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Interannual variability of shellfish toxicity in the Gulf of Maine: Time and space patterns and links to environmental variability

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ABSTRACT

Six metrics characterize annual aspects of the magnitude and timing of shellfish toxicity resulting from dinoflagellates of the genus *Alexandrium* at >100 monitoring stations over 21 years (1985–2005) along the coast of Maine, northeastern USA. Climatologies at each station show distinct geographic patterns, generally consistent with previous reports based fewer stations/years. Earliest initiation and dates of maxima are at far western coastal stations, latest in far eastern stations. Toxicity magnitudes are highest at exposed western coastal stations and at far eastern stations inside a bay with minima in the center of the study region. Multivariate statistics group years according to similarity in station toxicity magnitude and timing. Results (a) confirm that a year of extreme toxicity (2005) differs from recent years but show it to be similar to strongly toxic years of the late 1980s, (b) show 3 year-groups, 1980s–early 1990s of high toxicity, mid-1990s–early 2000s of lower toxicity, and 2004–2005 similar to the early years, and (c) show temporal autocorrelation suggesting that processes carrying from year to year are important in controlling toxicity. Multivariate statistics then group stations according to interannual co-variability. Resulting station-groups show strong regionality consistent with known hydrographic and circulation patterns and identify stations that differ from their neighbors. Annual means calculated within station-groups provide 21-year time series that are cross-correlated with concurrent monthly environmental metrics of Gulf of Maine oceanographic conditions calculated from field measurements, satellite data and numerical circulation model hindcasts. These analyses provide three main results. First, toxicity time series show an overall pattern of elevated magnitudes and increased duration in the 1980s, minimum values in the mid-late 1990s and then increasing again in the 2000s. Second, only station-groups geographically located in the western portion of the study area have correlations with any tested environmental metric. Third, toxicity in many western station-groups was positively correlated to interannual variability in early season (April–May) wind stress driving onshore Ekman transport, negatively correlated with summer (June–July) wind stress driving offshore Ekman transport and negatively correlated with summer (June–July) cross-shelf surface temperature gradients indicative of relatively warm coastal surface temperature patterns, consistent with patterns expected from the wind transport correlations. The data do not show significant correlation between station-group toxicity and along-shelf temperature structure (an indicator of fronts and alongshore flow connection), river discharge, surface temperature anomalies, modeled surface salinities or alongshore current velocities. These data provide a quantitative summary of Maine coastal toxicity over 21 years, a spatial toxicity geography and isolate dominant environmental forcing responsible for interannual variability.

1. Introduction

The Gulf of Maine (Fig. 1), a marginal sea on the northeast North American coast, harbors a diverse and highly productive phytoplankton community. Among these, dinoflagellates of the genus *Alexandrium* produce saxitoxin associated with paralytic shellfish poisoning (PSP) (Bricelj and Shumway, 1998). For the past 30+ years, regional management agencies have operated comprehensive shellfish toxicity monitoring programs to protect consumers from these harmful algal blooms (HABs). Shellfish beds are closed to harvesting if toxicity approaches or exceeds 80 μg toxin/100 g of shellfish tissue. Such closures result in severe economic losses; >$15 M to Massachusetts alone in 2005 (Anderson et al., 2005c). Understanding the causes of, and the possibility of predicting, these HAB events is thus a regional priority. However, the oceanographic ecology of *Alexandrium* and environmental pro-

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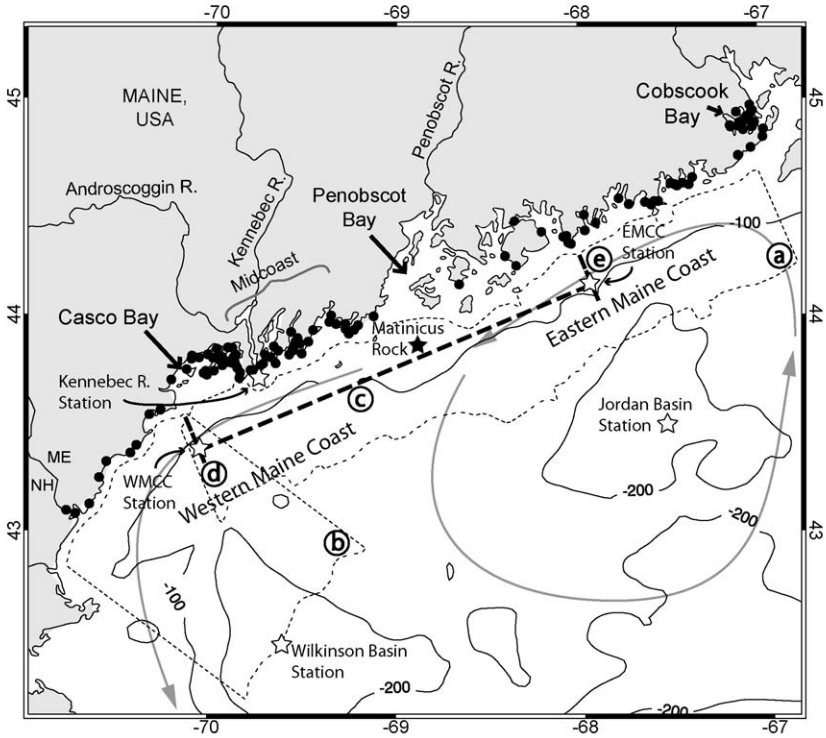

Fig. 1. The Gulf of Maine study area showing major geographic locations and region names along the coast, bathymetry, residual surface circulation patterns (grey arrows), the location of coastal shellfish toxicity sampling stations used in this study (black dots), and the sampling locations of environmental time series from (1) field data (wind, black star), (2) satellite image data (grey dashed polygons labeled a and b, and open stars) and (3) the numerical circulation model hindcasts (black dashed lines labeled c, d, e).

cesses that lead to increases in cell density and/or coastal toxicity events along the Gulf of Maine coast remain an active research topic (Anderson et al., 2005a). One approach to identifying environmental processes linked to *Alexandrium* dynamics is through the window afforded by long time series of data allowing examination of interannual variability in their timing, strength and location (Moore et al., 2009). Unfortunately, comprehensive maps of cell distribution are only available in a few years of intensive research (Anderson et al., 2005c; Townsend et al., 2001, 2005). Over 30 years of coastal shellfish toxicity data collected by the Maine Department of Marine Resources (DMR), however, provide a proxy for *Alexandrium* occurrence. Toxicity records potentially provide valuable insight into (1) the biogeography of HAB occurrence and its variability along the complex Maine coast, (2) interannual variability and trends in bloom magnitude, location and timing and, if coupled with concurrent environmental data, (3) links between HAB events and the dominant processes associated with them.

Shellfish toxicity in the Gulf of Maine has strong seasonality, usually peaking in early and late summer (Bricelj and Shumway, 1998; Hurst and Yentsch, 1981; Shumway et al., 1988). Within the overall Gulf, seasonal maxima often appear earliest in the west and latest along the east coasts (Anderson, 1997; McGillicuddy et al., 2005c), likely reflecting strong local differences in seasonal warming. Early examinations of toxicity (hereafter, toxicity refers to shellfish toxicity) spatial patterns at four stations over 4 years (Hurst and Yentsch, 1981) show a region of minimum occurrence in the Penobscot Bay region in the center of the Maine coast (Fig. 1). This pattern has been referred to as the “PSP sandwich”, with toxicity more prevalent both further east and to the west (Shumway et al., 1988). West of Penobscot Bay, however, seasonal toxicity often progresses from east to west (Franks and Anderson, 1992b; Shumway et al., 1988) in concert with the residual circulation (Pettigrew et al., 2005). Superimposed on this seasonality is strong interannual variability, both as regional averages (Anderson et al., 2005b) and at individual stations (Bean et al., 2005; Bricelj and Shumway, 1998; Hurst and Yentsch, 1981). Ten years of shellfish toxicity at 5 coastal stations along the western Gulf (Franks and Anderson, 1992b), show years of both episodic toxicity and sustained toxicity over several months. Analysis of 13 years of toxicity at 8 stations along the western Maine coast show strong overall interannual differences in the timing and strength of toxic events, with distinct differences between stations, even between those relatively close in geographic space (Luerssen et al., 2005). Five years of data (Bean et al., 2005) show geographic differences in magnitude and interannual variability between eastern and western stations. A systematic analysis of these toxicity data across decades to summarize mean patterns, to quantify similarity of the toxicity spatial patterns between years or similarity in interannual variability between stations has not been carried out.

Systematic analysis of the shellfish toxicity data, however, poses challenges common to many data sets whose sampling design reflects a different purpose than the proposed analysis. The highly effective monitoring program is carried out to protect human health and for maximum efficiency in managing commercially valuable fisheries. As such, it is not necessarily optimally designed for testing scientific hypotheses or statistical analyses. The same stations are not sampled every year, or necessarily sampled regularly, or randomly, either within a year, or from year to year over the decades. The same species are not always sampled. Both sampling frequency and location are often adjusted in response to developing toxicity events. Time and space gaps in sampling might be overcome by simple averaging to present dominant patterns. It is clear, however (Hurst and Yentsch, 1981; Luerssen et al., 2005), that toxicity is extremely variable in both time and space due to well documented extreme patchiness of cell densities during HAB events and by strong variability in toxin levels within the shellfish themselves (Shumway et al., 1994; White et al., 1993). Thus, sampling sites relatively close in geographic space may not exhibit the same toxicity history and simple averages over nearby stations may degrade or bias regional trends in time or space. This is especially true along a complex coastline like Maine's (Fig. 1), where highly localized effects should be expected. Grouping years or stations by toxicity characteristics requires a systematic, quantitative protocol.

Here we present a methodology for the extraction of dominant interannual and spatial patterns of coastal toxicity present in an extensive but gappy 21-year record from monitoring sites along a morphologically complex and hydrographically heterogeneous coastline. Multivariate statistics objectively quantify similarity, optimizing the temporal (interannual) and spatial (coastal geography) information in the historical record. We present climatological means/medians of 6 characteristics of annual toxicity. We then analyze the data for (1) recurring yearly patterns evident in magnitude and spatial pattern and (2) similarity in station interannual variability and any space pattern evident in these groups. We seek quantitative answers to four related questions regarding Maine coastal HAB toxicity events. Are there recurrent patterns of toxicity from year to year, or similar years, in terms of the spatial pattern of toxicity along the coast? Which stations behave similarly in terms of interannual variability? Do these stations map geographically into coherent regions? Using time series of annual means within similarly behaving station-groups, can we identify environmental variability consistently linked to shellfish toxicity events?

2. Regional background

The oceanography in the Gulf of Maine imposes a strongly seasonal and heterogeneous advective and mixing background within which *Alexandrium* ecology and toxicity events must be viewed. Residual circulation in the Gulf is generally cyclonic (see Fig. 1), broken, at least in summer months, into smaller cyclonic gyres over the deeper Jordan and Wilkinson Basins (Brooks, 1985; Pettigrew et al., 2005; Xue et al., 2000). Westward residual flow along the coast is divided into the Eastern Maine Coastal Current (EMCC) and the Western Maine Coastal Current (WMCC) (Fig. 1) (Pettigrew et al., 2005). The former is a strongly tidally mixed, cold flow with relatively strong alongshore velocities that extends along the eastern Maine shore from Grand Manan Island to approximately Penobscot Bay (Brooks and Townsend, 1989). At Penobscot Bay during summer, some fraction of EMCC water branches cyclonically offshore to form part of a recirculation around Jordan Basin, and the remaining fraction continues west along the coast (Pettigrew et al., 1998). Here the flow is joined by riverine input from larger Maine rivers to form the fresher, warmer (in summer), more stratified, but more diffuse Western Maine Coastal Current (WMCC) (Churchill et al., 2005). The WMCC flows cyclonically around Wilkinson basin, interacting with the western Maine shore and then the coasts of New Hampshire and Massachusetts. By late spring, heat flux, differences in tidal mixing and freshwater input create strong hydrographic differences between a warmer, more stratified and surface nutrient depleted surface regime west of Penobscot Bay and a colder, well mixed, more nutrient replete regime to the east (Townsend et al., 1987).

These features and their variability interact with the *Alexandrium* population in the Gulf and are a potential link between cell densities, their distribution and the coastal toxicity they impose. There is strong interannual variability in the spatial and temporal pattern of vegetative surface cells (Anderson et al., 2005c; Townsend et al., 2001, 2005), their benthic cysts (Anderson et al., 2005d) and toxicity events (Bricelj and Shumway, 1998; Franks and Anderson, 1992b). *Alexandrium* is widespread throughout the Gulf of Maine, is often present with maximum concentrations offshore, and is a consistent, although only episodically numerically dominant, member of the Gulf phytoplankton community (Townsend et al., 2001). Large concentrations of cells are often present in surface waters of the southern Bay of Fundy (Martin and White, 1988), immediately upstream from the Maine coast. Field work (Townsend et al., 2001) shows a strong spatial link between the well-mixed, nutrient-rich surface waters of the EMCC and elevated cell concentrations, suggesting that nutrient and light fields and interaction with the advective field are important in carrying cells downstream from a potential Bay of Fundy source. Early work (Franks and Anderson, 1992a, 1992b) along the western portion of the Gulf coast, hypothesized links of toxicity to local river input that modulates alongshore buoyancy-driven transport and its interaction with cross-shore wind-driven transport. A contrast between two years of strongly differing toxicity in western Maine coastal stations (Anderson et al., 2005b) showed the year with strong alongshore buoyant flow and downwelling winds to be significantly more toxic and over a larger geographic range than the year with upwelling-favorable winds and offshore transport. Select stations along the western Maine coast showed a link between their toxicity variability and interannual differences in the timing and strength of the surface temperature front separating colder EMCC water from warmer WMCC water (Luerssen et al., 2005), suggesting circulation, alongshore connectivity and delivery of cells to western regions from eastern sources may be important. Strong interannual variability is evident in the flux of water between the EMCC and the WMCC (Pettigrew et al., 2005).

3. Data and methods

The Maine DMR shellfish toxicity record for the 21-year period 1985–2005 has >64,000 records, spread over >350 different coastal stations, measured in >10 different species. Among these, over 58% are from the genus *Mytilus* (~38,000 records). To maximize our view of interannual variability and to reduce potential bias introduced by species-specific toxin uptake and depuration rates (Bricelj and Shumway, 1998), we focus our analysis on toxicity evident in *Mytilus*. Differing location names were resolved using maps and by communication with DMR operators. Each station was assigned a latitude and longitude location. Ambiguous and/or uncertain locations were discarded. Over the 21-year record, sampling frequency at an individual station varies, but is approximately weekly at the most regularly sampled "primary" stations (Bean et al., 2005). For each station, we bin average the toxicity record into 8-day periods, beginning January 1 within each year. These steps result in a 21-year time series of *Mytilus* toxicity at each station with a regular time step, but station-dependent irregular gaps due to the nature of the monitoring program. In the 21-year *Mytilus* record, toxicity was rarely (3 records) observed prior to March 1 or after November 1. The time series was truncated to this window providing 31 8-day time bins in each year at each station.

