Assessing genetic structure of thornback ray, Raja clavata

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CHAPTER 8

Summary-Discussion

Summary

Rays and skates are characterized by a slow growth rate, long generation time, late age at maturity, low fecundity and no pelagic larval phase. Consequently, they recover slowly to fisheries pressure in which they are a frequent part of the by-catch. Between 1956 and 1995, *Raja clavata*, disappeared from the waters along the continental coasts of the North Sea; and severely declined in most North European waters. This alarming decrease has led to concern about the sustainability of skate populations, and whether depleted areas can be naturally replenished from adjacent areas.

Tagging data suggested a small “home range” and philopatric behaviour based on seasonal movements from deeper waters in Autumn/Winter to shallower waters in the Spring/Summer, and the return of individuals in the same area every year. This combination of small home range and philopatric behavior led to the hypothesis of relatively strong population differentiation. The aim of this thesis was to test this hypothesis by assessing the genetic population structure of thornback rays. There were two initial questions:

What is the spatial scale and connectivity of genetically defined populations or stocks of the thornback ray, *Raja clavata*, in the North Sea/Northern Atlantic?

How well do indirect estimates of migration and connectivity, based on genetic data, correspond to direct estimates based on tagging data?

Population differentiation was first assessed at a regional scale, in British waters, using five newly developed microsatellite loci (Chapters 2 & 3). Fourteen locations were sampled in the North Sea, English Channel and Irish Sea. Some locations were sampled twice: in two different seasons (Autumn/Winter vs. Spring/Summer) or in the same season but at two different years. Temporal sampling made it possible to assess temporal stability of the population genetic structure. Significant global population differentiation was found ($F_{ST}=0.013 \, \, P<0.001$) although pairwise comparisons revealed no relationship with geography or with time. A first generation migrant analysis gave an estimation of 5-30% migrants. Locations sampled in Spring/Summer were more genetically differentiated than locations collected in Autumn/Winter. Altogether, these results strongly suggest that the population genetic structure of thornback rays is temporally and spatially dynamic, probably because of behavior. Genetic data indicated also that migration
distance is substantially larger than suggested by earlier tagging studies. Such discrepancies between tagging and genetic data are common given that tagging studies follow individuals for a maximum of 4-5 years (half a generation time for thornback ray), whereas population genetic studies integrate time over several generations. The main conclusions, in any case, are that dispersal capacity of thornback rays is greater than what had been previously reported, i.e., hundreds of kilometers vs. the 50-130 kms indicated by the tagging.

In Chapter 4, the population genetic structure was expanded to the European scale in order to take into account the historical, phylogeographic components of the population structure and to describe geographical barriers to gene flow. Twenty locations were sampled in European waters (Britain, Gulf of Biscay, Portugal, Corsica, Adriatic Sea, Black Sea and the Azores). Population differentiation was assessed using the microsatellite loci and a fragment of 290 bp of the mitochondrial cytochrome b (mtDNA). Strong population differentiation was found among the Mediterranean basin (Corsica, Adriatic and Black Seas), the Azores and the European continental shelf (Britain, Gulf of Biscay and Portugal), as well as a significant isolation by distance. Depth (continental margins), the Gibraltar Strait/Almeria-Oran front, and distance act as barriers to gene flow in thornback rays. Allelic and haplotypic diversities were high in Portuguese populations, consistent with the existence of a refugium along the Iberian peninsula. Unexpectedly, high diversity was also found in the English Channel/North Sea area. The distributions of two ancestral haplotypes: one common everywhere except in the Azores and one restricted to the Azores and British populations indicate that British waters have served as a secondary contact zone recolonized from at least two refugia—one around the Iberian peninsula and one possibly in the Azores. Finally, an historical demographic analysis indicated that thornback ray populations started to expand between 580,000 and 362,000 yr ago, which suggests that the Last Glacial Maximum (20,000 yr ago) mainly affected the distribution of populations rather than population size.

