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# Rapid declines across Australian fishery stocks indicate global sustainability targets will not be achieved without an expanded network of 'no-fishing' reserves

Graham J. Edgar[1] | Trevor J. Ward[2] | Rick D. Stuart-Smith[1]

[1] Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, Tasmania, Australia

[2] School of Life Sciences, University of Technology Sydney, PO Box 123, Broadway, New South Wales 2007, Australia

**Correspondence**
Graham J. Edgar, Institute for Marine and Antarctic Studies, University of Tasmania, GPO Box 252-49, Hobart, Tasmania, 7001 Australia.
Email: g.edgar@utas.edu.au

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## Abstract

1. A continuing debate between environmental scientists and fisheries biologists on the sustainability of fisheries management practices, and the extent of fishing impacts on marine ecosystems, is unlikely to be resolved without fishery-independent data spanning large geographic and temporal scales. Here, we compare continental- and decadal-scale trends in fisheries catches with underwater reef monitoring data for 533 sites around Australia, and find matching evidence of rapid fish-stock declines.
2. Regardless of a high global ranking for fisheries sustainability, catches from Australian wild fisheries decreased by 31% over the past decade. The biomass of large fishes observed on underwater transects decreased significantly over the same period on fished reefs (36% decline) and in marine park zones that allow limited fishing (18% decline), but with a negligible overall change in no-fishing marine reserves. Populations of exploited fishes generally rose within marine reserves and declined outside the reserves, whereas unexploited species showed little difference in population trends within or outside reserves.
3. Although changing climate and more precautionary fisheries management contribute to declining fish catches, fisheries-independent transect data suggest that excessive fishing also plays a major role.
4. The large number of fishery stocks that remain unmanaged or have poor data, coupled with continuing declines in the stock biomass of managed fish species, indicate that Aichi Target 6 of the Convention on Biological Diversity (i.e. 'by 2020, all fish and invertebrate stocks and aquatic plants are managed and harvested sustainably') will not be achieved in Australia, or elsewhere.
5. In order to maintain some naturally functioning food webs supported by large predators and associated ecosystem services in this era of changing climate, a greatly expanded network of effective, fully protected marine protected areas is needed that encompasses global marine biodiversity. The present globally unbalanced situation, with >98% of seas open to some form of fishing, deserves immediate multinational attention.

  

**KEYWORDS**

Convention on Biological Diversity, fish stocks, fisheries management, jackass morwong, marine protected area, marine reserve, overfishing, Reef Life Survey, reef monitoring, stock status

## 1 | INTRODUCTION

Effective marine management is needed now, more critically than ever. Coastal and offshore ecosystems are changing rapidly (McCauley et al., 2015), at a time when the history of fisheries management includes some successes and some highly publicized failures (Beddington, Agnew, & Clark, 2007; Pinsky, Jensen, Ricard, & Palumbi, 2011; Worm et al., 2009). The global wild fish catch peaked in the 1990s and is now declining (Pauly & Zeller, 2016; Watson & Tidd, 2018). Addressing these issues potentially involves both improved fisheries management and the application of 'no-take' marine protected areas (MPAs), i.e. 'marine reserves' (Costello et al., 2012; Edgar et al., 2014; Hilborn, 2016; Pendleton et al., in press). A single marine reserve can provide insurance against population declines for hundreds of species and improved fisheries outcomes, as long as it is well designed and regulated (Edgar et al., 2014; Ward, 2004). Yet despite the public desire and expectation for a greatly expanded and effective MPA network (Hawkins et al., 2016), marine reserves presently cover less than 2% of global marine waters (Boonzaier & Pauly, 2016).

Here, decadal time series were used to estimate the net benefit of marine reserves in enhancing the biomass of large reef fishes, relative to both marine parks with limited fishing permitted and to open-access waters where normal fisheries regulations apply. We integrate outputs from three broad-scale reef fish monitoring programmes (Stuart-Smith et al., 2017), which together span temperate and tropical waters around Australia.

Outcomes of field monitoring are compared with trends in fishery catches to test claims that Australian fisheries are managed sustainably using ecosystem-based approaches (Fletcher, 2006). Australia's fisheries encompass arguably the most complex and expensive management systems worldwide on a per unit catch-weight basis. Management practices ranked second for sustainability in a global marine performance assessment of 53 countries (Alder et al., 2010), with frequent praise from fisheries experts worldwide (e.g. Hilborn, 2016). Australia's approach to sustainability embraces the ratification of the Convention on Biological Diversity (CBD), which includes the obligation (Aichi Target 6) that 'By 2020, all fish and invertebrate stocks and aquatic plants are managed and harvested sustainably, legally and applying ecosystem based approaches, so that overfishing is avoided, recovery plans and measures are in place for all depleted species, fisheries have no significant adverse impacts on threatened species and vulnerable ecosystems, and the impacts of fisheries on stocks, species and ecosystems are within safe ecological limits' (https://www.cbd.int/sp/targets/rationale/target-6/). Given that Australia rates higher for fisheries sustainability than nearly all other CBD parties (which include all UN members other than the USA), a necessary condition for the achievement of Aichi Target 6 globally is that Australia's fisheries comply.

Clearly, the extent to which Aichi Target 6 is achieved will be difficult to measure, given an absence of data relating to the 'safe ecological limit' aspect of the sustainability for most fisheries. Furthermore, fishery sustainability can only be recognized amongst the small fraction of fisheries that are actively managed. Because of high management costs relative to fishery value, quantitative stock assessments involving population modelling and the collection of life-history information and fishing effort (including growth, size distribution, and maturity) cover <1% of species (Costello et al., 2012), and very few of these include annual fishery-independent assessments of population trends (including larval settlement and egg production proxies). Most stock assessments rely solely on trends in catch per unit effort (CPUE) or catch history (representing 52% of the 233 'key' Australian marine stocks reported by Flood et al., 2014).

## 2 | METHODS

### 2.1 | Ecological survey methods

Underwater visual surveys were conducted by divers along 5 m × 50 m transect blocks through three reef monitoring programmes: the Australian Institute of Marine Science Long Term Monitoring programme (Emslie, Cheal, Sweatman, & Delean, 2008; 276 sites); the Reef Life Survey (Edgar & Stuart-Smith, 2014; 127 sites); and the Australian Temperate Reef Collaboration programme (Edgar & Barrett, 2012; 119 sites). Data analysed are the same as those integrated for the 2016 Australian State of the Environment Report, and are plotted at the regional level in Figure 3 of Stuart-Smith et al. (2017), other than that sites surveyed on two or less occasions were excluded. Fish length and abundance estimates were converted to biomass using species-specific length–weight coefficients obtained from FishBase (www.fishbase.org), as applied in previous analyses using Reef Life Survey (RLS) data (Duffy, Lefcheck, Stuart-Smith, Navarrete, & Edgar, 2016; Edgar et al., 2014; Soler et al., 2015).

