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"Spring rise" of whaleworm (*Anisakis simplex*; Nematoda, Ascaridoidea) third-stage larvae in some fish species from Norwegian waters

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Abstract The seasonal variation in the infection of saithe (*Pollachius virens*), cod (*Gadus morhua*), and redfish (*Sebastes marinus*) from a coastal area of central Norway with *Anisakis simplex* third-stage larvae (L3) was studied over a period of 1 year. In all three host species there was an increase in the abundance of the parasite in spring, with a peak appearing in March and April. Cod displayed the most distinct seasonal variation, showing a clear abundance peak in April. The abundance peak in April for redfish was not as pronounced. In saithe the abundance over the seasons was less prominent, with a maximum appearing in March and another increase in abundance occurring during July. It is apparent that the causes behind the pattern of infection observed in this study are complex. However, possible explanatory mechanisms are discussed. Arguments are propounded to suggest that the increased supply of parasite eggs from northward-migrating whales in addition to the general spring bloom of plankton constitute the most important factors governing the phenomenon of "spring rise" in *A. simplex* L3 in the study area.

Introduction

Since the whaleworm (*Anisakis simplex*) was found to be of medical significance (Van Thiel et al. 1960), several papers have focused on the parasite and the disease "anisakinosis" (e.g., Smith 1983b). However, little is known concerning the seasonal dynamics of *A. simplex* third-stage larvae (L3). Polyanskii (1966) found no "essential" seasonal variation in the parasite fauna of cod and haddock (*Melanogrammus aeglefinus*) from the Barents Sea. Nevertheless, in a few parasites, including *A. simplex* and *Contraceacum* sp., another genus of anisakid nematodes, a decrease was registered during the winter period. In a study of herring (*Clupea harengus*) from the Baltic, Grabda (1976) showed a seasonal peak in the abundance of *A. simplex* in winter. Additionally, in a study of cod from northern Norway, Hemmingsen et al. (1995) found a significant seasonal variation of *A. simplex*, but in that study the infection peak appeared in autumn. Seasonal variation has also been shown in another anisakid nematode species, *Hysterothylacium aduncum* from the Oslo Fjord, where the abundance of L3 displayed a marked peak in March (Andersen 1993). The methodology used in different studies on the seasonal variation of *A. simplex* varies. This, in addition to the disparities associated with geographic conditions, makes it somewhat difficult to note distinct features in the occurrence of the parasite throughout the year. On the other hand, given the above-mentioned studies as a point of departure, it seems clear that seasonal variation as such is a condition that is largely linked to *A. simplex*, even in those instances in which such variation is present to a small extent in other species of parasites in the same hosts. The aim of this study was to throw further light on the phenomenon of seasonal variation in the abundance of *A. simplex* L3.

Materials and methods

The fish used in this study were caught north of the island of Vega in central Norway (650 46′N, 110 54′E) from January to December of 1990. Optimally, 20 specimens from each of the species saithe, cod, and redfish were collected by gill net on a monthly basis. However, owing to inclement weather conditions that made the gathering of material difficult, data are not available for October and November. A total of 568 fish were examined, including 187 saithe, 183 cod, and 198 redfish.

Within 4 h of being caught, the material was brought ashore and frozen. The fish were filleted and the musculature was examined on a light table using a pair of tweezers, whereas the viscera were examined under a dissecting microscope (40×). The otoliths were dissected and used to determine the age of the fish. In cod the otoliths were also used to assure that the material was from the stationary coastal stock and not from the migratory

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Arcto-Norwegian stock. As *Anisakis simplex* L3 in muscular tissue of fish are rarely found outside the abdominal lobes (i.e., the hypaxial musculature) surrounding the coelom, only this part of the fillet was examined (Young 1972; Wootten 1978; Arthur et al. 1982).

As the abundance of *A. simplex* L3 is positively correlated with age (Polyanskii 1966), the age structure in every monthly sample of fish would be of importance for the abundance. To compensate for the random composition of the samples we used analysis of covariance (ANCOVA) on log $(x+1)$-transformed data. The model applied contained the factors month, age, and age times month. A pairwise comparison of months with regard to the abundance was done with a Tukey test. The concepts "abundance" and "prevalence" are used according to definitions given by Margolis et al. (1982).

