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Movement and juvenile recruitment of mangrove jack, *Lutjanus argentimaculatus* (Forsskål), in northern Australia

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Abstract. *Lutjanus argentimaculatus*, tagged and released in coastal rivers and estuaries, were found to have made inter- and intra-riverine, coastal and offshore movements. A small proportion of the recaptures made offshore movements to reef habitats of up to 315 km and these recaptures were fish that were at liberty, on average, more than twice as long as those fish that had made intra-riverine movements. Most juvenile fish <400-mm length to caudal fork (LCF) resident in rivers were recaptured less than a kilometre from where they were released. The proportion of fish making sizeable movements increased with increasing recapture size, with about of 20% of larger fish (400–500-mm LCF) making offshore, inter-riverine or coastal movements. Larger fish were primarily caught offshore, whereas smaller fish <∼338-mm LCF were exclusively caught in estuarine and freshwater habitats. Recruitment of juveniles into estuarine and lower freshwater riverine habitats occurred from about February. There was temporal variability of recruitment of mangrove jack into some river systems and their relative abundance within the river system was inversely proportional to the distance from the sea. Overfishing of juveniles when they are concentrated in inshore areas could have adverse implications for mangrove jack stocks.

Extra keywords: Great Barrier Reef, lutjanids, migration, snappers.

Introduction

Mangrove jack, *Lutjanus argentimaculatus* (Forsskål, 1775), is a member of the snapper family and is widely distributed through the Indo-west Pacific from Samoa and the Line Islands to East Africa and from Australia northwards to Ryukyu Island, Japan (Doi and Singhagraiwan 1993). The species is also believed to have undertaken Lessepsian migrations from the Red Sea via the Suez Canal to the Mediterranean coasts of Israel and Lebanon (Anderson and Allen 2001). The species has excellent eating qualities and is a prized sportfish in northern Australia (Grant 1975). *Lutjanus argentimaculatus* occurs in a range of habitats, from brackish estuaries and the lower reaches of freshwater streams to offshore in deeper reef areas, sometimes penetrating to depths in excess of 100 m (Brouard and Grandperrin 1984; Allen 1985, 1987; Ludescher 1997).

Information available on the life history of *L. argentimaculatus* in Australia and in other areas is limited. In tropical Australia, the most common life-history pattern among estuarine nekton is saltwater spawning followed by recruitment of larvae, post-larvae or small juveniles into estuaries where they remain for some time before emigrating to join adult stocks (Robertson and Duke 1990). This pattern is reflected in the life history of some of the tropical snappers including mangrove jack. The spawning grounds for mangrove jack are believed to be offshore (Day *et al*. 1981; Doi and Singhagraiwan 1993). In Palau, spawning aggregations were found both in the reef lagoon and on the outer reef slope (Johannes 1978). Johannes (1978) noted that, in Palau, the timing of spawning activity of *L. argentimaculatus* peaked 14–18 days into the lunar month. Larvae and juveniles subsequently moved inshore and were found in coastal areas including seagrass beds (Doi and Singhagraiwan 1993) and freshwater areas (Munro 1967; Lake 1971). In eastern Australia, Sheaves (1995) suggests that estuaries are important development grounds for *L. argentimaculatus* and that estuarine populations appear to consist entirely of reproductively immature fish that are smaller than those caught offshore, but he noted that there is a paucity of direct evidence of movements from estuaries to offshore areas that needs to be rectified. In South Africa, Day *et al*. (1981) also observed that *L. argentimaculatus* seldom attained lengths of more than 400 mm in estuaries.

Movement studies of snappers have been confined largely to a few species that inhabit tropical reefs, although there have been several recent studies in south-eastern USA on red snapper (*Lutjanus campechanus*), which has a shallow-water, inshore phase in its life cycle. For example, Fable (1980) tagged and released 299 *L. campechanus*, of which 17 (5.6%) were subsequently returned. He noted that only a small

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number had moved and it was usually to adjacent banks or snags. In a larger study of the movements of *L. campechanus*, Patterson *et al*. (2001) found fish moved up to 352 km from their release location on artificial reefs. They observed that these movements were much greater than what has previously been recorded and speculated that these may facilitate stock mixing in the northern Gulf of Mexico. Similarly, Watterson *et al*. (1998) documented movements of red snapper on a spatial scale that would facilitate stock mixing and implicated the occurrence of large-scale climatic events, such as hurricanes, in the stock-mixing dynamics. Movement studies involving tagged juvenile *L. argentimaculatus* have been undertaken in Thailand (Doi *et al*. 1992; Doi and Singhagraiwan 1993). These studies have shown that juvenile fish moved inshore towards the coast and into estuaries from March to August and offshore from September to February (Doi and Singhagraiwan 1993).

In this paper, we document the movements of juvenile and sub-adult mangrove jack originally resident in rivers and estuaries, the recruitment of juveniles into estuaries and inshore areas and examine factors affecting recruitment variability. This work was part of a larger study into the biology, management and genetic stock structure of *L. argentimaculatus* in eastern and northern Australia.

Materials and methods

Study sites

Movement studies were undertaken using information from fish tagged and released in coastal streams in eastern and northern Queensland and northern New South Wales. These fish were tagged by either recreational fishers as part of an ongoing national recreational fishing tagging programme, or as part of a separate, three-year Department of Primary Industries research project. Most fish tagged as part of our research project were released in the upper tidal or lower freshwater reaches of selected eastern Queensland coastal streams (Fig. 1). Although these included the O'Connell and Calliope Rivers and Raglan and Baffle Creeks in central Queensland, in this paper most of the information presented is from mangrove jack tagged and released in the lower reaches of short, relatively fast flowing, north Queensland streams including the Endeavour, Daintree, Russell, Mulgrave, Johnstone (which bifurcates near the mouth into the North and South Johnstone Rivers) and Herbert Rivers and Crystal Creek (Fig. 1). Within each river, at least two sites were chosen for repeat electrofishing activities, with one of these sites close to the brackish water interface, and the others upstream but usually in freshwater areas under some tidal influence. Some electrofishing was also done opportunistically in the lower estuaries when occasional flood events temporarily depressed salinities. Small numbers ($\sim$3%) of *L. argentimaculatus* were opportunistically caught in other north Queensland estuaries and rivers by angling with lures and live and dead bait and these were also subsequently tagged and released.

