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Observations of *Alexandrium tamarense* (Dinophyceae) vegetative cells and oceanographic parameters in Scapa Flow, Orkney Islands, Scotland

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The toxic dinoflagellate *Alexandrium tamarense* was studied along with surrounding oceanographic parameters from May 1998 to May 1999 in Scapa Flow, Orkney. Nutrient concentrations were higher in winter and showed a phase of depletion in late spring and summer. Dinoflagellates tended to be abundant in late spring and summer. *Alexandrium tamarense* was detected in the water column almost year round, with the exception of the winter months (September to December). The growth of the *A. tamarense* population in Scapa Flow was not reflected in a monospecific bloom but rather in moderate to small biomass levels and always in co-occurrence with other species of diatoms and dinoflagellates. The highest concentration recorded was 1600 cells l^{-1} but concentrations of 200–400 cells l^{-1} were more typical. The oceanographic parameters indicate that the occurrences of vegetative cells of *A. tamarense* seem to be explained in part by instability of the water column, low temperature and low nutrient concentrations.

INTRODUCTION

There are approximately 31 *Alexandrium* species described in the literature (Steidinger & Tangen, 1997), and at least eight species are known to be toxic (Medlin et al., 1998). In the UK, the species which has been linked with paralytic shellfish poisoning (PSP) is the toxic dinoflagellate *Alexandrium tamarense* (Lebour) Balech (Wyatt & Saborido-Rey, 1993). Historically in the UK, *A. tamarense* was recorded mostly along the north-east coast of England, in recent years however, it seems to have become a conspicuous species within the Orkney Islands where it now commonly occurs resulting in widespread, recurrent outbreaks of PSP. Paralytic shellfish poisoning activity seems to be particularly prevalent in Scapa Flow.

The first recorded outbreak of PSP in Orkney was reported in 1991. Since then, annual outbreaks of PSP have been recorded, creating serious problems for the local shellfish industry which relies heavily on the exploitation of natural sources of mussels, scallops, queens, to name but a few. Toxicity episodes of PSP in Orkney have been variable with respect to magnitude, frequency and duration. Scapa Flow usually experiences the highest PSP values between June and August, but it is evident that toxicity can occur most of the year round (Joyce, 2001). The worst case of PSP recorded to date was in 1995, where maximum toxicities of 6919 μM/100 g shellfish flesh were recorded (Fisheries Research Services, Aberdeen, personal communication).

In any area, it is important to know the relationship between the occurrence of vegetative cells of *A. tamarense* and the local oceanographic conditions. Although a few studies on *A. tamarense* blooms have been conducted along the north-east coast of England (Lewis et al., 1995; Joint et al., 1997; Brown et al., 2001), information on *A. tamarense* in Scapa Flow is scarce. Little attention has been paid to the features of *A. tamarense* populations and the phytoplankton dynamics in Scapa Flow are not known. Scapa Flow is a semi-enclosed basin in which there is only limited water exchange with the open shelf waters. There have been no studies concerning the oceanographic conditions of Scapa Flow, and their possible influence on the occurrence of *A. tamarense*. This paper presents a preliminary analysis of the pattern of occurrences of the toxic dinoflagellate *A. tamarense*, coupled with observations of other phytoplankton species, and its relationship with physical and chemical data from May 1998 to May 1999, in an attempt to try and elucidate the population dynamics of *A. tamarense* in Scapa Flow, Orkney.

MATERIALS AND METHODS

Study area

The Orkney Islands are situated off the north-eastern tip of the mainland of Scotland, across the Pentland Firth, at the point of confluence of the North Atlantic and North Sea waters. Scapa Flow (Figure 1) is a semi-enclosed marine basin within the Orkney Islands archipelago, covering an area of roughly 130 km^2, with water depths ranging from 20–60 m. Within Scapa Flow there are two main entrances through which the tides and currents propagate, Hoy Sound in the north-west, opening to the Atlantic, and Hoxa Sound in the south, opening to the Pentland Firth.

Water column sampling and oceanographic data

Sampling was carried out, weekly to monthly from May 1998 to May 1999, at four stations in Scapa Flow (Figure 1).

