Perspective

Crinkles in connectivity: combining genetics and other types of biological data to estimate movement and interbreeding between populations

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Abstract. Marine species generally have large population sizes, continuous distributions and high dispersal capacity. Despite this, they are often subdivided into separate populations, which are the basic units of fisheries management. For example, populations of some fisheries species across the deep water of the Timor Trench are genetically different, inferring minimal movement and interbreeding. When connectivity is higher than the Timor Trench example, but not so high that the populations become one, connectivity between populations is crinkled. Crinkled connectivity occurs when migration is above the threshold required to link populations genetically, but below the threshold for demographic links. In future, genetic estimates of connectivity over crinkled links could be uniquely combined with other data, such as estimates of population size and tagging and tracking data, to quantify demographic connectedness between these types of populations. Elasmobranch species may be ideal targets for this research because connectivity between populations is more likely to be crinkled than for finfish species. Fisheries stock-assessment models could be strengthened with estimates of connectivity to improve the strategic and sustainable harvesting of biological resources.

Additional keywords: Australia, demography, dispersal, elasmobranch, fisheries management, migration, Timor Trench.

Introduction

'I believe then that the cod fishery, the herring fishery, pilchard fishery, the mackerel fishery and probably all the great sea fisheries are inexhaustible: that is to say that nothing we do seriously affects the numbers of fish. And any attempt to regulate these fisheries seems consequently from the nature of the case to be useless.' (Huxley 1884)

In 1884 Thomas Huxley believed that it was not necessary or possible to manage fisheries resources. One hundred and twenty-five years later, the potential of the oceans of the world to supply seafood has probably been reached. Worldwide, wild-capture fisheries produced ~92 million tonnes of product in 2006, comprising 82 million tonnes from marine waters and 10 million tonnes from freshwater (FAO 2009). Fifty-two per cent of fisheries stocks were fully exploited and 28% of stocks were overexploited, depleted or recovering. Some stocks (20%) were moderately exploited or underexploited and possibly capable of producing more. International variation is pronounced, however, and in Australia only 2% of 150 fisheries stocks were classified as overfished in 2012 (Flood *et al.* 2012).

In Australia and elsewhere, resource managers seek ways to sustainably harvest fisheries species, using knowledge from stakeholders as well as from biological, physical and social sciences. Mathematical models based on estimates of biomass, productivity and mortality are often used to predict the effect of harvest strategies. Biomass is inferred from catch-per-unit effort or other methods. Productivity is measured in terms of the number of new individuals produced each generation by the spawning stock (recruitment), and by the increase in the size of all individuals through time (growth). Mortality is the rate at which animals die naturally or as a result of harvesting (King 2007). The models apply to a fisheries population, which is defined as a demographically cohesive group of individuals that have similar age-specific birth, growth and death rates. Movement and interbreeding of individuals within the spatial extent of a population is the glue that binds it into a cohesive unit. Similarly, connectivity between populations binds them together into a single species and balances the diversifying forces of genetic drift, mutation and selection, which otherwise would combine to lead to evolution in isolation, and eventual speciation (Mayr 1970). The distribution and abundance of genes are commonly used to test for the free interchange of individuals that is the signature of connectivity between populations.

This perspective focuses on the use of genetics to identify population structure in marine species, and how that information could be used in new ways to investigate the extent of the movement and interbreeding between populations. New ways of
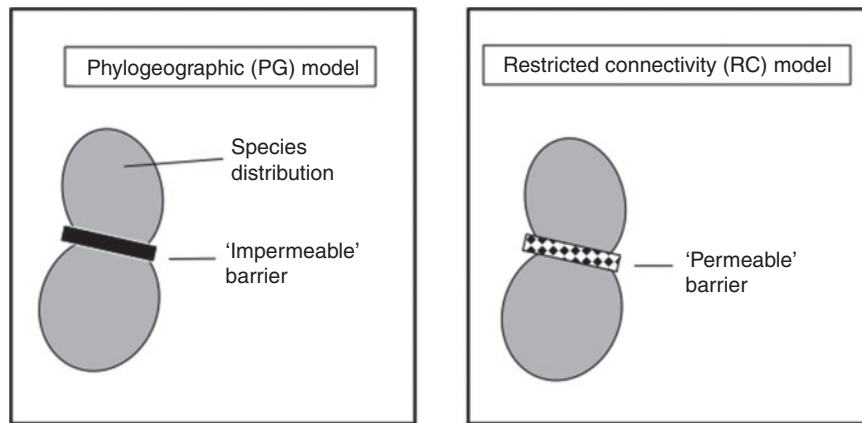
Fig. 1. Two basic models of connectivity that can explain the presence of separate populations (or stocks) in marine species.

