

Bridging the gap between fisheries genetics and management

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Abstract

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The work in this dissertation addresses a gap between fisheries management and population genetics. The first chapter uses landscape genetics to determine whether natural boundaries exist in the Pacific cod stock in the Bering Sea and Aleutian Islands (BSAI) region of Alaska. Results indicate that Aleutian Islands and Bering Sea Pacific cod constitute distinct populations, and that Samalga Pass appears to be a physical barrier between the two. Until 2012, Pacific cod in the BSAI was managed as a single stock, but since that time have been managed separately, partially owing to the results of this work. In the second chapter, a novel simulation framework is used to examine the range of migration possible between North Sea and Norwegian Skagerrak Atlantic cod, given the results of genetic studies. Chapter 3 is a management strategy evaluation to answer questions regarding the utility of genetics in management decisions, given the inherent error rate in genetic studies. This chapter is parameterized for Pacific cod in the BSAI to

examine the costs and benefits of incorporating genetic results into the determination of management units when two distinct populations exist. In general, incorporating the results of genetic studies into management framework increases catches and decreases the risk of population depletion below management goals. The fourth chapter examines a range of management strategies for populations subject to isolation-by-distance stock structure, a common type of population structure in marine fisheries. When disproportionate fishing effort exists, splitting a single management area into two provides less risk of depletion in individual spatial areas. Further improvement can be achieved when areas of similar fishing pressure are managed together.

Table of Contents

Introduction	7
References.....	11
Chapter 1: A landscape genetics approach to Pacific cod <i>Gadus macrocephalus</i> population structure in the Bering Sea and Aleutian Islands reveals isolation-by-distance and distinct populations.....	13
Abstract	13
Introduction	14
Methods	17
Results.....	22
Discussion	25
References.....	33
Chapter 2: Estimating dispersal rates in Skagerrak coastal cod from both genetic differentiation and population dynamics using an individual based model.....	52
Abstract	52
Introduction	53
Methods	55
Results.....	60
Discussion	64
References.....	72
Appendix 2.....	84
Chapter 3: The utility of genetics in marine fisheries management: a simulation study based on Pacific cod off Alaska.....	89
Abstract	89
Introduction	90
Methods	92
Results.....	98
Discussion	101
References.....	107
Appendix 3.....	123
Chapter 4: A simulation approach to managing isolation-by-distance stock structure in marine fish, Pacific cod and blackspotted rockfish: Where do we draw the line?	138
Abstract	138
Introduction	139
Methods	141
Results.....	145
Discussion	150
References.....	158
Appendix 4.....	172
Acknowledgements	186
Conclusions.....	187
References.....	191

Introduction

Marine fisheries resources are important recreationally, economically, and as a food resource. Marine fisheries must be managed sustainably to maintain these benefits. Sustainable fishing must include not only fishing to achieve optimum yield, consideration of the social and economic system, but also maintaining genetic structure and diversity (Hilborn 2005). The Magnuson-Stevens Fishery Management and Conservation Act, the primary Act governing marine fisheries management in the United States, defines its goal as “to provide for the preparation and implementation, in accordance with national standards, of fishery management plans which will achieve and maintain, on a continuing basis, the optimum yield from each fishery” based on “the best scientific information available” and “to foster and maintain the diversity of fisheries in the United States.”

Fish is the only major food source that is primarily taken from wild populations; even food to sustain aquaculture comes from wild-caught fish. Genetic population structure in marine fish species is relatively common (Hauser and Carvalho 2008); many marine species do not occur as a single homogenous group, but are divided into populations that are more or less isolated from each other. Such population structure has two main effects: first, isolated populations react independently to perturbation, such as environmental fluctuations and exploitation. Second, isolated populations may adapt to local environmental conditions, resulting in genetic differences in morphological and life history characters. Recognizing and maintaining population structure may thus help to reduce temporal fluctuations in species abundance and prevent overfishing of individual stocks (Hilborn et al. 2003; Schindler et al. 2010). Genetic populations showing differentiation at neutral genetic markers only exchange a few individuals per generation; therefore, differential fishing pressure on unrecognized stock structure can result in depletion of the more heavily fished stocks (Waples 1998).

Fisheries management organizations do not always include information on population genetic structure into management plans, due in part to uncertainty in the nature of stock structure and how to incorporate it into management. The idea that there may be distinct subpopulations of the same species began with work of Frederick Heincke, a German scientist, in the late 1800's. Today we recognize that two main types of stock structure exist in marine species: distinct populations and isolation-by-distance (Fig. 0.1). Lack of genetic population structure, or panmixia, is often considered a third type of population structure (Fig. 0.1). Distinct populations form when genetic drift is large relative to migration. This type of population structure can also occur if a population bottleneck or a founder effect occurs, and will be maintained when gene flow is minimal. Distance or environmental features can limit migratory exchange. In some cases, this results in a series of populations that are more connected to proximate than to distant neighbors, or isolation-by-distance stock structure (Selkoe et al. 2008). If distinct populations are separated at a known location or oceanographic feature, delineating management units can be straightforward. Isolation-by-distance, on the other hand, can leave a confusing picture of overall significant genetic differentiation without clear population boundaries.

Many examples exist of distinct stocks within a single management. On the U.S. west coast, evidence for population structure within management units has been observed in black rockfish, *Sebastes melanops*; Pacific hake, *Merluccius productus*; shortspine thornyhead, *Sebastolobus alascanus*; Pacific Ocean perch *Sebastes alutus*; canary rockfish, *Sebastes pinniger*; and yelloweye rockfish, *Sebastes ruberrimus* (Waples et al. 2008). Examples in the northeast Atlantic include Atlantic cod; haddock, *Melanogrammus aeglefinus*; whiting, *Merlangius*

merlangus; blue whiting, *Micromesistius poutassow*; European hake, *Merluccius merluccius*; and Atlantic herring (Reiss et al. 2009). Isolation-by-distance population structure has been identified in many commercially-managed species, including copper, brown, and grass rockfishes along the United States west coast (*Sebastes caurinus*, *S. rastrelliger*, and *S. auriculatus*; Buonaccorsi et al. 2002, 2004, 2005), Pacific ocean perch off Alaska (*Sebastes aleutus*; Palof et al. 2011), Northern rockfish in the Bering Sea and Aleutian Islands (BSAI) region of Alaska (*Sebastes polyspinis*; Gharrett et al. 2012), Atlantic cod off Newfoundland and Labrador (*Gadus morhua*; Beacham et al. 2002), blackspotted rockfish (*S. melanostictus*) in the BSAI (Spencer and Gharrett 2010), and Pacific cod within the BSAI (Cunningham et al. 2009; Spies 2012). Management plans have not yet been developed to incorporate isolation-by-distance population structure, despite its prevalence.

Successful implementation of stock structure into management plans involves a series of complicated steps, from identification of stock structure, to interpretation in a management context, and development of an appropriate plan for incorporating the information into management. Experiments to determine population structure must be designed to provide enough statistical power to answer the research hypothesis, and results that can be interpreted with regard to meaningful management units and dispersal rates (Waples 1998). Translating genetic differentiation into dispersal rates is not straightforward, but is of interest to fishery managers (Whitlock and McCauley 1999). There is often no predetermined method to incorporate genetic information into management plans; therefore evaluation of candidate management plans via simulation can aid managers in the decision making process.

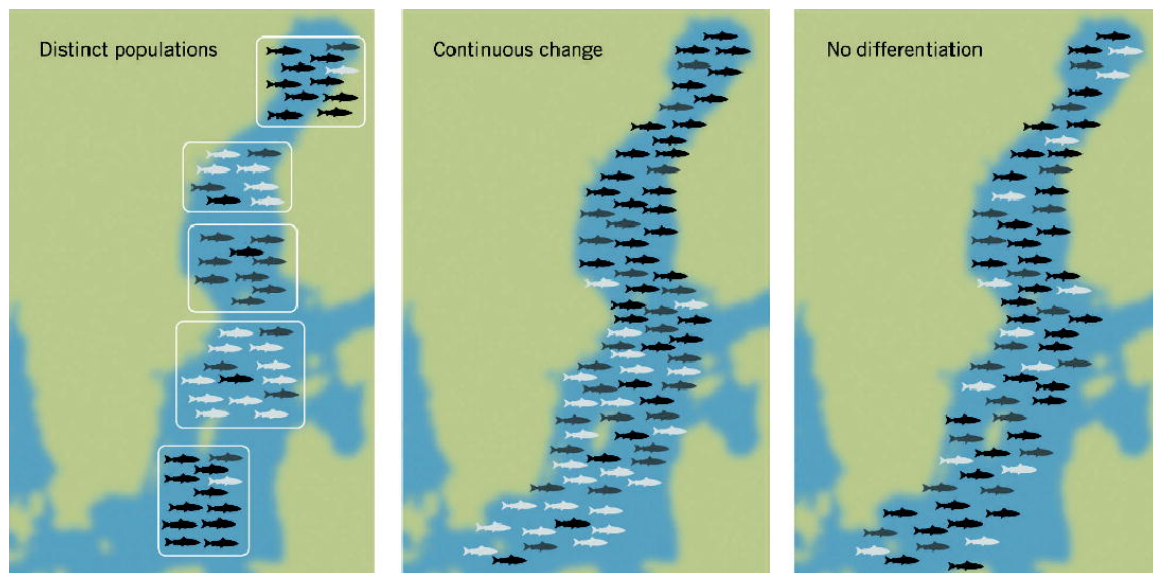


Fig. 0.1, from Laikre et al. (2005). Three general categories of genetic population structure are distinct populations, continuous change or isolation by distance, and no differentiation (panmixia).

The work in this dissertation addresses several current challenges to incorporating genetics into marine fisheries management. A landscape genetics approach is applied to Pacific cod, *Gadus macrocephalus*, in the Bering Sea and Aleutian Islands (BSAI) management area of Alaska (Chapter 1). This work was designed to identify relevant management units in an exploited marine fish species, based on oceanographic features specific to the BSAI. The second

chapter applies a novel simulation framework to existing information on genetic population structure in the highly exploited Atlantic cod, *Gadus morhua*, in the North Sea and Norwegian Skagerrak to examine dispersal rates. The third and fourth chapters examine how to apply genetic data on population structure in a management context. A management strategy evaluation (MSE), the process of using simulation testing to evaluate the effectiveness of management strategies, is implemented to address uncertainty associated with using plausible genetic hypotheses and the consequences (Chapter 3). This work is based on Pacific cod in the BSAI, and examines the performance of management strategies which incorporate genetic data, compared to ignoring such information, when two distinct populations are present in a management area. A similar analysis is performed in the fourth chapter, to examine several management strategies when isolation-by-distance stock structure is present.

Previous research found evidence for stock structure within the Bering Sea and Aleutian Islands management area. A comprehensive genetic analysis was needed to confirm the existence of stock structure, and to identify the location(s) of boundaries between subpopulations. Until 2013, this region managed as a single unit. The landscape genetics study performed in Chapter 1 was designed to address the needs of management. The study tests the hypothesis that the deep passes and dynamic oceanography of the Aleutian Islands deter migration of adults and restrict larval transport into the eastern Bering Sea. The cumulative effects of such mechanisms would lead to region-specific recruitment, and thus genetically distinct population units over smaller spatial scales than the BSAI management region. The approach examines potential physical and oceanographic barriers among ten samples across the BSAI region (nine locations, one sampled temporally) genotyped at 17 microsatellite loci.

The second chapter uses a novel simulation framework to examine dispersal based on genetic differentiation in North Sea and Skagerrak Atlantic cod. Dispersal is estimated based on simulations that incorporate population dynamics and biological parameters from actual populations for which information on genetic differentiation exists. Two pairs of Atlantic cod populations are examined: the North Sea vs. an outer Skagerrak fjord and the North Sea vs. an inner Skagerrak fjord. Empirical levels of genetic differentiation are not significant between the outer Skagerrak cod, but significant differences were found between the North Sea and the inner fjord. Genetic populations showing significant differentiation at neutral genetic markers only exchange a few, but reproductively successful, individuals per generation, and significance is generally evidence for distinct stocks (Waples 1998). However, lack of significant genetic differentiation may imply anything from complete panmixia to distinct ecological populations (Waples 1998). An upper level of ten percent migration has been suggested as a threshold between an ecological population and panmixia (Hastings 1993), and simulation results were compared with these theoretical expectations.

The third and fourth chapters examine management strategies for different types of population structure in marine species. The MSE in the third chapter addresses uncertainty in genetic results and stochasticity in recruitment and population dynamics, while evaluating the utility of such information for management. Parameters in the model are based on Pacific cod, *Gadus macrocephalus*, in the Bering Sea and Aleutian Islands (BSAI) region. Simulations use a spatially-structured individual-based model that combines multi-locus microsatellite genotypes and a traditional fish population dynamics model. Performance measures include the conservation status and yield of each of two populations.

The fourth chapter examines several management strategies for Pacific cod in the Aleutian Islands (AI) and blackspotted rockfish in the Eastern Bering Sea (EBS) and Aleutian Islands,

based on migration rates estimated from the extent of IBD stock structure. The mean dispersal distance, the distance traveled between parents and offspring per generation based on the IBD relationship, has been estimated at 500 km or less for blackspotted rockfish and less than 100 km for Pacific cod (Spencer and Rooper 2010; Cunningham et al 2009). These values are much smaller than the linear distance of the BSAI management unit, which spans approximately 1,000 km along the Bering Sea shelf and an additional 1,500 km along the Aleutian Island chain (Fig. 0.1). Arbitrarily implementing finer scale management units has been suggested as a precautionary approach to managing isolation-by-distance (Cunningham et al. 2009; Gharrett et al. 2012). However, there is a lack of information on how to manage stocks with IBD stock structure. Six management strategies are tested, and performance measures include the level of depletion of subpopulations within the management area, effective population size, and catch.

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Chapter 1: A landscape genetics approach to Pacific cod *Gadus macrocephalus* population structure in the Bering Sea and Aleutian Islands reveals isolation-by-distance and distinct populations

Abstract

Landscape genetics of Pacific cod *Gadus macrocephalus* within the Bering Sea/Aleutian Islands (BSAI) management area of Alaska was examined in samples from nine spawning locations, including one temporal replicate sample, using 17 microsatellite DNA markers. This study examined fine scale population structure of Pacific cod in the BSAI with the goal of identifying breaks in genetic continuity associated with physical barriers to migration and larval transport. Samples were taken from spawning fish collected from the western Aleutian Islands east to Unimak Pass and as far north as the Pribilof Islands. Overall, this work confirms the results of previous studies; genetic differentiation between samples is proportional to the distance between them. In addition, results indicate that dispersal is not continuous at a fine scale and several distinct genetic groups were identified that correspond to differences in the physical environment of the BSAI. The data suggest limited connectivity among spawning groups; in particular, there is evidence that a barrier exists between the Aleutian Islands and the Eastern Bering Sea. Results also indicate that within the Bering Sea, the Unimak Pass and Pribilof Islands spawning groups may be distinct from each other, and that samples west of Amchitka Pass in the western Aleutians may be distinct from those in the eastern Aleutians.

Introduction

Lack of migration among groups within a species can result in restricted gene flow, reproductive isolation, and complex population structure. Barriers to migration in terrestrial systems may consist of landscape features such as rivers or mountain ranges. Similar barriers exist in the ocean, in the form of currents (Gaylord and Gaines 2000), bathymetry (Schuller 2011), and temperature gradients (Wyllie-Echeverria 1995). When two populations are separated for many generations, their allele frequencies at neutrally evolving DNA loci will diverge and become distinct, primarily due to genetic drift. Over long time periods, such isolated groups may diverge into distinct species or remain as distinct evolutionary, or genetic, populations within a species (Waples and Gaggiotti 2006). Distinct genetic populations, or genetic stocks, are separated by limited or no gene flow, and can be recognized by significant and temporally stable genetic differentiation if enough time has passed for genetic differences to accrue (Bentzen 1998), while a single stock consists of individuals that are characterized by connectivity, or reproductive cohesiveness.

A primary goal of marine resource management is to match management units with biological populations to avoid unintended depletion of one or more distinct stocks that may otherwise have been managed as one composite unit (Taylor 1997; Laikre et al. 2005; Sterner 2007). As defined in the National Standard provision to the United States Magnuson Stevens Act, a specified management unit is a fishery or portion of a fishery that is based on management objectives that may include biological, geographical, economic, technical, social, or ecological criteria. Although other criteria exist for management units in fisheries around the world, this definition illustrates the fact that a management unit may be established for a variety of political or administrative reasons and may not necessarily reflect population structure (Hilborn 2005, Reiss et al. 2009). Preservation of locally adapted sub-populations is important for the stability of the stock complex (Schindler 2010), and fisheries that reduce the size of a population or maintain populations at a low level for an extended period could cause a loss of genetic diversity, which can result in lowered adaptability, compromised productivity and a higher risk of population loss (Lacy 1987; Hauser et al. 2002).

Pacific cod, *Gadus macrocephalus*, are important both economically and ecologically in the North Pacific Ocean. They comprise the second largest fishery in the United States, next to walleye Pollock, *Gadus chalcogrammus*, both by weight and value, and were 31st by weight

among worldwide marine capture fisheries from 2004-2008 (www.fao.org). In the United States, all but 1% of the total catch of Pacific cod is taken off Alaska, where cod are allocated into two management units, the Bering Sea and Aleutian Islands (although they were further allocated into Aleutian Island and Eastern Bering Sea management units beginning in 2014) and the Gulf of Alaska (GOA; Fig. 1.1). In 2009, Pacific cod catch in Alaska accounted for 15% of the total groundfish catch, or 228,200 mt (Hiatt et al. 2010), approximately 80% of which is taken from the BSAI. In this region, Pacific cod are primarily found along the Bering Sea shelf and the Aleutian chain. Many discrete spawning areas, each linked to a specific geographic location, have been identified throughout this range (Logerwell and Neidetcher 2008; Shimada and Kimura 1994). Cod are a key species in the ecosystem, both as predators, primarily of walleye pollock and other fish, crab, and shrimp (Lang and Livingston 1996), and as prey for halibut, *Hippoglossus stenolepis*, seabirds, and marine mammals, including the endangered Steller sea lion, *Eumetopias jubatus* (Sinclair and Zeppelin 2002).

In the biologically similar species, Atlantic cod, *Gadus morhua*, tracking data show that adults home to their natal spawning ground, a mechanism that has been used to explain localized population structure (Green and Wroblewski 2000; Robichaud and Rose 2001; Wright 2005). Distinct populations of Atlantic cod have been found as close as 30 km to one another, and gene flow appears to be influenced more by dispersal of pelagic larvae than by adult movement (Jorde et al. 2007; Knutsen et al. 2003; Stenseth et al. 2006). Indirect evidence associated with tagging studies suggests that Pacific cod may also exhibit site fidelity associated with spawning areas (Gustafson et al. 2000). Whether this represents fidelity to a natal spawning site is unknown; however, the presence of temporally stable distinct population structure would require limited dispersal at all life history stages and would imply natal spawning site fidelity.

Although mechanisms for natal spawning site fidelity are not known in Pacific cod, an overview of their life history from egg to adult provides insight into the potential for gene flow in this species. Demersal Pacific cod eggs hatch between 15 and 45 days after spawning depending on temperature, and at approximately 20 days in the Gulf of Alaska (Laurel et al. 2008; Rugen and Matarese 1988). Pacific cod larvae are pelagic until 3-4 months after hatching, after which they settle to depths of 30–50 m (Narimatsu et al. 2007); thus, larval dispersal may be influenced by current patterns. However, Pacific cod larvae have been observed to move into the upper water column where they are transported towards coastal nurseries (Rugen and

Matarese 1988; Hurst et al. 2010). Juvenile Pacific cod use inshore eelgrass in fjord-like habitats such as Prince William and Puget Sounds before migrating to deeper water as they mature (Gustafson et al. 2000). The maximum age observed for a Pacific cod is 25 years, and the age at 50% maturity in the BSAI is 4.9 years (Munk 2001; Stark 2007). Adult cod spawn in specific areas from January through March. Tagging studies in the Gulf of Alaska and the BSAI found that fish tagged in the summer and recaptured during spawning season migrated farther than fish recovered in other seasons, suggesting that cod migrate to feeding areas prior to returning to spawning areas (D. Urban, NMFS, Alaska Fisheries Science Center, Kodiak, Alaska 99615, USA, pers. comm. 2006; Shimada and Kimura 1994).

Adult cod prefer depths less than 260 m (Logerwell et al. 2005); therefore, deep passes could deter adult movement and provide an additional mechanism for reduced gene flow. Adults and juveniles reside near, but not on the bottom, generally from 80-260 m, and are not found deeper than about 500 m (Bakkala et al. 1984; Nichol et al. 2007). Bentzen et al. (1996) found significant differentiation among three northwest Atlantic cod populations (Flemish Cap, Scotian Shelf, and northern cod), each separated by submarine trenches that were up to 1,000 m deep. There are several major passes within the United States region of the Aleutian Chain that exceed 260 m depth (Hunt and Stabeno 2005), including Buldir Strait and Amukta and Amchitka Passes (Fig. 1.1, Table 1.1). In addition, the Aleutian passes define species distributions for 63 of 245 identified fish species, suggesting that the passes themselves may act as physical barriers to gene flow in this region (Logerwell et al. 2005).

Oceanographic flow may provide a third mechanism for constraining dispersal and gene flow (Gaylord and Gaines 2000); complex oceanography within the BSAI could form barriers to migration both to adult and larval Pacific cod (Fig. 1.1). The physical environment of the Bering Sea is extremely different from the Aleutian Islands; the Eastern Bering Sea is characterized by a single continental shelf adjacent to a deep sea basin while the Aleutian Islands form a chain of volcanic mountaintops separated by passes that allow transfer of water between the North Pacific Ocean and the Bering Sea (Hunt and Stabeno 2005). Along the Aleutian chain, physical and biological differences demarcate ecological shifts, most abruptly at Samalga Pass (169°W), an area that divides waters of the Alaska Coastal Current to the east and the Alaskan Stream to the west (Hunt and Stabeno 2005). To the east of Samalga Pass, the Alaska Coastal Current is comprised of warmer, nutrient-poor coastal water, while water to the west is oceanic, colder, and

rich in nutrients (Hunt and Stabeno 2005; Fig. 1.1). Those species with pelagic larvae are likely strongly influenced by oceanic currents and water mass origin (Logerwell et al. 2005, Hunt and Stabeno 2005); in addition, clockwise circulation patterns in the Aleutians have been identified that could entrain larvae (Ladd et al. 2005).

A broad-scale examination of the genetic population structure of Pacific cod found a sample from the Aleutians (Adak Island) to be distinct from both a Bering Sea (Unimak Pass) and a Gulf of Alaska (Kodiak Island) sample (Cunningham et al. 2009). This result led to the hypothesis that deep passes and current patterns may limit Pacific cod movement at all life history stages and create complex population structure (Cunningham et al. 2009). The sampling scheme in the current study was designed to address this question by investigating genetic structuring of Pacific cod in the BSAI on a fine scale. Samples were taken during spawning season from the western Aleutian Islands, spanning all the major North American passes of the Aleutian Archipelago, east to Unimak Pass and as far north as the Pribilof Islands. Several studies have found a lack of homogeneity and limited lifetime dispersal in other fish species that span the Aleutian Islands and Bering Sea, including Pacific ocean perch and northern rockfish (Palof et al. 2010, Gharrett et al. 2012). Therefore, we hypothesized that multiple populations of Pacific cod exist in the BSAI, and that both depth and current patterns define stock boundaries.

Methods

Samples, which consisted of fin clips collected at a particular location, span the Aleutian chain and a portion of the Bering shelf, from the Near Islands in the west, Unimak Pass in the east and Pribilof Island in the north (Table 1.2, Fig. 1.1). Whether the sample originated from the Aleutian Islands or the Eastern Bering Sea is specified in Table 1.2. All samples were stored in non-denatured ethanol and were collected during the spawning season (February-March), when the majority of commercial cod catches occur (Thompson et al. 2010). Most samples were taken from commercial fishing trawlers, with the exception of the Unimak Pass sample which was obtained during a research survey with pot gear. The Pribilof Island sample was frozen until ethanol became available. Two samples were collected north of Amlia Island, in 2006 and 2007, in order to investigate temporal stability. No samples were analyzed in previous studies. Because sampling was performed opportunistically, it was not feasible to record the spawning condition of all fish collected. The Unimak Pass samples were exclusively spawning fish, and maturity

state was recorded for the Near Island, S. Kiska Is. and Amchitka Is. samples. Spawning state was not recorded for the remaining samples. For the Near Island and the Amchitka Island samples, sufficient numbers of both spawning (Near: 136, Amchitka: 30) and immature fish (Near: 16, Amchitka: 20) were genotyped to assess genetic differentiation between them, while the Kiska sample consisted almost exclusively of spawning fish. DNA was extracted using Qiagen 96 Blood and Tissue kits (QIAGEN Inc., Valencia, CA) according to the manufacturer's instructions.

In order to determine how many samples and how many microsatellite loci are required to provide sufficient statistical power to reject the null hypothesis when it is false, a dataset was simulated with similar allele frequencies to the dataset of Cunningham et al. (2009) using POWSIM v.4.0 software. POWSIM estimates the statistical power associated with rejecting the null hypothesis of genetic homogeneity under varying numbers of microsatellite loci, sample sizes, alleles, and allele frequencies (Ryman and Palm 2006). The analysis indicated that 20 microsatellite loci and 100 samples per location would be sufficient to detect significant levels of allele frequency differentiation if F_{ST} was on the order of 0.001. In a previous study of Pacific cod within North America, F_{ST} values ranged from -0.0012 to 0.0163 and the smallest significant value was 0.006; thus the slightly more conservative value of 0.001 was chosen as an estimate of expected F_{ST} values for the current study.

To attain the goal of 20 microsatellite loci, 19 walleye pollock loci (O'Reilly et al. 2000), 19 Atlantic cod loci (Miller et al. 2000; Skirinsdottir et al. 2008; Stenvik et al. 2006; Wesmajervi et al. 2007), and 11 Pacific cod loci (Cunningham et al. 2009) were screened. One additional locus (*Gma107*) that had not been used previously (Canino et al. 2005) was also evaluated. Although 59 microsatellite loci have been developed for Atlantic cod, microsatellites were limited to tetra-nucleotides because they tend to have less stutter than di-nucleotides. Of the 38 pollock and Atlantic cod loci, 14 were variable and amplified well: *GmoG13*, *GmoG16*, *Gmo8*, *GmoG18*, *Gmo19*, *GmoC82*, *GmoC83*, *GmoC88*, *GmoG5*, *Tch5*, *Tch9*, *Tch13*, *Tch17*, and *Tch18*. Further screening of 96 samples revealed that only *GmoG13*, *GmoG16*, *Gmo19*, *GmoC82*, *GmoC83*, *GmoG5*, and *Tch13* were in Hardy-Weinberg equilibrium (HWE) and could be scored reliably (Table 1.3), for a total of 19 loci screened in the current study.

Polymerase chain reactions (PCR) were performed as described in Canino et al. (2005), with 55°C used as the annealing temperature for all loci. Reruns for the Pribilof sample were

performed differently since the tissue had degraded slightly before being stored in ethanol. For these PCR's, the Velocity PCR kit (Bioline, London, UK) in a 5µl volume was used following manufacturer's instructions, with 3% DMSO (v/v), 2mM MgCl₂, 0.4µM each primer, and 0.05U/µl Velocity DNA polymerase.

Two different types of genotyping platforms were used due to equipment failures. Seven loci (*Gma100*, *Gma101*, *Gma102*, *Gma103*, *Gma106*, *Gma109*, and *Tch20*) were run on one of two MegaBACE 1000 DNA sequencers (Amersham Biosciences/GE Healthcare, Uppsala, Sweden). All other loci were run on an ABI3730xl (Applied Biosystems/Life Technologies Corporation, Carlsbad, CA) via contract with Eurofins MWG Operon (Huntsville, AL). Cross-platform results were compared by running a set of 96 samples at each locus on each platform. MegaBACE data were scored using Genetic Profiler version 2.2 software (Amersham Pharmacia Biotech, Inc., Piscataway, NJ) and ABI data were scored using GeneMarker v1.85 (SoftGenetics LLC, State College, PA). Data quality was evaluated using a double-blind genotyping protocol, where two individuals score the gel image independently. This method was employed on all samples run on the ABI platform (12 loci), and multiple runs of the same sample were compared for reliability on samples run with the MegaBACE genotyping platform. All loci were rerun when scores were questionable to ensure scoring reliability, up to four times.

Several tests were performed in order to ensure that data met expectations of quality and neutrality. Tests for Hardy-Weinberg equilibrium (HWE), F_{IS} calculations and associated p -values were performed using GENEPOP on the web (<http://genepop.curtin.edu.au/>) with a burn-in period of 10,000 iterations, 1,000 batches and 10,000 iterations per batch. Observed and expected heterozygosity values and pairwise tests for linkage disequilibrium were analyzed in GENETIX 4.05 (Belkhir et al. 2000), and significance for pairwise tests was determined using 1,000 permutations of the data. Locus neutrality was assessed with *fdist2* (Beaumont and Nichols 1996) to determine whether any of the loci were under selection. *Fdist2* provides a comparison between observed F_{ST} values as a function of heterozygosity with those simulated with the same size and number as the actual data set, using the island model with 100 islands and an infinite alleles mutational model. This allowed 0.025, 0.5, and 0.975 quantiles for a selectively neutral distribution to be estimated. Micro-Checker v.2.2.3 was used to look for the presence of null alleles, upper allele dropout, and errors due to stutter (Van Oosterhout et al. 2004).

Tests for genetic differentiation between samples were performed using several standard methods, although samples were not assumed to represent populations. Pairwise theta (Weir and Cockerham 1984), an estimator of F_{ST} , was calculated in GENETIX, and significance was assessed with 1,000 permutations of the data. Pairwise theta and a 95% confidence interval for the combined Bering Sea samples versus the combined Aleutian Islands were calculated in FSTAT 2.9.3.2 (Goudet 2001). Exact tests for allele frequency differentiation among samples (genic tests) were performed using GENEPOP with the same burn-in, iterations, and batches as the F_{IS} calculations. Corrections for multiple tests were performed using the sequential goodness of fit metatest (SGoF) method, which increases the statistical power of the test as the number of comparisons increases, unlike the Bonferroni correction (Carvajal-Rodríguez et al. 2009). A locus-by-locus analysis of molecular variance, or AMOVA, was implemented in Arlequin, ver. 2.000 to examine divergence within and among groups of samples, with 15% missing samples allowed. Groupings were determined systematically using adjacent-sample pooling; adjacent sites were pooled to determine whether samples represented distinct populations. This method was chosen because isolation-by-distance population structure has been demonstrated in Pacific cod, implying that nearest neighbors are most likely to be similar (Canino et al. 2010; Cunningham et al. 2009). The best grouping was defined to be the one with the highest differentiation among groups (F_{CT}) and non-significant differentiation within groups (F_{SC}). Because theta is constrained to lower values at loci with high heterozygosity, a trend that was observed in the data, single estimates of D_{EST} were used to determine the most influential loci. D_{EST} is a standardized estimate of differentiation and both single and multi-locus D_{EST} values were calculated using software for the measurement of genetic diversity (SMOGD; Jost 2008; Crawford 2010).

To compare population structure to physical oceanographic and landscape features, approaches were used that incorporate genetic and geographic information from each sample. The maximum distance Monmonier algorithm is designed to transfer data contained in a genetic distance matrix onto a geographical map to identify boundaries (Manel et al. 2003; Monmonier 1973). This algorithm, implemented in the program BARRIER, v2.2 (Manni et al. 2004), creates a connectivity network among samples given a matrix of pairwise multi-locus genetic distance values. In this case, residual F_{ST} values based on the expected slope of the IBD relationship were used rather than F_{ST} estimates, which is recommended in the case of IBD (Manni et al. 2004).

Barriers were created by extending from the edge with the largest genetic distance to the edge of the adjacent network with the largest genetic distance until the edges of the network are reached. One drawback of this program is that it does not estimate the number of barriers; the user provides the number they suspect and the program provides the location. However, the significance of each barrier can be assessed using bootstrapping; 100 resampled datasets were created by randomly resampling original sample names. Pairwise theta was calculated in the bootstrapped datasets using the R package Geneclust v1.0.1. (Weir and Cockerham 1984; Ancelet and Guillot. 2006), and significance was assessed based on the proportion of resampled datasets that identified a barrier in the same location as the true data. Because the data included a temporal sample at N. Amlia, two datasets were constructed: one with all samples except N. Amlia 2006 and another with all data except N. Amlia 2007, so that the effect of the different temporal samples could be examined separately (Table 1.2). A second spatial analysis, Wombling (Crida and Manel 2007), takes into account both spatial information on an x,y grid, and multilocus genetic information in a systemic function:

$$(1) S(x,y) = \sum_j \|\nabla f_j(x,y)\|, \text{ where } f_j \text{ is the estimation of allele frequencies } j \text{ at each point on}$$

the (x,y) grid, $\nabla f_j(x,y)$ is the gradient of allele frequencies f_j with respect to coordinates x and y , and j is the summation over all alleles at all loci. Allele frequencies are estimated at each point using a local polynomial regression approximation. Calculations were performed using the R (2.12.1; R Development Core Team 2011) software package wombssoft, with settings implemented as suggested in Crida and Manel (2007). Statistical significance of boundaries was evaluated using a binomial test at a fixed p value ($\alpha = 0.05$), which determines whether the gradient of allele frequencies is greater than a given percentile, p_B . Population structure was further explored using Structure 2.3.3 (Pritchard et al. 2000); given genotype data, individuals are assigned to populations such that loci are in Hardy-Weinberg and linkage equilibrium. Preliminary trials indicated that a million MCMC iterations would be sufficient for convergence. Analyses, which were repeated five times, discarded the first 30,000 iterations and simulated $K=\{1,2,\dots,5\}$ populations. Simulations were performed both with and without using sample locations as priors. A further spatial analysis, Geneland, a bayesian model implemented with MCMC that uses individual multilocus geo-referenced genotypic data to identify spatial organization of populations, was implemented with R software. Like Structure, Geneland

clusters population genetics data from samples into populations such that each population is in Hardy-Weinberg equilibrium with linkage equilibrium between loci; however, it also takes into account spatial coordinates to group spatially proximate samples. Analyses were performed using 100,000 iterations and a burn-in of 200, thinning every 100th iteration (Guillot et al. 2005). To examine whether any geographic trends were present in genetic diversity, the average estimated number of alleles at a locus was calculated for each population (Leberg 2002; Appendix Table 1).

A Mantel test was implemented in IBDWS, “Isolation by distance, web service”, to determine whether genetic differentiation was correlated with geographic distance (Jensen et al. 2005). This program also calculated the slope of the relationship between the genetic and geographic distances using reduced major axis regression. Partial Mantel tests were implemented in the same program to determine whether a correlation was present between genetic differences and oceanographic features, after controlling for geography. Linearized F_{ST} , $F_{ST} / (1 - F_{ST})$ was used as input data for this test, which is standard for isolation-by distance testing (Rousset 1997) and was used for comparison with work by Cunningham et al. (2009). Distances between points were determined using Google earth software, v. 5.2.1.1588 (Microsoft Corp., Seattle, WA), and were calculated along the Aleutian chain rather than across the Bering Sea due to account for cod depth preference of less than 500 m. Four “indicator” matrices were used in the partial Mantel tests: the depth of the deepest pass spanned between points, whether any two points spanned Amchitka Pass, the deepest pass in the Aleutian chain, whether any two points spanned Samalga and Amukta Passes, and a fourth which tallied the number of passes over 260 m depth between points. Significance was determined using 1000 permutations of the data in all cases.

Results

Standard tests were applied to determine whether loci conformed to Hardy-Weinberg Equilibrium (HWE), were selectively neutral, and whether other problems existed that would warrant them being excluded from further analyses. All loci and populations conformed to HWE, with two exceptions: locus *Gma106* was discarded due to a clear excess of heterozygotes (data not shown), and locus *Gma107* was significantly out of HWE in 2 of 10 populations. The remaining 17 loci were in HWE, as were all 10 samples. Sample and locus statistics are given in App. Table 1.1, and significant F_{IS} values after SGoF correction are shown in bold. All loci

conformed to the assumption of neutrality, with the exception of *Gma107* (Fig. 1.2). The remaining 17 loci were all within the 95% quantiles expected for neutral loci. Allele frequency histograms by sample location were unremarkable at *Gma107*, discounting the possibility that this locus revealed selective differences. There was no evidence for null alleles, upper allele dropout or error due to stutter at any locus except for *Gma107*, which contained null alleles. These 17 loci were retained for further analyses, with the exception of *Gma107*. Of the 136 locus-by-locus comparisons for linkage disequilibrium, none were significant after SGoF correction.

Using these 17 loci, pairwise population differentiation statistics (genic tests, F_{ST} and D_{EST}) indicate differentiation among samples, both temporally and geographically, and were consistent with fine-scale population structure (Table 1.4). Global F_{ST} was 0.001, and the locus significance, based on single-locus D_{EST} values were (in order from highest to lowest D_{EST} value) *Gma100*, *Gma109*, *Tch20*, *Gmo37*, *Gmo19*, *Gma103*, *Gma101*, *Gma102*, *Gma104*, *GmoG13*, *Gma105*, *GmoG5*, *GmoC82*, *GmoG16*, *Tch13*, *GmoC83*, and *Gma108* (Appendix 1). The temporal samples at Amlia Is. were significantly differentiated from each other. Pairwise statistics showed that the Unimak samples had 6 out of 9 possible significant differences with the other samples whereas the Pribilof samples had 5 out of 9. When all samples from the Aleutian Islands were compared with all Eastern Bering Samples, the F_{ST} estimate was 0.006 (95% CI: 0.005, 0.008). Mature samples were not significantly differentiated from immature ones from the Near Islands and Amchitka ($F_{ST} < 0$ $p = 0.62$, $F_{ST} < 0$, $p = 0.74$, respectively), and removal of the immature samples did not change the F_{ST} value between the Near Islands and Amchitka samples. The AMOVA grouping pattern that included three groups (Unimak Pass, all Aleutian Island samples, and Pribilof samples; Table 1.5 and Fig. 1.3) resulted in significant differentiation among groups at the $\alpha = 0.05$ level ($F_{CT} = 0.0016$, $p = 0.0039$) but no additional significant differentiation within groupings ($F_{SC} = 0.0005$, $p = 0.0948$). However, the grouping that included four populations and further structuring within the Aleutian Islands appeared to be marginally better, with a slightly higher F_{CT} value ($F_{CT} = 0.0017$, $p \leq 0.05$). A break between Tanaga and Great Siskin Island, at Tanaga Pass, most fully accounted for this structure because it resulted in the highest overall F_{CT} .

With the exception of Structure and Geneland, spatial analyses were concordant with the AMOVA result; they identified the presence of a barrier between the Eastern Bering Sea and the

Aleutian Islands. Neither Structure nor Geneland analyses showed evidence for population structure. However, when three barriers were imposed on the Monmonier algorithm, both the N. Amlia 2006 and the N. Amlia 2007 samples identified barriers between Unimak and Pribilof, between Unimak and the Aleutian Islands, and between Tanaga and Great Siskin, and (locations A, B, and C respectively on Fig. 1.3). The proportion of bootstrapped datasets that randomly identified these locations as barriers, listed with values from the 2006 N. Amlia dataset followed by values from the N. Amlia 2007 dataset, were 0.060/0.060 between Pribilof and Unimak (barrier A), 0.003/0.001 between AI and Unimak, (barrier B) and 0.133/0.177 between Tanaga and Great Siskin (barrier C; Fig. 1.3). Wombling results supported two barriers: one between the Eastern Bering Sea and the Aleutian Islands and a second within the Aleutians west of Amchitka pass but lacked evidence of a barrier between the Unimak and Pribilof samples (Fig. 1.4). A range of values for the allele frequency gradient p_B between 0.05 and 0.5 resulted in the same pattern; both the Near Islands and Kiska samples were in the area of significant change in allele frequency, and an area of strong allele frequency change appeared between the Aleutian Islands and the Eastern Bering Sea. Above $p_B = 0.5$ and below $p_B = 0.05$, the signal disappears; therefore $p_B = 0.1$ was chosen because it clearly illustrates this pattern (Fig. 1.4). In addition to identifying a barrier between the Eastern Bering Sea and the Aleutian Islands, spatial analyses suggested the presence of additional barriers within the Bering Sea and within the Aleutian Islands.

The number of alleles per locus increased proportional to the number of fin clips per sampling station. A simple linear regression of the effect of genetic diversity on sample size was highly significant ($p < 0.001$). However, geographic location appeared to be uncorrelated with genetic diversity; comparisons of the five locations with 95 samples each (Pribilof, S. Atka, S. Kiska, Tanaga, and Unimak) had similar genetic diversity values (mean = 18.98, $s = 0.8$; Appendix Table 1). The sample with the highest genetic diversity was the farthest to the west; Near Island, which also had the highest number of fin clips. The lowest genetic diversity was in the Amchitka sample, which was also at the western end of the range, but had the lowest number of fin clips in the sample.

The Mantel test showed a significant isolation-by-distance pattern ($r = 0.4969$, $p[r \leq 0] = 0.0110$). The slope of the reduced major axis regression of genetic distance vs. geographic distance was 2.307×10^{-06} (95% CI: 1.730×10^{-06} , 2.885×10^{-06}) and the intercept was -7.175×10^{-04} (95% CI: -1.219×10^{-03} , -2.158×10^{-04} ; Fig. 1.5). After accounting for geographic

distances, three of the partial Mantel tests showed no significant correlation between genetic differences and any other factor. Results from the three tests were as follows:

The depth of the deepest pass between samples ($r=-0.3040$, $p[r\leq 0]=0.9200$),
whether two points span Amchitka pass ($r=-0.3667$, $p[r\leq 0]=0.9640$), and
number of deep passes between points ($r=-0.0350$, $p[r\leq 0]=0.6330$).

However, whether two samples spanned Samalga and Amukta Passes was marginally significant ($r=0.3495$, $p[r\leq 0]=0.0813$). These results indicated that depth or number of passes between sampling locations was not a factor limiting migration. In addition, Amchitka pass did not appear to be a significant factor preventing migration.

Discussion

Temporal differentiation, and sampling error

While the previous study on Pacific cod in North America found temporal stability in the two samples examined (Unimak Pass and Kodiak Island; Cunningham et al. 2009), the temporal samples at Amlia Island (2006 and 2007) were genetically different. The estimated F_{ST} value between the two samples (0.0017; Table 1.4) is on the order of those found between the Aleutian Islands and the Eastern Bering Sea (range = 0.0006-0.0034, mean over 11 pairs = 0.0020). The fact that the two samples are significantly different from each other with the genic test (but not F_{ST} estimate), suggests that temporal fluctuations may exist over time scales as short as one year. It was not possible to collect all fish from the same year and samples were taken from 2004-2007; thus the question of temporal stability is relevant. However, the fact that the AMOVA, Barrier, and Wombling results were robust with both years of the Amlia sample, the lack of stability at Amlia Island remains consistent with the conclusions of isolation by distance in this paper. Given temporal stability in two previous spawning areas (Cunningham et al. 2009), but not in the current study, the question of Pacific cod genetic variability within and between sites should be the focus of a dedicated sampling and research program.

Genetic differentiation between the Aleutian Islands and Eastern Bering Sea

Analyses of fine-scale population structure within this commercially important management unit consistently reject the null hypothesis of panmixia, or genetic homogeneity of Pacific cod. Higher numbers of polymorphic microsatellites typically result in higher statistical power

(Ryman and Palm 2006), and the 17 used in this study increased statistical power for detecting low levels of genetic differentiation typical of marine fish species over previous studies. With the exception of Structure and Geneland, which may have limited ability to identify small but significant levels of genetic differentiation that are often characteristic of marine fish species (Palof et al. 2011), analyses were fairly concordant. First, significant isolation-by-distance was observed; genetic differences between samples were proportional to the distance that separates them. This is consistent with previous work (Cunningham et al. 2009). Secondly, differentiation appeared to be discontinuous and marked by several barriers to gene flow that had previously been undetected. The most notable area of limited gene flow appeared to occur between the Aleutian Islands and the Eastern Bering Sea.

Research on genetics, oceanography, and species diversity all suggest that the BSAI is a complex ecosystem. Isolation-by-distance demonstrated in the present study is supported by two prior genetic studies of Pacific cod (Canino et al. 2010; Cunningham et al. 2009). The slope of the isolation-by-distance line is similar to that observed with coastal North American samples (Fig. 1.5, slope = 2.31×10^{-6} vs. 1.57×10^{-6} ; Cunningham et al. 2009). The previous analysis used this slope value to conclude that the mean dispersal per generation of Pacific cod is extremely limited, less than 100 km per generation, and the higher slope in the current study implies even more limited dispersal. All spatial analyses and F_{ST} results provide evidence for a barrier to gene flow between the Eastern Bering Sea and the Aleutian Islands, an area that includes two passes, Amukta and Samalga.

