



Chapter 15

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

Sara M. Francisco, Joana I. Robalo, André Levy
and Vítor C. Almada

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 (~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,

S. M. Francisco (✉) · J. I. Robalo · A. Levy · V. C. Almada
Eco-Ethology Research Unit, ISPA University Institute, Rua Jardim do Tabaco 34,
1149-041 Lisbon, Portugal
e-mail: sara_francisco@ispa.pt

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

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

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

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

69 Maggs et al. (2008) examined several population models, with varying degrees
70 of connectivity, for species distributed along a north–south gradient and expected
71 haplotype networks. Their review of eight benthic species revealed a variety of
72 patterns, and indicated that for some species the admixture of northern refugia
73 populations may lead to the unexpected pattern of greater haplotype diversity in
74 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 database¹ 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 Fishbase² (for fishes) and WoRMS³ (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

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

(continued)

Table 15.1 (continued)

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

109 identifying latitudinal patterns, remaining areas were considered central popula-
 110 tions. Nei's gene diversity (Nei 1987) was selected to represent genetic diversity.
 111 The population structure of a given species was assessed by analysis of molecular
 112 variance (AMOVA, Excoffier et al. 1992) and pairwise F_{ST} between locations. We
 113 considered that genetic discontinuity existed among locations when the respective
 114 pairwise F_{ST} was significant ($p < 0.05$). Due to the potential barriers to gene flow
 115 between the northeastern Atlantic and the Mediterranean, and the northeastern
 116 Atlantic and the North Sea, articles were searched specifically for the presence of
 117 significant F_{ST} involving these three seas. This task was facilitated by the fact that
 118 many studies included the assessment of these barriers as an explicit aim. Proposed
 119 marine refugia were recorded as: (1) Azores, Canaries, and northwest Africa; (2)
 120 southwestern Iberian Peninsula; (3) Mediterranean Sea; (4) western English
 121 Channel; (5) southwest Ireland; (6) Iceland and Faroe Islands; and (7) northern
 122 Norway (following Maggs et al. 2008). Statistical analyses were performed with

