Alexandrium Cyst Abundance in Nootka Sound Aquaculture and Towns

Jordan Omoto

University of Washington

School of Oceanography, Box 355351

Seattle WA 98195-5351

jdomoto@uw.edu

Advisors: Kathy Newell and Daniel Grunbaum

Abstract

This study measures the number of *Alexandrium* cysts from samples collected near fish farms found in Nootka Sound in December of 2015. This measurement can indicate the health of the marine environment and presence of a potential bloom due to the possible high concentrations of nutrients produced by fish farms causing a higher population of cysts. Stations closest to fish farms and towns had higher levels of *Alexandrium* cysts 275 cyst/cc to 575 cyst/cc. In conclusion this study established two things: 1) it supported previous findings that *Alexandrium* cysts are found in areas of fine grain material due their similarities in disposition, and 2) fish farms and towns had a greater amount of *Alexandrium* cysts possibly due to heightened nutrients.

Introduction

Over the past decade, toxic dinoflagellate blooms have been reported more frequently throughout the world, causing major concerns for both humans and the marine ecosystem. Fish farms and other anthropogenic sources (small towns and industrial plants) produce a large amount of nitrogenous waste that could induce more dinoflagellate blooms (Wild-Allen 2008). Because nitrogen is a limiting factor in many marine ecosystems, the introduction of nitrogen to the water from pesticides, fish waste, fish feed, and wastewater may increase the number of toxic dinoflagellates to the water (Wild-Allen 2008).

Dinoflagellates are marine protists with two flagella that allow them to move through the water column. Because of their ability to perform photosynthesis, dinoflagellates contribute toward the world’s carbon uptake. When nutrients are depleted, dinoflagellates enter a dormant stage in their life cycle and develop into cysts. Cysts are the last stage in the process of sexual reproduction whereby gametes are formed when the cysts stop growing. Two gametes merge together to form one cell and become a zygote, eventually sinking to the seafloor as a resting cyst. The cyst can remain on the seafloor for months to decades, until temperature and light levels increase. Once the dinoflagellates become cysts, they are immobile and discontinue photosynthesis and other metabolic processes. Most cysts are characterized by a thick shell made of organic sporo-pollenin or calcareous material (Matsuoka 2000). Many factors, such as nutrient concentration, salinity, grazing, temperature, and sediment type, can contribute to the formation of cysts (Dale 1976, Spector 1984, Sildever 2015, Mohamid 2011).

Thousands of species of dinoflagellates have been identified, but only 30 have been identified to produce toxins that can contribute to fish mortality (Taylor and Harrison 2002). It is calculated that around 2% of all phytoplankton are toxic (Landsberg 2002). This issue raises major concerns for aquaculture facilities because their success is heavily dependent on customer satisfaction, publicity, and the health of fishes.

The dinoflagellate genus, *Alexandrium* in particular, is a major concern for shellfish because they are a contributor to paralytic shellfish poisoning (PSP). PSP is caused by the toxin, saxitoxin, which accumulates in filter feeding shellfish and causes illness or death in both the consumer and the shellfish (Clark 1999). Saxitonin is known to block sodium flux, thus inhibiting the firing of action potentials by the organism (Hansen 1989). This blockage of voltage gated sodium channels causes disruption in the nervous system of infected organisms leading to illness and death. *Alexandrium* have also been found to impact fish health and mortality, affecting salmon gills using cytotoxin (Mardones 2015).

Toxic dinoflagellate blooms are a major economical concern for Canada, the fourth largest salmon producer in the world. Aquaculture exports contributed to approximately $983 million CAD in gross outputs in 2013 (Statistics Canada 2013). Most of the major salmon aquacultures are located near Vancouver Island. Harmful algal blooms (HABs) are considered to be the biggest cause of mortality in Canadian grown salmon, contributing to a loss of $16.135 million CAD in 2009-2012 (Trainer 2014). Nootka Sound is located on the western coast of Vancouver Island, British Columbia, Canada, the site of many fish aquaculture facilities. Most are located on the eastern coast of Bligh Island, in Williamson Pass, Concepcion Point (Grieg Seafood), and Gold River in Muchalat Inlet (Skuna Bay Salmon) (Figure 1). Muchalat Inlet has a mean depth of 200-220m, while the eastern waters of Bligh Island average between 150-180m in depth.

Nootka Sound is an estuary with river inputs into the sound from the eastern side from Gold River and the northern side from Tahsis River. Thus fresh water at the surface is replaced by cold salty water at depth. Sills are located at the entrance of each inlet and in Williamson passage where there is a sill located at the eastern end of the passage. In the summer, the Californian undercurrent upwells deep nutrient rich and saline water along the Canadian coastline. Some of the undercurrent is transported into the Sound and connected inlets such as Nootka (Thomson 1983). This increase in nutrients could induce more primary productivity and thus increase the amount of HABs into Nootka.

The abundance and distribution of *Alexandrium* cysts near fish farms can be an indicator of the health of the marine environment as well as the potential presence of a HAB. Studying these cyst beds near fish farms may allow for further insight into the potential effects on the fish farm. The objective of this study is to observe the distribution of *Alexandrium* cysts near fish farms in Muchalat Inlet, Tahsis Inlet, and around Bligh Island. This survey will also investigate the relationship between *Alexandrium* cyst abundance and various environmental factors such as nutrients, sediment size, and current input.

The hypothesized results are that a higher number of *Alexandrium* cysts would be found by the fish farms and towns most likely due to the increased nutrients, which could subsequently affect the ecosystem of the waters and fish health (Falconer 1993). This result could be especially valid since eutrophication is an indicator of HABs (Harvell 1999). Excess nutrients in the form of fish tissue and feed have been theorized to impact the growth of phytoplankton via eutrophication of the waters (Gao 2012).

Methods

Samples were collected from December 13th to 18th, 2015 in Nootka Sound, Canada onboard the R/V Thomas G. Thompson. Sampling occurred upon entering the target sampling site and was impartial to time of day and weather. A Seabird SBE-9 CTD with a niskin bottle rosette, shipek grab, and a multi-corer instrument were cast and used in data collection.

Station M04 (Figure 1) was sampled using an Ocean Instruments MC200 sediment multi-corer with coring cylinders 1m long and 10cm in diameter. A 5cc subsample of sediment was taken from the top layer sample from each core collected. The sample was then bagged and stored in a dark cold room for the remainder of the cruise.

Shipek grabs were used for the rest of the stations. Once the sediment was procured, the top layer of the sediment was extracted, bagged and stored in the same cold room as the multi-core sample. Samples were analyzed in the labs at the University of Washington.

