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Movement patterns of barramundi *Lates calcarifer*, inferred from $^{87}Sr/^{86}Sr$ and Sr/Ca ratios in otoliths, indicate non-participation in spawning

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ABSTRACT: The migration patterns of the large catadromous fish, barramundi *Lates calcarifer* in southern Papua New Guinea were examined by analysing $^{87}Sr/^{86}Sr$ and Sr/Ca ratios by MC-LA-ICPMS and LA-ICPMS, respectively. Individual migration histories between coastal and riverine habitats could be inferred from the $^{87}Sr/^{86}Sr$ ratios. These were used to calibrate the Sr/Ca ratios from a larger sample of fish and identify periods when the fish were resident in freshwater. The largest freshwater population of barramundi occurs in the middle reaches of the Fly River. We found that most adult barramundi from this population do not migrate annually to spawn on the coast. Fish vary in the age that they first enter freshwater, and most have arrived by sexual maturity (4 yr). We estimate that only half the adult fish in the Fly and nearby Kikori rivers have ever migrated back to the coast during their lifetime. This implies that many barramundi do not participate in spawning. Fish examined from the spawning ground were mostly marine residents, and some had spent short periods in rivers adjacent to their spawning ground. Tagging and scale chemistry studies from northern Australia have also found little evidence of movement of freshwater resident barramundi back to the sea. This implies that the phenomenon of non-participation in spawning may be widespread in this species. Our results suggest that freshwater fisheries for barramundi may have less effect on the spawning population than those in coastal regions and thus be able to sustainably remove a greater proportion of the population.

KEY WORDS: Barramundi · *Lates calcarifer* · $^{87}Sr/^{86}Sr$ ratios · Movement · Sr/Ca ratios · Spawning non-participation

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INTRODUCTION

The management of most fisheries worldwide assumes that most or all adults contribute to the spawning population. Reduced or delayed spawning has been recorded in some species, but it is not considered to be a common phenomenon (Woodhead 1979). Burton (1999) documented studies of several commercial species of fish where the spawning participation rates varied between 50 and 90% of the adult population. Other studies of both marine and freshwater fishes found that species often skip spawning when conditions are poor (Crim et al. 1992, Dion et al. 1994, Alekseyev et al. 1996, Rideout et al. 2000). Stock assessments of species with reduced spawning participation rates should be taken into account since population productivity may also be reduced.

Barramundi *Lates calcarifer* is a large centropomid fish that occurs throughout Southern and South East Asia, from India to northern Australia. It grows to over 20 kg in weight and is the largest species in freshwater reaches of rivers in northern Australia and adjacent southern Papua New Guinea. Barramundi are found in all the rivers and adjacent coastal parts of southwestern Papua New Guinea and are particularly abundant in the middle reaches of the large Fly River (Swales et al. 2000).

The life cycle of barramundi in Papua New Guinea is fairly well understood. They are protandrous herma-

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phrodites that spawn in marine salinities (>30) on the coast, 160 km west of the Fly River mouth during the monsoon wet season (November to March) (Moore 1979, 1982). Larvae enter coastal swamps filled by the monsoon rains and grow rapidly. They leave the swamps within a year and migrate to large rivers, particularly the Fly River, where they mature as males at about 500 mm TL and 3 yr of age. These males usually change sex between 75 (5 yr) and 1050 mm total length (TL) (10 yr old) (Moore 1979, Moore & Reynolds 1982) and the majority are female by 950 mm. Tagging studies have shown extensive movements of adult barramundi between the middle reaches of the Fly River and the coastal spawning ground (Moore & Reynolds 1982). Fish migrate from the Fly River to the spawning grounds during the pre-monsoon period (September to November). At this time, they are extensively caught by gill nets set along the banks of the lower estuary and form the basis of a valuable seasonal artisanal fishery in the region (Opnai & Tenakanai 1987, Kare 1995).

Based on these studies and similar findings from northern Australia (Davis 1986), most barramundi in Papua New Guinea are assumed to exhibit this life cycle. Thus, the large decline in catches of the seasonal artisanal fishery on the migrating adults in the mid 1990s was assumed to reflect a decline in the adult population as a result of overfishing of mature females (Milton et al. 1998). However, routine monitoring of fish populations in the middle Fly River found that although catches had declined, fish were still relatively abundant during the period when the artisanal fishery catch was negligible (Swales et al. 2000).

To better understand the dynamics of barramundi populations and manage the valuable artisanal fishery, we needed to re-examine the movement patterns of barramundi to ascertain the linkages between their coastal and freshwater populations. The contribution of freshwater fish to the spawning population can then be estimated and the 2 components managed more effectively. Recaptures from conventional tagging studies rarely provide evidence of the frequency of migrations by individuals because of their low number. Tagging studies of barramundi in Papua New Guinea and northern Australia (Moore & Reynolds 1982, Davis 1986) did show movements from freshwater to marine habitats but did not estimate migration frequency.

Migration frequency can be estimated from changes in the fish otolith concentration of elements such as Sr and Ba. These elements vary between marine and freshwaters and changes in their concentrations in otoliths have become a useful proxy to help understand the movements of fish between these environments. However, these relationships can be affected by a number of factors, such as fish physiology, growth rates and stress (Kalish 1992, Sadovy & Severin 1992, Secor & Rooker 2000). Sr/Ca ratios in otoliths vary widely among fish species collected in estuarine and marine waters (Secor & Rooker 2000). This can make inferences on fish movement from these data difficult to make (Milton & Chenery 2003). An alternative approach is to use $^{87}Sr/^{86}Sr$ ratios in otoliths (Kennedy et al. 1997). This approach has several advantages over Sr/Ca ratios. The isotopes are not selectively absorbed and thus closely reflect water ratios. The ratio is stable in marine waters (Hodell et al. 1989) but varies between river systems that differ in their underlying geology (Peterman et al. 1970). Thus, there is the potential to discriminate among river systems, or even branches of the same system (Kennedy et al. 2000, Milton & Chenery 2003).

Thus, the aims of this study were to (1) estimate the migration frequency between fresh and saltwater of barramundi populations resident in freshwater, particularly the middle Fly River, with $^{87}Sr/^{86}Sr$ ratios; (2) use the $^{87}Sr/^{86}Sr$ ratios to calibrate Sr/Ca ratios in a larger sample of fish in order to estimate the contribution of fish from freshwater, including the Fly River, to the spawning population; (3) examine available environmental catch monitoring data in the Fly River to assess the extent of seasonal changes in CPUE that are related to migration; and (4) review the life cycle of barramundi in Papua New Guinea and assess the implications for managing the coastal and inland fisheries.

MATERIALS AND METHODS

Sample collection. Otoliths were removed from adult barramundi caught with gill nets in the Fly, Strickland, Kikori, Mai, Morehead, Bensbach and Merauke rivers and on the coastal spawning grounds (Table 1, Fig. 1). Fish were measured (total length in mm), weighed (in g), sexed by macroscopic examination of gonads and otoliths dissected, washed with distilled water and dried with tissue paper before storage in polythene bags. All otoliths were removed from the fish within 1 h after capture, with the exception of the fish from Merauke River; these could not be processed until 3 h after the fish were caught, as they were purchased from the market.

