Chapter 15
In Search of Phylogeographic Patterns in the Northeastern Atlantic and Adjacent Seas

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Abstract We reviewed 54 studies on teleost fishes and crustaceans inhabiting European waters to test for the emergence of phylogeographic patterns. Concerning latitudinal variation of genetic diversity, we found that: (1) contrary to the predictions of the "central-margin hypothesis," only a minority of species ($\sim$10 %) revealed higher genetic diversity in the center of their distribution; (2) approximately a third of the fish had a peak of genetic diversity at their southern limit; (3) another substantial fraction of species (41 % for fishes and 72 % for crustaceans) showed little or no latitudinal variation of genetic diversity. Genetic structure expressed by significant FSTs varied widely among species from cases where Atlantic, North Sea, and the Mediterranean seem to correspond to distinct populations, to others where no structure could be detected across their entire range. Given the heterogeneity in sampling schemes we suggest that regular sampling across entire species ranges can improve our understanding of the marine phylogeography in Europe.

15.1 Introduction

The study of marine phylogeography in European shores is now *ca.* 15 years old (Magoulas et al. 1996; Borsa et al. 1997). Data accumulated and, as sequencing became more accessible, more labs were involved and more species were studied. During this period, techniques changed radically and while the initial emphasis was on enzyme electrophoresis it quickly moved to the analyses of mitochondrial DNA and increasingly incorporated nuclear markers, including microsatellites and introns (Sotelo et al. 2009; Almada et al. 2012). Analytical tools also changed and,

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in particular, estimation of the time to the most recent common ancestor (TMRCA) and of past demography of populations gained accuracy. At the same time, some initial assumptions were reconsidered, as many tools relied on concepts that seem unrealistic for populations subjected to a succession of climatic oscillations during the entire Pleistocene. Thus, models and statistical tools that assume that populations were in mutation-drift equilibrium, or those that assume that populations show a continuous type of growth, are being critically evaluated (Neigel 2002; Kuhner 2009).

The scope of geographical sampling also widened. As the cost of sequencing decreased, more individuals in more populations were included in phylogeographic studies of an increasing number of species, allowing for more fine-scale sampling and the study of local barriers, for the emergence of comparative phylogeography across diverse taxonomic groups, and for the detection of exceptions to broad patterns. For instance, for many years the Atlantic-Mediterranean seaway was thought to be a potential barrier for gene flow. However, the Atlantic-Mediterranean phylogeographic barrier proved to be effective only for some species, while others, often closely related, apparently cross it without restriction (for a review see Patarnello et al. 2007; Kettle et al. 2011).

The need for wide sampling coverage of populations and of comparing different species is particularly acute for the study of the Northeastern Atlantic: a transitional region between the tropics and boreal regions, whose climate has been very dynamic since the Pleistocene. While to a great extent it harbors warm and cold temperate species, it is also the northern limit of some tropical species and the southern limit of some boreal species, thus constituting both a central and marginal habitat (Almada et al. 2013). Furthermore, the climate in this region has changed considerably and often over the last glacial cycles, and during glaciations population ranges are thought to have been driven south or persisted in northern refugia. Evidence is also accumulating that many boreal and cold temperate species survived in peri-glacial refugia (for a review see Maggs et al. 2008).

The central-margin hypothesis (Eckert et al. 2008) assumes the center of a species distribution has a high and stable effective population size (N_e) and a high rate of gene flow (m). Thus, central populations (in this instance, southern populations) should exhibit the highest genetic diversity and harbor the overall most frequent haplotypes. In contrast, marginal (northern) populations should exhibit lower genetic diversity and higher genetic differentiation, and harbor private alleles. The pattern among populations in the Eastern North Atlantic, however, with its history of shifting ranges and patterns of populations connectivity (including presence of refugia), and fluctuations in local populations sizes is likely to be more complex and varied than expected by the central-margin hypothesis.

Maggs et al. (2008) examined several population models, with varying degrees of connectivity, for species distributed along a north–south gradient and expected haplotype networks. Their review of eight benthic species revealed a variety of patterns, and indicated that for some species the admixture of northern refugia populations may lead to the unexpected pattern of greater haplotype diversity in more northern populations. In addition, their coalescent simulations of haplotype

networks for a history of ancestral panmixia followed by geographic isolation call attention to the stochastic nature of genealogies. Overall, their examination indicates that genetic signatures, such as latitudinal patterns of genetic diversity, should be interpreted cautiously and that for a full understanding of population history several aspects should be considered in conjunction—haplotype diversity, monophyly, location of most frequent haplotype and of private haplotypes, rates of migration and identification of admixture events—and in conjunction with the coalescent simulation of different historical scenarios.

