



Contrasting life history characteristics of the eightbar grouper *Hyporthodus octofasciatus* (Pisces: Epinephelidae) over a large latitudinal range reveals spawning omission at higher latitudes

Corey B. Wakefield*, Stephen J. Newman, Ross J. Marriott, Dion K. Boddington, and David V. Fairclough

Western Australian Fisheries and Marine Research Laboratories, Department of Fisheries, Government of Western Australia, PO Box 20, North Beach, Western Australia 6920, Australia

*Corresponding Author: tel: +61 8 9203 0111; fax: +61 8 9203 0199; e-mail: Corey.Wakefield@fish.wa.gov.au

Wakefield, C. B., Newman, S. J., Marriott, R. J., Boddington, D. K., and Fairclough, D. V. 2013. Contrasting life history characteristics of the eightbar grouper, *Hyporthodus octofasciatus* (Pisces: Epinephelidae), over a large latitudinal range reveals spawning omission at higher latitudes. – ICES Journal of Marine Science, 70: 485–497.

Received 15 August 2012; accepted 26 January 2013; advance access publication 19 February 2013.

Demographic data on deep-water groupers are limited despite them being highly exploited throughout the Indo-Pacific. In Western Australia, the continuous distribution of the eightbar grouper, *Hyporthodus octofasciatus*, spans tropical to temperate waters over ~3500 km from 12°S–35°S. The maximum age was markedly higher in the northern tropical waters than in southern temperate waters, i.e. 47 vs 20 years. Females attained a significantly larger length-at-age in southern temperate waters. Macroscopic and microscopic examination of gonads and annual trends in mean monthly gonadosomatic indices (GSI) were used to determine that this monandric protogynous hermaphrodite spawns from late spring to summer (October–February) in northwestern Australia. In the temperate waters of WA, there was no evidence of reproduction and no males were observed south of ~30°S latitude. The lengths at which 50% of female *H. octofasciatus* matured and changed sex were estimated from northern tropical populations at 560 mm (6.1 years) and 1022 mm (≥11 years). Although the population connectivity of *H. octofasciatus* is unknown, the spawning omission in temperate waters suggests recruitment from the northern tropical areas and highlights the importance of preserving spawning stocks in those northern waters.

Keywords: age, deep-water, demography, global climate change, growth, maturity, protogynous hermaphroditism, reproduction, Western Australia.

Introduction

The eightbar grouper, *Hyporthodus octofasciatus* (Griffin, 1926), of the family Epinephelidae, is a large (~150 cm total length) and valuable deep-water demersal fish (Smith and Craig, 2007; Craig *et al.*, 2011). The monophyletic family Epinephelidae was resurrected based on the molecular analyses by Smith and Craig (2007) utilizing mitochondrial and nuclear DNA sequence data to resolve the relationships among serranid and percid fishes. Previously, *H. octofasciatus* had been assigned to the genus *Epinephelus* (Randall and Heemstra, 1991; Heemstra and Randall, 1993). Craig and Hastings (2007) resurrected the genus *Hyporthodus* based on genetic data from two nuclear and two mitochondrial genes as part of their examination of the molecular

phylogeny of the groupers of the subfamily Epinephelinae (Serranidae). *Hyporthodus* is characterized by having a much deeper body than species in the genus *Epinephelus* (this is particularly apparent in juveniles) and a drab brown or olive coloration that may or may not include several dark bars along the body (Craig and Hastings, 2007). A total of 14 species of groupers, including *H. octofasciatus*, have been accorded the genus *Hyporthodus* (Craig *et al.*, 2011).

Hyporthodus octofasciatus occurs in tropical to temperate waters and has a widespread Indo-Pacific distribution from east Africa (Somalia and South Africa) to the Marquesas Islands, extending north to Japan and south to Australia and New Zealand (Craig *et al.*, 2011). *H. octofasciatus* closely resembles

H. septemfasciatus (Randall and Heemstra, 1991; Heemstra and Randall, 1993; Craig et al., 2011). However, *H. septemfasciatus* has only been reported with certainty from Korea, China and Japan (Craig et al., 2011) and those records of *H. septemfasciatus* outside these localities appear to be based on misidentifications of *H. octofasciatus*. Furthermore, Randall and Heemstra (1991) determined that *H. octofasciatus* in Western Australia differs from all other localities in its distributional range by having a slightly rounded to truncate caudal fin with a distinctive white posterior border as an adult. In Western Australia, *H. octofasciatus* is distributed across almost the entire state from the north coast (12°S), south and east along the south coast as far as ca 35°S and 119°E (Figure 1).

The large size of *H. octofasciatus* and the high quality of its flesh, make this species highly valued by commercial and recreational fishers (Heemstra and Randall, 1993; Craig et al., 2011). The commercial landings of *H. octofasciatus* were first reported in Western Australia in 1986 (derived from compulsory catch statistics provided by commercial fishers to the Department of Fisheries, Government of Western Australia). Since then, annual statewide commercial catches have gradually increased, peaking at 83 tonnes in 2004, with an average annual catch of ca 26 t in the period from 1999–2009. In general, like most demersal fisheries in Western Australia, these annual commercial catches are low relative to fisheries elsewhere and may be indicative of a low productivity environment (Molony et al., 2011). This is of concern in Western Australia, given that there has been a possible shift in

fishing effort by both recreational and commercial fishers to deeper offshore waters, particularly in the Perth metropolitan region (31–33°S) following a marked decline in the abundances of many inshore demersal fish species (Wise et al., 2007).

At present, there is insufficient life history information on which to base a management strategy and stock assessment for this species along the coast of Western Australia or elsewhere, despite its broad distribution. Biological data on *H. octofasciatus*, and the *Hyporthodus* clade in general, is limited. The maximum age recorded for this genus was 85 years for *Hyporthodus flavolimbatus* from the Gulf of Mexico (Cook et al., 2009). Andrews et al. (2011) analysed the bomb radiocarbon composition of otoliths of *H. octofasciatus* and confirmed that estimates of fish age derived from growth zones in thin otolith sections are valid. Of the 14 species of *Hyporthodus*, five have been found to be protogynous hermaphrodites (e.g. Keener, 1984; Wyanski et al., 2000). The fact that *H. octofasciatus* is commonly misidentified and relatively rarely encountered throughout its range has led to a lack of reliable quantitative catch and effort statistics and thus a “Data Deficient” status according to the International Union for Conservation of Nature (IUCN) Red List classifications (To and Pollard, 2008). Knowledge of age, growth and reproduction are critical inputs to determine stock status and risks to sustainability from extractive fishing. Reliable biological parameter estimates will better inform fishery managers regarding sustainable management strategies for fishing this species, and for the offshore demersal scalefish resource in Western Australia, for which this species is used as an indicator (Department of Fisheries, 2011).

This study is the first detailed investigation of the age, growth and reproductive biology of *H. octofasciatus*. Specifically, we sought to determine the age, growth and reproductive parameters of relevance to satisfy base level information requirements for fisheries management of *H. octofasciatus* populations. Considering the very large latitudinal range that this species occupies along the Western Australian coast, samples were divided into those from generally tropical or temperate regions, with an arbitrary divide at 30°S. This was considered appropriate given the contrasting demographic characteristics exhibited by other demersal teleosts with similar widespread distributions along this coast (e.g. Wakefield, 2006). Thus, we compared biological parameters between tropical and temperate regions in order to evaluate the relative production potential of this species in different areas. Furthermore, we compared the results obtained from this study with available age-based demographic data for all 14 species of deep-bodied groupers in the genus *Hyporthodus* (Craig et al., 2011), including those listed as *incertae sedis* by Craig and Hastings (2007).

Methods

Sampling and somatic measurements

Samples of *H. octofasciatus* were collected from commercial (using lines, fish traps and fish trawls) and recreational catches (using lines only) from 1995–2012 across almost the entire north, west and south coasts of Western Australia (12–35°S, Figure 1). The total length (L_T) of each *H. octofasciatus* was measured to the nearest 1 mm, and when possible, the wet weight (W_w) of each whole individual was measured to the nearest 0.1 g. An allometric length (L_T) versus weight (W_w) relationship for females and males combined was derived from the log-transformed data and was

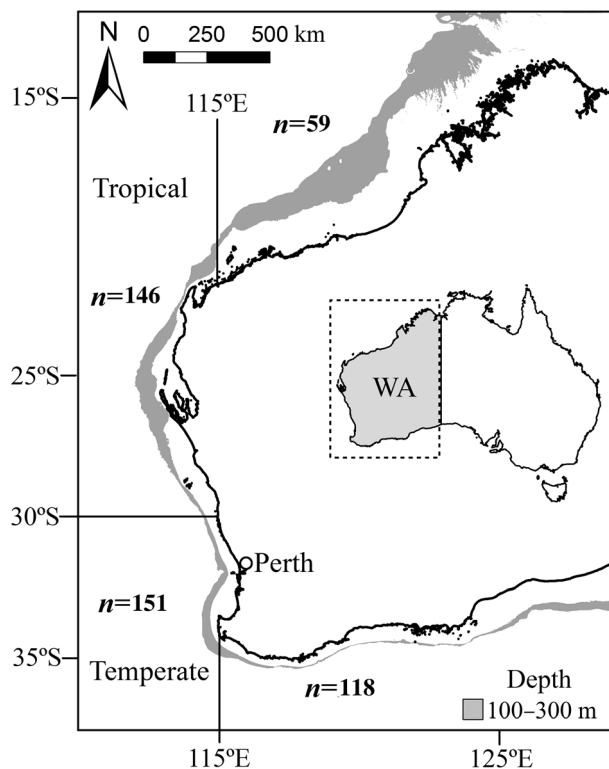


Figure 1. Map showing the tropical and temperate regions (relative to an arbitrary latitude of 30°S) and sample sizes of *Hyporthodus octofasciatus* collected from the north, upper west, lower west and south coasts of Western Australia (WA). The common depth range of this species is 100–300 m (grey shading).

used to estimate the weights of specimens that were unable to be sampled whole (Quinn and Deriso, 1999).

