Evidence for an increasing incidence and severity of Harmful Algal Blooms in the southern Benguela region

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Harmful Algal Blooms (HABs) may lead to catastrophic mortality over a range of trophic levels and impact on fisheries, local species' populations, conservation management and the health of both livestock and humans. Consequently, any increase in frequency and/or toxicity of these events is of concern. Recently this concern has been realized, with reported increases in the frequency of HABs from all continents except Antarctica. This reported rise is supported by data from the Benguela coast of western South Africa, where, since 1930, there has been a significant increase in the frequency of HABs and a slight increase in their average severity. There has been a sixfold increase in the number of HABs per decade since the 1960s, with the period 1990–2005 experiencing the greatest number of blooms, as well as the most severe in terms of associated mortality. The recent occurrence of previously unrecorded HAB-causing species in this region may go some way to explaining this trend, and further implies that the increase is unlikely to diminish in the near future.

Introduction

In 1832, Charles Darwin recorded a discolouration in the water off the coast of Chile,[1] the result of a high density of the phytoplankton *Mesodinium rubrum,*[2] a ciliate also recorded in the southern Benguela region and implicated in faunal mortality.[3] Such phytoplankton accumulations in this nutrient-rich upwelling system typically develop during mid to late summer, and form what were previously known as 'red tides', now more accurately described as Harmful Algal Blooms (HABs). These are differentiated from normal productive phytoplankton accumulations by an associated mortality of fauna and/or flora. HAB-forming plankton have been present for millions of years,[4] but are fairly rare: less than 2% of the approximately 5000 marine phytoplankton species are known to be toxin producers, although an increasing number are being recognized as toxin producers, due mainly to expanded research effort.[5–7]

There have been many misinterpretations about the causes and consequences of HABs. For example, a large fish mortality caused by a bloom in Gordon's Bay, near Cape Town, in 1931 was attributed to seismic activity following an earthquake in New Zealand.[8] More recently, a correspondent wrote that 'This (red) scum consists of protozoa cells and seems unable to thrive in cold water, so I do not think there is that grave danger here that exists on the Mexican Gulf Coast where the water is warm. Having the Benguela current passing near our shores around the Cape precludes these protozoa from multiplying'.[9] However, the north-flowing Benguela Current is a nutrient-rich upwelling centre, driven by strong southeasterly summer winds,[10,11] and is precisely the reason why HABs occur in this region so frequently.

During blooms, extreme phytoplankton concentrations may cause mortalities across several trophic levels, regardless of whether the plankton themselves are toxic. Toxic blooms, generally comprising dinoflagellates or diatoms,[7] impact either when the phytoplankton are filtered as food by shellfish, resulting in accumulation of toxins and their subsequent transfer up the food chain (e.g. by *Alexandrium catenella*[12]), or when toxins are released directly into the water (e.g. by *Karenia cristata*[13]). During non-toxic blooms, mortality results either from eutrophication and subsequent anoxia, or from mechanical damage to gills.

Decomposition of high densities of phytoplankton increases bacterial activity and reduces water oxygen content. Occasionally, anoxia leads to the death of all biodiversity within the affected region, such as the black tide event which occurred in St Helena Bay (18°03′E; 32°78′S) in 1994.[14] In the northern Philippines in 2002, intensively cultured milkfish *Chanos chanos* experienced mass mortality through anoxia caused by a *Prorocentrum minimum* bloom.[15] *Protoceratium reticulatum* (formerly *Gonyaulax grindleyi)* has also been implicated in a number of fish mortalities along the southern Benguela region through anoxia.[16] Several anoxia events in the southern Benguela region have led to mass 'walkouts' of commercially important west coast rock-lobster *Jasus lalandii.*[17] During 1990–1999, there was a 24-fold increase in estimated tonnage of stranded rock-lobsters on the South African west coast compared with the previous 30 years,[17] suggesting a possible increase in the severity as well as the frequency of such events.

Many marine phytoplankton have spiny protrusions which lodge in fish gills, indirectly reducing oxygen uptake efficiency through an overproduction of mucus, which may lead to death.[18] In 1972, in Japan, a bloom of the raphidophyte flagellate *Chattonella antiqua* killed US$500 million worth of farmed yellowtail *Seriola quinqueradiara.*[19] In the southern Benguela region, the haemolysing *Karenia cristata* [misidentified as *Gymnodinium mikimotoi* in South Africa (G.M. Hallegraeff, *in litt.)*] has been implicated in fish mortalities.[5,16]

There has been growing concern in recent years that both the frequency and toxicity of blooms are increasing.[5,20,21] Studies along the U.S. coastline, since 1972, suggest a growing frequency of HABs, an extension in their geographical range and the occurrence of previously absent toxic organisms such as *Pfiesteria piscicida,* discovered in 1991.[20] Along the Texas coast, the period 1996–2002 experienced the most HABs since records began in 1935.[22]

There was a general increase in dinoflagellate blooms in the Baltic Sea between 1979 and 1999,[23] possibly a result of mild, ice-free winters promoting the growth of dinoflagellates over diatoms.[24] On the Russian Pacific coast there has also been an increase in species richness and range sizes of potentially toxic species, including *Alexandrium* spp.[25–27]

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Table 1. The HAB severity index and its rationale.

