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Groundfish overfishing, diatom decline, and the marine silica cycle: Lessons from Saanich Inlet, Canada, and the Baltic Sea cod crash

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[1] In this study, we link groundfish activity to the marine silica cycle and suggest that the drastic mid-1980s crash of the Baltic Sea cod (*Gadus morhua*) population triggered a cascade of events leading to decrease in dissolved silica (DSi) and diatom abundance in the water. We suggest that this seemingly unrelated sequence of events was caused by a marked decline in sediment resuspension associated with reduced groundfish activity resulting from the cod crash. In a study in Saanich Inlet, British Columbia, Canada, we discovered that, by resuspending bottom sediments, groundfish triple DSi fluxes from the sediments and reduce silica accumulation therein. Using these findings and the available oceanographic and environmental data from the Baltic Sea, we estimate that overfishing and recruitment failure of Baltic cod reduced by 20% the DSi supply from bottom sediments to the surface water leading to a decline in the diatom population in the Baltic Sea. The major importance of the marginal ocean in the marine silica cycle and the associated high population density of groundfish suggest that groundfish play a major role in the silica cycle. We postulate that dwindling groundfish populations caused by anthropogenic perturbations, e.g., overfishing and bottom water anoxia, may cause shifts in marine phytoplankton communities.

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1. Introduction

[2] Atlantic cod (Figure 1a) are commercially valuable groundfish that prey on fish and benthic invertebrates [*Link and Garrison*, 2002]. The cod population in the Baltic Sea (Figure 2) crashed in the mid-1980s as a result of overfishing and has not recovered since [*Alheit et al.*, 2005]. This decline in the cod population is contemporaneous with a series of very sharp and distinct events [*Alheit et al.*, 2005]. These events occurred after the end of long-term environmental trends that started soon after WW II [*Conley et al.*, 2008] and stabilized during the 1970s [*Papush and Danielsson*, 2006]. Soon after the crash, the abundance and productivity of diatoms that constitute the base of the marine food chain [*Mann*, 1993] dropped sharply and remained low thereafter [*Alheit et al.*, 2005; *Wasmund et al.*, 1998]. Decrease in diatom productivity in the Baltic Sea was explained by (1) water stagnation related to mild winters resulting from the North Atlantic Oscillation [*Alheit et al.*, 2005] (see explanation in section 4.6); (2) shift in the ratio of Si to N and P in the riverine loads [*Rahm et al.*, 1996]; and (3) reduction in silica concentration in the surface water [*Danielsson et al.*, 2008]. This reduction in DSi was ascribed to its enhanced uptake by diatoms resulting from eutrophication [*Conley and Johnstone*, 1995] and to silica entrapment upstream from river dams [*Humborg et al.*, 2006]. However, the timing of the Baltic diatom decline and other related observations are inconsistent with these suggested mechanisms (see sections 4.4 and 4.5). This paper provides evidence linking sediment resuspension activity of groundfish to the marine silica cycle, thus providing a new explanation for the observed diatom decline.

[3] It was recently shown that sediment resuspension may greatly enhance DSi fluxes from the sediments, thereby increasing DSi concentrations in the water column [*Bonnin and Van Raaphorst*, 2004; *Tengberg et al.*, 2003]. While sediment resuspension in the marine environment is customarily attributed to physical factors such as currents, wind, and

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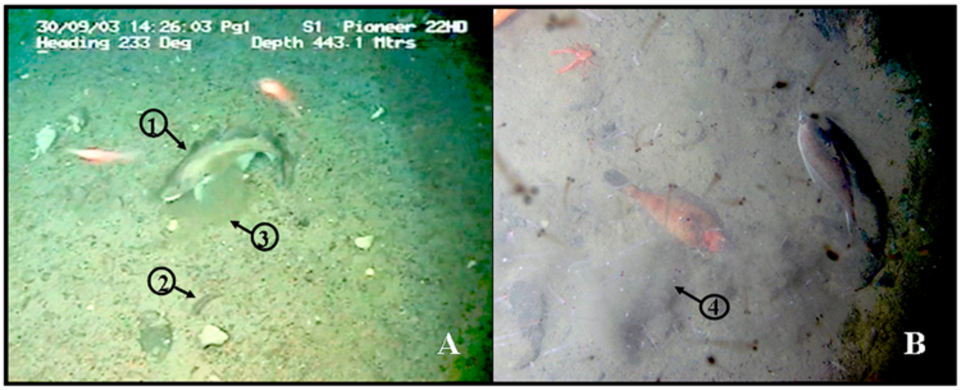

Figure 1. Groundfish activity resulting in sediment resuspension. (a) An Atlantic cod (*Gadus morhua*) (arrow 1) in the North Sea resuspends bottom sediments (sediment cloud marked by arrow 3) while hunting small fish (arrow 2) and benthic invertebrates. The picture frame was grabbed from a video taken by an ROV at depth of 443 m (see Movie S1, courtesy of the SERPENT Project: http://www.serpentproject.com). (b) Slender sole (*Lyopsetta exilis*; ~10 cm length) in Saanich Inlet. The species comprises about 90% of the flatfish population (~0.5 fish m^{-2}) in the depth range 80 m to the hypoxic zone. Above 80 m, other flatfish species become abundant. The fish in the photo (taken by the VENUS in situ camera at 93 m depth) is seen resuspending sediment (arrow 4), either moving around or trying to catch overhead zooplankton.

tidal energy [*Dezileau et al.*, 2000; *Ward*, 1985], biological factors have generally been neglected. Our recent studies showed, however, that groundfish are major agents of sediment resuspension during their search for food and shelter [*Yahel et al.*, 2008, 2002]. These studies led to the hypothesis of the present study that groundfish activity enhances sedimentary opal dissolution that controls DSi fluxes from marine sediments and silica supply to diatoms.

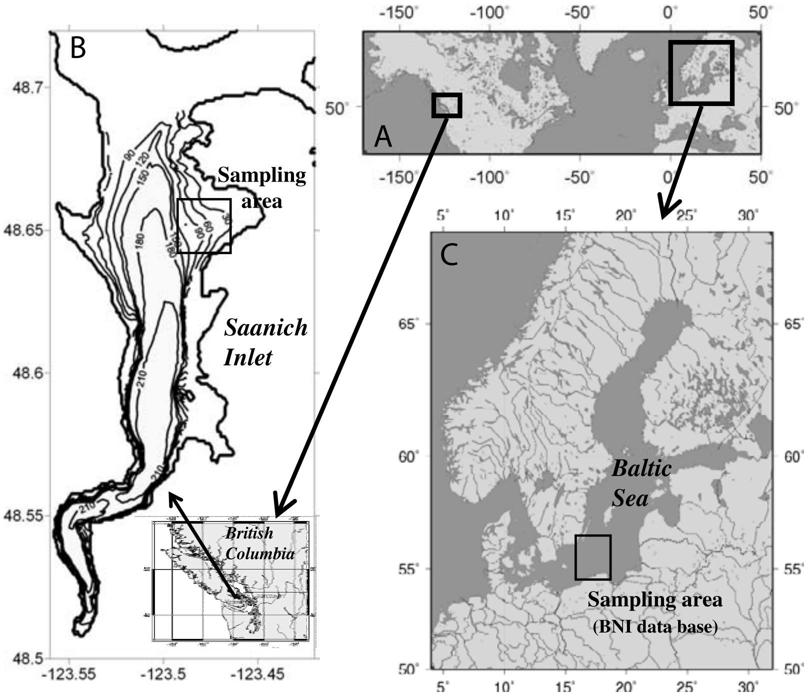

Figure 2. (a) Location map of Saanich Inlet and the Baltic Sea. (b) Map of Saanich Inlet. Anoxic and oxygenated regions are marked by shaded and white areas, respectively. Black frame at the northeast of Saanich Inlet marks our study site in Patricia Bay. Inset shows the location of Saanich Inlet in British Columbia, Canada. (c) Map of the Baltic Sea. Black frame in the Baltic proper marks the area from which historical DSi measurements were extracted.

