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Conservation Genetics Of Commercially Exploited Fishes With Case Studies On Leopard And Nassau Grouper

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CONSERVATION GENETICS OF COMMERCIALLY EXPLOITED FISHES WITH CASE STUDIES ON LEOPARD AND NASSAU GROUPER

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by
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Abstract

CONSERVATION GENETICS OF COMMERCIALLY EXPLOITED FISHES WITH CASE STUDIES ON LEOPARD AND NASSAU GROUPER

By Alexis Michelle Jackson

Overfishing is contributing to significant declines in marine species worldwide. Here, I evaluated the contribution of genetic data to enhancing conservation and fisheries management of commercially important fishes. First, I conducted two empirical population genetics studies on groupers that aggregate to spawn. I evaluated population structure of Nassau grouper (*Epinephelus striatus*) across the Caribbean Sea using mitochondrial DNA, microsatellites and single nucleotide polymorphisms (SNPs). Results suggested ocean currents and long distance migrations of adults to spawning sites may contribute to restricted gene flow and regional genetic differentiation among subpopulations, making it less likely that larvae settle beyond catchment areas of spawning sites. Regional patterns of genetic differentiation warrant international collaboration, standardizing fisheries management and conservation initiatives among countries within genetically isolated clusters. I then evaluated population structure of Leopard grouper (*Mycteroperca rosacea*) in the Gulf of California using mitochondrial DNA and microsatellites. I observed genetic differentiation and asymmetrical connectivity among subpopulations of *M. rosacea*, with divergence of lineages dating to the late Pleistocene and Holocene. Findings suggest a combination of marine reserves, catch quotas, and seasonal fishery closures as a potential management strategy for *M. rosacea* in the Gulf of California. Finally, I conducted a meta-analysis of 386 empirical genetics studies on marine and diadromous fishes in order to evaluate the implications of weak or strong population structure on the implementation of fisheries management. Quantitative adjectives used to describe varying magnitudes of genetic differentiation possessed statistically different mean F_{ST} values in studies utilizing mtDNA, microsatellites and allozymes. Additionally, mean F_{ST} values across stock management strategies were statistically different from one another. Results have major implications for standardizing reporting of metrics of genetic differentiation across empirical population genetics studies focusing on and prescribing stock management strategies for commercially important fishes.

To my family and friends for keeping me inspired, laughing and dancing

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Introduction

> "I believe, then, that the cod fishery, the herring fishery, the pilchard fishery, the mackerel fishery, and probably all of the great sea fisheries are inexhaustible; that is to say that nothing we do seriously affects the numbers of fish. And any attempt to regulate these fisheries seems consequently, from the case of nature, to be useless."
> ~ Thomas Henry Huxley

More than a century after Thomas Huxley's inaugural address at the 1883 Fisheries Exhibition, the rate of collapse in global marine fisheries continues to accelerate (Froese and Kesner-Reyes 2002; Worm et al. 2006). The power of fishing fleets has increased 10 to 25-fold, drastically reducing global marine yields from what they were even 50 years ago (Watson et al. 2013). There are ecosystem-wide consequences associated the overexploitation of marine taxa, as overfishing continues to result in both local and regional extinctions (Jackson et al. 2001; Dulvy et al. 2003). Significant declines in predatory fishes worldwide have shifted the global composition of fisheries landings towards short-lived, low trophic level invertebrates and plantivorous fishes (Pauly et al. 1998; Jackson et al. 2001; Myers and Worm 2003). Severe declines in predatory fishes also impact the interaction strengths between predators and prey within oceanic food web (Worm and Myers 2003), potentially altering community composition (Friedlander and DeMartini 2002; Myers and Worm 2003; Heithaus et al. 2008; Jaureguizar and Milessi 2008). Given the ecological consequences associated with global fisheries collapse and the decline of top predators, it is essential that we prioritize the development of sustainable fisheries management strategies (Pauly et al. 2002).

An initial step towards improving conservation decisions and fisheries management impacting threatened species is the application of genetic principles and molecular approaches (Hedrick and Miller 1992; Avise and Hamrick 1996). Genetic studies can address a variety of topics pertinent to wildlife management including fisheries-induced evolution, effective population size (N_e), adaptive variation, connectivity between populations, and spatial and temporal scales of genetic differentiation. From an evolutionary perspective, we are beginning to comprehend how fishing activities alter life history traits and compromise genetic variation essential to maintaining fitness and breeding success (Olsen et al. 2004; Walsh et al. 2006). Estimates of N_e have been useful in evaluating the risk of inbreeding in both captive breeding programs and wild populations (Taggart et al. 2001; Fraser 2008; Hauser and Carvalho 2008). Finally, understanding patterns of connectivity and population structure has important implications for identification of cryptic species and monitoring genetically distinct stocks (Jagielo et al. 1996; Jorgensen et al. 2005b; Burford and Bernardi 2008).

Knowledge of population structure and connectivity is essential when designing spatially explicit management strategies (Palumbi 2003; Shanks et al. 2003; Palumbi 2004; Palsboll et al. 2007). In the past, the effectiveness of such efforts was challenged by insufficient data on the geographic scale of dispersal for pelagic larvae and the extent of connectivity between populations (Sale et al. 2005). However, by analyzing patterns of genetic variation in molecular markers, it is possible to quantify the extent of larval dispersal occurring among groups (Avise 2004). Based on observed genetic differentiation between groups, inferences can be drawn about the abiotic and/or biotic factors inhibiting or driving divergence among populations (e.g. Bohonak 1999; Barber et al. 2002; Riginos 2005; Soria et al. 2012). Depending on the spatial scale across which distinct groups are identified, international management may be required if potential management units do not align with state or national boundaries (Avise 1998; Koljonen 2001; Payne et al. 2004).

The aim of my dissertation work was to use genetics approaches to enhance conservation and fisheries management of commercially exploited marine fishes. My primary objectives were: 1) to use molecular markers to determine suitable spatial scales for management of commercially exploited groupers that aggregate to spawn and 2) to observe how varying magnitudes of genetic differentiation impact conservation and fisheries management recommendations for marine fishes. To address these objectives I have organized this dissertation into three chapters: 1) Population structure and larval retention in Nassau grouper (*Epinephelus striatus*), a mass-aggregating marine fish, 2) Historical and ecological genetics of Leopard grouper (*Mycteroperca rosacea*) in the Gulf of California, and 3) How does the magnitude of population structure impact fisheries management strategies?

The first two chapters address objective one through empirical population genetics case studies on aggregating fishes, utilizing mitochondrial and nuclear markers. The spatial and temporal predictability of spawning aggregations guarantee fishermen high yields with minimal fishing effort, increasing their vulnerability to overfishing (Johannes 1978; Fulton et al. 1999). Aggregating fishes continue to be caught in large numbers once populations have begun to decline, as all reproductively viable adults migrate to and concentrate at spawning sites (Sadovy and Domeier 2005). Under this scenario, fishermen are not discouraged from fishing until a spawning aggregation has been completely fished out. The third chapter addresses objective two, reporting findings from a meta-analysis of empirical population genetics studies on marine and diadromous fishes. In it I describe the various ways in which conservation genetics results were used to guide fisheries management recommendations and whether there were inconsistencies among studies in the quantitative terms used to describe magnitudes of observed genetic differentiation.

Chapter 1

Population structure and larval retention in Nassau grouper (*Epinephelus striatus*), a mass-aggregating marine fish

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1.1 Introduction

In marine systems, connectivity refers to the exchange of larvae, juveniles or adults among locations, and is a crucial metric when managing populations (Roberts 1997; Palumbi 2003; Sale 2004). Due to the challenges associated with directly measuring connectivity in the field, molecular markers are used as a proxy to assess larval movement and dispersal of organisms (Avise 2004). Successful dispersal events between populations can be inferred based on patterns of genetic variation, as well as the demographic trajectories of populations over evolutionary time scales (Hellberg et al. 2002; Palumbi 2003; Avise 2004). Several biological and physical mechanisms may explain patterns of genetic connectivity and differentiation observed in marine systems. Genetic drift and local adaptation are the primary forces facilitating genetic subdivision when genetic exchange is limited. Additional factors, including ocean currents (Barber et al. 2002b; White et al. 2010), larval behavior (Kingsford et al. 2002), pelagic larval duration (PLD) (Selkoe and Toonen 2011), isolation by distance (Lavery et al. 1996; King et al. 2001b) and historical vicariance (Benzie 1999; Lessios et al. 2001), may also play important roles in either facilitating long distance dispersal or limiting genetic exchange among populations.

The reproductive behavior exhibited by reef fish that aggregate to spawn (Domeier and Colin 1997; Claydon 2004) may serve to further restrict connectivity between localities. A spawning aggregation is a gathering of conspecific fish for the purposes of reproduction and represents a mass point source of larvae for the subpopulation that it comprises (Domeier 2012). Such aggregations are ephemeral and highly synchronized and restricted in space and time, with frequency of spawning and persistence time varying among species (Domeier and Colin 1997; Domeier 2012). Adult fish migrate to spawning sites such that a spawning aggregation is an amalgamation of all reproductive individuals in a given geographic area (i.e. catchment area *sensu* Nemeth 2012). Ocean currents, pelagic larval duration, and the behavior of the larvae themselves will then influence dispersal patterns of larvae spawned at an aggregation site. The larger the catchment area, and the less overlap it has with the catchment of adjacent spawning sites, the smaller the likelihood that settling larvae originate from other locations and greater the potential for genetic subdivision among subpopulations.

Two primary hypotheses predict potential patterns of connectivity among spawning aggregations. The larval retention hypothesis predicts that spawning occurs at times when currents promote larval retention on natal reefs (Johannes 1978; Lobel 1978; Lobel and Robinson 1988). Jones et al. (1999) suggested five lines of evidence for self-recruitment in fishes, one of which is the observed genetic subdivision of some species. If larvae are locally retained, then genetic exchange may be limited among spawning aggregations, allowing them to diverge independently over time via processes of genetic drift and natural selection (Slatkin 1987). In contrast, the larval dispersal hypothesis predicts that spawning times and sites are synchronized to facilitate long distance transport of larvae (Barlow 1981). When larvae are transported long distances from natal reefs, genetic exchange among spawning aggregations is predicted to be high and genetic differentiation low

(Rosenblatt and Waples 1986). Alternatively, connectivity among subpopulations can occur through post larval movements (Love et al. 1991; MacPherson 1998; Dahlgren and Eggleston 2000), shifts in home ranges of adults, as well as adults spawning at multiple aggregation sites (Kramer and Chapman 1999). The extent to which any of these alternative factors contribute to connectivity is poorly understood for most species and assumed to be low, with extremely high fidelity to a single spawning site displayed by species for which data are available (Myrberg et al. 1988; Zeller 1998; Claydon et al. 2012). Thus, spawning aggregations may facilitate further genetic subdivision on a more local scale.

In the Caribbean Sea there is evidence of limited dispersal in both the larvae and adults of reef fishes. Larval dispersal kernels are not predicted to be greater than 200 km (Cowen et al. 2006) and movement of juveniles and adults are likely to range from 10 km to typically < 200 km (Chapman et al. 2005; Jones 2005; Verweij and Nagelkerken 2007). Because these distances are considerably smaller than the average range over which most Caribbean reef fishes occur [approximately 4,000 x 2,000 km for most species (Froese and Pauly 2011)], it is conceivable that there is limited connectivity at the regional scale. The broad geographic distribution of Nassau grouper (*Epinephelus striatus*) throughout the Caribbean Sea and western Atlantic Ocean makes it a suitable model species to investigate genetic subdivision at both regional and local scales in a mass-aggregating species.

Nassau grouper typically aggregate to spawn for about one week per month over a period that lasts up to three months, in association with water temperature, the moon phase and maximal tidal amplitudes (Colin 1992; Tucker et al. 1993; Carter et al. 1994). Individuals can migrate long distances to spawn [up to 240 km (Carter et al. 1994; Bolden 2000)] and larvae remain in the water column for 35 to 40 days before settling (Powell and Tucker 1992). Historically, spawning aggregations may have consisted of up to tens of thousands of individuals (Smith 1972; Colin et al. 1987; Colin 1992), however targeted fishing of spawning aggregations has drastically decreased population sizes and extirpated one third of all known aggregations (Sadovy de Mitcheson et al. 2008). As a result of its decline, Nassau grouper is now listed as Endangered on the IUCN Red List, largely as a result of aggregation focused fishing (Sadovy de Mitcheson et al. 2012b). Overfishing of such an important top predator has already impacted reef fish community structure (Sluka et al. 1998; Stallings 2008; Stallings 2009), census population sizes and may negatively impact levels of genetic diversity (Hauser et al. 2002), long-term viability and the economic and food benefits of this once common species.

To address patterns of connectivity in a mass-aggregating marine fish we analyzed patterns of genetic variation in mitochondrial DNA (mtDNA), microsatellites, and single nucleotide polymorphisms (SNPs) for Nassau grouper. Limited genetic work on Nassau grouper has focused on a narrow subset of the species' geographic range, used only a few microsatellite loci, and these previous studies have failed to resolve any regional or local scale genetic differentiation between subpopulations (Stevenson et al. 1997). In our study, we dramatically increased both the geographic distribution of samples and the number of molecular markers analyzed to determine whether Nassau grouper subpopulations represented in spawning aggregations exhibit population structure. Our expectation was that Nassau grouper would exhibit both local and regional differentiation among subpopulations due to its mass-spawning point source, spatially and temporally restricted reproductive behavior, as well as the variety of oceanographic conditions experienced across the broad Caribbean basin (approximately 2.754 million km^2). Given the decline of Nassau grouper across the region, our findings will have major implications for designing spatially explicit management and conservation strategies. While there are few obvious physical barriers to long-distance dispersal between most aggregation sites, if there is substantial genetic structure among aggregations then protection of aggregation sites may be the only means by which 1) distinct subpopulations can be maintained and 2) local natural resource management authorities can effectively ensure the long-term sustainability of fisheries dependent on aggregating species.

1.2 Materials and Methods

1.2.1 Sample collection and DNA extraction

We acquired a total of 620 Nassau grouper tissue samples (fin clips or muscle) from numerous research teams and fishermen from 19 sites across 9 countries, with samples collected between 1993 and 2013 (Figure 1, Table 1). Samples were either directly collected from spawning aggregations or in the time immediately before or after the fishery closure, depending on the year they were collected and the local fisheries management in place. We obtained samples from hook and line fisheries, from fish that were caught and released in the pursuit of scientific study, from Antillean fish traps, or collection using closed-circuit rebreathers. Samples were stored in a sarcosyl-urea solution, dimethyl sulfoxide (DMSO) solution or 95% ethanol. Sarcosyl-urea and DMSO samples were stored at room temperature. Samples in 95% ethanol were stored at -20°C. Genomic DNA was isolated following the manufacturer's protocol for the Qiagen DNeasy blood and tissue kit.

1.2.2 Genotyping and data analysis for mitochondrial markers

We genotyped samples for two mitochondrial markers: ATPase and cytochrome *b*. We amplified a 634-bp fragment of ATPase using primers L8331 and H9236. Polymerase chain reaction (PCR) used the following thermocycler parameters: an initial hold at 94°C/5 min, 35 cycles of 94°C/30 sec, 54°C/30 sec, 72°C/30 sec, followed by a final extension of 72°C/7 min. We then amplified a 785-bp fragment of cytochrome *b* using primers Gludgl and CB3H (Palumbi et al. 1991). Thermocycler parameters were as follows: initial hold at 94°C/5 min, 35 cycles of 94°C/45 sec, 45°C/45 sec, 72°C/45 sec, followed by a final extension of 72°C/7 min. Successfully amplified PCR products were sequenced on an ABI 3730xl DNA analyzer at the UC Berkeley DNA Sequencing Facility. Sequences were proofread and aligned, using the software Geneious (version 5.6, Biomatters Ltd.). Because of physical linkage between markers on the circular mitochondrial genome, ATPase and cytochrome *b* sequences were analyzed as concatenated sequences for a combined total of 1,419 bp. We used JModeltest 0.1.1 (Posada 2008) to select the nucleotide model of substitution that best fit the ATPase and cytochrome *b* datasets.

We calculated neutrality statistics and molecular diversity indices, including Fu's F_S, nucleotide diversity (π), and corrected haplotype diversity (h*). Under the Wright-Fisher neutral model of evolution, F_S is predicted to be zero. When F_S is negative, the number of segregating sites is greater than the pairwise nucleotide diversity, revealing an excess of neutral mutations due to a potential population expansion or following a selective sweep (Fu and Li 1993; Fu 1997). We corrected haplotype diversity using a rarefaction approach, as implemented in CONTRIB (Petit et al. 1998), to account for differences in sample size between sites based on a minimum sample size of $n = 8$ per site. We assessed phylogenetic relationships among sequences by generating a haplotype network in the software packages pegas and geiger in R.

1.2.3 Genotyping and data analysis for microsatellite loci

All samples were genotyped for nine polymorphic microsatellites previously designed for Gulf coney (*Hyporthodus acanthistius*), following published PCR protocols (Molecular Ecology Resources Primer Development Consortium et al. 2012). Amplification products were sized on an ABI 3730xl DNA analyzer at the UC Berkeley DNA Sequencing Facility, using the size standard LIZ-500 (Applied Biosystems). Microsatellites were scored using the genetics software GeneMapper version 3.7 (Applied Biosystems) and tested for null alleles, large allele dropout and scoring errors using Micro-Checker (Van Oosterhout et al. 2004). We calculated number of alleles, expected heterozygosity (H_e), observed heterozygosity (H_O) and performed exact tests to detect deviations from Hardy-Weinberg equilibrium (HWE) using Arlequin (Excoffier et al. 2005).

1.2.4 Genotyping and data analysis for single nucleotide polymorphisms

Restriction site-associated DNA (RAD) tag libraries were created using the protocol described in Hohenlohe et al. (2010). Genomic DNA was collected from a subset of tissues collected (n = 108) from four localities: Little Cayman (site 9), Glover's Reef, Belize (site 2), Long Island, Bahamas (site 16) and Antigua (site 19). DNA from each individual was digested with the restriction enzyme *SbfI*, and fragments were ligated to a unique, 6-bp barcoded adapter. The pooled single end libraries were sequenced on an Illumina Genome Analyzer IIx.

SNP discovery and genotyping were performed using modified Perl scripts (described in Miller et al. (2012)) and using the software package Stacks (Catchen et al. 2011; Catchen et al. 2013). Perl scripts trimmed sequenced fragments from the 3' end to a length of 92-bp and then filtered out low-quality reads with a probability of sequencing error greater than 0.10% (Phred score = 33). Reads without an exact match to the 6-bp barcode and 6-bp *SbfI* restriction site were filtered out, and the combined 12-bp sequence was trimmed off. Final filtered reads were then utilized in a population genomic analysis executed in Stacks. Putative SNPs were selected that met the following criteria: minimum depth coverage of 6X, present in at least 80% of individuals and present in individuals from all four sampling localities.

1.2.5 Population structure

We assessed population structure at both local and regional scales by estimating global and pairwise estimates of F_{ST} for all three marker types. Statistical significance of pairwise F_{ST} values was assessed after Bonferroni correction (mtDNA and microsatellites, critical p =0.00029; SNPs, critical p =0.00833). To test for evidence of regional genetic structure, we implemented an analysis of molecular variance (AMOVA) in Arlequin. We tested four regional hypotheses. The first two partitioned sites into regional clusters: 1) Mesoamerican Reef [sites 1-5], central Caribbean [sites 6-11] and eastern Caribbean [sites 12-19] and 2) Mesoamerican Reef [sites 1-5], central Caribbean [sites 6-11], the Bahamas [sites 12-14] and eastern Caribbean [sites 15-19]. The latter two partitioned sites based on connectivity regions identified in Cowen et al. (2006) and based on a meridional break between 67°W and 70°W, roughly separating the western and eastern Caribbean.

We used three methodologies to determine the location of potential barriers to larval dispersal, without *a priori* geographic assumptions using the mtDNA and microsatellite datasets. First we used a computational geometry approach implemented in the software package Barrier (Manni et al. 2004). Delaunay triangulation and Voronoi tessellation were used to visualize patterns of geographic variation. Triangular pairwise geographic distance matrices were generated using a

Geographic Distance Matrix Generator (Ersts 2013) and pairwise genetic distance matrices were generated in Arlequin. The thickness of barrier lines inferred by the software is inversely proportional to the permeability of the barrier and the frequency with which a given barrier is observed across replicate analyses. Next, we used a simulated annealing approach to maximize among group variance, as implemented by the software SAMOVA (Dupanloup et al. 2002) using the mtDNA and microsatellites datasets. Inferred groups are then tested for significance *a posteriori* via AMOVA. Finally, we used a Bayesian clustering algorithm to assign individuals to *k* groups, as implemented in the software Structure (Pritchard et al. 2000), using the microsatellite and SNP datasets. We ran 3 replicates for each value of *k* ranging from 1 to 19 for the microsatellite dataset and 1 to 4 for the SNP dataset. The Evanno method was implemented in the software Structure Harvester, in order to choose the *k* that best fit the data (Evanno 2005).

We performed partial mantel tests to determine whether significant isolation by distance exists among populations for all three marker types. Because hierarchal population structure can introduce bias to isolation by distance analyses (Meirmans 2012), partial mantel tests assess the correlation between geographic distance matrices and genetic distance matrices while also controlling for the effect of hierarchical population structure. Tests were implemented using the vegan package in R. Pairwise genetic distances were estimated in Arlequin and geographic distances between sampling localities were calculated using a Geographic Distance Matrix Generator.

1.3 Results

1.3.1 Mitochondrial DNA

We sequenced a combined total of 1,419 bp for ATPase and cytochrome *b* in 395 individuals, yielding 89 haplotypes (Table 2, Figure 2). The average distance observed between haplotypes was 1 to 2 bp, with a maximum distance of 16 bp. The two most abundant haplotypes were observed in 37.2% and 15.2% of the samples and were observed in all sampling localities. There was also a noticeable shift in the proportion of individuals associated with the Mesoamerican Reef for a given haplotype (Figure 2 in blue), in particular across a 16-bp break. The number of haplotypes (nH), corrected haplotype diversity (h*), nucleotide diversity (π) and Fu's F_S are reported in Table 2. Nucleotide diversity ranged from 0.0005 to 0.0089 and showed a decreasing east to west longitudinal trend across the Caribbean basin (R^2 = 0.271099, $p = 0.0156$). Corrected haplotype diversity ranged from to 0.500 to 0.954. Fu's F_S was significantly negative in 16 of 18 sampling localities, with the exception of Chinchorro Bank, Mexico and Dog Rocks, Bahamas. Such departures from neutrality indicate an excess of recent mutations (number of segregating sites > pairwise nucleotide diversity) due to a potential population expansion or following a selective sweep. Such selective sweeps may occur when favorable mutations rapidly increase in frequency, due to selection, potentially reducing levels of genetic diversity in surrounding linked regions in the genome.

1.3.2 Microsatellites

All nine microsatellite loci were polymorphic in Nassau grouper. The total number of alleles per locus per site ranged from 4 to 25 (Table A1). Allelic richness per locus ranged from 7.9 to 16.2 and there appeared to be no geographic trend in values. Observed heterozygosities ranged from 0.11 to 1.00. No significant linkage disequilibrium was observed between loci within subpopulations ($p > 0.05$, after Bonferroni correction). There was also no evidence of scoring error or null alleles. Significant departures from HWE were observed for 15 out of 171 exact tests ($p < 0.05$). One locus (A108) departed from HWE in 6 of 19 populations, with other loci departing from HWE in four or less populations. Deviations from HWE are consistent with fluctuations in population size as seen in F_S.

1.3.3 Single nucleotide polymorphisms

RAD tag libraries were created by individually barcoding 108 individuals from 4 spawning sites. One lane of sequencing yielded more than 221 million reads, which was reduced to approximately 9.1 million reads after stringent quality filtering. Within each population, we identified an average of 58,305 ± 4,594 stacks, where each stack is comprised of filtered reads representing a potential locus. After specifying minimum depth coverage of 6X and SNP presence in at least 80% of individuals in all 4 localities, using the populations script in Stacks, we identified a total of 4,234 SNPs within the RAD tag sequences that were variable among individuals from all four sampling localities.

1.3.4 Population structure

We detected genetic differentiation between subpopulations using mtDNA (Φ_{ST} = 0.48260, p <0.001; F_{ST} = 0.206, p < 0.001), microsatellites (F_{ST} = 0.003, p = 0.002) and SNPs (F_{ST} = 0.002, p = 0.001) (Table 3). Pairwise Φ_{ST} and F_{ST} comparisons confirmed patterns observed in global estimates from the mtDNA and SNP datasets (Table 4 and 5). After Bonferroni correction, only 52 of 330 total pairwise comparisons were significant (47, 0 and 5 significant comparisons for mtDNA, microsatellites, and SNPs, respectively). The majority of significant pairwise comparisons represent between-region comparisons (e.g. between spawning aggregations in the Mesoamerican Reef and eastern Caribbean). A closer examination revealed that Caye Glory, Belize was highly divergent, with 12 out of 18 statistically significant pairwise comparisons. We found no evidence for isolation by distance using partial mantel tests in the mtDNA (r = -0.04536, p = 0.670), microsatellite (r = 0.02296, p = 0.990) or SNP datasets (r = 0.09531, p = 0.790).

We tested for evidence of regional genetic differentiation using AMOVAs (Table 6). The three-region model, with genetic differentiation of the Mesoamerican Reef, central Caribbean and eastern Caribbean, was supported by the mtDNA datasets (p < 0.05). Approximately 22.45% of variance could be explained by regional differences. The four-region model, with genetic differentiation of the Mesoamerican Reef, central Caribbean, eastern Caribbean and a distinct Bahamas enclave, was supported by both the mtDNA and microsatellite datasets (p < 0.05). Regional differences accounted for approximately 18.09% of the variance in mtDNA and

0.10% of the variance in microsatellite datasets. Genetic differentiation was not significant for groups of samples pooled using connectivity units defined by either Cowen et al. (2006) or the 67° and 70°W meridional break ($p > 0.05$).

Three barriers to larval dispersal were identified using a computational geometry approach (Figure 3). The strongest barrier identified (barrier A) separates the eastern Caribbean and western Caribbean between Dock Rocks, N. Exuma and Lee Stocking. The next strongest barrier (barrier B) isolates the Mesoamerican reef from the remainder of the western Caribbean, and the weakest barrier (barrier C) isolates two coastal spawning sites from additional offshore sites in the Mesoamerican reef. Regional clusters defined by barriers A, B and C were genetically distinct from one another ($\Phi_{ST} = 0.20074$, $p = 0.02542$). These identified regions roughly confirm patterns seen from *a priori* testing of regional subdivision using AMOVAs.

Results from the simulated annealing approach further support regional genetic subdivision among clusters of subpopulations (Table 7). The mtDNA results indicate maximal variance among groups at $k = 2$, with one group comprised of three localities in Belize (sites 3-5) and another group comprised of all remaining sites (1, 2, 6-19). Microsatellite results indicate maximal variance among groups at $k = 4$. One group is comprised of 2 localities from Belize (sites 4 and 5), a second with the remainder of sampling localities in the Mesoamerican reef and central Caribbean (sites 1-3, 6-11), a third with all localities in the Bahamas (sites 14-16) and a final group with the remaining localities in the eastern Caribbean (sites 12, 13, 17-19).

