

Shifting-balance stock structure in North Pacific walleye pollock (*Gadus chalcogrammus*)

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High levels of gene flow are expected to produce genetic homogeneity among open-ocean populations of walleye pollock (*Gadus chalcogrammus*) because of few restrictions on migration. Although most genetic studies confirm this prediction, many surveys of morphology have detected differences among populations. Here, sequences of mitochondrial DNA cytochrome oxidase subunit I in nine samples ($n = 433$) from Japan to Puget Sound were used to evaluate genetic population structure. Two haplotypes varied clinally across the North Pacific. These clines are likely the result of the isolation of populations in ice-age refugia, secondary post-glacial contact, and restricted long-distance dispersal. Overall, $\Phi_{ST} = 0.030$ ($p < 0.001$), but the greatest partition was attributable to differences between Asian and North American populations ($\Phi_{CT} = 0.058$, $p = 0.036$). Isolation by distance was detected across the North Pacific, but differentiation among populations within regions was minimal ($\Phi_{SC} = 0.007$, $p < 0.092$). Climate variability on decadal–centennial scales produces shifts in local abundance, which prevent the appearance of genetically discrete stocks. These cycles of boom and bust, combined with high levels of gene flow, lead to different stock structures, as viewed with morphological, life history, and genetic markers.

Keywords: Bering Sea, cytochrome oxidase I, Gulf of Alaska, isolation by distance, marine fish, mitochondrial DNA.

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Introduction

Decadal climate-regime shifts influence the physical and biological marine environments that support populations of fish in the North Pacific (Mantua and Hare, 2002; deYoung *et al.*, 2008). These regime shifts produce a “Red Queen effect” (van Valen, 1973) that frequently forces populations to change in response to physiological challenges and altered foodweb dynamics (Benson and Trites, 2002). These responses involve plastic or selective shifts in life-history variables and feeding ecology. However, when populations cannot respond to local challenges, especially on short time-scales, the species’ geographic distribution shifts, contracting from suboptimal environments and expanding into optimal habitats (MacCall, 1990). These shifts in abundance complicate the identification of suitable population management units.

This study focuses on North Pacific walleye pollock (*Gadus chalcogrammus*) (= *Theragra chalcogramma*, 2006; Teletchea *et al.*, 2006), an abundant fish broadly distributed along the continental margins from the Yellow Sea in the Northwest Pacific to Puget Sound in the Northeast Pacific (Bailey *et al.*, 1999a). In the 1990s, the resource supported the world’s largest fishery, representing 10% of the total harvest of marine fish (National Research Council, 1996). Several features of pollock biology influence its stock structure. Pollock spawn in discrete locations in winter and early spring (Kendall and Nakatani, 1991) in at least 24

known areas (Bailey *et al.*, 1999a). However, these spawning areas are unlikely to harbour genetically discrete subpopulations, because of the potential for movement of adults and larvae between areas. Planktonic eggs hatch in 12–22 d and potentially drift considerable distances in coastal currents (Hinckley, 1987; Hinckley *et al.*, 1991). Mature adults may also move between spawning areas, and the distribution of juveniles can shift to avoid the “cold pool” in the eastern Bering Sea (Bailey *et al.*, 1995). The semi-pelagic habit of pollock adults produces spatially homogeneous populations over larger areas (e.g. eastern Bering Sea; Kotwicki *et al.*, 2005).

Coastal current patterns likely play an important role in structuring populations of pollock by controlling the movement of early life-history stages. The Alaska Coastal Current flows inshore over a wide continental shelf in the Gulf of Alaska and is influenced by many shelf canyons and a complex shoreline (Hermann *et al.*, 2002). The current narrows and combines with the fast-moving Alaska Stream along the southern edge of the Alaska Peninsula. A portion of the Alaska Stream filters through passages in the Aleutian Island chain and feeds a northwestern current over the broad, shallow continental shelf in the southeastern Bering Sea (Stabeno *et al.*, 2001). These fast-moving currents, with seasonal flows as fast as 100 cm s^{-1} (Hermann *et al.*, 2002), are expected to transport planktonic larvae over long distances.

Pollock stock structure is also influenced by North Pacific climate cycles that produce shifts in both local abundance and range-wide distributions (Stepanenko, 1997; Shima et al., 2001). In the North Pacific and adjoining seas, decadal ocean-climate changes alter primary and secondary productivity (Shuntov et al., 1996; Stabeno et al., 2001) and, hence, the abundance of mid- and high-trophic level fish (Vasil'kov and Glebova, 1984; Francis et al., 1998). The abundance of several marine fish has varied by at least an order of magnitude over the past several decades in response to climate shifts (Spencer and Collie, 1997). The effects of these environmental shifts on abundance have been incorporated into some harvest management strategies for pollock (e.g. Gulf of Alaska, A'mar et al., 2009), but have not been considered in defining the geographic extent of pollock stocks.

Management agencies currently recognize several fishery management regions for pollock. In the Northeast Pacific and Bering Sea, the North Pacific Fishery Management Council assesses populations separately in three areas: the Aleutian Islands, the eastern Bering Sea, and the Gulf of Alaska (Ianelli et al., 2008). The possibility of finer spatial resolution of stocks is recognized in the Gulf of Alaska, based on different spawning times of aggregates around the Shumigan Islands and those in Shelikof Strait, a few hundred kilometres away (Dorn et al., 2008). Two fishery regions are defined in the Russian Exclusive Economic Zone (EEZ) of the Bering Sea: a western Bering Sea stock in the Gulf of Olyutorski and a northern Bering Sea stock on the Navarin shelf from 171°E to the United States–Russia Convention line (Kotenev and Glubokov, 2007). Abundance of pollock is considerably less in areas to the south along the coasts of Asia and North America. Countries there generally employ community-based management, which effectively divides pollock populations into small management units, regardless of biological indicators of stock extent.

Although the census sizes (n) of pollock populations are large, as evidenced by harvests in the millions of tonnes, genetic effective population sizes (n_e) may be much smaller. Genetic estimates of n_e in other marine fish can be several orders of magnitude smaller than n (Hauser et al., 2002). Genetic differences between populations may arise through genetic drift, especially if regional populations are isolated from each other by shoreline configurations or currents. Surveys of genetic-marker variability can potentially identify barriers between populations. In general, surveys of genetic markers, including allozymes (Iwata, 1975; Grant and Utter, 1980; Olsen et al., 2002), mitochondrial (mt) DNA restriction fragment length polymorphisms (RFLPs; Mulligan et al., 1992; Shields and Gust, 1995; Kim et al., 2000; Olsen et al.,

2002; Brykov et al., 2004), microsatellites (Olsen et al., 2002; O'Reilly et al., 2004; Shubina et al., 2004, 2009), and the pantophysin gene (Pan I; Canino et al., 2005), show only weak population structure.

In this study, we used mtDNA cytochrome oxidase subunit I (COI) sequences to complement previous surveys of genetic variability among populations. Maternally inherited, haploid mtDNA markers experience greater levels of genetic drift, so higher levels of differentiation may appear between populations than with diploid nuclear markers. Inferences in previous studies of mtDNA variability were limited by small numbers of samples (Mulligan et al., 1992; Brykov et al., 2004) and by small sample sizes (Shields and Gust, 1995; Kim et al., 2000) that did not provide the statistical power to detect small differences between populations expected in a high gene-flow species (Waples, 1998). In those studies, surveys of variability were based on RFLP analysis, which limited the types of statistical analysis that could be used to infer stock structure. In addition to mtDNA sequence data, we compared the results of genetic studies with those from surveys of morphological and meristic variability. This provided a contrast between long-term events indirectly influencing genetic variability, with short-term processes directly influencing growth, reproduction, and recruitment. Finally, we revisited the postulate (Grant et al., 2006) that some mtDNA haplogroups in pollock may be influenced by selection.

