MORPHOLOGICAL AND ECOLOGICAL FEATURES OF *THEODOXUS FLUVIATILIS* (LINNAEUS, 1758) FROM BALTIC BRACKISH WATER AND GERMAN FRESHWATER POPULATIONS

M.L. ZETTLER[1]*, J. FRANKOWSKI[1], R. BOCHERT[1], M. RÖHNER[1]

Abstract *In an investigation of the differences and similarities within the species* Theodoxus fluviatilis, *we analysed 11 brackish water populations from the Baltic Sea and 8 freshwater populations from northern Germany.* T. fluviatilis *from the two habitats are primarily distinguished by different habitat preferences. We have never observed the migration or colonization of rivers by brackish water animals or vice versa. While mostly stones and wood serve as typical substrata in freshwater, we found both stones and plants* (Fucus, Potamogeton, Zostera) *as habitats in brackish water environments. In an analysis of morphology (shell size, operculum, radula), we found no significant differences between brackish and freshwater populations of* T. fluviatilis *in the Baltic Sea area. The variability of shell morphology and ecological behaviour of* T. fluviatilis *within and/or between brackish and freshwater populations is most likely based on different habitat conditions and demonstrates the large phenotypic plasticity of the species.*

Key words Theodoxus fluviatilis, *Baltic Sea, ecology, morphology, operculum, radula, brackish water, freshwater.*

INTRODUCTION

Since Linnaeus decribed two different species for the Baltic area in 1758, *Nerita fluviatilis* from freshwater and *N. littoralis* from brackish waters, opinions differ as to whether these are different species, subspecies, forms, varieties or adaptations. In recent decades the scientific opinion has concluded that these are simply two different forms of one species, namely *Theodoxus fluviatilis* (Linnaeus, 1758).

The freshwater form (*Theodoxus fluviatilis fluviatilis*) is very common in central Europe. Its range extends from Western Russia to Iberia and from southern Scandinavia to the Balkan peninsula. *T. fluviatilis* is more common in central-eastern Europe (Glöer, 2002). If we restrict our area of focus to the Baltic Sea, the freshwater *Theodoxus* is common in all continental Baltic states (Russia, Estonia, Lithuania, Latvia, Poland, Germany, Denmark). In Scandinavia (Norway, Sweden) and Finland freshwater populations are missing or are very sparse. Only the southern provinces of Sweden and the vicinity of Stockholm belong to the distribution area (Hubendick, 1944; 1947; Nyman & Skoog, 1977; von Proschwitz, 2001). In Finland, isolated freshwater populations are known only from the Åland islands (Segerstråle, 1945; Carlsson, 2000). From freshwaters in Norway *T. fluviatilis* was erroneously mentioned (see Økland 1990, p 165).

The brackish water form (*Theodoxus fluviatilis littoralis*) is found in moderate saline areas of the North Sea and Baltic Sea. In the North Sea we know it from the Scottish Orkneys (Boycott, 1936; Nicol, 1938) and from brackish habitats in Denmark (Fretter & Graham, 1978). It lives all over the Baltic Sea with concentrations in the less brackish areas of inner coastal waters in the southern part and in regions of decreasing salinities off the coast of the northern part (Fig. 1). The salinity varies from 2-3 psu in the inner parts of the large gulfs, to 6-8 psu in the Baltic proper, to 20-24 psu in the Kattegat. Given an available substratum, *Theodoxus* is able to colonize zones between coastal and offshore waters to a depth of 60 m (e.g. Wlodarska-Kowalczuk & Janas, 1996). In the more saline areas of the southern Baltic, *Theodoxus* is restricted to inner coastal waters like

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Bodden and Haffe. The salinity varies between 2 and 15 psu. From the Belt Sea (South) to the Baltic Proper (North) the salinity decreases within the Baltic. Below 7-8 psu we also find populations in off-shore waters. In the Arkona Basin we observed specimens on stones and boulders up to depths of 23 m. In Poland (Gdansk Basin) the species was observed at a depth of 60 m (Wlodarska-Kowalczuk & Janas, 1996).

Some important *Theodoxus* localities surrounding the Baltic are: Schlei estuary, Darss-Zingst Bodden Chain and Greifswalder Bodden in Germany; Puck Bay and Wisla lagoon in Poland; Curonian lagoon in Lithuania; Riga Bay in Latvia; Väinameri and the Gulf of Finland in Estonia; certainly all the way from Tvärminne, across the Archipelago Sea to the Åland Islands and along the Swedish east coast up to the northern most parts