3.1. Metrics of interannual variability

We define 6 metrics quantifying annual toxicity characteristics at a station and set criteria for valid retrieval of each. Criteria are subjective but based on tests against numerous example station/year series. They reflect an attempt to balance usage of as much data as possible, minimize biased retrievals due to gaps, retain the definition of the desired metric and to stabilize retrievals in the face of some highly temporally variable signals by reducing the impact of single sample events. We use the DMR value of 80 μg toxin/100 g shellfish tissue as a toxicity threshold to define the metrics. Within each year, at each station, we attempt to quantify:

(1) *Date of 1st toxicity*: defined as the first day of the 8-day period when toxicity first exceeds the threshold. Successful quantification requires at least 1 record below threshold within the preceding two 8-day time bins, and toxicity that stays above 80 μg toxin/100 g for at least 2 periods over a 3 period interval. Not defined for years/stations with <10 measurements and assigned a value of 0 if the data allowed definition, but no events exceed the threshold.
(2) *Duration of toxicity*: valid retrieval requires both the Metric 1 criteria (above) defining a start date, and mirror criteria at the end of the season (a toxic sample followed by at least 1 below-threshold sample within the following two 8-day periods at the end of an above-threshold measurement). Not defined for years/stations of <10 samples, and assigned a value of 0 if the data allowed definition, but no events exceed the threshold that year.
(3) *Magnitude of maximum toxicity*: defined as the mean of the 3 maximum toxicity measurements in the year, calculated only in years/stations with ≥10 valid measurements.
(4) *Total annual toxicity*: sums all records over a year and defined only in years/stations with ≥5 valid measurements. Resulting annual values did not appear normally distributed, and further calculations were done on data transformed as $\log(x+1)$ to handle stations with 0 annual toxicity.
(5) *Date of maximum toxicity*: defined as the first day of the 8-day period with the maximum annual toxicity. Valid only if at least two below-threshold measurements are present at the beginning and end of the year to indicate the toxic season. A value of 0 is assigned if no events exceeding the threshold were recorded at a station/year.
(6) *Presence/absence*: a binary metric, assigned a value if any measurement is available for that station/year, defined as present if any measurement exceeds the threshold. Although a crude characterization of toxicity, this is a metric allows utilization of as much of the data set as possible.

The ability to extract each metric in any 1 year/station depends on the nature of gaps in the time series. Metric criteria range from those for which a metric is definable at many stations in most years (e.g. #4, #6), to more stringent metrics for which definition is possible only for stations/years of reasonably continuous sampling over a year (e.g. #1, #2). We apply these metrics in each year and produce six 21-year time series of interannual variability in toxicity for each station. Within each metric, stations for which a valid retrieval was not possible in at least 6 of the 21 years were discarded. Table 1 documents the number of stations for each metric that meet this criterion.

3.2. Year similarity: by station toxicity

Station time series for each metric remaining after the previous steps were used as input to a multivariate hierarchical cluster analysis to group years within the 21-year record according to similarity in each year's station toxicity characteristics. Two steps are required.

First, for each metric an appropriate measure of between-year separation is required. For metrics 1–5, distance (similarity) between years is defined as the Euclidean distance in multi-dimensional station toxicity space, a distance metric that preserves the absolute magnitude of each metric. For the binary data (metric 6) we use the simple matching coefficient (Everitt, 1979). Clustering requires input of separation distances between all possible year-pairs. Gaps in the data record for each metric, however, mean that distances between all possible pairs cannot be calculated and Euclidean distances are intolerant of any missing data. Within each metric, stations were filtered such that only those with a maximum of 2 missing years in the 21-year time series remained. These 1 or 2 gaps were judged to contribute negligibly to the 21-year definition vector and filled using an iterative approach that selected the median value from the 2, 4 or 6 stations closest in geographic space within the same year, whichever returned a valid measurement first. Stations that still had missing data after this approach were discarded from further analysis. This filtering reduced the number of stations contributing to the quantification of between-year separation for each of the six metrics to (1) 49, (2) 33, (3) 50, (4) 56, (5) 33 and (6) 59, respectively. The benefit, however, is that all years enter into the multivariate analysis.

Second, an appropriate algorithm for hierarchically clustering is required. Choice is somewhat subjective (Pielou, 1977, 1984). Comparison of dendogram results from a number of algorithms showed that some were better at forming separate clusters early in the procedure, with a clearly branching hierarchy, while others tended to sequentially adhere individual years to preformed agglomerations (Lance and Williams, 1967). The latter, while mathematically acceptable, offer little ecological insight. Comparisons between the former showed they tended to form similar year-groupings, at least at the closest branches (most similar years). A weighted pairwise average linking procedure was chosen. Dendograms for each metric were calculated, showing year-groupings. The choice of how many groups to allow (a stopping rule) is also somewhat subjective (Pielou, 1977; Strauss, 1982). Group linking in each dendogram was sliced at a distance that defined 3–4 distinct year-groups. Years that linked at distances further than this threshold were left ungrouped.

3.3. Station similarity: by interannual toxicity variability

Station time series for each metric were also used as input to multivariate hierarchical cluster analysis to group stations of similar interannual variability. For metrics 1–5 we use correlative distance to quantify station separation in multi-dimensional year-space. In contrast to Euclidean distance, correlation places weight on similarity of covariance rather than absolute magnitude of the

Table 1
Number of stations in cluster analysis for each metric and cluster results for station similarity by interannual toxicity variability.

Metric	# of stations with valid metrics in ≥6 years	# of stations entering cluster analysis	# of ungrouped stations after clustering	# of stations in each station-group				
				1	2	3	4	5
1	80	44	2	4	4	18	16	
2	70	40	3	4	10	23		
3	80	65	20	8	3	8	23	3
4	80	71	12	22	23	3	11	
5	74	40	2	3	6	18	11	
6	140	85	3	40	16	12	16	8

toxicity metric and has the benefit of being more tolerant of missing data. For the binary data (metric 6) we again use the simple matching coefficient. As above, gaps in the data record for each metric, however, mean that distance between all possible station-pairs cannot be calculated. For each metric, the diagonally symmetrical station-pair correlation matrix was populated by all pairs that had >6 years of record in common. The resulting matrix for each metric still had some missing between-station distances. The number of missing distances in each row of the matrix was examined, and the station with the most missing values removed. The matrix was then reconstructed and the procedure repeated. This was continued until the matrix had no missing data values. The number of stations surviving this procedure and entering the cluster analysis for each metric is given in Table 1. Weighted pairwise average linking produced dendograms for each metric and these were sliced at a distance that defined 3–5 distinct groups. Stations that linked at distances further than this threshold were left ungrouped. Table 1 summarizes the number of (a) ungrouped stations, (b) groups identified for each metric and (c) stations in each group.

3.4. Cluster significance examination

Testing the statistical significance of the station or year similarity and clustering is challenged by a number of issues including difficulty specifying appropriate null hypotheses, uncertainty of the sampling distribution of the distance metrics used and the failure of these data to meet key assumptions in dendogram significance testing used in other fields (Everitt, 1979). We examined statistical significance of the cluster results using two tests. The significance of between-station distances for each station-pair in the 2d matrix used as input into the clustering algorithm was tested using a bootstrap (randomization) approach (Strauss, 1982). For each station, years were randomized and all station-pair distances recalculated and recorded for 10 iterations providing a new set of randomized station-pair distances, the number of which varied by metric (minimum of 8400 values). These were ordered by value, and the value of the entry in the location 95% up the ranking is taken as the 95% significance level. Station-pairs from the original data that clustered into the same group were compared to this value. Results showed that over all 6 metrics, all station pairs within each of the groups identified by the cluster analysis are significant at the 95% level, providing an estimate of the expectation that such a pair would be as close (in the same group) by random chance. The null hypothesis that the observed clustering in the data (our choice of slicing distance) does not differ significantly from that which might occur by random chance was tested using another randomization approach (Harper, 1978). The number of dendogram linkage nodes up to the similarity threshold used to define the groups was compared to the number created in dendograms formed from 100 randomizations of the 21-year interannual vector at each station. The null hypothesis was rejected at better than the 99% confidence level for all 6 metrics, providing an estimate of the extent to which similarity expressed in the dendogram of the original data might be expected by chance.

Statistical significance of the year-groupings in the 6 metrics was also tested with the two bootstrap approaches. For the Strauss (1982) estimate of significance of the between-year separations of years within our identified groups, randomization produced a look-up-table of 1890 values. The dendogram for Metric 2 (Duration of Toxicity) showed a single year-group of statistical significance and a large number of years linking late in the hierarchy, beyond the 95% significance level. We choose not to interpret these data further. Across the remaining 5 metrics, the statistical data suggest that 90% of our entries (5 metrics $\times$ 21 years) linked within groups have linkages significant at the 95% level. The remaining 10% are identified and interpreted with caution in the results below. The Harper (1978) test of the null hypothesis that the number of dendogram linkages up to the similarity threshold used in the year clustering would occur by chance was rejected at better than the 99% level.

3.5. Environmental data

Annual fields of hydrographic data in the Gulf of Maine over the complete 21-year study period are not available. Even individual sites sampled by fully instrumented oceanographic buoys at do not span the study period. Select measurements indicative of some environmental conditions are available and these were acquired and extracted for comparison to interannual variability evident in station-group toxicity.

Satellite images of sea surface temperature (SST, 4-6/day) from the National Oceanic and Atmospheric Administration (NOAA) satellite series are available from 1985 to present providing measurements of both SST and temperature patterns indicative of surface circulation (Luerssen et al., 2005; Townsend et al., 2001). Each image is cloud masked, land masked and remapped to a standard projection over the study area with ~1.1 km spatial resolution. To reduce data volume, noise and gaps due to cloud cover, the image series is averaged into monthly composites beginning in January of each year. From these composites, a climatological monthly annual cycle is formed and a monthly anomaly time series calculated. We extract a number of monthly SST metrics from the image time series for each year (Table 2). These include SST anomalies averaged over a number of regions, differences in SST between regions as a potential indicator of varying circulation pattern, cross-shelf SST structure in the WMCC and EMCC regions and alongshore SST structure through the frontal region off Penobscot Bay (Bisagni et al., 1996; Luerssen et al., 2005) separating the colder EMCC from the warmer WMCC (Fig. 1).

Wind data are hourly records from the NOAA site at Matinicus Rock (Fig. 1). Examination of satellite scatterometer and model wind fields (not shown) over the inner Gulf of Maine show that on the monthly and interannual time scales of interest here, winds at this location can be taken as generally representative of overall conditions along the Maine coast. Records were converted, using standard oceanographic parameters, to wind stress vectors and U^{*3}, a non-directional index of wind mixing strength. The alongshore components of stress were calculated using the coastline orientation representative of the large-scale study area. Monthly and bi-monthly metrics of upwelling-favorable, downwelling-favorable, and mixing wind forcing in each year are calculated from these daily time series (Table 2). We use cumulative winds rather than means in an attempt to better capture the wind-forcing history of each month.

Daily river discharge data are available from the United States Geological Survey (USGS). On the interannual time scales of interest here, discharge from the largest Maine river, the Penobscot (Fig. 1) and other major Maine rivers are strongly correlated both in timing and volume. We used values from the Penobscot River as representative of interannual variability in Maine coastal river discharge. Interannual variability is characterized as total monthly discharge in calendar months and also as total cumulative discharge over the first 6 months of each year, a period that effectively captures the entire spring freshet, the dominant feature in the annual cycle.

Field data capable of quantifying Gulf of Maine interannual variability in circulation and hydrography do not extend back in time to cover the period 1985–2005. As a proxy, interannual variability in general circulation and hydrographic characteristics

Table 2
Environmental data time series examined for relationships to shellfish toxicity (monthly values in each year).

Field data	
SST anomalies	
(regional means)	EMCC, JB, WB, WMCC, Over whole Gulf of Maine coast
(spatial differences)	WMCC – EMCC (alongshore difference) WB – WMCC (western cross-shore difference) JB – EMCC (eastern cross-shore difference)
SST patterns	
Cross-shore gradient	WMCC to WB (western coastal region) EMCC to JB (eastern coastal region)
Alongshore gradient	Midcoast to EMCC (alongshore continuity of structure)
PenBay Frontal Zone	Summer frontal zone strength (local alongshore gradient)
Wind	Cumulative upwelling-favorable stress (also 2-months totals) Cumulative downwelling-favorable stress (also 2-months totals) Cumulative U^{*3} (mixing strength)
River discharge	Monthly totals January–June cumulative
Model-derived data	
Velocity (spatial means along transects, see Fig. 1)	
Alongshore	Averaged over entire coastal study area
Alongshore	At western coast (WMCC) At eastern coast (EMCC)
Cross-shore	At western coast (WMCC) At eastern coast (EMCC)
SST	EMCC, WMCC, JB, WB, Kennebec River mouth region
Salinity (0 m)	EMCC, WMCC, JB, WB, Kennebec River mouth region
Density (0 m)	EMCC, WMCC, JB, WB, Kennebec River mouth region
Velocity (at specific locations)	
Alongshore	EMCC, WMCC, Kennebec River mouth region
Cross-shore	EMCC, WMCC, JB, WB, Kennebec River mouth region
EOF Mode 1	
SST	Averaged over alongshore transect EMCC to WMCC Cross-shelf structure at EMCC Cross-shelf structure at WMCC
Velocity	Cross-shore (averaged along transect EMCC to WMCC) Alongshore velocity EMCC, WMCC

EMCC (Eastern Maine Coastal Current), JB (Jordan Basin), WB (Wilkinson Basin), WMCC (Western Maine Coastal Current), see Fig. 1.

over the 21-year study period is simulated using hindcasts from an operational version of the Princeton Ocean Model (POM) for the Gulf of Maine currently used for Gulf of Maine forecasts as part of the Gulf of Maine Ocean Observing System (Xue et al., 2005). The POM Gulf of Maine forecast system reproduces the seasonal variability of the Maine Coastal Current (Xue et al., 2005) and different circulation regimes from 1 year to another (Xue et al., 2008). The model hindcasts for the study period are forced with concurrent winds, heat and fresh water fluxes from the North American Regional Reanalysis (Mesinger et al., 2006) and concurrent satellite derived SST is assimilated to reinforce the surface heat budget. The hindcasts also include real daily river discharge from USGS and tidal harmonics to mimic the tidal regime in the Gulf of Maine. Such set-up captures a full range of variability in all local forcing. Subtidal open boundary conditions rely on climatological values derived from multi-years (2001–2005) of the NCEP's Coastal Ocean Forecast System. As a result, any interannual variability imposed by remote ocean forcing is absent from the hindcasts. As these effects will be strongest at depth and our metrics are extracted from the more strongly surface forced (wind, heat flux, freshwater) upper layers, while not eliminated, biases are minimized. From the 3-hourly hindcast time series over the 21-year study period, we calculate monthly average velocity, temperature, salinity and density fields from which to calculate various metrics of physical oceanography for comparison to the concurrent toxicity time series. A total of 25 different metrics of ocean structure were extracted from the monthly model fields in each year (Table 2). Spatial variability in small scale structure in many of the fields potentially biases interannual signals of samples extracted from the model at specific locations (or transects). To overcome this and extract dominant signals of interest, the time/space fields for some extracted model variables were decomposed using empirical orthogonal functions (EOFs) (Emery and Thomson, 2001). Monthly SST and velocity variability over the 21 year time series along three profiles is effectively summarized by EOF decompositions that separate the variance into a series of independent, uncorrelated modes, ranked from the highest mode that explains the largest percentage of the total variance, to smaller ones. Each mode has a spatial pattern, showing modal structure along the profile and an associated time series. The 1st mode of this decomposition isolates the dominant time/space pattern (Thomas et al., 2003) and its associated time modulation. In each case, this mode captured the seasonal cycle and its interannual variability, explaining 52–99%, depending on variable, of the overall variance. We use the EOF time series associated with these patterns as the signature of the time-varying model variable of interest for additional comparisons to the station-group toxicity time series.

