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Evaluating the performance of otolith morphometrics in deriving age compositions and mortality rates for assessment of data-poor tropical fisheries

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Deepwater snappers (Family Lutjanidae) are important to artisanal and subsistence fisheries in Pacific Island countries. Most species of deepwater snapper are considered vulnerable to exploitation due to their extended longevity and low natural mortality rates. However, the sustainability of deepwater snapper fisheries in Pacific Island countries remains uncertain because there are limited resources available to collect the required data for comprehensive stock assessments. Reliable estimates of the age composition for exploited deepwater snapper populations are limited primarily because of the lack of skills and resources required for routine age estimation from sectioned otoliths. The development of alternative low-cost approaches to derive estimates of age for deepwater snappers is required. We evaluated the performance of using otolith morphometrics (weight, length, width, and thickness) to obtain estimates of age for the most important target species in these fisheries: *Etelis carbunculus*, *E. marshi*, *E. coruscans*, and *Pristipomoides filamentosus*. We compared age compositions and fishing mortality rates (F) derived from otolith morphometrics with those derived from counts of annual increments in otoliths. We then used the ratio of F to natural mortality (M) as a biological indicator to evaluate the potential effects on management responses by comparing estimates of F/M derived from otolith morphometrics with those derived from annual increment counts. Age compositions and estimates of F and F/M did not differ significantly between those derived from otolith morphometrics and those derived from annual increment counts for all species. These results demonstrate that management responses would likely be similar whether based on age estimates derived from sectioned otoliths, or predicted from otolith morphometrics. In the absence of sufficient resources to section otoliths for age estimation, we recommend that otolith morphometrics be used as a proxy for age in assessments of deepwater snapper fisheries in Pacific Island countries, and potentially for other similar data-limited fisheries.

Keywords: age, biological indicators, deepwater snapper, *Etelis*, mortality, otolith morphometrics, Pacific Ocean, *Pristipomoides*, random forest, reference points.

Introduction

Deepwater fisheries occur within all ocean basins with fishing effort typically concentrated on seamounts, continental slopes, and other

deepwater bathymetric features. Life histories of deepwater fish are characterized by high longevity, slow growth, delayed maturity, and low fecundity, indicating low production potential and resilience

(Koslow, 1996, 1997; Morato *et al.*, 2006; Norse *et al.*, 2012). As such, many deepwater species are considered more vulnerable to exploitation than shallow-water species (Koslow *et al.*, 2000; Morato *et al.*, 2006; Norse *et al.*, 2012), placing greater urgency for their conservation and management in the deepwater environment.

In the tropical and subtropical regions of the Pacific Ocean, most deepwater fisheries are small-scale artisanal and subsistence fisheries that have a strong local economic and cultural value in many Pacific Island countries (Dalzell *et al.*, 1996; Williams *et al.*, 2012). Deepwater fisheries provide an important source of protein to Pacific Islanders who are highly dependent on fish for food security. Snappers (Lutjanidae) are the main species targeted by deepwater fisheries in this region, but species of groupers (Epinephelidae) and emperors (Lethrinidae) are also harvested. Although catches are low relative to industrial-scale fisheries, deepwater snappers are considered vulnerable to exploitation, due to their life history traits and relatively low productivity potential (Newman and Dunk, 2003; Fry *et al.*, 2006; Williams *et al.*, 2013). Thus, developing management strategies to ensure ecological and economic sustainability of deepwater snapper fisheries has become a priority for Pacific Island resource management (Williams *et al.*, 2012).

Stock assessments of deepwater snappers in the Pacific Ocean have been limited to simple production models because of a lack of information on size and age composition of catches (Martell *et al.*, 2011). Furthermore, these assessments have been limited to just a few jurisdictions within the Pacific Ocean (e.g. Hawaii, Tonga, and Vanuatu) due to the absence of reliable catch and effort data in most Pacific Island countries. As such, there is substantial uncertainty in assessment outputs and the status of deepwater snapper fisheries in the region (Brodziak *et al.*, 2011). Improving future assessments through the collection of size and age information from catches will be important to reduce this uncertainty. However, the high degree of variation in size-at-age for deepwater snapper species results in many age classes accumulating within a narrow length range (e.g. Newman and Dunk, 2003; Fry *et al.*, 2006; Williams *et al.*, 2013). Therefore, length data alone would be of little value for estimating population parameters, and emphasis should be placed on estimating the age composition of the catch.

Fish age is most commonly and reliably estimated from counts of increments in sectioned otoliths (Campana, 2001). The preparation of otoliths for age estimation can be time consuming and costly, and the interpretation of otolith increments requires appropriate skills and experience. Therefore, age estimation using standard procedures is likely to be beyond the reach of available resources in most Pacific Island countries, and development of alternative low-cost approaches to derive estimates of age for deepwater snappers is required. The strong relationship between otolith morphometrics and age has precipitated many studies over the past three decades that have evaluated the utility of otolith morphometrics in predicting the age of fish (e.g. Boehlert, 1985; Pawson, 1990; Worthington *et al.*, 1995a; Newman *et al.*, 1996a; Lou *et al.*, 2005; Bermejo, 2014). These studies have demonstrated relatively high predictability of age (usually >70% of variance in age explained) from otolith weight, length, width, thickness, or area in a wide range of temperate (e.g. Doering-Arjes *et al.*, 2008; Lepak *et al.*, 2012; Britton and Blackburn, 2014) and tropical species (e.g. Newman *et al.*, 1996a; Pilling *et al.*, 2003; Lou *et al.*, 2005; Steward *et al.*, 2009). Estimating age using otolith morphometrics requires relatively little training, and is faster and less expensive than counting increments in otoliths (Boehlert, 1985). As such, the use of otolith morphometrics as proxies for age has been advocated in

situations where estimating age from counting increments in otoliths is problematic due to limited resources or insufficient skills (Pilling *et al.*, 2003).

Most studies have used a single variable, usually otolith weight (e.g. Pilling *et al.*, 2003; Lou *et al.*, 2005), when evaluating the performance of otolith morphometrics for predicting age. However, greater accuracy in age predictions can be gained by including multiple otolith morphometrics and biological characteristics (e.g. fish length, weight, and sex; Francis and Campana, 2004; Bermejo, 2007, 2014). Here, we evaluate the performance of using several otolith morphometrics (otolith weight, length, width, and thickness) to predict the age of four important target species of deepwater snapper: Ruby snapper (*Etelis carbunculus*), Flame snapper (*E. coruscans*), Pygmy ruby snapper (*E. marshi*), and Crimson jobfish (*Pristipomoides filamentosus*). We chose these variables because they can easily be measured by fisheries staff in Pacific Island countries with limited financial resources. We used a random forest analysis, an ensemble machine learning approach (Breiman, 2001; Strobl *et al.*, 2009), to predict ages from otolith morphometrics data because random forests can manage a large number of predictor variables, have high prediction accuracy, provide descriptive variable importance measures, and have the ability to model correlated variables and complex non-linear interactions (Cutler *et al.*, 2007; Strobl *et al.*, 2009). Thus, random forests are particularly suited to predicting age from otolith morphometrics data (Lepak *et al.*, 2012; Dub *et al.*, 2013). Previous applications of random forests to otolith morphometric data have focused on short-lived freshwater species (Lepak *et al.*, 2012; Dub *et al.*, 2013). We extend the results from these studies to a group of long-lived marine species, thereby testing the suitability of the random forest analysis of otolith morphometrics across a wider range of life histories.

