



Imprecise naming: the anadromous and the sea spawning threespine stickleback should be discriminated by names

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Abstract

Two ecological forms of the threespine stickleback *Gasterosteus aculeatus* – a strictly marine form and an anadromous form – are often merged in the literature as a single “marine” form. Because we know virtually nothing of the life style of the two oceanic ecotypes in the sea and consequently nothing on reproductive isolation and gene flow I argue for a precise use of the ecological terms “marine” and “anadromous” for these two ecotypes. These terms should be self-describing. The frequent use of terms incorrectly describing intraspecific variation and life style of ecotypes can bias studies on community composition and interactions of populations.

Keywords *Gasterosteus aculeatus* · Threespine stickleback · Anadromous · Marine · Ecotypes

Introduction

The threespine stickleback *Gasterosteus aculeatus* Linnaeus, 1758 is a rare case where an ancestral marine form possibly has coexisted with its derived forms over the past million years (Wootton 1976, 1984; Bell and Foster 1994; Baker et al. 2015), or where “the ancestral condition” is represented by a “present-day oceanic stickleback” (Baker et al. 2015). Additionally, this teleost is phenotypically and ecologically extremely plastic (Wootton 1976, 1984; Bell and Foster 1994). Besides several morphological forms, three major ecological forms are discerned: two oceanic types, a strictly marine ecotype that spends its entire life cycle in a marine environment, and an anadromous ecotype that migrates as juvenile from freshwater to saltwater and returns as adult to freshwater for spawning. The third, a strictly freshwater ecotype, spends its entire life cycle in

freshwater (Wootton 2009; Bell et al. 2004). The high phenotypic and ecological plasticity and an ancestral form coexisting with extant forms makes the threespine stickleback an excellent model species (Schluter 1993; McKinnon and Rundle 2002) and a species that has generated an innumerable number of publications (Wootton 2009).

The eighteenth century saw the start of an objective and scientific approach to nature and the creation of many scientific terms widely used today: e.g., “Stammzelle” (stem cell) (Haeckel 1868), “Biosphäre” (biosphere) (Suess 1875) ... and “anadromous” (Myers 1949). “Anadromous” was introduced for “fishes which spend most of their lives in the sea and migrate to fresh water to breed” (Myers 1949). Like many salmonids, the threespine stickleback is a partially migratory species, viz., the species are split into migratory (anadromous) and resident populations (Jonsson and Jonsson 2009). Nevertheless, within these species the threespine stickleback is unique in splitting not only into two, but into three forms: a strictly marine, a migrating anadromous, and a strictly freshwater form. If applied, I found no case in the literature where the term “anadromous” was used inappropriately. The problem was “if applied”. In a large number of studies, the term “marine” was used instead of the correct “anadromous” or both terms were used optionally (Online Resource 1: Table S1).

Many species developed distinct phenotypes along ecological gradients which result in discrete ecotypes (e.g. Schluter and McPhail 1992; Rogers and Bernatchez 2007; Seehausen and Wagner 2014; Ahnelt et al. 2015) and differentiation in

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discrete ecotypes as result of selection can lead to genetic modifications and finally influences evolution (West-Eberhard 1989). Some phenotypes have split in sympatric populations (“species pairs”), e.g. freshwater threespine sticklebacks in populations inhabiting the pelagic and benthic zone of a lake respectively (Schluter and McPhail 1992; Conte and Schluter 2012). These populations represent two discrete ecotypes so called “limnetics” (plankton feeders) and “benthics” (lake bed feeders) (e.g. McKinnon and Rundle 2002; Baker et al. 2015; Vines and Schluter 2006). Although gene flow between most of these sympatric populations persisted (Schluter 1996) these two ecological terms are used frequently in recent literature (Saint-Laurent et al. 2003; Vines and Schluter 2006; Kozak et al. 2011; Jones et al. 2012) characterizing ecologically (and morphologically) divergent populations. Therefore precise use of ecological terms e.g. for the marine spawning and anadromous ecotypes of the threespine stickleback is needed.

Methods

I reviewed 109 studies published between 2000 to June 2017 for the use of ecological terms applied to the oceanic type (marine plus anadromous) of the threespine stickleback (Online Resource 1: Table S1). [Actually, there were many more publications, but I avoided repeated citing of authors who used the same name for an ecotype in subsequent studies]. In these studies I compared sampling sites with ecotypes mentioned, e.g. “marine” threespine sticklebacks sampled in a river (actually anadromous sticklebacks) to distinguish following five categories: (i) marine was conveniently or incorrectly used instead of anadromous, (ii) anadromous was correctly used for migrating sticklebacks, (iii) marine was correctly used for strictly marine sticklebacks, (iv) marine was used for sticklebacks sampled in the sea but not checked for the ecotype (anadromous or marine or a mix of both), and (v) oceanic was used to unite anadromous and marine sticklebacks.

Results

Only in 9.2% ($n = 10$) of the studies was the term “marine” correctly applied. This number increased to 10% if I excluded those publications in which only the term anadromous was used ($n = 9$) (Online Resource 1: Table S1). In nearly two-thirds of the studies ($n = 69$, 63.3%), the term “marine” was used instead of “anadromous”, or both terms were used optional (Fig. 1, Online Resource 1: Table S1). In the remaining studies (<30%), “anadromous” and/or “oceanic” was applied.

