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The hydrographic features of anguillid spawning areas: potential signposts for migrating eels

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Running page head: *Hydrographic structure of anguillid spawning areas*

Abstract

Catadromous anguillid eels (Genus *Anguilla*) migrate from their freshwater or estuarine habitats to marine spawning areas. Evidence from satellite tagging studies indicates that tropical and temperate eel species exhibit pronounced diel vertical migrations usually between 150–250 m nighttime depths to 600–800 m during the day. Collections of eggs and larvae of Japanese eels (*A. japonica*) show they may spawn at these upper nighttime migration depths. How anguillid eels navigate through the ocean and find their spawning areas remains unknown, so the salinity, temperature and currents were analysed between 0–800 m depths within two confirmed and three hypothetical anguillid spawning areas during likely spawning seasons. Within all four ocean gyres many eels would encounter subducted Subtropical Underwater (STUW) during their nighttime ascents possibly providing odour plumes for orientation. Four spawning areas are located near the western margins of where subducted water masses form cores of elevated salinities (~35.1–36.7) around 100–300 m depths, while one is found near the center of subduction. ~~Low salinity surface waters and fronts occur above the areas with high salinity cores.~~ Spawning may occur at temperatures between 16–24°C where the thermocline locally deepens. At spawning depths, weak westward currents (c.a. >0.05–0.15 m s^{-1}) prevail, but at least three spawning areas include eastward surface countercurrents. Anguillid eels have acute sensory capabilities that are discussed in relation to potential signposts that may guide them to where they spawn.

Introduction

How catadromous anguillid eels are able to migrate long distances from their freshwater or estuarine habitats through the seemingly featureless ocean to reach their pelagic spawning areas has long been one of the great mysteries in eel biology, which continues to be understood to a very limited extent (Schmidt 1922, McCleave 1987, Tsukamoto 2009, Rigthon et al. 2012). After reproduction they die and their marine larvae, called leptocephali, drift with currents toward recruitment areas and become widely distributed in some subtropical gyres (Schmidt 1922, Shinoda et al. 2011, Miller et al. 2015a). Among the 19 anguillid species or subspecies, the European eels (*Anguilla anguilla*) migrate the longest distances of up to 7000 km (Aoyama 2009) to reach their spawning area in the Sargasso Sea of the western North Atlantic (WNA, Schmidt 1922). The western part of their spawning area is shared with American eels (*A. rostrata*, McCleave et al. 1987) that can migrate up to about 2500 km. Similar distances are covered by *A. japonica* in the western North Pacific (WNP, Aoyama 2009). These temperate anguillid eel migrations are among the longest one-way migrations known for any fish species (Alerstam et al. 2003). Even though some tropical species spawn offshore after only short migrations (Aoyama et al. 2003), all the eel spawning areas are over deep water (>1000 m) in places with warm surface currents, probably because the genus is derived from an ancestral mesopelagic eel species (Inoue et al. 2010).

Oceanographic fronts have been hypothesized to provide structures that define the spawning areas of anguillid eels. In the Sargasso Sea, two temperature fronts consistently form in the Subtropical Convergence Zone (STCZ) at about 22 and 24°C during the February to April spawning season (see Miller et al. 2015a) and gradually move northward with seasonal warming (Ullman et al. 2007). Leptocephali are consistently found south of the northern front (Kleckner & McCleave 1988, Munk et al. 2010). In the WNP *A. japonica* spawns within the westward flowing North Equatorial Current (NEC) along the seamount chain of the West Mariana Ridge (Tsukamoto et al. 2011, Aoyama et al. 2014). Adult eels, their fertilized eggs, and recently hatched preleptocephali were collected exclusively along the western and/or deeper southern end of the seamount ridge (Chow et al. 2009, Kurogi et al. 2011, Tsukamoto et al. 2011, Aoyama et al. 2014), which seems to act as a longitudinal signpost (Tsukamoto et al. 2003, 2011). The latitude of spawning appears to be influenced by a shallow salinity front formed by rainfall that can move north or south, with spawning occurring on the south side of the front (Kimura & Tsukamoto 2006, Tsukamoto et al. 2011, Aoyama et al. 2014). Spawning can take place at a wider range of latitudes when the front is absent (Aoyama et al. 2014).

Relatively few leptocephali of the 6 species sympatrically occurring anguillid eels have been collected and genetically identified in the western (WSP) and central (CSP) South Pacific (*A. australis*, *A. dieffenbachii*, *A. reinhardtii*, *A. marmorata*, *A. megastoma*, *A. obscura*) and the same is true for the 4 species in the western Indian Ocean (WIO, Jespersen 1942, Kuroki et al. 2008, Miller et al. 2015b; *A. marmorata*, *A. mossambica*, *A. bengalensis*, *A. bicolor*). Considerably more leptocephali of the Indian Ocean species were collected offshore of West Sumatra (Jespersen 1942, Aoyama et al. 2007). Catches of small leptocephali of the Celebes longfin eel, *Anguilla celebesensis*, and the Borneo eel, *Anguilla borneensis*, in the central Indonesian Seas indicate those species can spawn after comparatively short migrations (Aoyama et al. 2003).

It is still a mystery as to how silver eels navigate through the ocean to find their offshore spawning areas. They have several sensory systems such as vision, olfaction and a geomagnetic sense that could be used (McCleave 1987, Tesch 2003, Tsukamoto 2009), and orientation and navigation using the earth's magnetic field (Durif et al. 2011), temperature gradients, odor trails (Westin 1990, Van Ginneken and Maes 2005), and ocean currents (Rommel and McCleave 1973) have been proposed to potentially be used by migrating eels.

A new research approach of tagging migratory-stage silver eels with pop-up satellite archival transmitters (PSAT) has revealed information about their unknown spawning areas and migration behavior. The pop-up locations of New Zealand longfin eels, *A. diefenbachii*, have pointed towards a possible spawning area east of New Caledonia in the WSP (Jellyman & Tsukamoto 2010) that is generally consistent with estimates from modelling of larval transport (Jellyman & Bowman 2009). Silver eels of two tropical anguillids, the giant mottled eel, *A. marmorata*, and the Polynesian longfin eel, *A. megastoma*, that were tagged within the archipelago of Vanuatu in the WSP, both had their tags pop-up in a potentially shared spawning area between 8°S−12°S and 170°E−175°E (Schabetsberger et al. 2015).

Tagging studies showed that both temperate and tropical anguillid eels display a distinct diel vertical migration behavior (DVM) of usually swimming in the lower epipelagic zone (~ 150–250 m) during the night and then quickly descending to the deep mesopelagic zone (~ 600–800 m) after sunrise, where they remain during the day (Aarestrup et al. 2009, Jellyman and Tsukamoto 2010, Manabe et al. 2011, Wysujack et al. 2014, Schabetsberger et al. 2015, Béguer-Pon et al. 2015, Fig. 1). Some species such as the relatively small-sized *A. japonica* (Manabe et al. 2011) and *A. rostrata* (Béguer-Pon et al. 2015) and the large *A. dieffenbachii* (Jellyman and Tsukamoto 2010) sometimes entered the upper 100 m at night. However, during three long tracks of tropical silver eels that may have reached their spawning area in the WSP the eels almost never swam shallower than 100 m (Schabetsberger et al. 2013, 2015) as they would be expected to if they were searching for shallow oceanographic features. This raises the question about how migrating eels can detect the surface features of temperature or salinity fronts that are generally only present in the upper 150 m (Kleckner and McCleave 1988, Aoyama et al 2014) if they stay deeper. Predator avoidance probably governs this behaviour, because the eels remain deeper when moonlight is present thereby avoiding more nocturnally foraging fish (Schabetsberger et al. 2013, 2015, Chow et al. 2015).

