Attraction of migratory inanga (*Galaxias maculatus*) and koaro (*Galaxias brevipinnis*) juveniles to adult galaxiid odours

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Abstract   The response of migratory galaxiid juveniles, inanga (*Galaxias maculatus*) and koaro (*G. brevipinnis*), to the odours of adult galaxiids was tested in a two-choice chamber apparatus. Both conspecific and heterospecific odours were tested. Inanga juveniles were attracted to adult inanga (*G. maculatus*), banded kokopu (*G. fasciatus*), and koaro (*G. brevipinnis*) odours. However, they were not attracted to odours from common bullies (*Gobiomorphus cotidianus*). Koaro juveniles exhibited a species-specific attraction to adult koaro odours only. These results demonstrate inanga juveniles can discriminate and are attracted to adult galaxiids during their migratory phase, whilst migratory koaro juveniles exhibit a species-specific attraction to adult odours similar to the pheromonal attraction previously described for juvenile banded kokopu. This strengthens the hypothesis for the use of pheromonal cues in stream and habitat selection by amphidromous galaxiids.

Keywords   migration; cue; galaxiid; fish; pheromone; inanga; koaro

INTRODUCTION

New Zealand currently contains 17 species of the genus *Galaxias*, five of which are diadromous. As such, their larvae migrate to sea where they spend the winter developing into juveniles. During spring each year, mixed species shoals of these juvenile galaxiids return to fresh water in search of habitat for growth to adulthood. These mixed shoals are collectively termed "whitebait" and comprise a nationwide commercial and recreational whitebait fishery. Inanga (*Galaxias maculatus* Jenyns) and koaro (*G. brevipinnis* Günther), along with banded kokopu (*G. fasciatus*) are the three main whitebait species. The other two species, which are rare in the catch, are the giant kokopu (*G. argenteus*) and shortjawed kokopu (*G. postvectis*).

Koaro are selective in habitat and tend to occur in forested, rapidly flowing rocky streams with cold, clear waters. They are adept at climbing falls and will generally seek out forest or bush covered first-order streams, penetrating well inland to higher altitudes (McDowall 1990). In contrast, inanga are a lowland species that do not penetrate far inland and are less selective in habitat. Inanga will occupy a diverse range of habitats from clear to brown (tannin-stained) cold to warm waters, in open pasture or within forest cover but occur mostly in gently flowing or still water (McDowall 1990).

Most research on factors affecting the distribution and abundance of whitebait species is based on the correlation of fish to certain physical or environmental stream variables, such as abundance of suspended solids, stream gradient, volume of flow, presence of forest cover, and physical habitat features such as water velocity and substrate size (Hayes et al. 1989; Hanchet 1990; Jowett & Richardson 1996; Jowett et al. 1996; Boubée et al. 1997). However, fish could derive information about the upstream habitats by the chemical information dispersed within the water column. Rowe et al. (1992) found juvenile koaro exhibited river mouth selection that did not correlate to the presence of physical or environmental variables attributed to

their preferred habitat. They proposed that migrating fish choose streams based on the presence of species-specific pheromones. Recent studies by Baker & Montgomery (2001) found support for this hypothesis when banded kokopu juveniles exhibited a species-specific attraction to adult odours or pheromones. Adult pheromones would signify an established population of conspecifics and therefore accessible adult habitat for colonisation. Thus, the presence of pheromones could be used in stream selection by juveniles. In this paper, the term adult odours is used synonymously with pheromone as defined by Sorensen et al. (1998).

The pheromone hypothesis was first proposed by Nordeng (1971, 1977) as a method of home stream selection in anadromous salmonids. He challenged the imprinting hypothesis suggested by Hasler & Wisby (1951). Although it is generally agreed that salmon navigate their way back to their home stream using chemical cues present within the water column, the precise nature of the cues still remains controversial. Currently the strongest evidence for use of pheromonal cues in stream selection by migratory fishes is in the sea lamprey (*Petromyzon marinus*). Adult sea lamprey do not return to their home stream, instead they seek suitable habitat for spawning. Studies by Li et al. (1995), Li & Sorensen (1997), Bjerselius et al. (2000), and Vrieze & Sorensen (2001) provide strong evidence that adult sea lampreys select spawning streams based on a pheromone released by upstream larval fish which comprises unique bile acids.

