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PRIMARY RESEARCH PAPER

Response of two-spined blackfish *Gadopsis bispinosus* to short-term flow fluctuations in an upland Australian stream

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Abstract Environmental flows are applied to regulated rivers, predominantly with the aim of benefiting native fauna. However, the outcomes for biodiversity and the mechanisms that underpin changes due to these manipulations are poorly understood. We examined the effects of elevated water release, of the magnitude used for riffle maintenance, on the movement and habitat use of the locally-threatened two-spined blackfish, *Gadopsis bispinosus*, in the Cotter River, a regulated upland stream in south-eastern Australia. We compared the behaviour of radio-tagged individuals during baseline flow conditions (0.12 m^3 s^{-1}) and during elevated flow releases (1.74 m^3 s^{-1}). Eight individuals (196 ± 8 mm TL) were radio-tracked at one site over 22 days, and six individuals (180 ± 5 mm TL) were monitored by fixed telemetry stations at a second site for 1 month. At both the sites, two-spined blackfish were nocturnal and occupied small linear ranges (23 ± 6 m). They preferentially used pools, but also used runs and riffles. Elevated discharge did not significantly affect movement, activity or dispersal of two-spined blackfish. Two individuals utilised inundated vegetation during high flow. Despite a small number of behavioural changes, there was no response to elevated flow at the population level. It is likely that the benthic nature of this species precludes its behaviour being affected by a 15-fold increase in-stream discharge. However, the indirect effects of flows of this magnitude on two-spined

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blackfish, and their responses to discharges of greater magnitude, remain to be investigated.

Keywords Environmental flows · Flow response · *Gadopsis bispinosus* · Radio-telemetry · Home-range · Diel activity

Introduction

Rivers are among the most degraded of the world's ecosystems (Abell et al., 2008), and damming of rivers is considered the leading cause of the loss of freshwater biodiversity (Walker, 1985; Bunn & Arthington, 2002; Richter et al., 2006). A major impact from damming is the alteration of the natural river flow (Poff et al., 1997; Bunn & Arthington, 2002). To mitigate the adverse environmental impacts of altered flow regimes, water resource managers are increasingly implementing flow release regimes for the environment, with the aim of improving the quality and quantity, of riverine habitats (Arthington et al., 2006). Such "environmental flows" reflect the view that flow pattern and discharge is a critical factor in riverine ecology (Power et al., 1995).

By increasing the quality and quantity of riverine habitats, environmental flows are also expected to restore or protect biotic integrity (Stanford et al., 1996; Arthington et al., 2006; Richter et al., 2006; King et al., 2010). Unfortunately, knowledge of the flow requirements of particular species is often incomplete or lacking. Consequently, the advice that aquatic ecologists are able to give for setting environmental flows is usually based on untested assumptions and hypotheses (Bunn & Arthington, 2002). Frequently, the default environmental flow regime for a stream is derived from estimating a pattern of release that is considered likely to mimic natural flow variability, since such variability is believed to be linked to environmental integrity (Poff et al., 1997). However, constraints on water availability generally mean that environmental flows are reduced in magnitude compared to pre-regulation flows. Nevertheless, increased knowledge of the environmental flow requirements of particular catchments and their biota will lead to better adaptive management of what water is available for benefiting biodiversity (Norris & Nichols, 2011). Methods for environmental flow assessment have been well documented (e.g. Arthington & Zalucki, 1998; Tharme, 2003), including the effects on hydrology, geomorphology, macro-invertebrates and fishes (Lintermans, 2005; Dyer & Thoms, 2006; Clear et al., 2007; Alonso-González et al., 2008; King et al., 2010). However, documentation of community and population responses to environmental flows often neglect to identify relevant processes and mechanisms (Bunn & Davies, 2000).

A range of techniques have been employed to monitor individual fish responses to flow (see Murchie et al., 2008 for review). Monitoring of the short-term responses of fishes to flows released from dams has primarily been conducted using implanted radio transmitters to analyse changes in movements or activity following releases from hydroelectric dams (e.g., Geist et al., 2005; Scruton et al., 2008; Cocherell et al., 2010). The responses of fishes during high natural flows, especially floods, have also been documented (David & Closs, 2002; Koster & Crook, 2008; Makiguchi et al., 2009). Many short-term responses of fishes to changes in discharge have been identified. These include: displacement, changes in activity and movement, use of newly inundated habitats and migration (Ottaway & Clarke, 1981; David & Closs, 2002; Koster & Crook, 2008; Scruton et al., 2008). Despite advances in technology, and the increasing importance of environmental flows, there is a paucity of studies of fish behaviour during flows released for environmental purposes. Investigations into behaviour of fishes during environmental flow releases are likely to provide important information both for the sustainable management of water resources, and for the protection and maintenance of threatened species.

The two-spined blackfish, *Gadopsis bispinosus*, is a benthic fish endemic to the south-eastern Murray-Darling Basin, Australia (Lintermans, 2007). Some populations of the species have undergone recent declines (Koehn, 1990; Lintermans, 2007; Lyon & O'Connor, 2008), resulting in the species being listed as threatened in the Australian Capital Territory (ACT) (ACT Government, 1999b, 2007). As of 1999, environmental flows have been released in the Cotter River catchment (the only catchment in the ACT that contains two-spined blackfish), to protect instream habitat, encourage spawning and migration of this species, and another threatened fish, the Macquarie perch (ACT Government, 1999a, 2006). Two-spined blackfish typically occupy upland streams, and are closely associated with in-stream cover in the form of cobble and boulders, and structural woody habitat (Koehn, 1990; Sanger, 1990; Lintermans, 1998). Indications are that two-spined blackfish are nocturnal (Ebner et al., 2009a), and mark-recapture studies indicate they inhabit small home-ranges (<15 m) (Lintermans, 1998). However, the movement, diel activity and tendency for dispersal of two-spined blackfish remain poorly understood. Furthermore, how environmental flow releases affect the movement (including dispersal), activity, and habitat use of two-spined blackfish is unknown.

