Spawning migration and larval dispersal of tropical Pacific eels (*Anguilla* spp.) in the centre of their distribution ranges

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ABSTRACT: It is unknown how many spawning areas exist for tropical South Pacific eels (*Anguilla marmorata*, *A. megastoma*, *A. obscura*) populating island archipelagos between Papua New Guinea and French Polynesia. They could spawn at single centralised eastern and western locations, implying long-distance migrations by some eels, or at several local spawning areas. Larval catches, morphological and genetic investigations, and tagging experiments have provided no unequivocal answer. In this study, *A. marmorata* and *A. megastoma* were tagged with pop-up satellite archival transmitters at Samoa, in the centre of their distribution ranges. Tags surfaced prematurely after 11 to 25 d, 91 to 345 km from the point of release. One *A. marmorata* and one *A. megastoma* came within 180 and 230 km, respectively, from where a small *A. marmorata* leptocephalus was caught north of American Samoa during a recent research cruise, suggesting that eels may spawn near the archipelago. Silver eels exhibited diel vertical migrations between 180 m during the night and more than 700 m during the day. At their upper migration depths, eels migrated towards increasing salinity and towards local eddies, raising the question of whether they may actively search for these oceanographic features. Up to 15% of virtual larvae released near Samoa were retained within local eddies and could have recruited back to the archipelago. The remaining larvae drifted as far as Fiji and the Cook Islands to the west and east, respectively. The exchange of leptocephali probably connects several local spawning areas throughout the South Pacific Ocean, causing genetic exchange among areas.

KEY WORDS: *Anguilla* · Diel vertical migration · Larval dispersal · Migration routes · Satellite telemetry · Spawning

1. INTRODUCTION

The current state of knowledge is that the 16 species and 3 subspecies of the genus *Anguilla*, the catadromous eels, evolved from an ancestral mesopelagic tropical marine eel species in the Indo-Pacific region around 20 to 40 million years ago (for reviews see Tsukamoto et al. 2002, Aoyama 2009, Tseng 2016, Arai 2020). It is further hypothesised that this marine ancestor took advantage of food resources and shelter from apex marine predators in tropical freshwater habitats but returned to its place of birth in the sea for spawning (Inoue et al. 2010). Over evolutionary time scales, the migration loops between freshwater growth and tropical marine spawning habitats expanded (Kuroki et al. 2014). Species colonising temperate regions at higher latitudes developed the longest spawning migrations and larval durations (Tsukamoto et al. 2002, Kuroki et al. 2014). Continental drift further expanded the migration loops, especially for the European and American eels that migrate over thousands of kilometres back

to the Sargasso Sea for spawning (Schmidt 1922, Righton et al. 2016).

Today, understanding the marine phase of eels is vital for effective management of each anguillid eel species. Some populations have shown alarming declines in parts of their ranges (Dekker et al. 2003, Stone 2003), and the European eel is classified as Critically Endangered in the IUCN Red List (www. iucnredlist.org). It is still not clear if the driving forces are anthropogenic stressors in freshwater (e.g. overfishing, barriers to passage, habitat alterations, pollution, introduced parasites) or changes in oceanic conditions reducing survival of larvae (leptocephali, reviewed in Righton et al. 2012, Miller et al. 2016, Drouineau et al. 2018). Despite strong efforts to close the reproductive cycle of eels in captivity (Tanaka et al. 2001, Tanaka 2015), the aquaculture industry still relies on wild-caught glass eels. With catch restrictions in place on threatened temperate eels, the demand for glass eels of tropical species is increasing rapidly (Crook & Nakamura 2013, Crook 2014, Jacoby et al. 2015).

From the presumed evolutionary centre of anguillid eels in Southeast Asia, species numbers decline towards the Pacific Ocean; in the Indonesian Seas region, 8 of the 16 eel species occur (*A. bengalensis*, *A. celebesensis*, *A. borneensis*, *A. interioris*, *A. bicolor*, *A. marmorata*, *A. megastoma*, *A. obscura*). In the tropical western South Pacific (WSP, Papua New Guinea to Samoa), 5 species are found as far east as New Caledonia (*A. australis*, *A. reinhardtii*, *A. marmorata*,

A. megastoma, *A. obscura*), and from Fiji eastwards, 3 species of catadromous eels populate the islands all the way to French Polynesia (FP) in the central South Pacific (Indo-Pacific eel *A. marmorata*, Polynesian longfin eel *A. megastoma*, and Polynesian shortfin eel *A. obscura*, Fig. 1, see Aoyama 2009, Tsukamoto et al. 2020). Even further east, *A. megastoma* has been reported from Pitcairn Island (Ege 1939), and *A. marmorata* may infrequently reach the Galápagos Archipelago (McCosker et al. 2003).

However, even today, the spawning areas of the majority of these species remain unknown, although considerable effort has been made to find them. The Indo-Pacific has been targeted for the ship-based search for collecting leptocephali for more than 90 yr. It started with the Carlsberg Foundation's Oceanographical Expedition Round the World 1928–1930 and continued with large-scale surveys conducted until recently (Jespersen 1942, Castle 1963, Aoyama et al. 1999, Miller et al. 2006, Kuroki et al. 2008, 2020). Some tropical eels in Indonesia (*A. borneensis*, *A. celebesensis*) do not make long marine migrations and spawn near their freshwater habitats (Aoyama et al. 2003, 2007, 2018, Kuroki et al. 2014). In contrast, *A. marmorata* in the Indonesian Seas region and western North Pacific migrates to the northern equatorial region and spawns in an overlapping area with the Japanese eel *A. japonica* (Kuroki et al. 2009, Tsukamoto et al. 2011). The temperate trans-Tasman species (*A. dieffenbachii*, *A. australis*, *A. reinhardtii*)
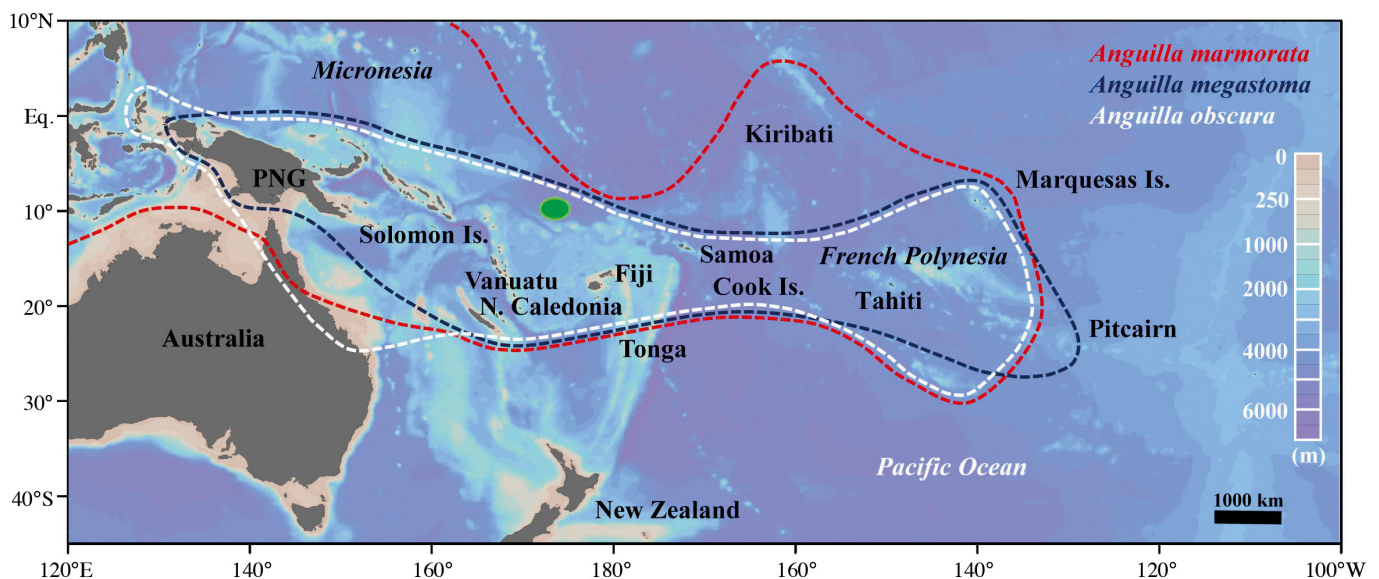

Fig. 1. Bathymetry of the study region and species ranges of the 3 tropical Pacific anguillid eels in the South Pacific. Range area of *Anguilla marmorata* extends north of the equator and westward into the Indian Ocean. A presumed spawning area based on larval catches and satellite tagging of *A. marmorata* and *A. megastoma* is indicated northwest of Fiji (green ellipse). Species ranges are based on Ege (1939), Marquet (1992), Sugeha et al. (2008), Thuesen et al. (2011), Watkins & Batoromaio (2014), Pike et al. (2020a–c), https://bie.ala.org.au. PNG: Papua New Guinea

have evolved typical long-distance migration loops, probably spawning somewhere north or northeast of New Caledonia (Jellyman & Bowen 2009, Jellyman & Tsukamoto 2010, Kuroki et al. 2020).

