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Habitat utilisation and movement of black bream *Acanthopagrus butcheri* (Sparidae) in an Australian estuary

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ABSTRACT: Acoustic telemetry was used to document patterns of movement by black bream *Acanthopagrus butcheri* (Munro, 1949) throughout Australia's largest estuary, the Gippsland Lakes. Forty-four fish were surgically implanted with acoustic transmitters and monitored over 12 mo (November 2005 to October 2006). Fish moved throughout the Gippsland Lakes at average rates of 8.7 km d^{-1} over 12 mo, with some fish moving distances of up to 2600 km. Fish frequently moved among the major estuarine rivers (Tambo, Mitchell and Nicholson rivers), sometimes moving up to 30 km in a day. Fish use of the rivers, river entrances and lakes varied strongly with the time of year. Fish spent more time in the lakes than rivers in late summer and early autumn, but began to use the rivers more than the lakes at the end of autumn. River use was greatest in early to mid-winter, then gradually decreased through spring. Fish also spent more time in some rivers than others, with use of their respective entrances peaking during transition phases when fish were moving from the rivers to the lakes and vice versa. Time of day was a weak predictor of regional patterns of fish use, but during the transitional phases (March through May) fish use of lakes was greater at night, while use of rivers was greater during the day. Monthly variation in time spent by fish in particular rivers varied positively with the discharge of freshwater (with a concomitant negative relationship between lake use and overall river discharge).

KEY WORDS: *Acanthopagrus butcheri* · Sparidae · Spatial behaviour · Acoustic telemetry · Gippsland Lakes

INTRODUCTION

Understanding the patterns of habitat use and movement by fish is critical to the sustainable management of aquatic resources (Fromentin & Powers 2005, Semmens et al. 2007). Spatial metrics on connectivity, residency, habitat affinities and behaviour are crucial in the development of models for resource management (Walters & Martell 2004). Recent technological advances have dramatically improved our ability to study the spatial behaviour of animals in aquatic environments (Lucas & Baras 2000). Biotelemetry methods provide valuable information on home range size, habitat selection and activity (Heupel et al. 2006). Observations on the change in behaviour of animals after environmental disturbance are increasingly important for predicting changes in resource structure and function with environmental perturbations.

Acoustic telemetry is one of the most widely used methods of documenting behaviour of fish and invertebrates, and has been used to explore questions of habitat use, movement and connectivity, and behaviour (Heupel et al. 2006). Acoustic telemetry has been used to quantify fish use of marine protected areas (Parsons et al. 2003, Lindholm 2005, Topping et al. 2005), artificial structures (Girard et al. 2004, Szedlmayer & Schroepfer 2005) and re-established aquatic habitat (Hindell 2007). More recently, acoustic techniques have been useful in describing subtle differences in movement and habitat use between stocked and nat-

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ural fisheries resources (Taylor et al. 2006), as well as documenting the degree of connectivity among disparate regions of large estuaries (Gudjonsson et al. 2005, Næsje et al. 2007). A common message from these studies is that the spatial behaviour of individuals changes dramatically over different temporal scales. Acoustic telemetry can provide more frequent monitoring of fish movement patterns and is beneficial in answering questions on the spatial behaviour of fish compared with traditional fish sampling methods, which provide only a 'snap-shot' of fish behaviour in time and space.

Acanthopagrus butcheri (Munro, 1949) is endemic to nearshore coastal areas, rivers and estuaries of southern Australia. *A. butcheri* is thought to be the only truly estuarine sparid in Australia and can tolerate a wide range of salinities, from 3 to 4 to hypersaline waters. In most estuaries, however, *A. butcheri* are most abundant in areas where salinities range from 15 to 25, particularly during the spawning period (late winter to early summer). Little is known about the movements of *A. butcheri*. Potter & Hyndes (1999) generally considered *A. butcheri* to be resident within estuaries, completing their entire lifecycle within a specific estuary. *A. butcheri* can, however, move considerable distances up and down estuaries (Hindell 2007), and some fish have been found to move among estuaries along the coast (Butcher & Ling 1958).

Acanthopagrus butcheri supports valuable recreational and commercial fisheries in the Gippsland Lakes (Walker et al. 1998), a large estuary in southeastern Australia. Historical catch and effort data from the commercial fishery suggests that abundances of *A. butcheri* in the Gippsland Lakes vary widely among years (Cashmore 2002). Since 2001 there has been a sharp decline in catches of *A. butcheri* in the Gippsland Lakes and current catches are at historically low levels. The reasons for the decline are unknown, but are thought to relate to recruitment and/or spawning failure as a consequence of unfavourable environmental conditions. There is some suggestion, however, that fish abundances may not have declined as seriously as data on catch suggest, and that lower catches may actually be an artefact of fish moving upstream and remaining in the rivers for longer periods of time (where they are not accessible to commercial fishers). Southeastern Australia has been impacted by a most severe drought in recent years and, as freshwater flows to the Gippsland Lakes have declined, high salinity waters (>30) have moved further upstream. Consequently, it has been suggested that *A. butcheri* may be moving further upstream in pursuit of lower salinities and, in the process, spending more time in the rivers than the lakes.

The present study aimed to document broad-scale patterns of movement by *Acanthopagrus butcheri* throughout the Gippsland Lakes and rivers. In doing so, the degree to which fish used different regions of the study area, including the rivers, river entrances and lakes, was quantified with respect to the time of year, time of day, and freshwater inputs.

