



*Evolutionary Ecology* **18:** 379–384, 2004.  
© 2004 Kluwer Academic Publishers. Printed in the Netherlands.

*Research article*

## **Unusual number of pectoral fin rays in an Icelandic population of threespine stickleback (*Gasterosteus aculeatus*) recently isolated in freshwater**

BJARNI K. KRISTJÁNSSON<sup>1,2,\*</sup>, SKÚLI SKÚLASON<sup>1</sup> and DAVID L. G. NOAKES<sup>2</sup>

<sup>1</sup>Hólar University College, 551, Skagafjörður, Iceland; <sup>2</sup>University of Guelph, Guelph, Ontario, N1G 2W1 Canada (\*author for correspondence, tel.: +354-455-6386; fax: +354-455-6301; e-mail: bjakk@holar.is)

Received 9 March 2004; accepted 27 August 2004

Co-ordinating editor: Kaitala

**Abstract.** Threespine stickleback most often have 10 pectoral fin rays, and it seems to be a highly canalized trait. We observed an unusually high frequency of stickleback with 11 pectoral fin rays in a population recently isolated from the marine environment in a freshwater lagoon in Iceland. These new morphologies may be beneficial for the fish in the new habitat but may disappear because of strong canalizing selection for the typical 10 pectoral fin rays.

**Key words:** divergence, isolation, rapid evolution

### **Introduction**

The threespine stickleback, *Gasterosteus aculeatus*, inhabits marine and freshwater habitats throughout its holarctic distribution (Wootton, 1984). It is believed to have originated in the ocean, but populations have repeatedly been isolated in freshwater (Bell and Foster, 1994). These populations adapt quickly to diverse freshwater environments and thus display a wide array of phenotypes often forming sympatric or parapatric morphs and species (Klepaker, 1993; Bell and Foster, 1994; Ziuganov, 1995; McKinnon and Rundle, 2002). These phenotypes usually differ from the marine ancestors, which appear to be more canalized in their morphology (Bell and Foster, 1994). West-Eberhard (2003) defined canalization as ‘the evolved ability to maintain a single phenotypic norm in the face of deviation-inducing genetic and environmental effects during ontogeny’.

Icelandic marine sticklebacks show some morphological variation, but much less than those in fresh water (Kristjánsson, unpublished; Kristjánsson *et al.*,

2002a; Skúlason *et al.* unpublished results). Icelandic freshwater sticklebacks are diverse, often with sympatric populations adapted to distinct benthic habitats in lakes showing differences in morphology and behaviour (Kristjánsson, unpublished; Kristjánsson *et al.*, 2002b; Doucette, unpublished; Doucette *et al.* 2004).

Threespine sticklebacks can evolve quickly after being isolated in freshwater (Klepaker, 1993; Bell and Foster, 1994; Ziuganov, 1995). This is clearly the case in Iceland, where sticklebacks in a lagoon in Hraunsfjördur show distinct morphological differences from their marine ancestors after being isolated for only 13 years. The fish in freshwater are smaller and have fewer armour plates, shorter spines and a smaller anal fin (Kristjánsson, unpublished; Kristjánsson *et al.*, 2002a). These recently isolated fish also show morphological divergence in relation to mud and lava habitats, indicating resource polymorphism within the new lagoon (Kristjánsson, unpublished; Kristjánsson *et al.*, 2002a).

Although, threespine stickleback are diverse in morphology they show clear canalization in some traits. One of those is the number of rays in the pectoral fins. The number of rays in the pectoral fin ranges from 8 to 11, but 10 rays is the most common (Bowne, 1994; Hermida *et al.*, 2002; Kristjánsson *et al.*, 2002b). This paper reports an unusual meristic phenomenon observed in the sticklebacks at Hraunsfjördur.

