



**Murdoch**  
UNIVERSITY

## MURDOCH RESEARCH REPOSITORY

*This is the author's final version of the work, as accepted for publication following peer review but without the publisher's layout or pagination.*

*The definitive version is available at*

<http://dx.doi.org/10.1016/j.fishres.2015.06.008>

**Prince, J., Victor, S., Kloulchad, V. and Hordyk, A. (2015) Length based SPR assessment of eleven Indo-Pacific coral reef fish populations in Palau. Fisheries Research, 171 . pp. 42-58.**

<http://researchrepository.murdoch.edu.au/28392/>



Copyright: © 2015 Elsevier B.V.

It is posted here for your personal use. No further distribution is permitted.

# Length based SPR assessment of eleven Indo-Pacific coral reef fish populations in Palau.

Jeremy Prince<sup>1</sup>, Steven Victor<sup>2</sup>, Valentino Kloulchad<sup>3</sup>, Adrian Hordyk<sup>4</sup>

5

<sup>1</sup> Corresponding Author: biospherics@ozemail.com.au

<sup>1</sup> Biospherics P/L, PO Box 168, South Fremantle, WA 6162, Australia

<sup>2</sup> The Nature Conservancy PO Box 1738, Koror, 96940, Palau

<sup>3</sup> Ebiil Society Inc. PO Box 3089, Koror, 96940, Palau

10 <sup>4</sup> Centre for Fish, Fisheries and Aquatic Ecosystems Research, School of Veterinary and Life Sciences, Murdoch University, Western Australia, Australia

## Abstract

The theoretical basis of a new approach to data poor fisheries assessment, length-based assessment of spawning potential ratio, has been recently published. This paper describes its first application over two years to assess 12 of the 15 most numerous species of Indo-Pacific coral reef fish in Palau. This study demonstrates the techniques applicability to small-scale data-poor fisheries and illustrates the type of data required, and the assessment's outputs. A methodology is developed for extending the principles of Beverton-Holt Life History Invariants to use the literature on related species within the Indo-Pacific reef fish assemblage to 'borrow' the information needed to parameterize assessments for Palau's poorly studied stocks. While the assessments will continue to be improved through the collection of more size and maturity data, and through further synthesis of the literature, a consistent and coherent picture emerges of a heavily fished assemblage with most assessed species having SPR <20% and many <10%. Beyond the technical aspects of this study, the relative simplicity of the data being collected and the underlying concept of spawning potential facilitated the involvement of fishers in collecting their own data and community ownership of the results.

## 1. Introduction

A persistent challenge for sustainable fisheries is the scale, complexity and cost of fishery assessment and management (Walters & Pearse 1996; Mullon *et al.* 2005). Conventional assessment methods on which fisheries management is predicated require large amounts of data, including good biological information for the exploited stock and historical time series of catch and effort data, so that the annual costs per assessed stock can be in the order of \$US50,000 to millions of dollars (Pauly 2013). Only a small fraction of exploited fish stocks can be assessed using conventional stock assessment methods

(Costello et al., 2012). By some estimates, 90% of the world's fisheries, which directly support 14 - 40 million fishers and indirectly support approximately 200 million people, are un-assessable with current methods (Andrew *et al.* 2007). In this context the development and demonstration of new methodologies for assessing stocks with limited biological information and fisheries data is of high priority.

Palau is a small independent island nation in Micronesia about 800km east of the Philippines (Figure 1). Palau has a population of approximately 12,000 resident nationals and approximately 8,000 resident guest workers mainly from the Philippines. With the main island group extending approximately 200km from north to south, and having a relatively small linearly shaped area of lagoon and fringing reef the scale of Palau's fisheries resource is small. Preston (1990) estimated total seafood production during the 1980s at 1,700t per annum, and observed that the 10 most important reef fish, *Naso unicornis*, *Bolbometopon muricatum*, *Hipposcarus longiceps*, *Scarus rubroviolaceus*, *Siganus canaliculatus*, *Siganus lineatus*, *Lutjanus gibbus*, *Lethrinus obsoletus*, *Lethrinus xanthochilus* and *Epinephelus* spp., comprised 52% of the Palau Federation of Fishing Association's landings (Perron 1983). Despite their small-scale, fishing plays a central role in the Palauan culture, economy and character. Traditionally Palauans depended on the sea for the majority of their protein, and subsistence fishing remains a major activity, but with the growth of paid employment and tourism, a local cash market for fresh fish developed and fishing became an important source of economic activity. A Forum Fisheries Agency study estimated that in 1992 fishing contributed 26% of Palau's GDP (FFA 1995). Since that time Palau has developed as prime destination for diving tourism, and over 100,000 tourists now visit annually, expecting to both see and eat Palauan fish, increasing the pressure placed upon Palau's fisheries resources.

Currently there are only a limited number of fishermen who fish exclusively for a living, although it is difficult to ascertain exactly how many. There are a limited numbers of reef fish buyers, mainly hotels and restaurants who buy directly from some fishers, and only one public fish market for reef fish, The Happy Fish Market situated in the main town of Koror, into which some fishers land their catch for direct sale to the public and restaurants. In 2014, Gleason *et al.* (2014) estimated that it takes about 6 fishermen operating out of 6-8 m outboard powered boat to catch 100-150kg of fish per night for the market, and that each fishermen received about \$125 for their share of catch. The boats of the fishermen fishing for a living typically go out 3-4 times per week, particularly on a good (dark) moon and on average fishermen fish about 150 nights per year. On a daily basis, approximately 400-500kg of fish moves through The Happy Fish Market, with a slight increase on weekends due to the increased participation of part-time fishermen.

The Palauans have been expressing concern about a perceived dwindling in the abundance of many species of food fish since at least the mid-1970s (Johannes 1991). A recent consultation found that there is a general perception that catch rates today are generally less than half what they were just 7 years ago, that reef fish in general are much smaller, and that local reefs are now being exhausted by the current level of local and tourism-driven demand for fresh fish (Gleason *et al.* 2014). In this context, few estimates of catch or effort are available, and apart from Kitalong and Dalzell's (1994) length based assessment of 10 species using Elefan, no quantitative assessments have been made. Only

a few legislated management controls are in place; a 300 mm minimum size limit and spawning season closure for plectropomids, a 50 mm minimum mesh size on nets, and a fishing ban on *B. muricatum* and *Cheilinus undulatus*.

85 This study was motivated by the two northernmost states of Palau, Ngarchelong and  
Kayangel who together fish an area known as the Northern Reefs. The state of  
Ngarchelong at the northern end of the main Palauan island of Babeldaob, has  
approximately 101 households and about 320 residents of which about 38 fish regularly.  
90 Kayangel is a low lying coral atoll island to the north of Babeldaob with about 28  
permanent households with ~70 residents, of which 15 people fish regularly. The main  
fishing techniques used are spearfishing, in daylight hours and at night with flashlights,  
and hand-line fishing using a wide range of hook sizes, which by all accounts are  
becoming smaller as average fish size declines. With declining fish abundance closer to  
105 the main town of Koror it is believed that about 30-50% of the reef fish being landed into  
the Happy Fish Market is now being taken from the Northern Reefs by fisherman resident  
in the main town of Koror (Gleason *et al.* 2014). These two communities have been  
expressing their concerns to The Nature Conservancy (TNC) for the last seven years,  
about the trends they have been observing in their fish stocks despite Palau having kept  
~40% of their reef area closed to fishing for the last 20 years.

100 A new approach to the length-based assessment of spawning potential ratio (LB-SPR) has  
recently been described, and its sensitivity to bias and variability in the input data tested  
with simulation studies (Hordyk *et al.* 2014a, Hordyk *et al.* 2014b). The new technique  
uses the life history ratios (LHR)  $M/k$  and  $L_m/L_\infty$  and the shape of a population's size  
structure, along with estimates of size of maturity, to estimate the ratio of fishing and  
105 natural mortality ( $F/M$ ) and spawning potential ratio ( $SPR$ ). The spawning potential ratio  
( $SPR$ ) of a stock is defined as the proportion of the unfished reproductive potential under  
any given level of fishing pressure (Mace and Sissenwine, 1993; Walters and Martell,  
2004). Its utility for data-limited assessment has been recommended because of its  
relative simplicity (Brooks *et al.*, 2010; Walters and Martell, 2004). Generic SPR-based  
110 reference points have been developed theoretically and through the meta-analysis of  
quantitatively assessed fisheries and have been recognized in international fisheries law;  
 $SPR_{40\%}$  is generally considered a conservative proxy for MSY, and  $SPR_{20\%}$  is proxy for  
when recruitment rates are likely to be impaired for finfish (Mace and Sissenwine, 1993;  
Restrepo and Powers, 1999; Walters and Martell, 2004). Extending the theory of  
115 Beverton-Holt Life History Invariants (Beverton & Holt 1959, Charnov 1993) it is  
proposed that LB-SPR can be applied to relatively unstudied stocks, by 'borrowing'  
information about poorly studied species from the literature for taxonomically related  
species (Prince *et al.* 2014). This paper describes the first application of LB-SPR  
technique to data collected for the purpose by fishermen in Palau. In August 2012 local  
120 fishermen were trained to begin collecting data on their catches and by August 2014 they  
had measured 6,852 fish from 106 species. This paper describes the initial assessments of  
12 of the 15 most numerous species in their catches, illustrating the potential utility of  
this new approach to other data-limited and small-scale fisheries.

## 2. Methods

### 2.1 Overview of LB-SPR Assessment

125 The LB-SPR assessment technique utilizes the fact that size structure and spawning  
potential ratio (*SPR*) in an exploited population are a function of the ratio of fishing  
mortality to natural mortality ( $F/M$ ), and the two life history ratios  $M/k$  and  $L_m/L_\infty$ ; where  
130  $M$  is the rate of natural mortality,  $k$  is the von Bertalanffy growth co-efficient,  $L_m$  is the  
size of maturity (SoM) and  $L_\infty$  is asymptotic size (Hordyk *et al.* 2014a). The inputs to the  
LB-SPR model are: (i) the  $M/k$  ratio, (ii) the mean asymptotic length ( $L_\infty$ ), (iii) the  
variability of length-at-age ( $CV_{L_\infty}$ ), which is difficult to estimate directly without reliable  
length and age data, and normally assumed to be around 10%; and (iv) a description of  
135 the size of maturity (SoM) schedule specified in terms of  $L_{50\%}$  and  $L_{95\%}$ , the size at which  
50% and 95% of a population matures. In practice the  $L_\infty$  of a stock is unlikely to be  
known in a data poor fishery, so the life history ratio  $L_m/L_\infty$  is combined with the estimate  
of  $L_{50\%}$ , which is more easily estimated, to estimate  $L_\infty$ . Given the assumed values for the  
 $M/k$  and  $L_\infty$  parameters and length composition data from an exploited stock, the LB-SPR  
model uses maximum likelihood methods to simultaneously estimate the selectivity  
ogive, which is assumed to be a logistic curve defined by the selectivity-at-length  
140 parameters  $S_{L_{50}}$  and  $S_{L_{95}}$ , and the relative fishing mortality ( $F/M$ ), which are then used to  
calculate the *SPR* (Hordyk *et al.*, 2014a, 2014b).

Estimates of *SPR* are primarily determined by the size of the fish in a sample, relative to  
SoM and  $L_\infty$ . At its simplest, if a reasonable proportion of fish in a sample attain sizes  
approaching  $L_\infty$  a high estimate of *SPR* will be derived, where as if there are few fish  
145 much larger than the SoM, a very low estimate of *SPR* is derived. Our sensitivity testing  
(Hordyk *et al.* 2014b) with the LB-SPR technique shows that at high levels of relative  
fishing pressure the technique has relatively little discriminatory power in estimating  $F/M$   
and selectivity, but still robustly estimates *SPR*. This is because the relationship between  
 $F/M$  and *SPR* is asymptotic, and determined by the selectivity parameters, so that at high  
150 fishing pressure, many combinations of  $F/M$  and selectivity produce similar values of  
*SPR*. Where as the estimate of *SPR* is strongly informed by the size of the biggest fish in  
the sample.

Like many length-based methods, the LB-SPR model is an equilibrium based method,  
and relies to differing degrees on a number of assumptions, which have to be made  
155 relatively arbitrarily in a data-poor fishery. These underlying assumptions include: (i)  
asymptotic selectivity, (ii) growth is adequately described by the von Bertalanffy  
equation, (iii) a single growth curve can be used to describe both sexes which have equal  
catchability, or that female parameters and length composition data can be used, (iv)  
length-at-age is normally distributed, (v) rates of natural mortality are constant across  
160 adult age classes, and (vi) growth rates remain constant across the cohorts within a stock.  
Simulation testing of the LB-SPR model has shown that the method is most sensitive to  
the under-estimation of  $L_\infty$ , and large rapid changes in recruitment rates (Hordyk *et al.*  
2014b). The LB-SPR assessment technique has not been developed to replace more  
precise, data-intensive assessment techniques. Rather it should be considered as a  
165 technique for applying a ‘weight of evidence’ approach to developing initial estimates of

stock status, and a means of implementing longer-term data collection processes that can lead towards the application of more precise.

## 2.2 Synthesis of Life History Ratios & Parameter Estimation

170 It is assumed that in the case of data-poor fisheries the biological knowledge needed to  
apply the LB-SPR technique will not be available from studies of the population being  
assessed, but that the two life history ratios (LHR) required might be estimated through  
175 synthesis of the scientific literature for species, and closely related species. The theory  
behind Beverton-Holt Life History Invariants (BH-LHI) is that the LHR are the formulaic  
expression of each species' life history strategy, and determine when, and in what  
180 proportion, energy budgets are switched from somatic growth into reproductive output  
(Charnov 1993). Consequently, while the individual life history parameters of a species  
are thought to be dynamic and changeable, with regard to environmental variability  
across a species' range, and changing population densities over generations. The LHR are  
185 expected to be more stable across species' ranges and equilibrium states, as well as across  
taxonomically related groups, and species with shared life history strategies than the  
individual parameters contributing to the LHR (Beverton & Holt 1959, Prince *et al.*  
2014). Following from this foundation, the overarching criteria which we apply most  
rigorously, is that the LHR cannot be robustly estimated by combining estimates of the  
individual parameters derived from different regions, or time periods that could  
190 encompass shifts in productivity regimes and population densities. The LHR should only  
be estimated from related studies that have been conducted in close temporal and spatial  
proximity to each other, so that they can be reasonably expected to reflect the parameters  
of a single stock around a specific equilibrium state.

190 Many of the families and species of interest here are long lived and grow slowly as adults  
causing the size distributions of differing age cohorts to overlap substantially with the  
consequence that length based techniques may not accurately estimate growth and  
mortality. Studies of growth and mortality based on ageing have been preferred over  
purely length-based studies, although when little other information is available length  
195 based studies maybe referred to as well. If conducted at a place and time when  
exploitation pressure was likely to have been relatively low, length-based estimates of  $L_{\infty}$   
have been considered potentially informative. Many published age and growth curves  
also surprisingly problematic in the way they estimate growth parameters (see Cailliet *et al.*  
2006, Pardo *et al.* 2013). Synthesizing the literature to reliably estimate the LHR  
200 parameters requires a degree of professional judgment, and in some cases the digitizing  
of published data so that growth curves can be re-estimated. This is discussed and  
described in more detail in the appendix. In applying our judgments the aim is to use  
whatever information is available to derive the best possible estimates of the LHR, rather  
than to rigidly apply rules that end up excluding what little information may exist.

