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SHORT COMMUNICATION

# Offshore spawning of *Conger myriaster* in the western North Pacific: evidence for convergent migration strategies of anguilliform eels in the Atlantic and Pacific

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**Abstract** The spawning area of the common Japanese conger, *Conger myriaster*, had remained unknown because spawning adults or its newly hatched larvae were never collected. Using genetic identification, we determined that *C. myriaster* spawns far offshore in the western North Pacific, just west of the spawning area of the Japanese eel, *Anguilla japonica*. In June 2008, six newly hatched *C. myriaster* larvae, 5.6–6.9 mm, were collected at the eastern edge of where many small unidentified *Conger* leptocephali (7–20 mm) were collected previously. The offshore spawning location of *C. myriaster* is analogous to that of the American conger eel, *Conger oceanicus*, and the American eel, *Anguilla rostrata*, in the Sargasso Sea, suggesting that convergent evolution of large-scale reproductive migration strategies in both anguillid and conger eels has occurred in the north Atlantic and Pacific subtropical gyres. The realization that two anguillids, *A. rostrata* and *A. japonica*, and two congers, *C. oceanicus* and *C. myriaster*, have evolved almost identical migration strategies in widely separated ocean basins suggests that natural selection for larval survival and recruitment success has resulted in long offshore spawning migrations in two phylogenetically distant taxa of anguilliform eels.

**Keywords** Anguilliformes · *Conger* · *Anguilla* · Leptocephali · Spawning area · Migration

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## Introduction

Schmidt (1922) discovered that two freshwater eel species, the European eel *Anguilla anguilla* and the American eel, *Anguilla rostrata*, make long migrations from Europe and North America to spawn in the Sargasso Sea of the western North Atlantic (Fig. 1a). More recently, Tsukamoto (1992) found that the Japanese eel, *Anguilla japonica*, migrates far offshore to spawn in the western North Pacific (WNP), where all oceanic stages of this species have now been collected, including spawning adults, eggs, and recently hatched larvae (Tsukamoto et al. 2011). These eels in both the Atlantic and Pacific spawn in similar westward flowing currents at the southern edges of the subtropical gyres in