As galaxiid juveniles are not known to return to a specific spawning site or home stream but instead are thought to seek suitable habitat for colonisation, as with sea lampreys, an established population of conspecifics could be a good predictor of suitable habitat. In this sense, species-specific pheromonal cues would provide a good mechanism for successful migration. This study tests whether inanga and koaro juveniles also show a species-specific attraction to adult pheromones, which may aid fish in stream selection and recruitment to upstream populations.

MATERIALS AND METHODS

Experimental animals

Inanga juveniles (*G. maculatus*, 47–51 mm total length (TL)) were collected from the Mokau River (NZMS R18 543754) in August 2000, during their annual migration up stream. Koaro juveniles

(*G. brevipinnis*, 39–55 mm) were collected below the spillway of the Upper Mangatawhiri Dam on the Mangatawhiri River (NZMS S12 022548), a tributary of the Waikato River, in October 2001.

Inanga were transferred to the University of Auckland and kept in a 15°C temperature controlled room. Koaro juveniles were kept in a 13°C temperature controlled room at the National Institute of Water and Atmospheric Research Limited (NIWA). Both species were kept under a 12:12 h light cycle and housed in a glass aquarium containing 120 litres of aerated brackish tap water (salinity 12‰). Brackish water was used to reduce the risk of disease and to help maintain their migratory response for as long as possible. In both aquaria, migratory responses were also maintained by creating a continual current flow within the housing arena using a Fluval® 303 filter pump. As an abundant food supply was necessary to feed all juveniles, both species of fish were fed daily on frozen bloodworms as opposed to the adult food supply of cultured whiteworms.

Experimental apparatus and protocol

Inanga trials were performed in two experimental apparatuses simultaneously (Fig. 1), those described by Boubée et al. (1997) and Baker & Montgomery (2001). Koaro trials were only performed in the apparatus of Boubée et al. (1997). Each apparatus consisted of a main chamber that gave fish access to two upstream choice chambers. The entrance to each upstream chamber was created by a funnel of 20 mm diameter, which allowed entry but limited the return of fish to the main chamber. Rubber bungs were inserted into the funnel openings to block entry until a trial began. The water used within the experimental tanks was aged, aerated tap water (fresh water). All trials were conducted during daylight hours. For inanga trials, a Philips 58 W double tube cool white fluorescent light was placed 60 cm above the centre of the two experimental tanks and for koaro trials, an Osram 40 W double tube cool white fluorescent light was placed 60 cm above the centre of the experimental apparatus. There was no difference in inanga performance between the two experimental test tanks.

Trials were conducted following the protocol described by Baker & Montgomery (2001). At the beginning of each trial, rubber bungs were inserted to block the entrance of each funnel and 10 fish were placed in the main chamber and left for 20 min to adjust. A volume of odour water was then introduced to an upstream chamber (for control trials no odour was added, each upstream chamber consisted of tap
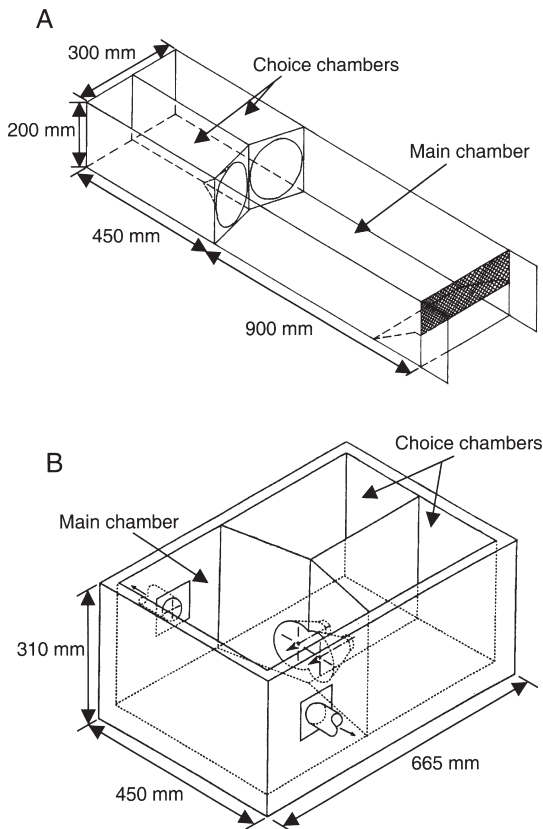
Fig. 1 Schematic diagram of **A**, choice tank used in Baker & Montgomery (2001); **B**, choice tank used by Boubée et al. (1997).

