FISH and FISHERIES

Ocean's eleven: a critical evaluation of the role of population, evolutionary and molecular genetics in the management of wild fisheries

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Abstract

Significant changes have occurred in the well-established partnership between fisheries managers and geneticists over the last 50 years. It is therefore timely to review and recalibrate the ways in which genetic technologies can assist the fishing industry to maintain productive and sustainable harvests. Our objective is to contribute to the mutual understanding of all stakeholders in the genetics–management partnership. Genetic technologies that are relevant to fisheries management are grouped into eleven themes, which are described in plain language for a non-specialist audience. The role that the genetic information plays in fisheries management is explained, along with an assessment of the challenges and barriers that may be preventing the uptake of the information into the fisheries management process. The compelling conclusion is that genetics offers a diverse collection of versatile and useful tools for informing fisheries managers about issues that have a biological basis. Presently, mainstream use of genetic tools focuses on a narrow set of fisheries management issues, but the diversity of genetic tools and the novel issues they can address indicates that uptake will grow, particularly as communication between geneticists and end-users improves.

Keywords environmental monitoring, genetic effective population size, genetic mark–recapture, product provenance, stock structure, unnatural selection

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Introduction

The science of genetics has assisted the management of wild fisheries and other marine life for over 50 years (Ryman and Utter 1987). During this time, approaches to fisheries management and genetic analysis have changed significantly. The breadth of issues considered by fisheries managers has increased substantially so that now, in addition to conventional management problems, issues such as ecosystem effects of fishing and surveillance of illegal fishing need to be considered. Similarly, genetics in the laboratory has undergone a revolution in the past two decades driven largely by advances in biomedical industries. There have also been significant theoretical advances in the analysis of genetic data. These changes are reflected by the recent rapid growth in scientific publications on fisheries genetics (Fig. 1).

In the light of these changes, there is a need to reassess the ways in which the science of genetics can contribute to fisheries. Fishery managers, researchers, industry representatives and fisheries geneticists need to be mutually aware of issues, requirements and capabilities to make the most out of new genetic technologies in the resource management sector. Previous reviews of the nexus between genetics and fisheries management have focused primarily on the use of genetic tools to define population units and how to best incorporate that information into fisheries stock assessments (Hauser and Carvalho 2008; Waples *et al.* 2008; Waples and Naish 2009). The scope of this review is broader and seeks to identify the com-

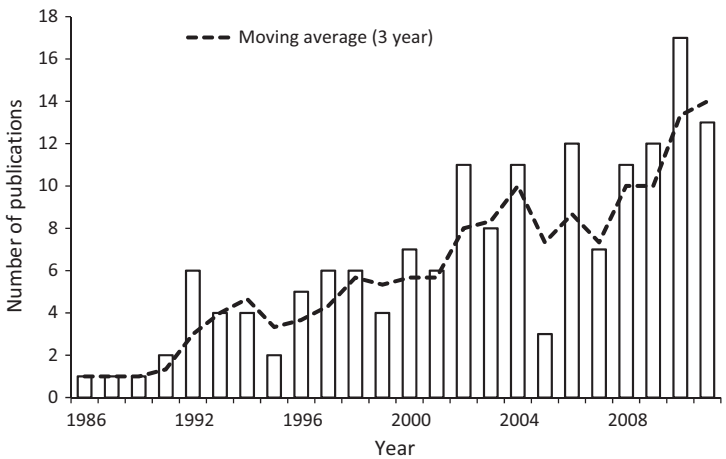

Figure 1 Number of peer-reviewed publications listed on the Web of Science Database related to fisheries management in Australia and that involved genetic analysis (Search: TS = [fishery AND (genetic OR DNA)] AND AD = Australia). The total number of publications listed is 144.

plete spectrum of new and existing genetic approaches that are likely to deliver significant advances to fisheries management, now and in the future, to stimulate new collaborative thinking that could improve the focus and impact in this area.

To this end, we describe eleven themes that encompass the ways in which genetic analysis can contribute to the management of naturally occurring fisheries resources. The themes align with four broad issues in fisheries management: (i) measuring the biological attributes of harvested species and the environment, (ii) measuring impacts of fishing on harvested species and the environment, (iii) biosecurity, and (iv) post-harvest regulation. The themes demonstrate the variety of genetic applications, but the divisions between them are artificial, and there is much complementarity and linkage. While we focus on the utility of genetics to inform fisheries management, other scientific disciplines make important contributions to this field. Comparison of the merits of genetics and other disciplines is outside the scope of this work, although such comparisons would undoubtedly be valuable for researchers and managers.

Each theme begins with the importance of the issue to fisheries management. The underlying principles of the genetic methods are provided briefly, and interested readers are encouraged to consult primary literature for further information. Australian and international case studies are provided for all themes to illustrate the application of the methodology to naturally occurring fisheries resources. They are also presented to highlight contrasts in management goals and the science of fisheries genetics between regions. Within each theme, the limitations of the use of genetic tools are discussed frankly, including knowledge gaps and challenges to the implementation of outcomes derived from genetic studies. The future of each genetic theme is also presented, balancing optimism with realism. A plain language summary of the eleven genetic themes is presented as a 'field guide to genetics in fisheries' (Table S1) as well as a Glossary (Data S1). In summary, the objective is to facilitate a more coordinated and consistent approach to the application of genetic technologies, greater uptake of research outcomes, and build an enduring platform for future successes in genetic research and fisheries management.

Attributes of harvested species

Theme I: Species identification

Why is it important to fisheries management?
Many aspects of fisheries management rely on the accurate identification of both harvested and non-harvested organisms. Individuals harvested from a fishery, unintentionally caught or otherwise affected, need to be identified to maintain accurate records to assist with fisheries management. Mapping species distributions, the discovery of cryptic species, recognizing larval stages, detecting toxic algal blooms, the identification of by-catch and the construction of food webs for ecosystem models assume species can be identified accurately. Cryptic species are particularly challenging for management, but once recognized using genetic tools, reliable diagnostic morphological characters may be identified (e.g. Smith *et al.* 2011). Species identification is also important for post-harvest issues, such as seafood processing and marketing, and this is dealt with in theme XI.

DNA analysis is a rapid, universal and highly accurate tool for assigning a specimen to a species, provided the species has been taxonomically described and regions of its DNA have been characterized. It is particularly useful if the specimen lacks the morphological characters for routine taxonomic identification (e.g. fish fillet), if morphological characters are poorly defined (e.g. pre-caudal vertebral counts in whaler sharks, Carcharhinidae), if no diagnostic morphological characters are known (e.g. cryptic species) or if the state of preservation precludes morphological analysis. Even though we use the term 'species identification' here, we do not endorse the use of DNA alone for taxonomic description of animal species. As originally emphasized in early discussions of DNA barcoding, DNA data are part of a suite of auxiliary taxonomic tools (Moritz and Cicero 2004; Naylor *et al.* 2012).

How does it work and what are the limitations?
The advantages of DNA as a data source for species identification have been incorporated into the 'DNA barcoding' approach (e.g. Hebert *et al.* 2003). DNA barcoding is the use of a specific mitochondrial DNA (mtDNA) gene region (cytochrome oxidase subunit 1; COI) to recognize animal species by comparison with validated reference sequences. However, any gene region

(mtDNA or nuclear DNA) can be used provided it is diagnostic for the species under consideration and reference sequences are available. Generally, a user obtains DNA sequence from their sample and compares it with a database of reference sequences. If a close match is made, the identity of the specimen can be inferred. If a close match is not made and if the accuracy of the sequence of both the sample and reference database is satisfactory, the sample may belong to a species that is not included in the reference data or to a species that is taxonomically undescribed. There are two public reference databases for matching sequences: FISH-BOL (www.fishbol.org) and GenBank (www.ncbi.nlm.nih.gov/genbank). FISH-BOL is part of the International Consortium of the Barcode of Life (www.ibol.org), and the database consists of several recognized DNA barcoding genes with high quality assurance requirements, whereas GenBank is a repository for all available DNA sequences, often with lower quality assurance requirements.

While conventional DNA barcoding employs sophisticated laboratory equipment to generate readable DNA sequences for comparison between a specimen and references, a variety of more streamlined and portable approaches to DNA barcoding exist (e.g. Fox *et al.* 2005; Berry and Sarre 2006; Chow *et al.* 2006; Morgan *et al.* 2011). These new methods rely on detecting DNA sequence differences between species, but do not involve direct visualization of DNA sequences. They permit faster, less expensive analysis and lend themselves well to field deployment where results can be obtained in near real time.

The accuracy of DNA barcoding rests largely on the validity of reference sequences. Well-established quality assurance processes exist to ensure the accuracy of reference data, such as linking DNA sequences to museum voucher specimens and documenting biological and collection data associated with specimens (Ratnasingham and Hebert 2007). Meta-analyses of the accuracy of DNA barcoding for numerous taxa have demonstrated it to generally be >90% (e.g. April *et al.* 2011). Nevertheless, in a minority of cases, the accuracy of DNA-based species identification may fall below what is required for a range of reasons including hybridization (Morgan *et al.* 2012) and pseudogenes (Moulton *et al.* 2010; Morgan *et al.* in press). The main challenge to the greater use of DNA barcoding in fisheries management, however, is the incompleteness of reference databases, especially for invertebrate taxa. Approximately 30% of fish species globally, for example, have been DNA barcoded to date using the COI gene (http://www.fishbol.org).

Case studies

DNA analysis for species identification is an excellent tool for linking life-history stages to adult forms. To assist fisheries management and conservation in waters surrounding the Yucatan Peninsula (Mexico), Valdez-Moreno *et al.* (2010) used a DNA barcoding approach to assign fish eggs, larvae, juveniles and adults to 179 teleost and two elasmobranch species. Major range expansions were recorded for some species, and larvae of the fish genus *Eucinostomus* (Gerreidae) were identified for the first time. New information about the spawning time and locality was obtained for the most commercially valuable species in Mexican waters of the Caribbean (hogfish, *Lachnolaimus maximus*, Labridae).

Assigning by-catch to species is relevant to ecosystem-based fisheries management. Globally, albatrosses (e.g. *Diomedea* spp. and *Phoebastria nigripes*; Diomedeidae) and other pelagic seabirds have suffered high mortality as by-catch in longline fisheries. Because these species are highly mobile and because by-catch carcasses may be highly degraded, it is difficult to attribute mortality rates to species. Genetic tools demonstrated that the species, subspecies, breeding colony and gender of albatrosses could be assigned with high accuracy (Walsh and Edwards 2005; Burg 2007), permitting the impacts of by-catch on the viability of specific populations or species to be more accurately measured.

Barriers to uptake

There are few barriers to the uptake of this genetic technology. Species identification using DNA is a burgeoning scientific field and probably the most rapidly growing area where genetic tools are being taken up for fisheries management. Fisheries species are particularly well represented in international DNA databases because of the ongoing, dedicated program designed to establish this baseline (Ward *et al.* 2009). The database will facilitate the uptake of barcoding technology in fisheries management, and enable more accurate and consistent attributions of catch and by-catch than have been possible in the past. From a fisheries manager's perspective, the reliance on skilled personnel and suitably equipped laboratories to perform the work may be a limiting factor. However, many laboratories in uni-

versities, museums and government institutions are equipped to collect genetic data, and it is common practice to outsource DNA sequencing where facilities do not exist.

