FISH and FISHERIES

Integrating genetic data into management of marine resources: how can we do it better?

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Abstract

Molecular genetic data have found widespread application in the identification of population and conservation units for aquatic species. However, integration of genetic information into actual management has been slow, and explicit and quantitative inclusion of genetic data into fisheries models is rare. In part, this reflects the inherent difficulty in using genetic markers to draw inferences about demographic independence, which is generally the information of the greatest short-term interest to fishery managers. However, practical management constraints, institutional structures and communication issues have also contributed to the lack of integration. This paper identifies some of the organizational, conceptual and technical barriers that have hampered full use of genetics data in stock assessment and hence fishery management and outlines how such use could be enhanced.

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Introduction

Management of living marine resources involves modifying anthropogenic impacts to achieve societal goals. It is widely recognized that sound management depends on scientific information, and a variety of international organizations have been established to facilitate collection and interpretation of scientific data for marine species in a management context (e.g. International Council for the Exploration of the Sea, ICES; International Whaling Commission, IWC; International Commission for the Conservation of Atlantic Tunas, ICCAT; North Pacific Marine Science Organization, PICES). In the USA, the three laws with the greatest direct impact on fisheries management at the national level are the Magnusson–Stevens Fisheries Conservation and Management Act (MSA), the Endangered Species Act (ESA) and the Marine Mammal Protection Act (MMPA). Each of these acts has different (and potentially conflicting) goals, but all have a common need for scientific advice on the likely consequences of alternative management actions.

Much of the scientific advice for fisheries management is based on outputs of stock assessment models. Several texts (Hilborn and Walters 1992; Quinn and Deriso 1999; Haddon 2001; Walters and Martell 2004) describe the plethora of methods used for fisheries stock assessment, which differ with respect to data requirements, complexity and the quantities they are designed to estimate. However, all involve (to at least some extent) three steps: (i) fitting a model

to data; (ii) using results of the model fitting exercise to make inferences about attributes of the population being assessed and (iii) using results of the population assessment to evaluate the ability of alternative management actions to satisfy management goals and objectives (which arise from legislation, international agreements and court decisions). In addition, all stock assessment methods require that the stocks/populations to be assessed are defined.

Some of the most fundamental (and vexing) problems in marine resource management are amenable to study with genetic methods. For example, in the 1950s, dissatisfaction with performance of phenotypic methods for stock identification encouraged early exploration of the usefulness of genetic markers (reviewed by Cadrin *et al.* 2005). Identification of genetically based differences among populations spurred development of statistical algorithms that can provide estimates of contributions of source populations to a mixed-stock fishery (Milner *et al.* 1985). The field of fishery genetics has greatly expanded in recent decades (Sweijd *et al.* 2000; Ward 2000; Hauser and Carvalho 2008), in parallel with (and due in no small part to spin-offs from) rapidly developing technologies in the field of human genetics. A recent meeting reviewing six decades of fishery genetics included, among many others, talks on genetic variation in reaction norms in fish, fishery-induced selection, parentage analysis to evaluate relative reproductive success, genetic analysis of domestication, insights into population histories using DNA from archived scales, gene

expression analyses to assess reproductive status, co-evolutionary relationships between IHNV virus and salmonid fishes and molecular tools for remote biosensing (see Waples *et al.* 2008 or http://www.nwfsc.noaa.gov/events/workshops/index.cfm for a meeting summary and agenda). More broadly, genetic data are widely used in many aspects of global biodiversity conservation, including identification of species (Hebert *et al.* 2004; Smith *et al.* 2006) and conservation units (Waples 1991; Moritz 1994; Crandall *et al.* 2000) and management of captive or artificially propagated populations (Frankham *et al.* 2002; Ryder 2003).

It is therefore somewhat ironic that, in spite of the considerable needs for scientific information by managers of living marine resources, and in spite of the demonstrated ability of genetic data to address questions of direct management relevance, formal integration of genetic information into fisheries management has been slow in many cases and uneven in even the most favourable situations. For example, on the West Coast of the USA, there is a rather imperfect correlation between the population units of groundfish species that have been identified with genetic markers and the units that are used for stock assessments (Table 1), and similar patterns can be found elsewhere in the world. This paper explores some of the reasons why this has occurred, where and how genetic information is currently being used in fisheries management, and how better integration of genetic information and traditional methods of fisheries stock assessment could substantially improve the quality of management advice. This is a large topic, so in this paper we have chosen to focus primarily on two widespread uses for genetic information in providing management advice: identification of populations or stocks and analysis of mixed-stock fisheries. We illustrate with examples drawn primarily from our experiences with the management of fisheries and whaling off Australia, South Africa and the West Coast of North America.

Factors contributing to the problem

Biological realities

Identifying populations and stocks
Andrewartha and Birch (1984) identified two major ways of thinking about populations: the ecological paradigm and the evolutionary paradigm (see Waples and Gaggiotti 2006 for more discussion).

Both paradigms invoke a cohesive force that unites individuals. In the ecological paradigm, the cohesive forces are demographic; a population is characterized by individuals that co-occur in space and time and have an opportunity to interact demographically. Important linkages between populations can largely be captured by the migration rate, *m*, which is the fraction of individuals in one population that were born in another population. The ecological paradigm is a natural way to approach the problem of defining populations or stocks because managers are typically interested primarily in population dynamic processes. One of the most common management problems is to identify populations that are demographically independent and can be modelled as separate entities. Information that indicates whether migration between two putative populations is low enough that they can be considered to be demographically independent (or, conversely, whether migration is high enough that they should be treated as a single demographic unit) is therefore of considerable interest to managers.

In the evolutionary paradigm, the cohesive forces are genetic; a population is characterized by individuals that interbreed. Most population genetic models are sensitive to the combined parameter mN_e, where N_e is the effective population size. The product mN_e represents the effective number of migrants per generation (roughly, those that actually reproduce and contribute genes to the new generation). This parameter is a key one in evolutionary biology; for example, it is central to Wright's (1931) famous equation that relates a measure of population genetic differentiation (F_{ST}) to the level of gene flow:

$$F_{ST} \approx 1/(1 + 4mN_e), \quad mN_e \approx (1/F_{ST} - 1)/4.$$

(1)

F_{ST} is easy to estimate in natural populations from samples analysed for molecular markers. Although Equation (1) is based on a simple, equilibrium model and assumptions that are rarely satisfied by natural populations (Waples 1998; Whitlock and McCauley 1999; Hedgecock *et al.* 2007), it still can provide useful insights into levels of population differentiation, and this equation (or variations thereof) has been widely used in studying patterns of connectivity in marine and terrestrial systems. However, the estimation of mN_e, is of little direct use to managers, who (as noted above) are generally interested in *m*. A consequence of these contrasting paradigms (ecological and demographic) is that, although

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Table 1 Genetic population structure and stock assessment units for West Coast groundfishes.

Species	Common name	Genetics		Stock assessment units
		Marker	Stock substructure	
Nearshore				
Hexagrammos decagrammus	Kelp greenling	NA	NA	2 units: CA and OR[a]
Ophiodon elongatus	Lingcod	al	2 stocks: PS stock and coastal stock (CA to AK)[1]	2 units: above and below 43° N.[b]
Platichthys stellatus	Starry flounder	NA	NA	2 units: CA and OR/WA[c]
Scorpaena guttata	California scorpionfish	NA	NA	1 unit: S. of Pt. Conception[d]
Scorpaenichthys marmoratus	Cabezon	mt	Minimum 2 stocks: N. and S. of Fort Bragg, CA; up to 8 stocks: WA, OR, and 6 in CA[2]	1 unit: C. CA to N. CA[e] 2 CA units: N. and S. of Pt. Conception[f]
Sebastes carnatus	Gopher rockfish	ms	No structure in CA[3]	1 unit: CA (N. of Pt. Conception)[g]
Sebastes melanops	Black rockfish	al	2 stocks: WA to mid-OR; mid-OR to CA[4]	1 unit: n. OR to WA[h]
		al	3 stocks: WA to n. OR, n. OR to n. CA north, n. CA south[5]	1 unit: CA to OR[i,j]
		al	None b/t OR and WA[6]	
		ms	2 stocks: WA; southern OR[7]	
		ms	2 stocks: w AK to Yakutat; Yakutat to WA[8]	
		ms	2 stocks: w. AK to Yakutat; Continental U.S; and a Brookings, OR outlier[9]	
Sebastes miniatus	Vermilion rockfish	ms	Cryptic speciation segregated by depth (break at 100m); Deeper species primarily south of Pt. Conception, CA[10]	2 unit: N. and S. of Pt. Conception, CA[k]
Sebastes mystinus	Blue rockfish	mt	2 stocks: N. of Mendocino, CA; S. of Mendocino, CA[11]	1 unit: Pt. Conception to OR[l]
		ms	None b/t San Miguel, CA and Fort Bragg, CA[12]	
		mt; ms	Two incipient types[13]	
Shelf/slope				
Anoplopoma fimbria	Sablefish	NA	NA	2 unit: above and below 43° N[m] 1 unit: CA to WA[n,o]
Atheresthes stomias	Arrowtooth flounder	NA	NA	1 unit: CA to WA[p]
Eopsetta jordani	Petrale sole	NA	NA	3 units: (1) above 43° N lat.; (2) 43° N to 40° 10′ N; (3) below 40° 10′ N[q] 2 units: above and below 43° N[r]
Microstomus pacificus	Dover sole	mt	Substructuring found from AK to CA, but no consistent geographic groupings[14]	1 unit: CA to WA[s,t]
Parophrys vetulus	English sole	NA	NA	1 unit (CA to WA), but 2 fisheries (break near Cape Mendocino)[u]
Merluccius productus	Pacific hake	al	2 stocks: coastal and PS[15]	1 unit: CA to WA[v]
		al	2 stocks divided at 28° N (Baja CA)[16]	
		al	3 stocks: coastal, PS, and Strait of Georgia[17]	

