Aquaculture 362–363 (2012) 264–272

Contents lists available at ScienceDirect

Aquaculture

journal homepage: www.elsevier.com/locate/aqua-online

Is salmon smoltification an example of vertebrate metamorphosis? Lessons learnt from work on flatfish larval development

Björn Thrandur Björnsson [a,*], Ingibjörg Eir Einarsdottir [a], Deborah Power [b]

[a] Fish Endocrinology Laboratory, Department of Zoology/Zoophysiology, University of Gothenburg, Box 463, SE40530 Gothenburg, Sweden
[b] Centro de Ciências do Mar and Faculdade de Engenharia de Recursos Naturais, Universidade do Algarve, Campus de Gambelas, P8005-139 Faro, Portugal

ARTICLE INFO

Article history:
Received 23 October 2009
Received in revised form 24 February 2011
Accepted 3 March 2011
Available online 9 March 2011

Keywords:
Metamorphosis
Smoltification
Parr–smolt transformation
Development
Flatfish
Salmonids

ABSTRACT

The terms metamorphosis and smoltification both describe developmental processes. However, the question on what specific criteria define these terms continues to engage scientists. At the same time, various views have been expressed on whether or not smoltification of anadromous salmonids should be regarded as an example of vertebrate metamorphosis. This short overview tries to summarize some of these discussions and starts by determining if smoltification meets any of the criteria used to define metamorphosis. In particular, it broadly compares the process of flatfish metamorphosis with that of salmonid smoltification from a morphological, endocrine, molecular and behavioral perspective. Tools and approaches developed and used in metamorphosis research which could be useful in continued work on smoltification are highlighted.

1. Introduction

The title of a recent overview paper asks the question "What is metamorphosis?" (Bishop et al., 2006). This echoes a similar fundamental question frequently raised in discussions at the International Workshops on Salmon Smoltification and similar forums—"What is salmon smoltification?" While the questions are seemingly straightforward—we all "know" what we mean when we use these terms, their simple definitions slip away when we start to consider borderline examples. Do roundfish species undergo metamorphosis? Do *Salvelinus* species smoltify? The purpose of this short review is to examine the related and intriguing question if salmon smoltification is an example of vertebrate metamorphosis? A more descriptive synonym for smoltification is parr–smolt transformation, and linguistically, the words *metamorphosis* and *transformation* are close synonyms. The question is therefore, in the case of smoltification, if they are biologically synonymous.

Such exercise is not just about terminology and semantics. Instead it highlights the issue of whether (and what) molecular, physiological, morphological, behavioral and ecological research and understanding of salmon smoltification as a developmental process can gain from insights and comparisons with metamorphic processes in other fish species such as lamprey, eel and flatfishes. Defining the terms metamorphosis and smoltification are ongoing discussion topics. However, from a physiological perspective, the most important question is if researchers working in the different fields can gain information and/or research approaches from each other.

2. Discussion

2.1. What is metamorphosis?

Metamorphosis is a widely used term in various fields of biology, but there is no clear consensus on its definition (see Bishop et al., 2006). Its literal translation from the Greek *metamorphoum* is "changing form" or "transform", with *meta* meaning change and *morphe* meaning form. Thus, in its broadest sense, the term metamorphosis describes biological "transformation" and is synonymous with morphogenesis. It can thus be argued that it can be used broadly to describe a life stage transition between a vegetative and sexually reproductive stage of any multicellular fungi, plant or animal (Bishop et al., 2006).

