Charles Darwin, ichthyology and the species concept

Daniel Pauly

Fisheries Centre, 2204 Main Mall, The University of British Columbia, Vancouver, BC, Canada, V6T 1Z4

Abstract

This contribution presents the ichthyological writings of Charles Darwin (1809–1882), by periods, viz. 'the years prior to the voyage of the *Beagle*' (about 1825–1830); 'the *Beagle* years' (1831–1836); 'from the return of the *Beagle* to the *Foundation of Origin*' (1837–1844); and 'the mature Darwin' (1845–1882). Overall, this material covers 45 000 words penned by Darwin, but represents only 0.7% of his lifetime output of about 6 million words, indicating a limited interest in fish. However, this sample, briefly described here, but analysed in great detail in a forthcoming volume on *Darwin's Fishes*, allows drawing inferences on Darwin's working style that were missed in conventional biographies. On the other hand, it is suggested, based on a close reading of the 6th (1876) edition of *Origin*, that Darwin was not particularly interested in the theoretical issues now associated with the species concept, nor indeed with other levels of the Linnean system.

Correspondence:
Daniel Pauly,
Fisheries Centre,
2204 Main Mall, The University of British Columbia,
Vancouver, BC,
Canada, V6T 1Z4
Tel.: +1 604 822 1201
Fax: +1 604 822 8934
E-mail: d.pauly@fisheries.ubc.ca

Received 3 Jun 2002
Accepted 10 Jun 2002

Keywords Darwin, evolution, ichthyology, species concepts

Introduction

This issue of *Fish and Fisheries*, devoted to the 'Species Concept in Fish', could benefit, one might think, from a brief review of what Charles Darwin (1809–1882), the founder of evolutionary biology, might have to say about fishes and the species concept.

Darwin, as every biologist knows, wrote numerous books on particular groups of organisms: barnacles, orchids, earthworms, but never on fishes. To compensate for this, I have assembled a book, titled 'Darwin's Fishes: An Encyclopedia of Ichthyology, Ecology and Evolution' based on a detailed analysis of material extracted from the work Darwin published during

his lifetime and the wealth of manuscript material published since (Pauly 2002). Here, I present a brief summary of this book's contents, to introduce Darwin's relationships to ichthyology, then turn to his species concept. *Darwin's Fishes* documents everything ever written by Charles Darwin on fishes and closely related groups in the form of 481 entries that are arranged alphabetically and structured around taxa, e.g. 'parrotfishes;' scientists, e.g. 'Weber' (he of the ossicles); or concepts, e.g. 'sexual selection', in this case one coined by Darwin and illustrated with many fish examples.

Entries were extracted from Darwin's books (here cited through their short, italicized title; see Freeman 1977 for publication details), his short publications (Barrett 1977), his notebooks (Barrett *et al.* 1987), other now published manuscripts (e.g. Stauffer 1975; Keynes 2000) and that part of his complete correspondence now published (Vol. 1–12, covering the years 1821–1864; see Burkhardt *et al.* 1985). One appendix to *Darwin's Fishes* presents his list of *Fish in Spirits of Wine*, while two others identify those fishes he collected that now are in the Natural History (London) and Zoology (Cambridge University) museums.

Overall, quotes comprising about 45 000 words were extracted. Given the overall extent of Darwin's writing (well over six million words), this indicates a limited interest in fishes. However, the sample of 0.7% of Darwin's lifetime written output covered in *Darwin's Fishes* allowed drawing of a number of inferences, some quantitative, that are missed in many conventional biographies. Examples are the high accuracy of Darwin's citations to his sources, his mining for and systematic re-publication of information relevant to natural selection, and the very high success rate of his many hypotheses.

The analysis of this literature allows a first evaluation of Charles Darwin's relationship to ichthyology, a theme developed below through four distinct periods.

The years prior to the voyage of the *Beagle*

Contrary to a widespread view, Darwin's youth and student years prepared him well for the role he assumed during the voyage of the *Beagle*.

Darwin's schooling appears to have been typical of boys of his social class and time, even if he claims, in his *Autobiography* (p. 46) that he 'was doing no good at school'. Far more interesting, at least to this account, is his extraordinary devotion to angling, which started at an early age, and lasted until well into the *Beagle* years. An extensive correspondence attests to this devotion, and related activities and readings, notably *The Compleat Angler* (Walton 1653). Izaak Walton's classic, which identifies (and names!) distinct populations of trout and other fish species in the British Isles, may have contributed, a decade or so later, to Darwin's dawning perception of within-species variability as a motor of evolution.