The concept "spring rise" was apparently used for the first time by Taylor (1935), who described the rise in epg (eggs per gram of feces) of gastrointestinal nematodes in ruminants during spring. In the present paper, "spring rise" is used in a general way to describe a distinct increase in the abundance of nematodes during the springtime.

Results

Saithe

The abundance recorded for the total sample of saithe was 22.1, varying between 11.6 and 38.4 throughout the year. The equivalent values for prevalence were found to be 97.2% and 85.0–100%, respectively. Saithe also had the highest overall rate of infection of the three species examined (Table 1). The progression of the abundance of *Anisakis simplex* in saithe (Fig. 1A) was relatively even from month to month, with the exception of two peaks in March to April and July, the spring peak being the most distinct. March, which had the highest abundance in the sample, did not differ significantly from the months of February, April, May, July, or December (Tukey; $P > 0.05$).

Cod

The abundance noted for the total sample of cod in this study was 14.0, varying between 3.6 and 52.4 during the sampling period. Equivalent prevalence values recorded for this species were 92.2% and 80.0–100%, respectively (Table 1). For cod the abundance in January to March followed a gradual course before a marked annual maximum set in during April, 1 month after the infection peak in saithe. This was followed by a marked reduction in abundance, and May to June showed a level equivalent to that seen during the months prior to the peak in April, followed by a further decrease in July to September. In December the abundance returned to the same level observed in January (Fig. 1B). This seasonal variation was more prominent in cod than in saithe, in that April differed significantly from all other months (Tukey; $P < 0.05$).

Redfish

The abundance recorded for the total sample of redfish was 5.5, varying between 1.9 and 20.4 throughout the year. The prevalence throughout the year fluctuated more in redfish than in the other two species of fish examined in this study, varying in the former between 35.0% and 80.0% (Table 1). For the total sample the prevalence was 60.1%. The abundance followed a course characterized by a relatively low level of infection with *A. simplex*, with a distinct annual maximum occurring in April (Fig. 1C). The seasonal variation was approximately similar to the pattern found in cod in that April differed significantly from all other months (Tukey; $P < 0.05$) except for February and March.

In none of the fish species was the pattern of infection throughout the year significantly influenced by the age composition of the monthly samples (ANCOVA; $P < 0.05$).

Discussion

With regard to marine parasites in general, seasonality has been reported in some cases from cold-temperature waters, though such patterns have been less prominent in other cases. In subtropical and tropical waters, where fewer studies have been undertaken with regard to seasonal variation, results indicate that seasonality, if it occurs, is far less pronounced than in colder waters (Rohde 1982). These conditions may indicate that the

Table 1 Abundance, prevalence, and total numbers of *Anisakis simplex* L3 recovered from every monthly sample in the three host species saithe (*Pollachius virens*), cod (*Gadus morhua*), and redfish (*Sebastes marinus*). Summed data for all months are given in *italics*

		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sept	Dec	*Total*
Saithe	Abundance	11.6	19.3	38.4	35.6	15.6	13.2	34.9	22.2	26.1	15.7	*22.1*
(n = 187)	Prevalence	100	100	100	92.9	100	100	100	93.3	85.0	100	*97.2*
	$\sum$ No. of worms	231	386	767	497	311	264	569	343	444	313	*4125*
Cod	Abundance	13.9	18.1	8.1	52.4	10.0	9.8	8.6	4.5	4.6	13.2	*14.0*
(n = 183)	Prevalence	94.1	90.0	100	100	93.3	100	85.0	80.0	80.0	100	*92.2*
	$\sum$ No. of worms	273	361	129	1048	140	147	148	72	74	264	*2620*
Redfish	Abundance	2.5	3.5	8.8	16.4	1.3	1.5	1.0	1.4	1.2	2.8	*5.5*
(n = 198)	Prevalence	52.6	68.4	75.0	80.0	35.0	75.0	50.0	40.0	60.0	65.0	*60.1*
	$\sum$ No. of worms	48	67	175	327	25	30	19	28	23	55	*797*

