

1 The hydrographic features of anguillid spawning areas: potential signposts 2 for migrating eels

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

18 19 20 21 Abstract

22
23 Catadromous anguillid eels (Genus *Anguilla*) migrate from their freshwater or estuarine
24 habitats to marine spawning areas. Evidence from satellite tagging studies indicates that
25 tropical and temperate eel species exhibit pronounced diel vertical migrations usually between
26 150–250 m nighttime depths to 600–800 m during the day. Collections of eggs and larvae of
27 Japanese eels (*A. japonica*) show they may spawn at these upper nighttime migration depths.
28 How anguillid eels navigate through the ocean and find their spawning areas remains
29 unknown, so the salinity, temperature and currents were analysed between 0–800 m depths
30 within two confirmed and three hypothetical anguillid spawning areas during likely spawning
31 seasons. Within all four ocean gyres many eels would encounter subducted Subtropical
32 Underwater (STUW) during their nighttime ascents possibly providing odour plumes for
33 orientation. Four spawning areas are located near the western margins of where subducted
34 water masses form cores of elevated salinities (~35.1–36.7) around 100–300 m depths, while
35 one is found near the center of subduction. ~~Low salinity surface waters and fronts occur~~
36 ~~above the areas with high salinity cores.~~ Spawning may occur at temperatures between 16–
37 24°C where the thermocline locally deepens. At spawning depths, weak westward currents
38 (c.a. >0.05–0.15 m s⁻¹) prevail, but at least three spawning areas include eastward surface
39 countercurrents. Anguillid eels have acute sensory capabilities that are discussed in relation
40 to potential signposts that may guide them to where they spawn.

41 42 43 Introduction

44
45 How catadromous anguillid eels are able to migrate long distances from their freshwater or
46 estuarine habitats through the seemingly featureless ocean to reach their pelagic spawning
47 areas has long been one of the great mysteries in eel biology, which continues to be
48 understood to a very limited extent ([Schmidt 1922](#), [McCleave 1987](#), [Tsukamoto 2009](#),
49 [Rigthon et al. 2012](#)). After reproduction they die and their marine larvae, called leptocephali,
50 drift with currents toward recruitment areas and become widely distributed in some
51 subtropical gyres ([Schmidt 1922](#), [Shinoda et al. 2011](#), [Miller et al. 2015a](#)). Among the 19

52 anguillid species or subspecies, the European eels (*Anguilla anguilla*) migrate the longest
53 distances of up to 7000 km (Aoyama 2009) to reach their spawning area in the Sargasso Sea
54 of the western North Atlantic (WNA, Schmidt 1922). The western part of their spawning area
55 is shared with American eels (*A. rostrata*, McCleave et al. 1987) that can migrate up to about
56 2500 km. Similar distances are covered by *A. japonica* in the western North Pacific (WNP,
57 Aoyama 2009). These temperate anguillid eel migrations are among the longest one-way
58 migrations known for any fish species (Alerstam et al. 2003). Even though some tropical
59 species spawn offshore after only short migrations (Aoyama et al. 2003), all the eel spawning
60 areas are over deep water (>1000 m) in places with warm surface currents, probably because
61 the genus is derived from an ancestral mesopelagic eel species (Inoue et al. 2010).

62 Oceanographic fronts have been hypothesized to provide structures that define the
63 spawning areas of anguillid eels. In the Sargasso Sea, two temperature fronts consistently
64 form in the Subtropical Convergence Zone (STCZ) at about 22 and 24°C during the February
65 to April spawning season (see Miller et al. 2015a) and gradually move northward with
66 seasonal warming (Ullman et al. 2007). Leptocephali are consistently found south of the
67 northern front (Kleckner & McCleave 1988, Munk et al. 2010). In the WNP *A. japonica*
68 spawns within the westward flowing North Equatorial Current (NEC) along the seamount
69 chain of the West Mariana Ridge (Tsukamoto et al. 2011, Aoyama et al. 2014). Adult eels,
70 their fertilized eggs, and recently hatched preleptocephali were collected exclusively along the
71 western and/or deeper southern end of the seamount ridge (Chow et al. 2009, Kurogi et al.
72 2011, Tsukamoto et al. 2011, Aoyama et al. 2014), which seems to act as a longitudinal
73 signpost (Tsukamoto et al. 2003, 2011). The latitude of spawning appears to be influenced by
74 a shallow salinity front formed by rainfall that can move north or south, with spawning
75 occurring on the south side of the front (Kimura & Tsukamoto 2006, Tsukamoto et al. 2011,
76 Aoyama et al. 2014). Spawning can take place at a wider range of latitudes when the front is
77 absent (Aoyama et al. 2014).

