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Habitat requirements, habitat variability, and altitudinal distribution of *Coenagrion hylas* (Odonata: Coenagrionidae) in the Lech-river valley and beyond (Tyrol, Austria)

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Abstract

Coenagrion hylas is the rarest Central European odonate species and – at present – populations are exclusively known from an extremely limited area of occurrence of about 42 km² in the North-western Tyrol. Since 1973 the species has been recorded at 27 single sites in Tyrol whereof 15 (currently 10), and all sites with larger self-sustaining populations, are situated in the Lech valley, which thus can be regarded as the European stronghold of the species. The perception of the habitat niche breadth of *C. hylas* and the knowledge about the range of its altitudinal distribution are still somewhat superficial and biased in the literature. In particular, the "mountain lake myth" persists, stating that *C. hylas* in Europe is mostly bound to clear mountain lakes in the submontane to lower montane zone. Here, we therefore analyse and compare habitat characteristics of the 27 Tyrolean sites and, in addition, offer a pictorial overview of the habitats used by *C. hylas* in Tyrol. Our compilation indicates that *C. hylas* in Europe has a broader habitat niche than expected from its Siberian origin and as stated in literature. According to the chemistry, size, depth, sources of water, and the predominant vegetation we were able to distinguish six main types of *C. hylas* habitats. These comprise rather different waters including clear cold mountain lakes (3 cases only), dystrophic bog lakes, fishponds, spring water swamps, and shallow flood plain pioneer habitats. However, despite this wide spectrum of habitats used by *C. hylas,* a closer analysis of the data reveals that the few habitats constantly used by larger populations for reproduction have a combination of specific habitat features in common. The presence of waterbodies with very shallow water and stands of the sedge *Carex rostrata* along or near to incoming (or outgoing) small spring creeks with cold water or zones with cold groundwater entering seems to be required. Since such conditions currently mainly seem to be fulfilled at about a dozen sites in the Lech valley, the strict preservation and enhancement of these places via management measures as well as the creation of appropriate steppingstone habitats in between are the main issue to conserve the species. Such measures are already in progress as part of the current LIFE-Lech program Dynamic River System Lech.

Zusammenfassung

Habitatansprüche, Habitatvariabilität und Höhenverbreitung von *Coenagrion hylas* im Tiroler Lechtal und im Tiroler Oberland (Odonata: Coenagrionidae) – *Coeangrion hylas* gilt als die seltenste Libellenart Mitteleuropas. Ihr Areal ist auf Nordwesttirol beschränkt und auch dort umfasst die eigentliche derzeit besiedelte Fläche nur etwa 42 km². Seit 1973 gelangen in Tirol Nachweise an 27 Einzelstandorten (Kleingewässern), davon stammen 15 (und rezent 10) aus dem Tiroler Lechtal, das zudem die größten Einzelpopulationen beherbergt und damit europaweit das Zentrum der Art darstellt. Über die Vertikalverbreitung, Lebensraumansprüche und Nischenbreite von *C. hylas* gibt es in der Literatur teilweise etwas einseitige Vorstellungen, die z.T. darauf zurückzuführen sind, dass die Art ursprünglich nur an klaren Bergseen der submontanen und unteren Montanstufe gefunden wurde. Wir haben hier deshalb Charakteristika, Gemeinsamkeiten und Unterschiede der 27 bekannten Standorte zusammenfassend analysiert und die Variabilität der von *C. hylas* genutzten Habitate in repräsentativen Bildern dargestellt. Dabei zeigt sich, dass die Art eine bislang unterschätzte Nischenbreite aufweist und unterschiedlichste Gewässer besiedeln kann, die zudem von der submontanen Talstufe bis in die subalpine Bergwaldstufe (790–1.540 m ü. NHN) liegen können. Nur drei der 27 Standorte entsprechen in etwa dem Typ „Klarer Bergsee", die restlichen Vorkommen haben wir grob fünf weiteren Habitattypen zugeordnet. Das Spektrum reicht von dystrophen Moorgewässern über röhrichtgesäumte Teiche mit Fischbesatz und flache, verwachsene Quellmoorsümpfe bis hin zu astatischen Pioniergewässern in der Flussaue. Allerdings haben vor allem die wenigen größeren und konstanten Vorkommen, an denen sich die Art regelmäßig erfolgreich entwickelt, eine Reihe von Gemeinsamkeiten: Sie werden auch im Sommer von kühlem Wasser durchströmt oder gespeist, das von Quellbächen oder unterirdischen Sickerwässern herrührt und haben ausgedehnte, vor allem von der Schnabelsegge *Carex rostrata* durchwachsene Flachwasserbereiche. Da solche für den Schutz der Art zentralen Hauptgewässer sich vor allem im Lechtal befinden, ist deren Bewahrung und Management vordringlich. Die Umsetzung entsprechender Maßnahmen (Verbesserung bestehender, Renaturierung verwaister sowie Neuanlage von geeigneten Biotopen) ist dementsprechend auch Teil des aktuellen EU-LIFE Lech Programms: „Dynamic River System Lech 2016–2021"