[4] The study was conducted in Saanich Inlet (Figure 2b), a partly anoxic basin in British Columbia, Canada, that served as a "natural laboratory" for examining the potential effect of groundfish activity on the silica cycle. The main relevant characteristics of Saanich Inlet are (1) only the oxygenated margins (about half of the basin area) are subjected to groundfish resuspension activity, whereas the deep intermittently anoxic basin is generally devoid of groundfish [*Yahel et al.*, 2008]; (2) diatom production and the downward export of opal frustules from the surface water are relatively high in the entire basin area [*Timothy et al.*, 2003]; and (3) physical resuspension of sediments is negligible because bottom currents are very weak [*Yahel et al.*, 2008]. In an earlier study we found that flatfish in the oxygenated margins of Saanich Inlet rework the entire seafloor about once every 2 to 3 days, resuspending ~1.3 L bulk sediment m^{-2} d^{-1} in 100 resuspension events m^{-2} d^{-1} [*Yahel et al.*, 2008]. These findings were the basis for the hypothesis that groundfish activity may play a major role in the marine silica cycle, which was tested for the first time in the Saanich Inlet study presented below. This new understanding was used to reexamine available fisheries, biological, and geochemical data from the Baltic Sea to infer a linkage between trends in groundfish and the marine silica cycle on a whole-basin scale.

2. Materials and Methods

2.1. Description of the Study Site at Saanich Inlet, British Columbia

[5] Saanich Inlet (Figure 2) is an intermittently anoxic fjord on southeast Vancouver Island, British Columbia, Canada. The basin is anoxic during most of the year as a result of high productivity and restricted water exchange through the shallow, 70 m deep sill at the mouth of the inlet. The maximum depth in the inlet is 230 m, and total surface area is 65 km^2 [*Gucluer and Gross*, 1964]. The inlet is highly productive (~490 g C m^{-2} yr^{-1}) [*Timothy and Soon*, 2001]; sedimentation of organic carbon and opal at the mouth of the fjord (45 m depth) is 130 and 670 g m^{-2} yr^{-1}, respectively [*Timothy et al.*, 2003]. The laminated sediments in the anoxic basin of the fjord reflect the annual sedimentation cycle in which the ratio of plankton (mostly diatoms) to terrestrial matter is high in summer and spring and low in winter [*Gucluer and Gross*, 1964; *Tunnicliffe*, 2000]. The study was conducted on the eastern slope of Saanich Inlet in Patricia Bay (48°39′N; 123°28′W) at a water depth of ~95 m. The sediments of the study area are oxygenated (no microbial mat or detectable H_2S odor), defined as "near-shore sediments" by *Gucluer and Gross* [1964]. Bottom current velocities (1 m above bottom) are 3.6 ± 2.4 cm s^{-1} and too slow to resuspend bottom sediments [*Yahel et al.*, 2008]. Many fish, mostly sole (*Pleuronectidae*) species, inhabit the seafloor (Figure 1b). Only a few flatfish inhabit the hypoxic zone between 100 and 130 m where the sediments contain dissolved sulfide that maintains *Beggiatoa* mats. For additional background information, see the Fisheries and Oceans Canada Web site: http://www.pac.dfo-mpo.gc.ca/sci/osap/projects/bcinlets/saanich_inlet_e.htm.

2.2. Work in Saanich Inlet

[6] Underwater work was conducted by the remotely operated vehicle ROPOS (see ROV specifications at http://www.ropos.com) operated from the CCGS *J.P. Tully*. ROPOS was equipped with video and still cameras, two robotic arms, and conductivity-temperature-depth (SBE 19 plus CTD, SeaBird), dissolved oxygen (SBE 43, SeaBird), and turbidity (SeaStar 25 cm Transmissometer, WetLabs) sensors.

[7] Eleven push cores, 20 cm long, 4.5 cm diameter (five in July 2005 and six in February 2006) were taken from the study site for pore water analyses, characterization of bulk sediment properties, and laboratory experiments (see section 3.3). Core sampling was monitored by the ROPOS video; cores that were agitated during sampling were immediately emptied and retaken. Thirty-two additional cores (7.6 cm diameter) were collected for infauna analyses on July 2005 and February 2006 using the processing analytical procedures of *Ramey and Snelgrove* [2003].

[8] Bottom waters for the laboratory experiments were collected in Niskin bottle casts from the ship. Bottles were refrigerated (4°C) until the laboratory experiments. Methods for estimating fish abundance, distribution, taxonomy, morphometrics, behavior, and rate of fish resuspension are described by *Yahel et al.* [2008].

2.3. Sediment and Water Analyses

[9] Water fraction and porosity in the bulk sediments were determined gravimetrically [*Hakanson and Jansson*, 1983]. Sediment was dried in a drying oven at 60°C, and weights were corrected for salinity of 31; dry sediment density was taken from *Gucluer and Gross* [1964]. Pore waters were extracted by sediment centrifugation (5000 RPM for 10 min), and DSi in the water was determined after dilution of 1: 20 by the molybdate blue spectrophotometric method [*Strickland and Parsons*, 1968] using Flow Injection Analyzer (Quick Chem 8000, Lachat Instruments) with precision of 0.05 μ mol L^{-1} or 0.8% in diluted samples. Sedimentary opal was determined by the alkaline extraction method [*Mortlock and Froelich*, 1989].

[10] Nutrients including DSi were analyzed at the geochemical laboratory of the Interuniversity Institute in Eilat, Israel. Quality check was provided by intercalibration with the laboratories of University of British Columbia (UBC) and the Institute of Ocean Sciences. Opal content in a subset of sediment samples from Pat-Bay, Saanich Inlet, was also determined at UBC.

2.4. Fish Resuspension Simulation Experiment

[11] The aim of the resuspension experiment was to quantify and study the dynamics of DSi release from resuspended Saanich Inlet sediments. In a series of trials, we examined DSi release from sediments following a brief resuspension event (simulating fish activity). Saanich Inlet oxygenated sediments were sampled with PVC corers from a depth of 95 m in Pat-Bay, ~1 day before starting the experiments. Each experiment started with a brief (10 s) resuspension of a preweighed, 2 cm thick slice of surface sediments in 2 L of either ambient or poisoned (+1% saturated $HgCL_2$ solution) bottom water in plastic vessels.