Weak but statistically significant genetic differentiation detected in microsatellite and SNP datasets did not yield clear visual geographic clustering of individuals in Structure (Figure 4). When population structure is weak, as seen in the microsatellite and SNP datasets, assignment methods are less effective at clustering isolated demes (Latch et al. 2006; Jones and Wang 2012). Using the Evanno method, patterns of microsatellite variability partitioned samples into $k = 3$ clusters (Figure 4A). Average levels of reassignment for each individual in the microsatellite dataset ranged from 0.085 to 0.810 to each cluster. Similar to results from the simulated annealing approach and pairwise Φ_{ST} comparisons, Caye Glory in Belize seemed to be somewhat divergent possessing some individuals with the highest assignment to an identified (white) cluster (< 0.70). Observed patterns of SNP variability partitioned samples into $k = 2$ clusters (Figure 4B). All individuals had high levels of assignment to a single cluster (> 0.939) with minimal assignment to an additional cluster (< 0.061) in the SNP datasets. Of the 4 sampling localities, the sampling locality in Belize (Glover's Reef) again possessed individuals with slightly higher assignment to an identified (white) cluster.

1.4 Discussion

Characterizing the connectivity of populations in open marine systems is challenging, but understanding how populations may be interconnected across geographic and political landscapes is crucial for the development of effective management and conservation strategies. Multiple hypotheses have been put forth to describe the potential fate of offspring from large-scale, aggregation-type spawning events. The primary hypotheses argue that aggregations either provide for long-distance dispersal opportunities (and therefore greater population connectivity) or facilitate a strong degree of local larval retention (resulting in discrete populations). Genetic subdivision among subpopulations has not been detected in the few previous genetic studies conducted to date on aggregating fishes in the Caribbean (Shulzitski et al. 2009; Carson et al. 2011). Such lack of population structure was viewed as support for the notion that larvae are not necessarily retained near spawning sites, with potential for long distance dispersal and extensive mixing among subpopulations.

We described for the first time evidence of restricted gene flow and genetic differentiation among subpopulations of a mass-aggregating marine fish, Nassau grouper, and detected barriers to larval dispersal in the Caribbean basin. Our findings contribute to the growing body of literature that demonstrates evidence of local larval retention and genetic subdivision of demes for marine species in the Caribbean Sea (Swearer et al. 1999; Swearer et al. 2002). In one of the most comprehensive genetic analyses in this region to date, we detected limited genetic connectivity among subpopulations across three classes of molecular markers. We discounted the potential for sex-biased dispersal or philopatry, despite a more than order of magnitude difference between *F*-statistics estimated from mtDNA, microsatellites and SNPs. Evidence from acoustic tagging studies suggests similar movement and migration patterns in male and female Nassau grouper (Semmens et al. 2006; Starr et al. 2007; Nemeth et al. 2009). Instead, discordance in the magnitude of genetic differentiation may be due to differences in the effective population size (N_e) of mitochondrial and nuclear markers (Moore 1995), and the inverse correlation between magnitude of genetic drift and N_e. In the marine system, where species are known to have large N_e, mitochondrial markers may show higher levels of differentiation in instances where there is weak isolation among groups or during the early stages of differentiation (Larsson et al. 2009). Despite differences in magnitude of observed genetic differentiation among marker types, evidence of similar patterns of reduced connectivity among Nassau grouper subpopulations generated from analyses of all three marker types may arise due to the interplay of numerous biophysical mechanisms, such as oceanography, site fidelity to aggregation sites, and self-recruitment and limited dispersal associated with highly restricted spatial and temporal spawning.

1.4.1 Timing of reproduction with ocean currents may facilitate larval retention

Larval pathways from spawning aggregations may alternate between local retention and export into mesoscale eddies (Hamner and Largier 2012). Coastal boundary layers, eddies and lateral trapping in embayments are the primary flow patterns suggested to facilitate local retention (Hamner and Largier 2012), thereby inhibiting long distance transport of propagules spawned at aggregation sites. Such oceanographic phenomena may retain larvae close to spawning sites for several days before potentially transporting them to offshore waters (Largier 2003). As a result, these retentive oceanographic conditions may limit dispersal away from aggregation sites thereby retaining larger proportions of settling larvae within the aggregation catchment area (Botsford et al. 2009b). For example, Colin et al. (1992) observed local retention using oceanographic drogues released from Nassau grouper spawning sites off Long Island in the Bahamas. Drogues remained on the insular shelf for several days before moving offshore. Such findings contradict earlier oceanographic and population genetics studies in the Caribbean Sea, which suggested significant potential for long distance dispersal of larvae, with extensive gene flow facilitated by pathways of major surface currents (Shulman and Bermingham 1995; Roberts 1997).

Given the evidence for potential larval retention via ocean currents, there is a possibility that some aggregating species may coordinate spawn timing to coincide with oceanographic regimes that enhance retention and may increase recruitment to natal areas (Lobel 1989). Temperate fishes, such as Atlantic herring, Atlantic cod, and haddock, are known to spawn at sites with predictable currents allowing for larval retention (Iles and Sinclair 1982; O'Boyle et al. 1984; Smith and Morse 1985). In the tropics, adult Nassau grouper may migrate several hundred kilometers to reach spawning sites (Colin 1992; Bolden 2000), though average migration distances may be considerably less depending on reef habitat continuity. Numerous hypotheses have been proposed to understand the possible adaptive advantages of concentrated site-specific breeding in mass-spawning organisms including increased mate encounter and mate choice facilitation, higher fertilization rates and decreased predation risk on spawning adults and larvae via dilution effect (Loiselle and Barlow

1979; Shapiro et al. 1988; Claydon 2004; Molloy et al. 2012). An additional hypothesis is that spawning aggregations may form at sites that place larvae in preferential locations for retention or to increase likelihood of survival. Pathways of satellite-based oceanographic drogues released in the Cayman Islands reveal eddies present at the time of spawning potentially retain Nassau grouper larvae close to where they were spawned (Heppell et al. 2011). Long-term patterns also suggest that pre-settlement grouper will be returned near spawning sites during the course of pelagic larval duration (PLD) (Sadovy de Mitcheson et al. 2012a). The fact that many aggregation sites host multiple species throughout the year provides additional evidence that placement of spawning sites may confer fitness or convergent genetic advantages (Whaylen et al. 2004; Whaylen et al. 2006; Heyman and Kjerfve 2008). This is particularly the case if coupling reproduction with oceanographic phenomena retain gametes and larvae close to the insular shelf increases chances of survival for future offspring (Johannes 1978; Cherubin et al. 2011), thereby contributing to the natal breeding population. While the majority of these hypotheses are untested, such concordance of group spawning behavior with oceanographic dynamics may help explain observed patterns of genetic subdivision among Nassau grouper subpopulations.

More detailed biophysical modeling that considers temporal variations in oceanographic regimes, to more reliably estimate potential recruitment pathways (Hamner and Largier 2012), would contribute greatly to our understanding of genetic connectivity among Nassau grouper subpopulations. While biophysical modeling has not been performed for Nassau grouper yet, results from numerous studies on ecologically similar aggregating fishes that migrate to spawning grounds in the Caribbean are available. Coupled biophysical modeling accounting for larval behavior, a stochastic Lagrangian scheme, and inter-annual varying currents suggested high levels of self-recruitment in five aggregating snappers of the genus *Lutjanus* (Paris et al. 2005) on the Cuban shelf. These five species have similar geographic distributions as Nassau grouper, with PLDs about 5 days shorter than those estimated for Nassau grouper (Victor et al. 2009). A numerical model parameterized on the oceanographic conditions surrounding a red hind (*E. guttatus*) spawning site in the U.S. Virgin Islands demonstrated that larval retention was maximized in the area surrounding the spawning site (Cherubin et al. 2011). Average current direction supported onshore transport of fertilized eggs onto shelves, potentially maximizing retention of eggs and larvae at multiple spawning sites (Nemeth et al. 2006). The spawning period for *E. guttatus*, similar to that of Nassau grouper, occurs during the winter full moons. Such knowledge of retentive oceanographic regimes in the Caribbean, combined with findings of strong genetic differentiation among subpopulations, may provide additional support for the larval retention hypothesis.

1.4.2 Evidence of limited dispersal in marine species

The Caribbean Sea was once considered a single biogeographic province lacking phylogeographic barriers (Mitton et al. 1989; Silberman et al. 1994; Veron

1995; McCartney et al. 2000; Haney et al. 2007). A number of well-known breaks have since been identified through genetic studies, including one between populations east and west of Mona Channel (Taylor and Hellberg 2003; Galindo et al. 2006; Taylor and Hellberg 2006) and others isolating the Bahamas (Taylor and Hellberg 2003; Lee and Foighil 2004,2005; Galindo et al. 2006). Some of the best known barriers in the region are outlined in biophysical modeling work done by Cowen et al. (2006). However, delineating concordant barriers for marine organisms in the Caribbean is challenging due to differences in life history among species (i.e. spawning timing, larval duration and fecundity), spatial and temporal variation in circulation patterns in the region, and variability in sampling schemes between studies. Despite these potential obstacles, barriers to larval dispersal defined in our work are similar to those seen for other invertebrate and fish species in the Caribbean basin, although ours do not perfectly mirror previously defined connectivity regions. Nevertheless, we find support for the presence of barriers identified as isolating groups of Nassau grouper subpopulations in the eastern and central Caribbean, Bahamas and Mesoamerican Reef. A combination of broad-scale oceanographic regimes and limited larval dispersal may explain regional patterns of genetic differentiation among Nassau grouper subpopulations observed in our study.

The strongest barrier (barrier A) detected in our dataset was in the central Bahamas, and corresponds to a previously documented barrier to marine dispersal (Taylor and Hellberg 2006; Diaz-Ferguson et al. 2010; Diaz-Ferguson et al. 2012a). Much debate exists as to whether the Bahamas represent a distinct genetic enclave.

In some genetic studies the Bahamas clustered well with the eastern Caribbean and islands of the Lesser Antilles (Diaz-Ferguson et al. 2010; Diaz-Ferguson et al. 2012a), while a number of hydrodynamic, seascape, and population genetic studies provide support for limited dispersal and genetic isolation of Bahamian populations (Gutierrez-Rodriguez and Lasker 2004; Cowen et al. 2006; Galindo et al. 2006). Pairwise genetic distances, clustering analyses, and results from AMOVAs support some degree of isolation for Nassau grouper populations in the Bahamas. Fishery landings data for Nassau grouper from the Bahamas may also provide evidence of genetic isolation of its stocks. Nassau grouper have become commercially extinct throughout large portions of their range. While they have also been heavily fished within Bahamian waters and have experienced noticeable decline there (Sluka et al. 1998), the Bahamas represent one of the few remaining areas where substantial landings of Nassau grouper are still obtained (Cheung et al. 2013). The extensive continental shelf surrounding the islands provides a large shallow water habitat for Nassau grouper, where there are evidently some remaining aggregations in less accessible (i.e. most distant from fishing centers) locations. The continued presence of these fish, despite heavy fishing pressures in the region and declining abundances, may suggest that Nassau grouper aggregations in the Bahamas are both isolated and potentially self-seeding. Evidence for this notion of potentially self-seeding demes of Nassau grouper may be supported by the apparent recovery of Nassau grouper in the Cayman Islands after a numerous years of protection (Heppell et al. 2012).

Geographic localities in the central and eastern Caribbean showed varying levels of genetic isolation for Nassau grouper. The central Caribbean has been viewed as a region of mixing, receiving larval inputs from other regions in the Caribbean (Taylor and Hellberg 2003; Cowen et al. 2006; Foster et al. 2012). There was no evidence for the presence of highly divergent subpopulations in this region, thereby confirming findings from oceanographic studies. In contrast, we detected significant evidence for genetic differentiation of eastern Caribbean subpopulations. Genetic isolation of populations in the Lesser Antilles is supported by studies of marine invertebrates, suggesting that the Antilles current may facilitate larval mixing among spawning aggregations off of these eastern Caribbean islands (Diaz-Ferguson et al. 2010; Diaz-Ferguson et al. 2012a). However, we were unable to detect a genetic break among populations on either side of the Mona Channel (off Puerto Rico). An inability to detect this break may be the result of inadequate sampling of subpopulations occupying sites adjacent to the channel.

Of all potential barriers observed in our study, those in the Mesoamerican Reef are the least discussed in the literature (Puebla et al. 2009; Salas et al. 2010; Puebla et al. 2012). Both barriers B and C, which isolate coastal Belizean aggregation sites and the Mesoamerican Reef as a whole, were more permeable than the barrier observed in the central Bahamas. Permeability of barrier C and weak genetic divergence observed among Mesoamerican reef subpopulations may be explained by fine scale sampling in this region (as few as 40 km). Weak genetic isolation observed in the Mesoamerican reef is also predicted by oceanographic studies (Roberts 1997; Cowen et al. 2006). Permeability of such barriers may be due to ongoing connectivity with other regions in the Caribbean. Historical oceanographic drifter tracks suggest potential connectivity of our sampling sites in the Mesoamerican Reef with sites in the central Caribbean, the Gulf of Mexico and Atlantic Ocean (Muhling et al. 2013). Some studies have grouped Belize with geographic localities in the central Caribbean, such as Cuba and the Cayman Islands, as they were unable to detect genetic isolation of the Mesoamerican Reef system (Foster et al. 2012). Nonetheless, currents moving northward along the Central American coastline and cyclonic gyres in the region may suffice to genetically isolate spawning aggregations in the Mesoamerican Reef (Shulman and Bermingham 1995; Heyman and Kjerfve 2008; Paris and Cherubin 2008). Slower speeds of drogue drifters have been observed in this region as they move northward along the Belizean Mesoamerican reef towards the Yucatan strait (Richardson 2005); reduced water speeds may facilitate local retention of larvae. Biophysical modeling suggests that levels of self-recruitment in Belize are upwards of 26% (Cowen et al. 2006). Thus, dispersal in the Mesoamerican Reef may be leptokurtic, with the majority of larvae being locally retained with occasional long distance dispersal events (Puebla et al. 2012). Despite evidence of potential connectivity with distant sites, local larval retention in coastal gyres may be sufficient to explain the genetic distinctness of some spawning aggregations in the Belizean Mesoamerican reef.

In addition to physical barriers to dispersal, limited larval dispersal has been proposed as a mechanism facilitating strong population structure in marine species

(Barber et al. 2002b; Jones et al. 2005; Almany et al. 2007; Buston et al. 2012). Circulation patterns in the Caribbean Sea are both spatially and temporally variable (Gordon 1967; Molinari et al. 1981; Kinder 1983; Kinder et al. 1985). The Caribbean Current represents the strongest flow in the region, moving from the southern Lesser Antilles westward through the Yucatan strait. Mesoscale eddies form within this current and take anywhere from 6 to 10 months to move across the width of the Caribbean, challenging the notion that flow in the region is purely westward (Kinder et al. 1985; Murphy et al. 1999). Coupled with knowledge of Nassau grouper's 35 to 40 day PLD, such eddies may serve to limit Caribbean-wide dispersal of larvae, potentially resulting in observed regional patterns of genetic subdivision. Additionally, with average current speeds of 1 to 2 km per hour in the Caribbean, it is unlikely that larval dispersal kernels of native reef fishes extend beyond 200 km (Cowen et al. 2000). Dispersal kernels provide us with a probability that individuals from one site will arrive at another, as well as the approximate spatial scale over which dispersal is likely (Largier 2003). Evidence from DNA parentage analyses studies have now allow us to estimate dispersal kernels more directly and to understand dynamics that produce the observed patterns of genetic differentiation (Jones et al. 2005; Almany et al. 2007; Jones et al. 2009; Buston et al. 2012). Work on linesnout goby (*Elacatinus lori*) in the Belizean Mesoamerican Reef showed low levels of export to nearby sites over a small spatial scale (D'Aloia et al. 2013). Further evidence from work done in the Pacific Ocean on an aggregating grouper (coral trout [*Plectropomus areolatus*]) demonstrated that 50% of larvae remain within

14 km of a given spawning site (Almany et al. 2013). In future work, parentage analyses studies may be an excellent means of elucidating mechanisms driving localized patterns of genetic divergence among Nassau grouper subpopulations.

1.5 Conclusion

We found evidence for restricted gene flow and genetic differentiation among Nassau grouper subpopulations, with indirect support for the larval retention hypothesis. Our results suggest that the absence of physical barriers to dispersal and potential for long distance dispersal of larvae has not resulted in genetic homogeneity among its subpopulations. Long migrations of adults to spawning sites may enhance differences among subpopulations by making it less likely that larvae settle beyond the catchment areas of the site from which they were spawned. Additionally, oceanography likely plays an important role in retaining larvae close to spawning sites at both local and regional spatial scales. Findings warrant additional detailed studies of ocean circulation patterns and dispersal kernels during the spawning period for a more direct investigation of the mechanisms driving genetic divergence among Nassau grouper subpopulations.

Our results yield important insights into the vulnerable status of Nassau grouper throughout its geographic range. Spawning aggregations are not resilient to heavy fishing, failing to reestablish once they are fished out (Warner 1988; Sadovy and Eklund 1999; Aguilar-Perera 2006). If subpopulations represented by spawning aggregations are heavily reliant upon self-recruitment, then persistence of the species may rely upon fisheries management and conservation efforts focusing on the maintenance of local genetic diversity and the implementation of management units at the regional scale, as suggested by genetic data. Regional patterns of genetic differentiation observed may also warrant standardization of fisheries management and conservation initiatives, particularly among countries within genetically isolated clusters.

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Table 1.1. Sampling localities for Nassau grouper

Region	Sampling Site	N_{mtDNA}	N_{msat}	N_{SNPs}
Mesoamerican Reef	1. Chinchorro Bank, Mexico*	7	24	0
	2. Glover's Reef, Belize	21	59	31
	3. Lighthouse Reef, Belize	4	32	0
	4. Turneffe Atoll, Belize	5	29	0
	5. Caye Glory, Belize	12	26	0
Central Caribbean	6. Corona San Carlos, Cuba	14	24	0
	7. Pardon del Medio, Cuba	17	41	0
	8. Grand Cayman, Cayman Is.	8	9	0
	9. Little Cayman, Cayman Is.	72	61	14
	10. Cayman Brac, Cayman Is.	27	28	0
	11. Florida Keys, U.S.A.	31	38	0
Bahamas	12. Dog Rocks, Northern Exuma	4	19	0
	13. Lee Stocking	4	23	0
	14. Long Island	23	37	32
Eastern Caribbean	15. South Caicos, Turks and Caicos$^+$	32	50	0
	16. Bajo de Sico, Puerto Rico $^+$	10	10	0
	17. Grammanik Bank, U.S.Virgin Is. $^+$	72	58	0
	18. N. of St. Thomas, British Virgin Is.	0	8	0
	19. Antigua$^+$	32	44	31

Sample sizes utilized for mitochondrial DNA (N_{mtDNA}), microsatellites (N_{msat}) and SNP (N_{SNPs}) analyses. Majority of tissue samples were stored in sarcosyl-urea unless denoted with (*) for dimethyl sulfoxide (DMSO) or ($^+$) for 95% ethanol.

Table 1.2. Molecular diversity indices for mitochondrial DNA for Nassau grouper

Sampling Site	*n*	nH	h*	π	F_S
1. Chinchorro Bank	7	5	0.857	0.0071 ± 0.004	-1.561
2. Glover's Reef	21	9	0.852	0.0070 ± 0.004	**-13.710**
3. Lighthouse Reef	4	2	0.667	0.0005 ± 0.001	**-3.989**
4. Turneffe Atoll	5	3	0.700	0.0006 ± 0.001	**-5.410**
5. Caye Glory	12	6	0.758	0.0008 ± 0.001	**-19.341**
6. Corona San Carlos	14	6	0.780	0.0009 ± 0.001	**-23.181**
7. Pardon del Medio	17	6	0.721	0.0032 ± 0.002	**-15.891**
8. Grand Cayman	8	6	0.893	0.0005 ± 0.001	**-8.040**
9. Little Cayman	72	26	0.776	0.0011 ± 0.001	**-27.953**
10. Cayman Brac	27	12	0.732	0.0008 ± 0.001	**-28.993**
11. Florida Keys	31	12	0.817	0.0011 ± 0.001	**-24.744**
12. Dog Rocks	4	3	0.833	0.0088 ± 0.006	0.576
13. Lee Stocking	4	2	0.500	0.0035 ± 0.001	**-4.644**
14. Long Island	23	11	0.834	0.0052 ± 0.003	**-19.421**
15. South Caicos	32	14	0.823	0.0053 ± 0.003	**-25.015**
16. Bajo de Sico	10	6	0.844	0.0064 ± 0.003	**-3.581**
17. Grammanik Bank	72	20	0.737	0.0089 ± 0.001	**-28.730**
18. N. of St. Thomas	---	---	---	---	**---**
19. Antigua	32	22	0.954	0.0070 ± 0.003	**-24.668**

Sample location, number of specimens (*n*), number of haplotypes (nH), corrected haplotype diversity (h*), nucleotide diversity (π) and the neutrality statistic Fu's F_S, as reported by Arlequin 3.5. Bolded values denote statistical significance of $p < 0.05$ for Fu's F_S.

Table 1.3. AMOVA results for mitochondrial DNA, microsatellites and SNPs for Nassau grouper

	d.f.	var	var%	F_{ST}	P-value
mtDNA					
Among populations	15	0.8216	20.29	0.2060	< 0.0001
Within populations	377	2.2612	79.40	0.2036	< 0.0001
Total	394	3.9770			
Microsatellites					
Among populations	16	0.0078	0.20	0.0023	0.0039
Within populations	1221	3.8413	99.77	0.0020	0.0088
Total	1239	3.8502			
SNPs					
Among populations	2	0.1159	0.02	0.0020	0.0140
Within populations	212	159.9480	1.05	-0.0490	1.0000
Total	215	157.4285			

Degrees of freedom (d.f.), variance components (var), percent variation (var %) and *F*-statistics to test for evidence of genetic differentiation among Nassau grouper subpopulations using mitochondrial DNA, microsatellites and SNPs. (*) denotes statistical significance of $p < 0.05$.

Table 1.4. Pairwise *F*-statistics for mitochondrial DNA and microsatellite loci for Nassau grouper

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
1. Chinchorro Bank	---	0.004	0.002	0.000	-0.002	0.001	-0.003	0.004	-0.001	0.001	-0.001	0.002	-0.001	0.004	0.006	0.001	0.005	0.014	0.007
2. Glover's Reef	-0.061	---	-0.002	-0.002	0.004	0.007	0.003	0.018	0.002	0.002	0.002	-0.001	0.002	0.011	0.008	0.004	0.000	0.022	0.003
3. Lighthouse Reef	0.378	0.344	---	-0.001	0.000	0.004	0.000	0.007	0.000	-0.004	-0.002	-0.002	-0.001	0.006	0.007	0.002	0.001	0.016	-0.001
4. Turneffe Atoll	0.404	0.356	**0.180**	---	0.001	0.004	0.002	0.012	0.001	0.000	0.000	-0.004	0.001	0.004	0.005	0.003	0.002	0.001	-0.003
5. Caye Glory	0.537	0.428	0.086	0.028	---	0.005	0.002	0.005	0.000	-0.001	0.003	0.000	0.006	0.001	0.005	0.001	0.004	0.010	0.005
6. Corona San Carlos	**0.407**	0.302	0.937	**0.936**	**0.800**	---	0.006	0.018	0.004	0.000	-0.001	0.000	0.005	0.006	0.005	0.009	0.001	0.022	0.004
7. Pardon del Medio	0.161	0.146	**0.760**	**0.766**	**0.933**	0.021	---	0.003	-0.003	-0.001	-0.002	-0.002	0.000	-0.001	0.007	0.003	0.001	0.014	0.001
8. Grand Cayman	0.301	0.250	0.922	0.922	**0.925**	0.000	-0.021	---	0.010	0.005	0.068	0.011	0.015	-0.003	0.020	0.008	0.014	0.026	0.013
9. Little Cayman	**0.574**	**0.477**	**0.915**	**0.915**	**0.916**	0.083	-0.021	-0.028	---	-0.002	-0.002	-0.002	-0.001	0.000	0.005	0.003	0.000	0.014	-0.001
10. Cayman Brac	**0.507**	**0.376**	**0.937**	**0.937**	**0.935**	0.054	-0.029	-0.003	-0.014	---	-0.006	-0.002	0.002	-0.002	0.007	0.006	0.003	0.019	-0.002
11. Florida Keys	-0.059	-0.026	0.416	0.425	**0.481**	0.217	0.081	0.173	**0.357**	**0.272**	---	-0.006	-0.001	-0.001	0.004	0.004	-0.002	0.016	-0.002
12. Dog Rocks	-0.174	-0.152	0.315	0.355	**0.519**	0.538	0.228	0.417	0.675	0.636	-0.104	---	0.002	0.005	0.004	-0.005	-0.004	0.008	-0.001
13. Lee Stocking	0.201	0.192	0.965	0.960	0.944	0.038	-0.045	-0.089	-0.126	0.525	0.114	0.307	---	0.010	0.005	0.004	0.001	0.018	0.002
14. Long Island	0.017	0.062	0.583	0.595	**0.646**	0.096	-0.014	0.057	**0.196**	0.138	0.019	0.057	-0.008	---	0.006	0.006	0.007	0.018	0.001
15. South Caicos	0.027	0.052	0.573	0.580	**0.623**	0.197	-0.114	0.054	**0.186**	0.133	0.010	0.041	0.001	-0.024	---	0.007	0.006	0.018	0.006
16. Bajo de Sico	-0.050	-0.002	0.187	0.205	**0.306**	**0.537**	**0.340**	**0.456**	**0.699**	**0.626**	0.057	-0.143	0.388	0.187	0.195	---	0.005	0.018	0.007
17. Grammanik Bank	**0.602**	**0.494**	**0.929**	**0.929**	**0.929**	-0.122	0.095	-0.020	-0.003	-0.006	**0.368**	0.707	-0.030	0.209	**0.198**	**0.720**	---	0.018	-0.002
18. North of St. Thomas	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	---	0.007
19. Antigua	0.015	0.058	0.109	0.091	**0.167**	**0.476**	**0.353**	**0.434**	**0.629**	**0.537**	**0.118**	-0.080	0.392	0.244	0.249	-0.053	0.641	N/A	---

Pairwise Φ_{ST} values for mitochondrial markers are below diagonal and pairwise F_{ST} values for microsatellites are above diagonal. Bolded values denote statistical significance of $p < 0.00029$ (mtDNA) and $p < 0.00027$ (microsatellites), using Bonferroni correction for multiple tests. N/A indicates pairwise comparisons that could not be generated due to poor amplification of mtDNA.

Table 1.5. Pairwise *F*-statistics for 4,234 SNP loci for Nassau grouper

	2	9	16	19
2. Glover's Reef	---			
9. Little Cayman	**0.003**	---		
14. Long Island	**0.004**	**0.001**	---	
19. Antigua	**0.006**	0.001	**0.003**	---

Pairwise F_{ST} values for SNP loci. Bolded values denote statistical significance of $p < 0.00512$, using Bonferroni correction for multiple tests.