Severity score	Rationale
1	Low mortality – few deaths of one species or genus.
2	Relatively low mortality affecting more than one species. Fairly localized event.
3	Medium to high mortality affecting several species and/or occurring over a large area.
4	Very toxic or eutrophic event, often over a large area, with associated mass mortality.
5	Extreme toxic event. Mass mortality across every trophic level – a black tide event.

Along the Chinese coast, 460 HAB events were recorded between 1933 and 2001, with a marked rise in the number of blooms between 1952 and 1998: the frequency of HABs more than doubled between 1980 and 1998 in the South and East China Sea.[28,29] Between 1988 and 2001, HABs expanded to an average of 500 km^2 per event, from an average of <100 km^2 prior to 1981.[28,29] In the same region, Tolo Harbour in northeast Hong Kong experienced a marked increase in HABs after 1980, a period of enhanced urban development and nutrient loading from untreated sewage and industrial wastes.[30] Since 1987, improvement in water quality has reduced the number of HABs from a peak of 39 in 1988 to 19 in 1997.[31]

Despite these records, long-term data sets are rare, the longest being from the Bay of Fundy in Canada, which has been monitored since 1944.[32] Consequently, determining whether these changes are part of a natural process or one exacerbated by human activity rests on a number of assumptions, not least the effort of past documentation of HAB occurrences.

Because global evidence indicates increases in HAB incidences as well as changes in the organisms causing them, this study compares HAB instances along the southern Benguela region from the South African/Namibian border (16°48′E; 28°53′S) south to Betty's Bay (18°96′E; 34°37′S), to assess whether this area has followed the same general pattern.

Methods

Incidences of HABs in the southern Benguela region were collated from reports in the main Cape newspapers, *The Argus* and *The Cape Times,* from 1930 to 2005, for the summer period January–April, when the frequency and magnitude of HABs in the southern Benguela region is greatest.[10] Because all newspapers had to be examined in unindexed microfilm, these searches were necessarily restricted to the times of year when HABs are most likely to form. The decision to include published data about HABs occurring at other times of year was made based on the assumptions that a) the most severe events would have been reported (even if not in newspapers), and b) the probability of such events being unreported remained constant throughout the study period. Data for the periods 1930–1946 and 1974–1985 were extracted from *The Argus* and *The Cape Times,* respectively. Data for the period 1947–1973 were obtained from the *Argus* oceanography clippings files, covering each month of the year. Fifteen of 29 incidences reported in newspapers were not used in analyses, as no associated mortality was reported and these could therefore not be categorized as HABs. Incidences between May and December, reported elsewhere in the literature and on the Internet, were included in analyses.

There are uncertainties associated with analysing 'data' drawn from media articles. In the early to mid-20th century, some incidences of HABs in the southern Benguela region may have been unreported, particularly along the northern coastline where human population density was low (although dependent on fishing). In the absence of reports, we assumed that had such incidences occurred, there was at most limited associated mortality and these events would not impact on detecting any trend in increasing severity of HABs; indeed, if anything, their exclusion would work against detecting such a trend. Further south, within the Table Bay and False Bay areas immediately adjacent to Cape Town, we assumed that the majority of incidences would have been reported. When local media headlines such as, 'The Queen goes for a walk' and 'Woman dies in hospital'[33] are commonplace, it seems unlikely (although admittedly not impossible) that a large mortality event or dramatic water discolouration would go unreported.

Reporter subjectivity (regarding exaggeration of an event and its mortality) was deemed unlikely to be significant. Prior to the 1960s, the events were poorly understood and their cause was undetermined. Blooms were reported factually as unusual phenomena attracting spectators through displays of extreme coloration or bioluminescence in response to wave action. Following discovery of the link between blooms and aquatic mortality or toxicity (and particularly human mortality), events were reported as shellfish consumption warnings, usually quoting an expert. For this reason, human mortality was not included in the analysis because later events would not have had the same impact due to a conscious avoidance of potentially contaminated seafood. Estimates of tonnage of rock-lobster strandings may be inaccurate to some degree, but all estimates were made by government marine inspectors, therefore error in estimation is assumed to have been consistent.[17]

Because mortalities associated with HABs are mostly reported qualitatively, or at best subjectively estimated quantitatively, it is difficult to rank the severity of events using strictly quantitative criteria. We opted in preference to base such a ranking on a combination of the number of individuals affected, diversity of taxa involved, and geographical area influenced by a bloom. The lowest-ranking events thus affected few individuals of few species and/or were highly localized (events scoring 1 out of a possible maximum of 5; Table 1). At the other end of the continuum were events resulting in large-scale mass mortality (only one such event, a black tide in St Helena Bay in 1994, qualified for inclusion in the highest-impact category). The severity scale is almost certainly non-linear, but available data make it impossible to assess the extent of this non-linearity. What is almost certain is that the categorization used underestimates the impact of large events relative to small ones. Basing our analyses on an implicit assumption of a linear index is thus a conservative approach in as much as infrequent and severe events will not have a disproportionately large effect on the analyses.