Age and growth

The sagittae of each *H. octofasciatus* were removed, cleaned and stored dry. The right sagitta of each fish was embedded in epoxy resin and sectioned transversely through the primordium in a direction perpendicular to the sulcus acusticus, using a low speed saw with a diamond tipped blade. Otolith sections were cut thinly, i.e. 0.11–0.15 mm, to improve growth zone clarity. Sections were mounted on glass slides with a cover slip using casting resin. The opaque zones on each otolith section were counted along an axis from the primordium to the crista superior (dorsal rim of the sulcus acusticus) under reflected light at x20 to x40 magnification, without any knowledge of the size of the fish from which they had been derived.

Bomb radiocarbon dating has been used to validate that a single opaque zone is deposited annually, and thus opaque zone counts from otolith sections can be used for determining ages of *H. octofasciatus* (Andrews *et al.*, 2011). The primary reader (CBW) examined each otolith section ($n = 418$), while a secondary reader (SJN) examined a subsample of these sections ($n = 108$). To establish the level of confidence that can be placed in the interpretation of the otolith structure, the precision of counts between readers was assessed using the Index of Average Percent Error (IAPE, Beamish and Fournier, 1981).

The age of each *H. octofasciatus* was estimated using a combination of the birth date, the time of year when the opaque zones on the otoliths of the majority of *H. octofasciatus* became delineated, and the number of opaque zones. The birth date of *H. octofasciatus* was considered to be the approximate onset of peak spawning (1 November), as determined from the annual trends in gonadosomatic indices (GSIs) for the tropical region.

Trends in the growth of female *H. octofasciatus* in both tropical and temperate waters were determined from the mean length at each year of age. A von Bertalanffy growth equation was fitted to the lengths at ages of individual fish, such that

$$L_t = L_\infty(1 - \exp^{-k(t-t_0)}),$$

where L_t = the predicted mean total length (mm) of fish at age t (years), L_∞ = asymptotic mean length (mm), k = the growth coefficient (year^{-1}), t = estimated age (years), and t_0 = the hypothetical age (years) at which fish would have zero length. The von Bertalanffy growth curves of females were compared between the tropical and temperate regions using a likelihood ratio test (Cerrato, 1990). The mean length of males (only recorded in the tropical region) was not positively correlated with age, and the distributions of their lengths at each age were comparable with those of females across the same age range. It is therefore likely that the growth of males is a continuation from that of females, and thus a von Bertalanffy growth curve was also fitted to the lengths-at-age of both sexes combined in the tropical region. A growth equation that combines data for both sexes would theoretically provide a better description of the length-at-age of older age classes and be more suitable for population model assessments. A comparison of available log-transformed weight–length data between tropical and temperate *H. octofasciatus* was also undertaken using analysis of covariance (ANCOVA) to evaluate if there was sufficient evidence to reject the null hypothesis of there being no difference in relative

condition between regions. Mean-square error terms derived from simple linear regressions were compared using Cochran's C test for homogeneity of error variances. Owing to heterogeneous residual variances (Cochran's $C = 0.70$ with 124 degrees of freedom), comparisons of groups with uneven sample sizes were made using Type III sums of squares.

Reproduction

The gonads of each fish were removed and weighed (W_G) to the nearest 0.01 g. Gonads were macroscopically classed as ovaries, testes or indeterminate. All ovaries were assigned a macroscopic stage based on Wakefield *et al.* (2010): I, immature/resting; II, developing; III, developed; IV, ripe/spawning; V, spent. GSIs were calculated for females with a total length greater than or equal to the length at 50% maturity ($L_T \geq L_{M50}$) using the equation:

$$\text{GSI} = 100(W_G/W_W).$$

Data for GSIs were pooled for each calendar month for tropical and temperate regions separately. Spawning periods of female *H. octofasciatus* were assessed for the two regions using annual trends in mean monthly GSIs and macroscopically staged ovaries.

Freshly dissected gonads were preserved in pH neutral 10% buffered formalin for investigating histological characteristics relating to ovarian development and suspected protogynous hermaphroditism for a subsample of specimens ($n = 61$), which included many of the gonads categorized as indeterminate. This was done to confirm the sex and developmental stage assigned to gonads macroscopically ($n = 500$). Medial transverse sections of the preserved gonads were embedded in paraffin wax, sectioned at 5 μm , mounted on slides, and stained with Mayer's haematoxylin and eosin. Ovarian developmental stages were assessed microscopically from the identification of the most developed oocytes (Yamamoto *et al.*, 1965; Wallace and Selman, 1981) and other relevant structures, such as the structural appearance of lamellae, thickness of the ovarian wall, intra-lamellar stromal tissue, atretic oocytes, brown bodies and postovulatory follicles, consistent with Burton *et al.* (1997), Bean *et al.* (2003) and Marriott *et al.* (2010). Gonads were classified as "transitional" *sensu* Sadovy de Mitcheson and Liu (2008) if they contained degenerating functional ovarian tissue (yolk granule or later stage oocytes and/or brown bodies) and developing testicular tissue (crypts comprising sperm cell stages earlier than spermatozoa) (Sadovy and Shapiro, 1987; Grier and Taylor, 1998; Sadovy de Mitcheson and Liu, 2008; Marriott *et al.*, 2010). This was consistent with an assumption that the presence of spermatozoa would indicate a functional testis, i.e. a male was ready to spawn or in the act of spawning and thus had completed the sex transition. Gonads were categorized as "bisexual" *sensu* Sadovy de Mitcheson and Liu (2008) if they contained both immature ovarian (previtellogenic oocytes) and testicular tissue (sperm cell stages earlier than spermatozoa), which does not indicate function of either sex. Additional microscopic evidence of suspected protogynous sex transition was the detection of vestigial ovarian structure and/or sperm sinuses in testes (Sadovy and Shapiro, 1987).

Estimates of sexual maturity and sex change

The lengths at which female *H. octofasciatus* from the northern tropical waters reached maturity were determined using data from the months when spawning occurred, i.e. mean monthly GSI > 1.5, and when some fish contained developing, developed,

spawning or spent gonads (Stages II–V). The lengths at which 50% of female *H. octofasciatus* attained sexual maturity (L_{M50}) were determined using a reparameterized form of the logistic equation (e.g. Punt and Kennedy, 1997; Hesp et al., 2004; Wakefield et al., 2007), to describe the relationship with length of the probability that a fish during the spawning period possessed gonads at Stages II–V. Therefore, it was assumed that during the spawning period, fish with gonads of these stages would have had the potential to spawn, were spawning or had recently spawned, and that fish with gonads at Stage I would have remained immature. The reparameterized logistic equation used was:

$$P_L = \left\{ 1 + \exp\left[-\log_e(19)(L_T - L_{M50}) / (L_{M95} - L_{M50})\right] \right\}^{-1},$$

where P_L = the proportion of mature *H. octofasciatus* at a particular total length L_T and L_{M50} and L_{M95} the estimated total lengths in mm at which 50% and 95% of female *H. octofasciatus*, respectively, attained sexual maturity. This logistic equation was fitted by maximizing the sum of the log-likelihoods such that, on the basis of its L_T , an immature (Stage I) fish would have a likelihood of P_L and a mature (Stages II–V) fish a likelihood of $1 - P_L$. Values of the L_{M50} and L_{M95} and their 95% confidence intervals were determined by bootstrapping, with replacement, each dataset to generate 2000 estimates of the parameters of the logistic equation. The parameters and 95% confidence intervals (CI) for the reparameterized logistic equation were calculated as the median, upper and lower 2.5 percentiles of the 2000 bootstrap estimates of each length class. Estimates of the length at which *H. octofasciatus* from the northern tropical waters changed sex were calculated using the same equation as above, but with the lengths at which 50% and 95% of individuals had become male, i.e. L_{S50} and L_{S95} , substituted for L_{M50} and L_{M95} , respectively. The proportions of females to males with increasing age were determined, but the age at which 50% of *H. octofasciatus* changed sex was not estimated, as the rate of change did not have a logistic trend.

Results

Length and age compositions, ageing precision and growth

In total, 162 females and 43 males were collected from the tropical region of Western Australia, compared with 295 females and no males from the temperate region. The relationship between total length (mm) and weight (g) was described using the equation:

$$W_W = 0.00001356L_T^{3.03} (n = 156, r^2 = 0.99).$$

All fish < 700 mm L_T from the tropical region were female (Figure 2). In this region the length composition of females was essentially unimodal at 750–799 mm L_T and ranged in length from 72–1509 mm L_T (Figure 2). The length composition of male *H. octofasciatus* from this region was also unimodal but at a larger size (1150–1199 mm L_T) and had a length range from 700–1385 mm L_T (Figure 2). In comparison, the unimodal length–frequency distribution of females from the temperate region (range, 262–1230 mm L_T) occurred at a slightly smaller mode, (600–649 mm L_T), compared to that of females from the tropical region (Figure 2).

