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High Heteroptera biodiversity

Low Heteroptera biodiversity

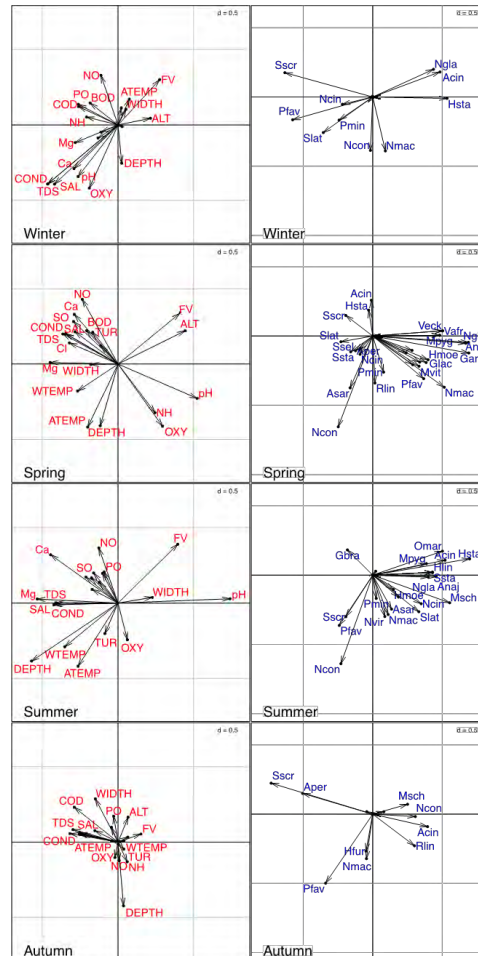
Spring & Summer

Autumn & Winter



Low salinity / conductivity
High dissolved Oxygen

High salinity / conductivity
Low dissolved Oxygen



Headwater
Riparian forest
Aquatic macrophytes

Lowland
Urbanisation
Pollution

**Unravelling the environmental correlates influencing the seasonal biodiversity
of aquatic Heteropteran assemblages in northern Africa**

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Abstract

Heteropteran communities form a key component of aquatic ecosystems but have not been widely studied compared to other freshwater faunal groups. This research examined the environmental parameters influencing the diversity, seasonal distribution and structure of aquatic Heteroptera assemblages in the Mediterranean region of Tunisia, northern Africa. Heteropterans were most abundant during spring and summer, coinciding with the emergence of several species and the most favorable environmental conditions for benthic aquatic fauna. Three-way multivariate analyses (combining community composition data from all sites and seasons) highlighted the longitudinal spatial organization of Heteropteran communities. Headwater regions were dominated by halophobic sensitive taxa, and lowland sites were characterized by high salinity resistant taxa (halophilic taxa). The longitudinal organization was driven by gradients of mineralization (salinity and electrical conductivity) and oxygen (DO, COD and BOD) concentrations. Taxonomic composition differed between river catchments, with significantly higher diversity (taxa richness) in the streams with adjacent riparian forest cover. These sites were characterized by the presence of endemic species, such as *Velia africana* and *Velia eckerleini*, and rare species, *Notonecta meridionalis*, and *Aquarius najas*. Results recorded highlight the importance of aquatic vegetation and water quality in driving the seasonal and spatial variability of Heteropterans, and provide important information to inform the management and conservation of freshwater biodiversity in Northern Africa.

Key words. freshwater ecosystems, water quality, macroinvertebrate, aquatic ecology, Mediterranean.

1 **Introduction**

2 Freshwater ecosystems in the Mediterranean region of North Africa are increasingly recognized as global
3 biodiversity hotspots (Beauchard et al., 2003). However, there remains a fundamental lack of research
4 considering the structure and functioning of north African Mediterranean freshwater ecosystems and in the insect
5 communities they support (Slimani et al., 2019). This limited ecological knowledge currently hinders our
6 scientific understanding of how aquatic ecosystems and their biodiversity will respond to anthropogenic
7 pressures across North Africa in the future (Schilling et al., 2012). The primary threats to the freshwater
8 biodiversity of north Africa, and globally, include excessive freshwater water abstraction (for domestic,
9 agricultural and industrial use) and the construction of engineered infrastructure (e.g. dams, weirs and
10 channelization), which have driven the rapid loss of natural freshwater habitats (Reid et al., 2019).
11 Anthropogenic flow regime modifications and projected climatic change threatens freshwater environments
12 (Döll and Schmied, 2012; Colin et al., 2016), their high biodiversity and the endemic freshwater fauna (including
13 the freshwater insects) they support (García et al., 2010) across North Africa.

14 Heteropterans represent a subgroup of the Hemiptera, an insect order forming an integral part of freshwater
15 ecosystems globally. There are over 4500 Heteropteran species thought to inhabit aquatic environments globally,
16 making a significant contribution to the biodiversity of freshwater ecosystems (Polhemus and Polhemus, 2008).
17 They have been recorded in virtually all aquatic habitats, including surface and subsurface environments
18 associated with lotic (e.g. headwater streams, lowland rivers) and lentic (e.g. pond, lakes, coastal rock pools)
19 waterbodies (Slimani et al., 2015, 2016, 2017). Heteropterans are important for the functioning of aquatic
20 ecosystems as they help regulate fluxes of energy and matter across aquatic food webs, through facilitating
21 nutrient cycling and providing a source of food for higher trophic levels (Brown and McLachlan, 2010; Amaral
22 et al., 2016). Aquatic Heteropteran taxa vary considerably in their ecological requirements (Aukema et al., 2013;
23 De Figueroa et al., 2013; Damgaard and Zettel, 2014; Turić et al., 2015), and many species display specific
24 habitat preferences (Bloechl et al., 2010; Carbonell et al., 2011; Annani et al., 2012; Dudgeon, 2012). As such,
25 Heteropteran communities are widely used as indicators of aquatic ecosystem health and to characterize
26 ecological responses to anthropogenic pressures (e.g., Hershey et al., 2010; Lock et al., 2013; Slimani et al.,
27 2017). In addition, many Heteropteran species are recognized as reliable surrogates for the wider biodiversity of
28 aquatic ecosystems and have been used to support the conservation and restoration of freshwater habitats
29 (Whiteman and Sites, 2008; Cunha and Juen, 2017).

30 Globally, the majority of aquatic Heteropterans belong to one of two major groups: Nepomorpha (water bugs)
31 which largely live below the water surface, and Gerromorpha (water striders) comprising species that inhabit the
32 water surface film (Polhemus and Polhemus, 2008). Both Nepomorpha and Gerromorpha are particularly
33 common within Mediterranean freshwater ecosystems (De Figueroa et al., 2013), including those of northern
34 Africa (Aukema et al., 2013; Slimani et al., 2015, 2016). The distribution and diversity of both subgroups may
35 be influenced by a range of environmental factors, including physicochemical conditions (particularly dissolved
36 solutes and oxygen concentrations), flow conditions (lentic or lotic habitats) and water temperature (Tully et al.,
37 1991; Hufnagel et al., 1999; Barahona et al., 2005; Karaouzas and Gritzalis, 2006; Skern et al., 2010). The size
38 and shape of the water body has been reported to strongly influence their distribution; with clear distinctions
39 between small shallow waterbodies and larger deeper lakes (Macan, 1954; Savage, 1994).

40 Heteropterans display a range of traits which allow them to survive extreme hydroclimatic conditions, from
41 torrential floods during winter to the severe summer droughts which occur consistently in the Mediterranean
42 region of North Africa (Annani et al., 2012). For example, species from the genus *Notonecta* spp. (Notonectidae)
43 have a prolonged period of development over multiple months and are typically be found in freshwaters at higher
44 altitude during the drier summer months (Annani et al., 2012). While a limited number of studies have explored
45 the taxonomic composition and diversity of aquatic Heteropteran communities in northern Africa (e.g. L'mohdi
46 et al., 2008 -Morocco; Annani et al., 2012 -Algeria; Slimani et al., 2015, 2016 - Tunisia), to our knowledge none
47 have tested their sensitivity to varying environmental conditions beyond individual river basins or seasons.

48 In order to better understand the key drivers underpinning the spatiotemporal distributions of aquatic
49 Heteropteran assemblages, we examined seasonal variations in community structure and environmental controls
50 across 45 sites within 4 catchments in northern Tunisian. A total of 21 environmental variables, identified as
51 drivers of aquatic Heteroptera assemblages were measured: including salinity, conductivity, dissolved oxygen,
52 water depth, and surface area of open water. The main objectives of the study were to: (i) examine differences in
53 Heteropteran community composition and diversity between the four river catchments examined; and (ii)
54 quantify the environmental correlates driving spatiotemporal variability of Heteropteran communities across the
55 catchments.

