Resilience of reef fish species on the Great Barrier Reef and in Torres Strait

Project Milestone Report

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Introduction

The status of many fisheries associated with coral reefs are in decline globally, putting the food security and livelihoods of millions of people at risk (Newton *et al.* 2007; Cinner *et al.* 2009). Declines in reef fish populations have also been linked to reduced ecosystem services and functions on coral reefs (McClanahan 2002). The ability to effectively manage exploited reef fish populations will thus enhance the health of coral reefs and the societies that rely upon them. A variety of management strategies are available for coral reef fisheries, across a range of complexities. While complex management strategies (e.g. individual transferable quotas, ITQs) can ensure exploitation of the maximum amount of available biomass they are difficult (and costly) to implement and enforce. This is especially true for coral reef fisheries as many are small-scale subsistence fisheries that operate at local scales. Alternatively, simpler strategies such as marine protected areas (Russ 2002) and size limits can be easier to implement and enforce, and may be more suited to many coral reef fisheries.

Coral reef fisheries management is also complicated by the fact that these habitats have very high fish diversity, with a wide range of different life history strategies (Choat and Robertson 2002). Thus the ability to sustain fishing pressure varies between species (Jennings *et al.* 1998), with some species able to sustain much higher levels of exploitation than others. In the absence of good information on life history, proxies such as maximum size have been used to identify species that may be more susceptible to fishing (Jennings *et al.* 1998). However, where good life history data can be used, a much clearer picture of the species within coral reef fish communities that are most susceptible to fishing can be more readily identified and management measures such as size limits targeted at vulnerable species (Goodyear 1993).

Coral reef fisheries worldwide, and especially in the Indo-Pacific, are dominated by a small number of speciose families – Serranidae (cods and gropers), Lethrinidae (emperors), Lutjanidae (tropical snappers), Scaridae (parrotfishes) and Labridae (wrasses and tuskfishes). Within-family life history variation is large (Choat and Robertson 2002; Gust *et al.* 2002). These families are the most common large-sized teleosts on reefs and as such, represent the preferred target species for exploitation. Their larger less productive species with particular life history characteristics (such as greater longevity, slow growth and late maturation) are more vulnerable to overexploitation and are rare in some coral reef fisheries which exploit smaller and/or more productive species (Musick 1999).

The Coral Reef Fin Fish Fishery (CRFFF) in the Great Barrier Reef (GBR) is considered to be one of the most well managed coral reef fisheries in the world. A range of complex management measures are in place, including Individual Transferable Quotas (ITQs) for commercial fishers, bag limits for recreational fishers, marine protected areas (through zoning of the Great Barrier Reef Marine Park), spawning closures, size limits, gear and effort controls, etc. Management measures are targeted at the two main species targeted in the commercial fishery – common coral trout (*Plectropomus leopardus*) and redthroat emperor (*Lethrinus miniatus*) – but also apply to a suite of >100 spp. of telesosts comprising the ‘other species’ quota group. These species constitute 27.7% commercial, 51.8% charter and almost 90% of recreational catch in GBR waters (Table 1). Identification and recording by fishers from different sectors can be less than accurate and despite extensive scientific investigation and management implementation, knowledge of the life history of most species is poor. With a highly diverse catch, the wide range of life histories indicates variation in resiliencies to exploitation. Thus, the ability to identify those species vulnerable to fishing, and assess the effectiveness of management measures, is limited.

The Effects of Line Fishing (ELF) project was a decade-long research initiative centred on a large-scale manipulative fisheries experiment aimed to improve the understanding of the fish and fisheries of the GBR. Catch surveys associated with the ELF Project collected substantial life history data and samples (reproductive organs and otoliths) from a wide range of species captured using commercial line fishing techniques. The current project used the data and samples collected during the ELF Project from the non-target species (i.e. not *P. leopardus* or *L. miniatus*) and additional samples from eastern Torres Strait (ETS) to determine life history parameters for >20 species from the families Lethrinidae, Lutjanidae and Serranidae Williams *et al.* 2007; Currey *et al.* 2008; Mapleston *et al.* 2009; Heupel *et al.* 2010). The objective of this section of work was to use this life history data to (1) identify the species with biological characteristics that make them most vulnerable to over-exploitation and other disturbances, and (2) evaluate the effectiveness of size-based regulations and gear characteristics in achieving sustainability of commonly caught species from three of the most important reef fish families of the Australian east coast.

Table 1. Percentage catch composition of teleosts from three sectors of the Coral Reef Fin Fish Fishery (summarised from MTSRF report, Simpfendorfer *et al.* 2005).

Common name	**Species**	**% Catch composition by weight**		
		Commercial	**Charter**	**Recreational**
CORAL TROUT*	*Plectropomus* spp.	50.3346	26.7582	10.4831
REDTHROAT EMPEROR*	*Lethrinus miniatus*	21.9267	21.437	8.6265
FISH MIXED REEF		5.0747	0.105	
FISH MIXED REEF B		3.3452	0.0165	
LARGE MOUTH NANNYGAI	*Lutjanus malabaricus*	2.4657	4.9749	5.5305
RED EMPEROR	*Lethrinus sebae*	2.4568	7.8324	10.1417
EMPEROR UNSPECIFIED	*Lethrinus spp.*	2.1669	8.9244	12.7807
COD UNSPECIFIED	Serranidae	2.0693	4.8013	11.0595
FISH MIXED REEF A		1.8524	0.0279	0.0219
HUSSAR PERCH	*Lutjanus adetti/vitta*	1.6848	3.3486	2.8422
JOBFISH UNSPECIFIED	*Aprion spp.*	1.4156	0.6166	0.042
SPANGLED EMPEROR	*Lethrinus nebulous*	1.266	3.8785	2.83
ROSY JOBFISH	*Pristipomoides filamentosus*	0.8276	0.6622	0.8277
GOLD BANDED SNAPPER	*Pristipomoides multidens*	0.5185	0.0006	0.0169
PARROTFISH UNSPECIFIED	Scaridae	0.4791	7.9686	2.1094
SMALL MOUTH NANNYGAI	*Lutjanus erythropterus*	0.3649	3.1159	1.6644
NANNYGAI UNSPECIFIED	*Lutjanus malabaricus/ erythropterus*	0.3398	1.24	6.4219
BARRAMUNDI COD	*Cromileptes altivelis*	0.2656	0.0834	0.7546
WRASSE UNSPECIFIED	Labridae	0.2492	0.1252	0.078
MAORI COD UNSPECIFIED	*Epinephelus undulatostriatus*	0.1566	0.4031	0.375
CORAL BREAM	*Gymnocranius audleyi*	0.1519	0.1242	2.4956
STRIPEY BASS	*Lutjanus carponotatus*	0.1167	0.2801	2.3758
SLATEY BREAM	*Diagramma pictum labosium*	0.0956	0.2993	2.3205
SEA PERCH UNSPECIFIED	*Lutjanus* spp.	0.0731	0.1644	0.8182
LONGNOSED EMPEROR	*Lethrinus olivaceus*	0.0324	0.1758	0.0357
FINGERMARK BREAM	*Lutjanus johnii*	0.0278	0.5094	3.0456
VENUS TUSK FISH	*Choerodon venustus*	0.0271	0.9822	4.1944
FLAME TAIL SNAPPER	*Etelis coruscans*	0.0241		
RUBY SNAPPER	*Etelis* spp.	0.0237		
RED BASS	*Lutjanus bohar*	0.0231	0.0074	0.1104
GREEN JOBFISH	*Aprion virescens*	0.0184	0.3589	0.4541