MATERIALS AND METHODS

Study area. The present study was done in the Gippsland Lakes, southeastern Australia (Fig. 1). The Gippsland Lakes are a network of temperate coastal lakes, marshes and lagoons covering an area of about 600 km^2. The Gippsland Lakes has a small tidal range of around 30 cm and is connected to the open ocean by an artificial channel that was cut across the beach at

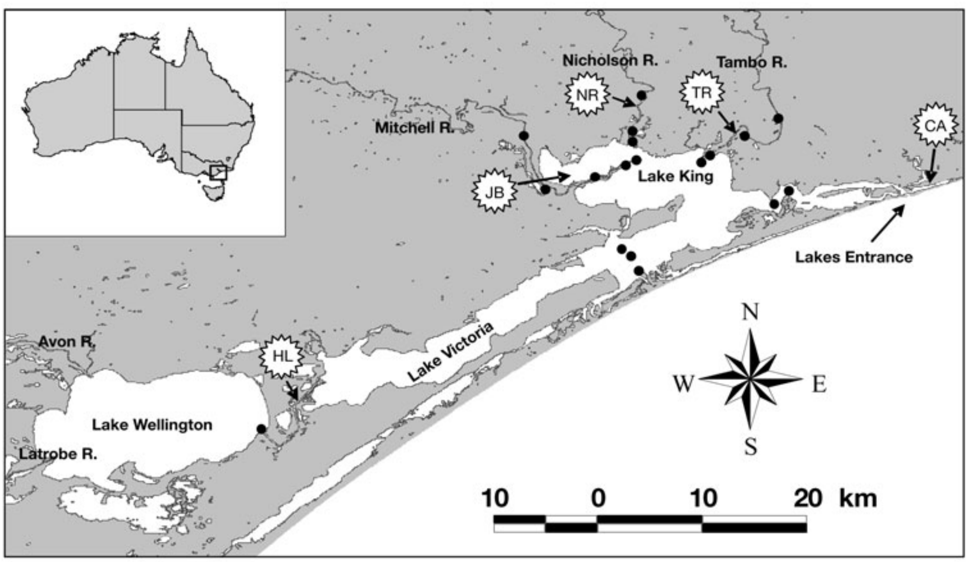

Fig. 1. Gippsland Lakes with locations of acoustic receivers (●) and release locations of fish (NR: Nicholson River; TR: Tambo River; CA: Cunningham Arm; JB: Jones Bay; HL: Hollands Landing)

Lakes Entrance to stabilise the water level, create a harbour for fishing boats, and open up the lakes to shipping.

Lake Wellington, Lake King and Lake Victoria are the largest of the lakes in the study area. There are 5 major tributaries entering the Gippsland Lakes: 2 in the west (the Avon and Latrobe rivers), and 3 feeding the central basin of Lake King (the Mitchell, Nicholson and Tambo rivers). The Gippsland Lakes are around 70 km long, forming the largest navigable network of inland waterways in Australia, and (with associated wetlands) are recognised under the Ramsar Convention as a site of international importance, supporting rare, endangered, and vulnerable plants and animals.

Rainfall in the Gippsland Lakes region between 2000 and 2006 was generally lower than, and subsequent annual discharge of freshwater to the Lakes from the 5 major tributaries (Fig. 1) was only 66% of, the long-term average (1 344 188 megalitres [Ml] yr^{-1} versus 2 018 794 Ml yr^{-1}; www.vicwaterdata.net/vicwaterdata/home.aspx). As a consequence, salinity at 4 sites within the lower and middle basins of the Gippsland Lakes has increased from around 20 to more than 30 (www.vicwaterdata.net/vicwaterdata/home.aspx), and there has been a concomitant movement and constriction of the salt wedge inland along the major tributaries; in the Mitchell, Tambo and Nicholson rivers, salinities as high as 27 to 28 have been recorded in surface waters at the most inland incursion of saltwater (J. S. Hindell pers. obs.).

Selection of study sites and application of acoustic telemetry. Acoustic receivers (VEMCO, VR2) were used to detect and record information from ultrasonic (69 kHz) signals emitted by acoustic transmitters in real time. Thirty receivers were placed strategically throughout the Gippsland Lakes, from Lakes Entrance to the western end of McLennans Strait (Fig. 1). Within the lakes, receivers were located to separate the study area into 5 broad regions (Fig. 1). Within each of the Tambo, Nicholson and Mitchell rivers, receivers were placed upstream to distances of around 15 km from the entrance to the lakes.

Receivers were attached underwater to available structure (such as woody debris or navigational piles) with plastic cable ties at depths between 2 and 3 m. Sensitivity analyses showed that acoustic receivers were able to detect acoustic transmitters (implanted within fish) at distances of up to 400 m in the rivers and 600 m in the lakes, even during periods when environmental variables, such as strong winds (increasing water turbulence), may interrupt the detection of acoustic signals.

Three types of data were recorded and stored when a tagged fish swam within the range of an acoustic receiver: (1) number of visits; (2) total time of visit; and (3) number of hits. The number of visits represents the number of times a fish visited a receiver over the course of the study. For example, a fish that is detected at a receiver, moves outside the detection range of a receiver, and then returns, would have 2 visits recorded. The theoretical minimum time between visits depends on the transmission delay of the acoustic transmissions from the transmitters (tags), which in the current study were set to occur randomly between 30 and 60 s. The total time of a visit (or visits), over the course of a study represents the total time elapsed (s) between the initial and final detection for a given visit (and is summed over all visits). The number of hits represents the number of times a given transmitter is detected within a single visit. For example, if a transmitter is set to transmit once every 30 s and a fish remains in the vicinity of a receiver for 2 min, 4 'hits' will be recorded.

Tagging fish. The methods for catching and tagging *Acanthopagrus butcheri* are outlined in detail by Hindell (2007). Briefly, fish for tagging were caught using recreational methods. Only lip-hooked fish were retained for tagging because of the high mortality of fish that swallow hooks (S. Conron unpubl. data). Fish were tagged at 5 different locations within the Gippsland Lakes, including outside the major rivers (Table 1, Fig. 1), to avoid potential effects of release location on movements. Fish were also tagged in a number of batches through time (Table 1) to ensure that adequate numbers of tagged fish were present in the study area over 12 mo; the tag manufacturer only guaranteed 300 d of battery power for the acoustic transmitters used here.

Fish were first anaesthetised to Stage III sedation (Ross & Ross 1999) with Benzocaine (2 g in 10 l of estuarine water), and the fork length (FL, mm) and weight (g) of each fish were recorded. A single, individually coded, acoustic transmitter (VEMCO V9-2L coded, random signal delay 20 to 60 s) was inserted into the peritoneal cavity via a 2 to 3 cm off-centre ventral incision in the body wall, which was then 'closed' with 2 to 3 simple sutures (Braided Polyglycolic Acid Suture, 3/8 circle, USP 3/0). The sutures were sealed with cyanoacrylate adhesive, with care taken to minimise direct contact with the skin of fish in case of irritation (Jepsen et al. 2002). All fish were also tagged with external anchor tags (T-bar), which were inserted into the dorsal musculature, adjacent to the dorsal fin. Once tagged, the wound areas of fish were swabbed with antiseptic, and fish were placed in a cubic (70 × 70 × 70 cm) holding net in water to recover. Once fish were able to maintain balance, they were released close to the point of capture.

