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Changes in the range of dragonflies in the Netherlands and the possible role of temperature change

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Abstract

The trends of 60 Dutch dragonfly species were calculated for three different periods (1980–1993, 1994–1998 and 1999–2003). Comparing period 1 and period 3 shows that 39 of these species have increased, 16 have remained stable and 5 have decreased. These results show a revival of the Dutch dragonfly fauna, after decades of ongoing decline. The species were categorized in different species groups: species with a southern distribution range, species with a northern distribution range, species of running waters, species of fenlands and species of mesotrophic lakes and bogs. The trends of these different species groups were compared with the all-species control group. As expected, a significantly higher proportion of the southern species show a positive trend than the all-species group. In the northern species group on the contrary, a significantly higher proportion of the species show a negative trend than the all-species group. Different explanations for these results are discussed, such as climate change, improved quality of certain habitats and degradation of other habitats. It is likely that the observed increase of southern species is at least partly caused by the increasing temperatures. The less positive picture of the northern species group is probably more influenced by other environmental factor than directly by climate change.

Three out of six southern species which have become established since 1990 have done so during the aftermath of large invasions. It is concluded that dragonflies are well capable of using changing climate circumstances to colonise new habitats.

Keywords

dragonflies, Odonata, climate change, invasion, trends, conservation, Netherlands

Introduction

During the last century, the Dutch dragonfly fauna has shown large changes. Destruction of habitats, canalisation of streams and rivers, desiccation, eutrophication, acidification and pollution led to an often strong decline of many species. This started in the first half of the 20th century, but was especially severe in the sixties and seventies of that century (Kalkman et al. 2002). Most affected were species of running waters and species of mesotrophic lakes and bogs (Wasscher 1994, 1999), some of which even disappeared from the Netherlands (*Coenagrion mercuriale*, *Nehalennia speciosa*, *Gomphus flavipes*, *Ophiogomphus cecilia*, *Oxygastra curtisii*, *Leucorrhinia caudalis*). The degradation of the Dutch dragonfly fauna reached a maximum in the 1980's. Since the start of the 1990's, many species have increased. This is very obvious for some species of running water and ubiquistic species for which the Netherlands lie on the northern limit of their distribution range. These species seem to have profited from the improving water quality (RIVM 2003) and the recent warm summer seasons (KNMI 2006). However, a number of species of other habitats, such as mesotrophic lakes and bogs, have also increased during last decade.

In this article we describe the revival of the Dutch dragonfly fauna, which seems to be happening. Special attention is given to the role of temperature change.

Methods

Database

The database used for this article is build and maintained by the Dutch Society for Dragonflies, Butterfly Conservation and the European Invertebrate Survey – the Netherlands. It contains over 307,000 records of 71 dragonfly species up to and including 2003, mainly submitted by volunteers. Each record constitutes a species on a date on a locality. The records are checked for mistakes by a committee of experts, based on the known distribution and flight period of the species. For records of rare species further documentation like a picture or a description is required.

More than 279,000 records are available from the period 1980–2003. By far the largest number of these records was collected from 1994 onwards, but the number of records prior to this period is large enough to give a good impression of the distribution of the species in that period.

The database gives good information on the distribution of species. However it is subject to influences of the differences between fieldwork done by the volunteers and large-scale professional projects. Therefore, results based on the database can only be interpreted correctly with a good knowledge of the database itself.

Calculation of trends

The data set was divided in three periods: 1980–1993 (period 1), 1994–1998 (period 2) and 1999–2003 (period 3). Relatively few records are available from each year in period 1. Therefore, this period includes fourteen years while periods 2 and 3 only include five years. The 5×5 kilometre squares which had been visited at least in three different months in the period May till August were selected for each year (table 1). Only records from these squares were used for the analysis. For eleven of the 71 Dutch species this resulted in usable records for only one or none of the three periods. Therefore these species, all extinct or very rare, were not included in the trend calculation.

Presence or absence of dragonfly species in the selected 5×5 kilometre squares was used, instead of the recorded number of individuals, as the latter is more prone to differences in recording behaviour. The consequence of this method is that a decrease or increase in observed numbers or in localities within a 5×5 kilometre square will go unnoticed.

For each species and period the relative abundance (RA) was calculated as follows:

> RA= (Number of squares in which a species is recorded)/(number of investigated squares) × 100%.

The RA's for each year were summed for each period and divided by the number of years. The relative change of a species was calculated as follows:

> Trend= (RA in recent period – RA in historical period)/(RA historical period × 100%

The trends were divided in five trend categories (table 2).

Southern and northern species group

The Dutch dragonfly species were categorized as southern species, northern species or species without a typical southern or northern distribution pattern. This categorization was based on distribution maps of Northwest Europe (NVL, 2002). A southern species was defined as a species of which the northern limit of its range runs through the southern tip of Sweden or more southwards. A northern species was defined as a species of which the southern border of its range runs through the Netherlands or Belgium and which is further south only found at higher elevations or in small, scattered populations.