Growth increments were visible as alternating translucent and opaque bands in sectioned otoliths when viewed under reflected light. One translucent followed by one opaque band was

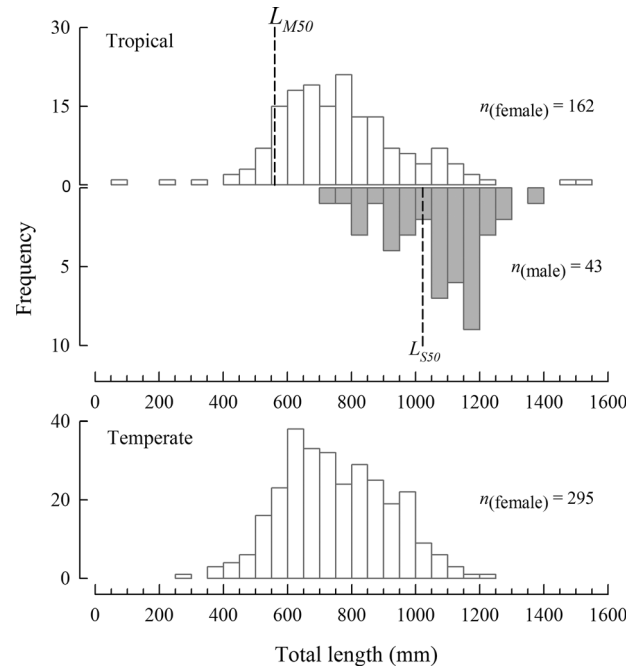


Figure 2. Length-frequency histograms for females (white bars) and males (grey bars) of *Hyporthodus octofasciatus* from the tropical region (above) and females only from the temperate region (below) of Western Australia (sample sizes shown, n). The dashed lines represent the corresponding lengths at 50% maturity for females (560 mm, L_{M50} , see Figure 7) and sex change to males (1022 mm, L_{S50} , see Figure 8) for the tropical region.

considered to represent growth over 12 months following age validation results from bomb radiocarbon analysis (Andrews et al., 2011). The IAPE between the counts of annuli from two readers was 4.9%. Annuli counts by the secondary reader for the randomly selected subset of otoliths concurred with 40% of the counts made by the primary reader. No annuli counts by the secondary reader differed by more than two from the primary reader.

The age of *H. octofasciatus* from the tropical region ranged from 0.7–46.6 years for females and 11.2–38.6 years for males (Figure 3). The age composition of females from this region increased from one individual in the 1+ age class to a maximum of 14 fish in the 9+ age class, before gradually declining in frequency through older ages (Figure 3). The maximum frequency of male *H. octofasciatus* in this region occurred at an older age with five fish recorded in the 19+ age class. In comparison, the age-frequency distribution of females from the temperate region peaked at a younger age (6+ age class) and frequencies in older age groups declined faster to a longevity of less than half that of the tropical region (i.e. 20.4 years, Figure 3). The youngest recorded female from the temperate region was 3.2 years. A smaller female at 262 mm L_T was sampled from the temperate region, however otoliths were not obtained and thus an age of ~16 months was estimated from the von Bertalanffy growth equation.

The mean total length of females from the tropical region increased from 517 mm at five years to 952 mm at 16 years (39.5 mm year⁻¹), with very little increase, typical of an asymptote, displayed after this age, e.g. mean L_T of 922 mm at 30 years (Figure 4). The mean length of females from the temperate region increased relatively linearly with age from 491 mm at four

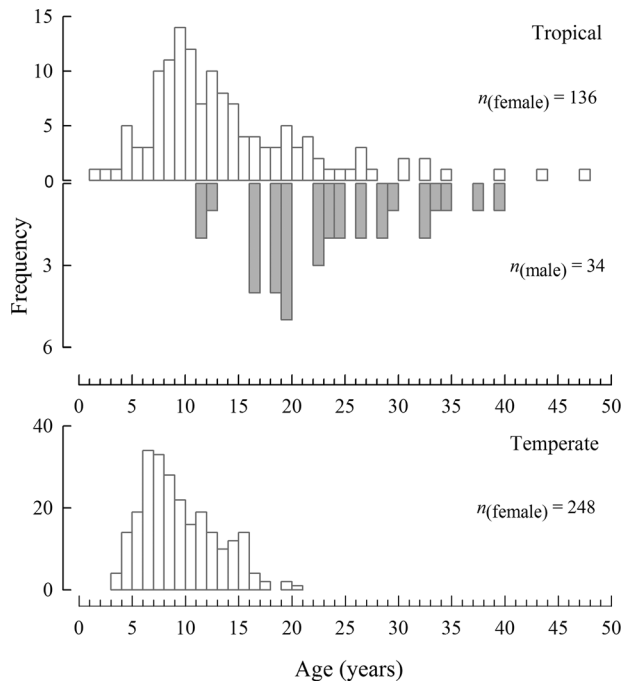


Figure 3. Age–frequency histograms for females (white bars) and males (grey bars) of *Hyporthodus octofasciatus* from the tropical region (above) and females only from the temperate region (below) of Western Australia (sample sizes shown, *n*).

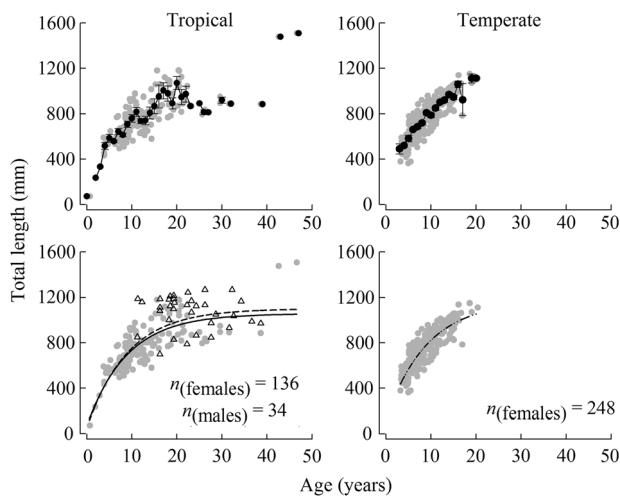


Figure 4. Mean length-at-age (± 1 s.e., above) and age–length relationships (below) fitted with von Bertalanffy growth curves for females (grey circles) of *Hyporthodus octofasciatus* from the tropical (left, solid line) and temperate (right) regions of Western Australia (sample sizes shown, *n*). Males (triangles, bottom left) were only recorded in the tropical region and have been combined with females in a second von Bertalanffy growth curve (dashed line).

years to 1059 mm at 16 years ($47.3 \text{ mm year}^{-1}$, Figure 4). As only three individual females > 17 years were recorded in that region, the trend in the mean length above that age was uncertain. The von Bertalanffy growth curves of females from the tropical and

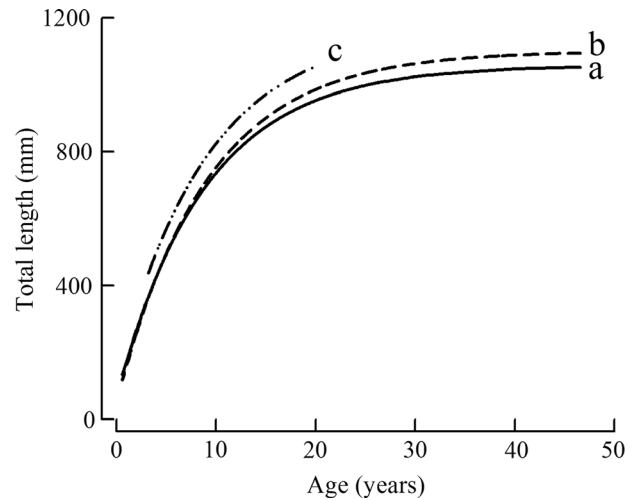


Figure 5. Comparison of von Bertalanffy growth curves of female *Hyporthodus octofasciatus* from the tropical region (a, solid line), females and males combined from the tropical region (b, dashed line) and females from the temperate region (c, dash-dot line) of Western Australia.

temperate regions were significantly different ($P < 0.001$, Figure 5, Table 1). However, there was insufficient evidence to reject the null hypothesis of there being no difference in the relative condition of *H. octofasciatus* between regions, from comparing the slopes ($F_{1,155} = 0.56$, $p = 0.46$) and intercepts ($F_{1,155} = 0.93$, $p = 0.34$) of the log-transformed linear weight on length relationships. The estimated L_T from the von Bertalanffy equations attained by females at ages 5, 10 and 15 years, from the tropical region were 502, 744 and 868 mm, compared with 569, 825 and 964 mm, respectively, from the temperate region. On average, the difference in the lengths of females from the temperate region, estimated from those curves, was always $\geq 9\%$ larger than that of the tropical region between the ages of two and 17 years, which were the ages best represented in the samples (Figure 5).

Spawning period

The mean monthly GSIs for female *H. octofasciatus* \geq the L_{M50} from the tropical region of Western Australia was relatively low (< 1.0) from June through August (Figure 6). The first appearance of gonadal recrudescence (Stages II and III) occurred in October and was accompanied by an increase in GSI to $1.7 (\pm 0.3 \text{ se})$, Figure 6). Note, it is possible that gonad development commenced one month earlier in September, but no samples were collected for that month. The highest mean monthly GSIs were recorded during November and January at ca 2.5 before declining to $1.7 (\pm 0.3 \text{ se})$ in February and to < 1.0 in both March and April (Figure 6). Ovaries containing hydrated oocytes (Stage IV) were recorded from October to February, with gonadal regression (Stage V) most prevalent in February and March. In contrast, mean monthly GSIs of female *H. octofasciatus* caught in the temperate region of Western Australia were less than 0.31 for all months of the year (Figure 6). Ovaries of all fish from the temperate region were always recorded as immature/resting (Stage I).