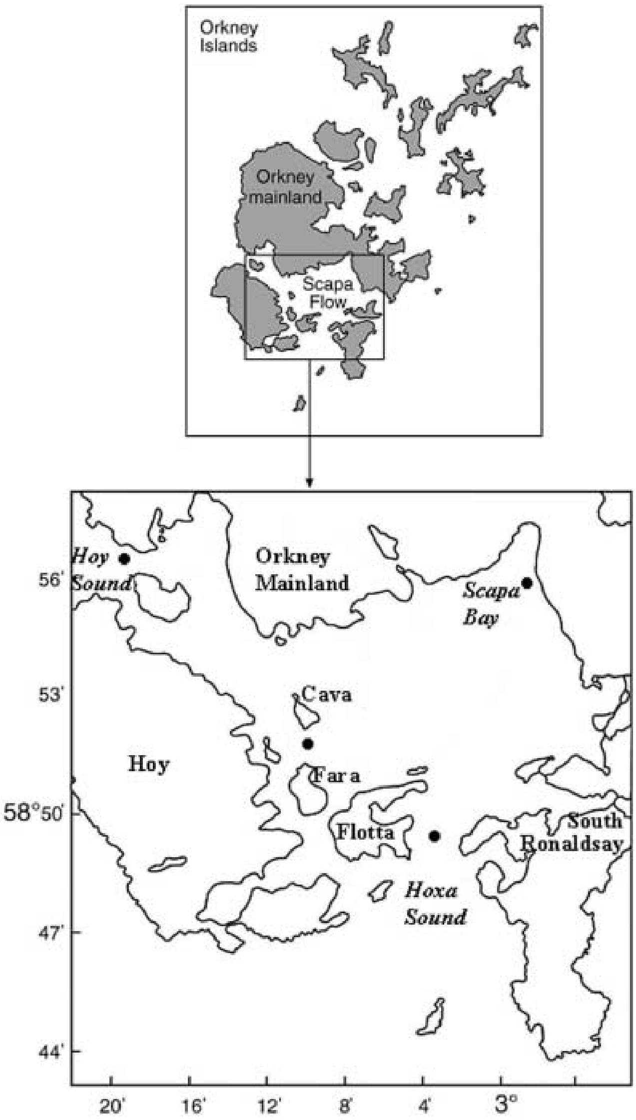

Figure 1. Map of the study area showing the location of Scapa Flow and the sites where water samples (●) were collected.

Water samples from discrete depths in the water column, 5, 10, 15, 20 m, and 30 and 40 m where depth allowed, were collected using 1-l bottles, for nutrient analysis and examination of the phytoplankton assemblage. From the 1 litre, 50 ml was removed, stored in sterile polypropylene centrifuge tubes and frozen immediately for nutrient analyis. Nutrient samples were analysed by means of an auto-analyser. From the 1 litre, 300 ml was removed and preserved with 11% gluteraldehyde solution for examination of the phytoplankton assemblage. From the 300 ml, a subsample of 100 ml was removed into a settling jar, the material was left to settle for 48 hours, then the top 90 ml was siphoned off by pipette, leaving the phytoplankton concentrated in the remaining 10 ml. This 10 ml was mixed, and 1 ml was removed by pipette and placed on a 1 cm^3 Sedgewick-Rafter slide. Phytoplankton cell counts were then performed using a Zeiss Standard 20 light microscope. At each station an Interocean STD 12 CTD profiler was used to construct water column profiles of salinity and temperature. Correlation coefficients and significance between oceanographic parameters and *Alexandrium tamarense* cell concentrations were computed and tested using the statistical package Statistica.

RESULTS

Vegetative cells of Alexandrium tamarense *and phytoplankton*

Alexandrium tamarense cells were observed almost year round in the water column; from May to September 1998 and from January 1999 onwards until the end of the sampling period in May 1999 (Figure 2). Coinciding with, or just shortly after, the detection of cells in the water column, paralytic shellfish toxins were detected in shellfish from Scapa Flow (Joyce, 2001). *Alexandrium tamarense* always occurred with other species of diatoms and dinoflagellates and was always outnumbered by these co-occurring species. Diatoms, in general, dominated the phytoplankton. Two peaks of diatoms were observed as a feature of the phytoplankton cycle throughout the sampling period (data not shown); the autumn peak extending from September to November 1998, dominated by *Skeletonema costatum*, *Paralia sulcata*, *Thalassiosira* spp., *Chaetoceros* spp., *Leptocylindricus* spp., and *Pseudo-nitzschia*