3.6. Environmental links to toxicity

We calculate 21 annual values for each station-group defined by the multivariate analysis of Section 3.3. Metrics defining time (Metrics 1, 2 and 5) are represented by the median among stations making up the group, metrics with magnitude (Metrics 3 and 4) use means and presence/absence data (Metric 6) is represented as the proportion (as a percentage) of stations within each station-group that were toxic in each individual year. These produce a 21-year time series vector of toxicity variability representative of each group. Correlations are used to examine similarity between these and environmental interannual variability. To address the possibility (and poorly understood relationships) of time lag between environmental conditions and toxicity signal, we calculate cross-correlations between the annual values of the toxicity time series and environmental variables in each month over a 7 month period, February–August, that may potentially influence *Alexandrium* ecology and resulting coastal toxicity,. We avoid issues of unknown underlying data distributions by using the non-parametric Spearman rank order correlation, with associated quantifiable estimates of 90 and 95% significance levels (Sokal and Rohlf, 1998).

Calculation of multiple correlations to examine potential linkages between variables suffers from the unavoidable problem of increasing the probability of making a Type 1 statistical error. The default approach to addressing this issue is the Bonferroni correction. While reducing Type 1 errors however, this correction is known to be strongly conservative, doing so at the expense of significantly increasing the probability of making Type 2 statistical errors (Nakagawa, 2004; Narum, 2006; Perneger, 1998). Other approaches are possible (Narum, 2006) and here we use a bootstrap technique modeled after that shown by Barton et al. (2003). Briefly, with multiple correlation calculations, we expect to observe by chance some values above the statistical significance level (Type 1 errors). If we see many, especially if they are grouped within a single environmental variable rather than apparently random occurrences, we wish to estimate the probability that the observed number and pattern of these significant correlations could occur by chance. For each instance where an apparently large number of significant correlations occur between an environmental variable and station-group toxicity variability, we assume that there should be no relationship between toxicity in 1 year and the environmental variable value in question from different years. We randomize the environmental variable time series and calculate its correlation to each station-group toxicity time series for 1000 iterations, building a ranked look-up-table of correlations and the number of instances a significant relationship occurs to derive a 95% confidence level. We then compare the number of instances of random correlations to those observed in the actual data correlations to estimate the probability that the observed number could occur by chance. We focus only on those toxicity record/environmental metric comparisons that return a larger number of significant correlations than the bootstrap 95% significance value.

4. Results

4.1. Climatological spatial patterns of toxicity

Climatological averages of each of the 6 metrics at each station and their associated interannual variability (Fig. 2a and b) provide a summary of regional toxicity characteristics and their relative stability over the 21-year study period. To provide broad coverage, a value is formed for any station with six or more values. These present a quantitative baseline against which interannual variability and future toxicity patterns can be viewed.

Timing of 1st toxicity (Metric 1) is earliest in the Casco Bay region (~days 115–130), slightly later in the mid-coast and western coastal regions (days 130–160), and latest in the extreme eastern stations and Cobscook Bay (days 160–220). Variability in timing is strongest in the stations along the western coast and some of the stations on the outer (seaward) edge of Casco Bay. Variability is small within Casco Bay, most of the mid-coast stations, and those in the far eastern portion of the study area. Duration of toxicity (Metric 2) has a less distinct geographic pattern. Most stations along the western coast average relatively long time scales, as do many in the Cobscook Bay area. In Casco Bay and the mid-coast region, duration of toxicity appears strongly station specific, with generally shorter durations at stations closest to Penobscot Bay. Variability about these means is also strongly spatially variable. The magnitude of maximum toxicity (Metric 3) shows relatively clear geographic pattern, with highest values (>170 μg/100 g) along the western coast and in the far eastern and Cobscook Bay area and lowest values in the center of the study area at stations closest to Penobscot Bay (<70 μg/100 g). Stations in the mid-coast and Casco Bay regions have intermediate values, with a tendency for those on the outer edge of Casco Bay to be higher than those on the mid-coast or inside Casco Bay. Variability about these means is strongest all along the western coast and Casco Bay area, intermediate along the mid-coast and Cobscook Bay regions and weakest in the vicinity of Penobscot Bay. Total annual toxicity (Metric 4) also shows clear patterns of highest values along the western coast, outer stations of Casco Bay and throughout the far eastern and Cobscook Bay stations. Intermediate value means are present at stations inside Casco Bay and along much of the mid-coast area, with weakest values at stations adjacent to Penobscot Bay. Variance about these means generally follows a similar pattern with the exception of Casco Bay, where the high values have less variability than those along the western coast and Casco

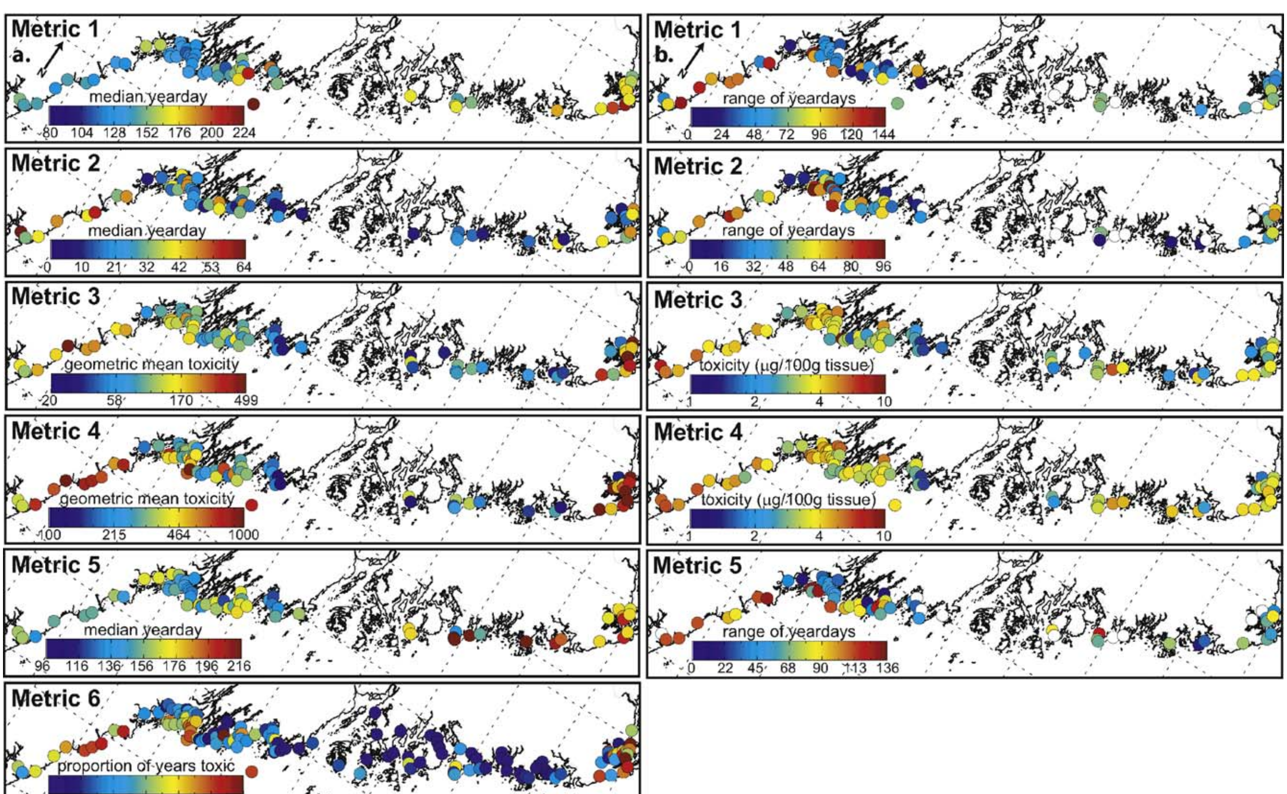

Fig. 2. Maps showing (a) (left column) climatological (21 years) values at each station of each of the 6 metrics (see Section 3.1) of shellfish toxicity annual variability and (b) (right column) the variability associated with these means. Variability is not calculated for Metric 6, the binary measure of presence/absence. Note the orientation of the maps has been rotated to conserve space.

Bay. Mean date of the annual maximum (Metric 5) has patterns generally similar to date of 1st toxicity (Metric 1), with earlier dates along the western coast and Casco Bay (~day 156), intermediate in the mid-coast area, and latest dates at stations east of Penobscot Bay (after day 170). Variability about this date is maximum along the western coast and stations along the outside of Casco Bay and in the mid-coast, weakest at stations deep in Casco Bay and in Cobscook Bay. We present the climatology of presence/absence of toxicity (Metric 6) as the proportion of years with a valid record that were toxic. There is a clear geographic trend for those stations along the west coast and those in Cobscook Bay to have the highest values (>60%), along with a group of stations at the eastern end of Casco Bay near the mouth of the Kennebeck River. Stations in and near Penobscot Bay and along the eastern coast have the smallest values (often <15%). Stations in the mid-coast and throughout the remainder of Casco Bay have intermediate values (30–50%).

4.2. Year similarity: by station toxicity

Results of clustering the years according to similarity in station toxicity are presented in Table 3, showing each year's group membership for each metric. Characteristics of each group are presented as maps (Fig. 3a–e) showing the geographic pattern of station toxicity averaged over the years within each year-group.

4.2.1. Timing of 1st toxicity (Metric 1)

Using this metric, years cluster into 3 groups (Table 3), with 3 years left ungrouped. Geographic patterns are characterized as the median date of 1st toxicity at each station within the grouped years (Fig. 3a). The largest group (Group 1) extends almost continuously from 1992 through 2004. The mapped medians for this group show that these are years when station median dates are zero (toxicity never develops). Years in Group 2 also have many stations whose medians are zero, located primarily in the mid-coast region, but also have some stations especially along the western coast where the median rises over day 90. Group 3 is of 2 years when virtually all stations have median start dates >0 and these occur relatively late in the season (> day 120). Ungrouped years 1985 and 1988 (not shown) link at distances beyond the 95% significance level, but subsequently link into Group 2 and so are most similar to these years. The year 1987 linked last in the dendogram, indicating station toxicity patterns dissimilar from all other years. This year (not shown) had a mix of stations including both relatively late start dates (> day 180) and day 0 (no toxicity), often among close neighbors, strongly dissimilar from other years and forming no easily described geographic pattern.

4.2.2. Duration of toxicity (Metric 2)

Year-groups are not statistically significant.

4.2.3. Magnitude of maximum toxicity (Metric 3)

Four year-groups are identified with 1 year remaining ungrouped at the chosen stopping level (Table 3). These 4 groups can be generalized as 2 of years with reduced/weak toxicity and 2 of years with elevated toxicity (Fig. 3b). Group 1 is composed of years of minimum toxicity across the entire region and many stations that fail to become toxic at all. In this group, the mean exceeds the 80 μg/100 g toxicity threshold at only 1 station and of those stations that do show toxicity, the mean is <50 μg/100 g. Years in Group 2 are also years of weak toxicity, but show a pattern of greater concentrations than Group 1, with most stations showing some toxicity. Stations in the mid-coast region have low mean toxicity in these years, with toxicity >80 μg/100 g only occurring along the western coast and in the far eastern end of the study area. Group 3 is composed of the most toxic years, with means of most stations exceeding 100 μg/100 g. Many stations, especially those along the western coast and in Casco and Cobscook Bays have means exceeding 300 μg/100 g. No stations included in this analysis average zero toxicity in these years. Group 4 is also of years with high toxicity, but is characterized by a few stations that do average zero toxicity, and others of generally weaker toxicity than those in Group 3. Station patterns in the ungrouped year (2000) show high toxicity at stations within Casco Bay (like Group 3), mid-coast station toxicity levels similar to Group 4, but with many more stations with zero toxicity than

Table 3
Membership of each year-group for each toxicity metric.

Toxicity metric	Year groups↓	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	00	01	02	03	04	05
1	1								X		X	X	X	X	X	X		X	X	X	X	
	2						X	X		X							X					X
	3		X			X																
	UG*	X		X	X																	
3	1												X	X		X		X	X			
	2	X							X		X	X			X					X		
	3		X		X	X	X															X
	4			X				X		X											X	
	UG																X					
4	1												X	X		X		X	X			
	2	X							X		X	X			X					X		
	3		X		X	X																X
	4			X			X	X		X											X	
	UG																X					
5	1							X		X							X					
	2	X							X		X	X	X	X	X	X		X	X	X		
	3		X		X	X	X															X
	UG			X																	X	
6	1	X						X	X		X	X	X	X	X	X		X	X	X		
	2						X										X					X
	3		X	X	X	X				X											X	

*UG: ungrouped years that do not cluster at the significance level.

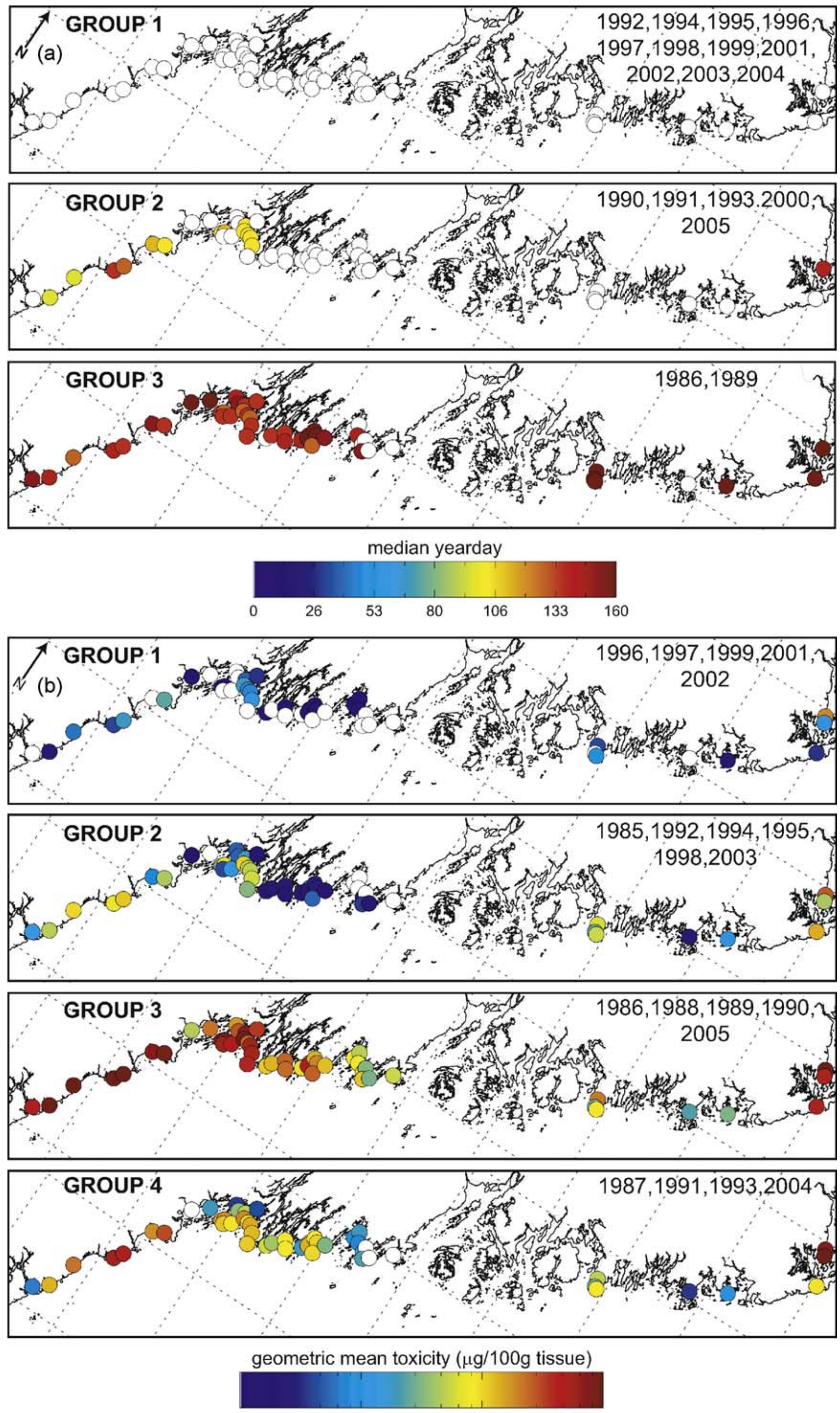

Fig. 3. (a) Year-group results of the multivariate analysis assessing year similarity based on station toxicity characteristics for Metric 1, the date of first toxicity. At each station, maps show the median yearday of first toxicity within the years of each of the 3 identified year-groups. White indicates a median start day of 0 (no toxicity development). Note the orientation of the maps has been rotated to conserve space. (b) The same as (a), but for Metric 3, the magnitude of maximum toxicity. Maps show the means at each station within each of the 4 clustered year-groups. White stations are those for which the group mean over the years is zero. (c) The same as (b), but for Metric 4, total integrated toxicity over a year. (d) The same as (a), but for Metric 5, date of annual maximum in toxicity. (e) The same as (a), but for Metric 6, presence or absence of any toxicity in a year-group. Maps show the proportion of years within each of the 3 identified year-groups that a station has toxicity.

either of these groups, including zero mean toxicity at far eastern stations.

