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Batch-like Arrival Waves of Glass Eels of *Anguilla japonica* in Offshore Waters of Taiwan

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ABSTRACT

Yu-San Han, Chau-Ron Wu, and Yoshiyuki Iizuka (2016) The larval stage of *Anguilla japonica* includes a long dispersal time over a long distance. In theory, the larvae should be distributed evenly throughout their transportation route when using both the NEC and Kuroshio, but the hypothesized new moon spawning of mature eels should lead to recruited glass eels exhibiting batch-like arrival waves, with a one-month-long cycle. However, environmental disturbances could mask the expected batch-like waves of glass eel recruitment. Thus, this phenomenon is best observed in glass eels collected from offshore waters, which are closer to the spawning site and less disturbed by these environmental factors. The offshore area of Yilan, Taiwan, is a suitable place to observe the arrival dynamics of the *A. japonica* glass eel. In this area, batch-like waves of glass eel arrival of *A. japonica* were observed, with peaks occurring between the last quarter and first quarter lunar periods, with a near one-month periodicity. No arrival peaks were found during the full moon period, suggesting that the glass eels exhibit light-avoidance behavior. Furthermore, all of the batches of arrivals were in the early pigmentation stage and similar in age (around 150-160 days), suggesting that they are likely a new arrival cohort. The tracer simulation showed that the mean tracer drift time, from the presumed spawning site to Yilan, was 155 ± 19.8 days. The observed batch-like arrival waves of glass eels in the offshore waters of Taiwan support the "New Moon Hypothesis," which suggests that there is synchronized spawning behavior of the eels during the new moon period.

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BACKGROUND

The Japanese eel *Anguilla japonica* (Temminck and Schlegel 1847) is a temperate catadromous fish that is mainly distributed in Taiwan, China, Korea, and Japan (Tesch 2003; Kuroki et al. 2009; Han 2011). Mature eels spawn in the western waters of the West Mariana Ridge (Tsukamoto 1992, 2006) mainly between May and August (Zenimoto et al. 2009; Han 2011; Han et al. 2012). After hatching, the larvae (leptocephali) passively drift from the spawning sites by way of the North Equatorial Current (NEC) and the Kuroshio at depths typically between 50 and 150 m for 4-6 months before reaching the East Asian coast (Tsukamoto 1992, 2006; Cheng and Tzeng 1996; Han et al. 2012). The larvae then metamorphose into glass eels and adopt a benthic sheltering behavior to escape from the oceanic current, and actively swim toward nearby estuaries and rivers for growth (McCleave and Wippelhauser 1987; Tesch 2003). Tsukamoto et al. (2003) analyzed the otolith microstructure of *A. japonica* leptocephali collected near the spawning area in July 1991 and estimated their age in order to determine the spawning times of *A. japonica*. These leptocephali had a total length of 10-30 mm and consisted of individuals hatched during the new moon periods of May and June. The “New Moon Hypothesis,” therefore, was proposed to explain the timing of eel spawning (Tsukamoto et al. 2003, 2011). Synchronized spawning and hatching is a well-known phenomenon that occurs in many marine animals, including corals, polychaete worms, crabs, and fish (Tsukamoto et al. 2003). The activity of migratory silver-stage Japanese eels peaked during the new moon period (Sudo et al. 2014), and a spawning event occurred at a depth of around 160-250 m (Aoyama et al. 2014). Thus, the lunar phase influences the spawning behavior of eels by mediating the synchronization of final maturation and spawning.

The larval stage of *A. japonica* includes a long dispersal time over a long distance. Based on conventional wisdom, the larvae should be distributed evenly throughout their transportation route when using both the NEC and Kuroshio; however, based on the New Moon Hypothesis, the abundance of recruited glass eels along their transportation route should be uneven and may exhibit batch-like waves with a one-month-long cycle. In the river estuaries of most sites, recruitment usually peaks during the new moon period due to high tidal currents (which push the glass eels towards the estuary) and lack of light (glass eels exhibit photopathy) (Jellyman 1979; McCleave and Kleckner 1982; Gascuel 1986; McCleave and Wippelhauser 1987; Boëtius and Boëtius 1989). In addition, the newly arrived glass eels may stay in the offshore area for several months in response to cold-water temperatures, before migrating into the river estuary (Han 2011). Furthermore, other factors, including water salinity, turbidity, pH, rainfall, freshwater discharge, river-water odor, and weather conditions, may influence, alone or in combination, the upstream migration of glass eels (Jellyman 1979; Tzeng 1985; Tosi et al. 1990; Jellyman and Lambert 2003; White and Knights 1997; Zompola et al. 2008; Hwang et al. 2014). These disturbances could mask the expected batch-like waves of glass eel recruitment. Thus, this phenomenon is best observed in glass eels collected from locations closer to the spawning site and from offshore waters, which are less disturbed by environmental factors.

