3.2 TIME TO BURROW

Galaxias cobitinis was able to pass through undisturbed substratum quickly. Within 10 minutes, fish had appeared in both experiments, and by 20 minutes, 10 and 15 fish were observed to have burrowed through the undisturbed gravel in Experiments 1 and 2 respectively. In the first experiment, 48% of *G. cobitinis* were able to move completely through the gravel; in the second experiment, 60% of *G. cobitinis* did this (Table 2).

For both experiments, the mean time taken for *G. cobitinis* to pass completely through 18.5 cm of gravel and into the bins was significantly less for fish in buckets with undisturbed substratum than for fish in buckets with disturbed substratum (Fig. 6; Table 3). Substratum treatment explained 41% and 15% of the variation in the factorial ANOVA models for Experiments 1 and 2 respectively (Table 3). However, the speed of the burrowing response was not affected by whether the water level was stable or declining (Fig. 6). The average time taken to burrow through the buckets was similar for both experiments, being c. 40 minutes. This is a conservative estimate, due to difficulties in measuring the exact time at which each fish emerged from the gravel.

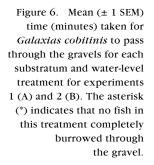
It was evident that more fish were able to pass through gravels and did so more quickly in Experiment 2 than in Experiment 1 (Fig. 6). To further investigate the effect of interstitial volume on the ability of *G. cobitinis* to burrow, interstitial volumes for each bucket were regressed against the average time taken for fish in that bucket to burrow through the gravels (Fig. 7). There was a significant negative correlation between the mean proportion of time taken for fish within a bucket to pass through the gravel and interstitial volume (r^2 =0.60, F=32.9, df = 1, 22, P<0.0001, β =-0.77), i.e. as interstitial volumes increased, fish passed through the gravel more quickly. However, in several cases fish were able, on average, to burrow through disturbed gravels at a speed similar to fish in buckets with large interstitial volumes. This suggests that particle packing and the architecture of interstitial spaces are also important considerations.

LEVEL (STABLE AND DECLINING) TREATMENTS IN EACH EXPERIMENT. TH	IERE WAS
A TOTAL OF TWELVE FISH PER TREATMENT.	

 TABLE 2.
 NUMBER OF Galaxias cobitinis THAT PASSED THROUGH THE GRAVELS

 WITH DIFFERENT SUBSTRATUM (DISTURBED AND UNDISTURBED) AND WATER

	DIST	URBED	UNDIS	STURBED
	STABLE	DECLINING	STABLE	DECLINING
Experiment 1	0	3	8	12
Experiment 2	4	4	10	11



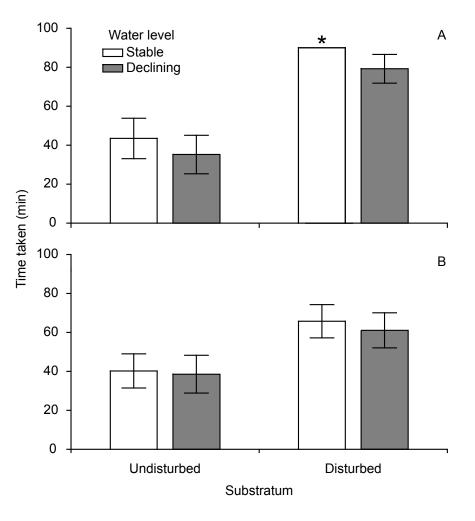
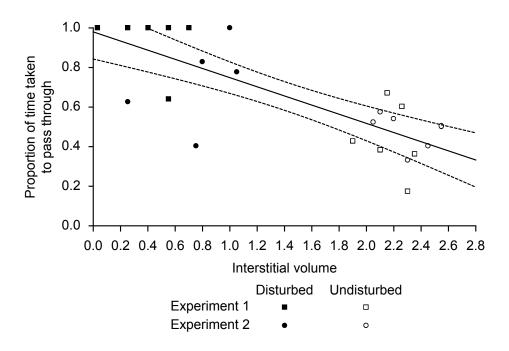


TABLE 3. RESULTS OF FACTORIAL ANOVA EXAMINING THE TIME TAKEN FOR *Galaxias cobitinis* TO PASS THROUGH THE GRAVEL IN EACH EXPERIMENT WITH DIFFERENT SUBSTRATUM (DISTURBED AND UNDISTURBED) AND WATER-LEVEL (STABLE AND DECLINING) TREATMENTS.

