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Abstract

Salinity is a limiting factor for many invertebrates, especially for Odonata which are typically associated with freshwater ecosystems. In Europe, 15 Odonata species inhabit brackish wetlands and only few detailed data on their tolerance toward salinity are available. We investigated Odonata fauna in 11 sampling stations situated in three estuarine areas (northern Adriatic coastline) which differed in salinity conditions (freshwater- polyhaline habitats) in order to assess affinity of Odonata species to brackish habitats and to describe their distribution pattern in coastal wetlands,. Adults, exuviae (the remains of the exoskeleton after the last larval instar), and the main chemical and physical water parameters were sampled every 2 weeks for 1 year in each station. In total, 25 species were detected and 56% of them were able to complete their life cycle in brackish water environments. Our results showed that freshwater and oligohaline ponds were the most favorable for dragonflies, with an overall higher species richness. There was a high species turnover along the salinity gradient, with a strong differentiation among the communities along the gradient. Considering the exuviae, we observed a high specificity with respect to the habitat conditions (seven species exclusive of freshwater sites and six of oligohaline ones, respectively). Among the adults, four species were found exclusively in freshwater habitats and no species seemed to be strictly connected with oligohaline habitats. Coastal wetlands, composed by a mosaic of different habitats, especially when freshwater and seawater are close together, support many Odonata species with different tolerance toward salinity conditions. They also provide useful insights for conservation and management actions.

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Dragonfly (Odonata) Diversity Patterns in Mixohaline Coastal Wetlands

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Abstract
Salinity is a limiting factor for many invertebrates, especially for Odonata which are typically associated with freshwater ecosystems. In Europe, 15 Odonata species inhabit brackish wetlands and only few detailed data on their tolerance toward salinity are available. We investigated Odonata fauna in 11 sampling stations situated in three estuarine areas (northern Adriatic coastline) which differed in salinity conditions (freshwater- polyhaline habitats) in order to assess affinity of Odonata species to brackish habitats and to describe their distribution pattern in coastal wetlands,. Adults, exuviae (the remains of the exoskeleton after the last larval instar), and the main chemical and physical water parameters were sampled every 2 weeks for 1 year in each station. In total, 25 species were detected and 56% of them were able to complete their life cycle in brackish water environments. Our results showed that freshwater and oligohaline ponds were the most favorable for dragonflies, with an overall higher species richness. There was a high species turnover along the salinity gradient, with a strong differentiation among the communities along the gradient. Considering the exuviae, we observed a high specificity with respect to the habitat conditions (seven species exclusive of freshwater sites and six of oligohaline ones, respectively). Among the adults, four species were found exclusively in freshwater habitats and no species seemed to be strictly connected with oligohaline habitats. Coastal wetlands, composed by a mosaic of different habitats, especially when freshwater and seawater are close together, support many Odonata species with different tolerance toward salinity conditions. They also provide useful insights for conservation and management actions.

Keywords Brackish water · Coastal wetlands · Community ecology · PERMANOVA · Salinity

Introduction

Odonata (Insecta: Zygoptera, Anisoptera) can be considered an amphibious group of insects (Wildermuth et al. 2005), whose taxonomy is widely accepted and whose adults (or imagoes) are quite easy to be identified (Simaika and Samways 2012). Q1 They are characterized by a relatively short generation time which begins from an aquatic larval stage (that can last many years) followed by a terrestrial adult phase (Askew 1988). Odonata are ecologically important because they are major predators in terrestrial and aquatic ecosystems (Corbet 1993; Samways and Steytler 1996; Clark and Samways 1996; Reece and Mcintyre 2009). Owing to their bipartite life cycle (they occupy the interface between aquatic and terrestrial ecosystems) and sensitivity to environmental changes (Balzan 2012; Cat et al. 2018), Q2 they are good indicators of habitat quality of both aquatic and terrestrial habitats (Sahlén and Ekestubbe 2001; Foote and Hornung 2005; Willigalla and Fartmann 2012). Most of the 5680 known larvae species depend only on freshwater habitats (Kalkman et al. 2008). For this reason, they are considered a “flagship” indicator group (Sharma et al. 2007; Balzan 2012; Hart et al. 2014) in freshwater ecosystems, where they also represent focal organisms for conservation (Samways 2008; Clausnitzer et al. 2009). The distribution of Odonata species

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in the environment is largely determined by the presence of suitable habitats, even though individuals commonly occur in environments with unsuitable abiotic conditions (McPeek 2008; Balzan 2012). Local abiotic and biotic factors such as temperature and water chemistry, as well as abundances of predators or parasites, can impact on the survival, growth, and fecundity of individuals (Askew 2004). The ecological requirements of Odonata and the autecological factors limiting species distribution in particular habitats are still unclear (McPeek 2008; Balzan 2012). Although Odonata are not common saltmarsh inhabitants (Cheng 1976), many species can withstand high level of salinity (Zinchenko and Golovatyuk 2013) and live in brackish environments such as saltmarshes (Catling et al. 2006). In these habitats, Diptera, Coleoptera, and Hemiptera dominate most of the insect fauna (Cheng 1976). On the other hand, Odonata represent ca. 3% of this assemblage only (Bowden and Johnson 1976). Specifically, Catling et al. (2006) noted that a "heterogenous assemblage of Zygoptera and Anisoptera can occupy brackish waters, usually of relatively low salinity compared with seawater", but only some of these taxa can survive in higher-salinity waters (Zinchenko and Golovatyuk 2013). According to Kelts (1977) and Corbet (1999), only one species may be considered a truly marine dragonfly (*Erythrodiplax berenice* Drury), and Dunson (1980) confirms that nymphs belonging to this species regulate hemolymph osmotic pressure from fresh water to 260% sea water (2.612 mOsm in controlled laboratory conditions; Dunson and Travis 1994).