Introduction

Coenagrion hylas (Fig. 1) is an East Siberian damselfly, an element of a cold-stenothermal fauna, that probably colonised Europe during the late Pleistocene or early Holocene (Dumont 1971; Lohmann 1992; Bernard & Daraż 2010). Westward of the Ural the species on the one hand is only known from a few sites in the Ural and Pinega river region of Russia, where it inhabits peat bog and fen habitats partly together with another North-east Asian Bluet, *Coenagrion glaciale* (Bernard & Daraż 2010; Wildermuth & Martens 2019). In Central Europe, however, populations of *C. hylas* are exclusively known from an extremely limited area of occurrence in the North-western Alps of Tyrol, Austria (Landmann A. et al. 2005; Landmann A. 2013; Landmann M. et al. 2021a). Accordingly, *C. hylas* is undoubtedly

the rarest Central European odonate species and is assessed as vulnerable in the IUCN Red List (Kalkman et al. 2010) – *C. hylas* will be upgraded to Endangered in the forthcoming update of the IUCN Red List status of European dragonflies – and listed in Annex II of the EU-FFH directive. It thus deserves special attention and protection on an international scale.

The species was originally described in Europe by Bilek (1954, 1957) from the Bavarian Zwingsee (690 m a.s.l.), a clear mountain lake with small sedge belts, and was rediscovered at a quite similar lake in Tyrol in 1973 (Weißensee, 1,082 m a.s.l.; Heidemann 1974), but vanished at both sites in 1967 and the late 1970's, respectively. A decade later, a third population was detected in the Lech-river valley at another lake surrounded by fens (Riedener See, 880 m a.s.l., Fig. 1; e.g., Kiauta & Kiauta 1991; Landmann A. et al. 2005) which still sustains a healthy population (Landmann & landmann 2020; Landmann M. et al. 2021a).

Hence, the "mountain lake myth" was born, stating that *C. hylas* in Europe has a small habitat niche and is mostly bound to clear mountain lakes in the submontane to lower montane belt (e.g., Ott 2003, 2006). Although we now know much more about the ecology and habitat demands of the species, as an outcome of specific studies in Tyrol (Müller 2000a, 2001; Landmann A. et al. 2005; Mungenast 2001, 2014; Landmann & Landmann 2020; Landmann M. et al. 2021a), the international perception of the habitat niche of *C. hylas* still seems to be somewhat superficial and biased (e.g., Boudot 2010: »In Europe, the species is confined to shallow and more or less peaty pools and small lakes with clear oligotrophic water and zones of slow shallow running and seepage water«).

Figure 1. A clear mountain lake in the Lech valley – the "classic" habitat of *C. hylas* (inset), 24-v-2019. – **Abbildung 1:** Ein klarer Bergsee im Lechtal – das „klassische" Habitat von C. hylas (Einschubbild), 24.05.2019. Photos: ML & S. Hofer

Here, we offer a pictorial overview of the habitats used by *C. hylas* and summarize the knowledge concerning the habitat demands of *C. hylas* based on (partly unpublished) data collected within the last two decades, and including our own findings which stem from a population survey conducted during the recent Dynamic River System LIFE Lech-program (Landmann & Landmann 2020).

Material and methods

Data from past projects

In Tyrol, *C. hylas* has been recorded at about two dozen single sites in the last two decades. At 17 sites successful reproduction of the species could be directly proved (records of hatching, exuviae) in at least one year. However, some of these and some of the other sites were only irregularly occupied, and at a few sites only reproductive behaviour (mating, oviposition) or only single individuals have been observed so far. The rectangle between the outposts of the known range covers an area of 600 km^2 in the North-western Calcareous Alps of Tyrol, but the real area of occurrence is only about 42 km^2 (Landmann A. 2013). Fifteen of the known sites are in the Lech valley, and most of these were discovered by Jochen Müller between 2000 and 2005 in connection with his thesis (Müller 2000 a, b, 2001) and a monitoring scheme accompanying a first LIFE Lech-river restoration program (2001–2007; Müller & Vorauer 2006; Amt der Tiroler Landesregierung 2007).

