

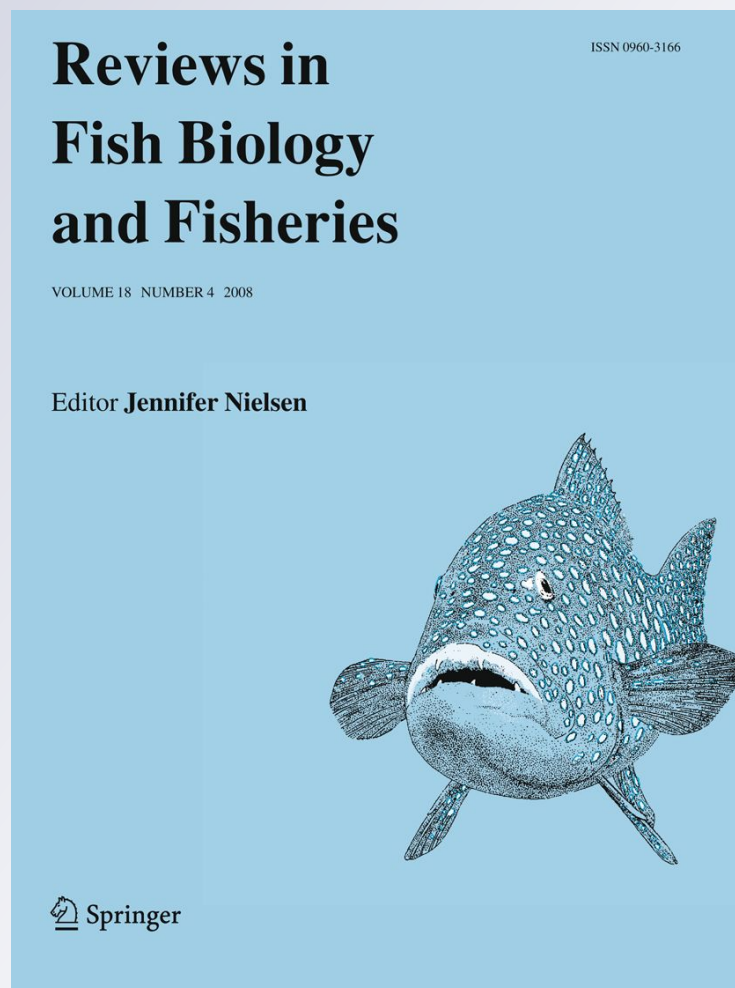
Evaluation of the larval distribution and migration of the Japanese eel in the western North Pacific

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Evaluation of the larval distribution and migration of the Japanese eel in the western North Pacific

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Abstract The distribution of all larval stages of the Japanese eel, *Anguilla japonica*, were examined using historical catch records and original data in the western North Pacific (WNP) to evaluate existing information about the larval distribution and migration of this species. A total of 148 preleptocephali, 2547 leptocephali, 6 metamorphosing larvae, and 21 glass eels were collected during 37 cruises over a 52-year period (1956–2007). Sampling effort was spatio-temporally biased in latitude/longitude among seasons with sampling effort being concentrated near the western margin of the subtropical gyre near Taiwan in the winter season and extensive effort occurring near the

spawning area to the east near the seamount chain of the West Mariana Ridge in summer during the spawning season. The distribution of preleptocephali (4.2–8.7 mm) was limited to a narrow area around 14°N, 142°E just west of the southern part of the seamount chain, while leptocephali (7.7–62.0 mm) were widely distributed at increasing size westward in the North Equatorial Current (NEC) to the region east of Taiwan. Metamorphosing larvae (52.7–61.2 mm) were collected only in the area 21–26°N, 121–129°E to the east of Taiwan, while glass eels (51.3–61.2 mm) occurred only within or west of the Kuroshio. These distributions suggest that leptocephali begin to

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metamorphose within or just east of the Kuroshio, then after completion of metamorphosis the glass eels detrain from the current and migrate inshore. The relationship between catch date and body size of leptocephali suggested that the spawning season is from April to August, but further sampling is needed to eliminate possible effects of sampling bias. This analysis is consistent with the existing hypothesis that Japanese eel larvae born near the West Mariana Ridge are transported westward in the NEC and then transfer to the Kuroshio to recruit to East Asia, although more sampling effort is needed for later stage larvae in the NEC bifurcation region to help understand the larval migration in relation to the possible impacts of ocean–atmosphere changes.

Keywords Eel larvae · Leptocephali · *Anguilla japonica* · North Equatorial Current · Kuroshio · Larval dispersal

Introduction

The Japanese eel, *Anguilla japonica*, is a catadromous eel that migrates thousands of kilometers through the ocean back to its spawning area as adults (Tsukamoto 2009), and then its larvae, which are called leptocephali, must migrate to their continental growth habitats using ocean currents (Tsukamoto 1990; Tsukamoto et al. 2003a, b). Its spawning area is located offshore in the western North Pacific (WNP) subtropical gyre (Fig. 1; Tsukamoto 1992), in a similar location and ocean current system in relation to its juvenile growth habitats as the location of the spawning area of the American eel, *Anguilla rostrata*, in the Sargasso Sea region of the subtropical gyre of the western North Atlantic (McCleave 2003). The spawning area of *A. rostrata* overlaps with that of the European eel, *A. anguilla*, in the Sargasso Sea (McCleave et al. 1987), and it has been shown recently that the giant mottled eel, *Anguilla marmorata*, also spawns in an overlapping area with the Japanese eel (Miller et al. 2002a; Kuroki et al. 2009).

Due to the spawning area of *A. japonica* being located so far offshore, its larval phase is long compared to most other types of fishes and is also long compared that of some tropical anguillid eels

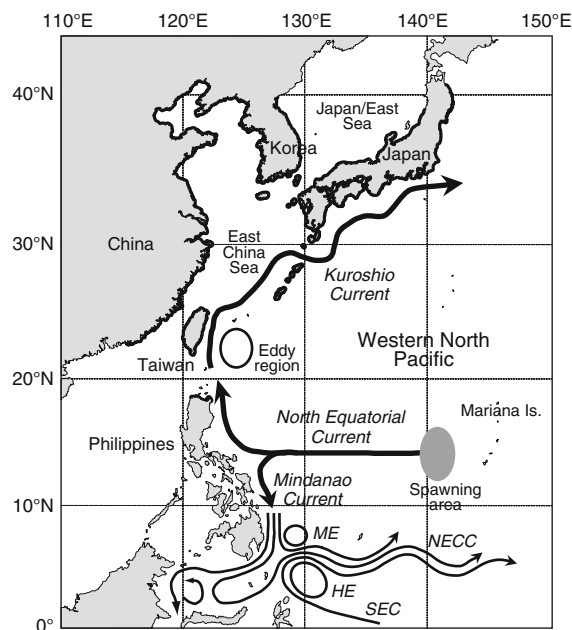


Fig. 1 Map of the western North Pacific region showing the general spawning area of the Japanese eel, *Anguilla japonica*, the coastline areas where it recruits and migrates into freshwater (black lines on coasts), and offshore ocean currents or eddies. The detailed patterns of currents are shown in the southern region (adapted from Lukas et al. 1991) where *A. japonica* leptocephali may be transported if they are entrained into the Mindanao Current instead of entering the northward flow into the Kuroshio Current and being transported to their recruitment areas. The North Equatorial Countercurrent (NECC), South Equatorial Current (SEC), Mindanao Eddy (ME), and Halmahera Eddy (HE) are also shown

(Marui et al. 2001) that have shorter spawning migrations (Aoyama et al. 2003). This larval dispersal migration is the first key event of the life history of anguillids, and the larvae of *A. japonica* grow up to about 60 mm as they migrate from their offshore spawning area to their growth habitats in the estuaries, freshwater rivers and lakes of East Asia (Tsukamoto et al. 2003a, b). In recent years however, most sampling effort has concentrated on locating the exact spawning sites of this species (Ishikawa et al. 2001; Tsukamoto et al. 2003a, b; Tsukamoto 2006, 2009). Due in part to this, the details about the distribution of its larvae and its long larval migration are still poorly documented compared to the literature about leptocephali of the Atlantic anguillid eels that presently includes detailed catch data from sampling surveys (e.g. Scoth and Tesch 1982; Wippelhauser et al. 1985; McCleave and Kleckner 1987; Kleckner

and McCleave 1988; Tesch and Wegner 1990; Munk et al. 2010), analyses of historical catch data (Boëtius and Harding 1985; Kleckner and McCleave 1985), reviews about the spawning areas and larval migrations (McCleave 1993, 2003; McCleave et al. 1998; Miller et al. 2009; Bonhommeau et al. 2010), and larval transport modeling studies (Kettle and Haines 2006; Bonhommeau et al. 2009a).