Sediment analysis

Sediment (5 g to 7 g) was placed in a jar mixed with dispersant solution (DI water and 0.05% sodium metaphosphate) in order to break down the clumps of sediment. The samples were then sonicated for 10 minutes to further break down the sediment as to ease the sieving process. The sample was then wet sieved through a 63 µm sieve and the material sieved out of the solution was placed in the oven at 60˚C to calculate the percent of sandy material. The sieved solution was placed in a 100 mL jar and run through a SediGraph III to analyze finer grain sediment (Poppe 2000).

Cyst processing

Sediment (5cc) was diluted in deionized water, sonicated, and sequentially sieved through 20 µm and 90µm nitex screens then placed in a centrifuge tube. The concentrated cysts were then fixed using a 10% formaldehyde solution, followed by storage in methanol for 48 hours in order to remove organic material that could conceal the cysts. The concentrated cysts were stained with primuline fluorescent dye and suspended in 5mL of deionized water then diluted to a 1:5 dilution of concentrated solution and DI water. This method is a modified version developed by Yamaguchi (1995).

In order to count the cysts, 1 mL of each stained sample was pipetted into a Sedgwick-rafter counting chamber for analysis. The samples were then placed into a Zeiss Axiovert 35 inverted microscope with epifluoresence. A mercury bulb with blue (420-490 nm) light excitation filter, and a 330-380 nm band pass excitation filter (for UV excitation) was used to activate the Primuline. The samples were viewed under 16x magnification and scanned for cysts. Counting and identification of the cysts was done manually (Yamaguchi 1995).

Nutrient data was taken at surface waters varying from 1 to 10 m in depth and then filtered through a 0.45 µm syringe filter into a 60 ml bottle and until stored in the freezer until the return to the University of Washington. The samples were then analyzed in the Marine Chemistry Lab, University of Washington Oceanography, using a Technicon AAII autoanalyzer.

Modeling

To determine where cysts might be most abundant in reference to fish farm locations, I used a model devised by Danny Grunbaum based on fluid dynamics analysis by Parker MacCready (MacCready, 2004). This model simulates transport of benthic marine invertebrate larvae and their deposition locations and rates into the sediment based on key estuarine properties from Willapa Bay in Washington. Because *Alexandrium* cells have a two-stage life cycle alternating between the water column and sediments similar to these larvae, I was able to adapt this model to simulate *Alexandrium* transport and deposition. The model was run using Octave-4.0.1. Release locations for cells were selected to match Nootka Sound fish farms in distance from the end of the inlet. Reported values suggest *Alexandrium* cells vary in sinking and swimming rates, depending on species and potentially other factors. Typically vegetative Alexandrium cells swim mostly in an upwards direction, while cysts sink in a directly downwards direction (in addition to transport by currents and turbulence). Simulations were run using a sinking rate of 100 µm/s, a value reported for *Alexandrium fundyense* (Aretxabaleta 2014). Swimming rates reported for two species of *Alexandrium* were used: 105 µm/s for Alexandrium *cantenella*, and 410 µm/s for *Alexandrium affine* (Smayda 2010). To assess potential impacts of pollution from fish farms, up-swimming cells were assumed to remain in the water column for 7 or 8 days before transitioning (Anderson 1997). A second parameter in the model determined how long cysts can survive in the water column before settling into sediments.

Because the literature suggests cysts are very tough and long-lived, this parameter was set such that cysts could stay in the water column for the duration of my simulations (100 days) (Anderson 1997). Cysts traveling beyond the distance corresponding to the mouth of Nootka Sound (55 km for Muchalat Inlet and 38.87 km for Tahsis Inlet) were considered to be exported from the estuary and not to contribute further to the resident population.

Results

Surface nitrate, nitrite, and phosphate concentrations in Muchalat were much lower in all stations compared to stations in Tahsis and Bligh Island (Table 1). Nutrient concentration in Muchalat was greatest in nitrate and nitrite near Gold River at station M04 with 0.15 µmol/L NO_2 and 8.13 µmol/L NO_3. Concentrations in Tahsis were greatest in nitrate, nitrite and phosphate at T06 where Tahsis and Esperanza intersect. In all three sections studied (Muchalat, Tahsis, Bligh Island), the waters near Bligh Island had the greatest concentration of nutrients in nitrate, nitrite and phosphate than all the other stations.

Alexandrium cysts found in this survey were of different sizes and shapes (Figure 2). Of the eight stations surveyed, stations M03 and BIO2 had the greatest number of *Alexandrium* cysts, while BI01 and T05 had the least number of *Alexandrium* cysts (Figure 1).

The greatest abundance of *Alexandrium* cysts occurred within 1.04 km of the fish farms (Figures 1, 3). Station BI02, which was 0.71 km from a fish farm, contained 337.5 *Alexandrium* cysts/cc and station M03 was 1.04 km from a fish farm contained 575 *Alexandrium* cyst/cc. Station T07, although not close to a fish farm, was the third most abundant having 275 *Alexandrium* cysts/cc and was 0.75km away from the town of Tahsis.

The sediment analysis of the stations with high abundances of *Alexandrium* cysts tended to be deposited with sediments that are around 85.47% to 89.44% fine grain sediment mostly comprising of clay material, with the exception of station TO7 which was 42.73% fine grain with similar percent values in clay and silty (Table 2) yet was the third most abundant station. Stations below and above that range tend to be low in *Alexandrium* abundance (Figure 4). Also stations in Tahsis have lower percent fine sediment than stations in Muchalat and near Bligh Island.

The model results suggest that in Muchalat most of the cysts released by the fish farms end up 5 km to ~25 km from the mouth of the Sound (Figure 6). Most of the *Alexandrium affine* cysts were transported out of the estuary at all release points in Muchalat except at station M04, as opposed to *Alexandrium cantenella* which mainly stayed in the estuary (Figure 6, 7). In Tahsis, the model suggest that the majority of *Alexandrium* cysts that could be influenced by the town of Tahsis are retained in the inlet (Figure 6, 7).

Discussion

Muchalat

The abundance of *Alexandrium* cysts varied in all stations. Muchalat station M03 contained the greatest abundance of cysts (Figure 2). This might be attributable to this station's proximity to a fish farm. Williamson Passage, where station M03 is located, has sills located on both sides of the passage. This location could potentially restrict flow out of the passage, and decrease the range which encysting *Alexandrium* could travel. Station M04, with the least number of *Alexandrium*, was within 3.71 km of a fish farm and 1.09 km from an industrial plant. The Gold River was within 1 km of the station and could have potentially transported the cysts further away from the station. Literature suggests that *Alexandrium* zygotes stay in the surface waters for at least seven days (Anderson 1997). Lastly, station M08 had a large number of *Alexandrium* cysts at 100 cysts/cc (Figure 2), but was within 1.05 km of two fish farms. This result could indicate that the flow of currents pushed the *Alexandrium* away from the fish farm or that there was an absence of a bloom in this location. The sediment data supports the findings in Mohamid (2011) paper, as cysts tended to be greater in number in places of finer sediment possibly due to having similar depositional properties (Figure 5).