Future

DNA barcoding relies on sound taxonomic descriptions and the availability of reference DNA sequences. This tool will progressively become more useful as large DNA sequence databases are generated and made publically available. The integration of DNA characters into formal taxonomic descriptions is a relatively new development. This is already underway at the Museum National d'Histoire Naturelle in Paris for mtDNA (Puillandre *et al.* 2012). Some regions worldwide lack taxonomic expertise (e.g. Africa; Swartz *et al.* 2008), and generally, the number of taxonomists is declining. The use of sequence data is an efficient use of resources and may attract new workers to the field.

Theme II: Fisheries stock structure

Why is it important to fisheries management?

The concept of a biological stock as a basic population unit for harvested species is central to the management of wild fisheries. In most cases, stock boundaries encompass groups of individuals within a single species that have similar demographic or genetic characteristics and thus will respond uniquely and independently to fishing. Stock boundaries are generally defined spatially, but may have a temporal component, for example, if a species' distribution changes during feeding, breeding or other life-history phases. It is desirable for management actions such as stock assessment, quota allocation or monitoring to operate at the biological stock scale.

How does it work and what are its limitations?

Stocks have many definitions, but in fisheries management, they usually represent demographically cohesive groups of individuals of one species (Carvalho and Hauser 1994). That is, changes to stock abundance are largely a function of local birth and death rates, not immigration and emigration. Stocks defined this way represent natural management units because a relationship between productivity and harvest rates can be established.

Stocks are commonly defined or identified in genetic terms, because: first, it may be desirable to manage genetic variation in its own right to ensure that a harvested species retains specific adaptive traits or enough genetic variation to adapt to environmental change (Carvalho and Hauser 1994; Kenchington *et al.* 2003). Such genetic resource issues are discussed further in themes VII and VIII. Second, and more often, genetic analysis is used as a way to identify demographically distinct stocks (Hauser and Ward 1998). Part of the appeal of genetic approaches is the difficulty of directly observing the movements of organisms in marine environments (Pineda 2007). In contrast, there is a simple theoretical relationship between the number of migrants exchanged between stocks and the level of genetic difference ('genetic structure') between those stocks (Waples 1998). Genetic structure is readily measured with genetic markers [e.g. microsatellite DNA, see Glossary (Data S1)], and broadly the detection of genetic difference between spatially or temporally separated samples implies existence of some level of demographic independence and presence of separate stocks (Bentzen 1998; Waples 1998; Waples and Gaggiotti 2006). An important benefit of the genetic approach is that it measures long-term (i.e. multi-generational) average levels of population connectivity.

Whilst genetic methodologies provide a rapid and cost-effective way to define biological stocks, there are important limitations (Waples 1998; Waples and Gaggiotti 2006). Foremost among these is that there are different thresholds for genetic and demographic connectivity between stocks (Lowe and Allendorf 2010). Such complexity arises because genetic connectivity depends upon the *absolute* number of migrants between stocks, whereas demographic connectivity depends on the *relative* contribution to population growth of migration versus local recruitment (Mills and Allendorf 1996; Lowe and Allendorf 2010). This means that small and demographically insignificant numbers of immigrants that successfully interbreed with recipient individuals can homogenize genetic structure, particularly in large populations. Genetic analysis therefore has a bias towards failing to detect demographically independent stocks, and the bias is worse in large populations. Such issues are especially acute for many harvested marine organisms because populations tend to be large and with high rates of dispersal (Hauser and Ward 1998).

The conventional strategy for conducting genetic assessments of demographic stock bound-

aries involves the following: (i) collecting samples of adult organisms from throughout a region either opportunistically during harvest or preferably during spawning when stocks are likely to be most genetically distinct, (ii) characterizing genetic diversity overall and within each putative stock, and (iii) testing whether genetic diversity is distributed randomly with respect to the putative stock boundaries or throughout the region of investigation. Where genetic structure is detected, it is a strong indication of limits to dispersal and usually is accepted as the basis for delineating different stocks (Carvalho and Hauser 1994). Recently, however, it has been argued that a more appropriate criterion is whether the limit to dispersal is demographically significant in the context of a particular management objective (Waples 1998; Palsbøll *et al.* 2007). The most effective way to understand links between demographic and population genetic processes is through coupled demographic–genetic simulations, which can set criteria for accepting stock structure based on case-specific conditions (Palsbøll *et al.* 2007; Lowe and Allendorf 2010).

Case studies

Genetic analysis of stock structure can reveal the most appropriate scale of management on a species-specific basis. This is illustrated by a series of genetic investigations of fished species in northern Australian and Indonesian waters. The taxa studied included sharks (Sphyrnidae and Carcharhinidae), mackerel (Scombridae) and snapper (Lutjanidae), and the molecular tools utilized included allozymes, microsatellite DNA and mitochondrial DNA sequencing [see Glossary (Data S1)]. A great variety of population structures existed among the species in this geographical region, including within each of the taxon groups, such that, surprisingly, life-history traits, bathymetry and hydrodynamics were not always effective predictors of population genetic structure. For example, two shark species (*Prionace glauca* and *Sphyrna lewini*) showed no evidence of stock structure, whereas pronounced structure was evident in another shark species (*Carcharhinus sorrah*) across the Timor Sea (Ovenden *et al.* 2009). In the lutjanids, two codistributed species showed strong correspondence in their stock structure (Salini *et al.* 2006) with the Timor Sea once again providing a barrier to movement, as it does also in the benthic lutjanid *Pristipomoides multidens* (Ovenden *et al.* 2004). In contrast, another codistributed lutjanid, *Lutjanus argentimaculatus* exhibited no structure in this region (Ovenden and Street 2003). These patterns of genetic subdivision implied that Australian stocks of some species had limited capacity to act as donors to the overexploited Indonesian stocks (Blaber *et al.* 2005). Similar multispecies analyses have been conducted in south-western Australia (Ayvazian *et al.* 1994; Watts and Johnson 2004) and elsewhere (Waples 1987; Pelc *et al.* 2009).

Investigation of population structure in salmonids (salmon, trout and charr; Salmonidae) has been instrumental for both the development of fisheries genetic techniques (Utter 1991) and the sustainable harvest of the resources (Altukhov *et al.* 2008). In part, this is because of their enormous economic value, which can support the cost of research, but it is also due to their unusual life history, which lends itself well to genetic analysis. Salmonids are renowned for their ability to return to their natal streams to breed. This behaviour, coupled with relatively small breeding populations within each stream, typically results in high levels of genetic differentiation and corresponding stock structure between drainages (Allendorf and Seeb 2000). Genetic structure is often evident not only spatially, but temporally, with different 'runs' within a single drainage being reproductively isolated from each other (Banks *et al.* 2000; Fillatre *et al.* 2003). Such high levels of fidelity mean that fine-scale stock structure must be taken into account in salmonid management (Shaklee *et al.* 1999). The combination of fine-scale stock structure and very high values is largely restricted to the salmonid fisheries, although there are other groups that exhibit similar levels of subdivision and support smaller scale fisheries (Ayvazian *et al.* 1994; Horne *et al.* 2011).

Genetic analysis can identify stocks with important adaptive differences, even when conventional genetic analysis cannot detect demographically distinct stocks. In Atlantic cod (*Gadus morhua,* Gadidae), conventional DNA analysis with neutral microsatellite DNA markers detected almost no genetic differences between regions, but genes with known function (i.e. under natural selection) showed stronger spatial differences. For cod, genetic differentiation in Icelandic waters at nine neutral microsatellite DNA markers was very low [F_{st} = 0.003, see Glossary (Data S1)], but with the Pantophysin gene (Pan I), substantial differentia-

tion was observed in the same region (F_{st} = 0.261; Ãrnason *et al.* 2009). The basis for this differentiation is that selection acts on Pan I genetic variants differently according to local temperature, salinity and depth conditions (Ãrnason *et al.* 2009). Additional analysis has shown that the association between temperature and particular genetic variants recurs along multiple temperature gradients (Bradbury *et al.* 2010). In cod, the strongly differentiated DNA markers could be used to identify stocks that experience unique environmental conditions and that retain genetic variants suited to those conditions. They could also be used as diagnostic markers for the geographical provenance of individual fish (Nielsen *et al.* 2012; see theme XI).

Barriers to uptake

Because the concept of stocks pervades so many aspects of fisheries management, stock identification is by far the most common use of genetic analysis in fisheries management. Yet, global uptake of genetic information into fisheries stock management has been slow and patchy. There are biological, practical and cultural reasons for slow uptake (Waples *et al.* 2008). One of the most significant biological barriers is the inherent limitations of conventional genetic techniques to detect stock structure in species that exhibit life histories common among harvested marine species (large populations, high capacity for dispersal; Carvalho and Hauser 1994). This issue has been partly resolved by the development of more informative and less expensive DNA markers (Balloux and Lugon-Moulin 2002), but the fundamental difficulty presented by the mismatch between genetic and demographic cohesion remains both a perceived and real barrier to greater uptake (Ovenden 2013).

Other challenges include mismatches in scale between biological and management units. For example, managers may not have the capacity to manage resources at the spatial scales indicated by the fine scale of stock structure or to adapt management frameworks to deal with non-discrete biological units such as clines of connectivity. There are also situations where the organizational cultures and structures that have evolved to govern fisheries management limit communication and collaboration between geneticists and fisheries scientists and managers (Waples *et al.* 2008).

Future

Genetic approaches to detect stock structure will continue to be an indispensable part of wild fisheries management. Some changes in this field will be incremental, involving increases in analytical power by boosting sample sizes and numbers of DNA markers (Waples and Naish 2009). Analyses are likely to increasingly rely on models of population structure focusing on the behaviour of individuals on ecological time frames rather than on the long-term average behaviours of entire populations (Christie *et al.* 2010; Harrison *et al.* 2012). New clustering methods have been developed that do not rely on predefined stock boundaries to frame the analysis. These flexible approaches work by grouping individuals in such a way that the most genetically cohesive groupings are identified. Such analysis both identifies the number of discrete genetic stocks and maps their distributions (Pritchard *et al.* 2000; Guillot *et al.* 2005), so works best when individuals are sampled evenly throughout the range of the target species. This approach lends itself well to combining genetic information with geographical, oceanographic or other environmental information to increase the explanatory power of the analysis (Fontaine *et al.* 2007; Galarza *et al.* 2009).

An extension of this approach is that individual organisms can be statistically attributed (assigned) to candidate stocks based on their genetic affinities (Manel *et al.* 2005). In doing so, recent migrants can be identified and counted. Unlike conventional genetic analysis, these methods can directly estimate the number of migrants between stocks on an ecological timescale and so are highly compatible with conventional ecological methods so long as stocks are sufficiently genetically differentiated (Cornuet *et al.* 1999; Berry *et al.* 2004; Manel *et al.* 2005). Individual-focused approaches to measuring the origins of individuals are discussed further in themes III, VI and XI.