We further extend previous research on otolith morphometrics by comparing age compositions and fishing mortality rates (F) derived from otolith morphometrics with those derived from counts of annual increments in otoliths for each species. We then evaluate the potential effects on management responses by comparing estimates of biological indicators (i.e. ratios of F to natural mortality) derived from otolith morphometrics with those derived from annual increment counts against established biological reference points (Wise *et al.*, 2007). This approach has broader application to other resource-limited settings where otolith morphometrics can provide comparable estimates of age compositions and mortality rates to those from sectioned otoliths.

Material and methods

Sample collection

Samples of *E. carbunculus*, *E. coruscans*, *E. marshi*, and *P. filamentosus* were collected across the South Pacific Ocean, from the waters of Fiji, New Caledonia, Papua New Guinea, Samoa, Tonga, Vanuatu, and Wallis and Futuna (Figure 1). *Etelis marshi* has only recently been recognized as a separate species from *E. carbunculus* (Andrews *et al.*, 2011), and we distinguished the two species based on colouration of the upper lobe of the caudal fin and the shape of the opercular spine (Wakefield *et al.*, 2014). Samples were collected during scientific surveys and from commercial and artisanal landings in port by trained fisheries staff between October 2012 and April 2014. Fish were captured during scientific surveys using four standardized vertical droplines connected to hydraulic reels, and the terminal rig consisted of 10 circle hooks (size 11/0), a steel weight of ~5 kg, and Pacific saury (*Cololabis saira*) and squid as baits. The fishing depth ranged between ~100 and 500 m. At each

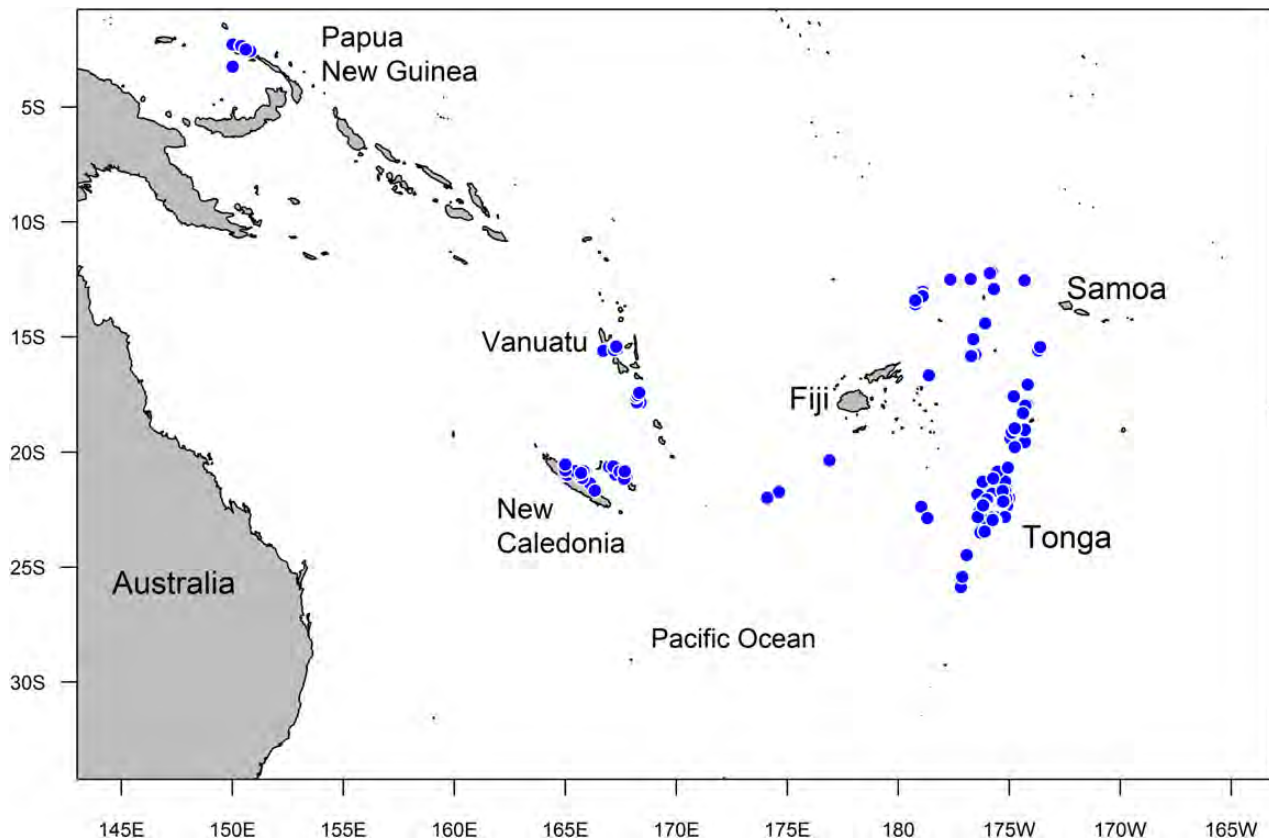


Figure 1. Locations where deepwater snapper were sampled in the South Pacific Ocean.

fishing location, the vessel drifted over the fishing area, and each drift lasted between 10 min and 1.5 h. Each dropline was deployed and retrieved usually once per drift up to a maximum of three times. Commercial and artisanal fishers use similar dropline fishing gear, except fishers usually deploy fewer hooks per reel and reels are manually hauled. The fork length (to the nearest 0.5 cm) of each fish was measured and otoliths were removed, cleaned, and stored dry in plastic vials.

Sample processing

Morphometric measurements were taken from an unbroken otolith from each fish. Otolith dimensions were measured using digital calipers to the nearest 0.01 mm and included (i) the length of the otolith from rostrum to postrostrum, (ii) the width of the otolith at the widest point approximately perpendicular to an axis through the rostrum and postrostrum, and (iii) the thickness of the otolith across the primordium, perpendicular to the sulcus acusticus. The weight of each otolith was measured to the nearest 0.0001 g using a calibrated balance with glass draft shields.

We used methods similar to other studies on deepwater teleosts to prepare thin otolith sections for age estimation (Wakefield *et al.*, 2010, 2013a, b). Briefly, the sagitta of each fish was embedded in epoxy resin and sectioned transversely through the primordium, in a direction perpendicular to the sulcus acusticus, using a low speed saw with a diamond tipped blade. Otolith sections were cut thinly (0.15–0.20 mm) to improve increment clarity. Sections were mounted on glass slides with a cover slip using casting resin. Opaque increments on each otolith section were counted using a

compound microscope under reflected light at $\times 50$ to $\times 100$ magnification. The opaque increments were counted primarily along an axis from the primordium to the otolith margin on the ventral rim of the sulcus acusticus (Figure 2) as this was typically the axis with the most well-defined increments. However, other axes were examined as a reference when opaque increments were unclear on the primary axis.

