

The formation of the population genetic structure of the European eel *Anguilla anguilla* (L.): a short review

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The complex life cycle of the European eel predestines unique formation of the population genetic structure. The sweepstakes reproductive success and the chaotic genetic patchiness are the characteristics of this species and its population genetic structure could be described as a genetic mosaic, whose formation is predetermined by the reproductively isolated groups of eels. Due to the fact that until now it was impossible to investigate the genetic parameters of the spawning eels in their spawning grounds the population genetic structure and its formation is still not understood. Currently three main models are available: panmixia, isolation by distance and isolation by time. In order to understand the formation of the population genetic structure of the European eel its intraspecific evolution should be more comprehensively studied and the multidisciplinary seascape genetics should be applied.

Key words: *Anguilla anguilla*, population genetic structure, formation, models

INTRODUCTION

The European eel *Anguilla anguilla* (L.) is a commercially important fish species (Dekker, 2004; Shiao et al., 2006) which belongs to the Anguillidae family (Bastrop et al., 2000) and is naturally distributed in the Atlantic Ocean and Europe (Albert et al., 2006). The European eel has been recently listed in Appendix II of CITES Red List of Endangered Species (Maes, Volckaert, 2007) according to regulation No. 1100/2007 by European Commission as the stock of this species significantly declined several decades ago and had not recovered since then in Europe (Åström, Dekker, 2007; Winter et al., 2007). Despite necessary restrictions and control in the exploitation and trade market of this species, the principal obstacles for the protection, conservation and management of the European eel are the deficiency of information regarding biology of this fish (Boëtius, Harding, 1985; Casellato, 2002; Dannewitz et al., 2005;

Bonhommeau et al., 2009) and the primary cause of its decline (Bonhommeau et al., 2008; Aoyama, 2009). The biology of this fish is not sufficiently studied because the life cycle of this species is quite complicated (Daemen et al., 2001; Lecomte-Finiger, 2003; Vasemägi, 2009). The complicated life cycle of the European eel is mainly characterized by the facultative catadromy (Edeline, 2007) and surely predestines unique formation of the population genetic structure of this species.

The population genetic structure, the formation of which depends on fish spawning, of any fish species could be defined as a pattern of distribution of genetic variation in space and time within and between populations (Laikre et al., 2005; Samuilovienė, Kontautas, 2012). An exhaustive examination of population genetic structure using different molecular markers provides us knowledge that ensures the opportunity to create the strategy of sustainable exploitation of resources at a genetic diversity level (Hauser, Carvalho, 2008) and preserve the genetic diversity of the species (Laikre et al.,

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2008). Whereas the information regarding the formation of the population genetic structure of fish species is important both for the theoretical and practical perspectives. Despite many investigations into the population genetic structure of the European eel it is still not completely studied (Avisé et al., 1986; Dannewitz et al., 2005; Maes et al., 2006; Cagnon et al., 2011) and understood (Vasemägi, 2009; Kettle et al., 2010; Avisé, 2011). In fact, thus far the accumulated molecular data gives only limited insights into the formation of the population genetic structure of this species.

The main objectives of this paper are to present what is currently known about the formation of population genetic structure of the European eel and how our understanding about this fundamental process could be improved.

MATERIALS AND METHODS

Main aspects of the European eel biology and genetics

The life cycle of the European eel. Due to the fact that the spawning sites of the European eel have not been found and spawning eels have not been observed by scientists yet (Boëtius, Harding, 1985) almost all available information concerning the biology of the eels in their breeding grounds was accumulated using indirect methods (Maes, Volckaert, 2007; Aoyama, 2009; Bianchini et al., 2009; Bonhommeau et al., 2009). It is generally accepted that the spawning of the European eel should take place in the Sargasso Sea because here >10 mm in size leptocephalus larvae was found and it is known that eels, inhabiting the water bodies of Europe, are capable of reaching this sea (5 000–6 000 km) (Van Ginneken, Maes, 2005; Van Ginneken et al., 2005). Experimentally determined 18.7–18.8 °C temperature and 250–302 m depth indicate that the spawning of eels should take place in the warm waters of the upper layers of the sea (Fricke, Kaese, 1995). Since the European eel is considered to be semelparous fish each individual presumably participates in the spawning process only one time, i. e. after the spawning eels die (Bastrop et al., 2000). It is supposed that the spawning of eels is collective and females are able to produce more than 9 million pelagic eggs that are 0.9–1.4 mm in size (Virbickas, 2000; Van Ginneken, Maes, 2005). From the fertilized pelagic

