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Original Article

Morphology-based classification of the flying capacities of aquatic insects: A first attempt

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Abstract

Flight is a key feature of the reproduction and dispersal of emerging aquatic insects. However, morphological measurements of insect flight are mostly available for terrestrial taxa and dragonflies, while aquatic insects have been poorly investigated. We analyzed 7 flight-related morphological parameters of 32 taxa belonging to 5 orders of emerging aquatic insects (Ephemeroptera, Trichoptera, Plecoptera, Diptera, and Megaloptera) with different life history traits related to flight (dispersal strategy, voltinism, adult lifespan, and swarming behavior). After correcting for allometry, we used an a priori-free approach to cluster the individuals according to their flight-related morphology. Then, we explored the levels of agreement between these clusters, taxonomy, and several life history traits of the taxa. All orders were scattered among several clusters, suggesting a large range of flight capacities, particularly for Diptera. We found swarming taxa in each cluster, showing that morphological adaptations to swarming are not identical in all aquatic insects. The clusters did not match the expected dispersal capacity of the taxa as derived from the literature or databases. Heavy wide-winged insects notably gathered taxa traditionally described as good or weak dispersers. Flight capacities based on morphology partly matched with the taxonomy and life-history traits of aquatic insect imagoes. Other parameters such as flight propensity, energy stores, and wing kinematics should help refine their flying and dispersal capacity.

Key words: allometry, dispersal, flight, freshwater, wing.

Aquatic insects are found in all freshwater ecosystems (rivers, streams, lakes, temporary ponds, etc.). They represent more than 100,000 species all over the world and belong to 12 orders (Dijkstra et al. 2014). Among orders, Ephemeroptera (mayfly), Plecoptera (stonefly), Trichoptera (caddisfly)—often referred to as EPT, Odonata and Megaloptera are almost entirely aquatic, whereas only a small number of Hymenoptera, Lepidoptera, and Neuroptera have an aquatic life stage (Dijkstra et al. 2014). Diptera makes up the most diverse order, including nearly 46,000 species belonging to 41 families (Adler and Courtney 2019) and truly aquatic Diptera (Chironomidae) represent more than 4,000 known species (Ferrington 2007). Aquatic insects spend at least one stage of their life cycle in the water, and most species exhibit aquatic larvae that emerge from the water as winged adults. Literature about the larvae of aquatic insects is abundant because they are used as bioindicators (Montes et al. 2012; Cortelezzi et al. 2020), whereas literature about the adult stage is scarce. Almost all imagoes (i.e., the last stage of the life cycle of insects—the adult stage) of aquatic species have wings and can fly (Nilsson 1996). Intensive research has been carried out about how insects fly (Ellington 1999; Dudley 2002; Harbig 2017). Flight relies on a number of different capacities: flight speed, maneuverability (the space needed to change the flight path while flying at a fixed speed), and endurance and agility (the speed at which an individual can change its flight trajectory). However, apart from Odonata, the distances that aquatic insects are able to fly are poorly known. Studies have often concluded that Plecoptera and Ephemeroptera stay close to the water and are "weak" flyers, while Trichoptera fly farther (Muehlbauer et al. 2014) and are considered as "good" flyers. The "weak/good flyer" dichotomy simplifies the complexity of insect flight and is not necessarily based on the real flight capacities of the insects.

Flight is particularly crucial for aquatic insects during two phases of their life cycle (Dudley 2002), namely mating and dispersal (Peckarsky et al. 2002; Nowinszky et al. 2014; Ptatscheck et al. 2020). Mating is highly dependent on the flight capacity. For example, male chironomids, most mayflies, and some caddisfly species fly in large groups to attract females (i.e., they swarm (Sullivan 1981)). In this study, we assumed that swarming required the following flight capacities: endurance, agility, and maneuverability. Dispersal is defined as the movement of individuals from one population to another, leading to successful reproduction in the new population and potential gene flow (Raffard et al. 2021). Aerial dispersal requires the capacity to fly long distances (i.e., endurance). Adult insects also tend to fly upstream to compensate for the downstream drifting of the larvae (i.e., longitudinal dispersal, also known as the freshwater insect colonization cycle (Müller 1982)). Although this trend does not seem to apply to all contexts (May 2019), studies on longitudinal

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dispersal have provided insights into the flight behavior of aquatic insects (Didham et al. 2012). More recent studies have focused on their lateral dispersal (i.e., dispersal away from a watercourse, as opposed to longitudinal dispersal). Lateral dispersal provides a better estimate of the distance that aquatic insects can fly from their water source than longitudinal dispersal does (Muehlbauer et al. 2014; Peredo Arce et al. 2021; Raitif et al. 2022; Gerber et al. 2023). Other characteristics, such as flight propensity—take-off capacity and its frequency (Asplen 2018)—are linked to the dispersal capacity. Insects that often take off are more likely to disperse, regardless of their flight capacities (Steyn et al. 2016).

Among the morphological characteristics studied in relation to dispersal, size is closely linked to the flight capabilities because aerodynamic forces change with scale. For example, aerodynamic constraints result in the vast majority of insects having to flap their wings to maintain flight; only the larger insects such as butterflies and dragonflies can glide briefly (Bhat et al. 2019). Moreover, wingbeat frequency is known to be closely related to size (Tercel et al. 2018). Dispersal strategies could also be indirectly affected by body size. Larger species can fly faster than the wind speed (Compton 2002) and thus “choose” their flight direction. These species—mainly EPT in our study—can be considered as active dispersers. Conversely, light species (e.g., Chironomidae) are more easily blown away by wind (Peredo Arce et al. 2021) and are most often considered as passive dispersers. In other words, climatic conditions may facilitate take-off depending on the species (Reynolds 2013).