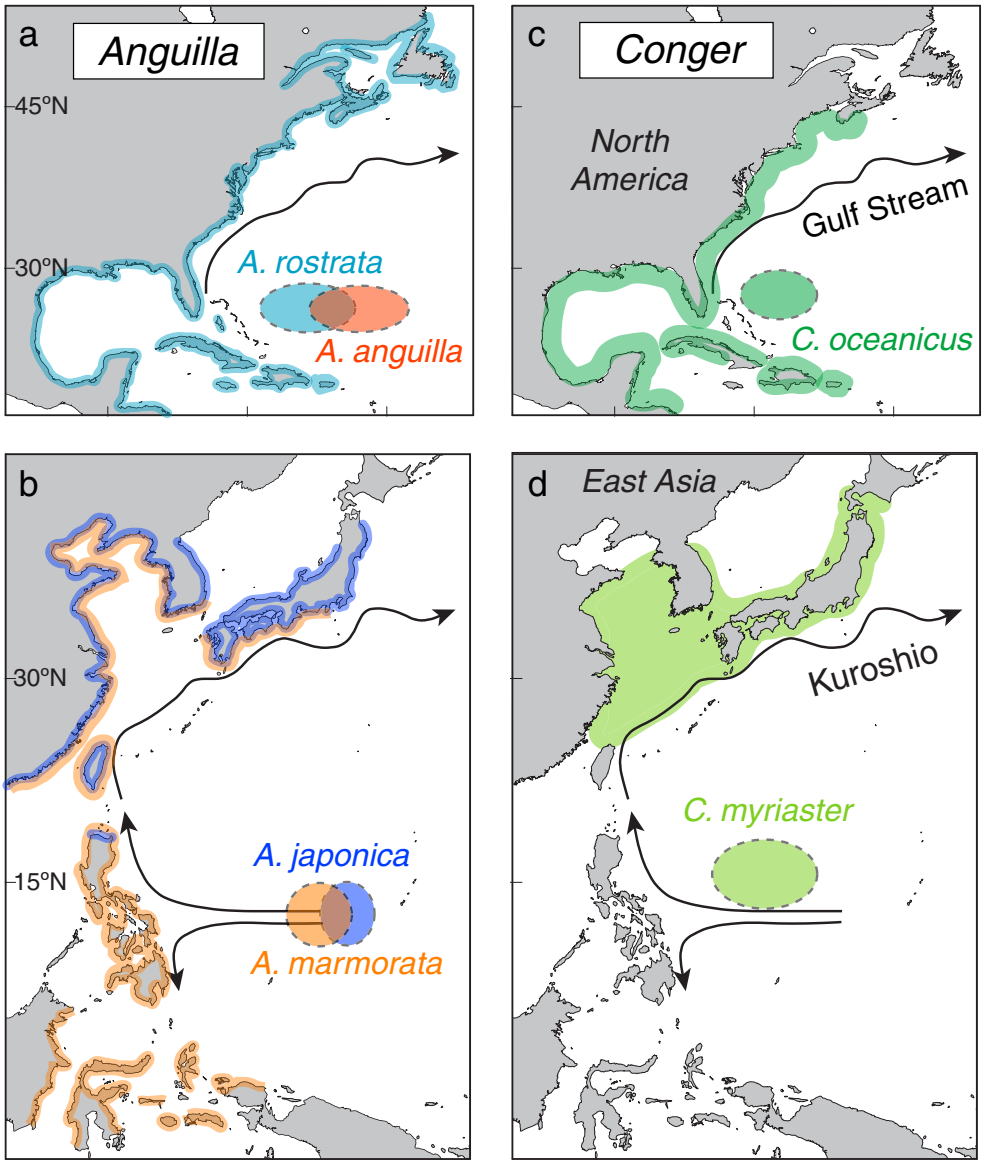


**Fig. 1** General locations of the offshore spawning areas of northern temperate freshwater eels and conger eels (*ovals*). **a**, **b** Freshwater eels of the genus *Anguilla* (from McCleave et al. 1987; Kuroki et al. 2009; Tsukamoto et al. 2011). **c**, **d** Marine eels of the genus *Conger* (from McCleave and Miller 1994; this study). Both types of eels spawn within westward currents in the subtropical gyres of the western North Atlantic (*top*) and western North Pacific (*bottom*) and their larvae enter western boundary currents (Gulf Stream, Kuroshio) that transport them northward in each geographic range. Some larvae also move east and south to other parts of their species ranges that are shown with *colored lines* on coastlines or *shading* (inland ranges of freshwater eels are not shown)

both oceans so their larvae (leptocephali) can be passively transported to recruitment areas while they feed and grow (Tsukamoto et al. 2002).

The long anguillid migrations to spawn far offshore have appeared to be unique among the >800 anguilliform species (Miller 2009), except for the American conger eel, *Conger oceanicus* (McCleave and Miller 1994), and possibly the bandtooth conger, *Ariosoma balearicum*, which may make a shorter spawning migration (Miller 2002). There are about 160 species of eels of the family Congridae that live on the continental shelf and slope around the world (Nelson 2006), but there is no evidence of any other species of congrids making long offshore spawning migrations similar to that of anguillids (Miller 2009). The first realization that some marine eels make long offshore migrations also resulted from the early surveys in the Sargasso Sea, when Schmidt (1931) reported finding the small leptocephali of conger eels offshore. He proposed that *C. oceanicus*, and the European conger eel, *Conger conger*, also migrated to spawn in the Sargasso Sea. However, more recent larval collections in the Sargasso Sea found that only leptocephali of *C. oceanicus* were present there along with those of a local tropical conger species, but not those of *C. conger* (McCleave and Miller 1994). The confirmation that *C. oceanicus* migrates offshore from North America to spawn in an overlapping area with *A. rostrata* (Fig. 1c) showed that two eel genera had evolved long offshore spawning migrations for reproduction in the North Atlantic.