4.2.4. Total annual toxicity (Metric 4)

Four year-groups are identified, with 1 year remaining ungrouped (Table 3). Both year-groupings and spatial pattern (Fig. 3c) are similar to those of Metric 3. Group 1 is composed of years when the majority of stations did not exhibit toxicity and the few stations that have toxicity average relatively low levels. Group 2 also has many stations with no toxicity, but fewer than the years in Group 1. Those stations with toxicity tend to be similar to those of Group 1, but average higher levels. Group 3 is of those years with the largest total annual toxicity. All stations exhibit means above zero and all stations along the western coast, in Casco Bay and the far eastern end of the study area average total annual toxicity >1000 μg/100 g in these years. Group 4 is of years with slightly weaker mean toxicity

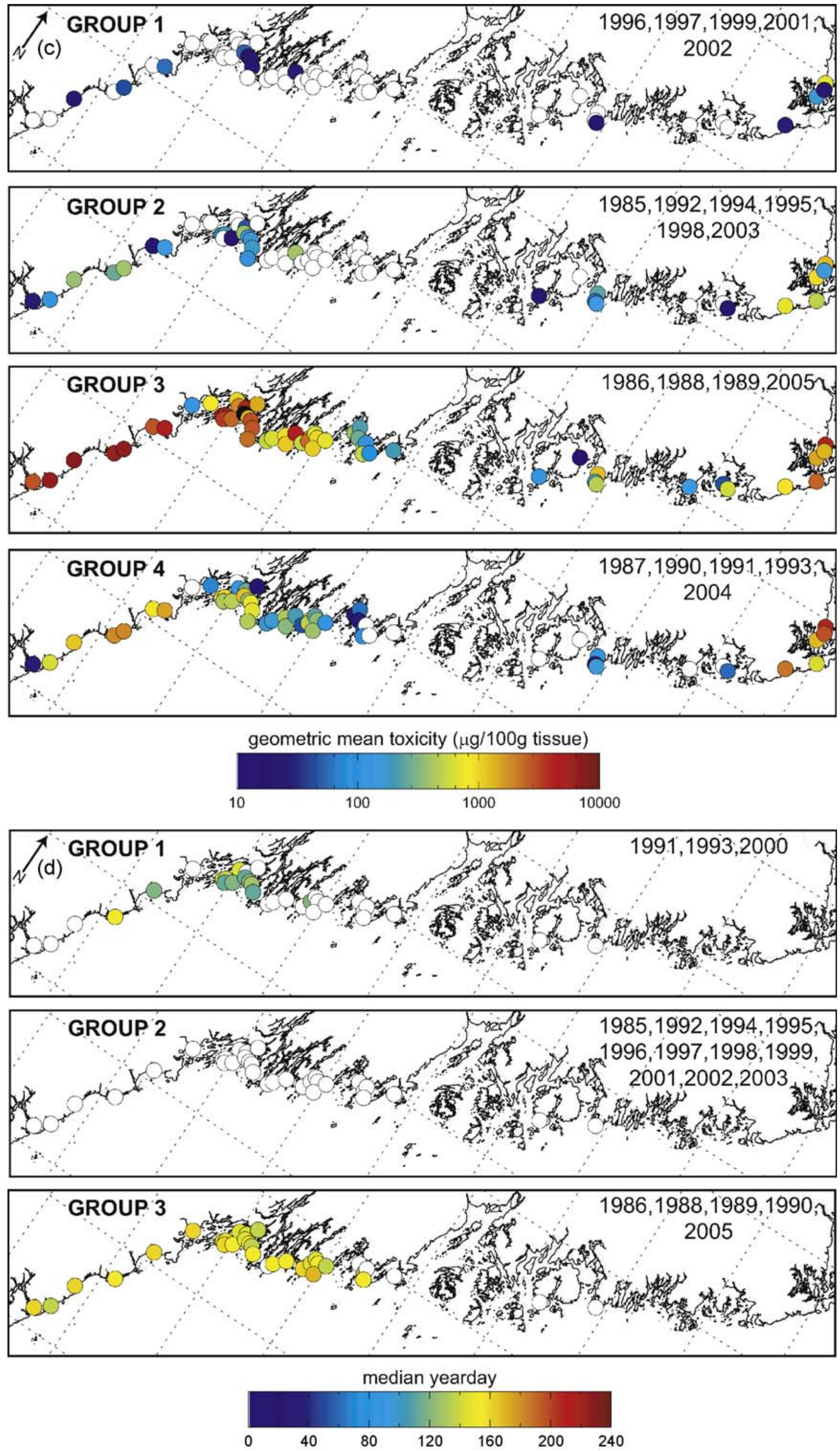

Fig. 3. (*Continued*)

than years in Group 3, with occasional stations having means of zero. Highest means are along the western coast and in the far eastern end of the study area (mostly >1000 μg/100 g). As in Metric 3, the year 2000 (not shown) has a significantly different toxicity geography and is left ungrouped. The station pattern in 2000 shows high toxicity in the Casco Bay region (similar to Group 3) but with more stations of zero toxicity and no toxicity in the far eastern stations.

4.2.5. Date of maximum toxicity (Metric 5)

Clustering results in 3 major year-groups (Table 3). Two years link late in the hierarchy and are not assigned to a group. No stations from the eastern end of the study area make it into the analysis. We characterize the station pattern as the median date of maximum in the years within each group (Fig. 3d). Group 1 is composed of 3 years when a number of stations have medians of zero (no date due to no toxicity), with other stations, primarily in the Casco Bay area, having medians mostly ~ day 120. Group 2 includes a large number of years. The map shows that median dates at all stations over these years have values of zero. Group 3 is of years with later dates of maximum. Most stations along the western coast and along the mid-coast and outer Casco Bay area have median dates ~ day 160. The ungrouped years (1987, 2004, not shown) are characterized by significantly later dates of maximum (many ~ day 200) than those in Group 3.

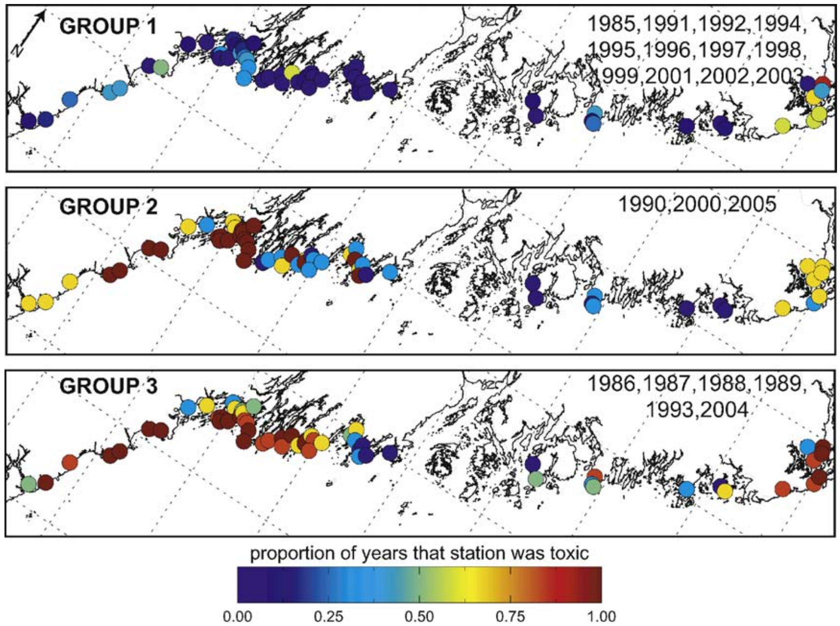

Fig. 3. (*Continued*).

4.2.6. Presence/absence (Metric 6)

Clustering assigns years into 3 groups based on simple presence or absence of toxicity (Table 3). Stations throughout the study area contribute to the analysis. Geographic pattern is presented as the proportion of years within the year-group with a positive (toxicity present) return (Fig. 3e). Group 1, the largest group, is of years with a large number of stations with low proportions of years with toxicity present. Stations in the mid-coast area and many in Casco Bay have toxicity in less than 25% of the years, and most stations have toxicity in less than 50% of the years. Both Groups 2 and 3 have a large number of stations that are toxic in 100% of the years. The primary difference between these groups appears to be their geographic pattern. Group 2 is composed of years when most of the stations in Casco Bay exhibit toxicity and stations in Cobscook Bay have less frequent occurrence. Group 3 is of years when fewer Casco Bay stations have 100% occurrence but the % occurrence in stations of Cobscook Bay is higher. Both Groups 2 and 3 show 4–5 stations along the western Maine coast reaching 100% occurrence.

4.3. Station similarity: by interannual toxicity variability

We present results of clustering the stations according to their interannual co-variability as maps (Fig. 4a–f, i and ii) showing station position and group affiliation in two views, the whole study area (i) and a close-up (ii) of the most densely sampled area in the Casco Bay – mid-coast region (Fig. 1).

4.3.1. Timing of 1st toxicity (Metric 1)

Relatively few stations entered the cluster analysis due to stringent definition criteria, with four major station-groups identified (Table 1). Geographic pattern of most of these groups shows strong regionalization (Fig. 4a). Group 1 is composed of stations at the eastern (upstream) end of the study area, all east of Penobscot Bay. Group 2 is restricted to stations in the midcoast area between Casco and Penobscot Bays. Group 3, although concentrated in the Casco Bay region, is the only truly cosmopolitan group, with members spread over the entire study area. Group 4 is composed of stations located entirely from the downstream portion of the study area, to the west of Penobscot Bay. Also of interest, Group 4 does not include any stations from the inner parts of Casco Bay or deep within other bays/inlets.

4.3.2. Duration of annual toxicity (Metric 2)

Definition criteria for this metric are also relatively restrictive and result in the fewest stations entering the cluster analysis (Table 1). Three station-groups cluster in interannual variability space, but only one group shows strong localization in geographic space (Fig. 4b). Group 1 is composed of 4 stations spread over the width of the study area. Group 2 is strongly localized in the mid-coast region, with stations generally located on the outer, more exposed, portions of the coast. Group 3 is primarily composed of stations west of Penobscot Bay, in Casco Bay and extending to the southern part of the study area. Two stations along the outer eastern coastline get included in the group.

4.3.3. Magnitude of maximum toxicity (Metric 3)

Many stations enter this analysis. Five station-groups are clustered and a number of stations dissimilar from any of the major groups are identified (Table 1). The groups separate well in geographic space (Fig. 4c) Groups 1 and 2 are located in the eastern part of the study area with Group 1 spread along the outer coast and Group 2 in Cobscook Bay. Group 3 is localized strongly in the eastern portion of Casco Bay. Group 4 represents a large group of stations spread over the western portion of the study area, beginning immediately west of Penobscot Bay and reaching to the western edge, with a single station from the east included. Group 5 is composed of only 3 stations with no obvious geographic pattern. Many other stations (19) entered the multivariate analysis, but differing interannual variability excluded them from clustering at significant levels.

4.3.4. Total annual toxicity (Metric 4)

Definition criteria allowed a substantially larger number of stations to enter this cluster analysis. Four station groupings are identified with a number of stations isolated as dissimilar from any of these groups (Table 1). In geographic space, each is strongly localized (Fig. 4d). Groups 1 and 2 represent the western study area, with some overlap. Group 1 is dominated by stations located in the mid-coast region between Penobscot Bay and Casco Bay. Group 2 stations represent areas to the west of Group 1, beginning in the mid-coast region, especially in eastern Casco Bay, and extending along the southern Maine coast to the western edge of the study area. Group 3 is comprised of only 3 stations, each in the mid-coast region

