Vertical migrations may control maturation in migrating female *Anguilla dieffenbachii*

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ABSTRACT: The marine spawning area of the New Zealand longfin eel *Anguilla dieffenbachii* is unknown. The present study used 3 popup tags to obtain information on the offshore swimming behaviour and possible swimming directions and destination of migrating eels. All 3 eels showed very consistent behaviour and underwent daytime dives to depths of 600 to 900 m, where they experienced temperatures of 6 to 7°C. These dives were followed by nighttime ascents to depths of 200 to 300 m. From the consistency of these dives, we propose that eels are using regular exposure to cool temperatures to regulate the rate of maturity. While swimming at depth could also reduce predation, the increased pressure would stimulate development of the ovaries, something mediated by ascent to shallower water. Comparisons of ascent locations and swimming speeds are consistent with spawning in the tropics, possibly in the South Fiji basin.

KEY WORDS: *Anguilla dieffenbachii* · Freshwater eel · Diving · Thermoregulation

INTRODUCTION

Freshwater eels *Anguilla* sp. are considered to be a marine genus that has invaded fresh water (Tsukamoto & Aoyama 1998). They have retained marine spawning, although, of the 16 species now recognized (Watanabe et al. 2009), the spawning areas of only 4 species are known. While tropical eels are presumed to undergo relatively short migrations to their spawning grounds (Aoyama et al. 2003), migrations of temperate eels are extensive — typically 5000 to 6000 km in the case of the European eel *A. anguilla* (van den Thillart et al. 2009). Classical means of delimiting spawning grounds have required the collection of progressively smaller larvae (e.g. Schmidt 1922, McCleave et al. 1987, Tsukamoto 1992), but the availability of pop-up tags (pop-up satellite archival transmitters, PSAT) that transmit data to satellites provides a new technique that does not require the use of expensive ocean research vessels. Rather, ascent of a number of tags at a similar location would provide strong evidence of a likely spawning area.

It is often assumed that to minimize the possibility of abnormal behaviour, the weight of a tag should not exceed 2% of the body weight of the fish (McCleave & Stred 1975, Baras & Jeandrain 1998), although, as pointed out by Jepsen et al. (2005), there is no generally applicable 'rule' for tag/fish size relationship. In the present study, the tag weight was ~1% of body weight, so the eels were assumed to be large enough to carry a popup tag. Two previous studies using these tags on migrating (silver) female *Anguilla dieffenbachii* (Jellyman & Tsukamoto 2002, 2005) have recorded significant diel vertical and offshore movements, but tags failed to remain attached for the duration of the programmed time (up to 7 mo). Further, the daytime diving behaviour meant that insufficient light recordings were available for subsequent estimation of locations of eels and tracking of migration routes.

The main objective of the present study was to obtain additional information on the diving behaviour of migrating female eels in the open ocean. Any consensus of popup tag locations might indicate general swimming directions to the tropical spawning areas and possibly potential spawning areas.

MATERIALS AND METHODS

The methods were similar to those used by Jellyman & Tsukamoto (2002, 2005). In brief, the tags used were popup archival tags (PAT5, Wildlife Computers) weighing 75 g. They were programmed to ascend after 210 d (7 mo), a period considered sufficient for eels to arrive at the spawning grounds. The option to commence transmission after depth remained constant for a nominated period (24 h) was enabled in case tags broke off prematurely. Upon ascent, tags transmitted data to ARGOS satellites for a period of up to 3 wk. Tags were tethered to the eels using a multifilament nylon bridle. A pressure-operated guillotine was included on the tether line so that should the eel descend to >1800 m, the bridle would be cut and the tag ascend to the surface.

