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# A polar insect's tale: Observations on the life cycle of *Parochlus steinenii*, the only winged midge native to Antarctica

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Antarctica and the sub-Antarctic islands include some of the world's most extreme and pristine terrestrial habitats. While they are characterized by low biodiversity and terrestrial communities that are comprised of small, often microscopic, noncharismatic species, they have become a focus of studies of adaptation and biological function in the face of multiple extreme environmental stresses (Convey & Biersma, 2023). Furthermore, they are highly sensitive to climate change and are considered natural laboratories to study and understand its impacts on biota (Contador et al., 2015; Convey & Peck, 2019). In the second half of the 20th century, the maritime Antarctic experienced considerable warming (Turner et al., 2014), causing deglaciation and the development of new ice-free areas and freshwater habitats, both along the coast and inland (Nędzarek & Pociecha, 2010), a process that is expected to continue (Lee

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et al., 2017). While the regional warming trends paused in the early 21st century (Turner et al., 2016), they are predicted to resume through the rest of the century (Bracegirdle et al., 2020), and a recent botanical study from Signy Island (South Orkney Islands) suggests this may already be happening (Cannone et al., 2022).

Maritime Antarctic lakes can experience extremely rapid physical ecosystem change, even magnifying the very rapid (in global terms) regional air temperature increases (of up to 2°C in mean annual air temperature) (Quayle et al., 2002, 2003). The lakes, streams and terrestrial habitats that make up Antarctica's land-based ecosystems are generally oligotrophic, small, and isolated. Many of their small invertebrates, lichens and microbes are found nowhere else on Earth (Convey et al., 2020; Convey & Biersma, 2023; Vincent & Laybourn-Parry, 2008). Other than the scavenging snowy sheathbill (*Chionis albus*), closely associated with marine vertebrate aggregations, the Antarctic terrestrial fauna consists only of small invertebrates, with just two native species of holometabolous insects, *Parochlus steinenii* Gercke, 1889 and *Belgica antarctica* Jacobs, 1900 (Diptera: Chironomidae), and two established nonnative species, *Eretmoptera murphyi* Schäffer, 1914 (Chironomidae) and *Trichocera maculipennis* Meigen, 1818 (Trichoceridae) (Convey & Block, 1996; Kozeretska et al., 2021; Potocka & Krzemińska, 2018; Volonterio et al., 2013). Of these, the terrestrial *B. antarctica* is strictly endemic to coastal regions of the western Antarctic Peninsula and the South Shetland Islands. In contrast, *P. steinenii* is not found on the Antarctic Peninsula, but occurs throughout the South Shetland Islands in the maritime Antarctic, sub-Antarctic South Georgia and the sub-Antarctic Magellanic ecoregion of southern South America (Contador et al., 2020; Gañan et al., 2021). Its larvae and pupae are aquatic, inhabiting lakes and streams, while the winged adults are terrestrial (Figure 1).

As parts of Antarctica undergo some of the most rapid changes worldwide in air temperature, glacial cover, and lake seasonality, polar flies face extreme changes in their environments. Insect life histories are influenced by changing temperatures, from physiology through development and voltinism (number of generations per year) to population dynamics and range (Contador et al., 2014). Climate change has significantly influenced the phenological patterns, distribution, and physiological adaptations of multiple species in different parts of the planet. Those distributed in alpine, subpolar, and polar regions are particularly affected (Walther et al., 2002). Studies of the life history, phenology, and stress tolerances of insects inhabiting aquatic ecosystems in these regions are critical for a better understanding of the ecological consequences of recent and ongoing climate change.

Antarctica's native and often endemic terrestrial invertebrate species appear particularly flexible in terms of their life history and ecophysiological strategies (Convey, 1996; Convey & Block, 1996). For example, recent studies have shown that *P. steinenii* has a wide thermal tolerance, ranging from −5 to +31°C (Contador et al., 2020; Pertierra et al., 2021), which could be an evolutionary consequence of the considerable magnitude of both short- and long-term variation in microenvironmental conditions within their habitats. However, while *B. antarctica* has been extensively studied as a model organism for a better understanding of the adaptations to extreme environments (Kozeretska et al., 2021), there has been much less research focused on *P. steinenii*, although studies of its phylogeny, physiology, and distribution patterns have increased in recent years (Allegrucci et al., 2006; Contador et al., 2020; Gañan et al., 2021; Pertierra et al., 2021). These species are of particular interest in terms of their ability to adapt and respond to changing environmental conditions, potentially being sentinel species of the ecosystem consequences of human-induced global environmental change (Kozeretska et al., 2021). In this context, we characterized the habitat preferences, life cycle, and phenology of *P. steinenii*, the winged Antarctic midge, to better understand how climate change may affect the phenological patterns of this species through time and space.