In the laboratory, the otoliths were weighed (±0.1 mg) and embedded in polyester resin. Traverse sections were made through the origin with a diamond saw. Thin sections (300 µm) were mounted on labelled microscope slides and polished with diamond pastes (3 and 1 µ) until the surface was smooth. The surface of the section was then wiped vigorously on 2 occasions with a piece of tissue paper moistened with 0.5 M HNO_3 (Aristar). The rims of the cleaned sections were examined with a stereo microscope and where residual resin or diamond paste remained, it was brushed with a clean nylon brush that

Table 1. *Lates calcarifer*. Mean (±SE) length (TL in mm), weight (in kg) and date of collection of adult barramundi (>500 mm) caught at sites in southern Papua New Guinea and adjacent west Papua (see Fig. 1)

Site	Collection date	Mean length	Mean weight	N
Merauke River	May 2000	735 ± 44	5.3 ± 0.7	19
Bensbach River	August 2000	618 ± 8	3.2 ± 0.1	107
Morehead River	December 2000	674 ± 22	3.7 ± 0.4	19
Mai River	August 2000	625 ± 16	3.9 ± 0.3	25
Spawning ground	November 1999	710 ± 12	3.9 ± 0.2	67
	February 2001	739 ± 14	4.4 ± 0.3	75
	February 2002	730 ± 18	4.6 ± 0.5	38
Middle Fly River	August 1999	680 ± 13	3.9 ± 0.2	106
	October 2000	687 ± 8	3.9 ± 0.1	51
	August 2001	646 ± 12	3.3 ± 0.2	53
Strickland River	August 2001	692 ± 15	4.0 ± 0.3	22
Lower Fly River	September 2000	840 ± 15	6.2 ± 0.3	10
Kikori River	October 1999	708 ± 14	3.9 ± 0.2	87

had been rinsed in the HNO_3. After brushing, the sections were re-examined to ensure that the surface particles had been removed. Brushing was required for about 20% of all the sections, and it removed any residual diamond paste that may have contaminated the ablations at the otolith rim. The slides were then dried in a laminar cabinet under a positive airflow before being placed into plastic bags until analysed.

Sr isotope analysis. We analysed the $^{87}Sr/^{86}Sr$ ratios in a random subsample of otoliths from all sites with a P54 (VG Instruments) Multi-collector Inductively Coupled Plasma Mass Spectrometer fitted with a VG Microprobe 2 laser (LA-MC-ICPMS) to measure the Sr isotope composition of samples with high precision (Walder 1997, Halliday et al. 1998). The MC-ICPMS is fitted with 9 Faraday cups for signal detection; in this case, the ions were arranged as follows: L2-$^{84}Sr^+$; L1-$^{85}Rb^+$; Axial-$^{86}Sr^+$; H1-$^{87}Sr/Rb^+$; H2-$^{88}Sr^+$; H3-$^{89}Y^+$.

Prior to each day's analysis, the LA-MC-ICPMS was optimised for maximum Sr and Y signals and stability with 100 µg l^{-1} NIST SRM 987 solution of Sr doped with 10 µg l^{-1} Y and ablations of the North Sea deep water coral *Lophelia pertusa*, which has a typical Sr concentration of 8000 µg g^{-1}. For this optimisation, argon gas was fed through a Cetac MCN6000 de-solvating nebuliser and the output was coupled through the laser ablation cell before reaching the injector of the MC-ICPMS. Typical running conditions for the P54 MC-ICPMS were: plasma r.f power of 1350 W, plasma coolant gas of 13.0 l min^{-1}, plasma auxiliary gas of 1.10 l min^{-1}, injector gas of 0.75 l min^{-1}, and nebuliser sweep gas of 0.53 l min^{-1} (Milton & Chenery 2003).

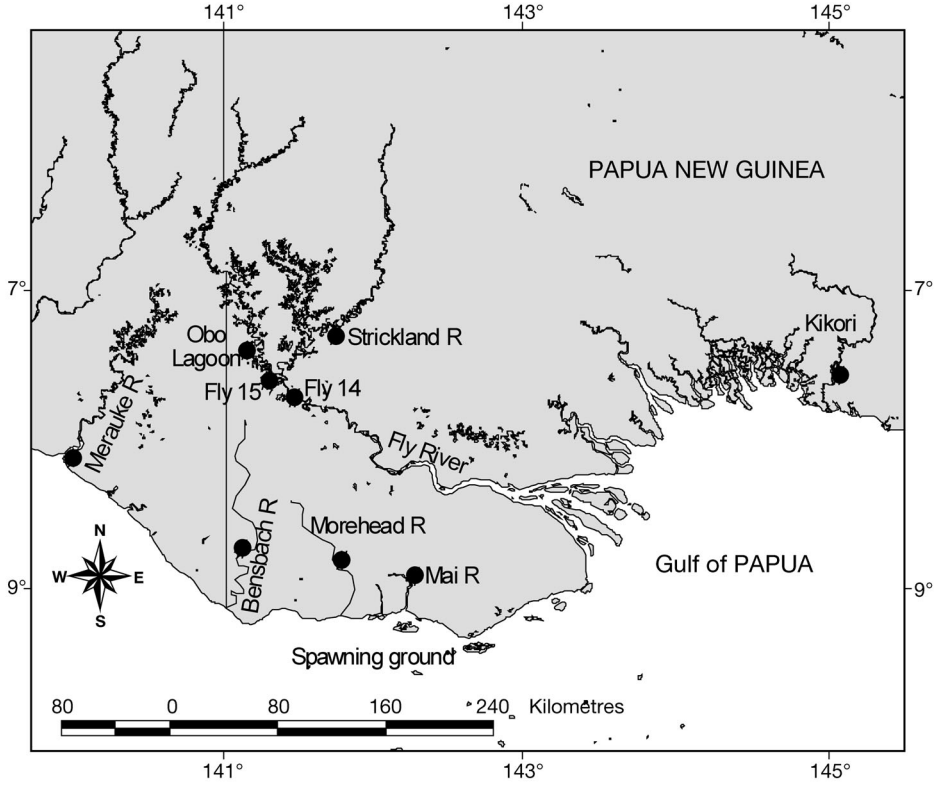

Fig. 1. Map of southern Papua New Guinea showing sites where fish were collected for otolith analysis and catch monitoring

The laser ablation system was a VG Microprobe 2, operating at 266 nm wavelength. Laser conditions, such as energy and beam size, were varied between sample types to give a total Sr signal of greater than 1 V where possible, depending on the minimum Sr concentration in the otolith. Sr concentrations in the otolith varied by up to a factor of about 6 (500 to 3000 µg g^{-1}). Typical laser parameters were 0.56 mJ pulse energy, 150 µm wide oval ablation path, 3 Hz firing and 10 µm s^{-1} stage translation. Laser conditions for ablating the coral *Lophelia pertusa* were somewhat less intense because of the higher Sr concentration.

Transects of up to 250 ablations were made in a continuous transect across the distal portion of the otolith from the rim to the core. Initially, we made multiple transects along different growth axes (distal and proximal) on 8 of the otoliths but found little variation between ablations in the same growth zone of different transects (<6%). Consequently, only 1 transect was undertaken on all other fish. These transects were made across the distal portion of the otolith because the growth axis was much longer than in the proximal direction. All of the transects were made perpendicular to the growth increments and a single ablation covered a maximum of approximately 2 mo of growth in the oldest fish.

Data acquisition was as a series of signal integrations of 10 s in a single block, with exponential corrections for mass bias using measured $^{88}Sr/^{86}Sr$ versus the true ratio. A correction factor was derived using an exponential mass bias model within the instrument software. Correction for Rb isobaric interference was made with the natural $^{85}Rb/^{87}Rb$ ratio. These corrections were normally small, as Rb had been previously measured in barramundi otoliths and was less than 1 µg g^{-1} (Milton et al. 2000). Each analysis was preceded by peak-centring on ^{89}Y, and zero-point correction at 0.5 atomic mass units from the peak. A minimum of 50 ratios (50 × 10 s integrations) was recorded for the SRM987 standard and the coral material. All ratios were electronically logged for transfer to an Excel spreadsheet for off-line processing of the data.