In the WNP, Kuroki et al. (2009) showed that the tropical giant mottled eel, *Anguilla marmorata*, also migrates offshore to spawn in an overlapping area with *A. japonica*. This species has multiple populations in the Indo-Pacific (Minegishi et al. 2008), and the WNP

population makes a long spawning migration, with its larvae recruiting to a wider area than *A. japonica* (Fig. 1b). This type of offshore migration may be unique among tropical anguillids because other species in the region make shorter local migrations (Aoyama et al. 2003).

The spawning area of the common Japanese conger eel, *Conger myriaster*, which is one of the most important fisheries species of marine eel in the world, has remained a mystery (Kimura et al. 2004). This species lives on the continental shelf in the East China Sea and around Japan and the Korean Peninsula, where it is extensively harvested (Tokimura 2001; Katayama et al. 2004) along with another species, the beach conger, *Conger japonicus*, which has a more limited species range along southwestern Japan and the Korean Peninsula. Catches of *C. myriaster* have declined in recent years (Fig. S1), making it essential to understand its life history and to facilitate conservation efforts. Its leptocephali can be collected in coastal waters of East Asia at sizes of about 80–110 mm shortly before metamorphosis into juveniles (Lee and Byun 1996; Kimura et al. 2004) when they have a distinct row of lateral pigment spots along the side of the body (Fig. 2c, d). However, no small larvae had ever been collected to indicate a spawning location.

The first clear hint about the spawning area came from two genetically identified larvae collected offshore in the WNP (Fig. 3a, 22.3, 45.0 mm) because only larger leptocephali had been collected in the East China Sea (Kurogi et al. 2002; Ma et al. 2007). These smaller *C. myriaster* leptocephali were found to lack the lateral pigment spots that are present in the larger larvae collected in coastal waters (Fig. 2; Ma et al. 2007), which had important implications for finding the spawning area of this species using its small larvae. The two larvae collected offshore in the WNP suggested for the first time that the spawning area was located offshore.

This paper presents the first clear evidence that the spawning area of *C. myriaster* is located far offshore in the WNP. This discovery was made by the collection and genetic identification of pre-feeding stage larvae (preleptocephali), which are the recently hatched larval stage of eels. We also describe the collection of many small *Conger* leptocephali in the same area in 1991 and 1995 that also may have been the larvae of *C. myriaster*. This finding that a species of the genus *Conger* migrates offshore to spawn near the anguillid spawning area in the WNP shows that similar migratory behaviors have evolved in anguillid and conger eels in both of the Northern Hemisphere subtropical gyres.

## Methods

Preleptocephali of *C. myriaster* were collected in a north–south transect of stations (every 1° from 9 to 20°N) along 137°E during a sampling survey for *A. japonica* in June and July 2008. Most stations during the survey were concentrated between 141 and 143°E and 12–16°N where all oceanic stages of *A. japonica* have been collected (Tsukamoto et al. 2011), and another transect of stations was made along 130°E (Fig. S2). Single oblique tows of an 8.7 $m^2$ mouth opening Isaacs–Kidd Midwater Trawl (IKMT) with 0.5 mm mesh were made at each station in the upper 300 m along 130°E and 137°E. Leptocephali were sorted fresh out of the plankton, but preleptocephali cannot be identified morphologically, so they were measured, photographed, and preserved in ethanol for later genetic identification.