Habitat groups

Next to the southern and northern species groups, three ecological species groups were selected: species of running water habitats (rheophilic species), species of mesotrophic lakes

Table 1. The number of well investigated 5×5 kilometre squares

Period 1		Period 2		Period 3	
Year	**Well investigated squares**	**Year**	**Well investigated squares**	**Year**	**Well investigated squares**
1980	5	1994	151	1999	235
1981	9	1995	260	2000	235
1982	16	1996	242	2001	241
1983	12	1997	205	2002	260
1984	11	1998	180	2003	372
1985	14	**Total**	**1038**	**Total**	**1343**
1986	19				
1987	20				
1988	14				
1989	20				
1990	28				
1991	23				
1992	45				
1993	68				
1994	151				
1995	260				
1996	242				
1997	205				
1998	180				
Total	**1342**				

and bogs and species of fenlands. For this categorization the habitat preference of Dutch dragonflies was used, as given in NVL (2002). Table 3 lists the species of the four selected species groups. Note that some species are appointed to more than one species group.

Statistics

χ^2-tests were conducted to test the differences between the all-species group and the selected distribution and habitat species groups. This was done by using Microsoft Excel 2000 software. Species with increasing (>20 %) and strong increasing trends (>100 %) were lumped together and tested as increasing species.

Results

The relative abundance for each period and the trend between the periods is given for each species in table 4. Table 2 gives the number of species showing a certain trend between the different periods.

Table 2. Categories of trend and the number of species showing this trend between periods

Trend		**In table 4 as**	**period 1 to 2**	**period 2 to 3**	**period 1 to 3**
Strong increase	>100%	++	19 (32%)	6 (10%)	13 (25%)
Increase	>20% and <100%	+	9 (15%)	19 (32%)	14 (25%)
Stable	-20% to 20%	0	19 (32%)	28 (47%)	16 (31%)
Decrease	<-20%	-	13 (22%)	7 (12%)	9 (17%)

Trends between the first and the third period could be calculated for 60 species. 39 species (65%) show a positive trend, 16 species (27%) remained stable and 5 species (8%) show a negative trend. Most increasing species show the strongest positive trend between the first and second period (see figure 1).

The results of the χ^2-tests are given in table 5.

Species with a southern distribution pattern

Within the southern species group, significantly more species show a positive trend than the all-species group, when period 1 is compared to period 2 and when period 1 is compared to period 3. Furthermore, a significantly lower proportion of the southern species remained stable, when period 1 is compared to period 3 (figure 2).

Species with a northern distribution

Within the northern species group, significantly more species show a negative trend than the all-species group, when period 1 is compared to period 2. Furthermore, a significantly lower proportion of the northern species remained stable, when period 2 is compared tot period 3 (figure 3).

Differences in trends between habitats

Within the species group of mesotrophic lakes and bogs, significantly less species show a positive trend than the all species group and significantly more species show a stable trend, when period 1 is compared to period 3 (figure 4).

Within the ecological species groups of running waters and fenlands, no significant differences are found for the three trend categories.

Discussion

The results show that the Dutch dragonfly fauna has recovered since the start of the 1990's, which is in sharp contrast with some other groups of invertebrates as but-

Table 3. Categorisation of the species in five different species groups.

Species	Southern	Northern	Running waters	Lakes and bogs	Fenlands
Aeshna affinis	x				
Aeshna grandis				x	x
Aeshna isoceles	x				x
Aeshna juncea				x	
Aeshna mixta	x				
Aeshna subarctica		x		x	
Aeshna viridis		x			x
Anax imperator	x				
Anax parthenope	x				
Brachytron pratense					x
Calopteryx splendens			x		
Calopteryx virgo			x		
Ceriagrion tenellum	x			x	
Coenagrion hastulatum		x		x	
Coenagrion lunulatum		x		x	
Coenagrion puella				x	
Coenagrion pulchellum					x
Cordulegaster boltonii			x		
Cordulia aenea				x	x
Crocothemis erythraea	x				
Enallagma cyathigerum				x	
Erythromma lindenii	x				
Erythromma najas					x
Erythromma viridulum	x				x
Gomphus flavipes			x		
Gomphus pulchellus	x				
Gomphus vulgatissimus			x		
Ischnura elegans					x
Ischnura pumilio	x				
Lestes barbarus	x			x	
Lestes dryas				x	
Lestes sponsa				x	x
Lestes virens	x				
Lestes viridis	x				x
Leucorrhinia dubia				x	
Leucorrhinia pectoralis					x
Leucorrhinia rubicunda		x		x	
Libellula fulva	x				x
Libellula quadrimaculata				x	x
Ophiogomphus cecilia			x		
Orthetrum brunneum	x		x		
Orthetrum cancellatum	x			x	x
Orthetrum coerulescens			x		