## 2.3 Assumptions Relating to Stock Structure

205 Through this study it is assumed that the Northern Reef study area contains units of stock  
(*sensu* Gulland 1969) for all the species assessed. This is a convenient assumption to  
make because it is the area from which we could collect sufficient data to analyze within  
the time period of our study. While the data we collected can be attributed to the

individual reefs named by Palauans sub-dividing the data reduces sample sizes. Our  
210 sensitivity testing (Hordyk *et al.* 2014b) along with the results presented here, suggest the  
sample sizes used are barely sufficient for our purpose. The extent to which our  
pragmatic assumption about stock structure reflects biological reality is open to  
conjecture as discussion about the scale of tropical reef fish stocks continues (Swearer *et*  
*al.* 2002). Originally thought to have scales of 100-1000 km, Cowen *et al.* (2000, 2006)  
215 who modeled meso-scale oceanography and assumed larvae are passive particles  
concluded the scale of self-recruiting populations should be considered to be 10-100km.  
While experimental studies in the field are now concluding self-recruiting populations of  
Indo-Pacific reef fish species can occur at scales of 1-10km (Jones *et al.* 1999, 2005,  
Almanny *et al.* 2007, Planes *et al.* 2009).

#### 220 2.4 Assumptions Relating to Sexual Ontogeny

Tropical teleost species exhibit a diverse range of sexual ontogenies; serranids, lethrinids  
and scarines are typically protogynous hermaphrodites, changing sex from female to male  
(Sadovy 1996, Sadovy de Mitcheson & Liu 2008, Taylor & Choat 2014). While the  
growth of lutjanids, which tend to be gonochoristic and remain the same sex throughout  
225 life, is often described with separate gender specific growth curves. With regard to gender  
specific growth curves of gonochoristic species, it was not feasible in this study to sex  
every fish measured and so simplifying assumptions have occasionally been necessary in  
our synthesis of the literature. Where authors have estimated gender combined growth  
curves and SoM we have used these estimates. Where only gender specific estimates  
230 have been published; males and females tend to comprise an upper and lower part of a  
shared growth curve or SoM rather than distinctly different curves and SoMs (e.g.  
Nanami *et al.* 2010). In these cases we have used the data presented to derive our own  
estimates of gender combined growth curves and SoMs. With regard to the growth of the  
protogynous hermaphrodites we assume, as have most other workers, that male growth  
235 represents a continuation of the female growth curve. With regard to the estimation of  
*SPR* for protogynous hermaphrodites we assume that the reproductive potential of males  
is a continuation of the population's reproductive output, albeit in a different form, and  
that reproductive output remains proportional to adult body weight. In this case we define  
SoM as the size at which 50% of females reach maturity, and we regard females  
240 transitioning into males as part of the adult population. We are still in a relatively early  
phase of our development of this approach and these working assumptions remain to be  
tested more fully with simulation modeling. It seems likely that in the case of the  
protogynous hermaphrodites *SPR* reference points will need to be adjusted upwards to  
ensure sufficient survival of larger males, but the analyses needed for that purpose have  
245 yet to be conducted.

#### 2.5 Bounding Estimates of *F/M* and Selectivity

As discussed above, the relationship between *F/M* and *SPR* is asymptotic, and  
determined by the selectivity parameters, so that at high fishing pressure, many  
combinations of *F/M* and selectivity produce similar values of *SPR*. Thus our estimates of  
250 selectivity and *F/M* are not considered as definitive as our estimates of *SPR*. In some  
cases implausibly high sizes of selectivity (e.g.,  $S_{L50} = L_{\infty}$ ) and high *F/M* fit the data just  
as well as more realistic values. The implausibly high estimates of the sizes of selectivity

may reflect the fact that the size compositions are so heavily truncated that fully mature size classes are rare, and so also uninformative for estimating the size of full selectivity. We addressed this issue by bounding the selectivity parameters. We initially ran the LB-SPR model on all 12 datasets with no constraints on the selectivity parameters. We then ran the model a second time, with the estimate for  $S_{L_{50}}$  bound between the minimum observed length and the modal length class (i.e., the length class with the highest number of observations). Overall, implementing this constraint resulted in very little difference in the estimated  $SPR$  and the resulting selectivity curves appear more ‘reasonable’. Similarly at high fishing mortality, estimates of  $SPR$  are relatively unaffected by differences in  $F/M$  (Hordyk et al. 2014a, b) and we capped all estimates of  $F/M$  to an upper limit of 5. These constrained estimates are reported in this study.

## 2.6 Quantifying Uncertainty

Length data that is representative of the exploited stock is crucial for the LB-SPR model. The LB-SPR model assumes that sampled length data adequately describes the size structure of the exploited stock. Poor quality or ‘noisy’ length data can add considerable uncertainty to the estimates of  $SPR$ . To describe the uncertainty in our estimates of  $SPR$  that is due to variability in the length data, we used a bootstrapping routine, where one thousand iterations were run for each species. The biological parameters were fixed at the “best estimates” (Table 1) and the length data were resampled with replacement. For example, Figure 2a shows the length composition for *Lethrinus xanthurus* which has the smallest sample size in our study ( $n=144$ ) and relatively noisy length frequency data. The variability in the estimates of  $SPR$  resulting from the uncertainty in the length data and estimated by boot-strapping is shown in Figure 2b. For comparison, Figure 3a shows the length composition data for *Lutjanus gibbus*, which has the largest sample size ( $n=1,225$ ) and most coherently shaped size composition. The corresponding less variable estimates of  $SPR$  from the bootstrapping routine reflect the higher quality length data (Figure 3b). While showing a single fit to the length composition data using what we consider to be the best parameters for each of the 12 species (Figure 4 a-l), for brevity we display the bootstrapped  $SPR$  estimates for the 12 species as boxplots in Figure 5a. The complete set of the histograms of bootstrapped  $SPR$  estimates for all 12 species are presented in the appendix (Figures A2b - A13b).

A second way in which variability in LB-SPR estimates can arise is from uncertainty in the input parameters (Hordyk et al., 2014b). It is difficult to obtain empirical estimates of  $CV_{L_{\infty}}$ , and because the LB-SPR model is least sensitive to error in this parameter (Hordyk et al., 2014b)  $CV_{L_{\infty}}$  was fixed at 0.1, and assumed to be without error. Our sensitivity analyses shows that our estimation routine is most sensitive to the mis-estimation of  $L_{\infty}$ , as individuals in a sample around this size are indicative of high  $SPR$ . The technique is moderately sensitive to misspecification of  $M/k$ , but in a direct sense relatively insensitive to uncertainty in the estimate of  $L_m$ . Superficially the SoM parameters are assumed to be estimated without error, but in reality the error associated with our estimation SoM, is compounded into the uncertainty we associate with  $L_{\infty}$  through our use of the  $L_m/L_{\infty}$  ratio to estimate  $L_{\infty}$ .

To account for the uncertainty in the biological parameters, we used a sampling-importance-resampling (SIR) algorithm, where we specified prior distributions for the



$M/k$ , and  $L_\infty$  parameters and updated the posterior distribution based on the conditional likelihood of each set of parameters. The upper and lower bounds for the  $M/k$ , and  $L_\infty$  parameters were chosen by examining the range of parameter estimates from studies of the same and closely related species in other parts of the world, and our own estimates of SoM. For each dataset, values for the  $L_\infty$  and  $M/k$  parameters were drawn from a uniform distribution, with the lower and upper bounds given in Table 1, and the corresponding likelihood (importance ratio) was calculated for each parameter set with the LB-SPR model. One thousand parameter vectors were then resampled with probability proportional to the importance ratio.

Our starting assumption was that the upper and lower bounds we select for the  $M/k$ , and  $L_\infty$  parameters should be broad enough to capture the plausible range but that the selection process is not critical, as the bounds only define the range over which the SIR algorithm calculates the likelihood profiles. We revisit this assumption in our discussion. Generally with the small data sets we are using, there is little information in the length data to inform the values of the life history parameters, and in most cases the posterior distribution for the  $L_\infty$  and  $M/k$  parameters are not appreciably updated from the uniform priors we assume (e.g. Figure 2c & d and 3c & d). Some combinations of the  $L_\infty$  and  $M/k$  parameters fit the data very poorly, and the SIR algorithm allows us to examine the uncertainty in the estimates of  $F/M$  (e.g. Figure 2g and 3g) and  $SPR$  (e.g. Figure 2h and 3h) and, to a lesser extent, the selectivity parameters (e.g. Figure 2e & f and 3e & f) that arises from our uncertainty about these input parameters. Note our capping of  $F/M$  can be seen in Figures 2g and 3g where a large proportion of the estimates of  $F/M$  from the SIR algorithm are stacked up at  $F/M = 5$ . For brevity, we only present boxplots of the estimates of  $SPR$  from the SIR algorithm for the 12 species in this analysis (Figure 5b). The complete set of histograms of the posterior distributions for the  $M/k$ , and  $L_\infty$  parameters, and the selectivity parameters,  $F/M$ , and  $SPR$  for all 12 species are presented in the appendix (Figures A2-13).

## 2.7 Data Collection

### 2.7.1 Scoping Trip & Training Program

An initial scoping study was conducted in November 2011, which concluded that the LB-SPR technique could be applicable to Palau, and that the Northern Reef communities were suitable community partners. In August 2012 a two day workshop was used to give 12 Palauan collaborators a basic training in the technique including the collection size of maturity and size frequency data, a data sheet with standardized Palauan / scientific nomenclature was developed, and fish measuring boards were made. Not all the collaborators were expected to continue collecting data, some were selected in the expectation that they would support the project in other ways; such as policy development, community leadership and technical support. Approximately half the trainees went on to collect data and train fellow fishermen to measure fish.

### 2.7.2 Length Measurements:

For simplicity the data measurers were taught:

- To measure length along the middle of the side of all species of fish i.e. fork length, or standard length depending on morphology.
- To measure the length of all the fish in the catch of a boat on any day to ensure that lengths were sampled non-selective.

### 2.7.3 Size of Maturity Studies:

The diverse range of sexual ontogenies observed in tropical species makes the classification of sexual development and gender challenging, even for professionally trained fisheries biologists, let alone the artisanal fishers used to collect the data for this study. Basic protocols were developed and taught to the fishers for classifying the gonad of a fish as either immature, or otherwise maturing and mature. The primary distinguishing features for mature, maturing or transitional gonads being:

- Whether the length of the gonads is longer than one third the length of the body cavity,
- The gonads have a distinct, three dimensional shape; lobed, and triangular in cross section, for testis, or sausage, tube, or sack-like for ovaries,
- In the case of mature ovaries an obvious network of blood vessels.

Many Palauans sell a portion of their daily catch, normally the larger more valuable fish in the catch, and are reluctant to cut open and inspect the gonads of the fish they intend to sell. Consequently the collection of gonad data was left up to the discretion of the measurers who were taught that fish could be selected from a catch they were measuring for maturity classification. This impeded the collection of SoM data but was considered necessary to ensure sufficient size data that was representative of the catch would be collected. A second factor that impeded the collection of SoM data was that the size structure of the assemblage being studied is heavily truncated so that it is difficult to find individuals from the size classes expected to be 100% mature. In an attempt to overcome these challenges, the proprietor of the fish market in Koror agreed to our training one of his staff to collect gonad information from fish processed for customers. These fish were generally the largest premium fish and not representative of the normal size structure of the catch, so this data was used only in the SoM studies. Many of the fish measured at the market will not have come from the Northern Reef Area, which is the focus of this study, the implicit assumption here is that the SoM of the fish measured in the market are still to some extent representative of the SoM of the fish in the Northern Reef Area. Considering the other assumptions being made to make these data-poor assessments possible this is not thought to be a critical assumption.

### 2.7.4 Estimating Size of Maturity

The size at which 50% ( $L_{50\%}$ ) and 95% ( $L_{95\%}$ ) maturity occurs was estimated by fitting a standard logistic curve, which was constrained to pass through selected data points by manually minimizing a sum of squares routine written in Excel. Because of the relatively low sample sizes, the complexity of categorizing the developmental stages of tropical fish, the truncated nature of size structures, and the relatively low level of training provided to the collaborating fishers, the SoM data for most species is sparse and very noisy. These are not the type of data that would normally be published as a part of a

380 biological study. The aim being to use informed interpretation to make the most of the  
limited data available, in this context we have evaluated these data using a weight of  
evidence approach which is described in the appendix to this study,.

### 3. Results

385 Here we begin by describing the results of our synthesis of the LHR literature for  
*Lutjanids*, *Lethrinids*, *Plecropomids* and Scarines. From these syntheses we derive  
estimates of LHR for these broader groups which we then use in the subsequent sections  
which deal with the 12 species assessments which are the primary focus of this study.

#### 3.1 Literature Synthesis

##### 390 3.1.1 *Lutjanids*

Eighteen publications were collected covering 16 lutjanid species, from which 21  
estimates of  $L_m/L_\infty$  and 28 estimates of  $M/k$  were derived (Davis and West 1992 and 1993,  
Grandcourt *et al.* 2006, Heupel *et al.* 2010, Kritzer 2004, Loubens 1980a & b, Luckhurst  
*et al.* 2000, Marriott *et al.* 2007, McPherson *et al.* 1992, Nanami *et al.* 2010, Newman *et al.*  
395 *et al.* 1996, Newman *et al.* 2000a, Newman *et al.* 2000b, Pember, M. B. *et al.* 2005,  
Shimose and Nanami 2014, Shimose and Tachihara 2005). Ten of the growth curves used  
were corrected so that the estimate of  $t_0$  conformed to the approximate size of settling  
post-larvae (Leis & Rennis 1983). Two studies produced LHR estimates that appeared  
anomalous and would have contributed disproportionately to the estimated variance of  
400 the estimates (Loubens 1980 a & b; Davis & West 1992a & b). Loubens produced  
estimates of growth, maturity and longevity for a wide range of the Indo-Pacific  
assemblage in Noumea, and for most of the species they studied, the LHR we derive  
conform closely to comparable studies and species, however the maximum age of two  
small bodied species of lutjanid (*L. vitta* & *L. kasmira*) are anomalously low (8 years)  
405 resulting in outlying estimates of  $M/k$  (1.00 & 1.58 respectively). These estimates were  
excluded from our analysis. Their results for a third small bodied species of lutjanid (*L.*  
*fulviflamma*) produced relatively low estimates of longevity (13 years), and relatively  
high estimates of  $M/k$  (0.70), but we included this value in our analysis. Davis & West  
(1992 & 1993) studied *L. vittus* on the northwest shelf of Australia and decided against  
410 reading otoliths, because in older fish they required sectioning, instead they decided to  
read urohyal bones which required little preparation, despite the fact that ‘checks in older  
fish were represented by a cluster of bands’. Their study produced anomalous estimates  
of female and male  $L_m/L_\infty$  (0.48, 0.38 respectively) and  $M/k$  (2.51, 3.8 respectively),  
which we also excluded from our analysis.

415 The mean LHR values (Table A2) derived by pooling the selected lutjanid studies ( $L_m/L_\infty$   
= 0.75 s.d. = 0.17, n = 21, range 0.62 – 0.85;  $M/k$  = 0.41 s.d. = 0.14, n = 28, range 0.22 –  
0.70) are the same as those derived using a single ‘best’ estimate (mean or single  
estimate) for each species ( $L_m/L_\infty$  = 0.75, s.d = 0.06, n = 14;  $M/k$  = 0.41, s.d.=0.09,  
n=15). The similarity of these estimates across the range of lutjanid studies collected is

420 quite remarkable, and suggests these average values provide a good proxy for lutjanid  
species for which the LHR are either unstudied or poorly estimated.