producing connectivity estimates of movement and interbreeding across different types of marine species could fine-tune fisheries models, and promote further collaboration and mutual understanding between geneticists and scientists who work in the field of fisheries. It is timely, given the increased level of interest in the use of genetics in wild-fisheries management (Dichmont *et al.* 2012) and the technological and theoretical improvements to population genetics that have occurred over the past 5 years (Allendorf *et al.* 2010; Helyar *et al.* 2011; Dudgeon *et al.* 2012; Hoban *et al.* 2012).

Types of connectivity between populations

There are two basic explanations for the presence of separate populations within a marine species (Fig. 1). In the first model, an impermeable barrier has separated a single population into two; the two new entities are called phylogeographic (PG) populations (Avise *et al.* 1987). Examples of impermeable barriers are mountain ranges, which can separate freshwater fish populations (Nock *et al.* 2011), and present (e.g. Isthmus of Panama, Knowlton *et al.* 1993) or past (e.g. Torres Strait, Chenoweth *et al.* 1998) land bridges. In the second basic model, connectivity is restricted (RC) within the range of a species by a permeable barrier (Fig. 1). Examples of permeable barriers include inshore sea conditions (e.g. Broderick *et al.* 2011) or prevailing ocean currents (e.g. Feutry *et al.* 2013). On a case-by-case basis, instances of the PG and RC models can be distinguished by factors such as concordance among the physical locations of populations across species, obvious barriers to gene flow (past and present) as well as biological data about the species (e.g. distribution, abundance and vagility). In these and other models, genetics provides a long-term perspective on connectivity among populations. It provides information not only on movement, but also on whether an animal has successfully reproduced in its adopted population. Methods such as conventional capture–mark–recapture and acoustic tracking measure animal movement, but do not detect whether the movement has resulted in reproduction in the adopted population. Thus, genetics uniquely adds the dimension of interbreeding to the study of movement.

Marine examples of PG are less common than examples of RC. However, the PG model appears to explain similar patterns of population subdivision across several co-distributed species to the north of Australia. The Timor Trench interrupts genetic connectivity between populations of some mackerel, snapper and shark species (Fig. 2), but not for all species studied (Table 1). The Timor Trench divides the shallow continental shelf of north-western Australian from the volcanic islands of Timor and central Indonesia and is 3000 to 5000 m deep. It is unclear how the Trench acts as a barrier to connectivity in some, but not all species. Adult body size in the subdivided species was large, and presumably individuals would be able to move across the Trench. The subdivided finfish species have pelagic larvae, which could be passively advected across the Trench by ocean currents (Gordon and Fine 1996). Regardless of the mechanism involved, the Timor Trench is the location of a major break in connectivity and has been used to shape management scenarios for commercial species (Blaber *et al.* 2005). It may also act as a species-specific filter of general southward movement into the relatively cooler waters of Australia when environmental change leads to elevations in seawater temperature in Indonesia.

