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Variation in growth, mortality, length and age compositions of harvested populations of the herbivorous fish *Girella tricuspidata*

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Commercial gillnet and beach-seine catches of *Girella tricuspidata* from seven estuaries in eastern Australia were examined for differences in fork length (L_F), sex and age composition, and populations were assessed for growth and mortality. Fish 220–350 mm L_F dominated landings across all estuaries sampled, regardless of gear type. Few fish >10 years of age were observed in the catches, with fish aged 3–5 years, and 4–7 years, being most abundant in the catches in the four most northern estuaries and three southern estuaries, respectively. There was considerable variation in the L_F of *G. tricuspidata* at any given age and the oldest male and female were 21 and 24 years, respectively. There were no consistent differences between sexes or latitudinal regions in the growth and mean L_F at age of fish in each individual age class between 3 and 8 years. Growth of females was greater than males in the northern region, but not elsewhere. Estimates of the instantaneous rate of total mortality (Z) were dependent on estuary and year, ranging from 0.30 to 1.01, whereas the corresponding estimates of fishing mortality (F) ranged from 0.12 to 0.90. Populations of *G. tricuspidata* appear to have been heavily exploited, primarily relying on young fish recruiting to the fishery. The ecosystem-wide effects of harvesting this dominant mobile teleost herbivore need to be assessed further.

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Key words: ageing; exploitation; fishery assessment; Girellidae; life history; management.

INTRODUCTION

The Girellidae is a family of fishes that inhabit shallow coastal and estuarine sub-tropical and temperate waters of the Pacific, Indian and Atlantic Oceans (Yagishita & Nakabo, 2000; www.fishbase.org). The family comprises 18 species, with all but one species belonging to the genus *Girella*. Most species of *Girella* are herbivorous (Clements & Choat, 1997; Yagishita & Nakabo, 2003), but very little is known about their general population biology and ecology and the fisheries that exploit them.

Four species of *Girella* occur in temperate waters of Australia (Miskiewicz & Trnski, 1998), the most common being *Girella tricuspidata* (Quoy & Gaimard), which inhabits estuaries and near-shore waters along the eastern and southern

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seaboard of Australia and around the north island of New Zealand (Kailola *et al.*, 1993; Miskiewicz & Trnski, 1998). *Girella tricuspidata* is important in estuarine and coastal commercial and recreational fisheries (West & Gordon, 1994; Gray, 2002; Gray & Kennelly, 2003; Steffe *et al.*, 2007), having been exploited in south-eastern Australia since at least the 1880s (Dannevig, 1904) and probably earlier by indigenous fishers. The species can reportedly attain a maximum total length (L_T) of 700 mm and mass of 4 kg (Kailola *et al.*, 1993), although very few individuals exceeding 500 mm and 2 kg have been observed in catches in recent years (Gray, 2002; Gray & Kennelly, 2003; Steffe *et al.*, 2005).

The commercial fishery for *G. tricuspidata* in south-eastern Australia is characterized by high local volume but low value, with recently reported annual commercial catches in the state of New South Wales (NSW) alone fluctuating between 350 and 500 t (Scandol *et al.*, 2008). The total commercial catches reported in NSW peaked at c. 800 t year⁻¹ in the late 1980s. Approximately 85% of the total commercial catch of *G. tricuspidata* in NSW is taken in estuaries, particularly the large coastal lagoons in central NSW, primarily using gillnets and beach seines. Fishing occurs year round, but commercial catches are generally greatest between March and August (autumn to winter) when the species is also targeted along ocean beaches using beach seines (Gray *et al.*, 2000; Broadhurst *et al.*, 2006). The estimated total recreational catch for *G. tricuspidata* in NSW of 270–550 t year⁻¹ is of a similar magnitude to the total commercial catch (Henry & Lyle, 2003). The recreational fishery is important and popular in many locations (West & Gordon, 1994; Steffe *et al.*, 2005); it is also specialized with fishers using unique rigs that utilize filamentous green algae as bait. The commercial fisheries that catch *G. tricuspidata* in NSW are managed by input controls, including gear restrictions (*e.g.* minimum and maximum mesh-sizes in nets and length of nets) and spatial and temporal fishing closures. A current minimum legal L_T (MLL) restriction of 270 mm (*c.* 240 mm fork length, L_F) applies to commercial and recreational fishers, with the latter also having a possession limit of 20 fish.

Some aspects of the biology of *G. tricuspidata* are known; notably it is primarily herbivorous, predominantly feeding on seagrass *Zostera capricorni*, filamentous green algae *Enteromorpha* spp. and *Ulva* spp., and red algae *Gracilaria* spp., although it also consumes small benthic invertebrates (Anderson, 1987, 1991; Raubenheimer *et al.*, 2005). The development of larvae and pre-settlement juveniles (Neira *et al.*, 1997; Miskiewicz & Trnski, 1998), the occurrence and horizontal and vertical distributions of larvae in coastal waters (Gray & Miskiewicz, 2000), the habitat relationships (Bell *et al.*, 1984; Middleton *et al.*, 1984; Gray *et al.*, 1996, 1998) and growth of juveniles (Worthington *et al.*, 1992; Smith & Sinerchia, 2004) have also been documented. The age and growth of *G. tricuspidata* have been investigated for populations in Morton Bay near the limit of its northern distribution (Pollock, 1981), but this was based on scale readings, which can be problematic (Campana, 2001). Despite the importance of the species to recreational and commercial fisheries throughout its distribution, little is known of the demographic characteristics (length, sex and age composition) of catches and how these vary spatially and temporally. Length and age-based information, including estimates of growth and mortality, are some of the most important life-history characteristics required to assess the status of exploited fish populations and to explore and test alternative fishery management strategies (Ricker, 1975; Megrey, 1989; Charnov, 1993; Campana, 2001).

This study examined spatial, temporal and gear-related differences in the length and age compositions of estuarine commercial catches of *G. tricuspidata* in NSW. It also investigated relationships between length and age, and determined whether estimates of growth and instantaneous rates of total and fishing mortality of *G. tricuspidata* varied among estuaries that were subject to different types and extents of commercial harvesting.

MATERIALS AND METHODS

SAMPLING COMMERCIAL CATCHES

Between 1995 and 1997, retained commercial catches of *G. tricuspidata* were sampled for length, sex and age composition from seven estuaries in NSW: Clarence River from 1995 to 1997; Wallis Lake in 1995 and 1996; Port Stephens in 1997; Lake Macquarie in 1996 and 1997; St Georges Basin in 1996 and 1997; Tuross River in 1995 and 1996; Wallaga Lake in 1995 and 1996 (Fig. 1). Sampling of catches took place when fishers landed their catches at each port (primarily fishing cooperatives) during peak seasonal production between February and July each year. Whole catches or random sub-samples of whole catches landed on each sampling day were measured (L_F to nearest 5 mm below the true length) and sexed by macroscopic examination of gonads. Because sampling was restricted to commercial landings, no fish below the MLL of 250 mm (c. 220 mm L_F) were examined. The specific gear type used for capture was obtained from each fisher at the time of sampling.