From among the East Asian countries, Taiwan is closest to the spawning ground of the Japanese eel, and it is the first country to receive recruitment waves of *A. japonica* (Fig. 1). Yilan County, Taiwan, is located at the edge of the East Asian continental shelf, and the warm Kuroshio main stream flows along its coast year round, with a mean depth between 50 and 150 m (Hsin et al. 2008). It is the biggest fishing area for the Japanese glass eel in Taiwan. Thus, the offshore waters of Yilan are a suitable place to observe the arrival dynamics of the *A. japonica* glass eel.

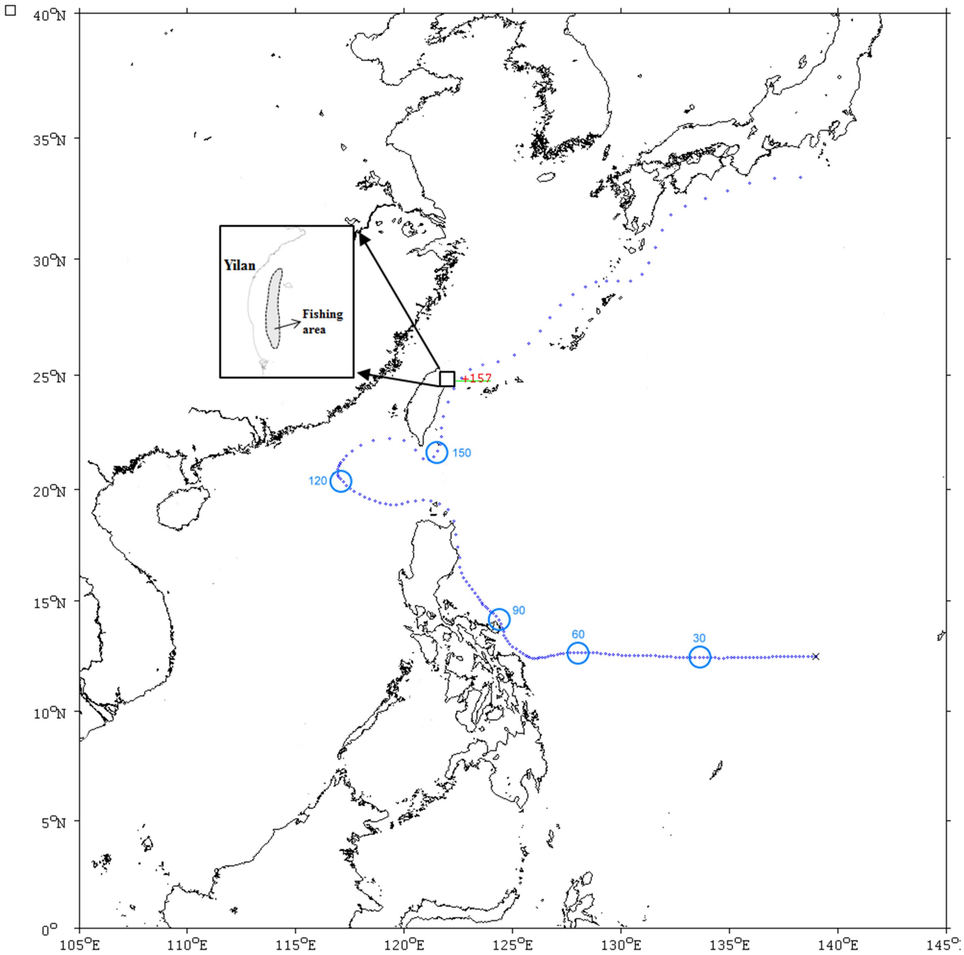

Fig. 1. Tracer drift map showing spawning, transportation, and sampling sites of *Anguilla japonica*

in East Asia. This is a representative map. The numbers along the North Equatorial Current (NEC) and Kuroshio indicate the cumulative drift days for the core batches of eel larvae from the spawning site to the offshore area of Yilan, Taiwan. The tracer experiment was performed at a depth of 100 m in June, starting at 139°E and 12.5°N.

