Predation, vegetation and habitat-specific survival of terrestrial eggs of a diadromous fish, *Galaxias maculatus* (Jenyns, 1842)

Michael J.H. Hickford *, Mathilde Cagnon, David R. Schiel

Marine Ecology Research Group, School of Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch 8140, New Zealand

ABSTRACT

Mortality from predation during the early life-stages of most teleost fishes can be extreme, and many species have developed specialized spawning strategies to reduce predation. In the diadromous fish *Galaxias maculatus* there is terrestrial development of eggs which restricts aquatic predation, but exposes them to terrestrial predators and a more extreme physical environment. We hypothesised that exotic slugs (*Milax gagates*, *Deroceras panormitanum* and *D. reticulatum*) and mice (*Mus musculus*) reduce the survival of developing eggs and tested this using laboratory and field predation experiments and sampling. We also tested the effects of riparian vegetation composition and density on egg survival. We found that exotic slugs (*M. gagates* and *D. panormitanum*) reduced the survival of eggs in laboratory experiments, but that neither slugs nor mice affected egg survival in field experiments. Egg densities were positively associated with the stem density of riparian vegetation and the thickness of the aerial root-mat. Egg survival was also positively associated with stem density and aerial root-mat thickness, but was not density-dependent. Although predation by mice and slugs did not appear to be a major cause of egg mortality in our study locations, mortality dynamics could be different in areas with greater densities of predators. Abiotic factors are important in egg survival and these are heavily modified by the height and density of riparian vegetation. It is likely that *G. maculatus* egg survival, therefore, co-varies with the composition of riparian vegetation.

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1. Introduction

The early life-stages of most teleost fishes have very high mortality rates (Bailey and Houde, 1989). It is widely accepted that mortality during the egg, larval and juvenile stages is principally caused by predation or starvation (Houde, 1987; Bailey and Houde, 1989; Houde, 1997; Sogard, 1997). Mortality is generally size-selective, so larger larval and juvenile life-stages are better able to escape predation and endure food shortages (Sogard, 1997). However, refuges from predation through size-selective mortality or behavior are not available to egg stages, and several studies, using aquaria and mesocosms, have shown that predation plays a large part in egg mortality (e.g. Fancett and Jenkins, 1988; Cowan et al., 1992). Spawning strategies that reduce access of predators may give eggs a major advantage. Many different strategies can be used, such as egg guarding, burial or deposition in specific habitats away from major predators (DeMartini, 1999). For example, Atlantic silverside, *Menidia menidia*, deposit their eggs only in the high intertidal zone, which is relatively free of aquatic predators. *M. menidia* eggs that were relocated to mid- or subtidal zones had

significantly greater mortality from predation (Tewksbury and Conover, 1987). For *M. menidia*, intertidal egg deposition appears to be adaptive.

Some fishes are highly specialized and occupy different habitats during their life-history. These include diadromous fishes such as salmonids and galaxiids that have marine and freshwater life-history phases. By doing so, they have developed many specific behaviors and habitat requirements for spawning, egg deposition, larval development and growth to maturity. However, use of these different habitats draws a separate suite of factors that affect survival and progression through life-histories. For example, degraded stream and river habitats and channelization are known to have major impacts on salmonids in North America (Smokorowski and Pratt, 2007). These impacts and sources of mortality may create bottlenecks in the life-history and population biology of such species.

In New Zealand, the major diadromous fish *Galaxias maculatus* spawns in the tidal reaches of waterways, immediately after the new and/or full moon, when the tidal range is maximal (Benzie, 1968; Richardson and Taylor, 2002; Taylor, 2002). Eggs are deposited supratidally within dense, terrestrial, stream-side vegetation that is inundated only by high spring tides (McDowall and Charteris, 2006). This type of terrestrial development of eggs is very rare among fishes, but is thought to have evolved independently several times (Martin et al., 2004). An adhesive coating on the newly laid eggs helps them to adhere to the stems and aerial root-mat of riparian vegetation (Taylor, 2002) where they develop for two to four weeks (McDowall, 1968). Egg hatching is triggered by re-

* Corresponding author. Postal address: School of Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch 8140, New Zealand. Tel.: +64 3 364 3049; fax: +64 3 364 2590.
  E-mail address: michael.hickford@canterbury.ac.nz (M.J.H. Hickford).

immersion in water during the following spring tides (Benzie, 1968; McDowall, 1968). Riverine and tidal currents flush the newly hatched larvae (5–7 mm) out to sea, where they develop for about six months until reaching the juvenile stage.

New Zealand's largest commercial and recreational freshwater fishery, of great cultural and economic importance, is for returning juveniles ("whitebait") of five species of galaxiids, but >90% of the catch is *G. maculatus* (McDowall, 1965). Although the fishery is not monitored well statistically, there is a widespread perception that catches have declined since the late 1900s. There is little direct evidence to confirm that overfishing is responsible for this decline, but destruction of habitat required for rearing and spawning is undoubtedly a factor (Taylor, 1996).