To date, most of the studies on dragonflies have focused chiefly on freshwater habitats (Willigalla and Fartmann 2012; Cai et al. 2018) or on understanding macroecological patterns of geographical species distribution (e.g., Kalkman et al. 2008; Keil et al. 2008). On a local scale, habitat features seem to have a primary role in shaping dragonfly assemblages (Remsburg and Turner 2009; Hart et al. 2014). In particular, floating macrophytes determined the formation of dragonfly species assemblages (Schindler et al. 2003) and macrophytes cover was significantly associated with dragonfly assemblage composition especially in spring and in summer (Briggs et al. 2019). In addition, it has been proven that odonata larvae are influenced by vegetation structure in both aquatic and riparian habitats (Remsburg and Turner 2009).

On larger spatial scales, such as regions or continents, diversity variations are often associated with a strong climatic signal (Heino 2002; Kalkman et al. 2008) which, in turn, may be explained by "water-energy" dynamics (Keil et al. 2008). The water-energy dynamic is due to Earth sphericity and axial tilt (O'Brien 1998). It explains that liquid water and liquid water-energy dynamics are necessary and fundamental to the existence of all sort of life and to all biotic dynamics, everywhere, and always (O'Brien 2006). Spatial variation in species richness are better explained by measures of energy, water, or water-energy balance than by other climatic and non-climatic variables (Hawkins et al. 2003). More, globally extensive plant and animal diversity gradients may be caused by the interaction between water and energy, where for animals, there also is a latitudinal shift in the relative importance of ambient energy vs. water moving from the poles to the equator (Hawkins et al. 2003). In angiosperm, the richest areas of the world are the hottest and the least lacking in water; the relationship between richness and heat depends on water availability, and the relationship between richness and water that depends on heat (Francis and Currie 2003).

To the best of our knowledge, there are no previous studies describing dragonflies' diversity patterns in brackish waters. For this reason, we sampled adults and exuviae of Odonata in three areas of NE Italy hosting habitats along a gradient (from freshwater to polyhaline habitat conditions). Our aims were (1) to identify dragonfly species tolerant to brackish environments or able to complete their biological life cycle in these environments and (2) to assess if there are differences in species richness and compositions along the salinity gradient. We hypothesized that few dragonfly species are able to colonize and breed in polyhaline waters. Therefore, we expected to find significant differences in species richness and composition along the salinity gradient. These aspects can be important to understand the ecology of coastal wetlands, and especially for the conservation and management of this considerable "flagship" group of species.

Materials and Methods

Study Area

Fieldwork was carried out in the few remaining natural coastal wetlands along the northern Adriatic coastline. Since the 1950s, most of the coastline in the region has been transformed and reclaimed due to increased tourism and urbanization (Nordstrom et al. 2009).

Specifically, three areas were selected between Monfalcone and Grado municipalities (Italy, Fig. 1): one belongs to the brackish biotope called "Lisert Zone," on the estuary of the Timavo River, and two are located inside the "Natural Reserve of the Isonzo River Mouth". The "Lisert Zone" is an area that lies along the northernmost coastal part of the Balkan Peninsula, and it is characterized by high mountains and rocky environments. Isonzo river mouth is characterized by low altitude and sandy environments (Poldini 2009). In the "Lisert Zone" and in the neighboring areas, the first man-made modifications date back to 1948–1950 (Michelutti et al. 2006), while the most recent one took place in 2006. After that, the area reverted to a more natural condition and the creation of many ponds occurred. During the study period, as usual, these wet zones underwent strong water fluctuations, with maximum water tidal wave level ranging from 60 to 74 cm.

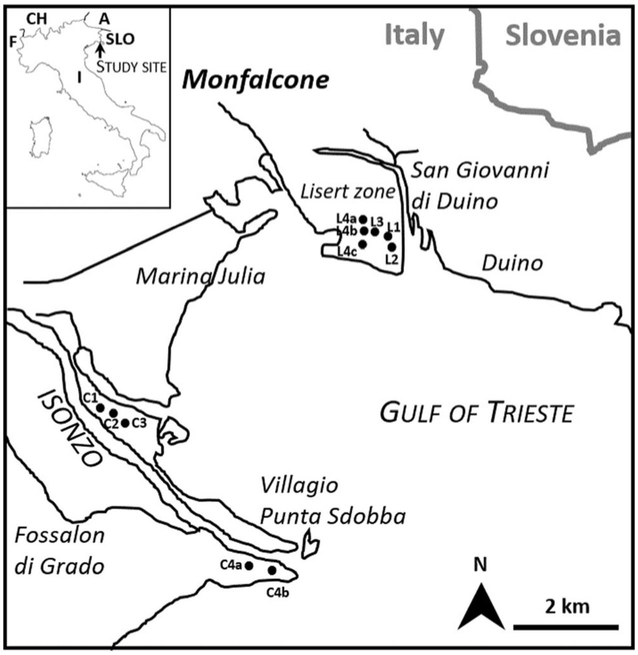

Fig. 1 Geographic position of the study site (inset) and of the 11 sampling stations at eight ponds (L1–L4, C1–C4) between Monfalcone and Grado, NE Italy. Letters denote different sampling stations at the largest ponds (L4a–c, C4a–b)

Water supply was partially due to rainfall, but it was also due to the tidal flooding. Despite the numerous modifications, the area currently displays a high biodiversity, with interesting coastal habitat characterized by autochthonous flora and fauna species.

The "Natural Reserve of the Isonzo River Mouth" was established in 1996 and consists of a complex lagoon structure situated in the easternmost side of Po River plain. It includes the last part of the high plain river areas, characterized by pebbly floodplains and the low valley areas characterized by muddy soils. In this stretch, the remains of floodplain woods and canalized spring water courses are still present. The southernmost part of the Reserve is situated at the Isonzo mouth and consists of marshes. It is characterized by clayish floodplains, sandy sediments, and many islets (Perco et al. 2006).