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Table 1 Continued.

| Species	Common name	Genetics		Stock assessment units
		Marker	Stock substructure	
Raja rhina	Longnose skate	NA	NA	1 unit: CA to WA[w]
Sebastolobus alascanus	Shortspine thornyhead	al	None from AK to CA[18]	1 unit: CA to WA[x]
		mt	3 stocks: AK, CA, and Cortez Bank[19]	
		mt	Substructuring found from AK to CA, but no consistent geographic groupings[20]	
Sebastolobus altivelis	Longspine thornyhead	mt	Substructuring found from AK to CA, but no consistent geographic groupings[20]	1 unit: CA to WA[y]
Sebastes alutus	Pacific Ocean perch	al	3 stocks: Gulf of AK; WA & OR; Prince William Sound[21]	1 unit: OR to WA[z]
		al	Low differentiation between AK & WA[22]	
		ms	3 BC stocks: Vancouver I.; E. Queen Charlotte; W. Queen Charlotte[23]	
Sebastes crameri	Darkblotched rockfish	ms	Low but significant differentiaion from N. CA to WA; no geographic groupings[24]	1 stock: 36° N to Canadian boarder[aa]
Sebastes diploproa	Splitnose rockfish	NA	NA	1 stock: CA to WA[bb]
Sebastes entomelas	Widow rockfish	NA	NA	1 stock: CA to WA[cc]
Sebastes flavidus	Yellowtail rockfish	al	None from WA to CA[21]	3 units: 40° 30′ N to 45° 46′ N; 45° 46′ N to 47° 20′ N; 47° 20′ N to 49° N[dd]
		rflp	None b/t Vancouver I., WA & CA[25]	
		mt; ms	2 stocks: N. of Cape Mendocino, CA; S. of Cape Mendocino, CA[9]	
Sebastes goodei	Chilipepper	al	None from WA to CA[21]	1 unit: CA to OR[ee]
Sebastes jordani	Shortbelly rockfish	ms	None from San Diego, CA to Cape Mendocino, CA[26]	1 unit in CA[ff]
Sebastes levis	Cowcod	NA	NA	1 unit: southern CA[gg]
Sebastes melanostomus	Blackgill rockfish	NA	NA	1 unit: CA[hh]
Sebastes paucispinis	Bocaccio	al	None from OR to CA[21]	1 unit: S. and C. CA[ii]
		ms	Ambiguous structure; most consistent above and below Pt. Conception, CA[27]	
Sebastes pinniger	Canary rockfish	al	2 stocks: WA to S. OR; S. OR to CA[21]	1 unit: CA to WA[jj]
Sebastes ruberrimus	Yelloweye rockfish	ms	2 stocks: WA to OR; PS[28]	1 unit: CA to WA[kk]
Sebastes rufus	Bank rockfish	NA	NA	1 unit: CA to WA[ll] 1 unit: CA[mm]

NA, not available; al, allozymes; ms, microsatellites; mt, mitochondrial DNA; rflp, restriction fragment length polymorphism; AK, Alaska; BC, British Columbia; CA, California; OR. Oregon; PS, Puget Sound; WA, Washington.

[1]Jagielo et al. (1996); [2]Villablanca & Nakamura (2007); [3]Narum et al. (2004); [4]Baker, unpublished data; [5]Wallace *et al.* (1999); [6]Baker (1999); [7]Miller et al. (2005); [8]L. Seeb and J. Seeb, unpublished data; [9]Hess, unpublished data; [10]Hyde et al. (2008); [11]Cope (2004); [12]Burford and Larson (2007); [13]Burford and Bernardi (2008); [14]Stepien (1999); [15]Utter and Hodgins (1969), (1971); [16]Vrooman & Paloma (1977); [17]Iwamoto et al. (2004); [18]Siebenaller (1978); [19]Stepien (1995); [20]Stepien et al. (2000); [21]Wishard et al. (1980); [22]Seeb & Gunderson (1988); [23]Withler et al. (2001); [24]Gomez-Uchida & Banks (2005); [25]McGauley & Mulligan (1995); [26]Constable (2006); [27]Matala et al. (2004); [28]Wallace et al. (2006).

[a]Cope and MacCall (2005); [b]Jagielo and Wallace (2005); [c]Ralston (2005); [d]Maunder et al. (2005); [e]Cope et al. (2004); [f]Cope & Punt (2005); [g]Key et al. (2005); [h]Wallace et al. (1999); [i]Ralston & Dick (2003); [j]Sampson (2007); [k]MacCall (2005); [l]Key et al. (2008); [m]Methot and Hightower (1990); [n]Methot (1992); [o]Schirripa 2007; [p]Kaplan & Helser (2007); [q]Sampson and Lee (1999); [r]Lai et al. (2005); [s]Sampson (2005); [t]Sampson & Wood (2001); [u]Stewart (2005); [v]Helser & Martell (2007); [w]Gertseva & Schirripa (2007); [x]Hamel (2005b); [y]Fay (2005); [z]Hamel (2005a); [aa]Hamel (2007); [bb]Rogers (1994); [cc]He et al. (2005); [dd]Wallace and Lai (2005); [ee]Field (2007); [ff]Field et al. (2007); [gg]Dick et al. (2007); [hh]Helser (2005); [ii]MacCall (2005); [jj]Stewart (2007); [kk]Wallace et al. (2006); [ll]Pearson (1994); [mm]Piner et al. (2000).

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fishery managers need information about migration, and genetic data can provide information about migration, it is not in a currency that is immediately useful to managers.

A second difficulty is that the transition between demographic dependence and independence occurs at a level of migration that is very high in evolutionary terms. Surprisingly, little attention in the literature has been paid to assessing the level of migration required to produce demographic coupling, but one simulation study (Hastings 1993) suggests that this might occur at about $m = 0.1$: populations connected by 10% or more migration are demographically coupled, whereas those experiencing less migration are demographically independent. Under what circumstances could genetic data distinguish between migration rates of, say, 5%, 10% and 20% – that is, half, equal to or twice the putative threshold for demographic independence? When populations are small ($N_e \approx 100$), these different migration scenarios have substantially different expected values of F_{ST} (Fig. 1). However, populations of most marine species are large and might have effective sizes of order 10^3 or higher, even allowing for relatively small ratios of effective size to census size (Hauser and Carvalho 2008). As illustrated in Fig. 1, for $N_e > 10^3$ the expected value of F_{ST} is extremely small for $m > 0.05$. This means that it is a very challenging task to use genetic data to distinguish between migration rates that do and do not lead to demographic independence, particularly given all the potential sources of noise (e.g.
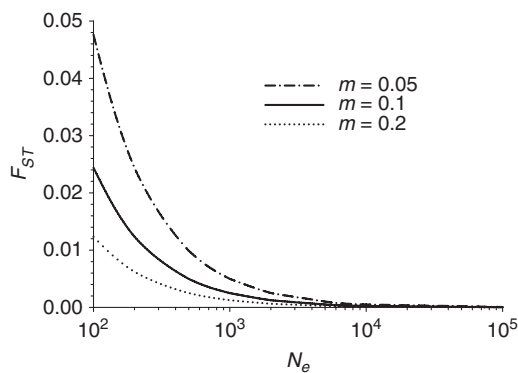
departures from random sampling; genotype scoring or recording errors) that could affect results (Waples 1998).

