



Contribution to the Symposium: 'International Eel Symposium 2014' Food for Thought

Did a “perfect storm” of oceanic changes and continental anthropogenic impacts cause northern hemisphere anguillid recruitment reductions?

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Miller, M. J., Feunteun, E., and Tsukamoto, K. Did a “perfect storm” of oceanic changes and continental anthropogenic impacts cause northern hemisphere anguillid recruitment reductions? – ICES Journal of Marine Science, 73: 43–56.

Received 28 November 2014; revised 20 March 2015; accepted 22 March 2015; advance access publication 14 April 2015.

The three northern hemisphere anguillid eel species experienced recruitment declines at similar times beginning in the 1970s and 1980s, but the exact causes of the declines have remained unclear. Attention focused on two categories of possible causes that included (i) anthropogenic impacts on eel growth habitats, such as dam construction, degradation and pollution of habitats, introduction of parasites, overfishing and (ii) changes in ocean-atmospheric conditions affecting their marine life-history stages. The cumulative effects of reaching peaks in dam construction, levels of pollution, and eutrophication just before the eel declines likely had reduced eel production in many areas, and contamination by metallic and organic compounds and parasites may have reduced reproductive success. Shifts in ocean-atmospheric conditions also occurred just before the eel declines that could have reduced feeding success of larvae or disrupted larval transport. If oceanic regime shifts reduced production of the marine snow food of eel larvae, it may have affected larval survival and recruitment success, especially if there is a critical time-window for successful larval first feeding when marine snow particles need to be abundant. A reduction of these particles could result in density-dependent early mortality of the larvae of each spawning event, and competition for marine snow particles with sympatrically spawning mesopelagic eel larvae would amplify this effect. Nutrient reductions causing shifts in the relative abundance of phytoplankton contributing to marine snow production and of ubiquitous cyanobacteria may mediate levels of larval survival in areas with high spawning activity. Reductions of eels reaching the spawning area from species range margins that spawn outside of peak spawning periods could have reduced recruitment further. It appears likely that a variety of impacts, oceanic and anthropogenic occurred simultaneously causing sudden declines of these eel populations.

Keywords: anguillid eels, anthropogenic impacts, density-dependent larval survival, oceanic regime shifts, population declines.

Introduction

In the last few decades of the 20th century, declines in recruitment and reduced standing stocks of the three species of northern hemisphere anguillid eels were observed that attracted considerable attention from scientists and helped to stimulate new research (Castonguay *et al.*, 1994a, b; Haro *et al.*, 2000; Feunteun, 2002; Casselman, 2003; Dekker, 2003a; Dekker *et al.*, 2003; Knights, 2003; Tsukamoto *et al.*, 2009). Recruitment to parts of the species ranges dropped to low levels, such as the Netherlands and other areas for the European eel, *Anguilla anguilla* (Dekker, 1998; ICES,

2014) and the St. Lawrence River at the northern edge of the range of the American eel, *Anguilla rostrata* (Castonguay *et al.*, 1994a; Casselman, 2003), or for the Japanese eel, *Anguilla japonica*, in many areas (Tsukamoto *et al.*, 2009). These three species are widely distributed across many countries within their large species ranges and have been commercially harvested to varying degrees during their glass eel, yellow eel, and silver eel stages (Casselman, 2003; Dekker, 2003a; Tsukamoto and Kuroki, 2014), so their declines have been a major concern. The declines in recruitment and catches of yellow and silver eels of these three species began at

various times in the 1960s to 1980s, and continued until the last few years, at least for the European eel (Figure 1; Casselman, 2003; Tsukamoto *et al.*, 2009; ICES, 2014); although the trends of recruitment levels of the American, Japanese, and European eels may have been more stable in some areas after the initial declines occurred (Sullivan *et al.*, 2006; Tzeng *et al.*, 2012; Adams *et al.*, 2013).

Human impacts on ecosystems within the regions where these eels live, along with species overexploitation/removal, are well-known, especially for fisheries species (Vitousek *et al.*, 1997; Lotze *et al.*, 2006; Humphries and Winemiller, 2009; Limburg and Waldman, 2009; Estes *et al.*, 2011). What is somewhat unusual about the case of catadromous anguillid eels compared with fisheries resources that appear to have declined as a result of overfishing (Lotze *et al.*, 2006) is that the exact causes of the eel declines have not yet been clearly determined. As described below, there are clear hypotheses for what could have happened, with various levels of support for some factors, but it is difficult to empirically determine causes of the declines primarily because it is impossible to assess the spawning stock abundance in their offshore spawning areas or even if this is linked to recruitment levels (Dekker, 2003b; Åström and Dekker, 2007). There is also only minimal information about escapement of the migratory reproductive-stage silver eels except to some extent for the European eel (Feunteun *et al.*, 2000; Dekker, 2003b; Åström and Dekker, 2007; ICES, 2013; Prigge *et al.*, 2013), making it difficult to link declines to any one factor. This inability to determine direct causes of the declines has in part resulted in many of the 19 anguillid species/subspecies in the world being recently listed in the IUCN Red List (IUCN, 2014), with the European eel being listed as critically endangered in 2010 and having its export banned by the Convention on International Trade of Endangered Species (CITES, 2006).

Two general types of causes have been proposed to be responsible for eel declines, which include (i) anthropogenic effects on their continental life-history stages and (ii) changes in ocean-atmosphere factors affecting their marine stages. Many types of information

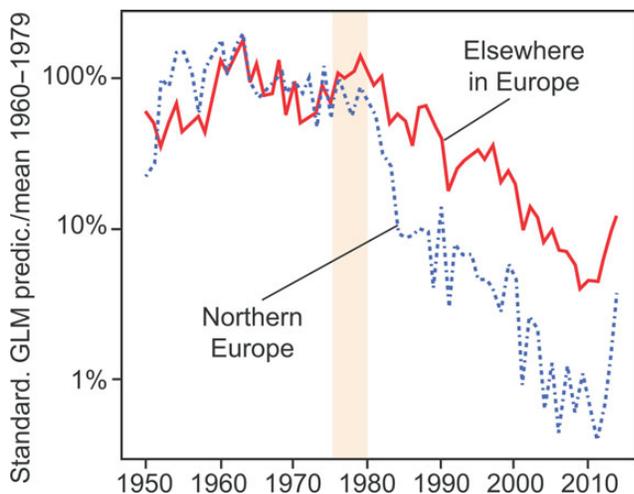


Figure 1. Historical changes in glass eel recruitment of the European eel, *Anguilla anguilla*, in the regions of northern Europe (areas with recruitment from the North Sea) and all other areas (excluding the Baltic Sea where no time-series data for glass eel catches are available) that are plotted on a logarithmic scale (adapted from ICES, 2013, 2014). The shaded bar shows the 1975–1980 period after which eel recruitment or abundance was declining. This figure is available in black and white in print and in colour at ICES Journal of Marine Science online.

indicate reductions in available habitats due to dams and river modifications, contaminants, parasite introduction, or overfishing have affected eels and therefore contributed to their population declines (Haro *et al.*, 2000; Feunteun, 2002; Robinet and Feunteun, 2002; Kirk, 2003; Geeraerts and Belpaire, 2010; Kettle *et al.*, 2011; Itakura *et al.*, 2014). Several studies have also correlated recruitment or eel abundance indices with ocean-atmosphere-related parameters (Knights, 2003; Friedland *et al.*, 2007; Bonhommeau *et al.*, 2008a, b; Kettle *et al.*, 2008; Durif *et al.*, 2011; Arribas *et al.*, 2012). These studies suggest that recruitment fluctuations may be influenced by aspects of spawning success, larval survival in the spawning area, or survival during larval growth and transport. However, because various time-lags have been used to find correlations between ocean-atmosphere parameters and eel recruitment/abundance data, these studies provide limited definitive proof of a cause-and-effect relationship between environmental factors and eel recruitment without more specific evidence being available.

