

## Chapter 2

# Paradigm Shifts in the Phylogeographic Analysis of Seaweeds

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**Abstract** The phylogeographic analysis of seaweeds faces numerous biological, methodological, and conceptual challenges. One challenge is to understand how life-history phases, mating systems, dispersal mechanisms, and physiological tolerances influence the distributions and persistence of local populations. A second challenge has been to develop genetic assay methods that allow us to trace unbroken gene lineages so they can be tested with models using coalescence theory. An integral part of this challenge has been to identify unrecombining sections of DNA with known modes of inheritance. For the most part, seaweed phylogeographic studies have used unrecombining organellar and plastid DNAs, but new methods of phasing haplotypes of nuclear DNA can provide an enormous amount of data to fine-tune hypotheses to distinguish the effects of demography and natural selection. Finally, phylogeography faces conceptual challenges, as we learn ever more about palaeoclimates, the historical shapes of shorelines, and the dynamics of ocean currents. A major advance is the marriage between demographic models and models of natural selection, because both interact to mold the shapes of gene genealogies.

**Keywords** Historical demography • Modes of inheritance • Modes of reproduction • Molecular markers • Natural selection • Phylogeography • Pleistocene • Population genetics

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This chapter is dedicated to Bob Vadas (University of Maine) who, by example, taught me to ask questions.

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## 2.1 Introduction

The central concept in phylogeography is the notion that the geographic distributions of gene lineages can be used to understand the ‘spatial and temporal dimensions of microevolution’ (Avice 2009). Monophyletic lineages are the primary units of analysis and have historically been estimated from nonrecombining, uniparentally inherited cytoplasmic DNAs, such as those in mitochondria and plastids (Avice et al. 1987). The origins of Phylogeographic patterns of genetic diversity among populations can be fully understood only by bringing together ideas from several disciplines, including not only genetics and molecular biology, but also ecology, reproduction and developmental biology, physiology, dispersal biology, paleoclimatology, geology, and oceanography (Dawson et al. 2013; Marske et al. 2013; Habel et al. 2015). This interdisciplinary approach can be seen in recent studies of seaweeds and is embodied in a long-standing research paradigm described by Huxley and Tinbergen, known as *explanatory pluralism* (Box 1) (Huxley 1916; Mayr 1961; Tinbergen 1963). Pluralistic explanations can lead to major breakthroughs in understanding the patterns of biological diversity.

### Box 1. Phylogeography and Explanatory Pluralism

Most biologists specialize in a particular area of research because time and funding restrict the use of a wide range of research methods. Unfortunately, such limitations can preclude broad understanding of a biological system. Phylogeography intersects with several disciplines that help to provide explanations for the patterns of genetic diversity among populations. These explanations fall into two broad categories reflecting *proximate* and *ultimate* causes (Tinbergen 1963; Dewsbury 1999). The distinction between these categories is whether the expression of a trait results from an event during the life of an individual, and by extension within the recent history of a population, or is the legacy of an individual’s, or population’s, evolutionary history.

Proximate causes include *mechanistic* explanations of how a phenomenon occurs. For example, why do some populations have less genetic diversity than other populations? One explanation might be that the amount of diversity in a population is proportional to the population’s effective size. Larger populations have higher levels of diversity because the effects random drift are less than in small populations. Proximate causes also include *ontological* explanations that in our example of explaining levels of genetic diversity might include a population’s response to climate variability or to the recent introduction of a predator into its ecosystem.

Ultimate causes can be rooted in the *phylogenetic* origins of an individual or population trait. Again in our example, genetic diversity in a population, or species, might reflect its evolutionary history, which we can reconstruct with a large toolbox of genetic methods and concepts. Finally, we can ask whether

genetic diversity has *adaptive value*. Are populations with high levels of genetic variability better able to survive short-term environmental challenges, or to adapt to long-term habitat changes?

Phylogeographic explanations typically include both *proximate* and *ultimate* factors to understand patterns in nature. Proximate mechanisms operate within the lifetime of an individual (or population), and *ultimate* mechanisms operate over long timescales. An understanding of how phylogeographic patterns arise depends on incorporating both kinds of factors from other disciplines. Proximate factors include life-cycle variation, mating strategies, environment–biological interactions, physiology, predation, and demographic processes. Ultimate factors include the phylogenetic and genetic legacies arising from a species' evolutionary history and adaptive traits that give rise to phylogeographic patterns. Importantly, phylogeographic explanations have to include information about the interaction of a species' biology with geologic, paleoclimatic, and oceanographic histories in a region.

The goals of this chapter are to explore the fundamental concepts of phylogeography and to outline biological variables in seaweeds that influence phylogeographic patterns. An overview of the literature shows that phylogeographic concepts have shifted in response to the development of new methods for surveying genetic variation and the creation of new theories and statistical models to interpret genetic patterns. These developments have led to the expansion of phylogeography beyond its original formulation. Phylogeographic studies now often include the analysis of nuclear genes, in addition to organellar genes and invoke ideas from numerous disciplines to explain phylogeographic patterns. A major future direction in phylogeography will be to weave demography and natural selection into more holistic explanations of microevolutionary processes.

## 2.2 Shifting Paradigms in Phylogeography

The term *phylogeography* first appeared in an article by Avise et al. (1987) to describe the association between the lineages in a gene genealogy and geography. The hallmark of phylogeographic inference has been the use of nonrecombining organellar DNA, chiefly from mitochondria and chloroplasts, to reconstruct gene genealogies. However, the development of new molecular markers has prompted an expansion of the methods and concepts used in phylogeography (Hickerson et al. 2010; Marske et al. 2013; Bowen et al. 2014). Phylogeographic studies now draw on a diversity of methods and concepts to infer contemporary and historical processes that influence population distributions and abundances (Hickerson et al. 2010; Marske et al. 2013). Population genetic models are used to interpret genetic variability in terms of equilibrium processes such as genetic drift, gene flow, and mutation (Crow and Kimura 1970). Seascape concepts borrow from work on land

plants (Sork et al. 1999) to understand the effects of currents, tides, shoreline topography, and temperature on the dispersal and settlement of spores and gametes (Galindo et al. 2006; Selkoe et al. 2008; Liggins et al. 2013). Species' distribution modeling (SDM), or ecological niche modeling (ENM), (Elith and Leathwick 2009) can predict both historical (Bigg et al. 2007) and contemporary (Jueterbock et al. 2013) geographic distributions of marine organisms. These and many other concepts provide a framework to test hypotheses of historical and contemporary population structures with molecular datasets.

## 2.3 Methodological Considerations

A seminal challenge in phylogeography is the use of genetic profiles in contemporary populations to understand the roles of historical demography and selection on microevolutionary processes. The chief genetic approach to understand the effects of historical climate change is coalescence analysis of gene genealogies, because historical population size, extirpations and colonizations, and founder events influence the depth of coalescence to a common ancestral haplotype in a genealogy (Fu and Li 1999). The shape of a gene genealogy can provide a window into the past demography of a population (Rogers and Harpending 1992; Hey and Nielsen 2004; Drummond and Rambaut 2007; Beaumont 2010).

A vexing problem in the phylogeographic analysis of seaweeds can be their different morphological forms, depending on environmental conditions. Related species sometimes differ little in their morphologies, making individual identifications difficult. Hence, a major focus of molecular methods in the past few years has been on systematics (Kraft et al. 2010; Saunders and Kucera 2010; Yotsukura et al. 2010; Boo et al. 2011; Lindstrom et al. 2011; Sutherland et al. 2011; Marins et al. 2012; Kirkendale et al. 2013; Lin et al. 2013), and on phylogenetic relationships among higher taxa based on DNA restriction fragment length polymorphisms (RFLP) (Bhattacharya and Druehl 1990) and DNA sequence markers (Saunders et al. 2004; Clarkson and Saunders 2010; Verbruggen et al. 2010). Several researchers routinely use the mtDNA barcode gene, cytochrome oxidase I (*coxI*) (Saunders 2005; McDevit and Saunders 2010), whereas others favor the chloroplast DNA gene, ribulose-bisphosphate carboxylase (*rbcL*) (Freshwater et al. 1994) for phylogenetic and phylogeographic studies.

### 2.3.1 Molecular Markers

The goals of phylogeography are first to describe genetic relationships among populations, or among closely related species, scattered across a seascape, then to infer the ultimate and proximal processes responsible for the observed genetic patterns. Phylogeographic studies require a careful choice of molecular markers to

be able to detect a particular effect size (magnitude of divergence) and appropriate temporal scale of events. Most importantly, a molecular marker must have a predictable mode of inheritance, which can be tested with breeding studies, with pedigree analysis, or with statistical analyses of population data. A molecular marker must be appropriately polymorphic to test a particular hypothesis and amenable to the analysis of large numbers of individuals to be able to provide enough statistical power to detect population structure (Ryman et al. 2006).

