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Towards an integrated assessment of the Arctic marine ecosystems in response to abrupt environmental changes: Contribution from the Arctic challenge for sustainability II (ArCS II) project

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ABSTRACT

The Arctic marine ecosystems, extending from microbial communities to the system response to environmental and human pressures, were investigated in the Arctic Challenge for Sustainability II (ArCS II) project, a nationally coordinated Arctic project in Japan. New findings and hypotheses emerged: a) bottom sediments on a continental shelf contained a significant amount of the bloom-causing viable diatom, and more primary production may be occurring over a water column than previously thought, b) particle flux containing biogenic opal increased over the 2010s, c) large copepod *Calanus glacialis/marshallae* exhibited flexibility on grazing in the Pacific Arctic Ocean, suggesting their high adaptation to environmental changes, d) a novel environmental DNA (eDNA) technique succeeded in the identification of polar cod distribution, e) there was an increase in species richness over the last 20 years due to the poleward shift of habitat ranges of marine predatory species, f) Arctic marine ecosystems may have a larger sensitivity to external forcings around the Pacific and Atlantic gateways. This article reviews and highlights these findings in the context of specific science questions and delivers Japan's contribution to the integrated assessment of Arctic marine ecosystems.

1. Introduction

A significant reduction of Arctic sea ice during recent years (Druckenmiller et al., 2020; Meier et al., 2023) is a symbolic symptom of our planet in response to anthropogenically driven global climate change. The retreat of the sea ice is now allowing a direct and unprecedented expansion of human activities into the Arctic with modern industrial machinery such as fishing, shipping, cruising, etc. (Stocker et al., 2020; Dawson et al., 2020). Despite such visible changes in the natural environment and the extent of human intervention in the Arctic, their impacts on marine ecosystems are not necessarily visible and poorly recognized. International efforts have been developed in various frameworks for the visualization (e.g. ICES, 2021; 2023, CAFF, 2021; PAME,2008, 2013) and earlier and recent studies in the Arctic have shown the differences in physical and biological structures among ecosystems (Kang et al., 2024; Rudels and Carmack, 2022; Drinkwater et al., 2021; Mueter et al., 2021a), stressing the need to understand regional ecological impacts. Some studies showed evidence of these impacts, for example, on species abundance (CAFF, 2013), recruitment (David et al., 2025), and biogeographic shifts of organisms (Kim et al., 2024; Orlov and Volvenko, 2024; Baker et al., 2023; Gordó-Vilaseca et al., 2023; Jørgensen et al., 2022; Stafford et al., 2022; Frainer et al., 2021) as well as future change in marine communities and biodiversity (e.g. Stroeve et al., 2025; Hodapp et al., 2023; Mueter et al., 2021a; Alabia et al.,

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2020). While Arctic research efforts are gaining momentum, climate change research remains comparably sparse in this region relative to other marine biomes, impeding conservation efforts (Deb and Bailey, 2023). Impact assessment of Arctic ecosystems due to the combined effects of natural and anthropogenic stressors is an urgent international task towards achieving sustainable ecosystem management against unregulated and overused environmental resources and ecosystem services in the Arctic.

Two nationally-organized projects for Arctic research, such as the Green Network of Excellence (GRENE) Arctic Climate Change Research project (2011–2016) (Yamanouchi and Takata, 2020) and the Arctic Challenge for Sustainability (ArCS) project (2015–2020) (Sueyoshi et al., 2021), were launched in Japan. Marine ecosystem studies have been conducted as one of Japan's contributions to the international efforts to understand the Arctic marine ecosystems. One of the significant ecological findings was the northward transport and shift of marine species across multiple trophic levels over the Bering and Chukchi Sea shelves, associated with sea ice decline (Hirawake et al., 2021, extensive references therein). In the follow-up ArCS II project (2020–2025), we further extended the efforts to the Arctic Ocean, from the Pacific gateway including Chukchi Sea to the Pan-Arctic waters, to find new unrecognized marine ecosystem processes and assess the ecosystems' variability and potential vulnerability. This article reviews and highlights these findings. The other topics with summaries of the research cruises, field campaigns, and modeling experiments in the ArCS II Ocean Research Program are reported in a companion article (Watanabe et al., 2025, in this issue).

