

# Spatial and temporal re-distribution of Naididae (tubificoid naidids and naidids s.str., Annelida, Clitellata) in Europe due to climate change: a review based on observational data

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## Abstract

Temperature is one of the most important factors affecting the life history characteristics and biogeography of aquatic oligochaetes in the family Naididae (both the tubificoid Naididae and the Naididae s.str. species). To understand the effect on oligochaetes of climate change in The Netherlands, the impact of temperature rise on tubificoid naidids and naidids s.str. is studied at temporal and spatial scale. The spatial scale includes the temperature change induced shift of biogeographic distribution patterns over The Netherlands. I took as hypothesis that, based on the climate change predicted for The Netherlands, Dutch waters would potentially be colonized by species presently occurring in the south-central parts of France. Species with their most southern distributional boundaries in The Netherlands will possibly become extinct. Climate change is a fast process; oligochaetes likely will be unable to adapt naturally within the accelerated climatological change we are now experiencing. The only way in which oligochaetes can easily be transported throughout Europe is by anthropogenic interference. If the introduction location is suitable, the species then will colonize. A change in the species list within tubificoid naidids and naidids s.str., perhaps ranging from 5% to perhaps 15%, could occur in the future.

In general, the number of potential immigrants and emigrants related to climatic change is low. This supports the conclusion that the expected climatic changes will not essentially modify the aquatic oligochaete fauna in Europe, particularly when compared with the contemporary long-distance anthropogenic introductions of many species.

The temporal scale includes the temperature change induced shift of life history stages of oligochaetes over the year. Therefore, the occurrence of different life history stages over major regions in Europe was used. The hypothesis of oligochaetes showing different life history features in population occurring between western and eastern Europe, and in populations occurring between northern and southern Europe was tested. Only slight support for this hypothesis could be documented, due in part to the scattered and unequally divided data availability over Europe. When going from western to eastern Europe, the mature stage lasted somewhat longer and reproductive periods somewhat shorter for tubificoid naidids. Naidids s.str. were present along this gradient for longer periods of the year. The north-south gradient lacked enough data. Several other observations can argue against our interpretation, primarily those related to the oligochaetes' (genetic) plasticity or adaptation, population dynamics, food, behavior, and tolerance to a range of environmental conditions.

## Introduction

Temperature is one of the most important factors affecting the life history characteristics and biogeography of aquatic macro-invertebrates (Sweeney 1984), including oligochaetes. Oligochaetes are poikilothermic animals whose life history characteristics (e.g., metabolism, growth, development and behaviour), are

determined by daily, seasonal and annual temperature regimes. Like other macro-invertebrates, oligochaetes, also possess life history strategies that enable them to distribute over large geographical areas and over different seasons.

Despite debates on the magnitude of climate change, it is clear that through – human activities – climate will continue to change over the next decades.

The general circulation model (GCM) suggests a more active hydrological cycle fed by a greater evaporation and resulting in a substantial shift in rainfall distribution (Schlesinger & Mitchell 1987). This will have a large impact on aquatic ecosystems. In the temperate zone, more extreme climate events will occur, e. g., heavy rainfall over short periods of time resulting in floods, dry periods with high air temperatures leading to droughts, warmer winters preventing ice cover, and storms that will disturb shallow water bodies by increasing the periodicity and extent of overturn. Of greatest concern, though, is the rise in temperature – directly affecting the life history characteristics of oligochaetes as well as their biogeographical distribution patterns.

Global average surface temperature on Earth increased by approximately 0.8°C over the last century and the Intergovernmental Panel on Climate Change (IPCC) predicted an increase in global average surface temperature of 1.4 °C to 5.8°C for the year 2100 (Houghton et al. 2001). The average surface temperature in The Netherlands rose by 1.6°C over the last hundred years (KNMI 2003). The largest temperature rise took place in the months February and March. Precipitation has increased by 20% since 1900. The KNMI climate change scenarios predict a future rise of 1-6°C in The Netherlands. The strongest temperature increase will occur during the late winter and early spring (van Oldenborgh & van Ulden 2003). Van den Hurk et al. (2006) concluded that temperature in The Netherlands will continue to rise, and mild winters and hot summers will become more common.

During this review, temporal and spatial effects of temperature change on Dutch freshwater oligochaetes were considered. Temporal effects may include shifts in timing of life cycle stages of oligochaetes over the year. The spatial scale includes the temperature change-induced shift of biogeographic distribution patterns over The Netherlands.

Two primary research questions were addressed during this review:

1. How does temperature change affect the life cycle characteristics of Dutch tubificoid naidids and naidids s.str.?

2. What shifts in biogeographical distribution of oligochaetes will take place in The Netherlands when climate changes?

One should keep in mind that the terms “naidid”

and “tubificid” have become more ecological in concept now that Erséus et al. (2002) have shown that traditional naidids are not monophyletic, and are nested within at least 2 tubificid clades.

Based on sequences of 18S rDNA and other molecular and morphological data, Erséus and Gustavsson (2002) and Erséus et al. (2002) concluded that the family Naididae is more correctly placed within a subfamily Naidinae of the Tubificidae, with ‘Naididae’ thus becoming a junior synonym of the family Tubificidae. A petition was then submitted by Erséus et al. (2005) to the International Commission of Zoological Nomenclature (ICZN, the Commission), requesting the family-group name Tubificidae *Vejdovský, 1876*, be given precedence over Naididae *Ehrenberg, 1828*. In 2007 the Commission recently voted against this proposal, maintaining precedence for Naididae over Tubificidae (ICZN 2007). Erséus et al. (2008) published a paper summarizing the short history of this issue, with the consequence being that the former tubificids (Tubificidae s.str.) should be regarded as members of the Naididae whenever the two names are regarded as synonyms. The five subfamilies of Tubificidae s.str. (Tubificinae, Rhyacodrilinae, Phallogrilinae, Limnodriloidinae, and Telmatodrilinae) are now included within the Naididae (Erséus et al. 2008). Throughout this paper, the vernacular term ‘tubificoid naidids’ will be used, inclusively of the former Tubificidae (taxa in the five subfamilies noted above) and the term ‘naidids s.str.’ will be used for taxa in the subfamilies Naidinae and Pristininae.

## Material and methods

### *Climate change in Dutch surface waters*

The KNMI climate change scenario is based on Hadley’s General Circulation Model (GCM: Houghton et al. 1996). The grid cell of the Hadley GCM chosen (Eastern Longitude between 5.625° to 9.375°, Northern Latitude between 51.25° to 53.75°) has its centre in the eastern part of The Netherlands (Verweij and Viner 2001). The Hadley weather variables used were daily values of precipitation (mm d<sup>-1</sup>), temperature (°C), relative humidity (%), and total downward surface short-wave flux (W m<sup>-2</sup> d<sup>-1</sup>). As the Hadley data for the current weather conditions deviate from those conditions that were measured, the Hadley weather series were downscaled and calibrated to this

region. The rising CO<sub>2</sub>-concentration in the future will affect evapotranspiration (Haasnoot et al. 1999). The change in the crop evapotranspiration factor is included in a different scenario – as a reduction of 10% for grassland and a reduction of 36% for arable land crops (van Walsum et al. 2001). The change in the daily and mean temperature involved in a climate scenario will result in a change in precipitation. The KNMI method for adjusting precipitation is described by Können et al. (1997) and results per degree Celsius in a long-term average increase of 1% of the mean summer and of 6% of the mean winter precipitation. Finally, wind directions and speeds as well as frequency of storm events will also change due to climate change. Thus, an 8% increase in the maximum wind speed for 2100 is predicted (Dorland et al. 2004). All variables were included in the scenario described.

#### *Biogeographical distribution patterns*

Climate change will influence the biogeography of aquatic macro-invertebrates. The current climate zones over Europe are illustrated in Figure 1. Changes in the temperature regime will affect the fitness of individual species in terms of survival/mortality, growth/fecundity, and production of viable offspring. If some species of macro-invertebrates, including oligochaetes, are unable to endure changing conditions, the only option to avoid extinction would be to actively disperse to a location with a more suitable climate (Sweeney et al. 1992). Oligochaetes will not actively disperse in response to changing climatic conditions. In past studies (e.g., Timm 1980, Milbrink 1980, Milbrink & Timm 2001) oligochaetes were only successful in reproducing and ‘staying alive’ at newly colonized sites through passive dispersal rather than as a result of ‘active moving’. A temperature change will not only affect the current distribution of oligochaetes resulting in local extinction of one or more taxa, but will also – over time – lead to immigration of one or more taxa from elsewhere in Europe. However, in The Netherlands a considerably immigration from overseas occurs, without any climatic shifts (e.g., bilge water replacement by ships, commercial pet industry). To study the current and expected distribution pattern of oligochaetes, the biogeographic information on oligochaetes listed in the Fauna Europaea (2004) was analyzed. The criteria within this

analysis to include a species were:

1. the focus is on species of tubificoid naidids and naidids s. str.;
2. the species must be present in the Atlantic region of the north-western European lowland plain; this means that the area included should have an altitude lower than 200 m above sea level.

Under the hypothesis that water temperature will increase by about 1-6 °C in 2100, the temperature regime in The Netherlands will become similar to the one that now present in France. Thus immigrants most probably will come from Belgium and the central parts of France (termed the “south”). For this analysis the immigrants comprise those species that currently occur in Belgium and/or France but are not yet present in (have yet to be reported from) the Scandinavian countries (termed the ‘north’). Emigrants are those species currently occurring in The Netherlands but are not yet present in (have yet to be reported from) southern countries (Belgium and France). Their distribution limits are predicted to shift towards the north. The species distribution in the United Kingdom and Germany is added to the list for purposes of comparison as these species could be absent in The Netherlands due to missing / unpublished data. These three countries (United Kingdom, Germany, The Netherlands) are termed the “middle”. Oligochaete species currently occurring in all three major areas (south, middle and north) will show no change in distribution range with respect to The Netherlands.

#### *Life cycle patterns*

It is generally accepted that aquatic oligochaetes are extremely euryoecous and inhabit occur in a variety of habitats. Only a few species, however, can be associated with specific habitats. Among the freshwater oligochaetes the family Naididae s.lat. (including both the tubificoid naidids and naidids s.str.) contains the highest number of species, reach the highest population densities, and are widely distributed. Tubificoid naidids and naidids s.str. are quite distinct (as groups) from one another with respect to for example, ecology, life cycles, and reproduction biology despite the fact that these two groups are now treated as a single family due to the conclusions of recent phylogenetic studies (see Erséus et al. 2008).

