

## Review Article Biomonitoring Climate Change and Pollution in Marine Ecosystems: A Review on Aulacomya ater

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The sedentarism and wide global distribution of the blue mussel *Mytilus edulis* have made it a useful bioindicator to assess changes in the health status of the marine ecosystem in response to pollution and other environmental stresses. Effective biomonitoring of an ecosystem requires, however, that multiple biomarkers be used to obtain an accurate measure of the cumulative effects of different sources of environmental stress. Here, we provide a first integrated review of the biological, economical, and geographical characteristics of another species of mussels, the ribbed mussel *Aulacomya ater*. We discuss the use of *Aulacomya ater* as a complementary biomonitor to the blue mussel to assess the impact of pollutants and climate change. Recent findings have indeed shown that *Mytilus edulis* and *Aulacomya ater* have distinctive anatomy and physiology and respond differently to environmental stress. Monitoring of mixed beds containing blue and ribbed mussels may thus represent a unique opportunity to study the effect of environmental stress on the biodiversity of marine ecosystems, most notably in the Southern hemisphere, which is particularly sensitive to climate change and where both species often cohabitate in the same intertidal zones.

### **1. Introduction**

Historically known as the Magellan mussel, Aulacomya atra (A. ater) belongs to the genus Aulacomya. Today, this mussel species is commonly known as "cholga" in Chile and Argentina and as "ribbed mussel" in South Africa and other countries. The New Zealand form (Aulacomya maoriana) is smaller than its South American counterpart and has a finer radial sculpture, suggesting that it could be a distinct species [1]. It should not be confused with Geukensia demissa, a native mussel species from the Atlantic coast of North America also commonly called "ribbed mussel." In South America and South Africa, the presence of *A. ater* is found on Pleistocene deposits, suggesting it has been in these regions for at least 2 million years [2]. It has probably evolved from Aulacomya anderssoni, which originated from the Antarctic during the Paleocene-Early Oligocene [3]. Its dispersion is likely to have been favored by kelp-rafting of juvenile and/or adult individuals and not by an anthropogenic dispersal mechanism [2].

A. ater is well known for its presence in deep water. In Punta Arenas Cove in Chile, for instance, natural banks of A. ater are found at depths of 15 m to more than 30 m, where temperatures vary from 12 to  $16^{\circ}$ C [4] (Figure 1). A. ater is also commonly found in nearshore kelp-bed communities and algae holdfasts in Central Chile, subantarctic and Antarctic waters [5–7] and South Africa [8]. We found some specimens in the cold and deep water of Port-aux-Français, in the Kerguelen Islands.

### 2. Anatomical Features of Aulacomya ater

In contrast to other mussel species, such as *M. edulis* and *M. galloprovincialis*, which have been studied in detail for many years, descriptions of anatomical features of *A. ater* remain relatively scarce. The biomechanical properties of its byssus have been reported by Troncoso et al. [9] but without comparison with other mussels species. Bivalves are well known to have a wide range of sensory organs for orientation, synchronization of gamete emission, and



FIGURE 1: Aulacomya ater. A specimen of A. ater collected in the deep subtidal water at Port-aux-Français, in the Kerguelen Islands.

mechanical reception of water currents [10]. They are also known to have light-sensitive cephalic and (in more evolved species) pallial eyes that are used to measure proximal light intensities emitted from different directions [11]. Zaixso et al. [12] have shown that *A. ater* has distinct anatomical and histological features with regard to its sensory organs. While the cephalic eyes are highly uniform among bivalves, the pallial eyes are structurally more varied and are localized on the outer, middle, or inner mantle folds. *A. ater* has a paired "pallial sense organ" that has no equivalent in *Mytilus* [12]. These eyes are located in the suprabranchial chamber of the pallial cavity, extending from the base of the foot to the anus, on the posterior adductor muscle.

