



Distribution of anguillid leptocephali and possible spawning areas in the South Pacific Ocean

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ABSTRACT

Seven South Pacific anguillid eel species live from New Guinea to French Polynesia, but their spawning areas and life histories are mostly unknown despite previous sampling surveys. A July–October 2016 research cruise was conducted to study the spawning areas and times, and larval distributions of South Pacific anguillid eels, which included a short 155°E station-line northeast of New Guinea and five long transects (5–25°S, 160°E–140°W) crossing the South Equatorial (SEC) and other currents. This survey collected nearly 4000 anguilliform leptocephali at 179 stations using an Isaacs-Kidd Midwater Trawl accompanied by 104 CTD casts. Based on morphometric observations and DNA sequencing, 74 anguillid leptocephali were collected, which in the southern areas included 29 larvae of six species: *Anguilla bicolor pacifica*, *A. marmorata*, *A. australis*, *A. reinhardtii*, *A. megastoma*, and *A. obscura* (all anguillid species of the region were caught except *A. dieffenbachii*). Small *A. australis* (9.0–16.8 mm) and *A. reinhardtii* (12.4, 12.5 mm) leptocephali were collected south of the Solomon Islands, other *A. australis* (10.8–12.0 mm) larvae were caught northwest of Fiji along with an *A. obscura* (20.0 mm) larva, and an *A. marmorata* (7.8 mm) larva was collected near Samoa. Considering collection sites, larval ages from otolith analysis, and westward SEC drift, multiple spawning locations occurred from south of the Solomon Islands and the Fiji area (16–20 days old larvae) to near Samoa (19 days old larva) during June and July in areas where high-salinity Subtropical Underwater (STUW, ~150 m depth) and the warm, low-salinity surface Fresh Pool were present. Five long hydrographic sections showed the strong Fresh Pool in the west and the STUW formation area in the east.

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1. Introduction

Catadromous freshwater eels of the genus *Anguilla* live in freshwater and estuarine habitats during their juvenile growth stage and then migrate into the ocean to reproduce. The 19 species and subspecies of anguillid eels live in areas adjacent to all major ocean gyres, except the South Atlantic and eastern Pacific (Ege, 1939; Watanabe, 2003; Watanabe et al., 2009). Many of these species have experienced population declines and there are concerns about their conservation status (Tsukamoto et al., 2009; Jacoby et al., 2015; Drouineau et al., 2018), so research efforts have increased in recent years to understand all aspects of their life histories to facilitate conservation efforts as many questions remain unanswered about these species (Righton et al., 2012).

A fundamental aspect of understanding the life history and population ecology of each anguillid species is where they spawn in the ocean and how their larvae are transported to their recruitment areas. The spawning areas of some species such as the European eel *Anguilla anguilla*, American eel *A. rostrata*, and Japanese eel *A. japonica*, were discovered by collecting smaller-and-smaller larvae (Schmidt, 1922; Tsukamoto, 1992), as reviewed in previous studies (McCleave, 2003; Tsukamoto et al., 2003; Shinoda et al., 2011; Miller et al., 2015, 2019). Their spawning areas were then evaluated from hydrographic perspectives in later years, which indicated that features such as oceanic fronts seem to help define where spawning is likely to occur (Kleckner and McCleave, 1988; Munk et al., 2010; Aoyama et al., 2014; Schabetsberger et al., 2016).

Efforts then shifted to discover where tropical species of anguillid eels in the Indo-Pacific spawn, after only one spawning area was found off Sumatra in the eastern Indian Ocean during the Danish Round the World expedition in 1928–1930 (Schmidt, 1935; Jespersen, 1942). Some anguillid leptocephali were collected in the South Pacific (Jespersen, 1942; Castle, 1963), but their body sizes were somewhat large to suggest the possible spawning area of the species.

Decades later, some small anguillid leptocephali were collected south of the Solomon Islands along the northeastern edge of the Coral Sea, and genetic identification, indicated that at least one of the subspecies of *A. australis* and *A. reinhardtii*, likely spawn in the South Equatorial Current (SEC) (Aoyama et al., 1999; Kuroki et al., 2008) and then recruit to either Australia or New Zealand (Shiao et al., 2001, 2002; Jellyman, 2003; Watanabe et al., 2006). It was also reported that some tropical eels such as *A. borneensis* and *A. celebesensis* spawn locally in the deep basins within the Indonesian Seas, without making long migrations to outside ocean areas (Aoyama et al., 2003, 2018). The North Pacific population of *A. marmorata* that recruits to the central Indonesian Seas as well as areas farther to the northwest was found to spawn in the North Equatorial Current (NEC) in an overlapping area with the Japanese eel (Kuroki et al., 2009). Efforts to understand the spawning areas and early life histories of anguillid eels in the Indian Ocean have produced some information about the leptocephali (Aoyama et al., 2007; Kuroki et al., 2007) and recruitment-stage glass eels (Robinet et al., 2003, 2008; Réveillac et al., 2009), but where the spawning areas are located are still only estimated from transport modeling studies (Pous et al., 2010).

The South Pacific region extending from Australia to French Polynesia in the central Pacific is inhabited by seven species and subspecies of anguillid eels (Jellyman, 1987, 2003), but many aspects of their life histories remain poorly understood. The geographic distribution ranges of each species extend across the boundaries and jurisdictions of many different countries in the region and require international cooperation for their management and conservation. Only *A. dieffenbachii* that is endemic in New Zealand is exclusively present in only one area, whereas other species (*A. marmorata*, *A. megastoma*, and *A. obscura*) are widely distributed across the South Pacific (Ege, 1939). *Anguilla reinhardtii* is distributed in northeastern Australia and nearby islands, and *A. australis* is separated into two subspecies that recruit to either Australia (*A. australis australis*) or New Zealand (*A. australis*

schmidtii).

The recruitment patterns of glass eels to tropical islands such as French Polynesia and Fiji have begun to be studied (Helme et al., 2018; Hewavitharane et al., 2019). Other efforts to find the spawning areas of tropical eel species in the South Pacific have been conducted using pop-up satellite archival tags (PSATs) on adult silver eels (e.g., Jellyman and Tsukamoto, 2002, 2010; Schabetsberger et al., 2013, 2019). However, there are major gaps in understanding most aspects of the life histories of all anguillid eel species in the South Pacific. Therefore, a wide range of research is needed to learn about when and where each species or population spawns, how their larvae are distributed, and what their recruitment patterns are. It has been considered that at least some eel species in the western South Pacific likely use the westward flow of the SEC to transport their larvae towards their recruitment areas in Australia and New Zealand (Jellyman, 1987, 2003; Shiao et al., 2001, 2002; Kuroki et al., 2008; Jellyman and Bowen, 2009). However, for the other species that live on the many offshore islands in the South Pacific, it is less clear where they spawn and how their larvae use current systems for transport.