There is also likely to be a shift in emphasis towards use of DNA markers under selection as opposed to neutral markers (theme VIII; Nielsen *et al.* 2009). Coupled with methods to assign provenance to individuals, these can potentially provide greater resolution of demographically relevant rates of migration than neutral markers and also reveal adaptive differences that may be key to future adaptability of fisheries resources. Many of these changes will be facilitated by the

rapid development of next-generation DNA sequencing technologies, which are revolutionizing all branches of molecular biology by providing vast volumes of DNA sequence data at a fraction of the cost of conventional DNA sequencing technologies (Mardis 2008). Finally, there is likely to be a shift in emphasis towards greater integration of genetics into multidisciplinary assessments of stock structure and connectivity (e.g. Selkoe *et al.* 2008; Berry *et al.* 2012), for example complementary analysis such as hydrodynamic simulations, micro-chemical analysis, fatty acid analysis, coupled demographic-genetic computer simulations, and Geographical Information Systems.

Theme III: Resolving mixed-stock fisheries

Why is it important to fisheries management?

Fisheries management becomes complicated when stocks overlap. A mixed-stock fishery contains individuals from two or more distinct (or component) stocks of a single species. When mixed stocks are harvested, the component stocks will be impacted according to the proportions represented within the mixed stock. For example, subadult Pacific salmon in the Northern Pacific Ocean form a mixed stock because they represent offspring from several freshwater breeding populations. Mixed-stock analysis is the process of quantifying the contributions of different stocks to a mixed-stock fishery, and genetic tools are commonly used to achieve this.

How does it work and what are the limitations?

The composition of mixed-stock fisheries is resolved by comparison with baseline (or reference) gene frequencies from the component stocks. Highly variable genetic markers, such as microsatellite loci and SNP [see Glossary (Data S1)], are commonly used. The collection of baseline data is often a consequence of the description of the genetic stock structure of the species. Baseline data should be collected over several years to check for temporal stability. Computer simulations are used to determine whether there is sufficient genetic differentiation between the component stocks to characterize a mixed sample. If so, individuals taken from the mixed fishery are genotyped and relative proportions of each component stock are estimated. Chemical composition of otoliths and other phenotypic characters can also be used to characterize breeding populations (e.g. Thorisson *et al.* 2011), often in combination with genetic data.

To undertake a mixed-stock analysis, there needs to be evidence that the species has discrete stocks but is harvested in an aggregated state. In many parts of the world, fishing occurs on species whose biology has not been well characterized. For these species, mixed stocks may or may not be present, and genetic technology is irrelevant until the need for the analysis is established. Also, there must be some genetic differentiation between the component stocks. For north-east Atlantic herring (*Clupea harengus*, Clupeidae), Bekkevold *et al.* (2011) showed that mixed-stock analysis was feasible at low population differentiation [e.g. $F_{st} < 0.02$, See Glossary (Data S1)]. However, if the composition of the mixed stock is significantly biased towards one or more component stock, the performance of the method will be poor (Stevens *et al.* 2010). Mixed-stock analyses, in contrast to assignment methods (see Theme 2), determine the relative proportions of two or more stocks in a mixed sample, rather than assigning individuals to stocks. Mixed-stock analysis is the preferred method when differentiation between stocks is low.

Case studies

Sockeye salmon (*Oncorhynchus nerka*) spawn in freshwater habitats on the western coast of North America and the eastern coast of Russia. Juveniles migrate to sea and grow to adulthood in the North Pacific Ocean. Mixed-stock analysis was used to determine the oceanic migration routes of immature sockeye to predict the effect of changing oceanic conditions on the numbers of returning adults. Habicht *et al.* (2010) used 45 SNP markers [see Glossary (Data S1)] to genetically characterize eight spawning populations in the Pacific Rim, from Russia to the United States. A large number (35 549) of immature salmon were taken from 304 high-sea locations in the North Pacific Ocean. Following testing to confirm accuracy, mixed-stock analysis showed that North American salmon migrated further westwards towards the Russian coast compared with the movement of Russian fish eastwards towards North America. The Russian exclusive economic zone was firmly established as a feeding area for immature North American sockeye salmon.

Barriers to uptake

There are no technical barriers to the uptake of this application of genetic technology in fisheries

management. The outcomes of a scientifically sound study that has been designed with the involvement of fisheries managers and scientists should be directly applicable to harvest strategies and conservation plans. However, there are practical barriers. Mixed-stock analyses are expensive and require a high level of expertise and infrastructure, and although with high throughput automation and declining costs, individuals can be screened at hundreds of genetic loci quickly (Nielsen *et al.* 2012). Methodology is most likely, however, to be adopted most frequently for species of high economic value where the sustainability of component stocks is of critical importance.

Future

New types of genetic markers (e.g. SNP) and markers under selection [see Glossary (Data S1)] have the potential to increase the ability to discriminate between component stocks and hence to increase the number of species that can be analysed as mixed stocks (Habicht *et al.* 2010). In future, separate breeding and feeding ranges may be discovered for some Australian fisheries species. For example, some species of sharks in Australia appear to return to certain locations to mate and give birth, which implies that removing individuals from non-breeding locations may deplete breeding populations (Blower *et al.* 2012; Tillett *et al.* 2012). Some other Australian commercial fisheries species have life histories encompassing freshwater, estuarine and marine habitats [e.g. *Mugil cephalus* (Mugilidae), *Lutjanus argentimaculatus, Scylla serrata* (Portunidae)] that may benefit from mixed-stock analysis in the future.

Theme IV: DNA as a biomarker for age

Why is it important to fisheries management?

Growth and recruitment are the two primary sources of productivity in fisheries populations; thus, accurate estimates are essential for fisheries stock assessment modelling. Growth estimates require knowledge of the ages of individuals in days, months or years. For most fisheries species, this is accomplished by counting growth rings in otoliths, scales or vertebrae. However, some marine taxa, such as crustaceans and molluscs, generally lack equivalent hard structures that show growth rings. Biomarkers for age are not dependent on growth rings in hard structures. Biomarkers can also be assayed from tissue samples taken as biopsies from living animals.

How does it work and what are the limitations?

Telomeric DNA is the most prominent alternative biomarker for age. Telomeres cap the end of chromosomes and consist of characteristic DNA sequence ('TTAGGG' in vertebrates), which are repeated thousands of times and interlaced with proteins. Telomeres have two main functions: to protect vulnerable chromosome ends from physical damage and to buffer the ends of chromosomes against shortening, which occurs during each cycle of DNA replication. The shortening process tracks the number of cell replications, which is proportional to the chronological age of the tissue. The principle of using telomeres as biomarkers for age relies on knowing the rate that telomeric DNA shortens with age.

Specific technical challenges face the development of biomarkers for age in fisheries species. Fisheries species for which age and growth information is most needed tend to be those that are not kept in captivity. Some of these species may also not have hard parts that can be sectioned for ring counting as an alternative method of estimating age. For these species, it is challenging to calibrate the rate of telomeric DNA attrition with age, because there are no animals for which age is known. Solutions may include using the rate of DNA attrition for closely related species or studying the attrition rate in animals at liberty from which regular tissue biopsies can be taken non-lethally.

Case studies

Several research groups in Australia have trialled the use of telomeric DNA as a biomarker for age. In abalone (*Haliotis rubra;* Haliotidae) from Tasmania, a small-scale study demonstrated an inverse relationship between telomere length and shell size ($R^2 = 0.833$, $P < 0.001$; Ovenden and Godwin 2011). A weak correlation between age and telomere length was detected in another mollusc species, the Sydney rock oyster (*Saccostrea glomerata,* Ostreidae; Godwin *et al.* 2012). However, there was no relationship between telomere length and body size in five Australian commercial crustacean species (Godwin *et al.* 2011). Two confounding issues were identified for crustaceans in this study: extracted genomic DNA degraded during storage in the laboratory (mimicking the effect of telomere attrition) and telomeres in these species were large, making them difficult to analyse. In two studies on the relationship between telomere length and age in pinnipeds, one showed no corre-

lation between age (from counts of growth layers in teeth) and telomere lengths in harp seals (*Pagophilus groenlandicus,* Phocidae; Lydersen *et al.* 2010), while the other showed that Australian sea lions (*Neophoca cinerea,* Otariidae) adults could be distinguished from pups and juveniles on the basis of their telomere lengths (Izzo *et al.* 2011).

In the Northern Hemisphere, fisheries examples are scarce. Almoth *et al.* (2012) measured a number of physiological markers associated with ageing (including telomere lengths) in male and female Atlantic cod. They sampled fish from a heavily fished area where there has been intense selection for reproduction at smaller sizes and younger ages and hence may have accelerated rates of ageing. Telomere length declined with age in males after approximately 3 years of life. Female telomere length was constant with age, possibly because of the presence of oestrogen has been shown to induce an enzyme (telomerase) that prevents telomere shortening with age, at least in humans. Compared with a population where fishing was banned in 1932, there was some evidence that males, but not females, from the heavily fished population were ageing prematurely.

Barriers to uptake

The main barriers to uptake are the knowledge gaps highlighted here. Additional challenges include the extent and effect of error in growth determinations and the start-up costs for each new species.

Future

While telomeric DNA shows promise as a biomarker for age, other molecular methods are worth exploring. Transcriptional profiling of electron transport genes showed an age-related decline in expression in humans, mice, flies and worms (Zahn *et al.* 2006). Using this method on eight genes in mosquitoes (Culicoidea), 87% of the variance in gene expression was explained by age (Cook *et al.* 2006, 2007). Another potential biomarker for age may be changes to the degree of DNA methylation in non-expressed genes (Lara *et al.* 2010). Methylation is a chemical change to the cytosine (C) nucleotide [see Glossary (Data S1)] in DNA that occurs during the lifespan of an individual. The potential of transcriptional profiling and methylation for fisheries species remains to be assessed.

Theme V: Ecosystem monitoring

Why is it important to fisheries management?

As fisheries managers increasingly adopt the principles of ecosystem-based management, tools to monitor the interactions between fisheries and the environment are more in demand (Levin *et al.* 2009). These interactions, however, are diverse, complex, hard to observe and therefore difficult to characterize accurately. Several emerging applications of genetic analyses to environmental monitoring have the potential to provide unique understandings of ecological processes in aquatic environments and to build stronger empirical underpinnings for ecosystem-based management. The applications highlighted here are as follows: dietary analysis for constructing food webs, detecting impacts on ecosystems of pollutants and other stressors, and monitoring evolutionary effects of climate change on harvested species.

How does it work and what are its limitations?

Food webs are networks of predator–prey dietary relationships amongst ecosystem components, which in the marine environment may be difficult to reconstruct because of their typical complexity and diversity (Ainsworth *et al.* 2010). Food webs provide vital input to whole of ecosystem models, which are increasingly used to evaluate alternative management strategies for fisheries (Fulton *et al.* 2011). DNA analyses of diets can be used to assemble food webs by identifying species without relying on expert taxonomic knowledge (Pompanon *et al.* 2012).