Of all the passes in the Aleutian Islands region, Samalga Pass appears to be a major biophysical transition area (Logerwell et al. 2005). In this study, the species assemblages appeared to change and the number of fish species sampled decreased from east to west of Samalga Pass; 14 of 43 demersal fish species found at Samalga Pass were absent to the west of Amukta Pass (Logerwell et al. 2005). Nearly all of these species have pelagic larvae, which are affected by current patterns. Similarly, the diet composition of fish species changes at Samalga Pass. West of Samalga Pass, Pacific cod samples indicated increased consumption of Atka mackerel (*Pleurogrammus monopterygius*), as well as shrimp, squid and other fishes, whereas east of Samalga these were relatively rare and the diet primarily consisted of walleye pollock (Logerwell et al. 2005). Of the two passes separating the Eastern Bering Sea and the Aleutians,

Samalga is the greater transition zone and this appears to be reflected in diet, species abundance and biophysical factors.

Oceanographic and current patterns have been shown to act as barriers to migration for particular species. This is also true within species, resulting in stocks that might be best considered as separate management units. For example, Cape Mendocino in California represents a flow-induced range boundary, where the predominantly southward California Current is diverted from shore creating a site of strong upwelling. Samples of vermillion rockfish *Sebastes miniatus* (Hyde and Vetter 2009), acorn barnacle *Balanus glandula* (Sotka et al. 2004), and yellowtail rockfish *Sebastes flavidus* (Hess et al. 2011) all demonstrate limited gene flow around the cape. Like Samalga Pass, differences in species assemblages as well as the ends of species ranges indicate that limited gene flow exists to the north and south of Cape Mendocino (Hess et al. 2011). Another example appears off the west coast of Canada where the Alaska Current and the California Current diverge. This location has been correlated with a barrier to gene flow in the rosethorn rockfish *Sebastes helvomaculatus* (Rocha-Olivares and Vetter 1999). Although divergent current patterns may affect species differently, they have been recognized as potential zones of change, both among and within species, as they limit gene flow.

Genetic differentiation between adjacent populations could be the result of both present and historical events. A study based on mtDNA and microsatellite markers that examined current and historical gene flow in Pacific cod across its range hypothesized that glacial maxima, which reduced available habitat and lowered global sea level by as much as 120 m, forced Pacific cod to move south along the western and eastern coasts of the Pacific Ocean (Canino et al. 2010). Such glaciations likely had a significant effect on the genetic differences that have been noted between Pacific cod from the eastern vs. western Pacific (Canino et al. 2010). Following the last glacial maxima 14,000-15,000 years ago, the southern refuge population in the eastern Pacific expanded northward, resulting in present day populations of cod in the Gulf of Alaska, the Bering Sea, and the Aleutian Islands. The effective population size of Pacific cod has increased from an estimated median of 1.2×10^6 before the last glacial maxima to a current estimate of 8.0×10^7 across the entire northeast Pacific (Canino et al. 2010). Considering the evolutionary history of the species, several hypotheses could explain the differentiation observed between the Aleutian and Eastern Bering Sea populations. First, as populations of Pacific cod expanded northward, founder effects could have accompanied colonization. Subsequently, oceanic

conditions that limited gene flow could have prevented groups from homogenizing. Alternatively, initial colonization could have represented a single panmictic group that experienced limited gene flow due between the Bering Sea and the Aleutian Islands and diverged over time. The lack of a geographic trend in genetic diversity among samples is consistent with the latter hypothesis and confirms results observed with mtDNA and microsatellites (Canino et al. 2010).

Differentiation within the Eastern Bering Sea

Some evidence suggests that Pacific cod that spawn at Unimak Pass may be a distinct population from the Pribilof spawning group. Both datasets used in the Barrier analysis indicated a barrier between the Unimak and the Pribilof samples (significance derived by bootstrap sampling of the data, $p = 0.060$). Permutation tests of F_{ST} values and the AMOVA, which also uses permutation to calculate significance, indicated that Unimak and Pribilof samples are genetically different, but genic tests and examination of allele frequency clines did not. Although permutation test results were concordant, these tests have been shown to have lower statistical power than Fisher's exact tests (Ryman and Palm 2006). Wombling analysis, which is based on changes in allele frequencies, showed no evidence of a break between these two samples. Therefore, more samples are needed to confirm the evidence for stock structure within the Eastern Bering Sea.

A transition zone (e.g., that of Samalga Pass) in species abundance or composition between Unimak Pass and the Pribilof Islands appears to be absent; however, physical mechanisms coupled with adult homing to natal spawning sites could account for the observed differences. Flow north of Unimak Pass diverges into an eastward component (the Bering Coastal Current) and a northward component (Aleutian North Slope Current) toward the middle and outer Bering Sea shelf (Fig. 1.1). It has been hypothesized that larvae spawned west of Unimak Pass are potentially influenced by currents that disperse them northward while larvae spawned on the slope are transported along the Eastern Bering Sea shelf towards the Eastern Bering Sea via basin and shelf currents (Lanksbury et al. 2007; Stabeno et al. 1999). In addition, spawning at the Pribilof Islands may occur later than at Unimak Pass due to the presence of ice along the Bering Sea shelf through spring months (Overland and Stabeno 2004). Thus, both current patterns and spawn timing may prevent mixing of Pacific cod larvae spawned at Unimak and those from the

Pribilof Islands area, which may not be unrealistic considering that distinct populations of Atlantic cod exist on much smaller geographic scales (Knutsen et al. 2003).

Further differentiation within the Aleutian Islands

There was evidence for some level of genetic structure within the Aleutian Islands, which corresponds with complex oceanographic forces and range limits for other demersal fish species (Logerwell et al. 2005). Amchitka Pass is the point of allopatric speciation between the Alaska skate (*Bathyrhaja parmifera*) and the congeneric Leopard skate (Spies et al. 2011). Taken together, flow through the central Aleutians (between Samalga and Amchitka Passes) exceeds $8.8 \times 10^6 \text{ m}^3 \text{ s}^{-1}$ and includes two passes over 260 m depth (Hunt and Stabeno 2005). In the Pacific cod data examined here, a strong cline in allele frequency was observed west of Amchitka Pass and several results indicated that a break exists between Great Siskin and Tanaga Islands, an area corresponding to Tanaga Pass. This pattern of genetic variation within the Aleutian Islands was evident with the Wombling and AMOVA analyses, and appeared with the Monmonier algorithm with both datasets but was not highly significant, $p = 0.133$ (2006 N. Amlia dataset), $p = 0.177$ (2007 N. Amlia dataset). A partial Mantel test, which examined the effect of Amchitka Pass on gene flow after accounting for geographic distance, was not significant. Similarly, the number of passes between samples and the depth of the deepest pass between samples had no significant effect on genetic differentiation. Because evidence was equivocal in terms of the exact location of a break, it is unclear whether isolation-by-distance alone or a specific barrier to gene flow is responsible for the observed patterns of differentiation within the Aleutian Islands.

Spawning state

The limited analysis of spawning vs. non-spawning fish did not provide evidence for genetic differentiation between them. Many of the samples were collected without regard to spawning state, and this result seems to indicate that those samples are a sufficient representation of fish that spawn in that area. McQuinn (1997) suggests that juvenile Atlantic herring learn migration patterns and the location of spawning grounds from mature adults. If this were the case for Pacific cod, juveniles would be expected to be related and therefore genetically similar to mature adults in spawning areas. However, the relationship between actively spawning fish and

immature fish on the spawning grounds is an important biological question that deserves further analysis before broad conclusions can be drawn.

Comparative life history

The life history of Pacific cod and the closely related walleye pollock and Atlantic cod may lend some additional insight into the mechanisms responsible for limited gene flow. Walleye pollock and Atlantic cod show very different patterns of genetic population structure. In walleye pollock, significant levels of genetic differentiation have been observed among populations from Asia vs. North America. However, within Alaska, tests for genetic differentiation appear inconsistent and may reflect temporal instability (O'Reilly et al. 2004; Olsen et al. 2002). In contrast, highly differentiated populations of Atlantic cod have been found at fine-scale resolution throughout their range (Bentzen et al. 1996; Knutsen et al. 2003; Pampoulie et al. 2006).

Both larval drift and adult migration are responsible for homogenization of genetic differences. Interestingly, these three species have similar periods of planktonic larval duration. Atlantic cod females produce multiple batches of pelagic eggs from February – April (Knutsen et al. 2007). Once they hatch after 2-3 weeks the larvae are planktonic for approximately 3-4 months (Lough et al. 1989). Walleye pollock spawn multiple batches of eggs in early spring, which diffuse horizontally and hatch after approximately 20 days in the Gulf of Alaska (Hinkley et al. 1991; Brodeur et al. 1996; Laurel et al. 2008). Pacific cod follow a similar pattern, except that each female deposits only a single batch of eggs, which are demersal and slightly adhesive (Sakurai and Hattori 1996; Hurst et al. 2010). After hatching at approximately 20 days in Alaska, Pacific cod larvae are transported towards coastal nurseries, whereas walleye pollock larvae are primarily pelagic, transported considerable distances by coastal currents (Rugen and Matarese 1988; Hinkley et al. 1991; Hurst et al. 2010). Gene flow in Atlantic cod appears to be directly linked to larval drift; eggs are retained in fjords and adults have a strong homing tendency (Stenseth et al. 2006; Knutsen et al. 2007). In walleye pollock, larval drift and migration, coupled with large effective population size, have been used to explain the lack of population structure (Olsen et al. 2002). In Pacific cod, some level of larval retention and homing to specific spawning areas could explain observed levels of genetic population structure (Shimada and Kimura 1994).

Conclusions and management implications

The results of population genetics studies are often difficult to translate into information that is meaningful for fisheries management. However, it is important to understand the impact of population genetics in a management context. Under Sewall Wright's infinite-island model, the number of effective migrants a population receives per generation is related to F_{ST} :

$F_{ST} \approx \frac{1}{4N_e m + 1}$ (Wright 1931). The island model assumes an infinite number of populations,

each with N_e diploid individuals, m migration rate, no selection or mutation, and equilibrium between migration and genetic drift (Wright 1931). In the model, migrants leave each year, form a migrant gene pool, and are randomly assigned to a new population, and the number of individuals refers to effective population size. Clearly, BSAI Pacific cod does not fit the island model; however, the equation relating F_{ST} and effective number of migrants can be used as a rough approximation (Neigel 2002), and the equation has been adapted for the case of two

populations $F_{ST} \approx \frac{1}{16N_e m + 1}$ (Wang 2004). Given that the estimate of F_{ST} between the combined

Aleutian Islands and the combined Bering Sea data is 0.006 (95% CI: 0.005, 0.008), the estimated effective number of migrants is 164 (95% CI: 124, 196). By extrapolating from estimated biomass using average fish weight, an estimate of the total number of cod in the combined Bering Sea and Aleutian Islands is 10^9 , and approximately 9% of the biomass is found in the Aleutian Islands and the remainder in the Eastern Bering Sea (Thompson et al. 2010). Although the ratio between effective and census size has not been determined for Pacific cod, the value is estimated at 4×10^{-5} in Atlantic cod (Hutchinson et al. 2003). Using this conversion ratio, this would imply that the effective size is on the order of 36,000 in the Aleutian Islands and 364,000 in the Eastern Bering Sea. Using the more conservative value of 36,000 results in a migration rate of 0.11% (95% CI: 0.09, 0.13) per generation. Generation time in Pacific cod has been estimated at 6 years; therefore, the current data suggests demographic independence between the Aleutian Islands and the Eastern Bering Sea and far less than 10% migration per year (Canino et al. 2010).

Through 2011, Pacific cod has been managed on a BSAI-wide basis, with a single total allowable catch (TAC) calculated for the entire management area (Thompson et al. 2010). Relative fishery exploitation rates in the Aleutian Islands are higher than in the Eastern Bering

Sea (22% vs. 17%) despite the fact that exploitable biomass in the Aleutians is more than five times smaller (Thompson et al. 2010). Single and multi-species estimates of biomass in the Aleutian Islands indicate that, since the 1970s, populations may have been in decline (Kinzey and Punt 2009), and the 2010 survey estimate for Aleutian Islands Pacific cod biomass is the lowest since the time series began in 1980 (Thompson et al. 2010). Since 2006, the Scientific and Statistical Committee for the North Pacific Fishery Management Council, which manages Pacific cod in the BSAI, has recognized that a precautionary approach to management would be to apportion catch allocations separately for the Eastern Bering Sea and Aleutian Islands. Efforts are ongoing to develop a protocol for such an allocation that minimizes competition among gear types and fairly disperses individual transferrable quotas while ensuring that harvest distribution remains consistent with biomass distribution and harvest strategy. In addition, starting in 2013, a separate age-structured model for Aleutian Islands cod will be prepared and in 2014 the Eastern Bering Sea and Aleutian Islands stock will be managed separately, with separate quotas.

Although previous research has provided evidence that multiple populations of Pacific cod exist in the BSAI (Cunningham et al. 2009), this study provides the most comprehensive evidence to date for genetic distinctiveness and lack of gene flow between the Aleutian Islands and Eastern Bering Sea. In addition, current work indicates that further population structure exists within the Eastern Bering Sea and the Aleutian Islands. The hypothesis that deep passes and current patterns may act as barriers to gene flow and result in complex population structure was partially confirmed. There was evidence that Samalga pass acts as a barrier between the Eastern Bering Sea and the Aleutian Islands but similar barriers were not identified within the Aleutian Islands. There is a strong relationship between geographic distance and genetic distinctiveness indicating low realized dispersal in this species, and the observed genetic differences are suggestive of limited gene flow both currently and historically. Evidence for limited gene flow in Pacific cod, Pacific ocean perch, and northern rockfish (Palof et al. 2010, Gharrett et al. 2012) implies that research on population structure is important for all commercial species in the BSAI, most of which are managed as a single unit, because optimal management units may be smaller than those currently implemented.

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Table 1.1: Northward oceanographic flow rates and depth of selected Aleutian Islands passes (Hunt and Stabeno 2005; Mordy et al. 2005). Flow through Tanaga and Amchitka are reported as combined and flow rate is not known for Buldir Pass.

Pass	Buldir	Amchitka	Tanaga	Amukta	Samalga	Unimak
Flow (m^3s^{-1})	-	4.4×10^6		4.0×10^6	4.0×10^6	1.0×10^5
Depth (m)	640	1155	235	430	200	52

Table 1.2. Sample locations, date, and number of samples at each location. Sample “group” refers to whether the sample is from the Aleutian Islands (AI) or the Eastern Bering Sea (EBS).

<i>Location</i>	<i>Group</i>	<i>Abbreviation</i>	<i>Number</i>	<i>Latitude</i>	<i>Longitude</i>	<i>Date (month/year)</i>
Near Islands	AI	NR	192	52.56°N	174.29°E	2/2005
S. Kiska Is.	AI	SK	96	51.80°N	177.79°E	3/2005
Amchitka Is.	AI	AM	50	51.20°N	179.80°W	2/2005
S. Tanaga Is.	AI	TN	96	51.67°N	178.27°W	3/2005
N. Great Sitkin Is.	AI	GS	118	52.10°N	175.86°W	3/2005
S. Atka Is.	AI	AT	96	51.97°N	174.38°W	3/2007
N. Amlia Is.	AI	A6	96	52.42°N	173.80°W	2/2006
N. Amlia Is.	AI	A7	96	52.28°N	173.69°W	2/2007
Unimak Pass	EBS	UP	96	54.50°N	165.30°W	3/2005
Pribilof Is.	EBS	PR	96	56.83°N	170.00°W	2/2004

Table 1.3. Microsatellite loci used in this study and associated information, in addition to those described in Canino et al. (2005).

<i>Locus</i>	<i>Repeat Sequence</i>	<i>Primer Sequence 5'-3'</i>	<i>Anneal- ing Temp.</i>	<i>Accession No.</i>	<i>Reference</i>
<i>Gmo19</i>	(GACA)	F: CACAGTGAAGTGAACCCACTG R: GTCTTGCCTGTAAGTCAGCTTG	50	AFI159232	Miller et al. 2000
<i>Gmo37</i>	(GACA)	F: GGCCAATGTTTCATAACTCT R: CGTGGGATACATGGGTACT	46	AFI159237	Miller et al. 2000
<i>GmoC82</i>	(TG) ₁₃	F: CCTGGAAGAGAACCCTTTTCA R: GTTTCTTGGGAACCTACATTCCCT ACTCTC	51	50353897	Stenvik et al. 2006
<i>GmoC83</i>	(TG) ₁₁	F: CGGTGCGTTGGATTTTCAT R:GTTTCTTAACTGCTCTCCTGATTTT GTTTT	51	50353980	Stenvik et al. 2006
<i>GmoG5</i>	(AG)	F: GTCTCTTGCCCTACGTTTGTTTCG R: GTTTCTTTTCTGGTTGTGGTGTGC CCTGAC	65	DQ836317	Wesmajervi et al. 2007
<i>GmoG13</i>	(GTCA)	F: ATGCGCTAGACACAGGGCTTGTT R:GTTTCTTGACGGACTGTGTCAGTGT CTGGTG	55	DQ648550	Wesmajervi et al. 2007
<i>GmoG16</i>	(TGTC)	F: GTCTGCACATCTTGGTGCGTGATT R:GTTTCTTTATGGTTTCAATACCGCC GGTTTC	55	DQ648552	Wesmajervi et al. 2007
<i>Tch13</i>	(GT)	F: TTTCCGATGAGGTCATGG R:AATCCACTGGTGCAGACC	54	AF178503	O'Reilly et al. 2000
<i>Tch20</i>	(GA) ₆ GGGAA(GGAA) ₃ GGAT(GGAA) ₂ GGAA T(GAAA) ₁₀ GAA G(GAAA) ₅	F: ACATTGTAAACGGCGATTTC R: TGGTTAGTCTGAGACCCAG	54	AF178509	O'Reilly et al. 2000

Table 1.4. Multi-locus pairwise population differentiation statistics with F_{ST} values above the diagonal and D_{EST} below. Significance for both F_{ST} and pairwise genic test results are given above diagonal: bold indicates significant F_{ST} values and asterisks indicate comparisons with significant genic test values (p -values not shown). F_{ST} and genic test p -values were corrected for multiple tests using the sequential goodness of fit metatest (SGoF) method (Carvajal-Rodríguez et al. 2009). D_{EST} values are the harmonic mean of locus-specific D_{EST} across loci.

	<i>N.Amlia '06</i>	<i>N.Amlia '07</i>	<i>G.Sitkin</i>	<i>Near</i>	<i>Pribilof</i>	<i>Amchitka</i>	<i>S.Atka</i>	<i>S.Kiska</i>	<i>Tanaga</i>	<i>Unimak</i>
<i>N.Amlia '06</i>		0.0017*	-0.0007	0.0009*	0.0023*	-0.0003*	-0.0002	0.0017*	0.0008	0.0019*
<i>N.Amlia '07</i>	0.0006		0.0000	-0.0002	0.0016	-0.0001	0.0003	0.0005	0.0008	0.0028*
<i>G.Sitkin</i>	0.0000	0.0000		0.0000	0.0025*	-0.0003	-0.0003	0.0021	0.0010	0.0006
<i>Near</i>	0.0003	0.0000	0.0000		0.0034*	0.0008*	0.0005	0.0011	0.0001	0.0021
<i>Pribilof</i>	0.0052	0.0000	0.0047	0.0049		0.0006	0.0016*	0.0032*	0.0019	0.0023
<i>Amchitka</i>	0.0000	0.0000	0.0001	0.0007	0.0010		-0.0007	-0.0008	-0.0010	-0.0002
<i>S.Atka</i>	0.0000	0.0000	0.0000	0.0002	0.0005	0.0000		0.0004	-0.0005	0.0013
<i>S.Kiska</i>	0.0002	0.0000	0.0000	0.0001	0.0003	0.0000	0.0000		0.0011	0.0026*
<i>Tanaga</i>	0.0003	0.0005	0.0020	0.0000	0.0007	0.0000	0.0000	0.0001		0.0022
<i>Unimak</i>	0.0008	0.0005	0.0000	0.0002	0.0013	0.0001	0.0002	0.0010	0.0033	

Table 1.5. AMOVA results for all loci: fixation indexes represent average over all loci; F_{ST} , variance of samples relative to total; F_{SC} , variance among samples within groups; F_{CT} , variance of samples among groups (sample abbreviations are from Table 1.2, bold values are significant at the $\alpha = 0.05$ level, asterisks indicate that $p \leq 0.1$, and highlighted lines represent the best grouping pattern).

<i>Grouping</i>	<i>groups</i>	F_{ST}	F_{SC}	F_{CT}
(PR) (UP,A7,A6,AT,GS,TN,AM,SK,NR)	2	0.00235	0.00077	0.00158
(PR,UP) (A7,A6,AT,GS,TN,AM,SK,NR)	2	0.00172	0.00068	0.00105
(PR,UP,A6) (A7,AT,GS,TN,AM,SK,NR)	2	0.00133	0.00079	0.00054
(PR,UP,A7) (A6,AT,GS,TN,AM,SK,NR)	2	0.00124	0.00086	0.00038*
(PR,UP,A7,A6) (AT,GS,TN,AM,SK,NR)	2	0.00106	0.00099	0.00007
(PR,UP,A7,A6,AT) (GS,TN,AM,SK,NR)	2	0.00101	0.00104	-0.00003
(PR,UP,A7,A6,AT,GS) (TN,AM,SK,NR)	2	0.00114	0.00089	0.00025
(PR,UP,A7,A6,AT,GS,TN) (AM,SK,NR)	2	0.00103	0.00102	0.00000
(PR,UP,A7,A6,AT,GS,TN,AM) (SK,NR)	2	0.00111	0.00095	0.00016
(PR,UP,A7,A6,AT,GS,TN,AM,SK) (NR)	2	0.00095	0.00106	-0.00011
(PR) (UP) (A7,A6,AT,GS,TN,AM,SK,NR)	3	0.00207	0.00045*	0.00162
(PR) (UP,A7) (A6,AT,GS,TN,AM,SK,NR)	3	0.00132	0.00077	0.00056*
(PR) (UP,A7,A6) (AT,GS,TN,AM,SK,NR)	3	0.00114	0.00089	0.00024
(PR) (UP,A7,A6, AT) (GS,TN,AM,SK,NR)	3	0.00110	0.00091	0.00019
(PR) (UP,A7,A6, AT,GS) (TN,AM,SK,NR)	3	0.00123	0.00065	0.00058
(PR) (UP,A7,A6, AT,GS,TN) (AM,SK,NR)	3	0.00117	0.00080	0.00036
(PR) (UP,A7,A6, AT,GS,TN,AM) (SK,NR)	3	0.00125	0.00072	0.00052
(PR) (UP,A7,A6, AT,GS,TN,AM,SK) (NR)	3	0.00125	0.00081	0.00044
(PR) (UP) (A7) (A6,AT,GS,TN,AM,SK,NR)	4	0.00162	0.00046*	0.00115
(PR) (UP) (A7,A6) (AT,GS,TN,AM,SK,NR)	4	0.00131	0.00062	0.00068*
(PR) (UP) (A7,A6,AT) (GS,TN,AM,SK,NR)	4	0.00123	0.00061*	0.00062*
(PR) (UP) (A7,A6,AT,GS) (TN,AM,SK,NR)	4	0.00182	0.00012	0.00171
(PR) (UP) (A7,A6,AT,GS,TN) (AM,SK,NR)	4	0.00124	0.00047*	0.00077
(PR) (UP) (A7,A6,AT,GS,TN,AM) (SK,NR)	4	0.00130	0.00039	0.00091
(PR) (UP) (A7,A6,AT,GS,TN,AM,SK) (NR)	4	0.00136	0.00044	0.00092*

Fig. 1.1. Bering Sea and Aleutian Islands (BSAI) with sample locations (black circles), major current patterns (grey arrows), 1,000 m and 100 m depth contours (dark and light bathymetry lines, respectively) and major passes. Islands west of Unimak Pass are considered the Aleutian Island chain. The eastern Bering Sea is north of Unimak Pass along the shelf, which follows the 1,000 m isobath. BSAI and Gulf of Alaska (GOA) management areas are shown in the inset.

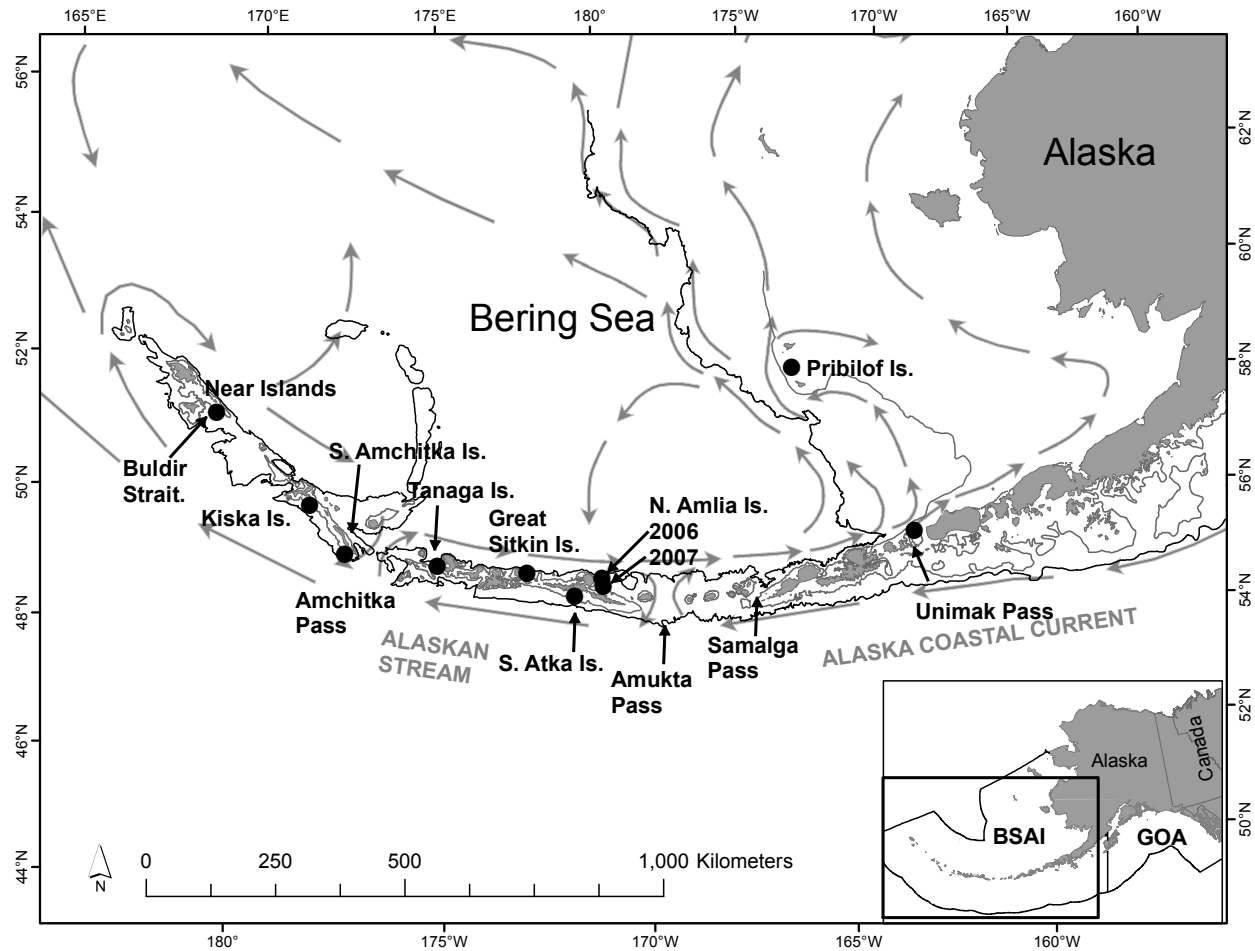


Fig. 1.2. F_{ST} values estimated from 18 microsatellite loci are all within the 95% confidence intervals expected for neutral loci, with the exception of *Gma107*.

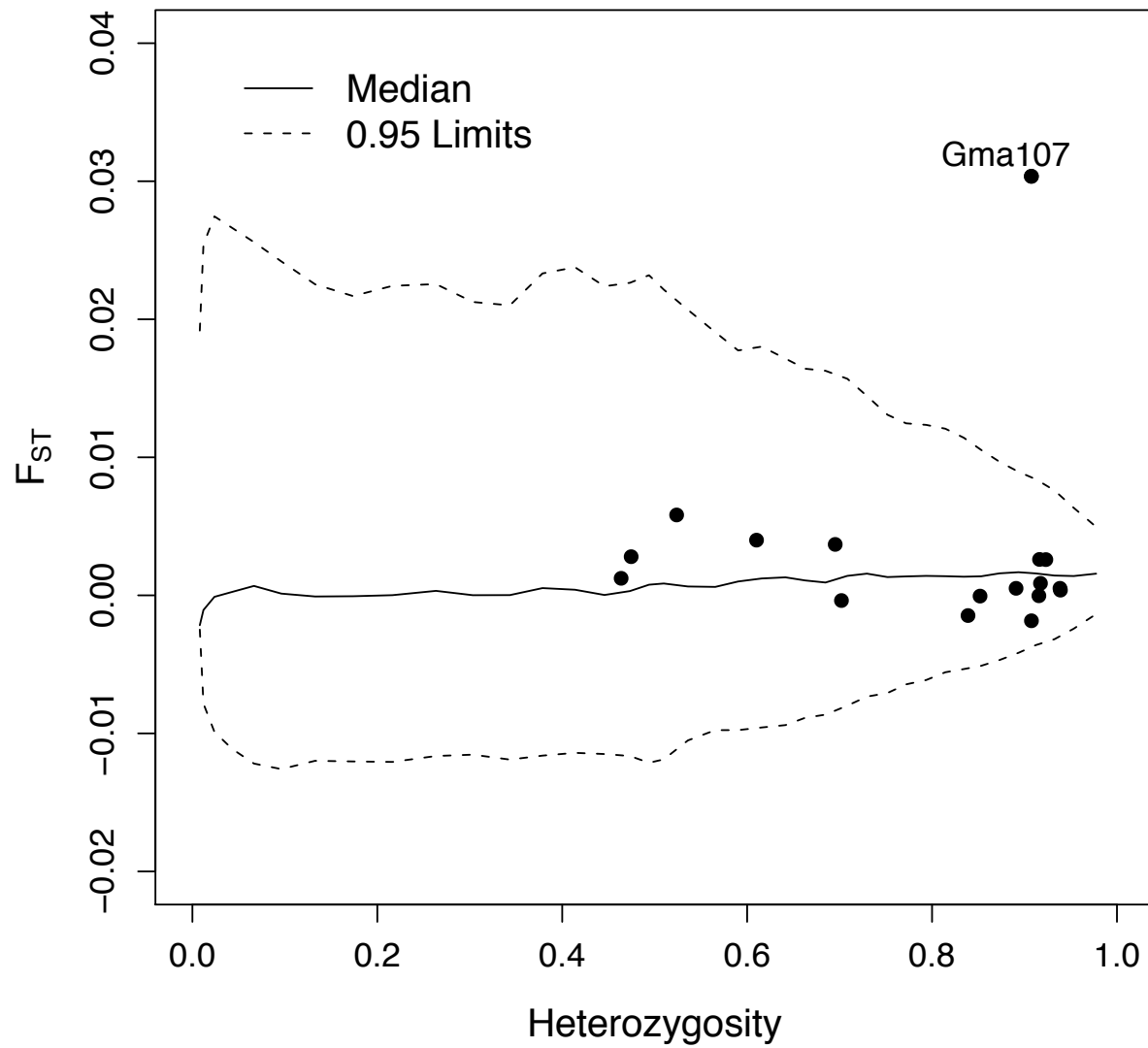


Fig. 1.3. Circles encompass significant AMOVA groupings when $\alpha = 0.05$, and lines represent barrier results. Significance values (representing the probability that the null hypothesis of no barrier is correct), from the 2006 N. Amlia dataset followed by values from the N. Amlia 2007 dataset, were 0.060/0.060 at barrier A, 0.003/0.001 at barrier B, and 0.133/0.177 at barrier C.

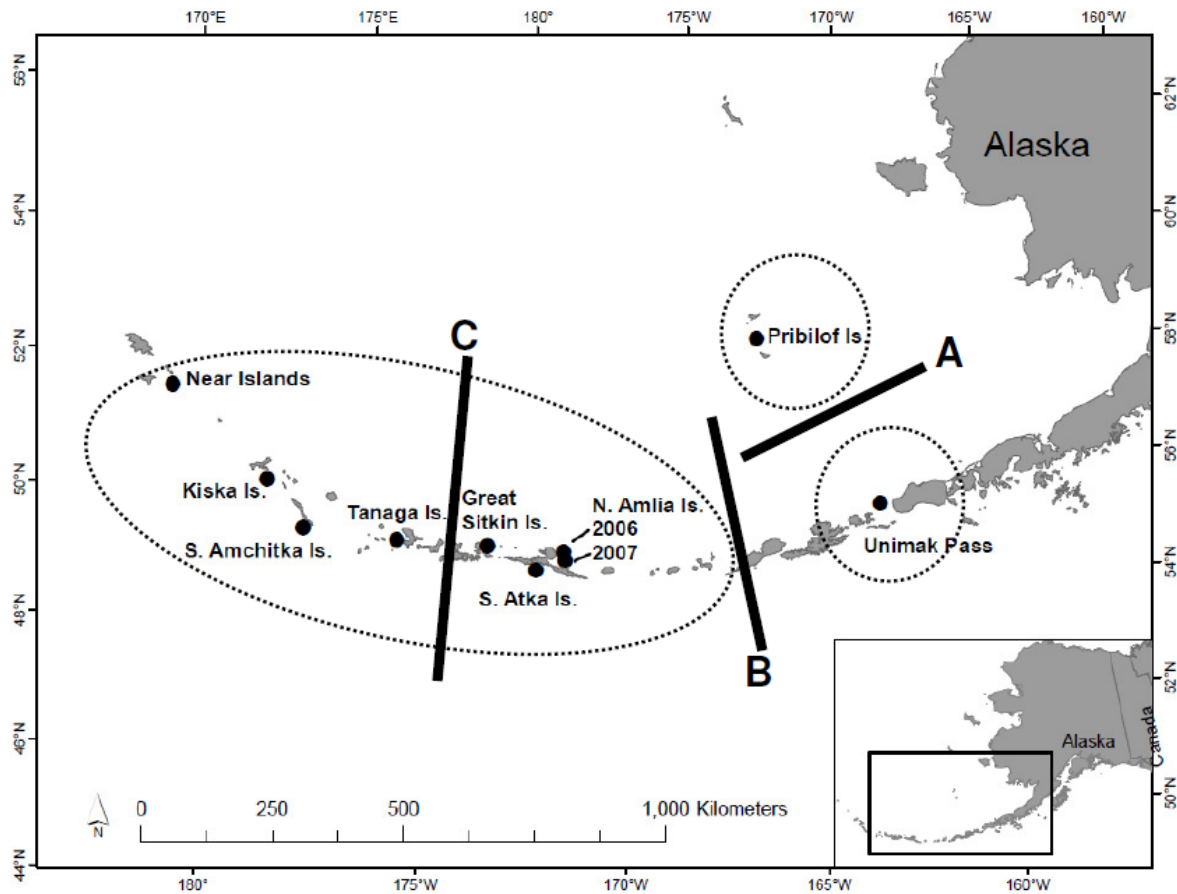


Fig. 1.4. Map of boundary elements that are significant at $p_B = 0.1$ (shown in light grey). Dark grey areas represent regions of no significant change.

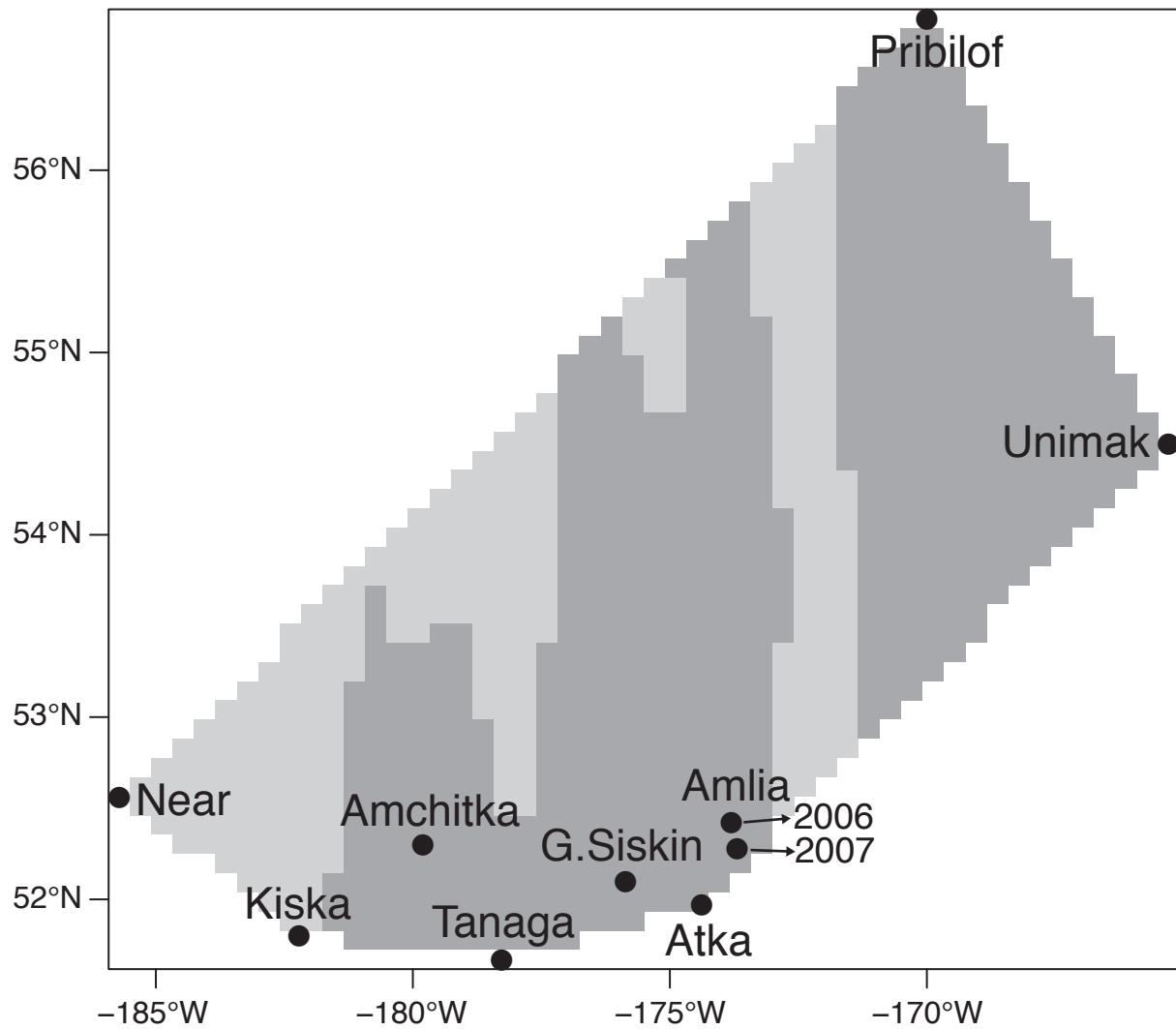
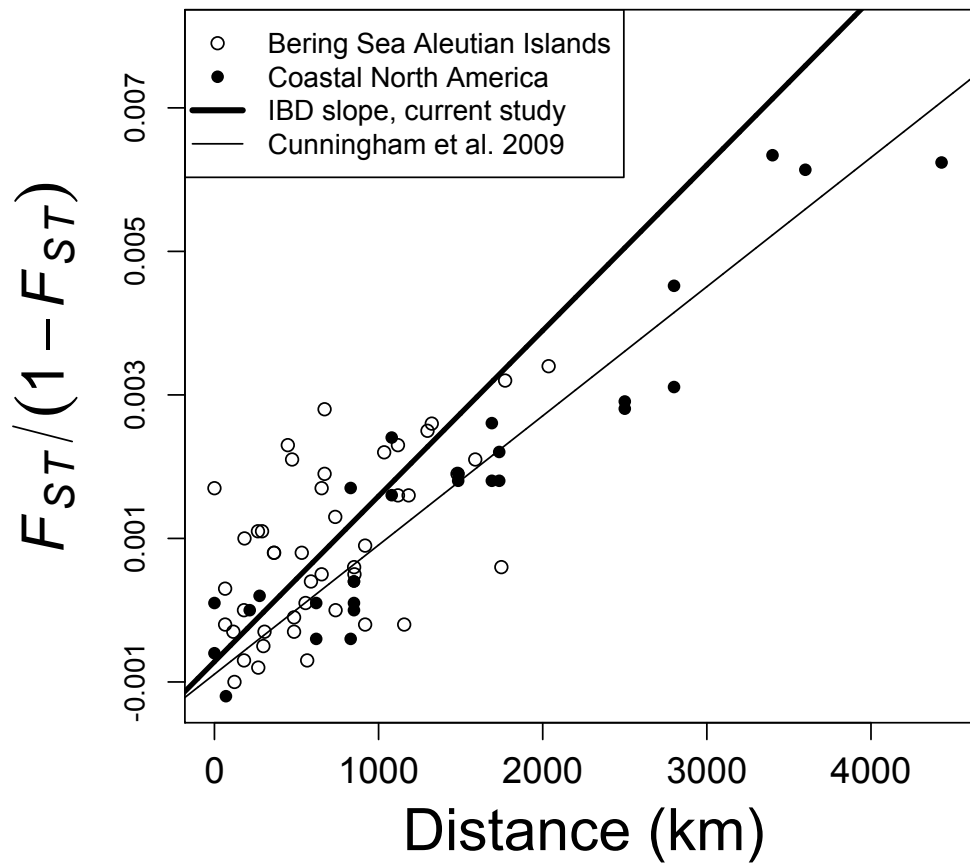


Fig. 1.5. Isolation-by-distance, with genetic “distance” represented by $F_{ST} / (1 - F_{ST})$. The thicker solid line represents the reduced major axis regression line through pairwise samples from the current study (empty circles) and the thin line corresponds to samples from the North American range of Pacific cod (solid circles; Cunningham et al. 2009).

Genetic vs. Geographic distance



Appendix 1

App. Table 1.1. Sample size (N), number of alleles (N_A), expected and observed heterozygosities (H_e and H_o), and estimates of F_{IS} (Weir and Cockerham 1984); significant F_{IS} values after SGoF correction are indicated by bold font.

