Population biology and vulnerability to fishing of deep-water Eteline snappers

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Summary

Deep-water fish in the tropical and sub-tropical Pacific Ocean have supported important fisheries for many generations. Observations of localised depletions in some fisheries have raised concerns about the sustainability of current fishing rates. However, quantitative assessments of deep-water stocks in the Pacific region have been limited by the lack of adequate biological and fisheries data. Estimates are provided of age-based demographic parameters for two important deep-water snapper species in the Pacific, *Etelis carbunculus* and *E. coruscans*. A spawner biomass-per-recruit (SPR) model was applied to determine fishing mortality rates for each species that would achieve specified biological targets (40% unexploited levels, SPR_{40}) and limit (30% unexploited levels, SPR_{30}) reference points, and examine the sensitivity of the model to variation in natural mortality and age at first capture. The maximum observed age, based on increment counts from sectioned otoliths, was 21 years for *E. carbunculus* and 18 years for *E. coruscans*. Total mortality (Z), estimated from the Hoenig regression, was 0.21 year^{-1} for *E. carbunculus* and 0.25 year^{-1} for *E. coruscans*. The best approximating growth models were the von Bertalanffy model (L_∞ = 896 mm fork length, k = 0.28, t_0 = 0.51) for *E. carbunculus* and the logistic model (L_∞ = 879 mm fork length, k = 0.32 year^{-1}, t_0 = 3.42) for *E. coruscans*. The spawner biomass-per-recruit analysis demonstrated that lower rates of fishing mortality were required for *E. coruscans* than for *E. carbunculus* to maintain spawning biomass above estimated biological reference points. Estimates of spawner biomass-per-recruit were more sensitive to variation in natural mortality than in the age at first capture, suggesting that regulating fishing mortality rather than gear selectivity would be a more effective management measure for both species. Maintaining fishing mortality <0.1 for both species is recommended as a cautious approach to management, given the uncertainty in estimates of natural mortality and mixed fishery considerations.

Introduction

Life histories of deep-water fish species are frequently characterised by extended longevity, slow growth rates, late maturity and low rates of natural mortality, indicating exceptionally low production potential (Koslow et al., 2000). As such, deep-water species are typically vulnerable to over-exploitation, and their biological characteristics have important implications for fisheries management (Cheung et al., 2005; Morato et al., 2006a,b). In virgin or minimally exploited stocks, high catch rates and capture of larger individuals are observed initially, but within only a few years after exploitation commences, depletion of the stock results in lower catch rates and a smaller size of captured individuals (Langi et al., 1992; Koslow et al., 2000).

In the tropical and sub-tropical region of the Pacific Ocean, most commercial fishing for deep-water stocks began in the 1970s and has persisted to today with different intensities and longevities, mostly supplying local markets (Dalzell et al., 1996). It has only been in a few places with abundant habitats that allow fishers to move between fishing grounds to support higher catch rates (e.g. Fiji and Tonga) and where larger commercial ventures have persisted (McCoy, 2010). There is, however, a renewed interest in developing deep-water fisheries by many Pacific Island countries and territories in recognition of the limited potential for further commercial development of shallow reef and lagoon fisheries in the region (Bell et al., 2009; McCoy, 2010). Given past observations of localised depletion in the Pacific Islands region, fishery managers are approaching such opportunities with caution. Quantitative assessments of the population dynamics of these species and the potential impact of fishing on their populations have been requested to support policies for their sustainable exploitation or conservation (Williams et al., 2012).

Ruby snapper *Etelis carbunculus* (Cuvier), and flame snapper *E. coruscans* (Valenciennes) are deep-water species within the subfamily Etelinae (Lutjanidae) that generally inhabit waters between 100 and 500 m (Carpenter and Niem, 2001). They are widely distributed in tropical and subtropical waters (30 °N–25 °S) of the Pacific Ocean (Carpenter and Niem, 2001) and are two of the main deep-water snapper species caught in the Pacific Islands region (McCoy, 2010). Expansion of the deep-water snapper fishery, whilst maintaining fishing rates within sustainable limits, is currently a priority for fisheries management in some Pacific Island countries.

In New Caledonia, fishing for deep-water snappers has focussed upon the southern and northern provinces of the main island and in the Loyalty Islands (Virly, 1997). Although the history of exploitation in each region has varied, all regions have some fishing history dating back to the

1970s and 1980s. Data reporting the exploitation of deep-water snappers have been collected in the Southern Province since 1991, in the Northern Province since 1993, and in the Loyalty Islands since 2006. Rarely, however, do the monitoring data separate the catches by species, identify locations beyond the broad region, or specify the allocation of effort.

Growth and mortality rates are essential parameters for most sustainable harvest models. Estimates of size at age and growth have been estimated for both deep-water snapper species using information derived from sectioned otolith examination in Papua New Guinea (Fry et al., 2006) and the Commonwealth of the Northern Mariana Islands (CNMI) (Ralston and Williams, 1988). However, the sample sizes in both studies were extremely small (20 individuals or fewer). Other published estimates are based on length frequency information which can substantially under-estimate age in long-lived species (Choat and Robertson, 2002). Moreover, previous studies on reef fish species have demonstrated variation in growth parameters at multiple spatial scales, suggesting that using growth parameters estimated from other areas for the same species can be prone to bias (Gust et al., 2002; Williams et al., 2003, 2007; Allman, 2007).