Results

HAB incidences in the southern Benguela region

The 33 HAB events in the southern Benguela region over the period 1930 to 2005 have been concentrated in two distinct 'hotspots', around Elands Bay in the north and False Bay in the south (Table 2, Fig. 1).

At least 26 phytoplankton species, both toxic and non-toxic,

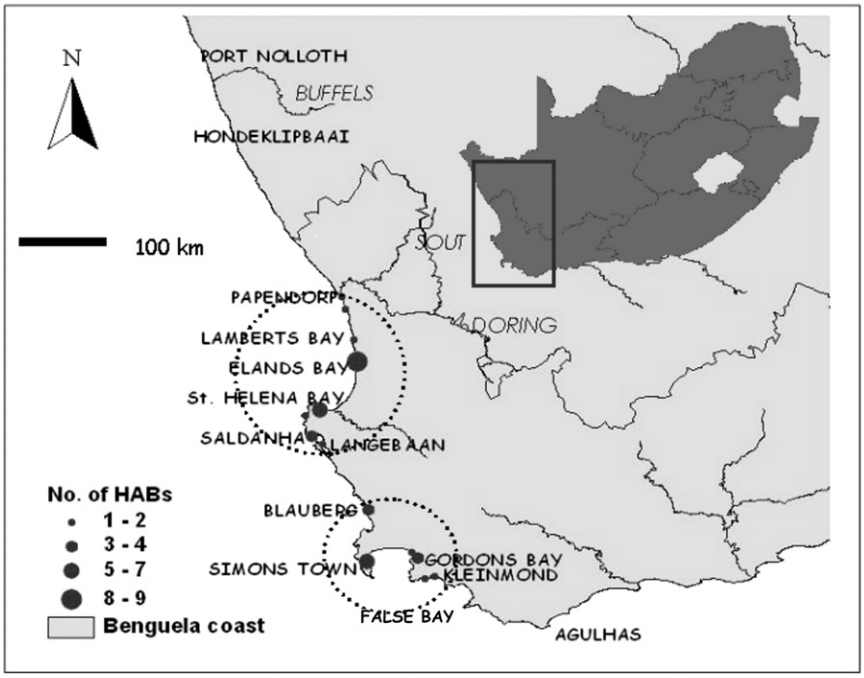

Fig. 1. Frequency of HABs in the southern Benguela region, 1930–2005.

have been identified as likely to cause mortality in the southern Benguela region through blooming (Table 3). Because many HAB incidents were recorded only from media articles, it was not possible in every incidence to isolate the predominant organism responsible. Additionally, the assumption is not made in Fig. 1 that organisms not shown in an area do not occur there, simply that they have not been dominant in blooms causing mortality in that area.

Apart from *Alexandrium catenella* and *Noctiluca scintillans,* which occur throughout the region, the dominant HAB-forming species differ greatly between the two HAB 'hotspots' (Table 4). Furthermore, the past 15 years have seen several species responsible for the formation of HABs being recorded in the southern Benguela region for the first time (Table 3). Because cell counts have been made only since 1991, it is possible, perhaps likely, that several species recorded for the first time recently may have been present for much longer. However, some recently recorded species almost certainly were not previously present: these include species with effects directly deleterious to humans (such as the aerosol toxin released by *Karenia cristata*[34]), or those with obvious and dramatic effects on the ecosystem (for instance, the 'brown tides' caused by *Aureococcus anophagefferens*[35]).

There is a slight but insignificant upward trend ($r = 0.24$, $P = 0.20$) in the severity of HAB events in the southern Benguela region (Fig. 2). While the 1990s experienced an exceptional number of rock-lobster strandings as well as the greatest frequency of HAB events on record, lack of a statistical long-term trend in HAB severity is due, in part, to the continuing occurrence of low-severity HABs.

Prior to the 1960s, HAB frequency in the southern Benguela region averaged one event per decade. This changed significantly ($r = 0.73$, $P = 0.002$) after 1960, when HAB frequency increased to an average of 6.2 incidents per decade (Fig. 3). The six-year period 2000–2005 experienced the highest frequency of HABs on record, almost equalling the frequencies in the entire 1990s, that experienced the most severe (average of 2.8 out of a maximum possible of 5.0) and highest frequency of events in a single decade. Indeed, the period 1995–2005 experienced 15 HABs (Fig. 3), with an average severity of 2.4. The overall pattern is mirrored by the subset of data from Table Bay (Fig. 4), presumed to be the most comprehensive (see Methods). HAB frequency in Table Bay remained stable until the 1960s, when there was a slight increase in frequency, followed by a large increase in the frequency of both toxic and non-toxic events from the 1990s. The Table Bay sample size is small relative to the full data set, but the trend is nonetheless marginally significant ($r = 0.50$, $P = 0.06$).

