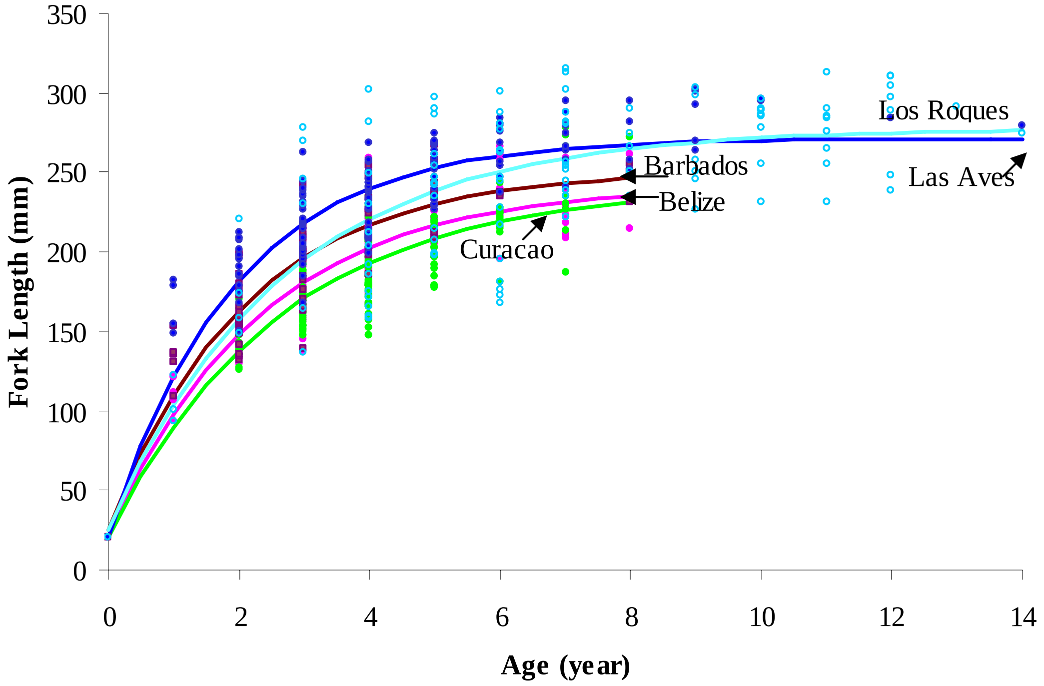


Figure 4-12. *C. cruentatus*, comparison of VBGF growth curves among location.

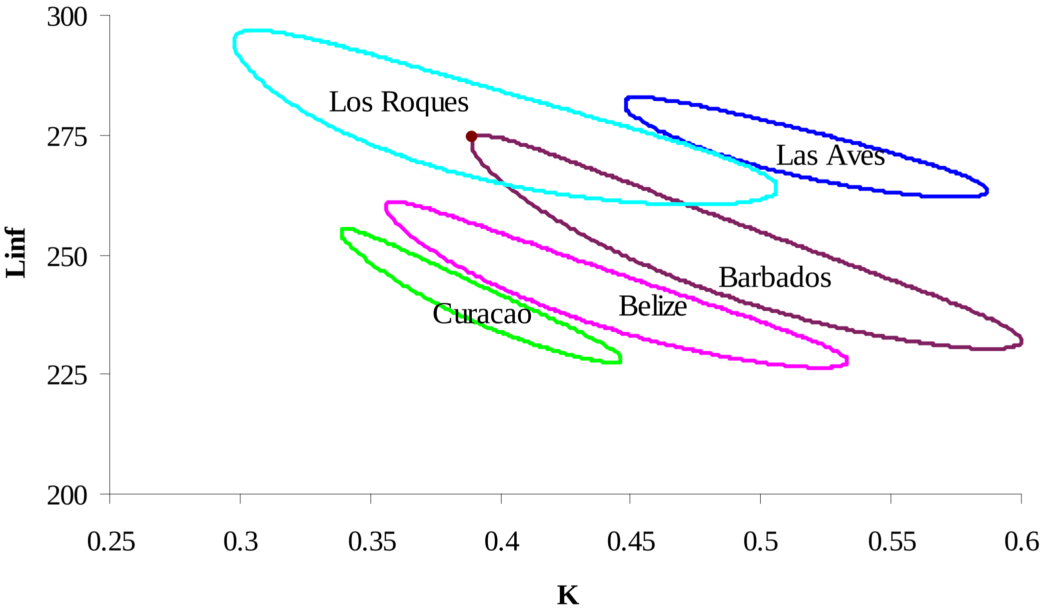


Figure 4-13. *C. cruentatus*, 95% confidence regions around least-squares estimate of *K* and L_∞, following Kimura (1980).

Age structure

Both Belize and Los Roques populations of *L. apodus* displayed multimodal age distributions (Fig. 4-14). Belize population had no representative samples for age 1. Modal age in Belize, where the species is exploited was 5 yr which is apparently the age *L. apodus* was fully recruited to sampling gear. One of the key findings in this study was the greater relative abundance in older age classes of *C. cruentatus* in Los Roques, where the species is unexploited (Fig. 4-15A). Also, locations where *C. cruentatus* subjected to intense fishing (Belize, Curacao, and Barbados) had truncated age distributions.

Except for Curacao, all the other populations of *C. cruentatus* had representative samples starting from very first year, suggesting they were subjected to sampling gear at the age of 1 year (Fig. 4-15A). Age classes 3 and 4 were most abundant in Belize, Curacao and Las Aves; ages 2 and 3 in Barbados, and ages 6 and 7 in Los Roques. Age-frequency distributions were unimodal for all the locations except Los Roques, where a second and third modes at ages 10 and 11 were present. With the exception of Los Roques, the abundance of fish > 4 declined rapidly. It is evident that *C. cruentatus* of ages 3 and 4, became fully recruited to the sampling gear.

Mortality

Table 4-4. Total instantaneous mortality rates (*Z*), annual percentage survivorships (*S*) and fishing intensities for *L. apodus* and *C. cruentatus*.

	Location	Instantaneous mortality rates, Z	Survivorship S (%)	Fishing intensity*
L. apodus	Belize	0.17	84.4	moderate
	Los Roques	0.08	92.3	very low
C. cruentatus	Belize	0.51	60.0	High
	Curacao	0.66	51.7	High
	Barbados	0.50	60.7	High
	Las Aves	0.38	68.4	moderate
	Los Roques	0.30	74.1	very low

* As described in Robertson et al. (2005b)

Total instantaneous mortality rate for *L. apodus* was considerably higher in Belize (0.17 yr^{-1}) compared to Los Roques (0.08 yr^{-1}) (Table 4-4, Fig. 4-14B). These mortality rates resulted in survivorship estimates of 84.4 and 92.3 for Belize and Los Roques, respectively.

Estimates of total instantaneous mortality rates for *C. cruentatus* were lowest for Los Roques (0.3) and highest for Curacao (0.66) (Table 4-4, Fig. 4-15B). Annual survivorships ranged from 60% in Belize to 74% in Los Roques. The low value of Z in Los Roques reflects the wider age distribution, and especially the high relative abundance of age 10 and 11 fish. ANCOVA revealed significant differences in Z among all locations (F=11.9, P=0.000, df=4). Pairwise comparison of slopes using Bonferroni test also predicted significant differences among all locations.

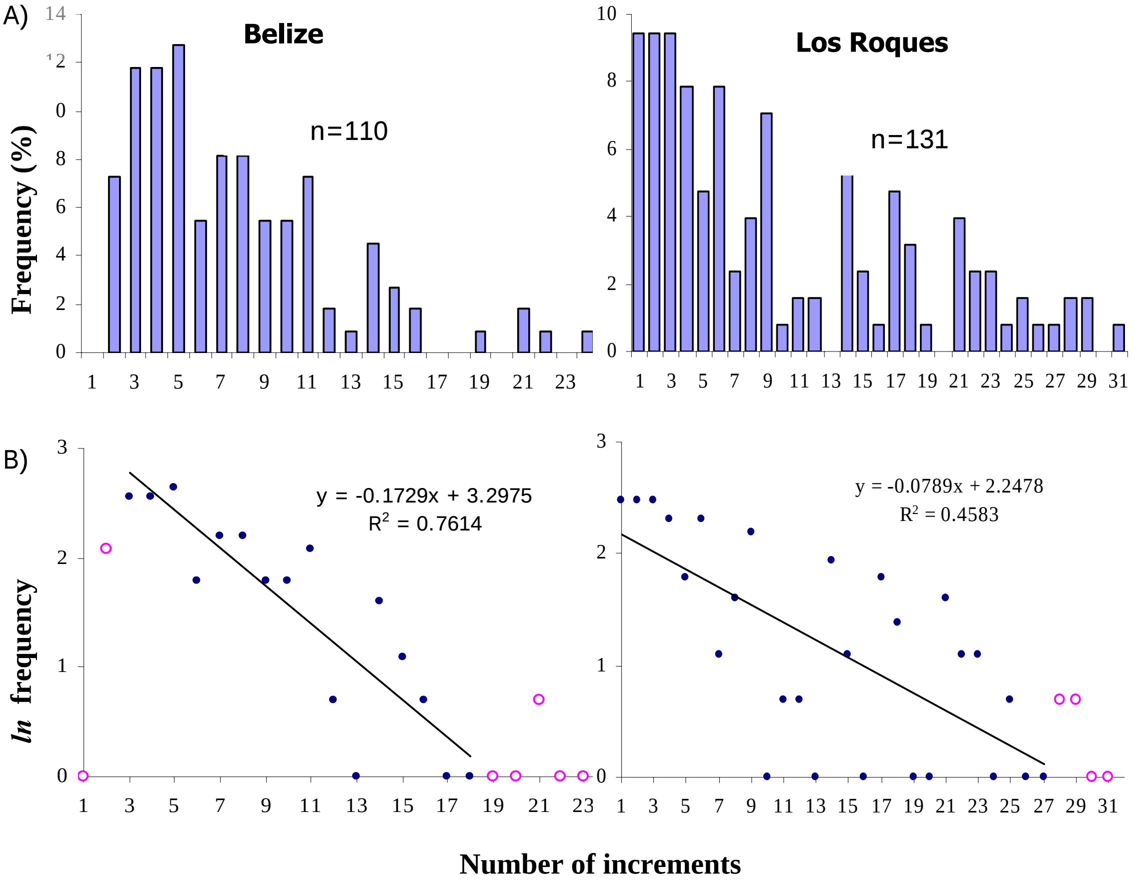


Figure 4-14 *Lutjanus apodus* (A) Age-frequency (%) distribution (B) log-linear regression of mortality rates plotted by region.