In early May 2006, 3 migrating female eels *Anguilla dieffenbachii*, 7.3 to 8.7 kg (Table 1), were obtained from a commercial eel fisher in Lake Ellesmere, east coast South Island, New Zealand. The lake is closed to the sea by a gravel bar, which is opened mechanically at preset water levels. Silver eels congregate at the southern end of this bar, attracted by saltwater seepage, and are caught in large (50 m wing) fyke nets. The 3 eels were held in a 0.62 m^3 aerated tank of fresh water to which equal amounts of artificial seawater salt mix were added at 4 h intervals to bring the water up to full strength sea water in 20 h. Despite the presence of the tag, the eels showed no signs of abnormal behaviour over this period. The tags were activated 24 h before release of the eels. Eels were transported to the sea in open bins and released at an open shoreline (43.860° S, 172.354° E) at 13:00 h on 11 May 2006. Water temperature during the acclimation period ranged from 12.6 to 13.3°C, and the sea temperature at the time of release was 13.2°C. Tags were programmed to record water temperature (0.05°C resolution) and depth (±0.5 m), with up to 32 sets of observations per day. The tags store data in 4 time bins (00:00–06:00, 06:00–12:00, 12:00–18:00, 18:00–24:00 h). Within each time bin, the minimum and maximum temperatures are recorded at 8 depths chosen dynamically to include the minimum and maximum depths detected, and 6 other depths arranged equally between them; data within bins are not stored in chronological order, meaning that it is not possible to assemble a true daily time series of swimming behaviour. For subsequent analysis, the data were pooled as either 'day' (06:00–12:00 and 12:00–18:00 h New Zealand Standard Time, NZST), or 'night' (18:00–24:00 and 00:00–06:00 h NZST). Occasionally the complete daily data set from all 4 bins was not available; in such instances, only those time bins that had the maximum number of sets of data (8) were included in analysis.

RESULTS

The tags from all 3 eels ascended prematurely after eels had been at liberty for periods of 65.5 to 90 d (Table 1). The percentage of the potential data available that was received from the tags ranged from 46 to 66%. As with a previous study (Jellyman & Tsukamoto 2005), no geolocation data were obtained as eels swam beyond the depth of detectable light.

Upon release, all 3 eels commenced similar swimming behaviour, with a daily descent and a nightly ascent. Although there appeared to be some initial exploratory dives (e.g. Eel 1 dived to 1160 m on Day 13 after release), after ~15 d at liberty, all 3 eels showed very consistent diving behaviour. During the night, eels usually swam at minimum depths between 100 and 200 m (Fig. 1); there was a slight tendency for the minimum depth to increase over time. In contrast, the maximum depth showed a marked increase over time. Maximum depth was highly correlated with minimum temperature ($R^2 = 0.80$, $p < 0.001$), while minimum depth was significantly correlated with maximum temperature ($R^2 = 0.17$, $p < 0.001$). With increasing time at liberty, as eels swam further north from New Zealand, the maximum water temperature they experienced increased while the minimum temperature declined slightly.

Time-at-depth (Fig. 2a) and time-at-temperature (Fig. 2b) histograms also showed considerable similarity between the 3 eels, with each eel showing different day and night depth and temperature usage. Comparison of depth profiles of the 3 eels on the same day sug-

Table 1. *Anguilla dieffenbachii.* Sizes of eel tagged, minimum and maximum temperatures and depths experienced by eels, and distances travelled