Sampling Design

Eight wetlands (ponds) were selected in the study area. In the "Lisert Zone," we identified four ponds with waters ranging from oligohaline to polyhaline (stations L1, L2, L3, L4: 45.778635 N, 13.575363 E). Four more ponds were selected in the Natural Reserve of Isonzo River Mouth, where three of them, characterized by freshwater conditions, were situated in the northern portion of the study area (C1, C2, C3: 45.754511 N, 13.500439 E). The fourth pond was mesohaline (C4: 45.724948 N, 13.541177 E), and it was situated in the southernmost portion of the Reserve (Fig. 1).

Pond areas range from 40 (L1) to 500 m^2 (L4). The number of sampling sites in each pond was selected as a function of the pond size in order to maintain a similar sampling intensity throughout the whole study area. Specifically, smaller than 100-m^2 areas (L1–L3, C1–C3) had only one sampling station, and larger than 250-m^2 ponds had two or three sampling stations (C4 with sampling stations coded as C4a and C4b, and L4 with sampling stations coded as L4a, L4b, and L4c; see Table S1 in supplementary material for details).

The Odonata sampling campaigns were conducted every 2 weeks from 14 May to 29 September 2010 and from 15 March to 23 April 2011. At each sampling station, we searched for adults along the pond banks on a predetermined transect 30–40 X 5 X 5 m in size (length, width, and height, relative to the surface of the ponds). Searches took place from 10 a.m. to 6 p.m. on sunny days, when temperatures were higher than 20 °C, and with low wind speed (Buchwald 1994). Adults were caught with an entomological net, identified (Dijkstra and Lewington 2006), photographed, and then released. Transects for exuviae collection were placed parallel to those for adults, using the same spatiotemporal scheme presented above, but in shallow water and where aquatic vegetation was present. However, in order to maximize the probability of collection, we considered a buffer area around the transect of 50 cm in each side (total wide 6 m) based on pond morphology and including also helophyte vegetation, bushes, and trees .

Therefore, the height of the exuviae transects was determined by bank vegetation and emergent vegetation from which exuviae were collected by hand and stored. Each exuvia was then identified to species in the laboratory (Gerken and Sternberg 1999; Askew 2004). Abundance classes were then assigned following Buchwald (1990): 1 for very few individuals (1–4 adults or exuviae), 2 for poor populations (5–10 adults or exuviae), 3 for medium populations (11–20 adults or exuviae), 4 for dense populations (21–40 adults or exuviae), and 5 for very large or mass populations (> 40 adults or exuviae).

Environmental Variables

Information about physical and chemical parameters, size of the ponds and vegetation around the ponds were acquired directly in the field (supplementary material, Table S1). Specifically, conductivity (mS cm^{-1}), pH, temperature (°C), and dissolved oxygen (mg l^{-1}) were recorded using field meters (instrument models: HI 8633 conductivity meter; HI 9025 pH and temperature meter; HI 9143 dissolved oxygen meter; all instruments manufactured by Hanna Instruments Inc., Woonsocket, Rhode Island, USA). Measures were performed every 2 weeks from 14 May 2010 to 23 April 2011, between 12 a.m. and 2 p.m., without rain and with low tides since these conditions were necessary to have access to the area. Since many ponds were located close to the sea, water chemical analyses were conducted to correlate the high conductivity values with salinity (presence of chloride ions); conductivity values were converted to practical salinity units (PSU).

Based on the chemical composition, each sampling station was assigned to a salinity category as follows: (1) freshwater (C1, C2, C3), oligohaline (L4a, L4b, L4c), mesohaline (C4a, C4b), and polyhaline (L1, L2, L3).

Data Analyses

A one-way analysis of variance (ANOVA) was used to detect changes in species richness (alpha diversity) across salinity gradient (four levels: freshwater, oligohaline, mesohaline, and polyhaline) in adults and exuviae, separately. After checking for residual normality and homogeneity of variances, post hoc Tukey's HSD test was applied when the omnibus test was significant. Non-metric multidimensional scaling (NMDS) was used to assess community composition of dragonflies for the 11 sampling stations. In order to further assess the relationships between dragonflies and different habitat types, we used indicator species analysis (Dufrêne and Legendre 1997) coupled with combinations of site groups according to De Cáceres and Legendre (2009) using R package "indicspecies."

A permutation analysis of variance (PERMANOVA; Anderson 2001) was performed to test for differences in community composition across different salinity levels (fixed factor, as defined before) using 4999 unrestricted permutations of the raw data. When tests were significant, we applied a posteriori pairwise comparisons based on pseudo t statistic and p values were calculated using Monte Carlo sampling. Both NMDS and PERMANOVA were based on a Bray–Curtis similarity matrix on square root-transformed abundance data. To investigate interconnections in species compositions among the sampling stations, species assemblages were inspected through unweighted pair groups method (UPGMA). The clusters of the sampling stations were interpreted according to the recorded environmental parameters (see Table 1). A distance matrix was computed using a Bray–Curtis index for the abundance classes data. For each cluster determined via the UPGMA analysis (including one or more than one pond), we characterized the diversity of each assemblages by calculating the following metrics (abundance values were not untransformed): (i) number of species, (ii) Shannon-Wiener index (H′, here with ln), (iii) Fishers's alpha (α), (iv) dominance ($D = 1 - $ Simpson index), and (v) evenness (equality: $E = H'/\ln N$; where N = number of species in the sample). Then, we estimated spatial species turnover rates among pairs of ponds and predefined groups of ponds by UPGMA using Whittaker's β-diversity index (β_W; see Hammer 2012 for formulae).

