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Rethinking research: the role of tradition in the study of marine invertebrates

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Scientific tradition is a key-element behind innovation and novelty in science. Relying on tradition provides a sense of security for the individual researcher but may also hamper scientific progress. By rethinking and reformulating previously stated research-topics and questions, science can profit from already existing data and knowledge. For this, however, a conceptual framework for critical thinking must exist for exchange of scientific ideas and findings. Tradition and critical thinking supply the framework for understanding data collected today in relation to previously accumulated information and scientific knowledge. This paper reflects upon these processes from the perspective of marine biological studies on soft-sediment invertebrates in Finland during the past 100 years exemplified by the works of Sven G. Segerstråle, with his education rooted in the old and traditional, and yet daring to think and work in innovative pathways.

Introduction

Scientific tradition is often thought of as a key-element driving innovation and novelty in society at large and within science more specifically. Relying on tradition provides a sense of security for the individual researcher but may also hamper scientific progress. By rethinking and reformulating earlier research-topics and questions, and by reformulating scientific hypotheses, science can profit from already existing data and knowledge. To do so, there must, however, exist a general framework for critical thinking and for exchange of scientific ideas and findings. One such arena is provided by scientific and learned societies and academies, which contribute to upholding the needed basic platform. *Societas pro Fauna et Flora Fennica* (SFFF), founded in November 1821 and thus being the oldest learned society in Finland, plays an important role in both collecting and conserving ideas and knowledge about the terrestrial and aquatic fauna and flora of Finland and its nearby regions (Wallgren 1996).

From originally striving to describe and record the biota found in Finland, SFFF today is one of several scientific organizations in Finland offering academic guidance as well as economic and logistic support both to young early-career scientists and to established researchers in their efforts to uphold the traditions of natural history as a foundation for the plethora of advanced and high-level research groups within biosciences and ecology in Finland at universities and museums as well as at various institutes. How, then, can the modern and often effectivity-driven science ('science for benefit') of today draw from the descriptive or strictly curiosity-driven science of previous times? Are not modern efforts elements of a completely different set of scientific academic traditions? My tentative answer is 'no they are not'. In this paper I exemplify this from the narrow perspective of specific marine biological studies on soft-sediment invertebrates in Finland during the past 100 years.

Knowledge beyond a static image of nature

The natural science of the past 200 years indeed forms the foundation upon which current analytical and predictive curiosity-driven and applicable research is based. In a way one can say that the natural sciences are built in part on a strong Humboldtian tradition – see for instance the biography on Alexander von Humboldt (1769–1859) by Wulff (2015) – and in part on the famed quote of Johann Wolfgang von Goethe (1749–1832) stating that '*All intelligent thoughts have already been thought; what is necessary is only to try to think them again*'. The need to observe, interpret and understand nature became increasingly strong during the utilitarian era of the 18th century (more prominent in Finland during the first decades of the 19th century) as well as a result of the era of enlightenment with scientists and thinkers such as Isaac Newton (1642–1727) and Voltaire (or Francois-Marie Arouet, 1694–1778) as prominent spearheads, which lead to the need for a systematization of what was observed. Hence the Linnéan (Carl von Linné 1707–1778) approach to classify the living nature became defining for much of our natural end environmental science even today, paving the way for in-depth analysis reaching beyond systematics during the 19th century, with Charles Darwin (1809–1882) being the founding father of modern evolutionary biology and ecology, in turn basing parts of his thoughts on the fathers of modern palaeontology and geology, namely Georges Cuvier (1769–1832) and Charles Lyell (1797–1875), who had set out the pathway of thinking beyond the concepts of creation and a static image of nature.

Accepting change, succession and evolution is fundamental to our current intra-disciplinary understanding of nature. *Societas pro Fauna et Flora Fennica* became the founder of museal collections and taxonomic compilations in Finland (Wallgren 1996). The work largely built on traditions inherited from Sweden (Linné and his disciples, and the Royal Swedish Academy of Sciences, founded already in 1739) as well as from Europe in a wider perspective with natural history museums being founded in countries and cities with strong universities at the time. During the 19th century, several leading natural scientists in Finland made their mark for these collections. Among them Evert Julius Bonsdorff (1810–1898) who's collections including skeletons of now extinct mammals are still part of the Natural History Museum in Helsinki (see Wikgren 1996 for an overview of the history of biology in Finland).