Common name	**Species**	**% Catch composition by weight**		
		Commercial	**Charter**	**Recreational**
GOLDSPOT COD	*Epinephelus tauvina*	0.0161	0.2951	4.0031
BAR COD	*Epinephelus ergastularius*	0.0159	0.0023	
MAORI BREAM	*Gymnocranius grandoculis*	0.0111	0.0228	0.157
HAPUKU COD	*Polyprion oxygeneios/* *P. americanus*	0.0096		
SEA BREAM	*Gymnocranius* spp.	0.0087	0.002	0
FUSILIER UNSPECIFIED	*Caesio* spp / *Pterocaesio* spp.	0.0085	0.007	
SPECKLEFIN COD	*Epinephelus ongus*	0.0078	0.0295	
CORAL COD	*Cephalopholis miniata*	0.0068	0.033	0.2507
FLOWERY COD	*Epinephelus fuscoguttatus*	0.0062	0.0539	0.2184
CATTLEDOG COD	*Epinephelus cyanopodus*	0.0057	0.0198	
BLACKFIN COD	*Epinephelus maculatus*	0.0046	0.0113	0.0614
BLUESPOT ROCK COD	*Cephalopholis cyanostigma*	0.0039	0.024	0.0552
SMALL-TOOTHED JOBFISH	*Aphareus furca*	0.0037		0.0291
COMET GROPER	*Epinephelus morrhua*	0.0027		
FOOTBALLER COD	*Epinephelus fasciatus*	0.0023	0.0024	
MOZAMBIQUE BREAM	*Wattsia mossambica*	0.0019		
EIGHT BAR GROUPER	*Epinephelus octofasciatus*	0.0017		
CHINAMAN	*Symphorus nematophorus*	0.0016	0.0571	0.2738
BLUESPOT TROUT	*Plectropomus laevis*	0.0015	0.0012	0.0133
RETICULATED EMPEROR	*Lethrinus semicinctus*	0.001	0.0026	0.0123
TOMATO COD	*Cephalopholis sonnerati*	0.0008	0.0046	0.0229
BLUE-BONED TUSKFISH	*Choerodon cyanopodus*	0.0007	0.0162	
MAORI SEA PERCH	*Lutjanus rivulatus*	0.0007	0.0051	0.1316
BIRDWIRE COD	*Epinephelus merra*	0.0004		
PALE SNAPPER	*Etelis radiosus*	0.0004		
YELLOWTAIL SWEETLIP	*Lethrinus atkinsoni*	0.0004	0.0004	0.1357
BLUBBERLIP BREAM	*Plectorhinchus gibbosus*	0.0002	0.0018	
CAMOUFLAGE ROCKCOD	*Epinephelus polyphekadion*	0.0002		
THREADFIN EMPEROR	*Lethrinus genivittatus*	0.0002	0.0546	0.0107
BLACKSPOT PIGFISH	*Bodianus vulpinus*	0.0001		
REDSPOT EMPEROR	*Lethrinus lentjan*	0.0001	0.029	0.0976
PURPLE TUSKFISH	*Choerodon cephalotes*	0.0001		0.0499
SADDLE-BACK SNAPPER	*Paracaesio kusakarii*	0.0001		

Common name	**Species**	**% Catch composition by weight**		
		Commercial	**Charter**	**Recreational**
TUSKFISH UNSPECIFIED	*Choerodon* spp.	0.0001		
JAPANESE LARGE EYE BREAM	*Gymnocranius euanus*	0.0000		0.1196
POTATO COD	*Epinephelus tukula*	0.0000	0.0052	0.0327
WHITELINED COD	*Anyperodon leucogrammicus*	0.0000	0.002	
REDEAR EMPEROR	*Lethrinus rubrioperculatus*	0.0000		
SOUTHERN FUSILIER	*Caesio* spp.	0.0000	0.0002	1.0861
YELLOWTAIL FUSILIER	*Caesio cuning*	0.0000	0.0001	0.0391
VARIEGATED SWEETLIP	*Lethrinus variagatus*	0.0000	0.0014	
FRECKLED COD	*Cephalopholis sexmaculata*		0.0003	
QUEENSLAND COD	*Epinephelus lanceolatus*		0.0004	
INDONESIAN SNAPPER	*Lutjanus bitaeniatus*		0.0095	0.2937
ORANGE STRIPED EMPEROR	*Lethrinus obsoletus*		0.0001	
PADDLETAIL	*Lutjanus gibbus*		0.0021	
DARK TAILED SEA PERCH	*Lutjanus lemniscatus*		0.0024	0.0043
STRIPED SEA PERCH	*Lutjanus vitta*		0.0089	
PIGFISH UNSPECIFIED	*Bodianus* spp.		0.0001	
SADDLEBACK PIGFISH	*Bodianus bilunulatus*		0.0028	
SURGEONFISH	*Acanthurus* spp../ *Ctenochaetus* spp.		0.0039	0.0046
BLACKSPOT TUSKFISH	*Choerodon schoenleinii*		0.0165	0.4411
YELLOW SPOTTED ROCK COD	*Epinephelus areolatus*		0.0000	

Methods

To evaluate the vulnerability of individual species to overexploitation the spawning potential ratio (SPR) approach (Goodyear 1993) was used. This approach is commonly used where abundance time-series data or stock-recruitment data are unavailable to investigate the productivity of a population in more detail (Walters and Martell 2004). It provides the ability to determine fishing mortality based biological reference points (target and limit) as well as evaluate the effectiveness of size-based regulations in enhancing sustainability.

Life history parameters were compared among species via two multivariate methods: cluster analysis and principle components analysis (PCA). These analyses illustrate the influence of a range of life history parameters among species by reducing the dimensionality of the data.

Source of data

Life history data was collated from 23 teleost species of from the families Lethrinidae, Lutjanidae and Serranidae caught as part of two projects: the Effects of Line Fishing (ELF: GBR) and Eastern Torres Strait (ETS) projects. This work formed part of the Marine and Tropical Sciences Research Facility (MTSRF) Project 4.8.3 publications (Williams *et al.* 2007; Currey *et al.* 2008; Heupel *et al.* 2009; Mapleston *et al.* 2009) and the Eastern Torres Strait Reef Line Fishery Project T1.1 (Williams *et al.* 2008). These summary data were supplemented with additional data, mostly weight-at-age data collected during the ELF Project.

For all samples of the 23 reef fish species, fork length (*FL*) was measured to the nearest millimetre and whole wet weight (*W*) measured to the nearest 10 g. For species with low sample sizes and where weight data was not available, weight was estimated (*Lutjanus fulviflamma n*=134, *Aprion virescens n*=14) using species-specific length-weight relationships ($W = a \times FL^b$; where *a* is the coefficient of the power function and *b* is the exponent). Age was estimated using sagittal otoliths for each species using standard methods (Currey *et al.* 2008; Mapleston *et al.* 2009; Heupel *et al.* 2010). The von Bertalanffy growth function (VBGF) was fitted by nonlinear least-squares regression of both *FL* and *W* on age for each species using the equations:

$$L_t = L_\infty (1-e^{-K\,(t-t0)})$$

$$W_t = W_\infty (1-e^{-K\,(t-t0)})$$

where L_t and W_t are the fork length or weight at age t, L_∞ and W_∞ is the mean asymptotic length or weight, K is the growth coefficient or rate at which L_∞ and W_∞ are approached, t is the age of the fish and t_0 is the age at which the fish have a theoretical length or weight of zero. To adjust for the absence of juvenile individuals in each dataset and poor fits to the VBGF, t_0 was constrained to zero for all species for length-at-age analyses to produce a more realistic estimate of growth. Fits of weight-at-age data to VBGF produced more reasonable values of t_0, thus t_0 was constrained to zero where t_0 <-5.

Sex and maturity data were collected for each specimen macroscopically (Lutjanidae) or histologically (Lethrinidae and Serranidae) and the proportions of females (and mature females) in each age class calculated for each species. For sex-changing species the proportions of females were derived from the fit to the logistic equation:

$$P_s = 1 - \left(1 + e^{-\ln 19(S - S_{50})/(S_{95} - S_{50})}\right)^{-1}$$

where P_s is the proportion of females (relative to males) in age s, and s_{50} and s_{95} are the lengths and ages at which 50% and 95% of the population are males for each species, respectively. Operational sex ratios were also calculated for each species as the ratio of mature females to mature males. Departure from a 1:1 sex ratio was tested using a chi-squared test using Yates correction for continuity.

Mortality rate analysis

Age-based catch curves using data from ELF and ETS samples were used to estimate the instantaneous rate of total mortality (Z) for each species. The log-transformed number of fish in each age class was regressed against the corresponding age, and the descending slope provided an estimate of Z. Regressions were fitted from the mode, the first age class that was fully selected by the sampling gear, through to the oldest age class that was preceded by no more than two consecutive zero frequencies.

Estimates of natural mortality (M) were calculated for each species using Hoenig’s (1983) equation:

$$Log_e\, M = 1.46\text{-}1.01\ log_e\, t_{\max}$$

where $t_{\max}$ is longevity in years. Estimating mortality via this method was deemed appropriate as the likelihood of obtaining individuals at maximum age ($t_{\max}$) was probable from the unharvested reefs (closed to fishing) which were sampled.

Spawning potential ratio

Spawning stock biomass per recruit (SSB/R) was estimated:

$$SSB/R = \sum_{t=t_m}^{t_{\max}} \left(fr_t \times W_t \times e^{-\sum_{i=0}^{t-1}\left(M+\left(F_t \times V_t\right)\right)} \right)$$

where fr_t is the proportion of females mature at age t, W_t the mean weight of females at age t, M is the natural mortality rate, F_t is the fishing mortality rate at age t and V_t is the vulnerability at age t. The spawning potential ratio was calculated as:

$$SPR = \frac{SSB/R}{SSB/R_{F=0}}$$

SPR for each species was estimated under different levels of fishing pressure (F = 0 to F = 1.5, in increments of 0.1). Three values of SPR were estimated based on different assumptions about vulnerability to fishing: a) SPR_{ALL} where F applied to all ages equally, b) SPR_{GEAR} where V_t was determined from ELF and ETS catch data (modal age from age frequency distributions was used as the age of full selection to the fishery and for each age class below this modal age, a proportion of vulnerability was calculated), and c) SPR_{REG} where V_t was determined from size limits that applied to the fishers within the GBR and ETS (Table 2). Where a species was a regulated no-take species, or where its maximum size fell below the minimum size, V_t was set to zero for all age classes.

