

Water temperature and upstream migration of glass eels in New Zealand: implications of climate change

Stella M. August · Brendan J. Hicks

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Abstract Glass eels migrating upstream in a New Zealand river showed a clear preference for water temperatures between 12 and 20°C, with an optimum of 16.5°C. Water temperatures <12°C and >22°C almost completely inhibited migration, which implies that warmer temperatures associated with global climate change might have a detrimental impact on glass eel recruitment in their current ranges. We established this by trapping glass eels of shortfin, *Anguilla australis*, and longfin, *A. dieffenbachii*, eels nightly from September to November. Eels caught in 2001 (50,287) outnumbered those caught in 2002 (19,954); shortfin glass eels dominated catches in both years, comprising 91–93% of the catch. Longfins were larger than shortfins, and size and pigmentation in both species increased as the seasons progressed. Temperatures within the migratory season in 2001 showed ~14-day intervals between maxima that appeared to be associated with the new and full moons.

Keywords *Anguilla australis* · *Anguilla dieffenbachii* · Freshwater eel · Invasion

Introduction

Water temperature is one of the environmental cues that has been implicated as a cue for the start and intensity of the upstream migration of glass eels (Jellyman 1977; Tongiori et al. 1986; Chen and Chen 1991; Pease et al. 2003). To investigate this, we observed the upstream spring migration of glass eels in the Tukituki River, Hawke Bay, New Zealand. Our objectives were (1) to examine the association between environmental variables and numbers of migrants and (2) to investigate species composition, size, condition, and pigmentation. We maximised the nights trapped as much as weather conditions permitted to elucidate the factors influencing recruitment.

Two species of anguillid eel are native to New Zealand; the longfin eel, *Anguilla dieffenbachii* (Gray) is endemic, but the shortfin eel, *Anguilla australis* (Richardson) also occurs in south-eastern Australia, Tasmania, New Caledonia, Lord Howe Island, and Norfolk Island (McDowall 2000). These eels support important commercial, traditional, and recreational fisheries. Mature anguillid eels migrate to oceanic spawning grounds where they spawn and die, but the precise location of the spawning grounds of New Zealand's shortfin and longfin eel remain unknown. Shortfin eels are believed to spawn in the region east of Tonga (Jellyman 1987), and recent tagging studies have proposed that long-

S. M. August (✉) · B. J. Hicks
Centre for Biodiversity and Ecology Research,
Department of Biological Sciences, School of Science
and Engineering, The University of Waikato, Private
Bag 3105, Hamilton, New Zealand
e-mail: stella.august@fish.govt.nz

finned eels might spawn east of New Zealand (Jellyman and Tsukamoto 2002) or east of New Caledonia (Jellyman and Tsukamoto 2005). Leptocephali larvae travel back to New Zealand and metamorphose into glass eels when they reach the continental shelf (Jellyman 1987; McCleave et al. 1987). Unpigmented glass eels 55–70 mm long migrate upstream from the sea into the rivers and streams at night (Jellyman 1977, 1979).

Each year from late winter to early summer, large numbers of shortfin and longfin glass eels enter the rivers and streams of New Zealand (Jellyman 1979). Low numbers of glass eels arrive during August, increasing to a maximum in September and October, followed by a decline in November and December (Jellyman 1977, 1979; Jellyman and Todd 1982; Jellyman et al. 1999; Jellyman and Lambert 2003). Migration of glass eels into fresh water from the sea occurs mainly at night (Jellyman 1977; Jellyman and Todd 1982; Silberschneider et al. 2001), beginning shortly after sunset, peaking at some point in the evening, and then declining until the run ceases (Jellyman 1977).

After the initial invasion into fresh water from the sea, upstream migration of the glass eels is delayed in tidal or estuarine areas while the eels undergo physical and behavioural transitions (Jellyman 1977, 1979). At entry into fresh water, longfin glass eels are longer and more pigmented than shortfin glass eels, and length and weight decline in both species as the season progresses (Jellyman 1977, 1979; Jellyman and Ryan 1983; Jellyman and Lambert 2003). The species composition of glass eels on the east coast of New Zealand is dominated by shortfins, whereas longfin eels form the majority of the glass eels in west coast rivers (Jellyman et al. 2002).

Materials and methods

The study site (39°36′02.44″ S, 176°56′12.55″ E) was 600 m from the coast in the lower tidal reaches of the Tukituki River (2,496 km² drainage area), situated in Hawke Bay on the east coast of the North Island, New Zealand (Fig. 1).

Glass eels were trapped nightly for the period 11 September–25 November in 2001, and 9 September–4 December in 2002. Trapping occurred on 59 nights out of the available 76 nights (78%) in 2001, and total of 67 nights out of 87 (77%) in 2002.