Having answered the basic questions, I moved on to the following ones:

**What is the effective population size in thornback rays and what is the impact of fishing on genetic diversity?**

The effective population size \(N_e\) is the number of individuals that mate and contribute to the next generation. Populations with small \(N_e\) are at higher risk for the loss of genetic diversity. In fish, \(N_e\) is usually several orders of magnitude smaller than the census population size \(N\). \(N_e\) was estimated from samples of vertebrae collected in the Irish Sea in 1965 and contemporary samples (2003/2004) (Chapter 5). Using a temporal method over four generations (i.e., 40 years), we estimated \(N_e\) to be 399 [113; 2213] with a \(N_e/N\) ratio between \(1.3*10^{-4}\) and \(8*10^{-4}\), showing that very few individuals contribute to the next generation (one individual out of 1250-7500). This small \(N_e/N\) ratio is most likely due to variance in reproductive success.
and/or fluctuations in population size. Finally, no evidence for a loss of genetic diversity was observed between 1965 and 2003/2004, suggesting that thornback ray populations may be at genetic risk on the long term but not on the short term. This is encouraging given that fishing-mediated loss of genetic diversity has been documented in a number of fish species. Nevertheless, the small $N_c$ must be protected against further reductions.

Is there evidence for multiple paternity?

The mating system is an important parameter for long term management. Thornback rays have a protracted spawning season, which may last several weeks or months. During this period, oocytes are fertilized in the nidamental gland, where sperm are stored. It was not known whether polyandry and possible multiple paternity are part of the mating system in *R. clavata*. As an evolutionary strategy, advantages of polyandry can increase genetic diversity of clutches, decrease genetic incompatibility and increase female fitness —such as increased female fertility and/or increased female reproductive lifetime. Egg clutches collected from four female *R. clavata* were analyzed to test for multiple paternity (Chapter 6). Using a reconstructed-multilocus-genotypes method to explain the progeny array, we determined that each of the four clutches analyzed contained embryos sired by a minimum of 4 to 6 fathers. Except for the hammerhead shark, *Sphyra tiburo*, polyandry is the most common strategy in viviparous sharks and may be explained by their high degree of philopatry and small census population size. In *R. clavata*, polyandry may maximize the likelihood of viable sperm during the long egg-laying season. The possibility of multiple paternity would ensure further fitness advantages. Whether *R. clavata* is naturally polyandrous or whether this strategy has developed as a result of fishing pressure remains a question and needs to be investigated.

What is the spatial scale of population genetic differentiation in another Rajidae taxa, the thorny skate, *Amblyraja radiata*, and how similar is this scale to *Raja clavata*?

Nineteen locations were sampled in the North Sea, the Kattegat, Norwegian, Icelandic and Newfoundland waters. Using the same fragment of 290 bp of the mitochondrial cytochrome b, genetic differentiation and phylogeographic structure were examined (Chapter 7). With the exception of the Kattegat, there was no detectable population differentiation. Thirty-four haplotypes were identified with the haplotype diversity being high and evenly distributed across the entire Atlantic ($h=0.8$); the only exception was the North Sea ($h=0.48$). Statistical parsimony revealed a star-like genealogy with an ancestral widespread haplotype. A subsequent nested clade analysis led to the inference of contiguous expansion. Altogether, these results showed that *A. radiata* has a high dispersal capacity. Historical demographic analysis showed that thorny skates underwent an even earlier population expansion than thornback ray at between 1.1 million and 690,000 years ago. Likewise, the Last Glacial Maximum probably had little effect on thorny skates.
The thorny skate and thornback ray offer some interesting similarities and differences. Both have similar life histories and overlapping ranges; both were apparently little affected by glacial episodes. At the same time, thornback rays showed strong population differentiation at the oceanic scale but not *A. radiata*. Depth may restrict gene flow in *R. clavata*, but not for *A. radiata*, as it is frequently fished deeper than 500 m.

**Discussion / Concluding Remarks**

At the oceanic geographical scale, the level of population differentiation was found to be similar for thornback rays, *Raja clavata* and the European plaice, *Pleuronectes platessa* (see Hoarau et al. 2002) despite major differences in life history type. In contrast, thornback rays and thorny skates, *Amblyraja radiata*, with similar life history types, have very different level of population differentiation, i.e., a $F_{ST}$ 30-fold higher for *R. clavata*. Thus, the hypothesis that a life history characterized by low fecundity, slow growth and an apparently small home-range is not a priori, a reliable predictor of population structure. In this study, bathymetric barriers are more important factors than life history to explain population structure in plaice and thornbacks; but not in the thorny skate.