Flow data. Freshwater input is a significant determinant of water quality (especially salinity and tem-

Table 1. *Acanthopagrus butcheri*. Summary of the release date and location of tagged fish; fork length (FL, mm) and weight (W, g) of tagged fish; time after release (days), estimated distance travelled (S, km) and mean rate of movement (km d^{-1}) of fish. See Fig. 1 for release locations. –: fewer than 20 data points on fish movement, so distance parameters not calculated

Tag ID	Date	Location	FL	W	Time	S	Rate
90	Nov 2005	Nicholson River	255	367	306	837.3	2.7
91			245	331	197	215.9	1.1
93			260	371	131	143	1.1
94			255	324	234	151	0.6
95			260	408	183	1282	7.0
96			255	347	198	729	3.7
97			275	425	207	388	1.9
98			270	424	326	513.4	1.6
99			265	403	330	1405.3	4.3
1205	Dec 2004	Nicholson River	243	309	314	195.1	0.6
1206			324	740	361	634.1	1.8
1207			227	257	337	1405	4.2
1208			213	208	342	515.9	1.5
1209		Jones Bay	215	230	327	530.9	1.6
1211		Nicholson River	309	668	359	539.6	1.5
1213		Tambo River	235	264	216	974.9	4.5
1214			209	192	344	463.6	1.3
1217		Nicholson River	225	244	336	1819.5	5.4
1219	Mar 2005	Tambo River	360	920	344	2463.1	7.2
1220			250	292	–	–	–
1224			260	350	72	408.7	5.7
1225			240	291	317	1544.9	4.9
1228			260	325	336	470.9	1.4
1229	Nov 2005	Nicholson River	270	428	329	331.4	1.0
1230	Oct 2005	Hollands Landing	255	405	–	–	–
1231	Mar 2005	Tambo River	240	305	306	2656.9	8.7
1232	Oct 2005	Hollands Landing	230	282	–	–	–
1234			245	327	318	99.3	0.3
1235			260	466	–	–	–
1237			400	1932	–	–	–
1240			240	301	190	59.9	0.3
1241			245	362	298	575.5	1.9
1242			305	640	340	214.4	0.6
1243	Aug 2005	Cunningham Arm	225	216	–	–	–
1245			225	237	–	–	–
1248			200	173	208	66.7	0.3
1249	Dec 2004	Jones Bay	213	210	361	1760.1	4.9
1250			195	165	197	741.8	3.7
1251		Nicholson River	211	192	81	258.8	3.2
1252			215	216	87	326.8	3.7
1254		Jones Bay	210	200	–	–	–
1255		Nicholson River	225	241	335	240.5	0.7
1258		Jones Bay	203	185	–	–	–
1260		Nicholson River	224	241	–	–	–

perature) in the Gippsland Lakes. Given the salinity preferences of *Acanthopagrus butcheri*, especially for spawning, it is possible that freshwater flows from the Nicholson, Tambo and Mitchell rivers may influence fish use of the rivers. Freshwater discharge (discharge, Ml d^{-1}) data are recorded for each river entering the Gippsland Lakes and are stored at the Victorian Water Resources Data Warehouse (www.vicwaterdata.net/vicwaterdata/home.aspx). Daily discharge data over the period of the present study were extracted and monthly averages calculated.

Data analyses. The Animal Movement extension (Hooge et al. 2000) for ArcView GIS 3.3 was used for preliminary assessment of movement patterns, data checking and to calculate rates of movement. Rates of movement for fish were calculated from the time differential s^{-1} divided by the minimum distance s^{-1} by water between consecutive acoustic receivers.

The present study provides time-integrated information on the time (s) and number of hits by each tagged fish at each acoustic receiver (n = 30) between November 2005 and October 2006. As in Hindell (2007), 2 broad rules were used to select data for analyses. First, to reduce effects of surgery-induced changes on fish behaviour, only data 1 mo post fish release were used in analyses. Second, fish had to be recorded for at least 3 mo within (or leading into) the year-long study; 3 tagged fish were 'lost' 2 mo after tagging, so these data were excluded from further analyses.

The placement of double receivers around the entrance to each river, one immediately adjacent to the entrance and the other 600 m upstream, enabled the separation of time spent by fish in the rivers versus the lakes. Detection ranges within the rivers were between 300 and 400 m, so we were always able to determine if a fish was swimming downstream toward the entrance or upstream. To further increase our understanding of fish use of the entrance region of the rivers, we estimated the time spent by fish outside the river but in the immediate vicinity (between 400 and 500 m into the Lakes) of the entrance. Overall, the average time required for fish to move between the entrance receiver and that immediately upstream was around 3 min. Subsequently, 4 rules were applied in calculating the times spent by fish in the river versus entrance versus lake regions: (1) all recorded time a fish spent near the entrance receiver was 'entrance time'; (2) if a fish, on moving away from the entrance receiver, was next detected upstream, the difference between the departure and arrival times was designated 'river time'; (3) if a fish was detected at the entrance receiver within 3 min of moving away from it (i.e. the fish swam just outside the detection range of the listing station and then back again), the difference between departure and arrival times was designated 'entrance time'; and (4) if a fish, on moving away from the entrance receiver, was next detected at a receiver outside the river, the difference between departure and arrival times was designated 'lake time.'

Once the amounts of time a fish spent in each region (lake, entrance and river) had been calculated, we divided the data by the number of days that fish was detected in the last month in which it was observed. For example, if a fish was detected every day until 20 July, but not again after that, time data for July were divided by 20. This ensured that the estimates of time for fish were not weighted by differences in the number of days in a month (or the number of days for which they were observed in their last month). Subsequently, the principle response variable describing fish use of the study area was time (s d^{-1}). Data were assessed for normality and homogeneity of variance prior to analyses using box plots and plots of residuals (Quinn & Keough 2002). Data that did not meet these assumptions were transformed (Log_{10}) and reassessed.