### 3.1.2 *Lethrinids*

A total of 18 publications on age, growth and longevity of 14 lethrinid species have been  
collected (Brown & Sumpton 1998, Currey *et al.* 2009, 2010, 2013, Ebisawa 2006,  
425 Ebisawa & Ozawa 2009, Grandcourt 2002, Grandcourt *et al.* 2002, 2011, Loubens 1978,  
1980a & b, Marriott *et al.* 2010, Taylor 2010, Taylor & McIlwain 2010, Toor 1964a & b,  
Trianni 2011) from which 29 estimates of  $L_m/L_\infty$  and 41 estimates of  $M/k$  were derived  
(Table A3). Nineteen of the growth curves used were corrected so that estimates of  $t_0$   
conformed to the approximate size of settling post-larvae (Leis & Rennis 1983). As for  
430 the lutjanids the average values derived by pooling all lethrinid studies ( $L_m/L_\infty = 0.70$ , s.d.  
 $= 0.11$ ,  $n = 29$ , range = 0.47 - 0.86;  $M/k = 0.62$ , s.d. = 0.23,  $n = 41$ , range = 0.24 - 1.25)  
are similar to the averages derived using a single 'best' value for each species ( $L_m/L_\infty =$   
 $0.72$ , s.d. = 0.22,  $n=13$ , range = 0.63 - 0.86;  $M/k = 0.60$ , s.d. = 0.15,  $n=14$ , range = 0.36 -  
435 0.89) and suggests these average values provide a good proxy for lethrinid species for  
which the LHR are either unstudied or poorly estimated.

### 3.1.3 *Plectropomids & Variola*

A total of 11 publications on 4 plectropomids were used (Currey *et al.* 2010, Ebisawa  
2013, Ferreira & Russ 1992, Grandcourt 2005, Heupel *et al.* 2010, Loubens 1978, 1980 a  
& b, Russ *et al.* 1998, Rhodes *et al.* 2013, Williams *et al.* 2008) to develop 8 estimates  
440 of  $L_m/L_\infty$  and 14 estimates of  $M/k$  (Table A4). Five published studies on 2 *Variola* species  
(*V. albigarginatus* and *V. louti*) were also collected and used to derive 2 estimates of  
 $L_m/L_\infty$  and 3 estimates of  $M/k$  for this genus (Currey *et al.* 2010, Grandcourt 2005,  
Loubens 1978, 1980 a & b). Nine of the growth curves used were corrected so that the  
estimate of  $t_0$  conformed to the approximate size of settling post-larvae (Leis & Rennis  
445 1983). The average values derived by pooling all plectropomid studies ( $L_m/L_\infty = 0.59$ , s.d.  
 $= 0.13$ ,  $n = 8$ , range = 0.43 - 0.80;  $M/k = 0.91$ , s.d. = 0.21,  $n = 14$ , range = 0.59 - 1.3)  
was relatively similar to the average values derived using a single 'best' estimate for each  
plectropomid species ( $L_m/L_\infty = 0.58$ , s.d. = 0.06,  $n = 4$ , range = 0.51 - 0.64;  $M/k = 0.91$ ,  
s.d. = 0.02,  $n = 4$ , range = 0.89 - 0.92), and not dissimilar to the mean LHRs derived by  
450 pooling all the *Variola* studies ( $L_m/L_\infty = 0.64$ ,  $n = 2$ , range = 0.54 - 0.74;  $M/k = 0.86$ ,  $n=3$ ,  
range = 0.58 - 1.13).

### 3.1.4 *Scarines*

Parrotfishes (Labridae: tribe Scarinae) are among the most diverse and abundant groups  
found on coral reefs and have highly plastic growth and complex sexual ontogenies, as a  
455 group, they encompass a variety of body sizes and can range considerably in maximum  
life span among species (Taylor & Choat 2014). A total of 7 publications describing age,  
growth and maturity in 17 scarine species of the genera of *Cetoscarus*, *Chlorurus*,  
*Hipposcarus* and *Scarus* have been collected to date (Choat and Robertson 2002; El-  
Sayed 2011; Gust *et al.* 2002; Grandcourt 2002; McIlwain and Taylor 2009; Sabetian  
460 2010; Taylor and Choat 2014) and were used to develop 21 estimates of  $L_m/L_\infty$  and 53  
estimates of  $M/k$  (Table A5). Only three of the growth curves used required re-estimating

so that  $t_0$  approximated the size of settling post-larvae (Leis & Rennis 1983). We did however, exclude from our analysis an estimate of  $M/k = 2.39$  for *Scarus rivulatus* which was derived from Choat and Robertson (2002). We excluded this estimate because it was so far outside the range of other estimates (0.25 - 1.27) and contributed disproportionately (>33%) to the estimate of variance if included.

The mean value for  $L_m/L_\infty$  derived by pooling all the studies of the remaining 16 species ( $L_m/L_\infty = 0.71$ , s.d. = 0.09, n = 21, range = 0.50 - 0.87) was similar to the average estimated using a single 'best' estimate for each species ( $L_m/L_\infty = 0.73$ , s.d. = 0.08, n = 13, range = 0.57 - 0.87), and similar to the estimate of 0.68 derived by Choat & Robertson (2002) for the genera *Chlorurus* & *Scarus* combined. Note that 6 of 21 estimates used here were derived from Choat & Robertson (2002).

The estimates of  $M/k$  derived by pooling all scarine studies ( $M/k = 0.62$ , s.d. = 0.34, n = 53, range = 0.12 - 1.31) is a little different to the ratio estimated using a single estimate for each species ( $M/k = 0.73$ , s.d. = 0.27, n = 13, range = 0.25 - 1.07). This difference is largely attributable to the 10 studies of *Scarus frenatus* derived from Choat and Robertson (2002) and Gust *et al.* (2002), which produce a range of comparatively low values (0.12 - 0.34). These studies lower the average estimated by pooling individual studies, but the effect of these studies are down-weighted, when a single 'best' value is used for each species. The multiple studies of *S. frenatus* are consistent in suggesting the species has a lower  $M/k$  than other the other scarines in our synthesis, and along with the high values of  $M/k$  estimated for some other species (*Hipposcarus longiceps*, *Scarus schlegeli*) seem indicative of the variability of this group of species. On this basis we conclude that estimating this LHR using a single 'best' estimate for each species, rather than by pooling all studies, provides the better estimate of an average  $M/k$  for this group of species. Considering the genera in isolation to each other, and estimating averages across species rather than by pooling individual studies suggests some degree of difference between the scarine genera, although these differences may also reflect low sample sizes and variable quality of results between studies (Table A5).

## 3.2 *Lutjanus gibbus*

### 3.2.1 Data Used

Up until August 2014 a total of 1225 *L. gibbus* had been measured for length and 449 had also been categorized by sex and maturity from which  $L_{50\%} = 257$  mm and  $L_{95\%} = 320$  mm was estimated (Table 1; Figure A1a).

### 3.2.2 Literature Synthesis & Parameter Estimation

Kitalong and Dalzell (1994) collected length data for *L. gibbus* in Palau and analysed modal progression with Elefan to produce estimates of growth ( $L_\infty = 398$ mm;  $k = 0.4$ ), and natural mortality ( $M=0.91$ ) using the Pauly (1980) technique. The results of that study imply that  $M/k = 2.28$  which is inconsistent with the average value (0.41) we derive from our synthesis of lutjanid studies. The results of an age and growth study of *L. gibbus* on the Great Barrier Reef (GBR) of Australia (Heupel *et al.* 2010) allow an estimate of  $M/k = 0.69$  to be derived, which while more consistent is still relatively high. Estimates of

505  $L_m/L_\infty = 0.76$  and  $M/k = 0.51$  can be derived from combining the gender based estimates of Nanami *et al.* (2010) from Okinawa. Given the low sample size and variability of these LHR for *L. gibbus*, but also their relative similarity to the generic estimates, we preferred to use the average LHR values ( $L_m/L_\infty = 0.75$ ;  $M/k = 0.41$ ) derived from all the lutjanid studies in our (Table A2).

510 When  $t_0$  is constrained to the approximate size of lutjanid post-larvae the corrected estimates of  $L_\infty$  derived from the literature for *L. gibbus* range from 340 – 398 mm. Combining our estimate of  $L_m = 257$  mm with the lutjanid estimate of  $L_m/L_\infty = 0.75$  we estimate  $L_\infty = 343$  mm in Palau. We assumed lower and upper bounds for the estimate of  $L_\infty$  (340 – 400 mm) based on the lowest and highest values reported in the literature for *L. gibbus* (Table 1). We assumed lower bound and upper bounds of 0.3 and 0.6 for  $M/k$  based on the range observed for 27 of the 28 species, choosing not to use the lowest value in our synthesis (0.22) which was derived for *L. synagris*, but to encompass the value derived for *L. gibbus* (0.57) which was the highest (Table 1A).

### 3.2.3 Assessment Results

520 With these assumed parameters and our size composition data (Figure 2a & 4a) we estimated  $SL_{50\%} = 224$  mm,  $SL_{95\%} = 252$  mm,  $SPR = 10\%$  and  $F/M = 4.1$  (Table 2). Bootstrapping the length composition data with our best parameter estimates (Figure 2b & 5a) suggests a reasonably good fit to this relatively large sample ( $n=1227$ ) and that all plausible estimates of  $SPR$  lie in the range 8-16%. Application of the SIR routine across our assumed range of plausible parameter values suggests the data is relatively uninformative with regard to  $M/k$  for which the uniform priors were barely updated (Figure 2c), somewhat informative with regard to  $L_\infty$  (Figure 2d) for which the uniform priors were updated to indicate a peak probability in the range (350 – 365 mm), and also with regard to the selectivity parameters (Figure 2e & f). A broad range (2.5 – 5+) of  $F/M$  estimates were compatible with a plausible range of parameters (Figure 2g) with most values clumping against our upper bound of  $F/M = 5$ . The application of the SIR routine suggest that using our best parameter estimates with our assumed plausible range of parameter estimates we can be confident that the  $SPR$  of *L. gibbus* in the Northern Reefs of Palau is  $< 20\%$   $SPR$  (Figure 2h & Figure 5b).

## 3.3 *Lutjanus bohar*

### 3.3.1 Data Used

535 A total of 137 *L. bohar* have been measured for length and 38 had been categorized by sex and maturity from which  $L_{50\%} = 365$  mm and  $L_{95\%} = 460$  mm was estimated (Table 1; Figure A1b).

### 3.3.2 Literature Synthesis & Parameter Estimation

540 Studies of *L. bohar* by Loubens (1980a & b) in New Caledonia and Marriott *et al.* (2007) on the GBR have been used to derive two estimates of  $M/k = 0.40$  (Table A2). The growth curve from Loubens (1980a & b) required correcting so that  $t_0$  approximates the size of settling lutjanid post-larvae. A single estimate of  $L_m/L_\infty = 0.76$  was derived from Marriott *et al.* (2007) on the GBR. Both these estimates of the *L. bohar* LHR are

545 extremely similar to the average values we derive from all studies of the lutjanid genus in  
our synthesis ( $M/k = 0.41$ ;  $L_m/L_\infty = 0.75$ ). For consistency and the larger sample size we  
have preferred the average values for the genus. Combining our estimate of  $L_m = 365$  mm  
with  $L_m/L_\infty = 0.75$  we estimate  $L_\infty = 487$  mm which lies between our corrected estimate  
550 from New Caledonia (460 mm) and the GBR estimate (567 mm). We selected lower  
(470 mm) and upper bounds (570 mm) for our estimate of  $L_\infty$  loosely on these other  
estimates, adding 10 mm to the lower New Caledonian estimate so that our lower bound  
is slightly larger than our estimate of  $L_{95\%} = 460$  mm. For  $M/k$  we assumed lower and  
upper bounds (0.3 and 0.6), based on the range observed across 27 of the 28 lutjanid  
species in our synthesis (Table A2). Again excluding the lowest value (0.22) derived for  
*L. synagris* but encompassing the highest value derived for *L. gibbus* (0.57).

### 555 3.3.3 Assessment Results

With these parameters and our size composition data (Figure 4b & A3a) we estimated  
 $SL_{50\%} = 265$  mm,  $SL_{95\%} = 347$  mm,  $SPR = 27\%$  and  $F/M = 1.4$  (Table 2). Bootstrapping  
the length composition data with our best parameter estimates (Figure 5a & A3b)  
560 indicates a poor fit to this small ( $n=145$ ) noisy sample and a relatively wide range of  
possible  $SPR$  estimates  $\sim 15$ -50%  $SPR$ . Application of the SIR routine across our assumed  
range of plausible parameter values suggests the data were relatively uninformative with  
regard to  $M/k$  (Figure A3c) for which the uniform priors were left relatively unchanged in  
the posterior, for  $L_\infty$  (Figure A3d) which the probability profile increases monotonically  
565 through our bounded range, and with regard to  $F/M$  (Figure A3g) for which a wide range  
of estimates (1.0 - 4.5) were plausible. The data were only informative for the selectivity  
parameters (Figure A3e & f) where the estimate of  $SL_{95\%}$  is smaller than  $L_m$  (347 mm, c.f.  
365 mm). The application of the SIR routine across our assumed range of parameter  
values suggests that  $SPR$  could lie in the range 5-30%  $SPR$  although 75% of the estimates  
were  $< 20\%$  (Figure 5b & A3h).

## 570 3.4 *Lethrinus rubrioperculatus*

### 3.4.1 Data Used

A total of 530 *L. rubrioperculatus* have been measured for length and 300 categorized by  
sex and maturity from which  $L_{50\%} = 214$  mm and  $L_{95\%} = 270$  mm have been estimated  
(Table 1; Figure A1c)

### 575 3.4.2 Literature Synthesis & Parameter Estimation

Studies of *L. rubrioperculatus* conducted by Loubens (1978, 1980a, 1980b) in New  
Caledonia, Ebisawa and Ozawa (2009) in Okinawa and Trianni (2011) in the Northern  
Mariana Islands allow the necessary LHRs to be estimated. In each case the estimated  
growth curves had to be corrected so that  $t_0$  approximates the expected size of settling  
580 lethrinid post-larvae. An average  $L_m/L_\infty = 0.66$  ( $n=3$ ; range = 0.62 – 0.70) and average  
 $M/k = 0.63$  ( $n=3$ ; range = 0.56 – 0.69). Being similar to the average values estimated  
across the larger number of lethrinid studies (Table A3) we prefer the estimates from the  
larger sample ( $L_m/L_\infty = 0.70$ ;  $M/k = 0.62$ ) and the range of values estimated across the 14  
species (0.35 – 0.89) has been assumed to provide lower and upper bounds for  $M/k$  (Table

585 1). Once corrected the estimates of  $L_\infty$  contained in the literature for *L. rubrioperculatus*, range from 303 – 370 mm. Combining our estimate of  $L_m = 214$  mm,  $L_m/L_\infty = 0.70$  we estimate  $L_\infty = 306$  mm in Palau. We assumed lower and upper bounds for our estimate of  $L_\infty$  (300 – 370 mm) based loosely on lowest and highest values reported in the literature (Table 1).

### 590 3.4.3 Assessment Results

With these parameters and data (Figure 4c & A4a) we estimated  $SL_{50\%} = 239$  mm,  $SL_{95\%} = 279$  mm,  $SPR = 23\%$  and  $F/M = 3.9$  (Table 2). Bootstrapping the length composition data with our best parameter estimates (Figure 5a & A4b) indicates a reasonable fit to this moderately sized ( $n=533$ ) length sample and although our  $SPR$  estimates ranged from 10-40%  $SPR$  some 75% of the estimates lie within 20-24%  $SPR$ . Application of the SIR routine across our assumed range of plausible parameter values suggests the data is relatively uninformative with regard to  $M/k$  and  $L_\infty$  (Figure A4c & d), and with regard to  $F/M$  (Figure A4g) for which a wide range of estimates (2.0 – 5.0) were possible, although most were clustered against our upper bound ( $F/M=5$ ). The data were only informative for the selectivity parameters (Figure A4e & f), which again may coincide with the maturity ogive ( $L_{50\%} = 214$  mm;  $L_{95\%} = 270$  mm). The application of the SIR routine across our assumed range of parameter values suggests that  $SPR$  could possibly lie in the range 2.5 - 40%  $SPR$  although the 75<sup>th</sup> percentile of the estimates was 8-15%  $SPR$  (Figure 5b & A4h).