We studied the habitat preferences and the life history of *P. steinenii* in Lake Kitiesh, Fildes Peninsula, King George Island (62° S, Maritime Antarctica; Figure 1D) over the austral summer seasons from 2014 to 2019, during short (several weeks) field expeditions organized by the Chilean Antarctic Institute (INACH); longer duration, including year-round, field sampling is not possible at this location due to logistic limitations, as is commonly the case in Antarctic field research. This lake hosts an abundant population of *P. steinenii* and is easily accessible from Professor Julio Escudero Station (INACH, Chile), allowing for continuous site monitoring during the expeditions and the deployment of year-round environmental monitoring equipment. Ice-free areas on King George Island include many temporary shallow meltwater ponds and permanent lakes (typically smaller than 100 $m^2$), which are generally ice covered for the majority of the year (Kim et al., 2020). Surrounding ice-free terrestrial habitats in their catchments are characterized by rich herb–moss communities including the Antarctic hairgrass *Deschampsia antarctica* and a diverse moss and lichen community.

Antarctic populations of *P. steinenii* are restricted to permanent deeper lakes, which are ice covered for 9–10 months each year, and are surrounded by ice-free areas (Contador et al., 2020; Hahn & Reinhardt, 2006). To characterize the terrestrial habitat in which adults are found, we established five line transects around the perimeter of Lake Kitiesh (Figure 1D). Two transects were located parallel to the main inflow and outflow streams, while the

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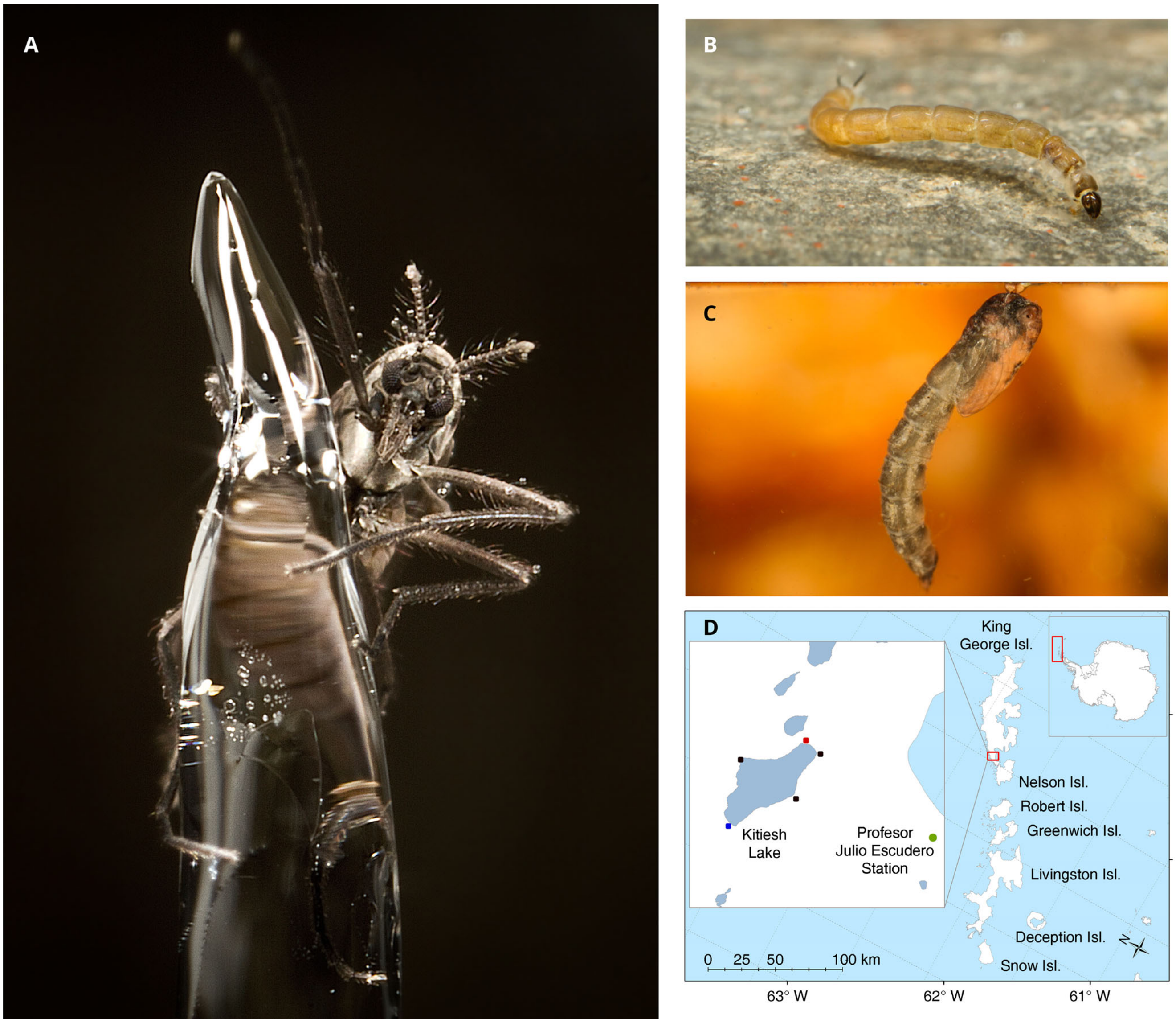