Size is an interesting characteristic in the study of dispersal, along with other morphological characteristics showed to be key components for understanding insect aerodynamics and flight mechanisms (Ellington 1984; Wootton 1992; Bhat et al. 2019). In this context, we aimed to 1) check for allometric relationships between morphological flight parameters and insect body length, 2) test whether morphological flight parameters were related to taxonomy, and 3) analyze the relationships between life-history traits (dispersal affinity, potential number of generations *per* year, adult lifespan and swarming behavior) and morphological flight parameters. More precisely, in 32 different taxa belonging to 5 orders of emerging aquatic insects (Ephemeroptera, Trichoptera, Plecoptera, Diptera, and Megaloptera), and encompassing a wide range of body sizes (from small Chironomidae to large Plecoptera), we selected 5 raw parameters (i.e., dry body mass, body length, thorax width, forewing length (FL), and total wing area) and two wing shape parameters based on raw parameter measurements (i.e., the radius of the second moment of wing area and the aspect ratio (AR)). Increased wing area leads to increased flapping wing force (Dudley 2002) and thorax width (which is related to the amount of flight muscles and therefore flight endurance (Marden 2000; Turlure et al. 2016; Crawford and Keyghobadi 2018)). The radius of the second moment of wing area (Ellington 1984) is related to the energy efficiency of flight, and the AR is related to the ratio between lift and drag (Bhat et al. 2019). The AR has been widely studied. Empirical studies on insect dispersal suggest that a low AR correlates with the dispersal capacity (Hassall 2015). This is consistent with recent results on insect aerodynamics indicating that the wing aerodynamic performance decreases as the wing AR increases (Harbig 2017).

Materials and Methods

Collection and identification of aquatic insects

Imagoes of aquatic insects (EPT, Megaloptera, and Diptera) were collected and sampled in Brittany and Normandy (France) from 2018 to 2021, using aquatic emergence traps (Cadmus et al. 2016), malaise traps, and mowing nets. Most of the samples were collected near streams or water points, but some Ephemeroptera and Trichoptera were caught far from water sources (>500 m). We also set up a citizen science program to enlarge the insect collection. Eight organizations were involved and collected around 25% of the individuals. The samples came from 32 different locations (Figure 1). They were stored in a freezer or in 96% ethanol.

We aimed to collect 30 individuals *per* taxon (15 individuals *per* sex and *per* taxon whenever possible), but this number eventually ranged from 18 to 35 because of the sporadic emergence of some species. Male *Dinocras cephalotes* (Plecoptera: Perlidae) were not considered because they cannot fly (they are brachypterous).

EPT and Megaloptera were identified to the genus or species level, and Diptera to the family level (Supplementary Material S1), except Chironomidae that were identified to the genus or species level.

Morphological measurements

After checking insect integrity, we took pictures of the dorsal and lateral views of each specimen. One forewing and one hindwing were carefully removed and flattened between a microscope slide and a cover slip. One picture of each wing was taken using a stereomicroscope (Leica M205 C) equipped with a binocular camera (Leica DMC4500). It was not possible to remove the very small hindwings (less than 8% of the total wing surface area) of *Baetis rodhani* (Ephemeroptera: Baetidae) and *Habrophlebia* spp. (Ephemeroptera: Leptophlebiidae) without damaging them. Consequently, only their forewings were analyzed. Afterward, the insects were freeze-dried for 24 h and weighed to the nearest 0.0001 mg (XP2U Mettler Toledo ultra-microbalance; Sartorius M2P microbalance).

$$\mathrm{RSM} = \sqrt[2]{\frac{S_2}{SR^2}}. \tag{1}$$

$$S_2 = \int cr^2 dr. \tag{2}$$

Five raw parameters were measured for each insect: 1) dry body mass (to investigate its relationships with body length), 2) body length from the antenna base to the genitalia, 3) thorax width between the forewings, 4) FL from the base to the tip of the wing (Ellington 1984), and 5) total wing area. Based on these parameters, two wing-shape parameters were calculated. Firstly, the radius of the second moment (RSM) of wing area was computed (Ellington 1984). The RSM (Equation (1)) describes the distribution of the wing area along the wing span. At low RSM values, most of the wing area is close to the insect body. At high values, most of the wing area is at its tip. The RSM was calculated from the second moment of wing area S_2 (Equation (2)), where S is the wing area and c the wing chord for a distance r along the wing span R. High RSM wings increase the energetic costs of flight and in turn lift force production (Lancaster et al. 2020). Secondly, the AR (Equation (3)) of the total wing area is the ratio of the FL over