DNA-based dietary analysis is a specialized example of DNA barcoding (see Theme I). Typically, it involves extracting DNA from gut or faecal samples and obtaining species-diagnostic DNA barcode sequences from either individual dietary items (Braley *et al.* 2010) or, increasingly, from mixed assemblages (Deagle *et al.* 2010). DNA sequences are assigned taxonomic identities by interrogating reference databases such as GenBank (http://www.ncbi.nlm.nih.gov/genbank) or FishBOL (Ward *et al.* 2009). DNA-based analysis offers several advantages over conventional microscopic sorting of dietary items. For example, as identification is based on a single universal and accurate criterion (a DNA barcode), taxonomic placement can be more consistent within and between investigations. Moreover, investigators typically do not require specialized training in morphological taxo-

nomic assessment. Finally, DNA analyses can identify items lacking diagnostic morphologies, such as soft-bodied organisms (Deagle *et al.* 2009). The greatest limitation of DNA-based analysis is the incompleteness of existing public reference sequence databases, which means identification must sometimes be made at genus, family or order level (Pompanon *et al.* 2012), although even these assignments may be at higher taxonomic resolution than morphological analysis.

A second emerging application of genetics to environmental monitoring is the direct measurement of functional gene responses to environmental stressors; a field called ecotoxicogenomics (Snape *et al.* 2004; Mehinto *et al.* 2012). Because harvested species are readily captured and identified, they are well suited as models for environmental quality (Cossins and Crawford 2005; Logan 2007; Sanchez and Porcher 2009). Directly monitoring responses to stressors at a genomic level provides an understanding of how stressors act at cellular and molecular levels, which means the effects may potentially be generalized across taxa and enable higher level ecosystem responses to be understood (Snape *et al.* 2004; Cossins and Crawford 2005). Ecotoxicogenomics permits fisheries managers and environmental regulators to monitor environmental quality and to anticipate potential risks to fisheries of new environmental stressors (Snape *et al.* 2004; Cossins and Crawford 2005). A challenge for ecotoxicogenomic approaches is to establish how the highly sensitive changes detectable via assays of gene expression link to functional impacts at the individual, population or ecosystem levels (van Straalen and Feder 2011).

Climate change has the potential to significantly affect the distribution and abundance of marine and aquatic organisms, including important fisheries species (Perry *et al.* 2005; Neuheimer *et al.* 2011). Fisheries managers are concerned with making predictions about future distributional ranges or behavioural changes in harvested species (e.g. Drinkwater 2005). Ideally, these forecasts should account for the capacity of species to adapt genetically to the selective forces introduced by climate change (Nielsen *et al.* 2009). Tracking genetic variants through time offers a direct approach to detecting evolutionary change. A major challenge for applying molecular tracking to harvested species is identifying the genes and regulatory mechanisms that underlie evolving traits and attributing changes in them to specific selective agents such as climate change (Hansen *et al.* 2012).

Case studies

A compelling demonstration of the power of next-generation DNA sequencing [see Glossary (Data S1)] to reveal the diet of an important marine predator was presented by Deagle *et al.* (2009). Analysis of faecal samples from Australian fur seals (*Arctocephalus pusillus*, Otariidae) provided over 20 000 DNA sequences that distinguished over 60 prey species. The diet diversity was similar to one determined from morphological analysis over a three-year period. However, the diet resolved through DNA analysis enabled the identification of soft-bodied and cartilaginous species that conventional analyses could not. Another encouraging aspect of this analysis was that it provided information on the relative contributions of prey species to the diet. Other examples of DNA-based analysis of marine species include the diets of the arrow squid (Ommastrephidae; Braley *et al.* 2010), the sevengill shark (Hexanchidae; Barnett *et al.* 2010) and the little penguin (Spheniscidae; Deagle *et al.* 2010).

Several commercially harvested marine species are used as 'sentinels' or 'biosensors' for pollution, and their responses are measured as differences in gene expression [see Glossary (Data S1)] (e.g. Williams *et al.* 2006). One example is mussels in the genus *Mytilus* (Mytilidae). Under controlled conditions, gene expression measured with microarrays [see Glossary (Data S1)] in *M. galloprovincialis* enables accurate identification of samples exposed to heavy metals or organic contaminants (Venier *et al.* 2006). This differential response of gene expression mirrors differences between mussels at sites in the ocean subject to high and low levels of contaminant (Venier *et al.* 2006). Further experimentation has demonstrated strong correlations between gene expression changes and conventional biomarkers for pollutants, although gene expression can respond more quickly, meaning that it is a more sensitive marker (Franzellitti *et al.* 2010). The European flounder (*Platichthys flesus,* Pleuronectidae) is another harvested species that is used as a biosensor (Williams *et al.* 2006).

Evolutionary effects of climate change on harvested marine species are an active area of research in the Northern Hemisphere (Nielsen *et al.* 2009; Kovach *et al.* 2012). As discussed in Theme II, genetic variants of the Pantrophysin (Pan I) gene in Atlantic cod vary spatially in the

north-eastern Atlantic Ocean with sea surface temperature (Ãrnason *et al.* 2009), and therefore, it is a candidate gene [see Glossary (Data S1)] to track climate change. However, analysis of DNA from archived otoliths revealed no change in the frequencies of Pan I variants with increased sea surface temperature since 1928 (Nielsen *et al.* 2007). A study of pink salmon (*Oncorhynchus gorbuscha*) in Alaska tracked molecular markers tied to the timing of breeding migrations through time. It documented a decrease in the abundance of genetic variants associated with late runs, thus a genetic change towards earlier migration, which was in line with expectations for the effects of climate change on this species (Kovach *et al.* 2012).

Barriers to uptake

The applications profiled here provide novel ways for fisheries managers and environmental regulators to assess the current and predicted state of ecosystems and are directed towards supporting long-term goals of ecosystem-based management rather than addressing conventional fisheries management questions (e.g. themes II and III). Where there is demand for information to support ecosystem-based management, and where facilities and expertise are available (see Table 1), there should be few barriers to adoption of these methods to complement conventional assessment tools.

Future

Environmental monitoring through DNA analysis is a rapidly growing field driven largely by technological developments such as next-generation DNA sequencing, quantitative PCR [see Glossary (Data S1)] and microarray analysis [see Glossary (Data S1)], as well as advances in bioinformatics (Taberlet *et al.* 2012). Applications such as those profiled in this theme and others (see Yoccoz 2012) deliver unique and highly informative data on a range of environmental parameters. As this becomes better appreciated outside of the research genetics communities, these tools are likely to receive increasing attention for the management of wild fisheries.

Impacts of fishing

Theme VI: Estimating harvest rates and abundance

> *'Counting fish is like counting trees, except that are invisible and they keep moving'* (John Shepherd in Hilborn 2002)

Why is it important to fisheries management?

Estimating the abundance and harvest rates of fisheries and non-target species impacted by fishing is one of the key requirements for determining sustainable yields or sustainable environmental impacts. Yet, these parameters are inherently difficult to measure in the marine environment. Capture–mark–recapture modelling (CMR) is a well-established set of statistical tools for estimating abundance and related population parameters in wild fish stocks (e.g. mortality, recruitment). Typically, CMR relies on marking organisms with a unique tag, and it is particularly effective for organisms that are easily captured in large numbers. However, CMR is difficult to implement for mobile and dispersed marine organisms because of low rates of recapture and tagging-induced mortality (Thorrold *et al.* 2002). Mortality is a particular problem for CMR investigations of wild fishes as capture often introduces significant trauma, especially in deepwater fishes (St John and Syers 2005).

Recently developed analytical tools combine conventional CMR with genetic analyses to directly estimate population parameters of harvested stocks while avoiding some of the difficulties associated with conventional CMR, such as tag loss and mortality. These methods can be grouped under the label 'genetic tagging' (Palsbøll 1999). Genetic tagging has been extensively used to monitor terrestrial wildlife (McKelvey and Schwartz 2004) and becoming increasingly applied to marine organisms (Palsbøll *et al.* 1997; Saillant *et al.* 2009; Harrison *et al.* 2012). It has the potential to be deployed for both baseline research and routine assessments of fisheries resources.

How does it work and what are its limitations?

Genetic tags are unique DNA fingerprints [genotypes; see Glossary (Data S1)] that are obtained by sampling organisms and assaying variable DNA markers such as microsatellites [see Glossary (Data S1)]. The high variability of these markers means that with repeat sampling genotypes function as unique identifiers or 'tags'. Two useful features of genetic tags are that first, unlike physical tags, they cannot be lost, and second, in some cases, DNA samples can be collected without capturing animals (e.g. from hair, skin, faeces, remotely collected biopsies), so monitoring need not influence behaviour or increase mortality (Mills *et al.* 2000).

The data obtained from genetic tagging is directly comparable with conventional tagging

Table 1 Possible team composition (by area of expertise; E, essential; D, desirable; O, optional) for research aligned with the eleven genetic themes that contribute to wild fisheries management.

Genetic Theme		Team Skills										
		Field biologist	Fisheries scientist	Fisheries manager	Taxonomist	Population geneticist	Molecular geneticist	Statistician	Mathematician	Software engineer	Bioinformaticist	Database manager
I	Species identification	O	E	E	E	E	O	O	O	O	O	D
II	Fisheries stock structure	E	E	E	O	E	O	D	O	D	O	D
III	Resolving mixed-stock fisheries	E	E	E	O	E	O	E	O	O	O	O
IV	DNA as a biomarker for age	O	E	E	O	O	E	E	O	O	D	O
V	Ecosystem monitoring	E	E	E	E	O	O	O	O	O	E	O
VI	Estimating harvest rates and abundance	E	E	E	O	E	O	E	E	E	O	E
VII	Genetic diversity, population abundance and resilience	E	E	E	O	E	D	E	E	E	O	O
VIII	Evolutionary responses to fishing	E	E	E	O	E	O	E	O	O	E	O
XI	Product provenance and fisheries surveillance	O	E	E	E	E	O	O	O	O	O	D
X	Detection of pathogens and invasive species	E	E	E	E	O	E	O	O	O	O	O
IX	Genetic effect of stock enhancement	E	E	E	O	E	O	O	O	O	O	O

data, so many of the existing statistical CMR approaches can be applied to it. To be used effectively, genetic tagging has a series of technical requirements. The first is identifying a source of DNA samples and obtaining sufficient numbers of samples. Like all CMR, precise and accurate parameter estimation relies on obtaining reasonable rates of recapture and so sample size is critical (Otis *et al.* 1978). Depending on the application, samples can be taken lethally or non-lethally (see case studies). Second, genetic tags must contain sufficient information to distinguish all individuals otherwise abundance will be under-estimated (Mills *et al.* 2000). In general, the information content of genetic tags is improved by increasing the number of markers or by including more variable markers. These issues are easily solved through calculation of summary statistics that establish the power of a panel of markers for a given population and experimental design (Waits *et al.* 2001; Jamieson and Taylor 2003). Third, genetic tags should not contain errors; otherwise, abundance will be over-estimated due to missed identification of recaptures (Mills *et al.* 2000). Errors can be introduced into the raw data at the laboratory or the databasing stage. Issues of data quality are not specific to genetic tagging, but it does generate unique error types. These are well-recognized and established protocols exist to deal with them (Wilberg and Dreher 2004; Lukacs and Burnham 2005; Macbeth *et al.* 2011).

Case studies

The first use of genetic tags to understand the dynamics of wild marine organisms was an investigation of the abundance and migration patterns of North Atlantic humpback whales (Balaenopteridae; Palsbøll *et al.* 1997). Based on 3060 biopsies collected throughout the North Atlantic Ocean, 2368 individuals were identified, including 692 recaptures. This permitted an estimate of total population size of 7698 whales, which was higher than estimates based on photo identifications. It also demonstrated high fidelity of individuals to particular migration routes between summer- and winter-feeding grounds, and differences in levels of feeding ground fidelity between males and females.