eggs larva hatches, which after a short growth period obtains specific features and is called leptocephalus larva (Miller, 2009). With the help of various sea currents, of which the Gulf stream is the most important, the leptocephalus larvae travel from the Sargasso Sea to Europe or the northern part of Africa (Bonhommeau et al., 2008). Thus far it is not clear whether the transportation of the leptocephalus larvae is passive or they are able to swim actively and in turn influence the final destination of their journey (Bonhommeau et al., 2009). When leptocephalus larvae reach the continent they metamorphose to the glass eels that are able to inhabit seas and estuaries or migrate upstream to the rivers (Edeline, 2007). The movement of the glass eels from the sea to the outfall of the rivers is determined by the chemoreception (Sola, Tongiorgi, 1996): it was experimentally demonstrated that some cues and water salinity (in other words, the particular molecules, their concentrations and their interactions with other molecules) have influence on the behaviour of the glass eels. It should be noted that the upstream migration of eels is also density- dependent, i. e. the greater density of eels predestines deeper inland invasions into the continent. After a short period spent in the continental water ecosystems the transparent bodies of the glass eels begin to lose transparency because of appearance of pigmentation and glass eels at first become elvers and when pigmentation process is completed they are called young yellow eels (Albert et al., 2006). In the continent yellow eels could live and grow from several years to several decades (Ringuelet et al., 2002). Pronounced sexual dimorphism is the characteristic of this species: the eel males tend to be smaller and mature faster compared to females (Winter et al., 2007; Kettle et al., 2010). The determination of sex is not dependent on the particular chromosomes, it mainly depends on the density of young eels in water volume (Huertas, Cerdà, 2006). The greater density of the individuals predestines the larger number of eel males. Growth rate, higher water temperatures and saline conditions may be also involved in the mechanism of sex differentiation (Davey, Jellyman, 2005). For instance, individuals experiencing rapid growth prior to gonad differentiation tend to develop as males, whereas eels that initially grow slowly are more likely to develop as females. Holmgren (1996) experimentally

demonstrated that water temperature influenced the observed sex ratios, but probably not through direct influence on the sex differentiation. Sexually maturing eels are called silver eels because after the silvering process the dominant color of their bodies is silver (Durif et al., 2005). The silvering process starts earlier in the eel males (>4 years old) compared to the females (>7 years old) (Van Ginneken et al., 2007). Before and / or during the final journey from the continent to the Sargasso Sea eels experience many morphological, physiological and ethological alterations (Fricke, Kaese, 1995; Lintas et al., 1998). For example, the body darkens, the size of eyes increases to ensure improved vision in the depth, jaws become more extended, the bones and the muscles demineralize, gonads develop, the digestive tract atrophies and eels stop feeding. From the conducted experiments it is known that the sexual maturation of eels can be completed only during their travel to the Sargasso Sea or when they reach their spawning sites (Palstra et al., 2008) and the distance of 6 000 km could be overcome within 180 days by silver eels (Van Ginneken et al., 2005). The migration of the European eel is mainly initiated by the temperature of the water, the moon phase and the photoperiod (Okamura et al., 2002). The migrations of eels from rivers and lakes can be massive and collective (Cullen, McCarthy, 2003). The time of the migration is diverse because it depends on the accumulated eel fat reserves (Svedäng et al., 1996) and geographical location (Maes, Volckaert, 2007). Eel females start their migration after the vacuolization of their oocytes (Virbickas, 2000). There are indications that even 57 years old eels are able to travel to the spawning grounds (Poole, Reynolds, 1998). During migration to their spawning sites, instead of feeding, eels are using accumulated fat reserves (Geeraerts, Belpaire, 2010). Ecological studies concerning eels migration to their spawning sites are currently lacking (Boëtius, Harding, 1985; Casellato, 2002; Chow et al., 2009). Several silver eels that were caught in the 220–660 m depth of the Mediterranean Sea indicate that eels could swim in groups to their spawning grounds (Bianchini et al., 2009).