### **Material and methods**

Hraunsfjördur in the Snæfellsnes Peninsula in NW-Iceland (Fig. 1) is a narrow fjord about 4 km<sup>2</sup>. In 1987, the fjord was dammed for an Atlantic salmon *Salmo salar* aquaculture operation, forming a freshwater lagoon (1.7 km<sup>2</sup>) that is inaccessible to fish from the sea (Sturlaugsson, 1994; personal communication). Because of porous lava, there is some brackish water in the lagoon close to the dam. Fish movement from the lagoon to the sea is not prevented. Brown trout, *Salmo trutta*, Rainbow trout, *Onchorynchus mykiss*, and Atlantic salmon are released into the lagoon for recreational fishing.

We caught sticklebacks on 9 July 1999 with unbaited minnow traps (Dynamic Aqua-Supply Ltd., mesh size 3.2 mm) as a part of a larger meristic and morphological study (Kristjansson *et al.*, 2002a). The fish were caught at three locations within the fjord: (1) Marine Site, a marine pond, in a lava field connected to the fjord by a narrow channel; (2) Lava Site, over a lava substrate within the freshwater lagoon, at a depth of 1–2 m, about 150 m from the dam; (3) Mud Site, over a mud substrate at the greatest distance from the sea in the freshwater lagoon, at a depth of about 1–1.5 m.

We preserved the fish (5% buffered formalin) and stained them with Alizarin Red in 1% KOH (e.g. Bell, 1981). The number of fin rays in the

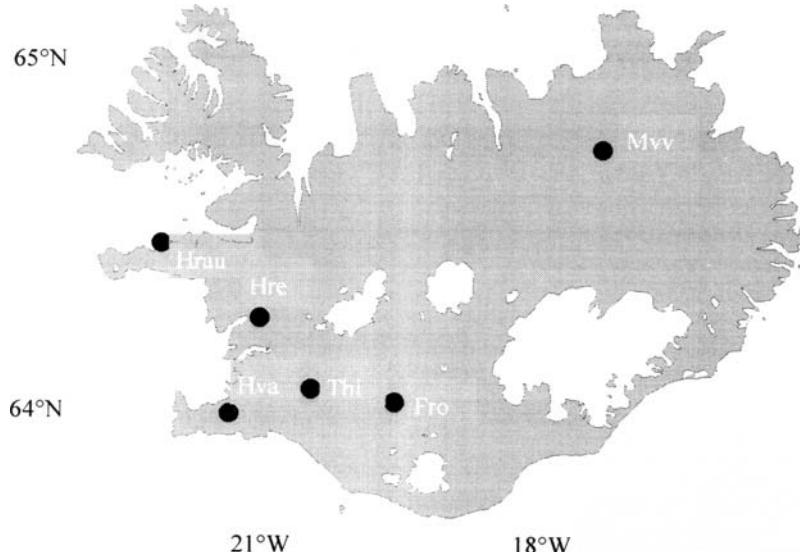


Figure 1. The sampling location Hraunsfjördur (Hrau) and the locations of comparison populations; Hredarvatn (Hre), Thingvallavatn (Thi), Myvatn (Myv), Frostastadarvatn (Fro) and Hvassahraun marine site (Hva).

left pectoral fins was counted on each fish. We counted the number of pectoral fin rays on 168 fish in the marine habitat (22.5–68.7 mm FL), 232 from the mud habitat (24.9–60.0 mm FL) and 150 fish from the lava habitat (27.7–59.9 mm FL). We compared these fish to 321 fish from five other Icelandic populations, four are apparently older freshwater populations while the fifth is marine (Fig. 1).

We compared pectoral fin ray counts of fish from the various locations within Hraunsfjördur using a  $\chi^2$ -test (Sokal and Rohlf, 1981). We compared pooled data from three sites in Hraunsfjördur to each of five other populations using a  $\chi^2$ -test (Table 1). In all cases of multiple comparisons we used sequential Bonferroni corrections to minimise the possibility of type I error (Rice, 1989).

## Results

We examined a total of 550 fish from the three sites in Hraunsfjördur. Of these, 55 had 11 rays in their pectoral fins (10.0%). Of the 150 fish caught within the lava habitat in the lagoon 25 had 11 fin rays (16.7%). The other two habitats had significantly lower proportion of fish with 11 fin rays (marine 6.5%, mud 8.2%, Table 1).