2. Plankton and settling particles

Phytoplankton, which forms the basis of marine ecosystems, is facing dramatic changes in its community composition (e.g., Li et al., 2009; Fujiwara et al., 2014), productivity (e.g., Pabi et al., 2008; Arrigo et al., 2011), and phenology (e.g., Ardyna et al., 2014; Nishino et al., 2015; Assmy et al., 2017; Waga and Hirawake, 2020) due to the recent climate change. They rapidly respond to the dynamic changes in available nutrients and light triggered by sea ice reduction and changes in ocean circulation (Ardyna and Arrigo, 2020 and references therein). One of the most notable scientific findings about the Arctic phytoplankton in recent years could be the discovery of under-ice bloom (Arrigo et al., 2012, 2014). Under-ice bloom is a spring phytoplankton bloom that occurs beneath the sea ice, which is hardly captured from the sea surface. In addition to their findings, we found another type of "hidden bloom" that underlies the sea floor of the vast shallow shelf region in the Arctic.

During the summer to early fall in the Arctic Ocean, surface nutrients are exhausted, resulting in low primary production (Hill et al., 2005; Tremblay et al., 2008; McLaughlin and Carmack, 2010). Phytoplankton thus cannot increase in the surface water and is most abundant in the subsurface layer (~40–50m) (Ardyna et al., 2013; Brown et al., 2015). This subsurface phytoplankton peak is called subsurface chlorophyll maximum (SCM). The phytoplankton in the SCM are regarded as low-productive and stable because they do not receive sufficient light and nutrients (Ardyna and Arrigo, 2020). However, in the Arctic Ocean, high primary production was occasionally observed in the SCM (Lowry et al., 2015; Martin et al., 2010). From repeated shipboard observations in the shelf region during the ArCS II project, Shiozaki et al. (2022) captured the development of the SCM near the seafloor in shallower waters north of 70°N, where higher irradiance reached the seafloor. Primary production significantly increased in the subsurface by the phytoplankton bloom near the seafloor. While the primary production monitored by satellite observation is generally assumed to be higher near the surface (e.g., Behrenfeld and Falkowski, 1997; Pabi et al., 2008), the new result highlighted that the bottom-associated diatom bloom could account for a large part of primary production on a local scale. Shiozaki et al. (2022) further estimated that the sediment-associated bloom accounts for 24 % of the shelf region in July in the eastern Siberian Sea, Canadian Arctic Archipelago, Foxe Basin, Chukchi Sea, and Barents Sea.

The bottom-associated bloom was mainly caused by diatoms (Shiozaki et al., 2022). Diatoms increase on the surface by spring bloom but sink and accumulate in the sediment (Leu et al., 2015). Diatoms produce resting stages to facilitate survival during periods that are less favorable for growth (McQuoid and Hobson, 1996), and they are distributed in sediments of the Arctic shelf (Tsukazaki et al., 2018). Resting stages of diatoms in sediments can resume growth in response to favorable light levels (Hollibaugh et al., 1981). Using a combination of physiological and microcosm experiments, Fukai et al. (2021) and (2022) confirmed abundant diatom resting stage cells broadly underly in the sediment across the Northern Bering and Chukchi shelf. From these findings from observational facts and experimental analysis conducted in the ArCS II project (Shiozaki et al., 2022; Fukai et al., 2021, 2022), a new hypothesis has emerged that the bottom-associated hidden bloom may now be widespread across the shallow Arctic shelf regions along with sea ice reduction due to climate change.

Observation of settling particle flux with a moored sediment trap in the Pacific Arctic from 2010 to 2022 showed that the particle flux for the late 2010s increased compared to the early 2010s (Onodera et al., in prep.) During summer, a relative increase of biogenic matter in the bulk component, probably the active biological production, was observed despite abundant shelf matter input mainly supplied by sub-surface ocean currents. Much of the biogenic opal was probably planktic diatoms and ice algae diatoms (Onodera et al., 2021). However, in winter, the contribution of radiolarian shells (Ikenoue et al., 2021) and resuspended fragments of siliceous microplanktons was relatively significant (Onodera et al., 2021).

