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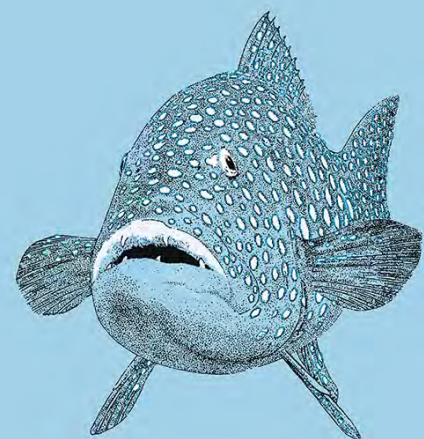
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REVIEWS

Review of the life history characteristics, ecology and fisheries for deep-water tropical demersal fish in the Indo-Pacific region

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Abstract Deep-water tropical fishes support locally significant commercial fisheries, high value recreational fisheries, and culturally and economically important artisanal and subsistence fisheries throughout the Indo-Pacific region. The main species captured by these fisheries are deep-water snappers (Lutjanidae), groupers (Epinephelidae), and emperors (Lethrinidae). Quantitative assessments of deep-water tropical fisheries have been limited by a lack of adequate biological and fisheries data. We review the biology and ecology of deep-water tropical fishes, discuss the implications for assessment and management of tropical deep-water fisheries, and provide perspectives on future research priorities. We found that biological and fisheries information is lacking for the majority of deep-water tropical fishes. Furthermore, many studies were constrained by low samples sizes and the use of methods that have not been validated or verified. Most species for which reliable information was available were reported to have extended longevities (>20 years), low rates of natural mortality ($M < 0.15$), and slow to modest growth rates ($K = 0.12$–0.25). These life history traits indicate a low production potential for many deep-water tropical fishes, and suggest that sustainable exploitation rates and potential yields may be low. There is a need for more representative and adequate studies of deep-water tropical fishes and for improved

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fisheries data collection and the use of consistent methods in addition to information sharing to facilitate the development of robust data-poor assessment techniques for these species.

Keywords Lutjanidae · Epinephelidae · Lethrinidae · Vital statistics · Traits · Mortality · Age · Growth · Reproduction

Introduction

Deep-water fisheries occur within all ocean basins and are typically concentrated on seamounts, continental and insular slopes, and other deep bathymetric features. In tropical and sub-tropical regions of the Indo-Pacific, most deep-water fisheries are small-scale artisanal and subsistence fisheries due mostly to a lack of knowledge of the existence of deep-water fish resources and/or the availability of appropriate fishing gear (Kramer et al. 1994; Dalzell et al. 1996; Newman et al. 2014a). These fisheries typically use low-technology fishing gear such as hand-powered wooden reels operated from relatively small vessels (<10 m) to target fish at depths between 100 and 400 m along deep reef slopes, shallow seamounts and banks (Dalzell et al. 1996). However, there are a small number of commercial fisheries, mostly in developed countries, that use more sophisticated fishing gear such as hydraulic or electric reels, trawl nets, traps and longlines. Catches from these fisheries are diverse, with over 200 species from 93 genera reported from fisheries in the western central Pacific Ocean (Dalzell and Preston 1992). The most common species harvested comprise members of the Lutjanidae, Epinephelidae and Lethrinidae families, with the eteline snappers (primarily the genera *Aphareus*, *Aprion*, *Etelis*, and *Pristipomoides*) the principle target species.

The propagation of suitable fishing gear in the 1970s allowed the development and expansion of deep-water fisheries throughout the Western Central Pacific region, including the development of some small export fisheries (Dalzell et al. 1996; Itano 1996a, b; Williams et al. 2012). The expansion in deep-water fisheries during the 1970s was soon followed by declines only two decades later, mainly as a result of declining catch rates, unreliable access to export markets, and a shift towards tuna long-lining, which was more profitable at the time (Dalzell et al. 1996). More recently, there has been interest in re-developing deep-water fisheries in recognition of the limited potential for further commercial development of shallow reef and lagoon fisheries in the region (Bell et al. 2009), and the perception that unexploited populations exist in more distant locations.

The harvest levels for many deep-water tropical fisheries are low relative to industrial scale fisheries; however, they support important domestic and export markets, particularly for small island states where the market value of some eteline species can reach ∼US\$20 kg^{-1} (reported in Loeun et al. 2014). Many tropical deep-water species are red in colouration, a culturally important colour to many countries in the Asia–Pacific region representing a sign of prosperity and providence. The high market value of these fishes provides economic opportunities for developing countries to progress sustainable fisheries to support export markets and to potentially distribute effort away from coastal fisheries.

Knowledge of life history attributes of fish populations is a fundamental requirement for developing effective fisheries assessment models and designing appropriate management and harvest strategies. Most deep-water fishes are intrinsically vulnerable to exploitation, as many species are long-lived, slow growing, and mature late in life (e.g. Newman and Dunk 2003; Fry et al. 2006; Andrews et al. 2011, 2012). However, quantitative assessments of tropical deep-water stocks have often been limited by a lack of adequate biological and fisheries data. As such, there are few reliable estimates of sustainable harvest levels for any deep-water fishery in the Indo-Pacific, and assessing the status of deep-water fish resources has become a priority for fisheries managers (Williams et al. 2012; Brodziak et al. 2014; Newman et al. 2015). Biological research for tropical deep-water fishes has been generally limited to isolated studies in geographically restricted areas, often focused on a few species and specific biological traits. There is a need to collate this information to evaluate the current state of knowledge for these species and provide direction for future research programs.

This review synthesises available data on the age, growth, and reproductive life history characteristics, related vital statistics and ecology of tropical deep-water fishes of importance to fisheries in the Indo-

Pacific region. The broad objective was to assemble and review all published material, including primary and grey literature, to identify knowledge gaps and provide direction for future research that would improve the assessment and management of these economically and ecologically important species.

The species examined in this review have either the centre of their depth distribution below 100 m and/or their depth range is deeper than 100 m, but not greater than 500 m (see Kramer et al. 1994; Newman and Williams 1996). As such, this review focuses on the deep-water snappers (Lutjanidae) of the subfamilies Etelinae and Apsilinae (Allen 1985), deep-water groupers (Epinephelidae) in the genera *Cephalopholis*, *Epinephelus*, *Hyporthodus*, *Saloptia* and *Variola* (Craig et al. 2011), and deep-water emperors (Lethrinidae, subf. Monotaxinae) including the mono-specific genus *Wattsia* (Carpenter 2001) that are of commercial, recreational, customary, or artisanal significance.

Taxonomy

In this review, we have followed the taxonomic reviews of Allen (1985) and Anderson and Allen (2001) for tropical snappers (Lutjanidae) and the taxonomic reviews of Carpenter and Allen (1989) and Carpenter (2001) for emperors (Lethrinidae). Recently, Wakefield et al. (2015a) used molecular techniques (cytochrome c oxidase subunit 1 barcoding gene sequences) to confirm that *Randallichthys* was within the subfamily Etelinae of the Lutjanidae and also confirm the related placement of other deep-water lutjanid genera within their respective subfamilies.

The Family Epinephelidae (formerly the subfamily Epinephelinae of the family Serranidae) has been used herein to represent the groupers, a family that was resurrected based on the molecular analyses of Smith and Craig (2007; see also Craig et al. 2011). It is notable that the genus *Hyporthodus* in the Epinephelidae was resurrected for 11 species of deep-bodied groupers, based on genetic information (Craig and Hastings 2007). Historically, species of *Hyporthodus* have been assigned to the genus *Epinephelus* (Randall and Heemstra 1991; Heemstra and Randall 1993). In addition, much of the literature on Indo-Pacific fishes has misidentified *H. (Epinephelus) octofasciatus* as *H. septemfasciatus*, which has a restricted northern hemisphere distribution (Heemstra and Randall 1993).

Advances in molecular genetic techniques have allowed teleost taxonomy to be refined and re-examined, resulting in the detection of cryptic speciation within taxa that were previously considered as valid species (e.g. Choat et al. 2012; Iwatsuki 2013; Iwatsuki et al. 2015). Resolving species identification issues is fundamental to fisheries science and stock assessment, as the misidentification of species and unresolved cryptic speciation can result in significant biases in fisheries assessments. Molecular techniques have recently identified cryptic speciation within the nominal species *Etelis carbunculus* (Andrews et al. 2016; see also Williams et al. 2012; Wakefield et al. 2014). As such, there will be a taxonomic reclassification within this species complex resulting in the verification of two valid species (nominally *E. carbunculus* and *E.* sp.). Both these species have now been identified to co-occur in many localities throughout the Indian and Pacific Oceans (Andrews et al. 2016); however, it is important to note that in Hawaiian waters, there is only one species, *E. carbunculus*.