Toxic and non-toxic HABs may both be detrimental to biodiversity, and in the southern Benguela region both have been recorded with increasing frequency (toxic: $r = 0.64$, $P = 0.01$; non-toxic: $r = 0.70$, $P = 0.004$ – Fig. 5). Non-toxic HABs were rarely recorded before 1960, with no events reported within the timeframe analysed in this study, either because there was insufficient knowledge of phytoplankton species at the time for mortalities to be attributed to non-toxic events, or because bloom densities have increased since1960.

Discussion

HAB incidences in the southern Benguela region

After the severe bloom in Gordon's Bay in 1962, which killed over 100 tonnes of fish and large numbers of invertebrates, it was reported that mass mortalities due to HABs were rare along the South African coast.[36] In fact, the 1960s was the decade when HAB events in this region became more frequent (Fig. 3), particularly in the Elands Bay area. Since 1960, the frequency of HABs in the southern Benguela region has increased 6-fold.

Although the frequency of HABs along South Africa's west coast has increased, the locations within which they have occurred has remained unchanged since 1930 (Table 2). However, within the Elands Bay and False Bay hotspots, several HAB-forming species have been reported for the first time since 1985 (G. Pitcher, pers. comm). For example, diarrhetic shellfish poisoning was unknown on the South African coast prior to 1991, when an incident was attributed to *Dinophysis acuminata,*[10] a species present in the 1994 St Helena Bay black tide.[14] Early records of HABs report *A. catenella* and *N. scintillans* as the predominant species (Table 2). However, since 1960 several new toxic and non-toxic species have predominated. Since 1988, *Karenia cristata* and *Dinophysis acuminata* have been recorded for the first time in False Bay, and *Ceratium* spp., *Aureococcus anophagefferens* and *Heterosigma akashiwo* have been recorded for the first time around Elands Bay (Table 4).

Until recently, the picoplankton *Aureococcus anofagefferens* was largely confined to the northeastern U.S.: it was discovered off Rhode Island in 1985[37] and has subsequently spread to many American bays,[38] where it has had major impacts on species abundance and diversity, e.g. in Narragansett Bay in Rhode Island, the bays of Long Island in New York, and in New Jersey.[37,39,40] This species first appeared in Saldanha Bay in the southern Benguela region in 1997[35] and recurred in 1998 in the adjacent Langebaan Lagoon (Table 2). Because this species can remain viable for up to 30 days in ships' ballast tanks,[41,42] there is a danger that it will be transported to other sheltered bays along the coast. Persistent shading by this species devastates eelgrass (*Zostera* spp.) beds and causes starvation and recruitment failure

Table 2. HAB occurrences along the South African west coast, 1860–2005.

