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# Larval Japanese eel (*Anguilla japonica*) as sub-surface current bio-tracers on the East Asia continental shelf

**YU-SAN HAN,[1,]* HENG ZHANG,[2] YU-HENG TSENG[3,]* AND MAO-LIN SHEN[3]**

[1]*Institute of Fisheries Science and Department of Life Science, College of Life Science, National Taiwan University, Taipei 106, Taiwan*
[2]*East China Sea Fisheries Research Institute, Chinese Academy of Fishery Sciences, Shanghai 200090, China*
[3]*Department of Atmospheric Sciences, College of Science, National Taiwan University, Taipei 106, Taiwan*

## ABSTRACT

Larval Japanese eel (leptocephali) are passively transported from their spawning sites of the North Equatorial Current to the Kuroshio and its branch waters for 4–6 months before reaching the East Asian coasts. The larvae mainly stay within water depths between 50–150 m. The dispersal dynamics of larvae thus should reflect the sub-surface oceanic currents on the East Asia continental shelf. An analysis of Japanese glass eel catch data in East Asian countries during 1985 to 2009, and for Taiwan from 1968 to 2008, indicates that the overall annual catch is generally correlated across countries of East Asia, and between north and west areas of Taiwan. The Kuroshio and its branch waters disperse glass eels throughout East Asian habitats, and the glass eel distribution matches the flow directionality of oceanic currents. Recruitment in western Taiwan occurs with a sequential southwestern to northwestern direction, suggesting that the Taiwan Strait Current penetrates the western coast of Taiwan in the sub-surface layer in winter. The monthly averaged sub-surface 50 m circulation pattern in the vicinity of Taiwan and modeled tracer experiments also support the northward winter sub-surface current in Taiwan Strait. These results suggest that the larval Japanese eel could serve as a valuable bio-tracer of sub-surface currents, and the earlier recruitment dynamics of Japanese glass eels in Taiwan could be a good predictor for the subsequent catch in other East Asia areas.

**Key words**: annual catch, dispersal, Kuroshio, leptocephali, Taiwan Strait

## INTRODUCTION

The East Asian continental shelf is relatively shallow, and is strongly affected by Asian monsoons, freshwater outflows, sea-floor topography, and the Kuroshio, forming complex circulation patterns (Chen, 2009). River discharge, especially the Changjiang, affects the circulation in the East China Sea in summer. In winter, strong northeast winds push coastal waters southward, while the Kuroshio moves the offshore warm waters northward (Hickox *et al.*, 2000; Ichikawa and Chaen, 2000; Su and Yuan, 2005; Chen, 2009). Although the surface currents around the East Asian continental shelf are well known (see Chen, 2009, for a general review), the sub-surface currents are less understood since no extensive spatial observations, such as the surface satellite images, can be obtained.

Taiwan is located at the edge of the East Asian continental shelf. The main axis of the Kuroshio (the major western boundary current in the western Pacific) flows by the eastern coast of Taiwan year round. On the other side of Taiwan (the Taiwan Strait), three primary water masses exist: the Kuroshio Branch Waters with high temperature and high salinity, the China Coastal Water with low temperature and low salinity, and the South China Sea Water with intermediate temperature and salinity (Jan *et al.*, 2010). The interactions of the three water masses in the Taiwan Strait in winter are complex (Shaw, 1989; Jan *et al.*, 2002, 2010; Yang, 2007; Chen, 2009). Yang (2007) suggested that a northward flow persists along the Taiwan Strait throughout the year despite the strong northeastward wind in winter time. When the Kuroshio flows along eastern Taiwan, enhanced friction sets a pressure gradient between the southern and northern tips of the island, forcing a northward flow against the wind along the Taiwan Strait. In contrast, Jan *et al.* (2010) suggested that, in summer, the Kuroshio surface currents hardly intrude into the

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*Correspondence. e-mail:yshan@ntu.edu.tw

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Taiwan Strait directly through the Luzon Strait. In winter, the modeled surface currents and simulated drifter trajectories suggest that the massive Kuroshio Branch Water conveys high salinity water to the southeastern Taiwan Strait through a loop-like route and rarely flows directly into the Taiwan Strait from the Luzon Strait (Jan *et al.*, 2010). The Kuroshio Branch Water may stay and accumulate around southwest of Taiwan.

The Japanese eel (*Anguilla japonica* Temminck and Schlegel) is a temperate catadromous fish mainly distributed in Taiwan, China, Korea, and Japan (Ege, 1939; Cheng and Tzeng, 1996; Tesch, 2003; Kuroki *et al.*, 2009). Mature eels spawn west of Mariana Island (Tsukamoto, 1992, 2006), mainly between June and August (Tsukamoto *et al.*, 1989, 1992, 2009; Ishikawa *et al.*, 2001; Zenimoto *et al.*, 2009). After hatching, the larvae (leptocephali) passively drift from the spawning sites on the North Equatorial Current (NEC) and then the Kuroshio for 4–6 months before reaching the East Asian coast (Tsukamoto, 1992, 2006; Cheng and Tzeng, 1996). The leptocephali of the Japanese eel are transported by currents at depths mainly between 50–150 m (Tsukamoto *et al.*, 2009). They then metamorphose into glass eels and transform into a benthic sheltering behavior (McCleave and Wippelhauser, 1987; Tesch, 2003), and actively swim toward nearby estuaries and rivers for growth. Thus the life histories of the Japanese eel include a larval stage with wide dispersive potential.