A reference point of $F_{SPR=0.2}$ was used to assess the vulnerability of a species to over-exploitation. A variety of reference levels of SPR have been suggested (Walters and Martell 2004) depending on the purpose. For setting sustainable levels (i.e. target reference points) SPR values of 0.3-0.5 are typically used, while for overfishing limits (i.e. limit reference points) values of 0.2-0.3 are common (Goodyear 1993; Chiang *et al.* 2009). We used an SPR value of 0.2 to indicate levels of F at which over-exploitation is likely to occur. Values of $F_{SPR_{ALL}=0.2}$ were used to demonstrate inherent vulnerability to over-exploitation. Lower values of $F_{SPR_{ALL}=0.2}$ (<0.2) were taken to indicate high vulnerability, values > 0.2 and < 0.4 indicated moderate vulnerability, and values > 0.4 indicated low vulnerability. Values of $F_{SPR_{REG}=0.2}$ were used to evaluate the ability of size regulations within the CRFFF and ETS to reduce the vulnerability to over-exploitation, and hence enhance the resilience of the populations. The value of $F_{SPR_{REG}=0.2} \big/ F_{SPR_{ALL}=0.2}$ was used to identify the level of reduction in vulnerability to over-exploitation as a result of regulations. Value of this ratio was <2 were taken to indicate limited reduction in vulnerability, values <4 to indicate moderate reduction in vulnerability and values >4 to indicate significant reduction in vulnerability. ANCOVAs were used to determine any significant difference among species in maximum size or age with values of $F_{SPR_{REG}=0.2}$.

Multivariate comparison of life history parameters

To determine the similarities and differences among species, a suite of life history parameters were compared using cluster analysis and principle component analysis (PCA). The 90th percentiles of age (A_{90}), length (L_{90}) and weight (W_{90}) estimated for each species were used as relative indices of senescence, longevity and growth potential. Hoenig's estimate of total mortality (Z) was used to calculate survivorship ($S = e^{-Z}$), growth parameter (K) from VBGF and SPR were compared for each species.

A cluster analysis was used to partition the species into subgroups (clusters) such that those in each particular subgroup were more 'similar' in life history characteristics than those found in other subgroups. Data was standardised by species total for each of the six life history parameters. A lower triangular resemblance matrix analysed between species using Bray Curtis coefficient of similarity. Results from the single-linkage cluster analysis were displayed by the two-dimensional graphical dendrogram.

To reduce the dimensionality of the data a PCA was used, with the original data normalised for the PCA because of the differences in scale between parameters, by standardising the variables against their means by their standard deviation. These were then transformed into principle components (PCs) – the weighted averages of the normalised estimates of life history parameters – and a PCA biplot produced. Vectors indicate the life history parameters associated with species in close proximity, with stronger relationships observed further from the vector origin.

Results

Life history data from the 23 coral reef teleost species assessed indicate a high degree of variation between and within families (Table 2). Life history patterns included small long-lived species to large fast-growing species. Maximum ages ranged from 7 to 46 years and maximum weights varied from 0.33 kg to 14.4 kg.

Table 2. Life history parameters for coral reef teleost species used in the analysis of spawning potential ratios. (^{a} t_0 constrained to zero, ^{b} Pauly's M was substituted as Z could not be estimated).

					Mortality		**Length-weight**		**Weight-at-age**			**Length-at-age**	
Family, *Species*	**Age$_{max}$ (yr)**	**A_{90} (yr)**	**L_{90} (FL)**	**W_{90} (g)**	**Z (yr^{-1})**	**Hoenig M**	**a (×10^{-8})**	**b**	**W_∞**	**K (yr^{-1})**	**t_0**	**L_∞**	**K (yr^{-1})**
Lutjanidae													
Lutjanus fulviflamma	17	15	304	481	0.14	0.25	2.00	2.98	0.36	0.40	0^a	267	0.41
Symphorus nematophorus	36	12	724	6430	0.20	0.25	2.23	2.95	8.95	0.15	-1.73	732	0.26
Aprion virescens	16	7	669	4691	0.56	0.47	2.12	2.95	5.52	0.37	-1.18	623	0.85
Lutjanus carponotatus	23	15	317	550	0.30	0.18	4.29	2.84	0.55	0.71	-0.11	291	0.66
Lutjanus gibbus	12	10	378	1201	0.63	0.35	0.07	3.58	1.50	0.19	-1.98	352	0.51
Serranidae													
Cephalopholis cyanostigma	46	28	289	350	0.16	0.09	4.11	2.81	0.30	0.20	0^a	271	0.22
Epinephelus fasciatus	21	14	300	380	0.38	0.20	4.55	2.79	0.34	0.28	-2.18	278	0.54
Epinephelus polyphekadion	44	27	565	2989	0.07	0.09	0.94	3.09	2.93	0.14	-2.46	547	0.20
Epinephelus fuscoguttatus	42	22	740	9800	0.07	0.10	0.14	3.05	11.39	0.10	-3.01	785	0.19
Epinephelus ongus	30	18	385	560	0.82	0.14	1.20	3.03	0.43	0.34	0^a	317	0.30
Epinephelus quoyanus	14	8	342	533	0.68	0.30	5.37	2.77	0.43	0.77	-0.18	322	0.74
Anyperodon leucogrammicus	27	16	493	1346	0.14	0.15	2.72	3.23	1.44	0.15	-3.96	472	0.33
Cephalpholis argus	39	25	421	1227	0.13	0.11	0.81	3.13	1.10	0.22	0^a	387	0.27
Variola albimarginata	12	8	326	644	0.44	0.35	0.69	3.15	0.49	0.50	0.03	315	0.51
Variola louti	7	5	459	1800	0.67	0.60	0.12	3.05	1.75	0.61	0^a	477	0.53
Plectropomus leopardus	17	8	557	1920	0.44	0.25	0.24	3.30	1.36	1.00	0^a	519	0.41
Plectropomus maculatus	13	6	575	2210	0.61	0.32	0.39	3.22	1.73	0.70	0^a	497	0.54
Plectropomus areolatus	14	8	590	2894	0.40	0.30	0.29	3.27	4.04	0.17	-4.07	572	0.35
Plectropomus laevis	16	6	710	5540	0.39	0.26	0.38	3.21	14.40	0.16	-1.04	788	0.30
Lethrinidae													
Lethrinus nebulous	24	12	540	2520	0.22	0.17	3.95	2.86	2.45	0.22	-3.26	477	0.63
Lethrinus olivaceus	15	7	603	2915	^{b}0.44	0.28	0.38	3.20	4.89	0.30	-0.76	660	0.47
Lethrinus atkinsoni	36	24	365	900	0.27	0.12	1.27	3.07	0.69	0.26	0^a	325	0.32
Lethrinus lentjan	19	12	345	710	0.21	0.22	7.20	2.75	0.55	0.71	-0.11	307	0.74

Spawning potential ratio

Spawning potential ratio values with three different assumptions about vulnerability to fishing (equal at all ages, commercial line fishing gear and Queensland/Torres Strait size regulations) at fishing mortality values from 0 to 1.5 yr^{-1} are shown in Figures 1 (Lethrinidae), 2 (Lutjanidae), 3 (Serranidae: Epinephelinae: *Anyperodon* spp., *Cephalopholis* spp., *Epinephelus* spp.) and 4 (Serranidae: Epinephelinae: *Plectropomus* spp., *Variola* spp.). The decline in *SPR* values was variable between and within families and the assumptions regarding vulnerability had different effects for different species. For example, there was little difference in the *SPR* trends for *Epinephelus fuscoguttatus* (Figure 3), but substantial differences for *Lethrinus lentjan* (Figure 1). The distance between the SPR_{ALL} and SPR_{REG} is a measure of the improvement in resilience that occurs from the size regulations.

