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FLORIDA GULF BAY SCALLOP (*ARGOPECTEN IRRADIANS CONCENTRICUS*) POPULATION GENETIC STRUCTURE: FORM, VARIATION, AND INFLUENTIAL FACTORS

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ABSTRACT Knowledge of changes in the interdependence of a species' populations for continued existence (connectivity) and of the forces driving connectivity patterns is critical for management and conservation of the species. Population genetics can be used to investigate population connectivity. Combining population genetics with climatic, environmental, and biological (external) factors that can influence population structure and connectivity can lead to a greater understanding of the forces influencing population dynamics. We deciphered the population genetic structure and connectivity patterns of bay scallops (*Argopecten irradians concentricus* Lamarck) from Florida Gulf of Mexico waters using allozyme-locus and mitochondrial DNA population genetics data from samples representing four consecutive generations. We evaluated bay scallop population genetic relationships within the context of habitat, hydrodynamic, and environmental variation, and concomitant spatial patterns in the abundance of adult and recently recruited scallops to infer the influence of these factors on bay scallop population structure. Florida Gulf bay scallops form a hierarchical, mixed-model, source–sink metapopulation with intergenerational variation in connectivity that seems to be influenced by the factors we considered. An El Niño event that occurred during 1 y caused climatic and environmental change that greatly reduced subpopulation connectivity, allowing us to understand more completely the potential relative importance of the other external factors on change in metapopulation connectivity over time. Our study illustrates the value of using multiple genetic markers, sampling for multiple years, and integrating data from multiple external factors for understanding the population genetic structure of species for adaptive management.

KEY WORDS: *Argopecten irradians*, bay scallop, external factors, fishery, Florida, Gulf of Mexico, metapopulation, population genetics, recruitment

INTRODUCTION

Knowledge of a harvested species' connectivity (successful exchange of individuals among local populations (Cowen & Sponaugle 2009, Le Corre et al. 2012)) is critical because management strategy should preserve that connectivity for the continued well-being of the species and the economic activity depending on it. "Successful exchange" involves recruitment at two levels: movement of individuals from one local population to another and the contribution of those individuals to the gene pool of the recipient population (Pineda et al. 2007, Lowe & Allendorf 2010). The relative dependence of local populations on one another for recruitment can be revealed by population genetics. The principal mechanism of recruitment for nearly all shallow-water benthic marine invertebrates is dispersal of pelagic larvae (Bode et al. 2006, Watson et al. 2012), which are very difficult to track directly. Genetic approaches for assessing patterns and degrees of connectivity are particularly valuable when tracking pelagic larvae is not possible (Botsford et al. 2009), because population genetic structure is the net product of the dispersal and survival that engender the connectivity (Whitlock & McCauley 1990, McCauley 1991, Bohonak 1999, Hellberg 2006). Therefore, patterns of genetic variation can be used to infer larval dispersal patterns (Palumbi 1994) and demographic

processes (Hellberg 2006). It is this link that makes population genetics studies so valuable for management.

However, population genetics cannot provide insight into the forces contributing to spatial and temporal variation in connectivity among local populations. Geophysical and environmental factors can strongly influence invertebrate larval dispersal (e.g., Ellien et al. 2000, Epifanio & Garvine 2001, James et al. 2002, Gouhier & Guichard 2007, Cowen & Sponaugle 2009). Knowledge of these factors is pivotal for understanding how they interact with the species' population biology to shape and vary the species' connectivity over time (Cowen et al. 2006). The explanatory and predictive powers of observed genetic patterns of variation are enhanced when an investigation of factors that may affect population genetic structure is included in a population genetics study.

Many single-year or single-generation studies have combined physical processes or biological factors with population genetic assessments to assess the effects of these external forces on the connectivity of local populations (e.g., Ingvarsson 1997, Ellien et al. 2000, Riginos & Nachman 2001, Gilg & Hilbish 2003, Jolly et al. 2003, Galindo et al. 2010, Selkoe et al. 2010, White et al. 2010a, Saenz-Agudelo et al. 2011, Schunter et al. 2011). Multiyear studies of this type are more informative, particularly when they capture intergenerational relationships (Carson et al. 2010), because they provide windows into the causes of spatial and temporal flux in connectivity across timescales relevant for understanding the potential effects of

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impacts such as harvesting (Smedbol et al. 2002, Hastings & Botsford 2006, Le Corre et al. 2012). However, multiyear or multigenerational investigations in which temporal and spatial variation in population genetic structure is compared with appropriately scaled, sufficiently detailed contemporary variation in multiple external factors that can influence connectivity are rare (Hellberg et al. 2002, Hellberg 2006, Hedgecock et al. 2007, and see also Weider et al. 2009) because in the marine environment, long-term, geographically expansive oceanographic and ecological studies are prohibitively expensive and time-consuming (Cowen & Sponaugle 2009). Thus, the most important type of population genetics study for conserving and managing marine resources is the least common type conducted.

A critical external factor influencing gene flow in marine organisms is hydrodynamics because it is usually linked tightly to dispersal (Sinclair 1988, Botsford et al. 1994, Xie & Eggleston 1999, Hamm & Burton 2000, Kritzer & Sale 2006, Morgan & Shepherd 2006, Cowen & Sponaugle 2009), sometimes to the point of driving population structure (Catalán et al. 2006, Cowen et al. 2006, Comerford & Brophy 2013). Other factors that influence population structure in shallow-water marine species include location of essential habitats; water quality; freshwater discharge; larval duration, behavior, and tolerances; and adult distribution and spawning season (e.g., Lipcius et al. 1997, Cowen et al. 2006, Banks et al. 2007, Fievet et al. 2007, Paris et al. 2007, Pringle & Wares 2007, Shima et al. 2010, Swearer & Shima 2010, Carson et al. 2011). We are fortunate to have a wealth of detailed information for many of these physical and biological processes to link with 4 y of population genetics data that we generated for the ecologically and economically important bay scallop (*Argopecten irradians* ssp. *concentricus* Lamarck). Specifically, we compare data from allozyme-locus electrophoresis and mitochondrial DNA (mtDNA) restriction fragment length polymorphism (RFLP) analyses of bay scallops from shallow (<5 m) Gulf of Mexico (hereafter, Gulf) waters off Florida with empirical data or detailed models for seagrass locations and expanses, current patterns, tropical cyclone (tropical storm and hurricane) pathways, red tide (the toxic dinoflagellate *Karenia brevis* Davis) extents and intensities, and rainfall amounts (together, environmental factors) and with empirical data for postsettlement juvenile (spat) and adult bay scallop abundances (biological factors), all available at the same geographical and temporal scales as our population genetics data.

Because they are essentially annual animals (Sastry 1965, Barber & Blake 1983), Florida Gulf bay scallops are ideal for studying spatial and temporal effects of external forces on the connectivity of a marine organism with pelagic larval dispersal. Connections between population genetic structure and external influences are not complicated by overlapping generations. Estimates of gene flow between populations should reflect the combined effects of external factors on the cumulative survival, transport, and reproductive success of individuals within and among subpopulations on an annual basis (Botsford et al. 2009), overlain on a background of genetic diversity framed by longer term ecological and evolutionary processes. This approach is important for understanding the sources of variation in population connectivity over time frames relevant to conservation or fishery management, particularly for species that are managed spatially (Gerber et al. 2003, White et al. 2010b), as are Florida Gulf bay scallops.

Our study complements Bert et al. (2011; in which this study was cited as Bert et al. in press) and constitutes the only long-term, comprehensive record of Florida Gulf bay scallop population genetics before any consequential stock enhancement, which has been conducted since 1998 on many local populations (hereafter, subpopulations) we sampled. Thus, this study can serve as baseline information for future examinations of the genetic diversity and population structure of Florida Gulf bay scallops, including assessments of possible genetic alterations imposed by stock enhancement efforts (see Bert et al. 2007).

Background on Florida Gulf Bay Scallops

Most Florida Gulf bay scallops live less than 2 y and spawn only one reproductive season (Loosanoff & Davis 1963, Sastry 1965, Castagna & Duggins 1971, Barber & Blake 1983). Bay scallops are hermaphroditic. Each individual spawns eggs and sperm in separate pulses (Arnold et al. 2005a, Arnold et al. 2005b), and self-fertilization can result in offspring production (Wilbur 1995). Florida Gulf bay scallops aggregate during the spawning season (Marelli et al. 1999) and aggregations spawn more or less simultaneously (Levitán & Petersen 1995, Arnold et al. 1998a, Marelli et al. 1999). Gametes are viable for only minutes to hours (Levitán 1995). Bay scallops have threshold densities below which spawning and recruitment do not support annual population renewal (Allee effect) (Greenawalt-Boswell et al. 2007).

The principal spawning season extends from September or October through December or January (Geiger et al. 2010). Peak spawning is most common in October, but can occur during any of those months or may be spread over several months (Arnold et al. 1997). Secondary local spawning bursts may occur in spring or early summer, and very low levels of spawning may occur during other months, but these occurrences yield little successful spat recruitment (Arnold et al. 1998a, Arnold et al. 2009, Geiger et al. 2010; Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute (FWRI), unpubl. data). Because spawning season is protracted and duration of the larval phase is 6–14 days (Sastry 1961, Sastry 1965, Arnold et al. 2005b), spawning and recruitment seasons overlap.

Bay scallop preference for *Thalassia testudinum* König/*Syringodium filiforme* Kütz (hereafter, seagrass) beds as benthic habitat is strong. Presettlement larvae must attach to seagrass blades to metamorphose into spat (Thayer & Stuart 1974, Barber & Blake 1983, Pohle et al. 1991), which remain attached to the blades until about 20-mm in shell height (Geiger et al. 2010). Juveniles and adults move about but travel only short distances (Barber & Blake 1983), remaining within seagrass meadows for the duration of their lives. High rainfall causes flooding that kills bay scallops by reducing salinity and increasing turbidity to intolerable levels (Tettelbach & Rhodes 1981, Leverone 1993); eggs and larvae are more sensitive to these environmental conditions than are juveniles and adults (Tettelbach & Rhodes 1981). Toxic dinoflagellate outbreaks (blooms) such as red tide kill bay scallops in any life phase (Marko & Barr 2007) through ingestion (Peterson & Summerson 1992) or by rendering large areas of water near seafloors hypoxic for extended time periods (Landsberg 2002). Bay scallop abundances can take years to recover from severe blooms (Peterson & Summerson 1992, Leverone et al. 2010). In the

Florida Gulf, *Karenia brevis* forms blooms essentially annually (Flaherty & Landsberg 2011).

Bay scallops are distributed patchily in the Florida Gulf (Marelli & Arnold 2001, Arnold et al. 2005a). Fluctuations in abundance have long characterized Florida Gulf bay scallop subpopulations (Arnold et al. 2005a); but, many historically abundant subpopulations, particularly those from Tampa Bay southward (Fig. 1), have declined enduringly in abundance and have become at least intermittently extinct (Arnold et al. 2005a, Leverone et al. 2006) as a result of habitat degradation (Leverone et al. 2006), red tide blooms (Arnold et al. 1998b), and overfishing (Marelli & Arnold 2001). Statewide, abundance had generally declined to a tiny fraction of its original size by the late 1980s (Geiger et al. 2006). By 1994, only the Deadman Bay and St. Joseph Bay (Fig. 1) subpopulations attained healthy abundance levels (≥ 25 scallops/600 m² (Arnold et al. 2005a, Greenawalt-Boswell et al. 2007)), but only during some years (Arnold et al. 1998a).

Florida Gulf bay scallops supported robust commercial and recreational fisheries during the 1950s (Murdock 1955, Rosen 1959). The abundance declines prompted the initiation of fishery management in 1985. The commercial fishery was closed statewide in 1994. In 1995, all recreational harvest was eliminated from the Suwannee River southward and from the mouth of St. Joseph Bay westward (Fig. 1) (Arnold et al. 2005a, Geiger et al. 2006). Between the Suwannee River and St. Joseph Bay, recreational harvest was permitted but restricted (very short harvest season, end of July through beginning of August; daily limits on amount taken per boat,

but no limit on the number of boats that could be deployed (Arnold et al. 1998a)).

Before 1998, attempts to supplement Florida Gulf bay scallop stocks were limited, sporadic (Arnold et al. 1999, Arnold 2001, Arnold et al. 2005a, Leverone et al. 2006, Arnold 2008, Leverone et al. 2010), and focused principally on Tampa Bay (Lu & Blake 1997) (Fig. 1). Low abundances after the recreational harvests from 1994 through 1996 prompted initiation of the first major stock enhancement effort during fall 1998—the stocking of spawner restoration stocks in Homosassa Bay, Anclote Estuary, and Tampa Bay (Arnold et al. 2005a, Wilbur et al. 2005). The first recruits from that stocking would have appeared in 1999.

Based on distributional patterns, prehistory and contemporary morphological variation, and spat recruitment patterns of Florida Gulf bay scallops, Arnold and colleagues (Marelli et al. 1997a, Arnold et al. 1998a, Marelli & Arnold 2001, Arnold et al. 2005a, Arnold 2008) postulated that Florida Gulf bay scallops were distributed as a series of disjunct subpopulations that together formed a metapopulation. Arnold et al. (1998a) postulated that the stable, high-density Steinhatchee subpopulation (Fig. 1) might be the main provider of migrants to other subpopulations (i.e., a source subpopulation, or source). Bert et al. (2011) showed that the Florida Gulf bay scallop population genetic structure differed from that of western Atlantic Ocean bay scallops and that bay scallops from Florida Bay (Fig. 1) were *Argopecten irradians* ssp. *concentricus* and not *Argopecten irradians* ssp. *taylorae*. They also described in detail previous population genetics studies that included samples of

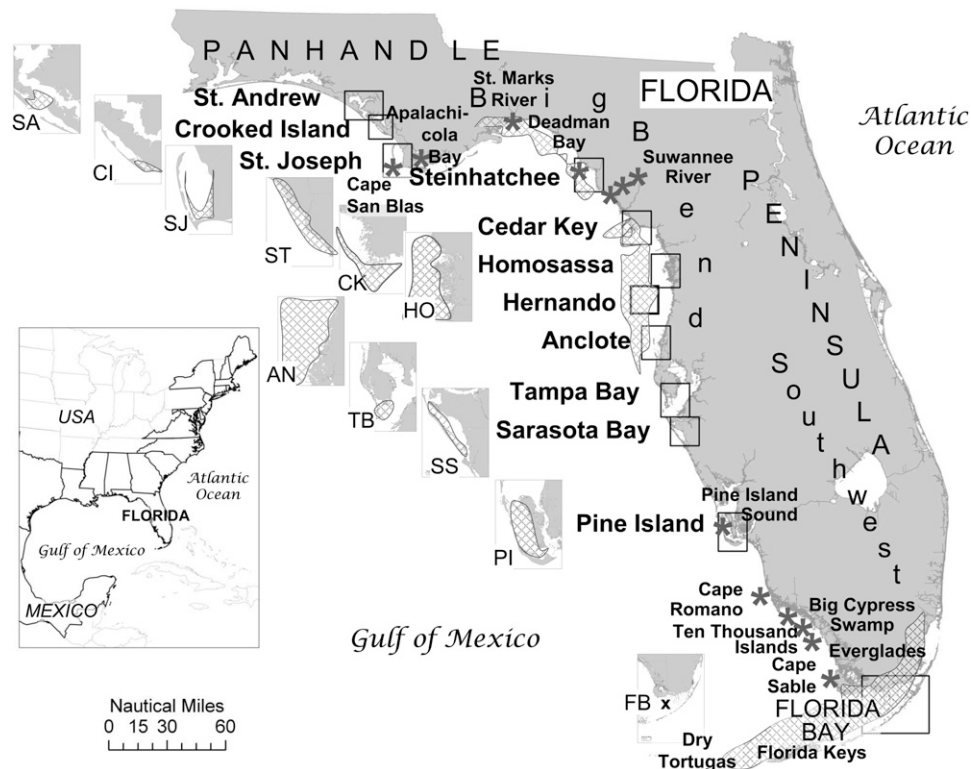


Figure 1. Bay scallop collecting locations. Large inset, location of Florida in eastern United States. Small insets, details of sampling locations and corresponding collection abbreviations (see Table 1; no inset for Hernando (HE)); hatched areas, approximate extent of sampled seagrass beds. Asterisks, locations of labeled features; x in FB inset, approximate location of Rabbit Key Basin.

Florida Gulf bay scallops (Blake & Graves 1995, Wilbur 1995, Marelli et al. 1997a, Marelli et al. 1997b, Bologna et al. 2001, Hemond & Wilbur 2011), including a genetic assessment of stock enhancement success (Wilbur et al. 2005). Based on comparisons of the relatively genetically distant Atlantic bay scallop (*Argopecten irradians* ssp. *irradians*) with only a few Florida Gulf bay scallop collections, those researchers concluded that Florida Gulf bay scallops, except those in Florida Bay, formed a single, more or less panmictic population. Our study was conducted to elucidate more fully the population genetic structure of Florida Gulf bay scallops and to test genetically the idea of Arnold and colleagues that those bay scallops formed a metapopulation.

MATERIALS AND METHODS

The Study Area

The Florida Gulf includes waters off the south-facing coast of the Florida panhandle (hereafter, panhandle) and the west-facing coast of the peninsula, as well as Florida Bay (Fig. 1). The seafloor off peninsular Florida slowly slopes down to 200 m (1 m depth/1–2.5 km distance (Li & Weisberg 1999)). The expansive shelf buffers heavy wave action in shallow water; only intense winter cold fronts and summer tropical cyclones result in waves more than 2 m high nearshore. The nearshore seafloor is a highly fragmented patchwork of seagrass flats, low rock outcrops, and bare sand. Interspersed along the coast are bays and rivers with restricted exchange with open water; large embayments, many times behind barrier islands, with freshwater marshes or estuarine mangrove swamps grading into seagrass flats or mixed seagrass/rock/sand; and sandy beaches facing open water. West of Cape San Blas (CSB), the seafloor slopes more rapidly and wave action is stronger. Relatively quiet waters are restricted to bays—which have a patchy seafloor of interspersed mud, sand, rocky outcrop, and seagrasses—behind barrier islands with few channels to open water. Florida Bay is composed of numerous shallow basins (most <1–3 m deep) connected by sparsely distributed channels through a network of sand bars, calcareous mud/sand banks, and small islands that, together, separate the basins. The network reduces tidal range, currents, and extreme wave action. Adjacent basins can have very different benthic habitats and ecosystems.

Field and Laboratory

Between 1995 and 1998, FWRI staff collected bay scallops during scuba diving surveys conducted in June of each year, before the annual harvest season. They collected the first ± 50 individuals encountered; or, if density was low, they searched or trawled, as time allowed, attempting to obtain at least 15 individuals. Multiple annual collections were made during the 4 y at some locations (hereafter, 2-y, 3-y, or 4-y subpopulations). Collections were not made at all locations in all years principally because bay scallops could not be found. Scallop samples were returned to the laboratory where, from each individual, a sample of adductor muscle, gill, and digestive gland was excised. The samples were wrapped, frozen immediately in liquid nitrogen, and stored at -80°C .

For allozyme electrophoresis, small pieces of the three tissue types were combined and homogenized in 0.1 M Tris-EDTA, pH 7.0; the supernatant was used as the enzyme source. Horizontal

starch gel electrophoresis was conducted according to Selander et al. (1971). The 4 buffer systems and the staining procedures used to resolve and visualize the 18 loci assayed are listed in Bert et al. (2011, Table 2). All gels were scored by at least 2 researchers. Alleles were identified by their mobility relative to that of the most common allele (designated as 100); the numerical code was translated into an alpha code (e.g., 100 = A) for some statistical analyses.