Given the spatial and temporal scales of ocean currents, the Japanese eel should form a panmictic population over ecological time scales. Microsatellite DNA studies have supported the hypothesis of a single population of Japanese eel (Han *et al.*, 2010). Since the NEC, Kuroshio and its branch waters, and coastal currents act together to transport eel larvae to East Asian habitats, the dispersal patterns of Japanese glass eels should generally reflect the current directionality, with some stochasticity. Interviews with glass eel traders indicate that glass eel recruitment in East Asia begins in late October in Taiwan. Later recruitment occurs in Japan and southern China (Fujian and Guangdong Provinces), and finally northern China (Jiangsu Province) and Korea around April of the following year. The recruitment dynamics of the Japanese glass eel in East Asian coasts therefore may provide a good context to study the regional sub-surface current regimes.

The Japanese eel is an important aquaculture species in East Asia countries. However, Japanese eel stocks have declined markedly in recent decades, and the annual glass eel catch in East Asia fluctuates greatly (Dekker, 2003; Han *et al.*, 2009). Accordingly, an understanding of the dispersal dynamics of the Japanese glass eel is very important for eel resource management. Thus, this study aims to: (1) identify the catch characteristics of Japanese glass eels in China, Japan, Taiwan, Korea, and also within different areas of Taiwan using correlation analyses, and (2) clarify the relationship between sub-surface current regimes in East Asian coastal waters, especially the Taiwan Strait, and larval dispersal patterns of the Japanese eels.

## MATERIALS AND METHODS

### *Eel catch data*

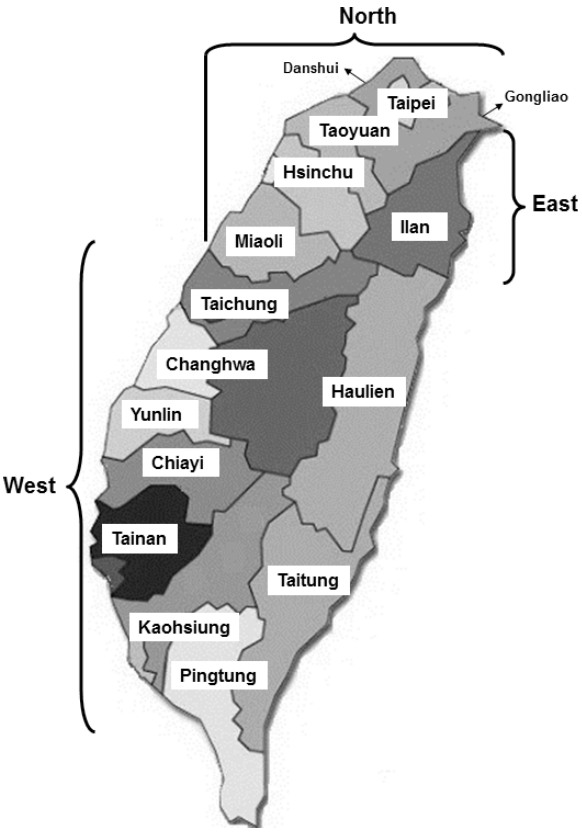
The analysis in this study includes annual glass eel catch data for the entire fishing season in each area. Annual Japanese glass eel catch data from 1985 to 2009 among Taiwan, China, Korea, Japan, and Shanghai City were gathered from the *Taiwan Fisheries Yearbook* (Fisheries Agency, Council of Agriculture, Executive Yuan, Taiwan), *Japan Aquaculture Information News* (The Nihon Yoshoku Shimbun, Tokyo, Japan), *Shanghai City Fisheries Yearbook* (ShangHai Agriculture Council, ShangHai City, China), and *China Eel Information News* (China Eel Net, Fujian, China). Information about glass eels catch in East Asia was also obtained from glass eel traders of Taiwan and China.

Annual Japanese glass eel catch data for each county of Taiwan, spanning 1968 to 2008, were gathered from the *Taiwan Fisheries Yearbook* (Fisheries Agency, Council of Agriculture, Executive Yuan, Taiwan). Since glass eel catch in the counties of Haulien and Taitung (Fig. 1) contributes to less than 1% of the total annual production (data not shown), the catch data of these two counties were excluded from analysis. The areas for glass eel recruitment in Taiwan are divided into East, West, and North, with each area comprising catch data of 1, 4, and 7 counties (Fig. 1). Data from the *Taiwan Japanese Glass Eel Reporting System* (Fisheries Agency, Council of Agriculture, Executive Yuan, Taiwan), obtained between October 31, 2009 and February 5, 2010, were used to trace the recruitment of Japanese glass eels at each location in Taiwan. Information about glass eels catch in Taiwan was also obtained from glass eel traders and fishermen in Taiwan.