56

57

58

59 **Materials and Methods**

60 **Study site**

61 This research was undertaken in northern Tunisia (Fig. 1 and Table S.1 in Supplementary Material), a
62 Mediterranean region located in the Maghreb (North Africa) and included 45 sites within four catchments
63 (Medjerda; Kroumirie-Mogods; Ichkeul; and Meliane-Cap Bon).

64 All sites maintained perennial surface water and encompassed the entire diversity of freshwater habitats
65 preferred by the target group, including streams, springs, ponds and lakes with both lotic/lentic water conditions;
66 comprising 34 lotic and 11 lentic waterbodies (Fig. 1, Table S.1 in Supplementary Material). Substrates within
67 the freshwater habitats were characterized by cobbles, gravel, sand, silt and clay; with some sites appearing
68 muddy and having a loamy character. Sampling sites were established on each catchment longitudinally from
69 upstream to downstream (St 1 to St 45). Site 1 was in the headwaters (upstream) of the Wadi Medjerda in North-
70 West Tunisia, and site 45 was located the furthest downstream on the Wadi Lebna in the North-Eastern
71 extremity of Tunisia in the Cap Bon region (A summary of sites is presented Table 1). The northern area of
72 Tunisia is characterized by a typical Mediterranean climate, ranging from humid to sub-humid and supports a
73 rich floral diversity including *Typha angustifolia* L., *Quercus canariensis* Willd., and *Quercus suber* L. This
74 northern region occupies 17% of the land mass but includes 60% of the national freshwater resource.

75 **Biological data**

76 Aquatic Heteroptera samples were collected on 4 separate occasions: February (spring), May (summer),
77 September (autumn), and December (winter) 2013 from the 45 sites (Fig. 1, Table S.1 in Supplementary
78 Material). The samples were obtained using a combination of both Surber samples (300 µm mesh net with an
79 opening 0.20 m wide and 0.10 m deep) and a kick / sweep net (filet Troubleau). A total of 25 minutes of
80 sampling and searching was undertaken at each site ensuring that the entire habitat heterogeneity was considered
81 at each site. Samples were preserved in 70% ethanol and returned to the laboratory for processing and species
82 level identification. Laboratory identification of fauna was undertaken using available identification keys
83 (Poisson, 1957; Tamanini, 1979; Jansson, 1986; Andersen, 1990; Zimmermann and Scholl, 1993), a binocular
84 microscope, and the Heteroptera collections deposited at the National Museum of Natural History in Paris and
85 the Naturalis Biodiversity Centre in Leiden to verify the identifications with the assistance of three experts.

86

87 **Environmental parameters**

88 The following environmental parameters were measured in situ at each site at the time of sampling aquatic
89 Heteroptera comprising pH, salinity (SAL), electrical conductivity (COND), total dissolved salt (TDS) and

90 dissolved oxygen (OXY) with portable probes (WTW, PP350). Air and water temperature (ATEMP, WTEMP)
91 were measured simultaneously in the field using a mercury glass thermometer graduated to 0.1°C. Altitude
92 (ALT) was calculated using a GPS (Garmin etrex 10). Flow velocity (FV) was measured using the time
93 (seconds) taken by a float (cork stopper) to cover a minimum distance of one meter. Visual estimates of
94 percentage substrate composition in shallow water and riparian cover were made at each site (Table S.1 in
95 Supplementary Material). Water samples were collected at each site using 4 L polyethylene bottles and
96 transported on ice back to the “Centre International des Technologies de l'Environnement de Tunis” CITET
97 laboratory for further analyses. Turbidity was measured in the laboratory using a turbidity meter (Hach model
98 2100A). Major cation and anion concentrations: Calcium (Ca^{2+}) and Magnesium (Mg^{2+}) were measured by
99 inductively coupled plasma optical emission spectrometry (ICP-OES). Chloride (Cl^-), and sulphates (SO_4^{2-}) were
100 measured by liquid chromatography (DX-120 Ion Chromatograph). The concentration of nutrients: nitrates
101 (NO_3^-), nitrite (NO_2^-), ammoniac (NH_4^+), and Orthophosphate (PO_4^{3-}), were measured by spectrophotometry
102 (JASCO V-530 UV/VIS) at 630 nm. Chemical oxygen demand (COD) was measured using the amount of
103 potassium dichromate ($\text{K}_2\text{Cr}_2\text{O}_7$) consumed by the dissolved solids in suspension. Biological Oxygen Demand
104 (BOD_5) was measured by incubation of the water sample in the presence of a solution of phosphate and allyl
105 thiourea in darkness and at 20°C over 5-days. Other parameters, including channel width (WIDT) and water
106 depth (DEPT) were measured in the field at each site. The concentration of NO_2^- was consistently below the
107 device's detection limit (0.4 mg L^{-1}), and therefore were not presented in the results below.

108 **Data analysis**

109 Statistical analyses were undertaken in the R environment (R Core Team, 2018). The STATICO multivariate
110 analysis method (Thioulouse et al., 2004; Thioulouse, 2011) was used to investigate the relationships between
111 aquatic Heteroptera communities and environmental variables (including morpho-dynamic parameters) over the
112 four seasons. The STATICO method is based on the use of two analyses: Co-inertia Analysis (Dolédec and
113 Chessel, 1994; Dray et al., 2003) and Partial Triadic Analysis (Thioulouse and Chessel, 1987; Thioulouse,
114 2011). This method allows the simultaneous analyses of three dimensions of the dataset: faunal matrix \times
115 environmental parameters matrix \times four seasons.

116 Co-inertia analysis was initially performed by building a crossed table between the two datasets: one comprising
117 the 21 environmental parameters and the other for the 36 Heteroptera species. Each of these contained 180 rows,
118 corresponding to the 45 sampling sites over four seasons (spring, summer, autumn and winter). Computations
119 were undertaken on these tables using the *statico* function in the *ade4* package (Slimani et al., 2017; Thioulouse

120 et al., 2018). Co-inertia analysis computes axes that maximize the covariance between the scores of the rows
121 (sampling sites) of the environmental parameters table, as well as the scores of the rows of the species table.
122 Partial Triadic Analysis is a K-tables data analytical method. The STATICO analysis consists of computing the
123 four (one for each season) crossed tables (environmental parameters x species) for the four corresponding co-
124 inertia analyses. A Partial Triadic Analysis is then undertaken on the series based on these four crossed tables.
125 The interstructure step computes a weighted mean of the four seasons (the compromise). The compromise step
126 includes a PCA using this table, providing environmental parameter scores and species scores. The intrastructure
127 step computes the scores of the rows (environmental parameters) and columns (species) of the four crossed
128 tables (one for each season) and of the rows of the initial tables (sampling sites of the environmental parameters
129 table and of the species table). The scores computed in the intrastructure step of the STATICO analysis describe
130 the temporal (within and between seasons) and spatial (within and between catchments) variability of the
131 associations between aquatic Heteropteran communities and environmental parameters.
132 When using the STATICO method, the variable scaling and the row weights must be chosen with great care, as
133 they imply different ecological considerations (Dray et al., 2003). In this study, the separate analysis of each
134 table was performed using a PCA because the species responses to the environmental parameters are
135 approximately linear (verified graphically in preliminary analysis). The table of environmental variables was
136 submitted to a “partial Bouroche standardization”, which means that it was first standardized (i.e. centered and
137 normalized) for the whole dataset (globally), and then standardized within each season. The PCA of species
138 abundance data was performed using $\log_{10}(x+1)$ transformed data to reduce the influence of highly abundant
139 species and also submitted to a partial Bouroche standardization. Sampling site weights were considered uniform
140 because the sampling method was homogeneous throughout the time-series and the taxonomic identification was
141 performed consistently by the same individual.

142 **Results**

143 **Environmental characterization**

144 Environmental factors displayed spatial and temporal differences between sampling sites and seasons
145 respectively (Table 1). One-Way Analysis of Variance (ANOVA) indicated significant seasonal differences for
146 the following physicochemical parameters between seasons: pH (DF = 3, F = 25.94, = P < 0.001, R² =0.30),
147 dissolved oxygen (DF = 3, F = 13.13, = P < 0.001, R² =0.18), turbidity (DF = 3, F = 9.69, = P < 0.001, R²
148 =0.14), water temperature (DF = 3, F = 258.35, = P < 0.001, R² =0.81), air temperature (DF = 3, F = 180.96, = P
149 < 0.001, R² =0.75), flow velocity (DF = 3, F = 15.32, = P < 0.001, R² =0.20), nitrate - NO₃⁻ L⁻¹ (DF = 3, F =

150 9.09, = $P < 0.001$, $R^2 = 0.13$), and ammonia - $\text{NH}_4^+ \text{L}^{-1}$ ($\text{DF} = 3$, $F = 4.57$, = $P < 0.001$, $R^2 = 0.07$). The PCA of
151 physicochemical data indicated that the first and second axes explained 22.91% and 12.46% of the variance in
152 the dataset, respectively (Fig. 2). PCA-axis 1 primarily reflected a gradient of altitude and mineralization, with
153 high altitude low mineralization samples located on the positive end and low altitude high mineralization
154 (COND, SAL, TDS) samples on the negative side of the axes. PCA-axis 2 reflected a gradient of dissolved
155 oxygen concentrations and pH on the positive side and temperature (air and water) on the negative side.