water only), both chambers filled with water and the bungs released. Upon releasing the bungs, water flowed through the funnels creating a decreasing current flow with an initial velocity of 0.1 m s^{-1}, which took 40 s to subside as the water levels equalised. Fish were given 10 min to move into an upstream chamber and after this time the bungs were replaced and the number of fish in each chamber were counted. After testing, fish were placed into another tank of the same size and attributes as the housing tank. The experimental tank was then emptied and rinsed out with tap water before being refilled for the next trial. In odour experiments, a double rinse of the odour chamber was performed. At each odour concentration, 20 trials were conducted (including the control) with a different set of 10 fish used for each trial (200 fish). Because of the difficulties in obtaining large numbers of juveniles, the same set of 200 fish was used for all

experiments. The odour chamber was randomised using a random numbers table (Wild & Seber 1992) with even numbers representing the left chamber and odd number representing the right chamber.

Odour water collection

For galaxiid odours, the three main whitebait species were used. Adult fish of all three species were captured and housed for c. 8 weeks before experimentation began. Every second day all adult fish were fed on whiteworms. All adult fish were sexually mature, with spawning season falling 1 month before capture.

For juvenile inanga trials, one adult banded kokopu, *G. fasciatus* (170 mm TL), one adult koaro, *G. brevipinnis* (225 mm TL) and, as adult inanga *G. maculatus* are considerably smaller than adult banded kokopu or koaro, four adult inanga (75, 78, 95, and 100 mm TL) were collected to give comparable biomass. Adult koaro and inanga were sea-run fish whereas the adult banded kokopu was collected from a landlocked population within the Nihotupu Reservoir, Waitakere Ranges, Auckland. Odour water of common bullies (*Gobiomorphus cotidianus*), a native fish often found in conjunction with inanga, was collected from eight fish ranging in size from 40 to 80 mm TL, also from a landlocked population within the Nihotupu Reservoir. Each species was housed in a separate bin containing 20 litres of fresh water. The presentation of each species odour water was mixed to ensure the juveniles were given attractive galaxiid odours after the presentation of common bully odours. Pilot studies were performed to determine an appropriate volume of odour water stimulant, i.e., the volume of odour stimulant was increased until juveniles showed an attraction, this gave odour volumes of 63 ml litre^{-1} for all adult species.

As juvenile koaro trials were performed the following season, a different set of adult fish were collected, one adult banded kokopu (220 mm TL), one adult koaro (194 mm TL), and six adult inanga (ranging from 60 to 100 mm TL) were used. All adult fish were taken from sea-run populations. Each species was held in a separate bin containing 30 litres of fresh water. As with inanga trials the presentation of adult odours was mixed ensuring inanga and banded kokopu odours were mixed between koaro odours. For each donor species, two volumes of odour stimulant were used, 6.25 and 50 ml litre^{-1}. These represent a relatively low and high concentration based on volumes used by Baker & Montgomery (2001).

To collect odour water, methods were adapted from Baker & Montgomery (2001). Fish were fed cultured whiteworms and left for an hour. Whiteworms were used to feed adult fish as being a live food source, any uneaten worms would aggregate and could be easily removed from the aquaria with minimal disturbance to the fish. A water change was then performed to remove any remnants of food with the tank refilled from the aged water supply used in the experimental apparatus. The fish were then left for 72 h for the juvenile inanga trials and 24 h for the juvenile koaro trials before the odour water was collected and measured into the appropriate volumes. That which was not used immediately, was frozen at –80°C. This ensured that fish were exposed to the same concentrations of chemicals present within the odour water for all 20 trials. All odour water was used within 2 days of freezing.

Otolith analysis

To determine if the koaro juveniles used in the study were sea-run fish that were trapped below the dam spillway, or were juveniles that could have originated from the landlocked population above the dam, an analysis of the strontium/calcium (Sr/Ca) ratio within the otoliths was performed. Sr/Ca ratios are higher when deposited in a marine environment compared with a freshwater environment (Kalish 1990; Tzeng 1996; Shen et al. 1998) and the ratios can be used as indicators of the environmental history of diadromous fish (Shen et al. 1998), determining if fish have had a marine phase. Otoliths were examined from six juvenile koaro used in attraction trials and seven adult koaro captured from Lilburne Stream (NZMS S12 035558), a tributary of the Mangatawhiri Reservoir. The otoliths were dissected from freshly killed and frozen fish. After removal, otoliths were dried, then embedded in an epoxy resin. Once the resin had set, otoliths were ground and polished to reveal the nucleus. To establish reference Sr/Ca ratios for a known sea-run fish, an otolith was examined from a juvenile inanga from the lower Waikato River (NZMS R12 730316).