The South Pacific, with its numerous archipelagos and the complex current patterns surrounding them, is an interesting region to study the spawning migrations and population structures of the 3 species of tropical anguillid eels that are found across more than half of the ocean basin. Is there one fixed mutual spawning area in each region, implying long-distance migrations for eels from distant archipelagos, or are there several local spawning areas in both the WSP and FP regions? For this study, we chose the isolated archipelago of Samoa in the centre of the distribution ranges of *A. marmorata*, *A. megastoma*, and *A. obscura* for learning more about their migration and possible recruitment strategies. Theoretically, adult eels could migrate either east or west for spawning, or they could remain close to the islands. With the prevailing zonal eastward or westward currents, long migrations to the north or south of the archipelago would render the return of larvae impossible.

The Samoan Archipelago (Independent State of Samoa, formerly Western Samoa: 2 main islands of Sava'i and Upolu, US Territory of American Samoa: Tutuila and the 2 smaller islands of Olosega and Faleasao, see Fig. 2) is situated near the northern edge of the South Pacific Gyre (Fenner 2019). Two major ocean current systems affect the oceanographic conditions near the archipelago (see Animation S1 at www.int-res.com/articles/suppl/m670p167_supp/). The eastward South Equatorial Countercurrent (SECC, ~8–13° S) is embedded within the westward South Equatorial Current (SEC, ~0–8° and ~13–19° S). Typical speeds are <10 cm s^{-1} and 10 to 20 cm s^{-1} for the SECC and SEC, respectively. However, the SECC varies greatly with season and year and is nearly absent from May to September (Chen & Qiu 2004). This shallow current propagates eastward above and within the upper thermocline (~200 m) overlying the westward flow of the SEC. Coupled with El Niño Southern Oscillation (ENSO) events, the SECC strengthens and the SEC weakens, while this pattern reverses during La Niña years (Reverdin et al. 1994, Johnson et al. 2000). The strong shear between the 2 opposite currents results in the seasonal formation of numerous irregular meanders and mesoscale eddies north and south of Samoa (Domokos et al. 2007). If eels from Samoa spawn locally, those currents could transport leptocephali back to the archipelago, which would result in a comparatively short migration loop.

Despite the larval sampling surveys that have been conducted, remarkably little is known about where the 3 species of tropical anguillids spawn throughout the South Pacific. Leptocephali of all 3 species have been caught northwest of Fiji (175° E, Kuroki et al. 2008, 2020). Eels from Vanuatu moved towards this area according to tagging studies using pop-up satellite archival transmitters (PSATs, Fig. 1). Genetic analyses confirmed hybridisation between the 3 species in this region (Schabetsberger et al. 2015, Gubili et al. 2019, Barth et al. 2020). Differences in the number of vertebrae suggest there could be WSP and FP populations of *A. marmorata* and *A. megastoma* but just 1 population of *A. obscura* (Marquet 1992, Watanabe et al. 2008, 2009, 2011). However, single *A. obscura* leptocephali have been caught both northwest of Fiji (20 mm, Kuroki et al. 2020) and near Tahiti (27 mm, Jespersen 1942), suggesting there are both eastern and western spawning areas. Molecular genetic data have not detected any population structure for the 3 species in the WSP (Gubili et al. 2019, Barth et al. 2020). Differences were found for *A. marmorata* between the WSP and FP regions (Ishikawa et al. 2004), but this was not confirmed in other studies (Minegishi et al. 2008, Gagnaire et al. 2011). The existence of several spawning areas is not in contradiction with the observation of a single gene pool in the WSP, as the oppositely flowing currents could disperse larvae over large distances. In 2016, however, the smallest *A. marmorata* leptocephalus ever caught was collected 200 km north-northeast of American Samoa, ~2000 km from both New Guinea and Tahiti, indicating some spawning occurs in the centre of the distribution range (7.8 mm long, 19 d old, Kuroki et al. 2020).

The tagging studies with PSATs have provided insight into the extraordinary marine migration behaviour of South Pacific eels (Schabetsberger et al. 2013, 2015, 2019). The distances covered to their spawning areas are further extended by distinct diel vertical migrations (DVMs) and sometimes by sweeping horizontal movements (Chang et al. 2020). The eels descend from shallow nighttime (100–300 m) to deep daytime (600–900 m) depths during crepuscular periods (Schabetsberger et al. 2015). The estimated horizontal zigzag movements could be related to searching for marine signposts or mates in the open ocean. It is still unknown if they typically migrate in groups or alone. Eels probably reproduce near their upper nighttime migration depths based on collections of eggs and preleptocephali of the Japanese eel (Tsukamoto et al. 2011, Aoyama et al. 2014).

Scientists have long marvelled about potential signposts that might guide migrating eels to their

spawning area (McCleave 1987). In the centre of all ocean gyres, where evaporation exceeds precipitation, high-salinity water (the Subtropical Underwater, STUW) is subducted into the thermocline (Price 2001, Johnson et al. 2016). In the WSP, this comparatively stable water mass propagates westward and equatorward around 150 m depths and conveys surface waters into the subsurface ocean (Qu et al. 2013). In the vicinity of Samoa, salinity maxima of subducted water masses and oceanic fronts forming at the edges of different currents may serve as landmarks for migrating eels to locate other eels for spawning (Schabetsberger et al. 2016).

In this study, we present information on 3 *A. marmorata* and 5 *A. megastoma* silver eels that were caught and tagged with PSATs on the Samoan island of Upolu (2017, 2019). We analyse oceanographic conditions during these 2 consecutive tagging campaigns using the HYbrid Coordinate Ocean Model (HYCOM) global ocean model. The migration behaviour data of 4 eels in 2017 presented previously in a short note (Schabetsberger et al. 2019) are combined with new data from 4 eels in 2019, and these are linked with the prevailing oceanographic conditions. To evaluate if one particular area around Samoa would be more favourable as a spawning location for larval self-recruitment, simulated trajectories of virtual leptocephali were analysed in areas where our tags popped up and where a small *A. marmorata* larva was found north of Samoa during a cruise in 2016. Finally, we consider the evidence regarding how many spawning areas might be used by South Pacific eels and how their wide-ranging larval dispersal and adult migration and mating behaviours might affect the genetic population structure, which can help guide future research to provide information for management and conservation of these anguillid species.

2. MATERIALS AND METHODS

2.1. Eel capture and tagging

Silver eels were caught by electrofishing or with scoop nets in 2 different river drainages on the southern side of Upolu, the eastern island of Samoa, between 20 February and 18 March 2017 and 5 March and 15 March 2019. The *Anguilla marmorata* were captured in the Leafe River near the village of Lotofaga, while the *A. megastoma* were caught in the island interior (Vaigafa River, outflow of Afolilo Dam, Fig. 2). In 2017, most of the hundreds of eels caught by electrofishing were released immediately after capture, but large eels (~80–112 cm total length) and those showing obvious signs of silvering (8 individuals, 52–80 cm) were transported in a cooler to the Ministry of Agriculture and Fisheries in Apia and kept in an aerated circular tank (1.5 m diameter) under a flow-through freshwater supply for up to 10 d. In 2019, only silver eels selected for tagging (4 individuals, 83–99 cm) were maintained for 1–3 d in a keep net at a tilapia farm in Lotofaga. During the first year, silver eels had to be transported across the island and then tagged and released from a boat north of the island off the harbor of Apia (13.78° S, 171.75° W, 6.3 km from shore). During the second year, a seaworthy vessel was available to transport tagged eels offshore on the island's southern shore from where they would have entered the ocean naturally (14.09° S, 171.81° W, 9.6 km from shore).