Terrestrial development of eggs in *G. maculatus* has both advantages and drawbacks (McDowall and Charteris, 2006). Hatching only occurs during elevated water levels at the time of peak spring tides and this is likely to improve downstream transport of hatched larvae into the sea. However, eggs may be stranded and die if subsequent tidal levels do not inundate the eggs before they exhaust energy reserves (McDowall, 1968). An obvious advantage of the terrestrial development of eggs is that aquatic predation is restricted to the times when the eggs are under water (i.e., immediately after spawning, during remaining spring tides and during riverine flooding). For example, Allibone (2003) observed cannibalism of *G. maculatus* eggs by adult fish, but only immediately after spawning when the eggs were still submerged.

G. maculatus eggs in the terrestrial environment are exposed to predation from a wide range of small predators that inhabit riparian vegetation. Baker (2004, 2006) observed exotic slugs, mud crabs (*Austrohelice crassa*) and field mice (*Mus musculus*) feeding on eggs, but did not quantify egg survival. In an experimental study of egg mortality, Mitchell et al. (1992) concluded that a combination of factors, including desiccation, thermal stress and predation, was more likely to affect egg survival than just the presence of slugs.

Because predators could potentially affect egg survival, and mortality of eggs can be extreme (Mitchell, 1991; Mitchell et al., 1992), we tested the impact of predation by mice (*M. musculus*) and slugs (*Milax gagates*, *Deroceras panormitanum* and *D. reticulatum*) on *G. maculatus* eggs in natural spawning habitats. We used surveys of spawning areas to identify potential predators and establish their densities, and then laboratory and field experiments to test the hypothesis that predation by mice and slugs reduces the survival of developing *G. maculatus* eggs. Finally, we used survey data to evaluate the effect of riparian vegetation composition and abiotic environmental variables on *G. maculatus* egg survival.

2. Methods

2.1. Predators in spawning areas

The relative densities of mice (*M. musculus*) and slugs were measured in *G. maculatus* spawning areas at three locations (Table 1;

Fig. 1): the Avon River (drains coastal plains and urban areas), Takamatua and Barrys Bay Streams (drain steep pastoral valleys). The spawning area at each of these locations is adjacent to an urban area and the riparian vegetation is a mixture of pasture grass, native rushes/sedges and invasive exotic plants.

To measure mice densities, 26 live-capture mouse traps (Tip-Trap, Kness Manufacturing Company, Iowa, USA) baited with peanut butter were placed in a 2 by 13 grid with 2.5 m trap spacing in each spawning area for two consecutive nights (Avon: 7–8 Apr 2008; Takamatua: 9–10 Apr) and inspected each morning. Mice caught during the first night were tagged with nail polish (to distinguish multiple catchings) and released. Slugs were counted in 50×50 cm quadrats ($n = 20$) placed haphazardly in the spawning areas at Avon (9 Apr 2008) and Barrys (15 Apr).

2.2. Laboratory predation experiments

The most commonly seen predators among the riparian vegetation were the exotic slugs *M. gagates* and *D. panormitanum* (Table 2). We used a laboratory experiment to test their abilities to eat *G. maculatus* eggs. In March 2008, *G. maculatus* eggs collected from the field were placed among the aerial root-mat of potted tall fescue (*Schedonorus phoenix*) plants. The pots were 7.5×7.5 cm and the grass had been trimmed to a height of 7 cm. There were 40 grass stems and 50 eggs per pot. The potted grass and eggs were placed inside a plastic container ($22 \times 22 \times 25$ cm) with a mesh lid. Experimental treatments were: inclusion of three *M. gagates* slugs, inclusion of three *D. panormitanum* and controls with no slugs. There were four replicates per treatment. The experimental containers were stored outside in the shade, and the temperature and relative humidity inside all containers were measured twice daily (0730 and 1800) using an HMI41 humidity and temperature probe (Vaisala, Vantaa, Finland). Relative humidity in the experimental containers was maintained between 84% and 98% by spraying the tall fescue plants with water. Remaining live *G. maculatus* eggs in each container were counted every 1–3 d for two weeks. Any dead (opaque) or decaying eggs were left in the containers and counted separately.

2.3. Field predation experiments

Experiments in spawning areas at three locations (Table 1; Fig. 1) tested the effects of mice and slugs on survival of *G. maculatus* eggs. At each location, the composition and height of the vegetation above discrete patches of eggs, and the thickness of the aerial root-mat that the eggs were within were measured. The density of vegetation was estimated by counting the number of stems in three 50 mm × 10 mm transects placed across each patch of eggs. At Avon and Takamatua, one of three treatments was applied to each plot to test for predation by mice: a) Mouse exclusion cage: mice were excluded by an inverted plastic bucket with its base removed (diameter: 27 cm, height: 25 cm,

Table 1
Summary of locations used for field predation experiments and natural *Galaxias maculatus* egg survival surveys. The latitude/longitude of each location and upstream distance to the mouth of the waterway "Mouth" are shown. The species composition and height of vegetation where *Galaxias maculatus* eggs were found are given. Plant species with >5% cover were averaged across replicates at each location and are presented in rank order: 1. *Agrostis stolonifera*; 2. *Schedonorus phoenix* (previously *Festuca arundinacea*); 3. *Ranunculus repens*; 4. *Carex virgata*; 5. *Trifolium repens*; 6. *Iris pseudocorus*; 7. *Holcus lanatus*; and 8. *Juncus edgariae*. The number of replicates at each location for experiments and surveys is given. Egg densities ($N/0.01$ m^2) at the start of each trial (T_0; see Fig. 2) are indicated.

