Microsatellite Population Structure in Herring at Three Spatial Scales

Arran A. McPherson
Dalhousie University, Department of Oceanography, Halifax, Nova Scotia, Canada

Christopher T. Taggart
Dalhousie University, Department of Oceanography and Marine Gene Probe Lab, Halifax, Nova Scotia, Canada

Paul W. Shaw
University of Hull, Department of Biological Sciences, Hull, United Kingdom

Patrick T. O'Reilly and Doug Cook
Dalhousie University, Marine Gene Probe Lab, Halifax, Nova Scotia, Canada

Abstract

We quantify population structure in herring at three spatial scales using 4-5 microsatellite DNA markers. Significant genetic structure was detected between putative species (Pacific vs. Atlantic herring), as well as among populations at ocean basin scales (northeast vs. northwest Atlantic) and at regional management scales (NAFO Division 4X). This study is the first that reports application of microsatellite markers to northwest Atlantic herring, where genetic support for population structure has been scant. Although the results are for 1 year only, and should therefore be interpreted with caution, these data imply that microsatellite analyses may enable detection of population structuring in Atlantic herring. The utility of the method and analyses are discussed and suggestions (related to sampling and interpretation) are provided.

Introduction

An objective of fisheries management is to ensure the integrity of a stock while maintaining (and even maximizing) harvests. Central to this concept is the identification of "populations" that are assumed to share a number of phenotypic traits (e.g., growth rate, fecundity, morphometric measurements) as well as, in the case of marine fish as reviewed by Carvalho and Hauser (1994), identifiable patterns of stock and recruitment. Identifying population structure within and among stocks therefore has the potential to greatly increase the ability to anticipate the effects of harvest levels among stock components.

Population structure can be delineated using a variety of techniques. Meristic, (e.g., variation in the number of vertebrae), morphometric, (e.g., variation in dimensions of body parts and/or rates of change), parasitic load (e.g., variations in number and type of parasites), and demographic (e.g., age structure, fecundity, and mortality) methods have long been used in the classification of groups of marine fish when the means and variance of these measurements have been observed to differ among populations (e.g., Messieh 1975). However, there are limitations associated with these techniques as the physical environment is known to influence the expression of traits over the life of the individual, therefore potentially converging nonheritable traits. This environmental influence is of greater consequence for a migratory species whose range could encompass a variety of environments, hence contributing to an increased variability in the nonheritable traits among populations. Therefore population-specific differences become difficult to interpret.

Neutral genetic variation can be used to differentiate among populations, and it is not thought to be subject to confounding environmental influences. However, the ability to reject the hypothesis of no population structure depends on a variety of factors, including the type and number of genetic markers used and the time-scale of divergence between populations. The successful application of molecular genetic markers in identifying population structure in freshwater and anadromous fish, that can be shown to be physically isolated (to some extent), has prompted marine fishery managers to consider genetic data in assessing population structure. Unlike the case for freshwater and anadromous fish, however, the environment of marine species may lack obvious physical barriers to dispersal and migration (Waples 1998). Therefore, delineation of marine populations with a "potentially" high capacity for gene flow (known, assumed, or otherwise) is problematic as complex oceanographic processes coupled with the migratory capabilities of the animals may create complex spatial patterns of population structure.

Given that relatively few successfully reproducing migrants are needed to reduce genetic differentiation to very low levels and that marine populations may be too large to markedly diverge by genetic drift (but note that variation in reproductive success may reduce the effective popula-

tion size and therefore increase susceptibility to drift; Hedgecock 1994), the genetic "signal" indicating population differences of marine fish may be small relative to the sampling "noise." Therefore, measures must be taken to optimize the probability of detecting differences when they occur (i.e., by increasing the signal-to-noise ratio).

Herring are an ideal model species for exploring the genetic basis of population structure because they are one of the most studied marine teleosts (e.g., there is more literature on herring than any other fish species as indexed by the Food and Agriculture Organization; FAO 1999) and several herring-specific population structuring mechanisms have been hypothesized (Iles and Sinclair 1982, Smith and Jamieson 1986, McQuinn 1997) which have provided a framework in which we may better articulate questions related to population structure in this species. From a more pragmatic perspective, Atlantic herring (*Clupea harengus*) are a valuable resource in the North Atlantic Ocean (> 2 million metric tons catch in 1995; FAO 1999), and recent fluctuations in catch on historical fishing grounds (e.g., Stephenson 1997) and the requirements for better conservation practices (e.g., Stephenson 1999) demand a clarification of the population structure of this species.