The aim of this study was to provide the first estimates of age-based demographic parameters for *Etelis carbunculus* and *E. coruscans* in New Caledonia using sectioned otolith increment counts. To assist managers with understanding the likely responses of the stock to fishing pressure, for each species an equilibrium spawner biomass-per-recruit analysis was applied to determine fishing mortality rates that would achieve specified biological target and limit reference points of spawning biomass per-recruit relative to unexploited levels.

Materials and methods

Sample collection and processing

A total of 96 *E. carbunculus* and 79 *E. coruscans* were sampled from commercial fishers operating in New Caledonian waters between December 2008 and June 2009 (Fig. 1). The fish were caught by electronic/motorised drop lines from small vessels fishing in three regions in New Caledonia (Southern Province, Northern Province and Loyalty Islands) and at depths between 150 and 400 m. Sampled fish were not necessarily representative of the catch because a proportion of the catch was sold before sampling could take place.
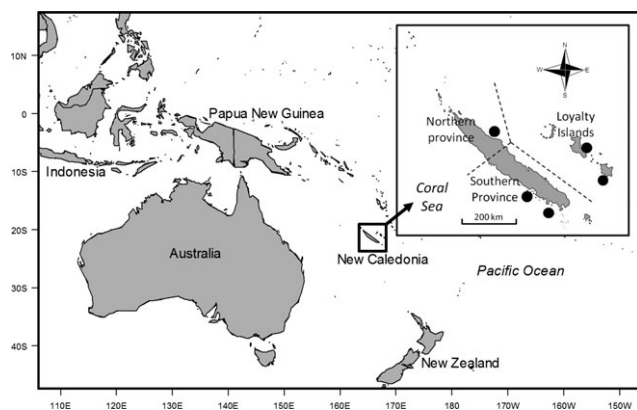
Fork length of all individuals was measured to the nearest millimeter and total wet weight to the nearest gram for a subsample of *E. carbunculus* (n = 31) and *E. coruscans* (n = 69) for which whole individuals were available. Sagittal otoliths were removed, cleaned of any residual material, and stored dry. Age was estimated for each individual using sectioned sagittal otolith increment counts, based on the assumption that opaque increments are formed annually. This assumption has been validated for a wide range of other lutjanids at similar latitudes to New Caledonia (Newman and Dunk, 2003; Choat et al., 2009). Otoliths were sectioned and read using similar methods applied to other lutjanids (e. g. Heupel et al., 2010). Briefly, otoliths were embedded in epoxy resin and cut transversely through the primordium with a diamond-tipped blade on a low-speed saw to produce a thin section of 300–400 μm. Sections were mounted on glass slides using Crystal Bond adhesive. Otolith sections were read under reflected light at 40× magnification and opaque increments were counted from the nucleus to the edge along the ventral margin of the sulcus acusticus. A single experienced reader counted opaque increments in each otolith at least twice, with a minimum of 24 h between consecutive counts and without reference to the previous reading, size of fish or capture date. A third count was made by the same reader if the first two counts differed; a match between the third and either of the first two counts was accepted as the final age. The median count was assigned as the final age estimate for those otoliths (26%) from which there were no agreements among three counts.

Age bias plots (Campana et al., 1995) were used to look for systematic differences and evaluate consistency of age estimates between readings. The precision of age estimates was compared between readings using the coefficient of variation (CV) expressed as a ratio of the standard deviation to the mean of age estimates for each fish (Chang, 1982):

$$CV_j = \frac{\sqrt{\sum_{i=1}^{R} \frac{(X_{ij} - X_j)}{R-1}}}{X_j}$$

where X_{ij} is the ith age determination of the jth fish, and R is the number of times each otolith was read – in this case two readings, as not all otoliths were read three times. The CV was averaged across all samples to determine the average precision between the first and second otolith readings.

Fig. 1. Map of New Caledonia. Black dots = collection locations of *Etelis carbunculus* and *E. coruscans* samples

Demographic analysis

The relationship between fork length (*FL*) and weight (*W*) was estimated using the power function:

$$W = a \times FL^b$$

where a is the coefficient and b is the exponent. The length–weight relationship was considered to be isometric if 95% confidence intervals of b included 3.00, meaning no or little change in shape with increasing length. Length and age frequency distributions were constructed for both species and the modes and ranges were compared qualitatively.