Advances in sequencing technology facilitate the use of large numbers of molecular markers used in phylogeographic studies. New approaches for developing molecular markers with restriction site-associated DNA (RAD) and next-generation sequencing (NGS) methods can now identify thousands to hundreds of thousands of DNA polymorphisms in populations of nonmodel species (Metzker 2010; McCormack et al. 2013; Toonen et al. 2013). Genotyping by sequencing small DNA fragments (50–500 bp), ‘amplicon sequencing’, promises to yield large numbers of genotypes at a much lower cost than current methods of SNP genotyping (Campbell et al. 2015). However, the massive amounts of genotypic data these methods produce require attention to genotype calling, quality control, and statistical analysis (Davey et al. 2011; Nielsen et al. 2011; Patel and Jain 2012). These technologies survey polymorphisms throughout the genome and open the door to investigate proximal and ultimate mechanisms operating on different timescales and to understand the effects of natural selection.

### ***2.3.2 Levels of Polymorphisms Influence Hypothesis Testing***

Genetic diversity ultimately arises through mutation, but the level of diversity in a population is influenced by the confounding effects of demographic history and natural selection. The mutation rate of a molecular marker and its level of polymorphism greatly influence the kinds of hypotheses that can be tested. The silent substitution rate of mtDNA is less than one-third of that of cpDNA in vascular land plants (Wolfe et al. 1987). The substitution rate in coding regions of nDNA is about twice that of cpDNA. However, nonsynonymous rates for mtDNA and cpDNA are similar. Sequences of DNA with higher levels of polymorphism are generally assumed to have larger mutation rates than less polymorphic sequences, and this assumption has been used, for example, to estimate mutation rates for one gene from another. Markers are most useful for phylogeographic analysis when their genealogies show a pattern of shared and unique lineages among populations that captures historical and contemporary events.

DNA sequences with low mutation rates might resolve relationships among species or higher taxa, but may not be useful for detecting fine-scale population structure, or for identifying individuals, to track the genetic effects of mating systems. On the other hand, molecular markers with high mutation rates may not resolve deep structure in a species or relationships among species, because of the loss of information through multiple substitutions (rapidly evolving sequences) or

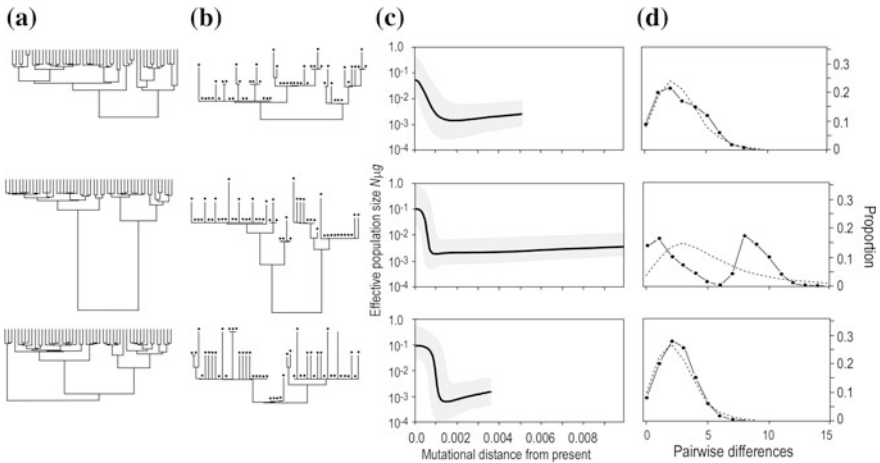
allelic convergence (microsatellites). Nucleotide saturation in a gene leads to underestimates of divergence between lineages in a gene genealogy, and the use of sequences with low levels of polymorphism may not resolve important features of recent phylogeographic structure. For example, a 629 bp portion of the mtDNA COI gene with 14 haplotypes provided greater resolution of population structure and colonization history of the kelp *Durvillaea antarctica* along the coast of Chile, than did a 886 bp portion of the cDNA *rbcL* gene that yielded only two haplotypes (Fraser et al. 2010).

Allelic convergence from the stepwise nature of mutation in microsatellites is especially problematic for comparisons between well-differentiated species, because the same microsatellite allelic state (size) can arise from alleles with different ancestries (Hedrick 1999; Rubinsztein et al. 1999; Ellegren 2004). Hence, the use of microsatellites for phylogenetic inference can be open to serious error. Microsatellite allelic convergence can even be a problem in delineating populations. For example, a survey of variability among populations of the red alga *Chondrus crispus* with biallelic single nucleotide polymorphisms (SNPs) and highly polymorphic microsatellites showed different patterns of diversity (Provan et al. 2013), which appeared to be due in part to the convergence of microsatellite alleles. Microsatellites can be plagued by other problems, including allele- and lineage-specific mutation rates and genotyping artifacts, such as null alleles and allelic dropout (Wattier et al. 1998).

When the goal of a study is to identify individuals, or parent–offspring pairs, or to illuminate the effects of mating systems, or life-history phase on genetic variability, markers with high levels of polymorphism may be needed to provide a unique genotype for each individual. For example, a survey on the Canary Islands of six populations of the green alga *Cladophoropsis membranacea* with highly polymorphic microsatellite markers indicated that intertwined mats of unattached filaments included individuals of both the haploid and diploid phases and that haploid plants significantly outnumbered diploid plants (van der Strate et al. 2002).

### 2.3.3 Use of Multiple Markers

Phylogeographic analyses of seaweeds have been based largely on sequence variability in chloroplast and mitochondrial DNA, chiefly because of their uniparental inheritance and apparent lack of recombination. Plastid DNA is generally circular and is about 70 kb to over 400 kb in size (Coleman and Goff 2004). Mitochondrial DNA in algae is generally smaller with genomic sizes of about 25–50 kb (e.g., Burger et al. 1999; Turmel et al. 1999). However, the use of multiple markers provides stronger insights into evolutionary processes than the use of a single-gene marker, because multiple markers mitigate for the large evolutionary variance among gene lineages (Edwards and Beerli 2000; Sunnucks 2000; Zhang and Hewitt 2003; Heled and Drummond 2008; Brito and Edwards 2009). Different modes of inheritance in organellar and nuclear genes provide complementary



**Fig. 2.1** Replicate gene genealogies in simulations of the same population model of a sudden population expansion of three orders of magnitude from  $N = 10^3$  to  $N = 10^6$  at 0.075 mutation units ( $\mu g$ ) in the past. Sample size  $n = 50$ . **a** Simulated gene genealogies. **b** Genealogies as recovered in neighbor-joining trees of mutations along a 500 bp sequence. **c** Bayesian skyline plots of the simulated sequences. **d** Mismatch distributions (*solid line*) with the expected distributions under a model of population expansion. (reprinted from Grant 2015)

insights into the same population events. Organellar DNA is generally inherited from one parent, generally from the maternal parent in higher plants (e.g., Dumolin et al. 1995), as it is in most animals (Giles et al. 1980), and comparisons with biparentally inherited nuclear DNA allow estimates of sex-biased dispersal, reproductive success in males and females and effective sizes of the total population.

An observed organellar DNA genealogy represents only one of an infinite number of possible evolutionary outcomes for a given population history (Rosenberg and Nordborg 2002). Gene genealogies simulated with the same population history illustrate this point (Grant 2015). Figure 2.1 shows three replicate genealogies in a population experiencing a sudden expansion (Fig. 2.1a). First, a molecular tree does not completely capture the topology of a genealogy (Fig. 2.1b). Second, the Bayesian skyline plots (Fig. 2.1c) and mismatch distributions (Fig. 2.1d) differ considerably among simulations, even though the genealogies were generated with the same population history. The results for each genealogy might provide the basis for constructing conflicting phylogeographic scenarios.

While the use of multiple nuclear loci can mitigate the randomness of individual genealogies, nuclear genes are also beset with the problem of recombination, which can mix gene genealogies during meiosis and violate a fundamental assumption of coalescence analysis. This problem can be overcome to some extent by the use of methods that estimate recombination events in a set of nuclear DNA sequences (Librado and Rozas 2009) and that establish the haplotypic or gametic phases of genotypes (Stephens et al. 2001; Stephens and Donnelly 2003; Scheet and Stephens

2006; Browning and Browning 2011; Garrick et al. 2010). The accuracy of phase estimation is improved by gene genealogies from family data, or by previously phased samples. Incorporating nuclear markers into phylogeographic analyses is especially important in the light of the development of next-generation sequencing that can produce genotypic data for an enormous number of polymorphic nucleotide sites.