These two species are very similar in phenotypic appearance although there are key differences. The significance of this recent taxonomic work is that much of the historical information available regarding life history parameters has used combined data from these two species and is thus likely to be confounded. These sympatric distributions and conservative morphologies create challenges for taxonomic identification. As these fish can be readily misidentified, a number of revised identification guides are required. Wakefield et al. (2014) have described a rapid and reliable method for distinguishing between these two phenotypically similar *Etelis* species based on otolith morphometry (length, width, thickness, and weight) and fish length that is particularly useful and important for fisheries assessment purposes (i.e. otoliths can be assigned to individual species for monitoring and assessment using ages to derive mortality rates).

Conservation status

The conservation status of most deep-water lutjanids and lethrinids considered in this review has not been assessed for the International Union for the Conservation of Nature (IUCN) Red List. More explicitly, species in the following genera have not been assessed

in the Indo-Pacific region; *Aphareus*, *Aprion*, *Pristipomoides*, *Parapristipomoides*, *Randallichthyes,* and *Wattsia*. Furthermore, only one species of *Paracaesio* (*P. caerulea*) and one species of *Etelis* (nominally *E. carbunculus*, but likely confounded as described above) have been assessed, and both are listed as data deficient. Of the 26 species in the genera listed above and considered in this review, 92 % have not been assessed.

In contrast, the conservation status of all epinephelids was assessed for the IUCN Red List. Of the species of epinephelids assessed in this review, one is listed as vulnerable, one as near threatened, 11 are species of least concern, and 14 are species classified as data deficient. The large number of data deficient species highlights the significant knowledge gaps. Importantly, for many species listed under the least concern category, little is known of their life history and there are uncertainties about their status.

There is however, information about the conservation status of two groupers. *Epinephelus bruneus* is listed as vulnerable on the basis of a decline of at least 30 % in the southern half of its relatively narrow range. Bottom trawling within its habitat along the coast of China is intensive. Fishing pressure appears to be increasing and declines are inferred in other parts of its range. There is negligible fisheries management across its range; thus, further declines in abundance are expected. *Hyporthodus quernus* has been assessed as near threatened due to several vulnerability characteristics, including a small global distribution, protogynous sex change at a large size (895 mm TL; DeMartini et al. 2011) and presumably a relatively extended longevity, and evidence of overexploitation.

Stock structure

Information on population structure of tropical deep-water fishes is limited to a small number of species of *Pristipomoides* and *Etelis*. Gaither et al. (2011) examined the phylogeography of *Pristipomoides filamentosus* across the tropical Indo-Pacific from 26 sample sites across a range of over 17,000 km from Hawaii to the Seychelles in the western Indian Ocean, with a major focus within the Hawaiian archipelago. This study was the first range-wide survey of a tropical deep-water Indo-Pacific snapper, and demonstrated that *P. filamentosus* is a highly dispersive species with

low, but significant population structure due entirely to the isolation of Hawaii. No evidence of any population structure was detected across 14,000 km of the Indo-Pacific ranging from Tonga in the central Pacific to the Seychelles in the western Indian Ocean using mitochrondrial DNA (mtDNA) and microsatellite markers, indicating widespread gene flow and high connectivity across the region. However, there was no evidence for connectivity between Hawaii and the remainder of the Indo-Pacific region. The genetic diversity in Hawaii was low, indicating a single archipelago-wide stock. These findings are similar to those of Shaklee and Samollow (1984) who reported similar allozyme frequencies across six populations of *P. filamentosus* extending across the entire Hawaiian Archipelago, suggesting a single archipelago-wide genetic stock. However, Gaither et al. (2011) detected several significant pairwise comparisons clustered around the middle of the archipelago (St. Rogatien, Brooks Banks, Gardner), indicating that these locations may be genetically isolated from the remainder of the Hawaiian Archipelago, or most likely receive gene flow from Johnston Atoll to the south.

The stock structure and connectivity of *Pristipomoides multidens* has been investigated across northern Australia (Gascoyne, Pilbara and Kimberley regions in Western Australia and locations in the Northern Territory), Indonesia, and Papua New Guinea (Newman et al. 2000a; Ovenden et al. 2002, 2004). In Indonesia, genetic subdivision was apparent over relatively small spatial scales (<500 km), suggesting that all life stages of this species may be relatively sedentary (Ovenden et al. 2004). In Australia, *P. multidens* populations in the northern Kimberley were found to be genetically distinct from populations to the south and east (Ovenden et al. 2002). The northern Kimberley population was different from populations sampled off Broome, the Pilbara coast, and off Ningaloo (Exmouth), which were all similar to each other (Ovenden et al. 2002). In addition, the northern Kimberley population was differentiated from populations sampled off the Timor and Arafura Seas, which were all similar to each other (Ovenden et al. 2002). The populations sampled off the Western Australia coast (Ningaloo (Exmouth), Pilbara and Broome) were also significantly different from populations sampled off the Timor and Arafura Seas (Ovenden et al. 2002).

Newman et al. (2000a) used stable isotope chemistry to identify separate and discrete management units or stocks of *P. multidens* among similar sampling locations. Separate management units were present along the WA coast: northern Kimberley; Broome; Pilbara coast, and Ningaloo (Exmouth), with gene flow between the Broome, Pilbara coast and Ningaloo (Exmouth) management units (Newman et al. 2000a; Ovenden et al. 2002). The evidence of any longshore movement between stocks was equivocal (Newman et al. 2000a). The available data for *P. multidens* (restricted gene flow amongst adjacent island and continental shelf populations) are in contrast to that of the congener *P. filamentosus* which exhibits extensive gene flow across the Indo-Pacific (Gaither et al. 2011).

Recently, Loeun et al. (2014) estimated the population connectivity of *Etelis* sp. and *Etelis coruscans* from three areas around New Caledonia separated by a minimum distance of 200 km using mtDNA. Loeun et al. (2014) detected minimal spatial differentiation in genetic structure between each of the three regions for each species, indicating that both species could be considered as a single genetic stock within New Caledonia.

Andrews et al. (2014) examined the genetic connectivity of *Etelis coruscans* and *E. carbunculus* at 16 locations across the Hawaiian archipelago using 436–490 bp of mtDNA cytochrome *b* and 10–11 microsatellite loci. The population genetic analyses of Andrews et al. (2014) detected little or no genetic structure across the Hawaiian archipelago, with the exception of genetically divergent populations occurring in the center of the archipelago (e.g., Gardner Pinnacles, St. Rogatien Bank, Brooks Banks, and Necker Island). In contrast, a genetically divergent population of *E. coruscans* was found outside of the mid-archipelago (Kaua'i Island). As hypothesised for *P. filamentosus,* evidence of genetic divergence for *E. carbunculus* and *E. coruscans* at the mid-Hawaiian archipelago may be driven by connectivity with Johnston Atoll, located outside of the Hawaiian Archipelago.

The studies described above, albeit limited to two genera, have assessed population genetic differences and stock structure among broad and fine spatial scales and thus provide information on the contrasting levels of gene flow and dispersal histories of these eteline snappers. For some species there is evidence for panmixia and in other species there is divergent, island

specific or population specific differences. This indicates that some species can be managed spatially in a robust manner as the level of mixing is very low.

In this review, we have not considered the study of Smith (1992) to be valid in regards to stock identification of *Etelis carbunculus* due to the presence of cryptic speciation. Smith (1992) compared Fourier descriptors and otolith shape indices to detect regional variation and population separation of *E. carbunculus*. However, it is likely that the locations sampled comprised separate distinct species and thus the results are confounded (see Wakefield et al. 2014; Andrews et al. 2016).

There is a need to assess the stock structure and dispersal capacity of the majority of tropical deep-water fishes. Ideally, this will involve studies examining the potential for shared stocks for these species, and hence the appropriate spatial scale(s) required for fisheries management. To facilitate this, a multidisciplinary holistic approach is required that utilises techniques such as molecular genetics (microsatellites, next generation sequencing and analysis), intergenerational markers, life history parameters, otolith chemistry, and the assessment of parasite faunal composition and incidence (Welch et al. 2015). These techniques in association with biophysical modeling will allow for an integrated understanding of connectivity and population subdivision.

Early life history

Tropical deep-water demersal fish species have not been well represented in ichthyo-plankton collections. Thus, knowledge of the early life history of tropical deep-water fishes is limited to a small number of species, or available only at the genus, subfamily, or family level. The larvae of tropical deep-water snappers and groupers are distributed mostly off the edge of continental shelves and offshore from oceanic islands (Leis 1987). Leis (1987) indicated that there was evidence of a vertical migration pattern in deep-water snapper and grouper larvae, in which larvae from these families avoided surface waters during the day.

For lutjanids, all eggs that have been described are pelagic, spherical, and small in size (0.77–0.85 mm), including species in the Etelinae (Leis and Carson-Ewart 2004). Larval development in the lutjanid

subfamilies Apsilinae and Etelinae have been described by Leis and Lee (1994), Leis et al. (1997), and Leis (2005).