MATERIALS AND METHODS

Glass eel catch and SST/salinity data collection

The offshore waters of Yilan County, Taiwan, were chosen for monitoring the arrivals of *A. japonica* glass eels (Fig. 1). *A. japonica* glass eels are easily separated from other eel species (*e.g.*, *A. marmorata*, *A. bicolor pacifica*, and *A. luzonensis*) by the lack of caudal cutaneous pigmentation (Tabeta et al. 1976; Han et al. 2012), and they are the target eel species for Taiwanese fisheries in winter. Pigmentation stage of the glass eel (V_A, V_B, VI_{A1}, VI_{A2}, VI_{A3}, VI_{A4}, and VI_B) was determined based on Tesch (2003). The main fishing season is from November to February, and the northeast monsoon wind is dominant during this period. The weekly catch data from eel ships in Yilan were collected by the Taiwan Japanese Glass Eel Reporting System (Fisheries Agency, Council of Agriculture, Executive Yuan, Taiwan) for six consecutive years, from October 2008 to February 2014 (unpublished). Glass eels hide in the seabed during the day, so all eel fishing occurs at night when the eels rise to the surface. Glass eels were collected using eel ships (approximately 200, contributing > 80% of the total catch for this area) with two trawling fyke nets beside the ship at depths of < 10 m, 5-10 km off the coast (Fig. 1). Although the CPUE (catch per unit effort) could not be precisely calculated, the data trend is close to the CPUE, based on the relatively stable catch activity during the fishing season. For comparison purposes, the Japanese glass eels were also caught daily using fyke nets at night in the Yilan River estuary (24.7162°N, 121.8352°E) between November 2013 and February 2014 with CPUE (individuals/net/hr). The daily sea surface temperature (SST) and salinity data for the area were obtained from the Central Weather Bureau and Environmental Protection Administration, Executive Yuan, Taiwan, respectively.

Numerical model description

Tracer simulation was performed to study the passive behavior of the larvae. This was based on the East Asian Marginal Seas (EAMS) model. The model covers a domain of 99-140° E and 0-42° N with a horizontal resolution of 1/8° × 1/8° and 26 sigma levels in the vertical. Hsin et al. (2008)

have given a detailed description of the EAMS model. The EAMS model was able to reproduce the flow patterns of the Kuroshio east of Taiwan and around the Luzon Strait (Hsin et al. 2008, 2012). The representative tracer experiment was performed at a depth of 100 m in June, during the main spawning season of *A. japonica*, starting at 139°E and 12.5°N. The overall mean tracer drift time from the presumed spawning site to Yilan between 1988 and 2007 was also calculated. Tracer drift times of > 200 days were excluded for having an irregular drift route affected by local eddies.

Otolith daily increment counts of glass eels

A. japonica glass eels were collected from the Yilan River estuary by fishermen in three consecutive Decembers between 2010 and 2012 (Table 1). Sagittal otoliths (n = 56) were analyzed for daily growth increments using scanning electron microscopy (SEM) according to the method described by Han (2011). Presumed daily increments in the otoliths were counted from the first ring outside of the core to the end of the otolith edge. The nine days of the preleptocephalus stage, during which no otolith ring is formed (Shinoda and Tsukamoto 2009), were added to the age.