Migration loops. During the analysis of the life strategies of the representatives of the *Anguilla* genus it is accepted to use the migration loop concept (Tsukamoto et al., 2002). The migration loop

is the migration route of the animal that migrates between the different environments, i. e. eels move from the ocean to freshwater ecosystems. Schematically the migration loop is presented as an ellipse, the different ends of which mark the spawning site and the growing grounds of the migrating fish, respectively. Due to distant migrations of the European eel the extent of the migration loop of this species (5.2×10^6 km²) is greater compared to other representatives of the *Anguilla* genus (Van Ginneken, Maes, 2005). The distance from the Sargasso Sea to the growing grounds varies from 2 500 km to more than 7 000 km (Kettle et al., 2010). In order to schematically represent three different groups of eels that are travelling from the Sargasso Sea to the Mediterranean Sea, the North Sea and the Baltic Sea it would be necessary to draw three migration loops. The number of the migration loops depends not only on the geographical distances but also on the different habitats, i. e. sea, estuary, lagoon, river, lake. The length of migration loops between different sexes of eels is different. Firstly, the journey from the continent to the spawning grounds of most male eels begins from the seas or lagoons while most females have to travel longer distances from their growing places in the continental freshwater water bodies (Virbickas, 2000). Secondly, the European eel is characterized by the sex-biased latitudinal distribution (Maes, Volckaert, 2007). For example, in the northern parts of Europe, such as the Baltic Sea region, females are more common. Sex-biased geographical distribution is mainly predetermined by the density-dependent migrations of young eels into the continent (Andersson et al., 2012). In the context of the decreasing population size of European eel during several decades period the density dependent changes in sex ratio (towards higher female:male proportion) were evident in European countries, such as Norway, Italy and the United Kingdom. It is noteworthy that in the Baltic Sea region lower recruitment was historically observed (Dekker, 2004). Consequently, due to poor stock conditions and low densities in this region females dominate not only in freshwater environment but also in the sea.

Sweepstakes reproductive success (SRS). Just as many other marine organisms the European eel is characterized by the following: the extensive geographical distribution, long age, late maturation,

great fertility, small number of survivors that reach their spawning sites due to the continuously changing conditions in the ocean (Daemen et al., 2001; Bonhommeau et al., 2008; Hedgecock, Pudovkin, 2011). All these aspects of the eel biology predetermine that the individuals from different generations differ genetically because in each spawning process a relatively small number of silver eels that produce many offsprings participate. Such situations are described by the SRS concept which explains how abundant marine organisms can have low effective population sizes (N_e).

Chaotic genetic patchiness (CGP). The groups of the glass eels that arrive to the same geographical locations in different times are called the recruitment waves (Pujolar et al., 2006). When the statistically significant genetic differentiation is determined between the recruitment waves, but not between the samples of the adult eels, then this phenomenon is defined by the CGP concept (Hellberg et al., 2002). In the marine organisms CGP could appear because of several fundamental reasons (Selkoe et al., 2006; Hedgecock, Pudovkin, 2011): young individuals come from the different populations (the distribution of these individuals could be affected by the sea currents), the natural selection on early life stages could winnow the genetic diversity of larvae and recruits, differential survival of genotypes after settlement and before sampling, SRS. It should be noted that nowadays there is a tendency to use the CGP concept in the situations when the major reason of the detected genetic differences between the samples of marine organisms is not clear (Selkoe et al., 2010; Pujolar et al., 2011a). Consequently, currently two different phenomena are described with just one CGP concept: i) statistically significant genetic differentiation is determined between the temporal samples of young organisms, but not between the samples of the adult organisms; ii) the major reason of the detected genetic differences between the samples of marine organisms is not clear because the determination of these genetic differences could not be explained by the spatial and temporal differences between the collected samples. In our opinion, in the future it would be rational to define a new concept for the situations when the genetic differences between the samples of marine organisms are statistically significant, but not stable in space and time.