Therefore, it has been difficult to reach clear conclusions about what are the primary driving factors of declines of northern hemisphere anguillid eels. It has been acknowledged, however, that a mixture of factors probably caused the declines, including both directly anthropogenic-related factors and more environmentally related factors in the ocean or atmosphere (e.g. Castonguay *et al.*, 1994a; Miller *et al.*, 2009; Kettle *et al.*, 2011; Hanel *et al.*, 2014).

In this paper, we briefly examine both the general types of anthropogenic factors that may have affected eels and how regime shifts in ocean-atmosphere conditions could have caused changes in the ocean that may also have affected eels. The timelines of possible occurrences of these factors are qualitatively examined in comparison with when eel populations began to decline, because although many factors could be affecting eel populations, some may not be the primary cause of the rapid declines that occurred at nearly simultaneous times for all three species. We propose a potential mechanism for how a shift in the fluctuations of relative abundances of eukaryotic and cyanobacteria primary producers could influence recruitment levels through regulating density-dependent early larval survival in the spawning area, and how this in combination with anthropogenically caused population reductions and species range and spawning time contractions may have acted synergistically to reduce overall eel recruitment each year. It is not our intention to attempt to comprehensively review all the literature associated with these subjects (see Knights, 2003; Tesch, 2003; Kettle *et al.*, 2008, 2011; Miller, 2009; Miller *et al.*, 2009; ICES, 2013, 2014 and previous reports for recent reviews; and literature cited by papers included in the present paper). Instead our goal is to provide some general historical perspective and propose a few new hypotheses to facilitate improving understanding of this subject. The fact that both anthropogenic factors and ocean-atmosphere changes seemed to converge during the same period when northern hemisphere anguillid eels began to decline is not in itself evidence of what the causal factors were, but it is suggestive of the possibility that a “perfect storm” of impacts on eels could have interacted to reduce their populations.

Timelines of anthropogenic impacts on eels

Anguillid eels move far upstream into freshwater river systems with large, older females being found upstream and a larger proportion of males and young eels being found in lower reaches and estuaries when eels are abundant (Feunteun *et al.*, 2003; Tesch, 2003). Therefore, eels are especially vulnerable to the blockages to upstream migration that occurred due to dam construction in the last 60 years

(Figure 2; World Commission on Dams, 2000; Lehner *et al.*, 2011). This has undoubtedly had a profound effect on the standing stock of eels in the northern hemisphere, because dams have made these areas have some of the lowest average free-flowing percentages of watercourse lengths in the world (Liermann *et al.*, 2012), thus blocking the passage of eels into vast drainages areas. Even if silver eels are able to pass upstream, hydroelectric dams can also adversely affect escapement of silver eels, because of mortality from downstream passage through turbines (McCleave, 2001). Many hydroelectric dams were built within the species range of the American eel (Figure 2D), with greatest densities being in the centre of the species range (Graf, 1999). More than 15,000 dams including 5000 dams ~7 m or higher were built in the North Atlantic coast drainages, blocking direct access to ~87% of river and stream reaches flowing into the Atlantic (Busch *et al.*, 1998), which has greatly reduced the present-day American eel inland range (see Miller and Casselman, 2013). Similarly, extensive dam construction across many regions of Europe (including > 1400 dams with reservoirs; Lehner *et al.*, 2011) and North Africa, resulted in some drainages having hundreds of obstructions (Kettle *et al.*, 2011; Van Looy *et al.*, 2014). In East Asia, many dams have been constructed, including 2675 large dams (>15 m high) in Japan that may have reduced abundances of eels by reducing access to upstream areas (Tatsukawa, 2003; Yoshimura *et al.*, 2005; Han *et al.*, 2008).

Extensive revetment and channelization of the lower reaches of most river systems in Japan and other parts of East Asia have likely affected eels (Yoshimura *et al.*, 2005; Chen *et al.*, 2014; Itakura *et al.*, 2014). The timing of construction of these dams and river modifications has varied to some extent among regions, with dam construction peaking slightly earlier in Europe than Asia and the number of dams being constructed decreasing in recent decades (Figure 2; Kettle *et al.*, 2011). Many wetland areas have been filled and converted into land within estuaries or further inland along rivers and lakes (Kettle *et al.*, 2011; Moreno-Mateos *et al.*, 2012; Chen *et al.*, 2014), which also represent a loss of growth habitat for eels. Anthropogenic modifications to river systems and estuaries that caused loss of habitat and connectivity have occurred far back in human history, for various purposes such as agriculture, mills, water level management, and flood control, but they greatly increased after the Industrial Revolution (Hoffmann *et al.*, 2010).

In addition to structural modifications to aquatic habitats, freshwater, and estuarine ecosystems have experienced a wide range of other anthropogenic impacts including sedimentation, chemical contamination, eutrophication, and fisheries harvests that can affect the community structure of the ecosystem there to various degrees (Jackson *et al.*, 2001; Robinet and Feunteun, 2002; Yoshimura *et al.*, 2005; Hering *et al.*, 2006; Lotze *et al.*, 2006;

