



Article Current Dependent Dispersal Characteristics of Japanese Glass Eel around Taiwan

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Abstract: Japanese eel larvae are passively transported to the East Asian Continental Shelf by the North Equatorial Current, Kuroshio and Kuroshio intrusion currents, and coastal currents. Previous studies have investigated the dispersal characteristics and pathways of Japanese glass eels. However, there are still limitations in these studies. According to long-term (2010–2020) catch data from the Fisheries Agency in Taiwan, the distribution and time series of glass eels recruitment to Taiwan are closely related to the surrounding ocean currents. Recruitment begins in eastern Taiwan via the mainstream Kuroshio and in southern Taiwan via the Taiwan Strait Warm Current. In central Taiwan, recruitment occurs from southern Taiwan, as well as from mainland China via the southern branch of the China Coast Current (CCC). The latest recruitment occurred in northern Taiwan and mainly comprised glass eels from mainland China via the northern branch of the CCC. A stronger monsoon during the La Niña phase could affect the recruitment time series in northern and eastern Taiwan. This study suggests that the recruitment directionality of glass eels is an indicator of the flow field of ocean/coastal currents and elucidates the dispersal characteristics of glass eels in the waters around Taiwan.

Keywords: Anguilla japonica; ENSO events; recruitment dynamics; Taiwan strait; weekly catch

1. Introduction

The Japanese eel (Anguilla japonica) is a catadromous species distributed throughout the western Pacific Ocean with high economic value in the East Asian countries of Japan, China, Korea, and Taiwan [1–3]. Mature eels mainly spawn between May and August during the new moon period near 12°-16° N, 141°-142° E in the North Equatorial Current (NEC), about 3000 km away from its habitat in East Asia [4–8]. After hatching, the larvae (leptocephali) passively drift from the spawning site on the NEC to the Kuroshio, from where they drift for 4–6 months before reaching the East Asian coast [1,2,4,8,9]. The NEC bifurcates into the north-flowing Kuroshio and the south-flowing Mindanao Current (MC) at its westernmost boundary off the coast of the Philippines. This is called the "NEC bifurcation" [10,11]. Leptocephali need to enter the Kuroshio in the bifurcation zone to reach their habitats in East Asian countries and avoid being entrained into the southflowing MC, where environmental conditions are unfavorable for this species [12,13]. The leptocephali are transported by currents, which are mainly 50-150 m deep, with diel vertical migration (DVM) [14,15], and metamorphose into glass eels as they approach their continental growth habitats. The glass eels then show a benthic sheltering behavior and actively swim toward nearby estuaries and rivers for further growth [3,4,16].

Large-scale commercial artificial propagation of the glass eel is yet to be undertaken. Therefore, the fry used in aquaculture can only be obtained by capture in estuarine and coastal waters during their upstream migration [17]. Japanese eel resources have been declining significantly since the late 1970s [18–21]. In response to this resource crisis, the



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Copyright: © 2022 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). Japanese eel was listed as an "endangered" species in 2013 by the Ministry of the Environment, Government of Japan. In 2014, it was listed in the IUCN Red List of Threatened Species as an "endangered" species [22,23]. Finally, in 2017, it was listed as a "critically endangered" species in the Freshwater Red List by the Forest Bureau of Council of Agriculture, Taipei, Taiwan. A combination of factors has caused this decline, including habitat degradation [20,24,25], overfishing [26–28], and fluctuations in oceanic conditions [21,28–33]. Therefore, it is crucial to elucidate the early life history of this species to allow for its sustainable use.