Sr/Ca ratios were measured by particle-induced X-ray emission (PIXE; Markwitz et al. 1999) under a proton beam produced by a 3 MeV van der Graaf accelerator at the Rafter Laboratory, Institute for Geological and Nuclear Sciences, Lower Hutt, New Zealand. Ca X-ray lines were 3.69 keV, and Sr X-ray lines were 14.1 keV (Markwitz et al. 2000). For the Sr measurements, a high-resolution Si(Li) detector was placed at a backwards angle of 45°. A 75 µm
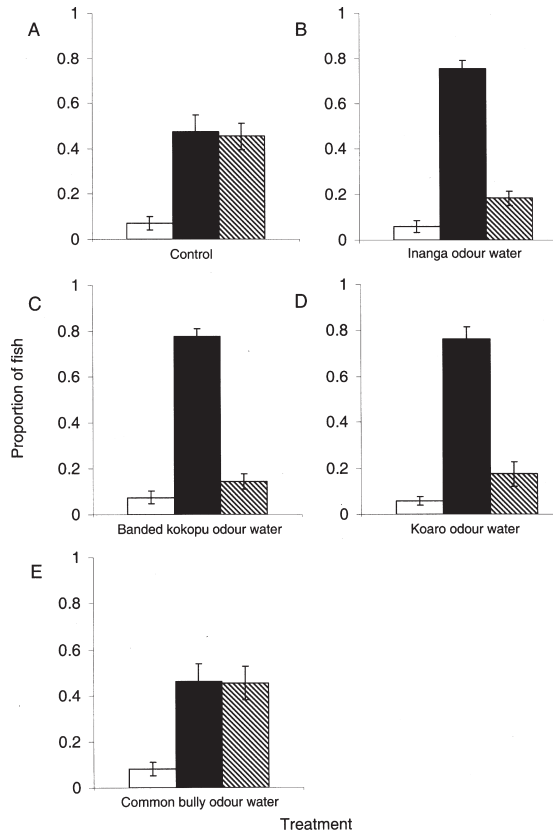
Fig. 2 Proportion of juvenile inanga (*Galaxias maculatus*) present in each chamber when subjected to odour water from various fish species. **A**, control, when no odour is added to either choice chamber (□, main chamber; ■, left chamber; ▨, right chamber); **B**, 63 ml litre^{-1} inanga odour water is added to one choice chamber; **C**, 63 ml litre^{-1} banded kokopu odour water is added to one choice chamber; **D**, 63 ml litre^{-1} koaro odour water is added to one choice chamber; **E**, 63 ml litre^{-1} common bully odour water is added to one choice chamber (□, main chamber; ■, odour chamber; ▨, non-odour chamber). Error bars represent ± one standard error.

aluminium window was placed in front of the detector to improve the signal-to-noise ratio of the Sr:Ca measurements. Area scans and line scans through the otolith cores were performed using integrated charges of typically 10°C. Pellets of $CaCO_3$ (NIST 610 standards) containing 1% and 10% $SrCO_3$ were used as standards.

RESULTS

Juvenile inanga

When trials were conducted in the absence of odour (Fig. 2A) there was no significant difference in the mean number of fish entering each of the choice chambers (Table 1). This shows no preference was exhibited towards either chamber.

When adult inanga, banded kokopu, or koaro odour water was added to one of the choice chambers (Fig. 2B–D), an attraction towards the odour chamber resulted, with a significantly higher number of fish entering the odour chamber compared with control trials ($P < 0.0001$, Table 1). Four and a half times more fish ($\pm$ 1.5 (1 standard error (SE))) entered the odour chamber than the non-odour chamber. Using a Kruskal-Wallis one-way ANOVA, there was no significant difference in the distribution of juveniles found in the odour, non-odour, or main chambers when inanga, banded kokopu, or koaro odours were presented ($P = 0.9669$).