## 605 3.5 *Lethrinus olivaceus*

### 3.5.1 Data Used

A total of 366 *L. olivaceus* have been measured for length and 155 categorized by sex and maturity from which  $L_{50\%} = 409$  mm and  $L_{95\%} = 500$  mm was estimated (Table 1; Figure A1d)

### 610 3.5.2 Literature Synthesis & Parameter Estimation

Only a single age and growth study of *L. olivaceus*, on the GBR of Australia by Currey *et al.* (2013), has so far been found. That study estimated  $L_\infty = 660$  mm and allows an estimate of  $M/k = 0.36$  to be derived. This estimate of  $M/k$  is considerably lower than the average (0.62) derived using all studies of the genus (Table A3). Currey *et al.* (2013) worked with a sample of just 53 individuals, most of which were < 5 y.o, although individuals up to 15 years of age were observed, thus along with the authors of that study, we are not entirely confident in that estimate. No studies have been found to date from which  $L_m/L_\infty$  can be estimated. On this basis the average lehrinid LHR ( $L_m/L_\infty = 0.70$ ;  $M/k = 0.62$ ) have been assumed for this species (Table 1), and the range of the 14 lehrinid species (0.35 – 0.89) has been assumed to provide lower and upper bounds for  $M/k$  (Table A3). Combining our estimate of  $L_m = 410$  mm with the lehrinid estimate of  $L_m/L_\infty = 0.70$  allows us to estimate  $L_\infty = 584$  mm in Palau. To bound our estimate of  $L_\infty$  we have used a value 10% larger than our estimate of  $L_{95}$  in Palau (500 mm) as the lower bound and Currey *et al.*'s (2013) relatively unconstrained estimate of  $L_\infty$  (670mm; Table 1) as the upper bound.



### 3.5.3 Assessment Results

630 With these parameters and data (Figure 4d & A5a) we estimated  $SL_{50\%} = 465$  mm,  $SL_{95\%} = 608$  mm,  $SPR = 10\%$  and the  $F/M = 5+$  was constrained (Table 2). Bootstrapping the length composition data with our best parameter estimates (Figure 5a & A5b) indicates a reasonable fit to this moderately sized ( $n=366$ ) length sample and a possible range of 8-18%  $SPR$ , with 75% of the estimates falling within the range 10-14%  $SPR$ . Application of the SIR routine across our range of plausible parameter values suggests the data is relatively uninformative with regard to  $M/k$  and  $L_{\infty}$  the selectivity parameters (Figure A5c, d, e, f). All the possible estimates  $F/M$  (Figure A5g) were high  $>4.0$  and most were  
635 constrained by our upper bound ( $F/M=5$ ). The application of the SIR routine across our assumed range of parameter values (Figure 5b & A5h) suggests all possible  $SPR$  are  $<25\%$  and 75% were  $<10\%$ .

## 3.6 *Lethrinus xanthochilus*

### 3.6.1 Data Used

640 A total of 144 *L. xanthochilus* have been measured for length and 103 categorized by sex and maturity from which  $L_{50\%} = 324$  mm and  $L_{95\%} = 380$  mm were estimated (Table 1; Figure A1e)

### 3.6.2 Literature Synthesis & Parameter Estimation

645 No age and growth studies of *L. xanthochilus* have been found to date. The only studies found to date come from length based studies conducted by Wright *et al.* (unpubl.) and Dalzell *et al.* (1989) which are cited in a species synopsis by Williams & Russ (1994). Those studies are cited as estimating  $L_{\infty}$  as ranging from 540 – 640 mm. The information cited from Dalzell *et al.* (1989) make it possible to derive estimates of  $M/k$  ranging from 2.65 – 2.79 which are inconsistent with lethriniid estimates derived from age and growth  
650 studies (Table A3) and so have been discounted here. Instead, as with *L. olivaceous*, we preferred the lethriniid average LHR ( $L_m/L_{\infty} = 0.70$ ;  $M/k = 0.62$ ) and the range of values estimated across the 14 species (0.35 – 0.89) to provide lower and upper bounds for  $M/k$  (Table 1). Combining our estimate of  $L_m = 324$  mm with  $L_m/L_{\infty} = 0.70$  we estimate  $L_{\infty} = 463$  mm for Palau. Our assumed lower bound for  $L_{\infty}$  (390 mm) is 10 mm larger than our  
655 estimate of  $L_{95}$  and the assumed upper bound (640 mm) is the largest of the length-based estimates (Table 1).

### 3.6.3 Assessment Results

660 With these parameters and data (Figure 3a & 4e) we estimated  $SL_{50\%} = 351$  mm,  $SL_{95\%} = 440$  mm,  $SPR = 13\%$  and  $F/M = 5+$  (Table 2). Bootstrapping the length composition data with our best parameter estimates (Figure 3b & 5a) suggests a poor fit to this small ( $n=144$ ) noisy sample and a possible range of 4 - 41%  $SPR$  but with 75% of estimates falling within the range 10-16%  $SPR$ . Application of the SIR routine across our plausible range of parameters suggests the data is relatively uninformative with regard to  $M/k$  and  $L_{\infty}$  (Figure 3c & d), and with regard to  $F/M$  (Figure 3g) for which almost any estimate is  
665 possible (0 – 5.0) although most estimates were constrained against our upper bound

( $F/M = 5$ ). Our estimates of the selectivity parameters (Figure 3e & f) were also constrained by our estimate of  $L_{\infty}$ , which was the upper bound. The application of the SIR routine across our assumed range of parameter values suggests that  $SPR$  could possibly have almost any value (0-1.0) although 75% of the estimates were  $<16\%$   $SPR$  (Figure 5b & 3h).

670

### 3.7 *Lethrinus obsoletus*

#### 3.7.1 Data Used

A total of 211 *L. obsoletus* have been measured for length and 83 categorized by sex and maturity from which  $L_{50\%} = 240$  mm and  $L_{95\%} = 300$  mm was estimated (Table 1; Figure A1f)

675

#### 3.7.2 Literature Synthesis & Parameter Estimation

Studies of age and growth of *L. obsoletus* conducted by Taylor (2010) in Guam, and by Ebisawa and Ozawa (2009) in Okinawa, allow the necessary LHRs to be estimated, although in both cases the estimated growth curves need to be corrected so that  $t_0$  approximates the size of settling post-larvae. The corrected estimates of  $L_{\infty}$  were 280 mm and 313 mm respectively. From these studies estimates were derived for  $L_m/L_{\infty} = 0.76$  ( $n=2$ ; range = 0.75 – 0.77) and  $M/k = 0.44$  ( $n=2$ ; range = 0.40 – 0.47). The estimate for  $L_m/L_{\infty}$  is similar to the average lethriniid value (0.70) although the estimate of  $M/k$  is somewhat lower than the lethriniid average (0.62). Considering the small number of studies involved, the average lethriniid LHR have been preferred for this species, and the estimated range (0.35 – 0.89) for the 14 lethriniid species (Table A3) has been used for the lower and upper bounds for  $M/k$  (Table 1). Combining our estimate of  $L_m = 240$  mm with the lethriniid estimate of  $L_m/L_{\infty} = 0.70$  allows us to estimate  $L_{\infty} = 343$  mm in Palau. Our assumed lower bound for  $L_{\infty}$  (330 mm) is 10% larger than our estimate of  $L_{95}$  and our assumed upper bound (365 mm) is approximately 10% larger than our best estimate (Table 1), and considerably larger than the largest estimate in the literature (313 mm). Note these criteria for selecting the bounds for  $L_{\infty}$  are more restrictive, than those applied for the other species.

680

685

690

#### 3.7.3 Assessment Results

We estimated  $SL_{50\%} = 260$  mm,  $SL_{95\%} = 325$  mm,  $SPR = 3\%$  and  $F/M = 5+$  (Table 2) and although the model appears unable to fit to this small ( $n=211$ ) sample neatly (Figure 4f & A7a), bootstrapping the length composition data with our best parameter estimates (Figure 5a & A7b) suggests all possible estimates of  $SPR$  are  $<5\%$ . Application of the SIR routine across our assumed range of plausible parameter values suggests the data is relatively uninformative with regard to  $M/k$  and  $L_{\infty}$  (Figure A7c & d), and we constrained our estimate of  $SL_{95}$  with our assumed  $L_{\infty}$ . Likewise all the estimates of  $F/M$  (Figure A7g) are constrained against our upper bound ( $F/M = 5$ ). Despite the limitations of the data, application of the SIR routine across our assumed range of parameter values suggests all possible estimates of  $SPR$  are  $<10\%$   $SPR$  (Figure 5b & A7h). Note the apparently very high confidence of these  $SPR$  estimates (Figure 5 a & b) coinciding with our assumption of tighter bounds for  $L_{\infty}$ .

695

700

705

### 3.8 *Plectropomus areolatus*

#### 3.8.1 Data Used

710 A total of 322 *P. areolatus* have been measured for length and 136 categorized by sex  
and maturity from which  $L_{50\%} = 383$  mm and  $L_{95\%} = 460$  mm was estimated (Table 21;  
Figure A1g)

#### 3.8.2 Literature Synthesis & Parameter Estimation

715 Three studies of *P. areolatus* were used to estimate LHR; Williams *et al.* (2008) from the  
eastern Torres Strait, Australia, Currey *et al.* (2010) from the GBR, Australia and Rhodes  
*et al.* (2013) from Pohnpei in Micronesia. With the exception of the Currey *et al.* study all  
the growth curves derived by these studies needed correction so that  $t_0$  reflects the size of  
settling plectropomid post-larvae. The re-estimated  $L_\infty$ 's range from 454 mm in Pohnpei  
to 660 mm in Eastern Torres Strait. Having made these corrections an average  $L_m/L_\infty =$   
0.64 (n=2, range = 0.48 – 0.80) and an average  $M/k = 0.94$  (n=3, range = 0.67 – 1.30)  
720 were derived. On the basis of the apparent similarity of the LHRs found in the  
plectropomid literature (Table A4), because of the larger sample size we preferred to use  
the average values for the genera ( $L_m/L_\infty = 0.59$ ;  $M/k = 0.91$ ). With fewer estimates  
available for *P. areolatus* than for *P. leopardus* (Table A4) we chose to use the lower  
bound of  $M/k$  estimated for *P. leopardus* (0.46) as the lower bound for *P. areolatus* and  
725 the highest estimate for *P. areolatus* (1.3) as the upper bound (Table 1). Using our best  
estimate for the genera of  $L_m/L_\infty$  (0.59) and our estimate of  $L_{50} = 383$  mm we estimate  $L_\infty$   
 $= 649$  mm in Palau. Because our estimate of  $L_{95} = 460$  mm is greater than the lowest  
estimates of  $L_\infty$  in the literature and our estimate of  $L_\infty$  is close to the largest, we chose to  
extend our possible bound of  $L_\infty$  estimates by using the range of  $L_m/L_\infty$  estimates we  
730 derived from the literature for this species (0.48 – 0.80; Table A4) to derive lower and  
upper bounds of 540 mm and 815 mm (Table 1).

#### 3.8.3 Assessment Results

735 With these parameters and size composition data (Figure 4g & A8a) we estimated  $SL_{50\%}$   
 $= 480$  mm,  $SL_{95\%} = 571$  mm,  $SPR = 5\%$  and  $F/M = 5+$  (Table 2). Bootstrapping the length  
composition data with our best parameter estimates (Figure 5a & A8b) suggests a  
reasonable fit to this moderately sized sample (n=322) all  $SPR$  estimates being in the  
range 2-8%. Application of the SIR routine across our assumed range of plausible  
parameter values suggests the data is relatively uninformative with regard to  $M/k$  and  $L_\infty$   
(Figure A8c & d), and all our estimates of  $F/M$  (Figure A8g) were constrained against our  
740 upper bound ( $F/M = 5$ ). Our estimates of selectivity parameters are apparently  
informative and hint at a link between maturation and selectivity ( $SL_{50} = 480$  mm, c.f.  $L_{95}$   
 $= 460$  mm). The application of the SIR routine across our assumed range of parameter  
values suggests that almost all possible estimates of  $SPR$  are  $<20\%$   $SPR$  and 75% of the  
estimates were  $<10\%$  (Figure 5b & A8h).

### 745 3.9 *Plectropomus leopardus*

#### 3.9.1 Data Used

A total of 186 *P. leopardus* have been measured for length and 53 categorized by sex and maturity from which  $L_{50\%} = 370$  mm and  $L_{95\%} = 440$  mm was estimated (Table 1; Figure A1h)

### 750 3.9.2 Literature Synthesis & Parameter Estimation

Four studies of *P. leopardus* were used to estimate the relevant LHRs of this species; Loubens (1978, 1980a&b) in New Caledonia, Williams *et al.* (2008) in the eastern Torres Strait, Australia, Currey *et al.* (2010) on GBR, Australia, and Ebisawa (2013) in Okinawa, Japan. With the exception of Currey *et al.* all the growth curves needed  
755 correction so  $t_0$  reflects the size of post-larvae. The re-estimated  $L_\infty$ 's range from 420 mm in New Caledonia to 620 mm in Okinawa. Having made these corrections an average  $L_m/L_\infty = 0.63$  (n=3, range = 0.47 – 0.71) and an average  $M/k = 0.89$  (n=5, range = 0.60 – 1.00) were derived for *P. leopardus* (Table A4). The ranges of both  $M$  (0.25 – 0.35) and  $k$  (0.24 – 0.41) estimated for *P. leopardus* are lower than for *P. areolatus* ( $M = 0.30$  – 0.43;  
760  $k = 0.30$  - 0.64) with the result that the average estimates of  $M/k$  for these two species are extremely similar (Table A4). On the basis of the apparent similarity of the LHRs found in the plectropomid literature we preferred to use the average values estimated across all species in the genera ( $L_m/L_\infty = 0.59$ ;  $M/k = 0.91$ ) because of the larger sample size.

Russ *et al.* (1998) used an aging study over time to track the abundance of a single strong  
765 cohort of *P. leopardus* in an area of the GBR closed to fishing over time, and estimated  $M$  for 7-9 y.o. fish as 0.115 – 0.189. They argued that other studies had over-estimated  $M$ . With regard to the studies we have used here; Currey *et al.* (2010) used samples from areas closed to fishing to estimate  $M=0.25$ , the same value estimated by Ebisawa (2013) from areas fished with a relatively high size limit, however the other two estimates (0.25  
770 & 0.35) were derived from areas open to fishing. If the mid-point of the Russ *et al.* estimates ( $M = 0.15$ ) is substituted into the studies we used, instead of the mortality rates derived by, or from, each study, a lower  $M/k = 0.46$  (n=5, range = 0.35 – 0.60) is derived. Notwithstanding the argument we advance in the methods section of the appendix that with stocks around equilibrium this LHR should be approximated by  $Z/k$ , here for  
775 interest, we used the estimate of  $M/k$  (0.46) derived with the Russ *et al.*  $M$  as the lower bound for  $M/k$ , and used the highest estimate ( $M/k$ ) derived from the studies in the literature (1.00) as upper bound (Table 1).

Using our Palauan estimate of  $L_{50} = 370$  mm and the estimate of  $L_m/L_\infty = 0.59$  we  
780 estimate  $L_\infty = 627$  mm in Palau, and in this case, because our estimate of  $L_{95} = 440$  mm is larger than the smallest estimates of  $L_\infty$  found in the literature and our estimate of  $L_\infty$  outside the range of estimates in the literature, we used our range of  $L_m/L_\infty$  estimates for this species (0.47 – 0.71) to derive lower and upper bounds of 521 mm and 787 mm for  $L_\infty$ .