It is known that changes in oceanic environmental conditions could significantly affect the larval transport processes and recruitment dynamics of the Japanese eel [34–37] El Niño–Southern Oscillation (ENSO) events are potentially important drivers of interannual variability across the equatorial Pacific. Kimura et al. [29] found that Japanese glass eel catches in Japan have declined in association with El Niño events. Zenimoto et al. [34] additionally demonstrated that the annual catch per unit effort (CPUE) of Japanese glass eels at Tanegashima Island, located in the southern part of Japan (30.35° N, 130.59° E), reaches its lowest during El Niño years and is relatively high during La Niña years. Hsiung et al. [32] further revealed that during El Niño years, the changes in salinity distribution and current velocity could cause a longer drifting time and total length for the leptocephali to reach the estuarine waters along the coast of the East Asian countries. In addition, a previous study found that the northeast monsoonal winds in the Taiwan Strait were relatively weaker during El Niño years [35]. The strength and direction of coastal currents are affected by the monsoon season [36], which suggests that the recruitment dynamics of Japanese glass eels across the Taiwan Strait might also be affected by ENSO events.

However, it has been suggested that the distribution of Japanese glass eels matches the flow directionality of oceanic currents [4]. Therefore, the larval Japanese eel may serve as a good bio-tracer for monitoring the variability of interannual sub-surface currents on the East Asian continental shelf [4]. The level of glass eel recruitment in Taiwan could also be a good predictor of the overall glass eel recruitment because glass eel recruitment begins earlier in Taiwan than in other areas of East Asia, with moderate correlation [4]. A previous study further combined the results of the otolith increment analysis of Japanese glass eels and a particle tracing experiment, and revealed that Ilan County in Taiwan is the first recruitment place for Japanese glass eels in East Asia and is associated with the lowest mean larval duration and age among the studied glass eel recruitment sites [17]. Furthermore, at least five main expected routes were proposed: (1) the main Kuroshio, (2) the Taiwan Strait Warm Current, (3) the Taiwan Warm Current, (4) the Yellow Sea Warm Current, and (5) the branch of the Yellow Sea Warm Current. These five blocks constitute the main recruitment dynamics of the Japanese eel on the East Asian Continental Shelf [17]. However, more sampling sites and sampling numbers from same-year cohorts should be collected to improve the age data resolution. In addition, using mainly simulation results might not be sufficient to further understand the dispersal characteristics of Japanese glass eels in the Taiwan Strait. Analyzing the long-term catch data in different parts of Taiwan and comparing it to the flow field status would help to elucidate the dispersal mechanism of the Japanese eel larvae as well as the recruitment dynamics of the coastal current on the East Asia Continental Shelf.

Accordingly, by combining the information from long-term detailed catch data at 10 sites in Taiwan and the flow field data, this study aimed to further clarify the dispersal route and time series of the Japanese glass eels recruited to the eastern and western Taiwan coasts, and to assess the impacts of ENSO events on the recruitment dynamics in the estuaries along the coasts in Taiwan for more specific and efficient resource management. to ensure the sustainable usage of the Japanese eel stock in Taiwan and all East Asian countries.

2. Materials and Methods

2.1. Glass Eel Catch Information

Weekly glass eel catch data (number of glass eels caught) from 10 sites in Taiwan between 2010 and 2020 were obtained from the Taiwan Japanese Glass Eel Reporting System (Fisheries Agency, Council of Agriculture, Executive Yuan, Taipei, Taiwan) (Figure 1). The glass eels were collected using either a hand-trawling net or fixed shore trap prior to the high tides which occurred at night. The catch data were collected by the person within the fisheries agency from the fixed cooperated glass eel wholesalers in each county. Since the data were not collected from all the wholesalers, it only reflects the fixed percentage of the whole catch in each area. Accordingly, the caught data were transformed to a percentage in this study, thus stably reflecting the long-term time series data for glass eel recruitment in each location, allowing us to compare and assess the time series of recruitment at different locations in Taiwan. The original catch data are shown in the Supplementary Material (Table S1).



Figure 1. Map showing the 10 selected sites for catch data analysis in Taiwan. Data from Tamsui (25.10° N, 121.26° E) and Hsinchu (24.54° N, 120.59° E,) represent northern Taiwan; data from Changhua (24.04° N, 120.26° E), Yunlin (23.45° N, 120.15° E), Chiayi (23.23° N, 120.09° E), and Tainan (23.08° N, 120.07° E) represent central Taiwan; data from Pingtung (22.28° N, 120.26° E) represents southern Taiwan; and data from Ilan (24.45° N, 121.47° E), Hualien (23.36° N, 121.31° E), and Taitung (22.37° N, 121.00° E) represent eastern Taiwan.