One-way ANOVA and boxplots were performed in R 3.5.1 (R Core Team 2018); NMDS and Permanova analysis in Primer 6 with the add-on package PERMANOVA+ (PRIMER-E Ltd., Plymouth, UK) (Clarke and Gorley 2006) and all other analyses in PAST (Palaeontological Statistics; Hammer et al. 2001).

Table 1 PERMANOVA output based on Bray–Curtis similarity calculated independently for Exuviae and Adults, respectively

	df	*SS*	*MS*	*Pseudo-F*
Exuviae				
Habitat	2	12,020	6010	5.23**
Residual	6	6899	1150	
Total	8	18,919		
Adults				
Habitat	3	9772	3257	4.70**
Residual	7	4849	693	
Total	10	14,621		

$^{**}P < 0.01$

Results

In total, we identified 4963 adults and 1907 exuviae belonging to 25 species of Odonata (Zygoptera: 7 spp., Anisoptera: 18 spp.). Considering the different habitat types (freshwater, oligohaline, mesohaline, and polyhaline water), 32% of species (*Coenagrion puella*, *Aeshna isoceles*, *Orthetrum albistylum*, *Libellula depressa*, *Coenagrion scitulum*, *Ischnura pumilio*, *Lindenia tetraphylla*, *Anax parthenope*) and 25% of species (*Sympetrum vulgatum*, *Aeshna cyanea*, *O. albistylum*, *Lestes parvidens*, *Sympetrum striolatum*, *L. depressa*, *C. scitulum*, *Hemianax ephippiger*, *Brachythron pratense*, *Aeshna affinis*, *Orthetrum cancellatum*, *Symetrum fonscolombii*, *I. pumilio*) were exclusive of only one habitat type for adults and exuviae, respectively. Moreover, 28% of adult species (*Anax imperator*, *O. cancellatum*, *Sympetrum meridionale*, *Erythromma viridulum*, *Ischnura elegans*, *Aeshna mixta*, *S. fusca*) were present in all habitat types, whereas none of all sampled species was breeding all along the gradient (Table S2 of supplementary material). We found a low share of rare species expressed as singletons and doubletons (namely the number of unique species represented by one or two individuals, respectively): one singleton (*L. tetraphylla*) and one doubleton (*A. isoceles*) for adults; for exuviae, four singletons (*I. pumilio*, *B. pretense*, *A. cyanea*, *H. ephippiger*) and no doubletons at all.

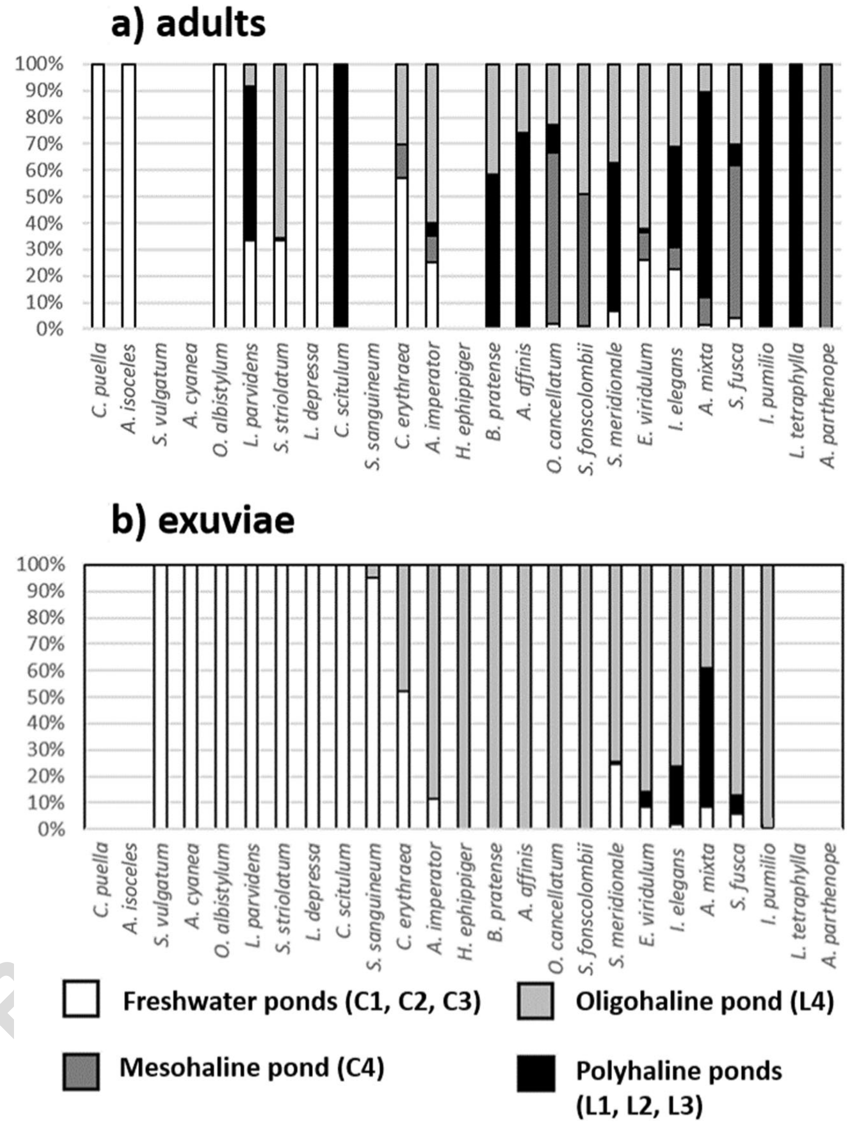

Fig. 2 Proportion of abundances (%) of Odonata species along the salinity gradient. **a** Adults. **b** Exuviae

As expected, freshwater habitats were more suitable for Odonata (Fig. 2); in these habitats, we found the highest number of species in terms of both adults (16) and exuviae (15) (in total: 956 adults, 543 exuviae). In contrast, mesohaline habitats showed no exuviae at all and only a reduced number of adults (in total adults belonging to 10 species and 513 adults) (Table S2 of supplementary material). Oligohaline habitats consisted of 13 species as adults and 14 species as exuviae (in total: 1601 adults, 1208 exuviae). In polyhaline habitats, we counted 14 species as adults, five species as exuviae (in total: 1893 adults, 156 exuviae). The most abundant species in the investigated habitats were *I. elegans* (adults), with a total of 1802 individuals sampled, and *S. meridionale* (exuviae), with 867 exuviae.