Field sampling techniques

Electrofishing

A 4.3-m electrofishing boat equipped with a Smith-Root Model 7.5 Generator Powered Pulsator (Vancouver, WA) was used as the survey vessel. Before the commencement of each survey, the conductivity at the site was measured to determine the settings required for efficient operations. Generally, the voltages of the pulsed DC current ranged between 135 and 1000 V. At each site, the vessel was manoeuvred upstream slowly, covering the area from the bank for a width of $\sim$5 m, and three individual sections of river bank were electrofished, each typically 100 m in length. The boundaries of these sections were identified by familiar bank-side structures that were recorded by GPS for repeat visits. The boat was manoeuvred such that the anodes were, where possible, in close proximity to suitable habitat, such as snags, overhangs and rocky structures. All *L. argentimaculatus* were netted using 3-m-long handle dip nets and placed in a 100-L recirculating live fish tank onboard the vessel. At the completion of each replicate, all untagged fish were measured (length to caudal fork, LCF), weighed and examined for evidence of tag wounds before most were tagged and released. A small number were retained for separate reproductive and ageing studies. Recaptured *L. argentimaculatus* were weighed and measured, their tag number was recorded and the placement of the tag was checked before the fish was released. As a measure of relative abundance, catch per unit effort (CPUE) was calculated as the number of fish caught per 1000 s of electrofishing time.

Tagging and recaptures

For *L. argentimaculatus* between 120- and 300-mm LCF, a Hallprint type TBF-2 (45 mm) fine anchor T-bar tag (Victor Harbour) was inserted between the ptyregiophores of the secondary soft dorsal fin rays using an Avery Dennison Mark III tag applicator (Phoenix, AZ). For fish greater than 300-mm LCF, a Hallprint 85-mm plastic-tipped dart tag was inserted between the posterior ptyregiophores of the first dorsal fin spines using a hollow tag needle. All tagging was done on the left-hand side. To correctly position the tag, a scale was lifted from the insertion location and the needle was inserted into the flesh until the tip passed between the ptyregiophores of the dorsal rays. After insertion, tags were then gently pushed into the flesh and then withdrawn slightly to ensure they were correctly anchored. Where the first tag was either not placed correctly or was broken, a second tag was inserted to the rear of this location. The flag of the tag contained a message requesting anglers to measure the fish and report the recapture to a freecall phone number. These data were then entered into a statewide recreational fishing tag-and-release database operated by SUNTAG, a programme of the Australian National Sportsfishing Association (Queensland).

Measuring and weighing

Fish were placed on an on-board measuring board adjacent to the live fish tank. This board was kept continuously moist to ensure minimal loss of slime on fish. Fork length (LCF) in millimetres was measured and the fish was placed in a cradle and weighed ($\pm$ 1 g) using Arlec digital scales (Melbourne).

Commercial and recreational catches

During the three-year study, commercial catches from the Great Barrier Reef line fishery were regularly examined at a local fish processor. Fish were measured (LCF to the nearest millimetre) and biological samples were taken for reproductive and ageing studies. The majority of samples were from the catch of a single fisher who worked year round mostly between 16°S and 19°S. The fisher generally provided approximate locations where individual fish were caught. Recreational fishers targeted *L. argentimaculatus* in coastal and offshore areas along most of the east Queensland coast and the northern Gulf of Carpentaria. Although recreational fishers are active in the rivers of the southern Gulf of Carpentaria, information in the SUNTAG database suggests that catches of mangrove jack in this area are minimal.

Laboratory and data analysis

The reproductive status of sampled fish was initially assessed macroscopically by assigning the gonads an index of maturity based on a