Location	Latitude	Longitude	Mouth (m)	Vegetation		Type	Replicates			T_0 eggs ($\overline{X} \pm$ SE)		
				Species	Height (mm)		Mar	Apr	May	Mar	Apr	May
Avon	43°30.022′	172°42.146′	10,650	1,2,6,4,3	323	Mice	10	10	–	101 ± 16	219 ± 25	–
				1,2,6,4,3	377	Slugs	10	10	–	334 ± 46	283 ± 30	–
Takamatua	43°46.897′	172°58.100′	140	1,2,5	281	Mice	7	9	–	103 ± 17	217 ± 37	–
Barrys	43°45.701′	172°54.597	80	1,2,7,3,5	195	Slugs	10	5	–	128 ± 28	306 ± 71	–
Te Kawa	43°39.797′	172°48.892′	170	1,2,8,7,3,5	233	Survey	–	17	5	–	479 ± 226	64 ± 19
Pigeon	43°41.389′	172°53.682′	210	2,1,8	222	Survey	10	12	10	183 ± 66	165 ± 21	190 ± 42
Robinsons	43°45.848′	172°57.750′	60	1,2,8	312	Survey	16	20	11	95 ± 26	563 ± 367	64 ± 17
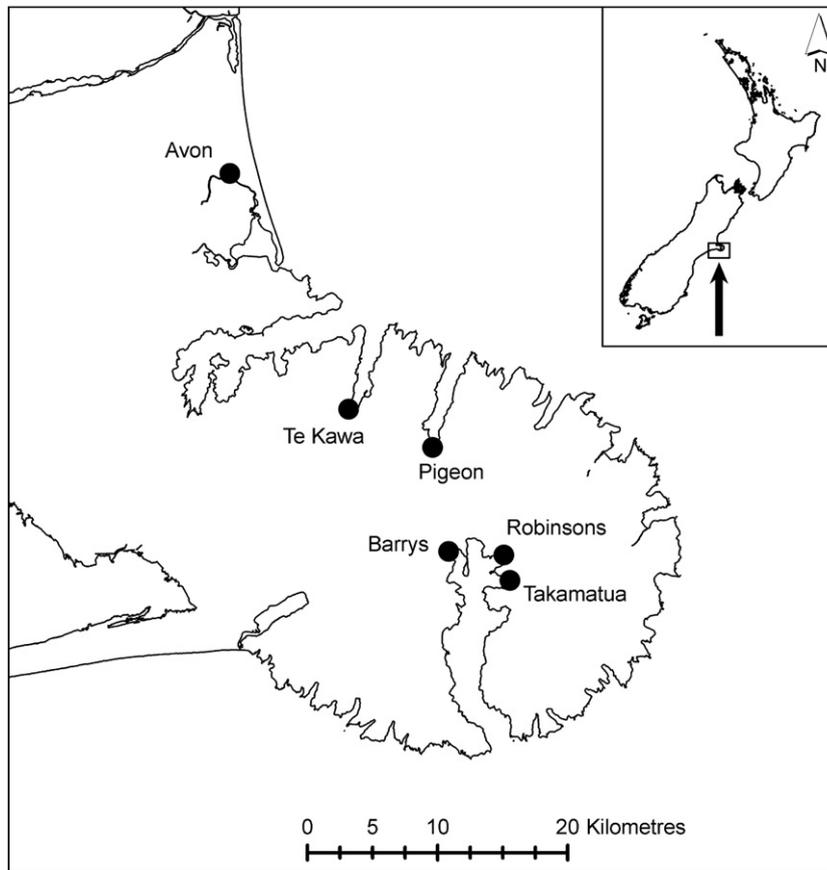
Fig. 1. Map of Banks Peninsula, New Zealand, showing the three locations used for field predation experiments (Avon, Takamatua and Barrys) and the three locations used for measuring *Galaxias maculatus* egg survival in natural habitats (Te Kawa, Pigeon and Robinsons).

and volume: 9.6 l); the bucket was anchored to the ground with metal pins, b) Open cage: mice were given access to the eggs by cutting four holes (6.5 cm diameter) at ground level in each plastic bucket, and c) Open control: no cage. To test the efficiency of the mouse exclusion cages prior to establishing the experiment, bait (peanut butter) was put inside five cages, five open cages and five open controls at Avon. Baits were checked the following morning, replaced if eaten, and re-checked three days later.