In general, both tubificoid naidids and naidids

s.str. have simple life cycles. Tubificoid naidids deposit eggs (1 to about 16) in cocoons. The embryonal development takes place in the cocoon and lasts (dependent on the presence of an embryonal diapause) from a few days up to 6 months. Juveniles hatch from the cocoon and grow to maturity in a period of time that can range from a few months to a year or more.

The worms breed once to several times before they die. Between reproduction periods they can resorb and regenerate the reproductive system. Such a post-breeding stage is characterised by a breakdown of the gonads, seminal vesicles and penis sheaths (Hunter & Arthur 1978). Asexual reproduction among tubificoid naidids occurs but is rare (Christensen 1984).

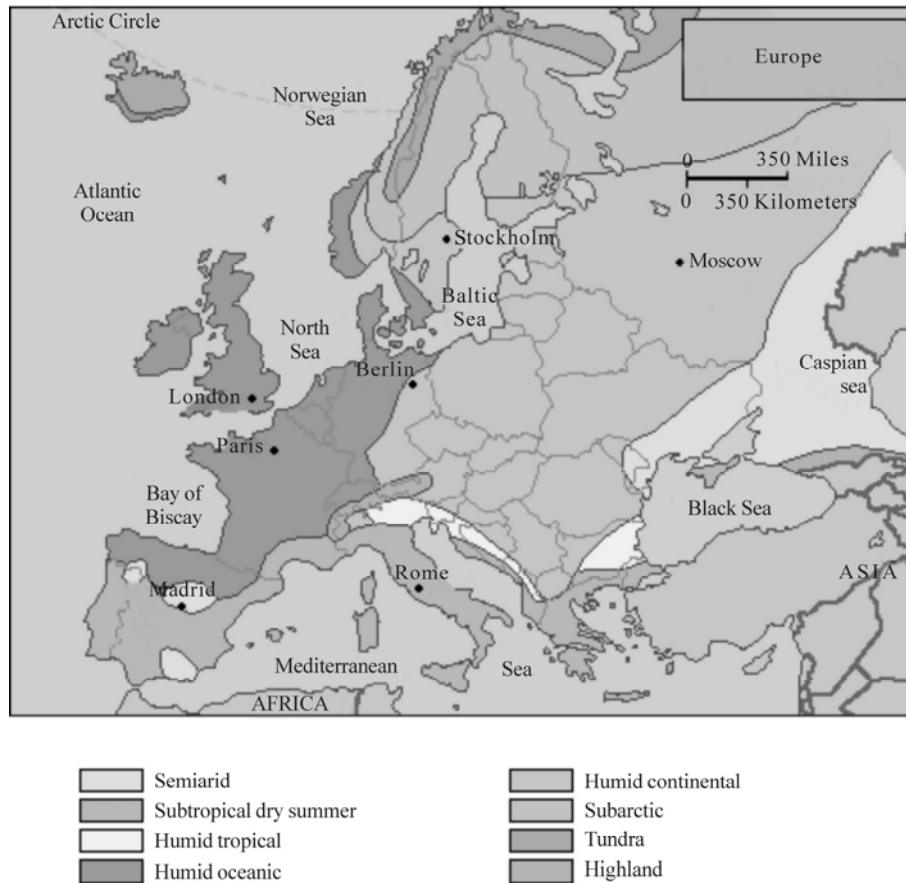


Figure 1. Map of Europe with climate zones indicated

Naidids s.str. also deposit cocoons, mostly with only one egg. The embryonal development takes place in the cocoon and lasts (dependent on the presence of an embryonal diapause) throughout most of the winter season. Furthermore, various forms of asexual reproduction occur among naidids s.str. (Christensen 1984), e.g., resulting in periods of mass abundances.

For this review, information on the timing of life cycle stages of tubificoid naidids and naidids s.str. was synthesized from a large number of studies over Europe. I included studies that recorded the months during which specimens of tubificoid naidids and naidids s.str. were observed in one of their life stages. Six life stages were distinguished for tubificoid

naidids: cocoons, newly hatched worms, young or immature worms, mature worms with fully developed genitalia, reproductively mature specimens containing spermatophores and eggs, and post-mature specimens (recognisable as lacking spermatophores and eggs, having absorbed the genitalia, but retaining the penis sheaths).

Two life stages were distinguished for naidids s.str.: presence and occurrence in mass abundances, and the occurrence of cocoons with mature (sexually developed) specimens.

Table 1 notes the regions in Europe discussed in this review, and the countries (with country code) assigned to these regions.

Next the country where the study was performed was noted and classified according to region in Europe (Table 1).

The first month in which a specific life stage of a specific species was recorded and the sum of observations for that species listed per European region are both presented in tables 5-13.

Table 1. Assignment of European countries to regions in Europe

European region	countries
north	Denmark (DK), Sweden (SE), Estonia (EE)
central	Germany (DE), Poland (PL), Switzerland (CH), Romania (RO)
south	France (FR), Italy (IT), Macedonia (MK)
west	United Kingdom (UK), Belgium (B), Netherlands (NL)
east	Russia (RU)

## Results

### *Climate change in Dutch surface waters*

The KNMI climate change scenarios (Table 2) predict a future rise in temperature of 1-6°C. The strongest temperature increase will occur during the late winter and early spring (van Oldenborgh & van Ulden 2003). More recently, van den Hurk et al. (2006) concluded:

1. Temperature in The Netherlands will continue to rise. Mild winters and hot summers will become more common.
2. On average, winters will become wetter and extreme precipitation amounts will increase.
3. The intensity of extreme rain showers in summer will increase. However, the number of rainy days in summer will decrease.
4. The calculated change in wind is small compared to the natural fluctuations.

An increase in precipitation will result from the increase in periods with extreme precipitation (more wet years) and will result in an increase in discharge peaks, especially in winter. Wetter periods will occur in winter and spring, and dryer periods in summer and autumn, but the latter will also experience more intense and heavier summer storms. Dryer summer periods will result in more intermittency and lower water levels. Warmer winters will result in less snow and shortening of ice cover periods.

### *Biogeographical distribution patterns*

In total, the Fauna Europaea (2004) included 55 Naididae s.str. species and 63 tubificoid Naididae

species that occurred in France, Belgium, The Netherlands, United Kingdom, Germany, Denmark, Norway and Sweden. Based on these biogeographical data it can be concluded that for the tubificoid naidids the southern part of the European Atlantic region recorded 48 species, the central region recorded 41, and the northern region 35 species (Table 3). For Netherlands, 5 potential tubificoid naidid immigrants (14%) and 2 emigrants (5%) were identified. Stygo-bionts were not considered as potential immigrants as they have not yet been reported from the Netherlands – a country devoid of subterranean habitats.

The south and the middle of the European Atlantic region recorded 47 and 48 species, respectively, and the northern region recorded 44 species of naidids s.str. (Table 4). For The Netherlands, 5 potential naidid s.str. immigrants (11%) and 3 emigrants (7%) were identified. Overall, the number of both tubificoid naidids and naidids s.str. species, together, would increase in The Netherlands.

Table 2. KNMI climate change scenarios for The Netherlands in the year 2050 based on the KNMI report (van den Hurk et al. 2006). (G= moderate scenario, W=warm scenario, extension += the scenario includes a strong change of circulation in winter and summer)

	moderate estimation		high estimation	
	G	G+	W	W+
average summer temperature (°C)	+0.9	+1.4	+1.7	+2.8
average winter temperature (°C)	+0.9	+1.1	+1.8	+2.3
yearly warmest summer day (°C)	+1.0	+1.2	+2.1	+3.8
yearly coldest winter day (°C)	+1.0	+1.5	+2.1	+2.9
average summer precipitation (%)	+2.8	-9.5	+5.5	-19.0
average winter precipitation (%)	+3.6	+7.0	+7.3	+14.2
precipitation on wettest summer day (%)	+4.6	+0.1	+9.1	+0.3
precipitation on wettest winter day (%)	+3.6	+6.0	+7.1	+12.1
evaporation (%)	+3.4	+7.6	+6.8	+15.2
wind speed	0	+1	0	+4

### *Life cycle patterns*

The seasonal occurrence of different life cycle stages over major regions in Europe was based on information summarized in Appendix 1.

For the tubificoid Naididae, I have summarized the results of studies on 21 species of in 11 countries published by 37 authors; for the Naididae s.str., I have summarized the results of studies on 37 species in 10 countries published by 34 authors. Most of these studies were performed in western Europe.

Table 3. Distribution of species of tubificoid naidids in the Atlantic European region (FR=France, BE=Belgium, NL=Netherlands, UK=United Kingdom, DE=Germany, DK=Denmark, NO=Norway, SE=Sweden, p=presence)(partly extracted from the Fauna Europaea, 2004 with additions based on literature data by T. Timm [ pers. Comm.]