Table 1. Analysis of otolith daily growth rings of *Anguilla japonica* glass eels collected from Yilan, Taiwan. Legend: values provided are mean ± SD; LZ: leptocephalus zone; MZ: metamorphosis zone; GZ: glass eel zone

Sampling time	n	LZ day	MZ day	GZ day	Total age* day (range)
Dec. 2010	18	100.3 ± 7.4	24.9 ± 1.8	22.8 ± 6.0	152.4 ± 11.6 (131-177)
Dec. 2011	19	105.8 ± 10.1	26.2 ± 3.7	20.7 ± 3.7	158.9 ± 11.4 (138-173)
Dec. 2012	19	102.2 ± 10.3	22.1 ± 3.1	22.8 ± 6.0	157.6 ± 13.3 (139-186)

*The 9 days of the preleptocephalus stage were added to the total age.

Data analysis

Differences in the total age (mean ± SD) between samples were tested using one-way analysis of variance (ANOVA) followed by Tukey's honestly significant differences (HSD) multiple-comparison test. Differences in the occurrence of arrival peaks among four moon phases were examined using the chi-square test of homogeneity. Linear regression was used to analyze the relationship between the SST and glass eel catch. SPSS (v. 16, IBM) software was used for the statistical analysis. Differences were considered significant when $p < 0.05$.

RESULTS

Glass eel arrival and SST/salinity data

Weekly catch data revealed periods of abundant catches throughout the fishing season (Fig. 2). In 2013-2014, the daily CPUE of glass eels in the Yilan River estuary was recorded, and three corresponding arrival events were observed between the offshore and estuary catches (Fig. 2f).