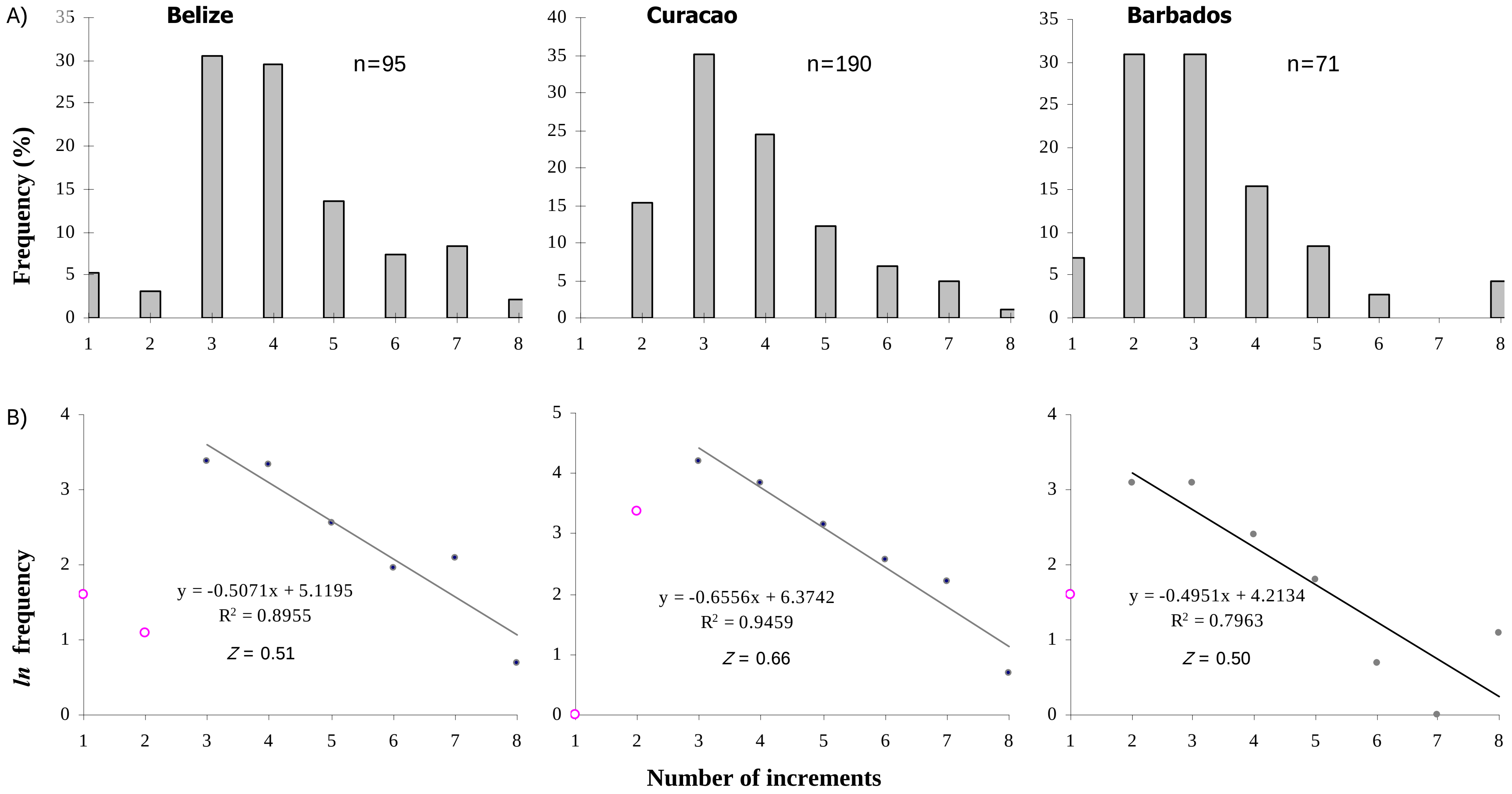


Figure 4-15. *C. cruentatus* **(A) Age-frequency (%) distribution (B) log-linear regression of mortality rates plotted by region. Age-classes represented in open circles were excluded from the analysis.**

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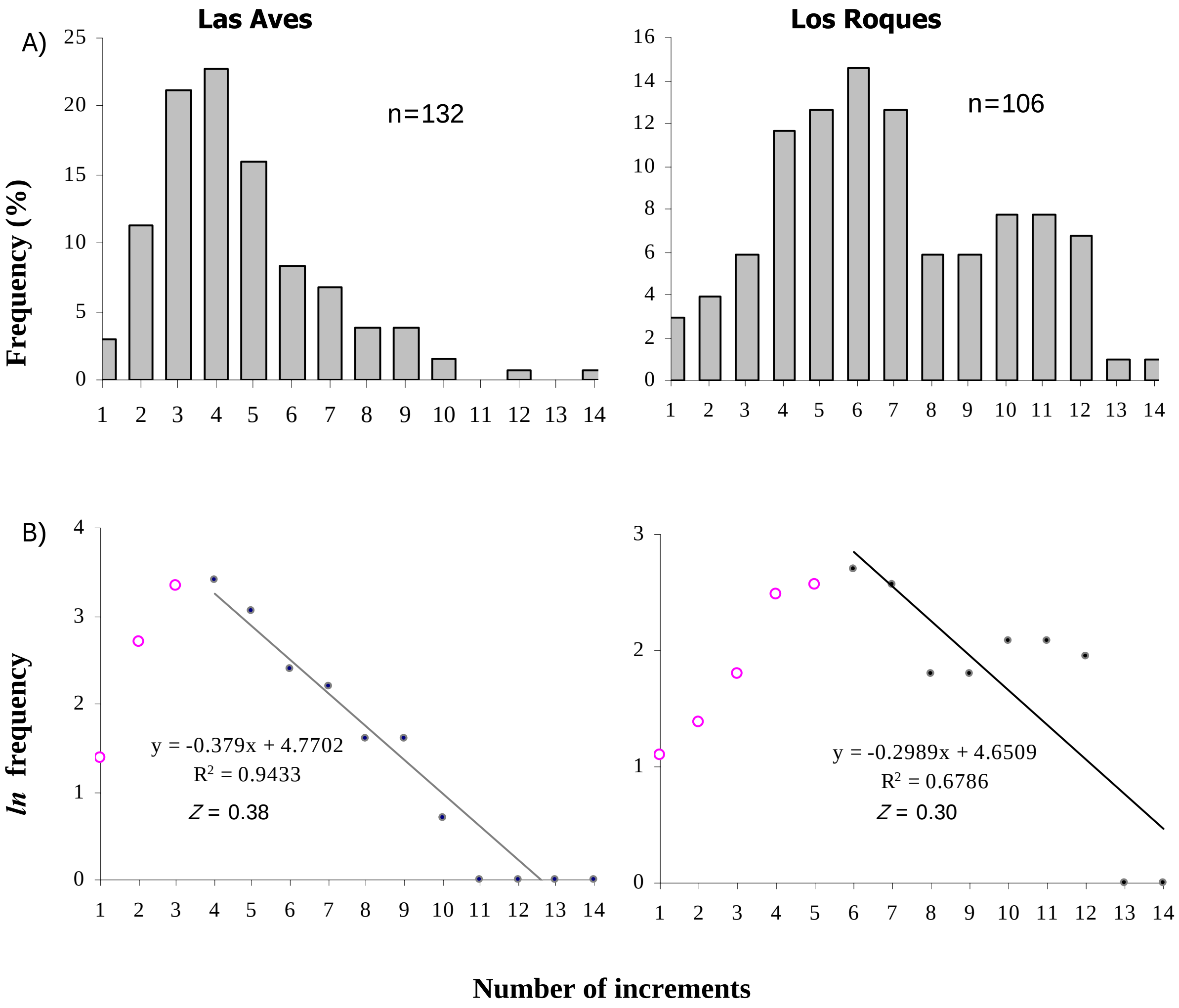