Table 1.6. AMOVA results to test for regional patterns of genetic differentiation in the Caribbean Sea

mtDNA	Source of variation	d.f.	%var	P-value
(1) Mesoamerican Reef, Central Caribbean, Eastern Caribbean	Among groups	2	22.45	0.02040
	Among populations within groups	15	20.64	< 0.00001
	Within populations	377	56.91	< 0.00001
(2) Mesoamerican Reef, Central Caribbean, Bahamas, Eastern Caribbean	Among groups	3	18.09	0.04208
	Among populations within groups	14	23.19	< 0.00001
	Within populations	377	58.72	< 0.00001
(3) Cowen et al 2006 Connectivity Regions	Among groups	2	0.28	0.48901
	Among populations within groups	15	20.31	< 0.00001
	Within populations	377	79.41	< 0.00001
(4) 67 to 70°W Meridional Break	Among groups	1	0.66	0.32931
	Among populations within groups	16	20.14	< 0.00001
	Within populations	377	79.20	< 0.00001
Microsatellites	Source of variation	d.f.	% var	P-value
(1) Mesoamerican Reef, Central Caribbean, Eastern Caribbean	Among groups	2	0.03	0.17400
	Among populations within groups	16	0.20	0.00489
	Within populations	1221	99.77	0.00978
(2) Mesoamerican Reef, Central Caribbean, Bahamas, Eastern Caribbean	Among groups	3	0.10	0.01564
	Among populations within groups	15	0.15	0.00293
	Within populations	1221	99.76	0.05963
(3) Cowen et al 2006 Connectivity Regions	Among groups	2	-0.02	0.52297
	Among populations within groups	16	0.24	0.00391
	Within populations	1221	99.79	0.00391
(4) 67 to 70°W Meridional Break	Among groups	1	-0.03	0.59335
	Among populations within groups	17	0.23	< 0.00001
	Within populations	1221	99.80	0.00293

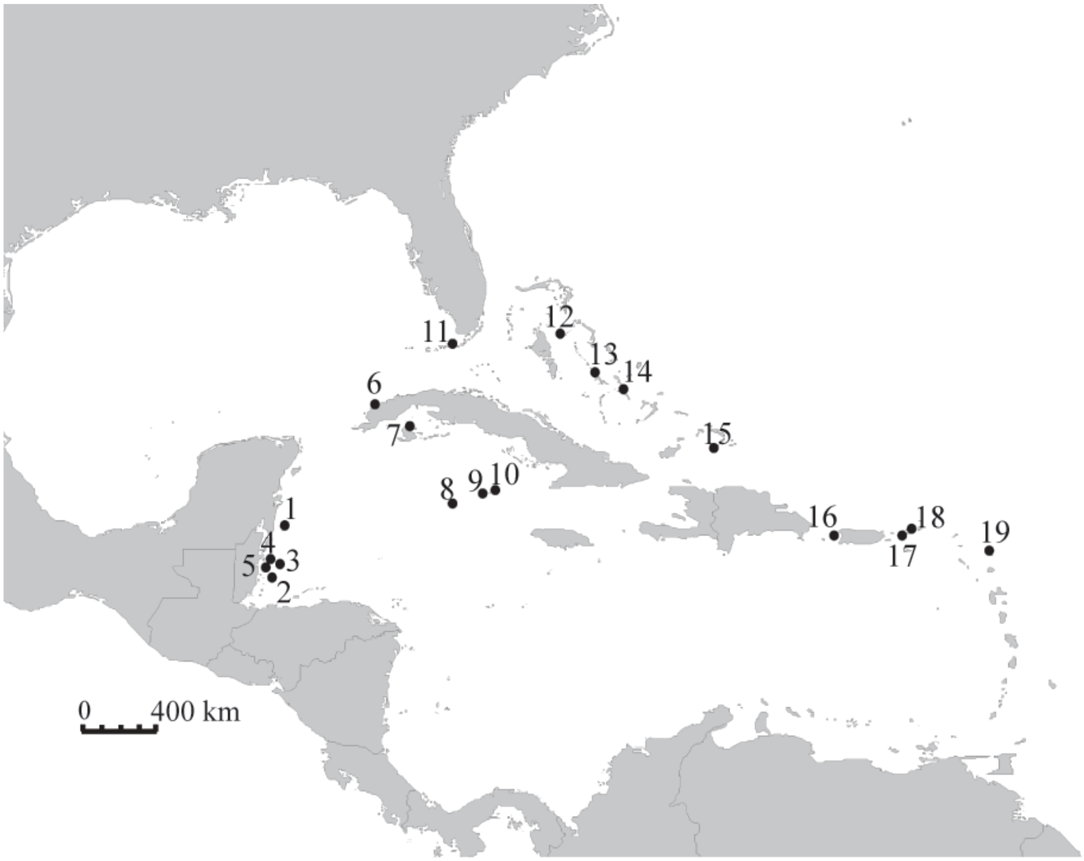
AMOVA results showing degrees of freedom (d.f.), variance components (var), percent variation (var%) and F-statistics to test for evidence of regional genetic differentiation among Nassau grouper subpopulations using mitochondrial DNA and microsatellites. (*) denotes statistical significance of $p < 0.05$.

Table 1.7. AMOVA results from simulated annealing approach for Nassau grouper

mtDNA	Source of variation	d.f.	%var	P-value
(1) Sites 3,4,5 and (2) Sites 1,2, 6-19	Among groups	1	62.9	< 0.00001
	Among populations within groups	16	9.84	< 0.00001
	Within populations	377	27.26	0.00196
(1) Sites 3,4,5, (2) Sites 11-14 and (3) Sites 1,2,6-10,15-19	Among groups	2	55.01	< 0.00001
	Among populations within groups	15	6.01	< 0.00001
	Within populations	377	38.98	< 0.00001
Microsatellites	Source of variation	d.f.	%var	P-value
(1) Sites 4,5, (2) Sites 1-3,6-11, (3) Sites 12-14 and (4) 15-19	Among groups	3	0.05	0.00391
	Among populations within groups	15	0.21	0.00880
	Within populations	1221	99.74	0.03431

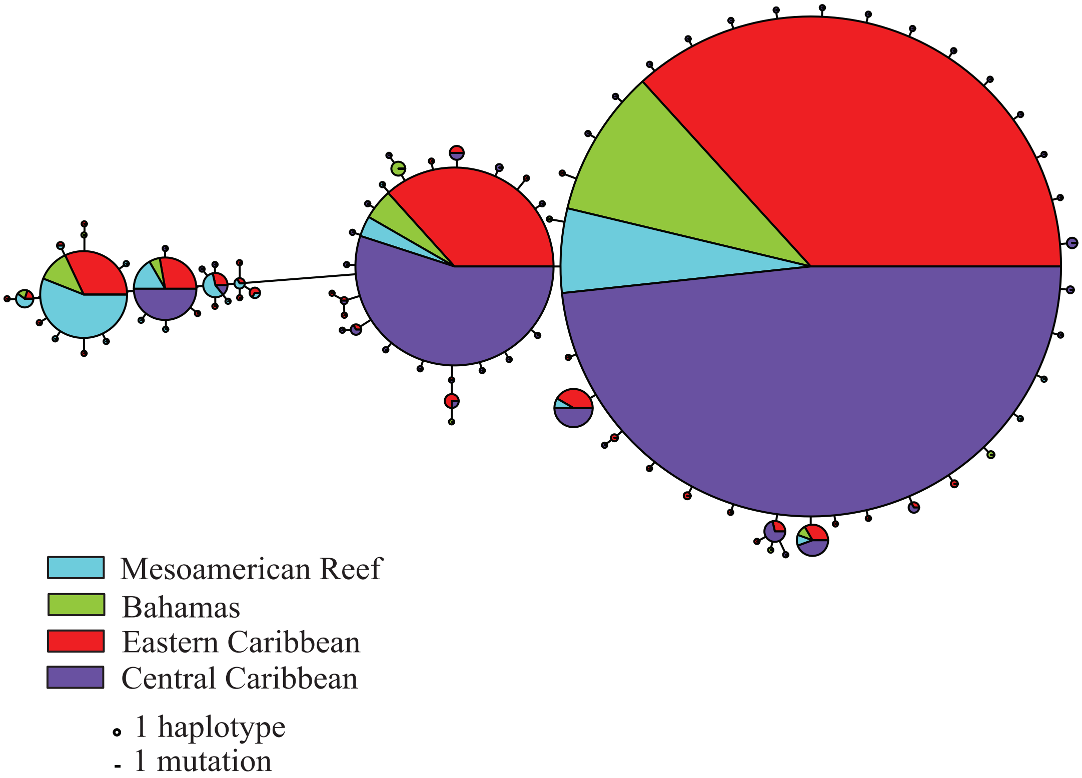
Degrees of freedom (d.f.), variance components (var), percent variation (var%) and F-statistics to test for evidence of regional genetic differentiation among Nassau grouper subpopulations using mitochondrial DNA and microsatellites. (*) denotes statistical significance of $p < 0.05$.

Figure 1.1. Nassau grouper sampling localities in the Caribbean Sea



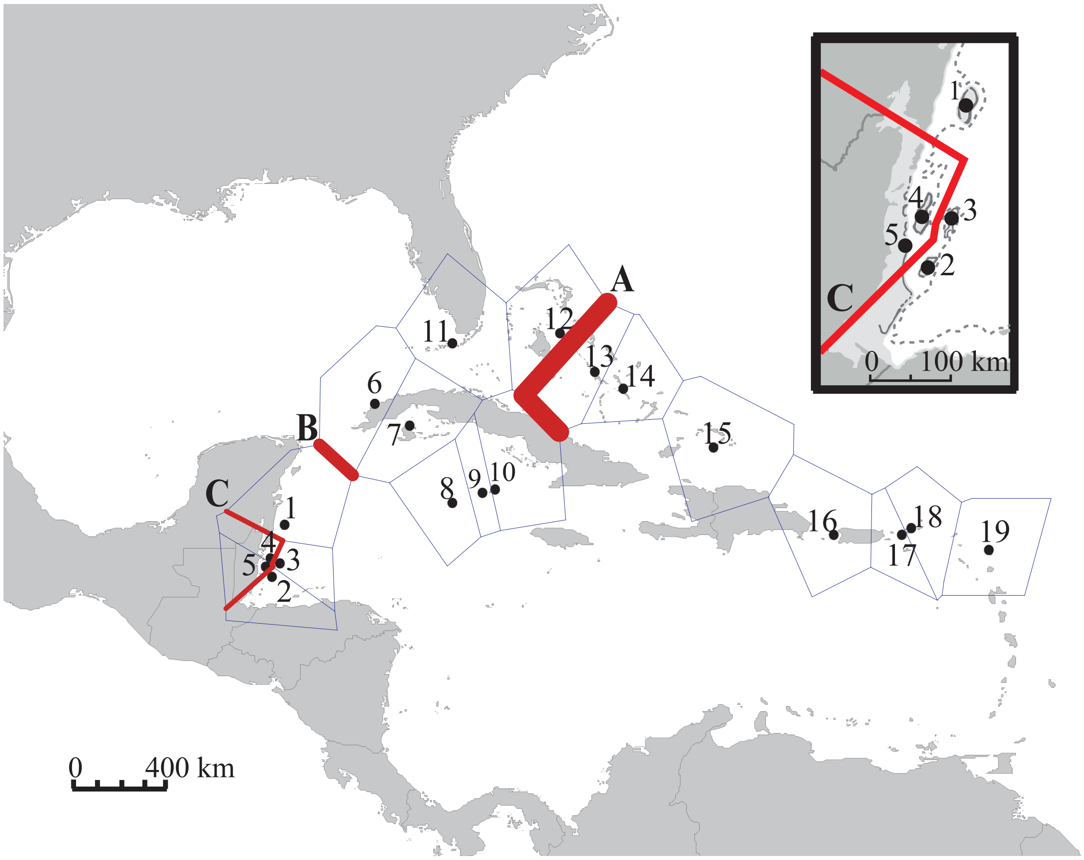
Sampling localities include: 1) Chinchorro Bank, Mexico, 2) Glover's Reef, Belize, 3) Lighthouse Reef, Belize, 4) Turneffe Atoll, Belize, 5) Caye Glory, Belize, 6) Corona San Carlos, Cuba, 7) Pardon del Medio, Cuba, 8) Grand Cayman, 9) Little Cayman, 10) Cayman Brac, 11) Florida Keys, 12) Dog Rocks, N. Exuma, 13) Lee Stocking, Bahamas, 14) Long Island, Bahamas, 15) South Caicos, 16) Bajo de Sico, Puerto Rico, 17) Grammanik Bank, U.S. Virgin Islands, 18) N. of St. Thomas, British Virgin Islands and 19) Antigua.

Figure 1.2. Haplotype network for Nassau grouper



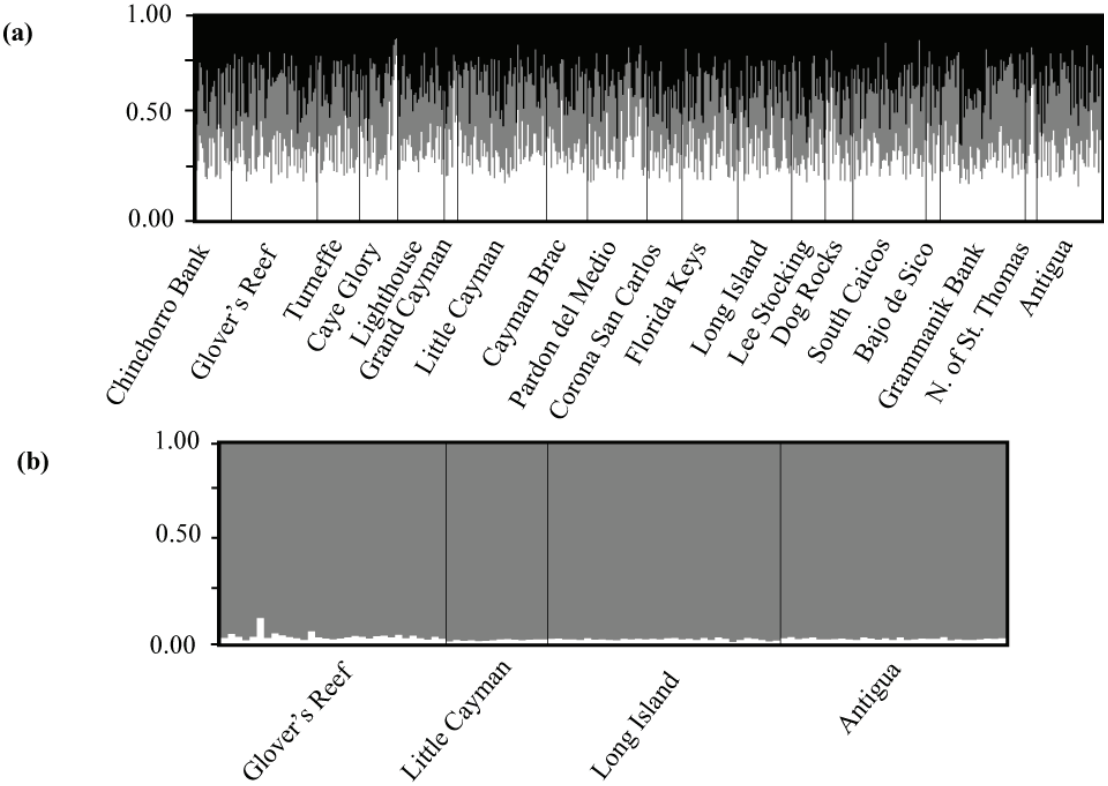
Circles are sized proportionately to the number of individuals that possess each haplotype. The pie chart within each haplotype represents the relative frequency of individuals from each color-coded region. A scale is provided to determine the number of mutations separating each haplotype.

Figure 1.3. Identified barriers to larval dispersal in the Caribbean Sea



Genetic barriers between Nassau grouper subpopulations, using Delaunay triangulation and Voronoi tessellation implemented in Barrier. Barriers are ranked in order of impermeability (A through C), with thickness of barrier lines proportional to the frequency with which a given barrier is observed in replicate analyses and inversely proportional to permeability.

Figure 1.4. Bayesian population assignment tests for Nassau grouper



Bayesian population assignment tests based on: A) 9 microsatellite loci and B) 4,234 SNP loci as implemented in Structure. *k* clusters were chosen for each data set. $k = 3$ (white, gray, black) for the microsatellite data set and $k = 2$ (white and gray) for the SNP data set. The y-axis provides the assignment likelihood for each individual belonging to a given cluster.

Chapter 2

Historical and ecological genetics of Leopard grouper (*Mycteroperca rosacea*) in the Gulf of California

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2.1 Introduction

Effective design of marine reserves for use in fisheries management requires a clear understanding of patterns of larval transport between populations (Sale et al. 2005; Levin 2006; Hauser and Carvalho 2008). While the small size of larvae make them challenging to track in the marine environment, genetic markers can be used as a proxy to assess larval dispersal patterns (Avise 2004). Phylogeographic and population genetics analyses of such markers then allow us to infer the extent of connectivity among populations (e.g. Pearse & Crandall 2004; Hedgecock et al. 2007), as well as historical and contemporary mechanisms driving divergence when connectivity is limited (Cowen and Sponaugle 2009; Hellberg 2009).

The Gulf of California (or Sea of Cortez) is a biodiverse marine ecosystem that could greatly benefit from increased conservation and fisheries management efforts (Ezcurra 2002; Roberts et al. 2002). Several authors have proposed establishing networks of marine reserves in the Gulf of California as a means of conserving biological diversity in the region (Sala et al. 2002; Enriquez-Andrade et al. 2005; Cudney-Bueno et al. 2009). The extent of connectivity between proposed reserves, and the extent of genetic differentiation among organisms within them, may be influenced by a number of historical and contemporary mechanisms. Previous studies in the Gulf of California have highlighted the role of vicariance events (Bernardi et al. 2003; Riginos 2005), environmental differences (Riginos and Nachman 2001), oceanography (Marinone et al. 2008; Peguero-Icaza et al. 2011;

Soria et al. 2012; Beldade et al. *in press*), and limited dispersal ability (Bohonak 1999; Hurtado et al. 2010) in subdividing populations of marine organisms.

A couple of vicariance hypotheses have been proposed to explain limited genetic exchange among populations in the Gulf of California. Climatic oscillations during the Pleistocene epoch (~2.5 million to 12 thousand years ago) could have restricted larval and adult movements between physically isolated regions (Munguía-Vega 2011). When sea levels fell 100 to 150 m during multiple glacial periods in the Pleistocene (Van Devender 2000), exposed shelves effectively served as geographic barriers. An alternative vicariance hypothesis is the opening of trans-peninsular seaways along the Baja California peninsula (Upton and Murphy 1997; Riddle et al. 2000; Lindell et al. 2006; Leache et al. 2007). While there is limited geological evidence to support these hypothetical seaways (Crews and Hedin 2006), they represented hard (impermeable) barriers between terrestrial subpopulations in the northern and southern peninsula (Riddle et al. 2000; Hurtado et al. 2010). However, for marine organisms a seaway is a soft (i.e. semi-permeable) barrier. The inflow of water from the Pacific Ocean may only partially prevent movement of larvae and adults between geographic regions north and south of the seaway. While evidence for a soft barrier was found in the Vizcaino region for some rocky reef fishes and intertidal isopods (Riginos 2005; Hurtado et al. 2010), the extent to which such seaways have restricted larval dispersal for other marine organisms warrants further study.

Regional differences in environmental conditions may also facilitate genetic divergence among populations in the Gulf of California (Riginos and Nachman 2001). Three biogeographic regions exist in the Gulf of California based on differences in ichthyofaunal composition and environmental conditions (Walker 1960; Thomson et al. 2000). In the shallow northern Gulf, marine organisms are subject to a variety of physical forces, such as wind-induced upwelling and low salinities (Thomson et al. 2000) as well as both extreme tidal oscillations and variation in sea surface temperature (Maluf 1983; Álvarez-Borrego 2002). In the central Gulf, south of Isla Ángel de la Guarda and Isla Tiburón, the Gulf has a thermohaline structure similar to the Eastern Tropical Pacific (Sverdrup 1941). There is the potential for genetic divergence driven by local adaptation to varying environmental conditions (Powers et al. 1991; Schmidt and Rand 1999). Additionally, intense tidal mixing in the Midriff Island region results in a sharp thermal front (Danell-Jimenez et al. 2009; Inda-Diaz et al. 2010) between the tropical waters of the central Gulf and the variable water masses in the northern Gulf. If larval survival or settlement is compromised by unfavorable thermal conditions (Lett et al. 2007; Annis et al. 2013), then tidal mixing in this region may serve as an ecological barrier inhibiting successful transport of larvae between the northern and central biogeographic regions.

Ocean circulation patterns can also play a particularly important role in restricting larval exchange between regions (Barber et al. 2002a; Barber et al. 2006). Seasonally dependent gyres in the northern and central Gulf may entrain larvae

(Lavín and Marinone 2003; Marinone 2003). In the northern Gulf, the directionality of the primary gyre is seasonally variable (Beier 1997; Lavín et al. 1997). In the central Gulf, there is a cyclonic gyre centered between La Paz Bay and Topolobampo (Emilsson and Alatorre 1997), as well as an anticyclonic gyre over the San Pedro Mártir Basin (Marinone 2003; Mateos et al. 2006). Movement patterns of satellite-tracked surface drifters also suggest the deflection of water masses along the geographic boundary between the northern and central Gulf (Danell-Jimenez et al. 2009; Inda-Diaz et al. 2010). Thus, oceanic circulation patterns may create a soft barrier, restricting gene flow between biogeographic regions in the Gulf of California.

We used mitochondrial DNA and microsatellites to investigate how the aforementioned mechanisms might impact connectivity among subpopulations of a commercially and ecologically important species in the Gulf of California. Leopard grouper (*Mycteroperca rosacea*) is currently the most intensely fished grouper in the Gulf, particularly during the months when they aggregate to spawn (Sala et al. 2004; Erisman et al. 2010). As top predators, groupers also play an ecologically important role in regulating species at lower trophic levels (Heithaus et al. 2008; Stallings 2008; Stallings 2009). Exploitation of top predators by artisanal fisheries in the Gulf has the potential to destabilize subtidal communities (Jackson et al. 2001; Sala et al. 2004). There may be genetic consequences associated with such overfishing including inbreeding and reductions in the genetic variability of wild populations (Hauser et al. 2002; Hoarau et al. 2005).

There is currently no management in place to regulate fishing activities for *M. rosacea* in the Gulf of California. Thus, we examined demographic history and patterns of connectivity, with the ultimate goal of informing fisheries management. Findings from this study are the logical first step in creating a sustainable fisheries management plan for *M. rosacea* as part of the Pesca Artesanal del Norte Golfo de California – Ambiente y Sociedad (*PANGAS*) project, an interdisciplinary, ecosystem-based management approach to fisheries management in the Gulf of California.

2.2 Materials and Methods

2.2.1 Sample collection and DNA extraction

Between 2006 and 2012 we sampled 551 *M. rosacea* pectoral fins from 21 localities in the Gulf of California (Table 1, Figure 1). Samples were collected at fish markets or directly from fishermen at harbors. Additional information was collected on the approximate localities where fish were caught. Samples were stored in 95% ethanol and kept at -20°C in the laboratory. DNA was extracted by incubating 20 mg of tissue in a proteinase K digestion in lysis buffer (10 mM Tris, 400 mM NaCl, 2 mM EDTA, 1% SDS) overnight at 55°C. Tissue digestion was followed by purification using standard phenol/chloroform and alcohol precipitation protocols (Sambrook et al. 1989).

2.2.2 Genotyping and data analysis for mitochondrial markers

We genotyped samples for two mitochondrial markers: ATPase and cytochrome *b*. For ATPase, we amplified a 726-bp fragment using species-specific primers (MYCROS Forward: 5’-TTCTCCCACTACCCTGATTC and MYCROS Reverse: 5’-TACGTAGGCTTGGATCATTG). Polymerase chain reaction (PCR) used the following thermocycler parameters: an initial hold at 94°C/5 min, 35 cycles of 94°C/30 sec, 54°C/30 sec, 72°C/30 sec, followed by a final extension at 72°C for 7 min. We then amplified a 787-bp fragment of cytochrome *b* using primers Gludgl and CB3H (Palumbi et al. 1991). Thermocycler parameters were as follows: initial hold at 94°C/5 min, 35 cycles of 94°C/45 sec, 45°C/45 sec, 72°C/45 sec, followed by 72°C for 7 min. Successfully amplified PCR products were sequenced on an ABI 3730xl DNA analyzer at the UC Berkeley DNA Sequencing Facility. Sequences were proofread and aligned using Geneious version 5.6. ATPase and cytochrome *b* sequences were subsequently analyzed as concatenated sequences for a combined total of 1513-bp. Both gene regions shared the same model of evolution, based on Akaike Information Criterion (AIC) implemented in JModeltest 0.1.1 (Posada 2008).

We calculated nucleotide diversity (π) and corrected haplotype diversity (h*) for each sampling locality. We corrected haplotype diversity using a rarefaction approach implemented in CONTRIB (Petit et al. 1998). Rarefaction accounted for differences in sample size between localities based on a minimum sample size of $n = 4$. Phylogenetic relationships among sequences were assessed by generating a haplotype network using the software packages pegas (Paradis 2010) and geiger

(Harmon et al. 2008) in R. We then plotted the frequency of distinct clades (bootstrap support > 95%) in each sampling locality as pie diagrams to illustrate the geographic distribution of haplotypes.

2.2.3 Genotyping and data analysis for microsatellite markers

All samples were genotyped for 12 species-specific microsatellites (Mros01 – Mros12), following PCR protocols described in Jackson et al. (2013). PCR products were sized on an ABI 3730xl DNA analyzer at the UC Berkeley DNA Sequencing Facility using LIZ-500 size standard (Applied Biosystems). Microsatellites were scored using GeneMapper version 3.7 (Applied Biosystems) and tested for null alleles, large allele dropout and scoring errors using Micro-Checker (Van Oosterhout et al. 2004). We calculated allelic richness, expected heterozygosity (H_e), observed heterozygosity (H_o), linkage disequilibrium (LD) between pairs of loci, and performed exact tests to detect deviations from Hardy-Weinberg equilibrium (HWE) using Arlequin (Excoffier et al. 2005). We corrected allelic richness using a rarefaction approach implemented in HP-Rare (Kalinowski 2005). Rarefaction accounted for differences in sample size between localities based on a minimum allelic richness of $n = 8$.

2.2.4 Divergence estimates and demographic patterns

We used JModeltest 0.1.1 (Posada 2008) to determine the most appropriate model of DNA substitution using AIC. AIC indicated SYM+I as the best fit model for cytochrome *b* sequence evolution. We calibrated a Bayesian skyline plot using a lognormal relaxed clock in BEAST version 1.7.5 (Drummond et al. 2012) in order to estimate divergence times for *M. rosacea* lineages. We excluded ATPase from this analysis as mutation rates in fishes are better understood for cytochrome *b*. Coalescent approaches implemented in Bayesian skyline analyses allowed us to explore demographic patterns as well as time to most recent common ancestor (tmrca) for all *M. rosacea* lineages. We used literature-derived mutation rates for cytochrome *b* (Maggio et al. 2005; Craig et al. 2009), allowing them to vary between 0.5 to 2% per million years. We performed three replicate runs sampling every 1,000 steps along a MCMC chain of length 50,000,000 and a burn-in of 15%. The three runs were combined, and 25% of the initial trees were discarded as the burn-in phase.