2.2. Area Classification of Glass Eel Data

In this study, 10 areas in Taiwan were selected and divided into four groups: (a) northern Taiwan, comprising Tamsui, Hsinchu, and Miaoli; (b) Central Taiwan, comprising Changhua, Yunlin, Chiayi, and Tainan; (c) Southern Taiwan, comprising only Pingtung; and (d) Eastern Taiwan, comprising Ilan, Hualien, and Taitung (Figure 1). The recruitment time series and the relationship between each possible cohort recruited to the four main parts (north, central, south, and east) of Taiwan was also investigated (Figure 1) to see if the different sites in the same part show similar recruitment time series.

In addition, to clarify the possible effects of ENSO events on the recruitment time of Japanese glass eels in Taiwan, this study further compared catch data from the west side of Taiwan: Tamsui, Yunlin, and Pingtung (from north to south) to catch data from the east side of Taiwan: Ilan, Hualien, and Taitung (from north to south) between 2010 to 2020. It is worth noting that the six sites selected to observe the effects of ENSO events were those with the most comprehensive catch data, and the data were not averaged with other sites to avoid mixing up the data from nearby sites and clarify the effects of ENSO events.

2.3. Temporal Extraction of the Glass Eel Data

To ensure the accuracy of the data usage, we extracted the catch data from November to February, which comprises data of the main Japanese glass eel fishing season in Taiwan. In addition, we used a proportion of the catch in a single fishing area to the total catch of the year instead of using the catch data directly as it is more suitable for observing the long-term fluctuations in Japanese glass eel recruitment dynamics and avoid possible misdirection that often occurs in the original catch data reported by glass eel traders and fishers [37].

2.4. Data Source to Distinguish the Phase of the ENSO Events

The El Niño/La Niña events were identified from the data collected by the Climate Prediction Center of the National Oceanic and Atmospheric Administration (NOAA, Washington, DC, USA) (https://origin.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5.php) (Accessed on 1 September 2021). Monthly values of ENSO index from 2010–2020 were based on the Oceanic Niño Index (ONI), which is derived from a three-month running mean of ERSSTv4 sea surface temperature anomalies in the Niño 3.4 region (5° N–5° S, 120°–170° W). El Niño events were defined when the threshold temperature of +0.5 °C for the ONI was met for a minimum of five consecutive overlapping months. La Niña events were defined when a threshold temperature of -0.5 °C for the ONI was met for a minimum of five consecutive overlapping months. In this study, the El Niño years were 2014–2015, 2015–2016, and 2018–2019; the La Niña years were 2010–2011, 2011–2012, 2016–2017, 2017–2018, and 2020–2021; and the normal years were 2012–2013, 2013–2014, and 2019–2020.

2.5. Current Velocity Data

GlobCurrent data were used to observe the flow field and current velocity. These data include the surface geostrophic current, Ekman current at the surface and at 15 m depth, and combined geostrophic and Ekman currents. The data were interpolated and collocated to a common grid with a spatial resolution of 25 km and temporal resolutions of 1 day for the geostrophic current and 2 h for the Ekman current and the combined currents. The data cover a 23-year period from 1993 to 2017 and can be accessed from http://www.globcurrent.org (Accessed on 1 May 2021). In this study, we chose the current at 0.25 m to observe the flow field.

