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UNIVERSITY OF MIAMI

IMPROVING STOCK ASSESSMENT CAPABILITIES FOR THE CORAL REEF FISHES OF HAWAII AND THE PACIFIC REGION

By

Marc-Olivier Nadon

A DISSERTATION

Submitted to the Faculty
of the University of Miami
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IMPROVING STOCK ASSESSMENT CAPABILITIES FOR THE CORAL REEF FISHES OF HAWAII AND THE PACIFIC REGION

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Coral reef fisheries provide livelihood and sustenance for hundreds of millions of people worldwide, particularly in poor tropical countries. Recently, stock assessment methods have been proposed for these typically data-poor fisheries that rely mainly on cost-effective abundance-at-size data and some basic demographic knowledge on growth, maturity, and longevity. However, even these simple data requirements are often unmet. Additionally, coral reef fishes are often monitored using disparate fisheries-independent and -dependent survey methodologies that cannot easily be combined into single datasets.

The goal of this dissertation was to develop a series of methods that allow for the efficient assessment of the sustainability of the coral reef fisheries of the Hawaiian Archipelago. To achieve this goal, the specific objectives of this dissertation were to: (1) develop a predictive model to generate standardization factors for species with sufficient fishery-independent survey observations and implement this statistical methodology in an automated, computer-based procedure, and; (2) develop a new approach for the generation of life history parameters that facilitates stock assessments for species with no published values.

Quantitative tools were developed to standardized underwater visual survey data collected by several methodologies, produce missing life history information key to assessments, and conduct the stock assessments of 27 coral reef fish species, including 8 species for which no life history information previously existed. These analyses indicated that about half of the stocks assessed in Hawaii are overfished (i.e., spawning potential ratio below 30%). This result was consistent with analyses conducted for other U.S. coral reef fisheries jurisdictions such as Florida and Puerto Rico. The methods and findings of this dissertation provides new tools for confronting data-poor situations, including, but not limited to, coral reef fisheries. The work presented here also provides the first archipelago-wide stock assessment of coral reef fishes in the tropical Pacific Ocean.

Dedication

À ma mère et à mon père.

Vous qui avez toujours cru en moi.

Merci.

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Chapter 1

Introduction

The sustainability of global fisheries has been the subject of recent debates among scientists (Myers & Worm 2003; Hampton et al. 2005; Sibert et al. 2006; Hilborn & Ovando 2014). The emerging view is that most stocks are overfished, although there have been encouraging signs that large, well-studied, and well-managed stocks are rebuilding (Worm et al. 2009; Pitcher & Cheung 2013), with notable exceptions such as the Atlantic cod (Hilborn & Litzinger 2009). The current status of smaller, typically un-assessed stocks is less clear. More specifically, the sustainability of coral reef fisheries has been questioned, mainly based on observed differences in fish abundance between heavily populated (and fished) areas and uninhabited areas (Chiappone et al. 2000; McClanahan & Arthur 2001; Sandin et al. 2008; Williams et al. 2011). Despite the economic and cultural importance of reef fisheries, there have been few formal stock assessments conducted other than those in Florida and Puerto Rico (Ault et al. 1998, 2005, 2008). The sustainability of reef fisheries in the tropical Pacific, for example, has yet to be evaluated and represents an important challenge to fisheries science and management. This state of affair is due to several factors: (1) lack of data required to conduct modern stock assessments such as time-series of age- or size-structured catches, associated fishing effort, and reliable demographic parameters (Quinn & Deriso 1999; Ault et al. 2008; Haddon 2010); (2) high fish species diversity in tropical coral reefs which precludes the concentration of efforts (e.g., field sampling, life history research) on a few stocks (Fenner 2012); and (3) lack of trained scientific and technical personnel.

The expert panel of a 2004 Western Pacific Regional Fisheries Management Council workshop pointed out several key limitations to conducting reef fish stock assessments in Hawaii and the Pacific region (Ault et al. 2004). First, the different underwater fish survey methodologies used across the region must be carefully standardized in order to be combined in a single, usable, dataset. Secondly, there are only a limited number of studies on the life history and population dynamic parameters of these reef fishes (i.e., growth, reproduction, longevity) which are necessary for modern length- or age-based stock assessment models. Thirdly, underwater visual surveys need to be carried out using an efficient population-scale sampling design to be useful for stock assessments (e.g., Smith et al. 2011). This last issue has been mostly addressed, at least within the Pacific Islands Fisheries Science Center's (PIFSC) – Coral Reef Ecosystem Division (CRED) and the National Marine Sanctuaries program. It involves a stratified random sampling design for underwater visual fish surveys that has been implemented since early 2007 and is continuously being improved. However, the two other issues present significant barriers to the conduct of reef fish stock assessment in Hawaii or the broader Pacific region. For example, only 20 species of exploited reef fishes, out of the more than one hundred exploited ones in Hawaii, have published life history parameters.

The overall goal of this Ph.D. dissertation was to improve the stock assessment capabilities for coral reef fisheries by developing new methodologies for data assimilation, statistical analyses, and computer model-building that facilitate the ultimate goal of conducting formal stock assessments of the principal targeted coral reef-associated fish species around the main Hawaiian Islands. To achieve this goal, the specific objectives were:

- **Chapter 2**: Develop an efficient, mostly automated, generalized linear model (GLM) procedure to standardize fishery-independent survey data collected using several different survey methods. This procedure also included the generation of statistical models to predict standardization factors for species with insufficient number of observations to run GLMs reliably;
- **Chapter 3**: Use the standardized length dataset and available life history parameters in a length-based modeling approach to conduct a first-step assessment of 19 exploited reef species in Hawaii;
- **Chapter 4**: Search the literature for key life history parameters for 6 families of reef fishes and run meta-analyses to generate probability density distributions of life history parameters. Use these distributions in Monte Carlo simulations to run population models;
- **Chapter 5**: Use the standardize length dataset and life history parameter probability distributions obtained through the new Monte Carlo simulation approach to conduct further stock assessment of Hawaii reef fishes.

Chapter 2

Standardization of high diversity reef fish population abundance datasets

Summary

Indices of population abundance are widely used in ecology and fisheries science by assuming a proportional relationships between observations per sampling unit and population size. However, indices collected using different sampling methods do not necessarily have the same proportionality with population size and therefore need to be standardized before being combined. The usual standardization approach employs generalized linear models (GLM), but this can be prohibitively time consuming when dealing with datasets containing information on hundreds of species, as is often the case for coral reef fish surveys. Furthermore, these datasets typically include hundreds of rare species with insufficient numbers of observations to run GLMs. Here we introduce a solution to these two dilemmas by: (1) developing a procedure to automate data processing and analyses associated with GLMs to obtain standardization factors; and (2) use these standardization factors to build predictive models using relatively simple explanatory variables such as family, rarity, swimming speed, habitat, and maximum size. We used a large underwater visual survey dataset collected using three different sampling methods around various U.S. Pacific reefs to generate standardization factors and to build predictive models. We applied these MCFs to standardize a dataset containing data on 208 species of coral reef fishes collected between 2005 and 2013 around the main Hawaiian Islands.

Background

Fisheries assessment and ecological research rely heavily on indices of fish abundance to evaluate population sizes and temporal trends, and determine ecological linkages in fish communities. There exists a great number of abundance indexes such as: fisheries-independent passive and active acoustic signals (Gannon 2008); underwater surveys by divers or cameras (Willis & Babcock 2000; Smith et al. 2011; Richards et al. 2011); as well as, fisheries-dependent catch-per-unit-effort (CPUE) for various fishing gears (Maunder et al. 2006). Fisheries assessment scientists typically rely on CPUE data due to their low costs and relatively broad spatial coverages. These can be integrated with precise and accurate fisheries-independent data which benefit from planned and controlled sampling designs, when available.

To complete spatial or temporal coverages, fish abundance index data derived from different observation methods often need to be integrated into a single dataset, especially when different observation methods are used in different areas or time periods. Before they can be merged together, fish abundance data need to be carefully standardized as observations-per-unit effort can vary widely between methods or fishing gears, even over equal sampling areas. The standardization of catch and effort data has long been employed in fisheries science (referred to as "fishing power" standardization, see Maunder & Punt 2004 for a review).

The use of abundance indices as relative measures of population size rests on the assumption that the number of observations per unit of effort (referred in the rest of the text as CPUE) is related to total population by the parameter q (CPUE = q $\overline{N}$), which is termed "catchability" and is defined as the fraction of the population removed or observed per unit of effort (Gulland 1956; Ault et al. 1998). At small spatial and temporal scales, $\overline{N}$ can be assumed to be the same and the differences in density obtained from multiple observation methods is related to their different catchabilities (q). Although it is rare to know the actual value of the catchability parameters (q), we can use the ratios of CPUEs collected by different methods over areas with similar $\overline{N}$ to estimate the relative magnitude of the methods' q values. We can thus convert one method's CPUE data to another method's equivalent by dividing the original CPUE data by that ratio (called the Method Standardization Factor or MCF). To calculate this ratio is to assemble a method comparison dataset where different observation methods are implemented over similar areas within a reasonable short timeframe and run a simple statistical model that describes CPUE as a function of the survey method used and space-time information. Although other approaches have been used, generalized linear modeling (GLMs; Fox 2008) has been the most commonly used tool for standardizing catch and effort data in commercial fisheries.

Standardization of data collected by different gears or methodologies has often been ignored in coral reef fish population and community dynamics research (Friedlander & DeMartini 2002; Mora et al. 2011; McClanahan et al. 2011; Edwards et al. 2013). A common misconception is that simply multiplying fish densities collected over different sampling areas by the ratio of these areas is sufficient to standardize fish counts (i.e., multiply counts from a 2m-wide belt transect by 2 to convert these to 4m-wide belt transects). The main reasons for omitting the standardization procedures are likely: (1) the costs and complexity associated with assembling a methods comparison dataset; (2) the time involved in running standardization analyses for the high number of species comprised in reef fish datasets; and (3) the important number of rare species with generally few comparative time-space block samples between methods.

The goal of this study was to address these last two reasons by: (1) developing a procedure that automates most of the data processing and GLM analyses to standardize fish abundance; and, (2) building a robust statistical model that facilitates prediction of standardization factors for a suite of data-poor species based on some easily obtainable predictor variables (e.g., taxonomic group, swim speed, habitat, size, etc.). We used a large underwater visual survey dataset collected using three different sampling methods around various U.S. Pacific reefs to generate standardization factors and to build predictive models obtain standardization factors for rarer species. The utility of this approach is demonstrated by standardizing a large underwater visual census dataset from the main Hawaiian Islands that was created using three different survey sampling methods.

Methods

Study area and survey design

The fish count data used in the current study came from the NOAA Pacific RAMP program which conducts coral reef fish surveys around 46 reefs in the Hawaiian archipelago, American Samoa, the Mariana archipelago, and various remote islands in the central Pacific (Ayotte et al. 2011; Fig. 2.1). From 2002 to 2007, the principal fish survey sampling method was belt transects; however, in 2007 these were replaced by stationary point counts (SPC) starting. During surveys conducted between 2007 and 2010, both methods were implemented at survey sites to build a dataset of paired fish counts for standardization analyses. Sampling sites around each islands were selected randomly within habitat-based strata defined by combination of reef zones (i.e., forereef, backreef, and lagoon) and depths (shallow, 0-6m; mid, 6-18m; and deep, 18-30m).

Belt transects consisted of a pair of divers slowly swimming along a 25 m transect line while recording and measuring all fish smaller than 20 cm in a 4 m-wide swath. Divers recorded and measured all fish larger than 20 cm in an 8 m-wide swath on the return swim. Since the two belt methods had different widths, we considered them as separate methods in our analyses, here referred to as the “small belt” and “large belt” methods. The third method, stationary point counts (SPC), were conducted by a pair of divers inside two contiguous 15 m-diameter cylinders extending from the seafloor to the surface following Brandt et al. (2009). Fish observations were recorded in two distinct steps. First, divers recorded a list of fish species observed during an initial 5 minute period. Second, divers went through this list, species by species, and recorded abundance and sizes of all fish present in their cylinder (sizes were total lengths estimated to the nearest cm). Fish densities for all three methods (SPC, small belt, and large belt) were converted to a standardized unit area (100 m^2) to simplify comparisons.

GLM for indices of abundance standardization

The method standardization approach used here is the “relative fishing power” method originally conceptualized by Gulland (1956) and Beverton and Holt (1956), and later formalized mathematically by Robson (1966).

It is generally assumed that catch or observations (we will use the latter term in the rest of the text), C, is proportional to average population abundance $\overline{N}$ such that

$$C = F\overline{N} = qf\overline{N} \quad , \qquad (1)$$

where, F is the instantaneous "viewing" rate, f is the nominal survey effort, and q is the fraction of total abundance that is captured or observed in one unit of effort (traditionally referred to as the catchability coefficient). Indices of fish abundance in terms of observation-per-unit-effort (CPUE) can be described by re-arranging Eq. 1 to

$$CPUE = \frac{C}{f} = q\overline{N} \quad , \qquad (2)$$

At each survey site s, the expected CPUE was a function of the space-time block i and method j, as described by a GLM model following Robson (1966)

$$CPUE_{ij} = \alpha + b_i + g_j + \varepsilon_{ij} \quad , \qquad (3)$$

where α is a constant, b_i are space-time block coefficients, g_j are method coefficients, and ε is an additive error term. The b_i are used to remove any potential effect of sampling time or location if sampling was uneven between methods (e.g., belt transect disproportionally sampling high fish abundance area vs. stationary point counts).

Eq. 2 shows that if catchability (q) is constant between CPUE abundance indices, these indices can be combined into a single dataset. This, however, is rarely the case and CPUE data collected from different methods typically need to be standardized to a single, standard, method. The usual way to do so is to divide the CPUE of the secondary method by the CPUE of the standard method (after controlling for sampling location/time effects on $\overline{N}$) to obtain a method standardization factor (MCF = λ_j)

$$\lambda_j = \frac{CP\hat{U}E_j}{CP\hat{U}E_S} \qquad (4)$$

The average CPUE for the secondary method divided by the MCF will convert abundance data collected using this method into their standard method equivalent, thus allowing the two datasets to be merged in an appropriate fashion.

When calculating method standardization factors (λ_j) we disregard these coefficients and write Eq. 3 as

$$\lambda_j = \frac{\alpha + g_j}{\alpha + g_s} \quad , \tag{5}$$

where g_s is the standardized method effect and g_j is the secondary method effect. Dividing the secondary method densities by the MCF converts those densities into standardized densities (i.e., as if fish counts had been recorded by the standard method).

CPUE data typically contain a large proportion of zero counts. It is almost always necessary to separate the CPUE into two components: (1) presence/absence; and, (2) positive-only densities, and model these independently (i.e., the delta modeling approach). To implement this approach, we first build a logistic regression model for the presence/absence data (0s and 1s) using a logit link (same structure as Eq. 3) which provides the probability of presence per unit effort for each method. We then build a regular linear regression model for the positive-only densities (again using Eq. 3). We reconstruct the CPUE for each method by multiplying the proportion of presence by the positive-only densities, and then use these CPUEs in Eq. 4. It is often necessary to log-transform the positive-only densities to obtain normally distributed residual errors. If the log-transformation fails to produce normal residuals, we can use a gamma distribution to model the positive densities.

Automating the GLM approach

Since the procedure described above would be almost impossibly time-consuming to run for hundreds of species, we created a procedure using the Java programing language (version 8.0.200) and R 2.15.3 (R Core Team 2013) to automatically manipulate and re-arrange high species diversity datasets and run the GLM analyses. Figure 2.2 describes this procedure: after loading the raw data, we first recognized all the species and space-time blocks present and split the dataset accordingly (all the following steps are run for each individual species, in turn). Next, we removed all space-time blocks with replicates from only one method (or without any positive counts). If there was an insufficient amount of observations left in a particular species' dataset after this step (e.g., non-zero $n < 10$ for either methods), we discarded this species from further analyses. If there was sufficient data, we evaluated the proportion of zero-counts in the dataset and decided whether to run a delta model or regular model (the proportion of zeroes minimum for delta modeling was set to 0.2 in our analyses). If the delta modeling approach was selected, we created two separate datasets: a presence/absence dataset (i.e., 0s and 1s) and a positive-only density dataset. For the presence/absence dataset, similarly to blocks with only zeroes, we filtered out blocks with no zero observations (a rare, but possible situation). For the positive-only density dataset, we filtered out blocks with positive observations from only one of the two methods. We then created dummy variables for the "method" variable and space-time blocks. Next, we ran the GLM model (delta or regular approach, as described in the previous section) and determined if the residuals were normally distributed by evaluating the skewness of the residuals. By definition, a normal distribution has a skewness of 0. We considered residuals with skewness outside of the -0.5 to 0.5 range to be non-normal and proceeded to log-transform the density data and re-run the GLM. If the log-transformation was unsuccessful in normalizing residuals, we ran the GLM again using a gamma distribution for errors, since the shape of this distribution is more flexible. If the GLM failed to converge on the shape and scale parameters, the species was discarded from further analyses. We calculated MCFs as described in the previous section. The uncertainty around the MCFs was calculated through Monte Carlo simulations: the R GLM procedure (R Core Team 2013) provides a variance-covariance matrix of the parameter estimates (b_0 and b_j from equation 4) from which we randomly sampled parameter values from a bivariate normal distribution, obtained a distribution of MCF values, and calculated the associated 95% confidence intervals (Preacher & Selig 2012). We rejected MCFs where the 95% confidence intervals were deemed too large and thus uninformative (CI > 2 log MCF).

MCF predictive model for data-poor species

In order to obtain MCF for species with insufficient paired data, we built a predictive model with the available MCFs as the dependent variable and various explanatory variables as independent variables. We tested the following predictive variables: genus, family, size, habitat, rarity, swimming speed, and schooling behavior. We used the maximum reported size for the size variable. “Habitat” referred to the typical species position in the water column (cryptic – inside holes, overhangs, or coral heads, bottom – resting on or hovering near the sea floor, and above – swimming at least 1m above the bottom). Rarity was defined as the average probability of presence for the secondary method (belt transect in our case) in the study area. Swimming speeds were classified in three categories (stationary – mostly immobile, slow – casual speed, less than 1m/s, winding trajectory, fast – faster than 1 m/s, usually straight trajectory). Finally, we used the average count on the SPC as a measure of schooling behavior (i.e., species with average counts around 1 are typically solitary while species with high average counts are more likely to be found in large schools). The MCFs, rarity, and schooling variables were log-transformed. We looked at potential collinearity between all explanatory variables by calculating correlation coefficients: Pearson's (continuous vs. continuous variables), polyserial (continuous vs. categorical variables), and polychoric (categorical vs. categorical variables) using the polycor procedure in R (Fox 2010). We selected the best model based on Akaike Information Criterion (AIC). We evaluated the normality of the model residuals by visualizing their distributions using histograms and QQ-plots.

Standardization of a Hawaiian Island reef fish survey dataset

We ran the procedure described above on the NOAA-CRED Pacific-wide dataset (Ayotte et al. 2011) in order to obtain MCFs for all species present in this dataset. We used those MCFs on the survey data for the main Hawaiian Islands (MHI) in order to test our standardization approach. Belt transects were used during survey cruises in 2005, 2006, and 2008, while stationary point counts were used in 2010, 2012, and 2013. We combined the years 2005-2006 and 2012-2013 since 2005 and 2013 had incomplete surveys of the MHI. Our goal was to standardize the fish densities data collected using belt transects to their SPC equivalent in order generate an unbiased time series of fish abundance from 2005 to 2013. We created two datasets: a small belt vs. SPC dataset for fish smaller than 20cm and a large belt vs. SPC dataset for fish larger than 20cm.

The next step was to obtain a MCF for each of the species present in this dataset (Fig. 2.3). If a species had enough observations to obtain a specific MCF through the GLM approach, we simply used this value. For rarer species without a species-specific MCF, we used our predictive model to obtain a likely MCF, as explained in the previous section. For each species, we divided the average belt densities in each year by their MCF to obtained densities standardized to the stationary point count method. The standardized and un-standardized time series of fish abundance were plotted by family and trophic group to visualize the potential bias associated with using an un-standardized dataset.

Results

From 2007 to 2010, paired surveys using both belt transect and stationary point count methods were conducted at 315 sites spread across 46 reef areas in the U.S. Pacific. To supplement this paired observation dataset, we also included surveys done in the same reef area, depth, and reef zones, but in different years (2008-2010) since surveys suggested small year to year differences in reef fish abundance (see chapter 3). Our space-time block variable was thus defined by reef area, depth, and reef zone (forereef, backreef, and lagoon) between 2008 and 2010. This added an additional 335 belt transect and 1003 SPC sites to our paired method comparison dataset.

The small belt-SPC dataset contained fish counts for 561 species, while the large belt-SPC contained data for 316 species. The automated standardization procedure successfully generated 191 MCFs for the first dataset and 81 MCFs for the second. Other species were rejected because of an insufficient number of non-zero observations ($n < 10$ for either method; Table 2.1). Furthermore, we discarded 18 MCFs from the small belt-

SPC dataset and 5 MCFs from the large belt-SPC dataset because the error associated with their MCF was high (>2 log of 95% CI). For the small belt-SPC dataset, MCFs ranged from 0.15 (*Melichthys vidua*, a triggerfish) to 16 (*Plagiotremus gosleinii*, a fang blenny) with an average MCF of 1.4 (i.e., belt densities were higher than SPC densities in general). For the large belt-SPC dataset, the MCFs ranged from 0.16 (*Gracila albomarginata*, a grouper) to 2.5 (*Anampses caeruleopunctatus*, a wrasse) with an average MCF of 0.9 (i.e., belt densities were lower than SPC densities in general).

We used the 173 MCFs obtained from the small belt-SPC dataset and 75 MCFs from the large belt-SPC dataset to build predictive models for the missing MCFs for both "density" and "occurrence" data (i.e., the first to convert belt fish density numbers to their SPC equivalent, the second to convert belt sighting probability numbers to their SPC equivalent). We first looked at the presence of multicollinearity among our explanatory variables. Swimming speed was highly correlated ($r>0.4$) with all variables except the taxonomic ones (family and genus) and rarity (Table 2.2). Maximum length was highly correlated with rarity ($r=-0.41$). We did not test two-variable models with highly correlated variables ($r>0.4$; Table 2.2). Since the "family" variable had a lower AIC than "genus" in the small belt-SPC and large belt-SPC datasets, we dropped the "genus" variable (both variables could not be kept since they are obviously highly correlated). For the density data, the model with the lowest AIC values for the small belt-SPC MCFs was "Family+Rarity" ($r^2=0.46$; Table 2.3). Since not all families in our dataset contained species for which we obtained a MCF, we also selected the best model that did not include a taxonomic variable ("Rarity+Habitat"; $r^2=0.26$; $\Delta_{AIC}=31$). The best models for the large belt-SPC density MCFs was "Family+Max size", "Family+Habitat", and "Max size" (equal AIC). We selected the single variable model with "Max size" since it was a simpler model with equal performance (r^2=0.25). We also calculated the MCFs for occurrence data only (i.e., probability of presence). For the occurrence data, the best model for occurrence data were "Family+Rarity" and "Rarity+Speed" for the small belt-SPC occurrence dataset and "Family+Max size" and "Max size" for the large belt-SPC occurrence dataset (Table 2.3).

We tested our standardization approach on a multiyear underwater visual census dataset for the main Hawaiian Islands containing quantitative data on 208 species. Of those 208 species, 173 were present in the small belt-SPC dataset. We successfully obtained direct MCFs for 105 of these, we used our taxonomic-level model ("Family+Rarity") to predict another 37 MCFs, and, finally, we had to resort to a non-taxonomic model ("Habitat+Rarity") for the remaining 31 species (Table 2.3). For the 117 species in the large belt-SPC dataset, we obtained 48 direct MCFs and used our non-taxonomic level model ("Max size") for 69 species (there was no taxonomic level model selected; Table 2.4). Table 2.5 presents the average MCF by family for both the small belt-SPC and large belt-SPC datasets.

Once we had a MCF assigned to all 208 species, we converted the 2005-2006 and 2008 average fish density collected on belt transects to their SPC equivalent by dividing those values by these MCFs. We first compared the time series of fish abundances for datasets that were un-standardized, standardized using species-specific MCFs, and standardized using MCFs from the predictive model (Fig. 2.4). Generally, the un-standardized time series showed a sharp decline in fish abundance around 2010 when the sampling methodology changed from belt to SPC, while the standardized time series (both for the species-specific MCF and predicted MCF) indicated a flat trend. For the hogfish *Bodianus bilunulatus*, the predicted-MCF standardized time series showed slightly higher pre-2010 abundances than the species-specific MCF time series. All three time series were similar for the snapper *Lutjanus kasmira*. We also looked at the un-standardized vs. standardized time series for several families and trophic groups. In general, the un-standardized time series showed a sharp decline in fish abundance around 2010 when the sampling methodology changed from belt to SPC, while the standardized time series indicated a flat trend (Fig. 2.5). This pattern was clear for surgeonfishes (Acanthuridae), hawkfishes (Cirrhitidae), wrasses (Labridae), damselfishes (Pomacentridae), and pufferfishes (Tetrodontidae). Groupers (Serranidae) showed the reverse pattern: the un-standardized time series displayed a sharp increase in densities while the standardized time series was flat (Fig. 2.5). A similar pattern was found for fish densities summarized by trophic group. The un-standardized dataset showed declines in herbivores and low-level carnivores while the standardized dataset showed flat temporal trends (there were no discernable difference between unstandardized and standardized trends for piscivores; Fig. 2.5).

Discussion

In this study, we present a practical approach to the standardization of large and complex species abundance datasets and we successfully demonstrated its utility by generating standardization factors using the Pacific-wide CRED diver dataset and standardizing a Hawaii reef fish dataset comprised of hundreds of species. This standardization effort represents the first large-scale standardization of reef fish abundance data collected using different sampling methodologies for the same resource. We achieve this by providing a solution to two important problems with high species diversity datasets: (1) prohibitive time investment required when manually running analyses for hundreds of species; and, (2) high proportion of species with insufficient numbers of paired observations to obtain reliable method standardization factors (MCFs). The automated standardization procedures used a GLM approach with the option of log-transforming fish densities or using a gamma distribution for highly skewed data, as well as modeling probabilities of presence and positive densities separately for zero-inflated datasets when necessary (delta models; Fletcher et al. 2005). GLM is commonly used in fisheries science to standardize catch and effort data, and has been used in one form or another over the last three decades (Gavaris 1980). Although other related modeling approaches have also been applied such as generalized additive models (GAMs; (Rodríguez-Marín et al. 2003) and generalized linear mixed models (GLMMs; Brandão et al. 2004), it is unclear how easily these models could be automated. Nevertheless, in our study, the relatively simple GLM approach successfully provided small belt-to-SPC MCFs for 173 out of 191 species with enough paired observations and did the same for 75 out of 80 species for the large belt-SPC dataset. All of these MCFs except for 2 were generated using delta models, reflecting the high proportion of zero counts typically encountered in underwater visual survey datasets.

We successfully used the 248 standardization factors generated by this procedure to build predictive models with easily obtainable explanatory variables such as family, rarity, habitat, swimming speed, and maximum size. For the smaller-bodied species found in the small belt-SPC dataset, “rarity” was clearly the most important explanatory variable, being included in all of our selected models for both density and occurrence-only datasets. Rarer species had lower small belt-SPC standardization factors. The presence of the "rarity" variable in our models suggests a non-linear relationship between small belt and SPC at certain abundances (i.e., if this relationship was linear, rare and common species would have similar MCFs, and "rarity" would not be an important variable in our models). A closer look at the relation between rarity and MCF shows that very rare species (i.e., those encountered on less than 5% of belt transects) also have some of the lowest MCFs (0.75 on average). More common species have MCFs generally above 1 (1.36 on average). This suggests that the "rarity" variable in our small belt-SPC models acts as a correction factor for MCFs when dealing with very rare species. The other important predictive variables for the small belt-SPC dataset were "habitat" (density model) and "swimming speed" (occurrence model) which are highly correlated (r = 0.65). Densities and probability of presence on the small belt were generally higher than for SPCs for stationary/cryptic species (i.e., higher MCF) while the opposite trend was seen for the fast/open-water species. Past studies have shown that cryptic species are under-represented in UVCs (Willis 2001; Edgar et al. 2004). We expected that certain methods would be more (or less) susceptible to this known source of bias. Since divers conducting small belt surveys are more focused on a small area vs. the larger SPC, it is not surprising that belt transects detect stationary/cryptic species more readily.

For the larger-bodied species found on the large belt-SPC dataset, we obtained simpler models that did not use taxonomic variables. The best model for predicting large belt-SPC MCFs for densities was one simply using "max size", where larger species had lower counts on the belt than on the SPC (i.e., lower MCFs for larger species). This pattern may be related to the larger survey area and longer timed count (i.e., 5 min) of the SPC. The larger species tend to be rarer and more mobile, and are likely more readily counted in a larger survey area. This may also be related to diver avoidance patterns which has been shown to be a source of bias in UVC (Watson & Harvey 2007; Januchowski-Hartley et al. 2011). The SPC diver stays stationary for a long period of time which may be sufficient for certain larger species to adjust to his or her presence and move within survey distance (7.5m). Finally, the best model for predicting large belt-SPC occurrence MCFs was “Family+Max size” and “Max size”, likely for similar reasons than for the density model.