When common bully odour water was added to a choice chamber (Fig. 2E), random entry was observed with no significant difference in the number of fish entering the two choice chambers. The number of fish entering each choice chamber or remaining in the main chamber was not significantly different to that found in control trials (Table 1).
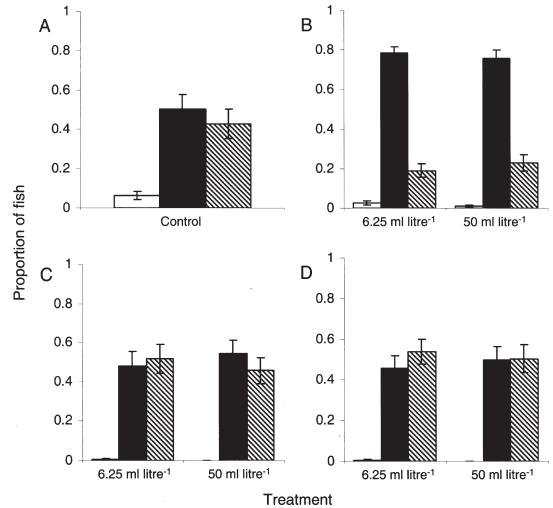
Fig. 3 Proportion of juvenile koaro (*Galaxias brevipinnis*) present in each chamber when subjected to odour water from various galaxiid species. **A**, control, when no odour is added to either choice chamber (□, main chamber; ■, left chamber; ◩, right chamber); **B**, 6.25 or 50 ml litre⁻¹ koaro odour water is added to one choice chamber; **C**, 6.25 or 50 ml litre⁻¹ inanga odour water is added to one choice chamber; **D**, 6.25 or 50 ml litre⁻¹ banded kokopu odour water is added to one choice chamber (□, main chamber; ■, odour chamber; ◩, non-odour chamber). Error bars represent ± one standard error.

Table 1 Chi-square analysis of the number of inanga (*Galaxias maculatus*) and koaro (*G. brevipinnis*) juveniles present in each chamber when exposed to various adult species odour water (values given to 4 significant figures). Sidak inequality was applied to each comparison, reducing the significance level for any individual comparison to $\alpha = 0.02$ to set the experiment-wise error rate at $\alpha = 0.05$.

Juvenile species	Experimental group	χ^2	d.f.	*P* value
Inanga	Control left versus control right	0.1684	1	0.4131
	Control versus inanga odour water	65.34	2	<0.0001
	Control versus banded kokopu odour water	81.48	2	<0.0001
	Control versus koaro odour water	70.16	2	<0.0001
	Control versus common bully odour water	0.3278	2	0.8488
Koaro	Control left versus control right	1.205	1	0.2727
	Control versus koaro 6.25 ml litre⁻¹ odour water	62.76	2	<0.0001
	Control versus koaro 50 ml litre⁻¹ odour water	53.66	2	<0.0001
	Koaro 6.25 ml litre⁻¹ odour water versus koaro 50 ml litre⁻¹ odour water	0.2563	2	0.8797
	Control versus banded kokopu 6.25 ml litre⁻¹ odour water	14.68	2	0.0006
	Control versus banded kokopu 50 ml litre⁻¹ odour water	13.92	2	0.0009
	Control versus inanga 6.25 ml litre⁻¹ odour water	17.69	2	0.0001
	Control versus inanga 50 ml litre⁻¹ odour water	15.66	2	0.0004
	Koaro 6.25 ml litre⁻¹ odour water versus inanga 6.25 ml litre⁻¹ odour water	109.2	2	<0.0001
	Koaro 6.25 ml litre⁻¹ odour water versus kokopu 6.25 ml litre⁻¹ odour water	95.78	2	<0.0001

Juvenile koaro

When no odour was added to either choice chamber (Fig. 3A), there was no significant difference in the number of fish entering either choice chamber (Table 1). This shows no bias is exhibited towards either chamber.

When 6.25 or 50 ml litre^{-1} adult koaro odour water was added to an upstream chamber, an attraction to the odour chamber resulted (Fig. 3B) with significantly more fish entering the odour chamber compared with control trials ($P < 0.0001$, Table 1). Over 4 times more fish (± 0.95 (1 SE)) entered the odour chamber compared with the non-odour chamber. There was no significant difference in the distribution of fish found in the odour, non-odour, or main chambers between the two odour volumes used (Table 1).