### 3.9.3 Assessment Results

785 With these assumed parameters and data (Figure 4h & A9a) we estimated  $SL_{50\%} = 334$  mm,  $SL_{95\%} = 419$  mm,  $SPR = 1\%$  and  $F/M = 5+$  (Table 2). Bootstrapping the length composition data with our best parameter estimates (Figure 5a & A9b) suggests a reasonable fit to this relatively small sample (n=185) with most estimates of  $SPR$  being

790 <2%. A thin tail of outlying estimates extending up to ~30% *SPR* relates to the  
measurement of a few larger (>400 mm) individuals which are poorly explained by the  
model but if given sufficient weight suggest higher *SPR* levels (Figure 4h). Application  
of the SIR routine across our assumed range of plausible parameter values suggests the  
data is relatively uninformative with regard to  $M/k$  and  $L_\infty$  (Figure A9c & d), and all the  
estimates of  $F/M$  (Figure A9g) were constrained by our upper bound ( $F/M = 5$ ). Our  
795 estimates of the selectivity parameters are apparently informed by the data and are again  
perhaps coincidental with our estimated maturity ogive ( $SL_{95\%} = 419$  mm, c.f.  $L_{95\%} = 440$   
mm). The application of the SIR routine across our assumed range of parameter values  
suggests that all possible estimates of *SPR* are <5% *SPR* (Figure 5b & A9h).

### 3.10 *Variola louti*

#### 800 3.10.1 Data Used

A total of 578 *V. louti* have been measured for length and 113 and categorized by sex and  
maturity (Table 1; Figure A1i)

#### 3.10.2 Literature Synthesis & Parameter Estimation

805 Studies of *V. louti* by Currey *et al.* (2010) on the GBR, Grandcourt (2005) and Loubens  
(1978, 1980a & b) in New Caledonia estimate  $L_\infty$  ranging from 390 – 510 mm and mean  
LHR values  $L_m/L_\infty = 0.64$  (n=2, range = 0.54 - 0.74) and  $M/k = 0.86$  (n=2, range = 0.58 -  
1.13) to be estimated (Table A4), which are similar to the average plectropomid values  
( $L_m/L_\infty = 0.59$ ;  $M/k = 0.91$ ). Given the close relationship between *Variola* and  
810 *Plectropomus* and the larger number of plectropomid studies available to us, we chose to  
use the plectropomid LHR as the best estimates for *V. louti* as well, and the range of  $M/k$   
values estimated for *Variola* as the upper and lower bounds (Table 1). Our SoM data for  
this species were noisy and uninformative, although not inconsistent with the only  
estimate of  $L_{50} = 290$  mm we found in the literature (Loubens 1980a) and an estimate of  
815  $L_{50} = 260$  mm we derived from Maplestone *et al.* (2009). On this basis we tightly  
constrained a logistic curve, to pass through our scatter of data, and assume  $L_{50} = 285$  mm  
and  $L_{95} = 350$  mm which when combined with our best estimate of  $L_m/L_\infty$  (0.59) enables  
us to estimate  $L_\infty = 483$  mm (Table 1). Again our estimate of  $L_{95}$  is larger than some  
estimates of  $L_\infty$  found in the literature, so we used our range of  $L_m/L_\infty$  estimates for  
*Variola* (0.54 - 0.74) to derive lower and upper bounds for  $L_\infty$  of 385 mm and 527 mm.

#### 820 3.10.3 Assessment Results

With these parameters and data (Figure 4i & A10a) we estimated  $SL_{50\%} = 203$  mm,  $SL_{95\%}$   
= 266 mm,  $SPR = 20\%$  and  $F/M = 1.4$  (Table 2). Bootstrapping the length composition  
data with our best parameter estimates (Figure 5a & A10b) suggests a relatively poor fit  
to this moderately sized (n=578) sample, with the model unable to fit the tails of smaller  
825 and larger individuals, resulting in a possible range of 10-30% *SPR*. Application of the  
SIR routine across our assumed range of plausible parameter values suggests the data is  
relatively uninformative with regard to  $M/k$  and  $L_\infty$ , with the probability profile of the  
latter increasing monotonically through our assumed range for this parameter (Figure  
A10c & d). The data were apparently informative for the estimation of the selectivity

830 parameters (Figure A10e & f), and in this case were considerably smaller than the  
maturity ogive we assumed ( $SL_{95\%} = 266$  mm, c.f.  $L_{50} = 285$ ) however the context for this  
is that our SoM estimate is very poorly informed by our data. The SIR routine suggests a  
wide range (1.5 – 5.0) of  $F/M$  estimates (Figure A10g) are compatible with our range of  
835 assumed parameter estimates, but that 75% our  $SPR$  estimates are <10% and all but a few  
outlier estimates are <20% (Figure 5b & A10h).

### 3.11 *Scarus rubroviolaceus*

#### 3.11.1 Data Used

A total of 159 *S. rubroviolaceus* have been measured for length and 116 categorized by  
sex and maturity from which  $L_{50\%} = 312$  mm and  $L_{95\%} = 400$  mm was estimated (Table 1;  
840 Figure A1j)

#### 3.11.2 Literature Synthesis & Parameter Estimation

Studies of age and growth in *S. rubroviolaceus* in the Seychelles by Grandcourt (2002),  
Sabetian (2010) in Taiwan and Seychelles, and Taylor and Choat (2014) from Micronesia  
have been used to estimate the relevant LHRs. All these studies constrained  $t_0$  to  
845 approximate the expected size of settling post-larvae so no correction was required. These  
studies estimate  $L_{\infty}$  as ranging from 308 - 459 mm,  $k$  from 0.43 – 1.05, and  $M$  or  $Z$  from  
0.18 – 0.63. From these studies  $L_m/L_{\infty} = 0.75$  (n=2; range = 0.72 – 0.78) was estimated,  
similar to the value we derived (Table A5) pooling all scarine studies (0.71), using a  
single ‘best’ value for each species (0.73), and also by Choat & Robertson’s (2002) for  
850 *Chlorurus* and *Scarus* genera (0.68). Given the small sample size for *S. rubroviolaceus*  
we prefer the estimate derived using the ‘best’ estimates for each of the 10 *Scarus* species  
(0.72) as being the most recent and comprehensive. Based on this estimate of  $L_m/L_{\infty}$  and  
our estimate of  $L_{50} = 312$  mm in Palau we estimate  $L_{\infty} = 433$  mm (Table 1). Given the  
lowest estimate of  $L_{\infty}$  in the literature (308 mm) is below our estimate of  $L_{50}$  in Palau (312  
855 mm), we assumed the lower bound on  $L_{\infty}$  to be 10 mm greater than our estimated  $L_{95}$  (410  
mm) and used the highest estimate of  $L_{\infty}$  in the literature (459 mm) as our upper bound.

From the collected studies of *S. rubroviolaceus* we estimate  $M/k = 0.51$  (n=4; range =  
0.27 – 0.95). The highest derived value of  $M/k$  is based on an estimate of  $Z$  (0.95) from a  
study by Taylor & Choat (2014) from the heavily exploited waters off Guam and is  
860 notably higher than the estimates of the other three studies. If this estimate is excluded,  
 $M/k$  for this species is re-estimated as 0.36 (n=3; range = 0.27 – 0.42) which is  
considerably lower than the average derived for the 10 *Scarus* species (0.53) in our  
synthesis (Table A5). Variability in the  $M/k$  ratio does seem to be an actual characteristic  
of the scarines, and not entirely attributable to noise in the data. In this situation, despite  
865 the low sample size we prefer the estimate of  $M/k = 0.36$  as our best estimate for this  
species. We use the estimate for *S. frenatus* (0.25), the lowest estimated for the *Scarus*  
species, as our lower bound and the average estimate for all *Scarus* species (0.79) as our  
upper bound (Table 1).

#### 3.11.3 Assessment Results

870 With these parameters and our data we estimated  $SL_{50\%} = 355$  mm,  $SL_{95\%} = 454$  mm,  $SPR = 7\%$  and  $F/M = 5+$  (Table 2). The model fit to this noisy small sample ( $n=159$ ) was relative poor (Figure 4j & A11a), however, bootstrapping the length composition data with our best parameter estimates (Figure 5a & A11b) suggests all but a few outlier estimates of  $SPR$  are  $<10\%$ . Application of the SIR routine across our assumed range of  
875 plausible parameter values suggests the data is relatively uninformative with regard to  $M/k$  and  $L_\infty$  (Figure A11c & d). Our estimates of the selectivity parameters were also not well informed by our data and instead constrained by our estimates of  $L_\infty$  (Figure A11e & f). Likewise our estimates of  $F/M$  (Figure A11g) were constrained by our upper bound ( $F/M = 5$ ). Nevertheless, taking into account the range of parameter estimates we  
880 considered plausible almost all possible estimates of  $SPR$  were  $<30\%$  and  $75\%$  were  $<18\%$  (Figure 5b & A11h).

### 3.12 *Chlorurus microrhinos*

#### 3.12.1 Data Used

885 A total of 150 *C. microrhinos* have been measured for length and 111 categorized by sex and maturity from which  $L_{50\%} = 315$  mm and  $L_{95\%} = 330$  mm was estimated (Table 1; Figure A1k)

#### 3.12.2 Literature Synthesis & Parameter Estimation

The LHR of *C. microrhinos* can be estimated from studies by Choat and Robertson (2002) from the GBR, by Sabetian (2010) from the GBR, Seychelles and Cocos Keeling  
890 Islands, and by Taylor and Choat (2014) from Guam. All these studies constrained  $t_0$  to the approximate of post-larvae and required no correction. These studies estimate  $L_\infty$  as ranging between 395 – 499 mm,  $k$  from 0.30 – 0.65, and  $M$  from 0.32 – 0.52. From these studies we derived estimates of  $L_m/L_\infty = 0.74$  ( $n=4$ ; range = 0.67 – 0.77), similar to the value we estimate (0.73) using the single ‘best’ estimates of each of the 15 scarine  
895 species in our synthesis, but slightly higher than the average (0.66) of the three *Chlorurus* species for which we have data, and the average (0.67) of all eight *Chlorurus* studies (Table A4). It is also slightly higher than the value (0.68) derived by Choat & Robertson (2002) for all *Chlorurus* and *Scarus* species. Given our relatively small sample size for *C. microrhinos* ( $n=4$ ), in this case we prefer the estimate derived by pooling all eight studies  
900 of *Chlorurus* (0.67). Based on this  $L_m/L_\infty$  and our estimate of  $L_{50} = 315$  mm in Palau we estimate  $L_\infty = 470$  mm (Table 1). We have used the range of  $L_\infty$  estimates in the literature for this species (395 – 500 mm) to define the upper and lower bounds (Table 1).

From the collected studies of *C. microrhinos* we initially estimated  $M/k = 0.91$  ( $n=6$ ; range = 0.53 – 1.26). This estimate of  $M/k$  is higher than the average of 16 *Chlorurus*  
905 studies (0.57), than the three *Chlorurus* species (0.62) and the average of ‘best’ estimates (0.70) for all 16 scarine species in our synthesis (Table A4). Again the highest value of  $M/k$  we derived for this species (1.26) uses an estimate of  $Z$  taken from the study by Taylor & Choat (2014) in Guam, although in this case, their estimate of total mortality (0.43) falls within the range of the other *C. microrhinos* estimates (0.32 – 0.52).

910 However, if for the sake of consistency, we also remove that value from our analysis we re-estimate  $M/k$  for this species as 0.84 ( $n=5$ ; range = 0.53 – 1.06) which while closer is

still above the average  $M/k$  estimated across all 16 scarine species in our sample (0.70). On this basis, and considering our relatively small sample size for *C. microrhinos* (n=6) we prefer the estimate of  $M/k = 0.70$  derived from all 16 scarine species. We use the range of estimates for *C. microrhinos* (0.53 – 1.26) to define our lower and upper bounds for this LHR (Table 1).

### 3.12.3 Assessment Results

With these parameters and data we estimated  $SL_{50\%} = 333$  mm,  $SL_{95\%} = 406$  mm,  $SPR = 21\%$  and  $F/M = 3.1$  (Table 2). The model fit to this small (n=150) noisy sample was relative poor (Figure 4k & A12a) and bootstrapping with the best parameter estimates (Figure 5a & A12b) suggested estimates of 10 - 50%  $SPR$  are compatible with the data, with 75% of the  $SPR$  estimates falling in the range 18-26%  $SPR$ . Application of the SIR routine across our assumed range of plausible parameter values suggests the data is relatively uninformative with regard to  $M/k$ ,  $L_{\infty}$  and the selectivity parameters (Figure A12c,d,e,f). Taking into account the range of parameter estimates we considered plausible the SIR routine suggests that almost any value of  $F/M$  (0 - 5) and  $SPR$  (0.1 - 1.0) is possible (Figure 5b & A12g,h).

## 3.13 *Hipposcarus longiceps*

### 3.13.1 Data Used

A total of 403 *H. longiceps* had been measured for length and categorized by sex and maturity from which  $L_{50\%} = 300$  mm and  $L_{95\%} = 330$  mm was estimated (Table 1; Figure A11)

### 3.13.2 Literature Synthesis & Parameter Estimation

Kitalong and Dalzell (1994) used length based techniques to study *H. longiceps* in Palau and estimated  $L_{\infty} = 439$  mm,  $k = 0.5$  and  $M = 1.02$ , suggesting  $M/k = 2.04$ , but we do not consider these estimates as reliable as the estimates based on aging studies. Three age and growth studies of *H. longiceps* have been used to estimate the LHR for this species; Choat and Robertson (2002) on the GBR, Sabetian (2010) from the Solomon Islands and Taylor and Choat (2014) from Pohnpei, Micronesia. These studies estimate  $L_{\infty}$  as ranging between 286 – 366 mm,  $k$  from 0.28 – 1.19, and  $M$  from 0.32 – 1.22. The only estimate of  $L_m/L_{\infty} = 0.87$  we could derive is based on Taylor and Choat (2014). Given the single sample involved and that the result is at the outer edge of the range observed for the other scarine studies (Table A5) we prefer to use the estimate derived by pooling all 21 scarine studies (0.71) and with our estimate of  $L_{50} = 300$  mm derive  $L_{\infty} = 423$  mm. Relatively arbitrarily, we have selected 360 mm as the lower bound for this estimate, being approximately 10% greater than our approximation of  $L_{95}$  (330 mm), and the estimate of  $L_{\infty} = 440$  mm derived by Kitalong and Dalzell (1994) using length based methods in Palau as our upper bound (Table 1).

An average estimate of  $M/k = 1.07$  (n=3; range = 0.93 – 1.26) is derived from the three age and growth studies collected, which is considerably higher than the single estimate (0.67) we derive for the other species in this genus for which we have data (*Hipposcarus harid*) and also the average (0.70) of all 16 scarine species (Table A5). Given the relative



consistency of the three *H. longiceps* estimates, the variability which seemingly characterizes scarine species, our own observation in Palau suggesting it is one of the species in this assemblage persisting longest under heavy fishing pressure, and despite the small number of studies, we think it likely this species does have a comparatively high  $M/k$  ratio. Consequently, in this case we chose to use the estimate we derived for *H. longiceps* (1.07) as our best estimate, the average derived across all 16 scarine species (0.81) as our lower bound, and the highest estimate for *H. longiceps* derived by age and growth studies (1.26) as our upper bound (Table 1).

### 3.13.3 Assessment Results

With these parameters and data we estimated  $SL_{50\%} = 276$  mm,  $SL_{95\%} = 313$  mm,  $SPR = 5\%$  and  $F/M = 5+$  (Table 2). The model fit to this moderately sized sample ( $n=403$ ) was reasonable (Figure 4l & A13a). Bootstrapping the length composition data with our best parameter estimates (Figure 5a & A13b) suggests all possible estimates are  $<10\%$   $SPR$ . Application of the SIR routine across our assumed range of plausible parameter values suggests the data is relatively uninformative with regard to  $M/k$  and  $L_{\infty}$  (Figure A13c & d), although estimates of the selectivity parameters are apparently informed by our data (Figure A13e & f) and again approximately coincide with the maturity ogive. Our estimates of  $F/M$  (Figure A13g) are relatively uninformed by the data, with all possible estimates being  $>2$  and most values being constrained by our upper bound ( $F/M = 5$ ). Taking into account the range of parameter estimates we considered plausible 75% of our  $SPR$  estimates are  $<10\%$  and all but a few outlier estimates are  $<20\%$  (Figure 5b & A13h).