The model suggests similar results to the actual data: Most *Alexandrium* cysts were found in the range of 5 km to 25 km away from the mouth of the Sound, which is where BI02, M03 and M08 are located (Figure 1, 6). The model results suggest an interpretation that *Alexandrium* cysts found in station M03 were most likely an accumulation of several sites further away from the mouth as well as *Alexandrium* at that site (Figure 7). The lower number of *Alexandrium* cysts found when compared to the other sites could be due the model being of Willapa Bay, not Nootka so there might be some differences in current, weather and salinity data or patchiness in *Alexandrium* cysts distribution in the sediment which were not addressed in the model.

Tahsis

Although the model suggests that there should be a high concentration of *Alexandrium* cysts at station T05, this was not the case. In Tahsis, the abundance of *Alexandrium* cysts was found to have less variation throughout the stations. Station T07 being close to a river delta, had the largest number of cysts among the Tahsis stations. This could be attributed proximity to the town of Tahsis (Figure 3), which may increase the amount of nutrients in the water. Additionally, since the town of Tahsis is close to the river delta, the depth of the water is shallower than in other parts of the inlet. This likely decreases settling time of sinking cysts, so if there was a bloom the cysts may be found in sediments much closer to the source. Thus for this to occur the cysts must have been deposited in fall when there is very little river input as opposed to spring when this model begins depositing the cysts. The low concentration at T06 could have been influenced by the Tahsis Narrows, which may flush water into the inlet and potentially move nutrients or the bloom itself away from this location.

Bligh Island

Because Bligh Island is located at the mouth of the sound, there will be more influence from the nutrients upwelled from the western coast in the summer, thereby providing the nutrients necessary for an *Alexandrium* bloom. This could explain the large abundance of *Alexandrium* cysts near station BI02. A fish farm located within 0.71 km of station BI02 and the waterway from the Zuciarte channel has a direct passageway from the ocean. This is opposite of BI01, which has no fish farm and contains 2 inlets before reaching the station (Figure 2). Another possible reason for this difference in the numbers of *Alexandrium* cysts found at station BI01 versus station BI02 are that blooms are occurring at the mouth of the sound in the summer and are being transported to stations in the Sound by currents from the Pacific Ocean and since BI01 is further from the mouth than BI02 fewer cysts are being deposited in that location. Also since currents around Bligh Island are predominately counter-clockwise (Nootka Coastal Land use Plan 2001) cysts would be more inclined to deposit at BI02 than BI01 as BI02 is the closest station relative to the movement of current.

Conclusion

This study found that, like previous studies, *Alexandrium* cysts are found in areas of fine grain material (mainly clay) due to their similarities in deposition (Dale 1975, Mohamid 2011). Also, fish farms could possibly affect the abundance of *Alexandrium* but more studies need to be done on the observed nutrients near fisheries and if the increase in nutrients is substantial enough to cause large blooms. As this study was conducted in the winter, the nutrient data is not indicative of the nutrients found in spring and summer when *Alexandrium* bloom and encyst. The nutrient profiles exhibit a baseline for future studies in the area. Additional studies need to be conducted in this region for the temperature variation in surface water, as well as to better understand if these waters are optimal for cysts to leave their cyst form.

Table 1: Surface nutrient data collected on the R/V Thomas G. Thompson in Nootka Sound along 8 different stations. Data were collected from the 13th to 18th December 2015. Concentrations of nutrients are in µmol/L, and depths are in meters.

Sample ID	**Depth**	**[PO_4]**	**[NO_3]**	**[NO_2]**
BI01	2	1.25	11.17	0.26
BI02	10	1.20	10.80	0.25
M03	2	0.82	7.60	0.14
M04	2	0.82	8.13	0.15
T05	1.3	0.82	8.58	0.12
T06	1.3	1.25	11.93	0.22
T07	10	1.06	10.40	0.17
M08	1.3	1.16	11.48	0.15

Table 2: Percent of sand, silt and clay in each sample.

	sand	**silt**	**clay**
BI01	7.41	18.42	77.78
BI02	10.67	20.99	69.41
M03	14.78	16.45	70.47
M04	50	18.70	33.60
T05	65.45	21.16	25.29
T06	17.07	22.97	62.78
T07	59.63	22.49	22.00
M08	10.40	15.77	76.52