We used an information theoretic, multi-model inference approach to determine the optimal growth model for both species (Katsanevakis and Maravelias, 2008). We fitted length-at-age data to a set of four candidate models commonly used for teleosts including the Gompertz (Gompertz,

1825), von Bertalanffy (VBGF: von Bertalanffy, 1938), Richards (Richards, 1959) and Logistic (Ricker, 1975) growth models. The form of each growth model was as follows:

Gompertz $\quad L_t = L_\infty e^{-e^{-k(t-t_0)}}$

VBGF $\quad L_t = L_\infty (1 - e^{-k(t-t_0)})$

Richards $\quad L_t = L_\infty [1 + (1/p)e^{-k(t-t_0)}]^{-p}$

Logistic $\quad L_t = L_\infty (1 + e^{-k(t-t_0)})^{-1}$

where L_t is the fork length at age t, L_∞ is the mean asymptotic length, k is a relative growth rate parameter (year^{-1}), t_0 is the age at which fish have a theoretical length of zero, and p is a dimensionless parameter in the four parameter Richards model.

Each growth model was fitted to length-at-age data using non-linear least squares in R version 2.13.2 (R Development Core Team, 2011). We evaluated the relative support for each model using Akaike's Information Criteria for small sample sizes (AIC$_c$: Burnham and Anderson, 2002). Models with an AIC$_c$ value within two of that calculated for the best approximating model (lowest AIC$_c$) were considered to describe the data equally well (Burnham and Anderson, 2002). The Akaike weight, w_i (Burnham and Anderson, 2002), of each model i was calculated to quantify the plausibility of each model, given the data and the set of five models using:

$$w_i = \frac{\exp(-0.5\Delta_i)}{\sum\limits_{k=1}^{5} \exp(-0.5\Delta_i)}$$

where $\Delta_i = \text{AIC}_{c,min} - \text{AIC}_{c,i}$. The Akaike weight is considered as the weight of evidence in favour of model i being the actual best model of the available set of models.

It was likely that the age frequency data collected for both species were not representative of the population or the catch, such that estimates of mortality from catch curves were potentially biased. Therefore, an estimate of total mortality (Z) was obtained for each species by fitting the linear equation:

$$\log_e(Z) = 1.44 - 0.982 \times \log_e(t_{max})$$

where t_{max} is the maximum age observed (Hoenig, 1983).

Spawner biomass-per-recruit analysis

Backwards extrapolation of the sampled age frequency distributions using the total mortality estimates was applied to estimate the probability of capture-at-age for each species (e. g. Grandcourt et al., 2011). All age classes older than, and inclusive of, the modal age were assumed to be fully selected by the gear. The proportion at age from the sampled age distribution was divided by the proportion at age from the backwards extrapolated age distribution to obtain estimates of the age-specific probability of capture for ages less than the modal age. Selectivity curves were generated by fitting logistic functions to the age-specific probability of cap-

ture. Estimated selectivity curves were then used to derive values of the mean age at first capture:

$$P_t = (1 + e^{-\ln(19)(t-t_{50})/(t_{95}-t_{50})})^{-1}$$

where P_t is the probability of capture at age t, t_{50} age at which the probability of capture is 50%, and t_{95} is the age at which the probability of capture is 95% (e.g. Haddon, 2001). The mean age at first capture was then assumed to occur at t_{50}.

Spawner biomass-per-recruit (SPR) was estimated for both species using the Beverton and Holt (1957) equation expressed as a proportion of the unexploited population size:

$$SPR = \sum_{t_m}^{t_{max}} (G_t \cdot W_t \cdot e^{-\sum_{t_{50}}^{t-1}(F+M)})$$

where W_t = mean weight-at-age from the VBGF for age t, G_t is the proportion mature at age t, t_m is the age at first maturity, t_{max} is the maximum age of fish in the population, t_{50} is the mean age at first capture, F is the instantaneous fishing mortality rate and M is the instantaneous natural mortality rate. The shape of the maturity function was assumed to be knife-edged. The parameter t_m was constrained to 3 years for *E. carbunculus* and 4.5 years for *E. coruscans* based on maturity estimates from Martinez-Andrade (2003). The value of t_{max} was based on the oldest age class observed in the sample and growth parameters were estimated in terms of weight by fitting a VBGF to weight-at-age data. Where weight data were not available, an estimated weight based on the length-weight relationship was used. F was assumed to be constant across all age classes above t_{50}.

The sensitivity of spawner biomass-per-recruit estimates to different values of M and t_{50} was examined. Two estimates of M (0.1 and 0.25) were used that captured the range of reported estimates (Fry et al., 2006), and the values of total mortality estimated here. Two estimates of t_{50} were used for *E. carbunculus* (3 and 4 years) and *E. coruscans* (2 and 3 years) that bounded the estimated value of t_{50} for each species.

Target and limit biological reference points were defined as the fishing mortality rates associated with maintaining relative spawner biomass-per-recruit at 40% (SPR$_{40}$) and 30% (SPR$_{30}$) of the unexploited population levels, respectively. These reference points were selected based on the meta-analyses of Mace (1994) given the absence of stock recruitment relationships for the study species. Fishing mortality rates were determined for each species that would achieve these biological reference points under different scenarios of M and t_{50}.

Results

The precision of age estimates, as indicated by the CV, was similar for *E. carbunculus* (CV = 11.5%) and *E. coruscans* (CV = 10.9%). There was no strong bias between age readings, although there was a tendency for the second reading to overestimate ages >7 years for *E. carbunculus* and underestimate ages >7 years for *E. coruscans* when compared to the first age reading (Fig. 2).

