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Assessing the use of different marine growth zones of adult Atlantic salmon scales for studying marine trophic ecology with stable isotope analysis

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ABSTRACT

The use of fish scales in stable isotope ecology studies is becoming increasingly prevalent, especially for rare species where non-lethal sampling methods are preferable. In studies of Atlantic salmon (*Salmo salar* L.) ecology, scale samples have been used to assess trophic interactions and migrations. The use of scales is complicated by their architecture and growth, with later overplating layers covering the lower older layers and biasing their isotope values. Despite the increase in scale use, there is no consensus as to what part of the scale should be used for stable isotope studies. Here, the stable isotope values for the marine growth zone of scales and its constituent growth zones (1st summer, 1st winter, 2nd summer) from non-maturing 1SW Atlantic salmon are investigated. Significant differences were found between the different sections of the marine growth zone, which, although small, were comparable to differences interpreted as biologically significant by other stable isotope studies. A mathematical model assuming isometric growth was used to correct for the biasing effect of later overplating. The method facilitates calculation of the "pure" stable isotope values for the different marine growth zones, and a "pure" value for the whole marine growth zone. Appropriate accounting for the differences between measured and "pure" values will assist in minimising the ecological inferential errors associated with the use of stable isotope analysis. Given the similarity between the measured and "pure" whole marine growth zone values, the measured whole marine growth zone can be used as a proxy for average marine feeding, while the commonly used 2nd summer growth zone was found not to be representative of earlier marine feeding.

1. Introduction

Stable isotope analysis (SIA) has become an important and commonly used tool for assessing fish diets alongside traditional methods of feeding assessment, such as gut content analysis (GCA) (Cabana and Rasmussen, 1994; Fry, 2006; Wolf et al., 2009). Stable isotopes of carbon and nitrogen provide a long-term integrated view of a fish's trophic ecology, compared with the "snapshot" of recently consumed food items provided by GCA (McCarthy et al., 2004). For salmonids stable isotopes have been used to: examine the nutritional status of migrating Atlantic salmon (*Salmo salar* L.) (Doucett et al., 1999), differentiate between wild and farmed Atlantic salmon (Dempson and Power, 2004), distinguish resident from anadromous brown trout (*Salmo trutta* L.) (McCarthy and Waldron, 2000), and assess fish migration in oceanic feeding areas (MacKenzie et al., 2011).

Commonly used tissues for fish SIA include dorsal muscle and liver (Pinnegar and Polunin, 1999; Dempson et al., 2010), which involve lethal sampling. Given that death of the fish is an undesirable sampling outcome, focus has shifted towards the use of tissues which can be collected non-lethally, e.g. fin clips and scales (McCarthy and Waldron, 2000; Dempson and Power, 2004; Kelly et al., 2006; Hammond and Savage, 2009; Sanderson et al., 2009; Fincel et al., 2012). Scales have the additional benefit of being easy to store and archive (Johnson and Schindler, 2012), and scales from commercially exploited fish are widely available in archived collections which may go back decades, due to their usefulness in assessing fish age, growth, and population structure (Wainright et al., 1993; Perga and Gerdeaux, 2003; Trueman and Moore, 2007). More recently archived scale collections have been used in genetic studies (e.g. Miller and Kapuscinski, 1997; Vähä et al., 2008) and their ready availability makes them useful in retrospective

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temporal studies of trophic ecology (e.g. Wainright et al., 1993; Perga and Gerdeaux, 2003; Pruell et al., 2003).

For SIA studies of Atlantic salmon ecology scales have been used to examine aspects of their life history such as diet and migration (MacKenzie et al., 2011; Dixon et al., 2012; Vuori et al., 2012), including a long term analysis of spatial and temporal variability in marine feeding (Sinnatamby et al., 2009). However, there are differences among studies in the protocols used for sampling scale sections for use in SIA that are linked with scale architecture and growth.

Scale growth begins with the formation of the overlying hard, well-mineralised external osseous layer (EL), followed by the growth of the poorly-mineralised fibrillary plate (FP), which consists mainly of collagen arranged in a “plywood-like structure” (Zylberberg and Nicolas, 1982; Sire and Géraudie, 1983; Trueman and Moore, 2007). The two layers are differentiated by a number of histochemical and histological features, with different processes of mineralisation taking place in each (Maekawa and Yamada, 1970; Zylberberg and Nicolas, 1982; Meunier, 1984). Scales grow in three dimensions with the EL growing outwards from the focus. Underneath the FP grows by the successive accumulation of collagen layers, with mineralisation of the FP occurring subsequent to that of the EL (Zylberberg and Nicolas, 1982; Ikoma et al., 2003). The scale, therefore, increases in thickness posteriorly towards the focus, as the older parts of the scale are overlaid with newer collagen lamellae (Hutchinson and Trueman, 2006). The overlaying of older collagen by younger collagen may affect the stable isotope signature, biasing the stable isotope (SI) values of the older scale material towards the SI values of the newly formed scale material such that vertical slices of the scale no longer purely reflect the diet the fish was consuming when the original scale material was formed (Hutchinson and Trueman, 2006; Sinnatamby et al., 2008).

