

Chapter 1

Seaweed Phylogeography from 1994 to 2014: An Overview

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Abstract Molecular phylogeographic approaches employed for studying genetic diversity and evolution of seaweeds experienced noticeable growth since the mid-1990s and have greatly expanded our understanding of factors and processes contributing to biodiversity, adaptation, and population genetic variation of seaweeds. Herein, we present a numerical synthesis of 126 published references on seaweed phylogeography during the past two decades. We summarize the progress, research hotspots, regional distribution of outputs, potential deficiencies, and future tendencies in this field at a global scale. We also highlight the importance of integrating a statistically rigorous and comparative phylogeographic framework with species distribution models (SDM) and model-based phylogeographic inferences, when exploring cryptic speciation and evolution of seaweeds in response to global climate change, environmental shift, and human interference.

Keywords Coastal ecosystem · Ecological adaptation · Habitat heterogeneity · Phylogeography · Population genetics · Seaweed

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1.1 Introduction

Phylogeography is a relatively young discipline seeking to explore the principles, patterns, and processes contributing to the geographic distributions of genealogical lineages, especially those found within species in evolutionary and ecological contexts (Avise 2000, 2009). Because the genetic variation found in extant populations or species resulted from thousands or millions of years of accumulation, phylogeography is closely allied with historical biogeography and has played a fundamental role in bridging the gaps between micro- and macroevolutionary processes which predominantly shaped modern patterns of biodiversity on earth. Since its inception (Avise et al. 1987), phylogeography has considerably influenced life and earth sciences and has expanded into many other subdisciplines such as ecology, biology, genetics, oceanography, environmental sciences, and geography (Beheregaray 2008). The rapid growth and extension of phylogeography is mainly ascribed to the accelerating integration of genetic data and mathematical modeling, emerging high-throughput DNA sequencing technologies and increasingly powerful computation algorithms and analysis programs.

The rapid growth of phylogeographic studies in less than three decades also promoted methodological and conceptual shifts in some fields such as statistical phylogeography (Knowles and Maddison 2002), comparative phylogeography (Arbogast and Kenagy 2001) and phylogeographic information systems (Kidd and Ritchie 2006). Such a trend in development probably is far beyond the imagination of the “Father of Phylogeography,” John C. Avise (the recipient of the 2009 Alfred Russel Wallace award), who initially described phylogeography as a discipline with conceptual and technical roots linked to the incipient field of molecular genetics in the 1970s. A recent global search in Web of Science database using the terms “phylogeography” or “phylogeographic” in abstracts found that there were more than 3000 articles published between 1987 and 2006 (Beheregaray 2008). Nevertheless, phylogeographic studies predominantly focused on terrestrial organisms and only a small proportion (17 %) on marine species. The paucity of phylogeographic studies on marine species is unfortunate because marine ecosystems are strongly influenced by environmental conditions, including complex oceanographic factors, the long-term influence of paleoclimate change, short-term environmental shifts and human activities. These forces have independently or interactively had fundamental impacts on the temporal and spatial distributions of biodiversity, population genetic differentiation, and evolutionary histories of marine organisms.

Seaweeds (marine macroalgae) are a diverse and widespread group of photosynthetic organisms, classified into three broad groups (red, brown, and green algae) based on pigmentation and cell structure. They can be found in almost all aquatic environments, from marine to brackish and freshwater, and from the tropical islands near the equator to polar regions. Seaweeds are an essential component of coastal marine ecosystems and play a significant role as benthic primary producers, providing food, habitat structure, breeding grounds, and shelter for many

coastal organisms. For seaweeds, drifting is an important characteristic allowing them to undergo long-distance dispersal driven by oceanic currents (Thiel and Haye 2006), thereby producing complex biogeographic patterns of population genetic differentiation.

In this chapter, we present a broad description of the state of phylogeographic studies of seaweeds, including some early studies using RAPD (Random Amplified Polymorphic DNA), RFLP (Restriction Fragment Length Polymorphism), SSCP (Single Strand Conformation Polymorphism) and microsatellites that explored environmental factors as contributors to population-level genetic connectivity and differentiation. Our synthesis of phylogeographic literature of seaweeds provides a global viewpoint to appreciate which genetic markers are more common and effective for deciphering intraspecific evolutionary histories, which taxonomic groups have intensively been surveyed, and where are the disparities of research productivity between different regions of the world. This information helps us to identify future research priorities that can promote and reinforce our understanding of adaptive genetic variation and evolution of seaweeds.