156 **Differences in Heteropteran communities between catchments**

157 A total of 36 aquatic Heteroptera species representing 19 genera and 13 families were recorded; 23 species
158 belonging to the Nepomorpha subgroup and 13 species representing Gerromorpha. The densities (individuals
159 m²) and percentage (%) contribution to abundance during the study period for all taxa recorded are presented in
160 Table 2.

161 Nepomorpha contributed 66.54% of the total relative abundance, with *Micronecta scholtzi* (Fieber) representing
162 the most abundant species (22.43%). The Gerromorpha species contributed 33.46% of the total abundance, with
163 *Aquarius cinereus* (Puton) being the most common (17.18%) (Table 2). Species richness and the distribution of
164 Heteroptera varied between catchments, reflecting the variable contribution of different species throughout the
165 study period (Fig. 3). The total density of Heteroptera was greatest at Meliane-Cap Bon (2382 ind/m²) and the
166 highest species richness was recorded at Kroumirie -Mogods (33 species).

167 The aquatic Heteroptera community compositions varied considerably between catchments (Fig. 3). The
168 Medjerda and Kroumirie-Mogods catchments were dominated by two species *Micronecta scholtzi*, and *Aquarius*
169 *cinereus*. The Ichkeul catchment was characterized by higher densities of *Micronecta scholtzi*, *Nepa cinerea* L.,
170 *Naucoris maculatus conspersus* (Stål). *Nepa cinerea*, *Naucoris maculatus conspersus*, and *Hydrometra*
171 *stagnorum* L.. *Parasigara favieri* (Poisson), *Sigara scripta* (Rambur), and *Notonecta maculata* (Fabricius) were
172 more abundant at Meliane-Cap Bon.. *M. scholtzi* and *A. cinereus* occurred at all sites at varying abundances. A
173 number of species were relatively rare in the study region: *Ranatra linearis* L., *Ochterus marginatus marginatus*
174 (Latreille), *Corixa panzeri* (Fieber), *Hesperocorixa linnaei* (Fieber), *Hesperocorixa moesta* (Fieber),
175 *Hesperocorixa furtiva* (Horvath), *Sigara stagnalis stagnalis* (Leach), *Sigara selecta* (Fieber), *Sigara nigrolineata*
176 *nigrolineata* (Fieber), *Notonecta meridionalis* (Poisson), *Hebrus montanus* (Kolenati) and two endemic taxa to
177 Maghreb (Algeria, Tunisia) - *Velia eckerleini* (Tamanini), and *Velia Africana* (Tamanini).

178 **Seasonal community responses to environment variables**

179 Weights obtained from the interstructure process of STATICO were 0.49, 0.50, 0.50, and 0.51 for Winter,
180 Spring, Summer and Autumn, respectively (Fig. 4A). This indicated that the four seasons had equal importance
181 and that the relationships between aquatic Heteropteran communities and environmental parameters could be
182 directly compared between seasons (Fig.4B).

183 The compromise step of the STATICO method identified the main environmental structures persisting across the
184 four seasons within the PCA. The first PCA-axis reflected the longitudinal gradient from headwater sites (high
185 altitude, high flow velocity, high dissolved oxygen and pH - higher axis values) to lowland sites (high salinity

186 and conductivity – lower axis values). The second PCA-axis reflected a pollution gradient; with sites with high
187 concentrations of nitrates, phosphates, sulfates, and higher values of BOD₅ and COD in the upper/positive sector
188 of the graph, and deeper sites with high dissolved oxygen levels on the lower/negative part of the graph (Fig.4C).
189 Heteroptera species were ordered along these two gradients reflecting their preferences in relation to the
190 environmental parameters (Fig.4D).

191 **Inter-catchment differences in community responses to different environmental parameters**

192 Within the infrastructure step of the analysis, the environmental parameters and Heteroptera communities were
193 averaged across all four seasons (Fig. 5). The first axis reflected a mineralization gradient with higher values of
194 salinity (SAL), electric conductivity (COND), and total dissolved salts (TDS) on the left, and high altitude
195 (ALT), flow velocity (FS), and pH on the right of the factorial plan. The second axis reflected a nitrate (NO)
196 gradient from the top of the factorial plan and dissolved oxygen (OXY), and depth (Dept) at the bottom of the
197 factorial plan. The structure of the species reflected the environmental gradient on the first axis (Fig. 4), with
198 species displaying saline intolerance (*Aquarius cinereus* (Acin), *Hydrometra stagnorum* (Hysta), and *Notonecta*
199 *glauca glauca* (Ngl)) located on the low mineralization side of the factorial plan (right) and halophilic species
200 (*Sigara scripta* (Sscr), and *Anisops debilis perplexus* (Aper)) on the high salinity side (left). Nepomorpha and
201 Gerromorpha species were distributed according to their individual salinity affinities. The distribution of the
202 species along the second axis indicated that *Parasigara favieri* (Pfav) *Naucoris maculatus conspersus* (Ncon)
203 and *Notonecta maculata* (Nmac) were associated with high dissolved oxygen concentrations and greater water
204 depth. As a result, the species–environment relationships primarily consisted of a salinity gradient linked to a
205 freshwater - brackish water faunal gradient. *Gerris brasili*, *Gerris maculatus*, *Hydrometra stagnorum*,
206 *Microvelia pygmaea*, *Velia africana*, *Velia eckerleini*, *Hesperocorixa linnaei*, *Hesperocorixa furtiva* and
207 *Notonecta meridionalis* were associated with low mineralization and relatively high altitude and higher flow
208 velocities. In contrast, *Sigara stagnalis*, *Sigara lateralis*, *Sigara selecta*, *Anisops debilis perplexus*, and *Anisops*
209 *sardeus sardeus* were associated with higher mineralization levels and relatively low altitude and reduced flow
210 velocities. *Parasigara favieri* were associated with high dissolved oxygen concentrations.

211 **Inter- and intra-basin variations in communities in relation to different environment controls**

212 The Infrastructure between the two sets of descriptors (environmental parameters - red labels- and aquatic
213 Heteroptera - blue labels) on the PCA of the compromise output for each catchment is presented in Figure 6. For
214 the Medjerda catchment, sites are roughly ordered along an upstream-downstream gradient from right to left
215 along the first axis. This reflects the mineralization and salinity gradient. In all seasons, site 5 appears at the top

216 of axis 2 due to increased pollution, higher water and air temperature, an absence of precipitation and reduced
217 flow velocities. The low values of dissolved oxygen (OXY) at these sites (0.3 mg/l) are consistent with this
218 interpretation (Fig. 6A). However, aquatic Heteroptera displayed clear seasonal variability mainly because of the
219 differences in the density of species between seasons (Fig. 6B).

220 For the Kroumirie-Mogods catchment, the environmental parameters clustered on the positive side of axis I,
221 associated with mild mineralization, linked to lithology; the catchment is dominated by clay-sandstone soils and
222 dense vegetation cover (Fig. 6A). The distribution of species from the sampling sites indicated a strong structure,
223 which indicates a good fit between the aquatic Heteroptera (corresponding to a majority to freshwater affinities)
224 and environmental parameters (the arrows were mostly short). In spring and summer, large differences were
225 observed for stations 1 and 9 when higher Heteroptera species richness and/or abundances were recorded (Fig.
226 6B).

227 For the Ichkeul catchment, during winter and autumn, environmental trajectories for most sites clustered at the
228 center of the axes. However, during spring and summer sites 11, 14 and 15 were located on the negative side of
229 axis I, reflecting an upstream-downstream gradient and seasonal variation of temperature and salinity (Fig. 6A).
230 Most species were located centrally and / or on the negative part of axis I (Fig. 6B). Environmental and aquatic
231 Heteroptera trajectories followed similar patterns for most seasons.

232 For the Meliane-Cap Bon catchment, the upstream-downstream gradient was less clear; site 9 was clearly
233 distinguished from other sites due to pollution and higher COD and BOD₅ (Fig. 6A). A poor association between
234 the fauna and the environment parameters was observed (Fig. 6B).