SOURCE	df	SS	MS	F	Р
Experiment 1					
Substratum	1	5.98	5.98	31.96	< 0.001***
Water level	1	0.27	0.27	1.42	0.24
Substratum × Water level	1	0.01	0.01	0.03	0.87
Error	44	8.24	0.19		
Experiment 2					
Substratum	1	2.16	2.16	7.79	< 0.008**
Water level	1	0.02	0.02	0.09	0.77
Substratum × Water level	1	0.02	0.02	0.06	0.81
Error	44	12.21	0.28		

Figure 7. The relationship between interstitial volume and the mean proportion of time taken for Galaxias cobitinis to pass through the gravels. Replicates are buckets, with four fish per bucket. Those buckets in which no fish completely passed through the gravels were assigned a proportion of 1. Results from both experiments have been combined. Dotted lines indicate 95% confidence intervals.

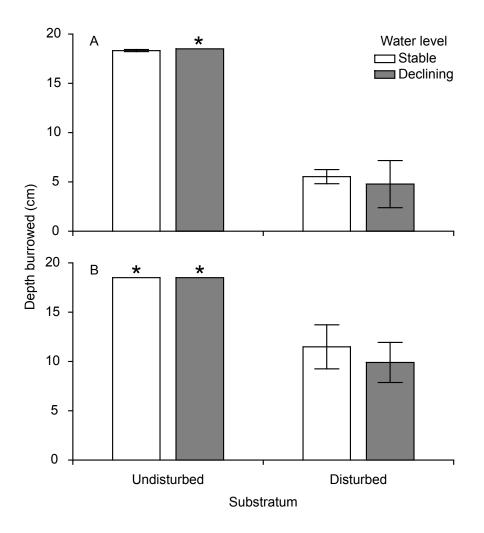


3.3 DEPTH BURROWED

In both experiments, *G. cobitinis* was able to burrow significantly deeper in buckets with undisturbed substratum than in buckets with disturbed substratum (Fig. 8; Table 4). Moreover, the substratum treatment explained 70% and 38% of the variation in the individual factorial ANOVA models for Experiments 1 and 2 respectively (Table 4). Interestingly, fish in Experiment 2 were able to burrow to approximately twice the depth of those in Experiment 1. However, there was no significant relationship between water-level manipulation and depth burrowed for either experiment (Table 4).

SOURCE	df	SS	MS	F	Р
Experiment 1					
Substratum	1	13.02	13.02	105.60	< 0.001***
Water level	1	0.02	0.02	0.18	0.68
Substratum × Water level	1	0.08	0.08	0.65	0.43
Error	44	5.42	0.12		
Experiment 2					
Substratum	1	4.47	4.47	27.88	< 0.001***
Water level	1	0.07	0.07	0.41	0.53
Substratum × Water level	1	0.07	0.07	0.41	0.53
Error	44	7.06	0.17		

TABLE 4. RESULTS OF FACTORIAL ANOVA EXAMINING THE DEPTH BURROWED BY *Galaxias cobitinis* IN EACH EXPERIMENT WITH DIFFERENT SUBSTRATUM (DISTURBED AND UNDISTURBED) AND WATER-LEVEL (STABLE AND DECLINING) TREATMENTS. Figure 8. Mean (±1SEM) depth (cm) burrowed by *Galaxias cobitinis* through the gravels for each substratum and water-level treatment. The asterisks (*) indicate that all fish either passed through the gravels and appeared in the bins or were found to have burrowed to the bottom of the buckets.



3.4 SURVIVAL

No mortalities occurred in treatments involving undisturbed substratum. However, in total, 9 out of 96 fish died during experiments. Eight of these deaths (four in each experiment) occurred in disturbed substratum with declining water levels, representing a third of the fish exposed to this treatment. The fact that they died within 90 minutes, in shaded, moist conditions, indicates that *G. cobitinis* has poor tolerance to emersion (being out of water). In addition, one fish died in a bucket containing disturbed substratum despite stable water levels. This fish was found at a depth of 15 cm, amongst coarse sand, and had an apparent head injury, as indicated by haemorrhaging, presumably sustained during its attempt to burrow through the fine substratum. That this fish had burrowed to this depth illustrates the tenacity with which they burrow.

In Experiment 1, three mortalities occurred in the same bucket, indicating that this substratum may have been particularly impenetrable, as no fish had entered the gravels. The fourth dead fish in Experiment 1 had burrowed but sustained head injuries (apparent from bruising), and was found wedged between cobbles 9.5 cm below the substratum surface. Head bruising was also present in live fish after the experiment; this is likely to have been sustained as fish probed for an accessible route through the gravel. In Experiment 2, three of the dead fish had

attempted to burrow, being located at shallow depths under surface cobbles. Live fish were also located in similar locations, suggesting individual variation in survival capabilities. In both experiments combined, the lengths of dead fish were not significantly different from those of fish that were alive at the end of experiments; similarly, there was no difference between the lengths of fish that remained in buckets and those that had completely passed through the gravels and into the bins.

