**Ecosystem recovery by benthic invertebrates after a sudden hypoxia caused by massive fish death**

**Mass fish death causes low-oxygen event with an ecosystem vipeout; the recovery of the benthic invertebrates**

**What happens when mass fish kill wipes out an ecosystem in a marine embayment?**

**The herr-binger of death**

JEJ, RAS, (AA, GVH, VS), JS

**Target rit? (JS vildi ekki Ecol Applications, Biogeosciences, eða Oecologia)**

Marine Biology Research? (JEJ og JS)

Marine Biology (JS)

Marine Pollution Bulletin (JS)

**Lykil orð (leitarorð):**

hypoxia (benthic invertebrates) “permanent hypoxia”, “coastal hypoxia”

Hvað er “okkar hypoxia”? “Sudden hypoxia” eða “episodic hypoxia” (Episodic er following flooding skv. Levin et al. 2009). 🡺 One-time hypoxic event varð fyrir valinu sbr. Josefson og Widbom og Nilsson og Rosenberg.

bæta “sediment” við leitirnar. mældur umhverfisparameter með gögnunum.

Organic pollution (benthic invertebrates)

**Introduction**

Kynnum Kolgrafafjörð inn eftir almenna umfjöllun um hypoxiu:

Látum þetta snúast um botndýr en ekki síld nema sem stressor.

Oxygen concentrations can vary within ecosystems but hypoxic conditions are a growing problem worldwide, and such events can even occur at seasonal, local and even at global and geological scales (Rabalais et al. 2001, 2010, Diaz & Rosenberg 2008, Levin et al. 2009, Zhang et al. 2010, Caswell & Frid 2017). An ecosystem becomes overflowed in nutrient stressors (sewage, waste, fertilizer or other organic material) and their subsequent breakdown requires more oxygen than the ecosystem can supply, leading to hypoxic (or anoxic conditions which are lethal or sub-lethal to benthic organisms and other metazoans. Ecosystem recovery can take years, even decades or longer (Jones & Schmitz 2009, Borja et al. 2010).

Hypoxic conditions commonly occur when water columns become stratified, which prevents oxygenated surface waters from mixing with lower-oxygen water near the bottom. Hypoxic conditions can be permanent or seasonal, but there exist three main types of hypoxic conditions: seasonal, episodic (“following flooding”) and permanent (Levin et al. 2009). Various taxa display differing thresholds for tolerance of low oxygen conditions (Vaquer-Sunyer & Duarte 2008, Belley et al. 2010), but such responses also depend on size of the affected area and duration of exposure (Levin et al. 2009). Wijnhoven et al. 2010 defined hypoxia (low oxygen) as O2<3 mg/l but anoxia (no oxygen) at O2<0.5 mg/l, whereas Rabalais et al. (2010) defined hypoxic conditions as O2<2 mg/l. Vaquer-Sunyer & Duarte (2008) found in a comparative study that the common definition of 2 mg O2/l as hypoxic was below empirical sub-lethal and lethal O2 thresholds for 50% the species tested, which implied that past, present and future distribution of hypoxic impacts on marine life generally have been underestimated.

Studies of single hypoxic events (one time hypoxic conditions with subsequent recovery for years without repeated hypoxic stressors), are relatively rare for marine/saline fjords but are more often related to eutrophication or other human-induced organic pollution, sometimes extreme cases hypoxic phases of seasonal cycles (Josefson & Widbom 1988, Fallesen et al. 2000, Nilsson & Rosenberg 2000, Hansen et al. 2002). Hypoxic conditions can be permanent and difficult for benthic animals to become re-established (Wijnhoven et al. 2010, Belley et al. 2010, Raman et al. 2015) but also occur seasonally in water bodies which are largely land-locked or have relatively narrow outlets relative to their volume. These often are estuaries, fjords, lagoons, or even land-locked oceans (i.e. Baltic and Black seas) which have relatively limited water exchange with sources of oxygenated water and relatively long residence times (Levin et al. 2009). Hypoxia can be indirectly associated with eutrophication acting as the nutrient stressor, leading to hypoxia as a secondary effect (Ærtebjerg et al. 2003, Diaz & Rosenberg 2008). To date, many of the fjord-like hypoxic ecosystems studied so far with respect to benthic fauna are estuaries with seasonal hypoxia, i.e. transition zones where freshwater from land and seawater mix with the occasional hyper abundance of fresh or saline conditions leading to stratifications (with seasonal nutrient or salinity overflows) and subsequent oxygen depletion, but also periods of recovery in between the seasonal stress (Leon-Morales & Vargas 1998, Como & Magni 2009, Yoshino et al. 2010, Díaz-Asencio et al. 2015).