The genetic mosaic. The population genetic structure of the European eel is characterized by a genetic mosaic, which is formed due to the existence of reproductively isolated groups (Daemen et al., 2001). The recent data (Ragauskas, 2013; Baltazar-Soares et al., 2014) shows that the appearance of the genetic mosaic in the species is mainly predetermined by the existence of the different genetic lineages, represented by phylogenies of different mtDNA regions, in this species. The appearance of the genetic mosaic in the European eel to a lesser degree is predetermined by the CGP and the SRS.

The main models of the formation of the population genetic structure of the European eel

Nowadays there are three main models explaining the formation of the population genetic structure of the European eel: panmixia, isolation by distance (IBD) and isolation by time (IBT). Schematically these models are presented in Figure.

Panmixia. Unpredictable conditions in the ocean, the variations of sexual maturity at age, the mixed groups of eels, which are migrating to their spawning grounds, prolonged spawning season, the sexual dimorphism and differences between the migration loops of males and females together with the information obtained from the studies of the population genetics of the European eel indicate that the formation of the population genetic structure of this species is best explained by the model of panmixia (Figure A) (Maes, Volckaert, 2007; Vasemägi, 2009; Avise, 2011). Due to the fact that several publications challenging the panmixia hypothesis were published quite recently (Daemen et al., 2001; Wirth, Bernatchez, 2001; Maes, Volckaert, 2002) currently the maintenance of the panmixia hypothesis requires the SRS and the CGP concepts (Pujolar et al., 2007, 2011a). These concepts are necessary because the population genetic structure of the European eel is characterized by a genetic mosaic, which indicates the existence of reproductively isolated groups (Kettle et al., 2010), and statistically significant genetic differentiation could be determined between the recruitment waves (Pujolar et al., 2006). Despite many recent publications confirming that SRS phenomenon is common in marine animals and the fact that it clearly explains how marked genetic differences

