**SUBJECT:** **PRELIMINARY INVESTIGATION INTO THE POTENTIAL DRIVERS THAT INITIATED THE 2025 SOUTH AUSTRALIAN HARMFUL ALGAL BLOOM**

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## KEY ISSUES

- Since March 2025, South Australia (SA) has experienced an unprecedented, coast-wide harmful algal bloom (HAB) dominated by multiple *Karenia* species, including the brevetoxin-producing *Karenia cristata* as a dominant taxon.

- The bloom has affected more than 20,000 km² (~30% of the state's coastline) and caused extensive mortality of fish, sharks, rays, invertebrates and other marine fauna, making it one of the most severe marine wildlife mortality events recorded in Australian waters.

- Available evidence indicates the 2025 HAB arose from the convergence of multiple interacting physical, chemical and biological drivers, rather than a single dominant cause, consistent with global understanding of HAB dynamics.

- Multi-decadal analyses show that the bloom developed following a period of prolonged environmental preconditioning, including several years of elevated phytoplankton biomass in the bloom origin region. This reflects sustained nutrient supply and primary production associated with the 2023 River Murray flood discharge and the record 2023–24 coastal upwelling event.

- These large-scale drivers are not considered direct or proximate triggers but rather may have pre-conditioned the regional environment in which *Karenia* populations could persist at elevated background levels prior to bloom formation.

- The bloom developed and intensified during an unprecedented marine heatwave. While temperature alone may not explain bloom initiation, the associated calm conditions, reduced wind mixing and enhanced water-column stratification are considered a key enabling factor, favouring motile dinoflagellates such as *Karenia*.

- Nutrient inputs from riverine discharge and upwelling did not align directly with bloom onset, indicating they likely acted as preconditioning influences, with proximate drivers more closely linked to physical conditions (e.g. stratification and retention) in the period immediately preceding bloom development.

- Multiple *Karenia* species, including *K. cristata*, have been present at low levels in SA waters for at least the past decade. The 2025 bloom is therefore consistent with rapid proliferation of a resident population under favourable conditions, rather than introduction of a novel species.

- The scale, duration and species composition of the 2025 event reflect a combination of favourable environmental conditions and species-specific ecological traits, including possible mixotrophy, broad environmental tolerances, and the capacity to exploit regenerated nutrients and suppress competitors, which may have contributed to bloom persistence.

- Comparison with the 2013 SA HAB event (associated with a different HAB taxa) indicates some shared features (e.g. warm conditions), but the 2025 event is distinguished by the magnitude and duration of preconditioning, including stronger upwelling and sustained elevated phytoplankton biomass in the bloom origin region over several years.

- Consistent with international experience, attribution of HAB drivers remains inherently complex and uncertain, even in well-studied systems. It is not yet possible to determine the relative importance of individual drivers, or whether all identified factors were necessary for bloom development.

- This advice note provides the most comprehensive synthesis of available evidence to date and establishes a conceptual framework for understanding HAB drivers in SA, while identifying key knowledge gaps.

- Critical next steps include applying more detailed statistical and modelling analyses to quantitatively assess the relative importance of the drivers identified in this initial study and to potentially identify new ones. The limited availability of key datasets underscores the need for expanded and sustained local monitoring and targeted laboratory-based biological and physiological research to resolve mechanistic, species-specific rates and environmental responses. These efforts should also support the development of early warning systems, risk frameworks and long-term resilience planning to improve both preparedness for, and the most appropriate responses to future HAB events.

## BACKGROUND

- Harmful algal blooms (HABs) are now recognised as a major and growing ecological and socio-economic issue in marine and freshwater systems worldwide. HABs can cause mass mortality of fish, marine mammals, seabirds, invertebrates and algae; contaminate seafood with biotoxins; impair human health via ingestion or aerosol exposure; and lead to prolonged closures of fisheries and aquaculture with substantial losses to tourism and coastal economies (e.g., Anderson *et al.* 2008, Brand *et al.* 2012, Wells *et al.* 2015).

- HAB taxa are diverse and include toxin-producing dinoflagellates, such as *Karenia* (brevetoxin - neurotoxic shellfish poisoning - NSP); *Alexandrium* (saxitoxin - paralytic shellfish poisoning – PSP), *Dinophysis* (okadaic acid and related toxins - diarrhetic shellfish poisoning - DSP); toxin-producing diatoms such as *Pseudo-nitzschia* (domoic acid - amnesic shellfish poisoning - ASP); fish-killing flagellates- (*Heterosigma*, *Chattonella, Vicicitus*); and cyanobacteria in marine, fresh and brackish waters. The global Intergovernmental Oceanographic Commission (IOC) of UNESCO Harmful Algal Event Database (HAEDAT) contains over 9,500 recorded HAB events worldwide since the mid-1980s, and although some regions are currently underrepresented, it demonstrates the extent to which HABs impact global coastal areas (Figure 1a).

- HAB events occur globally and range from short-lived episodes lasting weeks to persistent, recurrent events lasting months or longer (Hallegraeff *et al.* 2023). Although some systems experience one-off or sporadic HAB events, others have become persistent HAB centres where blooms recur over many decades (Figure 1b). Key examples include:
    - the West Florida Shelf (*K. brevis*, near annual) (Brand and Compton 2007, Walsh *et al.* 2006) ;
    - parts of the North Atlantic and European continental shelves (*K. mikimotoi*, *Dinophysis* spp.); (Bresnan *et al.* 2021);
    - Californian coast (*Pseudo-nitzschia*) (Smith *et al.* 2018);
    - Japan (*K. mikimotoi*) (Iwataki *et al.* 2022, Siswanto *et al.* 2013, Taniuchi *et al.* 2025);
    - China (*Karenia* spp.) (Su *et al.* 2024, Yu *et al.* 2023, Zhang *et al.* 2025).

- In Australia, most historically significant marine HAB events have involved paralytic shellfish toxin–producing *Alexandrium* spp. and *Gymnodinium catenatum* in Tasmanian and mainland estuaries, along with *Dinophysis* spp. and *Pseudo-nitzschia* on temperate coasts, typically expressed as

shellfish harvest closures and more spatially and seasonally constrained blooms (Ajani *et al.* 2013, Hallegraeff 1992, Hallegraeff *et al.* 2021b).

- In the years preceding the 2025 HAB event, SA coastal waters had experienced three notable HAB-related events: a spatially extensive bloom of the harmful diatom, *Chaetoceros coarctatus* in 2013 associated with fish kills and a significant marine heatwave (Roberts *et al.* 2019), a smaller *K. mikimotoi* bloom in the Coffin Bay region during summer 2014 that was responsible for localised fish kills over a two-month period (Roberts *et al.* 2014), and a bloom of the ichthyotoxic raphidophyte *Chattonella marina* in Port Lincoln in 1996 caused mass mortality of farmed southern bluefin tuna (Seger and Hallegraeff 2018).

- The 2025 SA HAB was characterised by a mixed *Karenia* assemblage including at least five species (*K. cristata, K. mikimotoi, K. brevisulcata, K. longicanalis and K. papilionacea*) with *K. cristata* newly identified as the brevetoxin producer and dominant species for much of the bloom period (Murray *et al.* 2025). Each of these taxa differ in their physiological and ecological preferences (see below). Of the co-occurring species, *K. mikimotoi* is notable for producing gymnodimine and generating high-biomass blooms that can deplete dissolved oxygen in bottom waters and may have contributed to widespread benthic mortality observed during the 2025 SA event. The bloom has extended from its initial detection near Victor Harbor (Waitpinga) in March 2025 across large areas of Gulf St Vincent, Spencer Gulf, the Fleurieu and Yorke Peninsulas and Kangaroo Island, with impacts still being recorded as of early May 2026.

- At the time the bloom was first detected near Waitpinga, the phytoplankton community comprised a mixed kareniacean assemblage in which *K. mikimotoi* was clearly present in March samples, consistent with early light-microscopy identifications. Subsequent metabarcoding and species-specific qPCR data from autumn and winter show that *K. cristata* became the dominant *Karenia* species across most sampled sites as temperatures cooled from about 18–21°C toward 14–18°C, with *K. mikimotoi* and other *Karenia* spp. typically present at lower abundances (Murray *et al.* 2025).

- Many *Karenia* species produce toxins and other bioactive compounds – including reactive oxygen species, polyunsaturated fatty acids (PUFAs) and brevetoxins – that can cause mortality in fish (ichthyotoxins) and other marine organisms during bloom events (Hallegraeff *et al.* 2023). High algal biomass further complicates impact attribution, as dense blooms not only generate large quantities of ichtyotoxins but can also produce mucilage, and under certain conditions, contribute to water column oxygen depletion. Consequently, it is often difficult to disentangle whether observed mortalities result from toxin or bioactive compound exposure, mucilage-related respiratory impairment, anoxia or a combination of these mechanisms (Brand *et al.* 2012, Hallegraeff *et al.* 2023).

- Prior to the 2025 SA HAB event, *Karenia brevis* was the only *Karenia* species known to produce brevetoxins at concentrations sufficient to cause widespread marine wildlife mortality; however, the cryptic and poorly studied species *K. cristata* was shown to produce significant concentrations of brevetoxin during the SA event (Murray *et al.* 2025). As brevetoxins are only weakly icthyotoxic, other toxins and bioactive compounds likely contributed more substantially to the observed mass mortalities. This is consistent with the broader HAB literature, where identifying the specific toxins responsible for fish kills frequently remains uncertain, even when the causative taxa are well established (Dorantes-Aranda *et al.* 2015, Hallegraeff *et al.* 2023).

- Following the identification of *Karenia cristata* by Murray *et al.* (2025), preliminary analyses of historical samples collected from the IMOS National Reference Stations in South Australia and Victoria indicate that *K. cristata* has been intermittently detected at these sites since sampling commenced in 2016 and 2025, respectively. Prior to the 2025 HAB, *K. cristata* HAB events had only been reported from South Africa, with a single detection also recorded off Newfoundland, and information on the species' spatial and temporal distribution and physiological tolerances remains extremely limited (Botes *et al.* 2003, Nézan *et al.* 2014).

- Plankton samples collected by IMOS and analysed using traditional microscopy methods, and more recently through archived genetic material, have revealed that multiple *Karenia* species have had an intermittent presence in SA shelf and gulf waters over the last decade. *Karenia* encompasses at least 11 species with broadly distributed representatives, and *K. cristata* in particular, may be more geographically widespread than previously recognised. A low-level,

persistent background population of *Karenia* spp. has been present in SA coastal and shelf waters for some years prior to the 2025 bloom event. The 2025 bloom is therefore more consistent with rapid population growth of a resident *Karenia* assemblage responding to favourable environmental conditions (Sommer 1989), and not consistent with recent dispersal from elsewhere.

- Advective physical processes such as upwelling (Kämpf *et al.* 2004) may have influenced local distribution and connectivity of *Karenia* populations but are unlikely to represent the primary explanation for bloom development (Anderson *et al.* 2008, Vandersea *et al.* 2020), however bloom development at the observed location may have been more strongly influenced by the release of nutrients from the remineralization of detritus resulting from the advection of material from the Bonney upwelling (Kämpf *et al.* 2025).
- Among the marine mass mortality incidents documented in HAEDAT, the 2025 SA HAB event ranks among the most severe ichthyotoxic blooms recorded globally, with millions of marine animals killed across more than 770 taxa (Murray *et al.* 2025, iNat mortality database).
- While several hypotheses have been proposed – including legacy River Murray flood nutrients, strong upwelling and a prolonged marine heatwave – the key drivers of the 2025 SA HAB remain unresolved (Murray *et al.* 2025).
- The aim of this advice note is to provide a preliminary assessment of the potential environmental drivers that initiated the 2025 SA HAB, informed by global HAB and *Karenia* science, and by analysis of available local environmental datasets, as a first step towards more detailed attribution work to be led by the Office of Algal Bloom Research (OABR).

## GLOBAL HAB EVENTS AND DRIVERS

International experience shows that HABs arise from a combination of favourable physical conditions, sufficient nutrient supply, and advantageous phytoplankton species traits, modified by local geography and climate.

Key characteristics from global HAB centres include (in no particular order):

### Stratification and calm conditions

- Many coastal HABs, including *Karenia* (Vandersea *et al.* 2020), develop under strongly stratified water columns associated with warmer conditions and/or low to moderate wind stress. Stratification suppresses turbulent mixing, favouring vertically migrating motile dinoflagellates – which can actively swim tens of metres through the water column on daily cycles to access both surface light and deep nutrient pools – over turbulence-adapted competitors such as diatoms (Anderson *et al.* 2008, Hallegraeff 2010, Margalef 1978, Smayda and Reynolds 2001, Zheng *et al.* 2023).
- The relationship between stratification, nutrient access and HAB development has been extensively reviewed by Berdalet *et al.* (2014) and is recognised as one of the most consistent physical preconditions for *Karenia* and other dinoflagellate blooms globally (Kudela *et al.* 2010, Wells *et al.* 2015). The *Karenia* species documented in the 2025 SA HAB are motile and phototactic and included species capable of vertical migrations exceeding 20 m, enabling them to exploit the decoupled light and nutrient fields characteristic of stratified water columns (Shikata et al. 2002; 2025).

### Nutrient enrichment and changing nutrient regimes

- Land based nutrient loads (particularly nitrogen (N) and phosphorus (P) from catchments, wastewater and agriculture), together with upwelling derived nutrients, can intensify or prolong coastal HABs, although relationships are often nonlinear and context-dependent (Anderson *et al.* 2008, Glibert *et al.* 2014, Wells *et al.* 2015). In coastal upwelling systems, upwelled pulses of dissolved inorganic N, P and Silicon (Si) initially favour diatom dominated blooms due to their competitive advantage under high turbulence and high new-nutrient concentrations (Lassiter *et al.* 2006, Margalef 1978) . As upwelling relaxes and the water column stratifies, inorganic Si and nitrate availability declines and is replaced by - regenerated and organic nutrient pools; under these conditions the phytoplankton community transitions from diatoms to flagellates, including mixotrophic dinoflagellates such as *Karenia* spp., that can exploit organic N, P and carbon (C) and, in some cases prey on other plankton (Anderson *et al.* 2008, Barth *et al.* 2020, Glibert *et al.* 2014,

Krimsky and Staugler 2025, Kudela *et al.* 2010, Lie *et al.* 2011, Ollison *et al.* 2023, Pitcher *et al.* 2010).

**Hydrodynamics, upwelling, downwelling and retention**

- Upwelling can deliver nutrient rich water that can seed or support blooms and has also been implicated in the shoreward transport of deep-water, offshore *Karenia* populations to the coast (Krimsky and Staugler 2025). Downwelling and upwelling relaxation are equally important: they can transport surface waters carrying accumulated phytoplankton biomass shoreward, driving coastal bloom accumulation and intensification (e.g., Crespo *et al.* 2006). Both mechanisms may operate at different stages of the same bloom event. Frontal zones have been proposed as "pelagic seed banks" that may support bloom development (Smayda 2002) and bays and semi-enclosed embayments can further facilitate retention that enables biomass to accumulate to harmful levels (Anderson *et al.* 2008, Barth *et al.* 2020, Brand *et al.* 2012, GEOHAB 2010, Kudela *et al.* 2010, Wells *et al.* 2015).

**Climate variability and change**

- Marine heatwaves, altered storm and rainfall regimes, and longer-term ocean warming all influence HAB risk by modifying stratification, circulation and nutrient delivery (Oliver *et al.* 2018). Evidence is emerging that climate change is increasing the frequency and intensity of HAB events in some regions, though this signal is not uniform globally and is partly confounded by expansion in monitoring effort (Hallegraeff *et al.* 2021a, Wells *et al.* 2015).