In this short review, we compiled information of 54 studies on teleost fishes and crustaceans inhabiting European waters, characterized their sampling, and summarized their phylogeography, in order to identify overall patterns.

15.2   Methods

To compile the set of chapters used in this mini-review, we searched ISI Web of Knowledge database[1] with the following keywords: phylogeograph*, northeastern Atlantic, fish, crustaceans, population structure*, genet* diversity. In addition, we included works that matched our criteria published in two representative journals (*Molecular Ecology* and *Molecular Phylogenetics and Evolution*) between 1997 and 2012. For the complete list of chapters analyzed see Table 15.1. For each chapter, the following data were recorded: distribution area of the species, sampling area, genetic diversity, population structure, time of coalescence estimated for the species, age of the populations, and proposed glacial refugia. When information on any of these items was not reported in a given publication, it was recorded as not available.

The species distributions were retrieved from Fishbase[2] (for fishes) and WoRMS[3] (for crustaceans) and recorded as presence/absence in 13 geographical areas: Arctic, Baltic Sea, North Sea, UK Atlantic coasts, Bay of Biscay, Western Iberian Peninsula, Southern Iberian Peninsula, northwestern African coast, western Mediterranean, eastern Mediterranean, Azores, Madeira and Canaries (Fig. 15.1). The geographic coverage of each study was expressed as the fraction of areas where samples were taken over the total number of areas where the species occurs. An important point in our study was to compare the levels of genetic diversity between northern and southern limits of each species. The southern limit of the species distribution was considered sampled if the geographical area that contains it was sampled in any point (likewise for the northern limit). For the purpose of

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[1] www.webofknowledge.com/.

[2] Fish Base (ed, by Froese R, Pauly D). Digital resource available at www.fishbase.org.

[3] WoRMS—World Register of Marine Species (eds by Appeltans W, Bouchet P, Boxshall GA, De Broyer C, de Voogd NJ, Gordon DP, Hoeksema BW, Horton T, Kennedy M, Mees J, Poore GCB, Read G, Stöhr S, Walter TC, Costello MJ). Digital resource available at www.marinespecies.org.

Table 15.1 List of species and publications considered in the present mini-review

	Species	Publication
Fishes	*Alosa alosa*	Faria et al. (2012)
	Alosa falax	Faria et al. (2012)
	Anguilla anguilla	Daeman et al. (2001)
	Aphanopus carbo	Stefanni and Knutsen (2007)
	Atherina presbyter	Francisco et al. (2009)
	Chromis chromis	Domingues et al. (2005)
	Chromis limbata	Domingues et al. (2006b)
	Ciliata mustela	Robalo et al. (2014)
	Conger conger	Correia et al. (2012)
	Coris julis	Aurelle et al. (2003)
	Coryphoblennius galerita	Domingues et al. (2007a)
	Dentex dentex	Bargelloni et al. (2003)
	Dicentrarchus labrax	Lemaire et al. (2005)
	Diplodus puntazzo	Bargelloni et al. (2005)
	Diplodus sargus	Domingues et al. (2007b)
	Engraulis encrasicolus	Magoulas et al. (2006)
	Gasterosteus aculeatus	Mäkinen and Merilä (2008)
	Halobatrachus didactylus	Robalo et al. (2013)
	Helicolenus dactylopterus	Aboim et al. (2005)
	Lipophrys pholis	Francisco et al. (2011)
	Lithognathus mormyrus	Bargelloni et al. (2003)
	Lophius budegassa	Charrier et al. (2006)
	Lophius piscatorius	Charrier et al. (2006)
	Merluccius merluccius	Lundy et al. (1999)
	Mullus surmuletus	Gallarza et al. (2009)
	Pagellus bogaraveo	Bargelloni et al. (2003)
	Pagrus pagrus	Bargelloni et al. (2003)
	Parablennius parvicornis	Domingues et al. (2008b)
	Parablennius sanguinulentus	Domingues et al. (2008b)
	Pholis gunnellus	Hickerson and Cunningham (2006)
	Platichthys flesus	Borsa et al. (1997)
	Pleuronectes platessa	Was et al. (2010)
	Pomatoschistus microps	Gysels et al. (2004)
	Pomatoschistus minutus	Larmuseau et al. (2009)
	Salaria pavo	Almada et al. (2009)
	Salmo salar	Consuegra et al. (2002)
	Sardina pilchardus	Atarhouch et al. (2006)
	Scomber scombrus	Nesbo et al. (2000)
	Scophthalmus maximus	Nielsen et al. (2004)
	Solea solea	Rolland et al. (2007)
	Spondyliosoma cantharus	Bargelloni et al. (2003)
	Sprattus sprattus	Debes et al. (2008)
	Symphodus melops	Robalo et al. (2012)
	Taurulus bubalis	Almada et al. (2012)