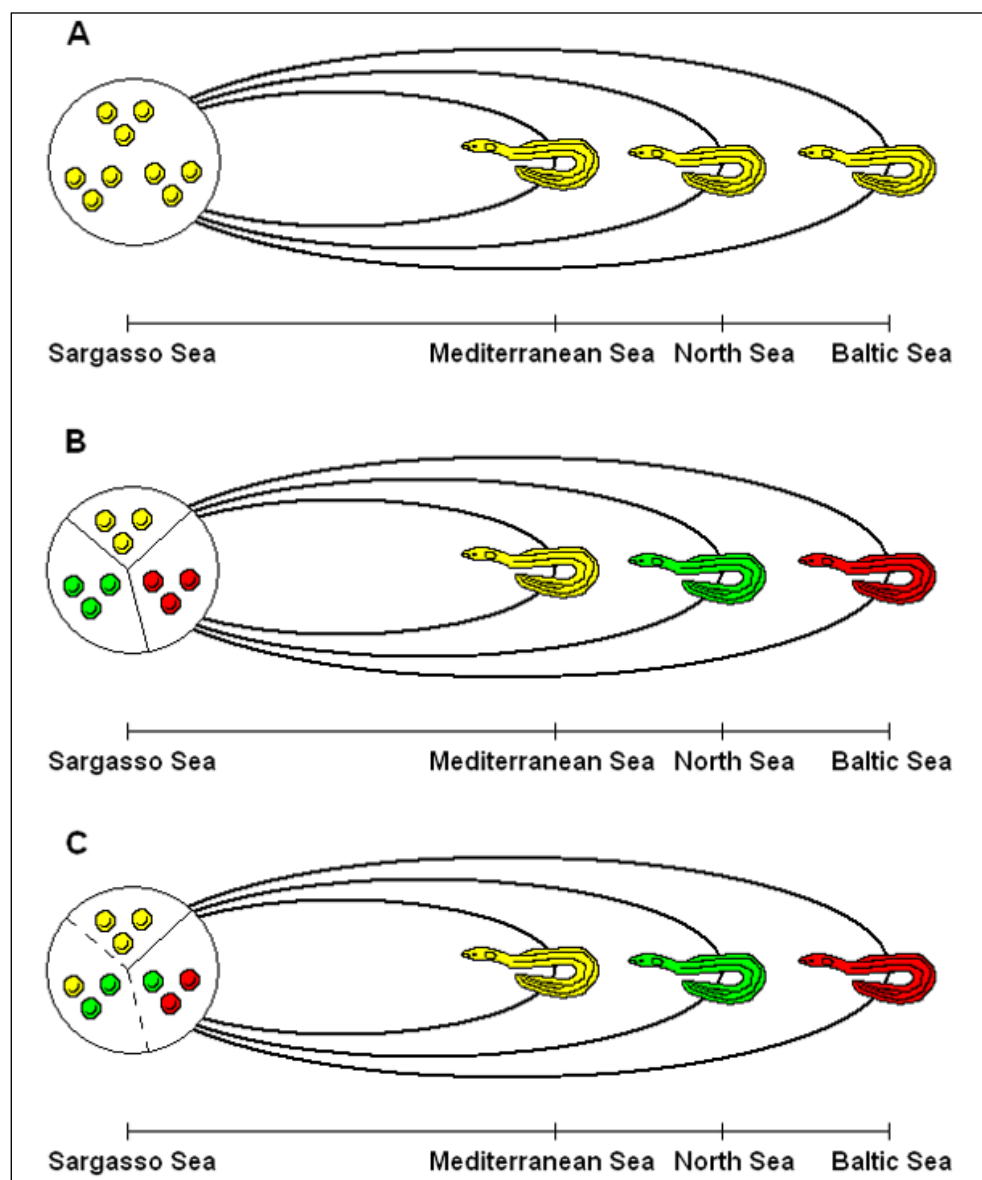


Figure. The main models of the formation of the population genetic structure of the European eel: **A** – panmixia; **B** – isolation by distance; **C** – isolation by time; migration loops of eels are represented by ellipses; different colors of silhouettes of eels and eggs represent their genetic differences; eggs in the circle represent spawning site or sites in the Sargasso Sea; dotted line shows that some individuals from the distinct populations can meet and spawn together in one particular spawning site

between the different groups of individuals can appear in panmictic species (Hedgecock, Pudovkin, 2011), based on the results of Selkoe et al. (2010) research it might be suggested that CGP is not an argument solid enough for validation of the panmixia hypothesis in the European eel. Firstly, the CGP may emerge not only due to stochastic processes in the ocean but it can have a biological meaning (Selkoe et al., 2008). Secondly, nowadays we still lack the essential information about

the formation of the population genetic structure of the European eel (Daemen et al., 2001; Vasmägi, 2009; Avise, 2011) because the collection of spawning eels samples in precise spawning sites is problematic. Finally, thus far there were no attempts to connect the seascape variables in order to explain the formation of the population genetic structure of this species. Other arguments for or against the panmixia hypothesis are presented in the work of Van Ginneken, Maes (2005).

Isolation by distance (IBD). The oldest alternative to the model of panmixia is the model of IBD (Figure B): different groups of the European eel migrate to mate non-randomly in at least two geographically separated spawning sites (Boëtius, Harding, 1985). Nowadays it is agreed that the spatial restrictions of the gene flow is likely to occur only between small groups of eels in the Sargasso Sea (Andrello et al., 2011). This is supported by the results of the investigations into population genetic structure of eel using DNA microsatellites: i) Dannewitz et al. (2005) demonstrated that the population genetic structure of this species is not stable over time; ii) the newest comprehensive research based on DNA microsatellites (Als et al., 2011) suggests that the spawning of the European eel takes place only in the Sargasso Sea. Whether the offsprings of these reproductively isolated groups of eels in the Sargasso Sea are able to return to the breeding grounds of their parents after their journey to the continent is unknown (Kettle et al., 2010), but the results of Kettle, Haines (2006) modeling and recent indications of female philopatric behaviour from the genetic studies using mtDNA markers (Ragauskas, 2013; Baltazar-Soares et al., 2014) do not reject this possibility. It is interesting to note that in the beginning of the 20th century it was hypothesized that eels living in the eastern part of the Mediterranean Sea could reproduce in this sea (Casellato, 2002; Bianchini et al., 2009) and in turn should be ascribed to the distinct population (Lintas et al., 1998). Nowadays this hypothesis is still not discarded and the results of some genetic investigations in part support it (Wirth, Bernatchez, 2001; Maes, Volckaert, 2002). Even so, thus far the spawning sites of the European eel in the Mediterranean Sea were not detected (Van Ginneken, Maes, 2005) and possibility that eels can breed here is very low.

