Vol. 129: 31-40, 1995 | MARINE ECOLOGY PROGRESS SERIES Mar Ecol Prog Ser | Published December 14

Large lutjanid and serranid fishes in tropical estuaries: Are they adults or juveniles?

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ABSTRACT: Two serranid fishes, *Epinephelus coioides* and *E. malabaricus*, and 2 lutjanid fishes, *Lutjanus argentimaculatus* and *L. russelli*, are common in estuaries of northeastern tropical Australia. Reviews of the literature suggest that, at least for *E. coioides*, *E. malabaricus* and *L. argentimaculatus*, both juveniles and adults occur in estuaries. I conducted the present study to determine if estuarine populations of these 4 species did in fact contain adults, or if they were comprised entirely of juveniles. I collected *E. coioides*, *E. malabaricus*, *L. russelli* and *L. argentimaculatus* from estuaries in northeastern Australia. I compared the size, age and reproductive maturity of fishes from estuaries to fishes of the same species from offshore areas. The estuarine populations of all 4 species seemed to consist entirely of reproductively immature fish. All fish from the estuaries possessed immature gonads, and for both serranids (protogynous hermaphrodites) all were females. Furthermore, all fish from the estuaries were much smaller and younger than the largest fish of the same species from offshore. This implies that estuaries are important juvenile development grounds for these lutjanids and serranids.

KEY WORDS: Estuary · Juvenile · Nursery ground · Life-cycle · Size · Age · Reproductive maturity

INTRODUCTION

It is generally considered that estuaries in tropical Indo-Pacific waters are dominated by small fishes, including the juveniles of many species (Blaber 1980, Blaber et al. 1985, 1989, Robertson & Duke 1987). While a number of studies have considered estuarine fish assemblages in the Indo-Pacific, the biology of individual species has received little attention. This is particularly true of habitat associated predators such as lutjanids and serranids. The structurally complex habitats used extensively by these species (Sheaves 1992) inhibit sampling with seine and gill nets, the gears employed in most studies. In consequence, members of these families have usually been sampled only in low numbers. Despite this, these fish comprised a major part of anglers' catches from an estuary in tropical Australia (Sheaves 1992), and fish trapping data (Sheaves 1992, 1995) suggests that gears which target appropriate habitats may produce quite high catch rates of lutjanids and serranids.

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Recent reviews (Randall & Ben-Tuvia 1983, Allen 1985, Allen & Talbot 1985, Randall 1987, Randall et al. 1990) list *Lutjanus argentimaculatus* and *L. russelli* as inhabitants of coastal and estuarine waters. These works suggest that within estuaries, *L. argentimaculatus* occurs as juveniles and sub-adults while *L. russelli* is present as juveniles only. However, few studies of Indo-Pacific estuarine fishes have reported the reproductive status or life-history stages of these species. Where such classification has been carried out, *L. russelli* populations have usually been classified as juveniles (Blaber 1986, Blaber & Milton 1990, Thollot et al. 1990). While most studies that have recorded *L. argentimaculatus* from estuaries have reported the presence of juveniles, a number of studies have also reported the presence of adults (Shine et al. 1973, Blaber 1980, Blaber et al. 1989, Blaber & Milton 1990, Thollot et al. 1990). While Blaber (1980) stated that 'all reproductively immature fish were classed as juvenile', in most cases the criteria used to evaluate reproductive status are unclear.

The life history of 2 serranids in Indo-Pacific estuaries is also uncertain. *Epinephelus coioides* and *E. mala-*

baricus are both known to inhabit coastal and estuarine waters (Randall & Ben-Tuvia 1983, Randall et al. 1990). Where life-history stages have been recorded, both juvenile and adult *E. coioides* (recorded as *E. suillus*, a synonym of *E. coioides*; Randall et al. 1990) (Blaber & Milton 1990) and *E. malabaricus* (Thollot et al. 1990) have been reported. However, the criteria used for these determinations were not presented. Thus, there is little direct evidence of the reproductive or life-history status of either the 2 lutjanids or these 2 serranids within Indo-Pacific estuaries.

In the present study, I determined the reproductive statuses of *Epinephelus coioides*, *E. malabaricus*, *Lutjanus argentimaculatus* and *L. russelli* within estuaries in tropical northeastern Australia. Assessment was made in terms of the maturity (macroscopic and histological) and relative size of gonads. I also compared the reproductive statuses and age and size structures of fishes of these 4 species from estuaries to fishes of the same species from offshore waters.