Maturity and sex change

On the basis of their macroscopic appearance, the smallest mature (Stage II–V) female sampled from the tropical region during the

Table 1. Comparison of von Bertalanffy growth parameters (L_{∞} , k , t_0), mortality estimates (Z , M , F), longevity and method of growth determination for the 14 species that comprise the monophyletic clade of the deep bodied grouper genus *Hyporthodus* in the Epinephelidae (Craig et al., 2011).

Species	Growth parameters			Mortality estimates			Max. Longevity (year)	Method of Ageing	Reproductive mode	Locality	Reference	IUCN Red List Classification
	L_{∞} (mm)	k (yr^{-1})	t_0 (yr)	Z	M	F						
<i>Hyporthodus acanthistius</i> (Gilbert, 1892)												Least concern
<i>Hyporthodus darwinensis</i> (Randall and Heemstra, 1991)												Data deficient
<i>Hyporthodus ergastularius</i> (Whitley, 1930)												Least concern
<i>Hyporthodus exsul</i> (Fowler, 1944)												Data deficient
<i>Hyporthodus flavolimbatu</i> s (Poey, 1865)												Vulnerable
	891	0.163					15		Prot. H.	South Carolina	(Keener, 1984)	
	831	0.191					27	TS		E Gulf of Mexico	(Bullock and Godcharles, 1984)	
									Prot. H.		(Bullock et al., 1996)	
	963	0.099	-0.08				35	TS		Trinidad & Tobago	(Manickchand-Heileman and Phillip, 2000)	
									Prot. H.		(Musick et al., 2000)	
							85	TS (B)		Gulf of Mexico	(Cook et al., 2009)	
<i>Hyporthodus haifensis</i> (Ben-Tuvia, 1953)												Data deficient
<i>Hyporthodus mystacinus</i> (Poey, 1852)												Least concern
					0.14							(Craig et al., 2011)
<i>Hyporthodus nigritus</i> (Holbrook, 1855)												Critically endangered
	2394	0.1156	-0.927				41	TS				(Manooch and Mason, 1987)
									Prot. H.		(Parker and Mays, 1998)	
									Prot. H.		(Musick et al., 2000)	
<i>Hyporthodus niphobles</i> (Gilbert and Starks, 1897)												Data deficient
<i>Hyporthodus niveatus</i> (Valenciennes, 1828)												Vulnerable
	1320	0.087	-1.013	0.175 ^a			27	TS	Prot. H.	Florida Keys	(Moore and Labisky, 1984)	
	1255	0.074	-1.92		0.15		25	TS		S Atlantic Bight	(Matheson and Huntsman, 1984)	
1993–1994 (com. SR)	1201	0.103	-1.149				29	TS	Prot. H.	N & S Carolina	(Wyanski et al., 2000)	
1982–1985 (res.)	948	0.122	-0.668					TS		N & S Carolina	(Wyanski et al., 2000)	
1993–1996 (com. LL)	1117	0.119	-1.1409					TS		N & S Carolina	(Wyanski et al., 2000)	
									Prot. H.		(Musick et al., 2000)	
<i>Hyporthodus octofasciatus</i> (Griffin, 1926)												Data deficient
Tropical (♀)	1057	0.11	-0.59		0.09		47	TS	Prot. H.	Western Australia	This study	
Tropical (comb)	1100	0.11	-0.41		0.09		47	TS		Western Australia	This study	
Temperate (♀)	1166	0.11	-1.00				20	TS		Western Australia	This study	
							43	TS (B)		Western Australia	(Andrews et al., 2011)	
<i>Hyporthodus perplexus</i> (Randall, Hoese & Last, 1991)												Data deficient
<i>Hyporthodus quernus</i> (Seale, 1901)												Near threatened
	1080–1186	0.119–0.126		0.233–					Prot. H.		(Craig et al., 2011)	
				0.253 ^b						Hawaii	(Moffitt, 2006)	
	823	0.157	-1.45				34	TS			(Nichols and DeMartini, 2008)	
<i>Hyporthodus septemfasciatus</i> (Thunberg, 1793)												Least concern
									Prot. H.		(Craig et al., 2011)	

TS = transverse sections, B = bomb radiocarbon dating used to validate age estimates derived from transverse sections of otoliths, comb = sexes combined, ♀ = female, Prot. H. = protogynous hermaphrodite, a = estimates of total mortality Z, derived from catch curves, b = estimates of natural mortality, M, derived mainly from the equation of Ralston (1987), com. SR = commercial snapper reels, res. = research surveys, comm. LL = commercial longline.

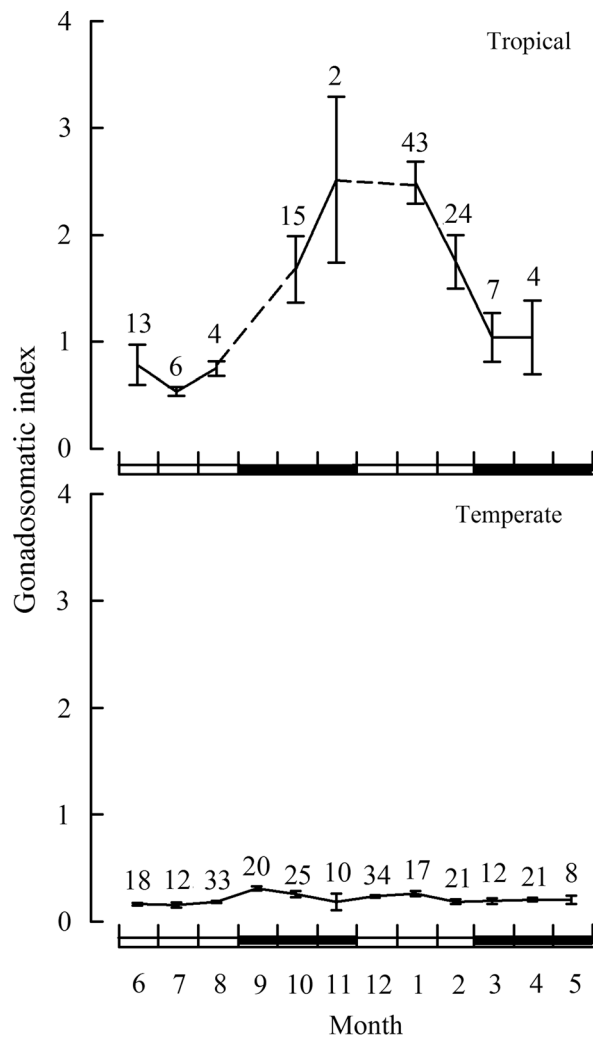


Figure 6. Mean monthly gonadosomatic indices (GSI, \pm 1 s.e.) of female *Hyporthodus octofasciatus* from the tropical and temperate regions of Western Australia. The data have been pooled for corresponding months (sample sizes shown) and are limited to fish \geq the length at 50% maturity of 560 mm (L_{M50} , see Figure 7). On the x-axis, white rectangles represent winter and summer, and black rectangles spring and autumn.

spawning season measured 495 mm L_T (Figure 7), and the youngest such female was 6 years of age. The proportion of mature females from this region increased from 50% in the 400–499 mm length class, to > 65% in the 500–899 mm length classes and 100% in fish \geq 900 mm L_T (Figure 7). The estimated length at which 50% and 95% of *H. octofasciatus* attain maturity in the tropical region was 560 and 900 mm L_B , respectively (Figure 7). The estimated ages from the von Bertalanffy growth equation (see below) at which *H. octofasciatus* reaches these lengths at maturity in the tropical region were 6.1 and 16.4 years, respectively. No mature (Stage II–V) females were recorded in the temperate region.

Microscopic examination of gonads was consistent with the conclusions of no males and an absence of evidence for spawning in the temperate region, although the number of specimens analysed from the temperate region was small ($n = 6$). Only inactive ovaries were observed, which were staged as either immature ($n = 2$) or inactive ($n = 4$). Immature ovaries were characterized

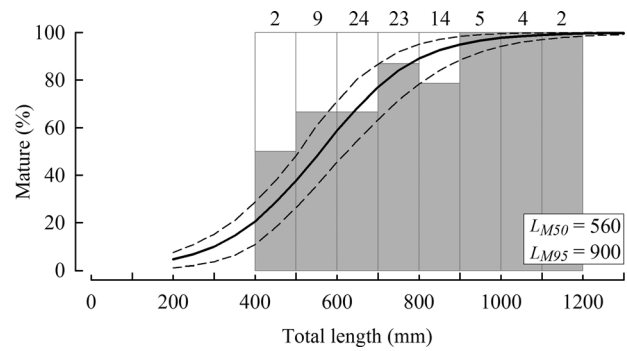


Figure 7. Percentage-frequency of immature (Stage I, white bars) and mature (Stages II–V, grey bars) females of *Hyporthodus octofasciatus* in sequential 100-mm length classes (< 1300 mm L_T) collected during the spawning months (October–February) from the tropical region of Western Australia (sample sizes noted above histograms). The logistic curve (solid line) and its 95% CI (dashed lines) represent the expected percentage of mature females at corresponding lengths.

by long thin lamellae that were densely packed with previtellogenic oocytes and relatively thin ovarian walls (Figure 8a). Inactive ovaries were characterized by a marked thickening in the ovarian wall, thicker and more prevalent eosinophilic intra-lamellar stromal strands, and lamellae that were less densely packed with previtellogenic oocytes and not as long and thin and more irregular than in immature ovaries (Figure 8b). Owing to the small number of samples examined histologically for the temperate region and the absence of definitive characteristics indicating prior spawning (e.g. brown bodies or atretic oocytes), it was not possible to identify with certainty any mature ovaries in that region. For tropical samples, asynchronous oocyte development was observed in developing ($n = 2$), developed ($n = 10$, Figure 8c), and spawning ($n = 14$) ovaries. Spawning ovaries were characterized by the presence of hydrated oocytes and/or postovulatory follicles (Figure 8d).