Isolation by time (IBT). The groups of spawning eels can be separated between each other not only by space but also by time (Maes et al., 2006). The temporal restrictions of the gene flow are represented by the model of IBT (Figure C) and appear due to some features of the life cycle of the European eel, such as the variation of age of mature eels and the differences in the length of migration loops of eels inhabiting the continent, and the continuously changing conditions in the ocean (Maes, Volckaert, 2007). The gene flow between the groups

of eels that arrive from the different geographical regions to spawn at similar time in the same part of the sea is possible. Nowadays it is accepted that not the spatial but the temporal restrictions of the gene flow have a greater influence on the formation of the population genetic structure of the European eel (Van Ginneken, Maes, 2005). Due to several reasons it is assumed that the primary reason for the detection of the statistically significant IBT is the stochastic processes in the ocean (Pujolar et al., 2007). Firstly, it is known that the population genetic structure of the European eel is not stable in time (Dannewitz et al., 2005). Secondly, thus far the statistically significant temporal restrictions were detected only between the samples of the glass eels, which represented the groups of eels that arrive to the continent in different years (Maes et al., 2006). Finally, statistically significant IBT was not detected using various samples of eels in the newest investigations into population genetic structure of the European eel (Palm et al., 2009; Als et al., 2011; Cagnon et al., 2011; Pujolar et al., 2011a).

Towards a better understanding of the formation of the population genetic structure of the European eel

Due to the fact that the present methodological problems prevent direct observations of the European eels both in their spawning sites and in the open ocean, the genetic and otolith investigations serve as the main tools for the extension of knowledge of eel biology, especially its ecology in the Atlantic Ocean (Casellato, 2002; Albert et al., 2006; Shiao et al., 2006; Maes, Volckaert, 2007; Aoyama, 2009). Unfortunately, the currently accumulated molecular data gives only limited insights about the formation of the population genetic structure of this species. This raises a question: what is supposed to be undertaken prior to detecting the spawning eels in their spawning sites?

Multidisciplinary seascape genetics. One of the solutions for increasing our knowledge about the formation of the population genetic structure of the European eel is the multidisciplinary seascape genetics (Selkoe et al., 2008). In fact, the combination of genetic approaches with other tools to test ecologically grounded hypotheses has already begun to reveal important insights into the patterns, causes and consequences of population structure and

connectivity of marine populations, and has helped to guide new approaches to fisheries management and marine reserve networks. Probably the most common area in the multidisciplinary seascape genetics is the landscape genetics, which in the context of marine environment is called 'seascape genetics' and attempts to connect the molecular data with geographical, physical and ecological data of marine environment (Manel et al., 2003; Selkoe et al., 2010). Other important areas of the multidisciplinary seascape genetics are reviewed by Selkoe et al. (2008). In general, these areas are the following: modeling, improved sampling design of larvae and recruits, statistical analysis and pairing of the molecular data with other non-genetic data (demographic, behavioural and data obtained from the natural and artificial tags). It is worth to emphasize that the best results are obtained when several different areas of the multidisciplinary seascape genetics are interconnected and used for answering particular ecological questions.