**Taxa specific responses.**

- Different HAB taxa respond to distinct environmental drivers and cannot be treated as interchangeable. *K. brevis* blooms on the West Florida Shelf are strongly influenced by physical transport and offshore–nearshore nutrient coupling (Krimsky and Staugler 2025, Vargo 2009); *K. mikimotoi* is often associated with low-salinity, nutrient-rich surface layers, with riverine inputs and rainfall-driven stratification playing a prominent role in European and Japanese systems (Barnes *et al.* 2015, Li *et al.* 2019); *Pseudo-nitzschia* toxicity can be closely linked to iron and silicate limitation, which can independently or synergistically stimulate domoic acid production (Trainer *et al.* 2012). Cyanobacterial HABs typically favour warm, stratified conditions and can proliferate under both N-rich and N-limited conditions (Paerl *et al.* 2016). Local geomorphology, water residence time and legacy nutrient inputs further influence which drivers dominate in any given system (Berdalet *et al.* 2014, Kudela *et al.* 2010).

This global context underscores that the 2025 SA HAB event is unlikely attributed to a single simple dominant cause, but rather reflects the likely convergence of multiple stressors and favourable conditions, some long-term (e.g., climate forcing, legacy nutrient enrichment) and others episodic (e.g., marine heatwaves, record upwelling anomalies) (Murray *et al.* 2025).

## GLOBAL UNDERSTANDING OF THE KEY DRIVERS OF *KARENIA* BLOOMS

- The genus *Karenia* includes several biotoxin- or ichthyotoxin-producing species that have caused major HABs worldwide, notably *K. brevis* (Gulf of Mexico), *K. mikimotoi* (Europe and Asia) and more recently, *K. cristata* in SA. Synthesis of global *Karenia* events highlights a set of common drivers, as well as species and region-specific differences (Barnes *et al.* 2015, Brand *et al.* 2012, Feki *et al.* 2013, Li *et al.* 2019, Murray *et al.* 2025, Wells *et al.* 2015, Yu *et al.* 2023).

- Evidence shows that marine warming (warm seasons or anomalously warm conditions), water column stratification (relatively calm, strongly stratified conditions favouring motile mixotrophic dinoflagellates over turbulence tolerant competitors), and access to multiple nutrient sources (offshore vs. nearshore; inorganic vs. organic) are central across systems, while species and site specific factors (e.g., salinity, circulation, grazing, sediment-pelagic coupling) modulate when and where blooms occur (Anderson *et al.* 2008, Barnes *et al.* 2015, Li *et al.* 2019, Vargo 2009, Wells *et al.* 2015, Yu *et al.* 2023).

- Considerable research has focused on identifying the ecological drivers of *Karenia* blooms, particularly the role of nutrients and other environmental factors (Barnes *et al.* 2015, Feki *et al.* 2013, Kok and Leong 2019, Medina *et al.* 2020, Rolton *et al.* 2022, Van Dolah *et al.* 2009). Nutrients such as nitrogen (N), phosphorus (P), and silica (Si) have been shown to play key roles

in driving *K. mikimotoi* blooms (Kok and Leong 2019), while both inorganic and organic forms of N and P have been linked to development of *K. brevis* blooms (Hall *et al.* 2024, Heil *et al.* 2014).

- However, because bloom dynamics reflect complex interactions between species-specific traits (including genetics, physiology and behaviour) and a range of abiotic and biotic environmental factors that are difficult to generalise. As a result, the specific drivers and termination mechanisms of individual *Karenia* blooms remain only partly resolved, even in intensively studied regions such as the Gulf of Mexico (Yu *et al.* 2023).

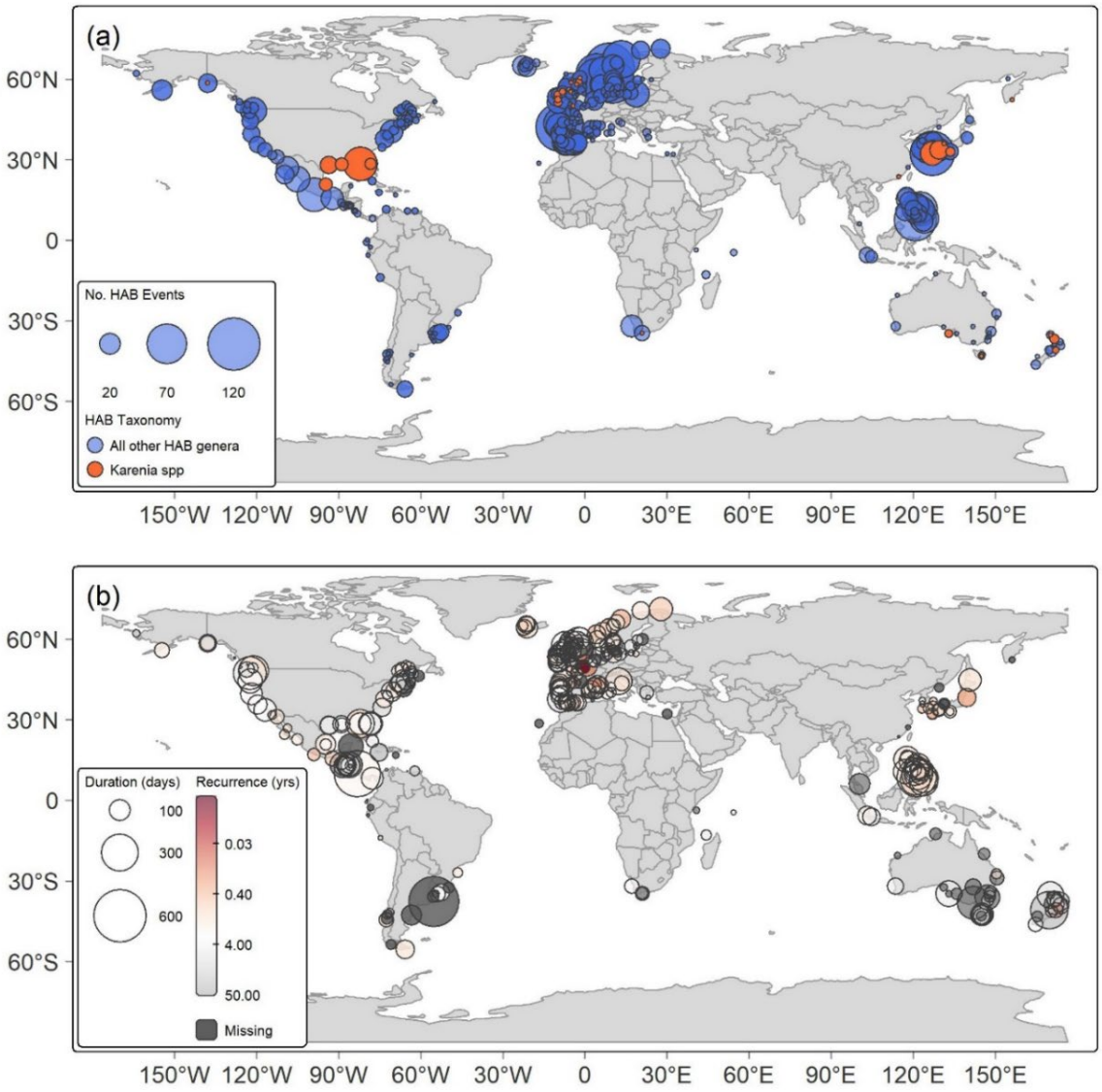


**Figure 1:** Global distribution of (a) Harmful Algal Bloom (HAB) event occurrence, and (b) average HAB event duration and recurrence, as reported in the Harmful Algal Event Database (HAEDAT). Note that HAEDAT records are not uniformly collected globally, and thus large expanses of coastline still have few or no records of HABs.

Common factors across *Karenia* blooms include:

**Thermal regime and heat anomalies**

- Many *Karenia* spp. have warm-water growth optima, for example, *K. brevis* grows optimally between 22 and 28°C (Vargo 2009), and *K. mikimotoi* has been recorded across 4–31°C but typically blooms under seasonally warm conditions (Li *et al.* 2019). Blooms of these species often coincide with seasonally warm conditions or marine heatwave periods that enhance stratification and growth rates (Oliver *et al.* 2018, Wells *et al.* 2015). *K. mikimotoi* isolated from the South Australian HAB performed optimally at temperatures between 15 - 20°C in pure cultures from the SARDI culture collection.

- There are important exceptions. *K. selliformis* includes cold-water strains with optimal growth documented at about 10–15°C in Chilean waters and 9.8–17.6°C in Japan and Russia, highlighting that thermal optima are highly strain-specific across the genus (Iwataki *et al.* 2022, Orlova *et al.* 2022, Uribe and Ruiz 2001, Vellojin *et al.* 2023). In these cases, cold-water anomalies have not been identified as the initiating cause of blooms; for example, cooling towards the colder end of the preferred range was associated with bloom decline in Japan (Hasegawa *et al.* 2022), and drivers of the Russia 2021 bloom remained unresolved.

- For *K. cristata* specifically, the thermal optimum remains poorly understood. Culture experiments on South Australian isolates indicate a preference for cooler, upwelling-influenced temperate conditions, with optimal growth around 13–15°C as observed within the SARDI cultures and slower growth at temperatures below about 10°C or above 20°C, consistent with the timing of *K. cristata* dominance during the 2025 SA event and with previous autumn blooms in South Africa (Botes *et al.* 2003, Murray *et al.* 2025). Further work is required to determine how general these responses are across strains.

**Stratification, hydrodynamics and transport**

- Strong stratification, often involving both temperature and salinity gradients, favours vertically migrating, motile *Karenia* cells, enabling them to optimise light and nutrient access and outcompete non-motile taxa (Barnes *et al.* 2015, Brand *et al.* 2012, Li *et al.* 2019, Smayda and Reynolds 2001, Vargo 2009).

- On the West Florida Shelf, *K. brevis* typically initiates offshore under stratified conditions, then is transported shoreward by shelf circulation, wind forcing, and upwelling–downwelling transitions. Nearshore intensification is linked to estuarine nutrient loads and organic N availability (Anderson *et al.* 2008, Brand and Compton 2007, Krimsky and Staugler 2025, Liu *et al.* 2022, Vargo 2009).

- In the western English Channel and northern Europe, *K. mikimotoi* blooms are linked to persistent summer stratification driven by rainfall-freshened surface layers overlying cooler, more saline waters, with riverine inputs and rainfall-driven stratification playing a prominent role (Barnes *et al.* 2015).

- Local circulation and physical retention can further concentrate biomass: in Tongxin Bay (China), distinct physical regimes characterise pre-bloom, bloom and post-bloom phases of *K. longicanalis,* with retention identified as a key factor enabling biomass accumulation (Yu *et al.* 2023).

**Multi-source nutrient supply**

- *Karenia* blooms commonly draw on a mosaic of dissolved inorganic and organic nutrient sources – offshore upwelled nutrients, riverine and estuarine inputs, groundwater, atmospheric deposition and regenerated nutrients – with different sources contributing at different bloom stages (initiation vs maintenance) (Anderson *et al.* 2008, Brand *et al.* 2012, Hall *et al.* 2024).
- For *K. brevis*, offshore diazotrophs (nitrogen-fixating microorganisms), have been shown to supply substantial quantities of ‘new’ nitrogen during bloom initiation (Lenes *et al.* 2001, Lenes and Heil 2010), while dissolved organic nitrogen (DON), sediment fluxes and regenerated ammonium

become increasingly important during bloom maintenance and persistence (Burkholder *et al.* 2008, Hall *et al.* 2024, Vargo 2009).

- Estuarine and riverine nutrient enrichment from developed catchments can significantly enhance bloom intensity and persistence in nearshore environments, with strong links reported between *K. brevis* presence and elevated dissolved inorganic and regenerated N in Florida estuaries (Hall *et al.* 2024, Li *et al.* 2021).
- Some *Karenia* spp. are capable of mixotrophy – combining photosynthesis and heterotrophic nutrition via phagotrophy (ingestion of prey) and uptake of dissolved organic compounds – which provides a significant competitive advantage in nutrient-depleted, stratified waters. *K. brevis* and *K. mikimotoi* (and related taxa) can utilise reduced inorganic N (e.g., ammonium) and organic forms (urea, amino acids, DON) and in some cases, ingest bacteria and small protists, enabling persistence and growth after diatoms have depleted inorganic N and Si (Burkholder *et al.* 2008, Heil *et al.* 2014, Jeong *et al.* 2010). Many dinoflagellates also exploit dissolved inorganic carbon and dissolved organic carbon sources under mixotrophic and heterotrophic modes, further increasing their flexibility under fluctuating resource conditions (Burkholder *et al.* 2008, Flynn and Mitra 2009).
- Nutrient ratios (N:P:Si) and nutrient forms are often more informative for predicting shifts in community composition than absolute concentrations alone. Low Si:N ratios following diatom drawdown, coupled with sufficient N and P (including organic fractions), favour dinoflagellates and other non-silicified HAB taxa. However, global syntheses consistently place these nutrient effects alongside, rather than above, the major physical drivers, and no single nutrient ratio or threshold has been shown to universally "trigger" *Karenia* blooms (Anderson *et al.* 2008, Heil *et al.* 2014, Li *et al.* 2019, Vargo *et al.* 2008).
- *K. mikimotoi* can thrive across a wide nutrient range, but often responds to nutrient-rich, low-salinity river inflows following persistent rainfall. Bloom development is frequently linked to shifts in nutrient form and availability, not simply to linear increases in total nutrient loads (Barnes *et al.* 2015, Li *et al.* 2019).
- Metatranscriptomic analyses of *K. longicanalis* in Tongxin Bay (China) suggest that bloom maintenance is more strongly associated with phosphorus and dissolved organic carbon availability than with inorganic N and Si, implying that organic nutrient pools and cellular energy status may be more important bloom-maintenance drivers than commonly measured inorganic nutrient parameters (Yu *et al.* 2023).

**Carbonate chemistry and ocean acidification**

- Recent studies in West Florida estuaries show systematic differences in carbonate chemistry ($pCO_2$, pH, alkalinity) between *K. brevis* bloom and non-bloom conditions, suggesting that changing $CO_2$ and pH regimes can influence *Karenia* competitive dynamics and biotoxin production (Hall *et al.* 2024).

- Dinoflagellates with efficient carbon-concentrating mechanisms and flexible carbon uptake pathways (including access to dissolved $CO_2$, bicarbonate and dissolved organic carbon under mixotrophic conditions) may gain a relative advantage in both low and high-$CO_2$ environments, depending on how competitors respond. Experiments have shown that rising $CO_2$ can promote *K. mikimotoi* growth relative to competitors and weaken allelopathic suppression by macroalgae (Wang *et al.* 2024). More broadly, species with adjustable carbon-concentrating mechanisms may be better placed to exploit future higher-$CO_2$, and more stratified coastal environments (Hall *et al.* 2024, Wells *et al.* 2015).

**Biological interactions (grazers, pathogens and competitors)**

- Some *Karenia* species have been shown to produce suites of ichthyotoxic and allelopathic compounds that confer strong competitive advantages. *K. brevis* exudates inhibit the growth of co-occurring diatoms and other phytoplankton, with allelopathy compromising competitor lipid biosynthesis, membrane integrity and photosynthesis (Kubanek *et al.* 2005, Poulin *et al.* 2018). Density-dependent allelopathy is also documented in *K. mikimotoi* and is considered a key trait promoting mono-specific bloom dominance once favourable physical–chemical conditions are established (Barnes *et al.* 2015, Li *et al.* 2019).