235

236 **Discussion**

237 Our results provide an important contribution to the study of freshwater communities from the north African
238 Mediterranean region including North Tunisia, which has been identified as a biodiversity hotspot (Marignani et
239 al., 2017; Abdou et al., 2018). This is consistent with previous Mediterranean ecosystem assessment studies, and
240 results that identified macroinvertebrate diversity as contributing disproportionately to ecological knowledge for
241 the North African region (Beauchard et al., 2003; Ball et al., 2013; De Figueroa et al., 2013; Slimani et al.,
242 2019). Benthic macroinvertebrates depend on a wide range of abiotic factors, including climate, water
243 physiochemistry, anthropogenic pressures and riparian habitat availability (White et al., 2019; Ceron et al., 2020)
244 and this study confirms that this is also true for aquatic insects such as Heteroptera. This study also supports the
245 finding of research linking the distribution and abundance of some Aquatic Heteroptera to water physico-

246 chemistry from other regions (Savage, 1994; Hufnagel et al., 1999). However, there were marked differences in
247 the Heteropteran assemblage in the semiarid Mediterranean study region (Northern Tunisia). The Heteropteran
248 fauna displayed significant differences in species richness and abundance. Richness of Heteroptera declined
249 from 33 species in Kroumirie-Mogods (Northern western) to 19 species in the Meliane-Cap Bon catchment
250 (Northern western), with a similar reduction in the relative density of individuals. This reflects changes in with
251 water quality, with the least impacted sites displaying a positive correlation between good water quality and
252 Heteroptera density for eight of the environmental parameters (out of 21). This indicates a strong link between
253 the faunal functional composition and local in-stream habitats conditions (micro-habitats) rather than the larger-
254 scale environmental conditions (Townsend and Hildrew, 1994).

255 The aquatic Heteroptera densities recorded in northern Tunisia displayed clear spatial variation reflecting
256 the preference and tolerances of individual species. *Micronecta scholtzi*, *Naucoris maculatus conspersus*, and
257 *Aquarius cinereus* occurred in high numbers highlighting their generalist characteristics in relation to most
258 abiotic, allowing them to thrive in extreme environmental conditions (Carbonell et al., 2011). The reduction in
259 macroinvertebrate densities in the Kroumirie-Mogods catchment may reflect interspecific competition at sites
260 with high species richness (Boumaiza, 1994). However, no species were recorded at all of the sampling sites.
261 This reflects the heterogenous abiotic conditions of the habitats studied as well as the preferences and
262 adaptations (ecological valence) of the individual Heteroptera species.

263 The results of STATICO analyses indicate that environmental and spatio-temporal gradients were
264 particularly important determinants of community structure in northern Tunisia (providing evidence to support
265 our hypothesis). The distribution of fauna reflected several physicochemical parameters which varied among the
266 four river catchments. The analysis highlights that the distribution of Heteroptera most strongly reflect a
267 mineralization gradient which has been shown to primary factor structuring communities (Verneaux and Tuffery,
268 1967). Other factors, such as altitude and flow velocity were also strongly correlated with mineralization. This
269 study provides further evidence that mineralization represents one of the principal forces driving heteroptera
270 community composition and distribution a global scale (Tully et al., 1991; Karaouzas and Gritzalis, 2006;
271 Bloechl et al., 2010; Carbonell et al., 2011; Scheibler et al., 2016). Previous studies on inland aquatic systems
272 have shown that richness and diversity decline with increasing mineralization (Sánchez et al., 2006; Kefford et
273 al., 2011; Millán et al., 2011; Slimani et al., 2019; Gutiérrez-Cánovas et al., 2019). In addition, mineralization
274 was reported to be the most important factor influencing the macroinvertebrate community richness of wetland
275 aquatic systems (Kefford et al., 2011; Millán et al., 2011; Cañedo-Argüelles et al., 2012; Velasco et al., 2019).

276 Our analysis demonstrated aquatic heteroptera diversity decreased downstream with increasing mineralization
277 (Fig.5). The salinity (SAL), electric conductivity (COND), and total dissolved salts (TDS) of stream waters were
278 identified as the primary factor controlling Heteroptera diversity. Many oligo- and mesotrophic taxa, such as
279 Veliidae and Notonectidae, were abundant in streams with low mineralization and higher DO concentrations, but
280 some Corixidae displayed an association with brackish water systems; comparable to results reported in other
281 studies (Slimani et al., 2015, 2016).

282 The specific richness of Heteroptera displayed a general reduction with increasing salinity from headwaters to
283 downstream (ST1 to ST44), and were absent from sites subject to high pollution stress (ST5 and ST45 - the site
284 with the highest BOD₅ and COD concentrations). This pattern was reflected in the Heteroptera species recorded,
285 with some species more common in freshwater, for example *N. meridionalis*, *V. eckerleini*, *V. africana* and *A.*
286 *najas* were only recorded in the Kroumirie-Mogods (SAL ≤ 0.23 PSU), where clayey-sandstone soils dominated
287 and riparian woodland occurred (oak - *Quercus canariensis* and cork tree - *Quercus suber*) (Boumaiza, 1994).

288 In the other catchments (SAL ≥ 1 PSU; EC ≥ 1900 μs/cm at 20°C), Heteroptera communities were characterised
289 by *A. cinereus*, *M. scholtzi*, *N. glauca* in the headwaters and *S. scripta*, *S. stagnalis*, *S. lateralis* and *N.*
290 *conspersus* in the more mineralized sites downstream. Such distributional patterns have also been reported
291 observed in other saline Mediterranean streams (Millán et al., 2011). In particular, some Corixidae appear to be
292 well adapted to osmotic stress and some, such as are *Sigara scripta* are considered halophilic taxa and indicative
293 of hypersaline streams (Savage, 1982, 1990; Millán et al., 2011; Slimani et al., 2015). There is great variation
294 among species regarding salinity tolerance with species-based ecophysiological and metabolically mechanisms
295 enabling them to tolerate such stress (Oren, 2000; Velasco et al., 2006; Elevi Bardavid and Oren, 2008).

296 Although Heteopterans are sensitive to anthropogenic pollution of the aquatic ecosystems, their respiratory
297 physiology (air breathing) and mating behavior enable them to persist even when exposed to harsh
298 environmental conditions (Lytle, 2015). However, in the current study Heteroptera were totally absent from the
299 most severely polluted sites at Kasseb and Lebna. These results are consistent with results reported by Zhang et
300 al. (2018) in response to chronic pollution and habitat modification. The ability of Heteroptera to withstand
301 relatively extreme environmental conditions may partially explain the negative correlations between water
302 temperatures, dissolved oxygen, depth and turbidity in this study and resulted in the high species richness
303 recoded during Spring and Summer. These observations support the findings of Slimani et al. (2017) and
304 previous studies in the study area highlighting correlations between aquatic macrophytes (Casagrande &

305 Boudouresque, 2007), phytoplankton (Casagrande and Boudouresque, 2010) and Coleoptera - water beetles
306 (Touaylia et al., 2013) with temperature and salinity.

307 The results reported suggest Heteroptera assemblages could be more widely used as indicators of freshwater
308 biodiversity in biomonitoring programs and the conservation of freshwater biodiversity in Mediterranean
309 freshwater ecosystems (Calapez et al., 2018). They have considerable utility for monitoring changes in
310 environmental parameters, as bioindicators of either deteriorating or improving habitat quality that may be
311 related to changing patterns of land use or other anthropogenic stressors (Buchwalter et al., 2003). The data from
312 this study could be used to inform the development of an index of biological richness and aquatic ecosystem
313 health when combined with wider data from the macroinvertebrate community from the region. These measures
314 could be used to provide measures of both biodiversity and wider environmental quality which could be
315 compared to those developed in adjacent regions in Europe and beyond. In addition, Heteroptera may have
316 utility as agents of biological control. With the exception of the omnivorous Corixidae, aquatic Heteroptera are
317 insect predators and have been recorded to help in the regulation of larval populations of the larvae of mosquito
318 vectors of disease (Aditya et al., 2004; Banerjee et al., 2010). Their use in the biocontrol of mosquitoes could be
319 used alongside the targeted application of insecticides to avoid or minimize the effects of chemical
320 contamination on wetland ecosystems.