The predictive MCF models allowed us to fill-in the remaining missing standardization factors for rare species with insufficient paired observations for species-specific MCFs. We applied this approach to our main Hawaiian Islands underwater visual survey dataset. We obtained species-specific standardization factors for 61% of the 173 species recorded in the small belt-SPC dataset and used predicted standardization factors for the rest. We only had species-specific standardization factors for 41% of the 117 species found in the large belt-SPC dataset (we resorted to predictive models to obtain the rest of the standardization factors). This is expected given that the larger fish recorded on the large belt transect (> 20 cm total length; e.g., large parrotfish) are usually rarer than smaller species found on small belt transects (<20 cm TL; e.g., surgeonfish, butterflyfish, damselfish). Once standardization factors were determined for all species, we converted the small and large belt transect fish densities from 2005-2006 and 2008 to their SPC equivalent and combined these survey years with the 2010 and 2012-2013 surveys done using SPCs. For small-bodied families, belt transect densities are generally higher than SPC densities (i.e., MCF > 1). The un-standardized time series for many families (and most of the 6 species analyzed individually) therefore showed a large drop in nominal fish densities between 2008 and 2010 when the survey method changed from belt transects to SPCs. The reverse pattern is observed for groupers, where the un-standardized time series shows a large increase in nominal densities while the standardized one shows a flat trend. These drops/increases are artifacts of combining different methods without standardizing their fish counts for changes in catchability. The standardized time series show mostly steady fish densities around the main Hawaiian Islands between 2005 and 2012 which was expected, especially for the non-exploited families (i.e., hawkfish – Cirrhitidae, wrasses – Labridae, damselfish – Pomacentridae, and pufferfish – Tetrodontidae). This example demonstrates the pitfall associated with re-creating a fish abundance time series without first standardizing counts collected with different methods. Similarly, we can imagine a situation where surveys are carried out around a relatively pristine island using mostly belt transects and other surveys are done around a heavily populated island using mostly SPCs. Researchers in this case would come to the conclusion that fish densities are much higher around the pristine island, even though this pattern may be due entirely to the different methodologies used.

Despite these clear issues, we have yet to find a coral reef fish study combining multiple underwater survey methods that have conducted a proper standardization of their dataset. It is common for researchers to assume that underwater counts obtained from different methods can be combined by insuring that their densities are expressed in the same unit of area. An accompanying paper showed that this is not necessarily the case. In our study, large belt transects had similar densities to the SPC (average species-specific MCF=0.9) while the small belt transects had, on average, higher densities than the SPC (average species-specific MCF=1.4). If unstandardized fish densities on large belt transects are half those on small belt transects, as is the case on average, this would obviously distort population size structures if we were to combine these datasets without standardizing them. This would lead to a biased estimation of size structure metrics, such as average lengths. This metric is often used to estimate total mortality rates (Ault et al. 2008). The lower average fish densities for lengths above 20 cm would lead to a lower average length and a high estimate of the true total mortality rate for this population. For all these reasons, we highly recommend not using different survey methods (i.e., large and small belt transects) for different size spectra when carrying out underwater visual surveys. We recommend using either belt transects of fixed width or the stationary point count method as described by Bohnsack and Bannerot (1986).

The approach to standardizing high species richness datasets presented here can easily be replicated elsewhere. Researchers interested in this approach can either write their own automated GLM procedure (as described in figure 2.2) in standard statistical software (i.e., SAS, R) or they can obtain our Java computer tool which includes a graphical user interface and greatly simplifies the analyses (available from contact author). For species with insufficient data for the calculation of species-specific standardization factors, researchers can either build predictive models by combining variables such as maximum size, rarity, swimming speed, and taxonomic grouping (as we did) or simply use taxonomic grouping which greatly simplifies the analyses (i.e., simply use the average MCF at the genus or family-level for species with missing MCFs). The failure to properly standardize fish abundance indices collected using different methods can lead to erroneous conclusions about fish populations, especially if methods with different catchability coefficients are implemented at different times or in different places, as demonstrated with the Hawaii dataset.

We see this approach as particularly useful in data-poor situations, where full stock assessment analyses are unlikely to be conducted. Although the recent trend in assessment has been to include CPUE indices from different sources directly into an assessment model (i.e., by allowing qs to be estimated in the model), this is unlikely for data-poor stocks. In this situation, using CPUE indices directly as trend indicators may be a more realistic approach to managing these stocks (Wilson et al. 2010)

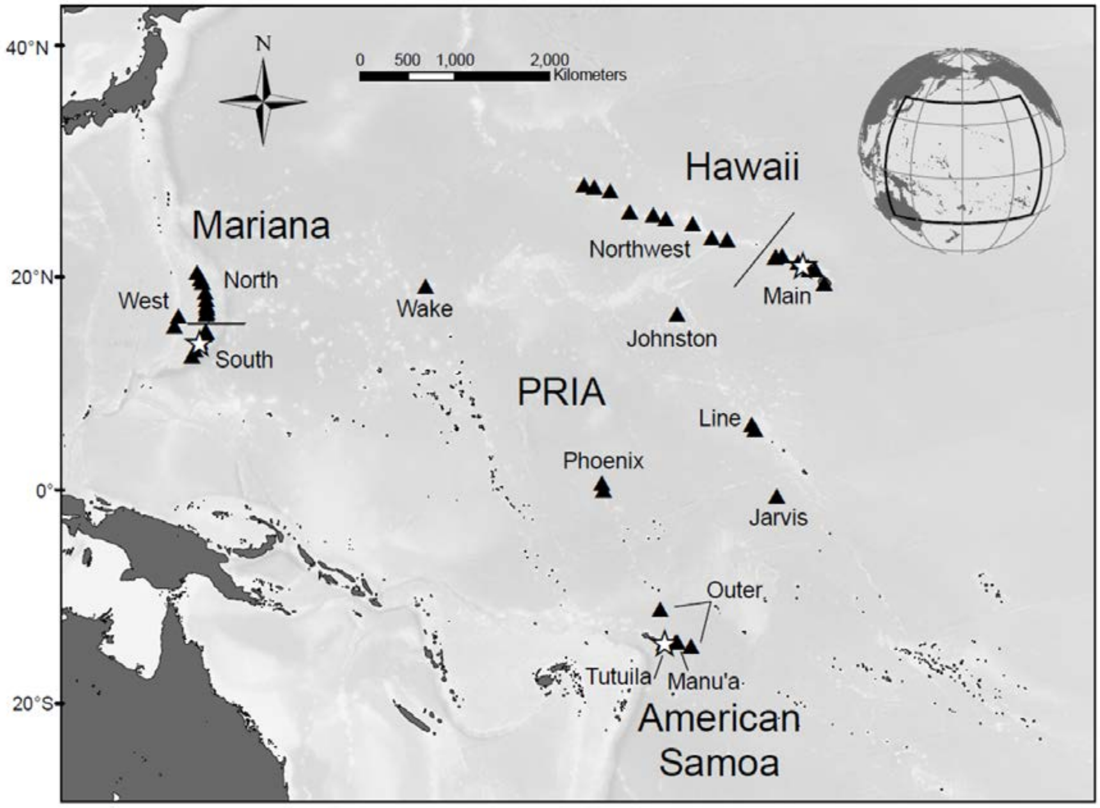

Figure 2.1 – Map showing the locations of the coral reef areas in the central and western Pacific Ocean sampled by the Coral Reef Ecosystem Division (CRED) of the NOAA Fisheries Pacific Islands Fisheries Science Center reef fish surveys between the years 2007 to 2012.

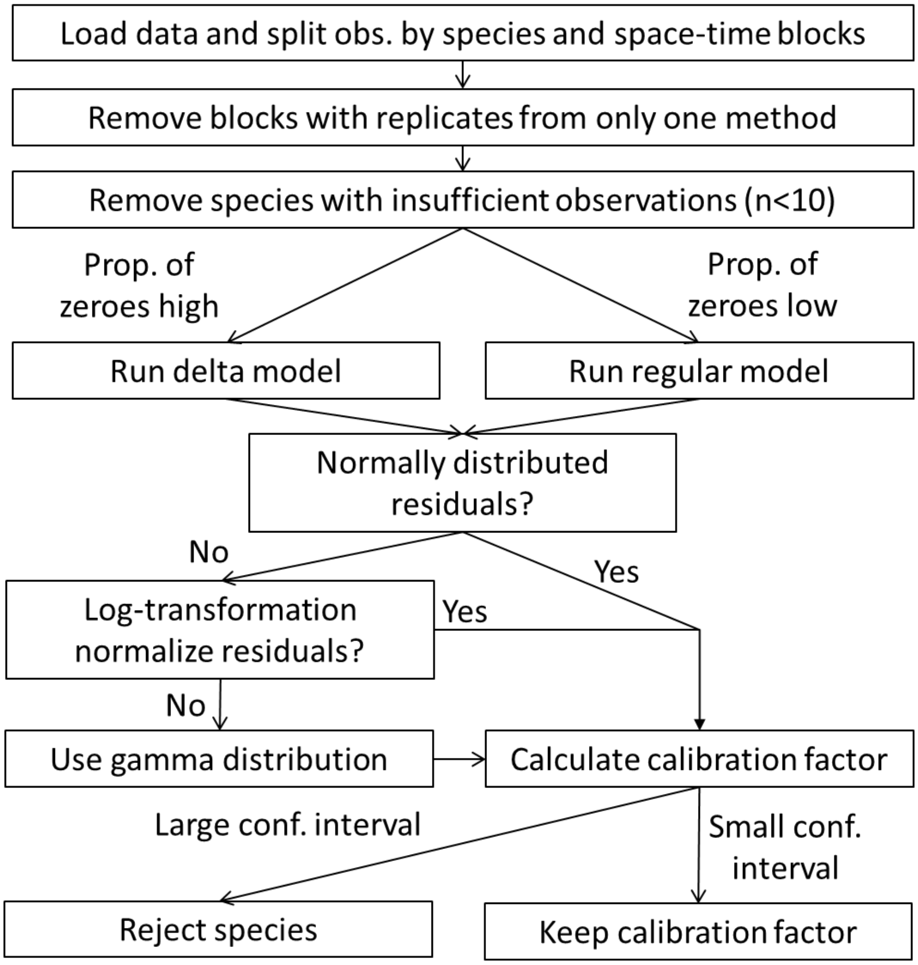

Figure 2.2 – Flow chart depicting the sequence of computations by the automated generalized linear models (GLM) computer algorithm to obtain method standardization factors (MCFs) for coral reef fisheries survey data.

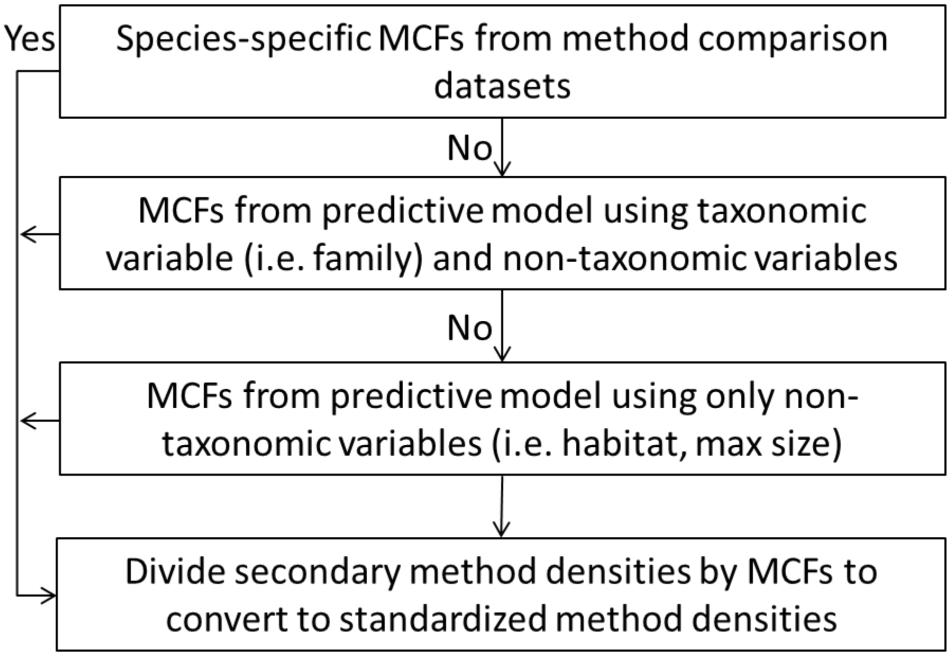

Figure 2.3 – Flow chart depicting the decision processes involved in assigning method standardization factors (MCFs) to each individual species in a particular dataset.

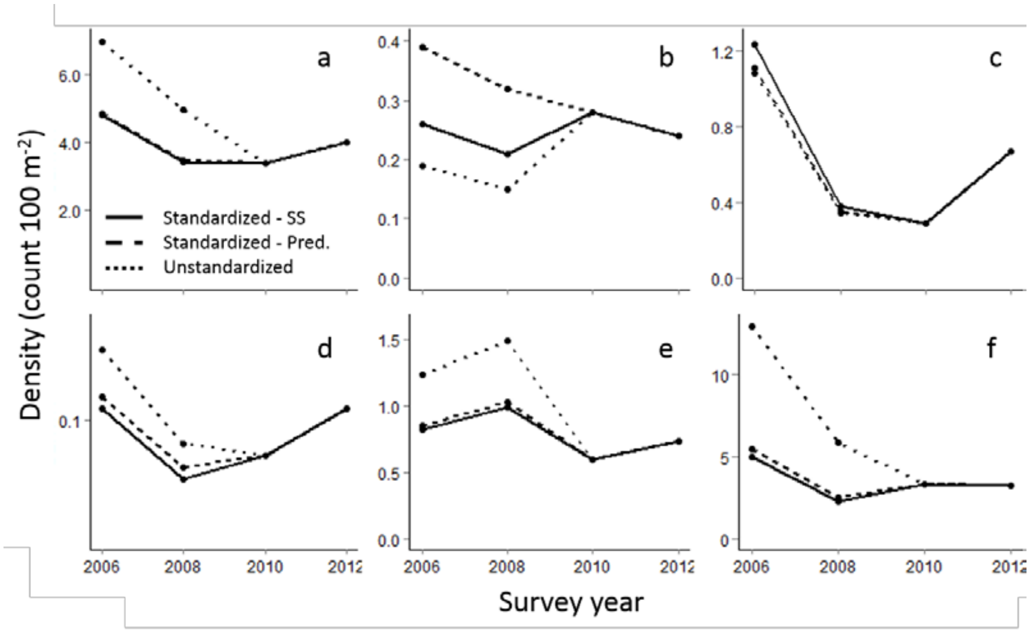

Figure 2.4 – Comparison of unstandardized (dotted line), standardized using species-specific factor (solid line), and standardized using predicted factor (dashed line) fish density time series for 6 species around Hawaii. (a) *Acanthurus nigrofuscus*, (b) *Bodiamus bilunulatus*, (c) *Lutjanus kasmira*, (d) *Paracirrhites forsteni*, (e) *Stegastes fasciolatus*, (f) *Thalassoma duperrey*.

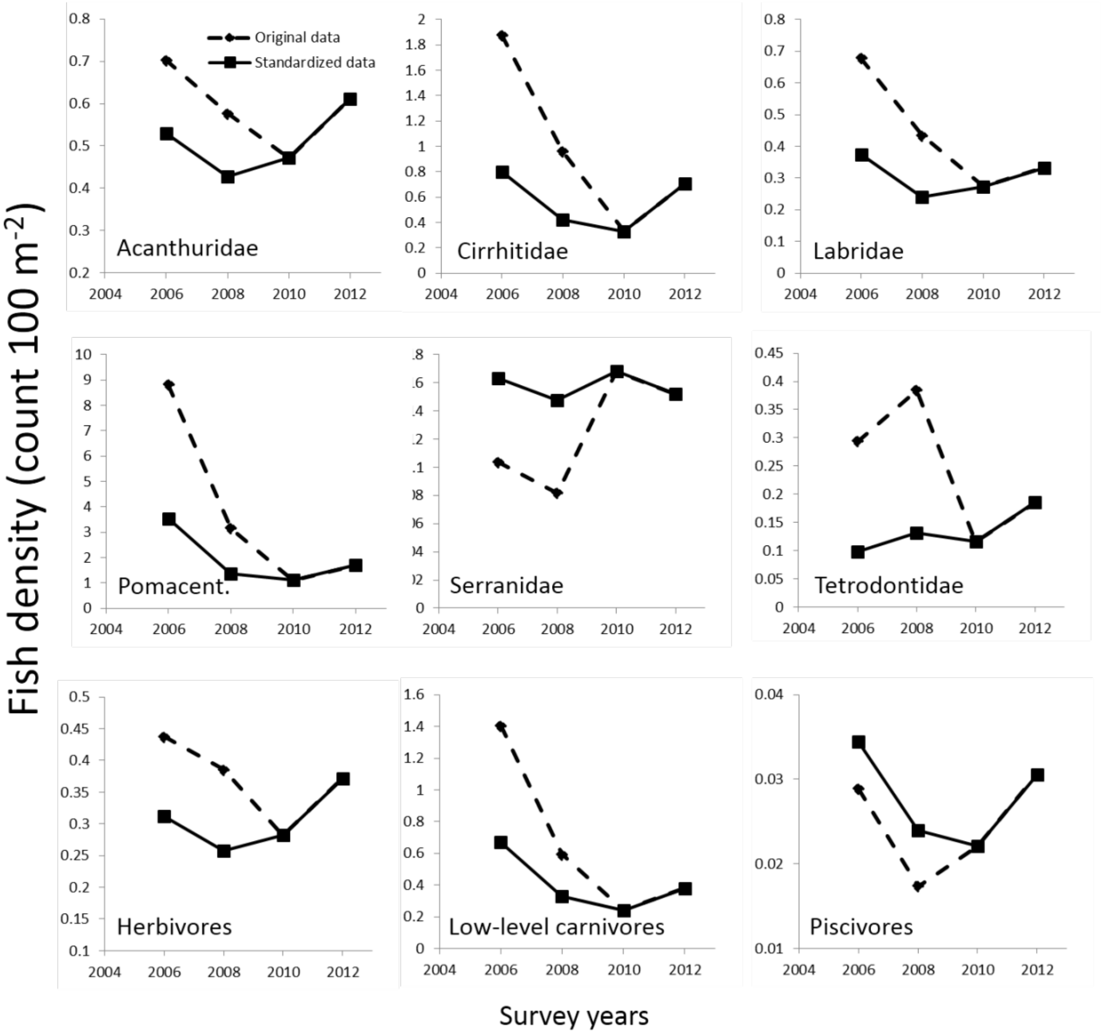

Figure 2.5 – Comparison of original belt transect (dashed line) and standardized to SPC (solid line) reef fish densities around the main Hawaiian Islands between 2005 and 2012 for six families and three trophic groups. Surveys were conducted from 2005 to 2008 using belt transect (BLT) methods while surveys after 2008 were done using stationary point counts (SPC). Belt densities were standardized to SPC equivalent densities (solid line before 2010). Year 2006 represents the 2005-2006 surveys while year 2012 represents the 2012-2013 surveys.

Table 2.1 - Results of the automated GLM standardization procedure to generate relative standardization factors from the reef fish survey dataset (including data outside of Hawaii).

Dataset	# of species	Sufficient obs. [a]	Regular model	Delta-normal model	Delta-log model	Delta-gamma model	Error < 2 [b]
Small belt – SPC	561	191	2	13	139	37	173
Large belt – SPC	316	80	0	2	52	26	75

[a] non-zero n >10 for both survey methods

[b] Error = log(97.5th percentile) – log(2.5th percentile) of method standardization factor distribution

Table 2.2 – Correlation matrix of predictor variables used in the method inter-standardization factors (MCF) model. (A) Includes “Family” variable. (B) Includes “Genus” variable. Significant correlation factors (>0.4) are shown in bold.

(A)

	Rarity	Max length	Schooling	Habitat	Speed	Family
Rarity	1.00	Pearson	Pearson	Polyserial	Polyserial	Polyserial
Max length	**-0.42**	1.00	Pearson	Polyserial	Polyserial	Polyserial
Schooling	0.19	-0.13	1.00	Polyserial	Polyserial	Polyserial
Habitat	0.03	-0.29	-0.30	1.00	Polychoric	Polychoric
Speed	0.30	**-0.67**	**0.40**	**0.65**	1.00	Polychoric
Family	0.07	-0.07	0.13	0.34	0.28	1.00

(B)

	Rarity	Max length	Schooling	Habitat	Speed	Genus
Rarity	1.00	Pearson	Pearson	Polyserial	Polyserial	Polyserial
Max length	**-0.42**	1.00	Pearson	Polyserial	Polyserial	Polyserial
Schooling	0.19	-0.13	1.00	Polyserial	Polyserial	Polyserial
Habitat	0.03	-0.29	-0.30	1.00	Polychoric	Polychoric
Speed	0.30	**-0.67**	**0.40**	**0.65**	1.00	Polychoric
Genus	0.01	-0.05	0.06	-0.19	0.05	1.00

Table 2.3 – Akaike Information Criterions (AIC) distances from model with lowest AIC (ΔAIC) for models explaining method standardization factors (MCFs). Four model sets are presented: small belt-to-SPC and large belt-to-SPC for both density and occurrence data. Numbers in bold represent selected models (overall best and non-taxonomic best models).

	Δ AIC			
Model	Small belt-SPC density	Large belt-SPC density	Small belt-SPC occurrence	Large belt-SPC occurrence
Null	88	22	152	22
Family	27	20	87	26
Genus	51	19	77	31
Habitat	73	19	142	22
Max size	72	**0[A]**	107	**3[B]**
Rarity	56	17	67	11
Schooling	86	23	151	24
Speed	66	16	113	18
Family+Habitat	29	21	86	27
Family+Max size	20	0	48	**0[A]**
Family+Rarity	**0[A]**	14	**0[A]**	12
Family+Speed	27	21	78	25
Family+Schooling	28	21	88	26
Habitat+Max size	64	0	105	5
Habitat+Schooling	69	21	139	24
Max size+Schooling	73	2	109	3
Rarity+Habitat	**40[B]**	14	54	10
Rarity+Schooling	57	17	69	12
Rarity+Speed	27	21	**47[B]**	3

[a] Schooling = log of average count on SPCs

[b] Speed = Typical swimming speed (stationary, slow, and fast)

[c] Rarity = log of probability of presence on belt transect

[A] Best model and [B] Alternate model (non-taxonomic variable)

Table 2.4 – Source of method standardization factors for the main Hawaiian Island datasets.

Dataset	Number of species	MCF source		
		Species-specific	Predictive model – taxon.	Predictive model – non-taxon.
Small belt – SPC	173	105	37	31
Large belt – SPC	117	48	-	69

Table 2.5 – Average standardization factors (MCF) for a subset of important families found in the main Hawaiian Islands dataset. n=number of species in the family group, % specific is the percentage of MCFs that are species-specific (i.e., not from predictive model).

Family	Small belt - SPC			Large belt - SPC		
	n	% specific	MCF	n	% specific	MCF
Acanthuridae	21	76	0.81	18	56	1.14
Apogonidae	2	0	1.29	0	-	-
Balistidae	8	50	0.31	6	33	1.12
Blenniidae	5	80	4.69	0	-	-
Chaetodontidae	19	68	0.81	0	-	-
Cirrhitidae	5	80	1.77	2	0	1.33
Holocentridae	7	57	1.32	7	43	1.18
Labridae	29	79	1.34	13	69	0.92
Lutjanidae	3	33	1.25	4	100	0.54
Monacanthidae	5	40	0.62	3	33	1.01
Mullidae	7	86	1.03	8	50	1.00
Pomacanthidae	4	75	1.19	1	0	1.63
Pomacentridae	15	80	1.37	2	0	1.38
Scaridae	6	100	1.21	7	86	1.04
Serranidae	1	100	1.23	1	100	0.41
Tetraodontidae	3	100	2.38	2	0	0.92

Chapter 3

Length-based assessment of coral reef fish populations in the Main and Northwestern Hawaiian Islands

Summary

The coral reef fish community of Hawaii is composed of hundreds of species and supports a multimillion dollar fishing and tourism industry, as well as being of great cultural importance to the local population. However, stock assessments of Hawaiian coral reef fish populations to determine their sustainability have yet to be conducted. Here we used the robust indicator variable "average length in the exploited segment of the population ($\overline{L}$)" estimated from size composition data from commercial fisheries trip reports and fishery-independent diver surveys to evaluate exploitation rates for 19 Hawaiian reef fishes. By and large, the average lengths obtained from diver surveys agreed well with those from commercial trip reports. We used these estimated exploitation rates, coupled with life history demographic parameters synthesized from the literature, to parameterize a numerical population model and generate various metrics of stock sustainability such as spawning potential ratio (SPR). We found good agreement between predicted average lengths in an unfished population (from our population model) and those observed from diver surveys in the largely unexploited Northwestern Hawaiian Islands. Of 19 exploited reef fish species assessed in the main Hawaiian Islands, 9 had SPRs below or very close to the 30% overfishing threshold. In general, longer-lived species such as surgeonfishes, the redlip parrotfish (*Scarus rubroviolaceus*), and the gray snapper (*Aprion virescens*) had the lowest SPRs, while short-lived species such as some

of the goatfishes and jacks, as well as two invasive species (*Lutjanus kasmira* and *Cephalopholis argus*), had SPRs above the 30% threshold.

Background

The Hawaiian coral reef ecosystem is inhabited by hundreds of reef fishes and macroinvertebrates and supports multimillion-dollar fishing and tourism industries (Cesar & Beukering 2004). The coral reef fishery is a mix of near-shore recreational/subsistence fishing combined with a modest commercial sector. Nearly a third of all Hawaiian households participate in recreational-subsistence fishing (Hamnett et al. 2006), and their catches have been estimated to exceed those of the commercial sector (Friedlander & Parrish 1997; Zeller et al. 2005; Williams & Ma 2013). The recreational-subsistence sector is characterized mostly by shore-based fishers using a range of gears that includes spears, hook-and-line, traps, and small gill and cast nets. The main targeted fish taxa include larger jacks and snappers, but also smaller reef-associated families such as surgeonfish, goatfish, soldierfish, and parrotfish (Friedlander & Parrish 1997). Commercial marine landings in Hawaii are dominated (>80% of catches) by coastal-pelagic species (DeMello 2004), but also include are the reef fishes targeted by the recreational-subsistence sector. The commercial fishery also includes an important aquarium-trade component focused on surgeonfishes and butterflyfishes. Although the direct monetary value of the near-shore fishery is only 10-20% of the pelagic fishery (Gulko et al. 2002), it is both culturally and socially important to the local population.

Observational studies have shown drastic differences in Hawaiian reef fish abundance along inferred fishing intensity gradients (Friedlander & DeMartini 2002;

Williams et al. 2008). For example, a recent study showed that snapper and parrotfish biomasses are about 3-4 times higher in the unpopulated and remote Northwestern Hawaiian Islands than in the populated main Hawaiian Islands (Williams et al. 2011). However, no formal quantitative analysis of stock sustainability has been conducted to date. This is mainly due to a lack of data such as demographic rates and time-series of age- or size-structured catches by species, and the associated fishing effort (Quinn & Deriso 1999; Ault et al. 2008; Haddon 2010). This "data poor" situation has been steadily improving in the Hawaiian Archipelago where implementation of large-scale fishery-independent coral reef fish surveys (Williams et al. 2008), along with an increased focus on life history and demographic research, now allows the possibility of more in-depth assessments of the sustainability of coral reef fish fisheries.

In this paper we employed a length-based assessment approach previously used to assess reef fish stocks in southern Florida and Puerto Rico (Ault et al. 1998, 2008) to conduct the first stock assessment of the exploited coral reef fish community in Hawaii. The general goal of stock assessment is to optimize yield while maintaining the reproductive capacity of a stock at a safe level (Quinn & Deriso 1999; Haddon 2010). Our first step was to estimate the fishing mortality rates currently applied to exploited stocks. We used a relatively straightforward length-based total mortality assessment method suitable to the data-poor situation typical of coral reef fisheries (Ehrhardt & Ault 1992). The principal data used for the mortality assessment were size-specific abundance data for 19 exploited reef fish species sampled by fishery-independent and fishery-dependent surveys. Next, we used the estimated mortality rates and other population-dynamic parameters (i.e., length-at-maturity, growth rates, maximum size/age) in a numerical cohort-structured population model to compute sustainability reference points (benchmarks). As an aid to fishery managers, we evaluated the species-specific benchmarks with respect to resource sustainability standards. Finally, the availability of an extensive fishery-independent dataset in a large pristine area (the Northwestern Hawaiian Islands) allowed us to test and validate the predictions of our stock assessment models and parameters

Methods

Study area

The Hawaiian Archipelago extends for 2600 km along a SE-NW axis from 19°N, 155°W to 28°N, 178°W (Fig. 1). The archipelago, consisting of 18 islands and atolls, is typically divided into two broad regions: (1) the inhabited main Hawaiian Islands (MHI); and, (2) the sparsely inhabited Northwestern Hawaiian Islands (NWHI). The MHI is composed of 8 geologically young, high (4,205 m maximum elevation) volcanic islands that are densely human-populated (1.39 million persons; dbedt.hawaii.gov/census). In contrast, the NWHI are relatively low-lying (275 m max. elevation) and sparsely inhabited (Table 1). The MHI were originally settled by Polynesians around AD 1250. Reef fish communities in the MHI have been exploited to various degrees throughout their history (Kittinger et al. 2011). In contrast, the NWHI were never permanently settled by Polynesians; however, they were the focus of some commercial fishing, particularly in the 19th century (Kittinger et al. 2011). Over the past century, the fishing fleet operating in the NWHI has remained relatively small at less than 12 vessels that were mainly focused on bottomfish (deepwater snappers) and lobsters (Kittinger et al. 2011). In 2006, the NWHI and surrounding marine environment, including associated coral reefs and other resources, were designated by a Presidential Proclamation as the Papahanaumokuakea Marine National Monument (PMNM) and protected under the co-management of several agencies of the U.S. federal government and the State of Hawaii.

