Ten years after the invasion: *Dicranopalpus ramosus* and *Odiellus spinosus* (Opiliones, Phalangiidae) in Denmark

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Abstract. The two harvestmen *Dicranopalpus ramosus* and *Odiellus spinosus* were first recorded from Denmark in 2007 and 2006, respectively. Two nation-wide surveys of the species in urban habitats were conducted in 2010 and 2017 providing information on their initial colonization and subsequent establishment and spread. By 2017, *D. ramosus* occurred in all parts of Denmark and was a frequent and abundant species in most of Jutland. On the Danish islands, the species was present but much less frequent. *Odiellus spinosus* occurred sporadically in eastern Jutland and more frequently on the islands. During the early years, new records of both species came from spaced-out locations, indicating arrival by long-distance jump dispersal possibly by independent colonisations from abroad and most probably mediated by human traffic. The range expansion of *D. ramosus* in northern Europe has occurred with a speed of 35–100+ km per year.

Keywords: alien species, colonization, introduced species, invasion routes, speed of range expansion, urban species

Zusammenfassung. Zehn Jahre nach der Invasion: *Dicranopalpus ramosus* und *Odiellus spinosus* (Opiliones, Phalangiidae) in Dänemark. Die beiden Weberknechtarten *Dicranopalpus ramosus* und *Odiellus spinosus* wurden 2007 bzw. 2006 erstmals in Dänemark nachgewiesen. In den Jahren 2010 und 2017 wurden zwei landesweite Kartierungen beider Arten in städtischen Lebensräumen durchgeführt und erbrachten Kenntnisse zur Kolonisierung, Etablierung und Ausbreitung der Arten. Im Jahr 2017 kam *D. ramosus* in allen Teilen Dänmarks vor und war in weiten Teilen Jütlands stetig und zahlreich zu finden. Auf den dänischen Inseln war die Art präsent aber weit weniger häufig. *Odiellus spinosus* kam im Osten Jütlands nur sporadisch vor und war auf den Inseln häufiger. Während der ersten Jahre wurden beide Arten an weit voneinander entfernten Orten gefunden, was auf Ausbreitung aus großen Entfernungen hindeutet, möglicherweise unabhängig voneinander aus dem Ausland mithilfe des menschlichen Fernverkehrs bzw. Gütertransportes. Die Erweiterung des Areals von *D. ramosus* in Nordeuropa fand mit einer Geschwindigkeit von 35–100+ km pro Jahr statt.

During several decennia, Northern Europe has witnessed repeated invasions of harvestman species originating from the Mediterranean region (Wijnhoven et al. 2007, Enghoff et al. 2014). Coming from Italy, *Opilio canestrinii* (Thorell, 1876) expanded through Central Europe during the 1960s, 1970s and 1980s (first records in European countries summarized by Vestbo et al. 2018). In those days, few people paid attention to harvestmen; therefore, observations are generally too haphazard to reflect the true routes and the speed by which the species expanded. For example, when discovered in Denmark in 1987, it was already of nation-wide occurrence and the second most abundant species in urban habitats (Enghoff 1988). It was clear, however, that the species had expanded very fast, but exactly how fast was impossible to tell. When other species followed suit during the 1990s and 2000s, the arachnological community was better prepared and could further take advantage of the creation of national public databases on the internet into which gifted amateur naturalist report their observations. This has tremendously enhanced the ability to follow fast faunistic changes, even if attention is not specifically directed towards harvestmen.

Dicranopalpus ramosus (Simon, 1909) originated from the Iberian Peninsula and Morocco (Wijnhoven & Prieto 2015). It turned up in southern UK in 1957 and slowly widened its distribution along the southern British coast (maps in Sankey & Savory 1974, Rambla 1986). Its northward expansion in western Europe became clear during the 1990s when it was recorded from the Netherlands (1993), Belgium (1994), Ireland (1994) and Scotland (2000) (summarized by Noordijk et al. 2007). In 2002 it was recorded from Germany (Schmidt 2004), in 2007 from Denmark (Toft & Hansen 2011), in 2012 from Sweden (Jonsson 2013) and in 2014 from Poland (Rozwałka & Rutkowski 2016). Noordijk et al. (2007) commented on the speed of spreading as the species was found in most parts of the Netherlands only 14 years after the first record. Based on a nation-wide survey of urban areas in 2010, Toft & Hansen (2011) reported on the early colonization and establishment in Denmark. They found that already within three years after the first discovery of the species it had reached most parts of the country, even locations as far from the presumed sources of immigration as is possible in Denmark. If these observations reflect the process of invasion correctly (see below), they underscore that the species was expanding extremely fast.