A trap net (1-mm mesh) with a mouth 1.5 m wide by 1 m deep was set on cobble substrate in water 0.50–0.75 m deep flowing at about 0.1–0.3 m s⁻¹ about 3–7 m from the water's edge. Two 1-mm mesh screens (1.5 m × 1 m) were used on the shore side to stop glass eels from migrating past the net, and a cobble weir was used as necessary to augment the screens. Fluctuations in river height of up to 6 m associated with tide phase and river flows necessitated moving the net, screens, and weir to maintain roughly constant water depth and velocity at the trap site.

Fishing began approximately 1 h before sunset, and the time spent fishing each night was determined by the catch rate of glass eels, concluding when glass eel numbers decreased over three successive 45-min trapping periods. When few glass eels were caught, or when a decline was not observed, we spent between 3.5 and 4.5 h fishing each night. The net was lifted every 45-min and the glass eels and by-catch were removed. The net was then set again and left to fish while the glass eels and by-catch from the previous capture were counted and recorded.

The eel species were not distinguishable in the field. To estimate the proportion of each species in the entire catch, a subsample of approximately 6 glass eels was removed from the catch after each 45-min interval if catches exceeded 6 eels. Each night, approximately 25 glass eels were retained alive for species identification in the laboratory. Before identification, glass eels were anaesthetised with a drop of clove oil (about 0.2 ml) dissolved in 500 ml of water. Individual total lengths were measured to the nearest 0.5 mm and individual weights were recorded in grams to three decimal places after surface water was removed with absorbent paper. Pigmentation was recorded based on a variation of Strubberg (1913; in Jellyman et al. 1999). Glass eels with a pigmentation stage equal to or less than 6_{A23} were considered “newly arrived” and those with a pigmentation stage

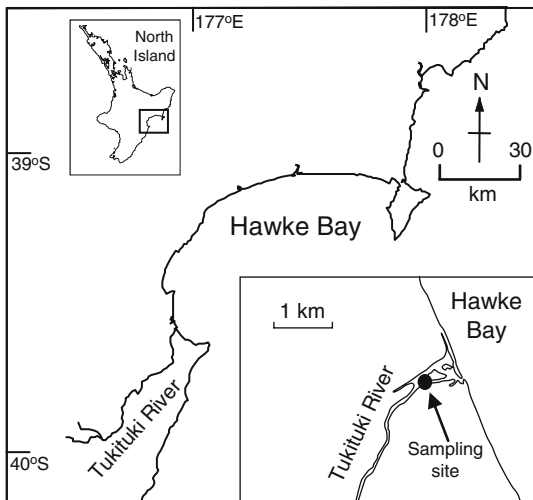


Fig. 1 The sampling site on the Tūkituki River, Hawke Bay, New Zealand

equal to or greater than 6_{A24} were considered “previously arrived” (Chisnall et al. 2002; Jellyman et al. 2002).

Most glass eels survived anaesthesia and examination and were released back into the Tūkituki River 0.5 km above the sampling site on the following night. Daily means of total lengths for each species were determined. Analysis of covariance (ANCOVA) was conducted to determine the difference in total length and condition factor between species (shortfin and longfin) and year (2001 and 2002). Time in days since the start of the migration season was used as a covariate. All statistical analyses were carried out using SYSTAT version 10.

River water temperature was measured at the sampling site and sea water temperature was measured at the mouth of the Tūkituki River once at commencement of fishing each night. River flow was measured at 30-min intervals about 10 km upstream from the sampling site; no major tributaries joined the river between these two points, and there were no obstructions. Wind, barometric pressure and solar radiation were measured at Lawn Road, Clive, about 5 km from the sampling site. All times are given as New Zealand Standard Time (NZST).

Results

Environmental variables and numbers of migrants

River and sea water temperatures and river flow were the environmental variables most associated with catches of migrating glass eels (Table 1), but river and sea water temperatures were themselves highly correlated. Water temperatures were also positively related to solar radiation, and negatively related to river flow. Glass eel numbers were negatively correlated to river water temperature in 2001, but positively correlated in 2002. River flow had no association with glass eel migration in 2001, but had a negative correlation in 2002 (Table 1). River flow increases were often associated with reduced catches, and the peak runs of glass eels occurred when river flow was low or normal ($\leq 22 \text{ m}^3 \text{ s}^{-1}$). Minimum river flows were similar in both years ($11 \text{ m}^3 \text{ s}^{-1}$), but the maximum river flow within the trapping periods was greater than in 2002 ($102 \text{ m}^3 \text{ s}^{-1}$) than in 2001 ($66 \text{ m}^3 \text{ s}^{-1}$; Figs. 2 and 3). A flood immediately preceding trapping in 2001 peaked at $116 \text{ m}^3 \text{ s}^{-1}$.