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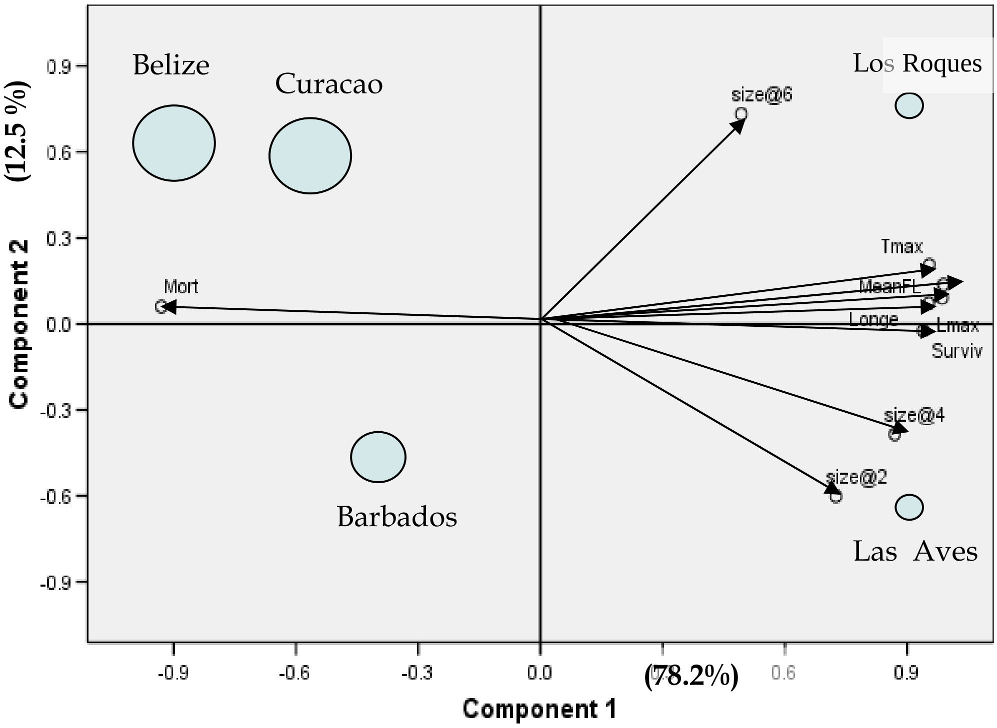
Relationship between life history variables and fishing intensity



he Principal Components Analysis performed on the life history variables. Descriptors were; mortality rates (mort), mean maximum age and size (Tmax & Lmax), mean fork length (mean FL), longevity (longe), survivorship (surviv) and size-at-age 2, 4 and 6 (size@age). Different sizes of the bubbles show fishing intensities (low, moderate and high).

A Principal Component Analysis (PCA) was conducted for *C. cruentatus* using a correlation matrix in order to test the relationship between life history variables and fishing intensity (Figure 4-16). Fishing intensity was the object and life history parameters were descriptors. Biplot representation was used to display the results. The first two axes of the PCA explained more than 90% of the total variation in life history parameters. PCA clearly separated locations based on low, moderate or high fishing intensity; also, a close relationship was observed among life history variables. Low fishing intensity (i.e., low mortality) resulted in larger sizes, longer lifespans and higher survival rates in Los Roques and Las Aves. In contrast, two of the three locations with high fishing intensity, Belize and Curacao were associated with smaller sizes, shorter lifespans, lower survivorships, and higher mortality rates. However, Barbados was separated from other locations without any association with life history variables.

4.4 Discussion

A sampling profile in this study incorporated different levels of fishing intensity, while controlling for the type of latitudinal variation identified in Chapter 3. Coral reefs lacking a history of intense exploitation set new baseline for evaluating human impacts and provide insights into the ecological function of these ecosystems (Stevenson et al. 2007).

The findings revealed demographic signatures of targeted species upon intense fishing. In both *L. apodus* and *C. cruentatus* mean maximum life spans were lower in areas subject to higher levels of fishing. In addition growth rates in fished areas were lower than those from protected sites, principally Los Roques.

Growth

Populations of *L. apodus* in Los Roques displayed continuous growth and attained a larger size compared to Belize population because of rapid growth after age of 6 years, although both populations had identical initial growth. The 95% confidence intervals around least squares estimate of K and L_∞ also revealed differential growth trajectories for Los Roques and Belize populations. Both Belize and Los Roques locations lie within the same latitude minimizing any latitudinal effects, thus the differential growth trajectories may be associated with different exploitation rates exerted on the two populations. Then, the smaller size-at-age observed in Belize could be a result of high fishing pressure and therefore, removal of older age classes.

VBGF curves for *C. cruentatus* revealed that the larger sizes observed in Los Roques and Las Aves populations would be a result of higher initial growth. Belize, Curacao and Barbados populations showed strikingly similar growth curves and VBGF growth parameters despite the fact that 95% confidence ellipses indicated different growth trajectories. Belize, Curacao and Barbados populations subjected to intense fishing and this would have been the reason for truncated size-at-age observed in all three populations. *C. cruentatus* is a protogynous hermaphrodite with growth is continuous for both sexes (Potts and Manooch 1999). The present study represents combined growth curves for both sexes. The theoretical growth curves previously obtained from back-calculated length at ages was L_t = 446 (1-e-0.12 (t+1.24), whereas equation derived from observed data was L_t = 446 (1-e-0.13 (t+ 1.54) (Potts and Manooch 1999). Nagelkerken et al. (2005) have derived a growth curve of Lt = 415 (1-e-0.13(t+0.94) for graysby based on their observations. Growth rates showed no positive relationship with sea surface temperature as predicted (Robertson et al. 2005). Sampling locations were within the same narrow latitude range, and that the maximum temperature variation among locations was 1 °C. Temperature difference in this magnitude seems not influence fish life history.

Estimates of VBGF parameters for *L. apodus* provided very reasonable L_∞ values (492 and 363 mm for Los Roques and Belize) which were very close to mean maximum sizes observed (510 and 381 mm, respectively). However, asymptotic size and mean maximum size showed a high degree of variation between locations.

Table 4-5. The life-history variables previously recorded for *L. apodus* (U- undetermined, M-male, F-female, L_m-length-at-maturity, t_m- age-at-maturity)

Location	Sex	t_0	L_∞	K	L_{max} mm	t_{max} yr	L_m mm	t_m yr	Source
S Florida	U	0.651	570	0.18	504	12	315	2	Ault & Johnson 1998 *
Jamaica	M	-0.769	630	0.18	601	17	255	2	Thompson & Munro (1983)
Jamaica	F	-0.769	630	0.18	601	17	255	2	Thompson & Munro (1983)
USA	U	-0.451	357	0.35	341	9	207	2	Randall 1963

* Length-based study

Table 4-6. The life-history variables previously recorded for *C. cruentatus* (NA= not available).

Locality	L∞	k	to	Age range yr	Size range FL, mm	Source
N Carolina	446	0.13	-1.51	4-13	180-405 TL	Potts and Manooch 1999*
Caribbean	415	0.13	-0.94	NA	NA	Nagelkerken 1979

* validated with MIA

For comparison, parameter estimates available in the literature derived for the study species are reported in Table 4-5 for *L. apodus* and 4-6 for *C. cruentatus*. A considerable variation in growth parameter estimates is observed even for the same species studied by different researchers. A number of factors, including geographical variation, different levels of fishing pressure, sampling bias or uncertainties in parameter estimations with length-based methods, may explain these discrepancies.

Growth parameters estimated for *C. cruentatus* in this study were also different to previous studies (table 4-6). Very high k values (0.37 – 0.52) were observed in present study for all the locations, indicating they attain asymptotic size quite rapidly. L_∞ estimates obtained were in confirmation with the maximum sizes observed. However, these values were very small compared to previous studies. The comparison of L_∞ and k parameters between studies suggests that *C. cruentatus* populations described in present study attained smaller asymptotic sizes but grew faster.

Otoliths and Sagittal weights

Sectioned otoliths of both *L. apodus* and *C. cruentatus* were readily interpretable with a high level of precision among replicate counts. However, the degree of readability of otoliths varied with sampling locality and readability appeared to be a characteristic of individual otolith. The consistent differences in the contrast of opaque increments in sagittal sections between the samples could be the result of a more pronounced seasonal growth oscillation for fish in the area. Double bandings were also visible in many instances that could be distinguished by discontinuous orbits around the focus of the false bands. There was a good representation of all the age classes within the observed age range, although samples were dominated by middle age classes. This under representation of younger and older age classes would be a result of sampling gear and methods.

Otolith weight showed a strong linear relationship with estimated age for both *L. apodus* and *C. cruentatus*, independent of fish size. This suggests that otoliths grow throughout the life of the fish and have regularly formed growth increments. Therefore, otolith weight can be used as a non-subjective methodology for determining age (Worthington et al. 1995). This would be particularly advantageous for large-scale stock assessment programs, where large samples are required on a regular basis.

Otolith validation

Alternating bands found in the sagittal otoliths of *L. apodus* are consistent with the patterns observed in other studies for the related species. Therefore, clear distinct bands observed for *L. apodus* were considered annuli. Given the importance of validation (Beamish and McFarlane 1983), further work is required to determine the periodicity of increment deposition. The annular deposition of the bands for *C. cruentatus* have been validated using marginal increment analysis (Potts and Manooch 1999).

Maximum and mean size

The largest schoolmaster snapper found in this study was 556 mm in size (FL) from Los Roques. Previously recorded maximum size for *L. apodus* was 570 mm FL (Froese and Pauly 2008). The largest individual found in Belize was only 406 mm. Estimated mean maximum size was smaller for Belize population (381 mm) compared to Los Roques (510 mm). Similarly, maximum size of 322 mm FL observed for *C. cruentatus* was also from Los Roques followed by Las Aves. Mean maximum sizes for *L. apodus* were 281 mm and 275 mm for Los Roques and Las Aves respectively. It has been shown that the locations subjected to high level of fishing showed smaller maximum sizes.