The estimated parameters and 95% confidence intervals of the *FL–W* relationship for *E. carbunculus* ($a = (2.77 \pm 7.13) \times 10^{-5}$, $b = 2.93 \pm 0.39$) and *E. coruscans* ($a = (3.18 \pm 2.67) \times 10^{-5}$, $b = 2.88 \pm 0.13$) indicate that both species
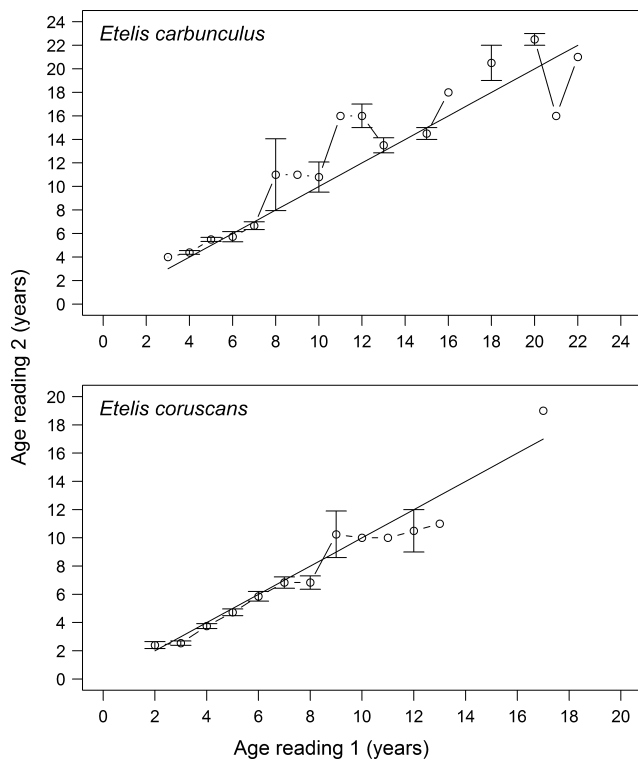
Fig. 2. Age bias plots for pairwise comparisons between otolith readings 1 and 2 for *Etelis carbunculus* and *E. coruscans*. Each point = mean age assigned from second reading of each otolith assigned an age from reading 1. Error bars = 95% confidence intervals. Solid black line = 1:1 equivalence

four growth models (Table 1). The VBGF model was found to be the best approximating model ($w = 0.37$) for *E. carbunculus*, although there was also substantial support for the Gompertz ($\Delta AIC_c = 0.46$, $w = 0.29$) and logistic ($\Delta AIC_c = 1.04$, $w = 0.22$) models. For *E. coruscans*, the logistic model was the best approximating model ($w = 0.37$), but there was substantial support also for the Gompertz model ($\Delta AIC_c = 0.81$, $w = 0.30$).

The size-at-age relationship described by the best-fit growth model differed between species (Fig. 5). The estimated L_∞ was higher for *E. carbunculus* compared with *E. coruscans* (Table 1). However, there was more uncertainty in L_∞ estimates for *E. coruscans*, as indicated by the larger standard errors (Table 1). Comparison of k and t_0 between models is not valid, as the definitions of these parameters differ between models. A semi-quantitative comparison of growth using the growth parameters from the best-fit models indicated that early growth was faster for *E. carbunculus*. *E. carbunculus* reached 50% of asymptotic length at a younger age (2.9 years) and at a lower percentage of potential longevity (14%) compared to *E. coruscans* (5.6 years, 31%).

The estimate of total mortality obtained from fitting Hoenig's (1983) equation was 0.21 year^{-1} for *E. carbunculus* based on a maximum age of 21 years, and 0.25 year^{-1} for *E. coruscans* based on a maximum age of 18 years. However, there was a difference of 6 years between the oldest and second-oldest (12 years old) individual *E. coruscans*. The mean age at first capture (t_{50}), based on backwards extrapolation of the sampled age frequency distributions using these estimates of total mortality, were 3.6 ± 0.01 (95% CI) years for *E. carbunculus* and 2.8 ± 0.16 years for *E. coruscans*.

The spawner biomass-per-recruit analysis revealed that the range of natural mortality values examined had a larger influence on relative biomass than t_{50} for both species (Fig. 6). The estimates of fishing mortality (F) that were required to achieve target and limit reference points are summarised in Table 2. For *E. carbunculus*, the target (40% biomass, SPR_{40}) and limit (30% biomass, SPR_{30}) biological reference points for a natural mortality of 0.1 were achieved when fishing mortality was 0.11 and 0.16, respectively. When natural mortality was 0.25, the target (SPR_{40}) and limit (SPR_{30}) biological reference points were achieved when fishing mortality was 0.25 and 0.38, respectively. For *E. coruscans*, the target (SPR_{40}) and limit (SPR_{30}) biological reference points for a natural mortality of 0.1 were achieved when fishing mortality was 0.09 and 0.12, respectively. When natural mortality was 0.25, the target (SPR_{40}) and limit (SPR_{30}) biological reference points were achieved when