Moon phase, though sometimes associated with glass eel invasion, was confounded by other environmental variables. In 2001, the largest nightly run totalling 18,619 glass eels occurred two nights after a new moon (Fig. 2). Only one spring tide occurs each month on the new moon at the Port of Napier, East Coast, New Zealand (NIWA, 2005). The largest glass eel run coincided with the largest spring tide for the spring months in 2001 (Fig. 2). In 2002, peak seasonal catches of glass eels occurred twice in October, on both occasions 3–4 days after a new or full moon (Fig. 3). Moonlight appeared to have no effect on glass eel recruitment; glass eels migrated into the Tūkituki River in varying degrees of moonlight ranging from complete darkness associated with new moons to bright moonlight during full moons.

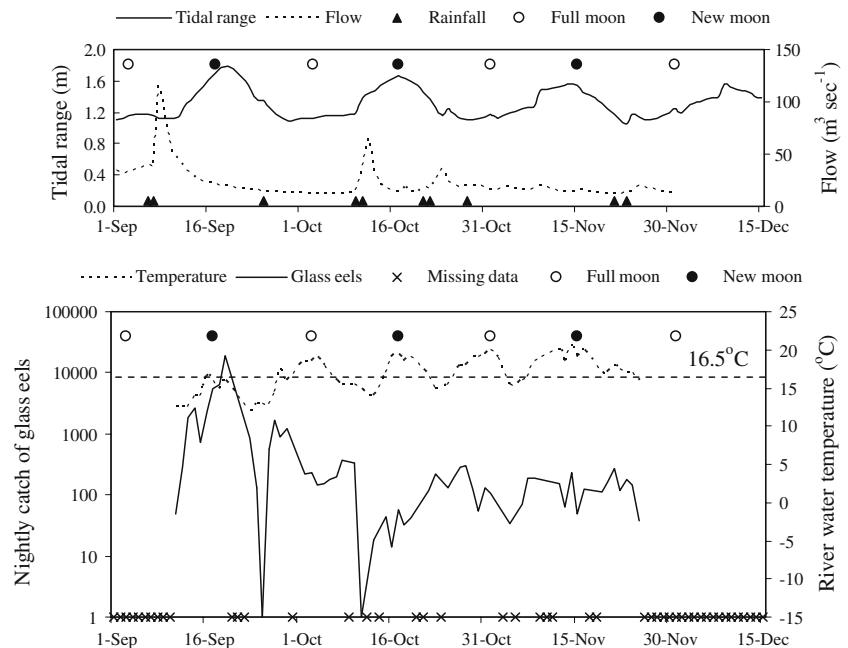
Glass eels entering the Tūkituki River showed a preference for moderate river water temperatures, avoiding extreme low and high temperatures. In 2002, when river water temperatures were mostly $<18^\circ\text{C}$ (Fig. 3), numbers of glass eels

Table 1 Spearman rank correlations between the daily total number of glass eels (*Anguilla australis* and *A. dieffenbachii*) migrating into the Tukituki River, Hawke Bay, New Zealand and environmental variables

| Variables | 1. | 2. | 3. | 4. | 5. | 6. | 7. |
|-------------------------------------------------------------|---------------|---------------|---------------|---------------|---------------|---------------|-------|
| <i>A. 2001</i> | | | | | | | |
| 1. Daily total number of glass eels | 1.000 | | | | | | |
| 2. Daily total rainfall (mm) | -0.148 | 1.000 | | | | | |
| 3. Solar radiation ($\text{MJ m}^{-2} \text{ day}^{-1}$) | -0.083 | -0.527 | 1.000 | | | | |
| 4. Daily average river flow ($\text{m}^3 \text{ s}^{-1}$) | -0.045 | 0.179 | -0.313 | 1.000 | | | |
| 5. River water temperature ($^{\circ}\text{C}$) | -0.297 | -0.042 | 0.560 | -0.379 | 1.000 | | |
| 6. Sea water temperature ($^{\circ}\text{C}$) | -0.473 | 0.130 | 0.522 | -0.195 | 0.878 | 1.000 | |
| 7. Barometric pressure (hPa) | 0.247 | -0.299 | -0.066 | 0.138 | -0.446 | -0.572 | 1.000 |
| <i>B. 2002</i> | | | | | | | |
| 1. Daily total number of glass eels | 1.000 | | | | | | |
| 2. Daily total rainfall (mm) | -0.040 | 1.000 | | | | | |
| 3. Solar radiation ($\text{MJ m}^{-2} \text{ day}^{-1}$) | 0.411 | -0.494 | 1.000 | | | | |
| 4. Daily average river flow ($\text{m}^3 \text{ s}^{-1}$) | -0.519 | -0.002 | -0.406 | 1.000 | | | |
| 5. River water temperature ($^{\circ}\text{C}$) | 0.420 | -0.309 | 0.485 | -0.545 | 1.000 | | |
| 6. Sea water temperature ($^{\circ}\text{C}$) | 0.340 | -0.068 | 0.306 | -0.454 | 0.707 | 1.000 | |
| 7. Barometric pressure (hPa) | -0.020 | -0.041 | -0.023 | 0.374 | -0.143 | 0.068 | 1.000 |