For the mtDNA analysis, various constraints required that we omit samples from 3 low-density subpopulations (CI, CK, HE). The mtDNA analytical techniques and solution formulas used are detailed in Seyoum et al. (2003) and Bert et al. (2011). Briefly, we assayed the restriction fragment patterns produced by digesting an 833-bp fragment that included a portion of the mtDNA 12s ribosomal subunit and the NADH dehydrogenase 1 coding region with 9 restriction enzymes: *Alu* I, *Ban* II, *Bgl* II, *Bsi*HKA I, *Hin*F I, *Rsa* I, *Scr*F I, *Tsp* 509 I, and *Taq*^α I. Entire digests were loaded onto low-melting point agarose gels and were electrophoresed. Fragment patterns were visualized by ethidium bromide staining and were photographed under UV light. Fragment sizes were determined from migration distances relative to known standards.

Statistical Analysis

Many statistical analyses were performed at both the collection level (allozyme, $n = 31$; mtDNA, $n = 21$) and the subpopulation level (all collections combined from a single location: allozyme, $n = 12$; mtDNA, $n = 9$; Table 1). Throughout this article, sample designations for collection-level analyses include both the location and year of collection (e.g., SA95) and designations for subpopulation-level analyses include only the location abbreviation (e.g., SA). When only 1 sample was collected from a location, that sample served in both collection-level (e.g., FB98) and population-level (e.g., FB) analyses.

Despite the possibility of overcorrecting for the possibility of type I statistical errors (Moran 2003, Nakagawa 2004), unless otherwise noted, significance levels of multiple tests of a single hypothesis were adjusted using the sequential Bonferroni technique (Rice 1989), which is designed to avoid type I errors. When many tests of a single hypothesis were conducted, we tempered the possibility of overcorrection for spurious significance by adjusting α levels using the number of significant tests rather than the total number of tests for the sequential Bonferroni adjustment, set significance at a higher level, or simply reported all significance levels (i.e., used a commonsense approach (Cabin & Mitchell 2000)).

Allozyme Loci

We originally used BIOSYS-1 (Swofford & Selander 1981) to calculate allele and genotype frequencies. We used GENEPOP (version 4.2 (Rousset 2008)) to calculate collection- and subpopulation-level statistics for all loci. All statistical tests were conducted on loci only in which the frequency of the most common allele was ≤ 0.99 . To examine the spatial and temporal nature of genetic diversity, we tested each locus for homogeneity of allele and genotype frequencies between multiple collections from each location, and for homogeneity of allele frequencies among subpopulations using the exact probability test. For every collection, we compared observed genotype frequencies for each locus with Hardy-Weinberg (H-W) equilibrium genotype frequency expectations using the Markov chain

TABLE 1.
Summary information for Florida Gulf bay scallop samples used to estimate population genetic structure.

Subpopulation, habitat	Collection/technique									
	1995		1996		1997		1998		Total	
	E	R	E	R	E	R	E	R	E	R
Saint Andrew Bay (SA), bay	30	—	46	—	28	—	25	25	129	25
Crooked Island Sound (CI), bay	42	—	22	—	—	—	—	—	64	—
Saint Joseph Bay (SJ), bay	30	15	45	15	49	14	30	25	154	69
Steinhatchee (ST) (Deadman Bay), open water	45	15	54	15	45	15	30	24	174	69
Cedar Key (CK), open water near islands	—	—	—	—	53	—	—	—	53	—
Homosassa Bay (HO), shallow, open water	47	15	53	14	50	18	30	40	180	87
Hernando County (HE), shallow, open water	—	—	—	—	30	—	11	—	41	—
Anclote Estuary (AN), high-salinity estuary between barrier islands and mainland	—	—	34	—	50	—	29	41	113	41
Tampa Bay (TB), bay	—	—	—	—	57	23	—	—	57	23
Sarasota Bay (SS), bay	—	—	—	—	—	—	35	24	35	24
Pine Island Sound (PI), bay	51	15	16	12	47	14	35	25	149	66
Florida Bay (FB; Rabbit Key Basin), semiencloded, high-salinity basin	—	—	—	—	—	—	35	21	35	21
Total	245	60	270	60	409	84	225	225	1,149	425

Subpopulation (all collections from a single collecting location) abbreviations in parentheses. mtDNA RFLP analyses performed on subsets of same individuals used for allozyme electrophoresis (E). Collecting locations shown in Figure 1. —, no analysis performed.

method. We also compared the percentage of loci deviating from H-W equilibrium among collections, subpopulations, and years (pooling collections within years) using the $R \times C$ G-test followed by the Simultaneous Test Procedure for frequencies (hereafter, collectively, the $R \times C$ test; BIOMstat, version 3 (Sokal & Rohlf 1995).

We calculated average direct-count heterozygosity per locus (\bar{H}_o), the percentage of polymorphic loci at the P_{95} and P_{99} levels (frequency of most common allele ≤ 0.95 or 0.99 , respectively), and mean number of alleles per locus (\bar{n}_a) at both the collection and subpopulation levels, and tested for correlations between those variables and sample size at both levels. We examined geographical and temporal variation in these genetic diversity measures by testing for correlations between the measures and latitude, by examining the values for collections within locations for directional pattern shifts among years when possible, and by testing for significant differences among collections taken in different years and among all collections and subpopulations. For all these tests, we used the Kruskal-Wallis test to establish significance followed by the Ryan-Einot-Gabriel-Welsch Multiple Range test (hereafter, collectively, the K-W test) to locate significant differences (Statistical Analysis System, version 9.1; SAS Institute Inc.).

We also used GENEPOP to test F_{IS} (inbreeding coefficient) values for significant differences among collections taken in different years, among all collections, and among subpopulations composed of two or more collections. We examined collections for the possibility of genetic bottlenecking using the BOTTLENECK program (Cornuet & Luikart 1996).

We investigated temporal and spatial population genetic associations by first testing allele frequencies collectively over all loci for homogeneity between each subpopulation pair (exact probability test). We calculated pairwise Nei's genetic distances (Nei's D (Nei 1972)) and pairwise Θ_{ST} values (Wright's F_{ST} analogue (Weir & Cockerham 1984)) over all loci (according to Slatkin (1993), in GENEPOP) between collections and between subpopulations. We used subpopulation Θ_{ST} values to generate

a global estimate of Θ_{ST} , to estimate the average gene flow according to Wright's island model (Wright 1943), and to test the statistical significance of Slatkin's (1993) isolation-by-distance (IBD; geographical distance was estimated by following major coastline contours using the ruler tool in Google Earth) among all subpopulations and among collections taken each year.

To further investigate population genetic structures, we used two methods to analyze temporal and geographical variation. First, STRUCTURE (Bayesian method, version 2.3.2 (Pritchard et al. 2000, Hubisz et al. 2009)) was used to test for temporal (among-year) differences in subpopulations, combining the data for collections within each year, and in collections within each subpopulation (for subpopulations with multiyear collections) and to test for geographical differences among subpopulations and collections (for both, all years combined), and for collections taken within each year. In STRUCTURE, we ran the Monte Carlo Markov Chain for 20^5 iterations after a burn-in period of 10^5 iterations for a range of number of populations ($1 - n$, where n is the number of collections or subpopulations in the analysis) using the default correlated allele frequencies and admixture options. The most likely number of populations (K) was estimated using the method of Evanno et al. (2005). Second, AMOVAs (ARLEQUIN, version 3.6 (Excoffier & Lischer 2011)) were conducted prior to tests to distinguish statistically different groups of pairwise genetic distance values (both Nei's D and Θ_{ST}). Unstructured AMOVAs were performed on the same data sets as those used for the STRUCTURE analyses. When an AMOVA revealed significant differences in frequencies among basic elements (years, collections, or subpopulations), we used the K-W test or Wilcoxon's 2-sample test (Sokal & Rohlf 1995), as appropriate, to locate significant differences among mean pairwise genetic distances. We tested for among-year differences in mean genetic distances among all collections taken within each year and among all collections within each year for each multiyear subpopulation (i.e., subpopulation represented by 2, 3, or

4 collections). To reveal geographical patterns, we conducted a hierarchical analysis in which we first tested for significant differences among means of the pairwise genetic distances for collections and, separately, for subpopulations, assuming no population structure. We then tested for higher level population structure among groups of collections or subpopulations as defined by the initial no-structure tests. For all calculations of mean pairwise genetic distances, we set individual negative pairwise genetic distances to 0 and transformed the data for the tests that included 0 values using $\log(n+1)$. Last, we tested for significant departure of each pairwise Θ_{ST} value from pairwise $\Theta_{ST} = 0$ (ARLEQUIN).

A complication of the second method was that the means calculated for some K-W tests involving pairwise genetic distances were not independent because some pairwise distances were used to calculate more than 1 mean within a particular analysis. However, it was obvious that some collections were sufficiently genetically differentiated from, or similar to, most or all others to drive the pairwise genetic relationships that included those collections, and that a multifaceted pattern of connectivity was present. Therefore, we opted to conduct the analyses because the effects of single populations or population clusters can be lost in general IBD analyses (Bossart & Prowell 1998), particularly when population genetic relationships are not linear geographically, as were ours. We used this approach also because it capitalized on many advantageous features associated with pairwise genetic distances based on statistics related to F_{ST} (see also Neigel (1997, 2002)), such as Nei's D and Θ_{ST} . First, the nonrandom distribution of small genetic differences is more convincing than a single tablewide genetic distance value calculated for an entire data set (Palumbi 2003). Second, underlying properties of dispersal can be revealed because genetic distance is frequently correlated with dispersal ability (Waples 1987, Bohonak 1999) and because even small pairwise distances indicate very little gene flow if they are significant (Palumbi & Warner 2002, Palumbi 2003), particularly if they are corroborated by environmental or biological data (Hellberg 2006, Selkoe et al. 2010, White et al. 2010b). Third, the relative differences among genetic distances speak more about population genetic structure than the absolute magnitude of those values (David et al. 1997, White et al. 2010b). Fourth, F_{ST} is relatively independent of the mutation process, so different genes in the same species may be compared (Pannell & Charlesworth 2000). Fifth, and last, population fluctuations can increase pairwise genetic distance estimates (McCauley et al. 1995, Pannell 2003), augmenting their value for interpreting population dynamics. The limitations of using pairwise genetic distances are that individual pairwise values may not be reliable; values are based on the assumption that the overall population is in equilibrium (Hellberg 2006); values can be affected by levels of variation within, as well as between, populations (Charlesworth 1998); and values can be inflated by anything that reduces within-population variation (Riginos & Nachman 2001). Thus, individual estimates of pairwise genetic distances may not be exact, but overall patterns that have statistical significance can provide insights into population boundaries.

While conducting the analyses that grouped pairwise genetic distance means, we noticed that means of collection-level pairwise genetic distances and variation around the means were possibly related. To test this idea, we performed correlations on the mean genetic distances versus their SDs using 4-y collection

pairs only, to eliminate any potential bias resulting from overall interannual differences in pairwise genetic distances.

Mitochondrial DNA

We calculated haplotype frequencies using REAP (version 4 (McElroy et al. 1992)) and used both Monte Carlo simulation (in REAP) and the $R \times C$ test to search for significant differences in haplotype frequencies among collections and subpopulations. Haplotypes other than the common haplotype were combined for the $R \times C$ tests. We calculated haplotype diversity (h) and nucleotide diversity (π) for each collection and subpopulation, and calculated pairwise π (Nei 1987) for each collection and subpopulation pair (REAP). The h and π values were tested for correlation with sample size at both collection and subpopulation levels; and 4-y subpopulations were tested for significant differences in mean h and π among years. Both diversity measures were tested for significant outliers within years using Dixon's method (Sokal & Rohlf 1995).

We calculated pairwise genetic distances (Φ_{ST} (Cockerham 1969, Cockerham 1973)) and nucleotide divergences (d (Nei 1987); REAP) and explored the pattern of mtDNA diversity by testing the Φ_{ST} values for significance (exact test, ARLEQUIN, version 2.0 (Schneider et al. 2000)) and comparing statistically the means of appropriate combinations of pairwise π values and pairwise d values for significant differences within and between years, collections, and subpopulations using the K-W test, similar to our approach for allozyme-locus pairwise genetic distances. We analyzed IBD by testing the geographical distances of (separately) all, within-year, and 4-y subpopulation pairwise combinations for correlation with the analogous linearized pairwise Φ_{ST} values (Slatkin 1993), and we tested for increasing genetic distance over time by substituting the number of years between collection pairs as the distance measure (all collection pairs and only 4-y collection pairs; Mantel test in ARLEQUIN). We also conducted AMOVAs (ARLEQUIN) on the same sets of data as those used for the allozyme-locus AMOVAs, but using pairwise Φ_{ST} values.

External Factors

We mapped the location and extent of the seagrass beds according to Yarbrow and Carlson (2013), and formed consensus maps of seasonal and unusual water currents based on the extensive oceanographic information available for the West Florida Shelf (see Results, External Factors). For each year, we constructed maps of the tracks of tropical cyclones, obtained from the U.S. National Oceanographic and Atmospheric Administration (NOAA) website (<http://www.nhc.noaa.gov/pastall.shtml>) and noted their timing; mapped the distribution and intensity of red tide blooms (drawn from direct cell density counts taken at precise locations during specific days; FWRI, unpubl. data), and documented their timing; and graphed the abundances of bay scallop adults (mean number/600 m²; n usually 20/600-m² transect per collection) and spat (mean number per collector per 42-day deployment period; range, 12–27 collectors per location) using data drawn from FWRI (unpubl. data) and annual reports (Arnold 1994, Arnold et al. 1995, Arnold et al. 1996, Arnold et al. 1997, Arnold et al. 1998b, Arnold et al. 1999).

Amounts of monthly rainfall were compiled from records for Florida maintained by NOAA. The U.S. National Oceanographic

and Atmospheric Administration partitions Florida into 7 geographical rainfall divisions. To categorize rainfall amounts, for each division we calculated the average precipitation (\pm SD) separately for each month using the monthly amounts from 1994 through 1998. Then, separately for each division-month combination, we classified rainfall amounts as follows: very wet, $\geq(\text{average} + \text{SD}) \times 1.25$; wet, $\geq(\text{average} + \text{SD})$ and $<[(\text{average} + \text{SD}) \times 1.25]$; average-wet, $\geq\text{average}$ and $<(\text{average} + \text{SD})$; average-dry, $\geq(\text{average} - \text{SD})$ and $<\text{average}$; dry, $\geq[(\text{average} - \text{SD}) \times 0.75]$ and $<(\text{average} - \text{SD})$; very dry, $<[(\text{average} - \text{SD}) \times 0.75]$. Because long-term average rainfall varies among months and divisions, a specific rainfall amount may be classified as, for example, dry for a given month/year/division but average-wet for a different month/year/division.

RESULTS

Genetic Variation

Allozyme-locus allele frequencies for the 10 polymorphic loci are given for bay scallop collections and subpopulations in Table 2. The frequency of the most common allele was ≥ 0.99 in two aspartate aminotransferase and two malic dehydrogenase loci, general protein, and in the hexonate dehydrogenase, isocitrate dehydrogenase, and superoxide dismutase loci. No geographical patterns in levels of polymorphism were discerned. Only 3 alleles were private alleles.

Within subpopulations, numerous collections varied significantly between years in allele frequencies, and five collections varied between years in genotype frequencies. The allelic variation was concentrated in panhandle collections; the genotypic variation was in panhandle collections only (both principally SJ). Most allelic and genotypic variation was at specific loci (e.g., *LAP*). All polymorphic loci except *PGD* differed significantly in allele frequencies among subpopulations.

Numerous loci did not conform to H-W equilibrium (Table 2), all but one resulting from heterozygote deficits. The percentage of loci deviating from H-W equilibrium in 1998 collections was significantly lower than the percentages in collections from 1996 or 1997 (Table 3A). Collections from Steinhatchee and St. Joseph had the greatest percentages of loci out of H-W equilibrium (Table 3B). Overall, the mean percentage of loci out of H-W equilibrium for 3-y- and 4-y subpopulations (70%; SD, 9%) was significantly greater than for 1-y and 2-y subpopulations (28%; SD, 12%; *t*-test for small sample sizes, $P < 0.001$ (Sokal & Rohlf 1995)).

Few measures of genetic variability for the Florida Gulf collections or subpopulations were related to sample size, geography, or time. At the collection level, \bar{n}_a correlated with sample size ($P < 0.0001$, $r = 0.73$). At the subpopulation level, \bar{H}_o correlated with sample size, year (both positively), and latitude (negatively) (P range, 0.05–0.001). The latitudinal and temporal correlations reflected the relatively high level of allozyme allelic variability in southwestern Florida 1998 collections (Table 2). Neither P_{95} nor P_{99} were correlated with any variable at either the collection level or the subpopulation level.

Inbreeding levels varied significantly among years ($P = 0.025$), collections ($P < 0.0001$), and subpopulations ($P < 0.001$). The level of inbreeding was significantly greater in collections from 1996 ($F_{IS} = 0.28$) than in collections from 1998 ($F_{IS} = 0.18$). Of all

collections, PI96 had, by far, the greatest F_{IS} value (0.40). Inbreeding levels also differed significantly between many collection pairs at very high probability levels.

The BOTTLENECK model assumes that populations are in H-W equilibrium. Because heterozygote deficits are common in our data, and other assumptions of the BOTTLENECK model may have been violated (e.g., Florida Gulf bay scallops show evidence of a recent population expansion (Bert et al. 2011, Figure 3)), results of the BOTTLENECK test were aberrant (e.g., T_2 was significant for many collections, but because of heterozygote deficits and not heterozygote excesses, as the model predicts). Therefore, we relied on other characteristics typically associated with bottlenecked populations to denote bottlenecks: comparatively low levels of polymorphism and numbers of alleles (Nei et al. 1975, Allendorf et al. 2008), and unexpectedly high pairwise genetic distances (Hellberg 2006). One collection, SJ96, had the requisite heterozygote excess (Wilcoxon's test, $P = 0.02$); PI96 and HE98 exhibited low P_{99} and \bar{n}_a ; SJ98 had low P_{95} , P_{99} , and \bar{n}_a ; and, although not significantly different than H_o values of other 1998 collections, H_o was notably high in FB98. In FB98, less common alleles often had greater frequencies than in other collections (e.g., *AAP-2D*, *PGM_F*), and multiple alleles rare in other collections were missing (Table 2).

The bay scallop samples yielded 43 mtDNA haplotypes (H). The estimated restriction fragment compositions for those haplotypes are presented in Bert et al. (2011, Table 7). Haplotype frequencies are listed here in Table 4.

Collection and subpopulation h and π values are provided in Table 5. Neither h nor π correlated with sample size at either the collection level or the subpopulation level, nor did mean h or mean π differ significantly among years for the 4-y subpopulations. Mitochondrial DNA diversity was notably low in 1995 collections, greater in ST than in other collections in 1995 (significantly) and 1996, comparatively high in HO and TB (significant for π) in 1997, and greater in SJ and PI (significantly for h) but significantly low (both h and π) in FB in 1998.

Population Genetic Structure

Allozyme Loci

Detecting Structure. Collectively over all loci, allele frequencies differed significantly between 89% of the subpopulation pairs (Table 6). At the tablewide level, TB, SS, and FB differed significantly from all or nearly all other subpopulations, whereas HE differed significantly from SS and FB only. Centrally located subpopulations were notably more similar to each other than to other subpopulations, as were panhandle subpopulations.

Although the estimated overall Θ_{ST} value for all subpopulations was small (0.015), at the collection level, pairwise Nei's D values varied more than 30-fold (range, 0.000–0.032) and pairwise Θ_{ST} values varied more than 70-fold (range, 0.000–0.071; Table 7A). The overall gene flow estimate was high (effectively, 6 individuals per generation), in part because only polymorphic loci were used (Smith et al. 1997); but gene flow was reduced significantly with increasing geographical distance ($y = -0.43x + 2.46$, $r^2 = 0.12$, $P = 0.006$). However, the proportion of the relationship explained was small (12%), and the only year in which gene flow and geographical distance were inversely related was 1997 ($y = -0.25x + 3.05$, $r^2 = 0.21$, $P < 0.0001$).

TABLE 3.

Temporal and spatial differences in percentage of allozyme loci deviating from Hardy-Weinberg genotype frequency equilibrium expectations.

(A) Differences among years.

Factor	Year				P value
	1998	1995	1996	1997	
Collections out of H-W equilibrium (%) ^{*†}	12	20	24	34	<0.01
Total no. H-W equilibrium tests	90	60	70	90	

(B) Differences among subpopulations.