The larvae of deep-water snappers (Apsilinae and Etelinae) are pelagic and most remain planktonic to a large size (Leis and Lee 1994; Leis et al. 1997; Leis and Carson-Ewart 2004; Leis 2005). The larvae of the *Etelis* genus remain pelagic until at least 51 mm, with *E. carbunculus* pelagic to at least 50 mm, and *E. coruscans* pelagic to at least 22 mm (Leis and Lee 1994). The larvae of the genera *Aphareus* (*A. rutilans*) and *Pristipomoides* (*P. auricilla*, *P. filamentosus*, *P. multidens,* and/or *P. typus*, *P. sieboldii*) are very similar and are pelagic to at least 54 mm (Leis and Lee 1994). In addition, the larvae of *Paracaesio* remain pelagic until at least 24 mm (Leis et al. 1997). While the larvae of some genera remain to be adequately described (e.g. *Lipocheilus*), Leis (2005) has described the larvae of *Randallichthyes filamentosus* from a 9.7 mm specimen.

The descriptions by Leis and Lee (1994) reveal that the largest *E. carbunculus* larvae were obtained from Hawaii and the smallest larvae were obtained from the Bismarck Sea. It is unclear whether the larvae from the Bismarck Sea are all *E. carbunculus* or whether they comprise both *E. carbunculus* and *E.* sp. There is a possibility that the larvae of *E. carbunculus* may be larger and as such possibly spend longer in the pelagic environment than *E.* sp., although this remains to be confirmed.

The pelagic larval duration (PLD) of most tropical deep-water fishes is poorly known. PLD is known for some species of *Lutjanus,* with a mean PLD of 40 days reported by Stobutzki and Bellwood (1997). In the absence of any data on PLD for *P. multidens*, Ovenden et al. (2004) assumed a PLD of ~40 days was practical based on the study of Stobutzki and Bellwood (1997). Gaither et al. (2011) suggest a PLD of 60–180 days for *P. filamentosus*, which is based on estimated ages of juvenile *P. filamentosus* from other studies (Moffitt and Parrish 1996; Leis and Lee 1994). This conclusion is supported by DeMartini et al. (1994) who estimated the age of the youngest juvenile *P. filamentosus* in their study to be 134 days old, while the smallest fish (84 mm *FL*) was estimated to be 160 days old. Moffitt and Parrish (1996) reported that juvenile *P. filamentosus* from Hawaii first appear in their juvenile habitat at 70–100 mm *FL*. Moffitt and Parrish (1996) further report that while it is not known

whether juvenile *P. filamentosus* are only recently settling after a long pelagic stage or whether they are immigrating from another benthic habitat, juvenile *P. filamentosus* of this size range or smaller have not been reported from other habitats. Further, juvenile *P. filamentosus* at a size of approx. 100 mm *FL* were estimated to be approx. 180 days old by Moffitt and Parrish (1996).

For epinephelids, all eggs that have been described are pelagic, spherical, and small to medium in size (0.5–1.2 mm; Leis and Carson-Ewart 2004). The larvae of deep-water groupers are pelagic (Leis and Carson-Ewart 2004). There have been few studies examining the early life history of deep-water groupers to date, the exception being the work of Kitajima et al. (1991), based on laboratory reared *E. septemfasciatus*. Kitajima et al. (1991) reported the eggs of *E. septemfasciatus* were pelagic and spherical (0.82 mm) with an oil globule present.

For lethrinids, all eggs of *Lethrinus* and *Gymnocranius* are pelagic, spherical, and small (0.68–0.83 mm; Leis and Carson-Ewart 2004). The larvae of the known lethrinids are pelagic (Leis and Carson-Ewart 2004). The early life history of the deep-water emperor *Wattsia mossambica* has not been studied to date.

Knowledge of the early life history of many deep-water snappers, groupers, and emperors is still incomplete, although the available information suggests a trend towards extended PLDs and larger sizes of pelagic larvae (suggestive of wide dispersal capacity) relative to shallow water species from the same families. Little is known of the PLD and age at settlement, the pelagic-benthic transition, swimming capacity, behaviour and position in the water column, and the feeding and vulnerability of larvae of deep-water tropical fishes.

The known juvenile habitats of deep-water snappers and groupers are very different from the adult habitats and there is distinct ontogenetic habitat partitioning. For example, juveniles of both *H. quernus* and *P. filamentosus* are found shallower than the adults and on flat banks (Moffitt 2006). Juvenile *P. filamentosus* occupy featureless sand and mud flats until a length of approx. 200 mm and then migrate to high relief hard bottom habitats (Moffitt 2006; Parrish et al. 2015). Moore et al. (2016) reported that the distribution of adult *E. carbunculus*, *E. coruscans* and *P. filamentosus* from Hawaiian waters are influenced by a unique combination of habitat conditions, with

depth, terrain (slope) and substrate (low lying unconsolidated sediments) being the three most important variables in shaping their distributions. Newman (unpublished data) found juvenile *P. multidens* in flat featureless sandy habitats in mixed schools with *Nemipterus* species in areas distinctly separate from the adult habitats. The partitioning of habitats from juvenile to adults may be a strategy in the life history of deep-water demersal fish in order to avoid predation.

Age, growth, and mortality

There has been no co-ordinated approach to determine age-based life history parameters and a plethora of methods have been used; some robust and some that derive misleading information. Estimates of age in tropical deep-water fishes have been obtained from length frequency analysis, increment counts from scales, fin spines, vertebrae, whole otoliths, sectioned otoliths, and from bomb radiocarbon and lead-radium histories derived from otoliths (see Supplementary Tables 1a–1c). As such, comparisons of age-based life history parameters among studies are challenging, but some broad trends are evident.

Age-based estimates of the von Bertalanffy growth function (VBGF) parameters (L_∞, K and t_0), instantaneous rates of natural mortality (M), total mortality (Z), and fishing mortality (F), and longevity for tropical deep-water fishes from the Indo-Pacific region are summarised in Supplementary Tables 1a–1c. In those cases where longevity data were available with no estimates of M, we derived proxy estimates of M using the general regression equation of Hoenig (1983) for fish, where: $\log_e Z = 1.46 – 1.01 \log_e t_{max}$ (t_{max} is the maximum age in years). This equation provides a reasonable approximation of M in tropical demersal fishes (e.g. Newman et al. 1996a, b, 2000b, c).

To test the differences among the four ageing methods [i.e. ages derived from: (1) length frequency data; (2) annuli counts from transverse sections of otoliths; (3) daily growth increment counts from otolith sections; or (4) vertebrae/scales] used to derive estimates of age-based life history parameters [i.e. maximum age (T_{max}) and VBGF parameters k and L_∞] in tropical deep-water fishes, we used an analysis of similarities (ANOSIM). This test is based on rank

similarity with significance assessed using the R statistic for global and pairwise comparisons. Studies that used ageing methods that differed significantly (i.e. $R < 1\%$) were further compared based on their distributions within a metric multidimensional scaling (mMDS) ordination. The estimates of maximum age (T_{max}) and VBGF parameters k and L_∞ from these studies were square root transformed prior to analyses to stabilise the variance among parameters. Considering these parameters are not on comparable scales, these square root transformed values were standardised prior to analysis, i.e.

$$Z_{(x)} = \frac{x - \mu}{\sigma};$$

where $Z_{(x)}$ is the Z-value for each age-based life history parameter x, μ = mean, and σ = standard deviation of each parameter. A Euclidean dissimilarity matrix was produced from the Z-values for the three age-based life history parameters and used to derive an mMDS ordination. The scale of relative distance between data points within the ordination was preserved from the input resemblance matrix by fitting a linear regression (through the origin) to their relationship with the corresponding Euclidean dissimilarities among all pairwise comparisons among studies ($n = 63$). This linear correlation was evaluated using a Shepard diagram and stress coefficient. Vectors for each life history parameter were overlaid onto the mMDS based on Pearson correlation coefficients to identify the strength and direction of their relationships within the data cloud. In addition, hierarchical agglomerative clustering with group-average linkage and an associated Similarity Profile test (1 % significance level, SIMPROF) based on Euclidean dissimilarity was used to identify significant group structure within the data cloud of the ordination.

Overall, there was a significant difference among the four ageing methods when estimating age-based life history parameters (ANOSIM global $R = 0.433$, $p = 0.1\%$). Pairwise comparisons between these four ageing methods showed that age-based life history parameters derived using annuli counts from thin transverse otolith sections differed significantly from those using ages derived from counts of daily growth increments (DGIs) on thin longitudinal otolith sections ($p = 0.1\%$, Table 1). These differences were consistent with results from the CLUSTER and SIMPROF procedures performed on the age-based life history

Table 1 R statistics and significance levels (P, %) for ANOSIM pairwise comparisons between four ageing methods (TS, transverse sections)

Groups	R	P (%)
Annuli counts (TS) vs. daily counts	**0.528**	**0.1**
Annuli counts (TS) vs. vertebrae/scales	0.003	38.7
Annuli counts (TS) vs. length frequency	0.204	10.7
Daily counts vs. vertebrae/scales	0.523	2.0
Daily counts vs. length frequency	0.325	9.1
Vertebrae/scales vs. length frequency	-0.167	60.0

Significant differences $P < 1$ % (bold)

Fig. 1 Metric multidimensional scaling (mMDS) ordination derived from the Euclidean dissimilarities among maximum age (T_{max}) and von Bertalanffy growth parameters k and L_{∞} (vectors for each parameter overlaid, *solid black lines*) derived from either annuli (*grey triangles*) or daily (*black circles*) growth increment counts among studies of deep-water demersal teleosts (see Supplementary Table 1a, b and c). Hierarchical agglomerative clustering (CLUSTER) and associated Similarity Profile test (1 % significance level, SIMPROF) used to derive significant groupings (*dashed grey lines*)

parameters, which almost exclusively separated studies into those that used either annuli or DGIs within the data cloud of the mMDS (Fig. 1). Studies that derived ages using annuli counts from transverse otolith sections resulted in higher estimates of maximum age (T_{max}) and lower estimates of the asymptotic length (L_{∞}), whereas estimates of the growth coefficient k were not strongly influenced by either annuli or DGI ageing methods (Fig. 1).