Species	Southern	Northern	Running waters	Lakes and bogs	Fenlands
Platycnemis pennipes			x		
Pyrrhosoma nymphula				x	
Somatochlora arctica		x		x	
Somatochlora flavomaculata				x	
Sympecma fusca	x			x	
Sympecma paedisca		x			x
Sympetrum danae				x	
Sympetrum flaveolum				x	
Sympetrum fonscolombii	x				
Sympetrum pedemontanum			x		
Sympetrum sanguineum					x
Sympetrum vulgatum				x	x

terflies and bees (Peeters and Reemer 2003; Swaay and Groenendijk 2005). Only 5 dragonfly species have declined, while a majority of 39 species has increased and 16 species remained stable. Out of the 27 species placed on the red list in 1999 (Wasscher 1999) 17 show an increase, 4 a decrease, 1 remained stable and 3 are still extinct. For the remaining 2 red-listed species (*Coenagrion armatum* and *Leucorrhinia albifrons*) no trend was calculated, as they were only recorded in one period. Populations of both species have recently been rediscovered (Van der Heijden 2001; De Boer and Wasscher 2006) in the Netherlands and although they are extremely rare, there is no evidence for an actual decline.

Two different causes can be pointed out for the increase or decrease of the different species. The first is climate change, the second is changes in the quality of habitats.

Climate change

The average temperature in the Netherlands in the last twenty years of the 20th century was 0,7 degree higher than the average temperature of the first twenty years of the 20th century (KNMI 2006). Especially the spring temperature has shown a strong increase. This increase in temperature caused several southern species to expand their range northwards, becoming more common in the Netherlands. This is at least the case for *Lestes barbarus*, *Aeshna affinis*, *Anax parthenope*, *Crocothemis erytraea*, *Orthetrum brunneum* and *Sympetrum fonscolombii*. *Coenagrion scitulum* expanded its range in northern France and Belgium and was first found in the Netherlands in 2003 (Goudsmits 2003). Also for more common southern species like *Lestes virens* and *Ceriagrion tenellum* a positive effect of increasing temperatures is expected.

Whether or not higher temperatures also play a role in the negative trend shown by some northern species is difficult to say, because the habitats of northern species are

Table 4. Relative abundance (RA) and trends for each species.

Species	RA period 1	RA period 2	RA period 3	trend 1st to 2nd period	trend 2nd to 3rd period	trend 1st to 3rd period
Aeshna affinis Vander Linden, 1820		1	0,6	++	-	++
Aeshna cyanea (O.F. Müller, 1764)	33,6	47,1	53,6	0	0	+
Aeshna grandis (Linnaeus, 1758)	36,3	36,3	40,9	0	0	0
Aeshna isoceles (O.F. Müller, 1767)	7,5	12,3	17,2	+	+	++
Aeshna juncea (Linnaeus, 1758)	18,1	13,5	13,4	0	0	0
Aeshna mixta Latreille, 1805	21,9	54,9	61,9	+	0	++
Aeshna subarctica Walker, 1908	0,4	0,9	0,5	++	-	+
Aeshna viridis (Eversmann, 1836)	1	4,2	6,4	++	0	++
Anax imperator Leach, 1815	23,5	59,5	73,2	+	0	++
Anax parthenope (Selys, 1839)		0,3	0,4	++	+	++
Brachytron pratense (O.F. Müller, 1764)	17,8	20,3	30,3	0	+	+
Calopteryx splendens (Harris, 1782)	33	32	32,4	0	0	0
Calopteryx virgo (Linnaeus, 1758)	5,2	3,2	3,1	-	0	-
Ceriagrion tenellum (de Villers, 1789)	11,9	8	13,8	-	+	+
Coenagrion armatum (Charpentier, 1840)			0,3			
Coenagrion hastulatum (Charpentier, 1825)	4,3	1,9	2,4	-	+	-
Coenagrion lunulatum (Charpentier, 1840)	19,3	8,3	9,5	-	+	-
Coenagrion puella (Linnaeus, 1758)	54,9	57,7	62,2	0	0	0
Coenagrion pulchellum (Vander Linden, 1825)	50,8	48,5	49,8	0	0	0
Coenagrion scitulum (Rambur, 1842)			0,1			
Cordulegaster boltonii (Donovan, 1807)	2	1,1	0,9	-	-	-
Cordulia aenea (Linnaeus, 1758)	28,8	22,7	24,7	0	0	0
Crocothemis erythraea (Brullé, 1832)		1,7	3,6	++	++	++
Enallagma cyathigerum (Charpentier, 1840)	63,7	59,6	64,1	0	0	0
Erythromma lindenii (Selys, 1840)	2,8	2,7	4,6	+	+	++
Erythromma najas (Hansemann, 1823)	28,3	44,3	42	+	0	+
Erythromma viridulum (Charpentier, 1840)	7,1	42,3	36,5	++	0	++
Gomphus flavipes (Charpentier, 1825)			2,8	++	++	++
Gomphus pulchellus Selys, 1840	10	8,7	8,2	0	0	+
Gomphus vulgatissimus (Linnaeus, 1758)	2	2,1	3,9	++	+	++
Hemianax ephippiger (Burmeister, 1839)		0,2				
Ischnura elegans (Vander Linden, 1820)	79,3	93	90,5	0	0	0
Ischnura pumilio (Charpentier, 1825)	6,2	4,9	9,1	0	++	++
Lestes barbarus (Fabricius, 1798)	2,2	16,9	15,7	++	0	++
Lestes dryas Kirby, 1890	14,7	14	11,7	0	0	0
Lestes sponsa (Hansemann, 1823)	62,9	50,9	48,2	0	0	0
Lestes virens (Charpentier, 1825)	5,1	7,1	12,3	+	+	++
Lestes viridis (Vander Linden, 1825)	32,7	51,4	54,2	0	0	+
Leucorrhinia dubia (Vander Linden, 1825)	18,6	11,2	12,3	-	+	0
Leucorrhinia pectoralis (Charpentier, 1825)	1,2	1,2	3,1	0	+	++
Leucorrhinia rubicunda (Linnaeus, 1758)	20,4	13,5	22,9	-	+	0