For examination of species identification and silvering characteristics, taking fin clip DNA samples, and tagging, the eels were anaesthetised in a freshwater bath containing 40 mg l^{-1} metomidate (Aquacalm, Syndel Canada) until motionless (described in detail in Schabetsberger et al. 2013, 2015). Silvering was confirmed through visual inspection of body colouration and the relative size of the eyes (Okamura et al. 2007). The morphological assignment to species through the dentition of the upper jaw was validated through nucleotide sequence analyses of the mtDNA control region following Schabetsberger et al. (2015). PSATs (MiniPAT, Wildlife Computers) were attached externally using a bridle and programmed to surface after 3 and 5 mo. Three hypodermic needles (20 gauge) were pushed subcutaneously through the dorsal skin for a length of approximately 3 cm, and a 0.8 mm surgical steel wire was then fed through the bore of the needles before they were removed. The ends of the wire were then twisted, and the transmitter was attached with a 3 mm nylon braid laced through the metal loops. This secured and held the transmitter, which then floated approximately 3 cm above the back of the eel. The tags were attached just anterior to the start of the dorsal fin. Before starting transmission after pop-up, the tags drifted for 3 d at the ocean surface. We estimated the actual pop-up locations with backward tracking within the prevailing surface currents (Fig. 2).

2.2. Oceanographic conditions

Temperature, salinity, and current fields were analysed for different time periods and depths: (1) when tagged adult eels were migrating in 2017 (10–
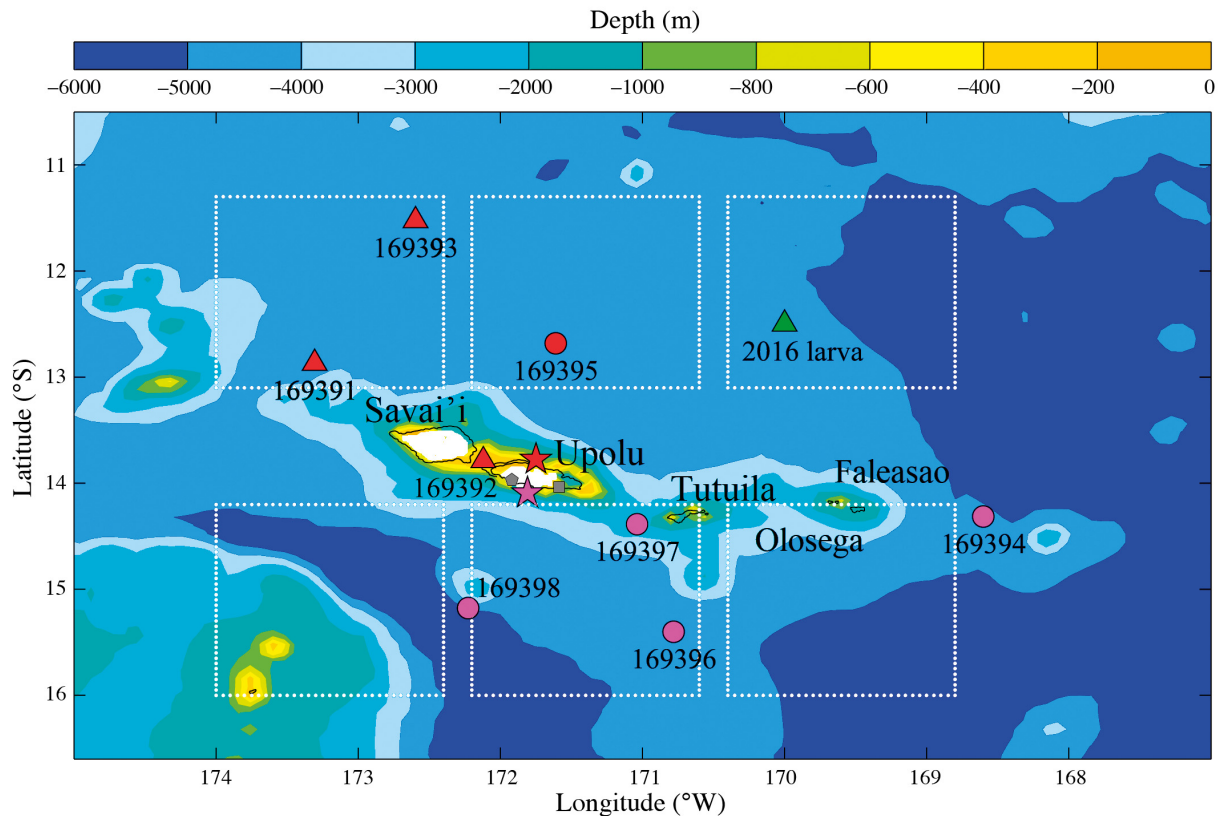
Fig. 2. Release locations (stars) and pop-up locations of satellite tags (serial numbers) of *Anguilla marmorata* (triangles) and *A. megastoma* (circles) in 2017 (red) and 2019 (magenta) around the Samoan Islands. Silver eels were caught in the Leafe (grey pentagon) and Vaigafa (grey square) rivers. The position of a 19 d old *A. marmorata* leptocephalus caught in August 2016 is shown (green triangle). Rectangles show the release domains of virtual larvae whose larval dispersal is shown in Fig. 7

29 March) and 2019 (12 March–9 April) at their median upper nighttime (2017: 186 m, 2019: 210 m) and lower daytime (2017: 718 m, 2019: 745 m) migration depths, (2) when the small *A. marmorata* larva caught in 2016 was drifting during its first 19 d of life (140 m), and (3) when virtual larvae (v-larvae) were released in March–April and August–September 2015 to 2019 (75 and 200 m, day and night depths, respectively). HYCOM (http://hycom.org) is a data-assimilative ocean circulation model that provides 3D currents and hydrological fields (Chassignet et al. 2009). The global analysis v. 3.1 was used in this work that has a 0.08° horizontal resolution and 32 vertical layers. The daily HYCOM used in the present study covers July 2014 to present. HYCOM has been validated against observations (Chassignet et al. 2003, Kelly et al. 2007) and has been widely used to analyse ocean dynamics in the world's oceans (Metzger et al. 2010, Shu et al. 2014).

2.3. Particle-tracking simulations

The 3D particle-tracking method (Ohashi & Sheng 2016) was used to simulate the movement of v-larvae

in this study. The tracking scheme was based on the fourth-order Runge-Kutta method (Press et al. 1992). A random walk displacement was included to represent unresolved subgrid turbulent flow and other local processes. The tracking time step was 3 h. The same tracking scheme has been used in previous studies to investigate the drift of Japanese eel larvae and adults in the western Pacific Ocean (Chang et al. 2016) and has also been applied to simulations of long-distance migration of adult American eels in the Atlantic (Béguer-Pon et al. 2016).

A release region was chosen surrounding Samoa (11.3–16° S, 168.8–174° W) covering the pop-up locations of the satellite tags and the location of the small *A. marmorata* larva (Fig. 2). The release region was further divided into 6 subdomains, and 288 000 v-larvae were released in each domain. We set the 2 release periods from March to April and from August to September 2015 to 2019 and staggered each release by a 15 d time interval. The release months and time periods were selected based on the pop-up of satellite tags and the discovery of the small *A. marmorata* leptocephalus larva. The results were expressed based on the 5 yr com-

posite. The tracking duration was set to be a conservative value of 120 d according to the approximate pre-metamorphosis larval durations of tropical anguillids (Arai et al. 1999, Marui et al. 2001), with the realisation that some larval durations could be longer if the oceanic glass eel stage is included (Hewavitharane et al. 2020). V-larvae were set to stay at 200 m for the first 10 d, and then DVM was assumed between 75 m nighttime and 200 m daytime depths (12:12 h day-night cycle, Castonguay & McCleave 1987). Larvae that arrived within 4 km from the coast of Western (Upolu, Savai'i) and American (Tutuila, Olosega, Faleasao, Fig. 2) Samoa after 120 d were counted as recruits.

