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Estuarine habitat preferences of *Anguilla australis* and *A. reinhardtii* glass eels as inferred from laboratory experiments

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Synopsis

We tested the habitat preferences of *Anguilla australis* (shortfin) and *A. reinhardtii* (longfin) glass eels using circular tanks in an aquarium, containing four types of estuarine habitat (sand, mud, rocks/cobbles and seagrass). Shortfin eels either showed a tendency to occur in heterogeneous habitats, or in rocks/cobbles. Longfin glass eels showed a significant preference for rocks/cobbles in both experiments. Tests on shortfin and longfin glass eels in tanks with only rocks/cobbles available showed that eels were not clumped, indicating that individuals select habitat for re-settlement independently. Therefore, we assumed that the uneven distribution of glass eels observed in the habitat type experiments were the result of habitat preference. Given a choice of habitats in tank experiments, shortfin and longfin glass eels preferred habitats containing structure, and in particular, rocks/cobbles.

Introduction

Spatial variations in the distribution of fish and aquatic invertebrates partly reflect their behavioural responses to various aspects of habitat quality (such as type of substratum, availability of refugia and food resources) or to post-settlement mortality. Environments studied in this regard include coral reefs (Shulman 1985, Hixon & Beets 1993, Booth & Beretta 1994), estuaries (Kenyon et al. 1997, Laegdsgaard & Johnson 2001) and streams (Heggenes et al. 1991, Fonesca & Hart 2001). In open populations, spatial variations in distribution may also reflect differences in the supply of new recruits to particular habitats (Fonesca & Hart 2001).

Eels of the genus *Anguilla* are one of the dominant taxa in freshwater fish communities in coastal regions of New South Wales, south-eastern Australia (Gehrke & Harris 2000). They are long-lived and spend most of their lifetime in freshwater and tidal habitats within coastal catchments. The leptocephalus larvae of *Anguilla australis* (Richardson), commonly and hereafter referred to as ‘shortfin’, and *A. reinhardtii* (Steindachner), commonly and hereafter referred to as ‘longfin’, are transported to the east coast of Australia via the East Australian Current (Jespersen 1942, Castle 1963, Jellyman 1987, Beumer & Sloane 1990). The leptocephali then metamorphose into glass eels (small unpigmented-slightly pigmented post-larval eels) before recruiting to estuaries and migrating upstream to a wide range of estuarine and freshwater habitats (Beumer & Harrington 1980).

During the upstream migration, glass eels exhibit a crepuscular and daytime shelter seeking behaviour (Tesch 1977, Jellyman 1979, Silberschneider et al. 2001). Factors affecting upstream glass eel migration, and consequently extending their time in the estuary, include local hydrographic conditions (McCleave & Kleckner 1982) such as tidal flow and estuary length, freshwater inflow (Sloane 1984), barriers to migration (Naismith & Knights 1988, Haro et al. 2000), and the time taken for glass eels to undergo a physiological adaptation from a highly saline to a freshwater environment. This physiological adaptation time is thought to be at least 2 weeks and occurs at the estuary/freshwater interface (Deelder 1958, Jellyman 1979, Pease et al. 2003). Glass eels will then remain in this area until they are physiologically able to move further upstream. A proportion of recruiting eels may remain in estuarine habitats until they reach sexual maturity (Arai et al. 2003, Kotake et al. 2003, Morrison et al. 2003, Tzeng et al. 2003). Thus, it is important to determine the preference for various estuarine habitats by glass eels as a first step in identifying which habitats should be conserved to maintain sustainable recruitment of these eel species to coastal catchments.

Habitat alteration and fragmentation have been suggested as contributing factors to the decline of *Anguilla rostrata* (American eel) populations (Haro et al. 2000), while the availability of daytime refuges was one of the main determinants of density, biomass and population structure of *A. anguilla* (European eel) at specific sites (Knights & Bark 2001). However, the value of specific types of habitat for growth and survival of eels has not been quantified (Haro et al. 2000). Much of the information on habitat preferences of *A. australis* and *A. dieffenbachii* is from studies in New Zealand, where sampling was conducted in freshwater lakes (Chisnall 1996, Glova et al. 1998, Jellyman & Chisnall 1999, Broad et al. 2001) and preference tests were performed under controlled conditions using freshwater (Glova 1999, Glova 2001). However, these studies have focussed on pigmented elvers and yellow-stage eels in freshwater; only limited information was obtained on glass eels (Jellyman & Chisnall 1999). There have been no studies that document estuarine habitat use and/or preferences by glass eels (defined in this study as post-larval eels that have not yet attained a pigmentation stage of VI_B1 (Strubberg 1913)). The aim of the present study was to determine whether shortfin and longfin glass eels show a preference for any particular type of estuarine habitat.