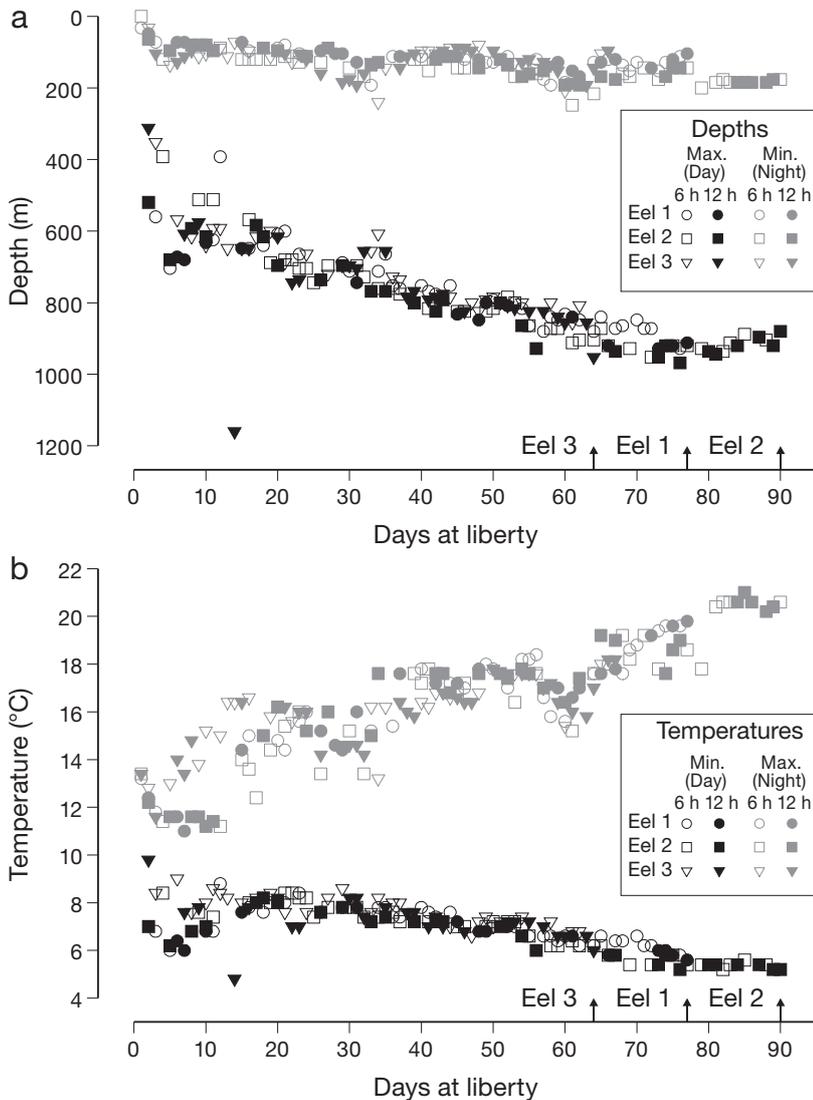| Tag	Size of eel Length (mm)	Weight (kg)	Data recovered (%)	Days at liberty	Day Min. (°C)	Max. (°C)	Min. depth (m)	Max. depth (m)	Night Min. (°C)	Max. (°C)	Min. depth (m)	Max. depth (m)	Distance travelled (km)	Average distance (km d^{-1})
1	1325	8.2	66	65.5	4.8	18.2	8	1160	8.4	18.2	32	408	1573	24.0
2	1416	8.7	60	90.0	5.2	18.0	24	968	7.8	21.0	64	608	2372	26.4
3	1297	7.3	46	77.3	5.6	17.8	80	928	8.2	19.8	32	336	1916	24.8

Fig. 1. *Anguilla dieffenbachii*. Minimum and maximum (a) depths and (b) temperatures received from the 3 tags. Grey symbols: night period; black symbols: day period. Filled symbols (labelled 12 h): average of a complete 12 h data set; unfilled symbols (labelled 6 h): data for a 6 h bin only available. Arrows labelled Eel 1, 2 and 3: end of liberty periods

gested that the eels were swimming separately (i.e. not schooling) but showing generally similar preferences for particular temperatures and depth. After the first 15 d 'settling period', the range of depths encountered during the night was 72 to 544 m compared with 80 to 1160 m during the day, indicating that the diving behaviour took place during the daytime period.

The ascent locations for the 3 tags (Fig. 3) lay along an almost straight trajectory due north of New Zealand. Distance travelled (measured as shortest distance over a great circle) ranged from 1573 to 2372 km, with average swimming speed being between 24.0 and 26.4 km d^{-1} (Table 1).

