First use of archival transmitters to track migrating freshwater eels *Anguilla dieffenbachii* at sea

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ABSTRACT: The spawning grounds of the New Zealand longfinned eel *Anguilla dieffenbachii* are unknown, but thought to be in the tropical region of the south Pacific Ocean. To determine whether pop-up tags could be used to provide information on the swimming speed and direction of migrating eels at sea, 4 female eels (7 600 to 11 400 g) were equipped with archival pop-up tags that were pre-programmed to surface after either 2 or 3 mo. All 4 tags ascended successfully at straight-line distances ranging from 368 to 1000 km offshore of the east coast of South Island, New Zealand. These estimated migration pathways showed that the eels moved substantial distances along inshore areas before moving offshore and eastward. There was no evidence of the expected northeast movement to tropical waters. Average swimming speed of all eels ranged from 15.1 to 31.3 km d^{-1}, but there was limited evidence of diel vertical movement within the water column. The results indicated that pop-up tags have considerable potential in tracking the marine migrations of the larger species of *Anguilla.*

KEY WORDS: Freshwater eel · *Anguilla dieffenbachii* · Pop-up tags · Satellite · Offshore movement

INTRODUCTION

Of the 15 species of freshwater eel, *Anguilla* spp., the spawning grounds of only the European *A. anguilla*, American *A. rostrata*, and Japanese eel *A. japonica* are known with reasonable certainty. Locating the spawning grounds of these species required the capture of progressively smaller larvae (e.g. Schmidt 1923, Tsukamoto 1992), a technique that is both labour intensive and costly.

New Zealand has 3 species of freshwater eel—the shortfinned eel *Anguilla australis*, the longfinned eel *A. dieffenbachii* and the recently discovered Australian longfinned eel *A. reinhardtii* (Jellyman et al. 1996). Spawning grounds of these species are unknown. Although a number of larvae of *A. australis* have been collected at sea (Jespersen 1942, Castle

1963, Aoyama et al. 1999a), no larvae of *A. dieffenbachii* have been identified. Based on a review of migration times and oceanic circulation, Jellyman (1987) suggested that a possible spawning area might lie to the east of Tonga. In the absence of larval material, it has not been possible to validate this suggestion.

With the development of archival 'pop-up' tags (i.e. external tags that collect environmental data, detach from fish at pre-programmed times, ascend to the surface and transmit information to satellites), it is now possible to track oceanic migrations of large pelagic fish. Such tags have been used to track tunas (e.g. Block et al. 1998), but to date they appear to have only been used on fish larger than 50 kg. We tested the use of pop-up tags on migrating female *Anguilla dieffenbachii* to see whether this technology could be used to track offshore migrating eels; if the technique was successful, then it could be used in the future to demarcate likely spawning areas.

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MATERIALS AND METHODS

Eels. During autumn (March to May), migratory eels accumulate in the south-west corner of Lake Ellesmere, South Island, New Zealand (172° 29′ E, 43° 47′ S), because the lake is normally closed to the sea by a gravel bar (Jellyman & Todd 1998). Twenty migrating longfinned females were caught from the lake by commercial eel fishers on 2 May 2000. The 4 largest were chosen for tagging and ranged from 1359 to 1520 mm total length (mean 1418 mm, SD 72 mm) and 7600 to 11 400 g total weight (mean 9290 g, SD 1572 g). The eels were retained in flowing freshwater (11°C) for 2 wk prior to tagging as the tags had been pre-programmed at manufacture to commence data recording on 17 May 2000. For tagging, eels were individually removed from a holding tank and anaesthetised with 2-phenoxyethanol; tagged eels were then returned to a 750 l aerated plastic tank, to which artificial sea salt was periodically added over 36 h—at the end of this period, the salinity measured 25‰.

For road transport to the sea, a distance of 7.5 km, individual eels were lightly anaesthetised (AquiS Fish anaesthetic at 0.0027 ml l^{-1}) and placed inside a plastic bag contained within a polystyrene container (1.2 long × 0.5 wide × 0.5 m deep) to which small quantities of the saline water and anaesthetic solution were added. At sea, fresh salt water was added to each container to revive the eels and provide some exposure to normal salinity salt water. Once the eels had recovered, they were individually carried into the sea and released in approximately 0.5 m water depth at 19:30 h on 17 May 2000. The release point was a steeply sloping oceanic beach where the immediate offshore area is comprised of gently shelving fine sediments.