Here, we present the influences of one-time, naturally induced hypoxic conditions within a fjord in Iceland in winter 2013 on the benthic fauna and the subsequent recovery in the summers of 2013-2017. This hypoxic event was caused by two successive mass deaths of herring schools (*Clupea harengus*), which formed a rotting mass of organic matter which caused rapid oxygen depletion within Kolgrafafjörður, West Iceland (Stefánsson & von Scmalensee 2013, Pétursson et al. 2015, Óskarsson et al. 2018). These sudden herring deaths happened two times but six weeks apart, leaving 55.000 tonnes of fish carcasses on the bottom and intertidal zones of the embayment, with dead benthic fauna found washed ashore in the intertidal zones. The herring schools seem to have caused their own death by depleting the oxygen supply within the Kolgrafafjörður embayment before the tidal cycle was able to replenish it with oxygenated seawater from outside Kolgrafafjörður (Óskarsson et al. 2018). This project was started immediately after the herring death and ran six years (2013-2018).

The project goal was twofold: 1) Estimate the effects of the hypoxia caused by the herring death on the benthos of Kolgrafafjörður, by comparing our data 2013-2017 to a dataset from 1999 (Ingolfsson 1999); 2) Quantify how species composition and number of individual macrofauna recover after the hypoxic shock and estimate the time period needed. Specifically we looked emergence of 1) species capable of breaking down the herring mass in hypoxic conditions and subsequently, 2) pioneer species that live in oxygenated conditions, and 3) species sensitive to low oxygen levels. Nefna AMBI og stuðla?

**Study area**

Kynnum Kolgrafafjörð og notum þær innlendu upplýsingar sem til eru, einkum seltustig og súrefnisstyrk, og allt sem segir hvernig Kolgrafafjörður hreinsar sig.

Kolgrafafjörður embayment (64°57′16″ N, 23°7′15″ W) is a 6 km long in-fjord (area 10 km2) on the north side of the Snæfellsnes peninsula, West Iceland and is an infjord of Breiðafjörður Bay. In its natural state, Kolgrafafjörður is a shallow, narrow fjord characterized by a shallow (≥12 m) 1 km wide inlet, shallow (≤15 m) intertidal zones, and two deeper central areas. The deepest area (30-50 m) is to the north where the fjord is widest (3 km), with a somewhat shallower (18-30 m) area to south (1.5 km wide). Here, we refer to Kolgrafafjörður as the embayment was defined in the historical sense, i.e. as the infjord south of Hjarðarbólsoddi and Kolgrafaroddi, whereas the sea to the north towards Akureyjar is termed Urthvalafjörður (Figure 1, sýna þetta á korti).

The fjord’s natural state is mostly maintained to the present day, with the exception that a road-bridge was built across the shallows surrounding the inlet in 2004. Elevations were raised on west and east sides, which were then bridged with a 210 m long stilt bridge, allowing tidal water exchange for a gap of 150 m (Figure 1 Map with depth profile). The bridge was built long enough to maintain natural exchange of tidal water between embayment and the outer fjord, i.e. similar water levels generally are observed outside and inside (Óskarsson et al. 2018). There are no reasons to expect the bridge to have caused the herring deaths (Pétursson et al. 2015). The fjord is in a rural area with a low anthropogenic impact; there is no industry near the fjord and no sewage entering the fjord except for that from two farms. Thus, the surroundings are fairly close to being completely natural.