Table 1. Water Fraction, Porosity, Opal Content, and Pore Water Silica in Cores[a]

	Depth in Core (cm)	Water Fraction (%)	Porosity (φ)	Opal (%)	DSi (μmol L^{-1})
July 2005	overlying water	-	-	-	58
	0–0.5	49 ± 3.8	0.79 ± 0.06	3.5 ± 0.3	400 (n = 1)
	0.5–1	48 ± 4.3	0.80 ± 0.07	4.0 ± 0.2	
	1–2	44 ± 1.8	0.70 ± 0.06	3.7 ± 0.2	
February 2006	overlying water	-	-	-	63 ± 4
	0–0.5	61 ± 0.1	0.83 ± 0.00	2.6 ± 0.1	380 ± 20
	0.5–1	54 ± 1.9	0.79 ± 0.01	2.8 ± 0.3	
	1–2	52 ± 1.4	0.77 ± 0.01	2.9 ± 0.3	450 ± 10

[a] Collected on two dates (July 2005 and February 2006) at a depth of 90 m on the margin of Saanich Inlet. Three cores were collected on each date, and the data shown are average ± standard deviations of the analyses.

The layer thickness was chosen to match the sediment depth range resuspended by slender sole, *Lyopsetta exilis*, which is the most abundant bottom fish at the site [*Yahel et al.*, 2008]. Thereafter, the waters were gently stirred at the surface, allowing sediment particles to settle while maintaining a homogeneously mixed water column. Water temperature in the vessels was 11–12°C, which is 1–2°C higher than ambient water temperatures. Water samples for DSi analyses were taken once prior to resuspension and 5 times in the 18 h after resuspension; samples were filtered using a syringe and syringe filters (0.2 μm pore size) to remove particulate matter.

2.5. In Situ Fish Exclusion Experiments

[12] Four cylindrical excluder cages (1 m^2 in diameter; 15 cm height with 2.5 cm plastic mesh) were deployed in Saanich Inlet at a depth of ~92 m where the flatfish were abundant. The cages prevented fish from reaching the bottom beneath them and reworking the sediment. Sediment cores for opal analyses and infaunal abundance were taken from the study site prior to deployment and again, 7 months later when the cages were removed and processed as described in section 2.3.

2.6. DSi Data From in the Baltic Sea

[13] DSi data collected in the southern Baltic Sea (Figure 2c) between the years 1970 and 2000 were obtained courtesy of the online database of the Baltic Nest Institute (2007, http://nest.su.se/).

2.7. Resuspension Activity of Atlantic Cod

[14] Cod resuspension behavior was observed in footage of Atlantic cod foraging over soft bottom taken by ROV in the North Sea at a depth of ~440 m (Movie S1).[1] This video was obtained courtesy of the SERPENT Project (http://www.serpentproject.com/).

3. Results

3.1. Resuspension by Fish in Saanich Inlet

[15] Below 130 m, the bottom water of Saanich Inlet is usually anoxic [*Anderson and Devol*, 1973], and the seafloor at these depths is devoid of groundfish. At shallower depths, the seafloor is oxygenated and inhabited by an abundant groundfish population, mostly pleuronectid flatfish. The bottom areas of the oxic and anoxic zones in Saanich Inlet are about equal, indicating that groundfish inhabit about half of the inlet's seafloor. The groundfish population above 80 m depth is quite diverse, whereas between 80–130 m, the groundfish community is dense (0.5–1 fish m^{-2}) and dominated by the small flatfish *Lyopsetta exilis* [*Yahel et al.*, 2008].

[16] Groundfish constantly rework the seafloor, resuspending sizable clouds of sediment as they bury themselves in the sediment or when emerging from it to change their location (Movie S2). Groundfish are the major cause for sediment resuspension in Saanich Inlet. Video, acoustic, and optic data show that the groundfish resuspension rate is ~100 major resuspension events m^{-2} d^{-1} [*Yahel et al.*, 2008]; numerous minor resuspension events were not included in the above estimate [*Yahel et al.*, 2008]. It should be noted that sediment resuspension was caused not only by benthic dwellers and benthic feeders but also by foraging piscivorous spiny dogfish sharks (*Squalus. acanthias*, Movie S3) and Pacific herring (*Clupea pallasii*) which are pelagic planktivores. These fish resuspended the sediment by either impacting the sediment directly or by generating strong turbulence in the overlying waters with their fins.

3.2. Sediment Characteristics

[17] The color of the oxygenated bottom sediments of the study area was olive green with no sulfide odor. The sediments were comprised mostly of fine sand. Fine gravels and sometimes even pebbles (up to 2.5 cm in diameter) were present 5 cm below surface in several cores (see other physicochemical characteristics of Saanich-Inlet sediments in Table 1). Opal content in the sediments at our study site (90 m depth) ranged between 2 and 5%. Opal concentrations within this range (4.8 ± 0.2%) were also measured at UBC in a subset of sediment samples from our study site (data courtesy of A. Chang, 2006). Counts show that infaunal abundance in the study site is comparatively low (see Figure S1).

3.3. Simulation Experiments of Fish Resuspension

[18] Following each resuspension event, DSi concentrations in the experimental vessel increased considerably with time (Figure 3a), and the final DSi concentrations were directly proportional to the amount of resuspended sediment (Figure 3a). There was no significant difference in the DSi release rate when equivalent weights of sediment were resuspended either in poisoned or "normal" bottom water (Figure 3a). This result indicates that opal dissolution rate was not controlled biologically. The DSi increase with time

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[1] Auxiliary materials are available in the HTML. doi:10.1029/2008GB003416.

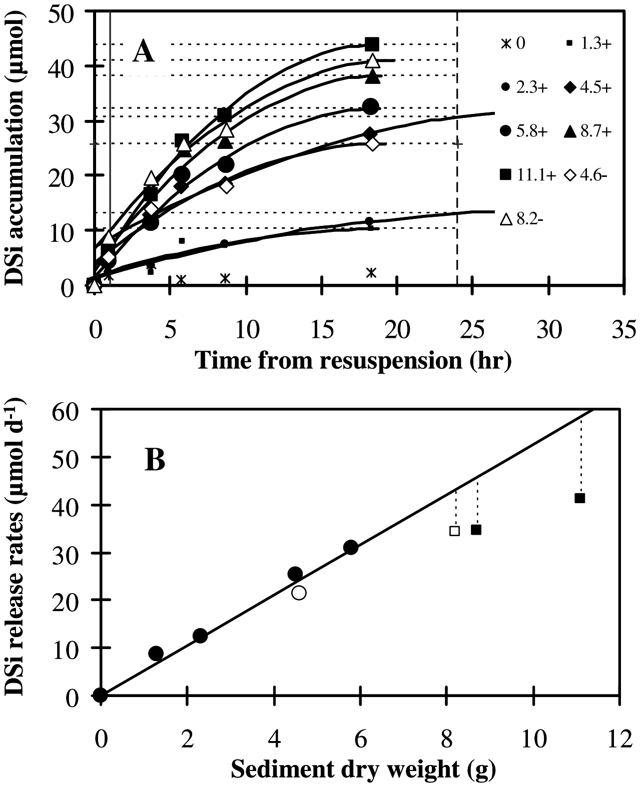

Figure 3. Laboratory resuspension experiments conducted on Saanich Inlet sediments. (a) Dissolved Silica (DSi) versus time. Different symbols mark experiments in which different amounts of sediments were resuspended (the legend indicates the dry weight in g); experiments with poisoned and ambient bottom water are marked with plus and minus signs, respectively. Solid lines are the second-order polynomial regression ($R^2 > 0.97$ in all experiments except the 1.3 g + in which $R^2 = 0.74$). The regression lines end where their time derivative reaches zero, indicating stop of excess dissolution (mostly within 1 day from resuspension). Horizontal dashed lines represent the extrapolated DSi concentrations for each simulation after 1 day. The vertical solid line marks the start of data collection (prior to this time, DSi increased also due to mixing of pore water enriched with DSi). (b) Daily opal dissolution (DSi release) rates versus the dry weight of resuspended sediments. Open and solid markers are the opal dissolution rates in experiments with ambient and poisoned bottom water, respectively. The slope of the regression line (5.26 μmol opal g dry weight^{-1} d^{-1}; $R^2 = 0.98$) gives the specific dissolution rate at the resuspended sediments. The squares represent experiments which were omitted from the regression (see section 3.3).

fitted a second-order polynomial ($R^2 > 0.97$ in all experiments except 1.3 g in which $R^2 = 0.74$). All DSi versus time curves approached a constant concentration indicating that the DSi release rate approached zero ~1 day after the induced resuspension event (Figure 3a). We therefore defined the "excess dissolution time" (τ) as 1 day (see calculations in section 4.1).