Near the Upper Tyrolean Inn valley another 11 sites used by *C. hylas* have been detected and investigated, mainly by Franz Mungenast between 1996 and 2014 (summarized in Mungenast 2001, 2014; Landmann A. et al. 2005).

Actual investigations

During the recent program "Dynamic River System LIFE Lech 2016–2021" we again surveyed the hitherto known sites in the Lech valley in the year 2019, and thereby not only investigated the genetic structure, dispersal abilities and local abundances of the local population (Landmann M. et al. 2021 a, b), but also examined biotic and abiotic structures at relevant sites. At seven important sites where the species has been known to regularly reproduce, we monitored fluctuations of the water level and water temperature from mid-May until the end of July 2019. The water depth was measured via self-constructed water level gauges, which could be observed from a distance via binoculars. Water temperatures were monitored via data loggers (tempmate® – S1, Modell: S1C10A01000) with a log-interval of 10 min, allowing a constant measurement over a running time of 110 days. Loggers and gauges were mounted in shallow water near the waterline and mostly close to the inflow of cold running or seepage water. In addition, we generated a photographic documentation of all sites and of important habitat structures (project report Landmann & Landmann 2020).

Data analysis

Including the Weißensee (abandoned by the species about 40 years ago) we overall can analyse habitat data from 27 discrete sites where *C. hylas* has been recorded in at least one year. Although some of these sites are close to each other (in part < 100 m), and thus may only serve as steppingstone habitats within a habitat complex, most were separated by forested areas or by otherwise inappropriate habitats or barriers, and somewhat differ in their overall habitat character.

In consideration of the size and structure of the water bodies, and of the predominating adjoining vegetation which could be used by the species for hunting, resting, mating, oviposition, and hatching, we assigned each site to one of six main habitat types and to different altitudinal belts (see results).

To indicate differences in the importance of the various habitats for the focus species we also distinguish four (Fig. 2) to five (Table 1) status classes according to the frequency of observations, the number and behaviour of observed adults and the reproductive status of the species at a site:

Class 1: Site constantly used for reproduction (exuviae/hatching recorded in at least three years), and population rather large (> 25 adults simultaneously recorded at least in two years);

Class 2: Site with probably regular reproduction (proof of reproduction in at least one year and/or mating behaviour/oviposition observed in several years), and with small to medium sized population (10–25 adults each year);

Class 3: Site probably used irregularly for reproduction; only small numbers of individuals (< 10) recorded infrequently, or even in single years only;

Class 4: Site without proof of reproduction, but mating/ovipositing individuals observed, albeit in only small numbers, and in only few or single years;

Class 5: Site with irregular records of few individuals; so far, no reproductive behaviour observed (steppingstone or foraging habitats?).

As "a picture expresses more than a thousand words" the result section is equipped with an extensive pictorial overview showing the main types of habitats actually and formerly used by *Coenagrion hylas* in Tyrol.

Results

Altitudinal distribution

Figure 2 shows the altitudinal distribution of all 27 Tyrolean sites where *C. hylas* has been recorded since 1973. The occurrences are allocated to 100 m altitudinal sections and to four status classes according to local population sizes and the regularity (or absence) of reproduction at a site. In accordance with Landmann A. et al. (2005), we distinguish four altitudinal belts: submontane (600–779 m a.s.l.), lower montane (800–999 m a.s.l.), montane (1,000–1,399 m a.s.l.), and high montane to subalpine (1,400–1,799 m a.s.l.).