Part of this difference is that research effort started later in the Pacific and the spawning area of the Japanese eel was discovered many decades after the spawning area of the Atlantic eels. After the discovery of the spawning area of the Atlantic eels in the Sargasso Sea in the early 1900's (Schmidt 1922, 1925), the history of surveys to determine the spawning area of *A. japonica* began in the 1930's with some limited research effort occurring in regions near Japan (Tsukamoto et al. 2003a, b). The sampling efforts in the 1960's and 1970's were mostly in the region to the east of Taiwan and south of the Ryukyu Islands where only large leptocephali were collected between November and March (e.g. Tabeta and Takai 1975b; Takai and Tabeta 1976; Ozawa et al. 1991), as has been overviewed previously (Tsukamoto et al. 2003a, b). In the 1980's leptocephali of about 40–50 mm TL with an age of 67–78 days after hatching were collected in September 1986 in more southern waters east of Luzon Island of the Philippines, 15°56'–22°02'N, 122°25'–129°37'E (Kajihara 1988; Tsukamoto et al. 1989). This was followed by collections of several even smaller *A. japonica* larvae of 24–32 mm in a more eastern area, 15°46'–16°22'N, 132°59'–138°43'E, in June–July 1988 (Ozawa et al. 1989), and 21 small leptocephali of about 20–25 mm were collected in one haul at 16°17'N, 139°12'E in July 1990 (Ozawa et al. 1991). These collections of leptocephali offshore in the subtropical gyre provided evidence that the spawning area of the Japanese eel must be located further to the east.

The search for the general spawning area of *A. japonica* then ended in the North Equatorial Current (NEC) to the west of the Mariana Islands with the offshore collection of many small leptocephali in 1991 (Tsukamoto 1992). The 1991 survey included 6 north–south transects within a large area between 10–22°N, 131–155°E, and *A. japonica* leptocephali were collected in the 3 western transects. The biggest catch of more than 800 leptocephali that were mostly

about 10–20 mm in length occurred along 137°E, just south of a salinity front (Tsukamoto 1992). This showed that the spawning had occurred upstream to the east in the NEC. In 1994, many *A. japonica* leptocephali were again collected offshore in the region 13–17°N, 133–141°E (Mochioka et al. 1995). Then in 1998, leptocephali as small as 10 mm were collected near seamounts of the West Mariana Ridge suggesting spawning had occurred near the ridge (Ishikawa et al. 2001). More recently, only 2 day post-hatching larvae, called preleptocephali (pre-feeding larvae) were collected west of the Suruga Seamount of the West Mariana Ridge, which was the first determination of a precise spawning location of *A. japonica* (Tsukamoto 2006). Examinations of the otolith increments of these preleptocephali and of larger leptocephali (Ishikawa et al. 2001; Tsukamoto et al. 2003a) and the timing of capture of adult eels (Chow et al. 2009) in the spawning area have indicated that *A. japonica* spawns only during the new moon periods of each month during its spawning season.

However, from the point of view of understanding the larval migration of *A. japonica*, even the data that has been published recently about the distribution of the leptocephali (e.g. Kajihara 1988; Mochioka et al. 1995; Ishikawa et al. 2001; Tsukamoto et al. 2003a, b; Tsukamoto 2006, 2009) has been strongly biased in terms of seasonal coverage and the areas of sampling effort, because the goal of the research cruises was focused on finding the spawning area of *A. japonica*. Furthermore, most previous reports on the distribution of *A. japonica* leptocephali have been concerned with only a few research cruises at most (e.g. Ozawa et al. 1991; Ishikawa et al. 2001) or included maps of simple regional presence or absence of larvae (Tsukamoto et al. 2003a, b; Tsukamoto 2006, 2009), so there has been no detailed quantitative analysis of the historical distribution, larval size or sampling effort of studies on this important commercial species.

The objective of this study was to evaluate the historical sampling effort of surveys for leptocephali of the Japanese eel and to examine what the data from these collections show about the larval migration of this species from sampling surveys in the WNP up until the year 2007. It is important to evaluate what is known about the larval migration, because recruitment declines have occurred for this commercially-fished

species (Tatsukawa 2003; Tsukamoto et al. 2009a) and the other Northern Hemisphere anguillid species (Dekker et al. 2003; Miller et al. 2009). It is especially important for the Japanese eel because changes in ocean conditions such as the position of the salinity front near the spawning area, flow patterns of currents, or even changes in productivity could be affecting its recruitment by acting on the larvae during their migration (Kimura et al. 2001; Kimura 2003; Kim et al. 2007; Bonhommeau et al. 2008b; Miller et al. 2009; Zenimoto et al. 2009).

Materials and methods

Historical data

Historical catch data of leptocephali and glass eels of *A. japonica* collected from 1934 to 1992 were examined from 30 previously published papers from studies designed to collect leptocephali (Table 1). These surveys were mostly along the western margin of the WNP before 1990 (e.g. Tabeta and Takai 1975a, b; Kajihara 1988), and then further offshore in the NEC in later years, except for a survey in the East China Sea in 2000 (Otake et al. 2006). Extensive fisheries surveys using small plankton nets for larval fishes or other types of gear with larger mesh sizes in this region were not included in this study, because small plankton nets ≤ 1 m are not effective for sampling leptocephali due to net avoidance, which can also occur with large plankton nets during the day (Castonguay and McCleave 1987; Miller and McCleave 1994; Miller et al. 2006; Miller 2009). The exception to this is that some of the glass eel catches were from surveys using various types of gear (Shojima 1966, 1967; Tabeta 1981; Shojima 1990), but the negative station data from these surveys were not included in Fig. 2. Similarly, some early papers about *A. japonica* leptocephali conducted along the western margin of the WNP did not plot the negative stations that were also sampled, so these locations are also not shown in Fig. 2. For the studies that were included in the analysis, as many parameters as possible were obtained from the papers and the data were standardized into the categories of the collection date, location, type of net, towing methods, filtering

volume, numbers of larvae collected, total length, and the developmental stage of each specimen.

Original data

Sampling surveys for the larvae of *A. japonica* were carried out during a total of 11 cruises from 1994 to 2007 (Table 1). Larvae were mainly collected with the Isaacs Kidd Midwater Trawl (IKMT) and the 3-m ORI-BF (BigFish) ring net. The ORI-BF is a large ring net attached perpendicularly to the trawl wire that has a large weight on the end. The IKMT and the ORI-BF ring net had 0.5 mm mesh and an 8.7 m² and a 7.1 m² mouth opening, respectively. The nets were fished in step tows or oblique tows primarily in the upper 300 m during both night and day. Although sampling within the spawning area has continued after 2007, which has included additional collections of preleptocephali, these data were not included in the present study (see Tsukamoto et al. In press).

During the sampling surveys leptocephali and glass eels were sorted fresh from the plankton samples, measured to the nearest 0.1 mm total length (TL) and were preserved in 99% ethanol after being identified. Some larvae were damaged, so TL data could not be obtained from them. They were not included in analyses of TL, but they are included in analyses of abundance. They were identified as being *A. japonica* larvae on board cruises based on their morphological characteristics according to Tabeta and Mochioka (1988) and Miller and Tsukamoto (2004), or using DNA sequencing when their morphological characteristics were undeveloped in young larvae or uncertain in damaged specimens (Aoyama et al. 1999, 2003; Watanabe et al. 2004; Minegishi et al. 2009).

Geographic distribution

All historical collection data were analyzed together with recent data on the distribution of leptocephali and glass eels in the WNP. The details of the surveys included in the analysis and the number and size of the larvae they collected are shown in Table 1. The locations (latitude and longitude) of each sampling station were pooled into 1 degree data bins for analysis of the geographic distributions of the different stages of *A. japonica* larvae.