Tags and method of attachment. The tags, PTT-100 (Microwave Telemetry), measured 18 cm in length with a 16 cm aerial, and weighed 65 g. Sensors collected hourly data on water temperature, light levels, and angle of the tag to vertical. Daylength and times of sunrise and sunset are used to estimate latitude and longitude respectively; tests on the accuracy of this method have indicated an average error of ±140 km (SDs of ±1.2° latitude and ±0.9° longitude (Welch & Eveson 1999), sufficient to allow assessments of open ocean migrations of fish. These daily estimates of latitude and longitude can then be used to calculate approximate directions and distances swum by individual eels. Tags were pressure tested to 750 m, with light level sensors capable of recording light (550 nm) to a maximum depth of about 250 m.

Two tags were pre-programmed to detach on 17 July 2000 and the other 2 on 17 August 2000, i.e. 2 and 3 mo respectively after release of the migratory eels. Detachment involves the tag passing voltage through the

wire embedded in the eye of the tag which then disintegrates over a few hours by electrolysis. Being positively buoyant, the tag then ascends to the surface and transmits data to ARGOS satellites. Interception of data is random, and the amount of data recovered each day depends on the number of satellites contacted and the trajectory of their orbits. The tag continues to transmit for several weeks, by which time most data should be recovered. Missing data sequences can be of 2 types: temperature data, but no latitude and longitude data because the light readings were beyond the limits acceptable to the tags (usually too 'faint' for accurate sunset/sunrise times to be estimated), or lack of both temperature and position data because the data sequences were not recovered by satellite. In both instances, a 10 d running mean (4 d prior to the missing date, 5 d after) was used to estimate daily position.

The manufacturer's recommended method of tag attachment, a dart, was rejected because of the comparatively small size of the eel; also it was considered possible that the constant 'vibration' caused by the trailing tag could prevent healing of the tagging wound, with the result that the dart and tag would fall off. The method used (Fig. 1) involved a nylon bridal
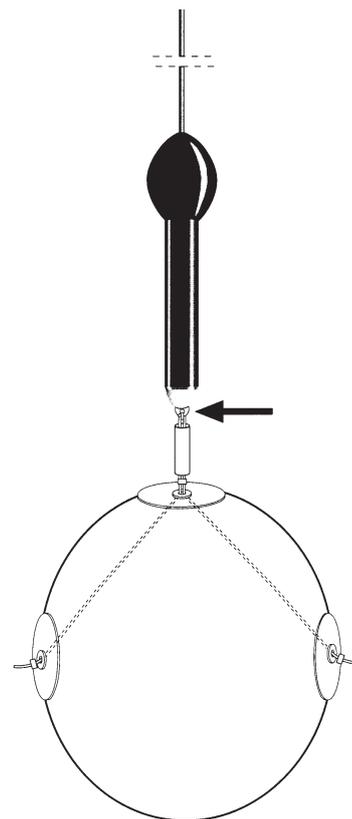

Fig. 1. The method of tag attachment (not to scale). Large circle (bottom) represents cross-section of an eel. Arrow indicates point of detachment of tag from nylon bridle

drawn through the dorsal musculature of the anaethse-tised eel and secured by a plastic disc on each flank.

Details of the tagging process were as follows: A 60 cm length of monofilament nylon (36 kg breaking strain) was threaded through the eye of the tag and knotted to form a tight loop. A 5 cm length of plastic tube was then pushed up the nylon to the base of this loop. A double (2-sided) brass crimp was slid up both lengths of nylon to the base of the plastic tube. The crimp was lightly squeezed to ensure it held the tube securely in place. Both ends of the nylon were then threaded through a 2.5 cm diameter plastic disc (1.5 mm polypropylene) to which a small brass washer had been glued to reduce any abrasion from the metal crimp.