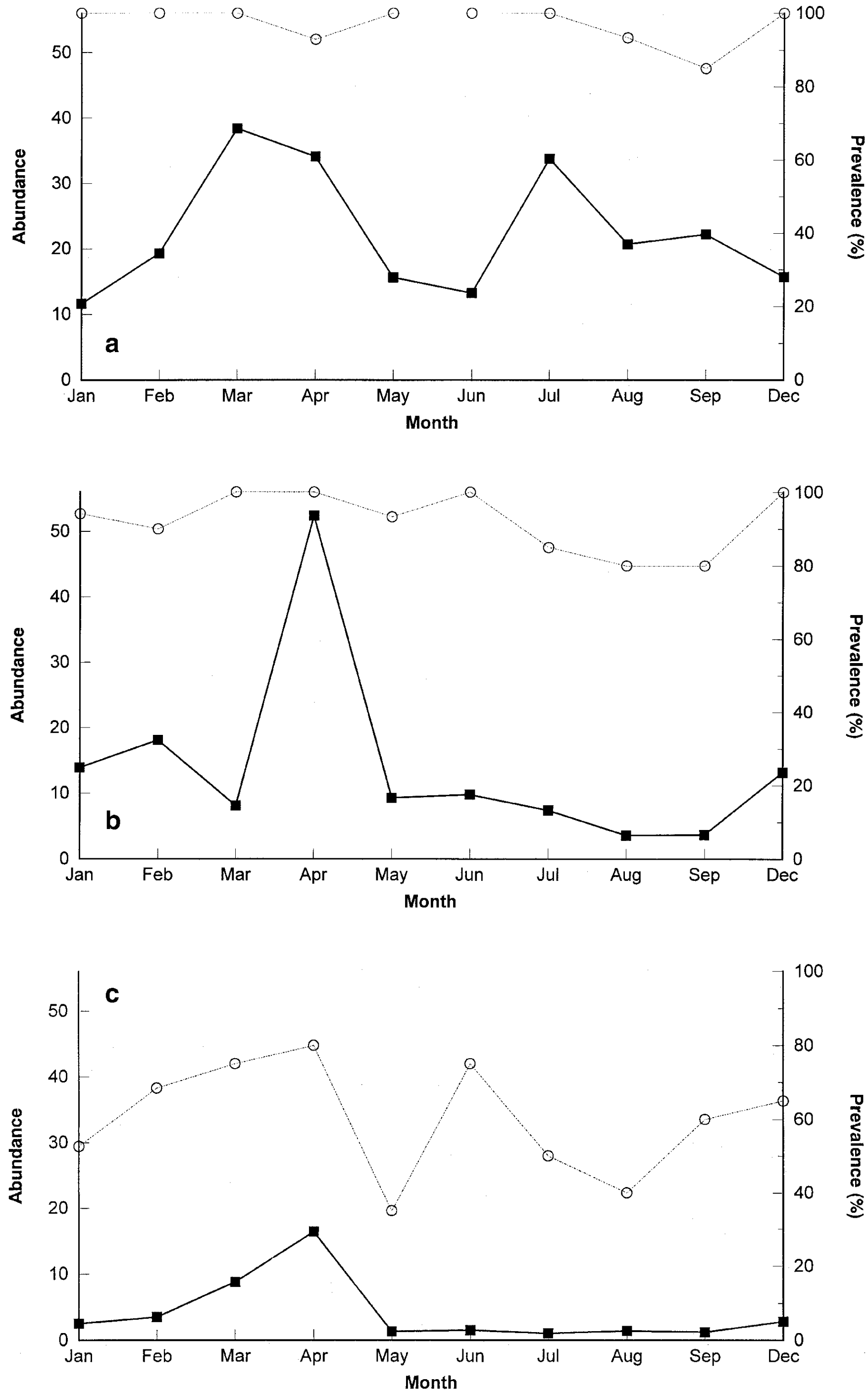

Fig. 1A–C Prevalence (*white circles*) and abundance (*black squares*) of *Anisakis simplex* L3 throughout the sampling period in **A** saithe, **B** cod, and **C** redfish

general seasonal variation in an area may be a determining factor as to whether parasites occur in a cyclic pattern throughout the year.