When 6.25 or 50 ml litre^{-1} of odour water from adult inanga or banded kokopu was added to an upstream chamber (Fig. 3C and D), no attraction towards the odour chamber was exhibited. Table 1 shows at both volumes, the distribution of fish was significantly different from control trials ($P = 0.0001$ and $P = 0.0004$ for inanga 6.25 and 50 ml litre^{-1} respectively and $P = 0.0006$ and $P = 0.0009$ for banded kokopu 6.25 and 50 ml litre^{-1} respectively) due to the reduced number of fish remaining in the main chamber. There was no significant difference in the distribution of fish in the odour, non-odour, or main chambers regardless of odour volume or species ($P = 0.8990$; Kruskal-Wallis one-way ANOVA). There was a large significant difference ($P < 0.0001$) in the distribution of fish entering each of the chambers when fish were exposed to banded kokopu or inanga odour water, compared with koaro odour water (Table 1).

The Sr/Ca ratios in the otoliths of juvenile and adult koaro were the same throughout their life history, with no evidence of an elevated core which might signify a period of marine residence (Fig. 4). However, an otolith from a 51 mm TL juvenile inanga from the Waikato River showed a central region with Sr/Ca ratios of c. 0.008.

DISCUSSION

The pheromone hypothesis as a method of stream selection in galaxiid fish was first suggested by Rowe et al. (1992). Baker & Montgomery (2001) provided further evidence for the role of pheromones as a migratory cue by demonstrating that banded
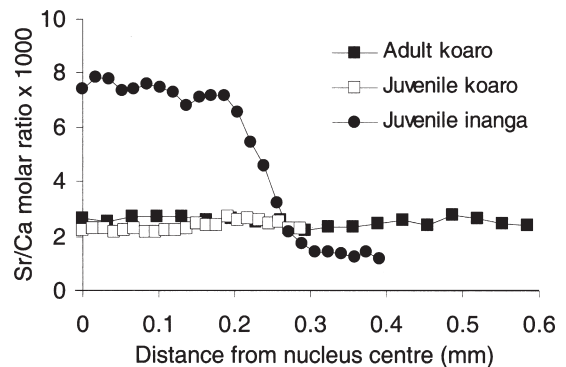

Fig. 4 Transects of strontium/calcium (Sr/Ca) ratios measured across otoliths taken from a juvenile koaro (*Galaxias brevipinnis*), an adult koaro (*G. brevipinnis*), and a juvenile inanga (*G. maculatus*) (one otolith from each fish). Each point represents a single measurement.

kokopu juveniles exhibited a species-specific attraction towards water-borne odours released by adult conspecifics. The present study has found that migratory koaro juveniles also exhibit a species-specific attraction to odours released by adult conspecifics. Although the use of pheromones by galaxiid juveniles in stream selection is yet to be tested in the field, the present study and work of Baker & Montgomery (2001) support the pheromone hypothesis in two species of galaxiid juveniles.

Laboratory results with koaro juveniles showed several behavioural differences from banded kokopu. Baker & Montgomery (2001) found that the migratory response of banded kokopu was reduced when they were exposed to relatively high concentrations of water containing adult odours (i.e., 9 ml litre^{-1}). A reduced migratory response was not found in juvenile koaro, even at 50 ml litre^{-1} odour water. Juvenile koaro also differed from banded kokopu in that they exhibited a much stronger rheotactic response to flowing water containing chemical cues. For example, koaro juveniles did not show any attraction to inanga or banded kokopu odour water, however, these odours stimulated greater upstream movement compared with control trials.

Koaro juveniles exhibit a marked desire for upstream movement over other galaxiid juveniles and both koaro and banded kokopu juveniles are known to climb vertical barriers by adhering to substrates using surface tension (McDowall 1990). When held in an aquarium, juvenile koaro will climb out of any opening in an upstream direction even

when a strong current flow is present (C. Baker pers. obs.). However, banded kokopu juveniles do not show such a pronounced upstream urge and only climbed out of aquaria when held in still water. The presence of chemical cues such as inanga and banded kokopu odours may provide a stimulatory cue which enhances the upstream movement of juvenile koaro compared with their upstream movement in tap water.