Other aspects of the hydrographic structure of the western South Pacific that have been considered to possibly help define the spawning areas of anguillid eels in the region (Schabetsberger et al., 2016) include the presence of the “Pacific Warm Pool” that forms from about 20°N and 15°S (Delcroix, 1998; Delcroix et al., 2000) and extends into the northern area, with decreasing water temperatures to the south, as well as some clear salinity structures. The shallow surface layer of low-salinity water (e.g. 34.4–34.7) referred to as the Equatorial Pacific “Fresh Pool” extends into the region north of Fiji, but may not extend much farther east (Delcroix and Picaut, 1998; Hénin et al., 1998). These features can be seen clearly in various types of hydrographic sections (Roden, 1998; Schabetsberger et al., 2016). Below the Fresh Pool in the western South Pacific is a layer of high-salinity water (e.g. 35.7–36.0) that has been referred to by names such as the southern Tropical Water (Gouriou and Toole, 1993), but is now realized to occur in specific regions throughout the world and is referred to as Subtropical Underwater (STUW) (see Schabetsberger et al., 2016). This water forms at the surface in specific areas where there is excess evaporation compared to precipitation, which results in surface salinity maximum areas forming in each ocean gyre (Gordon et al., 2015), including in the central South Pacific (Hasson et al., 2013), where it is subducted into the thermocline (Qu et al., 2008, 2013; Zhang and Qu, 2014).

The objective of the present study was to learn about the spawning areas, early life histories and possible patterns of larval transport of anguillid eel species in the South Pacific in relation to the hydrographic features of the region by conducting a sampling survey in 2016. The survey sampled for eel larvae in five long transects across the SEC, the collected larvae were aged using their otolith microstructure, and extensive hydrographic observations were made, which provided new information about the possible spawning areas of anguillid eels in the South Pacific.

2. Materials and methods

2.1. Sampling and oceanographic observations

The KH-16-4 research cruise from 10 July to 3 October 2016 by the R/V *Hakuho Maru* (JAMSTEC) was conducted mainly in the South Pacific (Fig. 1). Two stations (14°N and 16°N, 137°E) where anguillid leptocephali including *A. japonica* and *A. marmorata* were collected, and six stations (5.5–11.5°N, 149–164°E) where no anguillid leptocephali were collected in the North Pacific were excluded from the present study, because this study focuses on sampling in the southern areas that was conducted to continue the exploration of the spawning areas of anguillid eels by sampling across the South Pacific. These southern stations were sampled from 21 July to 11 September and included a short transect along 155°E from 5°N to 1°S and five long transects from

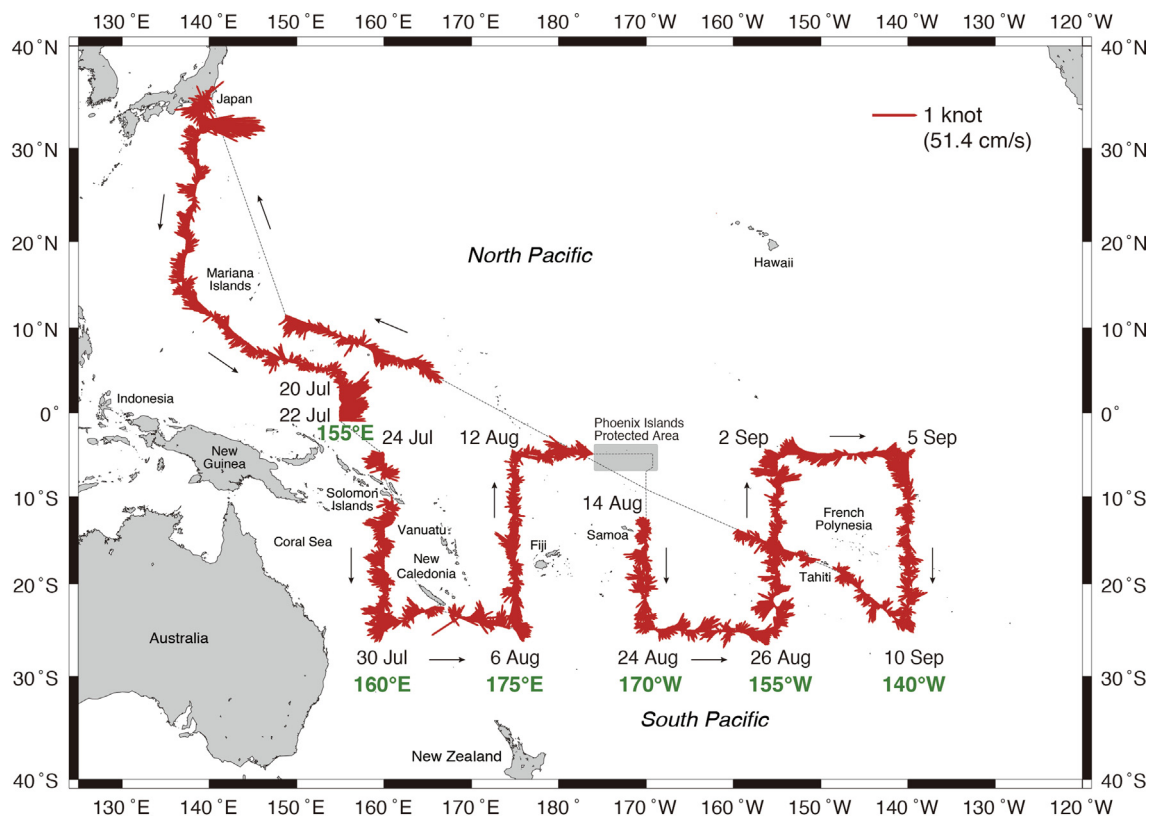


Fig. 1. Track chart of the R/V *Hakuho Maru* KH-16-4 cruise and Acoustic Doppler Current Profiler (ADCP) vectors that were measured at 100 m depth along the ship track during the cruise from July to October 2016. The Phoenix Islands Protected Area (PIPA) in the Republic of Kiribati was excluded from the ADCP observations.

5°S to 25°S along 160°E, 175°E, 170°W, 155°W, and 140°W (Fig. 1). Small islands and some EEZ (Exclusive Economic Zones) were avoided along the transects.

A total of 179 stations were sampled during the whole cruise, with the present study analyzing data from the 171 stations in the southern areas, which included 13 stations within the short transect and 158 stations in the five long latitudinal transects (Fig. 2). All net sampling was conducted using an 8.7 m² mouth opening Isaacs-Kidd Midwater Trawl (IKMT) with 0.5 mm mesh. The IKMT was fished using step tows at three depth layers from the surface to 200 m, with the depths of the towing layers being adjusted slightly according to the depth of thermocline or acoustic scattering layers using CTD and Acoustic Biomass Investigation System (ABIS, Furuno Electric Co., Ltd.) information. Each towing time was about 1–1.5 h and the ship speed during the tows was 2–3 knots.