Bold numbers indicate correlations that are significant at $P < 0.050$

Fig. 2 Daily catch of shortfin and longfin glass eels (*Anguilla australis* and *A. dieffenbachii*) migrating into the Tukituki River, Hawke Bay, New Zealand in 2001 compared to lunar phase, tidal range, mean daily river flow, rainfall events $>5 \text{ mm}$ per day (\blacktriangle), and river water temperature. X on baseline indicates missing data

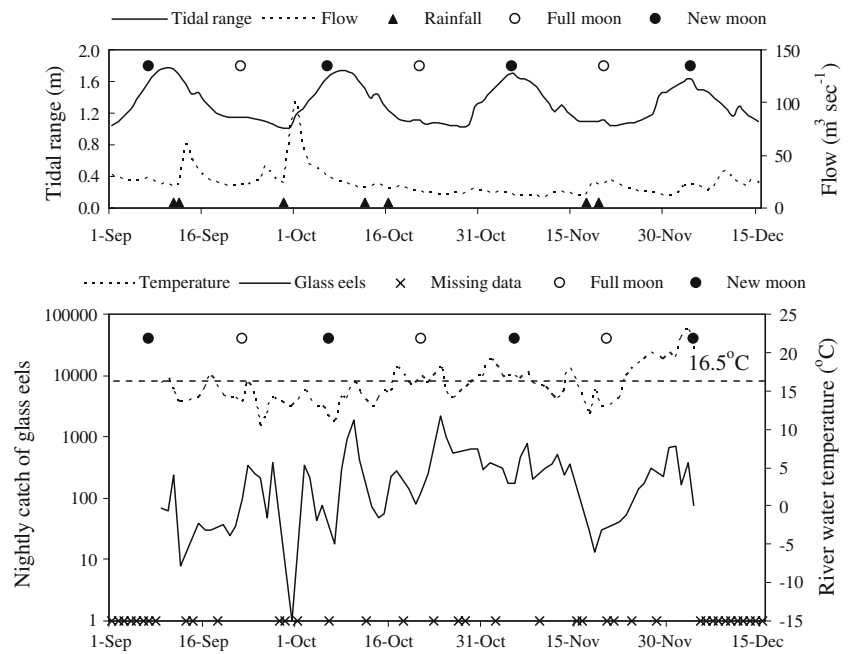


entering the river were positively correlated with water temperature (Table 1). A drop of 3–6 $^{\circ}\text{C}$ in river water temperature over 2–3 days reduced upstream migration of glass eels in 2002 on three occasions (Fig. 3). Decreases in river water temperature below 12 $^{\circ}\text{C}$ resulted in very few glass eels being caught in both years. In 2001, when river water temperatures often exceeded 18 $^{\circ}\text{C}$,

the highest temperatures also seemed to reduce glass eel numbers (Fig. 2).

River water temperature in 2002 was cooler at the start of the glass eel migration season than in 2001 but warmer at the end, ranging from 12.0 to 20.5 $^{\circ}\text{C}$ in 2001 (Fig. 2) and from 10.5 to 23.0 $^{\circ}\text{C}$ in 2002 (Fig. 3). Despite the smaller temperature range in 2001, mean river water temperature was

Fig. 3 Daily catch of shortfin and longfin glass eels (*Anguilla australis* and *A. dieffenbachii*) migrating into the Tukituki River, Hawke Bay, New Zealand in 2002 compared to lunar phase, tidal range, mean daily river flow, rainfall events >5 mm per day (▲), and river water temperature. X on baseline indicates missing data



warmer in 2001 ($16.7 \pm 0.6^\circ\text{C}$; mean \pm 95% confidence interval) than in 2002 ($15.7 \pm 0.6^\circ\text{C}$). In 2001, river water temperature showed a pronounced 14-day period in phase with the new and full moons (Fig. 2).