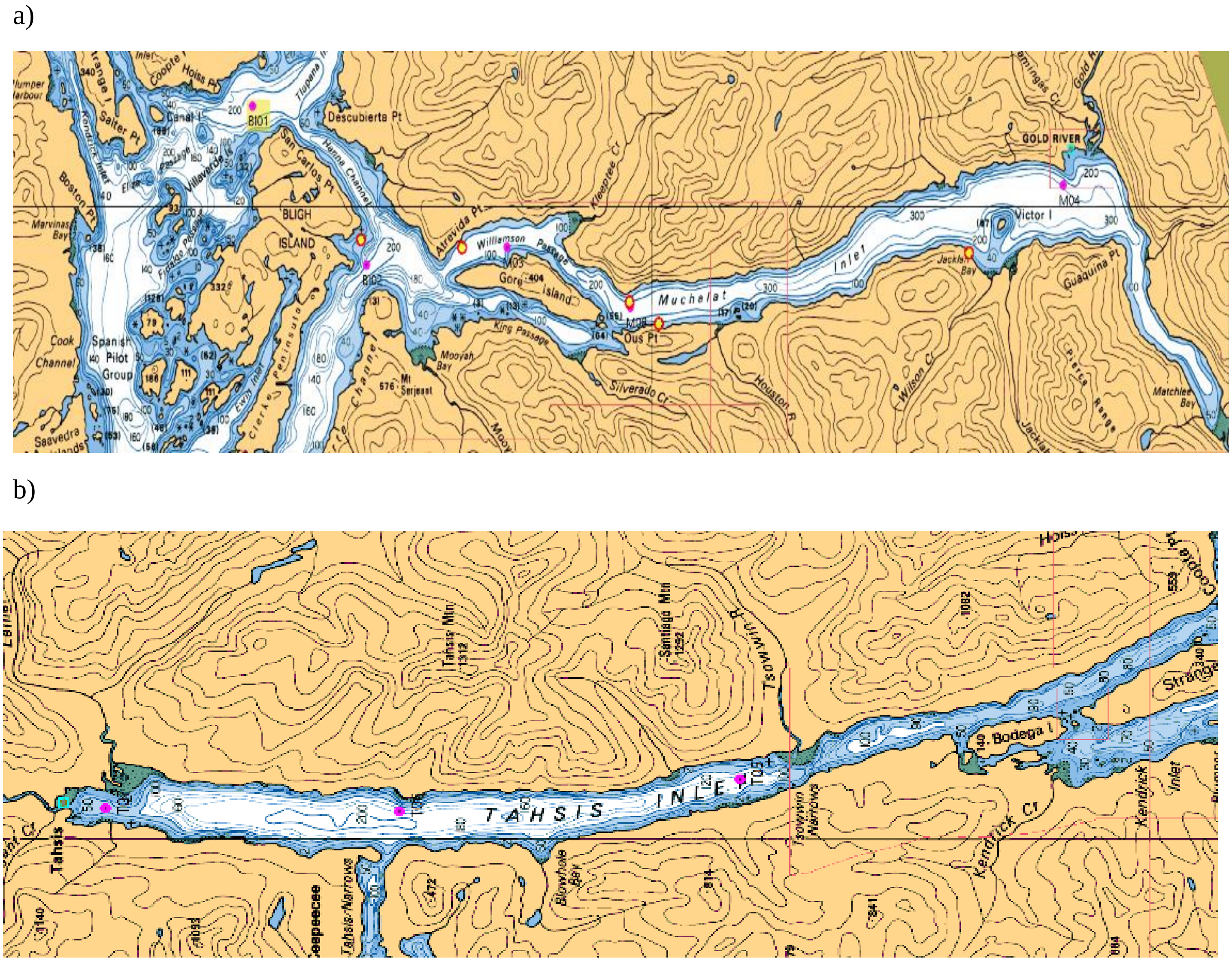


Figure 1

Maps of the sediment stations sampled in Nootka from Tahsis (a), Williamson Passage, Muchalat and Gold River (b). Pink dots: sampled stations; yellow dots: known fish farms; green squares: towns or industrial plants. In Tahsis Inlet, fish farms were observed visually, but the exact location of the farms were unknown so they were not be included in the figure. Station number 1 was the control, as there were no nitrogenous waste sources identified nearby.

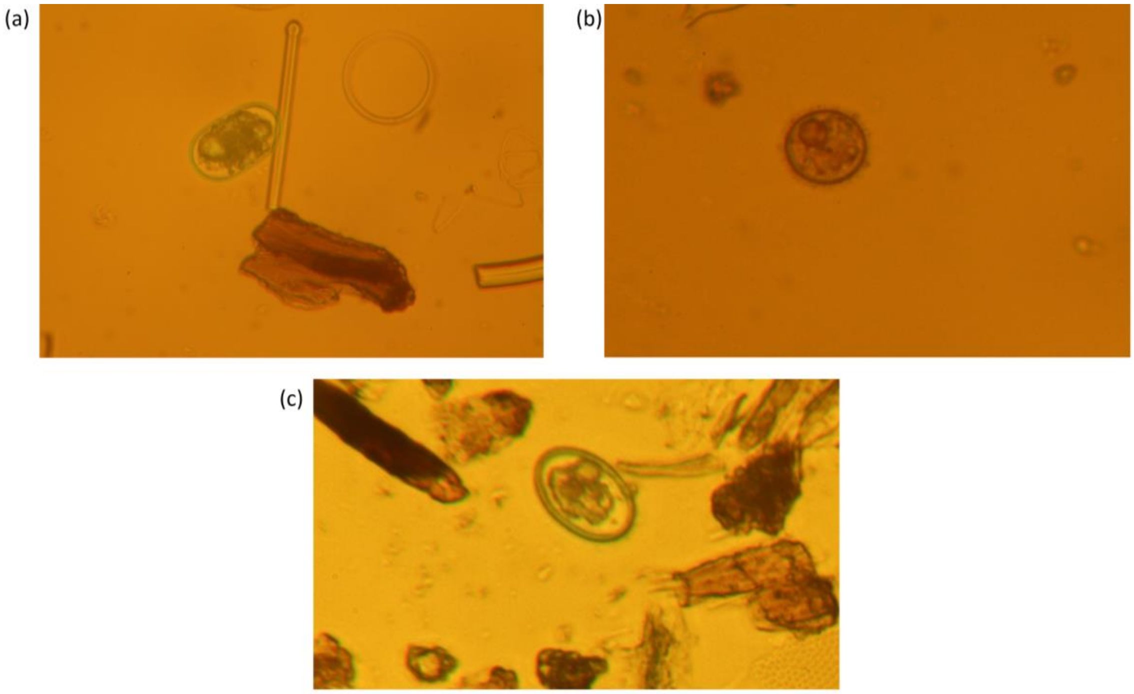


Figure 3

Alexandrium cysts (a-c) identified under an epifluorescent microscope stained with a 10% primuline solution viewed under tungsten light.

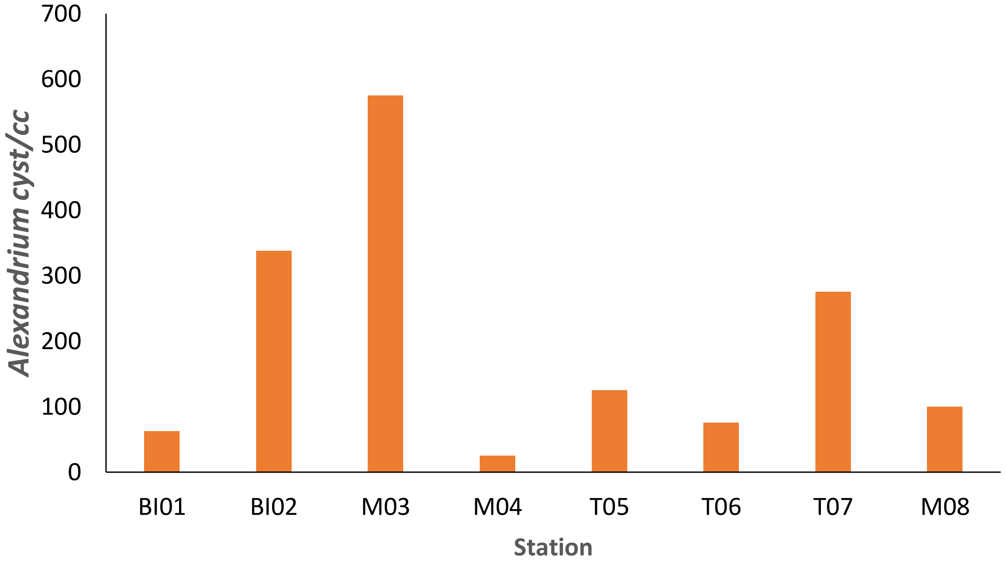


Figure 3

Abundance of *Alexandrium cysts*/cc of sediment with station number. The letter represents the location of the station (see Figure 1) while the number represents the station number.