1.2 Benchmark Progress

In contrast to the flourishing development of phylogeographic studies of terrestrial organisms soon after the discipline received its name in 1987 (Avice et al. 1987), the approach was only applied to seaweeds rather later. In 1994, Oppen and colleagues, led by Drs. Jeanine L. Olsen and Wytze T. Stam at the University of Groningen published an article entitled “Tracking dispersal routes: phylogeography of the Arctic-Antarctic disjunct seaweed *Acrosiphonia arcta* (Chlorophyta)” in the *Journal of Phycology* (Oppen et al. 1994), marking the pioneer phylogeographic study on (green) seaweeds (Fig. 1.1). Based on integrative evidence of RAPD and RFLP of nuclear ribosomal intergenic spacer (nrDNA IGS), these authors found that *A. arcta* populations in the Arctic and North Atlantic originated from the

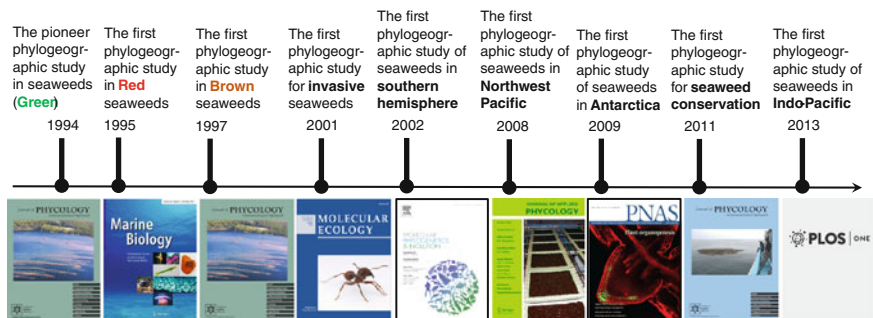


Fig. 1.1 Timeline of phylogeographic researches in seaweeds (key milestones)

Pacific. More importantly, the Arctic Greenland populations underwent independent colonization in contrast to the recolonization of the Antarctic Peninsula populations from southern Chile (Oppen et al. 1994). Afterward, the same research unit published a series of phylogeographic studies for other marine macroalgae (e.g., *Cladophora vagabunda*, Bakker et al. 1995; *Digenea simplex*, Pakker et al. 1996; Palmariaceae, Lindstrom et al. 1996), including the first phylogeographic work on red seaweeds (*Phycodrys rubens*, Oppen et al. 1995a, b) (Fig. 1.1).

In 1997, James Coyer collaborated with his previous colleagues (Olsen and Stam) to investigate genetic variability in the brown seaweed *Postelsia palmaeformis* on spatial scales of 1–250 km by integrating the complementary RAPD and M13 fingerprints (Coyer et al. 1997). They found that RAPDs can easily discriminate *P. palmaeformis* populations isolated by geographic distances of 16–250 km, despite no resolution in discriminating individuals separated by <1–25 m, whereas M13 fingerprinting detected decreased genetic relatedness as geographic distance increased to 25 m (Coyer et al. 1997). This was the first phylogeographic work on brown seaweeds (Fig. 1.1). Olsen and Stam initially introduced phylogeographic approaches to seaweed investigations and opened a window through which phycologists could link environmental variables and life-history features to population genetic differentiation and ecological adaptation of seaweeds over time and space. In 2012, they were awarded the Award of Excellence by the Phycological Society of America for several decades of research achievements in surveying biogeographic histories and evolutionary patterns of benthic seaweeds.

From the beginning of the twenty-first century, phylogeographic approaches have been extensively applied to seaweed research (Fig. 1.1). Based on the geographic distribution of specific chloroplast-encoded large subunit RuBisCo (*rbcL*) haplotypes and the genetic relatedness between source and invasive populations, McIvor et al. (2001) revealed two cryptic invasion routes of the red alga *Polysiphonia harveyi* from Japan to New Zealand and the North Atlantic Ocean, including two separate introductions from Japan (Hokkaido and Honshu) into the northern North Atlantic and a recent introduction from Honshu into at least two areas of California, North Carolina, and New Zealand. Other noteworthy milestones of phylogeographic theory applied to seaweeds include the first phylogeographic studies focused on benthic macroalgae in the Southern Hemisphere (*Halimeda*, Kooistra et al. 2002), the Northwest Pacific (*Ulva*, Shimada et al. 2008), the sub-Antarctic (*Durvillaea antarctica*, Fraser et al. 2009a, b), and the Indo-Pacific (*Sargassum polycystum*, Chan et al. 2013) (Fig. 1.1). In particular, the phylogeographic approach has been demonstrated to be able to provide valuable insights into conservation genetics of endangered seaweed species. Couceiro et al. (2011) used Amplified Fragment Length Polymorphism (AFLP) to investigate the genetic structure and population connectivity of the red alga *Ahnfeltiopsis pusilla*, a naturally rare species categorized as vulnerable in the Northwest Iberian Peninsula (NWIP), at different geographic scales (from <1 to 1200 km). The results indicated that five NWIP enclaves should be designated independently as management units

(MUs), and that the three southernmost sites harboring most of the genetic heritage of *A. pusilla* in NWIP are particularly valuable for conservation as evolutionarily significant units (ESUs).

1.3 Global Glance

Based on a survey of the database ISI Web of Knowledge and the terms “seaweed” and “phylogeography”/“phylogeographic” or “population genetics,” a total of 126 papers published from 1994 to 2014 were identified from 27 international journals such as *Proceedings of the National Academy of the Sciences of the United States of America*, *Proceedings of the Royal Society of Biology B: Biological Sciences*, *BMC Evolutionary Biology*, *Aquatic Botany* and *Journal of Phycology*. In general, phylogeographic studies on seaweeds experienced remarkable growth as measured by the number of papers published each year since 2000 (Fig. 1.2), which probably was due to the contribution of the book by Avise (2000) dealing with the history and formation of species, enabling more researchers to become acquainted with this emerging discipline. This tendency, as expected, is in line with the growth of phylogeographic studies at a global scale (Beheregaray 2008).