Factor	Subpopulation												P value
	FB	SS	HE	TB	CK	CI	PI	AN	HO	SA	ST	SJ	
Loci out of H-W equilibrium (%) [†]	20	20	20	30	30	50	60	60	70	70	80	80	<0.01
No. of collections in subpopulation	1	1	2	1	1	2	4	3	4	4	4	4	

* Number of loci out of Hardy-Weinberg genotype frequency equilibrium in each collection provided in Table 2.

[†] (A, B) Underlined groups of percentages are statistically similar. (B) Only statistical groupings that include the highest or lowest percentages are shown. Subpopulations are defined in Table 1. P, probability of homogeneity of percentages.

No STRUCTURE analysis divided the collections temporally or spatially into more than one population. STRUCTURE was designed to sort individuals into populations that conform to H-W equilibrium and to exhibit minimum linkage disequilibrium. The many departures from H-W equilibrium (Table 2) and close genetic relationships (small pairwise genetic distances) of Florida Gulf bay scallop subpopulations likely reduced STRUCTURE's statistical power (Kalinowski (2011) and references therein). Analyses of molecular variance indicated that variation attributable to differences among subpopulations was significant in 1998 ($P = 0.000$, 1.75% of all variation) and nearly significant overall ($P = 0.056$, 0.22% of all variation). These results and the nonrandom geographical patterns of variation in homogeneity of pairwise allele frequencies (Table 6) led us to speculate that significant but complex temporal and spatial population genetic structure existed in Florida Gulf bay scallops. As described in Materials and Methods, and shown in Tables 7 and 8, we used allozyme-locus pairwise genetic distances extensively to define this structure.

Building the Structure. The allozyme-locus pairwise genetic distances varied notably among collections from different years and locations, and between potential parent-offspring pairs (Table 7A). The 1998 bay scallop cohort had a markedly different population genetic structure than cohorts of other years in that many pairwise genetic distances were relatively large. The sequential-year 1997/1998 pairwise Θ_{ST} value was significant ($P = 0.003$), and the mean pairwise genetic distances for pairs that included 1998 collections were significantly greater than the means for pairs with collections from other years (Table 8A1). The high mean collection-level pairwise genetic distances for 1998 were a result of significantly high means for collection pairs from specific subpopulations (SA, SJ, HE; Table 8A2, analyses 5, 6, 9, 10, 15, and 16). Many pairwise genetic distances that included 1998 collections from those subpopulations were among

the highest (Table 7A). In contrast, 1995 was a year when all collections were genetically similar; the mean pairwise genetic distances of 1995 collections were low (Table 8A1).

Collections from ST and HO exhibited greater temporal and spatial genetic homogeneity than collections from other locations. The mean pairwise genetic distances with collections from ST to HO as pair members were low and genetically homogeneous among years (Table 8A2, analyses 11–14), whereas the means for collections from other subpopulations were not (Table 8A2, analyses 5–10 and 15–20). The average genetic distance of ST, HO, and AN parent-offspring pairs was significantly less than the average of pairs from other subpopulations (Table 7A; Wilcoxon's 2-sample test, $P < 0.05$ for both Nei's D and Θ_{ST}), and variation around the within-subpopulation ST- and HO-pair means was less than variation around the means with other pairs (Fig. 2). Most means of pairwise genetic distances that included a collection from either ST or HO were in the lower half of the ranges of means for both genetic distance measures (Table 8B1, analyses 21–24, bold print). At the subpopulation level, the mean pairwise genetic distances of pairs with ST and HO were among the lowest (Table 8B2, analyses 25 and 26, bold print)

The genetic stability of ST and HO through time, and their relatively close genetic relationship to each other and other subpopulations, led us to conclude that ST and HO formed a centralized source population (which we named Core; Table 7A). We then focused on defining the relationship between Core and other subpopulations. We reasoned that, if a subpopulation was part of Core, the mean pairwise genetic distance that included pairs with the collections from that subpopulation would not differ significantly from the means that included the collections from ST and HO; the mean distances would be similarly low. We first considered the remaining three 4-y subpopulations (Table 8C1, analyses 27 and 28). Nei's D indicated that the means of the pairwise genetic distances with collections

TABLE 4.
Haplotype frequencies for Florida Gulf bay scallops based on RFLP analysis.

H no.*	Designation†	Collection (subpopulation)																								
		SA 98	SJ 98	SJ 97	SJ 96	ST 96	ST 95	ST 94	ST 93	ST 92	ST 91	ST 90	HO 96	HO 97	HO 98	HO 98	HO 98	HO 98	HO 98	HO 98	HO 98	HO 98	HO 98	HO 98	HO 98	HO 98
1	AAAAA	25	15	15	15	15	15	25	70	15	14	18	40	87	41	23	24	15	12	9	10	13	25	66	21	
2	BABAA	1	1	1	2	1	1	1	3	1	1	1	1	1	1	1	1	1	2	1	1	1	1	3	1	
3	BAAA	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
6	BABBB	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
11	AAAAA	16	12	11	11	17	51	9	12	10	10	12	28	62	28	15	17	12	9	10	13	25	66	21		
13	AAAAA	2	1	1	2	1	3	1	1	1	1	1	1	2	3	1	1	1	1	1	1	1	1	1		
15	BABAA	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		
18	AAFA	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		
19	AAAA	1	1	1	1	3	3	1	3	1	1	1	1	1	1	1	3	1	1	1	1	1	1	1		
21	AAAA	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		
22	AADA	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		
23	AADAD	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		
24	AAAB	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		
25	AAAA	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		
26	BABAA	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		
27	ABDA	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		
28	AADA	1	1	1	1	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		
29	AAAA	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		
30	AAAA	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		
31	AAAA	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		
32	AAAA	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		
33	AACAA	1	1	1	1	1	2	1	1	1	1	1	1	3	1	1	1	1	1	1	1	1	1	1		
34	BAFA	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		
35	BAAAA	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		
36	AABAA	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		
37	AAAA	2	1	1	1	1	1	1	1	1	1	2	3	5	1	1	1	1	1	1	1	1	1	1		
38	AAEA	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		
39	AAAA	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		
40	AACA	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		
41	ABAA	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		
42	BABA	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		
43	AEAA	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		
44	AAFA	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		
45	BABA	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		
46	AADA	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		
47	DADA	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		
48	ACAA	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		
49	ADAA	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		

continued on next page

TABLE 4.
continued

H no.*	Designation†	Collection (subpopulation)																								
		SA 98	SJ 95	SJ 96	SJ 97	SJ 98	(SJ)	ST 95	ST 96	ST 97	ST 98	(ST)	HO 98	HO 97	HO 98	(HO)	AN 98	TB 97	SS 98	PI 95	PI 96	PI 97	PI 98	(PI)	FB98	
50	BBBAAAAA	—	—	—	—	—	—	—	—	—	1	(1)	—	—	—	—	—	—	—	—	—	—	—	—	—	—
51	BABABAAA	—	—	—	—	—	—	—	—	—	1	(1)	—	—	—	—	—	—	—	—	—	—	—	—	—	—
52	BABABAAAC	—	—	—	—	—	—	—	—	—	1	(1)	—	—	—	—	—	—	—	—	—	—	—	—	—	—
53	CAAAAAAAAA	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

* Haplotype numbers (H. no.) correspond with those in Bert et al. (2011, Table 8).

† Composite haplotype designations correspond to fragment patterns for restriction endonucleases in order listed in Bert et al. (2011, Table 7). Collection and subpopulation (in italics) abbreviations defined in Table 1.

from SA or SJ as pair members differed significantly from the mean of pairs with HO collections as pair members. Other previous analyses also demonstrated differences between SA and SJ versus ST and HO (e.g., Fig. 2, Tables 6 and 7A). Collectively, the evidence showed that SA and SJ were not members of Core. We therefore designated SA and SJ as a northern peripheral population and named it Panhandle.

To evaluate PI, we compared the mean pairwise genetic distance of collections including that subpopulation to the collection-level means of the combined Core subpopulations and of the combined Panhandle subpopulations (Table 8C1, analyses 29 and 30). Assignment of PI remained ambiguous. However, when the mean of the PI pairs was analyzed separately with the means of Core pairs and Panhandle pairs, the mean of PI pairs grouped with the mean for Panhandle pairs and not with the mean for Core pairs (Table 8C1, analyses 31–34). Based on this result and on PI generally higher collection-level pairwise genetic distances (Table 7A), we designated PI as a southern peripheral population and named it Southwest. Because the mean genetic distances of pairs with PI collections were nearly identical to the means of pairs with Panhandle collections, we grouped collection pairs with SA, SJ, or PI as pair members (collectively, peripheral collections) to categorize the remaining subpopulations.

The mean pairwise genetic distances of CI-collection/Core-collection pairs and CI-collection/peripheral-collection pairs grouped with the mean for peripheral collections and separately from the mean for Core collections (Table 8C1, analyses 35 and 36). That, and CI location within the same bay system as SA (Fig. 1), verified that CI was a component of Panhandle.

Because the 2 HE collections differed remarkably in their pairwise genetic distances with other collections (Tables 7A and 8B1, analyses 21 and 22), results for the comparisons of the HE-collection/Core-collection means or HE-collection/peripheral-collection means versus the means for Core collections or peripheral collections were ambiguous (Table 8C1, analyses 37–42). However, analyses equivalent to those conducted for PI pairs demonstrated that AN—HE’s neighbor to the south (Fig. 1)—was affiliated with Core subpopulations and not with peripheral subpopulations (together, SA, SJ, and PI; Table 8C1, analyses 43–48). In addition, the means and variances of AN–AN collection pairs (D , 0.003; Θ_{ST} , 0.004) were nearly as low as those of Core-population ST–ST pairs (Fig. 2); the means of AN collections paired with other collections were as low as those of Core collections paired with other collections (Table 8B1, analyses 21 and 22); and AN allele frequencies were generally similar to those of Core subpopulations (Table 6). Therefore, we included both HE and AN in Core.

Group membership tests performed for 1-y subpopulations (i.e., those represented by single collections) CK, TB, and SS were inconclusive. Those subpopulations were assigned to populations based on their geographical location and other analyses. Cedar Key bay scallops reside deep within Core, and nearly all CK/Core-member pairwise genetic distances were at or near 0 (Table 7A); thus, CK was included in Core. Tampa Bay and SS are outside the coastal region likely to receive recruits regularly from Core but are somewhat more likely to receive recruits from PI (as a result of regional currents, explained later); and both are extinct intermittently. Therefore, they belong with PI in Southwest. In contrast, the 1-y FB subpopulation clearly was genetically distinct from both Core

TABLE 5.

Mitochondrial DNA diversity estimators for Florida Gulf bay scallop collections and subpopulations (all years combined) based on RFLP analysis.

Year	DE	Collection								
		SA	SJ	ST	HO	AN	TB	SS	PI	FB
1995	<i>h</i>		0.36 L	0.63 H	0.36 L				0.36 L	
	π		0.90 L	1.27 A*	0.85 L				0.95 L	
1996	<i>h</i>		0.46 A	0.53 A	0.49 A				0.42 A	
	π		1.08 A	1.34 H	1.32 A				0.90 L	
1997	<i>h</i>		0.38 L	0.36 L	0.55 A		0.57 A		0.49 A	
	π		1.03 A	1.09 A	1.33 H		1.42 H		1.04 A	
1998 ²	<i>h</i>	0.58 A	0.52 A	0.48 A	0.51 A	0.53 A		0.49 A	0.72 H†	0.09 LL
	π	1.04 A	1.39 H	1.22 A	1.15 A	1.18 A		1.18 A	1.31 A	0.28 LL
Subpop.	<i>h</i>	0.58 A	0.46 A	0.51 A	0.47 A	0.53 A	0.57 A	0.49 A	0.62 H	0.09 LL
	π	1.04 A	0.94 L	1.15 A	0.92 L	1.18 A	1.42 H	1.18 A	1.61 H	0.28 LL

* This value was average compared with others in the table, but was a significant outlier among collections made that year.

† For each 1998 and subpopulation diversity estimator, FB98 was not included in calculations of row means for determining significant outliers. Collection/subpopulation (Subpop.) abbreviations are defined in Table 1; sample sizes are given in Table 4. DE, diversity estimator; *h*, haplotype diversity; π , nucleotide diversity ($\times 10^2$). Shaded values, significant outliers compared with other values in the same row (P range, 0.05 to < 0.005). Numbers in bold print, very high (H; value $>$ (row mean + SD)), low or very low (L or LL, respectively; value $<$ to \ll (row mean - SD)); numbers in normal print, average (A; (row mean - SD) $<$ value $<$ (row mean + SD)).

and peripheral collections. Many pairwise Θ_{ST} values with FB as a pair member were significant (Table 7A, B); mean genetic distances of FB pairs were significantly high (Table 8B, analyses 21, 22, 25, and 26); and mean genetic distances of FB paired with either Core or peripheral collections were uniquely greater than the means of either Core or peripheral collection pairs (Table 8C1, analyses 49–50).

Comparing mean collection- and subpopulation-level pairwise genetic distances among the 4 populations (Panhandle, SA-SJ; Core, ST-AN; Southwest, TB-PI; and unto itself, FB) exposed population-level relationships. The means of pairwise genetic distances between Core collections were significantly less than the means of other collections from other populations (Table 8C2, analyses 51–54), and the means of collection and subpopulation pairs with FB as a pair member were significantly greater than the means of other populations (Table 8C2, analyses 51, 52, 55, and 56). At the population level, FB was genetically more similar to peninsular populations, particularly Core, than to Panhandle (Table 8C2, analyses 55 and 56).

Last, pairwise genetic distances decreased through time; 1- or 2-y subpopulations were less genetically homogeneous with each other or with 3- and 4-year subpopulations than 3- or 4-y subpopulations were with each other (compare Tables 7B and 7C).

Mitochondrial DNA

The relatively high pairwise nucleotide diversity values for pairs with Core collections or peripheral collections in 1998 (Table 9A) reflected their individual relatively high π values (Table 5). Similarly, the low π value of FB98 resulted in low pairwise π values for FB98 pairs. Excluding pairs with FB98 (which were all $< 1\%$), the mean π value for pairs from 1998 was significantly greater than the mean for pairs from other years (all collections, $P < 0.001$; 4-y collections only, $P < 0.01$), principally because of significantly high means of pairs with SJ98 ($P < 0.0001$) and PI98 ($P < 0.02$). At the subpopulation level (Table 9B), pairs with the single-year SA and TB had the

highest π values, but only the mean of pairs with FB as a member differed significantly from the means with other subpopulations as pair members (FB pairs significantly low; $P < 0.001$). Among the 4-y subpopulations, within-subpopulation mean pairwise π values were significantly greater for ST collection pairs than for PI collection pairs ($P = 0.05$). Other than 1998, Core subpopulations generally had greater mtDNA diversity than peripheral subpopulations.

Thirteen of the 17 significant collection-level Φ_{ST} values had FB98 or SJ98 as a pair member (Table 9A). All PI-FB pairs were significant, and the distance between parental SJ95 and potential offspring SJ96 was highly significant. Within years, pairwise distances were significant for 1998 collections only (SA98/SJ98, SJ98/AN98, PI98/FB98). At the subpopulation level (Table 9B), 15 of the 17 positive Φ_{ST} values and the three significant values involved peripheral subpopulations. Few tests for significant differences among mean pairwise Φ_{ST} values were significant, and the pattern of significance was not clear (results not shown). Nonzero potential parent-offspring Φ_{ST} values occurred in all multiyear subpopulations except PI (Table 9A); some values were significantly high (SJ95/SJ96, ST96/ST97).

Nucleotide divergence was low. Most pairwise, collection-level d values were 0 or slightly negative (mean of all d , 0.0002; SD, 0.0002). The mean d for pairs with FB was 5 times to 10 times greater than the means of other pairs (data not shown). Of the 35 positive pairwise d values, 54% had FB as a pair member (mean d , 0.001; SD, 0.0005) and 34% had an ST collection (mean d , 0.0002; SD, 0.0002) as 1 or both pair members. The low nucleotide diversity of FB and high nucleotide diversity of ST contributed to the high frequencies of pairs with nonzero d values that included those collections.

Linearized pairwise Φ_{ST} values and geographical distances were related significantly for the 1997 collections ($r = -0.46$, $P = 0.02$) and 1998 collections ($r = -0.28$, $P = 0.05$). Geographical distance explained 21% of the variation in genetic distance in 1997 but only 8% in 1998. No tests for temporal IBD were significant. No AMOVA results were significant; variation

TABLE 6.

Significance levels for subpopulation-level pairwise tests for homogeneity of bay scallop allozyme-locus allele frequencies.

Spop.	SA	CI	SJ	ST	CK	HO	HE	AN	TB	SS	PI
CI	0	-	-	-	-	-	-	-	-	-	-
SJ	0.15	0.01	-	-	-	-	-	-	-	-	-
ST	***	***	***	-	-	-	-	-	-	-	-
CK	***	***	***	0.01	-	-	-	-	-	-	-
HO	***	***	***	***	0.14	-	-	-	-	-	-
HE	0.01	0.01	0.02	0.48	0.05	0.77	-	-	-	-	-
AN	***	***	***	0.05	0.09	0.01	0.25	-	-	-	-
TB	***	***	***	***	***	***	0.01	***	-	-	-
SS	***	***	***	***	***	***	***	***	***	-	-
PI	***	***	***	***	0.01	***	0.82	0.03	***	***	-
FB	***	***	***	***	***	***	***	***	***	***	***

Subpopulations (Spop.) are defined in Table 1. Shading reflects differences between subpopulation pairs: white, not significant; light gray, $0.01 < P \leq 0.05$ for pairwise comparison only; medium gray, $0.001 < P \leq 0.01$ for pairwise comparison only; dark gray, *** highly significant at $P \leq 0.001$ and significant tablewide at $P \leq 0.05$. Bars segregate geographically proximal subpopulation groups with comparatively similar allele frequencies over all allozyme loci.

within populations accounted for nearly 100% of the variation in all analyses.

Interannual Variation

The allozyme-locus pairwise genetic distances revealed notable interannual variation in genetic connectivity between collections and in the structure of that connectivity (Fig. 3, pairwise genetic distance matrices). In 1995, values for all pairwise genetic distances were small (Fig. 3A); and no pairwise Θ_{ST} values differed significantly from 0. In both 1996 and 1997, most collections were similar genetically, but collections from both extremes of the sampling range were more genetically differentiated from other collections, and the pattern of differentiation was reversed between years (Fig. 3B, C). In 1996, collections from the two northernmost adjacent subpopulations were significantly differentiated, and the collection from the southernmost subpopulation was differentiated from all collections north of HO. In 1997, collections from the two adjacent southernmost subpopulations were significantly differentiated, and the collection from the northernmost subpopulation was well differentiated from collections taken south of ST. The 1998 matrix of pairwise genetic distances (Fig. 3D) illustrates the patterns of significance that differentiated 1998 collections from others in Tables 8A and 8B (italicized). Pairwise genetic distances were, on average, much greater than in other years because collections from Panhandle were significantly differentiated from each other and from most other collections; and collections from some geographically proximal subpopulations were highly differentiated (notably, SA98/SJ98, HE98/AN98, SS98/FB98).

The geographical extent of the most genetically similar collection pairs (i.e., those considered to constitute Core) varied among years (Fig. 3A–D, boxes enclosing collections in pairwise genetic distance tables and dashed lines enclosing hatched

areas on Florida maps). In 1995, Core was discernible although all pairwise genetic distances were small. In 1996, Core extended from Panhandle (SJ) to AN, its broadest geographical extent. In 1997, Core was again located within the Big Bend but AN was excluded. In 1998, Core was small geographically (ST–HO) as a result of high levels of differentiation between HE98 and AN98 and other Core collections.