Elevated flows (in the order of 15-fold increase from base flow) are released in the Cotter River bi-monthly as part of an environmental flows release program (ACT Government, 1999a, 2006). Specifically, elevated flows are released to flush sediment from riffles for the purpose of maintaining interstitial spaces and cleaning hard substrata for fish habitat (ACT Government, 1999a, 2006). The effect of these elevated flows on the movement and activity of two-spined blackfish is unknown. It is expected that elevated flow releases may result in temporary relocation of individuals to refuge habitat and reduced movement and activity, to mitigate possible increases in energetic costs. Such responses have been found for pelagic species (e.g. Murchie & Smokorowski, 2004; Cocherell et al., 2010), but the response of benthic species has received negligible research attention. Displacement of two-spined blackfish from elevated flows is unlikely, due to the proclivity for instream cover (Lintermans, 1998, 2007) and the species' capability of occupying the boundary layer within the cobble-boulder stream bed. Two-spined blackfish may use elevated flows to disperse, as natural instream barriers to movement may be drowned out and newly inundated habitats become available, as found for river blackfish *G. marmoratus* (Koster & Crook, 2008) and giant kokopu *Galaxias argentus* (David & Closs, 2002). The aims of the current study were to use radio telemetry as a basis for advancing understanding of movement, activity and habitat use of two-spined blackfish, and to determine whether any of these characteristics change in response to elevated flows released to maintain riffle habitats (based on a 15-fold increase from base flow).

Study area

This study was undertaken in the Cotter River, ACT, Australia, between early-spring (20 September 2007) and mid-spring (25 October 2007). The Cotter River is 87 km long and the climate of its catchment is temperate, with an average annual rainfall of 980 mm (Maddock et al., 2004). Three reservoirs are situated along the river. Bendora Reservoir, which was the source of the riffle maintenance flows for this study, is the second largest (11.54 Gl of the three impoundments. Investigations were undertaken at two sites located between Bendora Reservoir and Cotter Reservoir. The more upstream site at Burkes Creek Crossing was 650 m in length. The more downstream site at Spur Hole was 850 m in length, and ~3.5 km below Burkes Creek Crossing (Fig. 1).

At both study sites, two native fishes; two-spined blackfish and Macquarie perch, *Macquaria australasica*, and three non-native fish species; rainbow trout, *Oncorhynchus mykiss*, brown trout, *Salmo trutta*, and Oriental weatherloach, *Misgurnus anguillicaudatus*

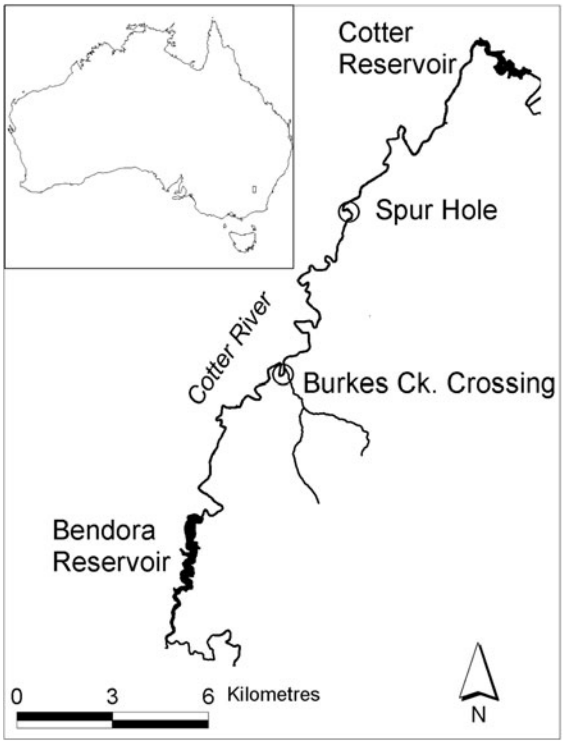


Fig. 1 Location of the two study sites on the Cotter River, Australian Capital Territory (*inset*: location of Cotter River catchment within Australia)

are present (Lintermans, 2000; Broadhurst and Ebner, unpublished data).

The catchment of the Cotter River upstream of the two study sites lies entirely within Namadgi National Park. Flow of the Cotter River is highly regulated as it is the primary source of domestic water for the city of Canberra (Maddock et al., 2004). Stream flow (median monthly flows and small flood events) in the Cotter River upstream of Cotter Reservoir is significantly lower since Bendora and Corin Dams were completed in 1969 (c.a., 55% reduction in median monthly flow for winter months and c.a., 73% reduction in median monthly flow during summer months) (Nichols et al., 2006). Environmental flows have been released from the three dams along the Cotter River since 1999 (ACT Government, 1999a; CRCFE, 2003; ACT Government, 2006). There are two components to the environmental flows that are released from the two most upstream impoundments on the Cotter River: an alternating weekly base flow of either 0.12 $m^3 s^{-1}$ or 0.35 $m^3 s^{-1}$, and a riffle maintenance flow of c.a., 1.74 $m^3 s^{-1}$ (ACT Government, 1999a, 2006). This regime has been set with the intention of creating flow variability, and maintaining spawning habitats and populations of threatened fish species, including two-spined blackfish (ACT Government, 1999a; CRCFE, 2003; ACT Government, 2006). Monitoring of the effectiveness of the environmental flow releases in the Cotter River catchment has focussed largely on macro-invertebrate communities (e.g. Chester & Norris, 2006; Nichols et al., 2006), and population monitoring of two-spined blackfish and Macquarie perch (Lintermans, 2005; Clear et al., 2007).

During this study, three cycles in flow discharge were delivered. Each cycle comprised 3 days of low flow (c. 0.12 $m^3 s^{-1}$) followed by 3 days of elevated flow (c. 1.74 $m^3 s^{-1}$). These flows are within the standard operating range of the river (i.e. 0.12–0.35 $m^3 s^{-1}$).