Sites where the species has been reproducing at least irregularly exist from 790 up to 1,530 m a.s.l. This means that *C. hylas* inhabits different altitudinal zones from submontane and lower montane valley regions up to the lower subalpine belt, and only about 250 to 300 m below the actual tree line in the Northern Alps. Hence, the species can reproduce over an altitudinal range of at least 750 m. Records between 1,200 and 1,480 m a.s.l. are missing, and about 70% of all sites can be found in the montane zone between 800 and 1,200 m a.s.l. Most of these sites and all permanent larger populations are spaced out over a stretch of 30 km along the Lech-river and adjoining terraces at altitudes between 890 and 1,200 m a.s.l. These sites are located within the EU-Natura 2000 area "Lechtal" (or, in two cases, close to its borders) which can thus be regarded as the actual European stronghold of the species (see Landmann M. et al. 2021a). High montane to low subalpine sites on the other hand so far are only known from the southern slopes of the Lechtal Alps close to the Inn valley. There, smaller to mid-sized populations are known to occur at altitudes between 1,480 and 1,540 m a.s.l., and for 25 years at least four sites have been permanently used for reproduction with no clear signs of decrease (Mungenast 2014, and pers. comm. 2021).

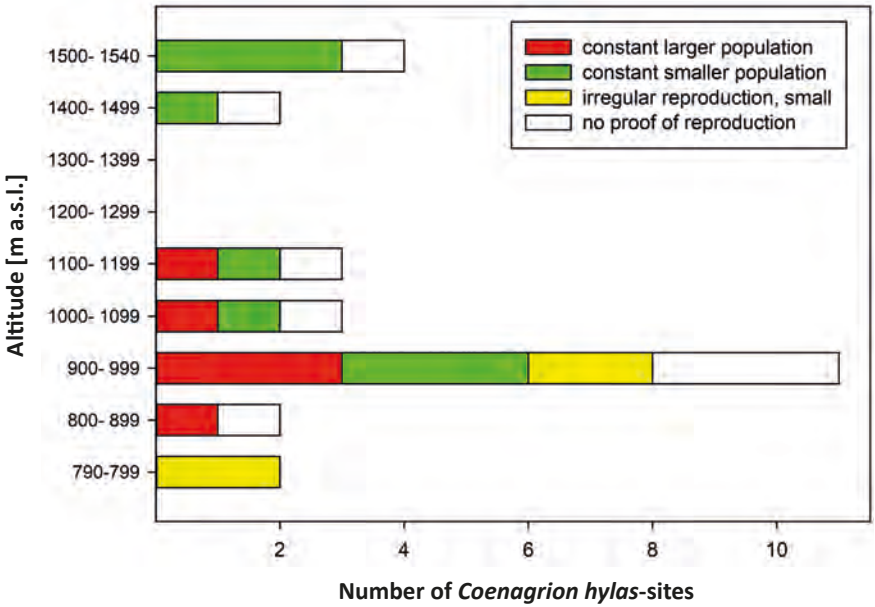

Figure 2. Altitudinal distribution of *Coenagrion hylas* in Tyrol. The 27 known sites of occurrence are assigned to four status classes (details see text). – **Abbildung 2:** Höhenverteilung der Fundorte von *Coenagrion hylas* in Tirol. Die 27 bislang bekannten Fundorte sind in vier Statusklassen unterteilt (Details s. Text).

Habitat characteristics and habitat variability

Coenagrion hylas has been recorded at quite different habitats and waterbodies since its first discovery in Tyrol in 1973 (Table 1, Fig. 3). In Table 1 we summarized the actual knowledge, by coarsely allocating the known aquatic sites of occurrence to six main habitat types and by listing the presence and dimension of some habitat features which we think, or which have already been shown (see Müller 2000 a; 2001, 2015; Landmann A. et al. 2005) to be important for the species and for the potential of a site for reproduction.

According to the chemistry, size, depth, sources of (open) water, and the predominant vegetation in and at the borders of the waterbodies we distinguish the following six main types of *C. hylas* habitats:

(I) Clear, open water dominated small mountain lakes ("classical" niche since Bilek 1954; e.g., Fig. 1, 3a);
(II) Old and mostly silted-up (fish) ponds and other artificial small ponds (e.g., Figs 3h–j);
(III) Dystrophic to mesotrophic (peat) bog habitats, including small boggy open waters and small moor-lakes (e.g., Figs 3k–l);
(IV) Spring water swamps with shallow water pools and with water fed by cold calcareous water inflow and/or by groundwater/interstitial seepage water (e.g., Figs 3b–d);
(V) Shallow flood plain waters of the Lech River (partly impounded by dams; e.g., Figs 3e-f);
(VI) Very shallow pioneer habitats in the Lech floodplain (clay-puddles; e.g., Fig. 3g).