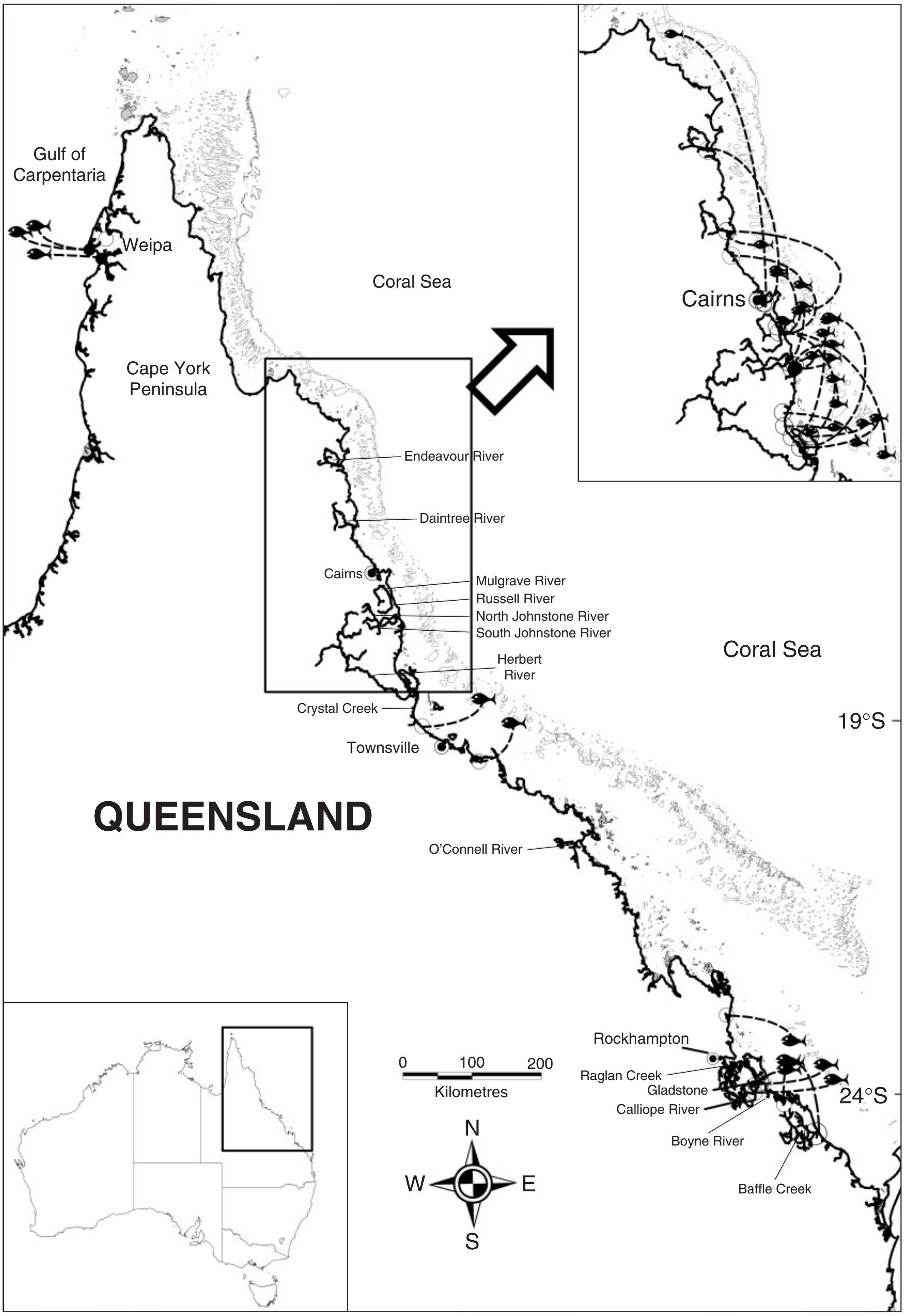

Fig. 1. Study sites and offshore movements of mangrove jack tagged in the current study and from the SUNTAG database. Open circle, release locations of recaptured fish; fish symbol, recapture locations. Note: there are multiple recaptures from some sites.

six-point gonad-maturity classification scheme (Davis 1982) and these were later confirmed using the following standard histological techniques. To determine if condition was a factor influencing offshore movements, Fulton's condition factor ($K = 100ML_F^{-3}$ where M is the mass of the fish in grams and L_F is the LCF in cm (Bagenal and Tesch 1978)) was calculated for those size classes (400–500-mm LCF) common to both inshore (estuarine and freshwater) and offshore habitat and compared using ANOVA and least-squares difference tests. A χ^2 test was used to compare the numbers of tagged fish moving upstream and downstream. Field data were collated in a Microsoft (MS) Access database (Redmond, WA) and data were graphically and geographically presented using MS Excel and MapInfo software (Troy, NY). Tag–recapture information was also extracted from the SUNTAG recreational fishing database current up to May 2004. This database contained records of *L. argentimaculatus* tagged or recaptured by recreational fishers throughout Queensland since 6 July 1985 and includes release and recapture locations and dates and lengths. Where length data were recorded as total length in the database they were allometrically converted to LCF for analyses using measurements obtained during the current study. Tagging data from the current study was also entered into the SUNTAG recreational fishing database, which has an established and efficient reporting and feedback procedure.

Results

In this study, between 20 May 1999 and 12 March 2002, 4303 mangrove jack were tagged in inshore coastal water, estuaries and freshwater reaches of rivers on the east Queensland coast between the Endeavour River (~15°30′S) and Baffle Creek (~24°30′S). Of these fish, most (3645, 85%) were tagged in the wet tropics of north Queensland (Fig. 1), 284 (7%) in central Queensland, 372 (9%) in south-east Queensland and two in the area around Endeavour River. Information on the movements of an additional 17 899 fish tagged by recreational anglers in Queensland and northern New South Wales were made available through the SUNTAG sportsfish database. Including the mangrove jack tagged as part of this current programme, the database contained records on 22 202 fish and included fish released on most of the east Queensland coast and the north-eastern Gulf of Carpentaria.

Of the fish tagged and released as part of the current study, 584 (13.6%) were subsequently recaptured. Of the mangrove jack released in the wet tropics area, 503 (13.8%) were subsequently recaptured; recaptures from other areas were 44 (15.5%) from central Queensland and 32 (8.6%) in south-east Queensland, with the remainder of recaptures (5) from other areas. In the SUNTAG database, the overall recapture rate in Queensland, including fish recaptured in this study, was 6.3%.

Offshore movements

In the SUNTAG database, there were records of 35 tagged fish moving offshore from riverine or coastal habitats where they were released. Of these, 9 fish were tagged in this study and all but one was released in the wet tropics area (between 19°S and 24°S, Fig. 1). The remaining fish was released in southern Queensland. Figure 1 shows the offshore movements of the fish tagged in the current study and those tagged by recreational fishers and recorded in the SUNTAG database. Offshore movements of tagged mangrove jack were recorded over much of the Queensland east coast and there were also offshore movements in the north-eastern Gulf of Carpentaria. In the current study, time at liberty for fish that moved offshore was between 63 and 799 days and the net distances moved varied between 17 km and 200 km. Similarly, the net distances moved by fish tagged by recreational anglers were up to 315 km (see Fig. 1).

No tagged fish (either tagged in this study or by recreational fishers) less than ~338-mm LCF were recaptured in offshore areas. In this study the average (± s.e.) size of fish recaptured offshore was 447 ± 18-mm LCF ($n = 9$, range 380–548-mm LCF), whereas the average size of recaptured fish tagged by recreational fishers was 455 ± 13-mm LCF ($n = 24$, range 338–606-mm LCF). Some records in the SUNTAG database did not include length information. There was no significant difference between the recapture lengths of fish tagged by recreational fishers and fish released as part of this study (t-test, d.f. = 31, $t = -0.34$, $P = 0.74$).

