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# Connectivity in the early life history of sandeel inferred from otolith microchemistry

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ABSTRACT

Connectivity is a central issue in the development, sustainability and effectiveness of networks of Marine Protected Areas (MPAs). In populations with site attached adults, connectivity is limited to dispersal in the pelagic larval stage. While biophysical models have been widely used to infer early dispersal, empirical evidence through sources such as otolith microchemistry can provide a means of evaluating model predictions. In the present study, connectivity in the lesser sandeel, *Ammodytes marinus*, was investigated using LA-ICP-MS otolith microchemistry. Otoliths from juveniles (age 0) were examined from four Scottish spawning areas predicted to differ in terms of larval retention rates and connectivity based on past biophysical models. There were significant spatial differences in otolith post-settled juvenile chemistry among locations at a scale of 100–400 km. Differences in near core chemistry pointed to three chemically distinct natal sources, as identified by a cluster analysis, contributing to settlement locations.

## 1. Introduction

Connectivity, the exchange of larvae, juveniles or adults across a species' range (Palumbi, 2003) is important to population dynamics, as it mitigates against local mortality events affecting population resilience and persistence (Hastings and Botsford, 2006; Prince and Hilborn, 1998). The extent of connectivity is a central issue in the development, sustainability and effectiveness of networks of Marine Protected Areas (MPAs) (Almany et al., 2009; Christie et al., 2010; Sale and Kritzer, 2008; Shanks et al., 2003) as, if a population within a network is to be viable, it needs to be self-persistent, either supplied by self-recruited or locally retained individuals (Burgess et al., 2014). Simulations of MPA network design indicate that where there is 'source-sink' dynamics (areas of net export and import respectively; Pulliam, 1988) it is arguably more beneficial to protect propagule sources (Roberts, 1997), which in turn should have a positive impact on the wider population and fishery yield (Gaines et al., 2010). MPAs are expected to benefit fish species that show a high level of site fidelity, in particular those that are highly substrate-associated, as protection will reduce fishing mortality (Polunin, 2002). However, finding appropriate ways to assess population connectivity remains a challenge, particularly in such site-attached species where dispersal is mostly dependent on an elusive planktonic early life stage, but needs to be addressed prior to implementing spatial management measures such as MPAs (Sale et al., 2005).

Otolith microchemistry provides a powerful tool for examining life stage dispersal and connectivity in regions where significant spatial differences can be detected (Campana et al., 2000; Gillanders and Kingsford, 1996; Thorrold et al., 2001; Vasconcelos et al., 2007). Trace metals from the local environment are permanently incorporated into the crystalline matrix of the otolith as they accrete continuously, are metabolically inert and increments are unlikely to be subject to resorption (Powles et al., 2006; Wright, 1990). Although otolith microchemistry can reflect a combination of local environmental chemistry and individual physiology, the resulting elemental composition can create a unique chronological 'signature' that can be used as a natural tag (Campana and Thorrold, 2001; Elsdon et al., 2008) to distinguish location and infer ontogenic change. Otolith microchemistry has previously been used to discriminate between capture location and detect the habitat shift from pelagic to bentho-pelagic behaviour in the sandeel *Ammodytes tobianus* (Laugier et al., 2015). Microchemistry has also been used to infer differences in natal origin from analyses of the chemical composition close to the otolith core i.e. the portion formed during embryogenesis (Di Franco et al., 2012).

Past studies of natal microchemistry have followed two types of statistical approach. The first is a supervised learning approach which relies on establishing a baseline sample of pre-dispersal life stages of known origin, ideally sampled in all spawning or nursery areas, in order to assign post dispersal individuals of unknown origin to sources characterised in the baseline sample based on their elemental

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signatures (e.g. Gillanders, 2002; Wright et al., 2010). The second type follows an unsupervised learning method, where clustering of the near core region of the otolith provides information on the number of contributing larval sources and their distinct elemental signatures (e.g. Di Franco et al., 2012). While the first method has the potential to assign settled fish to known spawning area, conducting a fully representative large-scale sampling of marine larvae from all potential source areas to compose the baseline is expensive and likely to be incomplete, therefore the utility of this approach, though sound, is limited (Campana et al., 2000; Munch and Clarke, 2008; White et al., 2008). Clustering does not allow assignment of fish to spatially defined larval sources, however, identifying the contribution of larval sources to distinct settlement locations provides useful information on the spatial scale over which larval dispersal takes place (Di Franco et al., 2012). Therefore, the second approach was adopted in this study as it can find the most homogenous groups within the individuals of unknown origin, identifying contributing sources by assigning them to distinct clusters.

The present study uses otolith microchemistry to examine connectivity in the lesser sandeel, *Ammodytes marinus* (Raitt) a species where dispersal is limited to early life history stages (Wright, 1996). Sandeels are small, elongate planktivorous fish which form an important prey source for numerous fish, seabirds and marine mammals (Daan, 1989; Santos and Pierce, 2003; Wanless et al., 1998) and also support the largest industrial fishery in the North Sea. Due to their importance to the food web they are one of the key species considered in the Scottish MPA network (The Scottish Government, 2015). *A. marinus* spawn eggs into sand between December and January (Gauld and Hutcheon, 1990; Winslade, 1971) and the larvae hatch between February and May (Langham, 1971; Macer, 1966; Wright and Bailey, 1996). The duration of this pelagic stage lasts between 32 and 90 days (Jensen, 2001; Wright and Bailey, 1996; Wright, 1993) and later stages begin schooling before settlement in late May to June (Wright and Bailey, 1996; Wright et al., 2000). As they need to bury in sandy areas with a low silt content (Holland et al., 2005; Wright et al., 2000), the distribution of settled juvenile *A. marinus* is patchy (Jensen et al., 2011; Macer, 1965). Following settlement, sandeels are rarely found further than 15 km away from known habitat (Engelhard et al., 2008; van der Kooij et al., 2008; Wright, 1996) and the maximum distance travelled by tagged individuals displaced from grounds was only 64 km over 1–3 years (Gauld, 1990).