Variability in time (s d^{-1}) was initially analysed using 3-factor randomised blocks analyses of variance for each month (November 2005 to October 2006) separately. Region (Lake, Entrance, River), and time of day (dawn: 04:00 to 08:00 h; day: 08:00 to 16:00 h; dusk: 16:00 to 20:00 h; night: 20:00 to 04:00 h) were treated as fixed factors. Fish were included in the model only as a random blocking factor. Planned comparisons were used to compare differences in time among regions.

Regression analyses were used to assess relationships between time (of all fish) and average monthly freshwater flows for each river individually (e.g. time spent by all fish in the Mitchell River versus flow in the Mitchell River), as well as time in the lakes versus total average monthly flows from the Mitchell, Nicholson and Tambo rivers.

RESULTS

All fish analysed in the present study survived surgery and were detected for more than 4 mo post release. Most fish (54 %) moved relatively large distances (>300 km, Table 1) during the study and there was little evidence of residency in a single river of the Gippsland Lakes (Table 1). Fish moved regularly among the Tambo, Nicholson and Mitchell rivers at an average rate (across all fish) of 2.8 km d^{-1}. Some fish were estimated to have moved distances in excess of 2600 km while at liberty, at an average rate of 8.7 km d^{-1} (e.g. Fish 1231, Table 1); rates of movement for other fish were as low as 0.6 km d^{-1} (e.g. Fish 1205, Table 1). There was no discernable relationship between the average rate of movement by fish and fish length (regression: df = 1,32, r^2 = 0.006, p = 0.667).

Release location had some influence on where fish were likely to move. Fish released in Cunningham Arm or at Hollands Landing were found to use the Tambo, Nicholson and Mitchell rivers despite the relatively large (up to 30 km) distances separating release and river locations (Fig. 2). Time spent by these fish in these rivers was less than that spent by fish released either directly into these rivers, or in the lake adjacent to the river entrances (i.e. Jones Bay). Fish released in a particular river did not remain in that river permanently (Fig. 2); most fish moved into a different river (or into the lake from the river) to that of their release location within days of tagging.

The degree to which fish used the river versus lake components of the Gippsland Lakes differed strongly among months (Table 2, Figs. 3 to 5) and varied in subtle ways with time of day (Fig. 4). Fish spent more time in the rivers than the lakes and least time around the river entrances in November and December (2005). January marked a period of transition, when the use of lakes and rivers was similar, although fish use of river entrances remained low (Fig. 4). In February and March, fish spent more time in the lakes than the rivers, with use of the river entrances still around half that of the lakes (Fig. 4). April was another period of transition, when fish use of the rivers and lakes was again similar but greater than use of the river entrances (Fig. 4). In May, fish began to spend slightly more time in the rivers than the lakes and there was little difference in fish use of the river entrances and the lakes. Between June and October there was a significant increase in the time that fish spent in the rivers, with the difference between the rivers and lakes peaking in June, July and August (Fig. 4). In September and October, fish were again spending similar periods of time in the lakes and river entrances.

The time spent by fish in the lakes was strongly influenced by fish that were released furthest from the rivers, which rarely used the rivers in the north–central regions of the Gippsland Lakes (Fish 1230 and 1232 to 1248, Table 1). To better assess the subtle diel variability, hour-to-hour variability in time spent in the different regions of the study area (entrance, river, lake) was plotted without 'lake-based' fish (Fig. 5). The exclusion of these fish did not increase the overall times that fish spent in the rivers, but reduced the difference between rivers and lakes for the periods when fish were previously associated more strongly with the lakes (February to April). Fig. 5 also demonstrates much stronger diel effects from February to May. Fish use of the rivers and lakes was the same in February regardless of diel period. In March, there was a trend for fish to use the lakes more than the rivers between 19:00 and 07:00 h,