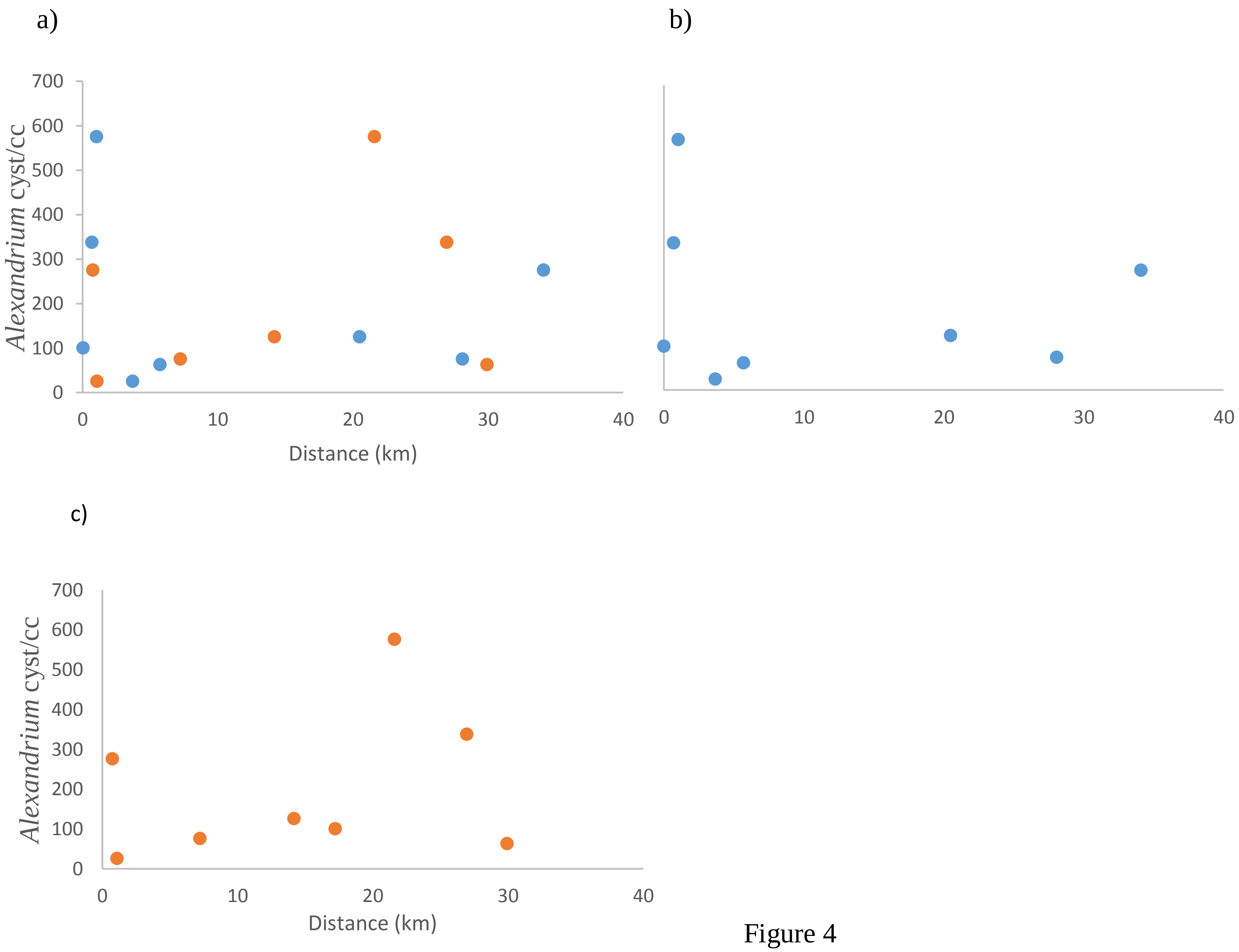


Figure 4

Alexandrium distributions relative to possible pollution sources. (a) Distance from the nearest nitrogenous waste source (fish farm or town/industrial plant) against *Alexandrium* cyst abundance for all stations (gray). (b) Distance to fish farms for all stations against the abundance of *Alexandrium* cysts (blue). (c) Distance to town/industrial plant for all stations against the abundance of *Alexandrium* cysts (orange).

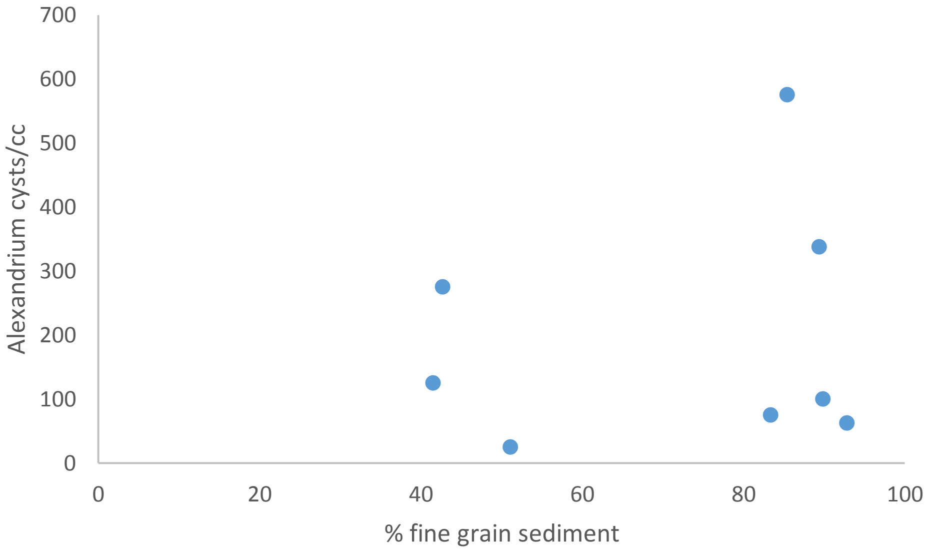
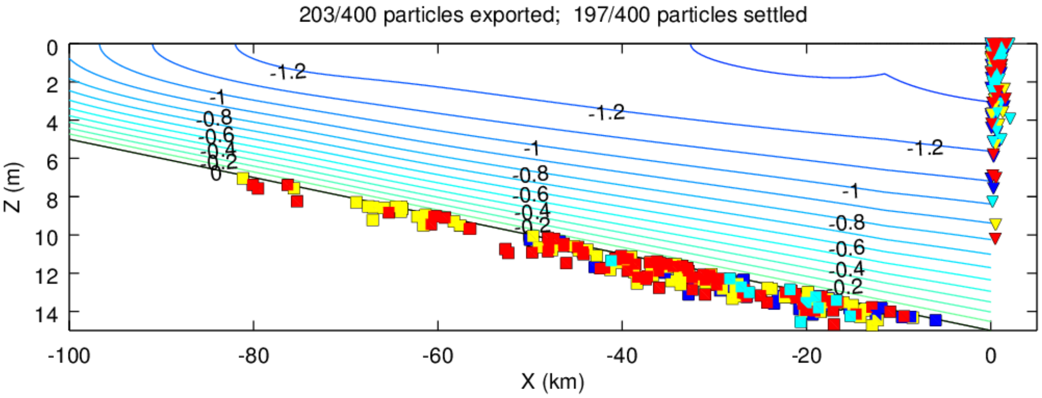