Length-based mortality model

The principal stock assessment indicator variable used to quantify the population status for the community of Hawaiian reef fishes was average length ($\bar{L}$) of the exploited phase of the population. Average length ($\bar{L}$) is highly correlated with population size (Kerr & Dickie 2001). For exploited species, $\bar{L}$ directly reflects the rate of instantaneous fishing mortality F through alteration of the population size structure (Beverton & Holt 1957; Ehrhardt & Ault 1992). As F increases, the probability of a fish reaching larger sizes decreases, and thus the mean of the exploited size frequency distribution $\bar{L}$ decreases accordingly. Theoretically, the average length $\bar{L}$ is generally expressed as

$$\bar{L} = \frac{F\int_{a_c}^{a_\lambda} N(a)L(a)da}{F\int_{a_c}^{a_\lambda} N(a)da} \quad , \tag{1}$$

where the exploitable phase is integrated from a_c (age at first capture) to a_λ (oldest age in the stock), $N(a)$ is the abundance of age class a, $L(a)$ is the expected length at age a, and F is the instantaneous fishing mortality rate.

A formula for estimating mortality rates using estimates of $\bar{L}$ was derived from Eq. (1) by Ehrhardt and Ault (1992). The first step in this derivation was to substitute $L(a)$ in Eq. (1) with the von Bertalanffy growth function and $N(a)$ with the exponential mortality model

$$N(a+\Delta a)=N(a)e^{-Z\Delta a} \quad , \tag{2}$$

where Z is the total instantaneous mortality rate and Δa is the age interval, normally one year. Step two was to integrate and algebraically solve for Z,

$$\left(\frac{L_\infty - L_\lambda}{L_\infty - L_c}\right)^{Z/K} = \frac{Z\left(L_c - \bar{L}\right)+K\left(L_\infty - \bar{L}\right)}{Z\left(L_\lambda - \bar{L}\right)+K\left(L_\infty - \bar{L}\right)} \quad , \tag{3}$$

where K and L_∞ are parameters of the von Bertalanffy growth equation (assumed to be constant over time), and L_c and L_λ are the mean sizes at first capture and oldest age, respectively. We selected Eq. (3) instead of the Beverton-Holt model (Beverton & Holt 1956) because of a known bias in their model associated with the assumption of an infinite lifespan (Ehrhardt & Ault 1992). Fishing mortality was obtained from F=Z-M, where M is the instantaneous natural mortality rate.

Data sources

Application of the average length mortality estimator (Eq. 3) and analyses of fishery sustainability (see below) required two types of information: basic demographic and life history information; and, length composition data. Life history demographic parameters for lifespan, growth in length and weight, and size-at-reproductive maturity were obtained from a synthesis of the scientific literature (Appendix, supplemental information). If size-at-maturity was different between sexes, we used the female size-at-maturity.

Length frequency composition data were obtained from two sources: (1) underwater diver-based visual surveys; and, (2) commercial fishery trip reports. Between

2007 and 2013, a team of highly trained divers from the NOAA Pacific Island Fisheries Science Center (PIFSC) conducted 770 and 764 visual samples throughout the MHI and NWHI, respectively. Survey sites around each island or atoll were randomly selected within strata defined by combinations of reef zone habitats (i.e., forereef, backreef, and lagoon) and depths (shallow, 0-6 m; mid, 6-18 m; and deep, 18-30 m). At each sample site, independent stationary point counts were conducted by two paired divers inside contiguous 15 m diameter cylinders that extended from the bottom to the surface (Brandt et al. 2009; Smith et al. 2011; Williams et al. 2011). A diver first recorded a list of fish species observed during an initial 5 minute period. The diver then worked through this list, species by species, recording counts and estimating sizes of all fish seen within the cylinder. Fish sizes were recorded as total lengths to the nearest cm. Fishes from species not listed during the initial 5 minute period, but present later in the sample, were also recorded but classified in a different data category. Before participating in the surveys, divers were extensively trained in size estimation using fish cut-outs of various sizes. Diver performance during and after survey efforts was evaluated by comparing size and count estimates between paired divers, where divers were continuously rotated between teams. Permits to conduct field surveys were obtained from the Hawaii Department of Land and Natural Resources (MHI surveys) and the PMNM authorities (NWHI surveys).

Commercial fisheries data from 2003 to 2012 were obtained from commercial trip reports submitted by fishers to the Hawaii Division of Aquatic Resources (DAR). Trip records were utilized from the 4 main fisheries gears used in inshore areas (hook-and-line, spearfishing, various nets, and traps). Because lengths were not directly reported, the catches in weight were divided by the number of fish caught to obtain average weights per species per individual trip over the total of 47,439 trip records. Average weights were then converted to total lengths using published standard allometric weight (W)-length (L) relationships (Appendix, supplemental information),

$$L = \left(\frac{W}{\alpha}\right)^{\left(\frac{1}{\beta}\right)} \quad , \qquad (4)$$

where α and β are model parameters. Average lengths and associated standard errors were calculated across trips using numbers caught per trip as a weighting variable. There were some concerns that converting average weight per trip to average length per trip would lead to a biased estimate of average length (Jensen's inequality caused by the non-linear length-weight relationship). However, for each species, we compared the average length calculated from trips with only 1 fish in the catch vs. the average calculated for all trips and did not find differences in average length. The resulting length observations for each trip were checked to ensure that no lengths were greater than the maximum reported for each species (this step was also done for the diver surveys).

Catch records for certain taxa that were not identified to the species level were not included in our analyses (e.g., parrotfishes and the "kala" group of surgeonfishes composed of *Naso unicornis, N. annulatus*, and *N. brevirostris*).

Estimation of average length and mortality rates

Mean lengths were evaluated for the exploited size range ($L \geq L_c$). Size at first capture L_c was set as the minimum length at full exploitation based on examination of the length converted fishery-dependent data for principal gears targeting Hawaiian reef fishes (hook-and-line, spearfishing, and fish traps). To do so, we looked for clear discontinuous breaks in the size structure histograms for the commercial dataset. For example, the commercial catch record for *Parupeneus porphyreus* did not have individuals below 20 cm, had a few individuals in the 20-22 cm and 22-24 cm ranges (~50), and a noticeably higher number of individuals in the 24-26 cm range (close to 200 fish). The number of fish in size bins above 24-26 cm increased steadily. This discontinuous jump between 22-24 and 24-26 cm appeared to be related to selectivity; consequently the L_c was set at 25 cm.

Species-specific average lengths were estimated for two broad geographical regions, the MHI and the unexploited Northwestern Hawaiian Islands (Fig. 1). To account for differences in size structures due to uneven sampling effort and/or uneven fishing pressure (inferred from humans per reef area values - Table 1) within the MHI region, $\overline{L}$ was estimated from average lengths for four subregions weighted by the respective shallow reef areas (depth <18m; Table 1). For two species not commonly found in the NWHI region, *Cephalopholis argus* and *Scarus rubroviolaceus*, length observations were imported from two other pristine areas (Wake and Johnston atolls) to make the unexploited state calculations.

Estimates of total instantaneous mortality rates Z were computed from Eq. (3) using a numerical procedure (Ault et al., 1996). Values of L_λ, mean length at maximum age a_λ, were estimated from the von Bertalanffy growth function using an observed maximum age.

Natural mortality rates M were estimated from lifespan applying the procedure of Alagaraja (1984) which is similar to Hoenig (1983) and Hewitt & Hoenig (2005), but assumes that 5% of a cohort survives to the observed maximum age (instead of about 1.5% in these papers):

$$M = \frac{-\ln(S)}{a_{\lambda}} \quad , \tag{5}$$

where S is the cohort survivorship to the maximum observed age (a_{λ}). We originally selected the 5% survivorship value to obtain a more conservative estimate of M than the one obtained with the 1.5% value. As an added precaution, we independently estimated S by using Eq. (3) to obtain Z in the NWHI for each species and fit a linear regression model between the estimates of Z and $1/a_{\lambda}$ (making the reasonable assumption that Z = M in the NWHI). To do so, we represented eq. (5) as $M = b_1 * 1/a_{\lambda}$ (no intercept parameter). The slope (b_1) of this regression is –ln(S) from which we derived S ($S = e^{-b1}$). Finally, fishing mortality F was obtained by subtracting M from Z. Natural mortality M was assumed constant for all ages, and F was assumed constant for ages above a_c.

Numerical population model and fishery sustainability analyses

Sustainability analyses involved comparison of various population metrics at current levels of fishing mortality relative to standard fishery management sustainability benchmarks (2008). Reference points for sustainability risk (spawning potential ratio, SPR) and fishery yield were computed using a length-conditional-on-age structured numerical model (following Ault et al. 1998) to simulate exploited fish populations. The computations were based on the mortality rates derived from $\bar{L}$ estimates and life history parameters synthesized from the literature. Numerical abundance at age *a* was estimated through use of an exponential mortality function (Eq. 2). Length at age was estimated from the von Bertalanffy growth equation, and converted to weight-at-age using the allometric weight-length relationship (Eq. 4). As an initial check on the validity of the population model and life history parameters, the model-calculated expected average length with no fishing mortality ($\overline{L}_{F=0}$) was compared with the observed average length in the pristine NWHI region.

The numerical model was used to obtain an important measure of stock reproductive potential, spawning stock biomass (SSB), at a given level of fishing mortality by summing over individuals in the population between the age of sexual maturity (a_m; age where 50% of individuals are mature, with knife-edge assumption) and oldest age a_λ,

$$SSB = \sum_{a_m}^{a_\lambda} \overline{N}(a) W(a) \quad , \qquad (6)$$

where $\overline{N}(a)$ is the average abundance at age a and $\overline{W}(a)$ is the mean weight of individuals at age a. Theoretically, a stock's maximum reproductive biomass occurs when there is no fishing. Spawning potential ratio (SPR) is a management benchmark that measures a stock's potential to produce yields on a sustainable basis. It was computed as the ratio of the current SSB relative to that of an unexploited stock

$$SPR = \frac{SSB_{\exp loited}}{SSB_{un \exp loited}} \quad . \qquad (7)$$

Estimated SPRs were compared to USA federal standards which define 30% SPR as the threshold below which a stock is no longer sustainable, i.e., is experiencing recruitment overfishing, a standard recommended for less well-known stocks (Gabriel et al. 1989; Restrepo et al. 1998; Clark 2002). An associated reference point, the average length when SPR is equal to 30% ($\overline{L}_{SPR30}$), was also evaluated as well as $L_{c\ SPR30}$, the size at first capture required to obtain an SPR=30% for current fishing mortality rates (Fig. 2).

The numerical population model was also used to examine growth overfishing, which occurs when fish are caught before they have reached their full growth potential thus limiting the harvested fish biomass (Beverton & Holt 1957). The population metric yield per recruit (YPR) was calculated as

$$YPR = \frac{1}{R}\sum_{a_c}^{a_\lambda} F\overline{N}(a)\overline{W}(a) \quad , \tag{8}$$

where R represents a fixed number of annual recruits (i.e., this number does not influence YPR values since yield is standardized to a single recruit), F is the fishing mortality rate, and a_c is the age of recruitment to the fishery (i.e., age at first capture). As a measure of growth overfishing, we calculated the expected percent increase in YPR from the current YPR associated with increasing the size at first capture (L_c) to its eumetric value (i.e., $L_{c\ eum}$= L_c that maximizes YPR for the current F; see Fig. 2).

Results

Average length and mortality estimates

Length composition data (Table 2) and life history information (Table 3) were available for 19 Hawaiian reef fish species: three parrotfishes, six surgeonfishes, three goatfishes, two snappers, three jacks, one grouper, and one squirrelfish. Annual estimates of $\overline{L}$ in the main Hawaiian Islands for the period 2003-2012 (commercial data) did not show any increasing or decreasing trends for 9 species with n>30 observations per year (Fig. 3), suggesting that these stocks were mostly at equilibrium (i.e., fishing mortality rates have been fairly constant, an important assumption of the length mortality model).

Length observations were subsequently combined across years by data source (commercial, underwater diver surveys) to increase the precision of average length estimates.

Table 2 shows average lengths by species and subregion. For most species, there was no clear pattern in average length between the more densely populated subregions (Maui Nui and Oahu) and the less populated ones (Hawaii and Kauai-Niihau) in the MHI region (Table 2). Notable exceptions were *Parupeneus porphyreus*, *Aprion virescens*, and *Caranx ignobilis*, which displayed clearer patterns of decreasing average lengths (and thus increasing Fs) across a human population density gradient (Tables 1 and 2). This was especially the case for *C. ignobilis*, which showed a clear difference in average length between combined data for Hawaii and Kauai-Niihau (758 mm) and combined data for Maui Nui and Oahu (677 mm; the latter island having by far the most densely populated coastline). Average lengths for the commercial dataset were generally in agreement with those from our underwater surveys (Fig. 4A) with some exceptions, such as *C. melampygus* (longer average lengths in commercial dataset), which may be due to a low number of observations in underwater surveys. For each species, we selected the data source with the most length observations for subsequent analyses.

The average lengths of species in the pristine NWHI were either larger (11 species) or similar (5 species) relative to the inhabited MHI (Table 2). Furthermore, 10 species had an overlap between their $\overline{L}$ 95% confidence intervals in the NWHI and their corresponding simulated $\overline{L}_{F=0}$ (Fig. 4B and Fig. 5). The remaining 6 species had average lengths close to the expected value at F=0, except for two species. The redlip parrotfish likely has a poor $\overline{L}$ estimate in the NWHI (even after including data from Wake and

Johnston Atoll) due to a low number of observations (n=47). The surgeonfish *Naso unicornis* had an average length in the NWHI much lower than the expected value (386 mm vs. 445 mm, respectively) and this may be due to a low estimate of M (see Discussion section for more details).

The regression of our Z estimates dependent on $1/a_\lambda$ in the NWHI (where Z was assumed to be equal to M) for 15 species gave a slope of $-\ln(S) = 3.143$ ($r^2 = 0.71$; Fig. 6), which is equivalent to a survivorship to the maximum age S of 0.043 (i.e., from $e^{-3.143}$). This value is very close to the S=0.05 used in our analyses.

Estimated fishing mortality rates in the MHI region varied greatly by species, ranging from 0.01 to 1.32 (Table 3). The two species with the highest fishing mortality rates were the goatfishes Parupeneus porphyreus (F = 1.32) and *Mulloidichthys flavolineatus* (F=0.46), followed by the snapper *Lutjanus kasmira* (F=0.36), and the jack *Caranx ignobilis* (F=0.30). The fishing mortality rates for all other species were less than 0.3.

Sustainability analyses

Of the species evaluated in this study, 53% had SPR estimates above the typical accepted lower limit of 30%, while 16% were between 25-35% SPR and 31% were below 25% SPR (Table 3; Fig. 7). In general, the 95% confidence intervals for estimates of $\overline{L}$ were much smaller than the interval between $\overline{L}_{SPR30}$ and $\overline{L}_{F=0}$, suggesting there was sufficient precision in F estimates to make appropriate conclusions on stock status (Fig. 5). Estimates of SPR were generally higher for parrotfishes (average SPR of 68%), goatfishes (58%), and jacks (41%), while surgeonfishes had generally low SPRs (26%).

The two invasive species analyzed, (*Cephalopholis argus* and *Lutjanus kasmira*), had very high SPRs (SPR > 60%).

Potential yield increases (from increasing L_c to its eumetric value), a measure of growth overfishing, was relatively low for most species (ranging between 1% and 44%; Table 3). Potential gains in yield exceeding 25% were found for *Naso unicornis*, *Caranx ignobilis*, and *Parupeneus porphyreus*.

Discussion

The sustainability of coral reef fisheries has been questioned (Newton et al. 2007; Costello et al. 2012), but this conjecture has generally been based on heuristic evidence such as observed differences in relative abundance between fished and protected or uninhabited areas (Chiappone et al. 2000; McClanahan & Arthur 2001; Sandin et al. 2008; Williams et al. 2011). There have been few formal stock assessments of tropical coral reef fishes other than those conducted in Florida, Puerto Rico, and Belize (Ault et al. 1998, 2005, 2008; Babcock et al. 2013). The sustainability of reef fisheries in other regions, such as the tropical Pacific, has yet to be assessed. Our study presents the first assessment of shallow water coral reef fish species in Hawaii. We used a relatively simple and reliable assessment method with minimal data requirements to obtain the mortality rates necessary to run population dynamic models. We show that more than half of the exploited species analyzed in this study have a spawning potential ratio above the US federal standard of 30% and are likely not experiencing recruitment overfishing. The species faring well were generally the shorter-lived ones with higher natural mortality rates (e.g., the small parrotfishes *Chlorurus spilurus* and *Scarus psittacus*, some of the goatfishes, and the jack *Caranx melampygus*), invasive species (the snapper *Lutjanus kasmira* and the grouper *Cephalopholis argus*), as well as more cryptic, nocturnal species (the squirrelfish *Myripristis berndti*). The species with lowest SPRs were generally the longer-lived, lower natural mortality species (e.g., the parrotfish *Scarus rubroviolaceus*, the snapper *Aprion virescens*, and the surgeonfishes) or the most highly prized ones (the goatfish *Parupeneus porphyreus* and the jack *Caranx ignobilis*). There is a well-established relationship between longevity and sensitivity of spawning potential to fishing pressure: longer-lived species have lower natural mortality rates and thus much of their pristine spawning biomass is represented by older individuals whose numbers become depleted even at relatively low fishing mortality rates (Goodyear 1993).

Another form of overfishing, growth overfishing, occurs when fish are harvested before they reach their optimum size (i.e., the size at which biomass loss to natural mortality equals the biomass gained from individual fish growth in a cohort), thus reducing yields (i.e., harvested biomass). We examined the potential increases in yields if the size at first capture (L_c) were set optimally (eumetric fishing) for the current fishing mortality rates. For the majority of species in our study, there was little gain in yield associated with setting L_c optimally, either because certain species had relatively low fishing mortality rates (e.g., *Myripristis berndti*, *Cephalopholis argus*, and *Chlorurus spilurus*) or had high individual growth rates accompanied by low natural mortality (i.e., maximum individual weights are reached quickly with little loss to natural mortality, thus reducing the influence of L_c in increasing yield; e.g., *Naso brevirostris*). The few species where large gains in yield could be achieved by setting L_c optimally were the higher fishing mortality (F>0.2) species such as *Naso unicornis* (44% potential yield gain), *Caranx ignobilis* (36%) and *Parupeneus porphyreus* (28%).

It is important to note that some fish stocks in the densely populated Oahu subregion had lower average lengths and thus higher fishing mortality rates and lower spawning potential ratios compared to other less populated MHI subregions. For example, the highly prized goatfish *Parupeneus porphyreus* had relatively high SPRs outside of Oahu (around 20%), but a very low value in this subregion (6%). The jack *Caranx ignobilis*, also a popular recreational target, had an SPR value for Maui Nui and Oahu around 16% but much higher values around Hawaii and Kauai-Niihau (>35%). Other species did not show differences in average lengths among subregions, which may have been due to a low number of observations, well-mixed populations, or similar fishing mortality rates for these particular species among subregions. It is still not entirely clear to what level the fish populations around the MHI are connected, or if larval exchanges or adult movements exist between Oahu and the other Hawaiian Islands. A recent tagging study failed to detect inter-island movements for tagged *Caranx ignobilis*, a large, highly mobile predator (2007). Genetic connectivity studies on reef fishes indicate that most species have no genetic structuring across the Hawaiian archipelago (Rivera et al. 2004; Craig et al. 2007; Gaither et al. 2010). However, the absence of structure does not imply that reef fish stocks are well connected at time scales relevant to the population dynamic processes. Population connectivity within the MHI is still an open question and will require further attention if potentially disconnected reef fish populations are to be managed sustainably, given the likely large differences in fishing pressures between subregions.

The reliability and robustness of conclusions regarding the state of Hawaiian reef fish populations depends on verification of a few assumptions. First, we assumed that the coral reef fish stocks analyzed in the current study were basically at equilibrium (i.e., mortality rates and recruitment have been fairly constant over the last decade or so). The lack of change in average length over time that we observed for 9 species was an indication that potential fluctuations in recruitment levels over time were not significant enough to affect our average length estimates and that fishing mortality was more or less constant. A second assumption was that size structure data were representative of the true populations around the MHI. Both the underwater visual survey and commercial trip report datasets have strengths and weaknesses. The underwater surveys by SCUBA divers did not reach depths beyond 30 m due to safety and time constraint issues, but were able to sample remote and exposed areas of the MHI that are likely visited less frequently by fishers. The abundance-at-size information for the visual survey dataset was thus more representative of nearshore, more easily accessible (and likely more heavily fished) communities, but also encompassed less heavily fished sections of relatively inaccessible coastlines. On the other hand, abundance-at-size data from commercial trip reports included information on deeper fish communities, but were less likely to be representative of inaccessible coastlines. Despite these potential biases, the size structure information from these two disparate datasets was remarkably similar suggesting that the average lengths used in the current study were likely representative of the real values. Another important assumption was that the life history parameters used in our analyses were representative of the local fish populations in Hawaii. For many species, we had to use life history parameters from other Pacific areas. It is possible that these values change geographically and with environmental conditions (Choat & Robertson 2002; Gust et al. 2002, although see Donovan et al. 2013). There is a clear need for more focused life history studies for the principal exploited shallow reef species in Hawaii. Having local length, age, and maturity raw data would also allow us to further investigate parameter uncertainty in future studies (beyond average length uncertainty) since few published growth studies report variability around fitted parameter estimates (L_{inf} K, L_{mat}) (see supplemental information).

The availability of an extensive underwater visual survey dataset for the relatively pristine NWHI allowed us to evaluate the validity of the length-based mortality model used in this study (Ehrhardt & Ault 1992; Ault et al. 1998) as well as the validity of our life history and demographic information. We first used our independent estimates of M from the NWHI (where Z derived from average length is assumed to be equal to M) to derive an estimate of average cohort survivorship (S) to maximum age (a_λ). We obtained a value closer to the one used for our analysis (0.043 vs. 0.05) than the one suggested elsewhere (0.015) (Hewitt & Hoenig 2005; Then et al. 2014). The S=0.015 value comes from empirical data that include mollusks, fish, and cetaceans, and thus may not be suitable for reef fishes. The exact survivorship value is linked to the sampling effort in the dataset from which a_λ is obtained (i.e., the larger the number of aged individuals, the greater the chance of finding extremely old individuals that are not representative of a 5% or even 1% cohort survivorship value) (Kenchington 2013). Since the a_λ value for reef fishes generally comes from life history studies with less than 100 aged individuals, it is possible that these values represent cohort survivorship higher than 1.5%, which is what our analysis suggests.

Furthermore, we used the length-mortality model to generate expected average length when only natural mortality is present (F=0), and we were able to compare these average lengths with observed values in the NWHI. For most species, the expected average lengths at F=0 fell within the 95% confidence intervals of the observed average lengths, while average lengths of the remaining species were close to predicted values. One exception was the parrotfish *Scarus rubroviolaceus* which may have been due to a small sample size in the NWHI. Another clear exception was the surgeonfish *Naso unicornis* which had an average length in the NWHI much smaller than the predicted pristine average (386 mm vs. 445 mm). A likely reason for this discrepancy is the natural mortality estimate derived from longevity (53 years) may be overestimated by the assumption that 5% of a cohort is left at that age (using the Alagaraja equation). This longevity estimate comes from an extensive ageing effort in the MHI and NWHI (Eble et al. 2009; n=186) combined with an unpublished bomb radiocarbon dating analysis which confirmed that the oldest aged individual was 53 years (A. Andrews, p. comm.). If we used the average length in the NWHI in Eq. (3) we would have obtained an M=0.16. However, even with this less conservative natural mortality estimates, the SPR for this species remains close to the 30% SPR limit at 36% (up from 8%). With the exception of these two species, the convergence between the expected average length when F=0 and the actual average length in the NWHI suggests that our length-mortality model, life history parameters, and size structure data were appropriate, and this strengthens our confidence in our conclusions concerning the state of reef fish stocks in Hawaii.

The coral reef fish of Hawaii appear to be in slightly better shape than in other U.S. jurisdictions (Puerto Rico and Florida). In the current study of Hawaii, about 47%

of the targeted species analyzed may be overfished (SPR < 30%). Studies elsewhere have shown a greater level of overfishing, e.g., in the Florida Keys (63% of species; Ault et al. 1998, 2005) and Puerto Rico (70% of species; Ault et al. 2008). The reduced level of overfishing in Hawaii could be related to the relative inaccessibility of much of the coastline (Williams et al. 2008) and the concentration of most of the human population on a single island (70% on Oahu).

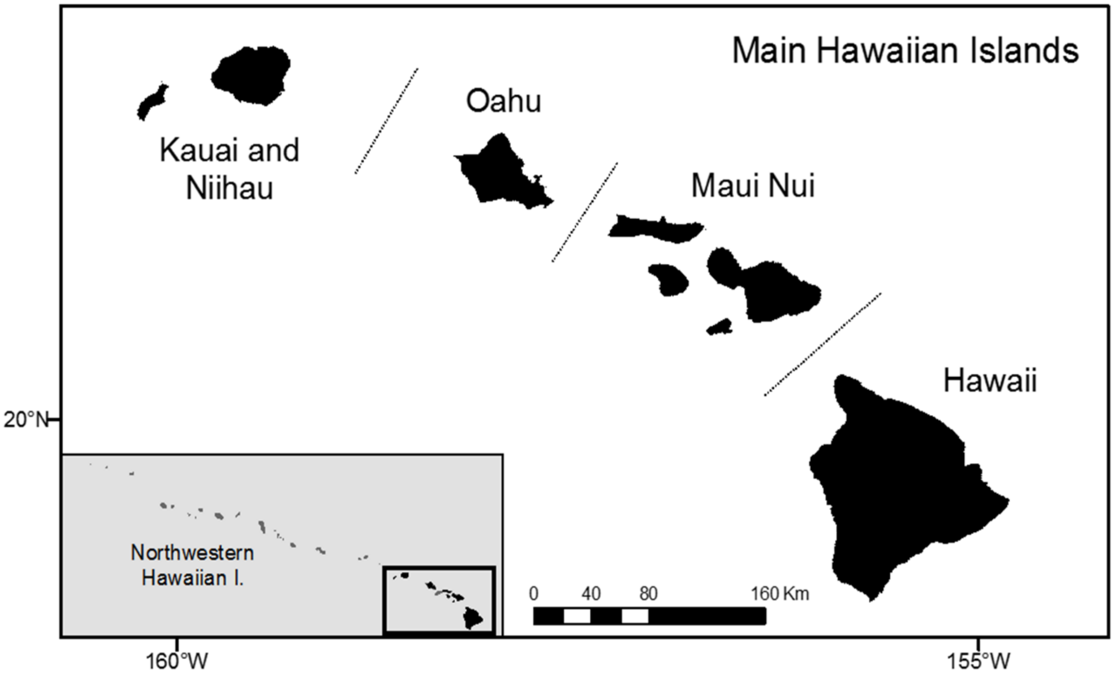

Figure 3.1 – Map of the Hawaiian Archipelago (inset shows the two principal regions) showing the four subregions of the main Hawaiian Islands used in the analyses.

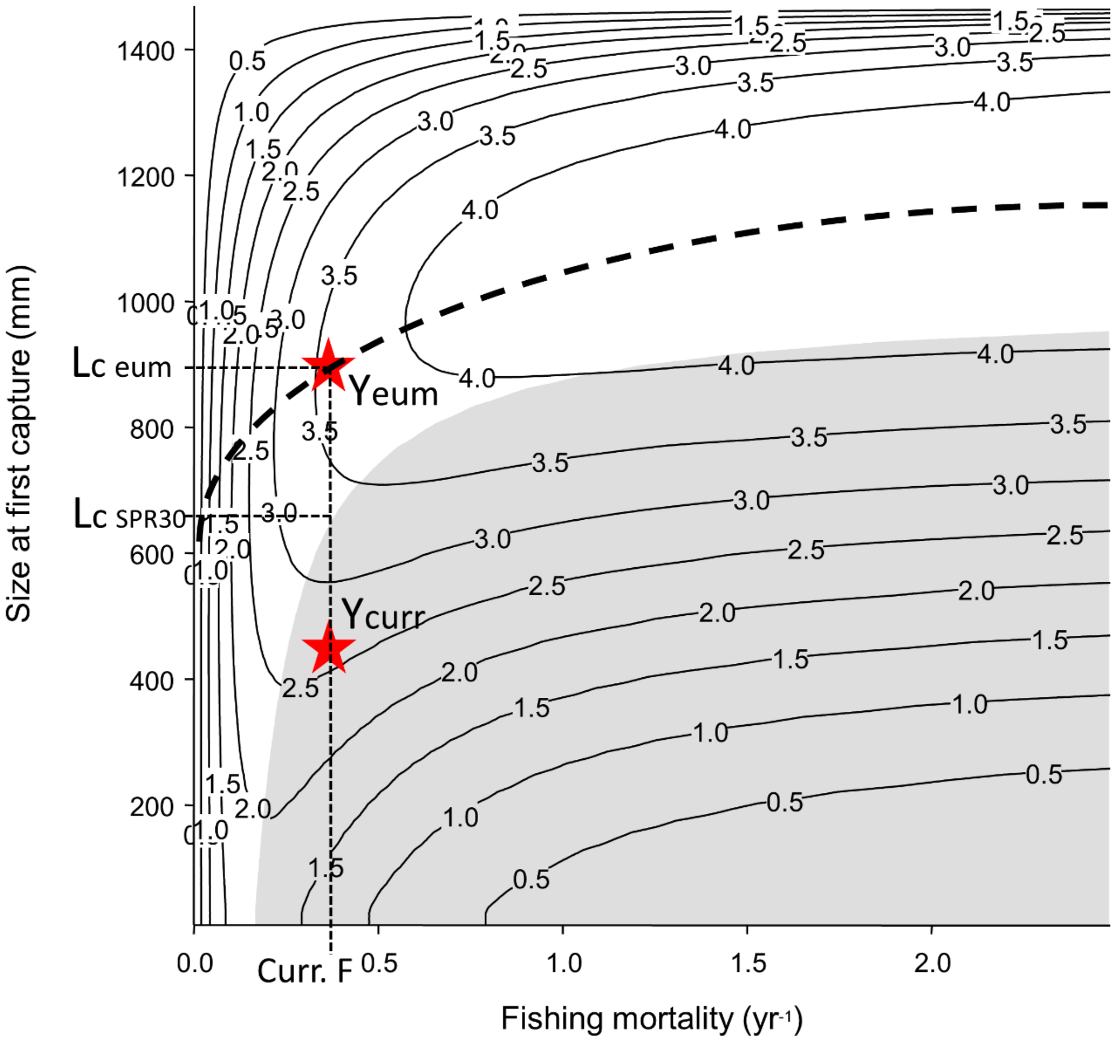

Figure 3.2 – Example of yield-per-recruit isopleths for the giant trevally Caranx ignobilis showing yield as a function of fishing mortality rates (F) and sizes at first capture (L_c). Y_{curr} represents current yield-per-recruit (in kg) in the fishery and Y_{eum} is the highest possible yield for the current F (Current F=0.4). The gray area represents combinations of F and Lc that result in SPRs below 30%. Lc eum is the minimum size limit that will maximize yield while Lc SPR30 is the minimum size limit that will lead to an SPR of 30% given the current F.