Genetic analyses of Atlantic herring based on allozyme and mtDNA markers (e.g., Ridgeway et al. 1971, Grant 1984, Ryman et al. 1984, King et al. 1987, Kornfield and Bogdanowicz 1987, Dahle and Eriksen 1990, Safford and Booke 1992, Jørstad et al. 1994) have been largely unable to reject the null hypothesis of no genetic differentiation among populations at management unit scales, nor in many cases at ocean basin scales. In contrast, evidence for homing from tagging studies (e.g., Wheeler and Winters 1984), for different population metrics among neighboring groups (e.g., Messieh 1975), and for predictable variations in spawning times and locations among groups (e.g., Sinclair and Tremblay 1984) is consistent with the existence of distinct populations. Thus, quantitative studies that focus on measuring the degree of genetic isolation among herring populations, and then construct testable hypotheses concerning the mechanisms that may maintain it, are essential to resolve the above inconsistencies. The conflicting evidence for herring population structure is not unique; it is shared with a variety of marine fish species.

Genetic analyses based on variation at a suite of microsatellite loci developed for Pacific herring (*Clupea pallasii;* O'Connell et al. 1998a) have provided evidence for significant population structure in Alaskan Pacific herring (O'Connell et al. 1998b) and northeast Atlantic herring (Shaw et al. 1999). Grant and Utter (1984) found allozyme-based differences in the northern Pacific herring that were not apparent in O'Connell et al. (1998b). However, the results of Shaw et al. (1999), that demonstrated subbasin and interocean scale differences among herring, suggest that microsatellite loci may be key in quantifying population structure in northwest Atlantic herring. Microsatellite markers may detect structure at finer spatial and

temporal scales than many other genetic methods due to higher levels of variability thought to be a result of high rates of mutation (Bentzen 1997).

Here we report an attempt to quantify population structure in herring at three spatial scales. Northeast (NE) and northwest (NW) Atlantic herring are compared to Pacific herring to quantify the degree of differentiation between groups that are clearly isolated geographically but whose life history similarities suggest a subspecies relationship (Svetovidov 1963 as outlined in Jørstad et al. 1994). Atlantic herring collected from the NE and NW Atlantic are then used to assess differentiation at the Atlantic basin scale, where the potential for genetic exchange might be presumed to be negligible. Finally, genetic variation among herring collected from three locations (NAFO Division 4X) in the NW Atlantic are then assessed at the management scale, where the potential for genetic exchange might be presumed to be greater than at the ocean basin scale.

Materials and Methods

Spawning-stage Atlantic herring (blood and/or muscle samples) were collected (Fig. 1) from the NW Atlantic at Spectacle Buoy (SB, 43.618°N, 66.124°W) and Scot's Bay (ScB, 45.224°N, 64.976°W). Mature fish (nonspawning) were also collected in the vicinity of Emerald Basin (EB, 44.294°N, 62.376°W). DNA extraction procedures for NW Atlantic samples follow Ruzzante et al. (1996). Five microsatellite loci, Cha 17, Cha 20, Cha 63, Cha 113 and Cha 123 were amplified (annealing temperatures were modified from those in O'Connell et al. 1998a) and scored. Four microsatellites (17, 20, 63, 113; allelic data were extracted from Shaw et al. 1999) were assayed in the NE Atlantic herring, represented by Barents Sea (BS, 70.53°N, 31.583°E) Norwegian spring-spawning herring (spawning stage), and the Pacific herring (nonspawning stage) collected seaward of Vancouver Island (PC). Single locus statistics (allele sizes, number of alleles, observed heterozygosity) were calculated for all herring samples and conformation to Hardy-Weinberg equilibrium (HWE) was tested for all loci in all collections (Miller 1997) to assess random allele assortment (nonassortative mating) within populations.