In addition to divergence dates, we estimated Fu's F_S and Tajima's D in order to detect signatures of recent population expansions. Under the Wright-Fisher neutral model of evolution, both F_S and D are predicted to be zero. When F_S is negative the number of segregating sites is greater than the pairwise nucleotide diversity, revealing an excess of neutral mutations common after a population expansion or selective sweep (Fu and Li 1993; Fu 1997). When D is negative, there is a often common, high frequency as well as a large number of rarer alleles. Such an allele frequency distribution is common in populations that are expanding (Hartl and Clark 2007).

2.2.5 Population structure

We assessed population structure at local and regional scales. We first estimated global estimates of F_{ST}, Φ_{ST}, or G''_{ST}. Φ_{ST} is an analogue of F_{ST} that incorporates genetic distances between sequences to assess allelic correlations among groups (Excoffier et al. 1992). G''_{ST} is an unbiased estimator of population structure, derived based on mathematical knowledge of high within-population heterozygosity values depressing estimates of F_{ST} (Hedrick 1999,2005; Meirmans and Hedrick 2011). Indices were estimated using Arlequin and Genodive (Meirmans and Van Tienderen 2004). We then estimated the statistical power of estimated indices using the software POWSIM (Ryman and Palm 2006). Statistical significance of pairwise F_{ST}, Φ_{ST}, or G''_{ST} values was assessed after Bonferroni correction (family-wise error rate = 0.050, corrected p-value = 0.002). We also performed partial mantel tests to assess the correlation between geographic distance and genetic distance, while controlling for the effect of hierarchical population structure (Meirmans 2012). Partial mantel tests were implemented using the vegan package in R.

We used three *a priori* methodologies to identify genetically differentiated subpopulations. We first used a computational geometry approach implemented in the software package Barrier (Manni et al. 2004) using the mtDNA and microsatellite data sets. Delaunay triangulation and Voronoi tessellation help visualize patterns of geographic variation and the frequency of a given barrier across replicate analyses. Triangular pairwise geographic distance matrices were generated using a Geographic Distance Matrix Generator (Ersts 2013) and pairwise genetic distance matrices were generated in Arlequin. Next we used a simulated annealing approach to maximize among group variance using the software SAMOVA (Dupanloup et al. 2002) using the mtDNA and microsatellite data sets. Inferred groups were tested for significance *a posteriori* via AMOVA (Analysis of Molecular Variance). Finally, we used a Bayesian clustering algorithm to assign individuals to *k* groups using the software Structure (Pritchard et al. 2000) using the microsatellite data set. Convergence of parameters (α, F, and likelihood) in preliminary runs was used to determine a suitable burn-in period (500,000) and MCMC chain length for each run (1,000,000). We used an admixture model that allows individuals to have mixed ancestry (Falush et al. 2007). We performed 10 replicate runs for each value of *k* ranging from 1 to 21. We then identified the most likely number of clusters using the Evanno method (Evanno 2005), as implemented in Structure Harvester (Earl and Vonholdt 2012).

2.3.6 Migration patterns

We estimated patterns of average, long-term connectivity between geographic regions in the Gulf using the Bayesian approach implemented in Migrate-n version 3.5.1 (Beerli and Felsenstein 1999). We evaluated a full migration model for the mitochondrial and microsatellite datasets. Running conditions for Migrate-n were as follows: 5,000,000 recorded steps, a burn-in of 1,000,000 steps, a static heating scheme using 20 temperatures, a tree swapping interval of 1, and an upper prior boundary for migration set to 7,500. We assessed convergence in Migrate-n across three replicate runs for each model by recording both effective sample size (ESS) and autocorrelation values. Values of ESS > 500 indicate convergence and proper length of MCMC chains.

2.3 Results

2.3.1 Genetic data: Mitochondrial markers

We identified 127 unique haplotypes. Haplotypes formed a star-like network, with a predominant central haplotype surrounded by many low frequency haplotypes (Table 1, Figure B1). The average distance between haplotypes was 1 to 2 bp, with a maximum distance of 4 bp. The most abundant haplotypes were observed in 26.9% (n = 148) and 9.1% (n = 50 for second and third most abundant) of the samples. The number of haplotypes (nH) and corrected haplotype diversity (h*) are reported in Table 1. Corrected haplotype diversity ranged from 0.673 to 1.000.

2.3.2 Genetic data: Microsatellite markers

All twelve microsatellite loci were polymorphic in *M. rosacea*. We excluded four loci (Mros01, Mros06, Mros08, Mros09) from our analysis due to evidence of null alleles and significant linkage disequilibrium. All reported statistics in Table B1 are from the remaining 8 loci. The total number of alleles per locus per site ranged from 6 to 40. Corrected allelic richness per locus ranged from 5.000 to 9.505. Significant departures from HWE were observed in 6 out of 168 exact tests ($p<0.0003$) after Bonferroni correction. Deviations from HWE may be consistent with fluctuations in population size observed in estimates of Fu's F_S.

2.3.3 Divergence estimates and demographic patterns

All *M. rosacea* samples coalesced to a most recent common ancestor that dated to the Pleistocene epoch (approximately 2.5 million to 11,800 years ago). Two major *M. rosacea* clades diverged approximately 113,000 years ago. The majority of lineages within these clades diverged < 20,000 years ago (Figure 2). Pie charts showing the geographic distribution of these clades confirm that lineage sorting has not yet occurred (Figure 3). However, three sites in the northern Gulf (San Felipe, Isla Patos and Isla San Esteban) had somewhat different profiles than the majority of sites, with > 50% of individuals belonging to the white clade.

Observed values of Fu's F_S and Tajima's D suggest that *M. rosacea* subpopulations are undergoing an expansion. Fu's F_S was significantly negative in 17 of 21 sampling localities, with the exception of Puerto Lobos, Isla Ángel de la Guarda, Isla San Lorenzo and Isla Tiburón (South) (Table 1). Tajima's D was significantly negative in 9 of 21 sampling localities. All D values in the central Gulf were statistically significant, a few in the northern Gulf and none in the Midriff Islands (Table 1). Departures from neutrality observed in both indices indicate an excess of recent mutations (number of segregating sites > pairwise nucleotide diversity) due to a potential population expansion or a selective sweep.

2.3.4 Population structure

We detected statistically significant genetic differentiation using mtDNA ($F_{ST} = 0.113$, $p < 0.001$; $\Phi_{ST} = 0.044$, $p < 0.001$) and microsatellites ($F_{ST} = 0.001$, $p = 0.028$; $G''_{ST} = 0.072$, $p < 0.001$). Power analyses indicated our ability to detect observed levels of genetic differentiation with a probability of 99% for our mtDNA data set and a probability of 95% for our microsatellite data set. Hypervariability of the microsatellites likely explains the order of magnitude difference in the degree of genetic subdivision uncovered between F_{ST} versus G''_{ST} (Table B1). As heterozygosity increases for a locus, the maximum value possible for F_{ST} is decreased (Hedrick 1999).

After Bonferroni correction, a large number of pairwise F_{ST} comparisons for the mtDNA data set were statistically significant (126 of 210) while few Φ_{ST} pairwise comparisons (6 of 210) were significant (Table B2). Pairwise F_{ST} values ranged from 0.051 to 0.249 and pairwise Φ_{ST} values from 0.091 to 0.161, with no clear geographic trends. For the microsatellite data set, only 6 out of 210 pairwise F_{ST} were statistically significant after Bonferroni correction (Table B3). Values ranged from 0.009 to 0.024, with all significant comparisons involving Isla Tiburón (North). The largest pairwise G''_{ST} values were observed in pairwise comparisons with San Felipe, Puertecitos and Isla Tiburón (North), though *p*-values could not be generated for pairwise G''_{ST} values. We found no evidence for isolation by distance. Results from the partial Mantel test yielded non-significant correlation coefficients when we controlled for both geographic distance (r = -0.386, p = 0.983) and hierarchical population structure (r = -0.104, p = 0.756).

A priori approaches for detecting genetic differentiation among subpopulations yielded largely concordant patterns. Two potential barriers to larval dispersal were identified in the northern Gulf using the computational geometry approach (Figure 4). The first barrier strongly isolated San Felipe and Puertecitos in the upper Gulf from sites on the mainland at similar latitudes. The second barrier isolated a large number of sites in the Midriff Islands from the remainder of the Gulf. Isla Tiburón (North) and Isla Patos were most divergent from mainland sites to their north. Simulated annealing approaches also confirmed genetic divergence of the Midriff Islands, with maximal genetic variance observed when sites in and around the Midriff Island region were clustered (Table 2). Finally, the Evanno method suggested k = 3 best explained patterns of microsatellite variability (Figure B2). Partial assignment to the blue and red clusters was seen among all sites. Assignment to the yellow cluster was highly variable among sites. The highest population level assignments to the yellow cluster were seen in Puerto Lobos (0.119), Isla Tiburón [North] (0.094), Isla Tiburón [South] (0.127) and Isla Patos (0.276). All sites with high population assignment to the yellow cluster were located in the eastern Midriff Islands or mainland sites just to the north of them. Genetic divergence in this region confirms patterns detected using computational geometry and simulated annealing approaches.

2.3.5 Migration patterns

Long-term migration rates estimated from mtDNA and microsatellites suggest asymmetrical larval dispersal is occurring between the northern and central Gulf. Based on mtDNA, an average of 132.1 (95% posterior distribution (PD) = 86.5 – 175.0) migrants per generation move from the northern to central Gulf, while only 26.2 (95% PD = 2.9 – 54.7) migrants per generation move in the reverse direction. Similarly in the microsatellite data set, an average of 581.9 (95% PD = 390.0 – 750.0) migrants per generation move from the northern to central Gulf, while 220.0 (95% PD = 72.5 – 320.0) migrants per generation move in the reverse direction.

2.4 Discussion

2.4.1 Demographic history

The majority of *M. rosacea* lineages have diverged since the last glacial maximum (LGM), when there was a dramatic drop in sea levels of 100 to 150 m (Figure 5). We found evidence of population expansions in sampling localities along continental shelf that would have been exposed during low sea level stands. Tajima's D values only reflected signatures of population expansion for some of the northernmost sites found on the large expanse of shelf exposed in the upper Gulf. Fu's F_S values, however, showed evidence of population expansions at all sites except Isla Ángel de la Guarda, Isla San Lorenzo, Isla Tiburón (South) and Puerto Lobos. Patterns of population expansion detected using Fu's F_S reflect sites along exposed shelves in the shallow upper Gulf (San Felipe, Puertecitos, Peñasco) and on landbridge islands with shallow channels connecting them to mainland (Tiburón, Datil, Patos, San Marcos, Carmen, Kino, San Pedro Nolasco). This may also explain why we did not find evidence of expansion around deep-water islands such as Isla Ángel de la Guarda or Isla San Lorenzo in the Midriff Islands. Additionally, the star-like topology of the haplotype network is common in species that have undergone population expansions (Avise 2000). Higher proportions of singleton haplotypes from the northern Gulf may demonstrate the reinvasion of *M. rosacea* as sea levels rose in the northern Gulf after the last glacial maximum.

2.4.2 Contemporary mechanisms restricting gene flow

The underlying mechanisms driving genetic divergence in the Gulf of California are not understood fully. While some studies have shown little to no structure for marine organisms within the Gulf (Terry et al. 2000; Bernardi et al. 2003; Pfeiler et al. 2005), others exhibit strong population structure (Riginos and Nachman 2001; Riginos 2005). Population structure has largely been observed in species with low vagility (e.g. Riginos 2005; Hurtado et al. 2010). *Mycteroperca rosacea* has a pelagic larval duration (PLD) of approximately 24 days (Aburto-Oropeza et al. 2007). If passive movement is assumed, then larvae have the potential to travel reasonable distances based on ocean current speeds (Soria et al. 2013). Given the limited amount of time since divergence and its PLD, we found considerable genetic differentiation among subpopulations of *M. rosacea*. A lack of support for isolation by distance suggests that observed patterns of genetic variation are driven by more complex dynamics than just linear distance alone.

Complex oceanography in the Gulf of California may be the primary mechanism driving broad scale connectivity between biogeographic regions as well as local retention of larvae. Results from migration analyses indicated high levels of connectivity between regions. Asymmetrical migration, with disproportionately more gene flow from the northern to central Gulf, has been observed in another serranid (Riginos 2005). Depending on the mode of larval dispersal, such asymmetrical differences in migration may be due to regional differences in environmental and oceanographic conditions (Wares et al. 2001). Results from three-dimensional modeling of circulation in the Gulf of California by Marinone (2003) may also explain observed asymmetrical migration. In May when larvae would be in the water column (Erisman et al. 2007), between region surface currents are predominately moving from north to south. Such asymmetrical migration between regions suggests that the northern Gulf may be a net exporter of larvae to populations in the central and southern Gulf.

The observation of high connectivity does not preclude the potential for reduced gene flow among or local retention within subpopulations. By local retention here we mean the proportion larvae produced at a site that are retained at the end of the PLD (Botsford et al. 2009a; Burgess et al. 2013). Identification of a potential genetic barrier between northern Isla Tiburón and sites directly to its north on the mainland may provide support for local retention in the Midriff Islands. Recent work by Iacchei et al. (2013) suggests that high genetic differentiation in sites may be due to localized recruitment. A biophysical oceanographic model accounting for pelagic larval duration, timing of flexion, and spawning time of *M. rosacea* provided evidence of larval retention in the region surrounding Isla Tiburón (Munguía-Vega et al., *in prep*). Minor contribution of larvae from this region and a strong break between sites around Isla Tiburón (and mainland sites to its north) has also been seen in the rock scallop (*Spondylus calcifer*) using a coupled biological-oceanographic model (Soría et al., *in prep*). Alternatively, results from a biophysical model described in Munguía-Vega et al. (*in prep*) also suggest that high genetic differentiation of sites around Isla Tiburón may be due to reception of larvae from a large number of diverse source populations. This may explain the different pie chart profiles seen for Isla Patos and San Esteban.

Habitat distribution and movement patterns of adults are alternative factors that might be driving geographic patterns in genetic variation. Discontinuity of suitable habitat can facilitate reduced gene flow among populations (Johansson et al. 2008; Fraser et al. 2010; Milana et al. 2012). Populations separated by open water may be more genetically distinct than populations along continuous stretches of rocky reef habitat in the Gulf (Riginos and Nachman 2001). While this does not explain divergence of San Felipe and Puertecitos, it could account for increased genetic divergence of some of the Midriff Islands. Movement patterns of some adult groupers also indicate that they may be less likely to migrate across deep channels (Colin et al. 1987; Starr et al. 2007). However, this may not apply to *M. rosacea*. A recent, small-scale study showed adults moving across deep channels between Espiritu Santo and Marisla Seamount (Erisman et al., *in press*). Whether this trend holds in other geographic regions in the Gulf will determine the relative importance of adult movement in either facilitating or inhibiting connectivity among coastal and island spawning stocks.

2.4.3 Relevance for conservation and fisheries management

A primary objective of fisheries management is to protect species from activities jeopardizing their future production of offspring (Jennings et al. 2001b). Deteriorating conditions in the Gulf of California's fisheries resources warrant an improvement of conservation and fisheries management efforts. According to the Carta Nacional Pesquera approximately 60% of fisheries in the Gulf of California are either at capacity or are overexploited [defined as harvesting stocks to the point of diminishing returns] (SAGARPA 2004).

Developing an effective management plan for *M. rosacea* has a two-fold benefit. First, it would assure the long-term sustainability of a profitable species for communities highly dependent on fishing-derived income (Cinti et al. 2009; Ainsworth et al. 2012). Second, enhanced management could help ameliorate negative genetic consequences associated with overfishing. The logical first step in the imposition of fisheries management is a detailed understanding of target fisheries' population structure, connectivity and demography. Though uncertainties still surround some of these topics, implementation of fisheries regulations should be implemented with the best readily available science. Thus, we recommend an adaptive management strategy that incorporates a combination of marine reserve implementation and seasonal closures. Implementation of marine reserves, in combination with other fisheries management tools, may allow broader achievement of fisheries and conservation objectives (Hilborn et al. 2004).

Several authors have proposed establishing a network of reserves in the Gulf of California (Sala et al. 2002; Enriquez-Andrade et al. 2005; Cudney-Bueno et al. 2009). Marine spatial planning requires an understanding of both potential placement, sizing and spacing within a network of reserves (Lubchenco et al. 2003; Palumbi 2003; Shanks et al. 2003). Based on high levels of genetic diversity and barriers to larval dispersal observed near Isla Tiburón and surrounding islands, this may represent a prime location to establish a reserve. Both fishing intensity and diversity of targeted species are high in the Midriff Islands relative to other areas in the northern Gulf, particularly in the region around Isla Tiburón (Moreno-Báez 2010). Despite inclusion of several of the Midriff Islands in biosphere reserves or marine parks, almost none explicitly designate specific no take zones, with the exception of Isla San Pedro Mártir. Thus, it would be prudent to promote more sustainable fishing in this region through placement of a large no-take reserve or by designating no-take regions in currently existing parks. Additionally, a no-take reserve in the Midriff islands could be linked to a few large reserves incorporating key habitat types in the separate biogeographic regions. High connectivity observed among the majority of sites suggests such marine reserves spaced at sizeable distances would be sufficient to maintain connectivity in a Gulf-wide network.

In conjunction with marine reserves, seasonal closures have been used as a management strategy for a number of aggregating reef fishes in the Caribbean Sea (Russell 2012). Seasonal closures protecting *M. rosacea* during their spawning period could potentially enhance reproductive stocks in the Gulf. The advantage of this approach is that while it does not specifically protect spawning sites, all reproductive stocks are protected regardless of whether explicit spawning sites are known. Regional differences in spawning time would need to be taken into consideration when designating the time frame of seasonal closures for *M. rosacea*. While the difference in the onset of spawning is not as drastic as once implied (Sala et al. 2003), analysis of gonad tissues from females suggests that spawning begins slightly earlier in the Midriff Islands (Erisman et al. 2007; Munguía-Vega et al., *in prep*).

It is crucial that we continue reevaluating the effectiveness of proposed measures via incorporation of data from new scientific studies and biological monitoring. Additional data on distances traveled by adult *M. rosacea* as well as larval dispersal kernels will aid in more precise area allotments for and spacing between marine reserves. Additionally, it will be necessary to reevaluate proposed regulations and marine reserve design when connectivity data becomes available for the other 5 focal species identified by *PANGAS*. In the meantime, some of our management recommendations may best be promoted through active conservation efforts being made by the non-governmental organization and partner in the *PANGAS* project, Comunidad y Biodiversidad, A.C. (COBI).

2.5 Conclusion

We observed genetic differentiation among subpopulations of *M. rosacea*, with divergence of lineages of *M.* rosacea dating to the late Pleistocene and Holocene. Complex oceanographic patterns in the Gulf of California may be responsible explain extensive connectivity observed between the northern and central Gulf, as well as pockets of larval retention in the northern Gulf. Based on our findings we recommend a combination of marine reserves and seasonal fishery closures as a potential management strategy for *M. rosacea* in the Gulf of California.

Acknowledgements

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Table 2.1. Molecular diversity indices for mitochondrial DNA for *M. rosacea*

Sampling Site	*n*	nH	h*	π	F_S	D
1. San Felipe	13	10	0.949	0.0015 ± 0.0010	**-6.695**	**-1.755**
2. Puertecitos	8	7	0.964	0.0019 ± 0.0013	**-3.393**	-1.283
3. San Luis Gonzaga	16	12	0.950	0.0016 ± 0.0010	**-8.513**	-1.707
4. Bahía de los Angeles	52	23	0.870	0.0016 ± 0.0010	**-17.754**	**-1.985**
5. Puerto Peñasco	25	13	0.810	0.0013 ± 0.0009	**-7.976**	**-1.863**
6. Puerto Lobos	11	7	0.909	0.0018 ± 0.0012	-1.976	-0.061
7. Puerto Libertad	55	21	0.874	0.0016 ± 0.0010	**-13.175**	-1.384
8. Isla Ángel de la Guarda	25	9	0.840	0.0015 ± 0.0010	-2.201	-0.052
9. Isla San Lorenzo	11	4	0.673	0.0011 ± 0.0008	-1.673	-0.077
10. Isla San Esteban	4	4	1.000	0.0013 ± 0.0011	**-1.872**	-0.780
11. Isla Tiburón (North)	18	12	0.922	0.0017 ± 0.0011	**-6.882**	-0.960
12. Isla Tiburón (South)	13	8	0.936	0.0023 ± 0.0014	**-1.773**	-0.966
13. Isla Datil	7	6	0.952	0.0013 ± 0.0010	**-3.409**	-1.129
14. Isla Patos	8	8	1.000	0.0026 ± 0.0017	**-4.670**	-1.096
15. Isla San Pedro Mártir	17	9	0.860	0.0014 ± 0.0010	**-3.648**	-1.498
16. La Jerga	23	17	0.949	0.0019 ± 0.0012	**-13.177**	**-1.896**
17. Isla San Marcos	51	20	0.783	0.0014 ± 0.0009	**-14.446**	**-2.060**
18. Isla Carmen	53	23	0.903	0.0017 ± 0.0011	**-15.850**	**-1.617**
19. Isla Cerralvo	51	23	0.902	0.0018 ± 0.0011	**-16.194**	**-1.834**
20. Bahía Kino	28	18	0.937	0.0016 ± 0.0010	**-14.726**	**-1.671**
21. Isla San Pedro Nolasco	62	32	0.938	0.0018 ± 0.0011	**-26.534**	**-1.903**

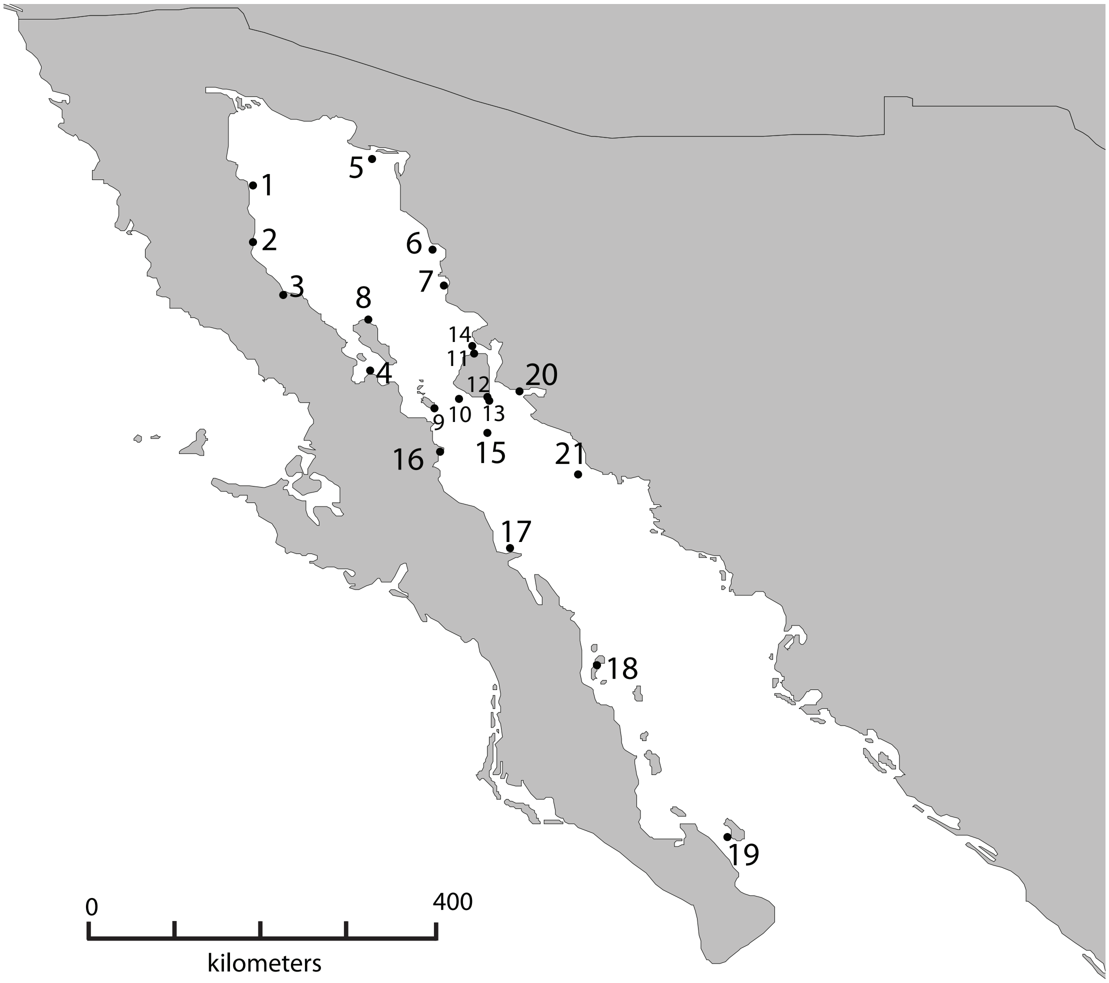
Sample location, number of specimens (*n*), number of haplotypes (nH), corrected haplotype diversity (h*), nucleotide diversity (π) and the neutrality statistic Fu's F_S and Tajima's D. Bolded values denote statistical significance of $p < 0.05$ for F_S and D values.

Table 2.2. AMOVA results from simulated annealing approach for *M. rosacea*

mtDNA	Source of variation	d.f.	var%	P-value
(1) Sites 3,4,8,11,12,14-16 and (2) Sites 1,2,5-7,9,10,13,17-21	Among groups	1	5.75	< 0.001
	Among populations within groups	19	0.77	< 0.001
	Within populations	530	93.48	< 0.001
(1) Sites 3,4,8,11,12,14-16, (2) Sites 1,2,5-7,9,12,17-21 and (3) Sites 10,13	Among groups	2	5.75	< 0.001
	Among populations within groups	18	0.61	< 0.001
	Within populations	530	93.64	< 0.001
Microsatellites	Source of variation	d.f.	%var	P-value
(1) Site 14 and (2) Sites 1-13,15-21	Among groups	1	0.90	0.046
	Among populations within groups	19	0.30	< 0.001
	Within populations	1021	98.80	< 0.001
(1) Sites 1, 14 and (2) Sites 1-13,15-21	Among groups	2	0.90	0.002
	Among populations within groups	18	0.10	< 0.001
	Within populations	1021	99.00	0.001

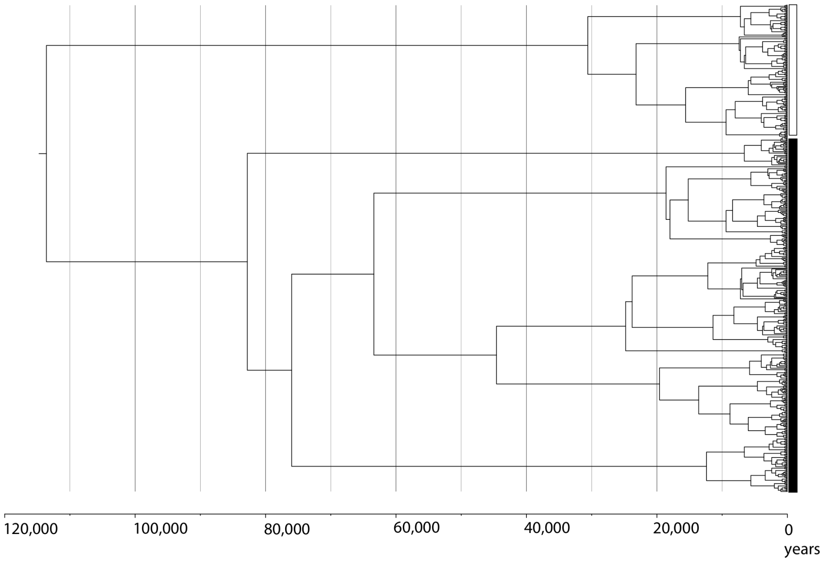
Degrees of freedom (d.f.) and percent variation (var %) to test for evidence of regional genetic differentiation among *Mycteroperca rosacea* sampling localities using mitochondrial DNA and microsatellites. (*) denotes statistical significance of $p < 0.05$.