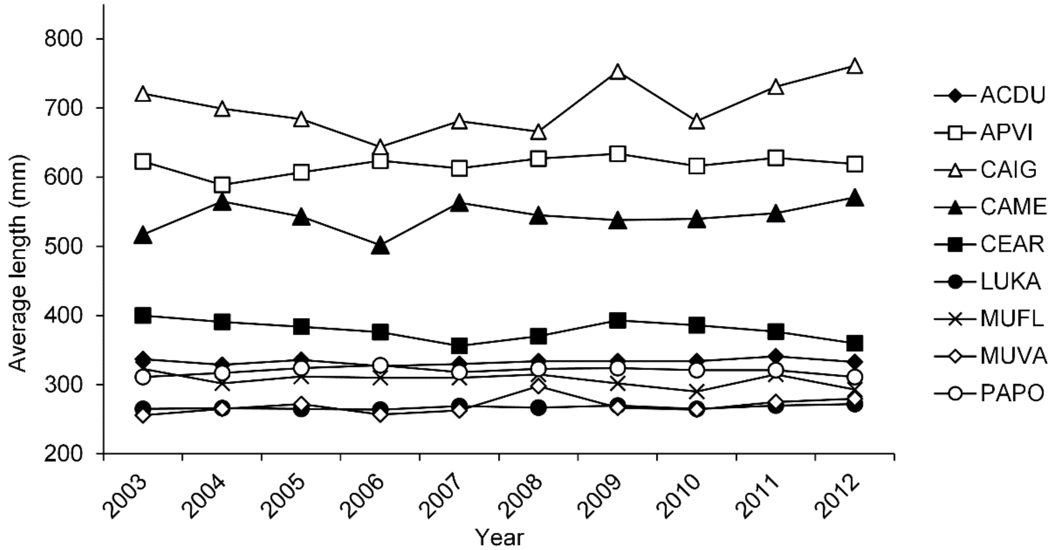

Figure 3.3 – Time-series of average lengths in the exploited phase of the population for 9 Hawaiian reef fish species in the MHI from 2003 to 2012. Species included in this analysis had at least 30 length observations per year. Data from commercial fishery reports. Species codes are defined Table 3.2.

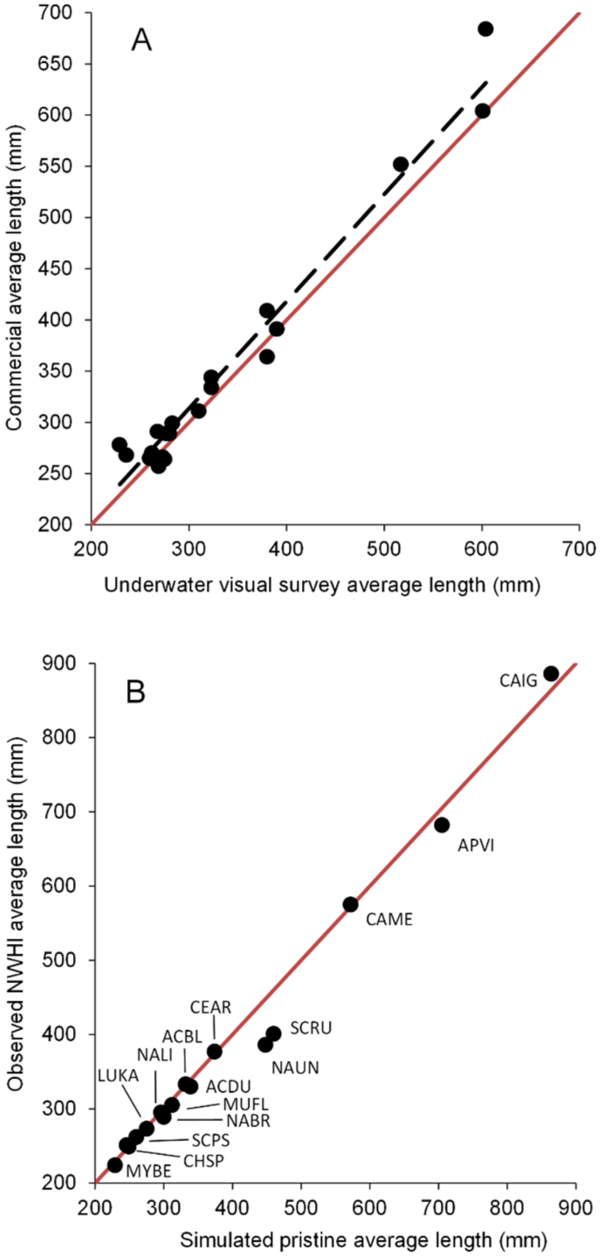

Figure 3.4 – (A) Comparison of average lengths in the commercial dataset versus the underwater visual survey dataset for the main Hawaiian Islands (MHI). Closed circles represent average lengths by species in different subregions of the MHI. (B) Average lengths observed in the Northwestern Hawaiian Islands versus simulated unexploited (pristine) average lengths. The red line represents perfect agreement between the two sets of average lengths. Species codes are defined Table 3.2.

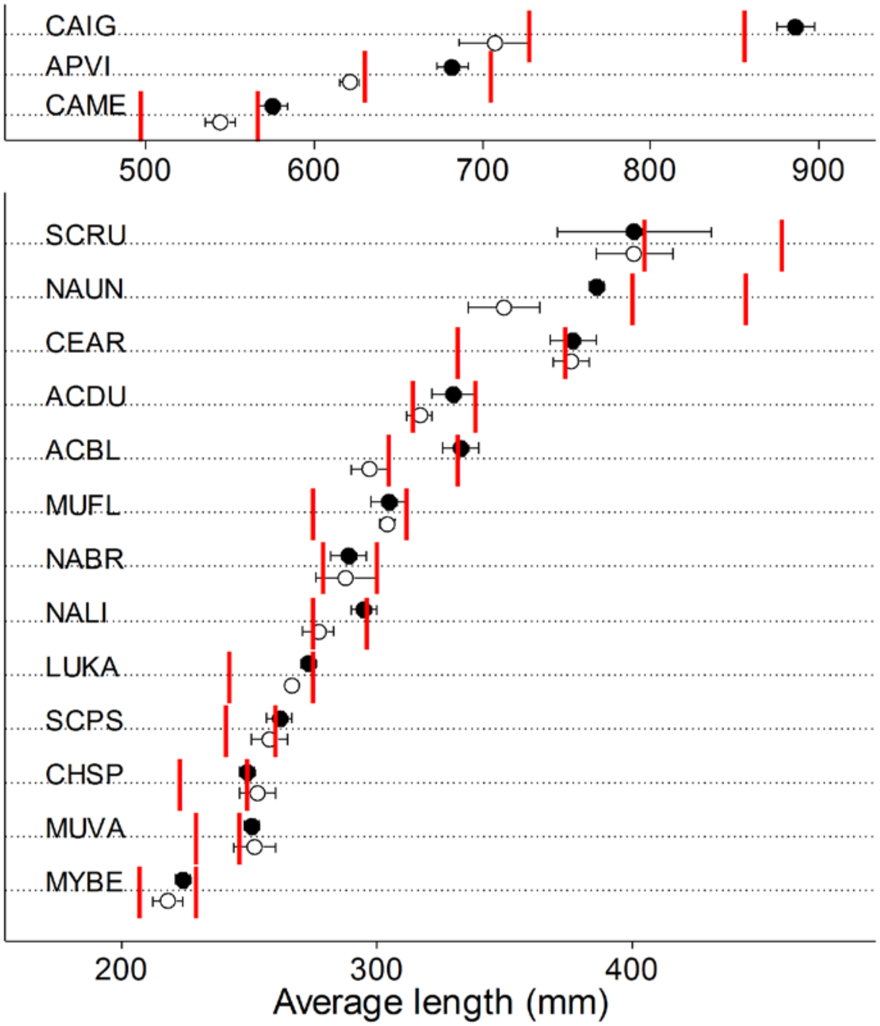

Figure 3.5 – Average lengths ($\overline{L}$) and 95% CIs for the main Hawaiian Islands (MHI; open circles) and the Northwestern Hawaiian Islands (NWHI; closed circles) along with two reference points: first red bar, $\overline{L}_{SPR=30\%}$ (average length when SPR = 30%); second red bar, $\overline{L}_{F=0}$ (average length when F=0). Species are ordered by maximum size. Only species with n>30 in the NWHI are presented. Species codes are defined Table 3.2.

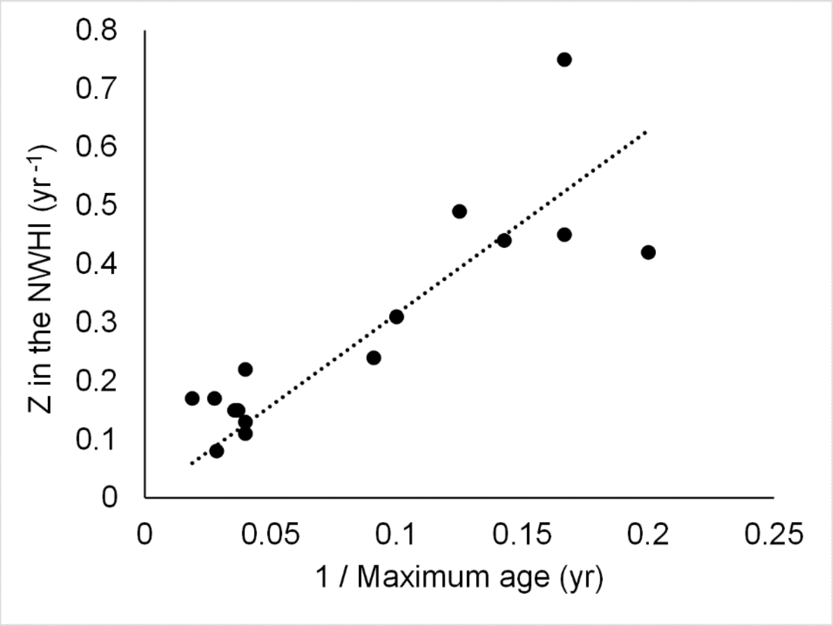

Figure 3.6 – Linear regression of total instantaneous mortality rate Z in the NWHI (assumed to be equal to M) derived from average length versus the inverse of published maximum age. The slope of this regression is equal to –ln(S)=3.14, where S (cohort survivorship to maximum age) is 0.043.

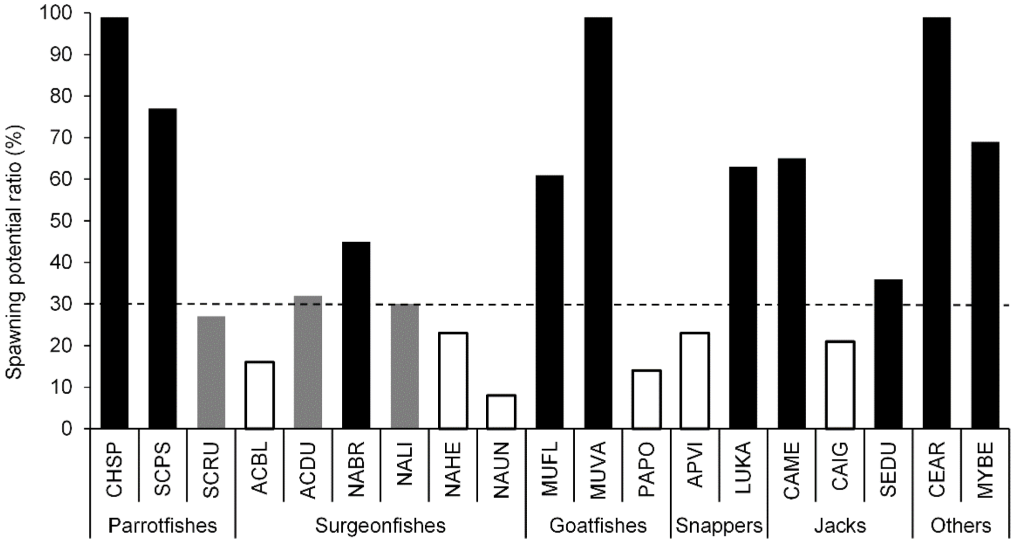

Figure 3.7 – Spawning potential ratio (SPR) for 19 Hawaiian reef fishes in the main Hawaiian Islands. White bars, SPR<25%; gray bars, SPR between 25%≤ SPR ≤ 35%; black bars, SPR > 35%. Species codes are defined Table 2. Dashed line denotes minimum SPR threshold of 30%.

Table 3.1 – Information summary of the two main regions the Hawaiian Islands, including the four main Hawaiian Islands subregions.

Region	Human population	Reef area (km2)	Prop. of total reef in region	Pop'n per reef area (# km-2)	Channel width a (km)
Main Hawaiian Is.					
Hawaii	185,079	194	0.16	954	48
Maui Nui	154,950	373	0.31	415	48-42
Oahu	953,000	375	0.31	2541	42-116
Kauai-Niihau	65,819	266	0.22	247	116-220
Northwestern Hawaiian Is.	~100	1595	-	~ 0	220

[a] Minimum distance between emergent land in different zones, ordered from SE to NW

Table 3.2 – Average size ($\bar{L}$) and standard error (TL mm) for 19 exploited Hawaiian reef fishes in the 4 main Hawaiian Islands subregions and Northwestern Hawaiian Islands (NWHI) region. Only $\bar{L}$ estimates with a minimum of n=10 observations are presented. The simulated average lengths when F=0 from our population model are also presented (Sim. Ref., $\bar{L}_{F=0}$).

Species	Code	Data source[a]	Hawaii		Maui Nui		Oahu		Kauai - Niihau		NWHI		Sim. ref.
			n	$\bar{L}$	n	$\bar{L}$	n	$\bar{L}$	n	$\bar{L}$	n	$\bar{L}$	$\bar{L}_{F=0}$
Chlorurus spilurus – P[b]	CHSP	UVS	96	277(6)	241	241(3)	-	-	-	-	853	249(2)	249
Scarus psittacus – P	SCPS	UVS	35	269(5)	121	252(3)	10	266(12)	14	262(6)	117	262(3)	260
Scarus rubroviolaceus - P	SCRU	UVS	141	379(7)	217	408(7)	15	445(22)	176	405(9)	47	401(16)[c]	459
Acanthurus blochii – S	ACBL	UVS	98	301(3)	101	290(4)	-	-	92	303(4)	203	333(4)	332
Acanthurus dussumieri - S	ACDU	UVS	256	323(2)	269	310(2)	-	-	150	323(3)	142	330(4)	339
		COM	643	334(1)	731	311(2)	2507	340(1)	103	344(4)	-	-	“
Naso brevirostris – S	NABR	UVS	41	271(6)	192	255(2)	25	251(7)	41	346(11)	303	289(4)	300
Naso lituratus – S	NALI	UVS	277	277(2)	384	280(2)	33	268(6)	186	285(3)	368	295(2)	296
		COM	233	289(2)	297	289(2)	210	291(3)	-	-	-	-	“
Naso hexacanthus – S	NAHE	COM	180	466(3)	82	528(5)	196	512(3)	-	-	-	-	551
Naso unicornis – S	NAUN	UVS	37	344(10)	103	356(6)	10	337(18)	100	347(6)	2107	386(2)	445
Mulloidichthys flavolineatus - G	MUFL	UVS	-	-	94	283(2)	16	355(4)	24	302(4)	124	305(3)	312
		COM	207	313(3)	253	299(2)	757	304(1)	14	291(8)	-	-	“
Mulloidichthys vanicolensis - G	MUVA	UVS	67	236(4)	318	229(1)	33	269(6)	43	273(5)	342	251(2)	246
		COM	199	268(2)	75	278(4)	688	257(1)	125	266(3)	-	-	“
Parupeneus porphyreus – G	PAPO	COM	1071	334(1)	259	326(2)	1709	294(1)	264	330(2)	-	-	392
Aprion virescens – Sn	APVI	UVS	15	579(22)	57	601(19)	-	-	80	604(13)	1042	682(5)	705
		COM	645	611(3)	1380	603(2)	738	600(3)	937	684(3)	-	-	“

(Table continued on next page)

Table 3.2 – Continued.

Lutjanus kasmira – Sn	LUKA	UVS	164	275(2)	208	260(2)	-	-	363	262(1)	367	273(2)	275
		COM	1511	264(1)	617	265(1)	1047	268(1)	560	270(1)	-	-	“
Caranx melampygus - J	CAME	UVS	11	433(17)	-	-	-	-	42	517(14)	858	575(5)	566
		COM	331	545(6)	485	538(5)	719	544(4)	563	552(5)	-	-	“
Caranx ignobilis – J	CAIG	UVS	-	-	-	-	-	-	-	-	1397	886(5)	856
		COM	140	769(21)	355	675(10)	923	678(6)	309	746(12)	-	-	“
Seriola dumerili – J	SEDU	COM	44	740(26)	56	827(29)	189	722(13)	141	793(12)	-	-	861
Cephalopholis argus - Gr	CEAR	UVS	96	380(5)	128	380(4)	-	-	63	390(6)	90	377(5)[c]	374
		COM	89	409(5)	664	364(1)	989	359(1)	38	391(10)	-	-	“
Myripristis berndti - So	MYBE	UVS	154	222(3)	88	212(3)	11	233(8)	207	224(3)	354	224(2)	229

[a] UVC, underwater visual census; COM, commercial report.

[b] Family: P, parrotfishes (Labridae); S, surgeonfishes (Acanthuridae); G, goatfishes (Mullidae); Sn, snappers (Lutjanidae); J, jacks (Carangidae); Gr, groupers (Epinephelidae); Sq, squirrelfishes (Holocentridae).

[c] Also includes data from Johnston and Wake Atoll.

Table 3.3 – Life history and demographic parameters, mortality rates, and sustainability benchmarks for 19 Hawaiian reef fishes. See text for description of life history parameters and symbols used. Only species with at least 30 length observations were analyzed. Potential yield increase is the increase in yield that would result if fishing is eumetric (Lc = Lc eumetric). Lc SPR30 is the minimum size at full selectivity for SPR to be equal to 30% under current fishing mortality rate (F). See the appendix for life history parameter references.

Species	L_∞ (mm)	K (y^{-1})	a_0 (y)	L_m (mm)	α	β	L_c (mm)	L_λ (mm)	a_λ (y)	M (y^{-1})	$\overline{L}$ (mm)	F (y^{-1})	SPR (%)	Potential yield increase (%)	L_c SPR30 (mm)	L_c eumetric (mm)
Parrotfish																
*Chlorurus spilurus**	289	0.44	-0.76	170	0.024	2.97	200	287	10	0.30	253	0.01	99	-	-	-
*Scarus psittacus**	278	1.65	-0.29	196	0.010	3.32	210	278	6	0.50	258	0.16	77	3	1	161
*Scarus rubroviolaceus**	563	0.29	-0.81	374	0.014	3.11	260	562	22	0.14	401	0.20	27	13	310	405
Surgeonfish																
*Acanthurus blochii**	363	0.25	-0.38	276	0.025	3.03	250	363	35	0.09	297	0.27	16	6	305	296
*Acanthurus dussumieri**	371	0.30	-0.29	282	0.025	3.03	260	371	28	0.11	317	0.18	32	1	251	279
*Naso brevirostris**	327	0.40	-0.21	269	0.011	3.24	220	327	25	0.12	288	0.11	45	1	1	236
*Naso lituratus**	322	0.34	-0.66	250	0.050	2.84	230	322	25	0.12	277	0.21	30	1	228	242
Naso hexacanthus	599	0.22	-0.22	511	0.042	2.85	410	599	44	0.07	509	0.13	23	2	480	461
*Naso unicornis**	512	0.17	-0.50	330	0.018	3.04	260	512	53	0.06	350	0.25	8	44	436	430
Goatfish																
Mulloidichthys flavolineatus	371	0.56	-0.36	199	0.009	3.21	260	364	6	0.50	301	0.42	61	5	1	220
*Mulloidichthys vanicolensis**	267	1.3	-1.1	206	0.017	2.96	210	267	5	0.60	251	0.01	99	-	-	-
Parupeneus porphyreus	547	0.54	-0.45	264	0.011	3.21	250	530	6	0.50	318	1.32	14	28	349	382

(table continued on next page)

Table 3.3 – Continued.

Snappers																
Aprion virescens	810	0.31	0	500	0.022	2.89	450	810	26	0.12	621	0.23	23	10	553	623
Lutjanus kasmira	340	0.29	-1.37	200	0.008	3.25	240	318	8	0.37	267	0.36	63	12	146	190
Jacks																
Caranx melampygus	1041	0.23	-0.04	475	0.024	2.94	370	839	7	0.43	544	0.16	65	1	1	394
Caranx ignobilis	2170	0.11	0.10	839	0.015	3.09	430	1523	11	0.27	707	0.30	21	36	639	902
Seriola dumerili	1272	0.23	-0.79	910	0.024	2.86	450	1237	15	0.20	773	0.14	36	6	1	681
Other families																
Cephalopholis argus – Grouper	506	0.08	-6.50	268	0.020	2.99	310	458	25	0.12	376	0.01	99	-	-	-
Myripristis berndti – Squirrelfish*	271	0.15	-4.48	175	0.028	3.00	180	268	27	0.11	224	0.04	69	5	1	130

* UVC data used for average length. All other species, commercial data used.

Chapter 4

A stepwise Monte Carlo simulation approach to determine missing life history parameters for data-poor fisheries

Summary

Tropical coastal fisheries are characterized by highly diverse species catch compositions and limited management resources which leads to a notably data-poor situation for stock assessment. Some parsimonious stock assessment approaches rely on cost-efficient size structure information, but these require key population demographic parameters such as growth (K, L_{inf}), maturity (L_{mat}), and longevity (a_{λ}). Past research has shown that these parameters are highly correlated across species. Further, certain parameter ratios (i.e., M/K, L_{mat}/L_{inf}) are often conserved within taxonomic groups. Here, we present an approach that uses these relationships to build complex multivariate probability distributions that can be used to parameterize stock assessment models in data-poor situations when no life history information is available. We first carried out a meta-analysis of the literature to build a life history parameter dataset for 6 coral reef fish families. For each family, we modeled the key relationships between these parameters: $L_{inf} \sim L_{max}$, $K \sim L_{inf}$, $M \sim K$, and $L_{mat} \sim L_{\lambda}$ (where L_{max} is the largest locally measured length, L_{inf} and K are parameters of the von Bertalanffy equation, M is the natural mortality rate, L_{mat} is the size-at-maturity, and L_{λ} is the expected size at maximum observed age). We then used these models to create multivariate LH parameter probability distributions by sampling random values in a stepwise fashion starting with a local estimate of the maximum size (L_{max}). We tested this approach on three well-studied species for which raw length, age, and maturity data was available. The probability

distributions from the data-poor approach compared relatively well with those obtained from the raw life history data and were sufficiently informative to be used for stock assessments or as prior information in Bayesian analyses.

Background

Coral reef fisheries provide livelihoods and sustenance for hundreds of millions of people worldwide, particularly in poor tropical countries (Pauly et al. 2005). These fisheries are often characterized by a highly diverse catch composition typically in the hundreds of species and are often managed with limited financial and human resources, if managed at all. For most of these fisheries, a limited amount of information exists on historical catches and baseline abundances (Fenner 2012). These issues make assessing coral reef fisheries highly problematic. Recently, methods have been proposed for data-poor situations that mainly rely on cost-effective abundance at size data and some basic biological knowledge such as growth, maturity, and longevity (chapter 3; Ault et al. 1998, 2008, 2014; Hordyk et al. 2014). However, even these simple data requirements are often unmet due to a lack of life history information. For example, the coastal fisheries of Hawaii target more than 200 species of reef fishes for which there exist only 35 growth studies, of which only 18 are local studies. This is despite the fact that Hawaii has a relatively low reef fish diversity and has many governmental agencies and universities conducting research on these species. This situation is likely even worst in poorer areas and is not only limited to reef-associated species: Froese & Binohlan (2000) estimates that only 1200 out of 7000 exploited species have some life history data. Here, we propose a novel way to obtain life history parameters for un-studied species by using a stepwise Monte Carlo simulation approach based on the meta-analysis of published life history parameters and some well-known relationships between LH parameters (i.e., Beverton-Holt invariants) to generate multivariate probability distributions of life history parameters.

Beverton and Holt (1959) and Beverton (1963) were the first studies to identify clear linkages between key life history parameters. They observed that (1) natural mortality rate (M) was positively correlated to the growth parameter K such that the M/K ratio is typically close to 1.5 (i.e., longer lived fishes tend to grow more slowly); (2) length at maturity (L_{mat}) is positively correlated to asymptotic length L_{inf} where the L_{mat}/L_{inf} ratio is generally around 0.66 (i.e., species tend to mature at a specific fraction of their maximum size); and (3) von Bertalanffy growth parameters L_{inf} and K are negatively correlated following a power function of the form $L_{inf} \sim K^{-h}$; where h is typically around 0.5. These ratios, generally referred to as Beverton-Holt invariants (Charnov 1993), have been shown to be related to the maximization of reproductive output (Jensen 1996, 1997; Charnov 2008) and thus likely conserved through natural selection, as originally theorized by Beverton and Holt (1959). Beverton and Holt (1959), as well as some recent studies (Prince et al. 2014), have noted that these “invariants” actually differ significantly between taxonomic groups and are thus better used within taxa.

One important interest in studying these relationships is to estimate elusive parameters such as M by relating these to more tractable ones, such as L_{inf}, K, and possibly water temperature (see Kenchington 2013 for a review of other empirical M relationships). Recent studies have proposed other relationships related to maximum length and optimum length (Froese & Binohlan 2000, 2003; Jarić & Gačić 2012). These studies have been mainly concerned with generating estimates for individual missing parameters. What is unclear is how to use these relationships to generate a complete multivariate distribution for all of the main life history parameters (L_{inf}, K, L_{mat}, a_{λ}) given that these are all correlated to various degrees. Standard multivariate distributions (e.g., multivariate normal distribution) can describe the variance-covariance structure of multiple parameters but preclude the use of more complex relationships between parameters (i.e., power, exponential, or multiple explanatory variables) and non-normal error distributions (e.g., log-normal, gamma).

As a solution, we propose using a stepwise Monte Carlo simulation approach that seeks to preserve the correlative structure linking these parameters with each other. We first reviewed the literature on the life history of 6 commonly targeted families of coral reef fishes to generate family-specific models linking the 4 main LH parameters ($L_{inf} \sim L_{max}$, $K \sim L_{inf}$, $M \sim K$, and $L_{mat} \sim L_{\lambda}$). With these models, it becomes theoretically possible to generate complex multivariate probability distributions of life history parameters for un-studied species by taking successive random samples from these relationships starting with an estimate of maximum length (L_{max}; the longest individual fish from a representative size dataset). We tested this approach for 3 well-studied species from Hawaiian waters for which we had access to raw length, age, and maturity data (the parrotfish *Scarus rubroviolaceus*, the surgeonfish Naso unicornis, and the jack Caranx ignobilis). We compared the probability distribution of life history parameters originating from single-studies vs. our novel data-poor approach. We also calculated spawning potential ratio (SPR: ratio of current mature fish biomass divided by pristine mature biomass) distributions from these life history distributions by using a numerical population model and compared these as well.

Methods

Life history parameter dataset

We collected life history parameters from the literature for 6 commonly exploited families of reef fishes: surgeonfishes (Acanthuridae), jacks (Carangidae), emperors (Lethrinidae), snappers (Lutjanidae), goatfishes (Mullidae), and parrotfishes (Scaridae) (see Appendix A.2 for citations). Unfortunately, we could not assemble a dataset composed of raw length, age, and maturity data given that such information is rarely published in growth studies and generally hard to obtain for the high number of species that we were targeting. This would have been useful in a hierarchical meta-analysis modeling context (Helser et al. 2007; Thorson et al. 2013). Instead, we obtained fitted parameters for growth (Von Bertalanffy: L_{inf}, K, a_0) and length at 50% maturity (L_{mat}), in addition to longevity (a_{λ}) and L_{max} (i.e., the longest measured length in the growth study where L_{inf} and K originated; see Table 4.1 for definition of all parameters). Although we could have potentially taken L_{max} values from other local sources (e.g., visual surveys, catch records), we had limited access to such datasets. If multiple studies existed for a single species, we kept the parameters from the most in-depth and recent study, with the exception of longevity for which we kept the highest value found in any study. If a study provided separate parameters for different localities, we averaged these parameters together (if the study did not already provide the average values). Growth parameters fitted separately for males and females were averaged together. For species with different length-at-maturity between sexes, the female L_{mat} was kept. L_{inf}, L_{mat}, and L_{max} parameters reported in standard or fork lengths were converted to total length (in mm) using published conversion factors. Time-based parameters (K, a_0, a_λ) expressed in units other than years were converted to that time unit. Finally, natural mortality rates M were estimated from longevity (a_λ) applying the procedure of Alagaraja (1984), similar to (Hoenig 1983), assuming that 5% of a cohort survives to the observed maximum age:

$$M = \frac{-\ln(0.05)}{a_\lambda} \quad , \qquad (1)$$

We used the 5% cohort survivorship value based on the analyses conducted in chapter 3 which showed that this is an appropriate value for coral reef fishes. We did not have independent estimates of M and had to rely on this maximum age approach. We rejected studies where growth parameters came from length-frequency or mark-recapture analyses (i.e., we only kept studies based on hard structure ageing), a_0 was very negative (< -2 years), the authors expressed concerns about their results, or parameter estimates were derived from empirical relationships. We also rejected life history studies from regions with annual mean sea surface temperature below 20 °C due to the effects of water temperature on growth and longevity (Pauly 1980; Choat & Robertson 2002). We decided not to add temperature as a variable in our models since the families targeted in the current study are mostly tropical and only a few studies were discarded because of this (15 out of 171, mostly jacks). However, we did keep growth and maturity information from 2 goatfish studies from colder water regions (i.e., Mediterranean Sea) because of a low sample size for this family. We did not retain the longevity values for these 2 studies, however.