For attachment to the eel, a syringe needle (12 cm, 17 gauge) was inserted through the lateral musculature of the eel and pushed upward to emerge at the dorsal mid-line approximately 10 cm anterior to the insertion of the dorsal fin. One end of the nylon suture was then pushed down through the hollow needle which was then removed, leaving the nylon inserted through the muscle. A similar technique was used on the other side of the eel, and the tag then secured against the back of the eel by gently pulling on both emerging lengths of nylon. Plastic discs were then threaded onto the emerging nylon, which was pulled taut, and the position of the disc secured with a brass crimp. Excess nylon was trimmed off.

The attachment technique was tested in the laboratory before being used in the field. For these trials, 2 non-migratory *Anguilla dieffenbachii* (750 and 820 mm) were fitted with dummy tags. After 4 wk, one eel had developed an infected wound on its back where both nylon sutures emerged, apparently because the sutures had not been pulled taut before crimping—this eel was removed from the test tank, the tag removed, and the eel released. The other eel was retained for a further 4 wk, at which time it showed no apparent ill-effects of tagging, and the tag remained secure. While it was suspected that drag caused by the tag could reduce the eel's swimming speed, this could not be tested in the laboratory.

In the absence of depth information, the possibility of early detachment of tags was examined by comparing the water temperatures recorded by the tags with sea-surface temperatures (SST) recorded by satellite (Udd-strom & Oien 1999) for the estimated daily location of each eel. In practice, daily SST were not always available because of cloud cover, so an average temperature was computed from the mean temperature of a 6 d period, with the day concerned being the midpoint of the period. Temperature profiles came from the Chatham Rise hydrological programme (NIWA unpubl. data). As a further check, the swimming tracks of the eels were compared with surface current patterns to examine whether these currents could account for the swimming paths of the eels. Swimming speeds were estimated by averaging the total distance swum by individual eels at 10 d intervals.

RESULTS

Geolocation of tags and the possibility of premature ascent

All 4 tags operated successfully. Transmissions from the 2 tags scheduled to ascend on 17 July were picked up by satellite on 11 July, indicating that the tags had ascended earlier than anticipated. Likewise, transmissions from the tags scheduled for ascent on 17 August were picked up on 15 August. Ascent locations, determined by Doppler shift, were accurately determined (depending on the class of reception data, these can be <150 m) and were reasonably close to the ascent locations estimated by the tags—ranging from differences of 33 (Eel 81) to 144 km (Eel 80).

Results from the inclinometer were equivocal, and could not be used to indicate whether the tags had detached prematurely. Likewise, comparisons of SST with temperatures recorded by the tags also failed to clarify this issue; for 2 eels (Eels 48 and 81) most SSTs exceeded tag temperatures, but the reverse was true for the other 2 eels. However, differences in daily mean temperature between the 2 data sets were generally small, with 74% of the differences (n = 136) being <1°C. Temperature profiles in the vicinity of where tags ascended show that the water is generally isothermal to a depth of 50 to 80 m (NIWA unpubl. data).

Continuity of data

There were some incomplete data sequences for all tags, especially for the 2 eels at sea for 3 mo. Eel 80 (55 d at sea) had 8 d of temperature and 10 d of position data missing, Eel 81 (55 d at sea) had 13 d of both temperature and position data missing, including the 7 d immediately before pop-up; Eel 48 (90 dat sea) had 47 d of both temperature and position data missing, including the 12 d immediately prior to pop-up. Eel 49 (90 d at sea) had 39 d of temperature and 52 d of location data missing, including the initial 22 d of the record following release, with the result that no estimates of position could be made for this period.