[19] The specific dissolution rate of opal from the resuspended sediments (υ) is the slope of the best fit to the plot of the daily DSi release rates (calculated from the horizontal dashed lines in Figure 3a) versus the dry weights of the resuspended sediment (Figure 3b). The rate υ was estimated from the regression to be 5.26 μmol opal g dry weight^{-1} d^{-1} ($R^2 = 0.98$). The three experiments that contained more than 8 g of resuspended sediments (marked by the vertical dashed lines in Figure 3b) were omitted from the regression. At that high sediment/water mass ratio (0.004), the DSi concentrations cross the critical degree of opal saturation beyond which the rate of opal dissolution drastically decreases [*Van Cappellen and Qiu*, 1997a].

3.4. Fish Exclusion Experiments

[20] The infaunal abundance below the fish exclusion cages increased by a factor of >2 within 7 months of isolation (see Figure S1), from 2500 (SD = 630; $n = 15$) to 7010 individuals m^{-2} (SD = 1330; $n = 7$). Infaunal abundance in the near vicinity of the exclusion cages at the end of their deployment was 3300 individuals m^{-2} (SD = 1210; $n = 4$), close to their abundance in the area at the time of deployment. Species richness of infauna was the same near and under the exclusion cages. Despite the large increase in the abundance of potential bioturbators, opal concentrations in the sediments under the exclusion cages increased almost threefold. Opal concentration in the surface sediments (0–2 cm depth) of the exclusion cages increased from 3.66% (range 3.6–3.7%; $n = 3$) before the deployment to 9% (range 6.2–11.4%; $n = 3$) 7 months later. The opal content of the sediments from the near vicinity of the exclusion cages at the end of the deployment was 2.8% (range 2.6–3%; $n = 2$), close to the opal content in the area at time of deployment. Apparently, the absence of fish activity on the bottom led to a substantial increase in opal accumulation.

4. Discussion

4.1. Opal Dissolution Rates Induced by Groundfish Activity: Saanich Inlet

[21] Groundfish in Saanich Inlet (primarily pleuronectid flatfish; see Figure 1b and Movie S2) rework the sediments of the seafloor at the oxygenated margins once every 2 to 3 days [*Yahel et al.*, 2008]. The fish resuspend bottom sediments at a rate of ~1.3 L bulk sediment m^{-2} d^{-1} [*Yahel et al.*, 2008]; equivalent to ~1 kg dry sediment m^{-2} d^{-1} (bulk volume m^{-2} d^{-1} × solids content (50%) × bulk density (1.6 g cm^{-3})). Sediment resuspension augments the flux of dissolved silica into depleted bottom water as a result of "injection" of DSi-enriched pore water and enhanced dissolution of "freshly" exposed opal particles as shown in the simulations in section 2.4 (Figure 3). The DSi flux that is produced from "injection" of pore water into overlying bottom water (J_{ri}) is relatively small, lasting only seconds to minutes after the resuspension event. J_{ri} was calculated to be 0.12 mol DSi m^{-2} yr^{-1} by multiplying the bulk sediment resuspension rate by the sediment porosity and by the calculated difference in DSi concentrations between pore water and bottom water (Table 1).

[22] The enhanced dissolution of resuspended opal occurs because of the change in the degree of undersaturation of the waters surrounding the opal particles [*Van Cappellen and Qiu*, 1997a]. During resuspension, opal particles are transferred from the pore water, where DSi concentration is about 400 μM, to the overlying water where DSi concentration is about 60 μM (Table 1). This is a large difference, particularly when considering that at high degrees of undersaturation there is a nonlinear dependence between opal dissolution rate and the degree of undersaturation [*Van Cappellen and Qiu*, 1997a] and possible hindering effects of aluminum in the pore water [*Van Cappellen and Qiu*, 1997b].

[23] Although resuspension activity of fish lasts only seconds at a time, it may take many hours for very fine resuspended opal particles to settle to the seafloor. Moreover, resuspended opal particles, mostly diatom frustules fractions, have larger surface area and lower specific density than other types of particles such as quartz and calcite. Thus, by winnowing, they are more likely to fall on top of the other faster settling particles, prolonging their stay at the sediment-water interface and their exposure to the overlying water.

[24] An estimate of the DSi flux caused by dissolution of resuspended opal (J_{rd}) was obtained from the laboratory resuspension experiments by the following equation:

$$J_{rd} = Rr_w\ \tau\upsilon \times 1000 \times 365 = 1.9 \text{ mol DSi m}^{-2}\text{yr}^{-1}$$

where Rr_w denotes the sediment resuspension rate by fish (1 kg dry weight m^{-2} d^{-1}); τ and υ were defined above (1 day and 5.26 μmol opal g dry wt^{-1} d^{-1}, respectively); and the numbers 1000 and 365 were used to match the units (1000 g kg^{-1} and 365 d yr^{-1}). The total fish-induced DSi flux, $J_{ri} + J_{rd}$, is therefore 2 mol DSi m^{-2} yr^{-1}.

[25] The time span between resuspension events is likely to affect the DSi release following resuspension. However, the sediments in the experiment were resuspended within 1 day after sampling so the time span from the previous, groundfish-generated resuspension was probably not very different than in nature [*Yahel et al.*, 2008].

[26] It appears that fluxes of DSi are more affected by brief resuspension events than other nutrients; possibly because the enhanced dissolution of opal following resuspension is hardly negated by adsorption and uptake in the deep, dark waters. In several laboratory and in situ experiments from Saanich Inlet and the Gulf of Aqaba (not reported here), very little change in nitrate flux occurred following brief resuspension events. Phosphate which, unlike nitrate, is easily released from the sediments following resuspension, depletes within a few hours to concentrations that are lower than these measured prior to resuspension; probably as a result of enhanced bacterial uptake and readsorption onto the suspended sediment particles.

[27] The DSi fluxes due to diffusion were estimated by Fick's first law [*Berner*, 1980] to be 0.7 mol m^{-2} yr^{-1} as follows:

$$J_{dif} = -\varphi D_s \left(\frac{dC}{dz}\right)_{z=0}$$

where J_{dif} is the DSi diffusive flux; φ is the porosity, D_s is the whole-sediment diffusion coefficient for DSi, and (dC/dz) is the DSi concentration gradient across the sediment-water interface.