### 3. Reproductive Cycle and Growth

In Northern Chile, A. ater spawns more than once a year, with variable intensities. The most intense spawning periods occur at the end of October/early November and during December/February, which coincide with periods of lower daily temperatures (recorded at 16 m depth) [4]. But spawning still occurs in winter (end of May/end of July). In Southern Chile, continuous gamete release has been reported over several months during the year, with clear peaks of prespawning stages in April (fall), August (early spring), November, and February (summer); this coincides with fluctuations in phytoplankton levels [20]. In females, the spawning stage peaks in July and December, while males release gametes from May to January [20]. Compared to other species, however, A. ater grows more slowly under optimal conditions and its growth is proportionally more sensitive to exposure to air than is the case for M. galloprovincialis [21, 22]. For example, while the growth rate of A. ater is approximately 35-40 mm in the first four years, that of *M*. galloprovincialis is approximately 70 mm for the same period of time. Moreover, while *M. galloprovincialis* is basically unaffected to continuous exposure to air for a period of one week, nearly all A. ater mussels will die following such an exposure [21]. To attain a minimum commercial size of 50 mm, M. chilensis will thus take approximately 7-8 years while A. ater will take 8-10 years, although the growth rate may vary depending of the regions and temperatures [23]. Thus Griffiths and King [24] reported a much faster growth

of *A. ater* at Ouderkraal, located just South of Cape Town in South Africa.

### 4. Geographical Distribution

The distribution of *A. ater* is widespread in both the Atlantic and Pacific coasts of South America, the Falkland Islands, and the Kerguelen Islands [2]. It is also found in a variety of different coastal environments (estuaries, harbors, sheltered, and exposed rocky shores) in New Zealand. A. ater is present along the Pacific Ocean from El Callao, Peru, to the Strait of Magellan in Chile, extending along the Atlantic Ocean from the south of Argentina to the south of Brazil. It is also present along the Atlantic coast of Africa, from Rocky Point in Northern Namibia to Port Alfred in the southeastern coast [8]. It is completely absent in the Northern hemisphere, although its presence has been reported in 1994 and 1997 in the deep water of the Moray Firth in Scotland, possibly following the passage of ships or barge hulls originating from South America [25]. The southernmost limits of its distribution are in the Beagle Channel (Tierra del Fuego, Argentina) and in the Kerguelen Islands, where they inhabit the intertidal and subtidal zones (Figure 2) [26].

### **5. Population Dynamics**

A. ater used to dominate the lower midlittoral banks in Patagonia. There are increasing indications, however, that it is gradually disappearing there. At least three reasons may explain such decline: (1) changes in the climate of marine ecosystems; (2) competition with invasive alien mussel species; and (3) shifts in the commercial production of mussels. For instance, its population has severely declined in many areas of South America, as suggested by the observed declines from natural banks in Peru and Patagonia during severe El-Nino Southern Oscillation (ENSO) or following competition with B. rodriguezii [20, 27, 28]. In Chile, its culture has declined steadily from 1991, being replaced by M. chilensis [29]. In 2014, it represented less than 2,000 tons as compared to more than 20 000 tons in the 70s-90s and more than 220,000 tons for M. chilensis. In South Africa, where A. ater is indigenous, its existence is compromised in many areas by the presence of alien species, such as the Mediterranean M. galloprovincialis, which was introduced in South Africa in the late 1970s and represents now the most abundant mussel species in South Africa [30]. Such dominance by M. galloprovincialis on exposed and semiexposed shores is attributed to multiple factors, including a faster growth rate and a higher resistance to exposure to air, compared to A. ater [22]. Only on sheltered shores is A. ater able to resist the increasing dominance of *M. galloprovincialis* [30]. The geographic overlap between *A*. ater and M. galloprovincialis is almost complete and both are often in the same intertidal zones. Because of its significantly higher filtration rate (approximately 3-4 times that of A. ater), its resistance to air exposure, and its faster growth rate and higher reproductive output, M. galloprovincialis threatens the existence of A. ater [30]. The coastline of South Africa is not the only site where A. ater faces competition. On the beach of Puerto Madryn, in Patagonia, up to four species of



FIGURE 2: Global distribution of *Aulacomya ater*. In red, hypothetical origin of *A. ater* from Antarctic coasts and actual coastal distribution of *A. ater*. In South America, it is found in Chile, Peru, and Argentina. It is also found on the Atlantic coast of South Africa, in the Kerguelen Islands (Port-aux-Français and other sites), New Zealand, and the Falkland Islands. In blue, invasion of the mediteraneen *M. galloprovincialis* worldwide (adapted from [30]). *M. galloprovincialis* has colonised and formed naturalised populations at nine localities outside of its native range. These include Hong Kong, Japan, Korea, Australia, America, Mexico, Canada, Great Britain, and Ireland. *M. galloprovincialis* has been listed as one of the World's Worst 100 Invasive Alien Species (GISD 2012).