Species	RA period 1	RA period 2	RA period 3	trend 1st to 2nd period	trend 2nd to 3rd period	trend 1st to 3rd period
Libellula depressa Linnaeus, 1758	23,9	40,7	53,2	+	+	+
Libellula fulva O.F. Müller, 1764	6,8	6,5	8,5	0	0	0
Libellula quadrimaculata Linnaeus, 1758	65,8	56	64,5	0	0	0
Ophiogomphus cecilia (Fourcroy, 1785)		0,2	0,3	++	+	++
Orthetrum brunneum (Fonscolombe, 1837)		1,6	1,2	++	-	++
Orthetrum cancellatum (Linnaeus, 1758)	42,1	80,2	81,6	+	0	+
Orthetrum coerulescens (Fabricius, 1798)	1,7	4,1	3,2	++	0	++
Platycnemis pennipes (Pallas, 1771)	17,2	18,6	18,4	+	0	+
Pyrrhosoma nymphula (Sulzer, 1776)	69,4	47,8	61	-	+	0
Somatochlora arctica (Zetterstedt, 1840)		0,2	0,4	++	++	++
Somatochlora flavomaculata (Vander Linden, 1825)	0,1	0,7	1,7	+	++	++
Somatochlora metallica (Vander Linden, 1825)	18,7	15,7	15,1	0	0	0
Sympecma fusca (Vander Linden, 1820)	0,4	6,2	8,3	++	+	++
Sympecma paedisca (Brauer, 1877)		0,3	1	++	++	++
Sympetrum danae (Sulzer, 1776)	51,4	45,6	45,7	0	0	0
Sympetrum depressiusculum (Selys, 1841)	1	0,5	0,1	0	-	-
Sympetrum flaveolum (Linnaeus, 1758)	24,4	38,4	20,2	++	-	+
Sympetrum fonscolombii (Selys, 1840)	0,4	4,8	6	++	0	++
Sympetrum pedemontanum (Allioni, 1766)	1,4	1	1,7	0	+	+
Sympetrum sanguineum (O.F. Müller, 1764)	37,1	64,3	58,3	+	0	+
Sympetrum striolatum (Charpentier, 1840)	13,2	39,2	41,8	+	0	+
Sympetrum vulgatum (Linnaeus, 1758)	38	44,5	48,3	0	0	+

more prone to negative influences of other environmental factors. Five out of seven northern species occur in mesotrophic lake and bog habitats, while there are no northern species occurring in running waters. It is clear that habitat degradation is an important factor to explain the results of the northern species group, possibly climate change makes this decrease more severe.

The northern distribution of many southern species seems to be directly limited by the summer temperatures, resulting in a direct expansion of their range when temperature permits (Appendix1). The southern border of northern species on the other hand does not seem to be limited directly by temperatures, but seems to be determined by habitats being absent more southerly and by competition with other species prevailing in warmer climates.

The decrease of northern species as a result of increasing temperatures would in that case be caused by degradation of habitats and by increasing competition from southern species. This would result in a slow decline, which is far more difficult to detect than the rapid increase shown by southern species.