**FIGURE 1** *Parochlus steinenii*, the Antarctic winged chironomid midge. (A) Adult female on ice stalactite. Adults aggregate on the shore of the lake to copulate and protect themselves from the harsh environmental conditions. Females lay eggs on the water surface and larvae hatch in the benthos, where they grow and develop (B). (C) Pupae rise to the surface during the austral summer; hydrophobic setae help them to stay buoyant and adults leave their pupal skin by emerging at the water surface. (D) The location of Lake Kitiesh, King George Island. The sites in which transects were established around the perimeter of Lake Kitiesh are shown as dark squares. The blue and red squares indicate the inflow and outflow direction, respectively. Along each transect, adult densities of *P. steinenii* were recorded at 0, 2, 4 and 6 m from the lakeshore. Photographs by Gonzalo Arriagada.

other three were oriented approximately in N, NE and S directions, in each case perpendicular to the lake and starting at the lake edge. Along each transect, we quantified adult densities using 50 × 50 cm quadrats (subdivided into 10 × 10 cm grids) at 0, 2, 4, and 6 m from the lake shore. Adults of *P. steinenii* were not observed beyond 6 m from the lake edge. Numbers of adult flies in each 10 × 10 cm grid were recorded, and a digital photograph of each entire quadrat was taken to allow assessment of habitat preferences (Canon PowerShot D20). We recorded rock, snow, mud, moss, and water proportions within each quadrat. We assessed differences in *P. steinenii* adult density around the lake shore using permutational multivariate analysis of variance (PERMANOVA), based on a Bray–Curtis similarity matrix. We also investigated the relationship between *P. steinenii* density (individuals/m$^2$) and habitat type (rock, snow, mud, moss, and water) using distance-based linear models (DistLM). Both analyses were run in PRIMER-E v7 with Permanova+add-on (Anderson, 2005).

The data obtained indicated that *P. steinenii* adults aggregated at the lake edge, where they reproduce during the austral summer, the females laying batches of eggs at

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the bases of rocks and stones at the shoreline (Hahn & Reinhardt, 2006). Densities were significantly different at 0, 2, 4, and 6 m distance from the lake shore ($p = 0.001$, 999 unique permutations, PERMANOVA), being greatest at the shoreline, where they averaged 200 individuals/m$^2$ and reached a maximum of 500 individuals/m$^2$. Density decreased significantly as little as 2 m from the shoreline (mean 35 individuals/m$^2$), and further to 17 individuals/m$^2$ at 4 and 6 m from the shoreline. To visualize densities and habitat preferences, a nonmetric multidimensional scaling analysis (nMDS) was performed, and the habitats assessed were overlaid in the nMDS as vectors (Pearson correlations) (Figure 2C). This indicated that adult flies

