How far do adult Trichoptera travel in the landscape?

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Resumé

Vi anvendte lysfælder til at undersøge spredningen af voksne vårfluer (Trichoptera). De i alt 46 lysfælder var placeret, så de dækkede størstedelen af Danmark. Vi anvendte data for 71 arter, som forekommer i forskellige typer af vandløb, i enkelte tilfælde søer, men ikke i damme. Vi forudsatte, at individerne af de forskellige arter var ankommet fra den nærmest kendte ynglende population. Uanset at denne antagelse formodentlig ikke er helt korrekt, viste vores analyser en statistisk signifikant sammenhæng mellem afstand til nærmeste potentielle ynglepopulationer og forekomst i lysfælderne, når vi anvendte en negativ potensfunktion til at beskrive sammenhængen. Denne sammenhæng var ens for hanner og hunner. Vores undersøgelse tyder på, at spredningen af individerne primært er passiv og drevet af vinden. Trods dette var der ingen klare tegn på, at arternes vingestørrelse havde nogen indflydelse på spredningen. Vores undersøgelse dokumenterer spredningsafstande op til 80 km, og i nogle tilfælde over åbne havområder. Vi finder det sandsynligt, at nutidens åbne landbrugslandskab, som dækker 62% af Danmarks areal, udgør en mindre barriere for spredningen sammenlignet med det skovlandskab, som dominerede, før mennesket for alvor ryddede skov til landbrugsformål. Resultaterne tyder dog også på, at rekolonisering af restaurerede levesteder i vandløb vil være meget langsom for sjældne og ikke mindst nationalt uddøde arter.

Abstract

The present study used light traps to infer dispersal in adult Trichoptera, including 46 sites geographically covering most of Denmark. We included 71 of the recorded species inhabiting various running water habitats, and in some cases lakes. Further, we presupposed that the nearest known breeding habitat of these species reflected arrival in the traps. Although this assumption may not be entirely true, analyses show a significant negative power relation between occurrences in traps and distance to nearest potential population. Further, males and females showed similar patterns. Our study indicates that transport is mainly passive and driven by wind. There were, however, no clear signs that wing size influenced the travelled distance. This study documents travelled distances of up to 80 kilometres and in some cases over the open sea. The Danish anthropogenically affected landscape probably promoted dispersal. Thus, the open agricultural landscape, which covers 62% of the area, may constitute a minor barrier to dispersal, compared to forests that would have dominated naturally. However, the results also indicate that recolonisation of former and now restored running water habitats may be very slow for rare – and not least regionally extinct – species.

Introduction

Caddisflies (Trichoptera) are a predominantly aquatic insect order whose larvae inhabit almost all kinds of stagnant and lotic freshwaters, and some species even occur in brackish habitats (e.g. Mackay & Wiggins, 1979; Wiberg-Larsen, 2010). The group is morphologically as well as biologically diverse, and the larvae exploit numerous different microhabitats and food resources (Mackay & Wiggins, 1979). Trichoptera is a sister group to Lepidoptera and shares several characteristics with it. One of these is the ability of the larvae to produce silk; thus, Trichoptera larvae spin portable cases and fixed retreats or, in the case of predacious species, capture nets. This is probably the main reason why Trichoptera have been evolutionarily successful in the aquatic environment (Mackay & Wiggins, 1979). At global scale, at least 17,279 species were known in the beginning of November 2023 (Morse, 2023), and the actual number may well exceed 20,000. Whereas most adult Lepidoptera have mouthparts specialised for feeding on nectar, fruit juice or honeydew, relatively few adult Trichoptera have a haustellum designed to nectar or honeydew feeding (Crichton, 1957). The lifespan of adult Trichoptera varies from only a few days in non-feeding species to up to 4-6 months in feeding species (e.g. Svensson, 1972). Feeding on honeydew not only prolongs the life length but may also promote mating (Syrnikov et al., 2005). Most adult Trichoptera are generally regarded as relatively strong fliers (e.g. Johnson, 1969; Gullefors & Petersson, 1993; Graham et al., 2017). In comparison, many species of Lepidoptera have a much stronger capacity for flight, and some carry out regular long-distance migration (e.g. Walker, 1980; Lundmark, 2010; Stefanescu et al., 2013). Especially species of the Trichoptera families Hydropsychidae and Leptoceridae are regarded as excellent fliers; the males perform species-specific swarming to attract the females, often in connection with so-called landscape markers like trees, bushes, reeds or simply the water surface (e.g. Benz, 1975; Shinn & Long, 1986; Gullefors & Petersson, 1993). Like many other aquatic insects, adult Trichoptera tend to stay relatively close to the site where they lived as larvae. Thus, a predominant part of the adult populations occurs within only a few meters wide zone alongside the banks of ponds, lakes and different kinds of streams (e.g. Sode & Wiberg-Larsen, 1993; Petersen et al., 1999). However, part of a population disperses further from the larval habitat (Kovats et al., 1996), allowing colonising and exploiting other habitats and exchanging genes with other populations. Unlike for Odonata (e.g. Russell et al., 1998) and Lepidoptera (e.g. Stefanescu et al., 2013), there are no well-documented examples of caddisfly mass migration and only few examples of long-distance dispersal (but see Svensson, 1974; Kovats et al., 1996). Generally, documentation of the dispersal range of Trichoptera is sparse, although it is evident from several studies that dispersal is primarily short ranged and varies considerably among species (e.g. Göthberg, 1973; Crichton & Fisher, 1978; Sode & Wiberg-Larsen, 1993; Hughes et al., 1998; Petersen et al., 1999; Wilcock et al., 2001).