The far-reaching contribution of phylogeographic approaches to seaweed research is evidenced in Table 1.1, which lists 10 subject categories substantially influenced by this scientific discipline. These studies can be primarily classified in the fields of ecology and evolution (56 %) and population genetics (19 %). The phylogeographic approach has also been extended to address some long-standing questions in seaweed ecology (e.g., hybridization and speciation). For example, Coyer et al. (2002) employed SSCP analyses of nuclear, chloroplast, and mitochondrial markers and confirmed the occurrence of hybridization between *Fucus*

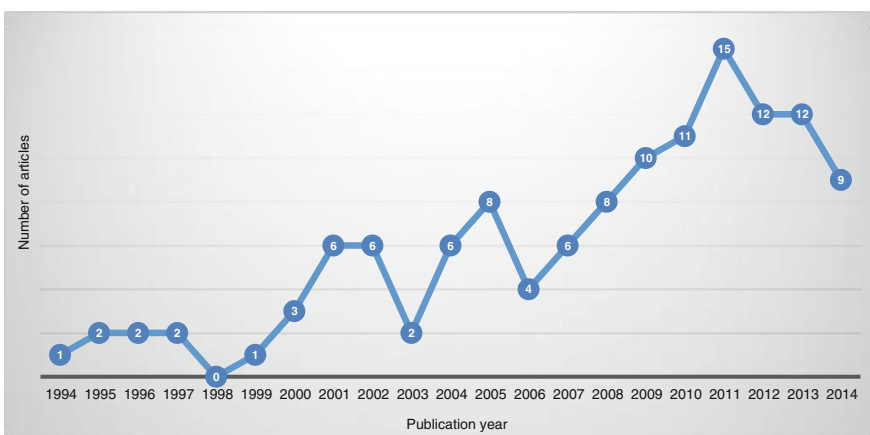


Fig. 1.2 Number of phylogeographic articles published between 1994 and 2014 in seaweeds

Table 1.1 The top 10 scientific journals published articles related to seaweed phylogeography and the contributions of phylogeographic approaches to relevant research areas in seaweed

Journal	No.	Subject category	Representative reference
<i>Journal of Phycology</i>	32	Population genetic structure	Faugeron et al. (2001)
<i>Molecular Ecology</i>	22	Evolutionary biology	Olsen et al. (2010)
<i>Marine Biology</i>	10	Cryptic/genetic diversity	Lee et al. (2013)
<i>Journal of Applied Phycology</i>	7	Environmental adaptation	Kostamo et al. (2012)
<i>Journal of Biogeography</i>	6	Invasive biology	McIvor et al. (2001)
<i>Phycologia</i>	5	Hybridization/speciation	Coyer et al. (2002)
<i>Molecular Phylogenetics and Evolution</i>	4	Biodiversity conservation	Couceiro et al. (2011)
<i>BMC Evolutionary Biology</i>	4	Heredity	Zuccarello et al. (1999)
<i>Botanica Marina</i>	4	Seascape genetics	Krueger-Hadfield et al. (2013)
<i>Aquatic Botany</i>	4	Molecular systematics	Kooistra et al. (2002)

serratus (dioecious) and *F. evanescens* (monoecious) in the Kattegat Sea, Denmark, when densities of *F. serratus* (F_s) and *F. evanescens* (F_e) exceeded 2 and 14 m⁻², respectively. However, the hybridization was asymmetrical since only the F_e egg × F_s sperm cross was successful and the reciprocal cross was ineffective. Moreover, Zuccarello et al. (1999) used SSCP analysis of the chloroplast-encoded RuBisCo spacer and revealed maternal inheritance of plastids in crosses between isolates of the red alga *Bostrychia radicans* and *B. moritziana*. Listed in Table 1.1 are journals representing the large proportion of published papers dealing with seaweed phylogeography (e.g., *Journal of Phycology*, *Molecular Ecology*, and *Marine Biology*).

1.4 Taxonomic Coverage

Among the 126 found articles on seaweed phylogeography, 92 % (115 papers) are research articles, whereas only 8 % (11 papers) are review articles or others (e.g., perspectives and short communications) (Fig. 1.3a). Sorting the papers by nature of the study (Fig. 1.3b) shows that 75 % of the articles investigated phylogeographic structure and evolutionary relatedness within one taxon. Comparatively, a smaller proportion of studies (25 % or 32 papers) focused on more than one taxon in the same genus; however, these papers did not use a comparative framework to explore congruency of evolutionary patterns and genetic structuring among the taxa.

The global publication effort on seaweed phylogeography is significantly biased toward brown seaweeds, which accounted for 50 % of all the articles (Fig. 1.4a).