Figure 5

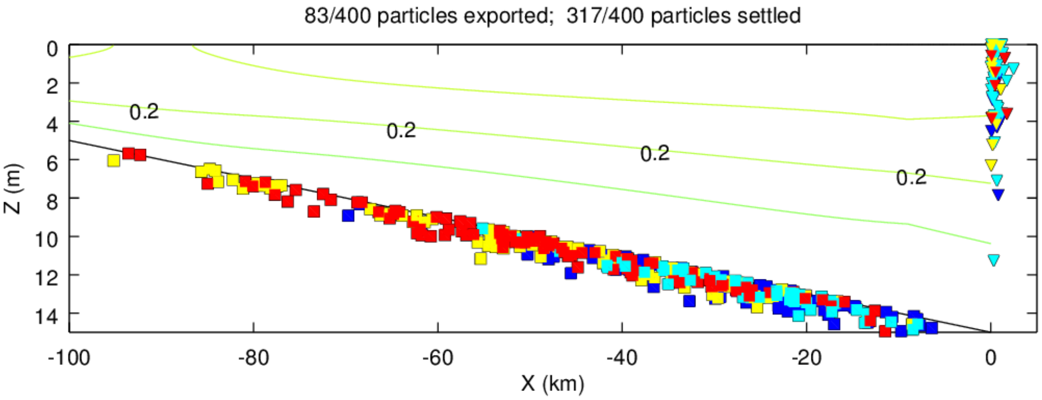
The percent silty or finer grain material (<63um) vs. abundance of *Alexandrium* cysts.

a)



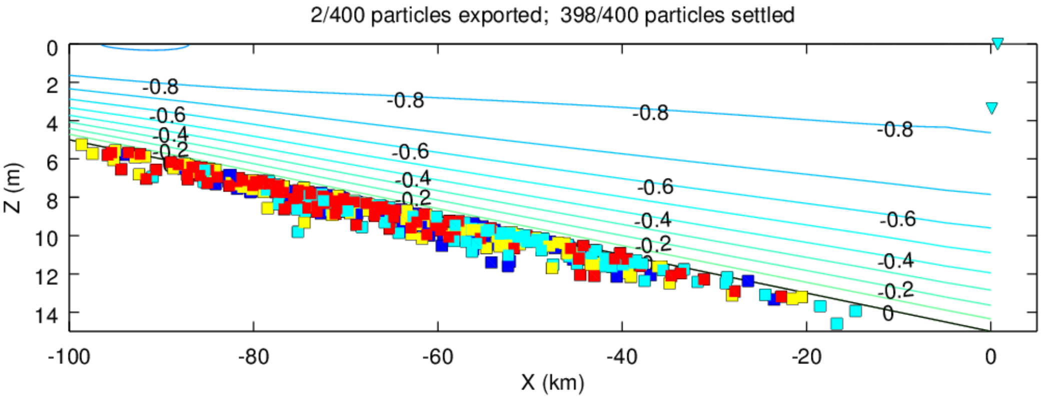
203/400 particles exported; 197/400 particles settled
Z (m)
0
2
4
6
8
10
12
14
-100
-80
-60
-40
-20
0
X (km)
-1.2
-1.2
-1.2
-1
-1
-1
-0.8
-0.8
-0.8
-0.6
-0.6
-0.6
-0.4
-0.4
-0.4
-0.2
-0.2
-0.2
0

b)



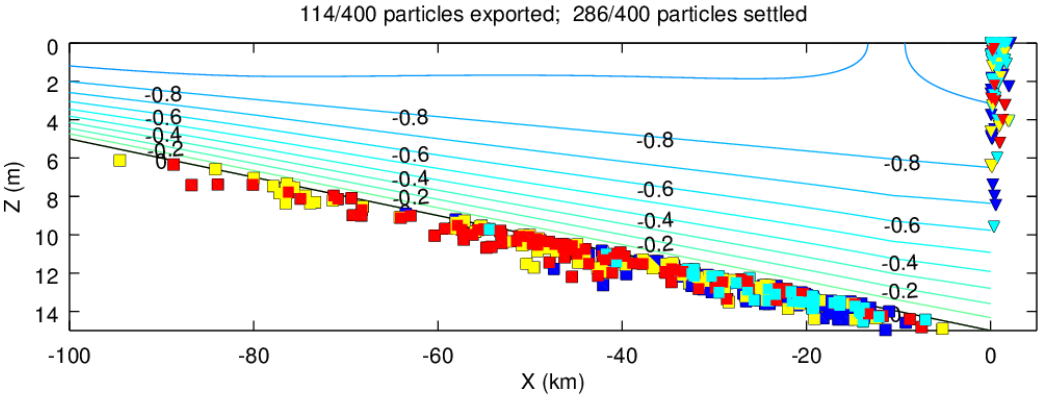
83/400 particles exported; 317/400 particles settled
Z (m)
0
2
4
6
8
10
12
14
-100
-80
-60
-40
-20
0
X (km)
0.2
0.2
0.2
0.2

c)



2/400 particles exported; 398/400 particles settled
Z (m)
0
2
4
6
8
10
12
14
-100
-80
-60
-40
-20
0
X (km)
-0.8
-0.8
-0.8
-0.8
-0.6
-0.6
-0.6
-0.6
-0.4
-0.4
-0.4
-0.4
-0.2
-0.2
-0.2
-0.2
0

d)


114/400 particles exported; 286/400 particles settled

e)