species name	country code							remark
	FR	BE	NL	UK	DE	DK	NO	
<b>widespread</b>								
<i>Aulodrilus limnobius</i> Bretscher, 1899	p	p	p	p	p		p	p
<i>Aulodrilus pluriset</i> a (Piguet, 1906)	p	p	p	p	p	p	p	p
<i>Branchiura sowerbyi</i> Beddard, 1892	p	p	p	p	p			p
<i>Ilyodrilus templetoni</i> (Southern, 1909)	p	p	p	p	p		p	p
<i>Limnodrilus claparedianus</i> Ratzel, 1869	p	p	p	p	p	p	p	p
<i>Limnodrilus hoffmeisteri</i> Claparede, 1862	p	p	p	p	p	p	p	p
<i>Limnodrilus profundicola</i> (Verrill, 1871)	p	p	p	p	p	p	p	p
<i>Limnodrilus udekemianus</i> Claparede, 1862	p	p	p	p	p	p	p	p
<i>Potamothrix bavaricus</i> (Oschmann, 1913)	p	p	p	p	p	p		p
<i>Potamothrix bedoti</i> (Piguet, 1913)	p	p	p		p		p	p
<i>Potamothrix hammoniensis</i> (Michaelson, 1901)	p	p	p	p	p	p	p	
<i>Potamothrix moldaviensis</i> Vajdovsky & Mrazek, 1903	p	p	p	p	p	p		p
<i>Psammoryctides albicola</i> (Michaelson, 1901)	p	p	p	p	p	p	p	p
<i>Psammoryctides barbatus</i> (Grube, 1861)	p	p	p	p	p	p	p	p
<i>Rhyacodrilus coccineus</i> (Vajdovsky, 1876)	p	p	p	p	p	p	p	p
<i>Rhyacodrilus falciformis</i> Bretscher, 1901	p	p	p	p	p	p	p	p
<i>Spirosperma ferox</i> Eisen, 1879	p	p	p	p	p	p	p	p
<i>Tubifex tubifex</i> (Müller, 1774)	p	p	p	p	p	p	p	p
<i>Tubifex nerthus</i> Michaelson, 1908	p	p	p*	p	p			
<i>Aulodrilus pigueti</i> Kowalewski, 1914	p		p		p			p
<i>Bothrioneurum vajdovskyanum</i> Stolc, 1886	p		p	p	p	p		p
<i>Haber speciosus</i> (Hrabe, 1931)	p		p	p			p	p
<i>Potamothrix heuscheri</i> (Bretscher, 1900)	p		p		p			p
<i>Potamothrix vajdovskyi</i> (Hrabe, 1941)	p		p	p				p
<i>Rhyacodrilus subterraneus</i> Hrabe, 1963	p		p		p		p	p
<i>Tubifex ignotus</i> (Stolc, 1886)	p		p	p	p	p	p	p
<i>Clitellio arenarius</i> (Müller, 1776)	p	p	p	p	p?	p		p
<b>Southern</b>								
<i>Abyssidrilus cuspis</i> (Erséus & Dumnicka, 1988)	p							southern species, potential immigrant, stygobiont
<i>Epirodilus pygmaeus</i> (Hrabe, 1935)	p							southern species, potential immigrant
<i>Gianius cavealis</i> Juget & Des Chatelliers, 2001	p							southern species, potential immigrant, stygobiont
<i>Gianius labouichensis</i> (Rodriguez & Giani, 1989)	p							southern species, potential immigrant, stygobiont
<i>Gianius riparius</i> (Giani & Martinez-Ansemil, 1981)	p							southern species, potential immigrant, stygobiont
<i>Haber pyrenaicus</i> (Juget & Giani, 1974)	p							southern species, potential immigrant
<i>Haber turquinae</i> (Juget & Lafont, 1979)	p							southern species, potential immigrant
<i>Krenedrilus sergei</i> Giani, Erséus & Martinez-Ansemil, 1990	p							southern species, potential immigrant, stygobiont
<i>Peristodrilus montanus</i> (Hrabe, 1962)	p							southern species, potential immigrant, stygobiont
<i>Rhyacodrilus amphigenus</i> Juget, 1987	p							southern species, potential immigrant, stygobiont
<i>Rhyacodrilus ardierae</i> Lafont & Juget, 1993	p							southern species, potential immigrant
<i>Rhyacodrilus balmensis</i> Juget, 1959	p							southern species, potential immigrant, stygobiont
<i>Rhyacodrilus carsticus</i> Kosel, 1980	p							southern species, potential immigrant, stygobiont
<i>Rhyacodrilus lindbergi</i> Hrabe, 1963	p							southern species, potential immigrant, stygobiont
<i>Spiridion phreaticola</i> (Juget, 1987)	p							southern species, potential immigrant, stygobiont
<i>Tubifex tubifex blanchardi</i> Vajdovsky, 1891	p							subspecies not considered
<i>Tubificoides galarzai</i> Giani & Rodriguez, 1988	p							southern species, potential immigrant, stygobiont
<i>Gianius aquaedulcis</i> (Hrabe, 1960)	p				p			southern species, potential immigrant
<b>southern-central</b>								
<i>Embolocephalus velutinus</i> (Grube, 1879)	p	p	p*	p	p			potentially migrating to Scandinavia
<i>Psammoryctides moravicus</i> (Hrabe, 1934)	p		p		p			potentially migrating to Scandinavia
<i>Quistadrilus multisetosus</i> (Smith, 1900)	p	p	p	p	p			North American immigrant
<b>western-central</b>								
<i>Aulodrilus japonicus</i> Yamaguchi, 1953			p		p			often mixed with <i>A. pluriset</i> a
<i>Limnodrilus maumeensis</i> Brinkhurst & Cook, 1966			p					North American immigrant
<i>Tubifex newaensis</i> (Michaelson, 1903)			p		p			Ponto-Caspian immigrant
<i>Tubificoides heterochaetus</i> (Michaelson, 1926)		p	p	p	p			brackish-water species
<b>western-central-northern</b>								
<i>Monopylephorus irroratus</i> (Verrill, 1873)			p	p	p	p		brackish-water species
<i>Limnodrilus cervix</i> Brinkhurst, 1963			p	p			p	North American immigrant
<b>Central</b>								
<i>Isochaetides michaelsoni</i> (Lastockin, 1936)					p			Ponto-Caspian immigrant
<i>Potamothrix danubialis</i> (Hrabe, 1941)					p			Ponto-Caspian immigrant
<i>Psammoryctides deserticola</i> (Grimm, 1876)					p?			Ponto-Caspian immigrant
<b>Northern</b>								
<i>Tubifex smirnowi</i> Lastockin, 1927								p
<i>Pararhyacodrilus ekmani</i> (Piguet, 1928)								p
<i>Pararhyacodrilus palustris</i> (Ditlevsen, 1904)						p		
<i>Peipsidrilus pusillus</i> Timm, 1977								p
<i>Peipsidrilus saamicus</i> (Timm, 1978)								p?
<i>Varichaetadrilus harmani</i> (Loden, 1979)			p		p?			p
<b>total number</b>	<b>48</b>	<b>23</b>	<b>37</b>	<b>28</b>	<b>38</b>	<b>20</b>	<b>18</b>	<b>31</b>

Table 4. Distribution of species of Naididae s.str. in the Atlantic European region (FR=France, BE=Belgium, NL=Netherlands, UK=United Kingdom, DE=Germany, DK=Denmark, NO=Norway, SE=Sweden, p=presence)(partly extracted from the Fauna Europaea, 2004 with additions based on literature data by T. Timm)

species name	country code							remark	
	FR	BE	NL	UK	DE	DK	NO		SE
<b>widespread</b>									
<i>Amphichaeta leydigi</i> Tauber, 1879	p		p		p	p	p		
<i>Aulophorus furcatus</i> (Oken, 1815)	p	p	p	p	p			p	southern species, in the north connected with sewage plants
<i>Chaetogaster crystallinus</i> Vejdovsky, 1883	p	p	p	p	p	p		p	
<i>Chaetogaster diaphanus</i> (Gruithuisen, 1828)	p	p	p	p	p	p	p	p	
<i>Chaetogaster diastrophus</i> (Gruithuisen, 1828)	p	p	p	p	p	p	p	p	
<i>Chaetogaster langi</i> Bretscher, 1896	p	p	p	p	p	p		p	
<i>Chaetogaster limnaei</i> Baer, 1827	p	p	p	p	p	p	p	p	
<i>Chaetogaster setosus</i> Svetlov, 1925	p				p		p		
<i>Dero digitata</i> (Müller, 1774)	p	p	p	p	p	p	p	p	
<i>Dero dorsalis</i> Ferroniere, 1899	p		p		p			p	
<i>Dero nivea</i> Aiyer, 1929	p		p		p			p	
<i>Dero obtusa</i> Udekem, 1855	p	p	p	p	p	p		p	
<i>Nais alpina</i> Sperber, 1948	p		p	p	p		p	p	
<i>Nais barbata</i> Müller, 1774	p	p	p	p	p	p	p	p	
<i>Nais behningi</i> Michaelsen, 1923	p		p		p			p	
<i>Nais bretscheri</i> Michaelsen, 1899	p	p	p	p	p	p	p	p	
<i>Nais communis</i> Piguet, 1906	p	p	p	p	p	p	p	p	
<i>Nais elinguis</i> Müller, 1774	p	p	p	p	p	p	p	p	
<i>Nais pardalis</i> Piguet, 1906	p	p	p	p	p	p	p	p	
<i>Nais pseudobtusa</i> Piguet, 1906	p		p	p	p	p	p	p	
<i>Nais simplex</i> Piguet, 1906	p	p	p	p	p	p	p	p	
<i>Nais variabilis</i> Piguet, 1906	p	p	p	p	p	p	p	p	
<i>Ophidonais serpentina</i> (Müller, 1774)	p	p	p	p	p	p	p	p	
<i>Paranaïs frici</i> Hrabe, 1941	p		p		p			p	
<i>Piguetiella blanci</i> (Piguet, 1906)	p		p	p	p		p	p	
<i>Pristina (Pristina) aequiseta</i> Bourne, 1891	p	p	p	p	p	p	p	p	
<i>Pristina (Pristina) longiseta</i> Ehrenberg, 1828	p	p	p	p	p	p	p	p	
<i>Pristina (Pristinella) jenkinae</i> (Stephenson, 1932)	p		p	p	p		p	p	
<i>Pristina (Pristinella) menoni</i> (Aiyer, 1929)	p		p	p	p		p	p	
<i>Pristina (Pristinella) osborni</i> (Walton, 1906)	p		p		p			p	
<i>Pristina (Pristinella) rosea</i> (Piguet, 1906)	p		p		p	p		p	
<i>Ripistes parasita</i> (Schmidt, 1847)	p		p	p	p	p	p	p	
<i>Slavina appendiculata</i> (Udekem, 1855)	p	p	p	p	p	p	p	p	
<i>Specaria josinae</i> (Vejdovsky, 1884)	p		p	p	p	p	p	p	
<i>Stylaria lacustris</i> (Linnaeus, 1767)	p	p	p	p	p	p	p	p	
<i>Uncinais uncinata</i> (Ørsted, 1842)	p	p	p	p	p	p	p	p	
<i>Vejdovskyaella comata</i> (Vejdovsky, 1884)	p		p	p	p	p	p	p	
<i>Vejdovskyaella intermedia</i> (Bretscher, 1896)	p	p	p	p	p	p		p	
<b>Southern</b>									
<i>Chaetogaster parvus</i> Pointner, 1914	p								southern species, potential immigrant
<i>Nais bihorensis</i> Pop, 1971	p								southern species, potential immigrant
<i>Pristina (Pristinella) notopora</i> Cernosvitov, 1937	p								southern species, potential immigrant
<i>Pristina (Pristinella) sima</i> (Marcus, 1944)	p								southern species, potential immigrant
<i>Pseudochaetogaster longemeri</i> Lafont, 1981	p								southern species, potential immigrant
<b>southern-central</b>									
<i>Haemonais waldvogeli</i> Bretscher, 1900	p		p						potentially migrating to Scandinavia
<i>Nais christinae</i> Kasprzak, 1973	p	p			p				formerly confused with variabilis s.l.
<i>Pristina (Pristinella) bilobata</i> (Bretscher, 1903)	p	p	p	p	p				potentially migrating to Scandinavia
<b>western</b>									
<i>Homochaeta lactea</i> (Cernosvitov, 1937)			p						South American immigrant?
<i>Pristina (Pristina) synclites</i> Stephenson, 1925			p						a widely distributed tropical species
<b>western-central-northern</b>									
<i>Amphichaeta sannio</i> Kallstenius, 1892			p	p	p	p		p	potentially disappearing from NL
<i>Pristina (Pristinella) amphibiotica</i> Lastockin, 1927			p	p	p			p	potentially disappearing from NL
<i>Arcteonais lomondi</i> (Martin, 1907)			p	p				p	potentially disappearing from NL
<i>Paranaïs litoralis</i> (Müller, 1780)			p		p				seashore species, even in subtropics
<b>Northern</b>									
<i>Pristina (Pristina) breviseta</i> Bourne, 1891								p	
<i>Vejdovskyaella macrochaeta</i> (Lastockin, 1921)								p	
<b>total number</b>	<b>46</b>	<b>24</b>	<b>45</b>	<b>34</b>	<b>43</b>	<b>28</b>	<b>27</b>	<b>41</b>	

Cocoons for tubificoid naidids were first observed during the months of January through May

in western Europe, although cocoons were also commonly observed in September through November

(Table 5). Observations of cocoon deposition, however, seemed to begin somewhat later in eastern Europe (February), and even later in northern Europe (April, May, or June). This could be a temperature related process, although the southern European observations also occurred during April and May.