Biophysical models that couple particle tracking and sea circulation models provide another approach to infer early dispersal in marine organisms with a planktonic phase (Cowen et al., 2006; Gallego et al., 2007; Miller, 2007; Nolasco et al., 2013). Several biophysical models of sandeel larval transport have been produced, differing in horizontal and vertical resolution of the underlying hydrodynamic models and the accuracy of biological parameters for particle tracking (Berntsen et al., 1994; Christensen et al., 2008; Gallego et al., 2004; Proctor et al., 1998). While such models lack the finer resolution and more realistic larval behaviour traits present in newer generation models (Petrik et al., 2015), the 2D, 35 km resolution sea circulation model used by Proctor et al. (1998) was based on reported hatch locations, times and pelagic larval duration and even this simple model appeared to explain the distribution of juvenile aggregations just prior to settlement. Moreover, results from a finer scale 3D bio-physical model that used North Sea sandeel fishing grounds to infer hatch locations (Christensen et al., 2008) produced comparable results, and both studies suggested an average larval transport among aggregations of <100 km apart, with similar levels of regional retention.

In this study we inferred natal sources and area-specific patterns of dispersal in settled juvenile sandeels using laser ablation-inductively coupled plasma-mass spectrometry (LA-ICP-MS) to quantify otolith trace elemental composition. Four areas around Scotland were selected as biophysical models suggest that they represent locations which exhibit different larval dynamics, namely acting primarily as sources (the North Minch and Orkney; Proctor et al., 1998), a sink (Shetland; see Wright, 1996) or as retentive coastal zone (the Firth of Forth; Proctor et al., 1998; Christensen et al., 2008). Specifically we investigated: (1) the scale of geographical variation among capture locations from an analysis of the elemental signature at the settled region of the juvenile otolith, (2) the number of possible chemically distinct natal sources settling to grounds in Scottish waters by cluster analysis of near-core chemistry and, (3) the degree of overlap between larval and settled juvenile populations by characterisation of the cluster elemental composition. The resolved scale of connectivity was discussed in context of spatial management measures.

## 2. Materials and methods

### 2.1. Juvenile sample collection

Juvenile sandeel (*Ammodytes marinus*) <10 cm in length from the 2014 year class were collected from areas of known larval abundance around the coast of Scotland (the North Minch, $N = 23$; East of Orkney, $N = 27$; Shetland, $N = 30$; Fig. 1) between 15 July and 14 August by dredge survey. Sampling platforms included Marine Scotland Science (MSS) research and charter surveys, conducted by the *MRV Alba na Mara* and *FV Sunbeam FR487* respectively. Samples were supplemented by a further collection of fish from the Firth of Forth (Bell Rock, $N = 28$) in early December during MSS's winter sandeel dredge survey (Fig. 1). Sandeel were measured at sea to the nearest 0.5 cm length class before being frozen for analysis back at the laboratory.

### 2.2. Study area

Sample locations are sited within or close to areas currently subject to spatial management measures. In July 2014, the Scottish Government designated a network of 30 Nature Conservation Marine Protected Areas (ncMPAs), of which 3 were for sandeels: southern Shetland, north-west Orkney and Turbot Bank off the east coast (The Scottish Government, 2015; Fig. 1). The Firth of Forth site is currently protected by the north east UK sandeel fishery closure. Potential connectivity routes between the areas are determined by both ocean circulation and local hydrographic conditions. Circulation in our study area is predominantly unidirectional, where Atlantic waters flow from the west coast, mixing with more coastal waters before entering the North Sea to the east of Shetland and through the Orkney-Shetland region via the Fair Isle current (Fig. 1; also see Turrell et al., 1990, 1996), where they continue eastwards into the central north sea as the Dooley current (Dooley, 1974). This Atlantic inflow is governed by seasonal variation in westerly wind regimes (Furnes, 1980; Winther and Johannessen, 2006) with maximum inflow occurring in the winter months. The ocean circulation to the west of Orkney is known to connect to the narrow shelf area to the west of the Shetland Islands (Hill et al., 2008). The Scottish coastal current (SCC) carries water northward from the Minches, flowing along the northern reaches of Scotland and into the North Sea (Simpson and Hill, 1986).

### 2.3. Otolith preparation

All equipment was washed in 10% nitric acid solution prior to use. Sandeels were re-measured for total length (±0.1 cm), total weight (±0.01 g) and both sagittal otoliths removed under laminar flow conditions with fine-tipped ceramic forceps. Otoliths were decontaminated by sonication in Elga ultra-pure (>18 MΩ·cm) water and preserved dry in plastic trays. After confirming 0-group status by macrostructural analysis of age, one sagitta from each pair was mounted on the sagittal plane with a droplet of Araldite CY212 resin (Agar Scientific, UK) onto a coverslip attached to a glass slide, as detailed in Donohoe and Zimmerman (2010). Thin sections were prepared by polishing the otoliths to just above the primordium, using a lapping machine fitted with 0.5–9.0 μm Ultraprep™ diamond lapping film discs (Buehler, UK). After