One method to infer Trichoptera dispersal is monitoring by malaise and light traps located strategically at different distances from a specific larval habitat (e.g. Sode & Wiberg-Larsen, 1993; Kovats et al., 1996; Petersen et al., 2004; Graham et al., 2017). Artificial light (especially with a high proportion of UV radiation) attracts most night-flying species (e.g. Larsson et al., 2016, and references in this). However, besides being highly influenced by weather, the methods suffer from obvious limitations due to the expectedly highly decreasing number of individuals recorded (e.g. due to dispersal in all directions) at a certain position with increasing distance from the emergence point. Recapture of radioisotope-labelled specimens carries the same limitations (e.g. Coutant, 1982). Additionally, performance of such controlled experiments is difficult and time consuming. Dispersal capacity has been inferred from the study of allozyme diversity and genetic markers in populations located at different distances from each other (e.g. Smith & Collier, 2001; Kelly et al., 2002; Wilcock et al., 2003). Although promising, the results can be difficult to interpret and relate primarily to dispersal over very long distances, and they are furthermore highly influenced by time scale. Other possibilities involve monitoring of the colonisation of newly established freshwater habitats or of habitats restored from a former deteriorated state and then relating the recorded larvae to the known small- and large-scale geographical occurrence of the species. This method may only indicate “minimum” dispersal distances, though. Thus, we presuppose that the observed individuals may have arrived from the nearest potential “inoculum” population although they may, in fact, have travelled from other sites than the nearest. Further, to be effective, the method demands routine long-time monitoring, which is highly time consuming.

A simple alternative is compilation of occasional light trapping of adults. Such trapping reflects the species composition in both near and distant larval habitats and the ability of the species to disperse (see above). Although many species arrive from unspecific larval habitats, i.e. typically many Limnephilidae from permanent or especially temporary ponds, some species are confined to more specific or even unique larval habitats. Knowing the exact position of these habitats makes it possible to infer distance to nearest potential inoculum. This is primarily possible for running water sites, typically located at a higher distance from each other compared to ponds, if the light trap is located relatively far from these. Thus, the method is of little value for pond dwelling species as these may occur everywhere. Of course, inferred dispersal data from single light traps may only have anecdotal and incidental character. Despite this, such data have been cited repeatedly in the scientific literature, although their value increases significantly when data from many light-trapping sites are compiled.

Consequently, the purpose of the present paper is to compile and analyse available data from light traps operated at a considerable number of Danish sites, aiming to contribute to the knowledge about how far adult Trichoptera may travel from their larval habitats.

Materials and methods

We used occurrences of adult Trichoptera from 46 light traps over a period of four decades. Data sets from these specific light traps were selected from a pool of more than 90 available light trap data sets. The criteria for the selection were: (i) the catches included species for which the closest potential larval habitat could be identified with certainty, and (ii) light trap positions were located more than 50 m from this site. The last criterion ensured that the data reflected adult dispersal beyond the riparian zone. This zone links the aquatic and terrestrial environment (for definition, see National Research Council, 2002), and its width varies depending on the type of water body. Overall, most populations of adult aquatic insects typically occur within a range of 20-30 m alongside the respective aquatic habitats (Collier & Smith, 1998; Petersen et al., 2004).

The 46 light trapping sites covered a considerable geographical range of Denmark (Fig. 1) and a wide spectrum of landscapes. Further, the position of the sites is in practice random in relation to Trichoptera larval habitats (see below). The sampled periods varied from one day

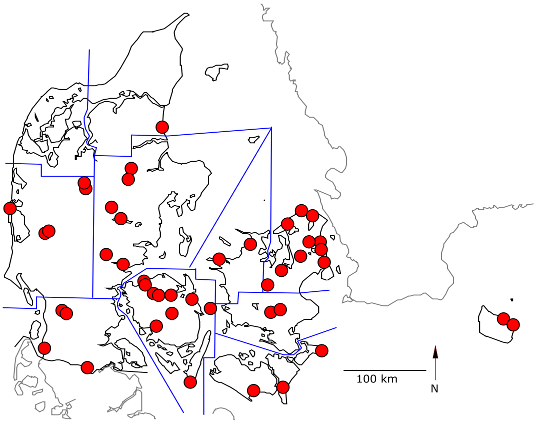

Figure 1. Positions of light traps with Trichoptera catches used in the present study.

to 7-8 months (within a specific year). Trichoptera was the target in seven traps (operated by the senior author), whereas the main target group was Lepidoptera for the rest, and Trichoptera therefore by-catches (and all specimens therefore not necessarily recognised and retained). The type of light traps varied (stationary or portable using generators or batteries), and the light sources were mercury lamps, UV-lamps, UV-tubes and other tubes predominantly emitting UV-radiation. In all, 18 different people and institutions were involved in the sampling (see Table 1). We identified all Trichoptera in the catches to species and sex and counted their numbers.

We calculated the distance from each light trap to its nearest potential inoculum population (DNPIP = Distance Nearest Potential Inoculum Population) for each species. We used topographic maps or aerial photos (Google Earth) and knowledge of the specific habitat requirements of the larvae (Table 2). Such linking was possible for species confined to running waters, scaling these from small to large, as assemblages of Danish Trichoptera are strongly related to stream size (Wiberg-Larsen et al., 2000). We were also able to infer DNPIP for a few species inhabiting specific larger and minor lakes. Further, we supplemented the documentation of DNPIP consulting the “National Monitoring Program for the Aquatic Environment and Nature” (NOVANA) that includes benthic macroinvertebrate data from more than 10,000 sites in streams and larger lakes. These data were primarily available from ODA, a national database (www.oda.dk).

We compiled data on the species-related forewing length from Malicky (2004).