At Avon and Barrys, one of two treatments was applied to each plot to test for predation by slugs: a) Slug exclusion cage: slugs were excluded by a copper fence (Newman and Showler, 2007) (diameter: 17 cm and height: 3 cm); the fence was pushed into the ground (~5 mm) and anchored with staples, and b) Open control: no copper fence. The efficiency of the copper fence was tested prior to establishing the experiment by putting bait (a paste of yeast, flour, sugar and water) inside five replicates of each treatment at Avon. Baits

were inspected the following morning, replaced if eaten, and re-checked three days later.

G. maculatus eggs were counted in a 10×10 cm quadrat inside each treatment immediately after the treatments were applied, and then 1–3 times before hatching (Fig. 2). All treatments at each location were surveyed on the same day.

To detect if cages affected internal temperatures, we placed Tidbit temperature loggers (Onset Computer Corporation, Bourne, MA, USA) at ground level inside replicate ($n = 2$) cages, open cages and open controls at Takamatua, recording temperatures every 2 min during the experiments.

2.4. Egg survival at other locations vs. environmental variables

Egg survival in natural habitats was measured at another three streams on Banks Peninsula (Table 1; Fig. 1). These drain steep valleys

Table 2
Number of predators at locations prior to experimental manipulations. The experimental area, number of traps and quadrats, number of mice caught in traps (+ traps where the bait was eaten) and density of slugs and slug eggs ($N/0.25$ m^2) are shown for each location.

Treatment	Location	Area (m^2)	Traps (n)	Quadrats (n)	Mice caught (+ bait eaten)		Density of slugs ($\overline{X} \pm$ SE)			Slug eggs
					Day 1	Day 2	*Milax gagates*	*Deroceras panormitanum*	*Deroceras reticulatum*	
Mice	Avon	75	26		2 (+8)	2 (+24)				
	Takamatua	75	26		2 (+0)	0 (+0)				
Slugs	Avon	96		20			7.8 ± 2.0	3.8 ± 1.3	0	15.6 ± 4.2
	Barrys	60		10			0	0	0.4 ± 0.4	1.6 ± 1.6
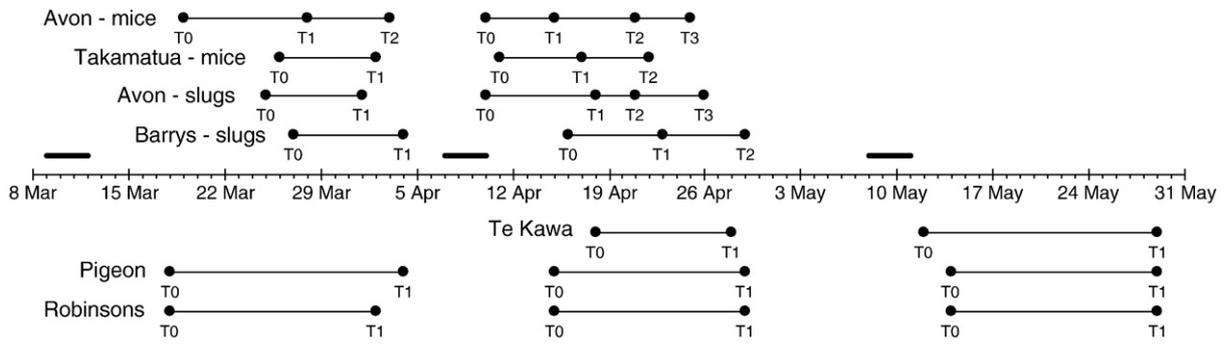
Fig. 2. Autumn 2008 timeline showing dates of field predation experiments measuring *Galaxias maculatus* egg survival at three locations (above abscissa) and dates of egg survival surveys at three locations (below abscissa). T_0 is date of first monitoring, T_1–T_n represent subsequent monitoring. Bold horizontal bars show *Galaxias maculatus* spawning events.

and the *G. maculatus* spawning areas are in coastal pastoral land. Riparian vegetation at all three locations is a mixture of pasture grass and native rushes/sedges. At each location, the species composition (percentage cover) and height of the vegetation above discrete patches of eggs, the thickness of the aerial root-mat that the eggs were within, and the vegetation density were measured. To test the effect of the composition and density of riparian vegetation on *G. maculatus* survival, eggs were counted in 10×10 cm quadrats immediately after spawning and again before hatching (Fig. 2).The elevation of the midpoint of each quadrat was measured using a real-time kinematic global positioning system (Trimble Navigation Ltd 4000SSI & 4400, Sunnyvale, USA). To test the effect of riparian vegetation on the physical environment at ground level, temperature and relative humidity were measured at the base of clumps of riparian vegetation ($n = 30$) in the spawning area at Pigeon Bay on 15 April 2008 using an HMI41 humidity and temperature probe (Vaisala, Vantaa, Finland).

2.5. Statistical analyses

To investigate the relative densities of predators at field locations, differences in slug and slug egg densities were tested with analysis of variance (ANOVA) for the effect of location. To examine the effects of slug predation in the laboratory experiment, differences in egg survival after 15 d were tested with ANOVA for the effect of predator inclusion. Differences in the abundance of dead eggs at days 3, 9 and 15 were tested with 2-way ANOVA for the effects of time and predator inclusion. Time was treated as a random factor. Temperature and relative humidity inside the experimental containers were tested with 3-way ANOVA for the effects of treatment, day and time. Day and time were treated as random factors.