Material and methods

Samples, DNA isolation, and sequencing

Walleye pollock ($n = 383$) were collected at eight spawning localities across the North Pacific (Table 1, Figure 1). Some of the samples were used in previous surveys of allozyme, microsatellite, and mtDNA RFLP variability (Olsen et al., 2002; O'Reilly et al., 2004). Fin clips were preserved in 95% non-denatured ethanol, and genomic DNA was extracted with a Qiagen Dneasy kit (Qiagen Inc., Valencia, CA, USA; note that reference to brand name does not imply endorsement by the National Marine Fisheries Service, NOAA) following the manufacturer's protocol. Additional sequences ($n = 50$) of pollock from Puget Sound (Port Townsend, WA, USA) were included to extend the geographic range of this study. This sample consisted of a 410-bp fragment of COI (GenBank accession numbers DQ385429–DQ385443; Grant et al., 2006).

A 630-bp fragment of mtDNA COI was amplified with the polymerase chain reaction (PCR) and primers COI gadid F (5'atcaccgctgattttctc 3') and COI gadid R (5' attgcccaagaattgatga 3';

Table 1. Sample locations, abbreviation, latitude and longitude, sample size (n), haplotype diversity (h), and nucleotide diversity (Θ_π) of mitochondrial DNA cytochrome oxidase subunit I (410 bp) in walleye pollock.

Location	Year	Abbreviation	Latitude	Longitude	Number of haplotypes	n	H	Θ_π
1. Funka Bay, Japan	1998	JP	45.30	143.20	9	38	0.716	0.0025
2. Kronotsky Bay, Russia	1999	KR	52.00	161.00	16	49	0.815	0.0034
3. Adak, Island, AK	2006	AD	52.30	–174.79	15	49	0.777	0.0031
4. Central Bering Sea	1999	CB	61.19	–177.72	14	49	0.838	0.0037
5. Bogoslof Island, AK	2001	BG	53.25	–169.00	14	49	0.741	0.0032
6. Unimak Pass, AK	1997	UN	54.41	–165.73	12	44	0.693	0.0027
7. Shelikof Strait, AK	1998	SH	57.60	–154.39	17	53	0.744	0.0034
8. Icy Bay, AK	1999	IB	60.08	–141.28	12	52	0.732	0.0033
9. Port Townsend, WA ^a	2003	PT	48.12	–122.77	15	50	0.736	0.0035

Sample numbers correspond to the numbers in Figure 1.

^aSample information from Grant et al. (2006).

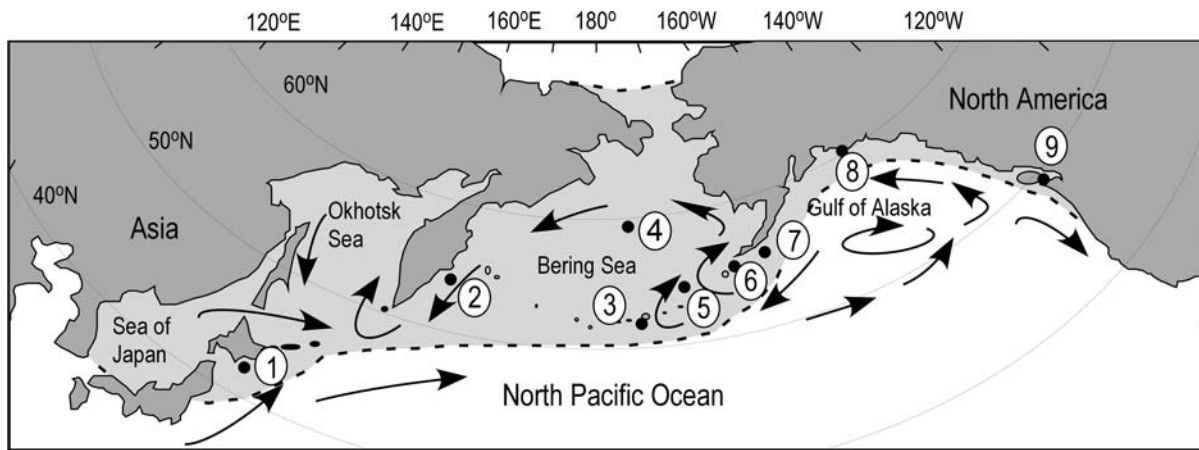


Figure 1. Map of the North Pacific showing the distribution of walleye pollock and the localities of the samples. Arrows indicate major ocean currents. Sample numbers as in Table 1.

Grant *et al.*, 2006). Sequences were amplified in a 10- μ l mix with ca. 100-ng template DNA, 10 mM Tris-HCl (pH 8.3), 50 μ M KCl, 2.5 mM MgCl₂, 2.0 mM each dNTP, 5 pM each primer, and 0.5 U Biolase *Taq* polymerase (Biolase Technology, Inc., San Clemente, CA, USA). Amplifications were made with a touchdown thermal cycle in an MJ Research PTC-100 Thermalcycler (MJ Research, Inc., Waltham, MA, USA). An initial denaturation step at 94°C (2 min) was followed by five cycles of 94°C (1 min), 56°C [1 min (-1°C cycle⁻¹)], and 72°C (1 min), then by 25 cycles of 94°C (30 s), 51°C (30 s), and 72°C (30 s), with a final extension at 72°C (10 min). Amplicons were treated with ExoSAP-IT^R (USB Corp., Cleveland, OH, USA) to degrade unincorporated primers and deoxynucleotides. PCR products were diluted to 6 ng μ l⁻¹ in dH₂O and sequenced in both directions on a high-throughput capillary sequencer at the University of Washington High Throughput Genomics Unit (<http://www.htseq.org>). Unique haplotype sequences were deposited in GenBank (accession numbers EU715523–EU715584). GeneBank accession numbers are abbreviated (E23–E84; D29–D43) for graphic presentation.

Statistical analysis

Haplotype (h) and nucleotide (Θ_m) diversities were estimated with ARLEQUIN 3.11 (Excoffier *et al.*, 2005). Geographic structure was inferred from only the eight spawning-area samples, because the sample from the central Bering Sea likely consisted of fish from different spawning areas. The 630-bp sequences in these eight samples were trimmed to 410 bp to include the sample from Port Townsend for geographic analyses. These edited sequences produced similar summary statistics and a similar 95% parsimony network to haplotypes based on 630 bp, indicating that little information was lost by truncating sequences (Table 1, and Tables S1–S3 in the Supplementary material). F -statistics and their analogue Φ -statistics were estimated with ARLEQUIN with 50 000 replicates to determine significance. F -statistics were estimated from haplotype frequencies, and Φ -statistics were estimated from both haplotype frequencies and sequence divergences between haplotypes. The HKY + I + G ($I = 0.695$, $\alpha = 0.604$) substitution model was used, as determined with MODELTEST (Posada and Crandall, 1998). Distributions of haplotype frequencies among samples were examined with the analysis of molecular variance

(AMOVA) in ARLEQUIN, using an adjacent-sample pooling analysis to test for genetic breaks between populations (Buonaccorsi *et al.*, 2004). This procedure was warranted because the samples used here were distributed linearly along the coast, and because isolation by distance in pollock (O'Reilly *et al.*, 2004) indicated that gene flow came predominantly from neighbouring populations. A 95% plausible parsimony network of haplotypes was constructed with TCS 1.21 (Clement *et al.*, 2002). Ambiguous connections between some haplotypes in the network were resolved with predictions from coalescence theory (Posada and Crandall, 2001). Isolation by distance was evaluated with Mantel's permutation test in IBDWS (Bohonak, 2002; <http://ibdws.sdsu.edu/~ibdws/distances.html>) and was tested with $\Phi_{ST}/(1-\Phi_{ST})$ and geographic distances (km) between samples with 10 000 permutations.