The preleptocephali were identified using the nucleotide sequences of their mitochondrial DNA 16s rRNA and cytochrome oxidase I (COI) genes that were compared to the *C. myriaster* sequences of Inoue et al. (2001) and Ma et

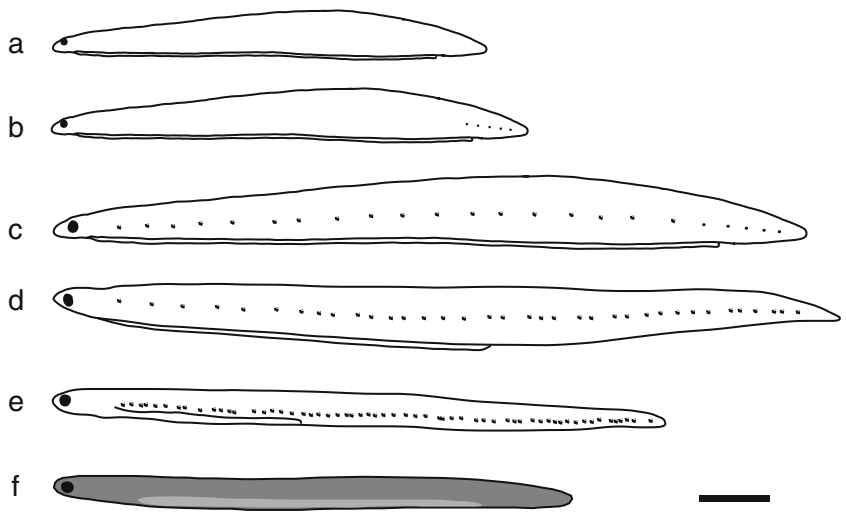


**Fig. 2** Ontogenetic change in larval pigmentation of *Conger myriaster* showing leptocephali of 62–108 mm lengths (**a**–**c**), metamorphosing leptocephalus (**d**), glass eel (**e**), and elver (**f**). Small larvae have no lateral pigment, but a complete row appears in the larger larvae (>75 mm) and glass eels, and total body pigmentation then forms in the elvers. Adapted from Ma et al. (2007) and Miller and Tsukamoto (2004). *Scale bar* shows about 10 mm for all stages