Once transferred to the spreadsheet, data on the SRM987 standard and coral were used to calculate both internal and external error statistics. If the data were outside the error of expected values for the SRM987 isotopic standard solution, otolith isotope ratios were further corrected for mass bias. The deep-sea coral *Lophelia pertusa* was used as a matrix-matched (calcium carbonate) reference sample for a seawater signature. This hard coral species was considered appropriate as it grows in large colonies at over 800 m in the North Sea northeast of Scotland. This is a location with no freshwater input and should provide a stable marine water $^{87}Sr/^{86}Sr$ signature (0.70918). The mean $^{87}Sr/^{86}Sr$ ratio in the coral was very similar to the marine water signature (0.70916 ± 0.00004). As a further calibration, we also analysed a transect across the otolith of a barramundi maintained for 4 yr in seawater with a flow-through water exchange system. This fish was fed trash fish every second day and was 990 mm TL and 10.8 kg when it was sacrificed. Data from the otoliths were smoothed with a 5 point rolling median to reduce high-frequency noise before plotting.

Ages at each ablation were estimated by examination under a light microscope after $^{87}Sr/^{86}Sr$ ratios had been acquired. Distances of each annuli from the otolith core were measured with an ocular micrometer (±0.01 mm) and their position related to the ablations based on laser speed and the time elapsed from the start of the transect. Ages at each Sr/Ca ablation were calculated in a similar manner.

Analysis of Sr concentration. All otoliths analysed by LA-MC-ICPMS in this study were also analysed by LA-ICPMS with methods outlined in Milton et al. (2000) and Milton & Chenery (2001). Transects of ablations were made along an axis parallel to that of the MC-ICPMS, but separated by approximately 300 µm to avoid any potential effects from the previous ablations. A larger sample of the largest fish (>700 mm TL) from all sites were also analysed for Sr by LA-ICPMS to provide a less precise, but more representative indication of their migration frequency (Secor 1992, Secor et al. 1995). Laser beam width was approximately 25 µm, and each ablation was discrete and separated from adjacent ablations by approximately 25 µm.

In order to calibrate the Sr/Ca ratios and identify periods when fish were in low salinity, we calculated Sr mixing curves for all the rivers with different $^{87}Sr/^{86}Sr$ ratios (Fly, Mai/Morehead and Bensbach rivers) with the equation of Ingram & DePaolo (1993). This equation required both end member Sr concentration and $^{87}Sr/^{86}Sr$ ratios. The water concentrations in each river were obtained from mid-water samples collected at the same time as the fish and acidified to a concentration of 1% trace metal grade HNO_3. These water samples were analysed by inductively coupled plasma atomic emission spectrometry (ICP-AES) (Milton & Chenery 2001, 2003). The $^{87}Sr/^{86}Sr$ ratios were estimated from the mean of the last 3 ablations of all the fish analysed from each system.

We then matched the $^{87}Sr/^{86}Sr$ and Sr/Ca ratios in the same fish from each river and obtained an estimate of the salinity at each Sr/Ca ablation. The data indicated that the salinity could only be reliably separated from marine salinities at low values (<5) in most fish (Fig. 2). The Sr mixing curves varied between rivers, being more discriminatory at higher salinities in the Fly River than either the Mai/Morehead River or the Bensbach

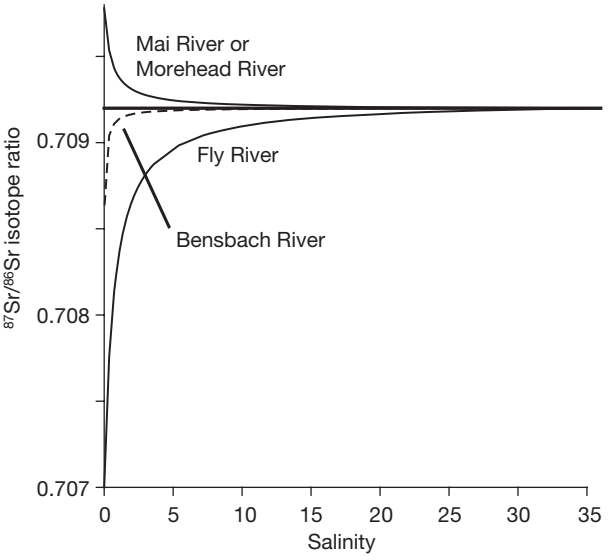

Fig. 2. Estimated Sr mixing curve for the Mai/Morehead, Bensbach and Fly rivers with the mean salinities calculated from water Sr concentrations and the mean $^{87}Sr/^{86}Sr$ ratios estimated from ablations taken in the rim of barramundi otoliths from the freshwater reaches of each river system

River (Fig. 2). The maximum Sr/Ca ratio was 1.58 mM M^{-1} at ablations where the $^{87}Sr/^{86}Sr$ ratios were detectably less than marine water values.

Catch monitoring. Adult barramundi (>500 mm TL; Moore 1979) catches from Ok Tedi Mining routine monitoring sites in the middle Fly River region (Fly 14, Fly 15 and Obo Lagoon: Fig. 1) between 1987 and 2001 were analysed for seasonal changes in catch rate (in kg 100 m net^{-1} d^{-1}). At each site, a standard suite of 13 gill nets from 50 mm (2″) to 152 mm (6″) were deployed for 3 d at quarterly intervals (Swales et al. 2000).

During this period, a commercial fishery for adult barramundi, based at Obo Lagoon (Fig. 1), began in 1999. The fishery employs up to 15 fisher groups who catch barramundi and sell their catch to the processing plant. Daily catch rates (in kg 1000 m net^{-1} d^{-1}) from all gill nets (178 mm or 7″) were recorded by the processing plant between February 1999 and July 2001. The mean daily catch rates from these nets were estimated for the same time interval as the Ok Tedi Mining monitoring to allow for direct comparison.

RESULTS

$^{87}Sr/^{86}Sr$ ratios

Fly River and Obo Lagoon. Twenty barramundi were analysed for $^{87}Sr/^{86}Sr$ ratios with the LA-MC-ICPMS (Table 2). Fish were collected between August 1999 and May 2001 and were all female, except for a single male from Obo Lagoon in the middle Fly River (Fly 1: Table 2). These fish showed a range of patterns in $^{87}Sr/^{86}Sr$ ratios and none showed evidence of any return migrations into marine waters (Fig. 3). The amount of time these fish spent in marine waters before moving into the Fly River varied from 3 to 8 yr. The single fish

Table 2. *Lates calcarifer*. Total length (mm), weight (kg) and age (increments) of barramundi analysed for Sr isotopes by MC-ICPMS

Region (habitat)	Site	Fish no.	Date	Sex	Total length	Weight	Age
Middle Fly River (freshwater)	Obo lagoon	Fly 1	May 2001	M	794	6.1	5
		Fly 2	March 2001	F	1300	20.5	14
		Fly 3	March 2001	F	1350	15.0	9
		Fly 4	March 2001	F	1280	9.7	7
	Fly River (Fly 14)	Fly 5	May 2001	F	867	9.9	6
	Strickland River	STR 1	August 1999	F	972	11.0	11
Spawning ground (marine)	Sigabaduru	SPAW 1	February 2001	F	940	8.6	6
		SPAW 2	February 2001	F	795	4.9	7
		SPAW 3	February 2001	F	970	8.9	7
		SPAW 4	February 2001	F	1005	9.7	12
		SPAW 5	February 2001	F	1015	10.9	12
		SPAW 6	February 2001	F	755	4.6	4
Coastal (freshwater)	Mai River	MAI 1	December 2000	F	800	7.0	5
Coastal (estuarine)	Mai River	MAI 2	December 2000	F	750	4.0	9
Morehead River (freshwater)	Site 1	MOR 1	December 2000	F	847	7.5	8
Bensbach River (freshwater)	Site 2	BEN 1	August 2000	F	885	8.3	5
Bensbach River (estuarine)	Site 1	BEN 2	August 2000	F	870	8.1	5
		BEN 3	August 2000	F	888	9.5	5
West Papua (marine)	Merauke	MER 1	May 2000	F	1130	15.2	9
		MER 2	May 2000	F	960	8.0	8