Another negative effect of increasing summer temperatures is increasing evaporation, resulting in lower surface and ground water tables. This can lead to desiccation of

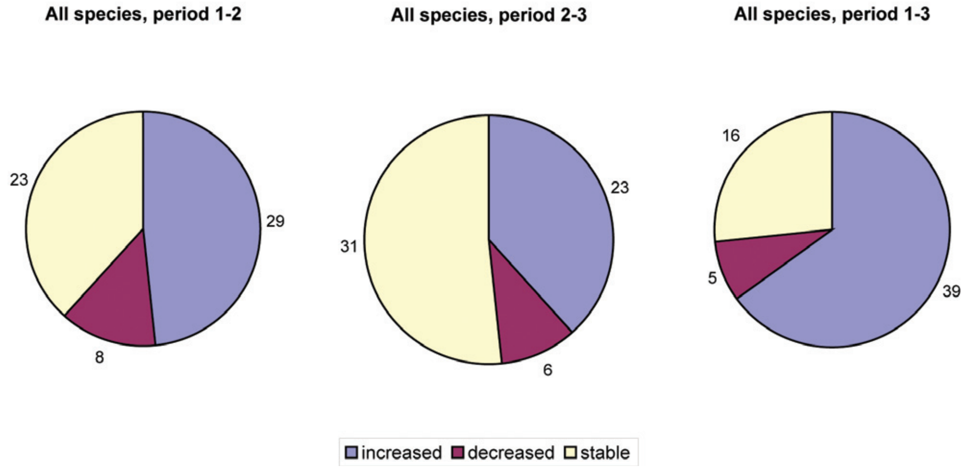

Figure 1. Distribution of all tested species over the trend categories. Three different periods were compared. Period 1 = 1980–1993, period 2 = 1994–1998, period 3 = 1999–2003.

important vegetation structures in the riparian zone of lakes and the upstream stretches of streams. This happens especially in late summer, when the first and most vulnerable larval instars of most species are present in the water. Furthermore, desiccation leads to the stagnation of ground water in seepage fed lakes and streams, causing acidification. Also the turn-over rate of organic matter increases when lake shores dry out, causing nutrient enrichment.

Coenagrion hastulatum, *Cordulegaster boltonii* and *Somatochlora arctica* are examples of threatened species which are known to react negatively on desiccation caused by human influences (e.g. intensive drainage in agricultural areas and drinking water collection) (Groenendijk 2002; Groenendijk 2005; Ketelaar 2001a; Ketelaar 2001b; Wasscher 1999). It is expected that hot summers contribute to this problem. On the other hand, temporary water specialist like *Lestes barbarus* and *Sympetrum flaveolum* might have profited from waters becoming shallower.

Changes in quality of habitats

The test failed to show that the species group of running water contains a significantly higher portion of increasing species than the all-species group. However, this is probably due to the low number of species included in the group, making it difficult to find significant results. Of the ten included species five show a strong increase, two a moderate increase, one is stable and two show a decrease when the first period is compared with the third. Most striking is the comeback of *Gomphus flavipes*, which from 1996 onwards reoccupied all large river systems in the Netherlands (figure 5), after an absence of more than 90 years (Kleukers and Reemer 1998;

Table 5. Results of χ2-tests of the observed proportions of trend categories within the different species groups. *p<0,05; **p<0,01.

	All species n=60	Southern species n=19			Northern species n=19		
		Observed	Expected	p	Observed	Expected	p
Period 1 compared to period 2							
Number of increased species	29	14	9.2	0.027*	4	3.4	0.641
Number of stabel / decreased species	31	5	9.8		3	3.6	
Number of decreased species	8	1	2.5	0.301	3	0.9	0.022*
Number of stabel / increased species	52	18	16.5		4	6.1	
Number of stabel species	23	4	7.3	0.121	0	2.7	0.037*
Number of increased / decreased species	37	15	11.7		7	4.3	
Period 2 compared to period 3							
Number of increased species	23	8	7.3	0.735	5	2.7	0.072
Number of stabel / decreased species	37	11	11.7		2	4.3	
Number of decreased species	6	2	1.9	0.939	1	0.7	0.705
Number of stabel / increased species	54	17	17.1		6	6.3	
Number of stabel species	31	9	9.8	0.708	1	3.6	0.048*
Number of increased / decreased species	29	10	9.2		6	3.4	
Period 1 compared to period 3							
Number of increased species	39	19	12.4	0.001**	4	4.6	0.663
Number of stabel / decreased species	21	0	6.7		3	2.5	
Number of decreased species	5	0	1.6	0.189	2	0.6	0.053
Number of stabel / increased species	55	19	17.4		5	6.4	
Number of stabel species	16	0	5.1	0.009**	1	1.9	0.459
Number of increased / decreased species	44	19	13.9		6	5.1	