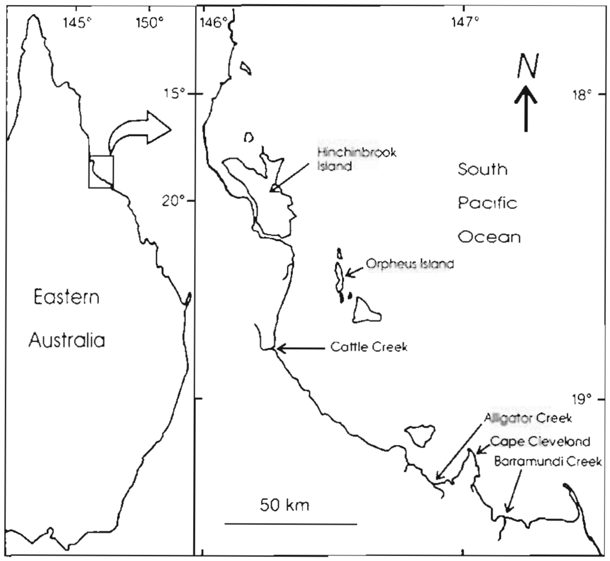

Fig. 1. Sampling sites for the collection of lutjanid and serranid fishes from estuarine and nearshore waters

MATERIALS AND METHODS

Collection of samples. Between October 1990 and November 1994, specimens of *Epinephelus coioides*, *E. malabaricus*, *Lutjanus argentimaculatus* and *L. russelli* were collected to provide size structure, gonad and otolith samples.

Estuary samples were collected from fish trap catches supplemented by line caught fish, either captured during research or supplied by anglers. Between October 1991 and August 1993, extensive fish trapping was conducted in Cattle, Barramundi and Alligator Creeks (Fig. 1), using 12 Antillean-Z fish traps (1800 mm long, 1100 mm wide, 600 mm high, plan area approx. 1.53 m^2, volume approx. 0.92 m^3) with 12.5 mm square galvanised steel mesh and straight entrance funnels (inner opening 260 × 150 mm). This sampling included estuaries spanning about 145 km of coast and consisted of 2736 trap sets. Trapping extended over the entire lengths of these creeks which could be navigated in a 3 m dingy (about 15 km for Cattle and Barramundi Creeks, and 7.5 km for Alligator Creek), and occurred once every 3 mo during the study period. The traps used and sampling procedures are described in detail in Sheaves (1995). Line caught fish originated from a large number of estuaries between Hinchinbrook Island (approximately 18° 10′ S, 146° 10′ E) and Barramundi Creek (19° 25′ S, 147° 10′ E), a length of coast extending approximately 220 km. In an attempt to ensure that fish of the largest sizes available in estuaries were obtained, all line fishing was aimed at catching large individuals, and pamphlets requesting large fish of the required species were distributed through angling clubs and displayed in fishing tackle shops. In addition, requests for samples were made directly of anglers encountered in the field.

Samples were also collected from waters offshore of the estuaries studied. Sampling was conducted on offshore reefs around Cape Cleveland (a coastal headland) and Orpheus Island (a near-shore island) (Fig. 1), utilising the same fish traps and trapping methods used for estuary sampling. These samples were supplemented by fish from angler donations, trawl samples from Cleveland Bay (Fig. 1), and fish collected during research trips for other projects.

Determination of reproductive status. Immediately upon capture or receipt of donated samples, fish were placed on ice where they were kept until dissected (less than 12 h). Gonads were preserved in FAAC fixative (formaldehyde 4%, acetic acid 5%, calcium chloride 1.3%; McCormick & Molony 1992). Gonads were weighed within 2 d of preservation and returned to the fixative where they were stored until histological preparation was carried out (within 1 mo).

Fish were initially classified as females, males or of indeterminate sex from the macroscopic appearance of their gonads. Histological examination was carried out on all gonads greater than approximately 1 mm diameter. Smaller gonads were not examined histologically as they were difficult to process and it was considered unlikely that they would be sexually mature. In support of this premise, most of the smaller gonads examined contained only oogonia or spermatogonia (precursors of oocytes or spermatozoa respectively) rather than more developed gonadial tissue.

A section from each of the anterior, central and posterior regions of 1 gonad from each fish was embedded in paraffin wax and transverse sections cut at 6 µm. The sections were stained with haematoxylin and eosin. The sex of each gonad was determined by microscopic examination and for each female, the stage of the most advanced oocyte was recorded.

Ovarian tissue was staged according to the scheme described by West (1990) as follows: Stage 1, chromatin nucleolar stage; Stage 2, perinucleolar stage; Stage 3, yolk vesicle formation; Stage 4, vitellogenic stage; Stage 5, ripe.

For each male, the most advanced stage of spermatic tissue present was recorded.

Growth from mark-recapture. In conjunction with fish trapping studies in Cattle, Barramundi and Alligator Creeks (Sheaves 1993, 1995, unpubl. data) between 14 October 1991 and 25 August 1993, *Epinephelus coioides*, *E. malabaricus*, *Lutjanus argentimaculatus* over 150 mm and *L. russelli* over 100 mm were tagged and released. In addition to fish tagged during fish trapping, fish captured by hook and line were also tagged. All fish were tagged with Hallprint medium T-bar anchor tags. Upon capture and recapture the fork length (FL) of each fish was recorded to the nearest millimetre. To prevent the use of non-independent samples, where fish were recaptured on more than one occasion only data from the longest period at liberty was used in the analysis of growth.