To gain a perspective on regional gene flow each year, we averaged the pairwise Θ_{ST} values within and between the defined populations. Genetic distances are inversely related to gene flow (Slatkin 1985) so relatively low genetic distance values connote relatively high gene flow (Fig. 3A–D, Florida maps: within-population gene flow represented by colored boxes around subpopulation abbreviations; between-population gene flow represented by colored lines). Gene flow was always high within Core, ranged from high (1995) to very low (1998) within Panhandle, and was moderate within Southwest. Gene flow between Core and Panhandle ranged from high (1996) to low (1998), whereas gene flow between Core and Southwest was more consistent among years (moderate, but high in 1997). Gene flow was high between Panhandle and Southwest only when it was high throughout the study range (1995); when populations were structured, gene flow between Panhandle and Southwest tended to be low. The high gene flow between FB and Core (Fig. 3D) may have been an artifact of high frequencies of common alleles in FB, or FB may have received recruits from Core. Between FB and peripheral populations, including geographically adjacent Southwest, little genetic exchange occurred.

External Factors

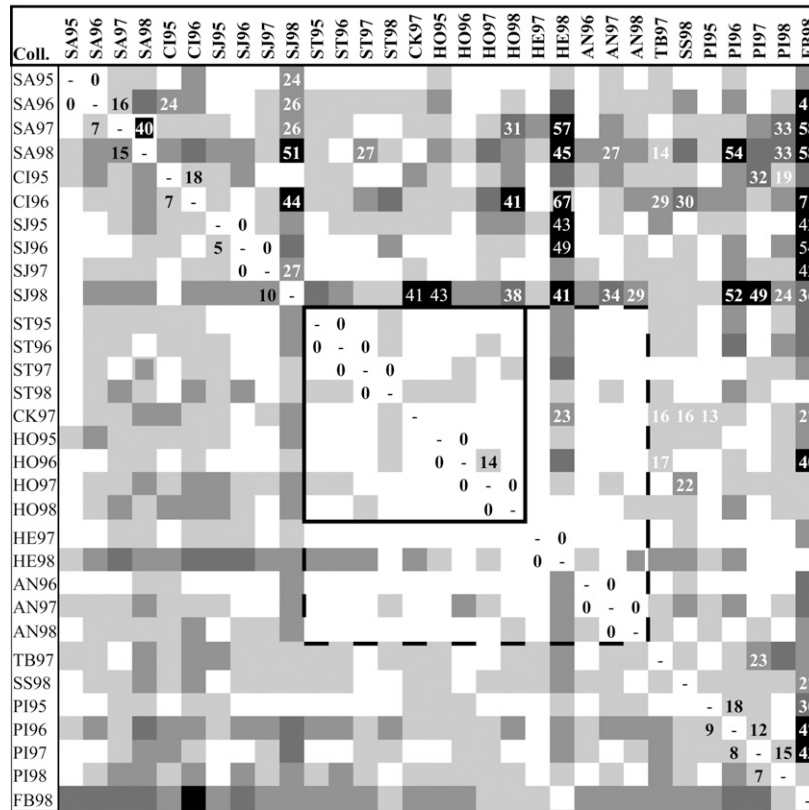
Expansive offshore seagrass flats extend between the St. Marks River and Anclote Estuary (Fig. 1). Both westward in panhandle waters and southward to waters off Cape Romano, substantial seagrass beds are within bays. From Cape Romano to Cape Sable, seagrass beds are very sparse; the seagrasses that exist are thinly distributed and usually are not *Thalassia* or *Syringodium*. In Florida Bay, only the westernmost and some southernmost basins typically contain dense seagrass beds; but, westward of Florida Bay, extensive seagrass beds exist along the Gulf side of the Florida Keys and throughout the Keys.

In the areas inhabited by bay scallops, seasonal currents interact with shoreline contours to form 4 regional current domains (Fig. 4A–D): (1) from CSB westward (includes SA–SJ), (2) the Big Bend (includes ST–HO and sometimes HE and AN); (3) southwestern Florida (includes TB–PI and sometimes HE and AN); and (4) Florida Bay (includes FB). From CSB westward, water currents are almost always strong, usually running westward from late spring through fall and eastward during winter and early spring (He & Weisberg 2002, He & Weisberg 2003). Overall, currents in this region run westward more than eastward (Ohlmann & Niiler 2005). When currents run eastward, some water moves around into the Big Bend, but a significant component veers offshore at CSB in an offshore jet (Fig. 5A), which generates upwelling off CSB (Ohlmann & Niiler 2005). From spring through fall or early winter (Yang & Weisberg 1999, He & Weisberg 2003), slow, variable currents moving generally northwestward to northeastward push water into the north end of the Big Bend, where it piles up and generates downwelling (Li & Weisberg 1999) (Fig. 4A–C).

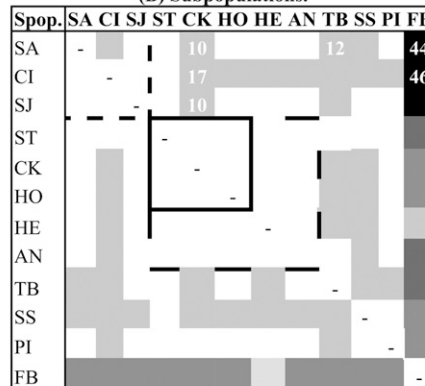
TABLE 7.

Matrices of Florida Gulf bay scallop allozyme-locus pairwise genetic distance estimators (Θ_{ST} , above diagonal; Nei's D , below diagonal).

(A) Collections.



(B) Subpopulations.



(C) 3- and 4-year subpopulations.

Spop.	SA	SJ	ST	HO	AN	PI
SA	-	1	3	5	7	2
SJ	0	-	3	6	5	3
ST	2	1	-	0	1	2
HO	2	2	0	-	1	2
AN	3	3	3	1	-	4
PI	1	2	1	1	2	-

Collection (Coll.) and subpopulation (Spop.) abbreviations are defined in Table 1. Ranges of values (both $\times 10^3$) are shown by shading for Nei's D : white, $\leq 0-4$; light gray, 5-9; medium gray, 10-19; dark gray, 20-29; black, ≥ 30 ; for Θ_{ST} : white, $\leq 0-9$; light gray, 10-19; medium gray, 20-29; dark gray, 30-39; black, ≥ 40 . (A, B). Values in white print differ significantly from pairwise $\Theta_{ST} = 0$ ($P \leq 0.005$). Solid lines enclose the initially defined Core population (i.e., subpopulations for which all pairs had very low pairwise genetic-distance values); long dashed extensions outline the expanded Core after further testing (see Building the Structure in the text and Table 8). (A) Bold-print numbers flanking diagonal divider, within-subpopulation parental cohort/offspring-cohort genetic distances. (B) Short dashes outline Panhandle population; solid line and long dashes as in (A). (C) Pairwise genetic distances over 4 generations.

TABLE 8.

Statistically homogeneous groupings of allozyme-locus average pairwise Nei's *D* (*D*) and Θ_{ST} values (from Table 7A, B) for bay scallop collections and subpopulations grouped by year, geographical location, or previous grouping (see Results).

OBJECTIVE Category Data set: pairs used; <i>n</i> values	Statistic and analysis number	Variable Mean ($\times 10^3$) of pairwise values included in specified variable, statistically homogeneous groupings underlined	<i>P</i> level
A. UNDERSTANDING INTERANNUAL VARIATION			
<i>A.1. Differences in mean pairwise genetic distances among collection pairs from different years.</i>			
All collections ¹ : means calculated for pairs with both pair members from the appropriate year; <i>n</i> = 15 for 1995, <i>n</i> = 21 for 1996, <i>n</i> = 36 for 1997 and 1998	<i>D</i> 1	1995 1997 1996 1998 <u>5²</u> <u>5</u> <u>5</u> <u>8</u>	0.019
	Θ_{ST} 2	<u>3</u> <u>5</u> <u>8</u> <u>20</u>	
4-year collections: means calculated as for analyses 1 and 2; <i>n</i> = 10 for each mean	<i>D</i> 3	1995 1997 1996 1998 <u>4</u> <u>6</u> <u>6</u> <u>9</u>	0.150
	Θ_{ST} 4	<u>8</u> <u>10</u> <u>12</u> <u>22</u>	0.026
<i>A.2. Differences in mean genetic distances between collection pairs from specific locations and other pairs¹</i>			
Collections: means calculated for pairs composed of SA within the appropriate year and every other collection except those with SA from the other three years; <i>n</i> = 27 for each mean	<i>D</i> 5	1995 ³ 1996 1997 1998 <u>4</u> <u>8</u> <u>9</u> <u>11</u>	0.0001 for both
	Θ_{ST} 6	<u>7</u> <u>16</u> <u>18</u> <u>26</u>	
Collections: means calculated as for analyses 5 and 6, but focusing on pairs from CI; <i>n</i> = 27 for each mean	<i>D</i> 7	1995 1996 <u>7</u> <u>17</u>	0.053
	Θ_{ST} 8	<u>16</u> <u>26</u>	0.025
Collections: means calculated as for analyses 5 and 6, but focusing on pairs from SJ; <i>n</i> = 27 for each mean	<i>D</i> 9	1997 1996 1995 1998 <u>5</u> <u>6</u> <u>7</u> <u>12</u>	0.0001 for both
	Θ_{ST} 10	<u>11</u> <u>13</u> <u>14</u> <u>29</u>	
Collections: means calculated as for analyses 5 and 6, but focusing on pairs from ST; <i>n</i> = 27 for each mean	<i>D</i> 11	1995 1997 1996 1998 <u>5</u> <u>5</u> <u>5</u> <u>6</u>	0.91
	Θ_{ST} 12	<u>10</u> <u>10</u> <u>11</u> <u>12</u>	0.73
Collections: means calculated as for analyses 5 and 6, but focusing on pairs from HO; <i>n</i> = 27 for each mean	<i>D</i> 13	1996 1995 1997 1998 <u>5</u> <u>6</u> <u>7</u> <u>7</u>	0.034
	Θ_{ST} 14	Neither the REGWQ nor Tukey's Studentized Range (Tukey's; Sokal and Rohlf 1995) tests separated the means. <u>9</u> <u>12</u> <u>13</u> <u>14</u>	0.31
Collections: means calculated as for analyses 5 and 6, but focusing on pairs from HE; <i>n</i> = 29 for each mean	<i>D</i> 15	1997 1998 <u>3</u> <u>13</u>	0.0001 for both
	Θ_{ST} 16	<u>5</u> <u>26</u>	
Collections: means calculated as for analyses 5 and 6, but focusing on pairs from AN; <i>n</i> = 28 for each mean	<i>D</i> 17	1996 1998 1997 <u>4</u> <u>6</u> <u>6</u>	0.004
	Θ_{ST} 18	<u>6</u> <u>11</u> <u>13</u>	0.001
Collections: means calculated as for analyses 5 and 6, but focusing on pairs from PI; <i>n</i> = 27 for each mean	<i>D</i> 19	1995 1998 1997 1996 <u>4</u> <u>7</u> <u>8</u> <u>11</u>	0.0001
	Θ_{ST} 20	<u>8</u> <u>13</u> <u>14</u> <u>21</u>	0.001
B. UNDERSTANDING BASIC RELATIONSHIPS AMONG COLLECTIONS AND SUBPOPULATIONS³			
<i>B.1. Relationships of collections to all other collections</i>			
All collections: means calculated for pairs composed of collection displayed and every other collection; <i>n</i> = 30 for each mean ¹	<i>D</i> 21	HE SA AN HO PI ST ST ST CK SJ HO ST AN HO HO 97 95 96 96 95 97 95 96 97 97 95 98 98 98 97 3 ⁴ 4 4 4 4 4 5 5 5 5 6 6 6 6 6	0.0001 for both
		AN SJ SS SJ PI TB PI SA CI SA CI SA PI SJ HE FB 97 96 98 95 98 97 97 96 95 97 96 98 96 98 98 98 6 7 7 7 7 7 7 7 9 11 11 11 11 12 15	
	Θ_{ST} 22	HE AN SA PI HO ST ST CK ST AN ST HO SJ AN HO 97 96 95 95 96 95 97 97 96 98 98 95 97 97 97 5 6 8 9 9 10 10 10 10 11 11 12 12 12 13	
		SJ HO PI PI TB SJ SS SA CI SA PI HE CI SA SJ FB 96 98 98 97 97 95 98 96 95 97 96 98 96 98 98 98 13 13 14 14 15 15 15 16 16 19 20 25 25 27 29 34	

continued on next page

TABLE 8.
Continued

OBJECTIVE Category Data set: pairs used; <i>n</i> values	Statistic and analysis number	Variable Mean ($\bar{X} \times 10^3$) of pairwise values included in specified variable, statistically homogeneous groupings underlined	P level
4-year collections: means calculated for pairs composed of collection displayed and every other collection from locations sampled for 4 years; <i>n</i> = 19 for each mean	<i>D</i> 23	SA HO PI ST ST ST SJ SJ HO ST HO HO SJ SA PI PI SA SA PI SJ 95 96 95 95 96 97 97 96 95 98 97 98 95 96 97 98 97 98 96 98 3 4 4 4 5 5 5 6 6 6 6 6 6 6 6 7 8 8 10 11 12	0.0001 for both
	Θ_{ST} 24	SA PI HO ST ST ST SJ ST SJ HO HO PI SJ SA HO PI SA PI SA SJ 95 95 96 95 96 97 97 98 96 95 97 97 95 96 98 98 97 96 98 98 6 8 8 8 10 10 10 11 11 12 13 13 13 13 14 15 17 21 25 30	
<i>B.2. Relationships of subpopulations to other subpopulations</i>			
Subpopulations: except FB, means calculated for pairs composed of subpopulation displayed and every other subpopulation except FB, <i>n</i> = 10 ⁵ ; for FB, mean calculated for pairs composed of FB and every other subpopulation; <i>n</i> = 11 for each mean	<i>D</i> 25	ST HO PI SJ AN SA CK CI TB SS HE FB 2 2 2 3 3 3 4 5 5 5 7 13	0.0001 for both
	Θ_{ST} 26 ⁶	ST PI HO AN SJ SA HE CK SS TB CI FB 4 5 5 5 6 7 7 8 12 12 12 32	
C. UNDERSTANDING POPULATION GENETIC STRUCTURE			
<i>C.1. Affiliation of subpopulations</i>			
4-year collections: means calculated for pairs composed of all collections with both pair members from the displayed subpopulation; <i>n</i> = 6 for each mean	<i>D</i> 27	HO/HO ST/ST PI/PI SA/SA SJ/SJ 3 ⁷ 4 7 8 8	0.005
	Θ_{ST} 28	7 7 11 19 20 Neither the REGWQ nor Tukey's tests separated this group.	0.040
PI			
4-year collections: means calculated for pairs composed of all collections with both pair members from the displayed subpopulations; <i>n</i> = 28 for ST,HO/ST,HO and SA,SJ/SA,SJ, <i>n</i> = 32 for PI/ST,HO and PI/SA,SJ, <i>n</i> = 6 for PI/PI	<i>D</i> 29	ST,HO/ PI/ SA,SJ/ PI/ PI/ ST,HO ⁸ ST,HO SA,SJ PI SA,SJ 3 6 7 7 8	0.0002
	Θ_{ST} 30	ST,HO/ PI/ PI/ SA,SJ/ PI/ ST,HO ST,HO PI SA,SJ SA,SJ 7 11 11 17 18	0.001
4-year collections: means calculated as described for analyses 29 and 30; <i>n</i> = 28 for ST,HO/ST,HO, <i>n</i> = 32 for PI/ST,HO	<i>D</i> 31	ST,HO/ST,HO PI/ST,HO 3 6	0.0005
	Θ_{ST} 32	7 11 Both the REGWQ and Tukey's tests separated the two groups.	0.063
4-year collections: means calculated as described for analyses 29 and 30; <i>n</i> = 28 for SA,SJ/SA,SJ, <i>n</i> = 32 for PI/SA,SJ	<i>D</i> 33	SA,SJ/SA,SJ PI/SA,SJ 7 8	0.71
	Θ_{ST} 34	17 18	0.98
CI			
Collections: means calculated as described for PI; <i>n</i> = 28 for ST,HO/ST,HO, <i>n</i> = 66 for SA,SJ,PI/SA,SJ,PI, <i>n</i> = 16 for CI/ST,HO, <i>n</i> = 24 for CI/SA,SJ,PI	<i>D</i> 35	ST,HO/ CI/ SA,SJ,PI/ CI/ ST,HO ST,HO SA,SJ,PI SA,SJ,PI 3 7 8 8 CI/CI = 7 (<i>n</i> = 1)	0.0001 for both
	Θ_{ST} 36	ST,HO/ SA,SJ,PI/ CI/ CI/ ST,HO SA,SJ,PI ST,HO SA,SJ,PI 7 17 19 19 CI/CI = 18 (<i>n</i> = 1)	

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TABLE 8.
Continued

OBJECTIVE Category Data set: pairs used; n values	Statistic and analysis number	Variable Mean ($\bar{X} \times 10^3$) of pairwise values included in specified variable, statistically homogeneous groupings underlined	P level
HE			
Collections: means calculated as described for PI; n = 28 for ST, HO/ST, HO, n = 66 for SA, SJ,PI/SA,SJ,PI, n = 16 for HE/ST,HO, n = 24 for HE/SA,SJ,PI	D 37	ST,HO/ HE/ SA,SJ,PI/ HE/ ST,HO ST,HO SA,SJ,PI SA,SJ,PI <u>3</u> <u>4</u> <u>8</u> <u>10</u> HE/HE = 4 (n = 1) <u>7</u> <u>11</u> 17 19	0.0001
	Θ_{ST} 38	HE/HE = 7 (n = 1)	0.0019
Collections: means calculated as described for PI; n = 28 for ST,HO/ST,HO, n = 16 for CI/ST,HO	D 39	ST,HO/ST,HO HE/ST,HO <u>3</u> <u>4</u> <u>7</u> <u>11</u>	0.20
	Θ_{ST} 40		0.0001
Collections: means calculated as described for PI; n = 28 for ST,HO/ST,HO, n = 16 for CI/ST,HO	D 41	SA,SJ,PI/SA,SJ,PI HE/SA, SJ,PI <u>8</u> <u>10</u> <u>17</u> <u>19</u>	0.40
	Θ_{ST} 42		0.24
AN			
Collections: means calculated as described for PI; n = 28 for ST,HO/ST,HO, n = 66 for SA,SJ,PI/SA,SJ,PI, n = 24 for AN/ST,HO, n = 36 for HE/SA,SJ,PI; n = 3 for AN/AN	D 43	AN/ ST,HO/ AN/ SA,SJ,PI/ ST,HO ST,HO SA,SJ,PI SA,SJ,PI <u>3</u> <u>3</u> <u>6</u> <u>8</u> AN/AN = 3 (n = 3) <u>5</u> <u>7</u> <u>11</u> <u>17</u>	0.0001 for both
	Θ_{ST} 44	AN/AN = 4 (n = 3)	
Collections: means calculated as described for PI; n = 28 for ST,HO/ST,HO, n = 24 for AN/ST,HO	D 45	AN/ST,HO ST,HO/ST,HO <u>3</u> <u>3</u> <u>5</u> <u>7</u>	0.53
	Θ_{ST} 46	Neither the REGWQ nor Tukey's tests separated the means	0.042
Collections: means calculated as described for PI; n = 66 for SA,SJ,PI/SA,SJ,PI, n = 36 for AN/SA,SJ,PI	D 47	AN/SA,SJ,PI SA,SJ, PI/SA,SJ,PI <u>6</u> <u>8</u> <u>11</u> <u>17</u>	0.048
	Θ_{ST} 48		0.037
HE			
Collections: means calculated as described for PI; n = 28 for ST, HO/ST, HO, n = 66 for SA, SJ,PI/SA,SJ,PI, n = 16 for HE/ST,HO, n = 24 for HE/SA,SJ,PI	D 37	ST,HO/ HE/ SA,SJ,PI/ HE/ ST,HO ST,HO SA,SJ,PI SA,SJ,PI <u>3</u> <u>4</u> <u>8</u> <u>10</u> HE/HE = 4 (n = 1) <u>7</u> <u>11</u> 17 19	0.0001
	Θ_{ST} 38	HE/HE = 7 (n = 1)	0.0019
Collections: means calculated as described for PI; n = 28 for ST,HO/ST,HO, n = 16 for CI/ST,HO	D 39	ST,HO/ST,HO HE/ST,HO <u>3</u> <u>4</u> <u>7</u> <u>11</u>	0.20
	Θ_{ST} 40		0.0001
Collections: means calculated as described for PI; n = 28 for ST,HO/ST,HO, n = 16 for CI/ST,HO	D 41	SA,SJ,PI/SA,SJ,PI HE/SA, SJ,PI <u>8</u> <u>10</u> <u>17</u> <u>19</u>	0.40
	Θ_{ST} 42		0.24
AN			
Collections: means calculated as described for PI; n = 28 for ST,HO/ST,HO, n = 66 for SA,SJ,PI/SA,SJ,PI, n = 24 for AN/ST,HO, n = 36 for HE/SA,SJ,PI; n = 3 for AN/AN	D 43	AN/ ST,HO/ AN/ SA,SJ,PI/ ST,HO ST,HO SA,SJ,PI SA,SJ,PI <u>3</u> <u>3</u> <u>6</u> <u>8</u> AN/AN = 3 (n = 3) <u>5</u> <u>7</u> <u>11</u> <u>17</u>	0.0001 for both
	Θ_{ST} 44		