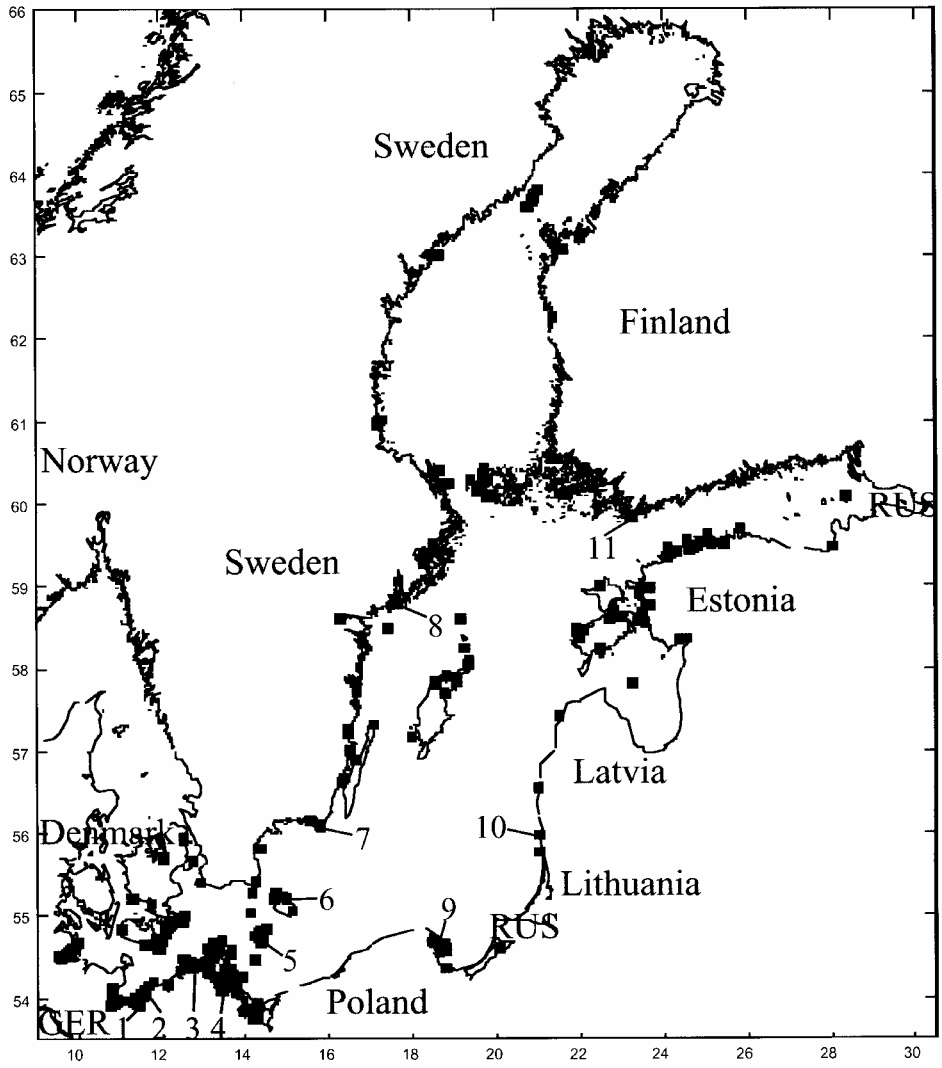

Figure 1 Distribution of *Theodoxus fluviatilis* within the Baltic Sea. The numbers indicate the sampling points of material which is included in this study and refer to table 1.

at Luleå; along the Finnish coast probably similarly distributed to the North; Bornhom and Roskilde Fjord in Denmark (see Figure 1). In Idefjorden (Skagerrak-Area), situated at the border between Norway and Sweden, an earlier record (19th century) of a brackish water population of *T. fluviatilis* exists (von Proschwitz, 2001). Due to heavy pollution during part of the 20th century it has probably died out there (Afzelius & Hardeng, 1995, von Proschwitz, 2001).

Apparently, it is extremely difficult to distinguish species of *Theodoxus* (Bandel, 2001). The main morphological features used for identification are size, colour patterns of the periostracum, the operculum and the radula, all of which are highly variable in this genus.

T. fluviatilis from brackish and freshwaters differ in the gross morphology of their shells. Specimens from freshwater on average become larger (Ulrich & Neumann, 1956; Kangas & Skoog, 1978) and have thicker shells than those from brackish water environments (Ulrich & Neumann, 1956). Some other differences between *Theodoxus* from brackish and freshwater habitats have been reported, including reproduction, behaviour, habitat demands and salinity tolerance (Bondesen, 1940; Neumann, 1960; Kangas & Skoog, 1978; Bandel, 2001; Glöer, 2002).

The aim of this study is to describe the ecological observations (salinity, substrata, abundance) and morphological features (shell size, operculum, radula) of brackish and freshwater populations of *Theodoxus fluviatilis*. Which differences could we find between these populations? Are there two different species in the Baltic Sea area, or merely one highly variable taxon?

Material and Methods

In order to assess the current distribution of *Theodoxus fluviatilis* in the Baltic Sea, the following papers were checked and analyzed in addition to our own observations:

Germany: For German Baltic waters several papers exist with information on *T. fluviatilis*. For more information of this area see the bibliography and database from Gerlach (2000) and Zettler *et al.* (in prep.). Some papers with important information on the distribution of *Theodoxus* are Krüger & Meyer (1937), Grahle (1932), Jaeckel (1940, 1952), Seifert (1938)

Poland: Falniowski *et al.* (1977), Falniowski (1989), Wlodarska-Kowalczuk & Janas (1996), Zmudzinski (1997), Haque et al. (1997), Kotwicki et al. (1999), J. Warzocha (pers. comm.)

Lithuania: D. Daunys (pers. comm.)

Latvia: Doss (1896), Knipowitsch (1909), Schlesch (1927, 1942)

Estonia: Knipowitsch (1909), Habermann (1935), Järvekülg (1979), Kotta & Kotta (1997)

Finland: Knipowitsch (1909), Segerstråle (1945), Boström & Bonsdorff (1997), Carlsson (2000)

Sweden: Knipowitsch (1909), Hubendick (1944, 1947), Skoog (1971), Kautsky *et al.* (1981, 1988), Kautsky (1989), Malm *et al.* (1999), von Proschwitz (2001)

Denmark: Schlesch (1934), Larsen (1936), Muus (1967), Rasmussen (1973)

[Norway: Afzelius & Hardeng (1995), von Proschwitz (2001), not included in Figure 1, because the Skagerrak and Kattegat were not taken into account in this paper]

Specimens were collected manually (handnet, diving) or by grabbing (Van Veen grab) at several brackish water and freshwater sites. Table 1 describes the assortment of the localities we used in this study. Shell length and shell height were measured using a stereo microscope (Stemi SV 11, CARL ZEISS, Germany). The indication of measurements are shown in Fig. 2. The dry weight of specimen was determined after