native mussels are found at the same site, including A. ater, M. edulis, Perumytilus purpuratus, and Brachidontes rodriguezii [31]. Mixed beds of A. ater, Choromytilus, and others have also been reported on the rocky intertidal shore of Central and Southern Chile [32]. Our team found mussel intertidal beds containing approximately equal numbers of M. desolationis and A. ater at Port-aux-Français, in the Kerguelen Islands [33] (Figure 3). To our knowledge, however, there is no data showing that such diversity is permanently maintained as in the previous cases. It is logical to believe, however, that the presence of pollutants or other sources of stress may alter such equilibrium. For example, when compared to other mussels species, A. ater has been shown to be very sensitive to copper when measuring mortality following exposure to concentrations of  $62.6-125 \,\mu\text{g/mL}$  for 48 h whereas other mussel species, such as Choromytilus chorus, have shown higher copper tolerance [34]. This equilibrium may also be threatened by distinct sensitivity to diseases, such a leukemia. This epidemic transmissible disease is caused by the insertion of retroviral sequences in the genome of the mussels and has recently been shown to spread horizontally [35, 36]. It is well known to affect many bivalves species, including Mya arenaria and Mytilus spp. Whether A. ater is more sensitive or resistant than other bivalves to the development of leukemia is currently unknown.

# 6. *A. ater* as a Sentinel Organisms for Marine Ecosystems

Marine bivalves have long been recognized as good biological indicators for monitoring the presence of a wide range of xenobiotics in marine environments. They are also used to monitor the effect of climate change. Although the majority of studies have used *M. edulis* as a sentinel organism to measure the presence of contaminants in marine ecosystems, several studies have used A. ater for assessing exposure and effect of pollutants in mussels [37]. In Northern Patagonia, where A. ater forms extensive beds on the rocky shores along the Patagonian coast of Argentina [38], this species has been used to monitor levels of metals (Fe, Cd, Zn, etc.) and activation of antioxidant enzymes. The authors found that the concentration of metals in the gills of A. ater varies according to the seasons, an observation similar to that which has been previously made with M. galloprovincialis [39, 40]. Measurement of the enzymatic activity of acetylcholinesterase present in the hemolymph has also shown to be potentially useful to detect the presence of low concentrations of organophosphate pesticides. Furthermore, A. ater has also been used for assessing the presence of cadmium in polluted marine environments on a more than 2000-kilometer-long coastline that extends from Walvis Bay



FIGURE 3: Mixed bed of *M. desolationis* and *A. ater*. The specimens were found in mixed beds located at Port-aux-Français in the Kerguelen Islands. On the left, the blue mussel *M. desolationis*. Each valve is elongated with a relatively smooth external surface that displays concentric growth rings. The anterior end is pointed and the posterior end is well rounded. The dorsal margin is convex and the ventral is weakly concave. On the right, *A. ater*, also known as the ribbed mussel, or Cholga or Cholgua, in South America. Its shell is multiform, with a concave ventral edge in most of the specimens. The dorsal edge is notoriously more prominent towards the rear half leaflet. Externally, it presents concentric grooves growth and marked ribs radials with band width decreasing progressively with increasing size.

in Namibia to Port Alfred on the coastline of South Africa [37]. In Chile and Argentina, A. ater is often used as a sentinel species to detect the bioaccumulation of pollutants, such as copper or cadmium, or toxic chemicals at different sites or following seasonal variations [14, 41-44]. It has also been used to study the disruptive effect of the natural estrogen E2 on male and female bivalves [45]. Natural hormones, such as  $17\beta$ -estradiol (E2), are well known for their potent endocrine disrupting effects on marine organisms and are released in the marine environment via domestic effluents [46, 47], livestock manure [48], and agricultural runoff [49]. A study in Argentina has also shown that A. ater can be used to monitor pollution from urban sewage [31]. The authors have shown that A. ater, M. edulis, and other bivalves (Perumytilus purpuratus and Brachidontes rodriguezii) seem to be equally sensitive to pollution by sewage [50]. Up to now, however, most of the biomarkers have been developed using M. edulis as the sentinel species. In the case of A. ater, most of the stress biomarkers have been focused on cellular (phagocytosis, apoptosis, oxygen consumption, oxidative damage, ammonia excretion, and lipid radicals) or enzymatic (acetylcholinesterase, superoxide dismutase, catalase, and glutathione S-transferase) activities [14, 33, 38, 51, 52]. Our knowledge of its immune functions also remains limited. Yet, biomarkers of the immune response are emerging as being extremely useful sentinels to monitor environmental stress in marine ecosystems. Only recently have we been able to get a glimpse of hemocyte functions in A. ater and the effect of cadmium or acute thermal stress in their viability and phagocytic activities [33]. The description of genes or sequence data in the case of A. ater also remains anecdotic at best or has been restricted to descriptions of partial DNA sequences aimed at rapidly identifying mussel species present in food products [53]. Yet, the use of