Thus far the investigations into the population genetic structure of the European eel did not incorporate the information about the marine environmental features. One of the fundamental reasons is that scientists still lack information about the ecosystem where eels spawning sites are located (Maes, Volckaert, 2007). Even so, it is obvious that both different currents in the Sargasso Sea and the temperature in the eel spawning sites, as well as the trophic conditions, surely affect the formation of the population genetic structure of the European eel (Kettle, Haines, 2006; Bonhommeau et al., 2008, 2009). Since Kettle, Haines (2006) modelling indicated that the silver eel spawners can develop strategies for spawning location and migration depth to preferentially target particular regions in the adult range it could be hypothesized that the restrictions of the gene flow in the Sargasso Sea could be predestined even by the variance in depth where the breeding eel groups mate. While our hypothesis remains to be tested there are examples in the scientific literature that the variance in depth could restrict gene flow between different fish populations. For instance, the depth as potential driver of genetic structure was proposed to the deep-sea redfish *Sebastes mentella* (Stefánsson et al., 2009). Consequently, the seascape genetics could and should be applied to the investigations into the population genetic structure of the European

eel. Thus far the applications of other important areas of the multidisciplinary seascape genetics to the genetic research of the European eel are also limited. For example, until now there has been no attempts to directly connect the molecular data with the data obtained from the natural and artificial tags. Even so, nowadays scientists are trying to combine oceanographic modeling with modern population genetics or incorporate the obtained molecular data into the new models. For instance, recently Baltazar-Soares et al. (2014) combined dispersal simulations using half century of high-resolution ocean model data with population genetics tools. It should be noted that this was done for the first time in the studies of the population genetics of the European eel. The main findings of their work are the following: i) regional atmospherically driven ocean current variations in the Sargasso Sea were the major driver of the onset of the sharp decline in eel recruitment in the beginning of the 1980s; ii) coastal genetic differentiation is consistent with cryptic female philopatric behaviour within the Sargasso Sea. Such results demonstrate the key constraint of the variable oceanic environment on the European eel population. Regarding the incorporation of the obtained molecular data into the new models, the first attempt to model the full life cycle of the European eel and its genetic structure was done by Andreollo et al. (2011). They presented a demographic-genetic model which expanded our knowledge regarding the influence of demographic processes on the formation of the population genetic structure of this species. This demographic-genetic model indicates that: i) in general, the European eel should be treated as panmictic species; ii) the different groups of breeding individuals can be separated in space and / or time. Based on the results of the modeling of Pujolar et al. (2011a) it could be suggested that in the Sargasso Sea should be approximately 2 000–5 000 reproductively isolated events and each of them should consist of 130–375 individuals (if we assume that 700 000 individuals could reach the spawning grounds). The relatively small numbers of the spawning eels in each reproductively isolated group suggest that the gene drift in this species may be more pronounced than previously anticipated. Even so, the most recent Pujolar et al. (2011b) study indicates that after the strong decline in the abundance several decades

ago the N_e of the European eel (3 000–12 000) was quite stable, i. e. the species did not experience the bottleneck effect.

Intraspecific evolution. Due to the fact that the currently existing population genetic structure of the species was affected by the various events in the past it has signatures of the population history (Bernatchez, Wilson, 1998). The concept of the population history encompasses the circumstances of the origin of the population, demographic processes in this population and its surrounding environment (Marko, Hart, 2012). The signatures of the population history can be detected by studying the intraspecific evolution of the species. The intraspecific evolution could be defined as evolution within the species and from the genetic point of view it deals with the historical population genetic structure of the species and its formation and shaping. When the information about the intraspecific evolution is supplemented with the biogeographic data a new research area, called phylogeography, emerges (Manel et al., 2003). The phylogeography is mainly concerned with the reconstruction of the population history of the species.

Thus far several investigations into the intraspecific evolution of the European eel using different mtDNA markers were conducted (Lintas et al., 1998; Daemen et al., 2001; Butkauskas et al., 2009; Ragauskas, 2013; Baltazar-Soares et al., 2014), but no publications of the purely phylogeographic studies of this species are currently available. The most recent data (Ragauskas, 2013; Baltazar-Soares et al., 2014) indicates that the different mtDNA lineages of eels exist in the European eel population. In fact, this data suggests a presumable existence of retrospective local populations, i. e. reproductively isolated groups of eels, characterized by juveniles ability to return to the spawning sites of their parents for at least several generations. While it is not clear whether the local populations of eels still exist today, the disappearance of the local populations of presumably non-panmictic species could be explained by the historical natural processes. For instance, it is known that the glaciations greatly affected the historical distribution of the European eel in Europe (Kettle et al., 2008). It could be hypothesized that the changes in the distribution at the growing grounds influenced eels breeding in the spawning grounds and in turn had a strong impact on the formation and shaping of the population ge-

