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Infection of Baltic herring (*Clupea harengus membras*) with *Anisakis simplex* larvae, 1992–1999: a statistical analysis using generalized linear models

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Anisakis simplex larvae were counted in the body cavity of Baltic herring sampled in the southern Baltic in 1992–1993, 1995–1997 and 1999. Generalized linear models (GLM) were used to model the prevalence and intensity of infection as dependent on year, quarter, area, length, condition factor, sex, and stage of gonad development. A binomial error distribution was assumed for the prevalence and a negative binomial distribution for infection intensity. The model for prevalence explained 71% of the deviance and all factors and variables tested were highly significant. The model for infection intensity explained 26% of the deviance and significant effects were length, year, quarter, area and sex. Prevalence increased with both length and condition factor, while decreasing eastwards and being higher in coastal areas than in offshore waters. Highest values were observed in the 1st and 2nd quarters (spawning season), and almost no infection was observed in the 3rd quarter. Both prevalence and intensity were higher in males than females. Prevalence has been stable from 1993 onwards, while intensity increased sharply in 1997 and 1999.

Keywords: *Anisakis simplex*, Baltic, GLM herring.

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Introduction

Nematodes of the family Anisakidae are common parasites of marine organisms world-wide. Stage 3 larvae of *Anisakis simplex* are found in many fish species, including herring (Berland, 1961). The ultimate hosts are cetaceans. In European waters, adult parasites have been reported in porpoise *Phocoena phocoena* from the western Baltic and the North Sea (Smith and Wootten, 1978; Herreras *et al.*, 1997; Siebert *et al.*, 2001; Wunschmann *et al.*, 2001) and in bottle-nosed dolphin *Tursiops truncatus* and white-sided dolphin *Lagenorhynchus albirostris* (Smith and Wootten, 1978). The eggs of *A. simplex* are shed with the faeces of the ultimate hosts and may infect marine crustaceans acting as intermediate hosts. Larvae have been found in five species of euphausids, including two from the North Sea (Smith, 1971, 1983). Plankton-feeding fish, such as herring preying on euphausids, become infected with 3rd stage larvae.

The presence of *A. simplex* larvae in Baltic Sea herring *Clupea harengus membras* was first recorded by Lubieniecki (1972) and Rokicki (1972). The fish are often heavily infected (Grabda, 1974; Lang *et al.*, 1990), but to date, there is no confirmation that herring become infected locally, because euphausids, the main intermediate host, do not occur in the Baltic Sea. Moreover, cetaceans are rare in the central and eastern parts. Only porpoises are regularly seen in Polish waters (Skóra, 1992), but Rokicki *et al.* (1997) found no *A. simplex* in specimens examined.

Local stocks of Baltic herring can be divided into spring- and autumn-spawning components. Some individuals among the coastal spring spawning herring undertake feeding migrations out of the Baltic to the Kattegat and Skagerrak, where they may become infected (Grabda, 1974; Kühlmorgen-Hille, 1979, 1983). During these annual migrations the fish may accumulate larvae because they can remain alive within the host for more than 3 years (Smith, 1984). Changes in the

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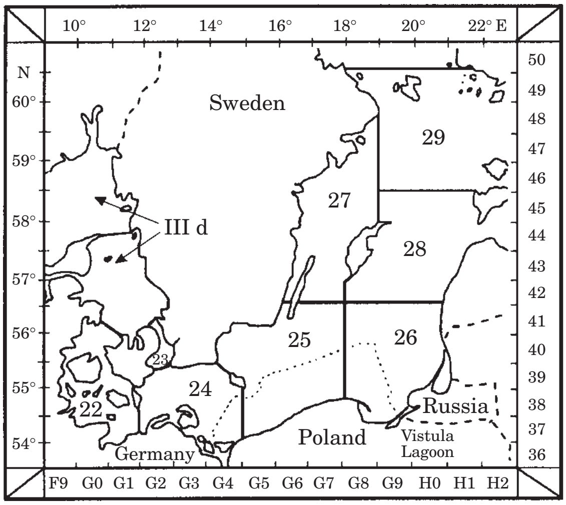

Figure 1. ICES Subdivisions in the Baltic Sea and Polish Fishery Zone (dotted line).

migration rate and the geographical extent of the migration may affect spatial and temporal differences in prevalence and intensity of infection.