Among all 19 *Anguilla* species, spawning-condition adult eels and eggs have only been collected for *A. japonica* and *A. marmorata* (adults only) and they were likely caught between 150 m and 300 m depths (Chow et al. 2009, Tsukamoto et al. 2011, Aoyama et al. 2014) corresponding to the upper nighttime migration depths of eels in the PSAT studies. This indicates that these water masses should be evaluated for potential oceanographic structures that eels may use to help locate their spawning areas. The most distinctive hydrographic feature at these depths is usually the high-salinity Subtropical Underwater (STUW) that is present in all the major ocean basins (Fig. 2A), which is formed by saltier water being subducted from the surface into the lower thermocline (Price 2001). This type of water is found within the spawning areas of the Atlantic eels (Kleckner and McCleave 1988), *A. japonica* (Aoyama et al. 2014) and in the presumed spawning regions in the WIO (Pous et al. 2010). The STUW in the WSP (Qu et al. 2013) is a prominent feature at the pop-up locations of *A. marmorata* and *A. megastoma* and has been hypothesized to possibly help migrating eels locate this area (Schabetsberger et al. 2013, 2015).

Now that data on the marine spawning migrations of eels are available that show they seem to predominantly migrate between 100 and 800 m depths, this behaviour can be related to the oceanographic conditions they experience during their presumed migration paths and within their spawning areas. The present study uses Argo float data to evaluate the hydrographic structure and current flow patterns of each subtropical gyre where anguillid spawning occurs or may occur, with the possible spawning depths being tentatively considered for inter-comparisons to be between 150−300 m in accordance with previous information from *A. japonica*. Ocean-Atmosphere changes have been suggested to be contributing to the declines of anguillid eels in recent decades (Knights 2003, Miller et al. 2009), with several species now on the IUCN Red List (Jacoby et al. 2015), so a better understanding of the oceanographic conditions the eels experience while migrating and at the spawning area may eventually facilitate management and conservation efforts.

Methods

Hydrographic analysis

The hydrographic structure of the 4 subtropical gyres where anguillid eels are present were examined (WNA, WIO, WNP, WSP, CSP). No catadromous eels occur in the warm Brazil Current of the South Atlantic or along the coastlines adjacent to the eastern Pacific (Tesch 2003, Aoyama 2009). Patterns of salinity, temperature, and currents at the two confirmed offshore spawning areas of the Atlantic and North Pacific eel species and within presumed eel spawning areas in the Indian and the South Pacific Ocean were studied.

The original data used in the interpolations were obtained from Argo floats (www.jamstec.go.jp/ARGO/argo_web/MapQ/Mapdataset_e.html). The Argo project has deployed a global array of about 3800 profiling floats that drift freely in the ocean while they measure temperature and salinity from 0–2000 m every 10 days (www-argo.ucsd.edu/). Interpolated temperature and salinity fields were gridded to a spatial resolution of 1 degree, with a temporal resolution of 1 month, and with 25 vertical levels from the surface to 2000 dbars. Zonal geostrophic currents were calculated with respect to a reference depth of 2000 m. Bathymetry data were gathered from the ETOPO 1-minute dataset (www.ngdc.noaa.gov/mgg/global/global.html).

Spawning areas

The Sargasso Sea spawning area of the Atlantic eels was the first to be discovered (Schmidt 1922; Fig 2A) and now the catch data of all collected leptocephali of both species has been combined into a database that shows the distribution of small (<11 mm) *A. anguilla* and *A. rostrata* larvae is predominantly between 24–30°N and 50–73°W and between 23–29°N and 60–76°W, respectively (Miller et al. 2015a). We made a section along 65°W in March 2014, since surveys to collect anguillid larvae were made across the Sargasso Sea in March and April of that year (P. Munk and R. Hanel, personal communication).

In the Indian Ocean a few leptocephali of *A. marmorata*, *A. mossambica*, *A. bengalensis*, and *A. bicolor* were collected during the Dana expedition (Jespersen 1942) in the Mozambique Channel and north of Madagascar. Based on otolith microstructure analyses of glass eels and elvers collected in rivers of islands in the WIO, a spawning area near the Mascarene Plateau (west of 60.5°E, 13–19°S) was predicted and evaluated by drift simulations (Robinet et al. 2008, Réveillac et al. 2009, Pous et al. 2010). Two sampling surveys for leptocephali were conducted there recently from November to February but no small anguillid larvae were collected (Miller et al. 2015b). We made a section along 65°E for October 2013, which is a month included in the estimated spawning times from otoliths (Pous et al. 2010). The Dana Expedition collected many small anguillid leptocephali off west Sumatra, which were probably mostly *A. bicolor* (Jespersen 1942, Aoyama et al. 2007). Small tropical anguillid leptocephali of *A. borneensis* and *A. celebesensis* were also collected in the central Indonesian Seas (Aoyama et al. 2003), but these more local spawning areas close to major landmasses (Fig. 2A) will not be examined in the present study.

The spawning area of *A. japonica* in the WNP has been studied since its discovery in 1991 (Tsukamoto 1992) with leptocephali and newly hatched preleptocephali being collected (Shinoda et al. 2011, Tsukamoto et al. 2003, 2011). In 2008 the first spawning adults of *A. japonica* and *A. marmorata* were caught along the ridge at depths above 350 m (Chow et al. 2009). Eggs of *A. japonica* were first collected in 2009 (Tsukamoto et al. 2011), and then again during consecutive cruises in 2011 and 2012 (Aoyama et al. 2014). Spawning occurs during new moon periods based on both backcalculated hatching dates of leptocephali and when the eggs and preleptocephali have been collected. The eels spawn between 12–16°N and 141–143°E somewhere below the thermocline because the eggs and preleptocephali appear to accumulate at about 150 m depths (Tsukamoto et al. 2011, Aoyama et al. 2014). The spawning area of *A. marmorata* overlaps with *A. japonica* (Kuroki et al. 2009), and the newly discovered anguillid species, *A. luzonensis* may also spawn offshore in the NEC. We made a meridional section along 141°E that corresponds to the June 2011 egg collections (Aoyama et al. 2014).