Observations of newly hatched juveniles in western Europe began in the months of February through July (Table 6). Too few observations were available from other regions to make a comparison.

The immatures of tubificoid naidids were collected all year around (Table 7). Mature specimens of tubificoid naidids were most commonly collected from January through April in western and central Europe (Table 8), though observations suggested they were present all year around in some localities.

Observations of reproductive specimens of tubificoid naidids began in January and continued to through June in western and central Europe, and in February through May in eastern and northern Europe (Table 9). The reproductive stage in the tubificoid naidids seems to be temperature related.

Cocoons of naidids s.str. were observed only incidentally throughout Europe during the period September through December (Table 10). Species of naidids s.str. were more often present from January through June in western, central and eastern Europe, with species also occurring in July in the latter two regions (Table 11). In the north most observations of cocoons began in May, June or July. First observations

of mass abundances of naidids s.str. began in February through July in western and central Europe (Table 12). In autumn periods fewer species occurred in masses. The low number of observations in the other European regions preclude comparison and conclusions. Observations of mature naidids s.str. began more often in the second half of the year (Table 13).

Taking the duration of each life cycle stage into consideration, immature Naidiae were always present (Figure 2). Mature specimens of naidids s.str. were present most of the year, while the other stages were collected during 6 to 8 months each year. Though cocoons and newly hatched individuals were clearly present longest for the longest period of time in central Europe and shortest period of time in northern Europe, the data do not demonstrate the effects of a real temperature gradient. All second occurrences of life cycle stages of naidids s.str. were observed for only one month each (data not presented herein).

Cocoons of naidids s.str. were observed for only one to two months throughout Europe (Figure 3). Naidids s.str. were present for about 4 months in northern Europe, but, on average, for seven to nine months in the other regions. The length of occurrence of naidids s.str. increased from western to eastern Europe (Figure 3). Mature specimens and mass abundances were observed, on average, for period of two months, except for eastern Europe where mass abundances of naidids s.str. were observed for more than three months.

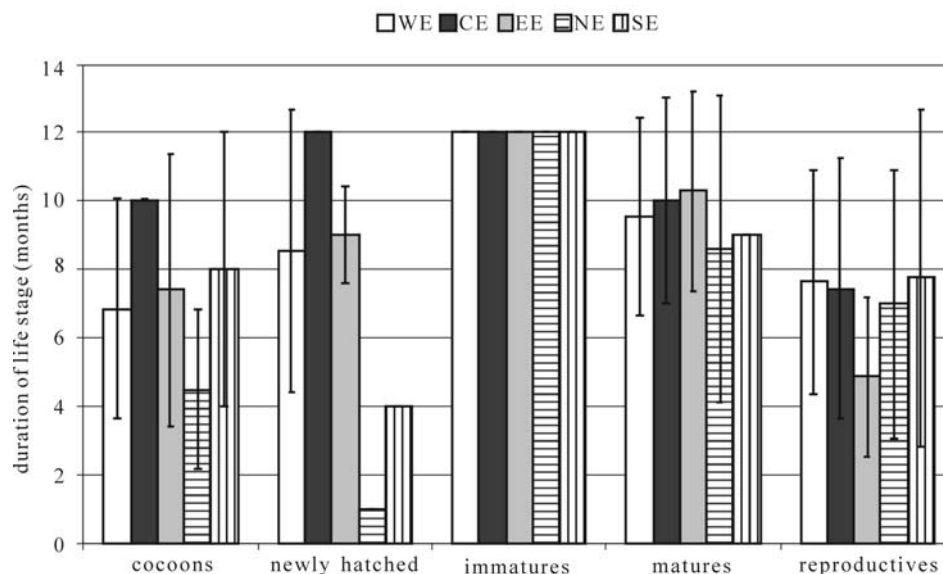
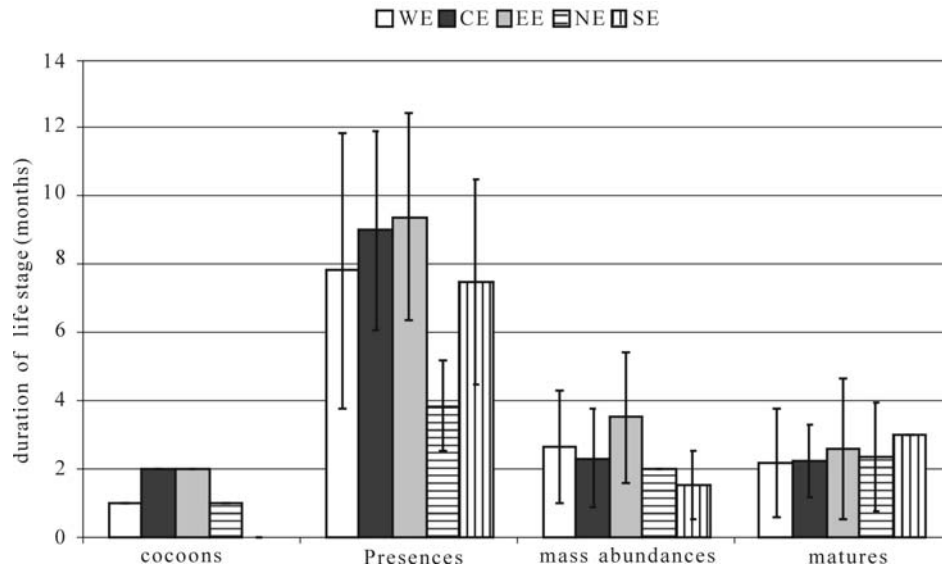


Figure 2. Duration (average and standard deviation) of life cycle stages of tubificoid Naididae (Tubificidae s.str.) in the major five European regions (for data see Appendix 1). (WE=western Europe, CE=central Europe, EE=eastern Europe, NE=northern Europe, SE=south-eastern Europe)





Figur 3. Duration (average and standard deviation) of life cycle stages of Naididae s.str. in the major five European regions. (WE=western Europe, CE=central Europe, EE=eastern Europe, NE=northern Europe, SE=south-eastern Europe)

Table 5. Month in which occurrences of cocoons of tubificoid naidid species were first recorded, over the five major regions in Europe based on the data in Appendix 1 (WE=western, CE=central, EE=eastern, NE=northern, and SE=southern Europe; number of high abundance observations are given between brackets)

cocoons	WE	CE	EE	NE	SE
all year	2		1		1
January	3 (1)				
February	2		1		
March	2 (3)	(1)	1 (1)		
April	1 (1)		2	2	1
May	1 (5)		(2)	2	1 (2)
June	1			2 (1)	
July					
August					
September	1		1 (1)		
October	1 (2)				
November	1				
December		1			

Table 6. Month in which occurrences of newly hatched juveniles of tubificoid naidid species were first recorded, over the five major regions in Europe based on the data in Appendix 1 (WE=western, CE=central, EE=eastern, NE=northern, and SE=southern Europe; number of high abundance observations are given between brackets)

newly hatched	WE	CE	EE	NE	SE
all year	4	1			
January					
February	1				
March	1 (1)				
April	1		1		
May	(1)				1
June	1 (1)	(1)			
July	1 (3)				
August				1	
September					
October			1 (1)		
November					
December					

Table 7. Month in which occurrences of immatures of tubificoid naidid species were first recorded, over the five major regions in Europe based on the data in Appendix 1 (WE=western, CE=central, EE=eastern, NE=northern, and SE=southern Europe; number of high abundance observations are given between brackets)

immatures	WE	CE	EE	NE	SE
all year	14	11	2	3	3
January					
February	(2)				
March	(1)				
April					
May		(1)			
June	(4)				
July	(3)				
August					
September					
October	(2)				
November					
December		(1)			

Table 8. Month in which occurrences of mature specimens of tubificoid naidid species were first recorded, over the five major regions in Europe based on the data in Appendix 1 (WE=western, CE=central, EE=eastern, NE=northern, and SE=southern Europe; number of high abundance observations are given between brackets)

matures	WE	CE	EE	NE	SE
all year	9	14	5	2	
January	1 (4)	2 (6)			
February	(2)	(1)		(2)	
March	1 (1)	3 (4)	1		
April	(1)	(3)			
May					
June	1 (1)	1 (3)			
July	2 (2)	(1)		1	
August	(1)				
September	(1)	2			
October	1 (1)	1	1		
November	3 (1)	1 (1)			1
December	3	(1)		2	

*Table 9.* Month in which occurrences of reproductive specimens of tubificoid naidid species were first recorded, over the five major regions in Europe based on the data in Appendix 1 (WE=western, CE=central, EE=eastern, NE=northern, and SE=southern Europe; number of high abundance observations are given between brackets)

reproductive	WE	CE	EE	NE	SE
all year	2	3		1	2
January	2	4 (1)			
February	1 (1)			2	
March	3 (1)	1 (7)	2 (1)	1 (1)	
April	1 (1)	1	1	(2)	1
May	(2)	(1)	4 (1)	(2)	
June	(1)	1			
July				2	
August	(1)				
September					1
October			1		
November	1	1		1	
December	1 (1)				