Infection rates are not uniformly distributed throughout the Baltic Sea, but may vary seasonally, annually and spatially. For many years, the highest percentages of infected herring were reported in spring in the most westerly spawning grounds (Grabda, 1974; Lang *et al.*, 1990; Podolska, 1996). More recently, the dynamics of invasion appear to have changed, and relatively high infection rates have been found in the eastern Baltic (Subdivision 26 and 28, Vistula Lagoon; Figure 1; Tshervontsev *et al.*, 1994; Rodiuk and Shukhgalter, 1997). However, so far no extensive statistical analyses have been published showing unambiguously how temporal, spatial and biological factors affect infection. Therefore, our objective is to investigate the influence of a variety of potential factors on prevalence and intensity of *A. simplex* infection in herring by means of generalized linear statistical models, assuming that there are biological reasons for the differentiation.

Material and methods

Stratified random samples of coastal spring spawning herring, with strata defined by host length, were collected from commercial catches in ICES Subdivisions 24, 25 and 26 and Vistula Lagoon (Figure 1) in 1992–99 with the exception of 1994 and 1998. Usually 4–5 herring were sampled for parasites at length and 12 to 20 samples were collected annually, covering all quarters and both inshore and off-shore areas (Table 1). The number of viable *A. simplex* larvae in the body cavity of each fish was recorded by macroscopic examination. In addition, total length (cm), weight (g), sex, and gonad stage according to Maier's scale (FAO, 1965) were recorded. The fish were classified as belonging to the spring spawner component according to Kompowski (1969) on the basis of otolith structure. The condition factor was calculated by Fulton's (1911) formula.

Intensity of infection is defined as the mean number of parasites in an infected host in a sample. Prevalence is expressed as the percentage of the host species infected (Margolis *et al.*, 1982; Bush *et al.*, 1997).

For statistical analysis, ICES Subdivisions 24, 25 and 26 were separated into coastal and offshore areas (Podolska, 1996), because huge pre-spawning and spawning concentrations of infected herring occur in inshore waters. Statistical rectangles with predominantly waters <20 m in depth were regarded as coastal. On the basis of these criteria, 7 areas were distinguished: coastal and offshore in each Subdivision and the Vistula Lagoon. Only herring in the 21–30 cm length range were included, because only one smaller fish was infected and the number of larger fish was very small. Generalized linear models (GLM) were used for the analysis. First, a model with first-order interactions was fitted:

$$\begin{gathered}\mathrm{G(inf)} = \mathrm{sex} + \mathrm{year} + \mathrm{quarter} + \mathrm{area} + \mathrm{gonad\_stage} \\ + \mathrm{length} + \mathrm{condition} + \mathrm{interactions} + \mathrm{error},\end{gathered}$$

where G is a link function, and inf represents prevalence or infection intensity. Length and condition were taken as covariates, while sex, year, quarter, area, and gonad stage were treated as factors. The model for intensity was fitted to infected fish only. In addition, a model without interactions was fitted to test approximate differences between the main effects if some interactions were significant but explained a relatively small amount of variance.

In the case of prevalence, error distribution was assumed to be binomial, and the logit link function was used. In the first attempt, the intensity was analysed assuming Poisson errors. However, because the data showed high over-dispersion, the final model was fitted with a negative binomial error distribution (Bishop and Margolis, 1955) and a logarithmic link function. Corner point parameterization was used, i.e. factor effects for level one were assumed zero for all factors. Thus the factor effects for other levels may be regarded as differences between effect at given level and effect at level one. The significance of factors, covariates and interactions was tested and only significant terms were left in the final model. Similarly, factor levels that did not produce a significantly different response were grouped into new factor levels. The tests were performed by deletion, i.e. only those terms whose deletion did not result in a significant increase in deviance (i.e. the GLM measure of discrepancy between modelled and observed values) were left in the final model. The significance of the effects and factor levels was tested by the χ^2 test. Model

Table 1. Number of coastal spring-spawning herring sampled by year and area.