### 2.3.4 Sampling Schemes and Statistical Power

The ability to resolve phylogeographic patterns also depends on sampling a sufficient number of populations. The number of individuals in a sample relative to the *effect size* influences the ability to detect phylogeographic structure. An effect size is the strength of the relationship between two variables (e.g., a correlation), or the size of the difference between means (Nakawaga and Cuthill 2007). When effect sizes are large, sample sizes needed to detect an effect can be relatively small compared to situations in which such signals are weak. Large samples are required to detect small allele- or haplotype frequency differences between populations (Ryman et al. 2006; Bird et al. 2011). Sample sizes needed to detect a given level of divergence between populations, as measured with  $F_{ST}$ , can be computed with simulations (Ryman and Palm 2006). Sample sizes also influence the ability of other analyses to detect demographic events. For example, simulations show that small samples from populations undergoing large expansions can fail to detect the expansion in a Bayesian skyline plot analysis (Grant 2015).

Third, an important consideration is the numbers and locations of samples. The numbers and locations of samples, of course, depend on the research problem, and often on the level of funding. However, sample design may be more important for testing a hypothesis than the generation of high-quality data (Meirmans 2015). An investigation of propagule dispersal distances might require collections over small and large distances, while a study of variation on a large geographical scale may require only widely spaced samples along a coast. For example, high and low intertidal populations of the red alga *Chondrus crispus* showed significant differences in microsatellite allele frequencies, and high intertidal populations showed small-scale genetic differentiation, which would not have been detected with coarse sampling (Krueger-Hadfield et al. 2013).

In addition to sampling challenges stemming from the biology of seaweeds and finite research resources, the locations and pooling of samples can influence the outcomes of some analyses (Grant 2015). When gene flow between populations is limited, the demographic analysis of a single population may not reflect the dynamics of a species, or regional group of populations, because of the population-specific histories (Städler et al. 2009). Hence, inadequate or unbalanced sampling among regions may produce misleading inferences about population structure or history. For example, a phylogeographic study of the brown intertidal seaweed *Ishige okamurae* used locations with high levels of contemporary diversity



to infer locations of glacial refugia (Lee et al. 2012). However, the conclusions of this study were misleading, because areas of high levels of diversity were also areas that had been disproportionately sampled (Hu and Duan 2013).

On the other hand, the pooling of samples from genetically differentiated populations may violate the assumptions of panmixia in many models. For example, when coalescence theory is used to estimate historical demography (Drummond et al. 2005), or migration and effective population size (Beerli and Felsenstein 2001), the pooling of heterogeneous samples pushes genotypic coalescence time frames deeper into the past, producing misleading results. Another sampling strategy is to pool a few individuals from numerous localities for statistical analyses. This approach is sometimes used when individuals are rare, or when conservation concerns or funding limit the number of individuals that can be analyzed. Simulations show that in some circumstances this ‘scattered’ sampling can provide a better picture of specieswide demography than the analyses of a few single-population samples (Städler et al. 2009; Chikhi et al. 2010). However, the dynamics of local populations cannot be resolved with this scattered sampling scheme.

### 2.3.5 *Molecular Clock Calibration*

DNA sequences and the molecular clock hypothesis can be used to date divergences between taxa and demographic histories. The calibration of a molecular clock requires the estimation of the mutation rate for a particular gene. Estimates of mutation rates are most commonly based on nodes in a phylogenetic tree that can be associated with a geological or climatic event. Deep divergences can sometimes be tied to geological plate separations, or to the formation of a geological barrier to dispersal. In marine research, the most recent rise of the Isthmus of Panama about 3.1–3.5 million years from uplift and volcanic accretion initiated divergences between populations in the western tropical Atlantic and eastern Pacific (Knowlton and Weigt 1998; Marko 2002). Comparisons between isolated sister populations, or sister species, yielded mtDNA divergence rate estimates of about 2 % divergence per one million years, and this ‘standard’ estimate has been used in a large number of studies. Substitution rates have also been estimated with various other geological events (e.g., Ketmaier et al. 2003; Marino et al. 2011), fossils (Gaunt and Miles 2002), climate and sea level history (Crandall et al. 2012; Grant et al. 2012), samples of ancient DNA (aDNA) (Prost et al. 2010), and pedigrees (Santos et al. 2005). Commonly used methods to estimate a mutation rate for a gene include the use of mutation rates in a related species (Bilgin et al. 2009), or in another gene (Qu et al. 2011). For the latter method, mutation rate estimates are adjusted by the relative levels of polymorphism for the two genes, by assuming that higher levels of polymorphism indicate a larger mutation rate. Many of these methods of calibration are not available for seaweeds, and researchers resort to using a standard rate, which appears to be slower in plants than in animals (Wolfe et al. 1987).

Mutation rates derived from ancient divergences generally push the timings of population events too far into the past (Ho et al. 2008, 2011), creating a mismatch between inferred population events and environmental causation. While substitution rates estimated from a phylogenetic tree are theoretically expected to equal mutation rates, contemporary mutation rates appear to be much larger. Mutation rates appear to be time-dependent and decline exponentially over a period of about one million years (Ho et al. 2005). It appears that mutation rates estimated from fossils, or from divergences precipitated by datable geological and oceanographic events, produce estimates of effectively population size and demographical timings that greatly overshoot the timings of the actual events (Ho et al. 2011; Grant 2015). Phylogenetically derived mutation rates often place population expansions before or during the Last Glacial Maximum, implying that glaciations did not impact population demography. However, resistance to major environmental changes during a period of global cooling is unlikely, given the effects that much smaller contemporary climate changes have on the abundances and distributions of seaweed populations (see Grant 2015 for detailed discussion).

### ***2.3.6 Reproductive Skew and Genealogical Models***

Many forms of data analysis are based on simulated genealogies using backward-looking coalescence models (Kingman 1982; Hudson 1991). One assumption, not only in these models, but also in forward Fisher–Wright models, is that nodes in a genealogy represent bifurcations. However, most marine species and seaweeds with high fecundities and large early life mortalities (type III life histories) show large differences in reproductive success among families (Hedgecock and Pudovkin 2011). This large variance in successful reproduction (reproductive skew) leads to multifurcations at the nodes in a genealogy, which can influence the phylogeographic analysis of genetic data (Eldon and Wakeley 2006). For example, a star-shaped genealogy is generally interpreted as evidence for a recent population expansion (or a selective sweep, see below) and a molecular clock calibration is used to date the expansion. Mismatch distributions or Bayesian skyline plots are used to make these kinds of demographic explanations and are reported in many phylogeographic studies of seaweeds. Unfortunately, when a genealogy contains numerous multifurcations at a coalescence node, these methods of data analysis tend to overestimate the timings of supposed population expansions and inflate estimates of effective population size. In the extreme, singleton haplotypes in a star-shaped genealogy may have arisen in the previous generation from a single highly successful family. Hence, temporal estimates of demographic events are intermediate between this extreme and the commonly used bifurcation models. The theoretical basis for simulation models that take these factors into account is in early stages of development (Eldon et al. 2015). Better recognition of the effects of reproductive skew on the genetic population structure of marine species will provide important insights into seaweed phylogeography.

## 2.4 Biological Variables Influencing Phylogeography

Phylogeographic patterns ultimately result from long-term interactions between the biology of an organism and environmental variability. Several features of seaweed biology influence patterns of genetic variability among populations, including the modes of inheritance of particular genes, life-history cycles, extents of sexual or asexual reproduction, self-fertilization, and dispersal ability.

### 2.4.1 Inheritance of Molecular Marker

The mode of inheritance of a molecular marker greatly influences how phylogeographic patterns can be interpreted. Nuclear genes are passed on to offspring by both parents in diploid organisms, whereas organellar genes are generally passed on to offspring by only one parent, generally the female. However, exceptions have arisen independently in several groups of seaweeds (Bock 2007; Nagasato et al. 2000). In isogamous species (male and female gametes are morphologically similar), organelles may be biparentally inherited but postzygotic mechanisms lead to the occurrence of only one parental organelle in the tissues of the plant. For example, in isogamous brown and green algae, chloroplasts can be biparentally inherited, but only maternal mitochondria remain after embryonic development from the zygote (Miyamura 2010; Nagasato et al. 2010). In the brown alga *Ectocarpus*, maternal inheritance of organelles is correlated with differences in the mobilities of the gametes (Peters et al. 2004). In anisogamous (different morphologies of male and female gametes) and oogamous (large female nonmotile gamete relative to motile male gamete), cpDNA and mtDNA are generally inherited through the female gamete (maternal inheritance) for most groups of seaweeds (Table 2.1) (Motomura et al. 2010).