Generally, the tidal cycle causes the water column to replenish its oxygen content on diurnal basis, independent of any seasonal fluctuations or stratifications. However, the fjord is comprised of two main parts, north and south areas: 1) the northern, deeper part is shaped like a cauldron in that the inlet is over a shallow area (10-12 m) but a deeper (30-50 m) basin but 2) the southern part of the fjord is shallow (1-25 m). This bathymetry affects the water exchange with Breiðafjörður as well as currents within Kolgrafafjörður, in that inflow is strong on the west side with relatively weaker outflow currents on the east side within the northern deeper part. Conversely, the shallower southern area is characterized by a slow-flowing, circular current which mixes with the stronger in- and outflow currents (Heimild? fengið úr <https://www.youtube.com/watch?v=uZPIBigjK6k&t=281s> ).

Kolgrafafjörður is up to 50 m deep (average 20 m) and represents a fjord- or embayment-type of a system that could turn hypoxic, except that the presence of a strong tidal cycle generally replenishes the water column and thus, generally maintains the oxygen levels at least at 2-7 ml 02/l or higher (Pétursson et al. 2015). The oxygen concentrations that were recorded in winter 2012-2013 were reported within the lower range of these values, i.e. lowest at 1.1–4.7 ml/L (Óskarsson et al. 2018). Thus, the herring deaths were not attributed solely to low oxygen concentrations caused by an excess of herring respiration, but a combination of those and “limited atmospheric-water gas exchange due to calm and cold weather prior to both incidents and sea ice on part of the fjord, and limited renewal of water coming in and out via tidal currents” (Óskarsson et al. 2018).

This fjord is marine (salinity 33-34 PSU) with limited freshwater input from mountain streams, and a tidal amplitude of 4-5 m. To date, there has been no repeat of herring deaths after winter 2013 but this one-time impact event allowed observation of subsequent recovery of benthic macrofauna under marine conditions. This study assumed that Kolgrafafjörður was not under hypoxic stress after 2013 and maintained stable water exchanges with the Breiðafjörður Bay (Pétursson et al. 2015). While fish deaths are often associated with hypoxic events (Levin et al. 2009), it is important to note here that the mass of dead fish remained within the study system and the rotting process further contributed to and prolonged the hypoxic conditions which initially caused the fish death.

Two separate herring deaths occurred in Kolgrafafjörður in winter 2013, i.e. 13 December 2012 an estimated 32.4 thousand tonnes of herring were killed in apparent hypoxic conditions when spring tides coincided with prolonged periods of still weather and starbright skies. A similar event re-occurred 1 February 2013 (6 weeks after first event) when an estimated 22.6 thousand tonnes of herring were asphyxiated; making the total 54.9 thousand tonnes, equating to 180 million herring (Óskarsson et al. 2018).

Levin et al. (2009) noted that although fish detect and avoid low oxygen concentrations, they find it relatively difficult to avoid hypoxia related to “diel cycling”, such as tidal fluctuations. Herring do not regularly migrate to Kolgrafafjörður or south of Breiðafjörður but large schools were present in winters 2007-2013 (Óskarsson et al. 2018). There are older historical accounts of herring collections in the intertidal zones of Kolgrafafjörður from the early 20th century.

We used grab samples to document succession of the benthic fauna at 6 stations over a 5 year period (2013-2017). Prior to our study, the only data on benthic macrofauna in Kolgrafafjörður was that of Agnar Ingólfsson (1999) who collected benthic samples for the environmental impact assessment for the bridge construction. Pre-disturbance data is rarely available for studies of eutrophication/hypoxia (Jones & Schmitz 2009).

**Methods**

Sampling benthos in the field

Grab samples (Shipek) were taken from the benthos within the Kolgrafafjörður embayment in June or July 2013-2017. Sampling was always done at spring low tides so the research vessels could enter Kolgrafafjörður by sailing under the bridge. Here, followed Ingólfsson (1999) but did not repeat all his stations but chose the stations with the highest biodiversity in the 1999 study, i.e. the seven stations classified as TWINSPAN-category II to effectively estimate how hypoxia caused by the herring death affected local biodiversity. Of these seven stations, station B0 was effectively destroyed by the bridge construction from 2004, filling this station with rocks, leaving six stations for the study. The distribution of these stations also represented the distribution of dead herring, with stations both inside and outside the dead herring mass at the bottom. There were three benthic samples taken at each station to facilitate statistical comparisons of stations, whereas the study of Ingólfsson (1999) was based on one sample per station. The two sampling stations farthest to the west coincided with the deepest part of the area covered with mass of dead herring (Óskarsson et al. 2018).