The 104 CTD (Conductivity, Temperature, and Depth) casts of the short transect from 5°N to 1°S at 155°E and five transects from 5°S to 25°S of latitude and from 160°E to 140°W of longitude in the western South Pacific were made at every other IKMT station (Fig. 2). As a result, casts were made at every one degree of latitude except for two transects where there were fewer stations due to the avoidance of the Solomon Islands in the 160°E transect and time constraints along 140°W (Fig. 1). This resulted in there being 21 CTD casts per transect, except in the westernmost (18 casts) and easternmost (16 casts) transects. The data from the CTD casts were used to plot hydrographic sections of temperature and salinity along each transect to a depth of 800 m using the Ocean Data View (ODV) program (<https://odv.awi.de/>). Current velocity vectors at 100 m were plotted using Acoustic Doppler Current Profiler (ADCP) current data from an ADCP device (38 kHz, TRDI) attached to the bottom of the ship except for the Phoenix Islands Protected Area (PIPA) in the Republic of Kiribati.

2.2. Morphology and genetic identification

The majority of the nearly 4000 anguilliform leptocephali that were collected in the survey were identified morphologically to be the larvae of many different families of marine eels. All anguillid leptocephali collected were examined morphologically on board using a stereo microscope while fresh following the identification methods of Miller and Tsukamoto (2004). Counts were made of the position of their last vertical blood vessel (LVBV), preanal myomeres (PAM), predorsal myomeres (PDM) and total myomeres (TM), and their number of anodorsal myomeres (distinguishes shortfin and longfin species) could then be determined from the PAM and PDM counts. The onboard myomere counts for the small larvae were only approximate. Some of the leptocephali from the southern region were photographed using a microscope camera (DXM1200F, Nikon) attached to a stereo microscope (SMZ-1500, Nikon). A portion of tissue of all specimens was preserved in 99% ethanol for further genetic analysis.

An onboard real-time PCR system was used to identify selected anguillid species (e.g., Tsukamoto et al., 2011), except in this case with more species potentially being present during the cruise. The final identifications were made by comparing about 500 base pairs of the mitochondrial DNA 16S ribosomal RNA gene sequences between the collected leptocephali and morphologically well-identified yellow eel specimens, as was done in a previous study following the procedure of Aoyama et al. (2007).

2.3. Otolith analysis

The ages of the southern region anguillid leptocephali collected in this study were analyzed using counts of their otolith daily growth rings and the ages were used to back-calculate their hatching dates. Each sagittal otolith was embedded in epoxy resin (Epofix, Struers), mounted on a glass slide, ground to near the core using a grinding machine (70

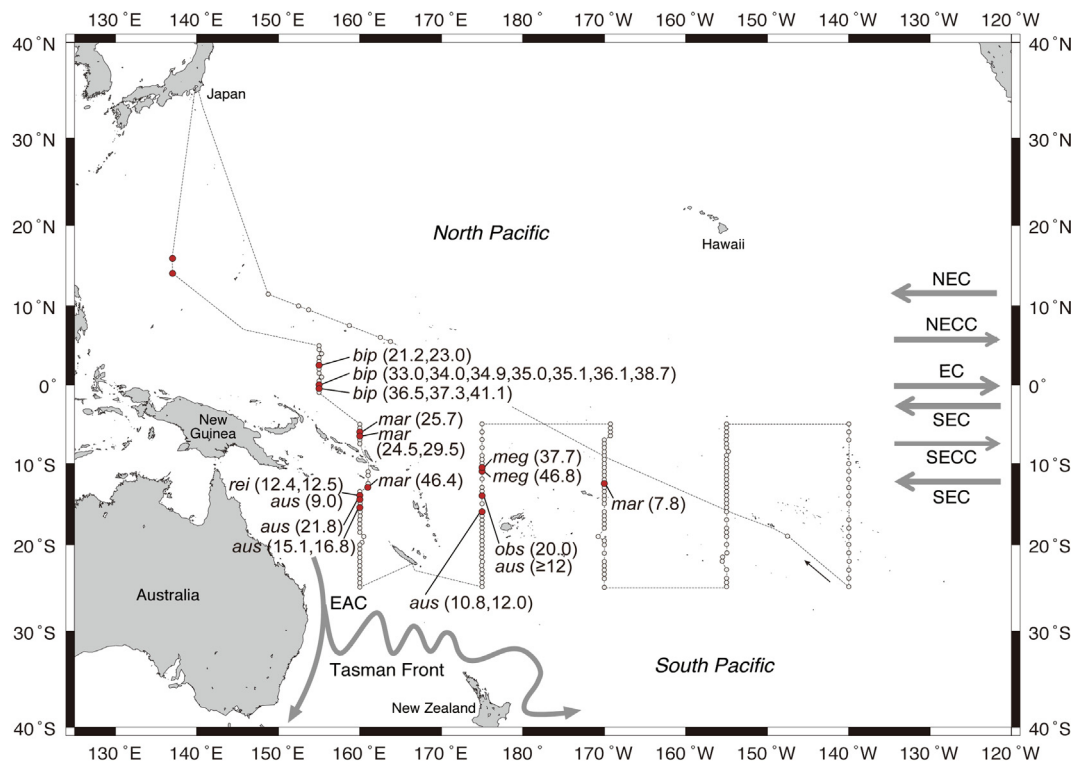


Fig. 2. Map of the sampling stations (open circles), major current latitudes or locations in the western Pacific, and collection locations (red circles) and total lengths (in parentheses) of anguillid eel leptocephali, which included *Anguilla bicolor pacifica* (*bip*), *A. marmorata* (*mar*), *A. megastoma* (*meg*), *A. obscura* (*obs*), *A. reinhardtii* (*rei*), and *A. australis* (*aus*). The latitudes of the North Equatorial Current (NEC), North Equatorial Countercurrent (NECC), Equatorial Current (EC), South Equatorial Current (SEC), South Equatorial Countercurrent (SECC) (arrows on right side of map), and the locations of East Australian Current (EAC) and Tasman Front are shown. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and 13 μm diamond cup-wheels, Discoplan-TS, Struers) and further polished to expose the core (3 μm Silicon Carbide grinding paper and OP-S suspension, Planopol-V, Struers). After cleaning the surface, each otolith was etched with 0.05 M HCl and vacuum coated with Pt-Pd in an ion-sputterer (E-1030, Hitachi) for scanning electron microscope observations (S-4800, Hitachi). The age of each specimen was determined by counting the number of successive daily rings from the hatch check to the otolith edge at magnifications of 600–1200 \times . Hatching date was back-calculated from age and collection date of each specimen.

3. Results

3.1. Hydrographic features and currents

The ADCP current vector data at 100 m depths showed some areas with strong currents, others with weak flow patterns and other areas that were possibly dominated by large mesoscale eddies. Strong eastward flows were observed within the North Equatorial Countercurrent (NECC), and the northern areas of the two eastern long transects had strong westward flows, which were likely part of the northern branch of the SEC. Strong westward flows also occurred at SEC latitudes along the 160°E transect and at two locations of the 175°E transect passing to the west of Fiji. At higher latitudes at 20–25°S, the current directions consistently alternated, suggesting large eddies were present (Fig. 1).