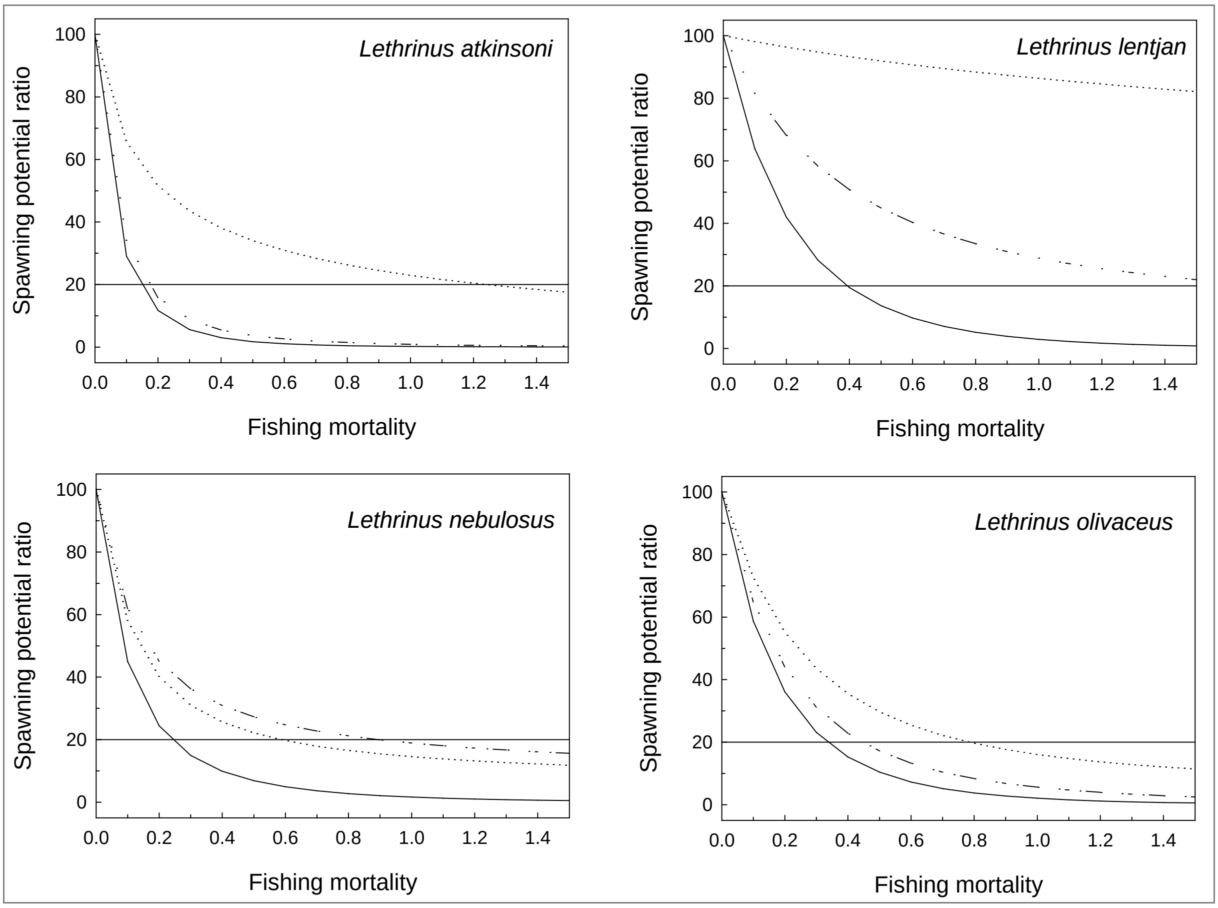

Figure 1. Spawning potential ratio plots for fish of the family Lethrinidae for three scenarios: age-independent fishing mortality (solid line), age-specific vulnerability from commercial reef line fishing gear (dotted line) and age-specific vulnerability from Queensland fishing regulations (dashed line).

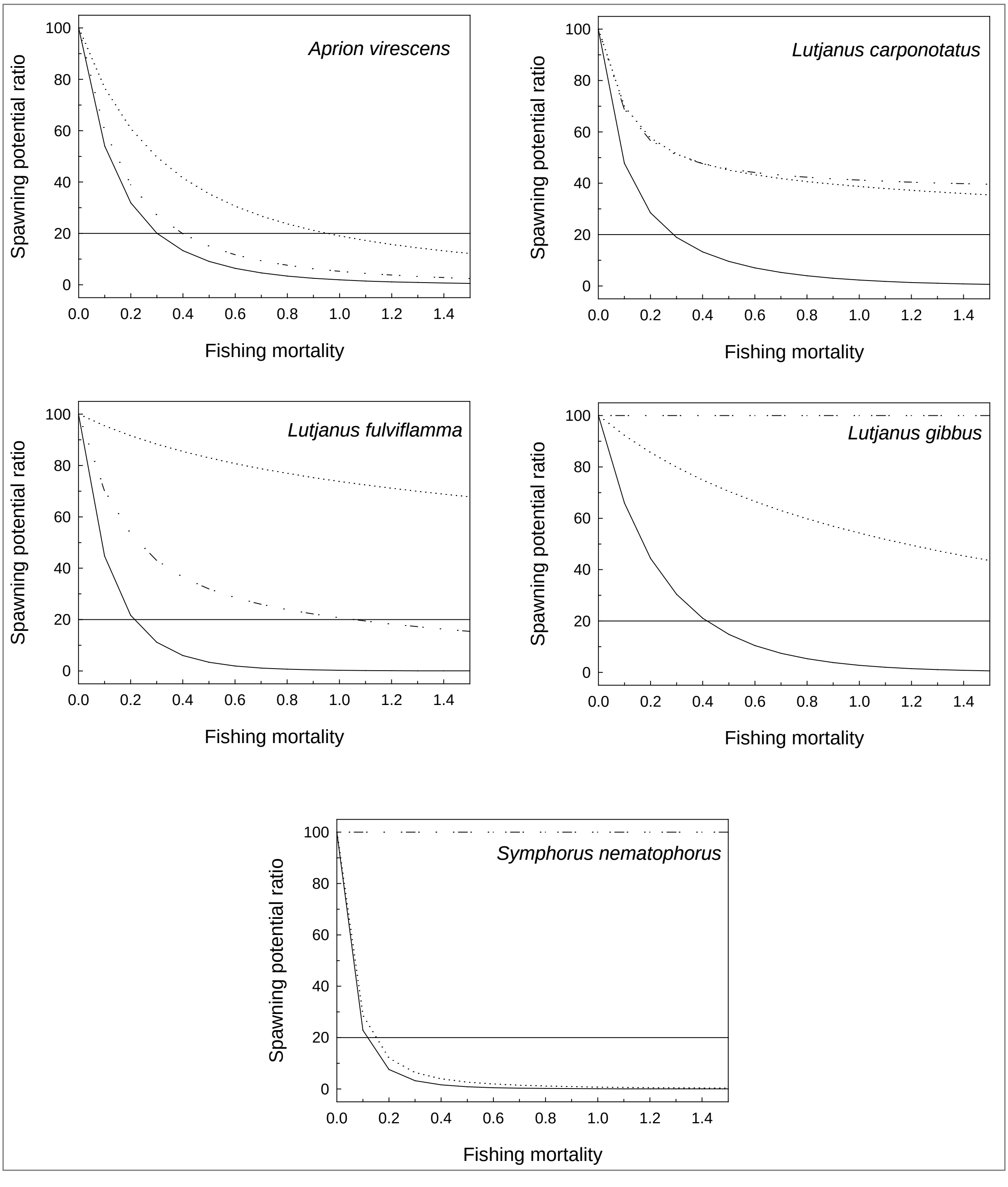

Figure 2. Spawning potential ratio plots for fish of the family Lutjanidae for three scenarios: age-independent fishing mortality (solid line), age-specific vulnerability from commercial reef line fishing gear (dotted line) and age-specific vulnerability from Queensland fishing regulations (dashed line).