Results

In the 410-bp dataset, 49 haplotypes were defined by 28 transitions and eight transversions at 34 polymorphic nucleotide sites. Haplotype diversity (h) ranged from 0.693 to 0.838 and was 0.779 overall. Nucleotide diversity (Θ_m) ranged from 0.0025 to 0.0037 and was 0.0034 overall. The haplotype genealogy was relatively shallow, consisting of one widely distributed haplotype (E52) in 44% of the fish and many low-frequency haplotypes (Figure 2).

The most abundant haplotype (E51) varied clinally across the North Pacific, from 0.34 in Japan to 0.50 in Port Townsend (Figure 3). A closely associated haplotype (E52), differing by one substitution, exhibited a reverse cline, in which frequencies among samples varied from 0.42 in Japan to 0.01 in Port Townsend. Mantel's permutation test between $\Phi_{ST}/(1-\Phi_{ST})$ and geographic distance (Figure 4) was highly significant ($r^2 = 0.535$, $p = 0.003$). Most of the IBD signal was attributable to long-distance comparisons between the two Asian samples and the remaining samples. No significant IBD appeared among the six North American samples ($r^2 = 0.0009$, $p = 0.58$).

An AMOVA of the eight spawning-area samples yielded an overall $\Phi_{ST} = 0.030$ ($p < 0.0001$) and an $F_{ST} = 0.022$ ($p = 0.0003$). AMOVAs structured by progressive adjacent-sample pooling across the North Pacific into two groups indicated a significant break between Northwest Pacific samples (JP and KR)

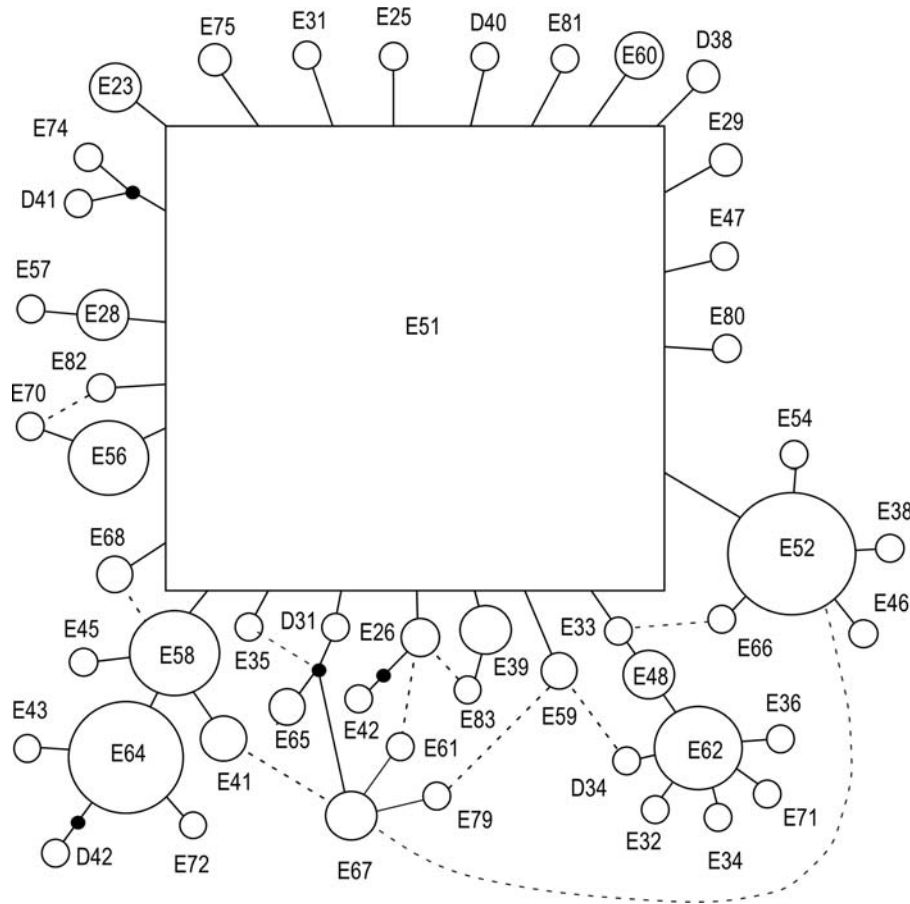


Figure 2. A 95% plausible parsimony network of mitochondrial DNA cytochrome oxidase subunit I haplotypes (410 bp) of pollock ($n = 433$). The sizes of the circles are proportional to haplotype frequency, the smallest circles representing a single haplotype. Dots represent hypothetical intermediate, but unobserved, haplotypes. The large square represents the plausible ancestral haplotype. Lines connecting haplotypes represent one mutational event. Ambiguous connections between haplotypes are indicated by dashed lines.

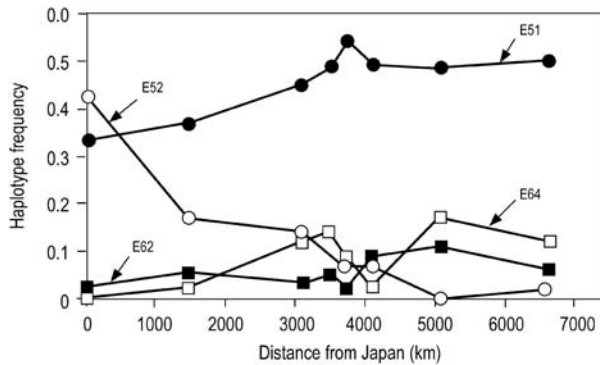


Figure 3. Frequencies of four haplotypes in samples of walleye pollock across the North Pacific and Bering Sea.

and Bering Sea and Northeast Pacific samples (AD, BG, UN, SH, IB, and PT; $\Phi_{CT} = 0.059$, $p = 0.034$), but also between JP, KR, AD, BG, UN, SH, IB, and PT ($\Phi_{CT} = 0.040$, $p = 0.018$; Figure 5 and Table S4 in the Supplementary material). Similar results were obtained in the analysis of only haplotype frequencies, except that the values of F_{ST} were marginally smaller (Figure 5 and Table S2 in the Supplementary material). No significant heterogeneity was detected among the five Northeast Pacific

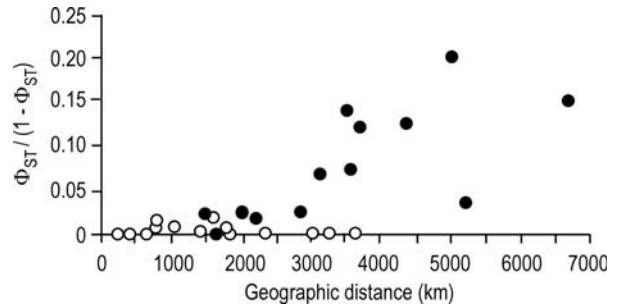


Figure 4. Isolation by distance between populations of North Pacific walleye pollock. Dots indicate comparisons involving Asian samples.

samples ($\Phi_{CT} = 0.003$, $p = 0.259$; $F_{ST} = -0.0002$, $p = 0.44$) nor between the two Northwest Pacific samples ($\Phi_{CT} = 0.023$, $p = 0.061$; $F_{ST} = 0.026$, $p = 0.065$).