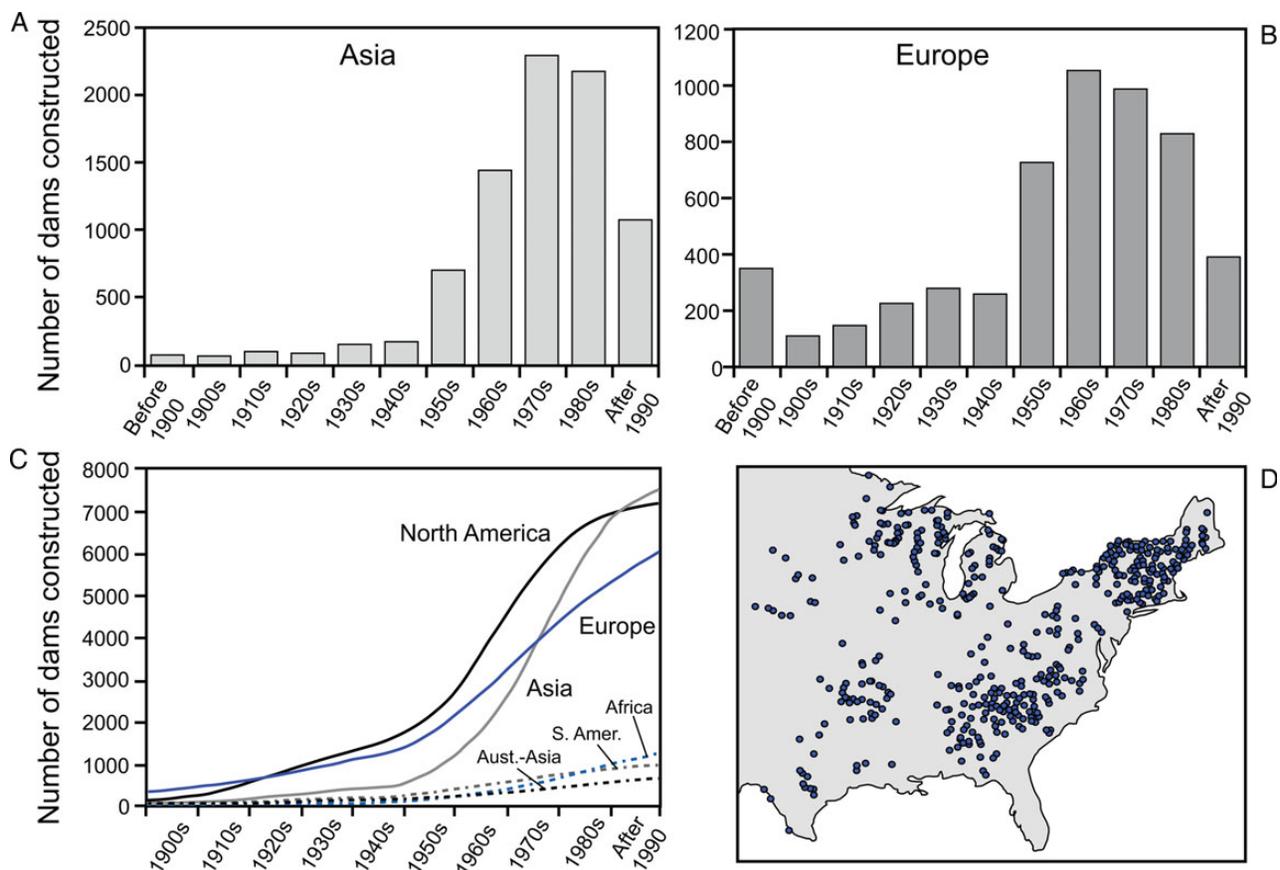


Figure 2. Plots of the number of dams constructed by decade in (A) Asia (excluding China) and (B) Europe (modified from World Commission on Dams, 2000), and (C) plots of the cumulative number of dams constructed by region, also excluding China that currently has more than 20,000 dams (modified from imagery from the International Commission on Large Dams, <http://www.icold-cigb.org/>). (D) The approximate locations of hydropower dams in the historical range of the American eel, *Anguilla rostrata*, in the continental US (modified from imagery from the US Energy Mapping System of the US Energy Information Administration: <http://www.eia.gov/>).

Søndergaard and Jeppesen, 2007; Humphries and Winemiller, 2009; Geeraerts and Belpaire, 2010) and likely affect the growth and survival of eels. Vast inland areas were deforested and replaced with urban areas, agricultural fields or second-growth forests (Williams, 2000), which would have caused extensive input of sediments into rivers and streams (Wilkinson and McElroy, 2007). Industrialization resulted in releases of heavy metals, polycyclic aromatic hydrocarbons, organochlorine compounds, dioxins, and other chemicals contaminants into rivers and streams (Meybeck and Helmer, 1989; Malmqvist and Rundle, 2002). Residential and urban development increased the amount of sewage entering aquatic systems until wastewater treatment facilities were built (Lofrano and Brown, 2010). Sewage effluents, the use of phosphate detergents, and fertilizer for agriculture (Figure 3A) all entered freshwater systems causing extensive eutrophication in many areas where eels would have been present (Litke 1999; de Jonge et al., 2002; Smith, 2003; Yoshimura et al., 2005; Savage et al., 2010). Use of pesticides and their entry into terrestrial and aquatic environments increased substantially starting in about the 1940s and reached maximum use in developed countries in the 1970s before levelling off, at which time they were replaced by new chemicals or

other pest control methods (Zadoks and Waibel, 2000; Stoate et al., 2009).

Sediment cores analysed in the northern hemisphere to examine the timelines of release of these types of pollutants indicate that there are similar historical patterns for levels of chemical contaminants and nutrient inputs to aquatic systems. Levels increased rapidly throughout 1920–1970 (Figure 3) that corresponds to the expansion of industrialization, agriculture, and urbanization. Levels usually decreased after regulations were imposed to control these problems (Litke, 1999; Balogh et al., 2009; Hosono et al., 2010; Savage et al., 2010; Wiener and Sandheinrich, 2010; Vane et al., 2011; Heim and Schwarzbauer, 2013). The exact timing of the occurrence, maximum levels, and eventual decreases depend on the location and input sources, but timelines are generally similar, because beginning around the 1970s, awareness of harmful effects of pollutants and excess nutrients on aquatic ecosystems increased and legislation began to be enacted to prevent further contamination (Litke, 1999; Wiener and Sandheinrich, 2010). There are exceptions to this pattern however, such as for mercury emissions from gold mining in North America, which peaked in the late 1800s then disappeared after ~1925, or some heavy metals or polycyclic aromatic hydrocarbons