Material and methods

We collected glass eels used in the laboratory experiments below the base of the Audley causeway on the Hacking River, southern Sydney, New South Wales, south-eastern Australia. The causeway is located 12 km upstream from the ocean and the water immediately below it ranges in salinity from 0 to 35 ppt. We collected shortfin and longfin glass eels during their peak estuarine recruitment seasons (May–August and February–April, respectively) and transported them in plastic buckets to the aquarium facility at the Cronulla Fisheries Centre (approx. 20 min drive). We then placed glass eels in an 86 l holding tank with flow-through ambient water from the Port Hacking estuary, where salinity ranged from 5 to 35 ppt. We collected separate batches of glass eels for each of the habitat preference experiments. The size of each batch varied but comprised enough eels to provide a sample size of between 24 and 30 eels for each experimental tank (a density of 0.28–0.35 glass eels l^{-1}). These densities were considered conservative since, in tank culture trials, Ingram et al. (2001) showed that stocking densities of glass eels at approximately 15 glass eels l^{-1} did not influence the growth or survival rates of shortfins.

We performed experiments with four 86 l fibreglass tanks (Figure 1). All tanks were supplied with filtered seawater from the Port Hacking estuary, had central outflow pipes ('standpipes') to

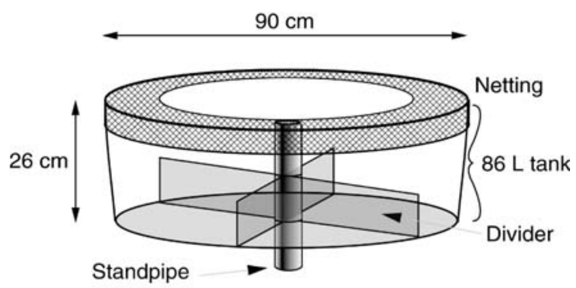

Figure 1. Diagram of a modified tank used in laboratory habitat preference experiments.

Table 1. Layout of habitats in each experiment for shortfin and longfin glass eels where S = sand, SG = seagrass, RC = rocks/cobbles and M = mud.

	Experiment 1				Experiment 2			
	Tank				Tank			
Section	1	2	3	4	1	2	3	4
Shortfin								
1	SG	M	RC	S	RC	SG	S	M
2	S	RC	SG	M	SG	S	M	RC
3	RC	S	M	SG	M	RC	SG	S
4	M	SG	S	RC	S	M	RC	SG
Longfin								
1	SG	M	RC	S	RC	SG	S	M
2	S	RC	SG	M	SG	S	M	RC
3	RC	S	M	SG	M	RC	SG	S
4	M	SG	S	RC	S	M	RC	SG

Note that tanks are circular so that habitats in sections 1 and 4 are adjacent.

maintain constant water levels, and air-stone diffusers to aerate the water. To prevent the glass eels from escaping, the top of each standpipe was covered with fine mesh netting, which was also placed around the outside of the tanks and extended inwards over the top of the tanks. The experimental tanks were distributed on one side of an enclosed room with no windows. Each tank was divided into four equal sections with perspex dividers (385 × 75 × 4 mm) that were sealed to the perspex base (Figure 1). Each substratum/habitat was placed in one of the four sections within 1 cm from the top of the divider so that all combinations of habitat placement were investigated (Table 1). The four types of substratum/habitat used consisted of two homogeneous (sand and mud) and two heterogeneous (rocks/cobbles and seagrass) types, with heterogeneous habitats defined as those habitats with more complex structure. The seagrass habitat consisted of a mixture of *Zostera* sp. and *Halophila* sp. in a sand substratum. All habitat types are representative of the predominant substrata/habitats in the Port Hacking estuary, with each substratum/habitat removed from the same area to maintain consistency between tanks and experiments. We collected each of these substrata/habitats from the Port Hacking estuary near the Cronulla Fisheries Centre and placed it in the tanks 1–2 days prior to the commencement of the experiments to allow sediments to settle out of the water column.