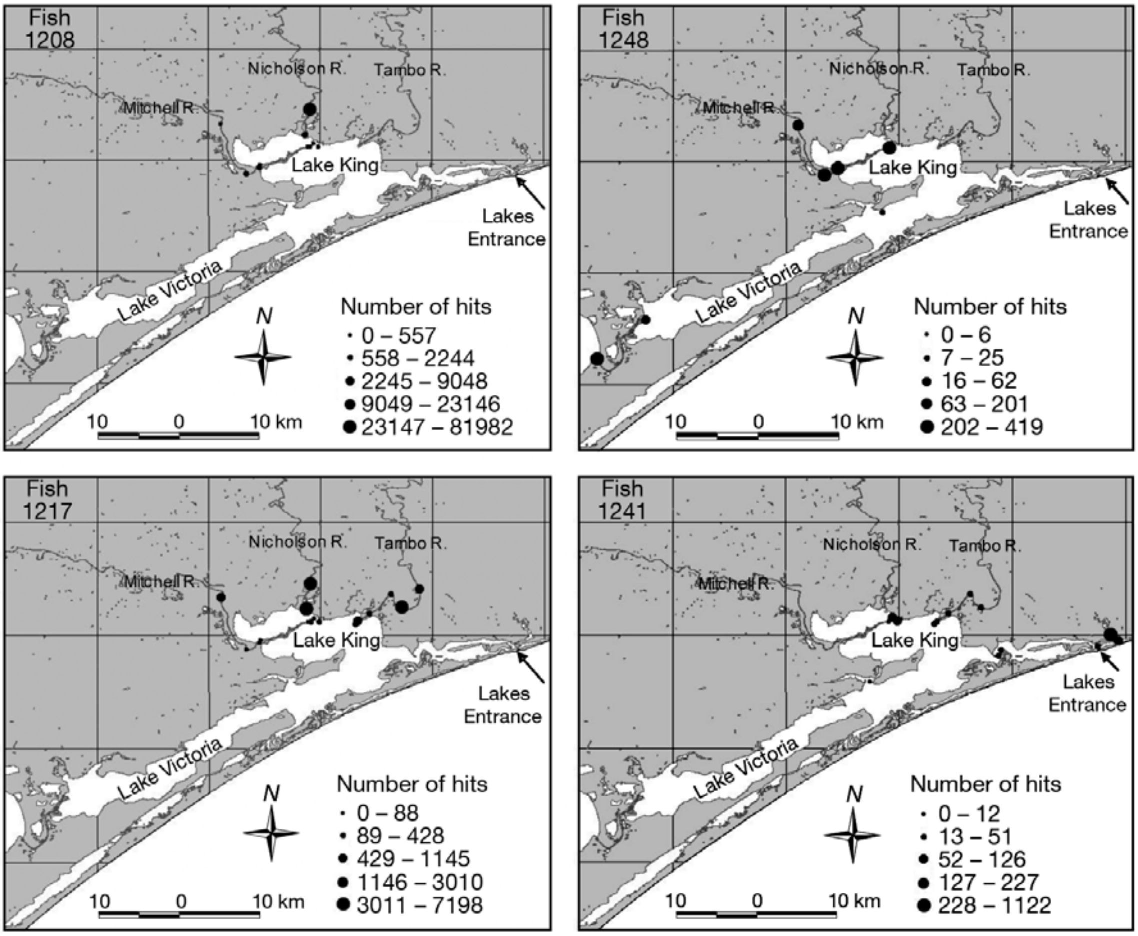

Fig. 2. *Acanthopagrus butcheri.* Typical patterns of use of different regions of the Gippsland Lakes, based on the number of times fish were detected (hits), by 4 individual fish (Fish 1208, 1248, 1217, 1241) over 12 mo

and for use to be similar between the rivers and lakes from 07:00 to 19:00 h. In April and May, fish use of the lake and entrance regions was always lower than that in the rivers, but, especially at river entrances, decreased markedly between 07:00 and 19:00 h (Fig. 5).

The time spent by fish in each of the rivers and lakes was compared with mean freshwater discharge for each river respectively at monthly intervals over the entire study period. The increase in times spent by *Acanthopagrus butcheri* in each of the Tambo, Nicholson and Mitchell rivers always occurred before peaks in freshwater flow (Fig. 6A–C). Fish use of the lakes peaked in February and March, corresponding with the lowest flows, while highest flows (collectively) into the lakes corresponded with the movement of fish into the rivers (Fig. 6D). For the Nicholson and Mitchell rivers, there were significant positive linear relationships between the average time spent by fish in a river and the average monthly flows (Mitchell River: df = 1, 8, $r^2 = 0.407$, $p = 0.047$; Nicholson River: df = 1, 10, $r^2 = 0.704$, $p = 0.001$). The time spent by fish in the lakes varied negatively with the total average flows from the Nicholson, Mitchell and Tambo rivers (df = 1, 10, $r^2 = 0.704$, $p = 0.001$), but average monthly flows in the Tambo River were a weak predictor of time used by fish (df = 1, 10, $r^2 = 0.205$, $p = 0.098$).

DISCUSSION

This is the first study to document and interpret broad-scale patterns of movement and rate of movement for a resident estuarine species (*Acanthopagrus butcheri*), with respect to seasons, times of the day and freshwater flows. Fish moved throughout the study area, sometimes moving up to 30 km d^{-1}. Most movements by fish were confined to the riverine regions of the study area, with the lakes serving as a thoroughfare among rivers. River and lake use varied strongly

Table 2. *Acanthopagrus butcheri*. Summary of probability values of 3-factor randomised block analyses of variance comparing the time (s d^{-1}) spent by fish (F) in different regions (rivers, R; lakes, L; river entrances, E) at different times of the day (T, dawn: 04:00 to 08:00 h; day: 08:00 to 16:00 h; dusk: 16:00 to 20:00 h; night: 20:00 to 04:00 h). Degrees of freedom shown in subscript. Bold values are significant at $p < 0.05$

	2005		2006									
Source	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct
Region (R)	**0.002**$_{2,68}$	**<0.001**$_{2,82}$	**0.002**$_{2,80}$	**<0.001**$_{2,76}$	**0.001**$_{2,68}$	**0.005**$_{2,68}$	**0.022**$_{2,66}$	**<0.001**$_{2,58}$	**<0.001**$_{2,46}$	**<0.001**$_{2,44}$	**0.001**$_{2,42}$	**0.026**$_{2,32}$
E = R	**<0.001**$_{1,68}$	**<0.001**$_{1,82}$	**0.004**$_{1,80}$	**0.014**$_{1,76}$	0.206$_{1,68}$	**0.004**$_{1,68}$	**0.006**$_{1,66}$	**<0.001**$_{1,58}$	**<0.001**$_{1,46}$	**<0.001**$_{1,44}$	**<0.001**$_{1,42}$	**0.001**$_{1,32}$
E = L	**0.019**$_{1,68}$	**0.003**$_{1,82}$	**0.001**$_{1,80}$	**<0.001**$_{1,76}$	**<0.001**$_{1,68}$	**0.005**$_{1,68}$	0.136$_{1,66}$	0.078$_{1,58}$	0.233$_{1,46}$	0.109$_{1,44}$	0.471$_{1,42}$	0.487$_{1,32}$
R = L	0.210$_{1,68}$	0.132$_{1,82}$	0.642$_{1,80}$	0.060$_{1,76}$	0.011$_{1,68}$	0.904$_{1,68}$	0.185$_{1,66}$	**<0.001**$_{1,58}$	**<0.001**$_{1,46}$	**0.002**$_{1,44}$	**0.002**$_{1,42}$	**0.004**$_{1,32}$
Time of day (T)	**<0.001**$_{3,102}$	0.235$_{3,123}$	0.165$_{3,120}$	0.301$_{3,114}$	0.100$_{3,102}$	**0.004**$_{3,102}$	0.717$_{3,99}$	0.098$_{3,87}$	0.053$_{3,69}$	**0.002**$_{3,66}$	0.358$_{3,63}$	0.353$_{3,48}$
Fish (F)	**<0.001**$_{34,204}$	**<0.001**$_{41,246}$	**<0.001**$_{40,240}$	**<0.001**$_{38,228}$	**<0.001**$_{34,204}$	**<0.001**$_{34,204}$	**<0.001**$_{33,198}$	**<0.001**$_{29,174}$	**<0.001**$_{23,138}$	**<0.001**$_{22,132}$	**<0.001**$_{21,126}$	**<0.001**$_{16,96}$
T × R	**0.002**$_{6,204}$	0.077$_{6,246}$	0.235$_{6,240}$	0.293$_{6,228}$	0.233$_{6,204}$	**<0.001**$_{6,204}$	0.162$_{6,198}$	**0.034**$_{6,174}$	0.192$_{6,138}$	0.001$_{6,132}$	0.187$_{6,126}$	0.600$_{6,96}$
F × R	**<0.001**$_{68,204}$	**<0.001**$_{82,246}$	**<0.001**$_{80,240}$	**<0.001**$_{76,228}$	**<0.001**$_{68,204}$	**<0.001**$_{68,204}$	**<0.001**$_{66,198}$	**<0.001**$_{58,174}$	**<0.001**$_{46,138}$	**<0.001**$_{44,132}$	**<0.001**$_{42,126}$	**<0.001**$_{32,96}$
F × T	**<0.001**$_{102,204}$	**0.005**$_{123,246}$	0.254$_{120,240}$	**<0.001**$_{114,228}$	0.072$_{102,204}$	**0.009**$_{102,204}$	**<0.001**$_{99,198}$	**0.011**$_{87,174}$	0.453$_{69,138}$	**<0.001**$_{66,132}$	**0.001**$_{63,126}$	0.111$_{48,96}$