Discussion

The results of this study, together with previous results for allozymes and microsatellites, indicate a general lack of genetic heterogeneity among samples from the Northeast Pacific and Bering Sea that could be used to define stocks of pollock. However, a

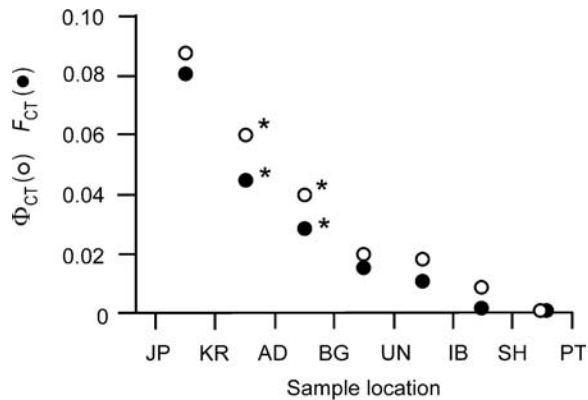


Figure 5. Adjacent-sample pooling analysis with AMOVA. Asterisks indicate significant ($p < 0.05$) values of Φ_{ST} and F_{ST} . Sample abbreviations as in Table 1.

moderate level of divergence exists between Asian and North American stocks. Haplotype-frequency clines across the North Pacific indicate that gene flow between populations at this geographic scale is somewhat limited. Nevertheless, limited gene flow has not produced definable stocks at smaller scales over the species' range, and we hypothesize that decadal climate shifts produce shifts in pollock abundance and distribution that prevent the accumulation of genetic differences between stocks, as measured with neutral molecular markers.

Origins of haplotype-frequency clines

Before developing this hypothesis, we consider the effect of using mtDNA variability constrained by selection to infer population structure. A previous summary of RFLP and sequence mtDNA data from several studies putatively resolved two mirror-image haplogroup clines on each side of the North Pacific. These clines were interpreted to reflect selection, because of correlations with latitudinal gradients in temperature (Grant *et al.*, 2006). The present study confirmed the presence of haplotype-frequency clines across the North Pacific, but the shapes of the clines differed from those previously postulated by Grant *et al.* (2006). The distributions of haplotypes based on sequences, rather than RFLPs, exposed the incorrect assumption that the common haplogroup in Puget Sound was homologous to the common haplogroup in Japan (this study). Hence, the haplotype-frequency clines resolved here extend across the North Pacific and are not mirror images of each other on each side of the ocean. A similar ocean-wide, mtDNA-frequency cline was observed in Atlantic cod (*Gadus morhua*) by Árnason (2004).

What are the origins of these clines? Associations between environmental variables and single-locus marker frequencies are often used to postulate the role of selection in shaping the clines (e.g. Slatkin, 1973). However, it is difficult to identify ocean-wide environmental gradients that would act as drivers of the clines in pollock across the North Pacific and in Atlantic cod across the North Atlantic. Moreover, Marshall *et al.* (2009) failed to find evidence of positive selection in a study of the whole mtDNA genomes of these two species. The lack of an association between haplotype frequency and environmental variables across the North Pacific and the lack of a selective signal in the whole mtDNA genome of pollock indicate that selection is unlikely to be responsible for these frequency clines.

Alternatively, these clines may have arisen by chance from restricted gene flow (Vasemägi, 2006) or from gene flow across a contact zone (Barton and Hewitt, 1985). A significant signal of IBD appeared overall across the North Pacific, but this was driven largely by comparisons between Asian and North American samples and not by restrictions on gene flow over distances of hundreds of kilometres in the sample-rich Northeast Pacific. This apparently scale-dependent IBD is typical of marine species (Bradbury and Bentzen, 2007) and is interpreted to be attributable to incomplete drift-migration equilibrium among populations (Bradbury and Bentzen, 2007). Although populations of pollock may not be in drift-migration equilibrium following ice-age disturbances, the lack of IBD in the Northeast Pacific argues against the chance formation of these clines.

A more probable explanation for the clines invokes historical isolation across the North Pacific by ice-age cooling and contemporary gene flow across a mid-ocean contact zone. Coastal glaciations during the Pleistocene apparently led to ocean-wide isolations and divergences in several marine fish, including Pacific herring (*Clupea pallasii*; Grant and Utter, 1984) and Pacific cod (*Gadus macrocephalus*; Grant *et al.*, 1987), which show major genetic partitions in the central North Pacific or Bering Sea. The major genetic partition observed in the mtDNA haplotype frequencies in pollock also likely reflects divergence during ice-age isolations. Subsequently, those groups expanded into the central North Pacific, and gene flow across the contact zone led to clinal haplotype frequencies. Experimental studies would be required to determine whether these are stable clines maintained by gene flow between two adaptive groups, or whether they are transient clines that would disappear after a long period of gene flow (Barton and Hewitt, 1985).

Stock structure

The major focus of this study, however, is on understanding short-term influences on stock structure. The task of assessing historical trajectories of abundance of a marine species to set harvest levels begins with a definition of appropriate management units. However, the criteria for defining threshold levels of migration between management units or populations differ between fishery managers and evolutionary biologists (Waples and Gaggiotti, 2006; Waples *et al.*, 2008). Fishery definitions generally focus on short-term environmental and ecological processes that influence population abundance and resilience under harvest scenarios. Evolutionary definitions of populations, in contrast, consider longer-term processes that lead to reproductive isolation between populations and drive genetic shifts. Ecological criteria for defining management units are more appropriate, given the management directives for sustainable harvests (Begg and Waldman, 1999).

In walleye pollock, allele-frequency shifts in the central North Pacific define two large ocean groups, but populations within these groups show little genetic differentiation from each other. Surveys with neutral genetic markers generally fail to resolve differences between populations on the same geographic scale (e.g. Olsen *et al.*, 2002; O'Reilly *et al.*, 2004), whereas results of phenotypic surveys unanimously show regional, and often fine-scale, differences among populations (see review by Gustafson *et al.*, 2000). For example, morphological differences defined four major populations located in the southeastern Bering Sea, northern Bering Sea, western Bering Sea, and Aleutian Islands (Serobaba, 1978). Contrasts in elemental profiles

of the otoliths of larvae also corresponded to many of these areas (Severin *et al.*, 1995; FitzGerald *et al.*, 2004). Patterns in parasite infections distinguished several groups of pollock in the Okhotsk Sea and western Bering Sea (Avdeev and Avdeev, 1989). On a larger geographic scale, vertebral, gillraker, and fin-ray counts resolved 12 stocks across the North Pacific (Koyachi and Hashimoto, 1977). Meristic differences also appeared between stocks in the Gulf of Alaska and those off the west coast of Canada (Koyachi and Hashimoto, 1977). In the Bering Sea, simulations of catch-and-effort data defined a single dynamically independent population of pollock (Cope and Punt, 2009). In Canada, several discrete spawning areas were apparent, and length frequency data indicated little mixing of adults among many areas (Saunders *et al.*, 1989).