While fish were often found under the same surface cobble, they were never in close proximity to each other, although some fish were curled around substratum particles (Fig. 9). When emersed, the skin of *G. cobitinis* appeared to dry quickly and became 'sticky', suggesting that increased mucus excretion did not occur. This resulted in relatively large particles adhering to the skin of fish. Several fish were found lying on their dorsal surface and others were bent into a deep U-shape. During the experiment and in subsequent handling, no fish were observed to retain an air bubble in their buccal cavity.



Figure 9. Stranded *Galaxias cobitinis* on the substratum surface of a disturbed-substratum bucket with declining water level at the end of Experiment 1. Note the deep U-bend shape (maintaining an upright stance) of two of the fish, one of which is curled around a pebble.

4. Discussion

Our experiments demonstrate that G. cobitinis is adept at burrowing into and moving through sub-surface gravels. That similar results were obtained in both experiments further substantiates these findings. Galaxias cobitinis appears to have greater gravel burrowing capabilities than other Galaxias species studied. For example, in a similar study, Dunn (2003) found that it took Galaxias paucispondylus Stokell and Galaxias vulgaris Stokell on average 101 minutes to pass through 15 cm of gravel, and that they burrowed to an average depth of 10 cm. This gravel had an interstitial volume of 2.1 L, which is similar to the undisturbed substratum used in the present study, through which G. cobitinis readily moved. It is likely that the small size and slender morphology of G. cobitinis contributes to this ability. Galaxias cobitinis did not respond to declining water levels by increasing its speed of burrowing. This may indicate that burrowing into the interstitial spaces plays a role in the general biology of G. cobitinis, rather than being a specific response to declining water levels and drought. Similarly, the closely related G. prognathus is considered to be 'a secretive fish, living amongst the boulders and gravel' (McDowall 1990: 137). It is also possible that burrowing is a response to perceived threat, which is often inherent in experimental manipulations. Additionally, other cues associated with drought may be important in eliciting a gravel burrowing response, such as low dissolved oxygen and a gradual reduction in water velocity as the river dries up.

Gravel burrowing ability was, however, influenced by the composition of the substratum, being significantly inhibited in gravels containing a high proportion of fine particles, and thus small interstitial spaces. Furthermore, several dead and surviving G. cobitinis had suffered bruising to the head in such gravels. Galaxias cobitinis was observed to probe the substratum, testing for accessible routes, and was able to reverse out of dead ends, yet some fish became wedged in pockets of finer substratum. Entrapment in such locations may have led to fish being crushed if substrata moved as water levels declined, or death due to stress and/or suffocation. This may also occur in the wild. Of the New Zealand galaxiids, Neochanna species are most commonly found burrowed into substratum and have a high physiological tolerance to survival without water. However, as noted by Eldon (1979: 345) of Neochanna burrowsius Phillipps, 'paradoxically the ability of mudfish to enter small spaces was often fatal'. These results for G. cobitinis concur with those of Dunn (2003) for G. paucispondylus and G. vulgaris, who concluded that large substratum sizes, and associated loose packing, create large interstitial spaces, which are essential for gravel burrowing to be an effective drought survival mechanism in gravel-bed streams with intermittent flow.

An important conclusion drawn from our experiments is that *G. cobitinis* is not particularly adept at surviving without water. We found that a third of all stranded *G. cobitinis* died within 90 minutes, despite the relatively benign conditions. In comparison, Meredith (1985) evaluated the emersion survival ability of nine galaxiids, including six *Galaxias* species, and found that all species survived for more than 1 day, except *Galaxias maculatus*, which suffered 50% mortality within 5 hours. Thus, at the onset of low flow and surface water loss, the survival of

G. cobitinis is dependent on being able to find suitable refugia, which may involve burrowing through the substratum into the groundwater. This finding emphasises the importance of adequate interstitial space and high groundwater levels.

A tendency to gulp air and to hold air bubbles in the buccal cavity during emersion has been observed in *Neochanna* and some *Galaxias* species, and is thought to be a crucial reflex enabling survival out of water (Meredith 1985). Observations of emersed *G. cobitinis* suggested that they may not be able to retain air bubbles in their buccal cavity; instead, they tended to gasp for air when removed from water, an act that desiccates the gills. Additionally, although emersed fish did appear to gulp an air bubble and inflate the buccal cavity sporadically, these bubbles quickly escaped. It is only speculative, but perhaps the mouth morphology of *G. cobitinis*, with its distinctly protruding lower jaw, precludes the ability to effectively retain an air bubble. Furthermore, increased mucus production, which occurs in *Neochanna* species, did not appear to occur in *G. cobitinis*. Mucus acts to keep gill surfaces moist and, importantly, improves the retention of air bubbles in the buccal and opercular cavities (Meredith 1985). These factors are likely to substantially reduce the ability of *G. cobitinis* to survive without water.