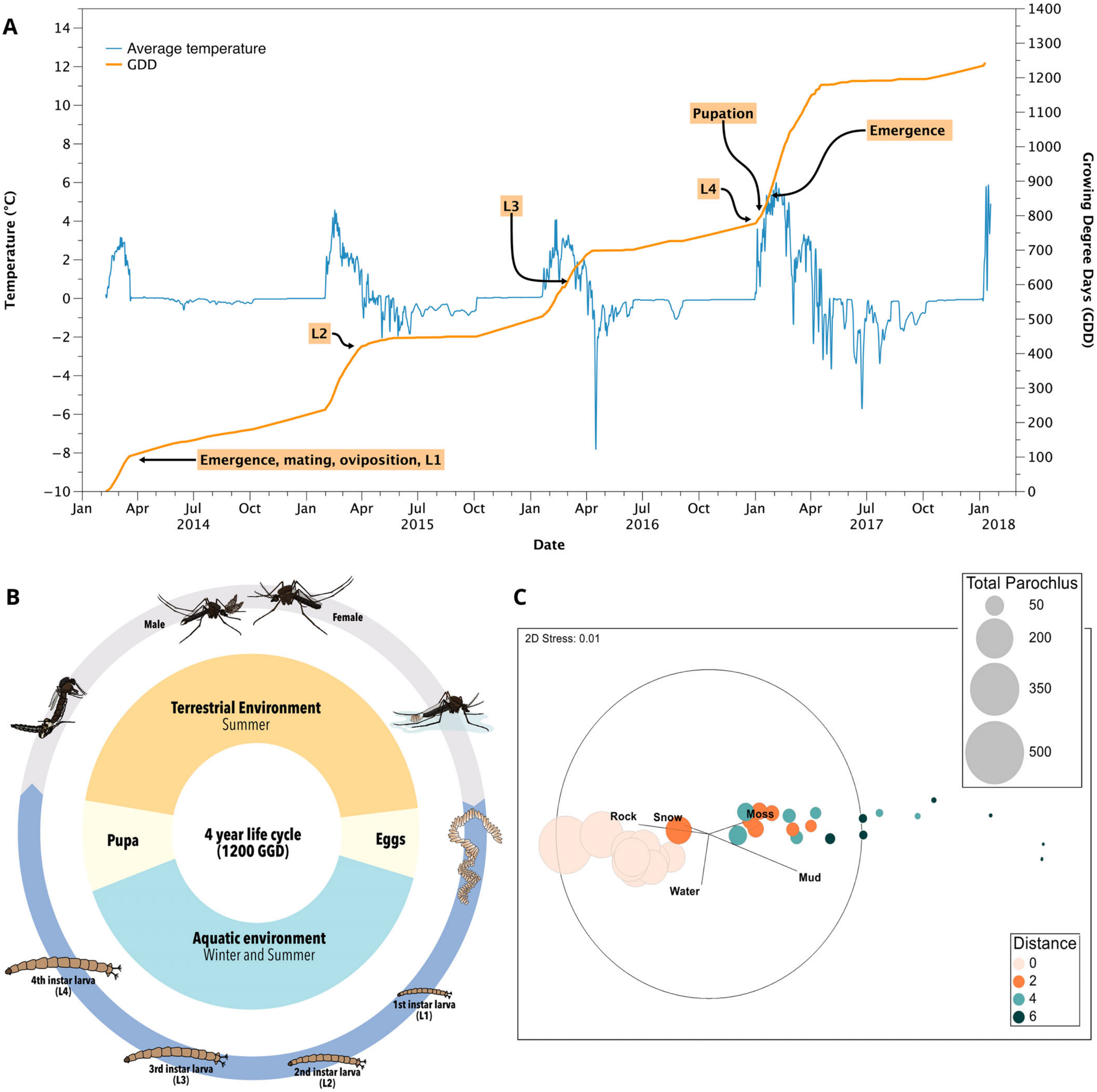

**FIGURE 2** Schematic illustration of the hypothetical multiyear life cycle of *Parochlus steinenii*. (A) Average temperature (blue line) and growing degree days (GDD) (orange line) recorded in Lake Kitiesh (King George Island, maritime Antarctic) from 2014 to 2019. Developmental events are highlighted in the GDD curve. (B) Conceptual scheme of the life cycle. L1, L2, L3, and L4 indicate developmental larval instars. (C) Nonmetric multidimensional scaling of *P. steinenii* densities (individuals/m$^2$) at 0, 2, 4 and 6 m from the shore of Lake Kitiesh (King George Island, maritime Antarctic). Bubble size and color indicate densities at different distances from the shore. The direction and length of each vector indicate the habitat preference and the strength of the correlation.

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preferred large rocks adjacent to the shoreline, particularly those oriented to protect them from exposure to wind and snow. Adults were also associated with moss patches, mainly at 2 and 4 m from the shoreline, and were rarely associated with mud (DistLM, $R^2 = 0.44$).

To assess the thermal characteristics of the aquatic environment in which *P. steinenii* develops from egg to adult, we anchored one temperature data logger (HOBO U22 Water Temp Pro V2) at a depth of 50 cm in Lake Kitiesh, corresponding to the depth at which high densities of larvae are commonly found during the austral summer. Minimum, maximum, and average daily water temperature (°C) were recorded from January 2014 to January 2019. Using these data, we calculated growing degree days (GDD), using the *pollen* package in R (Nowosad, 2019; R Core Team., 2021), which calculates GDDs available for development as the accumulated product of time and temperature above 0°C (noting that lake water temperatures are not likely to exceed the upper developmental temperature of *P. steinenii*, although this has not been formally assessed and that the larvae do not survive freezing) using daily maximum and minimum temperature data (Baskerville & Emin, 1969; Nufio & Buckley, 2019). To describe the life cycle of *P. steinenii*, we collected reproductive adults ($n = 200$) from rocks along the lake shore. Small rearing chambers (10 containers of 250 ml) were set up under controlled temperature conditions (4°C) in the laboratory of Professor Escudero Station as described by Harada et al. (2014). Each rearing chamber contained lake sediment, rocks, and water from the midge's habitat. Groups of ~20 reproductive adults were placed in each container, where mating occurred followed by oviposition on the surface of the rocks. The egg masses were then transported in the rearing chambers to the Wankara Laboratory (Universidad de Magallanes) in Puerto Williams, Navarino Island, Chile.

At the Wankara Laboratory, the chambers were maintained in an incubator with a 16 h light and 8 h dark cycle (LD = 16 h:8 h) at ~4°C (range achieved 4–4.5°C), monitored by a temperature logger (Hobo U22 Water Temp Pro V2) recording from the first day of observation until the hatching of the adults. Weekly observations of larval development were made until they reached the adult stage. Larval instar was assigned based on size, initially by eye and then followed by detailed measurements of head width and length (mm) using a microscope with a built-in camera (Leica DM750), calibrated for each image. Head capsule length (mm) was measured from the anterior margin of the frons to the posterior margin of the head's sclerites, while the width (mm) was measured as the distance across the eyes on the head capsule. This enabled larval development to be followed through four distinct developmental instars (L1, L2, L3, L4) (see Appendix S1). Growing degree days (GDDs, thermal units) needed to complete a cycle from egg to adult were then calculated. We obtained the GDDs required for each developmental stage and compared these with the GDD accumulation curve obtained from the water temperature recorded at 50 cm depth in Lake Kitiesh between 2014 and 2019. In the laboratory, after oviposition, a total of 53 eggs hatched close together after 109 GDDs and the L1 required $326 \pm 55$ ($n = 40$) GGDs to reach the next molt, with L2, L3, and L4 requiring ~$65 \pm 11$ ($n = 38$), $77 \pm 8$ ($n = 34$) and $192 \pm 31$ ($n = 32$) GDDs, respectively. The pupal stage required $166 \pm 38$ ($n = 29$) GDDs, meaning that the overall development from oviposition to adult emergence required $1056 \pm 41$ ($n = 12$) GDDs (Figure 2A). Similarly, in a simple preliminary laboratory trial in a varying temperature environment (6–12°C) overall development took ~1210 GDDs.