Date	Severity	Location	Organism	Associated mortality (and notes)
1869*	1	Stumpnose Bay	*Noctiluca scintillans*	Geelbek fish *Atractoscion aequidens*.[53,57]
1876*	1	Papendorp	*Alexandrium catenella?*	Black mussels *Choromytilus meridionalis.*[58]
1877*	1	Elands Bay	*A. catenella?*	Black and white *Donax serra* mussels.[59]
1888*	2	Simonstown	*A. catenella*	Chacma baboons *Papio ursinus* and white mussels.[7,53]
1901*	2	St Helena Bay	*A. catenella*	Tons of sardines *Sardinops sagax,* hundreds of seabirds (cormorant spp.[10,53]).
1907*	2	False Bay (Simon's Town)	*N. scintillans*	Fish and shellfish.[53,57]
1907*	2	Saldanha Bay	Unknown	Thousands of fish through anoxic conditions.[10]
1923*	3	St Helena Bay (Velddrif)	Unhnown	Mussels, fish and rock-lobster *Jasus lalandii.*[60]
1931	2	Gordon's Bay	*A. catenella?*	Thousands of fish.[61]
1948	2	Blauberg	*A. catenella*	Mussels, birds.[10]
1958	1	Paternoster	*A. catenella*	Black mussels.[10]
1962	3	False Bay	*Gonyaulax polygramma*	100 t of fish.[14,36]
1963	3	St Helena Bay (Velddrif)	'Reddish brown'	Last reported 40 years previously. Killed white mussels, large galjoen *Dichistius capensis,* geelbek, sharks, and small rock-lobster.[60]
1966	2	Elands Bay	*Protoceratium reticulatum* (=*Gonyaulax grindleyi*)	Hundreds of thousands of white mussels;[10,62,63] 'greatest mortality in 10 years'.[16]
1967	1	False Bay – Kalk Bay to Millers Point	*N. scintillans*	Dead fish 'but not unusual amount'.[3,64]
1967	1	Saldanha Bay	Unknown	Millions of krill.[65]
1967	2	Elands Bay (to north of Olifants River)	*A. catenella*	Entire white mussel population.[10]
1973	1	Velddrif	*Prorocentrum minimum*	White mussels.[3]
1974	1	Elands Bay	*P. reticulatum*	White and black mussels.[3,7,10]
1976	1	Gordon's Bay	*Gymnodinium* spp.	Hundreds of a wide variety of fish – mechanical damage.[7,10,66,67]
1978	4	Saldanha Bay	*A. catenella, Mesodinium rubrum*	Kelp gulls *Larus dominicanus,* Hartlaub's gulls *L. hartlaubi,* African black oystercatchers *Haematopus moquini*: walkout of crabs.[3,49]
1980	2	Elands Bay	*A. catenella*	5 million mussels.[14,67]
1988	2	False Bay	*Karenia cristata* (formerly identified as *Gymnodinium* cf. *mikimotoi.*)	Thousands of fish, also gastropods, chitons, octopus and starfish. First record of this species in the southern hemisphere.[67]
1989	3.5	Betty's Bay	*K. cristata*	30 t abalone *Haliotis* spp., fish, octopus.[67]
1993	2.5	Lamberts Bay	*Ceratium lineatum, Prorocentrum micans*	10 t rock-lobster walkout.[17]
1994	5	St Helena Bay	*P. micans, Ceratium furca, A. catenella, Dinophysis acuminata*	Black tide: total mortality, incl. 60 t rock-lobster, 1500 t fish.[14,68]
1995	1	False Bay	*Gymnodinium* spp.	Abalone larvae; caused toxicity in mussels. Also produced aerosol toxin.[69]
1996	2	Walker Bay	*K. cristata*	Abalone larvae.[10]
1997	4	Elands Bay	*C. furca; C. lineatum*	1700 t rock-lobster walkout[17,70] (Marine and Coastal Management, unpubl. data).
1997	3	Saldanha Bay	*Aureococcus anophagefferens*	Brown tide: growth arrest in oysters & mussels; some fish and seaweed mortality.[10,35]
1997	1	St Helena Bay	*A. catenella*	Sardines.[10]
1998	3	Langebaan	*A. anophagefferens*	Brown tide. Growth arrest in oysters & mussels; some fish mortality, extensive algal mortality.[10,35,71]
1999	3	Elands Bay	*A. catenella*	200 t rock-lobster walkout[17,72] (Marine and Coastal Management, unpubl. data).
2000	2	Blauberg	*A. catenella*?	30 million mussels washed ashore.[73]
2002	2.5	Elands Bay	*Ceratium dens, C. furca, C. lineatum, Dinophysis fortii, G. polygramma, P. micans, P. reticulatum, Scrippsiella trochoidea*	10 t rock-lobster walkout (Marine and Coastal Management, unpubl. data).
2002	4	Elands Bay	*Prorocentrum triestinum*	600 t rock-lobster walkout (Marine and Coastal Management, unpubl. data).
2002	2	Lamberts Bay	Unknown	Shellfish poisoning.[74]
2003	2	Table Bay	*Alexandrium minutum*	Shellfish poisoning. First record of this species on the South African coast (www.hab.org.za).
2004	2	Saldanha Bay	*Heterosigma akashiwo*	Mortalities not extensive though large shoals of disorientated fish in the shallows.[75]
2005	1	Blauberg	Unknown	Shellfish poisoning.[76]
2005	2.5	Doring Bay to Cape Agulhas	*A. catenella*?	Shellfish poisoning.[77]

*Not used in analyses as newspapers were not checked over this period.
? Assumed species from description.

Table 3. Toxicity and associated mortality of potential HAB-forming phytoplankton in the southern Benguela region. This table does not include all species present in the southern Benguela region, but focuses on those most likely to be implicated in a HAB.