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TABLE 8.
Continued

OBJECTIVE Category Data set: pairs used; <i>n</i> values	Statistic and analysis number	Variable Mean ($\bar{X} \times 10^3$) of pairwise values included in specified variable, statistically homogeneous groupings underlined	<i>P</i> level
		AN/AN = 4 (<i>n</i> = 3)	
Collections: means calculated as described for PI; <i>n</i> = 28 for ST,HO/ST,HO, <i>n</i> = 24 for AN/ST,HO	<i>D</i> 45	AN/ST,HO ST,HO/ST,HO <u>3</u> <u>3</u>	0.53
	Θ_{ST} 46	<u>5</u> <u>7</u> Neither the REGWQ nor Tukey's tests separated the means	0.042
Collections: means calculated as described for PI; <i>n</i> = 66 for SA,SJ,PI/SA,SJ,PI, <i>n</i> = 36 for AN/SA,SJ,PI	<i>D</i> 47	AN/SA,SJ,PI SA,SJ, PI/SA,SJ,PI <u>6</u> <u>8</u>	0.048
	Θ_{ST} 48	<u>11</u> <u>17</u>	0.037
FB			
Collections: means calculated as described for PI; <i>n</i> = 28 for ST,HO/ST,HO, <i>n</i> = 66 for SA,SJ,PI/SA,SJ,PI, <i>n</i> = 8 for FB/ST,HO, <i>n</i> = 12 for FB/SA,SJ,PI	<i>D</i> 49	ST,HO/ SA,SJ,PI/ FB/ FB/ ST,HO SA,SJ,PI ST,HO SA,SJ,PI <u>3</u> ⁹ <u>8</u> <u>12</u> <u>18</u>	0.0001 for both
	Θ_{ST} 50	<u>7</u> <u>17</u> <u>27</u> <u>41</u>	
<i>C.2. Relationships among populations</i>			
All collections ⁸ , with FB: means calculated for pairs composed of all collections with both pair members from within the ranges of displayed subpopulations; <i>n</i> = 91 for ST-AN/ST-AN, <i>n</i> = 45 for SA-SJ/SA-SJ, <i>n</i> = 15 for TB-PI/TB-PI, <i>n</i> = 140 for SA-SJ/ST-AN, <i>n</i> = 60 for SA-SJ/TB-PI, <i>n</i> = 84 for ST-AN/TB-PI, <i>n</i> = 10 for FB/SA-SJ, <i>n</i> = 14 for FB/ST-AN, <i>n</i> = 6 for FB/TB-PI	<i>D</i> 51	ST-AN/ TB-PI/ SA-SJ/ SA-SJ/ TB-PI/ SA-SJ/ FB/ FB/ FB/ ST-AN ST-AN SA-SJ ST-AN TB-PI TB-PI ST-AN TB-PI SA-SJ <u>4</u> ¹⁰ <u>6</u> <u>7</u> <u>7</u> <u>7</u> <u>8</u> <u>12</u> <u>15</u> <u>20</u>	0.0001 for both
	Θ_{ST} 52	ST-AN/ TB-PI/ TB-PI/ SA-SJ/ SA-SJ/ SA-SJ/ FB/ FB/ FB/ ST-AN ST-AN TB-PI ST-AN SA-SJ TB-PI ST-AN TB-PI SA-SJ <u>7</u> <u>10</u> <u>14</u> <u>16</u> <u>18</u> <u>18</u> <u>26</u> <u>33</u> <u>46</u>	
All collections, without FB: means calculated as described for analyses 51 and 52; <i>n</i> values reduced as appropriate	<i>D</i> 53	ST-AN/ TB-PI/ SA-SJ/ SA-SJ/ TB-PI/ SA-SJ/ ST-AN ST-AN SA-SJ ST-AN TB-PI TB-PI <u>4</u> <u>6</u> <u>7</u> <u>7</u> <u>7</u> <u>8</u>	0.0001 for both
	Θ_{ST} 54	ST-AN/ TB-PI/ TB-PI/ SA-SJ/ SA-SJ/ SA-SJ/ ST-AN ST-AN TB-PI ST-AN SA-SJ TB-PI <u>7</u> <u>10</u> <u>14</u> <u>16</u> <u>18</u> <u>18</u>	
All subpopulations (from Table 7B), with FB: means calculated for pairs composed of all subpopulations with both pair members from within the ranges of displayed subpopulations; <i>n</i> = 10 for ST-AN/ST-AN; <i>n</i> = 3 for SA-SJ/SA-SJ, TB-PI/TB-PI, FB/SA-SJ, FB/TB-PI; <i>n</i> = 15 for SA-SJ/ST-AN, ST-AN/TB-PI; <i>n</i> = 9S for SA-SJ/ TB-PI, <i>n</i> = 5 for FB/ST-AN	<i>D</i> 55	ST-AN/ SA-SJ/ SA-SJ/ TB-PI/ SA-SJ/ TB-PI/ FB/ FB/ FB/ ST-AN SA-SJ ST-AN ST-AN TB-PI TB-PI ST-AN TB-PI SA-SJ <u>1</u> ¹¹ <u>2</u> <u>4</u> <u>4</u> <u>4</u> <u>6</u> <u>11</u> <u>14</u> <u>17</u>	0.0001 for both
	Θ_{ST} 56	ST-AN/ SA-SJ/ TB-PI/ SA-SJ/ SA-SJ/ TB-PI/ FB/ FB/ FB/ ST-AN SA-SJ ST-AN ST-AN TB-PI TB-PI ST-AN TB-PI SA-SJ <u>2</u> <u>4</u> <u>8</u> <u>9</u> <u>10</u> <u>11</u> <u>26</u> <u>30</u> <u>44</u>	

¹Analyses performed with and without pairs that included FB98; without FB98, *n* values were reduced appropriately. Results without FB are not reported unless significance levels changed.

²For example, value is mean of all pairwise *D* values in Table 7A that included collections from 1995 only as pair members.

³Only the grouping with the lowest mean and 2 groupings with the highest means are shown.

⁴For example, the value is the mean of all pairwise *D* values in Table 7A with HE97 as a pair member.

⁵FB, an obvious outlier, was eliminated from the means calculated for other subpopulations because including FB greatly increased SDs and obscured significant relationships among other subpopulations. For example, ST includes all pairwise values in Table 7B with ST as a pair member, except ST/FB. The FB mean was calculated using all FB pairs. We also performed these analyses without FB-pair means; results were essentially the same as presented here.

⁶Groupings defined by Tukey's test (Sokal & Rohlf 1995), which in this case presented clearer results.

⁷For example, the value is mean of all pairwise *D* values in Table 7A that included only HO collections as both pair members.

⁸For clarity of presentation, year designations were omitted from collection abbreviations.

⁹For example, the value is the mean of all pairwise *D* values in Table 7A that include only ST and HO collections as pair members. Similarly, the value for PI/ST-HO is the mean of all collection pairs that included a PI collection and an ST or HO collection.

¹⁰For example, the value is the mean of all pairwise *D* values in Table 7A that include only ST, CK, HO, and AN collections as pair members.

¹¹For example, the value is the mean of all pairwise *D* values in Table 7B that include only subpopulations ST, CK, HO, HE, and AN as pair members. We conducted a total of 125 tests for significance of pairwise genetic distances and present tests with significant *P* values only and, when necessary, closely related tests to complete a testing series. All statistical groupings are underlined unless otherwise noted. Collection and subpopulation abbreviations are defined in Table 1. Analyses are numbered sequentially; in *B* analyses, bold-print collection abbreviations and italicized 1998 collections refer to Results in the text.

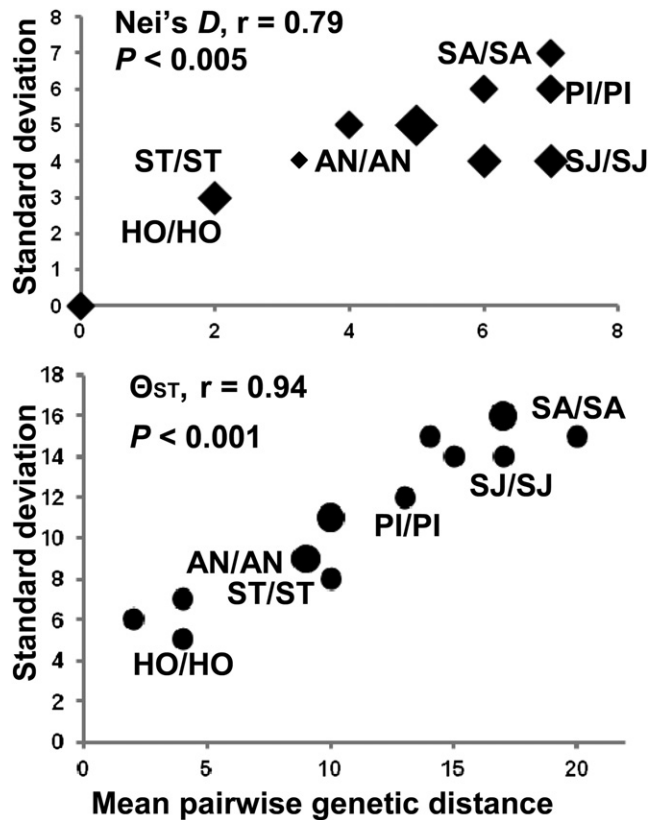


Figure 2. Relationship between the mean and variation around the mean in pairwise collection-level genetic distance measures of bay scallop subpopulations sampled 4 y (from Table 7A). Labeled points are the means of all within-subpopulation collection pairs (e.g., SA/SA is the mean of values for SA95/SA96, SA95/SA97 ... SA97/SA98). Other points are the means of other analogous groups of collection pairs (e.g., means of SA95/SJ95 ... SA98/SJ98). Larger points are proportional to the number of pairs with the same means.

From fall or early winter to spring, prevailing northerly winds drive an anticyclonal (clockwise) gyre—which is strongest in October through December (Yang & Weisberg 1999) and is enhanced by tides (He & Weisberg 2002)—that moves southeastward alongshore to the vicinity of Homosassa Bay or Anclote Estuary (Yang & Weisberg 1999), where it veers offshore and moves northwestward until encountering CSB, which deflects the water eastward to complete the gyre (Yang et al. 1999) (Fig. 4D). The gyre can generate upwelling off the Big Bend coast (Yang et al. 1999, Weisberg et al. 2001, He & Weisberg 2003); but, off CSB to Deadman Bay, currents typically remain weak to near 0, particularly during transition months (Hetland et al. 1999, Li & Weisberg 1999, Yang & Weisberg 1999, Weisberg & He 2003) (Fig. 4A, C), and annual net flow is usually near 0 (Ohlmann & Niiler 2005, Liu & Weisberg 2007). Currents between Deadman Bay and the Homosassa-Bay/Hernando vicinity are also very low if the wind is directly onshore or offshore (Li & Weisberg 1999) (Fig. 5B, C).

Summer and winter currents are generally stronger from Tampa Bay southward than in the Big Bend (Yang & Weisberg 1999), and both velocity and tidal amplitude increase with movement southward (He & Weisberg 2002) (Fig. 4B, D).

A strong, nearshore, southward-moving, upwelling-favorable coastal jet (Yang et al. 1999) is a common feature during fall, winter (strongest), and spring, particularly in waters between Tampa Bay and Pine Island Sound or Cape Romano (Li & Weisberg 1999, Liu & Weisberg 2005, Weisberg et al. 2005, Weisberg et al. 2009b, Liu & Weisberg 2012) (Fig. 4A, C, D). The coastal jet, together with the Big Bend gyre, generates upwelling off Tampa Bay (strongest October through January). During summer, the coastal jet is weaker, farther offshore, downwelling favorable, and northward flowing (Weisberg et al. 2009b, Liu & Weisberg 2012) (Fig. 4B). Net water movement is south to southwest offshore (He & Weisberg 2002, Ohlmann & Niiler 2005), but very nearshore, northward or shoreward countercurrents can develop (He & Weisberg 2002, Liu & Weisberg 2005).

Current flow in the western basins of Florida Bay is commonly westerly (Lee & Smith 2002), from the basins to open water or south-to-southwesterly through channels separating the Florida Keys (Lee & Smith 2002, Zheng & Weisberg 2012) (Fig. 4A–C). Inflow into western basins occurs sporadically during winter and spring, when cold front-associated west-to-northwest winds blow (Fig. 4D). Transport off the Ten Thousand Islands and Cape Sable is offshore (fall), northward (summer), or southwestward (winter/spring), bypassing Florida Bay (Lee & Smith 2002).

Tropical cyclones, red tides, and floods produced by heavy rains could affect a bay scallop cohort's population genetic structure by reducing abundance of, or eliminating, its parental generation as adults or the cohort generation itself at some life stage. Tropical cyclones also generate strong or atypical currents that can transport a cohort's larvae to unusual places, particularly those occurring during October. With this timeline in mind, and considering that tropical cyclone activity almost always occurred after we sampled in June, we included in the same figure as a cohort's pairwise genetic distances the tropical cyclone, red tide, and rainfall activity from the previous year (Fig. 3A–D). Occasionally, considering the timing of events that could affect a cohort's population genetic structure required viewing figures from two consecutive years.

Tropical cyclone activity varied among years (Fig. 3A–D, inset maps and black lines on main maps). Tropical cyclones swept through panhandle waters every year but through peninsula waters only some years. Throughout summer and fall 1995, the Gulf was besieged by tropical cyclones. During 1997, Florida was nearly unaffected by tropical storms.

The extent and intensity of red tide outbreaks varied greatly among years (Fig. 3A–D; main maps, enclosed areas shaded by diagonal lines and accompanying notes stating months of *Karenia brevis* outbreaks). Blooms occurred in panhandle waters most years, but location and intensity varied. The Big Bend was seldom affected by red tides. Between Anclote Estuary and Pine Island Sound, red tide blooms were broadly distributed and prolonged every year, particularly from Tampa Bay southward. Blooms could occur at any time of the year, but most occurred September through December. Blooms usually followed coastal contours, running alongshore and extending out into the ocean for varying distances (Fig. 3A–C). In 1997, red tide blooms assumed a very different configuration, extending from nearshore to offshore, with little alongshore development (Fig. 3D).

TABLE 9.

Matrices of ranges of Florida Gulf bay scallop pairwise nucleotide diversity (π , above diagonal) and genetic distance (Φ_{ST} , below diagonal, $\times 10^3$) based on mtDNA RFLP analyses.

(A) Collections.

Coll.	SA 98	SJ 95	SJ 96	SJ 97	SJ 98	ST 95	ST 96	ST 97	ST 98	HO 95	HO 96	HO 97	HO 98	AN 98	TB 97	SS 98	PI 95	PI 96	PI 97	PI 98	FB 98	
SA98	-																					
SJ95		-																				
SJ96			14																			
SJ97				0																		
SJ98					34																	
ST95						-																
ST96						70	10															
ST97							51	-														
ST98								0	-													
HO95										-												
HO96						34				0												
HO97						41				16												
HO98										0	-	12										
AN98						47																
TB97																						
SS98																						
PI95									17													
PI96																	0					
PI97																		0				
PI98																			0			
FB98				41	22	52	88			23							80	125	70	29		-

(B) Subpopulations.

Spop.	SA	SJ	ST	HO	AN	TB	SS	PI	FB
SA	-								
SJ		-							
ST			-						
HO				-					
AN					17				
TB						-			
SS							-		
PI								-	
FB									-

Ranges of values shown by shading for π values ($\times 10^3$): white, 5.9–7.9; light gray, 8.0–9.9; medium gray, 10.0–11.9; dark gray, 12.0–13.7; ranges for Φ_{ST} values: white, ≤ 0 ; light gray, 0.1–9.9; medium gray, 10.0–49.9; dark gray, 50.0–125.0. Significant Φ_{ST} values in bold white print; values significant after correction for multiple tests also underlined. Collection (Coll.) and subpopulation (Subpop.) abbreviations defined in Table 1. (A) Within-subpopulation parent–offspring genetic distances flank diagonal divide.

Of the 7 NOAA rainfall divisions, those affecting bay scallop habitats are divisions 1–5 (Fig. 3). Monthly rainfall patterns fluctuated greatly among those divisions within and between years (Fig. 6). In general, more rain fell May through August than during other months; but, in some years, one or more months between September and January were very rainy. Of note, heavy rains occurred in the panhandle and Big Bend area during summer and in southwest Florida during fall and early winter in 1994, in the panhandle during spring and in west-central and southwest Florida from summer through fall 1995, in the Big Bend area during March and from west-central through southwest Florida during early summer 1996, and from the panhandle through southwest Florida during April and early winter 1997 (Fig. 3A–D, rainfall notes on main maps; Fig. 6).

The maximum abundance of adult bay scallops varied nearly 5-fold among years, and abundance varied even more among subpopulations within some years (Fig. 7). Preharvest adult abundance was high in a Panhandle subpopulation and/or ST

1994 to 1996, but was low in all subpopulations in 1997 and, particularly, 1998. Postharvest abundance was very low compared with preharvest abundance in 1994 and 1995, declining as much as 95%, but was comparable with preharvest abundance in 1996 and 1997. Spat abundance also varied greatly among years and could be exceptionally high in single subpopulations during specific settlement seasons (e.g., SJ95–96, TB97–98).

