North Sea and Baltic houting

Gill raker morphometric differentiation between populations of the endangered fishes North Sea and Baltic houting

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Content

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General information

Abstract

Biodiversity loss is a global problem of increasingly dramatic proportions. The North Sea (NSH) and Baltic houting (BH) in Germany were near extinction. Due to intensive restoration efforts, they are now slowly coming back. With regard to conservation, it is of importance to determine whether the NSH and the BH houting each are evolutionary significant units (ESUs), i.e., whether they are populations that can be considered distinct for purposes of conservation.

In this study, the heritable gill raker counts were analysed for many different populations of NSH and BH, as well as closely related lake whitefish and vendace. Genetic study results (Dierking et al in preparation) finds hybridization between NSH and BH in many locations. Objectives were to find out, whether it is possible to distinguish reliably between NSH and BH by number of gill rakers. Secondly, differences between the populations of NSH respectively BH were analysed and assessed for intermediary numbers of gill raker, which could confirm the presence of hybridization. Thirdly, it was analysed whether variability in gill raker numbers can be partly explained by individual characteristics, e.g. fish length and sex. At last, consistency for right and left gill raker counts was observed.

I found significant differences in gill raker numbers between NSH and BH, but with overlap in range. Hybridization may be present, but the original populations Peene and Treene could still be distinguished. The Baltic houtings showed a pattern with two groups. One with gill raker numbers lower than North Sea houting and another with higher numbers than NSH and close to lake whitefish. The intermediate counts between BH and lake whitefish suggested that hybridizations is present, but in addition to hybridization with NSH, lake whitefish may also play a role. Gill raker numbers were not correlated with fish length and sex. Right and left counting were found to be equal. The combination of gill raker counts, genetics and ecological data for each fish may bring additional insights into these patterns in further studies.

Introduction

The threat of losing biodiversity is an ever more urgent issue and challenge. In 1992, the United Nations Conference on Environment and Development resulted in the United Nations Convention on Biological Diversity, which was signed by 154 nations and has the goal to conserve biological diversity (The Encyclopedia of Earth 2012). The European counterpart is the "Council Directive 92/43/EEC on the Conservation of natural habitats and of wild fauna and flora". In Europe, this issue exhibits itself in the fact that 37% of European freshwater fishes are threatened at present (Freyhof

and Brooks 2011). Recent examples for this are the IUCN redlisted North Sea houting (*C. oxyrinchus*) and Baltic houting (*C. lavaretus*), which both have a high priority status in the directive.

The North Sea houting (NSH) was near extinction with only a single population remaining in the Vidå, Denmark, by the 1980s (Jäger 1999). Due to intensive restoration efforts, it is now slowly coming back. In Germany, the NSH was reintroduced to the Treene River in 1987 by releasing fry produced from Vidå caught spawning adults (Jäger 1999). The first recatches succeeded in 1989 and the houting was subsequently introduced over much of its former range (Figure 1).

Similarly, regarding the Baltic houting (BH), within Germany, the group reexpanded from a remnant population in the Peene River (although more populations existed in the Eastern Baltic Sea). It has even gained in importance as a fishery species in the German state of Mecklenburg-Vorpommern, although the population appears to depend on stocking, as was shown by the strong decline in numbers during an interruption of the stocking program between 2002 and 2009 (Jennerich and Schulz 2011).

For both NSH and BH all stocking fry originates from only one population each.

Houtings are anadromous fishes that belong to the whitefishes, coregonids. Taxonomic controversy has surrounded the houtings. Reasons are their recent evolutionary history, low barriers in gene flow and frequent hybridizations. Many studies focused on this problem (Thienemann 1922, Freyhof and Schöter 2005, Jacobsen 2010). All of them used gill raker counts as a mean of taxonomy. Gill raker counts, including the number of gill rakers on the first right branchial arch, are a highly heritable trait and therefore a well-established method to distinguish between coregonid taxa. Today, genetic analyses can be used in addition.

Schöter did a thorough study of the existing literature and analysed gill raker counts in a wide range of populations. He states, that the historical Rhein houting C. oxyrinchus is now extinct and that all remaining houting populations in the North Sea and Baltic belongs to the species C. maraena. Furthermore, he differentiates between two sympatric species in the Baltic, C. maraena and C. widegreni (2002). The debate is still ongoing. For example Hansen (2006) lists persisting NSH populations as C. oxyrinchus.