River flow and water temperature examined together showed that catches were greatest at intermediate low flows ($<50 \text{ m}^3 \text{ s}^{-1}$) and water temperatures of about 13°C in 2001 and 16°C in 2002. The mean of average daily river flow was similar in both years ($17.9 \text{ m}^3 \text{ s}^{-1}$ in 2001, and $21.6 \text{ m}^3 \text{ s}^{-1}$ in 2002). When the data for both years were combined into a habitat suitability curve after the method of Bovee and Milhous (1978), there was a distinct optimum temperature of glass eel migration at 16.5°C (Fig. 4). River water temperatures $<12^\circ\text{C}$ and $>22^\circ\text{C}$ suppressed glass eel migration almost entirely.

Species composition, size, condition, and pigmentation

Shortfins comprised 91% of the 1,465 glass eels subsampled in 2001 and 93% of the 1,613 subsampled in 2002 (Table 2). No longfin glass eels were subsampled in December 2002 (Table 2). In 2001, a total of 50,287 of both

species of glass eel were caught, whereas fewer eels entered the river in 2002 (19,954; Table 2). The peak month of entry was earlier in 2001 (September) than in 2002 (October; Table 2). In 2001, 88% of the year’s total number of trapped glass eels was caught in September. Only 8% of this total was trapped in October in 2001. In contrast, in 2002 only 9% of the year’s total number of trapped glass eels was caught in September, and 54% (the highest monthly percentage) was caught in October (Table 2).

The total nightly catch of glass eels migrating into the Tukituki River varied throughout the arrival season from 1 to 18,619 in 2001 and from 0 to 2,205 in 2002. As the seasons progressed, the time each night when the most number of glass eels were caught advanced with the advancing time of sunset (Fig. 5). Irrespective of the time of sunset, glass eels began to enter the trap about 45 min before sunset, as light levels decreased, and numbers peaked 1–2 h after sunset. The duration of the migration decreased through the season, finishing approximately 5.25 h after sunset in September, 4.50 h after sunset in October, and 3.75 h after sunset in November.

Longfin glass eels were larger than shortfins, and length of both species increased as the season

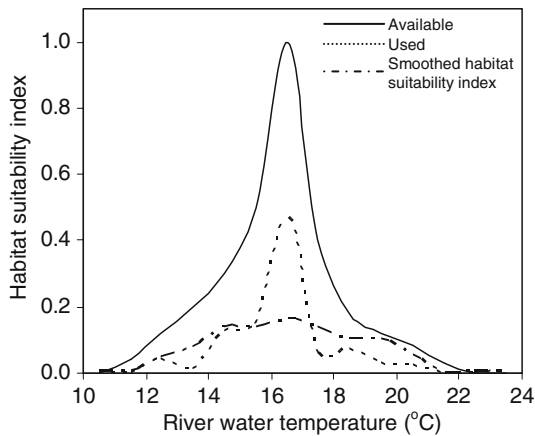


Fig. 4 Temperature preference for river water temperature of shortfin and longfin glass eels (*Anguilla australis* and *A. dieffenbachii*) migrating into the Tukituki River, Hawke Bay, New Zealand in spring 2001 and 2002

progressed (Table 3). In 2001, the difference in length between longfin and shortfin glass eels became greater with time. Longfin glass eels were the same size as shortfins in September, but increased in length faster as the season progressed and were longer than shortfins by November (ANCOVA, $P = 0.022$, $F_{1,93} = 5.39$). In 2002, both species increased in length at the same rate ($P = 0.131$, $F_{1,107} = 2.32$), but longfins were larger than shortfins (Table 3). Both species were larger in 2001 than in 2002, and increased in length at a greater rate in 2001 than in 2002 ($P < 0.001$, $F_{1,119} = 25.78$ for shortfins; $P < 0.001$, $F_{1,81} = 17.00$ for longfins).

The majority of subsampled glass eels (98–99%) were classified as “newly arrived” by their

pigmentation (between stages 5_B and 6_{A23}). Increased pigmentation was observed in both species of glass eel as the seasons progressed, and modal pigmentation stages of each species showed monthly differences between years (Fig. 6). Longfins were more pigmented than shortfin glass eels, suggesting earlier arrival than shortfins. Both species were less pigmented in November 2001 than in November 2002, suggesting earlier arrival in 2001.

Discussion

Environmental variables and numbers of migrants

We propose an optimum temperature for upstream migration of New Zealand glass eels (*A. australis* and *A. dieffenbachii*) of 16.5°C. This implies that warmer temperatures associated with global climate change might have a detrimental impact on glass eel recruitment. Our study appears to partially resolve the conflict between the variable responses shown by glass eels to moon phase. Water temperature itself was closely related to lunar phase in 2001, with temperature peaks occurring on new and full moons. The one new moon and spring tide in September 2001 that was associated with a very large run of glass eels coincided with a rapid increase in river water temperature.