The term metamorphosis is, however, most commonly used to refer to major developmental changes in holometabolous insects, marine crustaceans, amphibians, and certain fish species, most notably flatfish, eels, and lampreys (Youson, 1988). In line with the literal translation, a distinguishing feature of the developmental changes in these groups is the degree of morphological change, with larval and juvenile forms so distinct that they've often been thought to be different species, such as the case with the *Leptocephalus* larvae of the eel. In the context of salmon smoltification, anecdotally it can be noted that a similar confusion existed in early biology regarding different

* Corresponding author. Tel.: +46 31 7863691; fax: +46 31 7863807.
E-mail addresses: thrandur.bjornsson@zool.gu.se (B.T. Björnsson), ingibjorg.einarsdottir@zool.gu.se (I.E. Einarsdottir), dpower@ualg.pt (D. Power).

0044-8486/$ – see front matter © 2011 Elsevier B.V. All rights reserved.
doi:10.1016/j.aquaculture.2011.03.002

salmon life stages with William Yarrel (1836) concluding in his book "*A History of British Fishes vol. 2*" that the Atlantic salmon parr was a separate species, given the Latin name *Salmo salmulus*, and "not the young of the salmon".

Being polyphyletic, metamorphosis is not homologous among all animals. For example, in insects and mollusks, although some common transcriptional/translational events underlie metamorphosis, they are not homologous processes. As pointed out by Michael Hadfield (in Bishop et al., 2006), this lack of homology really rules out an absolute definition of the term metamorphosis. Instead, it is most important that authors using the word clearly define metamorphosis in the context of their writing.

Among the fourteen authors expressing their views in the recent overview paper "What is metamorphosis?" (Bishop et al., 2006), there's a broad consensus that the concept of metamorphosis includes (i) a habitat shift, (ii) a major morphological change, (iii) a change in adaptive landscape, and (iv) that the pre-metamorphic stage is post-embryonic. Majority also defines metamorphosis to include (v) a change in feeding mode, and (vi) usually being a pre-reproductive to reproductive stage transition. Metamorphosis is thus a change in form and function allowing the organism to transit between life-stages in order to exploit a new habitat in an optimal way. Thus, e.g. flatfish metamorphosis, with its dramatic changes in form and function (see Power et al., 2008a,b), enables the fish to transit from the pelagic to the benthic niche, profoundly changing their foraging behavior.

Without going into details at this point, salmon smoltification clearly fits the four major definition points for metamorphosis (i–iv), as well as the fifth (v). During smoltification, major morphological changes take place, both in body shape and coloration, preadapting the fish to a completely different environment, in which the fish gains competitive advantage through a new mode of foraging. It can be said that the change takes the smoltified salmon in an opposite direction of metamorphosing flatfish, from the adaptive landscape of a relatively stationary benthic existence to a free-swimming, actively predatory pelagic life.

Although discussions on metamorphosis often largely ignore the aspect of changed physiology (see Youson, 1988; Bishop et al., 2006) it is clear that changes in body shape, remodeling of organs and tissues, environmental conditions and behavior cannot take place without parallel changes in physiology of the organism, if the shift to a new adaptive landscape is to be successful. Recently, however, Paris and Laudet (2008) have taken a physiological view when suggesting that chordate metamorphosis should be defined based on the endocrine control of the morphological change. Thus, they define metamorphosis as a "postembryonic developmental stage characterized by a thyroactive compound-dependent morphological remodeling". Using this definition, they subsequently conclude that sexual maturation cannot be defined as metamorphosis as this life-stage transition is not driven by thyroid hormones (THs).

2.2. What is smoltification?

The life history of the anadromous salmonid is quite complex. Even at the larval–juvenile stages in fresh water, the fish undergo series of rather subtle physiological, morphological and behavioral changes, accompanied with shifts in habitat within the freshwater stream. For e.g. the Atlantic salmon (Fig. 1), after hatching of the egg in spring, the yolk-sack alevin stay in the gravel of the redd, showing negative photokinesis, positive geotaxis and positive rheotaxis, avoiding predators while absorbing the yolk sack. By the time the endogenous nutrition is exhausted, the alevin has turned into a fry, with cryptic (spotted) coloration. These move out of the gravel by positive photokinesis and negative geotaxis, but keep contact with the river bottom by thigmotaxis. Continued positive rheotaxis makes them face the current, allowing them to start feeding on drifting food particles. As the fry grow, between 8 and 11 regularly spaced oval-shaped marks appear on their