TABLE 1

Theodoxus fluviatilis material used in this study. The numbers of brackish water populations refer to Fig. 1. Besides we sampled and analysed some other populations (e.g. from Gotland and Öland)

site	country	year	Lat. [° N]	Long. [° E]	depth [m]	salinity [psu]	substrate
Baltic (1) -Poeldamm	Germany	2001	53.967	11.444	0.2 m	12.0	stones
Baltic (2) -Salzhaff	Germany	2002	54.064	11.599	0.3 m	11.0	stones
Baltic (3) -Barther Bodden	Germany	2002	54.414	12.769	0.4 m	8.3	plants
Baltic (4) -Greifswalder Bodden	Germany	2002	54.339	13.500	0.4 m	6.0	plants
Baltic (5) -Adlergrund	Germany	1999	54.459	14.232	12-23 m	7.4	stones
Baltic (6) -Bornholm	Denmark	2000	55.030	15.117	0.3 m	6.0 - 8.0	stones/ plants
Baltic (7) -Karlskrona	Sweden	2001	56.167	15.584	0.3 m	6.0 - 8.0	plants
Baltic (8) -Askö	Sweden	2002	58.483	17.420	0.2-5 m	6.0	stones/ plants
Baltic (9) -Puck Bay	Poland	1974	54.675	18.494	0.5 m	6.5 - 7.5	plants
Baltic (10) -Klaipeda	Lithuania	2002	55.975	21.034	14.1 m	7.0	stones
Baltic (11) -Tvärminne	Finnland	2003	59.833	23.201	0.5 m	5.0 - 6.0	plants
Lake-Großer Plöner See	Germany	2000	54.147	10.442	0.3 m	freshwater	stones
Lake-Mühlengeezer See	Germany	1997	53.762	12.060	0.3 m	freshwater	stones
Lake-Pinnower See	Germany	1997	53.608	11.540	0.3 m	freshwater	stones
Lake-Rudower See	Germany	1998	53.117	11.543	0.3 m	freshwater	stones
Lake-Schaalsee	Germany	1999	53.585	10.959	0.3 m	freshwater	stones
River-Alte Peene	Germany	1997	53.865	13.810	0.5 m	freshwater	plants
River-Bresenitz	Germany	2001	53.675	12.044	0.2 m	freshwater	stones
River-Randow	Germany	2002	53.615	14.103	0.5 m	freshwater	stones

drying in a heatchamber (60 °C, 24 h) and the shell weight after heating at 500 °C for 24 h (M 110, HERAEUS INSTRUMENTS, Germany) with laboratory balance (RC210P, SARTORIUS AG, Germany). The relationship between shell length and shell height and shell weight respectively were independently regressed. The software used was Excel. For the test of significance we calculated the confidence interval (95 %) for each regression. For a comparison of the different populations we analysed the radula from one specimen of each site. Three measurements of the central and two of the large intermediary teeth were taken (Fig. 2). Three different ratios were calculated (see Figure 2). The pictures were made by digital cam NIKON Coolpix 995 and by using REM (Cam Scan 44WEX).

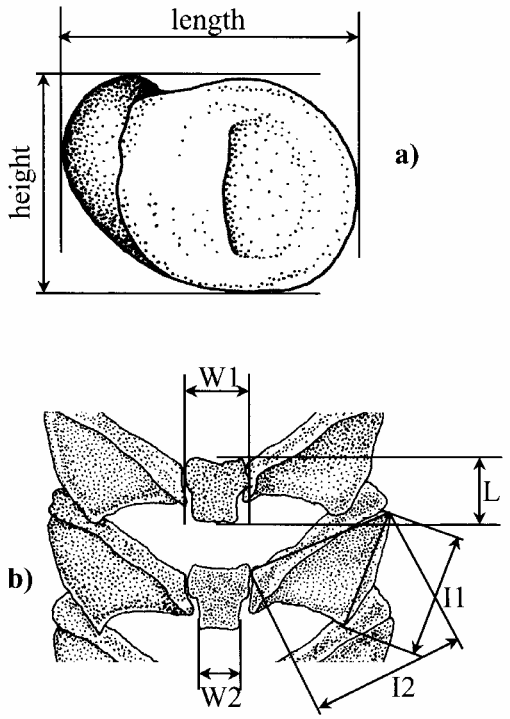

Figure 2 **a)** Scheme for the measurements of the shell length and height. **b)** Part of the *Theodoxus* radula (central and the two large intermediary teeth). Measurements of different radula features are indicated. Following relations were calculated: L/W1 and L/W2 for the central tooth, Q=I2/I1 for the large intermediary tooth.

RESULTS

ECOLOGICAL OBSERVATIONS

T. fluviatilis from brackish waters are distinguished from freshwater individuals by having different habitat preferences. We never observed the migration or colonization of brackish water animals into rivers or vice versa. Generally, we found a zone between both habitats which is not occupied by *Theodoxus*.

Individuals from freshwater occupy running waters or the littoral (lotic) zone of bigger lakes. These habitats are generally highly oxygenated. *Theodoxus* settles on hard substrata like stones, wood, and in some circumstances, on plants (*Phragmites australis*, *Nymphaea alba*, *Nuphar lutea*). In inner coastal waters and in nearshore waters off the coast (not deeper than 5-10 m) with moderate salinities (between 2 and 8 psu) *Theodoxus* mostly colonizes phytal substrata like *Fucus vesiculosus*, *Potamogeton* spp. or *Zostera marina*. We observed a maximum abundance between 200 and 1000 ind./m² in the boddens (shallow and sheltered coastal water of the southern Baltic with oligo- and mesohaline conditions) of Darss-Zingst. In more saline regions (10-20 psu) the species prefers hard substrata. In deeper areas (below 15 m and without plants) stones, boulders and sometimes *Mytilus*-aggregates are good habitats for *Theodoxus* as well. At the Adlergrund/Rönnebank, a shallow and stony area between the islands of Bornholm and Rugia, we found an abundance around 200 ind./m² in September 1999 and May 2002.