		Near Is. (192)	S. Kiska (95)	Amchitka (50)	Tanaga (95)	G. Sitkin (117)	S. Atka (95)	N. Amlia 2006 (83)	N. Amlia 2007 (81)	Unimak (95)	Pribilof Is. (95)
<i>Gma100</i>	N	181	83	41	78	110	91	74	59	90	86
	N_A	70	59	44	58	61	58	58	45	57	55
	H_e	0.9749	0.9727	0.9664	0.9721	0.9721	0.9734	0.973	0.9695	0.9733	0.9712
	H_o	0.9724	0.9518	0.9512	0.9744	0.9455	0.956	0.9595	0.9661	0.9667	0.9186
	F_{IS}	0.0054	0.0275	0.0280	0.0042	0.0320	0.0233	0.0207	0.0121	0.0124	0.0600
<i>Gma101</i>	N	178	94	38	87	105	85	74	74	90	64
	N_A	24	22	15	23	22	21	21	22	20	17
	H_e	0.9106	0.9182	0.8979	0.9113	0.9143	0.9066	0.9145	0.9137	0.9022	0.9088
	H_o	0.9101	0.8936	0.9211	0.8851	0.8952	0.8706	0.8919	0.8784	0.8444	0.9063
	F_{IS}	0.0034	0.0322	-0.0125	0.0346	0.0256	0.0457	0.0316	0.0455	0.0695	0.0107
<i>Gma102</i>	N	181	94	48	89	115	90	75	81	93	95
	N_A	15	13	14	14	12	12	13	17	16	14
	H_e	0.8897	0.883	0.8904	0.8847	0.8783	0.8797	0.8875	0.8891	0.8889	0.883
	H_o	0.8564	0.9149	0.8542	0.8764	0.8870	0.9222	0.9333	0.9136	0.8817	0.8316
	F_{IS}	0.0402	-0.0307	0.0512	0.0150	-0.0055	-0.0428	-0.0450	-0.0213	0.0135	0.0635
<i>Gma103</i>	N	176	94	48	92	117	91	77	77	95	82
	N_A	47	38	29	37	39	32	35	29	39	39
	H_e	0.8945	0.9239	0.9269	0.9231	0.9065	0.9121	0.9132	0.8857	0.9058	0.9225
	H_o	0.9091	0.8936	0.8750	0.9130	0.9316	0.9121	0.9351	0.9481	0.8842	0.8902
	F_{IS}	-0.0135	0.0381	0.0664	0.0164	-0.0234	0.0056	-0.0174	-0.0639	0.0291	0.0411
<i>Gma104</i>	N	183	79	49	91	110	88	81	77	94	48
	N_A	28	21	19	25	25	23	23	22	27	16
	H_e	0.9027	0.8964	0.8955	0.8988	0.9102	0.9117	0.9096	0.9133	0.9151	0.8819
	H_o	0.8852	0.8861	0.8980	0.8571	0.9091	0.8977	0.963	0.9091	0.9149	0.8333
	F_{IS}	0.0221	0.0179	0.0075	0.0519	0.0557	0.0211	-0.0525	0.0112	0.0056	0.0656
<i>Gma105</i>	N	187	91	49	92	110	94	78	80	94	81
	N_A	14	9	8	8	8	10	9	9	10	10

<i>Gma107</i>	H_e	0.8414	0.8277	0.8286	0.8233	0.8437	0.8292	0.8328	0.8445	0.8476	0.8349
	H_o	0.8610	0.8132	0.8367	0.8043	0.8000	0.8191	0.7821	0.8375	0.7979	0.8025
	F_{IS}	-0.0205	0.0231	0.0005	0.0285	0.0564	0.0174	0.0673	0.0146	0.0639	0.0450
	N	165	87	49	94	106	85	75	76	93	59
	N_A	21	17	15	21	20	18	17	16	16	15
<i>Gma108</i>	H_e	0.9133	0.8753	0.8884	0.9003	0.9073	0.8932	0.9010	0.9029	0.9014	0.9018
	H_o	0.7636	0.9195	0.8163	0.9043	0.8491	0.7176	0.8267	0.7237	0.9570	0.9492
	F_{IS}	0.1668	-0.0447	0.0913	0.0009	0.0689	0.2022	0.0891	0.2048	-0.0563	-0.0440
	N	187	93	46	95	116	94	82	81	95	95
	N_A	11	9	10	11	14	12	10	10	10	11
<i>Gma109</i>	H_e	0.4349	0.4775	0.5279	0.4619	0.4242	0.4726	0.5066	0.3829	0.4892	0.4622
	H_o	0.4759	0.4946	0.5652	0.4737	0.4052	0.4787	0.5244	0.3704	0.5158	0.4947
	F_{IS}	-0.0916	-0.0304	-0.0598	-0.0201	0.0491	-0.0076	-0.0290	0.0388	-0.0491	-0.0651
	N	174	84	43	86	111	91	74	78	90	80
	N_A	29	28	20	28	28	31	23	25	27	28
<i>Tch20</i>	H_e	0.914	0.9285	0.8997	0.9076	0.9224	0.9374	0.9088	0.9063	0.9132	0.9125
	H_o	0.8736	0.9167	0.9103	0.8721	0.8829	0.9451	0.8784	0.8846	0.9444	0.9125
	F_{IS}	0.0471	0.0187	0.0264	0.0449	0.0473	-0.0026	0.0403	0.0304	-0.0286	0.0063
	N	177	91	48	91	112	83	79	74	93	75
	N_A	25	21	22	24	23	23	21	23	23	22
<i>Gmo37</i>	H_e	0.9362	0.931	0.9249	0.9399	0.9305	0.9358	0.9194	0.939	0.9392	0.9335
	H_o	0.9774	0.9451	0.9167	0.9451	0.9107	0.8795	0.9494	0.9459	0.9247	0.96
	F_{IS}	-0.0412	-0.0096	0.0194	0	0.0258	0.0662	-0.0262	-0.0006	0.0208	-0.0217
	N	188	89	49	94	115	89	78	78	94	73
	N_A	44	37	31	35	36	39	35	34	37	38
<i>GmoG13</i>	H_e	0.9309	0.9354	0.9413	0.9217	0.9305	0.9322	0.9384	0.9303	0.9388	0.9251
	H_o	0.9468	0.8989	0.9184	0.9574	0.9304	0.9551	0.9744	0.9615	0.9149	0.9452
	F_{IS}	-0.0145	0.0446	0.0346	-0.0335	0.0044	-0.0189	-0.0318	-0.0271	0.0308	-0.0148
	N	186	93	49	94	112	94	79	80	88	71
	N_A	12	13	11	13	14	12	12	12	13	10
<i>GmoG16</i>	H_e	0.8471	0.8526	0.8519	0.8585	0.8374	0.8289	0.8519	0.8453	0.8539	0.8414
	H_o	0.871	0.8925	0.898	0.8936	0.8393	0.8617	0.8101	0.8125	0.8068	0.8732
	F_{IS}	-0.0255	-0.0414	-0.0437	-0.0356	0.0022	-0.0343	0.0554	0.0451	0.0608	-0.0308
	N	190	94	49	90	111	94	79	70	90	89
	N_A	6	4	5	5	5	5	4	5	6	3
	H_e	0.4743	0.5332	0.5185	0.5635	0.5064	0.5171	0.4976	0.483	0.5826	0.4992

<i>Gmo19</i>	H_o	0.4632	0.5426	0.5306	0.5667	0.4595	0.4681	0.443	0.4143	0.5667	0.6067
	F_{IS}	0.0262	-0.0122	-0.013	-0.0001	0.0972	0.1002	0.1159	0.1492	0.0329	-0.2099
	N	189	90	49	93	113	90	80	79	90	70
	N_A	30	23	23	27	26	33	28	24	29	21
	H_e	0.9219	0.9119	0.893	0.8898	0.9195	0.917	0.9073	0.9222	0.9262	0.8747
<i>GmoC82</i>	H_o	0.9206	0.9	0.8776	0.828	0.8761	0.9333	0.9	0.9367	0.9444	0.9286
	F_{IS}	0.0041	0.0186	0.0276	0.0749	0.0516	-0.0123	0.0143	-0.0094	-0.0141	-0.0544
	N	190	93	49	94	115	93	80	79	92	80
	N_A	8	5	5	5	5	5	6	6	7	4
	H_e	0.6204	0.6087	0.6187	0.6107	0.5894	0.6089	0.5912	0.5922	0.6434	0.5588
<i>GmoC83</i>	H_o	0.5632	0.5914	0.4898	0.5426	0.5913	0.6022	0.675	0.5823	0.6087	0.5875
	F_{IS}	0.0949	0.0339	0.2182	0.1169	0.0011	0.0165	-0.1355	0.0231	0.0594	-0.0450
	N	190	94	49	94	111	94	81	75	92	91
	N_A	3	3	3	3	3	3	3	3	3	3
	H_e	0.4829	0.4009	0.479	0.4595	0.4972	0.4663	0.48	0.4575	0.5077	0.4731
<i>Tch13</i>	H_o	0.4895	0.3723	0.449	0.5426	0.5405	0.4894	0.4568	0.4667	0.5326	0.5714
	F_{IS}	-0.0109	0.0766	0.0729	-0.1755	-0.0828	-0.0441	0.0546	-0.0133	-0.0435	-0.2026
	N	184	92	49	94	116	91	80	80	94	77
	N_A	9	6	7	7	8	7	7	8	7	7
	H_e	0.7268	0.6779	0.6976	0.7052	0.7323	0.6995	0.6737	0.6697	0.7355	0.666
<i>GmoG5</i>	H_o	0.7065	0.7826	0.7755	0.7128	0.75	0.6703	0.675	0.5625	0.7766	0.6709
	F_{IS}	0.0306	-0.1491	-0.1014	-0.0054	-0.0199	0.0472	0.0043	0.1662	-0.0505	-0.0021
	N	190	93	49	93	116	91	77	79	94	77
	N_A	6	4	4	4	4	4	5	4	5	5
	H_e	0.6869	0.7101	0.6847	0.6909	0.6646	0.7069	0.6767	0.6787	0.6993	0.6861
	H_o	0.6737	0.7527	0.6327	0.7204	0.6724	0.6593	0.6623	0.6456	0.6915	0.7143
	F_{IS}	0.0219	-0.0545	0.0863	-0.0374	-0.0075	0.0727	0.0277	0.0551	0.0165	-0.0345
<i>Genetic diversity</i>		22.41	18.53	15.94	19.24	19.59	19.41	18.41	17.53	19.76	17.76

Chapter 2: Estimating dispersal rates in Skagerrak coastal cod from both genetic differentiation and population dynamics using an individual based model

Abstract

Estimates of dispersal rate are important for managing marine fish stocks, and predicting how they will respond to fishing. Genetic data are commonly used to draw conclusions about dispersal. However, even significant genetic differentiation is difficult to translate directly into a dispersal rate. Interpretation of genetic data can be even more problematic when genetic differentiation is not significant, because it is difficult to determine whether there is complete panmixia or they appear connected using genetic methods due to modest dispersal rates. Here, a genetic individual-based, age structured population dynamics model was used to estimate the relationship between dispersal, genetic differentiation and demographic independence. The method was applied to inner and outer coast Skagerrak vs. North Sea Atlantic cod (*Gadus morhua*), which are connected by uncertain dispersal rates. Results suggest that significant genetic differentiation observed between the North Sea and an inner fjord (Søndeled) was most consistent with 55-80 age-0 immigrants into the inner fjord each year from the North Sea. Observed genetic differentiation between the North Sea and an outer fjord (Risør) was small and not significant; consequently, dispersal estimates were fairly high (1,300-6,000) and indicated that migration from the North Sea impacts the outer fjord demographically. The estimated number of migrants necessary to match empirical levels of genetic differentiation was sensitive to maturity-at-age and Skagerrak population size, depending on the level of genetic differentiation. Estimates of migration were also sensitive to the extent of fishing mortality and fishery selectivity.

Introduction

Dispersal is a fundamental consideration in fisheries management. Dispersal among populations can prevent extinction and aid in recovery from high fishing mortality if immigration is sufficiently high, a concept known as the demographic rescue effect (Brown and Kodric-Brown 1977). Therefore, information on dispersal can be used to determine whether populations could be safely managed as a single stock, or whether managing them separately is advised. When dispersal is limited among populations and multiple populations are managed within a single management unit, inadvertently high fishing effort could take place in some populations (Martien et al. 2013; Chapter 3). Populations that are characterized by low dispersal may have different life history parameters, which can increase the risk of overfishing or lead to sub-optimal yields if differences are unrecognized (Dougherty et al. 2013).

Dispersal is defined differently depending on whether it is applied to genetic or ecological populations. In an ecological population, dispersal is typically defined as the annual migration rate, while dispersal in a genetic population is considered in terms of the number of migrants per generation (Waples and Gaggiotti 2006). Genetic populations showing significant differentiation at neutral genetic markers only exchange a few, but reproductively successful, individuals per generation (Waples 1998). Significant genetic differentiation between populations is generally evidence for distinct stocks (i.e. Taylor 1997). However, lack of significant genetic differentiation may imply anything from complete panmixia to distinct ecological populations (Waples 1998). Populations that are interconnected by low enough dispersal to be defined as ecologically separate populations may exchange too many migrants to allow for genetic differentiation. An upper level of ten percent migration has been suggested as a threshold between an ecologically distinct population and panmixia (Hastings 1993).

Effective migration, migration of individuals that successfully breed in the new population, is difficult to estimate. Mark-recapture and otolith microchemistry can be used to determine movement patterns in both larval and adult life history stages (i.e. Hilborn 1990; Jones et al. 1999), but do not provide information on effective migration. Indirect formulae that are commonly used to estimate effective dispersal are often based on unrealistic assumptions (i.e. Whitlock and McCauley 1999). These formulae are based on ideal populations (Kimura and Ohta 1971). An “ideal” population is defined as a population with constant population size, equal

sex ratio, no immigration, emigration, mutation or selection that would experience the effects of genetic drift and inbreeding to the same extent as the population of interest.

This study uses a simulation approach based on a genetic individual-based population dynamics model incorporating movement, biological parameters, and multilocus microsatellite genotypes to estimate effective and census dispersal when genetic information is available. The model incorporates aspects of a true population, including census sizes, recruitment stochasticity, fishing, and complicated reproductive behavior. Dispersal in the model is estimated by varying the number of migrants until measures of genetic differentiation fall within the range of empirical estimates of genetic differentiation characterized by empirical levels of F_{ST} .

The approach is applied to a case study; dispersal between the North Sea and two fjord populations of Atlantic cod along the Norwegian Skagerrak coast. The North Sea stock of Atlantic cod is assessed by the International Council for the Exploration of the Seas (ICES), and includes the North Sea and the Skagerrak, a strait that reaches from the southeast coast of Norway, to the southwest coast of Sweden and the northern peninsula of Denmark (Areas IV (a, b, c), VII d, and III a; Fig. 2.1, Upper panel; ICES 2012). Numerous fjords reach inland as far as several kilometers along the Norwegian Skagerrak coast, and cod reside both within the fjords (inner fjords) and along the coast (outer fjords; Fig. 2.1, Lower panel). Atlantic cod in the Skagerrak strait comprise approximately 11% of the biomass of the North Sea cod stock. Cod also inhabit the inner and outer fjords of the Skagerrak coast of Norway, and are not included in the ICES, or any other, management plan. Two adjacent fjord populations were chosen for the case study: an outer fjord, the Risør archipelago, and an inner fjord, the Søndeled fjord (Fig. 2.1, Lower panel).

This case study was selected because it includes examples of both significant and non-significant estimates of genetic differentiation; cod from the inner fjord appear to be significantly genetically distinct from the North Sea, but cod from the outer fjord are not, and migration rates are unknown in either case. The empirical values of F_{ST} used here were based on a study using 13 microsatellite loci, in which two samples of 100 adult Atlantic cod from the North Sea, one from 2000/2001 and another from 2002, were compared with a sample of 88 adults from the inner fjord in 2005 and another sample of 101 adults from the outer fjord in 2000 (Knutsen et al. 2011). The F_{ST} estimate between the 2000/2001 North Sea sample and the inner fjord sample was 0.0039 ($p = 0.0013$), while the 2002 estimate was 0.0051 ($p = 0.0001$; Knutsen et al. 2011).

Unlike the inner fjord, it is unknown whether outer fjord cod are distinct from those in the North Sea or whether they represent part of the same population, because measured levels genetic differentiation are not significant at $\alpha=0.05$. The empirical F_{ST} estimate was 0.0001 ($p=0.7022$) between the outer fjord and the 2001 North Sea sample and 0.0003 ($p=0.3414$) with the 2000/2001 North Sea sample (Table 2.1). When juveniles from the outer fjord were pooled with the adult sample, F_{ST} dropped to a range of -0.0002 and 0.0001; therefore, zero was also considered as the level of genetic differentiation between the North Sea and outer fjord in simulation tests examining dispersal rates (P.E. Jorde pers. comm.).

Biological and oceanographic indicators add to the complexity of the situation. Long-term tagging studies suggest that adults are generally sedentary and spawn in the same location every year (Danielssen 1969; Rogers et al. In Press). However, strong currents that extend into the Skagerrak from the North Sea may be a mechanism for one-way dispersal of age 0+ juveniles (Stenseth et al. 2006; Knutsen et al. 2011). Maturity-at-age and growth rates differ between these two regions, possibly due to genetic differentiation, environmental differences or fishing pressure (Law 2000; Heath 1994; Olsen et al. 2005; Fig. 2.2). The goal of this study was to quantify the number of migrants from the North Sea into the inner and outer Skagerrak fjords using a simulation approach that incorporated these ecological and biological considerations. Sensitivity was also examined to changes in assumptions regarding stock size (both North Sea and Skagerrak inner and outer coast), fishing mortality rate, fishing selectivity, and maturity.

Methods

The three simulated populations considered here will hereafter be referred to as NSea-sim (the North Sea), inner-sim (the Søndeled fjord), and outer-sim (the Risør archipelago). A population dynamics model combined with a genetic individual-based model was used as follows. For each simulation, microsatellite alleles were randomly generated at 13 independent loci, based on characteristics of microsatellite loci in Atlantic cod and other marine fish species (Appendix 2). Alleles were assigned to each of two age-structured populations, whose size reflected the actual population sizes as closely as possible (NSea-sim and inner-sim or NSea-sim and outer-sim). In each year, a random proportion of fish, equal to the proportion mature-at-age, were selected as potential spawners. For each new recruit, one male and one female were randomly chosen from the group of spawning fish and the genotype of the new recruit was based on Mendelian

inheritance from parental genotypes. Fishing took place in each year at fishing mortality rates consistent with ICES estimates (ICES 2012). Models were run for an initial 600-year burn-in to achieve migration-drift equilibrium, because migration-drift equilibrium has likely occurred in reality (Appendix 2). Here, migration-drift equilibrium was achieved in fished, rather than unfished, populations for computational efficiency. During a 100-year simulation period, following the 600-year burn-in, F_{ST} was computed every five years using genetic information from every fish in each population. These total population F_{ST} values were used to avoid observation error or imprecision associated with a sample, although in specific cases samples of size 100 were randomly drawn without replacement. Each simulation scenario was replicated 100 times, including simulating new microsatellite markers. F_{ST} values were averaged over time and a coefficient of variation (CV) was calculated between the 100 replicates.

Parameterizing the model

Each population was simulated using a separate age-structured model, with life history parameters based on Atlantic cod in the Skagerrak and North Sea. Standard parameters for all simulations are shown in Table 2.2. The model included seven ages, from zero to 6, with the oldest age inclusive of all ages 6 and above, consistent with the ICES North Sea cod assessment (ICES 2012). Natural mortalities-at-age were also set to estimates from the ICES assessment (ICES 2012; App. Table 2.1). Selectivity-at-age estimates (mean and interquartile range over time) were computed from the annual fishing mortality-at-age (F_{age}) estimates over the years 1963-2011 by dividing all fishing mortality-at-age values for a given year by the highest F_{age} (the fully-selected fishing mortality rate, F_{Full}) in that year (ICES 2012; App. Table 2.1).

In the model, F_{Full} for both populations was randomly generated in each year from a lognormal distribution with variance equal to the assessment estimate, $\sigma^2 = 0.023 \text{ yr}^{-2}$ (ICES 2012; App. Table 2.2). The assessment tends to overestimate fishing mortality (ICES 2012); therefore, the mean fishing pressure for NSea-sim was adjusted from $\mu = 0.896 \text{ yr}^{-1}$ to $\mu = 0.69 \text{ yr}^{-1}$ so that age structure in the simulation model would be consistent with empirical estimates (Knutsen et al. 2011). Reports of fishing mortality are unavailable for the Skagerrak coast; for this component, the F_{Full} was tuned so that the age distribution was similar to that observed for the inner-sim and outer-sim populations (Knutsen et al. 2011; Fig. 2.3). This estimate was also $\mu = 0.69 \text{ yr}^{-1}$ (Table 2.2). Estimates of variability in recruitment were calculated from recruitment estimates in the ICES assessment; the coefficient of variation (CV) of recruitment from 1963-

2011 was 0.75 (App. Table 2.2). Estimates of maturity-at-age and weight-at-age differ between the North Sea and the Skagerrak coast (Heath et al. 2008; Knutsen et al. 2011; ICES 2012); therefore region-specific maturity and weight-at-age parameter values were assigned (Fig. 2.2).

The value for the steepness of the stock-recruitment relationship (h), the fraction of unfished recruits produced when spawning biomass is 20% of its unfished state, was based on work of Myers et al. (1999). This meta-analysis produced estimates of steepness from several Atlantic cod populations ($h=0.84$, 0.76, 0.9 – 20th and 80th percentile, respectively; Myers et al 1999). Steepness affects the number of recruits produced at a given stock size; high steepness allows for more recruits despite low stock size. A range of steepness values was considered in initial model runs. The observed age structure could not be matched with steepness values of 0.84 or less because the high fishing mortality rate resulted in too few recruits to sustain the population. Therefore, the value 0.9 was chosen because it was within the range of the distribution for steepness derived by Myers et al. (1999), and allowed for the observed age distribution to be matched using the model (Fig. 2.3).

The population sizes used in the model were based on estimates from Knutsen et al. (2011). The census size estimate for the inner Søndeled fjord is 1,847 fish, excluding age-0s (Knutsen et al. 2011). Using estimates of survival-at-age from Knutsen et al. (2011), the extrapolated total number, including age-0s is 5,380 (Table 2.2). The number of fish in the outer Risør archipelago was extrapolated from its estimated effective population size (N_e) of 542 (95% CI: 269 - ∞ ; Knutsen et al. 2011). The upper bound of infinity highlights uncertainty in population structure; it is uncertain whether the Risør archipelago comprises a distinct population, or whether it is a component of the North Sea population. The N_e/N_s ratio, where N_s represents the number of spawners, is 0.14 (Knutsen et al. 2011). The N_e/N ratio, or effective to census size ratio, is 0.037 in the inner fjord, given the census size estimate of 5,380 and the estimate of effective population size of 198. If the N_e/N ratio is similar for Søndeled and Risør, this would result in an estimate of 14,971, or roughly 15,000 (2.5% and 97.5% CI: 7,430 – ∞) total individuals in the Risør outer fjord (Table 2.2).

The North Sea Atlantic cod stock was estimated at 54,721 t in 2012 (ICES 2012), or approximately 7.6×10^7 fish. If the estimate of 15,000 fish in the inner fjord population is correct, then the North Sea stock is roughly 5,000 times larger than the outer fjord. Tagging, genetic, microchemistry, and morphometric studies have revealed significant differentiation of cod

populations within the North Sea, suggesting a metapopulation structure with various rates of mixing among the sub-populations (Horwood 2006; Heath 2008). Therefore, some components of the North Sea may interact with the Skagerrak coast while others may not. However, the North Sea cod stock is treated as a single large panmictic population in the simulations.

The model used estimates of census sizes for the Skagerrak populations but simulations of the North Sea cod stock were restricted to a feasible value, 6.4×10^4 fish, approximately 20 times larger than the biomass of the outer fjord (Table 2.2). Sensitivity to this and other population sizes used in the model were examined by varying the size of the North Sea population, as described below.

Unidirectional dispersal at the larval stage from the North Sea to the Skagerrak coast was specified in the model due to the absence of evidence to the contrary. Larvae appear to disperse into the Skagerrak coast from the North Sea, potentially dependent on currents (Knutsen et al. 2004; Stenseth et al. 2006). Dispersal was incorporated only at the larval stage, because adults are generally sedentary (Danielssen 1969; Rogers et al. In Press). Migrants were subject to the same level of fishery selection, fishing mortality, and natural mortality as fish from the recipient population. Dispersal was estimated by varying the annual number of migrants between the North Sea to the Skagerrak from zero upwards until the level of genetic differentiation measured by F_{ST} (averaged over simulations) matched empirical ranges. The ranges are based on empirical results; 0.0039-0.0051 between the inner fjord and the North Sea and 0.0001-0.0003 between the outer fjord and the North Sea (Knutsen et al. 2011; Table 2.1). The smallest amount of dispersal that resulted in $F_{ST} \approx 0$ was also estimated between the inner fjord and the North Sea. This is considered a low estimate of dispersal, because under higher migration, F_{ST} would remain essentially zero. The simulation was repeated 100 times for each level of migration, and the average F_{ST} was compared with the empirical values.

Sensitivity testing

Sensitivity tests were performed to examine the effects of a variety of factors on estimates of dispersal. Effective population sizes were calculated within the model using the following

equation $N_e = \frac{4N_1T}{V_k + 2}$ in order to assess the effect of different sensitivity parameters (Hill 1979;

Appendix 2):

Size of the inner Skagerrak population - Half and double the size of simulated inner and outer fjord populations were examined to determine whether the size of the Skagerrak population would affect the estimated level of migration.

Size of the outer Skagerrak population – Half and double the size of the outer-sim were also examined.

Fishery Selectivity - The effects of a range of fishery selectivity patterns for the North Sea fishery were examined by replacing mean selectivity with upper and lower interquartiles of the mean. Interquartiles higher than 65% resulted in such high mortality on ages 1 and above that the population was too unstable to simulate. Therefore, the 5% and 65% interquartile values were chosen to examine sensitivity to fishery selectivity (App. Table 2.1).

Fishing mortality rate - Decreasing fishing mortality in the North Sea has been a goal of ICES since 2008 when the North Sea Atlantic cod stock reached a record low of 30,000 mt (ICES 2012). In December 2008, the European Commission and Norwegian management agreed on a cod management plan that set the target fishing mortality at 0.4yr^{-1} . North Sea fishing mortality rate in the model was reduced from 0.69 to 0.12yr^{-1} while holding stock sizes constant. This was a greater contrast in fishing pressure than recommended by ICES, and was designed to examine the effect of lower fishing pressure on estimates of migration rates. This change increased the proportion of spawning biomass from <10% to ~40% of the unfished level. This analysis also provided insight into how results would change if stock assessment estimates were biased.

Maturity - The mean estimate of maturity-at-age of Skagerrak cod was replaced with the upper 95% interquartile intervals for maturity-at-age to examine the effect that the number of spawning individuals has on levels of genetic differentiation. Interquartile intervals were calculated using raw maturity data (Knutsen et al. 2011; P.E. Jorde pers. comm.), assuming that maturity data are binomially distributed (App. Table 2.1).

North Sea stock size - Sensitivity to the size of the simulated North Sea cod population was examined, while the size of the simulated outer fjord population, outer-sim, was held constant at approximately 15,000 fish. These runs were used to justify the use of a reduced NSea-sim census size. Runs were performed in which the NSea-sim biomass was 40x and 100x larger than that of the outer-sim to determine whether the number of migrants required to match F_{ST} values between 0.0001 – 0.0003 would change. This sensitivity test was only performed between the North Sea and the outer fjord because lower F_{ST} values are more sensitive to changes in migration.

Further testing: Is migration sufficient for a rescue effect?

A simulated population bottleneck was imposed on the inner and outer fjords during the first 10 years of the simulation following the 600-year burn-in, by reducing the number of fish in each age class to four individuals. The number of migrants each year was set to the more conservative lower end of the estimated range (55 for the inner fjord and 1,300 for the outer fjord), and fishing continued at the same rate (Table 2.2). The population size was monitored to determine whether migration was sufficient for the population to recover. Genetic differentiation, measured by F_{ST} , was monitored every 5 years. The high steepness value of 0.9 used in the model ensures that recruitment will occur despite small population sizes. Therefore, the number of migrants was also set to zero, to assess the change in the time required for population sizes to reach their unfished values with and without migration, and how genetic differentiation would change over time.

Results

Dispersal

Simulations were performed using a range of migration from the North Sea to the inner and outer fjords. The best estimates of migration were considered to be those that resulted in average simulated F_{ST} values that matched the empirical F_{ST} values in Table 2.1. Resulting average values over 13 simulated microsatellite loci (Tables 2.3 and 2.4) were compared with empirical F_{ST} estimates using 13 microsatellite loci (Table 2.1). Results from simulations using basic parameters are shown on the first lines of Table 2.3 (North Sea vs. inner fjord) and Table 2.4 (North Sea vs. outer fjord). Subsequent lines in Tables 2.3 and 2.4 provide estimates of migration

for simulations in which sensitivity to a variety of parameters was explored.

Model results suggested that 55-80 age-0 census migrants enter the inner fjord from the North Sea every year (Table 2.3). This range represented 1.6-2.3% of the average 3,450 age-0 cohort in the inner-sim population, and 1-1.5% of the total population of 5,380 individuals. Lower migration resulted in higher F_{ST} values; at 55 migrants per year from the North Sea, mean F_{ST} over 100 simulations was 0.0051 (5%, 95% CI: 0.0049, 0.0053) between the inner fjord and the North Sea, while at 80 migrants per year, F_{ST} was 0.0040 (5%, 95% CI: 0.0038, 0.0042; Table 2.3). Dispersal from the North Sea to the outer fjord was estimated to be 1,300-2,800 migrants per year (Table 2.4). The lower end of the range (1,300 migrants) was associated with mean F_{ST} values of 0.00030 (5%, 95% CI: 0.00028, 0.00032), while 2,800 migrants resulted in F_{ST} values of 0.00010 (5%, 95% CI: 0.00009, 0.00011). This was a large contribution (11-20%) to the age-0 cohort. Higher migration reduced F_{ST} to close to zero; zero was within the confidence interval (5%, 95% CI: -0.00001, 0.00001) of 100 simulated F_{ST} estimates when 6,000 migrants entered the outer fjord from the North Sea (Fig. 2.4). This represented a high proportion of the age-0 fish outer fjord cohort, 9,544 on average. However, the nature of the model and the limited number of mature individuals at each age allows for only a small proportion (13%) of individuals in the population to spawn (App. Table 2.1).

Sensitivity to the specifications of the analyses

Changes to certain parameter values affected the estimated range of migrants, as described below.

Size of the inner Skagerrak population – Changes to the size of the inner fjord population did not affect the estimated number of migrants required to achieve empirical levels of genetic differentiation. The range did not change significantly at half or double the estimated size of the inner fjord, and no trend was observed (Table 2.3).

Size of the outer Skagerrak population – The relationship between migration, genetic differentiation, and population size of the outer fjord was different than that for the inner fjord. The estimated number of migrants required to achieve empirical levels of genetic differentiation was sensitive to size of the outer fjord population. At half the estimated size of

the outer fjord, 7,500 fish, the estimated number of migrants ranged from 1,000-1,800, whereas at double the estimated size, 30,000 fish, the estimate number of migrants increased to 1,800-3,600 (Table 2.4).

Fishery Selectivity - Varying fishery selectivity-at-age in the North Sea population affected its relative age structure (Fig. 2.5). The number of older fish in the population increased when mean selectivity was replaced with the lower 5% interquartile, and the N_e/N ratio increased in the North Sea (Fig. 2.5). There was a less significant decrease in the number of older fish when mean selectivity was replaced with the upper 65% interquartile. Lower selectivity did not change the estimated number of migrants required to achieve empirical levels of genetic differentiation in the inner fjord (from 55-80 to 56-75), but did reduce the number slightly in the outer fjord, from 1,300–2,800 to 1,150-2,500 (Tables 2.3 and 2.4). Higher selectivity increased the number of migrants estimated to be required to achieve empirical levels of genetic differentiation, and decreased the N_e/N ratio in the North Sea. The number of migrants between the NSea-sim and outer-sim increased from 1,300–2,800 to 1,500-3,000, and from 55-80 between the inner-sim and NSea-sim to 68-80.

Fishing mortality rate – A lower fishing mortality rate changed the age structure of the North Sea population by allowing more fish to reach older ages, and increased the N_e/N ratio (Fig. 2.5). Because it increased the survival rate, it also increased the generation length from approximately 2.9 to 4.6 years. Decreasing the North Sea fishing mortality rate decreased the number of migrants estimated to be required to achieve empirical levels of genetic differentiation, in both the inner and outer fjord. The estimated number of migrants dropped from 55-80 to 48-69 between the inner-sim and the NSea-sim (Table 2.3), and from 1,300-2,800 to 1,000-2,000 migrants between the outer-sim and the NSea-sim (Table 2.4).

Maturity – Fewer migrants were required to achieve the same level of genetic differentiation when maturity-at-age was high in the Skagerrak population, and increased the N_e/N ratio in the Skagerrak populations. The number of migrants shifted from 55-80 to 49-71 for the inner fjord (Table 2.3) vs. N. Sea comparison and from 1,300-2,800 to 1,200-2,600 for the outer fjord vs. N. Sea comparison (Table 2.4). High maturity-at-age was applied to the inner and

outer fjord rather than the North Sea. More migrants were allowed to spawn; therefore fewer migrants were required for the same level of genetic differentiation.

North Sea stock size –The estimated number of migrants required to produce empirical levels of genetic differentiation between the outer-sim and the NSea-sim was not sensitive to increases in the size of the NSea-sim. The range did not change significantly for all population sizes examined (Table 2.4).

Is migration sufficient for a rescue effect?

The population biomass of both the inner and outer fjords recovered to their original size approximately 15 years following the end of a simulated population bottleneck, given conservative estimates for migration (55 between the inner fjord and North Sea and 1,300 between the outer fjord and North Sea; Figs. 2.6a, b). There was no difference in the rate at which recovery occurred when there was no migration (Figs. 2.6a, b vs. Figs. 2.6c, d), suggesting that migration would play a small role in recovery of the stock if an extreme bottleneck occurred. Levels of genetic differentiation increased significantly during and after the bottleneck (Fig. 2.6e, f, g, h). Genetic differentiation measured by F_{ST} reached a peak approximately 20 years after the bottleneck and slowly declined for the rest of the simulation, although it did not decrease as low as levels prior to the bottleneck (Fig. 2.6e, f, g, h; Appendix 2). F_{ST} increased from a mean of 0.00032 before to 0.01546 after the bottleneck between the outer fjord and the North Sea and from 0.0051 to 0.0157 between the inner fjord and the North Sea, due to increased genetic drift during the population bottleneck (Fig. 2.6e, f). Ordinarily, genetic differentiation would remain stable over time. Although F_{ST} values decreased after they reached a peak, there was not enough time for F_{ST} to decline to the pre-bottleneck level because more time was required to achieve equilibrium between genetic drift and migration (Appendix 2). Genetic differentiation increased to a greater extent during the population bottleneck when there was no migration (Fig. 2.6e vs. 2.5g and Fig. 2.6f vs. 2.5h). This was expected because lack of migration will increase genetic differentiation between populations, both before and after the bottleneck. Genetic differentiation decreased slowly following the bottleneck as the size of the inner (Fig. 2.6e, g) and outer (Fig. 2.6f, h) fjord populations increased. Genetic differentiation decreases more rapidly when there is no migration (Fig. 2.6e, f vs. Fig. 2.6g, h), but it never achieves levels

as low as when there is migration.

Discussion

This study illustrates an alternative to analytical formulae for estimating dispersal between two groups from genetic data. Estimates of dispersal are based on simulations that incorporate population dynamics and biological parameters. The simulation approach allows for much more flexibility than standard formulae, and can be tailored to two populations of unequal population size, population-specific parameters, and specific characteristics of migration, such as one-way dispersal at the larval stage. A similar approach has been taken to estimate dispersal among groups of western North Pacific minke whales (*Balaenoptera acutorostrata*), given observed rates of genetic differentiation, measured with mitochondrial DNA (Taylor and Martien 2004). The current study extends this type of evaluation to microsatellite markers and explores sensitivity to a variety of factors.

The case study focuses on Atlantic cod migration rates between the North Sea and the Norwegian Skagerrak inner and outer fjords, and provides insight into the behavior of genetic differentiation between two age structured populations connected by migration. The number of migrants between two populations at a given level of differentiation is sensitive to maturity-at-age and fishing mortality rate. The number of migrants is only slightly sensitive to population size and fishery selectivity; sensitivity to these parameters was only observed when F_{ST} was very small (0.0001 – 0.0003). The simulation approach provides a mechanism to account for these parameters, and may be worth the extra effort given their relevance.

A commonly employed method for estimating migration rates from genetic data is based on the assumptions of Wright's island model (Wright 1931; Whitlock and McCauley 1999). That model provides a relationship between the number of migrants into a population every generation and F_{ST} : $F_{ST} \approx 1/(4N_e m + 1)$, hereafter referred to as Wright's equation. Wright's island model assumes an infinite number of equally sized populations with random breeding within populations, non-overlapping generations and no mutation or selection. In addition, differentiation is assumed to be at equilibrium between genetic drift and migration (Waples et al. 1998; Whitlock and McCauley 1999). This model does not account for unequal population sizes or unidirectional migration. A version of this equation was derived in Hössjer et al. (2013, Eqn. 27) which accounts for a finite number of subpopulations of unequal size, s :

$$F_{ST} \approx \frac{1}{\frac{s}{s-1} 2\tilde{N}(1-(1-m)^2 - \frac{1}{2N_e}) + 1}, \text{ where } \frac{1}{\tilde{N}} = \frac{(1-m)^2}{N_e} + \frac{2m-m^2}{N}, \text{ and } N_e \text{ and } N \text{ are}$$

harmonic means of the two populations compared. Simulations indicated that this equation provides a close approximation of F_{ST} when mean unidirectional migration from the North Sea to the outer fjord was used (Per Erik Jorde pers. comm.). The F_{ST} estimates of 0.0001 between the North Sea and outer fjord and 0.005 between the North Sea and inner fjord were applied to this equation. Results estimate $N_e m$ from the North Sea to the inner and outer fjords to be 25.5 and 542 respectively, or $m = 0.13$ and 1. This contradicts the idea that if $m=1$, F_{ST} should be zero; this discrepancy may be due to stochasticity in allele frequencies in natural populations or sampling effects that cannot be represented in the Hössjer equation. If the N_e/N ratio in the model is applied to the estimate of $N_e m=25.5$ for the outer fjord comparison, then a rough estimate of the census migrants in the model would be 89, which is not far from the estimate in the present study (55-80). Other estimates for N_e/N are lower than those of Knutsen et al. (2011), and would provide lower estimates for census migrants (i.e. Therkildsen et al. 2010).

A genetic simulation experiment based on sequence data in natural populations revealed the stochastic nature of genetic systems (Taylor et al. 2000). Results showed that ϕ_{ST} , the analog for F_{ST} based on DNA sequence data, varied greatly over time. Management decisions could change over time based on random variation in estimates of genetic differentiation. Stochasticity in genetic differentiation over time was also observed in the current study, but was lower than the ϕ_{ST} results, due to the added statistical power of multiple loci. The CV of F_{ST} values among simulations was generally lower on average over all simulations and all tests for inner-sim vs. NSea-sim comparisons, 0.19, than for outer-sim vs. NSea-sim comparisons, 0.39. The effect of this stochasticity on management decisions was not examined here.

Specific migration rate estimates

There is much uncertainty regarding the population size of the outer fjord cod stock and its relationship to the North Sea. Genetic differentiation between the outer fjord and the North Sea has been found to be low and not statistically significant at $\alpha = 0.05$ (Table 2.1). However, the level of genetic differentiation between the North Sea and the inner fjord is significant, and estimates of population size are more precise. Relatively little migration appears to take place between the North Sea and the inner fjord. Simulations estimate that between 50-80 age-0 larvae

enter the inner fjord each year. Between 20-33 of these are expected to survive past their first year, and only 10-16 are expected to spawn, out of a total of 704 spawning fish on average. These do not represent “effective” migrants, rather the number of age-0 migrants expected to be selected as potential spawners. One male and one female are selected from potential spawners as parents of each offspring in the model, and there is variability associated with spawning success.

Similarly, for the outer fjord, the model estimates that approximately 1,300-2,800 age-0 migrants enter the outer fjord each year from the North Sea, based on observed F_{ST} values of 0.0001 and 0.0003 (Table 2.1). Of these, 758-1,634 will likely survive past the first year and only 266-573 will spawn, out of 1,952 spawning fish. Thus an average of 14 to 29% of the fish that spawn in the outer fjord each year is estimated to be of North Sea origin. This percentage is above the ten percent that has been considered as the threshold migration rate between ecological populations (Hastings 1993). Therefore, the population dynamics of the outer fjord is likely to be affected by larval drift from North Sea, as was found by Stenseth et al. (2006). Estimates of migration between the North Sea and the outer fjord are sensitive to the size of the outer fjord population. Larger population size would imply more migrants, but the migration rate does not increase proportionally with population size; if the outer fjord population size is 7,500 the migration rate is estimated between 13-24% of the total population size, whereas if the population size is 30,000, the migration rate is estimated to be much lower, between 0.06 – 0.12. $N_e m$ should stay constant given a certain F_{ST} , based on Wright’s equation, so increases in N_e result in decreases in m . However, the model is not based on ideal populations, and the migration rate decreases as effective size increases.

The true level of genetic differentiation between the outer fjord and the North Sea may be zero, which would imply that migration might be higher than 1,300-2,800 estimated using the empirical range of F_{ST} estimates, 0.0001-0.0003 (Table 2.4). Both non-significant F_{ST} values and the pooled juvenile and adult samples from the outer fjord suggest that F_{ST} may be zero, although the pooled sample has a higher proportion of juveniles (80%) than is found in the population (approximately 66%). An F_{ST} of zero could occur with migration as low as 6,000 individuals per year. Regardless of the true F_{ST} value or population size, the percentage of immigration is above the ten percent “threshold”, and likely to impact the recipient outer fjord demographically.

Estimates of migration from the current simulation are higher than previous estimates of dispersal between the North Sea and outer fjord; Stenseth et al. (2006) concluded, based on the

island model and observed average $F_{ST} = 0.0023$ among coastal populations, that 60,000 age-0 larval immigrants per fjord each generation enter the Skagerrak coast from the North Sea and 108 (95% CI: 71 to 227) will survive until adulthood (age 2+). The natural mortality-at-age values used in the present simulation are based on samples taken in the fall (Knutsen et al. 2011), whereas Stenseth et al. (2006) used estimates based on April samples, both from the Skagerrak region. Therefore, the estimate of 60,000 would be subject to high natural mortality rates between spring and fall, and would decline significantly. Due to this discrepancy, the number of adults is used for comparison rather than the number of age-0s. In the present study, 1,300-2,800 age-0 immigrants are estimated to enter the outer fjord from the North Sea each year, 758-1,634 migrants live past the first year, and between 145-312 of these survive past age 2+, compared to 27 per year estimated by Stenseth et al. (2006).

Sensitivity testing

The number of migrants required to achieve observed levels of genetic differentiation was more sensitive to changes in the size of the outer fjord than the size of the inner fjord population. The level of genetic differentiation between the inner fjord and the North Sea populations is much higher than that of the outer fjord and North Sea populations; $F_{ST} = 0.0039-0.0051$ vs. $0.0001-0.0003$; this was a key factor in the different responses to population size. Dispersal estimates are more variable when F_{ST} is low; Wright's equation illustrates why this is so. This relationship is a hyperbolic function in the first quadrant of the Cartesian coordinate system, with the number of effective migrants, $N_e m$, on the x-axis and F_{ST} on the y-axis (Fig. 2.7). The plot asymptotes at small values of $N_e m$ and F_{ST} , so for very small values of F_{ST} , there is a very large range of over which $N_e m$ could be chosen.

Sensitivity tests indicate that the number of migrants depends on selectivity-at-age, fishing mortality rate, and maturity-at-age. All tests were performed while holding stock size constant. Both selectivity-at-age and the fishing mortality rate affected the age structure of the population (Fig. 2.5), while maturity-at-age affects the number of individuals available to contribute genes to the next generation. These resulted in changes to the ratio of effective population size to census size (Tables 2.3 and 2.4). Wright's equation shows that F_{ST} is sensitive to the number of effective migrants, and changes to the number of migrants in sensitivity testing of selectivity, fishing mortality rate, and maturity are due to changes in the N_e/N ratio. Therefore, these are all important parameters to include when performing simulations such as these, and the accuracy of

the estimates may make a difference. The modeled populations are likely subject to less reproductive stochasticity than in reality; therefore, the N_e/N ratios generated from the model are likely higher than true values (i.e. Frankham 1995). However, they are accurate on a relative scale so only the relative changes in N_e/N are considered in sensitivity testing.

Fishery selectivity also plays a large role in estimating the number of migrants. High fishery selectivity in the NSea-sim population reduced the N_e/N ratio; because fewer larvae survive to spawn; so more migrants were required to achieve the same levels of genetic differentiation. Low fishery selectivity had the opposite effect on the NSea-sim population, by increasing the N_e/N ratio. Therefore, fewer migrants were required to transfer the same level of genetic diversity between the populations. This effect was more apparent in comparisons between the outer fjord and the North Sea than the inner fjord.

Recovery following a population bottleneck

The population bottleneck test was designed to examine how dispersal affects the relationship between the North Sea and the Skagerrak. High steepness allows a population to produce many offspring at even low population sizes, and a fairly high steepness was chosen in the simulation to achieve the empirical age distribution. A control experiment with no migration showed that the reproductive capacity of few individuals due to high steepness values is sufficient for demographic rescue to occur when the inner and outer fjords experience population bottlenecks (Fig. 2.6a, b). Results may not be realistic; steepness may be artificially high and depensation, although not considered in the model, could play a role in preventing recovery from a population bottleneck. It has also been hypothesized that recolonization of an empty niche may occur faster because there is no intraspecific competition (Waples 1998). In reality, Atlantic cod populations along the Skagerrak coast are severely depleted due to fishing, despite evidence for migration from the North Sea (Cardinale and Svedäng 2004.). Thus, there may be factors responsible for declines in population size despite suspected migration into the inner and outer fjords.

Migration and mutation-drift equilibrium

When a single population is split into two or more populations with limited genetic exchange, the populations begin to drift independently, and genetic differentiation, such as that measured by F_{ST} , will increase. Eventually, the combined effects of genetic drift and migration, as well as mutation, are expected to result in an equilibrium state at which the populations no longer

diverge. This has likely occurred between the Skagerrak and North Sea. The last glacial maximum took place in the northeast Atlantic 21,000 years ago (Mix 2001; Kettle et al. 2011). This corresponds to 5,000 Atlantic cod generations if the generation length is 4.2 years (Knutsen et al. 2011). Migration-drift equilibrium generally takes place in a shorter period than mutation-drift equilibrium, and the number of generations for F_{ST} to move halfway to the equilibrium

value is $T_{50} = \frac{\ln(0.5)}{\ln[(1-m)^2(1-1/(2N_e))]}$ (Whitlock 1992). In the case of unequal population sizes,

the single N_e in this equation can be estimated by the harmonic mean of the effective population size of each population. Low estimates for the number of migrants were used here because they provide the most conservative estimates (longest time until T_{50}); 1 migrant per generation for N. Sea vs. inner fjord and 10 migrants per generation for N. Sea vs. outer fjord. Effective population sizes for the inner and outer fjords were based on Knutsen et al. (2011); 542 for the outer fjord and 198 for the inner fjord. The N_e/N estimate of 0.14 from Knutsen et al. (2011) was applied to the North Sea census size of 7.5×10^7 . Current population size estimates are likely smaller than unfished, historical population sizes. T_{50} would be achieved in 1,372 generations between the N. Sea and the inner fjord and in 683 generations between the N. Sea and the outer fjord if historical population sizes were 20 times larger than current sizes, which is likely a conservative overestimate. Both cases suggest that migration-drift equilibrium has been reached in the North Atlantic cod since the last glacial maximum, using the estimate of 5,000 generations. The time until mutation-drift equilibrium can be estimated by $4N_e$ (Hartl and Clark 1988). In reality, most species are not expected to be at equilibrium between mutation and drift (Hartl and Clark 1988), and this study reflects such expectations.