Sagittal otoliths were collected opportunistically from random sub-samples of catches from each estuary. These collections were made during June and July in 1995 and between February and July in 1996 and 1997. Otoliths were cleaned in fresh water, dried and stored in paper envelopes until processing in the laboratory. Most otoliths were archived until 2004 and then examined. In addition to the annual sampling of fish, between 25 and 70 sagittal otoliths were collected on a monthly basis from landings in the Clarence River between September 1996 and September 1997 to investigate the periodicity of increment formation in otoliths from that estuary.

AGE ESTIMATION

Sectioned sagittal otoliths were used to estimate the age of fish, as preliminary examinations showed that whole otoliths were more difficult to interpret than those sectioned, particularly for older fish because of the stacking of growth zones near the otolith margin. One sagitta from each fish was **embedded in clear resin and sectioned** (c. 0.25–0.30 mm) in a transverse plane through the focus using a low speed saw fitted with two diamond blades. Both sides of the resulting thin section were then polished on 0.09 mm lapping film, after which the section was mounted on a standard glass slide and viewed under a binocular microscope ($\times 6$ –25 magnifications) with reflected light against a black background.

Most otolith sections displayed a pattern of narrow opaque (light) and broad translucent (dark) zones. Assignment of age was based on counts of completed opaque zones (*i.e.* number of opaque rings from the focus to the outer edge, usually along the line of the sulcus). Sections were interpreted without the knowledge of the L_F or sex of the fish or location of capture. **Twenty-five per cent of sections were read twice without the knowledge of the first interpretation and a coefficient of variation (c.v.) of successive reads was determined** (Kimura & Lyons, 1991). Assignment of age and year class was consistent across years and estuaries because all samples were collected within the same 6 month period each year. Preliminary analyses showed that during this 6 month period the previous opaque growth zone was complete, furthest from the otolith margin and therefore prior to the formation of a new opaque zone. There was no need to adjust assigned ages based on the time of collection of samples as the formation and completion of opaque growth zones in all fish occurred outside of the sampling period.

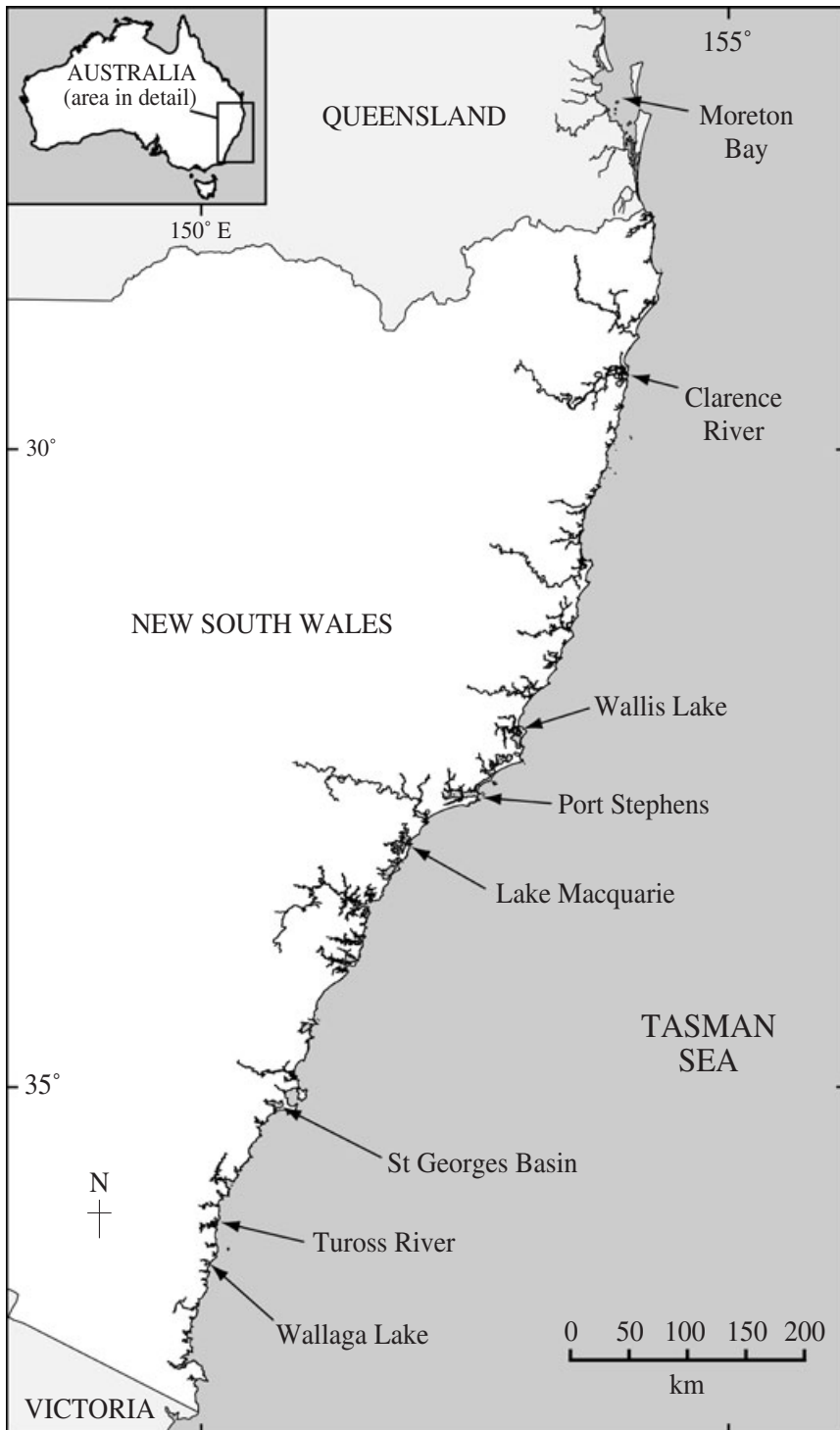


FIG. 1. Map of New South Wales showing the location of the seven estuaries where retained commercial catches of *Girella tricuspidata* were examined.

Marginal increment (I_M) analysis was used to determine the periodicity of formation of opaque zones in fish in the Clarence River. Sections were examined under a microscope (as described above), assigned an age, and whether the otolith margin was opaque or translucent was recorded. As above, 25% of sections were interpreted twice. A marginal ring was deemed to have formed where an opaque zone appeared on the edge with no translucent zone following. An image processor was used to measure the distance from the otolith focus to each successive opaque zone and to the otolith edge. All measurements were made along the dorsal edge of the sulcus to the nearest 0.05 mm. The I_M was expressed as 1 for fish with one opaque zone, the distance from the first opaque zone to the otolith edge as a proportion of the distance from the focus to the first opaque zone, and 2 for fish with two or more opaque zones, the distance from the most recently completed opaque zone to the otolith edge as a proportion of the last completed increment. Mean \pm S.E. I_M was calculated for each separate age group and for all ages combined for each month.