Figure 2.1. *M. rosacea* sampling localities in the Gulf of California



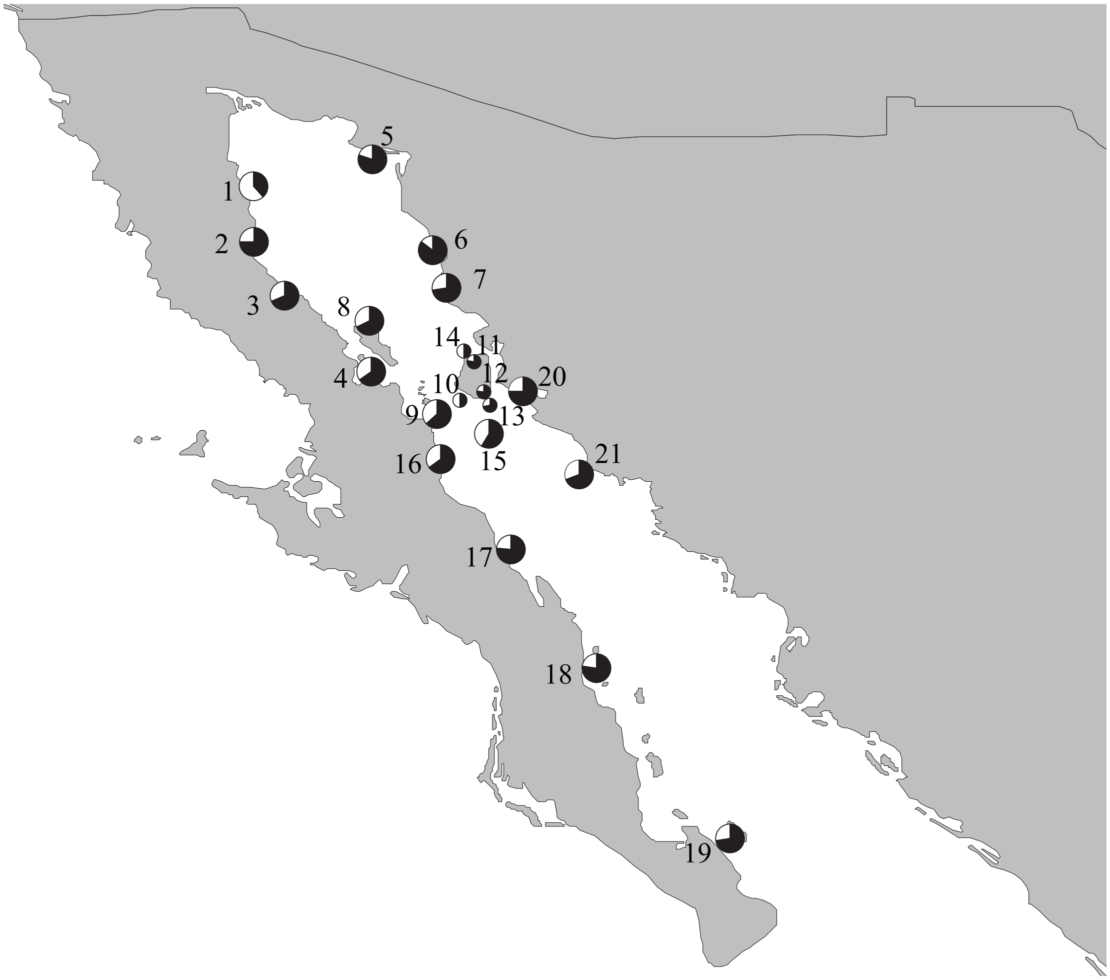
Sampling localities include: San Felipe (1), Puertecitos (2), San Luis Gonzaga (3), Bahía de los Angeles (4), Puerto Peñasco (5), Puerto Lobos (6), Puerto Libertad (7), Isla Ángel de la Guarda (8), Isla San Lorenzo (9), Isla San Esteban (10), Isla Tiburón (North) (11), Isla Tiburón (South) (12), Isla Datil (13), Isla Patos (14), Isla San Pedro Martír (15), La Jerga (16), Isla San Marcos (17), Isla Carmen (18), Isla Cerralvo (19), Bahía Kino (20) and Isla San Pedro Nolasco (21).

Figure 2.2. Coalescent genealogy for *M. rosacea*



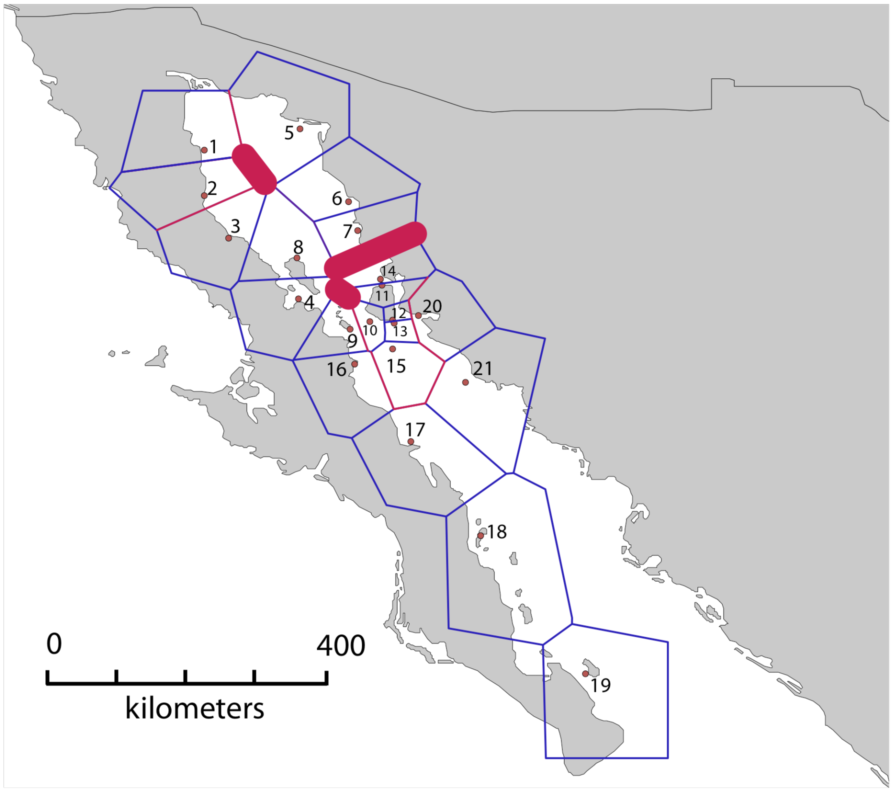
Coalescent genealogy generated in BEAST showing divergence dates for *M. rosacea*. Divergence dates are listed in years. Distinct clades are coded as black and white.

Figure 2.3. Pie diagrams for *M. rosacea*



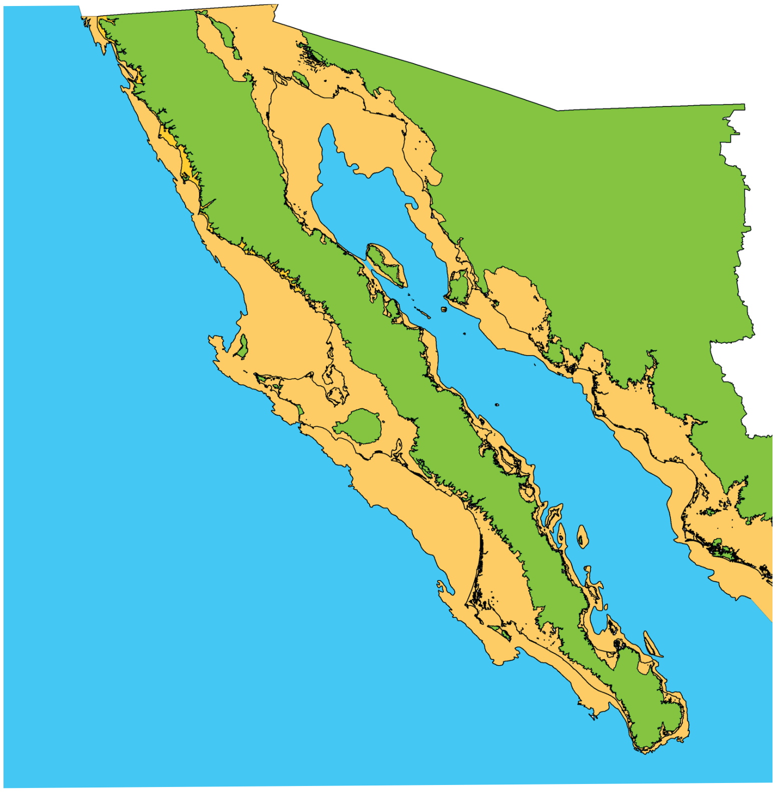
Each pie chart illustrates the relative frequency of clades identified in Figure 2.2 among samples within a sampling locality.

Figure 2.4. Identified barriers to larval dispersal in the Gulf of California



Genetic barriers between *M. rosacea* subpopulations, using Delaunay triangulation and Voronoi tessellation implemented in Barrier. Each sampling locality is located inside a blue cell, with thickness of barrier lines (in red) proportional to the frequency with which a given barrier is observed in replicate analyses and inversely proportional to permeability.

Figure 2.5. Reconstruction of Gulf of California coastline during last glacial maximum (LGM)



Gulf of California coastline during the last glacial maxiumum, using 100 m isobath as a reference. Blue areas represent ocean, green areas represent land and brown areas represent continental shelf exposed with decreased sea levels during the glacial cycle.

Chapter 3

How does the magnitude of genetic differentiation impact fisheries management strategies?

3.1 Introduction

Demands for seafood are growing as the human population continues to rapidly increase in size (Hilborn et al. 2003; Srinivasan et al. 2010). In the face of increasing demands, there have been drastic declines in commercially exploited species over the last few decades (Myers and Worm 2003; Worm et al. 2009; Watson et al. 2013). The primary objective of fisheries management is to ensure sustainable harvest while ultimately avoid population crashes in commercial species (Jennings et al. 2001a). Noticeable declines in species abundances are driving countries to improve their national and international fisheries management strategies and regulations (Mora et al. 2009). Implementation of sustainable management strategies will partly depend on the ability to match biological processes to suitable management actions (Worm and Branch 2013).

The fundamental biological unit in fisheries management has been the stock. A commonly used definition for a stock is "an intraspecific group of randomly mating individuals with temporal and spatial integrity" (Ihssen et al. 1981). Fished species may represent multiple stocks across a broad geographic range. Failure to properly delineate stocks or management units can result in decreased productivity, reduction in local populations, and in extreme cases local, regional or global extinction (Fu and Fanning 2004; Sterner 2007). Thus, it is crucial that we accurately define distinct stocks or management units for effective fisheries management, as such groups are likely to respond independently to fishing pressures.

There is a longstanding history of utilizing molecular markers to define stock structure and management units (Carvalho and Hauser 1994; Ward 2000; Hauser and Carvalho 2008; Ovenden et al. 2013). There are a number of advantages to defining stocks based on differences in their genetic composition. First, management of genetically distinct stocks or populations provides a means of monitoring levels of genetic variation in harvested species (Kenchington 2003; Allendorf et al. 2008). Utilizing population genetics theory to assess stock structure in commercial species is also helping to further address the longstanding question of whether populations of marine species are open or closed (Cowen and Sponaugle 2009), which has direct bearing on the resilience of a given stock. Genetic studies can increase our understanding of the extent of connectivity between stocks and the spatial scales across which they should be managed (Ward 2000; Reiss et al. 2009). Finally, knowledge of movement patterns of larvae and adults from natal sites and the magnitude of genetic differentiation among subpopulations can be used to size and space marine reserves (Palumbi 2003; Shanks et al. 2003; Palumbi 2004). Marine reserves have become an increasingly important tool in fisheries management that, if designed properly, can provide major benefits such as increased biomass for commercially important species (Roberts 1995; Halpern and Warner 2002) and enhancement of adjacent fisheries (Alcala and Russ 1990; Roberts et al. 2001).

The primary goal of this study was to examine the management implications of population structure by conducting a meta-analysis of results from empirical population genetics studies of marine and diadromous fishes. Though a number of invertebrate species are also exploited in global fisheries, I focused on fishes as they represent one of the most threatened groups of vertebrates (Baillie et al. 2004). In these studies, I specifically investigated the fisheries management strategies recommended as a direct result of varying magnitudes of genetic differentiation. If there is a lack of consistency across studies in how the magnitude of genetic differentiation is described for fishes, it could inhibit our broader understanding of how to best translate genetic estimates of stock structure into effective management strategies. The comparison of studies in the meta-analysis addresses this problem by extracting general patterns that link genetic differentiation and fisheries management strategies.

3.2 Methods

3.2.1 Literature review

I searched the available literature cited in the Web of Science database (year span: 1900 – 2013) to identify empirical population genetics studies of marine and diadromous fishes. The search covered all literature available up to December 3, 2013. Eight keywords used were combined into the following term combinations: “TS = (connectivity OR structure OR ‘gene flow’ OR dispersal OR ‘genetic differentiation’) AND TS = (‘marine conservation’ OR ‘fisheries management’ OR ‘marine reserve*’) ”. There were some factors limiting the scope of the search. First, I was limited to literature accessible based on database licensing held by the University of California Santa Cruz library system – Web of Science database, BIOSIS Previews and BIOSIS Citation Index. Within these databases my search was then limited to papers written in English and published in scientific journals (excluding grey literature, technical reports and the majority of conference proceedings). Nonetheless, I believe my approach was adequate since the goal of this publication was not to perform an exhaustive search of the literature.

3.2.2 Inclusion and exclusion criteria

After executing the initial search, studies were excluded if they did not meet key criteria. (1) The study should focus on fishes that spend either part of or their entire life cycle in the marine environment. Studies on both marine and diadromous fishes were considered, while studies on invertebrates, plants and freshwater fishes were excluded. (2) Only empirical genetics studies were considered. Review studies were excluded, as well as theoretical studies that estimated population structure or connectivity based on biophysical or numerical models.

3.2.3 Data collection and analysis

For each article, I assessed the species, major taxonomic grouping and basic life history (i.e. marine vs. diadromous) of each fish. I then recorded estimates of population structure and genetic differentiation (F_{ST} and its derivatives). All F_{ST} values that were not statistically significant were considered zero when means were later calculated. When explicitly stated, I also recorded the quantitative adjectives used by authors to describe the magnitude of observed genetic differentiation.

Because of the wide variety of synonyms used to describe certain magnitudes of differentiation, pending results, adjectives would be binned into the following categories – None (representing panmixia or no structure), weak, moderate and strong genetic differentiation. Finally, I recorded conservation or fisheries management recommendations made based on results of the study when they were explicitly stated.

In order to test the implications of weak or strong population structure on management it was first necessary to determine whether adjectives such as 'weak', 'moderate' and 'strong' used in the scientific literature actually correspond to statistically different magnitudes of genetic differentiation. Estimates of F_{ST} were plotted against quantitative adjectives, and the statistical difference between mean F_{ST} was evaluated using an ANOVA. Primary classes of markers expected were allozymes, DNA sequence (mitochondrial or nuclear), microsatellites and SNPs. ANOVAs were conducted separately for each marker type due to potential challenges associated with directly comparing indices generated from different markers. Pending results of the aforementioned analysis, I then assessed the magnitude of F_{ST} relative to stock management strategies (i.e. manage as a single stock, multiple stocks or as multiple species). Statistical differences among the mean F_{ST} for each management approach was determined via ANOVA.

3.3 Results and Discussion

3.3.1 Study characteristics

There were 15 possible keyword combinations based on the design of the Web of Science search. All combinations yielded a total of 9,380 articles after eliminating duplicate articles represented in more than one of the fifteen searches. After assessing article relevance, based on the aforementioned criteria, this number was drastically reduced to 386 relevant studies. All studies were conducted between 1984 and 2013. A total of eighty-five families and 275 species of fish were represented in these 386 research articles (Table C1, C2). Studies focused on diadromous fishes made up 18.09% of the total, with the remaining studies (71.91%) focused on marine species.

Certain groups of fish were better represented in the meta-analysis than others (Figure 1), comprising > 50% of the major taxonomic groups observed. Fish in the families Salmonidae (n = 37), Gadidae (n = 27) and Scombridae (n = 23) were best represented. Additionally, when families of sharks and rays were collectively grouped as elasmobranchs (n = 28) they were also well represented in the literature. Fish represented in these groups include salmon, cod, haddock, whiting, tuna, mackerel, sharks and rays. Increased scientific interest in these fishes may result from their economic value and/or biological vulnerability to overfishing. The majority of conservation genetics studies in marine systems are directed towards commercially important fish species (Avise 1998). The global value of fish traded is approximately US$111.8 billion (FAO 2012). While fisheries make minor contributions to overall economic activity in larger developed countries, in smaller countries they can contribute upwards of 50% the gross domestic product (Dalzell et al. 1996). In addition to economic value, the increased scientific interest in certain species may be due to their conservation status. For instance, the majority of genetic studies on sharks and rays yielded in the literature search were published in the past two to three years (e.g. Benavides et al. 2011; Galvan-Tirado et al. 2013; Vignaud et al., 2013). Increased focus on shark conservation in the literature may reflect increased awareness of shark finning and overall vulnerability of elasmobranchs to overharvest (Stevens et al. 2000; Clarke et al. 2006; Worm et al. 2013). Major efforts are being made to protect these important top predators at an international level, with the recent addition of five species to CITES Appendix II.

3.3.2 Quantitative adjectives for magnitudes of genetic differentiation

A number of adjectives were used to describe varying magnitudes of genetic differentiation. Synonyms were binned under 4 quantitative adjectives (none, weak, moderate and strong) used to describe varying magnitudes genetic differentiation (Table 1). However, all studies reviewed did not provide a quantitative adjective to describe the extent of genetic differentiation observed among groups. Approximately 19.94% of studies simply described the observed differentiation among groups with general terms such as ‘statistically significant’ or ‘genetically differentiated’.

F_{ST} values were grouped by marker type and then plotted against one of four quantitative adjectives (Figure 2). A Kruskal-Wallis one-way ANOVA was used as variances were not equal among quantitative adjectives, with variance values increasing as the magnitude of genetic differentiation increased (Table 2). Results from the ANOVA suggest that mean F_{ST} differs among quantitative adjectives used to describe magnitudes of genetic differentiation (based on a critical *p*-value = 0.05) for studies using allozymes ($p = 0.0013$), microsatellites ($p < 0.0001$) and mtDNA ($p < 0.0001$). This suggests quantitative adjectives across population genetics studies do in fact correspond to statistically different magnitudes of genetic differentiation. Thus, 'weak' genetic differentiation is in fact different from 'moderate' or 'strong' differentiation. Associated 95% confidence intervals around these mean F_{ST} values may provide ranges that can be referenced for each quantitative adjective in future studies of marine and diadromous fishes. In contrast, for studies using SNPs ($p = 0.1797$) and nDNA ($p = 0.0897$) it was not possible to determine if mean F_{ST} values for quantitative adjectives were statistically different from one another. However, this result is likely driven by an insufficient number of studies utilizing these markers (i.e. small sample size).

Wright (1978) suggested quantitative guidelines to assist with interpreting F_{ST} and different magnitudes of genetic differentiation. Quantitative adjectives ranged from little ($0 < F_{ST} \leq 0.05$) and moderate ($0.05 < F_{ST} \leq 0.15$) to great ($0.15 < F_{ST} \leq 0.25$) and very great ($F_{ST} < 0.25$). However, as the majority of Wright's theoretical work was based on terrestrial systems, it was unclear whether quantitative ranges defined would apply to marine and diadromous fishes with large effective population sizes, capable of long distance dispersal. Based on how I grouped adjectives in our analyses, I compared our ranges for ‘weak’ with Wright’s ‘little’, ‘moderate with Wright’s ‘moderate’, and ‘strong’ with Wright’s ‘great’ and ‘very Great’ (Table 3). Interestingly, mean F_{ST} and associated confidence intervals for our quantitative adjectives aligned reasonably well with Wright’s ranges. Mean F_{ST} values for quantitative adjectives for allozymes, mtDNA and microsatellites all fell within ranges defined by Wright for each adjective. Though confidence intervals defined by the meta-analysis did not perfectly align with Wright’s ranges for each quantitative adjective, significant overlap was seen. The best match was observed in studies using mtDNA. This implies that quantitative adjectives in population genetics studies could be standardized in the future (particularly for mtDNA studies) by using Wright’s quantitative adjectives to describe varying magnitudes of genetic differentiation.

3.3.3 Common fisheries management recommendations

Only 77.20% of the studies in the meta-analysis provided explicit fisheries management strategies based on genetic data provided. Remaining studies either yielded inconclusive results or made no statement about how results could be applied to fisheries management. The most frequent management strategies recommended could be grouped into 4 main categories (Figure 3). The most common strategy involved studies that designated genetically distinct stocks or proposed management units [MUs] ($n = 219$). Another category used genetic data to either confirm or re-evaluate current MUs, in cases where stocks or MUs were already designated for species ($n = 33$). In some of these studies, a single MU was recommended where a species was currently managed as multiple stocks (e.g. Safford et al. 1992; Gold et al. 1999; Cushman et al. 2009; Canales-Aguirre et al. 2010) or the reverse scenario (e.g. Lundy et al. 1999; Teacher et al. 2013). In other cases, genetic studies confirmed current internationally sanctioned or nationally defined MUs such as ICES or IUCN management units (e.g. Nakadate et al. 2005; Pampoulie et al. 2008; Dudgeon et al. 2009; Hyde and Vetter, 2009). A third category of studies focused on using genetic data to enhance the design or effectiveness of marine protected areas (MPA) and marine reserves ($n = 31$). A number of these studies utilized assignment tests and DNA parentage analyses to estimate dispersal kernels and extent of self-recruitment in order to assess efficacy of current reserves in place (e.g. Christie et al. 2010b; Berumen et al. 2012; Hogan et al. 2012; Saenz-Agudelo et al. 2012). The final category focused on monitoring genetic diversity in hatchery and/or wild stocks ($n = 8$), with some studies providing insight on monitoring genetic variation and controlling for inbreeding in commercial breeding programs (e.g. Skaala et al. 2005; An et al. 2011a; An et al. 2011b).

3.3.4 Relationship between magnitude of genetic differentiation and stock management strategies

A major question in fisheries management is what degree of divergence between groups is necessary to justify separate management (Palsboll et al. 2007; Waples et al. 2008). While there is a lack of consensus on this topic, results from the meta-analysis could be used to determine if there are trends in the data to further address this topic for marine and diadromous fishes. Since the designation of genetically distinct stocks or MUs was the most common fisheries management approach addressed in the literature, I assessed whether mean F_{ST} values were different among various stock management approaches (Figure 4). Results from a Kruskal-Wallis one-way ANOVA suggest that mean F_{ST} was statistically different for each of the stock management approaches ($p < 0.0001$). Mean $F_{ST} = 0.0122$ for studies recommending single stock management, 0.1572 for multiple stock management, and 0.6673 for management as distinct species (Table 4). If describing these magnitudes using Wright's quantitative adjectives, this would correspond to weak, moderate and very great genetic differentiation.

Despite statistically significant differences between mean F_{ST} values associated with stock management strategies, there was considerable variance around mean F_{ST} values, particularly in the multiple stock management category. Variance may be driven by biological differences among fish species, as well as a lack of consensus about the degree of genetic divergence required to justify distinct stock management. The broad range of F_{ST} values observed for multiple stock management recommendations highlights challenges associated with developing a general genetic framework for defining demographically distinct groups.

Fishes in the marine environment exhibit a wide variety of biological characteristics and life histories (Sweijd et al. 2000; King and McFarlane 2003). A number of factors including length of pelagic larval duration (Feutry et al. 2013), migratory behavior and natal homing (McCairns et al. 2012; Verspoor et al. 2012), spawning environment [pelagic vs. demersal] (Florin and Hoglund 2008) and marine environment occupied [pelagic vs. coastal] (Jackson et al., *in press*) may contribute to varying magnitudes of genetic differentiation and population structure. In this data set, the majority of high F_{ST} values in the multiple stock management category were associated with elasmobranchs. Elasmobranchs lack pelagic eggs and larvae, with dispersal potential entirely dependent on movement of juveniles and adults. Strong population structure has been associated with fishes lacking a pelagic larval stage (e.g. Bernardi 2000; Miller-Sims et al. 2008; Vagelli et al. 2008). Additionally, while minimal genetic structure is expected in marine fishes (Graves 1998; Waples 1998), certain biological factors such as sedentary behavior, disjunct distributions and reproductive philopatry can result in higher levels of genetic differentiation (Palumbi 1994). Both philopatry and disjunct distributions were observed in a number of elasmobranch species included in the meta-analysis (Schultz et al. 2008; Ahonen et al. 2009; Jorgensen et al. 2010; Karl et al. 2011; Phillips et al. 2011).

In contrast, similarity of biological traits among organisms with very low F_{ST} values (< 0.01) was less evident within the same multiple stock management category. In these cases, weak but statistically significant F_{ST} values were used as evidence to reject the null hypothesis of panmixia and to suggest the presence of more than one stock or MU (e.g. Charrier et al., 2006b, Fritsch et al., 2007, Kovach et al., 2010). Studies have cautioned against simply focusing on rejecting panmixia when delineating of MUs, as results can be misleading when there is sufficient statistical power to reject panmixia but populations are not demographically independent (Waples and Gaggiotti 2006). Such instances can lead to misallocation of limited resources to manage multiple stocks where only one exists. However, there are some instances where low but statistically significant structure is biologically significant (e.g. Knutsen et al., 2011), warranting adoption of fine-scale, multiple stock management strategies. Considerable overlap of F_{ST} values < 0.01 between the single-stock and multiple-stock management categories reflects this dichotomy, demonstrating a lack of consistency and arbitrary or biased assignment of stock management strategies by researchers when populations are weakly differentiated.

3.3.5 Potential biases associated with use of F_{ST} in designating management strategies

F_{ST} is one of many genetic indices that may be informative for fisheries management (Carvalho and Hauser 1994; Kenchington et al. 2003). A major complication associated with using F_{ST} to assess stock structure is that minimal genetic exchange is required between effectively isolated groups in order to observe a signal of genetic homogeneity. An ecologically insignificant number of migrants can be sufficient to maintain genetic panmixia, despite effective demographic independence of groups (Ovenden 1990; Utter 1991). Thus, a low F_{ST} value observed in a marine or diadromous fish species could be a reflection large effective population sizes and high connectivity between populations (e.g. Ward et al. 1994; Beheregaray and Sunnucks 2001; Bohonak 1999), or simply due to an inability of analyzed markers to detect true stock structure due to issues of sample size or lack of sufficient statistical power (Reiss et al. 2009).