Although the gradient was not strictly the same for adults and exuviae, there were obvious parallelisms in species composition between exuviae and adult stages. We detected that almost 4/5 of the species that were flying in the oligohaline habitats are connected to this habitat for reproduction; this proportion decreased to 3/5 of the species detected in freshwater habitats and to 1/5 of the species in polyhaline habitats (Table S1 of supplementary material). Even if many Odonata species (10) were observed flying in the mesohaline habitats, only one of those (*A. parthenope*) was recorded exclusively there. All the other species recorded in this habitat type were found also in oligohaline (two species) and in oligohaline and polyhaline habitats (seven species). However, no exuviae were found in mesohaline habitats. Furthermore, as shown by the spatial distribution of species abundances across different habitat types (Fig. 2), adults were less connected to a certain habitat than larvae. This was reflected in changes of species across habitat types that in all pairs of habitats compared were higher for exuviae than for the adults (Fig. S1 of supplementary material). Since no species was recorded to successfully complete its life cycle in mesohaline environments (C4), species turnover rates between this and any other habitat was 1 (i.e., 100% turnover rate).

We also detected a difference in species composition pattern along the salinity gradient. Accordingly, a set of species was detected to fly and/or breed in freshwater habitats only such as *C. puella*, *A. isoceles*, *L. depressa*, *S. vulgatum*, *A. cyanea*, and *O. albistylum*. On the contrary, *B. pratense*, *A. affinis*, *O. cancellatum*, and *S. fonscolombii* bred only in oligohaline habitats and flew in almost all the other habitats. *S. meridionale*, *E. viridulum*, *I. elegans*, *A. mixta*, and *S. fusca* showed no preferences for breeding or flying habitats, choosing also the saltiest habitats for reproduction. The rarest species were *H. ephippiger*, with one exuvia found in oligohaline habitats, and *L. tetraphylla*, with one male observed flying in polyhaline habitats. No exuviae were confirmed for the following four species: *C. puella*, *A. isoceles*, *L. tetraphylla*, and *A. parthenope*.

Diversity indices were in most cases the highest in freshwater habitats (but note the highest H′ = 1.97 for adults in oligohaline habitats) (adults: H′ = 1.74, $\alpha = 2.73$; larvae: H′ = 1.90, $\alpha = 2.86$) (Table S2 of supplementary material). Regarding the exuviae, the least diversified were mesohaline (H′ = 0, $\alpha = 0$) and polyhaline (H′ = 0.94, $\alpha = 0.99$) environments. Mesohaline environments were also the least diversified by the adults (H′ = 1.62, $\alpha = 1.76$). The dominance values were the highest in mesohaline environments for adults (D = 0.27), and polyhaline environments for exuviae (D = 0.46). Finally, the evenness values showed that species are most unequally distributed in oligohaline (adults, E = 0.55) and polyhaline (exuviae, E = 0.51) environments (Table S2 of supplementary material). Alpha diversity expressed as species richness showed significant differences among salinity types for exuviae ($F\ (3,7) = 21.15$, $P < 0.001$). In particular, polyhaline water hosted fewer species than fresh water and oligohaline water which shared similar values of species richness (Fig. 3). In contrast, adults showed no significant outcome ($P > 0.05$; Fig.3).

We found a good number of indicators species for adults (seven species) and exuviae (seven species), which are characteristic of different habitats and can be recognized as indicator species (Table S3 of supplementary material).

NMDS ordination provided a good representation of the sampled communities (Fig. 4) highlighting a strong differentiation along the salinity gradient, from freshwater to polyhaline habitats for both adults and exuviae. On adults, polyhaline species grouped on the extreme right of the plot, oligohaline in the middle, and freshwater on the bottom right. Mesohaline habitats laid on the left side relative to the others. As for exuviae, the division of habitats followed the gradient of salinity perfectly, with freshwater habitats on the right, oligohaline in the center, and polyhaline on the left side. Cluster analysis confirmed the same separation of the species assemblages into four groups according to the environmental parameters, and the groups are the same regardless of the dataset used (adults or exuviae; see Fig. S2 of supplementary material).

PERMANOVA outputs further corroborated this pattern (Table S1 of supplementary material). Specifically, strong and significant differentiation in both adults and exuviae was observed along the salinity gradient ($P < 0.01$). On adults, species dissimilarities differed among habitats ($P < 0.05$) excluding polyhaline vs oligohaline waters and oligohaline vs mesohaline waters ($P > 0.05$). On exuviae, species assemblages differed among all habitat pairs except for freshwater vs oligohaline ($P > 0.05$).