3. Zooplankton

Zooplankton are secondary producers of the marine ecosystem and comprise a vital link between primary production and higher trophic levels in the Pacific Arctic Ocean (Lowry et al., 2004; Ashjian et al., 2010). *Calanus glacialis/marshallae* are dominant large copepods in the region (Abe et al., 2020), but there is little information about regional and diel changes in population structure and grazing features. A remarkable early sea-ice reduction event observed in 2018 affected several marine trophic levels, resulting in delayed phytoplankton blooms (Kikuchi et al., 2020), phytoplankton community changes (Fukai et al., 2020), and a northward shift of fish stocks (Duffy-Anderson et al., 2019), but responses in zooplankton was unclear. Comparing the zooplankton community, population structure for dominant copepods, and size structure between 2017 and 2018, the response to the sea-ice reduction was investigated in the Chirikov Basin. While the zooplankton community in 2017 event included abundant Pacific copepods transported by the Anadyr water (Kimura et al., 2022), the community was dominated by small copepods (Duffy-Anderson et al., 2019), bivalve larvae and younger stages of large copepods (*C. glacialis/marshallae* and *Metridia pacifica*), which was likely caused by reproduction delays resulting from the early sea-ice reduction event (Kimura et al., 2022). Relating the dominance of small-sized species, low biomass and low transfer efficiency in the lower trophic levels were revealed by normalized size spectra analysis derived by a ZooSCAN (Kumagai et al., 2023). These results suggest the prevalence of low-nutrient foods for higher trophic levels in 2018 with early sea ice melt. Thus, a drastic sea-ice variation would impact the zooplankton community in the Pacific Arctic Ocean, but it was different between the regions (Abe et al., 2020). At the connecting area (e.g., Bering Strait), the zooplankton community was changed by increasing Pacific water inflow (Matsuno et al., 2011; Ershova et al., 2015). On the other hand, in the northern Chukchi Sea, a low-biomass community was found (Abe et al., 2020).

Climate changes could impact zooplankton in the Pacific Arctic (Skjoldal, 2022), but their intensity would vary depending on the flexibility in the physiology of the species (Balazy et al., 2021). *Calanus glacialis/marshallae* are dominant large copepods in the Pacific Arctic, but there is little information about regional and diel changes in population structure and grazing features. Ishihara et al. (2023) analyzed geographic and diel variations for *C. glacialis/marshallae* in population structure, body size, grazing activity, and fatty acid composition. It was found that *C. glacialis/marshallae* exhibited high flexibility toward environmental changes. In the northern Chukchi shelf, the populations also showed higher concentrations of fatty acids originating from dinoflagellates than those originating from the pan-Arctic Ocean, indicating low productivity in the region. In the basin, small and large forms of copepodite stage five were simultaneously found, and the small form exhibited a diel grazing activity pattern, but the large forms did not. These findings suggest their good adaptation to the changing of the Pacific Arctic Ocean.

According to the regional comparison of mesozooplankton trapped in sediment traps for 2010–2014 in the southern Northwind Abyssal Plain (NAP) (Tokuhiro et al., 2024), the timing of seasonal descent of *Calanus hyperboreus*, which is the representative herbivorous copepod in the Arctic Ocean, was different among NAP, the Fram Strait, and the MacKenzie Trough. The reproduction of *C. hyperboreus* at NAP in the early 2010s was less active than that in the Fram Strait and the MacKenzie Trough (Tokuhiro et al., 2024). However, this regional difference in the mesozooplankton population structure might be further changed with physical oceanographic changes after the late 2010s. The studied sediment trap captured a large amount of discarded Appendicularian "house" in summer (Onodera et al., 2021), which might be an important carbon transporter to the ocean interior in the region.

4. Polar cod

The polar cod (*Boreogadus saida*) is considered a key species in the Arctic ecosystem, supporting the food web as a primary prey for various predators (Geoffroy et al., 2023; Steiner et al., 2021). Increasing water temperature and retreating sea ice drive the distributional shift of polar cod (Levine et al., 2023; De Robertis et al., 2017) and potentially have a negative effect on its population (Huserbråten et al., 2019; Florko et al., 2021). Environmental DNA (eDNA), a composite of genetic materials originating from aquatic animals, can indirectly indicate the presence of source organisms (Barnes and Turner, 2016), such as the polar cod. eDNA can be detected using species-specific assay focusing on target species or metabarcoding to comprehensively describe the biodiversity across various taxa (e.g., Deiner et al., 2017; Shelton et al., 2022). Because the eDNA technique has sufficient sensitivity to evaluate the distribution of fish species in the ocean (e.g., Jensen et al., 2023; Shelton et al., 2022), it would provide valuable baseline data for understanding the ecological importance of polar cod.