For the field experiment, differences in egg survival were tested with 3-way ANOVA for the effects of location, time and predator exclusion. Location and time were treated as random factors. Internal temperature was tested with 3-way ANOVA for the effects of day, month and cage type. Day and month were treated as random factors. Partial correlation between egg densities and survival, while controlling for the effects of stem density, was used to examine effects further.

To examine the association between environmental variables and *G. maculatus* egg deposition and survival, a correlation analysis was done on initial egg densities, 28 d egg survival, vegetation height, stem density, thickness of aerial root-mat, and the percentage cover of individual vegetation species. Threshold levels of significance for correlation coefficients were adjusted for multiple comparisons ($k = 20$) by Bonferroni's correction, which resulted in a significance level of $\alpha = 0.0025$. Differences in initial egg densities and 28 d egg survival were tested with 2-way analysis of covariance (ANCOVA) for the effects of location and time, with stem density and thickness of aerial root-mat as covariates. Location and time were treated as random factors. Partial correlation between egg densities and survival, controlling for the effects of stem density were then done.

A correlation analysis was done on ground level humidity, temperature, stem density and thickness of the aerial root-mat.

Tukey's HSD post-hoc tests were used when ANOVA indicated significant effects. Unless otherwise specified, a significance level of $\alpha = 0.05$ was used for all tests. Data were log-, log $(x + 1)$- or arcsine-transformed when necessary to satisfy the assumption of homogeneity of variance, as detected by Cochran's test. If transformation did not alleviate heterogeneous variance, critical α was reduced to $\alpha = 0.01$ for the ANOVA to account for an increased probability of type I error (Underwood, 1997). Statistical analyses were done with Statistica 8 (StatSoft).

3. Results

3.1. Predators in spawning areas

Twice as many mice were caught over two days at Avon as at Takamatua (Table 2). When these capture frequencies were converted to catch densities (Caughley, 1977) the transformed indices indicated that the density of mice at Avon was 2.04 times that at Takamatua. This, coupled with evidence of mice readily consuming bait at Avon (Table 2), indicated that predation pressure from mice was likely to be higher at Avon than at Takamatua.

The species composition and density of slugs differed markedly between locations (Table 2). Two species of non-native slugs (*M. gagates* and *D. panormitanum*) were found only at Avon. A third non-native species, *D. reticulatum*, was found only at Barrys. Total slug densities were significantly higher at Avon ($F_{1,38} = 13.54$, $P < 0.001$). Unless *D. reticulatum* has markedly higher predation rates than the other two species, predation pressure from slugs was likely to be higher at Avon. Slug eggs were more abundant also at Avon than at Barrys ($F_{1,38} = 10.47$, $P < 0.01$; Table 2).

3.2. Laboratory predation experiments

Mortality of *G. maculatus* eggs in the control containers ($=$ no predators) was high with only 53% of eggs surviving until the end of the experiment (Fig. 3). After 15 d, survival was lower in the treatments containing slugs than in the controls ($F_{2,9} = 9.20$, $P < 0.01$), but the species of slug present did not significantly affect survival (Tukey HSD, not significant (n.s.)). Both species of slugs appeared to consume *G. maculatus*. Dead eggs initially turned opaque and then decayed over 2–3 d. The number of dead eggs in the containers increased between day 3 and days 9 and 15 across all treatments ($F_{2,27} = 384.14$, $P < 0.001$, Tukey HSD, $P < 0.01$), but there were no more dead eggs in the slug containers than in the controls ($F_{2,27} = 0.14$, n.s.). The temperature and humidity in the containers varied significantly during most days ($F_{1,270} = 92.44$, $P < 0.001$ and $F_{1,270} = 9.48$, $P < 0.01$ respectively; Fig. 3), but there were no significant differences between treatments ($F_{2,270} = 0.07$, n.s. and
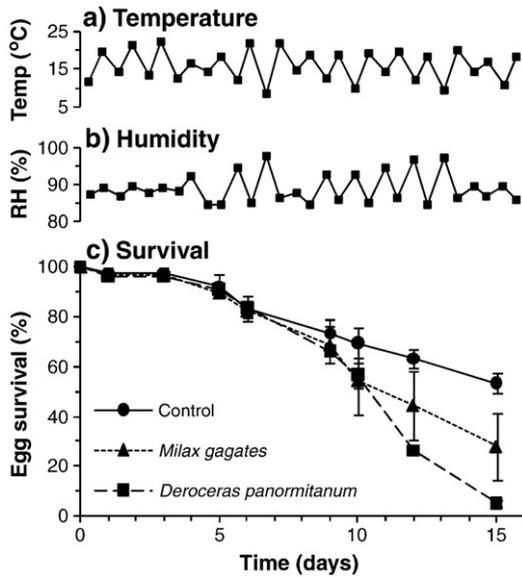
Fig. 3. Slug laboratory experiment. (a) Mean temperature and (b) mean relative humidity from morning (0730) and evening (1800) measurements ($n=12$) throughout the 15 d experiment in March 2008. (c) Mean ± SE survival of 50 *Galaxias maculatus* eggs in controls ($n=4$) and slug inclusion containers (either three *Milax gagates* ($n=4$) or three *Deroceras panormitanum* ($n=4$)).