### *Schematic of Kuroshio and coastal currents in Asian Marginal Seas*

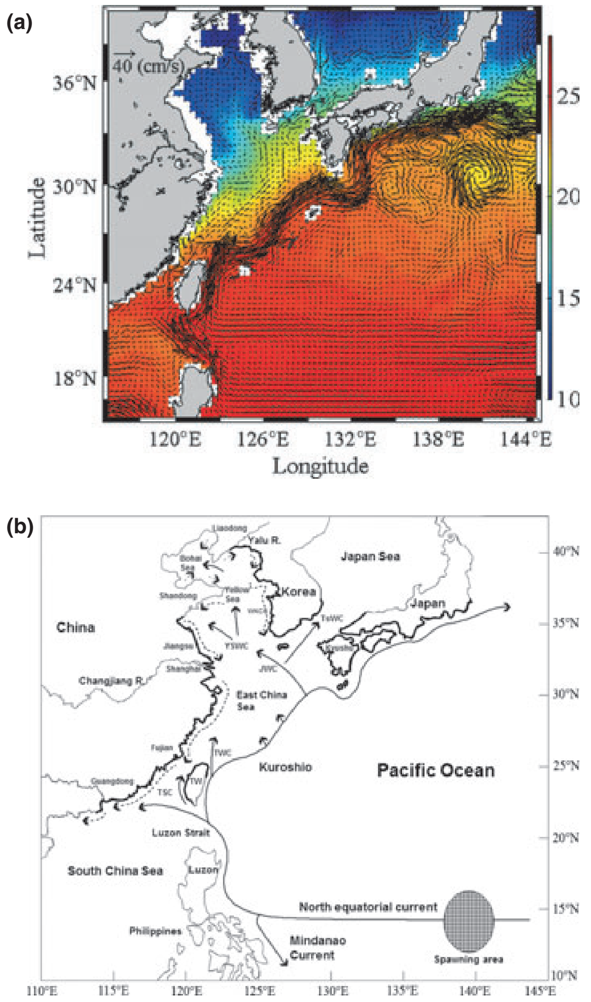
The schematic of the Kuroshio pathway, its branch water and coastal currents in Asian Marginal Seas (November–February) was based on a well-validated duo-grid Pacific Ocean model (DUPOM) (Chen *et al.*, 2010; Jan *et al.*, 2010; Tseng *et al.*, 2010, in press).

**Figure 1.** Map showing the counties of Taiwan. The glass eel catch was divided into three areas. The eastern area comprises Ilan County. The northern area is composed of Taipei, Taoyuan, Hsinchu, and Miaoli Counties. The western area includes Taichung, Changhwa, Yunlin, Chiayi, Tainan, Kaohsiung and Pingtung Counties.



The model domain covers the entire North Pacific Ocean ranging from 30°S to 60°N and 100°E to 80°W. To reduce overall computational time and emphasize the Asian Marginal Seas, the DUPOM is based on a duo-grid approach so that a 1/8° resolution is used in the domain west of 150°E, where it is necessary to resolve the detailed regional circulation, and a 1/4° resolution is used in the domain east of 150°E. The model is fully two-way-coupled at every time step of coarse resolution domain (time step is 200 and 600 s for the fine and coarse domains, respectively) with a single coarse grid overlapping (i.e. 2 × 2 in fine grid cells) (Fig. 2a). Meanders and eddy exchanges are seamless at the interface without inter-grid sponge layers or special treatments. Further details about the multiple-grid approach can be found in Tseng *et al.* (in press). The simplified sketch of major sub-surface currents in East Asian continental shelf during November–February was modified based on Hickox *et al.* (2000) and Chen (2009) (Fig. 2b).

**Figure 2.** (a) Map showing the modeled sub-surface (25–150 m) averaged velocity field in the western North Pacific during November–February, and (b) the simplified sketch map of major sub-surface currents in East Asian continental shelf during November–February. The dashed lines indicate coastal cold currents. The bold coast lines indicate the estimated distribution of the Japanese glass eel with high commercial catching activity. NEC: North Equatorial Current; MC: Mindanao Current; TW: Taiwan; TSC: Taiwan Strait Current; TWC: Taiwan Warm Current; JWC: Jeju Warm Current; TsWC: Tsushima Warm Current; YSWC: Yellow Sea Warm Current; WKCC: West Korea Coast Current.



Model bathymetry was established using unfiltered 2-min (~3.6 km) ETOPO2 depth data[1] supplemented with 1-min (~1.8 km) depth archive in the Asian

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[1] http://www.ngdc.noaa.gov/mgg/global/relief/ETOPO2/ETOPO2v2-2006/ETOPO2v2c/

seas from Taiwan's Ocean Data Bank. The vertical resolution is linear-exponentially stretched by 26 levels. The same vertical levels are used in both the coarser and finer grids.

Since this study aims to evaluate the pathway of source water from the south on climatological time scales, the Hellerman and Rosenstein wind stresses (Hellerman and Rosenstein, 1983) and the Levitus'94 climatology (Levitus and Boyer, 1994) were adopted to spin up the model. The surface wind forcing is obtained from the interpolated monthly Hellerman and Rosentstein wind stresses. The Levitus'94 climatology is used to initialize the model and determine surface fluxes of heat and freshwater (evaporation minus precipitation) using the non-damping approach described in Dietrich *et al.* (2004). The northern boundary is closed. Conditions at the southern boundary (30°S) are slowly nudged toward climatology in a sponge layer. The bottom is insulated, with no-slip conditions parameterized by a nonlinear bottom drag.