### 2.2 | Trends in total fish community biomass

The mean total biomass of all fishes ≥20 cm in length on transects at each site each year was standardized for temporal comparisons across sites, by dividing by the maximum biomass recorded at each site in any year (= 1). To remove spatial autocorrelation associated with clumped site distribution, site means were then calculated within $1^0 \times 1^0$ grid cells (latitude × longitude), and continent-wide means were calculated from the grid-cell means for each year. Sites were distinguished by local fishing regulation as 'reserve' (no fishing), 'limited fishing' (located within multi-zoned marine parks, where fishing with some gear types is allowed but where other gear types are prohibited), and 'open access' (outside MPAs, with general fishing regulations). Data were available for 36 $1^0 \times 1^0$ grid cells, including 33 cells with reserve data, 24 cells with limited-fishing data, and eight cells with open-access data. No open-access sites were surveyed in tropical waters, where long-term tropical surveys were restricted to the large multi-zoned Great Barrier Reef and Ningaloo marine parks. Generalized linear models with a quasi-binomial distribution were fitted to time-series data, and 95% confidence intervals calculated.

### 2.3 | Trends in species' abundances

The densities of common species were standardized amongst years by dividing by the maximum annual density of the species observed at each site from 2005 to 2015. Common species were those recorded in at least four years at 10 sites. A total of 190 common species were included, of which 11 were commercially exploited (Appendix 1). Decadal trends in mean standardized densities were calculated separately for reserve and fished sites, using the same procedures as for trends in fish biomass (see section 2.2 above). Fished sites were located in both limited fishing zones and open-access waters, given that there were insufficient open-access sites for this treatment to be analysed separately. In order for reserve and non-reserve trends to be directly compared, proportion data in plots were standardized to 1 for the year 2005.

### 2.4 | Continental analysis of fishery catches

The total Australian catches for all 213 reported fisheries for the years 1992–2014 were calculated using catch data distributed by the Australian Bureau of Agricultural and Resource Economics and Sciences (available at http://www.agriculture.gov.au/abares/publications/pubs?url=http://143.188.17.20/anrdl/DAFFService/pubs.php?searchphrase = fisheries). Catches for each fishery in each year were divided by the catch from the year of the maximum catch (= 1), and then the means of these annual standardized catches were calculated across all fisheries for different jurisdictions. In order for trends to be directly compared in plots, data for jurisdictions were standardized to 1 for the year 1992.

Following Pinsky et al. (2011), the number of 'collapsed' stocks was also calculated using a conservative definition of 'collapse' (<10% of mean catches in a 2-year period relative to the 5-year period with highest catches). The 90% decline threshold for collapse exceeds the magnitude of population decline required to classify species in unmanaged populations as 'critically endangered', the highest category of threat on the International Union for Conservation of Nature (IUCN) Red List (i.e. >80% decline over three generations; IUCN, 2006).

A caveat associated with the analysis of collapsed stocks is that because of the increasing span of data used for calculating the peak catch, the number of 'collapsed' stocks will statistically increase through time, even when stocks show random fluctuations about a stable mean (Branch, Jensen, Ricard, Ye, & Hilborn, 2011). Such a statistical artefact was assessed and found to be minor: e.g. in fisheries modelled with a 30% annual mortality, recruitment as a proportion of biomass, with a randomized annual error term added for variability and a stable biomass when averaged through time across 5000 stocks, only 0.5% of stocks (i.e. 1 of 213) would be incorrectly classified as having collapsed after 20 years.

### 2.5 | Case study: Eastern jackass morwong (*Nemadactylus macropterus*)

In order to better understand relationships between fishery model outputs, management decision making, trends in catches, and in-water outcomes, stock indicators associated with the eastern jackass morwong (*Nemadactylus macropterus*) fishery are considered in some detail. Jackass morwong, along with flathead (Platycephalidae spp.), was once the co-dominant target species in the largest multispecies Australian trawl fishery (Tuck, 2016). The management of this fishery is highlighted because decisions are supported by the most transparent documentation amongst Australian fisheries. Along with the bight redfish (*Centroberyx gerrardi*), the jackass morwong fishery is evaluated through the only comprehensive quantitative (i.e. Tier 1; Australian Fisheries Management Authority, 2009) stock assessment that we are aware of, where the modelled virgin stock biomass ($B_0$) and current stock biomass ($B$) are both provided in accessible public-domain documents for multiple recent years. Other Tier-1 assessments typically provide only the modelled ratio of current ($B$)/virgin ($B_0$) biomass, precluding an understanding of whether the modelled estimates of $B_0$, $B$, or both are changing.

## 3 | RESULTS

### 3.1 | Trends in total fish community biomass

The total biomass of large fishes ≥20 cm in total length, a key indicator of fishing pressure (Stuart-Smith et al., 2017), declined significantly ($P < 0.05$) on transects both in limited fishing zones (with a mean decline of 18%) and in reef sites that were open to fishing (with a mean decline of 36%) for the period from 2005 to 2015 (Figure 1). No significant overall trend in large fish biomass was apparent across sites in marine reserves (mean 4% rise).

### 3.2 | Trends in species' abundances

In order to assess the likelihood that large fish biomass declined at the fished sites as a result of broad-scale environmental change rather than fishing, population trends in the exploited and unexploited subsets of species were compared (Appendix 1), assuming that the latter group provided a counterfactual control unaffected by fishing. Declining fish populations of unexploited species were approximately balanced by the number of species showing increases. Slight, albeit non-significant ($P > 0.05$ for comparison with slope = 0), downward trends were evident across populations of unexploited species between 2005 and 2015 in reserve (16% decline) and in fished sites (11% decline; Figure 2), with no significant difference in the rate of change between these two groups ($P = 0.58$ for generalized linear model (GLM) comparison). By contrast, a downward overall population trend in exploited species at fished sites (with a mean decline of 33%) significantly differed in slope from an upward trend in exploited species within reserves (with a 25% increase; $P = 0.037$ for GLM comparison of slopes).

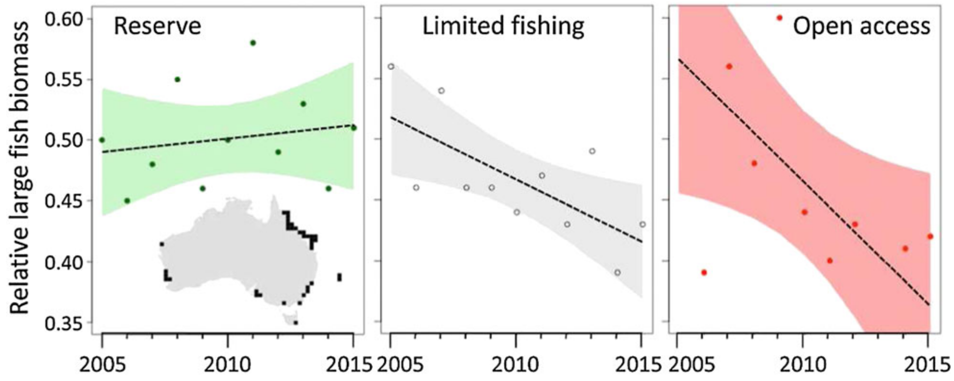


**FIGURE 1** Trends in the total biomass of large fishes (≥20 cm in length) observed during underwater transects around Australia. The inset map shows the distribution of 36 $1^0 \times 1^0$ grid cells with survey data, as integrated from three monitoring programmes for the 2016 Australian State of the Environment Report (Stuart-Smith et al., 2017). Data for each of 533 sites were standardized relative to the year of maximum biomass (= 1), and then the means were calculated for each $1^0 \times 1^0$ grid cell, before the calculation of the grand means for each year. Generalized linear models with a quasi-binomial distribution were fitted to these proportion data; 95% confidence intervals are shown by shading