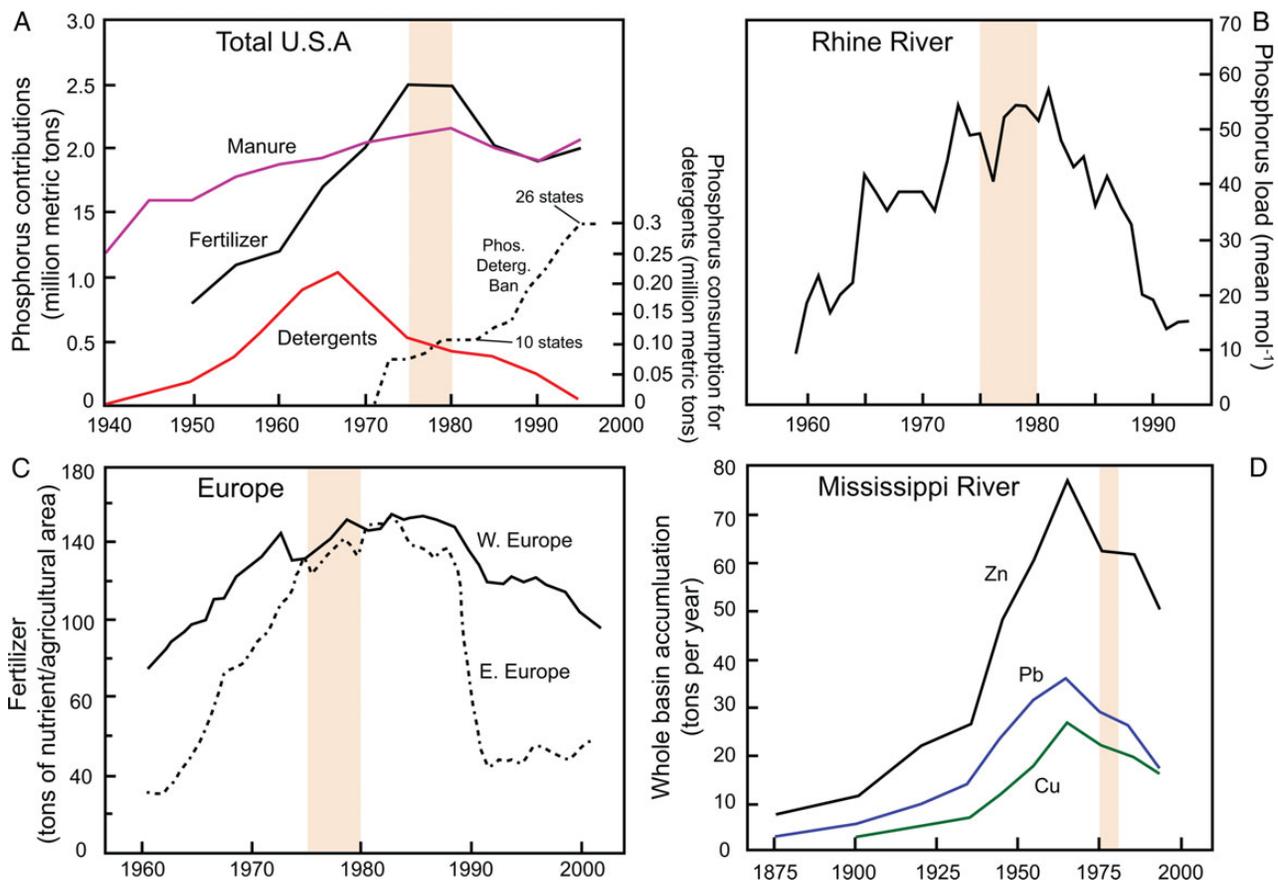


Figure 3. Historical changes in usage of phosphorus that could affect eutrophication of freshwater ecosystems as reflected by (A) contributions of phosphorus from fertilizer, livestock manure, and phosphorus used in detergents in the US, also showing the temporal trend of the number of states imposing a ban on detergents containing phosphorus (no y-axis scale shown) that was modified from Litke (1999), (B) phosphorus load in the Rhine River at the Germany–Netherlands border modified from de Jonge et al. (2002), (C) fertilizer use in western Europe (Austria, Belgium, Denmark, Finland, France, Germany, Ireland, Italy, The Netherlands, Portugal, Spain, Sweden, and UK) and eastern Europe (Bulgaria, Hungary, Poland, and Romania) modified from Stoate et al. (2009), and (D) whole basin accumulation rates of copper (Cu), lead (Pb), and zinc (Zn) in the Mississippi River in the central US modified from Balogh et al. (2009). The shaded bar shows the 1975–1980 period after which eel recruitment or abundance was declining. This figure is available in black and white in print and in colour at ICES Journal of Marine Science online.

that were mostly released in earlier years (Lima *et al.*, 2003; Balogh *et al.*, 2009; Heim and Schwarzbauer, 2013). The effects of contaminant releases can still be felt today however, since eel fisheries in some areas of Europe have been closed because the contaminant loads in eels make them unfit for human consumption (ICES, 2013), and contaminants are present in eels from many parts of Europe and North America (Geeraerts and Belpaire, 2010; ICES, 2013).

The effects of aquatic habitat modifications and community structure changes on eels are difficult to quantify, although growth rates of eels are slower in freshwater habitats where extensive impacts have occurred compared with brackish habitats (Cairns *et al.*, 2009; Marohn *et al.*, 2013); and many eels tend to leave freshwater and move to estuaries in some areas, or make seasonal movements between habitat types at high latitudes (see Jessop *et al.*, 2008; Clément *et al.*, 2014). In addition, the bioaccumulation of contaminants has been speculated to affect the migratory or reproductive capabilities of silver eels (Castonguay *et al.*, 1994a; Robinet and Feunteun, 2002; van Ginneken, 2009; ICES, 2013). This suggests that the collective effects of reduced growth or reproductive potential for eels from freshwater has occurred, especially if slow growth or poor body condition reduces the number of eels that have sufficient energy reserves to reach the spawning area and successfully reproduce (Belpaire *et al.*, 2009; Clevestam *et al.*, 2011).

Introductions of parasites or the occurrence of viruses have also affected eels in some areas. The parasitic swimbladder nematode, *Anguillicola crassus*, was introduced into European and North American waters in the early 1980s (Europe) and 1990s (N. America) then spread to many areas (Barse and Secor, 1999; Kirk, 2003). It affects the swimbladder of eels living in freshwater, but infection rates are lower in brackish water (Jakob *et al.*, 2009a; ICES, 2013). Infection may result in reduced swimming abilities in silver eels migrating to their spawning areas (Palstra *et al.*, 2007; Sjöberg *et al.*, 2009). Eels infected with viruses (van Ginneken *et al.*, 2004; Jakob *et al.*, 2009b) could also have reduced swimming abilities that might affect their chances to reach the spawning area and successfully reproduce (van Ginneken *et al.*, 2005).

Fisheries can likely reduce the number of silver eels escaping from continental waters each year, especially when they are harvested during their downstream migrations. Examining the timelines of fisheries harvests of the three species northern temperate anguillid eels is beyond the scope of this paper and this has been done previously (e.g. Casselman, 2003; Dekker, 2003b; Tatsukawa, 2003; Kettle *et al.*, 2008; ICES, 2013; Itakura *et al.*, 2014; Yokouchi *et al.*, 2014). Dataseries on harvest are complicated by changes in levels of fishing effort and the accuracy of catch reporting (Casselman, 2003; Dekker, 2003a, b; Itakura *et al.*, 2014), but harvests seem to reflect the trends in levels of recruitment that increased in decades leading up to the 1970s and 1980s then decreased thereafter (Gascuel *et al.*, 1995; Casselman, 2003; Dekker, 2003b; Tatsukawa, 2003; Tsukamoto *et al.*, 2009). Although fisheries catches may have sometimes reduced the number of eels in particular areas, especially perhaps for the Japanese eel whose glass eels are extensively captured for use in aquaculture (Tsukamoto *et al.*, 2009), we are unaware of any clear evidence that fisheries catches directly triggered the declines of the northern hemisphere anguillid eels.

This brief overview of anthropogenic influences on anguillid eels indicates that the population sizes, individual growth or survival, and possibly the success of silver eels to reach the spawning area and successfully reproduce were affected by some types of human activities in the last hundred years that included the Industrial

Revolution and continued human population growth and development of natural areas. Interestingly, the levels of occurrence of many of these activities such as release of contaminants and nutrients into freshwater (Figure 3) or the construction of dams (Figure 2) tended to reach a climax just before anguillid populations began to decline. However, often, the levels of these impacts were steadily reduced after that, yet the declines of eels continued or recruitment remained low. Possible exceptions may be the continued spread and presence of the *A. crassus* parasite (Barse and Secor, 1999; Kirk, 2003, Jakob *et al.*, 2009a; Marohn *et al.*, 2013), the sudden increase in dam construction in North Africa (Kettle *et al.*, 2011), the inputs of new types of contaminants or the persistence of contaminants in the sediments of eel habitats (Geeraerts and Belpaire, 2010). The massive loss of eel habitat area from dam construction may have reduced overall population sizes of these species causing recruitment reductions to areas at the margins of species ranges, such as the St. Lawrence River system for the American eel (Casselman, 2003) or the North Sea and Baltic Sea for the European eel (Dekker, 1998). In addition, Kettle *et al.* (2011) suggest that the loss of a large proportion of European eel production from the Iberian Peninsula and North Africa and reductions in rainfall may have been important factors affecting declines, since eels living there have the shortest migration distances, and thus may have greater success reaching the spawning area. Because anthropogenic effects may have been mostly decreasing or stable in recent decades in Europe, North America, and some parts of East Asia, it seems unlikely that those factors could be regulating interannual fluctuations in recruitment that have been observed both before and after the declines began, which suggests environmental factors also influence recruitment.