An important consequence of this reality is an asymmetry in the ability of equilibrium genetic methods to provide useful information regarding stock structure. If two putative populations really are connected by only low levels of migration, then (provided adequate samples can be collected) genetic methods generally will have considerable power to demonstrate this. However, if migration rates are high, genetic methods typically will struggle to distinguish between levels of connectivity that are and are not consistent with the need for separate stock management. That is, geneticists often can say quite confidently, 'Yes, the evidence strongly points to more than one stock', but it is very difficult, based on genetic data alone, to say something like, 'Yes, we are convinced that the two putative populations are connected by high enough levels of migration that they are demographically coupled'.

Taken together, these two biological realities pose considerable challenges to those wishing to use population genetic data to draw inferences of management relevance about population demography.

Mixed-stock fishery analysis

Populations or stocks that do not interbreed to any appreciable degree can nevertheless intermingle during part of their life cycle (e.g. on feeding grounds or during migrations), and effectively managing these mixed harvests to take advantage of abundant populations without overharvesting at-risk populations is one of the most challenging management problems for many aquatic species. Methods that take advantage of naturally occurring genetic markers have attracted a good deal of attention because application of physical tags is very labour intensive, and biological markers, such as scale patterns, can vary dramatically from year to year. The first genetic stock identification (GSI) methods for estimating the contributions of two or more stocks to a mixed harvest were developed in the late 1970s and applied to salmon (Grant *et al.* 1980; Milner *et al.* 1985). Since then, the rapidly expanding availability of highly variable genetic markers and refinements in statistical analyses (Pella and Milner 1987; Smouse *et al.* 1990; Pella and Masuda 2001; Koljonen *et al.* 2005) have considerably increased the ability to assess the proportions of different stocks in a mixed-stock

Figure 1 Expected equilibrium value of genetic differentiation (F_{ST}) for Wright's island model as a function of effective population size (N_e). Unless $N_e \ll 10^4$, genetic methods have little power to distinguish migration rates half, equal to or twice the putative threshold for demographic independence (migration rate, $m = 0.1$).

assemblage. Applications to a number of species have shown that these methods can provide information of direct management relevance (Utter *et al.* 1987; Brown *et al.* 1996; Beacham *et al.* 1999, 2004; Potvin and Bernatchez 2001). However, such information has not always been fully incorporated into fishery management. As discussed below in the example, this can be attributed in part to institutional and historical issues, but it also reflects the biological reality that the ability to resolve mixtures involving closely related populations can be limited.

Communication issues

Statistical significance vs. best available science
Many geneticists come from a hypothesis-testing background; a typical study design is to take samples of individuals from different localities and test whether one can reject the null hypothesis that the samples were drawn from a single, panmictic population. The hypothesis-testing framework is well suited to many types of scientific inquiry, where few or no practical consequences might ensue from making a type II error (failing to detect a true effect). In that case, it can be reasonable to stipulate a low α level to keep the type I error (false positive) rate low. Unfortunately, this approach has limited usefulness for fishery management, even though it is well grounded in statistical methodology. This is because the probability of obtaining a statistically significant result (power to reject the null hypothesis when it is false) depends not only on the effect size (true level of population differentiation – the biological signal of interest), but also on the amount of data (numbers of individuals, loci and alleles per locus). With limited data, important biological differences might be missed because of a lack of statistical power (Martien and Taylor 2003). Conversely, with modern techniques it might be possible to demonstrate that very small genetic differences are statistically significant, even if they are too small to be biologically meaningful in a particular context (Waples 1998).

More generally, a statistical test of panmixia is not often of much use to decision makers by itself. In most cases, there are sound biological reasons for believing that individuals from location A are more likely to breed with other individuals from location A than they are with individuals from location B. If that is true, then with sufficient effort it eventually will be possible to show that allele frequencies are

not identical in the two areas. What managers really want to know is *how much* more likely is local interbreeding than migration. This is directly related to the true level of population differentiation, or effect size. Notably, a *P*-value from a statistical test does not provide any information about effect size. Furthermore, in natural resource management, there can be severe (perhaps irreversible) consequences of making a type II error (e.g. failing to detect population structure when it exists). As a consequence, fishery scientists and managers typically work on the basis of 'best available science', in which various lines of evidence (including *P*-values and effect sizes, as well as associated sources of uncertainty and any other related information) are considered in an overall context before making a management decision. Application of 'best available science' approaches are designed to avoid some of management mistakes of the past, where, for example, fisheries managers sometimes assumed a null hypothesis of 'no depletion' and only acted to constrain fisheries if that hypothesis could be convincingly rejected.

Stock assessments of school shark (*Galeorhinus galeus*, Triakidae), which is considered overfished off Australia but sustainably harvested off New Zealand, illustrate these contrasting philosophies. Tagging studies document some migration between the two areas (Hurst *et al.* 1999), and at best weak evidence for genetic differentiation ($F_{ST} = 0.0014$ for allozymes and 0.0016 for mtDNA; both $P > 0.05$) has been found between school sharks in Australia and New Zealand (Ward and Gardner 1997; R.D. Ward, personal communication). Although the genetic analyses could not reject the hypothesis of a single stock at the nominal $\alpha = 0.05$ level, the school shark populations in the two countries are assessed and managed separately (Punt *et al.* 2000). This is done because the weight of evidence from the genetics data (a Bayesian analysis in which the one- and two-stock hypotheses are assigned equal prior probability) and tagging data (which suggest only low rates of movement between Australia and New Zealand and that only 'sub-adult' school sharks tagged in New Zealand had been recaptured in Australia) lend relatively more support to the hypothesis of two populations. Furthermore, treating Australian and New Zealand school sharks separately is more precautionary for the species in Australia because if the assumption were made that there is only one stock, there might have been no reason to reduce

harvest rates in Australia. It should be noted that, in this particular case, separate management (and assessment) would probably occur simply for administrative and logistical reasons because fish from one species are managed by two different national jurisdictions and hence under different objectives and legislation. It should also be noted that always treating putative population as separate stocks for assessment and management purposes is not always precautionary and that doing so unnecessarily can lead to loss of yield.

Disagreements and uncertainties among geneticists

As is typical of any rapidly evolving scientific discipline, evolutionary biology is characterized by energetic discussions among practitioners regarding the best approaches for experimental design, laboratory techniques, data interpretation and statistical and analytical methods. Inevitably, disagreements arise among scientists on some of these key issues. Although this is a natural part of the scientific process and can be a healthy way of advancing the field, real or perceived disagreements among geneticists can be confusing and troubling to managers, as can occasional publications that question the basic premise of applying genetic principles to conservation and management (Gauldie 1991; Backman and Berg 1992; Cronin 2007).

The genetic 'marker wars' of the past several decades are a case in point. For many years, allozymes were the universal workhorse genetic makers, and they made many valuable contributions to basic and applied conservation and management. Around 1980, the first applications of mitochondrial DNA (mtDNA) analysis to natural populations were published, and it was not long before some predicted that mtDNA would completely replace allozymes and provide answers to all key management questions regarding stock structure. Although mtDNA has indeed provided a wealth of new insights, it is not a panacea and has some limitations with respect to fishery management (e.g. it is clonal and maternally inherited, so provides no information about male migration or gene flow, and it is only a single marker and hence has much less power for some applications than a full suite of nuclear markers). In the 1990s, microsatellites muscled aside mtDNA and largely replaced allozymes as the markers of choice for population genetics studies. These highly variable markers have provided greatly increased power and opened up exciting new opportunities (e.g. parent-

age analysis and individual assignments) that were generally not feasible with allozymes or mtDNA. Again, some touted microsatellites as the silver bullet geneticists needed to answer management questions. However, microsatellites have not made (and cannot make) the biological realities discussed above go away. Managers who remember the overzealous promotion by some of mtDNA or microsatellites are understandably sceptical of subsequent (valid) claims by geneticists for the potential of new methods.