*Table 10.* Month in which the presence of cocoons of Naididae s.str. species was first recorded, over the five major regions in Europe based on the data in Appendix 1 (WE=western, CE=central, EE=eastern, NE=northern, and SE=southern Europe; number of high abundance observations are given between brackets)

cocoons	WE	CE	EE	NE	SE
September			1		
October				2	
November	1				
December		1			

*Table 11.* Month in which the presence of Naididae s.str. species was first recorded, over the five major regions in Europe based on the data in Appendix 1 (WE=western, CE=central, EE=eastern, NE=northern, and SE=southern Europe; number of high abundance observations are given between brackets)

present	WE	CE	EE	NE	SE
all year	4	10	5		
January	1				
February	2	2			1
March		6	1		
April	2				
May	1	1		1	
June	2	3		4	1
July		3	2	1	
August					
September					
October		3	2		3
November					
December		2			

*Table 12.* Month in which the presence of mass abundances of Naididae s.str. species were first recorded, over the five major regions in Europe based on the data in Appendix 1 (WE=western, CE=central, EE=eastern, NE=northern, and SE=southern Europe; number of high abundance observations are given between brackets)

mass abundances	WE	CE	EE	NE	SE
all year	14	11	2	3	3
January					
February	3	5			1
March	3	7			
April	1	7			
May	8	7	1		
June	2	8	2		
July	4	1	1	1	
August	2	2			
September		3			
October	3	1			2
November	2	2	2		
December		1			1

*Table 13.* Distribution of mature Naididae s.str. over the five major regions in Europe based on the data in Appendix 1 (WE=western, CE= central, EE=eastern, NE=northern, and SE=southern Europe; number of high abundance observations are given between brackets)

mature	WE	CE	EE	NE	SE
all year					
January	1				
February					1
March		1			
April	1	4			
May		2			
June	1	5		7	
July	1			8	
August	1	3	2	3	
September			2	3	
October	3	4			
November		3	1		
December					

## Discussion

I took as hypothesis that, based on the climate change predicted for The Netherlands, the Dutch waters would potentially be colonized by species currently occurring in the south-central parts of France. Native species with their most southern distribution boundary in The Netherlands will possibly become extirpated, at least locally. More specifically, the native species – as recent immigrants from anywhere would not have yet realized their full potential distribution pattern. Sweeney et al. (1992) suggested that increased water temperature could directly affect biogeographic dis-

tributions of aquatic organisms, as the authors showed for six species of mayflies. These authors suggested that, while the magnitude and rate of temperature do change, the genetic structure of populations and their phenology and life history traits will determine the capacity of aquatic organisms to respond to changes in temperature regime through migration or through adaptation. In the spatial analysis presented, the migration response of organisms is taken as a starting point. This immediately raised the question: Do oligochaetes possess dispersal capacity? In general, oligochaetes are slow in their dispersal, thus active dispersal can be ruled out (Timm 1980). Short-term dispersal is mainly related to downstream migration, rafting, cocoons and immatures/ – adults spread by bird and mammal vectors, discharge/ replacement of ballast water of ships, construction of new canals, transport of garden pond plants and fishes (Milbrink & Timm 2001). In their paper, Milbrink & Timm showed that the geographic expansion of the Ponto-Caspian genus *Potamothenis* into northern and north-western Europe took place in three waves:

1. The first wave in the early postglacial times included *Potamothenis hammoniensis* and *Psammoryctides barbatus* (Milbrink 1980). This wave was slow and natural.

2. The second wave took place in the 18-20<sup>th</sup> century and included *Potamothenis moldaviensis*, *P. bavaricus*, *P. moravicus* and *Tubifex newaensis* (Milbrink & Timm 2001). This wave was induced by the digging of waterways and shipping.

3. The third wave included *Potamothenis heuschleri* and *P. vejdvovskyi*, and is still continuing for the latter species (Milbrink 1999, Milbrink & Timm 2001).

Another interesting example of oligochaete dispersal pattern was the introduction and dispersal of the (sub)tropical species *Branchiura sowerbyi* in Europe (Aston 1968). Such introduced exotic species from warmer climate zones may provide a good indication of the biogeographic shift that will be realized when temperature rises. Arguments that *Branchiura* was introduced were threefold (Aston 1968):

1. It is the most abundant oligochaete species in eastern Asia.

2. In Europe it mainly occurs in botanical

gardens in warm water tanks.

3. It occurs in heated effluent receiving surface waters.

Although *B. sowerbyi* also was found in natural water bodies, Brinkhurst (1964) suggested that it only reproduced asexually under such conditions. Aston (1968) experimentally showed that the temperature required to produce viable cocoons was around 15°C, as is true for a number of indigenous tubificoid naids in Europe, although the optimum temperature for cocoon production was around 25°C. For most European tubificoid naids, however, the optimum may be around 15°C (see Timm 1987, p. 283: the English Summary). Aston (1968) also showed a positive correlation between growth of immature worms and temperature, and a negative correlation between growth of mature worms and temperature. Cocoon production of mature worms retarded growth. Thus, *Branchiura sowerbyi* was most probably introduced by man and is able to spread rapidly into areas where water temperatures are high relative to typical European temperature regimes. *B. sowerbyi* appears to exclude native oligochaetes near warm-water effluents (Milbrink 1980, Milbrink & Timm 2001).

The example of the dispersal of several species with the genus *Potamothenis* (above) shows that oligochaetes will disperse very slowly when natural processes prevail. Climate change is a fast process and natural dispersal of oligochaetes will not cope with that speed. The example of *Branchiura sowerbyi*, however, shows that when dispersal is facilitated by human activity – the most common way of current dispersal – species could easily be transported within Europe, and, when conditions at the introduction location are suited, species could colonize.

Apart from dispersal capacity, species must find suitable habitat. The list of potential immigrants from the south (Table 3) included a number of tubificoid naids of whom the habitat is listed as stygobionts: *Abyssidrilus cuspis*, *Ganius cavealis*, *G. labouchensis*, *G. riparius*, *Krenedrilus sergei*, *Peristodrilus montanus*, *Rhyacodrilus amphigenus*, *R. lindbergi*, *Spiridion phreaticola*, *Tubificoides galarzai* (Giani et al. 2001); *Rhyacodrilus balmensis* (Brinkhurst & Jamieson 1971); and *R. carsticus* (Juget 1987). Because their preferred (stygo-) habitat does not occur in The

Netherlands, it is unlikely that these species would colonize the country; this does not preclude, however, their collection as 'waif' specimens resulting from isolated introductions. This leaves only five potential immigrants (*Epirodilus pygmaeus*, *Ganius aquaedulcis*, *Haber pyrenaicus*, *H. turquinae*, *Rhyacodrilus ardierae*). Habitat is an important criterion for this analysis. A more detailed study on the ecology of potential immigrants, however, is necessary before drawing final conclusions. Only two emigrants were found (*Emboleocephalus velutinus*, *Psammoryctides moravicus*).

Temperature plays a major role in the ecology and evolution of all macroinvertebrates, including aquatic oligochaetes. As Ward & Stanford (1982) stated, "The thermal history to which an organism has been exposed shapes responses operative at the organism, population, and community levels of organization, which are manifest on both ecological and evolutionary time scales". Life history characteristics are the most important processes in which temperature plays a shaping role. The life cycle stages were classified as follows: cocoons, newly hatched or young specimens, immature specimens lacking reproductive features, mature specimens (mostly indicated by the presence of a clitellum), and reproductive specimens (those that have sperm in their spermatheca and/or eggs). Tubificoid naidids and naidids s.str. produce eggs that are sheltered by a cocoon. There was a positive correlation observed between number of eggs per cocoon and temperature for different tubificoid species (e.g., Aston, 1973, Poddubnaya 1980). Yet, in similar studies, Timm (1987), Timm (pers. comm.), and Jónasson & Thorhauge (1972) showed a negative correlation. Three possible explanations for the differences in the observations of the above studies are 1) the maximum number of eggs per cocoon occurs at the optimum temperature (which is quite low for *Potamothrix hammoniensis* and many other European species), or 2) higher temperatures accelerate cocoon laying rather than egg production, or 3) the last cocoons produced during the reproduction period contain fewer eggs.

The rate of development of embryos showed a positive linear relation to temperature (Thorhauge 1975). Thus, the higher the temperature, the shorter the developmental time will be. As was shown for a

number of species in other studies (Thorhauge 1976, Bonacina et al. 1987), the growth rate of tubificoid naidids increased proportionally with temperature.

Naidids s.str. generally show much more irregular developmental cycles or non-cyclic peaks in abundance (Wachs 1967, Learner et al. 1978). These peaks are due to asexual reproduction, and may only occur under optimal environmental conditions (Smith & Kaster 1986). Löhlein (1999) concluded that populations of Naididae s.str., at least early in the year, were limited by temperature in northern Germany. In early spring, a high production of diatoms attached to emergent vegetation sustained growing densities of *Chaetogaster diastrophus* and *Nais* spp. Later in the spring and on into summer, the exponential growth of naidids s.str. – through increased grazing activity – outweighed primary production by diatoms (which were being replaced by chorophytes). The naidid s.str. population was then observed to decline because of lower food quality. Löhlein's observations suggested a shift in naidid s.str. growth – from temperature control to food limitation.

The start of the breeding period for tubificoid naidids is strongly influenced by temperature (e.g., Brinkhurst 1964, Aston 1968, Ladle 1971). Generally, sexual maturation in naidids s.str. coincided with population density peaks (Smith & Kaster 1986). A number of causes have been postulated to explain sexual reproduction, such as food and oxygen (Stolte 1940), temperature and flow (Loden 1981), and temperature and food (Learner et al. 1978).

From all these observations we may conclude that life cycle is a process strongly influenced by temperature. Therefore, the hypothesis of oligochaetes showing different life history features – ranging geographically from western to eastern Europe, or from north to south – seems obvious. Plausible conclusions are that life cycles of oligochaetes are most influenced by higher summer temperatures in the east and south, and by harsher winters in the continental eastern areas.