Regime shifts and eel recruitment

Sudden ocean-atmosphere changes in a particular region, or regime shifts, have increasingly been recognized to affect the population dynamics of marine fish through changes in biological oceanography (Hare and Mantua, 2000; Weijerman *et al.*, 2005; Drinkwater, 2006; Lehodey *et al.*, 2006; Overland *et al.*, 2010). This has also been hypothesized to be the case for anguillid eels because they spawn in offshore oceanic areas and their larvae feed and grow in the ocean before recruiting to continental waters (Castonguay *et al.*, 1994b; Knights, 2003; Miller *et al.*, 2009). Changes in the North Atlantic Oscillation (NAO; Figure 4A) have occurred (Hurrell, 1995; Drinkwater *et al.*, 2003) and statistical correlations between recruitment indices of the European eel (Knights, 2003; Friedland *et al.*, 2007; Kettle *et al.*, 2008; Arribas *et al.*, 2012) or yellow and silver eel catches (Kettle *et al.*, 2008; Durif *et al.*, 2011) and the NAO index have been observed.

The larvae of anguillid eels, called leptocephali, appear to primarily feed on marine snow materials (Otake *et al.*, 1993; Mochioka and Iwamizu, 1996; Miller *et al.*, 2011, 2013), and the production of marine snow is linked to the primary productivity of phytoplankton (Alldredge and Silver, 1988; Alldredge and Jackson, 1995; Turner, 2002). Therefore, changes in primary productivity could influence the survival or growth rates of anguillid leptocephali (Knights, 2003). Correlations between sea surface temperature as a proxy of productivity and glass eel recruitment, especially for the European eel but also for the American and Japanese eel (Bonhommeau *et al.*, 2008a, b; Arribas *et al.*, 2012) support this concept. Warming of the ocean surface layer appears to result in reductions in productivity (Behrenfeld *et al.*, 2006; Boyce *et al.*, 2010) and therefore also may reduce marine snow production. Warming of surface waters has occurred in the Sargasso Sea and

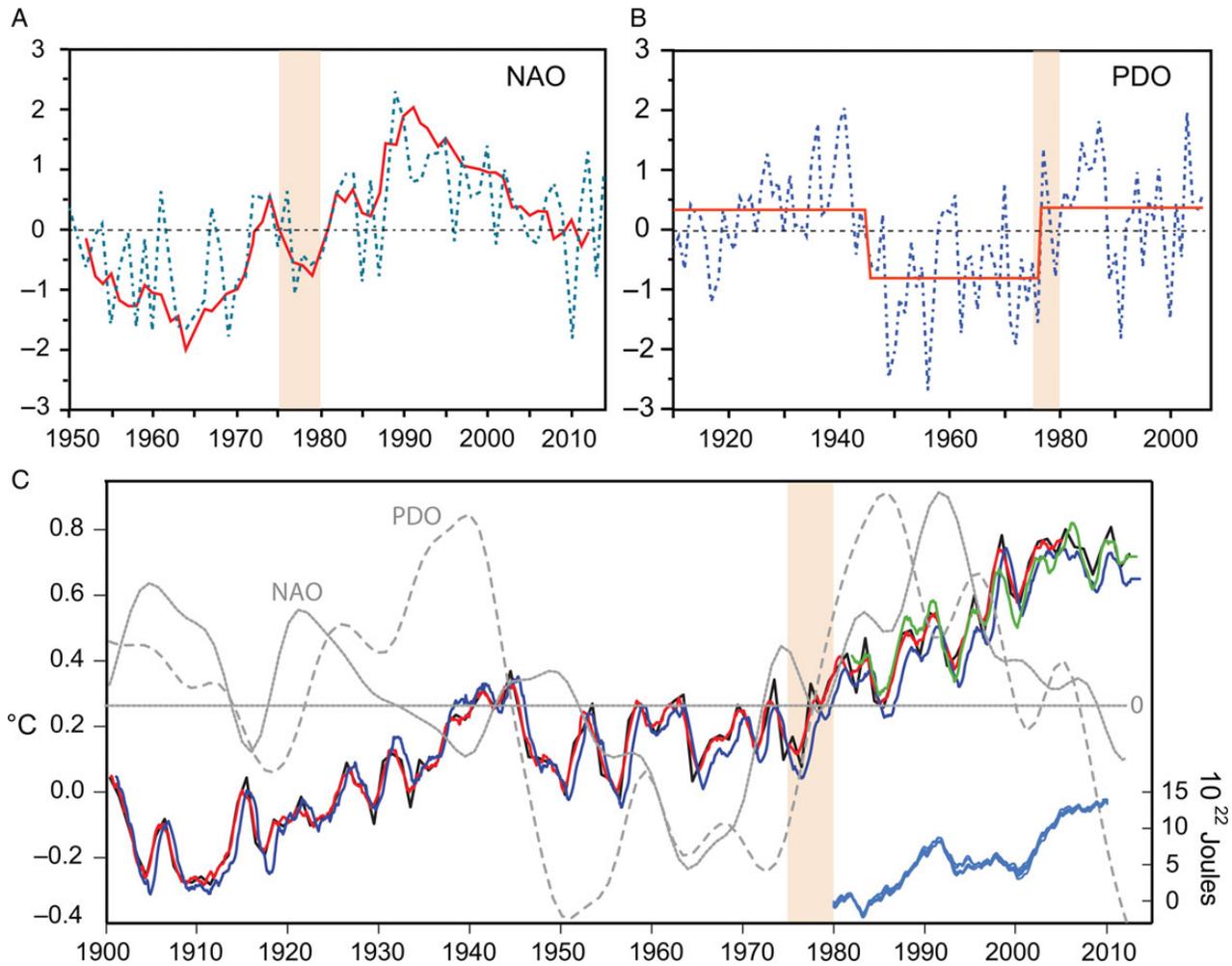


Figure 4. Time series of (A) the North Atlantic Oscillation (NAO) Winter–Spring Index showing the monthly index for January, February, and March for each year (dotted line) and the standardized 5-year running mean index (solid line) modified from a plot made by the US National Oceanic and Atmospheric Administration (NOAA) Climate Prediction Center (http://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/JFM_season_ao_index.shtml), (B) the winter Pacific Decadal Oscillation (PDO) (dotted line) and net displacements in the time series or regime shifts (solid line) modified from Overland *et al.* (2010), and (C) global mean temperature anomaly from multiple sources plotted as 24 month running means (relative to 1900–1949) compared with the decadal filtered PDO and NAO (December–March) indices (no y-axis scales), and also showing changes in heat content in the upper 700 m of the global ocean (bottom-right inset) after 1980, modified from Trenberth and Fasullo (2013). The shaded bar shows the 1975–1980 period after which eel recruitment or abundance was declining. This figure is available in black and white in print and in colour at ICES *Journal of Marine Science* online.

western North Pacific regions during the period of the recruitment declines (Levitus *et al.*, 2000; Polyakov *et al.*, 2005; Bonhommeau *et al.*, 2008a, b; Durif *et al.*, 2011) and global surface and ocean temperatures have also increased since the 1970s (Figure 4C; Trenberth and Fasullo, 2013). Changes in mixed layer depth or the actions of eddies, fronts, and winds are also thought to influence productivity (Knights, 2003; Palter *et al.*, 2005) and have been examined in relation to biological characteristics in the Sargasso Sea (Richardson *et al.*, 2014) and recruitment fluctuations (Friedland *et al.*, 2007).

