Food Webs with Population Models

Structured models should be chosen to stimulate the dynamics of several interacting species. The stage-based approach will be acceptable with few species, but quickly become intractable with increasing numbers of species. In this case, a community model based on size structure and using prey–predator size ratio is the alternative approach. There is a continuum of models from detailed size spectrum structure up to large size classes representing functional (trophic) groups in food web models. The detailed size spectrum approach is particularly useful when simulating the predation of a fish cohort on its prey, whereas large functional groups are required for large-scale ecosystem models. Numerous examples include models with size structure of herbivorous zooplankton populations and their prey, and their interactions, in a nutrient–phytoplankton–herbivore–carnivore dynamics model. Size-based plankton model with large entities consider the size range 0.2–2000 μm, picophytoplankton, bacterioplankton, nanophytoplankton, heterotrophic flagellates, phytoplankton, microzooplankton, and mesozooplankton.

See also

Biogeochemical Data Assimilation. Carbon Cycle. Fish Larvae. Fish Migration, Vertical. Fish Predation and Mortality. Gelatinous Zooplankton. Krill. Lagrangian Biological Models. Large Marine Ecosystems. Marine Mesocosms. Microbial Loops. Network Analysis of Food Webs. Nitrogen Cycle. Ocean Gyre Ecosystems. Patch Dynamics. Phosphorus Cycle. Plankton. Polar Ecosystems. Small-scale Patchiness, Models of. Small-scale Physical Processes and Plankton Biology. Upwelling Ecosystems.

Further Reading

Carlotti F, Giske J and Werner F (2000) Modelling zooplankton dynamics. In: Harris RP, Wiebe P, Lenz J, Skjoldal HR and Huntley M (eds) *Zooplankton Methodology Manual*, pp. 571–667. New York: Academic Press.

Caswell H (1989) *Matrix Population Models: Construction, Analysis and Interpretation*. Sunderland, MA: Sinauer Associates.

Coombs S, Harris R, Perry I and Alheit J (1998) *GLOBEC* special issue, vol. 7 (3/4).

DeAngelis DL and Gross LJ (1992) *Individual-based Models and Approaches in Ecology: Populations, Communities and Ecosystems*. New York: Chapman and Hall.

Hofmann EE and Lascara C (1998) Overview of interdisciplinary modeling for marine ecosystems. In: KH Brink and AR Robinson (eds) *The Sea*, vol. 10, Ch. 19, pp. 507–540. New York: Wiley.

Levin SA, Powell TM and Steele JH (1993) *Patch Dynamics*. Lecture Notes in Biomathematics 96. Berlin: Springer-Verlag.

Mangel M and Clark CW (1988) *Dynamic Modeling in Behavioral Ecology*. Princeton, NJ: Princeton University Press.

Nisbet RM and Gurney WSC (1982) *Modelling Fluctuating Populations*. Chichester: Wiley.

Renshaw E (1991) *Modelling Biological Populations in Space and Time*. Cambridge Studies in Mathematical Biology. Cambridge: Cambridge University Press.

Tuljapurkar S and Caswell H (1997) *Structured-population Models in Marine, Terrestrial, and Freshwater Systems*. Population and Community Biology Series 18. New York: Chapman and Hall.

Wood SN and Nisbet RM (1991) *Estimation of Mortality Rates in Stage-structured Populations*. Lecture Notes in Biomathematics 90. Berlin: Springer-Verlag.

Wroblewski JS (1982) Interaction of currents and vertical migration in maintaining *Calanus marshallae* in the Oregon upwelling zone – a simulation. *Deep Sea Research* 29: 665–686.

POPULATION GENETICS OF MARINE ORGANISMS

D. Hedgecock, Bodega Marine Laboratory, University of California, CA, USA

doi:10.1006/rwos.2001.0298

Introduction

This article provides a brief overview of the principles of population genetics and applications in ocean science. The specialized vocabulary of genetics is defined, and central concepts and approaches are summarized in an abbreviated historical context. Finally, specific topics that have been addressed in the marine biological literature illustrate major areas of application of population genetics in ocean science.