## 4. Discussion

This paper documents the first application of the LB-SPR approach advanced by Hordyk *et al.* (2104b) to developing an assessment of  $SPR$  in a small-scale and data-poor fishery. The LB-SPR assessment technique has not been developed to replace more precise, data-intensive assessment techniques, rather to provide a widely applicable and cost-effective starting point with which to begin longer term processes of data collection, assessment and management when little, if any, pre-existing data, and few if any other options exist. This first study of 12 species allows us to start evaluating the techniques' potential for real world implementation. In two years with the support of artisanal fishers to collect the data we have developed assessments for 12 of the 15 most abundant of the 106 species in the catch of the Northern Reefs of Palau (Table A1). Of the remaining three of the 15 most abundant species that we have been unable to assess, we have so far been unable to reliably estimate the LHR of one (*Siganus lineatus*), and have collected insufficient SoM data for the other two (*Naso unicornis*, *Cetoscarus ocellatus*), to begin formulating assessments.

### 4.1 Estimation of Life History Ratios

An expected limitation to the application of the LB-SPR technique, which we were interested in testing with this study, was the extent to which the required LHR might, or might not, be estimable using published studies of the species in question, and of taxonomically related species. This study demonstrates that the BH-LHI principles can be

995 used to borrow information from related species within the Indo-Pacific coral reef fish  
assemblage, and inform the LB-SPR assessment of less studied species. This study also  
begins developing a methodology for estimating from the literature the LHR required to  
parameterize LHR assessment. We found sufficient quality information for lutjanids,  
lethrinids, serranids and the scarines, to derive what we regard as robust starting estimates  
1000 to formulate assessments for those genera. Having made allowances for the variable  
quality of the growth curves described in the literature (Cailliet *et al.* 2006, Pardo *et al.*  
2013), we were agreeably surprised at the intra-genera consistency of LHR estimates for  
the lethrinids, lutjanids and plectropomids. On this basis we had little hesitation in  
1005 applying the average values for each of those groups to poorly or unstudied species of  
those groups. In contrast the scarines are acknowledged as being a highly variable group  
of species and genera (Taylor & Choat 2014), and this seems evident in the more variable  
LHR estimates that we derived for this species complex. At this stage it is difficult to  
determine to what extent this variation also reflects the variable quality of the results  
being synthesized.

1010 From what we have seen of the Indo-Pacific teleost literature so far, we expect there to be  
sufficient information based on aging studies to derive robust LHR estimates for the  
acanthurids, another important groups for the Indo Pacific coral reef fish fisheries of the  
Indo-Pacific, but that it is unlikely similar quality LHR estimates will be possible for the  
siganids, a sixth important species group for these fisheries. All the siganid studies we  
1015 have collected to date are length-based.

#### 4.2 Estimation of Size of Maturity

In developing LB-SPR we had anticipated that estimating asymptotic size from exploited  
data-poor stocks would be problematic, and for this reason developed the approach of  
1020 using estimates of  $L_m/L_\infty$  derived from the literature, together with *in situ* estimation of  $L_m$   
to estimate asymptotic size. We had not anticipated the difficulty we would encounter  
completing SoM studies with depleted stocks. In practice we found fully mature size  
classes difficult to sample because they have become rare in Palau. This made the  
estimation of SoM challenging. The reluctance of fishers wishing to selling their catch to  
1025 have their catch cut open for gonad inspection increased the difficulty of deriving good  
SoM estimates, a challenge we are also encountering in the Solomon Islands where we  
are also trialing the LB-SPR approach. In Palau we now seem to have overcome this  
problem by collaborating with the proprietor of the fish market to opportunistically  
collect data on selected larger fish. In the Solomon Islands we are resorting to buying the  
1030 fish we require for our SoM studies, a more expensive option. The complexity of the  
sexual ontogeny of tropical species further compounds the challenge of this aspect of the  
study, forcing us to adopt a weight of evidence approach to evaluating the SoM data  
gathered by the Palauan fishers, and accepting our resulting estimates of  $L_\infty$  have broad  
ranges of uncertainty around them. Undoubtedly accepting the added expense of having  
1035 trained scientists collect these data would improve the quality of these data and the  
resulting SoM analyses. Nevertheless we hope that by continuing to collect these data we  
will over time enlarge the sample sizes at the tails of our size distributions, and improve  
our current estimates, as well as extend the number of species.

1040 4.3 Evaluating the Uncertainty of LB-SPR Estimates

At this stage of our technique's development we have yet to develop an explicit means of quantifying uncertainty around the SoM estimates, and are conveniently compounding it into our uncertainty with regard to  $L_{\infty}$ , which we know from sensitivity testing is the most important determinant of LB-SPR assessments (Hordyk 2014b). Also lacking is a single comprehensive metric for evaluating the total uncertainty that comes from combining noisy length composition data with uncertain parameter estimates. Some multiplicative combination of the bootstrapping and sampling-importance-resampling we describe here, would provide the best holistic description of our uncertainty around these estimates. What is presented here is not an ideal solution to this issue, but our development of the LB-SPR methodology and software remains a work in progress. Although a strength of our current approach is that the different sources of uncertainty remain to some extent explicit and separable, enhancing our opportunity for learning from what we are doing, and informing our next steps in development.

The LB-SPR methodology is known to be extremely sensitive to the estimate of  $L_{\infty}$  (Hordyk 2014b). The SIR estimates suggest 11 of the 12 assessments have <20% SPR and are systematically lower than the bootstrapped values which suggest 4 or 5 stocks have ~20% SPR (Figure 5a & b). The SIR algorithm considers a wider range of  $L_{\infty}$  than the single 'best' estimate of the bootstrap routine, many of which are higher than the single 'best' bootstrap estimate, and equally compatible with the relatively uninformative size composition data. This mass of equally possible lower SPR estimates drags the distribution of estimates lower.

Ranking the variance estimated for each species by each technique 1 – 12, highest to lowest (Table 3) we see that with bootstrapping the five species with the lowest ranking and highest variance are; *Lutjanus bohar* (n=145), *Chlorurus microrhinos* (n=150), *Lethrinus rubrioperculatus* (n=533), *Variola louti* (n=578), *Lethrinus xanthochilus* (n=144). Ranking the variance of each species' SIR estimates the lowest ranking highest variance estimates were for *C. microrhinos* (n=150), *L. xanthochilus* (n=144), *L. rubrioperculatus* (n=533), *Scarus rubroviolaceus* (n=158), *Lutjanus bohar* (n=145). These two lists of most uncertain assessments are comprised of the four species with the smallest sample sizes, together with the second and third most numerous sampled species, *L. rubrioperculatus* and *V. louti*.

Generally the estimates of variance seem to decline and stabilize with  $n > 350$ , suggesting estimates can clearly be substantially improved by collecting more size data. In the case of *L. rubrioperculatus* and *V. louti* the 'noise' in their size composition histograms persists despite larger sample sizes than most other species. Noting that they are the smallest bodied members of this assemblage, it is tempting to attribute this to a greater degree of spatial variability, similar to that now being documented across reef profiles for other small-bodied Indo-Pacific coral reef species (Gust et al. 2002, Gust 2004). Some degree of finer data collection could be considered, along with tolerating the greater degree of uncertainty for these species.

The LB-SPR methodology is particularly sensitive to the under-estimation of  $L_{\infty}$  (Hordyk 2014b) because when the largest sized individuals in a sample begin to approach  $L_{\infty}$  estimates of  $SPR$  increase rapidly. The lower bounds we selected for the  $L_{\infty}$  apparently played a role in determining the upper limit of possible SIR estimates of  $SPR$  and confidence intervals. The order of the species in Table 3 has been determined by the ratio of the lower bound on  $L_{\infty}$ , and the  $L_{95\%}$  assumed for each species in our analysis. A value approaching 1.0 indicates the range assumed for  $L_{\infty}$  includes the lowest possible values (i.e.  $L_{\infty} = L_{95\%}$ ). Besides the influence of low sample size there also appears to be a co-occurrence with the species having the lowest  $L_{\infty}$  bounds (the top half of the table) also tending to have lower rankings and the higher levels of variance. With regard to  $L_{\infty}$  of a heavily fished species in a data-poor fishery there will always remain a sense of, ‘not being able to know what you don’t already know’. An argument can be made that we have systematically under-estimated our actual uncertainty about this parameter. Developing robust consistent protocols for setting the bounds for  $L_{\infty}$  will be essential for ensuring the comparability of SIR estimated confidence intervals.

#### 4.4 The Benefit of LB-SPR

While there is a lot of scope for further development the current weaknesses in our quantification of uncertainty around our estimates should not obscure the potential we think this new technique has for the field of data-poor assessments. Within two years of commencing our study we complete conclusive  $SPR$  assessments for 11 of the most important species in the Northern Reefs of Palau showing that these stocks are all currently around or below the  $SPR$  reference point at which recruitment impairment is likely. The relative simplicity of the data being collected, and the underlying concept of spawning potential, is a great advantage in the application of the technique, because they facilitate the involvement of fishers in collecting their own data, reducing costs and foster community ownership of the results. While basing our data collection program on the participation of local fishers may have added some noise into the data we collected, our judgment is that in the context of data poor fisheries, accurate determinations of scientific uncertainty are less important than a fishing community’s qualitative understanding and acceptance of the results. These results have been rapidly accepted by the Palauans, providing for them a convincing explanation of the changes they have been observing over the last two decades and confirming what they suspected, but were not acknowledging. We believe it is the involvement of the fishers in our study, as much as the results of our assessments, that has generated community support for implementing minimum size limits based on our estimates of size at  $SPR_{20\%}$ , and resulted in national and state laws being changed to support this occurring.

## 5. Acknowledgements

We gratefully acknowledge the support of The Nature Conservancy and of the David and Lucile Packard Foundation for making this project possible. We also thank Chuck Cook and Noah Idechong for the leadership, vision and relationship building over three

decades, that has given us receptive communities to work with, and Ann Singeo and the Ebiil Society of Ngarchelong for their development and support of data collection programs in the partnering communities. Finally we thank the communities of Palau's northern states for their enthusiastic participation in data collection and discussion of fisheries reform.

## 6. References

- 1125 Almanny, G.R. Berumen, M.L., Thorrold, S.R., Planes, S. (2007) Local replenishment of coral reef fish populations in a marine reserve. *Sci.* **316**, 742-743.
- Andrew, N.L., Bène, C., Hall, S.J., Allison, E.H., Heck, S., & Ratner, B.D. (2007) Diagnosis and management of small-scale fisheries in developing countries. *Fish Fish.* **8**, 277-240.
- 1135 Beverton, R.J.H., Holt, S.J. (1959) A review of the lifespans and mortality of fish in nature and the relation to growth and other physiological characteristics. *Ciba Foundation Colloquium on Ageing*, **5**, 142-177.
- Brooks, E.N., Powers, J.E. and Cortes, E. (2010) Analytical reference points for age-structured models: application to data-poor fisheries. *ICES J. Mar. Sci.* **67**, 000-000.
- 1140 Brown, I. and W. Sumpton (1998). Age, growth and mortality of red throat emperor, *Lethrinus miniatus*, from the Southern Great Barrier Reef, Queensland, Australia. *Bull. Mar. Sci.* **62** (3), 905-917.
- Cailliet, G.M., Smith, W.D., Mollet, H.F., Goldman, K.J. (2006) Age and growth studies of chondrichthyan fishes: the need for consistency in terminology, verification, validation, and growth function fitting. *Environ. Biol. Fish* **77**, 211–228. DOI 10.1007/s10641-006-9105-5
- 1145 Charnov, E.L. (1993) *Life history invariants*. Oxford University Press, New York.
- Choat, J. H., and Robertson, D. R. 2002. Age-based studies on coral reef fishes. In *Coral Reef Fishes: Dynamic and Diversity in a Complex Ecosystem*, pp. 57–80. Elsevier, San Diego, CA, USA.
- 1150 Costello, C., Ovando, D., Hilborn, R., Gaines, S.G., Deschenes, O., Lester, S.E., (2012) Status and solutions for the world's unassessed fisheries. *Science* **338**, 517–520.
- Cowen, R.K., Lwiza, K.M.M., Sponaugle, S., Paris, C.B., Olsen, D.B. (2000) Connectivity of marine populations: open or closed? *Sci.* **287**, 857-859.
- 1155 Cowen, R.K., Paris, C.B., Srinivasan, A. (2006) Scaling of connectivity in marine populations. *Sci.* **311**, 522-527.
- Currey, L.M., Simpfendorfer, C.A., Williams, A.J., 2010. Resilience of reef fish species on the Great Barrier Reef and in Torres Strait. *Project Milestone Report to the Marine*

- 1160 *and Tropical Sciences Research Facility. Reef and Rainforest Research Centre Limited, Cairns* (32pp.).
- Currey, L.M., Williams, A.J., Mapstone, B.D., Davies, C.R., Carlos, G., Welch, D.J., Simpfendorfer, C.A., Ballagh, A.C., Penny, A.L., Grandcourt, E.M., Maplestone, A., Wiebkin, A.S., Bean, K. (2013) Comparative biology of tropical *Lethrinus* species (Lethrinidae): challenges for multi-species management. *J. Fish Biol.* **82**, 764-788.
- 1165 Currey, L.M., Williams, A.J., Simpfendorfer, C.A., Ballagh, A.C., Penny, A.L. 2009. Comparative biology of key inter-reefal lethrinid species on the Great Barrier Reef. *Project Milestone Report to the Marine and Tropical Sciences Research Facility. Reef and Rainforest Research Centre Limited, Cairns* (29pp.)
- 1170 Dalzell, P., S. Sharma and Nath, G. (1992) Estimation of exploitation rates in a multispecies emperor (Pisces: Lethrinidae) fishery in Fiji, based on length frequency data. Papers on fisheries science from the Pacific Islands. *Inshore Fish. Res. Proj. Tech. Doc. No.1. South Pacific Commission, Noumea, New Caledonia.* **1**, 43-50.
- Davis, T. L. O., and G. J. West. (1992) Growth and mortality of *Lutjanus vittus* (Quoy and Gaimard) from the north west shelf of Australia. *Fish. Bull.* **90**, 395–404.
- 1175 Davis, T.L.O., West, G.J., (1993) Maturation, reproductive seasonality, fecundity, and spawning frequency in *Lutjanus vittus* (Quoy and Gaimard) from the North West Shelf of Australia. *Fish. Bull.* **91**, 224–236.
- Ebisawa, A. (2006) Reproductive and sexual characteristics in five *Lethrinus* species in waters off the Ryukyu Islands. *Ichthyol. Res.* **53**, 269–280. doi:10.1007/s10228-006-0345-3.
- 1180 Ebisawa, A, (2013) Life history traits of leopard coral grouper *Plectropomus leopardus* in the Okinawa Islands, southwestern Japan. *Fish Sci.* **79**, 911–921. DOI 10.1007/s12562-013-0669-7
- Ebisawa, A., Ozawa, T. (2009) Life-history traits of eight *Lethrinus* species from to local populations in waters off the Ryukyu Islands. *Fish Sci.* **75**, 553-566.
- 1185 El-Sayed Ali, T., Osman, A.M., Abdel-Aziz, S.H., Bawazeer, F.A. (2011) Growth and longevity of the protogynous parrotfish, *Hipposcarus harid*, *Scarus ferrugineus*, and *Chlorurus sordidus* (Teleostei, Scaridae), off the eastern coast of the Red Sea. *J. Appl. Ichthyol.* **27**, 840-846.
- 1190 Ferreira, B.P., Russ, G.R. (1992) Age, growth and mortality of the inshore coral trout *Plectropomus maculatus* (Pisces: Serranidae) from the central Great Barrier Reef, Australia. *Aust. J. Mar. Freshwater. Res.* **43**, 1310-12.
- Ferreira, B. P. (1995). Reproduction of the common coral trout *Plectropomus leopardus* (Serranidae: Epinephelinae) from the central and northern Great Barrier Reef, Australia. *Bulletin of Marine Science* **56**, 653–669.
- 1195