The proportion of males in samples from the tropical region increased with length and age (Figure 9). Given the observed length (72–1509 mm L_T) and age range (0.7–46.6 years) for the tropical region in this study, the fact that males were not sampled until 700 mm L_T and 11.2 years of age, which were greater than the L_{M50} of 560 mm and derived age at maturity of 6.1 years, respectively, is a good indication of monandric protogyny. The estimated lengths at which 50% and 95% of *H. octofasciatus* transitioned to male in the tropical region were 1022 and 1276 mm L_B , respectively (Figure 9).

Gonads of two individuals that were sectioned histologically contained both ovarian and testicular tissue that were intermixed on lamellar structures and were thus of the undelimited Type Two arrangement (Sadovy and Shapiro, 1987). The lamellae of one of those gonads comprised (degenerating) previtellogenic oocytes and both spermatogonia and spermatocytes in crypts, i.e. immature testicular tissue *sensu* Grier and Taylor (1998, Figure 10a). This individual was thus classified as bisexual. The lamellae of the other gonad were primarily comprised of testicular tissue, i.e. spermatocytes and spermatids, in conjunction with degenerating previtellogenic oocytes and also brown bodies (Figure 10b). Brown bodies provided evidence of previous ovarian function. This gonad was presumably at a late stage of

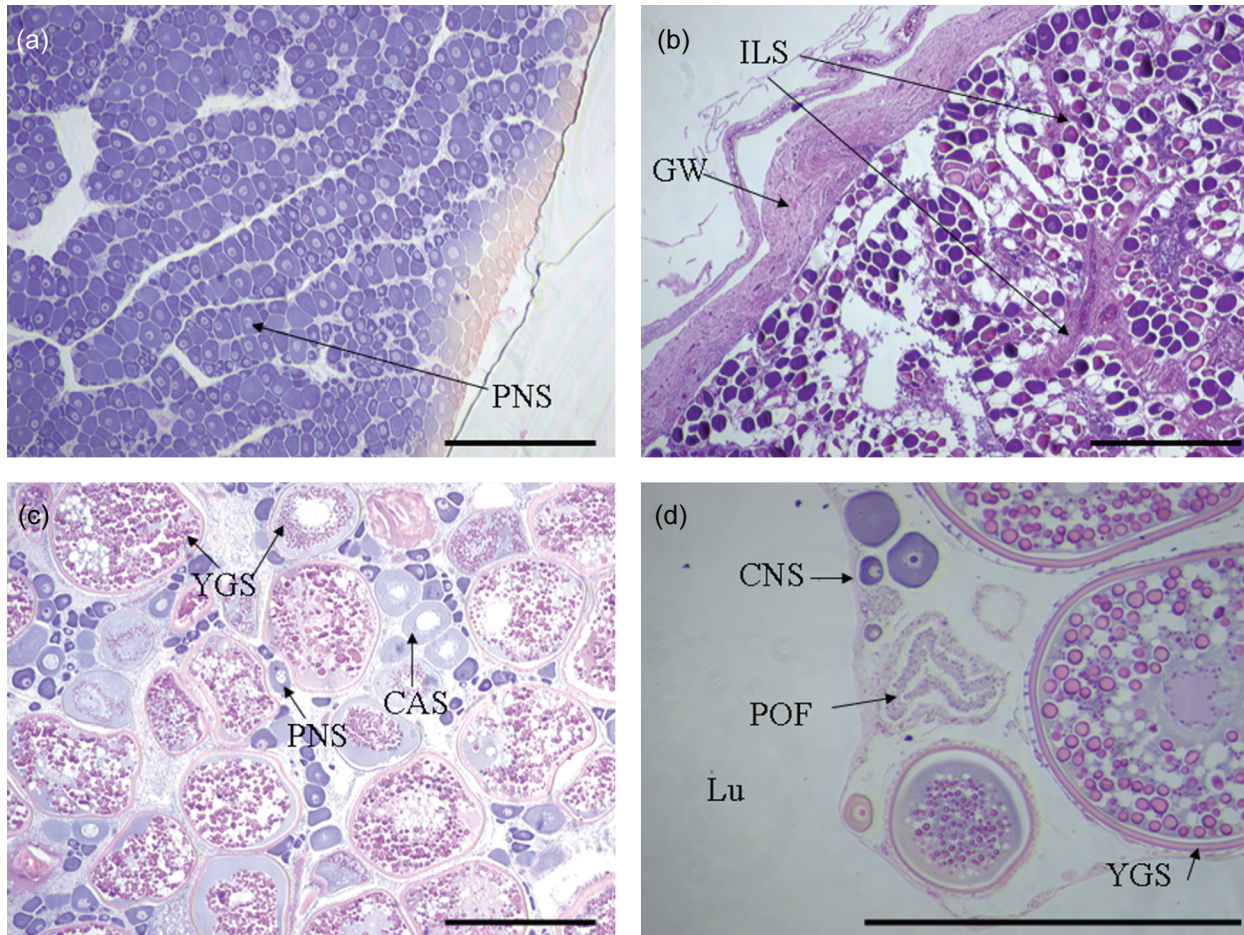


Figure 8. Histological features of ovarian development of *Hyporthodus octofasciatus* from tropical (a, c, d) and temperate (b) regions. a) Immature ovary from an individual measuring 559 mm in total length; b) inactive ovary from an individual measuring 817 mm and 10 years of age; c) developed ovary from an individual measuring 562 mm and 10 years of age; d) spawning ovary from an individual measuring 1180 mm and 15 years of age. CAS = cortical alveoli stage oocytes, CNS = chromatin nucleolus stage oocytes, GW = gonad wall, ILS = intra-lamellar stromal strands, Lu = lumen, PNS = perinucleolus stage oocytes, POF = postovulatory follicle, YGS = yolk globule stage oocytes (scale bar: 500 μm).

functional protogynous sex change and was categorized as transitional. Degenerating previtellogenic oocytes (Figure 10c) and brown bodies (Figure 10d) were also observed in functional testes, which exhibited spermatozoa located in sperm sinuses in the outer gonad wall, indicating further evidence in support of protogyny. All of the testes examined histologically contained a vestigial ventral *in situ* ovarian lumen, while mature testes also contained peripheral sperm sinuses in their gonad wall (Figure 10e).

Discussion

Rarely do studies on the age, growth and reproduction of a teleost span such a large latitudinal distribution as that covered in this study of *H. octofasciatus*. This species was sampled from the upper continental slope at depths of 105–480 m, over an exceptionally large latitudinal range (12–35°S) spanning tropical and temperate waters along the Western Australian coast (ca 3500 km). This is the first study investigating the life history characteristics of this species and thus could contribute towards the revision of its IUCN red list status from “Data Deficient” (To and Pollard, 2008). Further, the results of this study, in association with those from other species of the genus *Hyporthodus*, allow us to characterize the likely population parameters for this data-

limited group and to construct a general risk profile for this species in light of the potential for ongoing and increased rates of exploitation. Individuals of *H. octofasciatus* in samples reached a relatively large size (maximum 1509 mm L_T , estimated weight 66.5 kg), which combined with an excellent palatability increases their value among commercial and recreational anglers. Results on the life history characteristics of this species, and observed latitudinal variation throughout its range will therefore add to critical knowledge requirements for managing its harvest by all fishing sectors.

Age, growth and longevity

Ageing precision of *H. octofasciatus* based on counts of opaque zones from thin otolith sections were found to be within acceptable bounds, i.e. IAPE < 5.5% (Campana, 2001), but slightly less precise than other deep-water species (e.g. Wakefield et al., 2010). Both the mean length at each age and estimated lengths-at-age of females from the von Bertalanffy equation were markedly higher (>9%) in the temperate region. It is uncertain whether this larger length-at-age at higher latitudes represents the temperature-size relationship expressed by ectotherms in accordance with certain ecological theories (e.g. Metabolic Theory of Ecology,

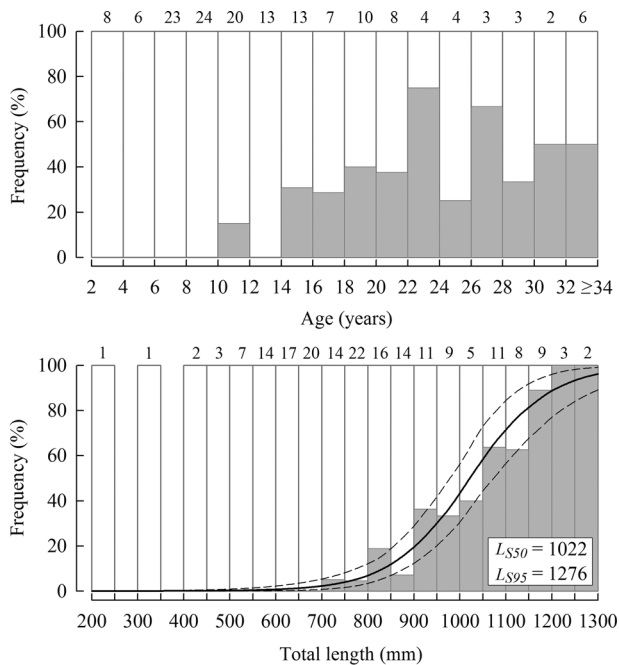


Figure 9. Percentage-frequency of female (white bars) and male (grey bars) *Hyporthodus octofasciatus* in two-year age-class categories (above) and sequential 50-mm length classes (<1300 mm L_T , below) from the tropical region of Western Australia (sample sizes noted above histograms). The logistic curve (solid line) and its 95% CI (dashed lines) represent the expected percentage of males at corresponding lengths.