Definitions and Historical Approaches

Population genetics is the branch of genetics that explores the consequences of Mendelian inheritance

at the level of populations, rather than families. Population genetics seeks to explain the most elementary step of Darwinian evolution, change in population genetic composition over time. Genetic composition is described by the frequencies, in population samples, of alleles (alternative states or forms of a particular gene or genetic marker that arise by mutation or recombination), phenotypes (the perceivable properties of organisms, such as their color or the banding patterns of their macromolecules following electrophoretic separation), or genotypes (the hereditary constitutions of individuals, usually inferred from their phenotypes), at particular genes or loci (singular, locus, the place on a chromosome where a genetic element is located). Genes are functional units of inheritance, whether they code for the synthesis of proteins or RNA or serve some regulatory or structural purpose, but nonfunctional portions of the genome are often used as genetic markers. The zygotes of higher organisms are mostly diploid, inheriting one copy of each gene from their parents. A diploid genotype, comprising two alleles that are identical either phenotypically or by descent, is said to be homozygous. A genotype comprising two different alleles is heterozygous. The proportion of heterozygous genotypes in a population, the heterozygosity, is an important measure of genetic diversity. Genetically determined traits or markers are said to be polymorphic when two or more forms or alleles occur in a population at frequencies greater than expected from recurrent mutation. Conversely, a monomorphic or fixed genetic trait or marker is represented by a single phenotype within a population comprising only homozygotes for a single allele.

The primary forces that change genetic composition over time are recurrent mutation, natural or artificial selection, gene flow among subpopulations, and random changes resulting from sampling errors in finite populations. In the absence of these forces, the genetic composition of a randomly mating population (i.e., one in which all possible matings or unions of gametes are equally likely) is stable through time and is described by the Hardy–Weinberg Principle. Under this basic principle, the frequencies of genotypes at a single, polymorphic locus are given by the expansion of the binomial (with two alleles) or multinomial (with three or more alleles) function of allelic frequencies. For example, at a locus with two alleles of equal selective value, A and a, having relative frequencies p and q ($p + q = 1.0$) in a large population, the frequencies of the genotypes, AA, Aa, and aa are given by the binomial expansion, $(p + q)^2 = p^2 + 2pq + q^2$, respectively. Populations conforming to this principle are said to be in Hardy–Weinberg (H–W) equilibrium. The H–W principle, which is easily extended to multiple alleles, simplifies enormously the description of populations, reducing the number of parameters to n alleles at a locus, rather than the $n(n + 1)/2$ genotypes formed by n alleles in diploid organisms.

There are three distinct and complementary approaches in population genetics. Empirical studies seek to document patterns of genetic variation in natural populations and to explain these patterns in terms of the primary forces acting on population genetic variation and the population biology of the species in question. Experimental studies seek to test the effects of inbreeding and crossbreeding, natural and artificial selection, and random genetic drift owing to population bottlenecks or finite population size, or to estimate the frequency and fitness effects of spontaneous mutations. Finally, theoretical studies continue to develop and elaborate the mathematical backbone of population genetics set down in the seminal works of Sewall Wright, Sir Ronald Fisher, and J.B.S. Haldane published in the early 1930s.

In the marine sciences, the bulk of population genetic studies fall into the empirical category. The earliest population genetic studies, carried out by Charles Bocquet in France and Bruno Battaglia in Italy in the 1950s and 1960s, described color polymorphisms in natural populations of copepods and isopods. The introduction, in the late 1960s, of methods for electrophoretic separation of allelic protein variants (or allozymes) allowed investigation of genetic variation in organisms not amenable to laboratory culture or lacking visible polymorphisms. Among the first allozyme studies of marine organisms were those by Fred Utter and colleagues on Pacific salmon, which provided a scientific basis for management of salmon ocean fisheries. Experimental genetic studies were initiated by Bocquet, Battaglia, and others working on small and easily cultured crustaceans, but have exploded over the past two decades in conjunction with the growth of aquaculture. The International Society for Genetics in Aquaculture was formed in 1985 and a triennial meeting on this topic has been held since 1982. A first International Symposium on aquatic genomics, held at the Tokyo University of Fisheries in November 2000, marked the beginning of a new millenium, in which advanced molecular biology, genomics, and bioinformatics will be applied to marine species.