These results indicate significant bias in the numerical integration techniques employed in those studies where counts were interpolated across expanses of the longitudinal otolith sections with no visible DGIs. Similarly, bias is also evident in age estimation from the use of length frequency analyses, scales, and vertebrae. These techniques all underestimate age, resulting in significant underestimates of longevity (see Andrews et al. 2012) and underestimates of correlated life history attributes such as rates of natural mortality (Hoenig 1983). Similarly, bias from the use of these techniques was also evident in estimates of L_{∞}.

DGIs have been used to estimate age for a range of deep-water lutjanid species in Hawaii, particularly for juveniles (e.g. Ralston and Williams 1989; DeMartini et al. 1994). Ralston and Miyamoto (1983) validated the deposition of daily increments in *P. filamentosus* otoliths up to approx. 3 years of age. However, direct age estimates from DGIs for older fish were difficult due to episodic otolith deposition. To address this issue, Ralston and Miyamoto (1981, 1983) developed an integration method, later refined by Ralston and Williams (1988) and Smith and Kostlan (1991).

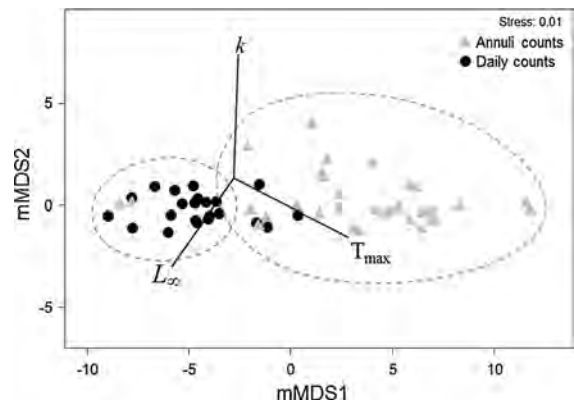This method uses the average increment widths of presumed DGIs in areas of otolith sections where

increments were considered unambiguous to extrapolate the total number of daily increments, and thus derive an estimate of age, for each otolith. As posited by Ralston and Miyamoto (1983), this DGI integration method is likely to produce underestimates of age. Unambiguous daily increments are likely to be more widely spaced than ambiguous increments, thus underestimating the total number of DGIs, and the width of DGIs decreases with increasing age, corresponding to an increase in the magnitude of ageing errors (Campana 2001; Williams et al. 2013a). Andrews et al. (2012) used bomb radiocarbon and lead-radium dating to confirm the longevity of *P. filamentosus* (see Supplementary Table 1a) and as such demonstrated that the otolith DGI numerical integration method considerably underestimated the true age.

Andrews et al. (2012) also used *P. filamentosus* age data estimated from otolith DGI counts on young fish (DeMartini et al. 1994), from numerically integrated DGIs (Ralston and Miyamoto 1983), and from bomb radiocarbon and lead-radium methods to describe a revised growth trajectory using all available information. It is possible that the resulting curve overestimates k and underestimates L_{∞} as a result of the inclusion of integrated DGI age underestimates, and

because the majority of the bomb radiocarbon length-at-age estimates in the 10–20 year age range lie below the curve rather than above it, while all of the bomb radiocarbon length-at-age estimates in the 30–50 year age range lie above the curve. These potential biases may result from the mix of aging techniques, opportunistic sampling, and non-random sampling when selecting otoliths for bomb radiocarbon and lead-radium analysis (i.e. selective sampling of the largest fish and/or heaviest otoliths; Andrews et al. 2012). Furthermore, the potential for sex-specific differences is not evaluated.

In addition, there is increasing evidence across many taxa, in particular lutjanids, that size and age are decoupled (Newman et al. 1996a; Newman 2002a, b; Newman and Dunk 2002, 2003), with large size not necessarily correlated with old age. This disconnection between size and age indicates that length-based analyses for long-lived deep-water fishes are misleading.

It is clearly evident that methodological differences in age estimation have the potential to unduly influence growth parameter estimation and may provide misleading impressions of the production potential of deep-water demersal fishes. A complete validated ageing protocol is non-existent for most species. Techniques such as length frequency analysis, use of scales, vertebrae, and DGIs extrapolated across otolith sections are all likely to underestimate the true age of deep-water demersal fish.

Considerable success has been achieved by using thin transverse sections of otoliths to estimate age of shallow (e.g. Mant et al. 2006; Marriott et al. 2011; Newman 2002a; Newman et al. 2010) and deep-water tropical fishes (e.g. Wakefield et al. 2013, b; Williams et al. 2015). This requires the use of sagittal otolith sections (preferably < 200 μm thick) that are subsequently polished, acid rinsed, and assessed using either transmitted or reflected light to allow annual opaque increments to be counted and cross-referenced between multiple reading axes of the otolith (e.g. Newman and Dunk 2003; Wakefield et al. 2013, 2016a, b). These approaches should be explored and consistently applied across taxa to ensure replication of reliable age-based data.

For species that are long-lived, the most unbiased methods for validation are derived from bomb radiocarbon and lead-radium dating of otolith material (Campana 1999). Andrews et al. (2013) described and utilised the bomb radiocarbon post-peak decline period (typically more recent than 1980) in the Gulf of Mexico for validating the age of fish with birth years more recent than the period of rising levels of bomb radiocarbon (late 1950s to late 1960s). Newman et al. (2015) noted that this method of bomb radiocarbon validation requires a strong slope to be present in the post-peak decline period and appears to be limited to the northern hemisphere due to air-sea exchange rates (e.g. Andrews et al. 2013), as the bomb radiocarbon signal in the southern hemisphere is attenuated and phase-lagged, with a long unusable post-peak period (e.g. Andrews et al. 2011, 2015). As such, the most reliable age class window for bomb radiocarbon validation is for fish with a birth year between 1958 and 1970 due to the phase lag (Campana 2001; Andrews et al. 2015) and these fish are now rare or only obtainable from archived collections. Furthermore, the bomb radiocarbon and lead-radium dating of otolith material also needs to examine whether there are sex-specific differences in longevity within species if sufficient material is available.

An additional benefit that can be derived from thin otolith sections is the capacity to develop a time series of annual growth using otolith increment measurements. Once these otolith growth chronologies have been detrended to remove ontogenetic effects, they can be correlated against environmental parameters (e.g. Nguyen et al. 2015; Ong et al. 2015, 2016). Strong correlations of these annual otolith growth chronologies with regional environmental drivers further contribute to the validation of fish age estimates (i.e., the concurrence of otolith growth trajectories with environmental signals over decadal scales, confirms estimates of longevity).