TABLE 1: Comparison of heavy metal mean content in whole *A. ater* with related bivalves.

	Cd	Cr	Pb	Cu	Zn	Mn	Mn
A. ater	1.7 <sup>a</sup>	2.5 <sup>a</sup>	7 <sup>a</sup>	0.575 <sup>b</sup>	13650 <sup>b</sup>	$0.84^{b}$	0.31 <sup>b</sup>
M. chilensis	1.5 <sup>a</sup>	2 <sup>a</sup>	$4^{a}$	0.67 <sup>g</sup>	15.7 <sup>g</sup>	2.85 <sup>g</sup>	_
M. edulis	1.26 <sup>c</sup>	_	_	0.98 <sup>c</sup>	61 <sup>c</sup>	$44.7^{\mathrm{f}}$	$5^{\mathrm{f}}$
M. galloprovincialis	1.3 <sup>d</sup>	1.6 <sup>d</sup>	$18^{d}$	21 <sup>d</sup>	183 <sup>d</sup>	14.1 <sup>e</sup>	56.3 <sup>e</sup>

Values are given in  $\mu$ g/g dry weight. Data was taken from Tapia et al., 2010 [13] <sup>a</sup>(Chili), Di Salvatore et al., 2013 [14] <sup>b</sup>(Argentina), Phillips, 1976 [15] <sup>c</sup>(Australia), Birch and Apostolatos, 2013 [16] <sup>d</sup>(Australia), Catsiki and Florou, 2006 [17] <sup>e</sup>(Greece), Szefer et al., 2002 [18] <sup>f</sup>(Baltic Sea), and España et al., 2007 [19] <sup>g</sup>(Chili).

A. ater as a sentinel species may provide some interesting benefits since it is one of the rare mussel species that is found in both subtidal and intertidal habitats, a property that could be very useful to assess the effect of environmental stress in two physically distinct habitats at a single site. Such difference in habitat is believed to explain the different sensitivity to copper and cadmium between A. ater and *Perumytilus purpuratus* in the Bay of Coliumo in Chile [41]. Because such distinct habitat is likely to make a difference in exposure, ingestion rates, and overall bioenergetics, it may also explain why the accumulation of toxins, such as paralytic shellfish poison, is less variable in A. ater than in M. chilensis [54]. Comparing the amounts of metals reported for M. edulis, M galloprovincialis, and A. atra (Table 1), the last species has a similar rate of accumulation and can be seen as an ecological equivalent from this point of view. Moreover, both genera have similar life span, reproductive cycles, and growth functions. In consequence they can be used equivalently to compare individuals of the same size. A. ater could be especially useful to monitor the impact of CC given its distinct physiology, reproductive cycle, and response to thermal stress when compared to other commonly used sentinel species. For example, it could be a convenient indicator of stressors that have limited impact on sentinel blue mussels. Such complementarity in biomarkers can provide significant benefits for monitoring of complex and high-risk ecosystems with borderline climatic conditions, such as the Kerguelen Islands.