Swimming tracks

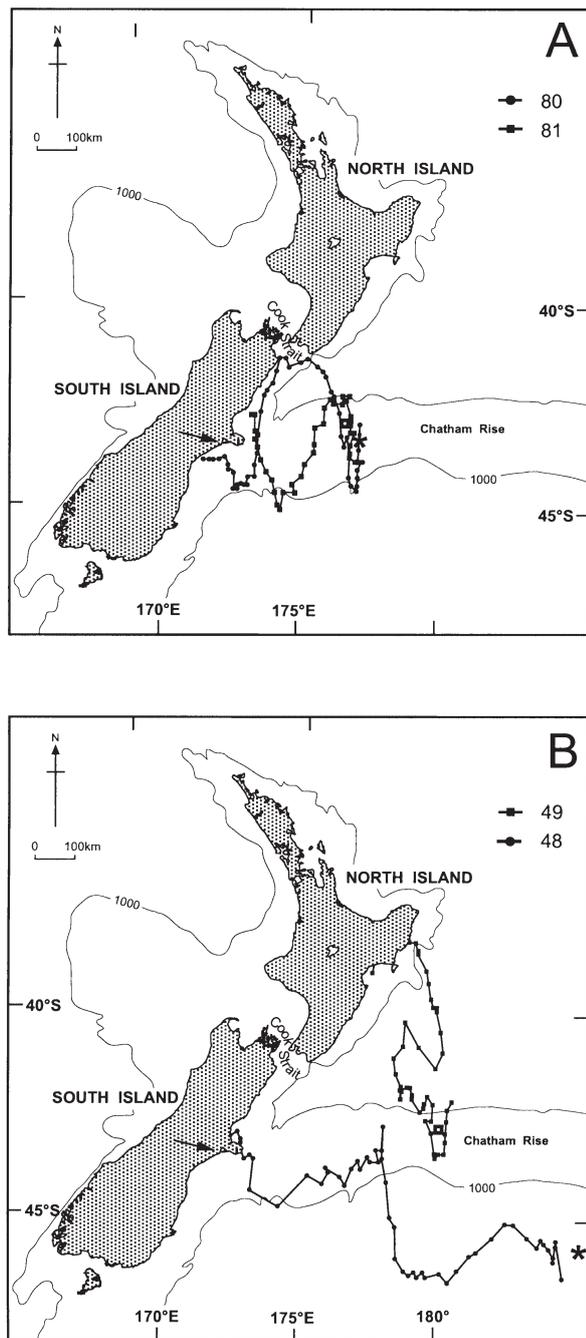The swimming tracks of all 4 eels are shown in Fig. 2. The estimated release point of Tags 48, 80 and 81

Fig. 2. Estimated swimming tracks of eels *Anguilla dieffenbachii* at sea for (A) 2 mo and (B) 3 mo. Note that all eels commenced from the release point indicated by the arrow, and that the initial track of Eel 49 is missing. Ascent (pop-up) locations of tags from Eels 81 and 49 (□) and from Eels 80 and 48 (∗) are shown. Individual points are estimated positions, mostly at 1 d intervals

ranged from 65 to 105 km from the actual release point. Eel 80 showed an initial southward movement before swimming due north to Cook Strait—once there the eel swam southeast and then due north

before the tag ascended on the Chatham Rise. The movement pattern of Eel 81 was rather similar, with initial southward movement followed by northward movement to the approximate latitude of the departure point before again moving south; tag ascension was 68 km south of that for Eel 80.

Eel 48 showed a more directed eastward movement until tag ascension south of the Chatham Rise. For Eel 49, tracking estimates commenced from 8 June, at which time the eel was estimated to be at 39.5° S— thereafter the track showed net southward movement until tag ascension again on the Chatham Rise (note that the estimated track of this eel shows some initial land-based movement, due to the inaccuracies of estimates of latitude and longitude).

Swimming speed and distance traveled

The estimated swimming speeds of eels varied considerably, ranging from 0 to 137 km d^{-1}. Mean swimming speed per 10 d period (Fig. 3) showed an initial slow speed of 15.1 km d^{-1}, but then reasonably constant averages ranging from 25.8 to 31.3 km d^{-1}. The total estimated distance traveled for Eels 80 and 81 (approx. 2 mo tracking period) were 1310 and 916 km respectively, compared with 2106 and 1551 km respectively for Eels 48 and 49. However, Eel 49 was first encountered off the east coast of the North Island, a straight line distance from the point of release of 700 km. Thus the minimum distance traveled by this eel was not less than 2250 km. Offshore (straight line) distances were 368 and 370 km for Eels 80 and 81 respectively, and 654 and 1000 km for Eels 49 and 48.