Methods

Capture and tagging

Single-winged fyke nets set overnight in pools and runs, and backpack electro-fishing in runs and riffles, were used to capture two-spined blackfish. Individuals exceeding 175 mm in total length (to ensure that radio-tag weight in air was not greater than 2% of the total weight of each individual (Winter, 1996)) were kept for tagging; smaller fish were immediately released. After capture the larger individuals were held separately in perforated containers situated in a flowing section of the stream. These fish were each fitted with a radio-tag (Ag317 internal coil antenna, 0.6 g Biotrack, UK) which was surgically inserted into the peritoneal cavity via an incision along the linea alba using the methods described in Broadhurst et al. (2009). Tagged individuals were held individually within containers in the stream until equilibrium was regained, after which individuals were placed within a large enclosure of stream water that had been salted (5 ppt NaCl) to minimise post-operative infection. After being held for 3 days post-tagging to allow initial healing (Broadhurst et al., 2009), fish were released at their site of capture. Tracking commenced 3 days after the release of fish to allow time for fish to resume natural behaviour (Broadhurst et al., 2009). There was no significant difference in the size of individuals between the two sites (Kruskal–Wallis test $\chi^2 = 2.8354$, DF = 14, $P = 0.0922$).

Radio-telemetry

Two different methods of telemetry were employed. Two-spined blackfish at Burkes Creek Crossing were monitored using manual tracking, while at Spur Hole they were monitored using fixed stations. At the Burkes Creek Crossing site, two-spined blackfish were manually located along a 650 m length of the Cotter River by triangulation using a scanning receiver (*Australis 2k*, Titley Electronics, Australia) and a three element yagi antenna (Titley Electronics, Australia). This method has an accuracy of c.a., 2 m in the Cotter River (Broadhurst & Ebner, 2007). Each individual was located daily over 22 days. Within this 22 days, individuals were tracked 3-h over a diel period (focal diel period), for a total of seven diel periods. Focal diel periods of tracking occurred once during each low flow ($n = 4$), and once during each high flow ($n = 3$) event. The locations of individuals were determined with respect to a pegged transect on the stream bank. Dominant meso-habitat type in a 2 m radius from the estimated location and a visual estimate of depth were recorded for each location. When an estimate of depth could not be made during a nighttime track, an estimate was made for that location at the first track the following day.

At the Spur Hole site, 24 three-element yagi antennae (Titley Electronics) were mounted 35 m apart, facing perpendicular to the stream, to provide a continuous array along a stream length of *c.* 850 m. Four antennas were each connected to one of six fixed stations (each station was comprised of an ATS DCC5041A data logger and an ATS R4100 receiver) via a switchbox (ATS 400A antenna switchbox) and lengths of coaxial cable (1/2″ Andrew Heliax™ LDF4-50A). Data loggers were programmed to continuously scan through pre-programmed control and implanted radio-tag frequencies. A control tag was secured to a weight and moored on the streambed under a randomly allocated antenna. Data loggers recorded a date and time associated with each positive record, along with signal strength from each antenna. Sensitivities of radio receivers were adjusted to eliminate potential false records from static. Scan time of each radio frequency was 8.96 ± 0.06 min, with the length of a scan cycle dependent upon the number of different frequencies detected at a site.

Habitat and depth use

Habitat and depth use were estimated using locations based on manual tracking at Burkes Creek Crossing. Habitat use was assessed based on the recognition of three habitat types: pools (no perceptible surface flow), runs (smooth visible surface flow), and riffles (visible flow with unbroken and broken surface water). Habitat use of individual fish was evaluated according to the dominant habitat type within a 2 m radius of the estimated location of that individual. Habitat was mapped at the Burkes Creek Crossing site under both base flow and high flow conditions, by estimating the proportion of riffle, run and pool per 10 m segment of the study reach. Habitat availability to each individual was calculated from the habitat composition of the extent of one diel range either side of the measured diel range of each individual, for each diel period that diel range was measured.

Statistical analysis

Total linear range (total length of river used by an individual over the entire study period c.f., Gerking (1953), diel range (length of stream used in a 24 h period), diel mobility (cumulative total distance of movements made by an individual in 24 h) and diel activity (percentage of diel mobility moved each 3-h tracking interval) were estimated using manual tracking data from the Burkes Creek Crossing site. Diel activity based on hourly signal strength variation (c.f., Thiem et al., 2010), was only measured at the fixed station site (Spur Hole). To determine differences in movement metrics, one-way analysis of variance (ANOVA) or equivalent non-parametric Kruskal–Wallis (KW) tests were performed and significant results further examined by planned comparisons to determine significant interactions. Bartlett's test for homogeneity of variance and Wilk–Shapiro normality tests were performed to determine if the assumptions of homogeneity of variance and normality were met. Data were transformed, where necessary, to achieve approximately normal distribution. Where approximate normal distribution could not be achieved, but distributions were similar, non-parametric Kruskal–Wallis tests were performed. To determine if there was a difference at the population level for metrics, mixed model analysis (MMA) was conducted, with individual fish as random factors. All tests were performed in SAS (v9.1 SAS Institute Inc., Cary, North Carolina), with the level of significance being 0.05. Values are reported as mean ± standard error unless otherwise stated.

Results

Movement

Two-spined blackfish occupied small total linear ranges (Table 1; Fig. 2) at Burkes Creek Crossing. Mean total linear range was 37 ± 11.8 m and ranged from 5.5–99 m (Table 1). There was no significant relationship between fish length and total linear range (Pearson's correlation: $r = 0.2650$, $n = 8$, $P = 0.5259$). Fish 4, 7 and 8 had larger total linear ranges than other individuals (Table 1). Two-spined blackfish moved only small distances, having moved their location on average 2.7 ± 0.7 m between daily fixes. They moved less than 3, 5 and 10 m between daily tracks on 74, 87 and 96% of occasions, respectively. The largest movements were exhibited by Fish 4 and 8, and comprised movements of 51 and 96 m, respectively. There was no significant difference in between day movements between individuals (KW $\chi^2 = 6.7954$, $DF = 166$, $P = 0.4505$). Two individuals

Table 1 Length, weight and movement metric estimates (home-range, diel range and diel mobility mean ± SE) of eight radio-tagged two-spined blackfish at Burkes Creek Crossing, Cotter River (Fish 1–8) and six radio-tagged individuals from the fixed station monitored Spur Hole site (Fish a–f)