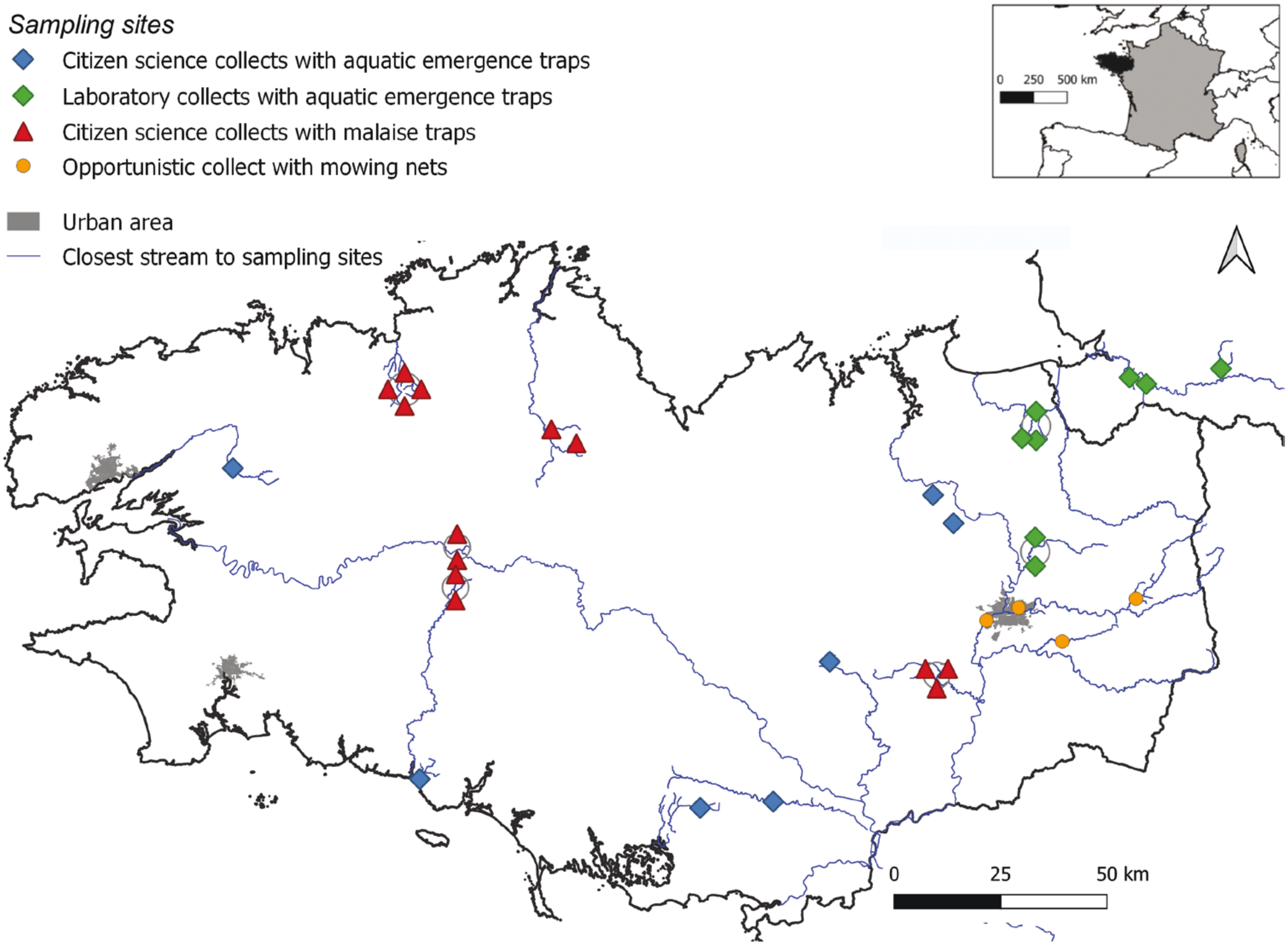

Figure 1 Map representing the sampling sites, Brittany region (France).

the wing area. High-AR wings are long and thin, while low AR wings are short and wide.

$$\mathrm{AR} = \frac{R^2}{S}. \tag{3}$$

Statistical analyses

Allometry analyses

The allometry analyses followed the procedure proposed by Warton et al. (2006). We conducted a standardized major axis (SMA) regression with the "Smatr" package and the *sma()* function (Warton et al. 2012) to determine the relationship between each morphological parameter as a response variable and body length as an explanatory variable, both log-transformed. Using the *sma()* function, we calculated the regression lines between the means of the morphological parameters and body length *per* taxon to remove intra-taxon variation. As the data were log-transformed, the slope b of the regression line was equal to the allometry coefficient (see Peig and Green 2009 for details). Length parameters (FL and thorax width), the AR, the RSM, and body length were proportional when $b = 1$ (i.e., they were isometric). As area A corresponded to the squared length L ($A = L^2$), wing area, and body length were isometric when $b = 2$. Dry body mass and body length were isometric when $b = 3$ (the volume V was related to the mass M, so that $M \approx V = L^3$ (Chown et Gaston 2010)). If $b > 1$ ($b > 2$ for wing area and $b > 3$ for dry body mass), the parameter value increased faster than body size (hyper-allometry). If $b < 1$, the parameter value increased more slowly than body size (hypo-allometry). Slope b was compared with the isometric value for each parameter by testing the correlation between residuals and fitted values.

Clustering of emerging insects based on flight-related morphological parameters

A principal component analysis (PCA) based on normalized data was carried out on all individuals using FL, allometry-adjusted thorax width, allometry-adjusted wing area, the AR, and the RSM ("FactomineR" package, *PCA()* function; Lê et al. 2008). Aerodynamic forces are strongly influenced by size. Therefore, we chose FL as a size parameter (i.e., without any allometric adjustment). A Euclidean distance matrix was calculated ("vegan" package, *vegdist()* function; Oksanen et al. 2015) from the mean of the PCA coordinates *per* taxon (i.e., the centroid of each taxon). Only the first 3 components were considered.

We allometrically adjusted the raw parameters using b obtained from the SMA regressions to allow for size-independent comparisons. The allometrically adjusted ratio was $\bar{Y}_i = Y_i/X_i^b$ (Albrecht et al. 1993). For each individual i, $\bar{Y}_{i_i}$ was the allometrically adjusted ratio of any given morphological parameter used in the further analyses. Y_i was the morphological parameter and X_i was body length. As the AR and the RSM were non-dimensional numbers and FL was needed for the size variable, no allometric adjustment was needed for these parameters.

The morphology-based classification was based on the coordinates of each taxon on the first 3 axes of the PCA following the procedure described by Borcard et al. (2011). We selected the methods that best fitted our data in an a priori-free manner. First, the clustering model of the distance matrix was selected by comparing several hierarchical cluster analysis (HCA) methods with the Gower distance ('stats' package, *hclust()* function; R Core Team 2021). The average method was selected to perform the HCA. Second, the number of clusters (k) was determined by computing the silhouette width S for each taxon after k-means consolidation. The average S was calculated for each cluster and partition ('cluster' package, *silhouette()* function (Maechler et al. 2021)). S ranged from −1 to 1: 1 indicated a perfect quality cluster and 0 a bad quality cluster (except for the clusters composed of only one taxon).

Relationship between flight-related morphological parameters and life-history traits

Four life-history traits drawn from the DISPERSE database (Sarremejane et al. 2020) were considered: 1) affinity for dispersal (weak affinity for dispersal, strong affinity for active dispersal, strong affinity for passive dispersal), 2) the potential number of generations *per* year (i.e., voltinism; 3 modalities: multivoltine, univoltine, semivoltine), 3) the adult lifespan (3 modalities: less than 1 week, 1 week to 1 month, 1 month to 1 year), and 4) the swarming behavior (two modalities: swarming or not swarming).

To test the relationships between flight-related morphological parameters, dispersal traits, and swarming, the mean coordinates of the first 2 principal components of each taxon were used as response variables, and the dispersal traits and swarming were used as explanatory variables. Comparisons were made using Kruskal–Wallis or ANOVA tests, depending on the normality and homoscedasticity of the data (checked using Shapiro–Wilk and Bartlett's tests).

All statistical analyses were performed with R software v. 4.1.1 (R Core Team 2021).

Results

We analyzed 898 individuals distributed into 5 orders and 32 taxa: 11 Diptera (including 6 Chironomidae), 5 Ephemeroptera, 1 Plecoptera, 1 Megaloptera, and 10 Trichoptera. Sexual dimorphism was not detected. Therefore, sex was not considered in the further analyses (Supplementary Material S2).

Allometry

Body length was highly related with raw parameters (i.e., FL, wing area and thorax width, minimum R^2 value > 0.92). Dry body mass and thorax width were proportional to body length (P values = 0.37 and 0.34, respectively). Consequently, body length was considered as a good proxy of size. The relationships between other raw parameters and body length were not isometric. FL ($b = 1.10$, P value = 0.008, Figure 2A) and wing area ($b = 2.57$, P value < 0.001, Figure 2B) increased with body size.