DISCUSSION

Population Genetic Structure and Environmental Influences

The Metapopulation

Interlocational, interannual, and intergenerational variation in population genetic structure is common in shallow-water marine organisms (e.g., Kordos & Burton 1993, Edmands et al. 1996, Moberg & Burton 2000, Carlin et al. 2003, Galindo et al. 2010); and genetic differentiation, often structured as a metapopulation, occurs in the face of potential gene flow in various

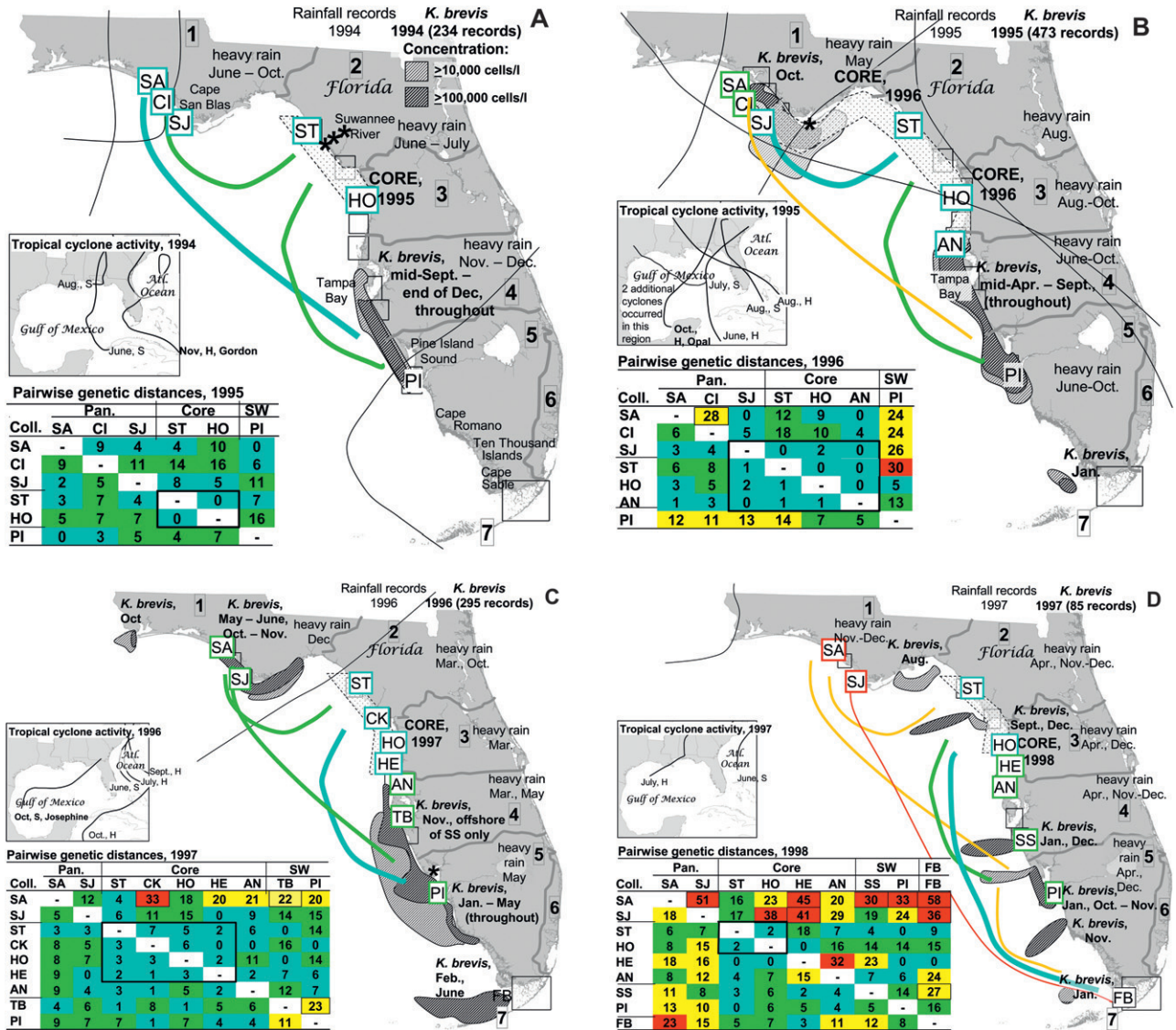


Figure 3. Interannual variation in cohort bay scallop allozyme-locus population genetic structure and in external factors potentially contributing to that variation over the time frame relevant to cohort larval dispersal and cohort survival. Matrices: Pairwise genetic distances ($\times 10^3$; Θ_{ST} above diagonal: blue, $\leq 0-9$; green, 10-19; yellow, 20-29; red, 30-71; Nei's D below diagonal: blue, $\leq 0-4$; green, 5-9; yellow, 10-19; red, 20-32) representing population genetic structure. Collections included in the Core population for each year are outlined in each matrix. Populations as defined by all analyses are shown in column and row titles (Pan., panhandle; SW, southwest). Extent of Core in any year may differ from analysis-defined Core. Collection (Coll.) abbreviations are defined in Table 1. (B-D) Boxed Θ_{ST} values differ significantly from $\Theta_{ST} = 0$. Inset maps: Full regional paths of tropical cyclones; S, tropical storm; H, hurricane; month abbreviation, month of principal activity affecting Florida. Maps of Florida: Colored boxes around collection abbreviations, mean within-population relative genetic distances; colored lines between populations, mean between-population relative genetic distances (Θ_{ST} coloration, as described earlier). Dotted area bounded by dashed lines, geographical extent of Core population. Hatched areas bounded by solid lines, maximum extents of red tide blooms; concentration ranges given in (A) apply also to (B-D). Dark gray lines, NOAA rainfall divisions, identified by boxed numbers; months of exceptionally high rainfall displayed within affected rainfall districts (Fig. 6). Black lines, pathways of centers of tropical cyclones.

scallop species (e.g., Heipel et al. 1998, Ridgway & Dahle 2000, Orensanz et al. 2006, Marko & Barr 2007, Owen & Rawson 2013). Florida Gulf bay scallops form a complex, mixed-model metapopulation (Harrison & Taylor 1997)—a combination between a pure source-sink metapopulation, in which all gene flow is from a donor source population to recipient sink populations (Tero et al. 2003), and a classic metapopulation, in which all populations have roughly

equivalent potentials to contribute recruits to all other populations (Levins 1970).

The Florida Gulf bay scallop metapopulation is also structured hierarchically (per Bilodeau et al. (2005) and Kritzer and Sale (2006)). In such metapopulations, gene flow and genetic isolation are dynamic processes that can occur at different scales (Le Corre et al. 2012), and can vary temporally and spatially in strength and duration. Genetic differentiation can

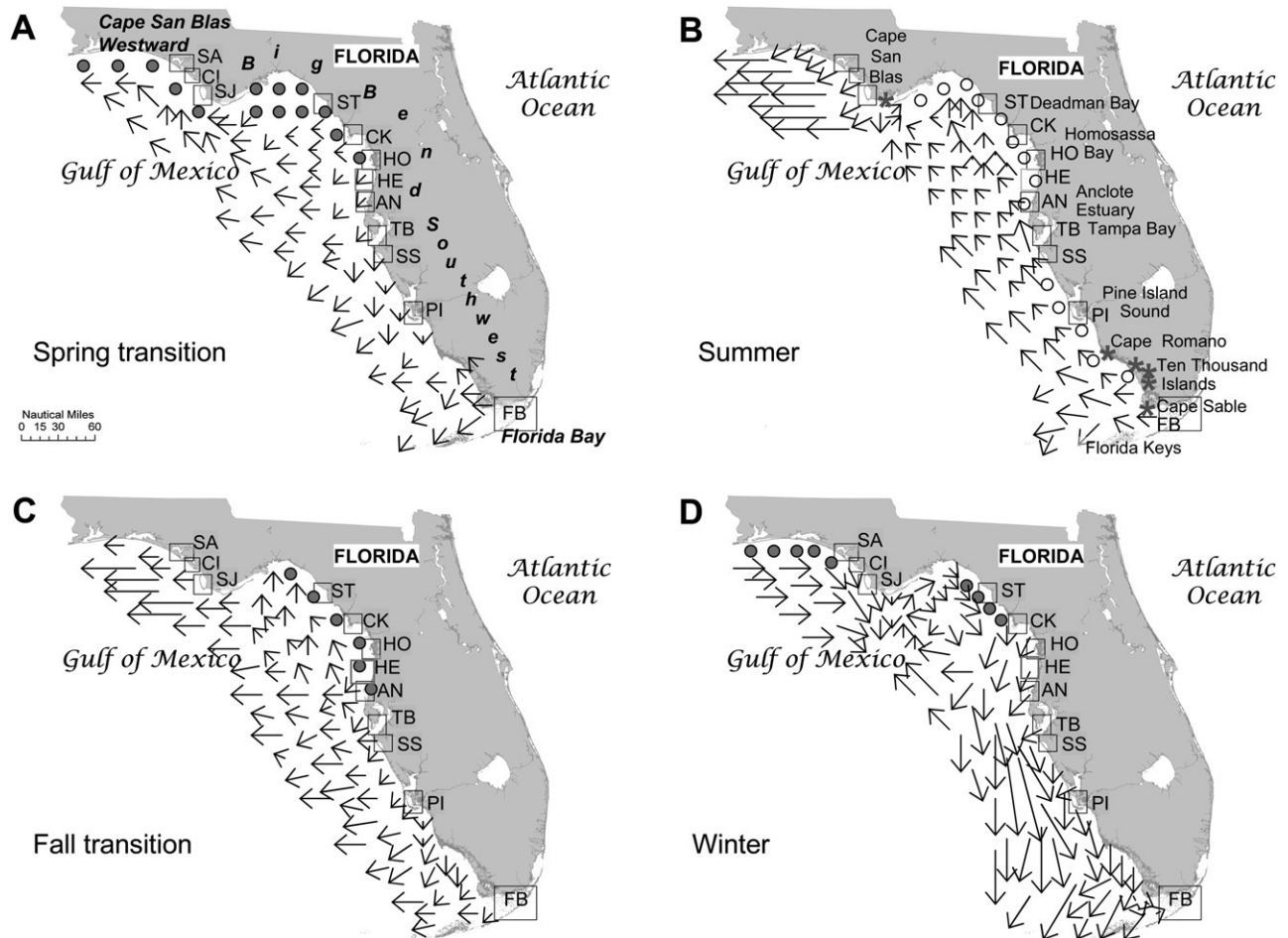


Figure 4. Consensus seasonal current flows along the West Florida Shelf. (A) Spring transition: March, April, or May. (B) Summer: April, May, or June to August or September. Names and geographical features are mentioned in the text. (C) Fall transition: September or October. (D) Winter: October or November to February, March, or April. Arrows approximately represent relative rate and direction of water flow; dots, very little net current flow. Collection abbreviations defined in Table 1.

be greater over short distances than over long distances and can be highly variable between cohorts from the same subpopulation. In the Florida Gulf bay scallop metapopulation, Core is the main source population; but, within every population is at least one subpopulation that could act as a local source (ST or HO in Core, SJ in Panhandle, PI in Southwest, and FB as its own source).

Luxuriant seagrass beds are essential in shaping the distribution of *Argopecten irradians* throughout its range, and currents guide the genetic relationships of many scallop populations, including *A. irradians* (Kraus et al. 1994, Wolff & Mendo 2000, Bogazzi et al. 2005, Tian et al. 2009, Bert et al. 2011). Vagaries in currents during periods of spawning or larval dispersal lend a perpetual element of intergenerational unpredictability to scallop population genetic structures (Tian et al. 2009); but, for Florida Gulf bay scallops, the location and extent of seagrass beds, together with the circulation patterns of the 4 Florida Gulf seasonal current domains, seem to be the basis for their metapopulation structure. Seagrass beds set the stage for the structure; seasonal water currents help maintain it.

We examined the validity of our proposed structure by submitting the population-level pairwise Θ_{ST} data to AMOVA.

The structure was highly significant ($P = 0.004$). Significant pairwise Θ_{ST} values (ARLEQUIN; P range, 0.03–0.005) also supported this structural model; Panhandle and Southwest were differentiated genetically from each other but not from Core, and FB was differentiated from all other populations. Overall, gene flow was high within Core, higher between Core and Southwest than between Core and Panhandle, and low to very low within and between peripheral populations (Fig. 8).

Juxtaposed on this population genetic structure is increasing genetic homogeneity over an increasing number of generations. Comparing single-year and multiyear pairwise genetic distances matrices revealed that, collectively over generations, subpopulations attained greater genetic homogeneity. Similar declines in genetic patterning over time were found theoretically by Galindo et al. (2010) in population genetics simulations of the Caribbean reef coral *Acropora cervicornis*, and empirically by Pruett et al. (2005) for Gulf of Mexico red snapper (*Lutjanus campechanus*). In our study, the increase in percentage of allozyme loci out of H-W equilibrium with an increasing number of generations sampled and the high percentage of loci out of H-W equilibrium in two consistent subpopulations (SJ, ST) together with other evidence (Table 10, characteristic 1)

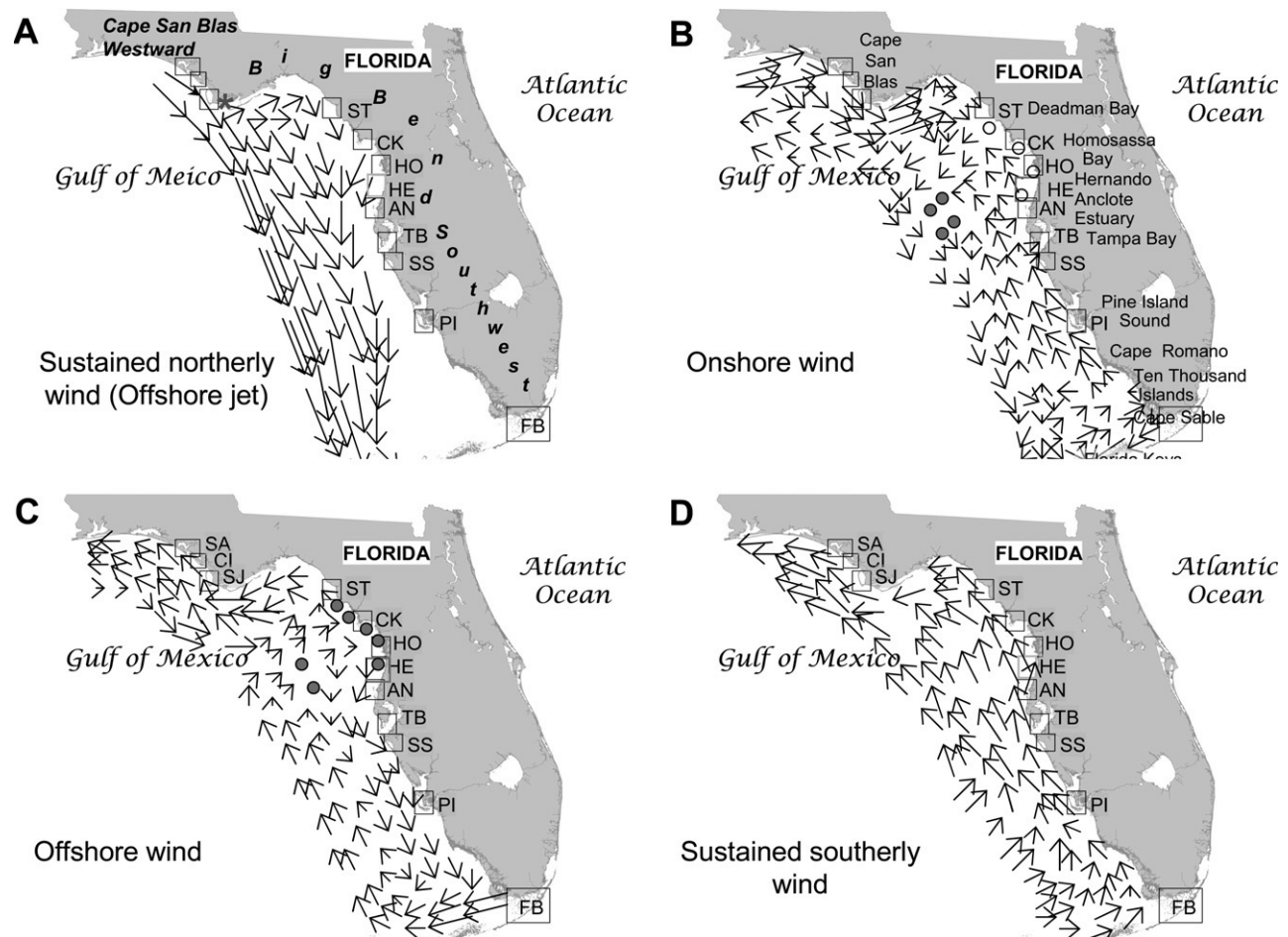


Figure 5. (A–D) Other current flows along the West Florida Shelf (depth averaged). Current patterns with sustained north-to-northwesterly wind (most common in winter) (A); strong, sustained west wind; names and geographical features mentioned in text (B); strong, sustained east wind (C); and sustained southerly winds (most common in summer) (D). Arrows approximately represent relative rates and directions of water flow; dots, very little net current flow. Collection abbreviations defined in Table 1.

indicate that the increase in homogeneity as generations are amassed may be the result of a Wahlund effect—the mixing of recruits from bay scallop aggregations with different allele frequencies. The aggregated distributional pattern of bay scallops during the spawning season (Marelli et al. 1999) is conducive to this type of genetic variation. Regardless of the reason, the increasing homogeneity among subpopulations as collections are amassed must be a result of a general averaging of the heterogeneous genetic diversities among cohorts.

Constituent Populations

Core. Genetic evidence indicates that Core is the largest and most stable population, and it is essentially self-sustaining (Table 10, characteristic 2). Core has the greatest genetic diversity (both allozyme and mtDNA) and connectivity. Although the geographical extent of Core varied among years, it always included the genetically diverse subpopulations ST and HO, indicating that gene flow from these subpopulations is important for maintaining the peripheral populations and the less stable Core subpopulations CK and HE, which exhibit high genetic relatedness to ST or HO and thus probably receive recruits from those subpopulations (Hellberg et al. 2002).

Evidence of genetic bottlenecks in HE98 (Table 10, characteristic 3) also implies that Core's less stable subpopulations are sometimes composed of offspring from only a few parental bay scallops. The southernmost AN is sufficiently differentiated genetically from other Core subpopulations in some years so as to be excluded from Core. It is the only Core subpopulation located in an estuary behind barrier islands and thus has physical barriers to gene flow that other Core subpopulations do not have, and it is subjected to red tides more frequently than other Core subpopulations.

Core exists and its discrete subpopulations (separated by 30 km or more (Arnold et al. 1995, Arnold et al. 1997)) have high connectivity because extensive seagrass beds are able to grow in the clean, quiet, shallow, open water of the Big Bend (Iverson & Bittaker 1986). The openness of Core provides the opportunity for current-driven larval dispersal within the population and between it and other populations. However, the upwellings generated offshore of the Cape San Blas and Anclote/Tampa Bay—area headlands and the slow, variable nearshore water currents that the headlands help to create in the Big Bend likely inhibit transport from Core both downstream and upstream (e.g., Cowen & Sponaugle 2009). In almost any current pattern, particles such as larvae are transported around within the Big

A 1994							
Rainfall Division							
Month	1	2	3	4	5	6	7
Jan	5.8	8.5	7.1	4.0	3.2	4.1	3.0
Feb	2.6	1.3	1.8	2.5	2.8	5.2	3.6
Mar	8.4	3.5	2.6	2.2	2.2	2.4	0.7
Apr	4.8	1.9	2.4	3.5	3.6	5.8	1.8
May	3.7	2.5	2.7	2.2	2.6	3.9	5.3
June	12.7	9.0	8.7	9.0	7.7	6.6	2.2
July	12.9	7.8	9.2	7.3	7.2	4.2	2.3
Aug	9.8	7.8	8.8	8.4	7.2	11.1	7.0
Sept	6.5	6.5	7.9	10.1	9.7	12.7	12.7
Oct	9.6	8.3	4.2	4.2	5.5	5.8	4.2
Nov	2.4	2.4	5.8	4.1	4.5	9.7	4.1
Dec	2.8	2.4	2.9	3.7	4.8	6.5	3.5
AVG	6.8	5.1	5.3	5.1	5.1	6.5	4.2

B 1995							
Rainfall Division							
Month	1	2	3	4	5	6	7
Jan	3.4	3.3	2.8	2.7	3.3	3.2	3.1
Feb	3.0	1.7	1.2	2.2	1.6	2.0	0.3
Mar	5.8	3.6	2.4	2.3	2.4	3.3	3.5
Apr	5.4	3.8	3.0	3.3	3.3	3.8	3.1
May	5.9	3.4	3.2	2.1	4.0	3.4	2.2
June	5.6	7.5	8.9	9.8	11.9	14.3	7.4
July	6.9	6.1	6.6	9.7	10.8	7.5	4.2
Aug	7.3	10.3	9.4	11.5	11.6	15.1	7.0
Sept	3.4	4.8	5.9	7.4	8.0	7.4	5.1
Oct	7.4	4.1	6.4	8.0	11.8	11.8	10.8
Nov	6.9	2.8	1.2	1.9	0.9	1.7	0.2
Dec	3.2	1.6	2.0	0.8	0.6	1.0	1.7
AVG	5.3	4.4	4.4	5.1	5.9	6.2	4.1

C 1996							
Rainfall Division							
Month	1	2	3	4	5	6	7
Jan	3.6	2.1	5.5	4.7	2.3	2.1	1.6
Feb	5.0	1.3	1.9	1.8	0.6	0.8	0.5
Mar	9.2	9.0	10.0	7.0	3.8	3.9	1.9
Apr	6.0	2.9	2.4	2.2	1.8	3.0	1.9
May	2.3	2.0	2.9	4.5	7.9	8.6	3.7
June	4.9	6.9	7.8	7.9	8.4	11.7	6.0
July	7.4	6.2	4.2	4.4	4.3	3.4	2.4
Aug	9.4	8.0	7.3	5.6	6.5	6.5	4.6
Sept	6.3	4.3	4.4	4.9	4.6	7.0	5.9
Oct	6.1	8.6	4.5	4.5	5.8	9.5	11.8
Nov	1.7	1.2	0.8	0.9	0.5	1.1	0.7
Dec	4.9	4.1	2.6	2.4	0.8	1.2	0.7
AVG	5.6	4.7	4.5	4.2	3.9	4.9	3.5

D 1997							
Rainfall Division							
Month	1	2	3	4	5	6	7
Jan	3.1	3.5	1.9	1.9	1.7	3.2	4.0
Feb	5.2	1.7	1.1	1.4	1.5	3.1	0.4
Mar	3.0	2.5	3.0	2.3	3.0	3.2	1.8
Apr	6.7	7.9	4.3	7.1	5.5	4.6	2.0
May	5.4	3.1	2.4	3.1	4.8	5.1	2.7
June	6.6	6.3	6.7	6.2	8.8	14.5	5.8
July	8.7	7.3	7.4	7.9	8.5	6.2	5.4
Aug	5.9	6.1	6.8	6.8	6.0	8.9	3.9
Sept	3.3	3.0	6.5	8.0	6.8	11.6	8.9
Oct	4.8	5.8	4.6	3.2	1.2	2.0	2.6
Nov	10.2	4.2	3.8	5.8	3.3	2.8	2.2
Dec	4.9	7.8	10.9	9.6	6.6	6.5	5.1
AVG	5.6	4.9	4.9	5.3	4.8	6.0	3.7

Bend, and only sometimes are eventually transported out (Ohlmann & Niiler 2005). Particularly during the fall/winter bay scallop spawning/recruitment season, northward-moving currents along the coast that stimulate downwelling in the northern part of the Big Bend (Fig. 4C) and the Big Bend winter gyre (Fig. 4D) could retain larvae within the Big Bend, and southward-moving currents that tend to veer offshore (Fig. 4D) could inhibit Core-to-Southwest larval transport along the peninsula. Sustained northwesterly winter winds could generate currents that promote larval transport from Panhandle to Core (Fig. 5A) and contribute to the intermittent genetic similarities between those two populations.