We focus mainly on the monthly averaged near-surface and sub-surface (50 m) circulation patterns in the vicinity of Taiwan (November to January). This time period is chosen because it covers most of the recruitment time of the Japanese glass eel in Taiwan. We further run additional tracer experiments to simulate the possible passive behavior of eels. The tracers are released from Luzon Strait at depths 6, 20, 36, 54 m in December and January, and from East China Sea at depths 6, 20, 36, 54 m in January to investigate the surface and sub-surface currents.

### *Data analysis*

Annual catch data for Taiwan, China, Shanghai, Japan, and Korea, and data from Taiwan counties did not fit normal distribution based on the Shapiro–Wilk test (Shapiro and Wilk, 1965). Thus correlation analysis between areas was then performed using Spearman's rho correlation on SPSS version 16. Correlations were considered significant at the $P < 0.05$ level. Glass eel recruitment indices of Japan, Taiwan, Korea, and China were normalized based on the average catch during 1985–2009. Glass eel recruitment indices within areas of Taiwan were normalized based on the average catch during 1968–2008.

## RESULTS

### *Sub-surface currents around East Asia and Taiwan in winter*

The Kuroshio originates in the westward-flowing NEC, turns northward east of Luzon, and flows past Taiwan into the East China Sea. Figure 2a shows the map of sub-surface (25–150 m) averaged velocity field in the western North Pacific (November – February). The main Kuroshio axis in the East China Sea typically flows along the steep continental slope (Fig. 2a). When the Kuroshio impinges on the East Asian continental shelf, portions of the Kuroshio branch out onto the continental shelf (Chen, 2009) (Fig. 2). The Kuroshio then bifurcates about 28°N south of Kyushu and the left branch of the Kuroshio moves onto the shelf. This separation creates the Tsushima Warm Current, Jeju Warm Current, and the Yellow Sea Warm Current (Hsueh *et al.*, 1996; Hsueh, 2000) (Fig. 2b). The Taiwan Warm Current flows northward all year round, even during the winter's strong northeast monsoons (Fig. 2). The impingement of the Kuroshio branch on the Luzon Strait forms the intrusion current and the Taiwan Strait Current (Shaw, 1989; Caruso *et al.*, 2006; Chen and Sheu, 2006; Yang, 2007) (Fig. 2b). The strong northeastern winds in winter push cold coastal waters southward along coastal China from the Bohai Sea to the Yellow Sea, East China Sea, and finally to the South China Sea. The northeastern winds in winter also push the West Korea Coast Current southward (Fig. 2b). It is clear that the areas influenced by these currents are in the vicinity of abundant commercial fishing activity for the Japanese glass eel (Fig. 2b).

The China Coastal Current intensifies with the stronger winter monsoon wind forcing and penetrates southward into the Taiwan Strait near the coast of China. However, it is mostly concentrated near the coast of Fujian (Fig. 3). Figure 3a–c show the monthly averaged near-surface (upper 50 m) circulation pattern in the vicinity of Taiwan. The intrusion of the Kuroshio in the central region of the Luzon Strait results in an anticyclonic circulation northeast of the South China Sea (Centurioni *et al.*, 2004; Caruso *et al.*, 2006). The transient winter circulation indicates that the Kuroshio intrusion reaches ~118°E in the northern South China Sea and turns anticyclonically back toward the southern tip of Taiwan. This is consistent with the finding of Jan *et al.* (2010) that the Kuroshio Branch Water conveys high salinity water to the southeastern Taiwan Strait through a loop-like route. Figure 3d–f further show the monthly averaged sub-surface (50–150 m or down to the bottom topography if the depth is shallower than 150 m) circulation pattern in the vicinity of Taiwan. For the topography shallower than 50 m, the first bottom layer above the topography is shown. It is interesting to see that a sub-surface northward flow exists in the Taiwan Strait (Fig. 3). Due to the blocking of Penghu islands, the