Bomb radiocarbon dating has validated that a single opaque zone is deposited annually in the otoliths of *E. carbunculus* (Andrews *et al.*, 2011), and that counts of opaque increments from otolith sections are accurate for determining ages. Although the periodicity in increment formation has not been directly validated for *E. marshi*, *E. coruscans*, and *P. filamentosus*, we presumed that opaque increments in these species were also deposited annually. Counts of opaque increments from each otolith section were obtained independently from a single read by two readers (MB and AJW). If increment counts were the same for each reader, that count was used as the final age. When increment counts differed between readers, an agreed final age was assigned after a joint reading by both readers. If agreement could not be reached, the mean age from the first two reads was used as the final age. If no pattern could be seen in the otolith section, a final age was not assigned. The total number of samples of each species that were collected for which a complete set of otolith morphometric measurements and age estimates was available is summarized in Table 1. These available data covered the full length and age range of fish collected, such that biases towards particular sized otoliths were unlikely. Maximum ages estimated from otolith sections were 43 years for *E. carbunculus*,

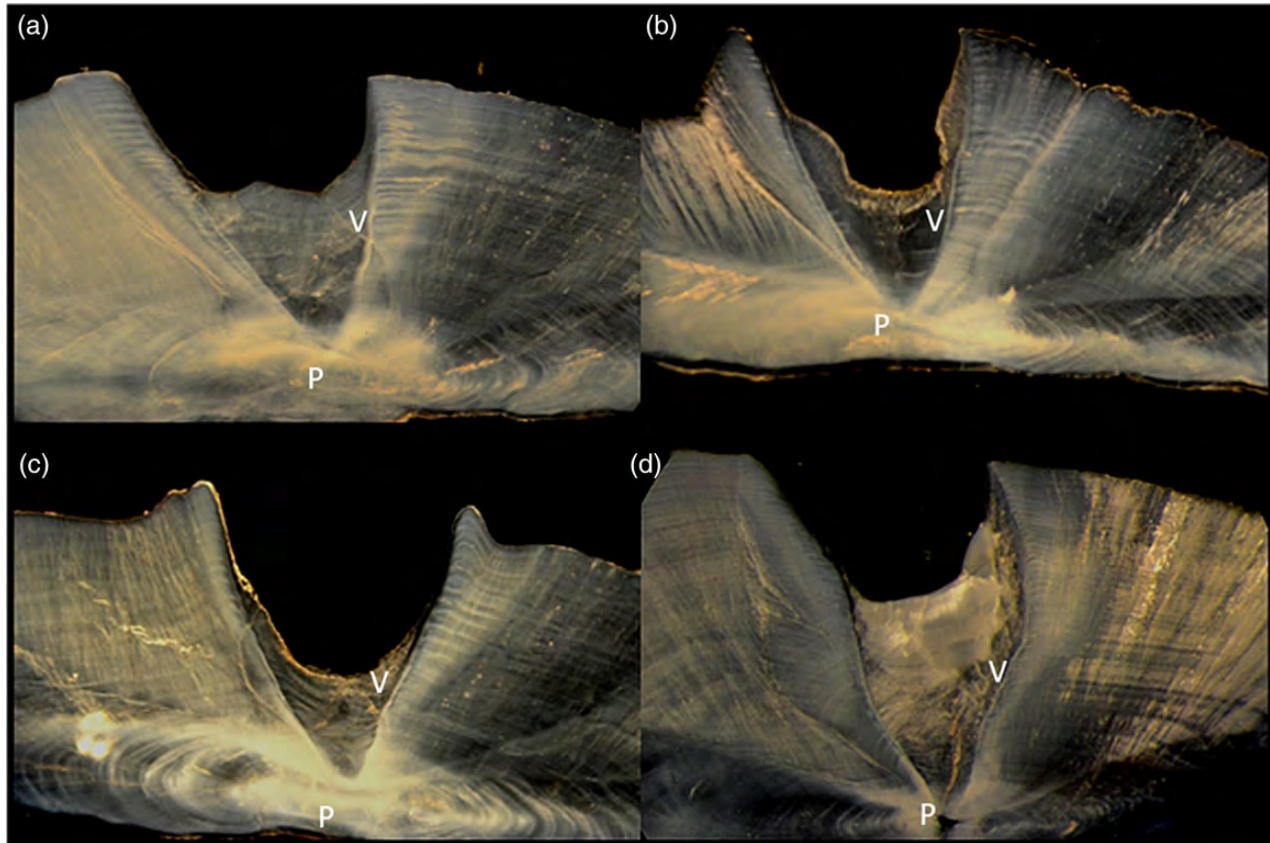


Figure 2. Transverse sections of sagittae from a 70-cm fork length (FL) *Etelis carbunculus* (a), 69-cm FL *E. coruscans* (b), 47-cm FL *E. marshi* (c), and 78-cm FL *Pristipomoides filamentosus* (d) viewed under reflected light at $\times 50$ magnification. Opaque increments were counted primarily along an axis from the primordium (P) to the otolith margin on the ventral rim of the sulcus acusticus (V).

Table 1. Number, fork length (FL), and estimated age range (from counts of increments in sectioned otoliths) of four deepwater snapper species sampled from the South Pacific Ocean from which otolith morphometrics were measured.

Species	n	Length range (cm, FL)	Age range (years)
<i>Etelis carbunculus</i>	130	14–115	3–43
<i>Etelis coruscans</i>	165	22–90	3–40
<i>Etelis marshi</i>	128	25–60	4–29
<i>Pristipomoides filamentosus</i>	85	30–78	11–64

40 years for *E. coruscans*, 29 years for *E. marshi*, and 64 years for *P. filamentosus* (Table 1).

Statistical analyses

We used random forest regression analysis to predict the ages of *E. carbunculus*, *E. marshi*, *E. coruscans*, and *P. filamentosus* from otolith morphometrics data. Random forests involve fitting an ensemble of regression trees, then averaging the predictions across all trees. The random forest algorithm first selects many (e.g. >500) bootstrap samples from the data, each of which contains $\sim 63\%$ of the original observations (Strobl et al., 2009). Observations that are not selected in each bootstrap sample are referred to as out-of-bag observations. A regression tree is then fitted to each bootstrap sample, but only a subset of randomly

selected predictor variables are used at each node. The trees are fully grown with no pruning, then each tree is used to predict the out-of-bag observations. The predicted value of an observation is calculated by averaging the out-of-bag predictions for that observation across all trees. The out-of-bag estimates are considered a cross-validation of the accuracy of estimates because they are not used in the fitting of trees. The relative importance of each predictor variable is then determined from the misclassification rate for the out-of-bag observations. More detailed descriptions of random forests and their application can be found in Breiman (2001), Cutler et al. (2007), and Strobl et al. (2009).