To illustrate patterns in growth and longevity, VBGF curves were plotted from examples of likely growth curve profiles (i.e. derived from thin transverse sections of sagittal otoliths) for several deep-water species (Fig. 2). The growth patterns for *Aprion virescens*, *E.* sp., and *E. coruscans* were characterised by high estimates of L_∞, with extended longevities (Fig. 2a). Growth of *E.* sp. is slow in comparison to the rapid initial growth of *A. virescens* and *E. coruscans* (Fig. 2a). Growth curves for the *Pristipomoides* species exhibited a precipitous incline before a long asymptote (i.e. square-like) in their profile, and were characterised by relatively high estimates of *k* and also extended longevities (Fig. 2b). In contrast, the growth
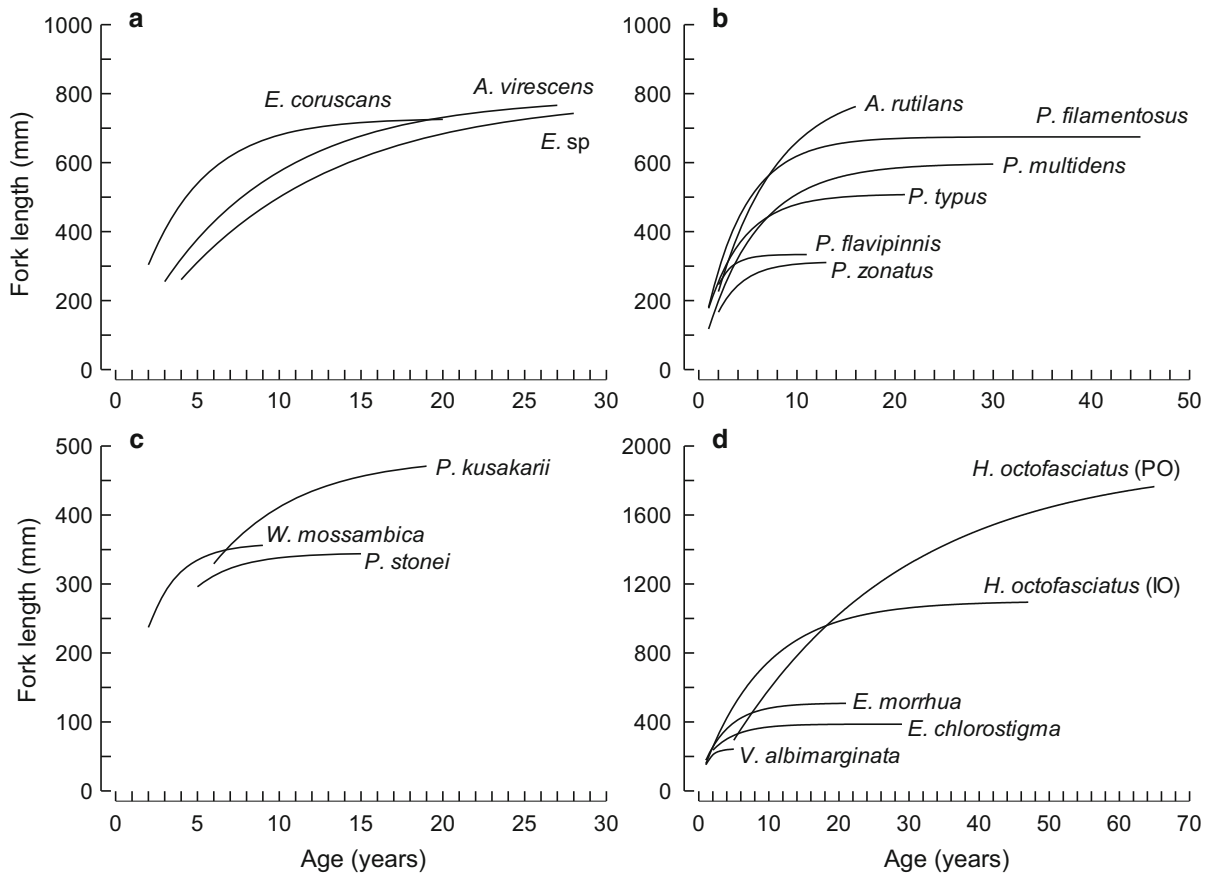
Fig. 2 Comparisons of von Bertalanffy growth trajectories and longevities for four deep-water demersal teleost groups. Data for **a** derived from Pilling et al. (2000) and Fry et al. (2006), longevity estimates for *E.* sp. were validated by Andrews et al. (2011). Data for **b** derived from Andrews et al. (2012), Fry et al. (2006), Newman and Dunk (2003) and Newman et al. (2001), longevity estimates for *P. multidens* were validated by Newman and Dunk (2003). Data for **c** derived from Fry et al. (2006). Data for **d** derived from Grandcourt (2002), Fry et al. (2006), Wakefield et al. (2013) and Wakefield et al. (2015b), longevity estimates for *H. octofasciatus* (Indian Ocean) were validated by Andrews et al. (2011)

curve of *Aphareus rutilans* did not appear to asymptote (Fig. 2b). Growth curves for *Paracaesio* species and *Wattsia* were similar to those of *Aphareus* and *Pristipomoides* with square growth profiles (Fig. 2c). Growth curves for *Epinephelus chlorostigma*, *E. morrhua*, *Hyporthodus octofasciatus,* and *Variola albimarginata* were highly variable, but all exhibit extended longevities (Fig. 2d). Significant differences between growth trajectories and longevities may also exist between the Indian and Pacific Oceans for conspecifics (e.g. *H. octofasciatus*, Wakefield et al. 2013, 2015b).

Estimates of longevity for tropical deep-water fishes derived from reliable studies indicate that most species exhibit longevities in excess of 30 years, with some species exceeding 40 or more years (see Supplementary Tables 1a–c). Where available, estimates of longevity among genera are similar. Furthermore, due to the inverse correlation between longevity and natural mortality, these long-lived deep-water fishes have low rates of natural mortality (see Supplementary Tables 1a–c). Growth rates are also slow for many species, thus the size and age at maturity may be delayed, placing greater importance on developing appropriate management measures.

The variation in parameter estimates among studies using similar age estimation methods (Supplementary Tables 1a–c, Fig. 2) suggests that populations of tropical deep-water fishes do not exhibit uniform age-based life history parameters among locations.

Population-level life history data are useful for informing fisheries management, as it may not always be valid to apply parameters from one population to another.

The age-based life history attributes of tropical deep-water fishes indicate low production potential. The eightbar grouper (*Hyporthodus octofasciatus*) is likely to be exceptionally vulnerable to exploitation and localised depletion (Wakefield et al. 2013, 2015b). Reports from across many Pacific Island countries are that this species is harvested initially in relatively large numbers (and sizes) during the early development phase of deep-water fisheries, and is rapidly fished down to levels of low abundance and commercial insignificance. For these species, there are few options available for fisheries managers, with the exception of spatial closures.

Reproduction

Deep-water snappers, groupers, and emperors are moderate to large predators that are commonly encountered in loose schools or groups. The mode of reproduction for these species is highly variable depending upon the family. Sexual dimorphism in anatomical features has not been reported in lutjanids, except by Kami (1973) for two *Pristipomoides* species (*P. auricilla* and *P. filamentosus*) from Guam. Kami (1973) reported that large males of both *P. auricilla* and *P. filamentosus* exhibit more yellow in their unpaired fins than do females and small males. The function of these colour differences are not known and have not been reported elsewhere. Recent, preliminary analysis suggests that *P. filamentosus* adult sex can be distinguished by macroscopic examination of the genital papilla (Luers, in prep.).

In many species of *Lutjanus*, male fish reach a larger size-at-age than female fish (e.g. Newman et al. 1996a; Newman et al. 2000a, b, c; Newman 2002a; Newman and Dunk 2002). However, there is no evidence of size-at-age differentiation between sexes in *Pristipomoides* (see Newman and Dunk 2003). Conversely, in the *Etelis* genus, females appear to reach a larger size-at-age than males (Wakefield et al. unpublished data). Females with a large body size may be reproductively advantaged by being more fecund as they can accommodate a large mass of hydrated eggs

prior to spawning, especially in a multiple male, multiple female spawning system.

All lutjanids studied to date are gonochoristic, i.e. individuals are born as male or female, do not undergo sex change, and remain the same sex throughout their life span (e.g. Allen 1985; Everson et al. 1989; Mees 1993; Newman et al. 2001; Nanami 2011). As gonochorists, the early gonad development of lutjanids proceeds from a gonad with a female germ cell directly into an ovary and from a gonad with a male germ cell directly into a testis.

The spawning period for most deep-water snappers is consistent with a spring-summer spawning season, regardless of region (Table 2). As such, spawning peaks generally coincide with periods of warmer annual water temperatures. Most deep-water lutjanids form aggregations to spawn (Table 2) and are broadcast or serial spawners, spawning multiple times over a protracted spawning season, and thus have indeterminate fecundity. For example, *P. multidens* forms multiple male, multiple female spawning groups during the spawning season, with males attempting to spawn with as many females as is practicable (Newman et al. 2001). In these species, sperm limitation does not appear to be an issue.

The length, at which 50 % of individuals mature relative to a species total length, is on average 57 % of their L_∞ for all deep-water species (Table 2). In those species where age protocols have been validated, the age at which 50 % of individuals attain maturity is relatively high (Table 2; Newman et al. 2001). While there are limited data, length at 50 % maturity for the deep-water Lutjanidae is on average 59 % of their L_∞ (range 40–79 %), while length at 50 % maturity for the female deep-water Epinephelidae is relatively smaller with an average of 46 % of their L_∞ (range 40–56 %). No reproductive data are available for *Wattsia*.