321 Future research is needed to combine the results of abiotic factors within a geographical information system
322 (GIS) to track species current and potential future distributions under climate change scenarios and
323 anthropogenic impacts. Many species of aquatic Heteroptera have been reported to be responding to climate
324 change by shifting their distributional ranges, changes in recorded abundances, phenology, voltinism,
325 physiology, behaviour and community structure, thereby serving as particularly good bioindications of climate
326 change (Musolin, 2007). Rabitsch (2008) referred to the process as Mediterraneanization, given that five new
327 species including *Micronecta scholtzi* (Corixidae), *Microvelia buenoi* (Veliidae), *Microvelia pygmaea*
328 (Veliidae), *Notonecta meridionalis* (Notonectidae), *Velia currens* (Veliidae) were recorded in Central Europe as
329 their geographical range expanded from their native Mediterranean region. Similarly, Klementová and Svitok
330 (2014) demonstrated that *Anisops sardeus* (Notonectidae), native to the Sahelo-Sindian area, was actively
331 expanding its geographical range from the Mediterranean and is now expanding its distribution in Central
332 Europe.

333

334

335 **Conclusion**

336 This study examined Heteropteran communities inhabiting the understudied Mediterranean region of north
337 Africa. The results presented highlight how different environmental parameters structure Heteropteran
338 communities, principally altitude, mineralization and dissolved oxygen levels. Strong seasonal differences in
339 environmental conditions in the study area resulted in the temporal variability of Heteropteran assemblages.
340 Moreover, intra- and inter-basin variations in environmental conditions associated with both natural and
341 anthropogenic resulted in a strong spatial structuring of Heteropterans. This study represents the first step
342 towards understanding the relationship between ecological factors and biodiversity of true water bugs, knowing
343 that freshwater management will become increasingly pivotal as increasing human populations and projected
344 climatic change threaten freshwater ecosystems. Findings from this study highlighted that some Heteropteran
345 taxa, including *N. conspersus*, *N. maculata*, *A. najas*, *Aquarius cinereus*, and *Micronecta scholtzi*, were indicative
346 of more pristine semi-natural environments and could provide the basis for characterising reference conditions
347 for other sites in the north African Mediterranean region. Our results also provide clear evidence of how aquatic
348 Heteroptera can be used as indicators of different environmental stressors, including water quality issues, and
349 could be used more widely in biomonitoring assessments across northern Africa.

350

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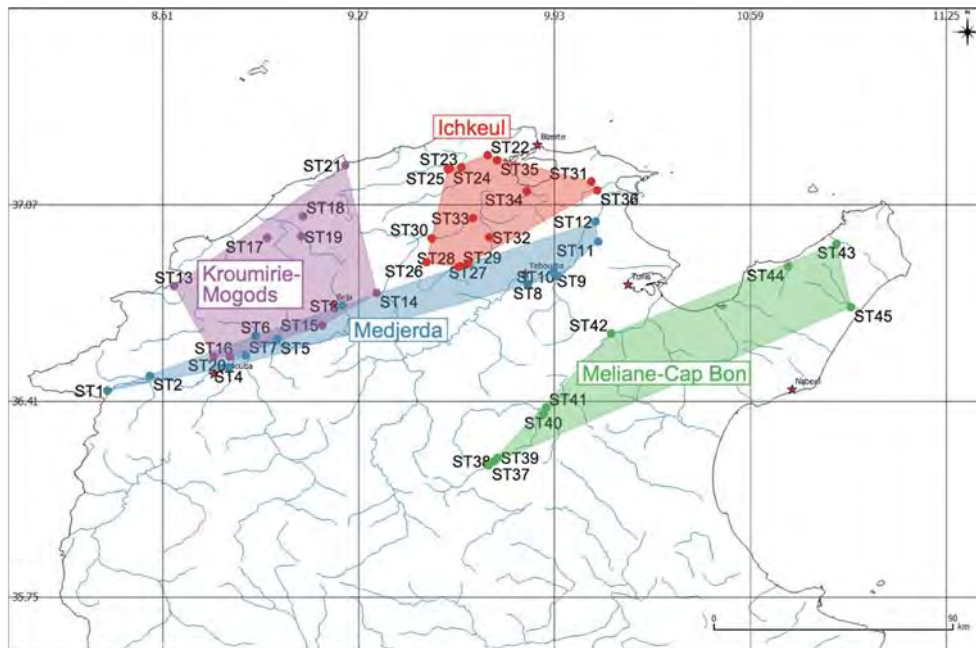


Figure 1.

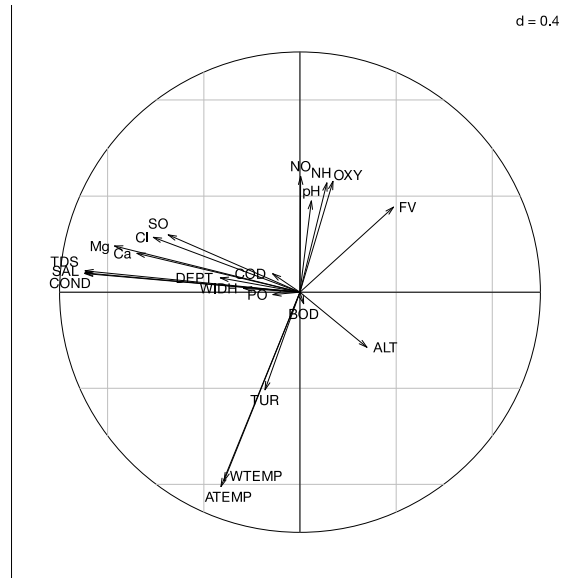


Figure 2.

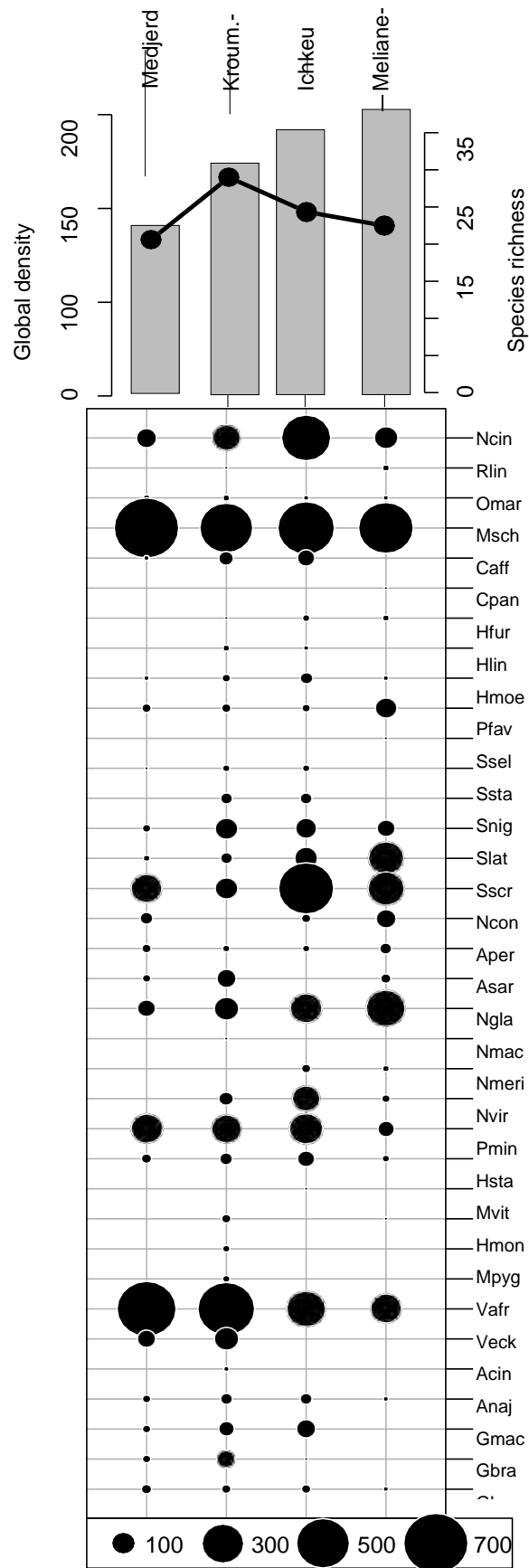


Figure 3.