[28] For the calculation of J_{dif} we used measured φ of 0.8 and dC/dz of 0.63 μmol cm^{-4} (Table 1); $D_s = 0.4 \times 10^{-5}$ cm^{-2} s^{-1} was taken from *van der Loeff et al.* [1984] who calculated it using temperature (10°C) and porosity values that were similar to those measured at the seafloor in our study site in Saanich Inlet. Using these values we estimated that the combined diffusive and bioturbation flux ranges between 0.7 mol DSi m^{-2} yr^{-1} (when considering only diffusive flux; see *van der Loeff et al.* [1984] and Figure S1) and 1.4 mol DSi m^{-2} yr^{-1} assuming that bioirrigation equals diffusion [*Hammond et al.*, 1999; *Tahey et al.*, 1994; *van der Loeff et al.*, 1984]. Therefore, in Saanich Inlet, groundfish activity accounts for 60% to 75% of the total DSi flux from the sediments (2.7 to 3.4 mol DSi m^{-2} yr^{-1}).

[29] In contrast to the high DSi flux from the oxygenated margins of the Inlet, the DSi diffusive flux from the anoxic basin is lower by threefold (about 1 mol DSi m^{-2} yr^{-1} as calculated from sediment data of *Murray et al.* [1978]. The ~24% opal content in the basin sediments [*Gucluer and Gross*, 1964] compared to ~5% in the oxygenated margins and much higher sedimentation of the anoxic basin may reflect this low opal dissolution rate. These findings emphasize the important role of groundfish in dissolving and mobilizing sedimentary silica because the anoxic basin is devoid of both bioirrigation [*Debret et al.*, 2006] and fish activity [*Yahel et al.*, 2008]. We conclude that groundfish that inhabit only half of Saanich Inlet seafloor have a marked effect on the silica cycle of the entire basin, reducing the overall opal accumulation by about 1 mol opal m^{-2} yr^{-1} (equivalent to enhancing the average DSi fluxes by ~50%).

[30] It is important to note that the groundfish-induced DSi flux cannot be measured by in situ benthic chambers and laboratory core incubations because they both exclude fish from reaching the incubated sediments. Hence, fluxes measured by benthic chambers considerably underestimate the "real" DSi fluxes in sites where groundfish are abundant. This conclusion is corroborated by reported enhancement in DSi fluxes in resuspension experiments in the Kattegat (Baltic Sea; *Tengberg et al.* [2003]), Saanich Inlet (north Pacific; *Yahel et al.* [2008]), and the Gulf of Aqaba (Red Sea; see Figure S2). The spatial spread of these locations indicates that sediment resuspension may control opal dissolution and accumulation in many locations around the globe.

4.2. Role of Groundfish in Controlling Diatom Productivity: Working Hypothesis

[31] In many marine environments, groundfish resuspend sediments while searching for food, shelter, or camouflage. The findings in Saanich Inlet can therefore be applied to other regions of the coastal ocean. The working hypothesis based on these findings was that a dramatic decrease in groundfish populations (e.g., as a result of overfishing or anoxia) may considerably reduce sediment resuspension, lowering the dissolution of sedimentary opal. This reduction is expected to reduce the DSi flux from the sediment and increase the burial efficiency of opal. DSi inventory in the

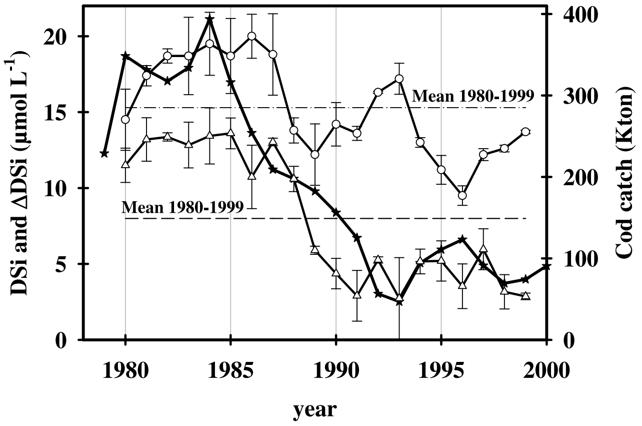

Figure 4. The Baltic Sea cod crisis. Time variations (1980–1999) in cod catch [*International Council for the Exploration of the Sea*, 2007] as a proxy for cod population (black stars); Dissolved silica (DSi) concentration in surface water before the spring blooms (blank circles); and the ΔDSi concentration (blank triangles with error bars, SE) which is the difference between prebloom and postbloom DSi concentration in three Baltic Sea stations [*Alheit et al.*, 2005; *Wasmund et al.*, 1998]. ΔDSi is a measure of silica uptake by the diatoms, a good proxy for diatom productivity [*Wasmund et al.*, 1998]. The cod catch started declining from 1987 and decreased until about 1991 showing no significant recovery ever since. The prebloom DSi stocks dropped by about 5 μmol L^{-1} (comparing 1980–1987 with 1988–1999 averages, $P < 0.01$ for all stations analyzed). The drop in diatom productivity is expressed by a ΔDSi decrease of 8 μmol L^{-1} that persisted from 1989 onward.

water column is then expected to decrease along with the supply of DSi to the surface water. Should DSi concentrations in the surface water become limiting for diatom growth, we expect diatoms to decline and nonsiliceous phytoplankton such as dinoflagellates to proliferate. This transition should be fairly rapid in shallow coastal seas, where the residence time of silica is short.

4.3. Baltic Sea Cod Crash as a "Natural Experiment": Testing the Working Hypothesis

[32] Cod is a major bottom-feeding groundfish capable of significant resuspension activity (Figure 1a and Movie S1). In the mid-1980s, the cod population in the Baltic Sea collapsed, decreasing by a factor of 5 [*Alheit et al.*, 2005]. This decline was a result of overfishing and recruitment failure, and the population has not recovered to date (Figure 4). Several explanations have been proposed to explain the recovery failure, including reduced salinity, enhanced predation of early life stages of cod by clupeid fish such as herring and sprat, and a decrease in spawning volume resulting from the expansion of bottom water anoxia [*Pers*, 2000; *Vallin et al.*, 1999]. This near extinction of Baltic cod, however, provided a "natural experiment" for testing our working hypothesis on the effect of groundfish on the marine silica cycle.

[33] DSi depth profiles conducted between 1970 and 2000 (Figure 5 and Table 2) in the southern part of the Baltic Sea (Figure 2c), an area that was not affected by bottom water anoxia, show a clear decrease in DSi flux from the seafloor following the cod crash. The profiles indicate that the near-bottom gradient of DSi decreased by ~20% after the cod crash (Figure 5 and Table. 2). It should be noted that we did not find any documented shift in deep water turbulence since the 1980s that could explain the gradient decrease by a physical mechanism. In addition, the DSi inventory in the water column between 0 and 90 m depth had decreased from ~1.8 mol m^{-2} before the cod crash (1985) to ~1.4 mol m^{-2} thereafter (Table 2). We propose that these phenomena were caused by the massive decline in cod population that decreased sediment resuspension and hence opal dissolution at the seafloor. Below we discuss additional observations from the Baltic Sea that corroborate this suggestion.