78 Relatively few leptocephali of the 6 species sympatrically occurring anguillid eels
79 have been collected and genetically identified in the western (WSP) and central (CSP) South
80 Pacific (*A. australis*, *A. dieffenbachii*, *A. reinhardtii*, *A. marmorata*, *A. megastoma*, *A.*
81 *obscura*) and the same is true for the 4 species in the western Indian Ocean (WIO, Jespersen
82 1942, Kuroki et al. 2008, Miller et al. 2015b; *A. marmorata*, *A. mossambica*, *A. bengalensis*,
83 *A. bicolor*). Considerably more leptocephali of the Indian Ocean species were collected
84 offshore of West Sumatra (Jespersen 1942, Aoyama et al. 2007). Catches of small
85 leptocephali of the Celebes longfin eel, *Anguilla celebesensis*, and the Borneo eel, *Anguilla*
86 *borneensis*, in the central Indonesian Seas indicate those species can spawn after
87 comparatively short migrations (Aoyama et al. 2003).

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

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

103 Tagging studies showed that both temperate and tropical anguillid eels display a
104 distinct diel vertical migration behavior (DVM) of usually swimming in the lower epipelagic
105 zone (~ 150–250 m) during the night and then quickly descending to the deep mesopelagic
106 zone (~ 600–800 m) after sunrise, where they remain during the day (Aarestrup et al. 2009,
107 Jellyman and Tsukamoto 2010, Manabe et al. 2011, Wysujack et al. 2014, Schabetsberger et
108 al. 2015, Béguyer-Pon et al. 2015, Fig. 1). Some species such as the relatively small-sized *A.*
109 *japonica* (Manabe et al. 2011) and *A. rostrata* (Béguyer-Pon et al. 2015) and the large *A.*
110 *dieffenbachii* (Jellyman and Tsukamoto 2010) sometimes entered the upper 100 m at night.
111 However, during three long tracks of tropical silver eels that may have reached their spawning
112 area in the WSP the eels almost never swam shallower than 100 m (Schabetsberger et al.
113 2013, 2015) as they would be expected to if they were searching for shallow oceanographic
114 features. This raises the question about how migrating eels can detect the surface features of
115 temperature or salinity fronts that are generally only present in the upper 150 m (Kleckner and
116 McCleave 1988, Aoyama et al. 2014) if they stay deeper. Predator avoidance probably
117 governs this behaviour, because the eels remain deeper when moonlight is present thereby
118 avoiding more nocturnally foraging fish (Schabetsberger et al. 2013, 2015, Chow et al. 2015).

119 Among all 19 *Anguilla* species, spawning-condition adult eels and eggs have only
120 been collected for *A. japonica* and *A. marmorata* (adults only) and they were likely caught
121 between 150 m and 300 m depths (Chow et al. 2009, Tsukamoto et al. 2011, Aoyama et al.
122 2014) corresponding to the upper nighttime migration depths of eels in the PSAT studies.
123 This indicates that these water masses should be evaluated for potential oceanographic
124 structures that eels may use to help locate their spawning areas. The most distinctive
125 hydrographic feature at these depths is usually the high-salinity Subtropical Underwater
126 (STUW) that is present in all the major ocean basins (Fig. 2A), which is formed by saltier
127 water being subducted from the surface into the lower thermocline (Price 2001). This type of
128 water is found within the spawning areas of the Atlantic eels (Kleckner and McCleave 1988),
129 *A. japonica* (Aoyama et al. 2014) and in the presumed spawning regions in the WIO (Pous et
130 al. 2010). The STUW in the WSP (Qu et al. 2013) is a prominent feature at the pop-up
131 locations of *A. marmorata* and *A. megastoma* and has been hypothesized to possibly help
132 migrating eels locate this area (Schabetsberger et al. 2013, 2015).

133 Now that data on the marine spawning migrations of eels are available that show they
134 seem to predominantly migrate between 100 and 800 m depths, this behaviour can be related
135 to the oceanographic conditions they experience during their presumed migration paths and
136 within their spawning areas. The present study uses Argo float data to evaluate the
137 hydrographic structure and current flow patterns of each subtropical gyre where anguillid
138 spawning occurs or may occur, with the possible spawning depths being tentatively
139 considered for inter-comparisons to be between 150–300 m in accordance with previous
140 information from *A. japonica*. Ocean-Atmosphere changes have been suggested to be
141 contributing to the declines of anguillid eels in recent decades (Knights 2003, Miller et al.
142 2009), with several species now on the IUCN Red List (Jacoby et al. 2015), so a better
143 understanding of the oceanographic conditions the eels experience while migrating and at the
144 spawning area may eventually facilitate management and conservation efforts.