Otoliths were obtained from one fish tagged in the Russell River and subsequently recaptured on an offshore reef 271 days later. At the time of recapture, the age of this fish (as estimated from reading otolith annuli) was 6+ years old, and therefore would have moved offshore between the ages of 5+ and 6+. This corresponds with the modal age of offshore movement of *L. argentimaculatus* from the Great Barrier Reef waters as determined by changes in otolith microchemical composition (Aumend 2003). In the current study, the average time at liberty differed significantly (t-test, d.f. = 584, $t = -2.19$, $P = 0.029$) for those fish that were recaptured in rivers and/or coastal areas (203 ± 10 days, $n = 577$, range < 1–1970 days) compared to those mangrove jack that had made offshore movements (385 ± 87 days, $n = 9$, range 63–799 days).

Coastal, inter- and intra-riverine movements

About two thirds of recaptured fish less than 400-mm LCF did not move more than a kilometre from their original release location (same area, Table 1). In the 200–300-mm size class, although nearly 22% ($n = 21$) made an upstream movement of more than a kilometre and ~11% ($n = 11$) made a similar downstream movement, the numbers moving upstream were not significantly greater. In the 300–400-mm size class, fewer fish (~13%, $n = 19$) made upstream movements and more fish (~17%, $n = 25$) made downstream movements. Small numbers of fish in the 300–400-mm and 400–500-mm size classes also moved to other river systems and along the coast, whereas the proportion of fish caught in offshore reef areas also increased with size (see Table 1). In the SUNTAG database, there are records of mangrove jack moving distances of up to 130 km from rivers or estuaries to other inshore coastal areas.

Table 1. Numbers (%) and size classes of recaptured mangrove jack undertaking various movements during the current study
Note: these data are only for fish at liberty for 100 days or more

Movement type	Size class (length to caudal fork, LCF)			
	100–200 mm	200–300 mm	300–400 mm	400–500 mm
Upstream		21 (21.6)	19 (12.9)	3 (14.3)
Offshore		0	5 (3.4)	4 (19.1)
Same area	38 (90.5)	65 (67.0)	94 (63.9)	10 (47.6)
Inter-riverine		0	3 (2.0)	0
Downstream	4 (9.5)	11 (11.3)	25 (17.0)	3 (14.3)
Coastal		0	1 (0.7)	1 (4.8)
Total	42	97	147	21

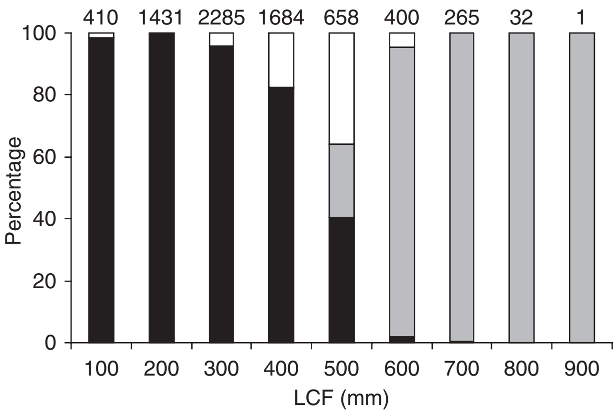

Fig. 2. Proportion of mangrove jack caught in freshwater (solid bars), estuaries (open bars) and offshore (grey) in each size class. Number at top of bars is the total sample size. Most fish caught offshore were from commercial catches; estuarine fish were angled by recreational fishers or electrofished; freshwater fish were mostly caught using an electrofisher.

Fish sizes in offshore and coastal areas

There was a clear partitioning of sizes of fish caught in offshore, estuarine and freshwater habitats (Fig. 2). All of the smaller size classes were sampled by angling or electrofishing in either estuaries or the lower freshwater reaches of rivers and creeks, whereas the larger size classes were made up almost exclusively of fish caught in the offshore line fishery. The smallest fish sampled in offshore commercial catches during this study was 370-mm LCF, whereas the smallest recapture in the SUNTAG database was ~338-mm LCF.

The smallest mangrove jack caught during the study were two 20-mm fish caught at Mutchero Inlet at the mouth of the Russell River during a flood event on 26 February 2001. The otoliths of these fish were extracted and, using daily growth increments, their age was calculated at 32 days, giving a hatch date of ~25 January 2001 (Russell *et al*. 2003). It was unusual to be able to electrofish this far down into the estuary but the flooding, combined with an ebbing tide, temporarily lowered the conductivity of the water sufficiently to allow electrofishing activities.

Condition of fish in freshwater, estuarine and offshore habitats

The average condition of fish in the 400–500-mm LCF range caught in estuarine habitats was 1.96 ($n = 36$), which was significantly greater ($P < 0.05$) than the condition factor of fish from a similar size range caught in either offshore habitats ($\bar{x} = 1.58$, $n = 124$) or freshwater habitats ($\bar{x} = 1.61$, $n = 228$).

Seasonality in recruitment

Most inshore recruitment occurs in the first half of the year (Fig. 3). Fish less than 50 mm long were sampled in all months between February and July, suggesting that juveniles were recruiting into freshwater riverine habitats over an extended period. Towards the end of the year, none of the smaller size classes were sampled. As most of the sampling sites were more than 5 km from their respective river mouths, it is possible that, to have penetrated that far upstream, recruitment could have commenced as early as November or December. Other studies assessing the reproductive condition of adult fish caught in offshore locations support this inference (D. J. Russell, unpublished data).