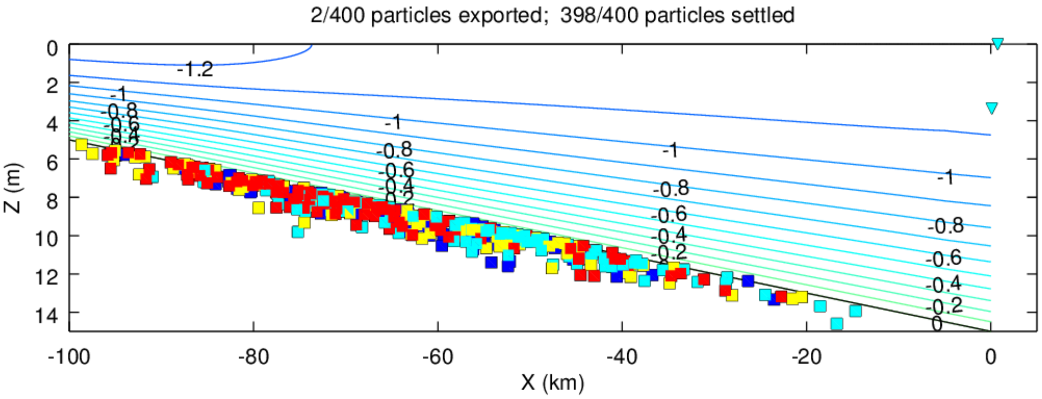
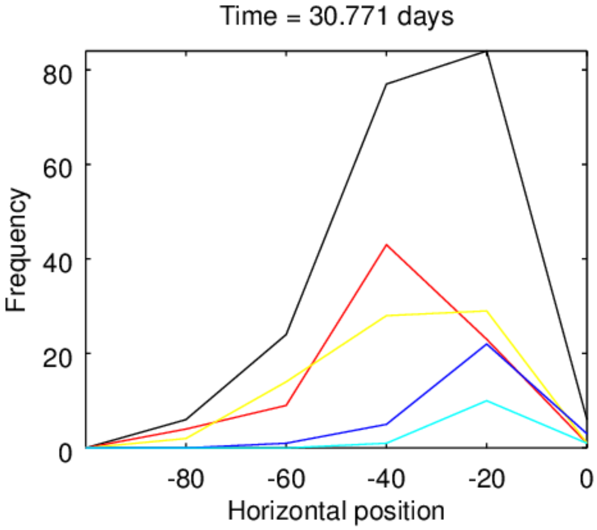

2/400 particles exported; 398/400 particles settled

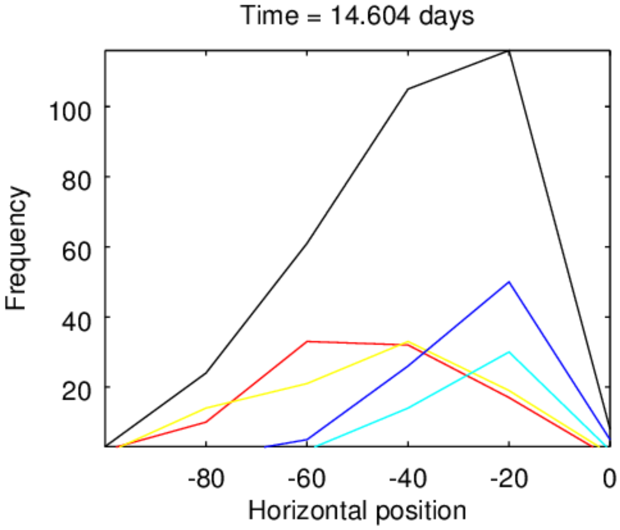
Figure 6:

Simulated distributions of *Alexandrium* cysts. (a) Graph of the final distribution of *Alexandrium* by fish farm near BI02, graph (b) is the final distribution of *Alexandrium* by fish farm near M03, graph (c) is the final distribution of *Alexandrium* by fish farms near M04, graph (d) is the final distribution of *Alexandrium* by fish farms near M08, graph (e) is the final distribution ease point of *Alexandrium* by town near T07. The Y-axis is the distance away from the mouth of the Sound in km, while the y-axis is the depth of the water in m. Contour lines represent horizontal velocity. The corresponding distances from the mouth of the estuary are 45 km for Muchalat Inlet and 61.13 km for Tahsis. Red: *Alexandrium cantenella* sinking at day 7, yellow: *Alexandrium cantenella* sinking at day 8, blue: *Alexandrium cantenella* sinking at day 7, cyan: *Alexandrium cantenella* sinking at day 8.

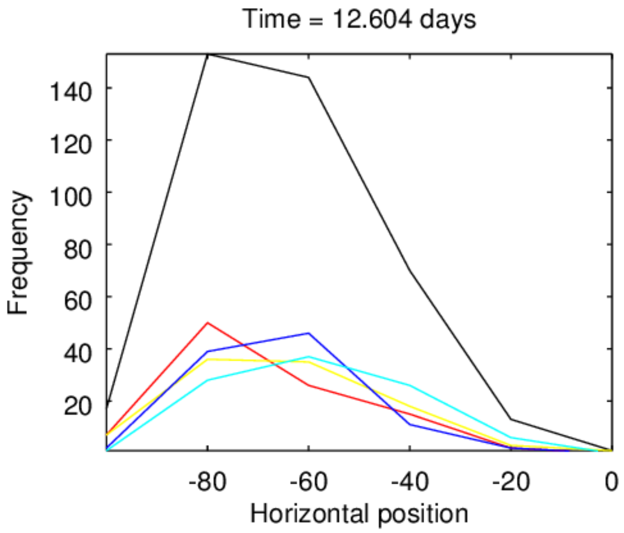
a)


Time = 30.771 days
Frequency
80
60
40
20
0
-80
-60
-40
-20
0
Horizontal position

b)

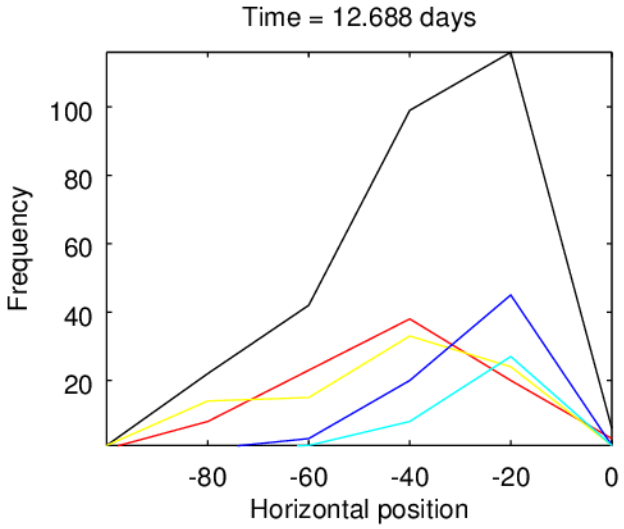

Time = 14.604 days
Frequency
100
80
60
40
20
-80
-60
-40
-20
0
Horizontal position

c)



Time = 12.604 days
Frequency
140
120
100
80
60
40
20
-80
-60
-40
-20
0
Horizontal position

d)



Time = 12.688 days
Frequency
100
80
60
40
20
-80
-60
-40
-20
0
Horizontal position

e)