Area	1992	1993	1995	1996	1997	1999	Total
Subdivision 24	78	189	285	60	263	144	1019
Subdivision 25	108	376	680	477	522	446	2609
Subdivision 26	452	675	823	551	600	581	3682
Vistula Lagoon			255	28	130	101	514
Total	638	1240	2043	1116	1515	1272	7824

assumptions and performance were evaluated by analysis of residuals, which were plotted against variables, factors, and fitted values. In the case of the binomial error structure, the residuals defined as signed square roots of the contributions to the deviance should be approximately normally distributed if the model is appropriate (Pierce and Schafer, 1986). For the intensity model, the standardized residuals were plotted against square root of the fitted values to check the assumption of negative binomial error structure. Autocorrelation in the data (up to 6th order) was investigated by means of the Durbin–Watson test.

All calculations were performed using the GLIM package, version 4 (Francis *et al.*, 1993). The negative binomial error structure was modelled using the macro developed by John Hinde (version 1.1 GLIM4, Feb. 1996, MSOR Department, University of Exeter: www.nag.co.uk).

Results

The analysis of residuals did not reveal marked departures from the assumptions of the GLM. The normal probability plot of errors for prevalence deviated to some extent from linear but appeared acceptable. The Durbin–Watson tests did not point at autocorrelation in the data. The correlation between condition factor and length was 0.19, showing no collinearity problem in the analysis.

Prevalence

In the model with interactions, the quarter-year, area-year and quarter-area interactions, as well as all covariates and factors were significant. However, in determining quarter-area interactions, 7 out of 18 parameters could not be estimated and had to be regarded as aliased. The interaction effect was based solely on the parameter estimates for offshore areas in Subdivisions 25 and 26. Therefore, these interactions were excluded in the final model (71% of deviance explained; main contributors: length, condition factor, quarter, area and area-year and quarter-year interactions; Table 2A). Figure 2 shows the factor effects and their standard errors. Gonad maturity stages higher than 3 (i.e. pre-spawning, spawning, and spent) were not significantly different and therefore were merged. Their effect was higher than the effect for immature fish and pre-spawning fish at stage 3.

Prevalence increased with host length and condition factor and was significantly higher in males than in females. Depending on year, first- or second-quarter effects were highest, while the effect for the third quarter was consistently lower than for the other quarters

Table 2. Analysis of deviance (A) for final prevalence model with interactions (adjusted $R^2=0.71$) and parameter estimates with standard error (B) for the corresponding model without interactions ($R^2=0.66$; Sd=Subdivision, VL=Vistula Lagoon).

A. Error source	Change of deviance	d.f.	p
Model	4531	59	<0.0001
Error	1768	2600	
Length	2929	1	<0.0001
Condition factor	714	1	<0.0001
Quarter	294	3	<0.0001
Area	116	6	<0.0001
Year	52	5	<0.0001
Sex	19	1	<0.0001
Gonads stage	21	2	<0.0001
Area-year	287	25	<0.0001
Quarter-year	101	15	<0.0001

B. Parameter	Estimate	s.e.
Intercept	− 26.18	1.06
Length	0.70	0.02
Condition	7.47	0.66
Sex males	0	Aliased
Sex females	− 0.34	0.08
Year 1992	0	Aliased
Year 1993–1999	0.93	0.15
Quarter 1 and 2	0	Aliased
Quarter 3	− 3.56	0.58
Quarter 4	− 0.80	0.17
Gonads 2	0	Aliased
Gonads 3 and 8	1.99	0.80
Gonads 4 to 7	2.58	0.80
Sd 24 offshore	0	Aliased
Sd 25–26 offshore	− 0.38	0.22
Sd 24 coastal	0.78	0.23
Sd 25–26 coastal+VL	0.32	0.21