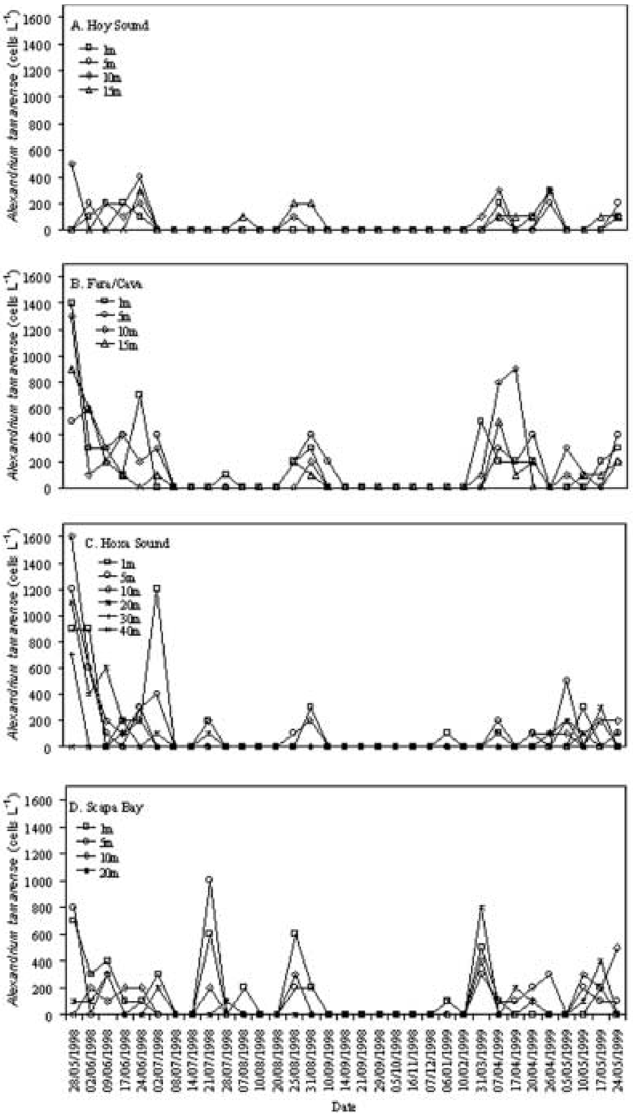

Figure 2. Cell density of *Alexandrium tamarense* at each depth layer at each sample station from May 1998 to May 1999.

spp.; and the spring bloom beginning in March 1999, dominated by *Chaetoceros* spp., *Rhizosolenia* spp., *Thalassiosira* spp. and *Pseudo-nitzschia* spp. However, during the summer (July) of 1998, massive peaks were observed at Hoy Sound and Scapa Bay sites (data not shown), these peaks were attributed to a bloom of *Pseudo-nitzschia* spp., which reached a maximum abundance of over 10^6 cells l^{-1}. Dinoflagellates tended to be abundant during late spring and summer (data not shown). *Ceratium lineatum* was the most important species achieving a maximum of over 10^4 cells l^{-1}. *Prorocentrum micans*, *Scrippsiella trochoidea*, *Dinophysis acuminata*, and *Heterocapsa triquetra* were also abundant in the summer. The pattern of *A. tamarense* distribution was similar at the four stations, the major difference being the tendency for higher densities of *A. tamarense* to occur at Fara/Cava, Hoxa Sound and Scapa Bay, and lower densities at Hoy Sound. At each site, cell densities ranged from undetectable to 500 cells l^{-1} at Hoy Sound, 1400 cells l^{-1} at Fara/Cava, 1600 cells l^{-1} at Hoxa Sound, and 1000 cells l^{-1} at Scapa Bay (Figure 2).