The six habitat classes compared in Table 1 may by divided into two subgroups: (1) habitats with dominance of open still water and at least in part deeper (> 70 cm or > 1 m) water bodies (No. I, II, III), and (2) small spring water swamps and tiny ponds with shallow to very shallow water bodies (10–< 50 cm) which mostly are dominated and perfoliate by sedge-, horsetail- and/or reed vegetation (No. IV–VI). The pictures in Fig. 3 give an impression of the variability and characteristics of the habitats used by *C. hylas* in the Lech valley (Figs 3a–h) and beyond (Figs 3i–l).

Structural and biological habitat features

As shown in Table 1 nearly all sites where at least smaller populations of *C. hylas* exist and have been proven to reproduce (status classes 1 & 2) are characterised by the inflow of cold to very cold water (for example see Fig. 4) which either originates from the intrusion of slow running surface water (small meadow or spring creeks) or from seeping spring water. At 12 out of 15 sites belonging to these status classes this habitat feature is dominant and conspicuous, at least

Table 1. Habitat features of 27 aquatic sites used by *Coenagrion hylas* in Tyrol: Differences and similarities between the six main habitat types distinguished in combination with the known local status of *C. hylas* (for habitat types and status classes see text). Lech valley sites are shown in bold (habitat type) and sites which are abandoned by *C. hylas* for at least five years are shown in brackets (status class). The specificity, dimension and importance of habitat features/structures is coarsely assessed: **++** feature/structure dominant/conspicuous, especially at places used by *C. hylas*; **+** feature/structure important, but slightly less dominant/conspicuous; **x** feature/structure present but not very important/conspicuous; **–** feature/structure not present or information is lacking (**?**). – **Tabelle 1:** Charakteristika der 27 Gewässer mit Nachweisen von *C. hylas* in Tirol. Unterschiede und Gemeinsamkeiten zwischen den sechs unterschiedenen Habitattypen (Lechtalstandorte fett; Details s. Text) in Verbindung mit dem jeweiligen Status (Klassen s. Text) von *C. hylas*. Dabei bedeutet **++** Merkmal/Struktur dominant/auffällig – v.a. in von *C. hylas* stärker genutzten Teilbereichen; **+** Merkmal/Struktur zwar wichtig, aber insgesamt doch etwas weniger ausgeprägt/auffällig; **x** Merkmal/Struktur zwar vorhanden, aber nicht sehr prägend/auffällig; **–** Merkmal/Struktur fehlt am Gewässer bzw. genauere Informationen dazu fehlen (**?**).

Habitat type	Status class	inflow of cold water	shallow open water	Carex rostrata	Equi-setum	reed Veget.	bushes, trees	fish stock
I	1	+	++	++	x	+	x	+
I	1	++	x	+	+	++	+	++
I	(2)	++	+	++	+	+	x	+
II	1	++	++	++	+	x	x	x
II	2	x	x	x	x	++	+	x
II	(3)	++	+	++	x	–	+	++
II	(3)	+	x	++	?	++	+	+
II	4	–	+	–	x	–	x	–
II	(5)	x	?	–	?	?	?	+
III	2	++	+	+	?	+	x	x
III	2	++	x	+	–	+	+	–
III	2	x	x	x	–	?	?	–
III	2	++	+	++	?	+	x	–
IV	1	++	x	++	x	–	+	+
IV	1	++	+	++	+	x	+	+
IV	2	++	++	x	x	–	+	x
IV	5	++	+	+	–	–	x	–
IV	5	x	x	+	++	–	x	-
IV	(5)	+	?	x	–	+	++	+
V	(1)	x	++	++	x	–	+	–
V	2	+	++	++	+	x	+	–
V	(2)	+	+	++	x	x	++	x
V	(3)	x	+	+	x	–	++	–
V	5	++	+	++	+	x	++	+
VI	(3)	x	+	x	+	x	+	–
VI	5	–	++	–	x	–	++	–
VI	(5)	x	+	x	+	+	++	–