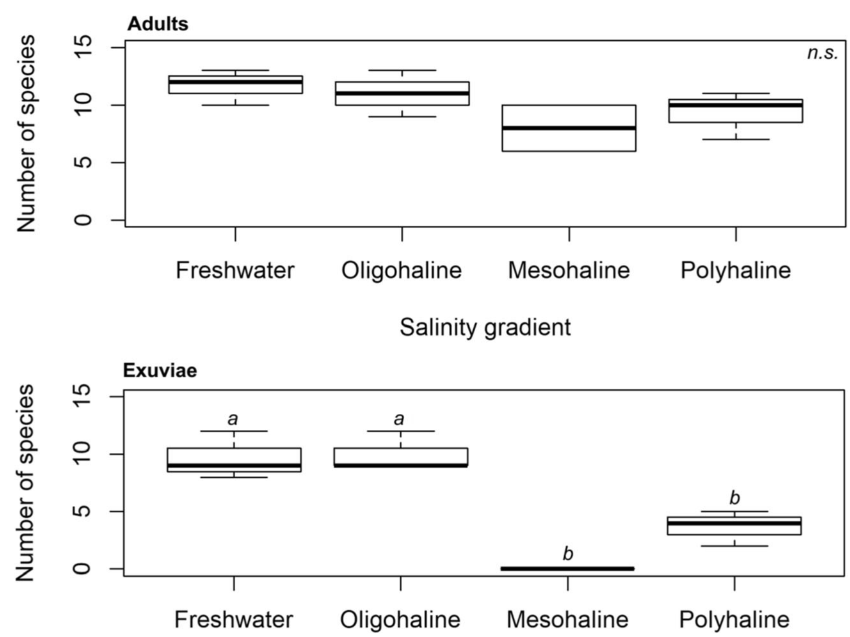

Fig. 3 Boxplots summarizing alpha diversity expressed as species richness along the salinity gradient for adults (top) and exuviae (down). Different letters indicate significant differences among groups ($P < 0.05$), while *n.s.* indicates no significant differences ($P > 0.05$)

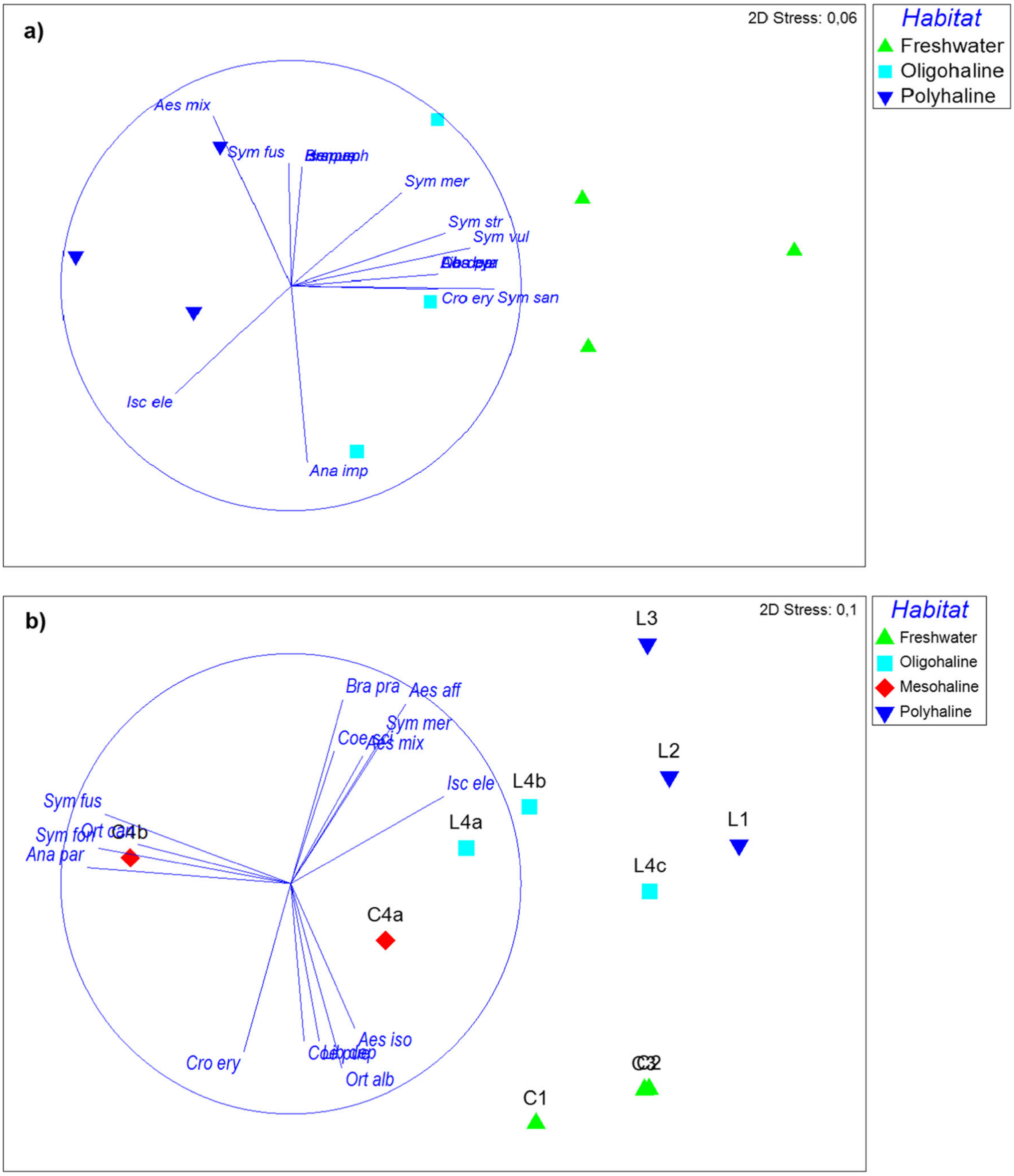

Fig. 4 Non-metric multidimensional scaling (NMDS) performed on Bray–Curtis similarity matrix of dragonflies' assemblage according to the salinity gradient. **a** Adults. **b** Exuviae. Please note that only the species which have correlation with axes > |0.6| were shown