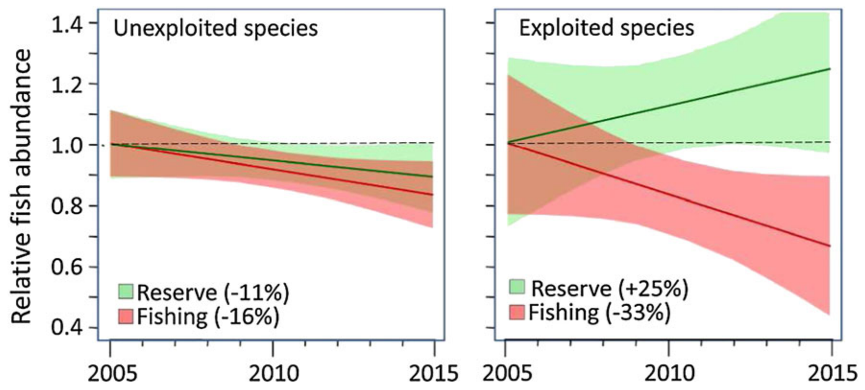


**FIGURE 2** Trends in the abundance of unexploited and exploited species at sites inside and outside no-fishing reserves. The mean decadal trend data for 179 unexploited and 11 exploited species are shown for the period 2005–15. Generalized linear models with a quasi-binomial distribution were fitted; 95% confidence intervals are displayed by shading; the overall decadal changes are shown in parentheses

## 3.3 | Continental analysis of fishery catches

Australian wild fishery catches have fallen rapidly over the past decade, with the total catch declining 32% from 2005 to 2014 (Figure 3a). Reported catches in different Australian management jurisdictions for 213 species or species groups show an average 31% decline since 2005 (Figure 3a, c, d). Only 23 fisheries show catches peaking in the most recent 6-year period (11% of total; Figure 3e).

Visual census data from inshore reefs (Figures 1 and 2) and commercial fishery catches (Figure 3) are not directly comparable because they encompass different spatial domains, with only a small overlap (for reefs with water depths of <20 m). Nevertheless, catch trends for the 36 commercial species that inhabit inshore reefs (abalone, lobsters, and fishes such as coral trout and luderick; Figure 3b) show a high degree of congruence with fishery-independent visual census data ($r$ = 0.75 for years 2005–13, $n$ = 9, 0.05 > $P$ > 0.01) and with offshore commercial catches ($r$ = 0.82 for years 1988–2013, $n$ = 26, $P$ < 0.001). Although the underlying cause of declining inshore biomass includes recreational as well as commercial fishing effort (the relative contributions of these cannot be separated), the close correspondence in these trajectories indicates that falling catches reflect declining fish populations, at least in part.

Despite steep continuing declines in catches, fishery stocks are considered to be in good condition by Australian management authorities. The proportion of Commonwealth Government-managed stocks reported as 'overfished' declined from 19% in 2004 to 12% in 2015, whereas 'not overfished' stocks increased from 27% to 74% through the same period (Flood et al., 2016). When state- and territory-managed fisheries are also considered, 30 of 238 stocks (13%) are now classed as 'overfished' or 'transitional–depleting' (Flood et al., 2014).

In contrast to the declining trend in the numbers of overfished stocks, an alternative method of classifying fisheries as 'collapsed' indicates a continuing increase since 1994, to 33 of 213 Australian stocks in 2014 (15% of total; Figure 3e). Although the rate of collapse is slowing (Figure 3e), the number of additional fisheries recovering from collapse each year remains fewer than the number of newly collapsed fisheries. A total of 48 fisheries (23% of total) were classified as collapsed in at least one year, including 15 that had recovered from a collapsed state by 2014.

## 3.4 | Case study: Eastern jackass morwong (*Nemadactylus macropterus*)

Annual catches of jackass morwong declined by 95% from around 2000 tonnes through the 1960s and 1970s to 109 tonnes in 2015/16 (Figure 4a). All other stock indicators – standardized CPUE (90% decline from 1990 to 2014; Figure 4b), fishery-independent survey results (71–82% decline from 2008 to 2014; Figure 4c), and modelled stock biomass (87% decline from 1965 to 2015; Figure 4d) – have also

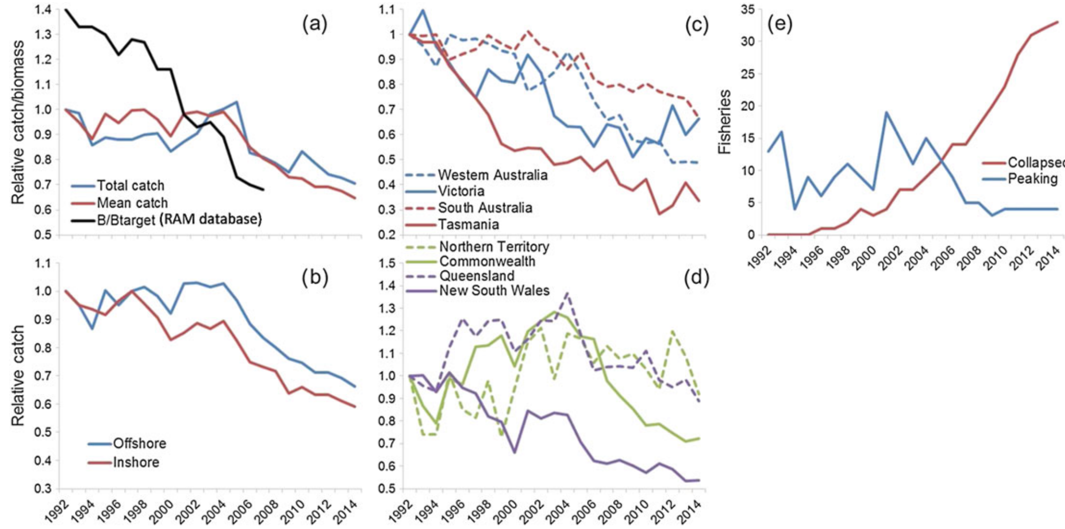


**FIGURE 3** Trends in Australian fishery catches. (a) Total Australian catch across all reported fisheries relative to 1992, mean catch across fisheries relative to 1992 after standardization of each fishery to year of maximum catch (= 1), and modelled stock biomass of 22 Australian fisheries assessed in the RAM Legacy Stock Assessment Data Base relative to stock size that maximizes sustainable yield ($B/B_{\mathrm{target}}$). (b) Mean catch for inshore and offshore fisheries relative to 1992 after standardization of each fishery to the year of the maximum catch. (c, d) Mean catch across fisheries in different jurisdictions relative to 1992 after the standardization of each fishery to the year of the maximum catch. (e) Total number of 213 reported Australian fisheries that peaked each year since 1988, and also those regarded as having collapsed according to the criteria described by Pinsky et al. (2011) (mean catches over a 2-year period are <10% of the mean catch over the 5-year period with the highest mean catch)

fallen continuously over recent decades. Modelling undertaken in the years 2007, 2010, and 2016 all identify rising stocks in the year of assessment, with fish biomass apparently recovering from lows 3–5 years earlier; however, with hindsight, subsequent stock assessments indicate that the turning points of 2007 and 2010 were illusory. Seven explicit assumptions were recognized during the modelling process (Tuck, 2016), including natural mortality $M$ = 0.15. The model output was found to be highly sensitive to this assumption, with $B/B_0$ decreasing from 36% with $M$ = 0.15 to 21% with $M$ = 0.10 in the 2015 model (Tuck, 2016).