Now the field seems poised to shift toward another type of marker, single-nucleotide polymorphisms (SNPs; Morin *et al.* 2004a, Hauser and Seeb 2008). Like allozymes, SNPs are generally diallelic, so each marker has less power than a single microsatellite locus. However, they occur in vast numbers throughout the genome; therefore, eventually large overall increases in power are possible. Furthermore, once developed, SNPs can be assayed more reliably and cheaply than microsatellites, which could be a considerable advantage in large-scale fishery management applications. However, development of sufficient numbers of SNP markers will be neither easy nor cheap, and analytical issues such as minimizing ascertainment bias (Clark *et al.* 2005) remain to be resolved. As a consequence, scientists hold diverse views on the best approach to take in the near future. Given uncertainties or disagreements among geneticists on such fundamental issues, it is not surprising that managers often elect to take a wait-and-see approach and defer major investments in genetic methodology until the situation has been clarified (see example below).

A related issue pertains to exciting opportunities provided by new analytical and statistical methods in population genetics. To take just one example, a nagging problem for genetic stock identification is a lack of certainty whether all populations contributing to the mixed harvest are represented in the genetic baseline. If not, the resulting stock composition estimates will be biased. An early attempt to address this problem (Smouse *et al.* 1990) provided a way to estimate contributions from a single population not included in the baseline. In the current decade, much more powerful and much more general genetic clustering programmes have been developed (Pritchard *et al.* 2000; Corander *et al.* 2004; Pella and Masuda 2006) which do not require any baseline data at all. These programmes attempt to identify component gene pools by form-

ing groups of individuals that minimize single-locus (Hardy–Weinberg) and multiple-locus (linkage) disequilibrium within groups, using only the multilocus genotypic information in a mixed sample. The new clustering programmes have been widely used, both in academic and applied management contexts, and are remarkably powerful in some situations. Indeed, the potential ability to identify multiple gene pools in a single sample, without *a priori* assumptions about the relationship between sample location and population membership, is of considerable management interest. However, power of these methods is not unlimited, and their ability to provide meaningful information when levels of population genetic differentiation are weak (as occurs with many marine species) has not been rigorously studied (Hauser *et al.* 2006; Latch *et al.* 2006; Waples and Gaggiotti 2006; Schwartz and McKelvey 2008). It is difficult to develop solid recommendations for appropriate uses in applied management contexts because rigorous evaluation of programme performance has not been conducted at low levels of genetic differentiation. Population geneticists have a range of views on this issue, as evidenced by heated discussions at some recent meetings of the Scientific Committee of the IWC (IWC SC) (IWC 2007a). Healthy discussions like this can ultimately promote successful implementation of genetic methods into fishery management, but only if the technical issues are worked through in a logical, transparent and systematic way. The longer the debates continue without this sort of resolution, the more disenchanted managers are likely to be with geneticists and genetic methods in general.

Sometimes multiple genetic studies produce conflicting results. In the case of the black rockfish (*Sebastes melanops*, Sebastidae), Wallace *et al.* (1999) suggested separate genetic stocks north and south of Cape Falcon, Oregon, while Baker (1999) found that samples from north and south of Cape Falcon were quite similar (Table 1). The studies had different sampling and experimental designs; so, without additional information it is difficult to determine which provides a more accurate picture of stock structure. Changes to the population structures underlying a stock assessment can have profound implications for stock status regionally and hence for management actions. Assessments of hoki (*Macruronus novazelandie*, Macruronidae) off New Zealand have considered one- and two-stock scenarios (Francis 2006). The possibility of two ('western' and 'eastern') stocks is

supported by consistent differences seen in morphometric and ageing studies (Livingston *et al.* 1992; Horn and Sullivan 1996; Livingston and Schofield 1996), but early genetic studies did not identify significant differences (Smith *et al.* 1981). The stock status is sufficiently different between assessments based on one- and two-stock scenarios potentially to be consequential for management decision making.

Institutional issues

Institutional uncertainty relates to the inability of institutional structures that underlie fisheries management to deal with the problems they confront (and how those problems change over time). Management systems in many jurisdictions have evolved from supporting development and expansion of fisheries and fishing fleets to focusing on conservation and sustainable utilization, but this transition has not always been smooth.

Mismatch between management units and biological units

The purpose of a stock assessment is to provide timely and appropriate scientific advice to management (see, for example, Fig. 2, which outlines the assessment and management process for federally managed species off the West Coast of the USA). Stock assessments always involve simplifications and assumptions that relate not only to biology, but also to the realities of providing management advice. In this section, we will focus on potential mismatches between units on which assessments and management are based and those inferred from biological data, but similar consideration apply for related issues. For example, assessments are almost always conducted for single species, whereas in reality stocks are influenced by multi-species effects. However, in the absence of accepted data and models for multi-species interactions, stock assessments will continue to be based on single-species models, the behaviour and data needs for which are well known and familiar to managers.

Stock assessments are generally based on a variety of sources of information, including catches, trends in abundance and size and/or age structure. Sampling designs for these data sources are often based on political or administrative boundaries. For example, data for groundfish species off the US West Coast are generally organized into regions defined by the International North Pacific Fisheries Commission (NPFMC), while management often occurs
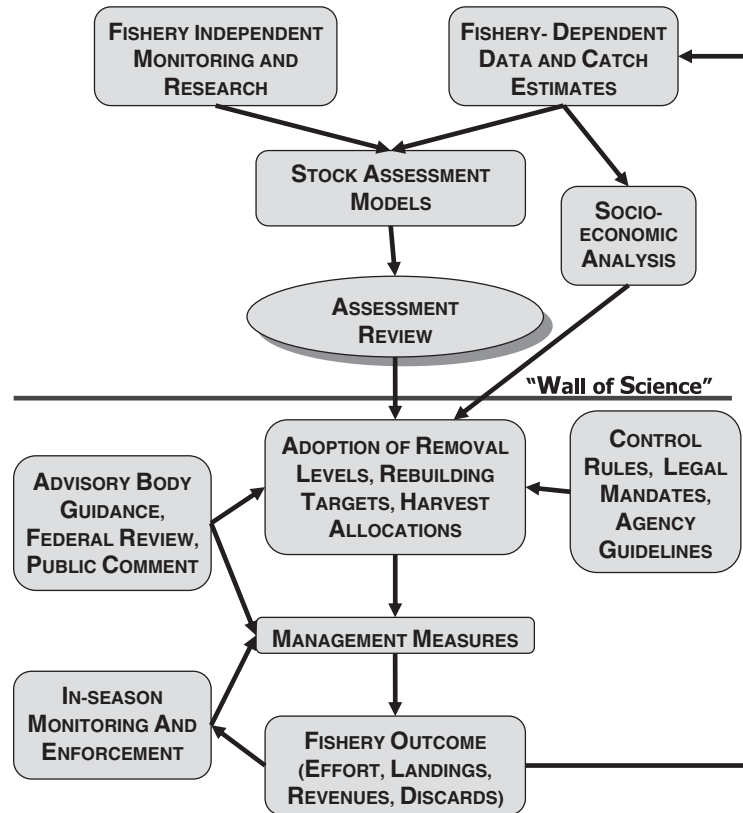
Figure 2 Overview of the management decision making and scientific advice processes for the fisheries managed by the Pacific Fishery Management Council (modified from Field *et al.* 2006, with permission).

at state (California, Oregon and Washington) levels and almost always along national lines (management arrangements for US West Coast groundfish can be very different between the USA, Canada and Mexico). The 2007 assessment of black rockfish *S. melanops* (Sebastidae, Wallace *et al.* 2007; Sampson 2007) involved an assessment boundary at Cape Falcon, OR, rather than at the Columbia River because Cape Falcon was the boundary for which most of the data were available. Had the Columbia River between chosen as the assessment boundary, it would have been difficult, if not impossible, to partition historical catches collected based on NPFMC boundaries to the new regions. Not surprisingly, the resulting discrepancy between biological and assessment boundaries can be frustrating for geneticists and managers alike.

Several factors probably contribute to the common mismatch between biological and management units evident in Table 1. The sampling design of genetic studies does not always match the geographic regions to which management controls

are applied. In addition, as noted above, different genetics studies sometimes give conflicting results, or are presented in a format or currency (e.g. *P*-values or estimates of gene flow) that is not very useful to managers. Finally, sometimes population structure identified using genetic methods is difficult to reconcile with standard stock structure models. This can happen, for example, if genetic methods find a clinal pattern, where genetic affinities change gradually over distance rather than with discrete breaks (Table 1). Although one might define an arbitrary boundary (or boundaries) within the range of a species that exhibits clinal structure and estimate migration between the putative stocks so defined this would require information on movement which is not available for the vast bulk of marine species.