As growth must be zero at time zero, for all species the regressions of growth on days at liberty were forced through the origin. As the variable 'days at liberty' was not under the control of the investigator, Model 2 regression was appropriate (Sokal & Rohlf 1981, p. 459). Thus, the reduced major axis (geometric mean) regression coefficient (b') and its standard error were calculated (Sokal & Rohlf 1981, p. 550) and used to calculate growth rates in preference to the simple least squares linear regression coefficient. Before calculating the regression equations, any outlying points (externally studentized residuals >2) or extremely influential points (leverage $>2p/n$, where p = number of explanatory variables and n = sample size) (Belsley et al. 1980) were omitted from the analyses.

Otolith aging. During this study, the sagittae of 92 *Epinephelus coioides*, 174 *E. malabaricus*, 298 *Lutjanus argentimaculatus*, and 423 *L. russelli* were used for age determination.

All otolith reading was conducted on sectioned sagittae. Right or left otoliths were selected at random for processing. Sectioning and counting were carried out as described by Ferreira & Russ (1992).

To determine if the opaque bands were annual marks, tetracycline marking of otoliths of tagged fishes of all species was carried out at Alligator Creek (approx. 19° 20′ S, 146° 55′ E) between January 1991 and March 1994. The fish were collected while fish trapping or caught on hook and line. Selecting only fish greater than 120 mm FL, 310 *Epinephelus coioides*, 219 *E. malabaricus*, 193 *Lutjanus argentimaculatus*, and 560 *L. russelli* were marked with T-bar anchor tags, injected with oxytetracycline (dosage of 50 mg kg^{-1} of body weight) into the coelomic cavity, and released. Recaptured, tetracycline-marked fish were processed and their otoliths prepared as described above for non-marked fish. The sectioned sagittae from these fish were observed microscopically under white light, ultraviolet light (UV) and a combination of both.

RESULTS

Comparison of size structures (estuary/offshore)

It was assumed that for all 4 species, the samples collected included fish of the largest sizes usually encountered in estuaries in the study area. It was clear from conversations with anglers that most tended to donate fish when they caught what they considered to be a large fish of that species. Thus, it is likely that few fish larger than those collected were caught from estuaries and not reported.

Samples were much more difficult to obtain from offshore areas than from estuaries. This is reflected in small offshore sample sizes (Table 1). Despite the small offshore samples for *Epinephelus coioides*, *E. malabaricus* and *Lutjanus russelli*, fishes of considerably larger sizes were trapped from offshore waters than from estuaries using the same fish traps. Apparently, if larger fishes of these species were available in these estuaries, they could have been trapped. Thus, given the spatially and temporally extensive trapping undertaken in estuaries during this study, it seems likely that the maximum sizes trapped reflected the normal maximum sizes of these species inhabiting estuaries of tropical northeastern Australia. This is supported by the fact that no *E. coioides*, *E. malabaricus* or *L. russelli* larger than those trapped were obtained from anglers fishing in the estuaries where trapping was carried out. Furthermore, for these species, only 1 individual larger than the largest trapped was obtained from any estuary within the study area. This was a line caught *L. russelli* (232 mm FL) which was slightly larger than the largest trapped (220 mm FL). During the study, *L. argentimaculatus* were only trapped occasionally in estuaries and not at all in offshore waters. However, the maximum size recorded for line caught fish from estuaries was substantially smaller than the maximum size from offshore (Table 1).

Reproductive status

Except for *Lutjanus russelli* in April, fishes of each species were collected from estuaries for gonad examination in all months (Table 2). Compared to fishes from offshore, the gonads of fishes of all 4 species from estuaries were small relative to body weight (Table 3, Fig. 2).

Table 1. Size ranges of *Epinephelus coioides*, *E. malabaricus*, *Lutjanus argentimaculatus* and *L. russelli* caught in Antillean-Z fish traps, and supplied by anglers

	Estuary FL range (mm)	n	Offshore FL range (mm)	n
E. coioides				
Trap	120-500	280	443-915	8
Angler collection	171-386	72	645-1085	7
E. malabaricus				
Trap	122-619	334	582-762	5
Angler collection	180-515	153	523-1199	5
L. argentimaculatus				
Trap	71-212	5	–	–
Angler collection	147-541	301	412-890	26
L. russelli				
Trap	28-220	2223	99-321	30
Angler collection	130-232	154	189-445	202

For all species, a number of fishes had gonads too small to enable confident macroscopic sex determination (Table 3). Of the fish from estuaries that could be sexed, all *Epinephelus* spp. were identified as females, while for *Lutjanus* spp. both females and males were collected in similar numbers. Histological examination of the larger gonads from estuary samples supported the results of macroscopic examination (Table 4). All *Epinephelus* spp. with gonads sufficiently developed to allow sex determination were females, while for *Lutjanus* spp. both females and males were identified.