Typically, harvested fishes are more difficult to sample non-lethally than whales. Recently, two novel applications of genetic CMR have been developed in Australia. Genetagging (Buckworth *et al.* 2012) has been applied to finfish and involves 'capturing' and 'recapturing' fishes without landing them. It does so by collecting biopsies from fishes with specialized hooks before immediately releasing the fish. The DNA contained in the biopsies is then analysed in a laboratory with DNA markers suitable for individual identification (e.g. microsatellites). The set of unique genotypes collected during one capture session is compared with sets of genotypes collected on subsequent sessions to identify instances of recapture. The data can be analysed with conventional CMR modelling approaches to estimate harvest rate and abundance (Otis *et al.* 1978; Pollock *et al.* 1990), although it requires rigorous error-checking systems. A particular advantage of genetagging over conventional tag and release for finfish is that capture is less likely to induce mortality than conventional tagging, and tags cannot be lost. Buckworth *et al.* (2012) have applied the method to Northern Territory populations of Spanish mackerel (*Scomberomorus commerson*, Scombridae) to monitor real-time harvest rate.

Close-kin genetics also relies on a mark–recapture analysis framework, but uniquely, recaptures are assigned across generations through parentage analysis (Bravington and Grewe 2007). Unique genotypes are obtained from discrete parental and offspring generations. The offspring are treated as a sample of individuals present in the parental generation and the parents as a second sample of that parental generation. These samples can be taken lethally from landed individuals or non-lethally via biopsies (e.g. Genetag hooks). Parentage analysis [see Glossary (Data S1); e.g. Marshall *et al.* 1998] is applied to the raw genetic data, and parent–offspring relationships (equivalent to recaptures) are enumerated. Variants of capture–recapture modelling are applied to the parentage data to provide direct estimates of population abundance in the parental generation. Bravington and Grewe (2007) have applied close-kin genetics to the southern bluefin tuna (*Thunnus maccoyii,* Scombridae) to estimate the number of spawners. The use of parentage analysis is not unique to investigations of abundance. Similar methods are being used to understand the extent of connectivity in marine populations in the context of the functions of marine protected areas (Planes *et al.* 2009; Christie *et al.* 2010), but equally could be applied to harvested species.

Barriers to uptake

Harvest rates and fisheries-induced mortality are fundamental measures of the impacts of fishing on resources, as well as measures of the effectiveness of management (Botsford *et al.* 1997). Similarly, measuring the impacts of fishing on non-target species such as marine megafauna is increasingly a requirement of management (Lewison *et al.* 2004). Although neither genetagging nor close-kin genetics has been widely adopted for these purposes, both have the potential to provide valuable baseline research or monitoring tools for wild fisheries that is difficult to obtain by conventional means.

There are biological and financial barriers to uptake of these novel methods by fisheries management. Genetic CMR is well suited to sedentary or aggregated species that suffer high mortality upon capture or release (or both). However, some marine species have life histories that present a greater challenge. For example, as is the case for conventional CMR tagging, large populations of mobile and dispersed species will require extensive effort to obtain sufficient recaptures for accurate and precise parameter estimation. In addition, fish 'marked' via remote biopsies are not landed, so their physical characteristics cannot be recorded, meaning that there is little scope for adding individual covariates to CMR models.

Close-kin analysis relies on being able to distinguish parental and offspring generations and sampling the generations independently. Species without obvious age classes or without spatial or temporal segregation by age are problematic. Similarly, parent–offspring pairs that occur together cannot easily be sampled independently (e.g. whales and calves, marine turtles and eggs). Because both genetagging and close-kin genetics employ a CMR analysis framework, both are well suited to *a priori* power analysis that can provide indications of the sampling effort required to accurately and precisely estimate the population parameters of interest (White and Burnham 1999).

An over-arching potential barrier to uptake by fisheries management is the requirement for *de novo* development of molecular tools for each new species. While these costs continue to decline, the significant time and financial commitment mean that genetic tagging's greatest appeal will be initially for high value and long-running research and monitoring programs.

Future

Because they address such important but often intractable issues in wild fisheries management, genetic tagging methods have the potential to become widely used both for generating baseline information about fish stocks and also for monitoring. Equivalent methods are now in mainstream use in terrestrial environments in situations where physical tags have limited use (Sawaya *et al.* 2012). Nevertheless, individual genetic tagging projects require significantly more customized development at start-up than conventional tagging projects, which effectively use off the shelf products. This inevitably adds time and cost to projects, which needs to trade against the potential for generating unique data. Increasing automation of laboratory procedures is likely to reduce costs and increase data accuracy, but genetic tagging is likely to have greatest use in high value fisheries requiring long-term research and monitoring.

Theme VII: Genetic diversity, population abundance and resilience

Why is it important to fisheries management?

Species impacted by fishing should be managed to minimize the loss of genetic diversity, which is a key measure of resilience and abundance. The amount of genetic diversity harboured by a population, and how it changes through time, is potentially a proxy for abundance. It can be estimated using genetics from a sample of individuals from the population without using the capture–mark–recapture paradigm. Resilience describes the ability of a population to withstand environmental challenges, such as pathogens or climate change. Resilience and abundance have special relevance to species that have smaller population sizes, such as by-catch species, or species that are endangered, threatened or protected, but the concepts are applicable across all fisheries species.

How does it work and what are the limitations?

Genetic diversity describes the set of genetic variants [also called alleles, see glossary (Data S1)] retained by a group of organisms, most commonly by a species or population. New genetic variants enter the gene pool by mutation and sometimes by interbreeding with other species (Arnold 2006). Alleles change in frequency due to natural selection and genetic drift. Alleles become more common by natural selection if they increase the

individual's lifetime reproductive success. Likewise, alleles become less common if fewer offspring are produced. Alleles can also become more or less common due to genetic drift [see Glossary (Data S1)]. Genetic drift leads to pronounced decreases in genetic diversity during prolonged periods of low population size. Genetic diversity may also be affected when the natural flow of genes between populations is changed, for example, by habitat loss or by alteration to patterns of connectivity.

Geneticists have a handy tool for monitoring genetic diversity called 'effective population size' (N_e), which reflects changes to the gene pool due to genetic drift (Wright 1931). Wright's N_e is often referred to as contemporary (CN_e) as it applies to recent changes in genetic diversity (i.e. over several past generations or years). The other type of N_e is historical (HN_e), which describes changes in genetic diversity over many past generations (Beerli 2009). Instead of indexing genetic drift, it is based on estimates of genetic diversity and mutation rate, taking advantage of the fact that larger populations retain more genetic variation than smaller populations. Genetic effective population size is part of a suite of methods available for genetic monitoring for management and conservation (Schwartz *et al.* 2006; Tallmon *et al.* 2010). A key aspect for fisheries science is that N_e is regarded as the number of breeding individuals that successfully transmit genes to the next generation (Frankham 1995), suggesting that it is a proxy for spawner numbers (N) (Ovenden *et al.* 2007; Luikart *et al.* 2010). Estimates of N_e can be made in the absence of CPUE or any other fisheries dependent data and would be worthwhile new data source for fisheries models. Time series of N_e can be produced suggesting it may be a valuable tool for tracking changes in abundance of threatened, endangered and protected marine species (e.g. Osborne *et al.* 2010; Charlier *et al.* 2012). However, for marine species with large population sizes, this remains to be demonstrated: estimates of CN_e remained stable over a severe decline in population size in sole (*Solea solea*) that was observed over a fifty-year period of harvesting in the North Sea (Cuveliers *et al.* 2011).

The relationship between N_e and spawner numbers (N) is not expected to be 1:1 (Frankham 1995; Nunney 1995), and there are methodological difficulties in determining the ratio. N_e can be measured in a variety of ways, and no consensus method has appeared yet, although LD (Waples and Do 2010) is a front-runner. The theory behind N_e methods is highly complex. Having navigated the perils of N_e estimation, researchers need to link estimates of N_e to the correct estimate of spawner abundance (N) (Palstra and Fraser 2012). The methods for measuring N may have wide confidence intervals, and this is particularly true for highly numerous marine species. Another issue that remains to be clarified is why the N_e/N ratio for marine species is small, around 10E-3 (Ovenden *et al.* 2007) to 10E-5 (Hauser *et al.* 2002). Other complicating factors such as the effect of varying life histories are being actively investigated (Hare *et al.* 2011; Waples and England 2011; Jorde 2012).

Estimates of HN_e represent long-term averages, so they have the potential to reveal historical abundances in species that are now heavily harvested. In doing so, they address the 'shifting baseline' effect, which is the acceptance through time of inappropriate and ever decreasing reference points for the size of fishery stocks (Pauly 1995). Demographic data are normally collected from a fishery resource after the onset of exploitation, and the collective memory of fishers often does not encompass pre-exploitation abundance or abundance changes over the course of a fishery. HN_e estimates are potentially pre-exploitation and thus may provide a measure of the extent of the decline of abundance and contribute to setting limits of fishing mortality. For example, HN_e estimates for Pacific grey whales (*Eschrichtius robustus*; Eschrichtiidae) led to an overall estimate of 96 000 individuals were several times larger than the current estimate of population size based on survey data of about 22 000 whales (Alter *et al.* 2007). As with CN_e, the estimation of HN_e is dependent on assumptions, not the least of which is the rate of mutation (Ho *et al.* 2011). There is potential for genetic data to estimate historic abundance providing the underlying genetic and demographic parameters are sound (Palsbøll *et al.* 2013).

Case studies

To explore the usefulness of CN_e for fisheries management, Ovenden *et al.* (2007) studied tiger prawns (*Penaeus esculentus,* Penaeidae) in Moreton Bay, Queensland. The population was selected as a simple model system; it did not have overlapping generations and was likely to be closed to immigration. The study demonstrated that even with a large fisheries population of invertebrates, precise

genetic estimates of effective population size could be made with eight microsatellite loci on a sample size of around 700 individuals. Furthermore, the estimates were stable between years: CN_e was 797–1165 for year 2001 and 866–1304 (95% CI) for year 2002, while ecological estimates (N) were 648 898 for 2001 and 464 627 for 2002. The ratio between N and CN_e was approximately 10^{-3}. Comparing census and CN_e estimates, it was possible to determine that the variance of reproductive success was large (V_k, 2200). Interestingly, the HN_e estimates approximated CN_e estimates, suggesting long-term stability of abundance over evolutionary timescales despite high harvest pressure.

As expected, the ratio between CN_e and N in a study on sharks was very different to tiger prawns; 0.5 and 1.0 for sharks compared with 10^{-3} for prawns. Portnoy *et al.* (2009) studied the heavily exploited sandbar shark (*Carcharhinus plumbeus*, Carcharinidae) in embayments on the eastern coast of the USA. Estimates of CN_e were similar to the magnitude of N, which were extrapolated from mark–recapture estimates of the numbers of young-of-the-year, average yearly reproductive success of females and the adult sex ratio. The similarity demonstrated between CN_e and N for this elasmobranch was a landmark for the application of N_e to marine species. For species with low fecundity and correspondingly low variance in reproductive success, it suggested that CN_e may have an important role in the assessment of abundance and hence biomass.