Fish	Total length (mm)	Weight (g)	Home-range (m)	Diel range (m)	Diel mobility (m)
1	180	30.1	10	3.7 ± 1.1	10.9 ± 2.7
2	215	51.3	16	5.8 ± 1.7	19.1 ± 6.2
3	180	38.4	6	1.8 ± 0.5	5.9 ± 1.9
4*	189	42.2	16 and 8 (69)	5.4 ± 2.0	13.4 ± 5.3
5**	231	72.7	25	16.8 ± 2.5	51.1 ± 12.7
6	177	30.1	18	5.4 ± 1.7	17.7 ± 5.9
7	176	28.1	54	11.1 ± 7.2	24.2 ± 13.9
8***	220	47.7	37 and 5.5 (99)	16.9 ± 13.5	22.6 ± 14.6
Mean	196 ± 8	43 ± 5	23 ± 6#	8.2 ± 2.0	20.1 ± 3.4
a	174	33	n/a	n/a	n/a
b	172	31	n/a	n/a	n/a
c	176	37	n/a	n/a	n/a
d	205	45	n/a	n/a	n/a
e	177	37	n/a	n/a	n/a
f	181	35	n/a	n/a	n/a
Mean	180 ± 5	36 ± 2			

Movement estimates based on manual tracking for 22 days and 7 diel periods

* Fish 4 made a home-range shift after 2 days of tracking. Figures reported are the two separate home-ranges and the total length of stream used by the individual over the study period (in parentheses)

** Fish 5 was tracked for 20 days and 6 diel periods only

*** Fish 8 made a home-range shift after 7 days of tracking. Figures reported are the two separate home-ranges and the total length of stream used by the individual over the study period (in parentheses)

Home-range estimates used from fish 4 and 8 were the larger of the home-ranges for each individual (excluding the overall length of river used—which incorporated a home-range shift)

(Fish 4 and 8) shifted their linear ranges (as mentioned above) during the study; both shifts were made during low flow periods (Fig. 2).

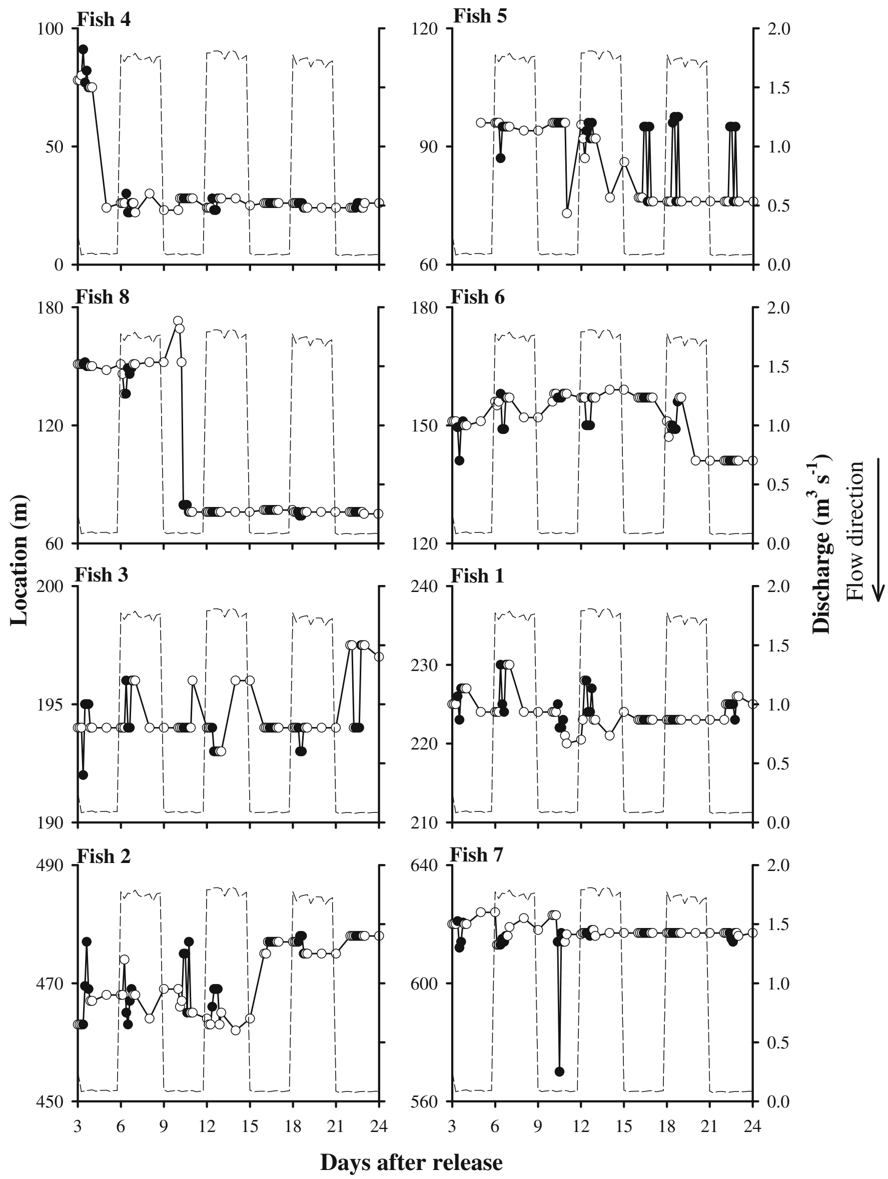
Two-spined blackfish used small (8.2 ± 2.0 m) lengths of stream within diel periods. The greatest length of stream used by an individual (Fish 8) within a diel period was 97 m. There were no significant differences in daily movements, diel range, or diel mobility for individuals between high and low flows, with the exception of Fish 6. Fish 6 had significantly higher diel mobility during high flows, than during low flows (KW $\chi^2 = 4.5818$, DF = 6, $P = 0.0323$).