(continued)

Table 15.1 (continued)

	Species	Publication
	Thalasoma pavo	Domingues et al. (2008a)
	Thunnus thynnus	Bremer et al. (2005)
	Trachurus trachurus	Karaiskou et al. (2004)
	Tripterygion delaisi	Domingues et al. (2006a)
	Xiphias gladius	Bremer et al. (2005)
Crustaceans	*Calanus helgolandicus*	Papadopoulos et al. (2005)
	Carcinus maenas	Roman and Palumbi (2004)
	Chthamalus montagui	Schemesch et al. (2009)
	Chthamalus stellatus	Schemesch et al. (2009)
	Crangon crangon	Luttikhuizen et al. (2008)
	Euraphia depressa	Schemesch et al. (2009)
	Gammarus duebeni	Rock et al. (2007)
	Homarus gammarus	Triantafyllidis et al. (2005)
	Idotea balthica	Wares and Cunningham (2001)
	Liocarcinus depurator	García-Merchán et al. (2012)
	Macropipus tuberculatus	García-Merchán et al. (2012)
	Maja brachydactyla	Sotelo et al. (2008)
	Meganyctiphanes norvegica	Papetti et al. (2005)
	Mesopodopsis slabberi	Remerie et al. (2006)
	Munida intermedia	García-Merchán et al. (2012)
	Necora puber	Sotelo et al. (2009)
	Nephrops norvegicus	Stamatis et al. (2004)
	Pagurus alatus	García-Merchán et al. (2012)
	Pagurus excavatus	García-Merchán et al. (2012)
	Palinurus elephas	Palero et al. (2008)
	Parapenaeus longirostris	García-Merchán et al. (2012)
	Plesionika heterocamrpus	García-Merchán et al. (2012)
	Pollicipes pollicipes	Quinteiro et al. (2007)