DISCUSSION

Maturation in eels is a deterministic process initiated in fresh water. Although triggering factors are uncertain, these will include attainment of sufficient fat reserves (Larsson et al. 1990) and minimum size (Vollestad & Jonsson 1986). Maturation is accompanied by morphological and biochemical adaptations (van Ginneken et al. 2007, Rousseau et al. 2009) to facilitate oceanic migration, including the capability of swimming at depth (Sebert et al. 2009).

The rate of maturation is affected by temperature (Boëtius & Boëtius 1980, Sato et al. 2006), pressure (Dufour & Fontaine 1985, Sebert et al. 2009) and even swimming itself (Palstra et al. 2007, 2009). Final maturation and hydration of oocytes probably occur at, or close to, the spawning grounds (Palstra et al. 2005, 2009). While warm temperatures are necessary to achieve full maturity, continued exposure to cool temperatures inhibits maturation. For example, in the Japanese eel *Anguilla japonica*, another temperate species, water temperatures of 18 to 22°C appear optimal for maturation (Sato et al. 2006, Dou et al. 2008), but cooler temperatures inhibit maturity, as final maturation could not be induced at 10°C (Sato et al. 2006), and spawning was not achieved at 14°C (Dou et al. 2008).

Observations on marine swimming behaviour of silver eels have invariably reported vertical diving (e.g. Tesch 1978, 1989, 1995, Tesch et al. 1991, Jellyman & Tsukamoto 2002, 2005, Westerberg et al. 2007, Aarestrup et al. 2009), with daytime diving and nighttime ascents, sometimes to the surface (Sasai et al. 2001, Westerberg et al. 2007). In shallow or continental waters, multiple dives have been observed within a single night (Tesch et al. 1991, Westerberg et al. 2007), but a single descent/ascent pattern becomes established in oceanic water (Tesch 1978, Jellyman & Tsukamoto 2002, 2005, Aarestrup et al. 2009, present study). Typically, ascents do not bring eels close enough to the surface for celestial navigation cues (Tesch 1989, Jellyman & Tsukamoto 2005), and geomagnetism is thought to be the more likely means of navigation (Tesch et al. 1992, Moore & Riley 2009). Whatever the reason for these dives, they must be ben-
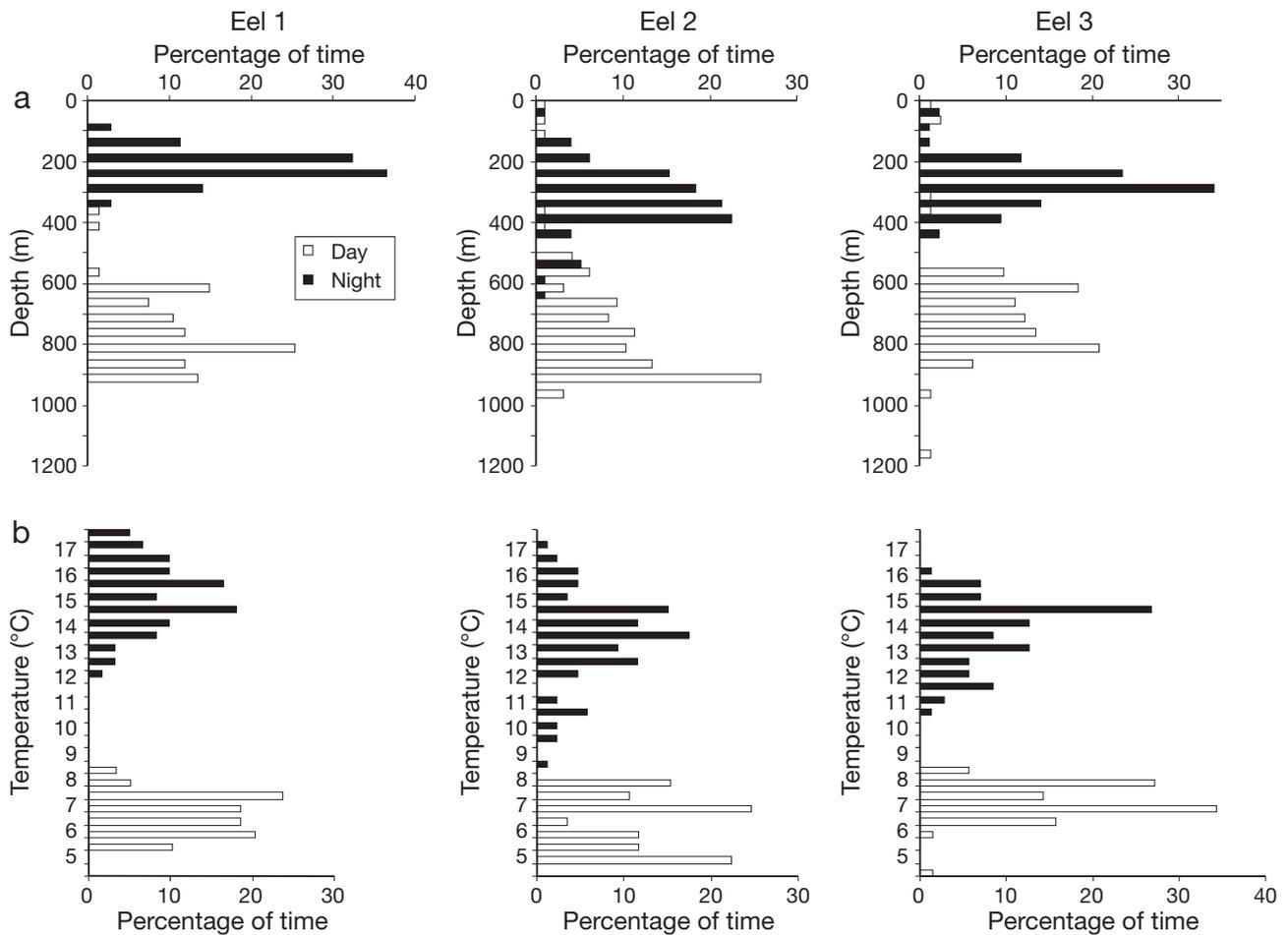
Fig. 2. *Anguilla dieffenbachii*. Percentage of time the 3 eels spent at different (a) depths and (b) temperatures during day and night