exhibit an isometric growth pattern (b ≈ 3), with a constant relationship between individual length and relative weight (Fig. 3). The length and age ranges were similar for *E. carbunculus* and *E. coruscans* (Fig. 4). Lengths of individuals ranged between 250 and 1010 mm fork length for *E. carbunculus*, and between 300 and 900 mm for *E. coruscans*. Ages of individuals ranged between 3 and 21 years for *E. carbunculus* and between 2 and 18 years for *E. coruscans*. Length distribution for *E. coruscans* had a single mode at 500 mm fork length, while the length distribution for *E. carbunculus* was multimodal. The age distribution for *E. carbunculus* was positively skewed with a single mode at 5 years, while that of *E. coruscans* was less skewed with a single mode at 4 years (Fig. 4).

None of the four candidate growth models was unambiguously the best model for either species as indicated by ΔAIC_c values <3 and Akaike weights between 0.11 and 0.45 for all
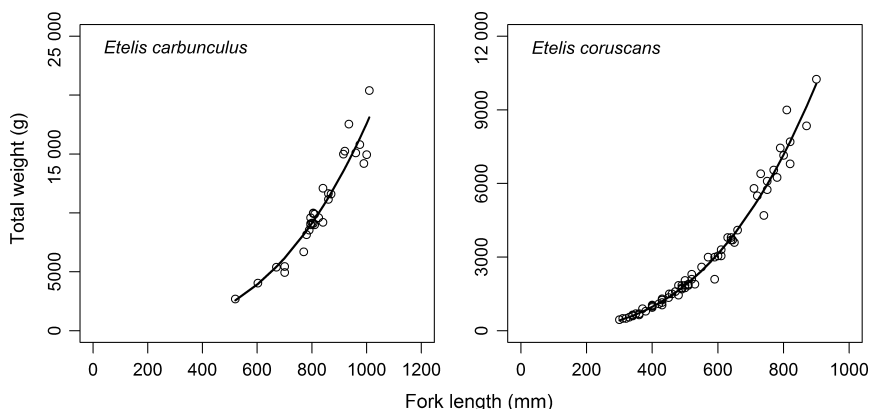

Fig. 3. Weight-at-length relationships and fitted power curves, *Etelis carbunculus* (n = 31) and *E. coruscans* (n = 79)
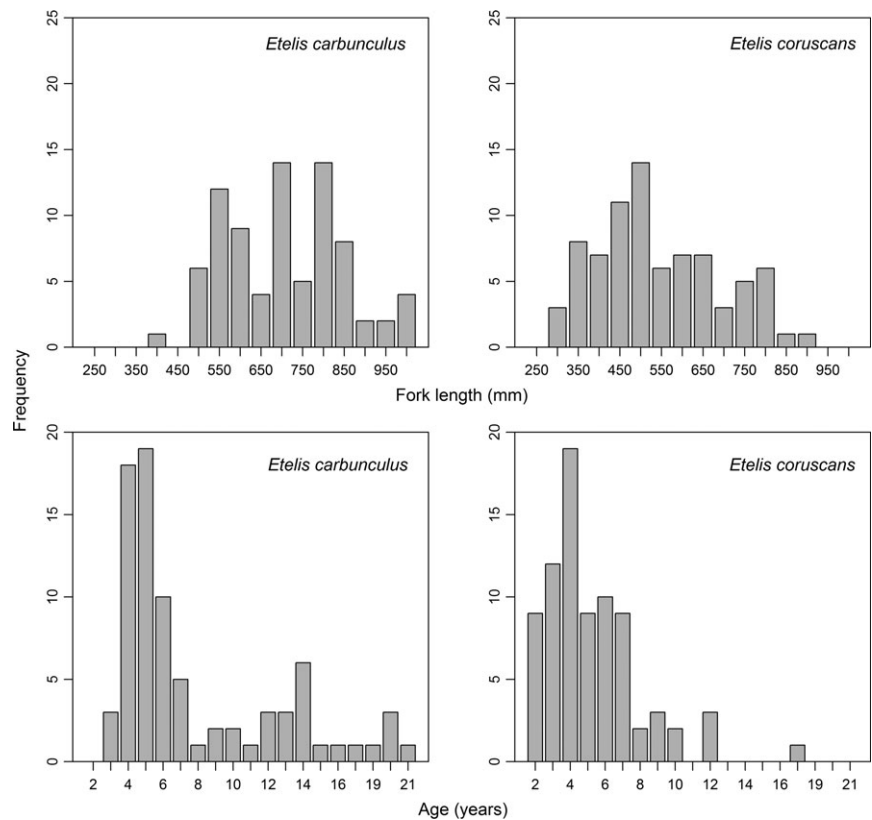
Fig. 4. Length and age frequency distributions, *Etelis carbunculus* (n = 81) and *E. coruscans* (n = 79)

Table 1
Parameter estimates (±standard error) from four candidate growth models for *Etelis carbunculus* and *E. coruscans* from New Caledonia