3. RESULTS

3.1. Marine migration of silver eels from Samoa

Eels released north (2017) or south (2019) of Upolu migrated to the northwest and the southeast, respectively, and never turned to swim to the opposite side of the island (Fig. 2). The tags popped up prematurely after 11 to 25 d of deployment. Eels travelled between 91 and 345 km from the point of release with speeds between 4 and 18 km d^{-1}. Except for 1 small *Anguilla marmorata* that was apparently not ready for marine migration (tag ID 169392, 0.7 kg, 67.6 cm, Fig. 3B), all silver eels exhibited distinct DVM (Fig. 3, Table 1). After release, both species steadily increased their daytime migration depths from around 500 m to more than 700 m depths within 1 wk. Overall median daytime migration depths were 731 m at 6.0°C. Median nighttime migration depths were 181 m for *A. marmorata* and 207 m for *A. megastoma* corresponding to 23.0 and 22.4°C, respectively (Table 1, Fig. 3). During new moon nights, eels migrated 33 to 47 m shallower than during full moon nights, corresponding to a temperature difference of 2.1 to 2.6°C, respectively (Fig. 3). One tagged *A. marmorata* and one *A. megastoma* came within 180 and 230 km, respectively, from where the small *A. marmorata* larva was caught north of American Samoa (170° W, Figs. 2 & 4). Temperatures experienced by the eels in both years were around ~23°C during nighttime (Fig. 4D,J, Table 1) and ~5.7°C during daytime (Fig. 4G,M, Table 1). Corresponding salinities were 35.8 to 36.0 psu at night (Fig. 4E,K) and ~34.4 psu during the day (Fig. 4H,N). In both years, the eels travelled along gradients of increasing salinity at nighttime depths. The silver eels moved towards a

clockwise (cyclonic) eddy northwest of Samoa in 2017 (Fig. 4F) and a counterclockwise (anticyclonic) eddy in 2019 (Fig. 4L) southeast of the archipelago encountering currents of <0.16 m s^{-1} during day and night (Fig. 4F,I,L,O).

3.2. Oceanographic features

The Samoan Archipelago lies at the southern edge of the equatorial Pacific warm water pool with temperatures around 27.2 to 29.5°C at the surface and >21°C at 200 m depth (Figs. 3 & 5A,B,G,H). The higher-salinity STUW (between ~100 and 350 m) propagates westward below the thermocline (Fig. 5C, D,I,J). Four major currents exist from north to south (Fig. 5): (1) the westward-flowing northern branch of the SEC (north of ~ 8° S, ~0.2 m s^{-1}), (2) the seasonal eastward-flowing SECC splitting the SEC (~8–13° S, ~0.15 m s^{-1} in March–April), (3) the meandering flow of the southern branch of the SEC (~13–19° S, ~0.15 m s^{-1}), and (4) a regularly occurring eddy south of the islands (Tonga Trench Eddy [TTE], ~15–19° S, 0.2 m s^{-1}, Kendall et al. 2011, see Animation S1) reaching down to the eels' deep migration depth in 2017 (Fig. 5F,L). The TTE may persist over several months without clear dissipation or propagation (see also Domokos et al. 2007). It fed an eastward countercurrent around 16° S east of Samoa (Fig. 5E,F,K,L). The SECC was stronger in March–April than in August–September (Fig. 5E,F). The shear at the boundaries of the SECC with the northern and southern branches of the SEC results in mild eddy formation in the north and many irregular meanders and eddies in the south.

3.3. Larval drift

The 19 d old *A. marmorata* larva caught in 2016 could have drifted westward, reaching a position about 300 km northwest of Samoa after 120 d (Fig. 6). The drift trajectories of v-larvae departing from the PSAT pop-up locations went in many directions except southwest and northeast (Fig. 6). V-Larvae were generally transported farther to the south compared to the north, regardless of which side of the islands they were released on (Fig. 7). Depending on season and year and which of the 6 release locations was considered, either none or up to 15% of larvae spawned near the Samoan Archipelago were retained and could have recruited back to the islands (Table 2). The central release region in the south
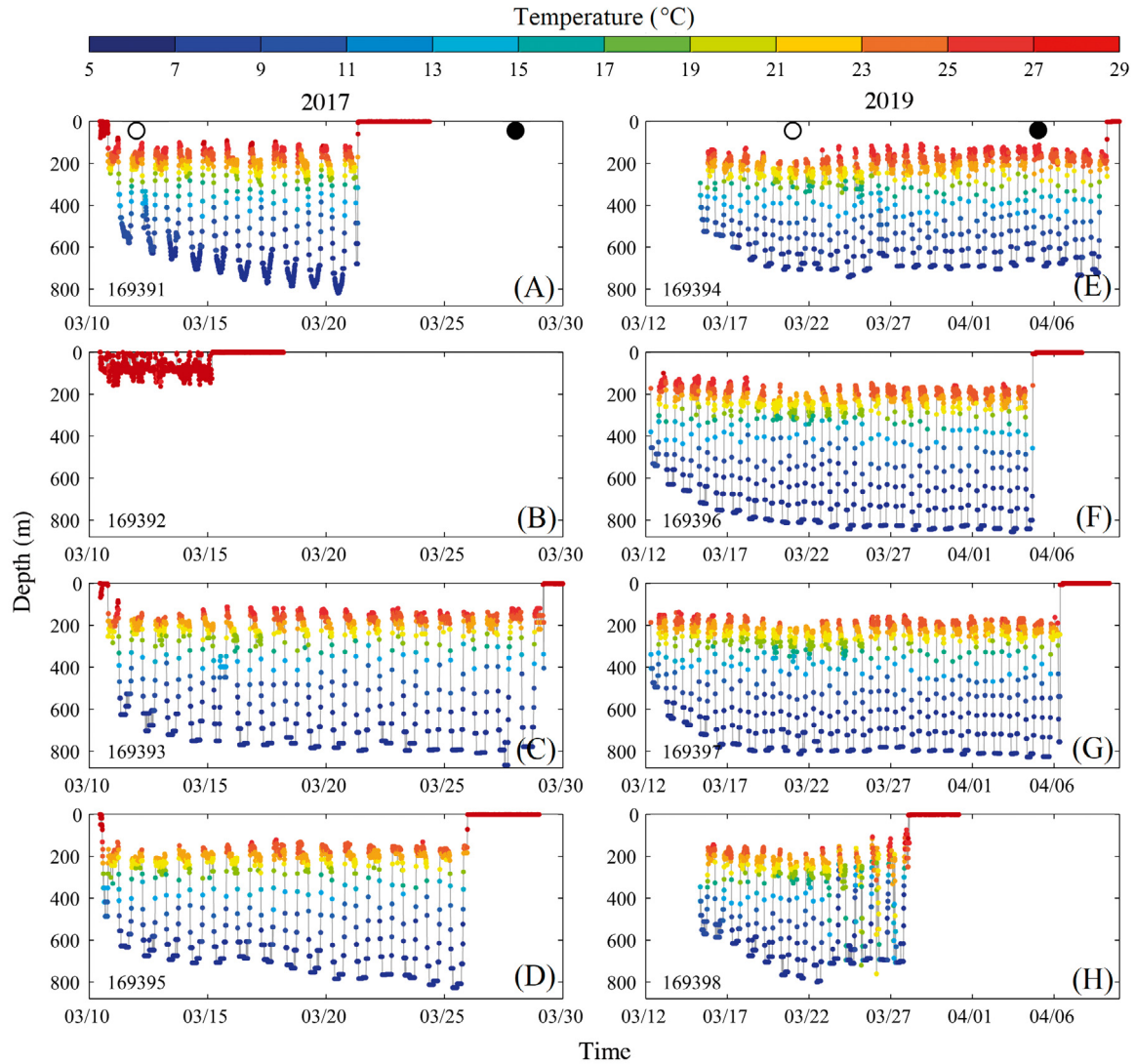
Fig. 3. Diel vertical migrations of (A–C) *Anguilla marmorata* (IDs 169391–169393) and (D–H) *A. megastoma* (IDs 169394–169398) tagged with pop-up satellite archival transmitters in 2017 (left panels) and 2019 (right panels). Temperatures experienced by the eels are shown on the colour bar. Open and solid circles shown in top panels represent full and new moons, respectively