The ovaries of all female fish from estuaries were thin [max. diameter: 7 mm *Lutjanus argentimaculatus* (540 mm FL); 3 mm *L. russelli* (228 mm FL), *Epinephelus coioides* (471 mm FL) and *E. malabaricus* (595 mm FL)] and less than $1/4$ the length of the body cavity. No oocytes were visible to the naked eye. For all species from estuaries, histological examination showed the most advanced oocytes to be chromatin nucleolar stage (Stage 1) or perinucleolar stage (Stage 2), even during months when reproductively active fish were present offshore (Fig. 2). Neither α or β stage atretic structures (Hunter

Table 2. Summary of *Epinephelus* spp. and *Lutjanus* spp. collected for sex status determination

Month	Location	*E. coioides* Max. FL (mm)	n	*E. malabaricus* Max. FL (mm)	n	*L. argentimaculatus* Max. FL (mm)	n	*L. russelli* Max. FL (mm)	n
January	Estuary	262	16	433	27	490	25	200	23
	Offshore	780	3	–	–	592	5	337	1
February	Estuary	384	14	544	21	475	23	183	17
	Offshore	915	3	–	–	–	–	382	23
March	Estuary	377	11	498	12	466	39	136	9
	Offshore	645	1	–	–	–	–	365	20
April	Estuary	387	9	545	11	411	12	–	–
	Offshore	436	2	–	–	445	31		
May	Estuary	405	18	525	13	422	16	159	16
	Offshore	–	–	687	2	636	5	362	37
June	Estuary	471	10	400	13	482	29	228	23
	Offshore	1085	1	–	–	615	1	296	10
July	Estuary	315	8	433	12	410	17	230	27
	Offshore	–	–	–	–	476	2	298	23
August	Estuary	333	11	595	16	288	11	158	14
	Offshore	–	–	–	–	–	–	360	5
September	Estuary	387	18	422	18	540	31	232	18
	Offshore	–	–	–	–	–	–	309	27
October	Estuary	394	13	594	26	541	44	204	23
	Offshore	–	–	–	–	654	7	405	13
November	Estuary	368	17	499	20	487	28	209	38
	Offshore	–	–	523	3	890	4	329	28
December	Estuary	420	11	562	19	450	23	205	21
	Offshore	–	–	–	–	528	1	410	8

Table 3. Summary of sexes and gonad sizes of *Epinephelus* spp. and *Lutjanus* spp. determined by macroscopic examination. The numbers of fish and the maximum proportion of body weight contributed by the female or male gonad are shown. Ind.: sex indeterminate

Species		Estuary n	Estuary Max. proportion of body weight ($\times 10^{-4}$)	Offshore n	Offshore Max. proportion of body weight ($\times 10^{-4}$)
E. coioides	♀	144	2.7	7	8.3
	♂	–	–	3	7.9
	Ind.	12	–		–
E. malabaricus	♀	185	8.9	–	–
	♂	–	–	3	6.8
	Ind.	23	–	2	5.0
L. argentimaculatus	♀	141	21.2	12	178.0
	♂	132	9.0	13	27.5
	Ind.	25	–	–	–
L. russelli	♀	53	22.4	108	406.0
	♂	55	7.5	114	40.3
	Ind.	121	–	4	–

& Macewicz 1985, Hunter et al. 1986, Kjesbu & Klungsoyr 1991) were found in the ovaries of any fish from estuaries. Thus, on the basis of gonad size and of macroscopic and histological examination of ovaries, all female fishes of all 4 species from estuaries were classified as reproductively immature.

The testes of all male *Lutjanus argentimaculatus* and *L. russelli* from estuaries were firm, narrow and strap-like, and comprised only a small proportion of body weight (Table 3). The most advanced spermatic tissue present in most *L. argentimaculatus* and *L. russelli* testes from estuaries were primary and secondary spermatocytes. However, as well as containing large areas of immature spermatic tissue, the testes of a sample of 3 male *L. argentimaculatus* (432 to 541 mm) collected from the mouth of Ross Creek (Fig. 1) in October 1993 contained some spermatids and spermatozoa. In these fish, the spermatids and spermatozoa were confined to the proximal (posterior) parts of the testes. As the testes of these males were very small and the area of reproductive development limited, it was assumed that they represented fish in early stages of reproductive maturity. Four large female *L. argentimaculatus* sampled at the same time were all reproductively immature. This included the largest female *L. argentimaculatus* (540 mm) obtained from estuaries during the study.

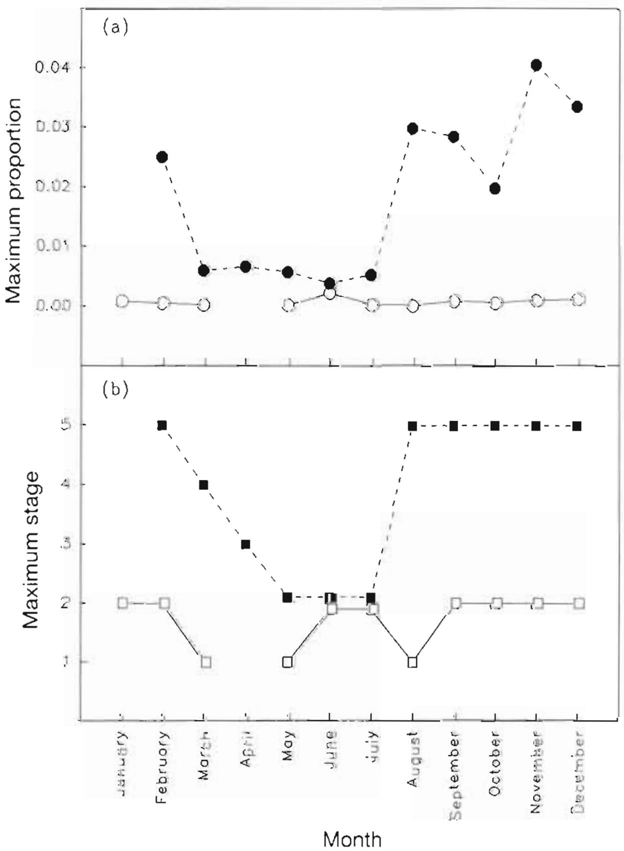

Fig. 2. Changes in relative gonad size and stage over time for *Lutjanus russelli* from (O, □) estuaries and (●, ■) offshore waters. Data presented are maxima of (a) gonad weight as a proportion of cleaned weight and (b) maximum gonad stage for each month