Over the past three decades, there has been growing interest on the part of biological oceanographers and fisheries scientists in the theory and practice of

population genetics, particularly as enhanced by molecular methods. Major scientific questions being addressed by population geneticists working with marine animals can be grouped under five headings: (1) identification of morphologically cryptic, sibling species; (2) amount and spatial structure of genetic diversity within species; (3) temporal genetic change, particularly in relation to recruitment; (4) retrospective analyses of historical collections; and (5) phylogenetic and phylogeographic analyses. Some of the prominent applications of population genetics in the marine environment concern the design of marine reserves, aquaculture and stock enhancement and their ecological affects, and mixed-stock analyses in fisheries.

Morphologically Cryptic, Sibling Species

A major contribution of population genetic studies to marine biology has been the identification of sibling or cryptic biological species within morpho-1logically defined taxa. When sympatric (occupying the same geographical area), cryptic species are most often recognized by obvious failures of the Hardy–Weinberg Principle at one or more markers. If the cryptic species are fixed for alternative alleles at a marker, one observes *AA* and *BB* homozygotes only and no or few *AB* heterozygotes, contrary to expectations for random mating. When cryptic species are allopatric (occupying nonoverlapping areas), inference of biological species status is less clear. Fixed differences at multiple genetic markers suggest an absence of genetic exchange, but additional evidence is needed to ascertain whether the populations are reproductively isolated. Morphologically cryptic speciation might also be suggested by large divergence in DNA sequences, but, again, ancillary evidence is required to ascertain whether this variation is concordant with reproductive isolation. The percentage nucleotide difference maintained within conspecific populations for mitochondrial DNA ranges from a few percent in many species to as much as 18% in the copepod Tigriopus californicus.

Cryptic species have been discovered in several well-studied taxa, including the blue mussel Mytilus, the worm Capitella, and the copepod Calanus. These discoveries, mostly serendipitous by-products of research directed at other questions, suggest that a systematic investigation of the frequency of sibling species in various taxa could eventually increase estimates of marine species diversity by an order of magnitude. Prudence dictates that the taxonomy of all target organisms of oceanographical study be confirmed by both traditional and molecular methods and that voucher specimens be kept. A major advantage of using DNA markers is that voucher specimens can often be preserved simply in ethanol.

Molecular diagnosis of cryptic species or of the cryptic stages of species should enable the extension of species diagnosis to early life stages. Correct species identification of larval stages should enable, in turn, the acquisition of data on species-specific patterns in dispersal and recruitment.

Amount and Spatial Structure of Genetic Diversity within Species

Early studies of protein polymorphism revealed widely varying levels of genetic diversity among marine taxa. Comparative studies of taxa differing in life history or ecological traits have provided few compelling general explanations for what maintains different levels of genetic diversity in different taxonomic groups. Certainly, the amount of diversity measured for a particular taxon depends largely on the particular type and set of genetic markers studied. However, the amount of genetic diversity in a species depends more fundamentally on the mating system and the balance among the forces of mutation, migration, selection, and random genetic drift owing to finite population size. We focus on the last factor first.

The Hardy–Weinberg Principle applies to infinitely large or very large populations. However, this important assumption of the H–W principle is often violated in real populations, which are finite in size. Therefore, to understand the maintenance and structure of genetic diversity in finite natural populations, we require an understanding of the concepts of random genetic drift and effective population size (N_e). Random genetic drift is defined as change in allelic frequency resulting from the sampling of finite numbers of gametes from generation to generation. One way to illustrate genetic drift is to consider the transition matrix that describes the probability of having i *A* alleles in generation $t + 1$, given j *A* alleles in generation t. The elements of this matrix are calculated from the binomial probability (eqn [1]).

$$\chi_{ij} = \frac{(2N)!}{(2N-i)!i!}\left(1-\frac{j}{2N}\right)^{2N-i}\left(\frac{j}{2N}\right)^{i} \qquad [1]$$

In this equation, $2N$ is the number of alleles and the frequency of *A* at generation t is $j/2N$.