The model

The model was designed to construct a framework as close as possible to the true Skagerrak and North Sea populations, with the caveat that it be computationally feasible to form the basis for analyses. The assumption of one-way larval dispersal is based primarily on tagging studies over many decades, which suggest that adults are generally very sedentary. Out of 3,302 recaptured individuals (from 9,528 tagged in three coastal areas), 25 were found in the North Sea, but the majority did not move out of the 20 km region where they were tagged (Rogers et al. In Press). An earlier study in which 1,244 cod were tagged in the Skagerrak coast led to 367 recaptures, the majority (82%) of which did not move from the Skagerrak coast (Danielssen 1969). In that

study, 13.6% of captures outside their tagging location were caught in the North Sea and 4.7% in the Kattegat, the extension of the Skagerrak bounded by Sweden and Denmark. These movements were highest in summer, and lowest during the winter spawning period, possibly suggesting that migrations outside the Skagerrak were temporary, and that fish returned to the Skagerrak to spawn (Danielssen 1969).

In the model, a proportion equal to the maturity-at-age of each age class spawns, while other individuals do not spawn. Each spawning individual has an equal chance to reproduce, and therefore an equal, but random, chance of contributing to the next generation. This may not be realistic; it has been suggested that older individuals may have a higher probability of successful reproduction than younger individuals (Knutsen et al. 2011). While this is not directly incorporated into the model in terms of older fish producing more larvae than smaller ones, older fish do have higher lifetime reproductive success than younger ones. The patterns observed here are not likely to change if older individuals were more fecund than younger ones.

Extending the model

Although examples here were limited to Atlantic cod in a specific region, conclusions can be extended to species with different life history parameters, such as steepness, age structure, population size, and maturity-at-age. Atlantic cod in the North Sea and Skagerrak rarely live past seven years. For species that are longer-lived, there may be more individuals that contribute to the gene pool. If so, these species would experience less genetic drift when populations were small, and fewer migrants would result in significant levels of genetic differentiation. However, the number of mature individuals is not always related to the age structure of the population; Pacific cod in the Eastern Bering Sea can live until age 20 but only 6.6% of the total population is reproductively mature on average (Thompson and Lauth 2012). The level of steepness considered here is higher than for many other commercially exploited marine fish species; gadidae (0.79), clupeidae (0.71), and enraulidae (0.62) (Myers et al. 1999). Lower steepness implies that fewer recruits will be produced when the population size declines; therefore, other species may be less resilient to population bottlenecks such as the ones simulated here (Fig. 2.6).

Here, a large population was compared with a smaller one. However, results may be different in larger populations or populations of equal size. F_{ST} typically depends on the quantity $N_e m$ (Wang 2004). The relationship between F_{ST} and $N_e m$ can be observed in the inverse relationship between the N_e/N ratio and the absolute number of migrants in Tables 2.3 and 2.4, although

simulation results indicated that this is not a direct relationship in a non-ideal population. If the (harmonic) mean of the effective population size increased, as it likely would in the case of equal population sizes or larger populations, the migration rate would decrease for the same level of genetic differentiation.

Summary

This study examined dispersal from the North Sea to the Skagerrak inner fjord and outer fjord using a simulation framework. Only 1-2% of the inner fjord age-0 cohort appears to be from the North Sea. Statistically significant levels of genetic differentiation between the North Sea and the inner fjord support this result. Estimates of migration into the outer fjord from the North Sea are higher and span a wider range, given some uncertainty in the level of genetic differentiation between these populations. If the estimate of $F_{ST}=0.0001-0.0003$ is accurate, then the model suggests 1,300-2,800 migrants per year from the North Sea to the outer fjord. If F_{ST} is zero, then at least 6,000 larval migrants could enter the Skagerrak from the North Sea, annually, based on natural mortality-at-age values from samples taken in the fall (Knutsen et al. 2011). All estimates of migration from the North Sea indicate that greater than 10% of the spawning population originates in the North Sea; therefore migration is likely to have a demographic influence on the outer fjord.

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Table 2.1: Empirical levels of genetic differentiation, measured by F_{ST} , between Atlantic cod samples from 1. the North Sea (2000/2001 and 2002 sample) and the inner fjord (2005 sample) and 2. the North Sea (2000/2001 and 2002 sample) and the outer fjord (sample from 2000). Asterisk * indicates statistical significance at $\alpha = 0.05$ (Knutsen et al. 2011; Per Erik Jorde, C.E.E.S., pers. comm.).

Comparison	SNPs (7,457 loci)	Microsatellites (13 loci)
N. Sea vs. inner fjord	0.0164-0.0565*	0.0039 ($p=0.0013$), 0.0051 ($p=0.0001$)
N. Sea vs. outer fjord	0.00012-0.00583	0.0003 ($p=0.3414$), 0.0001 ($p=0.7022$)

Table 2.2: Parameter values used in all simulations unless specified otherwise.

Parameter	Inner and outer fjord	N. Sea
Census population size	5,380 and 15,000	6.4×10^4
Fishing mortality	0.69 yr^{-1}	0.69 yr^{-1}
Between-year variance in fishing mortality	0.23	0.23
Length-at-age	App. Table 2.2	App. Table 2.2
Maturity	App. Table 2.1, mean value	App. Table 2.1, mean value
Natural mortality	App. Table 2.1	App. Table 2.1
Recruitment std. dev.	App. Table 2.2	App. Table 2.2
Selectivity	App. Table 2.1, mean value	App. Table 2.1, mean value
Steepness	0.9	0.9

Table 2.3: Estimates of migration between the inner fjord and North Sea resulting in F_{ST} values similar to empirical results (Table 2.1). The nature of the sensitivity test is indicated in the first column, followed by the census size (N), N_e/N ratio, and generation length (T) of each population, the number of migrants per year (mig), and the corresponding mean level of genetic differentiation between populations. The 5% and 95% confidence intervals for mean F_{ST} values over the 100 simulations are shown in parentheses for each level of migration. The first line is the base case scenario using basic parameters (Table 2.2), and the remaining tests are sensitivity tests.

Test	Inner fjord $N, N_e/N$, and T	N. Sea $N, N_e/N$, and T	mig	F_{ST}
Migration using base case parameters	$N=5,380$ $N_e/N=0.29$ $T=2.86$	$N=6.5 \times 10^4$ $N_e/N=0.28$ $T=2.89$	55- 80	0.0051 (0.0049, 0.0053)- 0.0040 (0.0038, 0.0042)
Lower inner fjord size (half base case size)	$N=2,730$ $N_e/N=0.28$ $T=2.86$	$N=6.5 \times 10^4$ $N_e/N=0.28$ $T=2.89$	55- 79	0.0051 (0.0049, 0.0053)- 0.0039 (0.0038, 0.0040)
Higher inner fjord size (double base case size)	$N=10,900$ $N_e/N=0.28$ $T=2.87$	$N=6.5 \times 10^4$ $N_e/N=0.28$ $T=2.88$	50- 74	0.0052 (0.0049, 0.0055)- 0.0039 (0.0037, 0.0041)
Lower selectivity-at-age	$N=5,380$ $N_e/N=0.29$ $T=2.86$	$N=6.5 \times 10^4$ $N_e/N=0.31$ $T=3.44$	56- 75	0.0050 (0.0048, 0.0052)- 0.0039 (0.0038, 0.0040)
Higher selectivity-at-age	$N=5,380$ $N_e/N=0.29$ $T=2.88$	$N=6.5 \times 10^4$ $N_e/N=0.23$ $T=2.82$	68- 80	0.0052 (0.0046, 0.0058)- 0.0040 (0.0039, 0.0041)
Lower fishing mortality rate	$N=5,380$ $N_e/N=0.28$ $T=2.86$	$N=6.5 \times 10^4$ $N_e/N=0.40$ $T=4.59$	48- 69	0.0052 (0.0050, 0.0054)- 0.0039 (0.0038, 0.0040)
Higher maturity-at-age	$N=5,380$ $N_e/N=0.32$ $T=2.74$	$N=6.5 \times 10^4$ $N_e/N=0.28$ $T=2.90$	49- 71	0.0052 (0.0050, 0.0054)- 0.0038 (0.0037, 0.0039)

Table 2.4. Outer fjord simulation results; the nature of the sensitivity test is indicated in the first column, followed by the census size (N), N_e/N ratio, and generation length (T) of each population, the number of migrants per year (mig), and the resulting mean level of genetic differentiation between populations. The 5% and 95% confidence intervals for mean F_{ST} values over the 100 simulations are shown in parentheses for each level of migration.

Test	Outer fjord $N, N_e/N$, and T	N. Sea $N, N_e/N$, and T	mig	F_{ST} (none were significant at $\alpha = 0.05$).
Migration using base case parameters	$N=15,000$ $N_e/N=0.28$ $T=2.88$	$N=6.5 \times 10^4$ $N_e/N=0.29$ $T=2.87$	1,300- 2,800, 6,000	0.00030 (0.00028, 0.00032)- 0.00010 (0.00009, 0.00011), 0.00000 (-0.00001, 0.00001)
Lower outer fjord size (half base case size)	$N=7,500$ $N_e/N=0.28$ $T=2.88$	$N=6.5 \times 10^4$ $N_e/N=0.28$ $T=2.89$	1,000- 1,800	0.00029 (0.00027, 0.00031)- 0.00010 (0.00001, 0.00012)
Higher outer fjord size (double base case size)	$N=30,000$ $N_e/N=0.29$ $T=2.88$	$N=6.5 \times 10^4$ $N_e/N=0.28$ $T=2.89$	1,800- 3,600	0.00030 (0.00028, 0.00032)- 0.00013 (0.00012, 0.00014)
Lower selectivity-at-age	$N=15,000$ $N_e/N=0.28$ $T=2.88$	$N=6.5 \times 10^4$ $N_e/N=0.31$ $T=3.45$	1,150- 2,500	0.00030 (0.00029, 0.00031)- 0.00010 (0.00009, 0.00011)
Higher selectivity-at-age	$N=15,000$ $N_e/N=0.28$ $T=2.88$	$N=6.5 \times 10^4$ $N_e/N=0.23$ $T=2.82$	1,500- 3,000	0.00032 (0.00031, 0.00033)- 0.00010 (0.00009, 0.00011)
Lower fishing mortality rate	$N=15,000$ $N_e/N=0.28$ $T=2.87$	$N=6.5 \times 10^4$ $N_e/N=0.40$ $T=4.59$	1,000- 2,000	0.00032 (0.00031, 0.00033)- 0.00010 (0.00009, 0.00011)
Higher maturity-at-age	$N=15,000$ $N_e/N=0.31$ $T=2.76$	$N=6.5 \times 10^4$ $N_e/N=0.28$ $T=2.88$	1,200- 2,600	0.00031 (0.00029, 0.00033)- 0.00010 (0.00009, 0.00011)
NSea-sim size (40x outer fjord biomass)	$N=15,000$ $N_e/N=0.28$ $T=2.87$	$N=1.3 \times 10^5$ $N_e/N=0.29$ $T=2.87$	1,100- 2,600	0.00033 (0.00032, 0.00034)- 0.00010 (0.00009, 0.00011)
(100x outer fjord biomass)	$N=15,000$ $N_e/N=0.28$ $T=2.86$	$N=3.3 \times 10^5$ $N_e/N=0.29$ $T=2.88$	1,100- 2,700	0.00028 (0.00027, 0.00029)- 0.00010 (0.00009, 0.00011)

Fig. 2.1: Upper panel: management units (ICES divisions and subdivisions in the NE Atlantic); areas IV (a,b,c), and VIId, and IIIa are included in the North Sea Atlantic cod management area (Figure adapted from Reiss et al. 2009). Lower panel: map of the Skagerrak coast, with the predominant ocean current indicated by the curved arrow, and the location of the inner (Søndeled) and outer (Risør) fjord (adapted from Knutsen et al. 2003).

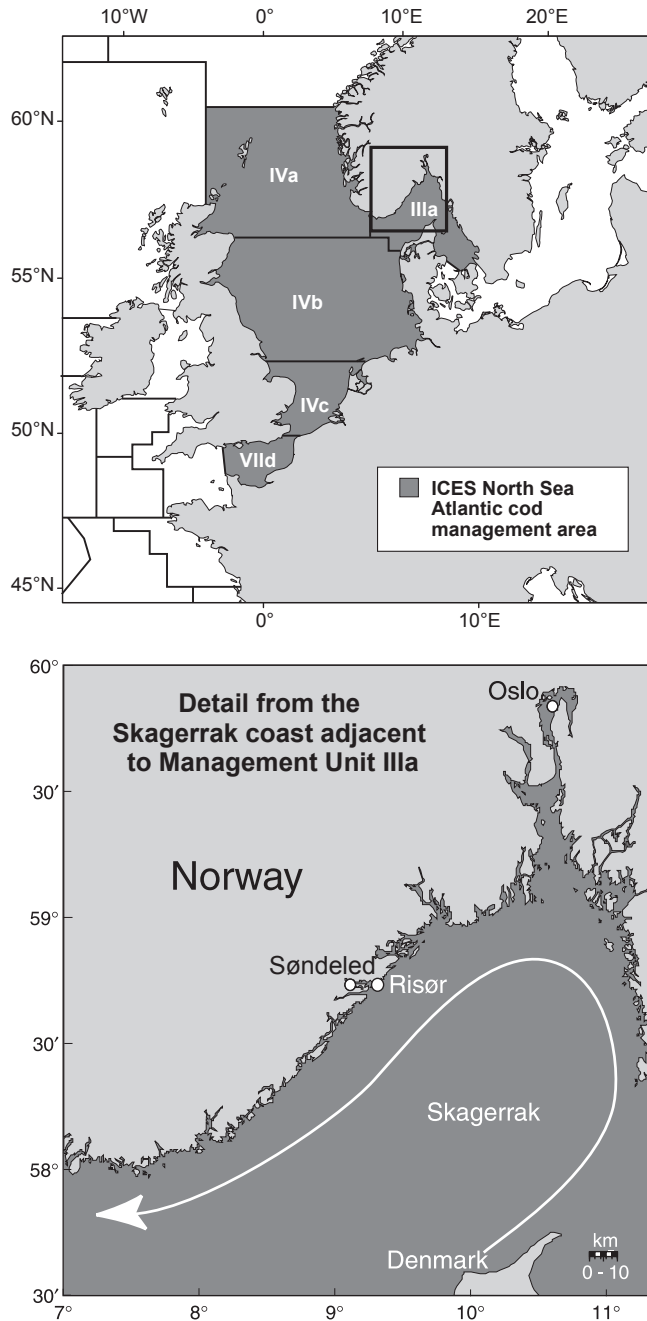


Fig. 2.2: a. Average weight-at-age estimated for the North Sea stock of Atlantic cod (Heath et al. 2008) and the Skagerrak coast (Knutsen et al. 2011), b. Maturity at age estimated for the North Sea (ICES 2012) and the Skagerrak coast (Knutsen et al. 2011).

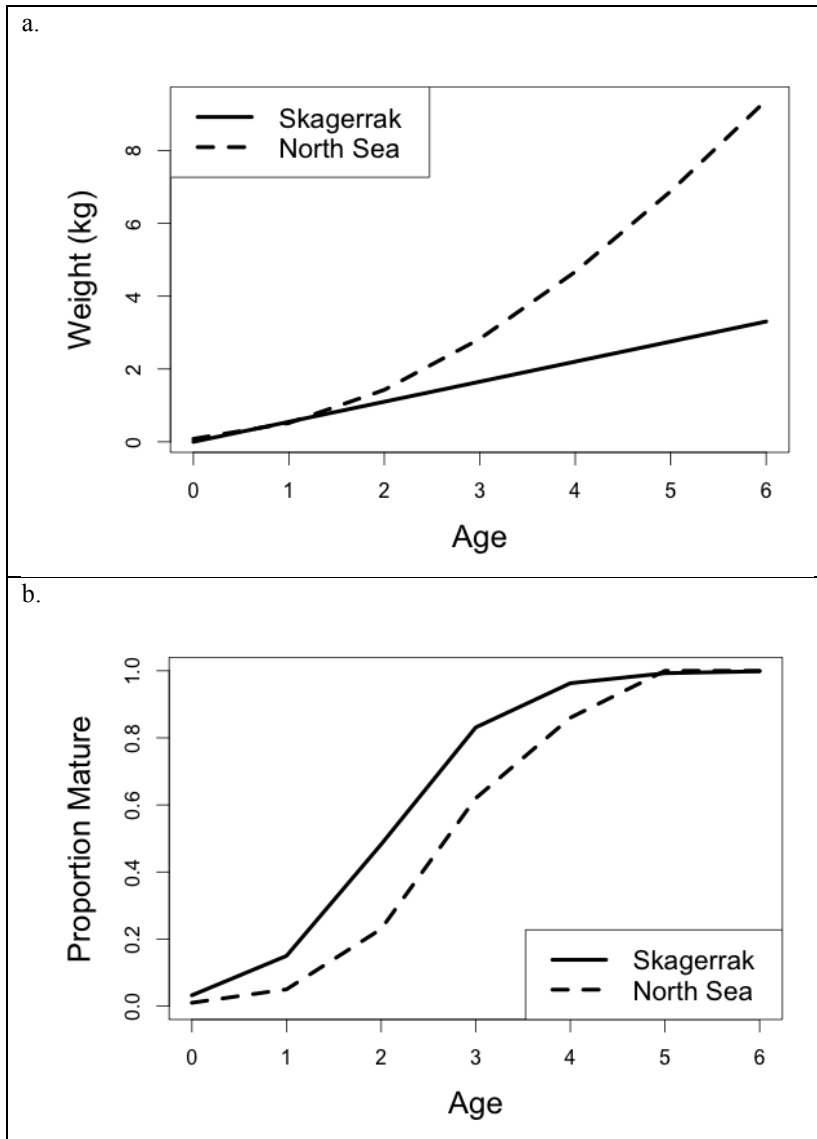


Fig. 2.3: Age structure of the Skagerrak and North Sea modeled populations, compared to observed age structure reported by Knutsen et al. 2011.

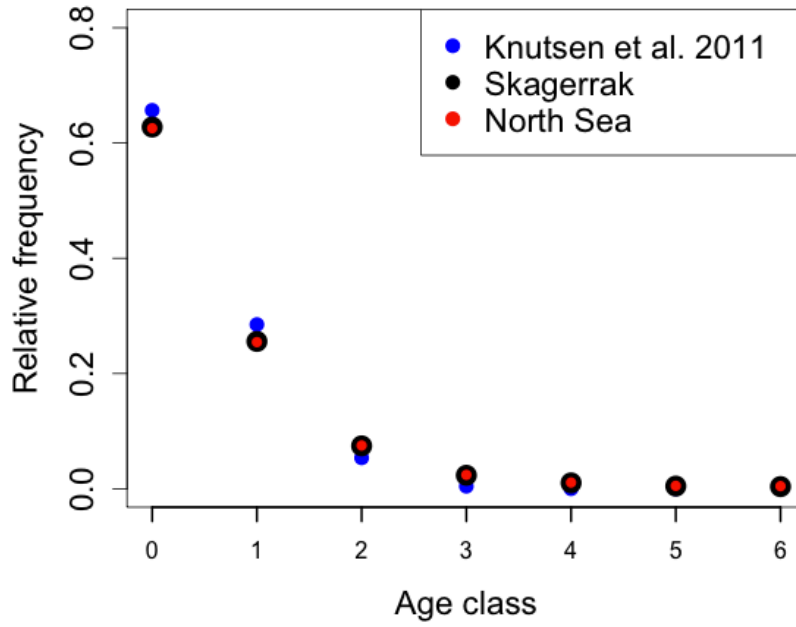


Fig. 2.4: The relationship between the number of migrants per year from the North Sea to the outer fjord, and F_{ST} .

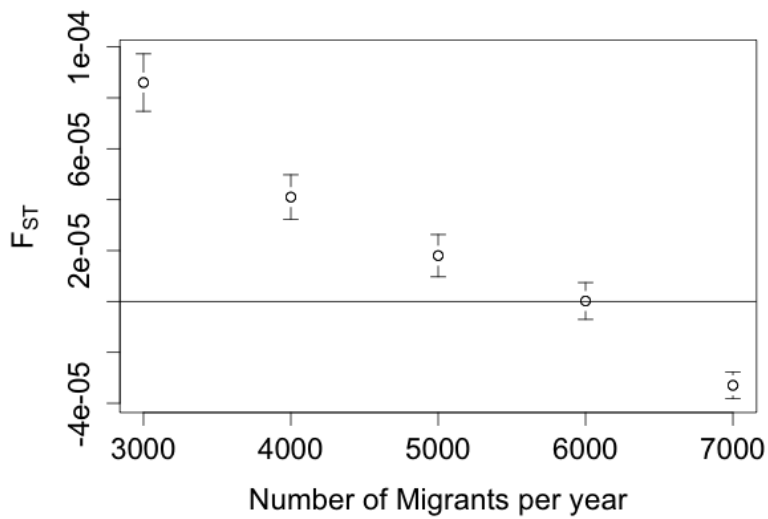


Fig. 2.5. Sensitivity of the age structure of the simulated North Sea population to changes in fishery selectivity and fishing mortality. Panel a. is plotted to show the full age range, b. is zoomed in to show detail of older ages. The legend applies to both panels.

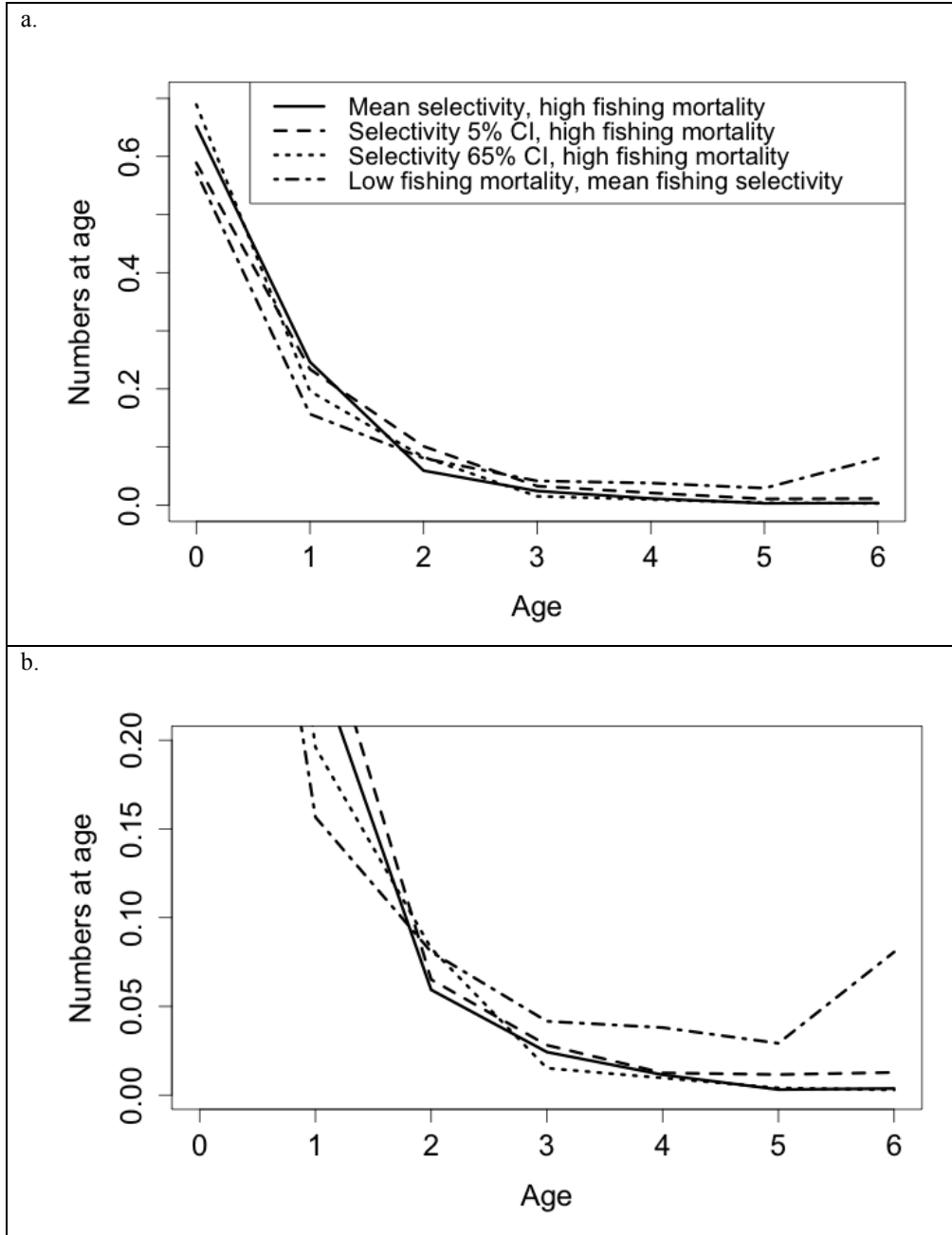


Fig. 2.6. Total biomass and genetic differentiation measured by F_{ST} before and after a simulated population bottleneck in the inner and outer fjords. Conservative values for migration are used: 55 per year between the inner fjord and North Sea populations and 1,300 per year between the outer fjord and North Sea populations. Biomass is shown with migration for the inner fjord (a) and outer fjord (b) and without (c, d), and F_{ST} with migration between North Sea and inner fjord (e), and outer fjord (f) and without (g, h).

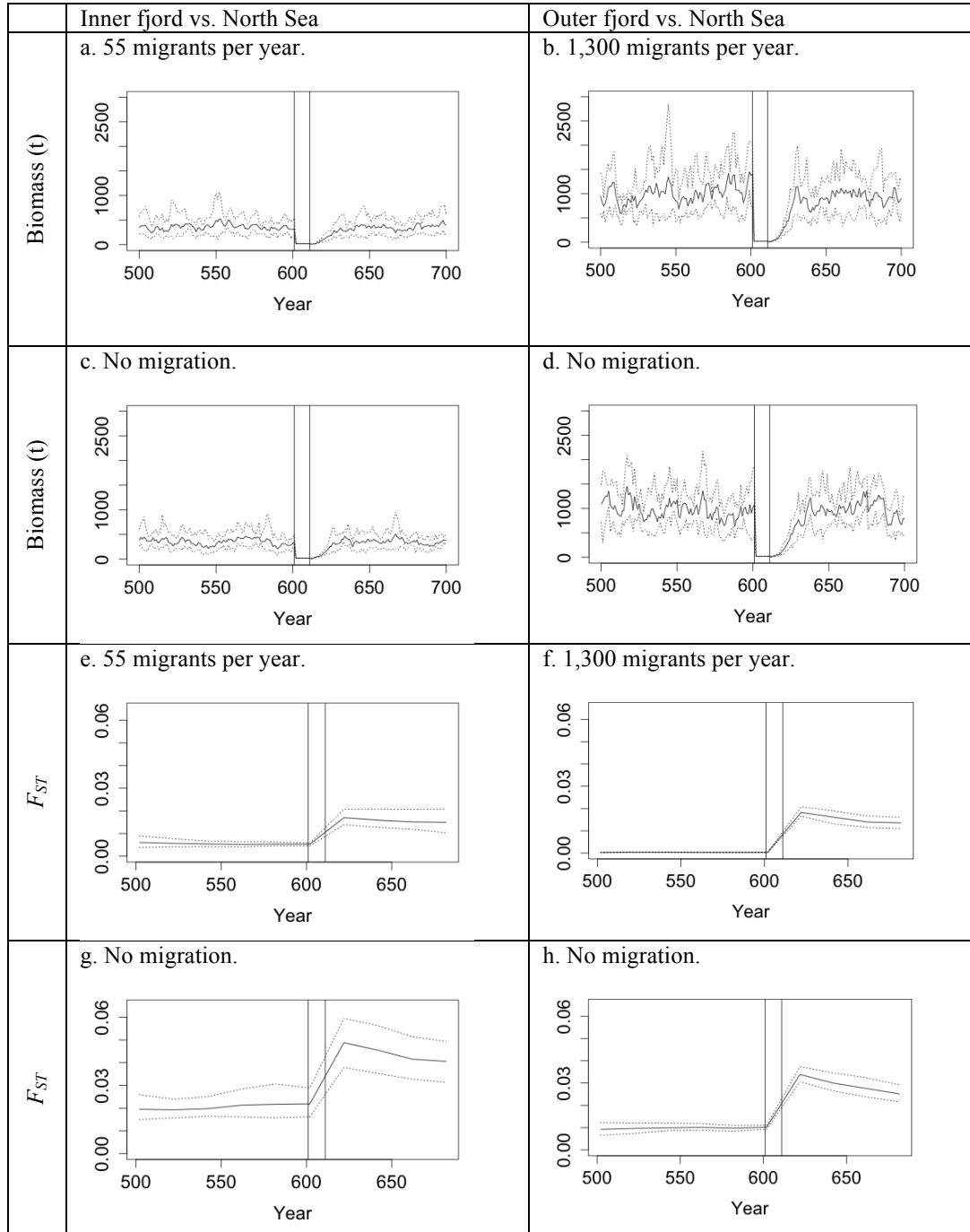
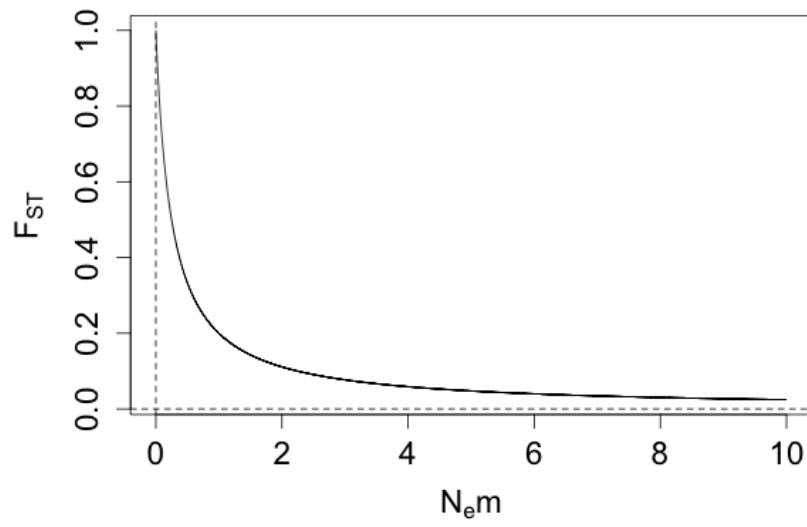


Fig. 2.7: The relationship between $N_e m$ and F_{ST} , based on Wright's equation.



Appendix 2

Details of the individual-based model

Initial allele frequency distributions for microsatellite loci were simulated under the stepwise mutational model (Ohta and Kimura 1973). This parameterization provided simulated alleles with average heterozygosity characteristic of marine fish; typically 0.79 ($\sigma = 0.26$), with 19 ($\sigma = 6.6$) alleles per locus on average (DeWoody and Avise 2000). This is similar to values found for Atlantic cod; in a survey of 18 microsatellite loci developed for Atlantic cod, there were 21 alleles per locus on average ($\sigma = 11.1$; Skirnisdottir et al. 2008). The mutation rates for each locus and simulation were drawn from a beta distribution parameterized to provide expected levels of heterozygosity, $\mu = 0.375$, $\sigma = 0.300$. The beta distribution provides values between 0 and 1; results were therefore scaled down by a factor of 100 to provide mutation rates in the range of those expected for microsatellites in marine fish (10^{-4} - 10^{-2}), and a maximum value of 10^{-2} . Mutation at this rate was allowed to continue each year during the simulation, converted from migration per generation.

Specifications of the age-based population dynamics model

The population dynamics of each population was modeled using an age-structured model with parameters given in App. Tables 2.1 and 2.2. The initial spawning biomass in each population (l) is \tilde{S}_0^l .

The initial number of recruits in each population (l) in the absence of fishing, R_0^l , was calculated using the equation:

$$(App. 2.1) \quad R_0^l = 2\tilde{S}_0^l / \sum_a W_a \tilde{N}_{init,a}^l Q_a,$$

where a indexed age class, W_a was weight-at-age, Q_a was maturity-at-age, and $\tilde{N}_{init,a}^l$ was the number of fish in each age class prior to exploitation relative to the number of age-0 fish. The latter quantity was calculated under the assumption that the population was in unfished equilibrium, given an instantaneous rate of natural mortality for animals of age a , M_a :

$$(App. 2.2) \quad \tilde{N}_{init,a}^l = \begin{cases} 1 & \text{if } a=0 \\ \tilde{N}_{init,a-1}^l e^{-M_a} & \text{if } 1 \leq a \leq x-1 \\ \tilde{N}_{init,x}^l e^{-M_a} / (1 - e^{-M_a}) & \text{if } a=x. \end{cases}$$

The numbers in each age class in each true population (l) were then scaled to the population size that would result from R_0^l recruits:

$$(App. 2.3) \quad N_{init,a}^l = R_0^l \tilde{N}_{init,a}^l.$$

For years $init+1$, $init+2$, etc., the numbers-at-age were computed allowing for fishing and a Beverton-Holt stock recruitment relationship (Beverton and Holt 1957):

$$(App. 2.4) \quad N_{y+1,a}^l = \begin{cases} \frac{4hR_0^l \tilde{S}_y^l}{\tilde{S}_0^l(1-h) + \tilde{S}_y^l(5h-1)} e^{(\delta_R - \sigma_R^2/2)} & \text{if } a = 0 \\ N_{y,a-1}^l e^{-(S_{a-1}F_y^l + M_a)} & \text{if } 1 \leq a \leq x-1 \\ N_{y,x-1}^l e^{-(S_{x-1}F_y^l + M_a)} + N_{y,x}^l e^{-(S_x F_y^l + M_a)} & \text{if } a=x, \end{cases}$$

where $N_{y,a}^l$ was the number of fish of age a in population l at the start of year y , S_a , was the selectivity-at-age for the fishery, h is steepness (Table 2.2), and F_y^l was the instantaneous fully-selected fishing mortality rate during year y for population l (Table 2.2). Variation with bias-corrected lognormal error was applied to the recruitment in each population in each year, i.e., $\delta_R \sim N(0; \sigma_R^2)$, and σ_R^2 was generated from the CV of recruitment (App. Table 2.2), using the equation

$$(App. 2.5) \quad \sigma_R^2 = \log(CV_R^2 + 1).$$

Spawning biomass in each population at the start of year y , \tilde{S}_y^l , is calculated subsequent to the initial year, using:

$$(App. 2.6) \quad \tilde{S}_y^l = 0.5 \sum_a W_a N_y^l Q_a.$$

The number of spawning males in each population was set equal to the number of spawning females, and was based on the proportion of individuals in each age group that were expected to be mature that year:

$$(App. 2.7) \quad SP_{y,a}^l = 0.5 N_y^l Q_a.$$

Catch in numbers of fish of age a in population l during year y , $C_{y,a}^l$, was a function of S_a , fishing mortality rate, natural mortality, and numbers-at-age,

$$(App. 2.8) \quad C_{y,a}^l = \frac{S_a F_y^l}{S_a F_y^l + M_a} (1 - e^{-(S_a F_y^l + M_a)}) N_{y,a}^l.$$

Finally, the total catch in weight from population l during year y , C_y^l , was calculated as:

$$(App. 2.9) \quad C_y^l = \sum_a W_a C_{y,a}^l.$$

Age was converted to weight using a von Bertalanffy growth function (von Bertalanffy 1957):

$$(App. 2.10) \quad W_a = \psi [L_\infty (1 - e^{K(a-A_0)})]^\gamma,$$

where L_∞ was the mean maximum length, K was a rate constant (year^{-1}), A_0 was the theoretical age at which length is zero, and ψ and γ determine the relationship between length and weight (App. Table 2.2). Maturity-at-age was governed by the relationship:

$$(App. 2.11) \quad Q_a = \frac{1}{1 + e^{-(A+aB)}},$$

where A and B were parameters (App. Table 2.2).

Effective population size

In the model only a proportion (Q) of the population reproduces each year, whereas effective population size calculations typically assume that each individual of the same age has an equal chance to reproduce (Felsenstein 1971; Hill 1972; Waples et al. 2011). Therefore, the effective population size was calculated specifically for the modeled populations based on average numbers-at-age (over 100 simulations), maturity-at-age, and survival of each age class. A simulation was performed in which a proportion of breeders, B , where $B = N_a * Q$, with N_a equal to the numbers-at-age, was selected from each age class, given estimates for Skagerrak maturity-at-age (Table 2.4), and equal age-specific birth rates. Simulating this population for 100 years and counting offspring over the lifetime of each individual yielded a lifetime variance in reproductive success (V_k). The generation length (T) was calculated as in Felsenstein (1971). The effective population size was then calculated using the Hill (1979) equation analogue for diploids,

$$(App. 2.12) \quad N_e = \frac{4N_l T}{V_k + 2} \text{ (Hill 1979, eqn. 8), where } N_l \text{ is the number of offspring. In reality}$$

N_e/N ratios are likely to be lower than those measured in the model, due to stochasticity that was omitted here.

App. Table 2.1: Age-specific parameters used in the model; North Sea parameters are annotated by an *, as obtained from ICES (2012), and Skagerrak parameters by †, as from Knutsen et al. (2011). Interquartile values used in sensitivity testing are shown in parentheses.

Age	Maturity* (Q)	Maturity† (Q) (5% and 95%)	Fishing Selectivity* (5% and 65%)	Natural Mortality*
0	0.01	0.032 (0.019, 0.046)	0.220 (0.201, 0.228)	1.038
1	0.05	0.149 (0.135, 0.164)	0.818 (0.656, 0.877)	0.698
2	0.23	0.482 (0.451, 0.514)	0.974 (0.891, 1.000)	0.490
3	0.62	0.831 (0.768, 0.895)	0.895 (0.783, 0.930)	0.233
4	0.86	0.963 (0.919, 1.000)	0.847 (0.742, 0.876)	0.2
5	1	0.992 (0.917, 1.000)	0.848 (0.743, 0.863)	0.2
6	1	0.999 (0.999, 1.000)	0.848 (0.743, 0.863)	0.2

App. Table 2.2: Parameter values used in the model.

Parameter	Application	Parameter value	Source
b	Weight-at-age	$0.5508 \text{ yr}^{-1}\text{kg}$	Knutsen et al. 2011
ψ	Weight-at-age	1.75×10^{-5}	Heath et al. 2008
γ	Weight-at-age	2.8571	Heath et al. 2008
L_{∞}	Length-at-age	197 cm	Heath et al. 2008
K	Length-at-age	0.1030 yr^{-1}	Heath et al. 2008
CV_R	Recruitment CV	0.75	ICES 2012
δ_R	Recruitment error	$\sim N(0; \sigma_R^2)$	App. Eqn. 2.5

Chapter 3: The utility of genetics in marine fisheries management: a simulation study based on Pacific cod off Alaska

Abstract

Although genetic population structure has been documented in many marine fish species, there is still uncertainty regarding the utility of such information for management. Simulations based on a spatially-structured individual-based model that combines multi-locus microsatellite genotypes and an age structured population dynamics model are used to evaluate the conservation status and yield of each of two populations, as well as the performance of microsatellite loci to detect changes in population size. Parameters in the model are based on Pacific cod, *Gadus macrocephalus*, in the Bering Sea and Aleutian Islands (BSAI) region of Alaska, although results are considered in terms of marine fish species in general. Population dynamics are projected under several management strategies, with annual stock assessments and fishing, for 100 years. Results show that managed fishing can result in reduction in stock sizes below target reference points when distinct stocks are not managed individually. In contrast, when stocks identified by genetic testing are managed separately, stock size is maintained at target levels, and catches may increase even given inherent error rates.

Introduction

Managing marine species at the level of the stock, or population, is considered the best approach for conservation of resources (Taylor 1997; Fu and Fanning 2004; Laikre et al. 2005). However, information on stock structure is not always incorporated into management (Waples et al. 2008; Reiss et al. 2009). Management at spatial scales larger than the genetic stock size is not uncommon in managed marine fish species (Waples et al. 2008; Reiss et al. 2009). Such a situation is problematic because genetic populations showing differentiation at neutral genetic markers only exchange a few individuals per generation (Waples 1998). If disproportionate harvest takes place on unrecognized genetic stocks, it may result in overharvest and/or loss of genetic diversity of some components of the population (e.g. Taylor 1997; Matala et al. 2004; Laikre et al. 2005). The problem can be exacerbated when genetically distinct stocks with different carrying capacities, natural mortality, or growth rates are managed as a single stock (e.g. Martien et al. In Press; Fu and Fanning 2004; Dougherty et al. 2013).

Incorporating information on population structure into fisheries management is difficult for many reasons (Waples et al. 2008). Population structure in marine fish is difficult to estimate. Otolith microchemistry can be used to determine movement patterns in both larval and adult life history stages and mark-recapture can achieve similar results in adult fish (i.e. Hilborn 1990; Jones et al. 1999); however, these techniques do not provide information on whether exchange of successfully breeding individuals takes place. Studies on genetic population structure are commonly undertaken using neutral genetic markers, markers that are not related to adaptive fitness. Such studies provide information on population structure and insight into whether migrants successfully reproduce, but issues associated with genetic studies can prevent them from being utilized in a management context. These issues include type I and type II errors, and whether the spatial and temporal coverage of sampling is adequate.

Marine populations are typically connected by relatively high gene flow, due to pelagic larval phases and few barriers to migration, which results in low levels of genetic differentiation (Ward et al. 1994; Waples 1998; DeWoody and Avise 2000). Marine fish species are typically associated with lower levels of F_{ST} , a common measure of genetic differentiation, than anadromous or freshwater fishes (Ward et al. 1994; Waples 1998). This results in a higher signal:noise ratio than would be observed in anadromous or freshwater fish species, which can increase measurement error and uncertainty (Waples 1998). Measures of genetic differentiation,

such as F_{ST} , can be imprecise due to the stochastic nature of genetic systems (Taylor et al. 2000). These circumstances can affect the utility of data to determine the number of stocks and the level of differentiation between them.

Another factor resulting in fisheries management at scales larger than the genetic population is how management entities deal with population structure. Some management entities do not have systems in place to incorporate genetic data, such as conventional top-down fisheries management systems applied to low-income fishing communities (Allison and Ellis 2001). Other fisheries management entities consider genetic stock structure and incorporate protocols to consider adapting their management strategies accordingly (e.g., Spencer et al. 2010). The relationship between science and management is not always straightforward; governance institutions that have established protocols to consider stock structure often move slowly by nature (Hartley and Glass 2010), and management constraints may prevent changes from being implemented (Waples et al. 2008).

Despite factors that could lead to high gene flow in the marine environment, observations of genetic population structure in marine fish species are numerous. Fewer barriers to migration exist in the ocean than on land, but they are still present in the form of currents (Gaylord and Gaines 2000), bathymetry (Schüller 2011), and temperature gradients (Wyllie-Echeverria 1995). Population structure has been found over a range of scales in Pacific cod, *Gadus macrocephalus*, and the closely related Atlantic cod, *Gadus morhua*. In Pacific cod genetic differences have been documented from 1000s of kilometers off Alaska (Spies 2012), to 10s of kilometers in the coastal waterways of the Salish Sea of North America (Canino et al. 2010). Similarly, genetic differentiation in Atlantic cod ranges from large scales in the oceanic environment (Sarvas and Fevolden 2005) to approximately 60 km in fjords along the Skagerrak coast (Knutsen et al. 2003). Population structure has also been observed in highly mobile species such as mackerel and Atlantic herring (Zardoya et al. 2004; Bekkevold et al. 2005).

The current study is a management strategy evaluation of the utility of using information on genetic population structure in fisheries management. The consequences of various fishery management strategies are examined in the context of a genetic individual-based model coupled with a population dynamics model. Parameterization of the framework is based on Pacific cod, a commercially exploited species in the Bering Sea and Aleutian Islands (BSAI) region of Alaska. Simulations represent the current state of management and the genetic population structure in

this region. Pacific cod spawning in the Aleutian Islands are genetically distinct from those in the eastern Bering Sea (Cunningham et al. 2009; Spies 2012). In the operating model, the Eastern Bering Sea (EBS) and Aleutian Islands (AI) are genetic populations, groups of individuals that can potentially mate with any other individual in that particular population, but rarely interbreed with individuals from other populations (Waples and Gaggiotti 2006).

At the time the study was undertaken, the AI and EBS cod stocks were managed as a single unit, although they are now managed separately (Thompson and Lauth 2012; Thompson 2013; Thompson and Palsson 2013). When the AI and EBS were managed together, average fishing pressure was disproportionately high in the AI between 1998-2012. The average relative fishing mortality, measured by catch relative to estimated biomass, was 15% higher in the AI than the EBS during that time period (G. Thompson pers. comm. NOAA Fisheries, 7600 Sand Point Way NE, Seattle, WA 98115). The highest discrepancy in fishing effort occurred in 2010 when fishing pressure in the AI was more than twice as high (215%) as the EBS. Biomass in the Aleutian Islands has been estimated to be 21% of the estimated unfished female spawning biomass, based on an age-structured model, whereas biomass in the EBS is above target levels (NPFMC 2012; Thompson and Lauth 2012).