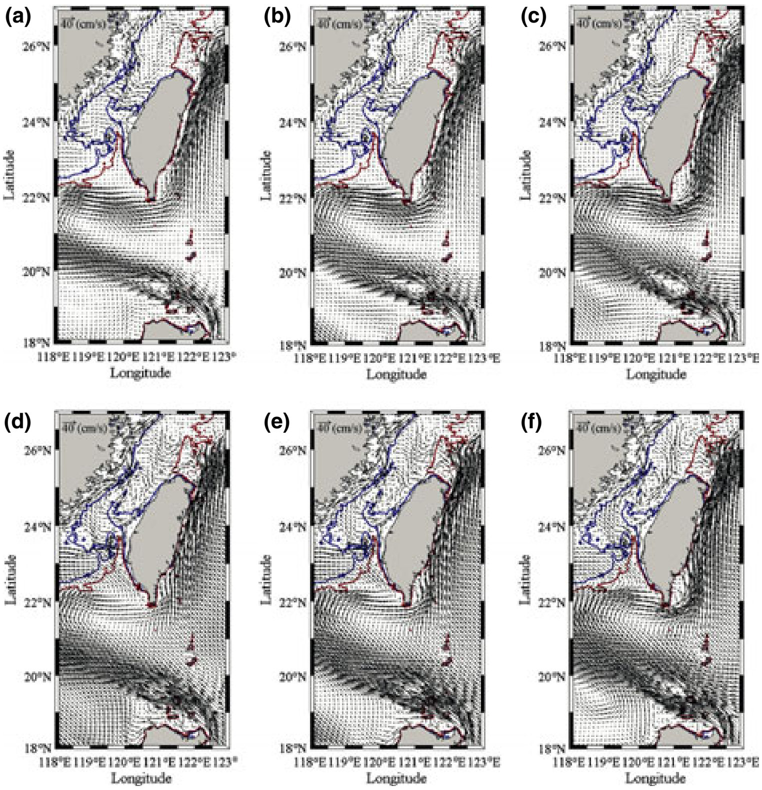


**Figure 3.** (a–c) Monthly averaged near-surface circulation pattern in the vicinity of Taiwan (from left to right: November, December and January, respectively). (d–f) Monthly averaged sub-surface 50 m circulation pattern in the vicinity of Taiwan (from left to right: November, December and January, respectively). For the topography shallower than 50 m, the first bottom layer above the topography is shown.

main northward stream flows northwestward and then turns northeastward close to the west coast of Taiwan. A small sub-surface anticyclonic circulation exists in the middle of Taiwan Strait.

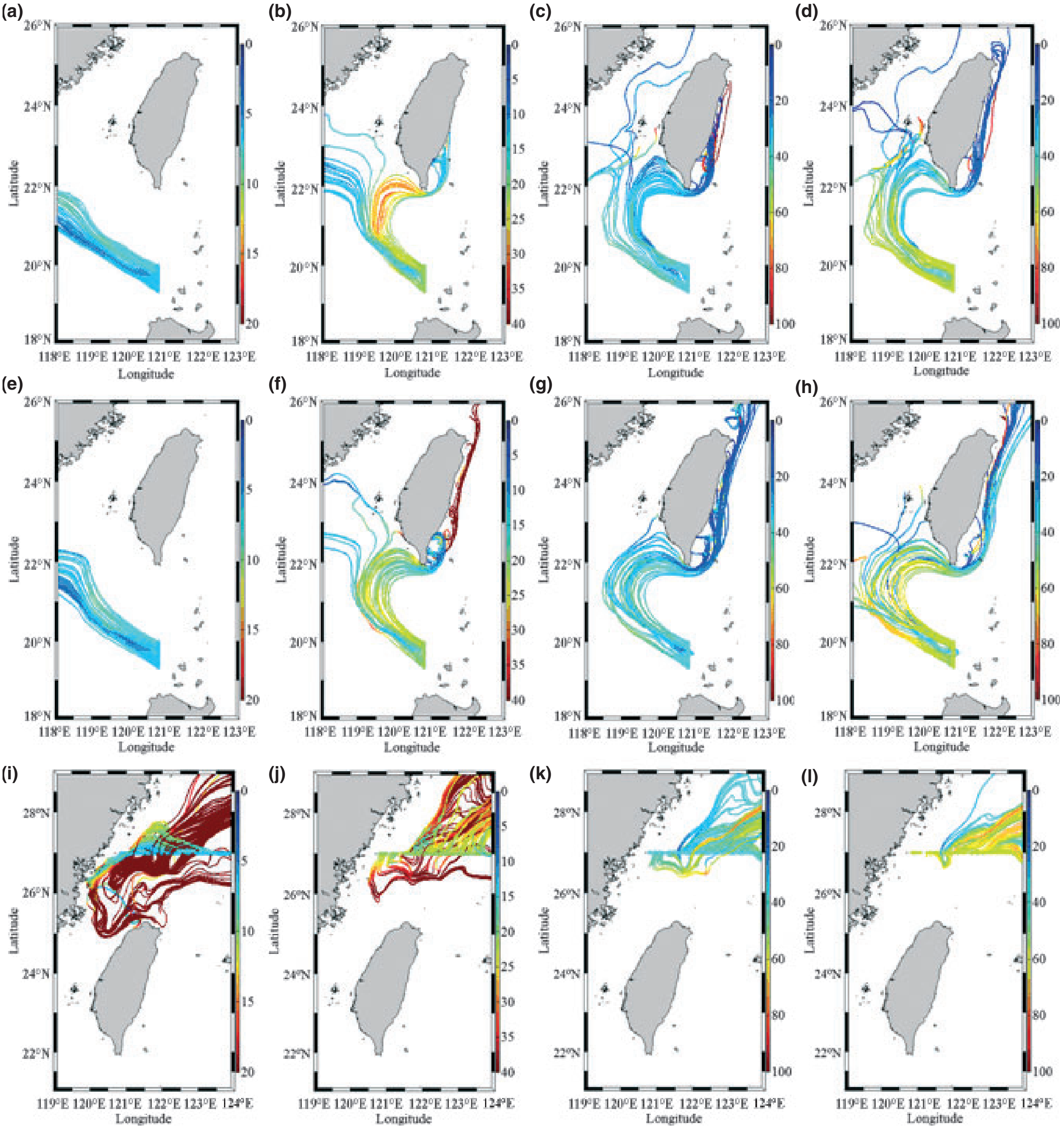
We performed more passive tracer experiments to examine the possible water mass distributions for the winter intrusion of the Kuroshio. These tracers are released across the Luzon Strait (19.5°N–20°N, where the northwestward Kuroshio dominates, i.e., most Kuroshio Branch Water) at depths 6, 20, 36, 54 m in December (from Fig. 4a–d, respectively) and January (from Fig. 4e–h, respectively). In December or January, most of the tracers deployed near the surface flows into the South China Sea (Fig. 4). Note that Kuroshio intrusion into Luzon strait is strongest in winter. The drifters deployed in the southern portion of the Luzon Strait move westward accompanying the cyclonic circulation in the South China Sea, consistent with Jan *et al.* (2010). A weak anti-cyclonic eddy exists south of Taiwan so that some tracers deployed at the north of the Luzon Strait may pass around the southern tip of Taiwan then drift along the east coast of Taiwan (Fig. 4). The released near-surface tracers (e.g., 6 m) never flow through the Taiwan Strait in winter (Fig. 4). Most of the sub-surface tracers flow along the main core of Kuroshio. Only the tracers deployed from Luzon Strait at the sub-surface (roughly 20–75 m) flow into the Taiwan Strait, mostly at depths of 20–54 m (Fig. 4). The waters may upwell and flow over Penghu channel or detour to the west where they further flow into the Taiwan Strait (Fig. 4). This is consistent with the monthly mean circulation patterns shown in Fig. 3. Most of the tracers are blocked by the shallower bathymetry, with only those flowing over the topography entering through the Strait and reaching north of Taiwan. Some tracers may turn towards the west across the southern Taiwan Strait and then move northward (Fig. 4). These are likely the primary northward pathways for eel larvae in winter.