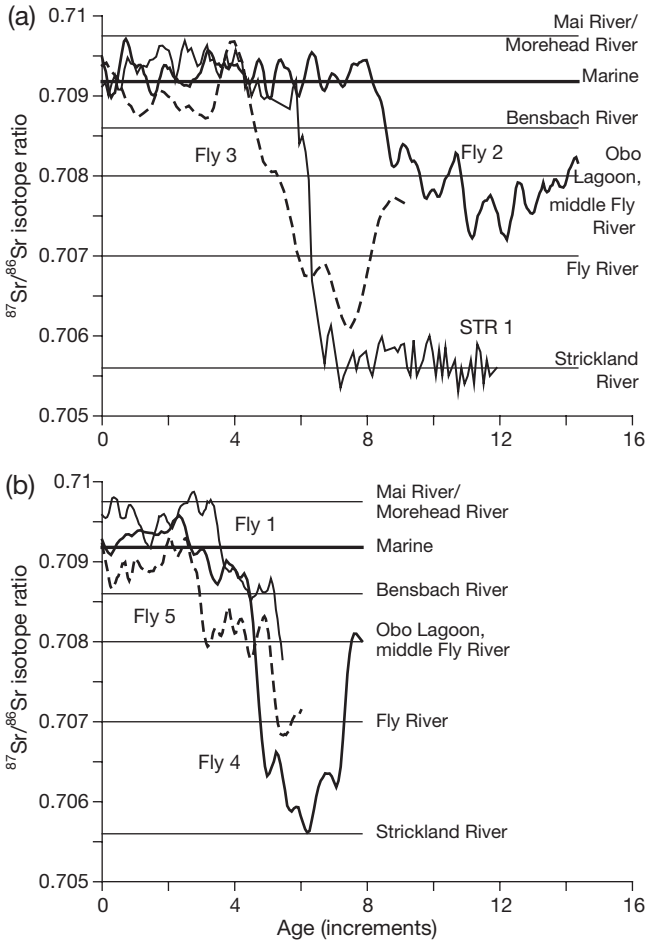

Fig. 3. *Lates calcarifer*. Transects of $^{87}Sr/^{86}Sr$ ratios from the core to the rim of otoliths of 6 barramundi caught in the middle Fly and Strickland rivers, Papua New Guinea. Fish nos. are (a) Fly 2, Fly 3 and STR 1, and (b) Fly 1, 4 and 5 (see Table 2). Lines corresponding to the mean $^{87}Sr/^{86}Sr$ ratios of the outer 3 ablations of fish caught in other rivers are shown for comparison. Thick horizontal line ('Marine') shows the marine water Sr isotope ratio (0.70918)

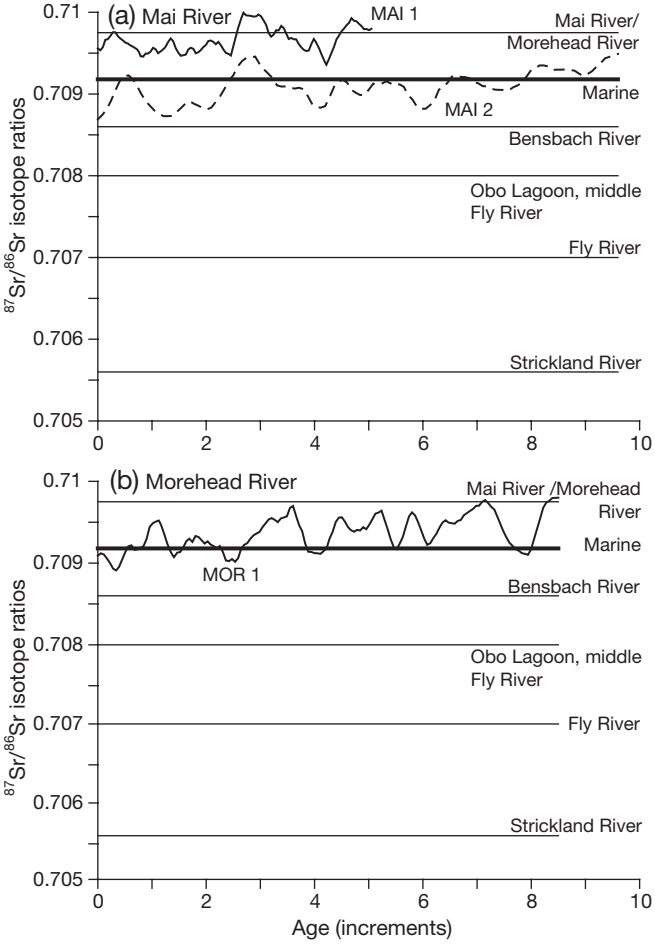

Fig. 4. *Lates calcarifer*. Transects of $^{87}Sr/^{86}Sr$ ratios from the core to the rim of otoliths of (a) 2 barramundi (MAI 1 and 2) caught in the Mai River adjacent to the spawning ground, and (b) 1 fish (MOR 1) caught in the freshwater reaches of the Morehead River. Lines corresponding to the mean $^{87}Sr/^{86}Sr$ ratio of the outer 3 ablations of barramundi caught in other rivers are shown for comparison

analysed from the Strickland River (STR 1) had a lower $^{87}Sr/^{86}Sr$ ratio in the freshwater period of its life than the fish in the Fly River and Obo Lagoon. These 2 sites could also be distinguished by their $^{87}Sr/^{86}Sr$ ratios, with fish caught in Obo Lagoon having a mean Sr isotope ratio of 0.7080 at the edge of their otoliths, whereas the fish analysed from the Fly River (Fly 5) had a ratio of 0.7070 at the edge of their otoliths (Fig. 3). Given the differences among the fish analysed from these sites, movements of fish among sites could be identified.

For example, Fly 4 appears to have spent time in the Strickland River after it migrated into freshwater in the Fly River at age 4. It was caught in the Obo Lagoon and had only recently arrived (Fig. 3). Fly 5 was caught in the Fly River downstream from the confluence of the Fly and Strickland rivers, but had spent about 2 yr in Obo Lagoon prior to its movement back into the Fly River. Other fish appear to have stayed largely in the one site, once they have migrated into the Fly River system.

Mai River and Morehead River. Among fish analysed from rivers west of the spawning ground, fish from the Mai River and Morehead River showed different patterns (Fig. 4). The isotopic signature of both the Mai and Morehead rivers were similar, with fish from both sites having an $^{87}Sr/^{86}Sr$ ratio of 0.7098 in the ablations at the edge of their otoliths. This is not surprising, given their close proximity and similar geology of their catchments (Fig. 1). One fish from the Mai River (MAI 1) appears to have remained largely within the Mai system, whereas the other fish appears to have spent most of its life in estuarine and marine waters (Fig. 3a). This fish (MAI 2) may have spent short periods