With this transition matrix, one can calculate how the distribution of allelic frequencies among

Table 1 The evolution of the allele-frequency distribution and heterozygosity (H) for a collection of populations, each of size three ($2N = 6$) and initial A frequency of 0.5

Number of A *alleles*	*Generation*						
	0	*1*	*2*	*4*	*8*	…	∞
0	0.0	0.0156	0.0728	0.196	0.353	…	0.5
1	0.0	0.0938	0.1326	0.1094	0.0538	…	0.0
2	0.0	0.2344	0.1893	0.1284	0.0617	…	0.0
3	1.0	0.3125	0.2106	0.1325	0.0631	…	0.0
4	0.0	0.2344	0.1893	0.1284	0.0617	…	0.0
5	0.0	0.0938	0.1326	0.1094	0.0538		0.0
6	0.0	0.0156	0.0728	0.196	0.353		0.5
Mean frequency	0.5	0.5	0.5	0.5	0.5	…	0.5
H	0.5	0.4167	0.3472	0.2411	0.1163	…	0.0

a collection of populations will evolve. The allele-frequency distribution is a vector, giving the proportion, $y_{j,t}$, of populations with jA alleles at generation t, the sum of which is 1.0. We can calculate the change in the allele-frequency distribution from one generation to the next by multiplying the matrix, $\mathbf{X}$, of probability transition values (i.e., the x_{ij} values) by the vector, $\mathbf{Y}$, of population states (i.e. the $y_{j,t}$ values), such that $\mathbf{Y}_{t+1} = \mathbf{X}\mathbf{Y}_t$. This is a recursive relationship, which, assuming an initial allele-frequency distribution $\mathbf{Y}_0$, can be generalized as $\mathbf{Y}_t = \mathbf{X}^t\mathbf{Y}_0$. An example of how the allele-frequency distribution and heterozygosity evolves by genetic drift in a small population is given in **Table 1**. Here, populations size is three ($2N = 6$), and the initial frequency of the A allele in all populations is 0.5 (i.e., $y_{3,0} = 1.0$).

Several important features of genetic drift are illustrated by **Table 1**. (1) The proportion of polymorphic populations (those with one to five A alleles) rapidly declines, until all populations become fixed with either zero or six A alleles. (2) The frequency of A across the collection of all subpopulations remains at the mean of 0.5, so that allelic diversity is conserved across groups. (3) Finally, heterozygosity for the total population declines from the initial H–W equilibrium value, $2pq = 2(0.5)(0.5) = 0.5$, to zero, as subpopulations become fixed. The heterozygosity at generation t can be calculated as in eqn [2].

$$H_t = 2\sum_{j=0}^{2N}\left(1 - \frac{j}{2N}\right)\left(\frac{j}{2N}\right)y_{j,t} \qquad [2]$$

The recursive relationship between heterozygosity at generation t and heterozygosity at generation $t + 1$ is readily solved, yielding the important fact that heterozygosity declines from one generation to the next by the factor $1/2N$. This is what makes the population size such an important parameter in population and conservation genetics, particularly in the context of hatchery enhancement of marine fisheries.

The finite populations discussed above are mathematically ideal populations that differ from real populations in a number of important ways. In the mathematically ideal population, there are equal numbers of both sexes, adults mate at random, and variance in number of offspring per adult is binomial or Poisson. In actual populations, the sexes may not be equal in number, mating may not be at random, or the variance in offspring number may be larger than binomial or Poisson. The effective size, (N_e), is the size of a mathematically ideal population that has either the same rate of random genetic drift or the same rate of inbreeding as the actual population under study. Variance and inbreeding effective sizes are similar unless the population experiences a rapid change in size. Here, we are concerned primarily with the variance effective size, which determines the rate at which genetic variants are lost or fixed by random genetic drift. The number of adults in the ideal population (N) is, by definition, equal to the effective size, and the ratio $N_e/N = 1.0$ in the ideal case. Owing to the nonideal properties of real populations, the N_e/N ratio for most terrestrial vertebrate populations is thought to lie between 0.25 and 0.75. However, as we shall see in the next section, this ratio may be much smaller in highly fecund marine species. In actual populations, N_e is substituted for N in theoretical calculations; for example, heterozygosity is lost at a rate of $1/2N_e$ per generation.