145

146 **Methods**

147

148 **Hydrographic analysis**

149 The hydrographic structure of the 4 subtropical gyres where anguillid eels are present were
150 examined (WNA, WIO, WNP, WSP, CSP). No catadromous eels occur in the warm Brazil
151 Current of the South Atlantic or along the coastlines adjacent to the eastern Pacific (Tesch
152 2003, Aoyama 2009). Patterns of salinity, temperature, and currents at the two confirmed

153 offshore spawning areas of the Atlantic and North Pacific eel species and within presumed eel
154 spawning areas in the Indian and the South Pacific Ocean were studied.

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

164

165 **Spawning areas**

166 The Sargasso Sea spawning area of the Atlantic eels was the first to be discovered ([Schmidt](#)
167 [1922](#); [Fig 2A](#)) and now the catch data of all collected leptocephali of both species has been
168 combined into a database that shows the distribution of small (<11 mm) *A. anguilla* and *A.*
169 *rostrata* larvae is predominantly between 24–30°N and 50–73°W and between 23–29°N and
170 60–76°W, respectively ([Miller et al. 2015a](#)). We made a section along 65°W in March 2014,
171 since surveys to collect anguillid larvae were made across the Sargasso Sea in March and
172 April of that year ([P. Munk and R. Hanel, personal communication](#)).

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

187 The spawning area of *A. japonica* in the WNP has been studied since its discovery in
188 1991 ([Tsukamoto 1992](#)) with leptocephali and newly hatched preleptocephali being collected
189 ([Shinoda et al. 2011](#), [Tsukamoto et al. 2003, 2011](#)). In 2008 the first spawning adults of *A.*
190 *japonica* and *A. marmorata* were caught along the ridge at depths above 350 m ([Chow et al.](#)
191 [2009](#)). Eggs of *A. japonica* were first collected in 2009 ([Tsukamoto et al. 2011](#)), and then
192 again during consecutive cruises in 2011 and 2012 ([Aoyama et al. 2014](#)). Spawning occurs
193 during new moon periods based on both backcalculated hatching dates of leptocephali and
194 when the eggs and preleptocephali have been collected. The eels spawn between 12–16°N
195 and 141–143°E somewhere below the thermocline because the eggs and preleptocephali
196 appear to accumulate at about 150 m depths ([Tsukamoto et al. 2011](#), [Aoyama et al. 2014](#)).
197 The spawning area of *A. marmorata* overlaps with *A. japonica* ([Kuroki et al. 2009](#)), and the
198 newly discovered anguillid species, *A. luzonensis* may also spawn offshore in the NEC. We
199 made a meridional section along 141°E that corresponds to the June 2011 egg collections
200 ([Aoyama et al. 2014](#)).

201 There is less information available about where spawning areas may be in the WSP.
202 Some large anguillid leptocephali were collected in the region predominantly between 5–20°S
203 and 160°E–175°W ([Jespersen 1942](#), [Kuroki et al. 2008](#)). These and more recent collections

204 of a few smaller leptocephali (Miller et al. 2006, Kuroki et al. 2008) indicated that some
205 species likely spawn within the westward flowing South Equatorial Current (SEC) that could
206 transport species like *A. reinhardtii* and *A. australis* towards Australia. The smallest
207 leptocephali of *A. marmorata* (Kuroki et al. 2008) were found close to the pop-up locations of
208 PSAT tags attached to adult *A. marmorata* and *A. megastoma* released in Vanuatu, which
209 pointed to a potential shared spawning area between 8–12°S and 170–175°E (Schabetsberger
210 et al. 2015). Presently, no leptocephali of the New Zealand longfin eel *A. dieffenbachii* have
211 been found, but they may spawn in potentially overlapping areas with *A. australis* and *A.*
212 *reinhardtii* somewhere between 10–25°S and 165–180°E (Jellyman and Bowen 2009).
213 That region of the WSP is probably not the only area where spawning occurs though, because
214 there is evidence that some species may have two populations within the South Pacific. The
215 analysis of differences in the numbers of vertebrae of adult eels indicated that there were
216 probably eastern and western spawning populations of *A. marmorata* and *A. megastoma* (Ege
217 1945). Molecular genetic evidence (e.g., Minegishi et al. 2008) and additional morphometric
218 analyses later supported this likelihood (Watanabe et al. 2008, 2009). From the arrival of
219 glass eels, Marquet (1992) hypothesized that an eastern spawning area is located west of the
220 Tuamotu archipelago between 15–20°S and 130–135°W (also see Jellyman 2003). We made
221 meridional sections for both South Pacific spawning regions that were along 173°E and
222 130°W, respectively, for July 2013, the year of the Schabetsberger et al. (2015) tagging study
223 in Vanuatu. Tropical eels may spawn throughout the year (Jellyman 2003), but the PSAT tags
224 surfaced in the presumed spawning area between May and September.