The month in which the start of different life stage occurred, and the length (in days) of each of the life stages, should therefore differ along both west-east and north-south gradients; however, only a slight support was found. This may be due, in part, to the scattered data available; in particular, these data were the result of localized or regional studies, rather than

from a more broad study encompassing all of Europe. Going from west to east, the mature period for tubificoid naids lasted somewhat longer while their reproductive period was somewhat shorter; the occurrence of naids s.str. increased during each period each year. The north-south gradient lacked sufficient data for analysis. Several other arguments complicate our interpretation – those specific to (genetic) plasticity or adaptation, population dynamics, food, behavior, and environmental conditions:

1. Tubificoid naids adapt to the environmental conditions where they occur. Reynoldson et al. (1996) compared the growth rate and reproduction of two populations of *Tubifex tubifex* in the laboratory at 22.5°C, one from Lake Erie (cold and lentic) in Canada and one from a small Spanish mountain stream (warm and lotic). Although the Spanish worms produced fewer cocoons and young per adult, the Spanish reproduction rate was higher. Furthermore, the Spanish worms had a lower and more variable growth rate (Reynoldson et al. 1996). The ability to reproduce and grow over a broader range of temperature is an adaptation to a greater temporal variability in the environment. Differences in growth rate can also be due to the responses of populations to available habitats present in lentic environments that differ from those present in lotic environments (Poddubnaya 1980). Adaptation could be a reason why the expected differences in life cycle characteristics were not observed in the field.
2. Tubificoid generations clearly overlap considerably (Lazim & Learner 1986). The growth rate differed per population (Adreani et al. 1984). High population densities delay maturation (Poddubnaya 1980, Adreani et al. 1984). Tubificoid naids become mature over a wide range of body sizes (Kosiorek 1974, Ladle 1971, Lazim & Learner 1987), but keep on growing after maturation (Kosiorek 1974). Mature specimens can undergo a regression of sexual organs and mature two or more times (Brinkhurst & Kennedy 1965). The number of ova decline with the increase of population density (Lazim & Learner 1987). It is important to observe the occurrences of life cycle stages as well as important to observe, but also the quantified population dynamics. These were not considered in this study.
3. Several observations showed a longer breeding period of tubificoid naids in more productive habitats (Kennedy 1966, Potter & Learner 1974). Food quality influences the life cycle characteristics at a site. When conditions become favourable, a fast asexual population growth of naids s.str. occurs, and more often in spring than during other seasons. This mass development ends by a collapse of the population and the occurrence of sexually mature specimens.
4. Homeostasis is the maintenance of an internal, stable state throughout a much wider range of environmental conditions. Homeostasis is achieved not only by physiological means but also by the appropriate behavioural responses (Pianka 1978). Poikilothermic organisms, like tubificoid naids and naids s.str., can maintain a fairly constant body temperature over a considerable range of ambient thermal conditions. Through different behaviours, oligochaetes can thus show comparable life cycle characteristics under different temperature regimes. An extreme example was described by Narita (2006) of the daily and seasonal migrations into horizons offering the most suitable temperatures for *Rhyacodrilus hiemalis*.
5. Tubificoid naids and naids s.str. inhabit different water types and habitats. Their euryoecous capacities allow great flexibility in habitat selection. Tubificoid naids show different vertical depth distributions. Factors causing a specific depth distribution can be adaptation in respiratory physiology (Chapman et al. 1982), predation by fish (Newrkla & Mutayoba 1987), and/or selective feeding (Brinkhurst et al. 1972). Species inhabiting the profundal, colder environments can also easily occur in cold areas in shallow waters. Naids s.str. often have swimming capacities and can move on a daily basis from shallow shorelines to open, deeper water. The euryoecous nature of

both tubificoid naidids and naidids s.str. provides the opportunity to survive in different water types in different regions in Europe, by selecting habitats where the environmental conditions are still more compatible.

In general, the number of potential immigrants and emigrants that have migrated (thus increasing or decreasing their general historical distributions) in response to climatic change is low. This supports the conclusion that the expected climatic changes will not essentially modify the densities, diversity, and distributions of the aquatic oligochaete fauna in Europe, particularly when compared with the potential for changes in the native fauna resulting from contemporary long-distance anthropogenic introductions of many species, and the possibility that native fauna may be extirpated. The analyses of observational data on spatial and temporal distribution of tubificoid naidids and naidids s.str. suggest that climate change may only trigger a marginal response in these oligochaetes. Increased observations and analyses of the population dynamics of individual species likely will reveal additional responses to climatic changes - in Europe, and elsewhere.

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Appendix 1 Summary of life cycle stages of tubificoid naidids recorded in Europe, as presented in published studies reviewed in this paper (p=present, a=abundant)

species	author	country	life cycle stage	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
<i>Aulodrilus plurisetus</i>	Brinkhurst 1964	UK	immature	p	p	p	p	p	p	a	p	p	p	p	p
			mature	p						a		p			
	Brinkhurst 1964	UK	immature	p		p	p	p	a	a	a	a	p	p	p
			mature						p	a	a	a	p		
<i>Branchiura sowerbyi</i>	Aston 1968		cocoons	(p)		p	p	a	p	a	p	p			
		UK	mature	p	p	p	p	p	p	p	p	p	p	p	p
	Casellato 1984	IT	cocoons				p	p	p	p					
			newly hatched					p	p	p	p				
<i>Ilyodrilus templetoni</i>	Frenzel 1983	CH	immature	p	p	p	p	p	p	p	p	p	p	p	p
			mature				p	a		a	a	a	p		p
<i>Isochaetides newaensis</i>	Timm 1970	EE	cocoons					p	p	p					
<i>Limnodrilus claparedianus</i>	Frenzel 1983	CH	mature	p		p	p		a		p				
	Dolidze 1994	RU	cocoons				p	p	p	p	p	p	p	p	p
			newly hatched				p	p	p	p	p	p	p	p	
			immature	p	p	p	p	p	p	p	p	p	p	p	p
			mature	p	p	p	p	p	p	p	p	p	p	p	p
			reproductive			p	p	p	p	p	p	p	p	p	p
	Pfannkuche 1977	DE	immature	p	p	p	p	p	p	p	p	p	p	p	p
			mature	a	a	a	a	p	p	p	p	p	p	p	p
			reproductive	a	a	a	a	a	a	p	p	p	p	p	p
			immature					p	p	p					
<i>Limnodrilus hoffmeisteri</i>	Poddubnaya 1960	RU	reproductive					p	p	p					
	Brinkhurst & Kennedy 1965	UK	newly hatched							a					
			mature	p	p	p	p	p	p	p	p	p	p	p	p
			reproductive			p									
	Kennedy 1966	UK	immature	p	p	p	p	p	a	a	a	a	a	a	p
			mature	a	a	p	p	p	p	p	p	p	a	p	p
			reproductive	p	p	p	p	p	p	p	p	p	p	p	a
	Kennedy 1966	UK	cocoons		p	p	a	p		p				p	
			immature	p	a	p	a	a	p	p	p	p	p	p	p
			mature	p	p	p	a	a	p	p	p	p	p	p	p
			reproductive	p	p	p	a	a	p	p	a	p	a	a	p
	Kennedy 1966	UK	cocoons		p	p	p	a	p	p					
			immature		p	p	p	p	p	a	p	p	p	p	p
			mature		p	p	p	p	a	p	p	p	p	p	p
			reproductive		p	p	p	a	p			p			p
	Aston 1973	UK	abundant	a	p	p	p	p	a	a	a	p	a	p	p
	Eyers et al. 1978	UK	abundant	p	p	p	p	p	p	p	a	a	a	p	p
	Pfannkuche 1977/1981	DE	immature	p	p	p	p	p	p	p	p	p	p	p	p
			mature	p	p	a	a	a	a	p	p	p	p	p	p
			reproductive	p	p	a	a	a	a	p	p	p	p	p	p
	Frenzel 1983	CH	mature	p		a	p		p	a	p	p		p	
	Lazim & Learner 1986	UK	cocoons	a	a	p	p	p	p	p	p	p	a	a	a
			newly hatched	p	p	p	p	a	a	a	a	a	p	p	p
			mature	a	p	p	p	p	p	p	p	a	a	a	a
	Dumnicka & Kownacki 1988	PL	cocoons	p	p	p	p	p	p	p	p	p	p	p	p
			mature	p	p	p	p	p	p	p	p	p	p	p	p
	Bonacina et al. 1996	IT	cocoons					a	a	a	a	a	a	a	a
			immature	p	p	p	p	p	p	p	p	p	p	p	p
			reproductive	p	p	p	p	p	p	p	p	p	p	p	p
			immature												
<i>Limnodrilus profundicola</i>	Frenzel 1983	CH	mature	p		p	p					p			
	Dumnicka & Kownacki 1988	PL	mature			p	p	p	p	p	p				
	Pfannkuche 1977	DE	immature	p	p	p	p	p	p	p	p	p	p	p	p
			mature	a	a	a	a	p	p	p	p	p	p	p	p
			reproductive						a						
			immature												
<i>Limnodrilus udekemianus</i>	Brinkhurst & Kennedy 1965	UK	newly hatched			p	p		p	a	a	a	p		
			immature	p	p	a	a	p	p	p	p	p	a	p	