L_F AT AGE AND GROWTH

Mean L_F at age was calculated separately for each sex and age class for three latitudinal regions: (1) Clarence River on the north coast; (2) Wallis Lake, Port Stephens and Lake Macquarie combined on the central coast (central estuaries) and (3) St Georges Basin, Tuross River and Wallaga Lake combined on the south coast (southern estuaries). The last two groupings were formed because of the relative paucity of data for many age classes from the individual estuaries, and the clear latitudinal distinction between groupings (Fig. 1). Truncated von Bertalanffy growth (VBG) curves (*i.e.* across only the age classes encountered that had >5 data points) were fitted to the L_F -at-age data separately for each sex and latitudinal region. The mean L_F -at-age estimates and growth curves were generated using data combined across years due to the paucity of data within each year in some zones.

Differences in growth between sexes and across the latitudinal regions were assessed by comparing the VBG curves using likelihood ratio (LR) tests (Kimura, 1980). Where the LR tests indicated no significant difference in growth curves between latitudinal categories for each sex, the relevant data were combined and one growth model fitted.

L_F AND AGE COMPOSITIONS OF COMMERCIAL CATCHES

Frequency histograms of the L_F and age compositions of commercial catches were generated for each year sampled in each estuary. A separate age- L_F key was generated for each year sampled in each estuary except the Tuross River, for which data were combined across 1996 and 1997 due to low sample sizes. The age compositions of fish in the retained catches were calculated by applying the age- L_F keys to the relevant commercial catch L_F -frequency data.

MORTALITY

Estimates of the instantaneous rate of total mortality (Z) were made for each year sampled in each estuary using the age-based catch curve method (Beverton & Holt, 1957; Ricker, 1975). The natural logarithm of the number of fish in each age class (N_t) was plotted against their corresponding age class (t) and a linear regression was fitted; Z was then estimated from the descending slope, b . The S.E. and r^2 values were calculated for each regression. The most abundant age class in each sample was assumed to be fully recruited for each catch curve analysis. These analyses assumed that the catchability of different sized fish, recruitment and growth were constant across years and that growth was asymptotic.

Estimates of the instantaneous rate of natural mortality (M) were determined by three separate methods: (1) $\ln M = 1.46 - 1.01 \ln t_m$ (Hoenig, 1983), (2) $M = -\ln(0.01)t_m^{-1}$ (Quinn & Deriso, 1999) and (3) $M = -0.0152 - 0.2790 \ln(L_\infty) + 0.6545 \ln(k) + 0.4634 \ln(T)$ (Pauly, 1980), where L_∞ and k are the von Bertalanffy growth coefficients, t_m is the maximum age in years (24 years), and T is water temperature ($^{\circ}$ C). The estimation method of Hoenig (1983) was based on the assumption that 1% of individuals reach the maximum attainable age of the

species, whereas the estimation method of Pauly (1980) was based on conservatively high average annual water temperatures: 21° C for Clarence River; 20° C for the central estuaries and 19° C for the southern estuaries; based on recent logged temperatures in the Clarence River (Ives *et al.*, 2009). The range of fishing mortality (F) was estimated by subtracting the highest and lowest estimates of M (of the three methods employed) from the corresponding estimates of Z , providing two estimates of the exploitation rate (E) from $E = FZ^{-1}$.

RESULTS

AGE DETERMINATION AND VARIATION IN L_F AT AGE AND GROWTH

The otoliths of *G. tricuspidata* displayed alternating wide translucent and thin opaque growth zones that were interpreted as annuli. The I_M values displayed an annual cyclical pattern with lower values in October to March (Fig. 2), identifying that one opaque and one translucent growth zone was deposited annually on the otoliths of *G. tricuspidata* in the Clarence River. The opaque zone was generally deposited between October and February (Fig. 2) and it was during this period that some otoliths had identifiable opaque zones near their edge (low I_M) while others still had a broad translucent edge (high I_M). The I_M for fish of all ages tended to increase from March to peak in October. The overall agreement between successive reads of sectioned otoliths was 64 and 97% for ± 1 year, with the corresponding c.v. value being 2.62.

The oldest age estimates for female and male *G. tricuspidata* were 24 and 21 years, respectively, and the largest female and male sampled were 560 and 480 mm L_F . All these specimens were from the Clarence River. The mean \pm s.e. L_F at age of 3 year olds from the Clarence River was 286.4 ± 1.9 mm for females and 276.9 ± 1.6 mm for males ($n = 123$ and 159 , respectively). The corresponding mean L_F of 3 year-old female and male fish were smaller in the central estuaries (261.1 ± 1.6 mm and 261.3 ± 1.9 mm; $n = 123$ and 94) and southern estuaries (258.6 ± 5.3 mm and 263.0 ± 5.0 mm; $n = 14$ and 23). Similarly, female and male 7 year-old fish had mean \pm s.e. L_F at age estimates of: 328.8 ± 4.3 mm and 317.0 ± 4.0 mm in the Clarence River ($n = 48$ and 42); 308.7 ± 4.4 mm and 309.1 ± 4.7 mm in the central estuaries ($n = 27$ and 28) and 301.2 ± 4.8 mm and 302.2 ± 4.2 mm in the southern estuaries ($n = 54$ and 44). It is noted that the estimated mean L_F at age for fish aged 2, 3 and 4 years are probably over-estimates due to the truncation of data at 220 mm L_F .