Table 1. Species, year, serial number (ID), body weight, total length (TL), distance travelled, speed, median (±SD) daytime and nighttime depth, and median (±SD) daytime and nighttime temperature of *Anguilla* eels tagged in 2017 and 2019 on the island of Upolu, Samoa. The last 2 lines show median values (±SD) for each species. ID 169392 was not ready for migration or was preyed upon and is not included (see Fig. 3)

| Species	Year	ID	Weight (kg)	TL (cm)	Distance (km)	Speed (km d⁻¹)	Depth (m) Day	Depth (m) Night	Temp. (°C) Day	Temp. (°C) Night
A. marmorata	2017	169391	0.6	64.3	197	18	686 ± 108	180 ± 37	6.2 ± 2.4	23.0 ± 2.0
A. marmorata	2017	169393	1.2	80.3	267	14	763 ± 100	183 ± 37	5.7 ± 2.0	22.9 ± 2.1
A. megastoma	2017	169395	3.3	115.0	123	8	707 ± 93	195 ± 33	6.0 ± 1.9	22.0 ± 1.7
A. megastoma	2019	169394	1.6	90.8	347	14	678 ± 65	193 ± 43	6.2 ± 0.9	23.3 ± 2.1
A. megastoma	2019	169396	0.9	91.0	184	8	812 ± 86	205 ± 42	5.4 ± 0.8	23.0 ± 2.2
A. megastoma	2019	169397	0.8	83.0	91	4	795 ± 80	216 ± 38	5.4 ± 0.9	22.1 ± 2.1
A. megastoma	2019	169398	1.8	99.0	129	10	695 ± 75	226 ± 73	6.6 ± 1.0	21.8 ± 2.8
A. marmorata			0.9	72.3	232	16	724 ± 104	181 ± 37	6.0 ± 2.2	23.0 ± 2.1
A. megastoma			1.6	91.0	129	8	737 ± 80	207 ± 46	5.9 ± 1.1	22.4 ± 2.2
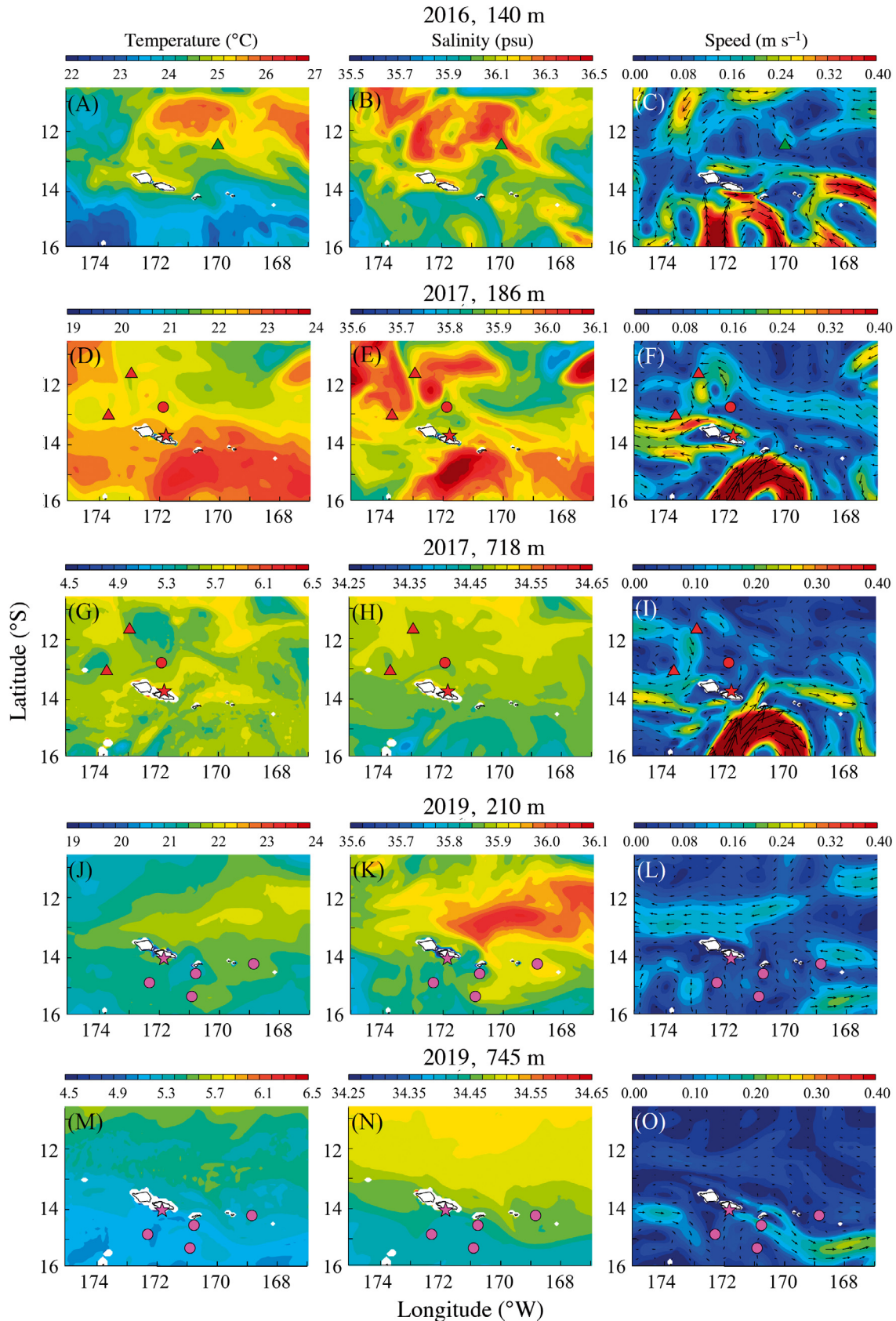
Fig. 4. Temperature, salinity, and current fields (vectors, speed shown by shading) (A–C) at the presumed depth of the 2016 *Anguilla marmorata* larva (green triangle) and (D–O) for the median (D–F, J–L) nighttime and (G–I, M–O) daytime migration depths of tagged *A. marmorata* (triangles) and *A. megastoma* (circles) in 2017 and 2019. Eel release locations are shown (stars). Note that the colour scales differ among different temperature and salinity panels
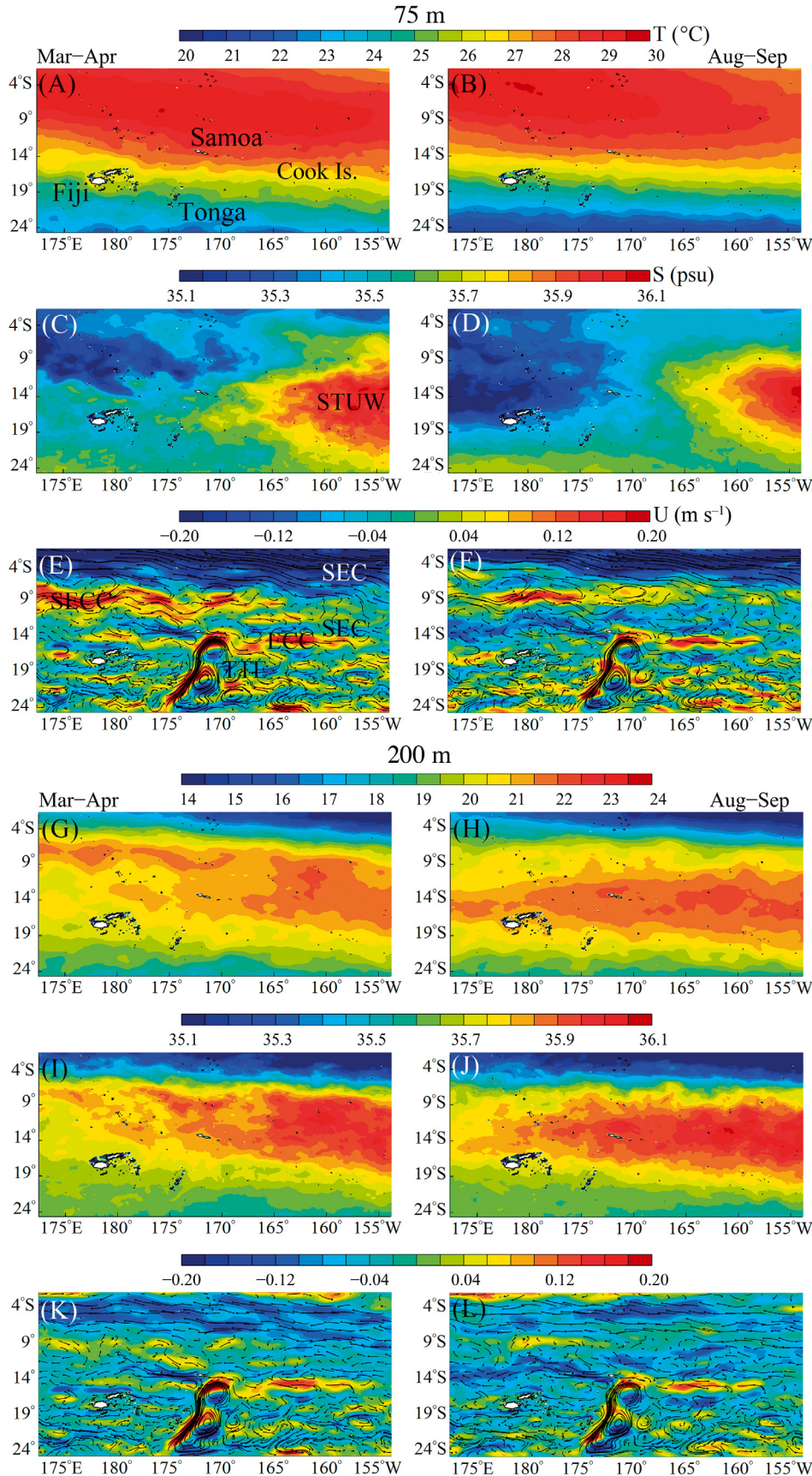
Fig. 5. 2015 to 2019 (A,B,G,H) mean temperature (T, °C), (C,D,I,J) salinity (S, psu), and (E,F,K,L) current fields (U, trajectories in black curves, zonal velocity indicated by shading, m s⁻¹) at 75 m (top panels) and 200 m (bottom panels) depths in March–April (left) and August–September (right). The high-salinity Subtropical Underwater (STUW), South Equatorial Countercurrent (SECC), northern and southern branches of the South Equatorial Current (SEC), Tonga Trench Eddy (TTE), and an unnamed eastward countercurrent (ECC) are indicated. Note that the colour scales differ among different temperature panels
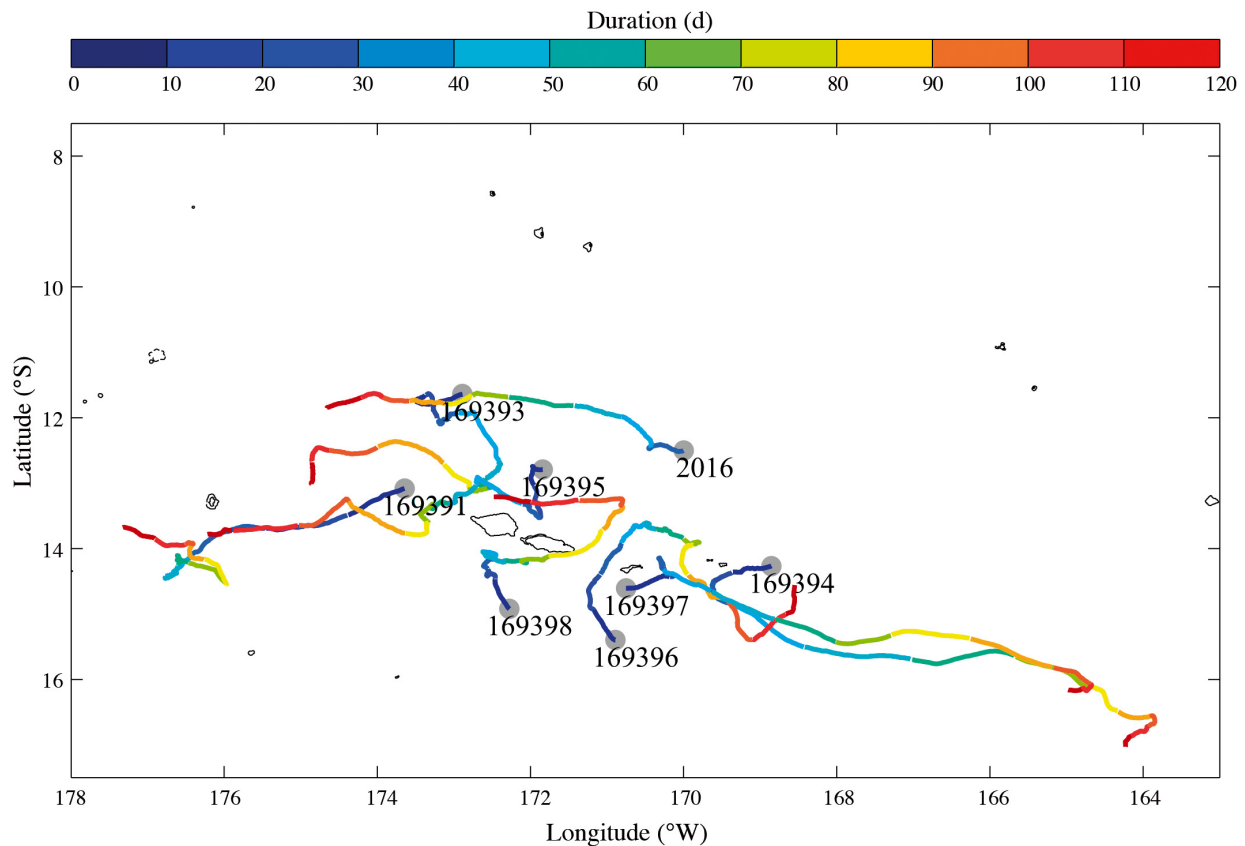
Fig. 6. Simulated trajectories of virtual larvae starting their drift from the positions where a 2016 larva was caught and from the points where the pop-up satellite archival transmitters surfaced. Colour codes refer to the duration of drift