netic structure. To a lesser degree spatio-temporal stability of the population genetic structure of the European eel probably was altered by the anthropogenic activity, especially restocking (Palm et al., 2009; Ragauskas, 2013). Restocking started in the beginning of the 20th century and could be defined as catching of glass eels, elvers or young yellow eels in the United Kingdom and France and their introduction to ponds, lakes or rivers of other countries (Dekker, 2004). Since this activity is not restricted just in European countries, nowadays the natural distribution of the European eel and several other species of *Anguilla* genus is changed (Maes, Volckaert, 2007). The assumption of panmictic breeding system was thought to limit any consequences of restocking, but recent work of Baltazar-Soares et al. (2014) suggests that this activity may have unexpected impacts and furthermore may affect the recovery of the European eel. Actually, more investigations into the intraspecific evolution of this species using larger number of geographical samples and archival material are needed in order to evaluate the impacts of various historical processes on the formation and shaping of the population genetic structure of the European eel. Due to the fact that the spawning grounds of both *A. anguilla* and *A. rostrata* species are located in the Sargasso Sea (Lecomte-Finiger, 2003) hybridization occurs (Als et al., 2011) and later viable hybrids are found exceptionally in Iceland (Albert et al., 2006). Consequently, after the investigations into the intraspecific evolution of different species of the Atlantic eels it is possible to study the historical hybridization between these species and its impact on the formation of the population genetic structure of the European eel. However, to our knowledge thus far there were no attempts to study the intraspecific evolution of the American eel using direct sequencing of different mtDNA fragments.

CONCLUDING REMARKS

The formation of the population genetic structure of the species is a fundamental process. The multidisciplinary seascape genetics enables scientists to answer many important questions about the biology of the European eel and is a valuable tool for the investigations into the formation of the population genetic structure of this species. The investigations into the intraspecific evolution of the European eel (especially coupled with the

biogeographic data) are also important because they could provide the crucial information about the historical population genetic structure of the species and its formation and shaping by the past events. Summing up the afore-said, it should be stated that in order to comprehensively investigate the formation of the population genetic structure of the European eel it is not enough to find the spawning sites of this species and to determine the genetic parameters of the spawning eels and their offsprings, but it is also necessary to obtain the information about the population history and to take into account the influence of the seascape variables on the reproduction process.

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**EUROPINIO UPINIO UNGURIO *ANGUILLA*
ANGUILLA (L.) POPULIACINĖS-GENETINĖS
STRUKTŪROS FORMAVIMASIS: TRUMPA
APŽVALGA**

S a n t r a u k a

Sudėtingas europinio upinio ungurio gyvenimo ciklas lemia unikalios populiacinės-genetinės struktūros formavimąsi. Rūšiai būdinga varžovų reprodukcinės sėkmės loterija ir chaotiškas genetinis nevienodumas, o jos populiacinė-genetinė struktūra gali būti apibūdinama kaip genetinė mozaika, kurios susiformavimą lemia produktyviai izoliuotų ungurių grupių egzistavimas. Kadangi iki šiol nėra galimybių ištirti europinio upinio ungurio nerštavietėje pagautų neršiančių ungurių genetinių parametrų, tad šios rūšies populiacinė-genetinė struktūra vis dar nepakankamai ištirta ir supраста, o jos formavimosi ypatumai aiškinami naudojant modelius. Šiuo metu yra pasiūlyti trys pagrindiniai europinio upinio ungurio populiacinės-genetinės struktūros formavimosi modeliai: panmiksija, erdvinė izoliacija ir laiko izoliacija. Siekiant atskleisti europinio upinio ungurio populiacinės-genetinės struktūros formavimosi dėsningumus, reikėtų taikyti metodus, naudojamus multidisciplininėje jūros kraštovaizdžio genetikoje, ir išsamiau ištirti šios žuvies vidurūšinę evoliuciją.

Raktažodžiai: *Anguilla anguilla*, populiacinė-genetinė struktūra, formavimasis, modeliai