F_{ST} estimates (Wright 1951 as amended by Weir and Cockerham 1984) of population structure were calculated using F-STAT (Goudet 1996) that assumes an Infinite Allele Model of microsatellite mutation and R_{ST} (Slatkin 1995) estimates were calculated using R_{ST}-CALC (Goodman 1997), that assumes a Stepwise Mutation Model. Allele size data were expressed in terms of standard deviations from the mean for R_{ST} analyses, as recommended by Goodman (1997) to minimize effects of unequal variance among loci and unequal sample sizes. Permutation tests (1,000 resampling trails per comparison) were used to determine significance values for all tests. We also employed an Exact test (Raymond and Rousset 1995) to assess the statistical significance of locus-specific allele frequency differences be-

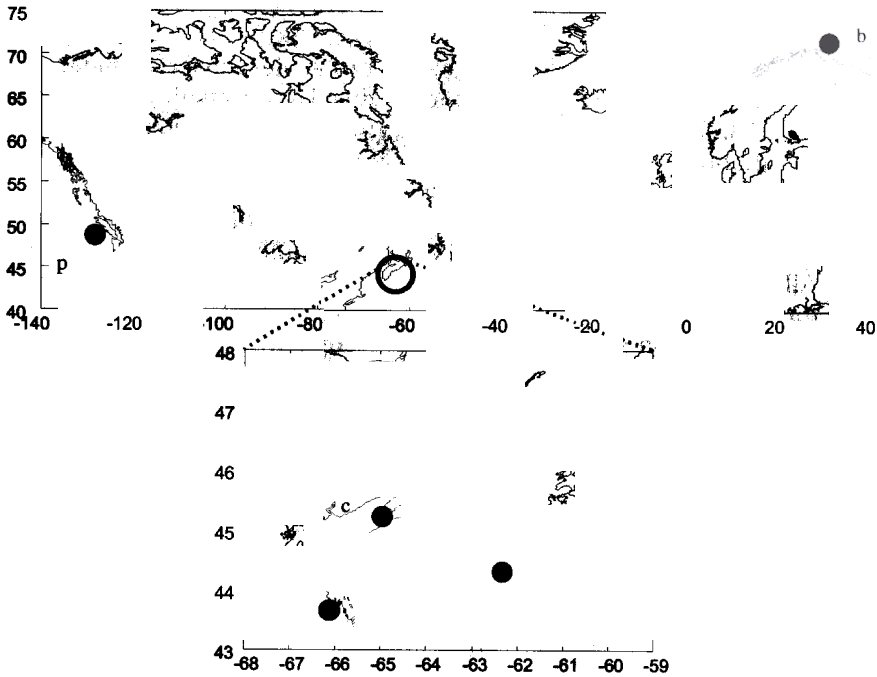

Figure 1. Sample locations of Atlantic and Pacific herring. Abbreviations are as follows: (p) Pacific herring collected seaward of Vancouver Island; (b) Atlantic herring from the Barents Sea; (e) Atlantic herring collected from Emerald Basin; (s) Atlantic herring collected from Spectacle Buoy; and (c) Atlantic herring collected from Scot's Bay.

tween pairs of population samples (Miller 1997) allowing an assessment of discriminatory utility at each locus.

Allele classes (base pairs; bp) were binned at each locus prior to parameter estimation in all pairwise comparisons to facilitate interlab comparisons of microsatellite data. The number of bins and bin-widths were determined at each locus by progressively increasing the number of bins and then comparing the binned frequency distribution to the original nonbinned distribution of all samples pooled for each locus respectively. The least number of bins (and thus bin width) that provided a frequency distribution not significantly different from the original distribution (Kolmogorov-Smirnov $P > 0.05$) was chosen to establish an objectively based binning criterion. In all cases, bin-widths were found to meet this criterion at 4 bp. Consequently, allele classes differ by 4 bp for each locus in all comparisons.

Results

Single locus statistics (allele sizes, number of alleles, observed heterozygosity) are similar across all samples (Table 1) and results for the NW Atlantic (SB, ScB, and EM) are consistent with those reported for Pacific and NE Atlantic herring (O'Connell et al. 1998b, Shaw et al. 1999). With the exception of one locus (Cha 20) in the Barents Sea population, no population deviated significantly from Hardy-Weinberg Equilibrium; i.e., consistent with samples being drawn from within randomly mating populations.

All pairwise R_{ST} and F_{ST} estimates between the Pacific (PC) and each of the four Atlantic (BS, SB, ScB, and EB) sites were significant (Table 2). Significant population structuring, as inferred by both F_{ST} and R_{ST} analyses, was also observed between the NE and NW Atlantic (see Table 2; pairwise comparisons between the NE and each of the NW samples). At the smallest spatial scale investigated (within the NAFO Division 4X region) significant structuring, using both F_{ST} and R_{ST}, was observed between herring from Spectacle Buoy and Emerald Basin, though the magnitude of differences were half those observed at the basin scale. No significant differences were observed between Scot's Bay herring and either Emerald Basin or Spectacle Buoy herring.