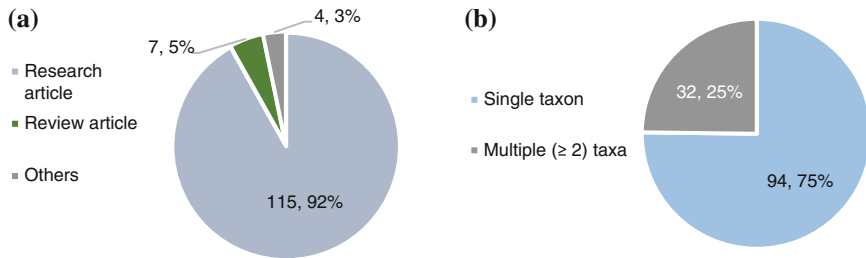


Fig. 1.3 Proportion of articles in seaweed phylogeography published between 1994 and 2014 according to type of articles (a) and nature of study (b)

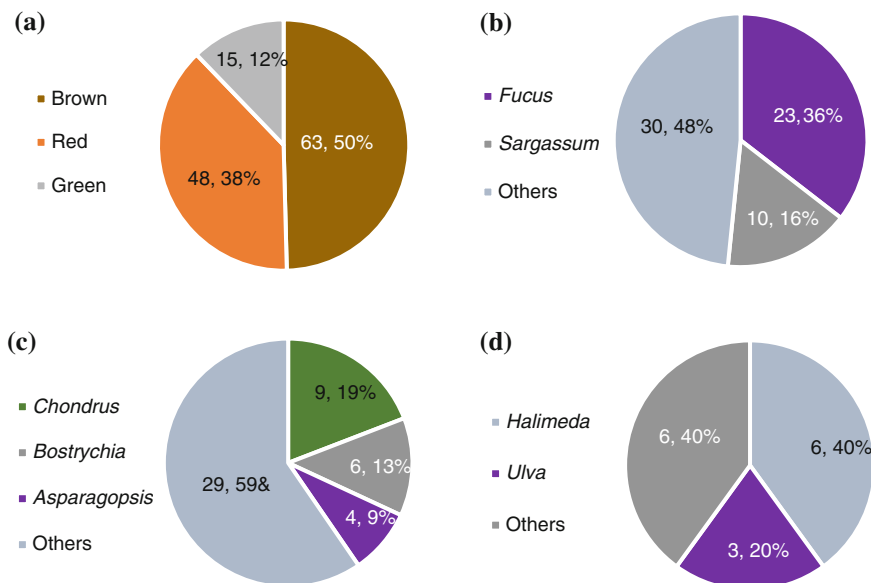


Fig. 1.4 Proportion of articles in seaweed phylogeography published between 1994 and 2014 according to taxonomic catalogs (a), the most common surveyed taxa in brown (b), red (c) and green (d)

Studies focusing on red seaweeds represented 38% (48 papers), and a much smaller proportion (12% or 15 papers) were focused on green seaweeds. Of the 63 articles published on brown seaweeds, the genera *Fucus* and *Sargassum* were the most common taxa surveyed to date, which comprised 23 and 10 articles, respectively (Fig. 1.4b). This taxonomically biased publication activity is probably due to two main reasons: First, the genera *Fucus* and *Sargassum* are characterized by wide geographic distributions from northern cold temperate to southern warm and

tropical regimes in the ocean enabling them to be representative models. For example, *Fucus* species' demographic histories, population genetic differentiation, and biogeographic evolution can be influenced by various factors, such as coastal topography and circulation patterns (Muhlin et al. 2008), range dynamics (habitat tracking), and dispersal restrictions (Neiva et al. 2012a, b), long-term climate change (e.g., the Quaternary ice ages) (Coyer et al. 2003, 2011a; Hoarau et al. 2007; Muhlin and Brawley 2009) and short-term environmental shifts (several decades of global warming) (Nicastro et al. 2013). Second, *Fucus* and *Sargassum* have biologically well-defined features, for example, some *Fucus* species can be found in highly heterogeneous marine coastal habitats, such as those with salinity gradients ranging from 2.7 psu to 33.0 psu on a 12 km geographic scale in the North Atlantic (Coyer et al. 2011b). Species of *Sargassum* can form drifting mats after being detached from the substratum and be transported for hundreds of kilometers driven by oceanic currents (Komatsu et al. 2008; Uwai et al. 2009; Cheang et al. 2010a; Hu et al. 2011a, 2013).