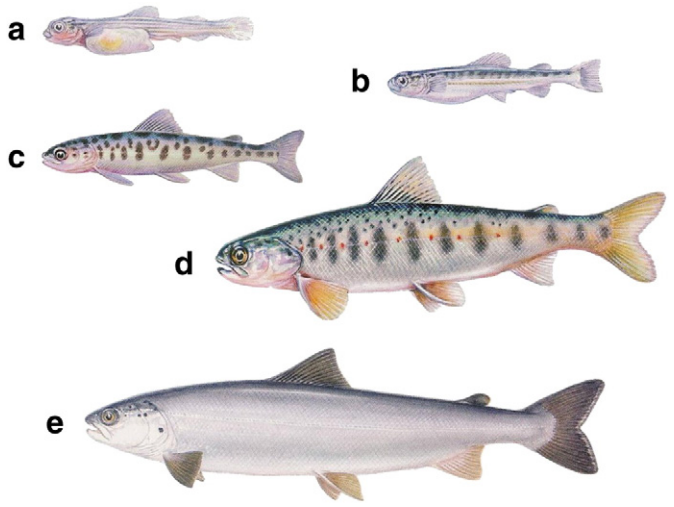

Fig. 1. Juvenile development of Atlantic salmon. (a) Alevin with yolk sack almost absorbed. (b) Fry. (c) Fingerling. (d) Parr. (e) Smolt. The paintings by Rodrick Sutterby, published in the book Atlantic Salmon, an Illustrated Natural History, and reproduced here with permission, are made from live specimens at Salmoniculture—The Conservatoire National du Saumon Sauvage, at Chanteuges, Auvergne, France.

sides, distinguishing them as parr. The behavioral pattern or the habitat does, however, not change radically, the parr still being a bottom-dwelling, upstream-facing, territorial juvenile. These freshwater developmental steps can take from one to several years to be completed, and are dependent on thermal and nutritional conditions of the stream.

At a certain point in time, dependent both on season and size, the parr–smolt transformation, or smoltification, is initiated. This process, which consists of complex changes in morphology, physiology and behaviour, preparatory for the marine phase of the anadromous life cycle, has been the subject of several general reviews (Hoar, 1976; Stefansson et al., 2008), as well as more specialized ones, focusing on physiology (McCormick and Saunders, 1987) and endocrine control (McCormick, 2009). The scope of this paper is not to review the smoltification process per se, but a set of "classic" illustrations (Fig. 2) can be used to highlight the size/season aspects (Kubo, 1974), the morphological changes (Gorbman et al., 1982) and the functional changes in osmoregulatory organs (McCormick and Saunders, 1987).

2.3. Is smoltification metamorphosis?

The question whether salmon smoltification is to be viewed as metamorphosis has been debated. Barrington (1961) wanted to include the physiological and behavioral changes of smoltification within what has been termed "second" metamorphosis (Wald, 1981), in contrast to "first" metamorphosis of fish which Youson (1988) claims is limited to lampreys, eels and flatfishes. Just et al. (1981) argued that smoltification does not meet criteria of chordate metamorphosis, whereas more recently Heyland (in Bishop et al., 2006) and Power et al. (2008a,b) have expressed the view that smoltification should be seen as metamorphosis.

These conflicting views have their basis in a number of aspects which need to be examined further. These include the broader concept of "roundfish metamorphosis", the idea of a series of metamorphic processes (first, second), and if metamorphosis is limited to larval-juvenile–transitions.

2.3.1. Roundfish metamorphosis

While the dramatic changes in external morphology which take place during the larval–juvenile transition of flatfish species makes it easy to term this to be metamorphosis, Power et al. (2008a,b) in a recent