- Several *Karenia* species show reduced grazing pressure during intense blooms; decomposition of bloom biomass recycles nutrients that can sustain bloom persistence (Anderson *et al.* 2008, Vargo 2009). Ichthyotoxic mass mortality events may further increase nutrient availability as prey decompose, providing positive feedback that supports continued bloom maintenance (Killberg-Thoreson *et al.* 2014, Walsh *et al.* 2009).

- In the *K. longicanalis* bloom in Tongxin Bay (China), bloom development occurred under low grazing pressure limited bacteria/viral attack; bloom termination coincided with increased top-down control (ciliate grazing, algicidal bacteria, viral infection) and competitive displacement from diatoms (*Chaetoceros* spp.) (Yu *et al.* 2023). This illustrates how biotic interactions can govern both bloom persistence and collapse, complementing the physical and chemical drivers.

**Key inter-specific differences and complexities**

- *K. brevis* is largely restricted to the Gulf of Mexico, with offshore initiation and onshore transport strongly governed by West Florida Shelf circulation and upwelling–downwelling dynamics, nearshore intensification is linked to estuarine nutrient loads and organic N availability, and allelopathy appears pivotal in building and sustaining dense blooms (Anderson *et al.* 2008, Brand and Compton 2007, Hall *et al.* 2024, Kubanek *et al.* 2005, Poulin *et al.* 2018, Vargo 2009).
- *K. mikimotoi* occurs across a broad latitudinal range and is often associated with low salinity surface layers overlying cooler saline waters, with riverine inputs and rainfall-driven stratification playing prominent roles; strong swimming, mixotrophy and allelopathy jointly promote dominance once favourable conditions are established (Barnes *et al.* 2015, Li *et al.* 2019).
- *K. longicanalis* blooms in Chinese coastal waters are strongly influenced by physical retention, with bloom formation and collapse linked to shifts in gene expression related to energy and nutrient acquisition and to biotic interactions (grazing, bacterial and viral pressures), underlining the importance of both physical–chemical and biological drivers (Yu *et al.* 2023).
- *K. selliformis* has shown links between nitrate, temperature and range expansion in Tunisia (Feki *et al.* 2013), and marine heatwaves and vertical nitrate supply have been identified as key preconditioning factors in recent Japan and Russia events (Hasegawa *et al.* 2022, Iwataki *et al.* 2022, Orlova *et al.* 2022).
- Data on *K. cristata* remain limited. Prior to the 2025 SA HAB, blooms of this species were confined to South Africa, occurring predominantly in autumn, suggesting a preference for cooler, upwelling-influenced temperate systems (Botes *et al.* 2003, Murray *et al.* 2025). Observations from the 2025 SA event and SA culture work align with this pattern.

In summary, *Karenia* species are prolific bloom-formers capable of producing large, dense, long-lasting events that cause extensive mortality of benthic and pelagic animals. They succeed because they combine a diverse array of nutritional and behavioural traits, including: 1) the ability to thrive under low light conditions; 2) broad salinity and temperature tolerances; 3) capacity to utilise diverse inorganic and organic nutrient sources through mixotrophy; 4) the ability to generate additional nutrients through the release of ichthyotoxins and other bioactive compounds that kill marine animals; and 5) allelopathic exudates that suppress or kill co-occurring algae (Anderson *et al.* 2008, Burkholder *et al.* 2008, Li *et al.* 2019).

## CHALLENGES IN ATTRIBUTING DRIVERS AND CAUSES

Attribution of the drivers of *Karenia* blooms is challenging because they are typically driven by stage specific drivers (offshore seeding vs coastal accumulation), occur within multispecies phytoplankton assemblages, and benefit from the regenerated nutrients derived from decaying biomass during mortality events as well as allelopathy that suppresses competition from co-occurring phytoplankton species. They are also influenced by long-term environmental change, and interannual variability that can obscure causal relationships. Compounding these ecological complexities, the level and consistency of monitoring effort can vary enormously across regions and through time – meaning that apparent changes in bloom frequency, extent or intensity may partly reflect changes in observational capacity rather than true changes in bloom dynamics, making robust attribution of drivers particularly difficult. Some key features that complicate attribution include:

**Multicausality and stage specific drivers**

- Blooms typically emerge from a sequence of processes – seed population accumulation, growth under favourable conditions, physical concentration, then maintenance – each potentially controlled by different drivers (Anderson *et al.* 2008, Vargo 2009, Yu *et al.* 2023).
- For *K. brevis*, offshore initiation may be more tightly tied to physical–biogeochemical shelf processes (upwelling, diazotrophs, submarine groundwater discharge, organic N), whereas nearshore maintenance and impacts are more sensitive to estuarine nutrient loading and hydrology (Anderson *et al.* 2008, Hall *et al.* 2024, Li *et al.* 2021, Vargo 2009).

**Limited concurrent measurements and in situ process data**

- Globally, many blooms are documented through cell counts and basic hydrography; however, simultaneous data on key ecophysiological and biogeochemical processes (e.g. groundwater fluxes, organic and inorganic nutrient uptake, autotrophic–mixotrophic switching, biotoxin synthesis, grazing, viral lysis) are often lacking. The absence of sustained pre-bloom monitoring and mechanistic process measurements can limit causal inference of the common drivers of bloom initiation, development and termination (Anderson *et al.* 2008, Brand *et al.* 2012).

- The 2025 SA HAB is no exception. Prior to the event, routine monitoring of marine coastal waters for HABs and associated environmental parameters was very limited. During the event itself, sampling was largely confined to nearshore and beach locations, brevetoxin measurements were limited, and detailed taxonomic analysis capable of distinguishing among the co-occurring *Karenia* species was largely absent in early samples. As a consequence, the spatially and temporally resolved data needed to elucidate the underlying mechanisms of bloom initiation and development remain a significant gap in our current understanding.

- Integrated molecular approaches – such as the metatranscriptomic study on *K. longicanalis* – illustrates the value of coupling phytoplankton molecular process data with community dynamics measurements, however, such studies remain rare and site specific, limiting generalisation to other systems (Yu *et al.* 2023).

**Distinguishing natural variability from anthropogenic forcing**

- Long historical records for *K. brevis* show that large blooms on the West Florida Shelf occurred well before intensive coastal development, implying a strong natural component, yet contemporary work clearly demonstrates that watershed nutrient enrichment and hydrologic alteration can intensify and prolong modern blooms (Anderson *et al.* 2008, Brand and Compton 2007, Li *et al.* 2021).

- Reviews on HABs and eutrophication emphasise that nutrient–HAB relationships are often nonlinear and context-dependent, varying with hydrodynamics, species traits, and background climate conditions, which complicates simple attributions such as “more N = more *Karenia*” (Anderson *et al.* 2008, Anderson *et al.* 2002, Wells *et al.* 2015).

**Climate change as an interacting, not isolated driver**

- Climate change simultaneously modifies multiple underlying controls – including temperature profiles, stratification, storm frequency, runoff patterns, and carbonate chemistry – making it difficult to separate its influence from local nutrient management or hydrological interventions (Hall *et al.* 2024, Wells *et al.* 2015).

- Projections for HABs stress that increased frequency of extremes (marine heatwaves, anomalous rainfall, compound events) is particularly important, but long time series that clarify these relationships specifically for *Karenia* remain limited (Wells *et al.* 2015).

**Species and strain level variability**

- Different *Karenia* species (and even strains within species) can differ in biotoxin profiles, growth optima, mixotrophic capabilities, and sensitivity to stressors. Yet most monitoring and many predictive models treat *Karenia* as a homogenous functional group, an approach that is unlikely to advance mechanistic understanding given the high ecological and physiological diversity within the genus (Li *et al.* 2019, Vargo 2009, Yu *et al.* 2023).

- This heterogeneity means that drivers inferred from one *Karenia* system (e.g., low salinity pulses for *K. mikimotoi* in Europe) cannot be uncritically transferred to another (e.g., *K. brevis* in Gulf of Mexico) without local validation (Barnes *et al.* 2015, Li *et al.* 2019, Vargo 2009).

**South Australian context**

- The 2025 HAB event represents the first large-scale, prolonged biotoxic *Karenia* bloom recorded in SA – and indeed Australian – waters. The event involved a complex assemblage of at least five *Karenia* species with shifting dominance over time, including the brevetoxin-producing *K. cristata*, as well as other ichthyotoxic taxa such as *Karlodinium veneficum* and *Takayama* spp. that may also have contributed to the observed marine mortalities (Murray et al. 2025). The inherent complexity of this multi-species assemblage limits the ability to clearly attribute impacts to any single taxon, and similarly constrains attribution of bloom initiation and persistence to specific environmental drivers (Anderson *et al.* 2008, Brand *et al.* 2012, Murray *et al.* 2025, Wells *et al.* 2015).
- Nevertheless, the global *Karenia* literature provides essential context for interpreting the SA assessment by:
    - identifying core drivers that should be examined (thermal regime and marine heatwaves, stratification and mixing, upwelling and circulation, multi-source nutrient supply including organic fractions, and biological interactions); and
    - highlighting the need for careful, multi-line-of evidence attribution, recognising that a single, unprecedented bloom event of a multi-species *Karenia* complex will inherently carry substantial uncertainty, and that predicting longer-term recurrence patterns from a single event is not yet possible (Anderson *et al.* 2008, Brand *et al.* 2012, Li *et al.* 2019, Murray *et al.* 2025, Wells *et al.* 2015, Yu *et al.* 2023).

## EXAMINATION OF POTENTIAL DRIVERS CONTRIBUTING TO THE SA HAB

### Approach

- To provide an initial assessment of potential environmental drivers of the 2025 SA HAB, we adopted a comparative, data-driven approach using existing observational and modelled datasets (physical, chemical, biological and climatic). Analysis focused on two coastal regions with contrasting exposure to suspected drivers:
    - (1) Zone 1 in the central South-East / Murray Mouth region, where the 2025 SA HAB was first detected and where influence from River Murray discharge and downstream enrichment from the Bonney Coast upwelling are potentially strongest; and
    - (2) Zone 2 in the Kangaroo Island / shelf-break region, where macro-nutrient inputs are dominated by coastal upwelling processes resulting in an area of nutrient enrichment and increased primary productivity separate from land-based (riverine) inflows, and importantly, includes sustained *in situ* measurements from the Integrated Marine Observing System (IMOS) Kangaroo Island national reference station.
- Within each zone, we examined multi-decadal time-series of sea surface temperature (SST), marine heatwaves, stratification proxies, wind and upwelling indices, chlorophyll-*a* as a proxy of phytoplankton biomass (Boyce *et al.* 2010) and a commonly used indicator of nutrient enrichment (Anderson *et al.* 2002, Boyer *et al.* 2009, Smith 2006), river flow and nutrient export, local nutrient observations, and large-scale climate modes (El Niño-Southern Oscillation - ENSO, Indian Ocean Dipole - IOD, Southern Annual Mode -SAM).

- This approach is consistent with global HAB attribution studies that combine long-term baselines with spatial contrasts to identify anomalous combinations of environmental drivers (e.g., Anderson *et al.* 2005). It allows conditions associated with the 2025 bloom to be assessed against the long-term climatology, and between two regions – one with river-influenced nearshore enrichment and one dominated by oceanic shelf enrichment from coastal upwelling. The long time series also enables comparisons with conditions experienced during the 2013 *Chaetoceros coarctatus* bloom event (Roberts *et al.* 2019).

## Methods

### Study areas

- The two reference locations are represented in Figure 2. Recent qPCR re-analysis of IMOS molecular samples collected since 2016 have indicated the intermittent presence of *Karenia cristata* in low concentrations since 2017. Additional information was also collated from the Murray River mouth, located north-east of Zone 1.

### Environmental time series

- Environmental parameters were selected based on their availability and their potential relevance to bloom development. The data sources and spatial-temporal resolution of each parameter are described in Table 1. Time series were restricted to the period 2009–2025 to capture environmental conditions preceding and encompassing both the 2013 and 2025 bloom events.

- The 2013 event was dominated by the chain-forming centric diatom *Chaetoceros coarctatus* and was spatially extensive, affecting shelf and coastal waters across a broad area encompassing both study zones (Roberts *et al.* 2019); it differed substantially in taxonomic composition, toxin profile and ecological impact from the 2025 *Karenia* bloom (Roberts *et al.* 2014). Despite these differences, comparison of environmental conditions associated with both events was undertaken to identify drivers common to both, as well as features that were unique to the 2025 *Karenia* event – with differences in bloom type explicitly acknowledged in the interpretation.

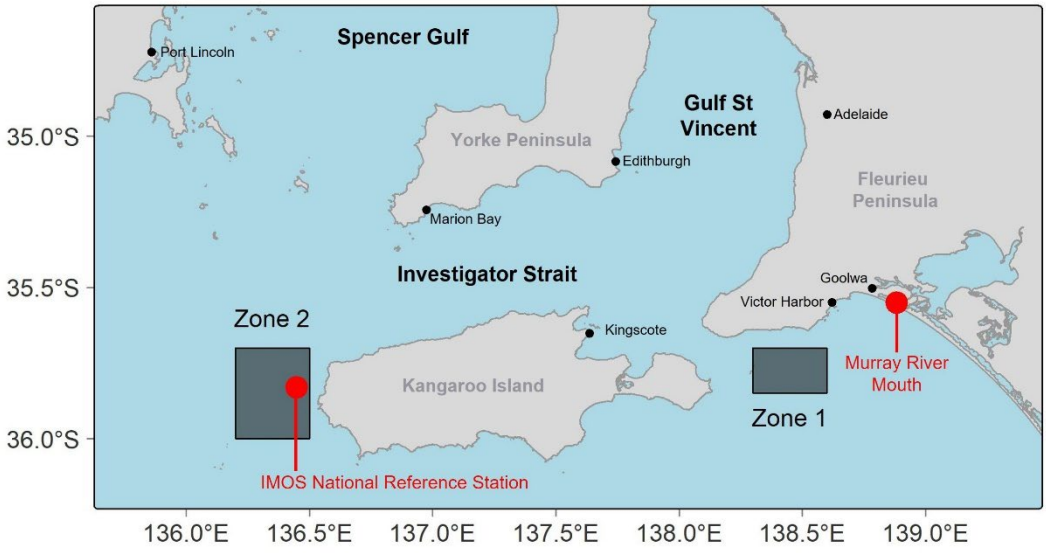


**Figure 2:** Locations used for collating environmental time series with Zone 1 positioned south-west of the River Murray mouth, adjacent to first detection of 2025 SA HAB (Waitpinga, Victor Harbor), and Zone 2 positioned west of Kangaroo Island, a zone of seasonal upwelling, also encompassing the IMOS national reference station.

**Data preparation and analyses**

- Spatial satellite data were extracted for each study area and averaged to produce a single value per time period (daily or monthly, depending on the initial data format). Chlorophyll-*a* and sea surface temperature (SST) data were smoothed using a 10-day running average to reduce short-term variability and highlight underlying trends.

- SST and wind speed anomalies were calculated – over the period 2009-2025. Nutrient data were standardised using z-scores (subtracting the mean and dividing by the standard deviation for each nutrient), allowing all nutrient types to be displayed on the same scale and facilitating comparison of their relative annual concentrations.

- An index of oceanographic upwelling was derived from bottom temperature measurements recorded at the IMOS National Reference Station west of Kangaroo Island (Figure 2). Bottom temperature anomalies were calculated in the opposite direction to the SST and wind anomalies: here, positive anomalies indicate anomalously cold bottom waters, reflecting the upward displacement of cold, nutrient-rich sub-thermocline water characteristic of upwelling events, rather than warm anomalies as in the SST index. These anomalies were then transformed (exponential function) to derive the upwelling index and facilitate interannual comparisons.