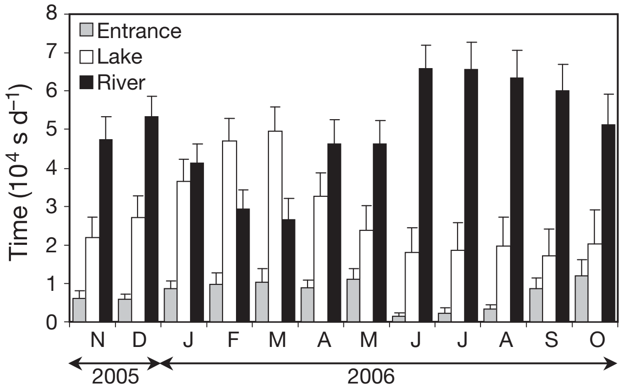

Fig. 3. *Acanthopagrus butcheri.* Mean (±SE) time spent by all fish in each region (entrance, lake, river) for each month of the study between November 2005 and October 2006

through time, and with freshwater flows. While the present study confirmed the status of *A. butcheri* as an 'estuarine resident', it also demonstrated the highly transient nature of this species, and its ability to undertake sub-daily movements over 10s of km among smaller estuarine tributaries.

Several *Acanthopagrus butcheri* in the present study demonstrated their propensity for sustained and rapid movements, in some cases travelling at >6 km d^{-1} and covering distances >2000 km yr^{-1}. Some fish displayed these patterns of movement by moving 20 to 30 km through the study area, but most fish achieved these distances moving only among the rivers in the north–central region of the Gippsland Lakes. As in Næsje et al. (2007), there was no significant relationship between the area of estuary used and the length of fish, with fish size being a poor predictor of movement behaviour. The rates of movement observed in the present study of 0.3 to 8.7 km d^{-1} were lower than those of estuarine species such as for mulloway *Argyrosomus japonicus*, which travelled up to 16 km d^{-1} (Taylor et al. 2006), but greater than those of the white stumpnose *Rhabdosargus globiceps* in South Africa, which travelled ~1.5 km d^{-1} (Kerwath et al. 2005, Attwood et al. 2007). The overall distances travelled by *Acanthopagrus butcheri* in this study were significantly greater than those observed for a related species (*Pagrus auratus*, Sparidae) in estuarine and marine water in New Zealand, which generally has small home ranges, on the order of 100s of meters in diameter (Hartill et al. 2003, Pittman & McAlpine 2003), and also greater than sparids such as *Rhabdosargus globiceps* and *Chrysoblephus laticeps*, which travel up to 16 and 4 km in estuarine and marine waters of South Africa, respectively (Attwood et al. 2007, Kerwath et al. 2007).

In the present study, patterns of use of the rivers, river entrances and lakes depended strongly on the time of year. Fish generally spent more time in the

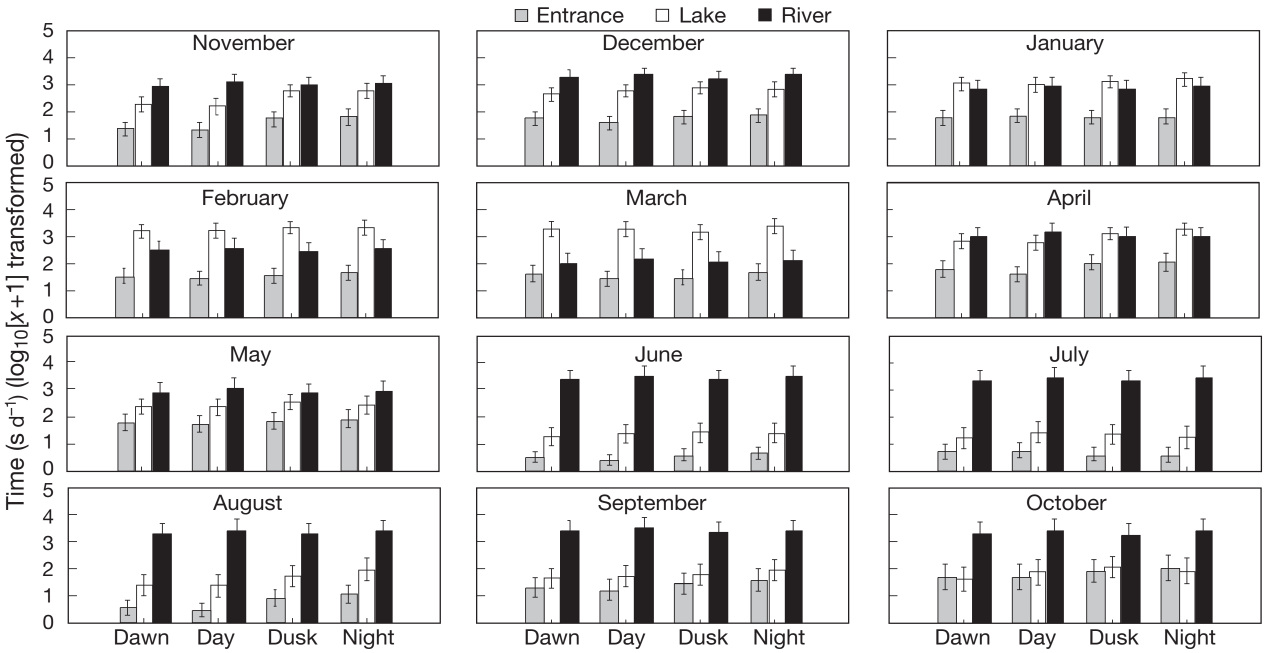

Fig. 4. *Acanthopagrus butcheri*. Mean (±SE) time spent by all fish in each region (entrance, lake, river) during each diel period (dawn, day, dusk, night) for each month of the study between November 2005 and October 2006