Two-spined blackfish, at the population level, exhibited no significant difference in diel mobility between high and low flows (MMA $F_{1,\ 31.124} = 0.102$ $P = 0.752$). Clear changes in movement patterns were not evident between high and low flows (Fig. 2), and no significant difference in daily movement, diel range, or diel mobility of each individual existed, with the exception of Fish 6. Fish 6 had significantly higher diel mobility during high flows, than during low flows (KW $\chi^2 = 4.5818$, DF = 6, $P = 0.0323$). Two individuals (Fish 4 and 8) undertook home-range shifts during the study, with both occurring during low flow periods (Fig. 2). Fish 6 and Fish 8 had overlapping home-ranges during the first week after release. Later (at day 10), Fish 8 moved further downstream; although it still inhabited the same pool (Fig. 2). Five individuals (Fish 3, 4, 5, 6 and 8) inhabited the same pool throughout the study. This pool was c.a., 170 m in length.

Activity

Two-spined blackfish were mostly nocturnal (MMA $F_{1,\ 31.124} = 32.139$ $P < 0.0001$), with peak activity occurring around 1800 h (Fig. 3a, b). There was no significant difference in the degree of nocturnal movement between high and low flows (MMA $F_{1,}$

Fig. 2 River discharge (m^3 s^{-1}) (*dashed line*) and location (m) along the study reach of eight radio-tagged two-spined blackfish at Burkes Creek Crossing based on daytime (*open circle*) and nighttime (*filled circle*) manual tracking fixes



$_{31.214} = 3.668$ $P = 0.065$). Activity at the Burkes Creek Crossing site was lowest during the 1200–1500 and 1500–1800 h tracking intervals (Fig. 3a), in comparison to activity during 2400–0300, 0300–0600 and 0900–1200 tracking intervals (KW $\chi^2 = 40.8272$, DF $= 440$, $P < 0.0001$). Fish 5 made large movements during the night on the last three of the seven diel periods over which it was manually tracked (Fig. 2). The lowest activity of blackfish at Spur Hole occurred from 0800–1100 h (Fig. 3b). Blackfish varied in their daily activity patterns, based on fixed station monitoring. Fish b, and to a lesser extent Fish c, commonly exhibited greater activity during night (Fig. 4). The largest spikes in activity for five of the six individuals (Fish a–e) were found either at night, or around sunset (Fig. 4). Based on signal strength variation, blackfish at Spur Hole exhibited significantly lower activity during the hours of 0800–1100 compared to the hours of 1700–2000 (ANOVA $F_{23,\ 3371} = 7.40$, $P < 0.0001$). There was no effect of flow on diel activity patterns (ANOVA $F_{1,\ 23} = 0.57$, $P = 0.9469$).

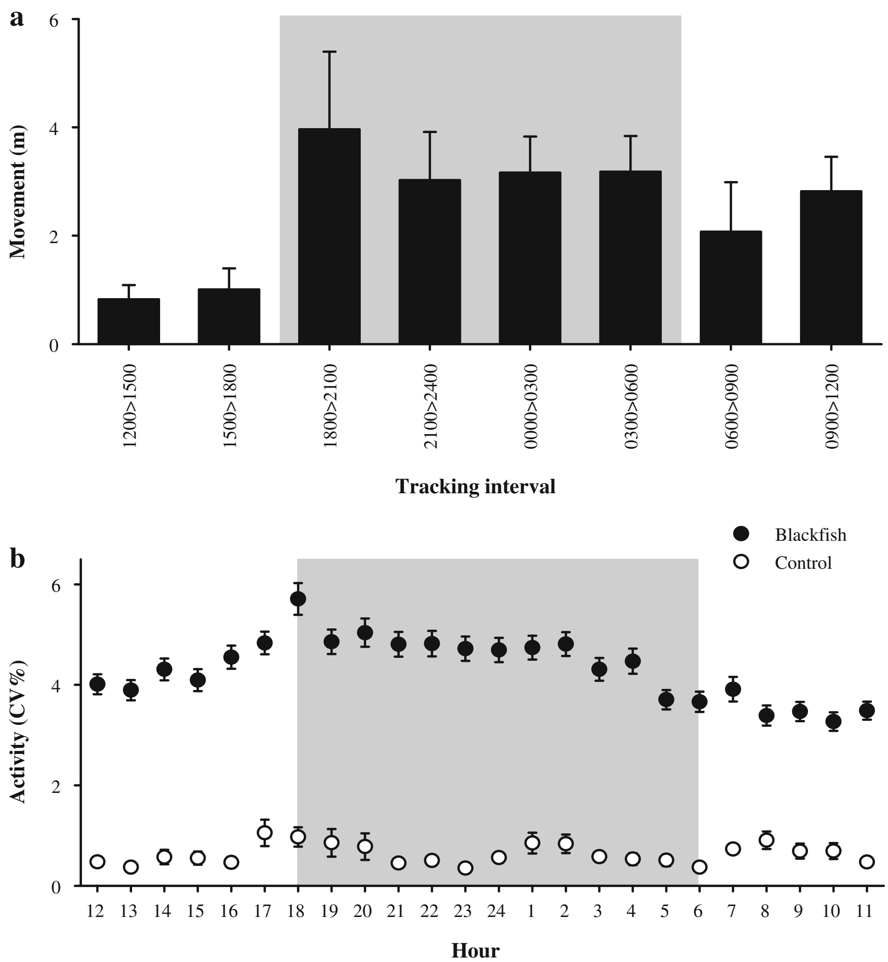


Fig. 3 Diel activity of two-spined blackfish measured by **a** movement per 3-h tracking interval using manual tracking at the Burkes Creek Crossing site ($n = 8$), and **b** variation in signal strength based on fixed station monitoring for two-spined blackfish at the Spur Hole site (*black circles*, $n = 6$), and a moored control tag (*white circle*, $n = 1$). *Shaded area* on each figure indicates night. Activity for fixed station site was estimated from remote telemetry loggers by calculating coefficient of variation (CV%) of hourly signal strength records (up to six records of signal strength per individual per an hour)