2.6. Statistical Analysis

The catch data were analyzed by one-way Analysis of variance (ANOVA, AB Electrolux, Stockholm, Sweden), (International Business Machines Corporation (IBM), Statistical Product and Service Solutions (SPSS), (Statistics 24.0, Armonk, NY, USA) to determine the differences in the amount of glass eel caught in northern, central, southern, and eastern Taiwan during the fishing season (November to next February). When a significant effect was found (p < 0.05), the least significant difference (LSD) test was conducted to compare means, and the abundance was considered to be significant between areas when the *p*-value is smaller than 0.05. Furthermore, Pearson's chi-squared test (IBM SPSS Statistics 24.0) was used to determine the difference between El Niño and La Niña years. It was considered to be a significant difference when the *p*-value is smaller than 0.05.

3. Results

3.1. Comparison of Glass Eel Recruitment Time Series from the Four Main Parts of Taiwan

The Japanese glass eel recruiting season occurred first in eastern and southern Taiwan, followed by central and northern Taiwan (Figure 2). The peak of the recruiting season was around December and January in Eastern Taiwan (Figure 2a,b), and the recruiting percentage decreased gradually until the middle of January (Figure 2a). In southern Taiwan, the recruitment season began in November (Figure 2c), approximately the same time as that in eastern Taiwan. The recruiting proportion reached its peak after a month and then gradually decreased until the end of the fishing season (Figure 2a).



Figure 2. (a) Order of the glass eel recruitment time series in northern, central, southern, and eastern Taiwan. Each point represents a catch proportion calculated from a number of the captured glass eel averaged over a week. (b–e) The amount of glass eel caught in different months in eastern, southern, central and northern Taiwan. Value is the means of caught in each month, where the values in each row with different superscripts are significantly different (p < 0.05) by LSD ANOVA post hoc test.

In central Taiwan, the glass eel recruiting season seemed to follow the trend of that in southern Taiwan before January (Figure 2d), with a time lag of about a week (Figure 2a). The peak of the recruiting season was in the middle of January, and a smaller peak could be observed in the middle of February (Figure 2a). The latest recruiting season seemed to occur in northern Taiwan from the middle to the end of December (Figure 2a). The peak of

the recruiting season occurred in February (Figure 2a), and the fishing season also ended late as compared to southern Taiwan (Figure 2e).

3.2. Time Series of Glass Eel Recruitment in Each Fishing Area in Taiwan

As shown in Figure 2, there were similar trends found in eastern and southern Taiwan (Figure 2b,c), with the significant lowest amount shown in February (p < 0.05), and the recruiting season seems to have started in November, peaked in December, and ended in January. In addition, the recruiting season in central Taiwan seems to have started in December, peaked in January, then decreased gradually, and ended in February (Figure 2d). The significant lowest amount was shown in November (p < 0.05) and the recruiting season seems to have started in December (p < 0.05) and the recruiting season seems to have started in November (p < 0.05) and the recruiting season seems to have started in December (p < 0.05) and the recruiting season seems to have started in December (the latest) in northern Taiwan (Figure 2e).

3.3. Effects of ENSO Events on the Glass Eel Recruiting Month

To examine whether ENSO events have affected the recruiting time series of the Japanese glass eel, this study further compared the monthly catch data during El Niño and La Niña years. The results showed that the peaks of the recruiting season occurred in the same month in Yunlin, Pingtung, Ilan, and Taitung in both ENSO phases (Figure 3). In contrast, the recruiting season began earlier in Tamsui and Hualien during La Niña years (Figure 3).



Figure 3. Comparison of the monthly catch data during El Niño and La Niña years in Tamsui, Yunlin, Pingtung, Ilan, Hualien, and Taitung. Bar charts with an asterisk (*) above are significantly different (p < 0.05).

3.4. Flow Field in Relation to Glass Eel Transport around Taiwan

Figure 4 shows the flow field around Taiwan, averaged every January from 2010 to 2017. Strong northeast winds push cold coastal waters southward, while the Kuroshio moves offshore warm waters northward in winter. The warm and cold waters mix on the East Asian Continental Shelf and form complex offshore and coastal currents that are affected by factors, such as local wind, water temperature and salinity, seabed topography,

and tides. The Kuroshio current intruding the central region of the Luzon Strait flows into the northeast of the South China Sea, with some flowing directly into the Taiwan Strait as the Taiwan Strait Warm Current (TSWC). It is worth noting that the southward China Coast Current (CCC) passing through western Taiwan flows not only into the northwest part, but also into another branch in the central part of Taiwan (Figure 4). The detailed transport pathways and time series of Japanese glass eels in Taiwan were constructed based on the information synthesized from the 11-year catch data analysis and the flow field that transports the glass eels to Taiwan (Figure 5).