Discussion

Assemblage Composition in Brackish Coastal Wetlands

To the best of our knowledge, this is one of the first studies investigating Odonata in European brackish coastal wetlands. As hypothesized, our results highlighted a strong differentiation of the Odonata assemblages along the salinity gradient (see Fig. 2). We detected in total 25 species of Odonata, almost half of the species present in Friuli Venezia Giulia region (62 species, Zandigiacomo et al. 2014). The two most common species in our study were *I. elegans* (adults) and *S. meridionale* (exuviae). *I. elegans* is a very widespread species that breeds in a wide variety of standing and slow flowing waters (Dow 2010). *S. meridionale* is often abundant across most of the southern parts of its range (Spain, France, Italy, the Balkans, the Mediterranean islands) (Askew 2004). It is a typical species of unshaded, hot, and often shallow standing waters which partially or totally dry up during summer (Kalkman 2014a). On the other hand, the rarest detected species were *L. tetraphylla* (one adult) and *H. ephippiger* (one exuvia). *L. tetraphylla* is a EU Habitat Directive species that in Italy has only a few fragmented populations in Tuscany, Campania, and Sardinia (IUCN 2014); disjunctive populations in the Balkans (Boudot et al. 2013); and a population close to the Italian border on Pag Island (Croatia) (Belančić et al. 2008; Vilenica et al. 2016). The habitat where the male was flying resembles the typical habitat of the species (Schorr et al. 1998), i.e., brackish, shallow, and warm water with abundant presence of *Phragmites australis*. *H. ephippiger* whose exuvia was found in oligohaline habitat is an obligate afro-tropical migrant species that is present in Italy in the mainland and in Sardinia and Sicily (Subramanian 2016). This exuvia is the first proof that the species reproduces in at least the north-eastern part of Italy (Uboni et al. 2018).

Zinchenko and Golovatyuk (2013) published a review about the salinity tolerance of many Odonata species: *Hemicordulia tau* and some of the genus *Ischnura* species were collected in rivers with salt concentrations up to 2.24 (all data on salinity from herein in PSU). Larvae of *Anax* spp. were found to colonize biotopes in the hyperhaline river upon its desalination to 3.5–6.8; species belonging to the families Coenagrionidae, Aeshnidae, Gomphidae, Libellulidae, Hemicorduliidae, and Lestidae inhabit river waters with salinity of 5.9–40, and larvae of *Sympetrum sanguineum*, *I. elegans* and *Aeshna* sp. have been found in mesohaline rivers at a salinity of 7.5–21.1. Experimental studies demonstrated a high tolerance toward water salinity for the larvae of *L. depressa* and *E. bimaculata*, up to 6.3–8.1 (Zinchenko and Golovatyuk 2013), and *Erythemis simplicicollis* showed a tolerance range between 7 and 18 (Smith and Smith 1996). The maximum salinity tolerance (25.8) was recorded on *Austrolestes annulosus*, belonging to the family Lestidae (Zinchenko and Golovatyuk 2013), and *Aeshna mixta* (27.8) belonging to the family Aeshnidae.

With respect to our current knowledge on the European Odonata species (Askew 2004; Dijkstra and Lewington 2006; Zinchenko and Golovatyuk 2013), only 15 dragonfly species are known to inhabit wetlands characterized by some level of salinity (*S. fusca*, *Lestes barbarus*, *Lestes macrostigma*, *I. elegans*, *I. pumilio*, *E. viridulum*, *B. pratense*, *A. affinis*, *A. mixta*, *H. ephippiger*, *O. cancellatum*, *Crocothemis erythraea*, *S. fonscolombii*, *S. sanguineum*, *S. striolatum*). Our results confirmed the "brackish/salty attitude" of almost all of the sampled species with the exception of *S. striolatum* (adults observed to fly everywhere and exuviae found only in freshwater habitats), and two species (*L. barbarus* and *L. macrostigma*), which were reported to have brackish affinity in literature but that were not found in our survey. The lack of these species in the study area may be explained by a general decline of both species and by the strong fluctuation in the population size within their ranges (Boudot et al. 2009; Clausnitzer 2009; Kalkman 2014b). Furthermore, we found out that *A. imperator* and *S. meridionale* can now be recognized for the first time as species inhabiting oligohaline and even polyhaline (*S. meridionale*) habitats. From the collected data, we observed that *S. meridionale* was very frequently found in freshwater and oligohaline environments and for this reason, it can be considered as an indicator species in such environments (Bakker 2008). In fact, the species favors well vegetated, unshaded, hot, and often shallow standing waters which partially or totally dry up during summer and it has frequently been observed also in coastal wetlands (Kalkman 2010).

Based on ecological features of the recorded Odonata species, we are able to group the species detected as follows: "polyhaline" species (*S. fusca*, *I. elegans*, *A. mixta*, *E. viridulum*, *S. meridionale*) that were able to breed in different aquatic environments along a fresh-polyhaline water *continuum* of habitat types, becoming the most tolerant species toward salinity in the study area. Hence, these species can complete their life cycle in water with a PSU range from 5.86 to 30.97. It must be underlined that *A. mixta* is the only species belonging to this group that emerges in higher numbers in polyhaline habitat than in fresh and oligohaline water bodies. Even if the "polyhaline" behavior of *A. mixta* (27.8 in Aguesse 1968) and *I. elegans* (21.7 in Zinchenko and Golovatyuk 2013) was already described, we noticed an increase of these values of tolerance for both species to 30.97.