The spatial structure of genetic variation within a species is, perhaps, the most thoroughly studied

aspect of marine population genetics. The question of how variation in mode of larval development, and therefore larval dispersal potential, affects the genetics and evolution of marine species was raised over a quarter of a century ago. To investigate this question, it is useful to review the theory of population divergence developed largely by Sewall Wright. We focus primarily on the balance between random genetic drift and migration. The role of diversifying selection in causing populations to diverge is not easily generalized; moreover, the specific consequences of any selection regime can depend on the underlying balance of drift and migration.

The genetic diversity of a species can be partitioned into components within and among population units, ranging from local, randomly mating populations (or demes) to subpopulations to the total species. Wright partitioned genetic variation within a species, using *F*-statistics, which measure the average genetic correlation between pairs of gametes derived from different levels in a population hierarchy. At the basal level of this hierarchy, the correlation between gametes drawn from different individuals within a deme is symbolized as F_{IS}. F_{IS} is zero in a randomly mating subpopulation but is positive when there are excesses of homozygotes relative to H–W expectations. Mating among related individuals can cause an excess of homozygotes, in which case F_{IS} is equivalent to the coefficient of inbreeding, f. Let us return to the example of a single locus with two alleles, A and a, having relative frequencies p and q in a particular local population. With partial inbreeding, the frequencies of genotypes AA, Aa, and aa are $p^2 + fpq$, $2pq(1-f)$, and $q^2 + fpq$, respectively. This is a generalization of the H–W principle, in which f (or F_{IS}) governs how alleles associate into genotypes. When f (or F_{IS}) is zero, the proportions of each of the three genotypes are the same as the H–W equilibrium; when f is 1.0, the population contains no heterozygotes. Most sexually reproducing marine populations conform to H–W equilibrium, so that F_{IS} is close to zero. Clonal marine populations, such as some sea anemones and corals, often have non-zero F_{IS}, owing to a mixture of sexual and vegetative propagation of genotypes.

If a species is subdivided into partially isolated, finite subpopulations, mating among individuals in the total population cannot take place at random. At the same time, there is genetic drift within each subpopulation. The effect on the proportion of genotypes in the species is analogous to the effect of inbreeding. Local populations tend towards fixation, with a decline in heterozygosity, but genetic diversity is preserved among rather than within subpopulations (**Table 1**). The genetic correlation between gametes drawn from different demes or subpopulations, with respect to allelic frequencies in the total population, is given by $F_{ST} = \sigma_p^2/\bar{p}(1-\bar{p})$. In this equation, $\bar{p}$ is the average frequency of allele A in the total population and σ_p^2 is the variance of p among subpopulations. Thus, F_{ST} is the ratio of the variance of allelic frequencies among subpopulations to the maximum variance that would obtain if each subpopulation were fixed for one of the alternative alleles without change in mean allelic frequency. When local populations diverge from one another, there is an excess of homozygotes and a deficiency of heterozygotes, with respect to random mating expectations in the total population. The frequencies of AA, Aa, and aa in the total population are, thus, $\bar{p}^2 + \sigma_p^2$, $2\bar{p}\bar{q} - 2\sigma_p^2$, and $\bar{q}^2 + \sigma_p^2$, respectively. Note the resemblance of these zygotic frequencies to those in an inbreeding population. The principle (the Wahlund effect) is readily understood at the extreme, in which each subpopulation is fixed for one allele or another; in this case, there are no heterozygotes in the total population. This partitioning of genetic diversity can be extended to any number of hierarchical levels.

In the absence of gene exchange among local populations of finite size, F_{ST} increases through time as local populations become fixed through the process of random genetic drift (**Table 1**). Local fixation can be prevented, however, by gene flow, the exchange of gametes or individuals among local populations. Suppose that a large population is subdivided into many subpopulations, with an average allele frequency $\bar{p}$, and that each subpopulation exchanges a proportion m of its population with a random sample of the whole population every generation. This is Wright's well-known 'island' model of population structure. If we consider a single subpopulation, the change in allelic frequency per generation will be $\Delta p = -m(p-\bar{p})$. Although this model is not realistic (e.g., exchange among all subpopulations is not likely to be equal), it illustrates the principle that the frequency of an allele in a subpopulation will be pulled toward the mean frequency of immigrants. When m is small, the equilibrium between genetic drift and gene flow in the island model is approximated by $F_{ST} = 1/(4Nm+1)$, which leads to a simple estimate of the number of migrants exchanged among demes. Such estimates from data on real populations must be regarded as provisional, however, as the numerous assumptions underlying the estimate are rarely, if ever, met.