Table 4. Summary of results of histological examination of gonads of *Epinephelus* spp. and *Lutjanus* spp. collected from estuary and offshore waters. Ind.: sex indeterminate

		Estuary n	Estuary Maximum stage (♀)	Offshore n	Offshore Maximum stage (♀)
E. coioides	♀	149	2	7	2
	♂	0	–	3	–
	Ind.	7	–	0	–
E. malabaricus	♀	199	2	2	2
	♂	0	–	3	–
	Ind.	9	–	0	–
L. argentimaculatus	♀	159	2	12	5
	♂	134	–	13	–
	Ind.	5	–	0	–
L. russelli	♀	93	2	108	5
	♂	108	–	116	–
	Ind.	28	–	2	–

Table 5. Summary of tagging and recapture data showing numbers of fish tagged and recaptured, the maximum days at liberty (DAL), and maximum growth between recaptures

Species	No. tagged	No. recaptured	Max. DAL	Max. growth
Epinephelus coioides	398	104	619	129
Epinephelus malabaricus	293	63	728	202
Lutjanus argentimaculatus	120	10	395	66
Lutjanus russelli	1070	43	238	44

Table 6. Summary of the correlation between growth rate (size increment per unit of time) and mean fork length (for the increment in question) for *Epinephelus* spp. and *Lutjanus* spp.

Species	r	n	p
Epinephelus coioides	-0.1018	104	0.3036
Epinephelus malabaricus	-0.0189	63	0.3957
Lutjanus argentimaculatus	-0.4478	10	0.1944
Lutjanus russelli	0.0448	43	0.7754

Table 7. Summary of the regression between growth rate and days at liberty for *Epinephelus* spp. and *Lutjanus* spp. For each species the reduced major axis (geometric mean) regression coefficient (b') and its standard error are presented together with the coefficient of determination (r^2)

Species	b'	SE	r^2	df
Epinephelus coioides	0.2253	0.0072	0.9042	95
Epinephelus malabaricus	0.2565	0.0100	0.9070	61
Lutjanus argentimaculatus	0.1780	0.0074	0.9896	5
Lutjanus russelli	0.1911	0.0107	0.8783	38

Growth from mark-recapture

Capture and recapture data for *Epinephelus coioides*, *E. malabaricus*, *Lutjanus argentimaculatus* and *L. russelli* from estuaries are summarised in Table 5. For each of the 4 species, growth rate (size increment per unit of time) and mean fork length were not significantly correlated (Table 6). Thus, for all species, the growth rate for estuary fishes was independent of fork length over the size ranges sampled.

For all 4 species, there was a strong linear relationship between growth and period at liberty (Table 7). For *Epinephelus coioides* (n = 104), interpolation suggested a growth rate of approximately 82 mm yr^{-1}, for *E. malabaricus* (n = 63), approximately 94 mm yr^{-1}, for *Lutjanus argentimaculatus* (n = 10), approximately 65 mm yr^{-1}, and for *L. russelli* (n = 43), approximately 70 mm yr^{-1}.

Otolith aging

Of the tetracycline-marked fish, 4 *Epinephelus coioides*, 5 *E. malabaricus*, 2 *Lutjanus argentimaculatus* and 1 *L. russelli* had been at liberty for more than a year. In each case, sectioned sagittae of the tetracycline-marked fish showed a single opaque band outside of the fluorescent tetracycline mark, indicating that the opaque bands did indeed represent an annulus.

Further evidence that the opaque bands represented annuli came from growth rates from mark-recapture. For each species, when a regression line derived from growth from mark-recapture data and centred on the mean size and count from otolith data was plotted with the otolith count data, the growth rate (slope) from mark-recapture corresponded well with the growth between age classes from otolith aging (Figs. 3 & 4).

Estuary samples

For each species, there was a broad variation in sizes at each count; however, there was a general trend for the number of annuli to increase with increasing fish size. From estuary samples, *Epinephelus coioides* (n = 87) displayed between 1 and 5 annual rings (Fig. 3a); *E. malabaricus* (n = 171), between 0 and 7 rings (Fig 3b); *Lutjanus argentimaculatus* (n = 276), between 0 and 8 rings (Fig. 4a); and *L. russelli* (n = 196), between 0 and 2 rings (Fig. 4b).