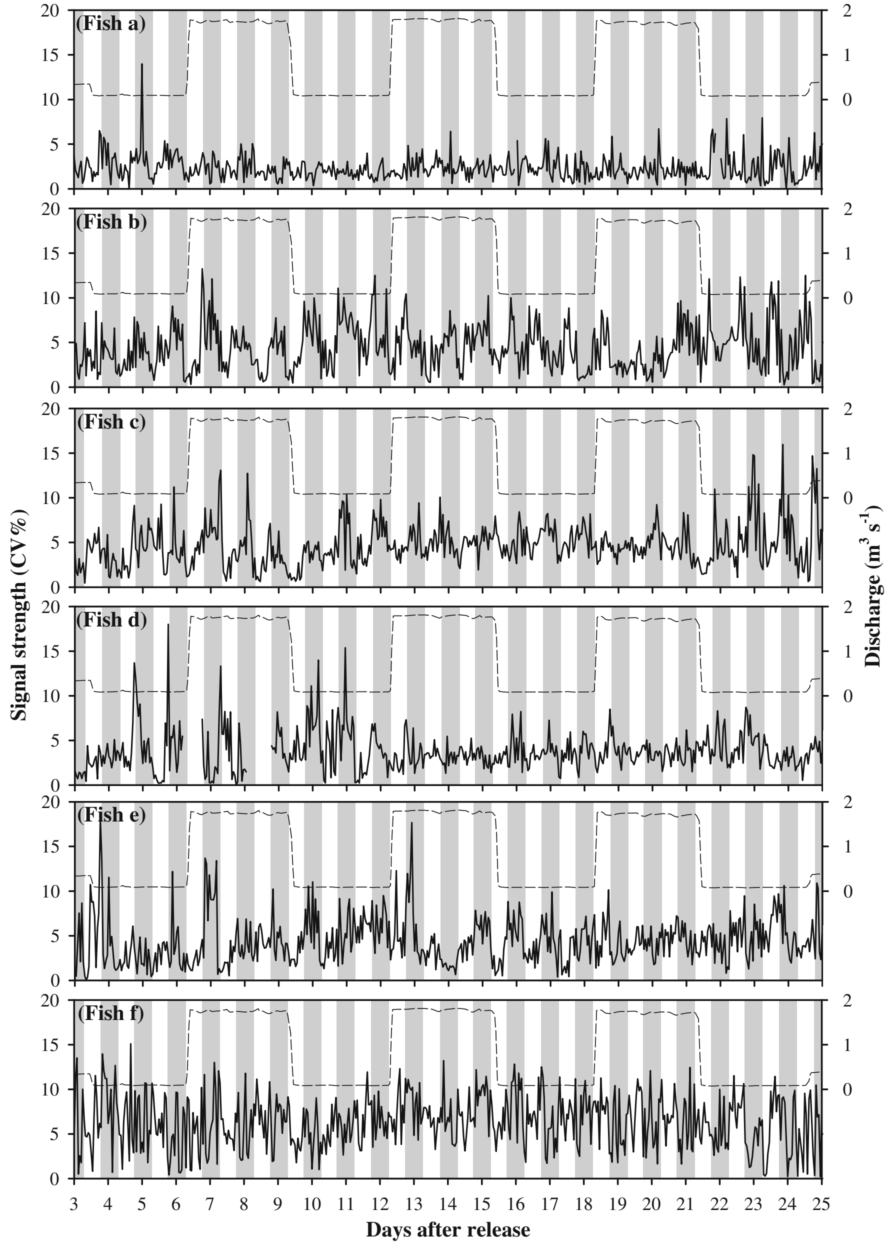
Habitat use

Daytime depths used by two-spined blackfish at Burkes Creek Crossing ranged from 0.15–2.5 m (mean 0.8 ± 0.03 m). Blackfish were found in water <1 m and <2 m depth on 55 and 98% of daily locations, respectively. Depth use did not differ significantly within diel periods (ANOVA $F_{7, 445} = 0.42$, $P = 0.8892$). Likewise, flow rate did not have a significant effect on diel depth use (ANOVA $F_{7, 445} = 0.26$, $P = 0.9690$).

The most commonly used habitat of two-spined blackfish during the day at Burkes Creek Crossing were pools (59% of locations), followed by runs (38% of locations), and riffles (3% of locations). During low flow, the study reach was dominated by runs (51%), followed by pools (44%) and riffles (5%). At high flows, the availability of these three habitats was greatly altered (runs 63%, riffles 23% and pools 15%). Within diel periods, pools were the most used habitat type, with use ranging from 61% (0600 h) to 70% (1200 h) of locations per 3-h tracking event. Runs were the next most frequented habitat type with use ranging from 29% (1200 and 2100 h) to 38% (1500 h) of locations per 3-h tracking event. Riffles were rarely used at any time of the day, however, peak use was at 0600 and 1200 h (3.7% of fixes at each of these times) during 3-h tracking.

Individual blackfish exhibited differing patterns in their habitat preference between high and low flow periods. Fish 4, 5, 7 and 8 showed increased preference for pool habitats during high flow (Fig. 5). Fish 3 showed a preference for run habitat during the first two low flow periods, but preferred pool habitat in the following two low flow periods (Fig. 5).

Fig. 4 Diel activity of six radio-tagged two-spined blackfish monitored by fixed stations, matched with hourly discharge at Spur Hole. *Grey bars* indicate night. *Solid line* indicates fish activity (based on signal strength variation), *dashed line* indicates river discharge ($m^3\ s^{-1}$)



Discussion

Neither the extent of movement nor diel activity of two-spined blackfish was affected by elevated discharge in this study. Two-spined blackfish are benthic, and often closely associated with instream cover, especially interstitial spaces in the streambed (Lintermans, 1998, 2007). It is likely that occupying spaces within the streambed afford this species adequate refuge from flow, even at elevated discharge. Flows were higher in the Cotter River pre-regulation (Nichols et al., 2006), and as a result, it appears as though two-spined blackfish are adequately adapted to maintain normal movement and activity at an elevated discharge. Previous studies have demonstrated mixed responses to variable discharge. For example, white sturgeon (*Acipenser transmontanus*) movements were similar at three different discharges, but the oxygen consumption and swimming speed were reduced during the lowest discharge investigated by Geist