- Annual maxima were calculated for all environmental time series except salinity and wind speed anomalies for which annual minima were calculated to identify anomalously low values. Lower salinity has been identified as a potential factor facilitating algal bloom development (Barnes *et al.* 2015, Li *et al.* 2019, Shi *et al.* 2024), and anomalously low wind stress may reduce turbulent mixing, enhance water-column stratification, and coincide with upwelling relaxation or downwelling favourable conditions that promote coastal bloom accumulation. All values were standardised using z-scores, and periods of strong to extreme anomalies and their co-occurrence across variables were identified to characterise environmental conditions preceding and during bloom events.

- Results are presented separately for each zone, except for large-scale climate drivers (ENSO, IOD, SAM), which are presented once because they apply to both zones. Data from the Murray River mouth are shown alongside Zone 1 data (Figure 3), and data from the IMOS Kangaroo Island reference station are shown alongside Zone 2 data (Figure 4)

- Principal Component Analyses (PCA) were conducted separately for each zone to compare interannual variability at the seasonal scale. Seasons were defined as summer (January–March), autumn (April–June), winter (July–September) and spring (October–December). This multivariate approach was used to distinguish seasons with similar environmental structures from anomalous ones and to identify which variables contributed most strongly to those differences. The first three principal components (PC1–PC3), which together explained more than 50% of the total variance in each zone, were retained for interpretation.

**Results**

**Phytoplankton biomass (chlorophyll-*a*):**

- In Zone 1, chlorophyll-*a* concentrations were above average early in 2011, 2012, and from 2022 to 2025, corresponding to years preceding, or coinciding with the two major algal bloom events – in 2013 and 2025 (Figure 3; Table 2). It is noted that elevated chlorophyll-*a* in winter–spring of 2012 may partly reflect the normal seasonal cycle of productivity rather than anomalous enrichment. Annual chlorophyll-*a* concentrations returned to average levels in the six months prior to the 2013 event, but remained elevated each year from 2022 to 2025, likely reflecting sustained nutrient enrichment associated with increased Murray River discharges (Figure 3 and 5) and the intense and prolonged 2024 coastal upwelling event (Figures 4 and 5); however, attribution of elevated chlorophyll-*a* to specific nutrient sources is not possible from these data alone without additional biogeochemical measurements (e.g. nitrogen isotope analyses), and is discussed further in the context of limitations below.

- In Zone 2, chlorophyll-*a* concentrations were above average in 2024, consistent with the intense and prolonged coastal upwelling event documented that year, but returned close to average levels in 2025 (Figure 4; Table 2). Elevated chlorophyll-*a* was also observed in Zone 2 in 2010 and 2016, years that coincided with strong upwelling events. Chlorophyll-*a* was notably low in 2013 in Zone 2, contrasting with conditions in Zone 1 around the time of the 2013 bloom.

**Sea surface temperature and marine heatwaves**

- In both zones, SST anomalies were positive in the years associated with the two major bloom events. In 2013, SST anomalies were clearly elevated in Zone 1 and classified as a marine heatwave. In 2024–2025, SST anomalies in both zones were classified as marine heatwaves of exceptionally high cumulative intensity and duration, exceeding nine months – reaching record levels in excess of +2°C in Zone 1 at the onset of the bloom (Figures 3, 4 and 5; Table 2). The relationship between SST anomalies and formal marine heatwave classification is discussed in Table 2.

**Upwelling and coastal circulation**

- The upwelling index demonstrates that upwelling occurs seasonally each year in SA, but with varying intensity (Figure 4; Table 2). In 2013 and 2024/25, the index was close to zero. Strong upwelling events were recorded in 2010 and 2016, and a strong but short-lived event occurred in 2015. A minor upwelling event was also evident in 2012. In 2023/24, upwelling was unprecedented in both intensity and duration, extending to approximately six months compared with a typical three-to-four-month duration. In 2024/25, the upwelling index was very low (negligible) during the months immediately preceding the March 2025 bloom onset. In early to mid-2024, prolonged negative SST anomalies in Zone 2 were consistent with the record-breaking coastal upwelling event (Figures 4 and 5). During this event, elevated phytoplankton biomass was distributed across SA shelf waters and adjacent coastal margins (Figure 5).

**Wind speed and stratification**

- Wind speed anomalies were negative in the early months of the 2025 HAB event (and notably also around the 2013 event), indicating reduced wind stress that would be expected to reduce turbulent mixing and promote water column stratification (Figure 3; Table 2). Anomalously low winds are also consistent with upwelling relaxation and the transition to downwelling-favourable conditions noted above.

**Murray River discharge and nutrients**

- Murray River discharge was above average in 2011, 2012, 2016 and from 2022 to 2023, with the highest discharge in nearly 70 years (Alluvium 2024) occurring in 2023. Short, elevated discharge events occurred in 2013 and 2014, while below-average discharge persisted between 2017 and late 2021 (Figure 3; Table 2).

- High river flows coincided with nutrient peaks at the river mouth in 2016 and in 2022/23; however, nutrient composition differed markedly between these periods. In 2016, a pronounced peak in silicate dominated, whereas 2022–2024 was characterised by elevated ammonium, phosphate and organic nitrogen (Figure 3; Table 2). No nutrient data are available for the 2013 bloom period.

**Salinity**

- In Zone 1, salinity decreased from 35.6 to 35.0 PSU between mid-2023 and end of 2024 – the longest period of such low salinity in the record – most likely reflecting the combined influence of elevated Murray River discharge followed by entrainment of lower-salinity water associated with the large 2023/24 coastal upwelling (Figure 3; Table 2). In Zone 2, salinity decreased more modestly, from 35.6 to 35.3 PSU over the extreme upwelling period in 2023/24 (Figure 4; Table 2).

**Climate drivers**

- The ENSO time series indicates three significant El Niño events over the past 17 years: 2009-2010, 2016-2017 and 2023-2024 (Figure 6; Table 3). El Niño events are associated with enhanced upwelling in South Australia (Middleton *et al.* 2007).
- The IOD time series indicates two significant positive events over the same period, in 2019-2020 and 2023-2024, with a moderate positive IOD also observed in 2015-2016 (Figure 6; Table 3). When a positive IOD event coincides with an El Niño event, the associated impacts are reinforced, amplifying dry, hot conditions associated with droughts (Ummenhofer *et al.* 2009). The co-occurrence of El Niño and positive IOD in 2023/24 is therefore notable as a potential compound climate driver of anomalous conditions preceding the 2025 bloom.
- The SAM time series was highly variable, with impacts that are season dependent. A positive SAM phase in summer is associated with contraction of the belt of strong westerly winds towards Antarctica, driving easterly longshore winds in SA that generally enhance the coastal upwelling system. Although positive SAM phases occurred frequently over the past 17 years, SAM was notably positive during summer 2023/24 (Figure 6; Table 3), consistent with the record upwelling event documented that year.

**Principal Component Analyses**

- In Zone 1, the PCA ordination on axes 1 and 2 (Figure 7A) explained 50% of the total variance and revealed a clear separation between spring 2022 and summer 2023. This separation was primarily associated with PC1, which was positively related to high river flow, elevated nutrient concentrations (including nitrogen, nitrate, phosphate, and phosphorus), and increased chlorophyll-*a*. PC2 was mainly driven by high sea surface temperature and temperature anomalies. The projection on axes 2 and 3 (PC2–PC3) (Figure 7B) highlighted additional patterns not captured by PC1. In this space, finer-scale differences became more apparent, particularly among summer 2013, spring 2024, and summer and autumn 2025, which were associated with higher temperatures along PC2. These seasons were negatively associated with salinity and associated with negative wind anomalies, suggesting lower salinity and more stable, stratified conditions during these periods. In contrast, spring 2023 and summer 2024 were more strongly associated with a positive IOD and a higher upwelling index.

- In Zone 2, the PCA ordination on axes 1 and 2 (Figure 8A) explained 43% of the total variance and revealed a clear separation of summer 2024. This separation was primarily associated with PC1, which was positively related to high upwelling index, elevated nutrient concentrations (including nitrate, phosphate, and silicate), increased chlorophyll-*a* and positive El-Nino index (ENSO). PC2 was mainly driven by high sea surface temperature and temperature anomalies. The projection on axes 2 and 3 (PC2–PC3) (Figure 8B) highlighted finer-scale differences, particularly among summer and autumn 2025, which were associated with higher temperatures along PC2.
- Overall, the PCA results are consistent with the time series analyses and Table 2–3, reinforcing that:
    - in Zone 1, years preceding the 2013 and 2025 bloom events were characterised by combinations of elevated river flow, nutrient enrichment and high chlorophyll a, followed by warm, low wind, lower salinity seasons; and
    - in Zone 2, summer 2024 stands out as a period of exceptional upwelling and nutrient delivery, while 2025 is distinguished more by warm, stratified conditions than by continued strong upwelling.

**Table 1:** Sources and spatial-temporal resolution of site-specific, regional and global environmental variables considered potentially relevant to SA algal bloom development.

| Variable | Description | Source | Spatial-temporal resolution | Forecastable |
|---|---|---|---|---|
| Long-term sea surface temperature (SST) | NOAA high-resolution daily optimum interpolation sea surface temperature (OISST) using multi-satellite sensor (AVHRR+VIIRS) data. | V2 High Resolution Dataset provided by NOAA PSL, Boulder, Colorado, USA at https://psl.noaa.gov | 1982 – 2025<br>Satellite 0.25° | Yes – Long term |
| Bottom Sea Temperature | IMOS National Mooring Network Facility daily bottom temperature is used as an index of the intensity of upwelling events. | https://portal.aodn.org.au/search | 2008 – 2025<br>National Reference Station (KI) | Yes – days to weeks |
| Sea surface salinity | Global gap-free Level 4 (L4) analyses of the monthly sea surface salinity from multiple satellite sources. | https://data.marine.copernicus.eu/product/MULTIOBS_GLO_PHY_S_SURFACE_MYNRT_015_013/services | 1993 – 2025<br>Satellite 1/8° | Yes – Long term |
| Chlorophyll-a concentration | Daily Aqua-MODIS chlorophyll-a concentration. | https://oceancolor.gsfc.nasa.gov/l3 | 2002 – 2025<br>Satellite 4 km | No |
| Wind | Daily wind components (U & V) and velocity. | https://cds.climate.copernicus.eu/datasets | 1940 -2025<br>Satellite 0.25° | Yes – Long term |
| Water discharge – Murray River Barrages | Barrage releases are generated by the Murray Darling Basin Authority's water balance hydrological model. | https://www.mdba.gov.au/water-management/water-resource-modelling | 2005 – 2025<br>Murray Mouth barrages | Yes – days to weeks |
| Nutrients – Murray River | Total export from the Murray-Darling Basin contained within all water sources (total combined natural flows plus managed environmental water). Daily concentrations for salinity, phosphate, particulate organic phosphorus, ammonium, particulate organic nitrogen, dissolved silica, chlorophyll-a. | https://data.gov.au/data/dataset/flow-mer-lower-murray-salt-and-nutrient-export | 2014 – 2023<br>Murray Mouth (138.88°E/35.56°S) | Yes – days to weeks |
| Nutrients – Kangaroo Island | IMOS combined biogeochemical parameters. Parameters include nutrients, comprising of ammonium, nitrate, phosphate and silicate. | https://portal.aodn.org.au/search | 2008 – 2025<br>National Reference Station (KI) | No |
| Marine Heatwave (MHW) | MHWs defined as a period when seawater temperatures exceed seasonally varying threshold (90th percentile) for at least 5 consecutive days. | https://www.marineheatwaves.org | 1982 – 2025<br>Satellite 0.25° | Yes – up to 4 months |
| Southern Oscillation Index (SOI) | Standardized index based on the observed sea level pressure (SLP) differences between Tahiti and Darwin, Australia. Prolonged periods of negative (positive) SOI values coincide with abnormally warm (cold) ocean waters across the eastern tropical Pacific typical of El Niño (La Niña) episodes. | https://psl.noaa.gov/gcos_wgsp/Timeseries | 1866 – 2025<br>Global | Yes – months |
| Dipole Mode Index (DMI) | Intensity of the Indian Ocean Dipole represented by anomalous SST gradient between the western equatorial Indian Ocean (50E–70E and 10S–10N) and the southeastern equatorial Indian Ocean (90E–110E and 10S–0N). | https://psl.noaa.gov/gcos_wgsp/Timeseries | 1870 – 2025<br>Global | Yes - months |
| Southern Annular Mode (SAM) | The Southern Annular Mode refers to the north-south shift of rain-bearing westerly winds and weather systems in the Southern Ocean compared to the usual position. | https://legacy.bas.ac.uk/met/gjma/sam.html | 1957 – 2025<br>Global | Yes - weeks |

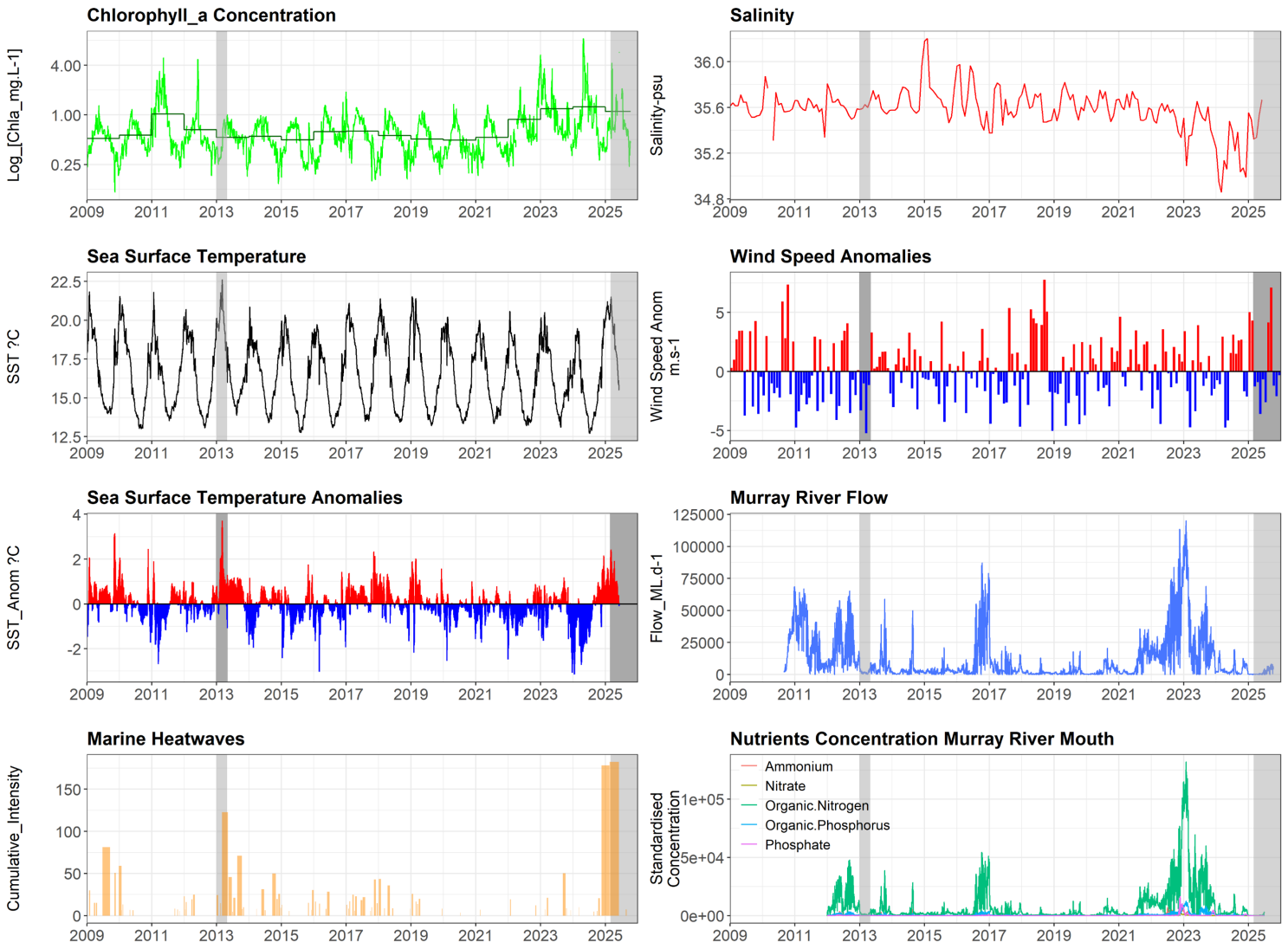


**Figure 3:** Time series of environmental data for Zone 1, positioned south-west of Murray River Mouth. The dark green line in chlorophyll-a plot represents the annual mean chlorophyll-a concentration (log(Chla mg L-1)). Gray shaded rectangles indicate the timing and duration of the two major SA algal bloom events (2013 *Chaetoceros;* 2015 *Karenia* and other taxa).