Swimming depth and water temperature

As water pressure was not recorded, no estimates of swimming depth were possible. However, with the exception of missing data, light data were available for all tracking days, indicating that the eels must have swum principally within the photic zone. Depths over the Chatham Rise primarily range between 250 and 500 m, indicating that the eels were not swimming near the bottom.

All records were discontinuous, with large portions of unrecovered data. With the exception of Eel 49, temperature tracks of individual eels (Fig. 4) show that eels experienced only 3 to 4°C variation in temperature over the 2 or 3 mo period (Table 1). There is some suggestion of small diel differences in temperature for Eels 80, 81 and 48, but these differences were only 0.2 to 0.4°C. Temperature profiles over the Chatham Rise
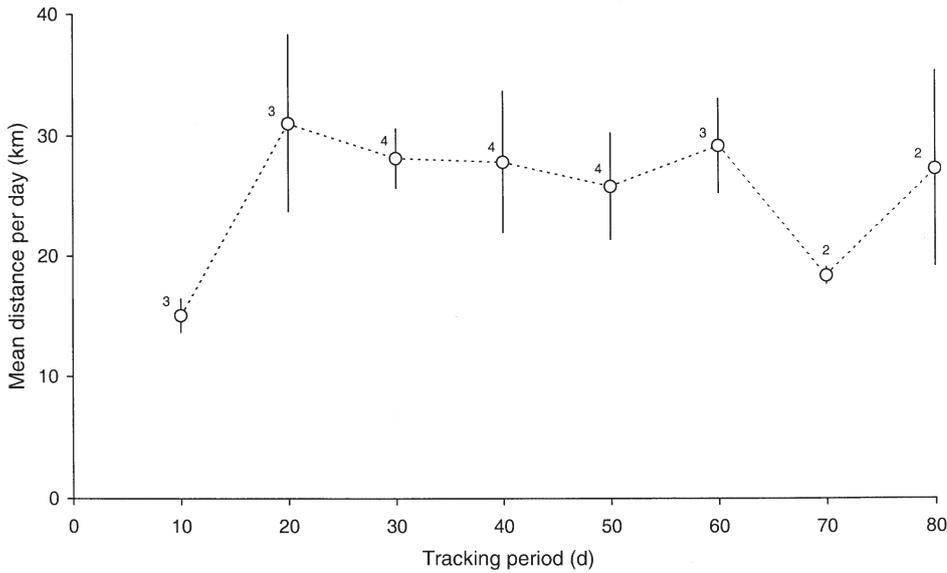
Fig. 3. Estimated 10 d mean swimming speed (km d^{-1}, ±1 SE) of *Anguilla dieffenbachii* at sea. The numbers are the number of eels for which data were available

indicate that differences of >0.4°C would take place at 50 to 150 m beneath the surface (Vincent et al. 1991, NIWA unpubl. data).

Eel 49 swam much further north than the other 3 eels; hence it encountered much warmer water. A 9 d portion of the temperature track of this eel (Fig. 5) shows a distinct diel pattern, with the eel regularly encountering 7.5 to 9°C water from 20:00 h to 05:00–06:00 h, and >11°C water for the remainder of the day. Presumably this corresponds to a daily descent in depth at 20:00 h and an ascent at 05:00–06:00 h. Thereafter the eel appeared to stop its daily vertical migrations, or encountered isothermal water.
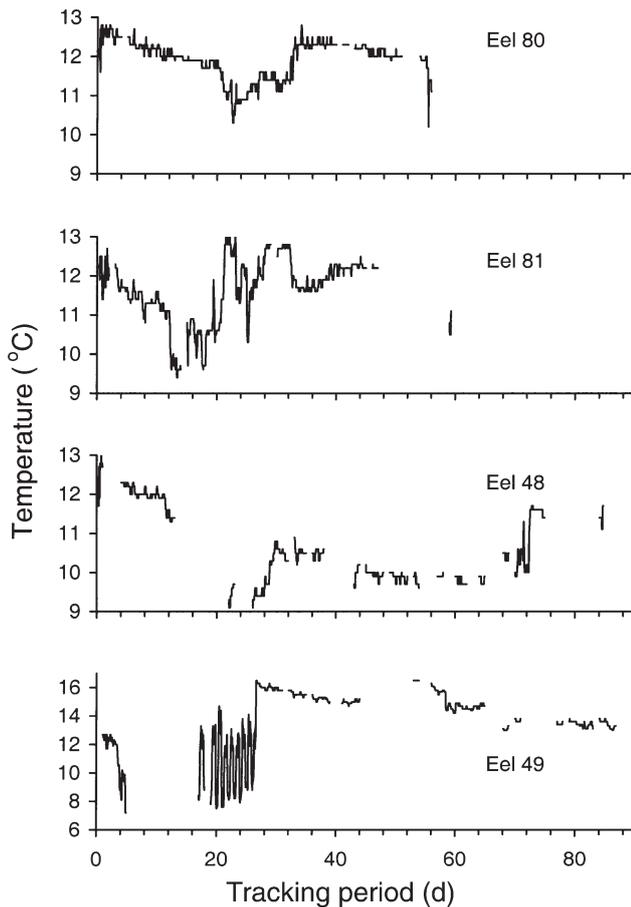