Several prezygotic and postzygotic mechanisms may be responsible for uniparental inheritance (Table 2.2). These mechanisms can be deterministic, when a cellular mechanism targets one parental organelle or the other, or they can be stochastic, when parental organelles are randomly sorted into cell lineages. In some species, organelles in male gametes may degrade during gametogenesis or after fertilization. This commonly occurs in isogamous green algae (Miyamura 2010). In other groups, organelles of one parent in zygotes may degrade, or the DNA of one parent may be selectively degraded (Miyamura 2010). In the oogamous brown algae *Undaria pinnatifida*, the mtDNA inherited from the male is digested toward the end of the one-cell zygotic stage (Kimura et al. 2010). The degradation of DNA in some gametes can be a source of sustenance to developing zygotes (Sears and Vanwinkle-Swift 1994). Generally, mitochondria of the sex with the higher energy requirements are destroyed in the zygote (Han et al. 2014). Another mechanism leading to effective uniparental inheritance includes the partitioning of one parental organelle or the other into separate cells at early stages of development, or

**Table 2.1** Examples of organellar inheritance in algae

Group/species	Mode <sup>a</sup>	Mechanism <sup>b</sup>	References
<b>Chlorophyta</b>			
<i>Bryopsis maxima</i>	cp/mt: M	1d	Kuroiwa and Hori (1986)
<i>Bryopsis plumosa</i>	cp/mt: M	1d	Ogawa (1988)
<i>Caulerpa</i> , 4 species	cp/mt: M	3b	Miyamura and Nagumo (2007)
<i>Chlamydomonas reinhardtii</i>	cp: variable	3b	Sears and Vanwinkle-Swift (1994), Lee and Lemieux (1986)
<i>Spirogyra</i> sp.	cp: M	3a	Smith (1950)
<i>Ulva mutabilis</i> (isogamous)	cp/mt: M	3b	Fjeld and Løvlie (1976), Bråten (Bråten 1971, 1973)
<b>Heterokontophyta</b>			
<i>Alaria esculenta-praelonga</i> hybrids	cp/mt: M		Kraan and Guiry (2000)
<i>Ectocarpus siliculosus</i> (isogamous)	cp/mt: M		Peters et al. (2004)
<i>Fucus vesiculosus</i>	cp/mt: M		Brawley et al. (1976)
<i>Fucus serratus</i> , <i>Fucus evenescens</i>	cp/mt: M		Coyer et al. (2002)
<i>Fucus serratus</i>	mt: M, H	2c	Coyer et al. (2004)
<i>Fucus serratus-evenescens</i> hybrids	mt: H	2c	Hoarau et al. (2009)
<i>Saccarhina (Laminaria) angustata</i>	cp/mt: M	1b	Motomura (1990)
<i>Scytosiphon lomentaria</i>	cp: B	4b	Nagasato et al. (2010), Kato et al. (2006)
	mt: M	3a or 3b	Han et al. (2014)
<i>Undaria pinnatifida</i>	mt: M	3a	Kimura et al. (2010)
<b>Rhodophyta</b>			
<i>Caloglossa leprieurii</i>	cp: M		Zuccarello et al. (1999a)
<i>Bostrychia radicans</i> , <i>B. moritziana</i>	cp: M	1b	Zuccarello et al. (1999a)
<i>Bostrychia moritziana</i>	cp/mt: M		Zuccarello et al. (1999a, b)
<i>Porphyra yezoensis</i>	cp & mt: M (86 %), B (11 %), P (2 %)	4b	Choi et al. (2008)

<sup>a</sup>cp chloroplast; mt mitochondria; M maternal; P paternal; B biparental; H heteroplasmy<sup>b</sup>Explanations of mechanisms listed in Table 2.1

**Table 2.2** Mechanisms of uniparental inheritance of chloroplastid and mitochondrial DNA (modified from Birky 1995)

Mechanism
<i>1. Prezygotic</i>
(a) Unequal cell division and differential growth: large female gametes, small male gametes
(b) Exclusion of organelles from gametes during meiosis
(c) Degradation of organelles in gamete
(d) Degradation of organellar DNA in gamete
<i>2. Fertilization</i>
(a) Exclusion of organelles of one parent from zygote
(b) No organelles exchanged
(c) Paternal leakage (heteroplasmy)
<i>3. Zygotic: deterministic</i>
(a) Selective silencing or degradation of organelle
(b) Selective silencing or degradation of organellar DNA
(c) Partitioning of parental organelles into separate cells
(d) Exclusion of organelles from embryonic cells
<i>4. Zygotic: random sorting among cell lineages</i>
(a) Exclusion of organelles from embryonic tissue
(b) Random replication and sorting

organelles may be selectively excluded from embryonic daughter cells leading to cell lineages. Random sorting in early embryonic cell division leads to the incorporation of either maternal or paternal cpDNA in the large sporophytes of *Scytosiphon lomentaria* (Kato et al. 2006). In the same species, mtDNA is maternally inherited, because paternal mitochondria are digested in male gametes or in fertilized eggs (Han et al. 2014). The mode of organellar transmission is a legacy of evolutionary processes, but proximate factors can alter how organelles are inherited. For example, individuals of the brown seaweed *Fucus serratus* were heteroplasmic for mtDNA in northeastern Atlantic areas previously covered with glaciers (Coyer et al. 2004).

The identification of the mode of inheritance in an alga is important in phylogeographic analyses using coalescence models. Since modes of inheritance can vary among species, they need to be experimentally verified with the distributions of molecular markers in an experimental family (Zuccarello et al. 1999a). Most analyses of chloroplast or mitochondrial sequences proceed by considering the genetic population structure or demography of only one sex, generally females, as the preponderance of cytoplasmic organelles are maternally inherited. When the abundances of the sexes are similar, inferences can be made about the entire population. Caution is needed, however, when organelles are biparentally inherited. For polymorphic gene markers, biparental inheritance appears as heteroplasmy, and it may be difficult to distinguish between markers passed on by one parent or the other, and hence to make population inferences with genealogical analyses.

### 2.4.2 *Effect of Life-History Phases on Phylogeography*

Seaweeds generally have multiple life-history stages that alternate between diploid and haploid forms. One exception includes furoid algae, in which the diploid stage produces gametes and zygotes that develop directly into the diploid form, without cycling through a free-living gametophyte phase. In red algae, the relative abundances of isomorphic gametophytic and sporophytic plants vary among groups, indicating an evolutionary legacy. The gametophytic phase is dominant among genera in the Gigartinales, but tetrasporophytes are dominant in the Gracilariales, Ceramiales, and Gelidiales (Thornber and Gaines 2004; Fierst et al. 2005; Dyck and DeWreede 2006b). In some brown and red algae, the sporophytic stage is large, and the gametophyte stage is small, just visible by eye. In red algae, the sporophytic and gametophytic stages can be isomorphic (e.g., *Mazzaella*) and are sometimes difficult to distinguish in the field (Hannach and Sanelices 1985; Hannach and Waaland 1986; Shaughnessy and DeWreede 1991). In yet other red algae, life histories progress through three stages consisting of a macroscopic diploid tetrasporophyte, haploid male and female macroscopic gametophytes, and a small diploid cystocarpic stage embedded in the female gametophyte (e.g., *Mastocarpus*). These minute cystocarps produce a multitude of mitotic diploid spores that greatly amplify a particular genotype and that develop into genetically identical free-living tetrasporophytic plants. Tetrasporophytes then produce meiotic tetraspores that develop into male and female gametophytes. Most brown seaweeds consist of large sporophytes alternating with microscopic gametophytes.

Inadvertent sampling of different life-history phases may introduce inferential errors, because chromosomal ploidy differs between alternate life-history phases. Mixed-phase sampling of isomorphic plants may introduce small-scale heterogeneity, which may be difficult to interpret in terms of dispersal and population structure. Although mixed-phase sampling is common in most phylogeographical studies of seaweeds, it may not substantially detract from phylogeographic inferences when organellar DNA markers are used. However, when nuclear markers are used, samples of unknown life-history type may produce ambiguous genotypes, because it is difficult to distinguish between homozygous and hemizygous genotypes. In large-scale studies of phylogeographic structure over distances of tens and hundreds of kilometers, mixed-phase sampling may not introduce substantial errors when population heterogeneity is much greater over large geographical distances than within sites (e.g., Wang et al. 2008).

The sampling of one life-history phase at one site and another phase at other sites may confound interpretations of allelic or haplotypic frequency distributions (Engel et al. 2004; Schiel and Foster 2006). The proximate factors regulating the relative abundance of one phase over the other are poorly understood. One possibility is that the propagules or mature plants in the different phases have different survival rates (e.g., Hansen and Doyle 1976; Kain 1982), because of ecological or physiological differences between phases (e.g., *Chondrus crispus*, Mathieson and Burns 1975; Carrington et al. 2001). In species with heteromorphic life-history phases,

microscopic gametophytes and large sporophytes inhabit different microenvironments and differences in abundance may be due to selection from ecological variables or to sweepstakes recruitment. Alternatively, differences in gametophyte and sporophyte abundances may be due to bottlenecks in the production of one phase (Santelices 1990). The results of models incorporating several reproductive variables show that fertilization rate and spore output, separately or together, can favor one life-history phase or another (Fierst et al. 2005). When fertilization rates are density dependent, the phase arriving first may then become dominant (Fierst et al. 2005). Phase dominance can shift among seasons, among years, and among sites (Dyck and DeWreede 2006a; Bellgrove and Aoki 2008), so that samples can potentially include individuals of different ploidies and ecologies.