In contrast, surveys along a coast with neutral genetic markers generally do not find differences between populations on small geographic scales (Olsen *et al.*, 2002; O'Reilly *et al.*, 2004). For example, allozyme frequencies (*Sod-2*) distinguished a genetic partition between subpopulations near Japan and in the southeastern Bering Sea (Iwata, 1975), but this difference was not echoed by mtDNA data (Kim *et al.*, 2000). Genetic differences were also reported within and between the Gulf of Alaska and the southeastern Bering Sea, but some of these differences were inconsistent from year to year (Olsen *et al.*, 2002). Microsatellite DNA markers showed both transoceanic and small-scale differences, but the latter were inconsistent among years (O'Reilly *et al.*, 2004). However, results from three of the same microsatellite loci used by Olsen *et al.* (2002) did not detect this transoceanic difference. An AMOVA (Grant *et al.*, 2006) of RFLP mtDNA haplotypes from Mulligan *et al.* (1992) indicated heterogeneity in the eastern Bering Sea, but the mtDNA data of Olsen *et al.* (2002) did not.

Despite the general genetic homogeneity among populations within regions, allele-frequency clines appeared for some molecular markers, indicating restricted gene flow. Shifts in frequencies of *Pan I* alleles appeared across broad oceanic areas and have been interpreted to reflect selection (Canino and Bentzen, 2004; Canino *et al.*, 2005). *Pan I* alleles also showed significant shifts among populations of Atlantic cod in response to temperature (Case *et al.*, 2005; Sarvas and Fevolden, 2005). Although the use of these selected gene markers may produce biased estimates of some population parameters when neutrality is assumed, they can provide a clear evidence of geographic differences between stocks.

Taken together, phenetic and genetic methods revealed patterns of variation between subpopulations, but these differences were not always consistent across marker types, at the same spatial scales, or over time. One reason for the discrepancy between the small-scale differences among populations detected with phenetic methods and the general lack of spatial resolution with genetic methods is likely the different time-scales that influence phenetic and genetic variation. Morphological and meristic differences between fish in different areas can arise rapidly in response to changes in environmental variables affecting growth. In contrast, frequencies of molecular markers shift only over longer time-scales in response to random drift, which is expected to be insignificant on short time-scales because of the large effective population sizes in pollock.

Shifting-balance stock structure

The patterns of genetic variability in pollock may be explained by a shifting-balance stock structure that is influenced on short

time-scales by environmental variability, in which subpopulations persist as long as local environmental conditions allow the completion of the species' life-history cycle (Smith and Jamieson, 1986). Responses to decadal changes in ocean temperature and productivity are clear examples of a shifting-balance population structure. In the British Isles, for example, the abundance of warm- and cold-water species shifts in response to decadal changes in ocean temperatures (Genner *et al.*, 2004). In another example, the latitudinal extents of anchovy (Engraulidae) and sardine (Clupeidae) populations around the globe periodically expand and contract in response to shifts in ocean temperatures (Schwartzlose *et al.*, 1999).

These populations experience repeated cycles of local displacement or extinction, and recolonization. The North Pacific is characterized by sudden ocean-climate changes on decadal and centennial scales that greatly influence the abundance and distribution of marine species (Mantua and Hare, 2002). These climate oscillations produce temperature shifts, large-scale current meanders, and disruptions in local upwelling that influence productivity and prey abundance. Pollock nursery areas diminish in size or disappear, even though the adults may persist (Wilson *et al.*, 2005). Survival at early life-history stages often depends on transport in mesoscale currents from spawning areas to inshore nurseries, away from cannibalistic adults (Schumacher and Stabeno, 1994; Wespestad *et al.*, 2000). Sudden changes in current patterns lead to atypical dispersals of larvae (Bailey *et al.*, 1999b), to local shifts in adult abundance, and to local extinctions (Vasil'kov and Glebova, 1984; Bailey *et al.*, 1999a; Nishimura *et al.*, 2001).

Short-term ocean-climate changes largely determine year-class abundance. Strong year classes often appear because of fortuitous ocean-climate conditions that reduce the mortality of larvae and juveniles. In the Okhotsk Sea, Bering Sea, and Gulf of Alaska, larval survival is greatest when warm temperatures follow spawning (Vasil'kov and Glebova, 1984; Bailey *et al.*, 1995). Enhanced survival in the Bering Sea, at least, can also result from reduced levels of cannibalism when juveniles move into shallow shelf waters away from offshore adults (Wespestad *et al.*, 2000). When unusually cool shelf waters prevent this separation, predation on juveniles by adults and other species greatly reduces the survival of the young of the year (Dwyer *et al.*, 1987; Livingston, 1993).

Recruitment of juveniles fluctuates considerably from year to year. In the eastern Bering Sea, 67% of the biomass in 1981 consisted of the 1978 year class (Bailey *et al.*, 1999a). That year-class bubble was synchronous among the Okhotsk Sea, western Bering Sea, Aleutian Basin, eastern Bering Sea, and the Gulf of Alaska. At other times, year-class strength among areas has not been synchronous (Dorn *et al.*, 2008; Ianelli *et al.*, 2008). Large 1982, 1989, 1992, and 1996 year classes appeared in the Bering Sea, but not in the Gulf of Alaska (Figure 6). Conversely, the 1976, 1977, 1979, 1988, 1990, and 1999 year classes were strong in the Gulf of Alaska, but not in the Bering Sea. These rapid asynchronous shifts in age classes indicate the independence of stocks in the Bering Sea and Gulf of Alaska and show a close coupling of pollock abundance with environmental variability. Shifts in abundance, in turn, influence patterns of dispersal and genetic connectivity between population groups.

In the past few decades, recruitment in some areas has dropped precipitously. In the late 1970s, biomass in the eastern Bering Sea declined, then recovered in the 1980s, dropped again in the early 1990s, and recovered in the mid-1990s and early 2000s, only to

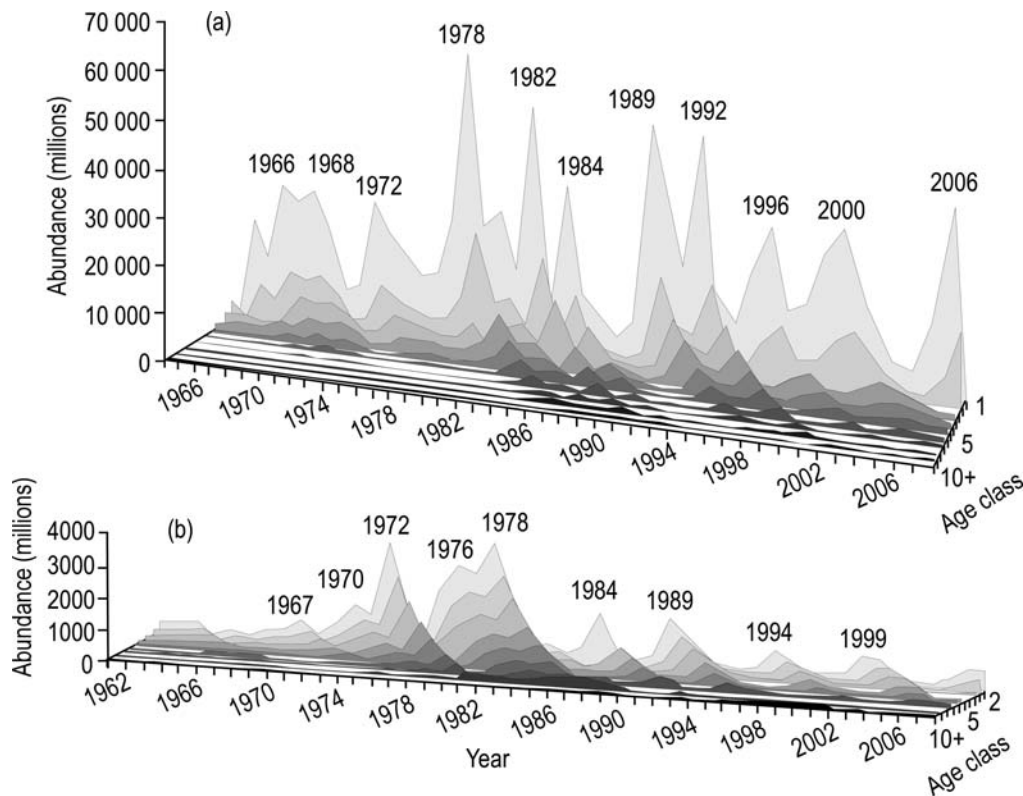


Figure 6. Year-class abundance of walleye pollock. Abundant year classes are indicated by dates at the peaks. (a) Eastern Bering Sea (from Table 1.20 of Ianelli *et al.*, 2008). (b) Gulf of Alaska (from Table 1.17 of Dorn *et al.*, 2008). Plots are generated from assessment model estimates of abundance.