The VBG curves significantly differed for females and males in the Clarence River (LR test, $P < 0.001$; Table I), with the mean L_F at age of females larger than that of males across all age classes (Fig. 3). In the cases of the central and southern regions, the VBG curves did not significantly differ between sexes (LR tests, $P > 0.05$; Table I). The VBG curves for females significantly differed among the three latitudinal regions (LR tests, $P < 0.01$ for each paired comparison), and the VBG curve for males in the Clarence River was significantly different from those for males in the central and southern estuaries (LR tests, $P < 0.001$ in each case). Growth curves of males in the central and southern regions, however, did not significantly differ (LR test, $P > 0.05$; Table I). The mean L_F at age of females and males was generally largest in the Clarence River. The final VBG coefficient estimates for

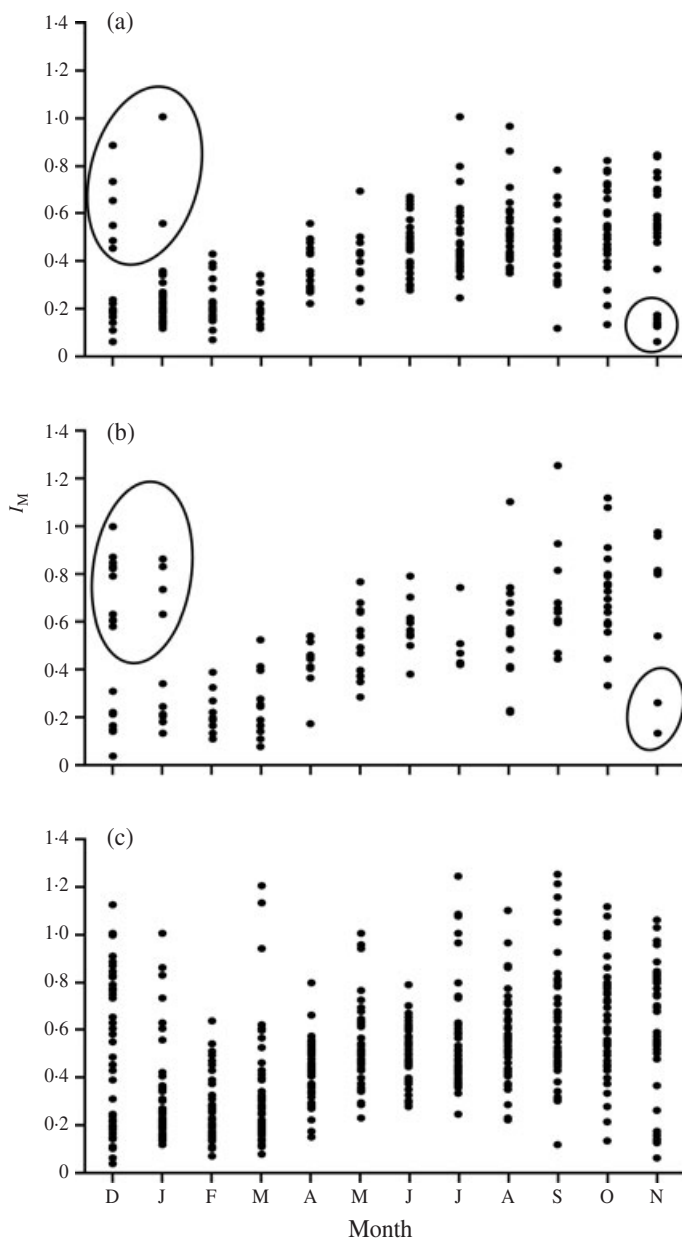


FIG. 2. Changes in the marginal increment (I_M) of otoliths of *Girella tricuspidata* from the Clarence River at (a) 2–3 years old, (b) 4–5 years old and (c) all ages combined. Some examples of the months when some otoliths had identifiable opaque zones near their edge (low I_M) and others had identifiable translucent zones near their edge (high I_M) are indicated by encirclement (O).

each sex in each of the latitudinal regions are summarized in Table II. Note that the male and female VBG coefficient estimates for the lower two regions were combined because it represented the simplest model supported by the data.

TABLE I. Likelihood ratio tests comparing von Bertalanffy coefficient (L_∞ , k and t_0) estimates for male and female *Girella tricuspidata* for each of the three latitudinal regions of New South Wales. The coefficient suffixes for L_∞ , k and t_0 refer to the dataset they are associated within the hypothesis. For the hypotheses where equality is being tested (odd rows), the coefficient values are displayed in the first suffix column

Hypothesis	$L_\infty 1$	$L_\infty 2$	$k 1$	$k 2$	$t_0 1$	$t_0 2$	Residual sums		n	d.f.	X^2	P -value
							of squares					
CRM \neq CRF	332	365	0.28	0.20	-3.46	-4.69	56.5		22			
CRM = CRF	347		0.24		-4.05		1289.0		22	3	68.80	<0.001
CEM \neq CEF	334	349	0.20	0.18	-5.00	-5.00	298.0		17			
CEM = CEF	334		0.22		-4.18		363.3		17	3	3.37	>0.05
SEM \neq SEF	346	368	0.17	0.14	-5.00	-5.00	513.9		15			
SEM = SEF	357		0.15		-5.00		576.2		15	3	1.72	>0.05
CRM \neq CEM	332	349	0.28	0.18	-3.46	-5.00	89.5		19			
CRM = CEM	342		0.20		-4.90		649.4		19	3	37.65	<0.001
CRM \neq SEM	332	346	0.28	0.17	-3.46	-5.00	261.6		18			
CRM = SEM	384		0.09		-10.00		1563.9		18	3	32.18	<0.001
CEM \neq SEM	334	346	0.20	0.17	-5.00	-5.00	470.1		15			
CEM = SEM	345		0.17		-5.00		540.9		15	3	2.10	>0.05
CRF \neq CEF	365	334	0.20	0.20	-4.69	-5.00	265.0		20			
CRF = CEF	353		0.19		-5.00		2789.1		20	3	47.08	<0.001
CRF \neq SEF	365	368	0.20	0.14	-4.69	-5.00	308.8		19			
CRF = SEF	358		0.18		-5.00		4357.0		19	3	50.29	<0.001
CEF \neq SEF	334	368	0.20	0.14	-5.00	-5.00	507.3		17			
CEF = SEF	362		0.13		-7.00		978.7		17	3	11.17	<0.05

CRM, Clarence River males; CRF, Clarence River females; CEM, central estuaries male; CEF, central estuaries female; SEM, southern estuaries male; SEF, southern estuaries female.

TABLE II. Summary of truncated von Bertalanffy growth coefficient (L_∞ , k and t_0) estimates for *Girella tricuspidata* for the three latitudinal regions of New South Wales. S.E. are shown in parentheses

Latitudinal region	Sex	L_∞	k	t_0
Clarence River	Female	364.8 (3.9)	0.20 (0.02)	-4.69 (0.39)
Clarence River	Male	332.0 (1.9)	0.28 (0.02)	-3.46 (0.26)
Central estuaries	Combined	333.6 (10.2)	0.22 (0.06)	-4.18 (1.27)
Southern estuaries	Combined	357.3 (9.4)	0.15 (0.01)	-5.00 (0.00)

VARIATION IN L_F AND SEX COMPOSITION OF COMMERCIAL CATCHES

Commercial catches of *G. tricuspidata* included fish 220–560 mm L_F , although the majority were between 250 and 350 mm L_F regardless of estuary or gear type (Fig. 4). The L_F compositions of catches shown are for gillnets (80–100 mm in mesh-size) in the Clarence River, Wallis Lake, Tuross River and Wallaga Lake, beach seines (50 mm bunt mesh) in Lake Macquarie and St Georges Basin and a modified beach seine set as a trap net in Port Stephens. The L_F compositions