The comparison of otolith microchemistry in koaro and inanga, showed that the koaro juveniles tested were not sea-run fish and had instead reared within a freshwater environment. This suggests that they either belong to the landlocked population above the Mangatawhiri Dam, or that they recruited from larvae rearing in the lower Waikato River without going to sea. Although the koaro juveniles tested had not gone to sea, an attraction and discrimination to an adult sea-run fish was still inherent. This would be expected from landlocked fish as larvae use lakes for development and then juveniles migrate into lake tributaries in search of suitable adult habitat. Stream selection in lakes may therefore be as important as river selection for diadromous stocks. The Upper Mangatawhiri Dam was constructed in 1965, creating a landlocked population of koaro and banded kokopu for the past 37 years. This is an extremely small time frame on an evolutionary scale and therefore if lacustrine stocks exhibit a species-specific pheromonal attraction, it can be assumed that it will also occur in diadromous stocks.

Migratory inanga juveniles did not exhibit a species-specific attraction to adult odours as found in both koaro and banded kokopu, but rather a heterospecific galaxiid attraction. The attraction to galaxiid odours was also difficult to evoke, requiring a markedly higher volume of odour water compared with that used in attracting juvenile koaro or banded kokopu to adult odours. Baker & Montgomery (2001) demonstrated an attraction of banded kokopu juveniles with the addition of as little as 0.2 ml litre^{-1} of adult odour water. In the present study, 63 ml litre^{-1} was needed to stimulate an attraction of inanga juveniles to adult galaxiid odours. Given the lack of sensitivity displayed by juvenile inanga, it is unlikely that the galaxiid attraction exhibited would be used as a principal cue in stream and habitat selection.

Both banded kokopu and koaro differ from inanga in having an amphidromous life cycle, i.e., fish migrate annually from fresh water to sea water and vice versa, not for the purpose of breeding but for growth and development (McDowall 1988). Both banded kokopu and koaro are also selective in their habitat requirements (McDowall 1990), seeking specific habitats for growth to adulthood. Pheromones produced by adults inhabiting tributary streams may well be used to identify rivers and streams containing such areas of suitable and accessible habitat.

The inanga, however, is the only whitebait species described as catadromous as it migrates to estuaries to spawn (McDowall 1988). Inanga also differ from the other galaxiid species in age of maturity and lifespan. The banded kokopu, shortjawed kokopu, giant kokopu, and koaro are all thought to reach sexual maturity at c. 2–3 years of age and survive spawning for many years. Inanga generally reach sexual maturity at 1 year of age, with the majority of fish dying after spawning (McDowall 1990). As inanga are essentially an annual species, few adults are generally present in streams at the time of juvenile migrations to release pheromonal cues for juveniles to detect. Inanga are also less selective in their habitat requirements and are capable of colonising very diverse habitats. Fish will occupy swift and gentle flowing water, still water, clear water, or deeply brown swamp waters, cold or warm waters, waters with high or low pH, and are found in the open and in the forest (McDowall 1990). In this respect, inanga may not need to utilise pheromonal cues as a method of locating suitable and accessible habitat.

Other studies on catadromous species have dealt with eels of the genus *Anguilla*. Migratory elvers show a strong attraction to freshwater streams containing odours originating from terrestrial and freshwater microbes (Miles 1968; Sorensen 1986; Tosi & Sola 1993). The odours of adult conspecifics are only weakly attractive and stream odours are preferred (Sorensen 1986). Inanga may also prefer chemical cues relating to habitat characteristics in stream selection over those cues released by adults.

In comparison, studies with anadromous or amphidromous species show a strong attraction of migrating fish to species-specific or population-specific pheromonal odours (Nordeng 1971; Quinn et al. 1983; Groot et al 1986; Quinn & Tolson 1986; Keefe & Winn 1991; Bjerselius et al. 2000; Baker & Montgomery 2001). Thus, pheromone-based selection of rivers and streams appears to be more evident for anadromous and amphidromous species, whereas habitat odours may be more important for catadromous species.

Other whitebait species such as the giant kokopu and the shortjawed kokopu are also assumed to share the amphidromous life cycle exhibited by both

banded kokopu and koaro (McDowall 1990) and as these species are also selective in habitat, they may also show a species-specific attraction to adult odours. Identification of a migratory cue used by amphidromous galaxiids could be used in the conservation of these rare species as well as for population enhancement of both koaro and banded kokopu.

In summary, juvenile koaro exhibited a species-specific attraction to adult odours consistent with the pheromonal attraction previously described for banded kokopu juveniles. Juvenile inanga were capable of discriminating galaxiid odours from those released by the common bully. These results strengthen the hypothesis that pheromonal cues may be used by amphidromous galaxiids for selection of streams where adult habitat is present.

ACKNOWLEDGMENTS

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