Barriers to uptake

There are no genetic diversity reference points for species impacted by fishing, and neither can the consequences of passing these points be predicted. Also, there are few strategies for reversing the decline of genetic diversity other than reducing harvest pressure. Genetic effective population sizes are regularly lower than census population sizes, and the mechanisms underpinning this need to be understood before N_e can be a proxy for abundance.

Future

Whole-genome sequences will revolutionize the ability to monitor genetic diversity, but several years may pass until it is feasible to apply the technology to a large sample of individuals from a fisheries population to establish baselines. Understanding the drivers of the relationship between N_e and abundance will be assisted by the dual application of genetic and demographic estimates across species that vary in life-history and exploitation characteristics. Waples *et al.* (2011) have recently produced a method (and software, *AgeNe*) for estimating effective population size from life-history tables. Implementing this method may have the added benefit of illuminating pathways for the integration of fisheries population models with estimates of N_e. Evaluation of alternate methods for estimating N_e will be assisted by the development of new software (Do *et al.*, in press). Close comparisons between CN_e and estimates of abundance derived from genetic mark–recapture studies have great potential to benefit both methodologies.

Theme VIII: Evolutionary Responses to Fishing

> *'Unnatural selection generally acts at cross purposes to the long-term goal of sustainable harvest of wild populations and can reduce the frequency of phenotypes valued by humans'* (Allendorf and Hard 2009)

Why is it important?

Evolutionary processes have rarely been considered in the management of wild fisheries (Swain *et al.* 2007). This is likely to change with the growing realization that fishing has the potential to introduce undesirable evolutionary changes to harvested populations, ultimately altering their distribution, abundance and productivity. Understanding these processes would enable fisheries managers to adapt practices to prevent or reduce their impacts on productivity (Kuparinen and Merilä 2007).

Fishing mortality is often many times larger than natural adult mortality. Furthermore, fishing mortality is typically non-random with respect to phenotypes [see Glossary (Data S1)]. Unless fishing mortality is reduced (Hutchings 2009), fishing therefore has the potential to exert 'unnatural' selection on life-history traits if those traits have a genetic basis (Allendorf and Hard 2009). This process can have implications for fisheries because the traits favoured by fishing are likely to be undesirable in terms of the long-term sustainability of fisheries. For example, because fishing often targets larger individuals, it inevitably selects for reduced size at maturity, which can ultimately reduce the productivity and stability of fisheries. Even where fishing is not selective for particular traits like size and merely

results in higher mortality overall, it has the potential to promote evolutionary change towards earlier maturation (Allendorf *et al.* 2008). Importantly, although evolutionary change in fisheries can occur rapidly (within decades), theoretical models demonstrate that it may be much slower to correct once harvest effects are removed (Walsh *et al.* 2006; Enberg *et al.* 2009; but see Edeline *et al.* 2007).

How does it work and what are its limitations?

Detecting evolutionary responses to past fishing pressure, or forecasting how organisms will respond, offers a way to identify species at risk and to adjust management strategies accordingly (Kuparinen and Merilä 2007; Hansen *et al.* 2012). Examples of ways to reduce the risk of evolutionary change in fisheries include the following: reducing the selectivity of fishing methods, reducing overall fishing mortality and maintaining large populations that retain the full range of phenotypes for natural selection to act upon, either by setting appropriate quotas or by implementing no-take areas that retain unselected phenotypes (Baskett *et al.* 2005; Hutchings 2009). Reviews on this topic are provided by Allendorf and Hard (2009), Hansen *et al.* (2012), Hutchings and Fraser (2008) and Law (2007).

The concept that harvest could have evolutionary effects with meaningful impacts on catch is well supported by theory and computer simulations (Brown *et al.* 2008; Hutchings 2009; Bromaghin *et al.* 2011). However, demonstrating it empirically is difficult because similar effects could result from natural environmental change or reflect plastic responses without genetic change [phenotypic plasticity; see Glossary (Data S1)] (Enberg *et al.* 2012). Historically, approaches to detection have mostly been based on observation, sometimes in combination with experimental manipulations and quantitative genetic modelling (Swain *et al.* 2007; Johnson *et al.* 2012). However, there remains debate about how best to demonstrate harvest affects while accounting for environmental effects and phenotypic plasticity (Dieckmann and Heino 2007; Law 2007). An alternative approach is presented by the growing availability of genomic resources [see Glossary (Data S1)], which has the potential to directly detect evolutionary changes by enabling the genes under selection to be monitored through time or in space (Nielsen *et al.* 2009; Hansen *et al.* 2012). At present, a significant challenge for this approach is our incomplete understanding of the genetic basis of most traits in wild fishes (Hansen *et al.* 2012), although genes underlying key traits such as growth are increasingly well characterized, and experimental tests have demonstrated a genetic basis for rapid phenotypic shifts in response to selection (van Wijk *et al.* 2013).

Case studies

The best-known example of fishing-induced selection associated with major changes in abundance and distribution comes from heavily exploited North Atlantic populations of the cod. After centuries of exploitation, Atlantic cod life histories have shifted towards maturation at earlier stages and smaller sizes in spite of environmental conditions favouring the opposite (Olsen *et al.* 2005; Swain *et al.* 2007). Cod stocks have failed to recover as fishing pressures were reduced, and permanent genetic changes are one of many factors that could explain this. Swain *et al.* (2007) used quantitative genetics modelling applied to length-at-age back-calculated from otoliths to demonstrate a genetically based reduction in growth rate in the Gulf of St Lawrence Fishery, whilst simultaneously documenting effects of density and temperature.

One example from Australia that may be explained by an evolutionary response to fishing is the western rock lobster (*Panulirus cygnus*, Palinuridae). The size at sexual maturity in this species has declined substantially in the past 35 years, and it has been argued that this may be partially a response to extremely high annual exploitation of adults (approximately 75%), together with a minimum carapace length in harvested animals (Melville-Smith and de Lestang 2006; Allendorf *et al.* 2008). One difficulty with this interpretation is that the change also coincided with increases in water temperatures over this period, which is expected to produce a similar pattern (Melville-Smith and de Lestang 2006). Further work is required to establish the relative importance of phenotypic plasticity, environmental- or fishery-induced selection in this species.

Barriers to uptake

Detecting and understanding the basis of evolutionary effects on fisheries allow managers to take action to reduce their impacts. Although the evidence for evolutionary effects of harvest is building (Allendorf *et al.* 2008; Kovach *et al.* 2012), few fisheries have adopted strategies designed to guard

against impacts (Allendorf and Hard 2009). This may reflect a lack of awareness of the issue, lack of compelling local examples or greater focus on more immediate and conventional fishing pressures (Law 2007; Allendorf and Hard 2009). Underpinning this is the difficulty of making clear links between environmental change, selection and evolutionary responses, and then extending the inference to meaningful impacts on fisheries productivity (Law 2007; Hansen *et al.* 2012).

Future

Theory has outpaced empirical evidence for evolutionary responses to fishing that have meaningful impacts on productivity (Marshall and Browman 2007). To date, most of the research on the selective effects of harvest in fisheries has been conducted in the Northern Hemisphere. Direct monitoring of the genes underlying traits has potential to provide robust tests of evolutionary predictions, but is currently limited by inadequate understandings of the genetic basis of many traits in wild fishes (Dieckmann and Heino 2007). Next-generation DNA sequencing tools, in combination with novel analyses and applied to temporal samples, hold promise to significantly advance this field and to enable a more global research effort (Nielsen and Hansen 2008; Hansen *et al.* 2012).

Theme IX: Genetic effect of stock enhancement

Why is it important to fisheries management?

Stock enhancement is commonly practised to meet the demands of commercial and recreational fishers (Laikre *et al.* 2010). It is most common in freshwater systems that are closed to migration, but is increasingly being used for marine species in estuarine and inshore habitats (Carson *et al.* 2009; Danancher and Garcia-Vazquez 2011). Some releases occur into vacant habitats, such as newly created water impoundments, or into habitats without a conspecific [see Glossary (Data S1)] resident population. Usually, however, the aim of stock enhancement programmes is to overcome recruitment failure of a local population by increasing the number of individuals available for capture. It can lead to serious genetic consequences for the local population of that species (Satake and Araki 2011), and if unchecked, it can lead to dependence on stock enhancement for future fishing opportunities.

How does it work and what are the limitations?

Interbreeding between endemic and captive-bred individuals has genetic consequences for the local population. Interbreeding introduces hybrids into the natural environment, which potentially lowers the productivity of the population. Adaptation to reproduction and growth in captivity leads to genetic changes in captive-bred individuals that are inevitable and unpredictable (Frankham 2008). As a result, captive-bred parents have lowered fitness in the wild compared with local endemics, and hybrid offspring also have lowered fitness. Of 70 studies, Araki and Schmid (2010) found 23 studies where captive-bred species had lower reproductive fitness than wild stocks and 28 studies where levels of genetic variation were lower in captive populations. There were no studies where captive-bred individuals had a higher fitness in the wild.

Genetics plays an important role in guiding captive breeding programmes and monitoring enhanced populations. Hatchery quality assurance programs (e.g. Rowland and Tully 2004) provide advice on the appropriate choice of broodstock from the wild (to match genotypes between endemic and captive stock) and on appropriate husbandry procedures (to minimize selection to captivity and to maximize genetic diversity). To prevent or to minimize post-release interbreeding between endemic and captive-bred individuals, technology exists to render captive-bred individuals sterile before release (Thresher *et al.* 2009) or broodstock can be selected to preclude interbreeding, although this is difficult (e.g. Seamons *et al.* 2012). Genetics can be used to identify released fish to determine post-release survival and is a cost-effective alternative to physically tagging millions of juveniles prior to release (Denson *et al.* 2012). Changes to genetic parameters of the population before and after enhancement is a good indicator of the likely impact of stock enhancement programmes (Carson *et al.* 2009).

Case studies

In North America, steelhead trout (*Oncorhynchus mykiss*) and Pacific salmon (*Oncorhynchus* spp.) populations are enhanced by the release of five billion captive-bred juvenile fish per year. While these juveniles are meant for harvest, captive-bred fish do reproduce in the wild and interbreed with native fish. Araki *et al.* (2007) and Araki and Schmid (2010) showed that the reproductive success

of captive-bred fish in the wild was less than wild fish. However, given continual contributions from captive-bred fish, the overall fitness of the wild population would progressively decrease. In the longer term, the population would become increasingly reliant on enhancement to maintain adequate numbers.

Barriers to uptake

There are no practical barriers to the use of genetic technology for the production of captive-bred individuals for stock enhancement, or post-release monitoring, assuming the infrastructure and expertise is close at hand. However, genetic monitoring is not a universal component of stock enhancement programmes. This could be due to factors such as lack of concern, awareness or resources.