There is less information available about where spawning areas may be in the WSP. Some large anguillid leptocephali were collected in the region predominantly between 5–20°S and 160°E–175°W (Jespersen 1942, Kuroki et al. 2008). These and more recent collections of a few smaller leptocephali (Miller et al. 2006, Kuroki et al. 2008) indicated that some species likely spawn within the westward flowing South Equatorial Current (SEC) that could transport species like *A. reinhardtii* and *A. australis* towards Australia. The smallest leptocephali of *A. marmorata* (Kuroki et al. 2008) were found close to the pop-up locations of PSAT tags attached to adult *A. marmorata* and *A. megastoma* released in Vanuatu, which pointed to a potential shared spawning area between 8–12°S and 170–175°E (Schabetsberger et al. 2015). Presently, no leptocephali of the New Zealand longfin eel *A. dieffenbachii* have been found, but they may spawn in potentially overlapping areas with *A. australis* and *A. reinhardtii* somewhere between 10–25°S and 165–180°E (Jellyman and Bowen 2009). That region of the WSP is probably not the only area where spawning occurs though, because there is evidence that some species may have two populations within the South Pacific. The analysis of differences in the numbers of vertebrae of adult eels indicated that there were probably eastern and western spawning populations of *A. marmorata* and *A. megastoma* (Ege 1945). Molecular genetic evidence (e.g., Minegishi et al. 2008) and additional morphometric analyses later supported this likelihood (Watanabe et al. 2008, 2009). From the arrival of glass eels, Marquet (1992) hypothesized that an eastern spawning area is located west of the Tuamotu archipelago between 15–20°S and 130–135°W (also see Jellyman 2003). We made meridional sections for both South Pacific spawning regions that were along 173°E and 130°W, respectively, for July 2013, the year of the Schabetsberger et al. (2015) tagging study in Vanuatu. Tropical eels may spawn throughout the year (Jellyman 2003), but the PSAT tags surfaced in the presumed spawning area between May and September.

Results

Salinity

Within all four investigated subtropical gyres there are tongues of subducted STUW present at the upper nighttime migration depths of eels around 150 m depth (Figs. 1, 2A). The areas of formation of the STUW indicated by high surface salinity occur in the eastern parts of the gyres (Fig 2A). The STUW flows obliquely towards the equator while being carried by horizontal circulation (Fig. 2B). Four oceanic spawning areas of *Anguilla* species are located near the western margins (Fig. 2A) of where subducted water masses form either cores of higher salinities around 100–300 m depths or inclined layers of subducted water masses stretch down from the surface and bend equatorward into the thermocline (Fig. 2A; WNA, Figs. 3A, 4A; WIO Figs. 3B, 4B; WNP, Figs. 3C, 4C; WSP Figs. 3D, 4D). The hypothetical spawning area in the CSP is located within the formation area of STUW (Figs. 2A, 3E, 4E). In the Pacific Ocean, the spawning areas are more or less congruent with the latitudinal extension of high salinity waters while in the Indian Ocean and the Atlantic they extend northeast of them (Fig. 2A). At the presumed spawning depths around 150 m salinities were highest in the WNA (~36.7), followed by the CSP (~36.1), WSP (~35.9), WIO (~35.2), and the WNP (~35.1, Fig. 3A-E, 4A-E). In three areas shallow lenses (<100 m) of lower salinity water masses are found (WIO, WNP, WSP) that have salinities ranging from 34.0-35.0.

Temperature

Within the spawning areas surface temperatures increased towards lower latitudes with a more gradual shoaling of isotherms in the WNP (Fig 2F-J). Within these broader latitudinal gradients temperature fronts may form locally, for example in areas where different currents meet (Fig 2K-L), but they are too narrow to show up in the temperature fields interpolated from Argo data (see Discussion). The estimated spawning depth zone were at temperatures between 16–24°C within or near the thermocline where along meridional sections warmer water reaches deeper down (Fig. 3F-J). Horizontally these elevated temperatures at 150 m show up as tongues of warmer water stretching east to west (Fig. 4F-J). Only in the WNA and the WIO spawning seems to occur just north of these elevated temperatures at spawning depths.

Currents

Predominantly westward surface currents were present in the anguillid spawning areas except for the WNP (NEC, SEC, Fig. 2B), but in the WNA (Fig. 3K), WSP (Fig. 3N) and the CSP (Fig. 3O) eastward countercurrents occur (Subtropical Countercurrent, SCC; South Equatorial Countercurrent, SECC, Fiji Basin Countercurrent, FBCC; SCC respectively, labelled in Fig. 3). In the WIO (Fig. 3L) the hypothetical spawning area is located just north of the eastward SCC. In the WNP (Fig. 3M) the spawning area is located south of the North Pacific Subtropical Countercurrent (SCC) and north of the North Equatorial Countercurrent (NECC). Weak westward currents prevailed at the presumed spawning depths (Figs. 4K-O; WNA: <0.05 ms^{-1}, WNP: ~0.15 ms^{-1}, WSP: <0.05 ms^{-1}, CSP: ~0.07 ms^{-1}, WIO: ~0.1 ms^{-1}). *Double check values after we hear back from Giorgio!*

Discussion

Hydrographic features of spawning areas

Since it was discovered that *A. anguilla* crosses the entire Atlantic Ocean to spawn in the Sargasso Sea, scientists and the general public have wondered about how silver eels find their way back to where they hatched as larvae. Eels have been hypothesized to use hydrographic features like major current patterns, or temperature and salinity fronts to help decide where to spawn (reviewed in Tsukamoto 2009), but understanding of the importance of these and other oceanic signposts and the sensory capabilities of eels to detect them are still at a very early stage. In the present study we compared salinity, temperature and current patterns derived from Argo float data on a global scale and at a fine-scale within two confirmed and three hypothetical spawning areas in four different ocean gyres. Common patterns were the proximity to subsurface subducted water masses as well as the presence of shallow features like countercurrents or temperature gradients and low-salinity pools that potentially cause the formation of oceanographic fronts.

One interesting observation is that the STUW water mass is present at the upper nighttime migration depths of eels in all of the spawning areas. This water is subducted from the mixed layer into the stratified thermocline and spreads horizontally over large areas of all 4 subtropical gyres. However, except for the estimated spawning location in the CSP, the analysed spawning areas are found along the western or northwestern edges of these tongues of higher salinity water where there may be zonal salinity gradients. Vertically, the spawning areas appear to be located within the lower edges of the cores of the STUW as previously seen in the WNP based on the distributions of egg and larval catches (Aoyama et al. 2014) and adult vertical migration data from satellite tags (Schabetsberger et al. 2015). The cores of these water masses are centered at about 150 m depths as also seen previously (Kleckner and McCleave 1988, Roden 1998, Miller et al. 2006, Aoyama et al. 2014), with absolute salinities that ranged from maximum values of ~36.7 in the WNA to minimum values of ~35.1 in the WNP.

These high salinity waters are subducted within the centres of the wind driven subtropical ocean gyres from the mixed layer into the thermocline (Qui & Huang 1995, Qu et al. 2013). The process consists of downward pumping from Ekman convergence and horizontal advection by lateral geostrophic flow (Huang & Qui 1998 and references therein). O'Connor et al. (2005) estimated the STUW subduction volumes in the North Atlantic (44-36 m yr^{-1}, 2 Sv; 1 Sv = 10^6 m^3 s^{-1}), North Pacific (26-17 m yr^{-1}, 4 Sv), South Pacific (32-33 m yr^{-1}, 7 Sv), and South Indian Ocean (22-25 m y^{-1}, < 1Sv), but global warming may decrease subduction rates due to decreasing lateral induction because of shallower winter mixed layer depths (Liu & Wang 2014). The renewal time for STUW appears to be 10–15 years (Price 2001). Qu et al. (2013) estimated that some STUW moves though the WSP to reach New Guinea within 2 years and extends over nearly the entire Pacific basin after 13 years, with highest concentrations remaining in the subtropical South Pacific. When these water masses are transferred beneath the mixed layer, they are shielded from the atmosphere and only slowly modify their properties through mixing in the ocean interior (Williams 2001). Hence they would seem to carry a long "memory" compared with the surface mixed layer, which as mentioned later may provide olfactory cues to migrating eels.