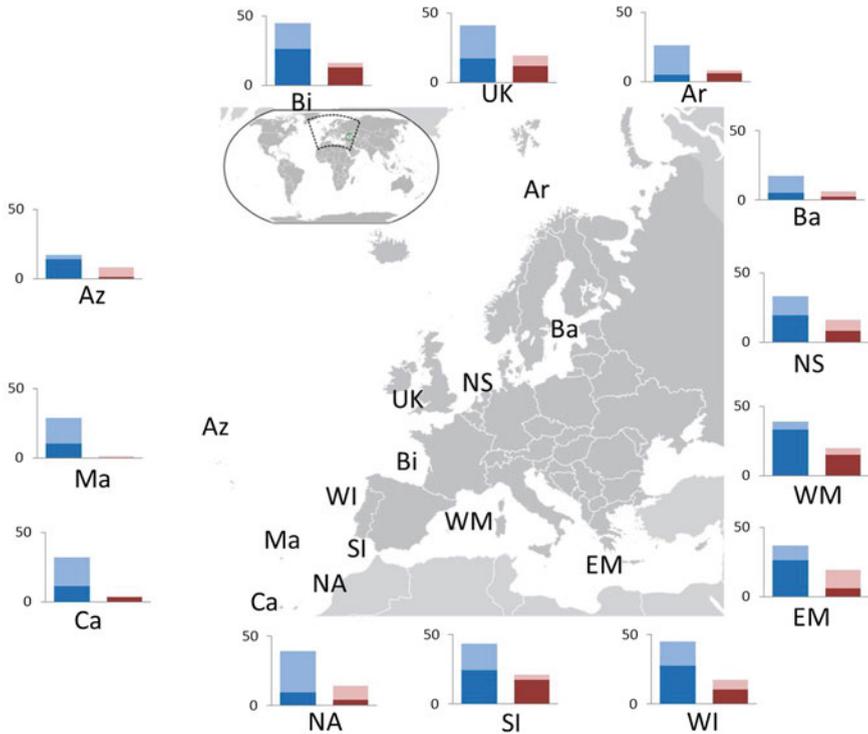


Fig. 15.1 Number of studied species of fish (*blue*) and crustaceans (*red*) present in the area (total height of the bars) and sampled (*dark shade*): Ar—Arctic, Ba—Baltic Sea, NS—North Sea, UK—UK Atlantic coasts, Bi—Bay of Biscay, WI—Western Iberian Peninsula, SI—Southern Iberian Peninsula, NA—Northwestern African coast, WM—Western Mediterranean, EM—Eastern Mediterranean, Az—Azores, Ma—Madeira, Ca—Canaries

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

15.3 Results

127 One major feature that emerges from this study is the existence of large gaps and
 128 differences in analyses conducted across studies. Very few works sampled the
 129 entire distribution area of the species (23 %). An important percentage of
 130 the chapters did not assess the age of the populations (74 %). On the positive side,
 131 the majority of studies evaluated the existence of population structure for the
 132 studied area (93 %). The average geographic coverage found was 54.26 %
 133 (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 (Arctic 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 Macaronesian samples found no population structure; 31 % found population differentiation 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 northern limit was slightly more sampled than the south (52 vs. 47 %). The

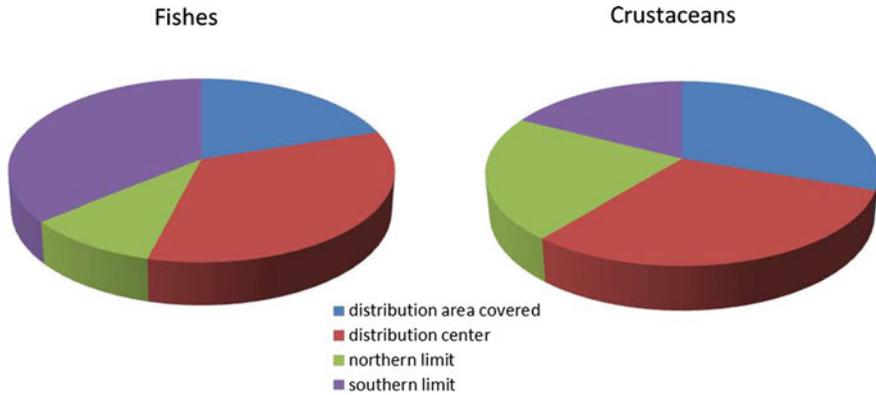


Fig. 15.2 Sampling schemes of the publications considered in this review. *Blue*—sampling covers the entire distribution area of a species; *red*—sampling only covers the center of the species' distribution; *green*—sampling only covers the northern limit and the center of the species' distribution; *purple*—sampling only covers the southern limit and the center of the species' distribution