Species	Model	L_∞ (mm)	k (year^{-1})	t_0 (year)	p	AIC$_c$	ΔAIC$_c$	w
Etelis carbunculus	Richards	905.10 (29.44)	0.23 (0.11)	1.50 (1.76)	0.57 (0.57)	898.58	2.14	0.13
	Logistic	880.48 (14.55)	0.44 (0.06)	2.71 (0.22)		897.49	1.04	0.22
	Gompertz	886.58 (15.75)	0.36 (0.05)	1.80 (0.31)		896.90	0.46	0.29
	VBGF	895.51 (17.73)	0.28 (0.04)	0.51 (0.47)		896.44	0	0.37
Etelis coruscans	VBGF	993.50 (86.14)	0.14 (0.03)	−0.93 (0.50)	0.68 (0.91)	884.76	2.88	0.11
	Richards	867.08 (57.61)	0.37 (0.19)	3.84 (1.67)		884.09	2.21	0.15
	Gompertz	917.78 (54.23)	0.23 (0.03)	2.03 (0.25)		882.69	0.81	0.30
	Logistic	879.33 (41.95)	0.32 (0.04)	3.42 (0.32)		881.88	0	0.45

AIC$_c$ is the small-sample bias-corrected form of Akaike's information criterion, Δ_i the Akaike difference, and w_i the Akaike weight. Note that the parameters k and t are defined differently in each model, such that values are not comparable across models

fishing mortality was 0.15 and 0.21, respectively (Fig. 6). Increasing the age at first capture by 1 year for each species resulted in a small increase in the fishing mortality required to maintain spawning stock biomass above SPR$_{40}$, except for *E. carbunculus* when natural mortality was 0.25 (Fig. 6).

Discussion

Management of deep-water snapper in the Pacific has been hindered by limited information on species demography and fisheries data. This study provides some of the first estimates of age-based population parameters for exploited deep-water snapper in the Pacific region. Moreover, it provides a foundation for contributing to formal assessments of the effects of fishing and evaluation of the likely benefits of alternative management and conservation efforts for these species in the Pacific region.

Previous studies have demonstrated that longevity within deep-water snappers varies greatly, from <15 to >30 years

(e.g. Smith and Kostlan, 1991; Williams and Lowe, 1997; Pilling et al., 2000; Newman and Dunk, 2003; Fry et al., 2006). Age estimates for the *Etelis* species have generally been at the younger end of this range (10–14 years; Ralston and Williams, 1988; Smith and Kostlan, 1991). Direct comparisons with studies from elsewhere in the Pacific are difficult due to differences in methods used to estimate age and low sample sizes (Table 3). However, the results from New Caledonia strongly support the results of Fry et al. (2006), who also used increment counts from sectioned otoliths, suggesting that the maximum age for *Etelis* species is greater than previously estimated and that the methods of using micro-increment widths to estimate age (e.g. Williams and Lowe, 1997) may under-estimate age. This study estimated ages for 96 *E. carbunculus* and 79 *E. coruscans,* which substantially increases the sample size of aged individuals for the western Pacific region. Age estimates for *E. carbunculus* were limited to 4 and 62 otoliths for the CNMI (Ralston and Williams, 1988; Smith and Kostlan, 1991), 20 otoliths in Papua New
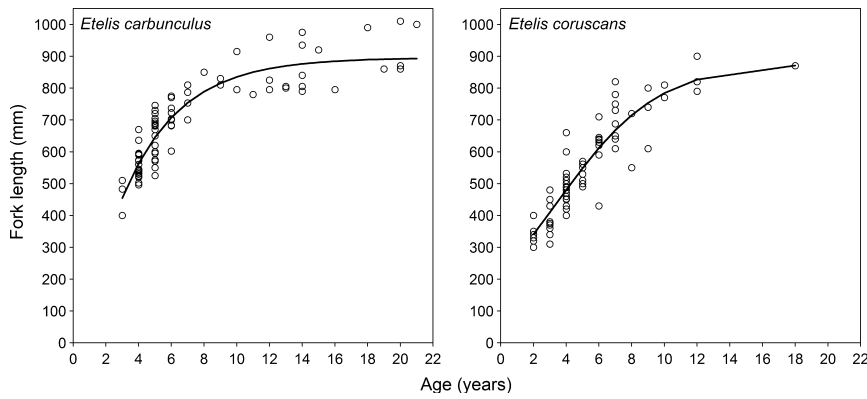
Fig. 5. Length-at-age relationships and fitted von Bertalanffy growth model for *Etelis carbunculus* and fitted logistic growth model for *E. coruscans*
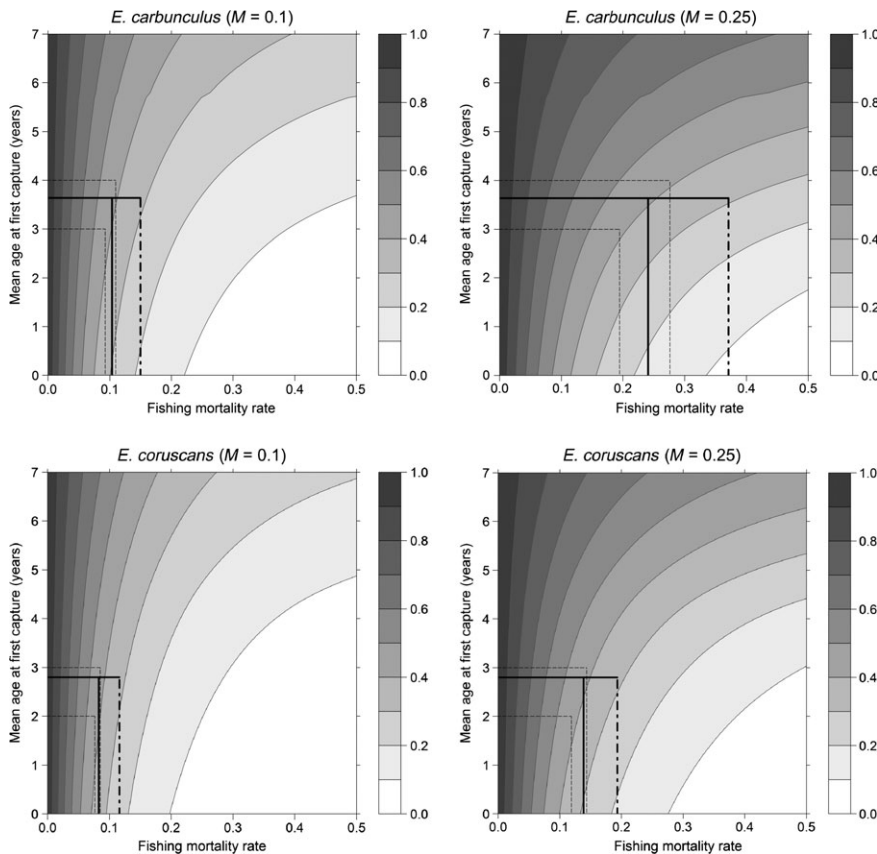