identifying latitudinal patterns, remaining areas were considered central populations. Nei's gene diversity (Nei 1987) was selected to represent genetic diversity. The population structure of a given species was assessed by analysis of molecular variance (AMOVA, Excoffier et al. 1992) and pairwise F_{ST} between locations. We considered that genetic discontinuity existed among locations when the respective pairwise F_{ST} was significant ($p < 0.05$). Due to the potential barriers to gene flow between the northeastern Atlantic and the Mediterranean, and the northeastern Atlantic and the North Sea, articles were searched specifically for the presence of significant F_{ST} involving these three seas. This task was facilitated by the fact that many studies included the assessment of these barriers as an explicit aim. Proposed marine refugia were recorded as: (1) Azores, Canaries, and northwest Africa; (2) southwestern Iberian Peninsula; (3) Mediterranean Sea; (4) western English Channel; (5) southwest Ireland; (6) Iceland and Faroe Islands; and (7) northern Norway (following Maggs et al. 2008). Statistical analyses were performed with
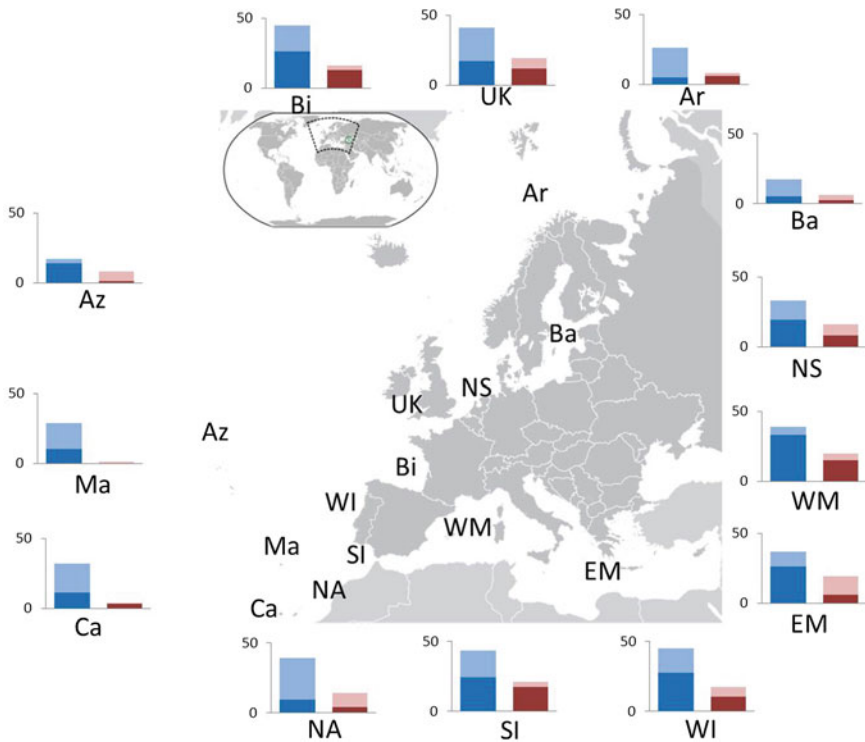
Fig. 15.1 Number of studied species of fish (*blue*) and crustaceans (*red*) present in the area (total height of the bars) and sampled (*dark shade*): Ar—Arctic, Ba—Baltic Sea, NS—North Sea, UK—UK Atlantic coasts, Bi—Bay of Biscay, WI—Western Iberian Peninsula, SI—Southern Iberian Peninsula, NA—Northwestern African coast, WM—Western Mediterranean, EM—Eastern Mediterranean, Az—Azores, Ma—Madeira, Ca—Canaries

the software STATISTICA (StatSoft 2003). Because areas in the Atlantic were less affected by the glaciations than the North Sea and Baltic, we compared gene diversity between these two areas.

15.3 Results

One major feature that emerges from this study is the existence of large gaps and differences in analyses conducted across studies. Very few works sampled the entire distribution area of the species (23 %). An important percentage of the chapters did not assess the age of the populations (74 %). On the positive side, the majority of studies evaluated the existence of population structure for the studied area (93 %). The average geographic coverage found was 54.26 % (S.D. 22.65 %, minimum 15.38 %, maximum 100 %).

15.3.1 Fishes

A total of 39 chapters were analyzed for teleost fishes (Actinopterygii), comprising 50 species belonging to 29 different families and involving 10 different molecular markers.

For the Actinopterygii, only 20 % of the works analyzed in the present review covered the entire area of distribution of the species (Fig. 15.1). In the remaining phylogeographic studies considerable parts of the species range were not sampled. In 34 % of the chapters the sampling was focused at the center of the species' distribution. The northern limit of the species was less sampled than the southern limit of their distribution (30 vs. 56 %) (Fig. 15.2). The sampling coverage was more deficient for the peripheries (Artic 19 %, Baltic 19 %, NW African coast 23 %, Madeira 34 % and the Canaries 34 %), with the exception of the Azores (82 % of the species studied) (Fig. 15.1).

The presence of population structure was not evaluated in only 8 % of the species. Considering the remaining works, 67 % of the species presented genetic structure in the sampled area (Fig. 15.3). Two-thirds of the species sampled in the European Atlantic and the Mediterranean exhibited population structure. Half of the species sampled in the Atlantic revealed genetic differentiation between temperate and North Sea locations. Concerning the Atlantic islands, the following results were found for population structure: 46 % of the studies involving Maca-ronesian samples found no population structure; 31 % found population differ-entiation between Azores and European coastal areas; and 23 % showed structure within the Macaronesian Islands.