drop again over the past few years (Ianelli *et al.*, 2008). The Aleutian Basin spawning subpopulation, which reached a biomass of almost 2 million tonnes in the late 1980s, has nearly disappeared (Ianelli *et al.*, 2008). Although fishing may have contributed, in part, to these population fluctuations, climate-regime shifts have an overriding influence on larval transport systems and ecosystem productivity (Wespestad *et al.*, 2000; Hinckley *et al.*, 2001; Shima *et al.*, 2001) and can lead to population declines. The cumulative effect of local extinctions and colonizations in pollock over long time-scales is expected to homogenize populations genetically. On short time-scales, regional environmental differences appear to produce phenotypically distinct populations, which are short-lived and do not accumulate genetic differences detectable with neutral molecular markers.

Conclusions

Patterns of mtDNA variability in pollock, together with the results of many studies of life-history variation and ecology, indicate poorly defined boundaries between regional stocks of pollock. Little genetic heterogeneity has been detected among populations within regions, despite a major subdivision across the Bering Sea and a weak pattern of isolation by distance, which indicate restrictions on dispersal. In this case, genetic homogenization appears to result from the “Red Queen” effects of subpopulation contractions, local extinctions, fissions, and expansions in response to low-frequency environmental variability. Under such circumstances, genetic differences between “populations” do not accumulate on small spatial and shorter temporal scales relevant to harvest management. Genetic markers are able to define only

large evolutionary population units in pollock that encompass the populations that are the focus of stock assessments and harvest management. The analyses of phenotypic and demographic population traits in pollock are more important for identifying local populations, because these variables reflect the short-term environmental drivers of larval survival and recruitment. Hence, the combined results of genetic studies on pollock do not provide information that would alter the present practice of managing pollock on the scale of continental shelf regions.

Supplementary material

Supplementary material is available at *ICESJMS* online, providing additional information on haplotype frequencies and summary statistics.

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References

A’mar, Z. T., Punt, A. E., and Dorn, M. W. 2009. The impact of regime shifts on the performance of management strategies for the Gulf of