In an attempt to get an uncontaminated comparison with our Kolgrafafjörður samples, we also initially added two stations north of the bridge in 2013; however, the benthic habitat there differed sharply from that within the embayment, and the southern station probably also was contaminated from the herring death anyway (Sigurðsson 2015).

Sample preparation and classification

On the boat immediately after obtaining the grab samples, samples were diluted with seawater and filtered using 60 micron sieve to remove mud from the samples. Formaldehyde solution and borax were added to each sample but removed xx hours after sampling and replaced with a 70% isoprophyl alchohol. A fourth sample was taken once for each station for sediment analysis.

Benthic macrofauna were sorted, identified and counted in a laboratory. Samples were subbed 2 times (4 parts) prior to identification and counting. Each sample was dyed with Bengal Rose to stain macrofauna prior to sample processing. Macrofauna was identied under á stereoscope. Macrofauna were identified to species when possible but otherwise to genus or class.

Sediment analysis (þýðing á kaflanum ms ritgerð VAS)

We estimated carbon content of sediment samples by using loss on ignition (Heiri et al. 2001). This was our annual index of the amount of organic matter present in the benthos upon sampling.

The sediment samples were dried at 60°C for 24 hours and stirred 2-3 times to prevent clot formation. The dried samples were then sieved with 4000, 2000, 1000, 250, 125 and 63 µm sieves, and each size groups weighed after sieving to obtain the proportion of each particle size group .

The organic matter content was estimated by burning the finest (clay) particles (63 µm); a small amount of these particles (2±0.05 g) was placed in porcelain melting pots and burned at 475 °C for 2 hours. The subsequent comparison of organic matter content between sampling stations is based on average values for 2 such particle sub-samples from each sampling station per year of study.

We compared total carbon among stations and years using generalized linear model, where year, station and their interaction were fixed effects.

**Niðurstöður (punktar)**

**Carbon content of sediment**

Carbon content was similar among stations (F 5, 30 = 1.8, P=0.14) but differed among years (F 4, 30 = 17.2, P=0.0001) in a consistent manner (the station \* year interaction was not significant: F 20, 30 = 1.2, P=0.31). Post-hoc test of differences among LSMEANS indicated that 2013 differed from all other years (P>0.0001) but that other years were similar to one another (P>0.083). The LSMEAN total carbon was 0.17 for 2013 but ranged 0.10-0.12 for the other years (Figure 2).

**Endurgera myndirnar töflurnar frá Valtý (2013 vs. 1999) og gera þær 2013-2017.**

Hlutfall lífræns efnis í setsýnum. Tafla 3.1:

Kornastærð í seti og bera saman milli stöðva. Þar gæti verið áramunur ef dýrin breyta setinu mikið. Mynd 3.1.

Samfélagsgerð, meginþátta og fylgnigreining (PC1 vs. PC2). Gætum gert PCA og skoðað hvernig meginþættir (PC1, PC2, PC3, o.s.frv.) svara árabreytileikanum.

Klasagreining út frá Bray-Curtis skyldleikastuðli

Prófílar stöðva eftir árum. Valtýr var með stöðvar á x-ás og tvær súlur við hverja stöð (1999 vs. 2013. Mynd 3.5 er fjöldi tegunda en mynd 3.6 fjöldi dýra á fermetra. Hér hallast ég að sex panelum per mynd, eina per stöð.

Kökurit: 10 algengustu tegundir (mynd 3.8).

Súlurit: Hlutfall mengunarþolinna/viðkvæmra tegunda í botngreiparsýnum eftir árum, aftur hallast ég að sér panel per stöð.

Shannon stuðull

Ambi stuðull.