Table 1 List of cruises that collected Japanese eel larvae, showing their locations, dates, nets used, and the references of each study

Vessels (Cruises)	Year	Period (Date)	No. of specimens collected	TL (mm)		Location	Type of net	Reference
				PL	Meta larvae			
Tsuru Maru	1934	29 May	1**	24.8		39°00'N, 128°18'E	–	Uchida (1935)
Shunkatsu Maru	1956	25 June	1**	55.7		23°15'0N, 142°40.0E	1.5mR	Matsui (1957)
Koyo Maru	1956	12 Feb	18**	12.2–23.0		24°32.0N, 128°57.0E	4mR	Matsui and Takai (1971)
Shunyo Maru	1961	29 Nov–17 Dec	2	45.9, 50.0		17°20.7N, 128°42.8E	Conical Net	Ozawa et al. (1991)
Yoko Maru	1962	21 Feb		53.5	1	33°01.2N, 122°21.0E	Larva Net	Tsukahara (1971) cited in Tabeta (1981)
Tsuru Maru	1965	19 Feb		56.0	1	29°50'N, 124°42'E	Larva Net	Shojima (1966)
Tsuru Maru	1966	18 Feb		53.0	1	29°37'N, 125°20'E	Larva Net	Shojima (1967)
Tenyo Maru	1967	8 Nov	1	53.5		21°40.5N, 121°08.5E	IKMT	Matsui et al. (1968)
Kaiyo Maru	1967	5 Dec		56.9	1	29°55.5N, 127°22.9E	1.3mR	Tsukahara (1971) cited in Tabeta (1981)
Yoko Maru	1968	5 Mar		58.1	1	31°52.3N, 128°59.8E	Larva Net	Tsukahara (1971) cited in Tabeta (1981)
Shoyo Maru	1971	25 Sep–25 Oct	1	41.5		18°50.5N, 143°29.0E	Conical Net	Ozawa et al. (1991)
Hakuho Maru (KH-73-2)***	1973	20 Feb–27 Mar		54.2	1	21°56.5N, 116°42.0E	4mR	Tabeta and Takai (1975a)
Hakuho Maru (KH-73-2)***	1973	20 Feb–27 Mar	1	52.7		21°01.4N, 121°00.8E	4mR	Nishiwaki et al. (1974)
Hakuho Maru (KH-73-5)***	1973	21 Nov–18 Dec	49	47.3–58.7		20°14.5–23°40.3N, 125°01.1–129°59.9E	4mR	Tanaka (1975), Tabeta and Takai (1975b)
Hakuho Maru (KH-73-5)***	1973	21 Nov–18 Dec	3	53.1, 58.4, 60.2		20°14.5–23°40.3N, 125°01.1–129°59.9E	4mR	Tanaka (1975), Tabeta and Takai (1975b)
Hakuho Maru (KH-75-1)***	1975	9 Jan–7 Feb	2	55.2, 56.5		19°57.5N, 128°44.6E, 17°00.9N, 126°16.3E	4mR, 1.6mR	Takai and Tabeta (1976)
No. 2 Kyooyo Maru	1978	4 Dec	1	59.2		24°06.2N, 125°46.8E	IKMT	Tabeta and Konishi (1986)
Hakuho Maru (KH-86-4)***	1986	26 Aug–2 Oct	21	33.9–47.0		15°56.0–22°02.0N, 122°25.0–129°37.0E	IKMT, 1.6mORI, MTD, 4mH	Kajihara (1988), Tabeta and Mochioka (1987)
Yoko Maru	1987	3, 4 Dec	3	57.2, 58.4, 61.2		30°14.9–30°50.0N, 128°41.0–128°51.9E	RMT-Y6	Shojima (1990)
Keiten Maru	1988	Jun–Jul	7	24.0–31.8		15°46.1–16°21.8N, 132°59.8–138°42.4E	1.6mR	Ozawa et al. (1989)

Table 1 continued

Vessels (Cruises)	Year	Period (Date)	No. of specimens collected			TL (mm)	Location Latitude, Longitude	Type of net	Reference
			PL	Lepto	Meta Glass larvae eels*				
Hakuho Maru (KH-88-4)	1988	21 Oct	1		55.8	20°59.5N, 129°52.7E	IKMT	Tsukamoto et al. (1992b)	
Keiten Maru	1990	13 Jun–10 Jul	21		19.5–25.4	16°29.3N, 139°20.8E	1.6mR	Ozawa et al. (1991)	
Hakuho Maru (KH-91-4)***	1991	14 Jun–22 Jul	958		7.7–34.2	12°00–19°00N, 131°00–137°00E	IKMT, 1.6mORI, MTD	Tsukamoto (1992), Mochioka et al. (1994)	
Seisui Maru	1992	21 Nov	1		61.1	26°31.7N, 128°21.9E	1.6mORI	Tsukamoto et al. (1995)	
Hakuho Maru (KH-94-2)***	1994	16 Jun–7 Jul	1110		10.6–31.1	14°00N, 140°00E (96.4% of total catch)	IKMT, 1.6mORI, MTD	This study	
Tansei Maru	1994	7 Feb		1	56.9	31°54.8N, 132°24.4E	IKMT	Sakakura et al. (1996)	
Fishery Research I	1995	8–28 Aug	3		27.4, 28.8, 31.4	12°30–14°30N, 131°30–140°30E	IKMT, 1.6mORI	Liao et al. (1996, 1999)	
Hakuho Maru (KH-95-2)***	1995	7 Jul–27 Sep	130		13.0–40.0	13°00–16°00N, 137°00–141°00E	IKMT	This study	
Tansei Maru***	1996	20–28 Nov	9		49.5–58.3	20°59.7N–23°30.1N, 123°00.1–128°01.0E	IKMT	Otake et al. (2006)	
Suruga Maru***	1997	2–7 Jun			–	14°12–15°39N, 142°45–142°54E	IKMT	This study	
Fishery Research I	1998	10–26 Aug	3		41.3, 45.9, 48.3	20°58–23°55N, 122°36–130°57E	IKMT	Liao et al. (1999)	
Fishery Research I	1998	14–20 Sep	1		47.5	23°00N, 123°40E	IKMT	Liao et al. (1999)	
Fishery Research I	1998	4–10 Nov	2		56.0, 62.0	23°26N, 122°55E, 23°55N, 122°36E	IKMT	Liao et al. (1999)	
Hakuho Maru (KH-98-2)***	1998	22 May–2 Jul	24		10.0–26.0	16°31.4–15°36.3N, 142°44.5–143°14.9	IKMT, 1.6mORI	Otake et al. (2000)	
Suruga Maru***	1998	17 Aug–14 Sep	14		21.1–43.2	13°10–17°05N, 136°59–137°01E	IKMT	Ishikawa et al. (2001)	
Tansei Maru***	2000	27 Nov–8 Dec	9		51.3–57.0	26°01.9–30°00.2N, 125°12.5–129°00.4E	IKMT	Otake et al. (2006)	
Suruga Maru***	2000	14 Jul–4 Aug	14		10.0–19.0	13°40.4–13°44.5N, 140°29.6–140°42.6E	IKMT	This study	
Hakuho Maru (KH-01-2)***	2001	13–23 Jul			–	12°01–25°29N, 136°29–143°10E	IKMT, 1.6mORI	This study	
Yokosuka***	2001	20–24 Aug			–	14°11–19°29N, 142°41–143°11E	IKMT	This study	
Hakuho Maru (KH-02-4)	2002	7 Nov–18 Dec	1		42.8	4°58.3N, 129°59.3E	IKMT	Miller et al. (2004, 2009)	

Table 1 continued

Vessels (Cruises)	Year	Period (Date)	No. of specimens collected			TL (mm)	Location	Type of net	Reference
			PL	Lepto	Glass larvae				
Hakuho Maru (KH-02-2)***	2002	5 Jul–15 Aug	25			8.4–32.9	12°00–17°00N, 137°00–140°00E	IKMT, 1.6mORI	Kimura and Tsukamoto (2006)
Tansei Maru	2002	29 Oct–6 Nov	1			61.2	34°50.3N, 138°29.3E	IKMT	This study
Hakuho Maru (KH-04-2)***	2004	16 May–28 Jun	60			7.7–27.0	14°30–17°00N, 137°00–142°00E	IKMT, 1.6mORI	This study
Hakuho Maru (KH-05-1)***	2005	31 May–14 Jul	110			4.2–8.7	13°45–14°31N, 141°59–142°15E	3mORI-BF	Tsukamoto (2006)
Hakuho Maru (KH-05-1)***	2005	31 May–14 Jul	68			11.7–18.1	13°01–16°00N, 139°00–141°00E	3mORI-BF, IKMT	Tsukamoto (2006)
Hakuho Maru (KH-06-1)	2006	23 Feb	1			55.5	35°51N, 142°33E	MOHT (5.3 m ² RMT)	This study
Hakuho Maru (KH-06-2)***	2006	26 Jun–31 Aug	20			11.3–38.3	14°30–17°00N, 133°30–143°00E	3mORI-BF, IKMT	This study
Hakuho Maru (KH-07-2)***	2007	9 Aug–15 Sep	38			3.7–6.6	13°30–15°00N, 141°45–142°45E	3mORI-BF	This study
Total			148	2547	6	21			