3.4 Conclusion

I conducted a meta-analysis to investigate the management implications of weak and strong structure in marine and diadromous fishes. The literature review and inclusion criteria yielded a total of 386 relevant studies. Quantitative adjectives used to describe varying magnitudes of genetic differentiation possessed statistically different mean F_{ST} values in studies utilizing mtDNA, microsatellites and allozymes. Mean F_{ST} values and confidence intervals for each quantitative adjective were similar to those defined in Wright (1978). Additionally, mean F_{ST} values across stock management strategies were statistically different from one another, though evaluation with additional methods may be warranted to evaluate stock management strategies for weakly differentiated populations.

Overall, results from this study have implications for standardizing reporting of metrics of genetic differentiation across empirical population genetics studies focusing on conservation and fisheries management for marine and diadromous fishes. While biological differences among species must be considered when developing suitable management strategies, results from this meta-analysis may provide also provide a first step in defining ranges of F_{ST} that can be used to prescribe single or multi-stock species management. If we continue to use F_{ST} to evaluate stock stucture, then it is crucial that we develop a basic criteria for assigning management strategies based on varying levels of genetic differentiation. Developing clear criteria may increase the likelihood that scientific data is incorporated into important conservation and fisheries management decisions.

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I would like to thank Devon Pearse for assistance with developing the concept for this study. I would also like to thank Giacomo Bernardi and Devon Pearse, for providing feedback on the manuscript.

Table 3.1. Quantitative descriptors of genetic differentiation

Quantitative descriptors of genetic differentiation	**Synonyms in literature**
None	negligible, none, lacking, panmixia, panmictic, homogeneous, homogeneity, absence
Weak	low, minor, small, weak, not great, fine, subtle, minimal, not extensive, shallow, limited, little, constrained
Moderate	moderate, modest, some, not unusually strong, sufficient, relatively strong
Strong	high, strong, pronounced, large, elevated, very high, great, dramatic, distinct, substantial, very strong, considerable, deeply divergent

Table 3.2. Mean F_{ST} values for quantitative adjectives for genetic differentiation

	Quantitative adjectives for genetic differentiation	**Mean**	**Variance**	**95% Confidence Interval**
Allozymes	None	0.0063	< 0.0001	-0.0046-0.0172
(n = 28)	Weak	0.0240	< 0.0001	0.0062-0.0418
	Moderate	0.1123	0.0080	-0.1093-0.3340
	Strong	0.2967	0.0877	0.0690-0.5243
mtDNA	None	0.0048	0.0004	-0.0023-0.0119
(n = 134)	Weak	0.0243	0.0016	0.0134-0.0352
	Moderate	0.1383	0.0074	0.0721-0.2046
	Strong	0.4982	0.1012	0.4057-0.5908
nDNA	None	0.0092	< 0.0001	-0.0304-0.0488
(n = 9)	Weak	0.0310	0.0018	-0.3502-0.4122
	Moderate	0.0870	0.0027	-0.3831-0.5571
	Strong	0.2911	0.0116	-0.6758-1.2580
Microsatellites	None	0.0020	< 0.0001	0.0005-0.0035
(n = 154)	Weak	0.0229	0.0011	0.0155-0.0304
	Moderate	0.0436	0.0015	0.0200-0.0672
	Strong	0.1746	0.0322	0.1086-0.2404
SNPs	Weak	0.0450	0.0054	-0.1379-0.2279
(n = 4)	Strong	0.1370	------	------
Wright (1978)	Little	------	------	0.0000-0.0500
	Moderate	------	------	0.0500-0.1500
	Great	------	------	0.1500-0.2500
	Very Great	------	------	0.2500-1.0000

Table 3.3. Relationship between meta-analysis quantitative adjectives and those defined by Wright (1978)

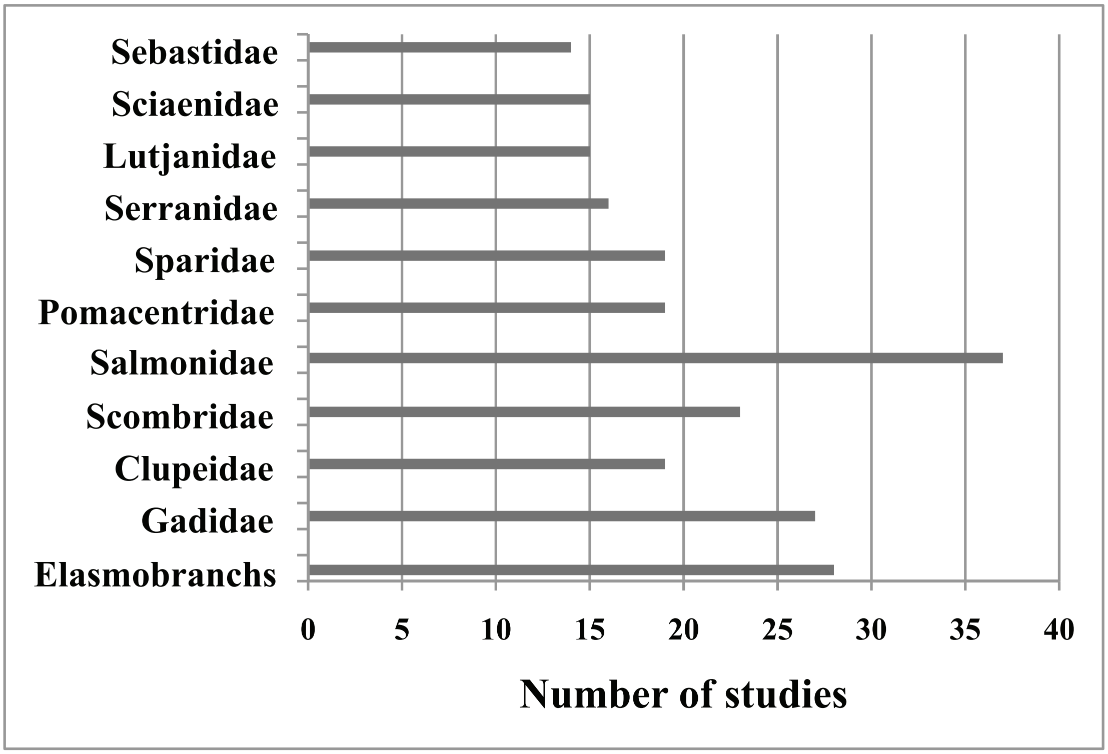
	Weak/*Little*	**Moderate/*Moderate***	**Strong/*Great or Very Great***
Wright (1978)	(0.00-0.05)	(0.05-0.15)	(0.15-0.25) (0.25 <)
mtDNA	0.02 (0.01-0.04)	0.14 (0.07-0.20)	0.50 (0.40-0.59)
microsatellites	0.02 (0.02-0.03)	0.05 (0.02-0.07)	0.17 (0.11-0.24)
allozymes	0.02 (0.01-0.04)	0.11 (-0.11-0.33)	0.30 (0.07-0.52)

Columns labeled with meta-analysis quantitative adjectives (normal font) and Wright's quantitative adjectives (in *italics*). Mean values of F_{ST} for each quantitative adjective, with associated ranges of F_{ST} provided in parentheses.

Table 3.4. Mean F_{ST} values for stock management approaches

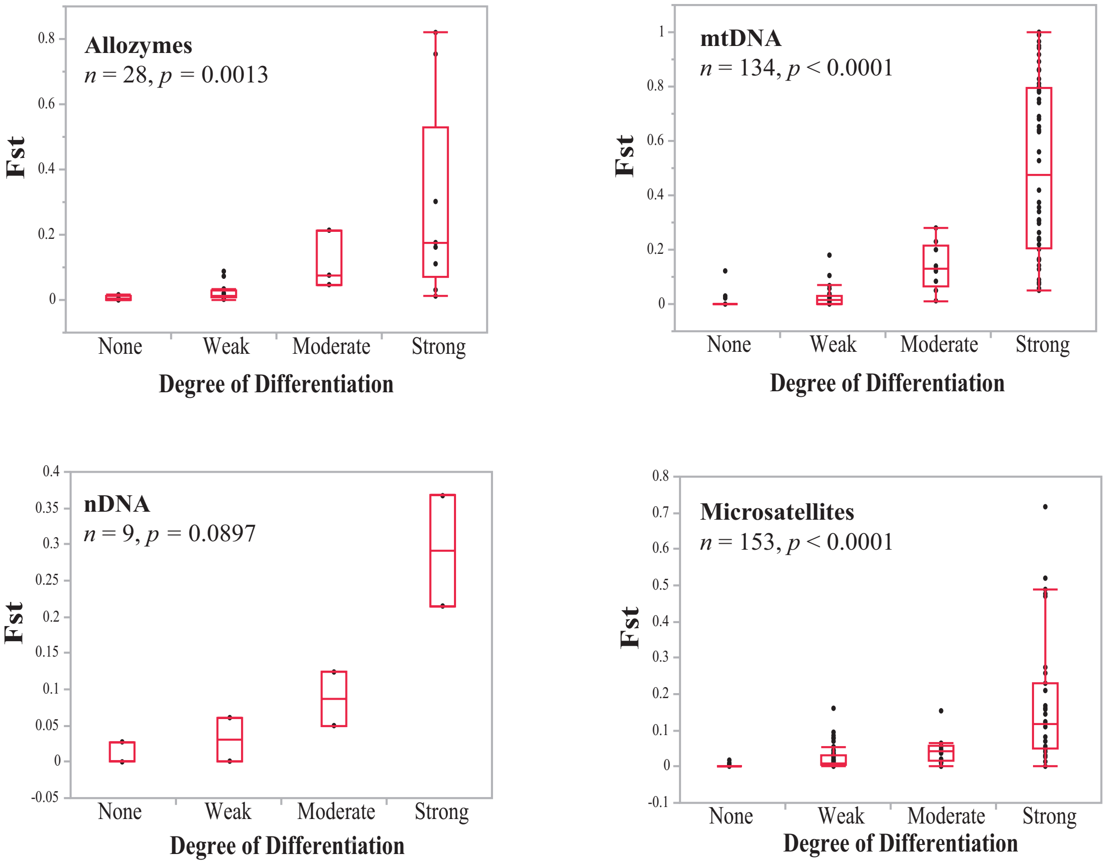
	Mean	**Variance**	**95% Confidence Interval**
Single stock	0.0122	< 0.0001	0.0057-0.0187
Multiple stocks	0.1572	0.0504	0.1253-0.1891
> 1 species	0.6673	0.0880	0.4192-0.9153

Figure 3.1. Taxonomic bias of studies



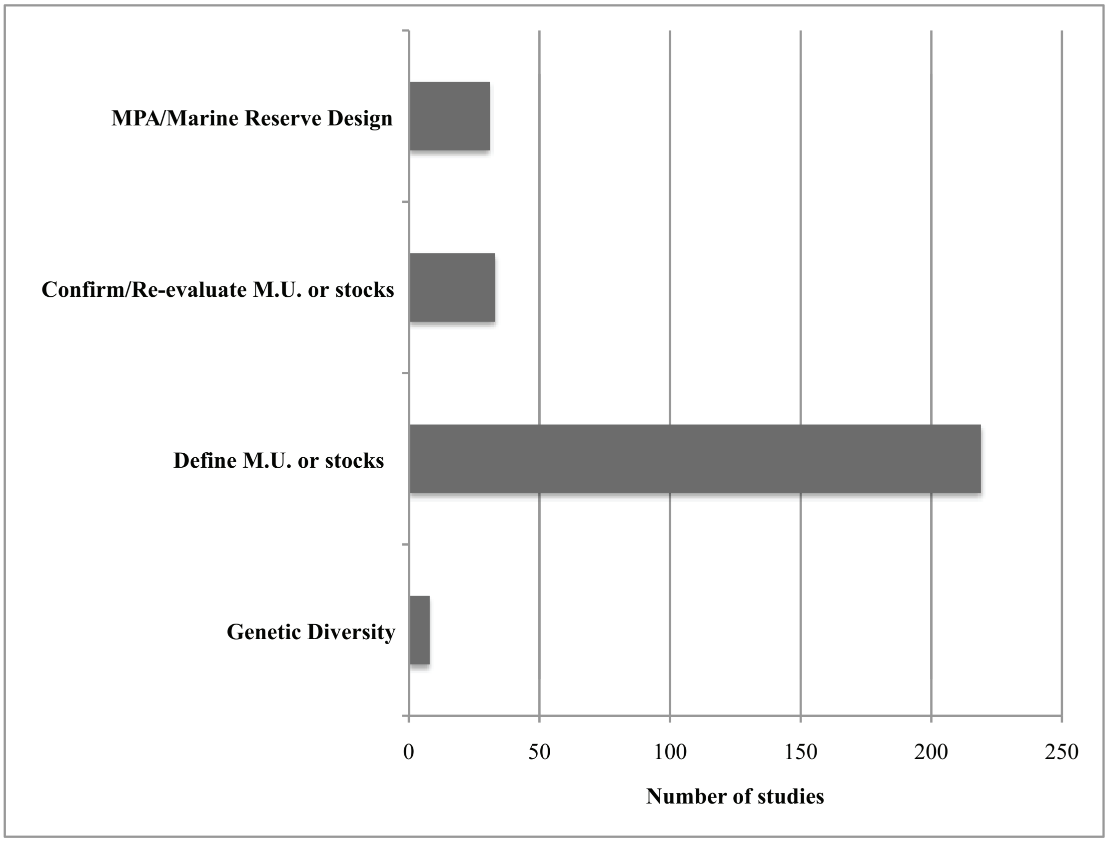
Taxonomic groups represented in more than 50% of studies in literature review. X-axis shows number of studies where focal species were from a given taxonomic group.

Figure 3.2. Relationship between F_{ST} and quantitative adjectives for genetic differentiation



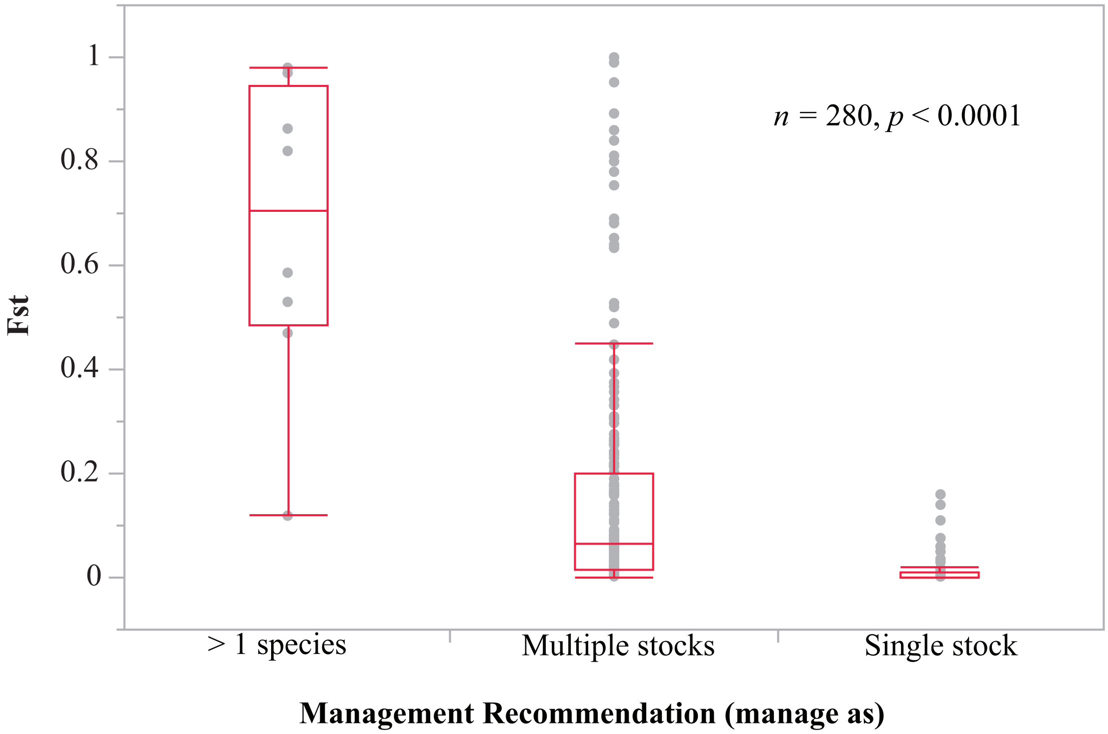
Results from Kruskal-Wallace one way ANOVAs to look at relationship between mean F_{ST} and quantitative adjectives of genetic differentiation. Results separated by major categories of molecular marker. F_{ST} represented on x-axis and quantitative adjectives for genetic differentiation along y-axis. Statistical significance of test determined by $p < 0.05$.

Figure 3.3. Recommended fisheries management strategies



Common fisheries management strategies suggested in literature. Suggested strategies were related to marine protected areas (MPA) or marine reserve design, defined management units (MUs) or stocks, confirmed or suggested re-evaluating existing MUs or stocks, or were related to monitoring genetic diversity levels. X-axis shows number of studies suggesting each approach.

Figure 3.4. Relationship between stock management approach and magnitudes of genetic differentiation



Results from Kruskal-Wallace one way ANOVAs to look at relationship between stock management approach and estimates of genetic differentiation (F_{ST}). Broad categories for management of stocks included managing as a single stock, managing as multiple stocks or managing as distinct species.

Appendix A. Supplementary Material for Chapter 1

Table A.1. Molecular diversity indices for Nassau grouper microsatellite data set

Sampling Sites		A113	D2	A6	A10	A108	A111	D8	A3	A117
1. Chinchorro Bank	nA	15	13	9	9	7	18	8	14	13
	H_o	**0.917**	0.833	0.792	0.875	0.750	0.958	0.625	0.750	0.875
	H_e	0.911	0.904	0.858	0.862	0.736	0.948	0.770	0.844	0.907
2. Glover's Reef	nA	20	17	10	10	7	27	8	20	16
	H_o	0.831	0.949	0.881	**0.814**	0.695	0.966	0.847	0.746	0.915
	H_e	0.908	0.889	0.849	0.868	0.663	0.947	0.802	0.772	0.921
3. Lighthouse Reef	nA	19	12	9	10	8	26	7	15	17
	H_o	0.938	1.000	0.938	0.781	0.719	1.000	0.906	0.781	0.969
	H_e	0.934	0.880	0.841	0.852	0.657	0.963	0.824	0.805	0.914
4. Turneffe Atoll	nA	17	17	8	7	7	20	10	16	16
	H_o	0.931	0.897	0.759	0.690	0.793	0.931	0.828	0.793	0.931
	H_e	0.930	0.901	0.844	0.852	0.740	0.953	0.818	0.852	0.913
5. Caye Glory	nA	18	17	14	13	11	22	7	17	16
	H_o	0.808	0.923	0.808	0.731	**0.731**	0.962	0.769	0.808	0.923
	H_e	0.922	0.931	0.899	0.884	0.742	0.959	0.844	0.904	0.911
6. Corona San Carlos	nA	15	14	7	9	6	21	8	11	12
	H_o	0.833	0.792	0.833	0.875	0.750	0.958	0.833	0.875	0.958
	H_e	0.897	0.891	0.783	0.836	0.647	0.957	0.810	0.866	0.899
7. Pardon del Medio	nA	18	19	10	9	7	29	9	17	17
	H_o	0.878	0.902	**0.707**	0.805	**0.610**	0.878	0.707	0.805	0.902
	H_e	0.924	0.908	0.843	0.842	0.683	0.957	0.774	0.843	0.901
8. Grand Cayman	nA	11	9	8	7	5	12	7	12	8
	H_o	1.000	0.889	0.778	0.667	**0.111**	0.889	0.778	1.000	0.556
	H_e	0.935	0.902	0.902	0.810	0.752	0.948	0.876	0.954	0.791
9. Little Cayman	nA	22	18	12	13	6	24	10	21	20
	H_o	0.869	0.951	0.820	0.836	0.607	0.967	0.770	0.803	0.852
	H_e	0.926	0.923	0.844	0.868	0.646	0.950	0.808	0.839	0.909
10. Cayman Brac	nA	16	15	10	11	7	22	10	11	15
	H_o	0.929	0.929	0.893	0.821	0.643	0.964	0.929	0.821	0.893

	H_e	0.932	0.919	0.836	0.851	0.641	0.959	0.846	0.849	0.881
11. Florida Keys	nA	21	17	10	12	6	24	9	16	17
	H_o	0.921	0.895	0.816	0.947	0.737	0.974	0.868	0.842	0.895
	H_e	0.934	0.907	0.817	0.869	0.653	0.956	0.809	0.850	0.891
12. Dog Rocks	nA	14	14	7	8	5	22	9	15	11
	H_o	**0.789**	**0.789**	1.000	0.842	**0.632**	**0.895**	0.947	0.944	0.833
	H_e	0.910	0.902	0.834	0.765	0.637	0.964	0.841	0.921	0.854
13. Lee Stocking	nA	14	14	8	10	5	22	7	14	15
	H_o	0.739	0.913	0.609	0.913	**0.565**	0.957	0.696	0.913	0.913
	H_e	0.858	0.906	0.790	0.877	0.675	0.966	0.789	0.875	0.889
14. Long Island	nA	16	14	10	9	7	22	7	18	17
	H_o	**0.811**	0.811	0.892	0.811	0.595	0.919	0.811	0.838	0.865
	H_e	0.890	0.877	0.834	0.854	0.651	0.955	0.782	0.867	0.913
15. South Caicos	nA	19	17	10	14	7	25	10	17	18
	H_o	0.820	0.880	0.900	0.900	0.640	0.960	0.740	0.800	0.940
	H_e	0.898	0.904	0.862	0.884	0.608	0.955	0.783	0.838	0.910
16. Bajo de Sico	nA	11	8	7	5	7	13	7	9	9
	H_o	0.900	1.000	1.000	1.000	0.800	1.000	0.900	**0.700**	1.000
	H_e	0.932	0.905	0.863	0.826	0.711	0.947	0.832	0.905	0.900
17. Grammanik Bank	nA	19	17	10	12	7	24	10	14	17
	H_o	0.897	0.897	0.845	0.810	0.759	**0.948**	0.759	0.862	0.931
	H_e	0.919	0.881	0.829	0.851	0.707	0.953	0.806	0.815	0.898
18. N. of St. Thomas	nA	8	9	7	8	4	11	8	8	8
	H_o	**0.500**	0.875	0.875	0.875	**0.250**	0.875	0.750	0.875	0.875
	H_e	0.883	0.933	0.867	0.850	0.692	0.950	0.758	0.875	0.875
19. Antigua	nA	20	19	10	12	7	24	9	16	17
	H_o	0.909	0.909	0.795	0.773	0.727	0.932	0.795	0.795	0.864
	H_e	0.919	0.913	0.857	0.859	0.659	0.950	0.775	0.835	0.905

Number of alleles (nA), observed heterozygosity (H_o) and expected heterozygosity (H_e) for 9 microsatellite loci. Bolded values violate Hardy-Weinberg equilibrium ($p < 0.05$).

Appendix B. Supplementary Material for Chapter 2

Table B.1. Molecular diversity indices for *M. rosacea* microsatellite data set

Sampling Sites		Mros02	Mros03	Mros04	Mros05	Mros07	Mros10	Mros11	Mros12
1. San Felipe	nA	14	16	16	13	12	16	11	12
	H_o	0.917	0.917	0.917	0.917	1.000	1.000	0.917	0.917
	H_e	0.942	0.964	0.946	0.942	0.909	0.957	0.888	0.902
2. Puertectitos	nA	10	11	12	10	13	12	10	11
	H_o	0.750	1.000	0.875	1.000	1.000	0.875	1.000	1.000
	H_e	0.925	0.925	0.967	0.933	0.967	0.950	0.942	0.950
3. San Luis Gonzaga	nA	18	19	16	16	14	20	11	13
	H_o	0.875	0.938	0.875	0.938	0.813	1.000	0.813	0.813
	H_e	0.944	0.950	0.956	0.931	0.925	0.958	0.891	0.921
4. Bahía de los Angeles	nA	37	26	25	31	25	34	16	19
	H_o	**0.854**	0.938	0.875	0.938	0.938	0.979	0.875	0.896
	H_e	0.966	0.958	0.947	0.954	0.954	0.961	0.918	0.936
5. Puerto Peñasco	nA	24	20	20	26	21	29	14	19
	H_o	0.957	0.957	0.957	0.913	0.957	0.957	0.870	0.826
	H_e	0.969	0.948	0.951	0.968	0.947	0.969	0.937	0.946
6. Puerto Lobos	nA	14	12	13	13	10	16	12	10
	H_o	**0.778**	1.000	0.889	1.000	1.000	1.000	0.667	1.000
	H_e	0.967	0.922	0.961	0.948	0.909	0.987	0.941	0.928
7. Puerto Libertad	nA	27	26	25	29	23	31	16	19
	H_o	**0.805**	1.000	0.927	0.927	0.829	0.976	0.854	0.854
	H_e	0.936	0.960	0.962	0.962	0.946	0.962	0.929	0.939
8. Isla Angel de la Guarda	nA	27	23	20	24	22	21	15	15
	H_o	0.875	0.958	1.000	1.000	1.000	0.875	0.958	0.917
	H_e	0.955	0.966	0.948	0.968	0.955	0.942	0.938	0.918
9. Isla San Lorenzo	nA	16	12	10	16	13	16	9	14
	H_o	0.818	0.909	0.909	0.909	1.000	0.818	0.818	1.000
	H_e	0.965	0.952	0.918	0.965	0.948	0.961	0.896	0.952
10. Isla San Esteban	nA	7	7	6	7	7	7	6	6
	Ho	1.000	1.000	0.750	1.000	1.000	1.000	0.750	1.000
	He	0.964	0.964	0.929	0.964	0.964	0.964	0.893	0.929
11. Isla Tiburón (North)	nA	17	15	17	20	23	21	12	14
	H_o	0.813	1.000	0.938	1.000	1.000	0.938	1.000	0.875
	H_e	0.921	0.944	0.944	0.962	0.978	0.970	0.917	0.919
12. Isla Tiburón (South)	nA	14	16	13	13	12	15	11	13
	H_o	0.727	1.000	0.818	1.000	0.818	0.909	0.818	0.818
	H_e	0.948	0.970	0.948	0.947	0.939	0.965	0.887	0.952

13. Isla Datil	nA	13	11	11	10	11	7	9	10
	H_o	1.000	1.000	1.000	1.000	1.000	0.714	1.000	0.852
	H_e	0.989	0.967	0.967	0.945	0.967	0.824	0.934	0.945
14. Isla Patos	nA	15	12	12	13	13	12	10	12
	H_o	**0.900**	1.000	1.000	**0.900**	1.000	**0.700**	0.900	1.000
	H_e	0.968	0.932	0.953	0.963	0.953	0.905	0.911	0.947
15. Isla San Pedro Mártir	nA	17	16	19	17	16	17	12	14
	H_o	0.867	0.933	0.933	1.000	0.933	0.933	0.933	1.000
	H_e	0.917	0.945	0.968	0.959	0.947	0.952	0.926	0.931
16. La Jerga	nA	24	22	22	22	22	24	18	18
	H_o	0.929	1.000	0.964	1.000	0.893	0.857	0.821	0.857
	H_e	0.955	0.951	0.953	0.948	0.964	0.949	0.921	0.935
17. Isla San Marcos	nA	37	28	25	30	28	35	18	20
	H_o	0.877	0.938	0.969	0.954	0.923	0.923	0.923	0.969
	H_e	0.955	0.957	0.951	0.956	0.955	0.957	0.921	0.933
18. Isla Carmen	nA	40	28	26	32	24	31	19	22
	H_o	0.845	0.983	0.948	0.966	0.931	0.931	0.862	0.966
	H_e	0.966	0.961	0.947	0.956	0.941	0.960	0.925	0.925
19. Isla Cerralvo	nA	35	24	24	30	22	31	20	18
	H_o	0.860	0.930	0.930	0.953	0.907	0.930	0.953	0.930
	H_e	0.958	0.940	0.945	0.964	0.946	0.960	0.928	0.932
20. Bahía Kino	nA	30	24	22	24	19	23	17	18
	H_o	0.929	0.929	0.929	0.096	0.857	0.929	0.929	0.964
	H_e	0.972	0.096	0.956	0.096	0.093	0.964	0.934	0.931
21. Isla San Pedro Nolasco	nA	26	28	26	26	26	33	16	20
	H_o	0.886	0.818	0.909	0.955	0.932	0.909	0.932	0.909
	H_e	0.942	0.960	0.956	0.949	0.958	0.969	0.923	0.934

Number of alleles (nA), observed heterozygosity (H_o) and expected heterozygosity (H_e) for 8 microsatellite loci. Bolded values violate Hardy-Weinberg equilibrium ($p < 0.05$).