Genetic and demographic connectivity

Under the RC model (Fig. 1), breaks in connectivity are less pronounced. Population genetics is able to detect the population structure because the type of genes (or alleles) and their frequency differ among individuals sampled from parts of the species range. If fish were freely moving and interbreeding between these areas, then the populations would have the same genes at the same frequencies. Many years ago, Wright (1949) proposed that at least one migrant per generation needed to be exchanged between populations to avoid the potentially harmful effects of genetic drift and inbreeding. This became the rule-of-thumb for the numbers of fish that needed to be exchanged between populations to maintain genetic differences. Below this number, alleles and their frequencies between populations would be significantly different; above this number, populations would be genetically the same. Thus, the presence of genetically different populations was thought to reflect a very small amount of movement between populations, namely, one fish per generation or fewer. Lowe and Allendorf (2010) pointed out, however, that populations could exchange more migrants than this and still remain genetically different. In fact, allele frequencies would
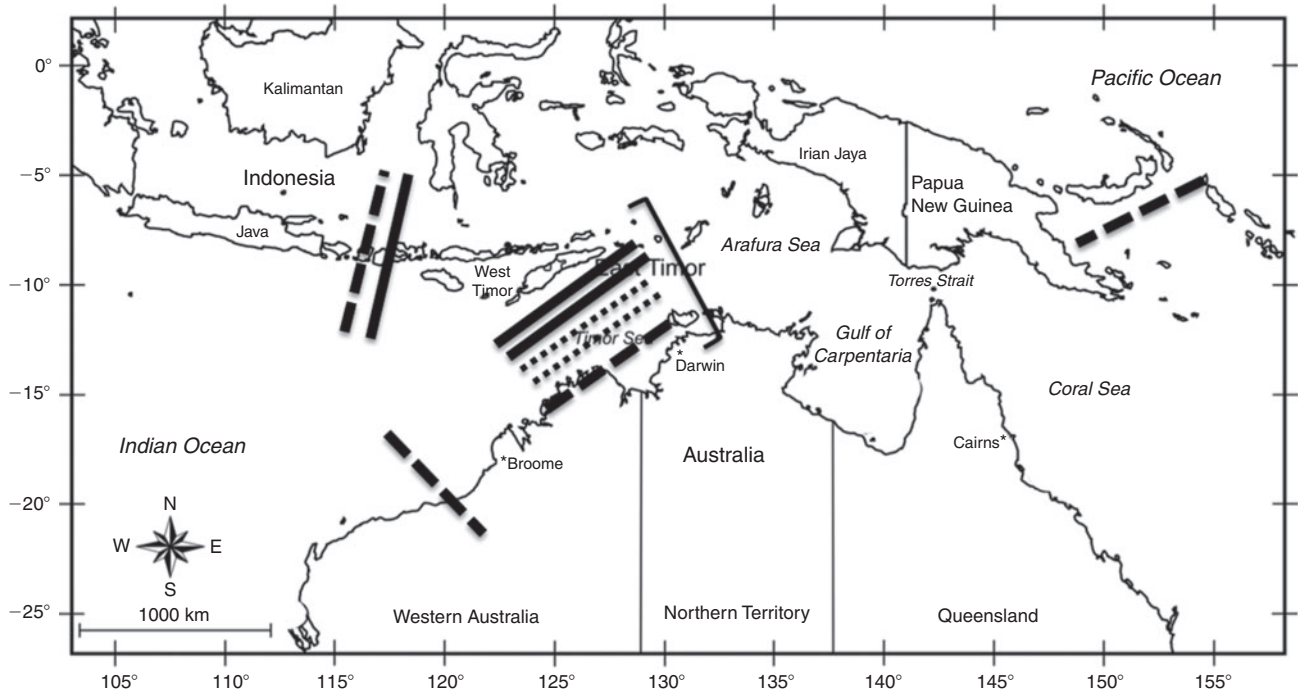
Fig. 2. The location of an interruption to connectivity between populations of mackerel species (*Scomberomorus commerson* and *S. fasciatus*; dashed lines), three shark species (*Carcharhinus sorrah*, *Rhizoprionodon acutus* and *Stegastoma fasciatum*; solid lines) and two species of snapper (*Lutjanus malabaricus* and *L. erythropterus*; dotted lines) to the north of Australia (Table 1). Five boundaries coincide with the Timor Trench (bracketed).