Seasonal and spatial recruitment variability

Figure 4 shows that there is considerable variability in the CPUE of small juveniles both between sites and over time. This suggests that there is also variability in recruitment of juvenile fish into rivers from year to year. In the northern wet tropics streams (Mulgrave, Russell and North Johnstone Rivers, Fig. 1), the CPUE of juvenile fish 100-mm LCF or less was generally significantly higher in 2001 than it was in 2000 (Fig. 4, Table 2). Evidence from ageing studies using otoliths suggests that the average size of 1-year-old fish is ~79-mm LCF (A. J. McDougall, unpublished data), so fish 100-mm LCF or less would be predominantly 0+. At two locations (Baffle Creek and Herbert River), it was difficult to determine seasonal trends in CPUE because of a reduced sampling effort from mid-2001 onwards. Unseasonably dry conditions during

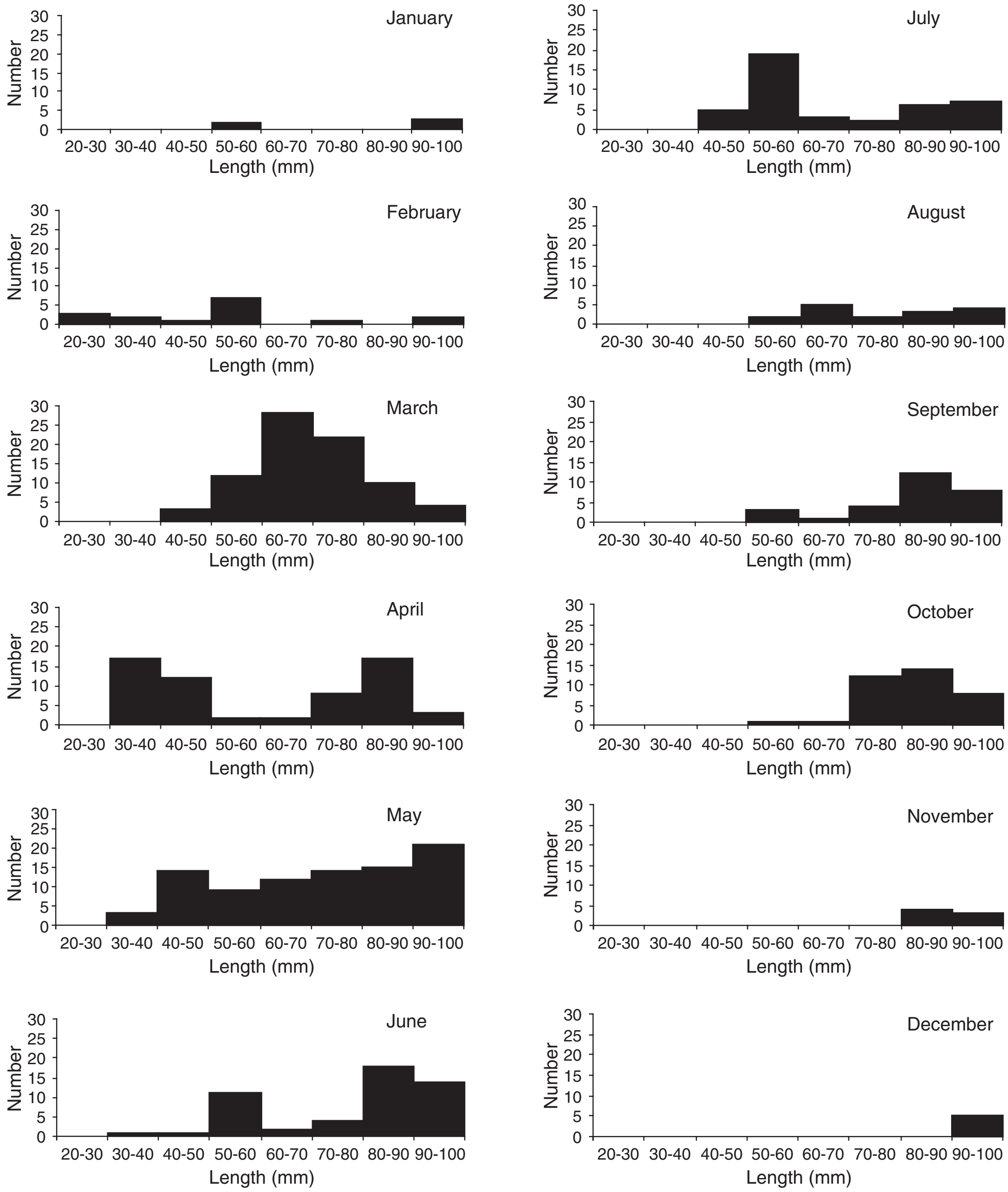

Fig. 3. Monthly abundance of juvenile mangrove jack pooled for all sites and all years.

this period increased the salinities at the study sites in these systems and this, in turn, severely restricted electrofishing activities.

The relative abundance (CPUE) of juvenile mangrove jack decreased exponentially with distance from the sea (Fig. 5). This model ($\text{CPUE} = 0.061 + 2.33 \times 0.828^{\text{Distance from the Sea}}$) explained 35% of variation. It suggests that juvenile habitat is largely restricted to the estuaries and the lower freshwater reaches of the study rivers. There was no significant relationship between the average size of juvenile fish and the distance they were caught from the river mouth in either 2000 or in 2001. There was also no significant relationship between the distance that tagged fish moved upstream and distance from the sea of their release locations. Most (73%) of the recaptured fish that had moved upstream were caught about a kilometre from where they were released.