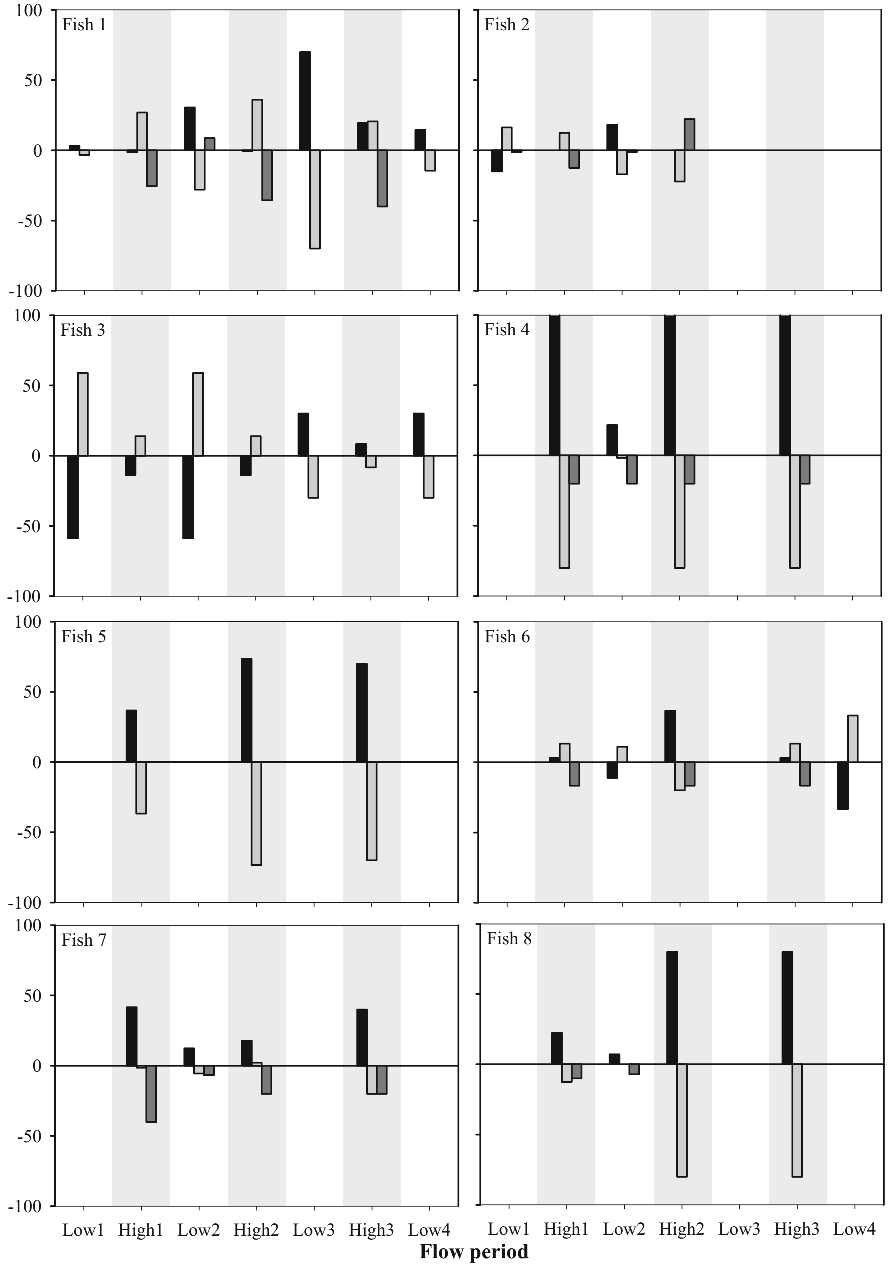


Fig. 5 Habitat use observed versus habitat use expected for two-spined blackfish at Burkes Creek Crossing for each flow period. Expected habitat values calculated from habitat composition ± 1 diel range either side of the actual diel range of each individual per flow period (low flow c.a., 0.12 m^3 s^{-1} *white background*, and high flow c.a., 1.74 m^3 s^{-1} *grey background*). *Black bars* pool, *dark grey* riffle, *light grey* run habitats. *Note*: positive values correspond to positive bias towards a habitat type; negative values correspond to a negative bias towards a habitat type

et al. (2005). Pelagic species have exhibited a range of behaviours in response to elevated flows. Individual landlocked Formosan salmon, *Oncorhynchus masou formosanus*, persisted in their locations during a large typhoon-induced flood by using boulders and deep pools for refuge (Makiguchi et al., 2009). Neither brook trout *Salvelinus fontinalis* nor walleyes *Sander vitreus* moved in response to a flow release, but the activity of both species increased with discharge (Murchie & Smokorowski, 2004), presumably in response to increased efforts to maintain position. Similarly, rainbow trout increased their energetic output during increasing flows (Cocherell et al., 2010). Although, once peak flow had been reached, these trout decrease their energetic output, suggesting that individual fish take refuge and cease foraging during peak flows (Cocherell et al., 2010). It is likely that movement and activity of benthic fish species is less likely to change in response to increased flow, when compared to pelagic species. It is possible that two-spined blackfish may exhibit a physiological response to elevated flows (c.f., *A. transmontanus* Geist et al., 2005), but this was not monitored in this study. The benthic nature and use of substrate interstices appears to afford two-spined blackfish adequate refuge from flow whilst completing daily activities, even at an elevated discharge.

An elevation in flow did not result in dispersal (via migration or displacement) of two-spined blackfish in the current study. It was expected that some individuals could make use of the drowning out of potential barriers to movement as a consequence of elevated flows. Two individuals (Fish 4 and 8) undertook home-range shifts, but these were made during low flows. An elevation in flows was coincident with upstream home-range shift in river blackfish *G. marmoratus* (Koster & Crook, 2008). In a similar sized stream in New Zealand, giant kokopu *Galaxias argentus* used elevated flows to ascend riffles which, at low flows, formed a barrier to upstream movement (David & Closs, 2002). A mark-recapture study of two-spined blackfish found that many individuals, especially large adults, rarely shifted home-range over the course of a year (Lintermans, 1998). Lintermans (1998) went on to hypothesise that larger individuals may become more sedentary, compared to smaller individuals, as indicated by a higher recapture rate of larger adult fish. Lintermans (1998) further postulated that "stray" individuals are potentially important for dispersal and colonisation. Certainly, two-spined blackfish are capable of dispersing and colonising over quite large distances when compared to their day-to-day movements (Lyon & O'Connor, 2008). The mechanism for dispersal, especially upstream, remains unclear for two-spined blackfish; though the current study suggests that elevated flows do not encourage adult two-spined blackfish to make upstream dispersal movements.