Lethrinids have been reported to undergo sex change in the form of protogynous hermaphroditism (e.g. Young and Martin 1982; Ebisawa 2006; Sadovy de Mitcheson and Liu 2008; Currey et al. 2013). However, lethrinids display a variety of hermaphroditic reproductive strategies that can be described as either functional gonochorism (rudimentary hermaphroditism) or protogyny. For example, Ebisawa (1990) and Marriott et al. (2010) provide evidence of functional gonochorism in *Lethrinus nebulosus* due to the pre-maturational protogynous sex change at a mean age of 2.3 years. In contrast, many other species

Table 2 Sexual pattern, maturity and spawning period (period in which females contained ovaries that were either ripe or or in spawning condition and the months when the largest proportion (peak spawning period) of those types of ovaries were recorded) of deepwater snappers

Species	Sexual pattern	Reproductive mode	Fish with ripe/spawning stage ovaries	Peak spawning period	Size-at-maturity (mm)	Age-at-maturity (years)	Location	References
A. furca	G	Aggregations/broadcast						Allen (1985)
A. ruilans	G	Aggregations/broadcast		Sept.–Feb.			Vanuatu	Allen (1985)
A. virescens					470 (FL)		Hawaii	Everson et al. (1989)
P. stonei					400		Papua New Guinea	Lokani et al. (1990)
P. argyrogrammicus	G	Aggregations/broadcast	Apr.–Aug.				Okinawa	Nanami (2011)
P. auricilla						2.4	Marianas	Polovina and Ralston (1986)
P. filamentosus					400 (FL)	3–4	Hawaii	Ralston and Miyamoto (1983)
P. filamentosus			June–Dec.	August	425 (FL)		Hawaii	Kikkawa (1984)
P. filamentosus					487 (FL)	1.8	Hawaii	Uchiyama and Tagami (1984)
P. filamentosus						2.0	Marianas	Polovina and Ralston (1986)
P. filamentosus					340		Papua New Guinea	Lokani et al. (1990)
P. filamentosus	G	Aggregations/broadcast	Oct.–Apr.	Feb.–Apr.	510–530 (FL)		Seychelles	Mees (1993)
P. flavipinnis	G	Aggregations/broadcast	All year	Dec.–Feb.			Vanuatu	Allen (1985)
P. flavipinnis						2.2	Marianas	Polovina and Ralston (1986)
P. multidens					310		Papua New Guinea	Lokani et al. (1990)
P. multidens	G	Aggregations/broadcast	Jan.–Apr.	Mar.	473 (FL) ♀	8.2	Western Australia	Newman et al. (2001)
P. multidens	G	Aggregations/broadcast	Jan.–Apr.	Mar.	470 (FL) ♂	8.0	Western Australia	Newman et al. (2001)
P. zonatus						3.25	Marianas	Polovina and Ralston (1986)

Table 2 continued

Species	Sexual pattern	Reproductive mode	Fish with ripe/spawning stage ovaries	Peak spawning period	Size-at-maturity (mm)	Age-at-maturity (years)	Location	References
E. carbunculus		Aggregations/broadcast	July–Sept.		300 (FL)		Hawaii	Everson (1984)
E. carbunculus					298 (FL)	1.1	Hawaii	Uchiyama and Tagami (1984)
E. carbunculus	G	Aggregations/broadcast	All year	Nov.			Vanuatu	Allen (1985)
E. carbunculus			Mar.–Oct.		298 (FL)		Hawaii	Everson (1986)
E. carbunculus						2.75	Marianas	Polovina and Ralston (1986)
E. carbunculus					610		Papua New Guinea	Lokani et al. (1990)
E. coruscans						4.1	Marianas	Polovina and Ralston (1986)
E. coruscans	G	Aggregations/broadcast			522		Hawaii	Everson et al. (1989)

Sexual pattern: *G* gonochoristic. Reproductive mode is derived mostly from testis weight relative to ovary weight, i.e. similar weights depict broadcast spawners, while relatively small testes weights depict social groups and/or pair spawning

Table 3 Sexual pattern and spawning period (period in which females contained ovaries that were either ripe or in spawning condition and the months when the largest proportion (peak spawning period) of those types of ovaries were recorded) of deepwater emperors and groupers

Species	Sexual pattern	Reproductive mode	Fish with ripe/spawning stage ovaries	Peak spawning period	Size-at-maturity (mm)	Age-at-maturity (years)	Location	References
Emperors								
W. mossambica					310		Papua New Guinea	Lokani et al. (1990)
Groupers								
C. aurantia	Pg							Heemstra and Randall (1993)
E. morrhua	Pg							Heemstra and Randall (1993)
E. radiatus	Pg							Heemstra and Randall (1993)
H. ergastularius	Pg				700–800			Rowling (1996)
H. octofasciatus	Pg							Heemstra and Randall (1993)
H. octofasciatus	Pg		Oct–Feb	Nov–Jan	560 (1022[a])	6.1 (≥11[a])	Western Australia	Wakefield et al. (2013)
H. octofasciatus	Pg						South Pacific	Wakefield et al. (2015b)
H. quernus	Pg							Craig et al. (2011)
H. quernus			Jan–Jun	Apr and Jun	580–620		Hawaii	Everson (1992)
H. septemfasciatus	Pg							Craig et al. (2011)

Sexual pattern: *Pg* protogynous

[a] Size/age at sex change

of lethrinid are reported as protogynous, with sex change occurring after maturity as a female and with large, older males participating in spawning events (e.g. Young and Martin 1982; Bean et al. 2003; Sumpton and Brown 2004; Ebisawa 2006; Williams et al. 2006; Currey et al. 2013). There is no evidence of sexual dimorphism in lethrinids. Little is known about the reproductive biology of the deep-water emperor *Wattsia mossambica* (Table 3) and further research is required to determine their mode of reproduction.

All deep-water groupers studied to date are monandric protogynous hermaphrodites, i.e. individuals in the population mature as females, and subsequently change sex later in life to males. This sequential reproductive function is best identified by the simultaneous (during sexual transition) or sequential (before and after transition) presence of mature, but degenerating ovarian tissue and mature, but proliferating testicular tissue in the gonads of the same individual. Some species such as those in the genus *Hyporthodus* reach a large size, with sex change similarly occurring at a relatively larger size and also age (see Table 3).

The spawning period for the deep-water groupers *H. octofasciatus* and *H. quernus* are similar, with both exhibiting a spring-summer spawning period (Everson 1992; Wakefield et al. 2013). Also, the length-at-maturity of both *H. octofasciatus* and *H. quernus* is similar (Table 3). The spawning behavior of deep-water groupers is not known.

The number of studies examining the reproductive mode and spawning season of deep-water snappers, emperors, and groupers is limited. Resolution of the spawning season and length- and age-at-maturity are key requirements for use in stock assessments and determining effective management strategies for these deep-water demersal fish and is considered to be a focal area for future research.

Fisheries

The tropical deep-water species considered in this review are harvested from a wide geographic distribution using a variety of different fishing gears that primarily focus on line-based methods (handline, hydraulic line, electric reels, longlines, and trotlines), but also include fish traps and fish trawls in some locations. The species compositions of tropical deep-water fisheries exploited across the Indo-Pacific vary between locations depending primarily on the availability and dispersion capacity of different species. However, in all tropical deep-slope environments, the dominant species in the catch are in the genera *Etelis*, *Pristipomoides, Aphareus, Paracaesio* and *Hyporthodus*.

Tropical deep-water species are harvested by commercial, recreational (including charter fishers), artisanal, and subsistence fishers, and in some locations there are resource sharing issues among these fishing groups. Many species considered in this review have only recently been exploited in many areas due to the depth that they inhabit. These depths have made it difficult for exploitation and the existence of relatively more abundant resources in shallower shelf areas has meant that there was little incentive to fish in such areas. In some locations, these species were initially exploited by artisanal and subsistence fisheries, with relatively low levels of harvest. The move to more commercial type fishing operations and more efficient fishing gear has placed additional strain on the sustainability of tropical deep-water fisheries.

For example, in the Pacific Islands, deep-water fish have been exploited on a subsistence basis for many centuries (Dalzell and Preston 1992). However, semi-commercial deep-water fisheries were developed during the 1970s, mainly to reduce pressure on shallow inshore reef fish populations (Dalzell and Preston 1992). This led to the development of fisheries for deep-water species in many Pacific Island countries (e.g. Tonga, Fiji, Vanuatu, Papua New Guinea (PNG), and American Samoa; Dalzell and Adams 1994; Itano 1996a, b). In Western Australia and the Northern Territory, significant commercial fisheries exist for deep-water fishes (Newman 2006; Newman et al. 2012, 2014b; Martin et al. 2014; Northern Territory Government 2014). In Western Australia, these fisheries have complex management arrangements that involve a system of total allowable effort, with individually transferable effort units. These fleets are highly mobile, efficient, and wide ranging and complex management arrangements are required to maintain breeding stock levels (Newman 2006).

Native Hawaiians fished for deepwater snappers and the endemic *H. quernus* from canoes hundreds of years ago. Today's fishery utilizes the typical modern technology (GPS, high resolution colour depth sounders, and electric or hydraulic reels). Reported landings in 2013 were approximately 106 tonnes, with

a catch value of approximately 1.5 million USD (Brodziak et al. 2014). These species are assessed and managed as a complex of the seven most important species known as the 'Deep-7' and the fishery operates under a Deep-7 complex catch limit.

Indonesia reported a catch of 3183 tonnes of *Pristipomoides* species in 2011 across all fishing areas. This was a minor component of their overall reported snapper landings. Landings from Australia's Indian Ocean Territories (Cocos (Keeling) Islands and Christmas Island) are small, but they are targeted by a range of fishing groups (Newman et al. 2014a). These islands are small and the available habitat is limited. Assessments of the status of populations of deep-water fish across the wider Indo-Pacific are limited due to a general absence of adequate life history data and catch and effort statistics.