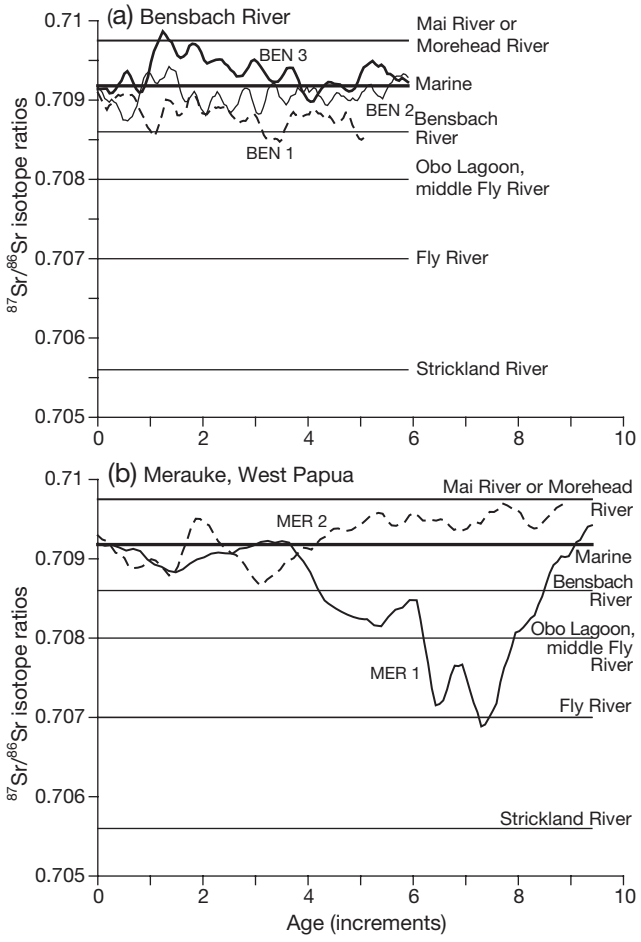

Fig. 5. *Lates calcarifer*. Transects of $^{87}Sr/^{86}Sr$ ratios from the core to the rim of otoliths of (a) 3 barramundi (BEN 1, 2 and 3) caught in the Bensbach River, western Papua New Guinea and (b) 2 fish (MER 1 and 2) caught in the Merauke River, Irian Jaya. Lines corresponding to the mean $^{87}Sr/^{86}Sr$ ratios of the outer 3 ablations of fish caught in other rivers are shown for comparison

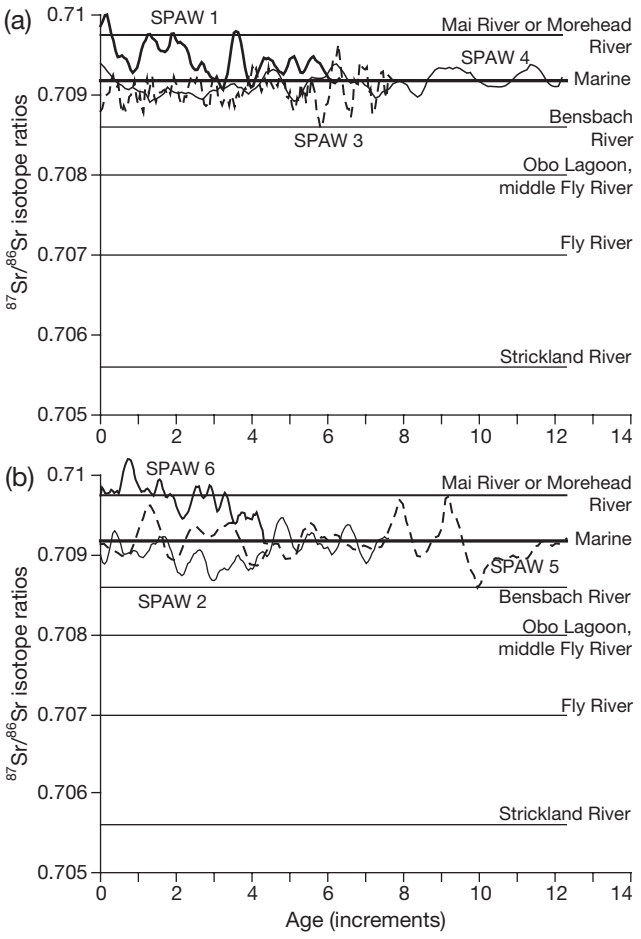

Fig. 6. *Lates calcarifer*. Transects of $^{87}Sr/^{86}Sr$ ratios from the core to the rim of otoliths of 6 barramundi caught on the spawning grounds during the 2001 spawning season. Fish nos. are (a) SPAW 1, 3 and 4 and (b) SPAW 2, 5 and 6. Lines corresponding to the mean $^{87}Sr/^{86}Sr$ ratios of the outer 3 ablations of fish caught in other rivers are shown for comparison

in freshwater reaches of the next most adjacent river, the Bensbach (Fig. 3a). The fish from the Morehead River (MOR 1) made at least 4 migrations into estuarine and marine waters after it matured (~ 4 yr of age).

Bensbach River and Merauke River. Fish analysed from rivers further west of the spawning ground also showed a variety of movement patterns. In the Bensbach River, the fish analysed from the freshwater site (BEN 1 and BEN 2) from the estuarine site showed a pattern that suggest they have been moving within the Bensbach River system and adjacent marine waters during their life (Fig. 5a). Whereas, the other fish (BEN 3) had $^{87}Sr/^{86}Sr$ ratios indicative of the Morehead and Mai rivers.

The 2 fish analysed from the Merauke River showed different patterns to those from adjacent rivers (Fig. 5b). One fish (MER 1) had spent several years in freshwater, moving between water bodies with different $^{87}Sr/^{86}Sr$ ratios. The $^{87}Sr/^{86}Sr$ ratios of these water bodies were similar to those measured in fish from the middle Fly River. However, it is extremely unlikely that this fish had been in the Fly River, as the Merauke and Fly rivers are separated by over 800 km of marine water, and that would have been recorded in the otoliths (Fig. 5b).

Spawning ground. We analysed the 6 largest spent females (from histological analyses of their ovaries: D.A. Milton unpubl. data) collected during the spawning season from the known spawning ground. These fish showed a range of patterns in $^{87}Sr/^{86}Sr$ ratios (Fig. 6). All appear to have spent their lives in coastal regions, with short periods in waters with $^{87}Sr/^{86}Sr$ ratios similar to the rivers close to the spawning ground. None showed any evidence of having been in the Fly River. The patterns in all fish were variable, and suggest that most have recently arrived on the spawning ground from freshwater habitats.

Calibration

The $^{87}Sr/^{86}Sr$ ratios of a captive barramundi kept in marine waters for 4 yr varied between 0.7090 and 0.7094 (Fig. 7) with a mean (±95% CL) of 0.70919 ± 0.0001. This is not significantly different from the marine water $^{87}Sr/^{86}Sr$ ratio of 0.70918. At the same ablations, the Sr/Ca ratio varied between 4.3 mM M^{-1} at the core and 2.2 mM M^{-1}, with a mean of 2.9 ± 0.6 mM M^{-1} (Fig. 7). By applying the Sr isotope mixing curve for the Fly River (Fig. 2), we were able to identify the period of otolith growth when barramundi were in freshwater (salinity <5). The Sr/Ca ratios of LA-ICPMS ablations measured during this growth period in the same fish were used to calculate a threshold Sr/Ca ratio value for their freshwater residency (<1.6 mM M^{-1}). This value was then used to estimate the number of times individual barramundi from each site analysed for Sr/Ca ratios had migrated to the sea after maturity (~4 yr old). Examples of how the $^{87}Sr/^{86}Sr$ and Sr/Ca ratios were related (Fig. 7) show that there was generally good agreement between Sr/Ca ratios below the threshold and $^{87}Sr/^{86}Sr$ ratios indicating freshwater residency.