The focus, however, on this study is not the taxonomy, but the investigation of differences between NSH and BH and due to the vast controversy, I will only refer to North Sea houting (NSH) and Baltic houting (BH) in the following. Likewise, I will refer to lake whitefish (classified as C. lavaretus, C. widegreni and others) as lake whitefish (LW) and to vendace (C. albula) as vendace (V).
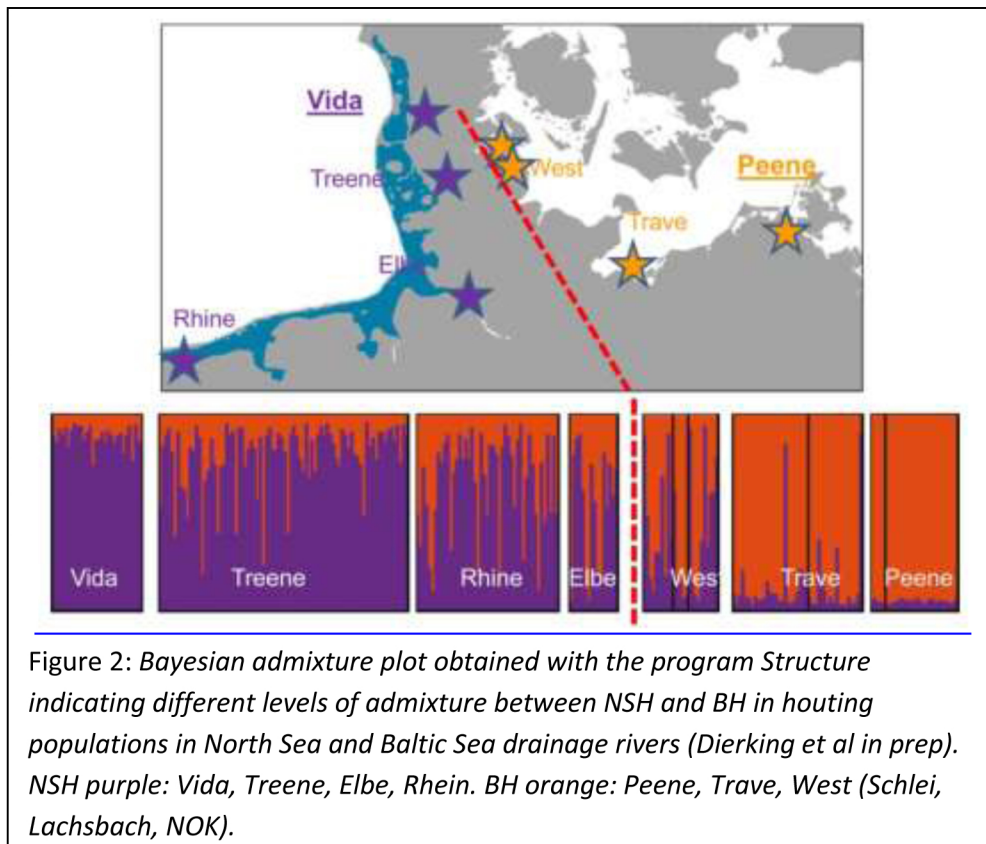

Figure 1: *Reexpansion of the NSH and BH within Germany, Denmark and the Netherlands.*
Arrows: Direction of reintroduction, from existing population to areas without fish. Yellow: BH. Purple: NSH. Red line: Border between NSH and BH. Numbers: years of reexpansion. Diagram amended after Dierking et al. (in preparation).

With regard to conservation, it is of crucial importance to determine whether NSH and BH each are evolutionary significant units (ESUs), i.e., whether they are populations that can be considered distinct for purposes of conservation. Measures commonly used to delineate ESUs include morphological or genetic distinctness and the consideration whether populations are following their own distinct evolutionary history (Holsinger 2011).

Meanwhile, a genetic study of NSH and BH (Dierking et al in preparation) finds evidence for admixture of the two taxa. Hybridizations might influence the status regarding taxa/ESU.

Figure 2: *Bayesian admixture plot obtained with the program Structure indicating different levels of admixture between NSH and BH in houting populations in North Sea and Baltic Sea drainage rivers (Dierking et al in prep). NSH purple: Vida, Treene, Elbe, Rhein. BH orange: Peene, Trave, West (Schlei, Lachsbach, NOK).*

In this study, the heritable gill raker counts were analysed for many different populations of NSH and BH, as well as closely related lake coregonids. The geographical resolution is higher than in Schöter's and others studies, and the number of tested fishes is higher in important groups. Genetic study results (Dierking et al in preparation) finds hybridization in many populations. Due to the fact that the number of gill rakers is a highly heritable trait, we expect intermediary gill raker numbers where hybridization occurs. The combination of gill raker counts as heritable trait, genetics and ecological data for each fish may bring additional insights into these patterns.

Objectives of the study were to find out whether it is possible to distinguish reliably between NSH and BH by number of gill rakers. Results might give new insights to the debate about the status as ESUs. Secondly, differences between populations were assessed. On the one hand, the expectation was homogenous taxa of NSH respectively BH due to the similar use of fry in stocking programmes (Figure 3a). On the other hand, intermediary

Figure 3a: *Schematic NSH, BH distinguishable. GRC on the x-axis, taxa/ populations on the y-axis.*
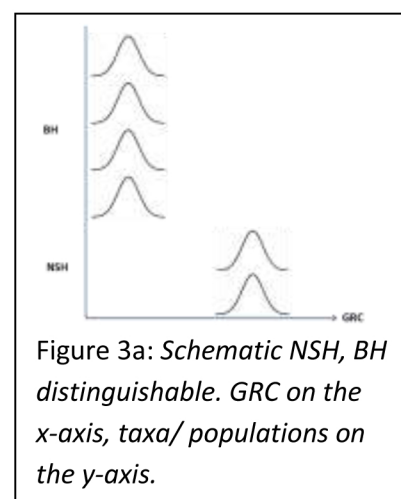
patterns of gill raker counts might occur in admixed populations due to potential hybridization (Figure 3b). Thirdly, it was analysed whether variability in gill raker numbers can be partly explained by individual characteristics, e.g. fish length and sex. The consistency for right and left gill raker counts was observed. In addition, I collected published data on gill raker counts for NSH and BH to compare my data with the literature.