MORPHOLOGICAL FEATURES

Regarding periostracum coloration *T. fluviatilis* is a highly variable species (Fig. 6, 7). In the outer coastal waters of the Baltic Sea the nearly black and often corroded form of shell is predominant (Fig. 6a, b) whereas in the inner (sheltered) parts of the coastal waters the yellowish-green form prevails (Fig. 6g-n). Marked differences exist among the freshwater populations as well. The background colour may be pale or the whole shell may be dark. The shell is ornamented with a pattern of yellow-white streaks (Fig. 7a, b), netlike structures (Fig. 7d, e) or dots (Fig. 7g-n). Excluding the largest individuals, the regressions between shell length and shell height of both freshwater and brackish water populations were very similar (Fig. 3). The difference between them is not significant. *T. fluviatilis* from brackish water habitats grew to a length of up to 9.3 mm and a height

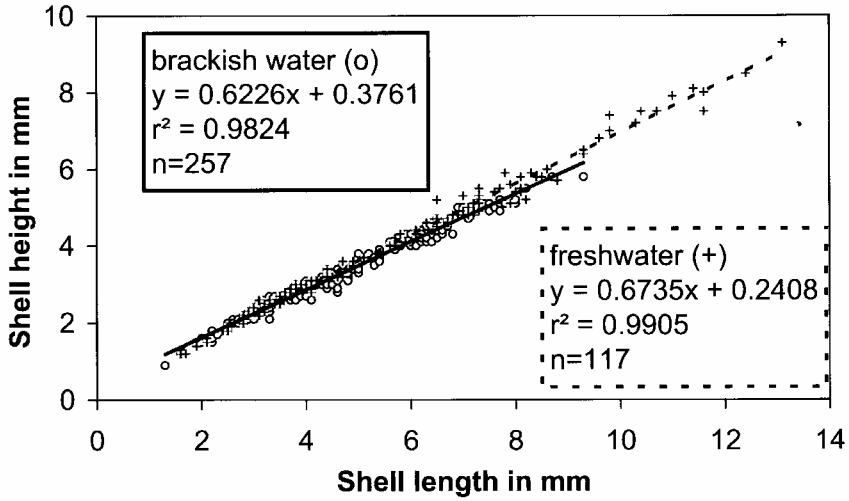

Figure 3 The regression line for shell length and shell height of *Theodoxus fluviatilis* from brackish and freshwater populations.

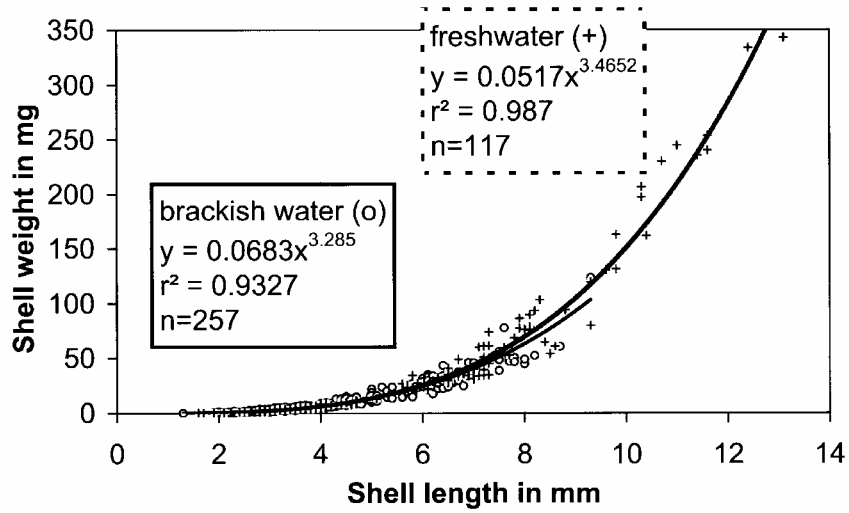

Figure 4 The regression line for shell length and shell weight of *Theodoxus fluviatilis* from brackish and freshwater populations.

of 5.8 mm. The maximum shell length of freshwater populations was 13.1 mm and the height reached was 9.3 mm. Also, the relations between shell length and shell weight are very similar across habitats (Fig. 4). We found no significant difference. Our data show that there is no change in the relationship between shell length and weight across the entire range of sizes. The maximum shell weight of brackish water *Theodoxus* was 124 mg whereas the shells of freshwater specimens weighed 343 mg at the most.

Regarding the radula measurements both the relations within the single central tooth (L/W1 and L/W2) and the large intermediary teeth (Q) showed no significant differences between *T. fluviatilis* from brackish water or freshwater habitats (Fig. 5). Even