Figure 4i–l show the tracers released along 27°N away from the coast of China. Almost all tracers move northeastward eventually no matter how deep they are. Although some surface tracers flow southward initially along the typical China Coastal Current (close to the China coast), they return and leave offshore from the northwest edge of Taiwan later on (Fig. 4i). These results are consistent with the velocity fields in Fig. 3.

### Eel catch analysis

Figure 5a shows the historical annual recruitment indices of Japanese glass eel in Taiwan, China, Japan, and Korea during 1985 to 2009. Although annual

**Figure 4.** Tracers released from Luzon Strait at depths 6, 20, 36, 54 m in December (a–d) and January (e–h), and from East China Sea at depths 6, 20, 36, 54 m in January (i–l). The depth of each tracer is shown as color.



catch from each area fluctuated somewhat, the annual catches among Japan, Korea, and China were generally correlated to each other ($P < 0.05$) (Table 1). The catches of Shanghai city were not correlated with those of other areas ($P \geqq 0.05$) except china (Table 1). Taiwan, Korea, China and Japan's average annual percentages of the total East Asian catch has been stable over the past 5 yr (Taiwan: 10.5%, Korea: 9.4%, China: 58.6%, Japan: 21.5%).

The historical annual recruitment indices of Japanese glass eel for counties of Taiwan during 1968 and 2008 are shown in Fig. 5b. Although fluctuations in the annual catch were observed in each area, the annual catches reported between north and west

**Figure 5.** (a) Estimated indices of recruitment of Japanese glass eels in Japan, Taiwan, Korea, and China during year 1985 and 2009. (b) Estimated indices of recruitment of Japanese glass eels within areas of Taiwan during year 1968 and 2008. Data from year 1974 is missing.

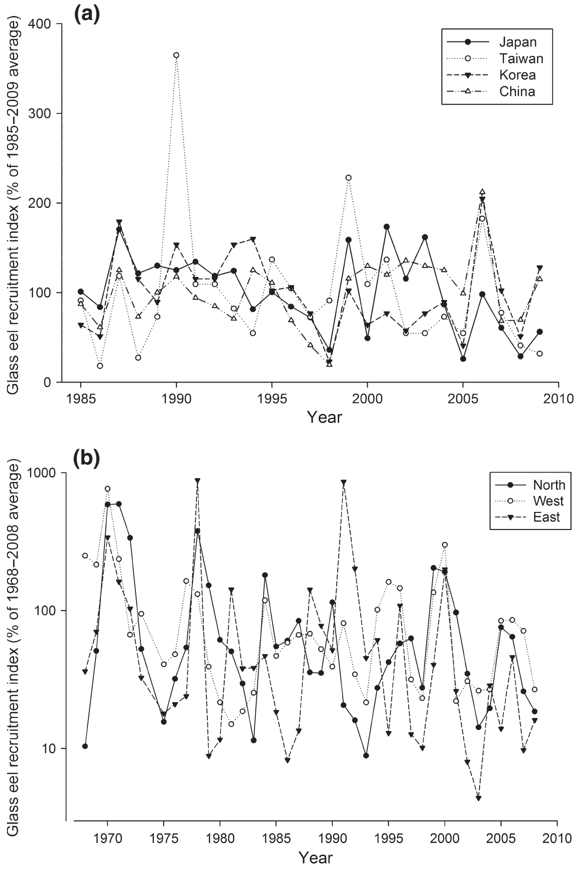


**Table 1.** Spearman's rho correlation analysis for annual catch data of Japanese glass eels during 1985 and 2009 in Japan (Jpn), Taiwan (Tw), Korea (Kr), China (Cn), and Shanghai city (Sh). Top- right above diagonal: correlation coefficient; Bottom- left below diagonal: $P$ value.

| | Jpn | Tw | Kr | Cn | Sh |
|---|---|---|---|---|---|
| Jpn | – | 0.43 | 0.40 | 0.36 | 0.21 |
| Tw | 0.03 | – | 0.36 | 0.26 | 0.32 |
| Kr | 0.04 | 0.08 | – | 0.28 | 0.30 |
| Cn | 0.08 | 0.21 | 0.17 | – | 0.54 |
| Sh | 0.32 | 0.12 | 0.15 | 0.01 | – |

Taiwan were significantly correlated ($P = 0.01$) (Table 2). The glass eel catch was more abundant in the west (contributed to 44.5% of the total historical catch on average) and east (38.1%) Taiwan than in the north Taiwan (17.4%).