$F_{2,270} = 0.28$, n.s.). Across all treatments, the temperature remained between 8.3 and 22.7 °C during the experiment, and relative humidity was greater than 81% at all times.

3.3. Field predation experiments

The plastic buckets and copper fences were effective at excluding mice and slugs respectively. None of the baits placed inside the mouse exclusion cages were eaten. In the open cages, four or five baits had disappeared at each inspection, and three or five baits in the open controls. Two slugs were found on the baits inside the copper fences, but 11 were found inside the open controls. This corresponds to an 82% efficiency of the barrier.
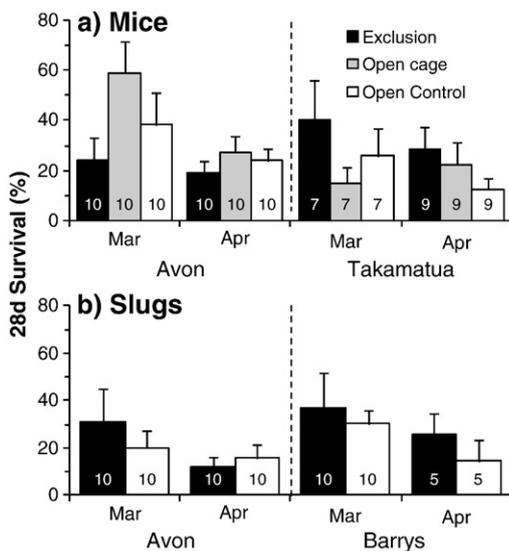
Fig. 4. Mice and slug field experiment. Mean + SE survival of developing *Galaxias maculatus* eggs in (a) two mice predation experiments (March and April) in exclusions, open cages and open controls at two locations (Avon and Takamatua) and (b) two slug predation experiments (March and April) in exclusions and open controls at two locations (Avon and Barrys). Replicate numbers are shown within bars.

In the mouse predation experiment, average survival in the open control plots over 28 d ranged from 13–38% (Fig. 4a). There was no effect of mouse exclusion on egg survival ($F_{2,96} = 0.39$, n.s.) with high variability among replicates obscuring any possible treatment effects. Overall, egg survival was better in March than April ($F_{1,96} = 4.44$, $P < 0.001$). Despite the differences in densities of mice at the two locations, there was no evidence of increased levels of predation at the location with more predators. Average survival rates in the open control plots at Avon (31%) and Takamatua (19%) were not significantly different (Tukey HSD, n.s.) despite twice as many mice being caught at Avon (Table 2). The average daily temperature in the experimental plots at Takamatua was cooler in April than in March ($F_{1,48} = 75.31$, $P < 0.001$), but there was no difference between the treatments ($F_{2,48} = 2.23$, n.s.).

In the slug predation experiment, average survival in the open control plots ranged from 15–30% (Fig. 4b). There was no effect of slug exclusion on egg survival ($F_{1,62} = 0.86$, n.s.), with high variability among replicates obscuring any possible treatment effects. Overall, there was no difference in egg survival between locations ($F_{1,62} = 1.10$, n.s.) or months ($F_{1,62} = 0.02$, n.s.). Survival rates in the open control plots at Avon (18%) and Barrys (22%) were not significantly different (Tukey HSD, n.s.) despite slug densities being 30 times greater at Avon (Table 2).

There was no evidence of density-dependent mortality of *G. maculatus* eggs in any of the field predation experiments. There was no correlation (controlling for stem density) between initial egg numbers in quadrats and subsequent egg survival ($r_{175} = 0.03$, n.s.), despite the more than 3-fold range in initial egg densities in the mice and slug field experiments (Table 1).