At a more regional scale of hundreds of kilometers, significant genetic differentiation could be detected but the patterns did not correspond to bays, coastlines or currents as one might expect. In general, it appears that most individuals probably do roam over a limited range of 50-130 km but that a significant percentage of individuals move over very long distances. Whether these are particular individuals or all individuals at some point in their life time, is unknown. Long-term tagging data are sorely needed in rays and skates if we are to better understand their demographic movements and long-term behavioral patterns. This could also shed light on mating behavior. The technical challenges associated with long-term tagging for thornback rays are formidable but better knowledge of mating sites, courtship, nurseries are really needed to clarify the temporal and dynamic population structure and to formulate a complete picture of population dynamics for thornback rays.

*Does the weak population differentiation have a biological meaning?*

One important question remains: how should we interpret weak population differentiation? Does it have biological meaning? As new classes of markers, more loci and increasingly sophisticated data analytical methods evolve it will be possible to detect weaker and weaker differences. The challenge is to decide at what point the differences matter and at what point we should consider “the population” as one panmictic unit. For thornback rays in British waters, it is probably not wise to define only one panmictic unit and thus one management stock. As discussed by Waples & Gaggiotti (2006), population genetics deals with the evolutionary time scale over several generations, whereas for conservation, scientists are interested in the
ecological time scale of only a few generations. The weak population differentiation found here represents an integration over time of the gene flow between several sampling sites; it may, therefore, be unrepresentative of contemporary gene flow. Moreover, migration rates estimated from genetic data need only to be very small to weaken the genetic differentiation; whereas ecologically meaningful migration may need to be much greater to maintain demographic units. Assignment methods provide an opportunity to assess migration in ecological time frames but require large number of polymorphic loci and large sample size. However, even small deviations from optimal conditions for such analysis, i.e. strong population differentiation, large number of loci and large sample size will significantly decrease the power. In wild and declining populations, optimal conditions for this type of analysis are difficult to achieve as population sizes are usually small, and developing further loci are costly and may only be considered for species of high economical value.

**Fisheries management**

Despite our rudimentary knowledge of the biology and population structure of thornback rays, this should not be used as an excuse to postpone management decisions (Mogensen & Fowler 2005). Protecting nurseries and mating grounds are fundamental for efficient conservation in elasmobranchs (Carrier & Pratt 1998), and the low $N_e$ and $N_e/N$, support the need to protect adults and mating grounds. Juveniles and immature rays must also be protected as their morphology and size makes them vulnerable to virtually all classes of nets. Relatively high abundance of juveniles has been reported in some coastal areas around the UK, suggesting the presence of nurseries. The Thames Estuary is one of these (possibly several nurseries) from where individuals seasonally migrate in and out. The higher level of population differentiation observed among Spring/Summer populations correlates with this seasonal migration, and suggests a certain level of philopatry, related to mating or egg-laying behaviour. Thus, as suggested by Hunter *et al.* (2006), extension of closed areas in Autumn/Winter for thornback rays should be considered, especially if mating occurred in the open sea. The establishment of closed areas for elasmobranchs along the Thames Estuary rim is under discussion (ICES 2005). While this is good news, it is not clear whether rays and skates will significantly benefit. As discussed by Hunter *et al.* (2006), flatfish fisheries take place in the same area that includes nurseries for thornback rays and the economic value of sole and other fisheries is far higher than that of skates. Thus, protected area design with closed areas will be difficult in the Thames Estuary. Moreover, even if one type of design proves to be efficient for thornback rays, there is a strong chance that it will not be for another species. This last remark is one of the main reason for a recent shift from single-species based management to ecosystem based management (Hilborn 2005), from which thornback rays may benefit more. Efforts to establish protected areas at the ecosystem level will be difficult and it is certain that
compromises will have to be found between exploitation of a single species and ecosystem management.

“The reserve design is never fixed - or at least it should never be fixed. It should always be open for amendment and improvement as new information becomes available. New threats to the primary habitat may require larger or more stringently enforced buffer zones. Unexpectedly vigorous population recoveries in target species may lessen the need for interventionist management and monitoring.” Kent Holsinger (Professor at the University of Connecticut, he is particularly interested in using knowledge of evolutionary and ecological principles to help solve a variety of conservation problems).

References