The correlations between shape parameters (AR and RSM) and body length were low ($R^2 = 0.31$ and $R^2 = 0.55$, respectively). The absolute value of the AR decreased when size increased ($b = -0.47$, P value < 0.001, Figure 2D). The RSM varied little with size ($b = -0.09$, P value < 0.001, Figure 2E).

We showed allometric relationships between body length and morphological parameters, except dry body mass and thorax width that were not proportional to body length, but the intensity (slope b) and direction varied.

Clustering of flight-related morphologies

The average silhouette width S was the highest for partitions $k = 6$ ($S = 0.390$, Figure 3A). Based on the silhouette analysis, 2 taxa (Diptera: Psycodidae, and Ephemeroptera: Ephemeridae) did not fit in with their specific clusters (cluster 1: $S = 0.088$; cluster 5: $S = 0.099$, respectively).

The taxa were structured by size, adjusted wing area and thorax width, and wing shape (AR and RSM). Size partly contributed to the three main axes (PC1, 17%; PC2, 21%; PC3, 10%). Wing shape mainly contributed to PC1 (36% and 35%, respectively), which separated clusters 3, 4, and 6 (only including Diptera with high RSM and AR values) from clusters 1, 2, and 5—with lower RSM and AR values. Allometrically adjusted thorax width and wing area mainly contributed to PC2, by 38% and 37% respectively, which separated clusters 1 and 4 (high adjusted thorax width and adjusted wing area) from clusters 2, 3, 5, and 6 (Figure 3C). Almost all the confidence ellipses of the taxa were flattened and oriented in the same direction, along the axis of adjusted wing area and thorax width (Figure 3B,C).

Each cluster was characterized by a different set of parameters (Figure 4). Cluster 1 included small insects with relatively high allometrically adjusted wing area and thorax width. It was represented by seven taxa, belonging to 3 orders (Trichoptera, Plecoptera, and Diptera). Cluster 2 included light insects characterized by a relatively narrow thorax (adj_TW). It included 4 Ephemeroptera taxa and 2 Plecoptera taxa. Cluster 3 included very small insects, with narrow wings (high RSM and AR) but a relatively small wing area. It only included Diptera (2 chironomids: *Brilla bifida* and Chironomini), Dolichopodidae and Empididae. Cluster 4 included the smallest taxa, all 3 chironomid taxa with very high RSM, and an allometrically adjusted wing area but narrow FL. Cluster 5 included large species (EPTM) characterized by wings larger at their base than at their tip. Cluster 6 only included Tipulidae (Diptera)— heavy insects with high RSM and AR but a very narrow thorax and a relatively low allometrically adjusted wing area.

Overall, morphological parameters differentiated the taxa along 3 axes: size, wing shape (AR and RSM), and raw parameters (allometrically adjusted wing area and thorax width).

Dispersal traits and swarming

Significant differences along PC1 (ANOVA; $P = 0.002$) were detected for affinity for dispersal (Figure 5A). According to the DISPERSE database, only 3 taxa out of 32 (Diptera only, in clusters 1 and 3) exhibited a strong affinity for passive dispersal (Table 1). The other dipteran taxa had a weak affinity for dispersal and represented 50% of the weak dispersers. Half of the taxa exhibited a weak affinity for dispersal. Weak dispersers were distributed among all six clusters. Thirteen taxa (mainly Trichoptera and Ephemeroptera in clusters 1, 2, and 5) were known to disperse actively (strong affinity for active dispersal, Table 1).

Swarming and non-swarming taxa differed along PC1 (Figure 5B). In general, the smaller species of our dataset