Ecological importance

The species discussed in this review appear to undergo limited movements along the deep continental slope. Some species also undergo limited vertical migrations and are likely to be involved in nutrient transfer in these ecosystems. The productivity of these deep slope environments is likely to be directly linked to the continental shelf or shallow reef near surface food webs, and may be enhanced in some submarine canyon areas although this remains to be quantified. In addition, these deep-water species are often associated with seamounts and isolated emergent or submerged atoll reef slopes.

These species occupy habitats and environments in the lower reaches of the epipelagic zone and in the upper reaches of the mesopelagic zone. These environments are dependent on the flux of epipelagic and mesopelagic taxa that flow across the shelf, down the slopes, and past the seamount and atoll reef slopes. They are also dependent on benthic associated species in these distinctive slope habitats. These deep-water species comprise a significant level of both biomass and abundance in deep slope habitats, and thus perform a significant ecological role. Many of these targeted species are high level predators. In many locations, it is the relative productivity of these habitats and resulting prey species that determines the population densities. For example, some locations have naturally low densities of deep-water species because of a lack of habitat and associated species in the required depth ranges. In those locations where key habitat characteristics and prey species are available, population densities are much higher.

Loss of deep-water fish populations resulting from overexploitation or perturbation may have major consequences for the associated ecosystems, which may become manifest in trophic changes in relation to reduced predator–prey interactions. Moreover, if climate variation increases habitat availability in more temperate regions, it is expected that these deep-water species will exploit these new habitats and expand populations if suitable prey species and environmental conditions are available (e.g. Wakefield et al. 2013, 2015b). It should be noted that any population expansion will also depend on suitable pelagic stage and juvenile habitats that can be quite different to the habitats of adult fish.

Discussion

Synthesis of life history information

Accurate age estimation is a critical issue for fisheries assessment and management. The estimates of longevity and related age-based demographic parameters derived from studies that have used age estimates from otolith thin sections and validated using robust and reliable methods such as bomb radiocarbon and Pb–Ra dating have indicated that deep-water species in the tropical Indo-Pacific region have life history attributes that are very different from those derived from previous studies that used more rudimentary age estimation methods that have underestimated true age.

The underestimation of fish age can lead to erroneous or misleading estimates of natural mortality and growth, and hence production potential and resilience to exploitation. The issue of underestimating fish age has proven problematical for tropical deep-water fishes in particular, as earlier works (see Supplementary Tables 1a–c) have utilised a range of techniques that over time have proven to be of little value in determining fish age accurately, particularly in long-lived fish (e.g. length frequency, scales, extrapolation of daily growth increments). Overcoming misconceptions of the production potential of deep-water fish stocks and their rational use is a challenge for fisheries management.

This review adds to the few existing studies that support the view that many tropical deep-water fishes are longer lived than previously inferred (sensu Wakefield et al. 2013, 2015b). For a number of these species, growth zones in thin, transverse otolith sections have been validated as annual. For example, Newman and Dunk (2003) successfully aged *P. multidens* using thin otolith sections, with analysis of otolith edge categories of individuals of all ages displaying a clear trend and demonstrating conclusively that annuli are formed once per year. However, the precision of otolith readings of *P. multidens* by Newman and Dunk (2003) was relatively low, with an IAPE (Index Average Percent Error) of 10.4 %. Newman and Dunk (2003) revealed that while a high level of variability was encountered among otolith reads, this level of IAPE reflected an average level of precision among otolith readings and indicated that the ageing protocol adopted was satisfactory. Furthermore, they observed that experience is a critical factor in increasing the agreement and hence precision or repeatability of annuli counts from sectioned otoliths. Thus, while interpretation of the otoliths of some species can be difficult, it is not insurmountable (Wakefield et al. 2016b).

To date, data from robust age-based studies reveal extended longevities, slow growth rates, and a large length/age at maturity. The consequence of a long life span in deep-water snappers, groupers and emperors is correspondingly low instantaneous rates of natural mortality, in the order of 0.1–0.2 year^{-1}; and less than 0.1 for some species. These biological characteristics of deep-water fish are generally consistent with K-selected life history strategies. That is, the productivity of populations of most species is low, resulting in low maximum sustainable yields.

Much of the vital life history data required for the management of deep-water snapper, grouper and emperor fisheries has revealed that many studies are constrained by low samples sizes and the use of ageing methods that have not been validated or verified. There is a need for more representative and adequate studies of these exploited fish species for increased precision and robustness of parameter estimation (see Newman et al. 2015).

Age-based life history information is required to provide a comprehensive basis for management and to understand the impacts of exploitation, especially given that the exploitation of deep-water reef fish stocks is increasing due to artisanal, recreational and commercial fisheries. Regional or country specific comparisons of life history attributes need to ensure that sampling to obtain age structures from which mortality estimates are to be derived is both representative and adequate. That is, sample sizes are large enough to enable robust parameter estimation and the sampling regime is sufficient to ensure that the age compositions used to determine instantaneous rates of mortality are reflective of spatial and temporal variability within the fishery system under assessment. In addition, there is a need for studies within each jurisdiction due to high likelihood of independent management units among island countries. Multi-scale sampling may also be required as life history patterns of reef fish can be expected to vary at both latitudinal and reef scales (e.g. Newman et al. 1996b; Cappo et al. 2013).

Fisheries management implications

Fishery managers need to be responsive to the inherent vulnerability of some tropical deep-water fish stocks to over-harvesting, as inferred from their life history attributes. These fish also exhibit internal trauma and haemorrhage associated with physoclistous over-expansion injuries (i.e. barotrauma) when captured from depth and are thus likely to suffer from high discard mortality. This complicates management regimes in multispecies fisheries that cannot successfully target individual species, and can restrict management options such as size limits and species-specific quotas, since any fish caught either below the size limit or above the species-specific quota are unlikely to survive release.

The maximum sustainable levels of exploitation of the tropical deep-water fish species assessed in this review are likely to be as low as 5–10 % of biomass, commensurate with levels of natural mortality (M) in many cases less than ~ 0.1 (Newman et al. 2012; Martin et al. 2014). This means that limit reference levels of biomass may be reached at a relatively rapid rate for some species with low levels of exploitation. This indicates that these fisheries will contribute modest total sustainable fishery production (catches), relative to species with faster growth and shorter longevity. With any species that has an extended longevity; many years of recovery (i.e. the number of years spanning the complete age structure of the

harvest) would be required to restore spawner biomass and age structure from a serious reduction below reference biomass levels.

It is important to note that growth parameters alone do not capture differences in longevity or natural mortality that can represent vastly different life history characteristics, in particular lifetime reproductive output (a bet hedging strategy against variable recruitment success; Newman and Dunk 2003). Extended periods of high exploitation rates are likely to result in decreases in the spawning stock biomass and constriction of the age structure of fish populations (removal of older fish), and thus diminish the number of reproductive events.

Tropical deep-water fish resources exhibit high diversity, with most fisheries composed of multiple species. Many fished locations are remote, which may provide refugia from fishing pressure but, this also makes them logistically difficult to monitor and assess. It is logistically impractical to monitor all stocks and species. It is thus advantageous to select indicator species for assessment purposes that are considered to be both inherently vulnerable to exploitation and representative of the exploited suite of species targeted. These species can then be targeted for comprehensive biological assessments.

It is evident that while many species in this group are harvested as a food source, there is little or no data available on species-specific catch statistics, and in some cases little or no data available in which to determine inherent vulnerability and/or stock status. There is also limited baseline biological information available in most countries (areas). Further research is needed on harvest levels, biology, and population trends of these species before a more accurate assessment of stock status can be ascertained. Furthermore, there is a need for detailed assessments within each jurisdiction due to the likelihood of independent management units and also spatial variation in life history parameters. Without detailed life history data from a variety of geographic, latitudinal, and habitat scales it will be difficult to generalise the likely trajectory of responses to environmental or anthropogenic perturbations.

Many deep-water fish species form schools or groups naturally, as well as to spawn and thus can be vulnerable to fishing pressure. The use of data from catches targeting large schools/groups can make it difficult to accurately assess population status because

of the possibility of hyperstability in the catch rate data. There is a need to develop new strategies to assess fish stocks rapidly in data poor situations.

Future research perspectives

There are a number of research areas for tropical deep-water demersal fish; however, the priority need for each of these research areas needs to recognize the varying risk levels between jurisdictions, regions, and also among species. Given these caveats, the priorities for research in the near future are diverse and include: resolution of taxonomic issues (particularly of commonly landed species); development of new species-specific identification guides; species-level monitoring and reporting of fisheries landings by countries and territories (and/or routine fisheries surveys); detailed biological studies with adequate and representative sampling that encompass any temporal patterns in reproduction and availability; establishing the degree of species-specific connectivity among Indo-Pacific countries and territories and defining population management units; and assessment of stock status using data poor assessment methods such as fishing mortality based approaches. Research activities also need to focus on post capture survival of released fishes to enhance survival of any discarded fish (O'Malley 2015).