An Exact test showed locus-specific significant differences among populations (Table 3). All loci were useful (i.e., reported significant differences) in discriminating among Atlantic and Pacific herring. However, as the geographic scale of the comparison decreased from ocean scale to management unit scale, fewer loci were of discriminatory value. In fact, two to three loci showed significant comparisons including Cha 123, a locus not used by Shaw et al. (1999). When pairwise comparison results were pooled over all loci, the same population pairs showed significant differences as were found using F_{ST} and R_{ST}.

Discussion

This study reports significant differences in herring at three spatial scales ranging from Atlantic vs. Pacific to those within a NW Atlantic management unit. The significant differences among Atlantic and Pacific herring are consistent with Svetovidov (1963 as outlined in Jørstad et al. 1994) who argued a subspecies relationship based on an analysis of biological traits, Grant (1984) who argued a distinct species relationship from genetic (allozyme) information, and with Domanico et al. (1996) who estimated a 3.1 million year divergence between Atlantic and Pacific herring when assessed using ribosomal DNA sequence variation.

The significant differences detected between NE and NW Atlantic herring are inconsistent with Grant (1984), who was unable to reject the hypothesis of no structure at basin scales using 40 allozyme loci. Our results suggest that microsatellites are valuable in detecting population structure at ocean basin scales. At the finest geographic scale considered (NAFO

Table 1. Descriptive statistics for microsatellite DNA analysis of herring samples showing sample size (*n*), the number of alleles per locus, the range of allele sizes in base pairs (bp), observed heterozygosity, and the χ^2 value/probability associated with Hardy-Weinberg equilibrium (HWE) estimates (Miller 1997).

	Pacific Vancouver $n = 30$	NE Atlantic Barents Sea $n = 50$	NW Atlantic Emerald Basin $n = 40$ Scot's Bay $n = 50$ Spectacle Buoy $n = 49$
Cha 17			
No. of alleles	21	22	23
Allele size (bp)	96-154	90-152	96-170
Heterozygosity	0.93	0.94	0.89
HWE	0.01/0.99	1.44/0.23	0.94/0.33 EM
			0.02/0.64 ScB
			1.65/0.19 SB
Cha 20			
No. of alleles	15	27	25
Allele size (bp)	108-180	96-158	96-186
Heterozygosity	0.77	0.72	0.93
HWE	0.020/0.66	8.62/**0.003**	0.16/0.69 EM
			0.11/0.65 ScB
			0.49/0.48 SB
Cha 63			
No. of alleles	17	13	13
Allele size (bp)	128-166	126-156	130-174
Heterozygosity	0.77	0.84	0.88
HWE	0.01/0.99	0.50/0.50	0.70/0.4 EM
			0.64/ 0.46 ScB
			1.23/0.27 SB
Cha 113			
No. of alleles	18	16	18
Allele size (bp)	100-150	104-134	94-132
Heterozygosity	0.87	0.77	0.93
HWE	0.54/0.46	3.26/0.06	0.01/0.94 EM
			0.5/0.5 ScB
			0.02/0.90 SB
Cha 123			
No. of alleles			23
Allele size (bp)			152-222
Heterozygosity			0.93
HWE			0.5/0.5 EM
			0.45/0.49 ScB
			0.30/0.58 SB

Table 2. **Pairwise F_{ST} above the diagonal (θ/P) and R_{ST} below diagonal (ρ/P) estimates of population structure in herring collected from the northeast (Barents Sea), northwest (Spectacle Buoy, Emerald Basin, and Scot's Bay) Atlantic and the Pacific.**

Location	Spectacle Buoy 5 loci	Emerald Basin 5 loci	Scot's Bay 5 loci	Pacific 4 loci	Barents Sea 4 loci
Spectacle Buoy		0.008/ $P < 0.01$	0.006/ $P = 0.11$	0.047/ $P < 0.01$	0.039/ $P < 0.01$
Emerald Basin	0.039/ $P = 0.002$		0.005/ $P = 0.16$	0.046/ $P < 0.01$	0.06/ $P < 0.01$
Scot's Bay	0.025/ $P = 0.15$	0.013/ $P = 0.21$		0.042/ $P < 0.001$	0.028/ $P < 0.01$
Pacific	0.098/ $P < 0.0001$	0.068/ $P = 0.001$	0.073/ $P < 0.001$		0.06/ $P < 0.01$
Barents Sea	0.193/ $P < 0.0001$	0.290/ $P < 0.0001$	0.180/ $P < 0.001$	0.185/ $P < 0.0001$	

All significant results remain significant at $P < 0.05$ after Bonferroni correction (Manly 1985).