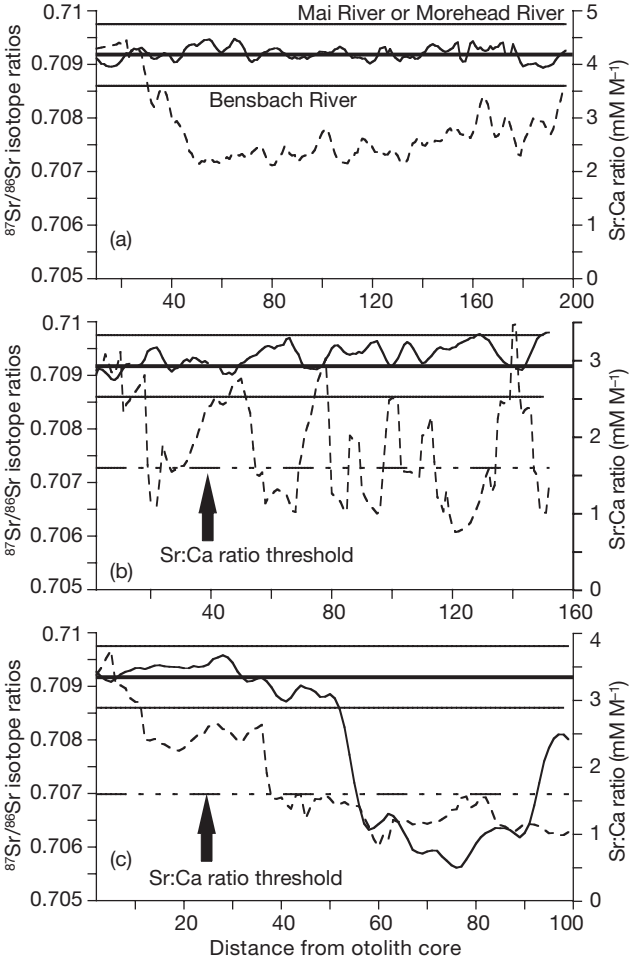

Fig. 7. *Lates calcarifer*. Transects of $^{87}Sr/^{86}Sr$ ratios (continuous line plot) and Sr/Ca molar ratios (dashed line plot) from the core to the rim of an otolith of (a) an adult barramundi kept in marine waters for 4 yr, (b) Fish MOR 1 and (c) Fish Fly 4. Lines corresponding to the mean $^{87}Sr/^{86}Sr$ ratios of fish caught in the Mai/Morehead rivers and Bensbach River are also shown; thick line: marine water ratio (0.70918). Line indicated by arrow in (b) and (c) corresponds to the calculated freshwater Sr/Ca ratio threshold (mM M^{-1}) from all fish analysed for both $^{87}Sr/^{86}Sr$ and Sr/Ca ratios

Migration patterns estimated from otolith Sr/Ca ratios

Sr/Ca ratios were measured in transects across the otoliths of 189 mature barramundi from throughout the species' distribution in Papua New Guinea and adjacent Indonesia (Fig. 1). The majority of fish from all sites demonstrated at least 1 migration after maturity (Figs. 8 & 9). Almost half the fish analysed either had not returned to the sea from freshwater or had not migrated to freshwater in the first place (spawners).

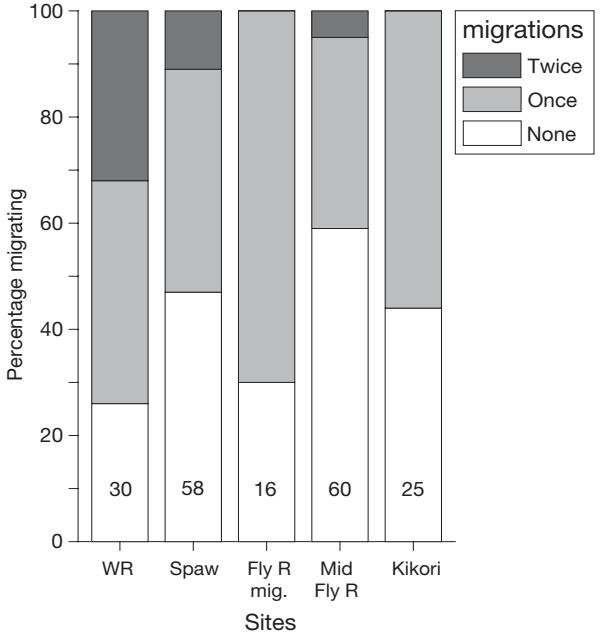

Fig. 8. *Lates calcarifer*. Percentage of barramundi examined for Sr/Ca ratios from different parts of their range that had migrated from marine waters into freshwater and returned. Migration into freshwater (salinity <5) was identified by a Sr/Ca ratio less than that measured in ablations of otoliths when the $^{87}Sr/^{86}Sr$ ratios were outside the range measured in fish caught in estuarine and marine waters (<1.6 mM M^{-1}). Western R (WR) refers to fish collected from the rivers west of the spawning grounds (Morehead, Bensbach and Merauke rivers). Fly R migrants (Fly R mig.) are fish collected from the Fly River estuary that were moving downstream during spring migration. Spaw: spawners; Mid Fly R: middle Fly River. Numbers at the bottom of each column are sample sizes at each site

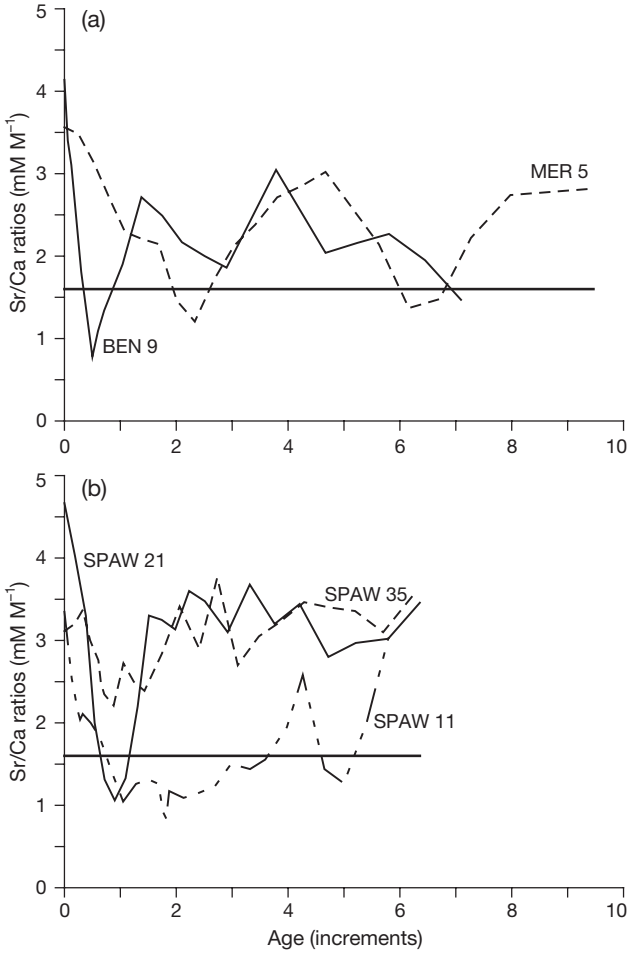

Fig. 9. *Lates calcarifer*. Examples of the range of movement patterns found in Sr/Ca ratios of fish analysed only for Sr/Ca. (a) Fish caught in coastal waters at Merauke (MER 5) and in freshwater in the Bensbach R (BEN 9). (b) The range of different movement patterns found among spawners. The heavy solid line represents the freshwater Sr/Ca threshold calculated from all fish analysed for both $^{87}Sr/^{86}Sr$ and Sr/Ca ratios

Fish analysed from the rivers west of the spawning ground showed the largest number of repeat migrants. The pattern of timing of movements between fresh and seawater showed a great diversity between fish (Fig. 9), with most not moving into freshwater until after maturity. Most of the fish caught in the mouth of the Fly River during spring downstream migration (Fly River migrants: Fig. 8) had previously migrated once, usually as males.

Migration patterns differed little between the sexes; about half the males and females did not migrate between freshwater and marine waters at all. The percentage of females migrating more than once was also similar to males (16 vs. 7%) ($p > 0.2$).

The proportion of barramundi undertaking at least 1 migration increased with age in fish caught in both coastal areas and freshwater (Fig. 10). Few fish caught in freshwater had made more than 1 migration, although 60 to 70% of fish over 6 yr of age had migrated to the sea at least once. The percentage making at least 1 migration was lower among fish caught in coastal areas, where about 45% had remained in the sea throughout their life.