The present study indicates that in the area of interest a seasonal variation exists in the occurrence of *Anisakis simplex* L3 in the fish species investigated. For cod the results are unambiguous in that the seasonal peak in April clearly differs from the pattern observed in all other months. In redfish the abundance peak in April does not differ significantly from the pattern seen during the previous two months. Of these three months, February shows the lowest abundance, whereas March is in an intermediate position. This indicates a gradual increase in infection during this period. Saithe exhibited the least pronounced seasonal variation in the pattern of infection. In this case, moreover, the highest abundance was registered in March, not in April as for the other two species. However, the infection maintains a high level in April as well, and this pattern does not differ significantly from that seen in March. It therefore appears as if the spring peak spans 2 months for this species. Furthermore, unlike cod and redfish, saithe displays a second peak in July. The high abundance observed in the latter case can partly be attributed to two extreme data points, but even if these were excluded from the Tukey test, this month would not differ significantly from March. It is apparent that saithe is the most migratory of the three species of fish and stays mainly in the upper waters of the open sea (Pethon 1985), where the density of L3 is the highest (Smith 1983a). The high level of exposure to *A. simplex* that this entails might explain the generally high level of infection observed in this species and, possibly, the more even pattern of infection observed throughout the year.

To a large extent, the infection peak, which is apparent in this study, coincides with the spring bloom of plankton in the relevant part of Norwegian coastal waters. Considering the primary production for the area in question, it is evident that the density of phytoplankton increases rapidly in March, normally reaching a maximum during April (Rey 1981). Over a period of 2 weeks a large production of organic material takes place, and this is undoubtedly of major importance for the secondary producers and the subsequent links in the production chain (Braarud and Nygaard 1978). This is also reflected in the production of zooplankton in general that has been under observation at permanent oceanographic stations along the coast of Norway since 1942. As expected, data from these stations show that the maximal volume of zooplankton for the study area is found in March to April (Wiborg 1978).

As far as the occurrence of *A. simplex* is concerned, Højgaard (1997) argues that the annual variation in the level of infection between age groups of saithe appears to correspond to changes in the occurrence of mesoplankton. This seems to happen because these intermediate hosts make up a considerable part of the mesoplankton and represent an important fraction of the nutritional basis for saithe. In addition, mesoplankton plays an important role as food for the other two species included in this study, cod and redfish (Pethon 1985). Højgaard (1997) points out that if the density of euphausiids is high, there is a greater possibility of saithe becoming infected by *A. simplex* larvae. A precondition for this supposition is a constant supply of *Anisakis* eggs to the system. However, an *increase* in the production of euphausiids, without a compensating supply of eggs, could lead to the opposite: a *dilution* effect. The density of infected intermediate hosts should in this case diminish, which would be followed by a reduction in the rate of infection. An explanation for the observed increase in the rate of infection must therefore be based on the assumption that there is a compensatory increase in the supply of eggs, leveling out the effect of a growing intermediate-host population.

Throughout the year the marine ecosystem appears to be supplied with a relatively even flow of parasite eggs from whales such as porpoises and killer whales, which occur along the Norwegian coast on a regular basis. The supply of *A. simplex* eggs contributed by these final hosts would therefore hardly account for the infection peak observed in the present study. However, a number of other host species are present along the coast of Norway during the relevant time of year. To all appearances, minke whales (*Balaenoptera acutorostrata*) play a central role due to their high abundance, but species such as the fin whale (*Balaenoptera physalus*), humpback whale (*Megaptera novaeangliae*), and blue whale (*Balaenoptera musculus*) also undertake marked seasonal migrations in spring on their way north to summer feeding grounds off the northernmost part of Norway and in the Barents Sea (Gambell 1985; Stewart and Leatherwood 1985; Winn and Reichley 1985; Yochem and Leatherwood 1985; Rice 1989). Given this rise in the occurrence of final hosts, the density of *A. simplex* larvae that are established in the crustacean intermediate hosts could increase in such a way as to compensate for the aforementioned dilution effect, thus providing an important explanatory variable for the peak in March to April. A relatively stable or increased density of infected euphausiids, coupled with a rise in fish consumption and a subsequent increase in the rate of infection during the spring bloom, make it reasonable to assume that the abundance of *A. simplex* would rise during this period.