Fig. 6. Relative spawner biomass-per-recruit (SPR) for *Etelis carbunculus* and *E. coruscans* from New Caledonia for two scenarios of natural mortality (M) and age at first capture (t_{50}). Grey-scale = proportion of spawner biomass-per-recruit relative to unexploited population levels. Solid black line and dot-dashed line = represent fishing mortality rates associated with SPR of 40% (SPR_{40}) and 30% (SPR_{30}), respectively, relative to unexploited population levels. Dashed lines = fishing mortality rates associated with SPR of 40% (SPR_{40}) of unexploited levels for two scenarios of mean age at first capture

Table 2
Estimated values of fishing mortality (F) required to achieve specified target (SPR_{30}) and limit (SPR_{40}) reference points for two natural mortality rates (M), *Etelis carbunculus* and *E. coruscans*

Species	M	F at SPR_{30}	F at SPR_{40}
Etelis carbunculus	0.10	0.16	0.11
	0.25	0.38	0.25
Etelis coruscans	0.10	0.12	0.09
	0.25	0.21	0.15

Guinea (Fry et al., 2006) and 37, 63 and 13 otoliths from Hawaii, French Polynesia and Vanuatu, respectively (Smith and Kostlan, 1991). Age estimates for *E. coruscans* were limited to 11 otoliths in the CNMI (Ralston and Williams, 1988) and 6 otoliths in Papua New Guinea (Fry et al., 2006), respectively. Maximum age from New Caledonian otolith counts was 21 years at 1000 mm fork length and 18 years at 870 mm for the two species, respectively, which is comparable to that estimated in the Lihir Island group, Papua New Guinea, where maximum age and length estimates of 28 and 20 years at 760 and 770 mm standard length were reported, respectively (Fry et al., 2006). However, recent bomb radiocarbon dating of *E. carbunculus* otoliths in Western Australia has extended the maximum reported age to at least 35 years (Andrews et al., 2011).

The growth pattern for many lutjanid species is characterised by rapid early growth followed by a protracted period of minimal growth (Newman et al., 1996, 2000a; Heupel et al., 2010). This results in the typical square-shaped growth curve (Choat and Robertson, 2002) whereby 50% of maximum size (L_∞) is reached at an age of <10% of potential longevity. The growth patterns for *E. carbunculus* and *E. coruscans* differed from this typical 'square-shaped' growth pattern, and were more akin to the slower growth

Table 3
Otolith sample size (n), estimated maximum age and method of age estimation, *Etelis carbunculus* and *E. coruscans,* from different studies in various locations in the Pacific region

Species	Location	n	Ageing method	Max. age (years)	Reference
Etelis carbunculus	CNMI	4	Otolith microincrement widths	3	Ralston and Williams (1988)
	CNMI	62	Otolith microincrement widths	6	Smith and Kostlan (1991)
	FP	63	Otolith microincrement widths	12	Smith and Kostlan (1991)
	Hawaii	37	Otolith microincrement widths	14	Smith and Kostlan (1991)
	Vanuatu	13	Otolith microincrement widths	9	Smith and Kostlan (1991)
	PNG	20	Annual increment counts	28	Fry et al. (2006)
	NC	96	Annual increment counts	21	Present study
	WA	10	Bomb radiocarbon dating	35	Andrews et al. (2011)
Etelis coruscans	CNMI	11	Otolith microincrement widths	9	Ralston and Williams (1988)
	PNG	6	Annual increment counts	20	Fry et al. (2006)
	NC	79	Annual increment counts	18	Present study