Above these subducted water masses, pronounced temperature (typically controlling density) and weaker salinity gradients may also provide possible signposts by separating different water masses. A temperature front in the Sargasso Sea appears to form the northern limit of where spawning by the Atlantic eels occurs based on the distribution of their small larvae (Kleckner and McCleave 1988, Munk et al. 2010, Miller et al. 2015a). A similar front can form in the WSP just north of Fiji where small anguillid larvae have been collected previously at the edges of the so called "western Pacific fresh pool" (Roden 1998, Miller et al. 2006, 2009), and also in the WIO (New et al. 2006). Our analyses showed there are areas of low-salinity water in the upper 100 m at the spawning areas in the WIO, WNP, and WSP. These lenses of low-salinity water are probably all caused by tropical rainfall. In the WIO a shallow layer (~50 m) of low-salinity surface water overlays a sharp halocline and may form salinity fronts at its northern and southern boundaries (New et al. 2006). In the WNP, the latitudinal position of a salinity front seems to influence the spawning locations of *A. japonica* (Kimura & Tsukamoto 2006, Tsukamoto et al. 2011, Aoyama et al. 2014).

Our analyses of geostrophic currents calculated from the Argo float data indicated that the anguillid spawning areas are predominantly within westward surface currents (NEC, South Equatorial Current, SEC). At 150 m depths weak but consistent westward flows were observed in most areas. Eastward flowing countercurrents were present within or near the spawning areas in the WNA (Subtropical Countercurrent, SCC), WNP (North Equatorial Countercurrent, NECC), WSP (South Equatorial Countercurrent, SECC, Fiji Basin Countercurrent, FBCC), and the CSP (SCC). Similarly, in the WSP the dynamic seasonal alternations between the strengths of the SEC and SECC (Chen & Qiu 2004) could result in leptocephali being transported to archipelagos both west and east of the presumed spawning area northwest of Fiji (Schabetsberger et al. 2015). The position of the spawning area in the CSP shown in the present study is uncertain because no small leptocephali have been collected yet, but both westward and eastward flow was indicated to occur at possible spawning latitudes. Within this region the SEC forms sharp boundaries with the SCC in the south and the Marquesas Countercurrent further North (Marquet 1992). The complex current patterns are influenced by ENSO events (Martinez et al. 2009) and similar to in the WSP, leptocephali may also be carried eastward, explaining the presence of *Anguilla* spp. at Pitcairn Island or the Galapagos Islands.

Eel migration behavior

Most PSAT studies of temperate and tropical anguillid eels all show surprisingly similar oceanic DVM patterns (Fig. 1). The eels migrate at 100–250 m depths during the night and then quickly descend to 600–800 m during dawn, remain there during the day and ascend again during dusk (Aarestrup et al. 2009, Schabetsberger et al. 2015), although movements up to very shallow water have also been observed (Béguer-Pon et al. 2015). Maximum daytime depths with temperatures of about 4°C may be actively sought to retard gonadal development (Aarestrup et al. 2009, Jellyman & Tsukamoto 2010, Manabe et al. 2011) or may reflect the physiological limit necessary to keep up a minimum metabolism (Schabetsberger et al. 2013). The upper nighttime migration depths seem to be adjusted in response to the amount of moonlight, presumably to avoid epipelagic predators (Schabetsberger et al. 2013, 2015, Chow et al. 2015).

For most species, eels tagged with PSAT's rarely entered shallow water in the open ocean, although most of them were still far from their destination. However, two *A. marmorata* tagged in Vanuatu that had their tags released on schedule after being attached for 3 and 5 months may have for the first time reached their spawning area northwest of Fiji (Schabetsberger et al, 2013, 2015). They almost never entered waters above 90 m throughout their entire journey and remained deep after reaching the area. Their diel vertical migration behaviour remained remarkably regular over up to 5 months indicating that they may have been largely unaffected by the tag compared to smaller *A. anguilla* tested under laboratory conditions (Burgerhout et al. 2011, Methling et al. 2011).

If eels deliberately and recurrently ascend to shallower water once they approach their spawning areas remains unknown until more telemetric data become available. In a recent study a tagged *A. rostrata* silver eel coming within reach of the spawning area in the Sargasso Sea frequently ascended to shallow water, although on average it migrated at 140 m during the night (Béguer-Pon et al. 2015). There is additional evidence that eels frequently enter waters above 75 m earlier during their migrations (Jellyman &Tusukamoto 2010, Manabe et al. 2011), but all 3 tagging studies used a more invasive attachment technique of penetrating the body musculature compared to only passing under the skin of the upper body (Okland et al. 2011). Eels seem to exhibit less regular DVM behaviour into shallower water when they are displaced or exhausted (Schabetsberger et al. 2015, personal observation). In a differently designed study, *A. japonica* also moved between 75 and 100 m at night (Chow et al. 2015). Long holding before release from a research vessel, implantation of ultrasonic tags, and in some cases punctured swimmbladders may have also affected their DVM behaviour though. More data from large eels released shortly after capture and tagged with minimally invasive techniques are needed to track eels all the way to their spawning sites. However, even if more data are obtained, it may still be impossible to detect spawning events from recorded depth and temperature tracks if spawning occurs at the regular upper migration depths without any changes in DVM behaviour.

Hydrographic signposts for eel orientation

The directions and distances that the eels migrate to reach the 5 spawning areas examined in this study must vary widely as would the conditions they experience. Silver eels leaving eastern North America, East Asia and eastern Australia must first cross powerful boundary currents overlapping with their nighttime migration depths (Gulf Stream, Kuroshio, East Australian Current respectively). Eels leaving Europe, North Africa, Madagascar, the Mascarene Islands, New Zealand and the various islands of the WSP region migrate through a variety of lower-velocity current systems and eddy-dominated areas (Fig. 2B). The growth habitats of most species are either widely distributed latitudinally or are on islands spread across wide regions, so the eels would be approaching their spawning areas from a variety of directions. Probably the most extreme example of this may occur for *A. rostrata* migrating to the Sargasso Sea from regions ranging from Atlantic Canada in the far north and to the Caribbean Sea in the far south.

Our global hydrographic analyses show that eels migrating at the observed nighttime migration depths would either start their migrations within the STUW or encounter it on their way to the spawning area. In either case, they would eventually experience weak gradients in salinity as they moved further towards the cores of the STUW. The salinity maxima around 150 m are crossed twice a day during DVM with the eels migrating below the STUW during the day and within it at night. In terms of temperature, the spawning areas seem to be located where the thermocline is weakening and extending deeper. The eels would therefore experience different types of vertical temperature gradients on the north or south sides of these areas during their DVMs. The temperature and salinity structures at deeper daytime depths do not seem to provide any clear markers of where spawning occurs though.