225

226 Results

227

228 Salinity

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

245

246 Temperature

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

255 the WIO spawning seems to occur just north of these elevated temperatures at spawning
256 depths.

257

258 **Currents**

259 Predominantly westward surface currents were present in the anguillid spawning areas except
260 for the WNP (NEC, SEC, Fig. 2B), but in the WNA (Fig. 3K), WSP (Fig. 3N) and the CSP
261 (Fig. 3O) eastward countercurrents occur (Subtropical Countercurrent, SCC; South Equatorial
262 Countercurrent, SECC, Fiji Basin Countercurrent, FBCC; SCC respectively, labelled in Fig.
263 3). In the WIO (Fig. 3L) the hypothetical spawning area is located just north of the eastward
264 SCC. In the WNP (Fig. 3M) the spawning area is located south of the North Pacific
265 Subtropical Countercurrent (SCC) and north of the North Equatorial Countercurrent (NECC).
266 Weak westward currents prevailed at the presumed spawning depths (Figs. 4K-O; WNA:
267 $<0.05 \text{ ms}^{-1}$, WNP: $\sim 0.15 \text{ ms}^{-1}$, WSP: $<0.05 \text{ ms}^{-1}$, CSP: $\sim 0.07 \text{ ms}^{-1}$, WIO: $\sim 0.1 \text{ ms}^{-1}$). *Double*
268 *check values after we hear back from Giorgio!*

269

270 **Discussion**

271

272 **Hydrographic features of spawning areas**

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

285 One interesting observation is that the STUW water mass is present at the upper
286 nighttime migration depths of eels in all of the spawning areas. This water is subducted from
287 the mixed layer into the stratified thermocline and spreads horizontally over large areas of all
288 4 subtropical gyres. However, except for the estimated spawning location in the CSP, the
289 analysed spawning areas are found along the western or northwestern edges of these tongues
290 of higher salinity water where there may be zonal salinity gradients. Vertically, the spawning
291 areas appear to be located within the lower edges of the cores of the STUW as previously seen
292 in the WNP based on the distributions of egg and larval catches (Aoyama et al. 2014) and
293 adult vertical migration data from satellite tags (Schabetsberger et al. 2015). The cores of
294 these water masses are centered at about 150 m depths as also seen previously (Kleckner and
295 McCleave 1988, Roden 1998, Miller et al. 2006, Aoyama et al. 2014), with absolute salinities
296 that ranged from maximum values of ~ 36.7 in the WNA to minimum values of ~ 35.1 in the
297 WNP.

298 These high salinity waters are subducted within the centres of the wind driven
299 subtropical ocean gyres from the mixed layer into the thermocline (Qui & Huang 1995, Qu et
300 al. 2013). The process consists of downward pumping from Ekman convergence and
301 horizontal advection by lateral geostrophic flow (Huang & Qui 1998 and references therein).
302 O'Connor et al. (2005) estimated the STUW subduction volumes in the North Atlantic ($44\text{-}36$
303 m yr^{-1} , 2 Sv; $1 \text{ Sv} = 10^6 \text{ m}^3 \text{ s}^{-1}$), North Pacific ($26\text{-}17 \text{ m yr}^{-1}$, 4 Sv), South Pacific ($32\text{-}33 \text{ m yr}^{-1}$,
304 7 Sv), and South Indian Ocean ($22\text{-}25 \text{ m yr}^{-1}$, $< 1 \text{ Sv}$), but global warming may decrease
305 subduction rates due to decreasing lateral induction because of shallower winter mixed layer

306 depths (Liu & Wang 2014). The renewal time for STUW appears to be 10–15 years (Price
307 2001). Qu et al. (2013) estimated that some STUW moves through the WSP to reach New
308 Guinea within 2 years and extends over nearly the entire Pacific basin after 13 years, with
309 highest concentrations remaining in the subtropical South Pacific. When these water masses
310 are transferred beneath the mixed layer, they are shielded from the atmosphere and only
311 slowly modify their properties through mixing in the ocean interior (Williams 2001). Hence
312 they would seem to carry a long “memory” compared with the surface mixed layer, which as
313 mentioned later may provide olfactory cues to migrating eels.