### 2.4.3 Asexual and Clonal Reproduction

The predominance of sexual or vegetative reproduction in a population can potentially shape phylogeographic patterns by influencing levels of genetic diversity and modes of dispersal between populations. In populations that depend on the recruitment of sexually produced propagules, gamete release and fertilization success are important determinants of abundance. In brown seaweeds, gamete release is influenced by interactions of daylight, concentrations of inorganic carbon, hydrodynamic conditions, and pheromones (Pearson and Brawley 1996; Pearson et al. 1998; Gordon and Brawley 2004; Serrão et al. 1996a, b). In species of the brown seaweed *Fucus*, light and available carbon for photosynthesis limit gamete release to periods of daylight hours during calm weather and minimal tidal currents (Berndt et al. 2002; Pearson and Serrão 2006). For species in the genus *Alaria*, water movement inhibits sperm release by diluting a sperm-releasing pheromone secreted by ripe eggs (Gordon and Brawley 2004). Fertilization success may also be influenced by male–male gamete competition or by female choice (Engel et al. 1999).

Asexual and clonal propagation can occur in different ways and to different extents among species. Reproduction through asexual spores leaves imprints that can be detected with molecular markers. For example, the low frequency of male gametophytes in the red alga *Chondrus crispus* was key to concluding that asexual reproduction was the dominant mode of reproduction in this alga (Prince and Kingsbury 1973; Frederica et al. 1992). In the red alga *Pterocladia capillacea*, asexual propagation occurred only in the northern British Isles, whereas sexual tetrasporic plants were found along the coast of France, and cystocarpic plants were found in northern Spain (Dixon 1965).

Clonal plants can arise by vegetative regeneration from perennial holdfasts, or from fragments of a thallus. In many species of red algae, population abundance is largely maintained by clonal propagation, even though spore release and germination occur. The frequency of sexuality in several seaweeds drops under poor ecological conditions and is especially common in populations at the edge of a

species' geographic range (Eckert 2002). A simulation study showed that sexually reproducing individuals tended to cluster in environmentally advantageous areas at lower latitudes, and asexual individuals were more frequent at high latitudes in ecologically marginal and resource-poor areas (Peck et al. 1998). For example, clonal reproduction in the red alga *Ceramium* in the Skagerrak–Baltic was highest in low-salinity areas in the inner Baltic, but absent in high salinity areas toward the open Atlantic (Gabrielsen et al. 2002). A similar increase in clonal reproduction appeared in populations of *Fucus* in the Baltic, where gametes were less viable in low salinities. In these populations, a skewed sex ratio (predominance of females), a short fertilization potential of eggs (about two minutes), and an environmentally driven short reproductive period led to reproductive failures in most years (Serrão et al. 1999). Hence, clonal reproduction was most important in these geographically and ecologically marginal populations (Box 2).

### Box 2. The Effect of Asexual Reproduction of Population Structure

Reproduction in brown algae generally occurs by sexually produced zygotes. However, in low-salinity areas in the Baltic Sea, the persistence of *Fucus vesiculosus* populations is facilitated by clonal reproduction. At its northern limit, fertilization success is generally low and fertilized eggs are susceptible to polyspermy, which is lethal (Serrão et al. 1999). At 5 psu, a dwarf form appears among the common larger form. This dwarf form largely reproduces clonally, as indicated by finding 70–80 % of the plants with identical microsatellite genotypes. A larger survey of *F. vesiculosus* (Morocco to Iceland) showed clonality only in Baltic Sea populations. A related species, *F. serratus*, does not show evidence of clonality over its distributional range, even in populations in marginal areas (Coyer et al. 2003).

*Fucus* is 'diplontic' with newly attached fronds arising from only sexually produced zygotes (Serrão et al. 1999). Clonal individuals can arise through vegetative fragmentation or budding. However, fragmentation in *Fucus* does not generally lead to attached fronds, except for fragments capable of producing adventitious branches. These fragments generate rhizoids from the wounded basal section that facilitate attachment. In addition to wounding, the growth of rhizoidal filaments appears to be stimulated by low salinities (Tatarenkov et al. 2005). Adventitious fragments with the capability of growing rhizoidal filaments have the potential for acting as clonal propagules.

Clonality tends to arise in environments in which sexual reproduction is impaired or impossible. Sexual reproduction is limited in brackish waters by forces that affect longevity and gamete motility (Serrão et al. 1996a, b). Clonality appears to reflect an in situ adaptive response to environmental conditions rather than dispersals in a source–sink system in which selection favors only some immigrant genotypes.



### 2.4.4 Self-Fertilization

Over 50 % of angiosperms show self-fertilization, at least occasionally (Barrett et al. 1996), and mixed mating systems have evolved in many groups of plants, despite the potentially negative effects of inbreeding (Goowille et al. 2005). The extent of self-fertilization in seaweeds is poorly known. Selfing can occur when an egg produced by a gametophyte is fertilized by spermatia from a male gametophyte originating from the same sporophytic plant. In the giant kelp *Macrocystis*, models of dispersal and field results showed that about half of the meiotic spores from large sporophytes disperse less than 100 m, and this limited dispersal led to aggregations of gametophytic plants from the same sporophyte. ‘Selfing’ in this case occurred when gametes from sibling gametophytes fused (Raimondi et al. 2004). Inbreeding from self-fertilization may explain periodic local extinctions of *Macrocystis* (Raimondi et al. 2004). These cycles of extinction and colonization produce metapopulation dynamics that affect genetic diversity and genetic population structure along a shoreline (Reed et al. 2000). The incidence of selfing is affected not only by recruitment dynamics along a shore but also by microhabitat differences at a single locality. For example, high intertidal zone plants of *Chondrus* showed greater gametophytic selfing than did lower-shore plants (Krueger-Hadfield et al. 2013). In *Fucus spiralis*, selfing occurred because gametes were released during periods of low water movement, and limited movement promoted fertilizations between gametes from the same individual (Coleman and Brawley 2005; Perrin et al. 2007).

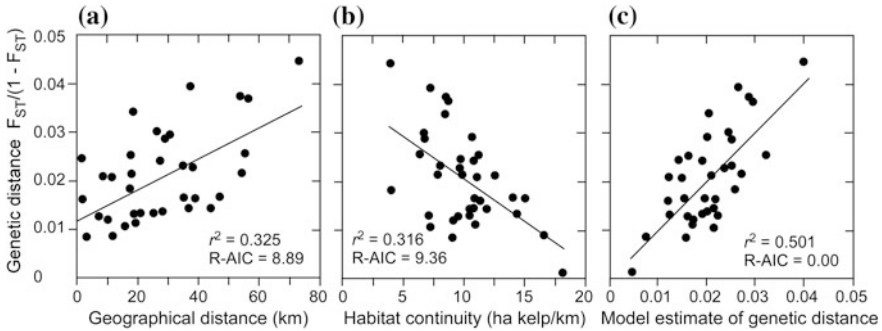
Self-fertilization can be advantageous or detrimental, depending on the ecological circumstances of a population. On the one hand, selfing can lead to inbreeding and the loss of local genetic diversity or the homozygotic exposure of deleterious alleles, which can retard growth, limit fecundity, and lower survival (Charlesworth and Charlesworth 1987). The example of *Macrocystis* appears to demonstrate the negative effects of selfing (Raimondi et al. 2004). While selfing can lead to deleterious effects, it may also be beneficial under some circumstances by boosting reproductive output when plants are rare or when gamete density is low and fertilization is not assured. Under some circumstances, selfing may be the last resort for producing recruits at low population densities in marginal habitats. Many models used by phylogeographers assume that samples are drawn from a randomly mating population. However, the complexity of mating systems in seaweeds may invalidate this assumption. Samples collected along a limited stretch of shore may not be representative of a population, because of the clumped recruitment from limited spore dispersal, or from selfing. Conversely, the sampling of individuals from different patches, genetic mosaics along shore, or between upper and lower tidal levels may produce misleading inferences about local mating dynamics.

## 2.4.5 Dispersal

Dispersal is the most important ecological variable shaping phylogeographic structure. Dispersals on ecological time frames can be realized by the movements of gametes, spores, fertile fronds, or zygotic propagules and are influenced by complex physical and biological variables, including spore swimming and sinking rates, height of spore release above the sea floor, and length of spore viability (Reed et al. 2004). Gamete and spore longevities define the scope for their movement in currents and depend to some extent on the presence of chloroplasts to provide energy (e.g., Amsler and Neuschul 1990; Reed et al. 1992). Gametes and spores of many seaweeds are viable for only a few hours, or a few days at most, and this generally leads to short-distance dispersals of only a few meters for many seaweeds (Destombe et al. 1992; Williams and Di Fiori 1996; reviewed in Santelices 1990; Forrest et al. 2000; Gaylord et al. 2002; Kusumo et al. 2006; Tellier et al. 2009; among several other studies). In the brown seaweed, *Sargassum muticum*, most spores settled within 2–3 m of the parent, but some germinated as far as 30 m away. Zygotic propagules, when they occur, may remain viable longer than gametes and spores but also do not disperse far (Deysher and Norton 1981; Kendrick and Walker 1995).