Although the potential of eDNA to investigate fish distribution is widely recognized, its application in the Arctic is limited, particularly for fish. In the Atlantic Arctic, Jensen et al. (2023) described latitudinal changes in the fish community around Greenland, which included cod species (Gadidae) such as polar cod, using eDNA metabarcoding. However, no eDNA study has been conducted to explore the distribution of polar cod in the Pacific Arctic. Kawakami et al. (2023b) successfully described the horizontal distribution of polar cod in surface water across the Bering and Chukchi Seas using a newly devised eDNA assay. Polar cod eDNA was detected primarily in the central part of the Chukchi Sea shelf, the marginal ice zone along 75°N, and the shelf slope off Point Barrow. The eDNA was most frequently and abundantly detected in the sites with cold, less saline water, while no eDNA was detected in the sites with warm and saline water. Current knowledge about the distribution and habitat of the polar cod (e.g., Forster et al., 2020; Geoffroy et al., 2023) was consistent with these findings, suggesting that eDNA can serve as a reliable tool to supplement or replace conventional methods. eDNA metabarcoding can evaluate interactions across multiple trophic levels (Deeg et al., 2023; Djurhuus et al., 2020), thus helping to assess how fluctuations in the polar cod population impact the ecosystem. Before applying the metabarcoding to the Arctic environmental sample, we evaluated how the sampling method affects the detection of fish eDNA (Kawakami et al., 2023a). We also used eDNA metabarcoding to investigate metazoan diversity and its environmental drivers in the Chukchi Sea, including a wide range of invertebrates that may occur sympatrically with polar cod (Verhaegen et al., 2025). Expanding eDNA techniques based on robust methodology will help fill the knowledge gaps Geoffroy et al. (2023) suggested about how various stressors influence polar cod.

5. Marine biodiversity

Sub-Arctic and Arctic seas have been increasingly exposed to rapid climatic changes over the last few decades, resulting in changes in their physical and biogeochemical characteristics (Polyakov et al., 2025; Nishino et al., 2023; Drinkwater et al., 2021; Mueter et al., 2021a). These significantly impact the marine ecosystem structure and function, evidenced by biogeographic shifts (Bernardo et al., 2024; Axler et al., 2023; Baker et al., 2023; Brandt et al., 2023; Levine et al., 2023; Jørgensen et al., 2022; Alabia et al., 2018) and future reorganization of marine communities (Årthun et al., 2025; Nilsen et al., 2025; Mueter et al., 2021a). While these emphasize the need better to understand the regional climate-driven ecological impacts on marine communities, our existing knowledge of marine biodiversity and stressors in these regions remains limited, as is our understanding of their trends and impacts (CAFF, 2013). Alabia et al. (2023) investigated recent marine biodiversity trends based on species richness and composition (Baselga, 2017) and pair-wise co-occurrences (Griffith et al., 2016), revealing an overall increase in species richness throughout the Arctic in the last 20 years. Further, regional biodiversity changes were accompanied by variations in co-occurring taxa over time, suggesting the formation of novel trophic interactions and potential trophic mismatches (Alabia et al., 2023).

Meanwhile, in a part of the Pacific Arctic region (i.e., Northeastern Bering and Southern Chukchi seas) and adjacent subarctic sea (i.e., southeastern Bering Sea), it was found that larger, longer-lived and more predatory fish and invertebrates would expand their ranges towards the north pole in response to warming waters and sea ice change, preying on and altering the composition and functions of the current Arctic communities (Alabia et al., 2020). Two distinct marine biodiversity refugia were also discovered in the north and south parts of the middle shelf of the southeastern Bering Sea, which overall covered less than 10 % of the study region yet harbored 91 % of the entire species pool (144 out of 159 species) over the last 29 years (Alabia et al., 2021). Climate buffering and sustained productivity within these areas potentially permit the persistence of stable communities and high marine biodiversity. These biodiversity refugia, albeit small, will be increasingly crucial for preserving marine communities in this climate-exposed yet highly productive ecosystem.