With respect to management decisions (Figure 4e), no change to the total allowable catch (TAC) was recommended by the relevant Southern and Eastern Scalefish and Shark Fishery Shelf Resource Assessment Group (ShelfRAG) when modelled $B/B_0$

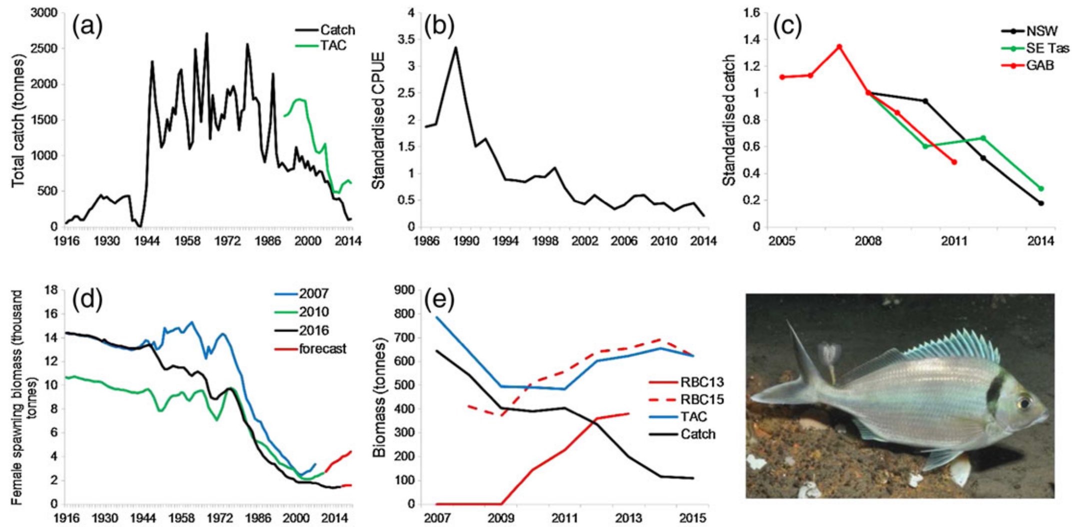


**FIGURE 4** Trends in stock indicators for the eastern jackass morwong (*Nemadactylus macropterus*) fishery. (a) Trends in total catch and total allowable catch (TAC) (Tuck, 2016). (b) Trends in standardized catch per unit effort (CPUE) (Tuck, 2016). (c) Biomass trends obtained from standardized experimental trawl surveys undertaken in three regions (Commonwealth grounds off New South Wales, south-eastern Tasmania, and the Great Australian Bight (GAB)) (Tuck, 2016; Wayte, 2013a). Biomass data are calibrated to 1 for the 2008 survey year. (d) Hindcast (blue, green, black) and forecast (red) trends in the modelled female spawning biomass for stock assessments reported in 2007 (Ricard et al., 2012), 2010 (Wayte, 2010) and 2016 (Tuck, 2016). (e) Recommended biological catch (RBC), TAC, and total catch for 2007–15, as agreed by the relevant Southern and Eastern Scalefish and Shark Fishery Shelf Resource Assessment Group (ShelfRAG) in 2013 for eastern stock, and 2015 for eastern and western stocks combined (Australian Fisheries Management Authority, 2015)

[Correction added on 3 December after first online publication: Legend for Figure 4(e) has been updated in this version.]

declined below the limit reference point of 0.2 in 2007, 2008, and 2009. This should have automatically triggered a recommended biological catch (RBC) of 0 tonnes (Wayte, 2013a); however, contrary to the downward catch and recruitment trends that lacked inflection, and to a precautionary approach, ShelfRAG agreed in 2011 that a 'climate-induced recruitment shift' (Wayte, 2013b) had occurred in 1988. The RBCs for 2008 and 2009 were retrospectively changed from 0 tonnes in the 2013 report (Wayte, 2013a) to 410 and 370 tonnes in the 2015 report (Australian Fisheries Management Authority, 2015).

## 4 | DISCUSSION

### 4.1 | Linkages between fish population declines and overfishing

Most fish populations, both exploited and unexploited, declined around Australia through the period 2005–15, probably largely as a negative consequence of recent warming and heatwaves experienced in south-eastern and south-western Australia (Day, Stuart-Smith, Edgar, & Bates, 2018; Last et al., 2011; Wernberg et al., 2013). Fishing apparently exacerbated the declines in population numbers amongst the exploited species, with a mean overall downward trend of 33%, compared with 16% and 11% for unexploited species outside and inside marine reserves, respectively. Marine reserves generally offset the continental-scale declines, with the population numbers of commercially exploited species increasing by an average of 25% in no-fishing zones. Thus, although regional change other than fishing was partly responsible for declining fish populations, fishing added to the declines for commercial fishes, thereby increasing the risk of recruitment failure in the absence of reserves to safeguard spawning stock.

Regardless of its reputation for sustainable fishery management, overfishing has apparently contributed to the field observations of the declining biomass of large fishes on Australian reefs. The overall declines in catches began 7 years later for offshore stocks compared with inshore stocks (in 2003 rather than 1996; Figure 3b), presumably because of the expansion of fisheries into progressively deeper offshore fishing grounds through the 1990s that counterbalanced the catch declines in the mature inshore fisheries. The issue of catch hyperstability, where total catch and CPUE are maintained at constant levels through improved technical efficiency and progressive expansion into more distant fishing grounds, appears to characterize Australian fisheries. Underlying stocks of the 24 mature Australian fisheries assessed in the RAM Legacy Stock Assessment Data Base (http://www.ramlegacy.org) – the largest synthesis of data for global fisheries – declined precipitously through the 1990s, during a period of stable total Australian catches (Figure 3a). These data affirm that continuing declines in Australian fish catches are linked to declining fish stocks rather than increasing regulatory precautions that leaves more fish biomass in the sea. Ironically, the recently announced global projections predict a 0–20% decline in the total catch for the Australian region for the period 2000–2050 (Golden et al., 2016), a level well exceeded already, given the average 31% decline for fish catches from 2005 to 2015.

