North Uist - the 'Scottish Galápagos': a hotspot of stickleback biodiversity

Carl Smith

Reader in Natural History, Bell-Pettigrew Museum of Natural History, School of Biology, Bute Building, University of St Andrews, St Andrews KY16 9TS (cs101@st-andrews.ac.uk)

Almost 40 years ago, the fish ecologist and conservationist Niall Campbell published an article in the *Hebridean Naturalist* that reviewed the remarkable morphological diversity of three-spined sticklebacks (*Gasterosteus aculeatus*) in the lochs of North Uist (Campbell 1979). Campbell (1979) ended his article by citing the work of Wootton (1976), who made a case for the three-spined stickleback as a model for understanding key evolutionary questions. Campbell (1979) endorsed this view, further proposing that the Outer Hebrides represented an unparalleled natural laboratory for research on the species.

Both Wootton and Campbell showed remarkable foresight. The stickleback has emerged as one of the most important vertebrate models for research on evolution, ecology and genetics, studied in laboratories throughout Europe, North America and Japan in just the way that Wootton predicted (McKinnon & Rundle 2002; Wootton 2009; Barber & Nettleship 2010). Further, research over recent years has demonstrated the remarkable status of North Uist sticklebacks, which show probably the greatest morphological diversity yet recorded in the species (MacColl *et al.* 2012; Spence *et al.* 2013; Klepaker *et al.* 2016).

Campbell was not the first scientist to investigate the sticklebacks of North Uist. The renowned marine biologist, Prof. William Carmichael M'Intosh, who held the prestigious Chair in Natural History at the University of St Andrews, reported collecting sticklebacks from North Uist in an expedition to the Island in the middle of the 19th Century (M'Intosh 1866). A further comprehensive exploration of North Uist was conducted by Edith Nicol, again from the

University of St Andrews, who catalogued the fauna of a set of lochs on the Island, including recording the presence of sticklebacks (Nicol 1936). Subsequent research by PhD students Nick Giles (Giles 1981) and Susan Coyle (Coyle 2007) from Glasgow University, as well as work by my own research group at the University of St Andrews (Spence *et al.* 2013; Smith *et al.* 2014; Klepaker *et al.* 2016) and researchers from Germany (Hiermes *et al.* 2015), England (MacColl *et al.* 2012) and Norway (Klepaker *et al.* 2013), have shown that North Uist supports an exceptional variety of stickleback body forms, which can shed light on how the process of natural selection operates.

In the UK there are three species of stickleback; three-spined and nine-spined sticklebacks (*Pungitius pungitius*) live in fresh, brackish and seawater, whereas the fifteen-spined stickleback (*Spinachia spinachia*) is confined to seawater. All occur in the Hebrides. Unlike most bony fishes, sticklebacks lack scales and instead possess a row of bony plates along their body which, along with bony dorsal spines and pelvic girdle and pelvic spines, protect them from predators, such as trout and birds. Three morphs have been described on the basis of the number and spatial arrangement of the lateral plates (Figure 1): 1. the *complete* morph has a continuous row of plates from immediately behind the head to the tail stalk; 2. the *partial* morph has an anterior row of plates, then a length of the body that lacks plates, succeeded by a posterior row of plates reaching to the tail; 3. the *low* morph has only an anterior row of plates and the remainder of the body is naked. Within a population there is variation in the exact numbers of plates within each morph, but the three are clearly defined.

While three-spined sticklebacks can live in a wide variety of aquatic habitats, they originate in the sea, and large numbers occur in coastal waters throughout the northern hemisphere. Marine populations of three-spined sticklebacks migrate into freshwater to lay their eggs (like salmon and seatrout) and some remain or are trapped there, evolving over subsequent generations and adapting to their new environment. An outcome is that three-spined sticklebacks show unusually high variation in a variety of features, including size, behaviour, jaw shape and body shape. It is this extraordinary diversity that has attracted the attention of biologists who use sticklebacks to understand ecological and evolutionary processes. In the case of three-spined sticklebacks from North Uist it is extreme variation in the development of the lateral plates, spines and pelvis, including the complete loss of these skeletal structures, that characterises their morphological diversity Other traits also show high levels of variation, with jaw development, body shape and predator avoidance behaviour also differing among North Uist lochs.