For many species, limited dispersals of gametes and zygotic propagules can lead to small genetic neighborhood sizes and to genetic mosaics along the shore (Williams and Di Fiori 1996; Coyer et al. 1997; Coleman and Kelahr 2009; Krueger-Hadfield et al. 2011). In species with long-lived propagules, particle tracking models indicate that spores can move several kilometers in coastal currents (Brennan et al. 2014). For example, spores were found up to 30 km offshore of the east coast of North America (Amsler and Searles 1980; Zechman and Mathieson 1985). Spores of green and bangiophycidean red algae were found at all depths, but spores of brown and florideophycidean red algae occurred only at greater depths in the photic zone. Spores from upper levels tended to be opportunistic species.

A pattern of isolation by distance (IBD) can arise among populations when gene flow is limited by short dispersals to nearby populations. In an unfragmented forest of the kelp *Laminaria digitata*, limited gamete and spore dispersal resulted in genetic differentiation between neighborhoods separated by 10 km without evidence of environmental boundaries (Billot et al. 2003). IBD models generally only include geographic distances between samples, but seascape features may also influence dispersal and their inclusion can improve IBD correlations. For example, Alberto et al. (2010) examined the effect of habitat continuity on IBD in the kelp *Macrocystis pyrifera* along the Santa Barbara Channel and found that genetic distances between samples were positively correlated with geographical distance between samples, but that habitat continuity was negatively correlated to genetic distance (Fig. 2.2). Geographic distance and habitat continuity did not covary, but operated independently to influence genetic distance. Increasing geographic distances between patches produced larger genetic distances, but habitat continuity between patches led to smaller genetic distances, because gene flow was enhanced.



**Fig. 2.2** Isolation by distance among populations of *Macrocyctis pyrifera* along the coast of California. **a** The effect of geographical distance of genetic distances between populations. **b** The effect of habitat continuity on genetic distance between populations. **c** A two factor model incorporating the effects of geographical distance and habitat continuity on genetic distances. (redrawn from Alberto et al. 2010)

Since spore dispersal is limited, movement across inhospitable habitats is rare. In Chilean populations of the rocky shore bull kelp *Durvillaea antarctica* genetic divergences between populations increased when sandy beaches separated the populations (Fraser et al. 2010). Sandy beaches are inhospitable to the recruitment of these kelps and thus inhibit gene flow between populations.

While small-scale genetic population structure can be attributed to restricted gamete and spore dispersal, some seaweeds show little genetic structure over hundreds or thousands of kilometers. This genetic homogeneity likely reflects rafting of detached reproductive fronds or vegetative fronds that mature during transport in currents. Floating seaweeds and beach-casts of seaweeds are common along seashores, but the effectiveness of drifting plants or fragments to facilitate gene flow varies considerably among species. Detached fragments of the fucoid *Hormosira banksii* produced viable gametes 8 weeks after detachment (McKenzie and Bellgrove 2008). Drifting reproductive fronds of the kelp *Macrocyctis pyrifera* produced viable spores for as long as 125 days (Hernández-Carmona et al. 2006). Drifting plants of *Macrocyctis pyrifera* were found on newly constructed artificial reefs, but kelp germlings appeared to have originated from spores released by a distant stand of kelps, rather than from drifters (Reed et al. 2004). In the bull kelp *Durvillaea antarctica* in New Zealand, the distributions of mtDNA haplotypes in beach-cast samples were largely consistent with the genetic structure of populations, indicating that the current systems shaping the genetic structures of sessile populations also influenced the movement of free-floating plants along the coast (Collins et al. 2010; Bussolini and Waters 2015).

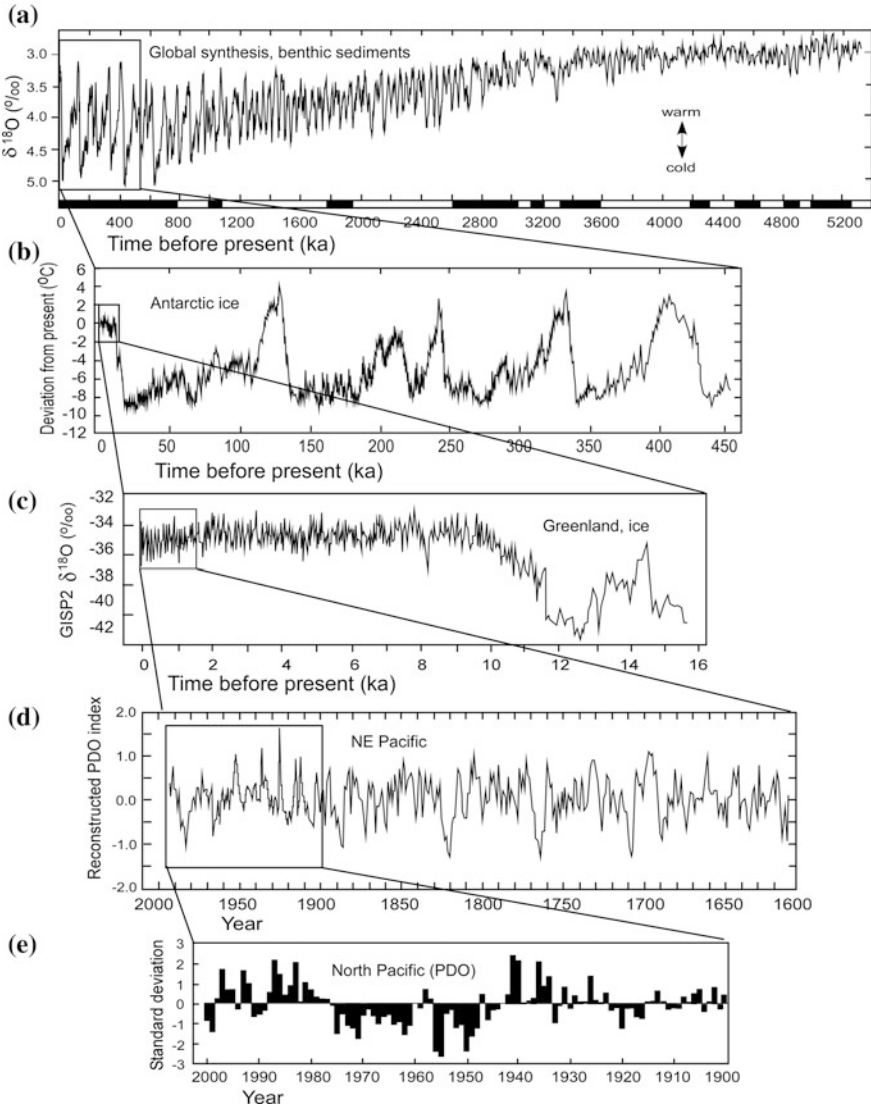
Long-distance dispersals of floating seaweeds have largely been inferred from genetic homogeneity among populations and from particle transport in ocean current models (but see Fraser et al. 2011). The time frames of postulated dispersals vary from contemporary movement in ocean currents to dispersals thousands of years ago. Contemporary movements of detached plants or fragments have been

invoked to explain genetic similarity between populations of *Fucus* spp. (Coleman and Brawley 2005; Muhlin et al. 2008) and *Sargassum* spp. (Hu et al. 2011, 2013; Chan et al. 2013, 2014). On longer timescales, rafting in ocean currents may be important for colonizations of distant shores across the open ocean (Waters 2008; Fraser et al. 2010; Hu et al. 2010; among others). Some studies have interpreted genetic homogeneity among populations to indicate postglacial population expansions (*Porphyra umbilicalis*, Teasdale and Klein 2010; *Chondrus crispus*, Hu et al. 2010; *Sargassum* spp., Hu et al. 2011; Chan et al. 2013, 2014), or interhemispheric dispersals (*Macrocystis pyrifera*, Coyer et al. 2001). Ocean currents can enhance or inhibit dispersal (White et al. 2010). Algae entrained in rapid offshore currents can potentially move large distances (Garden et al. 2014, whereas complex near-shore currents and eddies can impede long-distance dispersals (Hoffmann and Ugarte 1985; Hoffmann 1987).

## 2.5 Reconstructing Historical Population Events

A major goal of marine phylogeography is to construct hypotheses to explain the distributions of genetic diversity across a seascape. Placing historical population events into a time frame can clarify the environmental and biogeographic mechanisms influencing genetic variability and can ultimately reveal the evolutionary mechanisms shaping species' diversity. A wealth of theory can be used to interpret the results of molecular studies. However, several caveats are warranted in the applications of these theories to reconstruct demographic histories, because the assumptions in many theoretical models are not always realized in the sampling of natural populations (Karl et al. 2012; Grant 2015).