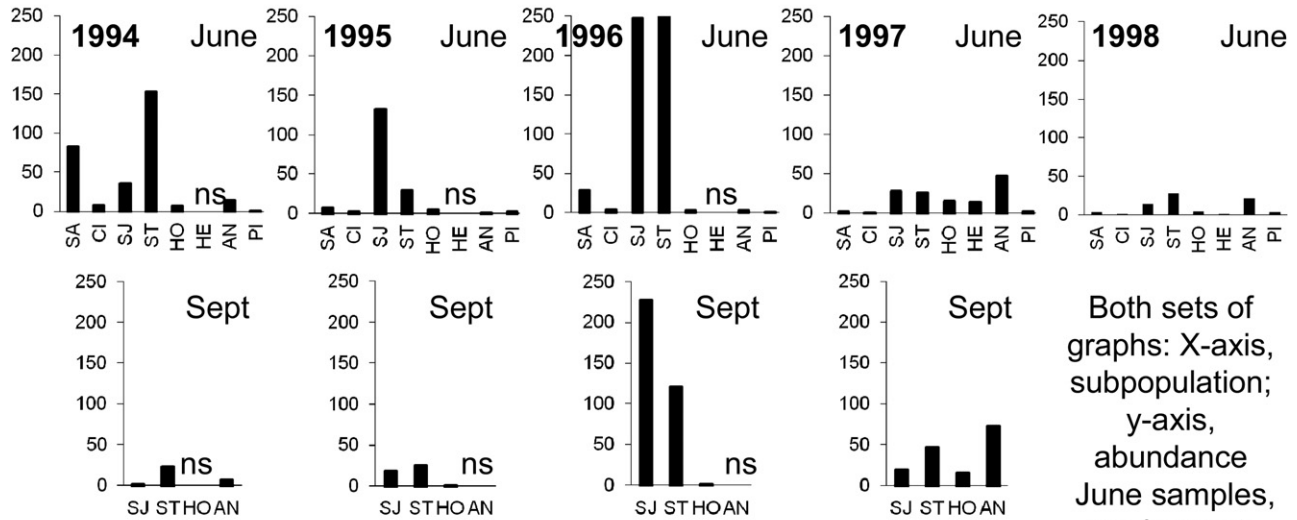
Red tides, which can render subpopulations extinct at any time of the year, were present in and offshore of Anclote Estuary more so than of other Core subpopulations. AN was almost completely eliminated by red tide in 1996 (Arnold et al. 1997). Red tides contribute to either genetic differentiation or genetic homogenization of subpopulations, depending on the sources and effective population sizes (Hedgecock 1994) of larvae reestablishing the decimated subpopulations. Despite the 1996 near-extirpation, the genetic diversity of AN97 was not notably low, and pairwise genetic distances between AN97 and other Core subpopulations were low (Fig. 3C), suggesting that gene flow was high.

Peripheral populations. Compared with Core subpopulations, peripheral subpopulations undergo greater temporal variation in genetic composition and genetic variation and, consequently, generally have greater pairwise genetic distances within and between subpopulations than Core. All peripheral subpopulations are located in bays where, to different degrees, limited exchange with open water impedes successful recruitment among subpopulations, and variation in salinity and temperature increases bay scallop mortality. Red tides and floods, which are more common in areas occupied by peripheral populations than in Big Bend waters (compare A–D in Fig. 3), also decrease abundance by increasing mortality and, thus, contribute further to the abundance fluctuations and intermittent extinctions experienced by these subpopulations. Consequently, all peripheral populations have multiple characteristics of nonequilibrium recruitment and population instability (Table 10, characteristics 1, 3, and 4), as well as enhanced genetic differentiation between subpopulations (Pannell & Charlesworth 2000).

Overall, similarities in allele frequencies and low subpopulation-level pairwise genetic distances (Tables 6 and 7B) suggest that Panhandle subpopulations could constitute a quasi-independent population. The UPGMA cluster analysis of Bert et al. (2011, Fig. 2A) supports that idea. However, relatively high pairwise genetic distances between potential parent–offspring pairs and between collections taken within a single year (Table 10,

Figure 6. (A–D) Annual rainfall for years 1994 to 1997, respectively. Rainfall amounts (in inches, as downloaded from <http://www.nhc.noaa.gov/pastall.shtml>) for NOAA rainfall divisions shown in Figure 3. Shading for monthly relative rainfall intensity levels, as defined in Methods and Materials: very wet, white print on black background; wet, white print on dark-gray background; average-wet, black print on medium-gray background; average-dry, black print on light-gray background; dry, black print on white background; very dry, bold black print on white background with black outline.

Standardized Adult Abundance



Spat Abundance

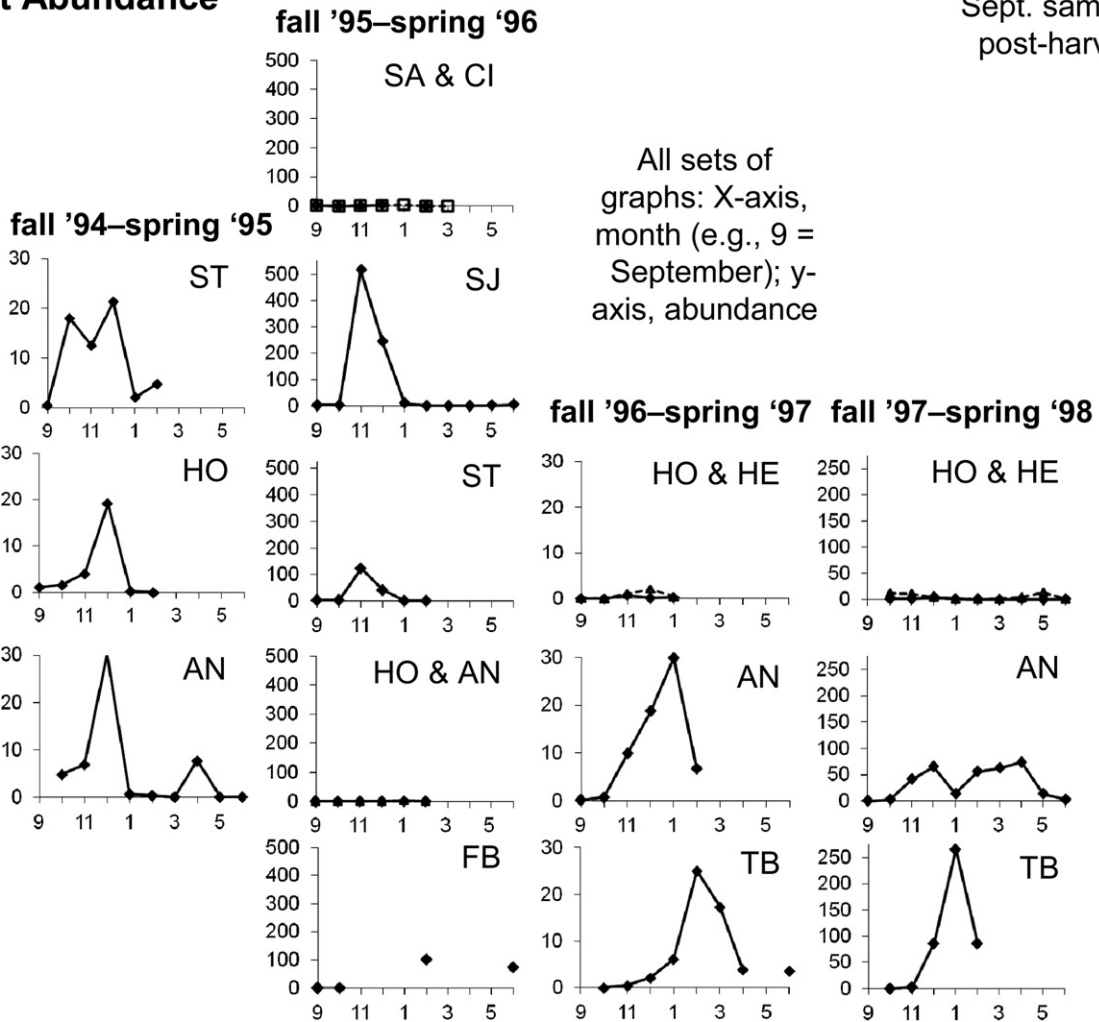


Figure 7. Florida Gulf bay scallop adult and spat abundances (note variation in scale among years in spat abundances). Abundances (defined in Methods and Materials) were not available for all collection in all years. The 1994 adult abundance is included because the September abundance of that parental-adult year class spawned the 1994/1995 spat that we sampled subsequently as adults (1995 cohort); other samples of parental adults, spat, and year cohorts are similarly related. Adult abundances: collection abbreviations (x-axes) defined in Table 1; June, scallops surveyed before opening of recreational harvest season; September, scallops surveyed after closing of recreational harvest season; ns, no sample. Spat abundances: x-axes, months of sampling (9, September; 11, November; 1, January; and so forth).

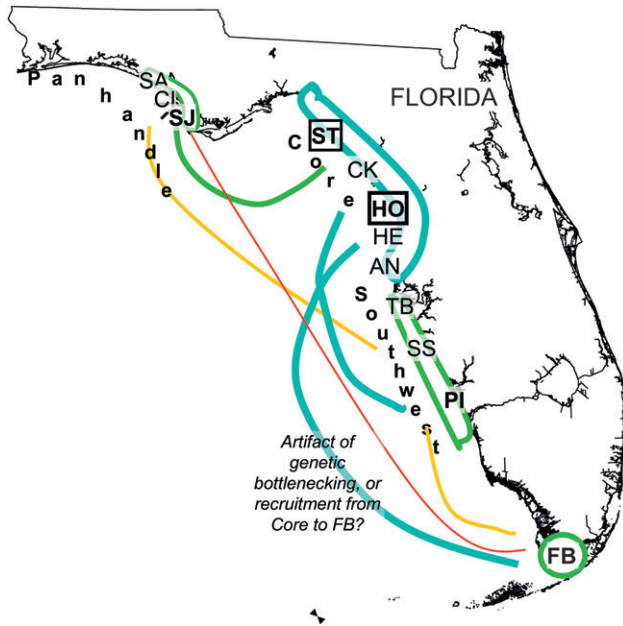


Figure 8. Relative magnitudes of gene flow pathways for Florida Gulf bay scallops, inferred from appropriate pairwise genetic distances (Θ_{ST} , which is inversely related to gene flow) in Figure 3, averaged over all years. Colored enclosed shapes, gene flow levels among subpopulations within populations (labeled); colored lines, gene flow between populations; blue, high (average $\Theta_{ST} < 0.009$); green, moderate (average $0.010 < \Theta_{ST} < 0.019$); yellow, low (average $0.020 < \Theta_{ST} < 0.029$); red, very low (average $\Theta_{ST} \geq 0.030$). Subpopulation abbreviations are defined in Table 1. Bold print, most likely source of subpopulations within each population; abbreviations for ST and HO, most likely main recruitment sources for the metapopulation also boxed.

characteristic 4, Panhandle), together with evidence of drift or bottlenecks (Table 10, characteristic 3, Panhandle), suggest that subpopulations are less stable than Core subpopulations and that self-seeding or exchange of larvae among subpopulations is highly variable. The broadly ranging connectivity levels between Panhandle and Core (from genetically indistinguishable in 1995 to well differentiated in 1998) illustrate further the variable nature of Panhandle compared with Core. However, the relationship of Panhandle subpopulations to Core varies; SJ is more closely related to Core than SA or CI, as exemplified by its inclusion in Core in 1996.

Several external factors contribute to the variation in Panhandle's population genetic structure. Cape San Blas and associated water currents tend to isolate Panhandle (Fig. 4) from peninsular populations, and SA and SJ are remote from open water and in different bay systems, rendering the likelihood of recruitment from peninsular populations and the regular exchange of recruits within Panhandle typically low. Panhandle is decimated periodically by floods, which can eliminate or impact populations severely in multiple ways (Etherington & Eggleston 2000, Wolff & Mendo 2000, Paerl et al. 2001, Burkholder et al. 2004, Mallin & Corbett 2006), sometimes for prolonged periods (Litaker & Tester 2003). Floods reduce Panhandle abundance, generating genetic bottlenecks and contributing to genetic drift and instability (Table 10, characteristics 3 and 4). Red tides can also decimate Panhandle subpopulations and inhibit larval dispersal. Nevertheless, Panhandle subpopulations, apparently, can attain very

high abundances within 1 generation (e.g., Fig. 7, SJ in 1996), a source of variation that could contribute further to high genetic distances or to generate greater genetic connectivity among Panhandle subpopulations and between Panhandle and peninsular subpopulations, depending on the origins and number of recruits.

Substantial numbers of bay scallops occurred historically throughout bays southward of Core to Pine Island Sound (Haddad 1989, Lu & Blake 1997, Marelli & Arnold 2001). Southwestern Florida seagrass beds are best developed near the seaward mouths of bays and channels (Yarbro & Carlson 2013), so gene flow among Southwest subpopulations should be common. However, Southwest subpopulations are not closely related, nor do they seem to form a quasi-independent population. Red tides, which have frequented the waters between Anclote Estuary and Pine Island Sound for decades (Tester & Steidinger 1997, Steidinger et al. 1998, Landsberg et al. 2009, Walsh et al. 2009), and typical offshore-directed and upwelling currents (Fig. 4), may contribute routinely to the lack of genetic cohesion in Southwest by depleting abundances and inhibiting larval transport. The low mean pairwise Φ_{ST} value for PI/PI pairs (0.000) compared with analogous Φ_{ST} means (SJ/SJ, 0.019; ST/ST, 0.016; HO/HO, 0.004 (K-W test separated PI/PI mean and SJ/SJ mean; $P < 0.01$)) suggests that PI, the only semipermanent subpopulation in Southwest, is mainly self-recruiting. But, genetic bottlenecks in PI96 (Table 10, characteristic 3) and chronically low PI census numbers (Arnold et al. 1994, Arnold et al. 1995, Arnold et al. 1996, Arnold et al. 1997, Arnold et al. 1998b, Arnold et al. 1999, Greenawalt-Boswell et al. 2007) indicate that recruitment is usually from small numbers of parental individuals. Allee effects may hinder reestablishment of sustainable, large subpopulations in Southwest after severe depletion (Marelli et al. 1999).

Currents offshore of Tampa Bay and Sarasota Bay are particularly variable and can be adverse to larval recruitment into the bays (Fig. 4). When successful recruitment occurs, it may be from multiple sources. The 1997 Tampa Bay cohort has characteristics of a subpopulation generated from multiple groups of larvae with some level of genetic differentiation between them (Table 10, characteristic 1). Or, recruitment may be successful because larvae bypass unfavorable open-water conditions. The large aggregation in Sarasota Bay (SS98) that occurred the year after the geographically proximal TB97 aggregation was found may have been composed of TB97 offspring. Recruitment, at least to spat size and possibly of TB97 offspring, was successful in nearby Tampa Bay in 1997–1998 (Fig. 7). Tampa and Sarasota bays are connected by an intracoastal waterway. Interbay larval transport could bypass open-water red tides and the unfavorable currents.

Genetic evidence presented here (Table 10, characteristic 4) and in Bert et al. (2011) indicates that FB is isolated from other populations and, along with census data, that FB has undergone repeated abundance reductions. The retention of high allozyme genetic variability indicates that the population crashes are short-term (Cornuet & Luikart 1996, Bowen & Grant 1997, Zenger et al. 2003). Bay scallops were sufficiently abundant for collecting scientific samples from western Florida Bay in 1979 and 1980 (T. M. Bert, unpubl. data), 1990 (Marelli et al. 1997a), 1993 (Blake & Graves 1995), and 1998 (current study), and spat were found in 1996 (Fig. 7). However, bay scallops were apparently absent during at least some intervening

TABLE 10.
Genetic evidence for characteristics of the Florida Gulf bay scallop metapopulation.