- Forum Fisheries Agency (1995). Marine Resources Profiles: Republic of Palau. *FFA Report 95/12* (250 pp).
- 1200 Gleason, M., Merrifield, M., Vermeer, L., Wilson, J. (2014). Trip report January 18-27, 2014 site visit to Palau's northern reefs fisheries project. *The Nature Conservancy Unpublished Report*. (26 pp).
- Grandcourt, E.M. (2002) Demographic characteristics of a selection of exploited reef fish from the Seychelles: preliminary study. *Mar. Freshwater Res.* **53**, 123–130.
- 1205 Grandcourt, E. (2005) Demographic characteristics of selected epinepheline groupers (Family: Serranidae; Subfamily: Epinephelinae) from Aldabra atoll, Seychelles. *Atoll Res. Bull.* **539**, 199-216.
- Grandcourt, E. M., Al Abdessalaam, T. Z. and Francis, F. (2006) Age, growth, mortality and reproduction of the blackspot snapper, *Lutjanus fulviflamma* (Forsskal, 1775), in the southern Arabian Gulf. *Fish. Res.* **78**, 203–210.
- 1210 Grandcourt E.M., Al-Abdessaalam, T.Z., Al-Shamsi, A.T., Francis, F. (2006) Biology and assessment of the painted sweetlips (*Diagramma pictum* (Thunberg, 1792)) and the spangled emperor (*Lethrinus nebulosus* (Forsskal, 1775)) in the southern Arabian Gulf. *Fish. Bull.* **104**,75–88.
- 1215 Grandcourt, E., Al Abdessalaam, T.Z., Francis, F. and Al Shami, A., (2010). Age-based life history parameters and status assessments of by-catch species (*Lethrinus borbonicus*, *Lethrinus microdon*, *Pomacanthus maculosus* and *Scolopsis taeniatus*) in the southern Arabian Gulf. *J. Appl. Ichthyol.* **26**, 381-389.
- 1220 Grandcourt, E.; Al Abdessalaam, T. Z.; Francis, F.; Al Shamsi, A. (2011) Demographic parameters and status assessments of *Lutjanus ehrenbergii*, *Lethrinus lentjan*, *Plectorhinchus sordidus* and *Rhabdosargus sarba* in the southern Arabian Gulf. *J. Appl. Ichthyol.* **27**, 1203–1211.
- Gulland, J.A. (1969) Manual of methods for stock assessment. Part 1. Fish population analysis. *F.A.O. Man. Fish. Sci.* **4**. (154pp).
- Gust, N. (2004) Variation in the population biology of protogynous coral reef fishes over tens of kilometres. *Can. J. Fish. Aquat. Sci.* **61**, 205–218.
- 1225 Gust, N., Choat, J.H., Ackerman, J.L. (2002) Demographic plasticity in tropical reef fishes. *Mar. Biol.* **140**,1039–1051.
- Heupel, M.R., Williams, A.J., Welch, D.J., Davies, C.R., Penny, A.L., Kritzer, J.P., Marriott, R.J., Mapstone, B.D. (2010a) Demographic characteristics of exploited tropical lutjanids: a comparative analysis. *Fish. Bull.* **108**, 420-432.
- 1230 Heupel, M.R., Williams, A.J., Welch, D.J., Davies, C.R., Adams, S., Carlos, G., Mapstone, B.D. (2010b) Demography of a large exploited tropical grouper, *Plectropomus laevis*: implications for fisheries management. *Mar. Freshw. Res.* **61**, 184-195.

- 1235 Hoenig, J.M. (1983) Empirical use of longevity data to estimate mortality rates. *Fish Bull.* **82**, 898–903.
- Hordyk, A., Ono, K., Sainsbury K., Loneragan, N., Prince, J.D. (2014a) Some explorations of the life history ratios to describe length composition, spawning-per-recruit, and the spawning potential ratio. *ICES J. Mar. Sci.* doi:10.1093/icesjms/fst235
- 1240 Hordyk, A., Ono, K., Valencia, S.V., Loneragan, N., Prince, J.D. (2014b). A novel length-based estimation method of spawning potential ratio (SPR), and tests of its performance, for small-scale, data-poor fisheries. *ICES J. Mar. Sci.* doi:10.1093/icesjms/fsu004
- Johannes, R. E. (1981) Words of the lagoon: fishing and marine lore in the Palau District of Micronesia. *Univ. California Press, Berkeley.* (245 pp).
- 1245 Johannes, R.E. (1991) Some suggested management initiatives in Palau's nearshore fisheries, and the relevance of traditional management. *South Pacific Commission, Inshore Fisheries Research Project Country Assignment Report* (39pp).
- Jones, G.P., Milicich, M.J., Emslie, M.J., Lunow, C. (1999) Self-recruitment in a coral reef fish population. *Nat.* **402**, 802-804.
- 1250 Jones, G.P., Planes, S., Thorrold, S.R. (2005) Coral Reef Fish larvae settle close to home. *Curr. Biol.* **15**, 1314-1318.
- Kitalong, A., Dalzell, P. (1994) A preliminary assessment of the status of inshore coral reef fish stocks in Palau. South Pacific Commission, *Inshore Fisheries Research Project Tech. Doc.* 6 (35pp).
- 1255 Kritzer, J. P. (2004) Sex-specific growth and mortality, spawning season, and female maturation of the stripey bass (*Lutjanus carponotatus*) on the Great Barrier Reef. *Fish. Bull.* **102**, 94–107.
- Leis, J.M., Rennis, D.S. (1983) The larvae of Indo-Pacific coral reef fishes. University of Hawaii Press, Honolulu. (269pp.)
- 1260 Loubens, G. (1978) Biologie de quelque especes de poisson du lagon neo-caledonien. I. Determination de age (otolithometrie). *Cah. ORSTOM Ser. Oceanogr.* **16**, 263–283.
- Loubens, G. (1980a) Biologie de quelques especes de Poissons du lagon Neo-Caledonien. II. Sexualite' et reproduction. *Cah. Indo- Pac* **2**, 41–72
- 1265 Loubens, G. (1980b) Biologie de quelques especes de Poissons du lagon Neo-Caledonien. III. Croissance. *Cah Indo-Pac.* **2**,101–153.
- Luckhurst, B.E., Dean, J.M., Reichert, M., (2000) Age, growth and reproduction of the lane snapper *Lutjanus synagris* (Pisces: Lutjanidae) at Bermuda. *Mar. Ecol. Prog. Ser.* **203**, 255–261.



- 1270 Mace, P., Sissenwine, M. (1993) How much spawning is enough? *Risk evaluation and biological reference points for fisheries management* (eds S. Smith, J. Hunt & D. Rivard), pp. 101-118. Can. Spec. Publ. Fish. Aquat. Sci. **120**.
- 1275 McIlwain, J.L., Taylor, B.M. (2009) Parrotfish population dynamics from the Marianas Islands, with a description of the demographic and reproductive characteristics of *Chlorurus sordidus*. *Final Report to the Western Pacific Regional Fisheries Management Council. University of Guam Marine Laboratory*. (61pp).
- McPherson, G. R., Squire, L., O'Brien, J. (1992) Reproduction of three dominant *Lutjanus* species of the Great Barrier Reef inter-reef fishery. *Asian Fish. Sci.* **5**, 15–24 .
- 1280 Maplestone, A., Currey, L.M., Williams, A.J., Pears, R., Simpfendorfer, C.A., Penny, A.L., Tobin, A., Welch, D.J. (2009) Comparative biology of key inter-reefal serranid species on the Great Barrier Reef. *Project Milestone Report to the Marine and Tropical Sciences Research Facility. Reef and Rainforest Research Centre Limited, Cairns* (55pp).
- Marriott, R.J., Jarvis, N.D.C. Adams, D.J., Gallash, A.E., Norriss, J., Newman, S.J. (2010) Maturation and sexual ontogeny in the spangled emperor *Lethrinus nebulosus*. *J. Fish. Biol.* **76**, 1396-1414.
- 1285 Marriott, R.J., Adams, D.J., Jarvis, N.D.C., Moran, M.J., Newman, S.J., Craine, M. (2011) Age-based demographic assessment of fished stocks of *Lethrinus nebulosus* in the Gascoyne Bioregion of Western Australia. *Fish. Manag. Ecol.* **18**, 89-103.
- 1290 Marriott, R.J., Mapstone, B.D., Begg, G.A. (2007) Age-specific demographic parameters, and their implications for management of the red bass, *Lutjanus bohar* (Forsskal 1775): A large, long-lived reef fish. *Fish Res.* **83**, 204-215.
- Mullon, C., Freon, P., Cury, P. (2005) The dynamics of collapse in world fisheries. *Fish Fish.* **6**, 111-120.
- 1295 Nanami, A., Kurihara, T., Kurita, Y., Aonuma, Y., Suzuki, N., Yamada, H. (2010) Age, growth and reproduction of the humpback red snapper *Lutjanus gibbus* off Ishigaki Island, Okinawa. *Ichthy. Res.* **57**, 240-244.
- Newman, S. J., Williams, D. M., Russ. G. R., (1996) Age validation, growth and mortality rates of the tropical snappers (Pisces: Lutjanidae) *Lutjanus adetii* (Castelnaud, 1873) and *L. quinquelineatus* (Bloch, 1790) from the central Great Barrier Reef, Australia. *Mar. Freshw. Res.* **47**,575–584.
- 1300 Newman, S. J., Cappo, M., Williams. D. M. (2000a.) Age, growth and mortality of the stripey, *Lutjanus carponotatus* (Richardson) and the brown-stripe snapper, *L. vitta* (Quoy and Gaimard) from the central Great Barrier Reef, Australia. *Fish. Res.* **48**:263–275.
- 1305 Newman, S. J., Cappo, M. & Williams, D. M. (2000b). Age, growth, mortality rates and corresponding yield estimates using otoliths of the tropical red snappers, *Lutjanus erythropterus*, *L. malabaricus* and *L. sebae*, from the central Great Barrier Reef. *Fish. Res.* **48**, 1–14.

- Newman, S. J., Dunk, I. J. (2003) Age validation, growth, mortality, and additional population parameters of the goldband snapper (*Pristipomoides multidens*) off the Kimberley coast of Northwestern Australia. *Fish. Bull.* 101:116–128.
- 1310 Pardo, S.A., Cooper, A.B., Dulvy, N.K. (2013) Avoiding fishy growth curves. *Meth. Ecol. Evol.* doi: 10.1111/2041-210x.12020
- Pauly, D. (1980) On the interrelationship between mortality, growth parameters and mean temperature in 175 fish stocks. *J. Cons. Int. Explor. Mer.*, **39**, 175-92.
- 1315 Pember, M. B. *et al.* 2005. Biological parameters for managing the fisheries for Blue and King Threadfins, Estuary Rockcod, Malabar Grouper and Mangrove Jack in north-western Australia. *FRDC project 2002/003*. Murdoch University, Western Australia, 2005. (224 pp.)
- 1320 Perron, F.E., Narao, A.M., Patris, S.J. (1983) The Palau reef fish production study: a baseline study of the commercial reef fishing industry in Palau and a blueprint for the development of a permanent fisheries management system. *Palau Div. Mar. Res.* (55 pp).
- Planes, S., Jones, G.P., Thorrold, S.R., Lubchenco, J. (2009) Larval dispersal connects fish populations in a network of marine protected areas. *Proc. Nat. Acad. Sci.* **106**, 5693-5697.
- 1325 Prince, J.D., Hordyk, A., Valencia, S.V., Loneragan, N., Sainsbury K., (2014) Revisiting the concept of Beverton-Holt Life History Invariants with the aim of informing data-poor fisheries assessment. *ICES J. Mar. Sci.* doi:10.1093/icesjms/fsu011
- Preston, G.L. (1990) Inshore fishery resource management in Palau. South Pacific Commission. Unpubl. Mss. cited in Johannes 1991 & Kitalong and Dalzell 1994.
- 1330 Restrepo, V.R., Powers, J.E. (1999) Precautionary control rules in US fisheries management: specification and performance. *ICES J. Mar. Sci.* **56**, 846-852.
- Rhodes K. L., Taylor B. M., Wichilmel C. B., Joseph E., (2013) Reproductive biology of squaretail coralgroupers *Plectropomus areolatus* using age-based techniques. *J. Fish Biol.* **82**, 1333–1350.
- 1335 Russ, G. R., Lou, D. C., Higgs, J. B., and Ferreira, B. P. (1998) Mortality rate of a cohort of the coral trout, *Plectropomus leopardus*, in zones of the Great Barrier Reef Marine Park closed to fishing. *Mar. Freshwater Res.* **49**, 507–511. doi:10.1071/MF97224.
- Sabetian, A. (2010) Parrotfish fisheries and population dynamics: a case-study from Solomon Islands. *PhD thesis, James Cook University.* (227pp).
- 1340 Sadovy, Y. J., (1996) Reproduction of reef fishery species. In: Reef fisheries. N. V. C. Polunin and C. M. Roberts (Eds). Chapman and Hall, London, pp. 15–59.
- Sadovy de Mitcheson, Y., Liu, M. (2008) Functional hermaphroditism in teleosts. *Fish Fish.* **9**, 1–43

- 1345 Shimose, T., Nanami, A. (2014) Age, growth, and reproductive biology of blacktail snapper, *Lutjanus fulvus*, around the Yaeyama Islands, Okinawa, Japan. *Ichthyol. Res.* **61**, 322-331.
- Shimose, T., Tachihara, K. (2005) Age, growth and maturation of the blackspot snapper *Lutjanus fulviflamma* around Okinawa Island, Japan. *Fish. Sci.* **71**, 48–55.
- Taylor, B.M. (2010) Life history and per-recruit assessment of *Lethrinus obsoletus* from Guam. *University of Guam Marine Laboratory Tech. Rep.* **128**, (16 pp).
- 1350 Taylor, B.M., Choat, J.H. (2014) Comparative demography of commercially important parrotfish species from Micronesia. *J. Fish Biol.* **84**, 383–402. doi:10.1111/jfb.12294.
- Taylor, B.M., McIlwain, J.L. (2010) Beyond abundance and biomass: effects of marine protected areas on the demography of a highly exploited reef fish. *Mar. Ecol. Prog. Ser.* **411**, 243-258.
- 1355 Toor H.S. (1964) Biology and fishery of the pig-face bream, *Lethrinus lentjan* Lacepede. II. Maturation and spawning. *Indian J. Fish.* **11**, 581–596.
- Toor H.S. (1964) Biology and fishery of the pig-face bream, *Lethrinus lentjan* Lacepede. III. Age and growth. *Indian J. Fish.* **11**, 597–620.
- 1360 Trianni, M.S. (2011) Biological characteristics of the spotcheek emperor, *Lethrinus rubrioperculatus*, in the Northern Mariana Islands. *Pac. Sci.* **65**, 345-363.
- Walters, C., and Martell, S. J. D. (2004) Fisheries Ecology and Management. *Princeton University Press, Princeton, NJ.* (399 pp)
- Walters, C., Pearse, P.H. (1996) Stock information requirements for quota management systems in commercial fisheries. *Rev. Fish Biol. Fish.* **6**, 21-42.
- 1365 Williams, A.J., Ballagh, A.C., Begg, G.A., Murchie, C.D., Currey, L. (2008) Population biology of coral trout species in the eastern Torres Strait: implications for fishery management. *Cont. Shelf Res.* **28**, 2129-2142.
- 1370 Williams D. McB., Russ, G.R. (1994) Review of data on fishes of commercial and recreational fishing interest in the Great Barrier Reef. *Great Barrier Reef Marine Park Authority (Australia) Res. publ.* Vol. 1., **33** (103 pp).