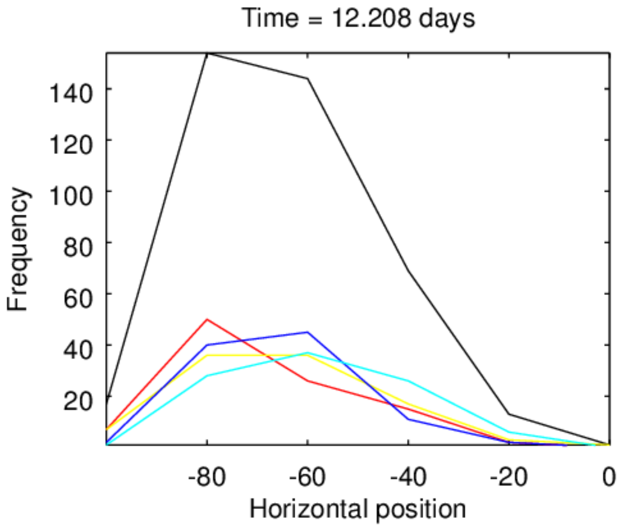


Figure 7: Final distribution of simulated cysts in estuary sediments. These plots depict where *Alexandrium* cysts settle and the number of simulated *Alexandrium* cysts that settle there. 45 km is the distance from the mouth from Muchalat Inlet and 61.13 km is the distance from the mouth from Tahsis. Red: *Alexandrium cantenella* sinking at day 7, yellow: *Alexandrium cantenella* sinking at day 8, blue: *Alexandrium cantenella* sinking at day 7, cyan: *Alexandrium cantenella* sinking at day 8, black: total *Alexandrium.*

Citations

Anderson, Donald M. "Bloom Dynamics of Toxic Alexandrium Species in the Northeastern U.S." Limnol. Oceangr. Limnology and Oceanography 42, no. 5_part_2 (1997): 1009-022. doi:10.4319/lo.1997.42.5_part_2.1009.

"Aquaculture Industry, by Selected Provinces (Canada)." Government of Canada, Statistics Canada. Web. 15 Nov. 2015.

Clark, R. F., Williams, S. R., Nardt, S. P., & Manoguerra, A. S. (1999). A review of selected seafood poisonings. Undersea & Hyperbaric Medicine, 26(3), 175-84.

Cosper, E.M. 1989. Novel phytoplankton blooms: Causes and impacts of recurrent brown tides and other unusual blooms. Berlin: Springer-Verlag.

Dale, B. 1976. Cyst formation, sedimentation, and preservation: factors affecting dinoflagellate assemblages in recent sediments from Trondheimsfjord, Norway. Rev. Palaeobot. Palynol.

Falconer, Ian R. 1993. Algal toxins in seafood and drinking water. London: Academic Press.

Gao, Yongli, Kedong Yin, Lei He, and Paul Harrison. "Phytoplankton Growth on Organic Nutrients from Trash Fish." AQUATIC ECOSYSTEM HEALTH & MANAGEMENT 15.2 (2012): 234-40. Print.

Hansen, Pj. "The Red Tide Dinoflagellate Alexandrmm Tamarense: Effects on Behaviour and Growth of a Tintinnid Ciliate." Marine Ecology Progress Series Mar. Ecol. Prog. Ser. 53 (1989): 105-16. Web.

Harvell, C. D., Kim, K., Burkholder, J. M., Colwell, R. R., Epstein, P. R., Grimes, D. J., Hofmann, E. E., et al. 1999. Review: marine ecology – emerging marine diseases – climate links and anthropogenic factors. Science 285:1505–10.

Mardones, Jorge I., Juan José Dorantes-Aranda, Peter D. Nichols, and Gustaaf M. Hallegraeff. "Fish Gill Damage by the Dinoflagellate Alexandrium Catenella from Chilean Fjords: Synergistic Action of ROS and PUFA." Harmful Algae 49 (2015): 40-49. Web.

Maccready, Parker. "Toward a Unified Theory of Tidally-averaged Estuarine Salinity Structure." Estuaries 27.4 (2004): 561-70. Web.

Mohamed, Z. A., & Al-Shehri, A. M. (2011). Occurrence and germination of dinoflagellate cysts in surface sediments from the Red Sea off the coasts of Saudi Arabia. Oceanologia, 53(1), 121-136. doi:10.5697/oc.53-1.121

Nock, Max, Darrell Robb, Earl Warnock, Ted Hall, Ron Lampard, Dave C. Chair, and Joe Truscott. "Nootka Coastal Land Use Plan." 31 May 2001. Web. 31 May 2016.

Poppe, L. J., A. H. Eliason, J. J. Fredericks, R. R. Rendigs, D. Blackwood, and C. F. Polloni. 2000. chapter1 @ pubs.usgs.gov. U.S. Geological Survey.Sildever, S., Andersen, T. J.,

Ribeiro, S., & Ellegaard, M. (2015). Influence of surface salinity gradient on dinoflagellate cyst community structure, abundance and morphology in the Baltic Sea, Kattegat and Skagerrak.

Smayda, T.j. "Adaptations and Selection of Harmful and Other Dinoflagellate Species in Upwelling Systems. 2. Motility and Migratory Behaviour." Progress in Oceanography 85.1-2 (2010): 71-91. Web.uarine, Coastal and Shelf Science, 155, 1-7. doi:10.1016/j.ecss.2015.01.003

Spector, David L. 1984. Dinoflagellates. Orlando: Academic Press.

Taylor, F.J.R., P., Harrison, 2002. PICES Scientific Report No. 23, 2002. Harmful algal blooms in western Canadian coastal waters. North Pacific Marine Science Organization (PICES). C/o Institute of Ocean Sciences, P.O. Box 6000, Sidney, B.C., Canada. V8L 4B2 http://www.pices.int.

Thomson, Richard E. Oceanography of the British Columbia Coast. Ottawa: Dept. of Fisheries and Oceans, 1981. Print.

Trainer, V.L. and Yoshida, T. (Eds.) 2014. Proceedings of the Workshop on Economic Impacts of Harmful Algal Blooms on Fisheries and Aquaculture. PICES Sci.

Wild-Allen, Karen, Mike Herzfeld, Peter A. Thompson, Uwe Rosebrock, John Parslow, and John K. Volkman. "Applied Coastal Biogeochemical Modelling to Quantify the Environmental Impact of Fish Farm Nutrients and Inform Managers." Journal of Marine Systems 81.1-2 (2010): 134-47. Web.

Zonneveld, Karin A. F., Ewa Susek, and Gerhard Fischer. "Seasonal Variability Of The Organic-Walled Dinoflagellate Cyst Production In The Coastal Upwelling Region Off Cape Blanc (Mauritania): A Five-Year Survey1." Journal of Phycology 46.1 (2010): 202-15. Web.