A more extreme form of the mismatch between biology and management units occurs when genetic data indicate that there are multiple species (rather than just stocks) in a putative managed species. For example, an assessment of blue rockfish (*Sebastes*

mystinus, Sebastidae) was conducted, even though genetic and other evidence suggests that two species are involved (Key *et al.* 2008, Table 1). This assessment combined data for the putative species because it is currently (and probably always will be) impossible to split the historical catches to species. Although conducting aggregate assessments is not ideal from a management viewpoint, it is better than not providing any management advice at all. Furthermore, simulation studies (Punt 1992) have shown that management objectives can be achieved if two stocks are assessed and managed as one, provided that the inherent productivity of the two stocks is similar and the catches by species reflect the relative abundance of each stock. A similar situation exists with the deepwater and Acadian redfish (*Sebastes mentella* and *S. fasciatus*, Sebastidae) from Atlantic waters of Canada. Although genetic data confirm these two closely related species are distinct (Sévigny *et al.* 2003), they are nearly impossible to tell apart in the field. As a consequence, although these redfish are managed separately in nine different areas of the North Atlantic, within each of the broad areas of sympatry (including the Gulf of St Lawrence, Laurentian Channel, Grand Banks and southern Labrador Sea), the two species are jointly managed as a single 'stock' (Morin *et al.* 2004b).

A different type of mismatch between biological and management units can arise from managing fisheries on a more regional basis. Interest in this approach has been spurred recently by two factors: (i) community-based efforts to collect more information on local stocks and (ii) the perception that these finer scale data will show that stock status in the local area is better than is reflected in coast-wide assessments. This approach can lead to more accurate allocation of local resources, provided that the spatial scales of interest for coastal communities match the scales of population-level processes that are naturally found within marine ecosystems (PMCC 2007). However, there is no reason to expect that natural population units will match the borders of local communities. If local management is implemented on too fine a scale, a single biological population could be subjected to independent and perhaps conflicting management regimes in different areas of its range.

Another factor that can limit use of genetic data in stock assessments is the trade-off between accuracy and precision. A typical stock assessment used for West Coast fish species has tens to hundreds of parameters. Dividing an area into multiple populations should, all else being equal, reduce bias caused by assessing several populations as one. However, there will also be a cost in terms of reduced degrees of freedom and hence possibly lower precision when data from a single region are partitioned into several assessment areas. The trade-off can be examined using simulation (Punt 2003) or more generally using management strategy evaluation (MSE) (see below).

Finally, often it is not clear that modifying management advice to match biology 'matters' in the sense of affecting how fisheries management decisions will be made and implemented. For example, the recommendation to reduce fishing mortality for an overfished stock is likely to be robust to the choice of management units. A key role for assessment biologists is therefore to highlight the trade-offs and uncertainties (with respect to effects on management decisions) associated with different modelling and biological assumptions. In many cases, for example, uncertainties about reliability of abundance indices will dominate those related to stock structure.

Allocation issues

Allocation of access rights is one of the most important issues in fisheries management, and effective management generally requires a well-defined approach for allocation. Above we discussed how new genetic information can, for historical reasons, be difficult to accommodate into stock assessments. The same scenarios can create enormous challenges in deciding how management controls should be implemented in systems in which access rights have been allocated spatially. Individual transferable quotas (ITQs) have been used extensively worldwide and have formed the basis for fisheries management in Iceland and New Zealand since the 1980s. It is now common for total allowable catches (TACs) to be modified annually based on information from stock assessments. Consider a hypothetical species managed over a single region based on a TAC that is allocated in the form of ITQs. Suppose that new genetic evidence suggests that the region contains two demographically independent stocks. Ideally, this would lead to separate assessments for each stock and stock-specific TACs. However, this could raise a thorny allocation issue if the allocation rules do not explicitly account for this possibility. How should ITQs for the original (single) management unit be divided into ITQs for the newly defined units?

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Moreover, what should happen if one of the two stocks is assessed to be overfished while the other is not? Each ITQ holder currently has been allocated a percentage of the TAC, and one solution might be to give each ITQ holder that same percentage for each of the new stocks. However, this might mean that ITQ holders get new rights for areas they do not fish at the cost of rights for areas they do fish. Alternatively, if rights are allocated based on where individuals have fished historically, only fishers who harvest the overfished stock would have their rights reduced. Unfortunately, when a rights-based system is implemented, considerable attention is typically given to how access rights (including shares of TACs) are allocated, but potential consequences of subsequent changes in the definitions of the management units are almost never considered. This problem has occurred for blue warehou (*Seriolella brama*, Centrolophidae) off southern Australia. Genetic and other analyses suggest that separate stocks occur east and west of Bass Strait (Talman *et al.* 2003), and stock assessments are conducted by stock (Punt 2006a). However, TACs pertain to both stocks combined, and there has been no restriction on the fraction of the TAC taken from each stock.

Organizational structure

A clear need exists for geneticists to be more aware of standards applied by assessment scientists (and *vice versa*) and for both groups to be aware of the needs of managers. However, interchange of ideas to achieve this is often hampered by the organizational structure of management agencies, which frequently group scientists by discipline rather than by species. For example, a typical agency might have a genetics unit and a stock assessment unit, with only episodic communication between them. It is also uncommon for scientists other than those who conduct stock assessments to attend assessment and management meetings, and hence see how information on population structure feeds into the management process.

An example – genetic stock identification of Chinook salmon

Chinook salmon (*Oncorhynchus tshawytscha*, Salmonidae) is the largest Pacific salmon and is prized by sport, commercial and tribal fishers. Harvest primarily occurs at sea or in major rivers, where individuals from a few to over 100 populations can comingle. A brief review of the history of mixed-stock fishery management for this species illustrates many of the complicating factors discussed above, as well as some novel ones.

Background

In the 1960s, development of the coded-wire tag (CWT: a small wire coded with alpha-numeric data that is inserted into the snout of juvenile fish) produced an effective means of tagging fish. Because the tags provide direct evidence of origin for individual fish, managers can use CWT data from samples of a fishery to shape the harvests (in space and time) to focus on abundant populations while keeping incidental take of at-risk stocks below acceptable levels. Valuable adaptive management information can also be obtained by differentially marking treatment groups within a hatchery. The CWT programme has been the cornerstone of salmon harvest management on the US West Coast for several decades and has been an integral part of international harvest management of Chinook salmon under the Pacific Salmon Treaty since the mid-1980s (Bernard and Clark 1996).

On the other hand, the CWT programme is expensive and labour intensive, as massive marking and recovery efforts must be conducted every year (Hammer and Blankenship 2001). Only a small fraction of fish is marked, so field workers have to either handle many fish to find the few with CWTs, or invest in expensive electronic wands to detect the tiny tags in the field. Because marking wild populations is difficult, virtually all available CWT information is for hatchery populations. Some tags are lost, and some errors occur in reading codes. Finally, with widespread population declines and associated harvest reductions, samples of marked fish are often too small to yield the desired precision.

Although the initial application of GSI was for sockeye salmon (*Oncorhynchus nerka*, Salmonidae, Grant *et al.* 1980), the first application on a coast-wide scale occurred with Chinook salmon. A major advantage of GSI over the CWT is that GSI depends on naturally occurring genetic marks and thus can provide valuable insights into contributions by wild populations. Still, in spite of a number of demonstrated successes with Pacific salmon and other species, application of GSI to harvest management of Chinook salmon has been limited. Here are some of the reasons why this has occurred.

Biological and technical challenges

Implementing GSI on a coast-wide (or Pacific Rim) scale requires extensive efforts to collect baseline data for populations from California to Alaska (or Asia) and to standardize laboratory procedures so that comparable data can be obtained by different state, federal and university laboratories (Shaklee *et al.* 1999; Seeb *et al.* 2007). This requires broad collaboration among laboratories and a willingness to share unpublished data for use in management – provisions that are a stumbling block for some potential participants. For the most part, no centralized funding is available for coast-wide GSI; therefore, funds have to be pieced together from diverse sources, typically on a year-to-year basis.

Chinook salmon GSI has experienced the 'marker wars' described above (see also Appendix 1). The transition from allozymes to microsatellites over the past decade required major groundbreaking efforts to standardize data collection (LaHood *et al.* 2002; Moran *et al.* 2006). Now, some favour another major shift to SNPs. While energetic discussions among geneticists on the markers of the future take place, managers are reluctant to commit major funds lest they end up backing a soon-to-be obsolete technology.

After decades of being accustomed to definitive information about origins of individual fish provided by CWTs, some managers find it difficult to accept probabilistic assignments based on genetic markers, even in cases where other aspects of experimental design and analytical methodology lead to greater accuracy and precision of overall stock composition estimates. Moreover, GSI cannot generally distinguish separate treatments or release groups within a population, as can be done with CWTs.