In the analyses, we used occurrences (presence) of species, not numbers, for several reasons: (i) numbers in several cases did not represent the actual values in a catch (see above), (ii) catch per unit effort (i.e. number of “trapping” nights) differed considerably (i.e. from one night to several months), not reflecting the flight period of all (or even most) species, (iii) catchability of light traps differed due to differences in tubes and effect (see above), and (iv) differed in position in relation to e.g. vegetation and wind. These reservations also affect presence/absence data, but to a minor degree.

Another important reservation when interpreting occurrences in relation to DNPIP may be that a relation between occurrence and DNPIP simply reflects rarity of species. Thus, one might expect that common species would dominate closest to the traps. We analysed this issue, first calculating a simple abundance metric, combining for each species its (i) general distribution and (ii) local abundance. We calculated the general distribution of occurrences in the eleven Danish faunal districts (Wiberg-Larsen, 2010) as a simple ratio: number occurrences/11. Further, we scaled local abundance of the larvae (as a common value): very rare (0.2), rare (0.4), median (0.6), common (0.8), and very common (1.0). The scaling was based on a survey of NOVANA data (see above) and the senior authors unpublished data covering a period of four decades. Multiplying the two metrics, we obtained an abundance index (overall scaling 0-1). When finally correlating this index with DNPIP for all occurrences, we however found no relationship ($r = -0.065$, $P = 0.31$).

For statistics, we used regression analyses to determine the number of occurrences depending on DNPIP after first grouping occurrences according to the following eight distance intervals (in km): < 0.675, 0.675-1.25, 1.25-2.5, 2.5-5, 5-10, 10-20, 20-40, and 40-80. We carried out analyses for each sex separately.

Table 1. Trapping localities with adult Trichoptera records used in the present study, including people responsible for sampling, year of sampling, and geographical position of light traps. Regions: J – Jutland; Z – Zealand; F – Funen; LFM – Lolland, Falster & Møn; B –Bornholm.

Locality	Legit	Year	Latitude	Longitude
Aarhus University, Silkeborg (J)	Peter Wiberg-Larsen	2009	56.1564	9.5613
Allerød (Z)	Jens Lyngsøe	2002	55.8645	12.3606
Allindelille Fredskov (Z)	Knud Bech m.fl.	2013	55.5159	11.7657
Annettevej, Vig (Z)	Søren Birkholm Hansen	1976-1982	55.8520	11.5274
Arboretet, Hørsholm (Z)	Erik Steen Larsen	2019	55.8664	12.5077
Borris, NW (J)	Uffe Terndrup	2014	55.9489	8.6658
Borris, Rabæk (J)	Uffe Terndrup	2014	55.9217	8.6219
Brandbjerg Sønderskov (J)	Benny Steen Larsen	1998	55.7641	9.4826
Bøtø (LFM)	Bjarne Skule	2006	54.6760	11.9607
Emmerlev Klev (J)	Uffe Terndrup	2014	54.9863	8.6645
Errindlev Havn (LFM)	Per Stadel Nielsen	2010	54.6466	11.5477
Eskildstrup (Z)	Jørgen Rosschou	2002	55.5297	10.0623
Fogense Pynt (F)	Otto Buhl	2007	55.5547	10.0355
Freltofte (F)	Peter Wiberg-Larsen	1980	55.2836	10.4236
Frøslev Mose (J)	Benny Steen Larsen	1999	54.8268	9.2500
Fussing Vandmølle (J)	Per Stadel Nielsen	2011	56.4802	9.8324
Gevninge (Z)	Per Stadel Nielsen	2014-2015	55.6419	11.9616
Gilbjerg Hoved (Z)	Flemming Vilhelmsen	2007	56.1219	12.2699
Gl. Ry (J)	Erik Dylmer	2016	56.0698	9.6944
Grisby (B)	Morten Top Jensen	2001	55.1194	15.1464
Gulstav Mose (F)	Per Stadel Nielsen	2013	54.7287	10.6879
Havneby, Rømø (J)	Uffe Terndrup	2013	56.3934	9.7931
Havrehed Sø (F)	Peter Wiberg-Larsen	1992	55.4464	10.1938
Holmegårds Mose (Z)	Per Stadel Nielsen	2001	55.2986	11.8066
Høstemark Skov, SE (J)	Uffe Terndrup	2013	56.8247	10.2694
Håstrup (F)	Ebbe Munk Andersen	1984	55.1819	10.2121
Karup, local bakery (J)	[Karup Bakery employee]	2004	56.3075	9.1776
Lundebro, Risinge (F)	Jens Holmkvist	2007	55.4098	10.7057
Lysholm, Haslev (Z)	Benny Steen Larsen	2009	55.3205	11.9337
Mandemarke (LFM)	Ole Karsholt	2017-2018	54.9671	12.4913
Rabis Bæk, OS Rabis Bro (J)	Peter Wiberg-Larsen	2021	56.3462	9.1631
Ravnholm (Z)	Per Stadel Nielsen	2006	55.8042	12.5119
Rue Hed, Morud (F)	Peter Wiberg-Larsen	1995	55.4457	10.2311
Rusland (Z)	Bjarne Skule	2020	56.0854	12.4027
Saltuna (B)	Morten Top Jensen	2001	55.1747	15.0272
Sandet, Asserbo (Z)	Per Stadel Nielsen	2019	56.0071	12.0487
Sjapmose (J)	Peter Wiberg-Larsen	1987	55.2898	8.9125
Sprogø (F)	Otto Buhl	2005	55.3302	10.9652
Stensbæk Plt. (J)	Peter Wiberg-Larsen	1987	55.2709	8.9474
Stige (F)	Jørgen Rosschou	2002	55.4413	10.4079
Stige, Odense (F)	Otto Buhl	2010	55.4359	10.4076
Søndervig (J)	Per Stadel Nielsen	2011	56.1198	8.1132
Vejle Fjord, north side (J)	Biowide	2014	55.6906	9.7361
Veksø (Z)	Bjarne Skule	2006	55.7532	12.2327
Vollerup Overdrev (Z)	Per Stadel Nielsen	2019	55.7325	11.0839
ZMUC, Copenhagen, roof (Z)	Ole Karsholt	1994-1995	55.7026	12.5594

Table 2. Distances (km) to nearest potential inoculum populations (DNPIP) for adult Trichoptera species recorded in 46 light traps (locations: see Fig. 1 and Table 1). N = number of DNPIP occurrences. Larval habitat for each species: SPR – spring or spring brook; ST – stream/river; LA – lake; PO –pond.