Life history parameter models

A preliminary look at the distribution of life history parameters and Beverton-Holt invariants (Charnov 1993) revealed important differences in the distribution and range of certain parameters between families (Table 4.2), as previously reported in other meta-analytical studies (Beverton & Holt 1959; Choat & Robertson 2002; Prince et al. 2014). We therefore conducted all analyses at the family level, as expected.

We described the empirical relationships between pairs of LH parameters using generalized linear models (GLM; Fox 2008) for each of the 6 families. We fitted GLMs to the parameter pairs with the closest relationships: $L_{inf} \sim L_{max}$, $L_{mat} \sim L_{inf}$, $K \sim L_{inf}$, and $M \sim K$ (Beverton & Holt 1956; Pauly 1980; Beverton 1992; Jensen 1996; Froese & Binohlan 2000, 2003; Binohlan & Froese 2009; Gislason et al. 2010). We also tested the use of a 2-variable model to predict M which included the L_{max} variable (in addition to K, similarly to the model described in (Pauly 1980). Additionally, we tested L_{λ} (average length at the oldest measured age) as a replacement for L_{inf} as a predictor of L_{mat} (Fig. 4.1). For all four GLMs, we tested three deterministic functions (linear, power, and exponential) and three error probability distributions (normal, lognormal, and gamma). We selected the best model based on an in-depth look at the distribution of residuals (to select an appropriate error distribution) and scatterplots (to select an adequate linear or non-linear function). The a_0 variable was described using a probability distribution independently from the other variables, as we did not observe any significant correlation between this variable and L_{inf} or K (as opposed to Helser et al. 2007).

Once these four LH parameter models were established for each family, it became possible to use the step-by-step iterative approach described in figure 4.1 to build multivariate probability distributions of the four main LH parameters (L_{inf}, K, M, and L_{mat}) for un-studied species (which we call the “data-poor approach”). The first step in the data-poor process was to use L_{max} (the maximum recorded length in a local abundance at size dataset) to draw a random L_{inf} from the $L_{inf} \sim L_{max}$ model (step A in Fig. 4.1). From this random L_{inf}, a K value was drawn from the $K \sim L_{inf}$ model (step B) which was then used to draw a random M from the $M \sim K + L_{max}$ model (step C). Finally, we tested two models to draw a random L_{mat}: using the $L_{mat} \sim L_{inf}$ model or using the $L_{mat} \sim L_{\lambda}$ model (step D). For the second model, we had to first calculate L_{λ} using the von Bertalanffy equation and the L_{inf}, K, and longevity parameters from the same iteration (longevity being derived back from M using eq. 1). We tested both model fits (using r^2) and ultimately decided on the $L_{mat} \sim L_{\lambda}$ model, which is the reason why it is presented as step D in fig. 4.1 (see Results for more details). This entire process (Fig. 4.1) was repeated for 5000 iterations in order to build a multivariate distribution describing the variance and covariance of all 4 life history parameters.

Testing the data-poor approach

We tested the precision and accuracy of the data-poor approach by comparing the probability distributions of LH parameters obtained in this way versus the probability distributions originating from well-conducted growth and maturity studies (i.e., data-rich situation). We selected 3 in-depth growth and maturity studies from Hawaii for which we had access to the raw length, age, and maturity data: *Scarus rubroviolaceus* (Howard 2008), *Naso unicornis* (Eble et al. 2009), and *Caranx ignobilis* (Sudekum et al. 1991). We first used the data-poor approach described above to obtain “data-poor” probability distributions of LH parameters for those 3 species. The L_{max} values used for this approach came from an extensive underwater visual census dataset collected by the National Oceanic and Atmospheric Administration in Hawaii (see chapter 3 for more details).

To generate probability distributions for the "data-rich" situation, we bootstrapped the raw length, age, and maturity observations for the 3 selected studies since these did not report the error associated with their fitted parameter estimates. Fish collected for growth/maturity studies are typically selected to be representative of an entire species' size range (i.e., once researchers have sufficient small specimens, they will shift their focus to capturing medium or large individuals until they have a representative size range). To reflect this, we stratified the bootstrapping of the raw dataset for each species in three size categories (small – bottom 20% of lengths, medium, and large – top 20% of lengths). We ran the bootstrapping procedure for 5000 iterations to obtain probability distributions of the life history parameters presented in these studies. Finally, we compared the probability distribution of all 4 LH parameters obtained this way with the ones obtained using our novel data-poor approach. We looked at the width of the data-poor distributions compared to the data-rich distributions to assess precision and the distance between the data-poor and data-rich distribution means to assess accuracy.

For both the data-poor and data-rich situations, we calculated a measure of stock status, spawning potential ratio (SPR), at three different levels of fishing mortality: light (F=0.01), moderate (F=M), and high (F=2M), where M is the natural mortality derived from the oldest age for all 3 test species. We used a length conditional on age structured numerical model (following (Ault et al. 1998) to make these calculations. In this model, numerical abundance at age *a* was estimated through use of an exponential mortality function. Length at age was estimated from the von Bertalanffy growth equation, and converted to weight-at-age using the allometric weight-length relationship. This numerical model was used to obtain spawning stock biomass (SSB) by summing over individuals in the population between the age of sexual maturity (a_m; age where 50% of individuals are mature, with knife-edge assumption) and oldest age a_λ,

$$SSB = \sum_{a_m}^{a_\lambda} \overline{N}_a \overline{W}_a \quad , \tag{5}$$

where $\overline{N}_a$ is the average abundance at age a and $\overline{W}_a$ is the mean weight of individuals at age a. Length-weight relationship parameters (α, β) necessary for SPR calculations were taken from the literature (i.e., Kulbicki et al. 2005). Theoretically, a stock's maximum reproductive biomass occurs when there is no fishing. SPR was computed as the ratio of the current SSB relative to that of an unexploited stock

$$SPR = \frac{SSB_{\exp loited}}{SSB_{un\exp loited}}$$

We compared the SPR distributions between the data-poor and data-rich scenarios in a similar way as for the life history distributions.

Results

Life history parameter dataset

We found growth information for 167 species out of the 560 species that are currently listed for the 6 families included in our analyses (from hard structure ageing studies only; Table 4.2). Of those 167 species, we found maturity-at-size information for 97. A total of 15 species were discarded because their growth and longevity information came from colder regions (mean SST < 20°C). Furthermore, 6 species were discarded in some of the models for being clear outliers. The L_{mat} values for *Lethrinus laticaudis* (Ayvazian et al. 2004) and *Lutjanus campechanus* (White & Palmer 2004) corresponded to very low reproductive loads (i.e., L_{mat}/L_{inf}; 0.46 and 0.37, respectively) which were far lower than for other species in their family. These values were also far lower than the predicted reproductive load based on the theoretical maximization of egg production (~0.66; Jensen 1996). We removed the L_{inf} and K values for the goatfish *Mulloidichthys vanicolensis* since they were clear outliers; the ageing for this species was done using un-validated annual otoliths rings, which may be a reason for this discrepancy, although this is not entirely clear (Cole 2009). Similarly, we discarded growth and longevity parameters for the surgeonfish *Acanthurus triostegus* since Longenecker et al. (2008) used un-validated daily growth rings that resulted in a lifespan estimate much lower than anything previously recorded for surgeonfishes (3 years vs. 20 years for the next surgeonfish species with the shortest reported lifespan). We removed the small parrotfish *Sparisoma atomarium* from our meta-analysis since this is an extremely small species (L_{inf} = 110 mm) with very fast growth (K=1.8) and short lifespan (3 years) that could not be properly modeled with other parrotfishes and was a clear outlier. Finally, we removed a very low (and unlikely) longevity estimate for the parrotfish *Calotomus carolinus* from a study in Guam (Taylor & Choat 2014) which may be related to the high fishing pressure around this island. For example, the parrotfish *Scarus rubroviolaceus* has a maximum lifespan estimate of 22 years around Oahu (Hawaii) while the estimate for the same species around Guam in Taylor & Choat (2014) is only 6 years.

Life history parameter models

Maximum size in a representative local sample (L_{max}) was generally a good predictor of L_{inf}, with a reasonably small standard error of about 2 cm for most families. We used a normal error distribution for most families except for jacks where we used a log-normal distribution to take into account increasing variability with size (i.e., the variance of the gamma and log-normal distributions is proportional to the square of their mean). We also had to use a size break point in our models for jacks and snappers, as there was an important increase in variability beyond certain max sizes that could not be taken into account by the properties of the log-normal or gamma distributions (900 mm TL for jacks and 500 mm TL for snappers). The growth parameter K followed a decreasing, curvilinear trend with increasing L_{inf} which was described using either an exponential or power function, depending on the family. Variability generally decreased with increasing L_{inf} which was properly described by either a gamma (emperors, snappers, parrotfishes) or log-normal (jacks) error distribution. Goatfishes where an exception with no clear trend between L_{inf} and K or increases in variability with L_{inf}. K values for this family were simply describe by their mean value with a normal error distribution. Natural mortality (M) generally followed a weak increasing curvilinear trend with higher K values and a weak negative curvilinear trend with L_{max} (i.e., larger species in general grew slower and lived longer). This was true for jacks, snappers, emperors, and parrotfishes (Fig. 4.2; Table 4.3). However, there was no clear relationship between M and K or L_{max} for either surgeonfishes or goatfishes (i.e., species in these families had a similar range of longevity regardless of size). Surgeonfishes were all fairly long lived, with lifespans between 20 years (*Acanthurus chirurgus*, a Caribbean species) and 53 years (*Naso unicornis*, a widespread Indo-Pacific species). Conversely, goatfishes were all short-lived (max lifespan of 6 years, or 11 years if colder water species are included). Lastly, L_λ (average size at maximum age) was an equal or better predictor of L_{mat} for all families compared to L_{inf}, especially for jacks and goatfishes (Table 4.4). The r^2 value for the $L_{mat} \sim L_\lambda$ regression was 0.91 vs. 0.83 for the $L_{mat} \sim L_{inf}$ regression for all families combined. We therefore selected L_λ as our predictor of L_{mat}, instead of the typical L_{inf} variable. A simple linear equation with a normal error distribution fitted the $L_{mat} \sim L_\lambda$ data for all families except for surgeonfishes and snappers where a log-normal error distribution was used due to the increasing variance with higher L_{mat} values.

Test of the data-poor approach

For the 3 species selected to test our approach, we compared the life history parameter probability density distributions obtained through the data-poor approach (i.e., only size structure data available) with those from the data-rich situation (i.e., single, well-conducted, growth and maturity study). We compared the width of these distributions as a measure of precision and the distance between the means of the data-poor distribution to the data-rich distribution as a measure of accuracy (i.e., we assume that the data-rich mean is closer to the "true" value). Figure 4.3 represents the result of these comparisons for all 3 species. The life history parameter estimates from the data-poor situation were all more variable than in the data-rich situation. This was especially true for the growth parameter K and natural mortality parameter M. The data-poor approach provided estimates of the L_{inf} and L_{mat} parameters that were fairly close to the data-rich estimates in terms of variability and accuracy. In general, the data-poor parameter estimates for the parrotfish *Scarus rubroviolaceus* were the most accurate and precise, with probability distributions closer to those originating from the data-rich situation for all parameters except L_{mat}, where the estimates were slightly higher (e.g., average of 430 mm vs. 375 mm for the data-rich situation). The estimates for the surgeonfish *Naso unicornis* were slightly less precise than for *S. rubroviolaceus* when compared to the data-rich situation (Fig. 4.3), especially for the growth parameter K. Both the L_{mat} estimates and M estimates were slightly higher than the data-rich estimates. Finally, the life history estimates from the data-poor approach fared slightly worst for the jack *Caranx ignobilis*. The L_{inf} and L_{mat} estimates were clearly lower than for the data-rich approach. The natural mortality estimates were higher.

The variability of the SPR probability density distributions for both the data-poor and data-rich approaches varied with fishing mortality, with lower variability at low (0.01) and high (2 x M) fishing mortality rates. The probability density distributions at moderate fishing mortality rates (F=M) where the most variable. The SPR distributions for the parrotfish *S. rubroviolaceus* where generally more precise and accurate than those from the other 2 species, at all fishing mortality rates (Fig. 4.4). The SPR distributions for both the surgeonfish *N. unicornis* and the jack *C. ignobilis* where moderately higher than for the data-rich situation. Overall, the data-poor approach had 95% confidence intervals about 3 times wider than for the data-rich situation.

Discussion

Past studies have shown how the Beverton-Holt life history invariants and other related relationships can provide basic estimates of individual, hard to obtain, life history parameters (Pauly 1980; Stamps et al. 1998; Binohlan & Froese 2009, 2009). In this study, we extend this concept and present a novel way of obtaining complete probability distributions for all key life history parameters (L_{inf}, K, L_{mat}, and M) in a data-poor situation where the only available information for a stock is taxonomic group (i.e., family) and an estimate of maximum size. It is well known that these parameters are all inter-correlated to varying degrees (Beverton & Holt 1959; Beverton 1992; Charnov 1993) and that, therefore, their probability distributions cannot be adequately described independently from each other (e.g., species with high L_{inf} typically have high L_{mat} but low K and low M). A multivariate probability distribution such as the multivariate normal distribution could be used, but this would limit the model to normal error distributions and linear relationships between parameters (unless transformations are used). As an alternative, we presented an intuitive stepwise approach to build a multivariate probability distribution for these four parameters that also preserve their correlative linkages. This approach also allows the use of maximum size (L_{max}) as an informative starting point to obtain the rest of the life history parameters.

The first step of our approach was to build models describing 4 core relationships connecting life history parameters with one another. These models allowed for an intercept similarly to Froese and Binohlan (2000) and so are not directly comparable to the B-H invariants which are typically calculated as ratios (e.g., M/K vs. M = b0 + b1*K). However, we did calculate two BH invariants (M/K and L_{mat}/L_{inf}) as well as the L_{max}/L_{inf} ratio as a first step comparison of the families in our study, as well as to compare these values with those from previous studies (Table 4.2). First, it was clear that these ratios vary by taxonomic group, in this case family, as reported in other studies (Beverton 1992; Prince et al. 2014). The families fell into two broad categories characterized by determinate (i.e., individuals reach an asymptotic size before dying) vs. indeterminate growth (i.e., few or no individuals reach an asymptotic size before dying). Jacks and goatfishes had relatively high M/K ratios (1.6 vs. less than 1 for other families) which correspond to an indeterminate growth curve (i.e., high natural mortality coupled with slow growth). This type of growth curve typically leads to maximum observed sizes (L_{max}) being smaller than L_{inf}, as indicated in the average L_{max}/L_{inf} ratios for these families which is less than 1 (Table 4.2). The other 4 families followed the more typical determinate growth patterns, with lower average M/K ratios (0.3 to 0.8) and L_{max}/L_{inf} ratios above 1.

The distinction between these two type of growth curves was also apparent for the reproductive load values as usually calculated (L_{mat}/L_{inf}) with low reproductive load values of 0.55 for the jacks and goatfishes (i.e., indeterminate growth) which was well below the expected value of 0.66 which theoretically maximizes reproductive output (Jensen 1996). However, we believe the low reproductive loads for families with indeterminate growth is actually an artefact of L_{inf} not being representative of the average size at the oldest age (L_{λ}) for these types of growth curves. In the case of highly indeterminate growth, L_{inf} becomes more of a fitting parameter than one with any biological meaning. For example, the L_{inf} value for the giant trevally *Caranx ignobilis* equals 1840 mm while L_{λ} is only 1260 mm (and the world-record is 1430 mm). We found the use of L_{λ} to be a better predictor of L_{mat} and the L_{mat}/L_{λ} ratio closer to the theoretical value of 0.66 for families with more indeterminate growth curves (0.63 instead of 0.55). As a side note, this observation is likely responsible for the previously reported negative relationship between the L_{mat}/L_{inf} and M/K ratios: as M/K increases, the biological significance of L_{inf} as a representation of the average maximum length (L_{λ}) decreases and the L_{mat}/L_{inf} ratio decreases accordingly (see Prince et al. 2014). Beverton (1992) showed a similar relationship between L_{mat}/L_{inf} and $K*T_{max}$ that is likely related to this artefact as well. These relationships were also apparent in our dataset when using L_{inf} but disappeared when we replaced L_{inf} with L_{λ}, which supports our argument. For this reason, we selected L_{λ} to infer L_{mat} in our model and we suggest replacing the L_{mat}/L_{inf} life history invariant with L_{mat}/L_{λ} in future studies.

Although we looked at the BH-LH ratios as a preliminary source of information, our primary focus was to go beyond simple ratios and explore more flexible models, an approach similar to Froese and Binohlan (2000). The $L_{inf} \sim L_{max}$ and $L_{mat} \sim L_{inf}$ relationships were the simplest to model using simple linear predictor with an intercept term and normal error distributions for most families. For a few families, we used a log-normal error distribution that appropriately modeled the widening variance with increasing mean value (e.g., surgeonfish $L_{mat} \sim L_{inf}$ and jack $L_{inf} \sim L_{max}$ relationships). For jacks and snappers, we divided the $L_{inf} \sim L_{mat}$ relationships in two separate size groups due to a much greater variability at larger sizes which could not be modeled by a log-normal or gamma error distribution. The higher variance for large species in these families may be related to the difficulty in obtaining very large individuals for growth studies since these families are typically heavily fished. This typically leads to un-reliable estimate of L_{inf} when fitting incomplete age-length data. On the other hand, the L_{max} value is fairly stable and well known for most small species, and this is likely due to the ease in obtaining a representative size sample for these species.

The K ~ L_{inf} relationships followed a similar, decreasing power pattern in all 6 families. This relationship was not very clear for goatfishes, but this is probably related to a small sample size and narrow L_{inf} range for this family. Similarly, the K ~ L_{inf} relationship for jacks was fairly linear probably due to a lack of smaller species in our dataset (i.e., the K ~ L_{inf} relationship typically follows a sharp decrease for L_{inf} values below 500 mm followed by a plateau). Interestingly, variability in K followed a decreasing trend with Linf (which was modeled using a gamma distribution for most families). The higher variability in K at smaller L_{inf} values may be related to the absence of juvenile in many growth studies, which often leads to uncertainty in the estimation of a_0 and K (Trip et al. 2014). It could also be linked to biological reasons, although this is not clear.

The M ~ K relationship was the least clear of all 4 relationships. We did not detect a clear pattern between these two parameters for surgeonfishes and goatfishes (which may be due to a small sample size for this family). However, the range of longevity (and associated M) values found in these families was consistent and fairly limited: surgeonfishes had the longest maximum age range (20-54 years) while goatfish had the lowest range (3-6 years). For these families and to a lesser extent the others as well, taxonomic group was more important in determining M than the K values by themselves. For surgeonfishes and goatfishes, there was also no significant relationship between M and L_{max}. Choat and Robertson (2002) also reported the lack of significant relationship between L_{max} and longevity for surgeonfishes. It is not clear why surgeonfish seem to so clearly violate life history invariance for the M/K. However, a lack of pattern between M and K has also been observed in other fishes, such as the walleye (Beverton 1987) and brown trout (Vøllestad et al. 1993).

For all three species tested, the life history parameter probability distributions obtained through the data-poor approach compared relatively well to the data-rich situation (i.e., parameters originating from a well-conducted biological study). The L_{inf} and L_{mat} parameters had the most precise and accurate estimates, overall. This was expected given that the $L_{inf} \sim L_{max}$ and $L_{mat} \sim L_{\lambda}$ models were generally the ones with the tightest confidence intervals. Overall, the 95% confidence interval of the L_{mat} distributions were about 2-3 times wider than for the data-rich situation. For L_{inf}, the data-poor probability distributions was very similar to the data-rich situation for S. rubroviolaceus, twice has large for *N. unicornis*, but surprisingly smaller than the data-rich situation for *C. ignobilis*. This is likely related to the highly indeterminate growth rate of *C. ignobilis* (Sudekum et al. 1991) where L_{inf} becomes more of a fitting parameter than an actual representation of maximum length. The probability distribution for K and M were generally less precise than for L_{inf} and L_{mat}, with confidence intervals about 4-5 time wider than for the data-rich situation. This was expected given that the growth parameter K and natural mortality M had the most variability associated with them.

The last step in this study was to calculate spawning potential ratios (SPR) for the three test species at various fishing mortality rates using the life history parameters provided by the data-poor approach and compare these with SPR values obtained through the data-rich situation. The SPR distribution obtained through the data-poor approach compared well, with probability distributions for SPR about 2-3 times wider than for the data-rich approach. The SPR estimates for the parrotfish *S. rubroviolaceus* were the closest to those from the single-study estimates, while the estimates for the jack *C. ignobilis* were further away, as well as generally less precise. The surgeonfish estimates were in between. The SPR distributions were more closely related to the natural mortality distributions. For example, the wider and positively biased M distribution for *C. ignobilis* matches the wider and positively biased SPR distribution for that species. The high uncertainty associated with the L_{inf} parameter for that species did not seem to impact the SPR estimates significantly.

Hordyk et al. (2014) present another approach to obtaining SPR for data-poor situations by using the Beverton-Holt life history invariants to solve directly for SPR. We see many advantages to our approach versus Hordyk et al. (2004)'s approach. First, our approach does not rely on ratios (i.e., L_{mat}/L_{inf}, M/K, etc.) and can model the relationships between LH parameters with more flexibility in both the shape and error distributions. Secondly, since we can obtain probability distributions for the actual LH parameters, these can be used in any stock assessment models, not just Hordyk et al. (2014)'s SPR approach. Finally, the various probability distributions provided by our approach can also be used as prior information in a Bayesian statistical analysis framework.

Conclusions

The stepwise Monte Carlo approach presented in this study appears to provide sufficiently precise and accurate estimates of life history parameters to conduct preliminary assessments of stocks in extremely data poor situations typical of coral reef fisheries where only size structure information is available. Although this study presented the models necessary to run this approach for 6 families, other families could easily be added (e.g., groupers), as the need arises. This study presented a way of obtaining SPR when fishing mortality rates are known, which is likely not the case in data-poor situations. However, it is possible to obtain fishing mortality rates through average length mortality estimators (Ehrhardt & Ault 1992; Gedamke & Hoenig 2006). We plan on testing this approach in the next chapter.

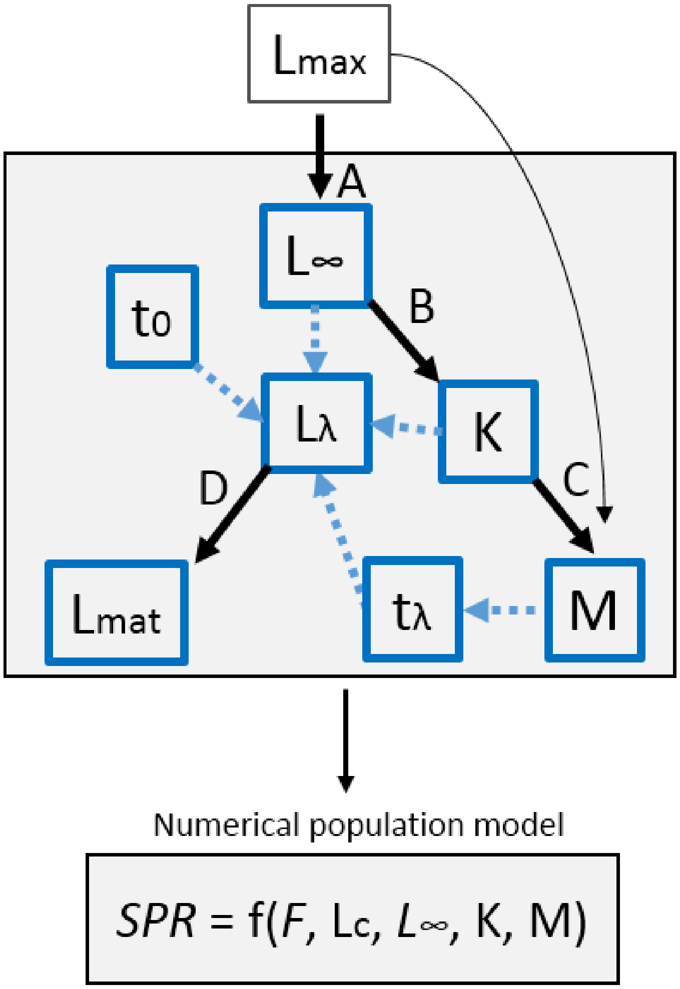

Figure 4.1 – Diagram presenting one iteration of the Monte Carlo simulation chain used to obtain a single spawning potential ratio (SPR) value. Solid black arrows represent steps that are derived using the four modeled relationships. Blue dashed arrows represent deterministic steps where certain values are used to calculate others.

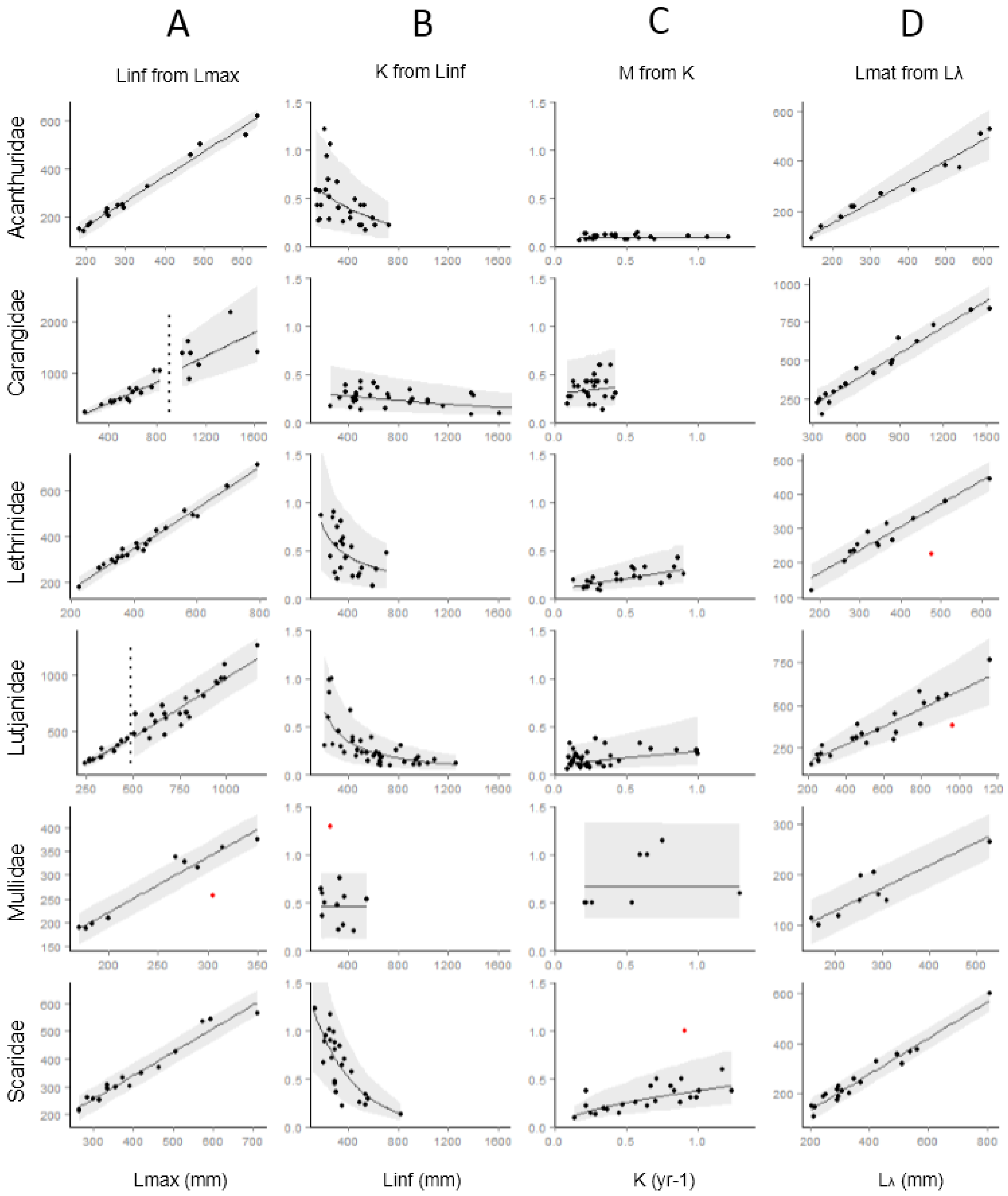

Figure 4.2 – Statistical relationships between life history parameter pairs for 6 families of reef fishes. Gray area is 95% confidence interval; red dots represent removed outliers (see text for justifications).