[34] Soon after the cod crash, diatom abundance and productivity declined and the dinoflagellate populations increased (Figure 4) [*Alheit et al.*, 2005; *Wasmund et al.*, 1998]. We think that the diatom population declined because of a decrease in silica supply to surface water as suggested by

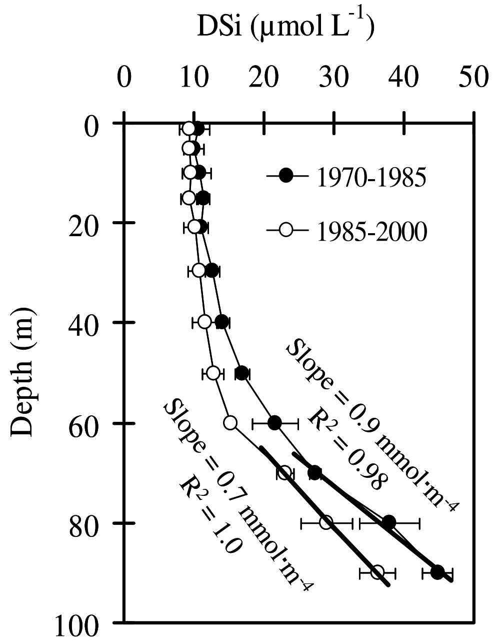

Figure 5. Composite depth profiles of DSi in the oxygenated waters of the southern Baltic Sea (54°45′–56°20′N, 16°28′–18°25′E). The profiles represent DSi data from all seasons (Baltic Nest Institute, 2007, http://nest.su.se/) averaged for two 15 year periods, first before the cod crisis (1970 to 1985) and second after the cod crisis (1985 to 2000). In order to overcome the uneven sampling frequency during the 15 year period, each profile was produced by averaging three 5 year intervals (±1σ is shown for each depth) assumed to have an equal weight (Table 2). DSi vertical gradients (bold trend lines) are the slopes of the best fit for DSi data below 70 m. The ratio of DSi fluxes from the bottom to the surface water before and after the cod crisis is estimated to be ~1.2 (assuming constant vertical eddy diffusivity during the relevant period, the ratio of the gradients equal to ratio of fluxes).

Table 2. Dissolved Silica in the Water Column Before and After the Cod Decline in the Baltic Sea[a]

	Years (September to September)	Number of 0–90 m Depth Profiles	DSi Inventory (mol m^{-2})	Deep DSi Gradient (μmol L^{-1} m^{-1})
Prior to cod crash	1970–1975	22	2.0	0.92 (R^2 = 0.91)
	1975–1980	20	1.77	0.79 (R^2 = 0.99)
	1980–1985	58	1,70	0.91 (R^2 = 1.0)
	1970–1985	100	1.82 (SD = 0.16)	0.87 (SD = 0.07)
After cod crash	1985–1990	88	1.45	0.70 (R^2 = 0.99)
	1990–1995	39	1.46	0.57 (R^2 = 0.92)
	1995–2000	17	1.40	0.71 (R^2 = 0.98)
	1985–2000	144	1.44 (SD = 0.03)	0.66 (SD = 0.08)

[a] The dissolved silica DSi inventory in the water column over six 5 year periods was calculated between the surface and 90 m depth. DSi gradient near the seafloor was calculated as d[DSi]/dz between depths of 90 and 70 m. The DSi data shown in this table (courtesy of the Baltic Nest Institute, 2007, http://nest.su.se/) are from an oxygenated area of the southern Baltic Sea. This area is shown by the black frame in the Baltic Sea map in Figure 2.

the decrease in deep water DSi gradient after the cod crash (Figure 5). This idea is supported by the mid-1980s increase in spring and summer low DSi events (DSi < 2 μmol L^{-1}) in the Baltic proper's surface water [*Danielsson et al.*, 2008]. DSi concentrations smaller than 2 μmol L^{-1} are limiting diatom growth [*Egge and Aksnes*, 1992]. Hence, these low DSi events may have contributed to the observed decline in the diatoms [*Danielsson et al.*, 2008] that occurred contemporaneously with the cod decline. Clearly, the low DSi events, observed in about 5% of the samplings [*Danielsson et al.*, 2008], cannot decrease annual averages of DSi concentrations (shown in Figure 5) to lowest values.

[35] Despite the obvious decrease in diatom productivity, opal accumulation rates did not decrease [*Olli et al.*, 2008] suggesting that the burial efficiency of opal had increased because of a decrease in its dissolution rate. These observations are explainable by the crash in cod numbers according to our working hypothesis (see section 4.2).

[36] It could be argued that the decrease in opal dissolution rate and silica supply into the overlying water stemmed from the exclusion of cod from anoxic areas that developed in the Baltic since the 1980s. However, if the cod population size remains the same and only their distribution changes, than we would not expect a change in their overall resuspension activity. The reduction in bottom trawling fishing activity in the Baltic Sea, which is known to resuspend bottom sediments, could be another cause for this phenomenon except that despite the decrease in cod catch, this fishing activity in the Baltic Sea has not changed since the 1980s [*Marchal et al.*, 2001], prior to the cod crash.

[37] Several alternative hypotheses were suggested to explain the DSi decrease and diatoms decline in the Baltic Sea. In sections 4.4 to 4.6, we critically discuss those hypotheses arguing that the observations and their timing are better explained by the link between cod decline and the silica cycle.

4.4. Damming Reduced DSi Inputs Into the Baltic Sea

[38] Decline in riverine DSi input into the Baltic Sea due to damming Silica trapping upstream from dams was suggested as an explanation for the DSi decrease in the Baltic Sea [*Conley et al.*, 2008; *Humborg et al.*, 2006]. While this hypothesis explains well the long-term DSi decline until the 1970s, the period of major dam construction [*Papush and Danielsson*, 2006], it has difficulties explaining the rapid DSi decrease of the late 1980s (Table 2); riverine supply of DSi did not change since the 1970s [*Papush and Danielsson*, 2006].

[39] Moreover, the observation that opal accumulation rates did not vary much since the late 1980s [*Olli et al.*, 2008] may suggest that the Baltic Sea silica cycle during that period was controlled by a decrease in opal dissolution (internal DSi recycling) rather than by a decline in riverine DSi supply (external DSi supply).

4.5. DSi Uptake due to Eutrophication

[40] Ongoing eutrophication has also been proposed as a possible mechanism for the observed DSi depletion in the Baltic Sea [*Conley and Johnstone*, 1995]. Accordingly, nutrients' (N, P) enrichment enhanced diatoms' productivity and DSi uptake, resulting in a twofold increase in sedimentary opal content since the middle of the 20th century [*Conley et al.*, 2008]; the enhanced DSi uptake resulted in the observed decrease in water column DSi. Certainly, this mechanism contributed to the DSi decrease in the Baltic Sea until the late 1970s. It is very unlikely, however, that this mechanism was responsible for the DSi decrease between the mid-1980s and 2000 (Table 2). This is because N and P inputs into the Baltic Sea had already leveled by the late 1970s [*Papush and Danielsson*, 2006], and diatom productivity had decreased in the late 1980s [*Alheit et al.*, 2005] (Figure 4).

4.6. Mid-1980s Shift in North Atlantic Oscillation

[41] The late 1980s shift in the North Atlantic Oscillation (NAO) stabilized the water column of the central Baltic Sea [*Alheit et al.*, 2005]. The timing of the NAO shift correlates well with the decrease in Baltic Sea diatom population and the increase in dinoflagellates. Both phenomena were attributed to the water column stabilization (induced by the NAO) because dinoflagellates thrive in a stratified water column while diatoms dominate in mixed waters [*Harrison et al.*, 1986]. In addition, the stratified water column may also limit DSi (and other nutrients) transport from deep water to the surface and hence limit diatom growth. We argue, however, that if the decrease in diatoms resulted solely from water column stabilization, then we should have witnessed an increase in the water column DSi inventory in the steady riverine input of DSi since the 1970s [*Papush and Danielsson*, 2006; *Savchuk and Wulff*, 2009] rather then the observed decrease (Figure 5 and Table 2).