Species	Family	Males (m)/ Females (f)	DNPIP – range (km)	N	Larval habitat
Ernodes articularis	Beraeidae	1f	0,33	1	SPR
Brachycentrus maculatus	Brachycentridae	928m/268f	0,6-8,6	4	ST
Ecnomus tenellus	Ecnomidae	5f	0,40-1,16	2	LA
Agapetus ochripes	Glossosomatidae	2m/2f	7,25-10,40	3	ST
Glossosoma boltoni	Glossosomatidae	18m/5f	0,60-0,82	2	ST
Goera pilosa	Goeridae	12m/18f	0,35-34	10	ST/LA
Silo nigricornis	Goeridae	2m/1f	0,7-4,06	3	ST
Silo pallipes	Goeridae	6m/12f	0,50-4,06	6	ST
Cheumatopsyche lepida	Hydropsychidae	9f	9,2-35	2	ST
Hydropsyche angustipennis	Hydropsychidae	17m/110f	0,50-7,0	15	ST
Hydropsyche bulgaromanorum	Hydropsychidae	1m	80	1	ST
Hydropsyche contubernalis	Hydropsychidae	1m	65	1	ST
Hydropsyche pellucidula	Hydropsychidae	6m/256f	0,80-50	11	ST
Hydropsyche saxonica	Hydropsychidae	1m	4,06	1	ST
Hydropsyche siltalai	Hydropsychidae	77m/299f	0,35-15,5	20	ST
Agraylea multipunctata	Hydroptilidae	178m/782f	0,40-5,40	2	LA
Agraylea sexmaculata	Hydroptilidae	9f	0,4	1	LA
Hydroptila cornuta	Hydroptilidae	1f	35	1	ST
Hydroptila sparsa	Hydroptilidae	2m/8f	0,40-8,8	7	ST
Ithytrichia lamellaris	Hydroptilidae	1m	0,8	1	ST
Orthotrichia costalis	Hydroptilidae	1f	0,4	1	LA
Crunoecia irrorata	Lepidostomatidae	1m	1,7	1	SPR
Lepidostoma hirtum	Lepidostomatidae	24m/36f	0,60-25	12	ST/LA
Adicella reducta	Leptoceridae	1f	0,8	1	ST
Athripsodes albifrons	Leptoceridae	2m/9f	0,40-4,3	5	ST
Athripsodes aterrimus	Leptoceridae	2f	0,4	1	LA/PO
Athripsodes cinereus	Leptoceridae	10f	0,4	1	ST/LA
Ceraclea albimacula	Leptoceridae	1m/75f	0,40-3,3	4	ST
Ceraclea annulicornis	Leptoceridae	2f	0,4	1	ST/LA
Ceraclea dissimilis	Leptoceridae	1m/177f	0,40-4,3	4	ST/LA
Ceraclea fulva	Leptoceridae	0m/2f	0,40-3,3	2	ST/LA
Ceraclea nigronervosa	Leptoceridae	1m/0f	0,8	1	ST
Leptocerus tineiformis	Leptoceridae	759m/2924f	5,4	1	LA/PO
Mystacides azureus	Leptoceridae	1m/16f	1,25-8,6	4	ST
Mystacides longicornis	Leptoceridae	12f	0,40-1,16	2	LA
Oecetis lacustris	Leptoceridae	19f	0,40-1,16	2	LA
Oecetis ochracea	Leptoceridae	40f	0,4	1	ST/LA
Ylodes simulans	Leptoceridae	65m/73f	0,60-1,0	3	ST
Anabolia furcata	Limnephilidae	1m/0f	0,3	1	ST/LA
Anabolia nervosa	Limnephilidae	12m/5f	0,60-0,80	2	ST/LA
Chaetopteryx villosa	Limnephilidae	2f	0,1	1	ST
Ecclisopteryx dalecarlica	Limnephilidae	1f	0,22	1	ST
Halesus radiatus	Limnephilidae	504m/562f	0,22-9,5	12	ST
Halesus tessellatus	Limnephilidae	503m/98f	0,30-2,17	5	ST
Ironoquia dubia	Limnephilidae	2m	1,5	1	ST
Limnephilus extricatus	Limnephilidae	2m/3f	0,35-1,95	3	ST
Limnephilus fuscicornis	Limnephilidae	15m/4f	0,80-1,15	2	ST

Table 2 (cont.).