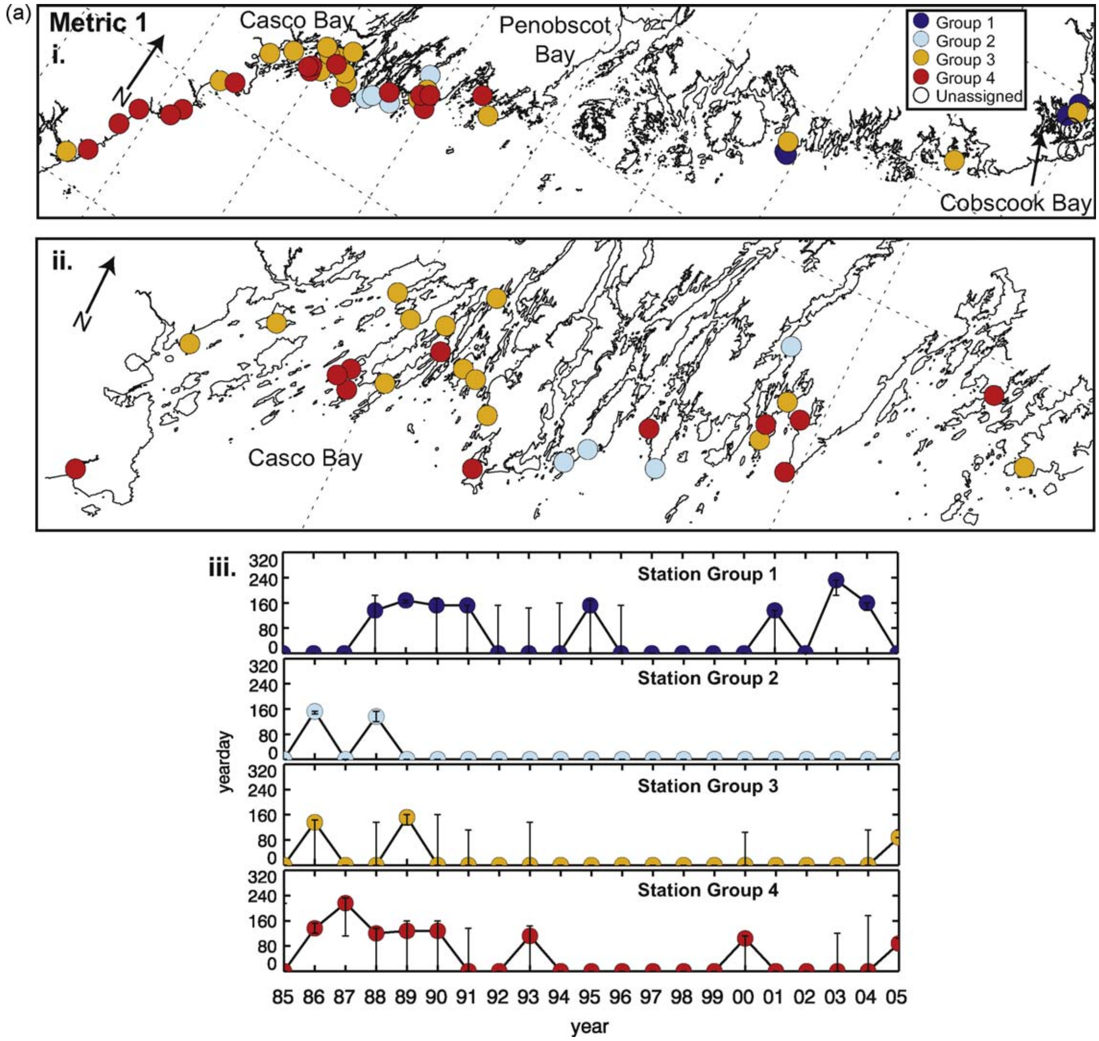

Fig. 4. (a) Maps showing station-group membership and location resulting from the multivariate analysis of station similarity based on toxicity interannual variability for Metric 1, date of the first toxicity event of the year. Maps show patterns (i) across the whole study area and (ii) the same data enlarged over the Casco Bay/mid-coast region of high station density. The lower panels (iii) show interannual variability over the study period for each station-group as the median of member stations each year. Whiskers on each station-group annual value are 50 percentile values. (b) The same as (a), but for Metric 2, the temporal extent of annual toxicity. (c) The same as (a), but for Metric 3, the maximum annual toxicity. Whiskers on each station-group annual value are standard deviations. (d) The same as (a), but for Metric 4, total toxicity over the year (annual integral). Whiskers on each station-group annual value are standard deviations. (e) The same as (a), but for Metric 5, date of annual maximum in toxicity. (f) The same as (a), but for Metric 6, presence/absence of any toxicity in a year (a binary metric). The annual value for each station-group (iii) is the proportion (0–1) of member stations that are toxic in each year. No measurement of station-group variability in each year is calculated.

and each relatively deep in bays, isolated from the open Gulf of Maine. Group 4, with 1 exception, is comprised of stations far to the east in the study area, including many stations in Cobscook Bay.

4.3.5. Date of annual maximum (Metric 5)

Four station-groups are identified by clustering of this metric (Table 1). Geographically (Fig. 4e), Group 1 is restricted to a strongly localized part of the eastern Maine coast represented by 3 stations. Group 2 is located from Casco Bay into the mid-coast region, overlapping Group 3 stations which are strongly concentrated in the mid-coast and Casco Bay area. Group 3 also includes one station far to the east and another immediately west of Casco Bay. Group 4 is dominated by stations from Casco Bay and the western coastline, but includes two stations from the east.

4.3.6. Presence or absence (Metric 6)

The relaxed criteria of this binary metric allowed the most stations to enter the multivariate analysis (Table 1). Five main station-groups of similar interannual variability are identified. In space (Fig. 4f), each has strong geographic coherence. Group 1 is the most cosmopolitan, dominated by stations along the eastern coast (but only one in Cobscook Bay) and mid-coast, including four stations deep inside Casco Bay. No stations west of Casco Bay are members. Three of the station-groups represent stations from the western half of the study area, all west of Penobscot Bay. Group 2 is dominated by stations in the mid-coast area and the inner regions of Casco Bay. It includes two stations in the extreme west of the study area. Stations in Groups 3 and 4 are concentrated in Casco Bay and the western coastline, but include a few representatives immediately east of Casco Bay. In the final group (Group 5), all stations are located in the extreme east of the study area, many within Cobscook Bay.

4.4. Interannual toxicity variability of station-groups

Spatial pattern of station-groups identified in Section 4.3 indicates the clustering isolates potentially useful bio-geographic information. Mean interannual variability within each station-

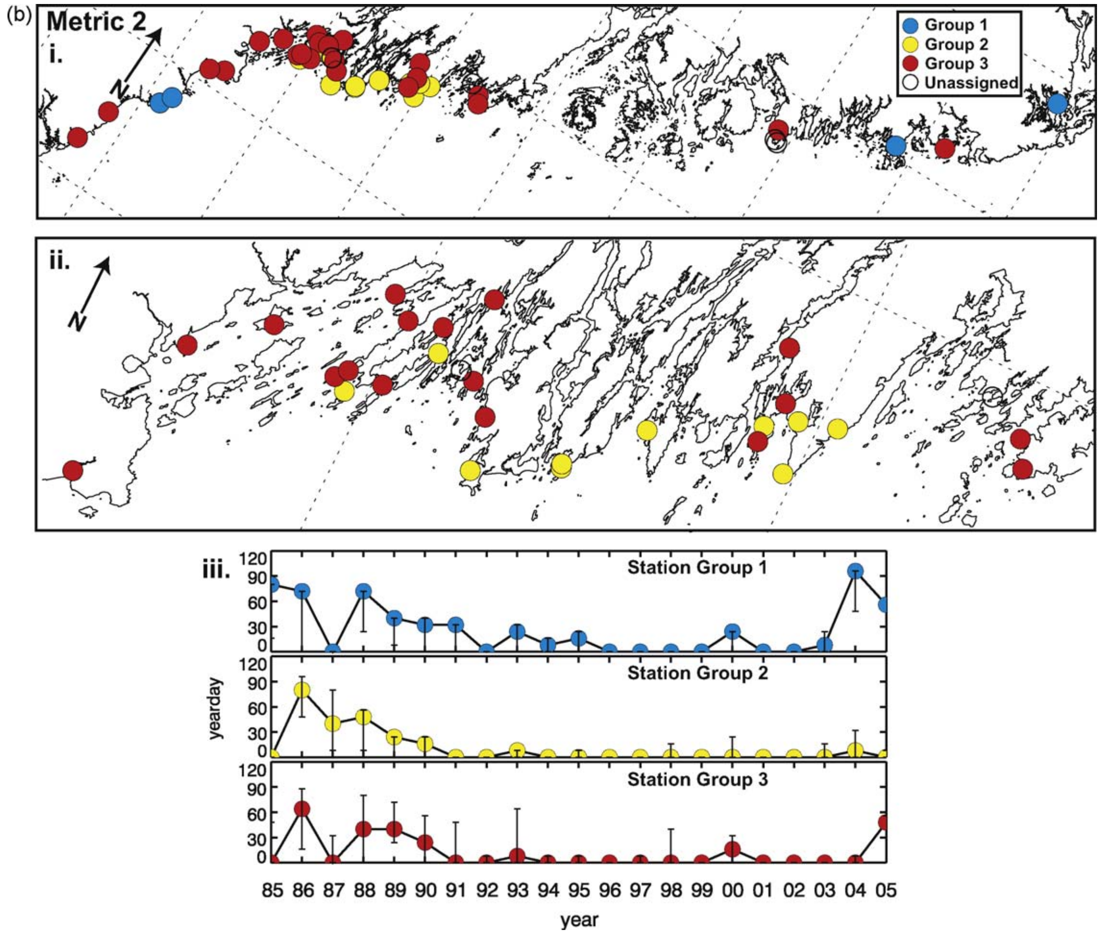

Fig. 4. (*Continued*)

group is presented as a time series over the 21-year study period (Fig. 4a–f, iii).

4.4.1. Timing of 1st toxicity (Metric 1)

Interannual variability in the timing of initial toxicity of the four major station-groups (Fig. 4a), shows two similar groups (Groups 2 and 3) that have most years in the 1990s and early 2000s within which most stations have no start date (they do not become toxic). Differences between these groups are in (1) the 1988–1989 period, (2) the variability between stations in each year (Group 2 has virtually no variance in years of 0 start date, Group 3 does) and (3) the delayed start date in 2005 evident in Group 3. Group 1, representing 4 stations in the eastern part of the study area, exhibits the latest start dates, averaging days 120–160 in the period 1988–1991 and 3 years at the end of the series (2001, 2003, and 2004) also with late start dates. Group 4, composed primarily of stations west of Penobscot Bay and dominated by stations along the western and mid-coast, is distinguished from Group 1 by later start dates in the late 1980s and more years with no (or very early) start dates at the end of the time series.

4.4.2. Duration of annual toxicity (Metric 2)

The mean interannual variability for each of the three groups (Fig. 4b) shows Group 1 stations have the longest durations and a have quantifiable toxicity duration in the most years. Stations in this group, however, are geographically scattered. Groups 2 and 3 are both dominated by stations west of Penobscot Bay with Group 2 localized to the mid-coast area. Both have time series that show longer durations in the 1980s and average much shorter (or zero) durations after this. The strongest difference between Groups 2 and 3 are toxicity durations during 1987 and 2004–2005. Both are distinguished from Group 1 by fewer years with a quantifiable event duration.

4.4.3. Magnitude of maximum toxicity (Metric 3)

The interannual vector of each of the five station-groups (Fig. 4c) shows that both Groups 1 and 5 had relatively low values throughout the time series and a number of years with values of 0. These stations are primarily located along the exposed portion of the east coast (Group 1) and scattered in the midcoast – Casco Bay areas (Group 5). Groups 2–4 have many years with high toxicity, especially in the 1980s and early 1990s. The primary difference between these groups is strong differences in the maximum toxicity values reached in the period 1999–2001. All station-groups show a general tendency for elevated levels early and late in the time series, with reduced values in the late 1990s.

4.4.4. Total annual toxicity (Metric 4)

Interannual variability within each of four identified groups (Fig. 4d) shows both western station-groups (1 and 2) are relatively similar. The primary difference between these groups is decreased toxicity in the mid-coast Group 1 in the mid-late 1990s compared to higher values throughout the study period in the more western Group 2. Both show elevated toxicity in the early part of the time series, a decrease until 1999, and an increase in the late part of the time series. Variability for Group 3 (only 3 stations, all within deep bays), is stronger than that of the other 3 groups and includes a number of years of no toxicity. Within Group 4 (eastern-most

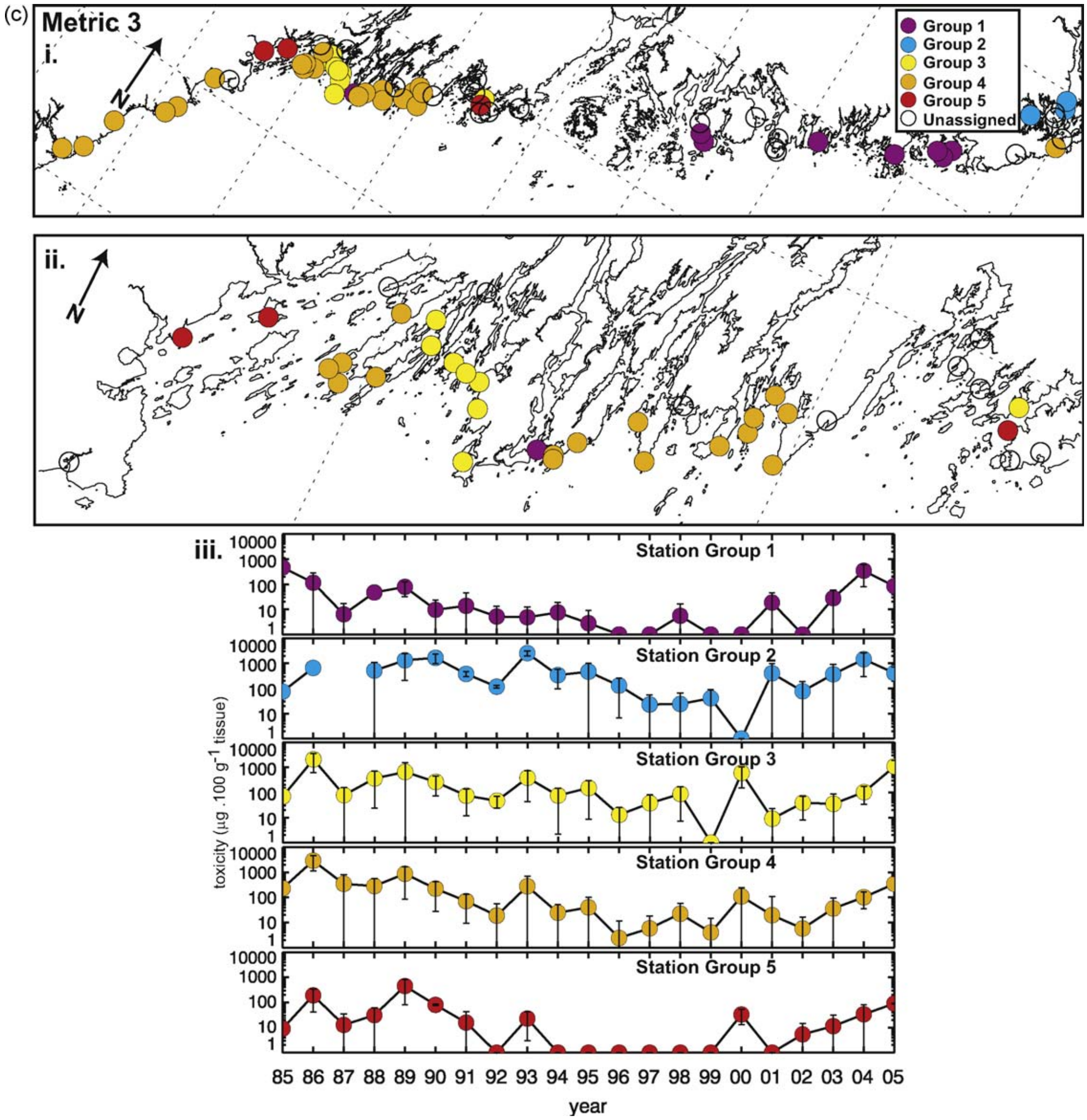

Fig. 4. (*Continued*)

stations), toxicity is highest of all groups, generally similar to Groups 1 and 2 early in the time series, with increasing differences towards the end of the time series (1998 and after).

4.4.5. Date of annual maximum (Metric 5)

Variability of date for the four station-groups (Fig. 4e), shows both Groups 1 and 2 are dominated by many years, especially in the mid-late 1990s, with no date of annual maximum (most of the stations in the group do not become toxic). Groups 3 and 4 have later dates of maximum, especially early in the time series. Of these, Group 4, comprised largely of stations to the far west, has the most years with a defined date of annual maximum, primarily in the first half of the time series.

4.4.6. Presence or absence (Metric 6)

Mean interannual variability in each of the five station-groups is presented as the proportion of stations within each station-group that were toxic in each individual year (Fig. 4f). The most cosmopolitan group (1) is dominated by relatively low values throughout the time series and a large number of years with no toxicity present, especially in the 1990s. Group 2, dominated by stations in the mid-coast and Casco Bay, also had a number of years with 0 (or very low) proportions, but has higher values in the early part of the time series than Group 1. Group 3 stations, primarily from Casco Bay and the western coast have the highest proportions over the years among the 5 groups, with only 1 year (1992) below the 50% value in the first 11 years of the time series, and only 1 year with 0 (1999). Over many years, 100% of these stations exhibit toxicity. Group 4 appears to covary with Group 2, but has many years of reduced proportion. Group 5 are all located in the far eastern portion of the study area and have a distinct interannual pattern. Years appear to have either very high proportions of stations that are toxic or very low proportions, with few intermediate values. Values are high in the first half of the study period (1985–1995) and again at the end of the study period (2001–2005) separated by a 5-year period of low proportions in the late 1990s.