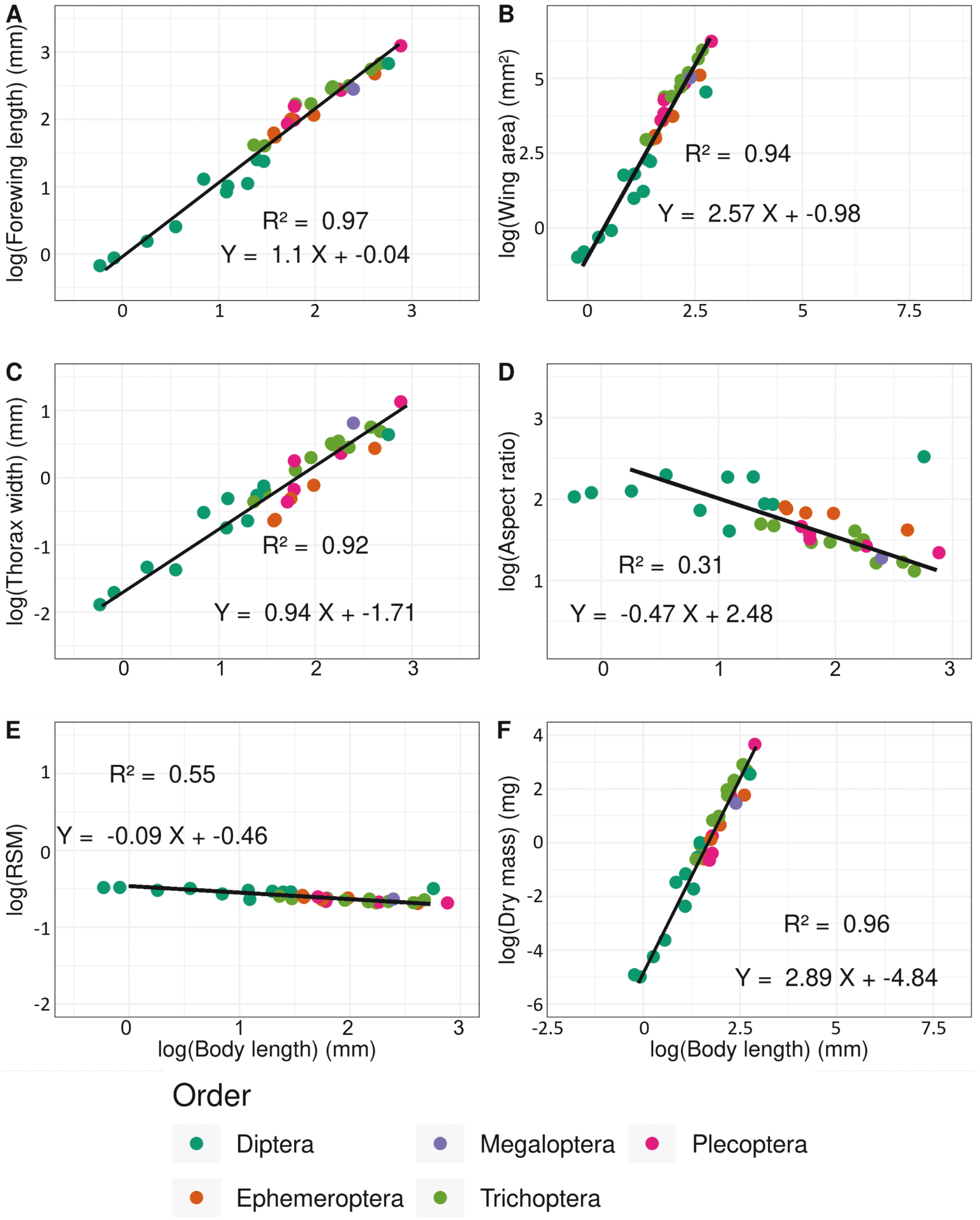

Figure 2 SMA regression between the log-values of body length (mm) and of (A) FL (mm), (B) wing area (mm²), (C) thorax width (mm), (D) the AR, (E) the radius of the second moment (RSM) of wing area, and (F) dry body mass (mg). All regressions were significant ($P < 0.001$). The linear equations include the slope (b) and elevation: $Y = bX +$ elevation. Coefficient R^2 is the correlation between residual and fitted values. Orders are showed for information purposes. The link between length parameters, the AR, the RSM, and body length is proportional (i.e., isometric) when $b = 1$. As area A corresponds to the squared body length ($A = L^2$), the link between wing area and body length is isometric when $b = 2$. Dry body mass and body length are isometric when $b = 3$ (volume V is related to mass M, so that $M \approx V = L^3$).

tended to swarm more than the larger species. All clusters included at least one taxon with swarming behavior so that no cluster was solely composed of non-swarming taxa (Table 1). In contrast, cluster 4 only included swarming taxa.

Significant differences along PC1 and PC2 (Kruskal–Wallis test; P values < 0.05) were detected for voltinism and adult lifespan (Figure 5C,D, respectively). All the taxa belonging to cluster 5 were either semi- or univoltine, while all the taxa belonging to cluster 4 were multivoltine. A short adult lifespan is mainly characterized by clusters 3 and 4.

A general link was highlighted between morphological parameters, size, and life-history traits. More specifically, the clusters did not reflect the life-history traits.

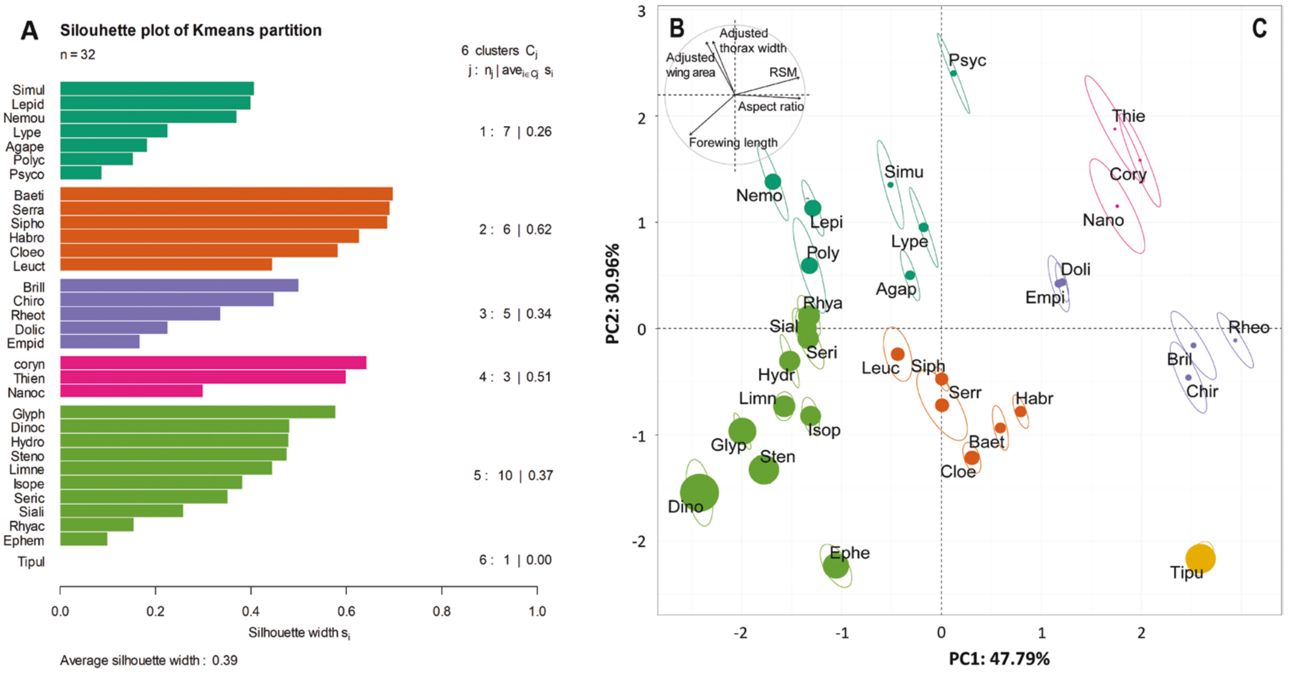

Figure 3 (A) Silhouette plot showing the quality of the clusters. The silhouette width *S* was computed for each taxon. The average *S* was calculated *per* cluster for each partition. Average *S* ranged from −1 to 1: 1 = a perfect quality cluster, and 0 = a bad quality cluster (except for clusters composed of only 1 taxon). (B) Circle showing the contribution of the variables according to components 1 and 2. RSM, radius of the second moment of wing area. (C) Principal component analyses on all individuals. Ellipses represent the 0.95 confidence interval for the individuals of each taxon around its centroid. Colors represent the 6 clusters. Point sizes are proportional to the mean size of each taxon. Short names are given in Table 1.