Alabia et al. (2024) investigated the future abundance changes of eight major commercial fisheries under contrasting CMIP6 climate and socio-economic narratives. They revealed that species abundance fluctuations led to pronounced changes in the future maximum catch, revenue, and profit potential, suggesting ensuing trade-offs of shifting fisheries resources under contrasting climate change scenarios. Projected redistributions of maximum catch potential adjacent to major fishing ports could further alter the future fishing fleet dynamics. These findings support the mounting evidence of exacerbated future climate impacts on marine ecosystems and their socioeconomic repercussions (Cheung et al., 2022; Tittensor et al., 2021; Boyce et al., 2020). Hence, it entails establishing and implementing climate-adaptive and forward-looking management strategies to mitigate their anticipated impacts (Free et al., 2020; Holsman et al., 2020).

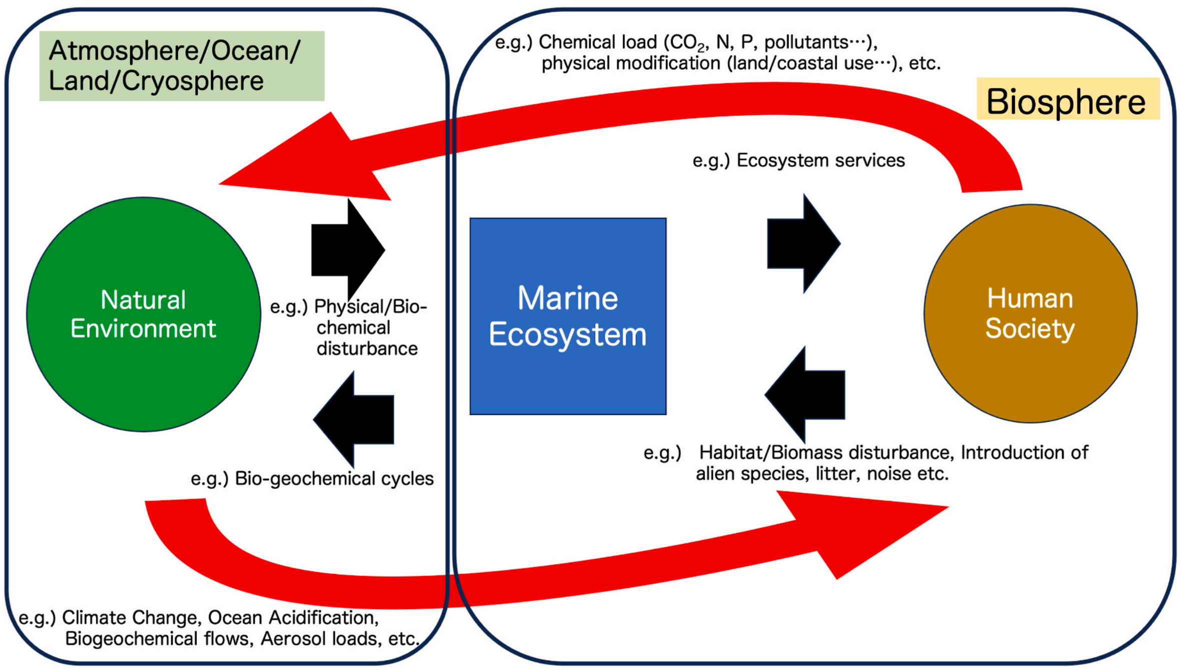

Fig. 1. Conceptual sketch of the marine ecosystem influenced by natural and anthropogenic pressures in the Earth system.

6. Ecosystem assessment

The recent retreat of sea ice in the Arctic Ocean, caused by climate change, has increased anthropogenic activities such as shipping and fishing (Berkman et al., 2022; Heaney et al., 2024; PAME, 2020). These activities, including shipping, oil/gas exploitation, fishing, etc., have threatened marine ecosystems by acoustically intruding on the habitats of marine species (Haver et al., 2017). Arctic ship traffic can also elevate exhaust levels of CO_2 and SOx (Eckhardt et al., 2013). They can significantly impact ocean pH and lead to ocean acidification (Hunter et al., 2011; Evans and Shibata, 2022), affecting marine organisms (AMAP, 2013, 2018). Moreover, commercial shipping is a significant cause of the introduction of non-native marine species (Miller and Ruiz, 2014). Invasive alien species are the critical drivers of biodiversity loss (Bellard et al., 2016), and the pathways of invasion in the Arctic include ballast water and hull biofouling from shipping activities, among others (CAFF and PAME, 2017). Thus, maritime traffic imposes various anthropogenic pressures on Arctic marine ecosystems. Yet, overall impact assessment on the ecosystem, which distinguishes but simultaneously considers natural and anthropogenic pressures, remains a challenge.