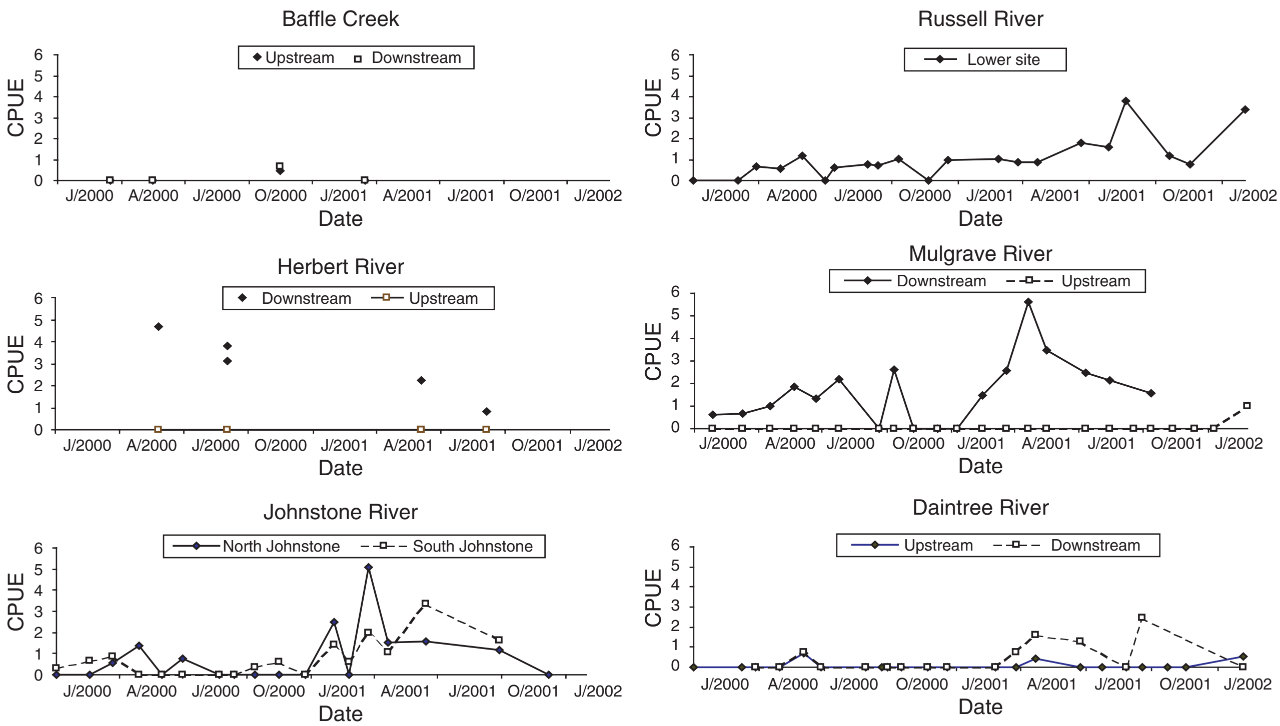

Fig. 4. Catch per unit effort (number of fish caught per 1000 s of electrofishing time) of juvenile mangrove jack (<100-mm length to caudal fork, LCF) at study locations along the Queensland coast.

Table 2. Average sizes (mm length to caudal fork, LCF) of juvenile fish <100-mm LCF and catch per unit effort (CPUE) at sampling locations in 2000 and 2001

Sample numbers are in parentheses. Average lengths and CPUE for each year were compared using single-factor ANOVA

Location (site number)	Average length (mm)		Average CPUE	
	2000	2001	2000	2001
Crystal Creek (1)	97.75 (4)	65.36 (14)**	n.a.	n.a.
Daintree River (2)	50 (1)	81.42 (12)	0.08 (18)	0.037 (19) n.s.
Herbert River (2)	81.73 (15)	89.23 (13) n.s.	n.a.	n.a.
Mulgrave River (6)	78.49 (51)	59.37 (91)**	1.03 (10)	2.42 (8)*
North Johnstone River (1)	80.29 (7)	62.26 (68)*	0.27 (10)	1.48 (8)*
O'Connell River (1)	87.44 (9)	n.a.	n.a.	n.a.
Russell River (1)	91.25 (12)	77.68 (28)**	0.50 (11)	1.63 (10)**
South Johnstone River (1)	78.3 (3)	81.60 (28) n.s.	0.27 (7)	1.11 (10) n.s.

*$P < 0.05$; **$P < 0.01$; n.s., not significant; n.a., sample size was too small to calculate average CPUE.

The average sizes of juvenile fish (<100 mm) caught in the North Johnstone, Mulgrave and Russell Rivers and in Crystal Creek were significantly higher in 2000 than those juveniles sampled in 2001 (Table 2). Given that the relative abundance of juvenile fish was significantly higher in North Johnstone, Mulgrave and Russell Rivers in 2001 than in 2000, these data suggest the presence of larger numbers of smaller fish in those systems in 2001.

Length–frequency plots from the Russell River and Baffle Creek (Fig. 6) also support the concept of recruitment variability. Fish appear to have fully recruited into the upper tidal areas in each system at a length of ~175-mm LCF. In the Russell River, the number of fish in the size classes from 175 mm to 375 mm remains relatively constant and then declines. Initially, the size–frequency plot for the Baffle Creek fish follows the same trend, rising to a high in the

175-mm size class and then sharply dipping before rising again.

Recruitment to offshore areas

Despite evidence of spawning activity in offshore areas (Allen 1985, 1991), no juvenile fish have been sampled in habitats other than in rivers, tidal creeks and gutters or in supra-littoral wetlands (D. J. Russell, unpublished data). The smallest fish that was sampled offshore from the commercial catches was 370-mm LCF and ~338-mm LCF in the recreational fishery.

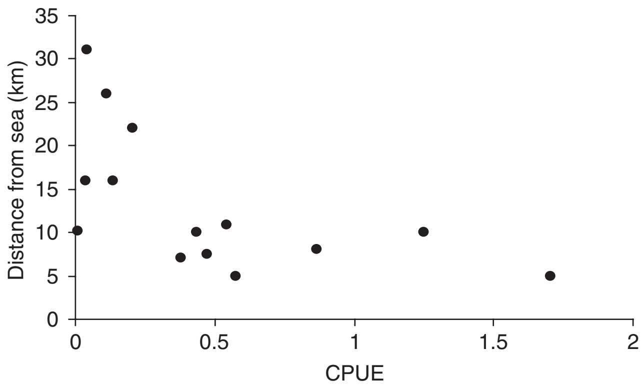

Fig. 5. Catch per unit effort (number of fish caught per 1000 s of electrofishing time) at major study sites for juvenile mangrove jack (<100-mm length to caudal fork, LCF) plotted against distance (km) from the river mouth. Data were pooled over the period January 1999 to February 2002.