Using the temperature data obtained from the natural lake habitat at 50 cm depth, the accumulation of ~1200 GDDs took 4 years. We therefore hypothesize that *P. steinenii* requires a multiyear life in this habitat at present. Furthermore, GDDs accumulated rapidly during only a short period in the austral summer (December–April) (Figure 2A) during which, we assumed, most biological activity (i.e., larval growth, pupation, adult hatching) would occur. However, we recognize that the larvae may move between different microhabitats in the lake benthos and thereby experience conditions that differ from those at the 50-cm depth where we obtained our lake temperature data. For instance, as oviposition takes place on rocks at the lake edge, hatching L1 will enter very shallow and likely warmer water before moving to greater depths. Hahn and Reinhardt (2006) noted that, in the very shallow water at the lake edge, larvae may complete the first two instars before experiencing their first winter. However, before winter they need to move to deeper parts of the lake in order to survive (Rauschert, 2008), and where they avoid ice formation which is fatal (Contador et al., 2020; Shimada et al., 1991). The extent to which larvae show coordinated or timed movements to and from deeper or shallower water is yet to be investigated. Thus, the balance between time spent at deeper and colder, and shallower and warmer, depths has the potential to both accelerate or decelerate development relative to the 4 years estimated here, and requires further research. However, the fact that all developmental stages were active together in Lake Kitiesh during the austral summers of our study is consistent with the presence of multiple overlapping generations.

We found that *P. steinenii* can be extremely abundant at the local scale. However, at the same time, it is very restricted in terms of its preferred microhabitat distribution. The adult stage is only found along the edges of Antarctic lakes, using rocks and mosses to protect it from

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harsh environmental conditions, and often most obvious when forming swarms on the ground (Figure 2B,C). While it is capable of flight, for instance being attracted to lit windows of research stations, in our field observations we did not note that adults were flying, rather they were mainly walking and present in large aggregations at ground level. During more windy conditions, we noted that adults sometimes were transported to areas further than 6 m from the lake shore, but such events occurred infrequently. Even though this fly is winged, such observations have suggested that aerial dispersal is a rare occurrence, which is consistent with the complete lack of records of vagrant individuals from the neighboring northern Antarctic Peninsula, which is only 90 km away and to where prevailing westerly winds might be expected to carry it. Additionally, paleolimnological evidence suggests that the species has not previously occurred in the northeast Antarctic Peninsula (Gibson & Bayly, 2007). Such a lack of aerial dispersal may also indicate that the populations of different lakes and islands in the South Shetland Islands may be more isolated in an evolutionary context than might be expected from their apparent physical proximity. However, while Allegrucci et al. (2006) gave a preliminary estimate that South Shetland Islands populations of the species have been isolated from those in South Georgia and southern South America for ~2 million years or more, ongoing molecular phylogeographic studies have yet to examine the differentiation between populations at finer spatial scales. Given these constraints, we asked three key questions as a basis for future research: (1) How could climate change affect the species' phenological patterns? (2) What is the potential of *P. steinenii* to be able to move and disperse beyond its current distribution in the maritime Antarctic? and (3) What could the impacts of climate change be on this species, given its highly restricted and specialized microhabitat characteristics?

Phenological patterns are changing worldwide due to global environmental change. Many cold environment insect species have long life cycles, resulting from very slow growth, repeated or prolonged periods of dormancy, or very long-lived adults (Danks, 1992). Among the invertebrate fauna, insects are strongly affected by thermal variation, as the thermal environment directly affects their growth rates and maturation, and their ability to survive when temperatures exceed their tolerance range. Accumulating evidence suggests that climate change affects the phenology, population sizes, distribution ranges, development, and activity of insects at all trophic levels, resulting in temporal decoupling that may in turn lead to population crashes or extinctions (Nufio & Buckley, 2019; Parmesan, 2006, 2007). In particular, Arctic Chironomidae often have life cycles extending over several seasons (Hodkinson et al., 1996) and adult emergence is highly synchronous, often triggered by rising temperatures (Butler, 1980). For *P. steinenii* we observed a synchronous pattern of emergence, extending through the austral summer (Figure 2A). Synchronous emergence appears to be an important adaptation to the harsh environmental conditions in Antarctic Chironomidae, as it is in Arctic insects. In this context, the physiological mechanisms for synchronization must be particularly effective, as cohorts may develop over several years allowing the opportunity to diverge in growth and development (Butler, 1980). The possession of an obligate diapause, particularly in the pupal stage, presents one mechanism by which emergence synchrony may be restored. However, the presence of diapause does not appear to have been specifically investigated in this species. Our own preliminary laboratory observations in a simple and thermally variable culture experiment did not suggest the presence of obligate developmental arrest in any life stage, but we did not attempt any temperature manipulation to mimic the presence of, for instance, a seasonal cooling cue activating a diapause phase. One of the many species' traits that has been used to link climate change to phenological shifts is the thermal requirement for development, which can be measured using GDD (Cayton et al., 2015). Integrating GDD data into models aimed at forecasting the impact of current climate change provides a powerful tool for assessing its effects on insect phenology, as it can account for both regional and temporal variations in temperature (e.g., Hughes et al., 2013).