The number and total length (TL) of each type of larvae is given for preleptocephali (PL), leptocephali (lepto), metamorphosing larvae (meta larvae), and glass eels. Various types and sizes (m = meter, diameter) of nets were used including the Isaacs Kidd Midwater Trawl (IKMT; 8.7 m² mouth opening) and various sizes of circular mouth opening ring nets (ORI, R, MTD, Conical net, Larva nets), or hexagonal (H) or rectangular (RMT) mouth opening nets. Latitudes and longitudes listed show the areas where larvae were collected during each survey, except for the cases where no larvae were collected that show the total sampling region

* Offshore catch

** Specimens were not *A. japonica* (Tabeta 1981), but were originally reported to be

*** Negative net tow station data included in the analysis

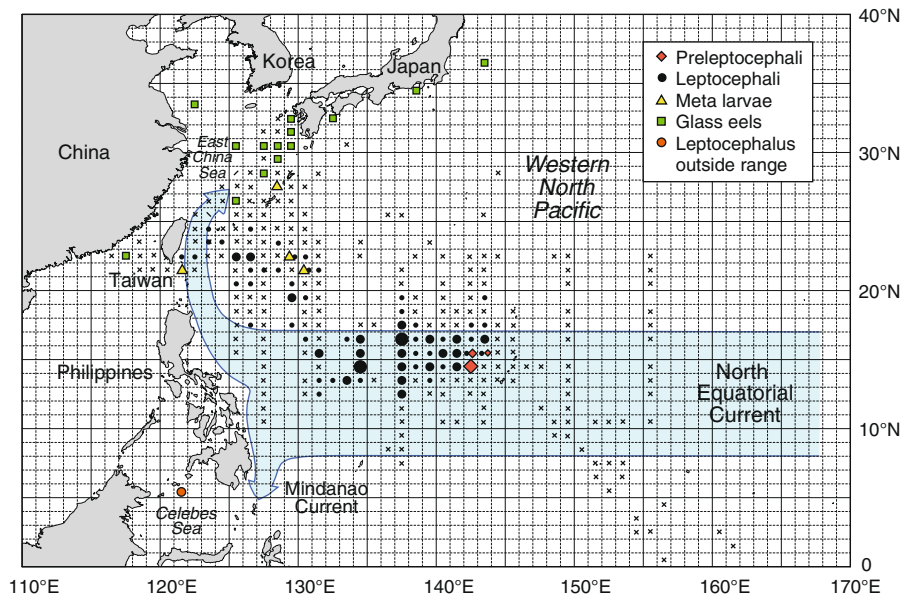


Fig. 2 Distribution of *Anguilla japonica* larvae from 1961 to 2007, with data pooled by every 1° of latitude and longitude. Different larval stages are shown with symbols: circles, leptocephali of any size; diamonds, preleptocephali collected in 2005 and 2007; triangles, metamorphosing leptocephali; squares, glass eels; crosses, negative stations. Symbol sizes of preleptocephali and leptocephali correspond to the total number of *A. japonica* larvae collected in each 1° square:

small, from 1 to 9 individuals; medium, from 10 to 99; large, over 100. The symbols for metamorphosing leptocephali and glass eels represent from 1 to 3 individuals. The blue shading shows the approximate region of the unbroken westward flow of the North Equatorial Current between 8 and 17°N (Reverdin et al. 1994; Kaneko et al. 1998), but the latitude of bifurcation into north and south currents can change seasonally and annually (Kim et al. 2004; Zenimoto et al. 2009)

Relative abundance

Because of the large variation in sampling methods among the cruises, we used two types of catch rate estimations. One was a simple value that was calculated as the numbers of specimens collected in each 1 degree square of latitude and longitude divided by the number of tows in the same area (inds./tow), which allowed a complete geographic coverage of the regions that have been sampled for leptocephali. The other was calculated from the number of specimens and the filtered water volume of each net tow. In those cases, the numbers of leptocephali at a station were converted to catch rates expressed as the number of individuals (inds.) per 10^5 m^3 of water filtered by the net (inds./ 10^5 m^3), using the flow meter revolutions, a calibration factor and the trawl mouth area (m^2), as has been done in previous quantitative studies on leptocephali catches (e.g. Kleckner and McCleave 1988; Miller and McCleave 1994, 2007; Miller et al. 2002b, 2006). This type of catch rate was used for the data collected by the 1.6 m-ORI net, MTD net

(Motoda-type multiple layer closing net), IKMT and ORI-BF net from 16 cruises (KH-86-4, KH-91-4, KH-94-2, KH-95-2, KH-98-2, KH-01-2, KH-02-2, KH-05-1, KH-06-2, KH-07-2, KT-96-19, KT-00-16, Suroga 97, 98, 00, and Yokosuka 2001). It was not feasible however, to distinguish between different types of towing methods during these cruises, so a general catch rate was calculated that includes both oblique and horizontal towing styles.

Body size versus day of collection

To evaluate if the general growth rate or mean hatching date of *A. japonica* leptocephali could be estimated from the historical catch data examined in this study, we calculated a linear regression between the TL and collection dates (Julian day) of the leptocephali. 1 January was defined as day one, and we assumed that large larvae (>50 mm) and juveniles collected from January, February and March were hatched in the previous year and added 365 days to their collection dates. Since anguillid eel leptocephali

decrease in TL during metamorphosis, we used only pre-metamorphosis leptocephali for this analysis.

Results

Geographic distribution

A total of 148 preleptocephali, 2,547 leptocephali, 6 metamorphosing larvae and 21 oceanic glass eels were collected in 37 cruises during a 52-year period in the WNP and marginal seas up until 2007 (Table 1). The geographic distribution of larvae was spread across a wide region of the WNP, but compared to the vast region of the WNP subtropical gyre, the larvae were only present in a very limited range of areas (Table 1, Fig. 2). There was a distinct lack of extensive sampling to the east and northeast of the Philippines though, in the region where larger larvae would likely be present, so various gaps are visible in the map in Fig. 2.

Examination of the data by larval stages shows clear geographic separations of the earliest and latest stages. The distribution of preleptocephali was limited to only a narrow area around 14°N, 142°E within the spawning area, just west of the Suruga Seamount of the West Mariana Ridge (Fig. 2), with the catches in June of 2005 being reported by Tsukamoto (2006) and catches also being made in August of 2007 (Tsukamoto et al. In press). In contrast to the distribution of preleptocephali, leptocephali were widely distributed in the area of 12–19°N, 131–143°E, which corresponds to the typical latitude of the main part of the NEC, and in the area east of Taiwan around 20–24°N, 122–132°E (Fig. 2). Generally, leptocephali have not been reported in other regions, although many fisheries-related surveys have widely covered the western North Pacific. The only leptocephalus of *A. japonica* that has been collected outside of its expected region of distribution was a 42 mm specimen collected in the Celebes Sea by an IKMT at 5°N, 121°E (Fig. 2; Miller et al. 2009).

The later stages of *A. japonica* larvae have also been rarely collected based on existing literature and surveys for eel larvae. Only six metamorphosing larvae were reported in the literature up to 1992, collected in the limited area of 21–26°N, 121–129°E east of Taiwan (Fig. 2). Collections of oceanic glass eels ($N = 21$) have only occurred in or to the west of

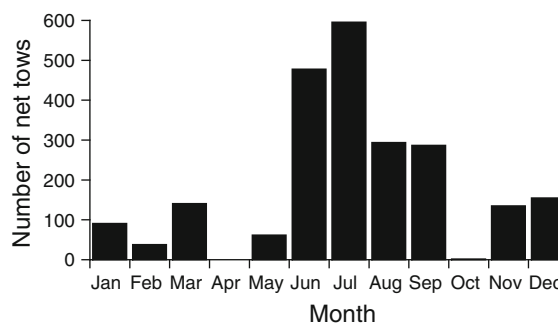


Fig. 3 Frequency distribution of the number of tows during each month of the year that were made during sampling surveys for collecting *A. japonica* larvae in the western North Pacific

the Kuroshio Current (Fig. 2; Sakakura et al. 1996; Otake et al. 2006), and one was caught at 31°N, 143°E in the Kuroshio Extension region in 2006 (Fig. 2; Table 1). The biggest catches of glass eels were made in late November and early December of 2000, when 9 early stage glass eels were collected in the Kuroshio Current region of the East China Sea (Fig. 2; Otake et al. 2006).