Other types of oceanic changes that are potentially linked to ocean-atmosphere factors also may have occurred such as shifts in the latitudes of fronts (Kimura *et al.*, 2001; Kimura and Tsukamoto, 2006; Friedland *et al.*, 2007), or the latitudes of bifurcation of currents (Kim *et al.*, 2007; Zenimoto *et al.*, 2009), which have the potential to influence eel recruitment levels by disrupting larval transport pathways. A shift in current patterns in the western Sargasso Sea has been hypothesized to be associated with the

onset of eel declines in the Atlantic (Baltazar-Soares *et al.*, 2014). Changes to the Gulf Stream system were also considered as possibly affecting recruitment of the Atlantic eels (Castonguay *et al.*, 1994b), and changes in the Gulf Stream and the North Atlantic gyre occur that appear linked to the NAO (Curry and McCartney, 2001). However, Bonhommeau *et al.* (2008a) did not find any statistical evidence of a correlation between recruitment and gyre circulation and Gulf Stream-related parameters (Gulf Stream Index and Transport Index) for the European eel. Kettle *et al.* (2008) suggested that the NAO might influence the numbers of silver eels migrating to the spawning area through climatic factors such as rainfall, with decreases in rainfall reducing the number of migrating eels.

In addition to the statistical correlations that have been found between interannual fluctuations in eel indices and ocean-atmosphere parameters, regime shifts occurred at about the same time as the northern hemisphere eels began to decline. Both the NAO and Pacific Decadal Oscillation (PDO) shifted phases in the 1970s and

1980s (Figure 4A and B; Hurrell, 1995; Hare and Mantua, 2000; Lehodey *et al.*, 2006; Overland *et al.*, 2010). In the Sargasso Sea, during low NAO index periods such as before the eel declines began, storm tracks shift to the south and cold air flows more frequently off North America, helping to cool surface waters, increase mixed layer depths, and cause increased nutrient levels (Drinkwater *et al.*, 2003). In the western Pacific where the Japanese eel has its spawning and recruitment areas, it is more difficult to establish direct links with the PDO (Tzeng *et al.*, 2012), whose effects are more related to the northeastern Pacific (Hare and Mantua, 2000; Lehodey *et al.*, 2006; Overland *et al.*, 2010). Changes in productivity have been observed in the western side of the North Pacific gyre though (Watanabe *et al.*, 2005; Ishida *et al.*, 2009), and shifts in the *El Niño* Southern Oscillation Index (ENSO) have been hypothesized to influence recruitment of the Japanese eel (Kimura *et al.*, 2001). The shifts that occurred in the NAO and PDO in the 1970s were accompanied by increases in global temperatures that included ocean surface temperature increases (Figure 4C; Levitus *et al.*, 2000; Polyakov *et al.*, 2005; Trenberth and Fasullo, 2013), and this could reduce ocean productivity and the feeding success of eel larvae as proposed by Knights (2003) and Bonhommeau *et al.*, (2008a,b).

Another change in the ocean that could have been important for eels is that Karl *et al.* (2001) proposed there was a “photosynthetic population domain shift” in the North Pacific gyre, which occurred at about the time that the eel declines began. There appeared to have been a shift to a prevalence of cyanobacteria and a reduction of diatoms or other phytoplankton that was driven by the globally widespread and abundant photosynthetic cyanobacterium *Prochlorococcus* (Partensky *et al.*, 1999; Flombaum *et al.*, 2013). Its abundance increased in the North Pacific gyre after 1976 (Karl *et al.*, 2001). There is also another common species of cyanobacteria species, *Synechococcus*, which co-occurs with *Prochlorococcus* worldwide, but is typically less abundant, with an inverse pattern of abundance fluctuations (Campbell *et al.*, 1994; Cavender-Bares *et al.*, 2001; DuRand *et al.*, 2001; Casey *et al.*, 2013; Flombaum *et al.*, 2013; Pasulka *et al.*, 2013). It appears that when nutrient levels are high, diatoms or other eukaryotic phytoplankton thrive and blooms occur, but when nutrients are low, *Prochlorococcus* is abundant, producing the tendency for an inverse relationship between the abundance of the two types of primary producers in both the Pacific and Atlantic oceans (Figure 5; Partensky *et al.*, 1999; Karl *et al.*, 2001; Rousseaux and Gregg, 2012; Casey *et al.*, 2013).

This may be important for eels because it is phytoplankton such as diatoms that are thought to be important for producing exudates that become transparent exopolymer particles (TEPs) containing carbohydrates, which provide the “glue” that facilitates the aggregation of marine snow (Alldredge and Silver, 1988; Alldredge and Jackson, 1995; Passow, 2002). Bacteria also release some TEP (Passow, 2002; Ortega-Retuerta *et al.*, 2010), and cyanobacteria can release various types of compounds depending on their habitat, some of which are toxic to other organisms, but also include carbohydrate and carboxylic acid exudates (De Philippis and Vincenzini, 1998; Bertilsson *et al.*, 2005; Sychrová *et al.*, 2012; López-Sandoval *et al.*, 2013). It is unclear though, how important cyanobacteria may be for releasing exudates that may contribute to marine snow production. Carbohydrates appear to coat the outer parts of cyanobacteria (i.e. *Synechococcus*; Biersmith and Benner, 1998), so laboratory measurements that found low percentages of “exudates” from *Synechococcus* and *Prochlorococcus* (Biersmith and Benner, 1998; Bertilsson *et al.*, 2005; López-Sandoval *et al.*, 2013) could be artificially high as a result of the effect of the filtration process releasing materials from the outer

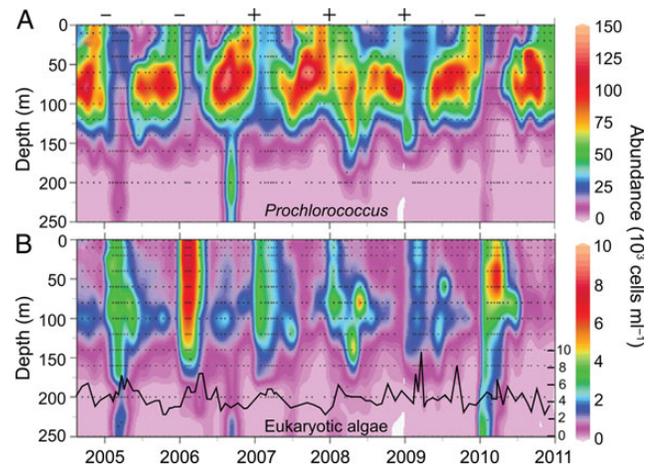


Figure 5. Time-series plots of the abundance of (A) autotrophic *Prochlorococcus* cyanobacteria, and (B) eukaryotic algae measured at the Bermuda Atlantic Time Series Station (BATS) in the northern Sargasso Sea using flow cytometry modified from Casey *et al.* (2013). Plots of biomass of eukaryotic algae indicated that the winter 2005 bloom was much larger than reflected in abundance data (not shown). Total particulate organic carbon (POC) fluctuations in the upper 250 m are shown as a black line in the bottom of (B) (units = g C m^{-2}). NAO phase is shown as “+” or “-” at the start of each year along the top of each year.

coating during the experimental measurement processes, which are not actually exudates.