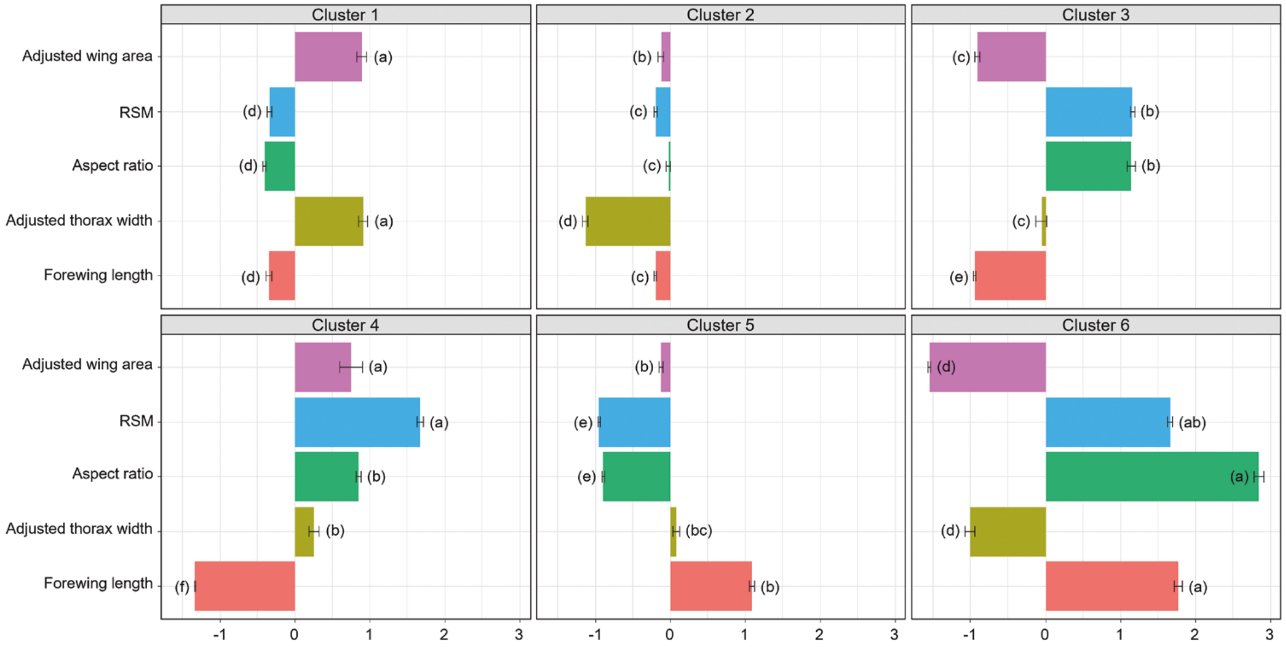

Figure 4 Characterization of the 6 clusters (1–6) determined by hierarchical clustering. Each bar represents the mean of a normalized parameter for a given cluster. RSM, radius of the second moment. For each morphological parameter taken independently, letters between brackets indicate significant differences between clusters, ranging from *a* (highest mean) to *f* (lowest mean). Error bars indicate standard errors.

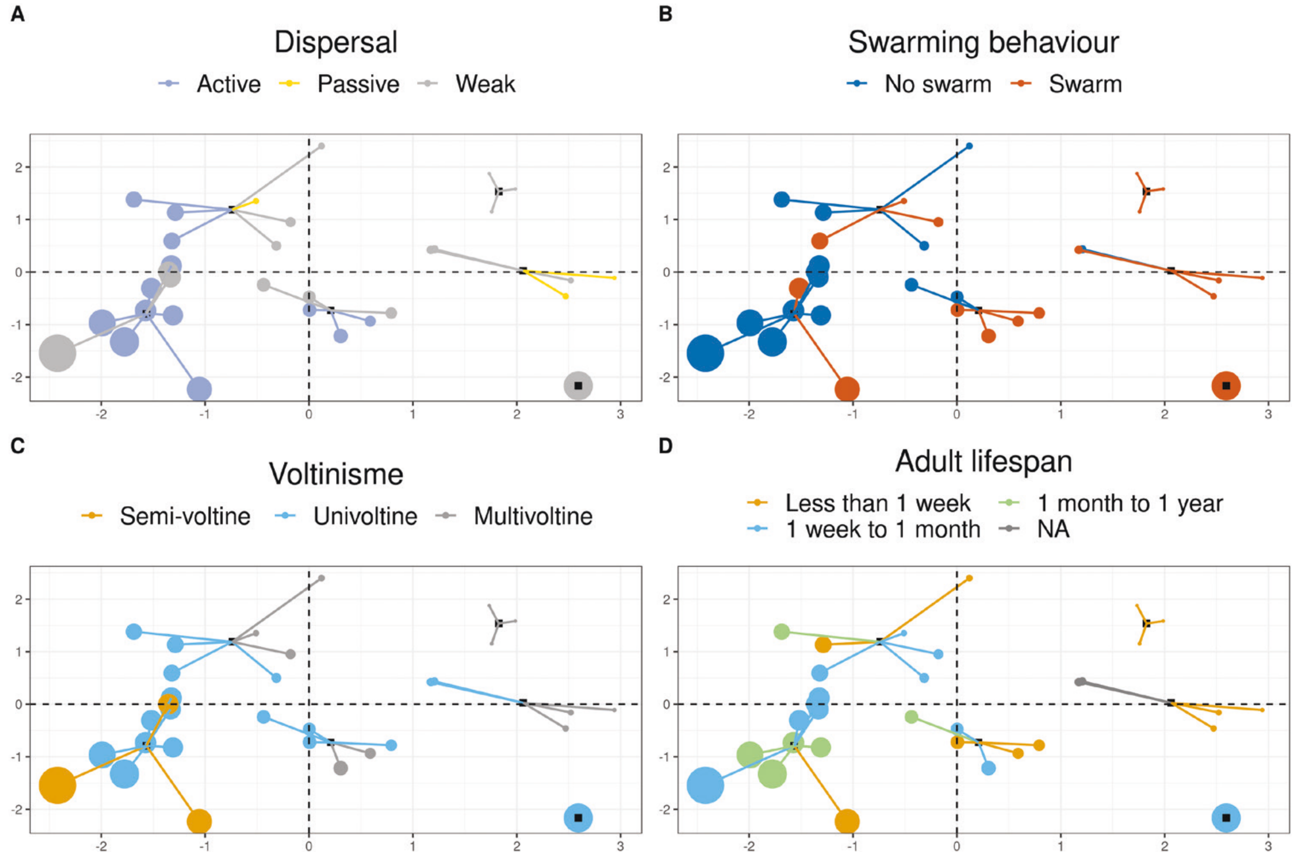

Figure 5 Principal component analyses on all individuals. Point sizes are proportional to the mean size of each taxon. Black squares, centroids of each cluster. Colors represent the projected trait modalities: (A) dispersal; (B) swarming behavior; (C) number of generations *per* year (voltinism); (D) adult lifespan. The adult lifespan of Dolichopodidae and Empididae is not known (NA).