### 7. Impacts of Climate Change and Pollution on Mixed Mussel Beds with *A. ater*

After changes in climatic conditions, invasive plants and animals are among the greatest threats to ecological diversity. Because they provide a habitat for other benthic macroinvertebrates, mussels are essential to maintain interrelatedness and persistence of associated organisms in aquatic ecosystems. Any major disturbance in their populations may thus have severe consequences in the biodiversity of these ecosystems. In North America, for example, Zebra mussels (*Dreissena polymorpha*), which were transported from Europe to North America in the ballast water of ships in the mid-eighties, have been shown to negatively impact aquatic ecosystems by harming native organisms by outcompeting other filter feeders or by adhering to shells of native mussels, turtles, and crustaceans [55]. Another example of invasion is the introduction in the Parana basin of an even more dangerous species, Limnoperna fortunei, which has a glochidia larvae that can attach to fishes to be transported upstream [56]. According to The Global Invasive Species Database (GISD), however, the most aggressive alien mussel species is probably M. galloprovincialis, a native from the Mediterranean coast and the Black and Adriatic Seas. It has successfully invaded numerous marine coastal lines around the globe, most notably those near important seaports where ship hull fouling and transport of ballast water are suspected to release alien mussel species [30]. A case in point is its dominance over the indigenous A. ater in South Africa. The question therefore arises as to whether climate change could exacerbate or revert the ability of an alien species such as *M. galloprovincialis* to invade a region like South Africa. One could easily envisage that extreme desiccation of rocky intertidal ecosystems, caused by strong dry winds and low rainfall, would provoke a selective pressure on these musseldominated beds that will impact their biodiversity. Such effect might be irreversible since we now know that biodiversity helps protect ecosystems from extreme conditions. This could be particularly important at sites with a rich diversity, such as the Wellington Harbour, where the endemic ribbed mussel A. maoriana and Perna canaliculus, together with M. galloprovincialis, dominate the intertidal zone in terms of their cover and biomass [57], or in Southern Chile, where rocky intertidal are dominated by Perumytilus purpuratus, Semimytilus algosus, M. edulis, M. chilensis, Choromytilus chorus, Brachidontes granulata, and Aulacomya ater [28]. It is also plausible that climate change will impact the ability of mussels to escape the effects of natural control agents such as parasites. In South Africa, for instance, it is well known that *M. galloprovincialis* is particularly sensitive to *Mastigocoleus*, an endolithic cyanophyte that contributes to the mortality of young (less than 40 mm shell length) *M. galloprovincialis* by weakening its shell at the point where the adductor muscle is attached and shell repair is impossible [58]. Because A. ater is less sensitive to Mastigocoleus, any environmental changes that favor the propensity of this bacteria will put M. galloprovincialis at a disadvantage relative to A. ater. In contrast, conditions that would favor growth of Polychaetes may have a more detrimental effect on A. ater than on M. edulis. While weak infestation by Polychaetes is usually not a threat for bivalves, heavy infestation can cause serious shell damage, reduce growth, and impair reproduction. The rough surface of the valves of A. ater, compared to smooth periostracum of *M. edulis*, probably explains why it is much more sensitive to polydorin (Polydora rickettsii) infestation [59].

Another factor to consider is how climate change will affect the vulnerability of mussels to predators, which play a critical role in the control of the structure and diversity of local mussel beds [60]. As suggested by Griffiths and Hockey [61], because predators attack younger and smaller mussels, *M. galloprovincialis* is less susceptible to predation compared to *A. ater*, which has a significantly lower growth rate in exposed and semiexposed sites [21]. However, because

*A. ater* has a significantly higher growth rate in sheltered sites, changes in the sea level that would impact the physical habitat of the mussel bed may favor *A. ater*, although one may argue that predation is likely to be more intense at sheltered sites. The rock-lobster is another predator that is particularly sensitive to environmental factors such as water temperatures, strength of the Leeuwin Current, and westerly winds [62, 63]. The scarce distribution of *A. ater* at Malgas Islands is indeed attributed to intense predation by rock-lobsters [64]. Changes in the population of *Nucella cingulata*, commonly found on the coast of South Africa, may also have a strong influence on the biodiversity of mixed beds with *A. ater* since this sea snail drills wider boreholes and preferentially selects bigger mussels such as *A. ater* [65].