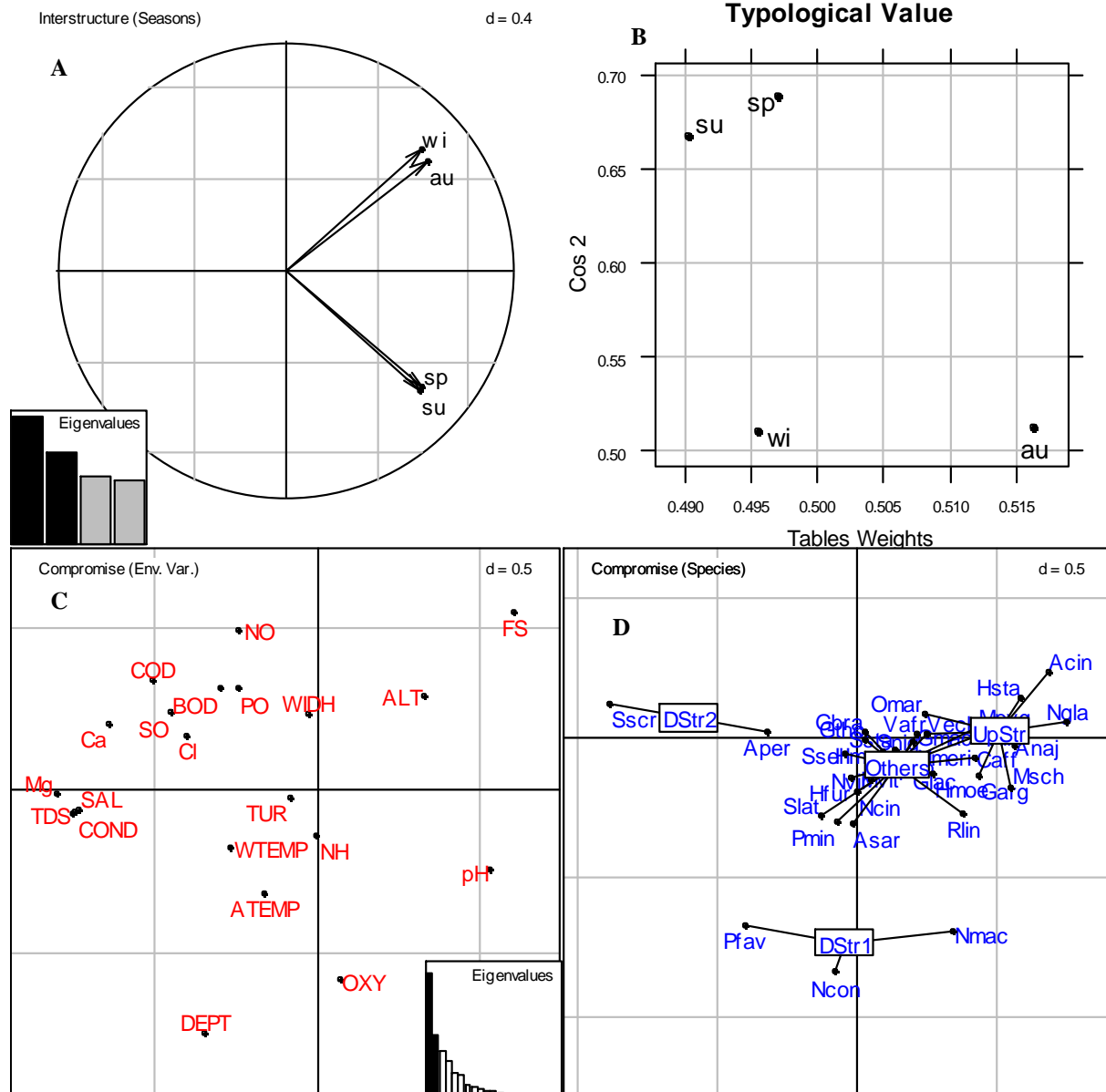


Figure 4.

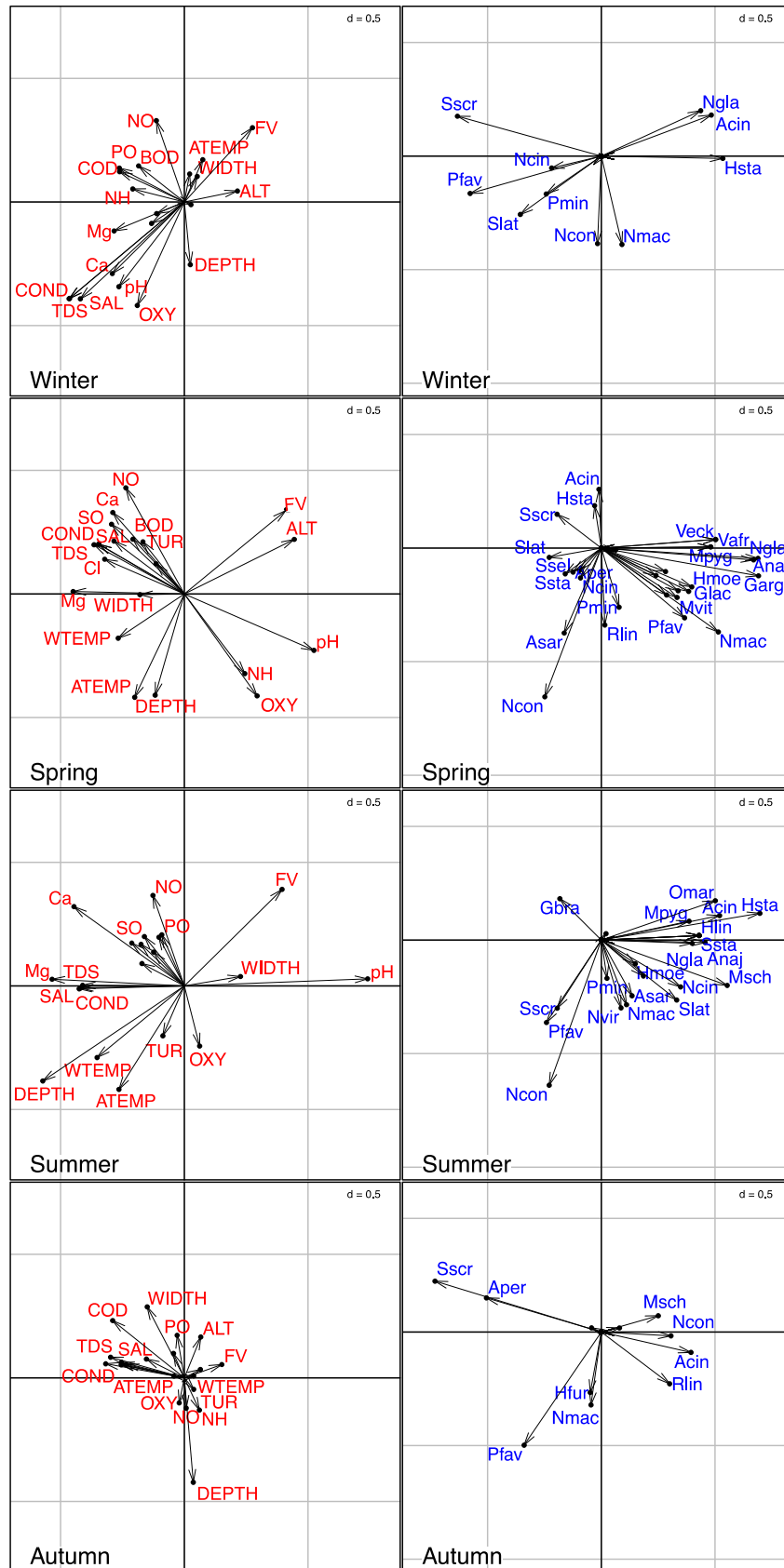


Figure 5.