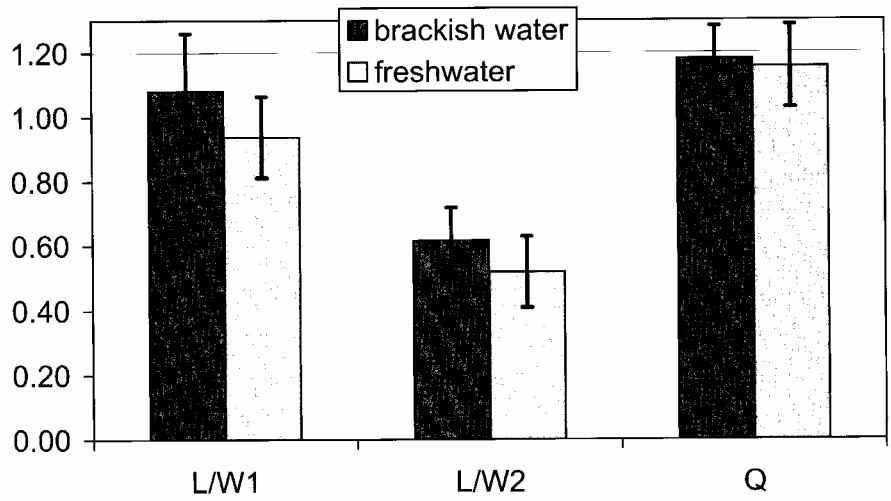

Figure 5 The relation between different radula features of the central tooth (L/W1, L/W2) and of the large intermediary tooth (Q) of *Theodoxus fluviatilis* from brackish and freshwater populations. The measurement of these parameters are shown in figure 2.

when the substrata (stones or plants) of the populations (see Table 1) were taken into account (not shown in figure), we never found characteristic features to justify separate radula shapes.

Microscopic inspection of the opercula revealed no differences between brackish water and freshwater individuals (Fig. 6, 7). The operculum is equipped with a ridge on the inner side, supporting the attachment of the columellar muscle. Usually in *T. fluviatilis*, there is no knob on the opercular hinge.

DISCUSSION

Considering coloration, *T. fluviatilis* is a variable species both in brackish water and freshwater habitats. The colour and the patterns of the periostracum are influenced by external factors like ionic composition of the milieu and possibly by the substratum and/or nutrition (Rotarides, 1932; Jaeckel, 1952; Neumann, 1959; Heller, 1979; Dillon, 2000). In the outer coastal waters of the Baltic Sea, the nearly black and often corroded form of shell is predominant, whereas in the inner parts of the coastal waters mainly the yellowish-green form prevails. Both forms are indicative of different substrata. The animals from lotic areas with stony substrata are more black. On soft bottom and in more sheltered areas *T. fluviatilis* is confined to vegetation like *Zostera*, *Potamogeton* and *Fucus*. In these areas the more yellowish-green and transparent shells dominate. This indicates the likely influence of habitats/substrata on shell colour variability. We report some differences between *T. fluviatilis* from brackish and freshwater habitats: The mean size of the shells in brackish water habitats is smaller than in freshwater (Glöer, 2002). In a brackish water population near Askö (near the same locality as our station 1) Skoog (1971) found a maximum shell length of 8.5 mm. *T. fluviatilis* from the brackish Lochs of Harray and Stennes (Scotland) reached a shell length between 6.5 and 9 mm (Nicol, 1938). During the cruise of Knipowitsch (1909) several hundred specimens were collected. The maximum shell length was 9.6 mm from the locality of Ytternäs

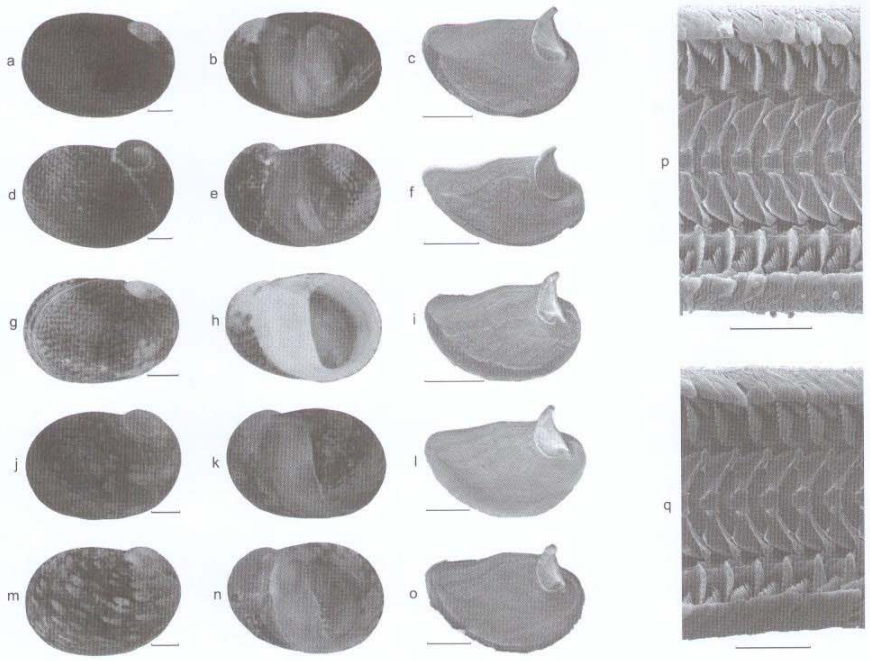

Figure 6 *Theodoxus fluviatilis* from different brackish water locations (see Table 1 for more information). **a-c)** Askö, Sweden, **d-f)** Tvärminne, Finland, **g-i+q)** Puck Bay, Poland, **j-l+p)** Barther Bodden, Germany, **m-o)** Greifswalder Bodden, Germany. The scale bar is always 1000 µm except for the radula which is 100 µm.

(Mariehamn) on Åland (Finland). The upper shell length in our study of brackish water specimens was 9.3 mm (Greifswalder Bodden). The maximum shell length of *T. fluviatilis* in freshwater was 13.1 mm (River Randow) which is in the upper range of this species (e.g. Falniowski, 1989; Glöer, 2002).