Owing to the three dimensional nature of scale growth, some researchers use only the last growth period portion of the scale as the section contains no material from previous seasons (e.g. Hutchinson and Trueman, 2006; Trueman and Moore, 2007; MacKenzie et al., 2011; Vuori et al., 2012). Other researchers use multiple scale growth zones as an indicator of average feeding status over a defined period of time, i.e. marine residency (e.g. Perga and Gerdeaux, 2003, 2004; Gerdeaux and Perga, 2006; Sinnatamby et al., 2008, 2009; Dixon et al., 2012) (Table 1). There is currently no consensus as to what portion of the scale should be used when performing SIA to study the trophic ecology of fishes. While some authors provide a rationale for their choice, such as to remove the influence of material laid down during an earlier life-stage when diet is known to be different (e.g. Rennie et al., 2009), others do not.

In adult anadromous Atlantic salmon, scales reflect both freshwater and marine growth, with the latter clearly able to partition winter versus summer phases, allowing for accurate aging of the fish and the ability to choose what sections of the scale to use in SIA (e.g. Friedland and Reddin, 2000; Hutchinson and Trueman, 2006). Salmon growth is reduced in winter months, as demonstrated by narrower and fewer circuli in the scale structure, with circuli laid down at a rate of approximately one per week in spring and summer, and approximately one per two weeks in winter (Friedland et al., 2005). In 1SW (one-sea-winter) fish there are three portions of the marine growth zone: the 1st summer following migration to the sea, the 1st winter; and the 2nd summer. Hence, a sampling strategy using only the last growth period (the 2nd summer for 1SW fish) disregards the portion of the marine growth zone of the scale that includes the first season of sea growth (i.e. the post-smolt stage or the 1st summer), and the first winter. This sampling strategy also limits the ecological inferences that can be made about feeding and location to the most recent growth period as a result of the disconnect between the portion of the life-history for which trophic information is obtained and the other portions of the life-history. Crucially, such a sampling strategy limits the ability to understand the ecology of Atlantic salmon during the initial part of the 1st summer where the largest amount of marine growth occurs (Power,

Table 1
Summary of various research investigations using stable isotopes extracted from fish scales and the comparative sections of the scales used in the analyses. Studies that used scale decalcification are denoted with an asterisk (*). 1SW, 2SW and MSW, respectively, indicate fish that have spent one, two or multiple winters at sea. † denotes studies where the use of whole scales was presumed, although not specifically stated.

References	Species	Life-stage	Section of scale used	Study theme
Hutchinson and Trueman (2006)	*Salmo salar*	1SW, 2SW	Freshwater, last summer at sea portions	Tissue comparisons
Johnson and Schindler (2012)	*Oncorhynchus nerka*	2SW	Whole scale	Trophic ecology
Perga and Gerdeaux (2003)*	*Coregonus lavaretus*	Mature adults	Whole scale	Trophic ecology, tissue comparisons
Pruell et al. (2003)	*Morone saxatilis*	3–5 year olds	Whole scale†	Trophic ecology, tissue comparisons
Wainright et al. (1993)	Multiple species (7)	~2 year olds	Whole scale†	Trophic ecology
Sinnatamby et al. (2008)	*Salmo salar*	All life-stages	Whole for smolt, marine portion for others	Tissue comparisons
MacKenzie et al. (2011)	*Salmo salar*	1SW MSW	Last growth zone for 1SW, penultimate growth zone for MSW	Marine feeding location assignment
MacKenzie et al. (2012)	*Salmo salar*	1SW, 2SW	Last growth zone for 1SW, Penultimate growth zone for 2SW	Marine feeding location assignment, trophic ecology
Sinnatamby et al. (2009)	*Salmo salar*	1SW	Marine portion	Trophic ecology
Galster et al. (2012)*	*Sander vitreus, Micropterus dolomieu*	Adults	Whole scale†	Food web structure
Vuori et al. (2012)	*Salmo salar*	Adults	Last growth zone	Trophic ecology
Fincel et al. (2012)	*Sander vitreus*	Adults	Whole scale†	Tissue comparisons
Hammond and Savage (2009)	*Notolabrus celidotus*	Adults	Specific to experiment	Trophic ecology
Quinn et al. (2012)	*Oncorhynchus mykiss*	1st time Adult spawners	Whole scale	Trophic differences
Kennedy et al. (2005)	*Salmo salar*	Age—0 juveniles	Whole scale†	Natal origin
Ramsay et al. (2012)	*Salmo trutta*	Juvenile, Adults	Whole scale†	Natal origin
Grey et al. (2009)*	*Rutilus rutilus*	Age 1+	Whole scale†	Trophic ecology
Syväranta et al. (2008)*	*Rutilus rutilus* *Perca fluviatilis*	Various ages	Last growth zone	Inter- tissue comparison
Gerdeaux and Perga (2006)*	*Coregonus lavaretus*	Ages 4, 5 (mature)	Whole scale	Trophic ecology
Perga and Gerdeaux (2004)*	*Coregonus lavaretus*	Adults	Whole scale	Trophic ecology
Rennie et al. (2009)*	*Coregonus clupeaformis*	Adults	3 mm core area removed	Trophic ecology