Oceanographic parameters

Summer water temperatures in Scapa Flow ranged from approximately 10°C to 13°C and winter water temperatures ranged from approximately 9°C down to 6°C, with very little difference between the four sites (data not shown). There was no pronounced thermocline, however, a weak thermocline was noticeable at Scapa Bay on 7 April 1999 that lasted for approximately 7–10 days, but did not exceed 5 m (Figure 3A). The vernal warming period began in March 1999. Salinity at all four sites was always around 34.5 psu. Very weak haloclines occurred occasionally at Hoy Sound but tended to be no deeper than 5 m (data not shown). Only on one occasion was there a more noticeable halocline that occurred on 7 April 1999 at Scapa Bay (Figure 3B). Phosphate, nitrate, and silicate concentrations were occasionally depleted in surface waters (data not shown), but, in general, phosphate levels ranged between 0.03–1.13 μM, nitrate between 0.1–9.7 μM and silicate between 0.1–4.6 μM. Nutrient concentrations were higher in winter and showed a phase of depletion in late spring and summer.

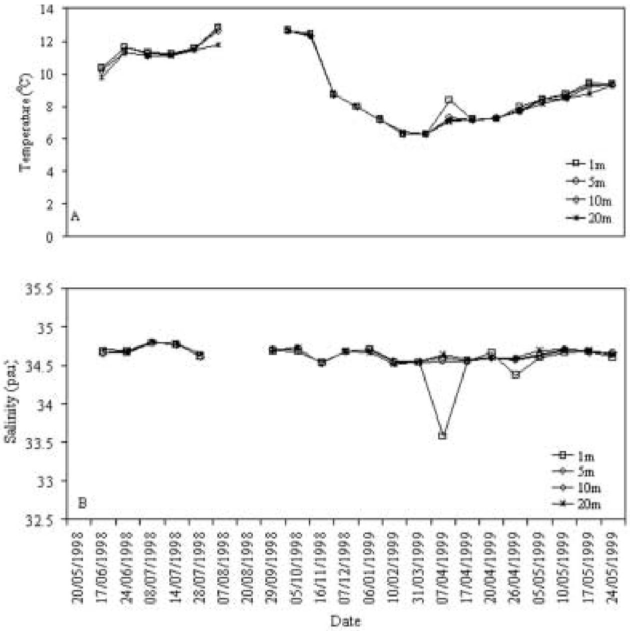

Figure 3. (A) Water temperature and (B) salinity, at each depth layer at the Scapa Bay site showing the periods of weak thermocline and halocline, from May 1998 to May 1999.

Relationship between oceanographic parameters and Alexandrium tamarense *cells*

The relationships between the surrounding water temperature, and salinity, and the cell density of *A. tamarense* are shown in Figure 4. There was no significant correlation between water temperature and cell density ($r = -0.10$, $P = > 0.01$) (Figure 4A). Relatively high cell densities of *A. tamarense* (>800 cells l^{-1}) were detected at temperatures between 7°C and 13°C, the maximum number was observed at 9.5°C degrees. Cell density was observed to decline around both the lower