Longevity and mean age

Theoretically, our expectation would be that the larger size attained should be attributed to greater longevities (Meekan et al. 2001) and in contrast, any heavily fished locality would have younger fish. The maximum age achieved for *L. apodus* in present study was 31 years from a protected reef environment (Los Roques) while maximum age recorded from a location subjected to fishing (Belize) was 24 years. Maximum longevity observed in present study for *L. apodus* (31 yr) is the highest recorded from anywhere in the world. Previously recorded maximum longevity was 17 yr (Thompson and Munro 1983). It was evident that *L. apodus* has remarkably greater longevity than previously reported.

Previously recorded maximum longevity for *C. cruentatus* was 13 years (Potts and Manooch 1999), however in this study, a maximum age of 14 years was observed for both Las Aves and Los Roques populations. It is possible that the longevity of *C. cruentatus* could exceed that recorded in this study, as fishing would have truncated the older individuals from the sampling populations. However, if the differences in longevity between studies are due to sampling bias, error-in age reading, or real differences in the age structure, is not clear. It is worth further investigation in order to ascertain the reason for this variation. *C. cruentatus* found in Las Aves and Los Roques attained larger mean sizes, much greater maximum ages than those found in Belize, Barbados and Curacao, which were subjected to intense fishing.

Manooch (1987) reviewed growth patterns of tropical snappers and groupers and argued that these two families were characterized as long-lived and slow growing with low rates of natural mortality. The finding of Russ and Alcala (1996), that for Indo-Pacific species at least, a replenishment and recovery rate of fished populations was slow, supports this characterization. *L. apodus* attained maximum age of 32 yr and *C. cruentatus* 14 yr. These ages are lower than those achieved by Indo-pacific lutjanids and serranids (Cappo et al. 2000, Ferreira and Russ 1992, 1996). This follows a general trend for reef fishes (Choat and Robertson 2002). However, there were substantial differences in the maximum ages achieved in populations from unfished and fished localities; *L. apodus* 31 vs 24 yrs, *C. cruentatus* 14 vs 8 yrs. As in both species and especially *L. apodus* size increases with age, the most credible explanation is size-specific fishing mortality. Moreover, both species showed reduced growth rates (seen in the size at age profiles) in localities subject to higher fishing intensity. However, growth differences were less pronounced and subject to greater among-locality variation than maximum age differences. This reflects the sensitivity of growth to habitat-related variables, (Robertson et al. 2005a).

CHAPTER 5

Demographic changes of blacktail snapper, *Lutjanus fulvus* (Forster, 1801) after introduction to new habitat.

5.1 Introduction

One of the consistent demographic signatures associated with fishing was a truncation of the size and age distributions in heavily fished localities (Chapter 4) relative to the protected or lightly fish localities of Los Roques and Las Aves. This was notable for the lutjanid, *L. apodus* and the serranid, *C. cruentatus*. In the latter there was evidence of rapid growth during the initial part of life in fished populations (Table 4-2). The main issue concerns the reliability of truncated size and age structures as a signal of overfishing. As shown in Chapter 3, maximum age co-varies positively with latitude, a pattern that is seen in other reef fish species (Robertson et al. 2006). Chapter 4 demonstrated that reduction in maximum age was consistent with increased fishing pressure. However, other factors including the biological environment in the form of site-specific competition could influence age structure. For larger mobile and long-lived reef fish there are few opportunities to test for the effects of biological mechanisms on demography.

Ideally, the demography of the target species should be studied in the presence and the absence of competitors. However, the possibility of a manipulative experiment in which competitors were removed from some sites but not from others is remote in large mobile reef fishes. The opportunity to carry out a partial test of the hypothesis that the biological environment would influence demographic traits was provided by the introduction of the lutjanid, *Lutjanus fulvus* into Hawaiian waters.

Nearshore snappers (Lutjanidae) and groupers (Serranidae) are most common in the tropical Indo-Pacific; however, they were absent in Hawaii before the 1950s

(Morales-Nin and Ralston 1990). Various hypotheses have been proposed to explain such an absence. Planes (1998) argued that this could be due to the geographic and hydrographic isolation of Hawaiian Archipelago in the Pacific.

L. fulvus occurs in tropical marine waters of the Indo-West Pacific, from the Red Sea, north to Japan, south to Australia and east to the Tuamoto Islands and also in the Hawaiian Islands after its introduction (Allen 1985a). It inhabits inshore coral reefs and lagoons at depths from 1m to 75m and may also enter mangrove areas and the lower reaches of rivers. Juveniles are sometimes found in shallow mangrove swamps and the lower parts of freshwater streams, and adults may grow up to 40cm in length (Morales-Nin and Ralston 1990).

L. fulvus was first introduced to Hawaiian waters in 1956 through fish brought from Moorea to Kaneohe Bay in Oahu (Planes 1998) and another batch was introduced into Kaneohe bay from the Marquesas Islands. This species became established in Oahu and spread to all other islands of the Hawaiian Archipelago. However, *L. fulvus* did not establish itself to the same degree as its introduced congener *Lutjanus kasmira* did (Schumacher and Parrish 2005). It has been suggested that this may be due to *L. fulvus* being a more preferred food fish than *L. kasmira* and *Cephalopholis argus* (also an introduced species), thus yielding better market prices, which in turn stimulated additional exploitation (Parrish et al. 2000). Because *L. fulvus* is not very abundant, it is currently not a big concern to fishery managers, however, due to its many biological similarities with *L. kasmira* (Tissot 1998), it may be worthwhile to monitor its demographical changes in the long-term.

Rapid growth and increased abundance have been documented in several introduced species (Koehn 2004, Laurenson and Hocutt 1986, McMahon 2002). Rapid growth may confer ecological advantages and increase survivorship of early juvenile fishes (Sogard 1997). Therefore, the selection of appropriate habitats for the fish being introduced has important demographic consequences (Forrester 1990, Levin et al. 1997, Petrik et al. 1999, Sogard 1992).

The primary aim of this chapter was to study the nature of demographic responses of *L. fulvus* after introduction to a new habitat. In a newly settled environment without many competitors, it is expected that *L. fulvus* will display a rapid growth compared to Moorea or Marquesas populations from where they originated. Using samples collected from the source populations (Marquesas and Moorea) and from the introduced populations from the southern islands of the Hawaiian archipelago, in this study I compared maximum life span, mortality and growth rates. The expectation of reduced life spans in Hawaiian populations was conservative for the following reason. Hawaii is located at higher latitude compared to either source populations. Based on the results presented in Chapter 3, the lifespan of the introduced populations should increase relative to that of the source populations if latitudinal position was the main determinant of that trait. This study also compared Pacific populations with the Cocos (Keeling) Island population (Indian Ocean) to obtain a wider picture on spatial variability in the demography of *L. fulvus*.

5.2 Materials and methods

Lutjanus fulvus were collected from three locations in the Pacific and two native habitats, Moorea and Marquesas, the source for the Hawaiian introductions. Samples were also collected from the Cocos (Keeling) Islands in the Indian Ocean in order to compare across ocean basins. A total of 120 *L. fulvus* were collected from the Cocos (Keeling) Islands (January - September 2004); 41 samples from Hawaii in July and August 2003; 24 from Marquesas in August 2003; and 50 samples from Moorea in August 2003. Sexual identity was available only for Moorea sample and therefore size-at-age data analysis discriminated by sexual identity was only possible for Moorea. Any temporal variation resulting from sampling in different time periods was assumed to not be a significant factor in the spatial patterns in the demographics and life history traits observed in this study.

Study areas

Cocos (Keeling) Islands: (Fishing intensity – very low). The Cocos (Keeling) Islands (12° 07′ S, 96° 54′ E) situated in the eastern Indian Ocean, is a territory of Australia. There are two atolls and twenty seven coral islands in the group. North Keeling Island is entirely surrounded by broken, irregular fringing reef, except at the north-west corner (Parks Australia North 2004). The marine reserve extends 1.5 km offshore from the Pulu Keeling National Park. North Keeling Island consist of world's most pristine coral reefs. The clear waters surrounding North Keeling island is home to a stunning array of fish, dolphins, marine turtles, and other marine species. Along the western side of the island is a wide coral terrace which drops into deep water. South Keeling Islands is an atoll consisting of twenty-six individual islets forming an incomplete atoll ring. About 528 species of fish have been recorded from the islands (Berry 1989). Compared with other oceanic atolls, the fish fauna is impoverished (Allen 1989). Most fish found in Cocos (Keeling) have distributions that cover large areas of the Indo-Pacific region (Allen and

Smith-Vaniz 1994). These are unpopulated group of islands and only 596 inhabitants in 2007.

Moorea: (Fishing intensity – very high). Moorea is a high volcanic island in French Polynesia, part of the Society Islands, 17 km northwest of Tahiti (17° 32′ S, 149° 50′ W). The total area is 134 square kilometers, 61 km of coastline with 16000 inhabitants in 2007. Moorea is encircled by a barrier reef which forms a 30 square km lagoon. There are fewer faunal species, a common characteristic of French Polynesia, mainly due to its isolation from other regions of the Indo-Pacific (Galzin, 1986a). Population density was 121 /km^2 in 2007.