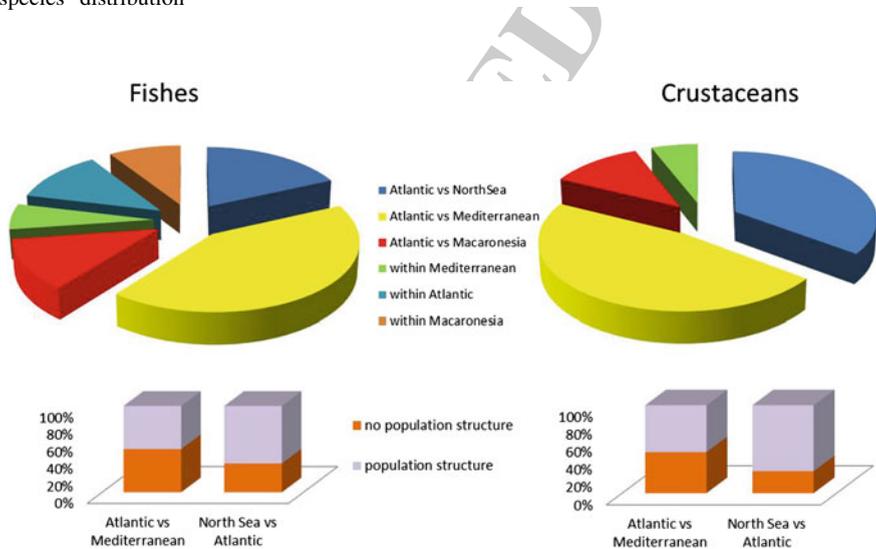


Fig. 15.3 Population structure across the studies compiled for this review: between Atlantic and North Sea (*dark blue*), Atlantic and Mediterranean (*yellow*), Atlantic and Macaronesia (*red*), within the Mediterranean (*green*), within the European Atlantic area (*light blue*) and within Macaronesian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

174 sampling for the crustacean chapters analyzed is more deficient in the peripheries
 175 (0 % for Madeira, 13 % for Azores and 33 % for the Baltic Sea) (Fig. 15.1).

176 The existence of population structure across the studied area was evaluated in
 177 96 % of the studies, with 54 % of the species presenting population genetic

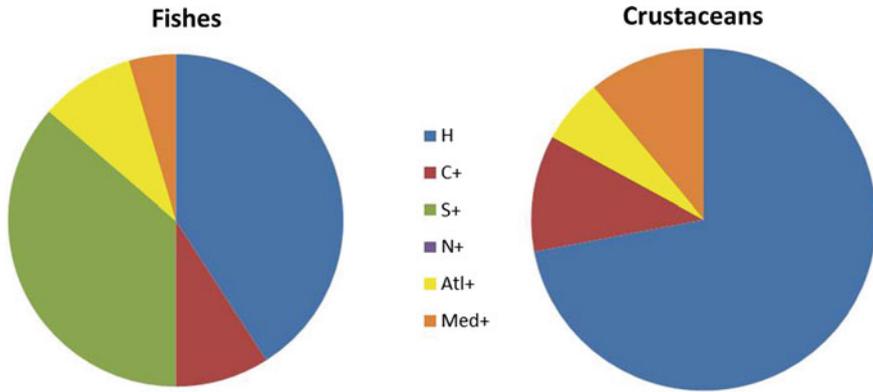


Fig. 15.4 Distribution of the genetic diversity along the sampled areas: H—homogeneous, C+—more diverse in the center of the distribution, S+—more diverse in the southern limit of the distribution, N+—more diverse in the northern limit of the distribution, Atl+—more diverse in the Atlantic than in the Mediterranean, Med+—more diverse in the Mediterranean than in the adjacent Atlantic

178 structure (52 % of the total of species) (Fig. 15.3). Population structure was found
 179 between the Mediterranean and the European Atlantic in 47 % of the studies that
 180 addressed this issue, while for the European Atlantic versus North Sea 67 %
 181 yielded population structure.

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

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

15.3.3 General Patterns

194 No significant differences in gene diversity were found when comparing the
 195 Atlantic coast (Biscay + Iberian Peninsula), North coasts (North Sea + Baltic
 196 Sea), and the Mediterranean with Kruskal-Wallis tests (Kruskal and Wallis 1952):
 197 total of 73 species: $H = 1.055$, $p = 0.590$, $df = 2$; fishes: $H = 4.018$, $p = 0.134$,
 198 $df = 2$; crustaceans: $H = 2.116$, $p = 0.347$, $df = 2$.