Figure 3b: *Schematic intermediary patterns. GRC on the x-axis, taxa/ populations on the y-axis.*
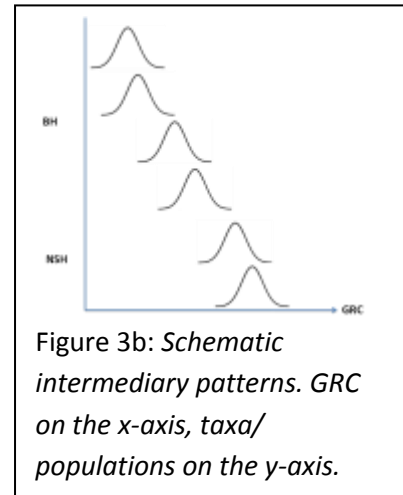
Materials and methods

Analytical methods

For this study, BH was collected from Peene, Trave, Kiel Canal, Lachsbach and Schlei; NSH from Elbe and Treene (Figure 5), and lake whitefish for comparison from Bordesholmer See, Pönitzer See, Drewitzer See and vendace from Selenter See (Table 1). Each individual was dissected. Sex, weight, standard length and total length were noted. A photo was taken for morphological comparisons; muscle biopsy samples were taken on the left side of each fish for stable isotope analysis to assess feeding ecology and migration. In addition, scales from the place of the biopsy were taken for age analysis, and a piece of the adipose fin was taken for genetic analysis (Figure 4).

Figure 4: *NSH from the Treene River (Photo: Dierking 2011). The numbers placed on the picture show a range of measurements and samples that were taken. 1: standard length (distance from the tip of the snout to the base of the caudal peduncle, 2: total length (distance from the tip of the snout to the end of the tail fin), 3: muscle biopsy (piece of muscle taken from the dorsal), 4: scales, 5: adipose fin (piece of the adipose fin was clipped).*

Stomach, heart, liver and gonads were taken out of the fish. The whole weight, gutted weight, liver weight and gonad weight were taken for the later calculation of condition factors. Next, the otoliths were taken for migration and age analysis. Finally, gills were taken for this study.

Population	Site	Number
North Sea houting	Elbe River	13
	Treene River	83
Baltic houting	Peene River	38
	Trave River	38
	Kiel Canal	13
	Lachsbach	4
	Schlei	17
Lake whitefish	Bordesholmer See	5
	Pönitzer See	29
	Drewitzer See	3
Vendace	Selenter See	29

Table 1: *Samples of the taxa NSH, BH, lake whitefish and vendace available for counts of gill rakers.*

Figure 5: *Map of populations. North Sea houting populations: T=Treene, E=Elbe. Baltic houting populations: S=Schlei, ON=Kiel Canal, L=Lachsbach, OS=Trave, RS=Peene.*

Gill raker morphometrics

The methodology for gill raker counts followed Kahilainen and Østbye (2005). The first right branchial gill arch was used. The gill raker count (GRC) as the number of all gill rakers was counted. In addition, the length of the central gill raker was measured (GRL) and the gill arch length (GAL) was taken as the sum of the short and the long gill arch part, all with a caliper (Figure 6).
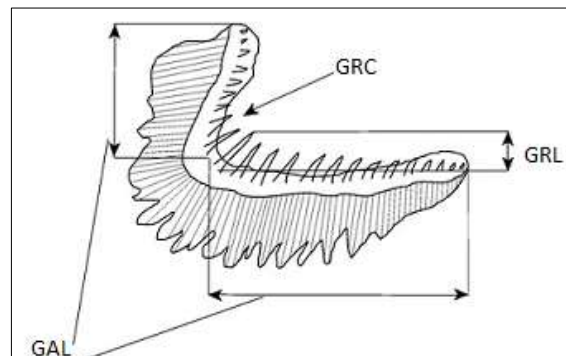
For juveniles, gill raker counts were counted under a dissecting scope (brand: Leica, type: MZ 9.5). The first right gill arch was photographed (camera: QIMAGING MicroPublisher 3.3 RTV, program: Image-Pro Plus 5.0). The lengths were measured on photos after calibration with millimetre paper.

For both adult and juvenile individuals, the left arch was used if the right arch was broken. In addition, both the right and left arch were counted and measured for some fishes for comparison.