Characteristics group*	Evidence	
	Allozyme locus	mtDNA
1. Recruitment from genetically differentiated aggregations	<p>Metapopulation: Many significantly different allele and genotype frequencies between collections; significantly greater percentage of loci out of H-W equilibrium in subpopulations composed of collections taken 3 y or 4 y than in subpopulations composed of collections taken 1 y or 2 y; greater percentages of loci out of H-W equilibrium in subpopulations composed of multiple annual collections than in their constituent collections; many highly significant pairwise F_{IS} values</p> <p>Panhandle: Generally high levels of differentiation in allele and genotype frequencies among collections from different years</p> <p>Core: Very high percentage of loci out of H-W equilibrium despite population stability</p> <p>Southwest, TB97: unusual allele frequencies at multiple loci; high heterozygosity; greatest average number of alleles per locus</p>	<p>Significant parent/offspring pairwise genetic distance (SJ95/SJ96)</p> <p>Significant parent/offspring pairwise genetic distance (ST96/ST97)</p> <p>High pairwise nucleotide diversity values</p>
2. Population stability, longevity, high gene flow, self-recruitment	<p>Core: Little variation in allele or genotype frequencies or in pairwise distances between generations and subpopulations; close relationship among subpopulations in UPGMA cluster analysis (Bert et al. 2011); sometimes, correlated adult–recruit abundances (Arnold et al. 1998a)</p>	<p>High pairwise nucleotide diversities; significantly high mean pairwise nucleotide diversity compared with peripheral populations</p>
3. Drift, bottleneck, low N_e	<p>Panhandle, SJ96: significant excess of heterozygotes according to BOTTLENECK model Panhandle, SJ98: low P_{95}, P_{99}, n_a</p> <p>Core, HE98: Greatly altered allele frequencies between HE97 and HE98; high pairwise genetic distances; low P_{99}, n_a</p> <p>Southwest, PI96: Lowest H_o, low P_{99}, n_a; low percentage of loci with heterozygote deficits; greatest inbreeding coefficient; very high F_{IS} value</p>	<p>High pairwise genetic distances</p> <p>Low genetic diversity values</p>
4. Population instability, intermittent extinction/recolonization, lower gene flow	<p>Peripheral populations: Comparatively high interannual variation in allele frequencies; higher between-subpopulation and interannual variation in pairwise genetic distances compared with Core</p> <p>Panhandle: Significant differences in genotype frequencies between collections within subpopulations; intermittent high pairwise genetic distances between neighboring subpopulations (SA/CI in 1996, SA/SJ, in 1998); high genetic distances between potential parent–offspring pairs (SA97/SA98, SJ97/SJ98) and between cohort pair SA96/CI96</p> <p>Southwest: Ephemeral subpopulations (TB, SS); relatively high mean pairwise genetic distances between subpopulations (TB97/PI97)</p>	<p>Compared with Core, overall lower mtDNA diversity (Hedgecock 1994), greater between-subpopulation and interannual variation in genetic distance</p> <p>Significant difference in haplotype frequencies, SA98/SJ98; significantly high genetic distance between potential parent–offspring pair SJ95/SJ96 and between cohort pair SA98/SJ98</p> <p>Variable pairwise genetic distances</p>

continued on next page

TABLE 10.
continued

Characteristics group*	Evidence	
	Allozyme locus	mtDNA
	FB: High genetic diversity measures as a result of higher frequencies of less-common alleles (frequencies, >0.05 to <0.25 in other collections) (Nei et al. 1975, Leberg 1992, Brookes et al. 1997); depleted in rare alleles (frequencies, <0.05 in other collections) (Nei et al. 1975); high percentage of allele frequencies significantly different from other subpopulations; very high pairwise genetic distances at both subpopulation and population levels (Chakraborty & Nei 1977)	Absence of haplotype diversity; (Wilson et al. 1985, Nei 1987, Birky 1991, Luikart & Cornuet 1998, Matocq et al. 2000, Carlin et al. 2003, DeYoung & Honeycutt 2005); high nucleotide divergence from other subpopulations; very high pairwise genetic distances at subpopulation and population levels, particularly Core ST and neighboring PI

* Inclusion in a group does not imply that all characteristics in the group apply to each collection or subpopulation listed. Characteristics are grouped according to similarities in population genetics measures that result from the effects of those characteristics. Collection and subpopulation abbreviations are defined in Table 1.

years (W. S. Arnold, unpubl. data; J. M. Stevely, Florida Sea Grant Program, pers. comm., January 2013). Although the Florida Keys seagrass beds are among the most extensive on earth (Fourqurean et al. 2002), bay scallops are rarely seen outside of Florida Bay basins, indicating that local recruitment is limited to within and among the basins. The close relationship of FB with Core (low 1998 pairwise allozyme-locus genetic distances) may be an artifact of the high genetic diversity of Core and high heterozygosity of FB. The near-absence of mtDNA diversity in our FB collections and high mtDNA diversity level recorded for FB by Blake and Graves (1995) demonstrate that gene flow from other populations into FB does not occur regularly.

Florida Bay is isolated in part because no seagrass flats capable of supporting bay scallops exist between the Florida Keys and FB's nearest neighbor, PI, which is more than 250 km northward and at the dispersal limit of some models for habitat-specific marine organisms (e.g., Cowen et al. 2006). Nor are currents conducive to larval transport from subpopulations farther north into western Florida Bay (Fig. 4C, D). Some FB population crashes may be associated with die-offs of seagrass beds in the western basins inhabited by bay scallops. Between 1987 and the early 1990s, a massive reduction in seagrass density and abundance occurred in western Florida Bay; some recovery had begun by 1994 (Hall et al. 1999). The bay scallop aggregation we sampled may have established or expanded since that seagrass die-off.

Interannual Variation

The basic metapopulation structure varies intergenerationally from nearly panmictic to highly subdivided. The interannual variation can be related to the external factors we considered—what happens, and when and where it happens.

In the Florida Gulf, tropical cyclones and seasonal storms are most common during fall and winter (Weisberg et al. 2001, Weisberg & He 2003)—the principal bay scallop spawning/recruitment season. Tropical cyclones, which move vast quantities of water abruptly, mix water columns down to at least 25 m, and greatly alter or reverse normal current flows (Ohlmann &

Niiler 2005, Weisberg et al. 2009a), can modify population genetic relationships by generating currents that transport larvae great distances or to unusual places relative to transport by normal currents (Caputi & Brown 1993, Shenker et al. 1993, Etherington & Eggleston 2000, Etherington & Eggleston 2003, Montane & Austin 2005, Briones-Fourzán et al. 2008, Eggleston et al. 2010). Before the 1994/1995 spawning/recruitment season, 2 tropical storms generated heavy rainfall over the panhandle (Fig. 3A), causing floods that, together with harvesting, reduced SJ parental adult abundance by 96% (Arnold et al. 1995). Then, Hurricane Gordon passed across southern Florida. Its winds may have helped to homogenize the 1995 cohort genetically. As it approached southern Florida, southeasterly winds would have set up northwestward-flowing currents that could move larvae from ST to Panhandle (Fig. 5D). As the hurricane traversed Florida, northeasterly winds could have dispersed the red tide temporarily (Burkholder et al. 2004) in southwestern Florida waters (Fig. 3A) and moved larvae from Core to Southwest. Mitochondrial DNA haplotype and nucleotide diversities were high in ST95 compared with other 1995 cohort collections, as might be expected if ST was the source and other subpopulations were recipients of subsets of the ST larval pool.

Huge tropical cyclones slowly traversing the central Gulf generate sustained winds for days (e.g., Weisberg et al. 2009a). Those moving south to north, such as Hurricane Opal in October 1995 (Fig. 3B) set up opposing regional gyres with rotational directions like those in Figure 5C. As they pass over the panhandle, wind circulation would change to that depicted in Figure 5B. During the principal bay scallop spawning season, these gyres could divide bay scallop larvae into northern and southern groups separated somewhere in west-central Florida waters, a model that fits the genetic distance pattern of the 1996 bay scallop cohort (Fig. 3B). Hurricane Opal may have established two genetically differentiated larval pools that separated ST and Panhandle subpopulations from PI and dispersed the red tide in the waters around Panhandle (red tide was not recorded again after passage of that hurricane; <http://www.nhc.noaa.gov/1995opal.html>; FWRI, unpubl. data), allowing Core larvae to enter St. Joseph Bay, genetically

homogenizing SJ and Core larvae (as indicated by the exceptionally broad Core observed in 1996). The genetic bottlenecking of PI96, perhaps the result of low parental cohort PI95 abundance (Fig. 7), contributed the genetic differentiation between PI and northerly subpopulations. Similarly, poor recruitment in SA and CI (Fig. 7) may have contributed to differentiation between those subpopulations.

The opposing pattern of genetic relatedness in 1997 compared with that of 1996 may have been influenced similarly by a tropical cyclone, but with a key difference in its path. As Hurricane Opal moved northward toward Florida, the winds affecting nearshore Florida Gulf waters would have been principally southerly, followed by southeasterly, then easterly, as the storm traversed the panhandle. As October 1996 Tropical Storm Josephine moved northeastward toward Florida, winds would have been principally southwesterly (Fig. 5B), followed by northeasterly (Fig. 5C) as the storm crossed northwestern Florida (Fig. 3C). Thus, the gyres generated by Tropical Storm Josephine could have transported larvae from Core to Southwest. Larval dispersal between TB and PI may have been inhibited by the red tide offshore of SS, which developed 3 wk after the cyclone passed (<http://www.nhc.noaa.gov/1996josephin.html>; FWRI, unpubl. data).

Winter storms, which have strong northeasterly to northwesterly winds that can be sustained for days and are strongest during October through December (Yang & Weisberg 1999)—the principal spawning/recruitment season—also generate current patterns like those shown in Figure 5A through C. Any of those current patterns would tend to generate gyres that separated larvae into regional groups with population genetic patterns similar to those seen in the 1996 or 1997 cohorts.

By any estimation, the time period from fall 1997 through 1998 was anomalous. Compared with bay scallop collections from other years, 1998 collections had a significantly low overall percentage of loci deviating from H-W equilibrium; significantly high allozyme-locus heterozygosity, particularly in southern subpopulations (HO-FB); significantly low level of inbreeding; significantly high mtDNA nucleotide diversity; and significantly high overall mean allozyme-locus and mtDNA pairwise genetic distances. Many allozyme-locus collection-level pairwise genetic distances were among the highest, including some between neighboring Core subpopulations (Fig. 3D), and mtDNA diversities were redistributed (peripheral subpopulations were more diverse). The 1998 cohort exhibited multiple examples of genetic drift, genetic bottlenecking, and low gene flow (Table 10).

Climatically, Florida was affected by a strong El Niño event. In Florida, El Niños alter wind velocities and patterns, change rainfall patterns and amounts, and suppress hurricanes (Schmidt et al. 2001), triggering a cascade of oceanographic and hydrological events that affect dramatically the shallow-water marine environment (Müller-Karger 2000). No tropical cyclones occurred during fall 1997. Thus, seasonal current domains (Fig. 4), which would tend to isolate bay scallop populations, probably prevailed during the spawning/recruitment season. The absence of strong currents also may have allowed red tides to proliferate and assume their unusual nearshore-to-offshore configurations (Landsberg et al. 2009) and to bloom in unusual places. The only year in which red tide bloomed in the Big Bend was 1997. Heavy El Niño-related rainfall caused extensive flooding (Del Castillo et al. 2001,

Jolliff et al. 2003), which lowered salinities in bays throughout the Florida Gulf and generated low-salinity plumes that swept along the panhandle west of CSB (Müller-Karger 2000) and down the peninsula from Cedar Key to Anclote Estuary (Jolliff et al. 2003). Nutrient-rich water in flooded panhandle bays stimulated phytoplankton blooms (Gilbes et al. 2002) that produced detritus-laden anoxic bottom layers, which killed benthic-dwelling organisms (Collard et al. 2000), including bay scallops. Freshwater outflows greatly damaged seagrass beds in the Big Bend (Carlson et al. 2003). Prolonged north-to-south current flow generated cold-water upwelling west of CSB and off the peninsula (Weisberg & He 2003). This extraordinary event overload reduced bay scallop abundances (Fig. 7) and apparently curtailed at least some larval dispersal, resulting in the unusual genetic diversity patterns and high levels of genetic differentiation (especially in Panhandle subpopulations), genetic bottlenecking (Panhandle and Core subpopulations), and genetic instability (Panhandle subpopulations) we recorded for the 1998 cohort (Fig. 3D; Table 10, characteristics 3 and 4).

Management of the Metapopulation

Status of the Metapopulation

Many scallop fisheries have collapsed as a result of reduction in habitat quantity and quality, coupled with overfishing (Orensanz et al. 2006). Habitat degradation and fishery-related abundance declines can affect metapopulations by reducing numbers of individuals and inducing changes in rates of migration, colonization, and extinction (Hui & Li 2003). These factors decrease genetic variation, accelerate its loss, and increase genetic drift (Saavedra & Peña 2005, Allendorf et al. 2008). The combined effects of prolonged intensive harvesting, loss of critical seagrass habitat, decline in water quality, and mortality resulting from red tides and floods have decreased the number of stable populations in the Florida Gulf bay scallop metapopulation to 1: Core. Other populations are, to temporally varying degrees, sinks. Moreover, the rates of near or total extirpation of all subpopulations, including those in Core, have increased greatly and have extended for longer periods of time in recent years (Marelli et al. 1999, Greenawalt-Boswell et al. 2007, Arnold 2008). The continued general reduction in bay scallop abundance and number of stable subpopulations after years of closure of most of the fishery and restrictions on open areas (Harrison & Taylor 1997) indicates the metapopulation is in decline.

Fishery Management Options

Understanding metapopulation structure and identifying source-sink connections is important for determining which subpopulations to protect (Warner & Cowen 2002, Figueira & Crowder 2006, Watson et al. 2012). One management strategy is to protect only the principal source subpopulation. Underpinning this strategy is the idea that a metapopulation can persist if it contains only one self-persistent subpopulation from which larvae are also exported to sink subpopulations (James et al. 2002, Tian et al. 2009, White et al. 2010b, Watson et al. 2011), because at least some sinks should persist or be recolonized (Shepherd & Brown 1993, Roberts 1997). Influx of alleles from the (usually the more genetically diverse) source is also needed to maintain genetic variation, which is important for long-term population resiliency, in sinks (Gaggiotti & Smouse 1996). If

source-to-sink larval dispersal is reliable, sinks can endure heavy fishing as long as the source is protected (Fogarty 1998, Yakubu & Fogarty 2006). However, as sinks become more chronically depleted, their dependence on the source for sustainability and maintenance of genetic diversity increases. Then, the need to maintain source abundance well above the level at which the Allee effect could negatively affect recruitment potential is paramount (Quinn et al. 1993).

At the other extreme is a strategy to conserve all subpopulations by managing each independently (Tuck & Possingham 2000, Smedbol et al. 2002). Underpinning this strategy is the idea that the metapopulation has an increased probability of long-term survival when its subpopulations are numerous and not depleted routinely (Thrall et al. 2000). When many subpopulations are depleted, stock replenishment from other subpopulations is reduced, especially when connectivity is low (Orensanz et al. 2006).

The stringency of managing the Florida Gulf bay scallop fishery should depend on the sensitivity of the metapopulation to extinction or change in form. Some characteristics of the metapopulation and of Florida Gulf bay scallops indicate that the metapopulation could be sensitive to total collapse. First, only 1 subpopulation in Core (ST or HO, but rarely both) is a stable source for the entire metapopulation. Second, smaller but important peripheral subpopulations (i.e., SJ, PI) are not stable and not connected reliably with other subpopulations. Thus, they and other peripheral subpopulations are at high risk of extinction (Hanski & Gaggiotti 2004). Third, and last, short-lived, semelparous species such as bay scallops lack the population-level buffering capacity of long-lived, iteroparous species (Sale et al. 2006). Other characteristics indicate that the metapopulation is resilient. First, Core could sustain itself and supply recruits to other populations, if all were managed properly. Second, Core is relatively stable. It has the highest genetic diversity and connectivity, occupies the highest quality habitat, and is not subject to high frequencies of the environmental impacts we considered.

Current Florida Gulf bay scallop fishery regulations include a component that is not advocated as a management strategy for metapopulations: heavy harvesting in source subpopulations. Harvest is allowed in SJ and in the important ST and HO, as well as CK and part of HE. In addition, since the 1995 regulations on the Florida Gulf bay scallop fishery were enacted, management has repeatedly relaxed regulations by extending both area fished and fishing season (Florida Administrative Code, Chapters 46–18 and 68B-18). Maintaining high Core abundances is critical to the long-term perpetuation of other subpopulations. Harvesting in ST has not contributed to ST's sustainability (FWRI unpubl. data; S. Geiger, pers. comm., January 2014). Harvesting in the now high-density HO may result in the same outcome. The general depletion of local sources in Panhandle and Southwest further enhances the importance of Core for maintaining the metapopulation, but it is not clear that Core's reproductive viability is sufficient to allow "rescue" of sink subpopulations (per Brown and Kodric-Brown (1977) and Hanski (1998)). More important, depletion of Core could change the fundamental metapopulation structure from core periphery to network, in which Core subpopulations are as much sinks as sources (Quinn et al. 1993). Network metapopulations, particularly those with small, fragmented subpopulations, such as those seen in Florida Gulf bay

scallops, require multiple protected subpopulations (i.e., much more complicated management) to increase the probability that the metapopulation persists and to maintain adequate gene flow throughout (e.g., Rozenfeld et al. 2008). However, pressure from stakeholders to increase harvest levels of productive subpopulations can be high and has been successful in easing regulations in the past (Geiger et al. 2006).

Based on the findings presented here, our suggestions for management and research are as follows: First, implement a "hybrid" management strategy that protects multiple potential source subpopulations to ensure better recruitment success for all subpopulations than a strategy that protects only 1 source subpopulation (Orensanz et al. 2006), particularly because the principal Core source subpopulation changes over time (ST when we conducted our study, HO now). This strategy could eventually result in an overall higher yield because sink subpopulations and historically productive Core subpopulations (e.g., AN) are more likely to increase in abundance (Tuck & Possingham 2000). Second, assess the effects of the recent regulatory expansions on subpopulation abundances. Adjust management if needed, using the recommendation presented above. Third, continue studies such as the one presented here. Intermittent population genetics studies are essential to determine metapopulation status and form, to determine recruitment sources, and to track changes in genetic diversity. Explore the potential for monitoring the external events we considered to generate timely, predictive models for subpopulation abundances and metapopulation structure (Fogarty & Botsford 2007, Werner et al. 2007) before harvest season. Fourth, continue stock enhancement efforts, but target source subpopulations, because higher frequencies of natural impacts in peripheral subpopulations reduce the probability of their long-term success through stock enhancement (Lipcius et al. 2008). Genetic monitoring must be an integral part of all stock enhancement efforts because many stock enhancement strategies can reduce genetic diversity and alter population genetic structure of supplemented populations through numerous avenues (Bert et al. 2007). Fifth, and last, continue improving water quality in historical bay scallop habitats. Numerous regional efforts are ongoing to improve water quality and, thereby, expand seagrass coverage in areas inhabited by bay scallops (Lewis et al. 1999, Johansson & Greening 2000), with some evidence of success (Greening & Janicki 2006). These efforts should be strongly supported.

Getting the Picture: Long-Term Studies, Multiple Markers, and External Factors Are Important

Identifying and classifying metapopulation structure using population genetics can be difficult in the marine environment because genetic distances between metapopulation components can be small and gene flow estimates high. To provide confidence in identifying and interpreting metapopulation structure of marine organisms, population genetics studies should be broad in geographical scope, extend over multiple years, include multiple genetic markers, incorporate a comprehensive array of statistical analyses, and draw on oceanographic, climatic, ecological, and life history information. The paucity of studies with these criteria belies their utility for management and conservation.

Studies conducted over broad spatial scales can provide a more holistic understanding of recruitment dynamics and can

elucidate complicated subpopulation connectivity patterns (Etherington & Eggleston 2000). Population genetic relationships can be fully understood only through multiyear studies (Hellberg 2006, Owen & Rawson 2013), because gene flow and isolation are dynamic processes that vary in intensity and duration through time and space (Pruett et al. 2005), especially when populations are not in mutation–drift equilibrium (Slatkin 1993), as is the case for many shallow-water marine invertebrates (Sponer & Roy 2002). Many population genetics studies have demonstrated the value of using multiple genetic markers to evaluate population genetic structure of marine animals, particularly those using both nuclear DNA and mtDNA markers (e.g., Ward et al. 1994, Edmands et al. 1996, Brookes et al. 1997, Smith et al. 1997, Grant & Bowen 1998, Shaklee & Bentzen 1998, Salini et al. 2006, Bert et al. 2011). In population genetics studies of marine organisms, thorough data analysis is essential because genetic differences are typically very small; any significant degree of genetic differentiation is evidence for restricted gene flow (Palumbi 2003). Even small genetic diversity values can provide insight into the origins, histories, and interactions of populations (Bohonak 1999, Hamm & Burton 2000, Pannell & Charlesworth 2000, Sherman et al. 2008). Moreover, the validity of small differences increases when many different statistics or replicas support a specific interpretation. Last, combining population genetic structure and climatic, ecological, and biological factors may lead to the ability to predict population dynamics for resource management. Using this analytical approach, we were

able to define the population genetic structure of Florida Gulf bay scallops, elucidate its annual variation, and document environmental and biological factors of potential influence in shaping the structure annually, represent the Florida Gulf metapopulation gene pool more fully than if we had sampled for a single year, identify the increasing genetic homogeneity among Florida Gulf bay scallop subpopulations over ecological time, and provide recommendations for future research and management of this complex and dynamic metapopulation.

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