Figure 4. The flow field around Taiwan at 0.25 m depth averaged every January from 2010 to 2017. The colors show the ocean bathymetry (m), and the arrow represents the current direction and velocity.



Figure 5. Schematic map combining information from the flow field related to the transport of Japanese glass eel around Taiwan and the time series of the catch data in eastern (1), southern (2), central (3), and northern (4) Taiwan. The numbers represent the order of glass eel recruitment. TWC, Taiwan Warm Current; TSWC, Taiwan Strait Warm Current; CCC, China Coast Current.

4. Discussion

According to the detailed transport pathways and time series of Japanese glass eels in Taiwan arranged in this study, after the larvae meet the NEC bifurcation, they have to enter the northward Kuroshio and avoid entering the southward MC to reach their habitats in East Asian countries. According to a previous study, the long-term statistics of the Japan Aquaculture Information News showed that the average recruitment abundances of the Japanese glass eel in China, Japan, Taiwan, and Korea were 50–60%, 30–40%, 5–10%, and 5–10%, respectively [17]. In Japan, more than 90% of glass eels are caught along the Pacific coast, meaning that approximately one-third of all Japanese glass eels are transported by the primary Kuroshio pathway each year [17]. In this study, the earliest glass eel cohort was transported to eastern Taiwan through the Kuroshio. Among the three sampling sites in eastern Taiwan, the trends of the recruiting time series were similar, but it seems that the recruitment peak in Taitung, Taiwan occurred slightly earlier than that in Ilan, Taiwan. This further verifies that the distribution of the glass eels followed the Kuroshio from south to north.

The Kuroshio intruding the central region of the Luzon Strait flows northeast of the South China Sea, with some flowing directly into the Taiwan Strait as the TSWC (the ratio was about 1:5 according to the data from Nan et al. (2015) [38], which occurs synchronously with the weakening of the upstream Kuroshio during winter [36,39,40]. In this study, other than those transported to eastern Taiwan via the Kuroshio, some of the glass eels entered the TSWC and were transported to the western coast of Taiwan (the ratios were about 1:7 and 1:7.9 calculated from the transport volume data from Nan et al. (2015) [38] and the glass eels recruitment data from Taiwan Japanese Glass Eel Reporting System), thus becoming the second cohort to arrive in Taiwan. According to the order of the glass eel recruitment time series in Taiwan, the recruitment of Japanese glass eels to southern Taiwan

started in November, reaching a peak around mid-December and gradually decreasing until the end of the fishing season. However, recruitment in central Taiwan showed an increasing trend until the end of January, which was close to the end of the fishing season. The results indicated that there might be two pathways for the glass eel to reach central Taiwan. Previous studies have suggested that glass eels along the southwestern coast of Taiwan were carried there via the CCC from the north [9,41], In contrast, Han et al. (2012) [4] showed that the recruitment of glass eels in western Taiwan started from Pingtung County and then proceeded from south to north. The results of this study seem to correspond logically with both of these findings.

The latest recruitment occurred in the northwestern region of Taiwan. This area is located at the end of the Taiwan Strait Warm Current, and the stock seems to be shared with other areas of western Taiwan [4]. However, this study further found that the recruitment proportion continued to increase in northern Taiwan, while it showed a decreasing trend in southern Taiwan, which might indicate that the glass eels come not only from southern Taiwan, but also through another pathway. The recruitment proportions in northern and eastern Taiwan showed a similar trend before the end of December. Considering that the earliest recruiting season occurred in eastern Taiwan, some individuals might have escaped eastern Taiwan through TWC to northern Taiwan. In addition, there seemed to be another small recruitment peak in northern Taiwan after February, while recruitments in other parts of Taiwan were about to end. This indicated that a significant portion of glass eels might have been recruited from mainland China via the CCC.