Marquesas: (Fishing intensity – moderate). The Marquesas Islands consist of ten volcanic islands and a few small islets, extend in a NW and SE direction between 7^0 S - 11^0 S and 138^0 W-141^0 W. With a combined land area of 1,049 km^2 (405 sq. miles), the Marquesas are among the largest island groups of French Polynesia. The population of the Marquesas Islands was 8,632 at the August 2007 census. Marquesas is exposed to an upwelling regime with a lower temperature compared to neighboring islands (Camoin et al. 2006). Population density was 8 /km^2 in 2007.

Hawaii: (Fishing intensity – high). The Hawaiian Islands (18° 55′ N, 154° 48′ W) comprise a total of 137 islands and atolls, with a total land area of 16,636.5 km^2. The Hawaiian archipelago is characterized by fringing reefs and Northwest Hawaiian islands which contains non-fringing reefs (Price 2002). Kaneohe Bay on the island of Oahu is an example of the fringing, patch and barrier reefs. Kaneohe Bay's barrier reef is often questioned if it really is a "true" barrier reef. It was not formed the same way as the Great Barrier Reef in Australia. Hawaii is the most isolated group of oceanic islands in the world and possesses one of the most endemic, fragile, and endangered biota on earth, containing about 40% of the threatened and endangered species in the United States (Cox 1999). Fishing plays a very important role in Hawaiian economy by way of subsistence and recreational fishing (DBEDT 2003).

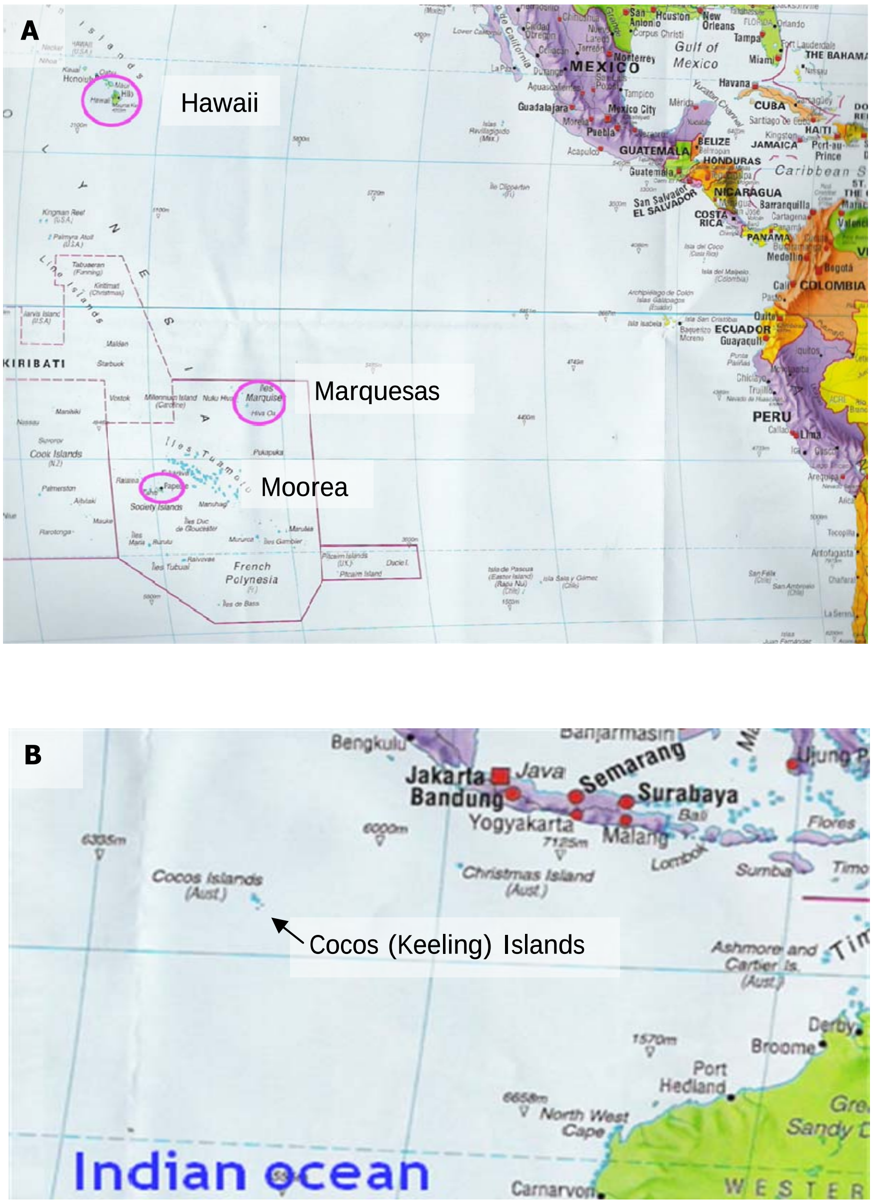


Figure 5-1 Map showing sampling locations of *Lutjanus fulvus;* A) Pacific sampling locations (Hawaii, Marquesas and Moorea), B) Indian Ocean location [Cocos (Keeling) Islands].

5.3 Results

A total of 235 *L. fulvus* otoliths were examined from 4 different locations (Table 5-1). Thin sagittal sections had distinct pattern of alternating translucent and opaque bands, and were readily interpretable for aging purposes.

5.3.1 Otolith weight versus age

Sagittal weight was linearly related to number of increments for each population of *L. fulvus* (Figure 5-2) for all the locations, indicating that sagittae continue to grow even in older ages. Otolith weight accounted for 89%, 76%, 66% and 88% of the variability in age for Hawaii, Cocos (Keeling), Marquesas and Moorea populations, respectively, and therefore could be used as a reasonable predictor for age in *L. fulvus.* ANCOVA revealed that the slopes of these relationships were significantly different among sample locations (F=24.4, p=0.000, df=3). Pairwise comparison of all 4 locations revealed that only Hawaiian-Cocos (Keeling) pair showed no significant relationship. Strongly significant relationships for all the other 3 locations indicate different sagittal growth patterns.

5.3.2 Maximum size and Longevity.

The largest *L. fulvus* collected in Hawaii, was 316 mm FL (Table 5-1). Mean maximum size ranged from 237 mm FL in Marquesas to 298 mm FL in Hawaii. The asymptotic size was also highest in Hawaiian (288 mm). The maximum longevity observed for *L. fulvus* was 10 yr in both Marquesas and Cocos (Keeling) compared to 7 yr in Moorea and 6 yr in Hawaii (Table 5-1). Estimated mean maximum age also followed a similar pattern as longevity (Table 5-1). The *L. fulvus* population in Moorea was relatively short-lived compared to Marquesas, i.e. the mean maximum age was about 25% less (6.4 vs 8.5 yr).

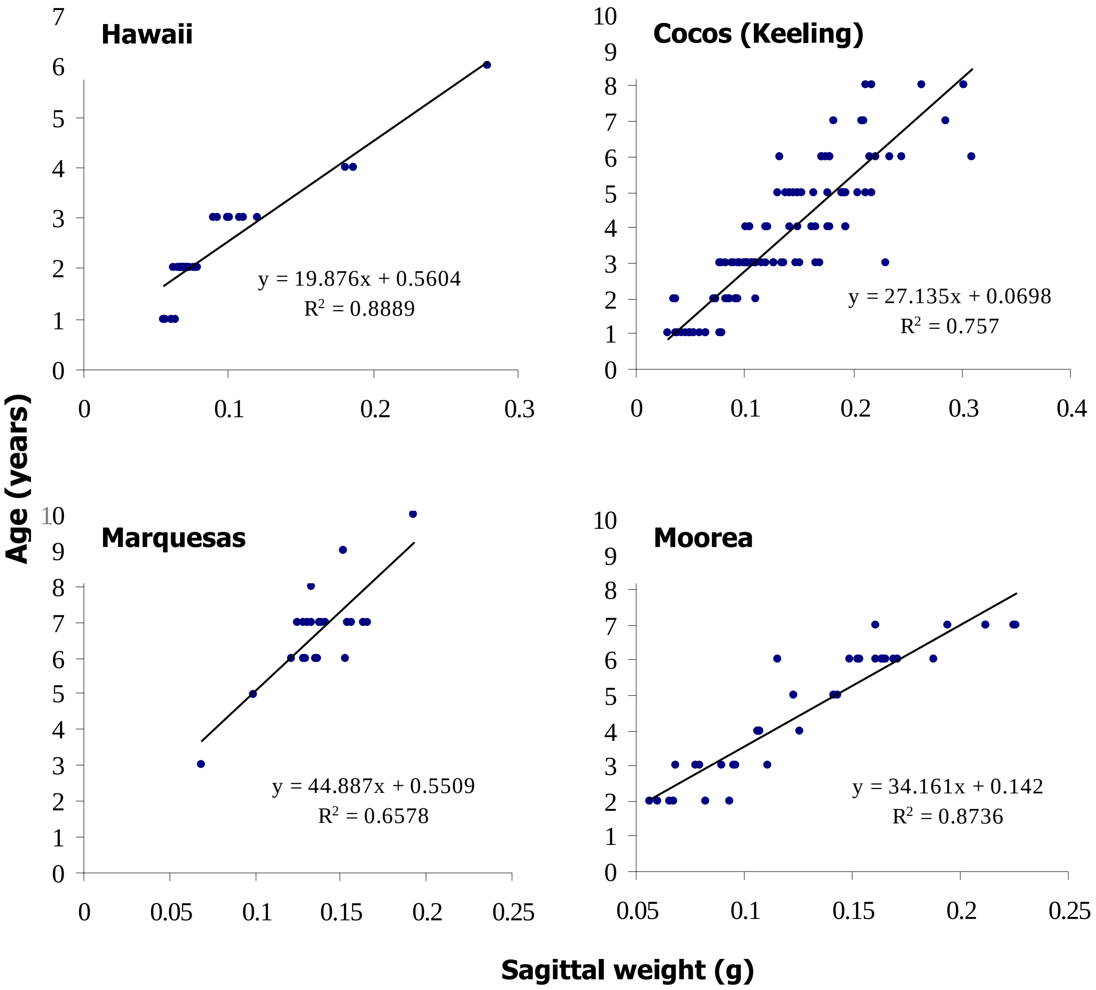


Figure 5-2. Least squares linear regression of sagittal weight on age for *L. fulvus* plotted by region.