The simulations undertaken here examine how performance measures (total catch, relative stock size, and probability of overfishing) change when: 1) management units are established using genetic data versus treating the entire area as a single management unit, 2) the data used for setting management regulations are based on the outcomes of simulated stock assessments, and 3) two harvest control rules are used: a simple (Tier 5) and more complex (Tier 3) rule, as implemented by the North Pacific Fishery Management Council, NPFMC (Fig. 3.1; NPFMC 2012). Other questions are designed to extend the conclusions of the simulation to marine fish in general, and include the sensitivity of results to the size of the unfished spawning biomass, dispersal rates, and target fishing mortality rates.

Methods

The model

The (operating) model representing the system being managed simulated both population dynamics and genetic population structure by linking a cohort-based population dynamics model to an individual-based model (IBM; Appendix 3). The operating model consisted of two

populations that were genetically differentiated according to empirical estimates for Pacific cod in the BSAI (Spies 2012; Chapter 1). This level of genetic differentiation was achieved by allowing a specific migration rate, 25 spawning migrants per generation. The model represented the true dynamics and individual-based genetic structure of two populations, and was a simplification of a complex system.

Each simulation began by assigning each individual in each population a 10-locus microsatellite genotype, with average allelic richness 20-25 alleles per locus, the expected value for Pacific cod and other marine fish species (DeWoody and Avise 2000; Spies 2012; Appendix 3). Other simplifications included equal numbers of males and females, and a proportion equal to the proportion mature at each age was randomly selected into the pool of potential spawners each year. One male and one female from these potential spawners were randomly selected as parents for each new recruit, and the genotype for each new recruit was generated via Mendelian inheritance from parental genotypes. A population dynamics model with overlapping generations was parameterized using estimates for growth, mortality, age structure, and maturity (App. Table 3.1) 3). In addition, population sizes were scaled down from those estimated for Pacific cod in the BS and the AI for computational efficiency.

The model followed a specified timeline. The populations were allowed to evolve for 2,000 generations, the estimated length of time since cod recolonized the North Pacific following the last glacial maxima (Canino et al. 2010). This was necessary to achieve migration-drift equilibrium, which has likely occurred in reality (Appendix 3). Fishing was implemented for an initial 10-year “burn-in” so that each simulation started in a fished state, a time period appropriate for the life history of Pacific cod. The populations were then projected forward with fishing under various management strategies for 100 years. A genetics study was performed at the start of the 100-year period to determine the location of perceived population boundaries. Another genetics study was performed after 50 years to provide information on the level of genetic differentiation between populations. Some management strategies incorporated information on genetic structure to select the number of management units. The entire simulation process was repeated 100 times under each management strategy to account for variability in the data.

The model used a spatial framework that consisted of 10 linear spatial units, and was intended to mimic the linear oceanographic configuration of many marine exploited species with

spawning sites along the continental shelf, specifically cod habitat from the Aleutian Islands chain to the Bering Sea shelf (Fig. 3.2; Spies 2012). Spatially biased fishing pressure was achieved via a single fishing port on the left side of the 10 spatial areas (Fig. 3.2). Fishing effort was based on a gravity model; effort by spatial area was proportional to the number of fish in each spatial area and inversely proportional to the distance from the fishing port (Appendix 3). In reality the largest fishing port for Pacific cod is Dutch Harbor on Unalaska Island between the AI and the EBS, but the model framework allowed for disproportionate fishing effort in the AI. The high relative fishing mortality rate recorded in 2010 in which the AI was fished 2.15 times harder than the EBS (G. Thompson pers. comm.) was used in the simulation. This value was chosen because the current study was designed to illustrate disproportionate fishing effort when distinct populations exist within a single management unit, rather than provide management advice for Pacific cod (App. Table 3.1). The population nearest the fishing port that received high fishing effort, hereafter referred to as population A, represented the Aleutian Islands stock of Pacific cod, while the stock representative of the Bering Sea stock of Pacific cod is referred to as population B (Fig. 3.3). Fish moved freely among spatial areas within true populations, and dispersal was limited between populations.

The two populations in the operating model were either of equal size, and a boundary was located between spatial units 5 and 6 (Fig. 3.3); or unequal, with a boundary between spatial units 2 and 3 so that population A was initially one quarter the size of population B (Fig. 3.3). The terms “equal” and “unequal” as defined here are used throughout the text. Under unequal spatial structure, relative population size was representative of Pacific cod populations in the EBS and AI, although the absolute magnitude was smaller in the simulation.

An age-structured model determined the population dynamics. In this model, age-classes were modeled as homogenous cohorts, recruitment was governed by a Beverton-Holt stock-recruitment relationship, and the instantaneous rate of natural mortality was assumed to be 0.34yr^{-1} (Thompson and Lauth 2012). Selectivity for a single fishery was a weighted average of selectivity from the three fisheries that comprise the Pacific cod fishery in the BSAI (Appendix 3; Thompson and Lauth 2012). Maturity-at-age was based on a logistic equation in which 50% of fish are mature at age 4.9 and almost all are mature by age 9 (Stark 2007). The maximum age of Pacific cod is approximately 20 years; therefore there were 20 age classes, with the oldest age class representative of all fish of age 20 and above.

Simulated survey data were collected from each of the 10 spatial areas in each year, and provided estimates of the number and biomass of animals. The data generation process accounted for autocorrelation among annual assessments and variability among survey estimates of spawning biomass. The mean coefficient of variation (CV) for assessed spawning biomass, CV_A , from 1982-2011 is 6.0%, the mean CV of the survey estimate for total biomass, CV_S , from the same time period is 8.4%, and the variance (σ_R^2) of the age-0 estimated recruitment from 1977-2012 is 0.408 (App. Table 3.1; Thompson and Lauth 2012). Research surveys and stock assessments were assumed to take place annually, which is true for stock assessments and Bering Sea research surveys, but Aleutian Islands surveys take place on a triennial or biennial basis. An assessment based on survey data within each management unit was conducted during each year of the 100-year fishing period, and determined the total allowable catch (TAC) and hence the fishing mortality rate.

The mean estimated spawning biomass from 1977-2011 from the BSAI Pacific cod assessment was 405,943 metric tons (t), based on EBS trawl surveys from 1977-2011 (Thompson and Lauth 2012). The unfished spawning biomass for the BSAI Pacific cod population is estimated at 10^6 t, given that fishing pressure for Pacific cod in the BSAI is $F_{40\%}$. A spawning biomass of 10^6 t would result from approximately 2.06×10^9 fish, given the age-weight relationship and estimated age structure in the population (Appendix 3). Simulations with populations of this magnitude were not feasible due to computational constraints, so the BSAI population size was scaled down to the largest practicable size, 8.3×10^4 , by a factor of 25,000. Population sizes of 1.66×10^5 and 8.3×10^3 were used in sensitivity testing (an order of magnitude below and double above the reference level). Results from the population dynamics model are scale invariant, as are genetic results, with some caveats (Appendix 3). The only analyses affected by the scaled down population sizes are effective population size and catch, which are presented in an absolute sense or scaled up.

The results of the simulations were summarized using the following performance measures in each year of the 100-year projection period: (a) total catch (by population and for both populations combined), (b) spawning stock biomass relative to spawning stock biomass at the start of the projection period (SSB/SSB_{init}), (c) the probability of individual stocks being overfished (below 20% of unfished spawning stock biomass, $B_{20\%}$), and (d) Felsenstein-Hill effective population size, chosen because it captures information regarding the number of

reproducing individuals in the population (Waples et al. 2011). Effective population size was compared with $N_e = 5,000$, a threshold that has been identified as necessary to maintain normal adaptive potential (Lande 1995). Performance measures were summarized over 100 different simulations.

Management strategies

A management strategy is the set of actions taken toward managing a fishery. The management strategy in this study includes collection of genetic data, interpretation of those data to establish management units, application of an assessment method to provide information on the state of the resource, and application of harvest control rules that provide the TAC based on the assessed state of the resource. The operating model is described above, while three management strategies are implemented under a Tier 3 harvest control rule (Fig. 3.1): (i) “combined” management, where the entire area is managed as one unit; (ii) “separated” management, where subpopulations, as determined using simulated population genetic testing, are managed individually; and (iii) “combined then separated” management, in which subpopulations are managed together as one unit for 50 years, followed by 50 years of “separated” management, with management units selected using the results of simulated population genetic testing. The “combined” management strategy was also implemented under a simple Tier 5 harvest control rule which uses fewer data than the Tier 1 harvest control rule but is more conservative (Fig. 3.1). Target fishing mortality rate was set to $F_{40\%}$, the fishing mortality rate which reduces spawning biomass-per-recruit to 40% of its unfished level, unless specified otherwise. To determine the effect of target fishing effort, the Tier 3 HCR was used with “combined” management and three levels of fishing mortality: $F_{40\%}$, $F_{35\%}$, and $F_{30\%}$. In addition to these basic types of management, the simulated population genetics studies, which were used to determine the location of management units for the “separated” and “combined then separated” strategies, were implemented using various sampling methods (i.e. the number of fish sampled in each spatial area) to examine how sample size affects identification of stock boundaries (Table 1).

Dispersal

Twenty-five migrants from the spawning population per generation provided levels of genetic differentiation on the order of those expected between the BS and AI under unequal population sizes. Dispersal rates an order of magnitude below and two orders above this were explored to

cover a range of estimates and account for error (Table 1). In addition, a scenario of 10,000 migrants was examined to test the effect of much higher dispersal. The model was configured so that the number of immigrants and emigrants are equal in the first year, but become unequal as the populations are fished down, proportional to their size, generally resulting in more immigrants from population B (the larger population) to population A.

Genetic testing

Genetic tests were designed to select the location(s) of the management units. A simple test was used to determine management units, which involved taking samples from adjacent (i.e. 1 vs. 2, 2 vs. 3, etc.) spatial areas. Weir and Cockerham's (1984) theta, θ , a commonly used estimator of Wright's pairwise F_{ST} , was calculated between each adjacent spatial area (Wright 1931). Significance of the test was determined by a permutation test, using an alpha level of 0.05. The permutation test was implemented as follows: individuals were permuted among samples, and θ was recalculated 100 times to assess the significance of each initial θ value ($\alpha = 0.05$). P -values were considered significant with respect to this alpha value, after correction for multiple tests using the sequential goodness of fit metatest (SGoF) method, which increases the statistical power of the test as the number of comparisons increases (Carvajal-Rodríguez *et al.* 2009). Adjacent spatial areas that were not significantly different were considered to be in the same population. Significant differences between adjacent areas were considered to be evidence for population boundaries. Distinct populations, defined by the simulated genetic test, were managed in separate management units under the "separated" and "combined then separated" management strategies.

In addition, F_{ST} was calculated using genotypes from all fish in each population, to assess levels of genetic differentiation without sources of error from small samples. These F_{ST} estimates are referred to as "true" F_{ST} values, whereas F_{ST} based on samples are "sample" F_{ST} estimates. How well different genetic sample sizes determined population structure was tested using: 1) 100 fish from each of the 10 spatial areas, 2) 200 fish from each of the 10 spatial areas, and 3) samples of differing size from each spatial area, with size proportional to the fishery catch, and a total of 1,000 fish. This sensitivity analysis was limited to the context of the model; a broad power analysis of this type has been performed elsewhere (Ryman *et al.* 2006).

Results

The model

Pairwise F_{ST} values, averaged over 100 simulations, were used to validate the model output. Empirical results produced $F_{ST} = 0.006$ (95% CI: 0.005, 0.008) using 192 individuals in samples from the EBS and 840 from the Aleutian Islands (Spies 2012). Using samples of the same size, the model estimated F_{ST} to be 0.0061 (95% simulation interval: 0.0040, 0.0089) when the true θ value, calculated using data from all individuals in each population, was 0.0035. This discrepancy was due to the fact that higher sample size reduces F_{ST} estimates. Therefore, a true F_{ST} of 0.0035 was considered to be the best estimate between the EBS and AI Pacific cod, and was used as the target level of differentiation between populations of unequal population size. Divergence levels reached the expected value of $F_{ST} = 0.0035$ (5% and 95% simulation interval limits: 0.0022, 0.0067) with two populations relative in size to EBS and AI cod with a total population size of 8.3×10^4 and 25 migrants per generation.

Management strategies

Six base-case analyses provided a comparison among management plans that did and did not implement management units based on the results of genetic testing. These base-case analyses (I-VI) included “combined”, “separated”, and “combined then separated” management for both equal and unequal initial population sizes, and performed management based on the Tier 3 HCR with a target fishing mortality of $F_{40\%}$ (Table 1). Relative fishing pressure for base case analyses was 215% higher in the AI than the EBS (populations A and B respectively), as described above. Genetic tests were performed on 100 samples from each spatial area in the first year of the projection period (following the initial 10-year “burn-in”) for cases III and IV, and in year 50 for cases V and VI.

The population near the fishing port (population A) was more vulnerable to overfishing due to disproportionately high fishing effort under “combined” management, particularly when it was the smaller of the two populations (Fig. 3.4, cases I and V). The relative spawning biomass (SSB/SSB_{init}) in population A was depleted below threshold levels (i.e., below $B_{20\%}$) under “combined” management when it was the smaller of the two populations in 33-38% of the simulations (Table 2, cases I and V). Depletion below threshold levels did not occur under

“separated” management (Fig. 3.4, cases III and IV) or equal population sizes (Fig. 3.4, cases II and VI). Spawning biomass in population A recovered to target levels when “separated” management was implemented after 50 years (cases V and VI), but not when management continued as “combined” for the entire projection period (cases I and II). Population B never fell below threshold levels; in fact it was underutilized under “combined” management and was above $B_{40\%}$ on average in cases I and II and during the first 50 years for cases V and VI (Fig. 3.4).

Average total catch among “separated” and “combined” management also depended on relative population size. Total catch was higher when populations were managed separately, even given that some genetic tests provided erroneous results, resulting in 13% higher average yearly catch for unequal initial stock sizes and 9% for equal initial stock sizes than managing populations together (Table 2). Catch also increased when “separated” management was implemented following “combined” management; the relative increase was 9.2% for unequal initial population sizes vs. 8.0% for equal initial population sizes (cases V and VI; Table 2).

The Felsenstein-Hill reproductive size did not decline significantly in a population of size 8.3×10^4 fished to $B_{20\%}$, despite the reduction in stock size, remaining at approximately 1.5×10^4 (Fig. 3.5a). When a smaller stock (8.3×10^3 individuals) declined to $B_{20\%}$, the Felsenstein-Hill effective population size declined below 5,000, and below 500 on average (Fig. 3.5b), which is a concern for populations of this size. However, 8.3×10^4 represents the BSAI population size scaled down by a factor of 25,000. If stock size were simulated at its actual size, the effective population size would remain above 5,000.

The performance of the Tier 3 (for three target fishing mortalities) and Tier 5 HCRs were contrasted (Fig. 3.6). All HCRs were implemented when management was “combined”, and the populations were initially unequal because this scenario led to a high probability of population A dropping below $B_{20\%}$ (Table 2). Spawning biomass declined in population A under the Tier 3 HCR proportional to target fishing mortality, but population B was not sensitive to this range of fishing mortality rates and remained above $B_{40\%}$ (Fig. 3.6a). The average catch increased with fishing mortality, with the highest catch of 125,800 t under $F_{30\%}$ and the lowest catch of 124,000 t under $F_{40\%}$ (Table 3). The probability that the stock would decline below $B_{20\%}$ increased with fishing mortality as well; the highest probability was 63% when the target fishing mortality was $F_{30\%}$ (Table 3). The Tier 5 HCR imposed lower fishing pressure than the Tier 3 HCR; spawning

biomass of both populations therefore remained well above $B_{40\%}$ under this HCR (Fig. 3.6b). However, and as expected, catches were noticeably lower under the Tier 5 HCR.

Dispersal

“Combined” management of populations that were initially of unequal size, with a total population size of 8.3×10^4 individuals, was used to explore the effect of dispersal rate (Fig. 3.7). Spawning biomass increased for population A, but not B, as the number of migrants increased, because the number of emigrants was proportional to relative population size, and population A was more depleted than population B. This effect rebuilt population A to approximately $B_{40\%}$ only when the initial number of migrants exchanged was 10,000. Spawning biomass in population B was insensitive to changes in dispersal because it received fewer migrants. F_{ST} was calculated between populations from generated data after 50 years of the 100-year managed fishing period, for each dispersal rate. The F_{ST} value between populations A and B was significant at the $\alpha = 0.05$ level when dispersal was 2.5 migrants per generation ($F_{ST} = 0.00397$, $p = 0.01$), but not for 2,500 ($F_{ST} = 0.00311$, $p = 0.08$) or 10,000 migrants ($F_{ST} = 0.00295$, $p = 0.12$); statistics were averaged over 100 simulations.

Genetic testing

Genetic tests were defined as successful when they correctly identified true population structure. Unsuccessful tests detected no genetic differentiation between the two populations, which were significantly genetically differentiated ($F_{ST} = 0.0035$ on average). Unsuccessful tests found no differentiation throughout the managed area or incorrectly identified the location of the boundary between distinct populations, and may have additionally identified populations that did not exist. When samples of 100 individuals were used, genetic tests had 80% power for unequal population sizes and 60% for equal population sizes, and 100% power when 200 samples were used (Table 3.4). When sample sizes were in proportion to catch in each spatial area, sample sizes from spatial area 1 to 10 were on average, respectively: 324, 177, 118, 88, 71, 59, 50, 44, 39, 29 for unequal population sizes in an unfished state. Success with this method was 50% when populations were equal in size, but 80% when population sizes were unequal, due to higher genetic differentiation with equal population sizes ($F_{ST} = 0.0035$ vs. 0.0018; Table 3.4). The base case simulations utilized equal sample sizes of 100 rather than sample sizes of 200 because

sample sizes of 100 are commonly used in population genetics studies and the 20-40% error rate was more meaningful for exploring errors due to genetic testing than perfect results associated with samples of size 200.

Discussion

The modeling framework provides information on how fishing and fisheries management affect effective population size, catch, and biomass of genetically distinct marine fish stocks. Several broad conclusions can be drawn from the results of this study. First, the probability of overfishing is lower and catches may be higher when management units take account of genetic population structure. Second, unrecognized populations that are inadvertently overfished under “combined” management will recover in size if management practices later manage populations separately based on management units identified using genetic tests. Finally, effective population size appears unlikely to drop below 5,000 for population sizes typical of marine fish species subjected to fishing pressure of $F_{20\%}$ or less.

There are several key differences in performance measures resulting from “separated” management based on genetic testing versus application of a single management unit to two genetically distinct populations, or “combined” management. Specifically, spawning biomass near the fishing port is higher and catches are larger when management units are based on genetic tests (Fig. 3.4; Table 2 – cases I and II vs. cases III and IV). Management based on genetic testing maintains all stock sizes above $B_{20\%}$ and generally near $B_{40\%}$. In contrast, population A may be depleted well below target levels, and even below threshold levels, when two genetically distinct populations are not managed at the level of the population. If this occurs, spawning biomass will begin to recover as soon as “separated” management is implemented, and total annual catch may increase as well (Fig. 3.4 and Table 3.2 – cases V and VI).

There are compelling economic reasons to implement management based on genetic testing. The mean value for whole Pacific cod was \$1,083 per metric ton between 1992-2010 (Fissel et al. 2011). A substantial increase in revenue resulted from higher catches under “separated” than “combined” management, when results were scaled up to the size of the actual BSAI population. The increase in catch value under “separated” management would provide an additional \$13,106,000, on average, under unequal population sizes and \$8,448,000 under equal population sizes annually in this simulated BSAI Pacific cod fishery.

Demographic rescue

The demographic rescue effect suggests that populations will escape extinction or bottlenecks by immigration from other populations in the same system if immigration is sufficiently high (Brown and Kodric-Brown 1977). However, dispersal rates that are low enough to result in significant genetic differentiation between two populations did not prevent the smaller population from declining below target levels under inadvertently high fishing pressure (Fig. 3.7). In fact, even dispersal rates two orders of magnitude higher than the ‘best’ estimates for Pacific cod were insufficient for demographic rescue (Fig. 3.7). Higher migration, 10,000 individuals from population B, was sufficient for population A to recover to $B_{40\%}$. Genetic differentiation between populations A and B associated with this level of dispersal was not significant. These results are important for those concerned with the demographics of populations and for those managing marine fish resources. This is the first example based on a genetic IBM simulation, but a review of appropriate spatial scales for management among significantly differentiated populations reached similar conclusions (e.g. Palumbi 2004).

Application to other species

Many examples of distinct stocks within a single management unit exist, some of which document unequal fishing pressure among stocks. On the U.S. west coast, evidence for population structure within management units has been observed in black rockfish, *Sebastes melanops*; Pacific hake, *Merluccius productus*; shortspine thornyhead, *Sebastolobus alascanus*; Pacific Ocean perch *Sebastes alutus*; canary rockfish, *Sebastes pinniger*; and yelloweye rockfish, *Sebastes ruberrimus* (Waples et al. 2008). Examples in the northeast Atlantic include Atlantic cod; haddock, *Melanogrammus aeglefinus*; whiting, *Merlangius merlangus*; blue whiting, *Micromesistius poutassou*; European hake, *Merluccius merluccius*; and Atlantic herring, *Clupea harengus* (Reiss et al. 2009). Norwegian spring herring that spawn off the coast of Norway and in the Barents Sea are managed as a single unit, but are considered two genetic and ecological stocks (Shaw et al. 1999). The coastal stock of Norwegian spring herring is subject to higher exploitation levels due to faster growth and earlier maturation (Holst and Slotte 1998). Disproportionate fishing effort of distinct stocks of northeastern United States and Canadian Atlantic cod stocks has been suggested as a cause for their 1992 collapse (Sterner 2007). Such examples demonstrate that the issues addressed here are not limited to Pacific cod, and may be

applied over a wide range of fish species.

Life history plays a role in how different species may react to the management strategies investigated here. Longer-lived species such as rockfish and groupers will react more slowly to higher fishing pressure, and will recover more slowly when fishing pressure is relaxed. Steepness, the fraction of recruits that are produced when spawning biomass is 20% of its unfished state, will affect whether populations will recover when fishing pressure is relaxed. The value of steepness applied in the model is 0.73, which is in the range of steepness estimated for other species; gadidae: 0.79, clupeidae: 0.71, and enraulidae: 0.62, scombridae: 0.52, sparidae (i.e. New Zealand snapper, *Pagrus auratus*): 0.95 (Myers et al. 1999). Simulations indicated that steepness of 0.9 was sufficient for depleted populations of Atlantic cod to recover regardless of migration rate (Chapter 4), and species with higher steepness will require fewer migrants to recover and vice versa.

Model assumptions

Many assumptions are made in the model, although it was designed to match biological reality as closely as possible. The model does not account for density-dependent factors other than through the relationship between recruitment and spawning biomass. Migration is modeled as a proportion of stock size regardless of the level of depletion, even though recolonization of an empty niche may occur at an increased rate due to a lack of interspecific competition (Waples 1998; Waters et al. 2012). Likewise, depensation, a phenomenon that has been hypothesized to be responsible for slow rates of recovery in Atlantic cod (Rowe et al. 2004) was not included. Depensation in Atlantic cod may be expected due to the fact that Atlantic cod spawn in large groups and fertilization is external; therefore insufficient numbers on the spawning grounds may result in low fertilization rates. Pacific cod may be susceptible to depensation as well, although there is no empirical evidence. Pacific cod spawning behavior is similar to that of Atlantic cod, except that Atlantic cod produce multiple batches of pelagic eggs while Pacific cod deposit only a single batch (Knutsen et al. 2007; Hurst et al. 2009).

The improvement in performance measures when management units are based on the results of genetic testing occurs despite the errors inherent in these tests. With 100 samples and 10 microsatellite loci, the chance of not correctly identifying population structure was 40% or less, and power was proportional to the level of genetic differentiation between populations (Table

3.2). The number of samples and markers required to achieve sufficient power to reject the null hypothesis should be considered before undertaking a genetic study (Ryman et al. 2006). However, 100 samples and 10 microsatellite loci are typical of many studies of marine fish species. The range of F_{ST} values examined is also typical of values observed in marine fish species: 0.0018 – 0.0069 (Waples 1998). The parameterization used here suggests that the application of management units based on the results of a reasonably well-planned out genetic study will be advantageous over a management plan that overlooks population structure.

Migration in the model was limited to spawning individuals, but simulating migration differently may affect the likelihood for demographic rescue. If migration were incorporated at different life history stages, more migrants would be required for the same levels of genetic differentiation. Migration patterns are not fully understood in Pacific cod, but consideration of what is known for this and related species can provide some insight. Gene flow in Atlantic cod appears to be directly linked to larval drift; eggs are retained in fjords and adults have a strong homing tendency (Stenseth et al. 2006; Knutsen et al. 2007). In walleye pollock, larval drift and migration, coupled with large effective population sizes, have been used to explain the lack of population structure (Olsen et al. 2002). In Pacific cod, some level of larval retention and homing to specific spawning areas could explain observed levels of genetic population structure (Shimada and Kimura 1994).

Loss of genetic diversity

An initial goal of this study was to examine whether fishing causes a reduction in genetic diversity in marine fish. Loss of genetic diversity that is associated with traits like local adaptation or evolutionary potential is of interest for conservation. Assessing traits that lead to local adaptation or short-term evolutionary potential in a population requires measuring quantitative genetic variation directly (Reed and Frankham 2001). However, the simulation framework was not a comprehensive tool for detecting loss of genetic diversity because it was limited to neutral markers. The number of alleles at neutral loci is expected to correlate with changes in the size of the population and has been used as a proxy for genetic diversity (Cornuet and Luikart 1996; Garza and Williamson 2001). Loss of genetic diversity at neutral markers has been observed for Hector's dolphin, *Cephalorhynchus hectori* (Pichler and Baker 2000) and New

Zealand snapper, *Pagrus auratus* (Hauser et al. 2002). These examples document loss of genetic diversity, but not all changes in genetic diversity can be observed with neutral markers.

Loss of alleles is more likely when population sizes are small or many rare alleles are present, such as in large populations at mutation-drift equilibrium. Mutation-drift equilibrium is unlikely to have occurred in most wild populations; it may take as long as $4N_e$ generations (Hartl and Clark 1988). The probability of an allele being lost from a randomly mating population in any given generation is $(1-p)^{2N_e}$, where p is the allele frequency (Fa et al. 2011). The number of rare alleles may vary among natural populations, but did not vary in the model because all simulations evolved for the same length of time and generated allele frequencies in the same manner (Appendix 3). Therefore, simulation results did not depart from results that would be predicted from the equation above. In populations the size of the Bering Sea and the Aleutian Islands, loss of neutral alleles did not appear to be a significant concern, even under high fishing pressure. This corresponds with the work of Ruzzante et al. (2001), who found no change in allele frequencies in Newfoundland Atlantic cod despite a decline in population size of two orders of magnitude between the 1960's and 1990s.

The analysis also examined effective population size, based on the Felsenstein-Hill method, which incorporates information on age-specific survival and fertility rates, as well as the concept that longer-lived individuals have more opportunities to reproduce (Waples et al. 2011). The effective population size for the simulated populations did not decline significantly and did not fall below 5,000 in a population of size 8.3×10^4 fished to $B_{20\%}$, remaining at approximately 1.5×10^4 (Fig. 3.5a). When a smaller stock (8.3×10^3 individuals) declined to $B_{20\%}$, the effective population size did decline as low as 500 (Fig. 3.5b). However, these population sizes were scaled down by a factor of 25,000 for computational purposes; therefore, the effective population sizes of the Bering Sea and Aleutian Islands would be proportionally larger as well. Population sizes, even in collapsed stocks are considerably higher than 8.3×10^4 , although this is not always the case. The northern cod, Flemish Cap, and Gulf of St. Lawrence stocks still measure in the millions of fish (Kiselya 1997; DFO 2012; Therkildsen et al. 2010); whereas, Norwegian fjord populations number as low as 1000's of fish (Knutson et al. 2011). A poisson scaling factor, the ratio between the mean and variance in reproductive success, is required when calculating effective population sizes based on the Felsenstein-Hill method (Waples et al. 2011). This value

was set to 1 in the model because no other information is available. However, it likely is much higher than 1, which would result in lower estimates of N_e .

Summary

This study attempts to incorporate the considerable uncertainty associated with incorporating spatial structure in fisheries management. The simulation framework provides an opportunity to investigate the utility of genetic studies in the management of exploited marine fish species in a way that field studies cannot. Results indicate that “separated” management, or incorporation of genetic stock structure information, should be considered as the default strategy to maintain the persistence of distinct stocks when disproportionate fishing effort exists. Incorporation of genetic data into management decisions has benefits to both yield and conservation of individual stocks.

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Table 3.1: Parameters that vary among scenarios: initial spawning biomass in metric tons (SSB_{init}), relative population size, approach for sampling genetics data, management method, harvest control rule, target fishing rate (Tier 3 harvest control rule only), and the number of effective migrants per generation. Asterisk * indicates parameters used in base case scenarios.

Initial BSAI population size	Relative population size	Genetics sampling plan	Management	Harvest control rule	Target Fishing rate	Effective migrants per generation
8.3×10^3	One single population	100 samples from each spatial area*	“Separated”*	40:10 (Tier 3)*	$F_{40\%}$ *	2.5
			“Combined”*			25*
		200 samples from each spatial area.	“Combined then Separated $F_{40\%}$ ”*		$F_{35\%}$	2500
8.3×10^4 *	Two populations (unequal sizes)*	Sample size relative to catch.	“Combined then Separated Tier 5”	Constant (Tier 5)	$F_{30\%}$	10000
1.66×10^5	Two populations (equal sizes)*		“Combined then Separated – Catch = 0”			

Table 3.2: Parameters and performance measures for the six base-case analyses: average catch, the average of the catch in each year of the 100-year projection period (x1000 t); $P(<B_{20\%})$, the proportion of the 100-year projection period that spawning stock size is below $B_{20\%}$ in population A/population B; average biomass, spawning stock biomass in year 100 relative to its unfished size in year 1 of the 10-year burn-in in population A/population B; and θ , which is measured in year 1/year 50 of the projection period. The success rate of the genetic test is shown in the last column, and is based on the genetic test in year 1 under “separated” management or in year 50 under “combined” management (specified in bold). Under “combined and separated” management, the average biomass, $P(<B_{20\%})$, and true θ for the first and second 50 years are shown separately on the first and second lines, respectively. All statistics are averaged over 100 simulations. All simulations were carried out with 25 migrants per generation, base case initial BSAI population size, and at $F_{40\%}$ under a Tier 3 HCR.

Case	Parameterization		Performance measures				
	Mgmt. type	Relative pop. sizes	Avg. catch	$P(<B_{20\%})$	Average biomass	θ (year 1/50)	% correct genetic tests
I	Combined	Unequal	113.4	0.38/0.00	0.22/0.45	-	-
II	Combined	Equal	116.9	0.00/0.00	0.32/0.49	-	-
III	Separated	Unequal	125.5	0.00/0.00	0.36/0.36	0.0035/ 0.0069	100%
IV	Separated	Equal	124.7	0.00/0.00	0.38/0.41	0.0018/ 0.0020	80%
V	Combined, Separated	Unequal	118.6/ 130.7	0.33/0.00 0.00/0.00	0.21/0.45 0.51/0.48	0.0035/ 0.0069	90%
VI	Combined, Separated	Equal	115.2/ 125.2	0.00/0.00 0.00/0.00	0.29/0.45 0.40/0.44	0.0018/ 0.0020	70%

Table 3.3: Sensitivity of the performance measures to target fishing mortality under the Tier 3 and Tier 5 HCRs. Results are for “combined” management, base case initial BSAI population size, and unequal initial population sizes. Tier level; target fishing mortality (F); average catch during the 100-year projection period, the average of the annual yearly catch during the 100-year projection period x1000 t; probability of the stock becoming overfished over all years, $P(<B_{20\%})$ (population A/population B); and spawning biomass in year 100 vs. unfished size in year 1 of the burn-in (population A/population B) are shown. All statistics are averaged over 100 simulations.

Tier	Target F	Avg. catch	$P(<B_{20\%})$	Average biomass
3	$F_{40\%}$	124.0	0.37/0.00	0.22/0.45
3	$F_{35\%}$	123.8	0.56/0.00	0.19/0.44
3	$F_{30\%}$	125.8	0.63/0.00	0.17/0.45
5	-	60.8	0.00/0.00	0.77/0.91

Table 3.4: Proportion of successful genetic tests with different sampling methods, relative population size, and population structure.

True F_{ST} (0.05, 0.95 quantiles)	Relative population size	Number of populations	100	200	Samples proportional to catch
0.0035 (0.0022, 0.0067)	0.2	2	80%	100%	80%
0.0018 (0.0015, 0.0024)	0.5	2	60%	100%	50%
Panmixia	-	1	97%	96%	91%

Fig. 3.1: Pacific cod control rules, Tier 3 control rule (left) and Tier 5 control rule (right; Thompson and Lauth 2012).

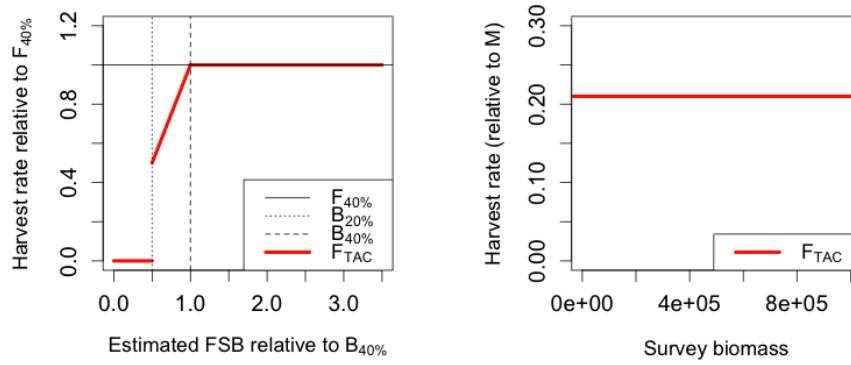


Fig. 3.2: Framework for simulation, including the operating model, selection of management units, stock assessment, harvest control rule, and performance measures.

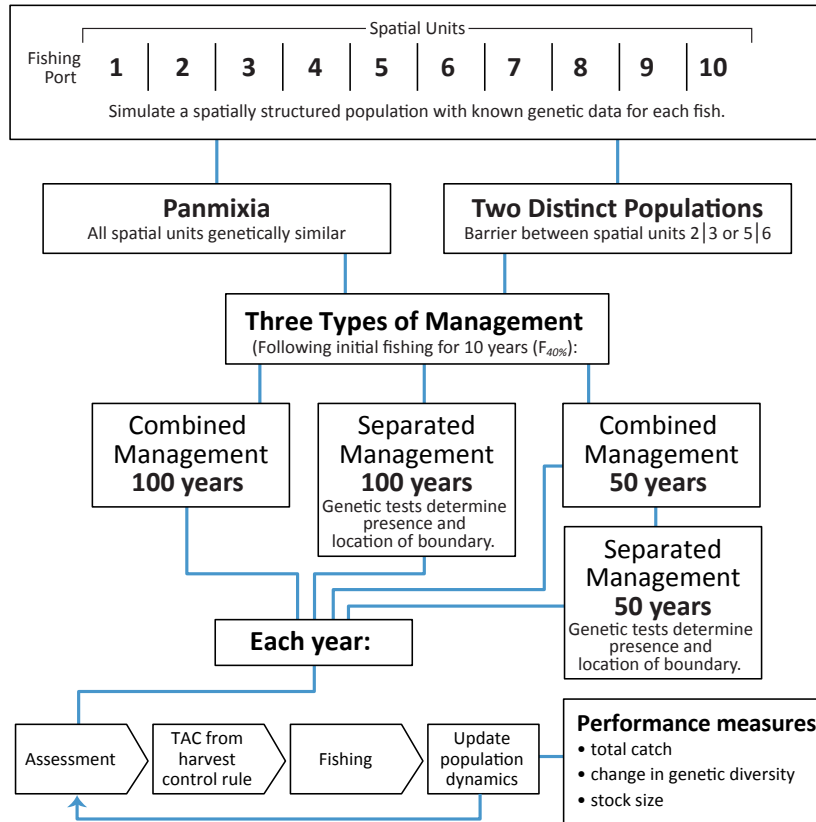


Fig. 3.3: Spatial areas and management units, along with the location of the fishing port. The upper case is referred to as unequal initial population sizes (barrier between spatial areas 2 and 3) and the lower case as equal initial population sizes (barrier between spatial areas 5 and 6). The population nearest the fishing port is referred to as population A and that on the right as population B. Here, management units match true populations, but this is not necessarily the case in a simulation if the genetics test fails to provide the correct result.

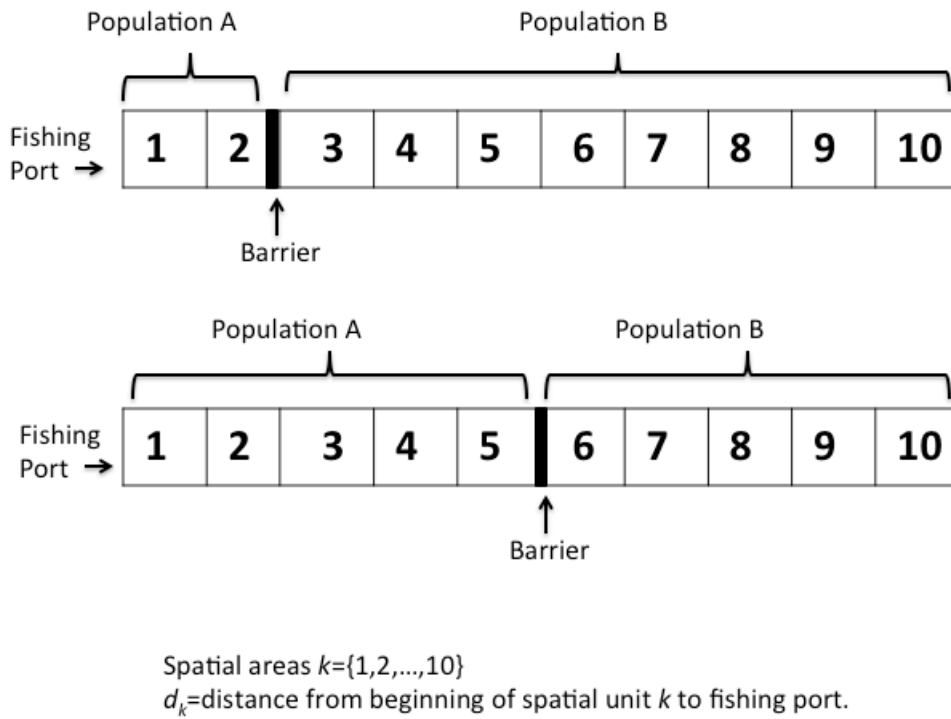
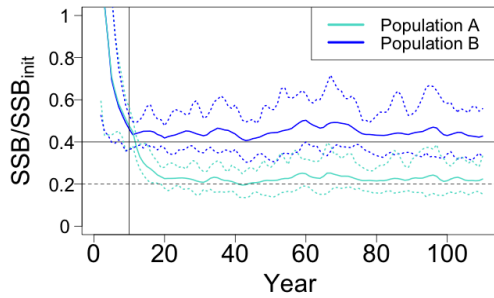
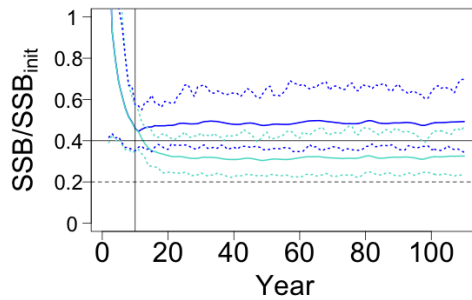


Fig. 3.4: Relative biomass (SSB/SSB_{init}) over the simulated fishing period for each of the six base-case analyses. The solid and dotted horizontal lines respectively demarcate $SSB/SSB_{init} = 0.4$ and $SSB/SSB_{init} = 0.2$, the vertical line at 10 years is the first year of the 100 year projection period, and the vertical line at 60 years indicates the year in which the genetics test is conducted after 50 years of “combined” management. Dotted colored lines represent 5% and 95% quantile intervals of simulated results. Management strategies are “combined” in cases I and II, “separated” in cases III and IV, and “combined then separated” in cases V and VI. Relative population sizes are initially unequal in the left column (I, III, and V) and initially equal in the right column (II, IV, and VI).

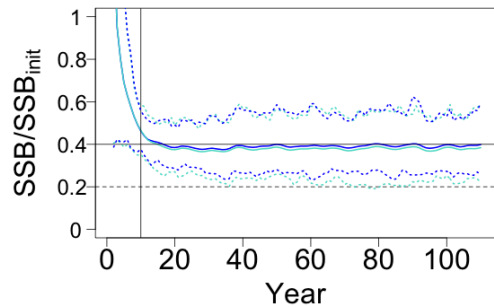
I.



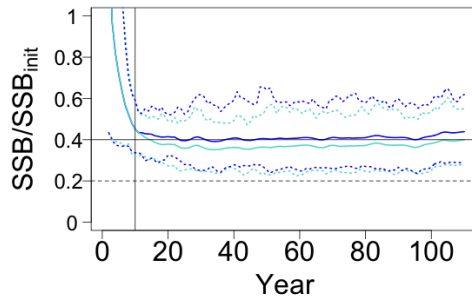
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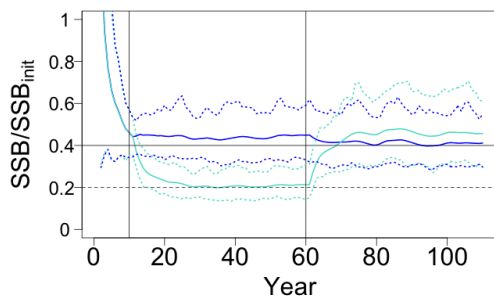
III.



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V.



VI.

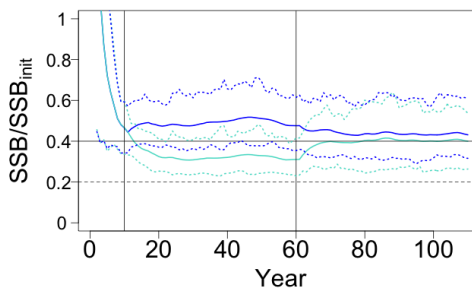
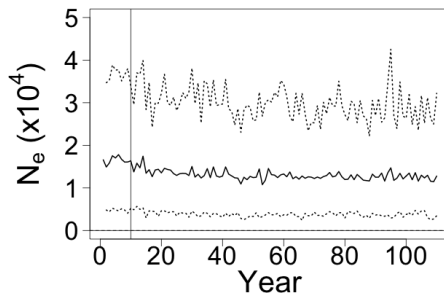


Fig. 3.5: Felsenstein-Hill effective population size (dotted lines are 5% and 95% confidence intervals) for initial spawning biomasses of 10^6 and 10^5 mt reduced to $B_{20\%}$. All statistics are means over 100 simulations. The horizontal line in panel b. highlights Felsenstein-Hill $N_e = 5,000$.

a. Initial stock size: 10^6 t.



b. Initial stock size: 10^5 t.

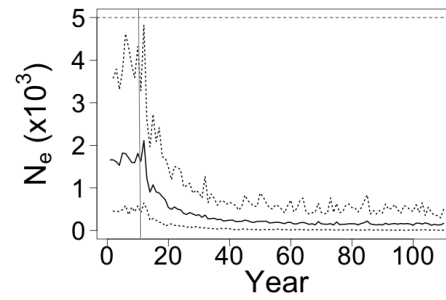
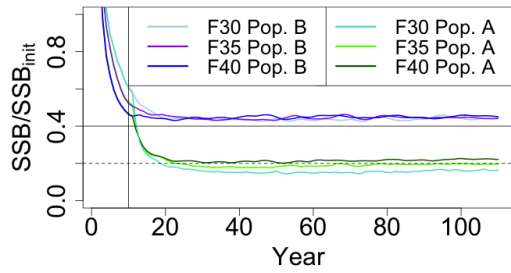


Fig. 3.6: Relative spawning biomass (SSB/SSB_{init}) for three target fishing mortality rates under the Tier 3 HCR ($F_{30\%}$, $F_{35\%}$, and $F_{40\%}$), unequal initial population sizes, an initial spawning biomass of 10^6 t, and “combined” management (panel a), and a Tier 5 HCR (panel b).

a.



b.