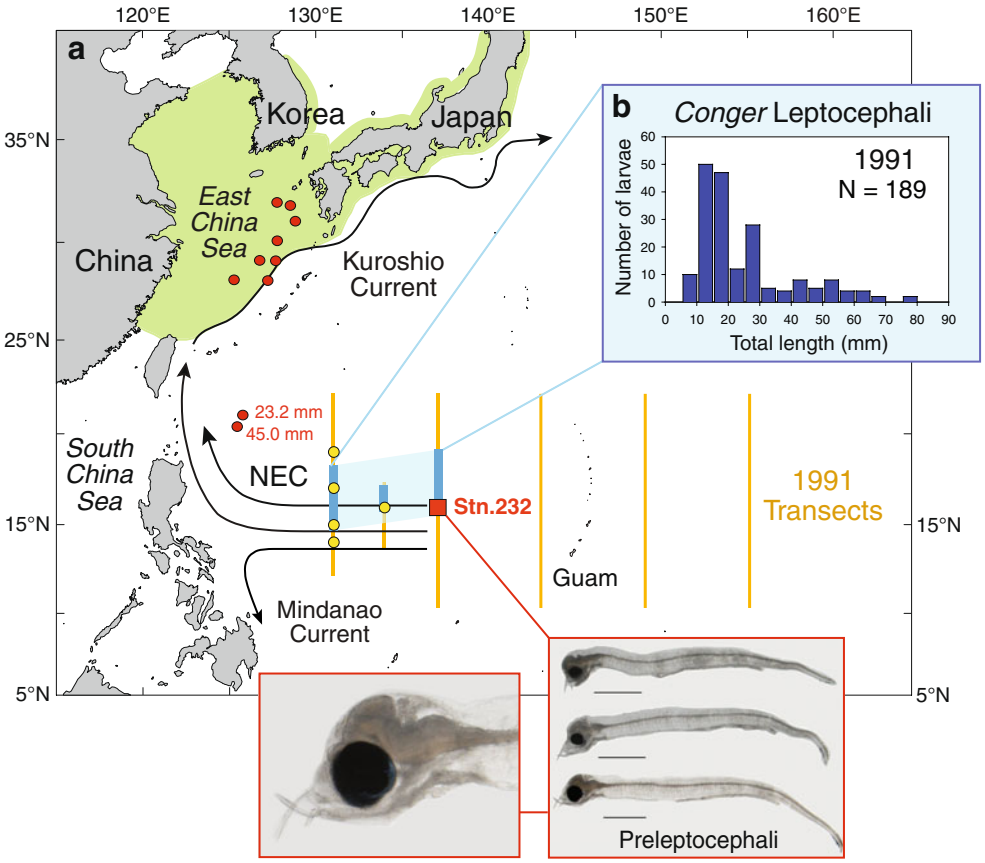


**Fig. 3** **a** Map of the areas where *Conger* leptocephali were collected in July 1991 (*thick blue lines*) in the North Equatorial Current (NEC) of the western North Pacific along the transects of sampling stations (*orange lines*). Station 232 is where six *Conger myriaster* prelepto-cephali were collected on 26 June 2008. **b** Graph of the body size of the *Conger* leptocephali collected in 1991. The greatest number of *Conger* larvae in 1991 was collected in the western transect along 131°E (*N*=137, 8.9–67.1 mm, 23.0±12.1 mm). All but two of the 49 larvae collected in the shorter middle transect (134°E) were 20 mm or smaller (6.9–50 mm, 15.8±8.9 mm), but only three were <20 mm in the eastern transect (137°E) where a wide range of sizes were collected at low abundances (12.9–77.0 mm, 45.0±16.3 mm). **c** Photographs of three of the *C. myriaster* preleptocephali (6.3, 6.1, and 6.9 mm in length, *top* to *bottom*) with the top larva still having its oil globule and the middle larva having two small spots on the posterior end of the gut. *Scale bars* are 1 mm. **d** Head of the bottom larvae in (**c**). The locations where the genetically identified leptocephali of *C. myriaster* were collected in November–December 2000 in the East China Sea (51.0–74.0 mm) and western North Pacific (23.2, 45.0 mm) (Ma et al. 2007) are shown with *red circles*, and locations where nine *Conger* leptocephali were collected in July 1995 (12.4–42.3 mm, 20.0 ±9.7 mm) are shown with *yellow circles* in (**a**). *Green shading* shows the approximate species range of *C. myriaster* juveniles and adults. See Fig. S2 for a map showing all sampling stations

al. (2007, 16s rRNA only). Total DNA was extracted from each larva using PureLink Genomic DNA kits (Invitrogen), and then PCR was performed with KOD plus ver. 2 DNA polymerase (TOYOBO). A partial fragment of the 16s rRNA gene was amplified with fish-versatile primers L1854 (5′-AAACCTCGTACCTTTTGCAT-3′) and H3059 (5′-CCGGTCTGAACTCAGATCACGT-3′). The COI gene was amplified with primers designed using *C. myriaster* sequences (Inoue et al. 2001), which were CmL5410 (5′-TGGCCTGGTAAGAAAAGGAA-3′ for tRNA-Cys to tRNA-Tyr region) and CmH7107 (5′-GACTGGCTT GAAACCGGTAA-3′ for tRNA-Ser region). Amplified products were purified with PEG8000 (Promega) and labeled with a BigDye ver. 3.1 kit (Applied Biosystems). Labeled fragments were analyzed by an ABI PRISM 3,100xl genetic analyzer (Applied Biosystems).

*Conger* leptocephalus catch data were obtained from a large-scale IKMT sampling survey for *A. japonica* in June and July 1991 and a smaller survey in July 1995. Sampling stations were mostly spaced at 1° intervals in five long latitudinal transects in 1991 and one shorter transect (Figs. 3 and S2). Many extra IKMT tows were made in the three western transects where *A. japonica* leptocephali were abundant (Tsukamoto 1992), and this is where most *Conger* leptocephali were collected. A smaller number of *Conger* leptocephali were also collected 17–29 July 1995 in the same area (sampling was conducted in three shorter transects corresponding to the three western 1991 transects in Fig. 3 as shown in Fig. S2). Leptocephali in both years were identified and measured (some were damaged and could not be measured) before being preserved in 10% formalin–seawater. These fixed specimens are no longer

available for genetic identification because of DNA degradation. All sampling in 1991, 1995, and 2008 was conducted by the R/V *Hakuho Maru*.