Table B.2. Pairwise *F*-statistics for mitochondrial DNA for *M. rosacea*

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1. San Felipe	---	0.044	0.051	**0.095**	**0.126**	**0.071**	**0.093**	**0.110**	**0.185**	0.031	0.065	0.058	0.050	0.027	0.097	0.051	**0.146**	**0.077**	**0.077**	0.058	0.057
2. Puertecitos	-0.022	---	0.043	0.091	0.124	0.065	0.088	0.106	0.191	0.020	0.059	0.051	0.042	0.018	0.093	0.044	**0.145**	0.071	0.072	0.051	0.051
3. San Luis Gonzaga	-0.008	-0.030	---	**0.093**	**0.123**	**0.070**	**0.091**	**0.108**	**0.180**	0.030	**0.064**	**0.057**	0.049	0.027	**0.095**	**0.051**	**0.143**	**0.076**	**0.076**	**0.057**	**0.057**
4. Bahía de los Angeles	0.000	0.003	-0.012	---	**0.158**	**0.113**	**0.128**	**0.144**	**0.209**	0.084	**0.106**	**0.101**	0.096	0.075	**0.134**	**0.093**	**0.173**	**0.113**	**0.114**	**0.098**	**0.096**
5. Puerto Peñasco	-0.014	-0.017	0.025	0.038	---	**0.146**	**0.155**	**0.175**	**0.249**	0.122	**0.136**	**0.132**	0.131	0.108	**0.166**	**0.121**	**0.205**	**0.140**	**0.141**	**0.126**	**0.121**
6. Puerto Lobos	0.037	-0.016	0.055	0.057	0.026	---	**0.111**	**0.129**	**0.209**	0.054	0.084	**0.077**	0.071	0.047	**0.117**	0.070	**0.165**	**0.094**	**0.095**	**0.076**	**0.075**
7. Puerto Libertad	0.050	0.025	0.089	**0.091**	0.022	0.012	---	**0.142**	**0.206**	0.081	**0.104**	**0.099**	0.094	0.073	**0.132**	**0.091**	**0.171**	**0.112**	**0.112**	**0.096**	**0.094**
8. Isla Angel de la Guarda	0.028	-0.014	-0.031	0.012	0.046	0.054	0.091	---	**0.232**	0.102	**0.121**	**0.116**	0.113	0.090	**0.150**	**0.106**	**0.191**	**0.127**	**0.127**	**0.111**	**0.108**
9. Isla San Lorenzo	0.022	0.003	0.073	0.038	0.003	-0.035	-0.009	0.070	---	0.204	**0.193**	**0.192**	0.201	0.174	**0.226**	**0.175**	**0.260**	**0.191**	**0.191**	**0.178**	**0.170**
10. Isla San Esteban	-0.080	-0.072	-0.058	-0.042	-0.053	0.020	0.039	0.017	0.077	---	0.048	0.038	0.027	0.000	0.087	0.032	0.144	0.062	0.063	0.040	0.039
11. Isla Tiburón (North)	0.066	0.030	0.005	0.015	0.119	0.061	**0.144**	0.003	0.095	0.047	---	0.072	0.065	0.043	**0.109**	**0.065**	**0.155**	**0.089**	**0.089**	**0.071**	**0.070**
12. Isla Tiburón (South)	0.004	-0.025	-0.004	0.008	0.040	-0.011	0.055	0.004	-0.011	-0.019	-0.008	---	0.057	0.034	**0.103**	0.057	**0.152**	**0.082**	**0.083**	**0.064**	**0.063**
13. Isla Datil	-0.010	-0.014	0.018	0.043	0.007	0.063	0.066	0.080	0.049	-0.090	0.133	0.049	---	0.023	0.099	0.050	0.152	0.077	0.077	0.057	0.056
14. Isla Patos	0.012	-0.015	-0.001	-0.002	0.069	0.002	0.085	0.013	-0.030	-0.030	-0.023	-0.030	0.043	---	0.076	0.028	0.129	0.056	0.056	0.035	0.035
15. Isla San Pedro Mártir	0.006	0.007	-0.020	-0.012	0.066	0.056	0.119	0.015	0.009	-0.039	-0.006	0.009	0.049	-0.016	---	**0.094**	**0.183**	**0.116**	**0.117**	**0.100**	**0.097**
16. La Jerga	-0.017	-0.038	-0.018	-0.005	0.015	0.019	0.060	-0.002	-0.006	-0.046	0.022	-0.006	0.012	-0.032	-0.006	---	**0.141**	**0.076**	**0.076**	**0.058**	**0.057**
17. Isla San Marcos	0.014	0.012	0.066	0.062	-0.012	0.031	0.009	0.077	0.045	0.010	0.148	0.045	0.041	0.087	0.102	0.033	---	**0.157**	**0.158**	**0.145**	**0.139**
18. Isla Carmen	0.000	-0.014	0.027	0.036	-0.011	-0.002	0.017	0.033	0.014	-0.022	0.078	0.014	0.037	0.035	0.055	0.015	-0.002	---	**0.098**	**0.081**	**0.080**
19. Isla Cerralvo	0.029	0.001	0.061	0.067	0.003	-0.002	-0.005	0.059	0.028	0.019	0.113	0.028	0.049	0.064	0.092	0.036	-0.006	-0.001	---	**0.081**	**0.080**
20. Bahía Kino	-0.017	-0.025	-0.001	0.021	-0.016	0.029	0.025	0.014	0.019	-0.048	0.076	0.019	0.003	0.037	0.038	0.004	0.004	-0.007	0.007	---	**0.063**
21. Isla San Pedro Nolasco	0.037	0.039	0.088	**0.094**	0.024	0.063	0.006	**0.108**	0.079	-0.010	**0.161**	0.079	0.045	0.105	**0.114**	0.070	0.024	0.038	0.024	0.029	---

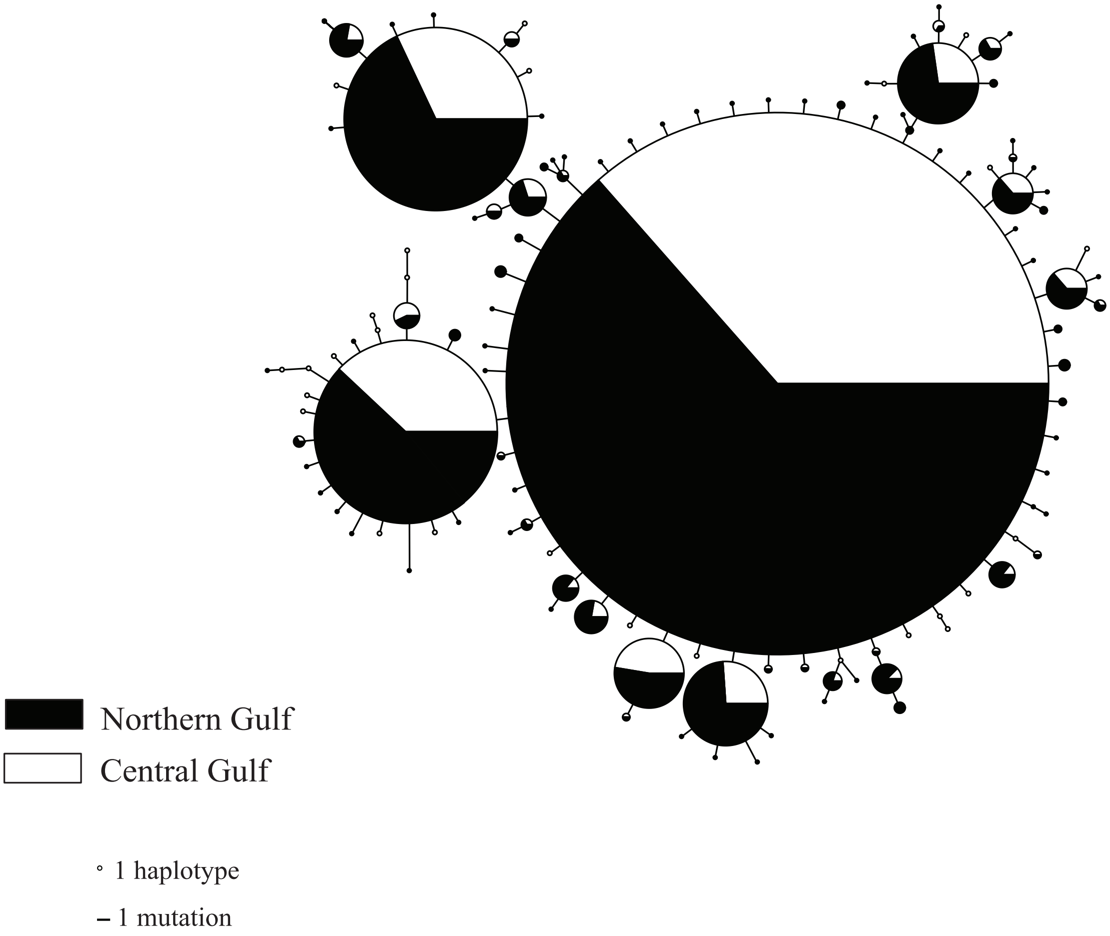
Pairwise Φ_{ST} values for mitochondrial markers are below diagonal and pairwise F_{ST} values are above diagonal. Grey shaded values denote statistical significance of $p < 0.05$. Bolded values denote statistical significance of $p < 0.002$, using Bonferroni correction for multiple tests.

Table B.3. Pairwse *F*-statistics for microsatellite loci for *M. rosacea*

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1. San Felipe	---	0.016	0.018	0.012	0.012	0.018	0.011	0.013	0.016	0.020	**0.024**	0.020	0.028	0.028	0.011	0.008	0.009	0.010	0.012	0.009	0.010
2. Puertecitos	0.165	---	0.018	0.010	0.011	0.022	0.007	0.011	0.013	0.011	0.020	0.009	0.011	0.029	0.001	0.009	0.013	0.009	0.004	0.005	0.007
3. San Luis Gonzaga	0.210	0.189	---	0.008	0.007	0.015	0.008	0.007	0.014	0.014	0.015	0.003	0.012	0.009	0.008	0.007	0.006	0.006	0.006	0.006	0.009
4. Bahía de los Angeles	0.153	0.104	0.094	---	0.000	0.006	0.000	0.002	0.009	0.006	**0.010**	0.006	0.003	0.011	0.003	0.001	0.002	0.001	0.001	0.001	0.002
5. Puerto Peñasco	0.158	0.112	0.080	-0.026	---	0.010	0.000	0.001	0.005	0.006	0.006	0.003	0.004	0.008	0.005	0.001	0.001	0.001	0.003	0.001	0.002
6. Puerto Lobos	0.202	0.233	0.157	0.050	0.107	---	0.004	0.008	0.016	0.023	0.013	0.003	0.020	0.014	0.015	0.003	0.008	0.009	0.010	0.007	0.008
7. Puerto Libertad	0.141	0.047	0.090	-0.019	-0.030	0.007	---	0.000	0.006	0.004	0.011	0.000	0.009	0.015	0.002	0.002	0.002	0.000	0.000	0.001	0.001
8. Isla Angel de la Guarda	0.176	0.123	0.068	0.007	-0.063	0.076	-0.022	---	0.004	0.010	0.009	0.001	0.012	0.011	0.002	0.001	0.002	0.001	0.000	0.001	0.002
9. Isla San Lorenzo	0.180	0.095	0.134	0.098	0.024	0.160	0.042	0.021	---	0.017	0.016	0.010	0.004	0.022	0.008	0.004	0.007	0.005	0.007	0.004	0.006
10. Isla San Esteban	0.211	-0.013	0.083	-0.019	-0.026	0.259	-0.076	0.096	0.142	---	0.013	0.013	0.024	0.017	0.017	0.012	0.008	0.005	0.000	0.013	0.008
11. Isla Tiburón (North)	0.323	0.236	0.173	0.136	0.059	0.132	0.157	0.129	0.185	0.100	---	0.012	0.021	0.015	**0.016**	0.008	**0.010**	**0.009**	0.010	0.008	**0.013**
12. Isla Tiburón (South)	0.234	0.016	-0.038	0.040	-0.026	-0.078	-0.069	-0.038	0.053	0.045	0.123	---	0.011	0.010	0.007	0.003	0.005	0.004	0.000	0.002	0.003
13. Isla Datil	0.352	0.045	0.097	-0.023	-0.001	0.212	0.074	0.131	-0.034	0.276	0.255	0.057	---	0.013	0.010	0.006	0.008	0.008	0.006	0.001	0.009
14. Isla Patos	0.354	0.358	0.054	0.127	0.079	0.125	0.200	0.155	0.261	0.127	0.173	0.056	0.105	---	0.016	0.013	0.011	0.010	0.008	0.002	0.012
15. Isla San Pedro Mártir	0.119	-0.083	0.069	0.005	0.049	0.156	-0.008	-0.007	0.057	0.161	0.201	0.036	0.079	0.180	---	0.004	0.003	0.002	0.004	0.006	0.002
16. La Jerga	0.080	0.069	0.070	-0.015	-0.020	-0.034	0.000	-0.046	0.006	0.085	0.089	-0.020	0.029	0.153	0.015	---	0.003	0.002	0.002	0.011	0.003
17. Isla San Marcos	0.107	0.159	0.069	0.022	-0.044	0.080	0.011	0.016	0.074	0.046	0.143	0.030	0.085	0.129	0.025	0.027	---	0.001	0.000	0.001	0.002
18. Isla Carmen	0.124	0.094	0.069	0.002	-0.039	0.096	-0.011	-0.004	0.039	-0.021	0.129	0.018	0.087	0.130	0.001	0.019	-0.029	---	0.001	0.000	0.001
19. Isla Cerralvo	0.154	-0.004	0.066	0.001	-0.096	0.118	-0.027	-0.033	0.063	-0.145	0.130	-0.069	0.040	0.070	0.022	-0.004	-0.016	-0.030	---	0.000	0.002
20. Bahía Kino	0.111	0.012	0.059	-0.015	-0.056	0.052	-0.018	-0.017	0.013	0.123	0.095	-0.034	0.036	0.132	-0.011	-0.013	-0.006	-0.029	-0.037	---	0.001
21. Isla San Pedro Nolasco	0.127	0.045	0.104	0.007	-0.003	0.076	-0.016	0.017	0.049	0.036	0.192	-0.014	0.083	0.154	-0.002	0.019	0.021	0.010	0.009	-0.012	---

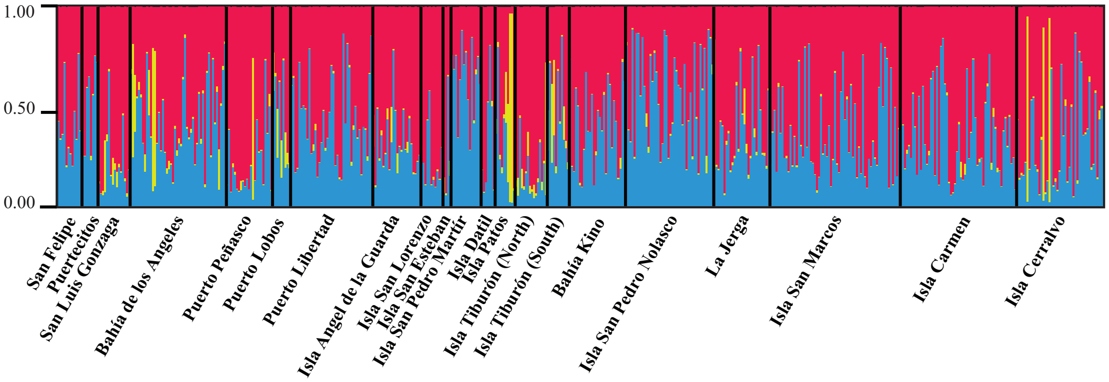
Pairwise G’’$_{ST}$ values for mitochondrial markers are below diagonal and pairwise F_{ST} values are above diagonal. Grey shaded values denote statistical significance of $p < 0.05$. Bolded values denote statistical significance of $p < 0.002$, using Bonferroni correction for multiple tests. *p*-values were not generated for G’’$_{ST}$.

Figure B.1. Haplotype network for *M. rosacea*



Circles are sized proportionally to the number of individuals that possess each haplotype. The pie chart within each haplotype represents the relative frequency of individuals from each color-coded region. Scaling is provided for the number of mutations between.

Figure B.2. Bayesian population assignment tests for *M. rosacea*



Bayesian population assignment tests based on 8 microsatellites as implemented in Structure. *k* clusters were chosen for each datasets using the Evanno method, which identified *k* = 3 (blue, red and yellow) clusters for the microsatellite dataset. The y-axis provides the assignment likelihood of each individual belonging to a given cluster.

Appendix C. Supplementary Material for Chapter 3

Table C.1. Empirical population genetics studies included in meta-analysis

Family	**Species**	**Citation**
Acanthuridae	*Acanthurus nigrofuscus*	(Eble et al. 2009; DiBattista et al. 2013)
Acanthuridae	*Ctenochaetus strigosus*	(Eble et al. 2009)
Acanthuridae	*Naso unicornis*	(Horne et al. 2013b)
Acanthuridae	*Zebrasoma flavescens*	(Eble et al. 2009; Christie et al. 2010b)
Acipenseridae	*Acipenser brevirostrum*	(Waldman et al. 2002)
Acipenseridae	*Acipenser oxyrinchus desotoi*	(Waldman et al. 2002)
Acipenseridae	*Acipenser oxyrinchus oxyrinchus*	(Waldman et al. 2002; Grunwald et al. 2008)
Acipenseridae	*Acipenser persicus*	(Ghasemi et al. 2011; Moghim et al. 2013)
Acipenseridae	*Acipenser stellatus*	(Norouzi et al. 2009)
Anarhichadidae	*Anarhichas denticulatus*	(McCusker and Bentzen 2011)
Anarhichadidae	*Anarhichas lupus*	(McCusker and Bentzen 2010; Pampoulie et al. 2012)
Anarhichadidae	*Anarhichas minor*	(McCusker and Bentzen 2011)
Anarhichadidae	*Anarhichas spp.*	(McCusker et al. 2008)
Anguillidae	*Anguilla anguilla*	(Dannewitz et al. 2005; Als et al. 2011)
Anguillidae	*Anguilla japonica*	(Tseng et al. 2006)
Anguillidae	*Anguilla rostrata*	(Cote et al. 2013)
Anguillidae	*Anguilla spp.*	(Maes et al. 2006)
Apogonidae	*Pterapogon kaudernii*	(Vagelli et al. 2008)
Atherinopsidae	*Atherinella brasiliensis*	(da Silva Cortinhas et al. 2010)
Atherinopsidae	*Leuresthes tenuis*	(Byrne et al. 2013)
Atherinopsidae	*Odontesthes argentinensis*	(Beheregaray and Levy 2000)
Berycidae	*Beryx splendens*	(Levy-Hartmann et al. 2011)
Blenniidae	*Lipophrys pholis*	(Francisco et al. 2011)
Caesionidae	*Caesio cuning*	(Ackiss et al. 2013)
Carangidae	*Caranx ignobilis*	(Santos et al. 2011)
Carangidae	*Lichia amia*	(Henriques et al. 2012)
Carangidae	*Seriola dumerili*	(Gold and Richardson 1998)
Carcharhinidae	*Carcharhinus brevipinna*	(Geraghty et al. 2013)
Carcharhinidae	*Carcharhinus falciformis*	(Galvan-Tirado et al. 2013)
Carcharhinidae	*Carcharhinus leucas*	(Karl et al. 2011)
Carcharhinidae	*Carcharhinus limbatus*	(Keeney et al. 2003)
Carcharhinidae	*Carcharhinus melanopterus*	(Mourier and Planes 2013; Vignaud et al. 2013)
Carcharhinidae	*Carcharhinus obscurus*	(Benavides et al. 2011)
Carcharhinidae	*Negaprion acutidens*	(Schultz et al. 2008)
Carcharhinidae	*Negaprion brevirostris*	(Schultz et al. 2008)
Carcharhinidae	*Rhizoprionodon acutus*	(Ovenden et al. 2011)
Carcharhinidae	*Rhizoprionodon lalandii*	(Mendonca et al. 2009)
Carcharhinidae	*Rhizoprionodon porosus*	(Mendonca et al. 2011a)

Carcharhinidae	*Rhizoprionodon spp.*	(Mendonca et al. 2011b)
Carcharhinidae	*Rhizoprionodon terraenovae*	(de Jesus Suarez-Moo et al. 2013)
Centrophoridae	*Centrophorus squamosus*	(Verissimo et al. 2012)
Centropomidae	*Centropomus undecimalis*	(Tringali and Bert 1996)
Chaetodontidae	*Chaetodon auriga*	(DiBattista et al. 2013)
Chaetodontidae	*Chaetodon lunulatus*	(Lawton et al. 2011)
Chaetodontidae	*Chaetodon tricinctus*	(van der Meer et al. 2013)
Chaetodontidae	*Chaetodon trifascialis*	(Lawton et al. 2011)
Chaetodontidae	*Chaetodon vagabundus*	(Berumen et al. 2012)
Channichthyidae	*Chaenocephalus aceratus*	(Papetti et al. 2009)
Channichthyidae	*Chionodraco spp.*	(Patarnello et al. 2003)
Channidae	*Chanos chanos*	(Ravago-Gotanco and Juinio-Menez 2004)
Cheilodactylidae	*Nemadactylus macropterus*	(Burridge and Smolenski 2003)
Clinidae	*Clinus cottoides*	(von der Heyden et al. 2008)
Clupeidae	*Alosa alosa*	(Jolly et al. 2012)
Clupeidae	*Alosa fallax*	(Volk et al. 2007; Jolly et al. 2012)
Clupeidae	*Alosa sapidissima*	(Hasselman et al. 2010)
Clupeidae	*Arripis georgiana*	(Ayvazian et al. 2004)
Clupeidae	*Clupea harengus*	(King et al. 1987; Safford and Booke 1992; Shaw et al. 1999; McPherson et al. 2001; McPherson et al. 2004; Jorgensen et al. 2005a; Ruzzante et al. 2006; Larsson et al. 2010; Teacher et al. 2012; Teacher et al. 2013)
Clupeidae	*Clupea pallasi*	(Jorstad 2004)
Clupeidae	*Sardina pilchardus*	(Atarhouch et al. 2006)
Clupeidae	*Sardinella zunasi*	(Ying et al. 2011)
Clupeidae	*Sprattus sprattus*	(Glover et al. 2011)
Clupeidae	*Tenualosa ilisha*	(Salini et al. 2004; Mazumder and Alam 2009)
Congridae	*Conger myriaster*	(Kimura et al. 2004)
Coryphaenidae	*Coryphaena hippurus*	(Diaz-Jaimes et al. 2006; Diaz-Jaimes et al. 2010; Tripp-Valdez et al. 2010)
Cyprinodontidae	*Aphanius fasciatus*	(Maltagliati 1998a,b; Triantafyllidis et al. 2007)
Dasyatidae	*Neotrygon kuhlii*	(Borsa et al. 2012)
Emperors	*Lethrinus nebulosus*	(Berry et al. 2012a)
Engraulidae	*Coilia mystus*	(Chen and Cheng 2012)
Engraulidae	*Coilia nasus*	(Yang et al. 2011)
Engraulidae	*Engraulis albidus*	(Bouchenak-Khelladi et al. 2008)
Engraulidae	*Engraulis encrasicolus*	(Borsa et al. 2004; Sanz et al. 2008)
Engraulidae	*Engraulis japonicus*	(Yu et al. 2002; Chen et al. 2010)
Fundulidae	*Fundulus parvipinnis*	(Bernardi and Talley 2000)
Gadidae	*Gadus macrocephalus*	(Cunningham et al. 2009)
Gadidae	*Gadus morhua*	(Mork et al. 1985; Ruzzante et al. 1999; Arnason et al. 2000;

		Hutchinson et al. 2001; Lage et al. 2004; Dahle et al. 2006; Hardie et al. 2006; Pampoulie et al. 2006; O'Leary et al. 2007; Westgaard and Fevolden 2007; Oresland and Andre 2008; Pampoulie et al. 2008; Nielsen et al. 2009; Kovach et al. 2010; Rose et al. 2011; Bradbury et al. 2013; Therkildsen et al. 2013)
Gadidae	*Merlangius merlangus*	(Rico et al. 1997; Charrier et al. 2007)
Gadidae	*Micromesistius poutassou*	(Ryan et al. 2005)
Gadidae	*Pollachius pollachius*	(Charrier et al. 2006a)
Gadidae	*Theragra chalcogramma*	(Olsen et al. 2002; Brykov et al. 2004; Shubina et al. 2004)
Glaucosomatidae	*Glaucosoma hebraicum*	(Berry et al. 2012b)
Gobiidae	*Bathygobius soporator*	(Lima et al. 2005)
Gobiidae	*Elacatinus lori*	(D'Aloia et al. 2013)
Gobiidae	*Eucyclogobius newberryi*	(Earl et al. 2010)
Gobiidae	*Pomatoschistus minutus*	(Stefanni and Thorley 2003)
Gobiidae	*Sicyopterus lagocephalus*	(Hoareau et al. 2007)
Haemulidae	*Haemulon flavolineatum*	(Purcell et al. 2006)
Hexagrammidae	*Hexagrammos otakii*	(Habib et al. 2011; Ren et al. 2013)
Hexagrammidae	*Ophiodon elongatus*	(Marko et al. 2007)
Hexagrammidae	*Pleurogrammus monopterygius*	(Lowe et al. 1998)
Holocentridae	*Myripristis berndti*	(Craig et al. 2007)
Holocentridae	*Neoniphon sammara*	(DiBattista et al. 2013)
Kuhliidae	*Kuhlia rupestris*	(Feutry et al. 2013)
Kyphosidae	*Girella nigricans*	(Terry et al. 2000)
Labridae	*Halichoeres hortulanus*	(Drew and Barber 2012; DiBattista et al. 2013)
Labridae	*Labrus bergylta*	(D'Arcy et al. 2013)
Labridae	*Larabicus quadrilineatus*	(Froukh and Kochzius 2007)
Labridae	*Thalassoma bifasciatum*	(Purcell et al. 2006)
Labridae	*Thallasoma hardwicki*	(Chen et al. 2004)
Lamnidae	*Carcharodon carcharias*	(Jorgensen et al. 2010; Blower et al. 2012)
Lateolabracidae	*Lateolabrax japonicus*	(Liu et al. 2006)
Lateolabracidae	*Lateolabrax maculatus*	(Liu et al. 2006)
Latidae	*Lates calcarifer*	(Zhu et al. 2006; Norfatimah et al. 2009; Yue et al. 2009)
Latridae	*Latris lineata*	(Tracey et al. 2007)
Lethrinidae	*Lethrinus miniatus*	(Van Herwerden et al. 2003)
Lophiidae	*Lophius budegassa*	(Charrier et al. 2006b)
Lophiidae	*Lophius piscatorius*	(Blanco et al. 2008)
Lutjanidae	*Lutjanus analis*	(Shulzitski et al. 2009)
Lutjanidae	*Lutjanus campechanus*	(Gold and Richardson 1998; Saillant et al. 2010)
Lutjanidae	*Lutjanus carponotatus*	(Evans et al. 2010; Veilleux et al.