Table 1.   Location of boundaries between populations of mackerel, snapper and shark species within and between northern Australia and Indonesia, on the basis of F_{ST} for nuclear genetic markers (microsatellites, msat; allozymes, allo)

n.a., not available

| Species	Northern Australia		Northern Australia and Indonesia		Reference
	F_{ST}	Location of presumed genetic break	F_{ST}	Location of presumed genetic break	
Mackerel					
Spanish – *Scomberomorus commerson*	0.006 (allo), 0.004 (msat)	Torres Strait	0.01 (allo), 0.04 (allo)	Numerous	Shaklee (2007), Sulaiman and Ovenden (2010)
Grey – *S. fasciatus*	0.04 (msat)	Kimberleys	n.a. (Australian endemic)	n.a. (Australian endemic)	(Broderick *et al.* 2011)
Snapper					
Mangrove Jack – *Lutjanus argentimaculatus*	0 (msat)	None	0 (msat)	None	Ovenden and Street (2003)
Red – *L. malabaricus*	0 (allo)	None	0.04 (allo)	Timor Trench	Salini *et al.* (2006)
Red – *L. erythropterus*	0 (allo)	None	0.04 (allo)	Timor Trench	Salini *et al.* (2006)
Shark					
Dusky – *Carcharhinus obscurus*	0 (msat)	None	0 (msat)	None	Ovenden *et al.* (2009)
Spot-tail – *C. sorrah*	0 (msat)	None	0.04 (msat)	Timor Trench	Ovenden *et al.* (2009)
Blue *Prionace glauca*	0 (msat)	None	0 (msat)	None	Ovenden *et al.* (2009)
Scalloped – hammerhead *Sphyrna lewini*	0 (msat)	None	0 (msat)	None	Ovenden *et al.* (2009, 2011)
Milk – *Rhizoprionodon acutus*	0 (msat)	None	0.04 (msat)	0 (msat)	Ovenden *et al.* (2011)
Zebra – *Stegastoma fasciatum*	n.a.	n.a.	0.06 (msat)	Wallace Line and Timor Trench	Dudgeon *et al.* (2009)
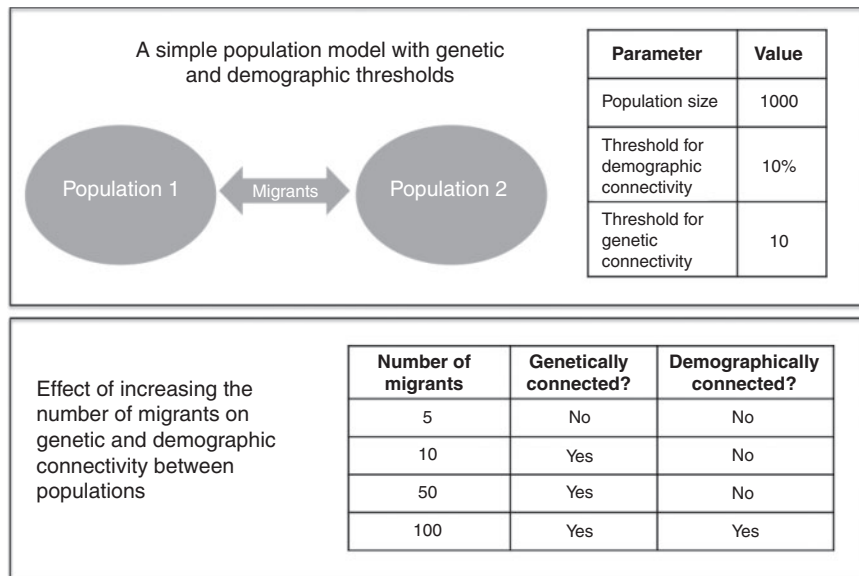
Fig. 3. A thought experiment to demonstrate the difference between genetic and demographic connectivity; as the number of migrants between two model populations is hypothetically increased, genetic threshold for connectivity is reached before the demographic threshold.

remain different unless the number of migrants (N_em) exceeded that predicted from the following equation:

$$F_{ST} = 1/(4N_em + 1) \text{ (Wright 1969).} \qquad (1)$$

Here, the value F_{ST} measures genetic difference between populations; if it equals zero, there is no genetic difference; if its larger than zero, then the populations are significantly different. Late last century, it was difficult to measure small values of F_{ST} (e.g. <0.1), whereas today, estimates as low as 0.01 (or lower) can be measured with accuracy. If F_{ST} is 0.01, then Eqn 1 predicts that the number of fish moving between the populations must be 25 per generation or fewer.