We established the first long-term study to improve our understanding of the ecology and life history of *P. steinenii*. It is already known that freshwater ecosystems in the maritime Antarctic may be strongly affected by climate change (Quayle et al., 2003). Therefore, the voltinism patterns and habitat suitability of *P. steinenii* could also be severely impacted. Further studies are now required to explore how phenological patterns and voltinism could be affected under different climate change scenarios, using GDDs to predict changes across space and time in the maritime Antarctic. Dispersal is another major life history trait and is particularly important in changing and extreme environments (Lakovic et al., 2017; Waters et al., 2020). We observed that *P. steinenii* has a very restricted microhabitat distribution, with the apparently rare occurrence of aerial dispersal events. These observations are especially important because migration toward more suitable regions is a common response to climate change (Arenas et al., 2012). Hence, the lack of dispersal capacity in this flying insect may increase its sensitivity to landscape/environmental variation, manifested by a reduced gene flow between even local populations,

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potentially driving speciation, and increasing susceptibility to extinction.

Placed in the context of more general awareness of Antarctic terrestrial diversity as well as the need for its protection, it is notable that most visitors to Antarctica are generally attracted by its charismatic marine fauna (penguins, seals, whales), spectacular scenery, and the all-too-familiar hostility of its environments; they express amazement that the continent's values include terrestrial biodiversity. There is virtually no awareness that Antarctica hosts insects or other terrestrial fauna, such as *P. steinenii*, or that these provide potentially key sentinels of the consequences of human-induced environmental change. To contribute to the compatibility of the conservation of the populations of this unique Antarctic dipteran in the face of greater intensity of long-term research, we designed nonextractive methods and prioritized ethical considerations in our study. We adapted the biocultural ethics approach to design methods that minimize collection through periods of field observation of behavior and population density (Contador, Rendoll, et al., 2022). Ecosystems and their component biota globally face multiple threats today and, therefore, it is essential to broaden the spectrum of ethical consideration beyond the historical focus on vertebrates (Rozzi, 2019). The conservation of *P. steinenii* should be motivated both by its intrinsic value as well as its instrumental value as a potentially effective sentinel of climate change in Antarctic terrestrial and aquatic ecosystems. The only winged Antarctic midge can alert us about changes in its thermal environment that may have significant impacts on its current habitats and phenological patterns, resulting in important structural changes in ecosystems in Antarctic regions.

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## CONFLICT OF INTEREST

The authors do not declare conflict of interests.

## DATA AVAILABILITY STATEMENT

Data (Contador, Gañan, et al., 2022) are available in Dryad at https://doi.org/10.5061/dryad.73n5tb31j.

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## REFERENCES

Allegrucci, G., G. Carchini, V. Todisco, P. Convey, and V. Sbordoni. 2006. "A Molecular Phylogeny of Antarctic Chironomidae and its Implications for Biogeographical History." *Polar Biology* 29: 320–6.

Anderson, M. J. 2005. *Permutational Multivariate Analysis of Variance*. Auckland: Department of Statistics, University of Auckland.

Arenas, M., N. Ray, M. Currat, and L. Excoffier. 2012. "Consequences of Range Contractions and Range Shifts on Molecular Diversity." *Molecular Biology and Evolution* 29: 207–18.

Baskerville, G. L., and P. Emin. 1969. "Rapid Estimation of Heat Accumulation from Maximum and Minimum Temperatures." *Ecology* 50: 514–7.

Bracegirdle, T. J., G. Krinner, M. Tonelli, F. A. Haumann, K. A. Naughten, T. Rackow, L. A. Roach, and I. Wainer. 2020. "Twenty First Century Changes in Antarctic and Southern Ocean Surface Climate in CMIP6." *Atmospheric Science Letters* 21: e984.

Butler, M. G. 1980. "Emergence Phenologies of some Arctic Alaskan Chironomidae." In *Chironomidae*, edited by D. A. Murray, 307–14. Pergamon: Elsevier.

Cannone, N., F. Malfasi, S. E. Favero-Longo, P. Convey, and M. Guglielmin. 2022. "Acceleration of Climate Warming and Plant Dynamics in Antarctica." *Current Biology* 32: 1599–1606.e2.