We used the *randomForest* package, version 4.6–7 (Liaw and Wiener, 2002) in R version 3.0.1 (R Core Team, 2013) to predict ages of *E. carbunculus*, *E. marshi*, *E. coruscans*, and *P. filamentosus* using the predictor variables otolith weight, length, width, and thickness. Fork length and location of capture (latitude and longitude) were included also as predictor variables in the random forest analysis because of the known relationship between fish length and age, and because samples were collected from a wide area of the South Pacific Ocean and previous studies have demonstrated significant spatial variation in the relationship between otolith weight and age (e.g. Lou et al., 2005). A sufficiently large number of trees (10 000) were used, and different random seeds were applied for each species to ensure stability in variable importance and predictions. We found only trivial differences in results when using different numbers of predictor variables at each tree node. Therefore, we used the default value applied in the

randomForest package (number of predictor variables divided by 3). Predicted ages for each individual fish were rounded to the nearest whole year to classify individuals by annual age class and to generate age frequency distributions. For each species, we used multidimensional contingency tables to compare age frequency distributions derived from estimated (counts of otolith increments) and predicted (random forest predictions from otolith morphometrics) ages.

We used age-based catch curves to estimate the instantaneous rate of total mortality (Z) for each species from estimated and predicted age frequency distributions. Catch curves were generated by fitting weighted linear regressions to the natural logarithm of the frequency of individuals in each age class against fish age, with the negative of the weighted regression slope providing an estimate of Z . We used weighted linear regression because it generally outperforms other mortality estimators (Smith *et al.*, 2012). An unweighted linear regression was fitted to all age classes with non-zero frequencies that were older than the youngest modal age (assumed age at full selectivity). The resulting regression model was used to predict log-transformed frequencies at each age, which were used as the regression weights in a subsequent fit using the same age range. The predicted log-transformed frequencies were occasionally zero, in which cases the weight of the age group was set to zero, with the remaining weights scaled to sum to one (Smith *et al.*, 2012). Estimates of Z from estimated and predicted age frequency distributions were compared using ANCOVA for each species, with age as the covariate.

Biological indicators and reference points

We evaluated the potential effects on management responses of using estimated or predicted ages by comparing estimates of biological indicators derived from each ageing method for each species and relating these to established biological reference points. Biological indicators and reference points relating the fishing mortality rate (F) to the natural mortality rate (M) have been established and applied to deepwater snapper fisheries in Western Australia in the Indian Ocean (Wise *et al.*, 2007). Specific biological reference points include a target level at $F/M = 0.67$, a threshold level at $F/M = 1$, and a limit level at $F/M = 1.5$. Potential management decision rules for each of these reference points are described in Table 2. We estimated M for each species by fitting the linear equation $\log_e(M) = 1.44 - 1.01 \times \log_e(t_{\max})$, where t_{\max} is the maximum age observed (Hoenig, 1983). Estimates of F were calculated as the difference between Z and M . We then compared ratios of F/M derived from estimated ages with those from predicted ages to evaluate whether management decisions would likely change as a result of whether ages were estimated from increment counts in otoliths or predicted from otolith morphometrics. It must be emphasized that the estimation of biological indicators was purely illustrative because mortality rates were estimated from samples collected

over a wide area, and may not have been sourced from the same stock. Therefore, the estimates of biological indicators may not necessarily reflect the status of deepwater snapper fisheries in the South Pacific Ocean.

Results

The relative importance of variables in predicting the age of individuals from the random forest analysis varied among species, but either otolith weight or otolith thickness was the most important predictor variable across all species (Figure 3). Fork length and otolith width were relatively important for predicting ages of *E. carbunculus*, but much less important for other species. Latitude and longitude were consistently of low importance for predicting age across all species. The random forest analysis did not predict accurately the age of many individual fish for all species, but the age of most individuals was predicted to within 2 or 3 years of the estimated age (Figure 4). There was also a slight tendency for predicted ages to overestimate the age of young fish and underestimate the age of older fish (Figure 4).

We did not detect any statistically significant differences between the age frequency distributions derived from predicted ages and those derived from estimated ages for *E. carbunculus* ($\chi^2 = 29.06$, d.f. = 34, $p = 0.71$), *E. coruscans* ($\chi^2 = 19.40$, d.f. = 31, $p = 0.95$), *E. marshi* ($\chi^2 = 26.45$, d.f. = 23, $p = 0.28$), and *P. filamentosus* ($\chi^2 = 37.28$, d.f. = 31, $p = 0.20$; Figure 5). The strong and weak age classes were consistent between ageing methods for *E. carbunculus*, *E. coruscans*, and *P. filamentosus*, but were not always predicted accurately for *E. marshi*. In addition, predicted age frequency distributions tended to underestimate the frequency of the youngest and oldest age classes from estimated age frequency distributions. However, we did not detect any significant differences in the estimates of Z from age-based catch curves (Table 3 and Figure 6) between estimated and predicted ages for *E. carbunculus* ($F = 0.54$, d.f. = 1, $p = 0.59$), *E. coruscans* ($F = 0.65$, d.f. = 1, $p = 0.52$), *E. marshi* ($F = 0.17$, d.f. = 1, $p = 0.87$), and *P. filamentosus* ($F = 0.22$, d.f. = 1, $p = 0.83$). Estimates of M derived from estimated ages were relatively low, ranging from 0.06 for *P. filamentosus* to 0.14 for *E. marshi* (Table 3).

We did not detect any statistically significant differences between estimates of biological indicators (F/M) derived from predicted ages and those derived from estimated ages across all species (Figure 7). Estimates of F/M from estimated and predicted ages were less than the target reference point of 0.67 for all species. However, the 95% confidence intervals for the estimates of F/M for *E. marshi* exceeded the target level, but not the threshold level (i.e. $F/M = 1$), for both estimated and predicted ages (Figure 7). It is highly likely, therefore, that the management response for each species would be similar whether biological indicators were based on age estimates derived from sectioned otoliths, or predicted from otolith morphometrics. For example, the estimates of F/M presented here and the biological reference points and decision rules in Table 2 would support management decisions to allow an increase in catch or effort for *E. carbunculus*, *E. coruscans*, and *P. filamentosus* and maintain current catch or effort levels for *E. marshi*.

Discussion

The sectioning and reading of fish otoliths for age estimation is a costly and time-consuming procedure (Worthington *et al.*, 1995b; Francis and Campana, 2004), which can impede the implementation of routine ageing programmes required for monitoring and

Table 2. Potential decision rules based on target, threshold, and limit reference points for assessments based on fishing (F) and natural (M) mortality rates [from Wise *et al.* (2007)].