3.4. Egg survival at other locations vs. environmental variables

The number of eggs laid increased with stem density ($r_{97} = 0.38$, $P < 0.001$; Fig. 5), and thickness of the aerial root-mat ($r_{97} = 0.30$, $P < 0.0025$) across all locations. Initial egg densities were lower at Robinsons in March and May than at Pigeon (ANCOVA with stem density and aerial root-mat thickness as covariates: $F_{2,70} = 5.07$, $P < 0.01$, Tukey HSD, $P < 0.05$; Fig. 6a). Egg survival was lower in March at Pigeon and Robinsons than in the later months (ANCOVA with stem density and aerial root-mat thickness as covariates: $F_{2,70} = 38.96$, $P < 0.001$, Tukey HSD, $P < 0.001$; Fig. 6b). Egg survival (over 28 d) was not correlated with the cover of any single species of riparian vegetation, the height of the vegetation ($r_{97} = -0.17$, n.s.) or
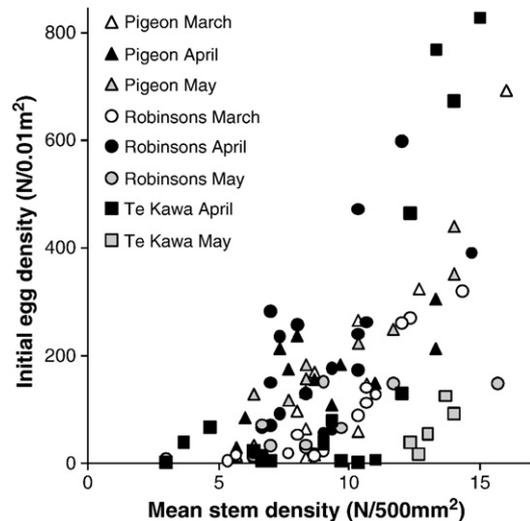
Fig. 5. The effect of stem density of riparian vegetation on *Galaxias maculatus* egg deposition at three locations (Pigeon, Robinsons and Te Kawa) during three months (March, April and May; only April and May for Te Kawa).
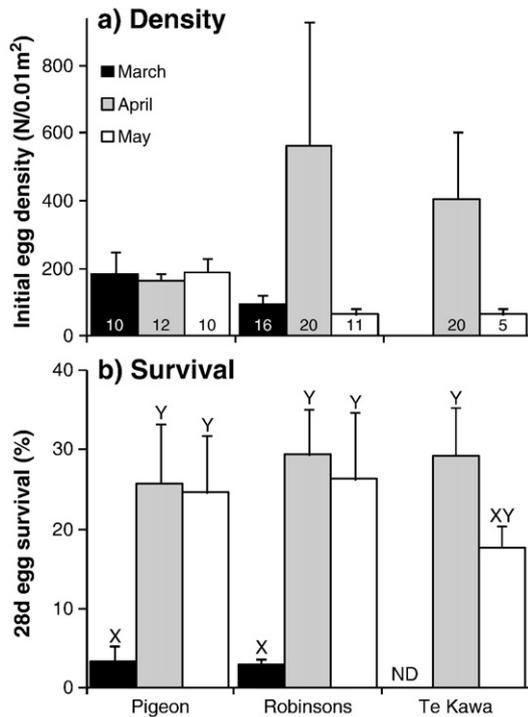
Fig. 6. Mean + SE *Galaxias maculatus* egg density (a) and survival (b) at three locations (Pigeon, Robinsons and Te Kawa) during three months (March, April and May). Replicate numbers are shown within bars. Different inset letters (*X*, *Y*, and *XY*) indicate significant differences among locations after Tukey comparisons (Tukey HSD, $P < 0.001$), ND = no data.

elevation ($r_{97} = 0.07$, n.s.), but survival was positively correlated with stem density ($r_{97} = 0.63$, $P < 0.001$) and thickness of the aerial root-mat ($r_{97} = 0.26$, $P < 0.0025$). Relative humidity (%) was positively correlated with stem density ($r_{28} = 0.88$, $P < 0.001$) and aerial root-mat thickness ($r_{28} = 0.83$, $P < 0.001$) in replicate clumps of vegetation in the riparian zone of Pigeon in April.

There was no evidence of density-dependent mortality of *G. maculatus* eggs in any of the egg survival surveys. There was no correlation (controlling for stem density) between initial egg numbers in quadrats and subsequent egg survival ($r_{104} = 0.15$, n.s.), despite the nearly 9-fold range in initial egg numbers surveyed across locations and months (Table 1).

4. Discussion

4.1. Predation effects on egg mortality

Mortality during the early life-history of fishes is extremely high, often variable spatially and temporally, and mainly due to predation and starvation (Bailey and Houde, 1989; Houde, 1997). Mortality of *G. maculatus* eggs in our study was very high, but we could not detect any overall difference in egg survival between predator exclusion treatments and open controls. The enclosures had negligible effects on the physical environment inside them, so there were no added effects on mortality due to increased temperatures or decreased humidity (Richardson and Taylor, 2002).

Baker (2006) observed mice feeding on *G. maculatus* eggs at a location where three mice were caught every four days on average. Over two nights, we caught four mice at Avon and two at Takamatua. However, differences in trapping methodology make comparisons difficult. Baker (2006) placed 12 traps at 20 m intervals along 240 m of river bank, whereas we placed 26 traps at 2.5 m intervals in a 2 by 13 grid. Slug densities are more amenable to comparison, although they have large temporal variability because they are closely linked to precipitation (Joe

and Daehler, 2008), and our surface searching method is likely to underestimate populations (Ferguson and Hanks, 1990). Mitchell et al. (1992) found slug densities of 65 m^{-2}, but even this number did not consume many *G. maculatus* eggs. Our laboratory predation experiment showed that it took very high densities (533 m^{-2}) and 12 d for the non-native slug *D. panormitanum* to significantly reduce egg survival. It seems likely, therefore, that in nature *G. maculatus* eggs represent only a small and facultative part of its diet.