314 Above these subducted water masses, pronounced temperature (typically controlling
315 density) and weaker salinity gradients may also provide possible signposts by separating
316 different water masses. A temperature front in the Sargasso Sea appears to form the northern
317 limit of where spawning by the Atlantic eels occurs based on the distribution of their small
318 larvae (Kleckner and McCleave 1988, Munk et al. 2010, Miller et al. 2015a). A similar front
319 can form in the WSP just north of Fiji where small anguillid larvae have been collected
320 previously at the edges of the so called “western Pacific fresh pool” (Rodén 1998, Miller et al.
321 2006, 2009), and also in the WIO (New et al. 2006). Our analyses showed there are areas of
322 low-salinity water in the upper 100 m at the spawning areas in the WIO, WNP, and WSP.
323 These lenses of low-salinity water are probably all caused by tropical rainfall. In the WIO a
324 shallow layer (~50 m) of low-salinity surface water overlays a sharp halocline and may form
325 salinity fronts at its northern and southern boundaries (New et al. 2006). In the WNP, the
326 latitudinal position of a salinity front seems to influence the spawning locations of *A. japonica*
327 (Kimura & Tsukamoto 2006, Tsukamoto et al. 2011, Aoyama et al. 2014).

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

345
346

347 **Eel migration behavior**

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

359 For most species, eels tagged with PSAT's rarely entered shallow water in the open
360 ocean, although most of them were still far from their destination. However, two *A.*
361 *marmorata* tagged in Vanuatu that had their tags released on schedule after being attached for
362 3 and 5 months may have for the first time reached their spawning area northwest of Fiji
363 (Schabetsberger et al. 2013, 2015). They almost never entered waters above 90 m throughout
364 their entire journey and remained deep after reaching the area. Their diel vertical migration
365 behaviour remained remarkably regular over up to 5 months indicating that they may have
366 been largely unaffected by the tag compared to smaller *A. anguilla* tested under laboratory
367 conditions (Burgerhout et al. 2011, Methling et al. 2011).

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

386

387 **Hydrographic signposts for eel orientation**

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

398 the Sargasso Sea from regions ranging from Atlantic Canada in the far north and to the
399 Caribbean Sea in the far south.

400 Our global hydrographic analyses show that eels migrating at the observed nighttime
401 migration depths would either start their migrations within the STUW or encounter it on their
402 way to the spawning area. In either case, they would eventually experience weak gradients in
403 salinity as they moved further towards the cores of the STUW. The salinity maxima around
404 150 m are crossed twice a day during DVM with the eels migrating below the STUW during
405 the day and within it at night. In terms of temperature, the spawning areas seem to be located
406 where the thermocline is weakening and extending deeper. The eels would therefore
407 experience different types of vertical temperature gradients on the north or south sides of
408 these areas during their DVMs. The temperature and salinity structures at deeper daytime
409 depths do not seem to provide any clear markers of where spawning occurs though.

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

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

439

440 **Sensory ecology of finding spawning areas**

441 The present study is not designed to determine what sensory systems may be used by
442 migrating eels, but enough is now known about eels and the environments they would
443 experience during migration to discuss this subject. Eels have several highly developed
444 sensory organs (Tesch 2003), and it is likely that they use several if not all of these during at
445 least some stage of their migrations. Once they reach the open ocean they move vertically
446 through about half a kilometre of water column every day over several months and therefore
447 have the chance to detect different water properties or changes in the magnetic field. Various
448 ideas have been proposed for the types of cues eels may use while migrating, or to detect the

449 features of their spawning areas (Rommel and McCleave 1973, McCleave 1987, Westin 1990,
450 Van Ginneken and Maes 2005, Tsukamoto 2009, Westerberg 2014), but none of these have
451 been validated through any kind of direct testing. For example it is unclear to what extent
452 eels might use “beaconing” (odour cues that build up a gradient), “trail following” (odour
453 trails from conspecifics), “route reversal” (memory of landmark series), “path integration”
454 (knowledge of own current position with respect to the goal in terms of distance and direction),
455 “compass orientation” (e.g. sun, moon, magnetic compass; genetic and/or experience based
456 components), “vector orientation” (genetic or acquired information about distance and
457 direction of the goal), or “true navigation” (navigation, map and compass mechanism) as
458 listed by (Papi 2006) during different stages of their journey.

459 Anguillid eels exhibit a consistent direction of orientation relative to the magnetic
460 field (Nishi et al. 2004, Durif et al. 2013). If they are also sensitive to large scale gradients in
461 the inclination and the intensity of the earth’s magnetic field (Durif et al. 2013), and potentially
462 even to the fine scale-mosaic of magnetic anomalies in the ocean floor (<1% of the total field
463 at the surface of the ocean; Walker et al. 2002, Lohmann et al. 2008) remains to be tested.
464 This sense has been found to probably be used during long-distance migrations in various
465 marine animals such as sea turtles or salmon (Walker et al. 2002, Papi 2006, Lohmann et al.
466 2008), so silver eels may be able to locate regions of the spawning areas through geomagnetic
467 information imprinted-on during their larval period.