Fig. 4. Water temperature encountered by individual eels. Gaps in the record indicate unrecovered data

Table 1. Summary of water temperature data collected by pop-up tags. n = total number of recordings

| Tag number | n | Water temperature | |
		Mean ± SD	Range
80	1223	11.9 ± 0.5	10.0–13.0
81	1048	11.6 ± 0.8	9.3–13.0
48	977	10.7 ± 0.9	9.1–13.0
49	1120	13.6 ± 2.2	7.2–16.5

DISCUSSION

Accuracy of geoposition estimates

Both the release locations and tag ascent locations estimated from light data were within the average geoposition calculation error of about 140 km. Potential sources of error for estimating geoposition from light levels include wave state (which affects light scattering), thickness of cloud cover, variable sensor angle, presence of shadows, presence of mountains in inshore areas, algal fouling of tags, movement of the fish between dawn and dusk, and the type of algorithm used (Welch & Eveson 1999). Fortunately, many of these errors work against each other, so that the potential error is not the sum of the parts (Gremillet et al. 2000). While the present system determined the time of dawn and dusk relative to reference levels, the use of maximum rate of increase or decrease in light levels has been proposed as a more accurate measure (Welch & Eveson 1999).
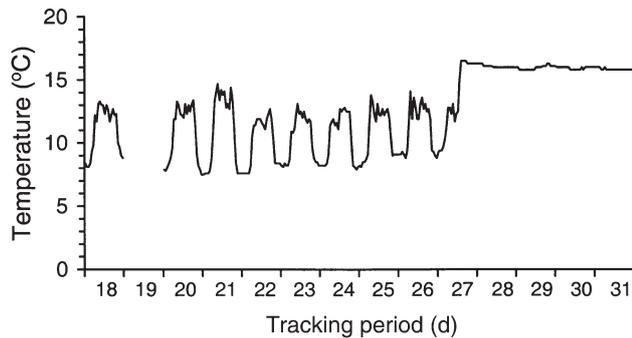
Fig. 5. Variation in water temperature recorded over a 9 d period for Eel 49 (*Anguilla dieffenbachii*). Note that data for Day 19 were unrecovered

Duration of marine migration

Freshwater eels are presumed to be derived from tropical marine species that later invaded fresh water (Tsukamoto & Aoyama 1998). Thus, the known spawning grounds of the temperate species *Anguilla anguilla*, *A. rostrata*, and *A. japonica* are in the tropics, and it seems reasonable to assume that spawning grounds of other temperate *Anguilla* spp. will also be in the tropics. The present paper describes the first attempt to partially track migrating *A. dieffenbachii* to such spawning areas.

The duration of the adult migration of New Zealand eels from fresh water to the spawning grounds is unknown. Based on an assumed larval life of 15 mo, and peak times of adult migration and glass eel recruitment, Jellyman (1987) suggested it could be as little as 4 mo for *Anguilla australis.* However, lengths of larval life determined from ages of glass eels are considerably less than this, with age of recruitment to fresh water for *A. australis* being 208 to 326 d (Arai et al. 1999, Maru et al. 2001, Shiao et al. in 2001). Equivalent estimates for *A. dieffenbachii* are 240 to 332 d (Maru et al. 2001).