Table 5-1. Summery of VBGF and other demographic parameters for *L. fulvus* derived from observed length-at-age data

Locality	L_∞	*k*	t_o	Age range (yr)	Mean max age (yr)	Size range (FL, mm)	Mean max size mm	n
Cocos (Keeling)	241	0.850	-0.129	1-10	7.0	133-282	260	120
Hawaii	288	0.613	-0.148	1-6	5.0	190-316	298	41
Marquesas	254	0.410	-0.253	3-10	8.5	180-260	237	24
Moorea	249	0.558	-0.190	2-7	6.4	161-268	251	50

5.3.3 Somatic growth

Maximum Likelihood Ratio test (Kimura 1990) was conducted only for Moorea population (figure 5-3), in order to examine any sex-biased differences in growth rates. Size-at-age did not differ between sexes in fish from Moorea, which allowed for sample pooling for further analyses. The von Bertalanffy growth curves, fitted to observed size-at-age data, were varied among locations (Figure 5-4). The Hawaiian population showed the fastest growth compared to other locations (Figure 5-5A) and Cocos (Keeling) population also showed similar fast initial growth as Hawaiian population. Blacktail snapper approached asymptotic sizes approximately at the ages of 4 years in Cocos (Keeling) and 7 years in Marquesas. However, Hawaiian population displayed a continuous growth without reaching an obvious asymptote.

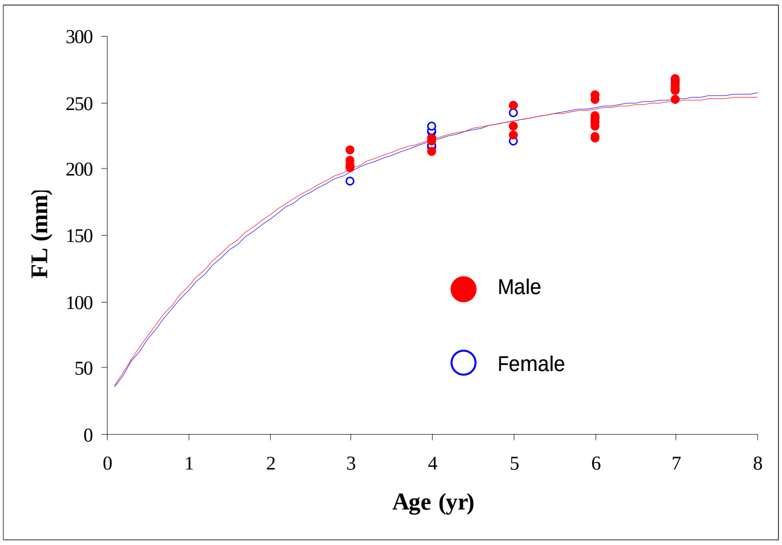


Figure 5-3. ***L. fulvus*, size-at-age plot by sex for Moorea population (after Kimura 1990). Circles represent the observed values while lines represent VBGF model values.**

The 95% confidence regions around the von Bertalanffy parameter estimates displayed overlapping of confidence ellipses between Moorea and Marquesas populations indicated they had similar growth trajectories (Figure 5-5B). The 95% confidence ellipses also showed that growth trajectory for Hawaii fish was more similar to that of the Cocos (Keeling) population than that of either Marquesas or Moorea where they originated.

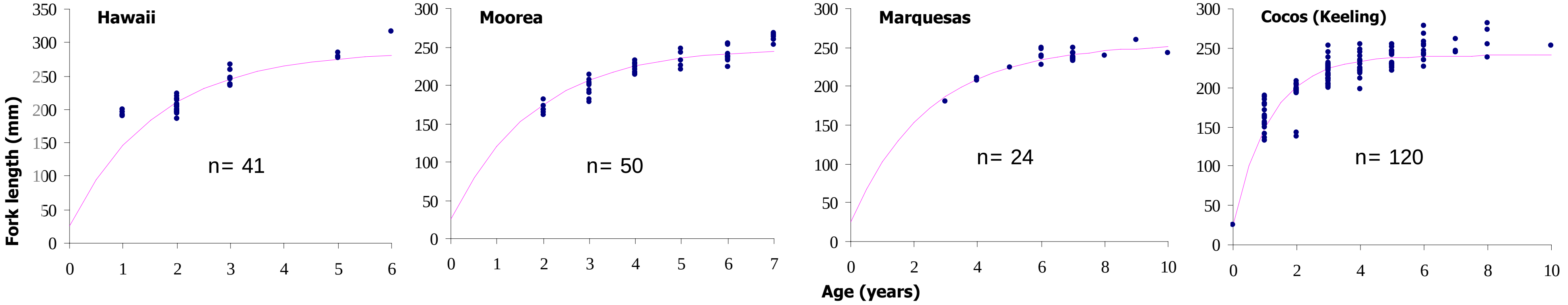


Figure 5-4. Size-at-age data with fitted VBGF for *L. fulvus*, plotted by region. Close circles indicate observed data and line represent the VBGF projections.

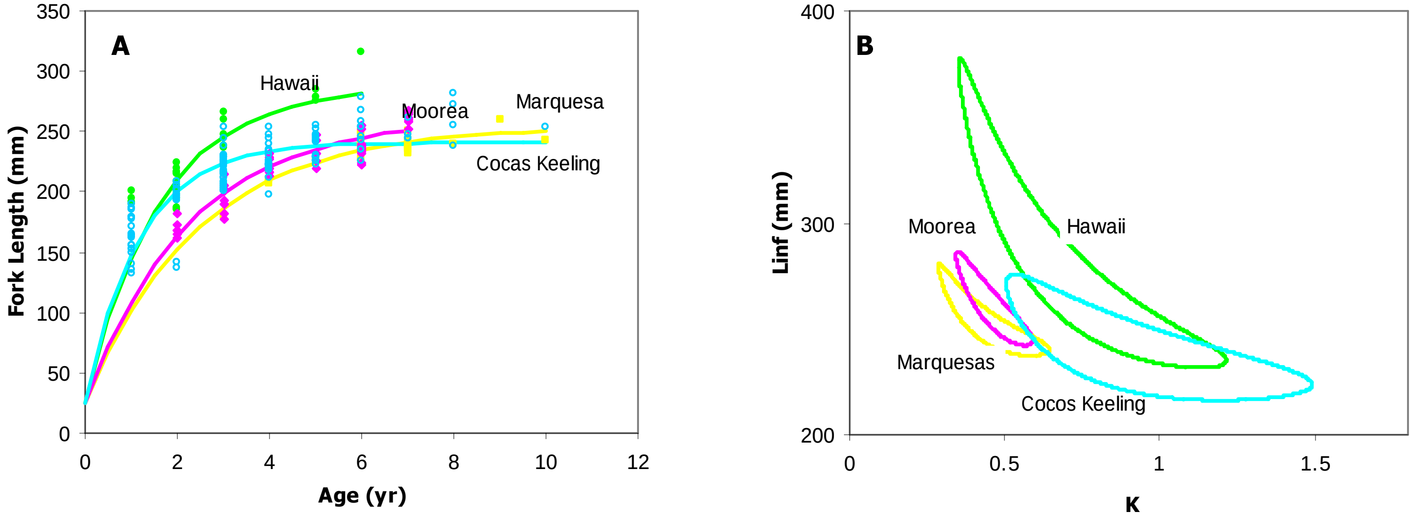


Figure 5-5A. Comparison of VBGF growth curves of *L. fulvus* among locations B. 95% confidence regions around least squares estimates of *K* and *L*$_\infty$.

5.3.4 Age structures and mortality.

Age distributions for *L. fulvus* (Fig. 5-6 A) were unimodal for all locations except Moorea, which was bimodal. The age structure in Hawaii was very truncated, with only one fish above age 4, whereas Marquesas had rapid decline in older age-classes. However, Moorea and Cocos (Keeling) populations had broader age structures with considerable numbers of older fish (> age 4)

The catch curve from Moorea has a very low r^2 and appeared to be nonsensical (Fig. 5-6B). The age distribution shows little or no evidence of a classical exponential decline. This could reflect some selectivity problem with sampling and relatively smaller sample size. The strong cohorts from ages 6 and 7 in Moorea also had the potential to skew the mortality curve upwards, thereby lowering the slope and underestimating mortality. Estimates of instantaneous total mortality rates, *Z,* ranged from 0.51 in Cocos (Keeling) to 0.85 (highest) in Hawaii (Table 5-2), corresponding to 60% and 43% annual survivorship respectively (Moorea was excluded). ANCOVA suggested significant differences in mortality between locations (df=3 *F*=13.5, p=0.000). Pairwise comparisons suggested significantly higher mortality rates in Hawaii compared to Marquesas and Cocos (Keeling).