Genetic diversity was never higher in the North Sea than in the Atlantic, while the opposite pattern (higher diversity in the south) was relatively common (36 %). The pattern of higher diversity in the center of species distributions occurred only in a minority of cases (9 %). Some species appear to have sufficient dispersal and migration (past or present) so that no difference in the distribution of genetic diversity was found along the whole sampled area (41 %) (Fig. 15.4).

Only 20 % of the studies accessed the age of the populations. In 70 % of the species analyzed one or more populations sampled were dated after the Last Glacial Maximum (LGM—18 kya). All studies estimated the age of one or more populations as dating from the last glaciation, before the LGM (120–18 kya).

15.3.2 Crustaceans

A total of 15 chapters were analyzed for the Crustaceans, comprising 23 species (18 from the class Malacostraca and five from the class Maxillopoda), belonging to 16 different families and involving six molecular markers.

Only 30 % of the studies analyzed covered the entire species distribution area (Fig. 15.2). Thirty percent focused on the center of the species distribution, and the
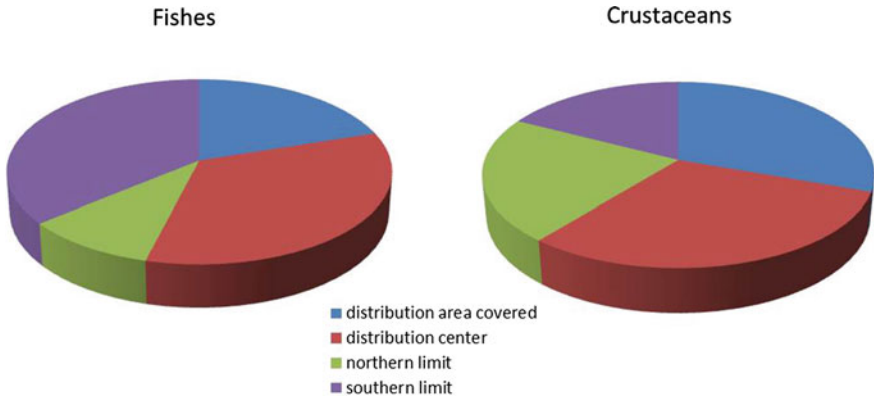
Fig. 15.2 Sampling schemes of the publications considered in this review. *Blue*—sampling covers the entire distribution area of a species; *red*—sampling only covers the center of the species' distribution; *green*—sampling only covers the northern limit and the center of the species' distribution; *purple*—sampling only covers the southern limit and the center of the species' distribution
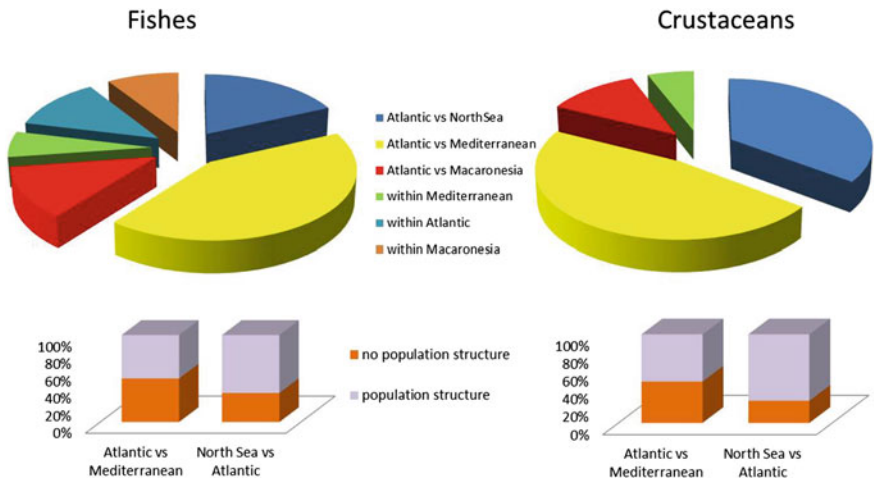