It may be unlikely that migrating eels can detect very gradual horizontal gradients of salinity and temperature, especially in the context of their vertical migrations, but these subducted water masses may contain other olfactory cues. The ages of silver eels are generally in the range of about 6 to 15 years (Jacoby et al. 2015) and hence they may still recognize information they imprinted on during their early larval life with their acute olfactory sense. Because these water masses are transferred beneath the mixed layer, they only slowly modify their properties (Williams 2001, Qu et al. 2015). Hence they carry a long "memory" compared with the surface mixed layer and may provide stable signposts for migrating eels that are comprised of distinctive odours even though they would be affected by a variety of biological activity.

The shallow hydrographic fronts that have been hypothesized to possibly influence where spawning occurs would seemingly require the eels to enter the upper 100 m at night to detect them, unless the fronts are linked to deeper features. In the Sargasso Sea (Kleckner and McCleave 1988) and the WSP (Roden 1998, Miller et al. 2006) the edges of the STUW cores correspond to where shallow temperature/density fronts occur, but it remains unknown if these features move latitudinally in synchrony. Both the salinity front within the *A. japonica* spawning area (Kimura & Tsukamoto 2006, Tsukamoto et al. 2011, Aoyama et al. 2014) and the temperature fronts in the Sargasso Sea (Kleckner & McCleave 1988, Munk et al. 2010) are most prominent above 100 m. Therefore, unless the eels can perceive altered patterns of sound or light transmission below fronts, or can detect chemical components of different water masses that sink downward on either side of fronts, they may not be able to detect the location of fronts without entering shallow water. It may be unlikely that eels would expose themselves to epipelagic predators potentially concentrating at fronts (Acha et al. 2015). However, swimming at the base of these hydrographic structures may provide sufficient sensory input to know their position in relation to the different water masses above. Some eel species such as *A. rostrata* (Béguer-Pon et al. 2015) might be adapted to search for shallow features, but it remains to be determined how important these fronts are as signposts, as *A. japonica* must have used other cues when the salinity front was absent (Aoyama et al. 2014) and if they are used, how they are detected.

Sensory ecology of finding spawning areas

The present study is not designed to determine what sensory systems may be used by migrating eels, but enough is now known about eels and the environments they would experience during migration to discuss this subject. Eels have several highly developed sensory organs (Tesch 2003), and it is likely that they use several if not all of these during at least some stage of their migrations. Once they reach the open ocean they move vertically through about half a kilometre of water column every day over several months and therefore have the chance to detect different water properties or changes in the magnetic field. Various ideas have been proposed for the types of cues eels may use while migrating, or to detect the features of their spawning areas (Rommel and McCleave 1973, McCleave 1987, Westin 1990, Van Ginneken and Maes 2005, Tsukamoto 2009, Westerberg 2014), but none of these have been validated through any kind of direct testing. For example it is unclear to what extent eels might use "beaconing" (odour cues that build up a gradient), "trail following" (odour trails from conspecifics), "route reversal" (memory of landmark series), "path integration" (knowledge of own current position with respect to the goal in terms of distance an direction), "compass orientation" (e.g. sun, moon, magnetic compass; genetic and/or experience based components), "vector orientation" (genetic or acquired information about distance and direction of the goal), or "true navigation" (navigation, map and compass mechanism) as listed by (Papi 2006) during different stages of their journey.

Anguillid eels exhibit a consistent direction of orientation relative to the magnetic field (Nishi et al. 2004, Durif et al. 2013). If they are also sensitive to large scale gradients in the inclination and the intensity of the earth' magnetic field (Durif et al. 2013), and potentially even to the fine scale-mosaic of magnetic anomalies in the ocean floor (<1% of the total field at the surface of the ocean; Walker et al. 2002, Lohmann et al. 2008) remains to be tested. This sense has been found to probably be used during long-distance migrations in various marine animals such as sea turtles or salmon (Walker et al. 2002, Papi 2006, Lohmann et al. 2008), so silver eels may be able to locate regions of the spawning areas through geomagnetic information imprinted-on during their larval period.

Eels are likely adapted for orientation in relation to water currents during their freshwater growth stage and during the downstream migration of silver eels, but in the open ocean they are immersed within the moving currents where there is a lack of stationary reference points (Montgomery et al. 2000). Alternatively, they may not feel the current itself, but sense the infrasound created at the edges of strong current systems or from strong turbulence with their otoliths (Sand & Karlsen, 2000). Rommel and McCleave (1973) proposed that eels might also sense weak electric fields induced by ocean currents flowing in the geomagnetic field of the earth, which may allow them to perceive the hydrodynamic field around them. Similarly, eels may be able to perceive magnetic signals generated by ocean circulation (Manoj et al. 2006). However, each current might carry a multitude of potentially specific odours that may also provide cues for orientation.

Navigation according to a direct sun- or moon compass during clear skies is unlikely at the depths most eels are migrating, as the discs of both celestial bodies would only be visible down to about 50 m in clear and calm ocean water (Partridge 1990). It is not known if eels can perceive light polarization, but if they do, they could theoretically gain an azimuth bearing for the sun down to several hundreds of meters (Waterman 2006). Solar and polarized light compasses would have to change their reference bearing with the sun's movement through the sky and are dependent on the latitude of the migrating eel. Nevertheless, the 24h cycle of underwater radiance provides a synchronizing time signal for the internal clock, which is critical for the timing of their distinct DVM.

As the eels get closer to the spawning areas, they may also rely on their highly sensitive olfactory system (Tesch 2003). It has been speculated that they back-track imprinted odour trails from specific biological communities within certain water masses (McCleave 1987, Westin 1990, Tsukamoto et al. 2003, van Ginneken & Maes 2005). They may also follow odours from other eels, as mucus, urine, and/or bile salts, potentially released with water passing through the shrunken gut of silver eels, are potential pheromones (Huertas et al. 2008). Eels can likely perceive strong horizontal and vertical salinity gradients with sensitive cells in the gills, olfactory organ, esophagus, oral cavity, and gastrointestinal epithelia (Evans et al. 2005, Kültz 2012) or with their olfactory organs. In general, the sensitivity of the otherwise highly sensitive nares to different ions seems poorly understood. In addition, eels have a complex set of additional osmosensors in their brain, pituitary gland, and vasculature (Kültz 2012).

Once within the spawning areas, there are vertical gradients of salinity and temperature that eels might use to detect their preferred spawning depths. For example, within the high-salinity cores, an eel ascending or descending at a speed of 5 m min^{-1} experiences salinity changes of more than 1.0 within an hour. Concurrently, eels can likely detect the thermocline during their DVM, assuming their sensitivity is similar to some freshwater fish that can detect rapid temperature changes down to 0.05°C (Bardach & Bjorklund 1957). Additionally, there is evidence that fish can accurately sense their depth with the swimbladder acting as a pressure receptor organ (Holbrook & Burt de Perera 2011).