- Alaska walleye pollock (*Theragra chalcogramma*) fishery. Canadian Journal of Fisheries and Aquatic Sciences, 66: 2222–2242.
- Árnason, E. 2004. Mitochondrial cytochrome *b* DNA variation in the high fecundity Atlantic cod: trans-Atlantic lines and shallow gene genealogy. *Genetics*, 166: 1871–1885.
- Avdeev, V. V., and Avdeev, G. V. 1989. A study of walleye pollock population structure and migration routes using parasitological indicators. In *Proceedings of the International Symposium Biological Management of Walleye Pollock*, pp. 569–590. Alaska Sea Grant Report No. 89-1, University of Alaska, Anchorage, AK, USA.
- Bailey, K. M., Bond, N. A., and Stabeno, P. J. 1999b. Anomalous transport of walleye pollock larvae linked to ocean and atmospheric patterns in May 1996. *Fisheries Oceanography*, 8: 264–273.
- Bailey, K. M., Canino, M. F., Napp, J. M., Spring, S. M., and Brown, A. L. 1995. Contrasting years of prey levels, feeding conditions and mortality of larval walleye pollock *Theragra chalcogramma* in the western Gulf of Alaska. *Marine Ecology Progress Series*, 119: 11–23.
- Bailey, K. M., Quinn, T. J., Bentzen, P., and Grant, W. S. 1999a. Population structure and dynamics of walleye pollock, *Theragra chalcogramma*. *Advances in Marine Biology*, 37: 179–255.
- Barton, N. H., and Hewitt, G. M. 1985. Analyses of hybrid zones. *Annual Review of Ecology and Systematics*, 16: 113–148.
- Begg, G. A., and Waldman, J. R. 1999. An holistic approach to fish stock identification. *Fisheries Research*, 43: 35–44.
- Benson, A. J., and Trites, A. W. 2002. Ecological effects of regime shifts in the Bering Sea and eastern North Pacific Ocean. *Fish and Fisheries*, 3: 95–113.
- Bohonak, A. J. 2002. IBD (isolation by distance): a program for analyses of isolation by distance. *Journal of Heredity*, 93: 153–154.
- Bradbury, I. R., and Bentzen, P. 2007. Non-linear genetic isolation by distance: implications for dispersal estimation in anadromous and marine fish populations. *Marine Ecology Progress Series*, 340: 245–257.
- Brykov, V. A., Polyakova, N. E., Priima, T. F., and Katugin, O. N. 2004. Mitochondrial DNA variation in northwestern Bering Sea walleye pollock, *Theragra chalcogramma* (Pallas). *Environmental Biology of Fishes*, 69: 167–175.
- Buonaccorsi, V. P., Westerman, M., Stannard, J., Kimbrel, C., Lynn, E., and Vetter, R. D. 2004. Molecular genetic structure suggests limited larval dispersal in grass rockfish. *Marine Biology*, 145: 779–788.
- Canino, M. F., and Bentzen, P. 2004. Evidence for positive selection at the pantophysin (*Pan I*) locus in walleye pollock, *Theragra chalcogramma*. *Molecular Biology and Evolution*, 21: 1391–1400.
- Canino, M. F., O'Reilly, P. T., Hauser, L., and Bentzen, P. 2005. Genetic differentiation in walleye pollock (*Theragra chalcogramma*) in response to selection at the pantophysin (*Pan I*) locus. *Canadian Journal of Fisheries and Aquatic Sciences*, 62: 2519–2529.
- Case, R. A. J., Hutchinson, W. F., Hauser, L., van Oosterhout, C., and Carvalho, G. R. 2005. Macro- and micro-geographic variation in pantophysin (*Pan I*) allele frequencies in NE Atlantic cod (*Gadus morhua*). *Marine Ecology Progress Series*, 301: 267–278.
- Clement, M., Posada, D., and Crandall, K. A. 2002. TCS: a computer program to estimate gene genealogies. *Molecular Ecology*, 9: 1657–1659.
- Cope, J. M., and Punt, A. E. 2009. Drawing the lines: resolving fishery management units with simple fisheries data. *Canadian Journal of Fisheries and Aquatic Sciences*, 66: 1256–1273.
- deYoung, B., Barange, M., Beaugrand, G., Harris, G., Perry, R. I., Scheffer, M., and Werner, F. 2008. Regime shifts in marine ecosystems: detection, prediction, and management. *Trends in Ecology and Evolution*, 23: 402–409.
- Dorn, M., Aydin, K., Barbeaux, S., Guttormsen, M., Megrey, B., Spalinger, K., and Wilkins, M. 2008. Gulf of Alaska Walleye Pollock. In *Stock Assessment and Fishery Evaluation Report for the Groundfish Resources of the Gulf of Alaska, Section 1*, pp. 53–168. Ed. by The Plan Team for the Groundfish Fisheries of the Gulf of Alaska. North Pacific Fishery Management Council, Anchorage, AK. (Available at <http://www.afsc.noaa.gov/refin/docs/2008/GOApollock.pdf>)
- Dwyer, D. A., Bailey, K. M., and Livingston, P. A. 1987. Feeding habits and daily ration of walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea, with special reference to cannibalism. *Canadian Journal of Fisheries and Aquatic Sciences*, 44: 1972–1984.
- Excoffier, L. G., Laval, G., and Schneider, S. 2005. Arlequin ver. 3.0: an integrated software package for population genetics data analysis. *Evolutionary Bioinformatics Online*, 1: 47–50.
- FitzGerald, J. L., Thorrold, S. R., Bailey, K. M., Brown, A. L., and Severin, K. P. 2004. Elemental signatures in otoliths of larval walleye pollock (*Theragra chalcogramma*) from the northeast Pacific Ocean. *Fishery Bulletin US*, 102: 604–616.
- Francis, R. C., Hare, S. R., Hollowed, A. B., and Wooster, W. S. 1998. Effects of interdecadal climate variability on the oceanic ecosystems of the NE Pacific. *Fisheries Oceanography*, 7: 11–21.
- Genner, M. J., Sims, D. W., Wearmouth, V. J., Southall, E. J., Southward, A. J., Henderson, P. A., and Hawkins, S. J. 2004. Regional climate warming drives long-term community changes of British marine fish. *Proceedings of the Royal Society, London B*, 271: 655–661.
- Grant, W. S., Spies, I. B., and Canino, M. F. 2006. Biogeographic evidence for selection on mitochondrial DNA in North Pacific walleye pollock *Theragra chalcogramma*. *Journal of Heredity*, 97: 571–580.
- Grant, W. S., and Utter, F. M. 1980. Biochemical genetic variation in walleye pollock, *Theragra chalcogramma*: population structure in the southeastern Bering Sea and the Gulf of Alaska. *Canadian Journal of Fisheries and Aquatic Sciences*, 37: 1093–1100.
- Grant, W. S., and Utter, F. M. 1984. Biochemical population genetics of Pacific herring (*Clupea pallasii*). *Canadian Journal of Fisheries and Aquatic Sciences*, 41: 856–864.
- Grant, W. S., Zhang, C. I., Kobayashi, T., and Ståhl, G. 1987. Lack of genetic stock discretion in Pacific cod (*Gadus macrocephalus*). *Canadian Journal of Fisheries and Aquatic Sciences*, 44: 490–498.
- Gustafson, R. G., Lenarz, W. H., McCain, B. B., Schmitt, C. C., Grant, W. S., Builder, T. L., and Methot, R. D. 2000. Status review of Pacific hake, Pacific cod, and walleye pollock from Puget Sound, Washington. NOAA Technical Memorandum NMFS-NWFSC-44. 275 pp.
- Hauser, L., Adcock, G. J., Smith, P. J., Bernal Ramírez, J. H., and Carvalho, G. R. 2002. Loss of microsatellite diversity and low effective population size in an overexploited population of New Zealand snapper (*Pagrus auratus*). *Proceedings of the National Academy Sciences of the USA*, 99: 11742–11747.
- Hermann, A. J., Haidvogel, D. B., Dobbins, E. L., and Stabeno, P. J. 2002. Coupling global and regional circulation models in the coastal Gulf of Alaska. *Progress in Oceanography*, 53: 335–367.
- Hinkley, S. 1987. The reproductive biology of walleye pollock, *Theragra chalcogramma*, in the Bering Sea, with reference to spawning stock structure. *Fishery Bulletin US*, 85: 481–498.
- Hinkley, S., Bailey, K. M., Picquelle, S. J., Schumacher, J. D., and Stabeno, P. J. 1991. Transport, distribution, and abundance of larval and juvenile walleye pollock (*Theragra chalcogramma*) in the western Gulf of Alaska. *Canadian Journal of Fisheries and Aquatic Sciences*, 48: 91–98.
- Hinkley, S., Hermann, A. J., Mier, K. L., and Megrey, B. A. 2001. Importance of spawning location and timing to successful transport to nursery areas: a simulation study of Gulf of Alaska walleye pollock. *ICES Journal of Marine Science*, 58: 1042–1052.
- Ianelli, J. N., Barbeaux, S., Honkalehto, T., Kotwicki, S., Aydin, K., and Williamson, N. 2008. Assessment of the walleye pollock stock in the eastern Bering Sea. In *Stock Assessment and Fishery Evaluation Report for the Groundfish Resources of the Bering Sea/Aleutian Islands Regions, Section 1*, pp. 47–136. Ed. by The Plan Team for the Groundfish Fisheries of the Gulf of Alaska.