Future

Fisheries managers require guidelines on the potential genetic consequences of stock enhancement programmes. This should include information on the key threatening processes, their risks, as well as ways to deal with the risks before and during stock enhancement. Two research topics are critically important to minimize the genetic and ecological effects of stock enhancement: addressing which genes and gene complexes are important to survival after release (Neff *et al.* 2011) and quantifying the extent of interbreeding in mixed populations using genetic monitoring (Denson *et al.* 2012). In Australia, there have been limited trials of marine restocking with species such as finfish (Butcher *et al.* 2003; Taylor and Piola 2008), prawns (Ochwada-Doyle *et al.* 2010) and abalone (Goodsell *et al.* 2006). To date, research has focussed on non-genetic methods of marking released individuals to monitor ecological effects. Little consideration has been given to the genetic consequences of enhancement programmes on endemic populations, possibly due to a lack of awareness of the issues.

Biosecurity

Theme X: Detection of pathogens and invasive species

Why is it important to fisheries management?

Pathogens and invasive species represent major threats to the productivity of wild fisheries (Darling and Mahon 2011; Johansen *et al.* 2011; Stentiford *et al.* 2012). Pathogens, such as viruses, bacteria and parasites, cause mortality or injury and can have indirect effects such as increased susceptibility to environmental stress and lowered fecundity. Invasive species are free living and do not cause disease, but have negative ecological impacts on harvested species. By definition, invasive species are a biosecurity risk outside their natural range, whereas pathogens are a biosecurity risk both within and outside their natural range. Action against harmful biological agents is an important part of wild fisheries management to forestall reductions in population size, mortality of live product prior to sale, adverse health outcomes in consumers (e.g. humans, aquaculture stock) and to control the spread through the environment.

Genetic tools are used to detect and monitor pathogens and invasive species because they offer detection assays that are rapid and highly sensitive, which facilitates a quick management response. Data from other sources can be slower to acquire, but are useful for confirming and extending conclusions based on DNA evidence. DNA analyses have been applied to ballast water for the detection of the planktonic stages of economically important invasive species: Australian examples include the invasive gastropod *Maoricolpus roseus* (Turritellidae; Gunasekera *et al.* 2005) and the Pacific oyster *Crassostrea gigas* (Ostreidae; Patil *et al.* 2005).

How does it work and what are the limitations?

Genetic tools for detecting and monitoring biosecurity risks to wild fisheries rely on PCR [including real-time PCR; see Glossary (Data S1)] of DNA, ensuring great sensitivity and the ability to analyse non-lethally collected samples. The technical challenges of using genetic tools for disease and invasive species detection in wild fisheries are largely the same as non-genetic tests. Robust sampling designs are difficult to implement in the extensive marine environment, and sampling is often biased towards the fished portion of the wild population. Biosecurity risks are often sporadic, spatially confined and occur at low levels. Also, unlike captive populations, wild populations are open to exchange with surrounding environments (Stentiford *et al.* 2012). DNA assays for pathogens and invasive species need to be developed and evaluated on a case-by-case basis and procedures

for dealing with type 1 (false negative results), and type 2 (false positive results) errors must be developed and implemented. Diagnosis of pathogens in wild populations is more challenging than captive populations and has rarely been applied to surveys of wild fish, and then only by research organizations. PCR-based tests cannot determine whether the pathogen is present in levels that could cause disease or be transmitted, and some knowledge of tissue prevalence is required for effective tissue sampling (Johansen *et al.* 2011). The tests cannot distinguish between viable and non-viable pathogens, thus are not useful to distinguish infected from immunized individuals.

DNA-based tests for detecting invasive species are referred to as eDNA (environmental DNA). The tests are applied to environmental samples such as filtered water, plankton tows and sediment cores, where the aim is to detect minute quantities DNA that originated from the individuals of interest (Thomsen *et al.* 2012). The tissue in the environmental sample could include living cells (e.g. eggs, larvae), shed body parts (e.g. skin cells, exoskeleton) or associated material such as faeces or mucus. As these methods are highly sensitive to low concentrations of DNA, precautions need to be taken to avoid sample cross-contamination (Darling and Mahon 2011). An important aspect of developing diagnostic tests for invasive species is the extensive testing for species specificity that is required before tests are deployed in the field.

Case studies

In 2005 and 2006, a disease was detected in abalone (*Haliotis laevigata* x *H. Rubra;* Haliotidae*)* farms on the south-eastern Australian coastline. It was identified as a herpeslike virus by electron microscopy and is now referred to as abalone viral ganglioneuritis (AVG). The disease caused high mortality in wild populations of abalone along the Victorian coastline. The Australian Animal Health Laboratory (Corbeil *et al.* 2010) developed a genetic [real-time PCR 'Taq-man'; see Glossary (Data S1)] assay for the detection of viral particles in tissue samples. A code of practice was subsequently developed to control the disease in the commercial, recreational, aquaculture and processing sectors (Gavine *et al.* 2007). Much remains to be understood, including the origin and range of the virus, its mode of action, whether it infects other species, its mechanism of action and ways to deactivate the disease.

In a large river and canal complex in the north-eastern USA, eDNA has been used to delimit the range of two species of invasive carp (Jerde *et al.* 2011). These species (silver and bighead carp *Hypophthalmichthys molitrix, and H. Nobilis,* Cyprinidae) have impacted fisheries and environmental quality in this region and their ranges continue to expand. eDNA testing detected both species ahead of the expected invasion front. In comparison with the conventional method of detecting carp via electrofishing, eDNA had a consistently higher catch per unit effort and detected carp in locations up to 8 months before they were detected via conventional means. Authorities are still debating the best course of action to protect the Great Lakes sports fishing industry and maintain open shipping links of economic importance between the Mississippi River and the Great Lakes; however, the science behind eDNA has come under intense and, in some cases, politicized scrutiny (Darling and Mahon 2011).

DNA assays can be used in marine systems for species detection. Thomsen *et al.* (2012) used eDNA and next-generation sequencing to record the presence of 15 fish species from filtered water samples taken from a temperate, inshore marine ecosystem in Denmark. Laboratory experiments showed that DNA in seawater samples degraded beyond detectability within a few days, suggesting that eDNA methods may be sensitive to localized changes in species presence and absence. This study brings together new developments in genetic technology [e.g. next-generation DNA sequencing, real-time PCR, reference sequence databases, see Glossary (Data S1)] and signals important new applications for genetics in wild fisheries management.

Barriers to uptake

For some DNA-based assays for pathogens and invasive species, such as those that use direct tissue sampling and species identification methodology, the technical challenges are largely under control. For eDNA, the technical challenges are being brought under control (Thomsen *et al.* 2012), but there are several other barriers to uptake (Darling and Mahon 2011; Johansen *et al.* 2011): first, authorities need to ensure that they have multifaceted, comprehensive information and advice about the problem. The biggest hurdle is to overcome the tendency to implement control rather than prevention programmes, which arises

from the perceived difficulty of confirming that an organism is present when it is likely to be very rare. Even if preventative actions may be less costly than control programmes, the cost of mounting a preventative campaign may be difficult to justify in the eyes of the public if there is no concrete evidence that the organism is present. Managers need to recall that DNA-based assays are designed to address this scenario and that similar methods have already been accepted in the legal world. Secondly, managers face a difficult problem in transparently communicating to stakeholders the uncertainty around the science and the rationale for their risk evaluation and chosen actions.

Future

> *'Increasingly, the science advances underpinning invasive species management must move at the speed of commerce'.* (Hulme 2009)

This is not only true for invasive species, but also for pathogen detection. The continued growth of aquaculture worldwide will lead to more species being cultured within their endemic range, increasing the risk of the transfer of pathogens into wild fisheries resources. Invasive species arise from escapees from aquaculture, but are also readily spread along international shipping routes. There is need for further developments in the area of DNA-based assays, including pathogen surveys in wild fish, the identification and role of reservoir individuals and species and in marine parasitology (Johansen *et al.* 2011). The future success of DNA-based assays depends on informed discussions among the general public, the commercial and recreational users of the natural resources as well as authorities such as managers, policymakers and developers of the methods.

Post-harvest regulation

Theme XI: Product provenance and fisheries surveillance

Why is it important to fisheries management?
Effective enforcement of management regulations relies on reliably identifying harvested organisms and their products. Often this can be difficult when species-diagnostic morphological characters are not evident. For example, fish fillets or trunks often lack heads, guts and tails following processing at sea. Product provenance is important to seafood producers to ensure consumer safety and confidence, which underpins profitable business. Product substitution, where a less valuable food product is illegally substituted for a more valuable product, is a well-described problem in the seafood industry (Rasmussen *et al.* 2009; Aranceta-Garza *et al.* 2011). The practice results in the loss of consumer confidence, devaluation of marketing tools, degradation of fisheries resources and potentially adverse effects on human health. This theme covers the post-harvest application of DNA technology to assign seafood products to categories such as species, geographical origin, family groups and individual carcasses.

How does it work and what are the limitations?
Genetic analysis of samples is widely used to enforce accurate labelling of seafood. This is the most straightforward of the provenance testing procedures and generally involves obtaining an mtDNA sequence from a specimen of interest and making a direct comparison with reference DNA sequence for known species. Genetic technology has been used to address the lack of standardization between common, marketing and scientific names for products (Yearsley *et al.* 1999; FDA 2010) as well as raising consumer knowledge of the species being purchased (Huxley-Jones *et al.* 2012).

Many wild fisheries operate under a management system where biological or jurisdictional stock boundaries are important. A range of genetic tools have been employed to assist the enforcement of such regulations. The FishPopTrace project (http://ec.europa.eu/research/bioeconomy/fish/projects/fishpoptrace_en.htm) used SNP markers to determine the unique genetic characteristics of fisheries stocks of major commercial species such as European hake (*Merluccius merluccius*, Merlucciidae), Atlantic herring, Atlantic cod and common sole (Martinsohn and Ogden 2009; Helyar *et al.* 2011). The FishPopTrace SNP database allows the assignment of individuals to fisheries stocks for enforcement and product tracing with correct assignments varying from 93 to 100%. Statistical methods enable probabilities of origin to be determined and also enable particular stocks of interest to be excluded as origins (e.g. Cornuet *et al.* 1999; Banks and Eichert 2000). Other fisheries have regulations covering the harvest of individuals of particular size, gender or reproductive

condition. For example, in Northern Ireland (United Kingdom), fishers are compensated for releasing female squat lobsters (*Munida rugosa* and *M. sarsi*, Munididae) carrying eggs. In the absence of fisheries officials, fishers take an egg and tissue sample from individual female lobsters at sea prior to the release of the lobster. Fishers are paid their allowance when subsequent genetic analysis demonstrates that the eggs are from one (and only one) female (e.g. Bailie *et al.* 2011). Genetic testing allows the rapid return of the females to the water, improving their survival, and is a transparent test that is popular with fishers and officials.

Another post-harvest application of genetic technology is the tracking of body parts from single individuals along the market chain. Products obtained from a single individual will be genetically identical. For example, in the Korean and Japanese whale markets, it provided a means of independently estimating the true catch as well as monitoring supply chains (Dalebout *et al.* 2002). The number of individuals for sale at any one time was estimated and the presence of the same individual among outlets suggested a common origin for processing. Likewise, the Norwegian minke whale (*Balaenoptera acutorostrata*; Balaenopteridae) register contains microsatellite genotypes of 7644 whales landed from 1997 to 2010, which allows trading in whale products that match registered genotypes (Glover *et al.* 2012).