The present paper follows up on the previous study (Toft & Hansen 2011). A new nation-wide survey was conducted in 2017, i.e. 10 years after the first Danish record of *D. ramosus* with the purpose of recording the changes that have occurred in the Danish distribution of *D. ramosus* during the intervening seven years. The combined data is then used to deduce the most likely routes and the most likely mechanisms of dispersal by which the species has colonized and established itself in Denmark.

Odiellus spinosus (Bosc, 1792) is another newcomer in Denmark, noticed for the first time in 2006 (Enghoff & Pedersen 2007) and also recorded during the urban surveys. It is native to southern and western Europe (Italy, northern Spain, France, Benelux and southern UK) (Martens 1978). Since the 1970s it has shown expansive tendencies by widening its area eastwards in Germany (Arachnologische Gesellschaft 2018) and adjacently Poland (Rozwałka et al. 2013). The species has spread in Denmark during the same period as *D. ramosus* allowing a direct comparison between the two with respect to area occupied and the speed of colonization and spreading.

The results are discussed in terms of two models of expansion (Hengeveld 1989): wave front expansion or jump dispersal. Either a species enlarges its range as a broad moving front progressing wavelike into the new range. Expansion happens

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by individual short-distance dispersal, induced by a surplus population being produced near the border of the original range. Alternatively, a species' range may expand as a result of long-distance displacements performed by a few individuals that successfully settle and establish themselves at a place far outside the normal range limit. Such pioneer (bridgehead) subpopulations may eventually become incorporated in the species' newly enlarged range by a combination of the two dispersal mechanisms: repeated jump dispersal events from the original range combined with local short-distance dispersal by offspring of the original colonizers. No direct information exists on the mechanisms of migration of these harvestmen; in accordance with Noordijk et al. (2007) and Vestbo et al. (2018) it is assumed that transportation by human traffic (trucks and cars) is the most likely means of long-distance dispersal for these harvestmen. Below I will also discuss the suggestion by Noordijk et al. (2007) that wind dispersal may be involved.

Material and methods

As the immigrant harvestmen were first discovered in urban settings and the animals are most easily observed on house walls, churchyard walls and similar vertical structures, registrations were made as surveys of cities and towns. Each registration was conducted as a one hour walk through (part of) the town, proceeding at a normal walking speed of ca. 3 km per hour, though some of the towns visited were too small to allow a full one-hour survey. Areas with plastered houses painted in light colours (white or yellow) were preferred, as the harvestmen are most easily discovered on such surfaces. In most cases, this means that older parts of the towns (from early 20th century) were included if available. These quarters also had the advantage that the house walls often faced the pedestrian pavement without enclosed gardens in front. All harvestmen seen between ground level and 2 m height were collected in 70 % alcohol and later identified under the binocular microscope.

At some localities these surveys were conducted repeatedly between 2008 and 2017. In the two years 2010 (Toft & Hansen 2011) and 2017, they included a large number of towns covering most of the country (61 and 64 locations, respectively). All records have been submitted to the public database Naturbasen (2018). In the distribution maps, the data from these surveys are supplemented by observations reported by others to the database. The pattern emerging from my own data and from the combined data set are the same, except that the latter provides a more complete geographical coverage.

An attempt, admittedly inaccurate, was made to estimate the rate of expansion of *D. ramosus* in northern Europe, using the locations of the first records of the species in the Netherlands and Germany and the early finds from Denmark. The distance from Ede (Netherlands) and Bochum (Germany) to Årslev (Funen, Denmark) was divided by the number of years between the respective finds (14 and 4 years, respectively). Similar calculations were made between the Ede and Bochum finds and the most remote (i.e. furthest away from assumed places of origin) Danish finds (Copenhagen, easternmost point of Zealand, 2009; Skagen, northernmost tip of Jutland, 2010) (names of main Danish regions/island indicated on Fig. 1A). *Dicranopalpus ramosus* is an extremely characteristic species due to its unique position of the legs during rest (all four legs directed straight to the side). Therefore, it will draw the attention of active field naturalists; they can easily recognize it and documentation by photos is unequivocal. In Denmark, the arrival of the species was anticipated (Toft 2004). It is therefore unlikely that the species had been present, widespread and abundant in Denmark before its first discovery. Similar arguments may refer to the situation in the Netherlands in the 1990s and to the records of *O. spinosus*. Furthermore, several locations in Denmark where *D. ramosus* later turned up were surveyed in 2003 without any trace of the species (Toft & Hansen 2011). Thus, in both countries the species may have first invaded a few years prior to discovery, but the time lag between arrival and discovery may be approximately the same.