Fishing mortality (F)	Decision rule for fishing licences
$F/M < \text{Target}$	Fishing effort and/or catches may increase
$\text{Target} < F/M < \text{Threshold}$	Fishing effort and/or catches remains constant
$\text{Threshold} < F/M < \text{Limit}$	Fishing effort and/or catches is reduced, e.g. 0–50%
$F/M > \text{Limit}$	Fishing effort and/or catches is reduced significantly, e.g. 50–100%

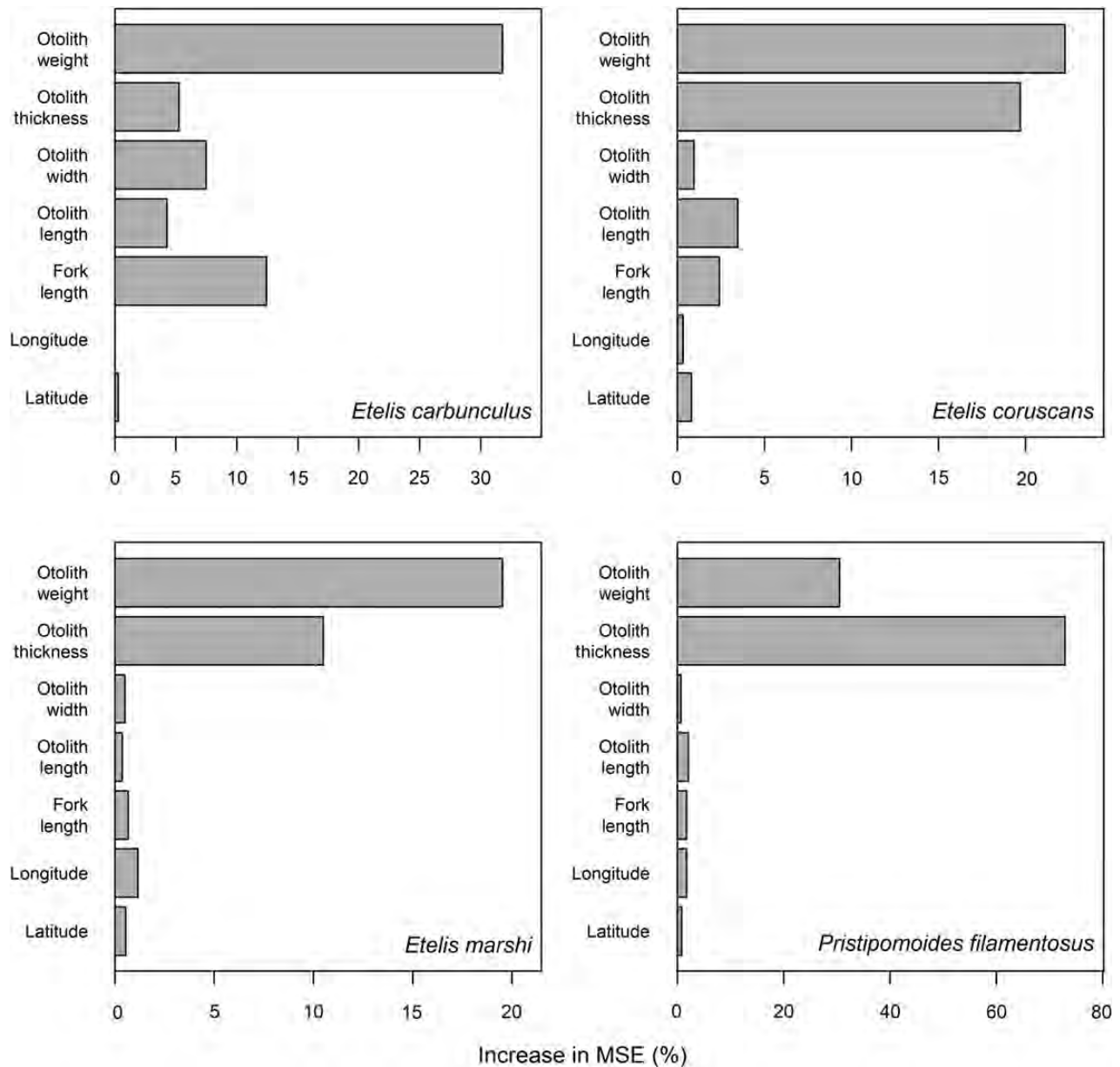


Figure 3. Variable importance for predicting ages of four species of deepwater snapper using random forests. MSE is the mean squared error.

assessment, particularly when resources are limited (Pilling *et al.*, 2003), and potentially delay the delivery of assessment results to stakeholders. We demonstrated that otolith morphometrics can provide similar estimates of age composition, mortality rates, and biological indicators to those derived from counts of increments in sectioned otoliths for four relatively long-lived deepwater snapper species. Importantly, our results demonstrate that management responses for these species, based on biological indicators related to estimates of fishing and natural mortality, would likely be similar whether age estimates were derived from sectioned otoliths or predicted from otolith morphometrics. Therefore, the use of otolith morphometrics represents an efficient approach to provide the data required for age-based assessments of deepwater snapper fisheries in resource-limited countries.

Our results indicated that otolith weight and thickness were the most important variables for predicting age, while other otolith morphometrics were far less important for the four species examined. This result is consistent with other studies that have evaluated the performance of multiple otolith morphometrics in predicting age (e.g. McDougall, 2004; Steward *et al.*, 2009) and is likely explained by the differential growth of otoliths that is common to many species. Growth in otolith length and width tend to slow with age, whereas otolith weight and thickness often increase linearly with age (Boehlert, 1985). Therefore, otolith weight and thickness are likely to be superior to other otolith morphometrics as predictors of age across a wide range of species. In contrast, latitude and longitude were the least important variables for predicting age for deepwater snapper, consistent with other species (Lepak *et al.*,