Gene flow is a powerful cohesive force holding populations together. Indeed, in the island model,

the exchange of one migrant every other generation ($Nm = 0.5$) is theoretically sufficient to prevent the chance loss or fixation of an allele with an initial mean frequency of 0.5 in most subpopulations. However, owing to departures from the ideal populations in the island model, the exchange of thousands of individuals per generation between neighboring subpopulations of a widely distributed species could be insufficient to prevent considerable random drift. Moreover, the balance between genetic drift and gene flow is established over many generations. Divergence (or convergence) following an interruption (or resumption) of gene flow can take hundreds of generations, so that genetic similarity is not sufficient evidence for current gene flow. On the other hand, genetic similarity owing to high gene flow does not mean that subpopulations are demographically linked. Ecological and genetic processes operate over very different timescales.

Spatial structure of genetic diversity or population subdivision is the topic of most interest to oceanographers, because it is tied to the hope that the geographic sources of recruitment to marine animal populations might be identified by their genetic makeup. However, for most species of interest, those that comprise the zooplankton broadly speaking, this hope is not well founded in logic or fact. Dispersal among geographic populations, perhaps even low levels of dispersal, can eliminate the very genetic differences among populations that would permit identification of provenance. The marine population genetics literature supports the generalization that species with dispersing, planktotrophic larvae have, as expected, much less geographic variation or population subdivision than species with poorly dispersing, lecithotrophic larvae. F_{ST} is generally much less than 0.05 for marine species with planktonic larvae.

The oceanographer's problem is to detect whether a sample of zooplankton is a genetic mixture and, if so, to determine the contributions of different geographic populations to the mix. This problem has been solved in mixed-stock fisheries, particularly for anadromous species. Sophisticated statistical analysis of genetic data can identify, with accuracy and precision, the relative contributions of discrete salmon stocks to ocean catches. With the advent of highly polymorphic microsatellite DNA markers, it is even possible to assign individuals to their population of origin. However, these methods work well for species like salmon because the source populations are identifiable in space and are genetically distinct, with F_{ST} values generally above 0.05 and as high as 0.5. These same methods are not likely to work for the many marine species that lack obvious spatial genetic structure. Although identification of sources and sinks of zooplanktonic populations is critical to understanding their distribution and abundance, it is unlikely to be achieved with indirect genetic methods. The fundamental limitation may be the dispersal biology of such species, which can easily homogenize the frequencies of alleles at all loci, whether allozymes or microsatellite DNA markers.

Studies of spatial genetic variation should be made as a part of any baseline population genetic description of a marine species. As a rule, one should not expect such studies to yield conclusive information about the sources of recruits or the water masses bearing them. Nevertheless, any given study might reveal an exception to this rule or a previously unrecognized barrier to dispersal that has resulted in a major genetic subdivision.

Temporal Genetic Change

Despite the generalization that marine species with planktonic dispersal tend to be genetically homogeneous over large geographic regions, allelic frequencies among samples, taken sometimes on scales of meters, often show unpredictable patchiness. Planktonic larvae and patterns of recruitment are thought to play a role in such paradoxical observations. Temporal genetic studies, which are few, further suggest that as much genetic variation can be observed among recruits to a single place as can be observed among adult populations on spatial scales of hundreds to thousands of kilometers. Thus, the population genetics of marine planktonic larvae or new recruits are spatially and temporally much more dynamic than expected, given that their adult populations are large and well connected by larval dispersal. This anomalous feature of marine population genetics, like patterns of larval settlement themselves, may be attributed to the dynamics of the ocean environment.