	All species n=60	Species of running waters n=10			Species of lakes and bogs n=24			Species of fenlands n=19		
		Observed	Expected	p	Observed	Expected	p	Observed	Expected	p
Period 1 compared to period 2										
Number of increased species	29	6	4.8	0.460	8	11.6	0.141	7	9.2	0.316

	All species n= 60	Species of running waters n=10			Species of lakes and bogs n=24			Species of fenlands n=19		
		Observed	Expected	p	Observed	Expected	p	Observed	Expected	p
Number of stabel / decreased species	31	4	5.2		16	12.4		12	9.8	
Number of decreased species	8	2	1.3	0.535	6	3.2	0.093	1	2.5	0.301
Number of stabel / increased species	52	8	8.7		18	20.8		18	16.5	
Number of stabel species	23	2	3.8	0.233	10	9.2	0.737	11	7.3	0.079
Number of increased / decreased species	37	8	6.2		14	14.8		8	11.7	
Period 2 compared to period 3										
Number of increased species	23	4	3.8	0.914	10	9.2	0.737	5	7.3	0.281
Number of stabel / decreased species	37	6	6.2		14	14.8		14	11.7	
Number of decreased species	6	2	1.0	0.292	2	2.4	0.785	0	1.9	0.146
Number of stabel / increased species	54	8	9.0		22	21.6		19	17.1	
Number of stabel species	31	4	5.2	0.460	12	12.4	0.870	14	9.8	0.055
Number of increased / decreased species	29	6	4.8		12	11.6		5	9.2	
Period 1 compared to period 3										
Number of increased species	39	7	6.5	0.740	10	15.6	0.017*	12	12.4	0.866
Number of stabel / decreased species	21	3	3.5		14	8.4		7	6.7	
Number of decreased species	5	2	0.8	0.182	2	2.0	1000	0	1.6	0.189
Number of stabel / increased species	55	8	9.2		22	22.0		19	17.4	
Number of stabel species	16	1	2.7	0.233	12	6.4	0.010*	7	5.1	0.316
Number of increased / decreased species	44	9	7.3		12	17.6		12	13.9	

Bouwman and Kalkman 2005). One extinct species (*Ophiogomphus cecilia)* and one absent species (*Onychogomphus forcipatus*) were found reproducing in the 1990's, in the river Roer in the south of the Netherlands (Geraeds 2000; Geraeds and Van Schaik 2004). *Platycnemis pennipes*, *Gomphus vulgatissimus*, *Orthetrum coerulescens, Orthetrum brunneum* and *Sympetrum pedemontanum* increased (van Eijk and Ket-

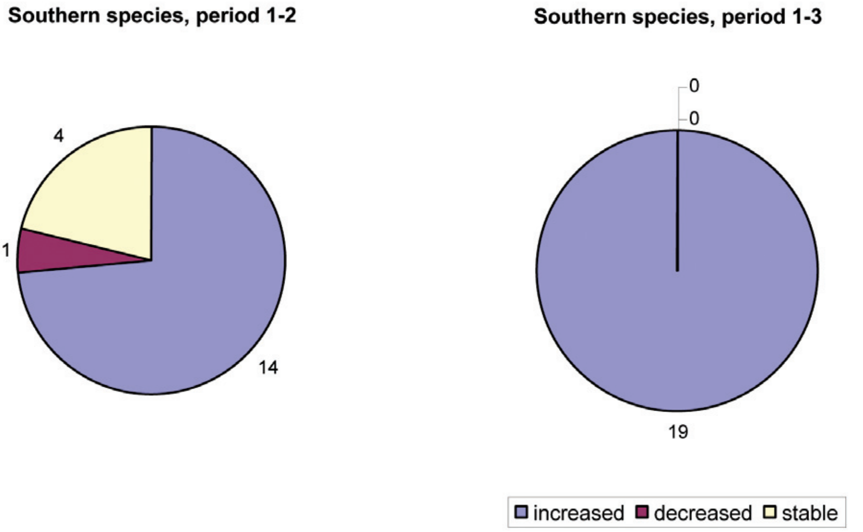

Figure 2. Distribution of the tested southern species over the trend categories. Three different periods were compared. Period 1 = 1980–1993, period 2 = 1994–1998, period 3 = 1999–2003.