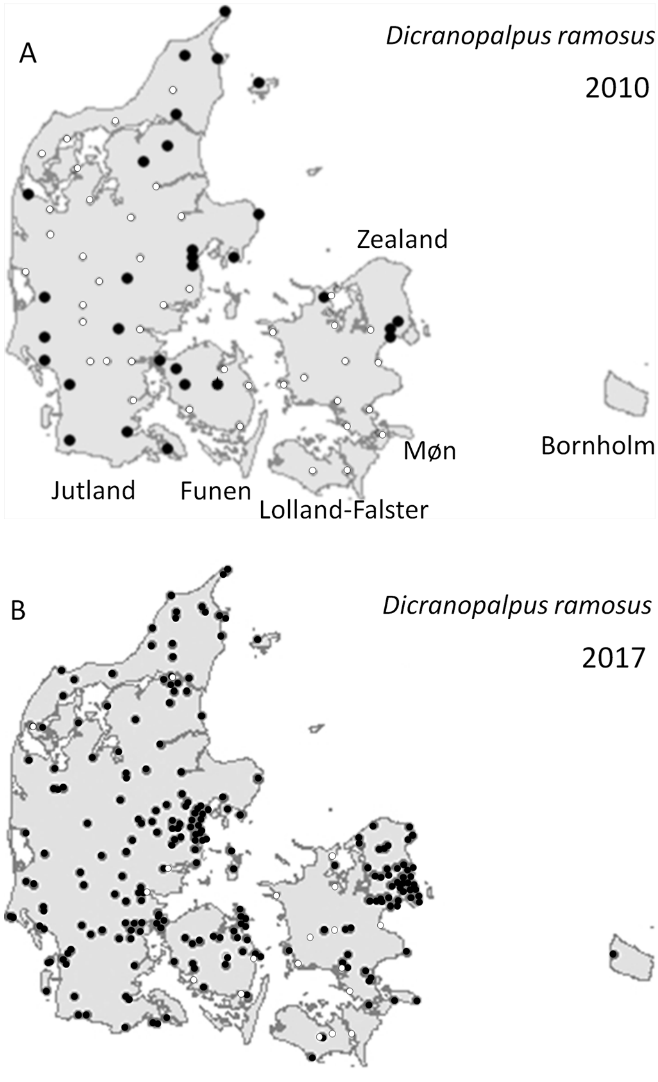

Fig. 1: Known distribution in Denmark of (**A**) *Dicranopalpus ramosus* at the end of 2010 (from Toft & Hansen 2011), (**B**) *D. ramosus* at the end of 2017. Star indicates point of first Danish record (2007). Closed circles: *D. ramosus* present. Open circles: localities searched, but *D. ramosus* was not found

Results

Already in 2010, *D. ramosus* had arrived to many parts of Denmark, but it was also absent from large areas (Fig. 1A; Toft & Hansen 2011). This early distribution can best be characterized as a widely scattered ("patchy") occurrence. At all locations where it was present the species was infrequent, 1-6 specimen (mean 2.4) being found during the one-hour searches. It was absent from central and northwestern Jutland, most of Zealand, as well as Lolland-Falster and Bornholm.

In 2017, *D. ramosus* had arrived to all parts of Denmark (Fig. 1B). In Jutland the species was nearly ubiquitous and was missed in only a very few survey visits (4 of 42 towns), indicating a more or less "continuous" distribution. On southern Funen, most of Zealand and Lolland-Falster, the species was present as indicated by reports to the database, but in any case it was missing in 15 out of 22 of the towns visited during the survey. The relative frequencies in Jutland and the islands are significantly different (Yates' χ^2 = 10.05, *df* = 1, *P* = 0.0015). The number of individuals per visit in Jutland was 1-10 (mean 3.6), while on the islands it was 1-2 (mean 1.6) (excluding locations without the species). The first record from the isolated island of Bornholm, situated in the Baltic Sea between Poland and Sweden, is from 2017.