Offshore samples

Few samples of *Epinephelus coioides* (n = 5) or *E. malabaricus* (n = 3) were available from offshore. However, for each species the largest individual from offshore displayed more rings (*E. coioides*, 16; *E. malabaricus*, 8) than did the largest estuary fish (Fig. 3a, b). *Lutjanus argentimaculatus* (n = 22) displayed up to 32 annuli, with growth appearing to slow in older fish (Fig. 4a). *L. russelli*, with an extensive offshore sample (n = 227), showed a maximum of approximately 17 annual rings with growth appearing to slow after approximately 3 yr (Fig. 4b). For *L. argentimaculatus*, and particularly *L. russelli*, growth appearsed to slow shortly after the transition from estuarine to offshore habitats.

DISCUSSION

The size, age, growth and reproductive data presented here strongly suggest that the estuary popula-

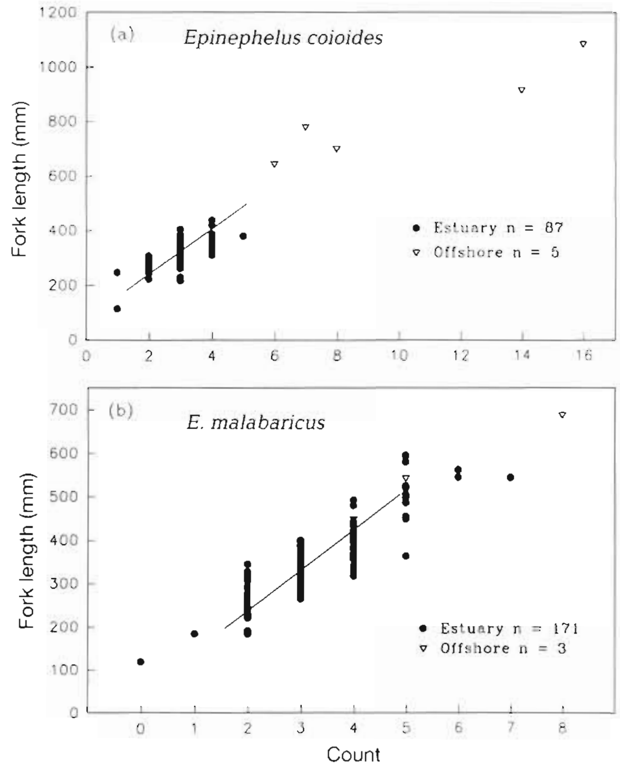

Fig. 3. Relationship between fork length and sagittal otolith counts for (a) *Epinephelus coioides* and (b) *E. malabaricus*. Line represents the growth from mark-recapture data. (●) Fish from estuaries, (▿) fish from offshore

tions of *Epinephelus coioides*, *E. malabaricus*, *Lutjanus argentimaculatus* and *L. russelli* studied were comprised of juveniles.

Size, age and growth

Even though fish trapping in estuaries in tropical north Queensland was extensive, both spatially and temporally, the maximum sizes of *Epinephelus coioides*, *E. malabaricus* and *Lutjanus russelli* trapped were considerably smaller than the largest sizes captured in the same traps from offshore waters. Similarly, collections from anglers fishing in estuaries produced relatively small individuals compared to fish collected from offshore. While *L. argentimaculatus* trapped poorly, considerable numbers of specimens were collected by angling or were donated by anglers. All the fish comprising these samples were relatively small compared to fish obtained from offshore waters. As *L. argentimaculatus* is an important recreational sportfish in North Queensland estuaries, and close contact was kept with local fishing clubs, it seems likely that few if any larger *L. argentimaculatus* were caught and not reported. The largest *E. coioides* (387 mm FL; Sheaves 1992), *E. malabaricus* (440 mm FL; Sheaves 1992) and *L. argentimaculatus* (320 mm standard length, SL; Blaber et al. 1989) previously reported from estuaries in tropical Australia are all smaller than the largest fish from estuaries in this study. The largest *L. russelli* (237 mm FL; Sheaves 1992) previously reported from Australian estuaries was of similar size to the largest individual captured during the present study (232 mm FL).

While many studies in both estuarine and offshore habitats in the tropical Indo-Pacific have reported at least one of these species, sample sizes have generally been small and fish sizes rarely quoted. Where sizes are available for *Lutjanus argentimaculatus* and *L. russelli* (Blaber et al. 1989) the same pattern as in the present study is seen: larger sizes from offshore locations than from estuaries.

There is some anecdotal evidence from the recreational fishing sector of large *Epinephelus* spp. occurring in estuaries in tropical northeastern Queensland. However, the discrepancy between the maximum sizes trapped in estuaries and the maximum sizes able to be caught in the same traps in offshore waters suggests that if larger fish were common in estuaries they would