When comparing the differences in the recruiting patterns during El Niño and La Niña years, the results showed that peaks in the recruiting season occurred in the same month in most of the sampling sites in Taiwan during the two ENSO phases. However, they appeared earlier in Tamsui and Hualien, Taiwan during La Niña years. According to previous studies, the East Asian–Western Pacific (EAWP) climate is significantly influenced by ENSO in the boreal winter. It has been proposed that El Niño (La Niña) can cause an anomalous lower-tropospheric anticyclone (cyclone) around the Philippines via Gill-type Rossby wave responses in peak winters [42,43]. Therefore, the East Asian winter monsoon (EAWM) tends to be weak (strong) during El Niño (La Niña) winters, with widespread warming (cooling) and more (less) precipitation observed in subtropical East Asia [44–50]. Although these climate anomalies are not exactly symmetric, they have broadly opposite signs in El Niño and La Niña winters [51]. The Taiwan Strait is under the East Asia monsoon regime. The weak southwest monsoon prevails from May to September, while the intense northeast monsoon dominates for the rest of the year. The transient monsoon system can significantly modulate the strait circulation [10,52], thereby affecting the transport and biogeochemical budgets for the East China Sea (ECS) [37,53]. Hu et al. (2019) [36] further proved that when northeastern winds are strong, the surface currents in the Taiwan Strait are primarily toward the southwest, while the surface flows are generally directed toward the northeast and veer offshore upon entering the ECS when along-strait winds are weak.

Some earlier observations have shown that the volume transport of the Kuroshio in northeast Taiwan changes seasonally, with a stronger magnitude in summer and a weaker magnitude in winter, and a main axis that is close to the continental margin in fall and winter shifts offshore in spring and summer [51,52], presumably in response to the East Asian monsoon winds [52]. Accordingly, the earlier recruiting peak that occurred in Tamsui during La Niña years could be due to a stronger volume transport of the CCC caused by a stronger northeast monsoon, which allows the glass eels from mainland China to arrive at northern Taiwan earlier. In contrast, the southward nearshore current on the east coast of Ilan seems to be greatly induced by a stronger northeast monsoon during La Niña years. This may be a reasonable explanation for the earlier recruiting peak that occurred in eastern Taiwan (Hualien, Taiwan).

5. Conclusions

The recruitment of Japanese glass eels in Taiwan began earlier than in other distribution regions, and the catch in Taiwan showed a moderate correlation with the overall catch in East Asia. In this study, long-term catch data from 10 sites in Taiwan were used to more comprehensively analyze glass eel recruiting dynamics and relationships with flow fields. According to the analysis in the present study, the Japanese glass eel recruiting season occurred first in eastern and southern Taiwan, with similar recruiting time-series trends found in the two parts. The glass eel recruiting season seemed to follow the trend of that in southern Taiwan, with a time lag of about a week in central Taiwan. The latest recruiting time series matched the flow directionality of oceanic currents well, highlighting the strong dependence of larvae on advection by ocean currents. Furthermore, the effects of ENSO events, especially stronger monsoons during the La Niña phase, could also be seen in the long-term glass eel catch data analysis in Taiwan.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/ 10.3390/jmse10010098/s1, Table S1: The original catch data from 2010 to 2020 (number of the glass eel) at the 10 sampling sites in Taiwan (Tamsui, Hsinchu Miaoli, Changhua, Yunlin, Chiayi, Tainan, Pingtung, Ilan, Hualien, and Taitung) were collected according to the Taiwan Japanese Glass Eel Reporting System (Fisheries Agency, Council of Agriculture, Executive Yuan, Taiwan). W represents the week; NA means no catch data has been reported during that week.

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