Figure 6: *Gill raker count measurement (Kahilainen and Østbye 2005). GRC: gill raker count (number of gill rakers). GRL: gill raker length (length of the central raker). GAL: gill arch length (length of the long and the short arch).*

Data analysis

To answer the research question regarding the presence of differences between North Sea and Baltic houting populations, and to assess differences in numbers of gill rakers for fish of different length or sex, an analysis of covariance (ANCOVA) was done with taxon and sex as fixed variables and fish length as covariate. The groups of NSH and BH consisted of all examined North Sea houtings respectively Baltic houtings. The group of LW consisted of all examined lake whitefish. Regarding the question of evidence for potential hybridizations, pairwise comparisons of population means were

Figure 7: *Explanation of a boxplot.*
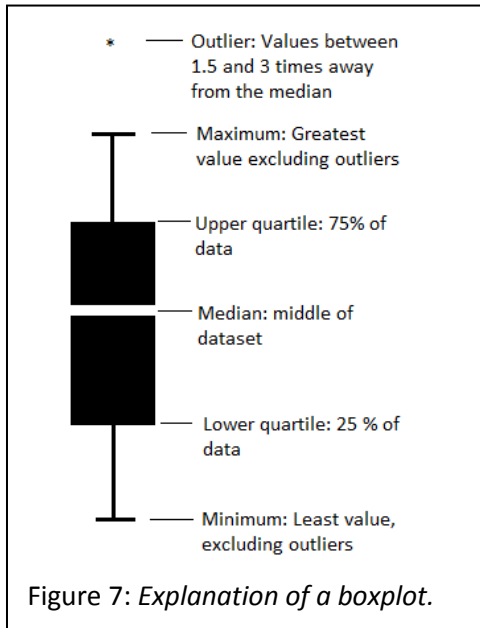
done within an ANCOVA. Hybridization would be recognizable as intermediary number of gill rakers. Consistency for counts obtained from left and right gill rakers were tested with a scatterplot and correlation analysis. For both taxon and population level, boxplots were used to show tendencies graphically. Figure 7 explains a boxplot.

To put my results into context, I did a literature review of published gill raker counts of coregonids in the same geographic area as my study objects.

Depending on availability, I noted taxon, population, year of catch, number of examined fishes, mean of gill raker numbers, standard deviation, median of gill raker numbers, the range from minimum to maximum number of gill rakers and the source of the data.

Results

When analyzed on the taxon level, gill raker numbers differed significantly between groups (ANCOVA, p< 0.001), but with overlap in range (Figure 8). In particular, BH showed significantly lower gill raker numbers than NSH which was followed by lake whitefish and vendace. Pairwise comparisons showed that each combination was significantly different (Table 2). Number of gill raker were not significantly correlated with fish length (ANCOVA, p=0.350).

These patterns are reflected by Figure Appendix-1. Likewise, sex was found not to be correlated with the gill raker numbers (ANCOVA, p=0.976).

When considered on the population level, the picture was more complicated (Figure 9). To the left, the NSH population Elbe starts, followed by Treene with lower gill raker numbers.

The figure shows that the BH populations had increasing gill raker numbers in the order Peene, Trave, Schlei, Lachsbach, and Kiel Canal (NOK). BH compared to NSH differed most between Peene and Treene (similar to Vidå). The BH populations showed a pattern with two groups. Group 1 consisted of Peene, Trave and Schlei and had lower gill raker numbers than NSH and group 2 consisted of Lachsbach and Kiel Canal and had higher gill raker numbers than NSH.

	North Sea houting	Baltic houting	Lake whitefish
North Sea houting			
Baltic houting	0.016		
Lake whitefish	<0.001	<0.001	
Vendace	<0.001	<0.001	0.008

Table 2: *The p-values of pairwise comparisons within an ANOCVA of the taxa BH, NSH, lake whitefish and vendace.*

The lake whitefish had higher gill raker numbers than both NSH and some of the BH populations. Lake whitefish from Drewitzer See stood out by having the lowest gill raker numbers of all populations, including much lower numbers than the other lake whitefish populations. The highest gill raker numbers were found in vendace from Selenter See.
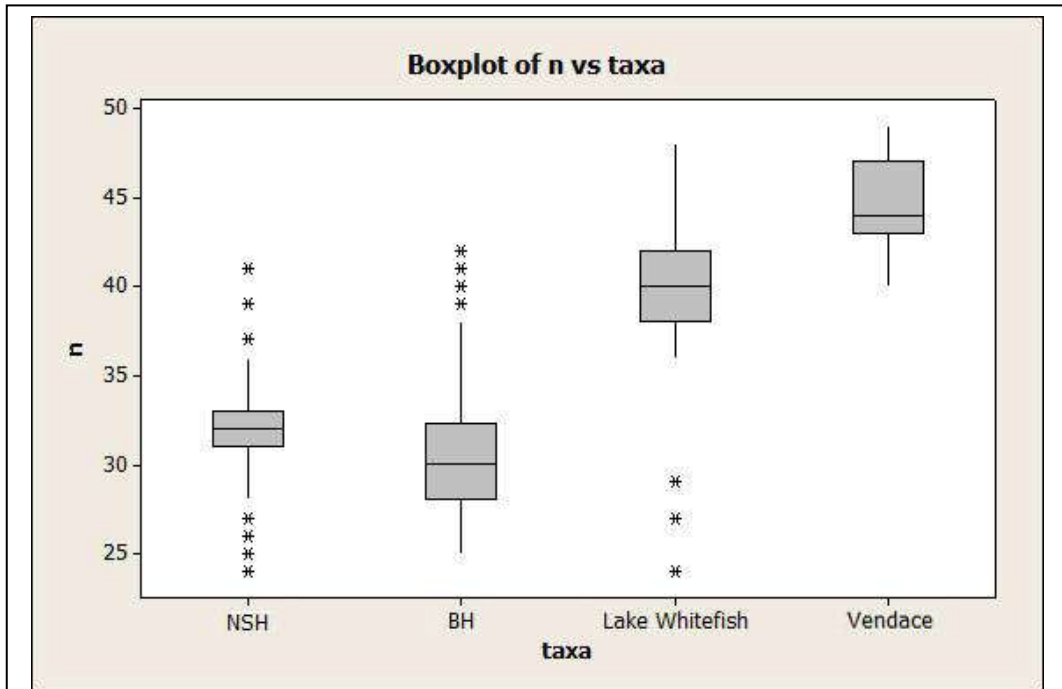
Figure 8: *Boxplot of gill raker numbers versus taxa. BH shows lower gill raker numbers than NSH which is followed by lake whitefish and vendace. The groups were formed by lumping all populations for each taxon. Every taxon is shown with a box and supplement. More details in the text. Further explanation of a boxplot in Figure 7.*