where *C. hylas* can be observed permanently. This is also true for the existence of extensive shallow water areas (conspicuous at 80% of sites with autochthonous populations) which mostly are overgrown or perfoliate by stands of bottle sedge *Carex rostrata* which is present at about 90% of all sites with records of *C. hylas* and is very conspicuous at all sites of the status class 1 (e.g., Figs 3 c, d, f, h). At sites where this sedge is merely present or not available as a dominant structure for mating, oviposition and hatching (e.g., Fig. 3b), other larger sedge species like tufted sedge *C. elata* or other swamp plants, in particular river horsetail *Equisetum fluviatile* and marsh bulrush *Eleocharis palustris (*or also deergrass *Trichophorum caespitosum* at bogs) may serve as essential plant structures as well. Reed Grass *Phragmites communis*, although conspicuous at some sites (Tab. 1, Figs 3a, i), is mostly absent or only present in small stands at sub-areas not heavily used by *C. hylas*, which hints at the species preference for oligotrophic waters, as reed is an indicator of more eutrophic conditions. However, dense reed vegetation at the edges of larger water bodies does not necessarily exclude a self-sustaining population. We know two such – rather isolated – sites at higher elevations, where at least medium sized populations constantly reproduced in the past 20 years (Figs 3a, j). At one of these sites *C. hylas* even uses Reedmace *Typha elata* predominantly as a substrate for mating and oviposition, and at the other site a rather dense stock of rainbow trout and other fishes exists (see Fig. 3a). Nevertheless, at most sites fish stocks are either absent or insignificant (Table 1). Also, bushes and trees are rarely dominating at *C. hylas* sites, although some shrubs and trees are present at all sites near the water line (Fig. 3) or even in the waterbodies (e.g., Fig. 3c).

Water depth and temperature

The results of our measurements of water temperatures and depths at seven important sites where individuals of *C. hylas* were mainly active, and where oviposition and hatching took place, are presented in Fig. 4 for three sites belonging to different habitat types and located at different elevations. Although our monitoring generated different values and seasonal patterns from site to site, overall the data revealed that sites inhabited by *C. hylas* are quite similar with respect to water depth and temperature:

(1) Most sites are rather shallow with flat land/water-transition zones and often with floating vegetation mats;
(2) Many sites exhibit some seasonal fluctuations in the water level with a tendency for a pronounced levelling from spring into the summer;
(3) Water temperatures are low to very low not only in spring, but mostly stay low even in mid-summer, and even at times and when the water is very shallow (Fig. 4). Even though, at most sites, the mean daily maximum values of water temperatures reached 19.1–21.5°C between late June and mid-July 2019, these maximum values stayed at 13.2 and 8.7°C at the two coldest sites exhibited in Fig. 4.

3a Habitat type I, above Lech valley; 1,200 m a.s.l., 16-vii-2019

3b Habitat type IV, Lech valley margin; 925 m a.s.l., 11-vi-2019

3c Habitat type IV, Lech valley margin; 930 m a.s.l., 18-v-2019

3d Habitat type IV, Lech valley margin; 990 m a.s.l., 16-vii-2019

3e Habitat type V, steppingstone habitat?; 1,030 m a.s.l., 16-vii-2019

3f Habitat type V (2013): now desiccated; 920 m a.s.l., 15-iii-2013

Figure 3. Variability and characteristics of *Coenagrion hylas*-habitats in the Lech valley (**a–h**) and in the vicinity of the Upper Inn valley (**i–l**). Definition/description of habitat types and habitat settings see text and Table 1. – **Abbildung 3:** Vielfalt und Charakteristik der

3g Habitat type VI (2000): now desiccated; 930 m a.s.l., no date

3i Habitat type II, near Inn valley; abandoned 790 m asl, 25-iii-2010

3k Habitat type III, bog at mountain terrace; 1,510 m a.s.l., 09.-vii-2008

3h Habitat type II, above Lech valley; 1,030 m a.s.l., 16-vii-18-v-2019

3j Habitat type II, above Inn valley; 1,130 m a.s.l., 30-ix-2012

3l Habitat type III, bog at mountain terrace; 1,530 m a.s.l., 08-vi-2007

Coenagrion hylas Habitate im Lechtal (**a–h**) und im Nahbereich des Inntals (**i–l**). Details zu den Habitattypen siehe Text und Tabelle 1. Photos: K. Blassnig (i), W. Egg (j), AL (a–e), J. Müller (g), F. Mungenast (k–l), A. Vorauer (f).

Discussion

A positive relationship between niche breadth and range size has been heavily disputed in ecology in the past, but overall is well documented across different taxonomic groups and spatial scales (e.g., Slatyer et al. 2013; Kambach et al. 2019; Cascadden et al. 2020; Sheth et al. 2020).