The Baltic Sea and its benthic invertebrates exemplify tradition in research

One hundred years after its foundation, in 1921 as *Societas pro Fauna et Flora Fennica* celebrated its first centenary, marine science was a young and fumbling branch of academic study and research in Finland. Some physical and oceanographic features of the sea had been monitored for a few decades, such as mareographs measuring variations of sea level, and other basic features of our coastal waters (Poutanen & Leppänen 2021). These data now provide valuable references for our current interpretation of climate change-related aspects of the Baltic Sea and the entire Baltic Sea region ranging from the sea itself to the terrestrial and atmospheric systems surrounding it (Meier et al. 2022, Viitasalo & Bonsdorff 2022).

Descriptive biological studies had begun during the last decades of the 19th century (Wikgren 1996, Pokki 2009), and as fishing and fisheries were socially and commercially important, the organisms that provide food for fish were collected and recorded, and so the first inventories of the zoobenthic fauna of our coastal and offshore waters had begun (Haahtela 1996, Poutanen & Leppänen 2021). The continued need for mapping and description of the fauna and flora of the Finnish coastal waters today is perhaps best documented in a recent book including an Atlas based on the national habitat-mapping and biodiversity inventory project VELMU (Viitasalo et al. 2021).

One specific field of descriptive zooecology in Finland is the study of aquatic (both limnic and marine) zoobenthos, displaying a great taxonomic and functional variability along the environmental Baltic Sea gradient (Bonsdorff 2006, Ojaveer et al. 2010, Gogina et al. 2016, Viitasalo et al. 2021). This stems from the fact that the benthic invertebrates constitute an important and reliable food source for benthic-feeding fish. To understand the dynamics of commercial fish-stocks as well as non-commercial fish populations in general, benthic surveys in the Baltic Sea were started already in the early 1900s, with the first systematic study partially covering Finnish offshore waters was a large survey by Hessle (1924). This study became a foundation for later monitoring-surveys up until today (Villnäs & Norkko 2011).

It is justified to ask why this field of zoology and ecology is of general interest, and the answer lies in the above-mentioned role of the benthic fauna as food for fish, but also in several overarching facts: the sediment-water interface in the oceans is the largest ecological interface on Earth, and the diversity at Phylum-level is highest in this ecological realm. The benthic invertebrates play key-roles in ventilating the sediments, thus contributing to the remineralization of nutrients and recycling of other important elements on a global scale. From a local or regional perspective, the relatively long-lived and stationary organisms have a high value as indicators of ecosystem-health (Janas et al. 2017, Thrush et al. 2021). Although the analytical methods have improved immensely during the last decades, and environmental mapping has become more precise, environmental monitoring as well as scientific interpretation of long-term changes in the Baltic Sea rely on basically asking and reformulating the same scientific questions over and over in true Goethean manner. The precision has improved, but the conceptual framework has remained surprisingly similar over time (Hessle 1924, Sjöblom 1955, Andersin et al. 1977, Laine 2003, Villnäs & Norkko 2011 illustrate a chain of examples encompassing Finnish coastal and offshore waters).