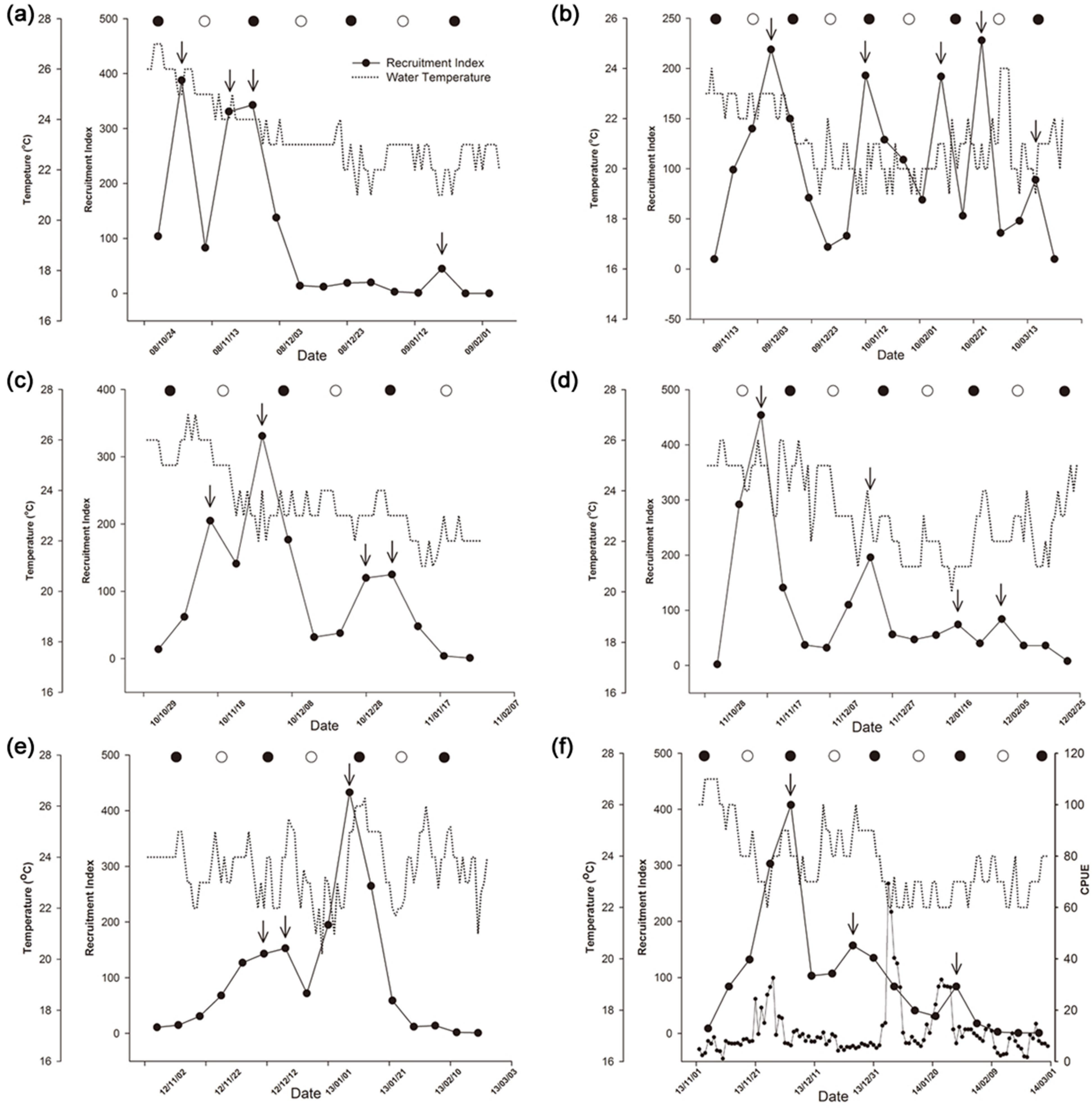

Fig. 2. The SST and catch data of *Anguilla japonica* glass eels in Yilan. The eel seasons represented are 2008 to 2009 (a), 2009 to 2010 (b), 2010 to 2011 (c), 2011 to 2012 (d), 2012 to 2013 (e), and 2013 to 2014 (f). Data were collected as weekly catch (individuals). In 2013-2014, the daily CPUE (individuals/net/hr) of glass eels in the Yilan River estuary (small dark circle) was also recorded (f). The recruitment index is represented as the percentage of the weekly catch relative to

the overall mean weekly catch during the fishing season. SST was measured at four stations offshore of Yilan, at the fishing area. The new moon is indicated by a black circle and the full moon by a white circle on the top of each legend. Arrows indicated visible recruitment peaks (median date of the catch period).

This validated the reliability of the Taiwan Japanese Glass Eel Reporting System. The peak interval during the six consecutive years ranged from 14-35 days, with a mean interval of 25.3 ± 8.4 days. Times of arrival peaks occurred during the first quarter (days 4-11), full moon (days 12-18), last quarter (days 19-26) and new moon (days 27-3) 5, 0, 11, and 7 times, respectively. Arrival peaks occurred during all lunar periods except the full moon period. A chi-square test of homogeneity for the occurrence of the arrival peak among the 4 moon phases showed significant differences ($\chi^2 = 10.913 > \chi^2(3, 0.025) = 7.815$). The SST ranged between 19°C and 27°C during the glass eel season. No regression correlation was found between the SST and arrival (Fig. 3, $R^2 = 0.04$, $p = 0.06$). The seawater salinity remained stable, between 33.5‰ and 34.5‰, during glass eel season from 2008 to 2014.