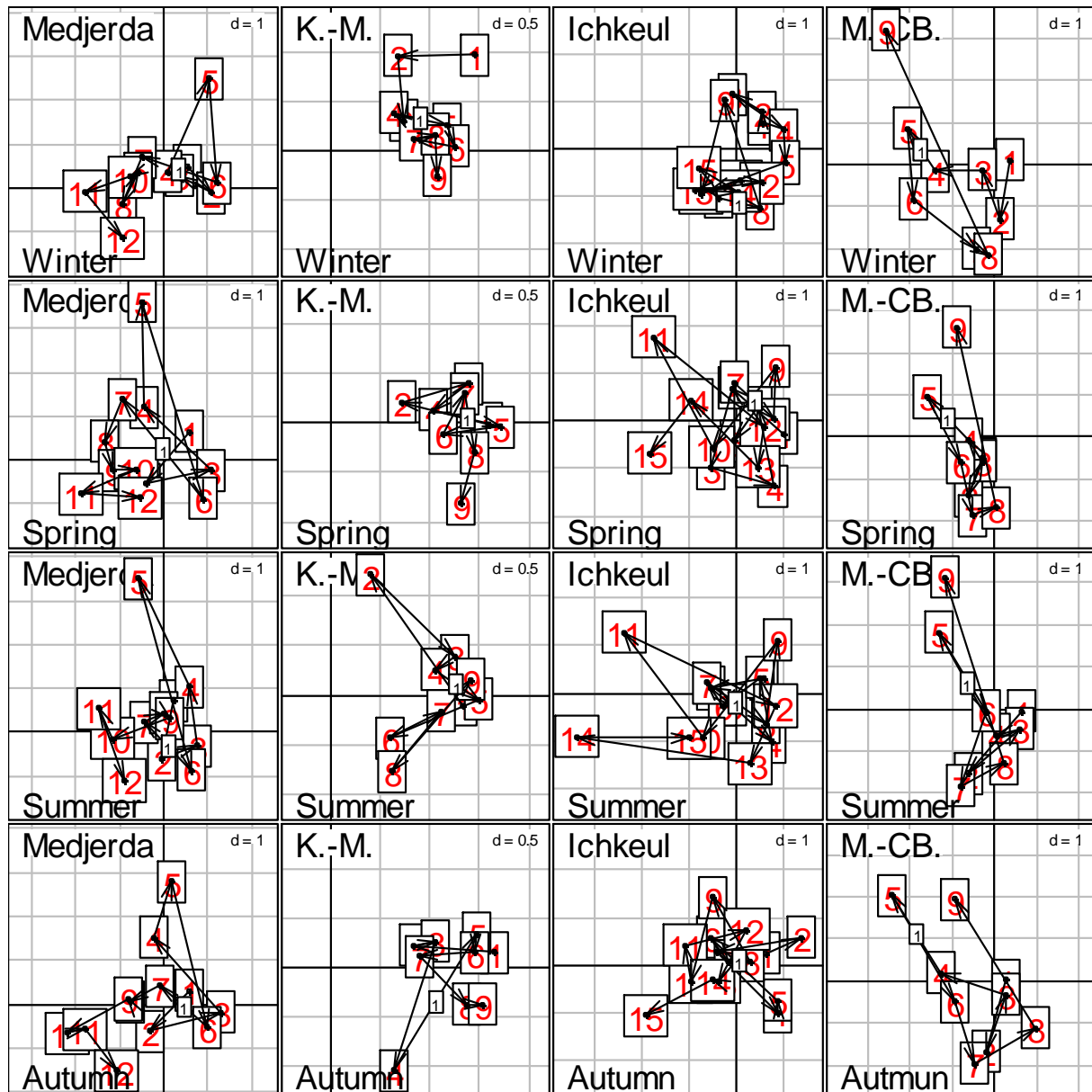


Figure 6A.

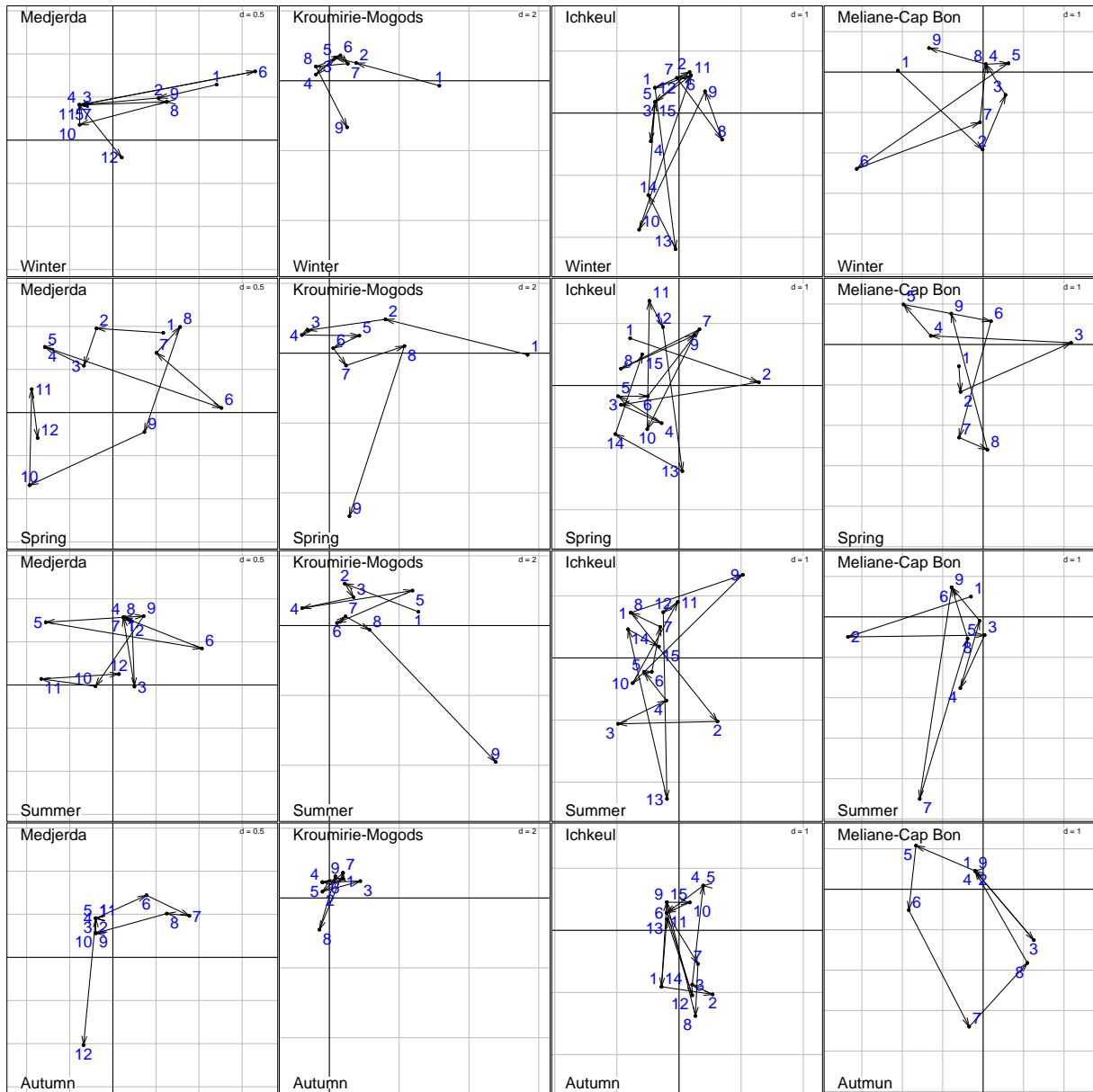


Figure 6B.

Figure 1. Map indicating the location of the study sites within the four catchments (Medjerda, Kroumirie-Mogods, Ichkeul and Meliane-Cap Bon) in northern Tunisia (Site codes and names are presented in Supplementary Table S1) .

Figure 2. PCA biplot of indicating the physicochemical variables with the greatest loading on the first two axes –see Table 1 for definition of environmental codes.

Figure 3. (a) Plot of the spatial changes in aquatic Heteroptera Global density (ind/m²) and Species richness during the study period (b) Plot of the spatial changes in mean density for each of the 36 species in the four catchments (Medjerda, Kroumirie-Mogods, Ichkeul and Meliane-Cap Bon) in northern Tunisia (codes for species names are defined on Table 2).

Figure 4. General plot of the STATICO method: Interstructure factor map (A) and the table weight and Cos² are shown in (B). Compromise factor map for environmental variables (C) and for taxa (D) using STATICO analysis on the 45 sites data in the four catchments of northern Tunisia from January to December 2013. See Tables 1 and 2 for definitions of environmental and taxonomic codes respectively.

Figure 5. Intrastructure plot of the STATICO analysis for environmental parameters (red, left) and water bugs (blue, right) at each season. See Tables 1 and 2 for definitions of environmental and taxonomic codes respectively

Figure 6A. Intrastructure plot of the STATICO analysis detailing the environmental parameters for the sampling sites by catchment and season. See Tables S1 for site names and further details.

Figure 6B. Intrastructure plot of the STATICO analysis of the water bugs for the sampling sites by catchment and season. See Tables S1 for site names and further details.

Table 1. Summary of environmental parameters for the 45 sites from the four catchments (Medjerda; Kroumirie-Mogods; Ichkeul; and Meliane-Cap Bon) in northern Tunisia during the study period. Definition of environmental parameter codes: channel width (WIDT) and water depth (DEPT), altitude (ALT), salinity (SAL), electrical conductivity (COND), total dissolved salt (TDS) dissolved oxygen (OXY), water temperature (WTEMP), air temperature (ATEMP), flow velocity (FV), calcium (Ca^{2+}), magnesium (Mg^{2+}), sulphates (SO_4^{2-}), chloride (Cl^-), nitrates (NO_3^-), nitrite (NO_2^-), ammoniac (NH_4^+), orthophosphate (PO_4^{3-}), chemical oxygen demand (COD), biological oxygen demand (BOD_5).