MTE, Atkinson, 1994; Arendt, 2010), or a result of energy partitioned toward growth in the absence of reproduction. The larger length-at-age of *H. octofasciatus* at higher latitudes is consistent with the growth patterns expressed by many teleosts along the Western Australian coastline, all of which are reproductively active (e.g. Cossington *et al.*, 2010; Lek *et al.*, 2012). In contrast, a parabolic relationship between length-at-age and water temperature (latitude) is expressed by *Pagrus auratus*, where a greater length-at-age is attained at the centre of its latitudinal distribution in Australia and New Zealand with reduced performance occurring towards the ends of that range (Wakefield, 2006). It cannot be ruled out that *H. octofasciatus* achieved a greater length-at-age in the temperate region as a result of energy partitioned toward growth in the absence of reproduction considering the mean length-at-age in the temperate region was conspicuously linear through all ages sampled, which extended past the ages at which this species matured in the tropical region. These varying growth trajectories for *H. octofasciatus* are consistent with that described by Lester *et al.* (2004), who postulated that growth of teleosts is best described using two models, reflecting two subsequent life history stages. This growth model proposed that prior to maturation somatic growth is relatively linear, and that the von Bertalanffy growth equation is more appropriate for describing post-maturational growth (Lester *et al.*, 2004).

Longevity estimates were more than twice that observed for the northern tropical than southern temperate region (i.e. 47 vs. 20). This trend contradicts the positive correlations that have been demonstrated between longevity and water temperature in accordance with the MTE (Munch and Salinas, 2009). The latitudinal trend in longevity recorded for *H. octofasciatus* in Western

Australia may be explained by the fact that settlement and survival of recruits in the southern temperate waters are reliant on spawning and transport from northern tropical waters, and thus subject to relatively large variations in environmental conditions. If the age structure of *H. octofasciatus* in the southern waters of Western Australia is a good indication of recruitment success, their consistent abundance in recent cohorts suggests conditions have been favourable since the early 1980s. It is possible that recent warming trends in water temperatures along the lower west coast of Western Australia since the 1950s, particularly during the austral autumn–winter, may have improved the chances of *H. octofasciatus* settling and surviving in more southern temperate waters in recent years (Pearce and Feng, 2007; Caputi *et al.*, 2009). The maximum longevity of 47 years for *H. octofasciatus* in this study is similar to that of other *Hyporthodus* species (e.g. Manooch and Mason, 1987; Manickchand-Heileman and Phillip, 2000; Wyanski *et al.*, 2000), but only about half that recorded for *H. flavolimbatus* from the Gulf of Mexico (e.g. 85 years, Table 1, Cook *et al.*, 2009).

Reproductive mode

Multiple macroscopic and microscopic characteristics of sampled gonads were used to determine the reproductive mode of *H. octofasciatus* (Sadovy and Shapiro, 1987; Sadovy de Mitcheson and Liu, 2008). In the tropical waters of Western Australia all *H. octofasciatus* < 700 mm L_T and 11 years of age were females. The length and age of the smallest and youngest male (700 mm L_T and 11.2 years) were much greater than the length at which 50% of females reached maturity ($L_{M50} = 560$ mm L_T) and the estimated age at which this occurred (6.1 years). The prevalence of males increased with increasing length, to essentially 100% of the largest fish collected (1200–1300 mm L_T). Although males were present in almost all age classes above 10 years in tropical waters, females were recorded in some of the oldest age classes, indicating that not all females change to male. Further sampling of the upper age range would help determine such prevalences. Microscopic examination of gonads sampled from the northern tropical waters identified one individual undergoing protogynous sex transition, which was evident from the presence of both degenerating female (previtellogenic oocytes and brown bodies) and developing male (germ cell stages less advanced than spermatozoa) characteristics in the gonads. Further, all testes of this species possessed a central lumen, and mature testes often contained spermatozoa located in sperm sinuses in the gonad wall. The combination of the above lines of evidence is consistent with monandric protogynous hermaphroditism, whereby all males are derived from mature females. This reproductive mode appears to be consistent among the *Hyporthodus* genus (e.g. Heemstra and Randall, 1993; Wyanski *et al.*, 2000). On this basis, the length at which 50% of *H. octofasciatus* change sex is ca 1022 mm L_T and ≥ 11 years of age.

Reproductive period and spawning omission in the temperate region

The spawning period of *H. octofasciatus* was determined from trends exhibited throughout the year by the prevalence of stages in gonad development and the mean monthly GSIs. Individuals in spawning condition were only recorded in the northern tropical region, where the majority of spawning occurred during the austral spring and summer from October to February.

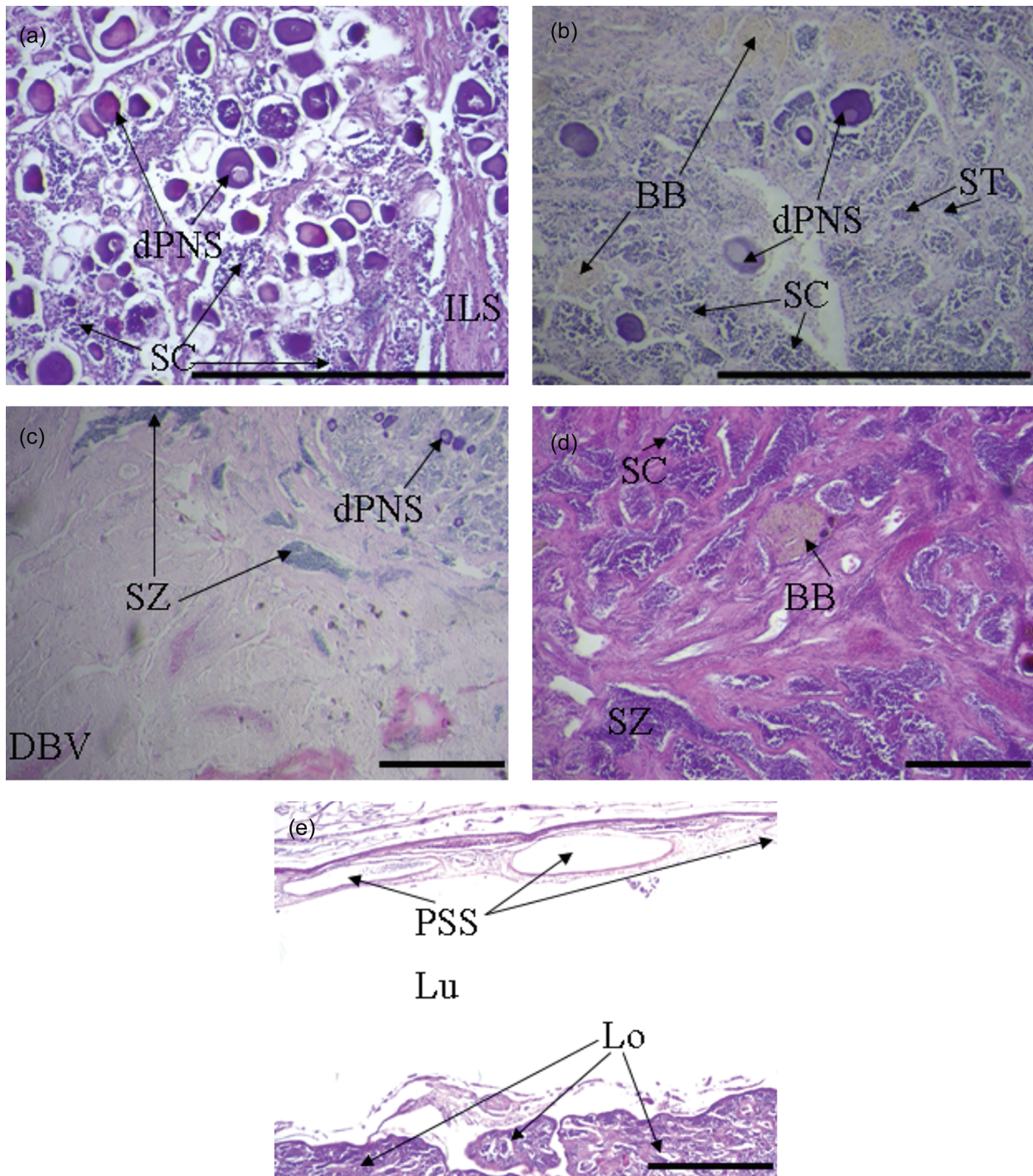


Figure 10. Histological evidence for protogynous sex change. a) Bisexual gonad comprised primarily of ovarian tissue with developing crypts of spermatocytes from an individual measuring 1177 mm and 20 years of age; b) transitional gonad showing signs of previous reproductive activity as a female by the presence of brown bodies, degenerating previtellogenic oocytes from an individual measuring 847 mm and 27 years of age; c) functional testis with small number of degenerating previtellogenic oocytes from an individual measuring 1082 mm and 16 years of age; d) testis containing brown bodies from an individual measuring 905 mm and 21 years of age; e) testis in (d) showing vestigial ovarian lumen with peripheral sperm sinus on the ventral side of the gonad. BB = brown body, CAS = cortical alveoli stage oocytes, DBV = dorsal blood vessel, dPNS = degenerating perinucleolus stage oocytes, ILS = intra-lamellar stromal strands, Lo = lobular tissue containing developing sperm, Lu = lumen, PSS = peripheral sperm sinus, SC = spermatocytes, ST = spermatids, SZ = spermatozoa (scale bar: 500 μm).