Galaxias cobitinis did, however, adopt postures likely to be conducive to survival while emersed or in very shallow water, such as a dorsal-ventral stance or lying on their dorsal surface. Maintenance of a dorsal-ventral or upright position is vital for an emersed fish; otherwise, ventilation is restricted through pressure on the opercular region. Meredith (1985) concluded that it was G. maculatus' inability to maintain this position that reduced its tolerance of emersion. However, G. cobitinis has small pectoral fins that are placed high on the body (McDowall & Waters 2002). Thus, instead of using its pectoral fins to maintain an upright stance, G. cobitinis tended to curl its body. Indeed, emersed G. cobitinis could adopt a deep U-bend stance, as commonly observed in emersed Neochanna species (McDowall 2003). Additionally, some G. cobitinis had rolled onto their dorsal surface during emersion. The physical act of rolling may assist the distribution and mixing of residual water within the opercular cavity and facilitate rehydration of the dorsal surface (Meredith 1985). Some fish were found curled around larger substrata, but no fish, even those under the same cobble, were touching one another. In contrast, Davidson (1999) found that during emersion tolerance experiments, Neochanna diversus Stokell that initially had been placed separately would end up in clusters, with fish coiled closely around one another. Such behaviour is thought to reduce the amount of exposed skin at risk of evaporative loss during prolonged emersion (Meredith 1985). These observations indicate that although G. cobitinis has behavioural adaptations allowing movement in little or no water, it does not have adaptations to enhance survival without water for extended periods.

Although no statistical difference was found between the two experiments in the interstitial volumes of disturbed substratum treatments, small differences relating to the amount of flushing that occurred during set-up may have had subtle and biologically important consequences. The substratum that was initially collected from areas disturbed by gravel abstraction had not subsequently received river flows. The removal of easily suspended fine particles to improve the visibility of fish simulated increasing amounts of water passing over the substratum, as would

occur when river waters flow over a recently disturbed area. The flow of water often acts to carve a channel through yielding substratum, and this was observed to occur during experimental set-up prior to the second experiment, influencing the structural arrangement of interstitial spaces. This process is likely to have influenced the ability of *G. cobitinis* to burrow through the gravels, resulting in more fish passing through, and fish, on average, being able to burrow more quickly and to deeper levels than in the first experiment. Thus, small differences in substratum embeddedness (the degree to which larger particles are surrounded or covered by finer particles) may have had a large effect on fish movement. Therefore, in addition to particle size composition analysis, quantitative measures of substratum embeddedness should be included in habitat assessments, as has been suggested for other species (Hudson et al. 2003).

Gravel abstraction on the Kauru River is necessary for flood protection, particularly in the vicinity of the Kakanui Valley Road Bridge; however, the river is also a major source of materials for the construction industry. Current gravel abstraction rates in the Kakanui River are 32 000 m³ per annum (Kelly et al. 2005). The major effect of gravel abstraction in the Kauru and Kakanui rivers has been to reduce overall particle size and increase embeddedness (Shirvell 2002; Kelly et al. 2005). Although large flushing flows covering much of the flood plain (such as the 24 m³/s flood in January 2005) can redistribute substratum and remove small particles and sediment that otherwise cause imbrication and armouring, unless surface flows are large, they may not be able to flush out fines from deep within the substratum. In contrast, the pressure of upwelling groundwater may flush out fine particles from deeper areas and maintain pathways to the underlying aquifer. This may, in part, explain the association between G. cobitinis and areas of groundwater upwelling (Dungey 2003); as stated by McDowall & Waters (2002: 49), 'the availability of pockets of really cool, upwelling ground water could be the key to the survival of this fish [G. cobitinis] in the Kauru River'.

In summary, the combined processes of summer droughts and gravel abstraction in the Kauru River are likely to adversely affect *G. cobitinis* populations. Although *G. cobitinis* was adept at burrowing through gravel, it had low emersion tolerances; thus, it is likely to require access to groundwater during droughts. Consequently, habitat modification that leads to the loss of interstitial space and inhibits gravel burrowing will have implications for the persistence of the species. However, the greater the volume of water that passes over an area modified by gravel abstraction before the onset of low flows, the higher the chances are of *G. cobitinis* being able to find access to the underlying water table. Thus, it may be necessary to modify the timing of gravel abstraction practices to enable this. Further, it may also be necessary to restrict the location of gravel abstraction, to avoid disturbance of upwelling areas that provide ready access to groundwater and support high abundances of *G. cobitinis*.