Species	**Family**	**Males (m)/ Females (f)**	**DNPIP – range (km)**	**N**	**Larval habitat**
Limnephilus lunatus	Limnephilidae	718m/265f	0,35-1,95	6	ST
Micropterna lateralis	Limnephilidae	12m/7f	0,35-0,70	4	ST
Micropterna sequax	Limnephilidae	115m/67f	0,35-5,6	7	ST
Potamophylax cingulatus	Limnephilidae	14m/13f	0,35-0,50	3	ST
Potamophylax latipennis	Limnephilidae	15m/37f	0,80-2,10	3	ST
Potamophylax nigricornis	Limnephilidae	4m/2f	0,35-13,6	3	ST
Stenophylax permistus	Limnephilidae	14m/4f	1,3	1	ST
Agrypnia varia	Phryganeidae	1f	0,4	1	LA
Phryganea bipunctata	Phryganeidae	9m/9f	3,3	1	ST
Phryganea grandis	Phryganeidae	8f	0,4	1	LA/PO
Cyrnus crenaticornis	Polycentropodidae	81m/47f	5,4	1	LA/PO
Neureclipsis bimaculata	Polycentropodidae	103f	0,4	1	ST
Plectrocnemia brevis	Polycentropodidae	18m/2f	0,5	1	SPR
Plectrocnemia conspersa	Polycentropodidae	67m/30f	0,35-5,6	9	ST
Polycentropus flavomaculatus	Polycentropodidae	5m/15f	0,40-8,20	7	ST/LA
Polycentropus irroratus	Polycentropodidae	9m/24f	0,40-7,2	6	ST
Lype reducta	Psychomyiidae	1f	1,11	1	ST
Psychomyia pusilla	Psychomyiidae	14m/79f	0,80-35	3	ST
Tinodes pallidulus	Psychomyiidae	3f	0,50-1,70	2	ST
Tinodes unicolor	Psychomyiidae	1f	0,65	1	ST
Tinodes waeneri	Psychomyiidae	1m/5f	0,40-5,4	2	LA
Rhyacophila fasciata	Rhyacophilidae	29m/9f	0,35-0,50	2	ST
Rhyacophila nubila	Rhyacophilidae	162m/23f	0,60-1,50	4	ST
Sericostoma personatum	Sericostomatidae	1f	0,35	1	ST
∑ species: 71	∑ families: 15	∑ 4433m/6618f		∑ 240	

Further, we analysed dependence of distance on size of the adults (using length of forewing as a convenient proxy, although this does not take body weight into account) based on the same grouping as above, although the last three groups were pooled into one (10-80 km) to obtain enough data in all groups. Differences in forewing length were analysed using Kruskal-Wallis test due to non-normality of the data, and as it was impossible to transform data by conventional formulas to obtain normality. Significance was decided at $P < 0.05$. Further, we tested the groups pairwise using Mann-Whitney U-test, using Holm correction to estimate the exact level of significance (Holm, 1979).

In addition, we similarly analysed dependence on wing morphology, in case Aspect Ratio (AR) and Relative Wing Area (RWA) according to Müller-Peddinghaus (2011):

$$AR = \text{wing span}^2 \cdot \text{total wing area}^{-1} \quad \text{and}$$

$$RWA = \text{total wing area} \cdot \text{forewing length}^{-1}$$

All values were taken from table 3.4 in Müller-Peddinghaus (2011). We tested the same groups as for forewing length.

SigmaPlot 13 was used for graphic presentations and statistical analyses.

Results

Using the 46 sampling sites, we established a data set with 240 records of long-distance dispersal (i.e. more than 50 m from DNPIP), including 71 species representing 15 families (Table 2). Of these, the majority (93%) inhabit different types of running waters (springs, brooks, streams and rivers) or the littoral zone of larger lakes (5%). The remaining species (2%) are primarily confined to lakes and ponds, only rarely occurring in running water. Full documentation of the records is available from the senior author upon request.

Generally, there were more records of females (190) than of males (129). The estimated DNPIP varied from 0.1 to 80 km with mean and median values of 3.9 and 1.2 km, respectively. The number of records correlated with DNPIP, following a (negative) power function (Fig. 2), for both males and females. The correlations were significant for both sexes (males $r^2 = 0.80$, females $r^2 = 0.74$; $P \leq 0.01$), and the patterns overall appeared identical for the two sexes.

We found an overall significant, but weak, difference in the length of forewings between the grouped DNPIP (Kruskal-Wallis test), for both males ($P = 0.048$) and females ($P = 0.026$). Further, pairwise comparisons of the groups only found a significant difference for female forewing length between the distances 1.25-2.5 and 10-40 km (Mann-Whitney U-test, P =

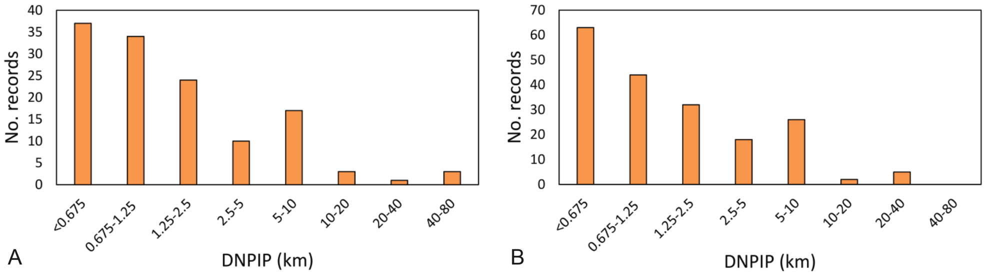

Figure 2. Relationship between number of records, NoR (no. occurrences) of adult Trichoptera in light traps (see Fig. 1) and the distance (km) to nearest potential inoculum population (DNPIP) of 71 species. The number of records is grouped for eight distance intervals of DNPIP. – A: males; relationship given by the equation $NoR = 25.578\ DNPIP^{-0.653}$. – B: females; relationship given by the equation $NoR = 38.109\ DNPIP^{-0.657}$.