The bee line distance between sites of first records in the Netherland (Ede) and Denmark (Årslev) is 482 km. This was accomplished by *D. ramosus* in 14 years, giving a displacement rate of 34.4 km/year. Records from Copenhagen 2009 and Skagen (northern tip of Jutland) in 2010 give displacement rates of 37.9 and 41.5 km/year, respectively. Similar calculations from the site of the first German record (Schmidt 2004) produce values of 119.5, 97.7 and 104 km/year, respectively. As it is unknown whether the immigrants to Denmark came from Germany or the Netherlands, 35-40 km per year may be considered the cautious estimate. In Sweden, however, *D. ramosus* was recorded from Uppsala only 5 years after the first Swedish record (Artportalen 2018) giving a rate of expansion of 103 km per year. The finding of an established population at Poznań, Poland, 440 km east of the nearest known German locality (Rozwałka & Rutkowski 2016) also indicates the possibility of fast expansion by very long jumps.

Odiellus spinosus (Fig. 2) has spread much less actively than *D. ramosus*. The number of localities and the total distribution area is smaller. It is widely scattered within its area which in 2017 included eastern Jutland and the islands (except Bornholm) with a relatively high concentration on the islands. The distributional pattern (Fig. 2) was as patchy as the early distribution of *D. ramosus*. It has been observed exclusively in or near towns and usually low in numbers (max. 2 individuals per one hour of search).

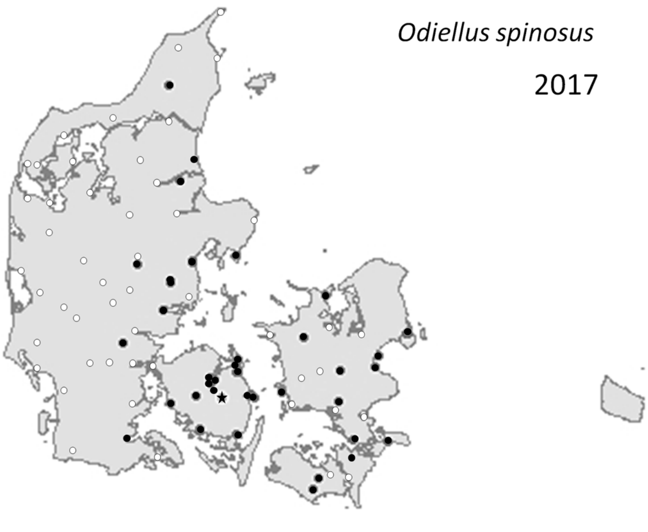

Fig. 2: Known distribution in Denmark of *Odiellus spinosus* at the end of 2017. Star indicates point of first Danish record (2006). Closed circles: *O. spinosus* present. Open circles: localities searched, but *O. spinosus* was not found. For names of Danish regions/islands, see Fig. 1A