It is uncertain whether these deep-water species of snappers, emperors, and groupers will be impacted by increased climate variability. Indeed, deep-water species may be somewhat impervious to all but major perturbations given their potential to access refugia by inhabiting a range of depth profiles. Shifts may occur in deep-water fish assemblages in accordance with local climate velocities or conditions (i.e. the rate and direction that climate shifts across the landscape will potentially influence deep-water fish assemblages; see Pinsky et al. 2013). As such, fishing grounds potentially may shift and either increase or decrease in size. There may also be species-specific changes, as many deep-water species recruit to shallow grounds that will be impacted by the complex mosaic of local climate velocities (Pinsky et al. 2013).

However, in order to assess possible effects of climate variability on these species, it is essential that we gather more robust data on life stage habitat requirements, seasonal abundances, and environmental variability in specific locations. In addition, the

potential impacts of climate variability on larval survivorship are not known. Indeed, climate induced changes to larval transport mechanisms could have potentially high negative population-level impacts if larvae settle in sub-optimal habitats. Conversely, there is the potential for positive population-level impacts or population growth if increased climate variability leads to the capacity for range expansion into new niches/habitats with the warming of temperate regions.

It is difficult to predict environmental impacts and how they may influence variables such as growth rate. There is a lack of long-term (decadal) data sets sufficient to investigate the relationships between vital rates of deep-water fishes in natural environments and variation in climate. The use of growth records from otoliths may provide these insights (Nguyen et al. 2015). In this approach, techniques developed in dendrochronology are applied to data extracted from otoliths so that growth records from many fish can be aligned and combined into a single time-series. This facilitates comparison of the common growth response to regional environmental drivers such as temperature, productivity, and current flow (e.g. Nguyen et al. 2015; Ong et al. 2015, 2016).

Many deep-water fish species have sympatric distributions and conservative morphologies (e.g. *Etelis carbunculus* and *E.* sp.) that in combination make taxonomic identification difficult (Andrews et al. 2016). The development of recent multivariate techniques using otolith morphometry has allowed species identification to be confirmed in both extant and archived otolith collections (Wakefield et al. 2014). However, there is a need to resolve species identification issues as they create a challenge for management. The use of molecular techniques to resolve taxonomic uncertainty and to create taxonomic baselines for these groups needs to be established. Intra-family phylogenetic relationships need to be investigated using all nominal species and genera. Specifically, this needs to examine divergence times within lineages, and the relatedness among species, and thus how this may have shaped and influenced the distribution and abundance patterns of present species.

Moreover, there is a need to investigate the connectivity and linkages among populations throughout their range and to assess the implications for the spatial management of fisheries. It is important to understand the evolutionary history and the potential

mechanisms that may have influenced gene flow among species (i.e. determining areas of genetic homogeneity or genetic discordance, and thus identifying geological or physical barriers to gene flow; e.g. DiBattista et al. 2016). The use of loci under selection, and the next generation of genetic techniques at fine spatial scales are essential to determine the dispersive capacity of species, extant gene flow, and thus the appropriate spatial scales of fisheries management.

The use of a holistic approach combining multiple techniques such as genetics (mitochondrial DNA, microsatellites; e.g. Broderick et al. 2011), parasite faunal compositions (e.g. Charters et al. 2010), otolith stable isotope compositions (e.g. Newman et al. 2009), and growth data (e.g. Ballagh et al. 2012) can be a powerful tool in providing greater certainty about the appropriate management units for deep-water fish stocks (Welch et al. 2015). As such, there is a need to assess pre- and post-settlement stock structure of deep-water fish species.

Little is known in regard to habitat preferences (niche delineations), ontogenetic changes in habitat, home ranges, and migrations (if any), in particular the level of movement between major biotypes (e.g. from seamount to seamount, atoll reef to atoll reef). Some of these issues can be resolved by otolith elemental and stable isotope analyses, however, these types of analyses can be expensive to undertake in a comprehensive manner. Tagging studies (conventional and acoustic) may also shed light on movement patterns and habitat utilization (e.g. Weng 2013) if the problems associated with barotrauma can be addressed (O'Malley 2015). Recently, Gomez et al. (2015) and Moore et al. (2016) employed predictive species distribution modelling approaches to accurately model and map sparse species distribution data across marine landscapes. These techniques could be applied to spare datasets to delineate species distribution patterns and habitat associations and assist in defining spatial management arrangements.

Resolving trophic pathways and food web interactions, including a need for quantification of linkages with continental shelf and shallow reef systems requires examination. For example, does the shallow reef link to the deep reef? Likewise, what is the habitat specificity among and between species and across what habitats do ontogenetic shifts occur? Critically, larval and juvenile habitats are poorly understood. What is the extent of the larval life (PLD) both

between and within species and where are these life stages located? More specifically, are there explicit juvenile habitats for all species such as those for *H. quernus* and *P. filamentosus* (Misa et al. 2013; Parrish et al. 2015), or are there inter-specific differences?

There is an ongoing need for reliable and accurate species specific reporting arrangements in the development phase of all emerging deep-water fisheries. These data collection approaches need to be extended into long-term programs aimed at incorporating a range of species, fisher, and fisheries data at fine spatial and temporal scales. The development of ongoing monitoring programs may also benefit from the use of fishery independent programs and techniques such as the use of remote stereo video systems (e.g., BRUVs, Harvey et al. 2012; BotCam, Merritt et al. 2011; MOUSS, Ben Richards, pers. comm). Video systems provide for a non-extractive, fishery-independent sampling and assessment technique that is cost-effective, repeatable, and robust across a range of habitats and depths (Harvey et al. 2012; Santana-Garcon et al. 2014b). Furthermore, the data collected by video systems can add insights into habitat and depth requirements across a range of deep-water fish species (Misa et al. 2013; Santana-Garcon et al. 2014a).

Comprehensive studies of the reproductive patterns and cycles of many species are needed, including estimates of fecundity by species, spawning mode and type, size and age at first maturity, and size at sex change if applicable. An important area of reproductive research is to examine the potential relationship between environmental parameters and spawning season timing and extent. It is important that these studies are undertaken in a standardised manner with similar methodologies in order to facilitate direct inter and intra species comparisons (Newman et al. 2015).

In conclusion, a number of key foci are emerging for both immediate and long-term future research, namely taxonomic resolution, population structure (connectivity), population status, long-term monitoring, foraging and reproductive ecology, habitat characterisation, and the effects of incidental bycatch. The technology and techniques required to address these questions are now largely in place as described above, allowing us to move away from an incidental, slow accumulation of data towards collaborative, international efforts targeted to understand the fisheries biology and ecology of these significant commercial, recreational, and artisanal species.

What is the future for deep-water tropical fisheries resources?

This is a difficult question, as the information presented in this review highlights the fact that little is known about the current stock status of many tropical deep-water fishes. Information relevant to sustainable management in many regions and/or localities is limited, patchy, and often outdated.

Little is known about the biology and/or the distribution patterns of many deep-water fish species. A number of species seem to appear in the development phase of fisheries and may be rapidly depleted as the fishery develops, whereas other species appear to be either uncommon throughout their range or not highly selective by the gears used to capture them (e.g. *Randallichthyes filamentosus*; Newman 2009; Wakefield et al. 2015a). Reliable and accurate species specific reporting arrangements in the development phase of emerging deep-water fisheries are needed and if practicable long-term monitoring of the relative abundance of these fish and fisheries.

For now, the available management (and enforcement) measures in many countries appear to offer limited effective protection of spawning stock biomass. It is also worth noting that the effective application of legislation through management plans requires robust frameworks and data which are not often available. Clearly, there is a need for reliable and pertinent spatial and temporal information to contribute to effective fisheries management arrangements. It is unfortunate that the development and promulgation of effective management arrangements for deep-water fisheries in some localities will remain a low priority area in terms of research and funding due to the importance of large scale tuna fisheries throughout the region and the revenue they generate.

However, there is considerable potential for developing sustainable tropical deep-water fisheries resources. In many countries, the amount of habitat available for deep-water fish populations is limited due to steep slopes and restricted continental slope areas, which also limits fishing to hook-and-line or trap methods and to fishers with considerable fishing skill and experience. Nonetheless, deep-water fishes are of both high domestic and export value.

These attributes in association with the intrinsic vulnerability of deep-water fish indicate that harvest strategies of low frequency or low intensity in conjunction with the protection of a substantial proportion of the spawning stock biomass of these fishes are optimal. Targeted fishery spatial area closures may also provide protection for a component of the spawning stock biomass and protect against recruitment overfishing. Clearly, community and country aspirations must be consistent with the production potential of the deep-water fish resources and the ecological systems that support them and in this regard, while low intensity high value fisheries can be developed, there is a low likelihood of any large-scale new fisheries being developed.

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