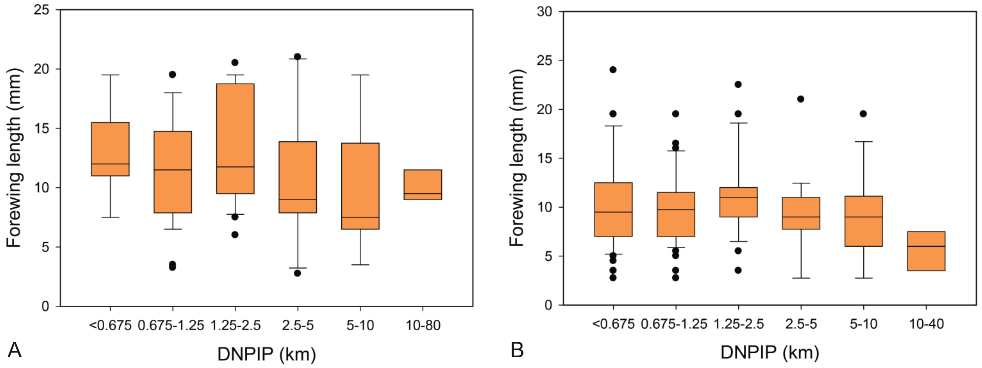

Figure 3. Box-Whiskers plot (median, 25 & 75% quartiles, 0 & 100 % percentiles, and outliers) of forewing length of adult Trichoptera in light traps (see fig. 1) in relation distance (km) to nearest potential inoculum population (DNPIP), including data for 71 species. Forewing lengths shown for 6 distance intervals of DNPIP. – A: males. – B: females.

0.003), the length of forewings being smaller for the 10-40 km group of species. Thus overall, the distribution of the forewing length of males and females was unrelated to minimum dispersal distance (Fig. 3).

Similar tests on the wing morphology characteristics AR and RWA showed no significant differences between the groups of minimum dispersal distances (Kruskal-Wallis test, P = 0.22-0.45; results not shown).

Of the species recorded, 24 (34%) representing 10 families, showed DNPIP values of 5 km or more (Table 2), without difference between sexes. Overall, the number of species decreased with DNPIP. Thus, within DNPIP ranges < 1 km, 1-2 km, 2-5 km, 5-10 km, 10-20 km, and > 20 km, we found 57, 32, 21, 21, 5, and 9 species, respectively, following a negative power function ($r^2 = 0.95$, $P < 0.001$). Among the long-distance (> 5 km) dispersing families, especially Hydropsychidae (88%) and Leptoceridae (65%) were well represented compared to their national species pool.

Going into details, one Hydropsychidae, *Hydropsyche bulgaromanorum* (1 male), recorded at the south coast of Lolland, represents the first record in Denmark ever and does not have obvious larval habitats within the Danish borders. Nearest potential larval habitats are major rivers located near the German coast (Berlin & Thiele, 2012), alternatively more distant rivers near the Polish coast (Czachorowski & Serafin, 2004). Similar oversea dispersal from the south, in this case 65 km, likely occurred for a single *H. contubernalis* male, trapped on South Falster. This species has Danish populations in Jutland and on Zealand, but these are located 150-250 km away, and dispersal from there is regarded unlikely (due to unfavourable wind direction before the incident).

Oversea dispersal of three other species (*Hydropsyche siltalai*, *Goera pilosa*, and *Potamophylax nigricornis*) must also have taken place, as these were trapped on the tiny island of Sprogø, located mid-way between the coasts of Funen and Zealand. As there are no larval habitats of these running water species on Sprogø, the individuals must have dispersed from habitats on adjacent islands. Furthermore, one specimen of *G. pilosa* trapped on south Langeland, where the species does not occur, may have dispersed over the sea from the nearest potential larval site on Fehmarn (northern Germany).

Discussion

This study clearly confirms the existence of long-distance adult dispersal of Trichoptera over a range of at least 0.1 to 80 km. Further, this dispersal declines with distance following a negative power function. Overall, this is in accordance with Kovats et al. (1996) who over a range of 1-5 km found that the number of Hydropsychidae declined with distance from riverbanks applying a negative log-log^2 model. However, comparable studies are few and of anecdotic character. Malicky (1987), using the same approach as in our study, reported dispersal of 3-5 km for *Micropterna* species inhabiting temporary larval habitats, but suggested that their maximum dispersal might be several dozens of kilometres. Further support of long-distance dispersal comes from interpretation of allozyme diversity and population genetic structure, although such dispersal is measured over a considerably larger time scale than in the present study. Nevertheless, Wilcock et al. (2001, 2003) suggest frequent dispersal of *Plectrocnemia conspersa* over tens of kilometres, more than found in the present study, while Smith & Collier (2001) point at maximum dispersal in the range of ten kilometres for *Orthopsyche fimbriata*. However, due to the limited number of studies, any extrapolation is precarious.

Our study further shows a significant decline in number of recorded species with increasing DNPIP, also following a negative power function. This is expected, as the number of recorded dispersals in the light traps must be positively correlated with the number of recorded species. We are not aware of studies that may place our results in perspective.

Interpretation of the results of the present study built on the premise that adult Trichoptera have reached the light traps from the nearest identified larval habitat. This is, of course, not necessarily true, as individuals may have originated from habitats further away. However, we expect that the general pattern observed is still overall correct. Thus, the decline in occurrence and number over long distances is consistent with and complements several studies of short-range dispersal (< 80 m from the larval habitat) for Trichoptera and other aquatic orders, like Ephemeroptera and Plecoptera (e.g. Sode & Wiberg-Larsen, 1993; Griffith et al., 1998; Collier & Smith, 1998; Petersen et al., 2004). Further, these orders generally follow a negative exponential or logarithmic function. However, Graham et al. (2017), studying lateral dispersal in streams in New Zealand, found most Trichoptera species in almost equal numbers in light traps located at different distances up to1500 metres from the stream, although some species did show a decline with distance.