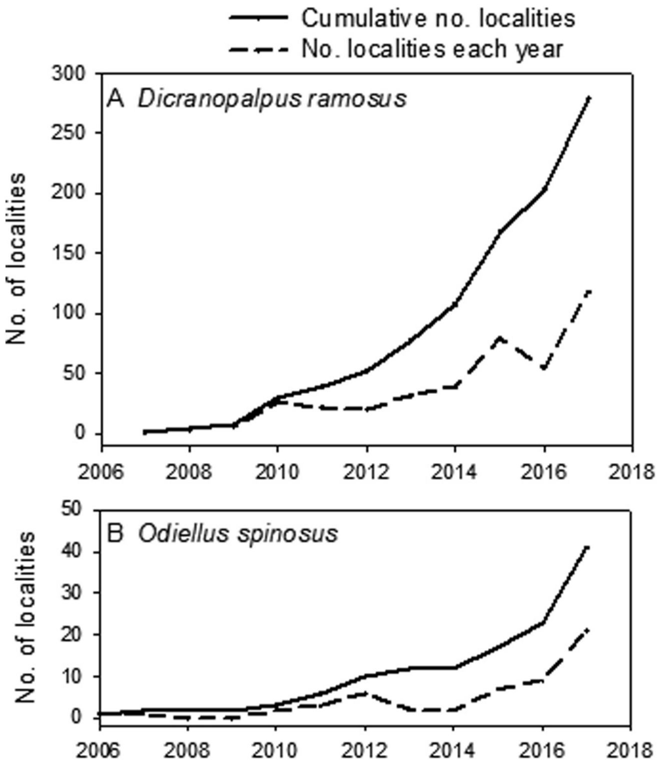

Fig. 3: Increase in the number of localities from which *Dicranopalpus ramosus* (**A**) and *Odiellus spinosus* (**B**) have been reported to Naturbasen (2018)

Discussion

Only since the early 1990s are the data about the occurrence of the two species of sufficient quality to allow analysis of the routes and speed of distributional expansion. According to its distribution before arriving in Denmark, *D. ramosus* must have come from the Benelux/western Germany area. At the subcontinental (north European) scale, there is some evidence of a dispersal front (Netherlands 1993, Germany 2002, Denmark 2007, Sweden 2012), but at the national Danish scale this disappears completely. The map of its occurrence in 2010 (Fig. 1A) indicates that neither distance nor sea water were barriers to dispersal. The species was soon found at locations far apart over most of the country, but at the same time it was missing in large areas. Such a distributional pattern signifies long-distance jump dispersal from the source area(s). Multiple independent immigrations from abroad represent a likely scenario and are compatible with the most probable mode of dispersal, i.e. transportation by human traffic (Noordijk et al. 2007, Vestbo et al. 2018). In fact, Fig. 1A may allow us to hypothesize in more detail about how this transportation took place. The occurrence in eastern Jutland, Funen and Copenhagen fits a pattern of immigration via the Danish highways, which extend the north German highway system northwards along the east coast of Jutland with a branch going east over Funen and Zealand to Copenhagen and Sweden, all of which are connected by bridges. Specifically, the first Danish records of *D. ramosus* (and also *O. spinosus*, Fig. 2) were from Årslev on the island of Funen (Fig. 1A & 2). Vestbo et al. (2018)

argues that this place houses a large horticultural centre that is a target of truck traffic from all of Europe, including not least the Netherlands. Interestingly, the early Swedish records of *D. ramosus* were from the Helsingborg and the Malmö/Lund area (Jonsson 2013, Artportalen 2018), i.e. the part of Sweden adjacent to Copenhagen. Thus, the species probably immigrated to Sweden via Denmark. No highways go up along the west coast of Jutland, but this area attracts high numbers of German tourists during the summer and early autumn. Thus, the areas in which *D. ramosus* became established very early are those which have relatively high traffic rates originating from south of Denmark. In contrast, central Jutland is characterized by east–west traffic and was colonized some years later. The first observation from the island of Bornholm, an isolated island in the Baltic Sea between Poland and Sweden, came in 2017. The late arrival here was expected due to limited traffic connections (ferries from Copenhagen, Germany and Sweden). Considering the Swedish distribution of *D. ramosus* in 2017 (Artportalen 2018), the traffic connections to Bornholm, and the absence of the species in eastern Germany (Arachnologische Gesellschaft 2018), immigration from the north via Sweden may be the most probable route.

Comparison of Fig. 1A and 1B shows that during the years 2010 to 2017, *D. ramosus* in Jutland has filled out much of the space between the locations initially colonized. In 2017 the species was missed in very few of the urban counts and only from one location in which it had been observed in previous years. Fig. 3 witnesses a dramatic increase in the number of new localities reported in precisely this period. Though transportation by cars cannot be excluded as partial explanation for the short-distance dispersal, self-accomplished dispersal may also be partly involved in the local filling of available habitat space. The species' preference for shrubby habitat (Noordijk et al. 2007, own observations) may facilitate corridor spreading e.g. along hedges. Unfortunately, no direct observations exist to evaluate the relative importance of dispersal mechanisms.