Discussion

Our analysis of the morphology of 32 taxa highlighted strong correlations between raw flight parameters and insect body length (Figure 2). When insect size decreased, the relative values of wing area and FL decreased too, while the relative values of thorax width increased. This pattern seems consistent for all insects, terrestrial ones included (Dudley 2002; García and Sarmiento 2012). Air viscosity is higher for small insects than for large ones (Tercel et al. 2018), so the cost of flight should be higher for small insects. However, the power required for flight is proportional to insect size, so the relative cost of flight does not increase when size decreases (Lyu and Sun 2021). The discrepancy between the facts that 1) the cost of flight is proportional to size, and 2) physical constraints vary according to scale is consistent with the existence of allometric morphological adaptation for flight among insects of various body sizes (García and Sarmiento 2012; Shyy et al. 2016). Correlations between body length and wing shape parameters do exist, but they are considerably weaker than those of raw flight parameters. According to Bhat et al. (2019), small insects have short and wide wings (i.e., a low AR) and a higher wingbeat frequency. Our results show that small aquatic insects except Tipulidae have a higher AR than large ones. The influence of the AR on wing flapping is complex and likely depends on the kinematics involved (Wootton 2020). The large number of taxa and the wide range of insect body sizes in our study could explain these apparent differences with the literature. The difficulties in establishing relationships between size and wing shape suggest that factors other than size, for example, wing kinematics, the flight metabolic rate (Niven and Scharlemann 2005; Tercel et al. 2018) or body stores (Gerber et al. 2022) also need to be investigated to study insect flight allometry.

Based on cluster analysis, we grouped or separated the taxa into six clusters according to their flight morphology, taking the AR, RSM, thorax width, and wing area into account (Figure 3). Each cluster significantly differed in size and size-dependent aerodynamical constraints (Dudley 2002). Since size was homogenous within the clusters, we can assume that morphological similarities within the six clusters induced similar flight capacities. We are aware of the limitations of this kind of analysis because many other parameters than morphology—ranging from kinematics to behavior—influence the way insects fly (Ellington 1999). However, empirical knowledge of flight is still lacking for most aquatic insects, and the present study provides part of the answer. Although more tests on the aerodynamics of insect flight are needed, our morphology-based classification allows studying and quantifying the flight of aquatic insects for the first time and improves knowledge on flight patterns. Our results show that taxonomy is partly related to flight-related morphology. This result makes sense because taxonomy underlies that morphology follows from evolutionary history. For example, the number of wing pairs (or the size of the hind wings) explains the general patterns of Diptera and EPT (Figure 2C). Two large pairs of wings relatively increase the wing area and decrease the AR (Figure 3B). Taxonomy is intermixed with the general differences observed for life

Table 1 Summary table of dispersal traits *per* taxon. Rows correspond to the lowest taxonomical taxon considered in the analyses.

Order	Family	Taxon	Short name	Cluster	Number of individuals per sex ♀:♂	Affinity for dispersal	Voltinism	Adult lifespan	Swarming behavior	Swarm references
T	Glossosomatidae	*Agapetus* spp	Agap	1	23:7	Weak	Univoltine	1 week to 1 month	no swarm	Müller-Peddinghaus (2011)
T	Lepidostomatidae	*Lepidostoma hirtum*	Lepi		13:17	Active	Univoltine	Less than 1 week	no swarm	Müller-Peddinghaus (2011)
T	Psychomyiidae	*Lype* spp	Lype		15:15	Weak	Multivoltine	1 week to 1 month	swarm	Müller-Peddinghaus (2011)
P	Nemouridae	*Nemoura cinerea*	Nemo		16:14	Active	Univoltine	1 month to 1 year	no swarm	Brittain (1990)
T	Polycentropodidae	*Polycentropus* spp.	Poly		20:3	Active	Univoltine	1 week to 1 month	swarm	Müller-Peddinghaus (2011)
D	Psychodidae	Psycodidae	Psyc		14:16	Weak	Multivoltine	Less than 1 week	no swarm	Downes (1969)
D	Simuliidae	Simulinae	Simu		17:13	Passive	Multivoltine	1 week to 1 month	swarm	Downes (1969)
E	Baetidae	*Baetis rodhani*	Baet	2	14:9	Active	Multivoltine	Less than 1 week	swarm	Elliott and Humpesch (1983)
E	Baetidae	*Cloeon dipterum*	Cloe		15:14	Active	Multivoltine	1 week to 1 month	swarm	Elliott and Humpesch (1983)
E	Leptophlebiidae	*Habrophlebia* spp	Habr		20:15	Weak	Univoltine	Less than 1 week	swarm	Bauernfeind et Humpesch (2001)
P	Leuctridae	*Leuctra* spp	Leuc		15:15	Weak	Univoltine	1 month to 1 year	no swarm	Brittain (1990)
E	Ephemerellidae	*Serratella ignita*	Serr		8:10	Active	Univoltine	Less than 1 week	swarm	Elliott and Humpesch (1983)
P	Chloroperlidae	*Siphonoperla torrentium*	Siph		15:15	Weak	Univoltine	1 week to 1 month	no swarm	Brittain (1990)
D	Chironomidae	*Brillia bifida*	Bril	3	15:15	Weak	Multivoltine	Less than 1 week	swarm	Moller Pillot (2014)
D	Chironomidae	Chironomini	Chir		14:16	Passive	Multivoltine	Less than 1 week	swarm	Downes (1969)
D	Dolichopodidae	Dolichopodidae	Doli		15:15	Weak	Univoltine	NA	no swarm	Downes (1969)
D	Empididae	Empididae	Empi		18:16	Weak	Univoltine	NA	swarm	Downes (1969)
D	Chironomidae	*Rheotanytarsus curtistylus*	Rheo		10:18	Passive	Multivoltine	Less than 1 week	swarm	Vallenduuk and Moller Pillot (2007)
D	Chironomidae	*Corynoneura* spp.	Cory	4	3:19	Weak	Multivoltine	Less than 1 week	swarm	Moller Pillot (2014)
D	Chironomidae	*Nanocladius spp*	Nano		9:19	Weak	Multivoltine	Less than 1 week	swarm	Moller Pillot (2014)
D	Chironomidae	*Thienemanniella* spp.	Thie		12:15	Weak	Multivoltine	Less than 1 week	swarm	Downes (1969)
P	Perlidae	*Dinocras cephalotes*	Dino	5	14:0	Weak	Semi-voltine	1 week to 1 month	no swarm	Brittain (1990)
E	Ephemeridae	*Ephemera danica*	Ephe		8:10	Active	Semi-voltine	Less than 1 week	swarm	Elliott and Humpesch (1983)
T	Limnephilidae	*Glyphotaelius pellucidus*	Glyp		14:16	Active	Univoltine	1 month to 1 year	no swarm	Gullefors and Petersson (1993)
T	Hydropsychidae	*Hydropsyche* sp	Hydr		18:12	Active	Univoltine	1 week to 1 month	swarm	Müller-Peddinghaus (2011)
P	Perlodidae	*Isoperla grammatica*	Isop		20:10	Active	Univoltine	1 month to 1 year	no swarm	Rupprecht (2009)
T	Limnephilidae	*Limnephilus* spp.	Limn		15:14	Active	Univoltine	1 month to 1 year	no swarm	Müller-Peddinghaus (2011)
T	Rhyacophilidae	*Rhyacophila dorsalis*	Rhya		19:11	Active	Univoltine	1 week to 1 month	no swarm	Müller-Peddinghaus (2011)
T	Sericostomatidae	*Sericostoma* sp	Seri		14:16	Weak	Univoltine	1 week to 1 month	no swarm	Müller-Peddinghaus (2011)
M	Sialidae	*Sialis* spp.	Sial		11:19	Weak	Semi-voltine	1 week to 1 month	no swarm	Elliott and Sutcliffe (2009)
T	Limnephilidae	*Stenophylax lateralis*	Sten		14:16	Active	Univoltine	1 month to 1 year	no swarm	Müller-Peddinghaus (2011)
D	Tipulidae	Tipulidae	Tipu	6	11:19	Weak	Univoltine	1 week to 1 month	swarm	Downes (1969); Sullivan (1981)