**FLEIRA?**

**Lykil atriði:**

**1999 vs. 2013, 2014, 2015, 2016 og 2017**

**5-10 tegundir sem standa upp úr eftir 6 ár?**

**mengunarþolnar tegundir: hverfa þær og mengunarfælnari sækja inn?**

**Parametrar:**

**Fjöldi einstaklinga, saman og per tegund/taxon**

**Fjöldi tegunda**

**Discussion (punktar héðan og þaðan í engri sérstakri röð), komment frá Árna og VAltý látin halda sér óbreytt í bili, enda er eftirfarandi á punkta- og hugmyndastigi.**

**Hvað gerðist, þ.e. hver eru fyrstu viðbrögð vistkerfisins á botninum?**

**Hvað breyttist þegar árin líða?**

**Hversu langt var í að allir taxa væru orðnir mælanlegir, þar með súrefnisháðir taxa?**

Spurningar tengdar efninu:

**1) Hvað er Kolgrafafjörður lengi að hafa vatnaskipti með sjávarföllum?**

**2) Er vitað hvað súrefnisstyrkur fór langt niður í Kolgrafafirði þegar síldin drapst?**

Óskarsson et al. 2018 segir “The measurements in Kolgrafafjörður following the mortality incidents showed oxygen concentration of 1.1–4.7 ml/L (Figures 4 and 5).”

Gætum borið saman dýpra svæðið og grunna svæðið m.t.t. tegundasamsetningar og notað það efni sem til er um súrefnisstyrk. Dýpri vs. grynnri svæði, gerist endurreisn lífríkis mishratt þar á milli? Manni sýnist það þegar stöðvarnar og datað frá Valtý eru borin saman við súrefnisprófílana.

**3) Hypoxia er rýrnuð vatnsgæði (súrefnisinnihald) fyrir “meðal tegundina” (Levin et al. 2009), en hvaða level gildi notum við fyrir Kolgrafafjörð og botndýr?** Ath. að gildi eru misjöfn eftir hopum og tegundum (Belley et al. 2010). Sýnist líka að Hafró (Óskarsson et al. 2018) leggi ekki í að segja að súrefnisþurrðin ein sér sé eini sökudólgurinn, heldur samspil hennar við veðurfar og takmörkuð sjávarföll “limited renewal of water coming in and out via tidal currents”.

Overall atburðarás. Taka 2013 sem ground zero, þ.e. kjarnorkusprengjan afstaðin? Það er eiginlega beint eftir ritgerð Valtýs eða því efni sem var til eftir hana.

AMBI o.fl. stuðlar. Stuðlar: alpha- og beta diversity stuðlar? (Líffræn fjölbreytileiki?) sjá t.d. Udalov et al. 2016.

Er fjörðurinn búinn að jafna sig? Eru öll kvikindin komin til baka? Berum saman við Agnar. Ef ekki, hverja vantar?

Ath Mariager fjord: settling order polychaetes & Bivalves – bivalves – cirripedians (we do not expect cirripedians because they are only intertidal animals in Icelandic waters OR only hard-bottom animals and we chose soft-bottom stations). However, from the crustacea, we found amphipoda in 2016-2017, possibly earlier. Also, are all the polychaetes oxygen-tolerant species?

Hvað ef Kolgrafafirði hefði verið lokað? sbr. hollensku rannsóknina Wijnhoven et al. 2010. Þar var firði lokað og myndaðist “þokkalegur drullupollur”.

One anecdote of a similar event exists from 1941, when British soldiers met a local farmer who collected herring from the intertidal zone at his farm. Herring is historically a fisheries species in Iceland but its winter distribution differs from year to year (Óskarsson et al. 2009). In 2007-2014, there were herring schools wintering in Breiðafjörður, whereas herring generally is rare in Breiðafjörður. The herring presence was observable via presence of the fishing fleet venturing into intertidal zones and extreme abundances of marine birds including gulls Larus spp. and Northern Gannets (*Morus bassanus*) (Yfirlit um jólatalningar okkar á fuglum).

A somewhat similar but considerably smaller-scale event (200-300 tonnes of herring left to rot) occurred in Alterosen (1 km long and 100-200 m wide), Norway in 1984 (Oug et al. 1991) but a herring death of the magnitude (thousands of tonnes) observed in this study is unprecedented to our best of knowledge. Ath líka Dommasnes (1994) sem Óskarsson et al. (2018) vitna til, það er norskt dæmi úr Oslófirði um áhrif síldargengdar á O2 styrk í Oslófirði.