species	author	country	life cycle stage	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
			mature			a	a	p	p	p	p		p	p	
	Brinkhurst 1965	UK	reproductive			p	p	p	a	p	p		p		
			cocoons						p	p	(p)				
			immature	p	a	a	p	p	p	p	p	a	p	p	a
	Timm 1970	EE	mature	p	a	p	p	p	p	p	p			p	p
			reproductive			p		a	p	p					
			cocoons						p	p	p				
	Eyers et al. 1978	UK	abundant	p	p	p	p	p	p	p	a	p	p	a	p
	Bird 1982	UK	cocoons	p	p	a	a	a	p	p	p				
			newly hatched	p	p	p	p	p	p	p	p	p	p	p	p
			mature	p	p	p	p	p	p	p	p				p
	Frenzel 1983	CH	mature						a	p	p			p	
	Lazim & Learner 1986	UK	cocoons	a	a	a	a	a	p	p	p				
			newly hatched	p	p	p	p	p	a	a	a	a	p	p	p
			mature	a	a	a	a	a	p	p	p				p
	Szarowska 1987	PL	cocoons		p		p	a	a	ap	a	p	p	p	
			mature	p	p	p	p	p	p	p	p	p	p	p	p
			reproductive				p	a	a	a	p		p		
<i>Pelosclex benedeni</i>	Hunter & Arthur 1978	UK	cocoons			p	p	a	a	p	p				
			immature	p	p	p	p	p	p	p	p	p	p	p	p
			mature	a	a	a	p								p
			reproductive			p	p	p	p	p	p	p			
	Pfannkuche 1977	DE	immature	p	p	p	p	p	p	p	p	p	p	p	p
			mature	p	p	p	a	a	p			p		p	p
			reproductive			p	p	a	a	p					
<i>Phalodrilus monospermathecus</i>	Pfannkuche 1977	DE	immature	p	p	p	p	p	p	p	p	p	p	p	p
			mature	p	p	a	a	p	p	p	p			p	p
			reproductive	p	p	a	a	a	a	a	p				
	Pfannkuche 1980	DE	immature	p	p	p	p	p	p	p	p	p	p	p	p
			mature	p	p	a	a	p	p	p	p	p		p	p
			reproductive	p	p	a	a	a	a	a	p				
<i>Potamothenix hammoniensis</i>	Sapkarev 1959	MK	reproductive									p	p	p	
	Poddubnaya 1960	RU	mature	p	p	p	p	p	p	p	p	p	p	p	p
			reproductive					p	p	p			p		
	Timm 1962/1970	EE	cocoons				p	a	a	p	p				
			mature	p	p	p	p	p	p	p	p	p	p	p	p
	Jonasson & Thorhaug 1972	DK	cocoons					p	p	p	p	p			
			immature	p	p	p	p	p	p	p	p	p	p	p	p
			mature	p	p	p	p	p	p	p	p	p	p	p	p
			reproductive	p	p	a	a	a	p	p	p	p	p	p	p
	Thorhaug 1975	DK	cocoons				p	p	a	a					
			newly hatched								p				
			mature	p	p	p	p	p	p	p	p	p	p	p	p
			reproductive	p	p	p	a	a	a	p				p	p
	Lang & Hutter 1981	CH	present	p	p	p	p	p	p	p	p	p	p	p	p
			abundant	p						p			p	p	
	Risnoveanu & Vadineanu 2002	RO	cocoons			a	a					a			
			newly hatched	p	p	p	p	p	p	p			a	p	p
			immature	p	p	p	p	p	p	p	p	p	p	p	p
			reproductive			a	p	p	a	p	a	a			
<i>Potamothenix heuseri</i>	Lang & Hutter 1981	CH	present	p	p	p	p	p	p	p	p	p	p	p	p
			abundant	p								p	p		p
<i>Potamothenix vejovskyi</i>	Lang & Hutter 1981	CH	present	p	p	p	p	p	p	p	p	p	p	p	p
			abundant	p							p	p			p
<i>Psammoryctides barbatus</i>	Ekman 1915	SE	reproductive							p	p				
	Timm 1970	EE	cocoons						p	p	p				
	Frenzel 1983	CH	mature	a		p	p		p	a	p	p		p	
	Ladle & Bird 1984	UK	newly hatched						p	p	p				
			immature	p	p	p	p	p	p	p	p	p	p	p	p
			mature	p	p	p	p	p	p	p	p			p	p
			reproductive	p	p		p	p	p						
<i>Spiridion insigne</i>	Pfannkuche 1977	DE	immature	p	p	p	p	p	p	p	p	p	p	p	p
			mature	p	a	a	a	a	p	p	p				p
			reproductive		p	p	a	a	a	a	p				

species	author	country	life cycle stage	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	
<i>Spirosperma ferox</i>	Pfannkuche 1980	DE	immature	p	p	p	p	p	p	p	p	p	p	p	p	
			mature	p	a	a	a	p	p	p						p
	Ekman 1915	SE	reproductive		p	p	p	a	a	p	p					
			reproductive								p	p				
<i>Tubifex costatus</i>	Timm 1962	EE	mature							p						
	Brinkhurst 1964	UK	cocoons									p	a			
			immature	p		p	p	p	a	a	p		p	p	p	p
	Frenzel 1983	CH	mature	p		p	p		p	p	p	p		p		
Knöllner 1935	DE	mature	p	p	p	p	p	p	p	p			p	p	p	
		reproductive				p	p									
		mature	p	p	p	p	p	p	p	p	p	p	p	p	p	p
		cocoons	p	p	p	p	p	a	p	p						
Bülow 1957	DE	mature	p	p	p	p	p	p	p	p	p	p	p	p	p	
		cocoons						a	p	p						
		newly hatched				p	p					p			p	
		immature	p	p	p	p	p	p	p	p	p	p			p	
Brinkhurst 1964	UK	mature	p	a	a	a	a	a	a	p					p	
		reproductive				p	a	p	p							
		immature	p	p	p	p	p	p	p	p	p	p	p	p	p	
		mature	a	a	a	a	a	a	p	p	p	p	p	p	p	
Pfannkuche 1974	DE	immature	p	p	p	p	p	p	p	p	p	p	p	p	p	
		mature	a	a	a	a	a	p	p	p	p	p	p	p	a	
		immature	p	p	p	p	p	p	p	p	p	p	p	p	p	
		mature	a	a	a	a	a	p	p	p	p		p	p	p	
Pfannkuche 1979	DE	reproductive	p	p	a	a	a	a	p	p						
		immature	p	p	p	p	p	p	p	p	p	p	p	p	p	
		mature	a	a	a	a	a	p	p	p	p		p	p	p	
		reproductive	p	p	a	a	a	a	p	p	p					
Birtwell & Arthur 1980	UK	immature	p	p	p	p	p	a	a	a	a	a	a	p	p	
		mature	a	a	p	p	p	p	p	p	p	p	p	a	a	
		reproductive	p	a	a	a	a	p	p	p	p					
		mature	p	a	a	a	a	p	p	p	p					
<i>Tubifex ignotus</i>	Frenzel 1983	CH	mature			p	p		a	p	p	p		p		
			reproductive					p	p	p						
			reproductive						p	p	p					
			reproductive						p	p	p					
<i>Tubifex newaensis</i>	Poddubnaya 1960	RU	reproductive					p	p	p						
			reproductive						p	p	p					
			reproductive						p	p	p					
			reproductive						p	p	p					
<i>Tubifex tubifex</i>	Brinkhurst & Kennedy 1965	UK	cocoons	p	p	a	p	a	a	p	p	p	p	p		
			newly hatched		p	a	p	p	p	a	p	p	p			
			immature	p	p	p	p	p	p	a	a	a	a	a	p	
			mature	a	a	a	a	p	p	p	p	p	p	p	p	
Brinkhurst & Kennedy 1965	UK	reproductive	p	p	a	p	p	p		p						
		cocoons	p			p	a	p	p	p						
		immature	p	p	p	p	p	p	p	p	p	a	a	p		
		mature	p	p	p	p	p	p	p	p		p	p	p		
Wachs 1967	DE	reproductive	p	p	p	p	p	p	p	p						
		mature			p	a	a	p								
		cocoons				p	p	p	p	p	p	p	p	p		
		abundant	p	p	p	p	p	a	p	p	p	p	p	p		
Eyers et al. 1978	UK	present	p	p	p	p	p	p	p	p	p	p	p	p		
		present	p	p	p	p	p	p	p	p	p	p	p	p		
		present	p	p	p	p	p	p	p	p	p	p	p	p		
		present	p	p	p	p	p	p	p	p	p	p	p	p		
Pfannkuche 1977/1981	DE	immature	p	p	p	p	a	a	a	a	a	a	a	p	p	
		mature	a	p	p	p								a	a	
		reproductive	p	p	a	a									p	p
		reproductive	p	p	a	a									p	p
Lang & Hutter 1981	CH	present	p	p	p	p	p	p	p	p	p	p	p	p		
		abundant		p							p	p	p			
		mature	a		p	p		p	a					p		
		abundant										p	p	p		
Frenzel 1983	CH	mature	a		p	p		p	a					p		
		cocoons	p	p	a	a	a	a	p	p	p					
		newly hatched	p		p	p	p	a	a	a	a	a	a	a		
		immature	a	a	a	p	p	p	p	p	p	p	p	a		
Graef 1985	DE	mature	p	a	a	a	a	a	p	p	p	p	p	p		
		reproductive	p	p	a	a	a	a	a	p	p	p	p	p		
		reproductive	p	p	a	a	a	a	a	p	p	p	p	p		
		reproductive	p	p	a	a	a	a	a	p	p	p	p	p		
Lazim & Learner 1986	UK	cocoons	p	p	a	a	p	p								
		newly hatched	p	p	p	p	p	p	p	p	p	p	p	p		
		newly hatched	p	p	p	p	p	p	p	p	p	p	p	p		
		mature	p	p	p	p	p	p					p	p		
Dumnicka & Kownacki 1988	PL	mature	p	p	p									p		
		mature	p	p	p									p		
		reproductive	p	p	p									p		
		reproductive	p	p	p									p		
<i>Tubifex pseudogaster</i>	Pfannkuche 1979	DE	immature	p	p	p	p	p	p	p	p	p	p	p		
			mature	a	a	a	a	a	p	p	p		p	p		
			reproductive	p	p	a	a	a	a	a	p					
			reproductive	p	p	a	a	a	a	a	p					

(country abbreviations: CH=Switzerland, DE=Germany, EE=Estonia, IT=Italy, MK=Macedonia, PL=Poland, RO=Romania, RU=Russia, SE=Sweden, UK=United Kingdom)

Appendix 2 Summary of life cycle stages of naidids s.str. recorded in Europe, as presented in published studies reviewed in this paper(p=present, a=abundant)