Annual catches also systematically fail to achieve the total allowable catch (TAC) when applied in most Australian fisheries. For example, of the nine species with readily accessible decadal data on TAC and actual catch in Australia's largest fishery (the Southern and Eastern Scalefish and Shark Fishery), only two species – the tiger flathead (*Platycephalus richardsoni*) and the pink ling (*Genypterus blacodes*) – achieved 50–100% of the allocated TAC in 2015, regardless of the fact that the TACs are based on stock models, and are regularly adjusted following analysis of the catch in the previous year (underlying data available at http://www.afma.gov.au/fisheries-services/catchwatch-reports). Catches of eastern school whiting (*Sillago flindersi*) were well over the TAC (166%), whereas catches of the other six species – blue grenadier (*Macruronus novaezelandiae*), deepwater flathead (*Neoplatycephalus conatus*), gemfish (Gempylidae spp.), jackass morwong, bight redfish, silver warehou (*Seriolella punctata*) – averaged 24% of the TACs. In most cases the TAC therefore appears irrelevant, declining through time and consistently annually overestimating the fish biomass available for catch, as in the case of jackass morwong (Figure 4).

### 4.2 | Decline of the eastern jackass morwong fishery

Trends in indicators for the Australian fishery with best publicly available documentation – the Commonwealth eastern jackass morwong trawl fishery (Figure 4) – illustrate the issues arising from inaccurate stock assessments and poor associated decision making. Modelling issues include a large number of statistical assumptions (seven explicitly recognized), the high sensitivity of model output to particular assumptions, and an apparent lack of consideration in models of the effect of technological improvements (other than changes in fleet type), the spatial expansion of the fishery footprint through time, or interactions with other species. All stock indicators have fallen continuously to low levels over recent decades; however, the fishery remains classed as sustainable.

Perversely, when stock numbers declined below a benchmark, triggering zero RBC and thus zero TAC, an increase in TAC was agreed on the grounds of an 'environmental regime shift' (Figure 4; Wayte, 2013b). The use of 1988 as the year of regime shift, rather than 1915, as the baseline year for assessing $B/B_0$ reference points (i.e. $B_0$ = 4080 tonnes rather than 14 402 tonnes (Tuck, 2016), representing a 72% reduction) allowed the TAC to be raised from 484 tonnes in 2011 to 601 tonnes in 2012. Thus, although originally proposed as a precautionary mechanism to address poor recruitment, the climate-induced recruitment shift theory was used to justify a management decision to increase the TAC. ShelfRAG minutes indicate that no member raised the possibility that overfishing could have contributed to the catastrophic declines in all stock indicators (minutes for 2009–16 available at http://www.afma.gov.au/), whereas anecdotal observations related to stock numbers were reported and presumably contributed to the decision making (e.g. 'as seen in on-water observations by industry members'; http://www.afma.gov.au/wp-content/uploads/2010/06/Minutes-ShelfRAG-9-10-November-2009.pdf). In the most recent 2015–16 assessment

[Correction added on 3 December after first online publication: In Section 3.4, a sentence about the volume of jackass morwong being caught in 2015 has been removed in this version.]

(Patterson et al., 2016), the eastern jackass morwong fishery was officially classed as 'not overfished' because only 17% of the 624-tonne TAC was captured, with the inference that the harvest was therefore well below sustainable rates, regardless of continuing declines in CPUE and all other indicators.

An alternative explanation, which we consider more parsimonious, is that the population has declined by >90% and should be categorized as 'critically endangered' on the IUCN Red List of Threatened Species (IUCN, 2006). Such a rating would not be appropriate if the threat was transitory; however, no amelioration of the threat posed by fishing to this species is foreseeable given the realpolitik associated with extensive fisheries closures, as would be needed to protect a wide-ranging species reduced from dominant to minor by-catch status within a large multi-species trawl fishery.

## 4.3 | Factors potentially contributing to catch declines

Considerable debate surrounds the use of catch history, as applied here, to identify collapsed stocks (Hilborn & Branch, 2013; Pauly, Hilborn, & Branch, 2013). Many biologists argue that overfishing is appropriately identified only through modelled stock assessments, with explicit consideration of confounding factors that influence the total catch, but are unrelated to stock size, such as changed regulations and fleet dynamics (Branch et al., 2011; Hilborn & Branch, 2013); however, modelled stock assessments depend on numerous assumptions that compound within the model, are rarely publicly documented, and are subjective, including the idiosyncratic adjusting of parameters. Such parameter 'tweaking' is, characteristically, explicitly described in only the best stock assessments, such as that of Leigh, O'Neill, and Stewart (2017) for the Australian east coast tailor (*Pomatomus saltatrix*) fishery. They note: 'a lower bound of ($M$) was applied to prevent the population going unrealistically low', 'we had to fix $r$ to values that produced sensible results', and 'the parameters $\mu$ and $\lambda$ also tended to go very low and we fixed them to the minimum values that we considered sensible'.

Moreover, the number of published stock assessments in Australia is so low that an overarching assessment of fisheries management outcomes is precluded. This was only possible here using catch data. Annual stock assessments are available for <10% of Australian fishery species with published catch statistics, relating to <1% of the fished populations in Australia. We also note that, regardless of the different perspectives on the use of modelled versus catch data, the estimated stock biomass provided through the RAM Legacy Stock Assessment Data Base showed similar or greater declines than the trends observed in catches (Figure 3a).

Fisheries managers generally offer three explanations for declining catches: (i) stock biomass is declining as a deliberate policy to remove large individuals and increase the average growth rates and productivity of the fishery; (ii) stock numbers are not declining but management is now more precautionary, undergoing recent structural reforms that include effort reduction and the declaration of MPAs that reduce catch; or (iii) populations are declining as a consequence of changing environmental conditions outside the influence of the fisheries intervention. These arguments have merit, but raise additional questions.

The deliberate fishing down of stocks only applies to newly developing fisheries, so has little relevance to mature fisheries, such as the inshore fisheries with declining trends depicted in Figure 3b. Moreover, the removal of large slow-growing fishes from ecosystems, although potentially useful in terms of maximizing fish production, is antithetical to ecosystem-based management, which requires the persistence of the full range of ecosystem functions, including those provided by larger predators and grazers in naturally structured populations.

Fisheries management in Australia is becoming more precautionary, including the introduction of harvest strategies that set the target biomass at 40% rather than 20% of the virgin biomass, and, in a few cases, by considering the maximum economic yield in addition to the maximum sustainable yield (Gardner, Hartmann, Punt, & Jennings, 2015). Nevertheless, implicit in the second precautionary argument is that mistakes were made in the past, with higher fishing levels than are now considered prudent, but that fisheries are at last sustainable following the lessons learned. This same argument has been made throughout history, however, often repeated annually, raising doubt as to whether this year is the turning point from which stocks will recover.

Structural reforms to the fishing industry also show little congruence with spatial or temporal trends in Australian catches. Amongst the states, Queensland fishers lost the most access to resources when an additional 28% of the Great Barrier Reef Marine Park was reassigned to no-fishing zones in 2004 (representing ~14% of the Queensland sea area; Grech, Edgar, Fairweather, Pressey, & Ward, 2014) and a \$A214 million structural adjustment package was implemented (Gunn, Fraser, & Kimball, 2010). Despite this re-zoning, Queensland catches have decreased less than catches in other Australian states during the past decade (Figure 3c, d), with the large no-take areas possibly buffering fisheries from decline.

By contrast, catches declined most in Tasmania, despite no additional marine reserves since 2004 nor any buyout of fishing effort (Figure 3c), although in one fishery the TAC was lowered because of a policy change from maximum sustainable to maximum economic yield (Gardner et al., 2015). As marine reserves comprise only a trivial proportion (~1%) of Tasmanian coastal waters (Grech et al., 2014), and are generally located in unproductive areas with few commercial resources (Devillers et al., 2015), the displacement of fisheries effort from marine reserves could not have contributed to the 65% decline in catch across all fisheries from 1994 to 2014.