Seasonal distribution of sampling effort

The sampling effort for Japanese eel larvae was greatest in summer, with a substantial amount of sampling also occurring in winter months (Fig. 3). Very few tows were made during April and October up to 2007. A total of 1,717 net tows (75% of total net tows) were carried out in the summer season (May–Sep) and 563 net tows (25% of total net tows) in the winter season (Oct–Mar). The locations of net tows were concentrated within the region of 13°–17°N, 134°–143°E in the summer season, and around 22°N, 126°E in the winter season (Fig. 4). These two large efforts corresponded to sampling in the waters east of Taiwan in the winter season and in the area around the West Mariana Ridge in summer near the spawning area during the spawning season.

Size of larvae

The sizes of the different stages of larvae varied greatly with preleptocephali (prefeeding larvae with an oil globule) being 5.4 ± 0.7 mm in mean TL \pm SD (range: 3.7–8.7 mm), leptocephali 18.6 ± 8.2 mm (7.7–62.0 mm), metamorphosing larvae 56.9 ± 3.6

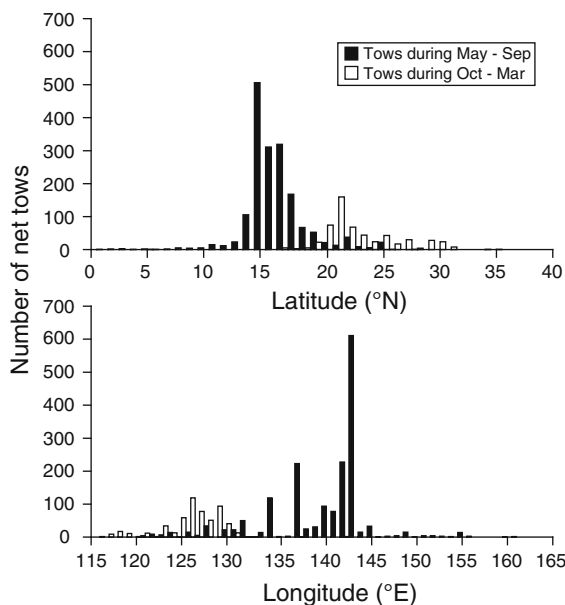


Fig. 4 Frequency distributions of the number of tows made at different latitudes and longitudes during the summer season (May–September, *black bars*) and winter season (October–March, *open bars*) during sampling surveys for collecting *A. japonica* larvae in the western North Pacific. *Upper panel* shows every 1° of latitude, *lower panel* shows every 1° of longitude

mm (52.7–61.2 mm), and glass eels 55.8 ± 2.7 mm (51.3–61.2 mm) (Table 1; Fig. 5). The length frequency distribution of leptocephali showed two peaks around 12 and 21 mm, each corresponding to the large catches of the Hakuho Maru cruises in 1991 (958 leptocephali 7.7–34.2 mm) and 1994 (1110 leptocephali 10.6–31.1 mm) (Table 1 and Fig. 5). The big catches in July 1991 were greatest just to the south of a salinity front that was thought to influence the location of spawning of *A. japonica* as reported by Tsukamoto (1992). At the larger larval size ranges, the leptocephali, metamorphosing larvae and glass eels overlapped in TL between 51 and 61 mm, suggesting that the Japanese eel may start metamorphosis at around 60 mm.

Analysis of the geographic distribution of all sizes of Japanese eel larvae shows that they increased in size with increasing latitude and in the westward direction of longitude (Fig. 6). Gaps in the presence of intermediate sized larvae between 30 and 40 mm were observed at latitude 19°N and longitude 130°E, which corresponds to the western region of the NEC before its westward flow begins to bifurcate. The

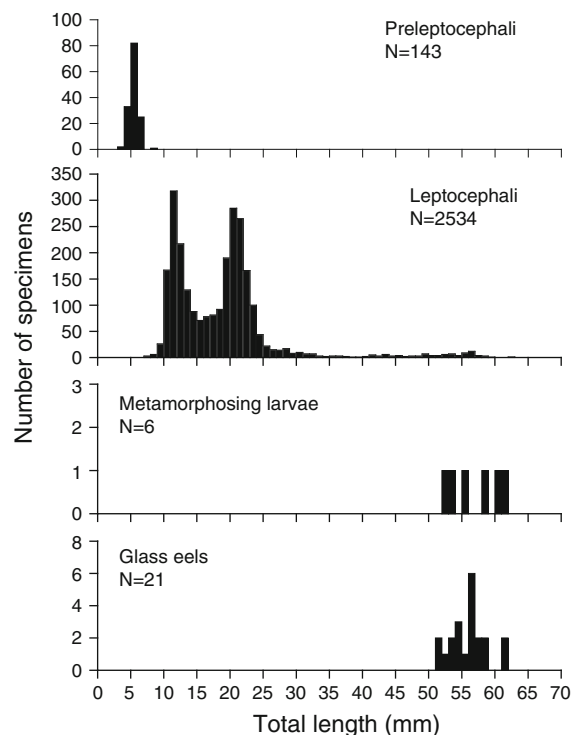


Fig. 5 Length frequency distributions of each developmental stage of *A. japonica* larvae collected during 1961–2007 surveys in the western North Pacific

larger specimens (>30 mm) occurred in the Kuroshio region or east of Taiwan. The smallest TL values show the locations of preleptocephali that were collected along 142°E at a latitude of 14°N.

Catch rate of larvae

The catch rates of larvae in each 1-degree latitude-longitude square calculated as mean individuals/tow were generally low except for some areas in the NEC region, and a few areas further to the northwest in the plot of Fig. 2. The catch rates plotted by latitude and longitude showed two areas of higher catches corresponding to the NEC and the region east of Taiwan in latitude, but only the longitudes corresponding to the NEC showed higher catch rates (Fig. 7).

The catch rates calculated based on volume of water filtered were spread out over a wide range of values (Fig. 8), with relatively high values being present in the area around 15°N and 135°E to the west of the estimated spawning area located along the southern part of the West Mariana Ridge (Fig. 7). The

Fig. 6 Box plots of total length of *A. japonica* larvae in each 1° square of latitude (*left panel*) and longitude (*right panel*) in the western North Pacific

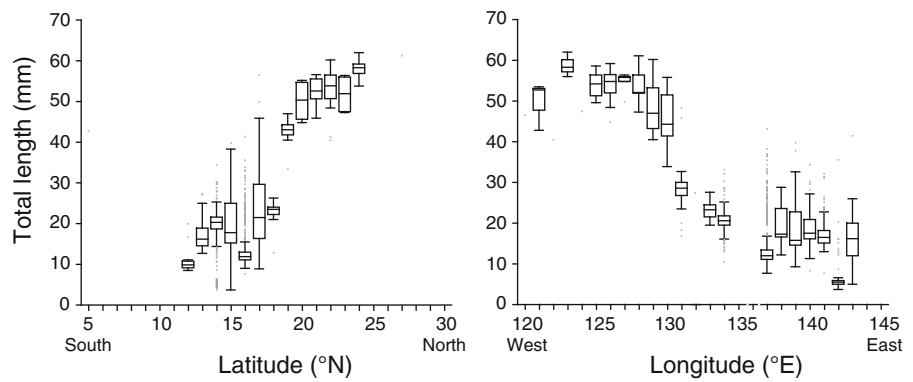


Fig. 7 Frequency distributions of catch rates per tow (individuals/tow) of *A. japonica* in each 1° square of latitude (*left panel*) and longitude (*right panel*) in the western North Pacific

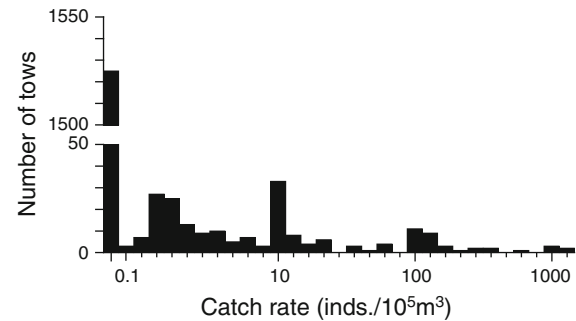
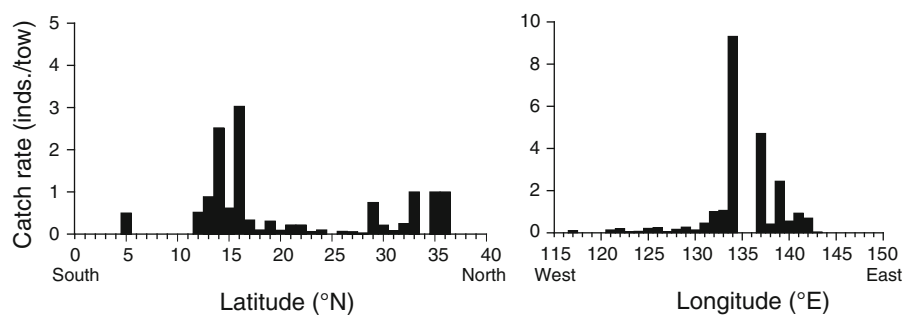