Institutional issues

The CWT programme for Chinook salmon has a long history that spans the entire careers of many scientists, and this promotes inertia and resistance to change. Because management rules and treaties (especially the Pacific Salmon Treaty) have been developed based on models that rely on CWT data, changes to the technology (GSI vs. CWT) would require completely revamping some management rules. However, major changes cannot be implemented unilaterally; even demonstrably imperfect methods can be perpetuated because they have survived hard-fought efforts to reach agreement among parties with disparate objectives and perspectives. In general, broad participation is essential in the development of any new methodology.

Communication

Geneticists have not always taken the time to fully understand the intricacies of the management process so that genetic information can be packaged in the most effective manner, and limitations of GSI have not always been portrayed accurately. For example, GSI proponents have sometimes failed to realize that computer simulations can lead to overly optimistic estimates of the power of GSI to resolve mixtures of specific salmon populations (see Anderson *et al.* 2008), which can erode credibility. Conversely, scientists and managers involved in the CWT programme have been slow to acknowledge and integrate into their assessment paradigm the many empirical demonstrations that GSI can provide valuable management information.

Solutions: some strategies for improving the use of genetic data in fisheries management

As the problems identified above have many causes, improvements must come from a variety of directions as well. Below we outline some measures that should help to more fully integrate genetic considerations into fishery management, beginning with perhaps the single most important area where progress can be made – communication.

Communication

Integration
Stock assessments, and hence the provision of management advice, are usually conducted by 'assessment teams' and peer-reviewed prior to being used for management (see boxes in Fig. 2 above the 'Wall of Science'). Historically, assessment teams have primarily included quantitative fishery biologists employed by fishery management agencies. In appropriate situations, the teams should be expanded to include geneticists as well as academics, statisticians and field biologists. This would improve understanding of the needs of managers, and it would also bring the latest technologies to the attention of those tasked with providing management advice. Adding geneticists to assessment teams would also help alleviate the perception that geneticists are 'ivory tower scientists' who seldom

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understand how their results can actually be used. However, geneticists are not the only group currently under-represented on assessment teams. For example, it is not uncommon for assessment teams not to include the field biologists who are most familiar with the bulk of the data sources used, and for managers (and other stakeholders) not to participate in meetings of assessment teams – thereby potentially rendering the assessment process uninformative for management purposes.

Unfortunately, most geneticists (and field biologists) are not exposed to the techniques of statistical model fitting and decision analysis that form the basis for modern stock assessment science. Therefore, it might be necessary for management agencies (perhaps in collaboration with academic institutions) to develop courses to prepare geneticists (and others) for work on assessment teams. Such courses are now standard for decision makers in Australia and the USA. Conversely, most managers and assessment biologist alike would benefit from a greater literacy regarding the evolutionary forces (and associated methods) that can profoundly affect the living resources for which they share stewardship responsibility. For the past several years, the US Fish and Wildlife Service has offered a course in Applied Conservation Genetics to managers and biologists (information available at http://doilearn. doi.gov/CourseCatalog/index.cfm; accessed August 2008). Consistent with the agency's mission, this course typically emphasizes terrestrial and freshwater species. A comparable course that focused on issues of particular relevance to marine species could help bridge the information gap between geneticists, managers and stock assessment biologists.

Improved dialogue
Scientists, managers and policymakers could work together more effectively to foster productive dialogue about the relationship between statutory definitions and management or conservation goals. Just as terms like 'population' or 'stock' do not have unique biological definitions, most management-related problems do not have a single, generic scientific solution. Therefore, it is important to clearly articulate the goals one is trying to accomplish and how key terms are being used so that scientific evaluations can be conducted and communicated in the most effective way. For example, within the USA, the MSA states that 'To the extent practicable, an individual stock of fish shall be

managed as a unit throughout its range, and interrelated stocks of fish shall be managed as a unit or in close coordination'. However, the MSA does not define what an 'individual stock' is, which leaves the term open to a wide range of interpretations. Similar issues apply to most other major pieces of legislation, such as the ESA and MMPA – management agencies are legally mandated to use scientific methods to achieve societal goals, but doing so requires dealing with poorly defined legal terms that have no precise biological definitions. As discussed above, the idea that stocks are demographically independent units lies at the core of much of marine conservation and management. To maximize the usefulness of genetic information for fishery management, geneticists could do a better job in focusing on questions related to demographic independence rather than (or in addition to) more traditional analyses that provide insights into levels of gene flow. For reasons outlined above, this will be challenging; so, it is reasonable to expect that improvements will come only incrementally.

In general, units are demographically independent if population dynamics is affected more by local demographic processes (births and deaths) than by immigration or emigration. However, the appropriate threshold to use in determining demographic independence can differ depending on which processes one is primarily interested in. For example, the concept of demographic independence is central to three landmark US laws that guide management of living marine resources, but each piece of legislation implies a different flavour of demographic independence (Eagle *et al.* 2008):

1. The ESA is primarily concerned with extinction risk. It is difficult to conduct meaningful viability analyses on units that are not demographically independent; therefore, identifying such units should be a key step in status assessments and recovery planning. In one framework that has been adopted to guide recovery planning for ESA-listed Pacific salmon (McElhany *et al.* 2000), populations are considered demographically independent if the level of immigration from other populations is low enough that it does not appreciably affect extinction risk on a 100-year time frame.
2. Goals of the MMPA include maintaining marine mammal stocks as functioning elements of their ecosystems. In defining stocks, therefore, it is important to consider units that might suffer

local depletion. It is easy to imagine that migration levels that can affect extinction probabilities over 100 years might be too small to have an appreciable effect in avoiding local depletions on ecological time frames.

3. Under the MSA, when a stock is considered overfished it triggers management actions that are projected to rebuild the stock within 10 years (with an adjustment to the recovery time if the stock cannot be rebuilt in 10 years). This implies a short time horizon; demographic linkages must be very strong for nearby populations to have an appreciable rescue effect within an MSA rebuild period.

These different flavours of demographic independence, each valid in its own context, mean that managers need to define in operational terms what they mean by 'demographic independence' or 'individual stock'. After management goals and operational concepts are clarified, it is the responsibility of scientists (including, but not limited to, geneticists) to develop analyses that will deliver information in the necessary format and currency. Although some common themes will emerge, these processes – both reviewing and articulating management goals and developing operational definitions for key terms – will be unique for each specific application.

An innovative programme in coastal Oregon and California employs out-of-work fishers to conduct widespread sampling of the marine distribution of salmon (Bellinger *et al.* 2007). Under this programme, samples collected are genetically analysed by using GSI methods to provide a more complete picture of stock composition in space and time than is possible with current sampling regimes. This collaborative, multi-stakeholder project could help bridge long-standing gaps between geneticists, fishery biologists, managers and fishers and could serve as a model for how to facilitate understanding of genetic data and its integration into fishery management.

Getting real

Over the last 25 years, geneticists have sometimes oversold the products they can deliver. These examples of 'crying wolf' are remembered by decision makers and assessment scientists, and this has helped to erode confidence in advice provided by geneticists. Scientists, managers and living marine resources alike will be better served in the future if geneticists (and other scientists as well) make a

concerted effort to understand the limitations as well as the power of the methods they use, and to understand appropriate (and inappropriate) applications in the management realm. Conversely, managers and fishery assessment biologists can 'get real' by showing more genuine interest in genetic and evolutionary processes and being receptive to the many geneticists who are capable of communicating complex topics to non-geneticists.

Analytical methods

Over the past decade, three factors have conspired to produce a veritable information explosion of genetic data: development of DNA technology that can identify large numbers of highly variable markers; development of sophisticated new statistical methods for analysing population genetic data; and continuing rapid increases in computational power (see Hauser and Seeb 2008). Some of the new analytical techniques, broadly known as assignment methods (Pearse and Crandall 2004; Manel *et al.* 2005), have the potential to study contemporary dispersal over ecological time frames, rather than relying on assumptions about long-term migration–drift equilibrium, as do most standard population genetic models. With careful application, these new methods should be able to provide information of management relevance. However, like the traditional methods, they are also constrained by biological and statistical realities. Power to detect migrants depends on genetic differences among populations, which are inversely related to levels of gene flow. Migrants can be most reliably detected in strongly diverged populations, but it is generally easy to show with traditional genetic methods that strongly diverged populations cannot be exchanging enough migrants to be demographically coupled. Conversely, when migrants are numerous, perhaps near the proportion required to produce demographic coupling, they will be genetically similar to resident individuals and thus difficult to detect using genetic markers (Paetkau *et al.* 2004; Manel *et al.* 2005). This limitation can be gradually eased with the use of more and more genetic markers, but the problem is likely to remain challenging for the foreseeable future.