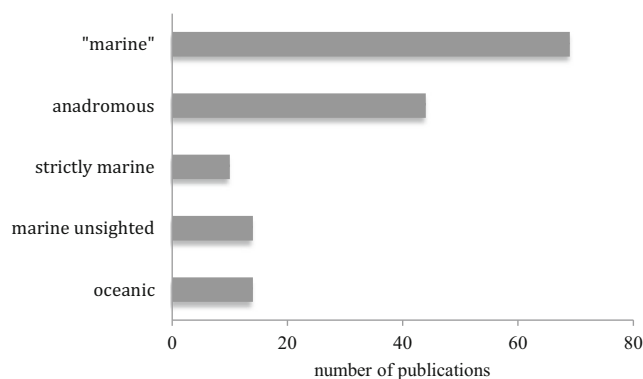


Fig. 1 Publications of the threespine stickleback from 2000 to 2017 broken down by five ecological categories: (i) “marine” = is used instead of anadromous; (ii) anadromous = is used correctly for migrating sticklebacks; (iii) strictly marine = is used correctly for strictly marine sticklebacks; (iv) marine unsighted = is used for sticklebacks recorded from the sea but not checked for the ecotype (anadromous or marine or a mix of both); (v) oceanic = is used to unite the anadromous and marine ecotypes. Because multiple ecological terms were used in some publications, the total sum of all publications shown in the table exceeds the total number of the investigated studies published ($n = 109$)

Discussion

The unusually high number of an inexact use of terms characterizing the life style of fish populations was surprising. A reason why “marine” is so often used instead of the correct term “anadromous” may simply be that relevant information on the lifestyle of the marine and of the anadromous ecotypes in the ocean is lacking (Bell et al. 2004; Barrett et al. 2008; Seehausen and Wagner 2014). Actually, the convenient use of the term “marine” is not rare in threespine stickleback literature and is repeatedly used optionally for “anadromous” (Online Resource 1: Table S1).

Why is “marine” so often used instead of “anadromous”? The question whether the strictly marine type and the anadromous type trace back to a common ancestor (Baker et al. 2015), or whether the anadromous threespine stickleback evolved from an extant marine stock has yet to be explored (MacColl 2009; Wund et al. 2012). Although sometimes mentioned (Bell et al. 2004; Barrett and Schluter 2008; Seehausen and Wagner 2014) no actual case has been documented where a strictly marine stickleback population evolved in the wild directly into a freshwater population. One reason why marine and anadromous ecotypes are merged into an “oceanic type” or a “marine type” (Bell et al. 2004; Wund et al. 2012) or why authors use “marine” for “anadromous” is possibly the low level of phenotypic variation of oceanic sticklebacks. Simply, we know virtually nothing of the life style of these two oceanic ecotypes in the sea (Walker and Bell 2000; Bell et al. 2009; MacColl 2009; Wund et al. 2012) and consequently we know nothing on reproductive isolation and gene flow.

The few studies on threespine sticklebacks inhabiting brackish waters revealed no definite results. In the Baltic Sea

significant evidence for adaptive differentiation along a salinity gradient and local adaptation of threespine sticklebacks because of restricted gene flow was found (DeFaveri and Merilä 2013; Guo et al. 2015) but not in the St. Lawrence River estuary, also a huge brackish water system (McCairns and Bernatchez 2012).

Seemingly, many authors use the term “marine” to conveniently lump marine and anadromous sticklebacks together (Hendry and Taylor 2004; Berner et al. 2010; Kaeuffer et al. 2012; Rennison et al. 2016). Other authors switch in the same publication between “anadromous” and “marine” (Barrett and Schluter 2008; McKinnon and Rundle 2002), and some use both terms differently in subsequent publications (Berner et al. 2008, 2010; Dalziel et al. 2009, 2012). Only in a small number of publications was the merging of anadromous and marine ecotypes indicated by the use of the term “oceanic” instead (Bell et al. 2004; Shaw et al. 2007; Kimmel et al. 2012) (Online Resource 1: Table S1).

Why does it matter: Because we know virtually nothing of the life style of the two oceanic ecotypes in the sea (MacColl 2009; Wund et al. 2012). Why do some sticklebacks breed in the sea and others in fresh waters? Just by chance or are brackish environments the link between both ecotypes? We know nothing on reproductive isolation and gene flow and nothing on morphological divergence of these sticklebacks in the wild. We currently can be certain of studying marine threespine sticklebacks only if the samples were collected or observed at their oceanic spawning sites (Wund et al. 2012). The anadromous ecotype spends most of its lifetime in the sea. Thus, sampling of threespine sticklebacks in the ocean (Barber 2003; Kristjansson 2005; Marchinko 2009; Schade et al. 2014) is not a guarantee of having sampled a strictly marine stickleback. Therefore, “marine” should only be used where the specimens were observed or sampled at a marine spawning site (Bell and Peeke 2012; Demchuk et al. 2015), i.e. both terms should be self-describing. If this is not the case I suggest using the neutral term “oceanic”, which combines strictly marine and anadromous ecotypes of threespine sticklebacks (Shaw et al. 2007; Baker et al. 2008; Furin et al. 2012) at least as long as it is demonstrated that a differentiation in these two ecotypes is not justified. The frequent use of terms incorrectly describing intraspecific variation and life style of ecotypes can bias studies on community composition and interactions of populations.

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