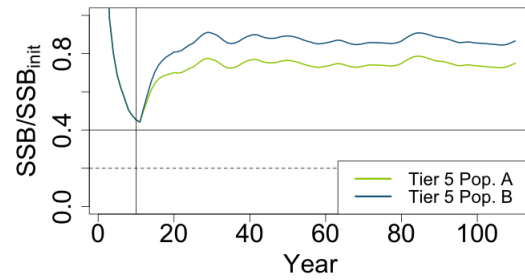
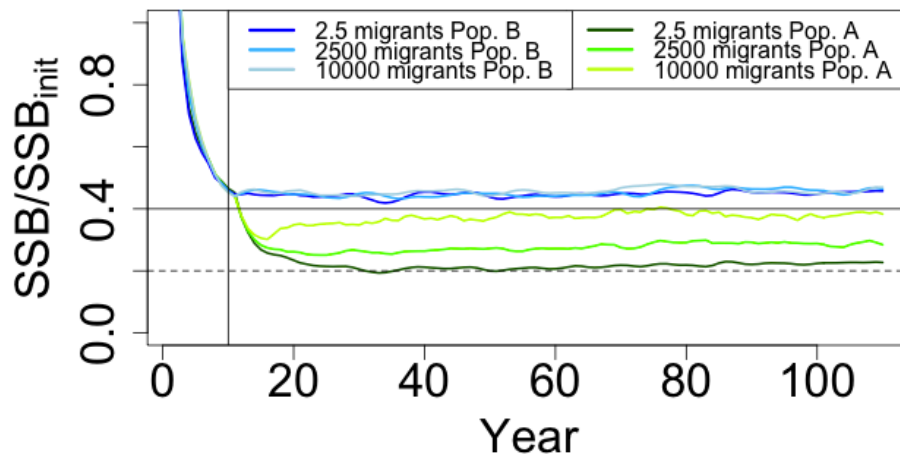


Fig. 3.7: Time-trajectories of expected spawning stock biomass relative to the initial SSB for three dispersal rates when the initial spawning biomass is 10^6 t. The legend refers to effective migrants. The solid and dotted horizontal lines demarcate $SSB/SSB_{init} = 0.4$ and $SSB/SSB_{init} = 0.2$.



Appendix 3

Details of the “true” age-based population dynamics model

The population dynamics of each true genetic population (l) is modeled using an age-structured cohort-based model with parameters given in Table 3.1. Once the initial spawning biomass (SSB_{init}) has been selected, it is converted to initial spawning biomass in each population, \tilde{S}_0^l , based on the relative size of each population and the number of spatial areas in which population l resides (n_l):

$$(App. 3.1) \quad \tilde{S}_0^l = \frac{n_l}{10} SSB_{init}.$$

The initial number of recruits in each true population (l) in the absence of fishing, R_0^l , is calculated using the equation:

$$(App. 3.2) \quad R_0^l = 2\tilde{S}_0^l / \sum_a W_a \tilde{N}_{init,a}^l Q_a,$$

where a indexes age class, W_a is weight-at-age, Q_a is maturity-at-age, and $\tilde{N}_{init,a}^l$ is the number of fish in each age class prior to exploitation relative to the number of age-0 fish. The latter quantity is calculated under the assumption that the population was in unfished equilibrium, given an instantaneous rate of natural mortality, M :

$$(App. 3.3) \quad \tilde{N}_{init,a}^l = \begin{cases} 1 & \text{if } a=0 \\ \tilde{N}_{init,a-1}^l e^{-M} & \text{if } 1 \leq a \leq x-1 \\ \tilde{N}_{init,x}^l e^{-M} / (1 - e^{-M}) & \text{if } a=x. \end{cases}$$

The numbers in each age class in each true population (l) are then scaled to the population size that would result from R_0^l recruits:

$$(App. 3.4) \quad N_{init,a}^l = R_0^l \tilde{N}_{init,a}^l.$$

For years $init+1$, $init+2$, etc., the numbers-at-age are computed allowing for fishing and a Beverton-Holt stock recruitment relationship (Beverton and Holt 1957):

$$(App. 3.5) \quad N_{y+1,a}^l = \begin{cases} \frac{4hR_0^l \tilde{S}_y^l}{\tilde{S}_0^l(1-h) + \tilde{S}_y^l(5h-1)} e^{\delta_R - \sigma_R^2/2} & \text{if } a = 0 \\ N_{y,a-1}^l e^{-(S_{a-1}^f F_y^l + M)} & \text{if } 1 \leq a \leq x-1 \\ N_{y,x-1}^l e^{-(S_{x-1}^f F_y^l + M)} + N_{y,x}^l e^{-(S_x^f F_y^l + M)} & \text{if } a=x, \end{cases}$$

where $N_{y,a}^l$ is the number of fish of age a in population l at the start of year y , \tilde{S}_y^l is the spawning biomass for population l at the start of year y , S_a^f is the selectivity-at-age for the fishery, F_y^l is the instantaneous fully-selected fishing mortality rate during year y for population l , and h is the steepness, or the fraction of R_0^l that is produced when spawning biomass is 20% of its unfished state (App. Table 3.1). Recruitment variation with bias-corrected lognormal error is applied to recruitment in each population in each year, i.e., $\delta_R \sim N(0; \sigma_R^2)$. Recruitment variance is obtained from the mean CV of recruitment estimates using $\sigma_R^2 = \log(1 + CV^2)$.

Subsequent to the initial year, spawning biomass in each population, \tilde{S}_y^l is calculated using:

$$(App. 3.6) \quad \tilde{S}_y^l = 0.5 \sum_a N_{y,a}^l Q_a.$$

The number of spawning males in each population always equals the number of spawning females, and is based on the proportion of individuals in each age group that are expected to be mature that year:

$$(App. 3.7) \quad SP_{y,a}^l = 0.5 N_{y,a}^l Q_a.$$

Catch in numbers of fish of age a in population l during year y , $C_{y,a}^l$, is a function of fishing effort, natural mortality, and numbers-at-age,

$$(App. 3.8) \quad C_{y,a}^l = \frac{S_a^f F_y^l}{S_a^f F_y^l + M} (1 - e^{-(S_a^f F_y^l + M)}) N_{y,a}^l.$$

Finally, the total catch in weight from population l during year y , C_y^l , is calculated as:

$$(App. 3.9) \quad C_y^l = \sum_a W_a C_{y,a}^l.$$

Definitions and acronyms for the model are given in App. Table 3.2.

Parameterizing the population dynamics model

Age is converted to weight using a von Bertalanffy growth function (von Bertalanffy 1957):

$$(App. 3.10) \quad W_a = \psi [L_\infty (1 - e^{K(a-A_0)})]^\gamma,$$

where L_∞ is the mean maximum length, K is a rate constant (year^{-1}), A_0 is the theoretical age, a , at which length is zero, and ψ and γ determine the relationship between length and weight. The populations have an equal number of males and females, but the sexes follow different growth trajectories (App. Table 3.1). The values for the parameters ψ and γ are an average of the regression parameters in each season, weighted by sample size (App. Table 3.1; Thompson and Lauth 2012). The remaining parameters in Equation A10 were estimated for Bering Sea Pacific cod by Stark (2007).

The maturity-at-age is governed by the relationship:

$$(App. 3.11) \quad Q_a = \frac{1}{1 + e^{-(A+ab)}},$$

where A and B are parameters in the relationship (App. Table 3.1). Similar to the 2011 Pacific cod assessment (Thompson and Lauth 2012), maturity-at-age is based on parameter estimates calculated in Stark (2007) from $n = 129$ cod for which the mean age at 50% maturity was estimated to be 4.9 years.

The stock assessment for Pacific cod includes nine fishing fleets (trawl, longline, and pot, during each of three seasons). Rather than modeling all nine fleets explicitly, fishery selectivity-at-age in the operating model, S_a^f , is an average over fleets, with the weights equal to the number of fish caught by each fleet (App. Fig. 3.1).

The Beverton-Holt stock-recruitment relationship does not fit the spawning biomass and recruitment data for Pacific cod well (Thompson and Lauth 2012) because recruitment is likely highly dependent on environmental factors (Tyler and Crawford 1991; Sinclair and Crawford 2005). The BSAI Pacific cod assessment model is not able to estimate a reliable stock-recruitment relationship and therefore does not estimate steepness (h). Pacific cod is assessed as a Tier 3 stock in which F_{MSY} is assumed to occur at $F_{35\%}$. For this study therefore, steepness is selected so that $F_{MSY} = F_{35\%}$: $h = 0.731283$. For the Tier 3 HCR, the TAC (which equals the

acceptable biological catch, ABC) is set based on a fully-selected fishing mortality rate of $F_{40\%}$. The TAC equals the amount of catch in each year.

Migration

Fish move freely among spatial areas, but migration is limited among true populations; therefore, the number of fish in the n_l spatial areas (k), within population (l) will have equal population size and age-structure at the start of each year prior to fishing:

$$(App. 3.12) \quad N_{y,a}^k = \frac{N_{y,a}^l}{n_l}, \text{ for } k \in l.$$

Migration among populations is considered “effective,” limited to individuals that successfully reproduce and therefore contribute genes to the recipient population. This property is implemented in the IBM by selecting effective migrants randomly from spawning individuals.

Dispersal among true populations is defined in the genetics simulations as dispersal per generation, and is rescaled into dispersal per year by dividing dispersal per generation by the number of years per generation. The generation length, defined as the average age of parents of a newborn cohort, is estimated to be approximately 6 years based on the demographic properties of the model, including the fishing mortality rate (App. Table 3.1) and the estimated maturity-at-age (Stark 2007; Waples et al. 2011). Dispersal between populations is defined by the probability matrix $P_{l=1,l=2}$ that is at equilibrium (equal number of migrants are exchanged) when populations are at their initial size:

$$(App. 3.13) \quad P_{l=1,l=2} = \begin{bmatrix} p_{1,1} & p_{1,2} \\ p_{2,1} & p_{2,2} \end{bmatrix},$$

where $p_{l,l+1} N_{init}^{l=1} = p_{l+1,l} N_{init}^{l=2}$, and N_{init}^l is defined as:

$$(App. 3.14) \quad N_{init}^l = \sum_a N_{init,a}^l.$$

After the first year, populations A and B will produce different numbers of emigrants depending on their relative population sizes.

Simulating genetics data in the individual-based model

Initial allele frequency distributions for 10 microsatellite loci were simulated under the stepwise mutational model (Ohta and Kimura 1973) in a single population that undergoes random mating and mutation for 1,000 generations, given an effective population size (N_e) of 3,000 and a mutation rate (μ). This parameterization provides simulated alleles with average heterozygosity characteristic of marine fish; typically 0.79 ($\sigma = 0.26$), with 19 ($\sigma = 6.6$) alleles on average (DeWoody and Avise 2000), while a recent study on Pacific cod using 17 loci reported average heterozygosity of 0.79 ($\sigma = 0.18$) and 22.4 ($\sigma = 17.9$) alleles per locus (Spies 2012). The mutation rate for each locus and simulation is drawn from the beta distribution with $\mu = 0.375$, $\sigma = 0.300$. The beta distribution provides values between 0 and 1; results are scaled down by a factor of 100 to provide mutation rates in the range of those expected for microsatellites in marine fish (10^{-4} - 10^{-2}), and a maximum value of 10^{-2} .

Once allele frequencies have been established, alleles (two per individual for each microsatellite locus) are selected randomly and with replacement for each individual from the initial distribution to establish a single homogeneous population of the effective population size of the entire system ($N_e \sim 83,000$). Prior to the model projection, this population is split and allowed to evolve for 2,000 generations, a time period selected to match that since cod recolonized the North Pacific following the last glacial maxima, based on the generation time of Pacific cod in its unfished state (approximately 8 years) and the estimated number of years since glaciers retreated and colonization was possible in the North Pacific Ocean (approximately 15,000-16,000 years ago; Canino et al. 2010). The signal of population expansion of Pacific cod predates 15,000-16,000 years ago, may be integrated over several ice-age cycles, and does not correlate with a particular climactic event (Canino et al. 2010). However, it provides a rough framework for the evolutionary past of these populations.

After 2,000 generations, populations are likely to have reached migration-drift equilibrium, but not mutation-drift equilibrium. Migration-drift equilibrium generally takes place in a shorter period of time than mutation-drift equilibrium, and the number of generations for F_{ST} to move halfway to the equilibrium value is $T_{50} = \frac{\ln(0.5)}{\ln[(1-m)^2(1-1/(2N_e))]}$ in an island model (Whitlock 1992). The N_e/N ratio has not been explored in the literature for Pacific cod; however, many estimates have been made for Atlantic cod. Using the N_e/N estimate (2.27×10^{-4}) by Therkildsen

et al. (2010) for southern Gulf of St. Lawrence Atlantic cod, the effective population size for Aleutian Islands and Eastern Bering Sea Pacific cod would be roughly 32,600 and 163,440, respectively. Applying the harmonic mean of these effective population sizes, 54,358, and the migration rate based on these values, 4.60×10^{-4} , results in a T_{50} estimate of 746 generations. Mutation-drift equilibrium can be estimated by $4N_e$, which is far longer than the time since the last glacial maxima (Hartl and Clark 1988). In reality, most species are not expected to be at equilibrium between mutation and drift (Hartl and Clark 1988). For each simulation, new populations of fish are generated and evolved as described above.

The number of individuals and spawners (individuals designated to produce the following year's newborn cohort) in each age group in each year is randomly rounded up or down to the nearest integer to overcome the discrepancy between the continuous cohort-based population dynamics model and the discrete IBM. Although the IBM distinguishes between males and females, the number of males and females is equal, as is the number of males and females that spawn at each age during each year. Mortality rates in the cohort-based model are used to update the number of individuals in the IBM.

The Felsenstein-Hill approach to measuring effective population size incorporates the generation length (L_{gen}), the variance in reproductive success (V_k), and the recruitment in population l in year y , R_y^l (Waples et al. 2011): $N_e = \frac{4R_y^l L_{gen}}{V_k + 2}$.

Fishing mortality

Two harvest control rules are used to determine future fishing mortality rates, the NPFMC Tier 3 and Tier 5 control rules (Fig. 3.1; NPFMC 2012). Fishing effort takes place with higher intensity in the spatial areas nearest to the fishing port within each management unit. A gravity model, a class of model designed to represent spatial interaction (Tinbergen 1963), is used to represent relative fishing effort E_y^k in each spatial area. The model is a function of the exploitable biomass in spatial area k at the start of year y , and the distance between the fishing port and that particular spatial area, d^k , i.e.:

$$(App. 3.15) \quad E_y^k = \frac{\frac{1}{(d^k)^\omega} S_a^f W_a N_{y,a}^k}{\sum_{k' \in J} \frac{1}{(d^{k'})^\omega} S_{a'}^f W_{a'} N_{y,a'}^{k'}} .$$

The term w is a scaling factor that is adjusted so that the ratio of the mean fishing mortality rate between the Aleutian Islands and the EBS matches desired value, i.e. 215%.

Within management unit l , fishing mortality in each spatial area is proportional to relative fishing effort, i.e.:

$$(App. 3.16) \quad F_y^k = E_y^k \tilde{F}_y,$$

where \tilde{F}_y is the fishing mortality rate by stock in year y .

Rationale for scaling down population sizes

The size of the individual based model was scaled down for computational efficiency from the estimated census size of 2.09×10^9 fish by a factor of 2.5×10^4 , to a base case size of 8.3×10^4 fish. Sensitivity to population size was tested using population sizes both half and double this base size. This adjustment did not affect the results because both the population dynamics and the N_e/N ratio are scale invariant. The number of migrants is not dependent on census population size, and was therefore held constant. An equation for estimating migration rates between two populations from genetic data based on the assumptions of Wright's island model (Wright 1931; Wang 2004, Eqn. 4) provides a relationship between the number of migrants into a population every generation and F_{ST} . Wright's island model makes several assumptions: an infinite number of populations exist, each with N_e diploid individuals. In addition, each population gives and receives a fraction m of its individuals into and from a migrant pool each generation, breeding is random, generations are non-overlapping, alleles are neutral, equilibrium has occurred between genetic drift and migration, and there is no mutation (Waples 1998; Whitlock and McCauley 1999). The equation can be expressed as $F_{ST} = \frac{1}{4\left(\frac{n}{n-1}\right)^2 N_e m + 1}$ (Wang 2004), where n is the

number of populations, and rewritten $\frac{1}{16\left(\frac{N_e}{N}\right)M + 1}$, in the case of two populations, where m is

migration rate ($m=M/N$), N is census size, and M is the number of migrants. The equation shows that if F_{ST} and the N_e/N ratio are held constant, then the number of migrants remains constant as well. This also requires that the level of allelic richness be held constant (O'Reilly et al. 2004).

Data generation from the population dynamics models

The “perceived” population dynamics is derived from the “true” state and dictates TAC. Fishing first occurs during the 10-year burn-in and then in each year of the 100-year projection period. Fishing mortality equals $F_{40\%}$ during the historical fishing period. This value was chosen because it is the target fishing mortality for a healthy fish stock according to the NPFMC, and will result in stock sizes near the target levels. The perceived population dynamics (for either one or two populations) is based on annual simulated stock assessments that provide estimates of total and spawning biomass.

Stock assessments estimate the number of animals of age a in management unit j at the start of year y , $\hat{N}_{y,a}^j$. These values are assumed to be unbiased and distributed about the true numbers-at-age at the start of the year, i.e.:

$$(App. 3.17) \quad \hat{N}_{y,a}^j = [\sum_{k \in j} N_{y,a}^k] e^{\varepsilon_y^j - (\sigma_A^j)^2/2}, \quad \varepsilon_y^j = \rho \varepsilon_{y-1}^j + \sqrt{1 - \rho^2} \eta_y^j, \quad \eta_y^j \sim N(0; (\sigma_A^j)^2),$$

where ε_y introduces autocorrelated error among annual assessments, η_y^j is a random normal variable based on the variance in the assessed estimate of abundance, and r is the parameter which determines the amount of autocorrelation (App. Table 3.1). This same error parameter is applied to recruitment estimates. The value of 0.707 was chosen for r , which implies that half the variance is due to autocorrelation. The proportion of variance in each management unit is determined by the CV for the estimate of abundance for the entire simulated area that includes all 10 spatial areas (CV_A) and the size of each management unit, n_j :

$$(App. 3.18) \quad (\sigma_A^j)^2 = \log \left(\frac{10}{n_j} CV_A^2 + 1 \right).$$

The perceived numbers-at-age are used to compute a time-series of perceived spawning biomasses for management unit j . The simulated estimates of spawning biomass from the surveys are generated using the equation:

$$(App. 3.19) \quad \hat{S}_y^j = 0.5 \sum_a W_a [\sum_{k \in j} \hat{N}_{y,a}^k] Q_a e^{\phi_y^j - (\sigma_S^j)^2/2}; \quad \phi_y^j \sim N(0; (\sigma_S^j)^2),$$

where σ_s^2 represents variability among survey estimates of biomass (App. Table 3.1). The variance in the estimates of spawning biomass for each management unit j is calculated as:

$$(App. 3.20) \quad (\sigma_s^j)^2 = \log \left(\frac{10}{n_j} CV_s^2 + 1 \right).$$

The two harvest control rules set the TAC as follows:

1. Tier 3: The ABC control rule (Fig. 3.1; Thompson and Lauth 2012) sets the target fishing mortality, \hat{F}_y^j , based on the status of the spawning biomass relative to $B_{40\%}$ and $B_{20\%}$. Because $B_{40\%}$ is not an obtainable quantity, a proxy implemented in NPFMC Pacific cod stock assessments is used:

$$\hat{B}_{40\%} = \bar{R} * SPR_{F=0.4},$$

where \bar{R} is the average estimated recruitment over the entire management period through the current year, and $SPR_{F=0.4}$ is the expected spawning biomass per recruit when fishing mortality is $F_{40\%}$ (Thompson and Lauth 2012). $SPR_{F=0.4}$ is calculated similarly to equation A3, except that fishing mortality is set at $F_{40\%}$. Fully-selected fishing mortality is set at $F_{40\%}$ if the perceived spawning biomass is higher than the perceived value for $B_{40\%}$, and declines linearly with biomass if perceived spawning biomass is between $B_{20\%}$ and $B_{40\%}$. Fishing ceases if perceived spawning biomass drops below $B_{20\%}$. Given the target fishing mortality, the TAC is computed using the equation:

$$(App. 3.21) \quad TAC_y^j = \sum_a W_a \hat{N}_{y,a}^j \frac{S_a^f \hat{F}_y^j}{S_a^f \hat{F}_y^j + M} \left(1 - e^{-(S_a^f \hat{F}_y^j + M)} \right).$$

2. Tier 5: The Tier 5 harvest control rule uses an estimate of natural mortality and simulated estimates of spawning biomass from the surveys to determine the TAC (NPFMC 2012). Here, the TAC is 21% of the product of natural mortality and the estimate of survey-selected biomass, i.e., $TAC = 0.21 \hat{S}_y^j M$.

The TACs (which are set by management unit, j) are used to calculate the actual fishing mortality rates by stock, \tilde{F}_y . There are four cases; in each case TAC_y is known for each management unit and \tilde{F}_y will be determined based on the following equations:

1. One population, one management unit. The value for \tilde{F}_y for year y is found so that:

$$TAC_y = \sum_k \sum_a W_a N_{y,a}^k \frac{S_a^f E_y^k \tilde{F}_y}{S_a^f E_y^k \tilde{F}_y + M} \left(1 - e^{-(S_a^f E_y^k \tilde{F}_y + M)} \right).$$

2. One population, multiple (n) management units. This case occurs when the genetic test incorrectly identifies a population boundary. The value of the parameter \tilde{F}_y for year y is found so that catch equals the sum of TAC in the n management units.

$$TAC_y^1 + \dots + TAC_y^n = \sum_k \sum_a W_a N_{y,a}^k \frac{S_a^f E_y^k \tilde{F}_y}{S_a^f E_y^k \tilde{F}_y + M} \left(1 - e^{-(S_a^f E_y^k \tilde{F}_y + M)} \right).$$

3. “Combined” management of two populations: two populations, one management unit. For each of the $l=2$ populations, the value of the parameter \tilde{F}_y for year y is found so that:

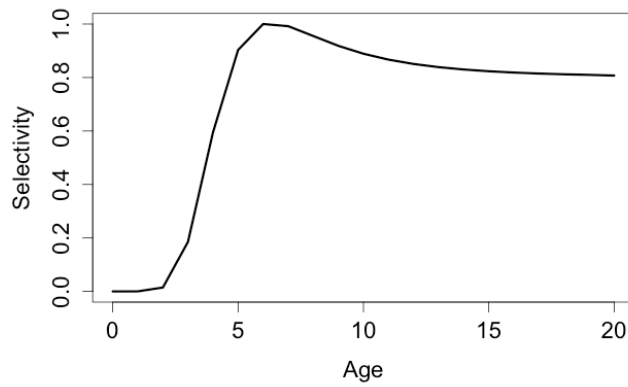
$$TAC_y = \sum_k \sum_a W_a N_{y,a}^k \frac{S_a^f E_y^k \tilde{F}_y}{S_a^f E_y^k \tilde{F}_y + M} \left(1 - e^{S_a^f E_y^k \tilde{F}_y + M} \right).$$

4. “Separated” management of two populations: Two populations, two management units.

- 1) The value of two parameters \tilde{F}_y^1 and \tilde{F}_y^2 for year y are found so that:

$$TAC_y^j = \sum_{k \in j} \sum_a W_a N_{y,a}^k \frac{S_a^f E_y^k \tilde{F}_y^j}{S_a^f E_y^k \tilde{F}_y^j + M} \left(1 - e^{S_a^f E_y^k \tilde{F}_y^j + M} \right).$$

App. Fig. 3.1: Selectivity-at-age for the fishery.



App. Table 3.1: Values for the parameters of the operating model.

Parameter	Application	Parameter values		Reference Parameter Values
		Males	Females	
ψ	Weight-at-age	6.537×10^{-6}		Thompson and Lauth 2012
Γ	Weight-at-age	3.164		Thompson and Lauth 2012
M	Natural mortality	0.34 yr^{-1}		Thompson and Lauth 2012
x	Maximum age	20yr		Thompson and Lauth 2012
L_{∞}	Length-at-age	110.06 cm	120.39 cm	Stark 2007
K		0.1449 yr^{-1}	0.1277 yr^{-1}	Stark 2007
A_0		-0.1814 yr	-0.2233 yr	Stark 2007
A (logistic y-intercept)	Maturity-at-age	-	-4.7143	Stark 2007
B (logistic slope)		-	0.9654	Stark 2007
CV_A	Assessment CV	0.060		Thompson and Lauth 2012
σ_R^2	Recruitment variance	0.408		Thompson and Lauth 2012
CV_S	Survey CV	0.084		Thompson and Lauth 2012
ρ	Autocorrelation parameter	0.707		Assumed
ϕ_y	Observation error (in year y)	$\sim N(0; \sigma_S^2)$		
η_y	Assessment error (in year y)	$\sim N(0; \sigma_A^2)$		
δ_R	Recruitment error	$\sim N(0; \sigma_R^2)$		
w	Relative fishing effort	1.15		This study – used to achieve 215% higher fishing mortality in population A

App. Table 3.2: Definitions and acronyms.

a	Index for age.
$B_{X\%}$	X% of the female spawning biomass that would result from an average cohort if fishing were eliminated.
$\hat{B}_{40\%}$	A proxy for $B_{40\%}$ based on average estimated recruitment and expected spawning biomass per recruit.
$C_{y,a}^*$	Catch in numbers in year y , at age a . Asterisk may represent one of three spatial scales: spatial area k , management unit j , or population l .
C_y^*	Total catch in weight in year y . Asterisk may represent management unit k, j , or population l .
d_k	Distance between spatial area k and the fishing port.
ϵ_y^j	A first order autoregressive standard random variable applied to assessment simulation applied to management unit j .
$E_{y,k}$	Normalized fishing pressure over all (n_j) spatial areas within each management unit j .
F_y^*	The instantaneous fishing mortality, or exploitation rate in year y . Asterisk can represent k, j , or l .
$F_{40\%}$	The fishing mortality at which spawning biomass-per-recruit is 40% of its unfished level.
F_{MSY}	The fishing mortality that produces the maximum sustainable yield, the maximum level at which a natural resource can be routinely exploited without long-term depletion.
F_{ST}	A measure of population differentiation based on genetic structure.
\tilde{F}_y^j	True fishing mortality rate in year y and management unit j .
\hat{F}_y^j	Target fishing mortality in year y and management unit j .
\tilde{F}_y	Fishing mortality rate by stock in year y .
h	Steepness, the fraction of R_0 when spawning biomass is 20% of its unfished state.
η_y^j	A random normal variable based on the variance in the assessed estimate of abundance.
i	Index for management-unit specific fishing mortality.
j	Index for the management units.
k	Index for the 10 spatial areas.
l	Index for true population.
L	Fork length in cm.
L_{gen}	Generation length.
M	The instantaneous rate of natural mortality.
Management unit	Adjacent spatial areas that are managed as a group.
N_{init}^l	Total population size when populations are at their initial size.
$N_{init,a}^l$	Total population size of age a fish when populations are at their initial size.
$\hat{N}_{y,a}^j$	Estimated number of animals of age a in management unit j at the start of year y . A k in place of the j indicates that the statistic refers to a spatial area.
$\tilde{N}_{init,a}^l$	Total initial population size of age a fish when there is one recruit.
$N_{y,a}^*$	Number of fish in year y , of age a . Superscript * may represent one of three spatial scales: spatial area k , management unit j , or population l .
N_e	Effective population size, a measure of the genetic diversity in the population (expressed in terms of number of fish).
N	The census size of the population.
n_j	The number of spatial areas within management unit j .
n_l	The number of spatial areas within population l .
P	Matrix of probabilities of fish movement among true populations in a given year.

$p_{l,l+1}$	The probability of a fish migrating from population l to population $l+1$ in a given year.
<i>Population</i>	Groups of individuals that can mate with any other individual, also known as genetic stocks.
Q_a	Proportion of fish mature at a given age.
\bar{R}	The average estimated recruitment over the entire management period through the current year
R_*^l	Recruitment to population l , where asterisk * can indicate at the start of year y in the absence of fishing, or at year 0.
S_a^f	Fishery selectivity at age a .
\tilde{S}_0^l	Initial spawning biomass in population l .
\tilde{S}_y^l	Spawning biomass in year y and population l .
\hat{S}_y^j	Estimated spawning biomass in year y and management unit j .
$SP_{y,a}^l$	The number of spawners at age a (same for both males and females) in year y and population l .
$SPR_{F=0.4}$	The expected spawning biomass per recruit when fishing mortality is $F_{40\%}$.
Spatial area	Each of the 10 boxes in the simulated spatial area.
SSB_{init}	Initial spawning stock biomass for the entire simulated area (10 spatial areas).
σ_A^j	Standard deviation of the survey estimates of total biomass in management area j .
σ_R	Standard deviation of recruitment.
σ_S^j	Standard deviation of assessed spawning biomass in management area j .
θ	Unbiased estimator of genetic population structure, based on Wright's F_{ST} (Wright 1965; Weir and Cockerham 1984).
<i>TAC</i>	Total allowable catch.
V_k	Variance in reproductive success.
W_a	Weight at age.
x	Maximum age.
y	Index for year.

Chapter 4: A simulation approach to managing isolation-by-distance stock structure in marine fish, Pacific cod and blackspotted rockfish: Where do we draw the line?

Abstract

There is no established management protocol for stocks subject to isolation-by-distance (IBD) stock structure. This study analyzes several management strategies for marine fish species subject to IBD using a simulation framework, Pacific cod in the Aleutian Islands (AI) and blackspotted rockfish in the Eastern Bering Sea (EBS) and Aleutian Islands. A one-dimensional stepping stone model with 10 demes was used for the simulation framework, and was intended to mimic the linear oceanographic configuration of the EBS and AI and other marine exploited species along the continental shelf. Estimates of movement rates between demes were based on the degree of isolation by distance observed in empirical studies. Overall, management strategies performed similarly for the two species, but the longer-lived rockfish declined and recovered more slowly. The performance of spatial assessment and management methods depended on how the range was split. Splitting anywhere within the range produced fewer demes falling below target and threshold biomass levels and higher catches than managing the entire range as a single unit. Optimal management strategies grouped management units by demes with similar relative fishing effort. Inbreeding effective population size remained above conservation thresholds of 5,000, regardless of management strategy. Catch was equally high when each deme was assessed and managed separately or under catch cascading; therefore, catch cascading was identified as an effective alternative to multiple stock assessments.

Introduction

Most marine fish species do not occur as a single homogenous group, but are divided into populations with some degree of isolation (Laikre et al. 2005). Such populations react independently to perturbations, such as environmental fluctuations and exploitation. Populations with limited connectivity may adapt to local environmental conditions, resulting in differences in morphological and life history characters. These aspects of population structure may be important for the survival of species in changing environments, may reduce temporal fluctuations in species abundance (Hilborn et al. 2003) and may prevent fisheries closures due to low abundance, a phenomenon known as the portfolio effect (Schindler et al. 2010). Dispersal among populations can prevent extinction and aid in recovery from high fishing mortality if immigration is sufficiently high, a concept known as the demographic rescue effect (Brown and Kodric-Brown 1977). Genetically distinct stocks with different carrying capacities, natural mortality, or growth rates that are managed as a single stock can be more vulnerable to overexploitation (e.g. Martien et al. 2013; Fu and Fanning 2004; Dougherty et al. 2013). If populations are lost, genetic diversity can also decline, which may result in compromised productivity and a higher risk of population collapse (Lacy 1987, Stephenson 1999, Sterner 2007, Holland and Herrera 2010). Therefore, information on stock structure can be important for the management of marine fishes. Unrecognized stock structure within a single management unit can result in overexploitation of more vulnerable populations when fisheries are localized (Taylor 1997; Fu and Fanning 2004).

Levels of migratory exchange may be limited by distance or environmental features, resulting in a series of populations that are more connected to proximate than to distant neighbors (Selkoe et al. 2008). Such a pattern can result in isolation by distance stock structure (Wright 1943; Slatkin 1993), where genetic differentiation increases with geographic distance. For management, this can leave a confusing picture of overall significant genetic differentiation without clear population boundaries.

Isolation by distance stock structure is common in marine fish species, likely due to a combination of continuous distributions and lack of barriers to migration. This type of population structure has been identified in species such as copper, brown, and grass rockfishes along the United States west coast (*Sebastes caurinus*, *S. rastrelliger*, and *S. auriculatus*; Buonaccorsi et al. 2002, 2004, 2005), Pacific ocean perch off Alaska (*Sebastes aleutus*; Palof et al. 2011),

Northern rockfish in the Bering Sea and Aleutian Islands (BSAI) region of Alaska (*Sebastes polyspinis*; Gharrett et al. 2012), Atlantic cod off Newfoundland and Labrador (*Gadus morhua*; Beacham et al. 2002), blackspotted rockfish (*S. melanostictus*) in the BSAI (Spencer and Gharrett 2010), and Pacific cod along the North American coast (Cunningham et al. 2009) and within the BSAI (Spies 2012).

The finding of isolation by distance in Pacific cod throughout their North American range and blackspotted rockfish in the BSAI represent two examples of IBD that have not been reconciled with fishery management (Cunningham et al. 2009; Spencer and Rooper 2010). The two species are found along the Aleutian chain and on the Eastern Bering Sea shelf and slope off Alaska, and are commercially exploited in that region. Blackspotted rockfish are managed as a species complex with rougheye rockfish in the BSAI (Spencer and Rooper 2010). This complex was managed as a single management unit in the Aleutian Islands until 2010 when information on stock structure motivated the total allowable catch (TAC) be split into two management units, 1) the Western and Central Aleutian Islands and 2) the Eastern AI and the EBS (Spencer and Rooper 2010). Pacific cod were managed under a single TAC in the BSAI until 2013, when separate assessments and TACs were implemented for the Bering Sea and the Aleutian Islands (Thompson 2013; Thompson and Palsson 2013).

The current analysis examines several management strategies for Pacific cod in the Aleutian Islands (AI) and blackspotted rockfish in the Bering Sea and Aleutian Islands (BSAI) based on their IBD stock structure. The model used here incorporates dispersal rates based on estimates from isolation by distance in empirical studies. The mean dispersal distance, the distance traveled between the birthplace of a parent and that of its offspring based on the IBD relationship has been estimated at 500 km or less for blackspotted rockfish (Spencer and Rooper 2010) and on the order of 100 km for Pacific cod (Cunningham et al 2009). These values are much smaller than the linear distance of the BSAI management unit, which spans approximately 1,000 km along the Bering Sea shelf and 1,500 km along the Aleutian Island chain (Fig. 4.1). Here, the subpopulation, or deme, is defined as a group of individuals who come from an area the size of the dispersal distance, a unit that can be estimated from the slope of the IBD relationship (Rousset 1997). The model imposes unequal fishing effort by simulating a single fishing port on one side of the spatial framework of 10 linearly arranged demes.

Pacific cod and blackspotted rockfish have considerably different life histories; the generation length of blackspotted rockfish has been estimated at 53 years but they have been observed as old as 121 years (Spencer and Rooper 2010). In Pacific cod the generation length has been estimated to be 8 years (Canino et al. 2010), and they live up to 25 years, reaching approximately 1 meter and 15 kg (Thompson and Lauth 2012). The age at 50% maturity for Pacific cod is estimated at 4.9 years in the BSAI (Stark 2007), and 19 years for blackspotted rockfish (McDermott 1994). Blackspotted rockfish mature later in life, grow slower and suffer lower natural mortality than Pacific cod (Spencer and Rooper 2010).

Arbitrarily implementing finer scale management units has been suggested as a precautionary approach to managing isolation by distance (Cunningham et al. 2009; Gharrett et al. 2012). The simulations of this paper are designed to test the following hypothesis: “splitting a management unit anywhere performs better than not splitting it at all.” The hypothesis is tested by splitting a single management unit, in which IBD stock structure is present, into two management units three different ways, representing three different arbitrary choices. These are compared with a “control”, in which the entire area is a single management unit. We also examine an unrealistically complicated scenario: splitting the simulated management area into 10 management units, in which assessments are conducted and Total Allowable Catch (TAC) is set for each management unit. Splitting a single management area into too many management units may result in loss of precision in estimates of abundance and status relative to reference points (Dougherty et al. 2013). Therefore, a catch cascading strategy (IWC 1994; Punt and Donovan 2007) was implemented as an alternative to splitting the entire management area into 10 management units. In this strategy, a single assessment is performed, but the TAC in individual management units is proportional to survey estimates of spawning biomass in that management unit (Fig. 4.2). The effectiveness of the various management strategies is summarized using several performance measures.

Methods

A standard one-dimensional stepping stone model was used for the simulation framework. The linear framework was intended to mimic the oceanographic configuration of the EBS and AI and other marine exploited species along the continental shelf. The stepping-stone model consisted of 10 “demes”, or subpopulations, along a linear framework, and migration was limited to adjacent

demes in each generation. The spatial scale of demes was based on the dispersal distance; 130 km was used in the case of Pacific cod (Cunningham et al. 2009) and 250 km in blackspotted rockfish (Spencer and Gharrett 2010).

An initial goal of the study was to estimate dispersal rates among demes based on observed slopes in the isolation by distance relationship. This was done for each species using theoretical models, estimates of the IBD slope, the N_e/N ratio, and unfished population size (Appendix 4). An operating model simulated the population dynamics of isolation by distance genetic population structure, and was parameterized two ways, one for each species (Appendix 4). The simulation framework followed a specific timeline: populations were fished at $F_{40\%}$, the fully-selected¹ fishing mortality rate that reduces the spawning biomass to 40% of its unfished size, for a 10-year “historical period” to produce a population in a fished state, and then the populations were projected forward under various management strategies for another 100 years. The populations were projected into the future 100 times under each management strategy to capture variability in the data available for assessment purposes as well as in the population dynamics. The operating model is described in detail in Appendix 4, and summarized below (Fig. 4.3):

1. Spatially-biased fishing pressure was achieved via a single fishing port on the left side of the linear spatial framework (Fig. 4.2). Fishing effort followed a gravity model so that it was proportional to the exploitable biomass in each deme and inversely proportional to the distance between the fishing port and that particular deme (App. Eqn. 4.17).
2. Initial population size was specified to match estimates of the census unfished population sizes of Pacific cod in the Aleutian Islands and blackspotted rockfish in the Bering Sea and Aleutian Islands.
3. Simulated survey data were collected from each of the 10 demes in each year, with uncertainty based on the standard deviations from the actual survey estimates. An assessment based on survey data within each management unit was conducted during each year of the 100-year fishing period. These data were used by six management strategies to determine the annual TAC, and hence the annual fishing mortality by deme.
4. Results were summarized over all simulations using the following performance measures: (a) spawning stock biomass of each deme, relative to the initial amount of spawning biomass, and compared to management target goals (b) fishing mortality in each deme, (c) average

¹ The fishing mortality rate applied to fish of the age with the highest probability of being caught by that gear.

annual fishery catch, measured in terms of the catch in the entire management area during the second 50 years of the simulation, and (d) effective population size.

Management strategies

All management strategies incorporated a Tier 3 harvest control rule, similar to protocols followed by the North Pacific Fisheries Management Council (NPFMC 2012; App. Fig. 4.1). Under this control rule, the target biomass is $B_{40\%}$, 40% of the female spawning biomass that would result from an average cohort without fishing, and the threshold biomass is $B_{20\%}$ (half of $B_{40\%}$). Fishing ceases when biomass is below $B_{20\%}$. The six management strategies evaluated are referred to as “combined”, “separated”, “catch cascading”, “split 2|3”, “split 5|6”, and “split 8|9” (Fig. 4.2). In combined management, all demes were assessed and managed as a single management unit, whereas in separated management, the 10 demes were assessed and managed separately. Catch cascading provides an alternative to separated management; all 10 demes are assessed as a single unit, and the TACs for each deme are based on the relative proportion of survey biomass in each deme. Unlike separated management, there is no need to conduct stock assessments for each deme.

Three management strategies split the 10 demes into two management units, but in different proportions. The “split 5|6” strategy split the demes into equal sizes of five demes each. The “split 2|3” strategy imposed two management units that were split between demes 2 and 3, and the “split 8|9” strategy created two management units by splitting between demes 8 and 9. Although the relative proportion of demes in the two management units were the same under “split 2|3” and “split 8|9”, the fixed position of the fishing port resulted in different fishing pressure by deme, and hence by management unit (Fig. 4.2).

Parameterization of the model

The populations in each deme were simulated using two separate age-structured models, with life history parameters based on either Pacific cod or blackspotted rockfish. The rockfish model included ages 0-45, with the 45th age group inclusive of ages 45 and older, while the Pacific cod model included ages 0-20, with the 20th age group including ages 20 and older. The model included growth, natural mortality, and fishery selectivity specific to each age class. The sum of the relative fishing effort in the five demes nearest to the fishing port was adjusted to be higher

by 50% than in the other five demes, within the framework of a gravity model (App. Eqn. 4.17). This value was chosen to represent disproportionate fishing effort, but not to specifically represent fishing patterns for Pacific cod and blackspotted rockfish, although it does fall in the range of observations (Chapter 3; P. Spencer, pers. comm.). This study was not designed to give management advice specifically for Pacific cod or blackspotted rockfish, rather to demonstrate how different types of management would perform when there is IBD stock structure and disproportionate fishing effort. Details of the model are further described in Appendix 4. Each model configuration was run 100 times and results are summarized over all simulations. Standard parameters for all simulations are shown in Table 4.1.

Migration

The model incorporated each species and management strategy at the low and high estimate of migration, which depended on the low and high N_e/N estimate for each species obtained from empirical estimates (App. Table 4.2). The N_e/N (effective to census size ratio) for blackspotted rockfish is 0.01-0.001 (Spencer and Gharrett 2010). Effective population size has not been estimated for Pacific cod; therefore a range of values was selected based on Atlantic cod. The N_e/N_s (effective to spawning size ratio) for Atlantic cod is 2.27×10^{-4} (Therkildsen et al. 2010) - 0.14 (Knutsen et al. 2011).

The range of migration estimates between demes in an unfished state was 813-8,130 migrants per year for blackspotted rockfish and 22,000- 1.4×10^7 for Pacific cod (App. Table 4.2). These estimates were based on the assumption of migration-drift equilibrium. The number of generations for F_{ST} to move halfway to the equilibrium value, T_{50} , was calculated using estimates for migration and effective population size (App. Eqn 4.24; Table 4.1; Whitlock 1992). The N_e/N and N_e/N_s ratios were applied to estimates of census sizes (blackspotted rockfish) and number of spawners (Pacific cod). This provided a range of effective population size estimates: 2.95×10^3 – 2.95×10^4 in blackspotted rockfish and 3,269- 2.02×10^6 in Pacific cod (App. Table 4.2). Migration between spatial areas was assumed to decline exponentially, i.e. m between adjacent areas and m^2 between areas two demes apart, etc.

The initial number of migrants was the same for each deme, and was converted to a migration rate based on the initial (equal) number of fish in each deme. The migration rate was converted to the number of fish emigrating from each deme. If the population sizes in two

adjacent demes differed, due to differential fishing effort and management strategy, the larger population would contribute more migrants than it received. Therefore, larger populations had the potential to increase the population size of smaller neighbors. Migrants were randomly selected from all age classes based on the relative frequency of each age class. This approach did not incorporate assumptions about the relative likelihood of migration by a given age class. The implications of such an approach are covered in the discussion.

Effective population size

Effective population size was measured two ways, inbreeding effective size and the Felsenstein-Hill, or reproductive effective size (Waples et al. 2011). The inbreeding effective population size was expressed in an absolute sense. It was averaged over the last 50 years of the simulation because it stabilized during the second half of the simulation period. The Felsenstein-Hill effective size was expressed in a relative sense, because this provided an indication of the proportion of reproductive potential that was lost. Inbreeding effective population size was compared with 5,000, the value considered necessary to maintain normal adaptive potential (Lande 1995).

Results

Migration

An upper and lower estimate of migration, the number of fish expected to move from one deme to an adjacent deme each year, was calculated for unfished stocks with demes of equal sizes, based on high and low N_e/N estimates (App. Table 4.2). For blackspotted rockfish, migration was 813-8,130 fish per year and in Pacific cod it was $2.2 \times 10^4 - 1.4 \times 10^7$ (App. Table 2). The Pacific cod estimate spanned a wider range due to the large discrepancy in N_e/N estimates. The equation used to estimate migration (App. Eqn. 4.14) is based on the assumption that migration-drift equilibrium has been reached. If migration-drift equilibrium has not occurred, App. Eqn. 4.14 would overestimate migration rates. Therefore, an estimate of migration an order of magnitude below the low estimate, hereafter referred to as “very low” migration, 81 for blackspotted rockfish and 2,200 for Pacific cod was also considered (Fig. 4.5; App. Table 4.2).

The number of generations required for F_{ST} values to reach half the size of those at migration-drift equilibrium, T_{50} , depended on estimates of effective population size (Fig. 4.4). In

Pacific cod, higher effective population size estimates indicated that migration-drift equilibrium would have taken 5,000 times longer than the lower estimate. The lower range indicated that T_{50} would take approximately 4,000 generations, or 32,000 years in Pacific cod. The range in blackspotted rockfish was 4,000-40,000 generations, or 20,000-200,000 years. These estimates are higher than the 15,000-16,000 years since glaciers retreated and colonization was possible in the North Pacific Ocean (Canino et al. 2010).

Emigration from each of the 10 demes was proportional to the biomass in that deme but not to the census size; census size and biomass were not correlated because fishing changed the age structure of the population. All 10 demes initially contained populations of the same size but population size declined in each deme depending on fishing effort and management strategy. Therefore, demes with small population sizes adjacent to demes with large population sizes received a net influx of migrants. Under combined management, net migration was typically toward the demes near the fishing port on the left side of the simulation framework, with the deme adjacent to the fishing port receiving the most migrants. Using this as a gauge of the relative movement between demes, the number of migrants entering deme 1 from deme 2 was 0.002%-2.0% of the population size of Pacific cod in deme 1 and 0.0019-0.0023% in blackspotted rockfish (Figs. 4.2 and 4.3), based on low and high migration rates.