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

203 15.4 Discussion

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

- 206 1. There are gaps in geographic coverage and substantial heterogeneity in ana-
 207 lytical procedures, a situation that reflects the rapid expansion of marine
 208 phylogeography and should guide future research in terms of sampling and
 209 statistical analysis. The pattern of diversity peaking in the center of the species
 210 distribution and decreasing towards the margins holds for only a small minority
 211 of species (9 % for fishes and 11 % for crustaceans). We suggest that, in
 212 temperate conditions where strong climatic oscillations prevail, the so-called
 213 central populations only rarely represent populations that persisted throughout
 214 the successive cycles (e.g., Eckert et al. 2008). Rather, many species must have
 215 moved up and down during glacial cycles tracking the changes of habitat
 216 (Kettle et al. 2011) so that what is now in the center of a distribution will
 217 usually reflect the historical contingencies that affected each species.
- 218 2. A considerable number of species (30 %) show no structure when different seas
 219 are compared (Fig. 15.3). This pattern may have several causes. Perhaps the
 220 most likely is that species with high dispersal capabilities and large effective
 221 population size may disperse in large numbers, exporting much of the genetic
 222 diversity across large geographical scales. This process may erode previous
 223 phylogeographic signals (like ancestral polymorphisms) if, after an initial
 224 colonization postdating the last glaciation, several millennia of dispersal and
 225 mixing elapsed.
- 226 3. The observed data underline the importance of the Atlantic as a post-glacial
 227 recolonization source for the North Sea. Nevertheless, several studies
 228 (e.g., *Carcinus maenas* in Roman and Palumbi 2004; *Taurulus bubalis* in Almada
 229 et al. 2012) suggest glacial refugia near the North Sea, and others demonstrate
 230 surprisingly long persistence north of the glacial ice for several glacial cycles
 231 (e.g., *Pholis gunnellus* in Hickerson and Cunningham 2006). With regard to the
 232 Mediterranean, it may have served as a refugium for some species, namely
 233 species that now extend to the adjacent Iberian Atlantic (e.g., *Chromis chromis* in
 234 Domingues et al. 2005; *Parablennius sanguinolentus* in Domingues et al. 2008b).
 235 This rule is, however, far from being universal, as many species may have sur-
 236 vived in the Atlantic part of the Iberian Peninsula, along the coast of northwest
 237 Africa, and other unglaciated areas in west Europe (see Maggs et al. 2008).

- 238 4. The origin of populations (especially in the Atlantic) was dated mainly from
239 the Lower and Middle Pleistocene. Populations with origin estimated after the
240 LGM occur primarily in the North Sea (for cold water species) and Macarone-
241 nesia, particularly in the Azores (for warm waters species).
- 242 5. For thermophilic species, the data seem to support the Azores colonization from
243 Madeira (e.g., Santos et al. 1995). Indeed, when migration was evaluated, more
244 migrants were detected from Madeira to the Azores than the reverse (e.g.,
245 *Chromis limbata* in Domingues et al. 2006b). Madeira is, in turn, biogeo-
246 graphically connected with the Canaries, and there are references that point to
247 links between Canaries and Mauritania (e.g., *Tripterygion delaisi* in Domingues
248 et al. 2006a). This colonization route, combined with high sea surface temper-
249 atures, probably explains why there are several fishes that are present in the
250 tropics and in the Macaronesian Islands, but not in Europe (e.g., *C. limbata* in
251 Domingues et al. 2006b; *Parablennius parvicornis* in Domingues et al. 2008b).

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

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

270 Several important projects like Corona,⁴ FishPopTrace⁵ and a recent MarinERA
271 Project⁶ are encouraging examples that mobilized researchers of different coun-
272 tries and did much to share ideas and samples giving rise to a good number of
273 important chapters. We suggest that marine phylogeographers need to advance
274 toward more daring projects. The idea of standardizing sampling patterns that are
275 adequate to represent populations is also a requirement for large scale monitoring
276 of marine communities, while the changes in time of population structure and
277 genetic diversity, in close articulation with oceanographic information, seems

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

5 <http://fishpoptrace.jrc.ec.europa.eu/>.

6 <http://biocongroup.eu/MarinEra/Welcome.html>.

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

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289 We dedicate this chapter in loving memory of Vítor Almada whose tragic loss we suffered
290 during the course of this work.

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