Seasonal catch rates

The seasonal changes in both monitoring and commercial catches showed a similar pattern (Fig. 11). Catch rates were lowest in December to February and highest in March to August. There was evidence of a

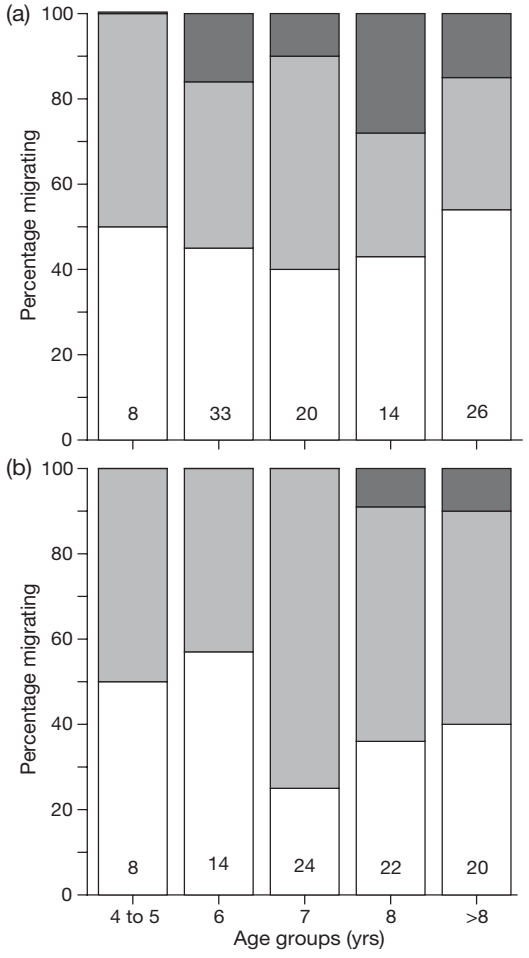

Fig. 10. *Lates calcarifer*. Percentage of barramundi examined for Sr/Ca ratios from different age groups in (a) freshwater and (b) coastal waters that had migrated from marine waters into freshwater and returned. Migration into freshwater (salinity <5) was identified by a Sr/Ca ratio less than that measured in ablations of otoliths when the $^{87}Sr/^{86}Sr$ ratios were outside the range measured in fish caught in estuarine and marine waters (<1.6 mM M^{-1}). Shading as in Fig. 8. Numbers at the bottom of each column are the sample sizes in each age group

reduced catch rate during the September to November migration period, but the mean catch rate was always at least 60% of the highest catch rates (March to August). Mean length in the monitoring catches (Fig. 11) also declined significantly (*t*-test; $p < 0.01$) during the same periods, implying larger fish had moved from the region.

DISCUSSION

This study clearly demonstrates that a large proportion of the barramundi population from southern Papua New Guinea living in freshwater are not spawning each year. All Fly River fish analysed with $^{87}Sr/^{86}Sr$ ratios and Sr/Ca ratios were sexually mature for at least 4 yr, and most had not undertaken more than a single migration to the sea and returned. A similar pattern was found among fish collected in the Kikori region. Both regions are quite remote from the spawning grounds (>300 km) and this may be contributing to their low migration frequency. Fish from rivers adjacent to the spawning grounds (Bensbach, Morehead and Mai rivers) appear to move to coastal areas and back into freshwater much more frequently (Figs. 4, 5 & 8).

Previous studies of barramundi migration in Papua New Guinea using tagging found that most adults moved less than 15 km between recaptures. Only a third was recaptured on the coast during the annual spawning migration (Moore & Reynolds 1982). Moore & Reynolds also found that the number of tagged fish migrating varied between years, depending on climatic conditions. In coastal areas, they found that over 70% of the fish made only local movements between tagging and recapture (Moore & Reynolds 1982). They interpreted these data to indicate that there was a resident coastal population of barramundi.

Similar movement patterns of barramundi were found in northern Australia (Davis 1986, Pender & Griffin 1996). Davis (1986) found that there was a general down-stream movement of tagged fish during the spawning season, but no evidence that the fish moved back into freshwater. Pender & Griffin (1996) examined the elemental composition of scales of fish from coastal, estuarine and freshwater habitats. They were able to distinguish 3 groups: freshwater resident, marine and mixed populations. They suggested that a large proportion of the population on the coast remained in that habitat and did not migrate into freshwater.

Our data are consistent with the results of these studies and indicate that a large percentage of the population in both marine and Fly River freshwater habitats are resident. For the fish in the Fly River, this means that many never (or rarely) contribute to the spawning population because this requires a salinity >30 (Moore 1982). This lifestyle does not appear to be adaptive, and why it has evolved is not clear. Reznick et al. (2002) found that when natural mortality is low and fecundity increases with age, species tend to have a long reproductive life-span. Barramundi is the largest fish species in the Fly River (Roberts 1978) and there is a strong relationship between size and fecundity (Moore 1982). This suggests that adult barramundi in freshwater habitats like the Fly River have few predators and thus may delay or defer migration to the spawning ground until conditions are most favourable.

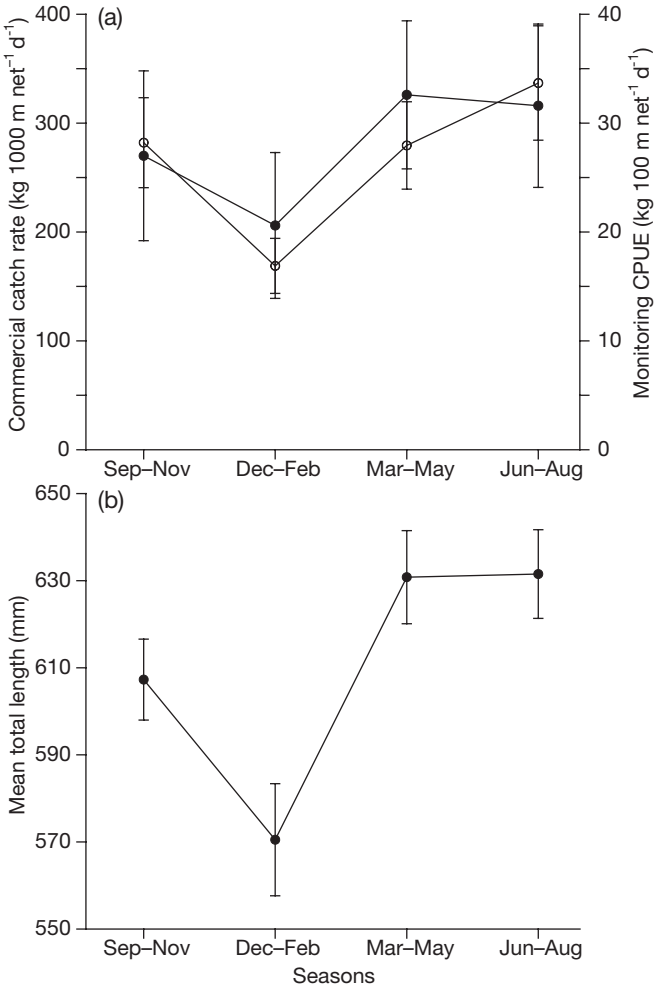

Fig. 11. *Lates calcarifer*. (a) Mean seasonal barramundi catch rates ±95% CL from commercial gill nets (—●—) and environmental monitoring (—○—) in the middle Fly River by Ok Tedi Mining between 1988 and 1999 with a standard suite of gill nets (Swales et al. 2000). (b) The seasonal change in mean total length of barramundi (in mm) ±95% CL from the same environmental monitoring

The largest fish that we examined for $^{87}Sr/^{86}Sr$ ratios from the middle Fly River had not migrated to the coast since entering the Fly River system. They were caught in a large oxbow lake (Obo Lagoon) connected with the main river. The $^{87}Sr/^{86}Sr$ ratios of these fish (Fig. 3)

show that barramundi move into the system after sexual maturity (>3 yr old). They also move within the system, between the large lagoon at Obo and the main river. The largest fish examined (Fly 2) remained in coastal waters until approximately 8 yr of age, before migrating upstream into the Fly River. This fish could have spawned for 4 yr prior to entering the Fly River and thus may have finished spawning.