Although the dominant paradigm in population genetic studies of natural populations still involves collecting individuals from two or more geographic locations and considering them putative populations,

landscape genetics – the study of spatial genetic patterns in continuously distributed species – is rapidly evolving (Manel *et al.* 2003; Guillot *et al.* 2005). Most landscape genetic methods have been developed with terrestrial species in mind, but they are beginning to be applied to marine species as well (Palumbi 2003; Galindo *et al.* 2006; Selkoe *et al.* 2008). These studies provide important insights into biological processes and, for example, can help guide decisions about optimal design and efficacy of marine reserves. However, the population structures these models describe cannot be easily accommodated by conventional population assessments. Taking advantage of new insights that are possible from the field of landscape genetics will require considerable dialogue between geneticists, stock assessment scientists and managers, as well as creative thinking on both sides to develop effective ways to integrate these insights into stock assessment and management.

Finally, because the signal of population differentiation is often weak in marine species, it is important to take advantages of all types of information that shed light on population structure. Geneticists could do a better job of integrating their data with other types of biological and oceanographic information; see Selkoe *et al.* (2008) for a number of recent, encouraging examples showing how this can be performed. Ideally, this would involve collaborations at the experimental design stage so that joint sampling and analytical efforts can be planned more effectively. In particular, it is difficult to develop an ideal sampling design for a genetic study without understanding the details of the life history of the target species and physical processes in the marine realm.

Institutional changes

Institutional changes typically occur very slowly because considerable inertia must be overcome. For example, the problem of how to reallocate rights if our understanding of stock structure changes will probably require resolution in the courts for those species whose rights have already been allocated. However, the possibility that such changes will occur in the future should be recognized and the processes for reallocating rights should be included in any future management plans that include individual rights (such as systems based on ITQs or territorial rights). Similarly, although lack of appropriate historical information might currently limit

the ability to separately manage some stocks (or even species) that are biologically distinct (see examples of black rockfish, blue rockfish and Acadian redfish cited above), we can begin now to collect the necessary information that in the future should reduce the discrepancy between biological units and management units. More generally, if serious efforts are made as outlined above to improve integration and dialogue, the institutional barriers to fuller use of genetic information in fishery management should be significantly weakened.

Being opportunistic

Historical factors have contributed to the lack of full integration of genetics into fishery management and still represent inertia that must be overcome. However, changes are possible under some circumstances, and geneticists and managers alike have to be ready to take advantages of opportunities as they arise. For example, in response to increasing logistical challenges to the coast-wide CWT programme (detailed above in the Example) and increasing awareness of the potential of GSI, the Pacific Salmon Commission sponsored two workshops in 2007 having the following objectives:

''To develop recommendations for integration of GSI information into a coordinated coast-wide management system to improve the ability of ocean fisheries to access abundant stocks within impact constraints established for other specific stocks and, to the extent possible, to identify and quantify the costs, implementation steps and timeframes to implement these recommendations''.

Following these workshops, a set of recommendations was developed (Pacific Salmon Commission 2008) that provides at least a partial roadmap for better integration of genetics into West Coast salmon management.

Emerging areas where genetic information can improve fisheries management

Management strategy evaluation

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The bulk of management actions designed to achieve the objectives of national legislation (e.g. ESA, MSA and MMPA in the USA) and multi-national fisheries management agreements (e.g. IWC and ICES) affect fisheries either directly or indirectly. These actions include restrictions on inputs through closed areas and limitations on

fishing effort, and on outputs through catch limits. For most resource management problems, the key uncertainties relate to how many populations exist and what their statuses are. Genetics has a role to play in informing both of these issues. Management strategies (sets of rules which specify the data on which management decisions are based and stipulate what management actions will be taken given what the data say about the status of the management system) have been developed in many jurisdictions. For example, management (or harvest) strategies have been adopted formally in South Africa for management of several of its most economically valuable fishery resources (Plagányi *et al.* 2007) and by the IWC for management of commercial and aboriginal whaling (Punt and Donovan 2007). In most jurisdictions that have not formally adopted management strategies, management decisions are nevertheless based in some way on decision rules which approximate fully specified management strategies (Smith *et al.* in press).

Management decision making, whether based on formal management strategies or not, depend on a variety of assumptions, some related to population dynamics and others to stock structure. It is important to determine which assumptions, if violated, will most seriously compromise the ability to achieve management objectives. This process, often referred to as Management Strategy Evaluation (MSE; Smith 1994), involves developing a number of alternative models (operating models) to capture plausible alternative hypotheses regarding the dynamics of the system to be managed, and then evaluating the management consequences or outcomes (summarized by the resulting status of managed stocks and of catches and other measures of management success) for each alternative hypothesis.

Management strategy evaluation has been described extensively elsewhere (Smith 1994; Butterworth *et al.* 1997; Punt 2006b). A key aspect of MSE for our purposes is to select an appropriate range of plausible stock structure hypotheses, because it is well known that performance of a management strategy can be poor in the face of this source of uncertainty (IWC 1992, 1993). Genetics (and other approaches to identifying stock structure) can be important in selecting and refining such hypotheses. For example, the IWC SC recently evaluated management strategies for Western North Pacific minke whales (*Balaenoptera acutoro-*

strata, Balaenopteridae) (IWC, 2004), motivated in part by the need to consider the implications of harvest during migration. Three major stock-structure hypotheses were considered: (i) two stocks (west and east of Japan); (ii) three stocks (one west and two east of Japan) and (iii) four stocks (one west and three east of Japan) (Fig. 3). The least complicated stock-structure hypotheses (two and three stocks; Fig. 3 upper two panels) were justified primarily by the lack of evidence for multiple populations from statistical hypothesis tests applied to a range of genetic and non-genetic data. The most complicated hypothesis (four stocks; Fig. 3 bottom panel) arose from the application of a clustering algorithm (Martien and Taylor 2001) to mtDNA data. Perhaps not unexpectedly, the operating models based on four stocks posed more of a challenge to the candidate management strategies, and uncertainty about stock structure led, in part, to the IWC SC being unable to reach agreement on relative weights for different stock structure hypotheses.

Thus, even when it is not possible to fully integrate genetic data into fishery management models, genetic information can be used through the MSE process to help assess the consequences of ignoring population structure. Only a limited examination of the implications of failure to correctly identify stock structure has been conducted to date (Punt 2006b, 2008), but this could be expanded considerably. This would help managers assess the consequences of incomplete information or situations where it proves impossible to formally integrate genetic information into management advice.

Novel applications

This paper has focused on two major themes (stock identification and mixed-stock fishery analysis), as these are among the most pressing management problems and the ones for which use of genetic information is most common. However, genetic data can potentially provide valuable insights into a number of other questions of direct management relevance. These include the following.