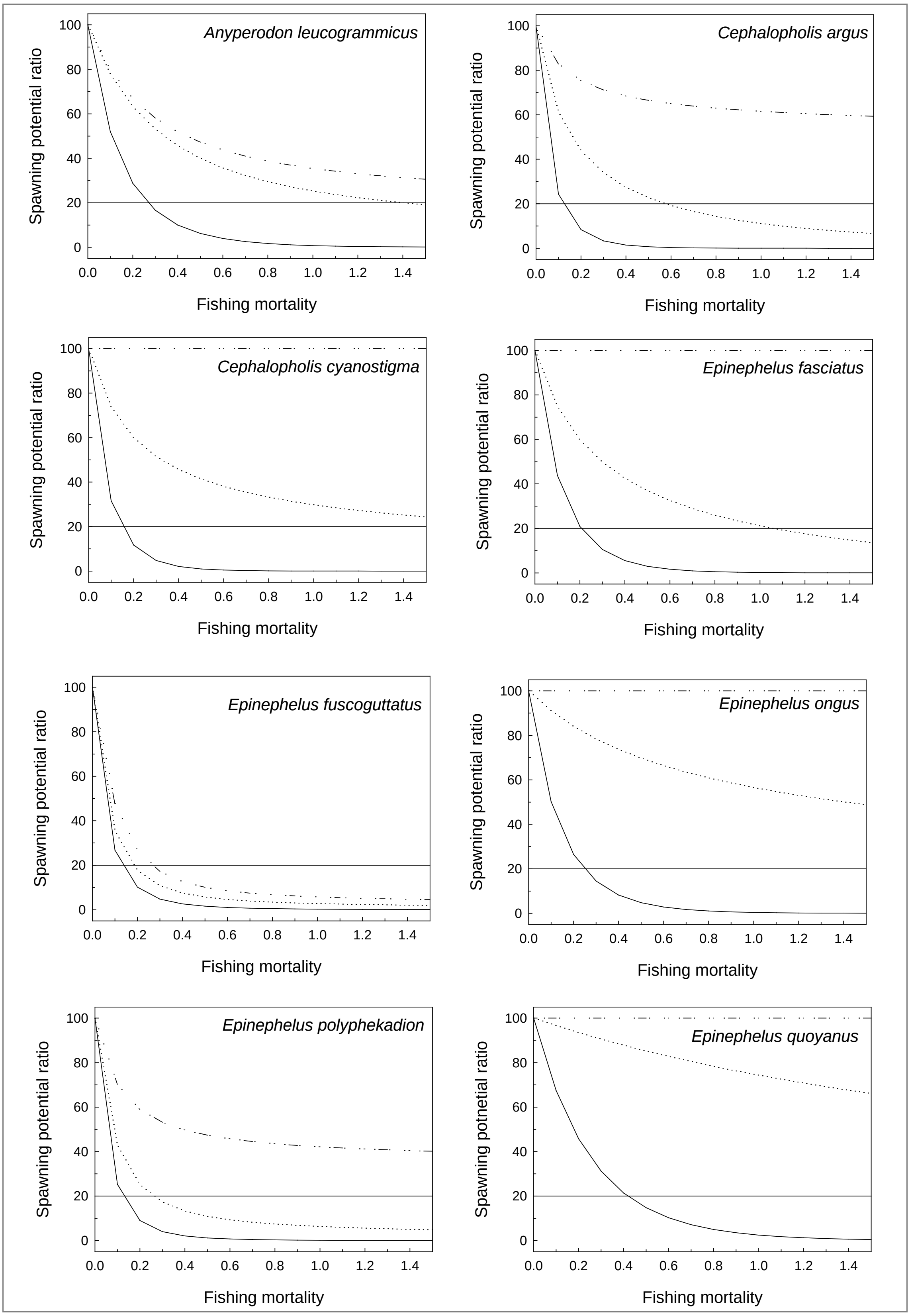

Figure 3. Spawning potential ratio plots for fish of the family Serranidae (Epinephelinae: *Anyperodon* spp., *Cephalopholis* spp., *Epinephelus* spp.) for three scenarios: age-independent fishing mortality (solid line), age-specific vulnerability from commercial reef line fishing gear (dotted line) and age-specific vulnerability from Queensland fishing regulations (dashed line).

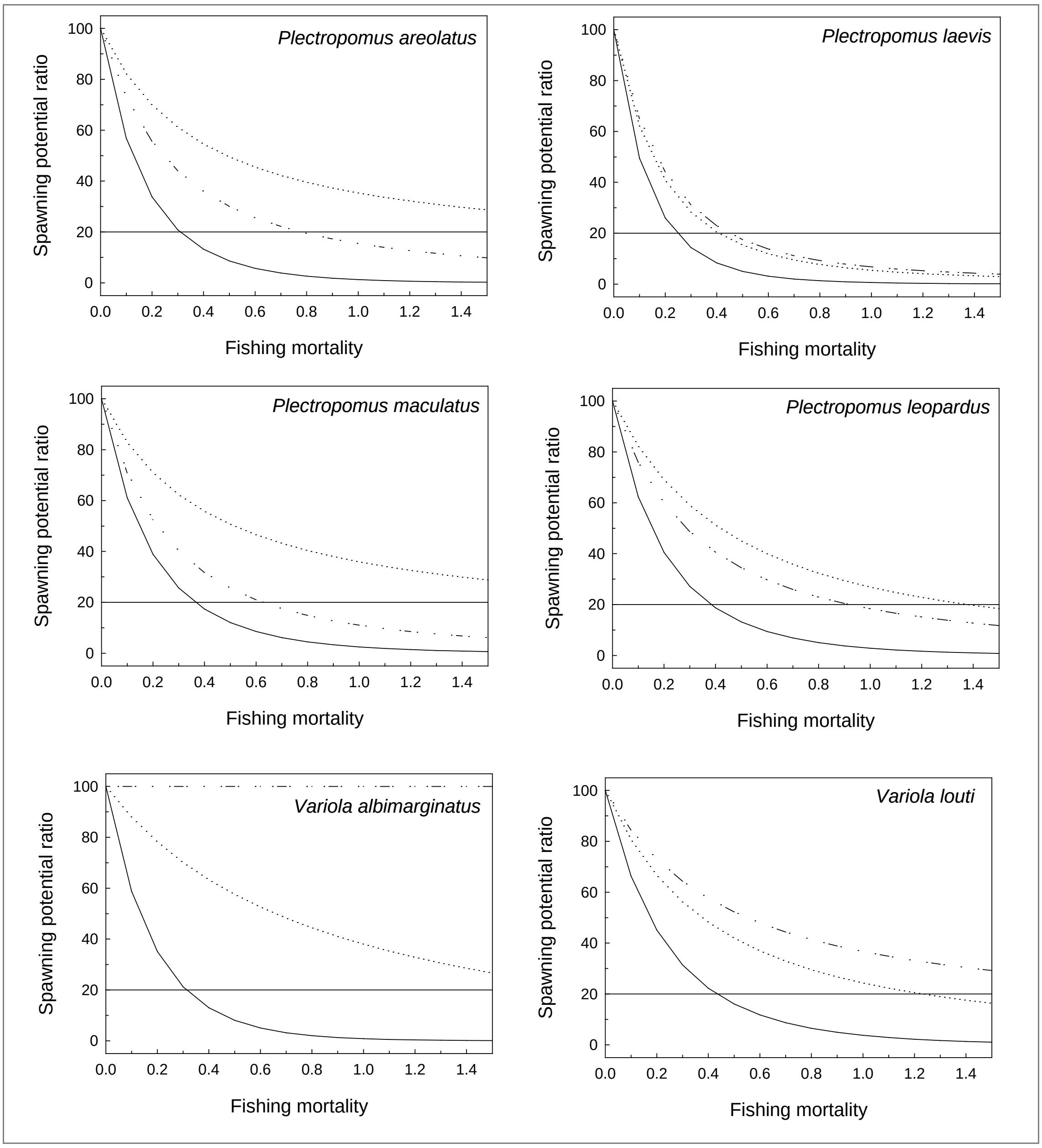

Figure 4. Spawning potential ratio plots for fish of the family Serranidae (Epinephelinae: *Plectropomus* spp., *Variola* spp. [coral trouts]) for three scenarios: age-independent fishing mortality (solid line), age-specific vulnerability from commercial reef line fishing gear (dotted line) and age-specific vulnerability from Queensland and Torres Strait fishing regulations (dashed line).

Values of $F_{SPR_{ALL}=0.2}$ ranged from 0.12 (*E. polyphekadion*) to 0.43 (*V. louti*) (Table 3). Three species (13%) had $F_{SPR_{ALL}=0.2}$ values that indicated low vulnerability, 14 species (61%) had moderate vulnerability and six species (26%) had high vulnerability. This indicates that without regulations the majority of the species assessed were relatively vulnerable to fishing. There was no relationship between the maximum size of species and their value of $F_{SPR_{ALL}=0.2}$ (Figure 5a), but a strong negative relationship with maximum age (Figure 5b; $r^2 = 0.72$; ANCOVA, $F_{1,19} = 54.75$, $p > 0.001$). Species with short life spans had the lowest levels of inherent vulnerability. The relationship between maximum age and $F_{SPR_{ALL}=0.2}$ was not significantly different between the three families investigated (ANCOVA, $F_{2,19} = 0.47$, $p = 0.63$), indicating that maximum age was an important indicator of the vulnerability of species to fishing in the absence of more complete data.

Consideration of vulnerability to standard commercial fishing gear and size regulations produced improvements in F_{SPR} values for all species (Table 3). This demonstrates that although about 90% of species were inherently vulnerable to fishing, this is moderated by one or both of these factors. The level of improvement, however, was variable among species. Examination of the ratio of $F_{SPR_{REG}=0.2}$ to $F_{SPR_{ALL}=0.2}$ (Table 3) allowed the effectiveness of the size regulations used in the Queensland coral reef fishery and the eastern Torres Strait to be assessed. These results showed that when size regulations were taken into account, 14 species showed a high level of improvement in F_{SPR} values and had limited (or no) vulnerability to overfishing. Three species had moderate improvements in vulnerability and six species had limited improvement. The six species with limited improvement were: *Aprion virescens*, *E. fuscoguttatus*, *P. maculatus*, *P. laevis*, *L. olivaceus* and *L. atkinsoni*. Two of these species (*E. fuscoguttatus* and *L. atkinsoni*) had high vulnerability to overexploitation under assumptions of equal susceptibility to fishing; the other four species had moderate vulnerability (Table 3).