Climate variability has an overriding influence on population demography. Climate swings occur on timescales ranging from decades to hundreds of thousands of years, and the challenge is to match genetic signals of demographic change with these climate changes (Fig. 2.3). Global and regional climates have continuously changed over the Holocene and Pleistocene Epochs, and the magnitudes of these changes progressively increase further into the past. Moderate environmental shifts, including El Niños (Philander 1983), Pacific Decadal Oscillations (Mantua et al. 1997) (Fig. 2.3e), and North Atlantic Oscillations (Hurrell 1995), occur in decadal and multidecadal time frames and produce poleward shifts in species' distributions during warm phases and equatorial shifts during cool phases (e.g., Russell et al. 1971; Stebbing et al. 2002). Even small contemporary changes in sea temperature can lead to ecological reorganizations in marine ecosystems (e.g., Hare and Able 2007; Francis et al. 1998; Stenseth et al. 2003). Climate shifts over only a few years can produce changes in sea temperature, nutrients, acidification, grazing, competition with other seaweeds and pathogen exposure, all of which can drive changes in local abundance and distribution (Ling et al. 2009; Wernberg et al. 2011; Wahl et al. 2015). Benthic seaweeds may be particularly vulnerable to environmental changes, because they are sessile and are at the mercy of local environmental



**Fig. 2.3** Scales of climate variability over the Quaternary, 2.6 Ma to present. **a** Synthesis of temperature proxy  $\delta^{18}\text{O}$  records in 57 benthic sediment cores distributed globally (redrawn from Lisiecki and Raymo 2005). **b** Temperature reconstructions from proxy deuterium isotope profiles in Antarctic ice cores (redrawn from Jouzel et al. 2007). **c** Temperature proxy  $\delta^{18}\text{O}$  records in Greenland ice cores from GISP2 (redrawn from Bond et al. 1997). **d** Extended reconstruction of the Pacific Decadal Oscillation from tree-ring time series along the western coast of North America (redrawn from Gedalof and Smith 2001). **e** Pacific decadal index (redrawn from Mantua and Hare 2002)

conditions (Harley et al. 2012; Koch et al. 2013). For example, shifts in abundances of brown seaweeds around the British Isles have been interpreted to reflect recent climate warming (Yesson et al. 2015).

Greater swings in climate have occurred on centennial timescales, shifts which—in historical times (Fig. 2.3d)—led to Medieval warming (950–1250 AD) and the Little Ice Age (1350–1850 AD) (Mann et al. 2009). These and other changes have been documented in ocean (e.g., Keigwin 1996) and lake sediments (e.g., Gill et al. 2009), tree rings (e.g., Villalba 1994), and historical records of fish landings (Alheit and Hagen 1997). The extent that these periods of regional cooling and warming led to expansions, contractions, or extinctions of seaweed populations is difficult to surmise, because of the lack of fossils or written records. On longer timescales of a few thousand years over the Holocene (Fig. 2.3c), climate swings influenced the structures of plant and animal communities in all of Earth's ecosystems (e.g., Hewitt 1996; Fauvelot et al. 2003; Staubwasser et al. 2003). On even longer timescales, the globe experienced orbitally driven ice ages at 100-thousand-year (kyr) 'Milankovitch' intervals, beginning about 800,000 years ago (Figs. 2.3a, b) (Bond et al. 1993). During these periods of global cooling, glaciers covered large high-latitude areas of North and South America, Europe, and Asia, and coastal areas were reshaped by drops of as much as 120 m in sea level at glacial maxima (Miller et al. 2005; Ludt et al. 2012).

Assessing the effects of Milankovitch climate oscillations on populations has been an enduring focus of phylogeographic research. As a general hypothesis, less genetic diversity within populations and less population structure are expected in high-latitude areas that experienced major disturbances, and greater diversity and population structure are expected in low-latitude areas harboring older diversity (e.g., Fraser et al. 2009). The concept of population contractions into refugia during climate extremes is deeply embedded in the phylogeographical literature and has been used to explain the distributions of mtDNA and cpDNA lineages in several species of seaweeds (e.g., Provan et al. 2005; Hoarau et al. 2007; Provan and Bennett 2008; Lee et al. 2012). However, the basic contraction–expansion model may not be relevant for all marine species. The distributions of some species may have merely been displaced more or less intact by temperature shifts or moved offshore by the exposure of continental shelf areas during drops in sea level without a decline in population size, or without compression into a small area. Hence, in some species, postglacial genetic structure may not show gradients in diversity or population structure. Some responses to historical environmental changes that produce genetic homogeneity may be mistaken for high contemporary levels of gene flow. The expectations of the null diversity model can also be modified by irregular shoreline topologies and ocean currents that create multiple hospitable local habitats during glaciations (Maggs et al. 2008). The genetic structure of populations within a refuge can additionally influence phylogeographic patterns after a postglacial expansion and produce patterns that may be mistaken for high latitude refugia (Gómez and Lunt 2007).

## 2.6 Comparative Phylogeography

Comparisons of phylogeographic patterns among codistributed species, or species complexes, can reveal general biogeographic patterns that may not be apparent from the analysis of a single species (Arbogast and Kenagy 2001; Hickerson et al. 2010). Phylogeographic concordances among species are especially important for detecting shared responses to historical seascape changes (Avice 2000). However, concordance does not necessarily mean that lineage distributions among species were shaped by the same environmental events, unless the timescales are the same. The careful application of the molecular clock hypothesis provides a means of dating dispersals, population expansions, and vicariances. Comparative phylogeography has been used to test mechanistic hypotheses about the effects of historical and contemporary dispersal barriers to gene flow and of ice age displacements and refugia on sympatric populations of different species.

Phylogeographical comparisons of codistributed seaweeds are already possible for several areas around the globe. In the Northwest Pacific, for instance, marine waters cooled during the LGM and a drop in sea level likely led to offshore and southward shifts in seaweed habitats. Large areas of the continental shelf were exposed, draining the Yellow Sea and largely isolating the Sea of Japan for a brief period during the LGM (Oba et al. 1991; Wang 1999). The rise in sea levels after the LGM led to colonizations over newly submerged areas of the continental shelf. Species of the brown algae *Sargassum* and *Ishige* show star-like haplotype genealogies, sometimes embedded in a complex haplotype network, that indicate recent populations expansions (*S. hornei*, Uwai et al. 2009; Hu et al. 2011; *S. fusiforme*, Hu et al. 2013; *I. okamurae*, Lee et al. 2012). These species also show strong haplotype frequency differences among areas, indicating periods of isolation, but the patterns of differentiation among species are not consistent with one another. Together these results show the profound impact of the last glaciation in displacing and isolating populations. However, the diversity of phylogeographic patterns indicates species-specific responses to climate variability.

In the southwestern Pacific, large areas of the Sunda Shelf were drained, uniting several of the large islands and reducing the extents of available shoreline habitats (Voris 2000). The Shelf was submerged again about 14 600 years ago (Hanebuth et al. 2000), stimulating a massive reoccupation by marine species. Marine species invading shelf habitats show molecular signatures of a recent expansion (Lourie et al. 2005; Crandall et al. 2012), including species of the brown seaweed *Sargassum* (*S. aquifolium* Chan et al. 2014; *S. polycystum*, Chan et al. 2013). In contrast to phylogeographical patterns in the northwestern Pacific, populations across Southeast Asia are largely genetically homogeneous, perhaps because each species was isolated in a single area during global cooling before expanding across the Sunda Shelf.

Another well-studied area is the southeastern Pacific along Chile. During ice age maxima, the Patagonian glacier in the southern part of South America reached to the sea as far north as about 41° S (McCulloch et al. 2000). These shores were most



recently open to colonization only after the LGM (0.026–0.019 Ma). A shift in the composition of marine species occurs at about 30°–33° S, but it was uncertain whether the environmental factors that produced the biogeographic transition also produced a genetic discontinuity in species with distributions spanning the biogeographical break. A multilocus survey of populations of the kelp *Lessonia nigrescens* with mtDNA, cpDNA, and nuclear markers resolved three major parapatric lineages, which were concordant with the biogeographical transition. A genetically intermediate lineage was limited to the transition zone. A second study of the red alga *Mazzaella laminarioides* using mtDNA and cpDNA markers revealed three strictly parapatric lineages, whose geographic distributions were not concordant with biogeographic breaks along the coast (Montecinos et al. 2012). It was uncertain, however, whether the geographic boundaries between genetic lineages reflected natural selection or founder events and high-density blocking of immigrants (Waters et al. 2013). A third study surveyed mtDNA and cpDNA markers in populations of the kelp *Durvillaea antarctica* located below the biogeographical break at 30° S (Fraser et al. 2010). One mtDNA lineage appeared along the shores of central Chile, and a second genetic lineage was restricted to the southern shores of Patagonia. This last lineage was closely allied with a lineage in the southern ocean, including New Zealand, and appeared to have colonized Patagonia after the LGM by long-distance rafting. These various comparisons show that species respond to environmental variability in different ways, and that it is difficult to generalize from the studies of only a few species.