(Figs. 2 & 7E,K) had higher recruitment success in both the March–April (end of rainy season, SECC strong) and August–September (dry season, SECC weak) periods, with values of 1.1 to 15.5% in all 5 of the simulation years. This was linked to the strong and persistent TTE and additional eddies in this region (Fig. 5). Three of the 4 PSAT pop-up locations were within or at the edge of that release region. The northeastern and southeastern regions had the lowest recruit percentages (0.2–0.6%). During 2015 and 2016, the northwestern region received 11.6 and 8.2% of recruits, respectively.

4. DISCUSSION

4.1. Marine migration of silver eels from Samoa

During their oceanic migrations, anguillid silver eels perform profound DVM between warm epipelagic and cold mesopelagic layers (reviewed in Righton et al. 2021). The migrating *Anguilla marmorata* and *A.*

megastoma silver eels released from Samoa also exhibited a remarkably similar behaviour to individuals released from Vanuatu: nighttime depths around 180 m (23°C), gradual increase in daytime depths from around 500 to >700 m within 1 wk after release, daytime depth of ~730 m (5.9°C), and a clear effect of moon phase on nighttime migration depths (~40 m shallower during the new moon). Swimming deeper at night during full moons and shallower during new moons has been observed in several anguillid species (Schabetsberger et al. 2013, Westerberg et al. 2014, Chow et al. 2015, Chen et al. 2018, Higuchi et al. 2018, Wu et al. 2018). These depth ranges were interpreted as a trade-off between predator avoidance and the necessity to maintain high enough metabolism for migration (Schabetsberger et al. 2013, 2015).