Environmental parameters	Global			Winter			Spring			Summer			Autumn			F values (df)
	Min	Max	Mean \pm SD	Min	Max	Mean \pm SD	Min	Max	Mean \pm SD	Min	Max	Mean \pm SD	Min	Max	Mean \pm SD	
ALT (m)	1	398	105.4 \pm 117	1	398	105.4 \pm 117	1	398	105.4 \pm 117	1	398	105.4 \pm 117	1	398	105.4 \pm 117	0
Width (m)	2	40	12.01 \pm 10.3	2	40	11.8 \pm 10	2	40	11.8 \pm 10	2	40	11.8 \pm 10	2	40	11.8 \pm 10	0.03
Depth (cm)	5	50	19.66 \pm 14.15	5	50	19.6 \pm 14.2	5	50	19.6 \pm 14.2	5	50	19.6 \pm 14.2	5	50	19.6 \pm 14.2	0
pH	6.8	8.69	7.8 \pm 0.33	7.2	8.45	7.82 \pm 0.34	7.4	8.7	8 \pm 0.24	6.8	8.06	7.5 \pm 0.26	7.3	8.42	7.84 \pm 0.28	25.94* **
SAL (psu)	0.1	7.6	1.2 \pm 1.15	0.1	3.8	1.06 \pm 0.97	0.1	3.8	1.4 \pm 1.1	0.1	7.6	1.5 \pm 1.4	0.1	3.5	1.16 \pm 1	1.52
COND ($\mu\text{S cm}^{-1}$)	212	13100	2515 \pm 2071	212	7400	2058 \pm 1736	382	7520	2806 \pm 2036	388	13100	2883 \pm 2495	245	6510	2314 \pm 1895	1.65
TDS (mg L ⁻¹)	154	10558	1864 \pm 1570	154	5508	1523 \pm 1302	259	5597	2080 \pm 1542	263	10558	2141 \pm 1930	179	4845	1710 \pm 1420	1.61
OXY (mg L ⁻¹)	1	11.8	6.38 \pm 2.11	1	11.8	6.59 \pm 2.8	1.4	9.25	5.83 \pm 1.83	1.2	6.68	5.36 \pm 1	1.1	9.77	7.74 \pm 1.53	13.13* **
Turbidity (NTU)	0	71	4.44 \pm 13.22	0.1	16	3 \pm 3.9	0.0	60	7.45 \pm 12.84	0.3	64	16.5 \pm 16.6	0.1	71	6.77 \pm 12.41	9.69* **
Water Temp (°C)	2	30	16.66 \pm 6.42	2	20	10.5 \pm 3.6	16	24	19.92 \pm 2.42	18	30	24.4 \pm 2.9	8	18.5	11.7 \pm 1.95	258.3* **
Air Temp (°C)	5	42	19.08 \pm 8.93	5	17	13.2 \pm 3.25	12	35	22.64 \pm 6.43	23	42	30 \pm 5	7	14	10.5 \pm 1.63	180.96* **
FV (cm s ⁻¹)	2.5	159	36.4 \pm 31.95	3.3	159	42.07 \pm 30	2.6	63	21 \pm 17.7	2.6	58.82	21.8 \pm 15.9	4.5	153	54.85 \pm 39	16.24* **
Ca ²⁺ (L ⁻¹)	14	540.8	156.1 \pm 90.9	14	341.3	136.9 \pm 78.6	30	540.8	167.8 \pm 103	33	540.8	166 \pm 96	30	389	153 \pm 82.2	1.12
Mg ²⁺ (L ⁻¹)	3.5	277.9	59.77 \pm 52.9	3.5	201.7	51.94 \pm 47.64	5.9	277.9	67.57 \pm 45.7	5.9	277.9	61 \pm 54.6	7.7	207	58.2 \pm 49.8	0.68

SO ₄ ²⁻ (L ⁻¹)	13.5	3100	239.3±568.1	13	872.3	176.72±185	21	3100	273.6±488	33	3100	304±492	13	872	202±197	1.16
Cl ⁻ (L ⁻¹)	0.1	2600	268.9± 457	0.1	1491	194.96±268	37	2600	324±589.7	37	2600	347±584	0.1	1491	209±267	1.3
NO ₃ ⁻ (L ⁻¹)	0.26	581.9	44.47±90.57	0.5	114	27.5±31	0.5	103.7	26.4±29.7	0.5	92	22.24±24.7	0.2	581	101±162	9.09* **
NH ₄ ⁺ (L ⁻¹)	0.02	81.2	2.3±14.47	0.06	12.3	1.7±2	0.02	2.34	0.64±0.54	0.1	2.42	0.7±0.49	0.03	81.2	6.3±16.7	4.57* **
PO ₄ ³⁻ (L ⁻¹)	0.1	8.73	0.31±0.77	0.1	8.73	0.38±1.28	0.15	2.6	0.28±0.43	0.15	4	0.31±0.68	0.1	2.47	0.28±0.4	0.15
COD (mg L ⁻¹)	15	1025	39.89±84.77	16	1025	57.87±155.2	16	181	31.1±26.8	16	33	33±34	15	323	37.5±52	0.94
BOD5 (mg L ⁻¹)	0.3	102	2.98±10.5	0.5	31	2.39±2.39	0.3	56	3.1±10.43	0.3	8.72	2.88±8.7	0.5	102	3.5±15	0.08

F values: between groups mean square/within-groups mean square.

Significant difference between sampled seasons: (***)p < 0.001).

Table2. List of species and their codes used in STATICO analysis.
Average (range) species density (ind/m²) and abundance (%) of aquatic Heteroptera during the study period.
Species in bold represent the most abundant species.

	Family	Species	Codes	Global density (ind/m ²)	Abundane (%)
Nepomorpha	Nepidae	<i>Nepa cinerea</i> L.	Ncin	508.33	7.82
	Ranatridae	<i>Ranatra linearis</i> L.	Rlin	25	0.38
	Ochteridae	<i>Ochterus marginatus</i> L.	Omar	16.66	0.26
	Micronectidae	<i>Micronecta scholtzi</i> F.	Msch	1458.33	22.43
	Corixidae	<i>Corixa affinis</i> L.	Caff	58.33	0.89
		<i>Corixa panzeri</i> F.	Cpan	8.33	0.13
		<i>Hesperocorixa furtiva</i> H.	Hfur	25	0.26
		<i>Hesperocorixa linnaei</i> F.	Hlin	16.66	0.26
		<i>Hesperocorixa moesta</i> F.	Hmoe	58.33	0.89
		<i>Parasigara favieri</i> P.	Pfav	100	1.54
		<i>Sigara selecta</i> F.	Ssel	8.33	0.13
		<i>Sigara stagnalis stagnalis</i> F.	Sstag	50	0.77
		<i>Sigara nigrolineata nigrolineata</i> F.	Snig	83.33	1.28
		<i>Sigara lateralis</i> L.	Slat	175	2.69
		<i>Sigara scripta</i> R.	Sscr	250	3.84
	Naucoridae	<i>Naucoris maculatus conspersus</i> S.	Ncon	658.33	10.13
	Notonectidae	<i>Anisops debilis perplexus</i> P.	Aper	91.66	1.41
		<i>Anisops sardeus sardeus</i> H.	Asar	50	0.77
		<i>Notonecta glauca</i> L.	Ngla	66.66	1.02
<i>Notonecta maculata</i> F.		Nmac	433.33	6.66	
<i>Notonecta meridionalis</i> P.		Nmer	41.66	0.13	
<i>Notonecta viridis</i> D.		Nvir	16.66	0.26	
Pleidae	<i>Plea minutissima</i> L.	Pmin	166.66	2.56	
Gerromorpha	Hydrometridae	<i>Hydrometra stagnorum</i> L.	Hsta	450	6.92
	Mesoveliidae	<i>Mesovelia vittigera</i> H.	Mvit	125	1.92
	Hebridae	<i>Hebrus montanus</i> K.	Hmon	8.33	0.13
	Veliidae	<i>Microvelia pygmaea</i> D.	Mpyg	33.33	0.51
		<i>Velia eckerleini</i> T.	Veck	33.33	0.51
		<i>Velia africana</i> T.	Vafr	33.33	0.5
	Gerridae	<i>Aquarius cinereus</i> P.	Acin	1116.66	17.18
		<i>Aquarius najas</i> De G.	Anaj	41.66	0.64

		<i>Gerris maculatus</i> T.	Gmac	50	0.26
		<i>Gerris brasili</i> P.	Gbra	58.33	0.89
		<i>Gerris lacustris</i> L.	Glac	116.66	1.79
		<i>Gerris argentatus</i> S.	Garg	91.66	1.41
		<i>Gerris thoracicus</i> S.	Gtho	50	0.77