Whilst flow period type (high or low) resulted in habitat availability differences in this study (i.e. pool habitat was reduced and replaced with riffle-run habitat under high flows and vice versa), two-spined blackfish did not generally shift their locations in response to these flows. Consequently, we interpret these results as indicating that microhabitat (individual boulder) may be more important than mesohabitat (pool or riffle-run) in influencing habitat selection when individuals are exposed to flows of the magnitude and duration observed in the current study. Sustained elevated flows may potentially result in mesohabitat relocations or dispersal, as has been observed previously for other species in small streams (David & Closs, 2002), however this is beyond the scope of this study. Two individuals were observed to use newly inundated vegetation during high flows, an observation consistent with that from the congeneric river blackfish (Koster & Crook, 2008). Whether this short-term shift is in response to a requirement for flow refuge, predation refuge or availability of a new food source remains unknown. Our study suggests that two-spined blackfish will not change their locations because of a short duration change to the meso-habitat type related to elevated flow releases.

Nocturnal behaviour was evident in all two-spined blackfish followed in this study. This is consistent with observations made using underwater video surveillance where a two-spined blackfish > 50 mm TL were found to be nocturnal over a diel period (Ebner et al., 2009a). Both these findings are in conformity with the diel behaviour reported in the congeneric river blackfish *Gadopsis marmoratus* by Koster & Cook (2008). These authors, found this species to be nocturnally active, although Khan et al. (2004) found no significant differences between the mean movements made by individuals of this species during day and night. Members of the closely related family Percicthyidae, including trout cod *Maccullochella macquariensis* (Thiem et al., 2008; Ebner et al., 2009b), Mary River cod *M. peelii mariensis* (Simpson & Mapleston, 2002) and Macquarie perch *M. australasica* (Ebner & Lintermans, 2007) have been found to have slightly varied diel activity, but all are generally inactive during the middle of the day. The temporal resolution arising from the use of fixed station monitoring provided a high degree of confidence in the diel activity patterns recorded. The two telemetry techniques employed in this study have each offered a resolution of spatial behaviours not previously achieved in studies of two-spined blackfish.

Since nocturnal activity appears to be present in river blackfish as well, it may be a inherent trait of the genus *Gadopsis*. Nevertheless, for extant populations of two-spined blackfish in the Cotter River, nocturnal behaviour may serve to increase access to prey, and may also serve to reduce competition and predation by non-native trout. Food items of two-spined blackfish, such as larval Ephemeroptera, Trichoptera and Chironomidae (Lintermans, 1998) generally become more available during the night (Elliott, 1967; Brittain & Eikeland, 1988). The propensity of two-spined blackfish to forage at night may be advantageous when two-spined blackfish co-occur with competitors and predators, such as trout (Lintermans, 1998). Trout, like other salmonids, are visual predators and so are generally diurnal feeders (Hoar, 1942; Angradi & Griffiths, 1990; Alanärä & Brännäs, 1997). The diets of two-spined blackfish and trout have been shown to overlap (Lintermans, 1998), and there is evidence that trout will aggressively defend foraging areas (Hearn, 1987). However, the nocturnal behaviour of two-spined blackfish could reduce interspecific competition with trout for both food and space.

Most two-spined blackfish in the present study occupied small total linear ranges. Small ranges have been found previously in this species based on a mark-recapture study (Lintermans, 1998), and in river blackfish based on radio-tracking (Khan et al., 2004; Koster & Crook, 2008). Similar findings have been made with members of the closely related family Percichthyidae (Simpson & Mapleston, 2002; Crook, 2004; O'Connor et al., 2005; Thiem et al., 2008; Ebner & Thiem, 2009; Koehn et al., 2009). Lintermans (1998) concluded that limited movement by two-spined blackfish was most likely due to a behavioural, not physical or mechanical, phenomenon, and that larger individuals appear to be more sedentary than smaller individuals. Considering the results of this study and the conclusions of Lintermans (1998), there are two possible behavioural explanations for small ranges of two-spined blackfish in this study. Firstly, this study was conducted around the known spawning period of two-spined blackfish, which is late spring to summer (Sanger, 1990; Lintermans, 1998). During the spawning period, males of the species maintain individual spawning sites and guard the fertilised eggs and larvae (Lintermans, 1998; O'Connor & Zampatti, 2006) and therefore would be expected to be sessile during this period. Secondly, it has been documented that smaller bodied fish occupy smaller home-ranges (Kramer & Chapman, 1999), which has been explained by a reduction in the area needed to provide suitable resources (Grant, 1997) or by increased relative cost of swimming (Brett, 1965). Whether two-spined (or river) blackfish have relatively low metabolic rates is unknown. However, in view of the extremely low proportion of red muscle in the myotomes of river blackfish (Dobson & Baldwin, 1982), it is plausible to suggest that Gadopsids may have low metabolic rates and so no need for large home-ranges.

Conclusions

This study details the diel movements and habitat use of two-spined blackfish, and offers rare observations on the behavioural response of a benthic fish to the release of riffle maintenance flows. Spatial and temporal behaviour of two-spined blackfish in the current study was not affected, at least in the short term, by sequences of riffle maintenance flow releases that involve a large (15-fold) increase in flow above baseline levels. The benthic nature of two-spined blackfish is the likely reason for the lack of response to flow. Two-spined blackfish did not make any expected upstream dispersal movements associated with high flows, nor were they displaced downstream. Further study is required to determine the mechanisms for dispersal and population maintenance for two-spined blackfish in upland streams. Two-spined blackfish were confirmed to be nocturnal and inhabit restricted home-ranges, and over the course of the 21 day study neither of these characteristics appeared to change despite the frequent large alterations in flow that took place. Elevated flows released for maintaining riffle habitats in the Cotter River catchment, did not appear to affect the movement and activity of mature two-spined blackfish.

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