In the northern Sargasso Sea though, a strong linear relationship was found between eukaryotic phytoplankton abundance and particulate organic carbon levels (Durand *et al.*, 2001) and the export of these particles from the surface layer appears linked to the abundance of large diatoms (Buesseler, 1998). High concentrations of TEP has usually been associated with phytoplankton blooms, especially of diatoms (Passow, 2002), with exudates of TEP carbohydrates originating in various types of phytoplankton including dinoflagellates, but to varying degrees (Biersmith and Benner, 1998; De Philippis and Vincenzini, 1998; López-Sandoval *et al.*, 2013). Further evaluation of TEP and marine snow production levels in the open ocean spawning areas of anguillid eels is needed, as has begun (Kodama *et al.*, 2014), especially for evaluating the role of *Prochlorococcus* and *Synechococcus*, which may contribute to particulate export in the northern Sargasso Sea, but at lower levels than eukaryotic phytoplankton (Lomas and Moran, 2011). It is possible, however, that it is not the cyanobacterial component that is primarily influencing marine snow production in these areas, at least when productivity levels are high.

Therefore, if there has been a trend towards generally greater cyanobacterial abundance and lower diatom or other phytoplankton abundance in recent decades, this might reduce the amount of marine snow that is available to leptocephali as food. Some evidence of this occurring, at least in terms of high cyanobacterial abundance and low diatom abundance, has been seen in studies in the Sargasso Sea eel spawning area, where *Prochlorococcus* was widespread and abundant, but diatoms were rare (Cavender-Bares *et al.*, 2001; Riemann *et al.*, 2011). *Prochlorococcus* is abundant in the central North Pacific (Campbell *et al.*, 1994; Karl *et al.*, 2001; Pasulka *et al.*, 2013) and western North Pacific (Flombaum *et al.*, 2013), but it is difficult to fully evaluate if there has been a shift in the

relative abundance of cyanobacteria such as *Prochlorococcus* and diatoms however, since the existence of *Prochlorococcus* was only discovered in 1988 (Chisholm *et al.*, 1988), which is after the declines of the eels began. *Prochlorococcus* is ubiquitously present in the upper 100–200 m from 40°N to 40°S, and may be the most abundant photosynthetic organism on earth (Partensky *et al.*, 1999; Flombaum *et al.*, 2013). However, recent research at the time-series station near Bermuda (BATS) in the northern part of the Sargasso Sea clearly documented the shift between high abundance of *Prochlorococcus* and eukaryotic phytoplankton, along with higher abundances of eukaryotic phytoplankton in winters with a negative NAO phase than those with a positive phase (Figure 5; Casey *et al.*, 2013).

Decreases in phytoplankton production or productivity appear to have occurred in both the North Pacific and North Atlantic (Martinez *et al.*, 2009; Boyce *et al.*, 2010) during the periods of eel declines, and decreases in nutrients, Chl-a, and larger phytoplankton such as diatoms were reported in the western North Pacific (Watanabe *et al.*, 2005; Ishida *et al.*, 2009) in the larval development area of the Japanese eel. However, because of the possibility of a shift towards cyanobacteria when nutrient levels and productivity are lower, these reductions in overall productivity (including cyanobacteria) may not fully reflect the changes in amount of marine snow that is available to leptocephali. The possibility that there have been substantial decreases in larger phytoplankton such as diatoms that contribute to marine snow should be considered, because this would not be detected in general indices of productivity that are now known to include the contributions of *Prochlorococcus* and *Synechococcus*, which are abundant when diatoms are at low levels. Studies that include time series of multiple types of both prokaryotic and eukaryotic autotrophic organisms such as that of Pasulka *et al.* (2013) in combination with evaluations of marine snow concentrations may provide a better understanding of these issues in relation to the early survival of eel larvae.

Effect of density-dependent early larval survival?

After it became known that leptocephali feed on marine snow materials, it was hypothesized that reductions in productivity in the ocean could reduce larval survival by reducing the food available to the larvae, and correlations between eel abundance indices and

time series of the NAO index or sea surface temperature have provided support for this possibility as described above (Knights, 2003; Bonhommeau *et al.*, 2008a, b; Kettle *et al.*, 2008; Arribas *et al.*, 2012). If there have been reductions in marine snow production or a shift in the composition of marine snow, this could affect levels of recruitment each year if density-dependent survival of the first-feeding early larvae occurs in the spawning area. Small early-stage larvae might be the most vulnerable to mortality because the larger leptocephali would have the ability to consume a wider range of marine snow particle sizes and would have a larger volume of energy reserves in their bodies to survive until food could be found. The small recently hatched larvae would require a relatively small size range of marine snow to ingest, unless they are able to break up larger particles, and there would theoretically be many small larvae looking for food at the same time after a spawning event took place (Figure 6). Although difficult to empirically establish as a primary mechanism regulating recruitment levels in marine fish populations, density-dependent survival of the first-feeding or later larvae as a result of food availability, or the existence of a “critical period” for first-feeding larvae as first proposed by Hjort (1914) remain as important hypotheses in fisheries ecology (Anderson, 1988; Myers, 2002; Houde, 2008; Robert *et al.*, 2014). Thus, this apparently can be considered as a possible factor affecting eel larvae feeding on marine snow.

Female anguillid eels may be able to spawn millions of eggs at one time and place due to their high fecundity (Barbin and McCleave, 1997; MacNamara and McCarthy, 2012), so many larvae could hatch out in the same area. The eggs would develop over several days before hatching out as preleptocephali, which then start feeding after they develop eyes and teeth (Miller, 2009). Some diffusion of the eggs and larvae would occur during the several days of drifting, but research on the Japanese eel suggests that both eggs and preleptocephali may become concentrated in a very narrow depth range at the top of the thermocline (Tsukamoto *et al.*, 2011; Aoyama *et al.*, 2014). Marine snow likely accumulates at density gradients within the thermocline (MacIntyre *et al.*, 1995), so these layers should be good feeding environments for the young larvae. However, accumulation of the larvae within a narrow layer could amplify the chance for density-dependent competition for food