The Danish distribution of *O. spinosus* (Fig. 2) differs from that of *D. ramosus* in that it is completely missing in western Jutland, and that it is found considerably more often on the islands (Funen, Zealand, Lolland, Møn) than in Jutland. Apart from showing much slower rates of expansion, this may indicate that the routes of immigration are partly different. The occurrences in eastern Jutland and Funen may have followed the same route as *D. ramosus*, i.e. via highway traffic from Germany. The relatively heavy concentration of the species on south Zealand, Lolland and Møn indicates another immigration route via the ferry from Germany to Rødby (southern coast of Lolland). The immigrants here may have originated from the population that have established in eastern Germany. The possibility of this immigration route is documented by the extreme number of rare southern species (insects, millipedes, centipedes, harvestmen) that have been found at an abandoned railway area near the ferry harbour (Enghoff et al. 2011).

Wind dispersal has been proposed as a possible mechanism of dispersal for the expanding harvestmen (Noordijk et al. 2007). There are neither direct nor indirect evidence for this, however. Firstly, I am unaware of any observations of "flying" harvestmen; in contrast to spiders and mites, harvestmen seem never to have been recorded in samples of aerial plankton whether recorded from planes (Glick 1939), high masts (Freeman 1946) or from boats far at sea (Hardy & Cheng 1986). Secondly, if the air was a main dispersal medium, the direction of spreading is expected to follow the main wind direction. The direction of expansion of most harvestmen has been towards the north, while prevailing winds are westerly (http://www.dmi.dk).

Development of the reports for each of the two species to Naturbasen (2018) (Fig. 3) indicate that the largest increase in the number of locations from which they were reported came in the latter half of the period, after a relatively slow increase in the first half. This picture is consistent with the hypothesis that the early finds were due to independent immigrations from abroad, while the later "filling up" is due to local (and possibly self-mediated) dispersal from each of the primary centres of establishment.

The 2017 distribution of *D. ramosus* on the Danish islands (Fig. 2B) indicates a situation similar to that in Jutland 2010 (Fig. 2A): the species is present, but not abundant enough to turn up at every one-hour observation event. The situation is a logical consequence of the fact that in 2010 the species was completely missing on most of the eastern islands (except in Copenhagen). In another seven years we can expect it to have become firmly established on these islands too.

Dicranopalpus ramosus were estimated to have invaded northern Europe with a speed of 35-100+ km per year. Range expansion rates at such speeds make it hard to imagine that the expansion could take place without human assistance. Though some flying insects (e.g. the harlequin ladybird beetle, *Harmonia axyridis*) may have spread with higher speeds (Brown et al. 2008, Hemptinne et al. 2012), most invasive winged insects have expanded with speeds in the same range as *D. ramosus* or slower (Hemptinne et al. 2012). Indeed, the spread of the harlequin beetle in Denmark has been considerably slower than that of *D. ramosus* (Steenberg & Harding 2009). Human vehicular transportation allows for dispersal by very long jumps also in species incapable of self-mediated long-distance dispersal. It even seems that the speed of expansion has increased as the species moved north. This may be due to increased truck traffic between countries of the European Union during the last decennia. Building of bridges between Funen and Zealand (1998) and between Zealand and Sweden (2000) may have reduced the tendency of the sea belts between these islands (Storebælt and Øresund) to function as dispersal barriers by facilitating terrestrial traffic.

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Electronic Appendix (pdf format): Numbers of *Dicranopalpus ramosus* and *Odiellus spinosus* collected during one-hour surveys of Danish towns during the period 2003 to 2017, with information on geographic position of towns and year/date (Month-Day) of collection.

Appendix. Numbers of Dicranopalpus ramosus and Odiellus spinosus collected during one-hour surveys of Danish towns during the period 2003 to 2017, with information on geographic position of towns and year/date (Month-Day) of collection. D = No. *D. ramosus*; O = No. *O. spinosus*