Reproductive characteristics of *H. octofasciatus* in southern temperate waters varied significantly from those observed in northern tropical waters in a manner that suggested no evidence

of reproduction south of ca 30°S in WA. Both macroscopic and microscopic examination of gonads revealed all *H. octofasciatus* sampled in the temperate region were immature or inactive

(Stage I) females. For inactive ovaries, there was no definitive histological evidence to indicate that any of these females had previously matured and spawned. In addition, the mean monthly GSIs were always lower than those recorded for any month in the tropical region where a spawning season was clearly identified. Monthly sample sizes of *H. octofasciatus* (collected throughout all months of the year) included a wide length (262–1230 mm L_T) and age range (3.2–20.4 years), and were thus considered to provide an adequate representation of seasonal reproductive activity for the temperate region. That a much smaller number of fish sampled from the tropical region were sufficient to demonstrate a seasonal pattern in reproduction lends further support to the observed lack of seasonal reproductive activity for the temperate region.

Reproductive seasonality in teleosts is common, with the primary environmental cues for spawning (or gonadal recrudescence) suggested to be water temperature and photoperiod (Pankhurst and Porter, 2003; Wakefield, 2010). Given the apparent spawning omission for *H. octofasciatus* in temperate waters, and considering this species spawns only during the warmer months, i.e. spring and summer, in the tropical region, it is expected that spawning of this species could be temperature-dependent. In which case, the annual maximum water temperatures in the temperate region may be lower than the threshold required for gonad recrudescence. Unfortunately, water temperature data from the depths occupied by this species in the tropical waters of Western Australia are currently unavailable. Therefore, the relationship between water temperature and reproduction in this poikilotherm could not be assessed. Further investigation into correlations between reproduction and environmental variables is required to elucidate the potential mechanisms influencing the spawning omission of *H. octofasciatus* at higher latitudes.

Management implications

Hyporthodus octofasciatus is part of the deep-water fish complex inhabiting the upper continental slope (typically >200 m depth) across all management Bioregions in Western Australia. Due to its high value, wide distribution and high inherent vulnerability this species has been selected as an indicator species for this suite of offshore demersal scalefish in all marine bioregions of the state (Department of Fisheries, 2011). This species, like others inhabiting relatively deep continental slope waters, and the majority of groupers in general, is long-lived, slow growing and has low rates of natural mortality (Morato *et al.*, 2006; Wakefield *et al.*, 2010; Sadovy de Mitcheson *et al.*, 2012). As such, the inherent vulnerability of this species is relatively high and the sustainable level of fishing exploitation is likely to be relatively low. Considering the depths this species inhabits, traditional management strategies such as bag, boat and size limits for single species within a multi-species fishery are not likely to be effective given the likely high rate of mortality associated with barotrauma. Current management arrangements for recreational fishers in Western Australia set a combined bag limit of two fish from a list of high risk species that occupy the continental slope (offshore demersal), per recreational fishing from boat license. The State-managed commercial fisheries for demersal scalefish in Western Australia are based on limited access and annual restrictions in total catch or fishing effort allocations in the northern and western coasts (Fletcher and Santoro, 2012); however, currently the commercial take of demersal scalefish from the south coast is not subject to such fishery-specific management regulations (Fletcher and Santoro, 2012).

Hyporthodus octofasciatus is also harvested by the Commonwealth-managed Great Australian Bight Trawl Fishery and Western Deepwater Trawl Fishery that operates in waters adjacent to, or overlapping, the west and south coast State-managed fisheries in depths between 200 m and the Australian Fishing Zone boundary. Thus, future stock assessments for this species need to consider catch and effort statistics from both State and Commonwealth fisheries, as they are all likely to be harvesting the same stock.

The apparent spawning omission of *H. octofasciatus* in the temperate waters of Western Australia suggests that recruits to this region are most likely originating from spawning in the northern tropical waters, with progeny transported southward by the dominant poleward-flowing Leeuwin current (Caputi *et al.*, 1996). If this is the case, then fishing exploitation of this species in the temperate region poses little risk to the breeding stock levels of the population. However, a higher emphasis may need to be placed on conserving spawning stocks in the northern tropical region to maintain the recruitment source for the broader Western Australian coastline. Until an improved understanding of the stock structure of *H. octofasciatus* is formed using more comprehensive methods (e.g. genetics or otolith microchemistry), the evidence provided in this study assumes the extensive distribution of *H. octofasciatus* in Western Australia represents a single population. Such limited genetic diversity has been found for other demersal species that occur along this coastline, e.g. *Glaucosoma hebraicum* (Berry *et al.*, 2012). Future monitoring and assessment programs for this species should incorporate sampling in southern waters of the state to determine if the spawning range of *H. octofasciatus* begins to extend southward, and how this relates with the long-term warming trend in water temperatures occurring in the temperate region of Western Australia (Pearce and Feng, 2007; Caputi *et al.*, 2009).

Acknowledgements

We would like to thank the crews of the RV “Flinders” and the RV “Naturaliste” and all the research staff, fishers and wholesalers across Western Australia who helped in the sourcing and collection of samples. We also thank Brett Molony and Shane O’Donoghue for providing useful comments on earlier versions of this manuscript.

Funding

We gratefully acknowledge logistical and financial support from the Department of Fisheries, Government of Western Australia.

References

- Andrews, A. H., Kalish, J. M., Newman, S. J., and Johnston, J. M. 2011. Bomb radiocarbon dating of three important reef-fish species using Indo-Pacific $\Delta^{14}\text{C}$ chronologies. *Marine and Freshwater Research*, 62: 1259–1269.
- Arendt, J. D. 2010. Size–fecundity relationships, growth trajectories, and the temperature-size rule for ectotherms. *Evolution*, 65: 43–51.
- Atkinson, D. 1994. Temperature and organism size – a biological law for ectotherms? *Advances in Ecological Research*, 25: 1–58.
- Beamish, R. J., and Fournier, D. A. 1981. A method for comparing the precision of a set of age determinations. *Canadian Journal of Fisheries and Aquatic Sciences*, 38: 982–983.
- Bean, K., Mapstone, B. D., Davies, C. R., Murchie, C. D., and Williams, A. J. 2003. Gonad development and evidence of protogyny in the red-throat emperor on the Great Barrier Reef. *Journal of Fish Biology*, 62: 299–310.