While this degree of variation among populations of North Uist three-spined sticklebacks is remarkable, North Uist is not unique. The Queen Charlotte Islands (or Haida Gwaii), off the coast of British Columbia, Canada also support an unusually diverse stickleback fauna, which has been the focus of research by North American scientists (Moodie & Reimchen 1976; Reimchen *et al.* 2013). There are also smaller pockets of morphological diversity in Alaska (Bell 2001) and Iceland (Lucek *et al.* 2012). What is most striking about the North Uist diversification is the degree of variation, the number of populations involved, and the rate of diversification, which have evolved in as little as 15,000 years following the end of the last ice age (Ballantyne 2010). The evolution of this amazing diversity of sticklebacks on North Uist is termed an 'adaptive radiation', with a single marine ancestor giving rise to a multitude of morphological forms (Figure 2). Adaptive radiations are thought to have occurred frequently during the evolution of life on earth and are considered by some evolutionary biologists to be one of the primary mechanisms by which biodiversity is generated. However, adaptive radiations also appear to be ephemeral, rapidly generating new species many of which subsequently become extinct (Schluter 2000). Perhaps one of the best known adaptive radiations is that of Darwin's finches on the Galápagos Islands. Here 30-100 individuals of a single species of seed-eating finch are thought to have arrived on the islands from the South

American mainland approximately 3 million years ago and established a viable population. This ancestral species radiated under contrasting selection pressures on different islands to fill a range of feeding niches, with species evolving to feed on seeds, insects, buds, fruits and cacti, which is manifested by variation in beak size and shape (Grant & Grant 2006). The North Uist three-spined stickleback radiation is considerably younger than the radiation of Darwin's finches, with the different stickleback forms considered separate 'ecotypes' but not discrete species. Different North Uist ecotypes are capable of producing viable offspring, at least in the laboratory, but probably do not do so under natural conditions due to mating barriers, which we are currently attempting to identify. Because it is at an earlier stage of development, the North Uist three-spined stickleback radiation offers an exceptional opportunity to investigate the evolutionary processes that drive the early stages of species formation.

While the adaptive radiation of Darwin's finches is underpinned by selection for feeding, the underlying cause for the radiation of North Uist three-spined sticklebacks is less clear. One hypothesis is that predators play a major role, with variation in brown trout (*Salmo trutta*) abundance among lochs the primary selection pressure; with a greater size and number of plates and spines a reflection of the impact of predators; this is the primary explanation put forward for the comparable radiation of three-spined sticklebacks in the Queen Charlotte Islands (Reimchen 1980). Another hypothesis relates to the availability of dissolved calcium. Giles (1981) noticed that spine and plate-reduced fish were always associated with lochs with low pH water and with extremely low levels of dissolved calcium. Giles (1981) argued that calcium limitation might compromise skeletal growth. Experimental studies in which young sticklebacks were deprived of calcium during development support this idea, showing that skeletal growth is substantially reduced when calcium is limiting (Spence *et al.* 2012). Other hypotheses relate to the effects of competition with nine-spined sticklebacks, which co-occur with three-spined sticklebacks in many lochs (MacColl *et al.* 2012), and also the role of parasites (de Roij 2010), though neither of these ideas are entirely convincing (Spence *et al.* 2013; Smith *et al.* 2014). Thus, the question of what drives the astonishing explosive radiation of three-spined sticklebacks on North Uist remains to be answered, as well as the subject of what underlying genetic mechanisms control this variation (Coyle *et al.* 2008).

While North Uist continues to serve as a natural laboratory for understanding the most fundamental of biological questions of how new species are generated by natural selection, it is also important to recognise the almost unique status of the three-spined stickleback populations on the Island. Three-spined sticklebacks have a circumglobal distribution and are abundant in freshwaters throughout the north temperate zone (Wootton 1976). As a species they are not threatened and receive no special protection in the UK or elsewhere. However, on North Uist their special status should, perhaps, be more fully recognised. There is growing acknowledgment by the scientific community of the value of North Uist sticklebacks for tackling fundamental biological questions. At a recent international meeting of stickleback biologists in Kyoto, Japan it was notable that a number of overseas research groups have been collecting sticklebacks in North Uist or have been acquiring them through a third party. While scientific study of these remarkable animals is to be encouraged, their unrestricted and undocumented collection is a potential threat since some North Uist lochs support populations that are both entirely unique and demographically small and, as such, risk depletion or even extinction through uncontrolled collecting. In these circumstances constraints on their collection need to be considered. It is worth recognising that if scientists wish to travel to the Galápagos Islands to study the radiation of finches there, they face highly restrictive controls, with the removal of birds or biological samples under strict regulation. Greater control of access to the more unique North Uist sites and fuller scrutiny of proposed scientific work on these populations should be considered.

In summary, North Uist supports an almost unique three-spined stickleback assemblage of huge scientific interest that can serve to further our understanding of some of the most profound problems in biology. Numerous questions regarding these populations of fish remain to be answered but it would be the utmost folly if this remarkable resource was damaged in the process of attempting to understanding its origin.

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Figure legends

Figure 1. External anatomy of the three-spined stickleback (*Gasterosteus aculeatus*) illustrating predator defence structures comprising lateral plates, dorsal and pelvic spines, and pelvic girdle in the *complete*, *partial* and *low* lateral plate morphs.

Figure 2. Adaptive radiation of three-spined sticklebacks from North Uist. The central fish is the marine ancestor of the surrounding 'ecomorphs', which show variation in lateral plate number and size, dorsal spine development and pelvic girdle and spines. Fish have been treated with alizarin solution, which stains bone red.