Locality	Latitude °N	Longitude °E	Year	Date	D	O
Assens	55.27	9.89	2017	10-18	2	2
Brande	55.90	9.13	2010	09-12	–	–
Brande			2017	10-09	1	–
Brønderslev	57.27	9.95	2010	10-08	–	–
Brønderslev			2011	10-13	–	–
Brønderslev			2017	09-24	6	2
Ebeltoft	56.20	10.68	2010	10-07	2	–
Ebeltoft			2017	09-22	5	–
Esbjerg	55.47	8.48	2010	10-10	2	–
Esbjerg			2017	10-27	1	–
Fjerritslev	57.09	9.26	2003	11-02	–	–
Fjerritslev			2010	10-08	–	–
Fjerritslev			2011	09-30	1	–
Fjerritslev			2017	09-28	2	–
Frederikshavn	57.45	10.54	2010	10-08	3	–
Frederikshavn			2011	10-13	1	–
Frederikshavn			2017	09-24	2	–
Fåborg	55.10	10.24	2010	09-29	–	–
Fåborg			2017	10-18	–	1
Grenå	56.41	10.89	2010	09-22	–	–
Grenå			2016	09-26	3	–
Grenå			2017	09-22	5	–
Grindsted	55.76	8.93	2010	09-12	–	–
Grindsted			2017	10-09	6	–
Haderslev	55.25	9.49	2008	09-28	–	–
Haderslev			2010	09-22	–	–
Haderslev			2011	11-02	1	–
Haderslev			2017	10-30	6	–
Herning	56.14	8.97	2003	11-01	–	–
Herning			2010	09-09	–	–
Herning			2011	10-04	–	–
Herning			2017	10-08	4	–
Hjørring	57.46	9.99	2010	10-08	3	–
Hjørring			2011	10-13	–	–
Hjørring			2017	09-24	1	–
Hobro	56.64	9.80	2010	09-30	–	–
Hobro			2011	09-30	–	–
Hobro			2013	11-03	3	–
Hobro			2017	09-14	2	–
Holbæk	55.71	11.72	2010	10-13	–	–
Holbæk			2017	10-14	–	–
Holstebro	56.36	8.62	2010	09-09	–	–
Holstebro			2011	10-04	–	–
Holstebro			2012	09-23	1	–
Holstebro			2017	10-08	5	–
Holsted	55.51	8.92	2010	09-12	–	–
Holsted			2017	10-27	4	–
Horsens	55.86	9.85	2010	09-12	–	–
Horsens			2017	09-15	–	1
Hurup Thy	56.75	8.42	2010	09-09	–	–
Hurup Thy			2012	09-23	2	–
Hurup Thy			2017	09-07	–	–
Ikast	56.14	9.16	2003	11-01	–	–
Kalundborg	55.68	11.09	2010	10-13	–	–
Kalundborg			2017	10-14	–	–
Frederiksberg	55.69	12.55	2009	11-01	–	–
Kolding	55.49	9.48	2010	09-12	–	–
Kolding			2017	10-27	–	–
Korsør	55.33	11.14	2010	10-12	–	–
Korsør			2017	10-15	1	1
Køge	55.46	12.18	2010	10-13	–	–
Køge			2017	10-14	–	1
Lemvig	56.55	8.31	2010	10-10	2	–
Lemvig			2011	10-05	3	–
Lemvig			2017	10-08	8	–
Maribo	54.77	11.50	2010	10-12	–	–
Maribo			2017	10-13	–	1
Middelfart	55.5	9.73	2010	09-29	4	–
Middelfart			2017	10-18	2	–
Nordby Fanø	55.45	8.40	2014	09-28	–	–
Nr.Snede	55.97	9.39	2010	10-09	1	–
Nr.Snede			2011	10-05	–	–
Nr.Snede			2017	10-09	7	–
Nyborg	55.31	10.79	2010	09-29	–	–
Nyborg			2017	10-18	–	1
Nykøbing Falster	54.77	11.87	2017	10-13	–	–
Nykøbing Mors	56.79	8.86	2010	10-09	–	–
Nykøbing Mors			2011	09-27	–	–
Nykøbing Mors			2013	11-03	2	–
Nykøbing Mors			2017	10-01	2	–
Nykøbing Sjælland	55.92	11.67	2010	10-13	–	2
Nykøbing Sjælland			2014	10-25	–	2
Nykøbing Sjælland			2017	10-14	–	–
Næstved	55.22	11.77	2010	10-13	–	–
Næstved			2017	10-15	–	–
Odder	55.97	10.15	2010	09-13	–	–
Odder			2017	09-15	4	–
Odense C	55.39	10.38	2010	09-29	–	2
Præstø	55.12	12.04	2003	10-25	–	–
Præstø			2010	10-12	–	–
Præstø			2017	10-13	1	–
Randers	56.47	10.02	2010	09-30	–	–
Randers			2011	09-30	–	–
Randers			2013	11-03	–	–
Randers			2017	09-14	2	–
Ribe	55.33	8.76	2008	09-28	–	–
Ribe			2010	09-22	2	–
Ribe			2011	11-02	1	–
Ribe			2017	10-30	6	–
Ringkøbing	56.09	8.25	2003	11-01	–	–
Ringkøbing			2010	10-10	–	–
Ringkøbing			2011	10-05	–	–
Ringkøbing			2017	10-08	2	–
Ringsted	55.44	11.79	2010	10-13	–	–