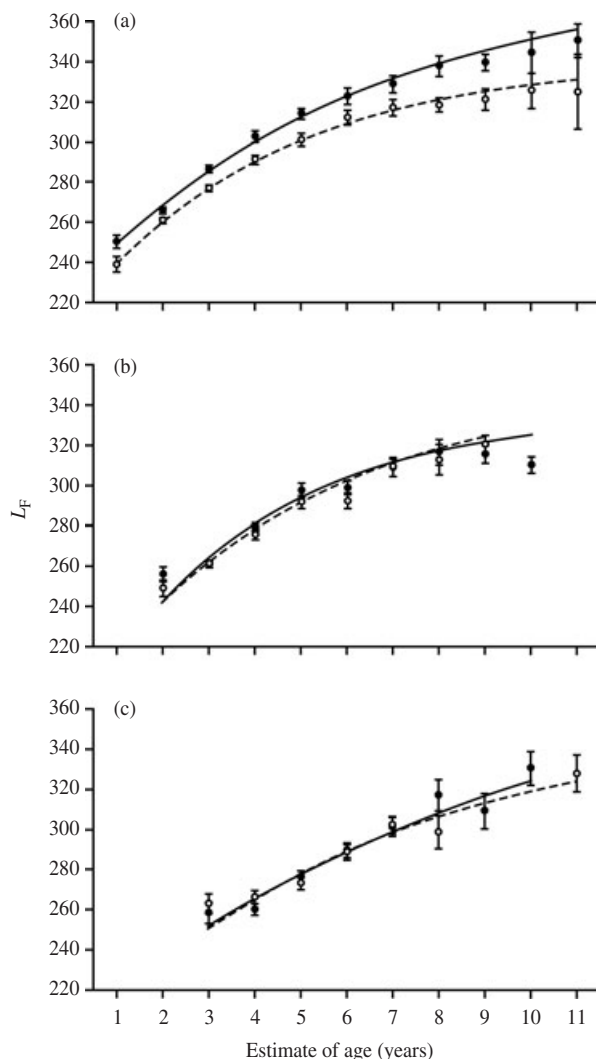


FIG. 3. Von Bertalanffy growth curves for male and female *Girella tricuspidata* from the three latitudinal regions examined in New South Wales: (a) Clarence River, (b) central estuaries and (c) southern estuaries (see Table II) (data combined across years).

of catches varied among estuaries and were not directly related to gear type. For example, the L_F compositions of the gillnet catches in Wallis and Wallaga Lakes were more similar to those from the beach-seine catches in Lake Macquarie and St Georges Basin compared to the gillnet catches in the Clarence and Tuross Rivers (Fig. 4). The mean L_F of *G. tricuspidata* sampled in landings was greatest in the Clarence and Tuross Rivers (*i.e.* gillnet catches) (Fig. 4).

With the exception of the Clarence River and Port Stephens, females were more numerous than males in the sampled catches combined across years in each estuary. The male to female ratios were: Clarence River, 1:0.91; Wallis Lake, 1:1.62; Port Stephens, 1:0.95; Lake Macquarie, 1:1.70; St Georges Basin, 1:1.17; Tuross River,

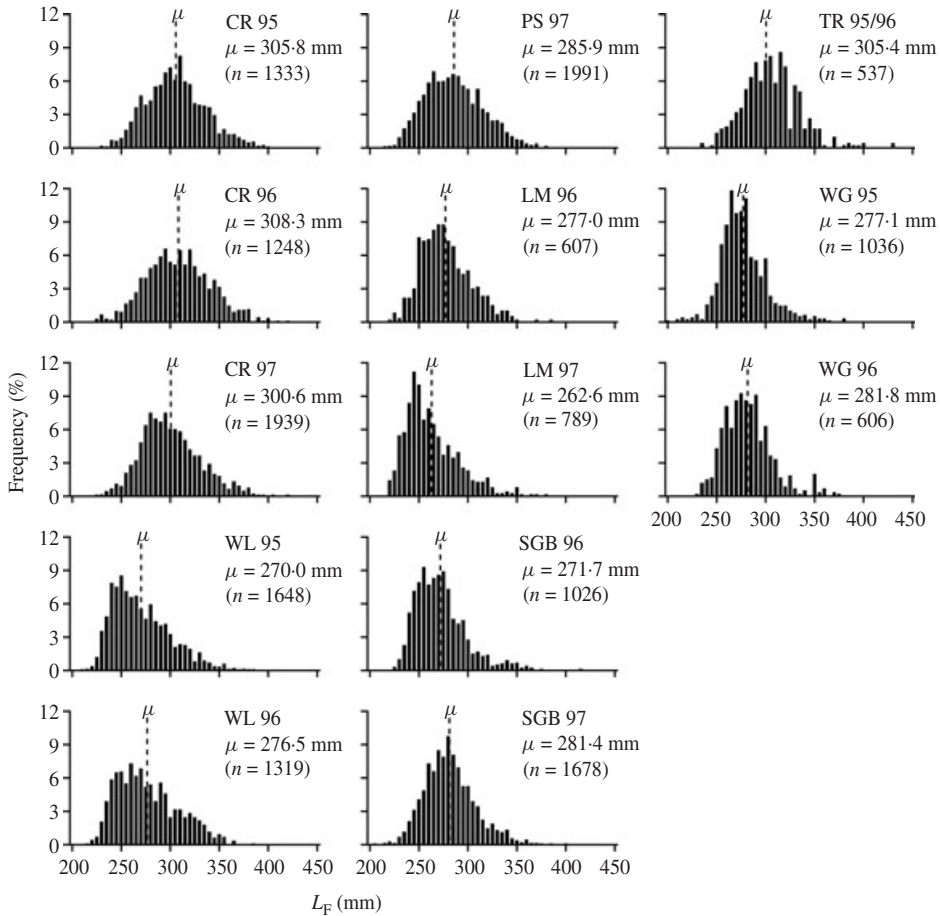


FIG. 4. Fork length (L_F) compositions of commercial catches of *Girella tricuspidata* in seven estuaries in New South Wales: Clarence River (CR), Wallis Lake (WL), Port Stephens (PS), Lake Macquarie (LM), St Georges Basin (SGB), Turrill River (TR) and Wallaga Lake (WG) 1995 (95), 1996 (96) and 1997 (97). μ = mean L_F and n = number of individuals. Catches in the Clarence River, Wallis Lake, Turrill River and Wallaga Lake were from gillnets and those in Port Stephens, Lake Macquarie and St Georges Basin were from beach seines.