Glass eels are very sensitive to changes in water temperature of as little as 1°C (Kim et al.

Table 2 Number of days fished each month and monthly totals of two glass eel species (shortfin, *Anguilla australis* and longfin, *A. dieffenbachii*) migrating into the Tukituki

River, Hawke Bay, New Zealand in 2001 and 2002 estimated from monthly subsamples

| Month | 2001 | | | | 2002 | | | |
|-------|-------------|---------------------|--------------------|--------|-------------|---------------------|--------------------|--------|
| | Days fished | Number of shortfins | Number of longfins | Total | Days fished | Number of shortfins | Number of longfins | Total |
| Sept | 16 | 39,618 | 4,402 | 44,020 | 17 | 1,714 | 190 | 1,904 |
| Oct | 25 | 3,493 | 460 | 3,953 | 24 | 9,845 | 974 | 10,819 |
| Nov | 18 | 2,152 | 162 | 2,314 | 22 | 5,662 | 236 | 5,898 |
| Dec | No trapping | – | – | – | 4 | 1,333 | 0 | 1,333 |
| Total | 59 | 45,263 | 5,024 | 50,287 | 67 | 18,554 | 1,400 | 19,954 |

–, Missing data

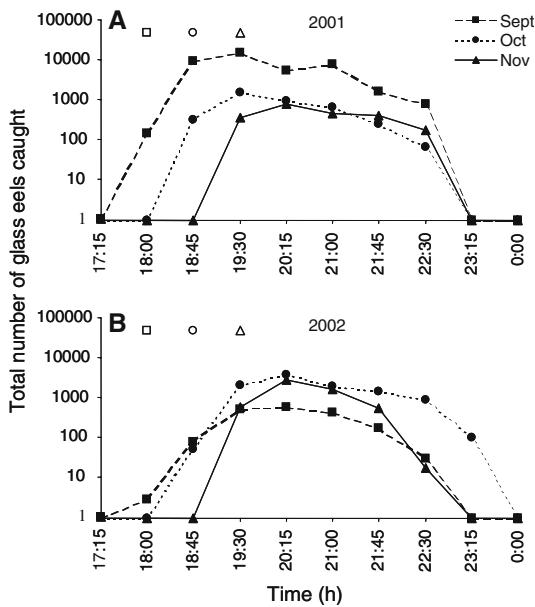


Fig. 5 Proportion of glass eels (*Anguilla australis* and *A. dieffenbachii*) migrating into the Tukituki River, Hawke Bay, New Zealand, in 45-min intervals each night during the migration seasons in 2001 and 2002. Open symbols indicate the mean time of sunset for each month (NB. The data for December 2002 have been omitted)

2002). Shortfin glass eels, *A. australis*, in Australia recruited to the Hacking River estuary and into fresh water when water temperatures were <18.5°C (Pease et al. 2003). Shortfin glass eels in Australia seem to prefer cooler temperature conditions and have a more restricted seasonal migration period than Australian longfin eels, *A. reinhardtii*, which migrated throughout the year, including at times when water temperatures reached 25°C (Pease et al. 2003). Sorensen and Bianchini (1986) found a link between water temperature and migration. For incompletely

pigmented elvers of American eels, *A. rostrata*, the onset of migration coincided with an increase in water temperature from 12 to 19°C over a week. This is similar to the lower thresholds for migration of American glass eels of 11°C (Helfman et al. 1984) and 12°C (Smith 1955). The migration of elvers and juvenile European eels into the rivers Severn and Avon, England, was also positively related to water temperature up to 20°C (White and Knights 1997). Jellyman (1977) found no evidence of a threshold temperature for entry of shortfin or longfin eels into New Zealand fresh waters, but suggested that sudden cold temperatures interrupted migrations. At temperatures lower than 14°C, acclimation temperatures are important (Tongiori et al. 1986). A threshold water temperature of 14–16°C was the statistically most robust predictor of elver migration in *A. anguilla* (White and Knights 1997), while Jessop (2003) proposed river temperatures of 10–12°C as thresholds for migrations of elvers of American eels in Nova Scotia.