Table 5-2. Instantaneous mortality rates, *Z* and annual percentage survivorships (S)

Locality	Instantaneous mortality rate, *Z*	Annual % survivorship, *S*
Cocos (Keeling)	0.51	60
Hawaii	0.85	43
Marquesas	0.78	46
Moorea	0.04	96

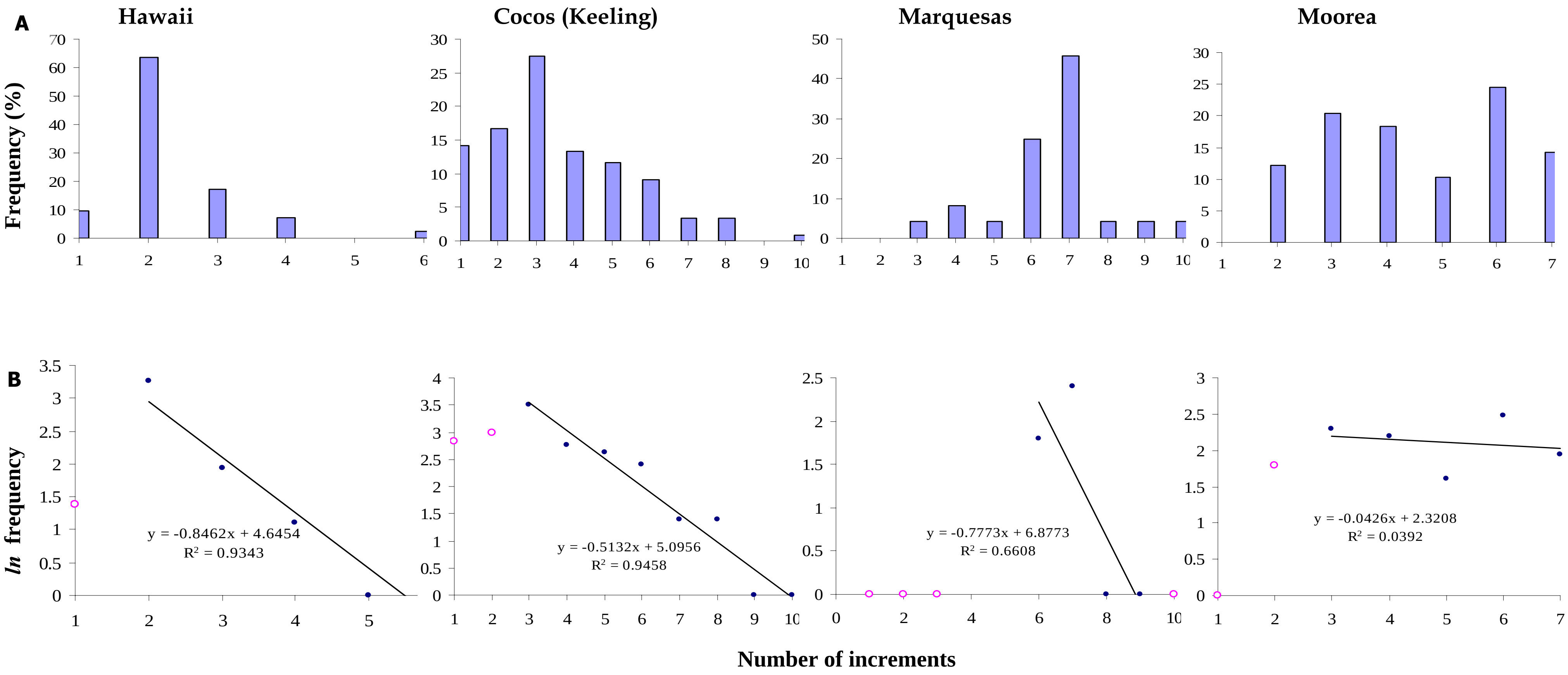


Figure 5-6. *Lutjanus fulvus* **(A) Age-frequency (%) distribution; (B) log-linear regressions of abundance on age by location.**

5.4 Discussion

The main interest in the *L.fulvus* demographic analysis lies in the comparison between the source and introduced populations. Fish from both Moorea and the Marquesas were introduced to the relatively depauperate reef system of Hawaii approximately 30 generations ago, and subsequently have become moderately abundant there. It is subject to a modest fishery. However, greater fishing pressure occurs in the source area, Moorea and to a lesser extent in the Marquesas. The introduced population demonstrated a number of properties that could be associated with rapid growth and population turnover, a predictable consequence of the release of a population into an environment with no other representatives of the family.

The comparison of the source and introduced populations is partially confounded by the possible interaction of fishing and habitat effects. In addition, the age structure of the samples and sample size was too low to allow a useful comparison of mortality rates or mean maximum age. To extend the comparison of *L. fulvus* populations, a sample was obtained from a similar habitat (deeper lagoon and outer reef slope) from an unfished population. This sample was collected from the Cocos (Keeling) Islands in the Indian Ocean and care was taken to obtain sufficient small individuals for estimates of size at age in the first three years of life.

The distinctive nature of the source and introduced populations is best seen in Fig 5-5B. The two source populations show almost complete overlap of k and L_∞. Marquesas samples had greater maximum age and mean maximum age compared to other Pacific counterparts. A more detailed comparison through size at age analysis was difficult due to the lack of samples from the younger age classes from Moorea and Marquesas. However, the growth curves supported the argument that the introduced population in Hawaii showed rapid growth in early stages of their life compared to the source populations. This is clearly seen in Fig 5-5B where the 95% confidence ellipse for the Hawaiian samples did not overlap with those of the source population at any point. Comparison of the 2nd and 3rd age classes of the Hawaii and Moorea populations demonstrate that by three years of age the Hawaiian individuals were approximately 25% larger than the Moorea individuals.

Predictably, the largest *L. fulvus* was collected in Hawaii. Mean maximum size and theoretical maximum size were also largest in Hawaii. Morales Nin and Ralston (1990) have also observed similar results for *L. kasmira,* another even more abundant introduced lutjanid in Hawaiian reef system. This suggests that large adult size is a consequence of rapid initial growth rates, a predictable consequence in species that achieve an asymptotic size relatively early in life, Laman-Trip (2004). This implies that conditions experienced during early life history will be critical in determining the adult size and associated demographics such as longevity, reproductive ability, ect.

The most plausible explanation for the enhanced growth rate and relatively short lifespan is that release into a relatively competitor- and predator-free environment would select for rapid population turnover rate and expansion into a new habitat (Morales Nin and Ralston 1990). Similar findings have been made with respect to the growth of the introduced *L. kasmira* in Hawaiian Islands in comparison to the Mariana Islands where the species is native (Ralston and Williams 1988).

The growth curves and their parameters illustrated in Fig 5-5A help clarify the relationship between growth rate, longevity and fishing. Firstly, initial growth rates in the Hawaiian and Cocos (Keeling) populations were similar which was reflected in the overlap of the confidence ellipses in Fig 5-5B. However, beyond age 3 the growth trajectories diverged as the Cocos (Keeling) population merged with the growth curves of the Moorea and Marquesas populations. The major distinction among the four populations is that the Cocos (Keeling), Moorea and Marquesas conformed to the typical asymptotic growth pattern that characterizes many lutjanids (Cappo et al. 2000), resulting in very similar L_∞ estimates. In contrast, the Hawaiian population maintained a higher growth rate throughout the life (which is unusual among known lutjanids), with the consequence of the highest L_∞ recorded in this study. The maximum life span was lowest in the Hawaiian population. This can be associated with earlier maturation and increased reproductive output (Robertson et al. 2005a).

A plausible interpretation of the changes in demographics that have occurred in *L. fulvus* in 30 generations since this species was transplanted from the southeastern Pacific is that they are mainly the result of biological rather than environmental influences. Both Moorea and Hawaii are similar distances from the equator. Although the Marquesas is at 10^{o} S, the reefs are subject to upwelling and have a lower temperature than predicted for their latitude. The three comparative populations, although spanning a wide range of locations and conditions, showed greater similarity to each other than to the Hawaiian population.

To determine if the introduced population is in fact in a rapid growth phase, a more comprehensive sampling program both from source, and introduced areas is required. Important objectives of such sampling would be to collect age-based reproductive data in order to establish the age at first maturity and to obtain larger, more representative samples of age structure to obtain more realistic estimates of mortality rates.

CHAPTER 6

General discussion

The primary goal of this study was to determine patterns of life history and demographic responses of reef fishes to environmental variation as well as how fishing on reef fish populations could be detected by an analysis of demographic features in the fishes concerned. For this study, the emphasis was on age-based features, growth rates, maximum age and population age structures. The major problem encountered in studies of this type is to separate the effects of fishing from the considerable variation in reef fish demographics that age-based studies are now revealing. It is known that reef fish demography is sensitive to changes in latitude (a proxy for temperature) and habitat structure. Accordingly, this study made a special attempt to control for the effects of latitudinal variation and to standardize the influence of habitats by sampling from equivalent habitats over the localities studied. In addition, it is known that biological features such as the presence of competitors may also influence the abundance and ecology of reef fishes.

In order to make the study more relevant to the fishery-related impacts, species with a history of fishing pressure - groupers, snappers and large wrasses - were selected. In addition, the study focused on the Caribbean, an area known for a long history of intensive fishing but one that also contains reserves protected from human activities. To attempt to resolve the issue of how reef fish populations might behave in the absence of competitors, a unique situation in which a reef fish had been introduced from a biologically complex coral reef locality to one lacking ecologically similar species was selected.