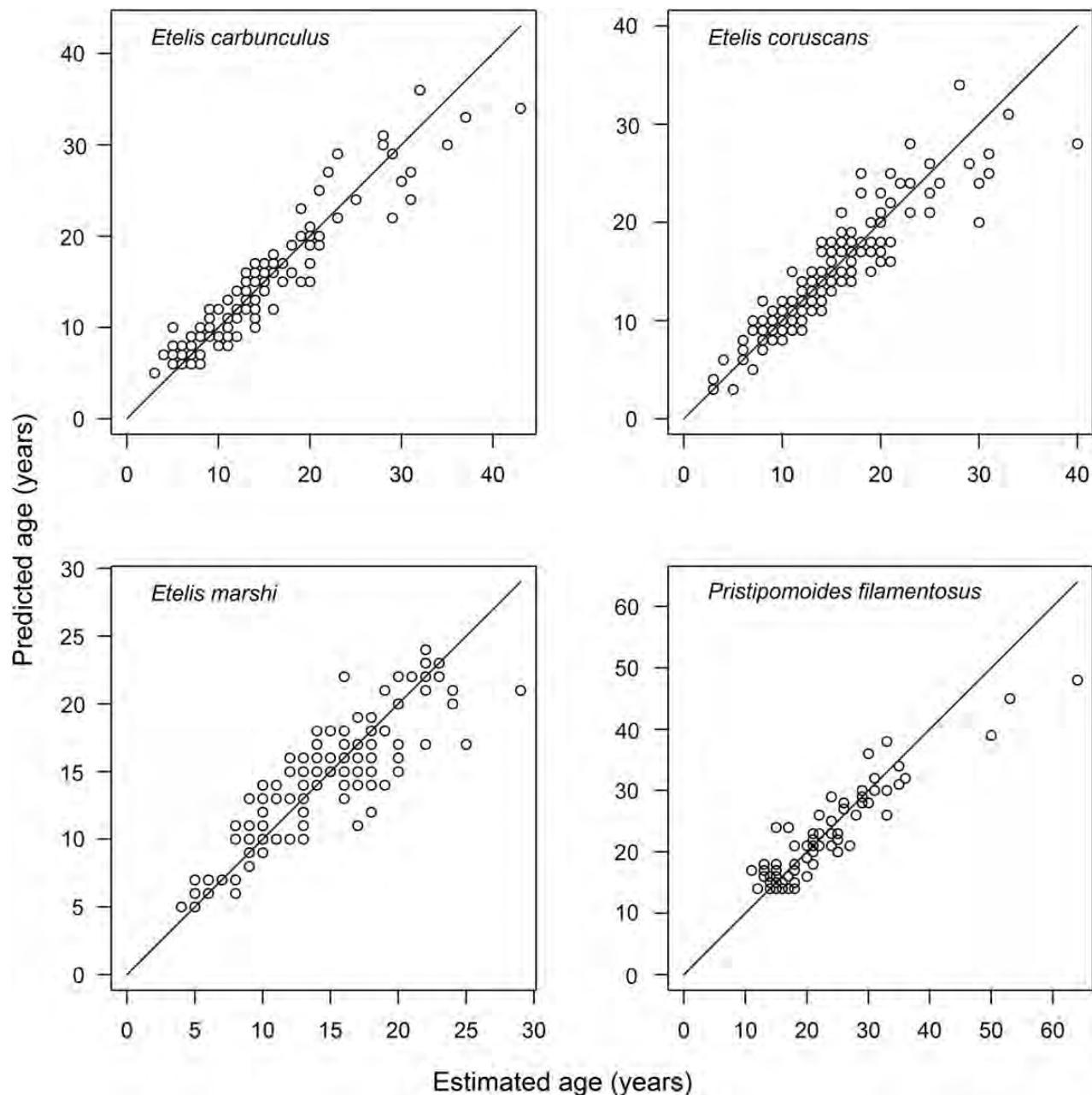


Figure 4. Scatterplot of estimated age from counts of increments in sectioned otoliths vs. the age predicted from the random forest out-of-bag estimates (out of bag error) for four species of deepwater snapper. Lines represent no difference between age estimates.

2012; Dub *et al.*, 2013), indicating that the location of capture had little influence on the ability to predict age. This has important implications for data-limited locations, such as most Pacific Island countries. A “Robin Hood” approach (e.g. Punt *et al.*, 2011) can be adopted in data-limited locations, whereby relationships between otolith morphometrics and age from a better studied region can be used to predict age compositions where only otolith morphometric data can be collected, without the need to estimate the age of individuals from sectioned otoliths from these areas.

We found that fork length was a poor indicator of age for three of the species examined, and only a moderate predictor of age for *E. carbunculus*. The larger maximum fork length of *E. carbunculus*, and broader length range, compared with the other species, may

partially explain why fork length provided more information on age for this species than for the other species. The poor relationship between length and age is a common feature of lutjanids, whereby many age classes accumulate within a narrow length range (Newman *et al.*, 1996a, b, 2000a, b; Newman and Dunk, 2003; Heupel *et al.*, 2010). As a result, length data alone are of limited value for estimating life history parameters and assessing the state of populations and the potential effects of different harvest strategies. This emphasizes the importance of using age-based assessments for species such as deepwater snapper to reduce potential biases in stock assessment outputs arising from the use of length data as a proxy for age.

Most studies that have evaluated the utility of otolith morphometrics to predict age have applied standard regression techniques

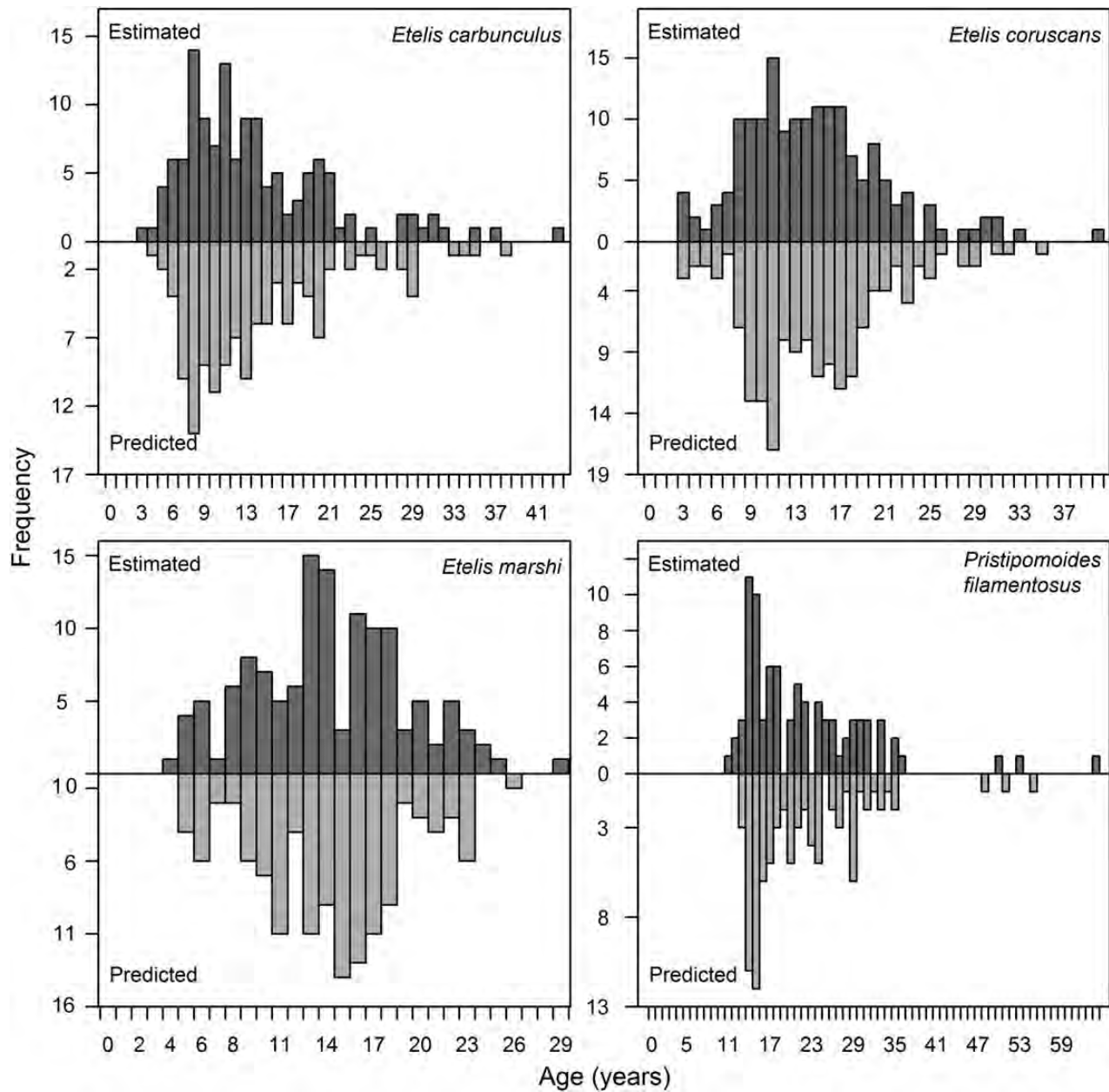


Figure 5. Age – frequency distributions for four species of deepwater snapper derived from counts of increments in sectioned otoliths (estimated age: top panels) and from otolith morphometrics (predicted age: bottom panels).