1:1-16; Wallaga Lake, 1:1-15. In the Clarence River, the overall mean L_F of female fish was larger than that of males (311 and 294 mm L_F , respectively). This was not the case, however, in the beach-seine catches from Lake Macquarie (female 291 mm and male 292 mm L_F) and St Georges Basin (female 279 mm and male 282 mm L_F), nor in the trap-net catches from Port Stephens (female 299 mm and male 300 mm L_F).

AGE COMPOSITION OF COMMERCIAL CATCHES

Commercial catches contained *G. tricuspidata* aged between 1 and 24 years, but the majority of fish were 3–7 years old, with very few fish exceeding 10 years (Fig. 5). Catches from the Clarence River, Wallis Lake, Port Stephens and Lake

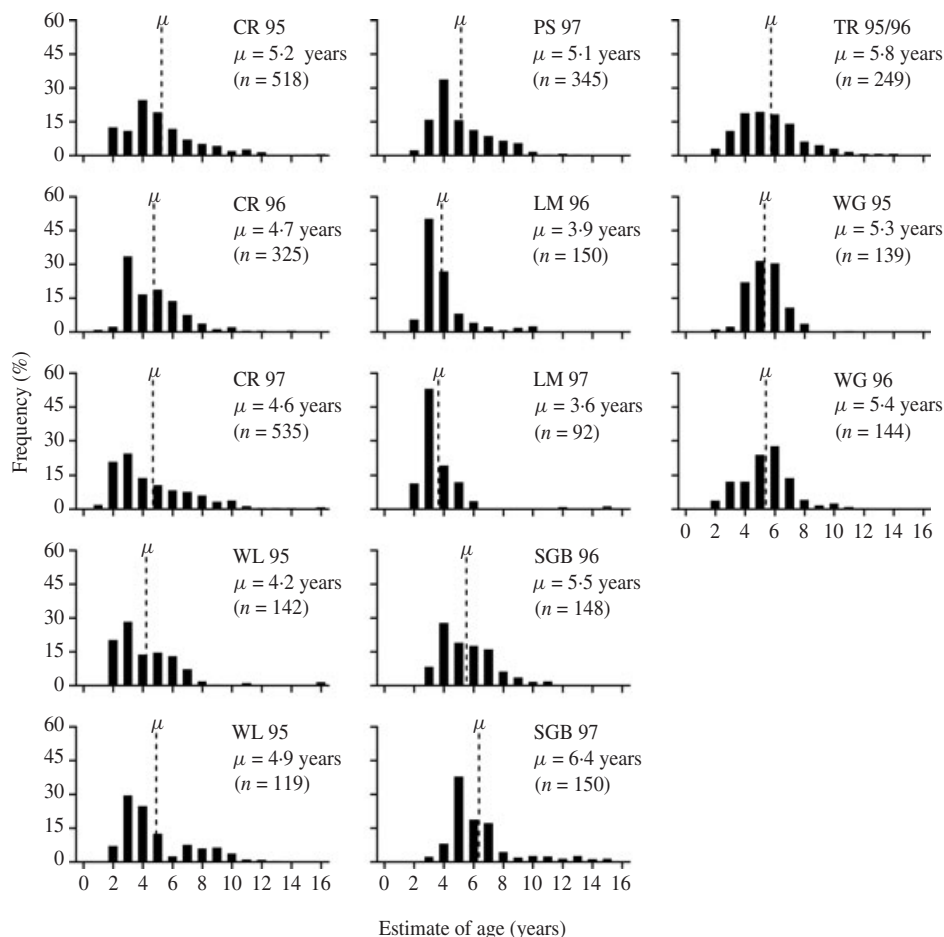


FIG. 5. Age compositions of commercial catches of *Girella tricuspidata* in seven estuaries in New South Wales (see Fig. 4). μ = mean age.

Macquarie were dominated by fish aged 2–6 years, with most of these fish aged 3 or 4 years. This was particularly evident in Lake Macquarie where the 3 year-old age class accounted for *c.* 50% of the catch in each of the 2 years sampled. In contrast, catches in St Georges Basin, Tuross River and Wallaga Lake were dominated by fish aged 4–7 years and included few fish <4 years old. The age compositions of catches were not related to gear type; the mean age of *G. tricuspidata* was least in the beach-seine catches in Lake Macquarie (3.6–3.9 years) and greatest in the beach-seine catches in St Georges Basin (5.5–6.4 years) and gillnet catches in Tuross River (5.8 years).

MORTALITY

Estimates of *Z* varied depending on the estuary and year (and age distribution used in each analysis), ranging from 0.30 (Wallis Lake 1995) to 1.01 (Wallaga Lake 1995) (Table III). There was considerable variation in the estimates of *Z* among years for

TABLE III. Estimates of total mortality (Z), natural mortality (M), fishing mortality (F) and exploitation rate (E) for *Girella tricuspidata* in each of the seven estuaries sampled along the New South Wales coast

Estuary	Year	Z	S.E.	r^2	M (Hoenig, 1983)	M (Quinn & Deriso, 1999)	M (Pauly, 1980)	F ($M = 0.16$) ($M = 0.30$)	E ($M = 0.16$) ($M = 0.30$)
Clarence River	1995	0.32	0.04	0.79	0.16	0.18	0.27	0.16	0.50
Clarence River	1996	0.51	0.03	0.95	0.16	0.18	0.27	0.35	0.68
Clarence River	1997	0.41	0.04	0.91	0.16	0.18	0.27	0.25	0.61
Clarence River	All	0.38	0.03	0.89	0.16	0.18	0.27	0.22	0.58
Wallis Lake	1995	0.30	0.10	0.54	0.16	0.18	0.30	0.14	0.47
Wallis Lake	1996	0.42	0.06	0.82	0.16	0.18	0.30	0.26	0.62
Wallis Lake	All	0.41	0.05	0.85	0.16	0.18	0.30	0.25	0.61
Port Stephens	1997	0.58	0.06	0.92	0.16	0.18	0.30	0.42	0.73
Port Stephens	All	0.58	0.06	0.92	0.16	0.18	0.30	0.42	0.73
Lake Macquarie	1996	0.53	0.13	0.73	0.16	0.18	0.30	0.37	0.70
Lake Macquarie	1997	0.33	0.14	0.54	0.16	0.18	0.30	0.17	0.52
Lake Macquarie	All	0.40	0.08	0.78	0.16	0.18	0.21	0.24	0.60
St Georges Basin	1996	0.46	0.06	0.92	0.16	0.18	0.21	0.30	0.65
St Georges Basin	1997	0.33	0.06	0.79	0.16	0.18	0.21	0.17	0.52
St Georges Basin	All	0.38	0.04	0.92	0.16	0.18	0.21	0.22	0.58
Turross River	1995–1996	0.31	0.04	0.84	0.16	0.18	0.21	0.15	0.48
Turross River	All	0.31	0.04	0.84	0.16	0.18	0.21	0.15	0.48
Wallaga Lake	1995	1.01	0.10	0.97	0.16	0.18	0.21	0.85	0.84
Wallaga Lake	1996	0.77	0.10	0.93	0.16	0.18	0.21	0.61	0.79
Wallaga Lake	All	0.76	0.09	0.93	0.16	0.18	0.21	0.60	0.79

each estuary. For example, Z values were 0.33 and 0.53 in Lake Macquarie, and ranged between 0.32 and 0.51 in the Clarence River. The precision of the estimates of Z also varied among estuaries and years. Most of these estimates of Z were generated using three as the minimum age (*i.e.* the most abundant age class), but in some places, like Wallaga Lake, the most abundant age class was identified as being as high as six.