		2011; Harrison et al. 2012)
Lutjanidae	*Lutjanus erythropterus*	(Zhang et al. 2006)
Lutjanidae	*Lutjanus kasmira*	(Planes and Lecaillon 1998; DiBattista et al. 2013)
Lutjanidae	*Lutjanus malabaricus*	(Sulaiman et al. 2008)
Lutjanidae	*Lutjanus peru*	(Rocha-Olivares and Sandoval-Castillo 2003)
Lutjanidae	*Lutjanus synagris*	(Gold et al. 2011)
Lutjanidae	*Pristipomoides filamentosus*	(Shaklee and Samollow 1984; Gaither et al. 2011)
Lutjanidae	*Pristipomoides multidens*	(Ovenden et al. 2002)
Macrouridae	*Coryphaenoides brevibarbis*	(White et al. 2011a)
Megalopidae	*Megalops atlanticus*	(Blandon et al. 2002)
Merlucciidae	*Antimora rostrata*	(White et al. 2011b)
Merlucciidae	*Macruronus magellanicus*	(Machado-Schiaffino and Garcia-Vazquez 2011)
Merlucciidae	*Merluccius bilinearis*	(Machado-Schiaffino et al. 2011)
Merlucciidae	*Merluccius capensis*	(von der Heyden et al. 2007)
Merlucciida	*Merluccius merluccius*	(Lundy et al. 1999; Lundy et al. 2000; Castillo et al. 2005; Pita et al. 2011)
Merlucciidae	*Merluccius paradoxus*	(von der Heyden et al. 2007)
Monocanthidae	*Stephanolepis cirrhifer*	(An et al. 2011a; Yoon et al. 2012; An et al. 2013)
Moronidae	*Dicentrarchus labrax*	(Garcia De Leon et al. 1997; Fritsch et al. 2007; Coscia and Mariani 2011)
Mugilidae	*Mugil cephalus*	(Rocha-Olivares et al. 2000; Liu et al. 2009a; Liu et al. 2009b; Livi et al. 2011)
Mullidae	*Mullus barbatus*	(Mamuris et al. 1998; Galarza et al. 2009)
Mullidae	*Mullus surmuletus*	(Galarza et al. 2009)
Myctophidae	*Electrona antarctica*	(Van de Putte et al. 2012a)
Myliobatidae	*Manta alfredi*	(Kashiwagi et al. 2012)
Myliobatidae	*Manta birostris*	(Kashiwagi et al. 2012)
Nototheniidae	*Dissostichus mawsoni*	(Parker et al. 2002)
Nototheniidae	*Trematomus bernacchii*	(Van de Putte et al. 2012b)
Nototheniidae	*Trematomus hansoni*	(Van de Putte et al. 2012b)
Nototheniidae	*Trematomus newnesi*	(Van de Putte et al. 2012b)
Odontaspididae	*Carcharias taurus*	(Ahonen et al. 2009)
Ophidiidae	*Genypterus blacodes*	(Canales-Aguirre et al. 2010)
Oreosomatidae	*Allocytus niger*	(Ward et al. 1998; Smith et al. 2002)
Oreosomatidae	*Allocytus verrucosus*	(Ward et al. 1998)
Oreosomatidae	*Pseudocyttus maculatus*	(Ward et al. 1998; Smith et al. 2002)
Osmeridae	*Osmerus mordax*	(Coulson et al. 2006; Kovach et al. 2013)

Osmeridae	*Thaleichthys pacificus*	(McLean et al. 1999; Beacham et al. 2005; Flannery et al. 2013)
Paralichthyidae	*Paralichthys lethostigma*	(Blandon et al. 2001; Anderson and Karel 2012; Anderson et al. 2012)
Paralichthyidae	*Paralichthys olivaceus*	(Xu et al. 2012a)
Pleuronectidae	*Platichthys flesus*	(Calves et al. 2013)
Pleuronectidae	*Verasper variegatus*	(Sekino et al. 2011)
Polynemidae	*Eleutheronema tetradactylum*	(Horne et al. 2012; Horne et al. 2013a)
Pomacanthidae	*Pygoplites diacanthus*	(DiBattista et al. 2013)
Pomacentridae	*Amblyglyphidodon orbicularis*	(Drew and Barber 2012)
Pomacentridae	*Amphiprion barberi*	(Drew and Barber 2012)
Pomacentridae	*Amphiprion mccullochi*	(van der Meer et al. 2012)
Pomacentridae	*Amphiprion ocellaris*	(Timm et al. 2012)
Pomacentridae	*Amphiprion percula*	(Planes et al. 2009; Berumen et al. 2012; Buston et al. 2012)
Pomacentridae	*Amphiprion polymnus*	(Jones et al. 2005; Saenz-Agudelo et al. 2009; Saenz-Agudelo et al. 2011,2012)
Pomacentridae	*Chromis limbata*	(Domingues et al. 2006)
Pomacentridae	*Chrysiptera talboti*	(Drew and Barber 2012)
Pomacentridae	*Pomacentrus amboinensis*	(Jones et al. 2010)
Pomacentridae	*Pomacentrus coelestis*	(Liu et al. 2010; Liu et al. 2012)
Pomacentridae	*Pomacentrus maafu*	(Drew and Barber 2012)
Pomacentridae	*Stegastes partitus*	(Ospina-Guerrero et al. 2008; Hepburn et al. 2009; Purcell et al. 2009; Christie et al. 2010a; Hogan et al. 2010; Villegas-Sanchez et al. 2010; Hogan et al. 2012)
Pristidae	*Pristis clavata*	(Phillips et al. 2011)
Pristidae	*Pristis microdon*	(Phillips et al. 2011)
Pristidae	*Pristis zijsron*	(Phillips et al. 2011)
Rachycentridae	*Rachycentron canadum*	(Phinchongsakuldit et al. 2013)
Rajidae	*Dipturus oxyrinchus*	(Griffiths et al. 2011)
Rajidae	*Raja clavata*	(Chevolot et al. 2006)
Rhincodontidae	*Rhincodon typus*	(Castro et al. 2007; Schmidt et al. 2009)
Rhinobatidae	*Rhinobatos productus*	(Sandoval-Castillo et al. 2004)
Salmonidae	*Coregonus lavaretus lavaretus*	(McCairns et al. 2012)
Salmonidae	*Coregonus maraena*	(Olsson et al. 2012)
Salmonidae	*Oncorhynchus clarki clarki*	(Wofford et al. 2005)
Salmonidae	*Oncorhynchus gorbuscha*	(Noll et al. 2001)
Salmonidae	*Oncorhynchus keta*	(Scribner et al. 1998; Beacham et al. 2008a; Afanas'ev et al. 2011)
Salmonidae	*Oncorhynchus kisutch*	(Small et al. 1998)
Salmonidae	*Oncorhynchus masou masou*	(Jia et al. 2012)
Salmonidae	*Oncorhynchus mykiss*	(Beacham et al. 1999,2000; Hendry et al. 2002; Winans et al. 2004; Pearse et al. 2011; Beacham et al.

		2012)
Salmonidae	*Oncorhynchus nerka*	(Beacham et al. 2004; Creelman et al. 2011; Russello et al. 2012)
Salmonidae	*Oncorhynchus tshawytscha*	(Gall et al. 1992; Heath et al. 1995; Beacham et al. 2008b)
Salmonidae	*Salmo salar*	(Verspoor et al. 1991; Jordan et al. 1992; O'Connell et al. 1995; King et al. 2001a; Wennevik et al. 2004; Skaala et al. 2005; Vasemagi et al. 2005; Palstra et al. 2007; Tonteri et al. 2009; Palstra and Ruzzante 2010; Ellis et al. 2011; Freamo et al. 2011; Verspoor et al. 2012)
Salmonidae	*Salmo trutta*	(Laikre et al. 2002; Hansen et al. 2007)
Salmonidae	*Salvelinus alpinus*	(Moore et al. 2013)
Salmonidae	*Salvelinus leucomaenis*	(Yamaguchi et al. 2010)
Scaridae	*Chlorurus sordidus*	(Dudgeon et al. 2000)
Scaridae	*Scarus frenatus*	(Dudgeon et al. 2000)
Scaridae	*Scarus ghobban*	(Visram et al. 2010)
Sciaenidae	*Argyrosomus regius*	(Haffray et al. 2012)
Sciaenidae	*Cynoscion nebulosus*	(King and Pate 1992; Gold and Richardson 1998)
Sciaenidae	*Larimichthys polyactis*	(Xiao et al. 2009; Li et al. 2013)
Sciaenidae	*Micropogonias furnieri*	(Levy et al. 1998; Pereira et al. 2009)
Sciaenidae	*Micropogonias undulatus*	(Lankford et al. 1999)
Sciaenidae	*Miichthys miiuy*	(Cheng et al. 2011)
Sciaenidae	*Nibea albiflora*	(Xu et al. 2012b)
Sciaenidae	*Pogonias cromis*	(Gold and Richardson 1998)
Sciaenidae	*Sciaenops ocellatus*	(Gold and Richardson 1991,1998; Gold et al. 1999; Seyoum et al. 2000; Gold et al. 2001)
Scomberesocidae	*Cololabis saira*	(Chow et al. 2009)
Scombridae	*Acanthocybium solandri*	(Garber et al. 2005)
Scombridae	*Euthynnus affinis*	(Kumar et al. 2012)
Scombridae	*Katsuwonus pelamis*	(Dammannagoda et al. 2011)
Scombridae	*Scomber australasicus*	(Tzeng et al. 2009)
Scombridae	*Scomber japonicus*	(Zeng et al. 2012)
Scombridae	*Scomber scombrus*	(Papetti et al. 2013)
Scombridae	*Scomberomorus cavalla*	(Gold and Richardson 1998; Gold et al. 2002)
Scombridae	*Scomberomorus commerson*	(Hoolihan et al. 2006)
Scombridae	*Scomberomorus semifasciatus*	(Broderick et al. 2011)
Scombridae	*Scomberomorus sierra*	(Dominguez Lopez et al. 2010)
Scombridae	*Thunnus alalunga*	(Takagi et al. 2001; Nakadate et al. 2005; Montes et al. 2012)
Scombridae	*Thunnus albacares*	(Wu et al. 2010)
Scombridae	*Thunnus obesus*	(Martinez et al. 2006; Chiang et al. 2008)

Scombridae	*Thunnus orientalis*	(Bremer et al. 2005)
Scombridae	*Thunnus thynnus*	(Riccioni et al. 2010)
Scombridae	*Trachurus trachurus*	(Abaunza et al. 2008; Cimmaruta et al. 2008; Comesana et al. 2008; Kasapidis and Magoulas 2008)
Scophthalmidae	*Lepidorhombus boscii*	(Danancher and Garcia-Vazquez 2009)
Scophthalmidae	*Lepidorhombus whiffiagonis*	(Danancher and Garcia-Vazquez 2009)
Scorpaenidae	*Pterois miles*	(Kochzius and Blohm 2005)
Sebastidae	*Sebastes alutus*	(Withler et al. 2001; Palof et al. 2011)
Sebastidae	*Sebastes atrovirens*	(Gilbert-Horvath et al. 2006)
Sebastidae	*Sebastes auriculatus*	(Buonaccorsi et al. 2005)
Sebastidae	*Sebastes caurinus*	(Johansson et al. 2008)
Sebastidae	*Sebastes inermis*	(An et al. 2011b)
Sebastidae	*Sebastes mentella*	(Roques et al. 2002)
Sebastidae	*Sebastes miniatus*	(Hyde and Vetter 2009)
Sebastidae	*Sebastes paucispinis*	(Matala et al. 2004)
Sebastidae	*Sebastes polyspinis*	(Gharrett et al. 2012)
Sebastidae	*Sebastes rastrelliger*	(Buonaccorsi et al. 2004)
Sebastidae	*Sebastes ruberrimus*	(Siegle et al. 2013)
Sebastidae	*Sebastes schlegeli*	(An et al. 2012)
Sebastidae	*Sebastes spp.*	(Pampoulie and Danielsdottir 2008)
Serranidae	*Centropristis striata*	(McCartney et al. 2013)
Serranidae	*Cephalopholis argus*	(Planes and Lecaillon 1998; DiBattista et al. 2013)
Serranidae	*Epinephelus coiodes*	(Sulaiman et al. 2008)
Serranidae	*Epinephelus itajara*	(Craig et al. 2009)
Serranidae	*Epinephelus labriformis*	(Craig et al. 2006)
Serranidae	*Epinephelus marginatus*	(De Innocentiis et al. 2001; Maggio et al. 2006; Schunter et al. 2011)
Serranidae	*Epinephelus morio*	(Gold and Richardson 1998)
Serranidae	*Hypoplectrus puella*	(Puebla et al. 2009)
Serranidae	*Mycteroperca microlepis*	(Cushman et al. 2009)
Serranidae	*Paralabrax clathratus*	(Selkoe et al. 2007)
Serranidae	*Plectropomus areolatus*	(Almany et al. 2013)
Serranidae	*Plectropomus leopardus*	(Van Herwerden et al. 2009)
Serranidae	*Plectropomus maculatus*	(Evans et al. 2010; Harrison et al. 2012)
Soleidae	*Solea lascaris*	(Pinheiro et al. 2005)
Soleidae	*Solea senegalensis*	(Diaz-Ferguson et al. 2012b)
Soleidae	*Solea solea*	(Guarniero et al. 2002; Cuveliers et al. 2012)
Soleidae	*Solea vulgaris*	(Guinand et al. 2013)
Sparidae	*Acanthopagrus butcheri*	(Farrington et al. 2000; Burridge et al. 2004)
Sparidae	*Acanthopagrus latus*	(Xia et al. 2008)
Sparidae	*Archosargus probatocephalus*	(Anderson et al. 2008)

	oviceps	
Sparidae	*Archosargus probatocephalus probatocephalus*	(Anderson et al. 2008)
Sparidae	*Chrysoblephus laticeps*	(Teske et al. 2010)
Sparidae	*Dentex dentex*	(Bargelloni et al. 2003)
Sparidae	*Dentex tumifrons*	(Xia and Jiang 2006)
Sparidae	*Diplodus puntazzo*	(Bargelloni et al. 2005)
Sparidae	*Diplodus sargus*	(Bargelloni et al. 2003; Lenfant 2003; Domingues et al. 2007; Gonzalez-Wangueemert et al. 2010; Pereira et al. 2010; Di Franco et al. 2012; Gonzalez-Wangueemert et al. 2012)
Sparidae	*Diplodus vulgaris*	(Pereira et al. 2010)
Sparidae	*Lithognathus mormyrus*	(Bargelloni et al. 2003; Sala-Bozano et al. 2009)
Sparidae	*Pagellus bogaraveo*	(Bargelloni et al. 2003; Stockley et al. 2005)
Sparidae	*Pagrus pagrus*	(Bargelloni et al. 2003)
Sparidae	*Sparus aurata*	(Rossi et al. 2006; Chaoui et al. 2009; Rossi et al. 2009)
Sparidae	*Spondyliosoma cantharus*	(Bargelloni et al. 2003)
Sphyrnidae	*Sphyrna lewini*	(Ovenden et al. 2011; Castillo-Olguin et al. 2012)
Stegostomatidae	*Stegostoma fasciatum*	(Dudgeon et al. 2009)
Stromateidae	*Pampus argenteus*	(Peng et al. 2009; Zhao et al. 2011)
Sygnathidae	*Hippocampus capensis*	(Teske et al. 2003)
Sygnathidae	*Hippocampus hippocampus*	(Woodall et al. 2011)
Sygnathidae	*Hippocampus kuda*	(Goswami et al. 2009)
Sygnathidae	*Hippocampus trimaculatus*	(Goswami et al. 2009)
Sygnathidae	*Syngnathus leptorhynchus*	(Wilson 2006)
Trachichthyidae	*Hoplostethus atlanticus*	(Varela et al. 2013)
Triakidae	*Mustelus antarcticus*	(Gardner and Ward 1998)
Triakidae	*Mustelus schmitti*	(Pereyra et al. 2010)
Trichiuridae	*Aphanopus carbo*	(Stefanni and Knutsen 2007)
Tripterygiidae	*Tripterygion delaisi*	(Carreras-Carbonell et al. 2007)
Xiphiidae	*Xiphias gladius*	(Grijalva-Chon et al. 1994; Bremer et al. 1995; Pujolar et al. 2002; Bremer et al. 2005; Bremer et al. 2006; Muths et al. 2009; Bradman et al. 2011; Garcia et al. 2011; Muths et al. 2013)
Zoarcidae	*Zoarces viviparus*	(Kinitz et al. 2013)

Table C.2. Complete list of fish species represented in meta-analysis

Family	Species
Acanthuridae	*Acanthurus nigrofuscus*
	Ctenochaetus strigosus
	Naso unicornis
	Zebrasoma flavescens
Acipenseridae	*Acipenser brevirostrum*
	Acipenser oxyrinchus desotoi
	Acipenser persicus
	Acipenser stellatus
Anarhichadidae	*Anarhichas denticulatus*
	Anarhichas lupus
	Anarhichas minor
	Anarhichas spp.
Anguillidae	*Anguilla anguilla*
	Anguilla japonica
	Anguilla rostrata
	Anguilla spp.
Apogonidae	*Pterapogon kaudernii*
Atherinopsidae	*Atherinella brasiliensis*
	Leuresthes tenuis
	Odontesthes argentinensis
Berycidae	*Beryx splendens*
Blenniidae	*Lipophrys pholis*
Caesionidae	*Caesio cuning*
Carangidae	*Caranx ignobilis*
	Lichia amia
	Seriola dumerili
Carcharhinidae	*Carcharhinus brevipinna*
	Carcharhinus falciformis
	Carcharhinus leucas
	Carcharhinus limbatus
	Carcharhinus melanopterus
	Carcharhinus obscurus
	Negaprion acutidens
	Negaprion brevirostris
	Rhizoprionodon acutus
	Rhizoprionodon lalandii
	Rhizoprionodon porosus
	Rhizoprionodon spp.
	Rhizoprionodon terraenovae
Centrophoridae	*Centrophorus squamosus*
	Centropomus undecimalis
Chaetodontidae	*Chaetodon auriga*
	Chaetodon lunulatus
	Chaetodon tricinctus
	Chaetodon trifascialis
	Chaetodon vagabundus
Channichthyidae	*Chaenocephalus aceratus*
	Chionodraco spp.
Labridae	*Thallasoma hardwicki*
Lamnidae	*Carcharodon carcharias*
Lateolabracidae	*Lateolabrax japonicus*
Channidae	*Chanos chanos*
Cheilodactylidae	*Nemadactylus macropterus*
Clinidae	*Clinus cottoides*
Clupeidae	*Alosa alosa*
	Alosa fallax
	Alosa sapidissima
	Arripis georgiana
	Clupea harengus
	Clupea pallasi
	Sardina pilchardus
	Sardinella zunasi
	Sprattus sprattus
	Tenualosa ilisha
	Conger myriaster
Coryphaenidae	*Coryphaena hippurus*
Cyprinodontidae	*Aphanius fasciatus*
Dasyatidae	*Neotrygon kuhlii*
Emperors	*Lethrinus nebulosus*
Engraulidae	*Coilia mystus*
	Coilia nasus
	Engraulis albidus
	Engraulis encrasicolus
	Engraulis japonicus
Fundulidae	*Fundulus parvipinnis*
Gadidae	*Gadus macrocephalus*
	Gadus morhua
	Merlangius merlangus
	Micromesistius poutassou
	Pollachius pollachius
	Theragra chalcogramma
Glaucosomatidae	*Glaucosoma hebraicum*
Gobiidae	*Bathygobius soporator*
	Elacatinus lori
	Eucyclogobius newberryi
	Pomatoschistus minutus
	Sicyopterus lagocephalus
Haemulidae	*Haemulon flavolineatum*
Hexagrammidae	*Hexagrammos otakii*
	Ophiodon elongatus
	Pleurogrammus monopterygius
Holocentridae	*Myripristis berndti*

Family	**Species**
Holocentridae	*Neoniphon sammara*
Kuhliidae	*Kuhlia rupestris*
Kyphosidae	*Girella nigricans*
Labridae	*Halichoeres hortulanus*
	Labrus bergylta
	Larabicus quadrilineatus
	Thalassoma bifasciatum
	Lateolabrax maculatus
Latidae	*Lates calcarifer*
Latridae	*Latris lineata*
Lethrinidae	*Lethrinus miniatus*
Lophiidae	*Lophius budegassa*
	Lophius piscatorius
Lutjanidae	*Lutjanus analis*
	Lutjanus campechanus
	Lutjanus carponotatus
	Lutjanus erythropterus
	Lutjanus kasmira
	Lutjanus malabaricus
	Lutjanus peru
	Lutjanus synagris
	Pristipomoides filamentosus
	Pristipomoides multidens
Macrouridae	*Coryphaenoides brevibarbis*
Megalopidae	*Megalops atlanticus*
Merlucciidae	*Antimora rostrata*
	Macruronus magellanicus
	Merluccius bilinearis
	Merluccius capensis
	Merluccius merluccius
	Merluccius paradoxus
Monocanthidae	*Stephanolepis cirrhifer*
Moronidae	*Dicentrarchus labrax*
Mugilidae	*Mugil cephalus*
	Mullus barbatus
Mullidae	*Mullus surmuletus*
Myctophidae	*Electrona antarctica*
Myliobatidae	*Manta alfredi*
Myliobatidae	*Manta birostris*
Nototheniidae	*Dissostichus mawsoni*
	Trematomus bernacchii
	Trematomus hansoni
	Trematomus newnesi
Odontaspididae	*Carcharias taurus*
Ophidiidae	*Genypterus blacodes*
Oreosomatidae	*Allocytus niger*
Oreosomatidae	*Allocytus verrucosus*
	Pseudocyttus maculatus
Osmeridae	*Osmerus mordax*
	Thaleichthys pacificus
Paralichthyidae	*Paralichthys lethostigma*
	Paralichthys olivaceus
Pleuronectidae	*Platichthys flesus*
	Verasper variegatus
Polynemidae	*Eleutheronema tetradactylum*
Pomacanthidae	*Pygoplites diacanthus*
	Amblyglyphidodon orbicularis
	Amphiprion barberi
	Amphiprion mccullochi
	Amphiprion ocellaris
	Amphiprion percula
	Amphiprion polymnus
	Chromis limbata
	Chrysiptera talboti
	Pomacentrus amboinensis
	Pomacentrus coelestis
	Pomacentrus maafu
	Stegastes partitus
Pristidae	*Pristis clavata*
	Pristis microdon
	Pristis zijsron
Rachycentridae	*Rachycentron canadum*
Rajidae	*Dipturus oxyrinchus*
	Raja clavata
Rhincodontidae	*Rhincodon typus*
Rhinobatidae	*Rhinobatos productus*
Salmonidae	*Coregonus lavaretus lavaretus*
	Coregonus maraena
	Oncorhynchus clarki clarki
	Oncorhynchus gorbuscha
	Oncorhynchus keta
	Oncorhynchus kisutch
	Oncorhynchus masou masou
	Oncorhynchus mykiss
	Oncorhynchus nerka
	Oncorhynchus tshawytscha
	Salmo salar
	Salmo trutta
	Salvelinus alpinus
	Salvelinus leucomaenis
Scaridae	*Chlorurus sordidus*
	Scarus frenatus

Family	Species
Scaridae	*Scarus ghobban*
Sciaenidae	*Argyrosomus regius*
	Cynoscion nebulosus
	Larimichthys polyactis
	Micropogonias furnieri
	Micropogonias undulatus
	Miichthys miiuy
	Nibea albiflora
	Pogonias cromis
	Sciaenops ocellatus
Scomberesocidae	*Cololabis saira*
Scombridae	*Acanthocybium solandri*
	Euthynnus affinis
	Katsuwonus pelamis
	Scomber australasicus
	Scomber japonicus
	Scomber scombrus
	Scomberomorus cavalla
	Scomberomorus commerson
	Scomberomorus semifasciatus
	Scomberomorus sierra
	Thunnus alalunga
	Thunnus albacares
	Thunnus obesus
	Thunnus orientalis
	Thunnus thynnus
	Trachurus trachurus
Scophthalmidae	*Lepidorhombus boscii*
	Lepidorhombus whiffiagonis
Scorpaenidae	*Pterois miles*
Sebastidae	*Sebastes alutus*
	Sebastes atrovirens
	Sebastes auriculatus
	Sebastes caurinus
	Sebastes inermis
	Sebastes mentella
	Sebastes miniatus
	Sebastes paucispinis
	Sebastes polyspinis
	Sebastes rastrelliger
	Sebastes ruberrimus
	Sebastes schlegeli
	Sebastes spp.
Serranidae	*Centropristis striata*
	Cephalopholis argus
	Epinephelus coiodes
Serranidae	*Epinephelus itajara*
	Epinephelus labriformis
	Epinephelus marginatus
	Epinephelus morio
	Hypoplectrus puella
	Mycteroperca microlepis
	Paralabrax clathratus
	Plectropomus areolatus
	Plectropomus leopardus
	Plectropomus maculatus
Soleidae	*Solea lascaris*
	Solea senegalensis
	Solea solea
	Solea vulgaris
Sparidae	*Acanthopagrus butcheri*
	Acanthopagrus latus
	Archosargus probatocephalus oviceps
	Archosargus probatocephalus probatocephalus
	Chrysoblephus laticeps
	Dentex dentex
	Dentex tumifrons
	Diplodus puntazzo
	Diplodus sargus
	Diplodus vulgaris
	Lithognathus mormyrus
	Pagellus bogaraveo
	Pagrus pagrus
	Sparus aurata
	Spondyliosoma cantharus
Sphyrnidae	*Sphyrna lewini*
Stegostomatidae	*Stegostoma fasciatum*
Stromateidae	*Pampus argenteus*
Sygnathidae	*Hippocampus capensis*
	Hippocampus hippocampus
	Hippocampus kuda
	Hippocampus trimaculatus
	Syngnathus leptorhynchus
Trachichthyidae	*Hoplostethus atlanticus*
Triakidae	*Mustelus antarcticus*
	Mustelus schmitti
Trichiuridae	*Aphanopus carbo*
Tripterygiidae	*Tripterygion delaisi*
Wolffish	*Anarhichas lupus*
Xiphiidae	*Xiphias gladius*
Zoarcidae	*Zoarces viviparus*

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