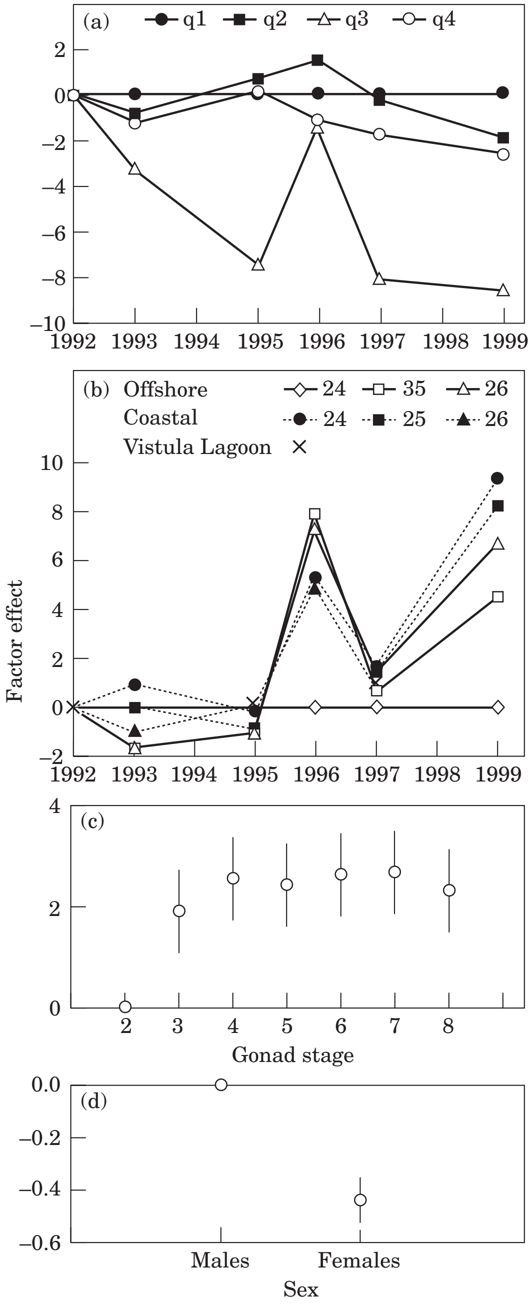

Figure 2. Interactions of quarter (a) and area (b) with year and effects of gonad stage (c) and sex (d) with their standard errors estimated in the prevalence model.