Table 3. **Pairwise Exact test results for allele frequency differentiation (Raymond and Rousset 1995) at each locus.**

Locations	Cha 17	Cha 20	Cha 63	Cha 113	Cha123
*PC-BS	$P = 0.0020$	$P < 0.001$	$P < 0.001$	$P < 0.001$	N/A
*PC-EB	$P = 0.055$	$P < 0.001$	$P < 0.001$	$P = 0.002$	N/A
*PC-ScB	$P = 0.008$	$P < 0.001$	$P < 0.001$	$P < 0.001$	N/A
*PC-SB	$P = 0.007$	$P < 0.001$	$P < 0.001$	$P < 0.001$	N/A
*BS-EB	$P = 0.56$	$P = 0.037$	$P < 0.001$	$P < 0.001$	N/A
*BS-ScB	$P = 0.31$	$P = 0.01$	$P < 0.001$	$P < 0.001$	N/A
*BS-SB	$P = 0.053$	$P < 0.001$	$P < 0.001$	$P < 0.001$	N/A
EB-ScB	$P = 0.65$	$P = 0.43$	$P = 0.100$	$P = 0.041$	$P = 0.049$
*EB-SB	$P = 0.88$	$P = 0.24$	$P < 0.001$	$P = 0.071$	$P = 0.050$
ScB-SB	$P = 0.65$	$P = 0.12$	$P = 0.14$	$P = 0.012$	$P = 0.030$

PC = Pacific; BS = Barents Sea; EB = Emerald Basin; SB = Spectacle Buoy; ScB = Scot's Bay. Shaded areas indicate significant differences ($P < 0.05$) between samples for that locus. * indicates combined Exact test probability over all loci is significant at $P < 0.001$. N/A: no data available for one of the populations at this locus.

Division 4X in the NW Atlantic), significant differences were observed between herring from Emerald Basin and herring caught at Spectacle Buoy. While it is necessary to test this pattern in subsequent years for it to be of direct use for management purposes, these results suggest microsatellite-based genetic evidence for management scale population structure of herring in the NW Atlantic, which is compelling as three different tests, based on different models, were used.

The implications of management-scale population differences are in some ways unique for 4X herring as Scotia-Fundy herring are currently managed using an "in-season management approach" as described by Stephenson et al. (1999). Each spawning ground is assessed (in season) and spawning ground-specific quotas are established accordingly. Therefore, the results presented here support the precautionary management currently employed. However, for most other marine fish management scenarios, there has not been this degree of success. The failure to recognize discrete populations within a stock complex may explain both the collapse and recovery failure in many marine fish populations (Frank and Brickman 2000). In fact, those authors suggest that when biological reference points are developed from aggregate (stock) data representing distinct (unit) populations and employed in conventional assessment models, the results are likely to be inaccurate and nonconservative.

However, the results of the within-management-unit comparisons should be interpreted with caution. As herring are thought to exhibit spawning ground fidelity (if not natal), and are known to mix at other seasonal stages (e.g., feeding), spawning stage herring collected from their spawning ground should be used to characterize population structure. While we can be reasonably confident that the Pacific herring have limited opportunity to mix with either the NE or the NW Atlantic populations, the assumption of no mixing is more problematic within the 4X management unit comparison, due to the close geographic proximity of sampling locations. This is particularly important when sampling different spawning groups that may overlap in time and space outside the spawning period or location, as is typically the case for comparisons at management-unit scales. Therefore, the state of the Emerald Basin herring sample (not in spawning condition) limits the utility of these results beyond providing evidence for small-scale population structure in the Nova Scotia and Bay of Fundy management unit. In addition, we recognize that the issue of temporal stability must be addressed as the next step in avoiding the sampling artifacts possible with such highly migratory fish (Waples 1998). However, we note that migration and mixing among adults does not necessarily imply reproductive mixing (i.e., gene flow) among putative populations, especially when considering those that exhibit spawning-ground fidelity.