Equation 1 is also important here because it shows that the genetic threshold is an absolute number, independent of the numbers of individuals in each population. In contrast, the numbers of migrants needed for demographic connectivity is dependent on the population size (Waples and Gaggiotti 2006; Lowe and Allendorf 2010). The demographic threshold is generally reached when the fraction of migrants in the receiving population is 10%. Above this, populations are demographically connected and below this, they are not connected. The demographic threshold may vary greatly among taxa and applications, and the actual value of the demographic threshold is not important here. A thought experiment is useful to explore the essential differences between demographic and genetic connectivity. Imagine two separate populations, each consisting of 1000 individuals, and which are connected by migration (Fig. 3). The genetic threshold is set at 10 migrants; below this the populations would be genetically different and above this they would be genetically similar. This number of migrants would not make the populations demographically connected. There would have to be 100 (i.e. 10% of population size) or more migrants to achieve this. At that point, the populations would be

genetically and demographically connected. Thus, a certain *number* of migrants are needed to tie stocks together in a genetic sense, whereas a certain *proportion* of migrants are needed for demographic connectedness.

Crinkles in connectivity

This example shows that if migration between populations is low, then genetics is a good guide to demographic connectivity and this may be the situation for populations on either side of the Timor Trench. The F_{ST} between them is ~0.04 (Table 1) and using Eqn 1, this equates to five migrants per generation. Because this is a small number of migrants, connectivity between these populations is regarded as broken both genetically and demographically, which is the rationale for treating them as separate biological stocks for the purpose of fisheries management (Blaber *et al.* 2005). However, if movement and interbreeding between populations had been higher, a point would be reached where two populations may be connected in a genetic, but not a demographic sense. Here, genetics would not be a good guide to demographic connectivity; genetically, there would be one population, whereas demographically, there would be two. A pair of populations like this would be regarded as having 'crinkled connectivity' (Fig. 4). The 'crinkle' would disappear at higher levels of connectivity, where there would be a single population that was genetically and demographically cohesive.

When connectivity between a population pair is crinkled, they are linked genetically but not demographically. In other words, they are demographically separate populations whose links just exceed the genetic threshold. Quantifying this type of linkage would provide additional valuable information for fisheries management. In future, it may be possible to do this, for example by obtaining migration estimates from an expanded
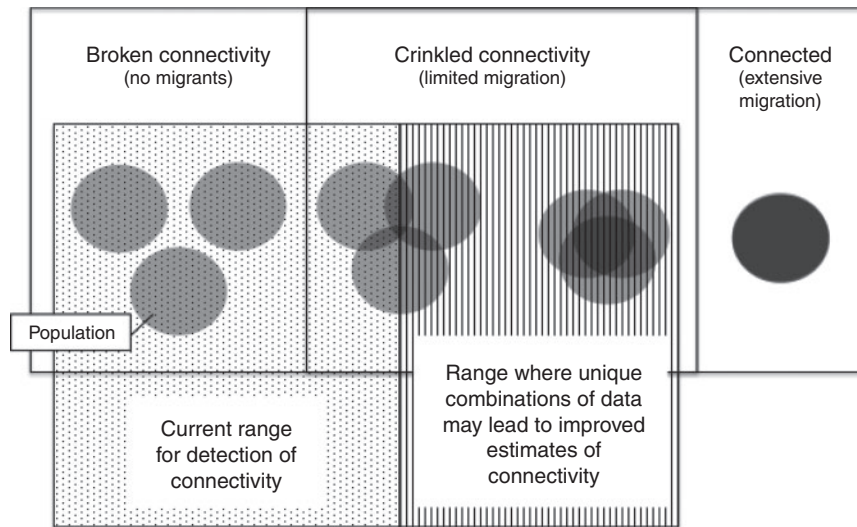
Fig. 4. Types of connectivity between populations, and the current and possible future scope for detecting connectivity using population genetics in combination with other data sources.

genetic dataset and using a revised, and more powerful, version of Eqn 1. Adding tagging and tracking data to genetic datasets could also lead to improved estimates of migration; e.g. non-genetic estimates of migration may account for the non-breeding migrants, whereas the genetic estimates account for the breeding migrants. Any improved estimates of migration would need to be converted to demographic estimates of connectivity, and for this, estimates of population sizes would be needed. This may be feasible with threatened, endangered or protected species, whose population sizes are small, or for well characterised fisheries populations. Another approach is to construct demographic models of connectivity, which could be used to predict genetic connectivity, and then specific hypotheses about connectivity could be tested with empirical genetic data.