The hydrographic sections plotted from the five long transects of CTD casts across the latitudes of the SEC region from 155°E to 140°W (Fig. 2) showed there was a generally consistent pattern of a warmer layer of surface water (25–30 °C) being present in the upper 100 m extending down to at least 20°S across the region (Fig. 3a–e). The surface water cooled slightly in the east, with maximum temperatures being 28 °C (155°W) and 27 °C (140°W), compared to mostly 29 °C in the western transects. In contrast, the salinity sections showed

considerable variations from west to east (Fig. 3f–j) that were caused by the low salinity surface-layer referred to as the Fresh Pool and the subsurface-layer of high salinity STUW. The Fresh Pool was distinctly present in the three western transects (minimum of 34.3 in 175°E), but it became less distinct in the two eastern transects (minimum of 35.2 in 140°W). The STUW forms in the eastern region of the South Pacific and extends westward, so it was least distinct in the westernmost transect, and the salinity values in each transect steadily increased in the eastern direction (maximum of 35.9 in the west and 36.5 in the east). The STUW extended farther north in the two eastern transects and it reached the surface in the easternmost transect because that transect was within the region of high evaporation where it forms. The shorter 155°E transect near the equator in the northwestern area showed some slightly different hydrographic characteristics (Fig. 4). There was a consistent and slightly deeper mixed layer of 29–30 °C water in the upper 75 m above the thermocline across those latitudes. The surface layer had slightly lower salinity (34.1) and the STUW also reached a lower value (35.6) compared to the transects. Comparing the ADCP data and the contour structure, the NECC was present in about the southern two-thirds of the short transect and there was no STUW north of the eastward NECC flow (Figs. 1 and 4).

3.2. Size and age of anguillid leptocephali

The onboard morphometric observations and subsequent DNA sequencing found that 29 anguillid leptocephali of six species; *A. bicolor* ($n = 12$), *A. marmorata* ($n = 5$), *A. australis* ($n = 7$), *A. reinhardtii* ($n = 2$), *A. megastoma* ($n = 2$), and *A. obscura* ($n = 1$), were collected in the equatorial region and the South Pacific (2.5°N–16°S, 155°E–170°W) during the period of July–August 2016 (Table 1, Fig. 2). No anguillid larvae were collected in the two eastern transects of 155°W and 140°W or at any of the southern stations from 16.5°S to 25°S, although

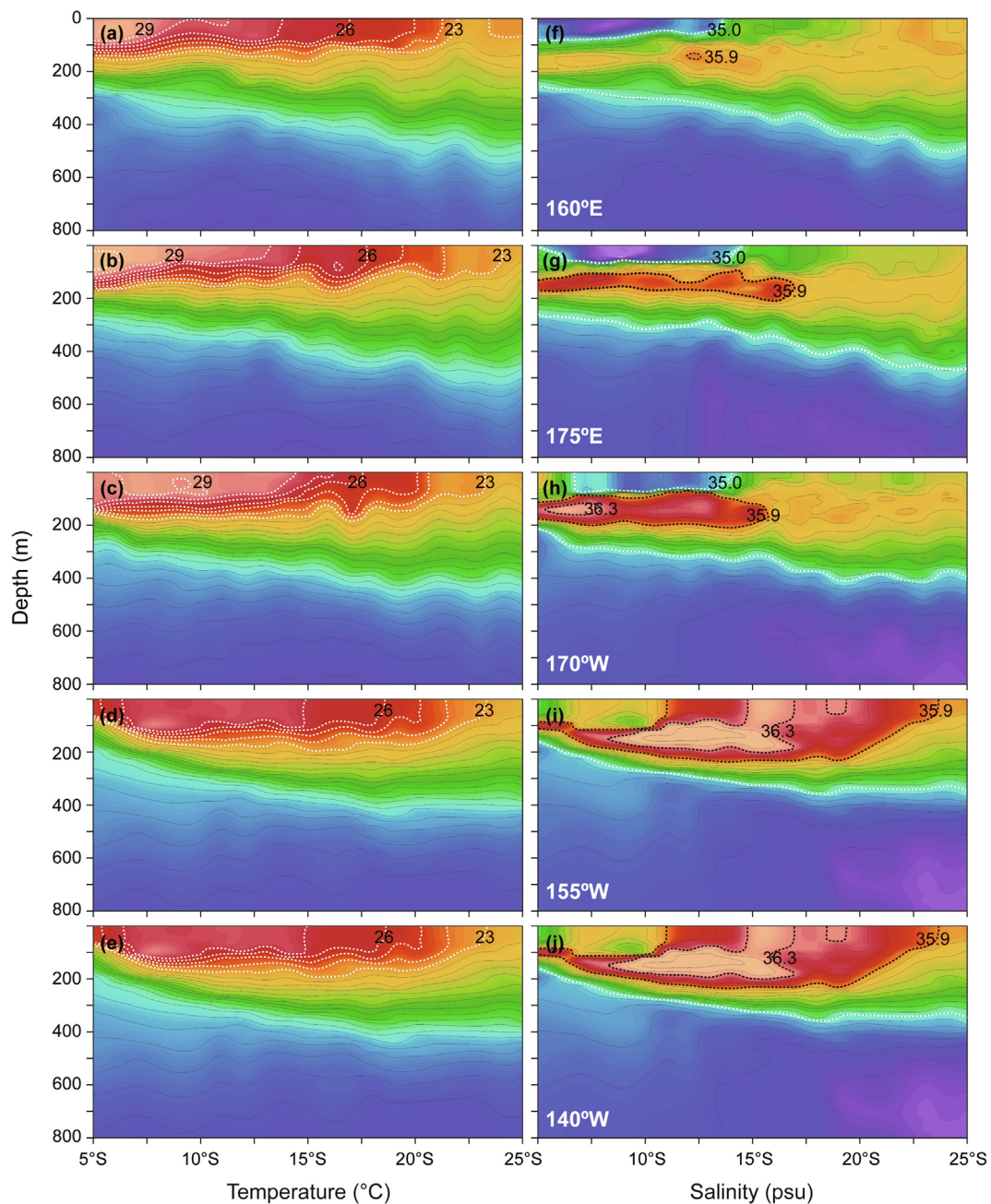


Fig. 3. Hydrographic sections of temperature ($^{\circ}\text{C}$) and salinity (psu) constructed using data from a conductivity temperature depth profiler (CTD) along the five transects of 160°E (24–30 July), 175°E (6–12 August 2016), 170°W (14–24 August 2016), 155°W (26 August–2 September 2016) and 140°W (5–10 September 2016) routes that are labeled in Fig. 1.

sampling was conducted in the same way in those areas.

Twelve middle-sized *A. bicolor* leptocephali (21.2–41.1 mm, 46–110 days) were collected in the NECC area to the northeast of New Guinea, but none were found anywhere else. Four middle to large-sized leptocephali of *A. marmorata* (24.5–46.4 mm, 46–120 days) were collected to the north and south of the Solomon Islands and a small leptocephalus of that species (7.8 mm, 19 days, Fig. 5a) was caught near the northeast side of Samoa (Fig. 2). That leptocephalus is the easternmost and the smallest specimen of that species ever found in the South Pacific.