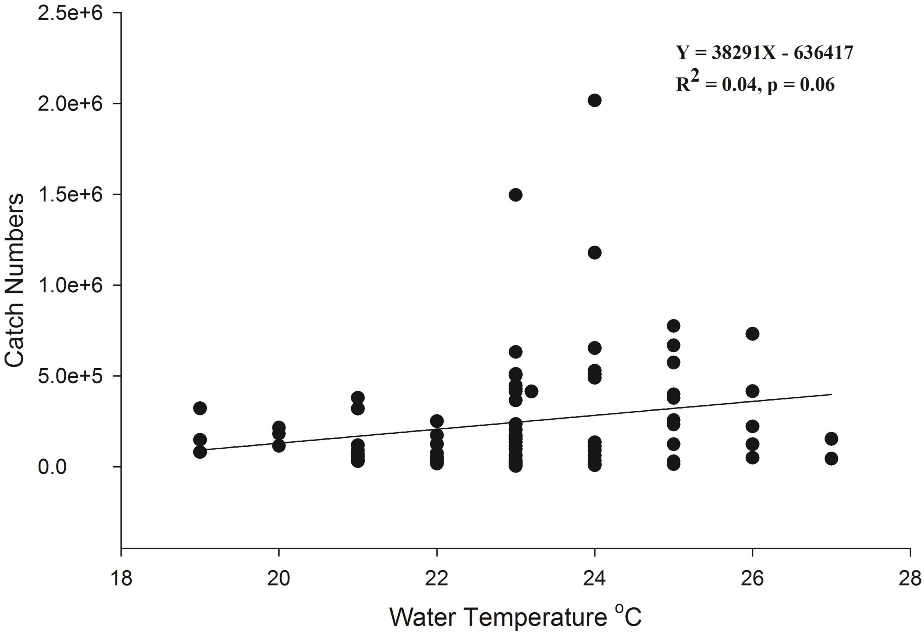

Fig. 3. Linear regressions of sea surface temperature on the total weekly glass eel catch. The sea surface temperature (SST) was calculated as the mean for the week corresponding to the catch period.

Otolith daily increment counts of glass eels

The majority of the glass eels caught offshore at Yilan were in the V_A and V_B developmental stages (data not shown); suggesting that each batch of glass eels mostly consisted of new arrivals. The mean age ranged from 131 to 186 (156.5 ± 12.2) days, including approximately 102.8 ± 9.4 days in the leptocephalus stage, 24.5 ± 3.3 days in the metamorphic stage, and 22.1 ± 5.3 days in the glass eel stage before they were caught (Table 1). The age composition of glass eel arrival batches in December of the three consecutive year classes had a normal distribution with a narrow range. No significant differences in mean ages were found between the three sampling years ($p > 0.05$).

Tracer experiments

The representative tracer simulation showed that the tracers (larvae) drifted in the main stream of the westward-flowing NEC, reaching the eastern coast of the Philippines three months later. They then entered the northward-flowing Kuroshio and finally approached the Yilan area of Taiwan after approximately 157 days (Fig. 1). The mean tracer drift time, from the presumed spawning site to Yilan, was 155 ± 19.8 days. Thus, the tracer simulation result is close to the otolith data, indicating that each batch of glass eels takes about five months to reach the offshore area of Yilan from their spawning site.

DISCUSSION

It is well known that the recruitment dynamics of glass eels in river estuaries are affected by multiple biotic and abiotic factors, such as the lunar cycle, tidal rhythms, water temperature, salinity, turbidity, freshwater discharge, water odor, pH, and weather conditions, causing glass eel migration to occur in waves of invasion for most sites (Jellyman 1979; McCleave and Wippelhauser 1987; Boëtius and Boëtius 1989; White and Knights 1997; Jellyman and Lambert 2003; Zompola et al. 2008; Hwang et al. 2014). For example, the recruitment season of the *A. japonica* glass eel generally starts in Taiwan (Southeast Asia) in November, and in northern areas of Korea in February of the following year. This represents a recruitment time lag of approximately three months (Han 2011). This time lag in the recruitment of glass eels in Korea can be explained by a longer leptocephalus stage in combination with a low-temperature-driven delay of upstream migration in winter (Han 2011; Hwang et al. 2014). Hwang et al. (2014) indicated that the first glass eels caught in the Geum River estuary were in early March, when the water temperature exceeded 5°C. Experiments and field observation both indicate that glass eels may starve, lose body weight, and remain in early pigmentation stages for a few months when in cold waters (Han 2011). Thus, low water temperatures could be the determining factor for the timing of upstream migration in cold areas like Korea, but not in Taiwan, where temperatures are not as cold in winter.

The waters offshore of Yilan are filled with the clean, warm Kuroshio flows (Hsin et al. 2008), with stable salinity (33.5‰-34.5‰) and no tidal current. Thus, some important factors, such as tidal rhythms, salinity, turbidity, and freshwater discharge, which may affect the recruitment of glass eels in the estuary, play little to no role in the Yilan offshore area. However, the SST variation between 19°C-27°C, due to the cold weekly northeast monsoon in winter, might affect the dynamics of the arrival batches. In this study, although the SST varied markedly during the fishing season, the short-term SST variation (over a few weeks) was generally less than 3°C. In addition, no significant correlation between the SST and glass eel catch was found (Fig. 3). Thus, the SST variation in the Yilan offshore area seems to play little role in the arrival dynamics of the glass eel.