- North Pacific Fishery Management Council, Anchorage, AK, USA. (Available at <http://www.afsc.noaa.gov/refm/docs/2008/EBSpollock.pdf>)
- Iwata, M. 1975. Genetic identification of walleye pollock (*Theragra chalcogramma*) populations on the basis of tetrazolium oxidase polymorphism. *Comparative Biochemistry and Physiology B*, 50: 197–201.
- Kendall, A. W., and Nakatani, T. 1991. Comparisons of early life-history characteristics of walleye pollock *Theragra chalcogramma* in Shelikof Strait, Gulf of Alaska, and Funka Bay, Hokkaido. *Japanese Fisheries Bulletin*, 90: 129–138.
- Kim, S.-S., Moon, D.-Y., and Yang, S. 2000. Mitochondrial DNA analysis for stock identification of walleye pollock, *Theragra chalcogramma*, from the North Pacific Ocean. *Bulletin of the National Fishery Research and Development Institute, Korea*, 58: 22–27.
- Kotenev, B. N., and Glubokov, A. I. 2007. Walleye Pollock *Theragra chalcogramma* from the Navarin Region and Adjacent Waters of the Bering Sea: Ecology, Biology, and Stock Structure., VNIRO Publishing, Moscow. 179 pp.
- Kotwicki, S., Buckley, T. W., Honkalehto, T., and Walters, G. 2005. Variation in the distribution of walleye pollock (*Theragra chalcogramma*) with temperature and implications for seasonal migration. *Fishery Bulletin, US*, 103: 574–587.
- Koyachi, S., and Hashimoto, R. 1977. Preliminary survey of variations of meristic characteristics of walleye pollock *Theragra chalcogramma* (Pallas). *Bulletin of the Tohoku Regional Fishery Research Laboratory*, 38: 17–40. (in Japanese with English summary).
- Livingston, P. A. 1993. Importance of predation by groundfish, marine mammals and birds on walleye pollock *Theragra chalcogramma* and Pacific herring *Clupea pallasii* in the eastern Bering Sea. *Marine Ecology Progress Series*, 102: 205–215.
- MacCall, A. D. 1990. *Dynamic Geography of Marine Fish Populations.*, University of Washington Press, Seattle, WA, USA. 200 pp.
- Mantua, N. J., and Hare, S. R. 2002. The Pacific decadal oscillation. *Journal of Oceanography*, 58: 35–44.
- Marshall, H. D., Coulson, M. W., and Carr, S. M. 2009. Near neutrality, rate heterogeneity, and linkage govern mitochondrial genome evolution in Atlantic cod (*Gadus morhua*) and other gadine fish. *Molecular Biology and Evolution*, 26: 579–589.
- Mulligan, T. J., Chapman, R. W., and Brown, B. L. 1992. Mitochondrial DNA analysis of walleye pollock, *Theragra chalcogramma*, from the eastern Bering Sea and Shelikof Strait, Gulf of Alaska. *Canadian Journal of Fisheries and Aquatic Sciences*, 49: 319–326.
- National Research Council. 1996. *The Bering Sea Ecosystem.* National Academy Press, Washington, DC, USA. 308 pp.
- Nishimura, A., Yanagimoto, T., Mito, K., and Katakura, S. 2001. Interannual variability in growth of walleye pollock, *Theragra chalcogramma*, in the central Bering Sea. *Fishery Oceanography*, 10: 367–375.
- Olsen, J. B., Merkouris, S. E., and Seeb, J. E. 2002. An examination of spatial and temporal genetic variation in walleye pollock (*Theragra chalcogramma*) using allozyme, mitochondrial DNA, and microsatellite data. *Fishery Bulletin US*, 100: 752–764.
- O'Reilly, P. T., Canino, M. F., Bailey, K. M., and Bentzen, P. 2004. Inverse relationship between F_{ST} and microsatellite polymorphism in the marine fish, walleye pollock (*Theragra chalcogramma*): implications for resolving weak population structure. *Molecular Ecology*, 13: 1799–1814.
- Posada, D., and Crandall, K. A. 1998. MODELTEST: testing the model of DNA substitution. *Bioinformatics*, 14: 819–818.
- Posada, D., and Crandall, K. A. 2001. Intraspecific gene genealogies: trees grafting into networks. *Trends in Ecology and Evolution*, 16: 37–45.
- Sarvas, T. H., and Fevolden, S. E. 2005. Pantophysin (*Pan I*) locus divergence between inshore v. offshore and northern v. southern populations of Atlantic cod in the north-east Atlantic. *Journal of Fish Biology*, 67: 444–469.
- Saunders, M. W., McFarlane, G. A., and Shaw, W. 1989. Delineation of walleye pollock (*Theragra chalcogramma*) stocks off the Pacific coast of Canada. In *Proceedings of the International Symposium on the Biology and Management of Walleye Pollock*, pp. 379–401. University of Alaska, Anchorage, AK, USA. Alaska Sea Grant Report 89–1,
- Schumacher, J. D., and Stabeno, P. J. 1994. Ubiquitous eddies of the eastern Bering Sea and their coincidence with concentrations of larval pollock. *Fisheries Oceanography*, 3: 182–190.
- Schwartzlose, R. A., Alheit, J., Bakun, A., Baumgartner, T. R., Cloete, R., Crawford, R. J. M., Fletcher, W. J., et al. 1999. Worldwide large-scale fluctuations of sardine and anchovy populations. *South African Journal of Marine Science*, 21: 289–347.
- Serobaba, I. I. 1978. Data on the population structure of the walleye pollock, *Theragra chalcogramma* (Pallas), from the Bering Sea. *Russian Journal of Ichthyology (translation of Voprosy Ikhtiologii)*, 17: 219–231.
- Severin, K. P., Carroll, J., and Norcross, B. L. 1995. Electron microprobe analysis of juvenile walleye pollock, *Theragra chalcogramma*, otoliths from Alaska: a pilot stock separation study. *Environmental Biology of Fishes*, 43: 269–283.
- Shields, G. F., and Gust, J. R. 1995. Lack of geographic structure in mitochondrial DNA sequences of Bering Sea walleye pollock, *Theragra chalcogramma*. *Molecular Marine Biology and Biotechnology*, 4: 69–82.
- Shima, M., Hollowed, A. B., and VanBlaricom, G. R. 2001. Changes over time in the spatial distribution of walleye pollock (*Theragra chalcogramma*) in the Gulf of Alaska, 1984–1996. *Fishery Bulletin US*, 100: 307–323.
- Shubina, E. A., Mel'nikova, M. N., Glubokov, A. I., and Mednikov, B. M. 2004. Analysis of the genetic structure of northwestern Bering Sea walleye pollock, *Theragra chalcogramma*. *Environmental Biology of Fishes*, 69: 177–185.
- Shubina, E. A., Ponomareva, E. V., and Glubokov, A. I. 2009. Population genetic structure of walleye pollock *Theragra chalcogramma* (Gadidae, Pisces) from the Bering Sea and Sea of Okhotsk. *Molecular Biology*, 43: 855–866.
- Shuntov, V. P., Dulepova, E. P., Radchenko, V. I., and Lapko, V. V. 1996. New data about communities of plankton and nekton of the far-eastern seas in connection with climate-oceanological reorganization. *Fisheries Oceanography*, 5: 38–44.
- Slatkin, M. 1973. Gene flow and selection in a cline. *Genetics*, 75: 733–756.
- Smith, P. J., and Jamieson, A. 1986. Stock discreteness in herrings: a conceptual revolution. *Fisheries Research*, 4: 223–234.
- Spencer, P. D., and Collie, J. S. 1997. Patterns of population variability in marine fish stocks. *Fisheries Oceanography*, 6: 188–204.
- Stabeno, P. J., Bond, N. A., Kachel, N. B., Salo, S. A., and Schumacher, J. D. 2001. On the temporal variability of the physical environment over the south-eastern Bering Sea. *Fisheries Oceanography*, 10: 81–98.
- Stepanenko, M. A. 1997. Variations from year to year in the spatial differentiation of walleye pollock, *Theragra chalcogramma*, and the cod, *Gadus macrocephalus*, in the Bering Sea. *Russian Journal of Ichthyology (translation of Voprosy Ikhtiologii)*, 37: 14–20.
- Teletchea, F., Laudet, V., and Hänni, C. 2006. Phylogeny of the Gadidae (sensu Svetovidov, 1948) based on their morphology and two mitochondrial genes. *Molecular Phylogenetics and Evolution*, 38: 189–199.
- van Valen, L. 1973. A new evolutionary law. *Evolutionary Theory*, 1: 1–30.

- Vasemägi, A. 2006. The adaptive hypothesis of clinal variation revisited: single-locus clines as a result of spatially restricted gene flow. *Genetics*, 173: 2411–2414.
- Vasil'kov, V. P., and Glebova, S. Y. 1984. Factors determining year-class strength of walleye pollock, *Theragra chalcogramma* (Gadidae), of western Kamchatka. *Russian Journal of Ichthyology* (translation of *Voprosy Ikhtiologii*), 24: 80–90.
- Waples, R. S. 1998. Separating the wheat from the chaff: patterns of genetic differentiation in high gene flow species. *Journal of Heredity*, 89: 438–450.
- Waples, R. S., and Gaggiotti, O. E. 2006. What is a population? An empirical evaluation of some genetic methods for identifying the number of gene pools and their degree of connectivity. *Molecular Ecology*, 15: 1419–1439.
- Waples, R. S., Punt, A. E., and Cope, J. M. 2008. Integrating genetic data into management of marine resources: how can we do it better? *Fish and Fisheries*, 9: 423–449.
- Wespestad, V. G., Fritz, L. W., Ingraham, W. J., and Megrey, B. A. 2000. On relationships between cannibalism, climate variability, physical transport, and recruitment success of Bering Sea walleye pollock (*Theragra chalcogramma*). *ICES Journal of Marine Science*, 57: 268–274.
- Wilson, M. T., Brown, A. L., and Mier, K. L. 2005. Geographic variation among age-0 walleye pollock (*Theragra chalcogramma*): evidence of mesocale variation in nursery quality? *Fishery Bulletin US*, 103: 207–218.

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