Darwin's angling years were also a period of avid beetle collecting, and this introduced him to Leonard Jenyns, who later described the fish Darwin collected during the voyage, the *Beagle* (Jenyns 1840–1842).

I present here only one element of Darwin's student years in Edinburgh: his dissection of a lumpfish, on March 16, 1827, under the guidance of his then mentor, Robert Grant. The importance of the written account of the lumpfish dissection derives from the fact that it is the first bit of scientific writing by Darwin ever found (Barrett 1977), and from the profound understanding of the relationship between scientific 'fact' and 'theory' that this documents:

> 'Procured from the black rocks at Lieth a large Cyclopterus Lumpus (common lump fish). Length from snout to tail 23 1/2 inches, girth 19 1/2. It had evidently come to the rocks to spawn & was left there stranded by the tide; its ovaria contained a great mass of spawn of a rose colour. Dissected it with Dr Grant. It appeared very free from disease & had no intestinal worms: its back however, was covered with small crustaceous animals.
>
> Eyes small. Hence probably does not inhabit deep seas? Stomach large. Liver without gall-bladder. Kidneys situated some way from the Vertebrae: an unusual fact in cartilaginous Fishes. Air bladder was not seen. Brain very small; the optic nerves being nearly as large as the spinal cord, neither the brain or spinal matter nearly filling its cavity. The valves in the heart were very distinct; the peduncle strong. The body was not covered with 'skin' scales, but slimy & remarkably thick. The sucker on its breast was of a white colour. I believe it is generally a reddish yellow? The plebs differ whether it is edible'.

Indeed, this account, while establishing that Darwin already then was a keen observer, quick to formulate and test fruitful hypotheses, also establishes that Grant, an early evolutionist, cannot have had on Darwin as little intellectual influence as claimed in the *Autobiography*. (A detailed analysis of this account is given in Pauly 2002.)

Darwin's years in Cambridge, where he relocated after giving up on medicine in Edinburgh, are rather well documented in various biographies, most of which emphasize the role of his mentor there, the botanist John Henslow. Nothing peculiar to ichthyology is reported from this period, which ends when Captain Fitzroy accepted Darwin as his companion and effective naturalist on the *Beagle*, after Jenyns had turned down the same offer.

The *Beagle* years (1831–1836)

Darwin's plan, when he embarked on the *Beagle*, was to collect enough material and observations to write on his return an account similar to von Humboldt's *Voyage aux régions exinoxiales du Nouveau Continent*, which he greatly admired. Moreover, as ichthyology in the early nineteenth century was completely dominated by French taxonomists, Darwin also had planned to collect fish specimens that would prove to be new species; the more the better. Thus, he concentrated his fish sampling effort in areas not previously, or little explored by French vessels. Hence the thoroughness of his collecting work in southern South America, and his more limited samples from the Indo-Pacific.

Darwin's conservative sampling strategy, dictated in part by the difficulties in preserving and shipping specimens back to England (with Henslow at the receiving end), did pay off, as illustrated by a letter of October 1839 to Jenyns, in which he congratulates himself: 'I am astonished & glad to hear how many new things you seem to have found – four new genera is something.' There would have been more, had not a part of the collection rotted away.

One important reason why the strategy worked is that Jenyns did a very competent job of describing Darwin's fishes, successfully navigating the waters between the Scylla of lumping distinct species, and the Charybdes of splitting mere variations into named species (see http://www.fishbase.org for a correspondence between his species names, and those now considered valid).

Darwin clearly believed, long before he conceived sexual selection (through which he explained sex-related differences in the colouration of birds, fishes and other animals), that colours matter and the descriptions of the live colours of most of his specimens, e.g. in *Fish in Spirits of Wine*, attest to this. Moreover, he did not let his imagination colour his descriptions, basing them, rather, on the colour-coded charts in a book he took with him for that very purpose (Syme 1821). Thus, we can attribute to Darwin the first rigorous treatment of colours in biology, in general, and in ichthyology, in particular.

This attention to details which other naturalists may have overlooked, is also evident from other aspects of his field work, e.g. by his collection in the Cape Verde and Falkland Islands. Notably, this involved performing simple – we might call them Baconian – experiments on the behaviour, ecology or physiology of various animals, including fishes. This involved, e.g. cutting open a marine iguana in the Galapagos (try that now!) to settle a long-standing dispute on whether they feed on underwater vegetation or on fishes, dropping marine fishes into freshwater to see if they could adapt, etc. (see Pauly 2002).