Figure 9: *Boxplot of gill raker numbers versus population. Every population is shown with a box and supplement. More details in the text. Further explanation of a boxplot in Figure 7.*

Pairwise comparisons of the populations were done with an ANCOVA (Table 3).

Within the group of BH, following groups were significantly different from each other: Lachsbach/Peene, Lachsbach/Trave and NOK/Peene,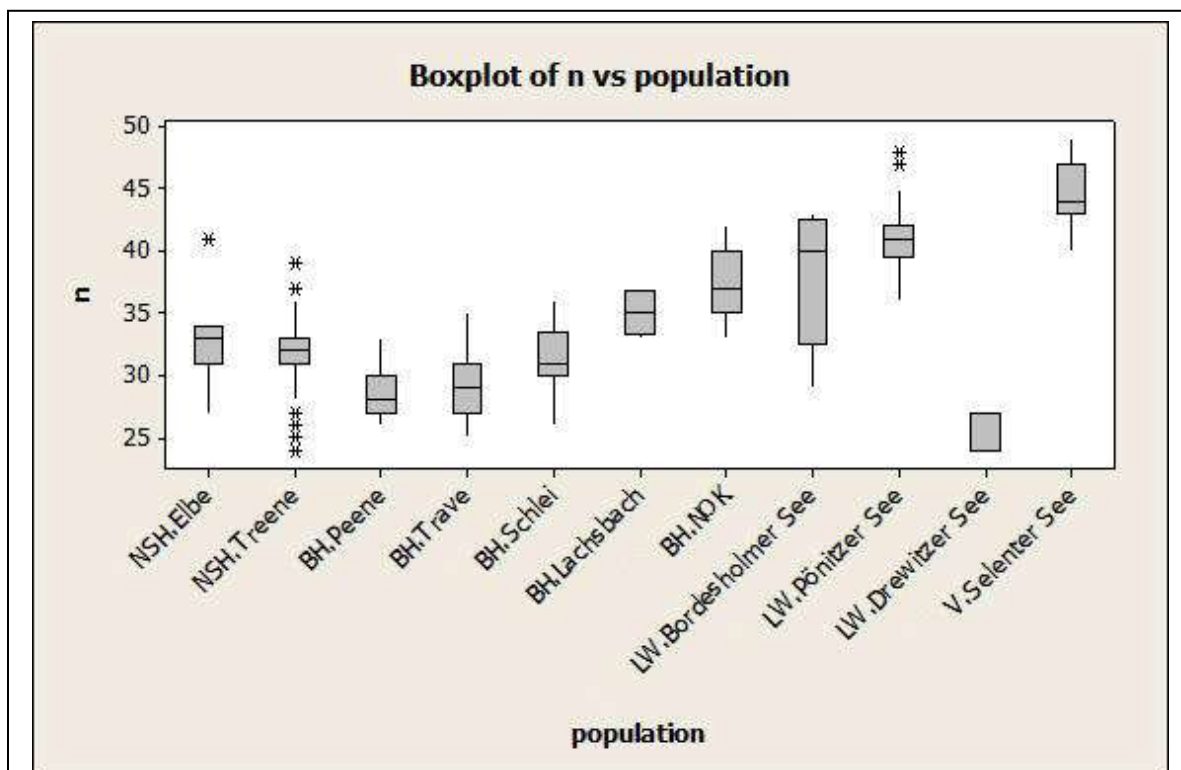 NOK/Trave, NOK/Schlei. Within the group of lake whitefish, Drewitzer See was significantly different from both Bordesholmer See and Pönitzer See.

There were some significant differences between NSH and BH, but not between NOK/Elbe, Lachsbach/Elbe, Lachsbach/Treene, Schlei/Elbe, Schlei/Treene. Likewise, there were no significant differences between following BH und LW populations: Bordesholmer See/NOK, Bordesholmer See/Lachsbach and Drewitzer See/Trave, Drewitzer See/Peene. The NSH population Elbe did not differ significantly from LW Bordesholmer See, and LW Pönitzer See did not differ significantly from vendace Selenter See.