Changing environmental conditions have undoubtedly promoted the decline in many fisheries, as is evident in Figure 2, where an overarching decline was noted outside reserves, including for species not targeted by fishers. Declining catches in Tasmania probably also partly result from a loss of oceanic productivity, as this state is a global hotspot for warming (Popova et al., 2016).

Regardless, few fisheries models consider changing environmental conditions, species interactions, or assign adequate leeway for error, despite the environmental domains of many fisheries now falling outside known bounds. Trends in sea temperature, and the increasing number and resolution of warming projections, should be considered in modelling and precautionary regulations (Brown, Fulton, Possingham, & Richardson, 2012; Melnychuk, Banobi, & Hilborn, 2014), rather than temperature anomalies used as *post hoc* justification for overstated catch projections and continuing declines.

For most assessments, a stable CPUE is regarded as indicative of stable population numbers and sustainable catch rates (Flood et al., 2014), even though fisheries biologists have long recognized that serial depletion (i.e. fishers maintaining stable catches by moving further afield as stocks close to home decline) and improvements in capture efficiency can obscure declining stocks. In particular, increased capture efficiency through improving technology (including GPS, acoustic sensors, weather forecasting, and boat and trawl design) and fisher knowledge can conservatively be estimated at 3% annually (Marriott, Wise, & St John, 2010; Tarbath & Mundy, 2015). Compounded, this equates to a 34% increase in real effort, and a 26% decline in stock, with stable CPUE in each decade.

## 4.4 | Towards improved sustainability

With some notable exceptions (Hobday et al., 2011), most recent attempts at moving fisheries management towards modern precepts of sustainability continue to face a steadfast focus on biomass production. This perspective is evident in the definition of 'overfished' used by Australian management authorities, which only covers recruitment overfishing of a stock (i.e. the reduction in biomass of spawning stock beyond the point where recruitment is inadequate to prevent stocks declining further; Flood et al., 2016). Knowing that fisheries are 'not overfished' provides little insight into ecological sustainability, including ecosystem impacts associated with trawl damage or changes to trophic structure. Consequently, even the best science underpinning gold-standard stock assessments does little to address the cumulative interactions and impacts of fisheries on biodiversity, including the many inter-dependent ecological relationships and consequent complexities that contribute to the structure and function of ecosystems (Rosenberg et al., 2014), and hence the true sustainability problem. Once tipping points are passed, hysteresis can make a return to formerly sustainable levels extremely difficult (Neubauer, Jensen, Hutchings, & Baum, 2013).

The lack of independent scrutiny in co-managed fisheries, including issues associated with industry capture of regulators, and researchers with grants dependent on fishers' support (Barkin & DeSombre, 2013), may also contribute to the setting of TACs that exceed sustainable and catchable limits. Although fisheries are a public resource, fisheries management committees in Australia are dominated by members aligned to, and typically funded by, the fishing industry. As in the case of the jackass morwong fishery described above, and the orange roughy (*Hoplostethus atlanticus*) fishery described by Bax et al. (2005), decisions on catch quotas consequently include only modest precautionary elements related to ecological and ecosystem issues, with stakeholders keen to push quotas as close as possible to the modelled maximum-sustainable or economic yield. When the knowledge base is limited or disputed, uncertainty is 'characterized almost uniformly by overly optimistic interpretations of the present and future states of the fishery' (Bax et al., 2005). Moreover, the underlying metrics for reporting the status of fish stocks change regularly, precluding accurate time-series comparisons amongst stocks that would better inform the estimates of actual trends in fish abundance.

Although focused on Australia, the outcomes reported here are relevant elsewhere, given the country's global leadership role in marine conservation (particularly MPA management), and the prevalence of declining and declined stocks worldwide. Fisheries statistics compiled within the RAM Legacy Stock Assessment Data Base (http://ramlegacy.org/) indicate two broad regional groupings in stock trends: Australian fisheries group with a set of regions that also include New Zealand, the Pacific, the Atlantic, and the US West Coast, exhibiting rapid declines in stocks from levels well above the maximum sustainable yield (MSY); a second large set of regions, including the US East Coast, the US Southeast, and non-EU Europe, have passed this phase through historical overfishing and are near or below the MSY when averaged across stocks, albeit with recent signs of improvement in some cases. Alaskan and South African fisheries are uniquely characterized by rising stocks that are well above the MSY on average.

Australian fisheries may differ from European, North American, and Asian fisheries in their comparative recent history and greater management focus on development (Worm et al., 2009). Compared with mature Northern Hemisphere fisheries, Australian fisheries lack an extended time series of data to calibrate models, and possess a relatively low total catch volume that translates to little research funding, public interest, or scrutiny. Regardless, most of the problems affecting the management of Australian fisheries (Box 1) probably also apply elsewhere.

**Box 1. Issues affecting fishery management practices in Australia and elsewhere**

Data availability

Problems

- Little or no catch or discard data are available for most species affected by fishing, including species caught as by-catch or that are difficult to identify to species level and are grouped in logbooks, for analysis or reporting
- Little or no fishery-independent data are available on population trends
- Comparable no-take scientific reference areas are rarely available for analytical partitioning of the contribution of fishing to declining stocks relative to impacts of climate change or other broad-scale pressures

Potential solutions

- Capitalize on the cost-effective collection of fishery-independent data over large scales through new technology (e.g. eDNA) and volunteer-based programmes, including the integration of existing citizen-science data streams into fishery management processes and the development of new citizen-science initiatives
- Establish benchmarks and fishery-independent trends in stocks through the investigation of effective marine protected areas (MPAs). This may require the establishment of new marine reserves or the better

enforcement of existing MPAs to provide effective fishery exclusion controls on a region-by-region basis

Stock assessments

Problems

- Detailed stock assessments are too expensive for widespread application, so are generally applied only in a few high-value fisheries
- Assessments are generally conducted with weak documentation and with assumptions that preclude replication and independent scrutiny
- Models generally ignore interspecific interactions, regardless that fisheries are increasingly framed within ecosystem-based management systems
- Models and quota-setting processes are rarely subjected to independent audit or scrutiny, and details are often withheld from the public domain
- With changing climate and habitat, models extrapolate outside the known environmental bounds
- Technological improvements that incrementally alter fishery characteristics and increase capture efficiency, biasing the catch-per-unit-effort (CPUE) calculations, are often ignored in models
- Fishery metrics used for reporting frequently change through time, complicating longitudinal comparisons

Potential solutions

- Establish transparent and publically accessible stock reporting tools that use consistent metrics and detailed documentation of methodology
- Allocate adequate resourcing to ecologists at research institutions mandated with fisheries science to contribute to stock assessments and decision-making support systems, including in the public domain
- Allocate adequate resourcing for the development of ecologically sensitive stock assessment systems able to be applied for all fished species, irrespective of catch value
- Develop empirical indices of stock status for all fished species that reflect direct and indirect ecological interactions, and are applied with high levels of precaution to reflect ecological and environment domain uncertainties