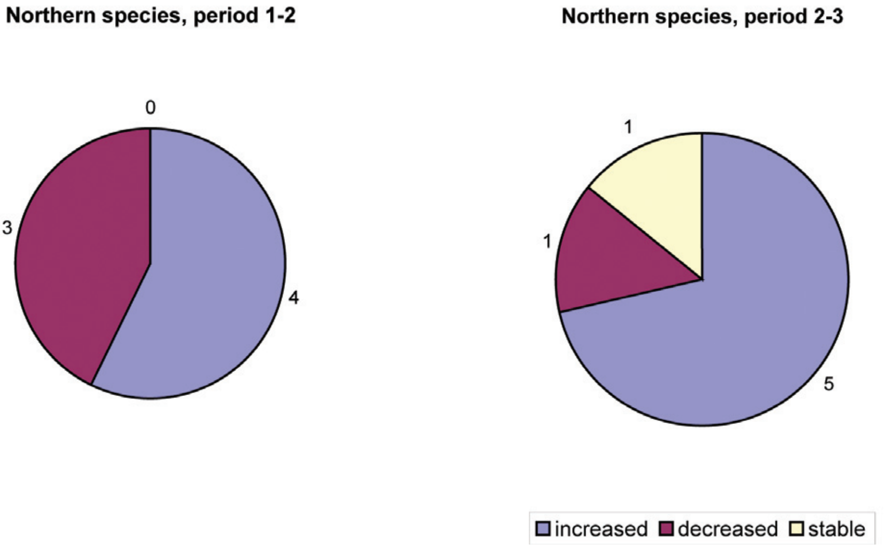

Figure 3. Distribution of the tested northern species over the trend categories. Three different periods were compared. Period 1 = 1980–1993, period 2 = 1994–1998, period 3 = 1999–2003.

elaar 2004; van Delft 1998; Mensing 2002), while *Calopteryx splendens* remained stable. *Calopteryx virgo* and *Cordulegaster boltonii* are the only rheophilic species showing negative trends, however the observed numbers of these species have increased recently and several new localities were found (Groenendijk 2002; Termaat

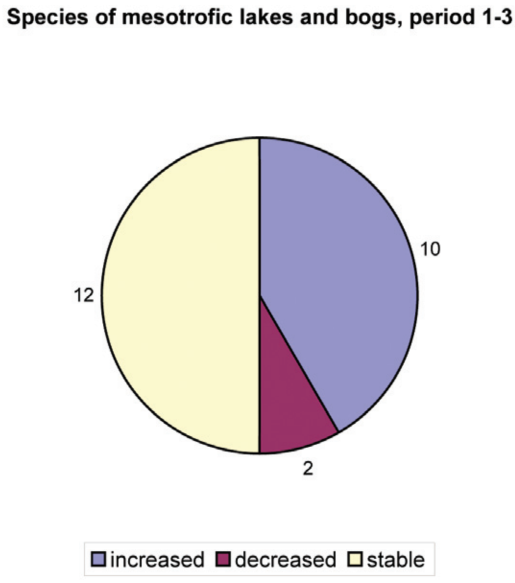

Figure 4. Distribution of the tested species of mesotrophic lakes and bogs over the trend categories. Three different periods were compared. Period 1 = 1980–1993, period 2 = 1994–1998, period 3 = 1999–2003.

and Groenendijk 2005). In our opinion, these findings leave no doubt that species of running water have increased strongly since 1980. Water quality improvement and restoration of the natural morphology of streams and rivers are likely to be the important causes for it. Some species probably profited from the higher summer temperatures as well. This is at least very likely for *Orthetrum brunneum, O. coerulescens* and *Sympetrum pedemontanum*.

Whereas the quality of running water habitats has improved, the threats for stagnant water habitats such as mesotrophic lakes and bogs are still present. Eutrophication, dessication and habitat fragmentation are still factors which explain why relatively few species in this species group show a positive trend. The intensity of eutrophication has reduced in recent years (RIVM 2003), but in many cases this has not lead to the recovery of lakes and bogs that have already been spoiled. The results of our analyses suggest that the negative trend of the species group of mesotrophic lakes and bogs stopped, but that they fail to recover. Especially *Coengrion hastulatum*, a species of mesotrophic lakes and bogs, is still declining in the Netherlands and is becoming increasingly endangered (Termaat 2006).

Conclusions

The analyses of the trends in the period 1980 to 2003 shows that the 55 Dutch dragonfly species for which a trend could be calculated remained stable or increased during

Figure 5. The distribution of *Gomphus flavipes* in the period 1996–2005. The species was not found in the Netherlands from 1902 to 1995.

that time period and that only 5 species have declined. Habitat degradation during the larger part of the 20th century resulted in a degradation of the dragonfly fauna in the eighties of that century. Improved water quality and increasing summer temperatures in the last two decades resulted in a revival of the Dutch dragonfly fauna.

Although our analyses failed to show that the species group of running water contains a significantly higher portion of increasing species than the all-species group, it is clear that especially species of running water have increased since 1980. This is probably largely due to the improved water quality of running waters and the restoration of the natural morphology of these systems.

The average temperature in the last twenty years of the 20th century was 0,7 °C higher than those of the first twenty years of the 20th century. As a result significantly more species with a southern distribution show a positive trend when compared with the all-species group.