To assess for measurement errors, I compared gill raker counts for both the right and the left side for 31 fishes (Figure 10). The two were highly correlated (Pearson correlation, $R^2=0.97$, $p=0.000$). 97% of the variability was explained by the model and only 3 % might be explained by error in measurement or variability.

The collected data were compared to published gill raker counts from NSH, BH, lake whitefish and vendace of interest (Table 4). Results were similar to the literature data for many populations. However, they also differed in some important patterns. This includes the strong differences between populations of BH observed here. Nobody ever observed such high gill raker numbers in BH as observed for Kiel Canal and Lachsbach. For Lachsbach, there was no overlap in range with the originally BH population Peene.

In general, it also looked as if ranges observed for most populations were higher than those in the literature. For example the range for NSH from this study was 24-41 while it is 28-35 in Freyhof (2005).
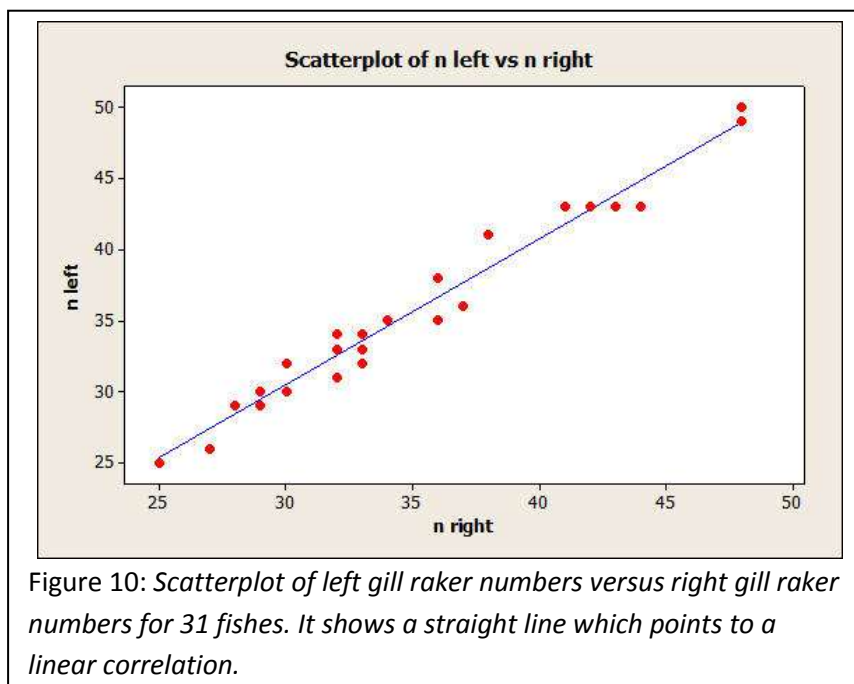

Figure 10: *Scatterplot of left gill raker numbers versus right gill raker numbers for 31 fishes. It shows a straight line which points to a linear correlation.*

Table 3: *Pairwise comparisons of populations. Upper half of the grid shows absolute differences between means, calculated as the mean for the population noted horizontal substracted from the population noted vertical. Lower half of the grid are p-values from an ANCOVA with population and sex as fixed variables and fish length as covariate. Significantly different results are bold.*

Taxon		NSH		BH					LW			V
Taxon	Population	Elbe	Treene	Peene	Trave	Schlei	Lachsbach	NOK	Bordesholmer See	Pönitzer See	Drewitzer See	Selenter See
NSH	Elbe		1.3	**4.6**	**4.1**	2	-1.8	-4.1	-4.8	**-8.5**	**8.2**	**-11.5**
	Treene	0.969		**3.3**	**2.8**	0.7	-3.1	**-5.4**	**-6.1**	**-9.8**	**6.9**	**-12.8**
BH	Peene	**0.012**	**<0.001**		-0.5	**-2.6**	**-6.4**	**-8.7**	**-9.4**	**-13.1**	3.6	**-16.1**
	Trave	**0.032**	**<0.001**	1.000		-2.1	**-5.9**	**-8.2**	**-8.9**	**-12.6**	4.1	**-15.6**
	Schlei	0.820	0.992	**0.043**	0.188		-3.8	**-6.1**	**-6.8**	**-10.5**	**6.2**	**-13.5**
	Lachsbach	1.000	0.396	**<0.001**	**0.001**	0.208		-2.3	-3	**-6.7**	**10**	**-9.7**
	NOK	0.495	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.954		-0.7	**-4.4**	**12.3**	**-7.4**
LW	Bordesholmer See	0.486	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.915	1		-3.7	**13**	**-6.7**
	Pönitzer See	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.001**	**<0.001**	0.362		**16.7**	-3
	Drewitzer See	**0.001**	**0.001**	0.519	0.334	**0.012**	**<0.001**	**<0.001**	**<0.001**	**<0.001**		**-19.7**
V	Selenter See	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.006**	0.164	**<0.001**	

Table 4: *Literature review. Sorted in Taxa and Populations. Year= Year of catch. N= number of fishes examined. Mean= mean of found gill raker numbers. SD= standard deviation. Median= median of gill raker numbers' distribution. Range= minimum-maximum gill raker number. Source= source of data.*