For shortfin eels, we conducted experiment 1 from 8 to 9 July and experiment 2 from 12 to 13 July 2001. Glass eels collected for these experiments were part of a glass eel recruitment study (Silberschneider et al. unpublished) and were allowed to acclimate in the aquarium for 17 days. The acclimation period depended on satisfying the sampling requirements for the recruitment study and allowing for the collection of substrata/habitats for the experiment. After acclimation, we dip-netted 30 glass eels and released them in each of the tanks by rotating the dip-net around the standpipe so that the glass eels were not released over one particular habitat. For longfins, we conducted experiment 1 from 4 to 5 April and experiment 2 from 8 to 9 April 2002. Because longfins experienced a high rate of mortality shortly after capture, we treated them with a formalin bath (1:10 000) to eradicate any ectoparasitic infestations, and used them in experiments only after mortalities had reached zero. We allowed these treated longfin eels to acclimate for 9 days. After acclimation, we dip-netted and released 24 glass eels into each of the tanks as described above. Feeding was not attempted prior to the experiments and glass eels of both species were released into the tanks at around midday.

Lights in the room were set to a 10:14 h light: dark cycle for shortfins and a 12:12 h light:dark cycle for longfins, which were the approximate natural cycles for the two respective times of year. After 24 h had elapsed, we checked tanks for signs of glass eel movement, removed the netting, and quickly inserted a partition that exactly fitted the shape of the tank and isolated each substratum/habitat. We siphoned off or scooped out the water and thoroughly checked each habitat for the presence of glass eels. We counted the glass eels collected from each section/habitat, euthanised them with benzocaine or clove oil, and stored them in labelled plastic jars containing 95% ethanol for confirmation of species.

We tested shortfin and longfin glass eels for habitat preferences monospecifically, as there are only 1 or 2 months of the year when their recruitment overlaps. Glass eels would undergo more stress if identified prior to experimentation, as they would have to be anaesthetised and viewed microscopically to identify them to species.

We performed analysis of variance (ANOVA) using a $4 \times 4 \times 4$ Latin square analysis (i.e. 4 tanks $\times$ 4 sections $\times$ 4 habitat types), based on the number of eels in each section, on the results of each experiment for each species (SAS version 6.12). When we found statistical differences among sections, we performed a Duncan's multiple range test to determine which treatment means were significantly different (SAS version 6.12). In all tests, we considered $p < 0.05$ as significant.

We did a separate series of experiments to determine whether any habitat preference detected in the previous series of experiments was due to a habitat choice or to aggregative behaviour of the glass eels (i.e. to test whether the individual eels were acting independently of each other). Two tanks were set up with the same habitat type in each section. We chose rocks/cobbles for this experiment because most glass eels in the experiments above were found in this habitat (see Results). We did experiments with shortfins from 20 to 21 and 24 to 25 June 2002, and longfins from 9 to 10 and 10 to 11 April 2002 (i.e. two experiments per species). In each experiment, we released 28 glass eels into each tank. We used χ^2 analyses (Statistica for Windows 2001) to test for deviations in the observed numbers of eels in each section from the expected frequencies. We calculated expected frequencies based on the assumption that the glass eels were distributed evenly through all sections. Any aggregative behaviour would result in an uneven distribution, indicating that habitat preferences of individuals were dependent on the preferences of other individuals.

Results

After glass eels had been released into the tanks we observed them swimming around the tank close to the substratum for approximately 2 min before they disappeared into the substratum/habitat. When the automatic lights switched off, in staggered 2 min intervals, we observed glass eels coming out of the substratum/habitat and swimming around the tank, some near the surface and others closer to the substratum. The dividers did not impede glass eels. On first inspection of each tank the following morning, there was no sign of glass eels swimming around the tank. Thus, we concluded that glass eels exhibited normal nocturnal behaviour.

Identification of glass eels on completion of the experiments confirmed that only one species had been used for each experiment. During the entire experimental series, we did not recover nine shortfins but we did recover all longfins. Mean length of the shortfins was 52.5 mm ± 0.4 (SE), with V_B as the most common pigmentation stage (only head and tail pigmentation; Strubberg 1913). Mean length of the longfins was 48.3 mm ± 0.07, with $VI_{A.IV}$ 1 as the most common pigmentation stage (distinct development of ventrolateral pigment; Strubberg 1913).