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

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

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

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

508 Willis et al. (2009) proposed the interesting hypothesis, that sharp descents and ascents
509 (50–605 m) during dawn and dusk, so called spike dives, provide cues for orientation in
510 bluefin tuna (*Thunnus maccoyi*). They may probe vertical profiles of polarized light and/or
511 detect magnetic field intensity, which both show characteristic patterns during crepuscular
512 periods. Although predator avoidance seems to be an important driving force behind the
513 large-scale DVM in eels (Schabetsberger et al., 2015), the concurrent detection of the range of
514 different environmental variables discussed above for obtaining cues for orientation might be
515 another function of DVM behavior.

516

517 **Concluding remarks**

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

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

549

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554

555

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767

768 **Figure Captions**

769

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

775

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

795

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

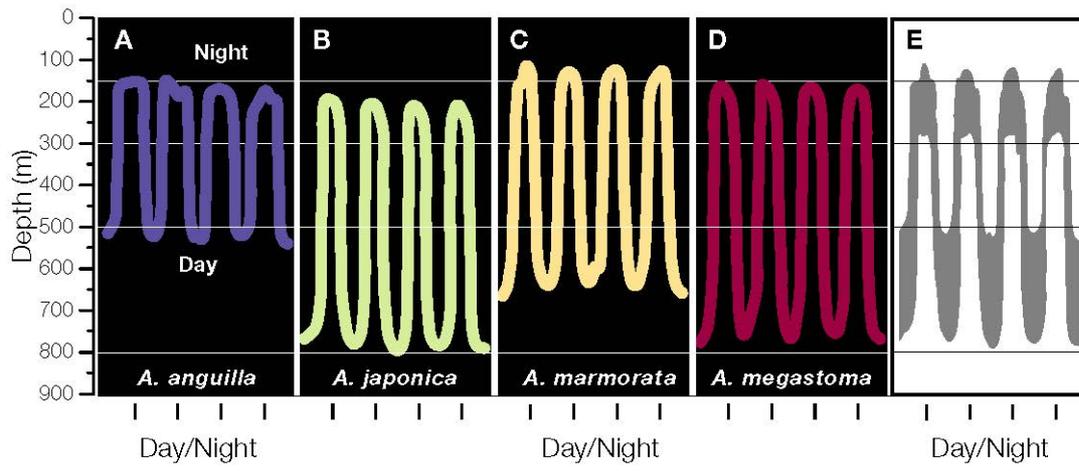
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805 **Fig. 4.** Maps of salinity (A-E), temperature (°C, F-J), and geostrophic currents (U, ms^{-1} , K-O,
806 red: eastward currents, blue: westwards currents) at a depth of 150 m during known and
807 presumed spawning times. Dashed rectangles indicate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

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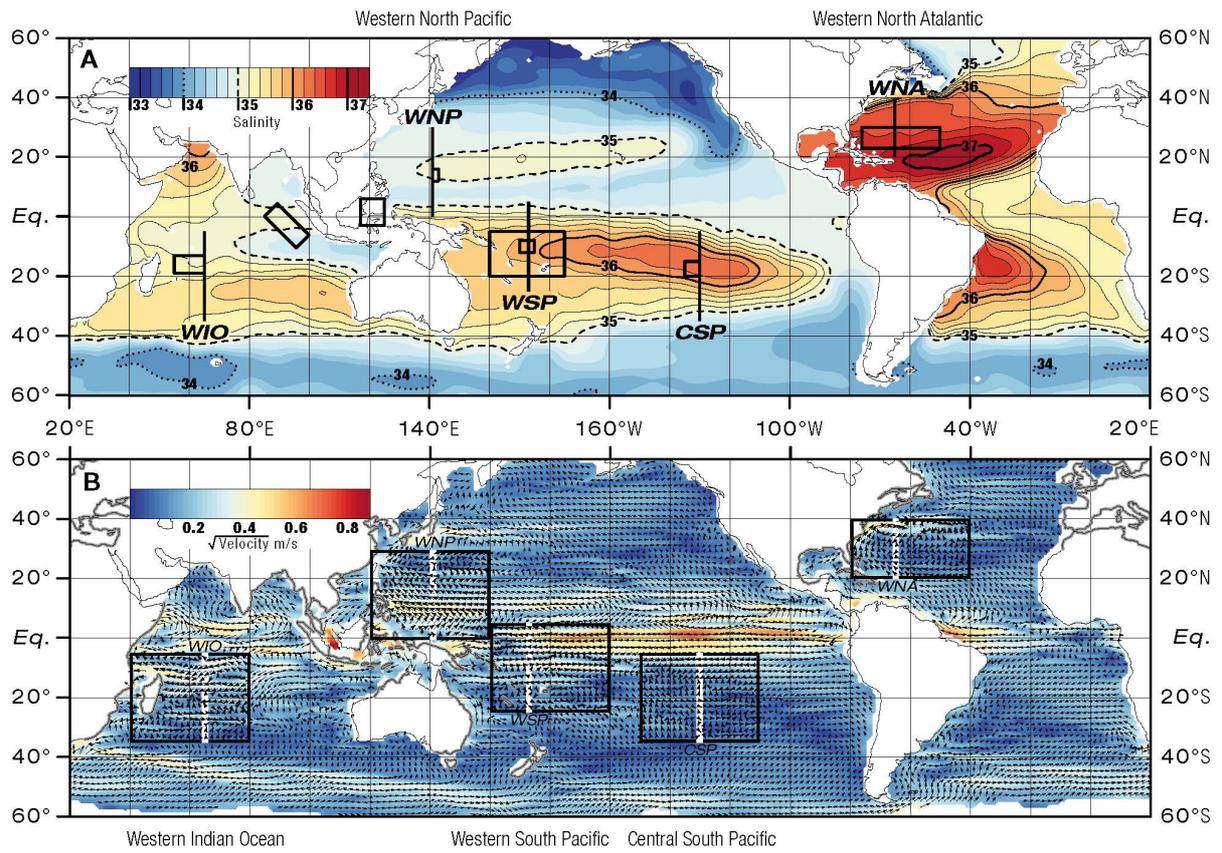