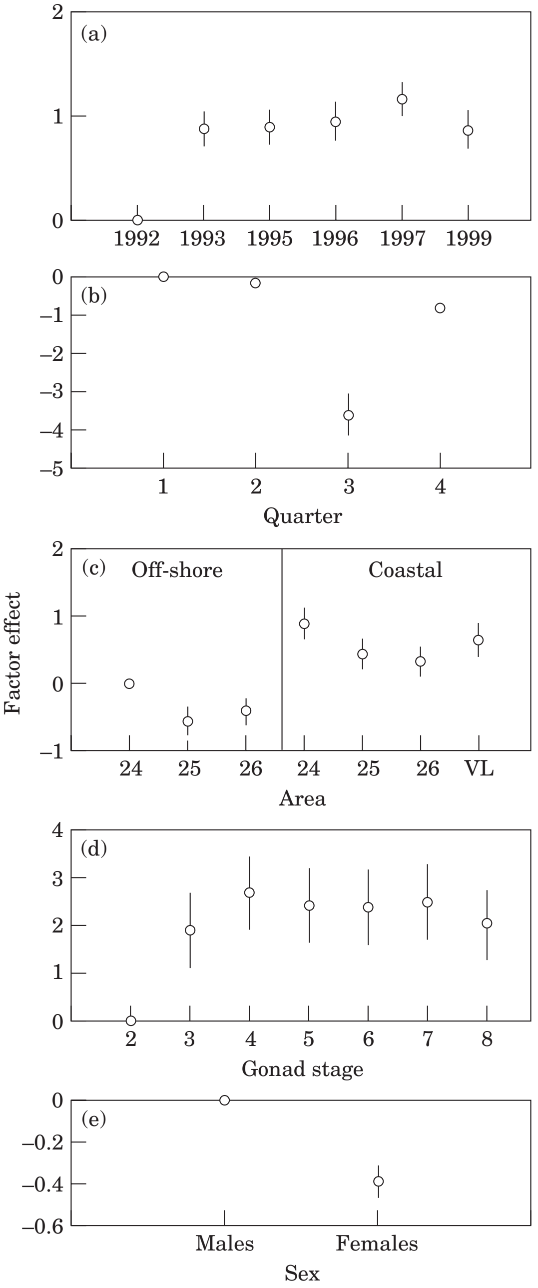

Figure 3. Effects (with s.e.) of year (a), quarter (b), area (c; VL: Vistula Lagoon), gonad stage (d) and sex (e) with their standard errors for the prevalence model without interactions.

(Figure 2a). The fourth-quarter effect was intermediate. The dependence of area effect on year effect is less conclusive (Figure 2b). With the exception of 1996, coastal area effects were higher than offshore area effects.

For the model without interactions, all factors and covariates were significant and explained 66% of the deviance (parameter estimates in Table 2B; factor effects in Figure 3). The model fitted with factor levels with insignificantly different effects merged explained only 0.5% less than the original model.

Length and condition factor had the highest effect on prevalence. To show what the parameters mean in terms of prevalence, the logit values were converted to

Table 3. Prevalence (%) of herring infection with *A. simplex* larvae estimated by the final prevalence model for some combinations of variables and factor levels (if not specified the following values apply: average length – 23.7 cm, average condition – 0.66, average sex, years 1993–1999, quarters 1–2, Sd 25–26+Vistula Lagoon, gonad stages 4–7).

Variable or factor	Coastal	Offshore
Length		
21 cm	5	3
25 cm	45	29
30 cm	97	93
Condition factor		
Mean − 10%	17	9
Mean	25	15
Mean + 10%	37	22
Year		
1992	12	6
1993–1999	25	15
Quarter		
1+2	25	14
3	1	0.5
4	13	7
Area		
Sd 24	35	20
Sd 25–26+VL	25	14
Sex		
Male	29	17
Female	22	13
Gonad stage		
2	3	1
3+8	16	9
4–7	25	14

percentages for some combinations of factors and variables assuming average values for the others (Table 3). For fish of 21–25 cm, the model estimates of prevalence for offshore areas are approximately half of the estimates for coastal waters. The difference decreases for larger fish, for which infection prevalence approaches its asymptotic value of 100%. For a condition factor ranging from 0.59 to 0.73 (± 10% of the average condition factor of 0.66), the prevalence approximately doubles.

Prevalence did not change much over time, with only the year effect for 1992 being significantly different from the others. Prevalences for the 1st and 2nd quarters were not significantly different and twice as high as for the 4th quarter, while in the 3rd quarter there was hardly any infection among the fish sampled.

Estimated prevalences in the offshore area in Subdivisions 25 and 26 were not significantly different and the same applied to those in coastal areas in these Subdivisions and in the Vistula Lagoon. Subdivision 24 was characterized by higher coastal and offshore prevalences than Subdivisions 25, 26 (and Vistula Lagoon).