In experiment 1, two of the four tanks had more shortfin glass eels in rocks/cobbles than in seagrass while, in the remaining two tanks, there were more shortfins in seagrass than in rocks/cobbles (Table 2). Only one and two eels were found in the mud habitat and one eel was found in the sand habitat. Despite the variation of glass eels in each habitat, there was no significant difference between the number of shortfins in any of the habitats (Table 3, $p > 0.05$). In experiment 2, there were significantly more shortfins in rocks/cobbles than in any other habitat (Tables 2 and 3, $p < 0.05$) with a total of 88 eels in rocks/cobbles and 23 in seagrass. There was only one glass eel found in the mud habitat, and no eels in the sand habitat.

There were significantly more longfin glass eels present in the rocks/cobbles habitat than in all other habitats in both experiments 1 and 2 (Tables 2 and 3, $p < 0.05$). In experiment 1, there were a

Table 2. Numbers of shortfin and longfin glass eels collected from each habitat type after each experiment.

	Experiment 1				Experiment 2				Totals
	Tank				Tank				
Habitat type	1	2	3	4	1	2	3	4	
Shortfin									
Seagrass	23	1	17	4	13	3	3	4	68
Rocks/cobbles	5	29	11	25	13	26	24	25	158
Sand	0	0	0	1	0	0	0	0	1
Mud	1	0	2	0	0	1	0	0	4
Totals	29	30	30	30	26	30	27	29	231
Longfin									
Seagrass	3	4	1	6	2	0	1	0	17
Rocks/cobbles	20	19	23	18	22	24	23	24	173
Sand	1	1	0	0	0	0	0	0	2
Mud	0	0	0	0	0	0	0	0	0
Totals	24	24	24	24	24	24	24	24	192

total of 80 glass eels in rocks/cobbles. Also, the means for seagrass were significantly larger than the means for mud in experiment 1 (Table 3, $p < 0.05$). In experiment 2, a total of 93 longfins were found in rocks/cobbles with the remaining three eels found in seagrass (Table 2), with no significant difference between the means of seagrass, mud and sand.

The ANOVA results also showed no significant difference in the number of glass eels among sections within tanks in the presence of the four different habitat types (Table 3, $p > 0.05$ in all cases). Similarly, there was no significant difference between the observed and expected frequencies of shortfin or longfin glass eels among sections within tanks when each tank was filled with rocks/cobbles only, indicating that there was no aggregative behaviour. In these single habitat experiments for shortfins, χ^2 and p values ranged from 3.43 to 7.71 and 0.0523 to 0.3301 respectively. For longfins, χ^2 and p values ranged from 0.86 to 4.29 and 0.2322 to 0.8358 respectively.

Discussion

The results from the tank experiments suggest that, given a choice of habitats, both shortfin and longfin glass eels prefer habitats with heterogeneous structure, in particular rocks/cobbles. The uniform distribution of shortfin and longfin glass eels in all

Table 3. Comparisons of mean number of eels per habitat type and tests of significance from ANOVA (Latin square) and Duncan's tests for habitat preferences of shortfin and longfin glass eels in experiments 1 and 2 when tested in tanks.

Habitat type	Shortfins		Longfins	
	Experiment 1	Experiment 2	Experiment 1	Experiment 2
Mud	0.75^{b}	0.25^{b}	0^{c}	0^{b}
Seagrass	$11.25^{a,b}$	5.75^{b}	3.5^{b}	0.75^{b}
Rocks/cobbles	17.5^{a}	22.0^{a}	20.0^{a}	23.25^{a}
Sand	0^{b}	0^{b}	$0.5^{b,c}$	0^{b}
Habitat $F_{3,3}$	4.64	21.14	99.91	794.25
Tank $F_{3,3}$	0.00	0.04	0.00	0.00
Section $F_{3,3}$	1.86	0.95	0.60	0.75
Habitat p value	0.0525	0.0014*	<0.0001*	<0.0001*
Tank p value	>0.9999	0.9878	>0.9999	>0.9999
Section p value	0.2369	0.4753	0.6357	0.5609

*indicates a significant difference between habitats.
[a, b, c] indicates Duncan's test groupings of significantly different means of glass eels between habitat types.

experimental tanks when only the rocks/cobbles habitat was present reinforces the conclusion that glass eels 'preferred' rocks/cobbles when given a choice of four habitats. Glass eels did not exhibit aggregative behaviour, thus each eel presumably made an individual choice. Shortfin glass eels also displayed a greater preference for seagrass than for the other types of substratum/habitat in two of the four tanks in experiment 1. The results from Glova (1999, 2001) support these findings. Small eels (<100 mm) of the species *A. australis* and *A. dieffenbachii* (the New Zealand longfin eel) preferred watercress, cobbles and, to a lesser extent, woody debris compared to more homogeneous habitats when tested in replicate channels. Glova (1999) also found that, when the species were mixed, the proportion of small *A. australis* in watercress was greater than *A. dieffenbachii* and, conversely, the proportion of *A. dieffenbachii* in cobbles was greater than *A. australis*. Thus, shortfins appear to inhabit macrophytes as well as rocks/cobbles.