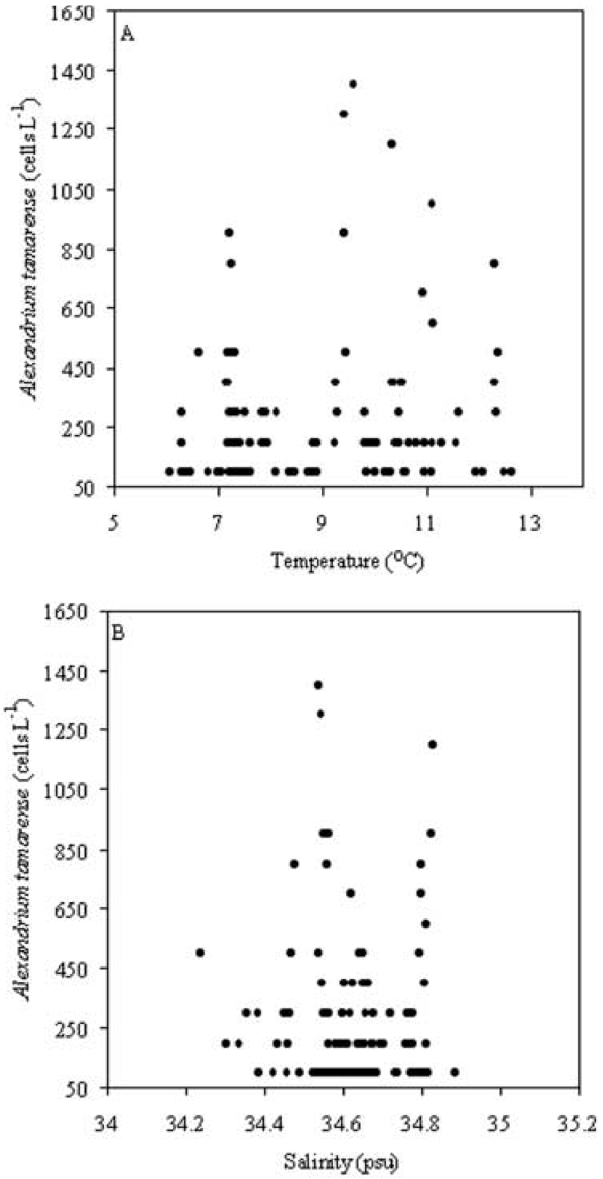

Figure 4. Observed relationships between (A) surrounding water temperature and (B) salinity, and cell density of *Alexandrium tamarense* over the study period, May 1998 to May 1999.

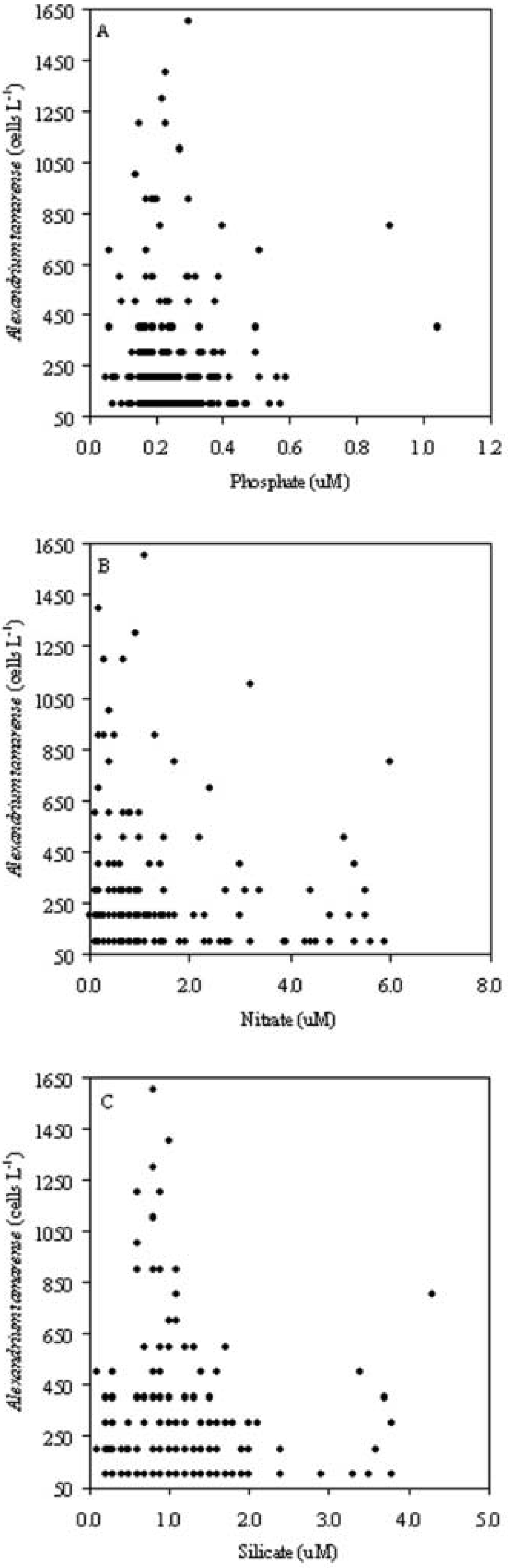

Figure 5. Observed relationships between surrounding nutrient concentrations: (A) phosphate; (B) nitrate; (C) silicate, and cell density of *Alexandrium tamarense* over the study period, May 1998 to May 1999.

and the upper temperature conditions. There was no significant correlation observed between salinity and cell density ($r=-0.04$, $P=>0.01$) (Figure 4B).

Figure 5 shows the relationship between surrounding concentrations of phosphate (Figure 5A), nitrate (Figure 5B) and silicate (Figure 5C) and the cell density of *A. tamarense*. There are similar trends shown in these relationships, in that, dense vegetative populations were observed at the lower concentrations for each nutrient. However, no significant correlation was shown for phosphate ($r=0.03$, $P=>0.01$). Very weak correlations were observed for nitrate ($r=-0.14$, $P=<0.01$) and silicate ($r=-0.96$, $P=<0.01$).