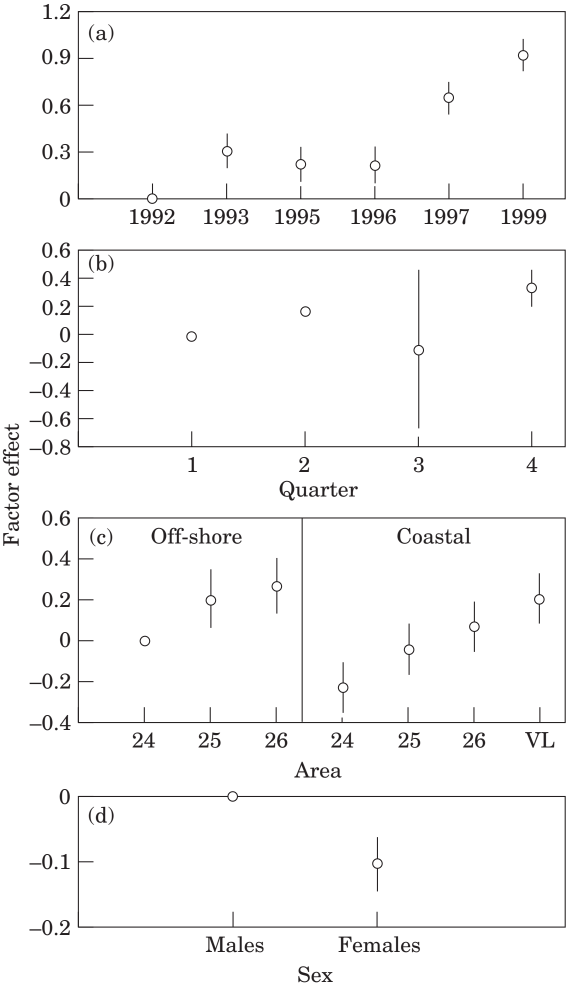

Figure 4. Effects (with s.e.) of year (a), quarter (b), area (c; VL: Vistula Lagoon), and sex (d) for the intensity model.

The prevalence of infection in males was slightly higher than in females for both coastal and offshore waters. Gonad effects could be merged into three groups. Immature fish (stage 2) were characterized by very low prevalences and the highest values were observed in the main (pre-)spawning stages 4–7.

Intensity

All interaction terms in the model for infection intensity were insignificant and so were gonad stage and condition factor. Other factors and covariates were highly significant (Figure 4), but explained only 26% of the deviance. The final model was fitted with factor levels not having significantly different effects merged (25% of the deviance explained; main contributors length and year; Table 4).

Table 4. Analysis of deviance (A) and parameter estimates and standard error (B) for the final intensity model (adjusted $R^2=0.25$; Sd=Subdivision).

A. Error source	Change of deviance	d.f.	p
Model	491	10	<0.0001
Error	1463	1838	
Length	267	1	<0.0001
Year	170	3	<0.0001
Area	38	4	<0.0001
Quarter	11.5	1	0.0007
Sex	5.3	1	0.02

B. Parameter	Estimate	s.e.
Intercept	− 3.20	0.33
Length	0.19	0.01
Sex males	0	Aliased
Sex females	− 0.10	0.04
Year 1992	0	Aliased
Year 1993–1996	0.22	0.11
Year 1997	0.61	0.11
Year 1999	0.90	0.11
Quarter 1	0	Aliased
Quarter 2–4	0.17	0.05
Sd 24 offshore	0	Aliased
Sd 25–26 offshore	0.23	0.12
Sd 24 coastal	− 0.24	0.13
Sd 25–26 coastal	− 0.01	0.12
Vistula Lagoon	0.16	0.13

Table 5. Intensity of herring infection with *A. simplex* larvae estimated by the final model for some combinations of length and factor levels (if not specified the following values apply: average length – 23.7 cm, average sex, years 1997–1999, quarter 1, Sd 25–26).

Variable or factor	Coastal area	Offshore area
Length		
21 cm	4	5
25 cm	8	11
30 cm	21	27
Year		
1992	3	4
1993–1996	4	5
1997–1999	7	8
Quarter		
1	7	8
2–4	8	10
Area		
Sd 24	5	7
Sd 25–26	7	8
VL	8	
Sex		
Male	7	9
Female	6	8

Table 5 provides model estimates of average intensity for some combinations of factors. Host length had the greatest effect on intensity. Intensity increased approximately 5-fold over a size range of 10 cm and values were slightly higher in offshore waters. The year effects for 1993, 1995, and 1996 did not differ significantly, nor those for 1997 and 1999. Overall intensity approximately doubled over the period.

Data for the 2nd, 3rd and 4th quarter could be grouped, because their effects were not significantly different. However, when the 3rd quarter was excluded (only three fish infected) and quarter was treated as a covariate, intensity increased significantly and linearly (Figure 4b).

For both coastal and offshore areas, the area effects in Subdivisions 25 and 26 were not significantly different and therefore these were grouped. Overall, coastal and offshore area effects increased eastwards. These trends were significant when areas are treated as covariates in the model (Figure 4c).