Tags popped up prematurely after only 11 to 25 d of deployment either due to predation or tag loss. Except for tag 169398 that surfaced in the middle of the night, all other tags came up during crepuscular periods or during daytime, which may indicate at-
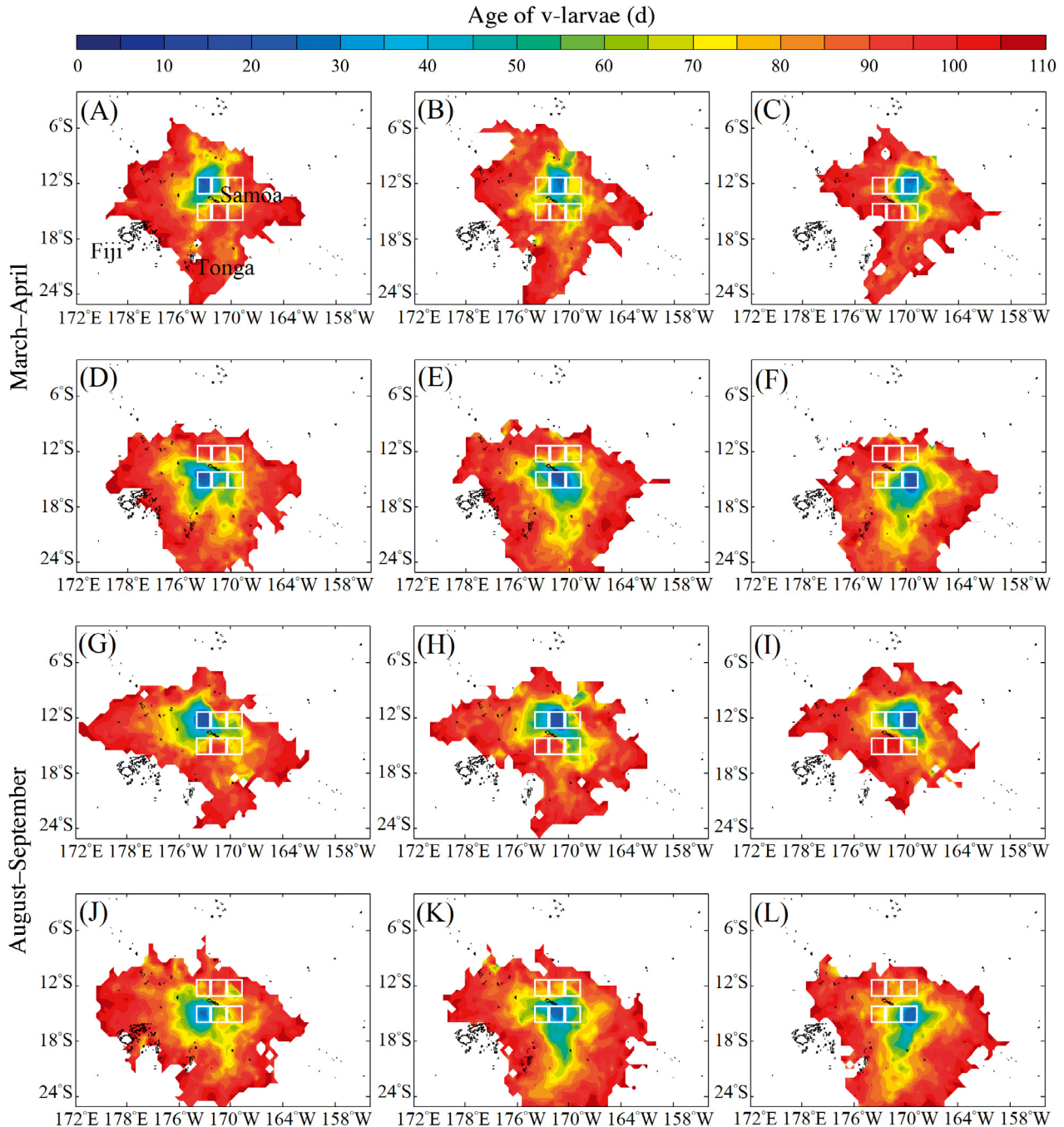
Fig. 7. Average age (d) of the virtual larvae (v-larvae) that entered each grid location and range of the final distance from Samoa of the larvae released within the 6 grids shown in Fig. 2 (white rectangles) after drifting for 120 d within prevailing ocean currents. Average current fields experienced during (A–F) March–April and (G–L) August–September 2015 to 2019 were used. The release locations of each panel are those with the most distinct blue colour

tacks by a visually hunting predator causing detach-ment of the tags from the eels. However, there were no unequivocal signs of predation such as the pas-sage of the tag through the digestive tract of a warm-blooded toothed whale (Wahlberg et al. 2014). Alter-natively, the tags may have broken loose, potentially

due to higher strain on the tags during upward and downward movements. We attached the PSAT rigs through the skin (Westerberg method, Økland et al. 2013), instead of piercing the swimming muscle, which trades minimal behavioural disturbance of the tagged fish against reduced retention rates. How-

Table 2. Percentage of larvae potentially arriving within 4 km of the shores of the Samoan Archipelago in different regions and seasons between 2015 and 2019 after being released from the 6 domains shown in Fig. 2

Release season and year	NW	N	NE	Grid SW	S	SE
Mar–Apr						
2015	11.6	4.2	0.9	1.6	1.1	0.4
2016	8.2	2.0	0.0	1.3	2.4	0.2
2017	1.3	5.7	0.8	1.9	5.1	0.4
2018	0.8	2.2	0.1	5.7	1.5	0.5
2019	0.5	0.3	0.3	3.9	12.5	0.3
Mean	4.5	2.9	0.4	2.9	4.5	0.3
Aug–Sep						
2015	1.5	2.5	0.5	0.7	3.5	0.3
2016	2.3	1.9	0.3	1.6	5.2	0.1
2017	5.9	1.5	0.1	0.7	2.4	1.3
2018	0.8	0.2	0.1	0.7	9.3	0.6
2019	0.0	0.0	0.0	9.1	15.5	0.7
Mean	2.1	1.2	0.2	2.6	7.2	0.6

ever, tag retention was similar to large-scale tagging experiments on European eels (~18 d, Økland et al. 2013). The linear migration speeds between release and pop-up locations (8–16 km d^{-1}) were within the range observed in our previous studies (Schabetsberger et al. 2013, 2015).

During both years, the eels appeared to move towards increasing salinities at their upper migration depths. The Samoan Archipelago lies inside the pathway of the STUW spreading below the thermocline (Fig. 5I,J). Earlier studies hypothesised that this corridor of subducted high-salinity water may offer cues for orientation and possibly provide favourable conditions for larval growth (Schabetsberger et al. 2016, Kuroki et al. 2020). The 2016 larva was caught near a salinity maximum at 140 m depth (Fig. 4B). Eels released either south or north of the island moved out into the open ocean and did not swim to the opposite side of the island, probably avoiding its shallower submarine flanks. However, taking eels from rivers draining south of the island to northern shores for release in 2017 — due to the unavailability of a seaworthy vessel that would have allowed a preferable release off the southern coast — was unnatural.

Also, during both years, the tags popped up near mesoscale eddies, raising the question of whether silver eels may be attracted to these oceanographic features (Braun et al. 2015). With their acute sensory capabilities, eels may be well equipped to perceive physical and biological properties that are associated with eddies and fronts (e.g. temperature and salinity gradients, weak electric and magnetic fields induced by ocean currents, odour, as discussed in Schabetsberger et al. 2016). Cotter (2008) suggests that the underwater soundscape could assist navigation, i.e. the geographic pattern of infrasound radiating from currents and eddies could provide a 3D image of the local environment. However, with the documented attraction of apex marine predators to frontal regions (Braun et al. 2015) — confirmed through the existence of a profitable tuna fishery in this region of increased eddy activity (Domokos 2009) — migrating silver eels would have to trade off their own survival (predator pit, Bakun 2006) with enhanced retention and feeding potential for larvae (Goldthwait & Steinberg 2008).

4.2. Larval drift from Samoa

V-larvae released near the Samoan Archipelago drifted in all directions, with small numbers recruiting back and others reaching distant islands. Cyclonic and anticyclonic eddies in the vicinity of the archipelago provide circular transport within these current loops and could result in variable degrees of larval retention in the area (Chang et al. 2017). Additionally, the feedback loops connecting the SECC with the SEC at ~165 to 170° W may act as a conveyor belt for leptocephali hatching near the archipelago, as previously predicted for reef fishes (Kendall et al. 2011). Late-stage leptocephali probably swim actively to detrain from oceanic currents (Miller 2009, Miller & Tsukamoto 2017, 2020, Chang et al. 2018). Hence, the number of eels recruiting back to Samoa if spawning occurred locally may exceed our estimates based on a threshold distance of only 4 km from land. Additionally, age estimates of the 3 species that recruited to Fiji indicate that the larval durations (Hewavitharane et al. 2020) can be approximately 1 mo longer than the 120 d dispersal period we used in the simulations.