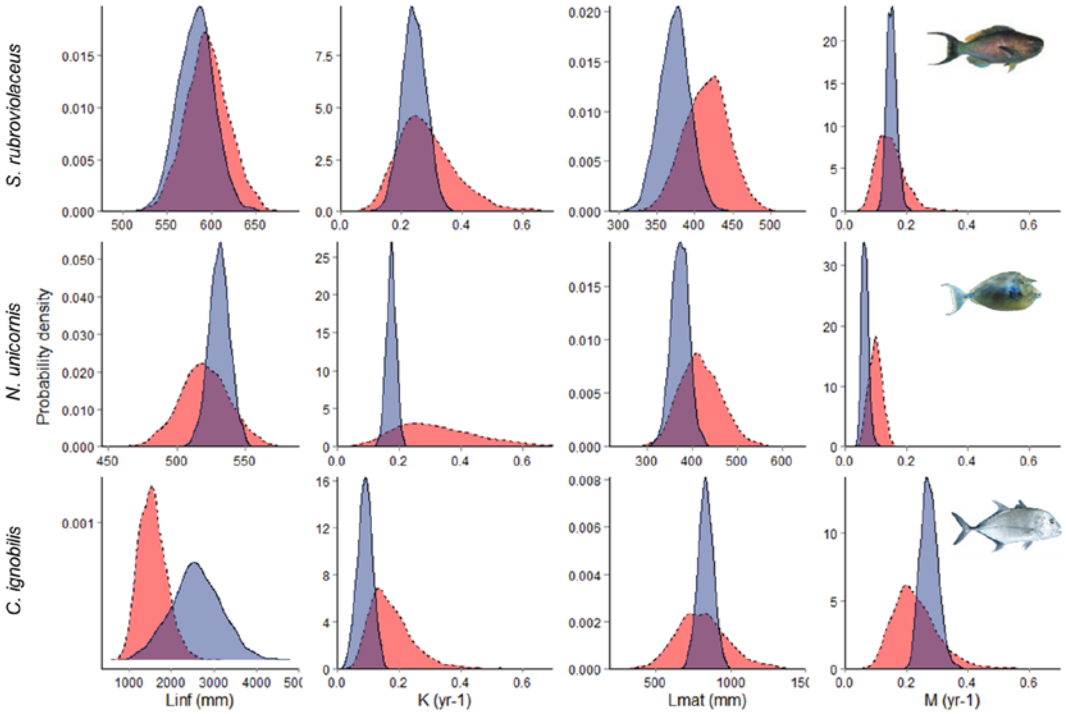

Figure 4.3 – Probability densities of various life history parameters from the data-rich situation (blue area; solid line) and our novel data-poor approach (red area; dashed line).

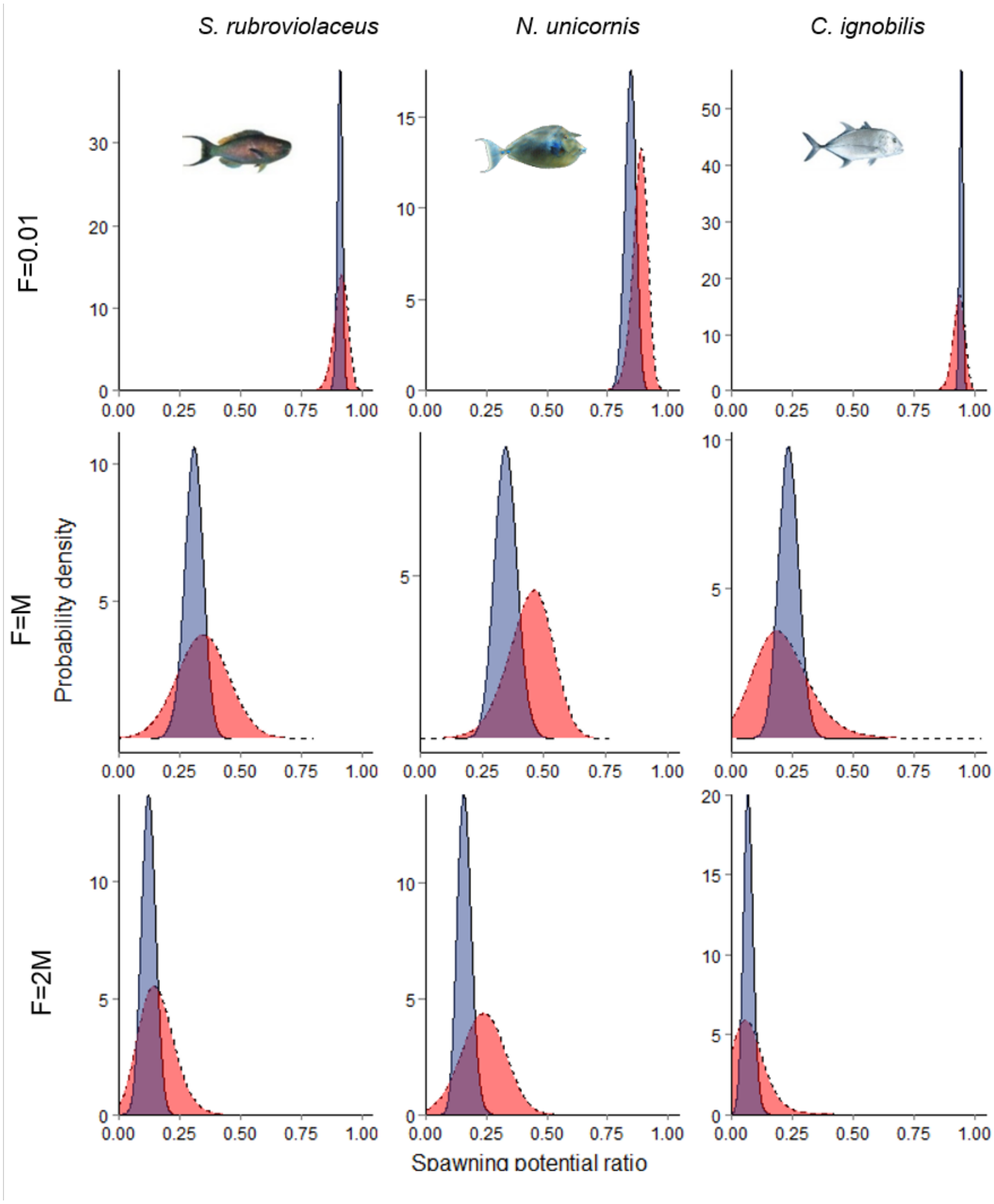

Figure 4.4 – Probability densities of spawning potential ratio for 3 different fisheries mortality rate using life history parameter from the data-rich situation (blue area; solid line) and our novel data-poor approach (red area; dashed line).

Table 4.1 – List of parameters with abbreviations.

Parameter	Definition
L_λ	Average length at the oldest recorded age
L_{mat}	Length at which 50% of a cohort reaches maturity
L_{inf}	Average length at infinite age
L_{max}	Maximum recorded length in a local study (i.e., not absolute record)
K	Individual growth rate or rate at which Linf is approached
a_0	Theoretical age at length zero
a_λ	Oldest recorded age
M	Instantaneous natural mortality rate

Table 4.2 – Summary of life history parameter dataset by family. L_{inf}, K, longevity are the ranges of these parameters. See Table 4.1 for parameter definitions.

Family	# of species	Growth studies	Mat. studies	SST < 20°C	Out-liers	Linf	K	a_{λ}	Lmax /Linf	M/k	Lmat /Lλ	Lmat /Linf
Acanthuridae	81	27	11	0	1	142-619	0.2-1.2	20-53	1.1(0.1)	0.3(0.1)	0.79(0.08)	0.79(0.08)
Carangidae	148	40	20	10	0	255-2170	0.1-0.4	5-23	0.9(0.2)	1.6(0.7)	0.63(0.08)	0.55(0.11)
Lethrinidae	38	22	14	0	1	180-712	0.1-0.9	7-36	1.2(0.1)	0.5(0.3)	0.78(0.07)	0.78(0.07)
Lutjanidae	110	39	22	0	1	216-1264	0.1-1.0	8-55	1.1(0.1)	0.8(0.6)	0.67(0.12)	0.64(0.13)
Mullidae	82	12	11	3*	1	187-547	0.2-0.8	3-11*	0.9(0.1)	1.6(0.6)	0.63(0.11)	0.55(0.09)
Scaridae	100	27	19	2	2	116-818	0.1-1.8	5-33	1.2(0.1)	0.5(0.3)	0.69(0.07)	0.68(0.08)
Total	560	167	97	15	6	116-2170	0.1-1.8	3-55	1.1(0.2)	0.8(0.7)	0.70(0.11)	0.66(0.13)

*Kept for growth and L_{mat}, but not longevity estimate

*Including cold water species.

Table 4.3 – Relations and residual probability distributions (N - normal distribution; LN - log-normal distribution; G - gamma distribution) of various life history parameters. Probability distribution for a_0 parameter is the same for all families: triangular(-2,0.5,-0.3).

	A) $L_{inf} \sim L_{max}$	B) $K \sim L_{inf}$	C) $M \sim K + L_{max}$	D) $L_{mat} \sim L_{\lambda}$
Acanthuridae	$E=-38.0+1.015*Lmax$ N(E, 18.1)	$E=0.7752*e^{-0.00165*Linf}$ G(5.465, E/5.465)	$E=0.0977$ N(E, 0.023)	$E=-13.11+0.829*L_{\lambda}$ LN(log E, 0.103)
Carangidae				
<=90cm Lmax	$E=18.7+1.023*Lmax$ LN(log E, 0.130)	$E=0.332*e^{-0.00046*Linf}$ LN(log E, 0.359)	$E=9.654*K^{0.0303}*Lmax^{-0.5151}$ LN(E, 0.307)	$E=36.6+0.570*L_{\lambda}$ N(E, 44.0)
>90cm	$E=-26.3+1.136*Lmax$ LN(log E, 0.205)	“	“	“
Lethrinidae	$E=-6.14+0.882*Lmax$ N(E, 17.1)	$E=36.25*Linf^{-0.735}$ G(5.583, E/5.583)	$E=2.677*K^{0.5123}*Lmax^{-0.3622}$ LN(log E, 0.298)	$E=35.5+0.673*L_{\lambda}$ N(E, 21.2)
Lutjanidae				
<=50cm Lmax	$E=-9.17+0.924*Lmax$ N(E, 21.1)	$E=143*Linf^{-1.0038}$ G(6.393, E/6.393)	$E=7.715*K^{-0.00928}*Lmax^{-0.6316}$ LN(log E, 0.392)	$E=62.2+0.522*L_{\lambda}$ LN(log E, 0.148)
>50cm	$E=-78.3+1.052*Lmax$ N(E, 91.0)	“	“	“
Mullidae	$E=-10.27+1.162*Lmax$ N(E, 16.7)	$E=0.468$ N(E, 0.173)	$E=0.674$ LN(log E, 0.348)	$E=39.3+0.447*L_{\lambda}$ N(E, 22.3)
Scaridae	$E=0.885+0.848*Lmax$ N(E, 23.2)	$E=1.799*e^{-0.00311*Linf}$ G(9.607, E/9.607)	$E=2.064*K^{0.5364}*Lmax^{-0.2989}$ LN(log E, 0.248)	$E=-12.7+0.725*L_{\lambda}$ N(E, 22.5)

Lmax: Maximum length in local dataset

Table 4.4 – Family and overall r^2 values for the linear models relating length-at-maturity (L_{mat}) as a function of either asymptotic length (L_{inf}) or expected length at oldest measured age (L_{λ}).

Family	$L_{mat} \sim L_{inf}$	$L_{mat} \sim L_{\lambda}$
Acanthuridae	0.95	0.95
Carangidae	0.85	0.95
Lethrinidae	0.93	0.93
Lutjanidae	0.79	0.77
Mullidae	0.77	0.84
Scaridae	0.94	0.96
All	0.83	0.91

Chapter 5

Assessment of Hawaiian coral reef fish populations using life history parameters obtained through a Monte Carlo simulation approach

Summary

Coastal fisheries in tropical areas usually target dozens, sometimes hundreds, of species and are typically managed with limited resources. Some recent approaches to stock assessment seek to tackle the problem of data-poor stocks by relying on easily obtainable length data. However, these methods require information on key life history parameter (growth, natural mortality, and maturity) which is missing for the majority of exploited tropical species. An accompanying study presented a new approach to obtain life history parameters by using information on maximum length, taxonomic group, and the relationships between these key parameters to obtain probability distributions for these parameters for un-studied species. Here, we continue this effort by presenting the complete process by which it is possible to conduct stock assessment on these data-poor species. We use this approach, combined with length data obtained through commercial and diver surveys, to calculated probability distribution of spawning potential ratios (a key sustainability metric) for 8 species of coral reef fishes in Hawaii. Of the 8 species assessed, half had 30% or more of SPR iterations below the 0.3 overfishing threshold, which we defined as overfished. The longer-lived species (surgeonfish and snappers) were typically overfished compared to shorter-lived ones (goatfishes and jacks). In addition, we compared the results obtained through this approach with the assessment conducted in chapter 3. We obtained good agreement between the data-poor and regular approach using published parameters. We demonstrate the implementation of a new data-

poor approach to stock assessment that will greatly help the management of tropical demersal fisheries.

Background

Tropical coastal fisheries are generally difficult to assess given that they typically involve hundreds of species, are of limited commercial importance, and therefore are usually managed with limited, thinly-spread resources (Pauly et al. 2002; Fenner 2012). For this reason, assessment efforts are typically limited to data-poor approaches, such as those based on size structure information (Ault et al. 1998, 2008; see Chapter 3). Although length data are often readily available, life history parameters such as growth and natural mortality rates are absent for a majority of coral reef fish species, as well species from other biomes (Froese & Binohlan 2000). For example, of the top 130 species caught by spearfishing around Guam, the Mariana Islands, and American Samoa, there exists basic life history information for less than a quarter of these species. This number is much lower if we only take into account local growth studies, which are generally preferable (Gust et al. 2002; Taylor & Choat 2014).

To address this critical issue, an accompanying study (chapter 4) presented a novel way of obtaining estimates of four key life history parameters (L_{inf}, K, L_{mat}, M) by using a stepwise Monte Carlo simulation approach. This approach is based on a meta-analysis of published life history studies and uses taxonomic group, maximum length, and basic relationships between life history parameters to generate multivariate probability distributions of these parameters for un-studied species. Chapter 4 showed that the life history parameter probability distributions obtained this way were comparable to the ones obtained from single growth studies, although with a lower level of precision, as would be expected. The study also showed that it is possible to generate spawning potential ratio distributions that are reasonably comparable to those obtained with life history parameters from single studies.

Chapter 4 was focused on presenting and testing this new approach to obtain life history parameters by comparing the LH parameter distributions obtained this way with those obtained directly from growth studies. For this reason, we fixed instantaneous fishing mortality rates (F) to specific values when calculating SPRs. In the current study, we complete the approach presented in that study by using a length-based mortality model (Ehrhardt & Ault 1992) to obtain F values, before combing these with other life history parameters in a numerical population model in order to obtain SPRs. We selected 8 species of targeted reef fishes in Hawaii for which we had size structure data but no growth information to implement the full data-poor assessment approach. We also ran these analyses for 17 species analyzed in chapter 3 in order to test the validity of our approach. We used length data obtained from commercial and underwater survey datasets to calculate average lengths in the exploited phase and uses the life history information obtain through the data-poor approach to first obtain F values and then SPR values.

Methods

Study area

The Hawaiian Archipelago extends for 2600 km along a SE-NW axis from 19°N, 155°W to 28°N, 178°W (Fig. 5.1). The archipelago, consisting of 18 islands and atolls, is typically divided into two broad regions: (1) the inhabited main Hawaiian Islands (MHI);

and, (2) the sparsely inhabited Northwestern Hawaiian Islands (NWHI). The MHI is composed of 8 geologically young, high (4,205 m maximum elevation) volcanic islands that are densely human-populated (1.39 million persons; dbedt.hawaii.gov/census). In contrast, the NWHI are relatively low-lying (275 m max. elevation) and sparsely inhabited by a few dozen government workers (Table 5.1). Over the past century, the fishing fleet operating in the NWHI has remained relatively small at less than 12 vessels that were mainly focused on deepwater snappers and lobsters (Kittinger et al. 2011). In 2006, the NWHI and surrounding marine environment were protected under the co-management of several agencies of the U.S. federal government and the State of Hawaii.

Data sources

Application of the average length mortality estimator and analyses of fishery sustainability using the numerical population model (both described below) required length composition data as well as some basic life history parameters for the 8 selected species of Hawaiian coral reef fishes.

Length frequency composition data were obtained from two sources: (1) underwater diver-based visual surveys; and, (2) commercial fishery trip reports. Between 2007 and 2013, a team of highly trained divers from the NOAA Pacific Island Fisheries Science Center (PIFSC) conducted 770 and 764 visual samples throughout the MHI and NWHI, respectively. Survey sites around each island or atoll were randomly selected within 9 strata defined by combinations of 3 reef zone habitats (i.e., forereef, backreef, and lagoon) and 3 depths (shallow: 0-6 m, mid: 6-18 m, and deep: 18-30 m). At each sample site, independent stationary point counts were conducted by two paired divers inside contiguous 15 m diameter cylinders that extended from the bottom to the surface

(Brandt et al. 2009; Smith et al. 2011; Williams et al. 2011). A diver first recorded a list of fish species observed during an initial 5 minute period. The diver then worked through this list, species by species, recording counts and estimated sizes of all fish seen within the cylinder. Fish sizes were recorded as total lengths to the nearest cm. Before participating in the surveys, divers were extensively trained in size estimation using fish cut-outs of various sizes.

Commercial fisheries data from 2003 to 2012 were obtained from trip reports submitted by fishers to the Hawaii Division of Aquatic Resources (DAR). Trip records were utilized from the 4 main fisheries gears used in inshore areas (hook-and-line, spearfishing, various nets, and traps). Because lengths were not directly reported, the catches in weight were divided by the number of fish caught to obtain average weights per species per individual trip over the total of 47,439 trip records. Average weights were then converted to lengths using published standard allometric weight (W)-length (L) relationships (Appendix, supplemental information),

$$L = \left(\frac{W}{\alpha}\right)^{\left(\frac{1}{\beta}\right)} \quad , \tag{4}$$

where α and β are model parameters. Catch records for certain taxa that were not identified to the species level were not included in our analyses (e.g., parrotfishes and the "kala" group of surgeonfishes composed of *Naso unicornis*, *N. annulatus*, and *N. brevirostris*). The resulting average length observations for each trip were checked to ensure that no lengths were greater than the maximum reported for each species.

Life history parameters were available for 17 species analyzed originally in chapter 3. We obtained probability distributions for life history parameters using a novel approach which uses stepwise Monte Carlo simulations described in greater detail in an accompanying chapter (Fig. 5.2; Chapter 4). For the 17 species analyzed in chapter 3, we compared the probability distribution of these parameters with published values. A summary of this approach is described further in this section.

Length-based mortality model

The principal stock assessment indicator variable used to quantify the population status for the community of Hawaiian reef fishes was average length ($\overline{L}$) of the exploited phase of the population. For exploited species, $\overline{L}$ directly reflects the rate of instantaneous fishing mortality F through alteration of the population size structure (Beverton & Holt 1957; Ehrhardt & Ault 1992). As F increases, the probability of a fish reaching larger sizes decreases, and thus the mean of the exploited size frequency distribution $\overline{L}$ decreases accordingly. Theoretically, the average length $\overline{L}$ is generally expressed as

$$\overline{L} = \frac{F\int_{a_c}^{a_\lambda} N_a L_a da}{F\int_{a_c}^{a_\lambda} N_a da} \quad , \qquad (1)$$

where the exploitable phase is integrated from a_c (age at first capture) to a_λ (oldest age in the stock), N_a is the abundance of age class a, L_a is the expected length at age a, and F_t is the instantaneous fishing mortality rate at time t.

A formula for estimating mortality rates using estimates of $\overline{L}$ was derived from Eq. (1) by Ehrhardt and Ault (1992). The first step in this derivation was to substitute L_a in Eq. (1) with the von Bertalanffy growth function and N_a with the exponential mortality model

$$N_{(a+\Delta a)} = N_a e^{-Z\Delta a} \quad , \qquad (2)$$

where Z is the total instantaneous mortality rate and Δa is the age interval, normally one year. Step two was to integrate and algebraically solve for Z,

$$\left(\frac{L_\infty - L_\lambda}{L_\infty - L_c}\right)^{Z/K} = \frac{Z\left(L_c - \bar{L}\right) + K\left(L_\infty - \bar{L}\right)}{Z\left(L_\lambda - \bar{L}\right) + K\left(L_\infty - \bar{L}\right)} \quad , \qquad (3)$$

where K and L_∞ are parameters of the von Bertalanffy growth equation, and L_c and L_λ are the sizes at first capture and oldest age, respectively.

Mean lengths were evaluated for the exploited size range $L \geq L_c$. Size at first capture L_c was set as the minimum length at full exploitation based on examination of fishery-dependent data for principal gears targeting Hawaiian reef fishes (hook-and-line, spearfishing, and fish traps). To do so, we looked for clear discontinuous breaks in the size structure histograms for the commercial dataset (see Chapter 3). Species-specific average lengths were estimated for two broad geographical regions, the MHI and the unexploited Northwestern Hawaiian Islands (Fig. 5.1). To account for differences in size structures due to uneven sampling effort and/or uneven fishing pressure (inferred from humans per reef area values - Table 5.1) within the MHI region, $\bar{L}$ was estimated from average lengths for four subregions weighted by the respective shallow reef areas (depth <18m; Table 5.1). For two species not commonly found in the NWHI region, *Scarus rubroviolaceus*, length observations were imported from two other pristine areas (Wake and Johnston atolls) to make the unexploited state calculations.

Estimates of total instantaneous mortality rates Z were computed from Eq. (3) using a numerical procedure (Ault et al., 1996). Values of L_λ, mean length at maximum age a_λ, were estimated from the von Bertalanffy growth function using an observed maximum age. Natural mortality rate M was estimated from lifespan applying the procedure of Alagaraja (1984) similar to (Hoenig 1983) assuming that 5% of a cohort survives to the observed maximum age:

$$M = \frac{-\ln(0.05)}{a_{\lambda}} \quad , \tag{4}$$

We selected the 5% value based on the analyses in chapter 2. Fishing mortality F was obtained by subtracting M from Z. Fishing mortality was obtained from F=Z-M, where M is the instantaneous natural mortality rate.

Numerical population model and fishery sustainability analyses

Sustainability analyses involved comparison of various population metrics at current levels of fishing mortality relative to standard fishery management sustainability benchmarks (2008). Reference points of sustainability risks, including spawning potential ratio (SPR) and fishery yields, were computed using a length conditional on age structured numerical model (following Ault et al. 1998) to simulate exploited fish populations; the computation were based on the mortality rates derived from $\overline{L}$ estimates, as described in the previous section. Numerical abundance at age *a* was estimated through use of an exponential mortality function (Eq. 2). Length at age was estimated from the von Bertalanffy growth equation, and converted to weight-at-age using the allometric weight-length relationship (Eq. 4).

The numerical model was used to obtain a measure of stock reproductive potential, spawning stock biomass (SSB), at a given level of fishing mortality by summing over individuals in the population between the age of sexual maturity (a_m; age where 50% of individuals are mature, with knife-edge assumption) and oldest age a_{λ},

$$SSB = \sum_{a_m}^{a_\lambda} \overline{N}_a \overline{W}_a \quad , \tag{5}$$

where $\overline{N}_a$ is the average abundance at age a and $\overline{W}_a$ is the mean weight of individuals at age a. Theoretically, a stock's maximum reproductive biomass occurs when there is no fishing. Spawning potential ratio (SPR) is a management benchmark that measures a stock's potential to produce yields on a sustainable basis. It was computed as the ratio of the current SSB relative to that of an unexploited stock

$$SPR = \frac{SSB_{\exp loited}}{SSB_{un\exp loited}} \quad . \tag{6}$$

Estimated SPRs were compared to USA federal standards which define 30% SPR as the threshold below which a stock is no longer sustainable for many species, i.e., is experiencing recruitment overfishing, a standard recommend for less "well-known" stocks (Gabriel et al. 1989; Restrepo et al. 1998; Clark 2002).

Monte Carlo simulation to obtain spawning potential ratio distributions

The Monte Carlo stock assessment approach presented here (Fig. 5.2) consisted of using the step-by-step iterative approach from Chapter 4 to build multivariate probability distributions of the four main LH parameters (L_{inf}, K, M, and L_{mat}) for all 8 new species and 17 previously assessed species selected for this study. In short, the approach consists of using an L_{max} (the maximum recorded length in a local abundance at size dataset) to draw a random L_{inf} from the $L_{inf} \sim L_{max}$ model (step A in Fig. 5.2). From this random L_{inf}, a K value was drawn from the $K \sim L_{inf}$ model (step B) which was then used to draw a random M from the $M \sim K + L_{max}$ model (step C). Finally, we used the random L_λ to draw a random L_{mat} (step D). L_λ was calculated using the von Bertalanffy equation and the L_{inf}, K, and longevity parameters from the same iteration (longevity being derived back from M using eq. 1). We compared the distributions of life history parameters obtained this way with the published parameters for the species analyzed in chapter 3.

At every iteration, a random average length ($\overline{L}$) was picked from the normal error probability distribution associated with the size structure data ($\overline{L}$ and standard deviation of $\overline{L}$) and used to obtain a total mortality rates (Z) and fishing mortality rates (F=Z-M; where M is a random value previously drawn). A spawning potential ratio was computed at each iteration using the numerical population model described above. Length-weight relationship parameters (α, β) necessary for SPR calculations were taken directly from the literature (Kulbicki et al. 2005).

This entire process (fig. 5.2) was repeated for 5000 iterations in order to build a multivariate distribution for all 4 life history parameters and posterior distributions of SPRs for the 17 species from chapter 3, as well as the 8 new species analyzed in the current chapter. For both sets of species, we calculated the percentage of iterations with SPR below the federal limit of 30%. We defined a stock as "overfished" when 30% of SPR iterations fell below SPR=30%.

Results

Size structure data and average length estimates

Length composition data (Table 5.2) were available for 8 species of Hawaiian reef fishes: three goatfishes (Mullidae), two snappers (Lutjanidae), two jacks (Carangidae), and one emperor (Lethrinidae) in addition to the 17 species analyzed in chapter 3. Annual estimates of $\overline{L}$ in the main Hawaiian Islands for the period 2003-2012 (commercial data) did not show any increasing or decreasing trends for 9 species with n>30 observations per year (Fig. 5.3), suggesting that these stocks were mostly at equilibrium (i.e., fishing mortality rates have been fairly constant, an important assumption of the length mortality model). Length observations were subsequently combined across years by data source (commercial, underwater diver surveys) to increase the precision of average length estimates.

Table 5.2 shows average lengths by species and subregion. For most species, there was no clear pattern in average length between the more densely populated subregions (Maui Nui and Oahu) and the less populated ones (Hawaii and Kauai-Niihau) in the MHI region. Two notable exceptions were *Monotaxis grandoculis* and *Scomberoides lysan* which had lower average lengths around the more populated islands of Maui Nui and Oahu. Average lengths for the commercial dataset were generally in agreement with those from our underwater surveys (Table 5.2) with some exceptions, such as *Aphareus furca* and *Monotaxis grandoculis* (longer average lengths in commercial dataset) which may be due to a low number of observations for *A. furca* and likely a bad length-weight conversion parameters for *M. grandoculis*. For each species, we selected the data source with the most length observations for subsequent analyses.

The average lengths of species in the pristine NWHI were either larger (4 species) or similar (3 species) relative to the inhabited MHI (Table 5.2).

Life history parameters and spawning potential ratio

Of the 4 primary life history parameters obtained using the data-poor Monte Carlo simulation approach (chapter 4), L_{inf} had the narrowest probability distributions (Fig. 5.4 and 5.5). The jacks had higher uncertainty associated with their L_{inf} estimates (Fig. 5.4. and 5.5), but this was expected given the higher uncertainty in the $L_{inf} \sim L_{max}$ relationship for this family (see chapter 4). The probability distributions for the growth parameter K were fairly wide, especially for the goatfish species, the surgeonfish *Naso lituratus*, and two small parrotfish species. The K distribution were narrower for the parrotfish *S. rubroviolaceus* and the jacks (Fig. 5.4 and 5.5). This, again, related to the precision of the $K \sim L_{inf}$ relationship established for these families (chapter 4). In the goatfish case, there was no clear $K \sim L_{inf}$ relationship, and K for this family is simply estimated from the mean value with normally distributed error. In contrast, the snapper and parrotfish families had a fairly clear $K \sim L_{inf}$ relationship with decreasing K variability at higher L_{inf} values (chapter 4). This is the reason for the lower uncertainty for the large snapper *Aphareus furca* (L_{max} = 55 cm) vs. the smaller snapper *Lutjanus fulvus* (L_{max} = 40 cm).

The jack species had the highest variability in L_{mat} which was linked to the high variability in their L_{inf} estimates (i.e., an iteration with a high L_{inf} random draw will lead to a high L_{mat} draw and vice-versa; Fig. 5.4 and 5.5). The snapper species also had relatively variable L_{mat} estimates, but these were linked to a less informative $L_{mat} \sim L_{\lambda}$ relationship then for other families (chapter 4). The parrotfish *S. rubroviolaceus*, the 3 goatfishes, and the emperor *Monotaxis grandoculis* had relatively precise L_{mat} estimates compared to the other families (Fig. 5.5). Finally, variability in natural mortality rate (M) estimates was highest for the goatfishes and lowest for the surgeonfishes. Interestingly, chapter 4 showed no clear relationship between K and M for these two families. However, their estimates of longevity (from which M is directly derived) were fairly constrained compared to the other families, with goatfish living between 3 and 11 years and surgeonfishes between 20 and 53 years. It is interesting to note that the narrow longevity range for goatfishes translates into a wide range of M values and vice-versa for the wider longevity range of the surgeonfishes. This is due to the highly non-linear relationship between longevity and M (eq. 4). M estimates were relatively precise for the parrotfish *S. rubroviolaceus*, the emperor *Monotaxis grandoculis*, and the two snapper species (Fig. 5.5).