4.5. Station-group toxicity relationships to environmental variability

Calculation of the interannual toxicity vector for each station-group (Fig. 4) allows comparison to interannual variability evident in various available concurrent environmental variables (Table 2) suggested from past work to be potentially important in development of toxicity. Most of the environmental variables we examined do not pass our bootstrap significant test, indicating no correlation with toxicity variability of the station-groups over

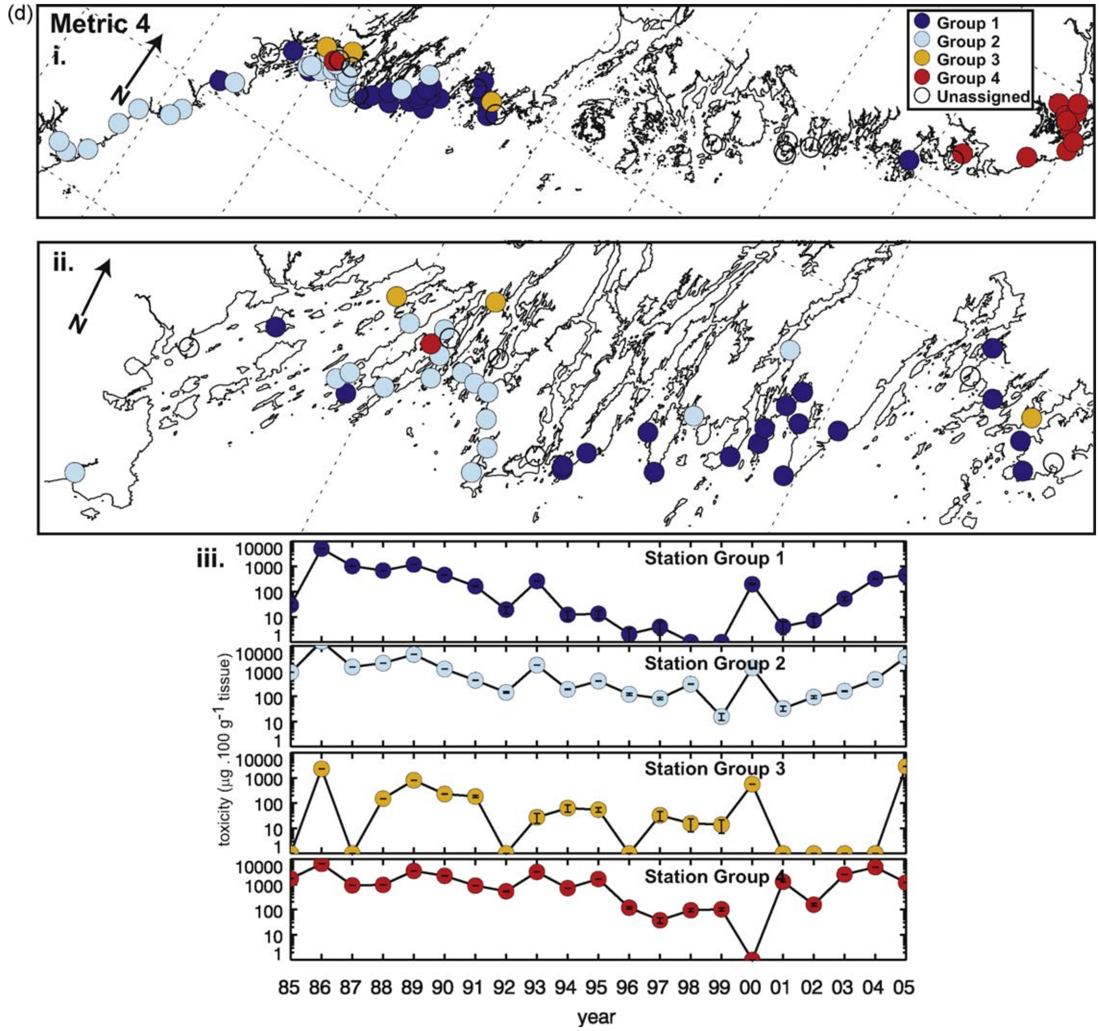

Fig. 4. (*Continued*)

the 21-year record. Select correlation results (Table 4) highlight those significant at >90%.

Results show significant negative correlation between western Gulf of Maine (WMCC) cross-shelf SST gradient (see Fig. 1) in June and July and toxicity variability in many metrics across many station-groups (Table 4). Interannual variability in WMCC cross-shelf SST gradients for the months April, May and August (and February–March, not shown) are not significantly correlated with variability in toxicity within any of the station-groups from any of the metrics. Winter and early spring months (February–April) not only precede the onset of any toxicity but also have very weak SST patterns. Lack of significant correlations in May and August, when stronger SST structure is present, however, provides a non-quantitative check on the potential occurrence of spurious correlations. Beginning in June (Table 2), and increasing in July, systematic correlations between monthly cross-shelf SST structure and toxicity metrics are present. Five station-groups, one in each toxicity metric, are significantly correlated with June cross-shelf SST gradients. In July, 10 of the 25 station-groups are significantly correlated with cross-shelf SST gradients over the 21-year study period (others are weakly correlated). The negative correlation values are indicative of covariance between relatively warmer coastal SST (and/or colder open Gulf SST) and increased toxicity metric values. Comparisons to space patterns (Fig. 4) show this relationship exists only for station-groups geographically located in the western portion of the study area.

Significant negative correlations also exist for these station-groups and cumulative upwelling-favorable wind stress in June–July (Table 4). The negative values indicate association of increased upwelling in this period with years of reduced toxicity metric value, oceanographically consistent with the correlations observed for cross-shelf SST patterns (increased coastal upwelling induces colder coastal SST). We observe significant positive correlations between cumulative downwelling-favorable wind stress early in the season (both March–April and April–May) and toxicity events at these same western station-groups. These correlations disappear by summer. There is a suggestion that increased cumulative monthly wind mixing in March is associated with reduced toxicity (many weak negative correlations). In July, these negative correlations increase in both significance and the number of station-groups showing relationships. Consistent with the previous significant correlations, these are present only for western station-groups, and suggest increased wind mixing reduces toxic events at these stations. The July correlations in mixing strength are likely associated with the upwelling wind stress discussed above.

A wide assortment of other available field-based environmental variables examined (Table 2) do not have significant correlations with the station-group toxicity interannual variability. Two examples are shown in Table 4; Wilkinson Basin SST anomalies and 6-month cumulative river discharge. Although a few correlations appear significant, they do not exceed our bootstrap

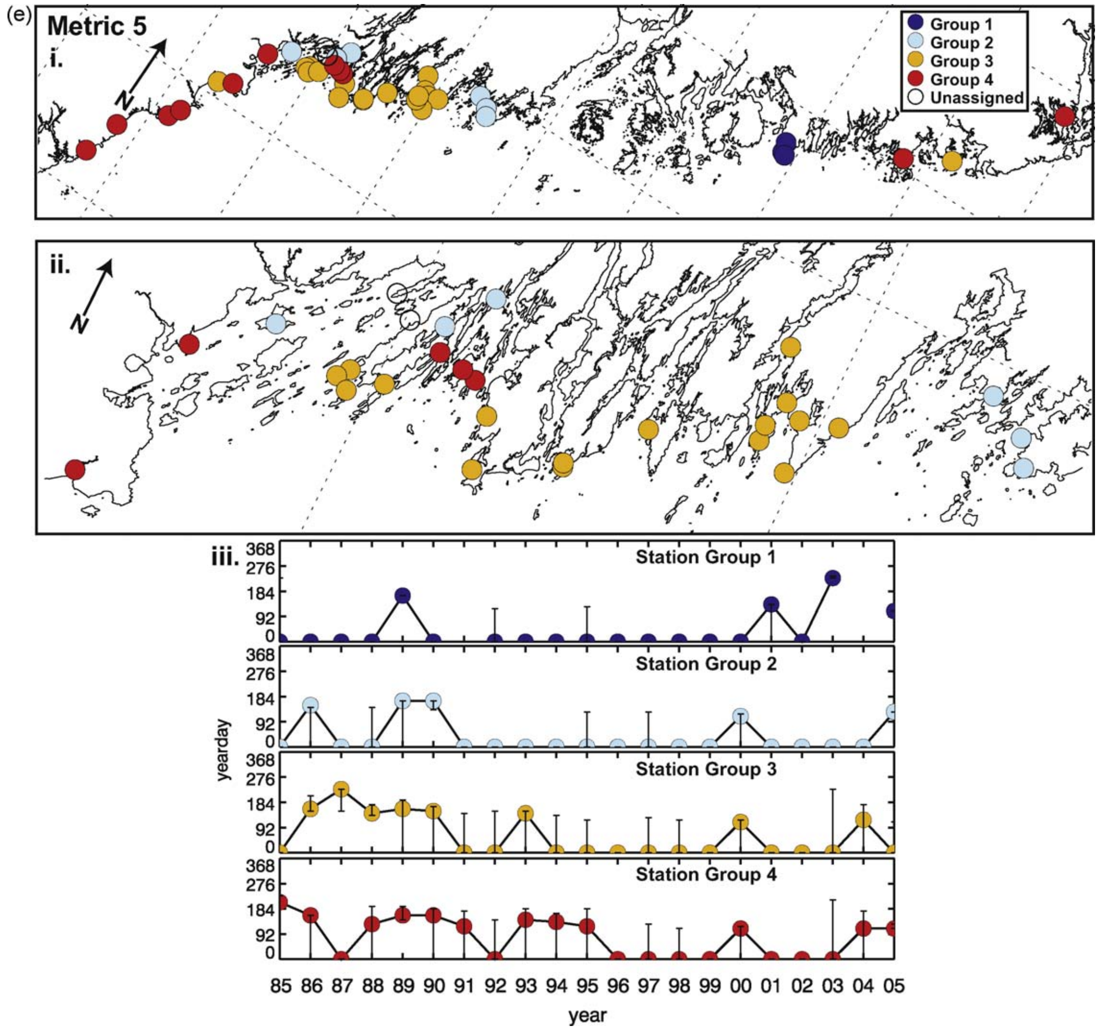

Fig. 4. (*Continued*)

significance test for the number that might be expected to occur by chance. Specifically, we do not observe any correlation of station-group toxicity using any metric with (a) SST anomalies from any tested region, (b) differences in SST anomaly between regions that might be indicative of interannual changes in surface hydrographic pattern, (c) cross-shore SST gradients along the eastern Maine coast (EMCC), (d) alongshore SST gradients, or (e) river discharge, either as monthly values in any month or as 6-month annual totals.

Most oceanographic metrics extracted from the numerical circulation model hindcasts (Table 2) showed no significant correlation with interannual variability in any metric of toxicity. Correlations of select model metrics are shown in Table 5. Cross-shelf surface velocities (v component), spatially averaged over 2 regions (EMCC and WMCC), both show positive correlations with many toxicity station-groups for early season (April) velocities. The sign of the correlation indicates an association of increased toxicity metric with increased onshore-oriented velocities. Geographically, the station-groups that are correlated with these velocities are those located in the western portion of the study area (Fig. 4). With a single exception (Metric 6, Group 5), eastern station-groups are not correlated with this model signal. Cross-shelf transport in June also shows a number of significant correlations, although fewer than those in April. Two aspects of these June correlations are inconsistent with previous correlation patterns. All are negative, indicating increased offshore velocities are associated with increased toxicity metric magnitude. Many of the correlated station-groups are located in the far eastern portion of the study area. No correlations for July (not shown) are significant.

Alongshore surface current velocities were examined at 3 coastal stations, EMCC, WMCC, and Kennebec (Fig. 1) for each of the months February through June. None of these co-vary significantly with any station-group toxicity signal (not shown). Surface density over the deep basins provides an indication of interannual variability of freshwater influences, vertical mixing, seasonal heating and resulting stratification. Early season density over Jordan and Wilkinson Basins does not have any systematic co-variation with toxicity metrics. In early summer, however, June surface density over both basins shows significant positive correlations with many station-groups: higher surface densities are associated with increased toxicity metric values. Examination of the location of the station-groups in question (Fig. 4) shows they are west of Penobscot Bay. These correlations are consistent with, but obviously not independent of, those observed for model SST in Jordan Basin. Model SST in early summer (June) from 2 eastern Gulf of Maine locations, EMCC and Jordan Basin, produced significant negative correlations with many of the toxicity station-groups from the western portion of the study area (years of cold SST associated with increased toxicity metrics). These were not observed in the satellite SST and likely reflect a strong model SST response to local wind forcing, heat flux and mixing. Station-groups along the eastern coast, geographically closer to these SST signals, do not show any relationship. Model SST from other

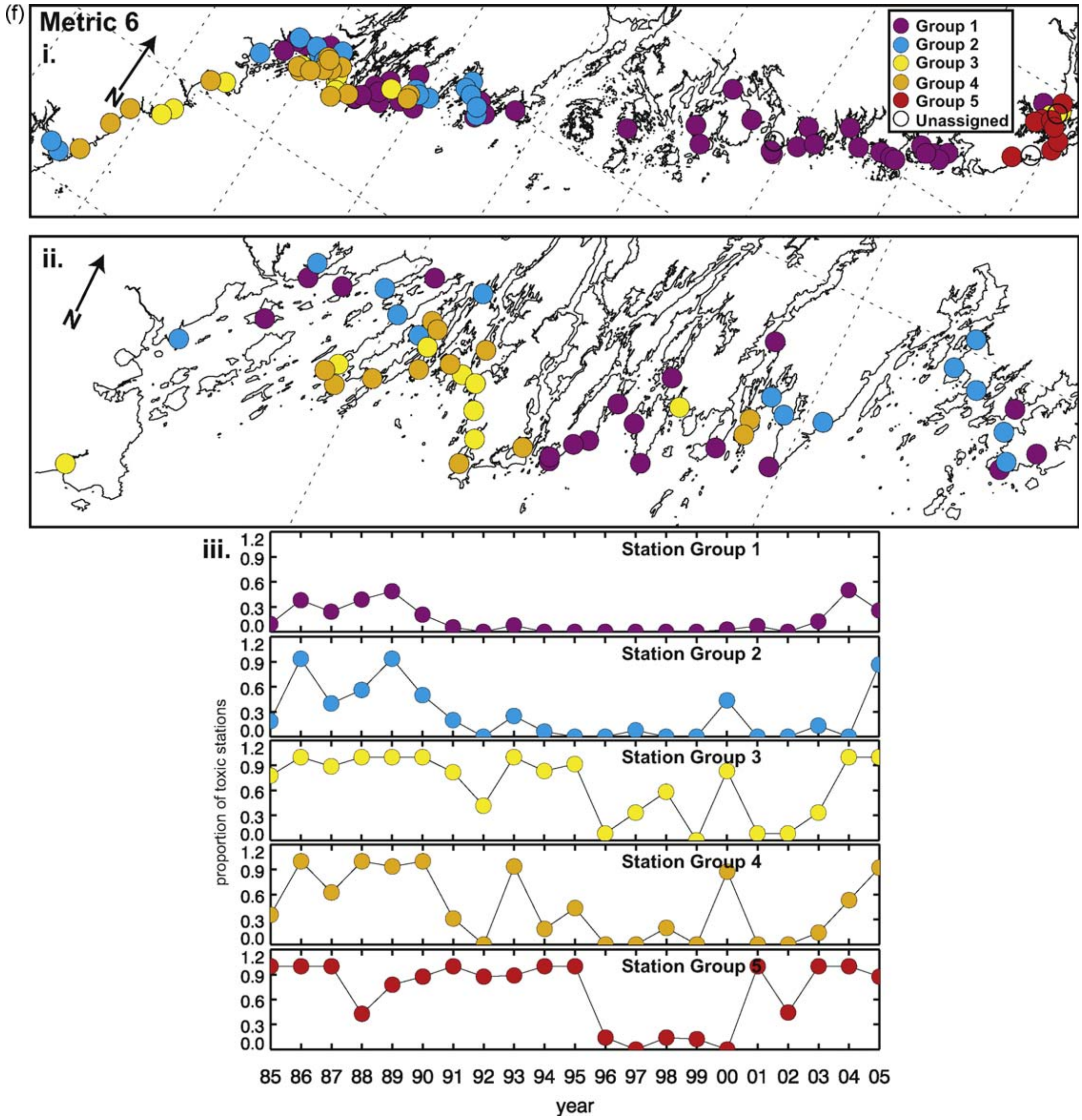

Fig. 4. (*Continued*).

examined locations (Table 2) is not significantly correlated with the toxicity of any station-group.