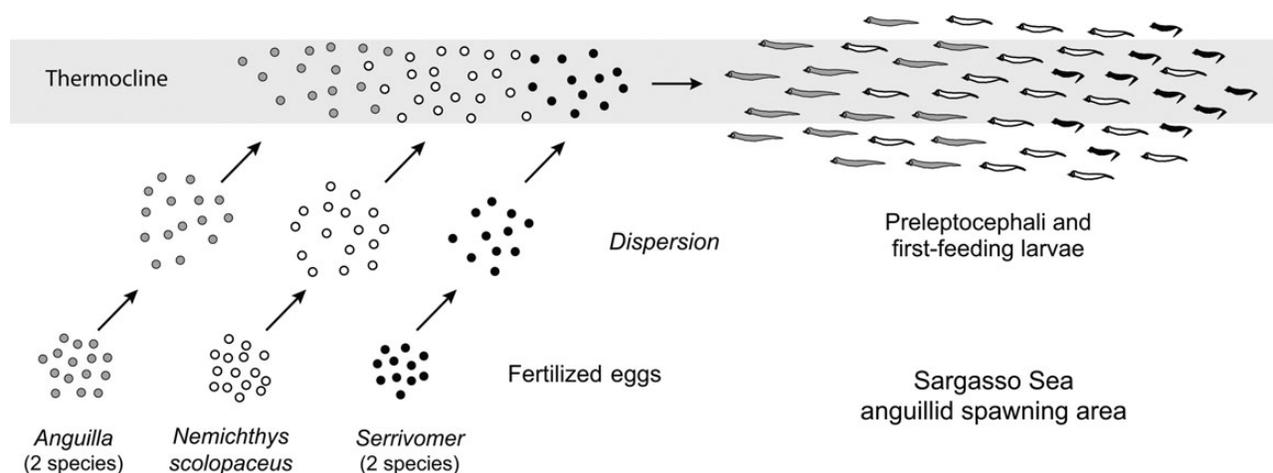


Figure 6. A diagrammatical representation of possible sympatric spawning of anguillid (*Anguilla anguilla* and *A. rostrata*) and mesopelagic eels in their Sargasso Sea spawning area showing how their eggs and pre-feeding larvae may float up and diffuse out from the spawning locations resulting in overlapping accumulation of their first-feeding larvae at density gradients in the thermocline as has been indicated by the depth distribution of eggs and preleptocephali of the Japanese eel, *Anguilla japonica* (Tsukamoto *et al.*, 2011; Aoyama *et al.*, 2014).

particles among the first-feeding larvae (Figure 6). If anguillid eels form spawning aggregations, that would further contribute to the potential for high densities of larvae in areas where spawning of several female eels has occurred. In addition to competition among different species of anguillid larvae in both of the northern hemisphere spawning areas (*Anguilla anguilla* and *A. rostrata* have overlapping spawning areas and *A. marmorata* spawns in an overlapping region with *A. japonica*; Kuroki *et al.*, 2009), other species of anguilliform eels of the mesopelagic eel taxa of Nemichthyidae, Serrivomeridae, and *Eurypharnx pelecanooides* also spawn at the same general places and times as the anguillid eels as evidenced by collections of their abundant small larvae (Miller and McCleave, 1994) or eggs (Yoshinaga *et al.*, 2011) as depicted in Figure 6. This might sometimes result in competition for marine snow particles by the first-feeding larvae of anguillid eels and mesopelagic eels, which if severe enough, could cause mortality of the larvae. The depth distributions of small larvae may change soon after successful feeding begins though, if they exhibit diel vertical migration as they do in the Sargasso Sea (Castonguay and McCleave, 1987).

A recent study in the Sargasso Sea spawning area of the Atlantic eels found lower larval abundance of both species of *Anguilla* during the spawning season in 2011 compared with the larval abundances in the same areas and months in 1983 and 1985 (Hanel *et al.*, 2014). This indicated that the low abundance of larvae (leading to low recruitment) likely begins within the spawning area and does not result primarily from low survival of the larger leptocephali during their drift towards their recruitment areas (Hanel *et al.*, 2014). A lower number of spawners reaching the spawning area is one explanation for the low larval abundances, and another is that reductions in early larval survival have occurred as a result of reductions in marine snow production. A much lower abundance of the smallest size class of *Nemichthys scolopaceus* larvae was observed in 2011, but these were among the most abundant types of leptocephali during the earlier period (Miller and McCleave, 1994), suggesting that there was low larval survival of the early stage larvae of both anguillid eels and *N. scolopaceus* in 2011 (Hanel *et al.*, 2014). However, more information is needed to be able to assess if density-dependent early larval survival is occurring within anguillid eel spawning areas, if later larval stages are also affected, or if low numbers are due to reduced numbers of effective spawners.

Possible synergistic effects on eel declines

Examination of the basic timelines of potential anthropogenic impacts on eels (e.g. Figures 2 and 3) and of the occurrences of ocean-atmosphere regime shifts (e.g. Figure 4) that could affect eels suggest that both types of factors could have contributed to the declines observed in the northern hemisphere anguillid eels (e.g. Figure 1). Habitat loss, habitat quality reductions, chemical contamination, parasite introductions, and fishing pressure could have all built up to the time of the declines, then oceanic regime shifts could have also occurred at the same time. These changes could have simultaneously affected their juvenile growth stage (slower growth due to greater competition for reduced food resources), the production of silver eels (reduced species ranges and population sizes, hydropower turbine and pump mortality), the oceanic migratory or reproductive success of silver eels (impacts of parasites, contaminants, or viruses) and their larval survival. It is also possible though that the two types of impacts could have acted synergistically at times to further amplify the reductions or fluctuations in recruitment. For example, if population contractions resulted in a reduction in variation in spawning times of each

species by reducing numbers of eels from the margins of the ranges, which might tend to spawn in the early or later parts of the spawning season, then spawning may have been more concentrated within the middle part of the spawning season. Some suggestion that this might occur can be implied from the possible loss of contribution to spawning of the large fecund female eels of the St Lawrence River (Casselman, 2003), or potential reductions in eels from the northern (long migration distance) or especially the southern parts (short migration distance) of the range of the European eel (Kettle *et al.*, 2011). If this occurred, it might result in a higher percentage of spawning occurring within a more limited period of the spawning season, when there could be higher levels of density-dependent mortality compared with during times with less spawning activity. If fewer eels spawn during early or later spawning periods when there might be lower levels of density-dependent early survival, then a loss of these eels from the population could have had a proportionally higher influence on recruitment reductions than the loss of eels from central parts of the ranges. More detailed evaluations of each aspect of this tentative hypothesis will be needed however, before it can be considered to have any validity.

There seems to have been slight increases in recruitment observed for these species in the last few years as reported for the European eel (Figure 1), which could be related to management actions resulting in increased spawner escapement (ICES, 2013, 2014). There may also have been shifts in oceanic conditions such as those related to the NAO and PDO returning to negative phases (Figure 4A and C) along with a slowdown in global surface temperature increases in recent years (Figure 4C; Li *et al.*, 2013; Trenberth and Fasullo, 2013), with the NAO reaching one of its lowest levels on record in 2010 (Taws *et al.*, 2011). These might have facilitated increased marine snow production through the mechanisms described above, resulting in greater larval survival and slight increases in recruitment. So it seems possible that both anthropogenic and environmental factors have the potential to be contributing to recent recruitment increases.

Summary

Despite uncertainty in linking the declines of the recruitment of northern hemisphere anguillid eels to any one specific cause, it seems possible that a variety of factors came together at about the same time to cause the drastic declines that were observed. Anthropogenic changes to the habitats used by yellow eels built up to a climax corresponding to the times of the declines, which likely reduced the production and health of silver eels, then for the Atlantic eels the swimbladder parasite *A. crassus* was introduced. Oceanic regime shifts also occurred simultaneously that might have resulted in reductions of larval survival. Synergistic effects resulting from species range contractions and a loss of silver eels reaching the spawning areas during times when there would be a lower effect of possible density-dependent early larval survival might also have occurred. Regardless of the exact contributions of each factor to the eel declines, these species experienced a wide range of potentially serious impacts building up to or occurring at the same time. The detailed effects of each type of impact will require continued evaluation in future years as the fate of anguillid eels unfolds around the world.

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Handling editor: Caroline Durif