"Order" column: D, Diptera; E, Ephemeroptera; M, Megaloptera; P, Plecoptera; T, Trichoptera. The "Short name" column refers to the name used in Figure 3. The "Voltinism," "Affinity for dispersal," and "Adult lifespan" columns are issued from the DISPERSE database (Sarremejane et al. 2020). "Voltinism" refers to the potential number of reproductive cycles *per* year. "Affinity for dispersal" describes whether the taxa have a weak affinity for dispersal ("weak"), a strong affinity for active dispersal ("active"), or a strong affinity for passive dispersal ("passive"). The "Swarming behavior" column refers to whether insects have a swarming behavior before mating (swarm) or not (no swarm).

history traits, swarming and dispersal. First, it goes against the commonly held belief that morphology and flight capacities are similar among families of a same taxonomic order (Tercel et al. 2018), highlighting the diversity of insect flight. Second, there is no congruence between flight-related morphology and life history traits and dispersal. For example, most of the taxa in cluster 5 are trichopterans known for their active dispersal (except *Sericostoma* sp., Table 1). Yet, they are morphologically close to female *Dinocras cephalotes* and to *Sialis* spp., which have been reported as weak dispersers and 'weak' or 'clumsy' flyers (Elliott and Humpesch 1983). Imagoes of *Sialis* spp. are primarily observed standing or walking on vegetation (Elliott and Humpesch 1983). This would suggest that the low dispersal capacity of *Sialis* spp. is related to their flight propensity—not to their flight capacities. This apparent contradiction between dispersal and flight-related morphology shows how carefully dispersal should be considered. Although insects from different taxa may share similar morphological traits, they may not have the same flying capacities (Lancaster and Downes 2017). Moreover, because flight is an energy-intensive activity (Marden 2000), we expected swarming taxa to be morphologically adapted to prolonged and energy-efficient flight (Akutsu and Morse 2020). Swarming species need to fly much longer than non-swarming species to reproduce (Dudley 2002; Lancaster and Downes 2013). Lightness and agility in flight might also be necessary for swarming (Peckarsky et al. 2002; Fyodorova and Azovsky 2003). However, each of our morphological clusters contained swarming taxa (Figure 5B), suggesting that swarming behavior of insects cannot solely be inferred from basic morphological traits. Swarming taxa notably have more fuel for flight (triglycerides) than non-swarming taxa (Gerber et al. 2022). Therefore, they can fly longer. Other factors influence the capacity for dispersal, such as flight capacities through wing kinematics and aerodynamics that interact with morphology (Hall et al. 2015), the navigation capacities (i.e., the ability to position oneself in space; Turlure et al. 2016), physiology (amounts of energy substrates for flight such as lipids, carbohydrates, or proteins), flight propensity (Steyn et al. 2016), or temperature (Mattila 2015). A broader approach combining these factors with flight-related morphology would provide a better understanding of aquatic insect dispersal.

In conclusion, using a wide range of emerging aquatic insects, the present study shows allometry between size and raw flight-related parameters. When body length increases, FL, and wing area relatively increase too, while thorax width relatively decreases. Conversely, wing shape parameters (i.e., the AR and the RSM) are not strongly correlated with body length. Based on flight-related morphological parameters, we clustered 32 taxa of aquatic insects according to their potential flight capacities. The various flight-related morphologies observed among taxa suggest highly variable flight capacities between and within orders. Six clusters of flight-related morphologies emerged, partly correlated with taxonomy or life-history traits of the taxa. Contrary to a commonly held belief, insect morphology alone is a questionable proxy for 'good' and 'poor' flyer categories. A more comprehensive approach combining morphology with physiology, kinematics, and behavior is now required for further understanding of the flight and dispersal of aquatic emerging insects.

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Conflict of Interest

None declared.

Author Contributions

B.B., J-M.R., and C.P. conceived the ideas and designed the methodology; R.G. conducted fieldwork; R.G. analyzed the data; R.G., C.P., and B.B. wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Ethical Approval

Ethics approval was not required for this study according to French legislation.

Data Availability

The datasets used and analyzed during the current study are available from the corresponding author upon reasonable request.

Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

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