*Table 1.* Number of pectoral fin rays in threespine stickleback, from three areas within Hraunsfjördur, and four freshwater and one marine habitat in Iceland. The proportion of 11 fin rayed fish in the lava habitat was compared with the two other Hraunfjordur habitats ( $\chi^2$ -test). The Hraunsfjördur fish were combined and compared with fish from five other habitats; four freshwater and one marine (Hvassahraun)

Location	Fish examined	11 rays	%	< 10 rays	%	Corrected <i>p</i> value
<i>Hraunsfjördur</i>						
Marine	168	11	6.5	0	0.0	<0.05
Mud	232	19	8.2	1	0.4	<0.05
Lava	150	25	16.7	0	0.0	
Combined	550	55	10.0	1	0.0	
<i>Other sites</i>						
Thingvallavatn	52	2	3.8	1	1.9	NS
Hredarvatn	60	0	0.0	0	0.0	<0.05
Frostastadarvatn	62	2	3.2	2	3.2	NS
Myvatn	105	2	1.9	3	2.9	<0.05
Hvassahraun	42	0	0.0	2	4.8	NS
Combined	321	6	1.9	8	2.5	<0.05

Samples differed between habitats within Hraunsfjordur, and the lava site fish were significantly different from the other two groups. Nevertheless, we combined the Hraunsfjordur fish for comparison to other populations (Table 1, Kristjánsson, unpublished; Kristjánsson *et al.*; unpublished result). The Hraunsfjördur fish did differ from almost all the other populations, among which the highest proportion of specimens with 11 pectoral fin rays was 3.8% in Thingvallavatn (Table 1).

## Discussion

The fish in Hraunsfjördur had an unusually high number of pectoral fin rays compared to other Icelandic freshwater and marine populations. This was true especially for the fish living in the lava area nearest to the sea.

Threespine stickleback, usually have ten pectoral fin rays, although the range from 8 to 11 rays has been reported (Bowne, 1994; Kristjansson *et al.*, 2002b). Coefficient of variation for pectoral fin ray number has been reported as 2.5% for *Gasterosteus aculeatus* (Hermida *et al.*, 2002); in general, variation in pectoral fin rays in fishes is low. It is likely that the unusual variation we observed is related to the recent isolation of the stickleback in freshwater in Hraunsfjördur. A similar phenomenon was seen in a Norwegian population recently isolated in freshwater, where many individuals had four dorsal spines. Over time the proportion of four-spined individuals decreased (Klepaker, 1993). This higher variation of otherwise canalized characters in recently isolated freshwater populations may indicate differences in the development of

fish in freshwater and seawater. The freshwater fish are experiencing a completely different physiological environment for the developing embryos than they have evolved to cope with in the sea. This changed environment may lead to new morphological variation because of phenotypic plasticity and/or genetic changes caused by a founder effect and genetic drift.

This new morphological variation can in some cases be a key to the divergence evolution of these fish in the new freshwater environment. However, these different morphologies often disappear from the population, as discussed for the Norwegian population (Klepaker, 1993). Similar observations were seen after the formation of the Salton sea in California, USA. After introduction to the Sea a high proportion of morphological abnormalities were seen in populations of Bairdiella (*Bairdiella icistius*) and Corvina (*Cynoscion xanthulus*), as densities grew in the lakes the number of abnormalities disappeared (Whitney, 1961a, b).

It is therefore possible that the new morphotype in Hraunsfjördur may be at a disadvantage as the population grows and intraspecific competition becomes more intense. They may thus be selected against and will eventually disappear from the population as in both the Norwegian example and the fish in the Salton Sea. Whereas, other morphotypes may be at an advantage and will, therefore, survive. These changes might also be caused by changes in the plastic response of the fish, and we feel this subject requires further study. It is therefore important to monitor this phenomenon in the Hraunsfjördur population, and other populations, over time.