Four leptocephali of *A. australis* (9.0–21.8 mm, 16–46 days) were collected at three stations south of the Solomon Islands in the northeastern Coral Sea along the 160°E transect and three other larvae of this species (10.8–12.0 mm, 19–30 days, Fig. 5b) were caught almost

1600 km to the east, not far to the northwest of Fiji along 175°E (Fig. 2). One ~12.0 mm *A. australis* specimen could not be accurately measured because of damage to the caudal fin.

Two small leptocephali of *A. reinhardtii* (12.4 and 12.5 mm, 20 and 26 days, Fig. 5c) were collected at one of the same stations (14°S , 160°E) with *A. australis* in the westernmost transect. Two *A. megastoma* (37.7 and 46.8 mm, 71 and 110 days) and one *A. obscura* leptocephali (20.0 mm, 37 days) were caught in the region to the northwest of Fiji (Fig. 2). The *A. megastoma* larvae were collected a little farther north than the *A. obscura* larva.

3.3. Hatching season

Hatching dates of each anguillid leptocephalus specimen in the

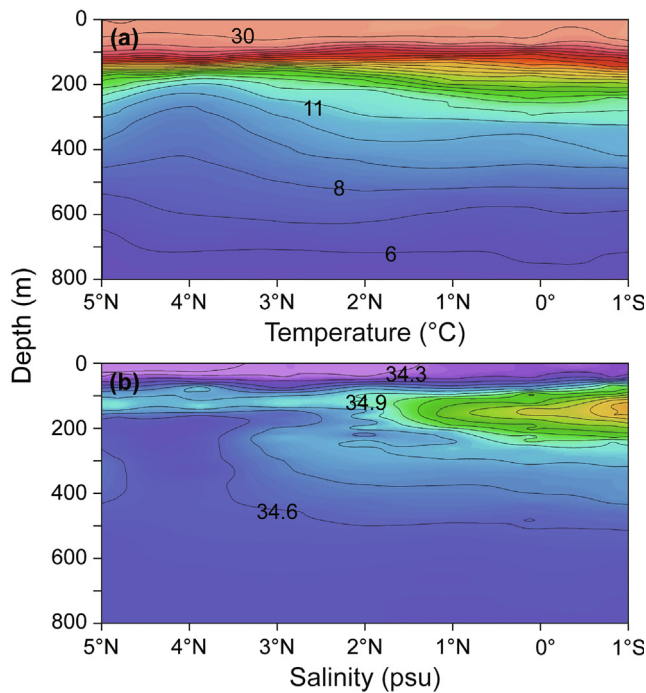


Fig. 4. Hydrographic sections of (a) temperature and (b) salinity constructed using data from a conductivity temperature depth profiler (CTD) along the 155°E transect (20–22 July 2016) northeast of New Guinea that is labeled in Fig. 1.

southern area were calculated from the estimated age determined from their otolith daily rings. The hatching season for the six species ranged across the five months from late March to late July 2016 before the larvae were collected in July and August, with the range of months for

Table 1

Collection data, total length (mm), total myomeres, and age (days) of the anguillid leptocephali collected in the southern region during the R/V *Hakuho Maru* KH-16-4 cruise.

No.	Collection date	St.	Latitude	Longitude	Species	Total length	Total myomeres	Age
257	22 July 2016	24	2°30'N	155°00'E	<i>A. bicolor pacifica</i>	23.0	103	55
258	22 July 2016	24	2°30'N	155°00'E	<i>A. bicolor pacifica</i>	21.2	105	46
268	23 July 2016	29	0°00'	155°00'E	<i>A. bicolor pacifica</i>	33.0	106	62
269	23 July 2016	29	0°00'	155°00'E	<i>A. bicolor pacifica</i>	34.9	106	84
270	23 July 2016	29	0°00'	155°00'E	<i>A. bicolor pacifica</i>	35.0	104	91
271	23 July 2016	29	0°00'	155°00'E	<i>A. bicolor pacifica</i>	35.1	104	78
272	23 July 2016	29	0°00'	155°00'E	<i>A. bicolor pacifica</i>	34.0	106	75
273	23 July 2016	29	0°00'	155°00'E	<i>A. bicolor pacifica</i>	36.1	105	83
274	23 July 2016	29	0°00'	155°00'E	<i>A. bicolor pacifica</i>	38.7	106	91
297	23 July 2016	30	0°30'S	155°00'E	<i>A. bicolor pacifica</i>	36.5	107	72
298	23 July 2016	30	0°30'S	155°00'E	<i>A. bicolor pacifica</i>	41.1	106	110
299	23 July 2016	30	0°30'S	155°00'E	<i>A. bicolor pacifica</i>	37.3	106	71
342	24 July 2016	34	6°00'S	160°00'E	<i>A. marmorata</i>	25.7	101	46
374	25 July 2016	35	6°30'S	160°00'E	<i>A. marmorata</i>	24.5	110	51
375	25 July 2016	35	6°30'S	160°00'E	<i>A. marmorata</i>	29.5	108	60
512	26 July 2016	42	13°00'S	160°00'E	<i>A. marmorata</i>	46.4	107	120
526	27 July 2016	44	14°00'S	160°00'E	<i>A. reinhardtii</i>	12.5	~113	26
527	27 July 2016	44	14°00'S	160°00'E	<i>A. australis</i>	9.0	~111	16
531	27 July 2016	44	14°00'S	160°00'E	<i>A. reinhardtii</i>	12.4	107	20
536	27 July 2016	45	14°30'S	160°00'E	<i>A. australis</i>	21.8	111	46
541	27 July 2016	47	15°30'S	160°00'E	<i>A. australis</i>	15.1	108	27
542	27 July 2016	47	15°30'S	160°00'E	<i>A. australis</i>	16.8	106	29
1260	9 August 2016	87	16°00'S	175°00'E	<i>A. australis</i>	12.0	~114	30
1261	9 August 2016	87	16°00'S	175°00'E	<i>A. australis</i>	10.8	~113	19
1267	9 August 2016	91	14°00'S	175°00'E	<i>A. obscura</i>	20.0	108	37
1280	9 August 2016	91	14°00'S	175°00'E	<i>A. australis</i>	12.0 ^a	77 ^a	25
1334	10 August 2016	97	11°00'S	175°00'E	<i>A. megastoma</i>	46.8	108	110
1345	10 August 2016	98	10°30'S	175°00'E	<i>A. megastoma</i>	37.7	112	71
1696	16 August 2016	130	12°30'S	170°00'W	<i>A. marmorata</i>	7.8	~110	19

^a Larva was not measured accurately due to damage.