Microspatial genetic heterogeneity and temporal change may both be explained by the hypothesis that highly fecund marine organisms may have a large variance in individual reproductive success. This variance in reproductive success may result from a sweepstakes-chance matching of reproductive effort with ephemeral oceanographic conditions conducive to spawning, fertilization, larval survival, and recruitment. According to this hypothesis, only small fractions (from 1/100 to 1/100 000) of spawning adults effectively reproduce and replace standing adult populations each generation. In this case, ratios of N_e/N may be far less than those observed in terrestrial animals (0.25 to 0.75), and random

genetic drift of allelic frequencies should be measurable in some populations. This prediction has been borne out by temporal studies, in which observed genetic drift implies effective population sizes that are many orders of magnitude less than the simple abundance of adults. Studies of larval populations and comparisons of recruits and adults have confirmed a second prediction, that specific cohorts of larvae or recruits should show genetic evidence of having been produced by only a segment of the potential parental pool.

This hypothesis establishes a connection between oceanography and population genetics in the study of recruitment and may explain how local adaptations and speciation can occur in seemingly large, well-mixed marine populations. Temporal genetic studies are therefore required to make sense of population genetic structure.

Retrospective Analyses of Historical Collections

Enzymatic amplification of specific DNA sequences by the polymerase chain reaction (PCR) can potentially be applied to the study of preserved zooplankton or fish scale collections. Molecular methods could facilitate rapid systematic treatment of these collections and establish genetic histories for particular species of interest. The power of such an approach is illustrated by a genetic study of Georges Bank haddock populations, which revealed significant heterogeneity in the frequencies of mitochondrial DNA genotypes between the 1975 and 1985 year-classes. Temporal change in this case was attributed to immigration rather than variance in reproductive success. Future collections of zooplankton should be stored in alcohol rather than formalin, which can chemically degrade nucleic acids.

Phylogenetics, Phylogeography, and Paleoceanography

Molecular genetic analyses are being used to reconstruct genetic phylogenies at all taxonomic levels and for many phyla. The application of phylogenetic methods to molecular as well as organismal traits, such as morphology, life history, and behavior, will undoubtedly shed new light on the evolution and systematics of marine organisms. Comparisons of genetic divergence within and between closely related species separated by barriers of known age (e.g., the Bering Strait or the Isthmus of Panama) are useful for calibrating rates of molecular evolution and reconstructing the history of faunal exchanges. Ultimately such studies may provide a basis for the development of biotechnological tools for rapid, automated classification of oceanographic samples and collections.

Since the 1990s, the application of phylogenetic approaches to molecular variation within species has yielded new insights into population histories and a synthesis of the traditionally separate disciplines of systematics and population genetics. Studies of mitochondrial DNA in several species living along the Gulf of Mexico and Atlantic coasts of the United States have revealed concordant patterns of major genetic subdivisions. In all of these species, Gulf genotypes give way to Atlantic genotypes across a previously recognized biogeographical boundary in south-eastern Florida. Gulf and Atlantic genotypes represent clades that separated over a million years ago. Thus, phylogeographic patterns reflect the persistence of historical events in the gene pools of organisms. Such information is relevant to management and conservation efforts and begs for interdisciplinary, paleoceanographic explanation. Other biogeographic boundaries should be similarly studied to assess whether they generally coincide with genetic discontinuities. A review of genetic differences between conspecific populations on either side of Point Conception failed to find a consistent pattern of discontinuity like that associated with the Florida Peninsula. Nevertheless, past dispersal, rather than present oceanographic connections, appear to be the messages written into the genetics of contemporary populations.

See also

Fishery Manipulation Through Stock Enhancement or Restoration. Coral Reef Fishes. Diversity of Marine Species. Mariculture, Environmental, Economic and Social Impacts of. Fishery Management. Fish Migration, Horizontal. Laridae, Sternidae and Rynchopidae. Mariculture Overview. Mariculture of Aquarium Fishes. Mariculture Diseases and Health. Mesopelagic Fishes. Salmon Fisheries: Pacific. Pelagic Fishes. Pelagic Biogeography. Hydrothermal Vent Fauna, Physiology of. Salmonids. Salmonid Farming. Seabird Conservation. Seabird Migration. Plankton.

Further Reading

Avise JC, Arnold J, Ball RM, Jr, *et al.* (1987). Intraspecific phylogeography: the mitochondrial DNA bridge between population genetics and systematics. *Annual Review of Ecology and Systematics* 18: 489–522.