Estimates of M ranged from 0.16, which was based on the lowest estimated mortality (method of Hoenig, 1983) with 1% of fish attaining the maximum observed age of 24 years, to 0.30, which was based on an average of the highest estimated mortality (method of Pauly, 1980). Estimates of F ranged from 0.14 in Wallis Lake 1995 to 0.85 in Wallaga Lake 1995 and the corresponding estimates of E in these two estuaries were 0.47 and 0.84, respectively (Table III). The estimates of F were greater than the lowest estimated value for M in most cases examined.

DISCUSSION

AGE DETERMINATION AND VARIATION IN L_F AT AGE AND GROWTH

The marginal increment analysis demonstrated that one opaque and one translucent growth zones were deposited on the otoliths of *G. tricuspidata* in the Clarence River each year, an occurrence previously observed for otoliths of *G. tricuspidata* that had been captured, marked with oxytetracycline, released back into the wild and subsequently recaptured 3 years later (Ferrell, 2000). The opaque zones probably began to form during the late austral winter and early spring (August to September), but were not observed as being completed (*i.e.* counted) on some individuals until late summer and early autumn (December to March). This timing of completion of opaque zone formation is in general agreement with that observed for a range of other species of coastal and estuarine fishes in south-eastern Australia, including *Platycephalus fuscus* Cuvier (Gray *et al.*, 2002), *Hyporhamphus regularis* (Günther) (Stewart & Hughes, 2007), *Nemadactylus douglasii* (Hector) (Stewart & Hughes, 2009), *Rhabdosargus sarba* (Forsskal) (Hughes *et al.*, 2008) and *Sillago maculata* Quoy & Gaimard (Kendall & Gray, 2009).

The maximum ages of *G. tricuspidata* of 21 and 24 years for males and females sampled here were greater than the 9 and 11 years reported by Pollock (1981) for the species in Moreton Bay (*c.* 500 km north of the Clarence River; Fig. 1). Pollock (1981) probably underestimated ages as they were based on interpreting scales rather than otoliths (Campana, 2001).

Sex and region were contributing factors to the observed variation in the L_F -at-age of *G. tricuspidata*. Both the largest and oldest fish sampled were female, indicating that they can potentially attain a greater length and age than males. Despite this, the analyses demonstrated that sex-specific differences in L_F at age and growth were not consistent between regions. Females had a greater mean L_F at age than males in the Clarence River, but this was not evident in the two more southern regions, where no differences in mean L_F at age and growth between sexes were observed. It was not possible to isolate the mechanisms and factors responsible for these discrepancies; however, genetic, physiological, behavioural and environmental conditions can all influence sex-specific rates of growth of fishes (Choat & Robertson, 2002).

The VBG coefficients estimated for *G. tricuspidata* differed among regions. Differences in the age compositions of samples could have contributed to some differences in coefficient estimates. For example, the far greater L_{∞} estimate for males in the southern region may have been a consequence of those samples having a greater proportion of older fish (Sainsbury, 1980). Nevertheless, regional and estuary-to-estuary intraspecific variation in growth among populations of fish is common (Sarre & Potter, 2000; Bedee *et al.*, 2002), and can be influenced by a range of biotic (*e.g.* food availability) and abiotic factors (*e.g.* water temperature) (Crecco & Savoy, 1985; Zalewski *et al.*, 1985; Claramunt & Wahl, 2000; Neuheimer & Taggart, 2007). It is notable that the variation revealed here was not unequivocally temperature related, with females apparently growing fastest in the central region and males growing fastest in the northern region.

The observed variation in the L_F at age of *G. tricuspidata* is also due in part to their extended (up to 9 months) spawning period in NSW (C. A. Gray, unpubl. data). Each age class within an estuary could contain fish spawned several months apart. Furthermore, initial rates of growth of small individuals may vary among different cohorts because of differing environmental conditions at the time of, and immediately following, settlement (Suthers, 1998; Smith & Sinerchia, 2004). It is also acknowledged that the movements of individual *G. tricuspidata* between estuaries and along the coast could mask specific estuary-to-estuary and regional differences in growth.

The VBG coefficients presented in Table II differed from those presented for *G. tricuspidata* in north-eastern New Zealand waters (Taylor & Willis, 1998). The latter study, however, was based on comparatively low sample sizes ($n = 126$), and the method and accuracy of ageing fish and the range of lengths and ages of samples were not reported. Nevertheless, the estimate provided for k (0.18) in that study was within the bounds of the estimates presented here. In contrast, the estimated L_{∞} value of 454 mm L_F for the New Zealand population was considerably higher than the highest estimate for L_{∞} provided here (365 mm for Clarence River females) even though samples were taken from similar latitudes (*i.e.* *c.* 36° 15' S). Although this may reflect differences in life-history characteristics of *G. tricuspidata* between these coastlines, high levels of fishing pressure can affect the life-history characteristics of populations of fishes (Rochet *et al.*, 2000; Reznick & Ghalambor, 2005; Andersen *et al.*, 2007); hence, this disparity in maximum lengths between the two coastlines could be a result of greater fishing pressure on the species in eastern Australia. Age class truncation and reductions in the numbers of old and large individuals in populations are common features of several exploited fish species in eastern Australia (Silberschneider *et al.*, 2009; Stewart & Hughes, 2009). More specific research would be required to test whether fishing is a contributing factor responsible for the observed differences in growth and population structure of *G. tricuspidata* between the eastern Australian and New Zealand coastlines.

COMPOSITION OF COMMERCIAL CATCHES

Commercial catches in all estuaries were dominated by fish <350 mm L_F (predominantly between 250 and 300 mm L_F) regardless of gear type, and the majority of fish retained in commercial catches were within 80 mm of the then current MLL of

220 mm L_F . The length compositions of recent recreational catches of *G. tricuspidata* display similar characteristics to those observed here (Steffe *et al.*, 2005).