Locality	Latitude °N	Longitude °E	Year	Date	D	O
Ringsted			2017	10-15	1	2
Roskilde	55.64	12.08	2010	10-13	–	–
Roskilde			2017	10-14	2	–
Sakskøbing	54.80	11.64	2017	10-13	–	–
Sønder Omme	55.84	8.89	2010	09-12	–	–
Sønder Omme			2017	10-09	1	–
Silkeborg	56.16	9.55	2003	11-01	–	–
Silkeborg			2010	10-09	–	–
Silkeborg			2011	10-14	–	–
Silkeborg			2017	09-14	2	–
Skagen	57.72	10.59	2010	10-08	2	–
Skagen			2011	10-13	–	–
Skagen			2017	09-24	3	–
Skanderborg	56.03	9.93	2017	09-18	2	2
Skive	56.57	9.03	2010	10-09	–	–
Skive			2011	09-27	–	–
Skive			2012	09-23	–	–
Skive			2013	10-10	2	–
Skive			2017	10-01	10	–
Skjern	55.95	8.50	2010	10-10	1	–
Skjern			2011	10-05	–	–
Skjern			2017	10-27	1	–
Skælskør	55.25	11.30	2017	10-15	–	–
Slagelse	55.40	11.36	2010	10-12	–	–
Slagelse			2017	10-15	–	–
Sorø	55.43	11.56	2017	10-15	–	–
Stege	54.99	12.29	2003	10-25	–	–
Stege			2010	10-12	–	–
Stege			2017	10-13	2	1
Struer	56.49	8.97	2010	09-09	–	–
Struer			2011	10-04	–	–
Struer			2012	09-23	1	–
Struer			2017	10-08	2	–
Svendborg	55.06	10.61	2010	09-29	–	–
Svendborg			2017	10-18	–	1
Sønderborg	54.91	9.79	2008	09-27	–	–
Sønderborg			2010	09-22	2	–
Sønderborg			2011	11-02	3	–
Sønderborg			2017	10-30	2	–

Locality	Latitude °N	Longitude °E	Year	Date	D	O
Thisted	56.96	8.69	2003	11-02	–	–
Thisted			2010	10-08	–	–
Thisted			2011	09-28	–	–
Thisted			2012	09-23	1	–
Thisted			2013	11-02	1	–
Thisted			2017	09-07	4	–
Tønder	54.94	8.86	2010	09-22	2	–
Tønder			2011	11-02	2	–
Tønder			2017	10-30	7	–
Varde	55.62	8.48	2010	10-10	6	–
Varde			2017	10-27	2	–
Vejen	55.48	9.14	2009	09-25	–	–
Vejen			2010	09-12	–	–
Vejen			2017	10-27	3	–
Vejle	55.71	9.54	2010	09-12	–	–
Vejle			2017	10-09	3	–
Vestervig	56.76	8.32	2013	11-02	2	–
Vestervig			2017	09-07	3	–
Viborg	56.45	9.41	2010	09-12	–	–
Viborg			2011	09-27	–	–
Viborg			2013	11-03	–	–
Viborg			2017	09-14	2	–
Videbæk	56.09	8.63	2003	11-01	–	–
Vordingborg	55.01	11.91	2010	10-12	–	–
Vordingborg			2017	10-13	–	1
Åbenrå	55.04	9.42	2008	09-27	–	–
Åbenrå			2009	10-03	3	–
Åbenrå			2010	09-22	2	–
Åbenrå			2011	11-02	3	–
Åbenrå			2017	10-30	5	–
Ålborg	57.05	9.93	2010	09-30	–	–
Ålborg			2017	09-24	–	–
Århus N	56.18	10.20	2010	09-21	4	–
Århus N			2012	10-26	1	–
Århus S	56.14	10.20	2009	09-21	1	–
Århus S			2010	09-13	2	–
Års	56.80	9.52	2010	09-30	2	–
Års			2011	09-30	1	–
Års			2017	09-14	4	–