The 17 species analyzed in chapter 3 had published growth information (see red bars in Fig. 5.4). Although this was not the focus of the current paper (see chapter 4), it is worth pointing out the similarities and differences between the publish parameters and those obtained from our data-poor approach. All in all, the data-poor approach performed remarkably accurately for these species with a few exceptions. For example, the published L_{inf} value for *Caranx ignobilis* was 2170 mm, but the median value from our data-poor approach was only 1100 mm. This is probably related to the highly indeterminate growth curve for this species, where L_{inf} becomes a fitting parameter un-related to average maximum size. For two species with high published K values (*Mulloidichthys vanicolensis* and *Scarus psittacus*), the data-poor approach provided low K estimates. The data-poor estimates for L_{mat} where overall fairly close to the published values (Fig. 5.4), as were the M values, with no noticeable bias.

The spawning potential ratio distributions obtained through the data-poor approach showed a clear patterns where distribution with low median SPR values (e.g., *Aphareus furca, Lutjanus fulvus*) had less variability than the distributions with higher SPR medians (e.g., *Parupeneus insularis, Mulloidichthys pfluegeri*, and *Carangoides orthogrammus*). The two snapper species and the emperor *M. grandoculis* were the stocks with the lowest SPR estimates (99% and 91% of iterations below SPR=0.3, respectively). The goatfish *Parupeneus cyclostomus* also had a significant number of SPR iterations below the 0.30 standard (39% and 75%, respectively). Two goatfish species (*M. pfluegeri* and *Parupeneus insularis*), and the jack *Carangoides orthogrammus* had a relatively high proportion of their SPR iterations above 0.3 (>80% above this standard in all cases). The results for *S. lysan* were the least clear, but 36% of iterations were below the 0.3 standard. For the 17 species analyzed in chapter 3, the data-poor approach correctly predicted 9 out of 9 overfished stocks as overfished and 4 out of 8 non-overfished stocks as non-overfished (Table 5.3). The data-poor approach mis-classified 4 stocks as overfished when the results in chapter 3 showed them to be non-overfished. No stocks classified as overfished in chapter 3 were mis-classified as non-overfished using the data-poor approach (Table 5.3). There thus seems to be a slight conservative bias in the data-poor approach.

Discussion

In chapter 3, I used length data combined with published life history parameters to assess 19 exploited coral reef fishes around the main Hawaii Islands. At the time, I could not conduct further assessments due to a lack of published life history information for other species with sufficient length data. This is a commonly encountered problem when trying to assess coral reef fishes and other poorly studied species. Chapter 4 proposed a solution to this limitation by presenting a novel way of obtaining complete probability distributions for all core life history parameters (L_{inf}, K, L_{mat}, and M) in these data-poor situations. The approach uses maximum size (L_{max}) as an informative starting point to obtain the rest of the life history parameters by using family-specific relationships between LH parameters and calculating spawning potential ratio for various known fishing mortality rates. The present study successfully pushed this idea further by integrating a length-based mortality model (Ehrhardt & Ault 1992) to obtain fishing mortality rate and conduct complete assessments for 8 Hawaii reef fish species with no life history information, as well as testing this approach on 17 species from chapter 3 with published LH parameters.

The final output of our procedure is a probability distribution of spawning potential ratios (SPR). It is thus necessary to define what proportion of iterations falling below SPR=30% (a standard limit use in the U.S. for less well-known stocks; Restrepo et al. 1998) will classify a stock as "overfished" and this can vary between management entities according to how much risk they deem is acceptable. For the sake of the current discussion, we defined a stock as overfished when 30% of iterations fall below SPR=30%. According to this definition, half of the stocks in our study are overfished (the snappers *Aphareus furca* and *Lutjanus fulvus*, the emperor *Monotaxis grandoculis*, the surgeonfish *Naso lituratus*, and the parrotfish *Scarus rubroviolaceus*) and the other half are not (the jacks *Carangoides orthogrammus* and *Scomberoides lysan*, and three goatfish species). This pattern falls relatively well into line with those observed in chapter 3, where the relatively short-lived goatfish and jack species were, for the most part, not overfished versus the longer-lived surgeonfishes and snappers.

Furthermore, for the 17 species for which we had actual life history parameters, our data-poor approach arrived mostly at the same conclusion as in chapter 3, with 13 stocks status classified accurately and 4 mis-classified as “over-fished” when the results in chapter 3 suggested otherwise. Two of these stocks were likely mis-classified due to low measured longevity estimates compared to expected longevity based on the data-poor approach. *Caranx melampygus* has an observed maximum age of 7 years vs. a median of 12 years in the data-poor results. Similarly, *Lutjanus kasmira* had a maximum age of 8 years vs. 18 years. For both of these species, this represented a potential underestimation of natural mortality rate which resulted in these stocks being classified as overfished. Another species, *Naso brevirostris* was likely mis-classified as non-overfished in chapter 3 due to an inappropriate growth curve where Linf was only 33 cm (this species as been observed to 60 cm in our diver dataset). The data-poor approach gave a likely more realistic L_{inf} of 42 cm and its classification of this stock as overfished is probably correct.

This study’s conclusions regarding the state of Hawaiian reef fish populations depends on a few important assumptions. The first is that the coral reef fish stocks analyzed in the current study are mostly at equilibrium (i.e., that fishing mortality rates have been fairly constant over the last decade or so). If fishing mortality, recruitment, and natural mortality are constant and stocks are near equilibrium, the average lengths should be stable from year to year. This was apparent for nine species in the commercial dataset which had sufficient observations to separate the data by year, suggesting that these species were near equilibrium. A second assumption is that our size structure data are representative of the true population size structure around the MHI. Chapter 3 had a more in-depth discussion of the underwater visual census data vs. the commercial data and I do not wish to simply repeat this discussion here. However, it is worth noting that, for the most part, these two datasets provided relatively similar average length values. The main exception was *Monotaxis grandoculis* (emperor family) were the commercial length data gave a much higher average length than the diver datasets (433 mm vs 333 mm), despite both datasets having a decent number of observations. The most likely explanation for this disparity is that the length-weight relationship parameters used to convert weights to lengths in the commercial dataset may not have been appropriate for Hawaii (i.e., it was taken from New Caledonia lagoon in Kulbicki et al. 2005). Although chapter 3 reported a slight tendency for commercial average lengths to be higher than diver data, this is the only example we found with such a clear disparity in average length between both datasets. This example does underline the need for caution when using this type of dataset when seeking size structure data.

Finally, this study added 8 species to the list of 19 already assessed coral reef fish stocks in Hawaii from chapter 3. Of the top 50 exploited reef fish populations in Hawaii (by numerical catch in the commercial dataset), 27 species have thus been assessed and another 6 species could potentially be assessed (i.e., some life history and length data exists). Seven of the remaining species cannot be assessed at the moment since they lack life history information and belong to rare or poorly-studied families (i.e., kyphosids) which precludes the use of the approach presented in chapter 4. The remaining 10 species on this list are small, fast growing species such as wrasses and surgeonfishes which are hard to assess using length-based methods due to a lack of size differentiation with age (e.g., the small surgeonfish *Acanthurus olivaceus* reaches 90% of its maximum length in just 2 years and remains close to this size for up to 33 years). For these remaining species, a different approach, probably based on abundance indexes, will be necessary (e.g., tracking CPUE trends inside and outside protected areas; Wilson et al. 2010).

Conclusions

The complete stepwise Monte Carlo approach presented in this study provides sufficiently precise and accurate estimates of life history parameters to conduct preliminary assessments of stocks in extremely data poor situations typical of coral reef fisheries where only size structure information is available. It is important to note that we see this approach as a stop-gap measure and not as a replacement for conducting more life history studies given that assessments using actual LH parameters have greater precision and accuracy. The probability distributions generated by this approach can also be used as prior information in Bayesian analyses.

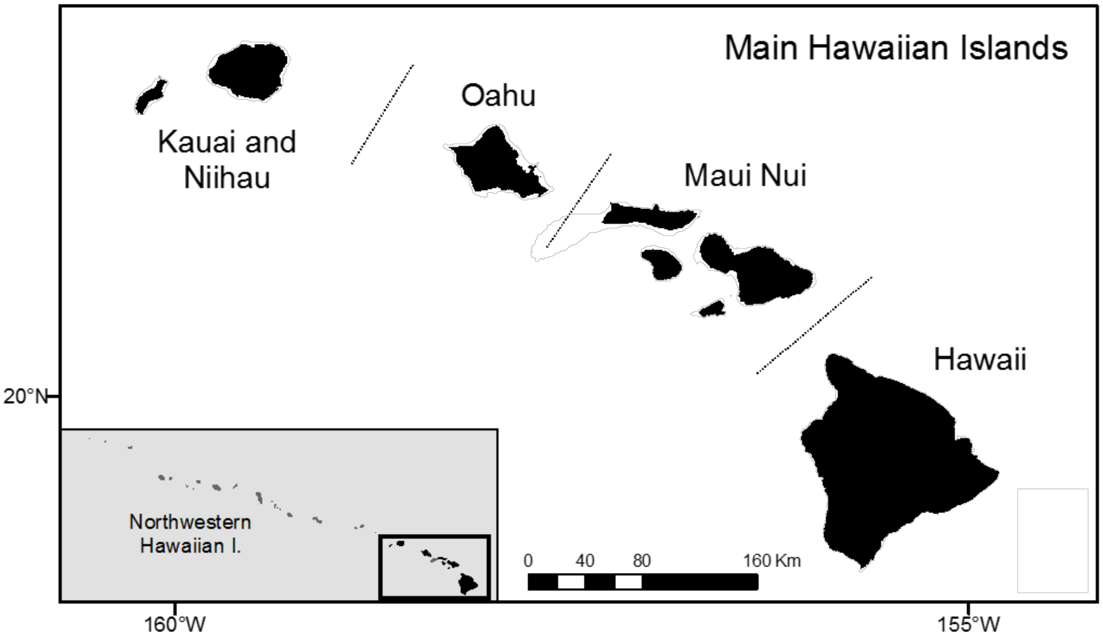

Figure 5.1 – Map of the Hawaiian Archipelago showing the four subregions of the main Hawaiian Islands used in the analyses (inset shows the two regions of the Hawaiian archipelago).

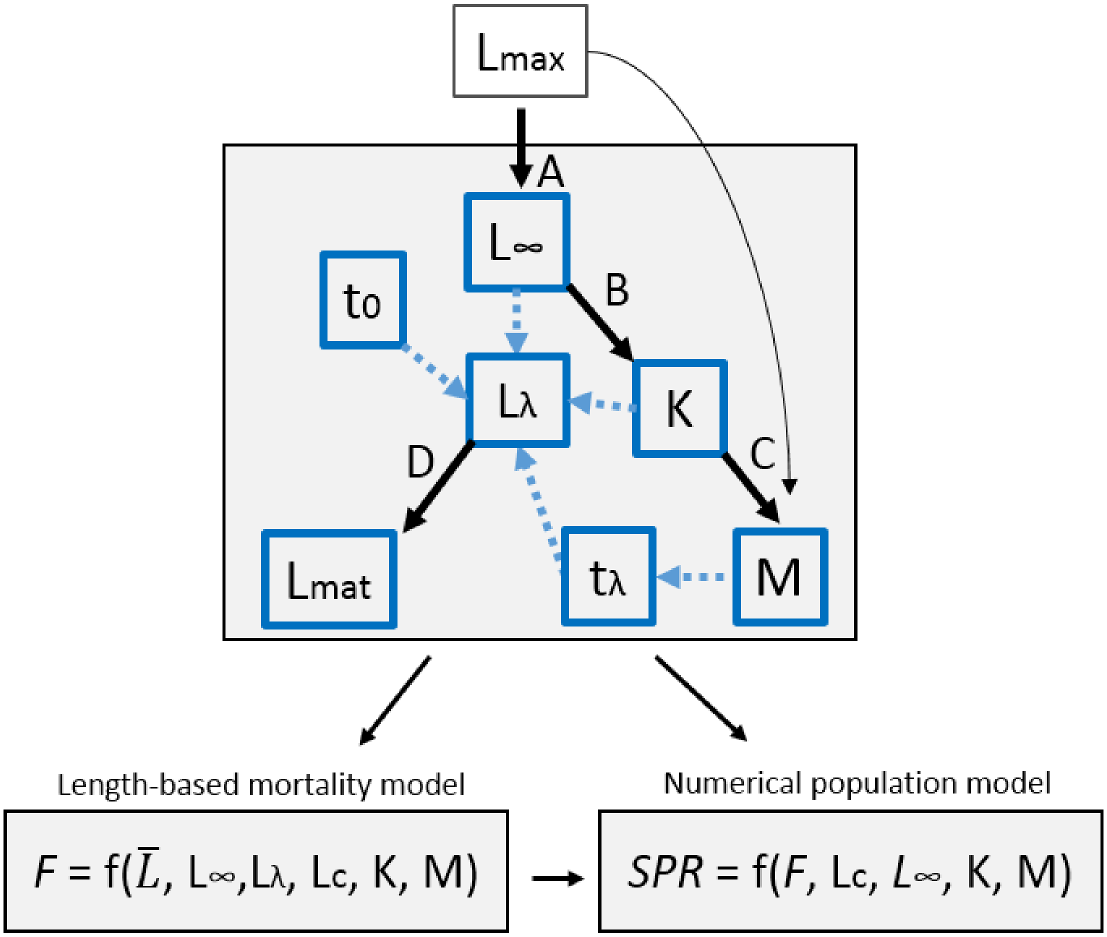

Figure 5.2 - Monte Carlo simulation chain used to obtain a single spawning potential ratio (SPR) value.

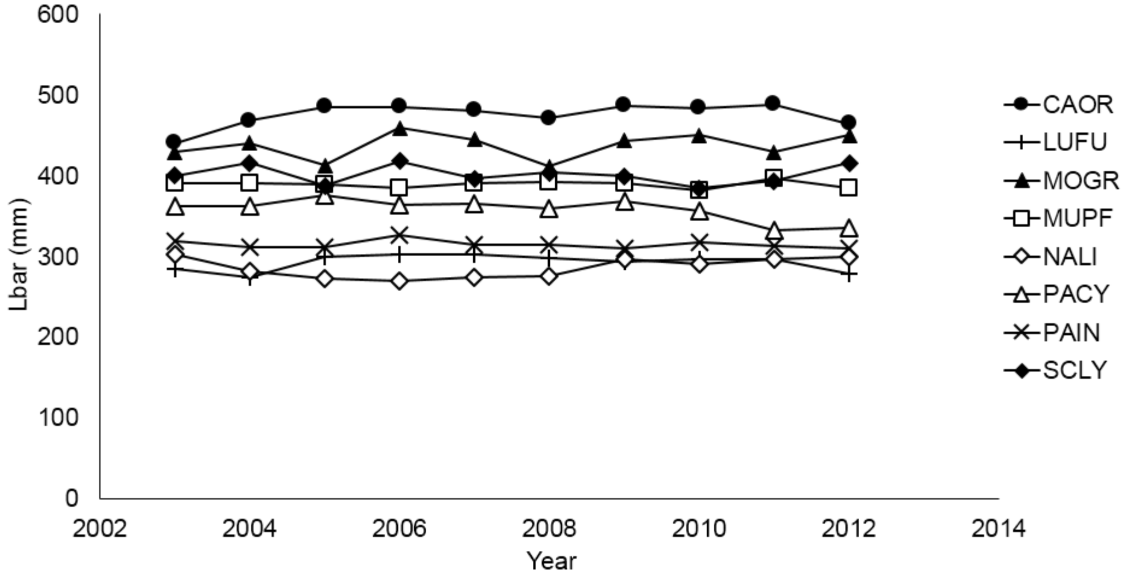

Figure 5.3 – Average lengths for 9 Hawaiian reef fish species in the MHI with marginally sufficient length observations (n>30 for every year) for an analysis of temporal trends from 2003 to 2012. Data from commercial fishery. Species codes in Table 5.2.

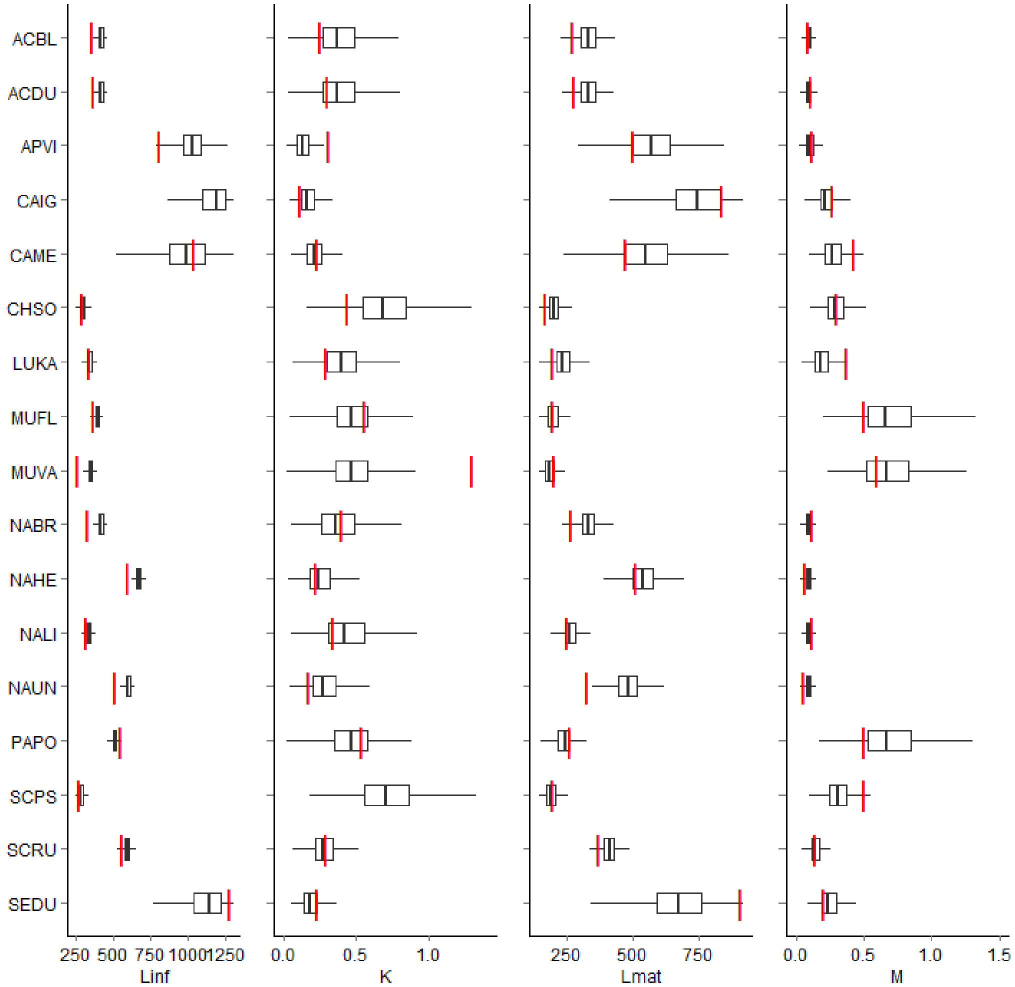

Figure 5.4 - Distribution of life history parameters obtained through the Monte Carlo simulation approach for 17 species of reef fishes previously assessed. Red vertical bars represent published parameter values. Vertical bars represent the median, the boxes represent the 25th and 75th percentile, and the horizontal bars represent the 95% confidence interval. Species codes in Table 3.2.

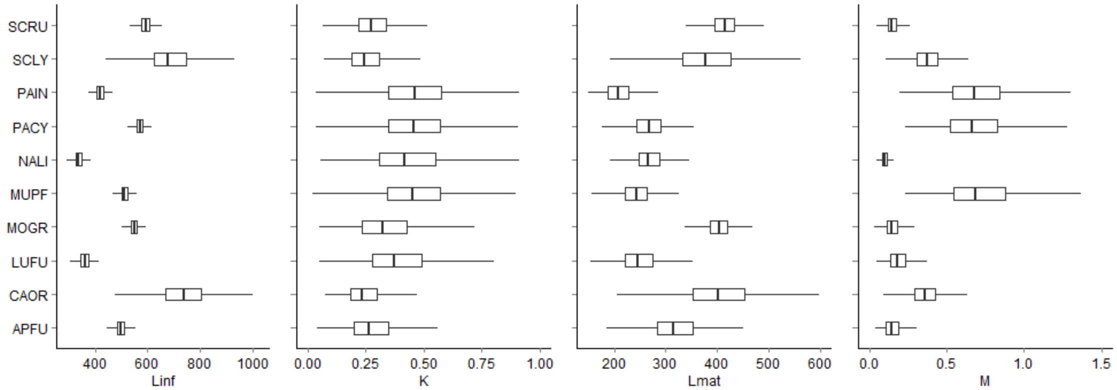

Figure 5.5 – Distribution of life history parameters obtained through the Monte Carlo simulation approach. Vertical bars represent the median, the boxes represent the 25th and 75th percentile, and the horizontal bars represent the 95% confidence interval. Species codes in Table 5.2.

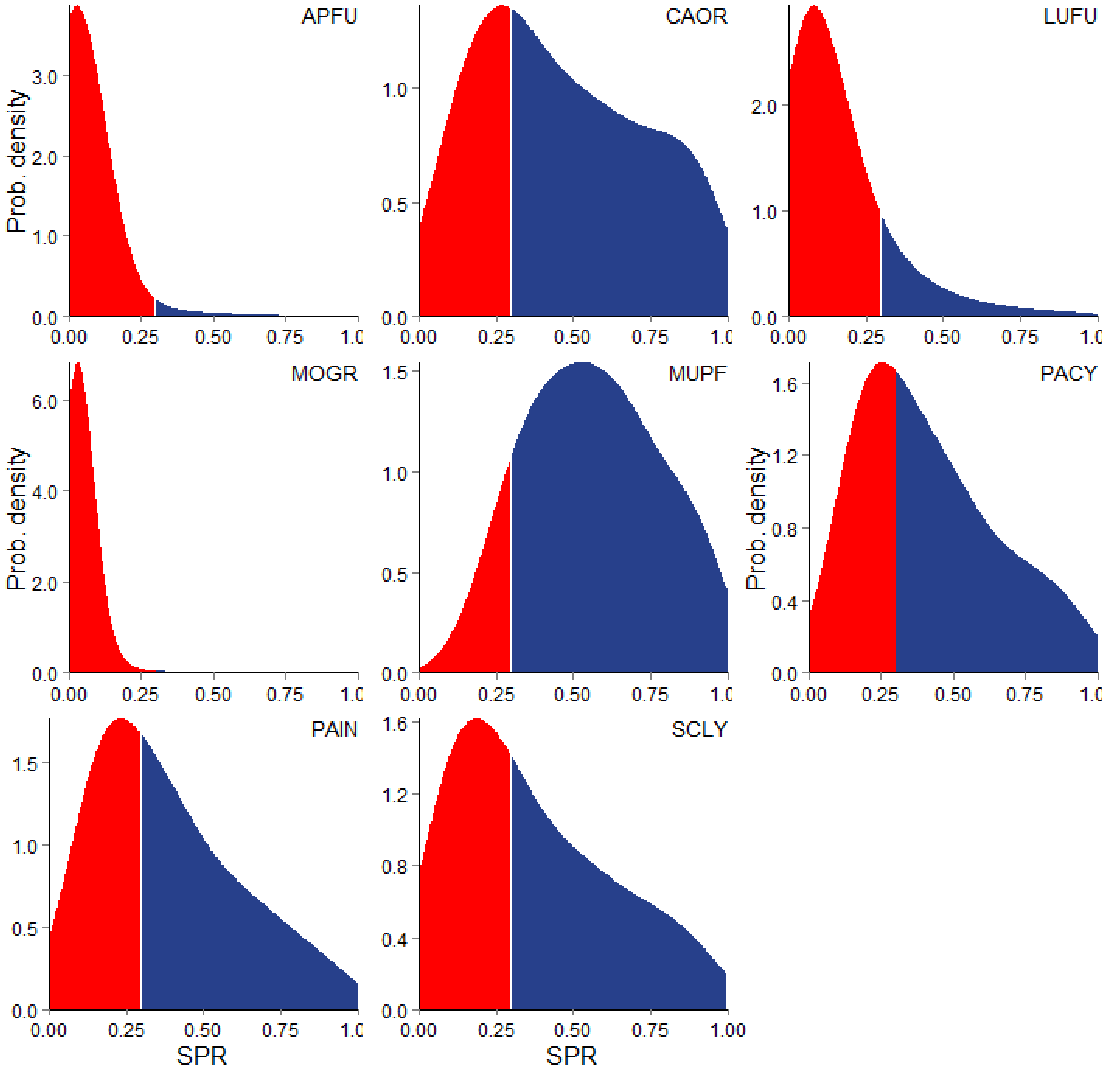

Figure 5.6 – Probability distribution of spawning potential ratios obtained through the Monte Carlo simulation approach. Red color indicate iteration below SPR=0.3, blue color indicate iteration above 0.3. Species codes in Table 5.2.

Table 5.1 – Information summary on the two main regions the Hawaiian Islands, including the four main Hawaiian Islands subregions.

Zone	Human pop.	Reef area (km^2)	Prop. of total reef in region	Pop. per reef area (# km^{-2})	Channel width [a] (km)
Main Hawaiian I.					
Hawaii	185,079	194	0.16	954	48
Maui Nui	154,950	373	0.31	415	48-42
Oahu	953,000	375	0.31	2541	42-116
Kauai-Niihau	65,819	266	0.22	247	116-220
Northwest. Hawaiian I.	~100	1,595	-	~ 0	220

[a] Minimum distance between emergent land in different zones, ordered from SE to NW

Table 5.2 – Average size ($\bar{L}$) and standard errors (TL mm) by region for 8 exploited reef fishes in the main Hawaiian Islands (MHI), as well as in the Northwestern Hawaiian Islands (NWHI). Only $\bar{L}$ with a minimum of 10 observations are presented.

Species	Code	Lc	Lmax	Data[a]	Hawaii		Maui Nui		Oahu		Kauai - Niihau		MHI		NWHI	
					n	$\bar{L}$	n	$\bar{L}$	n	$\bar{L}$	n	$\bar{L}$	n	$\bar{L}$	n	$\bar{L}$
				COM	233	289(2)	297	289(2)	210	291(3)	-	-	740	290(2)	-	-
Mulloidichthys pfluegeri - G	MUPF	330	450	COM	277	366(2)	427	398(1)	698	383(1)	382	395(1)	1784	388(1)	-	-
Parupeneus cyclostomus - G	PACY	260	500	UVS	34	313(9)	46	322(6)	-	-	36	354(12)	116	330(9)	60	344(8)
				COM*	682	353(2)	325	343(3)	907	352(1)	165	353(4)	2079	350(3)	-	-
Parupeneus insularis - G	PAIN	250	370	UVS*	33	279(4)	13	284(7)	-	-	40	286(5)	73	283(5)	13	274(8)
				COM	425	301(1)	67	327(3)	629	312(1)	26	289(6)	1121	316(2)	-	-
Aphareus furca - Sn	APFU	250	550	UVS*	76	290(4)	33	296(7)	-	-	22	320(9)	109	294(6)	57	352(8)
				COM	70	348(5)	14	403(16)	17	279(13)	26	349(13)	70	348(5)	-	-
Lutjanus fulvus – Sn	LUFU	220	400	UVS*	53	265(5)	79	259(4)	-	-	130	264(3)	262	262(4)	-	-
				COM	1118	301(1)	233	285(3)	1768	280(1)	186	298(3)	3305	289(2)	-	-
Carangoides orthogrammus - J	CAOR	310	700	UVS	-	-	-	-	-	-	-	-	-	-	40	470(16)
				COM*	51	433(13)	821	498(2)	564	465(3)	145	448(6)	1581	466(5)	-	-
Scomberoides lysan - J	SCLY	260	650	UVS	-	-	12	338(16)	-	-	-	-	-	-	-	-
				COM*	44	446(8)	74	372(4)	551	371(3)	23	467(17)	669	387(4)	-	-
Monotaxis grandoculis - E	MOGR	250	630	UVS*	48	309(10)	47	356(10)	-	-	54	319(8)	149	333(9)	662	356(3)
				COM	563	463(2)	154	424(5)	661	416(3)	56	447(7)	1434	433(4)	-	-

[a] UVC, underwater visual census; COM, commercial report.

[b] Family: G, goatfishes (Mullidae); Sn, snappers (Lutjanidae); J, jacks (Carangidae); emperors (Lethrinidae).

[c] Also includes data from Johnston and Wake Atoll.

Table 5.3 – Number of species with correct or incorrect stock-status classification between the original (chapter 3) results versus the classification presented in the current chapter using the data-poor approach.

Data-poor results	Original results	
	Overfished	Non-overfished
Overfished	9	4
Non-overfished	0	4

Chapter 6

Summary and recommendations

Tropical coastal fisheries are difficult to assess given that they typically involve hundreds of species, can be of limited commercial importance, and therefore are usually managed with limited, thinly-spread resources, especially in poor countries (Pauly et al. 2002; Fenner 2012). Although abundance at length data are sometimes available, they are often collected using different survey methodologies which need to be standardized before being combined. This usually straight-forward exercise can be prohibitively time consuming for high species diversity datasets. Further, even with sufficient size structure information, life history parameters are needed to run the data-poor stock assessment approaches that have recently been proposed (Ault et al. 1998, 2014; Hordyk et al. 2014). Unfortunately, life history parameters used to described growth, maturity, and longevity (from which we can derive an estimate of natural mortality) are absent for a majority of coral reef fish species, as well species from other biomes (Froese & Binohlan 2000). The primary goal of this dissertation was to begin the gigantic task of assessing the status of the coastal fish species of the tropical U.S. Pacific, starting with Hawaii. To do so, my specific objectives were to build new computer tools and methodological approaches to address the two problems highlighted above.