Decision making

Problems

- Decisions prioritise short-term catch maximization over precaution
- Modellers and managers both tend towards optimism when dealing with uncertainty
- Decisions in co-managed fisheries are generally made by committees dominated by industry-aligned members
- Scientists with ecological expertise contribute little to committees and decisions
- Benchmarks (e.g. total allowable catch) are often set at irrelevant levels
- Lessons learned from poor decision making can be obscured by revisionary history
- Large-bodied individuals of target species are deliberately fished down as a specific management goal, contrary to ecological sustainability goals
- Wider effects of fishing on ecosystems are overlooked

Potential solutions

- Mandate decision making that is explicitly precautionary, recognizing the ecological uncertainties, and provide for public domain contestability
- Formalise a ‘red team’ approach to data analysis, through the consideration of pessimistic as well as optimistic scenarios
- Increase the input from independent voices on management fora. Consistent under-catches of total allowable catches should trigger a detailed investigation of stock trends by an independent and public-domain audit process
- Expand targeted food-web modelling and ecological studies to investigate the system-specific ecological importance of targeted species and large individuals
- Develop management models and decision support based on age/size cohort objectives to facilitate the ecosystem-based management of target species that explicitly reflects the population-level ecological structure and function of target species
- Integrate fishery and biodiversity conservation management processes, including the expanded application of no-fishing reserves

Just as for Australia, the global community remains as far as ever from achieving Aichi Target 6 related to fisheries sustainability. Given the large number of fisheries with declining stocks and the predominance of fisheries that lack any accounting, an overall global improvement in fisheries sustainability over the past decade remains debatable, let alone the hope that fisheries are approaching the 2020 target that ‘all fish and invertebrate stocks and aquatic plants are managed and harvested sustainably’. This has become an aspirational rather than a practical target.

An improved understanding of factors affecting fisheries sustainability, particularly biases associated with stock assessment, could be achieved by retrospective analysis of the best-practice stock assessments on the RAM Legacy Stock Assessment Data Base for 331 fisheries stocks worldwide (Ricard, Minto, Jensen, & Baum, 2012). The difference between the estimated stock size in the last year of RAM assessment and the stock size re-assessed for that year using more recently updated models provides an index of accuracy. Individual stock errors can thus be aggregated to identify any consistent regional and global assessment biases. Although such a retrospective audit is beyond our resources, we note that stock biomass in 2007 in the two Australian fisheries with sufficient publicly accessible data to allow such a test was overestimated by 93% (jackass morwong) and 63% (bight redfish), according to 2015 stock assessments (Tuck, 2016).

The implementation of a relatively small number of solutions could make substantial progress towards addressing issues with current fisheries management practices (Box 1). The key issue of the availability of independent data can be partially covered for inshore systems through the expansion of citizen-science monitoring programmes, as has been achieved in Australia through the Reef Life Survey (RLS) (Edgar & Stuart-Smith, 2014; Stuart-Smith et al., 2017). Diver- and recreational fisher-based citizen science provides a direct cost-effective strategy for assessing key aspects of the sustainability of shallow-water stocks. Following appropriate selection and training, volunteer divers can generate data of scientific research quality (Edgar & Stuart-Smith, 2009) across geographic and temporal scales that are orders of magnitude larger than scientific teams can cover (Edgar, Stuart-Smith, Cooper, Jacques, & Valentine, 2017).

### 4.5 | Need for an expanded marine reserve network

Despite myriad complexities in the socio-ecological system that controls the human use of marine habitats (Fulton, Smith, Smith, & van Putten, 2011), improvement in both fisheries and conservation outcomes is possible (Ward, 2004; Ward, Heinemann, & Evans, 2001). Developing an adequate safety net of effective marine reserves, increasing the input from independent voices on management fora, considering pessimistic scenarios using a 'red team' approach (Burkus, 2017), and applying a more ecologically sensitive precautionary approach when regulating fishing effort all offer the prospect of achieving a win–win outcome for both fishers and the oceans. If managed more conservatively, fish stocks could expand in the future to help meet human food needs (Costello et al., 2012). Unfortunately, substantial change towards ecological sustainability within fisheries policy is unlikely to happen rapidly, other than through an expanded network of no-fishing marine reserves, which is a management tool with widespread public interest and support (Hawkins et al., 2016).

Notwithstanding the limited current extent of marine reserves, additional spatial restrictions on fishing for conservation purposes are opposed by many fisheries practitioners on the grounds that the removal of fish within well-managed fisheries has little impact on biodiversity (Kearney, Buxton, & Farebrother, 2012; Pendleton et al., in press). This contention profoundly affects government policies on marine conservation in Australia, a nation that has pioneered the development of multi-use MPAs (Day & Dobbs, 2013), and with a widely acknowledged global leadership role in this field. The current national roll-out of Australian Marine Parks, the largest national MPA network globally, is specifically designed to avoid fisheries operations (Buxton & Cochrane, 2015; Devillers et al., 2015; Edgar, 2017). Consequently, no-fishing zones are almost completely lacking in the proposed network in water depths of <500 m, where threats are concentrated. As one example, the eastern region, which extends 1600 km from Victoria to southern Queensland, includes only two small pre-existing marine reserves (of 1 and 2 km in diameter) on the continental shelf (Devillers et al., 2015). Our study refutes the central assumption underlying this zoning strategy: that MPA zones with selective fishing allowed provide adequate biodiversity safeguards, including for fish stocks (Figure 1). Issues similar to those identified here (Box 1) affect other nations and their fisheries to various extents.

Marine reserves should be viewed as a core management tool, even in locations with intensely managed fisheries. Due to much greater conservation effectiveness, 'no-fishing' marine reserves should also be considered separately from marine parks that allow limited fishing when accounting towards national and multinational MPA area targets (e.g. Aichi Target 11 of the CBD; https://www.cbd.int/sp/targets/). Unfortunately, because of idiosyncratic reporting by governments, the current global extent of marine reserves is unknown. The primary global MPA resource, the World Database on Protected Areas (https://www.protectedplanet.net/marine), currently (19 December 2017) lists 2.3% of the marine domain as 'no-take'; however, this total includes many large areas with fishing allowed or with management plans not yet enacted. We conclude that further declines in stocks and catches across the oceans are inevitable unless a greatly expanded global safety net of representative marine reserves is developed.