The impact of natural and anthropogenic pressures on Arctic marine ecosystems was assessed using the biodiversity of marine species (Kaschner et al., 2019) and primary production (Kahru et al., 2016) as key ecological indicators. To represent the natural pressures, a dimensionality reduction analysis was carried out over Planetary Boundaries processes (Rockström et al., 2009; Steffen et al., 2015). The anthropogenic pressure was determined from the same analysis over transit time, source-level noise, and exhaust (NOx + SOx) of >20,000 ships using marine traffic data obtained from the Automatic Identification System (IMO, 2002). The response of marine ecosystems to the pressures was evaluated by comparing the variability among the ecosystem and pressures. Marine ecosystem response was geographically heterogeneous over the Arctic Ocean; a relatively large response to these external pressures was inferred in the Arctic gateways on both the Pacific and the Atlantic sides from the present analysis (Hirata et al., in preparation). The ecosystem response on the Pacific gateway might be affected mainly by natural environmental pressure rather than anthropogenic pressure. In contrast, the response on the Atlantic gateway was suspected to include some impacts from anthropogenic pressure. The greater ecosystem response on the Arctic gateways found in the analysis was ecologically consistent with the independent analysis of underlying physics (e.g., Woodgate, 2018; Polyakov et al., 2020) as well as biogeography of marine communities (e.g., Csapó et al., 2021; Mueter et al., 2021b; Alabia et al., 2023). These implications, together with Ecosystem Overviews (Jørgensen et al., 2021; ICES, 2023) and ecological resilience research (e.g., Griffith et al., 2019), add to the scientific basis required for ecosystem-based management in the Arctic (Arctic Council, 2013; Wienrich et al., 2022).

7. Summary and outlook

In the second phase of the Arctic Challenge for Sustainability project, marine ecosystem research was extended to biodiversity and system response from the previous phase while further elaborating various knowledge gaps at different trophic levels. New scientific findings here, such as changes in Arctic marine communities at both trophic and ecosystem scales, unveiled the invisible impacts of visible sea ice reduction in the Arctic. A new hypothesis of the possible significance biological production near seafloor also emerged for further investigation. We successfully added a scientific basis valuable for ecosystem-based management through these multi- and cross-scale investigations, with the development of eDNA technique that will effectively allow them. The emergence of new issues, such as marine plastics (e.g. Bergmann et al., 2022; Ikenoue et al., 2023), which were not covered here, emphasizes the importance of including human impacts in ecosystem assessments on trophic and ecosystem scales. Evaluating their direct and indirect effects should be integrated into the ecosystem assessment. There is a growing need for a systematic evaluation of Arctic ecosystems that incorporates the human dimension into the conventional concept of the Earth system (Fig. 1).

CRediT authorship contribution statement

Takafumi Hirata: Writing – review & editing, Writing – original draft, Formal analysis, Investigation, Conceptualization. **Irene D. Alabia:** Writing – review & editing, Formal analysis. **Amane Fujiwara:** Writing – review & editing, Formal analysis. **Yuri Fukai:** Writing – review & editing, Formal analysis. **Jorge García Molinos:** Supervision,

Investigation. **Akihide Kasai:** Investigation, Supervision, Formal analysis. **Tatsuya Kawakami:** Formal analysis, Writing – review & editing. **Kohei Matsuno:** Formal analysis, Writing – review & editing. **Jonaotaro Onodera:** Formal analysis, Writing – review & editing. **Takuhei Shiozaki:** Formal analysis, Writing – review & editing. **Hiromichi Ueno:** Investigation, Writing – review & editing. **Eiji Watanabe:** Writing – review & editing, Funding acquisition, Investigation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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