[42] Clearly eutrophication and the hydrological regulations had long-term effects on the Baltic Sea silica cycle.

Table 3. Compatibility Between Suggested Mechanisms Explaining the Late 1980s Shift in the Silica Cycle and Reported Observations From the Baltic Sea[a]

Mechanism Observation	Eutrophication[b]	Damming[c]	NAO[d]	Cod Crash[e]
Decrease in surface water DSi	1	1	?	1
Decrease in bottom water DSi	0	1	0	1
Decrease in diatoms' productivity	0	1	1	1
Sustained opal accumulation rates	1	0	0	1
Water column changes occurring between 1985 and 1990	0	0	1	1
Decrease in DSi flux from the seafloor	0	1	1	1

[a] The late 1980s shift in the silica cycle is given in the columns, and the reported observations are given in the rows. Unity indicates a success of a mechanism in explaining the particular observation on the Baltic Sea, and zero indicates a failure. A brief description of the mechanisms is given in the footnote. Note that the cod crash is the only mechanism proposed to date that fully explains all the relevant observations.

[b] N, P eutrophication caused diatom blooms, depleting the DSi from surface water and transporting the extracted silica to the sediments as opal frustules [*Conley and Johnstone*, 1995].

[c] Damming of rivers inflowing into the Baltic trapped the dissolved and particulate silica behind the dams, thus reducing the inputs of silica into the Baltic Sea [*Humborg et al.*, 2006].

[d] North Atlantic oscillation (NAO) enhanced water column stratification, a condition that favors dinoflagellates over diatoms [*Alheit et al.*, 2005].

[e] Cod crash in the mid-1980s reduced both opal dissolution from the bottom and DSi fluxes from the sediment (this study).

The pioneering studies that noted these factors and recorded the decrease in dissolved Si until the late 1970s are fundamental in understanding the current silica condition in the Baltic Sea. The suggested effects of the mid-1980s "cod crash" on the silica cycle would be much harder to note without those starting conditions. It seems to us, however, that neither damming nor eutrophication can fully explain the timing and sequence of events observed in the Baltic silica cycle between the late 1980s and the end of the century (see Table 3 for summary).

[43] All the hypotheses explaining the mid-1980s shift in the Baltic Sea silica cycle, including the "cod crash hypothesis" suggested here, are speculative and based on circumstantial evidence. We suggest, however, that the sequence of events that have transpired in the Baltic Sea since the mid-1980s and the timing of these events are best explained by the "cod crash hypothesis" (Table 3).

[44] This study demonstrates the importance of groundfish to the silica cycle of marginal basins. We believe that groundfish impact the silica cycle most extensively in the global marginal ocean because these locations support the largest groundfish populations [*Kallianiotis et al.*, 2000], and they are the sites of highest diatom productivity [*Ragueneau et al.*, 2000] and ~40% of the oceanic opal accumulation [*DeMaster*, 2002]. We hope, therefore, that this study will stimulate similar studies in other areas of the marginal ocean to establish the global importance of this newly discovered pathway in the marine silica cycle.

5. Summary and Conclusions

[45] In this study we found that, by resuspending bottom sediments, groundfish in Saanich Inlet considerably enhance sedimentary opal dissolution. The DSi flux from the sediments resuspended by fish activity was ~2 mol m^{-2} yr^{-1}- which is ~3 times greater than the ambient diffusive DSi flux (~0.7 mol m^{-2} yr^{-1}). As a result, we predicted that a dramatic decrease in groundfish population (e.g., overfishing) would result in a decrease in the dissolution of sedimentary opal and enhancement of its burial efficiency and therefore a reduced supply of DSi to surface water. We tested this hypothesis with data from the Baltic Sea. Analysis of this data reveals that the sequence of events that followed the cod crash of the 1980s fits well the scenario we present in this study. In light of our findings in Saanich Inlet and corroborating circumstantial evidence from the Baltic Sea, we suggest a novel link between the activity of groundfish and the productivity of diatoms in the ocean. Sediment resuspension by groundfish enhances opal dissolution and DSi fluxes from the seafloor, ultimately controlling silica availability to diatoms in the surface water. We suggest that groundfish activity should be incorporated into geochemical and oceanographic models that deal with the silica cycle and with bentho-pelagic coupling. We further conclude that anthropogenic interventions that affect the fate of groundfish populations may have far reaching consequences for phytoplankton community structure and productivity.

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Text S1

BENTHIC CHAMBER EXPERIMENT IN THE GULF OF AQABA

In the paper we suggest that sediment resuspension by marine groundfish enhances DSi fluxes from bottom sediments and that neglecting fish-induced DSi fluxes may lead to severe underestimation of the "real" DSi fluxes from the seafloor. The manuscript describes enhanced opal dissolution following simulated resuspension experiments conducted on Saanich Inlet sediments (Fig. 3). In order to examine the generality of this observation we conducted an *in situ* simulated resuspension in a benthic chamber deployed in the Gulf of Aqaba, Red Sea, where groundfish constantly resuspend the sediment ((Yahel et al. 2002); SVideo 4). The simulation was conducted in shallow, sandy sediments overlain with warm (23^{o}C) oligotrophic waters, a fundamentally different oceanographic setting then Saanich Inlet.

Description of the simulated resuspension experiment

An opaque cylindrical benthic chamber (internal volume 5.45 L, cross section area 278 cm^2) was deployed on a sandy seafloor at a depth of 10 m in the northern tip of the Gulf of Aqaba (29^{O}32' N 34^{O}58' E). SCUBA divers gently inserted the chamber into the bottom sediment. Care was taken not to resuspend the sediments during the process. The lid of the chamber was closed after an overnight acclimation period. The overlying waters inside the chamber were continuously stirred with a magnetic stirrer throughout the 32 h long experiment. Eight hours after the lid was closed we resuspended sediments inside the chamber with a jet of water from a 100 ml syringe (injection lasted 2-3 sec). Six water samples (in duplicates), were taken from the chamber with 60 ml plastic syringes: three samples during the 8 hr period before the simulated resuspension, and three more (0.2 hr, 15.5 hr and 23.7 hr) following the simulated resuspension event. Ambient bottom water was sampled in each dive to correct for the difference in DSi between the sampled water from the chamber and the ambient seawater that replaced it.The dimensions of the small pit formed by the water jet were measured at the end of the experiment to estimate the volume of the sediments resuspended during the simulation.