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Appendix 1

COMPOSITION OF UNDISTURBED AND DISTURBED SUBSTRATUM SAMPLES

Summary statistics from GRADISTAT (Blott & Pye 2001) analyses of the substratum composition of three buckets from each substratum treatment. Particle sizes are given in terms of phi (ϕ), where $\phi = -\log_2$ diameter of particle (mm); *d* refers to particle diameter. See Blott & Pye (2001) for further description of technical terms.

METHOD	DESCRIPTOR	UND	UNDISTURBED SUBSTRATUM	TUM	DI	DISTURBED SUBSTRATUM	NM
		SAMPLE 1	SAMPLE 2	SAMPLE 3	SAMPLE 1	SAMPLE 2	SAMPLE 3
	Sample type	Polymodal, poorly sorted	Polymodal, poorly sorted	Trimodal, poorly sorted	Polymodal, very poorly sorted	Polymodal, very poorly sorted	Polymodal, very poorly sorted
Textural group	Gravel	Gravel	Gravel	Gravel	Gravel	Gravel	
	Sediment name	Very coarse gravel	Very coarse gravel	Very coarse gravel	Very coarse gravel	Very coarse gravel	Very coarse gravel
Method of moments (Logarithmic (ϕ))	Mean	-6.578	-6.478	-6.402	-5.338	-4.925	-4.874
	Sorting	1.600	1.599	1.541	2.724	2.510	2.657
	Skewness	1.318	1.161	1.684	0.768	0.794	0.638
	Kurtosis	4.067	3.716	5.824	2.178	2.177	1.931
Folk & Ward method (\$)	Mean	-6.557	-6.508	-6.602	-5.287	-4.929	-4.835
	Sorting	1.705	1.706	1.297	2.878	2.566	2.678
	Skewness	0.507	0.497	0.581	0.487	0.635	0.631
	Kurtosis	1.681	1.589	1.785	0.816	0.754	0.718
Folk & Ward method (Description)	Mean	Very coarse gravel	Very coarse gravel	Very coarse gravel	Very coarse gravel	Coarse gravel	Coarse gravel
	Sorting	Poorly sorted	Poorly sorted	Poorly sorted	Very poorly sorted	Very poorly sorted	Very poorly sorted
	Skewness	Very fine skewed	Very fine skewed	Very fine skewed	Very fine skewed	Very fine skewed	Very fine skewed
	Kurtosis	Very leptokurtic	Very leptokurtic	Very leptokurtic	Platykurtic	Platykurtic	Platykurtic
	$d_{10}(\phi)$	-8.244	-8.221	-7.490	-8.219	-7.347	-7.406
	$d_{50}(\phi)$	-7.146	-7.098	-7.034	-6.323	-6.146	-6.146
	$d_{\rm on}(\phi)$	-4.046	-4.073	-4.081	-0.378	-0.350	-0.317

I-continued	
Appendix	

METHOD	DESCRIPTOR	UN	UNDISTURBED SUBSTRATUM	TUM	DI	DISTURBED SUBSTRATUM	MU.
	I	SAMPLE 1	SAMPLE 2	SAMPLE 3	SAMPLE 1	SAMPLE 2	SAMPLE 3
Folk & Ward method (Description)	% Gravel	99.8	99.8	0.06	86.8	85.7	84.2
(continued from previous page)	% Sand	0.2	0.2	1.0	13.2	14.3	15.8
	% Mud	0.0	0.0	0.0	0.0	0.0	0.0
	% Very coarse gravel	83.0	81.5	85.3	64.7	60.2	58.2
	% Coarse gravel	7.7	10.0	5.6	8.1	10.8	8.8
	% Medium gravel	6.1	5.5	4.9	4.5	6.1	8.0
	% Fine gravel	2.8	2.6	2.7	6.6	6.3	6.8
	% Very fine gravel	0.2	0.3	0.5	2.8	2.2	2.4
	% Very coarse sand	0.2	0.2	1.0	13.2	14.3	15.8
	% Coarse sand	0.0	0.0	0.0	0.0	0.0	0.0
	% Medium sand	0.0	0.0	0.0	0.0	0.0	0.0
	% Fine sand	0.0	0.0	0.0	0.0	0.0	0.0
	% Verv fine sand	0.0	0.0	00	0.0	00	0.0