Such a positive relationship would suggest that a specialist species with a small range like *Coenagrion hylas* is more vulnerable to habitat loss and possibly also to effects of climate change due to synergistic effects of a narrow niche and small range (Slatyer et al. 2013; Cascadden et al. 2020). Thus, detailed information about habitat requirements of an endangered restricted-range species and about the range of habitats and altitudes is not only interesting from a general biological point of view but it is also essential for the planning of sound conservation measures.

The range of habitats used by *C. hylas* and its comparatively broad altitudinal distribution in Tyrol might at first suggest a rather large niche breadth for a species with such a small regional range. This somewhat contrasts with several statements in the literature assuming *C. hylas* to have a rather narrow ecological niche (see Ott 2003, 2006; Boudot 2010). Regarding the vertical distribution, for in-

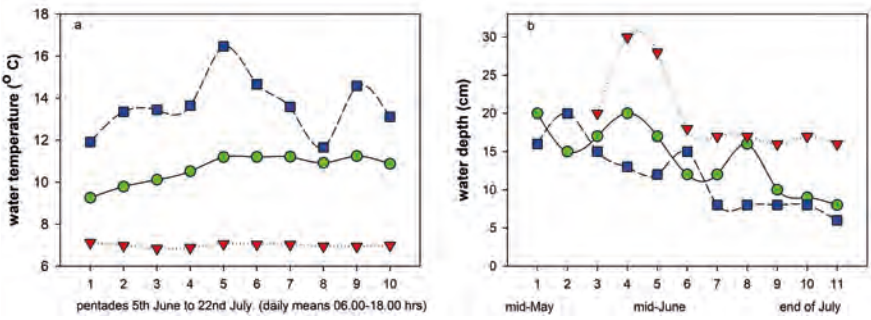

Figure 4. Seasonal variation of water temperatures (**a**) and water depth (**b**) at three sites in the Lech valley where *Coenagrion hylas* is known to reproduce regularly. **–n–** habitat type IV (990 m); **–l–** habitat type V (980 m); **–t–** habitat type I (1,200 m). Temperature: means from 360 thermo logger out reads (10 min intervals at daytime) in each pentad; depth: nine to 11 values from water level gauge reads between mid-May and the end of July 2019. The loggers and gauges were mounted in shallow water near the shorelines and close to the inflow of cold running or seepage water. – **Abbildung 4:** Saisonale Variation der Wassertemperatur (**a**) und Wassertiefe (**b**) an drei Gewässern im Tiroler Lechtal, an denen *C. hylas* sich regelmäßig fortpflanzt. **–n–** Gewässertyp IV (990 m); **–l–** Gewässertyp V (980 m); **–t–** Gewässertyp I (1.200 m). Temperaturwerte = Mittel aus je 360 Messungen/Pentade (Zehnminutentakt, tagsüber). Wassertiefe: Ablesungen an 9–11 Tagen zwischen Mitte Mai und Ende Juli 2019. Messungen erfolgten in Ufernähe (Flachwasser) und in der Nähe des Eintritts von kühlem Fließ- oder Sickerwasser.

stance, Schmidt (1991) speculated that the species would be restricted to the lower montane zone due to the lack of sheltering winter ice cover at lower elevations and upwards by insufficient warming of the inhabited waters in the summer. On the contrary, our data show that *C. hylas* can not only reproduce at cold bog waters in the subalpine zone, but also in high montane waterbodies which remain very cold in summer, and in valley waters which do not develop an ice cover in winter due to the influence of incoming running water.

However, even if the Tyrolean data, and especially the findings within the Lech-river valley have revealed that *Coenagrion hylas* is able to use a surprisingly wide range of habitats and waterbodies distributed over an altitudinal range of at least 800 m, a closer analysis of the data at hand yields a more complex picture and indicates rather specialized habitat demands which, overall, also raise some concerns about the future prospects of the species.

At first, despite the high variability of the habitats where *C. hylas* has been recorded, the few habitats where the species was constantly present over the last 20 to 30 years and reproduced in countable numbers, have rather similar features. Secondly, *C. hylas* seems to be restricted to locations in the western Northern Alps of Tyrol. This mountain area is characterised by long, snow-rich winters and cool, wet summers. In principle, for these climatical as well as for topographical and geological reasons, Northwest Tyrol is especially rich in small lakes, peat bogs, sedge swamps, and fens, cold spring waters and artificial ponds that might serve the habitat requirements of *C. hylas*. However, most sites of occurrence and the very few larger self-sustaining populations, which can comprise several hundred adult males (see calculations by Landmann M. et al. 2021a) are situated in the semi-open montane zone between 800 and 1,200 m a.s.l. Records between 1,200 to 1,480 m a.s.l. are currently missing , which might be the consequence of our incomplete knowledge, albeit one should keep in mind that possibly there are only a few appropriate habitats for *C. hylas* in the densely forested higher montane zone in the Northern Calcareous Alps.