Discussion

Mangrove jack in northern Australia, depending on their size, are found in a variety of locations including inshore coastal, estuarine or riverine habitats or offshore in areas of the Great Barrier Reef. During the current study, all of the smaller juvenile and sub-adult fish were sampled in inshore areas, whereas catches from offshore areas were made up of fish larger than ~338-mm LCF. In a study of lutjanids and serranids in northern Australia, Sheaves (1995) also observed that estuarine populations of *L. argentimaculatus* seemed to consist entirely of reproductively immature fish and that these were much smaller and younger than typical fish from offshore. He suggested that this inferred a migration offshore away from estuaries, but conceded that few offshore movements had been documented and that, because tagged fish in reef waters have a low probability of recapture, a substantial tagging and recapture effort would be required to demonstrate movement offshore. During the current study

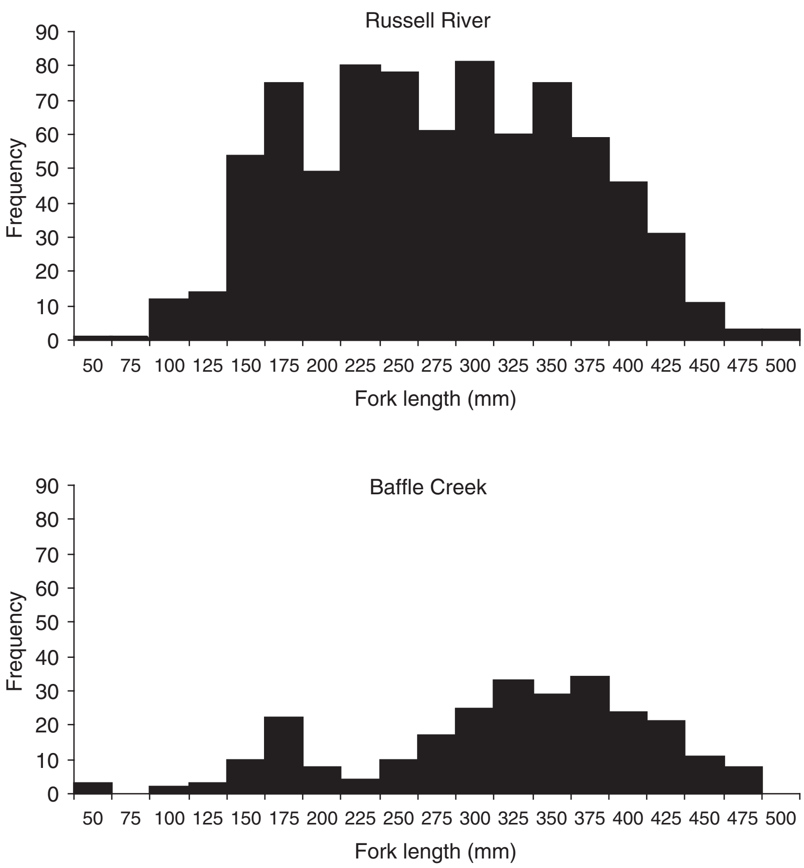

Fig. 6. Length–frequency of mangrove jack from the Russell River and Baffle Creek.

over 4300 tagged mangrove jack were released and data were available on an additional ~17 900 tagged fish in the SUNTAG database. In the current study, only small numbers of fish were recaptured in offshore areas, although the percentage increased with increasing size. For example, of the 21 fish recaptured in the 400–500-mm LCF size cohort, 19% were either caught on the Great Barrier Reef or offshore adjacent to a continental island. Similarly, the number of offshore recaptures of fish tagged by recreational fishers in the SUNTAG database is correspondingly small (26); however, it supports the contention that there is a general offshore migration of larger *L. argentimaculatus*. Very little is known of the movements of mangrove jack once they have migrated offshore, although it appears that they are capable of travelling substantial distances. For example, in the SUNTAG database, there is a record of one mangrove jack that was recapured on a reef ~315 km north of the estuary where it was released.

A study by Ovenden and Street (2003) of the genetic stock structure of mangrove jack in Australia supports the argument that the species is relatively mobile. Evidence from their mtDNA analyses suggests that the vagility of mangrove jack populations is high enough to homogenise populations in eastern Australia and possibly the whole Australian continent (Ovenden and Street 2003; Russell *et al*. 2003). This is in contrast to another catadromous (inshore spawning) species, *Lates calcarifer*, which has a high level of genetic subdivision with 16 Australian sub-populations of which four are in eastern Queensland (Keenan 1994).

Although larger mangrove jack are found predominantly in offshore habitats, large fish are also found in rivers, estuaries and along coastal foreshores particularly associated with structures such as rocky headlands. For example, during the current study 31 (<1% of total fish sampled) fish longer than 500-mm LCF were sampled either in estuaries or in the lower freshwater reaches of rivers, with the largest fish (610-mm LCF) captured in a seasonally isolated freshwater lagoon. Of these larger fish, the reproductive status was available for 16 fish and in all but three, the gonads were either immature or resting (stage I or II); the others were developing (stage III ($n = 2$) and stage IV ($n = 1$)). The presences of a small sample of male *L. argentimaculatus* from one estuary that showed some reproductive development led Sheaves (1995) to speculate that they were part of a larger group preparing to migrate offshore. The low recapture rate of fish that had moved offshore was probably a result of a combination of factors including tag shedding and low levels of fishing effort, either recreational or commercial, for this species in offshore waters. Cappo *et al*. (2000) suggested that these same factors also may make it difficult for the long-term recovery of useful sample sizes of oxytetracycline-marked lutjanids in Great Barrier Reef waters. Juveniles and sub-adult mangrove jack made up almost the entire catch in inshore areas and we found no evidence of smaller, juvenile fish in offshore areas. Sheaves (1995) noted sporadic reports of low numbers of juvenile *Lutjanus argentimaculatus* from offshore locations, but did not elaborate on the types of offshore habitat where they were found or the sizes of fish sampled.