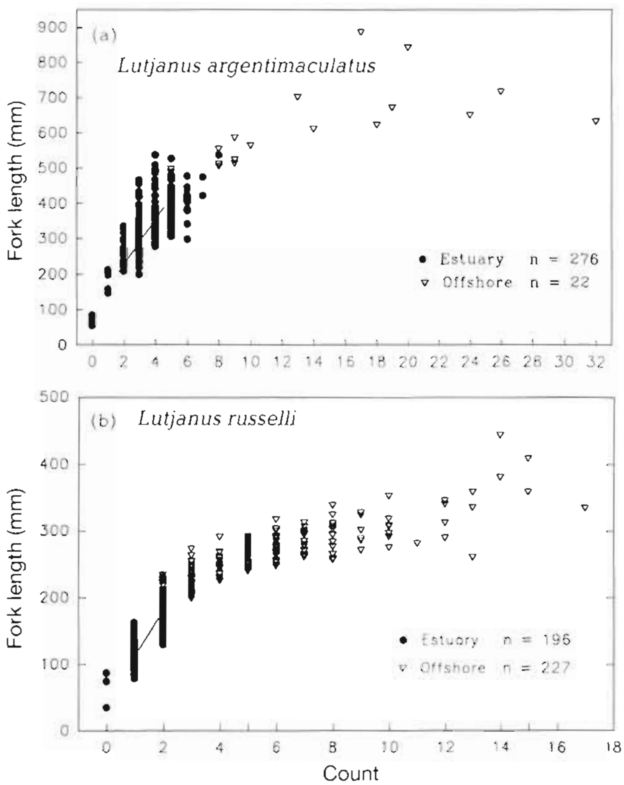

Fig. 4. Relationship between fork length and sagittal otolith counts for (a) *Lutjanus argentimaculatus* and (b) *L. russelli*. Line represents the growth from mark-recapture data. (●) Fish from estuaries, (▿) fish from offshore

have been captured. It appears that if large *Epinephelus* spp. do occur in estuaries, they probably constitute only a minor part of the main estuary population.

From the otolith data it seems that the maximum period spent in estuaries was about 5 yr for *Epinephelus coioides*, 7 yr for *E. malabaricus*, 8 yr for *Lutjanus argentimaculatus* and 2 yr for *L. russelli*. The exact period of residency of these species in estuaries is difficult to determine. The process of reading sectioned otoliths is subjective (Campana & Neilson 1985, Thresher 1988, Talbot & Doyle 1992), particularly for young fish, as it is difficult to determine exactly what period of time has elapsed prior to the deposition of the first annulus. While the counting of daily rings may overcome this, a second problem remains. The aging of fish from an estuary only tells the age of fish still resident within the estuary. Unless fish can be sampled immediately on exiting an estuary and it can be demonstrated clearly that those fish have originated from that estuary, it is impossible to determine the range of ages at which fish actually migrate from estuaries.

For each of the 4 species studied here, maximum ages determined for fish from estuaries were considerably younger than those for fish from offshore waters. Additionally, for each species the size at age determined from sectioned otoliths agreed well with the growth data from mark-recapture. Furthermore, as the growth of fish is expected to follow a curvilinear trajectory, with reduced growth at larger sizes (Pauly 1984), the linear growth of all 4 species in estuaries, implied by the mark-recapture data, is consistent with rapid growth in the rising part of an asymptotic growth curve. This suggests that the fish from estuaries were sampled over a restricted section of the lower part of the growth curve only.

Reproductive status

All female *Lutjanus argentimaculatus*, *L. russelli*, *Epinephelus coioides* and *E. malabaricus* collected from estuaries were found to be reproductively immature. No reproductively active individuals were found. This included periods when reproductively active females were present in samples from offshore. As the juvenile period lasts until maturation of the first gametes (Balon 1984), all the female fish sampled from estuaries can be considered juveniles. Although a sample of 3 male *L. argentimaculatus* from one estuary showed some degree of reproductive maturity, it is assumed that these were fishes in the early stages of reproductive development only. The testes of these males were very small, and mature spermatic tissue was limited to proximal regions of the gonads. Furthermore, 4 large females sampled at the same time showed no sign of reproductive development, suggesting that the spermatic development was not related to spawning at that time. It is possible that these were a group of large fish preparing to migrate from the estuary. Of the *E. coioides* and *E. malabaricus* possessing gonads advanced enough for sex determination, all individuals of both species were found to be females. As *Epinephelus* spp. are recognised as protogynous hermaphrodites (Bannerot et al. 1987, Randall et al. 1990) the presence of only non-reproductive females with poorly developed gonads suggests that the populations consisted of pre-reproductive individuals. Taken together, the data presented here strongly suggest that *L. argentimaculatus*, *L. russelli*, *E. coioides* and *E. malabaricus* do not become reproductively active within the estuaries studied. This implies that the estuarine populations of these species consist of juveniles. This is comparable with the situation in South Africa, where a large number of fish species use estuaries as juvenile habitats but return to the sea before attaining sexual maturity (Blaber & Cyrus 1983, Cyrus & Blaber 1984, Whitfield 1990). Similarly, in Florida, USA, juvenile *Sciaenops ocellatus* are found in estuaries but adults spawn in nearshore waters (Peters & McMichael 1987), and juvenile *Lutjanus griseus* are found in mangrove areas although adults spawn on offshore reefs (Starck & Schroeder 1970).