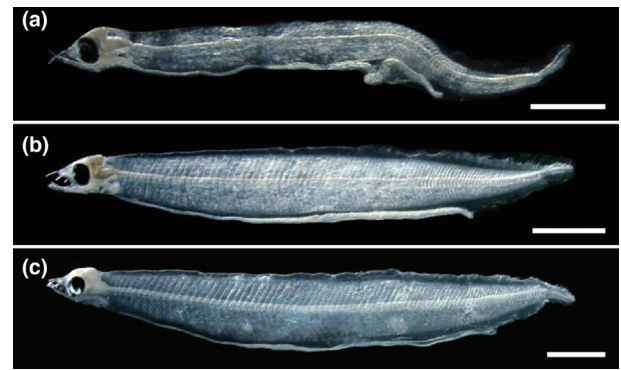


Fig. 5. Photographs of leptocephali showing (a) *Anguilla marmorata* (No. 1696, 7.8 mm) collected at 12.5°S, 170°W, on 16 August 2016, (b) *A. australis* (No. 1261, 10.8 mm) collected at 16°S, 175°E, on 9 August 2016, and (c) *A. reinhardtii* (No. 526, 12.5 mm) collected at 14°S, 160°E, on 27 July 2016. Scale bars indicate 1 mm.

each species depending on the size range of the collected larvae (Fig. 6). The wide range in sizes of *A. marmorata* larvae resulted in hatching dates from late March to late July. The other species were apparently hatched across ranges of within one to three months.

4. Discussion

4.1. Possible spawning areas of three anguillid eel species

The extensive sampling grid and hydrographic data of the 2016 survey that included the short transect northeast of New Guinea and five long transects, provided several types of interesting new information and clues about the spawning areas of anguillid eels in the region. Leptocephali < 15 mm were collected of three species; *A. marmorata* (smallest 7.8 mm), *A. australis* (smallest 9.0 mm), and *A. reinhardtii*

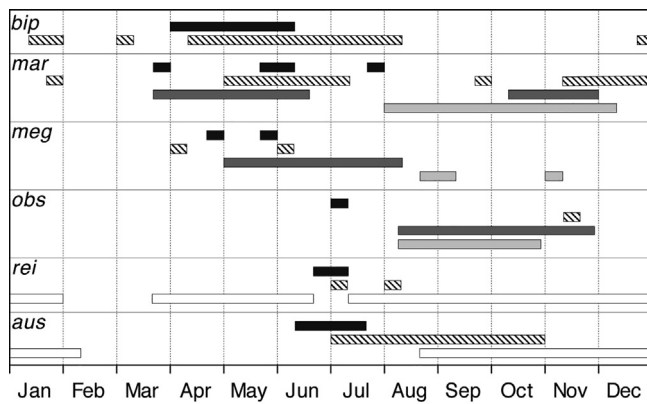


Fig. 6. Hatching seasons of *Anguilla bicolor pacifica* (*bip*), *A. marmorata* (*mar*), *A. megastoma* (*meg*), *A. obscura* (*obs*), *A. reinhardtii* (*rei*), and *A. australis* (*aus*). Hatching seasons were estimated from leptocephali collected in this cruise (black bars) and previous cruises (striped bars) from Kuroki et al. (2006) for *bip* in both the North and South Pacific, and from Kuroki et al. (2008) for five other species collected in the South Pacific, and for glass eels recruited to Fiji (dark gray bars) from Hewavitharane et al. (2019), glass eels recruited to Tahiti (light gray bars) from Sasal et al. (unpublished data), and glass eels recruited to Australia and New Zealand (white bars) from Shiao et al. (2001, 2002).

(smallest 12.4 mm). Each location where these small larvae were collected provides information about where the larvae could have been spawned when they are combined with the otolith aging estimates and the possible current flows in each area. The back calculated hatching data also provided useful information about when these eels may spawn. Combining the results of both present and previous studies estimated from leptocephali (Kuroki et al., 2008) and glass eels (Shiao et al., 2001, 2002; Helme et al., 2018; Hewavitharane et al., 2018, 2019), the spawning of each species appears to occur over a wide range of months. Hatching date estimates of *A. marmorata* from the various studies occurred in almost all months of the year, and almost to the same extent for *A. australis* and *A. reinhardtii* (Fig. 6).

As the survey moved south into the eastern Coral Sea the smallest *A. australis* larva ever collected (9.0 mm) was caught along with several 15–20 mm larvae and similar sized *A. reinhardtii* larvae. The morphology of these species of small larvae was quite similar to other small anguillid larvae (Fig. 5). This is the same location where 20–34 mm larvae of these species were also collected at about the same season of year in 1995 (Kuroki et al., 2008). The 9 mm *A. australis* larva collected about 700 km west of Vanuatu was estimated to be only 16 days old, so considering the general ADCP measurements and the likely presence of eddies (20 cm/s current would transport a larva approximately 276 km in 16 days), this larva was probably spawned on the west side of the Vanuatu Archipelago (Figs. 1 and 2). A few small 10–12 mm *A. australis* larvae were also collected to the northwest of Fiji in the 175°E transect. That location is almost 1600 km east of where the other small *A. australis* larvae were collected. Therefore, regardless of possible counter-current transport, it seems unlikely that the two groups of larvae were spawned in the same area. There were also small anguillid leptocephali ($n = 25$, 8.8–12.9 mm) collected in the same area northeast of Fiji (14–15°S, 175°E) in mid-August 1995 (Aoyama et al., 1999; Miller et al., 2006) that could not be genetically identified (formalin preserved), which could also have included *A. australis* larvae.

The 2016 specimens themselves though, are enough to suggest that there could be two different or overlapping spawning areas of *A. australis* in this western SEC region. Two anguillid species are known to spawn in overlapping areas in the Atlantic and North Pacific (Schmidt, 1922; Kuroki et al., 2009). But in the case of the two subspecies of *A. australis*, and considering the presence of the distinct geographic landmarks of large islands and the Vanuatu Archipelago, the two subspecies may have evolved separate spawning areas within the same

region, which would help maintain their morphological and genetic differentiation that has been observed (Watanabe et al., 2006; Shen and Tzeng, 2007). Schmidt (1928) had speculated that *A. australis australis* from Australia might spawn on the west side of the New Caledonian submarine ridge and that *A. australis schmidtii* from New Zealand might spawn on the east side of the ridge. Various other studies have subsequently evaluated where the spawning locations of these eels might be within the same general region between New Caledonia and Tahiti (e.g., Jespersen, 1942; Castle, 1963; Jellyman, 1987). The possible routes/distances of silver eel migration and durations of larval drifting before reaching recruitment areas might be two factors to consider when speculating about where it might be more adaptive for migrating silver eels of *A. australis schmidtii* from New Zealand or those of *A. australis australis* from Australia to spawn, if they do actually spawn in slightly different areas.

The larvae of *A. reinhardtii* were only collected to the west of Vanuatu during this and the previous surveys (Castle, 1963; Kuroki et al., 2008), suggesting their spawning area is only in one region of the SEC in the northeastern edge of the Coral Sea. That area seems to be the only area where *A. reinhardtii* leptocephali have been collected so far, and their glass eels recruit to areas ranging from northeastern Australia (farther north than *A. australis australis*) to eastern Tasmania, but not quite as far south as *A. australis australis* (Sloane, 1984; Shiao et al., 2002). Studies on the glass eels in Australia found that both *A. reinhardtii* and *A. australis* have a cline in age at recruitment from younger and smaller in size in the north to older and larger in the south (Shiao et al., 2002).