CNMI, Commonwealth of the Northern Mariana Islands; PNG, Papua New Guinea; FP, French Polynesia; NC, New Caledonia; WA, Western Australia.

patterns for the larger *Lutjanus* species such as *L. sebae*, *L. malabaricus*, *L. erythropterus* (Newman et al., 2000b) and *L. bohar* (Marriott et al., 2007). The youngest and oldest fish were probably under-represented in the distribution of size-at-age data collected for *E. carbunculus* and *E. coruscans*, which could be attributed to the selectivity of the gear. Larger sample sizes of small juvenile and larger adult fish would have helped to define the lower and upper ends of growth trajectories and improve parameter estimates for both species. Nevertheless, in contrast to most lutjanid species, the relatively high longevity and slow growth for *E. carbunculus* and *E. coruscans* indicates that these species have a relatively low production potential and higher vulnerability to the impacts of fishing (Cheung et al., 2005).

Fisheries managers in the Pacific region have called for stock assessments and evaluation of management strategies for the region's deep-water snapper stocks (Williams et al., 2012). Assessments of deep-water snapper stocks have been completed only in Tonga (MRAG, 1994) and Hawaii (Brodziak et al., 2011) where sufficient fisheries data have been collected. However, Hawaii is the only region in the Pacific where regular stock assessments are done. In the absence of fisheries monitoring data, stock assessments are limited to simplistic equilibrium models such as per-recruit-models. Notwithstanding the limitations of equilibrium models, the spawner biomass-per-recruit analysis has, for the first time, provided fisheries managers in New Caledonia with estimates of the dynamics of deep-water snapper populations that can be used to help guide management decisions. Estimates of spawner biomass-per-recruit were more sensitive to variation in natural mortality than in the mean age at first capture, suggesting that conservation measures for both species are more likely to be effective if they control fishing mortality rather than gear selectivity, but sustainable exploitation and maximization of yield could be achieved only by regulating F and selectivity simultaneously. The analyses also suggest that *E. coruscans* is more vulnerable to over-fishing than *E. carbunculus* due to its older age at maturity and younger age at first capture. The spawner biomass-per-recruit analysis demonstrated that lower rates of fishing mortality were required for *E. coruscans* than for *E. carbunculus* to maintain spawning biomass above the biological reference points of 30 and 40% spawning biomass, particularly when natural mortality was high (0.25). However, the revised longevity estimate for *E. carbunculus* (35 years) from Andrews et al. (2011),

suggests that natural mortality for *E. carbunculus* is approximately 0.13 based on the Hoenig (1983) regression. This estimate is close to the lower value of natural mortality (0.10) used here, suggesting that fishing mortality for *E. carbunculus* most likely needs to be relatively low (<0.11) to achieve stock persistence (assuming the 40% spawning biomass threshold). Maintaining fishing mortality <0.1 for both species is, therefore, the most cautious approach to managing the fishery, given the uncertainty in estimates of natural mortality and the fact that the two species are caught in a mixed fishery.

The challenge for fisheries managers in New Caledonia will be to implement monitoring procedures that allow estimation of natural and fishing mortality. The most feasible method for estimating these parameters for *E. carbunculus* and *E. coruscans* will be through the collection of otoliths from populations that have been exploited and those that are as close to unexploited as possible (Williams et al., 2012). Catch curves derived from unexploited populations would provide estimates of natural mortality, while those derived from exploited populations would provide estimates of total mortality, from which fishing mortality can be estimated. This approach would require more samples than available in the current study to provide representative age distributions and robust estimates of mortality. A fisher collection programme (e.g. Starr, 2010), whereby fishers are enlisted to collect biological samples and associated data, would be an ideal approach to collect otoliths from exploited populations. Some remote and lightly exploited habitats within New Caledonia could provide opportunities to collect otoliths.

Conclusions

Clearly there is a need for improved capacity to manage deep-water snapper in the Pacific region. For a few countries with a long time-series of fisheries monitoring data, evaluations of stock status and the ability to use quantitative methods to help guide management responses are feasible. For most countries in the Pacific region, however, such time-series of data are not available and resources have not been directed towards establishing fisheries data-collection programmes for deep-water snapper. The data and model predictions in this study have increased the sample size of otolith-derived age estimates. However, further and more comprehensive studies on age composition for both species

would greatly improve our understanding of the vulnerability of these species to fishing throughout the Pacific region. In the absence of robust estimates of natural and fishing mortality, it is appropriate that fisheries managers apply the precautionary principle to manage these vulnerable species. This should include *inter alia* ensuring that there are no major increases in the current fishing effort for deep-water snapper until reliable estimates of fishing and natural mortality are available.

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