In contrast, phylogeographic studies on red seaweeds have expanded into more areas. Some genera such as *Chondrus*, *Bostrychia* and *Asparagopsis* have received relatively more attention, with each genus comprising 9, 6, and 4 papers, respectively (Fig. 1.4c). For *Chondrus*, phylogeographic surveys have overwhelmingly concentrated on the North Atlantic endemic species *C. crispus*. Early phylogenetic analyses proposed that the North Pacific ancestor of *C. crispus* migrated to the Arctic via the opening of the Bering Strait *c.* 3.5 million years ago (Ma) and subsequently colonized both sides of the North Atlantic (Hu et al. 2007a). Recent integrative phylogeographic evidence showed that *C. crispus* experienced large-scale population decline caused by marine glaciations during the late Pleistocene and survived in at least three scattered refugia in the northeastern Atlantic (e.g., southwestern Ireland, the English Channel and the northwestern Iberian Peninsula) (Hu et al. 2010, 2011b). With the retreat of the Last Glacial Maximum (hereafter LGM, 0.026–0.019 Ma), *C. crispus* underwent multidirectional step-stone expansions in the northeastern Atlantic centering on the late Pleistocene refugia and trans-Atlantic migration from Europe to North America (Provan and Maggs 2011; Hu et al. 2011b). More importantly, *C. crispus* exhibits an excellent potential as a research model for seascape genetics, e.g., to explore the ecological role of microgeographic environmental variables in shaping phylogeographic dynamics along coastal communities. A recent study revealed that tidal heights not only contributed to genetic differentiation between high- and low-shore stands, but also restricted genetic exchange within the high-shore stand, extending our understanding of the population genetic structure and evolutionary patterns of *C. crispus* from macrogeographic scale (>500 km) to microgeographic scale (<100–200 m) (Krueger-Hadfield et al. 2013; Hu 2013). The feature of intraspecific hybridization, taxonomic complexity, and highly differentiated lineages in *Bostrychia* (Zuccarello et al. 1999, 2006, 2011; Zuccarello and West 2003; Muangmai et al. 2015), and the nature of rapid global invasion in *Asparagopsis* (Andreakis et al. 2007, 2009; Sherwood 2008), make these red algal taxa amenable to becoming research foci concerning cryptic genetic diversity, evolutionary history and invasive processes.

The genera *Halimeda* and *Ulva* are the two top-ranked taxa in limited phylogeographic studies on green seaweeds (Fig. 1.4d). *Halimeda* species consist of phenotypically complex segmented, calcified thalli and are common in reefs and lagoons throughout the tropics (Kooistra et al. 2002). After reproduction, the calcified *Halimeda* segments became the most important contributors of aragonite sediments (up to 90 %) in modern tropical and subtropical carbonate environments (Freile et al. 1995). Historically, *Halimeda* was an important member of the Late Miocene Mediterranean carbonate factory after the Tethyan Seaway was closed during the middle Miocene (Braga et al. 1996). Currently, *Halimeda* species are globally distributed and flourish in variable environments at depths ranging from <1 to 150 m (Kooistra et al. 2002; Verbruggen et al. 2009). These factors enable *Halimeda* to be an ideal model to survey genus-level biogeographic history associated with paleobiogeographical and macroecological processes, and to characterize evolutionary niche dynamics in the ocean (Verbruggen et al. 2005, 2009; Reuter et al. 2012). The green seaweed *Ulva* exhibits considerable morphological plasticity and can grow under variable salinities. Previous molecular research has demonstrated that *Ulva* species have some important phylogeographic imprints of climate change-induced historical reduction of genetic diversity in the Northern Hemisphere (Leskinen et al. 2004; Shimada et al. 2008). Recent genetic surveys indicated that *Ulva* species may be used as models to resolve how intertidal seaweeds adapt to thermal stress and salinity gradients and why some species exhibit more extensive spatial and temporal distribution ranges than others (Ogawa et al. 2015).

1.5 Regions and Countries

Our literature survey shows that the Northeast Atlantic was the most intensively studied region with 23.5 % (32 papers) of all the articles (Fig. 1.5), also see chapters by Neiva et al. (2016) and Li et al. (2016) in this volume. A good portion of studies were conducted for systems from the Northwest Pacific (13.5 % or 17 papers) and from the Northern Hemisphere oceans (14.3 % or 18 papers) in which sampling covered both the North Pacific and the North Atlantic. On the other hand, a relatively small proportion of references (4.8 % or 6 papers) used samples from the Southern Hemisphere oceans, Australia and New Zealand. A smaller proportion of studies (5–7 papers) were focused on the Southeast Atlantic, Indo-Pacific, Antarctic and Sub-Antarctic. There was only one paper each published on seaweed phylogeography in the Mediterranean and South Africa waters. This was surprising since recent evidence indicates that these phylogeographically unexplored regions are important marine biodiversity hot spots (Coll et al. 2010; Griffiths et al. 2010). Collectively, phylogeographic studies on seaweeds were predominantly performed in the Northern Hemisphere oceans but the research effort was not equally distributed among regions (e.g., Northwest Atlantic vs. Northeast Atlantic, North Atlantic vs. North Pacific).

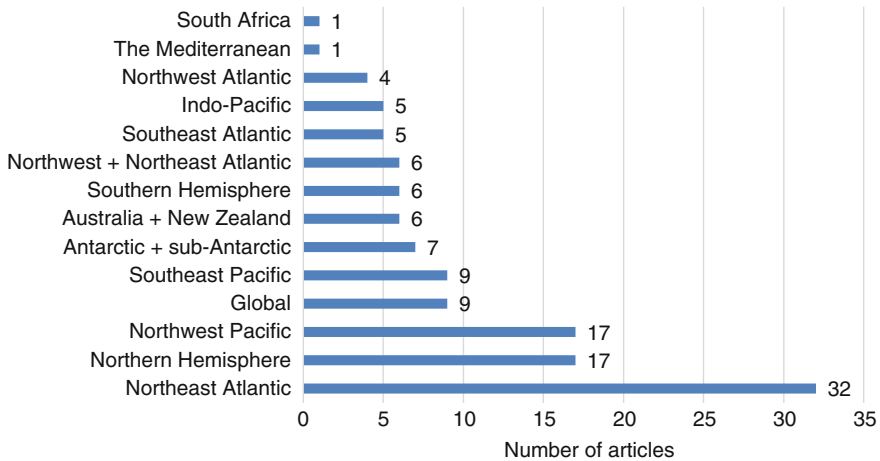


Fig. 1.5 Regional distribution of articles in seaweed phylogeography published between 1994 and 2014 based on the location of organisms studied