Furthermore, the increase in abundance may be influenced by immigration of fish from other areas with higher infection burdens than the area covered by the present study. However, according to what is known about the migratory pattern of the three fish species involved, this is not likely to be an adequate explanation. Among the three species investigated in the present study, saithe display the most migratory behavior. The principal migration activity in this species is associated with the movement to and from the three main spawning areas along the Norwegian coast (Godø 1995b). This migratory behavior is initiated as the fish become sexually mature at the age of 5–6 years (Pethon 1985). Up to this age, saithe might undertake short seasonal migrations toward the coast during summer and a few kilometers off the coast during winter (Godø 1995b). In our material, only 22 of 187 specimens were as old as 5 years; the rest were immature, ranging from 2 to 4 years in age. This observation implies that only a minor fraction of the material could be expected to have undertaken wide-ranging migratory movements far from the study area. Cod and redfish apparently display a more stationary way of life in the area of interest. To some extent, redfish undertake seasonal migration, but apparently these movements are normally of short range (Nedreaas 1995). Cod seems to be the most resident of the three species included in this study. The coastal cod stock along the Norwegian coast is made up of a number of local populations characterized by short-distance migratory patterns (Jørstad and Nævdal 1989; Godø 1995a). Thus, it would be reasonable to assume that the observed dynamics in the occurrence of *A. simplex* L3 reflect actual changes in the supply of eggs and larvae to the study area.

The present material provides no basis for an explanation of the marked decrease in abundance seen in May, and we can only speculate that this phenomenon may be associated with an increase in the immune response of the fish.

If the plankton spring bloom is part of a basic mechanism controlling the seasonal fluctuations observed in *A. simplex*, the studies of Grabda (1976) and Hemmingsen et al. (1995) indicate that local conditions are also of importance in modifying the infection pattern. Grabda (1976) explains a difference between the seasonality in herring and cod in the Baltic Sea by pointing out that cod are stationary in this area of low abundance of *A. simplex*, whereas herring undertake annual migrations in autumn to the North Sea, where the fish are exposed to the parasite. In an examination of 13 parasite species in cod from a fjord in northern Norway, Hemmingsen et al. (1995) found a clear seasonality with regard to abundance only in *A. simplex*. This is accounted for by the worms' accumulating during autumn, only to be largely removed by the large winter seal population that possibly feeds selectively on heavily infected cod. With regard to what was stated above concerning the spring bloom, it may be noteworthy that this event occurs approximately 1 month later in the area considered by Hemmingsen et al. than in the area from which our material was collected (late May to early June; Rey 1981). If any of the above-mentioned explanations linked to the spring bloom are relevant in a fjord system such as this, the reasons for the delay between the plankton-bloom peak and the parasite-abundance peak in autumn remain to be accounted for. However, we might speculate that a general slowdown in ecological processes due to lower water temperatures in this northerly area could be of importance in producing a lag in the system as compared with the findings in our material, collected further south. As pointed out with reference to the present material, the fish population in the study from northern Norway comprised stationary coastal cod. Therefore, immigration of more infected fish from other areas in this case would not be a likely explanation for the observed rise in infection.

Stavn (1971) has outlined five causal mechanisms central to the distribution pattern in free-living organisms in aquatic environments: physicochemical conditions such as light, temperature, and nutrients; mass transportation of material by wind or water currents; reproductive circumstances such as eggs' being laid patchily; social conditions such as shoal behavior; and coactive circumstances such as competition and predation. In addition, distribution patterns also ensue from combinations of the above-mentioned mechanisms. It would be reasonable to assume that the geographic incidence and distribution of parasites is indirectly influenced by the same mechanisms that power the distribution pattern in the host species. Under all circumstances this highlights some of the complexity in the system considered herein. In such a complex system it is obviously not feasible to explain seasonal fluctuation, or a lack thereof, on the basis of simple causal relations. Moreover, the present study does not provide grounds for an unambiguous conclusion based on the ensuing results. However, the observation emerges that *A. simplex* and, possibly, other anisakid nematodes show a tendency toward a "spring rise" and a subsequent seasonal variation in abundance. As thus far determined, the spring bloom in the ocean appears to be a very important, albeit complex, factor influencing this phenomenon.

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