From the return from the *Beagle* to the *Foundation of Origin* (1837–1844)

Particularly revealing to anyone who ever edited a book is the series of letters Darwin sent to Jenyns upon his return from the *Beagle* voyage to convince him to start, then to complete the job of describing the specimens Darwin called 'my fishes.' These letters are fully documented by Burkhardt *et al.* (1986), with additional context provided in *Darwin's Fishes*.

Darwin even used nationalism: 'For the credit of English zoologists, do not despair and give up; for if you do, then will it be said that there was not a person in Great Britain with knowledge sufficient to describe any specimen which may be brought here.' (December 4, 1837).

As well, Darwin pleaded with Jenyns for the incorporation into the fish descriptions of his field notes on colours and behaviour. Jenyns went along, and this made *Fish* (Jenyns (1840–1842) rather lively, at least by the standard of their time. One example, from p. 87: 'In Mr Darwin's notes, it is stated that (*Salarias atlanticus*) bites very severely, having driven its teeth through the finger of one of the officers in the ships company. Its two very long sharp canine teeth at the back of the lower jaw are well calculated to inflict such a wound'. The point about Darwin though is not any of this, but that he discovered natural selection. His post-*Beagle* notebooks, now available in their entirety (Barrett *et al.* 1987), make clear that this discovery happened in late 1838, with various scholars even venturing specific dates.

This led to an immediate change in the way Darwin read: before, he absorbed ideas from a wide range of books, almost haphazardly, with what we

might wish to call an 'open mind'. He describes his reading during this period thus: 'I worked on true Baconian principles and without any theory collected facts on a wholesale scale. . .'. This statement has misled many because it describes a period which ended when Darwin hit on natural selection. Thereafter, his readings became more targeted, with all that he read being evaluated (often through critical marginalia pencilled right onto the offending pages) in term of its support – or lack thereof – for the nascent theory.

The role played by fish in this phase of Darwin's personal evolution is hard to pin down. The distributions of fishes clearly played an important role. Notably, Darwin expected isolated islands to have a relatively large fraction of endemics among their coastal fishes, and one even gets the impression, with regards to the Galápagos at least, that he expected being able to document, using fish species distributions, the peculiar role that isolated islands play in generating biodiversity, and now commonly illustrated with 'Darwin's Finches'. This couldn't be done at the time, due to the state of fish taxonomy, and Darwin gradually abandoned this theme, though he continued to discuss fish distribution when contrasting freshwater with marine habitats, and insisting that the former served as refuge to ancient 'ganoid fishes', which have 'apparently been saved from fatal competition by having inhabited a protected station'. (*Origin,VI*, p. 105).

In *Foundation of Origin*, the two manuscripts Darwin wrote in 1842 and 1844 to ensure that his discovery would not be lost (he had his wife promise to publish them, should he die prematurely), 'fish' also served as Darwin's shorthand for ancestral vertebrates, especially in terms of their anatomy, habitat and perceived tendency toward hermaphroditism, a feature much emphasized in subsequent writings (see Pauly 2002).

Also of note is Darwin's membership in the Strickland Commission, which originated the predecessor to the International Code for Zoological Nomenclature (Strickland *et al*. 1843). None of this, however, added to our knowledge of fishes *per se*.

The mature Darwin (1845–1882)

Darwin's contribution to ichthyology, for the period from 1845 to his death were both indirect and direct. The indirect contribution, obviously, is that he developed the evolutionary context within which biology must now be done, if it is to mean anything.

That story, culminating in the 1859 publication of the first edition of *Origin of Species* has been told in uncounted biographies and texts, and does not need rehashing here.

However, *Origin*, which ran in six editions during Darwin's lifetime, contains a multitude of direct references to fishes, notably on sexual selection, on relict forms (variants of the ganoid story), on the position of fishes in term along the complexity 'scale' and on various 'difficulties of the theory', i.e. the seeming lack of transitory forms explaining the eyes of fishes and other animals; flying fishes; swim bladders, erroneously presented as lung precursors; electric fishes; the metamorphoses of flatfishes; the pregnancy of male seahorses; the 'sudden appearance' of teleosts in the fossil record and more. Also discussed are the impact of sea surface temperatures and geographical barriers on ichthyofauna formation, including an interesting volte-face from the first edition, concerning the impact of the Isthmus of Panama; and the results of his field experiments on how seeds in fish stomachs are distributed by piscivorous birds. Overall, *Origin* is a firework of ichthyological ideas (detail, in Pauly 2002).