Table 3. Estimates of fishing mortality at which spawning potential ratio values equal 0.2. Shading for $F_{SPR_{ALL}=0.2}$: green indicates low vulnerability, yellow moderate vulnerability and orange high vulnerability. Shading for $F_{SPR_{REG}=0.2} / F_{SPR_{ALL}=0.2}$: green indicates large improvement in resilience (i.e. reduced vulnerability), yellow indicates moderate improvement and orange indicates limited improvement.

Family, *Species*	Minimum size limit (cm *TL*)	Maximum size limit (cm *TL*)	$F_{SPR_{ALL}=0.2}$	$F_{SPR_{VUL}=0.2}$	$F_{SPR_{REG}=0.2}$	$F_{SPR_{REG}=0.2} / F_{SPR_{ALL}=0.2}$
Lutjanidae						
Lutjanus fulviflamma	25		0.21	>100	1.05	5
Symphorus nematophorus	no-take		0.15	0.14	no-take	>10
Aprion virescens	38		0.30	0.48	0.40	1.33
Lutjanus carponotatus	25		0.29	8.12	>100	>10
Lutjanus gibbus	no-take		0.41	3.74	no-take	>10
Serranidae						
Cephalopholis cyanostigma	38		0.14	2.18	>100	>10
Epinephelus fasciatus	38		0.21	1.06	>100	>10
Epinephelus polyphekadion	50	70	0.12	0.26	>100	>10
Epinephelus fuscoguttatus	50	70	0.13	0.18	0.26	2.00
Epinephelus ongus	38		0.25	10.31	>100	>10
Epinephelus quoyanus	38		0.42	17.88	>100	>10
Anyperodon leucogrammicus	38		0.27	1.40	>100	>10
Cephalopholis argus	38		0.12	0.57	>100	>10
Variola albimarginata	38		0.31	1.94	>100	>10
Variola louti	38		0.43	1.23	2.98	6.93
Plectropomus leopardus	38		0.38	1.40	0.92	2.42
Plectropomus maculatus	38		0.36	2.83	0.63	1.75
Plectropomus areolatus	38		0.31	2.95	0.78	2.52
Plectropomus laevis	50	80	0.24	0.41	0.45	1.88
Lethrinidae						
Lethrinus nebulous	45		0.23	0.58	0.89	3.87
Lethrinus olivaceus	38		0.33	0.78	0.44	1.33
Lethrinus atkinsoni	25		0.14	1.24	0.17	1.21
Lethrinus lentjan	25		0.39	>100	1.72	4.41

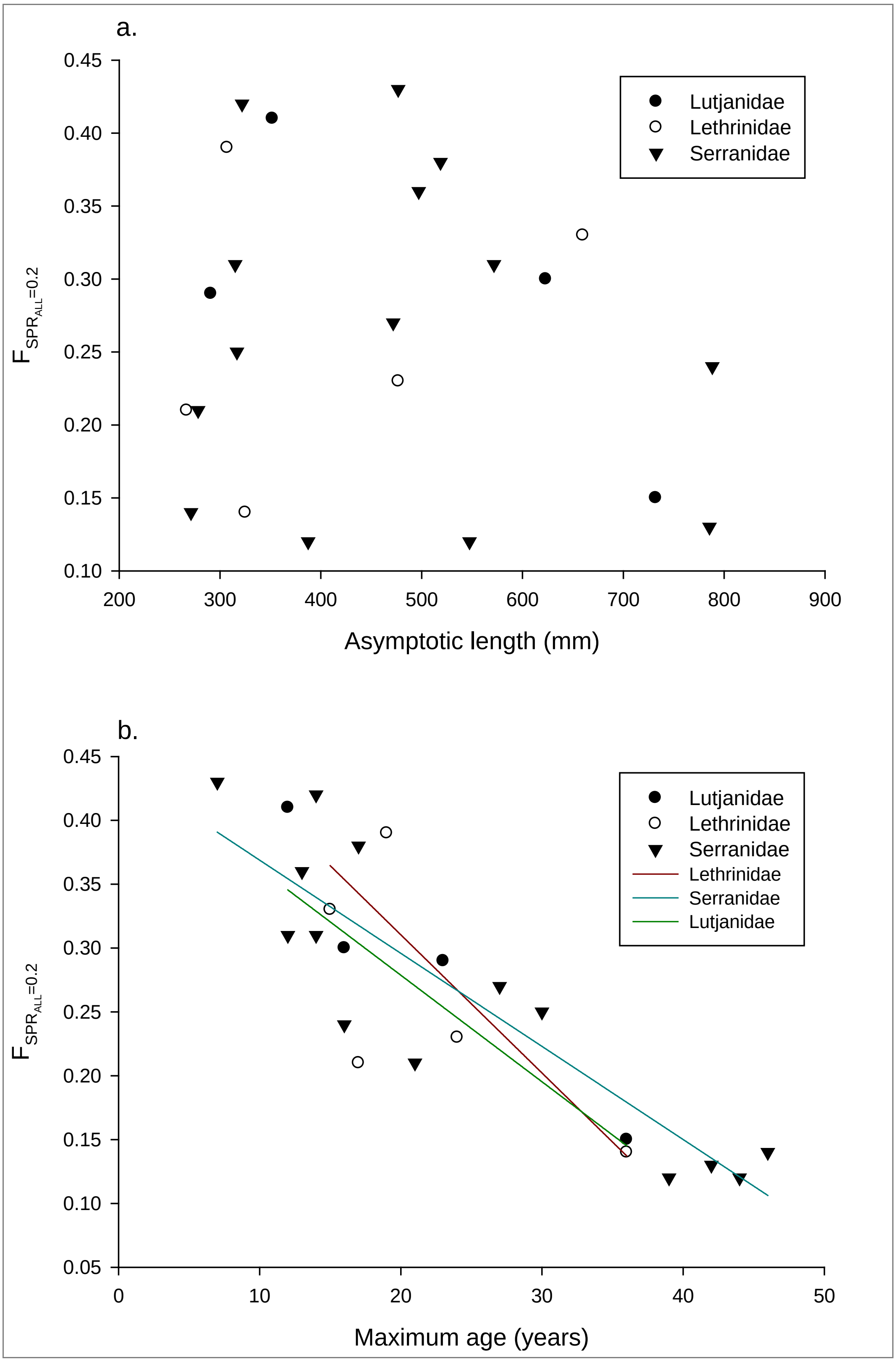

Figure 5. Relationship between the fishing mortality level at which SPR_{ALL} = 0.2 as a function of (a) asymptotic length (L), and (b) maximum recorded age, for three families of coral reef teleosts from the Great Barrier Reef and Torres Strait. Lines showing significant relationships are indicated.

Multivariate comparison of life history parameters

Multivariate analyses highlighted differences among species and that species were not grouped as families (Figures 6 and 7). Using six parameters (A_{90}, L_{90}, W_{90}, *S, K* and *SPR*) the cluster analysis illustrated three main clusters (indicated by boxes) at 96.4% similarity: small; medium; and large sized species (Fig. 6). The first main cluster was further split into three subclusters: *Variola albimarginata* and *Lethrinus lentjan* were very similar in growth (L_∞, W_∞, *K*) (a) and the older species *Cephalopholis cyanostigma* and *Epinephelus fasciatus* (c) were isolated from species in cluster (b). The medium sized species were clearly separated from *Lethrinus atkinsoni* (YTE) with the highest age$_{max}$ (d), *Anyperodon leucogrammicus* (WLC) and *Cephalopholis argus* (POC) were similar in Hoenig's mortality estimates and *K* for length (f), similar W_∞ and *K* parameters for length (g) differed from the species in cluster (e). The large species of cluster (h) were further separated into the older *E. fuscoguttatus* (FLC) from *Symphorus nematophorus* (CHM), *Aprion virescens* (GJF) and *Plectropomus laevis.*