The main months of longfin glass eel arrival in New Zealand are September to October (Jellyman et al. 1999), while most seaward migrating longfin females depart from New Zealand during May and June (Todd 1981a). Using these dates, together with an average larval life of 10 mo, it is likely that spawning of *Anguilla dieffenbachii* takes place about January—if this is correct, then the migration and spawning of female longfin eels would average about 6 to 7 mo.

Did the tags detach prematurely?

There were 2 issues here. Firstly, transmissions for all tags were first picked up between 2 and 6 d before the scheduled dates, indicating a small error in the programmed ascent times. The second and more important issue was whether the tag bridle broke before the scheduled pop-up time, and the tags then drifted at the surface, meaning that the swimming tracks were at least partly surface drift. In the absence of depth information, it is not possible to answer this question unequivocally. The failure of the inclinometer to produce consistent results indicated that eels did not swim continuously, with the result that the tags sometimes assumed a vertical position rather than the off-vertical position associated with continuous swimming. Unfortunately, comparison of water temperatures recorded by tags with satellite SSTs, also failed to produce clear evidence of differences between the 2 data sets, consistent with the tags being within the water column rather than at the surface. Failure to find such temperature differences may have been because most eels swam in the vicinity of the Chatham Rise, where temperature patterns are often complex, due to the convergence of sub-tropical water and sub-Antarctic water (Heath 1985, Carter et al. 1998).

Comparison of the tracks of individual tags with generalised surface current patterns indicates that it was unlikely tags had detached prematurely and were drifting at the surface. For example, Tags 80 and 81 showed contrasting patterns of movement, with Tag 80 moving north then southeast, and Tag 81 moving southeast, northeast, and then south. As there is a general eastward surface current in the vicinity of 42 to 43° S (Heath 1985), the track of Tag 80 could conceivably be explained by surface drift, that of Tag 81 could not—the pattern of inshore surface currents along the northeast coast of the South Island represents a strong northeast current that extends beyond Cook Strait to the lower east coast of the North Island (Carter et al. 1998). Further, once both tags ascended, their positions were tracked for an additional 10 d, during which time they both moved in a clockwise direction, presumably within an eddy. Such circular movement was in complete contrast to the directed movement from the estimated swimming tracks.

Swimming direction

Assuming that the spawning grounds of *Anguilla dieffenbachii* are tropical, then overall northeast movement was expected. In practice, after some initial longshore movement, all 4 eels swam along, or in the vicinity of, the Chatham Rise. This rise is the shallowest region extending offshore on the east coast of New Zealand and is responsible for the separation of northern (sub-tropical) and southern (subantarctic) water masses (Vincent et al. 1991). Passage along the rise

would result in eels remaining over New Zealand's continental shelf for an extended period.

Swimming speed

The tags were pre-programmed to ascend after 2 or 3 mo. Based on the estimates of an adult migration of twice this duration, and assuming a constant swimming speed, the eels could have covered up to half the distance to the spawning grounds within 3 mo. In practice, maximum straight line distances offshore achieved by the tagged eels were 1000 km. Given that distances from New Zealand to possible tropical spawning areas could be as much as 5000 km (Jellyman 1987), it is difficult to believe that the eels would have swum the remaining distance within 3 more mo.

There are 2 possible explanations for this observation. The first is that *Anguilla dieffenbachii* does not spawn in tropical areas, but in closer temperate areas to the east of New Zealand. This possibility is at variance with the known spawning habits of other temperate *Anguilla* species and is considered unlikely. However, it is consistent with the observation by Todd (1981b) that *A. dieffenbachii* is more sexually advanced at migration than *A. australis* and may not travel as far to spawn. The second possibility is that the presence of the tags inhibited the swimming speed of the eels.