eficial as they represent additional swimming distance to a starving (non-feeding) fish. For example, a daily vertical dive pattern from 100 to 850 m and return would add 6% to the total swimming distance, although this would halve if the dive angle was not as steep. Such a pattern might also result in reduced energy expenditure as diving by powerless gliding followed by active ascent swimming can result in significant energy savings in negatively buoyant fish like eels (Weihs 1973).

In a previous paper (Jellyman & Tsukamoto 2005), we postulated that the reasons for the diel vertical migrations we observed in migrating female *Anguilla dieffenbachii* were a combination of predator avoidance and thermoregulation. Potential visual predators like tuna, sharks, toothed whales, and billfish are able to dive for short periods to the 800+ m achieved by migrating eels, but temperatures encountered at such depths (5 to 6°C) were considered too cold for continuous swimming by eels. Certainly, activity of yellow phase *A. dieffenbachii* ceases at such temperatures

(Jellyman 1991, 1997). We suggest that the consistency of diving to encounter specific depths and especially temperatures observed in the present study indicate that predator avoidance is unlikely to be the only reason for these dives.

Diving to encounter particular thermal regimes, especially thermoclines and deep sound scattering layers (SSL), has often been associated with feeding in species like tuna (e.g. Dagorn et al. 2000, Kitagawa et al. 2000, Musyl et al. 2003) and ocean sunfish (Cartamil & Lowe 2004). Tuna also use such dives to regulate body temperature (e.g. Kitagawa et al. 2000, Musyl et al. 2003). Perhaps migrating eels use regular exposure to cooler water to regulate the rate of maturation? As indicated previously, swimming itself promotes maturation (Palstra et al. 2007, 2009), and achieving maturity well in advance of arrival at spawning grounds would be disadvantageous. The later stage of oogenesis, egg hydration, occurs within a few weeks and results in a substantial increase in the girth of the female abdomen. For example, pho-
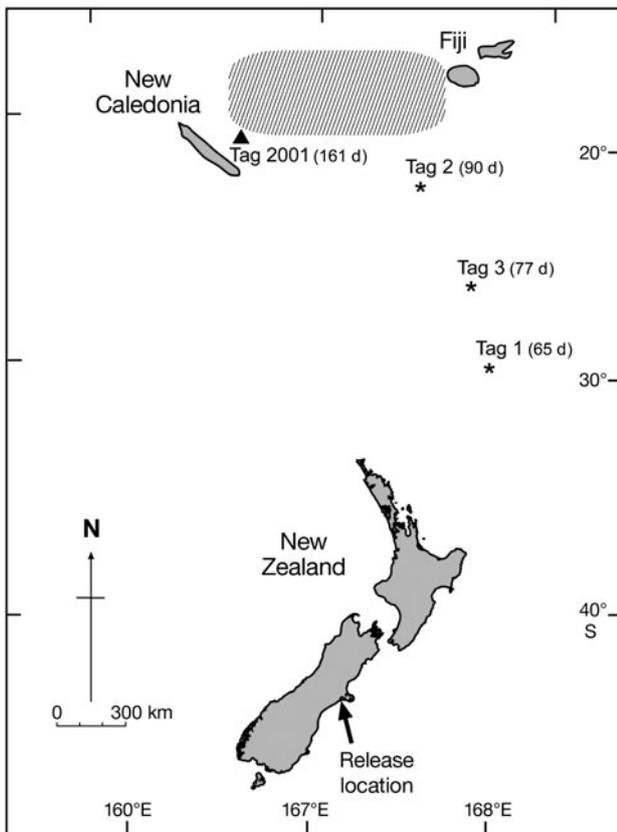
Fig. 3. *Anguilla dieffenbachii*. Ascent locations (with days at liberty in parentheses) of the 3 tags, and estimated ascent location of a tag (Tag 2001) from a previous study (Jellyman & Tsukamoto 2005). Suggested spawning ground of *A. dieffen-bachii* (striped area) given by Jellyman & Bowen (2009)

tographs of spawning female *Anguilla anguilla* (Tesch 2003, van Ginneken & Maes 2005) indicate that at this stage, the depth of the abdomen is twice that of an early stage silver eel: this results in a 4 times increase in cross-sectional area. The associated increased drag on this distended abdomen would be considerable, and energetically demanding. So, we agree with the suggestion of van Ginneken & Maes (2005) and Aarestrup et al. (2009) that female eels seek cooler temperatures to regulate over-maturation. If this is correct, we expect that cessation of this behaviour would indicate arrival at the spawning grounds; unfortunately, eels in the present study did not retain tags long enough to observe whether this phenomenon occurred or not.

Male *Anguilla dieffenbachii* depart on their oceanic migration about a month earlier than females (Todd 1981) and, being smaller, will swim slower but presumably coincide with females on their arrival at the spawning ground. The imperative for males is to initiate spermatogenesis but delay sperm production until arrival at the spawning grounds. Final maturity will be partly achieved by proximity to other mature males (Huertas et al. 2006). Unlike females, males do not appear to change body shape significantly at maturity and, if our thermoregulation hypothesis is correct, males would have less need to use water temperatures to influence the timing of maturity. Accordingly, we suggest that males would undergo less extensive dives than females. Possible lack of deep diving by males would be contrary to the suggestion by Scaion & Sébert (2008) and Scaion et al. (2008) that males are better adapted to increased pressure and deep water than females, and hence are likely to swim at greater depths.