Willis et al. (2009) proposed the interesting hypothesis, that sharp descents and ascents (50–605 m) during dawn and dusk, so called spike dives, provide cues for orientation in bluefin tuna (*Thunnus maccoyi*). They may probe vertical profiles of polarized light and/or detect magnetic field intensity, which both show characteristic patterns during crepuscular periods. Although predator avoidance seems to be an important driving force behind the large-scale DVM in eels (Schabetsberger et al., 2015), the concurrent detection of the range of different environmental variables discussed above for obtaining cues for orientation might be another function of DVM behavior.

Concluding remarks

The present study briefly evaluated the hydrographic structures associated with 2 confirmed and 3 hypothetical spawning areas of anguillid eels and discussed these features in relation to what is known about the oceanic migration behaviour and sensory systems of eels. Although it is clear that the mystery remains about how they can find their spawning areas during such long migrations, our study suggests some hypotheses about various features and senses that may be involved during the different stages of their migration. All spawning areas are associated with the STUW and with shallower hydrographic fronts, and the water masses associated with either one or both features could be imprinted-on by the larvae and later used to return. These possibilities and whether or not the migrating eels enter the upper layer of the ocean more frequently once they have reached their spawning areas, remain to be determined.

For effective protection and management of eels, more information is urgently needed on the marine part of their life cycle (Jacoby et al. 2015). Important steps are to locate more of the spawning areas in the Indo-Pacific, to determine how the eels find their spawning areas, and if changes in ocean-atmosphere conditions may affect that ability (Tsukamoto 2009, Miller et al. 2009, Righton et al. 2011). So far, the oceanic spawning areas of four species have been found through research cruises targeting the collection of smaller and smaller leptocephali over several years or decades. Satellite tags now provide a comparatively cheap way to narrow down the search areas. They will also provide information on the behaviour of eels that can then be related to environmental conditions observed with remote sensing technologies. Satellite tags with extra or improved sensors (salinity, low light) may provide additional information on the environmental conditions experienced by eels during migration. At present, geo-location underwater through measurement of light levels during daytime is only possible in shallow, well-lit surface waters (Lam et al. 2008). With the exact knowledge of the positions of eels, migration paths could be overlaid with environmental conditions measured with autonomous devices such as Argo floats. Additionally, the sensitivity of eels to magnetism, ion concentrations, infrasound, and polarised light could be further evaluated in laboratory experiments. By using a range of research approaches, including the possibility of direct observations of eels in the ocean (Fukuba et al. 2015), more progress will hopefully be made in the long quest for understanding the enigmatic migration and reproductive behaviour of eels in nature.

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Figure Captions

Fig. 1. Diel vertical migrations (DVM) of individual migrating anguillid silver eels tagged with pop-up satellite transmitters. *Anguilla anguilla* in the western North Atlantic (A, Aarestrup et al., 2009), *A. japonica* in the western North Pacific (B; S. Watanabe Unpubl. Data), *A. marmorata* (C) and *A. megastoma*, (D) in the western South Pacific (Schabetsberger et al. 2013, 2015).

Fig. 2. (A) Global map of salinity at 150 m depth (Time x-y) from Argo float data. Rectangles indicate spawning areas of anguillid eels (Western North Atlantic, WNA; Western Indian Ocean, WIO; Western North Pacific, WNP; Western South Pacific, WSP; Central South Pacific, CSP). Spawning in the WNA (*A. anguilla*, *A. rostrata*) and the WNP (*A. japonica*, *A. marmorata*, A. luzonensis?) has been confirmed by collection of small developmental stages. Hypothetical spawning areas in the WIO (*A. marmorata*, *A. mossambica*, *A. nebulosa*, *A. bicolor*), WSP (*A. australis*, *A. dieffenbachii*, *A. reinhardtii*, *A. marmorata*, *A. megastoma*, *A. obscura*) and the CSP (*A. marmorata, A. megastoma, A. obscura*) are based on estimates of larval drift or theoretical considerations. The small embedded rectangle in the WSP (*A. marmorata*, *A. megastoma*) depicts a spawning area predicted from satellite tagging results (see Materials and Methods for delineation of spawning areas). Transect lines indicate meridional sections shown in Fig. 3. The tilted rectangle west of Indonesia corresponds to the likely spawning area of *A. bicolor* and the rectangle in central Indonesia shows the region where *A. celebesensis* and *A. borneensis* spawn, but are not analyzed in this study. (B) Monthly (?) averages of global ocean surface currents derived from satellite altimeter and scatterometer data for the year 2013 (Near realtime Global Ocean Surface Currents – NOAA –). Black transect lines and enclosing rectangles refer to meridional sections and enlarged maps shown in Figs. 3 and 4, respectively. Grey areas indicate freshwater distribution of anguillid eels.

Fig. 3. Meridional sections through spawning areas between 0–800 m depth of salinity (A-E), temperature (°C, F-J), and geostrophic currents (K-O, U, ms^{-1}, red: eastward currents, blue: westwards currents) during known or presumed spawning times (see Materials and Methods). Dashed rectangles indicate latitudinal and vertical extensions of spawning areas. The major west- and eastward currents are identified (West: North Equatorial Current, NEC; South Equatorial Current, SEC, Gulf Stream, GS; East: Subtropical Counter Currents, SCC; North Equatorial Counter Current, NECC, South Equatorial Counter Current, SECC; Fiji Basin Counter Current, FBCC).

Fig. 4. Maps of salinity (A-E), temperature (°C, F-J), and geostrophic currents (U, ms^{-1}, K-O, red: eastward currents, blue: westwards currents) at a depth of 150 m during known and presumed spawning times. Dashed rectangles indicate latitudinal and longitudinal extensions of spawning areas. Black vertical lines show the positions of meridional sections in Fig. 3.