External tags are known to affect swimming speeds of fish, but most authors have reported few problems when tags do not exceed 2% of the fishes bodyweight (e.g. McCleave & Stred 1975, Moser et al. 1990, Thorstad et al. 2000). In studies using surgically implanted dummy (Baras & Jeandrain 1998) and actual transmitters (Baras et al. 1998) in *Anguilla anguilla*, tags weighed <0.6% of body weight, and none were expelled. In the present study, tags weighed <1% of body weight (range 0.6 to 0.9%), well below the 2% threshold. While the positive buoyancy of the tags might result in some initial swimming difficulties, this would be overcome by the highly functional swim bladder of migratory eels (Kleckner & Krueger 1981, Yamada et al. 2001). Although the tags are relatively streamlined, the effect of drag could inhibit swimming speed.

The swimming speeds of eels in the present study averaged 1.06 km h^{-1}, and were generally similar to the average speeds calculated from tracking studies of *Anguilla anguilla*. For example, Tesch (1974) recorded speeds of migrating eels of 2 km h^{-1}, and subsequently 0.5 km h^{-1} (Tesch 1978, Tesch et al. 1991) and 0.83 to 1.69 km h^{-1} (Tesch 1989); more recently, McCleave & Arnold (1999) found that migrating eels swam at 0.79 to 2.09 km h^{-1}. Various factors that may affect swimming speed have been suggested, including diel periodicity, moonlight and lunar phase (Tesch 1989), depth

(Tesch 1989), and tidal currents (McCleave & Arnold 1999). Artificially matured eels have either shown little movement (Fricke & Kaese 1995, Kuo et al. 1996), or similar swimming speeds to silver eels (Tesch 1989).

Swimming depth

Evidence of diel movement within the water column (Eel 49) indicates that eels were able to adjust their swimming depth. Such diel movement was not recorded regularly, and these 9 d were the only ones where temperature variations were sufficient to indicate significant diel movement. Migratory *Anguilla anguilla* tracked in inshore marine areas have generally shown similar 'classical' diel vertical movement, ascending at dusk and descending at dawn (e.g. Tesch 1978, 1989, Westerberg 1979, Tesch et al. 1991, McCleave & Arnold 1999), although both *A. anguilla* and *A. rostrata* have also shown reverse diel movements, i.e. ascending during daylight and descending during night (Stasko & Rommel 1974, Tesch 1978, McCleave & Arnold 1999).

Migrating eels are known to swim within the water column and not along the sea bottom (e.g. Stasko & Rommel 1974, Tesch 1989, Tesch et al. 1991). Swimming depths vary diurnally—for instance: 196 m during darkness and 344 m during daylight (Tesch 1989); 50 to 215 m at night and >400 m during daylight (Tesch 1978). Artificially matured *Anguilla anguilla* released in the Sargasso Sea did not descend beyond 300 m (Fricke & Kaese 1995), while partially matured *A. japonica* swam at mean depths ranging from 81 to 172 m (Aoyama et al. 1999b). Experimental evidence from maintenance of swimbladder volume (Kleckner 1980) and temperatures required for gonad maturation (Boetius & Boetius 1967) are also consistent with migration and spawning within 200 m of the surface. Although depth was not recorded during the present study, the fact that light levels could be recorded on most days indicated that eels remained within the euphotic zone, at least during daylight hours. The depth of this zone varies seasonally according to plankton productivity, but during the period when the eels were at large it would range as deep as 100 to 200 m (M. Gall, NIWA, pers. comm.).

CONCLUSIONS

The primary purpose of the study was to ascertain whether pop-up tags could be used to provide information on the direction and swimming speed of migrating *Anguilla dieffenbachii*. Given that adult marine migration could last for 6 mo or more, it was not expected that the tag ascent locations would indicate

spawning areas, but rather there would be some consensus of direction and swimming speed by all 4 eels. Somewhat surprisingly, all 4 eels showed a definite eastward movement, sometimes after initial longshore (north and south) movements. On the assumption that the spawning grounds of *A. dieffenbachii* are tropical, definite northward movement was expected but not found. Given the small number of tags deployed and the limited tracking time of the eels, further speculation on the possible location of the spawning ground is not warranted. The results indicate that further studies using pop-up tags of increased duration could be extremely useful in demarcating probable spawning grounds of *A. dieffenbachii.* Of course, any reduction in size of the tags would be advantageous, and would allow tracking of smaller species of *Anguilla.*

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