In brackish water the size of the egg capsules is smaller and the number of eggs within each capsule is lower (about 40%) (Bondesen, 1940; Graham, 1988). Further differences occur with respect to their behaviour. *T. fluviatilis* in freshwater is restricted (with some exceptions; *Phragmites australis*, *Nymphaea alba* and *Nuphar lutea*) to hard substrata, scraping food with its radula (Bandel, 2001). For example stones offer a counterpart for the radula when the animal is grazing on diatoms (Ulrich & Neumann, 1956; Neumann, 1961; Carlsson, 2000; Zettler, 2000). In the laboratory it was possible to keep the animals on plants for a restricted time only (Neumann, 1961). Carlsson (2000) found *T. fluviatilis* in one lake on the Åland Islands under the leaves of water lilies (*Nuphar lutea*), which may be explained by the fact that the plants are offering the same kind of substratum as stands of bladder-wrack (*Fucus vesiculosus*) and eelgrass (*Zostera marina*) on which it is often found in the Baltic Sea (Boström & Bonsdorff, 1997; Malm *et al.*, 1999; this study). These findings may indicate that there are differences in the construction of the radula of *Theodoxus* from both habitats (brackish water or freshwater, stones or phytal). No evidence for this hypothesis was found in the present study. The radular features (central and intermediary teeth measurements) showed no significant differences between brackish and freshwater specimens and between individuals from stony or phytal substrata.

Some investigations have been made on the adaptability of *T. fluviatilis* from

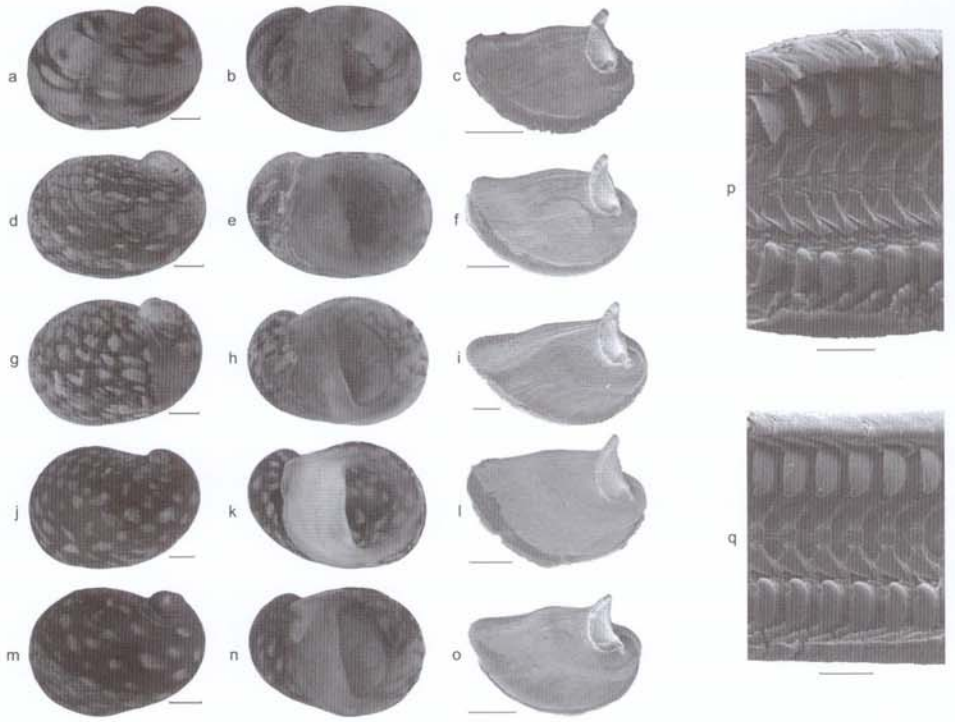

Figure 7 *Theodoxus fluviatilis* from different freshwater locations (see Table 1 for more informations). **a-c)** Bresenitz, Germany, **d-f+p)** Mühlengeezer See, Germany, **g-i)** Schaalsee, Germany, **j-l)** Randow, Germany, **m-o+q)** Rudower See, Germany. The scale bar is always 1000 µm except for the radula which is 100 µm.

brackish and freshwater habitats. Investigations of the salinity tolerance of individuals from different salinity regimes revealed differences between populations which are correlated to their origin (Kangas & Skoog, 1978; Neumann, 1960). Individuals from brackish water and freshwater populations were investigated by Neumann (1960) to assess their physiological adaptability by slowly and rapidly changing the salinity. He found a correlation between an animal's origin and its salinity tolerance. The brackish water individuals tolerate higher salinities than those from freshwater. A similar result was obtained for three populations from the northern Baltic Sea and one population from a Swedish freshwater lake (Kangas & Skoog, 1978). They found that freshwater animals were much less tolerant of salinity changes than brackish ones, and the brackish individuals vary in their ability to tolerate changes with respect to the degree of salinity in their original habitat.

Regarding morphology (shell size, operculum, radula), we found no significant differences between brackish water and freshwater populations of *T. fluviatilis* in the Baltic Sea area. The variability of shell morphology and ecological behaviour of *T. fluviatilis* within and/or between brackish water and freshwater populations demonstrates the large ecological and morphological variation within this one species. It would be of further interest to investigate populations from brackish waters and freshwaters with respect to genetic differences to obtain further knowledge regarding the species status of *Theodoxus* in the Baltic area. Some results indicate no differences between speciemens from fresh and brackish environments (Nyman & Skoog 1977, P.

Bunje, pers. comm.). According to our results, maintenance of *T. fluviatilis* as one species is justified.

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REFERENCES

AFZELIUS L. & HARDENG G. 1995 Faunaen i Enningdalsvassdraget og Indre Iddefjord, med oversikt over naturfaglig litteratur *Fylkesmannen I Ostfold, miljovernavdelingen, rapport nr.* **8**: 1-39

BANDEL K. 2001 The history of *Theodoxus* and *Neritina* connected with description and systematic evaluation of related *Neritomorpha* (Gastropoda) *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg* **85**: 65-164.