Intensity of infection was higher in males than in females, but the difference is only one parasite.

Discussion

The suitability of GLM for analysing parasitic infection is supported by Wilson *et al.* (1996), who showed that GLM with negative binomial error structure performed much better than did classical linear models on log-transformed data and only slightly better than GLM with Poisson errors and an empirical scale parameter. In contrast, models assuming Poisson errors for Baltic herring produced a smaller number of significant effects on *Anisakis* intensity than did models assuming negative binomial errors.

The dependence of prevalence and infection intensity on host length as well as no infection in herrings <19 cm have been reported by many authors (Grabda, 1974; Strzyzewska and Popiel, 1974; Weber and Neudecker, 1988; Lang *et al.*, 1990), suggesting that smaller fish do not migrate to the Kattegat. Horbowy and Podolska (2001) presented evidence that the relation between intensity and length is curvilinear. The models presented here implicitly assume a curvilinear relationship, because we used the log link function when fitting the model. The relationship with host size existed irrespective of geographical origin, a feature that has also been observed in herring from British waters (Khalil, 1969; Davey, 1972) and from the North Sea (van Banning and Becker, 1978), as well as in other host species for *Anisakis* sp. such as hake *Merluccius gayi* from the south-eastern Pacific Ocean (George-Nascimento, 1996) and red rockfish *Sebastes capensis* from northern Chile (Gonzales and Acuna, 2000).

Podolska *et al.* (1997) found that the condition factor is higher for infected than for non-infected fish when the

Table 6. Comparison of reported (a) prevalence and (b) mean intensity with comparable model estimates by area, quarter and length for recent years (for Sd 22 model estimates for Sd 24 have been used).

Reference	Area/quarter/length	Period	Reported estimate	Model estimate
a. Prevalence				(1993–1999)
Grabda, 1974	Sd 24 coastal, q 2, 23–26 cm	1973–1974	48	49
	Sd 24 offshore, q 2, 23–26 cm	1973–1974	39	29
Kühlmorgen-Hille, 1983	Sd 22, q 1–2, 20–30 cm	1978–1982	30	26
	Sd 22, q 4, 20–30 cm	1978–1982	9	8
Weber & Neudecker, 1988	Sd 22, q 1–2	1973–1988	27.7 cm*	25.2 cm*
Strzyzewska, 1987	Sd 25, q 2, 27–30 cm	1978–1980	60	80
Lang *et al*., 1990	Sd 25–26 offshore, q 4,20–27 cm	1987–1988	1–3	6–7
b. Mean intensity				(1998–1999)
Grabda, 1974	Sd 24, q 2, 21/30 cm,	1973	1/15	4/23
Lang *et al*., 1990	Sd 22–24, q 4, 21/30 cm	1987–1988	2/10	4/27
Strzyzewska, 1987	Sd 25, q 2, 25/30 cm	1978–1980	7/10	12/30

*Length of 50% infection.

gonad stage is accounted for, but the differences observed were not tested statistically. Fulton's (1911) condition factor is dependent on gonad developmental stage and is highest for gonad stages 5 and 6. However, this does not affect our conclusion that fish with higher condition factor have a higher prevalence, because gonad stage has been incorporated as an explanatory factor. A better condition is likely to reflect better feeding conditions and therefore a higher chance of infection. Condition had no significant effect on infection intensity. This may result from the higher variance in the intensity data than in the prevalence data.

The model can be used to compare prevalence and intensity data reported here with those reported historically. With knowledge of sampling season and area, it is a straightforward matter to assess the infection rate for a given length, assuming the current year effect and an average condition factor (Table 6). Subdivisions 22–24 show no increase in prevalence in the 1990s compared with results reported for the 1970s and 1980s. Only the length of 50% infection reported by Weber and Neudecker (1988) suggest a lower prevalence before 1990 than after. In contrast, prevalences for Subdivisions 25–26 appear to have increased, as well as infection intensity throughout the Baltic. An increase in intensity might be explained by a higher infection rate of euphausids, or by more extensive migrations into the Kattegat area, but suitable data are lacking.