The Sr/Ca ratios of barramundi from the middle Fly River showed a similar pattern, with most fish not entering freshwater until >3 yr of age. Among the older fish examined (>8 yr old), about 40% had not left freshwater after they entered it as a 3 to 5 yr old (Fig. 10). Given the low mortality rates in inland areas (Davis 1986), the large population of barramundi in the middle Fly River (Swales et al. 2000) and the dramatic increase in fecundity with length (Moore 1982), there is considerable reproductive potential being lost in these large, older non-spawning females.

A large proportion of the barramundi spawning population are marine residents, similar to the pattern found in northern Australia by Pender & Griffin (1996). Among the 6 fish analysed for $^{87}Sr/^{86}Sr$ ratios, none had been in the Fly River system. Three fish appear to have spent time in the Mai or Morehead rivers and 2 probably had spent short periods in the Bensbach River (Fig. 6). $^{87}Sr/^{86}Sr$ ratios in these fish were more variable than fish from freshwater sites or other species (e.g. Hilsa *Tenualosa ilisha*: Milton & Chenery 2003). This may be due to salinity varying more widely in coastal waters as they receive large volumes of freshwater during seasonal flooding rains.

Multi-collector ICPMS can produce highly accurate and precise measurements of $^{87}Sr/^{86}Sr$ ratios in otoliths (Milton & Chenery 2003). However, the utility of this approach to infer movement histories of fish is related to 2 factors. The first factor is the speed that fish move between water bodies and the amount of otolith ablated. As fish age, the sensitivity of the MC-ICPMS to detect changes in $^{87}Sr/^{86}Sr$ isotope ratios will diminish as growth increment width is reduced. The effect will be to make short incursions into marine waters less easily detected. This would be more of a problem for fish analysed from rivers adjacent to the spawning ground (Bensbach, Morehead and Mai rivers) as these have $^{87}Sr/^{86}Sr$ values more similar to those of marine waters. Additionally, some fish analysed for $^{87}Sr/^{86}Sr$ ratios did not show marine $^{87}Sr/^{86}Sr$ values at their core. There is published evidence that barramundi can spawn in salinity as low as 5, so these fish must have entered freshwater shortly after hatching (Moore 1982).

The other factor is the geology of the parent rock in the river catchment where the species occurs (Kennedy et al. 2000). ^{87}Sr derives from the decay of ^{87}Rb, which is enriched in continental crust and depleted in the earth's mantle (Hodell et al. 2004). Thus, the $^{87}Sr/^{86}Sr$ ratios of a rock are dependent on the initial $^{87}Sr/^{86}Sr$ composition, its original concentration of ^{87}Rb and the time elapsed since formation. Thus, sialic rocks tend to contain high ^{87}Rb and have high $^{87}Sr/^{86}Sr$ ratios (mean 0.716), whereas volcanic rocks have low ^{87}Rb and $^{87}Sr/^{86}Sr$ values (mean 0.704) (Hodell et al. 2004).

We know little of the $^{87}Sr/^{86}Sr$ ratios in the rivers of southern Papua New Guinea. However, we know that the Fly River rises in the high central highlands of Papua New Guinea where soils are derived from mostly sedimentary rocks (Loffler 1979, Bleeker 1983). The headwaters of several branches of it major tributary, the Strickland River, rise in recent volcanic soils further east (Loffler 1977, Bleeker 1983) and thus would be expected to have the lower $^{87}Sr/^{86}Sr$ ratios in the otoliths of barramundi from that river. By comparison, the rivers close to the spawning ground, the Kai, Morehead and Bensbach rivers, have catchments with soils of mostly unconsolidated alluvial deposits (Loffler 1977). Thus, their $^{87}Sr/^{86}Sr$ ratios will be more directly influenced by rainfall and marine derived Sr (Capo et al. 1998).

We could not distinguish between $^{87}Sr/^{86}Sr$ ratios in the otoliths of barramundi from the Morehead and Mai rivers. Fish analysed from the Merauke River also have $^{87}Sr/^{86}Sr$ ratios during parts of their periods of freshwater residency that were similar to those in the Fly River. This is not surprising as the Merauke River rises in near the western edge of the Fly River catchment in mountains with similar geology (Loffler 1979) and probably similar $^{87}Sr/^{86}Sr$ ratios. Thus the value of using otolith $^{87}Sr/^{86}Sr$ ratios in fish movement studies relies heavily on differences in the geology among catchments.

An approach that combines studies of both $^{87}Sr/^{86}Sr$ and Sr/Ca ratios appears to be more powerful for understanding movement patterns at a population level. This is more cost-effective than $^{87}Sr/^{86}Sr$ ratios, but uses the power of that approach to more accurately define when a fish has been in freshwater. Using this combined approach, our data shows that there are a large number of adult barramundi living in the Fly and other rivers remote from the spawning ground that are not contributing annually to spawning. Many of these fish appear to never spawn after entering freshwater, or have spawned only once since sexual maturity.

Moore & Reynolds (1982) showed that some fish do migrate between most of these rivers and the spawning ground. However, the recapture rates were low (<10%), and most fish had moved less than 15 km since capture. The similarity of our results to those of Davis (1986) and Pender & Griffin (1996) in northern Australia suggests that irregular contribution to

spawning by freshwater resident barramundi may be widespread.

We have no estimates of the population size of barramundi, but a companion study of barramundi population structure (J. Salini et al. unpubl. data) found a single breeding population with 69 distinct mt DNA control region haplotypes in 208 fish. This result implies that barramundi have a high genetic diversity in Papua New Guinea and that the effective (spawning) population size is very large. If this is true, then the number of barramundi apparently not contributing to the spawning population may actually be a relatively small proportion of the total population. This is despite it being a large proportion of the population present in the middle Fly River.

Are these freshwater resident fish not migrating because they are physiologically incapable of spawning? This is unlikely, given that Moore (1982) found adults that had enlarged gonads throughout the distribution range during the spawning season. The range of ages present in the middle Fly River is also similar to those found on the coast (Moore & Reynolds 1982). Rather, it appears that the proximate cues for migration of barramundi from freshwater are complex (McDowall 1988) or are linked to rare climatic events. Rainfall, temperature, moon phase, olfaction and fish condition have all been identified as important cues for migration of many freshwater and marine fishes (McDowall 1988, Naslund et al. 1993, Boubee et al. 2001, Hodgson & Quinn 2002, Okamura et al. 2002). Similar cues are probably involved in barramundi migration.

Moore & Reynolds (1982) found that there was an inverse relationship between river height in the Fly River and commercial catch on the coast near the spawning grounds. They found that low water levels in September to October forced fish from the large off-river water bodies in the middle Fly River and into the deeper main river. However, if the water level rose, the fish moved back into the water bodies. Their results, combined with our data, suggest that conditions for barramundi migration from freshwater occur irregularly. Fish that are resident in deeper lakes and swamps away from the coast may never migrate, despite their being reproductively active. This has implications for barramundi fisheries in freshwater throughout the geographic range. If these fish do not migrate to spawn for several years, they are effectively 'dead' (McDowall 1988) and their capture and removal may not significantly affect the spawning population.

In developing the management plan for the barramundi fishery in Western Province, the National Fisheries Authority of Papua New Guinea set a total allowable catch of 260 t for the entire fishery and this was allocated 50:50 between the coastal and inland fisheries (Anonymous 2003). The catch from the middle Fly River has been over 170 t for the last 2 yr, without declines in catch rates, whereas the catch from the coastal fishery has been only about 50 t. Previously, this would be of concern to managers, but our studies suggest that the high catch from the middle Fly River may not be impacting the spawning population to the extent previously thought (e.g. Milton et al. 1998).

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