### 8. Economical Perspective

Aquaculture is a rapidly growing economic sector that has shown a steady increase over the last 50 years [66]. According to a report published in 2013 by Transparency Market Research, the global market for aquaculture was valued at \$135.10 billion in 2012 and is expected to reach \$195.13 billion in 2019. Aquaculture provides half of the seafood products worldwide. Production of mussels is the third most important among bivalves, after clams and oysters, reaching approximately 1.5 million tons in 2010. This market is largely dominated by the blue mussels, which have a wide geographical distribution and which have been cultured by intertidal wooden poles for several centuries in Europe. Given the extreme southern geographical distribution of A. Ater, its production is much more limited. Historically, the production of A. ater has been exclusively derived from artisanal capture methods along the coast of Chile. Its commercial potential had steadily grown since the end of 1950s, reaching a plateau of approximately 15 000 to 20000 tons in the seventies [67]. This method has been gradually replaced by aquaculture production. Production of A. ater is usually done using suspended systems and takes 14-24 months before harvest [68]. Despite such new methods, over the last 15-20 years, its overall production has steadily declined (http://www.fao.org/fishery/species/3533/en) [69]. In 2005, the production of A. ater barely reached 800 tons. This is extremely low compared to productions of M. edulis and M. galloprovincialis (approximately 400 000 and 115 000 tons, resp.) [70]. In South America, the production of M. chilensis reaches more than 80 000 tons, exceeding hundredfold that of A. ater. In countries such as Chile, where mussel production concentrates around three distinct species, M. chilensis, Choromytilus chorus, and A. ater, and exceeds that of the Pacific oyster and the Northern scallop, the industrial development and the greatest commercial potential are now focused on M. chilensis [26]. In 2010, the production of M. chilensis reached 221,522 tons, 1,736 tons for A. ater, and 757 tons for C. chorus. Considering that the global market of bivalves is consistently increasing, reaching 13.6 millions metric tons (mt) in 2005, and that mussels dominate the global trade, it is clear that A. ater captures only a small share of the bivalve market taking into account consumer's preference for blue mussels.

A. ater, however, may still have some unexploited potential when considering the emergence of bioinspired engineering research for the development of innovative biotechnological applications. The global market for such plant and animal biological adhesives is believed to reach more than \$6 billion in 2019 (http://www.marketsandmarkets.com/). Like other mussels, A. ater possesses some highly developed macroadhesion mechanisms that are extremely efficient in a humid environment and that are necessary to resist the shear force of turbulent intertidal zones. A gland in the foot of byssus-forming mussels produces adhesive polyphenolic proteins rich in dopa, lysine, and other hydroxylated amino acids. These proteins, which have low immunogenicity and are nontoxic, biodegradable, and nonpolluting, have been considered as potentially attractive for coating different types of surfaces for biotechnological usage, including immobilization of antigens on solid support for ELISA testing [71]. Compared to other mussels species, A. ater contains 15-20 times more adhesive polyphenolic proteins than any other mussels [72]. Protocols aimed at optimizing large scale production of these biological adhesive for their industrial usage have recently been developed and may accelerate the use of such bioinspired proteins in various biomedical and tissue engineering fields [73, 74].

### 9. Perspectives

Compared to A. ater and other mussel species, blue mussels have received much more attention from scientists and aqua farmers not only because their global production is increasing at a rapid pace, but also because it is found almost everywhere in the world and is capable of dominating indigenous mussel species, which will eventually face local and regional extinction. In contrast, A. ater, which has been historically a driving force in the economy of many countries, has seen its position in the global market of bivalves steadily declining in favor of other mussel species. This is largely due to several factors, including the fact that its geographical distribution is restricted to the Southern hemispheres and that its growth rate is slower than that of the blue mussel. For scientists, the wide distribution of blue mussels also makes it a very useful tool for monitoring the effect of environmental stress on marine ecosystems on a global scale. It is clear, however, that more attention needs to be paid to A. ater. Its progressive disappearance from the coast of South Africa is an indication of its sensitivity to the dominance by the blue mussels. Given its limited geographic distribution, one could wonder whether such dominance by the blue mussel may severely compromise the existence of A. ater. Whether climate change and pollution will exacerbate this trend is a question that deserves attention. Because of their distinctive anatomy and physiology, it is logical to believe that both species will respond differently to climate change and exposure to pollutants. Our recent comparative study between A. ater and M. desolationis supports this hypothesis [33]. Monitoring of mixed beds containing A. ater may thus represent a unique opportunity to study the effect of climate change and pollution on the biodiversity of marine ecosystems. In fact, a better knowledge of A. ater could provide a

new and complementary tool for monitoring global climate changes in marine ecosystems in the Southern hemispheres, which is particularly sensitive to climate change.

### **Competing Interests**

The authors declare that they have no competing interests.

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