- Berry, O., England, P., Fairclough, D., Jackson, G., and Greenwood, J. I. M. 2012. Microsatellite DNA analysis and hydrodynamic modelling reveal the extent of larval transport and gene flow between management zones in an exploited marine fish (*Glaucosoma hepbraicum*). *Fisheries Oceanography*, 21: 243–254.
- Bullock, L. H., and Godcharles, M. F. 1984. Life history aspects of the yellowedge grouper, *Epinephelus flavolimbatus* (Pisces: Serranidae) from the eastern Gulf of Mexico. Marine Research Laboratories. Annual Report, Florida Department of Natural Resources. 28 pp.
- Bullock, L. H., Godcharles, M. F., and Crabtree, R. E. 1996. Reproduction of yellowedge grouper *Epinephelus flavolimbatus*, from the eastern Gulf of Mexico. *Bulletin of Marine Science*, 59: 216–224.
- Burton, M. P. M., Penney, R. M., and Biddiscombe, S. 1997. Time course of gametogenesis in Northwest Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences*, 54 (suppl. 1): 122–131.
- Campana, S. E. 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *Journal of Fish Biology*, 59: 197–242.
- Caputi, N., de Lestang, S., Feng, M., and Pearce, A. 2009. Seasonal variation in the long-term warming trend in water temperature off the Western Australian coast. *Marine and Freshwater Research*, 60: 129–139.
- Caputi, N., Fletcher, W. J., Pearce, A., and Chubb, C. F. 1996. Effect of the Leeuwin Current on the recruitment of fish and invertebrates along the Western Australian coast. *Marine and Freshwater Research*, 47: 147–155.
- Cerrato, R. M. 1990. Interpretable statistical tests for growth comparisons using parameters in the von Bertalanffy equation. *Canadian Journal of Fisheries and Aquatic Sciences*, 47: 1416–1426.
- Cook, M., Fitzhugh, G. R., and Franks, J. S. 2009. Validation of yellowedge grouper, *Epinephelus flavolimbatus*, age using nuclear bomb-produced radiocarbon. *Environmental Biology of Fishes*, 86: 461–472.
- Cossington, S., Hesp, S. A., Hall, N. G., and Potter, I. C. 2010. Growth and reproductive biology of the foxfish *Bodianus frenchii*, a very long-lived and monandric protogynous hermaphroditic labrid. *Journal of Fish Biology*, 77: 600–626.
- Craig, M. T., and Hastings, P. A. 2007. A molecular phylogeny of the groupers of the subfamily Epinephelinae (Serranidae) with a revised classification of the Epinephelini. *Ichthyological Research*, 54: 1–17.
- Craig, M. T., Sadovy de Mitcheson, Y. J., and Heemstra, P. C. 2011. *Groupers of the World: a Field and Market Guide*. NISC Pty Ltd, Grahamstown, South Africa.
- Department of Fisheries. 2011. Resource assessment framework (RAF) for finfish resources in Western Australia. Department of Fisheries, Government of Western Australia. Fisheries Occasional Publication No. 85. 28 pp.
- Fletcher, W. J., and Santoro, K. 2012. Status Reports of the Fisheries and Aquatic Resources of Western Australia 2011/12: the State of the Fisheries. Department of Fisheries, Government of Western Australia. 370 pp.
- Grier, H. J., and Taylor, R. G. 1998. Testicular maturation and regression in the common snook. *Journal of Fish Biology*, 53: 521–542.
- Heemstra, P. C., and Randall, J. E. 1993. *FAO species catalogue. Vol. 16 Groupers of the world. (family Serranidae, subfamily Epinephelinae)*. An annotated and illustrated catalogue of the grouper, rockcod, hind, coral grouper and lyretail species. Food and Agriculture Organization of the United Nations, Rome.
- Hesp, S. A., Potter, I. C., and Hall, N. G. 2004. Reproductive biology and protandrous hermaphroditism in *Acanthopagrus latus*. *Environmental Biology of Fishes*, 70: 257–272.
- Keener, P. 1984. Age, growth and reproductive biology of the yellowedge grouper, *Epinephelus flavolimbatus*, off the coast of South Carolina, p. 65. MSc thesis, College of Charleston, Charleston, SC, USA.
- Lek, E., Fairclough, D. V., Hall, N. G., Hesp, S. A., and Potter, I. C. 2012. Do the maximum sizes, ages and patterns of growth of three reef-dwelling labrid species at two latitudes differ in a manner conforming to the metabolic theory of ecology? *Journal of Fish Biology*, 81: 1936–1962.
- Lester, N. P., Shuter, B. J., and Abrams, P. A. 2004. Interpreting the von Bertalanffy model of somatic growth in fishes: the cost of reproduction. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 271: 1625–1631.
- Manickchand-Heileman, S. C., and Phillip, D. A. T. 2000. Age and growth of the yellowedge grouper, *Epinephelus flavolimbatus*, and the yellowmouth grouper, *Mycteroperca interstitialis*, off Trinidad and Tobago. *Fishery Bulletin*, 98: 290–298.
- Manooch, C. S., and Mason, D. L. 1987. Age and growth of the warsaw grouper and black grouper from the southeast region of the United States. *Northeast Gulf Science*, 9: 65–75.
- Marriott, R. J., Jarvis, N. D. C., Adams, D. J., Gallash, A. E., Norriss, J., and Newman, S. J. 2010. Maturation and sexual ontogeny in the spangled emperor *Lethrinus nebulosus*. *Journal of Fish Biology*, 76: 1396–1414.
- Matheson, R. H., and Huntsman, G. R. 1984. Growth, mortality, and yield-per-recruit models for speckled hind and snowy grouper from the United States South Atlantic Bight. *Transactions of the American Fisheries Society*, 113: 607–616.
- Moffitt, R. B. 2006. Biological data and stock assessment methodologies for deep-slope bottomfish resources in the Hawaiian archipelago. *In Deep Sea 2003: Conference on the governance and management of deep-sea fisheries. Part 2: Conference poster papers and workshop papers*, pp. 301–308. Ed. by R. Shotton. FAO Fisheries Proceedings No. 3/2. Rome, FAO, Queenstown, New Zealand.
- Molony, B. W., Newman, S. J., Joll, L., Lenanton, R. C. J., and Wise, B. 2011. Are Western Australian waters the least productive waters for finfish across two oceans? A review with a focus on finfish resources in the Kimberley region and north coast bioregion. *Journal of the Royal Society of Western Australia*, 94: 323–332.
- Moore, C. M., and Labisky, R. F. 1984. Population parameters of a relatively unexploited stock of snowy grouper in the lower Florida Keys. *Transactions of the American Fisheries Society*, 113: 322–329.
- Morato, T., Watson, R., Pitcher, T. J., and Pauly, D. 2006. Fishing down the deep. *Fish and Fisheries*, 7: 24–34.
- Munch, S. B., and Salinas, S. 2009. Latitudinal variation in lifespan within species is explained by the metabolic theory of ecology. *Proceedings of the National Academy of Sciences of the United States of America*, 106: 13860–13864.
- Musick, J. A., Harbin, M. M., Berkeley, S. A., Burgess, G. H., Eklund, A. M., Findley, L., Gilmore, R. G., et al. 2000. Marine, estuarine and diadromous fish stocks at risk of extinction in North America (exclusive of Pacific salmonids). *Fisheries*, 25: 6–30.
- Nichols, R. S., and DeMartini, E. E. 2008. Preliminary estimates of age and growth for the endemic Hawai'ian grouper (Hapu'upu'u, *Epinephelus quernus*, F. Serranidae). Pacific Islands Fisheries Science Center, National Marine Fisheries Service, NOAA, Honolulu. Pacific Islands Fisheries Science Center Administrative Report H-08-06. 19 pp.
- Pankhurst, N. W., and Porter, M. J. R. 2003. Cold and dark or warm and light: variations on the theme of environmental control of reproduction. *Fish Physiology and Biochemistry*, 28: 385–389.
- Parker, R. O., and Mays, R. W. 1998. Southeastern U.S. deepwater reef fish assemblages, habitat characteristics, catches, and life history summaries. U.S. Department of Commerce. NOAA Technical Report NMFS 138. 41 pp.

- Pearce, A., and Feng, M. 2007. Observations of warming on the Western Australian continental shelf. *Marine and Freshwater Research*, 58: 914–920.
- Punt, A. E., and Kennedy, R. B. 1997. Population modelling of Tasmanian rock lobster, *Jasus edwardsii*, resources. *Marine and Freshwater Research*, 48: 967–980.
- Quinn, T. J., and Deriso, R. B. 1999. *Quantitative Fish Dynamics*. Oxford University Press, New York.
- Randall, J. E., and Heemstra, P. C. 1991. Revision of Indo-pacific groupers (Perciformes: Serranidae: Epinephelinae), with descriptions of five new species. *Ichthyology*, Bernice Pauahi Bishop Museum, Honolulu Hawaii.
- Sadovy de Mitcheson, Y., Craig, M. T., Bertoni, A. A., Carpenter, K. E., Cheung, W. W. L., Choat, J. H., Cornish, A. S., *et al.* 2012. Fishing groupers towards extinction: a global assessment of threats and extinction risks in a billion dollar fishery. *Fish and Fisheries*, 448: 93–104.
- Sadovy de Mitcheson, Y., and Liu, M. 2008. Functional hermaphroditism in teleosts. *Fish and Fisheries*, 9: 1–43.
- Sadovy, Y., and Shapiro, D. Y. 1987. Criteria for the diagnosis of hermaphroditism in fishes. *Copeia*, 1: 136–156.
- Smith, W. L., and Craig, M. T. 2007. Casting the percomorph net widely: the importance of broad taxonomic sampling in the search for the placement of serranid and percid fishes. *Copeia*, 2007: 35–55.
- To, A. W. L., and Pollard, D. 2008. *Hyporthodus octofasciatus*, IUCN 2011. IUCN Red List of Threatened Species. Version 2011.2.
- Wakefield, C. B. 2006. Latitudinal and temporal comparisons of the reproductive biology and growth of snapper, *Pagrus auratus* (Sparidae), in Western Australia. PhD thesis, p. 162. Centre for Fish and Fisheries Research, Murdoch University, Western Australia.
- Wakefield, C. B. 2010. Annual, lunar and diel reproductive periodicity of a spawning aggregation of snapper *Pagrus auratus* (Sparidae) in a marine embayment on the lower west coast of Australia. *Journal of Fish Biology*, 77: 1359–1378.
- Wakefield, C. B., Moran, M. J., Tapp, N. E., and Jackson, G. 2007. Catchability and selectivity of juvenile snapper (*Pagrus auratus*, Sparidae) and western butterflyfish (*Pentapodus vitta*, Nemipteridae) from prawn trawling in a large marine embayment in Western Australia. *Fisheries Research*, 85: 37–48.
- Wakefield, C. B., Newman, S. J., and Molony, B. W. 2010. Age-based demography and reproduction of hapuku, *Polyprion oxygeneios*, from the south coast of Western Australia: implications for management. *ICES Journal of Marine Science*, 67: 1164–1174.
- Wallace, R. A., and Selman, K. 1981. Cellular and dynamic aspects of oocyte growth in teleosts. *American Zoologist*, 21: 325–343.
- Wise, B. S., St John, J., and Lenanton, R. C. J. 2007. Spatial scales of exploitation among populations of demersal scalefish: implications for management. Part 1: Stock status of the key indicator species for the demersal scalefish fishery in the West Coast Bioregion. Department of Fisheries. Final report to Fisheries Research and Development Corporation on Project No. 2003/052. Fisheries Research Report No. 163. 130 pp.
- Wyanski, D. M., White, D. B., and Barans, C. A. 2000. Growth, population age structure, and aspects of the reproductive biology of snowy grouper, *Epinephelus niveatus*, off North Carolina and South Carolina. *Fisheries Bulletin*, 98: 199–218.
- Yamamoto, K., Oota, I., Takano, K., and Ishikawa, T. 1965. Studies on the maturing process of the rainbow trout, *Salmo gairdnerii irideus*. I. Maturation of the ovary of a one-year old fish. *Bulletin of Japanese Society of Scientific Fisheries*, 31: 123–132.

Handling editor: Francis Juanes