Variation in the length compositions of catches between estuaries could not solely be attributable to the different gear types. For example, the length compositions of the retained gillnet catches in Wallis Lake and the Clarence River were most disparate than that observed between the gillnet catches in Wallis Lake and the beach-seine catches in Lake Macquarie and St Georges Basin. The gillnet catches from the Clarence River, however, overall comprised a greater proportion of *G. tricuspidata* >300 mm L_F and had a greater mean L_F of retained fish compared with gillnet and beach-seine catches from the other estuaries. This is despite beach seines being considered less size selective than gillnets (Broadhurst *et al.*, 2007). Although this result may have been partly due to a greater prevalence of larger fish in the Clarence River, more fishers in this river used gillnets with larger mesh (95 and 100 mm) compared with the standard 80 and 83 mm mesh most commonly used in the other estuaries. Previous studies have shown that the mean L_F of *G. tricuspidata* is generally larger when caught in gillnets with 100 mm mesh compared with 80 mm mesh (Gray, 2002; Broadhurst *et al.*, 2003; Gray *et al.*, 2005). Generally, the L_F compositions of catches reported here were consistent with direct observations of catches of *G. tricuspidata* in these fisheries (Gray, 2002; Gray & Kennelly, 2003; Gray *et al.*, 2005).

The commercial fishery for *G. tricuspidata* in each estuary was based on several age classes, but the dominant age classes varied among estuaries and years. In general, fish aged 3–5 years dominated landings in the four most northern estuaries (*i.e.* those located north of Sydney), whereas fish aged 4–7 years dominated landings in the three southern estuaries. Pollock (1981) reported that *G. tricuspidata* aged 4–6 years were most abundant in the commercial fishery in Moreton Bay in the early 1980s, although this conclusion should be interpreted with caution for reasons stated above. The differences in age structures observed among estuaries in this study cannot be solely attributable to differences in rates of growth between regions or due to differences in gear types. The predominance of older fish in Wallaga Lake may be the result of this estuary being intermittently closed to the sea (between May to October 1995 during this study), restricting the recruitment of young fish from outside the estuary to the fishery. Consequently, the age structures of populations in estuaries that intermittently close and open could vary considerably through time depending on their opening and closing regimes. The age composition of catches in the other study estuaries (all permanently open to the sea), notably the Clarence River, also varied between years, but strong and weak year classes could not generally be followed through time.

The recruitment of juvenile *G. tricuspidata* to the shallow regions of estuaries varies considerably in space and time (Worthington *et al.*, 1992; Smith & Sinerchia, 2004). Hence, the timing and magnitude of recruitment to the fishery probably also vary substantially between estuaries, affecting the age structures of populations. This, together with the large variation in length at age, probably results in a protracted recruitment of fish to the commercial fishery across several age classes, which may provide some protection to individual age classes from over-harvesting. This would also reduce the noticeable effects of strong and weak years of recruitment on productivity, with less reliance on any one particular age class dominating

the fishery. It would also make it harder to follow the success of any particular age class through time.

The occurrence of only a few old (>8 years) age classes of *G. tricuspidata* in catches despite a maximum age of at least 24 years suggests that the species has been heavily fished and predominantly based on the young fish entering the fishery. This was confirmed by the fact that the majority of the estimates of fishing mortality were greater than the estimated natural mortality. The general absence of larger and older fish in catches is not a gear selectivity issue; the selectivity of the nets used in the fishery does not exclude the capture of larger (>350 mm L_F) and presumably older *G. tricuspidata* (Broadhurst *et al.*, 2003).

MORTALITY

The estimates of Z (0.30–1.01) varied greatly among estuaries and were high for a species that can potentially live up to 24 years. In the case of Wallaga Lake, the high value of Z may be a consequence of it having been closed to the sea and therefore limiting recruitment, as discussed above. Such a situation may not be stable, being dependent on the state of the estuary mouth at any given time and the history of it opening and closing. In any case, the range of the estimates of Z provides a further demonstration of the dynamic nature of estuarine fish populations.

It was estimated that fishing mortality was greater than natural mortality, and thus the exploitation rate was >0.50 , for virtually all of the estuaries at the lowest bound of M (0.16). Fishing mortality was only greater than the highest bound of M (0.30) for Wallaga Lake. The range of estimates of M is similar to that of other species of fish in eastern Australia with similar life histories (*i.e.* mature at 2–3 years and live >20 years), including *Acanthopagrus australis* (Günther) and *N. douglasii* (Gray *et al.*, 2000; Stewart & Hughes, 2009). While the difficulty in estimating mortality rates in exploited fish populations is acknowledged, the confidence is high that the ranges of estimates presented here are reasonable. Nevertheless, continued monitoring of populations over many years may facilitate more accurate estimates of mortality by allowing estimation of changes in individual age cohorts through time (Ricker, 1969).

CONSEQUENCES FOR FUTURE ASSESSMENTS

This study has demonstrated the dynamic and complex characteristics of populations of *G. tricuspidata* in eastern Australia and the uncertainties in assessing their life-history variables. Nevertheless, the data presented here indicate that *G. tricuspidata* has been subject to high levels of fishing and total mortality. Since these samples were collected, reported total commercial catches of *G. tricuspidata* have reduced to *c.* 400 t year⁻¹ due to the complete or partial removal in 2002 of commercial fishing in 30 estuaries in NSW, including Lake Macquarie, St Georges Basin and the Tuross River. Now only recreational fishing (hook and line) of finfish is permitted in these estuaries. In 2005 the MLL for *G. tricuspidata* was increased from 250 to 270 mm L_T , providing greater protection to immature fish. The low market value of *G. tricuspidata* also continues to deter many commercial fishers from targeting this species, further reducing some effective fishing mortality. Catch-per-unit-of-effort data of the estuarine commercial gillnet catches (combined across

all estuaries) of *G. tricuspidata* over the past 5 years have been stable, indicating a stable stock throughout NSW (Scandol *et al.*, 2008).

Although current management arrangements appear to be sufficient for the sustainable harvesting of this species at present levels of extraction, the fishery is primarily dependent on the harvesting of new recruits upon reaching the MLL. Should commercial or recreational catches greatly escalate above current levels, then a reassessment of the status of populations of *G. tricuspidata* will be required. This would best be done by assessing changes in the age compositions and mortality rates of populations. Because of the considerable variation in the length at age of *G. tricuspidata*, using length alone to monitor populations for resource assessment may not prove effective. Fishery-independent sampling may be required to provide consistent and scientifically rigorous assessments of populations of *G. tricuspidata*, as well as populations of other key species, across estuaries subject to different management regimes. Finally, the effects of harvesting large quantities of the dominant mobile teleost herbivore in these estuarine systems are unknown. Elsewhere, dominant herbivorous fishes have been shown to be important in structuring reef ecosystems and the large-scale removal of such fishes can have negative consequences on reefs (McClanahan, 1995; Bellwood *et al.*, 2004; Graham *et al.*, 2006). The potential ecosystem-wide effects of harvesting *G. tricuspidata* need to be considered in future fisheries management plans.

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