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814 Fig. 1

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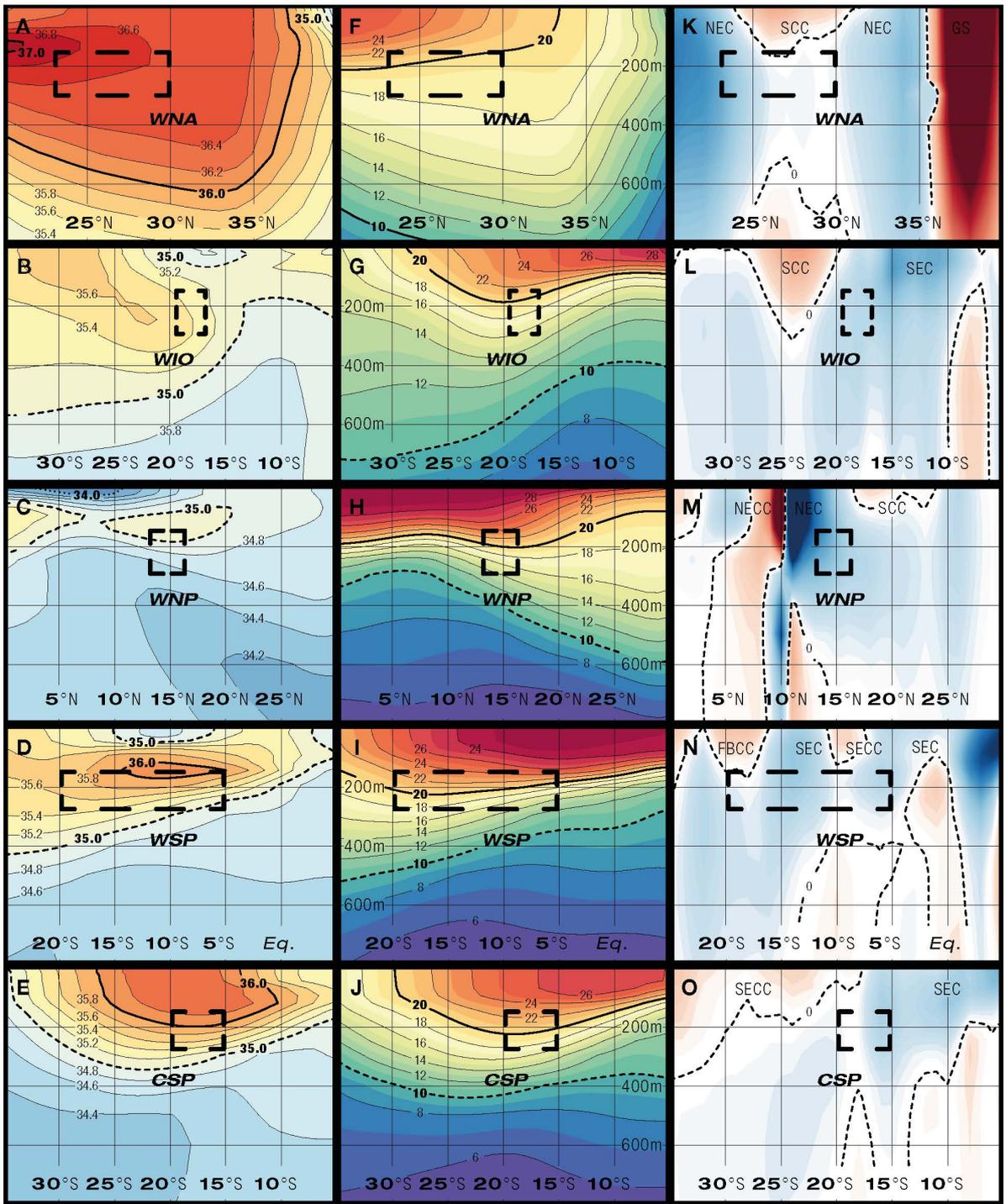
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819 Fig. 2