Our data set primarily included species from running waters, with fewer from the littoral zone of larger lakes. Thus, we omitted species inhabiting small lentic habitats like ponds and pools, especially the ones that regularly dry out during summer. These are expected to show a higher capacity of dispersal than the species included in our study (e.g. Svensson, 1974; Müller-Peddinghaus, 2011). Representatives of Limnephilidae are especially adapted to such dispersal as they are long-lived and feed on nectar (see below), and the males search for females that excrete attractant pheromones (e.g. Houghton, 2013). However, the exact dispersal potential of such species is practically unknown (but see Malicky 1987).

Fundamentally, aerial transport of flying insects depends on two factors, (i) active flight by wing movements and (ii) passive transport by wind. Active flight depends on the flight morphological characteristics of the species such as wing length, total wing area, wing area to body size ratios and, not at least, muscle strength, establishing a relationship between morphology and function (Wainright, 1994). Once in the air, sufficiently strong wings/wind may carry an insect over considerable distances, and under such conditions, wing morphology may play an important role. Mayflies (Ephemeroptera) seem to be especially well suited for passive wind transport due to their sail-formed wings with many folds like the sails of a yacht (Smith & Collier, 2006). In addition to the above-mentioned factors, weather conditions (most of all air temperature) influence the activity patterns of adult Trichoptera and, thus, also their flight (Waringer, 1991; Wiberg-Larsen, 1996).

Hoffsten (2004) inferred differences in the dispersal and flight ability of 17 lotic and lentic Trichoptera species from 10 families, linking morphology and site occupancy, the latter acting as a proxy for dispersal. He found evidence that characteristics like total body mass, relative thorax mass, relative wing area and aspect ratio of forewing and hindwing combined were all associated with site occupancy. Our study, however, which included considerably more families and species, did not reveal significant indications, that long-range dispersal depends on wing morphology, although relatively smaller females tended to disperse further away than larger ones. Accordingly, Graham et al. (2017) found no difference in dispersal distance among Trichoptera families, covering a large spectrum of sizes.

In the context of adaptations to active flight and passive aerial transport, the behaviour of adult insects may be an important factor. The males of especially the Trichoptera families Philopotamidae, Polycentropididae, Psychomyiidae, Hydropsychidae, Goeridae, and Leptoceridae carry out swarming as part of their mating (e.g. Benz, 1975; Becker, 1987; Gullefors & Petersson, 1993; Wiberg-Larsen, 1995; Müller-Peddinghaus, 2011), during which these and the attracted females may easily be caught by sudden strong winds. However, there are also indications that females of Hydropsychidae and Leptoceridae are active dispersers, and consequently occur more often in light traps than males (e.g. Wiberg-Larsen & Karsholt, 1999; Wiberg-Larsen, unpublished data).

Data from the Danish Meteorological Institute support the importance of facilitated wind transport for the longest dispersing adult Trichoptera in the present study. Thus, the specimens of *H. bulgaromanorum* and *H. contubernalis* trapped at the south coasts of Lolland and Falster after days with strong southern winds (> 10 m/s) combined with air temperatures up to 30°C undoubtedly arrived oversea from northern Germany. Further, the two *Hydropsyche* species likely had very large populations in the major rivers from which they must have dispersed and, thus, a higher chance of being captured when dispersing (see below).

Further, at first strong eastern, then strong northern winds occurred prior to the trapping of *C. lepida*, *P. pusilla*, and *H. cornuta* at Søndervig on the west coast of Jutland (Tables 1 & 2). This supports the conclusion that the individuals arrived from the nearest known habitat, which is Storå at Holstebro (35 km from light trap). Additionally, *H. siltalai*, *G. pilosa* (Fig. 4A), and *P. nigricornis* trapped on the little island Sprogø must have dispersed from habitats on the island of Funen facilitated by relatively strong westerly winds combined with air temperatures of up to 20-25°C. The high temperatures no doubt favoured flight activity, being positively correlated with air temperature (Crichton, 1960; Nimmo, 1966; Andersen, 1978; Waringer, 1991; Wiberg-Larsen, 1996; Wiberg-Larsen & Karsholt, 1999). In a study of Danubian river Trichoptera, Waringer (1991) further demonstrated that light trap catches primarily correlated positively with night maximum air temperature (just after dusk), which was more important than wind speed and precipitation.

Figure 4. Two long-dispersing species in the present study. – A: *Goera pilosa* breeds in middle-sized to large streams and at shores of larger lakes, the larvae inhabiting wind-exposed stony/gravelly substrates. – B: *Lepidostoma hirtum* breeds in large streams and occasionally in large lakes. Larvae inhabit sandy bottoms with accumulation of coarse dead organic plant material. (Photos: Per Stadel Nielsen).

Other factors may affect aerial dispersal. The longer adults live, the higher is the chance of long-distance dispersal. Life expectancy of adult Trichoptera varies considerably from few days to up to 4-6 months (e.g. Svensson, 1974). In the latter case, species have a summer diapause and no doubt feed. According to Crichton (1957), adult Trichoptera have a protrusible haustellum, derived from the hypopharynx, by which they take up fluid. Thus, they are capable of drinking water, but some species also feed regularly on nectar or honeydew. However, direct studies of feeding are few, and most knowledge is anecdotal. For example, Frings & Frings (1956) compiled scattered feeding records from various authors and additionally described the presence of sucrose sensitive chemoreceptors on the ventral surfaces of all the tarsi, the tips of the maxillary and labial palpi and the haustellum. Petersson & Hasselrot (1994) found that the males and females of the psychomyiid *Tinodes waeneri* ingested nectar from open nectary flowers located at a lakeshore, i.e. close to the larval habitat, and suggested that adults mainly used this energy supply for mechanical activities, including flying. Feeding on sugar solutions promoted longevity and induced mating in *Rhyacophila nubila*, *Hydropsyche angustipennis*, and *Anabolia laevis* (Syrnikov et al., 2005). Moreover, Hoffmann (1997) documented that female *Lepidostoma basale* produced more eggs and lived longer when feeding on honey solution in the laboratory, and he found evidence for their feeding on aphid honeydew in the wild. In addition, there are scattered records of adults of *Limnephilus affinis*, *L. flavicornis*, *L. luridus*, *L. stigma*, *Grammotaulius nigropunctatus*, *Micropterna sequax* (Limnephilidae), and *Agrypnia varia* (Phryganeidae) attracted by and feeding on sugar baits intended for Lepidoptera (Findal, 1931; Andersen, 1983). We may add *Stenophylax permistus* from the present study to the list of sugar feeders (Fig. 5). However, feeding may likely be a more general phenomenon than reported and may include more species in our study.