Although differences were detected at all spatial scales observed, the magnitude of differences observed at the species/subspecies comparison ($F_{ST} < 0.05$) of Atlantic and Pacific herring suggest limited differentiation. This may be due to the high rates of mutation expected at microsatellite

loci and the potential for convergence of allele sizes. F_{ST} was designed for characters that are considerably less polymorphic than microsatellites. Nevertheless, it is routinely applied to allele frequency data generated by any of several molecular markers (including mtDNA and microsatellites). The statistic can be interpreted as a ratio of the expected heterozygosity of an individual in an equivalent random mating total population minus the expected heterozygosity of an individual in an equivalent random mating subpopulation, to the expected heterozygosity of an individual in an equivalent random mating total population. Thus, F_{ST} estimates inbreeding in subpopulations relative to the total population. In doing so, the magnitude of the statistic is influenced by high levels of heterozygosity. Consider an extreme example involving two populations, each with an expected heterozygosity of 95% but with no alleles in common. The maximum pairwise F_{ST} value possible would be 0.05 (i.e., less than the homozygosity). Therefore, as Hendrick (1999) illustrated, the actual upper limit of the F_{ST} statistic is limited by the homozygosity (1–heterozygosity). Therefore, should we consider standardizing the F_{ST} value reported against the maximum F_{ST} possible given the observed homozygosities? If shown to be robust, this may prevent misleading interpretations of small F_{ST} values, that may correspond to very significant differences among groups of marine fish as responsible managers faced with difficult decisions may not fully appreciate the subtleties of the statistic that is easily and mistakenly interpreted (in its most frequently used form) as the proportion of the maximum possible differentiation.

When applying F_{ST} to address marine fish population structure, the magnitude of the error associated with each estimate is of significance. For potentially high gene flow marine species, the expected F_{ST} error estimates (due to nonrandom sampling) can be of a similar magnitude to the estimate itself when small samples sizes are used (<50). Therefore, following Waples (1998), expected random sampling error ($1/2n$) should be estimated for a given sample size (n) and be used when interpreting results. For example, the significant ($P < 0.05$) Emerald Basin to Spectacle Buoy comparison had an estimated F_{ST} value of 0.008 relative to the error associated with that estimate at 0.01. Therefore, our result falls within what may be attributed to sampling error or unexplained fluctuations in allele frequencies. Thus, temporal stability, which is required to substantiate the results reported here, is essential for confidence that differences are biologically meaningful in the context of stock identification and can be used to interpret spatial patterns in marine fish populations.

Because of the complexities involved with interpreting results averaged over loci (i.e., the error is dependent on sample size and independent of the significance of F_{ST}), we advocate considering the pairwise population comparisons at each locus (e.g., Exact test; Table 3). Significant differences at two to four loci were found in each pairwise comparison suggesting that all populations (including those within management

unit 4X) are at least partially reproductively isolated and should therefore be considered distinct if differences can be shown to be reproducible and temporally stable. Bentzen (1997) advocates that if even one of several loci yield a significant result, it may be biologically meaningful given the obstacles (huge population sizes, sampling biases) faced in detecting legitimate population differences in the marine environment.

An additional, and somewhat more intuitive, hazard when comparing two populations for discriminatory purposes, is the influence that the number of "uninformative loci" (relative to "informative" loci) have on population structuring estimates when averaged over all loci. We do not advocate arbitrarily abandoning uninformative loci for a variety of reasons. However, one could argue that an "informative" locus is being maintained by selection, and if indeed the population differences did accrue through selection, there remains evidence of limited gene flow and thus of population structure at time scales that are relevant to management. Remembering that selection can result from differential fishing practices, the consequence of such a process in the short-term (several generations) evolution of population structure and dynamics is unclear. Alternatively, the differentiation might equally be a biologically meaningful result of the frequently assumed neutral variation that is detectable using at least the one locus that has been identified by chance. Thus, given the clearly debatable quandary, we argue, regardless of the driving mechanism, resolving variation that arises from sampling error and unexplained temporal fluctuations in allele frequencies is deserving from a tractable research perspective when we are increasingly faced with collapsing populations, the resultant concerns about genetic biodiversity, and the demand for precautionary fishing practices.

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