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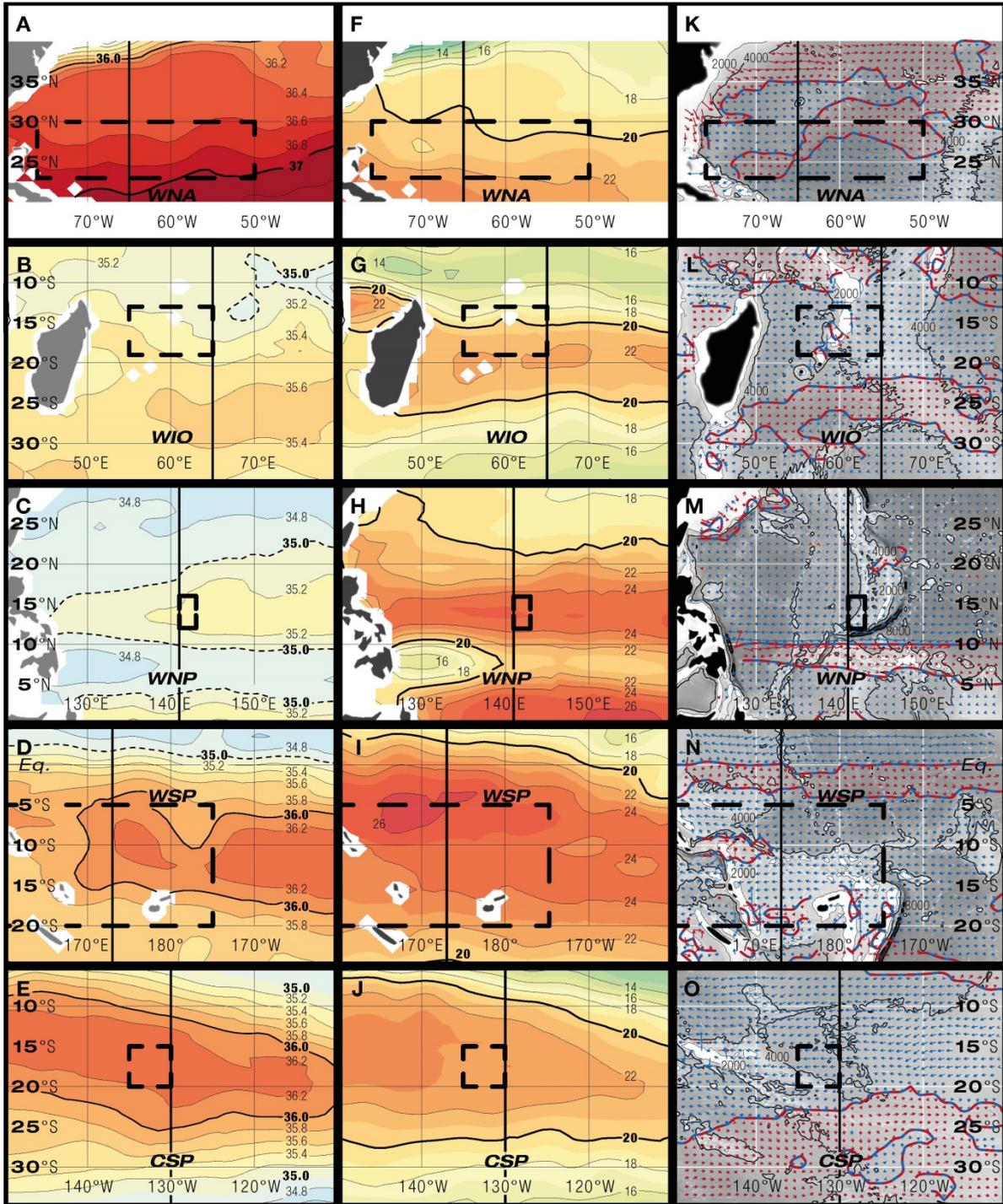


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823 Fig. 3

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828 Fig. 4