In summary, this study identifies strong demographic trends in reef fish age structure and growth rates over latitudinal gradients in the absence of significant fishing pressure. Correcting for the effect of latitude by examining the same species over a longitudinal gradient in which fishing pressure varied suggested that fishing did indeed have a measurable effect on reef fishes, especially in the reduction of lifespans. This was confirmed by a more detailed analysis of fishing pressure in two widely distributed reef fishes, a serranid and a lutjanid. Finally, the analysis of the demography of a lutjanid introduced into a new environment demonstrated that shifts in life span and growth rate could occur in response to biological changes as well as due to human influence. These results provide a more rigorous framework for analyzing the effects of fishing than one that simply monitors fished populations.

A number of life history variables were examined in order to understand the demographic patterns of reef fish at several spatial scales over a large geographic range and across ocean basins. There were obvious variations in age structures, growth and size maxima for most of the populations studied across the regions. Regional-scale patterns in demographics also differed among species, indicating complex spatial variability. However, again, there were contradictions because of variations in demography even within a single region.

Growth

There were striking differences in the growth characteristics of the populations examined. Growth curves were asymptotic in many instances; however, one of the consistent patterns observed was that the populations subjected to heavy fishing pressure showed continuous growth without reaching an obvious asymptote. There was considerable variation in demographic characteristics even within single latitude and that variation cannot be explained by latitudinal effects only.

Most growth occurred within the first third of the lifespan for long-lived *L. griseus* from Bermuda, indicating faster growth in high latitude populations compared to low latitude counterparts. This appeared not a universal explanation, as the low latitude Los Roques population of *L. maximus* also showed faster growth and attained larger size. These findings however need to be evaluated with caution, as fishing might have influenced such variability. In addition, wrasses are known to have complicated and inconsistent life histories (Choat et al. 2006) compared to snappers and groupers, and this might be another plausible explanation for such variability. Size increase would be achieved through rapid growth, resulting in large but relatively young individuals, or slower growth with increased longevity, providing longer opportunity to reach large sizes. The present study shows that large size can be achieved through rapid growth, resulting populations with larger but younger individuals.

Some species' demographics were more similar to regions in a different area than regions in the same area. For example the *L. fulvus* population from Hawaii showed similar growth trajectories with Indian Ocean [Cocos (Keeling) Islands] populations than Marquesas and Moorea populations where they originated.

Longevity

This study recorded the highest longevities reported for 3 of the 6 species studied, namely *L. griseus* (34 yr), *L. apodus* (31 yr) and *C. cruentatus* (14 yr). Previously recorded maximum ages were 28, 17 and 13 years for these species, respectively. Long lifespans act as a buffer against occasional recruitment failures. However, it is also associated with greater vulnerability to fishing and lengthy recovery times after episodes of population depletions (Jennings et al. 1999a). Estimates of greater longevity and therefore lower natural mortality rates in snappers suggest that they are more vulnerable to over-fishing than other species with shorter life spans and higher natural mortalities (Newman et al. 2000). However, longevities of more than 20 yr may actually benefit a species by ensuring a relatively long reproductive span and thus minimizing the risk that prolonged periods of unfavorable environmental conditions will lead to the loss of a stock (King and Mcfarlane 2003).

The high latitude Hawaiian population of *L. fulvus* was expected to have a longer lifespans compared to the lower latitude populations of Marquesas and Moorea; however, this study showed that *L. fulvus* in Hawaii is shorter-lived. This unexpected result may be related to the relatively faster growth observed in the Hawaiian population. Generally, faster growing individuals attain larger sizes and therefore have higher turnover rates resulting in shorter lifespans (Charnov 1993).

A consistent pattern observed in Bermudian populations of *L. apodus* and *L. maximus* was that they were relatively long-lived and displayed strongly multimodal age structures, indicating presence of occasional strong or dominant year classes. This would be a very important aspect to look at in future studies.

Body size

Bermudian populations also attained larger body sizes compared to other counterparts. This latitudinal increase in size has been observed among ectotherms (Atkinson 1994, Atkinson and Sibly 1997), including tropical and subtropical reef fishes (Choat et al. 2003, Luckhurst et al. 2000). Larger body size and extended lifespan in Bermudian populations could be an adaptive response to lower average temperatures (due to its high latitude location) experienced during development (Atkinson 1994). Choat and Robertson (2002) also noted that an increase in average annual temperature negatively correlates with maximum age in some fishes. Countergradient growth represents a mechanism that compensates for shorter growing seasons resulting from low temperatures in high latitudes (Conover 1990). The inverse relationship between growth and temperature I observed for *L. griseus* is consistent with such countergradient growth.

Age distributions

My findings provide strong evidence that all the species studied showed truncated age distributions in locations subject to heavy fishing. Differential growth trajectories may be associated with populations under different exploitation rates. Then, observed smaller sizes-at-age could be a result of selective removal of larger, therefore, presumably older age-classes in the population. Similarly, locations subjected to high level of fishing showed smaller mean maximum sizes.

Studies have shown positive relationship between initial size and adult size (Laman-Trip, 2004) my findings for *L. griseus* from Bermuda also comply with above relationship. This indicates that large amount of plasticity found in growth is driven by a mechanism of faster growth. Therefore, large body size is most likely due to increased growth during their early years of life. This is consistent with the countergradient growth model which explains the mechanism of variation in growth rates with latitude in temperate species (Conover 1990, Conover et al. 1997, Conover and Present 1990, Yamahira and Conover 2002). Higher temperatures in tropical waters are not necessarily associated with higher rates of somatic growth and points to the presence of compensatory mechanisms in growth to environmental factors such as length of growing season or colder temperatures as demonstrated for many temperate species (Conover and Present 1990, Schultz et al. 1996).

VBGF

A number of growth models are known to fit size-at-age data. However, the von Bertalanffy growth function with t_o constrained to size-at-settlement was chosen because it fit well with the available data. Constrained fittings of the VBGF (t_o to size-at-settlement), provided a conservative estimate of regional variation in growth, and these variations were usually larger when t_o was not constrained (Williams et al. 2003). Von Bertalanffy growth function known to give a biologically-realistic estimate of size-at-age and this also allow comparisons with other studies. The forcing of

VBGF models through zero in other studies may have contributed to some of the differences in growth parameters noted between previous studies and present study. However, in this study I did not force VBGF through zero. Some of the L_∞ values I estimated using the VBGF appeared unrealistically high, a common occurrence in species with continuous growth throughout life (e.g. Choat and Robertson 2002).

There is controversy over the use of the von Bertalanffy growth function to model fish growth (e.g. Day and Taylor 1997, Roff 1980). Further, there are serious doubts about its applicability to protogynous hermaphrodites (Appeldoorn 1996, Sadovy 1996), primarily because growth analyses have shown distinct differences in the sizes of equal age males and females (Garratt et al. 1993).

Significance and implications of the findings

Importance goes well beyond satisfying human curiosity in scientific investigations. The knowledge that gains from present study has immense significance in our current era of massive and excessive fisheries exploitation and grooving impact of climate change. This is also important contribution to dissemination of the scientific knowledge. Species specific information provided here will be available to fishBase consortium for integration in to global database.

This is the first record of such finding from Atlantic on demographic variability of large exploited reef fish at such large spatial scales, and will be valuable to fishery managers and stock assessment biologists in the region (and beyond) trying understand stock and sub-stock structure and move towards more spatially discrete management. Also, observed pattern in fisheries demographic and life history data are fisheries, environment or biological effects. Finding of this study will help in improving our understanding of species' population dynamics and their responses to environmental and fishing effects.

The findings on blacktail snapper will be valuable in predicting and understanding the effects of patterns associated with introduced species, whether the introduction was purposeful or accidental, such as the current situation with Pacific lionfish quickly spreading up the SU Atlantic coast, in to the Bahamas and Mexico and probably the Gulf of Mexico.

Limitations and future recommendations

In many instances, individuals were selectively sampled in order to obtain a comprehensive set of points for growth curves. Samples derived from fisheries that targeted larger fish were obviously biased towards larger size-classes. Because of this bias towards larger and older individuals, there was a potential to inflate estimates of survivorship. Estimates of mortality rates presented herein should therefore be treated with caution. Ideally, they should be calculated with repeated sampling through time. However, samples collected for this study had no regular temporal distribution and mortality rates were estimated using log-linear models which assume there is no long-term trend in levels of recruitment (Pauly 1984).

It is important to distinguish between the validation of increment periodicity and absolute age (Campana 2001). Although some studies have provided empirical evidence for an annual pattern of increment formation, the absolute age for the species examined in this study remain to be validated using mark and recapture technique or chemical marking of juveniles. However, such empirical studies looking at validating increment periodicity are challenging with snappers and groupers, which are difficult to rear.

Age-based demographic analysis of reef fish is a powerful tool in the context of management. However, to progress, the field has two critical requirements. Firstly, a better understanding of the reproductive biology of the study species is required, with a focus on obtaining realistic estimates of annual fecundity. This is a difficult task in reef fishes as some spawn year round while others are more episodic. However, changes in growth rate may well be linked to the magnitude of reproductive outputs, which in turn can be linked to the pattern of environmental seasonality. Secondly, the basis of demographic changes in terms of the underlying mechanisms, phenotypic or genetic, must be investigated. The most successful studies in this context are those of Conover and his colleagues and have been achieved through the use of common garden experiments. There are formidable challenges in accomplishing this with long-lived reef fishes.

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