**Table 2.** Spearman's rho correlation analysis of the annual Japanese glass eel catch between north, west, and east Taiwan during 1968 and 2008. Top- right above diagonal: correlation coefficient; Bottom- left below diagonal: $P$ value.

| | North | West | East |
|---|---|---|---|
| North | – | 0.43 | −0.13 |
| West | 0.01 | – | −0.09 |
| East | 0.41 | 0.57 | – |

Recruitment of Japanese glass eel at each location of Taiwan is shown in Table 3. Recruitment first occurs in the east (Ilan county), then the northeast (Gongliao) and southwest (Kaohsiung and Pingtung counties), followed by the west-central region, and finally in northwestern Taiwan (Danshui) (Fig. 1, Table 3). Recruitment in western Taiwan occurs from south to north (Table 3). The time difference in sighting of glass eel at Ilan and Pingtung was around 7–21 days, and that between Pingtung and Danshui was around 14–30 days, according to the *Taiwan Japanese Glass Eel Reporting System* and information obtained from Taiwanese glass eel traders and fishermen (Chen WC, Wang KF, He SF, personal communication).

## DISCUSSION

Our previous study, based on 7 polymorphic microsatellite DNA loci, supports the existence of a single, panmictic Japanese eel population in East Asia (Han *et al.*, 2010). If this hypothesis is true, then Japanese glass eels should match the flow directionality of oceanic currents in East Asian habitats because the leptocephali have limited swimming ability and are primarily transported by the oceanic currents. The analysis of catch data over the past 25 yr in this study indicates a markedly correlated recruitment pattern of glass eels throughout different East Asian regions. This reflects the generally stable Kuroshio and its branch waters. The Japanese eel appears to spawn in a restricted area, and the NEC transports the larvae for 3 months to the eastern Philippines (Zenimoto *et al.*, 2009), where they enter the Kuroshio on their way toward East Asian habitats. The Kuroshio intrusions distribute the larvae to western Taiwan, China, Japan Sea coast of Japan, and Korea. The Yellow Sea Warm Current flows northward toward the Yalu River estuary and westward toward the southwest coast of the Shandong Peninsula (Fig. 2b). The eastward Tsushima Warm Current (TsWC) flows into the Japan Sea and is blocked by the cold Oyashio. Interestingly, there

**Table 3.** Weekly eel catch data from the indicated areas of Taiwan between October 31, 2009 and February 5, 2010, according to the *Taiwan Japanese Glass Eel Reporting System*. Unit: individual.

| | Area | | | | |
|---|---|---|---|---|---|
| Date | Ilan | Gongliao | Kaohsiung -Pingtung | Yunlin -Tainan | Danshui |
| 09/10/31–09/11/06 | 0 | 0 | 0 | 0 | 0 |
| 09/11/07–09/11/13 | 8150 | 0 | 0 | 0 | 0 |
| 09/11/14–09/11/20 | 48205 | 0 | 0 | 0 | 0 |
| 09/11/21–09/11/27 | 186630 | 0 | 0 | 0 | 0 |
| 09/11/28–09/12/04 | 275303 | 5372 | 760 | 0 | 0 |
| 09/12/05–09/12/11 | 402722 | 710 | 21247 | 5170 | 0 |
| 09/12/12–09/12/18 | 281875 | 2095 | 12892 | 82560 | 19735 |
| 09/12/19–09/12/25 | 125978 | 3097 | 15956 | 74043 | 47000 |
| 09/12/26–10/01/01 | 46141 | 1752 | 2976 | 44608 | 37050 |
| 10/01/02–10/01/08 | 66560 | 2303 | 32151 | 68590 | 51782 |
| 10/01/09–10/01/15 | 338172 | 8263 | 56542 | 87049 | 24335 |
| 10/01/16–10/01/22 | 243264 | 21558 | 35152 | 536354 | 17200 |
| 10/01/23–10/01/29 | 214392 | 3326 | 62380 | 745232 | 183237 |
| 10/01/30–10/02/05 | 114122 | 3823 | 3473 | 637270 | 32500 |

are very few glass eels along the Bohai Sea coast, Shandong Peninsula, Liaodong Peninsula, eastern coast of Korea, and Japan Sea coast of Japan. The distribution areas of the Japanese glass eel with abundant commercial catching activity match the flow directionality of oceanic currents, highlighting the strong dependence of larval advection by ocean currents. The analysis of 40-year glass eel catch data between west and north Taiwan also suggests a significant correlation, indicating that these glass eels are transported by Taiwan Strait Current along the western coast of Taiwan.