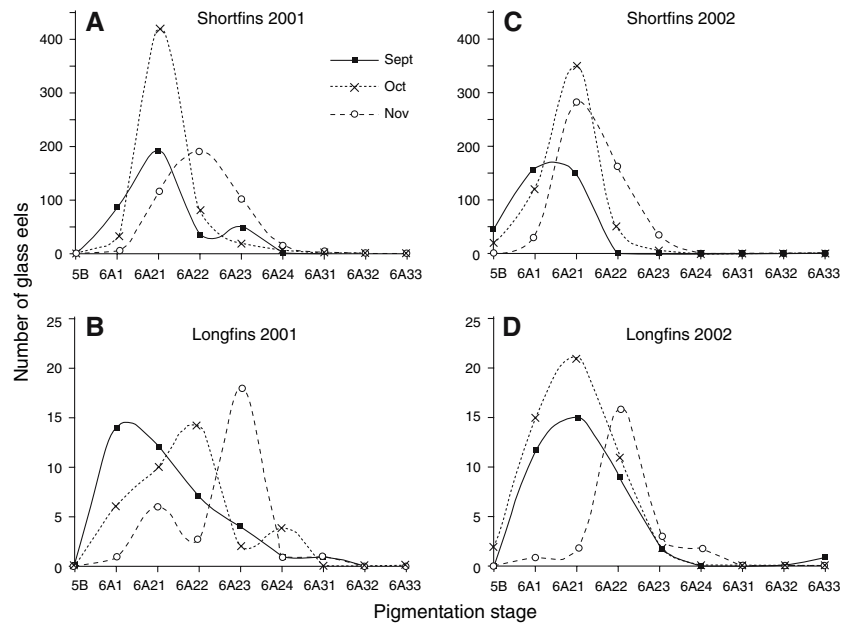
There was significant interannual variation in the river water temperature and the number of glass eels caught in 2001 and 2002. During the warmer spring in 2001 when river water temperatures frequently exceeded 18°C, glass eel catches were negatively correlated with river water temperature. In the cooler spring of 2002 when temperature maxima in were mostly below 18°C, glass eel catches were positively correlated with river water temperature. Increases in river water temperature stimulated migration resulting in the observed positive correlation. We suggest that the temperature maxima (18–20°C) in 2001 exceeded the optimal temperature range suitable for glass eel migration.

Table 3 Relationship between daily mean length of shortfin (*Anguilla australis*) and longfin (*A. dieffenbachii*) glass eels and progression of the migration season for the Tukituki River, Hawke Bay, New Zealand in 2001 and 2002

| Species | <i>N</i> | <i>b</i> | <i>a</i> | <i>r</i> ² | <i>P</i> |
|-------------|----------|----------|----------|-----------------------|----------|
| <i>2001</i> | | | | | |
| Shortfins | 57 | 0.121 | 53.3 | 0.887 | <0.001 |
| Longfins | 40 | 0.155 | 53.4 | 0.721 | <0.001 |
| <i>2002</i> | | | | | |
| Shortfins | 66 | 0.084 | 53.0 | 0.832 | <0.001 |
| Longfins | 45 | 0.062 | 58.6 | 0.266 | <0.001 |

Least-squares regression equation $Y = a + bX$, where *Y* = daily mean length (mm) and *X* = days since 1 August

Fig. 6 The number and pigmentation stages of glass eels (shortfin, *Anguilla australis* and longfin, *A. dieffenbachii*) migrating into the Tukituki River, Hawke Bay, New Zealand in September, October, and November in 2001 and 2002 (NB. The data for December 2002 have been omitted)



Water temperature can affect the swimming ability of larval fish by effects on both metabolism and the kinetic viscosity of water (Hunt von Herbing 2002). Acclimation temperature also affects the temperatures selected by glass eels (Tongiori et al. 1986; Chen and Chen 1991). Migratory behaviour of larval fish may also be regulated by interacting physiological and environmental factors (body condition, water temperature and salinity) as Edeline et al. (2006) suggest for glass eels. In whitebait, a delayed larval stage of New Zealand inanga, *Galaxias maculatus*, that migrates upstream in spring, the water temperature associated with the greatest swimming speed (17°C; Bannon and Ling 2004) was similar to the 16.5°C optimal temperature we propose for glass eels. River water temperatures <12°C and >22°C depressed glass eel catches in our study irrespective of other prevailing environmental conditions.

Periodicity in numbers of migrants corresponding to tidal currents can be caused by delays while glass eels rest in tidal areas (Ciccotti et al. 1995). Though some studies have shown links between moon phase, especially the new moon and peak migration of glass eels (e.g., Jellyman and Lambert 2003), it is not clear whether moon phase or some associated environmental factor such as tidal currents and selective tidal transport was the real cue for migration (Sugeha et al. 2001). Glass eels seem

to have no innate response to moon phase independent of other environmental factors, as wild glass eels of *A. japonica* held in laboratory did not exhibit lunar cycles of activity (Dou and Tsukamoto 2003). Initiation of the nightly migration by the onset of darkness, and the duration of the migration (4–5 h) is consistent with the activity observed under controlled lighting conditions (Dou and Tsukamoto 2003). In our study, varying levels of darkness also initiated the nightly glass migration, as the onset of migration became progressively later with the seasonal delay in sunset. The duration of the glass eel run reduced from 5.25 h in September to 3.75 h by November.