BONDESEN P. 1940 Preliminary investigations into the development of *Neritina fluviatilis* L. in brackish and fresh waters *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening* **104**: 283-318.

BOSTRÖM C. & BONSDORFF E. 1997 Community structure and spatial variation of benthic invertebrates associated with *Zostera marina* (L.) beds in the northern Baltic *Journal of Sea Research* **37**: 153-166.

BOYCOTT A.E. 1936 *Neritina fluviatilis* in Orkney *Journal of Conchology* **20**: 199-200.

CARLSSON R. 2000 The distribution of the gastropods *Theodoxus fluviatilis* (L.) and *Potamopyrgus antipodarum* (Gray) in lakes on the Åland Islands, southwestern Finland *Boreal Environment Research* **5**: 187-195.

DILLON R.T. 2000 *The Ecology of Freshwater Molluscs*. University Press, Cambridge.

DOSS B. 1896 Zur Kenntnis der lebenden und subfossilen Molluskenfauna in Rigas Umgebung, insbesondere des Rigaer Meerbusens *Korrespondenzblatt des Naturforschervereins zu Riga* **39**: 110-128.

FALNIOWSKI A. 1989 Prosobranchs (Prosobranchia, Gastropoda, Mollusca) of Poland. I. Neritidae, Viviparidae, Valvatidae, Bithyniidae, Rissoidae, Aciculidae *Folia Zoologica* **35**: 1-148.

FALNIOWSKI A., DYDUCH A. & SMAGOWICZ, K. 1977 Molluscs from Puck Bay (Baltic Sea) collected in 1973 *Acta Zoologica Cracoviensis* **22**: 507-531.

FRETTER V. & GRAHAM A. 1978 The prosobranch molluscs of Britain and Denmark. Part 3. Neritacea, Viviparacea, Valvatacea, terrestrial and freshwater Littorinacea and Rissoacea *Journal of Molluscan Studies* **Suppl. 5**: 101-152.

GERLACH S.A. 2000 Checkliste der Fauna der Kieler Bucht und eine Bibliographie zur Biologie und Ökologie der Kieler Bucht *Bericht Bundesanstalt für Gewässerkunde BFG* **1247**: 1-376

GLÖER P. 2002 Mollusca I. Die Süßwassergastropoden Nord- und Mitteleuropas. Bestimmungsschlüssel, Lebensweise, Verbreitung *In* Groh, K. & C. Groh (eds) *Die Tierwelt Deutschlands und der angrenzenden Meeresteile nach ihren Merkmalen und nach ihrer Lebensweise* 1-327 ConchBooks, Hackenheim.

GRAHAM A. 1988 Mollusca: Prosobranch and pyramidellid gastropods. Key and notes for the identification of the species *In* Kermack, D.M. & R.S.K. Barnes (eds)*Synopsis of the British Fauna (New Series)* 1-662 E.J. Brill & W. Backhyus, Leiden.

GRAHLE H.-O. 1932 Zur Molluskenfauna Schleswig-Holsteins I *Archiv für Molluskenkunde* **64**: 136-145.

HABERMANN H. 1935 Vesikinga (*Theodoxus fluviatilis* L.) levi kust Eestis *Eesti loodus*: 8-10.

HAQUE A.M., SZYMELFENIG M. & WESLAWSKI J.M. 1997 Spatial and seasonal changes in the sandy littoral zoobenthos of the Gulf of Gdansk *Oceanologia* **39**: 299-324.

HELLER J. 1979 Visual versus non-visual selection of shell colour in an Israeli freshwater snail *Oecologia* **44**: 98-104.

HUBENDICK B. 1944 *Theodoxus fluviatilis*, en av vara sötvattensnäckor *Svensk Faunistisk Revy* **6**: 3-7.

HUBENDICK B. 1947 Die Verbreitungsverhältnisse der limnischen Gastropoden in Südschweden *Zoologiska Bidrag fran Uppsala* **24**: 419-559.

JAECKEL S.G.A. 1952 Zur Ökologie der Molluskenfauna in der westlichen Ostsee *Schriften des Naturwissenschaftlichen Vereins für Schleswig-Holstein* **26**: 18-50.

JAECKEL S.H. 1940 Die Brackwassermollusken der deutschen Meeresküsten *Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin*: 114-130.

JÄRVEKÜLG A. 1979 *Donnaja fauna vostotschnoj tschasti Baltijskogo Morja* Balgus, Tallin.

KANGAS P. & SKOOG G. 1978 Salinity tolerance of *Theodoxus fluviatilis* (Mollusca, Gastropoda) from freshwater and from different salinity regimes in the Baltic Sea *Estuarine and Coastal Marine Science* **6**: 409-416.

KAUTSKY H. 1989 Quantitative distribution of plant and animal communities of the phytobenthic zone in the Baltic Sea *Contributions from the Askö Laboratory* **35**: 1-80.

KAUTSKY H., WIDBOM B. & WULFF F. 1981 Vegetation macrofauna and benthic meiofauna in the phytal zone of the Archipelago of Luleå – Bothnian Bay *Ophelia* **20**: 53-77.

KAUTSKY H., KAUTSKY U. & NELLBRING S. 1988 Distribution of flora and fauna in an area receiving pulp mill effluents in the Baltic Sea *Ophelia* **28**: 139-155.

KNIPOWITSCH N.M. 1909 Otcetch o rabotach v Balticeskom more N.M. Knipowitscha i S.A. Pawlowitscha letom 1908 g. po sobiraniju morskoy fauny dlja Zoologiceskago Museja Imperatorskoy Akademii Nauk *Annuaire du Musee Zoologique de l'Academie Imperiale des Science de St.-Petersburg* **14**: 131-245.