The present study was carried out in the Danish landscape that is highly influenced by human activities. Thus, 62% is used for agricultural activities, whereas roads and built-up areas account for 10% (see https://www.eea.europa.eu/soer/2010/countries/dk/land-use-state-and-impacts-denmark). Heath and meadows account for 9%, whereas forest, that naturally dominated following the latest glacial period, only covers 13%. The resulting overall open landscape probably makes aerial dispersal easier, contrary to a landscape with a higher proportion of forests acting as a kind of filter/barrier. Smith & Collier (2006) concluded that open country promoted the dispersal of short-lived and weak flying Trichoptera, whereas forests might act as a physical barrier for dispersal, further dampening the effect of winds. Similarly, Graham et al. (2017) suggested that Trichoptera dispersed farther in open than in

Figure 5. The Limnephilid *Stenophylax permistus* feeding on “thin” sugar solution. Feeding on sugar permit individuals to live for several months prior to mating and egg-laying in autumn. (Photo: Per Stadel Nielsen).

forested landscapes. Accordingly, Briers et al. (2002) found that the lateral dispersal from a stream of the plecopterans *Amphinemura sulcicollis*, *Leuctra fusca*, and *L. nigra* decreased with increasing forest cover in the riparian zone.

Urban areas with high concentrations of artificial light may influence the distribution of adult Trichoptera (Larsson et al., 2016). Consequently, the amount of adult Trichoptera was high during nighttime in a light trap operated 17.5 m above the ground in the city of Copenhagen (Wiberg-Larsen & Karsholt 1999), indicating high dispersal probably facilitated by elevated air temperatures due to heat accumulation during daytime. However, cities may also act as a giant light trap due to their illuminated roads (e.g. Brehm et al., 2021).

Long distance migrations are recorded in Lepidoptera and Odonata, insect orders encompassing strong flying species. Some Lepidoptera are seasonal migrants and travel regularly from their breeding sites to other areas and back again (Eitschberger et al., 1991); others, emigrants, travel from their original habitats but do not return. This last behaviour may be uncommon and induced by, for instance, over-exploitation of food resources (larvae feeding on specific plant species) and thus an act of searching for new resources (e.g. Stefanescu, 1997). Global warming apparently promotes migration of both orders (Sparks et al., 2007; Grewe et al., 2013). Although Trichoptera is a sister group to Lepidoptera, there are apparently no examples of representatives performing annual/regular long-distance migration. The present study did not trace any such migration either. Trichoptera larvae typically feed on microorganisms associated with decaying plant material, micro-algae, and animal prey, and they only rarely feed on fresh aquatic higher plants. In practice, most species are food generalists and feeding on “whatever is available” (Thorp & Rogers, 2011). This indicates that food resources are not likely to be exhausted. Finally, migrating Lepidoptera are considerably better flyers than Trichoptera and able to undertake longer flights with the possibility to tank up energy during their travel/energy on the way.

Because of the high human impact on Danish nature, many aquatic habitats have disappeared or been severely altered. Thus, most streams are regulated, physically managed by dredging and weed cutting, and to a certain extent polluted by sewage, pesticides etc. (e.g. Wiberg-Larsen et al., 2012). Although the water quality has improved considerably over the last two to three decades due to better treatment of urban wastewater, recolonisation by pollution-sensitive macroinvertebrate taxa is delayed, because the number of locations from where species may disperse is too small and the distance too far (Wiberg-Larsen et al., 2012). Unpublished data by Wiberg-Larsen show, that Trichoptera females of 60 Danish species (from 19 families), produce up to 800 eggs each, with a mean of 275 eggs. Although the potential dispersal is, as described in the present study, not the same as successful recolonisation, it can be regarded as a proxy for this process as, in theory, only a few successful females are needed to start new populations. Studies of dispersal within the riparian zone indicate that only approx. 10% of Trichoptera populations disperse more than 50 m from their breeding habitat (Briers et al., 2002). If dispersal curves from the present studies are ‘added’, then just 2% of these populations may e.g. disperse 20 km from the breeding site as potential colonisers. However, if colonising females carry fertilised eggs, mortality until these eggs are deposited and during the following life stages until the next eggs are deposited at the ‘new’ site must be considered. Unfortunately, studies of mortality during all these stages are few. Enders & Wagner (1996) found an adult mortality as high as 80% for *Apatania fimbiata*, ascribing this to high mortality during the egg stage, whereas Boonstra et al. (2018)

found approx. 75% mortality during the larval stages for *Holocentropus insignis*. Consequently, successful colonisation of very distant suitable habitats is problematic, and it may take rare species many decades to recolonise previously degraded habitats that were restored and made suitable for them. This is certainly the case for running water species like *Oxyethira frici*, *O. tristella* and *Micrasema setiferum* that were known from only 1-2 Danish sites and are now extinct (Wiberg-Larsen, 2019), their nearest known populations in nearby countries being located at least 250-400 kilometres away.

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