My first chapter tackled the issue of the standardization of complex fish abundance datasets by introducing an automated approach to the generalized linear model (GLM) standardization analyses. This effectively reduced the time needed to generate standardization factors for hundreds of species from weeks to a few minutes. Furthermore, this chapter also addressed the issue of generating standardization factors for species with insufficient observations to run individual GLMs by demonstrating the use of simple predictive models using variables such as rarity, maximum length, and taxonomic group to generate standardization factors. This chapter successfully standardized a complete coral reef fish dataset composed of hundreds of species collected using 3 different survey methods, which is, to my knowledge, the first such exercise.

My second chapter was a first step assessment of the status of coral reef fish stocks in Hawaii for species with sufficient life history information and length data. It presented the spawning potential ratios for 19 species of reef fishes and also showed that our length-based model could effectively predict the average length of a dozen populations of reef fishes in the almost pristine Northwest Hawaiian Islands, thus demonstrating the usefulness and validity of this relatively simple, data-poor approach to stock assessment. The third chapter was concerned with developing, demonstrating, and testing a novel approach to obtain probability distributions of life history parameters for species with no published information. This approach used the known relationships between parameters, taxonomic group, and an estimate of maximum length to generate complex multivariate distributions of four key parameters: asymptotic length, growth rate, length at maturity, and natural mortality. The precision and accuracy of these estimates compared relatively well with those from single-species life history studies, demonstrating the usefulness of this approach as a first step assessment or to build prior distributions for Bayesian analyses. The final chapter of my dissertation used this approach to add another 8 species of Hawaiian reef fishes to the 19 species already assessed in chapter 3, for a total of 27 assessed stocks. In this chapter, I also ran analyses for 17 of the 19 species assessed in chapter 3 using the data-poor approach. This approach successfully predicted the status of 9 of the 9 overfished stocks in that chapter and 4 of the 8 non-overfished stocks. It mis-classified 4 stocks as overfished that were not found to be in this condition in chapter 3 (no overfished stocks were classified as non-overfished by the data-poor approach). This demonstrated the utility of this approach.

This dissertation represents a significant advancement to the field of tropical coastal fisheries, especially in Hawaii, where it represents the first effort of its kind. However, an enormous amount of work still lies ahead of us.

First, a better understanding of the stock-recruitment relationship in tropical coastal species is key to improving the quality of the current assessments which rely on per-recruit analyses. Recruitment is the main production process of a stock and assuming that there is no penalty or danger in keeping spawning stock biomass above 30% of its pristine value may be optimistic. Further, stocks below 30% SPR (in per-recruit terms) probably have even lower SPR values in reality since recruitment is likely compromised in these stocks (thus further reducing adult spawning biomass). Given the difficulty in establishing valid stock-recruitment relationships in well-studied stocks, it is not clear if we will ever achieve this for reef fishes. However, the presence of long-term underwater visual surveys which record both juvenile and adult abundance may provide the datasets needed to explore this issue in the future. Secondly, chapter 3 and 5, which concerned themselves with assessing Hawaiian fish stocks, discussed the issue of population connectivity in the main Hawaiian Islands. Without repeating the discussion here, it is currently unclear how the reef fish populations are connected between islands and these chapters assumed they were connected, mainly because of data and management limitations. Hopefully, future study involving new genetic tools will resolve this question and inform fisheries scientist on the appropriate spatial scale suitable to the management of these populations. Finally, there has been much discussion concerning the need for ecosystem-based management in the coral reef world. One way forward may be to slowly integrate ecosystem components into single-species assessments, such as including harvesting limits aimed not only at insuring safe spawning-potential-ratios or optimizing yields, but also at maintaining key ecosystem functions, such as herbivory.

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APPENDIX

Appendix A.1 – Source of life history parameters for the reef fish species included in the sustainability analyses for chapter 3.

Species	Code	Longevity (a_λ)	Growth rate (Linf, K, a_0)	Maturity (L_m)	Length-weight parameters (α, β)
Parrotfish (Scaridae)					
Chlorurus spilurus	CHSP	(Choat et al. 1996)	(Page 1998)	(Page 1998)	(Kulbicki et al. 2005)
Scarus psittacus	SCPS	(Taylor & Choat 2014)	(Page 1998)	(Page 1998)	(Kulbicki et al. 2005)
Scarus rubroviolaceus	SCRU	(Howard 2008)	(Howard 2008)	(Howard 2008)	(Smith & Dalzell 1993)
Surgeonfish (Acanthuridae)					
Acanthurus blochii	ACBL	(Choat & Robertson 2002)	(Choat & Robertson 2002)	(Choat & Robertson 2002)[a]	(Kulbicki et al. 2005)
Acanthurus dussumieri	ACDU	(Choat & Robertson 2002)	(Choat & Robertson 2002)	(Choat & Robertson 2002)[a]	(Kulbicki et al. 2005)
Naso brevirostris	NABR	(Choat & Robertson 2002)	(Choat & Robertson 2002)	(Choat & Robertson 2002)	(Kulbicki et al. 2005)
Naso lituratus	NALI	Unpublished[b]	Unpublished[b]	Unpublished[b]	(Smith & Dalzell 1993)
Naso hexacanthus	NAHE	(Choat & Robertson 2002)	(Choat & Robertson 2002)	(Choat & Robertson 2002)	(Choat & Axe 1996)
Naso unicornis	NAUN	Allen Andrews p. comm.	(Eble et al. 2009)	(Eble et al. 2009) [c]	(Kulbicki et al. 2005)
Goatfish (Mullidae)					
Mulloidichthys flavolineatus	MUFL	Estimated [d]	(Holland et al. 1993)	(Cole 2009)	(Holland et al. 1993)
Mulloidichthys vanicolensis	MUVA	(Cole 2009)	(Cole 2009)	(Cole 2009)	(Jehangeer 2003)
Parupeneus porphyreus	PAPO	(Moffitt 1979)	(Moffitt 1979)	(Moffitt 1979) [e]	(Kulbicki et al. 2005) [f]

(Appendix continued on next page)

Appendix A.1 - Continued

Snappers (Lutjanidae)					
Aprion virescens	APVI	(Loubens 1980a)	(Loubens 1980a)	(Everson et al. 1989)	(Kulbicki et al. 2005)
Lutjanus kasmira	LUKA	(Loubens 1980a)	(Morales-Nin & Ralston 1990)	(Allen 1985)	(Kulbicki et al. 2005)
Jacks (Carangidae)					
Caranx melampygus	CAME	(Fry et al. 2006)	(Sudekum et al. 1991)	(Sudekum et al. 1991)	(Seki 1986)
Caranx ignobilis	CAIG	(Fry et al. 2006)	(Sudekum et al. 1991)	(Sudekum et al. 1991)	(Kulbicki et al. 2005)
Seriola dumerili	SEDU	(Manooch III & Potts 1997)	(Manooch III & Potts 1997)	(Kožul et al. 2001)	(Manooch III & Potts 1997)
Other families					
Cephalopholis argus	CEAR	(Donovan et al. 2013)	(Donovan et al. 2013)	(Myers, 1999)	(Kulbicki et al. 2005)
Myripristis berndti	MYBE	(Craig & Franklin 2008)	(Craig & Franklin 2008)	(Murty 2002) [g]	(Kulbicki et al. 2005)

a Length at maturity is set at 76% of Linf (average lmat/linf ratio for surgeonfishes).

b Data from specimens collected by the NOAA Pacific Islands Fisheries Science Center in the Northern Marianas in 2009. Processing and analyses carried out at James Cook University.

c Size-at-maturity is average between males and females.

d No longevity estimate. Best estimate of longevity based on similar goatfish in Hawaii (*Mulloidichthys vanicolensis* and *Parupeneus porphyreus*).

e Size at first reproduction

f Used relationship for *Parupeneus multifasciatus*; g Size at maturity taken for a similar species, *M. murdjan*

Appendix A.2 - Source of life history parameters for the reef fish species included in the meta-analysis for chapter 4.

Family	Scientific name	Longevity source	Growth source	Maturity source
Acanthuridae	*Acanthurus auranticavus*	(Choat & Robertson 2002)	(Choat & Robertson 2002)	
Acanthuridae	*Acanthurus bahianus*	(Mutz 2006)	(Mutz 2006)	
Acanthuridae	*Acanthurus blochii*	(Choat & Robertson 2002)	(Choat & Robertson 2002)	
Acanthuridae	*Acanthurus chirurgus*	(Mutz 2006)	(Mutz 2006)	
Acanthuridae	*Acanthurus coeruleus*	(Mutz 2006)	(Mutz 2006)	
Acanthuridae	*Acanthurus dussumieri*	(Choat & Robertson 2002)	(Choat & Robertson 2002)	
Acanthuridae	*Acanthurus lineatus*	(Choat & Axe 1996)	(Choat & Robertson 2002)	(Choat & Robertson 2002)
Acanthuridae	*Acanthurus maculiceps*	(Newman et al. 2000b)	(Choat & Robertson 2002)	
Acanthuridae	*Acanthurus mata*	(Choat & Robertson 2002)	(Choat & Robertson 2002)	
Acanthuridae	*Acanthurus nigricans*	(Choat & Robertson 2002)	(Choat & Robertson 2002)	
Acanthuridae	*Acanthurus nigrofuscus*	(Hart & Russ 1996)	(Hart & Russ 1996)	
Acanthuridae	*Acanthurus olivaceus*	(Choat & Robertson 2002)	(Choat & Robertson 2002)	(Choat & Robertson 2002)
Acanthuridae	*Acanthurus pyroferus*	(Choat & Robertson 2002)	(Choat & Robertson 2002)	
Acanthuridae	*Acanthurus xanthopterus*	(Choat & Robertson 2002)	(Choat & Robertson 2002)	(Choat & Robertson 2002)
Acanthuridae	*Ctenochaetus striatus*	(Choat & Robertson 2002)	(Choat & Robertson 2002)	(Choat & Robertson 2002)
Acanthuridae	*Ctenochaetus strigosus*	(Langston et al. 2009)	(Langston et al. 2009)	(Langston et al. 2009)
Acanthuridae	*Naso annulatus*	(Choat & Robertson 2002)	(Choat & Robertson 2002)	
Acanthuridae	*Naso brachycentron*	(Choat & Robertson 2002)	(Choat & Robertson 2002)	
Acanthuridae	*Naso brevirostris*	(Choat & Robertson 2002)	(Choat & Robertson 2002)	(Choat & Robertson 2002)
Acanthuridae	*Naso hexacanthus*	(Choat & Robertson 2002)	(Choat & Robertson 2002)	(Choat & Robertson 2002)
Acanthuridae	*Naso lituratus*	NOAA-CRED unpublish.	(Kitalong & Dalzell 1994)	NOAA-CRED unpublish.
Acanthuridae	*Naso tuberosus*	(Choat & Robertson 2002)	(Choat & Robertson 2002)	(Choat & Robertson 2002)
Acanthuridae	*Naso unicornis*	A. Andrews - p. comm.	(Eble et al. 2009)	(DeMartini et al. 2014)
Acanthuridae	*Naso vlamingii*	(Choat & Robertson 2002)	(Choat & Robertson 2002)	
Acanthuridae	*Zebrasoma flavescens*	(Claisse et al. 2009)	(Claisse et al. 2009)	(Bushnell 2007)

Family	Scientific name	Longevity source	Growth source	Maturity source
Acanthuridae	*Zebrasoma scopas*	(Choat & Robertson 2002)	(Choat & Robertson 2002)	
Acanthuridae	*Zebrasoma veliferum*	(Choat & Robertson 2002)	(Choat & Robertson 2002)	
Carangidae	*Alectis indica*		(Edwards & Shaher 1991)	
Carangidae	*Alepes djedaba*		(El-Sayed 2005)	(Reuben et al. 1992)
Carangidae	*Carangoides chrysophrys*	(Al-Rasady et al. 2013)	(Al-Rasady et al. 2013)	(Al-Rasady et al. 2012)
Carangidae	*Carangoides ferdau*		(Edwards et al. 1985)	
Carangidae	*Caranx caballus*	(Cruz-Romero et al. 1993)	(Gallardo-Cabello. et al. 2007)	
Carangidae	*Caranx caninus*	(Espino Barr et al. 2008)	(Espino Barr et al. 2008)	
Carangidae	*Caranx crysos*	(Goodwin & Johnson 1986)	(Goodwin & Johnson 1986)	(Goodwin & Finucane 1985)
Carangidae	*Caranx ignobilis*	(Fry et al. 2006)	(Sudekum et al. 1991)	(Sudekum et al. 1991)
Carangidae	*Caranx lugubris*	(Fry et al. 2006)	(Fry et al. 2006)	(Garcia-Cagide et al. 1994)
Carangidae	*Caranx melampygus*	(Sudekum et al. 1991)	(Sudekum et al. 1991)	(Sudekum et al. 1991)
Carangidae	*Caranx rhonchus*	(CECAF 1979)	(CECAF 1979)	(Do Chi 1994)
Carangidae	*Caranx ruber*	(Garcia-Arteaga & Reshetnikov 1985)	(Garcia-Arteaga & Reshetnikov 1985)	(Garcia-Cagide et al. 1994)
Carangidae	*Caranx sexfasciatus*	(Fry et al. 2006)	(Munro & Williams 1985)	(Whitfield 1998)
Carangidae	*Caranx tille*	(Fry et al. 2006)	(Fry et al. 2006)	
Carangidae	*Chloroscombrus chrysurus*	(Cergole et al. 2005)	(Cergole et al. 2005)	(Cergole et al. 2005)
Carangidae	*Decapterus macarellus*	(Shiraishi et al. 2010)	(Shiraishi et al. 2010)	(Shiraishi et al. 2010)
Carangidae	*Gnathanodon speciosus*	(Koob 2011)	(Koob 2011)	(Koob 2011)
Carangidae	*Parastromateus niger*	(Tao et al. 2012)	(Tao et al. 2012)	(Tao et al. 2012)
Carangidae	*Pseudocaranx dentex*	(Williams & Lowe 1997)	(Williams & Lowe 1997)	(Seki 1986)
Carangidae	*Scomberoides commersonnianus*	(Griffiths et al. 2006)	(Griffiths et al. 2006)	(Griffiths et al. 2006)
Carangidae	*Seriola dumerili*	(Manooch III & Potts 1997)	(Harris 2004)	(Harris 2004)
Carangidae	*Trachinotus carolinus*	(Murphy et al. 2008)	(Murphy et al. 2008)	(Garcia-Cagide et al. 1994)
Carangidae	*Trachinotus falcatus*	(Crabtree et al. 2002)	(Crabtree et al. 2002)	(Crabtree et al. 2002)
Carangidae	*Trachurus capensis*	(Hecht 1990)	(Hecht 1990)	(Hecht 1990)
Carangidae	*Trachurus indicus*	(Edwards & Shaher 1991)	(Edwards & Shaher 1991)	

Family	Scientific name	Longevity source	Growth source	Maturity source
Carangidae	*Trachurus japonicus*	(Kim et al. 1969)	(Kim et al. 1969)	
Carangidae	*Trachurus lathami*	(Saccardo & Katsuragawa 1995)	(Saccardo & Katsuragawa 1995)	
Carangidae	*Trachurus picturatus*	(Vasconcelos et al. 2006)	(Vasconcelos et al. 2006)	(Vasconcelos et al. 2006)
Carangidae	*Trachurus*	(Wengrzyn 1975)	(Wengrzyn 1975)	(Kerstan 1995)
Carangidae	*Trachurus trecae*	(Do Chi 1994)	(Do Chi 1994)	
Lethrinidae	*Gymnocranius audleyi*	(Laursen et al. 1999)	(Laursen et al. 1999)	
Lethrinidae	*Gymnocranius euanus*	(Loubens 1980a)	(Loubens 1980a)	(Loubens 1980b)
Lethrinidae	*Gymnocranius grandoculis*	(Loubens 1980a)	(Loubens 1980a)	
Lethrinidae	*Lethrinus atkinsoni*	(Currey et al. 2013)	(Currey et al. 2013)	
Lethrinidae	*Lethrinus borbonicus*	(Grandcourt et al. 2010)	(Grandcourt et al. 2010)	(Grandcourt et al. 2010)
Lethrinidae	*Lethrinus enigmaticus*	(Lebeau & Cueff 1975)	(Lebeau & Cueff 1975)	
Lethrinidae	*Lethrinus erythracanthus*	(Fry et al. 2006)	(Fry et al. 2006)	
Lethrinidae	*Lethrinus genivittatus*	(Loubens 1980a)	(Loubens 1980a)	(Loubens 1980b)
Lethrinidae	*Lethrinus harak*	(Lasi 2003)	(Lasi 2003)	(Lasi 2003)
Lethrinidae	*Lethrinus laticaudis*	(Ayvazian et al. 2004)	(Ayvazian et al. 2004)	(Ayvazian et al. 2004)
Lethrinidae	*Lethrinus lentjan*	(Currey et al. 2013)	(Currey et al. 2013)	Grandcourt 2011
Lethrinidae	*Lethrinus mahsena*	(Grandcourt 2002)	(Grandcourt 2002)	
Lethrinidae	*Lethrinus microdon*	(Grandcourt et al. 2010)	(Grandcourt et al. 2010)	(Grandcourt et al. 2010)
Lethrinidae	*Lethrinus miniatus*	(Williams et al. 2007)	(Williams et al. 2007)	(Ebisawa 2006)
Lethrinidae	*Lethrinus nebulosus*	(Andrews et al. 2011)	(Ebisawa & Ozawa 2009)	(Ebisawa & Ozawa 2009)
Lethrinidae	*Lethrinus obsoletus*	(Lasi 2003)	(Lasi 2003)	(Lasi 2003)
Lethrinidae	*Lethrinus olivaceus*	(Currey et al. 2013)	(Currey et al. 2013)	
Lethrinidae	*Lethrinus ornatus*	(Ebisawa & Ozawa 2009)	(Ebisawa & Ozawa 2009)	(Ebisawa & Ozawa 2009)
Lethrinidae	*Lethrinus ravus*	(Ebisawa & Ozawa 2009)	(Ebisawa & Ozawa 2009)	(Ebisawa & Ozawa 2009)
Lethrinidae	*Lethrinus rubrioperculatus*	(Ebisawa & Ozawa 2009)	(Trianni 2011)	(Trianni 2011)
Lethrinidae	*Lethrinus variegatus*	(Loubens 1980a)	(Loubens 1980a)	(Loubens 1980b)
Lethrinidae	*Wattsia mossambica*	(Fry et al. 2006)	(Fry et al. 2006)	

Family	Scientific name	Longevity source	Growth source	Maturity source
Lutjanidae	*Aphareus rutilans*	(Fry et al. 2006)	(Fry et al. 2006)	
Lutjanidae	*Aprion virescens*	(Loubens 1980a)	(Loubens 1980a)	(Everson et al. 1989)
Lutjanidae	*Etelis carbunculus*	(Andrews et al. 2011)	(Ralston & Williams 1988)	(DeMartini & Lau 1998)
Lutjanidae	*Etelis coruscans*	(Ralston & Williams 1988)	(Ralston & Williams 1988)	(Everson et al. 1989)
Lutjanidae	*Lutjanus adetii*	(Newman et al. 1996)	(Newman et al. 1996)	(Loubens 1980b)
Lutjanidae	*Lutjanus analis*	(Burton 2002)	(Burton 2002)	(Garcia-Cagide et al. 1994)
Lutjanidae	*Lutjanus argentimaculatus*	(Fry et al. 2006)	(Fry et al. 2006)	
Lutjanidae	*Lutjanus argentiventris*	(García-Contreras et al. 2009)	(García-Contreras et al. 2009)	
Lutjanidae	*Lutjanus bohar*	(Marriott et al. 2007)	(Marriott et al. 2007)	(Marriott et al. 2007)
Lutjanidae	*Lutjanus boutton*	(Fry et al. 2006)	(Fry et al. 2006)	
Lutjanidae	*Lutjanus buccanella*	(Espinosa & Pozo 1982)	(Espinosa & Pozo 1982)	(Garcia-Cagide et al. 1994)
Lutjanidae	*Lutjanus campechanus*	(White & Palmer 2004)	(White & Palmer 2004)	(White & Palmer 2004)
Lutjanidae	*Lutjanus carponotatus*	(Newman et al. 2000a)	(Newman et al. 2000a)	
Lutjanidae	*Lutjanus cyanopterus*	(Baisre & Paez 1981)	(Baisre & Paez 1981)	
Lutjanidae	*Lutjanus ehrenbergii*	(Grandcourt et al. 2011)	(Grandcourt et al. 2011)	(Grandcourt et al. 2011)
Lutjanidae	*Lutjanus erythropterus*		(Newman et al. 2000b)	
Lutjanidae	*Lutjanus fulviflamma*	(Grandcourt et al. 2006)	(Grandcourt et al. 2006)	(Grandcourt et al. 2006)
Lutjanidae	*Lutjanus gibbus*	(Nanami et al. 2010)	(Nanami et al. 2010)	
Lutjanidae	*Lutjanus griseus*	(Fischer et al. 2005)	(Fischer et al. 2005)	(Garcia-Cagide et al. 1994)
Lutjanidae	*Lutjanus guttatus*	(Amezcua et al. 2006)	(Amezcua et al. 2006)	
Lutjanidae	*Lutjanus jocu*	(Previero et al. 2011)	(Previero et al. 2011)	(Garcia-Cagide et al. 1994)
Lutjanidae	*Lutjanus kasmira*	(Loubens 1980a)	(Morales-Nin & Ralston 1990)	(Allen 1985)
Lutjanidae	*Lutjanus malabaricus*	(Newman et al. 2000b)	(Newman et al. 2000b)	
Lutjanidae	*Lutjanus peru*	(Rocha-Olivares 1998)	(Rocha-Olivares 1998)	
Lutjanidae	*Lutjanus purpureus*	(Manickchand-Heileman & Phillip 1996)	(Manickchand-Heileman & Phillip 1996)	(Manickchand-Heileman & Phillip 1996)
Lutjanidae	*Lutjanus quinquelineatus*	(Newman et al. 1996)	(Newman et al. 1996)	(Loubens 1980b)
Lutjanidae	*Lutjanus russellii*	(Sheaves 1995)	(Sheaves 1995)	(Sheaves 1995)

Family	Scientific name	Longevity source	Growth source	Maturity source
Lutjanidae	*Lutjanus sebae*	(Loubens 1980a)	(Newman et al. 2000b)	
Lutjanidae	*Lutjanus synagris*	(Johnson et al. 1995)	(Johnson et al. 1995)	(Manickand-Dass 1987)
Lutjanidae	*Lutjanus timoriensis*	(Fry et al. 2006)	(Fry et al. 2006)	
Lutjanidae	*Lutjanus vitta*	(Newman et al. 2000a)	(Newman et al. 2000a)	(Loubens 1980b)
Lutjanidae	*Ocyurus chrysurus*	(Manooch III & Drennon 1987)	(Manooch III & Drennon 1987)	(Garcia-Cagide et al. 1994)
Lutjanidae	*Paracaesio kusakarii*	(Fry et al. 2006)	(Fry et al. 2006)	
Lutjanidae	*Paracaesio stonei*	(Fry et al. 2006)	(Fry et al. 2006)	
Lutjanidae	*Pristipomoides filamentosus*	(Andrews et al. 2012)	(DeMartini et al. 1994)	(Mees 1993)
Lutjanidae	*Pristipomoides flavipinnis*	(Fry et al. 2006)	(Fry et al. 2006)	
Lutjanidae	*Pristipomoides multidens*	(Newman & Dunk 2003)	(Newman & Dunk 2003)	(Lokani et al. 1990)
Lutjanidae	*Pristipomoides sieboldii*	(Ralston & Williams 1988)	(Ralston & Williams 1988)	(DeMartini & Lau 1998)
Lutjanidae	*Pristipomoides zonatus*	(Ralston & Williams 1988)	(Ralston & Williams 1988)	
Lutjanidae	*Rhomboplites aurorubens*	(Potts et al. 1998)	(Potts et al. 1998)	(Boardman & Weiler 1980)
Mullidae	*Mulloidichthys flavolineatus*		(Holland et al. 1993)	(Cole 2009)
Mullidae	*Mulloidichthys vanicolensis*	(Cole 2009)	(Cole 2009)	(Cole 2009)
Mullidae	*Mullus barbatus*	(Stergiou et al. 1997)	(Stergiou & Karachle 2006)	(Stergiou et al. 1997)
Mullidae	*Mullus surmuletus*	(Stergiou et al. 1997)	(Mehanna 2009)	(Morales-Nin 1992)
Mullidae	*Parupeneus barberinus*	(Wahbeh & Ajiad 1985)	(Wahbeh & Ajiad 1985)	(Vijay Anand & Pillai 2002)
Mullidae	*Parupeneus heptacanthus*	(Al-Absy & Ajiad 1988)	(Al-Absy & Ajiad 1988)	
Mullidae	*Parupeneus multifasciatus*	(Pavlov et al. 2013)	(Longenecker & Langston 2008)	(Longenecker & Langston 2008)
Mullidae	*Parupeneus porphyreus*	(Moffitt 1979)	(Moffitt 1979)	(Moffitt 1979)
Mullidae	*Pseudopeneus maculatus*	(Santana et al. 2006)	(Santana et al. 2006)	(Munro 1976)
Mullidae	*Upeneus pori*	(Ismen 2006)	(Ismen 2006)	(Ismen 2006)
Mullidae	*Upeneus tragula*	(Sabrah & El-Ganainy 2009)	(Sabrah & El-Ganainy 2009)	(Sabrah & El-Ganainy 2009)
Mullidae	*Upeneus vittatus*	(Sabrah & El-Ganainy 2009)	(Sabrah & El-Ganainy 2009)	(Sabrah & El-Ganainy 2009)
Scaridae	*Bolbometopon muricatum*	(Choat & Robertson 2002)	(Choat & Robertson 2002)	(Hamilton et al. 2008)

Family	Scientific name	Longevity source	Growth source	Maturity source
Scaridae	*Calotomus carolinus*	Taylor & Choat 2014)	Taylor & Choat 2014)	(Taylor & Choat 2014)
Scaridae	*Calotomus japonicus*	(Kume et al. 2010)	(Kume et al. 2010)	
Scaridae	*Cetoscarus bicolor*	(Choat & Robertson 2002)	(Choat & Robertson 2002)	(Choat & Robertson 2002)
Scaridae	*Chlorurus frontalis*	(Taylor & Choat 2014)	(Taylor & Choat 2014)	(Taylor & Choat 2014)
Scaridae	*Chlorurus gibbus*	(Choat et al. 1996)	(Choat et al. 1996)	(Page 1998)
Scaridae	*Chlorurus japanensis*	(Page 1998)		
Scaridae	*Chlorurus microrhinos*	(Choat & Robertson 2002)	(Taylor & Choat 2014)	(Taylor & Choat 2014)
Scaridae	*Chlorurus sordidus*	(Taylor & Choat 2014)	(Taylor & Choat 2014)	(Page 1998)
Scaridae	*Hipposcarus longiceps*	(Choat & Robertson 2002)	(Taylor & Choat 2014)	(Taylor & Choat 2014)
Scaridae	*Scarus altipinnis*	(Taylor & Choat 2014)	(Taylor & Choat 2014)	(Taylor & Choat 2014)
Scaridae	*Scarus chameleon*	(Choat & Robertson 2002)	(Choat & Robertson 2002)	
Scaridae	*Scarus forsteni*	(Taylor & Choat 2014)	(Taylor & Choat 2014)	(Taylor & Choat 2014)
Scaridae	*Scarus frenatus*	(Choat et al. 1996)	(Choat et al. 1996)	(Taylor & Choat 2014)
Scaridae	*Scarus ghobban*	(Grandcourt 2002)	(Grandcourt 2002)	
Scaridae	*Scarus iseri*	(Choat & Robertson 2002)	(Choat & Robertson 2002)	
Scaridae	*Scarus niger*	(Choat et al. 1996)	(Choat et al. 1996)	(Choat & Robertson 2002)
Scaridae	*Scarus oviceps*	(Page 1998)		(Page 1998)
Scaridae	*Scarus psittacus*	(Taylor & Choat 2014)	(Taylor & Choat 2014)	(Taylor & Choat 2014)
Scaridae	*Scarus rivulatus*	(Choat & Robertson 2002)	(Choat & Robertson 2002)	(Barba 2010)
Scaridae	*Scarus rubroviolaceus*	(Howard 2008)	(Howard 2008)	(Howard 2008)
Scaridae	*Scarus schlegeli*	(Taylor & Choat 2014)	(Taylor & Choat 2014)	(Taylor & Choat 2014)
Scaridae	*Sparisoma atomarium*	(Choat & Robertson 2002)	(Choat & Robertson 2002)	
Scaridae	*Sparisoma aurofrenatum*	(Choat & Robertson 2002)	(Choat & Robertson 2002)	(Garcia-Cagide et al. 1994)
Scaridae	*Sparisoma chrysopterum*	(Choat & Robertson 2002)	(Choat & Robertson 2002)	
Scaridae	*Sparisoma cretense*	(Pallaoro & Dulcic 2004)	(Pallaoro & Dulcic 2004)	
Scaridae	*Sparisoma rubripinne*	(Choat & Robertson 2002)	(Choat & Robertson 2002)	(Garcia-Cagide et al. 1994)
Scaridae	*Sparisoma strigatum*	(Choat & Robertson 2002)	(Choat & Robertson 2002)	

Family	Scientific name	Longevity source	Growth source	Maturity source
Scaridae	*Sparisoma viride*	(Paddack et al. 2009)	(Paddack et al. 2009)	(Garcia-Cagide et al. 1994)