Species	Type	Toxin(s)	Associated mortality
Alexandrium catenella	Dinoflagellate	c1–c4 toxins, saxitoxins and gonyautoxins.[78,79] Ichthyotoxin production reported in cultured media of *A. catenella.*[80] First species linked to paralytic shellfish poisoning (PSP).	Shellfish, fish, wide variety of seabirds; instances of Chacma baboons *Papio ursinus,*[53] domestic cats *Felis catus* and Alaskan sea otters *Enhydra lutris.*[81]
A. minutum	Dinoflagellate	PSP gonyautoxins.[82]	Mammals, birds and fish.[83,84] Widespread toxic species first recorded in South Africa in Saldanha Bay, 2003 (www.hab.org.za).
Ceratium dens	Dinoflagellate	Non-toxic – causes oxygen depletion at high densities.[7]	Mass rock-lobster strandings in South Africa (Table 2) (Marine and Coastal Management, unpubl. data)
C. furca	Dinoflagellate	Non-toxic – causes oxygen depletion at high densities.[85]	Fish deaths, mass rock-lobster strandings in the Benguela.[10]
C. fusus	Dinoflagellate	Non-toxic – causes oxygen depletion at high densities.[6]	Harms invertebrate larvae, but mechanism unknown.[6]
C. lineatum	Dinoflagellate	Non-toxic.[7]	Rock-lobster strandings.[17]
Dinophysis acuminata	Dinoflagellate	Okadaic acid.[86,87]	Shellfish.[88] First reported in South African in 1991(www.hab.org.za).
D. fortii	Dinoflagellate	Dinophysistoxins1 and 2, and okadaic acid.[87,89]	Shellfish poisoning.[12] First reported in South Africa in 1991 (www.hab.org.za).
D. hastata	Dinoflagellate	Okadaic acid.[90]	Shellfish.[90]
D. rotundata	Dinoflagellate	Okadaic acid and dinophysistoxin.[87] North American strains non-toxic.[86]	Fish and shellfish.[87]
Gonyaulax polygramma	Dinoflagellate	Non-toxic.[84]	Massive fish and invertebrate kills due to anoxia and high sulphide and ammonia levels.[84,91]
G. spinifera	Dinoflagellate	Probably non-toxic.[92]	Shellfish mortality through anoxia.[7,92]
Karenia cristata (formerly identified as *Gymnodinium* cf. *mikimotoi*)	Dinoflagellate	Indication of haemolytic and ichthyotoxic substances.[84,90]. Gymnodimine extracted from shellfish in Southland, New Zealand: produces mortality in both laboratory mice and fish.[93]	Fish, gastropods, chitons and other marine invertebrates.[67,94]
Akashiwo sanguinea (formerly *Gymnodinium sanguineum*)	Dinoflagellate	Toxic, but toxin yet to be determined.[30]	Oysters.[7]
Gyrodinium zeta	Dinoflagellate	Non-toxic (T. Probyn, pers. comm.).	No associated mortality but high biomass blooms indicate a potential for anoxia (T. Probyn, pers. comm.).
Gyrodinium sp.	Dinoflagellate	Toxic, but toxin yet to be determined.[7,95]	Fish and mussels.[96–98]
Noctiluca scintillans	Dinoflagellate	Non-toxic, but accumulates and excretes toxic levels of ammonia.[99]	Linked to massive fish and marine invertebrate kills.[100,101]
Prorocentrum balticum	Dinoflagellate	Unconfirmed, although possibly toxic.[102]	Fish.[7]
P. micans	Dinoflagellate	Assumed non-toxic.[103] However, suspected to excrete substances inhibiting diatom growth, but apparently without affecting organisms at higher trophic levels.[104]	Shellfish.[3,108] Cormorants *Phalacrocorax* spp. off the coast of Chile.[106]
P. minimum	Dinoflagellate	Controversy over toxicity affecting organisms higher up the food chain.[107]	Shellfish poisoning documented in Japan, Portugal, Norway and USA.[107] In Hong Kong, incidence strongly linked to increased human population and consequent nutrient loading.[30]
Protoceratium reticulatum (formerly *Gonyaulax grindleyi*)	Dinoflagellate	Yessotoxin.[108]	Shellfish, squid, holothuroids, rock-lobsters, sucker fish *Chorisochismus dentex.*[63]
Peridinium sp.	Dinoflagellate	Non-toxic.[6]	Fish.[6]
Scrippsiella trochoidea	Dinoflagellate	Non-toxic.[7]	Large fish kills (together with *H. akashiwo*).[7]
Pseudonitzschia australis	Diatom	Domoic acid.[7]	Birds and marine mammals.[47,109] Common in the Benguela, but with no sign of toxin (www.hab.org.za).
Heterosigma akashiwo	Raphidophyte	Gill clogging through increased mucous secretion. Probably contains haemolytic substances, e.g. polyunsaturated fatty acids.[110,111] Possibleproduction of superoxide radicals.[112]	Large fish kills.[7] Present in both northern and southern Benguela region, but not yet linked to mortalities.[10]
Aureococcus anophagefferens	Pelagophyte	'Dopamine-mimetic compound'.[7,113,114]	Causes brown tides. Occurs at high densities, when shading affects fish, crustaceans and algae.[37] First recorded in the southern Benguela region in 1997.[35]

in bivalves.[39,42] The establishment of this species in Saldanha Bay and Langebaan Lagoon is of concern both economically and ecologically, as this is not only an important area for bivalve cultivation[35] but for South Africa's most endangered marine mollusc, *Siphonaria compressa,* which is endemic to Langebaan and Knysna lagoons, where it is dependent on the eelgrass *Zostera capensis.*[43,44]

Conservation concerns: other mortalities associated with HABs

In addition to fish and invertebrates, many bird species worldwide have been affected by HABs, including European shags *Phalacrocorax aristotelis,* common guillemots *Uria aalge,*[45] terns *Sterna* spp.,[46] brown pelicans *Pelecanus occidentalis,*[47] and Magellanic penguins *Spheniscus magellanicus.*[48]

At Penguin Island, Lamberts Bay, South Africa, between 1997 and 2002 HABs were the fourth most important cause of seabird mortality and the primary cause of mortality for gulls *Larus* spp. and terns (A.J. Williams and V.L. Ward, unpubl. data). The majority of common terns *Sterna hirundo* that died on Penguin Island did so soon after their arrival following southward migration (A.J. Williams and V.L. Ward, unpubl. data). Newly arrived migrant birds are considered particularly susceptible to HAB toxins, having depleted energy reserves and hence reduced

Table 4. Spatial distribution of HAB-causing phytoplankton in the southern Benguela region.