Estuaries as juvenile habitats for lutjanid and serranid fishes

Most previous studies have classified *Lutjanus russelli* from the tropical Indo-Pacific estuaries as juveniles (Allen 1985, Allen & Talbot 1985, Blaber et al. 1985, Blaber 1986, Blaber & Milton 1990, Thollot et al. 1990). The results of the present study agree with this classification. Where life-history stages have been recorded, previous studies (Shine et al. 1973, Blaber 1980, Blaber et al. 1985, Blaber & Milton 1990, Thollot et al. 1990) have classified estuary populations of *Epinephelus coioides*, *E. malabaricus* and *L. argentimaculatus* in the Indo-Pacific as being comprised of both juveniles and adults. The present study does not support this. Despite extensive collections, no female fish of any of the 3 species collected from estuaries possessed mature gonads. Along with the fact that fish collected from estuaries during this study were smaller and younger than those from offshore, this indicates that the populations of these species within the estuaries studied probably contain few adults, if any. However, it should be noted that as there are infrequent reports of anglers sighting large (>1 m) groupers in estuaries in northeastern Australia, it is possible that large *E. coioides* or *E. malabaricus* may occasionally be found in the estuaries studied.

The pre-reproductive statuses of *Lutjanus argentimaculatus*, *L. russelli*, *Epinephelus coioides* and *E. malabaricus* in the estuaries studied implies that they move offshore to spawn. The lack of large, old, reproductively active individuals suggests that adults of these species generally do not return to estuaries. In South Africa, 3 species of *Gerres* that leave estuarine juvenile habitats to spawn offshore do not usually return to estuaries (Cyrus & Blaber 1984). This is the case for most fish in South Africa that spawn offshore but use estuaries as juvenile habitats (Day et al. 1981). Previous workers have asserted that *L. argentimaculatus* (Johannes 1978, Thollot et al. 1990), *E. malabaricus* and *L. russelli* (Thollot et al. 1990) migrate offshore. Other studies have suggested that *L. argentimaculatus* and *L. russelli* (Allen 1985, Allen & Talbot 1985, Randall et al. 1990) occur as juveniles in estuaries and adults in offshore habitats, inferring migration away from the estuaries. Despite the necessity of a spawning migration for these fishes, few offshore movements have been documented for any of these species. One *L. argentimaculatus* tagged during a sportfish tagging program moved from an estuary on Hinchinbrook Island (Fig. 1) to a reef about 80 km to the northeast (ANSA 1991). An *E. malabaricus* tagged during the present study (length at release 480 mm FL) also moved offshore. It was tagged in Barramundi Creek (Fig. 1) and captured by an angler 17 mo later on Lodestone Reef, some 75 km to the north. The paucity of direct evidence of movement from estuaries to offshore habitats needs to be rectified. It may be that, while recapture rates are reasonably high within the estuaries where the fish are tagged, when tagged fish move out of estuaries, they mix with fish from other estuaries and spread out over large areas of offshore reef water, resulting in low probabilities of recapture. If so, a substantial tagging and recapture effort would be required to demonstrate movement offshore.

These species either can't or don't spawn in estuaries. However, the reasons why they migrate offshore and the cues that initiate migration are unknown. There are many possible reasons for spawning offshore rather than in estuaries. Perhaps the sperm or ova of these species are not viable in the extreme physical conditions prevalent in estuaries. Alternatively, an offshore migration may represent a mechanism for increasing genetic mixing. This could occur in 2 ways. Fish migrating offshore would be likely to breed with fish from other estuaries, and, after a planktonic larval stage followed by an offshore spawning migration, the offspring they produced would be unlikely to return to the location where they were spawned.

Estuaries are not the only habitats where juvenile *Lutjanus russelli* and *L. argentimaculatus* are found. Small *L. russelli* have been reported in small numbers from coastal seagrass beds (Blaber et al. 1992, Coles et al. 1993). Other studies of coastal seagrass beds (Robertson & Duke 1987) in tropical northern Australia failed to produce any *L. russelli* or *L. argentimaculatus*. As juvenile *L. argentimaculatus* and *L. russelli* have been reported from offshore habitats only sporadically and in low numbers, the importance of these areas as juvenile habitats is unclear. It is uncertain if juvenile *Epinephelus coioides* or *E. malabaricus* occur in habitats other than estuaries. Studies that have reported these species from coastal or reef habitats (e.g. Blaber et al. 1994) have not clearly identified the life-history stages present. Notwithstanding the potential for alternative habitats to provide nursery grounds for these 4 species, the presence of large numbers of functionally juvenile *E. coioides*, *E. malabaricus* and *L. russelli* in trap catches during this study, along with the fact that all 4 species are common components of estuary angling catches (Sheaves pers. obs.), suggests that these species are common in estuaries of northeastern Australia. This implies that estuaries are important nursery areas for these species, probably supplying a large part of the adult population found in offshore waters.

Acknowledgements. I thank all those who assisted in this project with the supply of fish for dissection. My particular thanks go to all the anglers who supplied fish and to the members of the Australian Institute of Marine Science, Fish Biology unit who supplied many fish from offshore. I also extend special thanks to B. Molony, G. Russ and D. Williams for their invaluable advice and support during this project.

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This article was presented by D. M. Alongi (Senior Editorial Advisor), Townsville, Australia

Manuscript first received: February 8, 1995
Revised version accepted: July 21, 1995