Field sampling using habitat collectors (unpublished data) during the same time period as the tank experiments did not show distinct habitat preferences. Shortfins were found in all habitats tested, and longfins were found in all habitats except rocks. Cairns (1941) observed that elvers are often found buried in sand and mud substrata, as well as under logs and boulders in the lower reaches of freshwater rivers in New Zealand. Beumer & Harrington (1980) noted that glass eels seek shelter within the estuary in mud or vegetation.

It has been well documented that glass eel migration through the estuary occurs at night during new moon periods on flood tides (Tesch 1977, Jellyman 1979, Sorensen & Bianchini 1986). It is assumed that when the ebb tide begins, glass eels seek cover in the substratum and remain there until the following night's flood tide so as not to be forced back downstream (Usui 1974, Beumer & Harrington 1980, McCleave & Kleckner 1982, McCleave & Wippelhauser 1987, Gascuel et al. 1995, Silberschneider et al. 2001). Thus, in the wild, glass eels may seek a particular habitat in which to hide, but may be forced to hide in less desirable habitats if the flood tide delivers them to an area where the preferred habitat does not occur. The study by Fonesca & Hart (2001) on the colonisation and habitat preference of black fly larvae found that processes governing the supply of colonists to substrata sometimes prevent them from reaching their preferred habitats. If fluid-mediated transport does not reliably deliver organisms to their preferred habitats, then the ability to disperse again or move about locally following settlement is likely to be a critical factor affecting fitness (Fonesca & Hart 2001).

We suggest that the onset of the ebb tide induces glass eels that are travelling through the estuary towards freshwater to seek shelter in the substratum with only a very limited time to search the surrounding area for available habitat. However, once glass eels reach the estuarine/freshwater interface, their behaviour is modified and they have time to search and select highly preferred habitat types. Our observations during a separate study at the Audley causeway (Silberschneider et al. 2001) showed that glass eels were accumulating around the freshwater outflows during the night and were sheltering in the surrounding substratum/habitat during the day, presumably whilst undergoing their physiological adaptation to freshwater. It was during this time that glass eels were caught in large numbers in artificial habitat collectors. Thus, we concluded that glass eels located the collectors during their nightly movements out of the substratum and found them to be a favourable alternative habitat. In turn, these nightly movements would also enable glass eels to find preferred habitat types which almost certainly provide more suitable refuge from predation.

We believe that the observed habitat preference behaviour is primarily based on the desire to use the most effective shelter for minimising the probability of predation. Other research has shown that post-settlement mortality is reduced in structurally diverse habitats because they provide a refuge from predation (Tupper & Boutilier 1997, Moksnes et al. 1998, O'Beirn et al. 1998, Steele 1999, Lindholm et al. 2001). Thus, glass eels may be more visible and accessible to predators when in unstructured or homogeneous habitats (e.g., sand and mud) compared to heterogeneous habitats (e.g., rocks and seagrass) which contain small interstitial spaces to shelter in. Glova (2001) tested the cover preferences of juvenile eels in the presence of subadult longfin eels and found that small eels co-occurred with subadult longfins in watercress, presumably because small eels found adequate shelter in this heterogeneous habitat.

The ability of glass eels to burrow into the substratum, as well as their ability to live in small interstitial spaces (Glova 2001), potentially allows them to use all available habitats in estuaries. However, this study is the first to identify the preference of glass eels for different estuarine habitats. Rocks/cobbles and, to a lesser extent, seagrass are the preferred habitats of shortfins, and rocks/cobbles are the preferred habitat of longfin glass eels. We believe that these preferred habitats offer increased shelter from predation compared to homogeneous sand and mud habitats. Because glass eels will spend at least 2 weeks in the estuary (Sloane 1984, Pease et al. 2003) and a proportion may remain in the estuary until they reach sexual maturity (Arai et al. 2003, Kotake et al. 2003, Morrison et al. 2003, Tzeng et al. 2003, Walsh et al. 2003), maintenance of preferred glass eel habitats will help to ensure the sustainability of eel populations in the coastal catchments of south-eastern Australia.

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