### Acknowledgements

We thank G.Á. Ólafsdóttir and L. Doucette for their valuable help with field sampling. We want to thank Andrea Bergmann Halldórsdóttir for counting pectoral fin rays, and M. Bell, J. Sturlaugsson, B.R. Hansen, T. Tunney, H. Thorarensen, B. Jónsson and two anonymous referee for useful comments and discussion. The aquaculture company Hvurslax e.hf. gave permission for the sampling. The Icelandic Research Council and NSERC Canada generously funded this study. The animal care committee at Hólar College approved all sampling.

### References

- Bell, M.A. (1981) Lateral plate polymorphism and ontogeny of the complete plate morph of threespine stickleback (*Gasterosteus aculeatus*). *Evolution* **35**, 67–74.
- Bell, M.A. and Foster, S.A. eds. (1994) *The Evolutionary Biology of the Threespine Stickleback*. Oxford University Press.

- Bowne, P.S. (1994) Systematics and morphology of the Gasterosteiformes. In M.A. Bell and S.A. Foster (ed.) *The Evolutionary Biology of the Threespine Stickleback*. Oxford University Press, pp. 28–60.
- Doucette, L.I., Skúlason, S. and Snorrason, S. (2004). Risk of predation as a promoting factor of species divergence in threespine sticklebacks (*Gasterosteus aculeatus* L.). *Biol. J. Linn. Soc.* **82**, 189–203.
- Hermida, M., Fernández, C., Amaro, R. and San Miguel, E. (2002) Heritability and “evolvability” of meristic characters in a natural population of *Gasterosteus aculeatus*. *Can. J. Zool.* **80**, 532–541.
- Klepaker, T. (1993) Morphological changes in a marine population of threespine stickleback, *Gasterosteus aculeatus*, recently isolated in fresh water. *Can. J. Zool.* **71**, 1251–1258.
- Kristjánsson, B.K., Skúlason, S. and Noakes, D.L.G. (2002a) Rapid divergence in a recently isolated population of threespine stickleback (*Gasterosteus aculeatus* L.). *Evol. Ecol. Res.* **4**, 659–672.
- Kristjánsson, B.K., Skúlason, S. and Noakes, D.L.G. (2002b) Morphological segregation of Icelandic threespine stickleback (*Gasterosteus aculeatus* L.). *Biol. J. Linn. Soc.* **76**, 247–257.
- McKinnon, J.S. and Rundle, H.D. (2002) Speciation in nature: the threespine stickleback model system. *Tree* **17**, 480–488.
- Rice, W.R. (1989) Analyzing tables of statistical tests. *Evolution* **43**, 223–225.
- Sokal, R.R. and Rohlf, F.J. (1981) *Biometry, second edition*. W.H. Freeman and company, New York.
- Sturlaugsson, J. (1994) The food of ranched Atlantic salmon postsmolts (*Salmo salar* L.) in coastal waters, W-Iceland. *Nord. J. Fresh. Res.* **69**, 43–57.
- West-Eberhard, M.J. (2003) *Developmental Plasticity and Evolution*. Oxford University Press.
- Whitney, R.R. (1961a) The bairdiella, *Bairdiella icistius* (Jordan and Gilbert). In B.W. Walker (ed.) *The Ecology of the Salton Sea, California, in Relation to the Sportfishery*, State of California Dept. Fish and Game, Fish Bull. 113.
- Whitney, R.R. (1961b) The orangemouth corvina, *Cynoscion xanthulus* (Jordan and Gilbert). In B.W. Walker (ed.) *The Ecology of the Salton Sea, California, in Relation to the Sportfishery*, State of California Dept. Fish and Game, Fish Bull. 113.
- Wootton, R.J. (1984) *Functional Biology of Stickleback*, Croom Helm.
- Ziuganov, V.V. (1995) Reproductive isolation among lateral plate phenotypes (low, partial, complete) of the threespine stickleback, *Gasterosteus aculeatus*, from the White Sea basin and the Kamchatka peninsula, Russia. *Behaviour* **132**, 15–16.