A few *A. reinhardtii* seem to recruit to northern New Zealand (McDowall et al., 1998), and *A. dieffenbachii* whose leptocephali have never been collected and identified, only recruits to New Zealand. The glass eels of *A. australis schmidtii* that recruit to the South Island of New Zealand were not much different in size or age than those of *A. australis australis* from southern Australia (Shiao et al., 2001), suggesting that the leptocephali take similar periods to reach both areas. The mean ages of *A. dieffenbachii* glass eels recruiting to New Zealand were found to be older than those of *A. australis schmidtii* (Marui et al., 2001). Considering the limited number of early life history studies on glass eels, and the mixture of sampling locations, times and years among the studies, it is difficult to reach any conclusions yet about the precise spawning areas and larval migrations of these Australian and New Zealand anguillid eel species and subspecies beyond what can be determined from the collection data of their small larvae in the SEC, and their absence at other latitudes.

It is similarly difficult to understand the spawning areas and life histories of other anguillid species in the South Pacific, because of their wide species distributions on most of the islands across the region and the possibility that they have more than one spawning population. *Anguilla marmorata* is the most widely distributed anguillid species because it is present across the entire Indo-Pacific from the western Indian Ocean to French Polynesia (Ege, 1939; Watanabe, 2003). Population genetic and morphology research indicates there are multiple populations of this species across its range, and there may be some population segregation between the eastern side (French Polynesia) and western side (Samoa, Fiji, New Caledonia, New Guinea) of the South Pacific (Ishikawa et al., 2004; Minegishi et al., 2008; Watanabe et al., 2008). Two tropical eel species of *A. megastoma* and *A. obscura* are similarly widely distributed and inhabit the same islands sympatrically with *A. marmorata* across the region (Jellyman, 2003; Watanabe, 2003), with *A. obscura* using the lower reaches of rivers, *A. marmorata* using the middle reaches, and *A. megastoma* using the upper reaches (Marquet and Galzin, 1991). Vertebral counts have also suggested there may be eastern and western populations of *A. megastoma*, but no differences were found for *A. obscura* (Watanabe et al., 2011). The present study provided the first clear evidence of a spawning location for these three species when the 7.8 mm *A. marmorata* leptocephalus (19 days old) was collected near Samoa. The region northeast of Vanuatu and northwest

of Fiji is where biologging research using PSATs on silver eels from Vanuatu have suggested there is a sympatric spawning area of *A. marmorata* and *A. megastoma* (Schabetsberger et al., 2013, 2016). Larvae of both those species have been collected in that area before the 2016 survey, including a 19.0 mm *A. marmorata* (Kuroki et al., 2008). There were also relatively small *A. marmorata* larvae ($n = 4$, 16.5–18.3 mm), about a month after hatching, collected at 8°S, 170–180°E in February 2013 (Kuroki et al. unpublished data) farther north closer to the pop-up locations of the PSATs. The 7.8 mm *A. marmorata* larva from this study would not be from that area though, and it seems unlikely that the larvae from northwest of Fiji would have been transported that far to the northwest from near Samoa, so at least this species may spawn at two different locations in the more western region of the South Pacific. A more recent PSAT study released eels of *A. marmorata* from Samoa and did not find evidence of the eels attempting to make a long migration away from that area (Schabetsberger et al., 2019), which is consistent with the collection of the 7.8 mm larva there.

4.2. Larval distribution of other anguillid eel species

The western Pacific subspecies of *A. bicolor pacifica* is one of the species for which there is little evidence about the location of their spawning area, and the short transect northeast of New Guinea sampled during the first part of the 2016 survey collected relatively small leptocephali (21.2, 23.0 mm) as well as larger ones within the strong eastward flow of the NECC. The previous collection of *A. bicolor pacifica* (24.0 mm) near New Guinea in 1995 (Kuroki et al., 2006) and the newly collected larvae that would have been transported eastward, suggests that their spawning area might be somewhere north of New Guinea as previously suggested (Kuroki et al., 2006; Miller and Tsukamoto, 2017). The other subspecies of *A. bicolor bicolor* inhabits the Indian Ocean and has at least one spawning area there off West Sumatra (Jespersen, 1942; Aoyama et al., 2007; Kuroki et al., 2007). The apparent spawning area of *A. bicolor pacifica* is in an area with interconnecting currents and eddy systems (Miller and Tsukamoto, 2017) that could result in the larvae becoming widely distributed to areas where they recruit, such as the Indonesian Seas (Sugeha et al., 2001), the Philippines (Shirotori et al., 2016), and as far north as southern Japan (Yamamoto et al., 2001). However, no larvae of this species have been collected and identified at sizes < 20 mm so far.

The same lack of collections of small larvae of several of the anguillid species in the South Pacific make it difficult to estimate the locations of their spawning areas, but some life history information is beginning to be obtained from studies on their glass eels. The 20.0 mm *A. obscura* caught northwest of Fiji was the smallest leptocephalus of that species ever to be collected and identified. This 37 days old larva could have been transported a considerable period by the SEC or eddies. *Anguilla obscura* is often the most abundant species that recruits to a small river area along the southern coast of the main island of Fiji, taking 141–204 days until recruitment there, which was somewhat longer than *A. megastoma* (126–163 days) and *A. marmorata* (124–183 days) that also recruited there (Hewavitharane et al., 2018, 2019). Two *A. megastoma* leptocephali (37.7 and 46.8 mm) caught at about 10°S to the northwest of Fiji were too large to provide any spawning location information. The glass eels of *A. megastoma* were much less abundant in Fiji (Hewavitharane et al., 2018). These tropical species having some glass eel recruitment during at least two periods of year or throughout most of the year (e.g., Sugeha et al., 2001; Hewavitharane et al., 2018) is different than the life-histories of temperate eel species that have single recruitment seasons.

One limitation of the present survey for determining the origins of both the large and small leptocephali collected during the survey and exactly where their spawning areas are located was the wide spacing between transects. The long transects were effective to establish the latitudinal zones where larvae may have been present, but there were

wide regions between the transects where many anguillid larvae could have been present. For example, it is possible that anguillid larvae may have been more abundant in the areas between the transects in the west, which may be one explanation for the low catches during the survey. This may also be one of the reasons why no anguillid larvae were collected in the two eastern transects. The 155°W transect did not pass near any major island groups where eels might live, and spawning far from any recruitment habitats at that longitude may not be advantageous. Similarly, the easternmost 140°W transect could have been on the upstream side of the majority spawning locations near the larger islands to the west where anguillid eels are known to live, such as Tahiti and the Marquesas Islands (Marquet and Galzin, 1991; Helme et al., 2018). The westward flow of the SEC in that region appears to be slow (5–10 cm/s), with frequent eastward countercurrents (Rougerie and Rancher, 1994) along with seasonal variability in the current flows (Martinez et al., 2009), so local spawning strategies may be effective. In that case, our two eastern transects may have been too far west and also too far east of the areas where most larvae were distributed. Our sampling could also have occurred during a time period when few larvae were present in those locations. It was recently reported that most recruitment of glass eels of the three species, *A. marmorata*, *A. megastoma*, and *A. obscura*, occurs from December to January in Tahiti and Moorea, with *A. marmorata* being by far the most abundant species at the single sampling locations on each island that have been studied (Helme et al., 2018).