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## ORCID

*Graham J. Edgar* http://orcid.org/0000-0003-0833-9001

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Source data on fisheries catches are available through the Australian Bureau of Agricultural and Resource Economics (ABARES) at their website http://www.agriculture.gov.au/abares/publications/pubs?url=http://143.188.17.20/anrdl/DAFFService/pubs.php?searchphrase=fisheries, and for Reef Life Survey ecological monitoring data at https://reeflifesurvey.com/reef-life-survey/survey-data/

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## APPENDIX 1

## FISH SPECIES INVESTIGATED IN THE ANALYSES OF TRENDS IN FISH ABUNDANCE.

| |
|---|
| **Temperate exploited species** |
| *Acanthopagrus australis* |
| *Achoerodus viridis* |
| *Cheilodactylus fuscus* |
| *Choerodon rubescens* |
| *Chrysophrys auratus* |

(Continued)

| |
|---|
| *Girella tricuspidata* |
| *Notolabrus fucicola* |
| *Notolabrus tetricus* |
| |
| **Tropical exploited species** |
| *Coris bulbifrons* |

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| *Lethrinus miniatus* |
| *Plectropomus leopardus* |
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| **Temperate unexploited species** |
| *Acanthaluteres vittiger* |
| *Aplodactylus lophodon* |
| *Apogon limenus* |
| *Apogon victoriae* |
| *Atypichthys strigatus* |
| *Austrolabrus maculatus* |
| *Cheilodactylus nigripes* |
| *Chelmonops curiosus* |
| *Chelmonops truncatus* |
| *Chromis hypsilepis* |
| *Coris auricularis* |
| *Coris picta* |
| *Dinolestes lewini* |
| *Diodon nicthemerus* |
| *Enoplosus armatus* |
| *Epinephelides armatus* |
| *Eupetrichthys angustipes* |
| *Halichoeres brownfieldi* |
| *Heteroscarus acroptilus* |
| *Hypoplectrodes maccullochi* |
| *Kyphosus cornelii* |
| *Kyphosus sydneyanus* |
| *Labracinus lineatus* |
| *Latropiscis purpurissatus* |
| *Mecaenichthys immaculatus* |
| *Meuschenia flavolineata* |
| *Meuschenia freycineti* |
| *Meuschenia galii* |
| *Meuschenia hippocrepis* |
| *Notolabrus gymnogenis* |
| *Notolabrus parilus* |
| *Olisthops cyanomelas* |
| *Ophthalmolepis lineolatus* |
| *Parma mccullochi* |
| *Parma microlepis* |
| *Parma occidentalis* |
| *Parma unifasciata* |
| *Parma victoriae* |
| *Parupeneus spilurus* |
| *Pempheris affinis* |
| *Pempheris compressa* |
| *Pempheris klunzingeri* |
| *Pempheris multiradiata* |
| *Pictilabrus laticlavius* |
| *Pomacentrus milleri* |
| *Pseudocaranx georgianus* |
| *Pseudolabrus biserialis* |
| *Pseudolabrus guentheri* |
| *Pseudolabrus luculentus* |

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| *Pseudolabrus mortonii* |
| *Schuettea scalaripinnis* |
| *Scorpaena cardinalis* |
| *Scorpis georgiana* |
| *Scorpis lineolata* |
| *Trachinops brauni* |
| *Trachinops noarlungae* |
| *Trachinops taeniatus* |
| *Trachurus novaezelandiae* |
| *Upeneichthys lineatus* |
| *Upeneichthys vlamingii* |
| |
| **Tropical unexploited species** |
| *Acanthochromis polyacanthus* |
| *Acanthurus blochii* |
| *Acanthurus dussumieri* |
| *Acanthurus lineatus* |
| *Acanthurus nigricans* |
| *Acanthurus nigrofuscus* |
| *Acanthurus olivaceus* |
| *Amblyglyphidodon curacao* |
| *Amblyglyphidodon leucogaster* |
| *Amphiprion akindynos* |
| *Cephalopholis cyanostigma* |
| *Cetoscarus ocellatus* |
| *Chaetodon aureofasciatus* |
| *Chaetodon auriga* |
| *Chaetodon baronessa* |
| *Chaetodon citrinellus* |
| *Chaetodon ephippium* |
| *Chaetodon flavirostris* |
| *Chaetodon kleinii* |
| *Chaetodon lineolatus* |
| *Chaetodon melannotus* |
| *Chaetodon ornatissimus* |
| *Chaetodon pelewensis* |
| *Chaetodon plebeius* |
| *Chaetodon rainfordi* |
| *Chaetodon tricinctus* |
| *Chaetodon trifascialis* |
| *Chaetodon trifasciatus* |
| *Chaetodon unimaculatus* |
| *Chaetodon vagabundus* |
| *Cheilinus fasciatus* |
| *Chelmon rostratus* |
| *Chlorurus microrhinos* |
| *Chlorurus sordidus* |
| *Choerodon fasciatus* |
| *Chromis atripectoralis* |
| *Chromis atripes* |
| *Chromis lepidolepis* |
| *Chromis margaritifer* |
| *Chromis nitida* |

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| *Chromis ternatensis* |
| *Chromis weberi* |
| *Chromis xanthura* |
| *Chrysiptera rex* |
| *Chrysiptera rollandi* |
| *Chrysiptera talboti* |
| *Ctenochaetus* spp. |
| *Dascyllus reticulatus* |
| *Dischistodus melanotus* |
| *Dischistodus prosopotaenia* |
| *Epibulus insidiator* |
| *Forcipiger flavissimus* |
| *Gomphosus varius* |
| *Halichoeres hortulanus* |
| *Hemigymnus fasciatus* |
| *Hemigymnus melapterus* |
| *Hipposcarus longiceps* |
| *Labroides dimidiatus* |
| *Lutjanus bohar* |
| *Lutjanus carponotatus* |
| *Lutjanus fulviflamma* |
| *Lutjanus gibbus* |
| *Lutjanus lutjanus* |
| *Macolor* spp. |
| *Monotaxis grandoculis* |
| *Naso lituratus* |
| *Naso tuberosus* |
| *Naso unicornis* |
| *Neoglyphidodon melas* |
| *Neoglyphidodon nigroris* |
| *Neoglyphidodon polyacanthus* |
| *Neopomacentrus azysron* |
| *Neopomacentrus bankieri* |
| *Parma polylepis* |
| *Plagiotremus tapeinosoma* |
| *Plectorhinchus flavomaculatus* |
| *Plectroglyphidodon dickii* |
| *Plectroglyphidodon johnstonianus* |
| *Plectroglyphidodon lacrymatus* |
| *Pomacentrus adelus* |
| *Pomacentrus amboinensis* |
| *Pomacentrus bankanensis* |
| *Pomacentrus brachialis* |
| *Pomacentrus coelestis* |
| *Pomacentrus grammorhynchus* |
| *Pomacentrus lepidogenys* |
| *Pomacentrus moluccensis* |
| *Pomacentrus nagasakiensis* |
| *Pomacentrus philippinus* |
| *Pomacentrus vaiuli* |
| *Pomacentrus wardi* |
| *Prionurus microlepidotus* |
| *Scarus altipinnis* |

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| *Scarus chameleon* |
| *Scarus flavipectoralis* |
| *Scarus forsteni* |
| *Scarus frenatus* |
| *Scarus ghobban* |
| *Scarus globiceps* |
| *Scarus niger* |
| *Scarus oviceps* |
| *Scarus psittacus* |
| *Scarus rivulatus* |
| *Scarus rubroviolaceus* |
| *Scarus schlegeli* |
| *Scarus spinus* |
| *Siganus corallinus* |
| *Siganus doliatus* |
| *Siganus puellus* |
| *Siganus punctatus* |
| *Siganus vulpinus* |
| *Stegastes apicalis* |
| *Stegastes fasciolatus* |
| *Stegastes gascoynei* |
| *Thalassoma lunare* |
| *Thalassoma lutescens* |
| *Zanclus cornutus* |
| *Zebrasoma scopas* |
| *Zebrasoma veliferum* |