One of the model time/space signals simplified by the EOF decomposition has significant correlations with toxicity. Time series of the dominant EOF mode (72% of total variance) of alongshore velocities in the EMCC indicate increased eastward velocities (these are anomalies, so equivalent to decreased westward alongshore transport) in the early season (March) are associated with increased toxicity metrics for many of the station-groups. With a single exception, these station-groups are all located in the western portion of the study area. The same relationship was not observed with velocities in the WMCC region.

5. Discussion

5.1. Space and time patterns of toxicity

Our toxicity metrics provide six views of the climatological coastal shellfish toxicity pattern over the 21-year study period (Fig. 2). These views are consistent with previous views based on fewer stations and/or years (Anderson, 1997; Hurst and Yentsch, 1981; McGillicuddy et al., 2005b; Shumway et al., 1988). We include them here as they represent a first systematic quantification of these toxicity properties over decadal time scales, over the entire coast and using so many stations. They provide a background against which the interannual variability examined here and future toxicity patterns can be compared. General climatological characteristics are of earlier seasonal starts and toxicity peaks in western areas compared to eastern areas, likely due to earlier seasonal warming in the western Gulf of Maine (Anderson, 1997). A weak trend for stations along the western coast to develop toxicity after those in and around Casco Bay, following circulations patterns, is evident in Metric 1, a pattern pointed out by Franks and Anderson (1992b). The figure also quantifies increased toxicity totals and maxima along the exposed western coastline, the outer stations of Casco Bay and in the far eastern and Cobscook Bay area compared to reduced toxicity occurrence and levels in the vicinity of Penobscot Bay, the ‘‘PSP sandwich’’ (Shumway et al., 1988).

Multivariate analysis extracts dominant year-to-year similarity based on geographic patterns of toxicity (Table 3 and Fig. 3). We comment on three of the most obvious aspects of these results. (1) In the literature, 2005 is identified as a year of particularly widespread and anomalously high toxicity (Anderson et al., 2005c). Our results are consistent with this but also place this

Table 4
Correlations between select environmental variables and toxicity metrics by station-group.

Metric	Group	WMCC–WB cross-shore SST gradient					Wind: cumulative upwelling					Wind: cumulative downwelling					
		Apr	May	Jun	Jul	Aug	Mar–Apr	Apr–May	May–Jun	Jun–Jul	Jul–Aug	Feb–Mar	Mar–Apr	Apr–May	May–Jun	Jun–Jul	Jul–Aug
1	1	–	–	–	–	–	−0.44	–	–	–	–	–	–	–	–	–	–
	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	3	–	–	–	**−0.58**	–	–	–	–	**−0.50**	–	–	–	–	–	–	–
	4	–	–	**−0.52**	**−0.61**	–	–	–	–	**−0.54**	**−0.62**	–	**0.50**	**0.59**	–	–	–
2	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	2	–	–	–	−0.44	–	–	–	–	**−0.46**	−0.42	–	**0.47**	0.39	–	–	–
	3	–	–	–	**−0.56**	–	–	0.42	–	**−0.55**	−0.40	**0.48**	–	0.43	–	–	–
3	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	3	–	–	**−0.52**	**−0.56**	–	0.44	**0.49**	–	**−0.49**	–	**0.54**	**0.48**	**0.53**	–	–	–
	4	–	–	−0.41	**−0.49**	–	–	–	–	**−0.52**	–	–	0.40	**0.61**	–	–	–
	5	–	–	–	−0.43	–	–	–	–	**−0.61**	–	–	–	**0.56**	–	–	–
4	1	–	–	−0.41	**−0.51**	–	–	–	−0.40	**−0.60**	−0.44	–	0.42	**0.61**	–	–	–
	2	–	–	**−0.49**	**−0.57**	–	–	0.42	–	**−0.52**	–	–	0.42	**0.61**	–	–	–
	3	–	–	–	−0.43	–	–	0.41	–	**−0.56**	–	**0.55**	–	–	–	–	–
	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
5	1	–	–	–	–	–	–	–	–	–	–	–	–	–	0.44	–	–
	2	–	–	**−0.54**	**−0.61**	–	–	0.41	–	–	–	**0.51**	–	0.44	0.42	–	–
	3	–	–	−0.43	−0.44	–	–	–	–	**−0.46**	**−0.53**	–	**0.58**	**0.49**	–	–	–
	4	0.42	–	–	–	–	–	0.40	–	–	–	–	–	–	–	–	–
6	1	–	–	–	–	–	–	–	–	−0.45	–	–	–	0.45	–	–	–
	2	–	–	–	**−0.53**	–	–	0.40	–	**−0.66**	**−0.49**	–	–	**0.58**	–	–	–
	3	–	–	**−0.47**	**−0.48**	–	–	0.44	–	−0.44	–	–	0.43	**0.48**	–	–	–
	4	–	–	−0.46	**−0.49**	–	–	–	–	**−0.48**	**−0.46**	–	0.43	**0.53**	–	–	–
	5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

Metric	Group	Wind: cumulative mixing (U^{*3})							SST anomaly (Wilkinson Basin)						River discharge
		Feb	Mar	Apr	May	Jun	Jul	Aug	Feb	Mar	Apr	May	Jun	Jul	First 6 months
1	1	–	−0.40	–	–	**−0.61**	**−0.46**	–	–	–	**−0.50**	–	–	–	–
	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	3	−0.44	–	–	–	–	**−0.53**	–	–	–	–	–	–	–	–
	4	–	−0.40	–	–	–	**−0.58**	**−0.47**	–	–	–	–	–	–	–
2	1	–	–	–	–	–	–	–	–	–	–	–	−0.47	–	–
	2	–	**−0.48**	–	–	–	**−0.56**	–	–	–	–	–	–	–	–
	3	–	–	–	–	–	**−0.62**	**−0.53**	−0.39	–	–	–	–	–	–
3	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	2	–	–	–	–	–	**−0.64**	–	−0.48	–	–	–	–	–	–
	3	–	−0.43	–	–	–	**−0.49**	–	–	–	–	–	–	–	–
	4	–	–	–	–	–	**−0.54**	–	–	–	–	–	–	–	–
	5	–	−0.42	–	–	–	**−0.60**	–	–	–	–	–	–	–	–
4	1	–	**−0.56**	–	–	–	**−0.67**	–	–	–	–	–	−0.42	–	–
	2	–	−0.42	–	–	–	**−0.50**	–	–	–	–	–	−0.41	–	–
	3	−0.42	–	–	–	–	–	–	–	–	–	–	–	−0.47	**0.51**
	4	–	−0.43	–	–	–	**−0.62**	–	–	–	–	–	–	–	−0.43
5	1	–	–	–	–	−0.40	**−0.47**	–	–	–	–	–	–	–	–
	2	–	−0.44	–	–	–	**−0.52**	−0.43	–	–	–	–	–	–	–
	3	–	**−0.50**	–	–	–	**−0.51**	–	–	–	–	–	–	–	–
	4	–	–	–	–	–	–	–	–	–	–	–	−0.45	–	–
6	1	–	−0.40	–	–	–	**−0.58**	–	–	–	–	–	–	–	–
	2	–	–	–	–	–	**−0.51**	–	–	–	–	–	–	–	–
	3	–	**−0.48**	–	–	–	**−0.52**	–	–	–	–	–	−0.40	–	–
	4	–	−0.42	–	–	–	**−0.54**	–	–	–	–	–	–	–	–
	5	–	–	−0.41	–	–	–	0.39	–	–	–	–	–	–	−0.42

Significance levels: 90% and **95%**, geography of station-groups is shown in Fig. 4.

year in greater historical context. The year-groups (Table 3) show that 2005 is rarely grouped with any recent year. Only in date of first toxicity (Metric 1) and the presence–absence metric (Metric 6) is 2005 similar to another recent year (2000). However, the other four metrics each group 2005 with years in the mid-late 1980s, other years with high mean toxicity values. The year 2000 fails to group with other years for both maximum and total toxicity (Metrics 3 and 4). Examination showed this was not because of anomalously high or low values but due to strong differences in spatial pattern. In 2000, elevated western Maine toxicities were accompanied by very low (or no) toxicity at far eastern stations, a clear departure from climatological patterns (Fig. 2). (2) Comparisons of Table 3 with Fig. 3b and c show three generalized periods of overall toxicity magnitude (Metrics 3 and 4): elevated in the 1980s into the early 1990s, reduced in the mid-1990s–early 2000s, and elevated again in 2004–2005. (3) Year-groups in Table 3 show

Table 5
Correlations between select model-extracted metrics of ocean structure and toxicity metrics by station group.

Metric	Group	V Velocity – EMCC					V Velocity – WMCC					Density – Wilkinson					Density – JB				
		Mar	Apr	May	Jun	Jul	Mar	Apr	May	Jun	Jul	Mar	Apr	May	Jun	Jul	Mar	Apr	May	Jun	Jul
1	1	–	–	–	–	–	–	–	–	**−0.73**	–	–	–	–	–	–	–	–	–	–	–
	2	–	–	–	–	–	–	–	–	–	0.45	–	–	–	–	–	–	–	–	0.42	0.41
	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	4	–	**0.63**	–	−0.39	–	–	–	–	–	–	–	–	–	0.41	–	–	–	–	**0.48**	–
2	1	–	–	–	–	–	–	0.39	–	−0.41	–	–	−0.41	–	**0.51**	–	–	–	–	–	–
	2	–	0.45	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	**0.50**	–
	3	–	**0.52**	–	−0.41	–	–	**0.50**	–	–	–	–	–	–	0.41	–	–	–	–	–	–
3	1	–	–	–	–	–	–	–	–	**−0.48**	–	–	–	–	–	–	–	–	–	–	–
	2	–	–	–	**−0.60**	–	–	–	–	**−0.53**	–	–	–	–	–	–	–	–	–	–	–
	3	–	0.44	–	–	–	–	**0.54**	–	–	–	–	−0.38	–	**0.54**	–	–	–	–	–	–
	4	–	**0.51**	–	–	–	–	–	–	–	–	–	–	–	**0.55**	–	–	–	–	–	–
	5	–	**0.54**	–	–	–	–	0.45	–	–	–	–	–	–	0.42	–	–	–	–	–	–
4	1	–	**0.54**	–	–	–	–	0.40	–	–	–	–	–	–	**0.51**	–	–	–	–	0.44	–
	2	–	**0.48**	–	–	–	–	0.42	–	–	–	–	–	–	**0.58**	**0.49**	–	–	–	**0.48**	–
	3	–	–	–	–	–	–	0.44	–	–	–	–	–	–	–	–	–	–	–	–	–
	4	–	–	–	−0.40	–	–	–	–	**−0.64**	–	–	–	–	–	–	–	–	–	–	–
5	1	–	–	–	–	–	–	–	–	−0.45	−0.44	–	–	–	–	–	–	–	–	–	–
	2	–	–	–	–	–	–	**0.51**	–	–	–	–	–	–	–	–	–	–	–	–	–
	3	–	**0.53**	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.39	–	**0.46**	–
	4	–	–	–	−0.39	−0.39	–	**0.50**	–	–	–	–	–	–	**0.55**	–	–	–	–	0.41	–
6	1	–	0.44	–	–	–	–	–	–	**−0.49**	–	–	–	–	–	–	–	–	–	–	–
	2	–	**0.56**	–	–	–	–	0.41	–	–	–	–	–	–	**0.48**	–	–	–	–	0.43	–
	3	–	0.41	–	–	–	–	0.45	–	–	–	–	–	–	**0.52**	–	–	–	–	–	–
	4	–	**0.55**	–	–	–	–	0.45	–	–	–	–	–	–	**0.61**	–	–	–	–	0.44	–
	5	**0.47**	–	–	–	–	–	–	−0.42	−0.43	–	–	–	–	–	–	–	–	–	–	–

Metric	Group	Temp. – JB					Temp. – EMCC					EOF U Velocity – EMCC				
		Mar	Apr	May	Jun	Jul	Mar	Apr	May	Jun	Jul	Mar	Apr	May	Jun	Jul
1	1	–	−0.40	–	–	–	–	–	–	–	–	–	–	–	–	0.42
	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	3	–	–	0.41	–	–	–	–	–	–	–	–	–	–	–	–
	4	–		–	–	–	–	–	–	−0.45	–	–	–	–	−0.40	–
2	1	–	–	–	−0.41	–	0.40	–	–	–	–	**0.61**	–	–	–	–
	2	–	–	–	–	–	–	–	–	**−0.53**	–	0.39	–	–	–	–
	3	–	–	–	–	–	–	–	–	–	–	0.41	–	–	−0.41	–
3	1	–	–	–	–	–	–	–	–	–	–	0.43	–	–	–	–
	2	–	–	–	–	–	–	–	–	–	–	–	–	–	−0.42	−0.40
	3	−0.39	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	4	–	–	–	−0.41	–	–	–	–	–	–	**0.50**	–	–	–	–
	5		–	–	−0.42	–	–	–	–	−0.41	–	**0.59**	–	–	–	–
4	1	–	–	–	**−0.46**	–	–	–	–	**−0.47**	–	**0.53**	–	–	–	–
	2	–	–	–	**−0.46**	–	–	–	–	−0.40	–	**0.46**	–	–	–	–
	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	4	–	–	–	–	–	–	–	–	–	–	0.43	–	–	–	–
5	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	**−0.55**
	2	–	–	–	–	–	–	–	–	–	–	0.39	–	–	–	–
	3	–	–	–	–	–	–	–	–	**−0.54**	–	0.45	–	–	–	–
	4	–	–	–	−0.43	–	–	–	–	–	–	**0.61**	–	–	–	–
6	1	–	–	–	–	–	–	–	–	–	–	**0.52**	–	–	–	–
	2	–	–	–	−0.40	–	–	–	–	–	–	**0.56**	–	–	–	−0.39
	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	4	–	–	–	−0.40	–	–	–	–	–	–	**0.47**	–	–	–	–
	5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

Significance levels: 90% and **95%**, V is cross-shore, U alongshore, EMCC (Eastern Maine Coastal Current), JB (Jordan Basin), WB (Wilkinson Basin), WMCC (Western Maine Coastal Current), see Fig. 1.

definite temporal autocorrelation; sequential years tend to group together. This suggests some control by ecological and/or environmental processes that persist from year to year, rather than processes controlled by episodic annual events. Two possible examples of such persistent processes are: (a) the deposition of benthic cysts by the previous year's population (Anderson et al., 2005d; Matrai et al., 2005), with years of large population density tending to produce large responses in the following year and vice versa and (b) changes in residual circulation and/or water properties related to overall Gulf of Maine hydrographic structure (e.g. Pershing et al., 2001; Thomas et al., 2003).