4.3. Hydrographic features and spawning areas

An important aspect of the present survey were the five long hydrographic sections that could be plotted and compared to the catch locations of the larvae and the ADCP current velocity data. From a hydrographic perspective, these high-resolution transects of CTD casts at each station provided a geographic view of the hydrographic structure across a wide longitudinal zone of the South Pacific during one time period. For example, these sections provide clear documentation of the structure of the longitudinal changes in the STUW, which previously has been only evaluated through modelling or sources of data other than high-resolution salinity sections (e.g., Hasson et al., 2013; Qu et al., 2013). Four of the long hydrographic transects of the World Ocean Circulation Experiment (Koltermann et al., 2011) were made across this region in 1991–1993 (one was analyzed by Roden, 1998). But these hydrographic observations were made during various different months and years, which makes interpreting geographic differences more difficult.

Comparisons of the hydrographic structure to the catches of leptocephali during the 2016 survey showed that the small larvae of *A. australis* and *A. reinhardtii* were collected in a narrow area (~14–15°S) of the 160°E transect that was along the southern edge of the warm surface pool of water (Pacific Warm Pool; Delcroix, 1998; Delcroix et al., 2000) and also the low salinity Fresh Pool (Delcroix and Picaut, 1998; Hénin et al., 1998) (Fig. 3a,f). The small *A. australis* and *A. obscura* were collected along 175°E northwest of Fiji (~14–16°S) in a similar location in relation to these hydrographic features, and the small *A. marmorata* was caught slightly farther north along 170°W. The edge of these surface features may be likely locations for fronts to form, and both temperature (European and American eels) and salinity fronts (Japanese eel) appear to affect where spawning of the eels occurs (Kleckner and McCleave, 1988; Tsukamoto, 1992; Kimura and Tsukamoto, 2006; Aoyama et al., 2014). These locations in the western South Pacific were also above subsurface cores of the high salinity STUW, and both types of features have been hypothesized to potentially be able to provide hydrographic signposts that could be used by migrating anguillid eels as recently overviewed by Schabetsberger et al. (2016).

These larval catch locations were also likely associated with the westward flow of the SEC that occurs in the upper 300–400 m of the

region and usually has a two-core structure with speeds that can reach > 20 cm/s (Delcroix et al., 1987; Kessler and Taft, 1987; Roden, 1998). It breaks up into several branches as it reaches the island groups of Vanuatu and New Caledonia, and then also bifurcates off north-eastern Australia, with the southern branch becoming the East Australian Current (EAC) (Ganachaud et al., 2014; Hu et al., 2015). This seems important for the species that recruit to eastern Australia after entering the southward flowing EAC, which is the western boundary current of the western South Pacific (Ridgway and Dunn, 2003; Hu et al., 2015), and those recruiting to New Zealand that must also enter the eastward flow across the Tasman Front (Tilburg et al., 2001).

There are various other complex seasonal currents or jets in the western region of the South Pacific however, which have likely influenced where spawning areas have been formed and how the larvae become distributed. Westward current jets can form such as north and south of New Caledonia and there are also eastward countercurrents that form at least during some seasons (Gourdeau et al., 2008; Ganachaud et al., 2014). Between the two branches of the SEC in the east, the South Equatorial Countercurrent (SECC) forms seasonally at about 5–10°S (Delcroix et al., 1987, 1992; Kessler and Taft, 1987; Roden, 1998), with peak flows in March (Chen and Qui, 2004). The western South Pacific can be viewed as a subtropical gyre with westward SEC flow in the north and eastward return flow to the south starting between New Zealand and Fiji (Morris et al., 1996; Hu et al., 2015). The current flows in the central part of the South Pacific such as in the French Polynesia region where three species of anguillid eels are present (Marquet and Galzin, 1991) and may spawn locally, seem less studied (Rougerie and Rancher, 1994; Martinez et al., 2009).

This complexity of current flows may be one reason why there is no evidence of a single regional spawning area for more than one species, because in the western South Pacific there is likely no single area that can result in the larvae reaching all the potential recruitment habitats. Therefore, it may be likely that some specific spawning areas have formed that enable recruitment to specific areas, such as the present study and previous information appears to indicate for *A. marmorata* (e.g., Robinet et al., 2008; Kuroki et al., 2014).

While the numbers of anguillid leptocephali collected in 2016 was relatively fewer than the previous survey in 1995 conducted in a similar season that included twice the number of IKMT tows per station (Aoyama et al., 1999), it is also important to note that the stations where anguillid larvae were not collected also provide useful information that can be compared to the hydrographic data. No anguillid leptocephali were collected to the south of the latitudes of the SEC. The hydrographic sections showed an interesting pattern of the highest levels of fluorescence from chlorophyll of phytoplankton being in the northern half of each transect (not shown). Those high-fluorescence areas corresponded to being within the thermocline below the warmer northern waters at latitudes where the westward flowing SEC would be. Those are the latitudes where the anguillid eels appear to spawn based on this study and previous collections of their larvae (Kuroki et al., 2008). This may suggest that those latitudes not only provide good westward flow for the leptocephali that need to go in that direction (also eastward just to the north in the SECC), but they also would provide a favorable environment for feeding (Miller et al., 2013; Feunteun et al., 2015; Liénart et al., 2016).

5. Summary and conclusions

The large-scale 2016 sampling survey to collect leptocephali in conjunction with extensive CTD casts in a short transect in the NECC northeast of New Guinea and along five long transects (5–25°S) crossing the SEC in the South Pacific provided new information about anguillid spawning areas and showed the hydrographic structure across the region. The sizes and ages of small leptocephali indicated spawning likely occurred in three different areas within the latitudes of the western SEC. *Anguilla reinhardtii* leptocephali were only collected on the west

side of the Vanuatu Archipelago, whereas *A. australis*, which consists of two subspecies, was collected in widely separated areas on both sides of the archipelago. Combined with information from logging or population structure studies, species such as *A. marmorata* appear to spawn in at least two areas within the New Caledonia to Samoa region, and also somewhere in French Polynesia, where no anguillid leptocephali have been collected yet. The warm Fresh Pool in the surface layer fades out in the eastern region where the high-salinity STUW is formed and extends subsurface within the thermocline into the western region. It is unclear if these hydrographic features help define any of the spawning areas that may be present. Future sampling surveys can now focus on a narrower range of latitudes to obtain further information about the spawning areas and larval ecology of the anguillid species in the South Pacific, and a more closely spaced series of transects sampled in the most likely spawning season will be useful for collecting the first anguillid leptocephali in the French Polynesia region. Other approaches using advanced techniques such as otolith microchemistry (e.g. isotope mapping), environmental DNA, numerical simulations, and high-precision PSAT tagging could also be informative about the early life histories and migration of the anguillid eels in the South Pacific.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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