Most of the mangrove jack tagged in rivers and estuaries were recaptured within a kilometre of where they were released. Small proportions of fish moved in either a net upstream or a net downstream direction. Although tag–recaptures provided convincing evidence of offshore movements during this study, there were no records of fish moving a net distance of more than 12 km upstream into freshwater reaches of rivers. Other studies in north Queensland rivers have reported large upstream movements. For example, Merrick and Schmida (1984) noted the presence of juveniles and sub-adult mangrove jack 130 km up the Burdekin River and well upstream (~80 km) in the Tully River.

The absence of large, adult fish in inshore areas suggests that once fish migrate offshore, they do not return to inshore areas. However, small juveniles, and possibly post-larvae, are recruited into coastal areas and estuaries and, later, into the lower freshwater reaches of rivers where they can remain for a considerable time. For example, the age of a 610-mm LCF, stage III female mangrove jack caught in a freshwater lagoon in central Queensland was estimated from otolith analysis to be 9 years old (A. J. McDougall and D. J. Russell, unpublished data). During this study, the smallest juveniles caught in an estuary/river was 20 mm LCF, and this is probably around the smallest size that occurs in these habitats. In eastern Thailand, large numbers of juveniles, mostly 20–30-mm TL, but as small as 16-mm TL, were observed migrating into river estuaries during late October to January (Doi *et al*. 1992, 1994). In a later study of the swimming characteristics of *L. argentimaculatus*, Doi *et al*. (1998) suggested that it would be possible for juveniles larger than ~16-mm TL to acquire swimming or cruising ability strong enough to migrate to coastal waters or river estuaries and noted that increased stomach sizes and therefore enhanced food storage capacity in this size fish may facilitate shifting habitats. It is feasible that onshore currents may also assist in larval transportation and this has been documented for other species in north Queensland. For example, Dennis *et al*. (2001) document the transport of *Panulirus ornatus* phyllosomas by surface onshore currents from the Coral Sea onto the Queensland coast.

In Australia, Davis (1988) found that although *L. argentimaculatus* was a dominant species in the tidal Leanyer Swamp in the Northern Territory, they are transient, with juveniles using the upper estuary and swamp as a nursery. He found that the number of juvenile *L. argentimaculatus* entering the swamp was correlated with month and tidal height. Higher tides provide greater assistance for the upstream movement of juvenile fish and also enable them to penetrate further into upstream areas to access wetlands (Davis 1988). In central Queensland, juvenile mangrove jack appear to move up into the freshwater riverine habitats in late summer or early autumn. At the Ben Anderson tidal barrage, 24-km upstream from the mouth of the Burnett River in south-east Queensland, 10 juvenile mangrove jack between 24- and 36-mm LCF were captured moving upstream through the vertical slot fishway in April 1999 after a freshwater runoff event the previous month (A. Berghuis, personal communication). In subsequent monitoring, no other juvenile mangrove jack were caught moving through the fishway.

The life cycle of mangrove jack in north-eastern Australia has offshore and inshore phases. Juvenile fish recruit into inshore coastal areas, moving into estuaries and upstream into the lower freshwater reaches of rivers. The trigger for moving inshore is unknown, although Doi *et al*. (1994, 1998) noted that juvenile fish appeared to move into the estuaries after the wet season and suggested that their upstream movement is governed by freshwater runoff resulting from high seasonal rainfall. Although capable of moving large distances upstream (Merrick and Schmida 1984), juvenile mangrove jack abundance decreases with increasing distance upstream and most intra-riverine movements are relatively small. Mangrove jack can remain resident in estuaries and rivers for considerable periods and during this study the maximum age of fish sampled in inshore areas was 11 years (Russell *et al*. 2003). The length–frequency histogram for fish in the Russell River (Fig. 6) shows the number of fish in the size classes from 175 mm to 375 mm to be relatively constant and then decline for larger sizes, mainly owing to offshore movements and perhaps some increase in fishing mortality. The length–frequency histogram for mangrove jack in Baffle Creek is bimodal (Fig. 6), suggesting the possility of variable recruitment in one or more year classes.

Both the tagging studies and the almost complete absence of larger individuals in inshore catches strongly suggest that older fish unidirectionly move to offshore areas, where they become reproductively active (Day *et al*. 1981; Allen 1987; Sheaves 1995). Sheaves (1995) speculated that possible reasons for spawning offshore could include reduced sperm viability in the extreme physical conditions prevalent in estuaries or that it may be a mechanism for increased genetic mixing. Given that fish in coastal aquaculture facilitaties and ponds can spawn naturally (Leu *et al*. 2003) the former is unlikely. However, Ovenden and Street (2003) showed that in eastern Australia there is a single evolutionary significant unit indicating considerable genetic mixing. Improved foraging opportunities does not appear to factor in triggering offshore movements. The condition of fish found in offshore habitats was not significantly different from fish of similar sizes caught in fresh water. The condition factor of estuarine fish was significantly higher than that in fish caught either offshore or in fresh water, but this should be viewed cautiously because the sample size of estuarine fish in the 400–500-mm LCF range was small ($n = 36$).

The biphasic life cycle of mangrove jack presents several unique management issues for the fishery. First, despite a minimum size limit, the fish that are targeted by mainly recreational fishers in rivers and estuaries are almost all immature and overfishing in these areas could have severe implications for the stock. The adult, reproductively mature fish in offshore areas are much less vulnerable to overfishing compared to fish resident in rivers because they disperse over considerable distances and, in Great Barrier Reef waters, are not currently heavily targeted by either commercial or recreational fishers. Indeed, recent management changes substantially increasing the percentage of no fishing, protected areas in the Great Barrier Reef marine park may further lessen fishing pressure on this species. This may be different in other parts of Australia, for example in the Gulf of Carpentaria, where fish appear to school at certain times and are occasionally caught in fish trawls (Russell *et al*. 2003). Fisheries managers need to be cognisant of the potential damage that excessive targetting of adults and particularly juveniles, concentrated in coastal waters and estuaries, can have on *L. argentimaculatus* stocks.

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