Burton RS (1983). Protein polymorphisms and genetic differentiation of marine invertebrate populations. *Marine Biology Letters* 4: 193–206.

Hedgecock D (1994) Does variance in reproductive success limit effective population sizes of marine organisms? In: Beaumont AR (ed.) *Genetics and Evolution of Aquatic Organisms*, pp. 122–134. London: Chapman and Hall.

Hedgecock D, Tracey ML and Nelson K (1982). Genetics. In: Abele LG (ed.) *Biology of the Crustacea* pp 284–403. New York: Academic Press.

Hedrick PW (2000). *Genetics of Populations*, 2nd edn. Sudbury, MA: Jones and Bartlett.

Knowlton N (1993). Sibling species in the sea. *Annual Review of Ecology and Systematics* 24: 189–216.

Nelson K and Hedgecock D (1980). Enzyme polymorphism and adaptive strategy in the decapod crustacea. *The American Naturalist* 116: 238–280.

Utter F and Ryman N (1993) Genetic markers and mixed stock fisheries. *Fisheries* 18: 11–21.

Whitlock MC and McCauley DE (1999). Indirect measures of gene flow and migration: $F_{ST} \neq 1/(4Nm + 1)$. *Heredity* 82: 117–125.

PORE WATER CHEMISTRY

D. Hammond, University of Southern California, Los Angeles, CA, USA

doi:10.1006/rwos.2001.0181

Introduction

As marine sediments are deposited, they trap sea water in the pore space between grains. This pore water (sometimes called interstitial water) may represent more than 90% of the volume of the bulk sediment in fine-grained deposits near the sediment–water interface. The volume fraction of the bulk sediment that is water is called the porosity. Porosity usually decreases rapidly with increasing depth through the uppermost sediments, with the profile depending on lithology and accumulation rate. Ultimately, porosity may decrease to only 5–20% as the sediment becomes lithified. As sediments are compacted during burial, the pore fluid is squeezed upward, traveling through fractures, burrows, or perhaps the sediment pore space itself.

As sediment is buried, its composition may be modified by chemical reactions, a process called chemical diagenesis. Pore water provides a medium that permits a solute to migrate from a site where it is produced to another site where it may be removed. For example, in organic-rich sediments, pyrite (FeS_2) is a common end product of diagenesis. While the intermediate steps in pyrite formation are not fully understood, they involve sulfate reduction to sulfide at sites where reactive organic matter is found, and reduction of insoluble ferric oxides to form soluble ferrous iron at sites of iron-bearing minerals. Iron sulfides have very low solubility, and their deposition is usually localized at one of the two sites. If sulfide is released faster than ferrous iron, the sulfide diffuses from its site of production on an organic-rich particle to the mineral containing iron, where it forms insoluble iron sulfides. This can produce pyrite overgrowths on iron-bearing minerals. Alternatively, if the iron is more readily released, it diffuses to form iron sulfides near the sites of organic particles such as shells or localized pockets of organic substrate.

Because diagenesis may alter only a small fraction of the solid phases, its impact may be difficult to detect from studies of solid phases alone. Pore water chemistry is much more sensitive to such changes. For example, in a sediment of 80% porosity, dissolution of 0.1 weight percent $CaCO_3$ from the solid phase (near the detection limit measurable in solid phases) would make a change of 6 mmol kg^{-1} in the concentration of dissolved calcium. This change in pore water would be easily detectable because it results in a concentration 60% greater than that in the starting sea water. Of course, this calculation assumes that the pore water acts as a closed system, which is generally not the case as noted below. However, this example illustrates that pore water chemistry is more sensitive than solid phase chemistry to diagenesis.

Studies of pore waters have become a standard tool for understanding the biogeochemical processes that influence sediments, and considerable efforts have been invested during the past several decades to develop techniques to collect samples, evaluate whether vertical profiles exhibit artifacts introduced during collection and handling, and develop approaches to model the observed profiles and obtain quantitative estimates of reaction kinetics and stoichiometry. Usually, modeling approaches assume steady-state behavior, but when time-dependent constraints can be established, nonsteady-state approaches can be applied.