Seven species very rare or absent prior to 1990 became established in the Netherlands, probably due to the increase in temperature. Three of these established themselves by means of large invasions. These invasions were very effective, showing once more that dragonflies are highly capable of colonising new areas. No evidence could be provided to state that species with a northern distribution are decreasing due to the higher temperatures. The habitats where these species live (mostly mesotrophic lakes and bogs) have been strongly influenced by eutrophication, acidification and desiccation in the 1960[th] and 1970[th] resulting in a decline of most of these species. This decline might have masked the influence of climate change.

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Appendix I

Southern species and invasions

Six southern species rare or absent in the 1980's are now well recognised members of the Dutch odonate fauna: *Lestes barbarus*, *Erythromma lindenii*, *Aeshna affinis*, *Crocothemis erytraea*, *Orthetrum brunneum* and *Sympetrum fonscolombii*. *Anax parthenope* is expected to become established in the coming years, as it recently became a regular guest and has reproduced successfully. The way in which southern species became established in the Netherlands differs among the species. *E. lindenii*, *C. erytraea* (figure 6) and to a lesser extent *O. brunneum* gradually expanded the northern border of their range. The other three species *L. barbarus*, *A. affinis*, and *S. fonscolombii* became established after invasions, being rare in the years preceding these invasions (see table 6). The invasion of *Lestes barbarus* started in July 1994 (Ketelaar 1994) During the invasion records were made in most areas of the country with a strong emphasises on the dunes and the Pleistocene areas. At the majority of these localities several (up to 40) individuals were found. Almost all records were made at shallow, warm waters such as dried-out bogs and smaller dune lakes. In many cases the species established itself at these localities. Probably several smaller invasions occurred since 1994 but these went largely unnoticed as the species was already established. In the period since 1994 the species is found yearly in suitable habitat all over the Netherlands. Preceding the 1994 invasion the northern border of the distribution of *L. barbarus* was situated to the south of the Netherlands. The invasion in 1994 therefore resulted in a northwards expansion of its range of well over 300 km.

The invasion of *A. affinis* started mid July 1995. All 39 records from 1995 came from the southern part of the Netherlands, most of them from the coastal dunes or from the Pleistocene areas. Almost all individuals were found at drying or dried-out waters, with low reeds or bulrushes. Of the 81 sexed specimens only four were females. This might be partly due to the inconspicuous behaviour of the females. Since the 1995

Figure 6. The distribution of *Crocothemis erythraea* in the periods 1980–1993, 1994–1998 and 1999–2003, showing its gradual northwards expansion.

Table 6. Southern species rare during the eighties which have become established since 1990. The second column states whether or not the species became established during a large invasion or gradually expanded northwards.

Species	Established due to	Number of records in the 10 years prior to invasion	Number of records in year of invasion
Aeshna affinis	Invasion in 1995	1	39
Anax parthenope	Gradually (1)		
Crocothemis erythraea	Gradually		
Erythromma lindenii	Gradually		
Lestes barbarus	Invasion in 1994	14	79
Orthetrum brunneum	Probably gradually		
Sympetrum fonscolombii	Invasion in 1996	1	135

(1) *Anax parthenope* is not yet established but has become a regular guest and is likely to become established in the future.

invasion the species is found several times a year in all parts of the Netherlands. The first proof of successful reproduction was found in 2005 (Wasscher 2005) although it is likely that small (temporary) populations have existed since 1995.

In end May and begin June of 1996 a massive invasion of *Sympetrum fonscolombii* reached Northwestern Europe (Lempert 1997; Dijkstra and Van der Weide 1997). As with *Lestes barbarus* the species was recorded all over the country with a strong emphasises on the dunes and the Pleistocene areas. Most records were made at unshaded, standing waters with sparse vegetation and often sandy banks. The species managed to establish itself at many of these localities. Since 1996 the species is found every year at numerous localities across the country, although it has become less abundant than in 1996.

The invasions of *L. barbarus*, *A. affinis*, and *S. fonscolombii* have two things in common:

1 During the invasion almost all specimens were found at suitable habitats and not seldom successful reproduction was noticed in later years;
2 Most records during the years of the invasions referred to more than one specimen.

The three species which invaded The Netherland in 1994, 1995 and 1996 were rarely seen at unsuitable sites. This stresses the fact that these species are highly capable of localising suitable habitats. This is further emphasised by the fact that in most cases more than one individual was found at a locality. These species do not fly in clustered groups making it likely that the individuals from one locality all located the habitat on their own.

Probably these species used their ability to recognise polarized light combined with visual cues on vegetation structure to detect suitable habitat from some height as has been shown for some species of dragonflies (Corbett 1999). This makes that a relatively high portion of the individuals taking part in the invasion is able to reproduce at a potentially suitable location. These examples show that at least these species are capable of taking advantage of favourable circumstances in an extremely effective way.