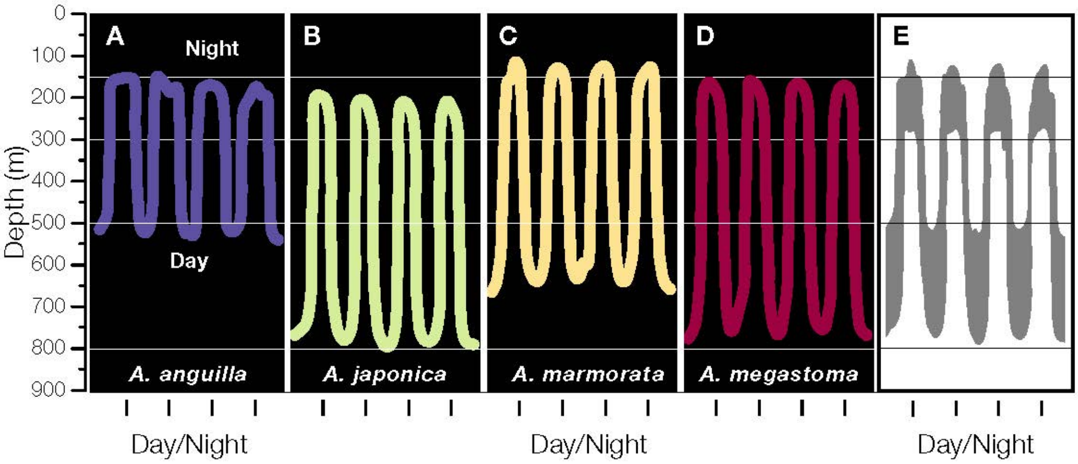
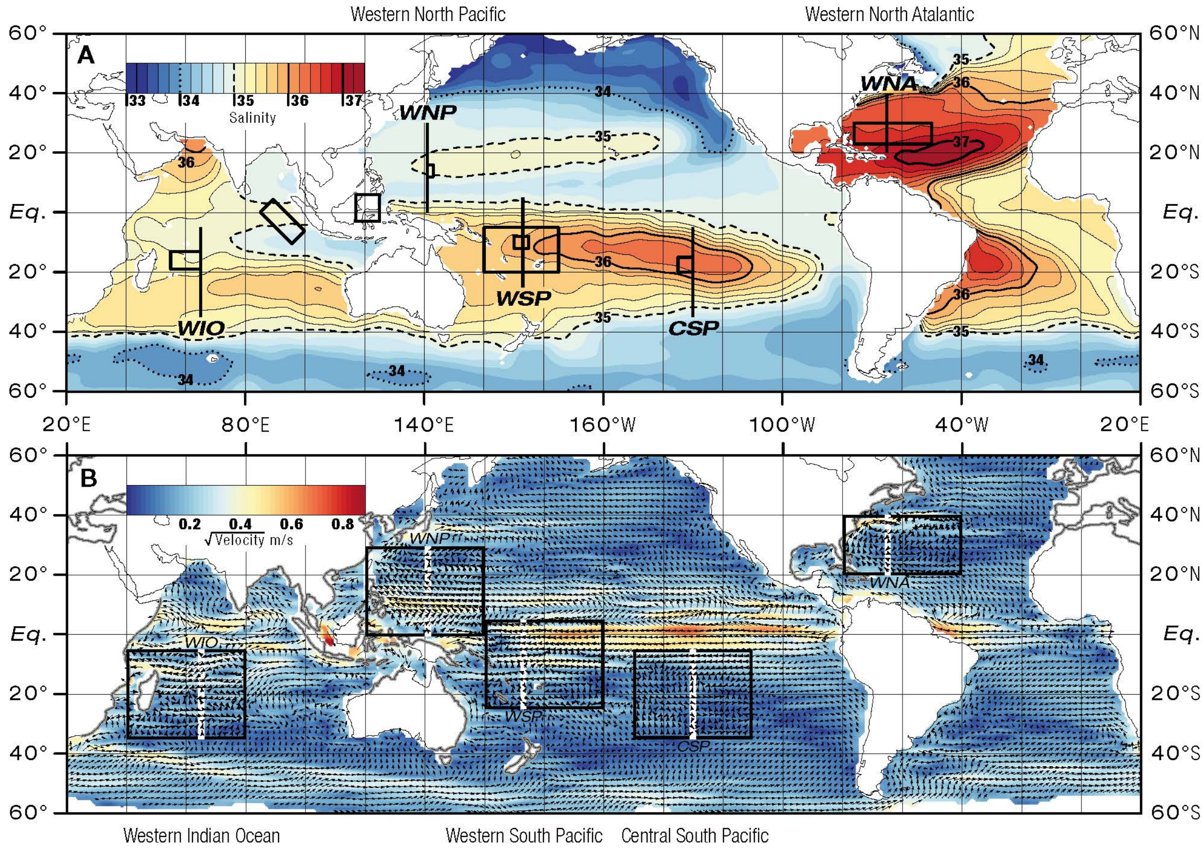

A
B
C
D
E
Night
Day
Depth (m)
0
100
200
300
400
500
600
700
800
900
A. anguilla
A. japonica
A. marmorata
A. megastoma
Day/Night
Day/Night
Day/Night

Fig. 1



Western North Pacific
Western North Atalantic
A
33
34
35
36
37
Salinity
WNP
WNA
WIO
WSP
CSP
60°
40°
20°
Eq.
20°
40°
60°
60°N
40°N
20°N
Eq.
20°S
40°S
60°S
20°E
80°E
140°E
160°W
100°W
40°W
20°E
B
0.2
0.4
0.6
0.8
√Velocity m/s
Western Indian Ocean
Western South Pacific
Central South Pacific