DISCUSSION

The results of this study showed that the occurrence of *Alexandrium tamarense* was observed almost year round, in low to moderate biomass levels. Throughout the sampling period, salinity was always within a range that is considered suitable for the growth of *A. tamarense* vegetative cells under laboratory conditions, i.e. 15–35 psu (Achiha & Iwasaki, 1990; Yamamoto & Tarutani, 1997). Scapa Flow does not receive any freshwater run-off from rivers, and its salinity, approximately 34.5 psu, is thus relatively stable. However, water temperature was always below the lower limit that is considered suitable for growth under laboratory conditions, <15°C (Anderson et al., 1984; Anderson, 1998). The water temperature in Scapa Flow never rose, or rises, above 13°C, which is the summer maximum. Thus, temperature seems to be an important limiting factor restricting growth of *A. tamarense* in Scapa Flow.

In contrast to these laboratory results described above, field results from north-eastern Japan show blooms of *A. tamarense* are frequently observed at temperatures lower than 15°C (Fukuyo, 1982). Likewise, in Cape Cod, most bloom development occurs at water temperatures that are considered non-optimal for rapid growth of vegetative cells, once the water reaches temperatures in the field at Cape Cod, that are considered optimal in the laboratory, blooms are already typically on the decline (Anderson, 1998). Similarly, Han et al. (1992) found that *A. tamarense* disappears from the water column of Chinhae Bay, Korea, at temperatures well below those that support optimal growth in the laboratory. So, even at lower water temperatures high biomass levels of *A. tamarense* can be attained, so there must be other limiting factors restricting the growth of *A. tamarense* in Scapa Flow.

High-biomass monospecific *A. tamarense* blooms that discolour the water (red tides) have previously occurred on the north-east coast of England (Ayres & Cullum, 1978), but never in Scapa Flow. As well as the effect of low water temperatures, this could partially be explained by the homogeneity of the water column, observed at all four stations throughout the sampling period. Due to the shallowness of the water column and the mixing effects of primarily wind-driven, and to a much lesser extent, tidal currents, the water column in the Flow remained mixed throughout the year. This turbulent motion of the water disperses cells through the water column, and counters any would-be stratification resulting from increasing temperatures. *Alexandrium tamarense* is known to favour stratified, stable conditions for optimum growth. Wind is one of the most significant features of the Orkney weather. The prevailing wind in Orkney is from the south-west. During a typical year, some 70% of all winds are between 13 and 24 mph, while on average, gales (47–54 mph) occur on 29 days per year. The water column was isohaline and thermohaline for the majority of the year, with only slight vertical variations in spring 1999. The turbulent motion of the water not only disperses cells through the water column, but affects the cells physiologically, *A. tamarense* is fairly fragile and could be damaged by turbulent mixing (White, 1976). Therefore, turbulent mixing generated by wind and/or tidal movement could be expected to inhibit bloom formation of this species in Scapa Flow.

Previous studies of *A. tamarense* populations on the east coast of England observed that the vegetative cells were only present in the water column for a short period of time. Ayres & Cullum (1978) and Lewis et al. (1995) state that the vegetative stage of *A. tamarense* is usually present in the water column from April to July. In contrast, the results of this study show that the occurrence of *A. tamarense* was observed almost year round. This study of Scapa Flow did not detect cells of *A. tamarense* in the water column only during the winter months, from September to December 1998. The vegetative cell density, distribution and length of period in the water column of *A. tamarense* are affected by the water exchange rate of Scapa Flow.