Relative spawning biomass

Relative spawning biomass among demes was similar regardless of species under all management strategies, despite different life history parameters (Fig. 4.5). Spawning biomass stabilized in Pacific cod during the first 5 years of the historical fishing period (Fig. 4.6a, b). Blackspotted rockfish achieved a stable state more slowly than Pacific cod due to their longer generation length (Fig. 4.6a vs. 4.6c). Mean relative spawning biomass, spawning biomass divided by the unfished biomass averaged over 100 simulations depended on the management strategy, with some demes falling below $B_{40\%}$ for most management strategies. More than half of all demes fell below $B_{40\%}$ under combined management (Fig. 4.5a, c). Relative spawning biomass under catch cascading and separated management was generally stable across demes, and higher under separated management due to the added precision of calculating harvest control rules for each deme (Fig. 4.5b, d).

Average long-term relative spawning biomass changed depending on how the 10 demes were split into two management units (Fig. 4.5a, c). Splitting closer to the fishing port, where fishing pressure was expected to be high (“split 2|3”), resulted in less extreme reductions in biomass on average in demes subject to high fishing pressure (i.e. in demes within management units closest to the fishing port). When the region to be managed was split further away from the fishing port (“split 8|9”), one deme was reduced to approximately $B_{20\%}$ (“split 8|9”), but when this region was split near the fishing port (“split 2|3”), the most heavily fished deme was reduced to approximately $B_{30\%}$ or higher. Splitting the managed area evenly (“split 5|6”) provided intermediate results between the other two management strategies that split the entire region into two management units (Fig. 4.5).

Migration rates provided a demographic rescue effect and reduced discrepancies in relative biomass among demes, and the effect was most pronounced in blackspotted rockfish even though the relative proportion of migrants was higher in Pacific cod. The natural mortality rate in blackspotted rockfish is much lower than that of cod (App. Table 4.1); therefore, a single blackspotted rockfish migrant could typically reproduce for more years than a Pacific cod. Relative biomass was generally higher with the higher migration rate in this species (Fig. 4.5). Low and high migration rates resulted in different levels of spawning biomass, but the very low and low migration rates resulted in similar average relative biomass estimates (Fig. 4.5).

Mean relative biomass was higher under high migration and separated management (Fig. 4.5d) because increased migration did not produce proportional increases in fishing mortality rate. Migration was not proportional to age-class abundance, rather it took place at equal rates for each age in the model. This resulted in a disproportionately large number of migrants in older age classes, relative to recruits, compared to the age structure of the population. The harvest control rule is based on the simulated estimate of spawning biomass relative to $B_{40\%}$, which incorporates an estimate of average recruitment (App. Eqn. 4.23). Under high net migration into a deme, spawning biomass will increase but recruitment will not increase in proportion to the age structure of the population. This effect reduces the estimate of spawning biomass below what the harvest control rule would otherwise calculate. This does not occur under catch cascading because TAC is allocated based on relative survey estimates of biomass, but it is a factor in the other four management strategies under high migration.

Catch cascading and separated management resulted in similar profiles of relative biomass over the 100-year simulation period in blackspotted rockfish, because the population dynamics do not fluctuate as quickly as in Pacific cod (Fig. 4.5b and d; Fig. 4.6). Quantiles for relative biomass span approximately double and half of the mean in blackspotted rockfish, which used a slightly higher assessment error than the Pacific cod model (Table 4.1). In Pacific cod, catch cascading and separated management produced distinct profiles of relative biomass (Fig. 4.6a, b). The additional error due to higher assessment error in small management units, coupled with the shorter generation length and higher natural mortality in Pacific cod, resulted in more variable population size estimates in this species under separated management. The overall effect was higher variance in estimates of relative biomass under separated management, which resulted in more conservative fishing mortality rates under the harvest control rule (App. Fig. 4.1), and consequently higher biomass in Figure 4.5b and d under separated management. This is also the cause of the fixed lower quantile interval for relative biomass under separated management in Pacific cod (Fig. 4.6a); the lower bound of relative biomass is set by the harvest control rule. In all cases represented in Figure 4.6, the lower 5% intervals remain above zero, indicating that population collapse is not expected at the simulated fishing pressure.

Sources of error

Overall results varied among simulations and years, primarily due to variance in recruitment, survey estimates of biomass, and assessment error. The largest source of variance was due to recruitment, which was assumed to be related to oceanographic and climactic conditions and therefore correlated spatially. Survey and assessment errors were not correlated among management units, and did result in variation among demes. Errors due to surveys and assessments were inversely related to the size of the management unit; therefore higher assessment error was incorporated under separated management (App. Eqn. 4.19). Catch cascading was the only management strategy that included survey error; TACs for catch cascading were allocated based on the survey estimate of population size in each deme (App. Eqns. 4.19, 4.22). The relative relationship of spawning biomass among demes was generally consistent, regardless of stochasticity in the model; therefore trends observed in the mean over all simulations were likely to hold true on a case-by-case basis.

Fishing mortality in each deme

Relative instantaneous fishing pressure among demes was similar regardless of species, but was lower in blackspotted rockfish; $F_{40\%}$ is 24% for Pacific cod and 3.5% for blackspotted rockfish (Table 4.1; Fig. 4.7). The highest relative fishing pressure occurred under combined management in the deme nearest the fishing port (Fig. 4.7a, c). All demes experienced similar levels of fishing pressure under separated management and catch cascading (Fig. 4.7b, d). Fishing pressure was slightly lower than the target level in separated management. Stochasticity and the harvest control rule were the cause of this discrepancy; when spawning biomass was above its target level, fishing pressure remained at $F_{40\%}$ and when it fell below, the harvest control rule reduced the fishing mortality rate, causing lower fishing mortality and higher spawning biomass than target levels (App. Fig. 4.1). Therefore, stochasticity in stock size resulted in a more conservative level of fishing pressure. Separated management imposed lower fishing effort than catch cascading due to the added variance of computing 10 stock assessments versus one. When the 10 demes were split into two management units, the “split 8|9” generated the highest relative fishing pressure, in deme 1, followed by deme 1 under the “split 5|6”, and “split 2|3” with the lowest relative fishing pressure (Fig. 4.7a, c).

Average annual fishery catch

Catch was lower under combined management than almost all other management strategies. Management strategies that split the management area into two management units resulted in higher catch than combined management on average (Table 4.2). The amount of increase depended on several factors, including where the split took place, the level of migration, and the life history of the species. Catch was highest under the “split 2|3” strategy, followed by “split 5|6” and finally “split 8|9” under low migration, because depletion in spawning biomass was lowest under “split 2|3” and highest under “split 8|9” (Fig. 4.7). The benefits of the “split 2|3” were not observed under high migration in terms of increased catches because the harvest control rule did not increase fishing mortality rate proportional to spawning biomass (Table 4.2). This is the same effect that generated increased spawning biomass in blackspotted rockfish under separated management and high migration (Fig. 4.5d).

Effective population size

The relative patterns of inbreeding and Felsenstein-Hill effective size were very similar by deme and management strategy; therefore, only the Felsenstein-Hill effective size is presented visually (Fig. 4.8). Both Felsenstein-Hill effective and census size decline over time as fishing is imposed, and reach a stable state after 20 years. The overall magnitude of change in N_e/N based on the management strategy is very small. The poisson scaling factor, the ratio between variance and mean lifetime reproductive success, is set to one, because there is no empirical value available for either species.

Inbreeding effective size is also included because it can be interpreted in an absolute sense. The lowest inbreeding effective population size occurred under the highest fishing pressure; in deme 1 under combined management; 5.15×10^7 in Pacific cod and 2.14×10^6 in blackspotted rockfish. Inbreeding effective population sizes remained high relative the theoretical threshold of 5,000 considered necessary to maintain normal adaptive potential.

Discussion

Isolation by distance is the most commonly observed type of spatial genetic population structure (Bradbury and Bentzen 2007). Not only does it suggest limited migration (Slatkin 1993), it may signify that biological differences exist between distant groups (Bradbury and Bentzen 2007). This simulation study confirms that management strategies should take into account isolation by distance population structure. Performance measures such as relative biomass and catch improve when a single management unit subject to isolation by distance stock structure and disproportionate fishing effort is split into multiple management units. Relative biomass in approximately half of the demes falls below target levels when they are managed as a single unit because higher fishing mortality occurs in those demes than intended by management (Fig. 4.7a and c). In contrast, management strategies that divide the area into two management units result, on average, in lower levels of depletion, fewer demes falling below target levels, and higher overall catch.

Splitting a management area into two management units between demes 2 and 3 optimizes biomass relative to target levels and increases overall catch. Other spatial configurations of two management units also improve upon combined management but result in higher depletion in some demes (Fig. 4.7a, c). The difference depends on how well management units group areas of

similar fishing effort into the same management unit. Performance measures are not affected by the size of the management unit or the number of subpopulations. Managers can use the rule of thumb that if IBD stock structure is present, and disproportionate fishing mortality exists at the scale of the dispersal distance, then areas of high fishing mortality rate, or a proxy thereof such as fishing effort, should be managed separately from areas of low fishing effort. This rule could be extended to more than two management units. Other simulation studies confirm these results for the case of distinct populations; one stock is more likely to be depleted below target or threshold levels when the management area is managed as a single management unit (Taylor 1997; Fu and Fanning 2004; Chapter 4).

Catch cascading is an effective alternative to multiple management units that provides separate TACs for each deme (IWC 1994; Punt and Donovan 2007). Results show that the mean relative biomass under catch cascading is near the target level for all demes, with less discrepancy among demes than combined management or strategies that split the area into two management units. Catch cascading is currently used to manage Pacific ocean perch in the Gulf of Alaska; the total allowable catch is apportioned into three separate areas by survey data (Hanselman et al. 2013). Catch cascading requires only a single assessment, whereas in separated management, in which each deme represents a management unit, a stock assessment is required for each. This involves applying available data for each year to the assessment model, determining biomass relative to $B_{40\%}$, and applying that estimate to the harvest control rule to determine fishing pressure. In many management organizations, each assessment must be independently evaluated and approved by a panel of experts, which would make separated management administratively undesirable. Therefore, catch cascading offers a precautionary approach to management of IBD stock structure with relatively little extra effort.

Results also provide information on inbreeding and Felsenstein-Hill effective population sizes. Inbreeding effective size emphasizes the effect that in small populations, inbreeding will occur more frequently, and as a result, heterozygosity can be lost from the population. The Felsenstein-Hill effective population size incorporates information on age-specific survival and fertility rates and considers that longer-lived individuals have more opportunities to reproduce. It specifically provides information in the case of size-selective harvest that can truncate age structure, such as the several management strategies implemented in the simulation (Waples et al. 2011). Typically, the variance in lifetime reproductive success among will be greater than the

mean, even if the variance in reproductive success is random. Climactic and oceanographic events, high reproductive success of a limited number of individuals, and other factors likely will create much higher variance in reproductive success. Increasing the poisson scaling factor would reduce the magnitude of N_e , but patterns in the N_e/N ratio would not change. Therefore, results are interpreted in terms of the relative patterns in N_e/N rather than the absolute magnitude (Fig. 4.8).

Fishing reduces the N_e/N ratio to a greater extent in blackspotted rockfish in heavily fished demes than in Pacific cod. This may be due to a combination of factors, including maturity-at-age, reproductive capacity in an age-truncated population, and fishing pressure. This reflects the hypothesis that managing to maintain stable age structure can protect the reproductive capacity of a population (Berkeley 2006). The inbreeding effective size was compared with an effective population size of 5,000, because this value has been suggested to be a threshold that is necessary to maintain normal adaptive potential (Lande 1995). No demes fell below this threshold in either species; therefore, there was no evidence that any of the management strategies explored here would result in loss of heterozygosity, as measured by inbreeding effective size.

Estimates of migration

In general, dispersal is defined differently depending on whether it is applied to genetic or ecological populations. In an ecological population, dispersal is defined as the annual migration rate, while dispersal in a genetic population is considered in terms of the number of migrants per generation (Waples and Gaggiotti 2006). Genetic definitions of migration are generally based on ideal populations and effective population sizes (Waples 1998). Migration in the model is based on an ecological rather than genetic perspective; net flow into each deme is considered and populations are modeled based on demographic parameters for each species. The model defines individuals in each population as those that spawn there; this is analogous to assessing a stock during spawning season. Therefore, this framework accommodates movement patterns such as natal and repeat homing, in which adult animals return to their birthplace to reproduce.

Estimates of migration rate in blackspotted rockfish are complicated by uncertainty in the IBD relationship, whereas the IBD slope is more certain for Pacific cod. Migration estimates for Pacific cod are based on an IBD slope that has been confirmed by two independent studies

(Table App. 4.2; Cunningham et al. 2009; Spies 2012). The migration rate for blackspotted rockfish is based on a significant IBD relationship ($p=0.0049$) from four samples, two from the Aleutian Islands and two from the Bering Sea (Spencer and Gharrett 2010). Further genetic analysis using more samples has not confirmed the IBD relationship (A. Gharrett pers. comm.). However, there are many reasons to suspect that migration is limited in this species. First, isolation by distance and limited migration are commonly observed in rockfish species in general, as exemplified by the finding of IBD in *Sebastes caurinus*, *S. rastrelliger*, *S. auriculatus*, *S. aleutus*, and *S. polyspinis*. Secondly, exploitation rates in the Western Aleutians are higher than estimated stock production rates, and biomass in that area appears to be in decline. Biomass from 2000-2010 averaged 1,059 t, and was consistently below estimates from 1991-1997, which averaged 3,156 t (Spencer and Rooper 2012). Declines would be expected to occur under high fishing pressure unless migration was sufficient to replace depleted stocks, but it has not recovered in the Western Aleutians (Spencer and Rooper 2012).

Incorporating migration only at the larval phase may be more consistent with fish behavior than assuming that migration takes place randomly across age groups. Many fish species have extended pelagic larval and juvenile stages, including rockfish (Buonaccorsi 2002) and Pacific cod (Narimatsu et al. 2007), and these species are relatively sedentary as adults or exhibit natal homing. If migration were implemented at the larval phase, and the number of migrants were constant, it would likely result in less overall migration because larvae are subject to higher natural mortality and are less likely to reach maturity. However, it would not change the overall results or the relative patterns among demes.

Isolation by distance; theory and pitfalls

In theory, the slope of the relationship between genetic differentiation and distance in isolation by distance stock structure will increase after colonization from a single panmictic population until migration-drift equilibrium occurs. Many recent studies have drawn conclusions about dispersal distance when IBD stock structure is present (i.e. Buonaccorsi et al. 2005; Cunningham et al. 2009; Pinsky et al. 2010) using theoretical methods (Rousset 1997). Whether or not stocks have reached equilibrium is an important consideration when using IBD to estimate dispersal distance because theoretical equations that provide such estimates assume equilibrium (Rousset 1997).

Migration-drift equilibrium may take place very slowly following colonization by a single panmictic population over a large area, and estimates may be further complicated if colonization involved multiple founding populations or factors that limit dispersal. Migration-drift equilibrium may take thousands of years when demes are characterized by low migration rates and connected by large distances (Whitlock 1992; Bradbury and Bentzen 2007). When migration-drift equilibrium has not occurred, the IBD relationship may be non-linear (Slatkin 1993; Jorde et al. 2006). When populations are not in migration-drift equilibrium, the slope of the IBD relationship will be smaller among more distant demes (Slatkin 1993; Jorde et al. 2006). This non-linearity is particularly common in marine organisms due to limited dispersal and large habitat ranges (Bradbury and Bentzen 2007). A meta-analysis revealed only a weak relationship between the slope of the IBD relationship and the time since colonization, possibly due to limited dispersal ability, geographic barriers, or distance to glacial refugia (Crispo and Hendry 2005).

The time until migration-drift equilibrium was examined for both blackspotted rockfish and Pacific cod; however, some assumptions were made due to limited information on each species. Estimates of the number of generations for F_{ST} to move halfway to the equilibrium value, T_{50} , were based on an island model (Whitlock 1992) and assumed one single panmictic founding population. Subpopulations exchanging genes tend to be genetically similar to each other in a stepping stone model; consequently, migration is less effective at reducing differentiation than in an island model and may take place more slowly (Allendorf et al. 2013). Migration was modified to account for the discrepancy between the two models by assuming that migration between demes declined exponentially, as in a stepping stone model (Figure 4.4). If colonization occurred from multiple panmictic equations, then estimating the time until equilibrium could be further complicated; equilibrium is reached more quickly in smaller populations but the level of genetic differentiation between founding populations would also affect the IBD relationship and is impossible to ascertain.

Estimates of T_{50} are high relative to the 15,000-16,000 years since glaciers retreated and colonization was possible in the North Pacific Ocean (Canino et al. 2010), suggesting either that migration-drift equilibrium has not occurred or that colonization was not a simple process from a single panmictic population (Figure 4.4). The low estimate of T_{50} was based on the lower value for effective population size; 4,500 generations (36,000 years) in Pacific cod in the Aleutian Islands and 4,000 generations (20,000 years) in blackspotted rockfish in the BSAI (Figure 4.4).

A lack of a geographic trend in genetic diversity in Pacific cod is suggestive of a single founding population (Spies 2012), but details regarding blackspotted rockfish in the BSAI have not been closely examined. Blackspotted rockfish are found in deep water (150-500 m; Orr and Hawkins 2008); therefore, they may not have been affected by the recent glacial period.

Costs and benefits

Spatial management can be costly; therefore the value of implementing it should be thoroughly evaluated (Rassweiler 2012). Justification of spatial management often requires knowledge of the biology, fishery, and environment (Rassweiler 2012). To identify IBD stock structure, genetic analysis must be performed. Such data collection is typically expensive, requiring research surveys, specialized equipment, and trained technicians. Individual transferable quotas (ITQ), a portion of the total allowable catch that is allocated to individual stakeholders, can also incur hidden costs. There are often no pre-determined means to allocate pre-existing ITQs if the initial management unit is split spatially (Waples et al. 2008). Stakeholders may be required to fish in less desirable locations if an ITQ applies to a given area that is later found to contain two distinct stocks. Spatial management that requires at-sea enforcement can also be costly, depending on the level of vessel monitoring systems that are already in place (Holland 2003; Rassweiler 2012). This cost would be incurred in all the management strategies presented here as alternatives to combined management.

On the other hand, there are many benefits to appropriately implemented spatial management. It has the potential for adaptive management and more efficient harvest, in addition to obvious effects such as higher stock sizes (Botsford et al. 1997). Effective population size can also benefit. Fishing practices did not change the effective population size of Pacific cod significantly, but did affect that for blackspotted rockfish. The effective size of blackspotted rockfish in the demes with the highest fishing effort fell to 30% of its initial size when migration was low. Spatial management practices may be particularly beneficial when growth is slow and effective population sizes are low, such as in small or fragmented populations. When growth is slow, a precautionary approach such as spatial management is warranted because populations are slow to recover. In the case of low effective population sizes, spatial management will help prevent depleting adaptive potential.

Generalizations based on life history

The contrasting life histories of blackspotted rockfish and Pacific cod emphasize the relationship between migration and population dynamics in IBD stock structure. Bradbury and Bentzen (2007) observed a similar relationship between life history and IBD; they found a decrease in IBD slope with increasing body size across species. Here, the effects of migration were related to species longevity. Long-lived species with high fecundity later in life such as rockfish may experience stronger than expected rescue effects under low migration, whereas shorter-lived species such as gadidae will not benefit from the same levels of migration. This is unlikely to change if dispersal were modeled at the larval level because the relative number of migrants that survive to spawn would be the same regardless of species. Therefore, both the slope of the IBD relationship and life history play a role in determining the level of spatial isolation among populations subject to IBD.

Blackspotted rockfish and Pacific cod have considerably different life history traits. Blackspotted rockfish are k-selected species, with long generation time, late maturity, slow growth rates, and have been observed as old as 120 years. Pacific cod grow more quickly, mature as young as 3 years, and rarely live past 20 years (Table 4.1). These differences influence some of the results shown here, but do not change the long-term responses to different management strategies when isolation by distance stock structure is present. The slower growth rate and long generation length in blackspotted rockfish result in slower reaction to changes in fishing pressure under the various management strategies. After approximately 40 years the population reaches stable levels of relative spawning biomass in each deme. Pacific cod react much more quickly to changes in fishing pressure, achieving stable levels of relative biomass in less than 10 years, but the relative levels of spawning biomass at equilibrium are similar. This suggests that many marine fish species subject to isolation by distance stock structure would react similarly to different management strategies, but that reaction times would vary depending on generation length.

Summary

Results show that the initial hypothesis is true; in the case of isolation by distance, performance measures improve when the management area is split anywhere rather than managed as a single management unit. These results are based on a management area that is larger than the size of the

dispersal distance. Splitting the management area into two management units resulted in a lower chance of individual demes falling below target and threshold biomass levels, as well as higher catches. The optimal configuration of management units placed demes with similar fishing effort into the same management unit. If separate management units are not possible, management that precautionarily employs catch cascading, or spatial apportionment – dividing the managed area into individual quota regions based on estimated biomass by region, may achieve similar benefits, depending on the location of distinct populations (IWC 1994; Punt and Donovan 2007).

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Table 4.1. Values for the parameters of the operating model. References: * Thompson and Lauth 2012, § Stark 2007, † Forrest et al. 2010, ‡ Spencer and Rooper 2010, °McDermott 1994, [◇] estimated within the model.

Parameter	Application	Parameter values			
		Pacific cod		blackspotted rockfish	
		Males	Females	Males	Females
Ψ	Weight-at-age	$6.537 \times 10^{-6}^*$		$6.6 \times 10^{-6}^\ddagger$	
γ	Weight-at-age	3.164^*		3.237^\ddagger	
M	Natural mortality	0.34 yr^{-1}^*		$0.0333162 \text{ yr}^{-1}^\ddagger$	
x	Maximum age	20yr^*		45yr^\ddagger	
L_∞	Maximum length	110.06 cm^\S	120.39 cm^\S	51.18088^\ddagger	
K	Growth rate	$0.1449 \text{ yr}^{-1}\S$	$0.1277 \text{ yr}^{-1}\S$	0.057572^\ddagger	
A_0	Theoretical age-at-zero-size	-0.1814 yr^\S	-0.2233 yr^\S	-4.06516^\ddagger	
<i>slope</i>	Maturity-at-age	$0.9654 \text{ yr}^{-1}\S$		$0.3196 \text{ yr}^{-1}^\circ$	
$a_{50\%}$		4.8833 yr^\S		18.8935 yr°	
<i>slope</i>	Fishery selectivity	See Appendix 4.*		0.34	
$a_{50\%}$	Fishery selectivity	See Appendix 4.*		17.77	
h	Steepness	0.731283		0.67^\dagger	
$F_{40\%}$	Fishing mortality rate	0.2389 yr^{-1}		0.03522 yr^{-1}	
CV_A	Assessment CV	0.178^*		0.105^\ddagger	
σ_R^2	Recruitment variance	0.408^*		0.411^\ddagger	
CV_S	Survey CV	0.188^*		0.270^\ddagger	
ρ	Autocorrelation	0.707^\diamond		0.707^\diamond	
ϕ_y	Observation error (year y)	$\sim N(0; \sigma_S^2)$		$\sim N(0; \sigma_S^2)$	
η_y	Assessment error (year y)	$\sim N(0; \sigma_A^2)$		$\sim N(0; \sigma_A^2)$	
δ_R	Recruitment error	$\sim N(0; \sigma_R^2)$		$\sim N(0; \sigma_R^2)$	

Table 4.2: Average catch over simulations during the last 50 years of the simulation for the six management strategies, “combined” (comb.), “separated” (sep.), “2|3 Split” (2|3), “5|6 Split” (5|6), “8|9 Split” (8|9), and “catch cascading” (C.C.). Results are shown for each species and for both high and low migration rates. Catch as a percentage of catch under combined management is shown in parentheses for each management strategy.

	Comb.	Sep.	C.C.	2 3	5 6	8 9
Pacific cod (x1000 t)						
Low migration rate	71.6	77.1 (107.7%)	77.1 (107.7%)	73.5 (102.7%)	73.2 (102.2%)	72.2 (100.8%)
High migration rate	72.4	78.8 (108.8%)	77.1 (106.5%)	73.8 (101.9%)	73.8 (101.9%)	73.2 (101.1%)
blackspotted rockfish (t)						
Low migration rate	613.4	680.2 (110.9%)	690.4 (112.6%)	667.0 (108.7%)	651.5 (106.2%)	637.9 (104.0%)
High migration rate	683.8	773.1 (113.1%)	681.7 (99.7%)	719.8 (105.3%)	731.6 (107.0%)	721.4 (105.5%)

Fig. 4.1. The Eastern Bering Sea and Aleutian Islands area of Alaska, with management areas. The line within the Aleutian Islands management area demarcates western and Central Aleutians from Eastern Aleutians.

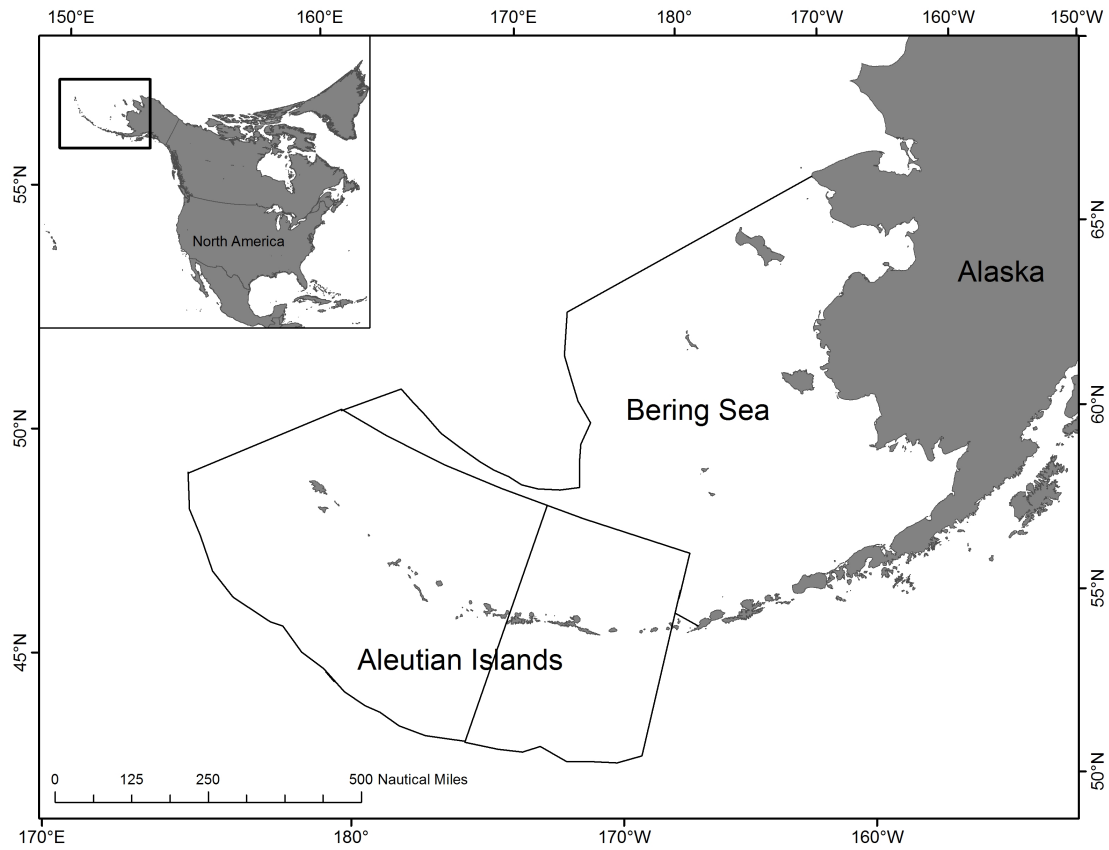


Fig. 4.2. The six management strategies: “combined”, “separated”, “catch cascading”, “2|3 split”, “5|6 split”, and “8|9 split”. Demes are numbered 1 to 10, with deme 1 closest to the fishing port.

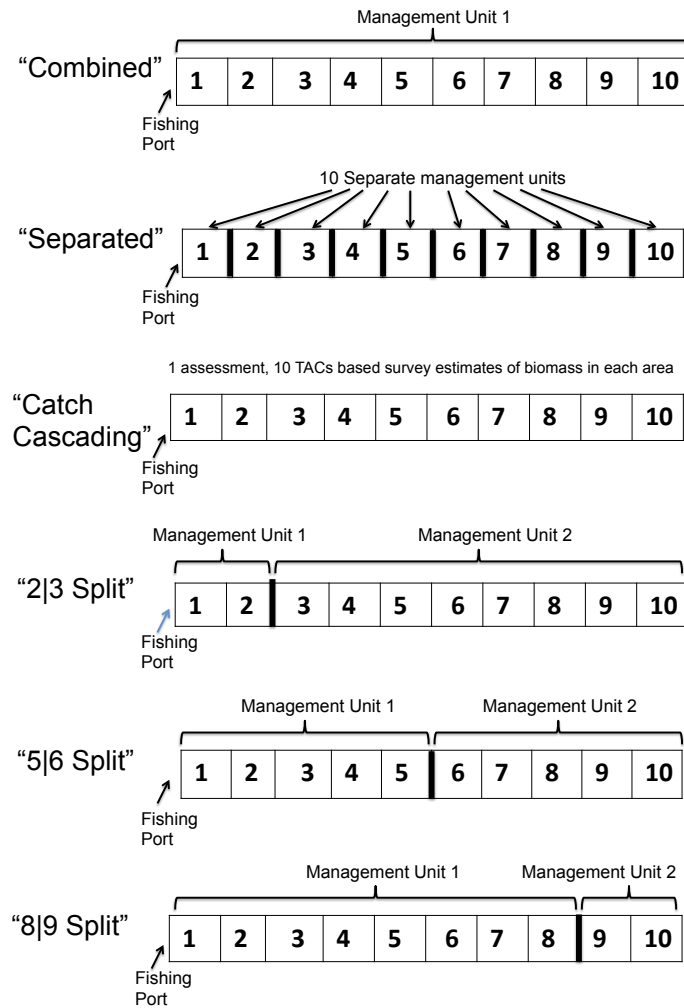


Fig. 4.3. Flow chart describing the operating model.

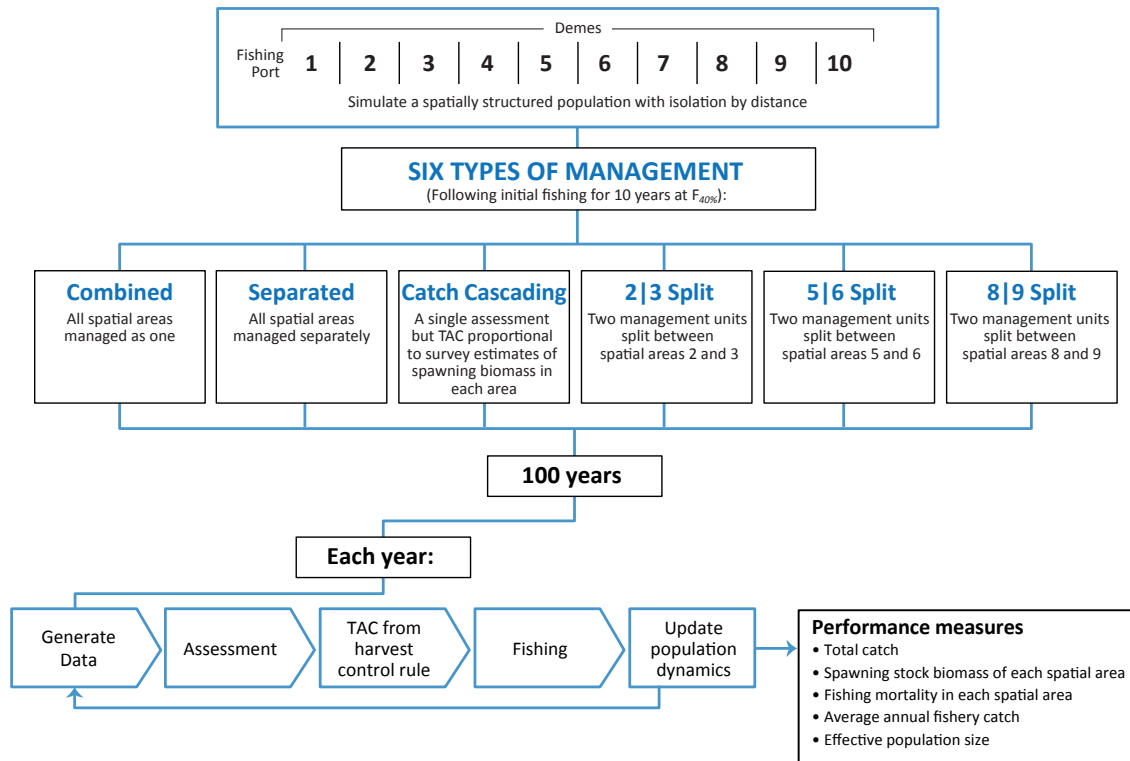


Fig. 4.4. The number of generations required for F_{ST} values to reach half the size of those at migration-drift equilibrium, T_{50} , in generations for blackspotted rockfish (panel a.) and Pacific cod (panel b.). The legend in panel a. applies to both panels. Low and high estimates for N_e and m are presented in Table 4.1. High N_e estimates resulted in T_{50} approximately 5,000 times higher in Pacific cod (right axis labels) than low N_e estimates (left axis labels).

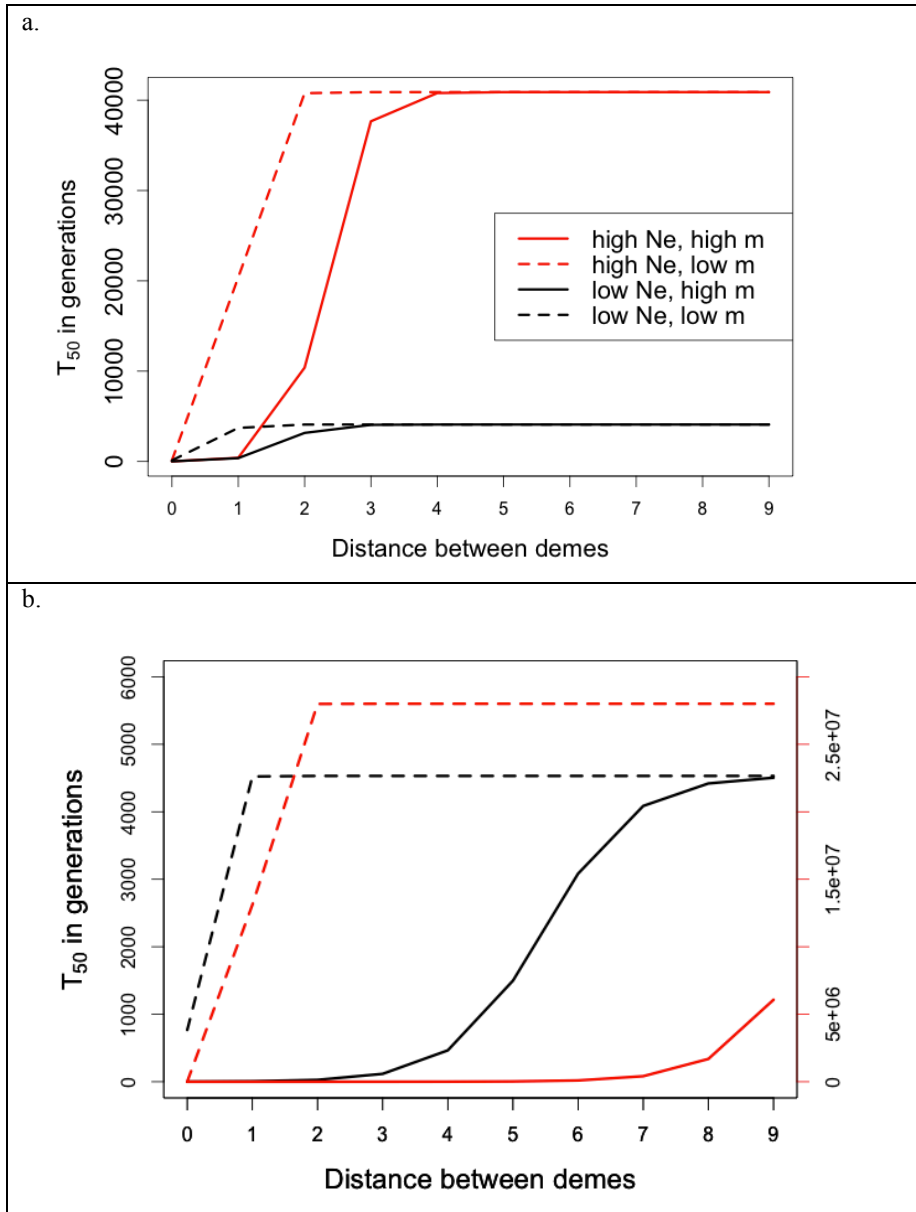


Fig. 4.5. Mean relative biomass, spawning biomass (SSB) in a given year divided by the unfished spawning biomass, averaged over 100 simulations and the last 50 years for each area. Dashed lines are for the higher migration rate and the solid lines for the lower migration rate, specified in App. Table 4.2. Dotted lines represent very low migration (App. Table 4.2). The horizontal lines indicate $B_{40\%}$ and $B_{20\%}$. Panels a. and b. represent Pacific cod and panels c. and d. blackspotted rockfish. Panels a. and c. show all management strategies except for “separated” and “catch cascading,” which are shown in panels b. and d.

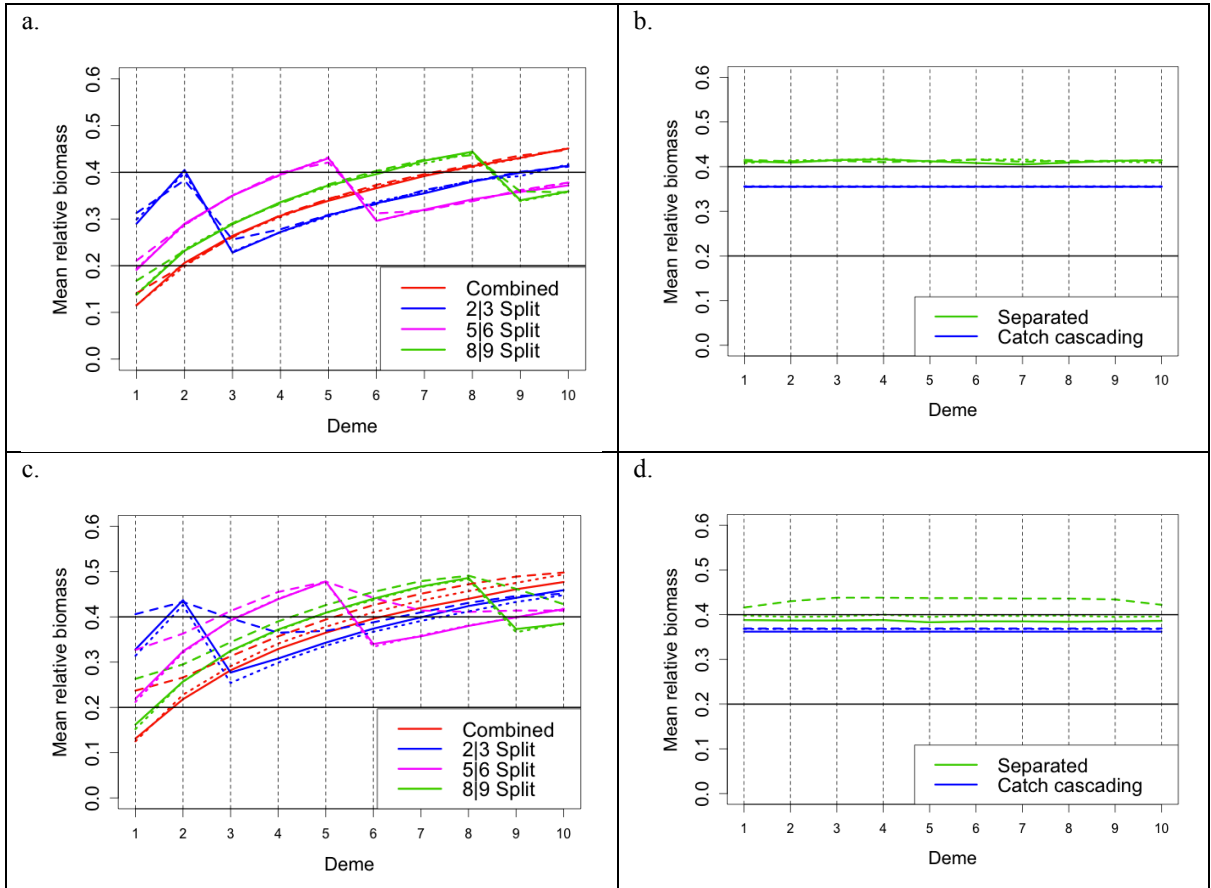


Fig. 4.6. Mean relative biomass and 90% quantile intervals over 100 simulations for catch cascading and separated management in deme 1 using the low migration estimate for separated and catch cascading management; 813 migrants in blackspotted rockfish and 22,000 migrants in Pacific cod (App. Table 4.2). Panels a. and b. represent Pacific cod and panels c. and d. blackspotted rockfish, and both simulations are based on the lower migration rate (App. Table 4.2). Panels a. and c. show relative biomass under catch cascading, while panels b. and d. used separated management. The vertical line indicates the end of the historical 10-year fishing period.

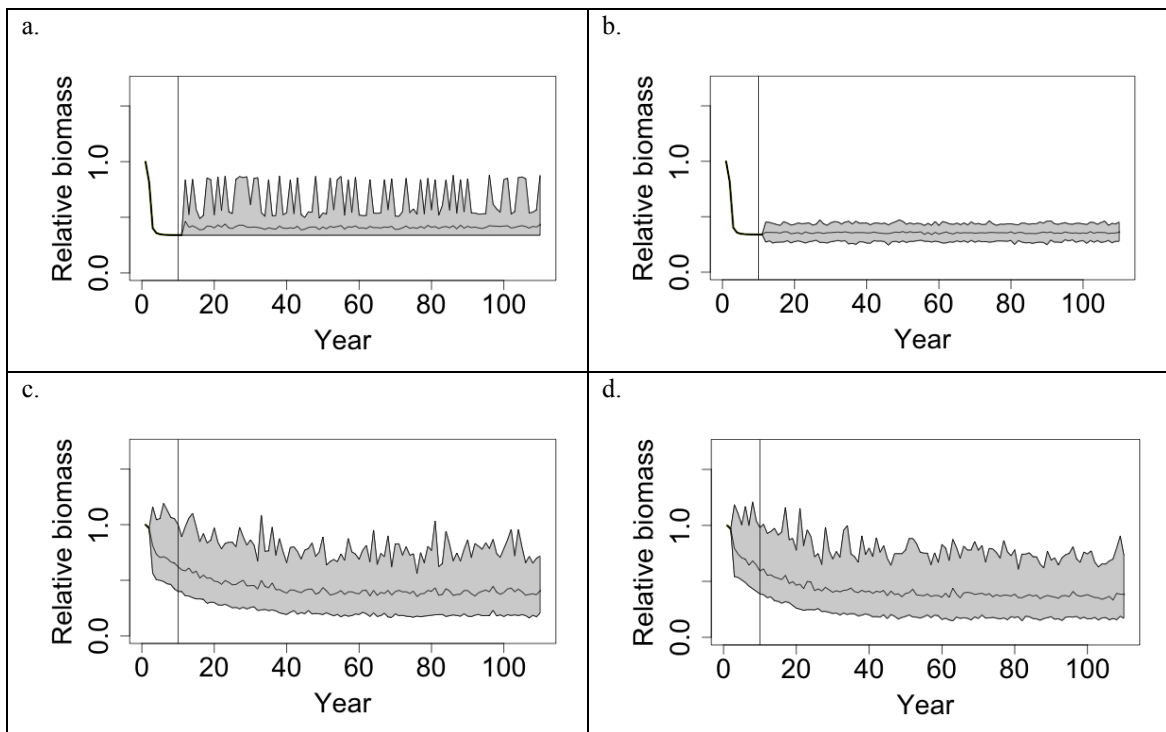


Fig. 4.7. Mean fishing mortality rate over 100 simulations during the last 50 years of managed fishing for all six management strategies. Dotted lines are for the higher migration rate and the solid lines for the lower migration rate, specified in App. Table 4.2. Panels a. and b. represent Pacific cod, while panels c. and d. represent blackspotted rockfish. The left column represents all management strategies except “separated” and “catch cascading,” which are shown in the right column.