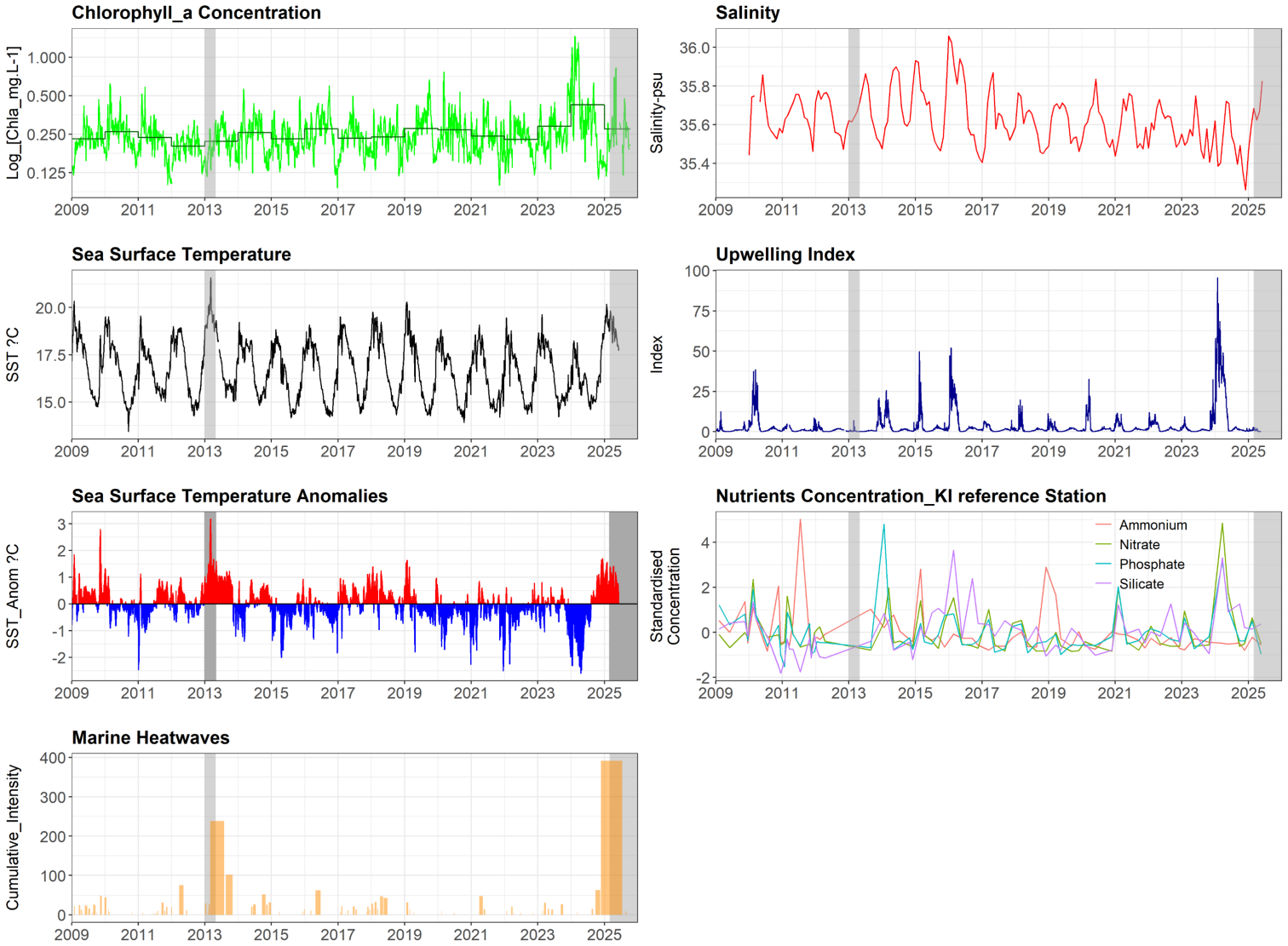


**Figure 4:** Time series of environmental data for Zone 2 and IMOS reference station. The dark green line in chlorophyll *a* plot represents the annual mean chlorophyll *a* concentration. Gray shaded rectangles indicate the timing and duration of the two major algal bloom events in SA (2013 *Chaetoceros;* 2015 *Karenia* and other taxa).

**Table 2:** Synthesis of environmental driver anomalies for Zone 1 and River Murray mouth, as well as Zone 2 and IMOS reference station. Values represent standardised maxima for each variable, either intensity (Int.) or duration (Dur.), except for salinity and wind anomalies (Anom.) for which standardised minima were calculated. Dark-blue cells highlight values > 2 and indicate extreme anomalies. Blue cells highlight 1 < values < 2 and indicate strong anomalies. Light-blue cells highlight 0.5 < values < 1 and indicate moderate anomalies. For salinity and wind, dark-plum cells highlight values < -2 and indicate extreme negative anomalies. Plum cells highlight -2 < values < -1 and indicate strong negative anomalies, while light-plum cells highlight -1 < values < -0.5 and indicate moderate negative anomalies. Gray shaded years indicate timing of major SA algal bloom events. Empty cells indicate missing data.

| | Zone 1 | | | | | | | | | | | | | Zone 2 | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | Nutrients Murray River | | | | | | | | | | | | Nutrients KI Upwelling | | | |
| Year | Chl-a | SST | SST Anom | MHW Int. | MHW Dur. | Salinity | Wind Anom. | River Flow | $PO_4$ | $NH_4$ | Organic N | Nitrate | Organic P | Chl-a | SST | SST Anom. | MHW Int. | MHW Dur. | Salinity | Upwell. Index | $NO_3$ | $PO_4$ | Silicate | $NH_4$ |
| **2009** | -0.7 | 1.11 | 1.28 | 0.48 | 1.61 | 0.73 | 1.27 | - | - | - | - | - | - | -0.5 | 1.07 | 1.23 | -0.19 | -0.31 | -0.02 | -0.56 | -0.81 | 0.17 | -0.24 | 0.28 |
| **2010** | -0.7 | 0.74 | 0.01 | -0.75 | -0.86 | -0.42 | -1.11 | 0.46 | - | - | - | - | - | 0.05 | -0.1 | -0.28 | -0.54 | -0.66 | -0.03 | 0.55 | 0.98 | 0.68 | 0.48 | 0.73 |
| **2011** | 0.88 | 1.07 | -0.54 | -0.57 | -0.73 | -0.25 | -0.56 | 0.41 | - | - | - | - | - | -0.1 | 0 | 0.03 | -0.37 | -0.34 | 0.3 | -0.73 | 0.41 | -0.06 | -0.75 | 2.67 |
| **2012** | 0.8 | -0.3 | -0.14 | -0.54 | -0.45 | 0.64 | 1.15 | 0.36 | -0.23 | 0.43 | 0.2 | 0.82 | 0.07 | -1.1 | -0.8 | 0.22 | 0.08 | 0.06 | 0.52 | -0.77 | -0.63 | -1 | -1.3 | -0.67 |
| **2013** | -0.8 | 2.11 | 1.93 | 1.23 | 1.08 | 0.89 | -1.83 | 0.18 | -0.36 | 0.08 | -0.03 | -0.24 | -0.13 | -0.9 | 2.78 | 2.33 | 1.73 | 1.77 | 1.19 | -0.21 | -1.4 | -1.2 | -0.98 | 0.06 |
| **2014** | -0.8 | -0.1 | 0.05 | -0.08 | 0.14 | 0.94 | 0.96 | -0.07 | -0.41 | 1.28 | -0.29 | 0.13 | -0.34 | -0.2 | -0.5 | 0.34 | -0.16 | -0.11 | 0.55 | 0.01 | 0.69 | 2.78 | 0.06 | -0.11 |
| **2015** | -0.8 | -0.8 | -0.79 | -0.44 | -0.55 | 0.46 | 0.55 | -0.89 | -0.42 | 0.06 | -0.73 | -0.3 | -0.7 | -0.4 | -1 | -1 | -0.53 | -0.65 | 0.35 | 1.02 | 0.26 | -0.16 | 0.25 | 1.22 |
| **2016** | -0.4 | -1.5 | -0.81 | -0.47 | -0.23 | 0.11 | 0.87 | 0.98 | -0.31 | 0.75 | 0.37 | 0.07 | 0.21 | 0 | -0.7 | -0.84 | -0.05 | 0.21 | -0.27 | 1.12 | 0.36 | -0.1 | 2.4 | -0.66 |
| **2017** | -0.5 | 0.19 | 1.42 | -0.21 | -0.3 | -0.05 | 0.34 | 0.6 | -0.31 | -0.04 | 0.16 | -0.17 | 0.03 | -0.4 | -0.1 | 0.78 | -0.46 | -0.41 | -0.73 | -0.78 | -0.04 | -0.28 | -0.2 | -0.78 |
| **2018** | -0.7 | 0.53 | 0.48 | -0.2 | -0.2 | 0.49 | -0.89 | -1.12 | -0.43 | -0.51 | -0.84 | -0.49 | -0.79 | -0.7 | 0.28 | 0.69 | -0.21 | -0.06 | 0.1 | -0.25 | -0.41 | -0.43 | -0.43 | 1.28 |
| **2019** | -0.7 | 0.71 | 0.5 | -0.52 | -0.58 | 0.57 | -0.19 | -0.97 | -0.42 | -1.05 | -0.7 | -0.63 | -0.68 | 0.24 | 1.01 | 0 | -0.36 | -0.44 | 0.31 | -0.75 | -0.81 | -0.78 | -0.49 | 0.47 |
| **2020** | -0.6 | -1 | -0.8 | -0.92 | -0.95 | 0.52 | 0.65 | -0.9 | -0.42 | -0.89 | -0.64 | -0.59 | -0.63 | 0.62 | -1 | -1.23 | -0.59 | -0.66 | 0.7 | 0.29 | -1.12 | -0.84 | -1.08 | -0.59 |
| **2021** | -0.7 | -1.2 | -0.65 | -0.86 | -0.95 | 0.57 | -0.28 | -0.48 | -0.38 | -0.47 | -0.3 | -0.44 | -0.35 | -0.5 | -0.7 | -1.01 | -0.2 | -0.11 | -0.12 | -0.6 | 0.68 | 0.76 | 0.38 | -0.66 |
| **2022** | 1.01 | -0.5 | -1.06 | -0.63 | -0.79 | -0.26 | -0.39 | 1.73 | 3.2 | 2.12 | 1.92 | 3.13 | 1.64 | -0.6 | -0.1 | -0.83 | -0.47 | -0.49 | 0.6 | -0.59 | -0.59 | -0.59 | 0.41 | -0.77 |
| **2023** | 1.07 | -0.6 | -0.45 | -0.08 | -0.08 | -1.66 | -1.63 | 1.91 | 1.08 | 0.75 | 2.37 | 0.19 | 2.7 | 0.28 | 0.1 | -0.41 | -0.37 | -0.38 | -0.67 | 0.28 | -0.09 | -0.24 | -0.3 | -0.79 |
| **2024** | 2.39 | -1.1 | -1.64 | 2.23 | 1.67 | -2.97 | 1.36 | -0.93 | -0.15 | -1.22 | -0.55 | -0.74 | -0.21 | 3.32 | -1.3 | -1.15 | 3.28 | 3.19 | -3.25 | 2.97 | 2.86 | 1.61 | 2.12 | -0.92 |
| **2025** | 1.24 | 0.69 | 1.21 | 2.31 | 2.17 | -0.34 | -0.28 | -1.26 | -0.44 | -1.29 | -0.94 | -0.74 | -0.82 | 0.87 | 0.85 | 1.13 | -0.59 | -0.61 | 0.44 | -0.98 | -0.32 | -0.34 | -0.33 | -0.76 |

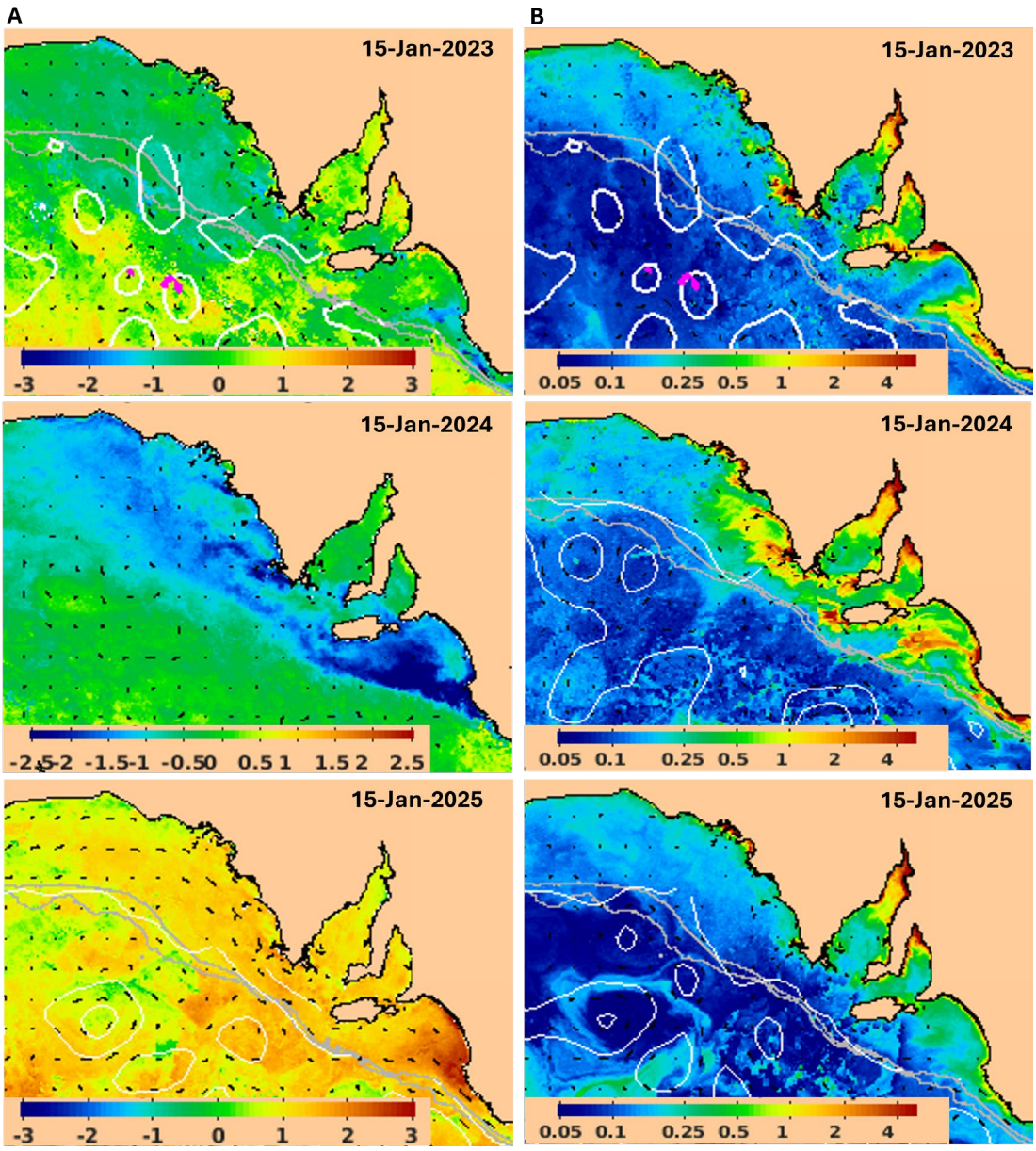


**Figure 5:** Monthly average (A) sea surface temperature anomaly (°C) and (B) chlorophyll-a concentration (mg $m^{-3}$) for January 2024 (middle panes) illustrating the extent of the seasonal upwelling and contrasting with the conditions in January 2023 and 2025. Source: https://oceancurrent.aodn.org.au (IMOS).