When local area catches (such as Shanghai city or different areas of Taiwan) are compared with those of other areas, however, the degree of correlation may become obscure (Table 1). Caruso *et al.* (2006) indicates that strong inter-annual variability exists in the intrusion of the Kuroshio Branch Waters into the Luzon Strait. The Kuroshio and the coastal currents also exhibit considerable mixing and stirring (Chen, 2009). This explains that the annual glass eels recruitments from Shanghai city are not significantly correlated with other countries, and recruitments from the eastern coast of Taiwan are not significantly correlated to those from the western coast of Taiwan (Table 2; Fig. 5b). However, when larger areas and longer time spans are included for analysis, correlations in the distributions (as indexed by catch) appear.

On the basis of the ages estimated from otolith daily growth rings, Cheng and Tzeng (1996) suggested that the time that elapses between the metamorphosis of glass eels to their arrival at estuaries is slightly longer in samples from the southern portion of Taiwan than in the northern portion. They supposed that glass eels along the southwestern coasts of Taiwan are carried there via the China Coastal Current from the north (Tzeng and Tsai, 1992; Cheng and Tzeng, 1996). However, in the present study, the recruitment of glass eels in western Taiwan starts from Pingtung County, then proceeds from south to north (Table 3). Interviews with glass eel fishermen and traders confirm that the northward direction of occurrence of the Japanese glass eel in western Taiwan is consistent year by year. Besides, the tracers released along 27°N away from the coast of China show that although some surface tracers flow southward initially, they return and leave offshore from the northwest edge of Taiwan later on (Fig. 4i). All other depths of sub-surface tracers move northeastward (Fig. 4). McCleave (2008) found that aging of glass eels can easily be confounded, especially at the post-metamorphosis stage, due to low temperature (Umezawa and Tsukamoto, 1991; Fukuda *et al.*, 2009), starvation (Fukuda *et al.*, 2009), and possible re-absorption of marginal otoliths (Cieri and McCleave, 2000).

In the Gongliao of eastern Taipei County, recruitment occurs 2 weeks earlier than that observed in the western Taipei County of Danshui (Fig. 1, Table 3). The glass eels in eastern and western Taipei County may be recruited from different sources. The Gongliao area is located near the main stream of the Kuroshio, which flows through eastern Taiwan. Some glass eels may be carried to this area several days later than those in Ilan County. Danshui of Taipei County is located at the end of the Taiwan Strait Current. Recruitment occurs latest there, and the stocks are shared with other areas of western Taiwan.

Yang (2007) stated that a persistent northeastward current exists in the Taiwan Strait throughout the year, despite the strong southwestward wind stress in winter, due to a strong northward pressure gradient. Jan *et al.* (2010) suggested that there is hardly a persistent surface northeastward warm current in the Taiwan Strait against the strong northeast monsoon in winter, which is confirmed by our near-surface tracer fields (Figures 3 and 4). However, we further clarify that the sub-surface current may detour (mostly) or flow over the topography (some) and then flow northward although the strength is weak (Fig. 3).

Only a few simulated tracers released in the Luzon Strait can flow and penetrate into the Taiwan Strait (Fig. 4) while most of the tracers flow along the main stream of the Kuroshio. Most of the tracers flowing into the Taiwan Strait are the sub-surface (released at 20–50 m deep). It is known that the larval Japanese eel has a vertical migration behavior (Tsukamoto *et al.*, 2009). When larvae are transported into the shallow Taiwan Strait, they may stay close to the sea floor and the sub-surface current could assist their northward migration, although the surface zonal front (Li *et al.*, 2006) may block their northward transport. That is, although the surface waters of the northwestern coast of Taiwan may be occupied by the China Coast Current (Figures 3 and 4), the sub-surface waters may still include the northward Taiwan Strait Current. The boundary between the cold China Coast Waters and warm Kuroshio Branch Waters occurs at Yun- Chang Ridge, the shallower seabed at the central areas of western Taiwan. Interestingly, the glass eel catch was more abundant in west Taiwan (44.5% of the total historical catch) than in north Taiwan (17.4%). The counteraction of these two water masses at Yun- Chang Ridge may block the northward transport of larval Japanese eels to some extent, suggesting a key role of the regional circulation in their distribution.

China and Japan's mean annual percentages of the total eel catch in East Asia contribute approximately 60% and 20%, respectively, in recent years. Based on reports of *Japan Aquaculture Information News*, the glass eel catch in Japan could have exceeded 200 metric tons each year before the 1970s. Thus, the estimated available annual glass eel production for the East Asian region may exceed 1000 metric tons prior to the 1970s. This suggests that the present Japanese eel stock is less than 10% of what it was four decades ago, highlighting the emergency steps now required for eel management and conservation. In conclusion, this study suggests that the distribution of the Japanese glass eel matches the flow directionality of oceanic currents. The larval Japanese eel may serve as a good bio-tracer for monitoring the variability of inter-annual sub-surface currents on the East Asia continental shelf, where observed data are usually insufficiently. Because glass eel recruitment in Taiwan begins one to several months earlier than in other regions, and the glass eel catch in Taiwan shows a moderate correlation with overall catch in East Asia, the level of glass eel recruitment in Taiwan could also be a good predictor of the overall glass eel recruitment in a given year.

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