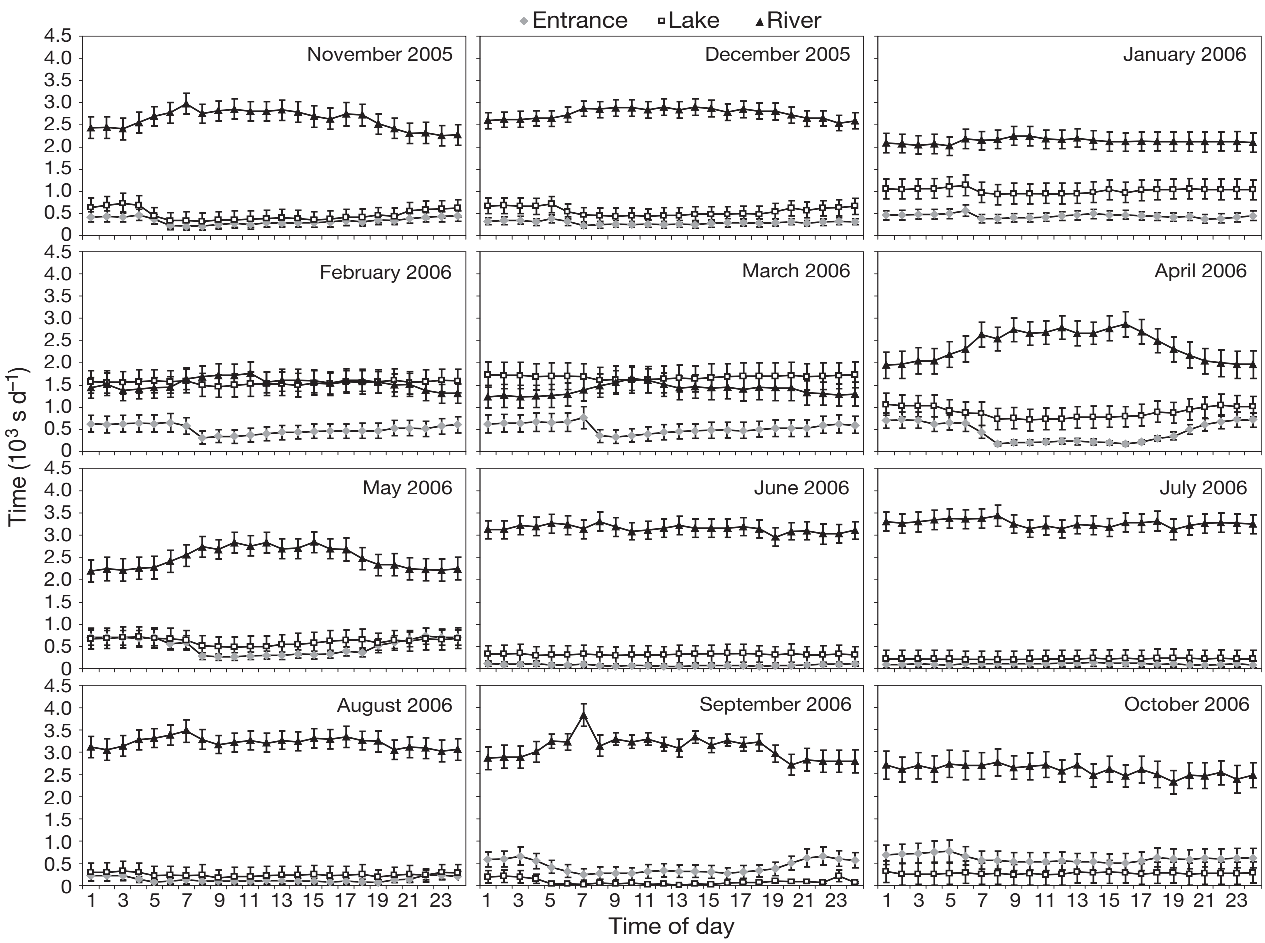

Fig. 5. *Acanthopagrus butcheri*. Mean (±SE) time spent by fish in each region (entrance, lake, river) over 24 h during each month between November 2005 and October 2006