**Table 3:** Synthesis of climate driver anomalies, including the El Niño Southern Oscillation (ENSO), the Indian Ocean Dipole (IOD) and the Southern Annual Mode (SAM). Values show standardised maxima for each variable, expressed as intensity (Int.) or duration (Dur.). Dark-blue cells indicate extreme anomalies (> 2). Blue cells indicate strong anomalies (1-2). Light-blue cells indicate moderate anomalies (0.5 – 1). Gray shaded years highlight major SA algal bloom events.

| Year | ENSO Int. | El Niño Dur. | IOD Int. | IOD Dur. | SAM Int. | SAM Dur. |
|---|---|---|---|---|---|---|
| **2009** | 0.89 | 0.72 | -0.25 | -0.04 | -1.58 | -1.45 |
| **2010** | 0.83 | 0.35 | -0.31 | -0.76 | 0.73 | 0.35 |
| **2011** | -1.08 | -0.77 | -0.49 | 0.67 | 0.17 | -1.45 |
| **2012** | 0.19 | -0.02 | -0.35 | -0.04 | -0.14 | -0.25 |
| **2013** | -0.66 | -0.77 | 0.06 | 0.31 | -0.56 | -0.85 |
| **2014** | -0.11 | -0.77 | -0.68 | -1.11 | -1.05 | -0.25 |
| **2015** | 1.98 | 2.96 | 0.54 | 1.38 | 2.03 | 1.56 |
| **2016** | 1.55 | 0.72 | -1.03 | -1.47 | 1.33 | 0.35 |
| **2017** | -0.61 | -0.77 | -0.60 | -0.40 | -0.14 | -0.25 |
| **2018** | 0.03 | -0.02 | -0.51 | -0.40 | -0.56 | 0.35 |
| **2019** | 0.03 | -0.02 | 2.40 | 2.10 | -0.62 | -1.45 |
| **2020** | -0.64 | -0.77 | 0.43 | -0.04 | -1.26 | 0.35 |
| **2021** | -1.18 | -0.77 | -0.77 | -0.76 | -0.69 | 0.35 |
| **2022** | -1.51 | -0.77 | -0.90 | -1.11 | 0.52 | 2.16 |
| **2023** | 0.78 | 1.10 | 2.36 | 1.74 | 1.58 | -0.25 |
| **2024** | 0.57 | 0.35 | 0.30 | -0.04 | 0.10 | 0.96 |
| **2025** | -1.08 | -0.77 | -0.20 | -0.04 | 0.12 | -0.25 |

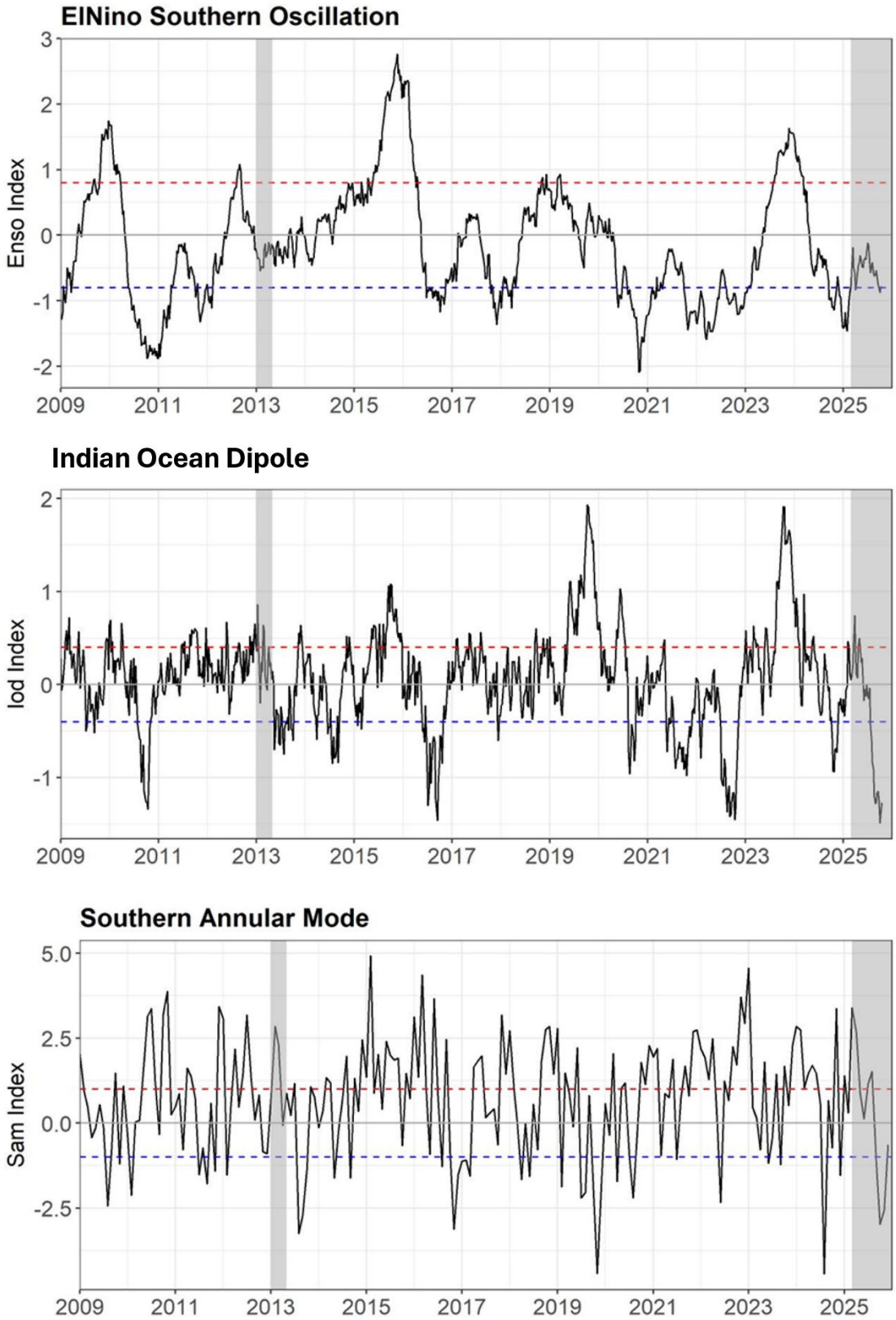


**Figure 4:** Time series of three climate drivers influencing environmental conditions in South Australia. El Niño events are indicated as ENSO index > 0.8 (red dotted line, top plot). Significant positive IOD events are indicated as IOD index > 0.4 (red dotted line, middle plot). A positive SAM phase is defined as SAM index > 1 (red dotted line, bottom plot). Gray shaded rectangles indicate the timing and duration of the two major SA algal bloom events.

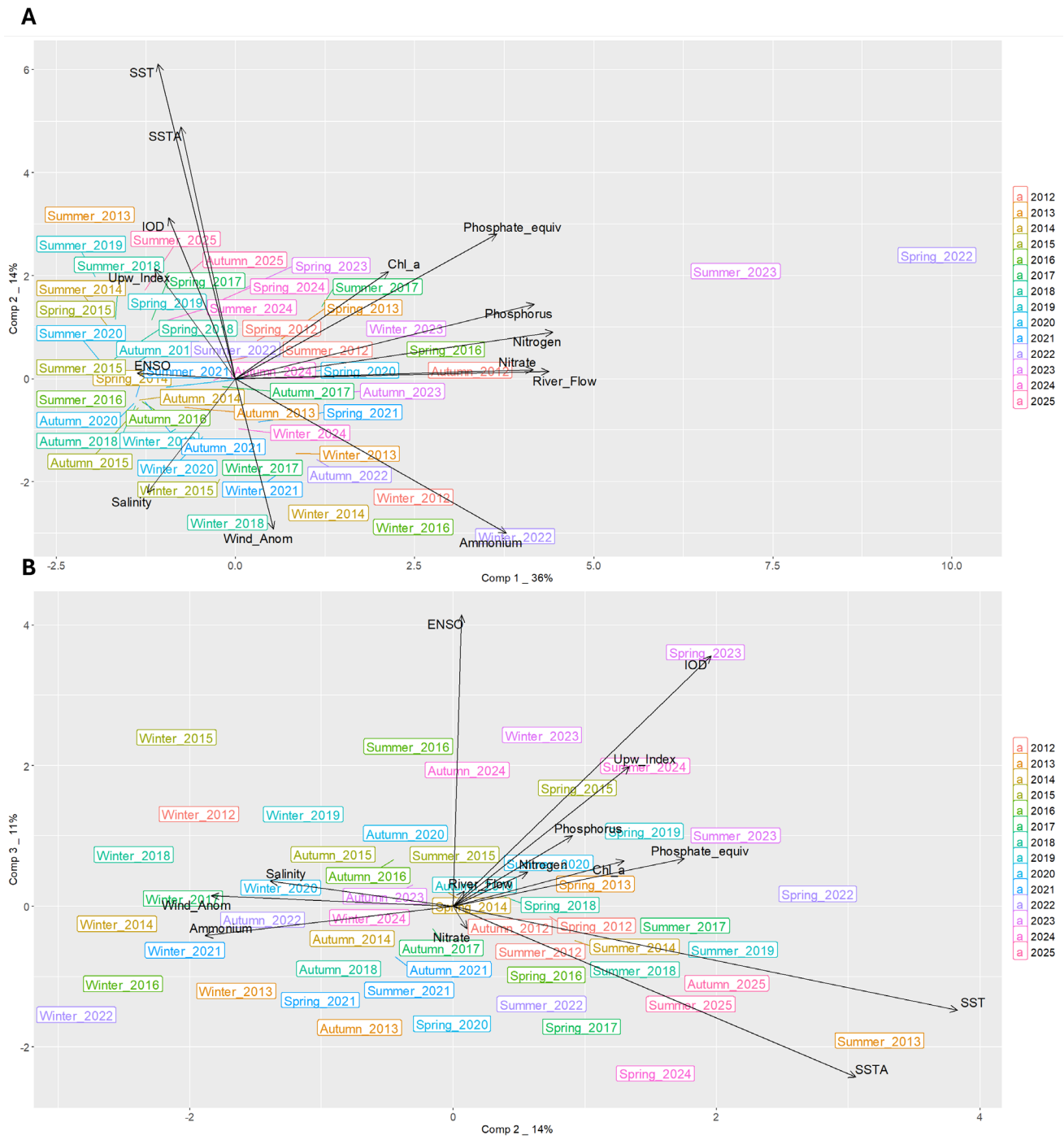


**Figure 7:** Principal Component Analysis (PCA) ordination plots for Zone 1 showing the distribution of inter-annual seasons along the principal axes. (A) Projection on axes 1 and 2 (PC1 vs. PC2), which capture the largest proportion of total variance (50%). (B) Projection on axes 2 and 3 (PC2 vs. PC3), highlighting additional structure in the data not explained by PC1. The relative positions of the seasons reflect similarities in multivariate environmental conditions; environmental variables with the longest vectors contribute most to the separation observed along each axis.

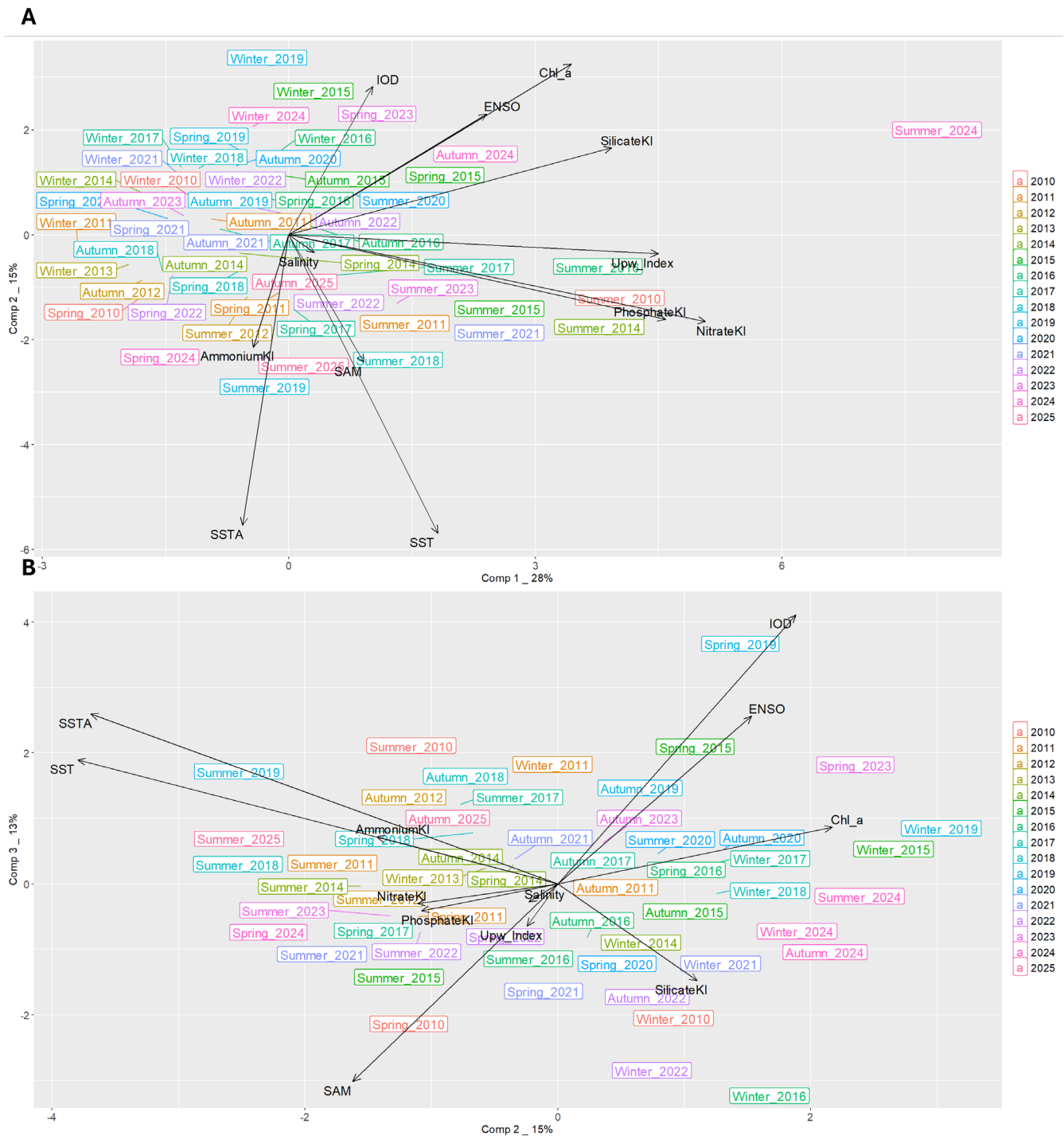


**Figure 8:** Principal Component Analysis (PCA) ordination plots for Zone 2 showing the distribution of inter-annual seasons along the principal axes. (A) Projection on axes 1 and 2 (PC1 vs. PC2), which capture the largest proportion of total variance (50%). (B) Projection on axes 2 and 3 (PC2 vs. PC3), highlighting additional structure in the data not explained by PC1. The relative positions of the seasons reflect similarities in multivariate environmental conditions; environmental variables with the longest vectors contribute most to the separation observed along each axis.