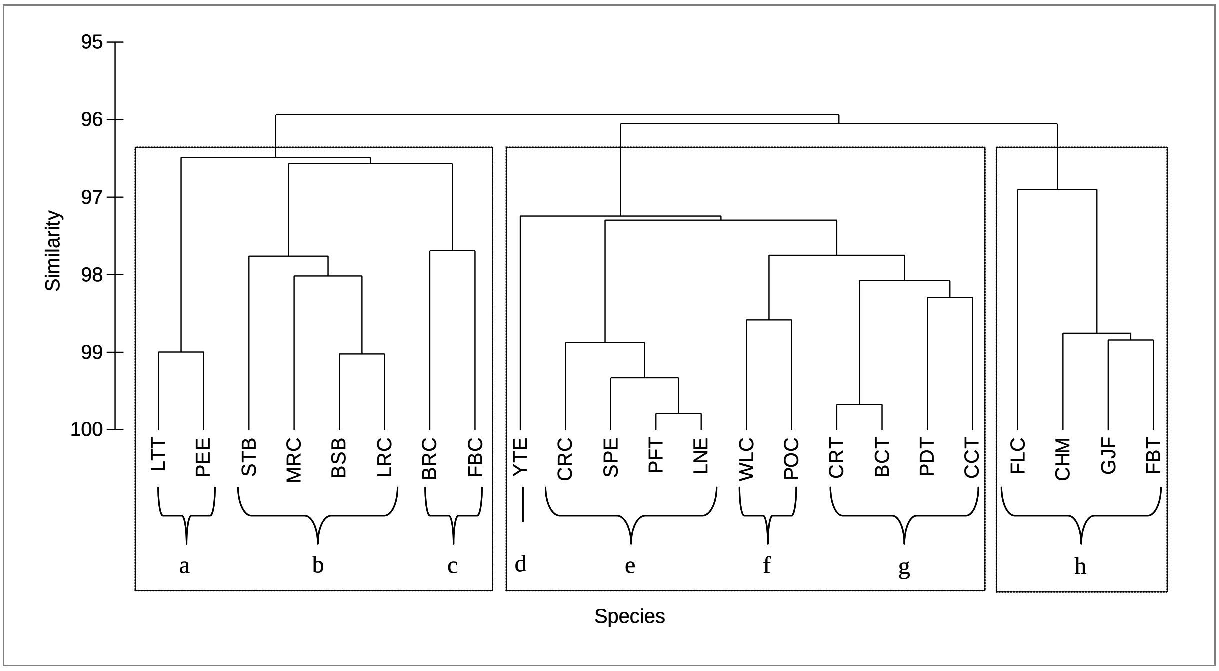

Figure 6. Cluster analysis dendrogram displaying species similarities indicating three main splits (boxes) with clusters a-h.

PCA the identified three significant PCs (>5%) for the 23 species (Table 4). The first two PCs described 87.5% of the variation therefore other PCs could be discarded without the loss of descriptive information. The biplot produced similar results to the cluster analysis in relation to size (Fig. 7). *SPR* and A_{90} were the main parameters underlying the effect of PC1, whilst PC2 was influenced by L_{90} and W_{90} (body size) (values in bold, Table 4). Similar PC1 values were observed for *Variola louti* (CRT), *Epinephelus quoyanus* (LRC) and *Aprion virescens* (GJF) with relatively high *SPR* values and young A_{90} (and were fast growing, *K*)(Table 5). High PC1 values (lower *SPR* and older A_{90}) were shared by a number of the Serranid species, particularly *Cephalopholis cyanostigma* (BRC), *C. argus* (POC) *Epinephelus fuscoguttatus* (FLC) and *E. polyphekadion*, as well as the lethrinid *Lethrinus atkinsoni* (YTE). Two of these species, *Cephalopholis cyanostigma* (BRC), and *Epinephelus fuscoguttatus* (FLC) represented the smallest and largest species respectively in body size.

Epinephelus fuscoguttatus (FLC), *Symphorus nematophorus* (CHM) and *Plectropomus laevis* (FBT) were strongly associated with high PC 2 values, large body size, with greater length (L_{90}) and weight (W_{90}) than other species (Figure 7, Table 5). Despite the same management strategy, the similar-looking serranids *Epinephelus polyphekadion* (CRC) and *E. fuscoguttatus* shared a similar maximum age and survival estimate (PC2 values), however the PC1 highlighted the much larger size of *E. fuscoguttatus*.

A regression of *SPR* against PC1 loadings produced from the PCA indicated PC1 was a good predictor of *SPR* (r^2 = 0.714, Figure 8a). Additionally, *SPR* was also well predicted by maximum age, with longer lived species having lower *SPR* values than shorter lived species (r^2 = 0.749, Figure 8b).

Table 4. Principle components (PC) values for each life history parameter among 23 species.

	PC1	PC2	PC3
A_{90}	**0.501**	-0.246	0.183
L_{90}	0.056	**0.681**	0.051
W_{90}	0.148	**0.652**	0.250
K	-0.458	-0.125	0.872
S	0.494	-0.182	0.291
SPR	**-0.521**	-0.040	-0.238
% Variation	52.7%	33.7%	6.7%

Table 5. Principle components (PC) 1 and 2 values for each species among six life history parameters.

Species	PC1	PC2
Lutjanus fulviflamma	0.245	-1.275
Symphorus nematophorus	1.237	2.512
Aprion virescens	-2.255	1.799
Lutjanus carponotatus	-0.485	-1.496
Lutjanus gibbus	-1.691	-0.563
Cephalopholis cyanostigma	2.645	-1.924
Epinephelus fasciatus	0.050	-1.447
Epinephelus polyphekadion	2.976	0.126
Epinephelus fuscoguttatus	3.074	2.991
Epinephelus ongus	1.021	-1.101
Epinephelus quoyanus	-2.304	-1.072
Anyperodon leucogrammicus	0.727	-0.325
Cephalopholis argus	2.443	-0.975
Variola albimarginata	-1.378	-0.847
Variola louti	-2.950	0.427
Plectropomus leopardus	-0.916	0.448
Plectropomus maculatus	-1.549	0.711
Plectropomus areolatus	-0.555	1.014
Plectropomus laevis	0.144	2.367
Lethrinus nebulous	-0.074	0.198
Lethrinus olivaceus	-0.933	0.996
Lethrinus atkinsoni	2.067	-1.312
Lethrinus lentjan	-1.540	-1.253

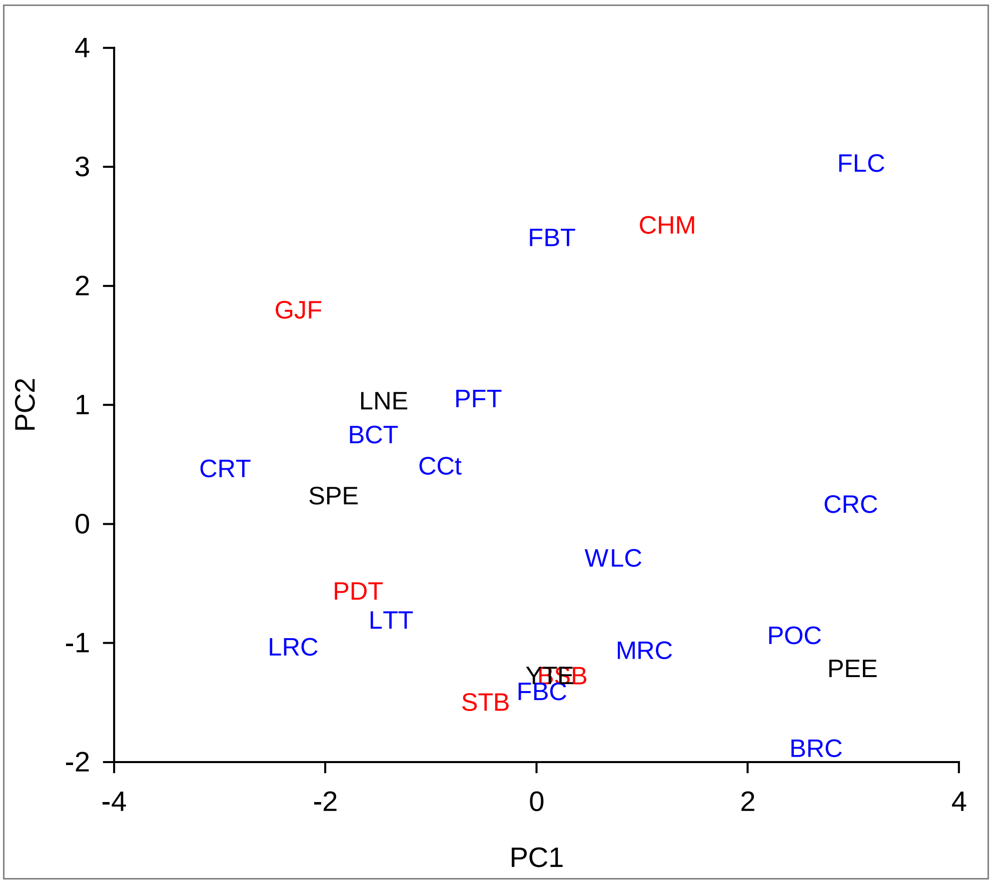

Figure 7. Biplots of data for six normalised multivariate life history parameters, principle components (PCs) 1 and 2 for 23 reef fish species from the families Lethrinidae, Serranidae and Lutjanidae.