Fig. 15.3 Population structure across the studies compiled for this review: between Atlantic and North Sea (*dark blue*), Atlantic and Mediterranean (*yellow*), Atlantic and Macaronesia (*red*), within the Mediterranean (*green*), within the European Atlantic area (*light blue*) and within Macaronesian islands (*brown*). For the Atlantic versus Mediterranean and North Sea versus Atlantic areas, the proportion of population structure found is shown below the pies

northern limit was slightly more sampled than the south (52 vs. 47 %). The sampling for the crustacean chapters analyzed is more deficient in the peripheries (0 % for Madeira, 13 % for Azores and 33 % for the Baltic Sea) (Fig. 15.1).
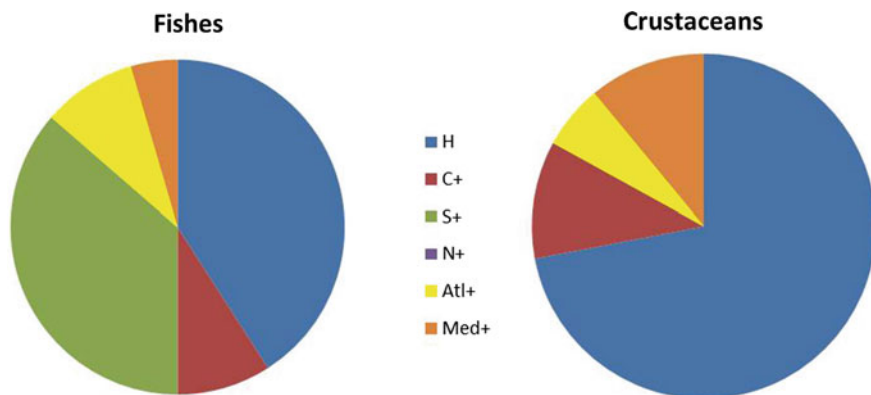
Fig. 15.4 Distribution of the genetic diversity along the sampled areas: H—homogeneous, C+—more diverse in the center of the distribution, S+—more diverse in the southern limit of the distribution, N+—more diverse in the northern limit of the distribution, Atl+—more diverse in the Atlantic than in the Mediterranean, Med+—more diverse in the Mediterranean than in the adjacent Atlantic

The existence of population structure across the studied area was evaluated in 96 % of the studies, with 54 % of the species presenting population genetic structure (52 % of the total of species) (Fig. 15.3). Population structure was found between the Mediterranean and the European Atlantic in 47 % of the studies that addressed this issue, while for the European Atlantic versus North Sea 67 % yielded population structure.

A majority of the studies (72 %) revealed a homogeneous distribution of the genetic diversity across the sampled area (Fig. 15.4). Only 11 % of the species presented a higher genetic diversity in the center of the sampled area. No chapters reported more genetic diversity in the north or south of the species range. Concerning the transition between the Atlantic and the Mediterranean, 6 % of the species presented higher genetic diversity in the Atlantic, while 11 % showed the opposite trend.

The age of the populations was considered in 39 % of the studies, with 44 % of the species with one or more populations dated after the LGM. For 67 % of the works the estimated age of one or more populations was in the last glaciation, before the LGM.

15.3.3 General Patterns

No significant differences in gene diversity were found when comparing the Atlantic coast (Biscay + Iberian Peninsula), North coasts (North Sea + Baltic Sea), and the Mediterranean with Kruskal-Wallis tests (Kruskal and Wallis 1952): total of 73 species: $H = 1.055$, p = 0.590, df = 2; fishes: $H = 4.018$, p = 0.134, df = 2; crustaceans: $H = 2.116$, p = 0.347, df = 2.

Only 21 species were evaluated for their potential glacial refugia. Of these, the Mediterranean may have served as a refugium for five species, namely species that now extend to the adjacent Iberian Atlantic, northern areas for six species and the Iberian Peninsula for nine species.

15.4 Discussion

Several interesting patterns emerge that are supported by both fishes and crustaceans.

1. There are gaps in geographic coverage and substantial heterogeneity in analytical procedures, a situation that reflects the rapid expansion of marine phylogeography and should guide future research in terms of sampling and statistical analysis. The pattern of diversity peaking in the center of the species distribution and decreasing towards the margins holds for only a small minority of species (9 % for fishes and 11 % for crustaceans). We suggest that, in temperate conditions where strong climatic oscillations prevail, the so-called central populations only rarely represent populations that persisted throughout the successive cycles (e.g., Eckert et al. 2008). Rather, many species must have moved up and down during glacial cycles tracking the changes of habitat (Kettle et al. 2011) so that what is now in the center of a distribution will usually reflect the historical contingencies that affected each species.