Fig. 8 Frequency distributions of catch rates for *A. japonica* larvae per 10^5 m^3 of water filtered (individuals/ 10^5 m^3) in all tows during 1986 to 2007. Note that catch rates are plotted on a log scale, with the highest interval being pooled as 1000–2000 individuals/ 10^5 m^3

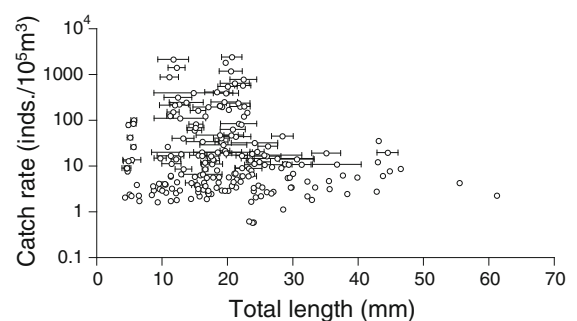


Fig. 9 Scatter plot of total lengths and catch rates of *A. japonica* showing individual larvae (1 specimen caught in a tow) and mean values when more than one was caught in a tow (*bars* show standard deviation)

catch rates of each tow ranged between 0.6–2,410.1 inds./ 10^5 m^3 , with 1,525 of the 1,727 tows (88.3% of total tows) not catching any larvae. Only 34 tows (2.0% of total tows) showed catch rates higher than 100 inds./ 10^5 m^3 (Fig. 8). These 34 tows were made during 1–2 July 1991 at 16°N, 137°E (12 tows), 21–22 June 1994 at 13°N, 133°E (3 tows) and at 14°N, 134°E (17 tows), 24 July 1995 at 13°N, 137°E (1 tow), and

10 June 2005 at 14°N, 142°E (1 tow). These tows collected a total of 1,963 preleptocephali and leptocephali, which accounts for 70.5% of the larvae collected. There was no clear relationship between the TL of larvae within a tow and the catch rate, but the larger specimens (>30 mm) were only caught at low catch rates (Fig. 9). The highest catch rates were of specimens between about 10 and 25 mm.

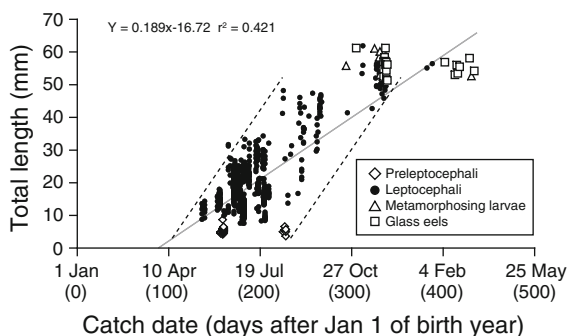


Fig. 10 Scatter plot and regression (grey line) of total length and catch date of the 4 different stages of *A. japonica* larvae, which are shown with different symbols. Catch date is shown as days after January 1 of the birth year (Julian date). The dashed lines qualitatively show the slope of lines representing a growth rate of 0.4 mm/day, as discussed in the text

Larval size versus collection date

The collection dates (Julian dates) of each developmental stage of *A. japonica* larvae ranged from 7–10 June (day 157–160) and 14–18 August (225–229) for preleptocephali, from 16 May–24 January (136–388) for leptocephali, from 21 October–7 March (294–431) for metamorphosing larvae, and from 2 November–10 March (305–434) for glass eels (Fig. 10). Preleptocephali and small leptocephali (<10 mm) were collected from 16 May to 18 August (136–229). The linear regression of TL (Y ; mm TL) and collection dates of leptocephali (X ; Julian date) was: $Y = 0.197x - 17.49$ ($r^2 = 0.489$, $P < 0.001$, Fig. 10).

When the TL of larvae at hatching is defined as 3 mm (Yamamoto and Yamauchi 1974; Tanaka et al. 2001), the mean hatching date based on the X-axis intercept of the regression line was 15 April (day 104). The growth rate of *A. japonica* leptocephali estimated from the slope of the regression line was 0.20 mm/day or 5.9 mm/month. However, as discussed later, both of these estimates do not appear to be very accurate due to biases in the catch data used in the regression.

Discussion

Larval distribution and transport

The examination of the collection records and catch data of 2,722 specimens of all the larval stages of the

Japanese eel in the last 50 years presented here provides the first detailed overview of the sampling effort and what has been learned about the larval migration of this important East Asian catadromous fish species. This analysis showed that the various stages of larvae have been collected over a wide area to the west of the West Marina Ridge, but none have been collected to the east of the ridge (Fig. 2). The preleptocephali were only collected at the eastern edge of the larval distribution area, metamorphosing larvae were only collected at the western edge of the WNP, and glass eels were only collected in the East China Sea or along the Pacific coast of Japan. Leptocephali were clearly collected only in the northern region of the westward flow of the NEC (Fig. 2), which extends as far south as 8°N (Reverdin et al. 1994; Kaneko et al. 1998). This pattern of distribution of the different stages of larvae is consistent with the present view of the early life history of this species, which is thought to spawn in the NEC with their larvae being transported westward where they enter the northern branch of the NEC bifurcation before being transported northward by the Kuroshio (Fig. 1; Tsukamoto 1990, 1992; Tsukamoto et al. 2003a, b; Kimura et al. 1994, 2001; Zenimoto et al. 2009).

The limited area in which the smallest size of *A. japonica* leptocephali or preleptocephali have been collected support the hypothesis that the spawning area of this species is small in size as was proposed by Tsukamoto (2006). All but one of the small larvae <20 mm were collected from 12–17°N, which corresponds to being within the latitudinal range of the westward flow of the NEC (Reverdin et al. 1994; Kaneko et al. 1998; Kawabe and Taira 1998), with the region to the north consisting of alternating east and west flowing currents and countercurrents (Kaneko et al. 1998; Qiu and Chen 2010). The longitudinal range of <20 mm leptocephali was somewhat wider though, from 136–143°E, suggesting some variations in spawning location or in the speed of early larval transport from the area near the West Mariana Ridge where preleptocephali have been collected, as has been suggested by modeling studies of larval transport (Kim et al. 2007; Zenimoto et al. 2009).

The spatial distribution of the *A. japonica* larvae as they get larger showed a clear pattern of an increase in latitude and a westward shift in longitude with greater TL (Fig. 6). However, in Fig. 2 it is

evident that there has not been enough sampling in areas east of the Philippines to be able to know much about the size and distribution of leptocephali as they enter the bifurcation region of the NEC. The steady westward flow of the NEC is known to split into northward and southward flows in this region (Fig. 1; Toole et al. 1990; Qiu and Lukas 1996), with the latitude of this bifurcation shifting with season and among years (Qu and Lukas 2003; Kim et al. 2004; Zenimoto et al. 2009). The larvae of the Japanese eel must enter the northward flow that enters the Kuroshio, and they must avoid the southward flow that becomes the Mindanao Current (Fig. 1), which flows into the Celebes Sea (Lukas et al. 1991). The strong northward flow originating from the NEC is very close to the eastern margin of the Philippines (Kashino et al. 2009), but there has been no sampling for leptocephali in this area of strong flow (Figs. 1, 2). There also have been few tows during the season when larvae should be entering the western bifurcation region, and fewer tows in general there compared to further east near the spawning area (Figs. 3, 4). This lack of sampling in the western areas of the NEC has resulted in few leptocephali >30 mm being collected in comparison with smaller sizes (Fig. 5).