Haahtela (1996) in his presentation and paper for the 175-year anniversary seminar of *Societas pro Fauna et Flora Fennica*, presented an inventory and a literature-overview of the basic faunistics of invertebrates of both marine and inland waters of Finland. He provided a thorough taxonomic overview, including a large bibliography regarding all key taxa, with 295 adequate references. Haahtela (1996) is still an important and valuable reference for the faunistics of the Finnish marine and brackish-water invertebrates. There is, however, one sector within the taxonomy of Baltic Sea invertebrates which has changed significantly since the 1990s, namely the so called non-native and invasive species, several of which have established viable populations during the last 20–30 years. These newcomers have not yet changed the rationale of the research, be it documentation or experimentation in the field or in aquaria. The methods have, however, diversified (such as molecular analysis for taxonomy, and numerical tools for validating findings in statistical terms), and open databases facilitate our efforts to stay updated on the distributions of species, but the basic questions as to what species are found under which conditions and why remain surprisingly similar over time. For the non-native invasive ones, the database AquaNIS (www.corpi.ku.lt/databases/index.php/aquanis/) provides an accurate and up-to-date source of basic information, and the ecological implications of them are summarized in Ojaveer et al. (2021).

Scientific tradition, Sven G. Segerstråle and the importance of curiosity-driven research

Scientific tradition is, as illustrated above, oftentimes linked to certain individual scientists who have dared challenge the knowledge and scientific 'truth' of their respective times. When it comes to the marine invertebrates, Finland clearly has had one outstanding forerunner at the national and international levels, namely Professor Sven G. Segerstråle (1899–1994), who according to WorldCat (worldcat.org) published 173 publications in three languages (among them 73 papers in English, 43 in German, and several in Swedish). The two most widely cited ones are Segerstråle 1957a (a comprehensive book chapter on the Baltic Sea as a system) and Segerstråle 1973 (the *Macoma-Pontoporeia* theory). Both these works can be classified as 'citation classics' for the invertebrate fauna of the Baltic Sea. A word-cloud based on the titles of his works shows that he covered a wide range of topics between the late 1920s and the early 1980s, and he published scientific papers during no less than 7 decades. The most impressive aspect of the word-cloud is that any benthic ecologist of today would be proud to have such a wide array of topics, species and environments covered during their careers. The top-tier of words is: Baltic Sea, Gulf of Finland, Gulf of Bothnia, Atlantic Ocean, Marine animals, Marine biology, Glacial lakes, Salinity, Amphipoda, Isopoda, Mysidae, Gammaridae, *Pontoporeia*, *Macoma* to name just a few.

What, then, were the main topics of his research, and how have these in turn affected others later and in parallel to him, what is his legacy for Finnish marine invertebrate zoology and ecology, apart from being the first one to pick up on the international trends of studying organisms that few people even know are there? Apart from having an extraordinary career in his field, Segerstråle played a key-role in the foundation of the Nordic Council for Marine Biology, which between 1956 and 1994 provided opportunities for several thousand Nordic students of marine biology to learn from all aspects of the field in just about every corner of the Nordic marine network of field stations (Wikgren 1996, Pokki 2009, Poutanen & Leppänen 2021). Wikgren (1996) specifically points out the importance of Segerstråle in the formulating and testing of specific hypotheses (which was not common in the early half of the 20th century) and following up on his thinking through extensive field work leading to experimental testing of both intra-and interspecific interactions of the zoobenthos (an approach largely neglected until the 1980s and 1990s). Through his examples in both research and education, he gave the younger generations a chance to realise the importance of knowing the scientific heritage and past thinking in order to understand and comprehend the present, and even be able to predict future responses to environmental change (as an example, Segerstråle 1957a mentioned non-native invasive species before they were discussed at all for our coastal waters, perhaps because general zoogeography and the distribution of glacial relict-species as well as paleofossil remains of bivalve shells were among his themes – see Segerstråle 1957b). To name just a few, Segerstråle as a person and through his publications significantly and positively influenced the thinking and work of Finnish benthic ecologists such as V. Sjöblom, P. Bagge, P. Tulkki, E. Leppäkoski, J. Lassig, A.-B. Andersin, H. Sandler, R. Varmo, E. Bonsdorff and A. Norkko. Through them there is now an active and gender-balanced generation of researchers at universities and research institutes (M. C. Nordström, H. Nygård, A. Törnroos-Remes, A. Villnäs and others).