Cayton, H. L., N. M. Haddad, K. Gross, S. E. Diamond, and L. Ries. 2015. "Do Growing Degree Days Predict Phenology across Butterfly Species?" *Ecology* 96: 1473–9.

Contador, T., M. Gañan, G. Bizama, G. Fuentes-Jaque, L. Morales, J. Rendoll, F. Simoes, J. Kennedy, R. Rozzi, and P. Convey. 2020. "Assessing Distribution Shifts and Ecophysiological Characteristics of the Only Antarctic Winged Midge under Climate Change Scenarios." *Scientific Reports* 10: 9087.

Contador, T., M. Gañan, J. Rendoll-Cárcamo, C. Maturana, H. Benitez, J. Kennedy, R. Rozzi, and P. Convey. 2022. "A Polar Insect's Tale: Observations on the Life Cycle of *Parochlus steinenii*, the Only Winged Midge Native to Antarctica." Dryad, Dataset. https://doi.org/10.5061/dryad.73n5tb31j.

19399170, 2023, 3, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1002/ecy.3964 by British Antarctic Survey, Wiley Online Library on [27/03/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Contador, T., J. Kennedy, J. Ojeda, and P. Feinsinger. 2014. Ciclos de vida de insectos dulceacuícolas y cambio climático global en la ecorregión subantártica de Magallanes: investigaciones ecológicas a largo plazo en el Parque Etnobotánico Omora, Reserva de Biosfera Cabo de Hornos. Bosque.

Contador, T., J. H. Kennedy, R. Rozzi, and J. O. Villarroel. 2015. "Sharp Altitudinal Gradients in Magellanic Sub-Antarctic Streams: Patterns along a Fluvial System in the Cape Horn Biosphere Reserve (55° S)." *Polar Biology* 38: 1853–66.

Contador, T., J. Rendoll, M. Gañan, J. Ojeda, J. Kennedy, P. Convey, and R. Rozzi. 2022. In *Underwater with a Hand Lens: Ecological Sciences and Environmental Ethics to Value Freshwater Biodiversity*, edited by R. Rozzi, A. Tauro, and R. May. Switzerland: Springer International Publishing.

Convey, P. 1996. "The Influence of Environmental Characteristics on the Life History Attributes of Antarctic Terrestrial Biota." *Biological Reviews* 71: 191–225.

Convey, P., and E. M. Biersma. 2023. "Antarctic Ecosystems." In *Encyclopedia of Biodiversity*, 3rd ed., edited by S. M. Scheiner. Amsterdam, The Netherlands: Elsevier EISBN-13: 9780323984348: in press.

Convey, P., E. M. Biersma, A. Casanova-Katny, and C. S. Maturana. 2020. In *Refuges of Antarctic Diversity. Chapter 10 in: Past Antarctica*, edited by M. Oliva and J. Ruiz-Fernández, 181–200. Burlington: Academic Press. https://doi.org/10.1016/B978-0-12-817925-3.00010-0.

Convey, P., and W. Block. 1996. "Antarctic Diptera: Ecology, Physiology and Distribution." *European Journal of Entomology* 93: 1–13.

Convey, P., and L. S. Peck. 2019. "Antarctic Environmental Change and Biological Responses." *Science Advances* 5: eaaz0888.

Danks, H. V. 1992. "Long Life Cycles in Insects." *The Canadian Entomologist* 124: 167–87.

Gañan, M., T. Contador, J. Rendoll, F. Simoes, G. Carolina Pérez, S. Graham, J. K. Castillo, and P. Convey. 2021. "Records of *Parochlus steinenii* in the Maritime Antarctic and Sub-Antarctic Regions." *ZooKeys* 1011: 63–71.

Gibson, J. A. E., and I. A. E. Bayly. 2007. "New Insights into the Origins of Crustaceans of Antarctic Lakes." *Antarctic Science* 19: 157–64.

Hahn, S., and K. Reinhardt. 2006. "Habitat Preference and Reproductive Traits in the Antarctic Midge *Parochlus steinenii* (Diptera: Chironomidae)." *Antarctic Science* 18: 175–81.

Harada, E., R. E. Lee, D. L. Denlinger, and S. G. Goto. 2014. "Life History Traits of Adults and Embryos of the Antarctic Midge *Belgica antarctica*." *Polar Biology* 37: 1213–7.

Hodkinson, I. D., S. J. Coulson, N. R. Webb, W. Block, A. T. Strathdee, J. S. Bale, and M. R. Worland. 1996. "Temperature and the Biomass of Flying Midges (Diptera: Chironomidae) in the High Arctic." *Oikos* 75: 241–8.

Hughes, K. A., M. R. Worland, M. A. S. Thorne, and P. Convey. 2013. "The Non-native Chironomid *Eretmoptera murphyi* in Antarctica: Erosion of the Barriers to Invasion." *Biological Invasions* 15: 269–81.