Taxon	Population	Year	n	Mean	SD	Median	Range	Source
NSH	Elbe (E)	2010	13	33,2	3,9	33	27-41	This study
	Elbe	1916	11	31,5	–	–	27-35	Thienemann 1922
	Elbe C. maraena	1860	2	32,5	3,5	32,5	30-35	Schöter 2002
	Treene (T)	2009-2011	83	31,9	2,6	32	24-39	This study
	Treene C. maraena	2000	19	32	1,7	–	28-35	Schöter 2002
	NSH (E, T)	2009-2011	96	32,1	2,8	32	24-41	This study
	North Sea C. maraena	–	70	–	–	32	28-35	Freyhof 2005
	Rhein C. oxyrinchus	1844-1906	14	–	–	40	38-46	Freyhof 2005
	Rhein historical C. oxyrinchus	1844-1906	9	40	1,7	–	38-43	Schöter 2002
	Rhein recent C. spec.	1967-1997	13	33	4,0	–	23-36	Schöter 2002
	Rhein recent C. maraena	1996-1997	4	32	3,4	–	28-36	Schöter 2002
	Nipså 1921	1921	3	29,3	1,5	29	28-31	Wulff Jacobsen
	Ribe 1879	1879	2	33	2,8	33	31-35	Wulff Jacobsen
	Ribe å	2009	6	29,2	1,7	29	27-31	Wulff Jacobsen
	Vesterhavet	1890	3	31,3	2,1	32	29-33	Wulff Jacobsen
	Danish North Sea inflows	1845-1890	10	30	1,9	–	28-34	Schöter 2002
BH	Kiel Canal (ON)	2010-2012	13	37,3	3,0	37	33-42	This study
	Lachsbach (L)	2011	4	35	1,8	35	33-37	This study
	Peene (RS)	2010-2011	38	28,6	1,8	28	26-33	This study

	Peene C. maraena	2000	23	30	1,6	–	25-31	Schöter
	Schlei (S)	2010-2011	17	31,2	2,5	31	26-36	This study
	Schlei	1918-1919	16	31	–	–	25-34	Thienemann 1922
	Schlei C. maraena	2000	27	28	3,5	–	23-33	Schöter 2002
	Schlei/Peene C. widegreni	2000	7	25	1,0	–	24-27	Schöter 2002
	Trave (OS)	2010-2011	38	29,1	2,7	29	25-35	This study
	BH 1 (RS, S, OS)	2010-2011	93	29,3	2,5	29	25-36	This study
	BH 2 (L, ON)	2010-2012	17	36,8	2,9	36	33-42	This study
	BH (ON, L, RS, S, OS)	2010-2012	110	30,4	3,7	30	25-42	This study
	Lebasee	1916	2	29	2,8	29	27-31	Thienemann 1922
	Baltic C. maraena	–	59	–	–	28	23-33	Freyhof 2005
LW	Bordesholmer See (MB)	2011	5	38	5,7	40	29-43	This study
	Pönitzer See (PS)	2010	29	41,7	2,7	41	36-48	This study
	LW (MB, PS)	2010-2011	34	40,6	3,4	41	29-48	This study
	Drewitzer See	2010-2011	3	25	1,7	24	24-27	This study
	Schaalsee	1916-1917	10	25,0	–	–	22-27	Thienemann 1922
V	Selenter See (CA)	2011	29	44,7	2,4	44	40-49	This study
	Selenter See	1916	15	44	–	–	40-46	Thienemann 1922

Discussion

Objectives included finding out whether it is possible to distinguish reliably between NSH and BH by number of gill rakers. Secondly, differences between populations were assessed. Thirdly, it was analysed whether variability in numbers of gill rakers can be partly explained by individual characteristics, e.g. fish length and sex. The consistency for right and left gill raker counts was observed. In addition, published data on gill raker counts for NSH and BH were collected to compare data of this study with literature.

Concerning the first objective, I found significant differences between gill rakers numbers in NSH and BH as well as lake whitefish and vendace, but with overlap in range. BH was expected to have lower gill raker numbers than NSH. For some populations this fitted, but others had higher gill raker numbers than NSH (Table 4). Over all, it was not possible to reliably distinguish between NSH and BH only by the number of gill rakers.

When lumping all populations by taxon, results of this study appear to be similar to literature values. The means for NSH are around 31-33 (Table 4), compared here 32.1 and the means for BH are around 28-30 (Table 4), compared here 30.4 including populations with higher gill raker numbers than NSH and 29.3 without those. Nevertheless, it was still possible to distinguish clearly between the original populations Treene for NSH and Peene for BH. However, ranges in this study were mostly higher than those in the literature.

It would endanger the ESU status of NSH and BH if they cannot be distinguished due to hybridization and it would hamper the effectiveness of conservation programmes.

Hansen (2008) states that Danish lake whitefish populations and NSH has a recent common postglacial ancestry while the BH have another, based on genetic analyses with samples from Peene representing BH. BH and NSH have been separated for several thousand years in which local adaptation may probably have occurred. Meanwhile, hybridization between NSH and BH was found.