Fig. 2

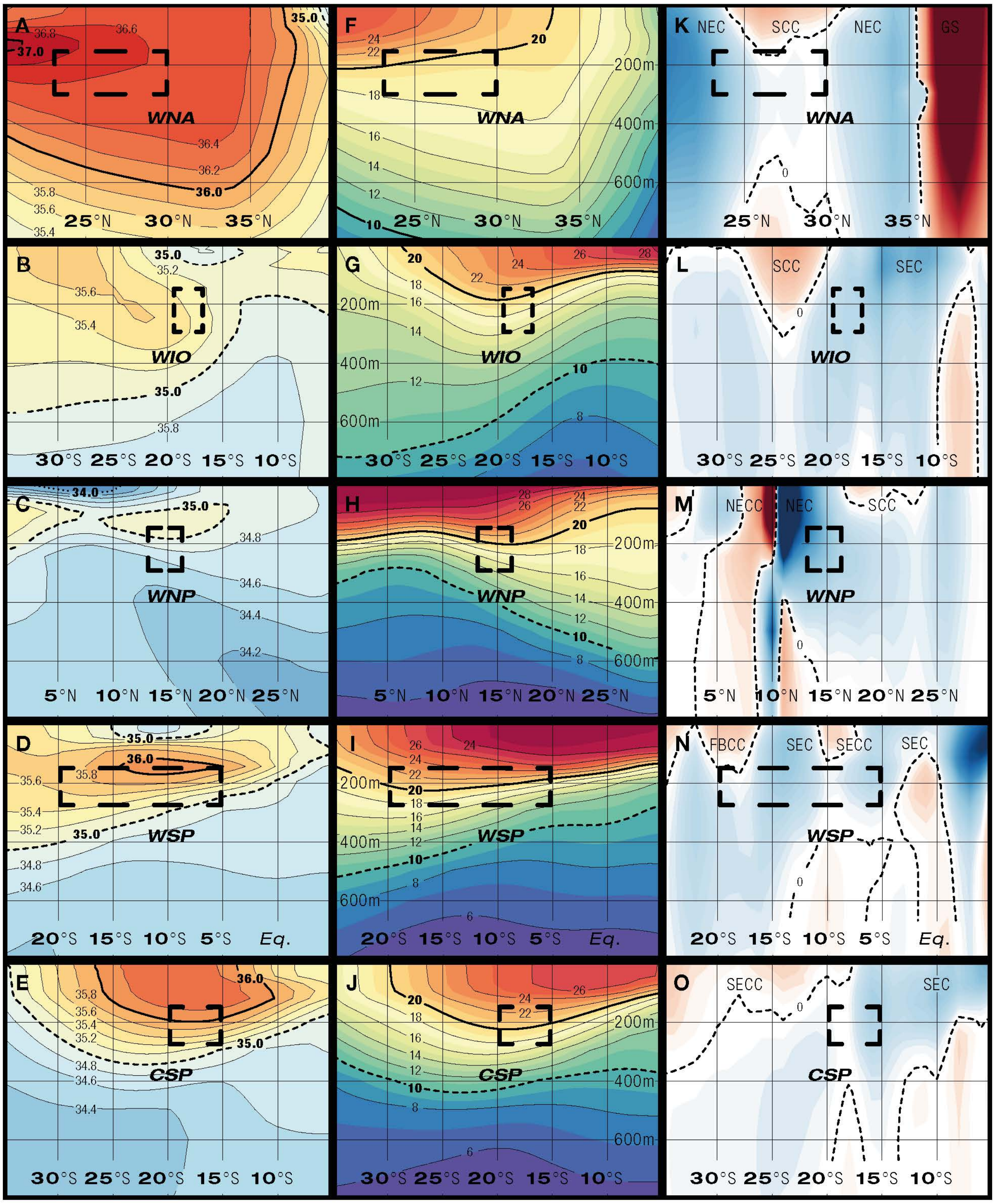

A
37.0
36.8
36.6
35.0
WNA
36.4
36.2
36.0
35.8
35.6
35.4
25°N 30°N 35°N
F
24
22
20
18
16
14
12
10
200m
400m
600m
WNA
25°N 30°N 35°N
K NEC SCC NEC GS
WNA
0
25°N 30°N 35°N
B
35.0
35.2
35.6
35.4
WIO
35.0
35.8
30°S 25°S 20°S 15°S 10°S
G
20
24
26
28
22
18
16
14
12
10
8
200m
400m
600m
WIO
30°S 25°S 20°S 15°S 10°S
L SCC SEC
0
WIO
30°S 25°S 20°S 15°S 10°S
C
34.0
35.0
34.8
WNP
34.6
34.4
34.2
5°N 10°N 15°N 20°N 25°N
H
28
26
24
22
20
18
16
14
12
10
8
200m
400m
600m
WNP
5°N 10°N 15°N 20°N 25°N
M NECC NEC SCC
WNP
0
5°N 10°N 15°N 20°N 25°N
D
35.0
36.0
35.8
35.6
35.4
35.2
35.0
WSP
34.8
34.6
20°S 15°S 10°S 5°S Eq.
I
26
24
22
20
18
16
14
12
10
8
6
200m
400m
600m
WSP
20°S 15°S 10°S 5°S Eq.
N FBCC SEC SECC SEC
WSP
0
20°S 15°S 10°S 5°S Eq.
E
36.0
35.8
35.6
35.4
35.2
35.0
34.8
34.6
34.4
CSP
30°S 25°S 20°S 15°S 10°S
J
20
18
16
14
12
10
8
6
24
22
26
200m
400m
600m
CSP
30°S 25°S 20°S 15°S 10°S
O SECC SEC
0
CSP
30°S 25°S 20°S 15°S 10°S

Fig. 3

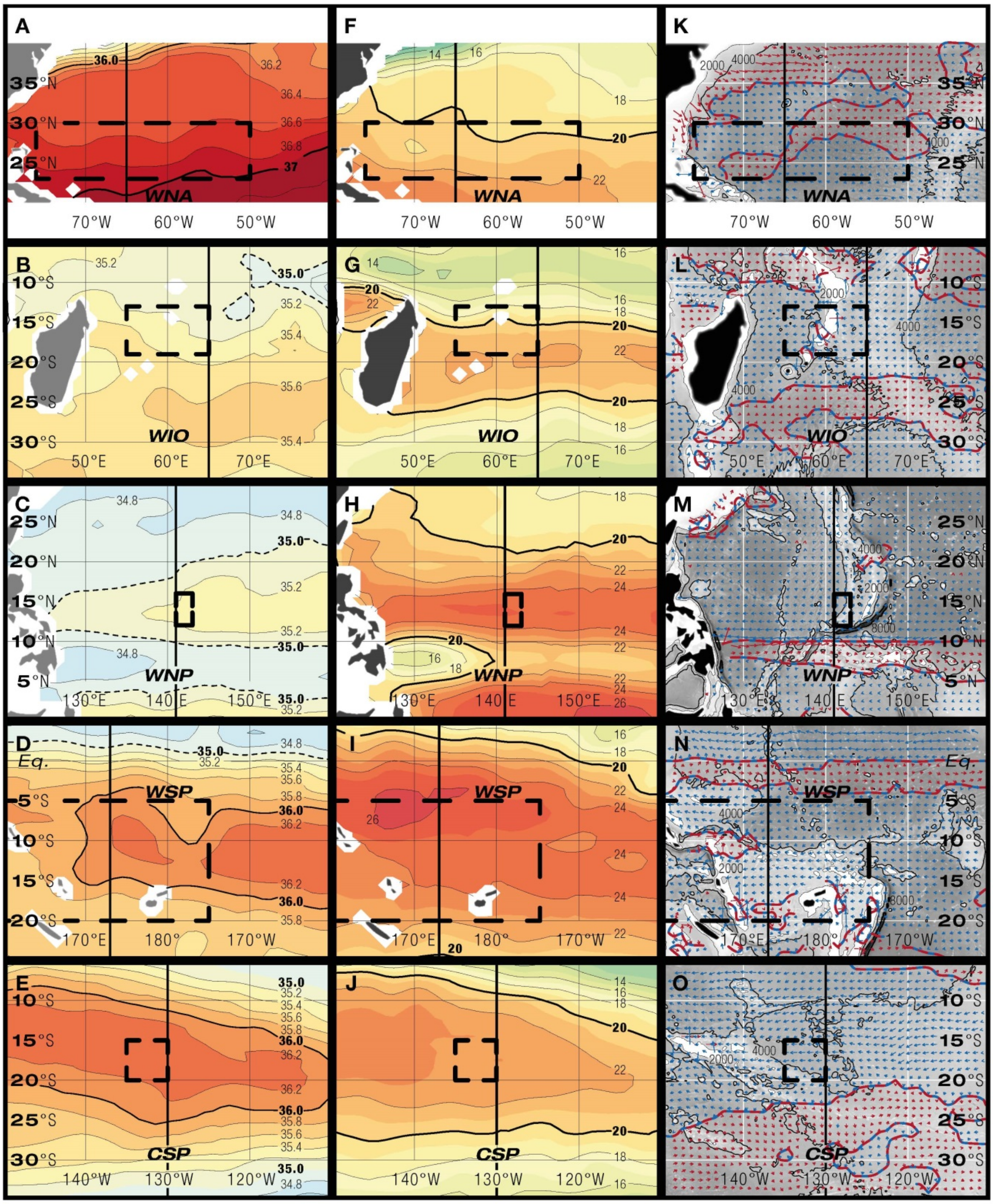

A
F
K
WNA
70°W
60°W
50°W
35°N
30°N
25°N
B
G
L
WIO
50°E
60°E
70°E
10°S
15°S
20°S
25°S
30°S
C
H
M
WNP
130°E
140°E
150°E
25°N
20°N
15°N
10°N
5°N
D
I
N
WSP
Eq.
170°E
180°
170°W
5°S
10°S
15°S
20°S
E
J
O
CSP
140°W
130°W
120°W
10°S
15°S
20°S
25°S
30°S

Fig. 4