(e.g. McDougall, 2004; Lou *et al.*, 2005, 2007; Ochwada *et al.*, 2008; Britton and Blackburn, 2014), but very few have exploited the analytical advantages of recursive partitioning methods such as random forests (e.g. Lepak *et al.*, 2012; Dub *et al.*, 2013). Random forests have substantial advantages over standard regression analyses for analysing otolith morphometric data, because they can deal with strong correlations and complex non-linear interactions among a large number of variables. Otolith morphometrics are typically highly correlated (e.g. McDougall, 2004; Steward *et al.*, 2009), which complicates standard regression approaches and often results in the need to transform or exclude variables from models. Random forests allow strongly correlated predictor variables to be included without transformation or exclusion and provide unbiased

predictions and estimates of variable importance (Strobl *et al.*, 2009). Furthermore, the ability of random forests to simultaneously analyse multiple otolith morphometric variables can provide substantially greater predictive power than when only single variables are used (Francis and Campana, 2004; Bermejo, 2014), although we did not evaluate this for our specific dataset.

Although age compositions were predicted well by otolith morphometrics, individual fish age was not predicted accurately for many individuals across all species. Therefore, otolith morphometrics should not be used as a proxy for age for these species when the goal is to derive the age of individuals. For monitoring and assessments of exploited species, however, the goal is typically not to estimate individual ages, but to estimate the age composition and

Table 3. Estimates of total mortality (Z), natural mortality (M), fishing mortality ($F = Z - M$), and the ratios of F to M as a performance indicator for four species of deepwater snapper and two ageing methods.

Species	Ageing method	$Z (\pm CI)$	M	$F (\pm CI)$	$F/M (\pm CI)$
<i>Etelis carbunculus</i>	Estimated	0.11 (0.02)	0.10	0.01 (0.02)	0.10 (0.16)
	Predicted	0.11 (0.01)	0.10	0.01 (0.01)	0.15 (0.14)
<i>Etelis coruscans</i>	Estimated	0.13 (0.01)	0.10	0.02 (0.01)	0.22 (0.13)
	Predicted	0.12 (0.02)	0.10	0.02 (0.02)	0.20 (0.17)
<i>Etelis marshi</i>	Estimated	0.23 (0.05)	0.14	0.09 (0.05)	0.60 (0.34)
	Predicted	0.22 (0.06)	0.14	0.08 (0.06)	0.55 (0.42)
<i>Pristipomoides filamentosus</i>	Estimated	0.08 (0.02)	0.06	0.01 (0.02)	0.17 (0.25)
	Predicted	0.08 (0.02)	0.06	0.02 (0.02)	0.28 (0.33)

Estimated refers to ages estimated from counts of opaque increments in sectioned otoliths, and predicted refers to ages predicted from otolith morphometrics. M was assumed to have no error. CI, 95% confidence intervals.

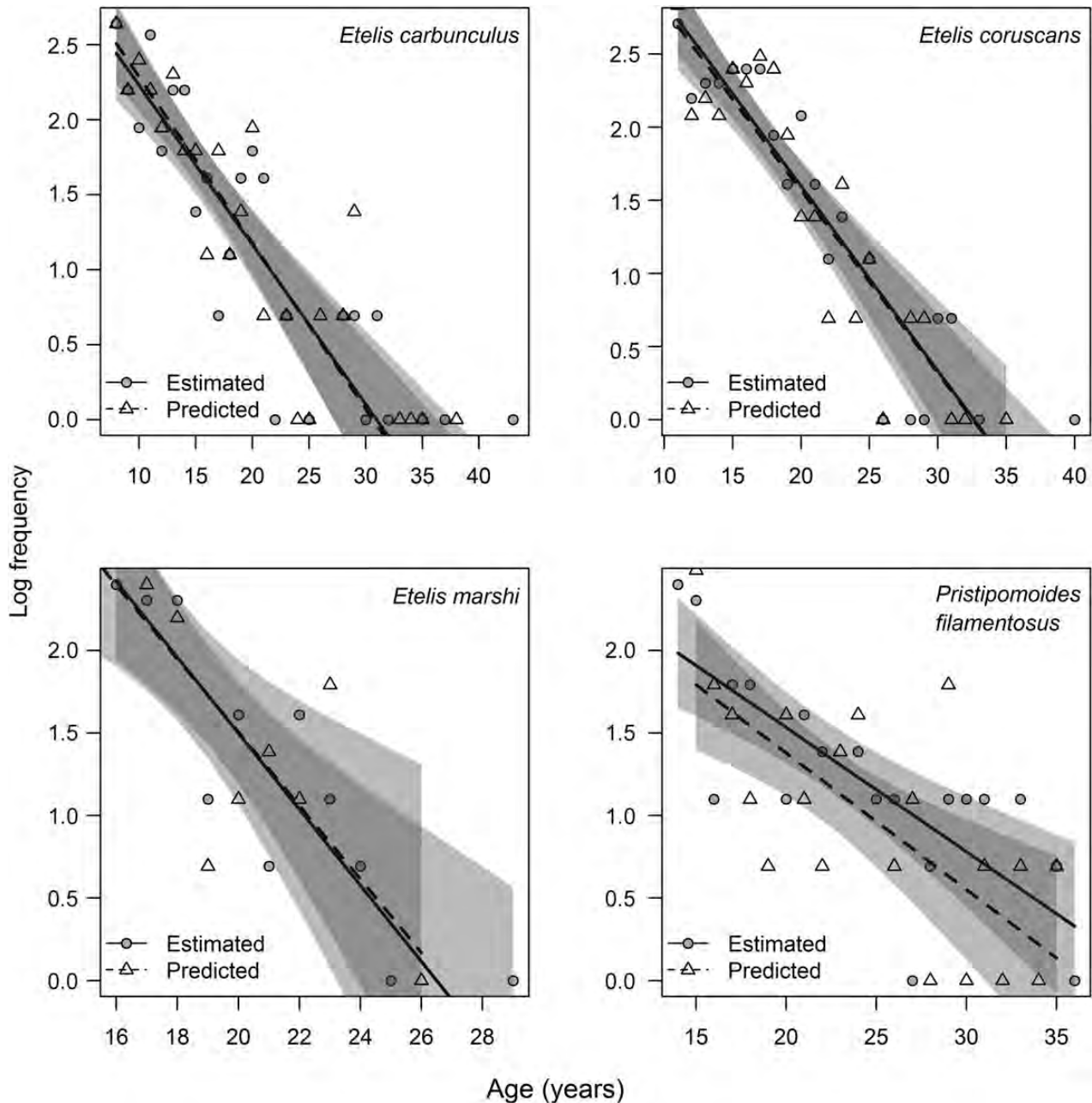


Figure 6. Catch curves for four species of deepwater snapper derived from counts of increments in sectioned otoliths (estimated) and from otolith morphometrics (predicted). Shaded areas indicate 95% confidence intervals with darker shading indicating where confidence intervals overlap.