When references were classified based on the nationalities of the corresponding authors of the articles (Fig. 1.6), the Netherlands was the most productive country with 14.3 % of all articles (18 papers), followed closely by China with 11.9 % (15 papers) and the USA with 11.1 % (14 papers). The large proportion of phylogeographic studies on seaweeds from the Netherlands was mainly due to the prolific contributions of Drs. Olsen and Stam at the Groningen University and their decades of continuous endeavor in this field (Oppen et al. 1994; Bakker et al. 1995; Peters et al. 1997; Miller et al. 2000; Coyer et al. 2002, 2003, 2006, 2011a, b; Hoarau et al. 2007; Olsen et al. 2010). China's productivity was largely thanks to Dr. Put O. Ang Jr. at the Chinese University of Hong Kong and Dr. Zi-Min Hu at the Institute of Oceanology, Chinese Academy of Sciences (Cheang et al. 2008, 2010a, b; Chan et al. 2013, 2014; Hu et al. 2007b, 2010, 2011a, b, 2013; Wang et al. 2008; Li et al. 2015). There were more than five institutions involved in population genetics and phylogeography of seaweeds in the USA with Drs. Susan H. Brawley (University of Maine) and Walter H. Adey (National Museum of Natural History) producing a considerable number of publications (Muhlin et al. 2008; Muhlin and Brawley 2009; Brawley et al. 2009; Adey and Steneck 2001; Adey et al. 2008; Adey and Hayek 2011). The Korean research unit led by Dr. Sung Min Boo published 11 papers on population genetic diversity and phylogeography of seaweeds, with the geographic sampling mostly restricted to the Korean Peninsula and adjoining areas (Yang et al. 2008, 2009; Bae et al. 2013; Lee et al. 2013; Kim et al. 2010, 2012, 2014). The research unit at the University of Algarve, Portugal led by Dr. Ester A. Serrão made important contributions to phylogeographic studies of seaweeds with nine publications (Moalic et al. 2011; Nicasastro et al. 2013; Neiva et al. 2010, 2012a, b, 2014). Dr. Giuseppe C. Zuccarello at Victoria University of Wellington and Dr. Ceridwen I. Fraser at the University of Otago, New Zealand led

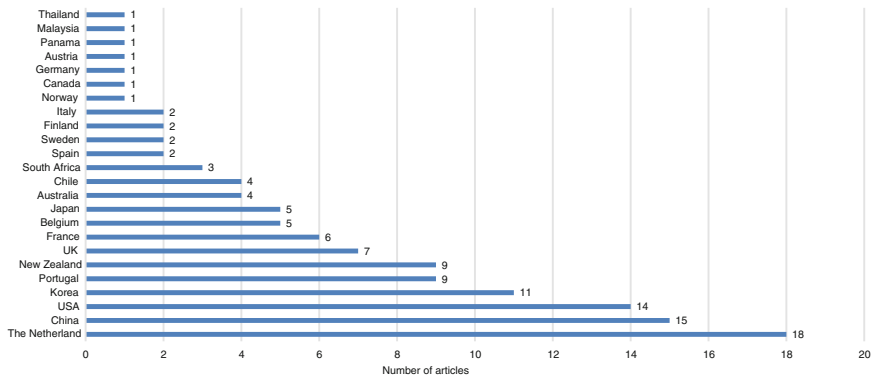


Fig. 1.6 Country distribution of articles in seaweed phylogeography published between 1994 and 2014 based on the location of organisms studied

the phylogeographic studies of seaweeds around Antarctic and sub-Antarctic areas (Zuccarello et al. 1999, 2003, 2006, 2011; Buchanan and Zuccarello 2012; Fraser et al. 2009a, b, 2011, 2013). In the United Kingdom, Drs. Jim Provan and Christine A. Maggs at the Queen’s University of Belfast have also demonstrated much endeavor in phylogeographic studies of seaweeds (Provan et al. 2005a, b, 2008, 2011, 2013). Dr. Myriam Valero at the Station Biologique de Roscoff, France and Dr. Marie-Laure Guillemain at the University of Austral de Chile, Chile have published important insights into the phylogeographies of seaweeds in the southeast Pacific (Montecinos et al. 2012; Guillemain et al. 2014; Krueger-Hadfield et al. 2011, 2013; Robuchon et al. 2014). Finally, the Phycology Research Group and Center for Molecular Phylogenetics and Evolution, Ghent University led by Dr. Olivier De Clerck have developed a broad interest in diversification and evolutionary dynamics of seaweeds through the integration of phylogenetic techniques and niche modeling into a Geographic Information System (GIS) framework (Verbruggen 2005, 2009), which may enable us to broadly understand how seaweeds shift their geographic distributions in response to global climate change. Although there are also many other excellent researchers working on seaweed phylogeography, the above examples highlight a few of the most productive groups in the field.