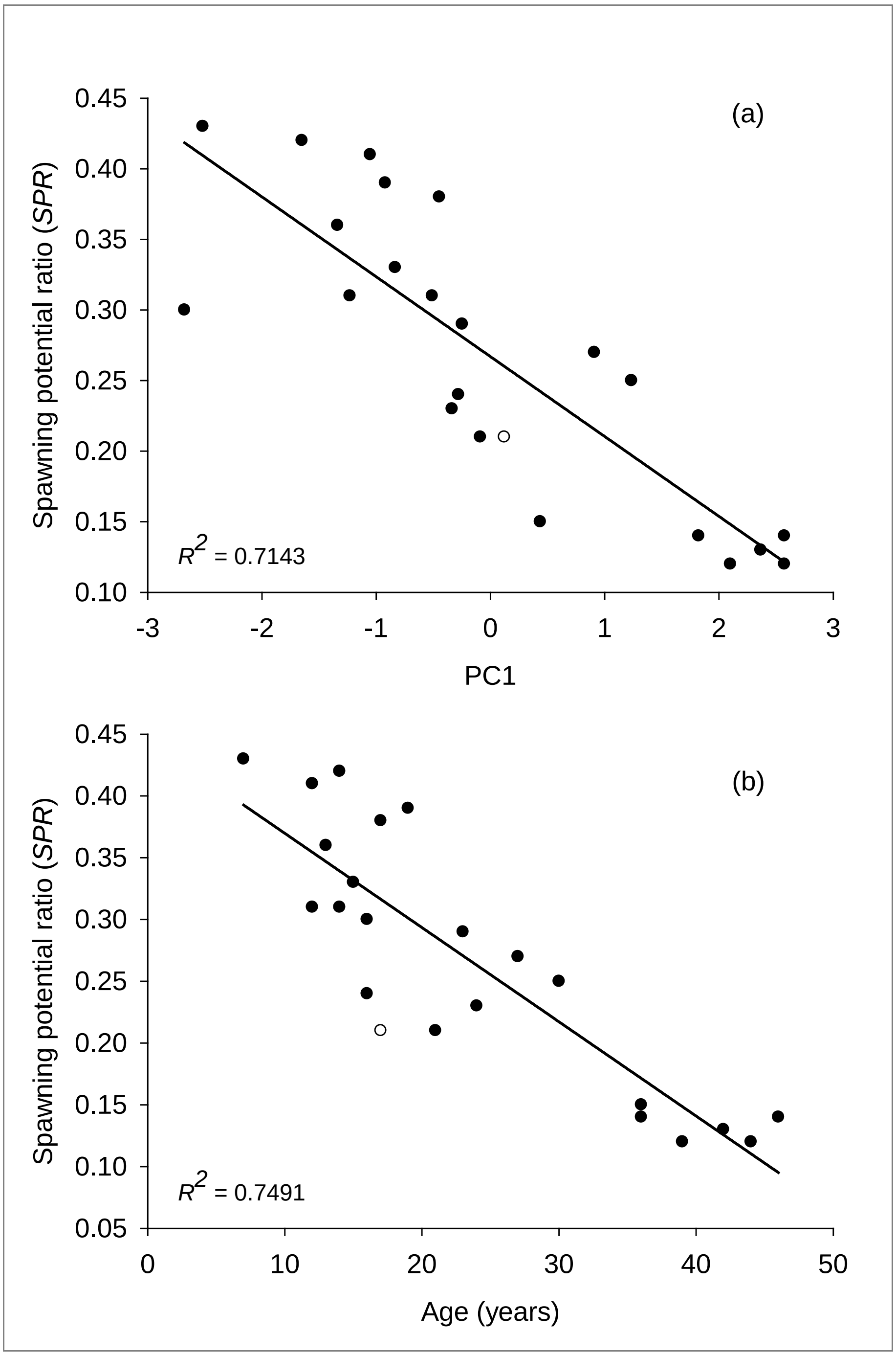

Figure 8. Linear relationships of spawning potential ratio (*SPR*) with (a) PC1 loadings (SE = 0.056) and (b) age (SE = 0.053).

Discussion

The results of these analyses demonstrate that many species of coral reef teleosts exploited by fisheries in the Great Barrier Reef, Torres Strait and more broadly in tropical regions around the globe, are inherently vulnerable to overexploitation. This is a result of varied life history characteristics that limit their ability to recover from high levels of depletion. In particular, long life spans for many species appear to be a key contributing factor.

Despite this inherent vulnerability to overexploitation, species-specific vulnerability was assessed using estimation of the spawning potential ratio (*SPR*). The results of the *SPR* analysis clearly demonstrated that in the majority of cases, size limits implemented by fisheries regulators (i.e. Fisheries Queensland [GBR] or Australian Fisheries Management Authority [Torres Strait]) provide effective protection from overexploitation. Six species were identified as requiring further investigation to determine if changes in size limits are required to further reduce their vulnerability to overexploitation.

For two of these species (*Epinephelus fuscoguttatus* and *Lethrinus atkinsoni*) fishing pressure greater than 0.2 under current size limits resulted in spawning potential ratios less than the recommended 0.2 limit reference point for overfishing. Firstly, *Epinephelus fuscoguttatus* and *E. polyphekadion* are similar in appearance which complicates species differentiation by fishers, thus they are managed under the same regulations by Fisheries Queensland. Research by Pears *et al.* (2006; Pears *et al.* 2007) identified differences in life histories (namely size and maturity) for these species, resulting in the 50-100 cm legal size slot limit reduced to the current 50-70 cm total length limit. This was to enable the protection of some males and larger breeding females of *E. fuscoguttatus*, which are much larger in size than *E. polyphekadion* (whereby males and fecund females are protected below 50 cm *TL*). Despite this change in management, the present study indicated the size regulations were ineffective at protecting this species from fishing pressure (at a level of 0.2) because the spawning potential ratio remained low. Thus *E. fuscoguttatus* is highly vulnerable to overexploitation, with perhaps this upper limit not protecting a sufficient number of the highly fecund females. Further research and ongoing monitoring is needed to ensure sustainability of this species, which is potentially at much greater risk in countries without size-based regulatory measures in place.

Secondly, *Lethrinus atkinsoni* also indicated low resilience to fishing pressure, and with consideration of the current size regulations included, these size limits appeared ineffective in reducing vulnerability. However as this species constitutes a low proportion of the catch by industry and recreational fishers in GBR waters and is typically discarded, it does not appear threatened. Additionally, *L. atkinsoni* was fully recruited (most vulnerable) to the fishery from 16 years, thus the fishery gears do not select for the smaller, immature individuals. As a long-lived non-target species that matures prior to capture by the GBR fishery, *L. atkinsoni* would be more susceptible to overexploitation only if there was a shift to increase harvest on the Australian east coast. In other areas worldwide where these lethrinids comprise targets in fishery catch (e.g. Ryuku Islands, Japan (Ebisawa 1999; Ebisawa and Ozawa 2009), this species may be more vulnerable and thus of greater concern. At a broader scale however, for the majority of cases these results demonstrate that in regions where overexploitation of reef fish populations is occurring (or likely to occur) then the introduction (and enforcement) of size limits can be an effective option.

Similarly, while maximum size has been suggested as a reasonable proxy for the vulnerability of coral reef fishes to overexploitation (Jennings *et al.* 1999), it was particularly interesting that another life history parameter, maximum age (and PC1), also provides a reliable indicator. This highlights the need by managers for biological data, as they face the constant challenge to ensure sustainable exploitation of diverse fisheries comprised of species with varied life histories. Comparative multivariate analysis for reef fishes in the current study provided an excellent method to illustrate the spread of biological differences, separating species by age (A_{90}) and *SPR* and body size (L_{90} and W_{90}). Species with greater longevity and reduced *SPR* were separated from shorter-lived, higher *SPR* species and by body size into small, medium and large sized species groups, across the three families. The relationship of maximum age with *SPR* gives the ability to speculate that species with longer lifespans have lower spawning potential ratios than short-lived species. This suggests that longer-lived coral reef fishes are more susceptible to overexploitation in multispecies fisheries, and can thus be identified in other regions which have little available data.

Previous assessments of the vulnerability of GBR teleosts to overexploitation have been based on qualitative ecological risk assessments using expert opinion (e.g. Smith and McCormack 2008) when biological data has been limited. These expert-based ecological risk assessments identified only large cods (e.g. *E. fuscoguttatus* and *E. polyphekadion*) as having an elevated risk level. The results of the current study therefore, represent an improvement in the ability to assess the risks to individual species in a quantitative way. In regions where fisheries are heavily exploited the ability to obtain biological data may be more limited, thus results from studies such as this can assist in estimating the vulnerability of reef fishes to exploitation in these areas. Utilising this knowledge of life histories (including *SPR*) with minimum legal size limits as a regulatory measure, could assist other multi-species fisheries with sustainable harvest.

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