M. musculus feed mainly on insects and plant seeds in New Zealand (Badan, 1986; Miller and Webb, 2001). These were abundant and ubiquitous in our study locations, but *G. maculatus* eggs were found only in a narrow band near the water. Availability may mean that *G. maculatus* eggs do not comprise a major portion of mice diets at our study locations and thus mice did not have a significant effect on egg survival.

Mice and at least some species of slugs do appear to be able to eat *G. maculatus* eggs, but only as opportunistic predators. Their predation effects could be significant at times, but haphazard and spatially variable as they encounter clusters of eggs. High variability in *G. maculatus* egg survival between plots, independent of predation, means that our field experiment would not detect this sporadic loss of eggs. Overall, we conclude that either mice and slugs do not commonly feed on *G. maculatus* eggs, or the apparent absence of predation reflects low predator densities when the locations were surveyed.

4.2. The effect of abiotic factors on egg survival

Similar to our study, Mitchell et al. (1992) found that *G. maculatus* egg survival was highly variable on a small spatial scale and that survival was independent of predation. This suggests that each plot may have unique characteristics affecting egg survival. Initial egg density is an obvious factor that may influence survival. However, density-dependent mortality at the egg stage in fishes is rare, particularly for large-bodied, pelagic spawning species of commercial fishes for which most egg mortality estimates exist (Bailey and Houde, 1989). Although density-dependence could occur in relatively less-studied species having clumped, demersal egg masses, our data do not support a density effect for *G. maculatus*.

Physical factors, however, do have a major effect on *G. maculatus* egg survival. Elevated temperatures enhance the rate of development of *G. maculatus* eggs (Benzie, 1968) so that they are capable of hatching sooner. This should improve survival by reducing the cumulative effect of mortality. However, higher temperatures can also increase mortality through dehydration. Even if the air temperature above a spawning area is uniform, ground level temperature and humidity will vary with vegetational characteristics, especially density and height (Geiger et al., 2003). We found better egg survival in riparian vegetation with dense stems and a thick aerial root-mat, which modified the ground-level environment by keeping temperatures lower, humidity higher and both more constant. Particular species of riparian vegetation (e.g., *Juncus edgariae*, *Schedonorus phoenix* and *Holcus lanatus*) provide dense stems and a thick aerial root-mat more frequently than other, sparser vegetation (e.g., *Isolepis cernua*). Dense riparian vegetation may also protect developing eggs from exposure to ultraviolet light (particularly UVB) which has been shown (Christopher Hickey, unpublished results) to be particularly lethal to *G. maculatus* eggs (LD50 = 3.6 kJ m^{-2}). It is likely that a combination of factors, therefore, including ambient temperature and humidity creates fine-scale environments that greatly influence *G. maculatus* egg survival.

4.3. Is the mortality of G. maculatus eggs lower than in species with aquatic egg development?

McDowall and Charteris (2006) listed several possible advantages of terrestrial egg development in diadromous galaxiids, including separation from aquatic predators. However, does this separation reduce

the mortality of *G. maculatus* eggs? Houde (1987) reviewed daily mortality rates throughout the life-cycle of several marine fishes. During the egg phase, the daily mortality rate was 5% for Atlantic herring (*Clupea harengus harengus*) and Atlantic cod (*Gadus morhua*), 10% for striped bass (*Morone saxatilis*), 20% for French grunt (*Haemulon flavolineatum*) and 69% for bay anchovy (*Anchoa mitchilli*). Unwin (1986) estimated the daily mortality rate of Chinook salmon (*Oncorhynchus tshawytscha*) eggs at 1.6% during their aquatic demersal development. Over our six study locations in April, the daily mortality rate for *G. maculatus* eggs in the open control treatments and surveys was ~7.5%. This is comparatively low, but the egg phase in *G. maculatus* (around 28 d, McDowall, 1990) is considerably longer than that of Houde's (1987) marine species (12, 14, 2, 1 and 1 d respectively). From our surveys, only ~11% of *G. maculatus* eggs survived to hatch, compared to 31–81% in the marine species. The egg stage of *O. tshawytscha* is very long (130–150 d, Unwin, 1986), but the low daily mortality rate means that 30% of eggs survive to hatch.

We may have overestimated the mortality of *G. maculatus* eggs by assuming that eggs that disappeared from our experimental plots had not survived. *G. maculatus* eggs can be displaced once they have lost their initial adhesiveness (after 5–7 d, McDowall, 1968) and heavy rain, riverine flooding or further tidal flooding may have washed eggs out of our quadrats. These eggs could have been deposited downstream and may have survived. Notably, however, the long planktonic larval duration (100–200 d, Rowe and Kelly, 2009) of *G. maculatus* will further decrease survival, with considerable mortality likely during the oceanic phase.

Predation by non-native species did not appear to be a major cause of mortality for *G. maculatus* eggs in our study locations, but it might be an additional stressor on an already heavily-impacted life-history. The cumulative effects of spawning habitat degradation, through intensified farming, urban development and channelization, and egg predation, together with increasing fishing pressure may disrupt the balance between productive sources and population sinks.

Acknowledgements

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