## Results

The genetic analysis confirmed that six *C. myriaster* preleptocephali 5.6–6.9 mm TL (mean±SD—6.3± 0.52 mm TL) were collected in one net tow at Stn. 232 (net was fished from 16–00.0°N, 137–00.6°E to 15–58.3°N, 137–01.2°E) on 26 June 2008 (Fig. 3). Comparisons of the sequences of the 16s rRNA gene (1,216 bp) of the preleptocephali (see Fig. S3 for DDBJ/EMBL/GenBank accession numbers) with those of a *C. myriaster* adult specimen ($n$=1; Inoue et al. 2001) and large leptocephali ($n$= 20; Ma et al. 2007) found sequence identities of 99.3–100% (Fig. S3). Sequence identities of 99% or higher are within the range of intra-species nucleotide substitutions (Ma et al. 2007). In contrast, the six preleptocephalus 16s rRNA gene sequences were only 97% and 96% similar to those of *C. japonicus* and the North Atlantic species *C. oceanicus*, respectively. The COI gene sequence (1,563 bp) of the six preleptocephali (see Fig. S3 for accession numbers) showed 99.7–100% similarity with that of *C. myriaster* (Inoue et al. 2001). Nucleotide substitutions were found at four sites among the six preleptocephali and adult, all at the third base, and no variation was found in their deduced amino acid sequences. Accordingly, these data show that the six preleptocephali collected offshore were those of *C. myriaster*. The preleptocephali had black tail pigment and some had two small gut spots (Fig. 3c). Their shape and pigment was consistent with earlier-stage artificially spawned *C. myriaster* larvae (Horie et al. 2002).

The finding of the newly hatched larvae of *C. myriaster* so far offshore in June 2008 has important implications for the species identity of the many *Conger* leptocephali offshore in July 1991. Recently, genetic identification of *Conger* leptocephali found that their leptocephali undergo an ontogenetic change from having no lateral pigment spots, to having a single row of lateral spots at the time of recruitment (Fig. 2; Ma et al. 2007). This ontogenetic pigmentation change indicated that their small larvae could have been collected historically, but were assumed not to be *C. myriaster* because they lacked lateral pigment. There were 215 morphologically identified *Conger* leptocephali collected at a wide range of sizes in 32 of the tows (1–20 per tow, 1–18 July) made along the three westernmost transects during the 1991 sampling survey (Fig. 3b). They had no lateral pigment, so they were assumed not to be the larvae of *C. myriaster* at the time. Similarly, in July 1995, nine *Conger* leptocephali mostly 12–15 mm were also collected in this area (1–4 per tow, 17–22 July).

## Discussion

The collection of *C. myriaster* preleptocephali in June 2008 provided the first proof that this species migrates offshore to spawn. This is consistent with the 22.3 and 45.0 mm leptocephali collected in the WNP (Fig. 3a; Ma et al. 2007), which would have been transported there by the westward flow of the subtropical gyre. The collection of larvae 10 mm or smaller in July 1991 and <15 mm larvae in July 1995 indicated that conger eels migrated offshore to spawn in this area in those years also because there are no landmasses nearby where these eels could have spawned without making an offshore migration. Due to the lack of genetic identification of the leptocephali in 1991 and 1995, however, it cannot be determined if some of these may also have been other species such as *C. japonicus* whose spawning area is also not known. The genetic identification of the six preleptocephali at the eastern edge of this region in 2008, though, strongly suggests that *C. myriaster* had also been spawning offshore in both 1991 and 1995 and that this offshore region is the typical spawning area of *C. myriaster*. A spawning area in this location would allow the larvae to feed and grow as they are transported westward towards the Kuroshio Current and East China Sea where they have been collected at larger sizes (Kurogi et al. 2002; Ma et al. 2007). This life history pattern is similar to that of *A. japonica* that recruits to East Asian estuarine and freshwater habitats after spawning offshore.