Many of these themes are amplified in the books that Darwin wrote to boost the argument in *Origin*, notably *Variation* (1871, 1877), and *Descent* (1871, 1877), his only works with sections explicitly dedicated to fishes. In *Variation*, a two-page section deals with the origin and forms of goldfish (*Carassius auratus*). In *Descent*, a section discusses the sex ratios of pike, salmonids and cyprinids, while another discusses the secondary sexual characters of a large number of fish species, from shark and rays to highly derived teleosts.

In the process of analysing this material, and reading essentially all that Darwin has ever written, I never noted any attempt by Darwin's part to discuss theoretical issues of taxonomy and/or to define the categories used by taxonomists (in fact he argued that his discovery of natural selection would not change the practice of taxonomy). For example, the otherwise very useful *Glossary of the principal scientific terms used in the present volume*, which Darwin added to the sixth edition of *Origin*, and which defines 223 terms, does not include 'species', nor for that matter, any other level of the Linnaean hierarchy. Thus, I can only confirm the often stated quip that *Origin of Species* does not deal with species, nor, really, with their origins.

The closest one can get in *Origin* to a species definition is this:

'I look at the term species as one arbitrarily given, for the sake of convenience, to a set of individuals closely resembling each other, [. . .] it does not essentially differ from the term variety, which is given to less distinct and more fluctuating forms. The term variety, again, in comparison with mere individual differences, is also applied arbitrarily, for convenience sake.'

As for speciation itself, the following is perhaps Darwin's best definition:

> 'The passage from one stage of difference to another may, in many cases, be the simple result of the nature of the organism and of the different physical conditions to which it has long been exposed; but with respect to the more important and adaptive characters, the passage from one stage of difference to another may be safely attributed to the cumulative action of natural selection, hereafter to be explained, and to the effects of the increased use or disuse of parts. A well-marked variety may therefore be called an incipient species; but whether this belief is justifiable must be judged by the weight of the various facts and considerations to be given throughout this work'.

Clearly, we are on our own when we discuss the species concept: the master is not going to help us.'

References

Barrett, P.H. (1977) *The Collected Papers of Charles Darwin*. University of Chicago Press, Chicago.

Barrett, P.H., Gautrey, P.J., Herbert, S., Kohn, D. and Smith, S. (1987) *Charles Darwin's Notebooks, 1836–1844: Geology, Transmutation of Species, Metaphysical Enquiries*. British Museum (Natural History), London and Cornell University Press, Ithaca, New York.

Burkhardt, F., Smith, S., Browne, J., Kohn, D. and Montgomery, W. (1986) *The Correspondence of Charles Darwin*, Vol. 2. Cambridge University Press, Cambridge, pp. 1837–1843.

Burkhardt, F., Smith, S., Kohn, D. and Montgomery, W. (1985) A calendar of the correspondence of Charles Darwin, Garland Publishing, New York, pp. 1821–1882.

Freeman, R.B. (1977) *The Works of Charles Darwin, an Annotated Bibliographical Handlist*, 2nd edn. Wm Dawson & Sons Ltd, Folkestone.

Jenyns, L. (1840–1842) Fish. In: *The Zoology of the Voyage of H.M.S. Beagle, Under the Command of Captain Fitzroy, R.N. During the Years 1832–1836* (ed. C. Darwin). Smith, Elder Cornhill, London. (in four parts: i-xvi + 1–172, p. Plates 1–29).

Keynes, R.D. (2000) *Charles Darwin's Zoology Notes and Specimen Lists from H.M.S Beagle*. Cambridge University Press, Cambridge.

Pauly, D.(2002) *Darwin's Fishes: an Encyclopedia of Ichthyology, Ecology and Evolution*. Cambridge University Press, Cambridge (in press).

Stauffer, R.C. (1975) *Charles Darwin's Natural Selection: Being the Second Part of His Big Species Book*. Cambridge University Press, Cambridge.

Strickland, H.E. *et al.* (1843) Series of propositions for rendering the nomenclature of zoology uniform and permanent. *Annals and Magazine of Natural History* **11**, 259–275.

Syme, P. (1821) *Werner's nomenclature of colours, with additions, arranged so as to render it highly useful to the arts and sciences, particularly zoology, botany, chemistry, mineralogy and morbid anatomy. Annexed to which are examples selected from well-known objects in the animal, vegetable and mineral kingdoms*. William Blackwood, Edinburgh and T. Cadell, London.

Walton, I. (1653) *The compleat angler, or the contemplative man's recreation: being the discourse of rivers, fishponds, fish and fishing not unworthy of the perusal of most anglers*. T. Maxey for R. Marriot, London.