Furthermore, we detected five "oligohaline" species that were mainly connected to oligohaline habitats (*A. affinis*, *B. pratense*, *H. ephippiger*, *O. cancellatum*, *S. fonscolombii*), breeding in water with a PSU range from at least 1.33 to 3.59. A set of three species (*B. pratense*, *A. affinis*, *I. elegans*) were more typical of polyhaline and oligohaline environments than of other habitat types. Hence, they were defined as indicator species for the two mentioned habitat types (Bakker 2008). Similarly, other two species (*O. cancellatum* and *S. fonscolombii*) were considered to be indicator species of oligohaline habitats only. Finally, seven species (*L. parvidens*, *C. scitulum*, *A. cyanea*, *L. depressa*, *O. albystilum*, *S. striolatum*, *S. vulgatum*) can be defined as stenoecious and seem to be strictly associated only with freshwater habitats. Among these species, four of them (*C. puella* and *O. albistylum*, *S. vulgatum*, *S. sanguineum*) proved to be the indicator species of freshwater habitats. It is important to underline that *L. depressa* in this study is present only in the freshwater habitats, despite laboratory results showing that this species can tolerate up to 6.3–8 (Zinchenko and Golovatyuk 2013). On the other hand, we were not able to confirm the tolerance range of 7.5–21.1 (Zinchenko and

Golovatyuk 2013) for larvae of *S. sanguineum* since we found the vast majority of them in freshwater (95%) or oligohaline habitat (5%). It was interesting to observe that *C. erythraea* was the only species that emerged as indicator species in all the investigated wetland types. An explanation of this particular result can be found in the "expanding" behavior of the species (Walther 2001) indicating that *C. erythraea* is the best example of how dragonfly distribution is changing in the last decades (Ott 2010). Even if this species is widespread in Africa, southern Europe, the Middle East, and western Asia (up to Yunnan in China, Clausnitzer 2016), it recently expanded its range in northern Europe becoming now naturalized in most countries where previously it did not occur (Ott 2007). The expansion trend of this species is documented on many countries, including Germany, UK, Denmark (where arrived in 2009), Ukraine, and Luxemburg (Ott 2010).

Diversity Patterns along the Salinity Gradient

Adult Odonata species richness is very different along the salinity gradient, presenting richer freshwater and oligohaline habitats than the others. The same pattern can be observed on breeding species, with the highest values of successful breeding in freshwater (15 species) and oligohaline habitats (14 species), with eight species in common between them. Only a small amount of these freshwater-oligohaline species (five species) were able to complete their metamorphosis in polyhaline waters too. It should be noted that the abundance of exuviae is higher in oligohaline habitats (63.3% of all collected exuviae) than in freshwater bodies (28.5%), followed by polyhaline (8.2%) and mesohaline (0%) environments. This result indicates that in environments with lower species diversity, many species can become highly abundant (Brower and Zar 1977); in our case, in oligohaline habitats, the euryoecious *S. meridionale* represents 45% of total collected exuviae. In these environments, salinity probably one of the main limiting factors affecting species assemblage(see supplementary material, Table S2), as reported also for other invertebrates (Hauton 2016). The lack of exuviae in mesohaline habitats may result more from other factors affecting dragonfly species such as wind exposure or scarcity of vegetation which may reduce or completely prevent certain behaviors which are important for completing their life cycle. The presence of developed vegetation is an essential factor in Odonata distribution and assemblages (Korkeämaki and Suhonen 2002), because it provides a substrate where individuals can copulate, warm up, display their behaviors (e.g., territoriality), and lay eggs. Submerged vegetation also represents a suitable habitat for larvae, and when the vegetation emerges from it represents a substrate where individuals can emerge (Buchwald 1990). Finally, exposure to strong winds also negatively affects the diversity of adults since strong winds may create problems in flight and feeding. It is well known that habitat characteristics may affect dragonfly assemblages across the world (e.g., Fulan et al. 2008; Hart et al. 2014), even along a gradient of disturbance from city center to rural areas (Willigalla and Fartmann 2012).

The effect of habitat is evident in our results on both adults and exuviae (see Fig.4 NMDS, Table 1 PERMANOVA). Interestingly, 75% of adults flying on oligohaline water used it as breeding site; this value decreases to 65% in freshwater reaching 23% and 0% in polyhaline and mesohaline habitats, respectively. On one hand, this pattern suggests a certain fidelity of species to their proper habitats (this is more evident at lower salinities), and on the other hand, it corroborates the idea that Odonata sightings of the adults may not always accurately predict the distribution of larvae (Painter 1998; Painter 1999; Corbet 1999; McPeek 2008; Balzan 2012).

Conclusions

In this study, we focused on the fauna and ecology of Odonata living in some coastal wetlands in the northeastern part of Italy. Our primary aims were to determine if there were species able to breed in brackish coastal wetlands, and to describe diversity patterns along the salinity gradient. We observed a strong and significant relationship between salinity and the Odonata assemblage and structure. Moreover, our results highlighted that in a relatively small area, freshwater habitats may be considered hotspots for dragonflies, having the highest species richness and the most number of indicator species. Moreover, the gradient of salinity allows a higher number of species and individuals to occur in the same study area.

In addition, oligohaline habitats acted as a "corridor" between freshwater and polyhaline habitats, having also the higher correspondence between adults and exuviae and hosting a mosaic of species spread across all the salinity gradient. Finally, we showed, once again, that coastal wetlands are important in displaying high biodiversity and sustaining natural ecosystem functions (Camacho-Valdez et al. 2013).

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AUTHOR QUERIES

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Q1. Ref. "Simaika and Samways 2012" is cited in the body but its bibliographic information is missing. Kindly provide its bibliographic information in the list.

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Q4. The citation "Boudot 2013" has been changed to "Boudot et al., 2013" to match the author name/date in the reference list. Please check if the change is fine in this occurrence and modify the subsequent occurrences, if necessary.

Q5. The sentence "The effect of habitat is evident in our results…" has been modified for clarity. Please check if the intended meaning was retained and amend as necessary.

Q6. Please supply/verify the standard expanded of the journal name in References Fulan et al (2008), Zinchenko and Golovatyuk (2013).

Q7. References [Bakker, 2014, Teixeira et al, 2014, Turner et al, 2000] were provided in the reference list; however, this was not mentioned or cited in the manuscript. As a rule, all references given in the list of references should be cited in the main body. Please provide its citation in the body text.