This study also suggests that the spawning area of *C. myriaster* is located northwest of that of *A. japonica*. In 1991, when many small *A. japonica* leptocephali were collected offshore, the greatest abundance of *Conger* leptocephali (131°E) was west of the biggest catches of *A. japonica* (137°E; Tsukamoto 1992). Preleptocephali of *A. japonica* have also been consistently collected further east and more to the south (Tsukamoto et al. 2011). Spawning of *A. japonica* can shift to the south when a salinity front moves southward (Kimura and Tsukamoto 2006) as was the case in June 2008 when *C. myriaster* preleptocephali were collected at 16°N (137°E), but *A. japonica* preleptocephali were collected at 12–13°N (141–142°E). Future sampling surveys are needed to determine the latitudinal and longitudinal extent of the *C. myriaster* spawning area and if its location can shift similar to that of *A. japonica*.

Two anguillid species having overlapping spawning areas in the WNP, and a *Conger* species spawning to the west, is remarkably similar to what occurs in the Sargasso Sea (Fig. 1). Both *A. rostrata* and *C. oceanicus* migrate offshore to spawn, and *C. oceanicus* also appears to spawn further west than *A. rostrata* (McCleave and Miller 1994). There is presently not enough known about the two *Conger* spawning areas or the migration behaviors and transport

routes of conger and anguillid leptocephali to know why they appear to have slightly different spawning locations. It could be related to the different maximum sizes (*Conger*> *Anguilla*) or growth rates of their larvae or other behavioral or life history differences among the species. The migrations of *A. anguilla* are different though, despite spawning in an overlapping area with *A. rostrata* (McCleave et al. 1987) because their leptocephali must cross the North Atlantic basin to reach Europe and North Africa.

Finding that both conger and anguillid eels in these two subtropical gyres have evolved offshore spawning migrations suggests that there is an important adaptive advantage to migrating that outweighs other costs. Offshore spawning in westward flowing ocean currents enables the larvae to feed and grow in the relatively predator-free open ocean as they are passively transported to their juvenile growth habitats. This strategy may be successful because leptocephali feed on readily available particulate organic material, which may typically contain a variety of small organisms (see Riemann et al. 2010), but probably not on larger free-swimming zooplankton like most fish larvae (Miller 2009). By placing their larvae far offshore to enable growth before reaching the continental margins, the larvae of these species reach the predator-dense coastal areas at large sizes and are ready for metamorphosis into juveniles.

The geographic separation of the two gyres and the phylogeny of anguillid eels suggest that these offshore spawning migrations may have evolved separately. This is possible because the Atlantic anguillids and *A. japonica* appear to be in separate lineages based on molecular genetic phylogenies of all the anguillid species (Minegishi et al. 2005; Aoyama 2009), and the long migrations of these temperate species are thought to have independently evolved from the shorter migrations of tropical anguillids (Tsukamoto et al. 2002). Congrid and anguillid eels also do not appear to be closely related and may have diverged about 150 million years ago (Inoue et al. 2005). In addition, anguillid eels appear to be derived from deep-ocean eels, with conger eels being deeply nested within a different lineage of marine eels that does not contain any species known to make long offshore migrations (Inoue et al. 2010). The phylogeny of conger eels is not known, but since most marine eels including other species of congrid eels (Miller et al. 2002) do not migrate far offshore to spawn (Miller 2009), the offshore migrations of *C. myriaster* and *C. oceanicus* could have been established independently. If this is true, the present study shows that convergent evolution of offshore spawning migrations has occurred in two phylogenetically distant genera of eels, whose life histories became adapted to the similar patterns of ocean currents that exist in the subtropical gyres of the north Atlantic and Pacific oceans.

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