Kolgrafafjörður provides an excellent model system to study effects of hypoxia on benthic ecosystems in the absence of seasonal (or otherwise repeated) hypoxic conditions, in the absence of any salinity stratifications and in almost completely marine (not an estuary) environment. Such a response to a hypoxic event can shed light on benthic changes related to changed oxygen concentrations caused by climate change and resulting changes in ocean circulations, and/or flow patterns of organic matters on the seafloor (Belley et al. 2010, Diaz & Rosenberg 2011), either from present-day, future or historical perspectives (Caswell & Frid 2017). Observing the recovery of benthic communities also is useful to identify pioneer species which can break down organic material to restore oxygenated conditions within an affected ecosystem, which in turn may aid in biological breakdown of sewage or otherwise accumulated organic materials.

Capitella:

Capitella dominated 2013, hvað svo? Josefson & Widbom 1988 in Gullmarsfjord, Oug et al. 1991 in Alterosen, Gamenick et al. 1998, fleiri? Eigum Wade grein frá 1972 í Skýrslu til Vegagerðar.

Josefson and Widbom 1988 mention Heteromastus filiformis with C. capitata, but in Kolgrafafjörður only one specimen found at U2 in 2013 (µ 2015).

Aðrir burstaormar? Aðrar tiltölulega mengunarþolnar (en samt mengunarþolnar) tegundir?

Hver er alþjóðleg þýðing burstaorma (Capitella og svipaðir) fyrir gums niðurbrot.

Hvenær koma molluska og crustacea inn? Þeir eru sagðir þola súrefnisskort hvað verst…

Þýðing rannsóknar fyrir ….súrnun sjávar, loftslags, urbanization, lífræn mengun o.s.frv. Sewage mál etc. (umræður)

Getum borið einstök ár í okkar gögnum saman við svokölluð Oxygen minimum zones (Raman et al. 2015). M.t.t. til hypoxiu höfum við mestan áhuga á dýrum sem vitað er að eru sjaldgæf á slíkum svæðum, þ.e. lindýrum molluska og krabbadýrum Crustacea. (umræður)

Hvað er svæði lengi að jafna sig eftir að þekkt magn lífræns efnis hefur verið losað en jafnframt komið í veg fyrir frekari losun, t.d. ef menn hættu að losa klóak, fiskafóður, kræklingarækt etc…Hvað þarf til? (rannsóknaspurning?)

Mariager Fjord (Fallesen et al. 2000): “In 1997, the summer in Denmark was unusually warm, sunny and calm. The wind induced very little mixing of the surface water and the input of oxygen from the air was therefore very limited. At some point, the limited oxygen input could not meet the mussels’ and other organisms’ oxygen demand. The Inner Fjord [2 km or narrower, 40 km in length] became anoxic and sulphidic to the very surface for a distance of 20 km.” og “It is thus concluded that the long period of calm and unusual warm weather reducing the mixing in the surface was the triggering factor — but the form of the fjord and the high concentrations of nutrients mostly discharged from land were the basic causes of the disastrous oxygen depletion.” The story from Mariager Fjord in 1997 suggests that wind is important on its own, possibly more so than tidal activity, [tidal range in Mariager Fjord is “micro-tidal with a tidal range of only 20–30 cm”. However, Kolgrafjörður probably is more affected by tidal cycles, with wind only occasionally important. We should note that Denmark uses A LOT of fertilizer, which is implicated as the cause for the hypoxic event (Fallesen et al. 2000).

Eru einhver ferskvatnsáhrif á næringarefnaflæði eða sýrustig? Sennilega veikburða við hliða sjávarfallasveiflunnar? Samt mikið af plöntuleifum í syðstu stöðinni sbr. Árna.

Sölupunktur: Systems like Kolgrafafjörður useful as models for OMZ or human-induced hypoxic zones?

Halda umfjöllun um efnafræði og vatnafræði í lágmarki – erum ekki með mælingar á slíkum parameterum.

Ætlum við að ganga út frá botngerð og týpum stöðva eins og Valtýr/Agnar? Endurskoða það eða ákveða að þetta sé einsleitt m.t.t. botngerðar úr því B0 er farin út?

Er þarna einhver lagskipting sem við vitum um? Ættu sjávarföllin ekki að þurrka það út a.m.k. 2x á sólarhring?

**Conclusion punktar:**

First study to link hypoxia with benthic animals within the Northern Atlantic? (Grænland, Ísland, Færeyjar, Svalbarði?)

Rannsóknin mikilvæg alþjóðlega vegna þess að…so what…because….

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