## 7. List of Tables

- 1375 Table 1. The assumed parameter estimates, with bounds, and the sample sizes, used to assess 12 Indo-pacific reef species of reef fish in Palau,  $M/k$  – the ratio of natural mortality ( $M$ ) and von Betalanffy growth coefficient ( $k$ ),  $L_{\infty}$  - asymptotic size,  $L_{50\%}$  - size of 50% maturity,  $L_{95\%}$  - size of 95% maturity,  $L_m/L_{\infty}$  - the ratio of size of maturity and

asymptotic size,  $n$  - Length Comp. - length frequency composition sample size,  $n$  - SOM - sample size for size of maturity estimate.

1380 Table 2. Point estimates of spawning potential ( $SPR$ ), fishing pressure ( $F/M$ ) and selectivity ( $SL_{95\%}$ ,  $SL_{50\%}$ ) derived with ‘best’ estimate parameters from the length-based assessment of 12 Indo-pacific reef species of reef fish in Palau.

1385 Table 3. Listing of the 12 assessed species with their sample size ( $n$ ), the ranking of the variance around their assessment (Figure 5 a & b), from highest (1) to lowest 12 for each of the estimated based on Bootstrapping the size data (BS Var) and SIR analysis of parameter uncertainty (SIR Var). In this table the species are ordered from low to high, by each species ratio of, our assumed lower bound on  $L_{\infty}$ , and the  $L_{95\%}$ . As this value approaches 1.0, the bounds placed upon  $L_{\infty}$  this parameter reach a lower maximum, thus the assessments with lowest ratios, at the top of this table, have a tendency to coincide with higher variance ranking (lower numbers).

1390

## 8. List of Figures

Figure 1. Map of Palau showing its size and position in the western Pacific Ocean, and the location of the Northern Reef Area, the location of this study..

1395 Figure 2. An examples of output from the length-based  $SPR$  assessment software for *Lutjanus gibbus*; a) length-frequency histogram with fitted size composition curve (dashed line), b) frequency distribution of  $SPR$  estimates from one thousand bootstrapped iterations of the length-frequency data, and SIR estimated posterior distributions across the assumed plausible range of c) for  $M/k$ , d)  $L_{\infty}$ , e)  $S_{L50}$ , f)  $S_{L95}$ , g)  $F/M$  estimated similarly, and h)  $SPR$ .

1400

Figure 3. An examples of output from the length-based  $SPR$  assessment software for *Lethrinus xanthochilus*; a) length-frequency histogram with fitted size composition curve (dashed line), b) frequency distribution of  $SPR$  estimates from one thousand bootstrapped iterations of the length-frequency data, and SIR estimated posterior distributions across the assumed plausible range of c) for  $M/k$ , d)  $L_{\infty}$ , e)  $S_{L50}$ , f)  $S_{L95}$ , g)  $F/M$  estimated similarly, and h)  $SPR$ .

1405

Figure 4. Length composition histograms for 12 Indo-pacific species of reef fish in Palau with curves fitted by the Length Based  $SPR$  assessment software; A- *Lutjanus gibbus*, B - *Lutjanus bohar*, C- *Lethrinus rubrioperculatus*, D - *Lethrinus olivaceus*, E - *Lethrinus xanthochilus*, F - *Lethrinus obsoletus*, G - *Plectropomus areolatus*, H - *Plectropomus leopardus*, I - *Variola louti*, J - *Scarus rubroviolaceus*, K - *Chlorurus microrhinos*, L - *Hipposcarus longiceps*.

1410

Figure 5. Two sets of box plots depicting the uncertainty expected around the  $SPR$  estimates from the 12 assessments; a) distribution of  $SPR$  estimates from bootstrapping the length frequency data, and b) distribution of  $SPR$  estimates based on SIR resampling of the plausible range of parameter estimates (Table 1). In these plots the 25th, 50th (median) and 75th percentiles are shown by the bottom, middle and top lines of the box

1415

1420

respectively. The broken line ‘whiskers’ extend to 1.5 times the interquartile range from the box, and all observations outside this range are presented as open circles. Horizontal dotted lines indicate  $SPR_{20\%}$  and  $SPR_{40\%}$ .

## Tables

Species	M/k Best	M/k Upper	M/k Lower	$L_{\infty}$ Best	$L_{\infty}$ Upper	$L_{\infty}$ Lower	$L_{50}$	$L_{95}$	$L_m/L_{\infty}$ Best	n - Length Comp.	n - SOM
<i>Lutjanus gibbus</i>	0.41	0.60	0.30	343	400	340	257	320	0.75	1227	449
<i>Lutjanus bohar</i>	0.41	0.60	0.30	487	570	470	365	460	0.75	145	38
<i>Lethrinus rubrioperculatus</i>	0.62	0.89	0.35	306	370	300	214	270	0.70	533	300
<i>Lethrinus olivaceus</i>	0.62	0.89	0.35	584	670	550	409	500	0.70	366	155
<i>Lethrinus xanthochilus</i>	0.62	0.89	0.44	463	640	390	324	380	0.70	144	103
<i>Lethrinus obsoletus</i>	0.62	0.89	0.44	343	365	330	240	300	0.70	211	83
<i>Plectropomus areolatus</i>	0.91	1.30	0.46	649	815	540	383	460	0.59	322	136
<i>Plectropomus leopardus</i>	0.91	1.00	0.46	627	811	537	370	440	0.59	185	53
<i>Variola louti</i>	0.86	1.50	0.58	483	527	419	285	350	0.59	578	113
<i>Hipposcarus rubroviolaceus</i>	0.36	0.79	0.25	433	459	410	312	400	0.72	159	116
<i>Chlorurus microrhinos</i>	0.70	1.26	0.53	470	500	395	315	380	0.67	150	111
<i>Hipposcarus longiceps</i>	1.07	1.26	0.81	423	440	360	300	330	0.71	403	181

1425

Table 1

Species	SPR (%)	F/M	$S_{L50\%}$ (mm)	$S_{L95\%}$ (mm)
<i>Lutjanus gibbus</i>	0.10	4.1	224	252
<i>Lutjanus bohar</i>	0.27	1.4	265	347
<i>Lethrinus rubrioperculatus</i>	0.23	3.9	239	279
<i>Lethrinus olivaceus</i>	0.10	5+	465	608
<i>Lethrinus xanthochilus</i>	0.13	5+	351	440
<i>Lethrinus obsoletus</i>	0.03	5+	260	325
<i>Plectropomus areolatus</i>	0.05	5+	480	571
<i>Plectropomus leopardus</i>	0.01	5+	334	419
<i>Variola louti</i>	0.20	1.4	203	266
<i>Scarus rubroviolaceus</i>	0.07	5+	355	454
<i>Chlorurus microrhinos</i>	0.21	3.1	333	406
<i>Hipposcarus longiceps</i>	0.05	5+	276	313

Table 2

1430

<i>Species</i>	<i>n</i>	BS Var	SIR Var	Low $L_{\infty}/L_m$
<i>Lutjanus bohar</i>	145	1	5	1.02
<i>Scarus rubroviolaceus</i>	159	8	4	1.03
<i>Lethrinus xanthurus</i>	144	5	2	1.03
<i>Chlorurus microrhinos</i>	150	2	1	1.04
<i>Lutjanus gibbus</i>	1227	9	10	1.06
<i>Hipposcarus longiceps</i>	403	10	9	1.09
<i>Lethrinus obsoletus</i>	211	12	10	1.10
<i>Lethrinus olivaceus</i>	366	7	6	1.10
<i>Lethrinus rubrioperculatus</i>	533	3	3	1.11
<i>Plectropomus areolatus</i>	322	11	7	1.17
<i>Variola louti</i>	578	4	8	1.20
<i>Plectropomus leopardus</i>	185	6	11	1.22

Table 3

1435 **Figures**

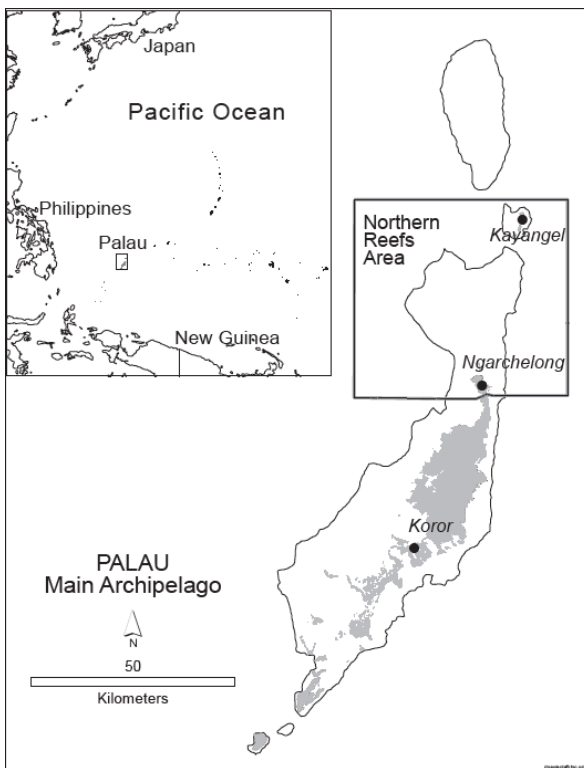
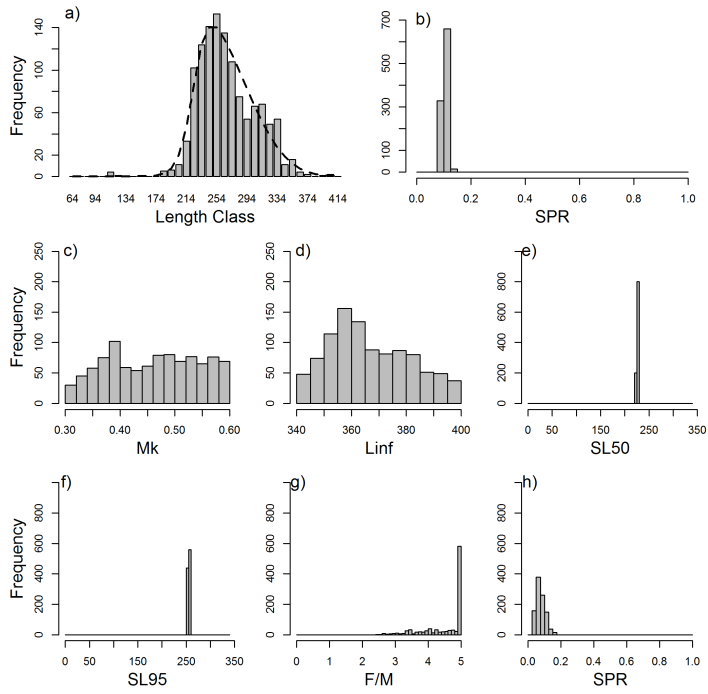
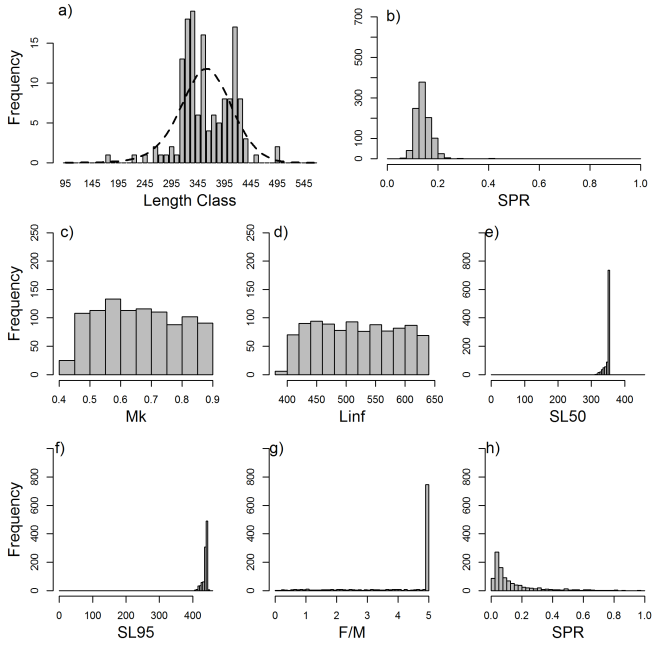


Figure 1.

1440



1445 Figure 2.



1450 Figure 3.

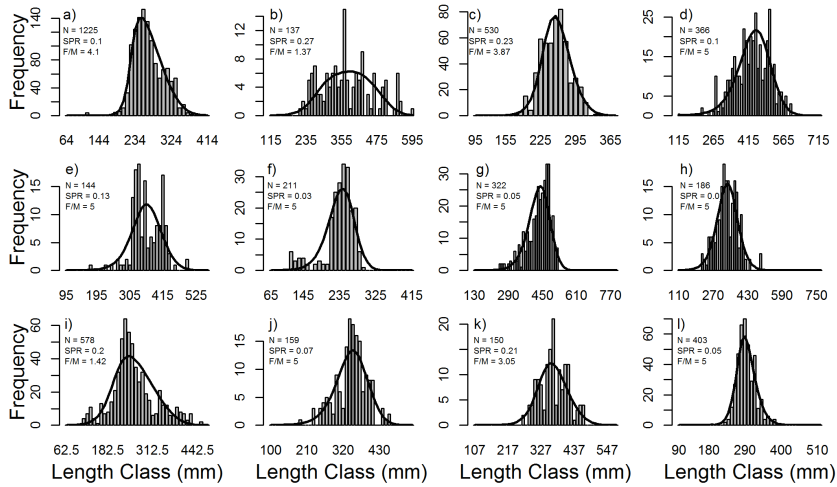


Figure 4.

1455



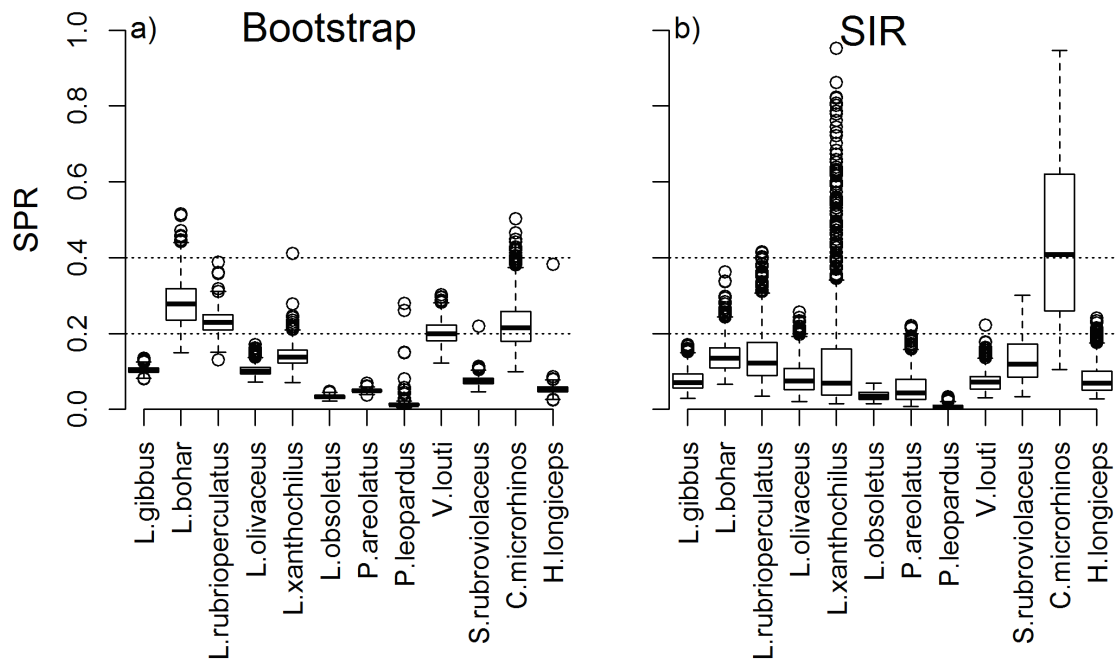


Figure 5.