The central areas of Scapa Flow are not readily flushed of water, due to a very low to negligible affect by tidal currents, there is a residence time of approximately 700+ days (Buller et al., 1974). Anything present in the water column e.g. cells of *A. tamarense*, is likely to remain for a while in the absence of regular flushing. Surface currents that may affect the central areas of the Flow are dependent on the wind, and seeing as the prevailing wind direction is from the south-west, there is little opportunity for cells to be carried out of the Flow. Also due to the effect of wind, cells are kept mixed throughout the water column avoiding transport out of the Flow in surface waters. Another factor to consider is the vertical migration behaviour of *A. tamarense* (MacIntyre et al., 1997), this may enable a population to stay in a location longer than expected. This could also be a possible explanation as to why *A. tamarense* cells are resident slightly longer in Scapa Flow than has been reported for the north-east coast of England. The diel vertical migration pattern of *A. tamarense* could be such that it keeps cells at depth, in periods of less wind stress, subsequently avoiding transport out of the Flow, either by surface current movements or by wind induced movement. This coupling between organism behaviour and the hydrography of the system within Scapa Flow may restrict the extent to which cells of *A. tamarense* can move out of the Flow. This would also allow *A. tamarense* populations within Scapa Flow to either accumulate to levels where toxicity levels can become a threat, or remain in the water column for longer periods extending the length of toxicity.

Alexandrium tamarense is often considered a 'background' species, in that it is often outnumbered by co-occurring phytoplankton species. In Scapa Flow, *A. tamarense* cells in the water column always occurred concurrently with other species, and was always out numbered by these species. The maximum abundance of *A. tamarense* observed in the water column of Scapa Flow was 1600 cells l^{-1}. Even though observed cell concentrations of *A. tamarense* in the Flow were lower than concentrations observed from many other regions, these less concentrated populations still caused significant shellfish contamination. It seems it is possible for these less concentrated populations to cause significant shellfish contamination, especially if the population can persist for an adequate period of time. This is true for the Bay of Fundy (Prakash, 1967), St Lawrence estuary (Cembella et al., 1988), Gulf of Maine (Franks & Anderson, 1992), and now it would seem Scapa Flow too. All these places, frequently suffer toxic shellfish incidents in the absence of dense aggregations of cells.

The occurrence of vegetative cells of *A. tamarense* in the water column of Scapa Flow always seemed to coincide with periods of low nutrient concentrations. Preceding the main growth periods of *A. tamarense* in spring of 1998 and 1999 were diatoms including *Chaetoceros* spp., *Rhizosolenia* spp., *Thalassiosira* spp. and *Pseudo-nitzschia* spp. These diatoms are known to deplete inorganic nutrients in the water column. A continuous decrease in nutrient concentrations indicated that the spring diatom bloom occurred during this period. Considering that silicate continued to decline, even during the period of *A. tamarense* growth, this suggests that the growth of *A. tamarense* appears to develop subsequently to, or concomitantly with, the diatom spring bloom. Dinoflagellates do not need silicate, so the spring bloom is followed by dinoflagellates in summer, supported by phosphates and nitrates. The dinoflagellates quickly use up these nutrients so nutrient concentration is always lower during the summer months.

The appearance of motile cells of *A. tamarense* in Scapa Flow might be attributed to an allochthonous mechanism, through cell transport via Hoy Sound during flood tide. However, it is proposed, an autochthonous mechanism via germination of cysts seems more likely to occur in the Flow. This is supported by; the observation of cells in the water column at Scapa Bay in January 1999, before cells were observed at other sites; and by a survey of resting cysts of *A. tamarense* in samples of surface sediments taken from the Flow (Joyce, 2001, 2004). Cysts of *A. tamarense* were found to be present and widespread throughout the Flow, and higher cyst densities were observed in central areas, indicating potential seedbeds for initiation of future vegetative growth and subsequent outbreaks of paralytic shellfish poisoning.

CONCLUSION

With the exception of this study, no systematic field investigations of phytoplankton, in particular *Alexandrium tamarense* motile cells, have been carried out in Scapa Flow. The present study describes the relationship between the seasonal growth of *A. tamarense* and the surrounding oceanographic conditions in Scapa Flow from May 1998 to May 1999. The dynamics of the vegetative population are partially explained by the physical and chemical environment. Temperature and salinity data, together with nutrient data, are indicative of a very well mixed system with very little indication of significant horizontal or vertical stratification. The combined effects of tidal currents and, principally, wind keep the water column in Scapa Flow well mixed all year round. Instability of the water column, low water temperatures and low availability of nutrients seem, at present, to be major factors limiting the growth of *A. tamarense* in Scapa Flow. However, *A. tamarense* is known to have a meroplanktonic life cycle, and resting cysts of this species likely play an important role in the population dynamics.

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