## EVALUATION OF POTENTIAL CONTRIBUTING FACTORS

The datasets used in this assessment combine satellite observations and *in situ* monitoring stations with varying spatial and temporal resolution. Gaps in long-term physical (e.g., water column stratification), chemical (e.g., inorganic and organic nutrients) and biological observations (e.g. phytoplankton community composition, grazing and other ecological interactions) in the area where the bloom first developed limit formal attribution of causal drivers. Accordingly, this initial evaluation focuses on identifying plausible contributing factors and assessing their consistency with established HAB and *Karenia* drivers, rather than attempting definitive causation.

### Pre-bloom environmental preconditioning

- Environmental conditions in the years preceding the 2025 SA HAB were highly anomalous relative to the historical record. Chlorophyll-*a* concentrations – a proxy for phytoplankton biomass and an indicator of eutrophication – increased markedly from 2022 and remained elevated through 2023/24 and into 2025 in the region where the bloom developed, indicating sustained primary production over multiple years.

- A consistent pattern is apparent in the observational record: elevated Murray River discharge and above-average chlorophyll-*a* co-occurred prior to both the 2013 and 2025 bloom events, with two or more years of above-average flow preceding each event. A similar, though weaker, association between increased flow and modestly elevated chlorophyll-*a* was also apparent in 2017. This recurring pattern suggests a strong link between anomalous river discharge and elevated phytoplankton biomass in Zone 1, likely reflecting the delivery of land-derived nutrients to coastal waters.

- Nutrient enrichment from Murray River flood discharge – particularly the record-high flows in 2022/23 – is likely to have been a significant contributor to the sustained elevated productivity observed from 2022 to 2024. This is likely to have been further supplemented by delayed release of nutrients through benthic remineralisation of deposited organic matter, and by the exceptional 2023-2024 coastal upwelling event, which provided an additional oceanic nutrient source via the possible remineralisation of detrital matter advected from the Bonney upwelling (Kämpf 2025) and further sustained elevated productivity.

- Upwelled waters are characteristically colder and slightly fresher than surface waters because they originate from deeper water masses compared to warmer, evaporated surface waters. In combination with elevated Murray River discharge and anomalously low wind-driven mixing associated with the developing marine heatwave, the intense upwelling of 2023/24 is likely to have contributed to the reduced salinity and enhance density stratification in near-coastal waters from mid-2023 to mid-2024.

### Marine heatwave, stratification and bloom development

- From mid-2024, warm sea surface temperatures intensified into an unprecedented marine heatwave that persisted for nearly ten months. During the early period of bloom development (March–May 2025), wind speeds were relatively low, favouring stable water-column stratification and reduced vertical mixing. While direct stratification measurements in nearshore inshore waters are limited, the combination of record SST and reduced winds is consistent with promoting strong surface stratification.

- This combination of warm, stratified conditions, increased photosynthetically active radiation and sustained nutrient availability is consistent with physical settings known to favour motile dinoflagellates such as *Karenia*, which are capable of diel vertical migration - descending to nutrient-rich deeper waters at night to acquire coloured dissolved organic matter (CDOM) (Hu *et al.* 2016), and ascending to the surface during the day to access light for photosynthesis - enabling them to exploit surface light and deep nutrient pools in a way that non-motile competitors cannot (Margalef 1978, Smayda and Reynolds 2001).

- Across the available evidence, the development and persistence of strong, anomalously warm and stratified conditions, emerges as a critical enabling factor for bloom maintenance.

**Role of upwelling, relaxation and downwelling in bloom transport**

- The South Australian shelf hosts one of Australia's most productive coastal upwelling systems, driven by seasonal south-easterly winds that generate Ekman transport and the shoaling of cold, nutrient-rich sub-thermocline water. The physical oceanography of this system, including shelf-slope circulation, Flinders Current dynamics and submarine canyon upwelling south of Kangaroo Island, has been characterised through sustained observational and modelling studies (Kämpf 2010, Kämpf *et al.* 2004, Middleton and Bye 2007, Richardson *et al.* 2020). Upwelled waters are characteristically nutrient-rich but low in silicate (Kämpf *et al.* 2023, Richardson *et al.* 2020) – a signature of their Southern Ocean Central Water origin – with direct implications for phytoplankton community structure, favouring non-silicified taxa such as *Karenia* over diatoms following upwelling events (Richardson *et al.* 2020).

- Upwelling in SA occurs as a series of discrete events between November and May, with significant interannual variability in intensity and duration (Kämpf 2010, Kämpf *et al.* 2004, Middleton and Bye 2007). El Niño events enhance upwelling intensity along the SA coast through their influence on large-scale wind and pressure fields (Middleton *et al.* 2007), and the co-occurrence of El Niño and positive IOD in 2023/24 is consistent with the record-intensity upwelling documented that year. During 2023/24, the extreme upwelling delivered cold, nutrient-rich water to the SA shelf, sustaining elevated phytoplankton production across coastal margins (Figure 5). Upwelling may also have transported deep-water *Karenia* seed populations to shallower shelf depths where growth conditions were more favourable (Krimsky and Staugler 2025).

- In the months immediately preceding bloom onset in March 2025, the upwelling index was low, consistent with a transition to upwelling relaxation or downwelling-favourable conditions (van Ruth *et al.* 2018). This transition is ecologically significant: downwelling and upwelling relaxation can transport surface waters - and any accumulated phytoplankton biomass - shoreward, facilitating coastal bloom accumulation and intensification (Crespo *et al.* 2006, Krimsky and Staugler 2025). Upwelling could therefore be considered a nutrient- delivery mechanism during 2023/24, with downwelling or upwelling relaxation as a potential bloom transport and concentration mechanism in the lead-up to and during the March 2025 bloom event.

**Large-scale climate forcing**

- There is no clear evidence that a single large-scale climate index directly triggered the 2025 bloom. However, the co-occurrence of El Niño and positive IOD conditions in 2023/24 is consistent with enhanced upwelling along southern Australia and the intrusion of nutrient-rich waters onto the SA shelf.

- Across the 17-year record, co-occurrence of El Niño and positive IOD conditions has been relatively infrequent, with the 2023/24 event being the most intense such co-occurrence in the record. A moderate positive IOD in 2015–2016 coincided with a weaker El Niño, but without the same magnitude of upwelling or productivity response observed in 2023/24. A positive SAM phase during summer 2023/24 further reinforced upwelling-favourable easterly wind conditions. These large-scale conditions may have acted to precondition the system for elevated productivity, with local oceanographic and meteorological conditions influencing bloom development and persistence.

- The environmental patterns observed in SA align closely with the global HAB and *Karenia* literature, which consistently highlights the importance of anomalously warm conditions and marine heatwaves, enhanced stratification, elevated inorganic and organic nutrient supply from multiple sources (including dead and decaying biomass); and physical settings that promote retention and accumulation of phytoplankton biomass. These drivers recur across major *K. brevis* blooms on the West Florida Shelf and *K. mikimotoi* blooms in the western English Channel and East China Sea, among other systems.

**Comparison with the 2013 event**

- The 2025 event shares some similarities with the 2013 SA bloom, including warm SSTs, and marine heatwave conditions, but key differences are evident:
    - The 2024–25 marine heatwave was longer-lasting and of far greater cumulative intensity than that recorded in 2013.
    - Elevated phytoplankton biomass persisted for multiple years prior to the 2025 bloom, whereas chlorophyll-*a* returned to average levels six months before the 2013 HAB event.
    - River Murray discharge prior to the 2025 event was substantially higher and sustained over a longer period than in the years preceding 2013, contributing – alongside the extreme 2024 coastal upwelling event – to a prolonged reduction in near-coastal salinity not observed in the lead-up to 2013.
    - The 2024 coastal upwelling event was unprecedented in both intensity and duration and had no equivalent in the 2013 record.
    - The 2025 event involved a complex, multi-species *Karenia* assemblage (among other ichthyotoxic taxa) producing potent biotoxins, whereas the 2013 event was dominated by the non-toxigenic diatom *Chaetoceros coarctatus.*

- These differences indicate a substantially stronger degree of physical and biogeochemical preconditioning in the lead-up to the 2025 event compared with in 2013.

**Nutrient dynamics and community succession**

- The combination of extreme upwelling, substantial River Murray inflows, and multi-year elevated phytoplankton biomass from 2022 to 2025 (Figure 3) indicates a prolonged period of elevated primary production and eutrophication in the region where the bloom was first detected in March 2025. The subsequent weak upwelling season in 2025 would be expected to reduce the supply of new nutrients, and reduced winds in combination with marine heatwave conditions lead to increased stratification.

- Under such conditions, a shift from diatom dominated communities associated with upwelling, towards communities favouring dinoflagellates, including mixotrophic *Karenia* spp., would be expected, as warmer waters, increased stratification and accumulated dissolved organic matter collectively favour taxa able to exploit regenerated and organic nutrient pools (Chen *et al.* 2026).

- However, because there are currently no time-resolved coastal N:P:Si measurements or detailed diatom–*Karenia* succession data from the bloom origin region, we cannot quantify the extent to which changes in specific N:P:Si ratios or nutrient-form shifts were necessary precursors for the 2025 event, nor can we separate their influence from that of the clearly anomalous marine heatwave, upwelling and stratification identified in this assessment.

**Overall synthesis**

Taken together, the available evidence suggests that the 2025 SA HAB arose from a convergence of interacting drivers rather than a single trigger. An unprecedented marine heatwave, extreme and sustained upwelling in 2023/24, prolonged elevated phytoplankton biomass, freshwater-derived nutrient inputs, and the subsequent transition to a weak upwelling state and stratified conditions at the site of the bloom origin, collectively may have created conditions that were highly favourable for *Karenia* bloom development and persistence. The relative importance of each driver cannot be determined from this assessment, and it is possible that not all were necessary conditions – i.e., some may have been reinforcing rather than essential.

- **Preconditioning versus proximate triggers.** The three major environmental events – River Murray flood discharge, the record 2023–24 coastal upwelling event, and the prolonged marine heatwave – are not proposed as direct or proximate triggers of the 2025 bloom. Rather, the sustained period of elevated chlorophyll levels – indicative of increased eutrophication – that followed them, is proposed as a defining feature of the regional environment in which the bloom developed. This prolonged preconditioning period may have maintained *Karenia* spp. populations at an elevated baseline from which bloom densities could be reached rapidly once proximate physical conditions – notably stratification and calm seas – aligned.

- **Spatial evidence for regional preconditioning.** The Zone 1 vs. Zone 2 comparison provides important circumstantial evidence for this view. Background conditions in Zone 1 – proximate to the Murray Mouth and in the path of Bonney coast upwelling – diverged markedly from those at the offshore Zone 2 reference site over the preceding three to four years, with sustained above-average chlorophyll-*a* and anomalous enrichment in Zone 1 absent from Zone 2. This spatial contrast underscores that proximity to the River Murray and the downstream deposition of detrital (organic) matter advected from the Bonney upwelling, may have provided multi-year (and cumulative) biogeochemical legacy, a defining characteristic of the region where the bloom concentrated.

- **Role of the marine heatwave.** The marine heatwave is unlikely to have acted as a direct driver through providing an extended or shifted seasonal thermal window suited to *Karenia* growth. Several *Karenia* spp. present in the 2025 SA HAB assemblage have broad to cool temperature preferences, and warm SSTs alone are not consistently identified as a proximate bloom trigger in the global literature. The heatwave's more plausible role was through the calm sea conditions, reduced wind mixing, and enhanced water column stratification it promoted, creating a stable, buoyancy-stratified environment that strongly favours motile, vertically migrating dinoflagellates such as *Karenia* over turbulence-adapted competitors.

- **Physical structuring versus nutrient availability.** Given the capacity for mixotrophy documented across multiple *Karenia* species – enabling acquisition of organic nitrogen, phosphorus and carbon in addition to dissolved inorganic forms – it is possible that nutrient availability was not a limiting or proximate driver of bloom development. This does not diminish the importance of the multi-year eutrophication period as a predisposing regional condition, but it does mean the relative importance of nutrient versus physical drivers cannot be resolved from available data alone.

- **Why *Karenia* and not other phytoplankton?** South Australian coastal waters are oligotrophic, characterised by low standing crop of other phytoplankton taxa. *Karenia* species, on the other hand, possess an unusually broad suite of competitive traits that help explain their capacity to dominate once favourable physical–chemical conditions are established: broad temperature and salinity tolerances, the ability to access multiple inorganic and organic nutrient forms through mixotrophy, allelopathic suppression of competitors, and the capacity to exploit nutrient pulses released from decaying animal biomass – effectively creating a positive feedback that sustains bloom persistence (Anderson *et al.* 2008, Burkholder *et al.* 2008, Kubanek *et al.* 2005). It is important to note, however, that these traits are well documented for *K. brevis* and *K. mikimotoi*, but have not yet been fully demonstrated across all species in the SA assemblage and should be regarded as plausible, rather than confirmed explanations pending targeted laboratory studies.

- **Distinctive features of the 2025 event.** The spatial extent, duration and multi-species *Karenia* assemblage composition – including the brevetoxin-producing *K. cristata* as a dominant component – further distinguish this event from many documented global examples. Regenerated nutrients from widespread animal mortalities, and the allelopathic capacity of *Karenia* spp. to suppress co-occurring phytoplankton, may have provided additional positive feedbacks, sustaining bloom maintenance beyond its initial development phase.

Consistent with global syntheses, this assessment reinforces the view that HABs emerge from the interaction of multiple co-occurring physical, chemical and biological factors, and that attributing any single bloom to a dominant driver is rarely straightforward, even in well-studied systems. Climate-driven changes are increasing the frequency and intensity of several of these drivers, while anthropogenic nutrient inputs remain among the few contributing factors that can be directly managed across local to regional scales. Given the documented presence of multiple HAB-forming taxa in SA waters, there is a clear need to strengthen monitoring, experimental and modelling capacity to better understand the mechanisms responsible for initiating and maintaining HABs in order to better predict, anticipate, manage and mitigate future events.

## LIMITATIONS AND UNCERTAINTIES

Interpretation of these preliminary results is subject to several important limitations.

### Single unprecedented event

- This analysis is based primarily on the single, unprecedented 2025 HAB event, with comparison only to the 2013 bloom, which involved a taxonomically and ecologically different dominant taxon (*Chaetoceros coarctatus*). It therefore remains unclear whether the combination of drivers observed in 2025 represents a recurrent pattern for SA *Karenia* blooms or a rare convergence of conditions.
- This contrasts with many global *Karenia* systems (e.g., West Florida Shelf, western English Channel) where multi-decadal bloom records allow for clearer characterisation between 'typical' versus 'extreme' driver configurations and enable more robust statistical attribution.