Plankton species	Elands Bay	St Helena Bay	Saldanha Bay	Table Bay	False Bay
A. catenella	●	●	●	●	●
C. furca	●	●			
P. micans	●	●			
P. triestinum	●				
S. trochoidea	●				
C. lineata	●				
P. reticulatum	●				
D. acuminata		●			
P. minimum		●			
M. rubrum		●			
N. scintillans		●			●
A. anophagefferens			●		
H. akashiwo			●		
D. fortii				●	
A. minutum				●	
K. cristata					●
G. polygramma					●

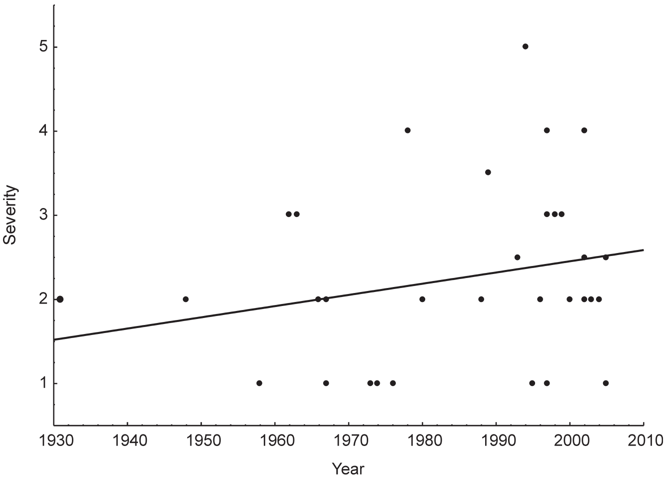

Fig. 2. Severity of HABs in the southern Benguela region in relation to year of occurrence.

immunity to toxins.[48]

A toxic bloom of *A. catenella* in Saldanha Bay in 1978 caused a 53% mortality among the local African black oystercatcher *Haematopus moquini* population,[49] a species classified as globally near-threatened.[50] This event was first erroneously attributed to *Mesodinium rubrum*,[3] a non-toxic species.

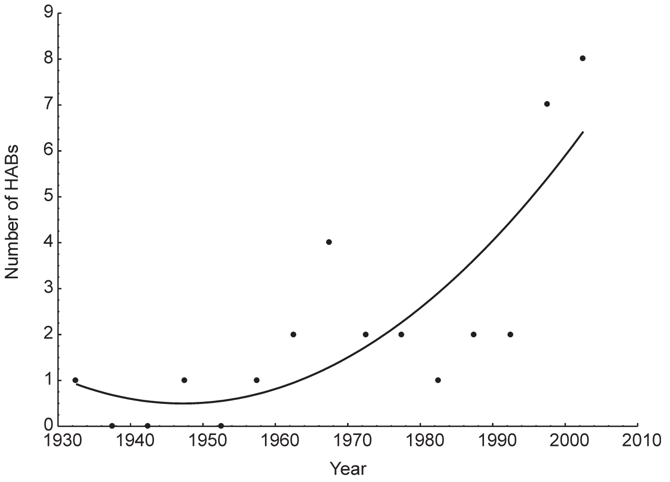

Fig. 3. Frequency of HABs in the southern Benguela region for the period 1930–2005.

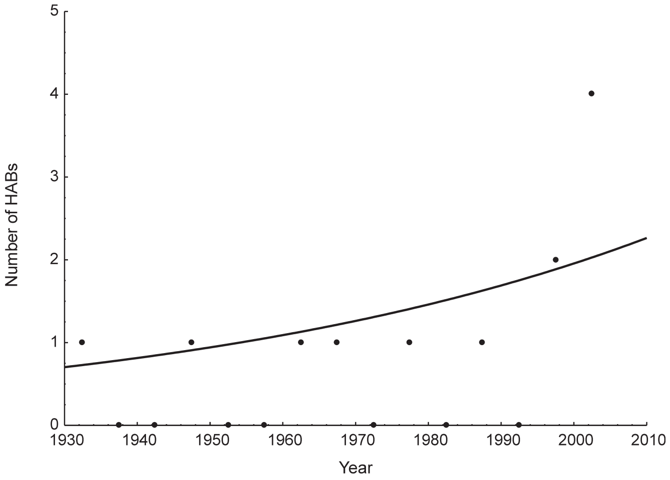

Fig. 4. Frequency of HABs in Table Bay and False Bay for the period 1930–2005.

If the observed trend of increasing HAB severity is correct, the consequences could be severe for several regionally endemic bird species (Table 5), especially those that breed colonially.

Marine mammals have also experienced HAB-related mortalities, including whales, dolphins, Florida manatees *Trichechus manatus*,[51,52] and monk seals *Monachus monachus*.[7] Deaths of terrestrial animals have also been reported, including cats, chickens, and baboons.[10,53] Additionally, human deaths and severe illness were reported from the southern Benguela region as early as 1888.[53]

Quo vadis?