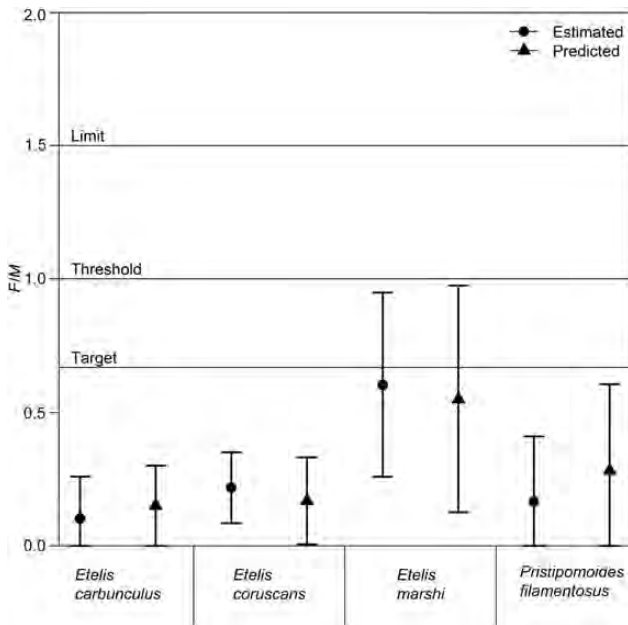


Figure 7. Estimates of the biological indicator [ratio of fishing mortality (F) to natural mortality (M)] for four species of deepwater snapper derived from counts of increments in sectioned otoliths (estimated) and from otolith morphometrics (predicted) relative to the target ($F/M = 0.67$), threshold ($F/M = 1$), and limit ($F/M = 1.5$) reference levels. Error bars are based on 95% confidence intervals for F , assuming no error in M .

population parameters such as mortality rates. It is surprising, therefore, that few studies have evaluated the performance of otolith morphometrics to predict secondary parameters derived from predicted ages such as age compositions, mortality, and growth [but see [Worthington et al. \(1995a\)](#) and [Lou et al. \(2005\)](#)], and we are not aware of any studies that have evaluated the flow-on effects on assessments and potential management responses. It should be noted, however, that the random forest analysis tended to overestimate the age of the youngest individuals, and underestimate the age of the oldest individuals. Therefore, there is a risk that this approach may fail to detect truncation of age structures caused by increased mortality (e.g. fishing mortality) or poor recruitment. Ensuring that sufficient otolith morphometric and age data are collected from individuals at the extremes of the age distribution will improve age predictions for the oldest and youngest individuals.

The accuracy of age predictions from otolith morphometrics is unknown because we did not know the true age of fish. Furthermore, the error in age predictions from otolith morphometrics will always be greater than that in age estimates from which the relationships with otolith morphometrics were derived ([Francis and Campana, 2004](#)), in this case counts of increments in sectioned otoliths. However, we did not detect any differences in age structures, mortality rates, or biological indicators, whether they were derived from otolith morphometrics or increment counts in sectioned otoliths, which would impact a management decision. Therefore, the effects of any increase in ageing error due to the use of otolith morphometrics to predict age were negligible.

[Francis and Campana \(2004\)](#) argue that cost–benefit analyses are a necessary part of any evaluation of the performance of otolith morphometrics in predicting age. Such analyses should

compare the cost of obtaining age estimates from otolith morphometrics with that of the traditional counts of annuli in sectioned otoliths ([Francis and Campana, 2004](#)). [Boehlert \(1985\)](#) estimated that over five times as many otoliths can be measured per hour than can be sectioned for age estimation, which represents a potentially large efficiency gain. In Pacific Island countries, the skills and equipment required to section and read otoliths are not readily available, and the only option at present is to send otoliths to an otolith laboratory in another country for processing. The cost of doing so would be variable, but a conservative estimate would be at least \$20USD per otolith, given the longevity (>40 years) and difficulty in interpreting increments in deepwater snapper otoliths. To process 500 otoliths for four species, each year would be ~\$40 000USD annually, which is well beyond an acceptable cost for Fisheries Departments in any Pacific Island country for their deepwater snapper fisheries. The measurement of otolith morphometrics (otolith weight, length, width, and thickness) requires no special training because they are objective quantities, and they can be measured simply with digital calipers and a balance. The ongoing cost of measuring otolith morphometrics is likely to be minimal as at least 40 otoliths can be measured per hour ([Boehlert, 1985](#)), such that 500 otoliths for four species could be measured in 50 h, at a cost of less than \$5USD per hour (~\$250USD annually) for an untrained technician in Pacific Island countries. Thus, the use of otolith morphometrics to predict age of deepwater snapper in Pacific Island countries offers substantial efficiencies over traditional age estimation methods.

It must be emphasized that the estimation of biological indicators in this study was for illustration purposes only, and does not necessarily reflect the status of deepwater snapper fisheries in the South Pacific Ocean. Our results may not reflect fishery status because mortality rates and biological indicators were estimated from samples collected over a wide area, and may not have been sourced from the same stock. Genetic research has revealed limited population structure in deepwater snapper species in the Indo-Pacific region (e.g. [Gaither et al., 2011](#)), although most research has been restricted to specific locations such as Hawaii ([Andrews et al., 2014](#)) and New Caledonia ([Loeun et al., 2014](#)). Therefore, more research is required to determine the population structure of deepwater snapper species in the Pacific and to delineate management units.

A useful extension of our work would be to evaluate the performance of otolith morphometrics in deriving other reference points related to age and reproduction. For example, the percentage of fish at a mature age, the percentage of fish at optimum age for maximizing yield, and the percentage of fish at an age with high fecundity (e.g. [Froese, 2004](#)) would be particularly useful to evaluate for long-lived species such as deepwater snapper. Having multiple indicators available to monitor a fishery from simple otolith morphometrics would be a substantial advantage over a single indicator such as F/M ratios. However, the evaluation of these additional indicators would require data on the sex and maturity stage of individuals to be collected, which are unavailable for most species of deepwater snapper at this stage.

Our results clearly demonstrate that otolith morphometrics provide an efficient approach for estimating age compositions, mortality rates, and biological indicators for deepwater snapper. Furthermore, the application of random forests to otolith morphometrics is likely to reveal that this approach is efficient for a range of other species. Therefore, in the absence of sufficient resources to section otoliths for age estimation, we recommend that otolith morphometrics be used to obtain age frequency distributions of the

catch from deepwater snapper fisheries in Pacific Island countries, and that this approach be evaluated in other similarly data-limited fisheries. Age-based assessment models can then be developed for these fisheries, greatly reducing the uncertainty from previous assessments and providing relevant information for developing appropriate management strategies.

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