Our hypothesis on the role of vertical movements during marine migrations of sliver eels is as follows: freshwater eels, including temperate species, are physiologically adapted to warm water (Owen et al. 1998, Graynoth & Taylor 2000). Their migration strategy involves tradeoffs between their preference for warm temperatures (e.g 17 to 20°C, Haro 1991), predator avoidance, the risk of over-maturation, and the need for energy conservation. As both swimming itself and residence in warm water promote maturity, eels mediate this effect by daily exposure to cooler water. However, they cannot remain indefinitely at the associated depth (600+ m) as the increased pressure would promote maturity, while the water temperature (6 to 8°C) is below the metabolic optimum of the eels. Hence, the eels ascend daily to warmer, shallower water. An increase in temperature associated with continuous swimming in the shallower water could be a trigger to final maturation (Palstra et al. 2009), and would also increase the likelihood of eels encountering olfactory cues that they might use to find conspecifics at the spawning area (Tsukamoto 1992). Spawning is likely to take place in depths of 200 to 300 m (Chow et al. 2009).

There may be associated physiological benefits to the daily descent/ascent rhythm, as pressure changes can affect such parameters as buoyancy and gas exchange (Sébert et al. 2009), aerobic metabolism (Scaion et al. 2008) and efficiency (Theron et al. 2000). However, any overall metabolic benefit is presently unknown (Sébert et al. 2009). Whatever the benefits, they must outweigh those of choosing a fixed intermediate swimming depth and temperature, where eels could experience water cooler than near-surface, and possibly avoid the necessity of daily dives. Why the dives are carried out regularly each day is uncertain, but we suggest that the thermoregulation regime is superimposed on the diel predator avoidance diving regime we suggested in an earlier paper (Jellyman & Tsukamoto 2005). Having some ability to control the rate of maturity could be very important to a species

like *Anguilla dieffenbachii*, where migratory eels from southern New Zealand would need to swim up to 2000 km further than eels from northern New Zealand to reach the spawning grounds, yet presumably both groups are able to arrive at the spawning grounds at the same level of maturity.

The alignment of popup locations of the tags in the present study suggests that the eels were using a similar migration route. The use of similar routes is likely within enclosed waterways like the Baltic Sea (Westerberg et al. 2007), but relatively few silver eels have been caught in the open ocean (Todd 1973, Sasai et al. 2001, Chow et al. 2009). As silver eels are known to use magnetic orientation at sea (e.g. Tesch et al. 1992, Tesch & Rohlf 2003), some convergence of eels along a common pathway seems likely, and the present results are the first that could indicate such behavior.

Mean swimming speed of the 3 eels in the present study averaged 25.1 km d^{-1}, (1.04 km h^{-1}), which equated to ~0.22 BL (body length) s^{-1}. These speeds are very similar to estimates for silver female *Anguilla dieffenbachii* of 1.06 km h^{-1} (Jellyman & Tsukamoto 2002), and female *A. anguilla* of 0.83 to 1.69 km h^{-1} (Tesch 1989) and 0.79 to 2.09 km h^{-1} (McCleave & Arnold 1999). A popup tag from a previous study (Jellyman & Tsukamoto 2005) remained attached longer (161 d) than those in the present study. Unfortunately, this tag drifted at the ocean surface for 61 d before commencing transmissions; using surface water velocities estimated from satellite altimetry data, the most likely popup location for this tag (Fig. 3) was 2630 km from the release point, giving an average swimming speed of 0.68 km h^{-1}, considerably slower than observed speeds in the above studies. The estimated popup location of this tag was at the margins of the area suggested by Jellyman & Bowen (2009) as being a likely spawning area for *A. dieffenbachii*, so it is possible that this eel had slowed its swimming because of proximity to the spawning area. However, based on observations from one eel, such a suggestion remains speculative, and further popup tag trials or capture of larvae, would be required to confirm the location of the spawning area.

Final confirmation of migratory routes and spawning areas could come from the use of further (smaller) popup tags, as the smallest presently available (40 g) are approaching a size where they could be deployed on migrating male *Anguilla dieffenbachii* as well as females. As migrating eels travel too deep to record light levels and hence reconstruct actual routes, future research could use a smaller popup 'pinger' tag that simply used surface transmissions to indicate location rather than the larger and more expensive archival tag used in the present study and those of Jellyman & Tsukamoto (2002, 2005).

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