Case studies

Atlantic Cod products are highly sought after in the British Isles, but this species has experienced extensive fisheries collapses. Miller and Mariani (2010) used genetic technology to determine the species identity of cod products on sale in Ireland. They purchased fresh, frozen and smoked Atlantic cod products from local fish shops and supermarkets, largely in Dublin. DNA analyses showed that around 28% of all samples, and up to 93% of smoked product, were mislabelled. The products were from a range of similar species, including Pacific (*G. macocephalus*) and Greenland (*G. ogac*) cod, saithe (*Pollachius virens*, Gadidae) and pollack (*P. Pollachius*, Gadidae). The outcome of the study increased accountability in product labelling that will lead to an increase consumer confidence. Ultimately, and with the provision of the right information, the consumer can choose to purchase if a product is from a sustainably managed fishery.

In the state of Queensland (Australia), it is illegal to possess female mud crabs (*Scylla serrata*). Genetic methods were used to achieve a successful prosecution in the case of female possession. The defendants claimed that females in their possession were derived from another state, the Northern Territory, where there are no gender-specific possession rules. Genetic analysis of the females revealed that they possessed a mtDNA haplotype (COI region) that was unique to Queensland populations on the north-eastern coast (Gopurenko and Hughes 2002).

Barriers to uptake

Genetic analysis has immense value as a tool for enforcement of fishing and marketing regulation because it provides higher-resolution provenance information than virtually all the alternatives. Nevertheless, the power of genetic provenance testing relies on the adequacy of reference data sets. As highlighted for Theme I, the collection and curation of reference collections require coordinated, strategic long-term planning. Without this, the benefits of genetic provenance testing will not be maximized.

Future

Seafood-processing companies may take the initiative to certify their products in terms of their origins and identities as part of a catch documentation scheme (CDS; Baker 2008) or as part of certification by the Marine Stewardship Council. Similar approaches have been used by the Norwegian whaling industry to register all legally killed individuals with a microsatellite DNA genotype (Palsbøll *et al.* 2006), and there is a close parallel in certification of timber products.

SNP markers [see Glossary (Data S1)] may take over from microsatellite DNA markers because they are better suited to automation, may be less prone to error, and reference data are easily transferred between laboratories or genotyping technologies (Helyar *et al.* 2011).

To be most effective, genetic information needs to stand up to cross-examination in a court of law. Geneticists may be called as expert witnesses, but often are not trained in court procedure or the provision of evidence. Procedures that are common in human forensic laboratories, such as chain-of-evidence, sample-logging and blind verification of results, are usually not in place in laboratories that generate DNA information for fisheries species.

Discussion

As illustrated by the diversity of genetic tools and applications profiled here, genetic analysis has never been better equipped to assist with wild fisheries management and conservation. In spite of this, in Australia and elsewhere, funding support for research has been narrowly focused and centred largely on fisheries stock structure and biosecurity issues (Fig. 2). It is unclear whether this represents need, perceived need or unawareness of other applications due to the rapidly evolving nature of the genetics discipline. Nevertheless, a compelling case is presented here for diversifying research outcomes across all eleven genetic themes based on the spectrum of pressing issues in fisheries management that genetic tools can address. This synthesis of applications of fisheries genetics allows a unique opportunity to compare and contrast among themes to identify common threads and predict where new and important contributions to fisheries management are most likely to occur.

Two major technical developments in biomedical industries are having an ever-increasing impact on genetics in fisheries. 'Next-generation' DNA sequencing technologies provide large volumes of DNA sequence data with unprecedented speed and economy. The new technologies have reduced the cost of genetic marker development. It will increase the power of analyses because more markers and samples will be assayable. It will also facilitate new types of analyses, from the study of genes directly involved in evolutionary change to the use of genetics for environmental monitoring. The second important development is the automation and miniaturization of laboratory procedures and equipment. Such advances will reduce costs, increase the repeatability of analyses, facilitate large monitoring projects (e.g. Seeb *et al.* 2011), produce data in a more timely manner for management decision-making (sometimes in real time) and pave the way for field-deployed or autonomous analyses (e.g. Ryan *et al.* 2011).

In the past, the cost of collecting data was sometimes a real or perceived barrier to the uptake of fisheries genetics. However, our experience is that other methods employed in fisheries science, such as tracking and tagging technology or chemical analyses of otoliths, have equivalent costs. With new technological developments, genetic data can be collected quickly and can be outsourced increasingly to specialist laboratories. As with all technologies, a significant challenge is to balance the value of new information against costs of acquiring it. Practically, this means that there is a direct relationship between the value of the fisheries resource and the research or monitoring resources that can be devoted to its management. Other factors are important also, such as the flexi-

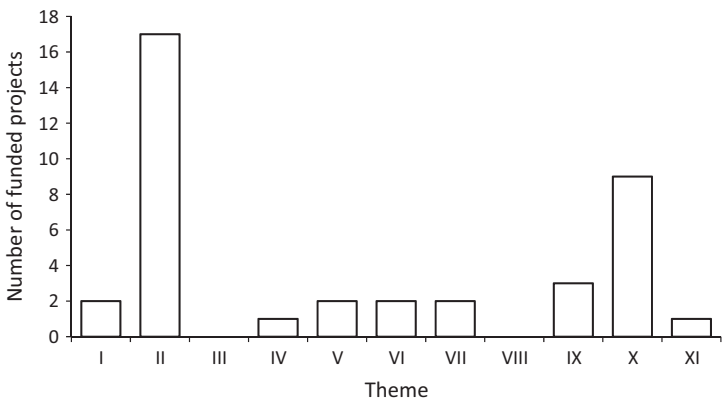

Figure 2 Allocation of financial support from a major Australian Research and Development Organisation (Australian Fisheries Research and Development Corporation) towards eleven genetic themes, based on data retrieved from a search of the FRDC online project database (www.FRDC.com.au/research) with search items Fisheries AND (Genetics OR DNA) and through discussions with researchers in Australia (1987–2011). Themes are indicated by their numeric codes as follows: I: species identification, II: fisheries stock structure, III: resolving mixed-stock fisheries, IV: DNA as a biomarker for age, V: ecosystem monitoring, VI: harvest rates and abundance, VII: monitoring genetic diversity, VIII: evolutionary responses to fishing, X: pathogens and invasive species, IX: consequences of stock enhancement, XI: product provenance and surveillance.

bility of harvest strategies to take into account new and more detailed information. A relatively new overhead cost for fisheries genetics is the collection, maintenance and administration of reference data, which is essential for many genetic themes such as DNA for species identification, mixed-stock analysis, ecosystem monitoring, detection of pathogens and invasive species and product provenance. There are numerous programmes underway to provide reference data for fisheries. To maximize their value, they need to be coordinated and developed strategically, and they require ongoing support from the private and public sector. Historical tissue sample collections need to be incorporated into these programmes (Nielsen and Hansen 2008). Methods for non-destructively extracting DNA from historical samples preserved under varying conditions are continually advancing (e.g. Garrigos *et al.* 2013).

Generally, genetics is used to provide baseline information on the nature of fisheries resources or the environment, for example, identifying fisheries stock structure. Increasingly, however, genetics in fisheries will be used as a monitoring tool: for example, estimating abundance and spawner numbers through genetic mark–recapture, determination of product provenance and detection of pathogens. Baseline research has typically been funded by grants of short duration. An important question that needs addressing will be whether funding bodies and research institutions will support ongoing genetic monitoring, as well as baseline research. Monitoring is generally not regarded as research (although research is needed to develop new monitoring techniques), and the responsibility for monitoring is often thought to lie with government and other authorities. The timeframe for monitoring is also potentially open-ended, requiring continual allocation of resources. It seems certain that developed and emerging genetic technologies will be ideal tools for fisheries monitoring, and their cost-effectiveness will only improve with technological advances. The monitoring of spatial and temporal variance in genetic diversity is as valid an activity as the monitoring of various demographic or morphological characters. Such inclusion will allow genetic markers to be more commonly deployed on medium to low value fisheries.

The single biggest issue that limits the effective use of genetic tools in fisheries management and that may partially explain the narrow focus illustrated in Fig. 2 is poor communication between geneticists and end-users (Waples *et al.* 2008). Like many specialized scientific disciplines, the science of genetics is highly technical, and understanding and communicating the basic concepts can be challenging. Fisheries managers therefore generally rely on geneticists and fisheries scientists to guide their understanding of genetic principles and outcomes as they apply to fisheries management in practical terms. However, responsibility for communication must be shared so that the needs of fisheries managers, geneticists and fisheries scientists are mutually understood. A promising mechanism to achieve this outcome is through the use of existing formal processes. In Australia, it is fisheries scientists, not geneticists, who usually serve on fisheries management committees, and therefore, the most effective partnership development is likely to be between fisheries scientists and geneticists, with scientists acting as a conduit to managers for relevant genetic information via the advisory groups. Other ways to improve the integration between key fisheries and genetics personnel are for a team approach to genetic research projects (Pullin and Stewart 2006). The skills and experience of fisheries managers and scientists are essential for successful experimental design, implementation, analysis and extension alongside population and molecular geneticists, statisticians, mathematicians, software engineers, bioinformatics and database managers (Table 1). Training of geneticists in fisheries science and of fisheries scientists in genetics would provide the common language needed for effective communication.

Clearly, the capability of genetic tools to address fisheries management issues is diverse and continually developing. In saying this, we recognize the limitations of some tools at their current stage of development. Examples of these include genetic mark–recapture, DNA as a biomarker for age and the use of genetics to detect evolutionary responses to fishing. Although further development may be required, the rewards are high as they are tools that can help address some of the most significant management issues of the future. Taking on innovative approaches that adapt existing high-end genetic technologies, for example, from the biomedical area, will rely on fisheries geneticists working in new collaborative contexts. As with existing technologies that have been widely applied in other fields, the risk will not be in the methodology itself but in the adaptation of that technology to a fisheries management context.

The genetic tool most likely to deliver significant advances for fisheries management in the short term is continued work on the identification of fisheries stock structure. Spatial information on fisheries resources underpins sustainable management, and genetic methods for defining stock boundaries are well developed. Many fisheries, particularly outside Europe and North America, lack this basic information. Increasingly, stock structure information will be used to assign provenance to fishery products. In the medium term, new methodologies such as genetic mark–recapture and estimation of genetic effective population size show promise for measuring spawning biomass, catchability and harvest rates independently of data collected from fisheries. In the longer term, genetics will provide fisheries managers with information and tools for detecting (and ameliorating) the effects of climate change and fishing on fisheries species, and for environmental monitoring and food-web analyses. Accessible, standardized reference databases that are developed in coordinated and strategic ways will underpin much of the future application of genetics in fisheries. Genetic tools have the potential to provide information that is unlikely to be obtained elsewhere, justifying on-going investment in their development. However, future investment should also be complemented by investment into the development of communication strategies designed to cross disciplinary boundaries to ensure that tools are appropriately and optimally used and that uptake of research outcomes are maximized.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. A field guide to genetics in fisheries: a plain language summary of the eleven past, present and emerging themes in which genetic technology can assist in the maintenance of productive and sustainable harvesting. See http://frdc.com.au/research/genetics/Pages/field_guide.aspx.

Data S1. Glossary.