Kim, J., S.-W. Jeen, H. S. Lim, J. Lee, O.-S. Kim, H. Lee, and S. G. Hong. 2020. "Hydrogeological Characteristics of Groundwater and Surface Water Associated with Two Small Lake Systems on King George Island, Antarctica." *Journal of Hydrology* 590: 125537.

Kozeretska, I., S. Serga, P. Kovalenko, V. Gorobchyshyn, and P. Convey. 2021. "*Belgica antarctica* (Diptera: Chironomidae): A natural model organism for extreme environments." *Insect Science* 29: 2–20.

Lakovic, M., O. Mitesser, and T. Hovestadt. 2017. "Mating Timing, Dispersal and Local Adaptation in Patchy Environments." *Oikos* 126: 1804–14.

Lee, J. R., B. Raymond, T. J. Bracegirdle, and I. Chadès. 2017. "Climate Change Drives Expansion of Antarctic Ice-Free Habitat." *Nature*.

Nędzarek, A., and A. Pociecha. 2010. "Limnological Characterization of Freshwater Systems of the Thomas Point Oasis (Admiralty Bay, King George Island, West Antarctica)." *Polar Science* 4: 457–67.

Nowosad, J. 2019. "pollen: Analysis of Aerobiological Data." https://CRAN.R-project.org/package=pollen.

Nufio, C. R., and L. B. Buckley. 2019. "Grasshopper Phenological Responses to Climate Gradients, Variability, and Change." *Ecosphere* 10: e02866.

Parmesan, C. 2006. "Ecological and Evolutionary Responses to Recent Climate Change." *Annual Review of Ecology, Evolution, and Systematics* 37: 637–69.

Parmesan, C. 2007. "Influences of Species, Latitudes and Methodologies on Estimates of Phenological Response to Global Warming." *Global Change Biology* 13: 1860–72.

Pertierra, L. R., P. Escribano-Álvarez, and M. Á. Olalla-Tárraga. 2021. "Cold Tolerance Is Similar but Heat Tolerance Is Higher in the Alien Insect *Trichocera maculipennis* than in the Native *Parochlus steinenii* in Antarctica." *Polar Biology* 44: 1203–8.

Potocka, M., and E. Krzemińska. 2018. "*Trichocera maculipennis* (Diptera)-an Invasive Species in Maritime Antarctica." *PeerJ* 6: e5408.

Quayle, W. C., P. Convey, L. S. Peck, C. J. Ellis-Evans, H. G. Butler, and H. J. Peat. 2003. "Ecological Responses of Maritime Antarctic Lakes to Regional Climate Change." *Antarctic Research Series* 79: 159–70.

Quayle, W. C., L. S. Peck, H. Peat, J. C. Ellis-Evans, and P. R. Harrigan. 2002. "Extreme Responses to Climate Change in Antarctic Lakes." *Science* 295: 645.

R Core Team. 2021. "R: A Language and Environment for Statistical Computing." Version 4.1.2.

Rauschert, M. 2008. "Beobachtungen an der Chironomide *Parochlus steineni* auf der Insel King George (Südshetlandinseln, Antarktis) (Diptera, Chironomidae). Mitteilungen aus dem museum fur naturkunde in Berlin." *Deutsche entomologische zeitschrift* 32: 183–8.

Rozzi, R. 2019. "Taxonomic Chauvinism, No More!: Antidotes from Hume, Darwin, and Biocultural Ethics." *Environmental Ethics* 41: 249–82.

Shimada, K., Y. Ohyama, and C. X. Pan. 1991. "Cold-Hardiness of the Antarctic Winged Midge *Parochlus steinenii* during the Active Season at King George Island." *Polar Biology* 11: 311–4.

Turner, J., N. E. Barrand, T. J. Bracegirdle, P. Convey, D. A. Hodgson, M. Jarvis, A. Jenkins, et al. 2014. "Antarctic Climate Change and the Environment: An Update." *The Polar Record* 50: 237–59.

Turner, J., H. Lu, I. White, J. C. King, T. Phillips, J. S. Hosking, T. J. Bracegirdle, G. J. Marshall, R. Mulvaney, and P. Deb. 2016.

19399170, 2023, 3, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1002/ecy.3964 by British Antarctic Survey, Wiley Online Library on [27/03/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

"Absence of 21st Century Warming on Antarctic Peninsula Consistent with Natural Variability." *Nature* 535: 411–5.

Vincent, W. F., and J. Laybourn-Parry. 2008. *Polar Lakes and Rivers: Limnology of Arctic and Antarctic Aquatic Ecosystems*. Oxford: Oxford University Press.

Volonterio, O., R. P. de León, P. Convey, and E. Krzemińska. 2013. "First Record of Trichoceridae (Diptera) in the Maritime Antarctic." *Polar Biology* 36: 1125–31.

Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. "Ecological Responses to Recent Climate Change." *Nature* 416: 389–95.

Waters, J. M., B. C. Emerson, P. Arribas, and G. A. McCulloch. 2020. "Dispersal Reduction: Causes, Genomic Mechanisms, and Evolutionary Consequences." *Trends in Ecology & Evolution* 35: 512–22.

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Additional supporting information can be found online in the Supporting Information section at the end of this article.

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