species	reference	country	life stage	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
<i>Arctonais lomondi</i>	Weerekoon 1956	UK	mature							p	p	p			
	Timm 1970	EE	mature								p				
<i>Amphichaeta sannio</i>	Koene 1981	NL	present mature					p						p	p
	Pfannkuche 1977/1981	DE	mass abundance			p	p	p	p			p	p		
<i>Amphichaeta leydigii</i>	Frenzel 1981	CH	mass abundance		p	p	p	p				p	p		
	Frenzel 1983	CH	present	p	p	p	p	p	p	p	p	p	p	p	p
			mass abundance			p	p								
			mature			p	p	p	p						
	Pfannkuche 1977/1981	DE	mass abundance		p	p							p		
	Grimm 1979	DE	mass abundance			p									
	Pfannkuche 1977	DE	mass abundance		p	p	p								
<i>Aulophorus furcatus</i>	Dumnicka & Kownacki 1988	PL	present							p	p	p	p	p	
<i>Chaetogaster cristallinus</i>	Grimm 1979	DE	present						p	p	p	p	p		
<i>Chaetogaster langi</i>	Sperber 1948	DE	mass abundance						p						
	Frenzel 1981	CH	mature					p	p	p					p
	Vaghin 1946	RU	mature								p				
<i>Chaetogaster diaphanus</i>	Timm 1970	EE	mature							p					
	Frenzel 1981	CH	present	p	p	p	p	p	p	p	p	p	p	p	p
<i>Chaetogaster diastrophus</i>			mass abundance						p	p					
	McElhone 1978	UK	mass abundance			p		p	p	p					
	Kahl & Konopacka 1981	PL	mass abundance							p				p	
	Timm 1970	EE	mature									p	p		
	Poddubnaya 1968	RU	mass abundance					p	p	p	p	p	p		
			mature									p	p		
			cocoons									p	p		
	Grimm 1979	DE	present	p	p	p	p	p	p	p	p	p	p	p	p
			mass abundance				p								
	Sperber 1948	SE	mature							p	p				
<i>Chaetogaster limnaei</i>	Frenzel 1981	CH	mass abundance					p	p	p					
	Frenzel 1983	CH	present			p	p	p	p	p	p	p			
			mass abundance				p	p	p	p	p				
	McElhone 1978	UK	mass abundance		p	p		p	p	p				p	
<i>Chaetogaster limnaei</i>	Löhlein 1996	DE	mass abundance		p	p	p								
	Grimm 1979	DE	present	p	p	p	p	p	p	p	p	p	p	p	p
			mass abundance				p								
<i>Chaetogaster limnaei</i>	Sperber 1948	SE	mature							p	p				
	Poddubnaya 1960	RU	present	p	p	p	p	p	p	p	p	p	p	p	p
<i>Chaetogaster langi</i>	Frenzel 1983	CH	mature	p	p	p	p	p	p	p	p	p	p	p	p
	Sperber 1948	CH	mature							p	p				
<i>Dero digitata</i>	Dumnicka & Kownacki 1988	PL	present							p	p	p	p	p	
	Krodkiewska 2005	PL	present	p	p	p	p						p	p	p
<i>Dero dorsalis</i>	Timm 1970	EE	present			p	p	p	p	p	p	p	p	p	p
		EE	mature								p				
<i>Dero obtusa</i>	Grimm 1979	DE	present	p				p		p	p	p	p		p
<i>Homochaeta naidina</i>			mass abundance								p	p			
	Grimm 1979	DE	present	p					p	p	p				p
<i>Nais alpina</i>			mass abundance						p						
	Learner et al. 1978	UK	present	p	p		p	p	p	p	p	p	p	p	p
			mass abundance							p	p	p			
<i>Nais barbata</i>			mature	p					p	p	p				
	Dumnicka 1982	PL	present	p	p	p	p	p	p	p	p	p	p	p	p
			mass abundance							p	p			p	p
<i>Nais barbata</i>	Timm 1970	EE	present						p	p	p				
			mature									p	p		
	Learner et al. 1978	UK	present						p	p	p	p	p		

species	reference	country	life stage	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
	Frenzel 1983	CH	mass abundance			p	p	p	p	p					
	Grimm 1979	DE	present	p	p	p	p	p	p	p	p	p	p	p	p
			mass abundance					p							
<i>Nais bretscheri</i>	Piguet 1909	CH	mature						p	p	p	p	p		
	Timm 1967	EE	mature									p	p		
	Learner et al. 1978	UK	present						p	p	p	p	p		
			mass abundance							p					
<i>Nais communis</i>	Dumnicka 1982	PL	present	p	p	p	p	p	p	p	p	p	p	p	p
	Grimm 1979	DE	mass abundance					p	p	p	p			p	p
			present		p	p		p	p	p			p	p	
			mass abundance			p									
<i>Nais communis/variabilis</i>	Piguet 1909	CH	mature										p	p	
	Piguet 1909	CH	mature						p	p					
	Timm 1970	EE	mature						p						
	Giani 1984	FR	present		p		p		p				p		p
<i>Nais elinguis</i>			mass abundance												a
	Wachs 1967	DE	mass abundance									p	p	p	
	Learner et al. 1978	UK	present		p		p	p	p	p	p	p	p		
			mass abundance							p	p	p	p		
<i>Nais communis/variabilis</i>	Verdonschot 1999	NL	mass abundance					p							
	Frenzel 1983	CH	present			p	p	p	p	p	p	p	p	p	
	Bowker et al. 1985	UK	present				p	p	p						
	Piguet 1909	CH	mature						p	p					
<i>Nais elinguis</i>	Szczesny 1974	PL	present							p	p	p			
	Little 1984	UK	present	p	p	p	p								
			mass abundance				p								
	Pfannkuche 1977	DE	mass abundance			p	p	p	p						
<i>Nais elinguis</i>			mature				p	p							
	Pfannkuche 1981	DE	mass abundance			p	p								
	Dumnicka & Kownacki 1988	PL	present	p	p	p							p	p	p
	Eyers et al. 1978	UK	present	p	p	p	p	p	p	p	p	p	p	p	p
<i>Nais pardalis</i>	Schönborn 1985	DE	mass abundance				p	p	p	p					
			present	p	p	p	p	p	p	p	p	p	p	p	p
			mass abundance		p	p	p	p							
	Giani 1984	FR	present		p		p		p				p		p
<i>Nais pardalis</i>			mass abundance		a		a								
	Giani & Martinez-Ansemil 1981	FR	mature		p	a	p								
	Timm 1970	EE	present	p	p	p	p	p	p	p	p	p	p	p	p
			mature						p	p	p	p	p	p	p
<i>Nais pardalis</i>			cocoons										p		
	Timm 1967	EE	mature							p	p	p	p	p	p
	Learner et al. 1978	UK	present	p	p	p	p	p	p	p	p	p	p	p	p
			mass abundance		p	p	p	p	p				p		
<i>Nais pardalis</i>			mature				p	a	a	p	p				
	Verdonschot 1999	NL	mass abundance	p				p	p				p	p	
	Grimm 1979	DE	present	p	p	p	p	p	p				p	p	p
			mass abundance				p								
<i>Nais pardalis</i>	Learner et al. 1978	UK	present		p		p	p	p	p	p	p	p		
			mass abundance					p		p	p				
	Verdonschot 1999	NL	mass abundance					p							
	Dumnicka 1982	PL	present		p	p	p	p	p	p	p	p	p	p	p
<i>Nais pseudobtusa</i>			mass abundance						p	p			p	p	
	Frenzel 1983	CH	present			p	p	p	p	p	p	p	p	p	
	Grimm 1979	DE	present	p		p	p		p	p	p	p	p	p	p
			mass abundance								p	p			
<i>Nais pseudobtusa</i>	Piguet 1909	CH	mature									p			
	Schönborn 1985	DE	present	p	p	p							p	p	p
	McElhone 1978	UK	mass abundance		p	p			p						
			mature										p		
<i>Nais simplex</i>	Löhlein 1996	DE	mass abundance					p							
			mature										p		
	Piguet 1909	CH	mature									p	p	p	
	Timm 1970	EE	mature						p	p					
<i>Nais simplex</i>	Verdonschot 1999	NL	mass abundance					p							
	Piguet 1909	CH	mature								p	p	p		

species	reference	country	life stage	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
<i>Nais variabilis</i>	Lochhead & Learner 1984	UK	cocoons												p
	Pfannkuche 1977	DE	mass abundance			p	p	p	p						
			mature				p	p							
	Pfannkuche 1981	DE	mass abundance				p	p							
	Timm 1970	EE	mature						p	p	p				
	Löhlein 1996	DE	mass abundance					p							
			mature											p	
	Kownacki et al. 1997	PL	mass abundance							p	p	p	p		
	Learner et al. 1978	UK	present				p		p	p	p	p	p	p	
			mass abundance								p	p		p	
Verdonschot 1999	NL	mass abundance						p						p	
Grimm 1979	DE	present	p		p	p	p	p	p	p	p	p	p	p	p
		mass abundance						p							
Piguet 1909	CH	mature							p	p					
Timm 1970	EE	mature							p	p					
Grimm 1979	DE	present	p		p				p		p	p			
		mass abundance							p						
<i>Paranais litoralis</i>	Pfannkuche 1981	DE	mature					p	p						
	Bennike & Berg 1948	DK	mature								p				
	Timm 1970	EE	present						p	p	p				
			mature						p	p	p				
Pfannkuche 1977/1981	DE	mass abundance						p	p	p					
		mature							p	p					
		mass abundance				p	p	p	p	p					
		mature						p	p	p					
<i>Paranais frici</i>	Pfannkuche 1977/1981	DE	mass abundance					p	p						
			mature				p	p							
<i>Pristina amphibiotica</i>	Verdonschot 1999	NL	mass abundance								p	p			
<i>Pristina jenkiniae</i>	Giani 1984	FR	present						p				p	p	
[as <i>idrensis</i> ]			mass abundance										a		
<i>Pristina rosea</i>	Giani 1984	FR	present		p		p		p				a	p	
			mass abundance										a		
<i>Piguetiella blanci</i>	Frenzel 1983	CH	present	p		p	p			p	p	p	p	p	
<i>Ripistes parasita</i>	Timm 1970	EE	present						p	p	a				
			mature								p				
<i>Slavina appendiculata</i>	Timm 1970	EE	mature							p	p				
Verdonschot 1999	NL	mass abundance						p							
<i>Specaria josinae</i>	Frenzel 1983	CH	present			p	p	p	p	p	p	p	p	p	
			mature									p		p	
<i>Stylaria lacustris</i>	Dumnicka & Kownacki 1988	PL	present							p	p	p	p	p	
	Lindegaard & Dall 1988	DK	present					p	p	p	p	p			
			mass abundance								p	p			
	Wachs 1967	DE	mature									p	p		
	Frenzel 1983	CH	mature								p				
	Timm 1970	EE	present						p	p	p	p	p		
			mature						p	p	p	p			
			cocoons											p	
	Lohlein 1996	DE	mass abundance						p	p					
			mature											p	p
		cocoons	p											p	
McElhone 1978	UK	mass abundance				p					p	p	p		
Verdonschot 1999	NL	mass abundance											p		
Frenzel 1983	CH	present			p				p	p	p	p	p		
		mature									p				
Grimm 1979	DE	present				p	p	p	p	p	p	p			
		mass abundance							p						
Weerekoon 1956	UK	mature									p				
Timm 1970	EE	mature								p					
Frenzel 1983	CH	present	p		p	p	p	p	p	p	p	p	p		
<i>Vejdovskyella intermedia</i>	Frenzel 1983	CH	present	p	p	p	p	p	p	p	p	p	p	p	
			mature				p	p	p	p					
			mass abundance						p	p					

(country abbreviations: CH=Switzerland, DE=Germany, DK=Denmark, EE=Estonia, FR=France, IT=Italy, MK=Macedonia, NL=Netherlands, PL=Poland, RO=Romania, RU=Russia, SE=Sweden, UK=United Kingdom)