Our model yielded the highest numbers of returning recruits south of Upolu within the TTE or within a local anticlockwise eddy in 2019 (Fig. 4L). The persistent clockwise TTE over the Tonga Trench has been present over several months (Kendall et al. 2011) and has a distinct twin gyre structure further south (Fig. 5, Animation S1). These recirculating currents probably develop from the Tonga-Kermadec Ridge blocking the flow of the SEC (see Webb 2000). Coincidentally, the greatest number of silver eels seem to reach the ocean on the southern side of the island. The windward southern to southeastern side

of Upolu (mean precipitation in September: 350–400 mm) receives more rainfall than the rain-shadowed northern to northwestern region (100–150 mm) (Samoa Meteorology Division, www.samet.gov.ws). After fishing in almost all rivers around the island, the majority of large silver eels were caught in the Vaigafa River in the southeast. It is probably one of the primary habitats for freshwater eels in the entire archipelago especially for *A. megastoma*, which have to surmount the Sopoaga Waterfall to reach their upstream habitat. This suggests that the TTE and other eddies may enhance recruitment to this important watershed if the eels spawn near the islands in the southern release grid areas of our simulations. However, the northwestern grid occasionally received high recruitment when the Samoan Islands were sandwiched by the southward-shifting SECC and SEC. A clockwise eddy formed between the 2 currents and transported larvae southward towards the archipelago, but there are no major rivers to recruit to on this dry side of the island.

Larvae not entrained in local eddies could be taken eastward and westward to distant archipelagos. Within 120 d, v-larvae drifted as far as Fiji, Tonga, and the Cook Islands. Eastward transport within the SECC is strongest during March–April and increases during El Niño years (Reverdin et al. 1994, Johnson et al. 2000). Additionally, the westward SEC was split by an eastward countercurrent extending from the TTE (Fig. 5E,F,K,L). Hence, leptocephali spawned near Samoa could theoretically be carried east as far as FP. Westward transport is possible year-round within the SEC. A constant supply of larvae in both directions might occur through extended spawning periods that are suggested by the occurrence of migrating silver eels in the rainy season (March) and the catch of a small larva during the dry season (August). Extended periods of recruitment of tropical species have been reported (Sugeha et al. 2001) and imply lasting escapement of silver eels throughout the year. Hence, the leptocephali may be transported east and west over long distances, assuming they are able to delay metamorphosis in the absence of triggering stimuli (e.g. chemical compounds or low salinity associated with freshwater habitats, Miller 2009).

4.3. Multiple spawning areas in the South Pacific

The discovery of the smallest *A. marmorata* larva north of Samoa is strong evidence that spawning occurs near the archipelago. Our tagged eels did not migrate to a single well-defined spawning area, but

1 *A. marmorata* and 1 *A. megastoma* came within ~200 km from where this leptocephalus was collected (170° W, Kuroki et al. 2020). Hence, spawning of both species may occur in the vicinity of the archipelago, although maximum attachment lengths of PSATs of 3.5 wk were too short to speculate about the final destinations of the eels. The larval dispersal simulations of our study indicate that local spawning could result in some larvae returning to the islands of Samoa.

There is evidence for several spawning areas across the large geographic species ranges spreading ~9000 km from New Guinea to the Marquesas Islands and Pitcairn. *A. marmorata* may even infrequently reach the Galápagos Archipelago within the Equatorial Countercurrent another 6500 km east of FP (McCosker et al. 2003). Within the WSP, catches of leptocephali of *A. marmorata* <50 d old occurred over a wide range of longitudes (160° E to 170° W, Kuroki et al. 2008, 2020), a distance of more than 3000 km. Tagging experiments in Vanuatu suggested that there is a shared spawning area of all 3 species northwest of Fiji (175° E, Fig. 1, Schabetsberger et al. 2015), 1700 km to the west of Samoa, which is supported by the observation of frequent hybridisation between species (Barth et al. 2020) and larval catches (Kuroki et al. 2008, 2020). At an even larger scale, the morphological (Watanabe et al. 2008, 2009, 2011) and possible genetic (Ishikawa et al. 2004) differences indicate some isolation between eels from the WSP and FP (150° W). Separated by more than 3700 km, small larvae (20 and 27 mm) of *A. obscura* were caught just northwest of Fiji (Kuroki et al. 2020) and northeast of Tahiti (Castle 1963, Kuroki et al. 2008), respectively. These 2 larvae could not have come from the same spawning area.

Seasonal patterns of glass eel arrival and age at recruitment studies in Fiji and FP do not suggest random arrival from distant areas or show larval ages long enough to account for frequent long-term drifting across these distances (Helme et al. 2018, Hewavitharane et al. 2018, 2020, P. Sasal unpubl. data). In Fiji, they range from 4 to 6 mo with mean ages of 168 d for *A. obscura*, 153 d for *A. marmorata*, and 141 d for *A. megastoma* (Hewavitharane et al. 2020). These ages are similar to those of tropical eels in Indonesia but are younger than the temperate species that recruit to Australia and New Zealand (Arai et al. 1999, 2001, Marui et al. 2001). The larvae arriving in Fiji could originate from 1 or several locations in the WSP — explaining the lack of genetic differentiation observed in this region (Gubili et al. 2019, Barth et al. 2020) — but they cannot reach the archi-

pelago from FP in large quantities. Nevertheless, an infrequent exchange of larvae between these distant regions may occur through drift within oppositely flowing currents, and this could breach the full genetic segregation of these otherwise reproductively isolated subpopulations (Gagnaire et al. 2009, 2011, Watanabe et al. 2009).

How genetic exchange occurs also depends on the migration and mating behaviours of the silver eels. For example, eels born at an eastern spawning area near Samoa could drift away from the archipelago as shown by our larval dispersal simulations and recruit to rivers farther west, such as in Vanuatu and Fiji. After completing their juvenile growth phase, they might follow their congeners born northwest of Fiji back to this closer spawning area instead of returning to their own place of birth near Samoa. Conversely, eels born near Fiji could recruit to Samoa. Eels from various areas could integrate into different breeding pools, resulting in genetically homogeneous populations in the WSP, even if there are different spawning locations. They could achieve this either by migrating in groups or by tracking the odour trails of conspecifics to a final spawning location they were not born at themselves (see Westin 1990, Huertas et al. 2008, Bruijs & Durif 2009). However, exchange of leptocephali in both directions may be sufficient for the entire juvenile population on each island to appear genetically homogeneous, even if each individual returns to its original place of birth.

There may not be selection for imprinting on rigid spawning areas when recruitment success depends on the larvae interacting with highly dynamic current patterns and possible recruitment areas being in many locations. Even temperate European and Japanese eels spawn over large geographical ranges of either longitude or latitude (Tsukamoto et al. 2011, Aoyama et al. 2014, Miller et al. 2015, 2019), although the geography of major currents (Gulf Stream, Kuroshio Current) flowing towards their continental distribution ranges restricts spawning to a single general area. Tropical South Pacific eels may just migrate away from the islands searching for congeners in suitable spawning habitats at various distances from their islands to spawn. The exceptionally high proportion of hybrids between different Pacific species found on the Vanuatu island of Gaua may indicate that eels follow each other to an established spawning area and recruit back to their freshwater habitats (Barth et al. 2020). The highly variable larval dispersal then results in the formation of an interwoven network of sink and source meta-populations

spanning from Papua New Guinea to FP and Pitcairn that are connected by eastward and westward current systems (Minegishi et al. 2008, Watanabe et al. 2009). In this respect, a key question is whether the eels either try to return to their place of birth or are adapted to spawn in a different location. Understanding how many spawning areas exist and how these meta-populations are interlinked is important for effective management.

A unique aspect of managing the anguillid eels in the South Pacific is that highly dynamic current systems with changing directions, positions, and strengths connect the small islands that are widely spread across a vast ocean basin, that provide more limited freshwater habitats compared to continents or large islands. Intensifying ENSO events due to climate change now further reduce the predictability of ocean currents (Ham 2018). Multiple spawning areas, shorter migration loops, and flexibility in timing and location of spawning may ensure successful reproduction and recruitment to these islands. However, at small population densities that could result from changing oceanic conditions in combination with overexploitation in freshwater, low numbers of spawning eels could cause drastic population declines (Winter et al. 2020). As long as our understanding of the reproductive biology of anguillid eels prevents a well-managed fishery (Righton et al. 2021), freshwater habitats and their eels should be protected. However, fishing pressure from local communities located at the lower stretches of rivers is high throughout the Pacific (R. Schabetsberger pers. obs.) and may increase if Pacific island nations start serving the demand from international markets. Enquiries from traders for glass eels and adults are increasing (Anon 2017). The attention of local authorities, scientists, stakeholders, and conservationists is required to safeguard the survival of Pacific eels. They are mythical creatures for human societies in Oceania (Flood et al. 1999), and they could act as flagship species that will help guide future conservation efforts (Itakura et al. 2020).

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