Similar seasonal variations in infection rate with a peak during the first half of the year have been observed before by Grabda (1974), Kühlmorgen-Hille (1983) and Lang *et al.* (1990). These are caused by the cyclic migration patterns of Baltic herring. The highest concentrations of infected fish are usually found in spring on the spawning grounds. After spawning, these fish undertake a feeding migration into the Kattegat and the North Sea. In the 3rd quarter, prevalence of herring within each area is close to zero. The quarter effect depended on year. Peak spawning usually takes place in March or April and variations therein may explain why in some years highest prevalences were observed in the 1st quarter and in the 2nd quarter during others.

The results on spatial differences are consistent with existing information. Grabda (1974) showed that prevalence was higher in coastal than in offshore waters of Subdivision 24 and Lang *et al.* (1990) observed the same pattern in Subdivision 25. The relatively high prevalence and infection intensity (32% and 7.2, respectively, for herring of 24 cm) in the Vistula Lagoon is remarkable. Infection in the lagoon has been sporadic before the 1980s (Tshervontsev *et al*., 1994), while Gayevskaya and Krasovskaya (1986) reported a prevalence of only 0.5% and usually not more than three parasites per infected fish of 23–25 cm in April 1985.

The results show that infection intensity, in contrast to prevalence, increases eastwards in both coastal and offshore areas. This trend is difficult to explain. One could venture the hypothesis that the greater the distance between spawning area and feeding area, the longer fish would have to spend in the feeding area, with an associated larger chance of eating infected food items to build up sufficient energy for the longer spawning migration. The findings of Slotte and Fiksen (2000), showing a more extensive spawning migration of Norwegian spring-spawning herring that are larger and in better condition, support this hypothesis. Also in contrast to prevalence, intensity in offshore waters was consistently higher ($p<0.05$) than in coastal areas, although the difference is small and amounts to 1–2 individuals only.

Although direct comparisons are problematic because of the multitude of factors affecting infection rates, the level of infection in Baltic herring is generally lower than observed in other areas. Only larger fish (25–30 cm) on coastal areas at spawning time show infection rates close to observed in other waters. The 8-year study by van Banning and Becker (1978) showed prevalences in North Sea herring on their spawning grounds usually in the range of 80–100% and a mean intensity in the range of 4–40 parasites at host age 3 to 5. Ellemann (1989) reported 60% prevalence and 1–10 parasites per infected herring in the Skagerrak and Kattegat in 1988.

Kühlmorgen-Hille (1979) and Lang *et al.* (1990) observed a slightly higher prevalence in males than in females of the same length in Subdivision 22 herring, but the difference was not tested statistically. Hemmingsen *et al.* (2000) reported a significantly higher prevalence of the Anisakid nematode *Contracaecum* sp. in male cod from Balsfjord in northern Norway and suggested potential differences in feeding behaviour between sexes. In contrast, Davey (1972) and van Banning and Becker (1978) reported similar levels of infection in herring for the two sexes. According to van Banning and Becker (1978), biological knowledge of the means of infection and the feeding habits of herring give no reason to suspect sex differences in the degree of infection. Because size and condition factor are significant explanatory variables in our analysis, we suggest that sex dimorphy in feeding behaviour is not likely. There may be other biological reasons for males being more infected than females, as has been reported for some other vertebrate species (Swansson *et al.*, 1984; Poulin, 1996). For instance, Zuk and McKean (1996) hold testosterone responsible for this phenomenon, because it can induce immune suppression in the male host.

Kühlmorgen-Hille (1979) reported that in Subdivision 22 over 50% of herring at age 2 were mature but only 2% of these were infected. After spawning, a large proportion of these fish migrates northwards, after which they first contract infection. While infection rate increased with age, the percentage of infected herrings was always lower than the percentage of mature fish. The results of the prevalence model suggest also that only a small proportion of immature herring migrate to feeding grounds outside the Baltic, or at least that their migration does only extend into areas where infection rate of their food is still relatively low.

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