1.6 Genetic Markers

In the survey, we divided the genetic markers employed into three major classes: Class I, mitochondrial DNA (mtDNA) and chloroplast DNA (cpDNA); Class II, nuclear ribosomal DNA (nrDNA) sequences, RAPD, AFLP, SSCP and single nucleotide polymorphism (SNP); Class III, microsatellites. Phylogeographic information and population genetic diversity derived from Class I molecular markers represented 82 studies (51 %), whereas Class II and III molecular markers were used

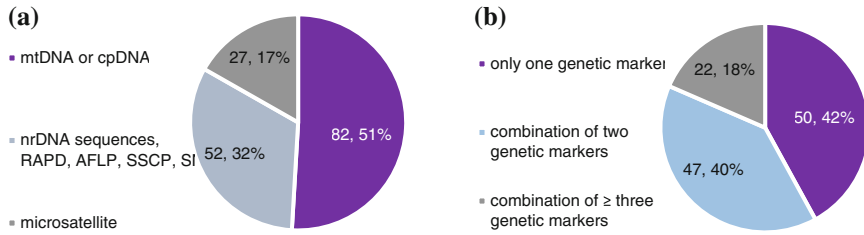


Fig. 1.7 Proportion of articles in seaweed phylogeography published between 1994 and 2014 sorted by classes of genetic marker(s) (a) or marker combinations (b)

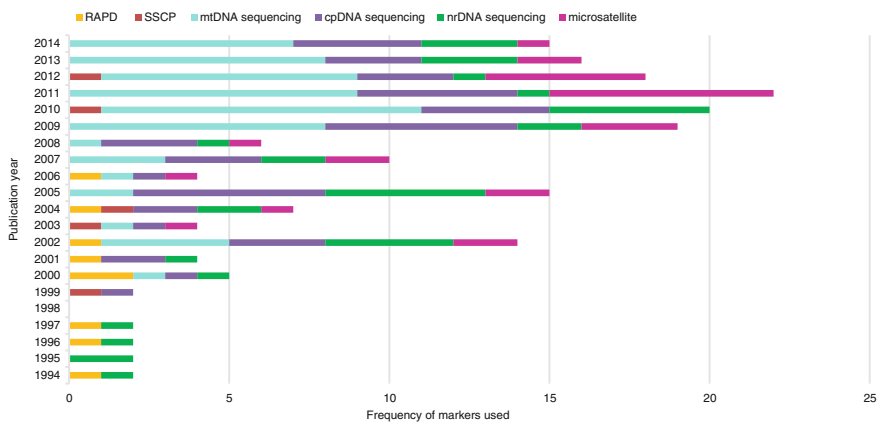


Fig. 1.8 Distribution of genetic marker(s) used for data collection in seaweed phylogeography published between 1994 and 2014

in 52 (32 %) and 27 studies (17 %), respectively (Fig. 1.7a¹). Among the 126 papers surveyed, 50 papers (42 %) used only one genetic marker, and 47 papers used two genetic markers, whereas 22 papers used ≥ 3 genetic markers to investigate population-level phylogeographic patterns and genetic differentiation (Fig. 1.7b).

Several interesting trends can be identified when each of the six representative genetic markers (RAPD, SSCP, mtDNA, cpDNA, nrDNA, and microsatellite) are sorted by year (Fig. 1.8). RAPD and nrDNA sequencing (e.g., internal transcribed spacer) were the predominant markers used for seaweeds before 2000. Afterward, nrDNA sequencing showed an intermittently increasing frequency until 2010, whereas the frequency of RAPD decreased significantly and was discontinued after 2006. SSCP was occasionally used for seaweeds from 1999 but gradually lost its advantages when high-throughput sequencing techniques emerged. On the other

¹The paper which employed more than one genetic markers will be counted for multiple times.

hand, the uniparentally inherited mtDNA and cpDNA markers were used about ≤ 5 times during the 2000s but have had a continuously increasing popularity in the last 6 years. Microsatellite technology, which was first used for seaweed phylogeography in 2002 as complementary evidence to sequencing data sets, has also shown a trend of increasing frequency since 2007.

1.7 Concluding Remarks and Perspectives

Phylogeographic studies on seaweeds have experienced a noticeable increase over the past two decades, although seaweeds still account for only a small proportion of several thousands of phylogeographic studies. Importantly, these empirical studies have not only expanded our knowledge of how seaweeds respond to severe climate change and environmental shifts via derived adaptive biological characteristics, but have also made valuable contributions to our knowledge of basic biology, intertidal ecology, conservation genetics and the adaptive evolution of seaweeds. Nevertheless, seaweed phylogeography is still confronted with several key challenges.