Based on observations in the field, Segerstråle (1927) reformed the understanding of possible migratory behaviour of bivalves. *Tellina – Macoma - Limecola baltica* (*balthica*) seemed to move towards deeper waters along the surface of the sediment. His reasoning was almost 70 years later supported by Bonsdorff et al. (1995). Thus, already from the onset of his scientific career, Segerstråle dared ask questions for the sake of advancing science and inspiring novel research. Segerstråle's main field studies were on the benthic infauna along the southern Finnish coast, specifically in the archipelagos of Pellinge and Tvärminne. Finding similar patterns of species assemblages, and in population dynamics, he was able to reconstruct and interpret settling of juveniles, and both positive and negative correlations between species as well as population dynamics for the bivalve *Macoma* (*Limecola*) *balthica* and the amphipod *Pontoporeia* (*Monoporeia*) *affinis*, as well as between communities and their environmental drivers, notably salinity, temperature, and depth (Segerstråle 1933, 1962). A key-factor for his understanding of the animal-sediment interactions was the fact that ground-breaking work on sediment-chemistry was being conducted simultaneously at the Finnish institute of marine research, where Segerstråle was employed (Gripenberg 1934, Poutanen & Leppänen 2021). In addition, Segerstråle (1933, 1962) initiated and inspired the long-term studies of coastal and archipelago benthic infauna that later became the foundation for modern area-specific monitoring and interpretations of mechanisms driving population- and community change for coastal zoobenthos used as indicators of ecosystem health (Bonsdorff et al. 2003, Rousi et al 2013, Hewitt et al. 2016, Forsblom et al. 2021).

Studying distributional patterns within and between the local benthic invertebrate assemblages on the coast of the Gulf of Finland (most notably around Tvärminne zoological station, where accompanying environmental parameters were continuously recorded), Segerstråle (1957a) was able to draw general conclusions comparable to the global ones made by Gunnar Thorson in Denmark (1957). His zoogeographical interests expanded to encompass the concept of glacial relicts (Segerstråle 1957b), with special focus on marine, limnic and brackish water crustaceans (isopods, amphipods, and mysids), thus setting the stage for later genetical studies concerning speciation driven by gradual geographical isolation (for example Väinölä et al. 1994).

Biological interactions such as competition, predation, and physical disturbance are hard to analyse in the field. Yet Segerstråle in his seminal papers (1969, 1973) put forward the famous *Macoma-Pontoporeia* theory, in which he postulated that the negative correlation found in the field between newly settled individuals of the bivalves and high abundances of the amphipod is due to predation by the amphipod. *Pontoporeia* was generally considered to be deposit-feeding on sediment-particles and organic matter rather than showing predatory behaviour, and colleagues elsewhere doubted and contested his theory (notably Ankar 1976). Segerstråle (1978) defended his findings and his theory, but it took another 20 years before he was proven right (Ejdung & Elmgren 1998), after experiments first confirming that the *Macoma*-spat was indeed a favourable food-item for other invertebrate predators and omnivores (Ejdung & Bonsdorff 1992, Aarnio et al. 1998). The *Macoma-Pontoporeia* theory in many ways became a classic and a starting-point for modern-day food web studies of the Baltic Sea (Kortsch et al. 2021).

Conclusive remarks

As can be seen from the above, it is possible for individual scientists to become forerunners within their fields of science, and even shape the pathways their entire research subject (in this case marine benthic ecology) takes for decades. Simultaneously it is evident and important to acknowledge the role of tradition and history within science irrespective of field or topic. Without the inspiration of insightful thinkers such as von Linné, Humboldt, Darwin and others, there would perhaps not have developed a need for collecting specimen for museum-purposes, and without such collections the concepts of studying organisms in their environment and the interactions between them, be they natural or anthropogenically modified. Sven G. Segerstråle was one of perhaps a handful of such marine scientists in Finland. Through his biological and ecological curiosity-driven interests and works, strong generations of scientists were fostered, and today we see how such broad and long-term knowledge allows us to contribute to the scientific debate on a basin-wide and even on a global scale (Reusch et al. 2018). It is safe to say that for scientific progress we need both an understanding of and respect for scientific tradition, and an open innovative and curiosity-driven research agenda.

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