The transparent waters off the Yilan coast, which can be penetrated by moonlight, may affect the arrival dynamics of the glass eel. In the present study, arrival peaks occurred most often during the last quarter through the first quarter, but not during the full moon. This suggests that the photopathy behavior of glass eels may play an important role in catch abundance. Tzeng (1985) indicated that *A. japonica* glass eels at early developmental stages (V_A and V_B) are light sensitive, and they do not migrate during the full moon. The glass eels caught at the Yilan offshore area were in early developmental stages and seemed to avoid the strong moonlight penetrating the transparent seawater during the full moon period by remaining hidden in the deep water at night. If this were true, these glass eels would be caught in the subsequent last quarter. This is supported by the highest frequency of arrival peak events during the last quarter. Although the age difference between few individuals of the same arrival batch may exceed 30 days (Table 1), each batch showed a small standard deviation value, suggesting that most individuals in the arrival peaks were spawned in the same month and belonged to the same cohort. Furthermore, tracer simulation also supported the observation that each batch of glass eels takes about five months to reach the offshore area of Yilan from their spawning site. Tsukamoto et al. (2003) collected *A. japonica* leptocephali near the spawning area in July 1991, which consisted of individuals hatched during the new moon periods of May and June, suggesting that the mixing events between monthly cohorts did occur even at a sampling site near the spawning ground. It is possible, however, that the local eddy currents (Tzeng et al. 2012) along the transportation route may trap some leptocephali and result in mixing between monthly cohorts at a small scale. The main force of the monthly glass eel cohorts is possibly transported away from the spawning site by the high speed NEC, thus reducing the mixing degree between monthly cohorts.

The most likely explanation for the batch-like arrival pattern of *A. japonica* glass eels in the Yilan offshore area is the new moon spawning behavior of the parental generation. Interestingly, a similar phenomenon was also observed in the glass eels of *A. marmorata* in the Philippines, which is close to the spawning site (Han et al. unpublished data). This causes batches of eel larvae to be transported with near one-month periodicity. In this study, the peak interval ranged between 14 and 35 days, with a mean interval of 25.3 ± 8.4 days. Variation in the intervals between arrival peaks may reflect variation in the current speed during larval transportation from the spawning site to the Yilan offshore area for each batch. Alternatively, these batches of glass eels may have been spawned at different sites in the range of 12-16° N during the new moon period, and then drifted along somewhat different routes on the NEC and Kuroshio to the Yilan offshore area. For glass eels caught at locations far from the spawning site, or with complex coastal currents and low temperature disturbances (e.g., China, Japan, and Korea), the eel larvae of different monthly cohorts could be mixed significantly, thus masking the theoretically recruitment waves.

From among the East Asian countries, Taiwan is the nearest country to the spawning ground of the Japanese eel, and is the first place to receive the recruited eels, up to several months earlier than other areas (Han 2011; Han et al. 2012). Yilan County contributes about 40% of the total glass eel catch in Taiwan each year (Han et al. unpublished data). Therefore, the dynamics of glass eel arrivals in the Yilan offshore area may serve as a useful assessment of (1) monthly larval cohorts from the spawning ground, and (2) subsequent glass eel recruitment in other countries. For example, the main arrival peaks in 2008/2009 (Fig. 2a), 2011/2012 (Fig. 2d), and 2013/2014 (Fig. 2f) occurred earlier than those in 2012/2013 (Fig. 2e). This reflects the spawning dynamics of the eel in the spawning site and corresponded with the subsequent recruitment patterns seen in other places in Japan (Han et al. unpublished data). The Japanese eel was categorized as an endangered species by the IUCN Red List in 2014. The Taiwan government also announced the banning of glass eel fishing between March and October since 2013. However, the main recruitment season of the glass eel occurred between November and February, a range that does not include the fishing restriction period. Thus, this study also provides information for the Taiwan government to better evaluate suitable regulation policies for Japanese glass eel catching.

CONCLUSIONS

The synchronized spawning behavior of *A. japonica* during the new moon may form a batch, containing individuals of the same cohort, which is transported by the NEC and Kuroshio to the Yilan offshore area, forming arrival waves with approximately one-month periodicity.

List of abbreviations

CPUE: catch per unit effort
EAMS: East Asian Marginal Seas
NEC: North Equatorial Current
SST: sea surface temperature

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