The NEC bifurcation region may be a key area for influencing the recruitment success of the Japanese eel based on the fact that climate related factors can affect both the currents in this region and the latitude of spawning (Kimura et al. 2001; Kimura and Tsukamoto 2006; Miller et al. 2009; Zenimoto et al. 2009). It has been hypothesized that the larger leptocephali use diel vertical migration into shallow layers near the surface at night as they enter the bifurcation zone to increase their northward transport towards the Kuroshio Current system due to Ekman transport (Kimura et al. 1994), and this may be facilitated by an increase in buoyancy that has been observed in the larger sized leptocephali of this species recently (Tsukamoto et al. 2009b). This hypothesis has not been tested, so it is presently unclear how leptocephali enter the northward flow that transports them towards their recruitment areas. Modeling studies have shown that a slight decrease in the latitude of spawning has the potential to greatly reduce the number of larvae that enter the northward branch of the NEC, due to much greater entrainment into the Mindanao Current (Kim et al. 2007;

Zenimoto et al. 2009). This southward shift in spawning is thought to occur when a salinity front that may be used by migrating silver eels as a cue to stop migrating and form spawning aggregations shifts southward (Kimura et al. 2001; Kimura and Tsukamoto 2006; Tsukamoto 2009).

This southward shift of the salinity front appears to frequently occur during El Niño years as a result of reduced tropical precipitation, and has shown evidence of being correlated with glass eel recruitment in southern Japan (Kimura et al. 2001). It is also apparent in Fig. 2 that there has been a lack of sampling effort in the Mindanao Current area where larvae that enter the wrong current would be distributed. There is proof that entrainment into the Mindanao Current sometimes occurs though, because a 42 mm *A. japonica* leptocephalus has been collected in the Celebes Sea in November 2002 (Fig. 2; Miller et al. 2009). Japanese eel leptocephali have not been collected in other larval sampling further south in the Celebes Sea though (Aoyama et al. 2003; Kuroki et al. 2006) and glass eels have not been detected yet in studies on recruiting glass eels on northern Sulawesi Island (Arai et al. 1999, 2001; Sugeha et al. 2001), so how many *A. japonica* larvae enter the Celebes Sea is unknown.

The potential importance of the bifurcation region in determining possible southward transport into the Celebes Sea and for influencing recruitment indicate that future sampling effort needs to target the bifurcation region to fill in gaps in our knowledge about this critical period of the larval migration. For example, if the potentially greater buoyancy of leptocephali (Tsukamoto et al. 2009b) in this region causes a more shallow depth distribution and northward Ekman transport as has been hypothesized (Kimura et al. 1994), this may reduce the huge losses of larvae that are suggested by modeling studies to occur in some circumstances (Kim et al. 2007; Miller et al. 2009; Zenimoto et al. 2009). However, these modeling studies have not simulated the transport of larvae at depths shallower than 50 m, and little is actually known about the depth distributions of leptocephali in the bifurcation region or elsewhere. Out of 31 papers published about collections of *A. japonica* larvae, only two have reported on the vertical distributions of the larvae (Kajihara et al. 1988; Otake et al. 1998). Because of the potential importance of the NEC bifurcation region for larval

migration success of the Japanese eel, studies of vertical distribution of *A. japonica* leptocephali in this region are needed along with surveys of leptocephali in the Mindanao Current to be able to obtain a better understanding of the annual fluctuations of glass eel recruitment in East Asia.

Area of leptocephalus metamorphosis

The present study found that only a few metamorphosing larvae of *A. japonica* have been collected and reported in the literature, so more information is needed about this aspect of the larval migration of this species. The few metamorphosing leptocephali included in the present study were collected either far offshore southeast of Okinawa, near Taiwan, or just northeast of Okinawa (Fig. 2). A similarly small number of metamorphosing American eel leptocephali have been reported in the North Atlantic, with some being caught after they moved to the west out of the Gulf Stream and few being caught offshore (Kleckner and McCleave 1985). In contrast however, no metamorphosing leptocephali of *A. japonica* have been collected on the west side of the Kuroshio (Figs. 1, 2).

Additional evidence that metamorphosis of *A. japonica* larvae may typically occur before they enter the Kuroshio in the East China Sea comes from a larger number of metamorphosing leptocephali ($N = 19$; 51.4–59.2 mm) that have been collected recently in the region to the east of Taiwan during 8–13 November 2004 (N. Mochioka unpublished data). This region often contains large eddies (Hasunuma and Yoshida 1978) and has a high degree of eddy variability (Qiu and Chen 2010). The large eddies appear to frequently interact with flow of the Kuroshio as it passes by the east coast of Taiwan (Yang et al. 1999). In this region just east of Taiwan and Luzon Island of the northern Philippines at longitudes of 122–125°E where the strongest northward current flows are likely to be present, the scarcity of tows make it difficult to determine what proportion of leptocephali may actually get entrained into the eddy region east of Taiwan compared to those that get transported directly into the Kuroshio. The leptocephali that reach this area have likely achieved appropriate sizes to begin metamorphosis, so future research in these areas will be important for helping to improve understanding of what triggers metamorphosis in this species.

Evidence from otolith studies suggest however, that the age at which metamorphosis is triggered in this species may vary by at least 2 months, which may be related to different speeds or routes of transport or the amount of time trapped in eddies. Although little has been reported about metamorphosing *A. japonica* leptocephali, the age at which metamorphosis occurs and its duration have been estimated using the otolith microstructure of their glass eels. Fully grown leptocephali of this species ($N = 5$, 49.8–58.3 mm), presumably just before metamorphosis, that were collected to the east of Taiwan in November 1996 were aged at 94–134 days old using their otoliths, and glass eels collected at Tanegashima Island, Japan in December of the same year were estimated to have begun metamorphosis at ages of about 100–160 days (Arai et al. 1997). Mean ages at metamorphosis at several sites across the species range were reported to range from 115.8 to 137.8 days using glass eel otoliths (Cheng and Tzeng 1996). Another more extensive study found mean ages of metamorphosis of *A. japonica* that ranged from 100.8 to 138.8 days for glass eels from 10 sites (Shinoda 2004).

Presently no glass eels of *A. japonica* have been collected offshore outside of the East China Sea, except for a few along the east coast of Japan (Fig. 2). The biggest single catch was made in late fall and early winter of 2000, when 9 early stage glass eels were collected in the East China Sea within or close to the flow of the Kuroshio (Fig. 2; Otake et al. 2006). Due to the strong velocities of the current in this region these larvae likely began metamorphosis much further south from where they were collected, and possibly even outside of the East China Sea in the far western part of the WNP. Therefore, the locations of glass eel collections and those of metamorphosing larvae suggest that metamorphosis in the Japanese eel is completed after they enter the Kuroshio, but there probably has not been enough sampling with large sized plankton nets along the western margins of the WNP to determine this for certain.

Density of leptocephali

The spatial and temporal patterns of larval density of the Japanese eel along its migration route in the NEC and Kuroshio Current system were examined in the present study, but it was clear that there have been

significant spatial and temporal gaps in sampling effort and problems with a lack of standardization of towing methods. The analyses of fishing effort and catch rates showed that the number of tows made during each month of the year was heavily skewed towards the summer months, and the locations of most of the tows were concentrated at longitudes near the spawning area (Figs. 3, 4). The actual catch rates calculated based on amount of water filtered by each tow varied widely from 0 for a majority of tows, to as high as 1000–2000 inds./ 10^5 m³ (Fig. 8). For the tows that did collect leptocephali, most nets had catch rates of ≤ 10 inds./ 10^5 m³, with a lesser number of tows having rates as high as 100 inds./ 10^5 m³; which are values in a similar range to previous studies that collected anguillid leptocephali in the Sargasso Sea (Wippelhauser et al. 1985; Kleckner and McCleave 1982, 1988; McCleave and Kleckner 1987) or the western South Pacific (Miller et al. 2006).

Much of the variability in catch rates in the present study was likely due to either sampling in areas both inside and outside of where the larvae were distributed and also the different types of nets or towing techniques used in the various sampling surveys. The various sampling techniques have included different fishing depths and towing methods such as basic oblique tows and oblique tows with the net being towed horizontally at one or more depth layers (step tows). The towing time at a particular depth or how deep the net reaches during each tow can greatly affect the relative amount of fishing time in the depth layers where anguillid leptocephali are most abundant, which is generally in the upper 100 m at night (Castonguay and McCleave 1987; Kajihara et al. 1988; Otake et al. 1998; Miller 2009). For example, the catch rate values as high as 1000–2000 inds./ 10^5 m³ observed in the present study are much higher than the catch rates of anguillid or leptocephali of other anguilliform taxa in previous studies (Wippelhauser et al. 1985; Kleckner and McCleave 1988; McCleave and Kleckner 1987; Miller and McCleave 1994, 2007; Miller et al. 2006). These were the result of horizontal tows focused in areas and at depths where high densities of *A. japonica* leptocephali were expected. Even higher catch rates of anguillid leptocephali were reported by Schoth and Tesch (1982) in the Sargasso Sea in areas where recent spawning had occurred, but that study reported their catch rates based on the amount of time that the net

was towed at the depths thought to be preferred by the larvae, and not on the total amount of time that the net fished during each deployment as was done in other studies.