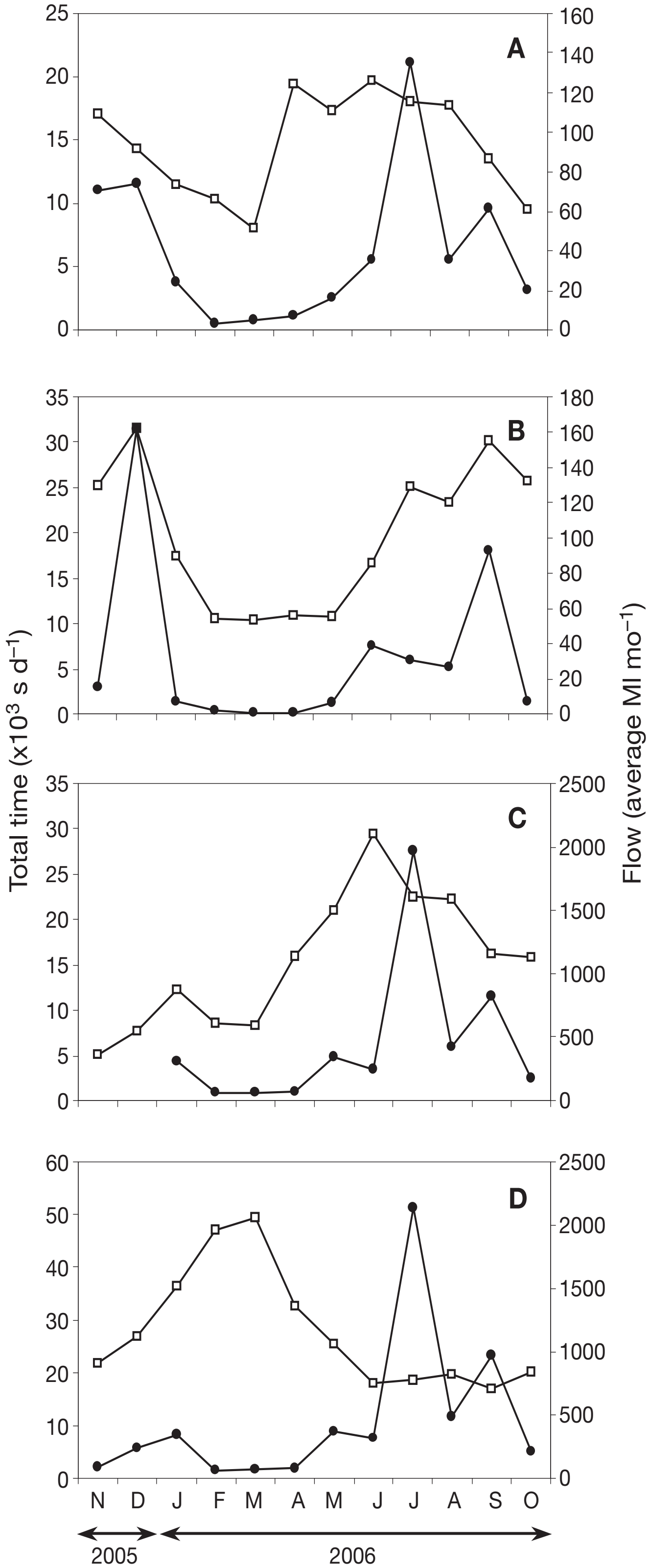

Fig. 6. Monthly variability in flow (●) and total time spent by fish (□) in each of the (A) Tambo, (B) Nicholson, and (C) Mitchell rivers, and (D) in the lakes. Note different *y*-axis scales

lakes than the rivers in summer and were also moving more widely in the lakes region of the study area at this time. Autumn (March–May) represented a transition time for the movement of fish into the rivers. Fish residency time in the rivers peaked in early to mid-winter, when fish were spending high proportions of time in the most upstream regions before gradually beginning to move back into the lakes during spring. These general patterns of movement are consistent with a model whereby *Acanthopagrus butcheri* forage throughout the lakes from late summer to autumn and then begin moving into the upper, salt wedge-dominated regions of the estuaries to spawn in late winter and spring (August to November), where haloclines of 17 and 20 support productive zones for the survival of eggs and larvae. Throughout the present study, freshwater discharge to the rivers was at historically low levels because of an extended period (up to 6 yr, 2001 to 2007) of drought and salinities of 17 to 20 that are appropriate for spawning were restricted to the uppermost regions of the major tributaries (such as the Nicholson, Tambo and Mitchell rivers).

While there was a clear movement of fish into the upper reaches of rivers in winter, around the time that *Acanthopagrus butcheri* begin to spawn, there was also a brief period in summer when river flows increased (due to localised heavy rain in the catchments) and fish use of the rivers increased. The movement of fish into the rivers at this time was unlikely to be for spawning, as most spawning is restricted to the July–November period, with a peak in October (Butcher 1945). Reasons for the fish moving from the lakes into the rivers at this time are unclear. Estuarine fish may move into lower-salinity water to feed and/or remove parasites; however, this is purely speculative and further research is required to address these hypotheses.

Diel periods can be strong determinants of fish movement and spatial behaviour. Hartill et al. (2003) found that *Pagrus auratus* remained in relatively small home ranges during the day, but moved out of the main channel onto surrounding shallow banks at night. Smith & Smith (1997) found that up-estuary movements and penetration of non-tidal regions by Atlantic salmon were more likely to occur at night. For most of the present study, there were no clear differences between night-day patterns of movement or use of the river versus lakes. Between February and May, however, fish use of rivers, river entrances and lakes varied with time of day. In February, there was no difference in time spent in the lakes versus river, regardless of the time of day. In March, there was a trend for fish to spend more time in the lakes than the river, except for a brief period between 07:00 and 11:00 h, when fish use of the rivers and lakes was similar. In April and May there were clear increases in the time spent by fish in the rivers between 06:00 and 18:00 h, with a peak around midday; there were also subtle increases in fish use of the river entrances and lakes at night during these months. Previous work by Hindell (2007) has suggested that movements of *Acanthopagrus butcheri* out of estuarine tributaries at night are probably related to foraging. Patterns of movement observed in the present study support these earlier observations and could be interpreted as fish moving from the rivers to the lakes to forage at night, then returning to the rivers in the day to shelter within large woody debris (Hindell 2007).

The present study demonstrates that, over 12 mo, *Acanthopagrus butcheri* spent, on average, twice as much time in the rivers of the Gippsland Lakes than the lakes per se, with a small amount of time spent around the river entrances. Despite this spatial behaviour changing with the time of year, these patterns could theoretically explain some of the decreases in commercial catches of black bream (which is restricted to the lakes region of the study area) in the Gippsland Lakes over the past 5 to 6 yr. Two alternative sources of data, however, suggest that this scenario is not likely. A fishery-independent survey of *A. butcheri* across the Gippsland Lakes, in which an 'experimental' haul seine is used to quantify the abundance of *A. butcheri* 'recruiting' to the fishery, and recreational angler diaries for the rivers both suggest a decline in abundances of *A. butcheri* (Morison & Conron 2007). If changes in commercial catches of *A. butcheri* in the Lakes were simply due to the movement of fish up the rivers, we could expect concomitant increases in recreational catches within these regions of the Gippsland Lakes, but this is not the case. It is more likely that there has been a decline in fish abundances throughout the Gippsland Lakes, perhaps as a result of spawning and/or recruitment failure and possibly related to the extended drought conditions experienced in the region.

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