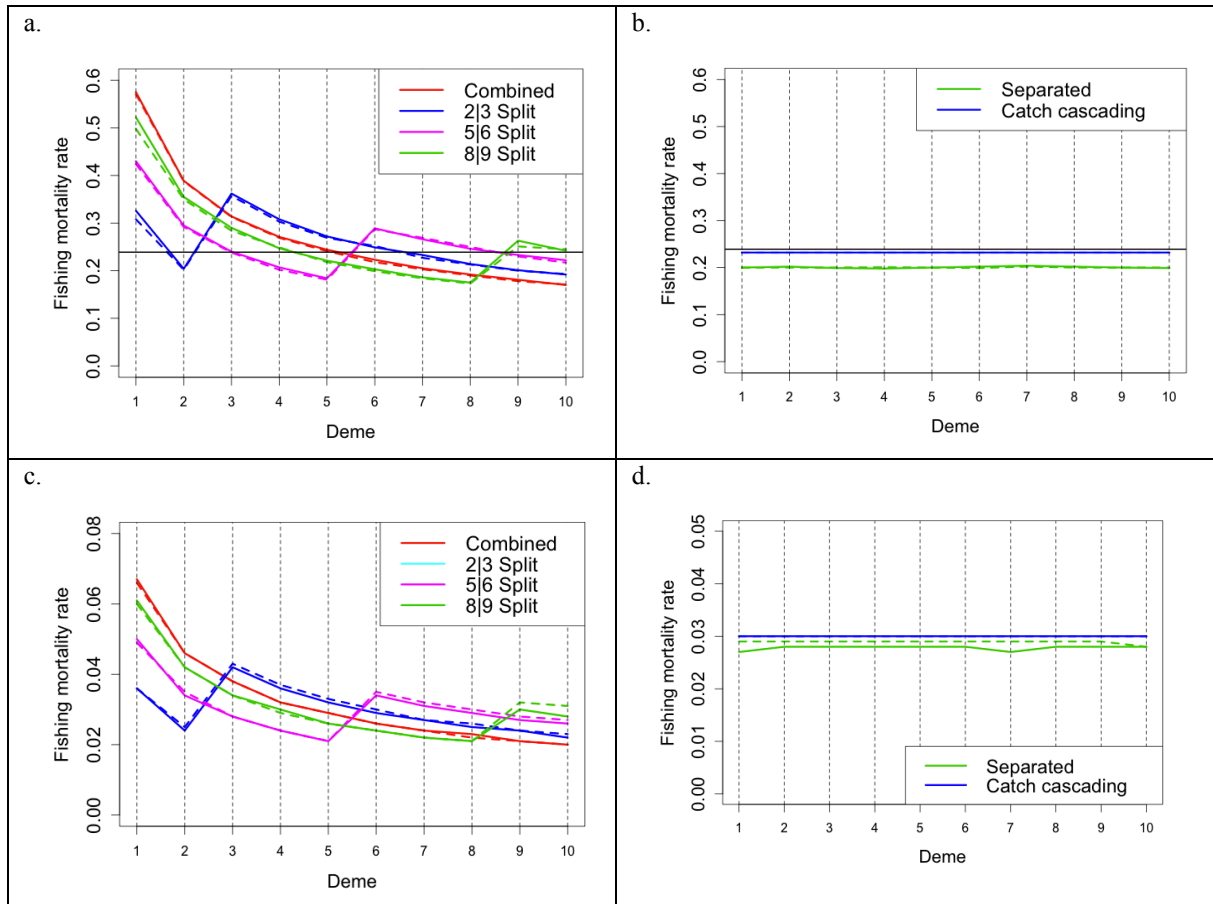
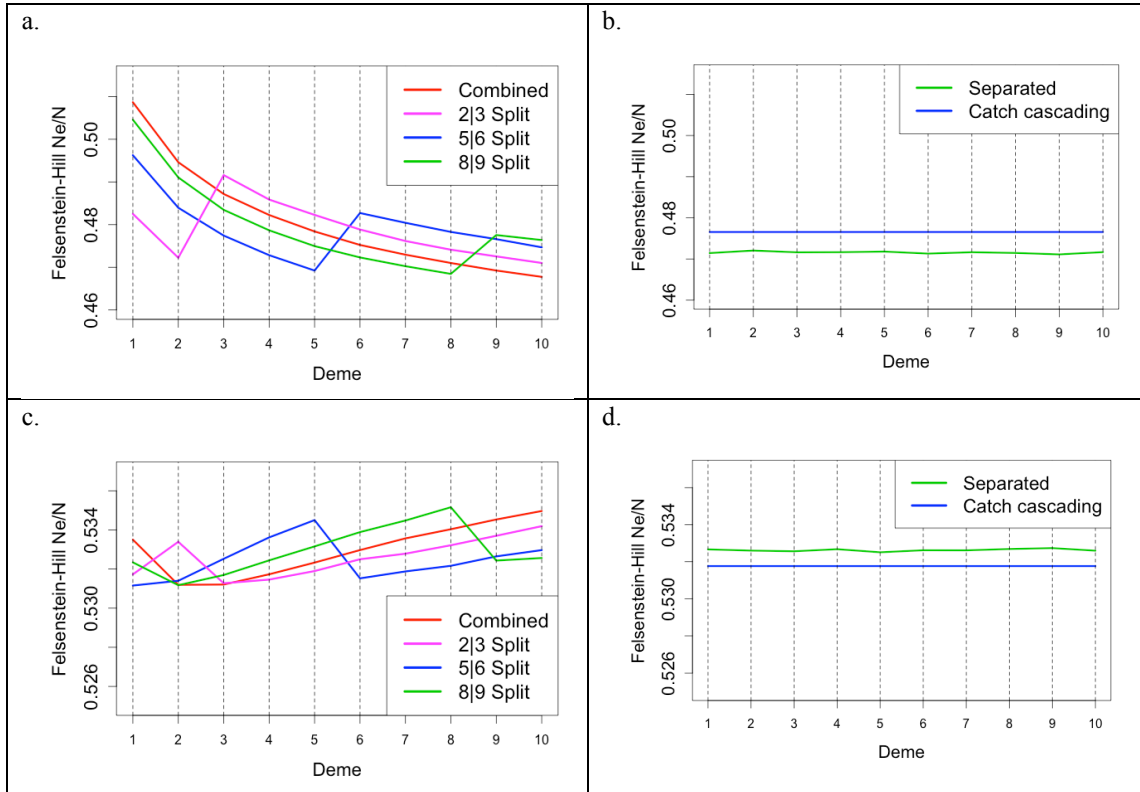


Fig. 4.8. The Felsenstein-Hill N_e/N ratio; the ratio of effective to census size averaged over 100 simulations, excluding the historical fishing period and the first 10 years of managed fishing. Demes are shown on the x-axis, with deme 1 nearest the fishing port. Panels a. and b. represent Pacific cod and panels c. and d. blackspotted rockfish. The left column shows all management strategies except “separated” and “catch cascading,” which are in the right column. Simulations were performed at the lower migration rate, specified in App. Table 4.2.



Appendix 4

Details of the “true” population dynamics model

The population dynamics in each of the 10 demes (Fig. 4.2) was simulated using an age-structured model with parameters given in Table 4.1. Definitions and acronyms for the model are shown in App. Table 4.1. The total initial (unfished) spawning stock biomass (SSB_{init}) was selected based on the estimated census size, and was split equally among the demes ($l \in \{1, 2, \dots, 10\}$):

$$(App. 4.1) \quad \tilde{S}_0^l = \frac{1}{10} SSB_{init},$$

where \tilde{S}_0^l is the initial (unfished) spawning biomass for deme l .

The initial number of recruits in each deme (l) in the absence of fishing, R_0^l , was calculated using the equation:

$$(App. 4.2) \quad R_0^l = 2\tilde{S}_0^l / \sum_a W_a \tilde{N}_{init,a}^l Q_a,$$

where a indexes age class, W_a is weight-at-age, Q_a is maturity-at-age, and $\tilde{N}_{init,a}^l$ is the number of fish in each age class prior to exploitation in deme l , relative to the number of age-0 fish. The latter quantity was calculated under the assumption of unfished equilibrium, given an instantaneous rate of natural mortality, M :

$$(App. 4.3) \quad \tilde{N}_{init,a}^l = \begin{cases} 1 & \text{if } a=0 \\ \tilde{N}_{init,a-1}^l e^{-M} & \text{if } 1 \leq a \leq x-1 \\ \tilde{N}_{init,x-1}^l e^{-M} / (1 - e^{-M}) & \text{if } a=x. \end{cases}$$

The numbers in each age class in each deme (l) were then scaled to the population size that would result from R_0^l recruits:

$$(App. 4.4) \quad N_{init,a}^l = R_0^l \tilde{N}_{init,a}^l.$$

For years $init+1$, $init+2$, etc., the numbers-at-age were computed allowing for fishing and a Beverton-Holt stock recruitment relationship (Beverton and Holt 1957):

$$(App. 4.5) \quad N_{y+1,a}^l = \begin{cases} \frac{4hR_0^l \tilde{S}_y^l}{\tilde{S}_0^l(1-h) + \tilde{S}_y^l(5h-1)} & \text{if } a = 0 \\ N_{y,a-1}^l e^{-(S_{a-1}^f F_y^l + M)} & \text{if } 1 \leq a \leq x-1 \\ N_{y,x-1}^l e^{-(S_{x-1}^f F_y^l + M)} + N_{y,x}^l e^{-(S_x^f F_y^l + M)} & \text{if } a=x, \end{cases}$$

where $N_{y,a}^l$ is the number of fish of age a in deme l at the start of year y , \tilde{S}_y^l is the spawning biomass for deme l at the start of year y , S_a^f is the selectivity-at-age for the fishery, F_y^l is the instantaneous fully-selected fishing mortality rate during year y for population l , and h is the steepness, or the expected fraction of R_0^l that is produced when spawning biomass is 20% of its unfished state (Table 4.1). Recruitment variation with bias-corrected lognormal error, i.e. $e^{\delta_R - \sigma_R^2/2}$; $\delta_R \sim N(0; \sigma_R^2)$, was applied to recruitment. Recruitment among demes is assumed to be perfectly correlated; therefore the same recruitment deviation is applied to the population in each deme in each year.

Subsequent to the initial year, spawning biomass in each deme, \tilde{S}_y^l was calculated using:

$$(App. 4.6) \quad \tilde{S}_y^l = 0.5 \sum_a W_a N_y^l Q_a.$$

The number of spawning individuals was used to determine the numbers of individuals available to reproduce in each year in the IBD model. The number of spawning males in each deme was set to the number of spawning females, and was based on the proportion of individuals in each age group that were expected to be mature that year:

$$(App. 4.7) \quad SP_{y,a}^l = 0.5 N_y^l Q_a.$$

Catch in numbers of fish of age a in deme l during year y , $C_{y,a}^l$, was a function of fully-selected fishing mortality, natural mortality, and numbers-at-age,

$$(App. 4.8) \quad C_{y,a}^l = \frac{S_a^f F_y^l}{S_a^f F_y^l + M} (1 - e^{-(S_a^f F_y^l + M)}) N_{y,a}^l.$$

Finally, the total catch in weight from deme l during year y , C_y^l , was calculated as:

$$(App. 4.9) \quad C_y^l = \sum_a W_a C_{y,a}^l.$$

Parameterizing the model

The biomasses in the simulation model are consistent with those for Pacific cod in the Aleutian Islands and blackspotted rockfish in the BSAI, and were taken from current stock assessments (Thompson and Lauth 2012; Spencer and Rooper 2012). Spawning biomass estimates for Pacific cod based on AI trawl surveys from 1980-2012 were examined to establish initial spawning biomasses (App. Table 4.2). The mean estimated spawning biomass over this time period was 115,773 metric tons (t). Initial spawning biomass assumed in the model was for an unfished population, and the 2012 estimate of 58,911 t is estimated at less than a quarter of the initial stock size. Therefore, the model used a rough estimate of 5.0×10^5 t for the unfished spawning biomass for the AI Pacific cod population. The estimated mean unfished biomass of Pacific cod in the Aleutian Islands would result in 9.44×10^8 individuals in the population for ages 0-20+, based on the average weight-at-age (App. Eqn. 4.10 and Table 4.1), and 1.44×10^8 reproductively mature individuals.

Applying corrections to the total biomass estimates, based on the species complex (96% of relative biomass in the Aleutians and 64% in the Bering Sea consists of blackspotted rockfish, for assessment time series dating to 1977) produced a mean blackspotted rockfish biomass estimate of 18,912 t (Spencer and Rooper 2012). The unfished spawning biomass of blackspotted rockfish in the BSAI was estimated at 2.8×10^4 t, based on the assumption that the population has been at $B_{40\%}$, on average between 1980-2012. This assumption draws from the $F_{40\%}$ fishing mortality rate management objective of the North Pacific Fishery Management Council (NPFMC 2012). Blackspotted rockfish have historically been managed as a complex with rougheye rockfish in the BSAI so historical information on the stock size of this stock is not available. The population dynamics model predicts that 2.95×10^7 blackspotted rockfish are equivalent to this estimate of unfished biomass.

Variance parameters come from the stock assessments for each species (Table 1). Variance estimates for Pacific cod come from the 2012 BSAI stock assessment ("Model 3"), and were based specifically on data for the AI. The mean coefficient of variation (CV) for assessed spawning biomass, CV_A , was applied to the true numbers-at-age, to simulate spawning biomass from a stock assessment (App. Eqns. 4.19 and 4.20). The CV_A for Pacific cod from 1991-2012 is 0.178, and in blackspotted from 1977-2013 it is 0.105. For blackspotted rockfish, the CV of the Aleutian Islands assessed biomass was used to calculate variance in the model because there are

few rougheye rockfish in the AI (Spencer and Rooper 2012). The mean CV of the survey estimate for total biomass, CV_S , from 1980-2012 is 0.188 in Pacific cod and 0.270 in blackspotted rockfish from 1980-2012. This value was used in simulated spawning biomass estimates from the raw survey data, which allocated catch under catch cascading management. The coefficient of variation of the age-0 estimated Pacific cod recruitment from 1977-2013 ($CV_R = 0.737$) was used to calculate the recruitment variance $\sigma_R^2 = 0.408$, using the equation $\sigma_R^2 = \log(1 + CV^2)$ (Thompson and Lauth 2012). The coefficient of variation (CV_R) of the age-0 estimated recruitment from 1977-2007 is 0.77, corresponding to $\sigma_R^2 = 0.411$.

Age was converted to weight using a von Bertalanffy growth function (von Bertalanffy 1957):

$$(App. 4.10) \quad W_a = \psi [L_\infty (1 - e^{K(a-A_0)})]^\gamma,$$

where L_∞ is the mean maximum length, K is a rate constant (year^{-1}), A_0 is the theoretical age at which length is zero, and ψ and γ determine the relationship between length and weight. Males and females follow different growth trajectories for Pacific cod, whereas the sexes follow the same growth trajectory for the blackspotted rockfish model (Table 1). For Pacific cod, the values for the parameters ψ and γ (Table 1) were an average of the regression parameters in each season provided in Thompson and Lauth (2012), weighted by sample size.

The maturity-at-age was governed by the logistic relationship:

$$(App. 4.11) \quad Q_a = \frac{1}{1 + \exp(-\text{slope}(a - a_{50\%}))},$$

where slope and $a_{50\%}$ are parameters in the relationship (Table 1) and a represents age. Similar to the 2012 Pacific cod assessment (Thompson and Lauth 2012), maturity-at-age was based on parameter estimates calculated by Stark (2007) from $n = 129$ cod for which the mean age-at-50%-maturity was estimated to be 4.9 years. Estimates for blackspotted rockfish indicate that the age-at-50%-maturity is approximately 19 years (McDermott 1994; Table 1). Maturity was set to zero for the first two Pacific cod and the first five blackspotted rockfish ages, to match observed maturity-at-age.

The stock assessment for Pacific cod includes nine fishing fleets (trawl, longline, and pot, during each of three seasons). Rather than modeling all nine fleets explicitly, fishery selectivity-at-age in the model, S_a^f , was an average over fleets, with the weights equal to the number of fish

caught by each fleet (App. Fig. 4.2). For blackspotted rockfish, fishery selectivity was assumed to be a logistic function of age (Table 1; App. Fig. 4.2).

The Beverton-Holt stock-recruitment relationship does not fit the spawning biomass and recruitment data for Pacific cod well in reality because recruitment is likely highly dependent on environmental factors (Tyler and Crawford 1991; Sinclair and Crawford 2005; Thompson and Lauth 2012). The BSAI Pacific cod assessment model is not able to estimate a reliable stock-recruitment relationship and therefore does not estimate steepness (h). Pacific cod is assessed as a Tier 3 stock in which F_{MSY} is assumed to occur at $F_{35\%}$. For this study, steepness was selected so that $F_{MSY} = F_{35\%}$, which results in $h=0.73$. Steepness has been specified in a similar manner for other species in BSAI region (e.g. Szuwalski and Punt 2012). The TAC for the Tier 3 management strategy (which equals the acceptable biological catch, ABC) was set based on a fully-selected fishing mortality rate of $F_{40\%}$. The TAC equals the amount of catch in each year. For blackspotted rockfish, the steepness was set to 0.67, based on a meta-analysis of rockfish species (Forrest et al. 2010).

Migration

Migration was estimated between demes using parameters in App. Table 4.2 and an equation based on the slope of the isolation by distance regression relationship (Jorde et al. 2006; Rousset 1997). In a one-dimensional infinite stepping-stone model with l demes,

$$(App. 4.12) \quad \frac{\beta_l^*}{1 - \beta_l^*} \approx \frac{A_l}{4N_e\sigma} + \frac{1 - e^{-\sqrt{2\mu}l/\sigma}}{4N_e\sigma\sqrt{2\mu}}, \text{ where } \beta_l^* \equiv (\theta_0 - \theta_l)/(1 - \theta_l) \text{ is the correlation of}$$

genes within demes with respect to genes at some distance l , θ_l is the probability of identity by descent of a pair of genes l steps from each other, μ is mutation rate per generation, σ is the square root of the variance of offspring position relative to its parent, A_l is a constant that depends on the dispersal distribution, and N_e is the effective population size in each deme (Eqn. 5 in Rousset 1997). Under the assumption that $F_{ST} \approx \beta$ when migration rates are low, and taking the limit of the above equation as $\mu \rightarrow 0$, results in

$$(App. 4.13) \quad \frac{F_{ST}}{1 - F_{ST}} \approx \frac{A_l}{4N_e\sigma} + \frac{l}{4N_e\sigma^2}.$$

The right side of the equation consists of a constant term and a term that varies with distance, l .

Taking the derivative with respect to l provides an equation for the slope of $\frac{F_{ST}}{1-F_{ST}}$ vs. the

number of steps between demes, $slope = \frac{1}{4N_e\sigma^2}$. In a one-dimensional framework, a proportion

m of the population will move a distance of length 1 from their original deme, while a proportion $1-m$ will remain. The variance in parental position relative to offspring can be calculated

$\sigma^2 = m * 1^2 + (1-m) * 0^2 = m$, so that the slope of the IBD relationship in an infinite stepping-stone model can be expressed:

$$(App. 4.14) \quad slope = \frac{1}{4N_e m},$$

when $\frac{F_{ST}}{1-F_{ST}}$ is plotted with respect to the number of steps between demes, rather than distance.

The relationship in equation App. 4.14 is discussed in Slatkin (1993). The slope of the IBD

relationship was rescaled from empirical values in Table 1 to $\frac{F_{ST}}{1-F_{ST}}$ with respect to the number

of steps between demes for each species (a scale from 1 to 9), resulting in a slope of 0.0029 for blackspotted rockfish and 0.00038 for Pacific cod. Two estimates of the IBD slope were available for Pacific cod, 1.38×10^{-6} (Cunningham et al. 2009) and 2.31×10^{-6} (Spies 2012). These values were close enough that they did not change migration rates; the value of 2.31×10^{-6} was chosen because samples were taken over shorter distances and considered a more accurate representation of IBD slope at migration-drift equilibrium (Jorde et al. 2006). The number of effective migrants used in the model was based on m (App. Eqn. 4.14) and then scaled up to the number of census migrants using estimates of N_e/N or N_e/N_s ratios, and estimates for census or spawning size for each species (Table 4.1; App. Table 4.2).

Dispersal between demes 2-9 was defined by the probability matrix $P_{l=1, l=2}$ that is at equilibrium (equal number of migrants are exchanged) when populations are at their initial size:

$$(App. 4.15) \quad P_{l=1, l=2} = \begin{bmatrix} p_{1,1} & p_{1,2} \\ p_{2,1} & p_{2,2} \end{bmatrix}, \text{ where } p_{l, l+1} N_{init}^{l=1} = p_{l+1, l} N_{init}^{l=2}, \text{ and } N_{init}^l \text{ is defined as:}$$

$$(App. 4.16) \quad N_{init}^l = \sum_a N_{init, a}^l.$$

Demes 1 and 10 only exchanged migrants with demes 2 and 9, respectively. The age class of migrants was randomly chosen proportional to the age structure of the population in a fished state.

Fishing mortality

The NPFMC Tier 3 harvest control rule, with target fishing mortality at $F_{40\%}$ was used to determine fishing mortality rates for all management strategies (App. Fig. 4.1; NPFMC 2012). Fishing effort occurred with higher intensity in the demes nearest to the fishing port within each management unit (Fig. 4.2). A gravity model, a class of model designed to represent spatial interaction (Tinbergen 1963), was used to represent relative fishing effort E_y^l in each deme. The model is a function of the exploitable biomass in deme l at the start of year y , and the distance between the fishing port and that particular deme, d^l , within each management unit j , i.e.

$$(App. 4.17) \quad E_y^l = \frac{\frac{1}{(d^l)^w} \sum_a S_a^f W_a N_{y,a}^l}{\sum_{l' \in j} \sum_a \frac{1}{(d^{l'})^w} S_a^f W_a N_{y,a}^{l'}}.$$

The term w is a scaling factor that was adjusted so that the ratio of the mean fishing mortality rate matches empirical values. This term was adjusted so that mean relative fishing pressure over 100 years and 100 simulations was 50% higher in the half of the management area near the fishing port.

Within management unit j , fishing mortality in each deme was proportional to relative fishing effort, i.e.:

$$(App. 4.18) \quad F_y^l = E_y^l \tilde{F}_y, \text{ where } \tilde{F}_y \text{ is the fishing mortality rate by stock in year } y.$$

Data generation from the population dynamics models

The “perceived” population dynamics is derived from “true” state and dictates TAC. Fishing first occurred in the model during the historical fishing period and then in each year of the 100-year projection. Fishing mortality was set to $F_{40\%}$ during the historical fishing period. This value was chosen because it is the target fishing mortality for a healthy fish stock according to the NPFMC,

and results in stock sizes near the target levels. The perceived population dynamics were based on annual simulated stock assessments that provided estimates of total and spawning biomass.

Stock assessments estimate the number of animals of age a in management unit j at the start of year y , $N_{y,a}^j = \sum_{l \in j} N_{y,a}^l$, by incorporating estimates of assessment error into the true values. The proportion of variance due to assessments and surveys $((\sigma_A^j)^2$ and $(\sigma_S^j)^2$) in each management unit was determined by the CV (CV_A or CV_S) for the entire simulated area that included all 10 demes as well as the size of each management unit, n_j :

$$(App. 4.19) \quad (\sigma^j)^2 = \log \left(\frac{10}{n_j} CV^2 + 1 \right).$$

Estimated numbers-at-age were assumed to be unbiased and distributed about the true numbers-at-age at the start of the year, i.e.:

$$(App. 4.20) \quad \hat{N}_{y,a}^j = N_{y,a}^j e^{\varepsilon_y^j - (\sigma_A^j)^2/2},$$

where ε_y introduces autocorrelated error among annual assessments as follows:

$\varepsilon_y^j = \rho \varepsilon_{y-1}^j + \sqrt{1 - \rho^2} \eta_y^j$. The variable η_y^j is random normal based on the variance in the assessed estimate of abundance, $\eta_y^j \sim N(0; (\sigma_A^j)^2)$, and r is the parameter which determines the amount of autocorrelation (Table 1). The value of 0.707 was chosen for r , which implies that half the variance is due to autocorrelation. The perceived numbers-at-age were used to compute a time-series of perceived assessment-based spawning biomasses for management unit j . The simulated estimates of spawning biomass in stock assessments were generated using the equation:

$$(App. 4.21) \quad \hat{S}_y^j = 0.5 \sum_a W_a \hat{N}_{y,a}^j Q_a.$$

Under catch cascading, estimates of relative biomass in each deme from survey data were used to allocate the amount of catch in that deme. This required an estimate of survey error be applied to the true numbers-at-age:

$$(App. 4.22) \quad \hat{N}_{y,a}^j = N_{y,a}^j e^{\phi_y^j - (\sigma_S^j)^2/2}, \text{ where } \phi_y^j \sim N(0; (\sigma_S^j)^2).$$

This value was used to estimate survey spawning biomass in each deme using Eqn. 21, in place of $\hat{N}_{y,a}^j$.

Pacific cod and blackspotted rockfish are managed under a Tier 3 harvest control rule in the BSAI (Spencer and Rooper 2010, Thompson and Lauth 2012). This harvest control rule sets the

TAC as follows. The ABC control rule (App. Fig. 4.1) sets the target fishing mortality, \hat{F}_y^j , based on the status of the spawning biomass relative to $B_{40\%}$ and $B_{20\%}$. Because $B_{40\%}$ is not an obtainable quantity, a proxy implemented in NPFMC Pacific cod and blackspotted rockfish stock assessments was used:

$$(App. 4.23) \quad \hat{B}_{40\%} = \bar{R} * SPR_{F=0.4},$$

where \bar{R} is the average estimated recruitment over the entire management period through the current year. $SPR_{F=0.4}$ is the expected spawning biomass-per-recruit when fishing mortality is $F_{40\%}$ (Thompson and Lauth 2012, Spencer and Rooper 2010). $SPR_{F=0.4}$ was calculated similarly to equation 3, except that fishing mortality was set at $F_{40\%}$:

$$(App. 4.24) \quad SPR_{F=0.4} = 0.5 \sum_a W_a \tilde{N}_{F=0.4,a}^l Q_a, \text{ where}$$

$$(App. 4.25) \quad \tilde{N}_{F=0.4,a}^l = \begin{cases} 1 & \text{if } a=0 \\ \tilde{N}_{F=0.4,a-1}^l e^{-(S_{a-1}^f F_y^l + F_{40\%})} & \text{if } 1 \leq a \leq x-1 \\ \tilde{N}_{F=0.4,x}^l e^{-(S_{a-1}^f F_y^l + F_{40\%})} / (1 - e^{-(S_{a-1}^f F_y^l + F_{40\%})}) & \text{if } a=x. \end{cases}$$

Fully-selected fishing mortality was set at $F_{40\%}$ if the perceived (assessment-based) spawning biomass was higher than the perceived value for $B_{40\%}$, and declined linearly with biomass if perceived spawning biomass was between $B_{20\%}$ and $B_{40\%}$ (App. Fig. 4.1). Fishing ceased if perceived spawning biomass dropped below $B_{20\%}$. Given the target fishing mortality, the TAC was computed using the equation:

$$(App. 4.26) \quad TAC_y^j = \sum_a W_a \hat{N}_{y,a}^j \frac{S_a^f \hat{F}_y^j}{S_a^f \hat{F}_y^j + M} \left(1 - e^{-(S_a^f \hat{F}_y^j + M)} \right).$$

Estimating effective population size in the simulation model

The Felsenstein-Hill effective population size is a measure of the effective population size that incorporates the generation length (L_{gen}), the variance in reproductive success (V_k), and the recruitment in deme j during year y , R_y^j (Fig. 4.8; Waples et al. 2011):

(App. 4.27) $N_e = \frac{4R_y^j L_{gen}}{V_k + 2}$. Felsenstein-Hill effective population size calculations assume the

population has stable age structure and vital rates, such as survival-at-age and reproduction (Waples et al. 2011). However, in the model, survival is defined based on numbers-at-age in each year and is subject to stochasticity. Basing the survival-at-age on numbers-at-age allows for the effects of natural and fishing mortality to be incorporated into the estimate, because fishing mortality changes over time and depends on management strategy. By averaging results over 100 simulations, the effects of stochasticity are mediated. The relationship between the mean and the variance of reproductive success, the poisson scaling factor, is set to 1, since we are only interested in how the ratio changes over time rather than its absolute value. In blackspotted rockfish, only modeled ages 1-44 were used in the calculation, because the incorporation of the plus group resulted in negative D_x values (Waples et al. 2011), and unrealistically low variance (V_k). The inbreeding effective size, the size of the ideal population that would allow for the level of inbreeding as the actual population, was estimated using the harmonic mean of the census size of the population over time.

Migration-drift equilibrium generally takes place in a shorter period of time than mutation-drift equilibrium, and the number of generations for F_{ST} to move halfway to the equilibrium value is:

(App. 4.28) $T_{50} = \frac{\ln(0.5)}{\ln[(1-m)^2(1-1/(2N_e))]}$ in an island model (Whitlock 1992). Estimates for

T_{50} were based on a range of estimates for migration rate and effective population sizes for each deme (Table 1) and varied primarily due to migration rate, with smaller migration rates resulting in longer T_{50} values. Migration between spatial areas was assumed to decline exponentially, i.e. m between adjacent areas and m^2 between areas two demes apart, etc.

App. Table 4.1. Definitions and acronyms for the model.

a	Index for age
$B_{X\%}$	X% of the female spawning biomass that would result from an average cohort if fishing were eliminated.
$\hat{B}_{40\%}$	A proxy for $B_{40\%}$ based on average estimated recruitment and expected spawning biomass per recruit.
$C_{y,a}^*$	Catch in numbers in year y , at age a . Asterisk may represent management unit j , or deme l .
C_y^*	Total catch in weight in year y . Asterisk may represent management unit j , or deme l .
d_l	Distance between deme l and the fishing port.
ϵ_y^j	A first order autoregressive standard random variable applied to assessment simulation applied to management unit j .
E_y^l	Fishing effort in deme l , within management unit j .
F_y^*	The instantaneous fishing mortality, or exploitation rate in year y . Asterisk can represent j or l .
$F_{40\%}$	The fishing mortality at which spawning biomass-per-recruit is 40% of its unfished level.
F_{MSY}	The fishing mortality that produces the maximum sustainable yield, the maximum level at which a natural resource can be routinely exploited without long-term depletion.
F_{ST}	A measure of population differentiation based on genetic structure.
\tilde{F}_y^j	True fishing mortality rate in year y and management unit j .
\hat{F}_y^j	Target fishing mortality in year y and management unit j .
\tilde{F}_y	Fishing mortality rate by stock in year y .
h	Steepness, the fraction of R_0 when spawning biomass is 20% of its unfished state.
η_y^j	A random normal variable based on the variance in the assessed estimate of abundance.
j	Index for the management units.
l	Index for the 10 demes.
L	Fork length in cm.
L_{gen}	Generation length.
M	The instantaneous rate of natural mortality.
Management unit	Adjacent areas that are managed as a group.
N_{init}^l	Total population size in deme l when populations are at their initial size.
$N_{init,a}^l$	Total population size of age a fish when populations are at their initial size.
$\hat{N}_{y,a}^j$	Estimated number of animals of age a in management unit j at the start of year y from the simulated stock assessment.
$\dot{N}_{y,a}^j$	Estimated number of animals of age a in management unit j at the start of year y from the simulated research survey.
$\tilde{N}_{init,a}^l$	Total initial population size of age a fish when there is one recruit in deme l .
$N_{y,a}^*$	Number of fish in year y , of age a . Superscript * may represent management unit j or deme l .
N_e	Effective population size (expressed in terms of number of fish).
N	The census size of the population.
n_j	The number of areas within management unit j .
P	Matrix of probabilities of fish movement among demes in a given year.
$p_{l,l+1}$	The probability of a fish migrating from deme l to deme $l+1$ in a given year.

<i>Population</i>	Groups of individuals that can mate with any other individual, also known as genetic stocks.
Q_a	Proportion of fish mature at a given age.
\bar{R}	The average estimated recruitment over the entire management period through the current year
R_*^j	Recruitment to management unit j , where asterisk * can indicate at the start of year y in the absence of fishing, or at year 0.
S_a^f	Fishery selectivity at age a .
\tilde{S}_0^j	Initial spawning biomass in management unit j .
\tilde{S}_y^j	Spawning biomass in year y and management unit j .
\hat{S}_y^j	Estimated spawning biomass in year y and management unit j .
$SP_{y,a}^j$	The number of spawners at age a (same for males and females) in year y and management unit j .
$SPR_{F=0.4}$	The expected spawning biomass per recruit when fishing mortality is $F_{40\%}$.
deme	Each of the 10 stepping stones in the simulated area.
SSB_{mit}	Initial spawning stock biomass for the entire simulated area (10 areas).
σ_A^j	Standard deviation of the survey estimates of total biomass in management unit j .
σ_R	Standard deviation of recruitment.
σ_S^j	Standard deviation of assessed spawning biomass in management unit j .
TAC	Total allowable catch.
V_k	Variance in reproductive success.
W_a	Weight at age.
x	Maximum age.
y	Index for year.

App. Table 4.2. Parameters used to estimate migration and the time until migration-drift equilibrium in blackspotted rockfish and Pacific cod.

Species	blackspotted rockfish	Pacific cod
Generation length	53 years [†]	8 years [‡]
Estimates of the N_e/N ratio		
Low	0.001 N_e/N [†]	$2.27 \times 10^{-4} N_e/N_s$ [*]
High	0.01 N_e/N [†]	0.14 N_e/N_s ^{**}
IBD slope	1.04×10^{-5} [†]	2.31×10^{-6} [‡]
Unfished total biomass estimate	28,000 t	500,000 t
Unfished census size estimate ^a	2.95×10^7	9.44×10^8
Number of mature individuals	-	1.44×10^8
Modeled area and linear distance between areas (km)	EBS and AI (2500 km)	AI (1300 km)
Migration rate (m)	0.00292 [†] -0.0292 [†]	0.000375*-0.23175**
Number of census migrants per generation/per year, low-high, and (very low) ^b	43,070-430,700 813-8,130 (81)	1.8×10^5 - 1.1×10^8 22,000 – 1.4×10^7 (2,200)

^a Based on population dynamics parameters and age-structured model.

^b The lower estimate of migration is based on Eqn. 14 using the smaller N_e/N estimate and vice versa. This value is the product of census size in each deme and m, divided by two to represent migration to each adjacent deme.

[†] Spencer and Gharrett 2010.

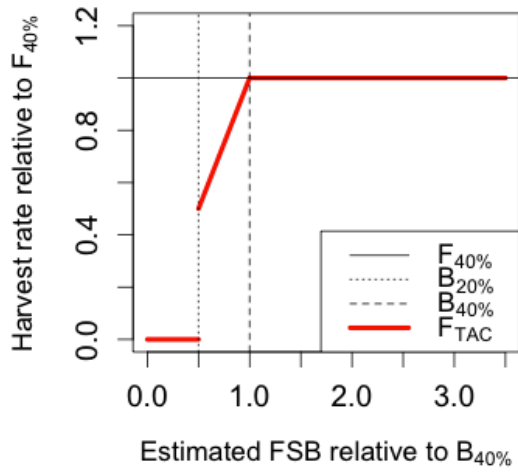
[‡] Cunningham et al. 2009.

^{*} Therkildsen et al. 2010.

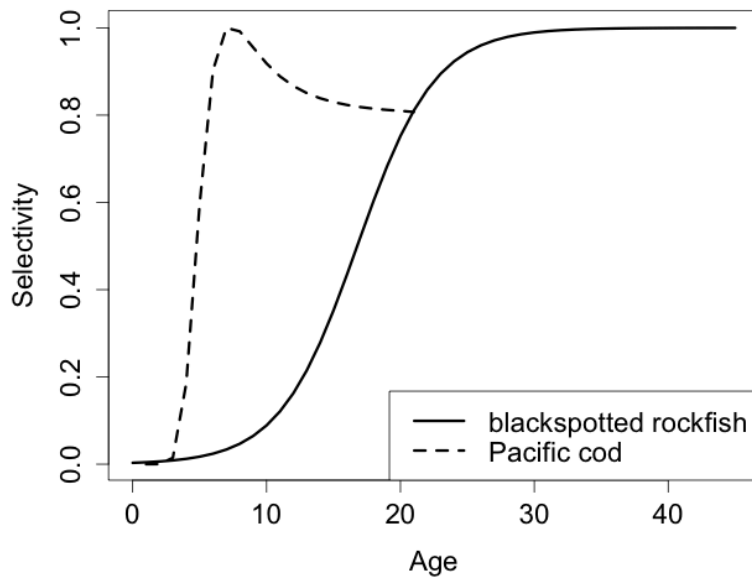
^{**} Knutsen et al. 2011.

[§] Spies 2012.

App. Fig. 4.1. Modified tier 3 harvest control rule used to set harvest rate in the simulated management strategies (Thompson and Lauth 2012).



App. Fig. 4.2: Fishery selectivity-at-age for Pacific cod and blackspotted rockfish.



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Conclusions

This work is neither the beginning nor the end of the ongoing discussion on how to incorporate stock structure into management plans. An early debate on this topic occurred with regard to stock structure at the turn of the 20th century. Gunder Dannevig, a fisherman and founder of the Flødevigen Marine Research Station, believed that there were local fjord populations of cod in the Norwegian Skagerrak fjords, and that an extensive hatchery program was needed to sustain the populations under fishing pressure. Johan Hjort, a Norwegian fisheries scientist, believed that coastal cod belonged to one large oceanic population that migrated over large areas, and disagreed with Dannevig (Dahl and Dannevig 1906). His hypothesis was that the coastal population would generate large numbers of larvae that would be transported inshore and sustain coastal cod, and would provide many more larvae than a hatchery program.

Discussions on incorporating population genetics into fisheries management continued into the 1980s, during which time the first genetic markers were applied to fish stocks. Nils Ryman and Fred Utter summarized ongoing issues between population genetics and fishery management, arguing that management frameworks did not take genetic population structure into account (Ryman and Utter 1987). They noted that population genetics was not included in books on the topic of fisheries management or required coursework for fishery students. This was despite the fact that the goal of fishery management, providing optimum yield from fisheries, cannot be achieved without recognizing the existence of subpopulations and genetic stock structure.

Since the 1980s, technology has advanced in the field of genetics research; microsatellites, single nucleotide polymorphisms and whole genome sequencing are relatively inexpensive and feasible, providing much more information on genetic stock structure than was possible in the past. Researchers are no longer limited by technology; the tools to analyze genetic differentiation exist and are relatively inexpensive. However, information on genetic stock structure is still not easily translated into management policy (e.g. Waples et al. 2008; Reiss et al. 2009). How to use information on genetic stock structure in management policy to optimize yield, stock size, and genetic diversity remains partially unresolved.

The research in this dissertation addresses several current areas to improve the cohesiveness between population genetics and marine fisheries management in the current era. This goal is addressed by example in Chapter 1, where landscape genetics was used to identify physical boundaries between subpopulations of Pacific cod within a single management area. In Chapter 2 a novel simulation approach was developed to evaluate dispersal between two populations when genetic population structure is known. The dispersal of a stock over management boundaries is of interest to fisheries managers, but is not directly estimable based on levels of genetic differentiation. This development provides an alternative to deterministic equations by using a simulation approach that incorporates information on population dynamics and genetic differentiation. In Chapter 3, the performance of management strategies formulated with and without genetic data were evaluated when two populations are present. This provided guidance on the utility of such information for marine fisheries management in general, although it is parameterized for Pacific cod. In Chapter 4, a general framework was provided for incorporating isolation-by-distance stock structure into management strategies: when and where to split a management area when this type of stock structure exists.

Each chapter is summarized in more detail below.

Chapter 1

This landscape genetics study provides the most comprehensive evidence to date for genetic distinctiveness and lack of gene flow between Pacific cod in the Aleutian Islands and Eastern Bering Sea, with more samples and microsatellite markers than used in past work. It was motivated by previous research that provided evidence for multiple populations of Pacific cod in the BSAI (Cunningham et al. 2009). The hypothesis that deep passes and current patterns may act as barriers to gene flow and result in complex population structure is partially confirmed. There is evidence that Samalga pass acts as a barrier for Pacific cod between the Eastern Bering Sea and the Aleutian Islands. There is also a strong relationship between geographic distance and genetic distinctiveness, indicating low realized dispersal in this species. The observed genetic differences are suggestive of limited gene flow both currently and historically.

Through 2012, Pacific cod was managed as a single stock in the BSAI, with a single total allowable catch (TAC) calculated for the entire management area (Thompson and Lauth 2012). Relative fishery exploitation rates have been disproportionately high in Aleutian Islands, compared to the Bering Sea (Thompson and Lauth 2012). Single and multi-species estimates of biomass in the Aleutian Islands indicate that populations may have been in decline since the 1970s (Kinzey and Punt 2009), and the 2010 survey estimate for Aleutian Islands Pacific cod biomass was the lowest since the time series began in 1980 (Thompson and Lauth 2012). Pacific cod in the Aleutian Islands and Bering Sea were managed separately beginning in 2013, as a result of strong evidence for population structure and management efforts to address declines in the Aleutian Island stock. There were many factors leading to this management decision, but the landscape genetics study in Chapter 1 helped solidify our understanding of Pacific cod stock structure in the BSAI and identified a boundary between the Aleutian and Bering Sea stocks.

Chapter 2

This study examines dispersal from the North Sea to the Skagerrak inner fjord and outer fjord using a simulation framework. Statistically significant levels of genetic differentiation between the North Sea and the inner fjord support the model result that 1-2% of the age-0 cohort appears to be from the North Sea. Estimates of migration into the outer fjord from the North Sea are higher and reflect uncertainty in the level of genetic differentiation between these populations. The model suggests 1,300-2,800 migrants per year from the North Sea to the outer fjord if the estimate of $F_{ST}=0.0001-0.0003$ is accurate. If F_{ST} is zero, then at least 6,000 larval migrants could enter the Skagerrak from the North Sea, annually, based on natural mortality-at-age values from samples taken in the fall (Knutsen et al. 2011). All estimates of migration from the North Sea indicate that greater than 10% of the spawning population originates in the North Sea; therefore North Sea migrants are likely to have a demographic influence on the outer fjord.

The simulation approach allows for much more flexibility than deterministic formulae, and can be tailored to any specific situation, in this case two populations of unequal population size, population-specific parameters, and one-way dispersal at the larval stage. Deterministic equations exist to estimate dispersal based on genetic differentiation, but they do not take into account stochasticity associated with multiple alleles or variation in population dynamics parameters such as maturity-at-age or selectivity (e.g. Wang 2004, Hössjer et al. 2013).

Chapter 3

This study incorporates the uncertainty associated with incorporating genetic population structure in fisheries management. The simulation framework investigates the utility of genetic

studies in the management of exploited marine fish species in a way that field studies cannot. Results indicate that managing stocks identified as significantly genetically distinct should be considered as the default strategy when disproportionate fishing effort exists. Incorporation of genetic data into management decisions has benefits to both yield and conservation of individual stocks. If that is not possible, management that precautionarily employs catch cascading, or spatial apportionment – dividing the managed area into individual quota regions based on estimated biomass by region, may achieve similar benefits, depending on the location of distinct populations (IWC 1994; Punt and Donovan 2007).

This simulation study was parameterized for Pacific cod, but results would be similar for other species. The microsatellite diversity simulated in the individual-based model was based on marine fish in general, which have similar genetic characteristics at microsatellite loci (DeWoody and Avise 2000). The simulated genetics study was based on 10 microsatellite loci, a standard number for this type of analysis. Therefore, management strategies that incorporate the results of similar genetic studies would be advantageous over those that do not, regardless of the specific marine fish species. Life history plays a role in the reaction to management changes; longer-lived species such as rockfish and groupers react more slowly to higher fishing pressure, and recover more slowly when fishing pressure is relaxed.

Chapter 4

The isolation-by-distance simulation study provides information on whether and how to split a single management unit subject to IBD stock structure into multiple management units. When a management area subject to IBD structure is managed as a single management unit, higher fishing mortality rates than management rules intend can occur in certain areas. Splitting the managed area into two management units improves the ability of management to meet its goals in each area. The optimal management unit configuration is one that equalizes relative fishing mortality rates between the two management units. This concept could be implemented in reality by grouping areas of similar fishing effort into the same management unit. The dispersal distance, which can be calculated from the slope of the IBD relationship, can be used to ascertain the spatial scale to consider (Rousset 1997). This rule could be extended to more than two management units. Catch cascading provides an alternative to this type of analysis, and optimized catch in the simulated area, without requiring specialized analysis.

The simulation was parameterized for two species: blackspotted rockfish and Pacific cod. These species have different life histories, but show similar long-term responses to different management strategies when isolation-by-distance stock structure is present. The slower growth rate and long generation length in blackspotted rockfish result in slower reaction to changes in fishing pressure under the various management strategies. After approximately 40 years the population reaches stable levels of relative spawning biomass in each area. Pacific cod react more quickly to changes in fishing pressure, achieving stable levels of relative biomass in less than 10 years. The relative levels of spawning biomass at equilibrium were similar among species. This suggests that many marine fish species subject to isolation-by-distance stock structure would react similarly to different management strategies, but that reaction times would vary depending on generation length.

The field of population genetics is likely to continue to grow and achieve new technological breakthroughs and tools. Forming a cohesive relationship between population genetics and fisheries management will require innovation, education, and communication. Simulation studies

will be necessary to understand how management strategies will perform in a variety of demographic situations. Fisheries managers need to be educated in the field of population genetics, and likewise, geneticists should be versed in the politics and modeling tools required of stock assessment scientists. Communication between the fields is also essential for genetics to be successfully incorporated into fisheries management, through presentations by both sides during conferences, seminars, and management meetings.

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