## 2.7 Effects of Natural Selection on Phylogeographic Structure

The construction of demographic hypotheses fundamentally assumes that DNA sequence polymorphisms are ‘neutral’ to natural selection and that the shape of a genealogy is due solely to genetic drift and gene flow. Unfortunately, genetic imprints from drift and gene flow can look the same as those from various forms of natural selection. For example, background selection prevents slightly deleterious mutations from drifting to higher frequencies, producing an allele frequency spectrum with an excess of low-frequency alleles that resembles a spectrum in a recently expanded population (Charlesworth et al. 1993). Additionally, strong directional selection at a locus can produce a ‘selective sweep’ as genes linked to a selected locus are carried along to higher frequencies (Smith and Haigh 1974). A selective sweep can lead to the loss of genetic diversity that is indistinguishable from the loss of diversity from a bottleneck in population size (Nei et al. 1975).

Departures from neutrality are generally interpreted only in terms of demographic process, because it is difficult to construct testable hypotheses for the many possible forms of selection. Several statistics can be used to test for departures from neutrality, but they cannot always distinguish the effects of population history from natural selection (Tajima 1989; Fu and Li 1993; Fu 1997; among others). Even so,

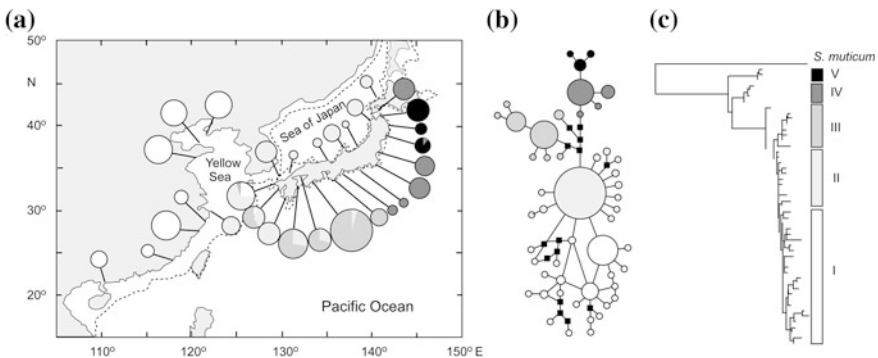


the potential effects of natural selection cannot be ignored in constructing phylogeographical hypotheses (Gagnaire et al. 2015) (Box 3). Benthic seaweeds may be more affected by climate changes than other marine species, because seaweeds are sessile, are restricted to the photic zone, and are sensitive to physical variables associated with climate change (Harley et al. 2012; Clark et al. 2013; Koch et al. 2013).

### Box 3. Confounding Effects of Demography and Natural Selection on Gene Genealogies

The geographical distributions of mtDNA (*Cox3*) haplotypes among populations of the brown seaweed *Sargassum horneri* along the coasts of China and Japan show strong regional differences among five lineages (Fig. 2.4a) (Hu et al. 2011). Haplotype and nucleotide diversities tended to be larger in southern areas and smaller in northern areas, even considering differences in sample sizes. This pattern was interpreted to reflect isolations in multiple refugia during the late Pleistocene, followed by postglacial secondary contact. Contemporary dispersals in ocean currents were further postulated to explain patterns of connectivity between populations. These explanations invoke only demographic processes. However, the pattern also supports an alternative explanation involving selection, and illustrates the potentially confounding effects of demography and selection on phylogeographic structure.

A parsimony network shows a linear arrangement of lineages corresponding more or less to the geography of the samples, indicating a close genetic relationship between lineages in adjoining regions (Fig. 2.4b). This



**Fig. 2.4** Phylogeographic analysis of mtDNA *Cox3* in *Sargassum horneri* populations in the NW Pacific. **a** Map showing frequencies of haplotypes in lineages I–IV. Dashed line indicates shoreline at the LGM about 0.019 Ma. **b** Parsimony haplotype network. Sizes of circles are approximately proportional to haplotype frequency, and lines connecting haplotypes represent one mutational step. Black rectangular blocks represent hypothetical, but unobserved haplotypes. **c** Neighbor-joining tree of haplotypes. Lineages indicated by shaded boxes. (Redrawn from Hu et al. 2011)

arrangement could be interpreted to have resulted from progressive post-glacial colonizations that led to reduced diversity in northern populations, the pioneer mode of colonization (Hewitt 2000). However, an alternative scenario is possible. The shoreline along this coast was warmed by the north-flowing Kuroshio Current during glaciation, so that populations may have not been forced into southern areas, but displaced offshore during lower sea levels. A neighbor-joining tree of the *Cox3* haplotypes, rooted by the outgroup *S. muticum* (Fig. 2.4c) shows ancestral lineages in the north and derived lineages in the south. This polarization of haplotypes does not support a postglacial expansion from the south.

An alternative scenario invokes both natural selection and demography, in which a cold-adapted, northern lineage expanded into southern waters only after beneficial mutations allowed individuals to complete a life-history cycle in warmer waters. Individuals with beneficial mutations progressively expanded into southern areas, producing a demographic signature of a population expansion with an excess of low-frequency haplotypes and star-shaped haplotype genealogies. The beneficial mutations need not be linked to the sequence that was surveyed in the study, but may be part of the mitochondrial–nuclear unit of selection (Dowling et al. 2008). If this is the case, the effects of selection and demography are confounded and cannot be teased apart by standard phylogeographic analysis. Additional studies of physiology are required.

Seaweeds may be particularly vulnerable to environmental changes because life-history phases may have different ecological requirements (e.g., Moring et al. 2014). One of the major population markers used in phylogeographical studies, mtDNA may be particularly subject to selection. Mitochondrial DNA encodes several protein subunits, which together with subunits encoded by nuclear genes, form functional respiratory proteins (Dowling et al. 2008). Numerous studies show that the distributions of mtDNA haplotypes are correlated with environmental variables, particularly temperature, in fishes (Consuegra et al. 2015; Silva et al. 2014), and humans (Mishmar et al. 2003), and with altitude in birds (Cheviron and Brumfield 2009) and lizards (Jezkova et al. 2013). The development of technologies that can be used to probe entire genomes will allow researchers to understand the effects of proximate environmental variables on evolutionary responses to short- and long-term climate changes.

## 2.8 Conclusions

The goals of this chapter have been to explore the myriad life-history and environmental variables that shape phylogeographic structure in seaweeds and to examine the methodological and conceptual challenges to understanding microevolutionary mechanisms. The mechanisms producing phylogeographic patterns can only be understood by holistically examining the variables influencing the abundances and distributions of local populations. The Huxley–Tinbergen research questions (Box 1) provide a framework to investigate proximate and ultimate causes. Phylogeographic patterns in seaweeds are largely interpreted by addressing the first three questions. First, what are the proximate mechanisms controlling vertical and geographic distributions? These include physiological responses to sea temperature and salinity variability, morphological responses to substrate variability and responses to herbivory, among many other variables. Second, how do the ontologies of plants influence their distributions? Numerous studies show that mating systems and life-history variability can influence abundances and distributions of populations. Third, what are the ‘phylogenetic’ relationships among populations? Phylogeographic research largely falls into this category with a focus on the analysis of gene genealogies. Answering the fourth question—how can we understand the evolutionary significance of variation—is a more difficult research objective. However, the continuing development of next-generation genomic and functional genetic approaches will provide avenues for understanding adaptive responses to natural selection in ever-changing marine environments.

Importantly, a phylogeographic study represents only a snapshot of dynamic processes influenced by continuous climate changes. Attributing phylogeographic patterns to specific climate events is a daunting task, made difficult by large errors in calibrating marker- and species-specific molecular clocks. In the light of the continuously changing climates on all temporal scales around the globe (Fig. 2.3) and frequent miscalibrations of molecular clocks, few reconstructions of historical demography are likely to reflect reality.

Lastly, many phylogeographic studies focus on reconstructing historical demography using models with simplifying assumptions that restrict the construction of broader explanatory hypotheses. The use of neutral models with easily testable hypotheses to explain phylogeographic patterns can lead to a biased view of the nature of microevolutionary processes. Natural selection has doubtlessly shaped, and continues to shape, the patterns of genetic diversity observed in contemporary populations. A growing body of literature demonstrates the influence that natural selection has on respiratory and metabolic genes encoded in the nuclear and organelles. New sequencing technologies capable of producing massive amounts of genomic data are beginning to provide insights into how natural selection targets particular genes (Holsinger 2010). The recognition that natural selection has to be considered in explanations of the origins of phylogeographic patterns are leading to conceptual shifts beyond the original formulation of phylogeography in the 1980s.

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