Other factors affecting the catch rates of *A. japonica* larvae in the present study are that, depending on exactly where and when spawning had occurred during each particular month, the distribution of leptocephali may be very patchy, with leptocephali being abundant only in certain areas at certain times (Tsukamoto 1992, 2006). This concept is supported by the many no-catch tows, the low number of tows that had high catch rates, and the very high catch rates observed in some targeted tows in areas of high leptocephali densities. The two major factors contributing to the occurrence of many no-catch tows seem to be that the Japanese eel spawns only during new moon periods, and that the spawning area often shifts to the south as discussed previously. The pattern of new moon spawning of this species has been shown by catches of adults (Chow et al. 2009) and preleptocephali (Tsukamoto 2006) near new moon and from back-calculated hatching dates from the otoliths of leptocephali (Ishikawa et al. 2001; Tsukamoto et al. 2003a; Tsukamoto 2006). As a result of the new moon spawning time, most sampling within the spawning area far before new moon will not catch any larvae, because the larvae spawned in the previous month will have been transported further to the west. Similarly, if sampling was targeted at higher latitudes where catches were made in previous years, but spawning had shifted to the south during that particular month or year such as in 2002 (Kimura and Tsukamoto 2006), then most tows would be negative. Some tows also have been made specifically in areas to show the absence of spawning as well.

Spawning time and growth rate

The analyses of all the larvae of the Japanese eel that have been collected up until 2007 allowed an evaluation of their spawning season and the subsequent growth of the larvae based on the time of capture of the different sizes of larvae (Fig. 10). The plot of larval length vs catch date suggested the spawning season may start in April and extend at least until August based on the size of the earliest collected leptocephali in May and the collection of

preleptocephali in 14–18 August 2007. The collections of preleptocephali (within 1 week after hatching) were limited to only June and August, and small leptocephali (less than 10 mm; within 2 weeks after hatching) appeared from May to August (Fig. 10). The mean day of hatching estimated from the regression line does not appear to be correct however, because as discussed below the slope of the regression line appears to be biased and not accurately representing the true growth rate of the leptocephali.

An estimate of a spawning season of about April to August however, is roughly consistent with the analyses of daily otolith increments in *A. japonica* leptocephali that found hatching dates from May to July (Tsukamoto et al. 1989; 1992a; Liao et al. 1996; Tsukamoto et al. 1998; Ishikawa et al. 2001). Some spawning of the Japanese eel may continue through the autumn season, as suggested by otolith ageing studies on glass eels (Tsukamoto 1990; Cheng and Tzeng 1996; Shinoda 2004); but the mismatches between spawning times estimated from the catch data of small leptocephali in the Atlantic and from the ages of glass eels estimated from their otoliths (McCleave 2008) indicate that hatching dates estimated from glass eels are probably not accurate indicators of spawning times in all individual glass eels. This is supported by the observations that low temperature can cause otolith deposition to stop in glass eels in the laboratory (Umezawa and Tsukamoto 1991; Fukuda et al. 2009) or affect otolith growth patterns in wild anguillid larvae migrating through cold waters (Kuroki et al. 2008).

As was the case for evaluating the possible spawning season, estimates of the overall growth rates of leptocephali from regressions using multi-year collection data are also likely not very accurate. The regression line generated from the lengths and catch dates of the leptocephali in Fig. 10 of the present study is likely not a good representative of the growth rate of these larvae for at least two reasons. One reason is the lack of many larvae in the 35–60 mm size range in the late summer and fall; and the other reason is that otolith analyses have shown that the growth rates of anguillid leptocephali appear to slow down greatly as the larvae reach their maximum sizes (Kuroki et al. 2006). These two factors, and a potential bias from the large number of leptocephali from the two surveys in 1991 and 1994, resulted in the growth rates estimated from the

regression line (0.20 mm/day) in Fig. 10 being much lower than the growth rates of *A. japonica* leptocephali estimated from otolith studies examining daily growth increments (0.43–0.56 mm/day; Tsukamoto and Umezawa 1990; Ishikawa et al. 2001; Shinoda 2004). Lines with slopes corresponding to a more reasonable minimum growth rate of 0.4 mm/day are also shown qualitatively in Fig. 10, which suggest the catch data in the present study are roughly consistent with the growth estimates obtained from otolith studies.

Estimates of the growth rates of anguillid leptocephali using historical catch data in the Atlantic also have been slower than the growth rates estimated from otolith increments of leptocephali. Regression of lengths and catch dates of historical collections of American eel leptocephali found an estimated growth rate of 0.24 mm/day (Kleckner and McCleave 1985). Other estimates of the larval growth rates of both species of anguillid leptocephali in the Atlantic using various analyses of larval length data were similarly low or even lower (Boëtius and Harding 1985; Tesch 1998). The only otolith aging study done so far on the Atlantic eel leptocephali found a higher growth rate of 0.38 mm/day (Castonguay 1987). This slightly lower growth rate than that from otolith studies on *A. japonica* leptocephali may be due in part to the colder water temperatures in the Sargasso Sea spawning area of the Atlantic eels (see Kleckner and McCleave 1988), which is located at a higher latitude than the spawning area of the Japanese eel.

Comparisons of the different types of assessments of larval growth rates in both oceans however, suggest that due to spawning of these anguillids occurring over a period of several months and growth rates slowing down at larger sizes as noted for both the Atlantic (Boëtius and Harding 1985) and Indo-Pacific (Kuroki et al. 2006) species of anguillid leptocephali, an accurate estimate of the larval growth can not be typically obtained from plots of larval length and catch date. It has also been hypothesized that the larval growth rates of anguillid leptocephali may be related to the distance of migration of each species, with species with shorter migration loops having faster larval growth rates than those with longer migration loops (Kuroki et al. 2006). There has only been one small study on the age and growth of Atlantic eel leptocephali (Castonguay 1987) however, and a relatively low number have

been examined for anguillid leptocephali in the Pacific as well. This indicates that more otolith studies using larger sample sizes and a wider size range of leptocephali are needed to confirm the larval growth rates of the Japanese eel and also for the Atlantic eels, which have been studied even less.

A greater understanding of the larval ecology of the Japanese eel and also of the Atlantic eels is important so the possible impacts of ocean–atmosphere changes in the regions where they develop during their larval migration can be evaluated. It is presently unknown if changes in productivity in the ocean can affect the growth rate of *A. japonica* or other species of anguillid leptocephali (Knights 2003; Friedland et al. 2007; Bonhommeau et al. 2008a, b; Miller et al. 2009), and so far there has only been one preliminary estimate of mortality rates of these larvae during their migrations (Bonhommeau et al. 2009b). Some useful information is beginning to be obtained from artificially spawned and reared *A. japonica* leptocephali (Tsukamoto et al. 2009b; Yamada et al. 2009), but clearly much more information about all aspects of the ecology of anguillid leptocephali during their long migrations from their offshore spawning areas to their recruitment areas is needed worldwide.

Summary and future perspectives

The present study used the collection data of 2,722 larvae at various stages of development to examine the spatial and temporal patterns of the larval distribution of the Japanese eel and also evaluated the sampling effort that has been made to study this species. These data confirm the general paradigm of the larval migration of *A. japonica* from its spawning area in the NEC to its yellow eel growth habitat in East Asia. The analysis revealed however, that there are considerable biases in where and when the majority of the sampling efforts have been made, which leaves important gaps in our detailed understanding of the early life history of this commercially important fish species. Although research on the spawning area has been ongoing even after the present study, it is apparent that there has been insufficient sampling effort during the later stages of the larval migration as the leptocephali enter the NEC bifurcation region, which may be a critical time for determining the recruitment success of each larval

year class. There is a similar lack of information about these larvae as they begin to metamorphose at the western margin of the subtropical gyre as they approach the Kuroshio Current. Future sampling surveys are needed that cover a wider seasonal range and that emphasize the later stages of the larval migration to fill in critical gaps in the knowledge about the remarkable larval migration of the Japanese eel from far offshore to the various regions of East Asia where they live in estuaries, rivers and lakes.

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