There is an evident bias of taxonomic coverage in terms of research objectives as brown and red seaweeds were relatively well represented in the phylogeographic literature (Fig. 1.4a). Publications on green seaweeds represented only 12 % of all publications, despite their important biogeographic and evolutionary roles. In fact, green seaweeds (e.g., *Ulva*) occur globally from the cold temperate to tropical regions and the poles, and under strong salinity gradients. These taxa are therefore ideal models for studying environmentally induced adaptive evolution and the interactions between the complex life-histories of seaweeds and their geographic distributions at both vertical and horizontal scales. In addition, there is a wealth of phylogeographic studies on seaweeds from the Northern Hemisphere oceans, but relatively few from the Southern Hemisphere (Fig. 1.5). The disproportional number of surveys of seaweed phylogeography between the Northern and Southern hemispheres is due in part to the vast majority of scientists who live in the Northern Hemisphere, and there are more research institutions there. Empirically, the competitive scenarios of glacial survival versus postglacial recolonization in the Northern Hemisphere appear to receive much more scientists' attention. Coastal areas of North Atlantic and North Pacific were covered by ice sheets during Quaternary glaciations and were recolonized after the ice retreated. Seaweed species in previously glaciated areas show similar phylogeographic patterns (Hewitt 2000; Beheregaray 2008), which are informative about the influence of paleoclimate change on population genetic structure, demographic history and range shifts of seaweeds. However, explanations of the generalized patterns observed in seaweeds in the Northern Hemisphere may not be applicable to the Southern Hemisphere populations or extended to other parts of the world because considerable differences in geomorphologic, environmental, and paleoclimatic history exist among these areas. Currently, phylogeographic knowledge of seaweeds is

either inadequate or simply nonexistent for seaweeds inhabiting some key regions on earth, such as southern Africa, the Mediterranean, the Antarctic and sub-Antarctic, Australia, Indo-Pacific (the Coral Triangle) and the Arctic and sub-Arctic. Some of these regions harbor high levels of seaweed endemism and species richness (Lindstrom 2001, 2009; Kerswell 2006; Adey et al. 2008; Coll et al. 2010; Griffiths et al. 2010), providing excellent opportunities to investigate the mechanisms and processes contributing to diversification and evolution of seaweeds at a global scale.

Seaweed phylogeography studies have predominantly been made at macrogeographic scales (>100 km) to test for the influence of long-term environmental factors on population genetic differentiation and demographic modes from the perspective of historical biogeography. Some studies were elaborately designed at moderate geographic scales and revealed significant insights into cryptic genetic diversity, genetic structure, and the influence of ecological variables on morphological variations of seaweeds (Coyer et al. 1997; Bergström et al. 2005; Tataronov et al. 2007; Fraser et al. 2009b). However, the knowledge of whether mating systems and microhabitats contribute to genetic differentiation and diversity of coastal seaweeds is still limited. This is surprising since the various physical conditions (e.g., turbidity, wave exposure gradients, and tidal excursion distances) in the intertidal zone make it an ideal ecosystem to explore the genetically and evolutionarily interactive patterns and processes of seaweeds (Hu 2013). Recent surveys have highlighted the significant role of sexual reproduction, inbreeding, and tidal height in substructuring population genetic differentiation in the red seaweed *Chondrus crispus* (Krueger-Hadfield et al. 2011, 2013), opening up an exciting avenue to investigate the relative roles of life-history and microhabitats in shaping phylogeographic connectivity and adaptive evolution of seaweeds.

The integrative comparison of phylogeographic data from multiple co-occurring taxonomic groups can help to discover prevalent patterns and previously unrecognized cryptic biogeographic imprints, enhancing our understanding of why co-distributed organisms have different levels of biodiversity and distributional ranges (Arbogast and Kenagy 2001). Maggs et al. (2008) reanalyzed genetic data for eight benthic marine taxa, including two seaweeds species *Palmaria palmata* and *F. serratus*, identified nine potential marine glacial refugia and refined concordant, nonconcordant and indeterminate biogeographic patterns in North Atlantic. Thereafter, many phylogeographic studies were performed for seaweeds from North Atlantic and North Pacific. We can expect that comparative analysis based on these patterns may help to understand some cryptic and basic information on general evolutionary histories for seaweed phylogeography.

Model-based phylogeographic inferences, which estimate parameters under different assumed models using likelihood, Bayesian or approximate Bayesian computation (ABC) approaches, have been greatly strengthened as the computational algorithms progressed. They have shown excellent promises to examine the relative support for various hypotheses about demographic histories of marine organisms when a wide range of plausible models are included (Hickerson and Meyer 2008; Ilves et al. 2010). These phylogeographic inferences may enable us to test the

proposed hypotheses inferred from molecular data on seaweeds. Finally, integrating phylogeography with species distribution models (SDM) or ecological niche models (ENM) can help us to explicitly elucidate how the species distribution range is affected by climate change, vicariance or dispersal, genetic introgression, and natural selection (Kozak et al. 2008). Based on the species' distribution range shifts between ancestral populations (obtained from paleo-ENM) and current populations, the historical and environmental parameters associated with population demography can be inferred (Richards et al. 2007). A few recent studies have been conducted in this area for intertidal seaweeds (Verbruggen et al. 2009; Neiva et al. 2014) and have provided important phylogeographic insights into range shifts of seaweeds with lower dispersal capability in response to climate change since the LGM. There is still an urgent need to assess, through integrative ecological and evolutionary approaches, the unknown aspects and specific details concerning adaptation and distribution of seaweeds.

Acknowledgements We would like to thank Ceridwen Fraser and an anonymous reviewer for valuable comments on this chapter. This study was partially supported by National Natural Science Foundation of China (31370264) granted to Z.M. Hu.

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