Population abundance

The two most important outcomes from any stock assessment are current status (the current population size (N) and the population size relative to management reference points) and productivity. Several genetic approaches can provide information
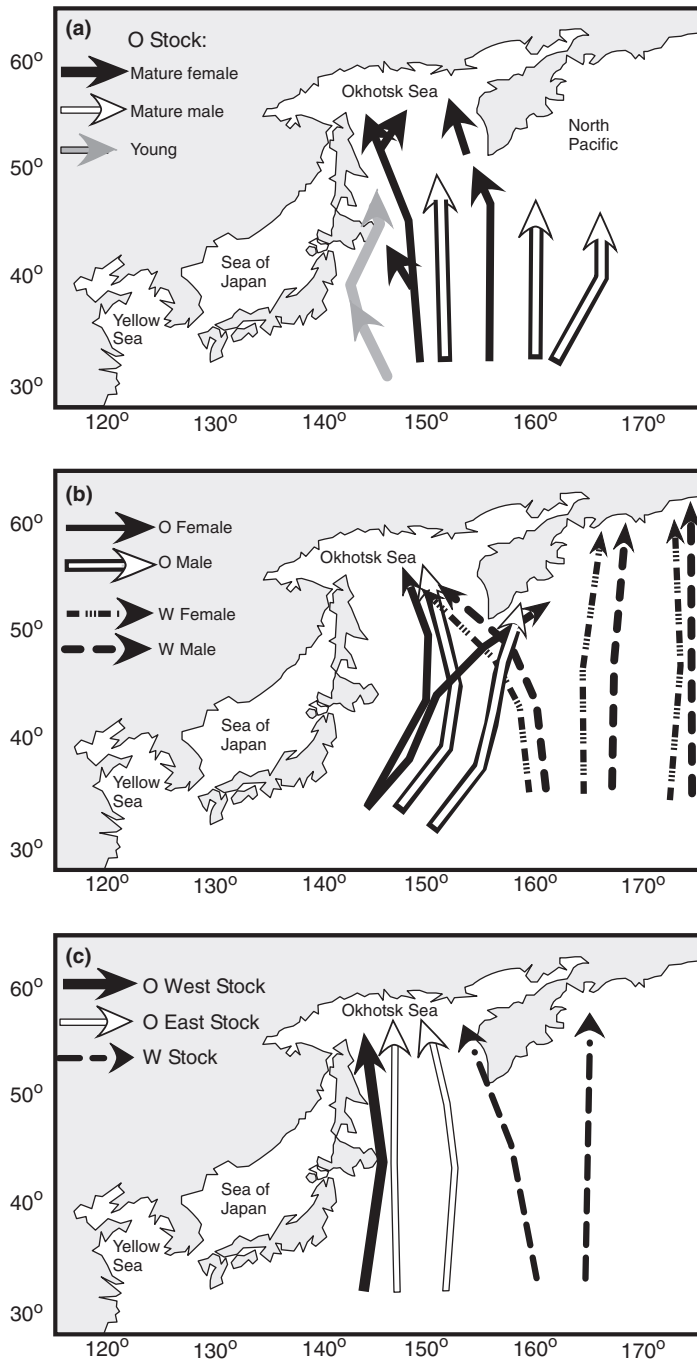
Figure 3 Summary of three major stock structure hypotheses (a, b, c) examined by the IWC SC during its evaluation of management strategies for the Western North Pacific minke whales. Arrows show putative migration routes between breeding and feeding grounds. The stock structure hypotheses arise from different ways of interpreting genetic and non-genetic information. In each panel, another stock (J, not shown) occurs to the West of Japan; each hypothesis also includes minor variants not shown here. Adapted from IWC (2004), with thanks to Greg Donovan and Kathleen Neely.

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about population abundance. The widely used mark–recapture method can be implemented effectively using multilocus genotypes as unique genetic marks. For terrestrial species, abundance estimates can be based on non-invasive sampling of scat, hair or feather samples (reviewed by Schwartz *et al.* 2007). Marine species present some special chal-

lenges, but this approach can be feasible if population size is not too large (Palsbøll *et al.* 1997). Highly polymorphic markers can produce unique multilocus genotypes for each individual, so these methods can be used not only to estimate *N* but also to track movement of individuals in space and time. Australian scientists have developed a special hook

that can take small biopsies for DNA marking (Buckworth *et al.* 2008), and a variant of this approach has been used to study abundance and distribution of rockfish (*Sebastes* spp.) within a conservation area in the Pacific Northwest (Hague 2006).

Although census size is generally of primary interest to managers, effective population size is of considerable evolutionary and conservation relevance and can be estimated using genetic markers (Schwartz *et al.* 1998; Leberg 2005). Furthermore, if the ratio N_e/N is known or can be estimated (see Hauser and Carvalho 2008), a genetically based estimate of N_e can provide a rough indication of N (Laurent and Planes 2007). A single-sample estimator of N_e based on linkage disequilibrium (Hill 1981) has seen relatively few practical applications, but has considerable potential to provide useful information about contemporary N_e (Waples and Do 2008). A novel application of a related method used current diversity of mtDNA to estimate the minimum (bottleneck) population size of cetaceans at the time commercial whaling was suspended (Jackson *et al.* 2008). Minimum bounds on population size obtained in this way have been included in recent cetacean stock assessments in the southern hemisphere. Assessments without the bound tend to indicate that humpback whale stocks were reduced to very low levels (below the minima implied by the genetic bounds) and have faster recovery rates (Johnson *et al.* in press). Other genetically based methods for estimating N in marine species include kinship analysis (Skaug 2001) and paternity analysis (Nielsen *et al.* 2001). Parentage analysis can also be used to study mating systems and patterns of realized reproductive success (Bekkevold *et al.* 2002) in marine species.

A global testing of genetic techniques for management purposes

Difficulties in using genetic data in stock assessments are compounded by the plethora of genetic methods, most of which have not been tested within a management context. To address this problem, the IWC SC has sponsored a global effort (testing of spatial structure models; IWC 2007b) to compare the performance of different genetic methods on common data sets. Importantly, performance is evaluated not only in terms of correctly identifying the 'true' number of populations, but also with respect to achieving management goals of sustainable utilization.

Miscellaneous

Other potential genetically based methods, all with empirical demonstrations of applicability to aquatic species, are too numerous to treat in detail here. These include analysis of fishery bycatch (Baker *et al.* 2006), identification of early life stages (Graves *et al.* 1990), forensic analysis of species at risk and product labelling (Schwenke *et al.* 2006, Ogden 2008), identifying origins of invasive species (Audzijonyte *et al.* 2008; Hess *et al.* in press), studying maturation and reproductive potential (Swanson *et al.* 2008), population genomics (Goetz and MacKenzie 2008), the link between the genotype and the phenotype (Naish and Hard 2008) and analysis of historical DNA samples to provide a temporal perspective on population genetic structure (Nielsen and Hansen 2008).

Conclusions

Numerous factors have contributed to the imperfect integration of genetic data into management of marine species. Some factors are inherently biological and relate to the relatively low signal-to-noise ratio for population structure in many marine species. Increasingly powerful laboratory and analytical techniques will make incremental progress in reducing these limitations. Considerable room for improvement exists on many communication issues involving geneticists, fishery biologists and managers. Historical factors that are largely out of the control of geneticists also impede integration of genetic information, and progress in these areas is likely to be episodic and opportunistic. However, even when historical factors impede full integration, genetic data can still be used to help assess the likely consequences of ignoring particular types of population structure, and this information can be valuable in the interim and, potentially, help the transition to a more effective management framework.

Consistent with the theme of this special issue, our paper has focused on the use of genetic information in fishery management. Some of the issues discussed above (especially those dealing with communication) are particularly challenging for geneticists because fishery stock assessments and fishery management are based primarily on ecological rather than evolutionary principles. These two fields of study are still imperfectly integrated, even in academic institutions where they are housed in the same department. Other

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challenges to better integration of genetic data (e.g. the need to produce timely information of management relevance in a currency that is useful to decision makers; difficulties associated with replacing outdated but accepted methods with promising new technologies; the importance of providing realistic assessments of both the power and limitations of each method, as well as associated uncertainties and the consequences of making different types of errors) are simply new twists on themes that have long affected the use of science in fishery management (Francis and Shotton 1997; Dayton 1998). In a broader sense, the topics discussed here reflect parallel issues about the appropriate relationship between science, management and environmental policy (Meffe *et al.* 1998). Although this relationship has a troubled history (Houck 2003), clear opportunities exist for science to better inform fishery management, and better integration of genetic data can help advance that enterprise.

Acknowledgments

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Appendix 1: Fred Utter's take on the genetic marker wars (unpublished data)

Hello SNPs

With allozymes dying, fish workers were trying to replace now-defunct data bases that for decades had grown and become widely known as the key to identify places where fish populations from various nations and regions were all intermixing.

Allozymes got expensive as they got less extensive and support for them rapidly nixing.

Allozymes hit the basement. To find a replacement, new DNA tools claimed the day.

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Each crowing their merits, they were dangled like carrots,
    asking management bodies to pay to develop,
    then sample – until data were ample to reach a
    new peak very fast for mixture solution with more
    resolution than allozymes did in the past.
Mitochondrial genomes were first seen as phenoms
    to reclaim salmon management's crown,
    but these female lines even failed to define
    what was known - this made managers frown.
Microsatellites came with immediate fame
    and abounding in loci, alleles.
Very soon major groups had the management troops
    strongly sniffing at microsat's heels.
Different groups had their foci on different loci.
    Different setups weren't very repeatable.

Analytical squeals from six dozen alleles
    suggested this tool was defeatable.
Among other blips, crept a tool known as SNPs
    with apparent explicit simplicity,
    proclaiming its wares based on nucleotide pairs,
    from proponents of zeal and felicity.
    This tool at this place is the primary basis
    of research intended to be
    a model – of course – for revealing the source
    of – sometime – every fish in the sea!!
Though it seems a bit chilling – living up to this billing
    is our intention right from the get go.
So come one and all. We are having a ball.
    Your problems we pledge never to let go.

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