### Limited knowledge of *K. cristata* ecology

- Environmental and physiological information specific to *K. cristata* is very limited. To our current knowledge, the 2025 SA HAB is the largest and most extensively documented *K. cristata* event worldwide, with only a few smaller blooms previously recorded in South Africa and a detection off Newfoundland (Botes *et al.* 2003, Murray *et al.* 2025). As a result, the global understanding of *Karenia* bloom drivers is derived predominantly from other *Karenia* species – principally *K. brevis* and *K. mikimotoi* – and it is plausible that *K. cristata* differs in ecologically important respects (e.g., narrower or cooler temperature preferences, distinct nutrient acquisition strategies, or particular associations with upwelling-influenced water masses).
- Establishment of pure cultures at SARDI using 2025 SA isolates indicate that *K. cristata* favours cooler, upwelling-influenced temperate conditions, with optimal growth at 13–15°C and poor performance at higher temperatures. In SA, *K. cristata* appeared suppressed during peak summer warmth but increased again during cooler months. This suggests that the marine heatwave – while contributing to stratification and broader bloom preconditioning – may not have been a direct positive driver for *K. cristata* specifically, and that the relationship between warm SST anomalies and *K. cristata* dynamics is more complex than simple thermal forcing. This remains an important unresolved question requiring targeted culture and field studies.

### Multi-species assemblage

- The 2025 SA HAB event involved a complex, temporally shifting assemblage of at least five *Karenia* species. Environmental relationships inferred at the community level therefore cannot be attributed clearly to *K. cristata* or any single species. Species and strain-level responses to temperature, salinity, nutrients and mixing are likely to differ, elucidating species-specific environmental tolerances and responses, using samples and cultures collected over the course of the bloom, is a priority for future research.
- Beyond broad regional drivers, site-specific factors – including local bathymetry, frontal dynamics, and the depth and stability of the pycnocline at bloom sites – together with strain-level physiological characteristics of the *Karenia* assemblage present in SA waters, are likely to be as important as large-scale physical and chemical drivers in determining when and where bloom development occurred. These factors are poorly characterised for SA *Karenia* populations and represent a priority for future research.

### Bloom origin and population source

- The processes by which a *Karenia* population first grew to bloom densities in SA coastal waters – including where those initial cells came from, what conditions triggered their rapid growth, and how the bloom subsequently spread – remain unknown, and the available datasets do not allow these questions to be resolved.
- The Zone 2 (IMOS Reference Station – west coast Kangaroo Island) dataset was used in this assessment as a contrasting offshore reference site with available long-term in situ observations, not as a proposed site of bloom origin or a source of cells that seeded the bloom. Drawing direct analogies with the offshore-initiation and onshore-transport model developed for *K. brevis* on the West Florida Shelf would be premature, as that model is highly system- and species-specific, and - as noted

elsewhere in this assessment - site, species and strain-level differences are critically important in *Karenia* bloom dynamics. The degree to which SA *K. cristata* blooms conform to patterns established for other *Karenia* species in other systems remains unresolved.

- Characterising the conditions and location of initial bloom development is identified as a priority for future observational and modelling work.

**Data gaps and qualitative nature of the assessment**

- The available environmental and biological datasets provide circumstantial evidence consistent with several plausible driver combinations, but do not permit definitive attribution of the 2025 SA HAB to any single mechanism or factor combination.
- In the absence of quantitative data sufficient to rule out any individual driver, it would be premature to eliminate any factor from consideration. The datasets demonstrate anomalous co-occurrence of multiple environmental conditions but do not provide the mechanistic resolution required to rank or exclude candidate drivers. Consistent with standard practice in novel bloom events where process-level understanding is limited, all plausible drivers identified in this assessment should be regarded as working hypotheses pending further targeted investigation.
- Even if River Murray flood-derived nutrients had no direct proximate influence on the 2025 bloom – for example because inorganic nutrients were rapidly taken up by the phytoplankton community following discharge – those inputs contributed to a multi-year period of elevated organic enrichment and productivity in the bloom region. This elevated background may have sustained *Karenia* spp. populations at a level from which bloom conditions could be reached more quickly once physical conditions optimised, but this mechanism cannot be confirmed or excluded with current data.
- Although the environmental datasets used here are relatively rich compared with many coastal systems, significant gaps remain in spatial and temporal coverage. Key limitations include:
    - absence of broad-scale *Karenia* and other phytoplankton abundance data prior to and during bloom initiation;
    - limited in situ nutrient, stratification and biogeochemical measurements at offshore locations;
    - reliance on satellite-derived and index-based proxies of upwelling, stratifications and large-scale climate forcing; and
    - absence of time-resolved N:P:Si data from the bloom origin region.
- As a consequence, this assessment is necessarily qualitative, based on the co-occurrence of anomalous environmental conditions rather than formal statistical or mechanistic attribution. More detailed statistical analysis and coupled physical-biogeochemical-ecological modelling will be required to quantify the relative contributions of individual drivers, assess their interactions and test alternative hypotheses.
- Progress toward addressing these observational gaps has already begun through the deployment of new moorings and sensor platforms providing enhanced biogeochemical and physical monitoring at key locations. These investments will–be critical for generating the higher-resolution, species-integrated observations needed to better relate future HAB events to their environmental drivers and to support the development of early warning and forecasting capability. Establishment of pure cultures of selected taxa from the 2025 SA HAB and the marine biotoxin capability will facilitate ecophysiological investigations to underpin the influence of physico-chemical and biological parameters in promoting the bloom and the biosynthesis of toxins.

## PRIORITIES AND NEXT STEPS

Building on this preliminary assessment, further work should be advanced through close collaboration between the Office for Algal Bloom Research (OABR), national research partners (e.g., CSIRO, Australian universities) and the broader international HAB science community. The scale and complexity of the questions raised by the 2025 event exceeds what any single agency can address alone, and meaningful progress will require coordinated, multi-institutional investment across three complementary streams.

**1. Enhanced analysis and attribution of the 2025 event**

- Apply quantitative statistical and modelling approaches to better resolve the relative roles of marine heatwaves, upwelling, riverine inputs, phytoplankton nutritional physiology, circulation and large-scale climate modes in bloom initiation and maintenance.
- Use coupled physical–biogeochemical and ecological models to simulate and test mechanistic hypotheses (e.g. with and without the 2024 upwelling anomalies, or under altered River Murray flow scenarios) and examine how combinations of drivers could reproduce the observed spatial and temporal progression of the bloom.
- Modelling efforts should follow a deliberate sequence from simple to complex: beginning with conceptual models before progressing to more sophisticated coupled models that incorporate HAB physiology, nutrient dynamics, grazing and other ecological processes – recognising that very few models of the latter level of complexity currently exist for HAB systems globally.
- Prepare a more substantive technical report and peer-reviewed publications on the 2025 SA HAB and its drivers, in collaboration national and international partners, ensuring that new findings on *K. cristata* and the multi-species *Karenia* assemblage are rapidly incorporated into the global literature.

**2. Targeted monitoring and process studies**

**Regional monitoring**

- Establish a comprehensive regional HAB monitoring program providing situational awareness across both gulfs and nearshore coastal zones – not limited to a small number of fixed coastal stations. The program should be capable of tracking where *Karenia* and other HAB populations are developing, whether they are being transported shoreward, and how populations are moving within coastal systems. It should integrate improved satellite observations, routine molecular and taxonomic identification using conventional and novel approaches (e.g., Imaging FlowCytobot) and regular biogeochemical sampling.
- Strengthen biogeochemical, physical and ecological observations in priority regions, including organic and inorganic nutrient and carbonate chemistry sampling, stratification and mixed-layer depth measurements, and targeted moorings in upwelling-influenced areas. Deployment of oceanographic moorings with phytoplankton and environmental monitoring sensors at key locations has already begun to advance this objective.
- Establish dedicated nutrient and phytoplankton community monitoring at regularly sampled stations in the primary bloom initiation region (e.g. central South-East / Murray Mouth), combining regular dissolved (N:P:Si) and organic nutrient measurements with high-resolution phytoplankton community data – including diatom vs *Karenia* assemblage composition. Early warning indicators should extend well beyond chlorophyll-*a* to include phytoplankton community data, which will be critical for detecting future assemblage shifts and distinguishing *Karenia* from other HAB taxa.

**Process studies**

- Support targeted process studies on *K. cristata,* and co-occurring *Karenia* and other HAB species (e.g. temperature and nutrient response experiments, biotoxin production under different regimes, grazing and allelopathic interactions, sediment-pelagic coupling) to resolve both their physiological optima and their competitive optima – the conditions under which *K. cristata* is best able to establish, persist and dominate over co-occurring taxa, which are not necessarily the same as those that maximise growth rate in isolation. Single-cell isolate cultures to ascertain key drivers for vegetative growth, toxin biosynthesis, allelopathic activity, and nutrient dose-response. Measurements of C:N:P:Si ratios in HAB algal tissue, combined with stable isotope analyses, will provide important information on nutrient sources supporting bloom growth.
- Where archived bloom biomass material is available, retrospective stable nitrogen isotope ($\delta^{15}N$) analyses should be considered as a cost-effective approach to attributing the relative contributions of upwelling-derived, riverine, benthic and local organic nutrient sources to bloom development.
- Incorporate molecular and transcriptomic and biochemical approaches (e.g. metatranscriptomics, targeted species and biotoxin detection/quantification and gene-expression assays) retrospectively (to archived samples), and during future bloom events to resolve guild-specific physiological responses

and shifts in metabolic priorities under nutrient stress, helping to distinguish nutrient-driven from physically forced changes in community composition.

- Develop conceptual models of *Karenia* and other HAB dynamics in SA coastal waters as a necessary foundation for predictive modelling (e.g., Figure 7). Simple, well-constrained conceptual models that identify and rank key environmental drivers and their interactions in our specific coastal setting using data collected by the expanding ocean mooring network, are the most appropriate starting point, guiding the progressive development of more sophisticated numerical models.
- Develop a series of models of increasing complexing, including hydrodynamic models used to forecast bloom trajectories, to more complex ecological models of HAB population dynamics incorporating key environmental and trophic controls, to evaluate drivers of initiation, maintenance and dissipation, explore persistence and recurrence under future climate scenarios. SA is already investing in forecasting hydrodynamic models and ecosystem-scale ecological modelling capability, the latter of which is currently being applied to provide a system-wide assessment of HAB impacts and to support recovery planning. This represents a potentially world-leading application of ecological modelling to a HAB event, with few precedents globally, and positions SA well to contribute novel methodological advances to the international HAB literature.

### Bloom control and mitigation

- Bloom control and mitigation at the spatial scale of the South Australian gulfs and shelf waters presents significant practical and cost challenges, and the 2025 HAB event demonstrated that many proposed intervention approaches were unlikely to be feasible or cost-effective at the required scales. It is recommended that SA actively monitor and evaluate developments in bloom control and mitigation technologies as they are trialled and assessed globally, with a view to identifying approaches that may be scalable or adaptable to SA conditions as the science and technology matures. This work should be coordinated with national and international HAB research networks to ensure SA benefits from global advances without duplicating efforts already underway elsewhere.

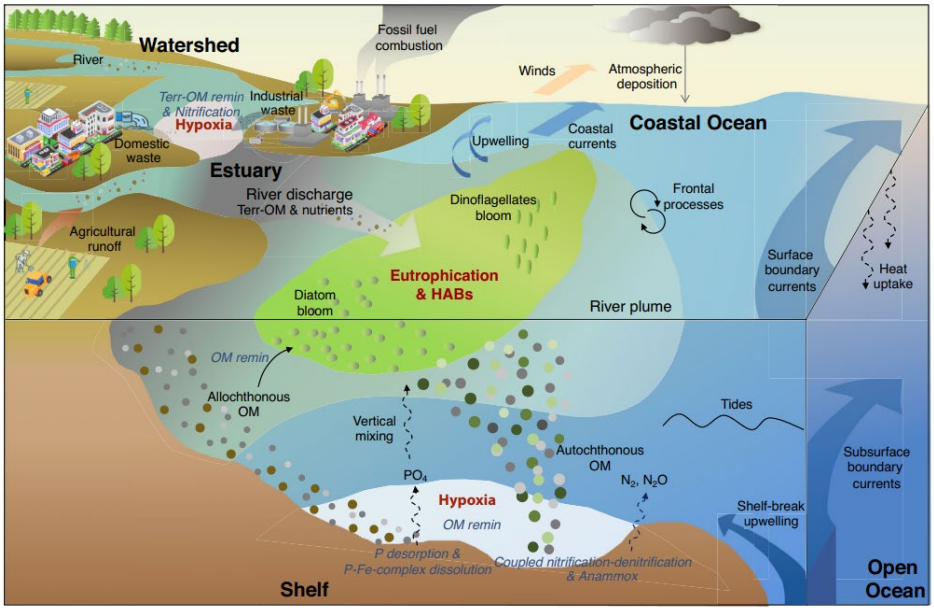


**Figure 7.** Conceptual diagram of the drivers of and interactions between physical, biological and chemical drivers in coastal systems taken from Dai *et al.* (2023). Eutrophication results in changes in nutrient ratios which promote HABs. Development of predictive models for HAB events requires conceptualisation and evaluation of relative importance of the common drivers and their interactions in our coastal waters. Excessive inputs of inorganic nutrients elevate the production of algae (autochthonous organic matter) in coastal regions, leading to an increase in the rate of organic matter supply to the bottom water and sediments. Certain environmental conditions may result in increased vertical stratification, restricted lateral advection or mixing changes in nutrient ratios, which may promote HABs.

**3. Longer-term risk assessment and communication**

- Combine lessons from the 2025 HAB event, together with global *Karenia* and HAB experience to develop risk frameworks and early-warning indicators for SA, using metrics such as marine heatwave indices, upwelling strength, satellite and in-situ observations, measures of HAB associated phytoplankton community compositions and biomass anomalies, and river discharge to signal elevated HAB risk.
- Integrate HAB considerations into broader marine heatwave and coastal climate impact assessments, recognising that similar compound extremes are likely to recur under future climate scenarios.
- Continue collaboration with national (CSIRO, universities) and international HAB experts – including Florida based expertise in *Karenia* (e.g. University of Maryland Center for Environmental Science, Florida Fish and Wildlife Research Institute, Woods Hole Oceanographic Institution) – and contribute to IOC-UNESCO HAEDAT/HAIS reporting and comparative global studies to ensure that new findings on the SA *Karenia* assemblage are rapidly incorporated into global management and policy contexts.
- Together, these steps will advance the current work from a qualitative, single-event assessment towards a more robust, evidence-based understanding of the conditions that initiate and sustain *Karenia* and other HAB taxa in SA waters, while supporting the development of practical monitoring, preparedness and response frameworks.

**FINAL REMARKS**

At this stage, the evidence is insufficient to identify a single dominant driver or definitive causal pathway for the 2025 bloom. It is possible (perhaps likely, that all the factors identified – prolonged regional nutrient enrichment, upwelling-derived nutrient supply, marine heatwave-intensified stratification, site-specific physical conditions, combined with *Karenia*-specific biological and community interactive factors – converged to produce the 2025 *Karenia* bloom. Alternatively, only a subset of these – perhaps those operating in the weeks immediately prior to bloom detection, such as stratification and calm conditions – may have been the proximate determinants, with earlier factors relevant as background preconditioning, and subsequent conditions intensifying and sustaining the bloom event.

This Advice Note provides the most comprehensive synthesis of available evidence to date and establishes the conceptual and empirical framework from which targeted future investigations can be designed. It does not – and cannot yet – provide definitive answers regarding driver attribution. The value of this synthesis lies in clearly mapping the landscape of plausible drivers, identifying the spatial and temporal patterns most consistent with each, and prioritising the data and analyses needed to distinguish between them.

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## Disclaimer

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