Crinkled connectivity and dispersal

Most harvested marine species fall into two broad categories based on the dispersal characteristics of their life-history stages. The first category includes species where dispersal is more common during pre-adult (egg, larvae and juvenile forms) than the adult stages. Reef fish are an example of this; adults are generally sedentary in defined home ranges, whereas dispersal occurs in the larval phase. The second category of marine species is the reverse, where dispersal mainly occurs during the adult stage and pre-adult dispersal is low. The best examples of this are shark and ray species, some of which have inshore nursery grounds and wide-ranging adult grounds (e.g. Blower *et al.* 2012; Tillett *et al.* 2012). The actual number of migrants in transit between populations will differ among species in the first and second dispersal categories. Pre-adult life forms are naturally more abundant than adults, so for species in the first category, there may be large numbers moving between populations. For species in the second category, there will be fewer migrants. However, mortality during migration will be high for pre-adult migrants compared with adult migrants, so the overall

amount of interchange between populations may be similar between the categories.

Assuming that the magnitude of successful migration between populations is similar for species in both categories, species in the first category (where dispersal occurs during pre-adult stages) are more likely to be genetically connected than are species in the second category (where dispersal occurs during adult stage). Although this seems counter-intuitive, it is because the species in the first category are more likely to breed successfully in their adopted population than are the species in the second category. For the species in the first category, migrants will consist of early life-history stages, and once they have overcome the high mortality rates associated with migration, they will assimilate into the local population and reach adulthood alongside local individuals. In doing so, they have the same chance of becoming part of the successful spawning population as have local individuals, assuming there is no inherited component to spawning behaviour. This is in contrast to species in the second category. Migrants between populations from these species are likely to be adults, who have a good chance of surviving the dispersal event and joining the local population. However, their chance of successfully contributing to spawning may be low. They may not be in reproductive phase with the local spawning stock or be able to recognise and join local breeding aggregations.

Little is known about patterns, mechanisms and functions of social and non-social aggregation behaviour in elasmobranchs (Jacoby *et al.* 2012). Coastal shark species regularly return to aggregation sites if they coincide with nursery areas, although fidelity to aggregations for breeding purposes has been observed only for a few species (Speed *et al.* 2010). Assuming elasmobranchs do aggregate for mating, it is feasible that incoming adult migrants may not have the behavioural knowledge to successfully engage with foreign aggregations. Recent work by Blower *et al.* (2012) on white sharks suggested that both genders regularly return to particular inshore regions in

Australia for mating. So, even though demographic linkages between population pairs from species in the first and second category may be similar, populations in the second category may be more likely to follow the RC model (Fig. 1). This suggests that elasmobranchs may be the most likely taxa to have crinkled connectivity, and thus they may be the best research targets for the use of genetics combined with other methods for the estimation of levels of demographic connectivity.

Conclusions

Obtaining food for humans from wild fisheries is less detrimental to natural ecosystems than the production of marine protein in captivity (Grigorakis and Rigos 2011). The key to a guaranteed supply of raw material to fishers and seafood to consumers from wild fisheries is a detailed understanding of individual species and their ecosystems, combined with sound, enforceable harvesting strategies. Scientific research is the main way to achieve understanding, and is particularly important for countries such as Australia and other nations in south-eastern Asia that generally do not have a long scientific tradition and where biodiversity is high and unique. Population genetics is a popular research tool for the spatial definition of fisheries populations. Although it provides valuable information about connectivity when it is low or broken, it currently lacks precision when connectivity is crinkled. Crinkled connectivity occurs when connectivity is large enough to make the populations genetically similar, but not large enough to make them demographically linked. Research on crinkled populations in wild fisheries may allow the estimation of the movement between them, particularly for species where dispersal occurs during the adult not the pre-adult life stage, such as elasmobranchs. The leap from genetic to demographic estimates of connectivity will open a window of opportunity to refine fisheries population models and improve the strategic management of wild fisheries in Australia and worldwide.

Acknowledgements

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