2. A considerable number of species (30 %) show no structure when different seas are compared (Fig. 15.3). This pattern may have several causes. Perhaps the most likely is that species with high dispersal capabilities and large effective population size may disperse in large numbers, exporting much of the genetic diversity across large geographical scales. This process may erode previous phylogeographic signals (like ancestral polymorphisms) if, after an initial colonization postdating the last glaciation, several millennia of dispersal and mixing elapsed.

3. The observed data underline the importance of the Atlantic as a post-glacial recolonization source for the North Sea. Nevertheless, several studies (e.g., *Carcinus maenas* in Roman and Palumbi 2004; *Taurulus bubalis* in Almada et al. 2012) suggest glacial refugia near the North Sea, and others demonstrate surprisingly long persistence north of the glacial ice for several glacial cycles (e.g., *Pholis gunnellus* in Hickerson and Cunningham 2006). With regard to the Mediterranean, it may have served as a refugium for some species, namely species that now extend to the adjacent Iberian Atlantic (e.g., *Chromis chromis* in Domingues et al. 2005; *Parablennius sanguinolentus* in Domingues et al. 2008b). This rule is, however, far from being universal, as many species may have survived in the Atlantic part of the Iberian Peninsula, along the coast of northwest Africa, and other unglaciated areas in west Europe (see Maggs et al. 2008).

4. The origin of populations (especially in the Atlantic) was dated mainly from the Lower and Middle Pleistocene. Populations with origin estimated after the LGM occur primarily in the North Sea (for cold water species) and Macaronesia, particularly in the Azores (for warm waters species).

5. For thermophilic species, the data seem to support the Azores colonization from Madeira (e.g., Santos et al. 1995). Indeed, when migration was evaluated, more migrants were detected from Madeira to the Azores than the reverse (e.g., *Chromis limbata* in Domingues et al. 2006b). Madeira is, in turn, biogeographically connected with the Canaries, and there are references that point to links between Canaries and Mauritania (e.g., *Tripterygion delaisi* in Domingues et al. 2006a). This colonization route, combined with high sea surface temperatures, probably explains why there are several fishes that are present in the tropics and in the Macaronesian Islands, but not in Europe (e.g., *C. limbata* in Domingues et al. 2006b; *Parablennius parvicornis* in Domingues et al. 2008b).

We are well aware that our sampling is not exhaustive and likely some pertinent literature may have failed to be included in this study. We hope, however, that this survey yielded a representative sample of the scope and patterns of the research being done. Due to lack of time, other important groups could not be included namely mollusks, echinoderms, algae and sea grasses. One major limitation of this survey is that different works often use different molecular markers. There is a substantial probability that slowly evolving markers did not capture the signature of recent events which rapidly evolving ones can retain. The number of studies that we surveyed was not very large, thus separating them by molecular marker would result in a serious loss of information.

Although marine phylogeography is a relatively young science, the evolution of problems and methods of analysis has been very profound. This review included studies with poorly calibrated markers and analytical techniques that differed greatly among studies. A closer communication among laboratories and the building of international projects that cover the entire distribution area of species, with regularly spaced sampling, can have a key role in the evolution of our knowledge. The same holds for quality control of statistical tools and software available, and a better understanding of their underlying assumptions.

Several important projects like Corona,[4] FishPopTrace[5] and a recent MarinERA Project[6] are encouraging examples that mobilized researchers of different countries and did much to share ideas and samples giving rise to a good number of important chapters. We suggest that marine phylogeographers need to advance toward more daring projects. The idea of standardizing sampling patterns that are adequate to represent populations is also a requirement for large scale monitoring of marine communities, while the changes in time of population structure and genetic diversity, in close articulation with oceanographic information, seems

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[4] www.biology.duke.edu/corona/.

[5] http://fishpoptrace.jrc.ec.europa.eu/.

[6] http://biocongroup.eu/MarinEra/Welcome.html.

critical to improve our ability to predict the impact of different climate change scenarios. But to achieve this, more long term financing is needed to assure a minimum stability of the networks. So, monitoring at a regular basis seems to us an essential forward step in our field. Finally, a closer cooperation with palaeo-climatologists and palaeoceanographers will add more and more realism to the scenarios we postulate for the glacial conditions, relating the phylogeographic patterns with population models, ocean circulation models and more realistic patterns of larval dispersal.

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