As the lower montane zone and its waterbodies in general are more greatly impacted by human influences and pressures (recreational demands, insertion of fishes) than habitats at higher elevations, this pattern is already unfavorable for the future of the species. Accordingly, recent records of *C. hylas* are lacking at a third of the sites used by the species ten to twenty years ago (5 out of 15 in the Lech valley, 10 of 27 overall; cf. Table 1), and all of them are located at or near valley floors in the low montane zone. Besides direct human habitat alterations, climate warming also causes problems, because the small and very shallow waters preferred by the species are prone to desiccation, as happened in the flood plains of the Lech-river valley at four places in the last two decades. In addition, despite the seemingly wide spectrum of habitats used (Figs 3a–l) it is obvious that the requirements of *C. hylas* are not easily fulfilled and that most habitats suitable for constant reproduction need to have a combination of specific habitat features in common, which also distinguishes them from places where the species can be observed sometimes but it does not reproduce (see Table 1).

The habitat demands of both the larvae as well as of the imagines of this rare damselfly have already been investigated by Müller (2000a, b, 2001) in the Lech valley and his basic findings are supported by the data of our enlarged compilation. A combination of waterbodies with very shallow water, perfoliate, with jagged (but not too dense) stands of sedges (preferably *Carex rostrata*) along or near to incoming (or outgoing) small spring creeks, with chilly water or at zones where presumably cold underground seeping water is entering, seems to be essential. Even at the high-altitude bog habitats, where *C. hylas* can be found together with arcto-alpine and boreal Odonates like *Aeshna subarctica, Somatochlora alpestris, S. arctica* and *Leucorrhinia dubia* (Landmann A. et al. 2005), and which somewhat might represent conditions of the core range in Siberia and isolated habitats in northeast Russia (see Wildermuth & Martens 2019), *C. hylas* mainly flies along incoming small cold-water brooks and moor runoffs. But, even at these isolated high-altitude sites, the odonate communities face an increasing pressure from grazing by cattle and horses and from recreational use. It is unclear to what extent a greater fish stock impairs successful reproduction of *C. hylas* at small lakes and ponds. Although it does not seem to completely exclude a local occurrence of the species, it is obvious that at most sites inhabited by *C. hylas* fish stocks are either absent or insignificant (Table 1), and then mostly consisting only of Eurasian minnow *Phoxinus phoxinus*, a species that possibly does not harm the larvae of *C. hylas* (see Schmidt 1991). Finally, the data compilation in Table 1 reveals that bushes and trees, which may be important for the species (e.g., for perching, for shelter, or for resting during mating), are rarely dominant at *C. hylas*-sites. This is in line with the fact that *C. hylas* has very specific demands with regards to sunshine (Müller 2000a; Landmann M. et al. 2021a), and thus is sensitive to a strong shadowing of the waterbodies inhabited.

Conclusion and implications for conservation

Our compilation supports the notion that *C. hylas* in Europe is a member of a post-glacial, cold adapted stenothermal relict fauna, but has a broader habitat niche than expected, compared with its Siberian origin and as stated in parts of the literature. Nevertheless, at present there are only about a half dozen larger self-sustaining populations in Central Europe which are bound to very small waterbodies (< 0.1 to 0.3 ha, see Landmann M. et al. 2021a) that exhibit specific habitat features; these are sensitive to desiccation and human impacts. We thus agree with Müller (2015) that the strict protection and sound management of these few core sites must be the main concern and are imperative to save the species. Fortunately, the species has pronounced dispersal abilities (Landmann M. et al. 2021a) so that not only the preservation and upgrading/restoration of the main source habitats, but also the creation of stepping-stones and new potential reproduction habitats in between existing sites seem to be promising conservation measures. Such measures to protect this "entomological gem" already are implemented into the LIFE-Lech-program and are currently in progress in the river valley at six sites (Landmann & Gstrein 2020).

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