River flow was negatively correlated with numbers of migrating glass eels in 2002 but showed no association in 2001, probably because river flow within the period of trapping was more variable in 2002 than in 2001. *A. rostrata* elvers used the boundary layer to maximise distance swum and to minimise energy expenditure; the time spent resting in the substrate increased at higher water velocities (Barbin and Krueger 1994). Increased rainfall and high river flow appeared to stimulate glass eel migration, but heavy rainfall and extreme high river flows inhibit migration (Domingos 1992). In our study, high river flows (>60 m³ s⁻¹) depressed glass eel catches.

Species composition, size, condition, and pigmentation

In contrast to previous studies (Jellyman 1977, 1979; Jellyman and Ryan 1983; Jellyman and Lambert 2003), the size and condition of glass eels in our study increased throughout the arrival season. Longfins in the Tukituki River were larger than shortfins in both years, consistent with other studies (Jellyman 1977, 1979; Chisnall et al. 2002; Jellyman and Lambert 2003).

Limited pigmentation and active swimming suggest that the glass eels migrating into the Tukituki River were newly recruited each night. Trapped glass eels always swam upstream immediately upon released, supporting this conclusion. Jellyman (1979) found that there were no physical or behavioural differences that distinguished the species of glass eel during capture, suggesting that the proportions of both species of glass eels trapped each night were representative of the numbers of each species migrating into the Tukituki River.

Progression of pigmentation in our study during the season supports the hypothesis that new eels were caught each night. Pigmentation generally advances during the arrival season in New Zealand (Jellyman 1977, 1979; Jellyman et al. 1999; Chisnall et al. 2002), and Australia (Sloane 1984). Glass eels caught in the Tukituki River were less pigmented than many northern hemisphere studies, where the transition from glass eel to pigmented elver appears to take place before entry into fresh water (e.g., Dutil et al. 1989; White and Knights 1997). The shortness of the Tukituki River estuary (<1 km) may account for this difference.

Shortfins dominated the glass eel recruitment into the Tukituki River, which is consistent with the predominance of shortfin eels (81%) in samples of the commercial catch in the North Island (Speed et al. 2001). In the South Island, however, longfin eels comprised 81% of the commercial catch (Speed et al. 2001), and Jellyman et al. (2002) found no evidence of declining longfin recruitment. The pastoral development of the lower Tukituki River might have influenced the high proportion shortfin glass eels, as this species shows more of a preference for water

from pastoral streams than longfin eels (McCleave and Jellyman 2002).

The extent to which nightly catches of glass eels reflected real fluctuations in numbers of migrants depends on trap efficiency, which we did not estimate. However, visual observations suggested that no more than 5% of the migrating glass eels escaped entrapment. The reaction of benthic fish to floods was to move with the river margin and maintain constant depth (Jowett and Richardson 1994). Fish swimming in the water column such as inanga, *Galaxias maculatus* (Jennyns), tend to travel in consistent water velocities rather than at constant depths (I. G. Jowett, NIWA, Hamilton, personal communication). By maintaining our trap in consistent water depths and velocities as the water level rose and fell, we accommodated the behavioural responses of fish to tidal fluctuations and increases or decreases in river flow.

The number of shortfin and longfin glass eels migrating into the Tukituki River followed the arrival pattern found by other studies on glass eels in New Zealand. The seasonal arrival pattern of glass eels into rivers and streams of New Zealand occurs between late July and December, peaking in September and October (Jellyman 1977, 1979; Jellyman and Todd 1982; Jellyman et al. 1999; Chisnall et al. 2002). Densities of glass eels migrating into the Tukituki River were highest in September, declining in October and further still in November in 2001. In 2002, densities were low in September, highest in October, decreasing in November and December. It is likely that glass eel recruitment into the Tukituki River started before sampling started in both 2001 and 2002.

Summary

Variation between years in recruitment of glass eels may be regulated by interacting environmental influences, but water temperature appears to be an overriding factor. The occasional link that we observed between water temperature and lunar phase offers a plausible physiological mechanism for the variable association between lunar phase and glass eel migrations in the Tukituki

River and possibly worldwide. The generality of the negative effects of high water temperatures on glass eel invasions, with its implications for global climate change, remains to be confirmed.

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