Multivariate analysis clusters stations according to similarity of toxicity interannual variability. Results show strong regionality when viewed in geographic space, with relatively few cosmopolitan station-groups. This suggests gradients and/or regionalized differences in environmental conditions that are important to

Alexandrium ecology and the annual development of toxicity across the study area. Clustering also identifies those stations that, although geographically close, exhibit interannual variability dissimilar to their neighbors. Summarized in different words, stations similar in interannual variability tend to be close in geographic space, but not all stations in an area necessarily belong to that group. We note that use of correlative distance to quantify similarity means that station-groups are determined by covariance of interannual variability rather than absolute magnitude of metric values. The methodology allows calculation of annual means among station-groups that behave similarly, thereby (1) avoiding inclusion of dissimilar stations that would degrade or bias a simple regional average and (2) allowing averaging over data gaps at any one station to produce a regional mean signal that retains the dominant interannual variability.

Geographic pattern of station-groups within the 6 metrics (Fig. 4) shows a number of features that reflect established oceanographic characteristics of our study area and regionality that suggests similarity of interannual forcing. The pattern of station-groups repeatedly demonstrates a discontinuity in station membership east and west of Penobscot Bay with a region of low toxicity magnitude/occurrence between. The area in the vicinity of Penobscot Bay is well known as a region of reduced toxicity occurrence (the PSP "sandwich") (Hurst and Yentsch, 1981; Shumway et al., 1988). Because toxicity is rare in this area, few stations are sampled frequently enough to make it into our analysis. Those that do, however, often fail to cluster significantly with more toxic stations further east and west (Fig. 4). This discontinuity is consistent with circulation patterns and climatological differences in surface hydrography along the Maine coast, as pointed out by Anderson (1997). Residual circulation along the coast means that stations east of Penobscot Bay are upstream of those in the west (Xue et al., 2000). Furthermore, stations along the eastern Maine coast are subjected to the cold, tidally mixed, and relatively strong alongshore flows of the Eastern Maine Coastal Current (EMCC) (Townsend et al., 1987). Those to the west of Penobscot Bay are subjected to surface conditions that become strongly stratified in summer with warmer surface temperatures, summer surface nutrient limitation and weaker alongshore flows of the Western Maine Coastal Current (Pettigrew et al., 2005). The persistent spring-summer offshore branching of the EMCC in the vicinity of Penobscot Bay (Bisagni et al., 1996; Brooks and Townsend, 1989) creates a discontinuity in coastal SST regime and alongshore connection. There is interannual variability in this discontinuity and the connection it represents between the eastern and western Maine coast (Luerssen et al., 2005; Pettigrew et al., 2005).

Stations in Cobscook Bay tend to cluster together, distinct from other stations in the analysis (Fig. 4, Metrics 3, 4 and 6). These stations are the furthest upstream, exposed to the strongest tidal mixing and are relatively isolated from circulation and forcing of the open Gulf of Maine.

South of Casco Bay, along the more exposed and relatively straight western Maine coast, stations also often group together, although groups often include membership from some stations in Casco Bay and/or the mid-coast region (Metrics 1, 3, 4 and 5). Similarly, many metrics show a separation of stations in the mid-coast region from those further to the west. On a smaller scale, the data also suggest a relatively consistent tendency for stations at the eastern end of Casco Bay to group together (most strongly in Metrics 3 and 4). This is a region most directly exposed to the influence of Kennebec River discharge (Franks and Anderson, 1992a; Keafer et al., 2005b) where freshwater and resulting density patterns likely play a role in both cross-shelf surface circulation and near-shore retention (Janzen et al., 2005).

5.2. Station-group links to environmental variability

Earlier work in the Gulf of Maine (Anderson et al., 2005b; Franks and Anderson, 1992a, 1992b) suggests that local river discharge, resulting alongshore transport within a buoyant plume and the interaction of this plume with upwelling wind forcing influences toxicity along the western coast of Maine. Keafer et al. (2005a) point to the influence of wind and salinity patterns controlling toxicity differences between two years in Casco Bay. Averaged within station-groups and viewed over a 21-year record, our data do not show correlations between river discharge and station-groups, suggesting that variability in freshwater discharge each year does not consistently influence interannual differences in coastal toxicity. We note, however, that other metrics of freshwater discharge (e.g. timing, peak monthly values, precipitation, etc.) are possible, but not examined here and our correlations are based on averages within station-groups. It possible that individual stations and/or stations excluded from our analysis correlate with interannual variability in discharge.

Correlations from the 21-year time series, however, are completely consistent with the above studies and many others that suggest wind driven surface transport plays a role in coastal HAB events (Figueiras et al., 2006; Kudela et al., 2005), both in the onset of coastal toxicity through onshore transport (Fraga et al., 1988; Trainer et al., 2002) and in bloom dissipation through offshore transport (Tester and Steidinger, 1997). Our data show onshore Ekman transport and, in summer, cross-shelf SST structure with relatively warm coastal SST linked to increased coastal toxicity characteristics of station-groups in the western portions of the study area. Both are indicative of the onshore advection of Gulf surface waters. This parallels mechanisms noted along many coastlines, where wind-induced downwelling events are linked to HAB events, for example along the northern Iberian peninsula (Crespo et al., 2006), in the California Current (Trainer et al., 2000) and the Benguela (Pitcher et al., 1998). McGillicuddy et al. (2005a) suggest that Gulf of Maine offshore cell populations vary little from year to year. If this is true, the strong interannual variability of coastal toxicity (Fig. 4) argues for differences in transport and/or local coastal environmental processes as controlling mechanisms. Wind variability is strongly correlated with current structure in the WMCC (Churchill et al., 2005) and imposes interannual differences in alongshore transport of other plankton in the coastal Gulf of Maine (Xue et al., 2008). Field data from a few years (Janzen et al., 2005) suggest strong coherence between low salinity coastal water, wind stress and on-shelf currents at the entrance to Casco Bay that act as a retention mechanism. Our data show strong regionality in these relationships. Station-groups located in the eastern portion of the study area (east of Penobscot Bay) do not show relationships to wind forcing or cross-shelf SST structure. These eastern station-groups are upstream within our study area, subjected to the cold and more strongly advective EMCC and less susceptible to interannual variability in surface forcing by wind. Stations within Cobscook Bay are even more strongly isolated from general Gulf of Maine forcing and circulation. One explanation of the observed timing difference between the correlations of wind and SST structure (Table 4) is that SST pattern is a poor tracer of circulation and surface hydrography early in the season, before heat flux induces heterogeneous stratification and surface warming.

Links between HAB events and indices indicative of climate have been documented in other regions (e.g. the northwest USA (Moore et al., 2009), and the North Sea (Edwards et al., 2006)). Previous work (Bisagni et al., 1996; Thomas et al., 2003) shows dominant spatial patterns of SST interannual variability in the Gulf of Maine. On a seasonal basis, climatological patterns of toxicity (Fig. 2) show earlier development in western portions of the study area, consistent with earlier and stronger seasonal stratification and warming in this region. However, correlations between interannual SST anomalies from a number of locations extracted from the satellite data and the toxicity interannual vectors from each station-group showed that none were significant (Table 4). On the interannual time scales of toxicity and monthly time scales of SST anomaly examined here, absolute surface temperature in the Gulf of Maine does not appear related to coastal toxicity.

Metrics extracted from the model hindcast of physical structure are consistent with the observed link between increased downwelling-favorable wind stress and increased toxicity. We note that these are not independent views of linkage, as the model is forced with daily wind stress. These results, however, do provide some assurance that the interannual signals generated by the physics in the model reflect aspects of concurrent field observations. The sign of the correlation with April onshore-oriented (v) velocities in both the EMCC and WMCC indicates an association of increased toxicity metric with increased onshore transport. Geographically, the station-groups that are correlated with these velocities are those in the western portion of the study area (Fig. 4). There are also some significant correlations with onshore transport in June, although fewer than those in April. Two patterns from these June correlations, however, are inconsistent with previous linkages. All are negative, indicating increased offshore velocities (or weaker onshore velocities) are associated with increased toxicity metric magnitude and many of the correlated station-groups are in the far eastern portion of the study area. A plausible mechanism linking June offshore cross-shelf velocities in the WMCC and eastern toxicity variability is not obvious to us.

The dominant EOF mode of EMCC alongshore velocity suggests that increased eastward velocities (these are anomalies, so equivalent to decreased westward alongshore transport) in the early season (March) are associated with increased toxicity metrics for many of the station-groups. With a single exception, these station-groups are all located in the western portion of the study area. This relationship was not observed for velocities of the WMCC, likely due to these being both weaker and more spatially variable than those of the EMCC (Pettigrew et al., 2005). Correlations were also not observed with the EMCC transect velocities likely due to increased variability removed by the EOF. One possible mechanistic link between reduced EMCC alongshore velocities in the early spring and increased western toxicity is an earlier and increased warming and stratification of the western coastal Gulf of Maine due to reduced cold, dense EMCC water delivery, but such is not evident at the surface in satellite SST data or model results.

Notable among model metrics that did not correlate with the toxicity signal from any of the station-groups were surface salinity, coastal surface densities and SST in any location west of Penobscot Bay. These findings are consistent with the observation that river discharge showed no significant correlation to any toxicity signal and the lack of correlation of toxicity with satellite SST. Again, neither should be regarded as independent observations of the same relationship, as the model uses both satellite SST and river discharge as forcing input. Alongshore velocities at both an EMCC and WMCC location, indicative of alongshore transport in these regions, were not correlated with toxicity variability. Because the seasonal component of EOF decomposition of EMCC velocity does have correlations to toxicity, it is possible that variability in the velocity structure reduces relationships below significance levels.

Circulation patterns mean that elevated concentrations of *Alexandrium* cells in EMCC water (Townsend et al., 2001) and in the southern Bay of Fundy (Martin and White, 1988) are a potential source for cell delivery to western coastal areas. Data from 2001 suggest that early season development of cells within a nearshore low salinity band along the cold eastern Maine coast influences western coastal toxicity (Keafer et al., 2005b) and there is strong interannual variability in the connection between EMCC water and hydrographic characteristics west of Penobscot Bay (Pettigrew et al., 2005; Pettigrew et al., 1998). Luerssen et al. (2005) show that early and strong (late/weak) development of a summer SST front, indicative of the relative connection between colder EMCC water and warmer regions along the western Maine coast, is linked to reduced (enhanced) toxicity at the eight western coastal stations they examined. The systematic treatment of all stations over the 21-year record presented here did not replicate this finding. Three differences between these studies likely explain this inconsistency. Luerssen et al. (2005) view the actual toxicity values at eight individual stations as opposed to metrics describing annual toxicity characteristics. Their individual station records differ from the group means examined here, and the 8 stations did not all fall into the same station-groups. They also examine 13 years of data, rather than the 21 years treated here.

6. Conclusions

Twenty-one years (1985–2005) of toxicity monitored at stations along the Maine coast are used to provide insight into spatial pattern, interannual variability and potential relationships to environmental conditions. Six metrics of annual toxicity characteristics quantify aspects of both timing and magnitude. Climatological means of these metrics at each station show dominant patterns of timing and magnitude consistent with previous work based on fewer years and stations but quantified here as 21-year means.

Multivariate statistics allow insight into between-year similarity and then station similarity based on interannual toxicity variability. The geographic pattern of station-groups suggests regionality of environmental conditions potentially linked to variability in toxicity. Superimposed on the climatological mean patterns, the dominant interannual signal that emerges from station-groups is of elevated values and increased duration of toxicity signals at the beginning of the time series examined, in the late 1980s to early 1990s, a period of reduced toxicity metrics in the mid-late 1990s and increasing values towards the end of the time series (2000–2005). Another, simpler, "HAB index", shows similar temporal trends (Don Anderson, Wood Hole Oceanographic Institute, personal communication and manuscript in preparation).

A number of questions of potential importance to coastal management are addressed.

- Would regional averages using all local stations reflect regional interannual variability? The station clustering shows strong regionality, but clearly identifies stations in close geographic proximity that do not group with their neighbors. Simple averages across all stations in a localized region would likely bias or blur dominant trends.
- What are the dominant regions with respect to differences in interannual variability? Viewed across all metrics, the regions consistently defined by station-groups and/or their boundaries are (1) Cobscook Bay and far eastern stations, (2) mid-coast stations between Penobscot Bay and Casco Bay, (3) Casco Bay and the western Maine coastline. These are consistent with Gulf of Maine circulation and seasonal hydrographic patterns.
- Are years of early initial toxicity also years of early seasonal maxima? Qualitatively, there is strong concordance between these two metrics.
- Are years of highest toxicity maxima also years of high integrated annual toxicity? Qualitatively there is extremely strong concordance between these metrics.

- Do year-groups show relationships between timing and magnitude? There is a strong concordance between year-group membership in early timing and weak magnitudes, and between later timing and stronger magnitudes. We caution that this is driven by the obvious similarities between year-groups with no median start date and low (or no) toxicity in the late 1990s and early 2000s. Beyond these groups, there is still concordance between years-groups of elevated toxicity and those of late timing.
- Is there evidence of increased toxicity levels in later years? Metrics 3 and 4 (indices of toxicity level) show that recent years are not grouped together and, with the exception of 2005, years in the 2000s are not in the highest toxicity year-cluster.
- In recent years, is toxicity developing systematically earlier or later, or lasting longer? Metrics 1 and 5 quantify timing of events. In these year-groups, no systematic shift towards years in the 2000s being early, late or more persistent is evident.

Averaging within groups develops mean regional toxicity signals suitable for comparison to concurrent environmental data. A similar approach on the northwest US coast highlights difficulties in isolating environmental metrics related to highly localized toxicity records (Moore et al., 2009). Among the measures of environmental variability tested here, two mutually consistent metrics emerge as linked to interannual patterns in toxicity. Wind forcing components related to onshore cross-shelf surface transport are correlated with multiple station-groups. Cross-shelf SST patterns along the western Maine coast indicative of relatively warm coastal areas, consistent with onshore Ekman transport of surface water are correlated with multiple station-groups. Station-group geography points to distinct regionality of these conclusions. Linkages were evident only in station-groups located in the western portion of the study area, the region subject to the strongest seasonal warming, stratification and relatively weak alongshore advection. Toxicity variability at station-groups to the east of Penobscot Bay, in the upstream, colder, more advective portion of our study area, were not correlated with these wind or SST patterns. Our results support previous assertions about the importance of wind forcing and onshore Ekman transport in creating toxic conditions based on a few years of cell distributions and/or examination of a few coastal stations. Here we show this to be a statistically dominant interannual pattern based on over 100 stations and 21 years of variability.

Temporal correlations between interannual toxicity characteristics and environmental variables do not imply causality. They do, however, point to environmental conditions that statistically co-vary with toxicity metrics. This suggests that significant components of interannual variability in coastal toxicity at these stations are linked to environmental conditions. Ecological mechanisms that connect the environment to actual *Alexandrium* dynamics, and these dynamics to coastal toxicity events await further field and physiological research. With the additional knowledge of such mechanisms, our results form the basis by which future prediction models might operate to both forecast toxicity events and optimize monitoring and management strategies.

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