Dierking (et al in prep.) has investigated admixture between different houting populations. The result was that hybridization between NSH and BH occurred. The admixture was strong in areas with little distance between NSH and BH and in Elbe and Rhein. Lake whitefish was not included in that study. The hybridization might explain the overlap of ranges in the results of this study. It might also explain the high variability in populations. It was found that neither sex nor fish length had a significant influence on the variability. Errors with regard to left or right counting could be excluded after checking this for consistency.
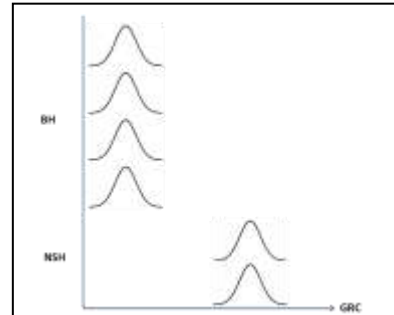

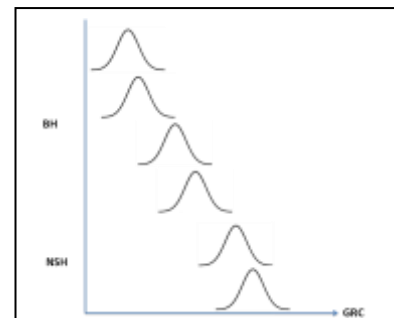Figure 11a: *Schematic NSH, BH distinguishable. GRC on the x-axis, taxa/ populations on the y-axis.*

Figure 11b: *Schematic intermediary patterns. GRC on the x-axis, taxa/ populations on the y-axis.*
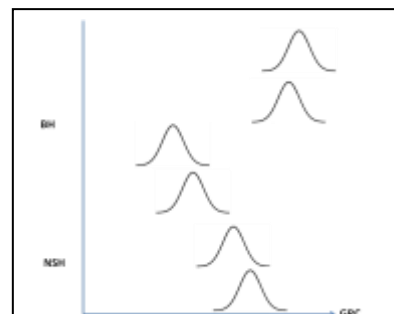

Figure 11c: *Schematic study results. GRC on the x-axis, taxa/ populations on the y-axis.*

When taking a closer look on the population levels, the picture became much more complicated. Assessing populations for differences and patterns revealed interesting details. The expectations had accounted for two possible outcomes. One with clearly separated gill raker counts of NSH and BH (Figure 11a) and another with intermediary gill raker counts (Figure 11b).

BH fell into two groups. One with gill raker numbers lower than NSH and another with higher numbers than NSH close to lake whitefish (Figure 11c).

One reason for the unexpected high gill raker numbers in the second group might be hybridization with lake whitefish with relatively high gill raker numbers (Table 4). Another intriguing outcome was the significant difference between Lachsbach and Trave despite they were geographically close to each other (Figure 5).

In other studies, the influence of environmental factors, e.g. diet and food availability or temperature, has been found to influence gill raker counts (Lindsey 1981, Todd 1998). However, the differences in gill raker counts found in this study were so large that hybridization and admixture is more probably. A second important point is the time frame. Almost all populations were introduced, alternatively reintroduced or stocked. Environmental selection could probably not have led to such big changes over a short time with few generations.

The lake whitefish population in Drewitzer See is said to be autochthon and comparable with the historic Schaalsee and Selenter See population (N. Schulz, personal communitcation). The much lower mean gill raker numbers compared to other lake whitefish (n=25 vs. n=40.6 LW, see Table 4) and the similarity with counts for the historic autochthonous Schaalsee population (n=25) (Thienemann 1922) that is now thought to be extinct (Schöter 2002), support this idea. However, the results should be confirmed, considering the low available sample size in this study.

Concluding, the results of this study showed that it is not possible to distinguish reliably between NSH and BH by gill raker numbers, but, nevertheless, NSH and BH might be handled as ESUs. They are following their own distinct evolutionary history (Hansen 2008) and they are genetic distinct. Hybridization between BH and NSH occurs, but also with lake whitefish which raises important new questions.

Outlook

Upon this, further research would be to connect gill raker counts to genotype both on the population and especially on the individual level, to see whether gill raker counts and intermediary patterns show the same as the genetics. Moreover, lake whitefish genetics should be included to explain the high numbers of gill rakers for certain BH populations.

In coregonids, gill raker counts and feeding ecology are strongly related (Lindsey 1981, Thienemann 1922). It will therefore be interesting to correlate gill raker counts and trophic level, e.g., by applying stable isotope analysis on fish analyzed on gill raker numbers for this study.

The shape of the fish and especially the head is another characteristic mark for the houting (Freyhof und Kottelat 2005). The shape of the samples should be analysed to see if there are similar patterns within the populations and differences between them. Sex, age and size have to be considered in conclusion of these results. Furthermore, it is often stated, that NSH has longer snouts than BH (Thienemann 1922). The results of the gill raker count analysis should be correlated with the head shape results to find out whether there is a correlation of gill raker counts and snout length and whether both lead to the same conclusions.

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Appendix

Figure A-1: *Scatterplot of gill raker numbers (n) versus fish length (fish TL). This figure shows the individual fish length plotted against the individual gill raker number. The colored symbols show the different individuals sorted in populations. The lines in the plot show patterns for each population. The populations do not all show the same pattern. Thus, fish length is not correlated with number of gill rakers.*