Results and discussion

The DSi flux from undisturbed sediment during the 8 h before the simulated resuspension was 90 µmol m-2 d-1 (Fig S3). Twelve minutes after the resuspension event, DSi in the chamber increased by 0.7 µmol, mainly due to porewater mixing (see below). After this initial stage, DSi was released from the sediments due to diffusion from the undisturbed sediments and due to enhanced dissolution of the opal particles that were resuspended during the event. The opal dissolution rate in the chamber increased 5 fold from 0.11 µmol h^{-1} to 0.51 µmol h^{-1} (Fig. S3). We can therefore calculate that During the 24h following the resuspension event some 12.2 µmol of DSi were released into the benthic chamber, only 2.6 µmol of it were related to molecular diffusion and infaunal bioirrigation; ~9.6 µmol DSi were released as a result of the resuspension of a ~17 cm^2 patch of sediment with the water jet.. The volume of sediments that were resuspended during the event (see above) was estimated to be ca.35 cm^3. This volume is similar to the volumes of feeding pits formed by the local goatfish that inhabit the study site (see SVideo 4). Accordingly, we estimate that a single resuspension event of a similar size conducted once a day in an area of 1 m^2 would increase the DSi flux from the sediment by about 10 %. It should be noted however that goat fish are capable of resuspending bottom sediments at much greater frequency (Yahel et al. 2002). The generality of the fish induced DSi flux is further corroborated by experiments conducted in the Kattegat, at the Baltic Sea outlet (Tengberg et al. 2003)

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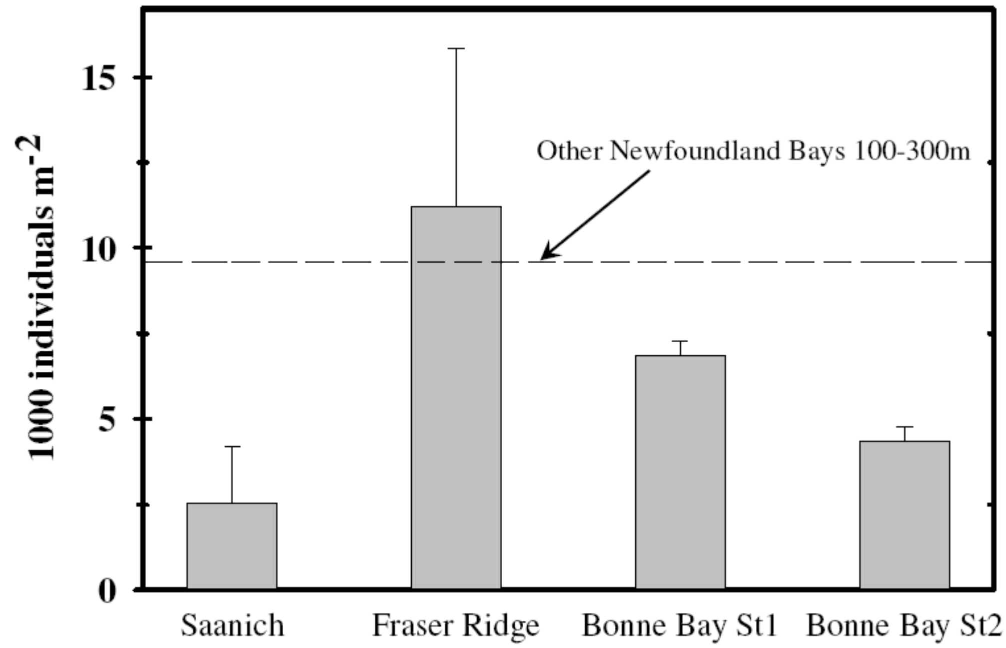
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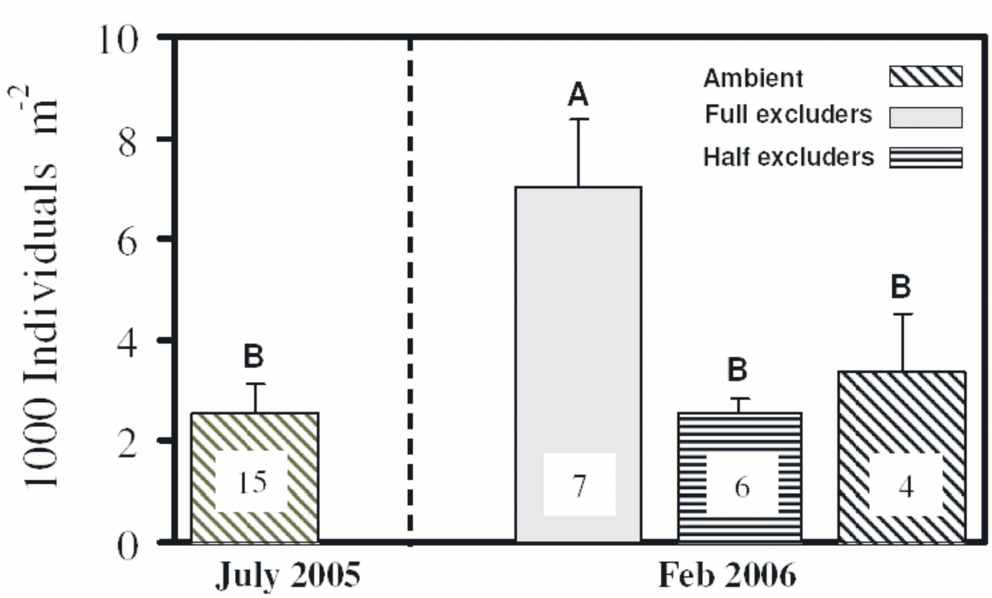
5
10
15
Other Newfoundland Bays 100-300m
Saanich
Fraser Ridge
Bonne Bay St1
Bonne Bay St2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8
10
July 2005
Feb 2006
Ambient
Full excluders
Half excluders
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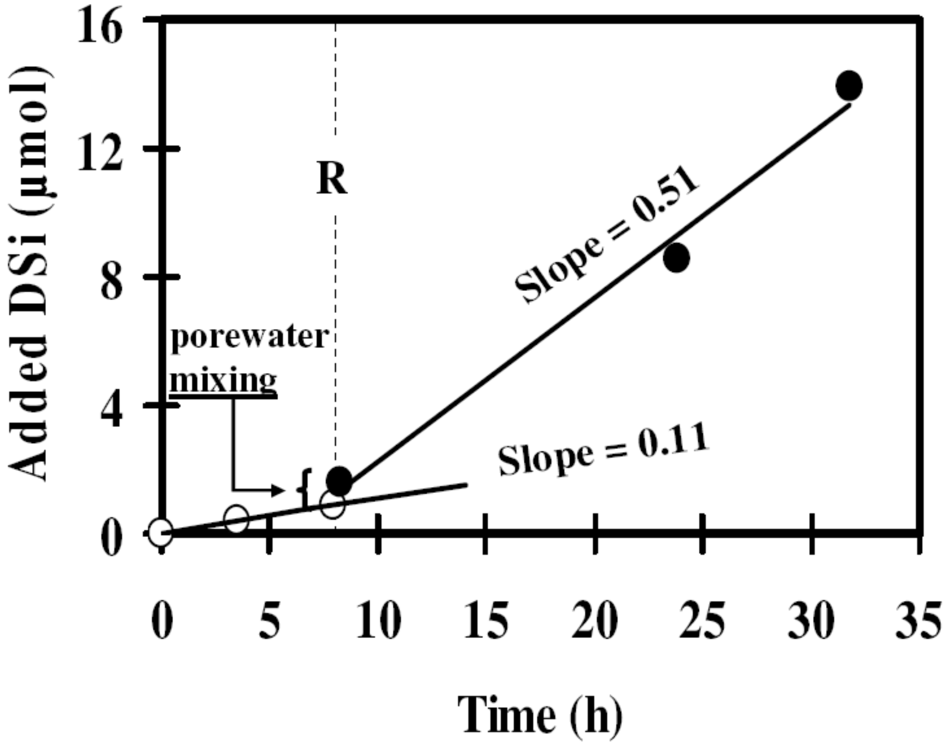
B
B
B
15
7
6
4



Added DSi (µmol)
0
4
8
12
16
Time (h)
0
5
10
15
20
25
30
35
R
Slope = 0.51
Slope = 0.11
porewater
mixing