KOTTA J. & KOTTA I. 1997 Do the towns of Helsinki and Tallin oppress the zoobenthos in the adjacent sea? *Estonian Marine Science Institute Report Series* **8**: 54-71.

KOTWICKI L., WLODARSKA-KOWALCZUK M. & WIECZOREK P. 1999 Macrozoobenthos of the sandy littoral zone in the military area between Hel and Jurata *Oceanological Studies* **28**: 97-107.

KRÜGER K. & MEYER P.-F. 1937 Biologische Untersuchungen in der Wismarschen Bucht *Zeitschrift für Fischerei und deren Hilfswissenschaften* **35**: 665-703.

LARSEN L. 1936 The distribution of the invertebrates in the Dybsö Fjord, their biology and their importance as fish food *Report of The Danish Biological Station to the Ministry of Agriculture and Fisheries* **41**: 1-35.

LINNAEUS C. VON 1758 *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis* Halae Magdeburgicae.

MALM T., ENGKVIST R. & KAUTSKY L. 1999 Grazing effects of two freshwater snails on juvenile *Fucus vesiculosus* in the Baltic Sea *Marine Ecology Progress Series* **188**: 63-71.

MUUS B.J. 1967 The fauna of Danish estuaries and lagoons *Meddelser fra Kommissionen for Danmarks Fiskeri- og Havundersogelser* **5**: 1-316.

NEUMANN D. 1959 Morphologische und experimentelle Untersuchungen über die Variabilität der Farbmuster auf der Schale von *Theodoxus fluviatilis* L. *Zeitschrift für Morphologie und Ökologie der Tiere* **48**: 349-411.

NEUMANN D. 1960 Osmotische Resistenz und Osmoregulation der Flußdeckelschnecke *Theodoxus fluviatilis* L. *Biologische Zentralblatt* **79**: 585-605.

NEUMANN D. 1961 Ernährungsbiologie einer rhipidoglossen Kiemenschnecke *Hydrobiologia* **17**: 133-151

NICOL E.A.T. 1938 The brackish-water Lochs of Orkney *Proceedings of the Royal Society of Edinburgh* **58**: 181-191.

NYMAN L. & SKOOG G. 1977 Species specific enzymes in some snail species (Mollusca, Gastropoda) from fresh and brackish water in Sweden *Zoologica Scripta* **6**: 327-330.

ØKLAND J. 1990 *Lakes and snails. Environment and Gastropoda in 1,500 Norwegian lakes, ponds and rivers* Universal Book Services/Dr. W. Backhuys, Oegstgeest, 516pp.

PROSCHWITZ T. VON 2001 Faunistiskt nytt 2000 – snäckor, sniglar och musslor inklusive något om afrikansk konsnäcka *Afropunctum seminium* (Morelet) och större vallsnäcka *Monacha cantiana* (Montagu) – två för Sverige nya, människospridda landsnäckor *Göteborgs Naturhistoriska Museum Årstryck*: 19-36.

RASMUSSEN E. 1973 Systematics and ecology of the Isefjord marine fauna (Denmark) *Ophelia* **11**: 1-507.

ROTARIDES M. 1932 Über die Variabilität und die Struktur der Schalenzeichnung bei den Neritinen *Zoologischer Anzeiger* **100**: 257-265.

SCHLESCH H. 1927 Zur Kenntnis der Molluskenfauna des Ostbaltikums mit besonderer Berückschtigung der in Lettland vorkommenden Arten *Korrespondenzblatt des Naturforschervereins zu Riga* **59**: 92-126.

SCHLESCH H. 1934 Revidiertes Verzeichnis der dänischen Land- und Süßwassermollusken *Archiv für Molluskenkunde* **66**: 233-312.

SCHLESCH H. 1942 Die Land- und Süßwassermollusken Lettlands, mit Berücksichtigung der in den Nachbargebieten vorkommenden Arten *Korrespondenzblatt des Naturforschervereins zu Riga* **64**: 246-360.

SEGERSTRÅLE S.G. 1945 Über die Verbreitung der Süßwasserschnecke *Theodoxus* (*Neritina*) *fluviatilis* (L.) in Finnland *Commentationes Biologicae Societas Scientiarum Fennica* **9**: 1-4.

SEIFERT R. 1938 Die Bodenfauna des Greifswalder Boddens. Ein Beitrag zur Ökologie der Brackwasserfauna *Zeitschrift für Morphologie und Ökologie der Tiere* **34**: 221-271.

SKOOG G. 1971 Variations in the distribution of *Theodoxus fluviatilis* on stony locations in the northern Baltic proper *Thalassia Jugoslavica* **7**: 363-372.

ULRICH H. & NEUMANN D. 1956 Zur Biologie einer Salzwasserpopulation der Flußdeckelschnecke (*Theodoxus fluviatilis* L.) *Natur und Jagd in Niedersachsen*: 219-222.

WLODARSKA-KOWALCZUK M. & JANAS U. 1996 Hydrogen sulphide and other factors influencing the macrobenthic community structure in the Gulf of Gdansk *Oceanologia* **38**: 379-394.

ZETTLER M.L. 2000 Bewertung des ökologischen Zustandes von Fließgewässern in Mecklenburg-Vorpommern über die Malakofauna als Indikatororganismen *Natur und Naturschutz in Mecklenburg-Vorpommern* **35**: 3-63.

ZETTLER M.L., LEUCHS H., RÖHNER M. & KÖNIG B. in prep. Atlas zur Entwicklung und Verbreitung des Makrozoobenthos der Ostsee zwischen Fehmarnbelt und Usedom - Daten von 1839 bis 2001 *BfG-Schriften.*

ZMUDZINSKI L. 1997 Resources and bottom macrofauna structure in Puck Bay in the 1960 and 1980 *Oceanological Studies* **26**: 59-73.