As yet, no single cause can be identified to explain the global increase in HABs. A popular explanation for the recent range expansions of several species is dispersal by shipping ballast water. Because the use of ballast water far predates the recent spread of HABs, and the Cape of Good Hope is an important global port, it is surprising that so many species have been recorded only in the last 20 years, although this could be linked to the initiation of cell counts in 1991. Some species may have been transported in ballast water for decades, but were detected only when they formed noticeable blooms.[54] Other species are seen to be recent arrivals, such as *A. anophagefferens*: in this case ballast water is implicated as the most likely vector.

In sheltered bays along the southern Benguela region, nutrient input from sources such as sewage outlet pipes may become localized, fuelling blooms. In line with this prediction, HAB

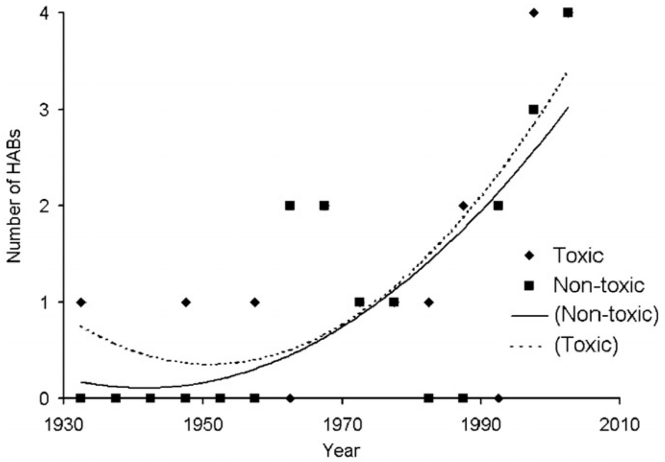

Fig. 5. Relative frequencies of toxic and non-toxic HABs in the southern Benguela region for the period 1930–2005.

Table 5. Avian species potentially at risk from more frequent and severe toxic blooms in the southern Benguela region.

Species	IUCN status[50]	Diet[115]
‡African black oystercatcher *Haematopus moquini* Endemic*	Near-threatened	Mussels and limpets.
African penguin *Spheniscus demersus* Endemic	Vulnerable	Fish, crustaceans, squid.
Bank cormorant *Phalacrocorax neglectus* Endemic	Endangered	Fish, crustaceans including rock-lobsters, and octopus and molluscs.
Crowned cormorant *P. coronatus* Endemic	Near-threatened	Small fish, molluscs and polychaetes.
Cape gannet *Morus capensis* Endemic	Vulnerable	Fish, incl. anchovy *Engraulis encrasicolus* and sardines *Sardinops sagax.*
‡Hartlaub's gull *Larus hartlaubii* Endemic	Least concern	Fish, molluscs incl. mussels, and crustaceans and polychaetes.
‡Arctic tern *Sterna paradisaea* Intercontinental migrant	Least concern	Small fish and crustaceans.
‡Common tern *S. hirundo* Intercontinental migrant	Least concern	Small fish and crustaceans.
Damara tern *S. balaenarum* Breeding endemic	Near threatened	Small fish, including anchovy.
‡Sandwich tern *S. sandvicensis* Intercontinental migrant	Least concern	Surface-dwelling fish; some crustaceans and molluscs.
‡Swift tern *S. bergii* Endemic subspecies; local migrant	Least concern	Pelagic shoaling fish.

‡ Known mortality caused by HABs in the southern Benguela region[49] (A.J. Williams and V.L. Ward, unpubl. data).
*Endemism status refers to southern Africa.

frequency in Table Bay has increased significantly since 1930 (Fig. 4): during the same period, the human population around Table Bay increased almost 3-fold from 301 450 in 1936 to 827 200 in 2001 (Statistics South Africa (2005), *in litt.*). Additionally, in 2004 alone, the Western Cape received about 1.5 million tourists.[55] Despite this apparently corroborative evidence, the fact that the same pattern of increasing HAB frequency has occurred along the open coast, where human population densities are low, suggests that other factors, as yet unidentified, are controlling the incidence of HABs.

While cause cannot as yet be convincingly determined, there has been and continues to be an increasing trend in the frequency of both toxic and non-toxic HABs along the South African west coast. Recent events suggest that the average severity of HABs is also increasing, although as yet the very conservative approach used in analyses in this study suggests that this trend is only approaching significance ($P = 0.14$). If the suspected non-linearity of our severity index is anything more than minor, what is currently a statistically insignificant finding may well represent biological reality.

Because of the economic dependence of the South African west coast on fisheries and tourism, these trends have economic, conservation and health implications. The recent discovery of several previously unrecorded HAB-forming species suggests the situation may worsen. If the trend of increasing severity is correct, the consequences could be severe, not only for species of conservation concern (Table 5), but also for commercially exploited species such as rock-lobster (Table 2), stocks of which have yet to recover from their decline in the late 1990s, following a succession of HAB-related walkouts.[56]

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