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Animal-Sediment relationships reexamined, a meta-analysis

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Abstract:

The patterns associated with the influence of grain size on the spatial variation of the deposit and suspension-feeding groups have been studied since the late 1950s. The foundational paper for the theory, Sanders (1958), proposed that a higher proportion of clay and silt-sized grains in the sediments correlates with a higher proportion of deposit feeders compared to suspension feeders. This theory has become widely accepted and taught in textbooks despite subsequent papers indicating differing observations. Through a meta-analysis, this study examines whether the observation from Sanders (1958) was indicative of a general rule or an anomaly. Additionally, this study aims to determine that this spatial distribution pattern covaries with food availability in the water column, measured by surface chlorophyll content gathered via satellite data using a meta-regression. The meta-analysis found the general effect size of grain size, measured as percent silt-clay, was a correlation coefficient of 0.13 across the nine studies. Indicating that a high proportion of fine grain sediment is not a consistent measure of increases in deposit feeder abundance. The meta-regression did not reveal any pattern associating the effect sizes of the individual studies with surface chlorophyll concentration. Suggesting that chlorophyll concentration is not a covarying factor influencing the spatial variation of feeding modes. While the pattern associating grain size with feeding mode spatial variation was determined not to covary with surface chlorophyll concentrations, other factors may include facultative feeding, larval dispersal, trophic group amenalism, and interactions with predators. Regardless, the pattern observed by Sanders (1958) is not generalizable and the inclusion of this pattern in textbooks should be retired.

Introduction:

The theory that sediment grain size can predict the proportion of deposit feeders to suspension feeders has been studied since Sanders (1958) first reported the trend in Buzzards Bay, Massachusetts. Sanders (1958) found that sediments consisting primarily of silt and clay possessed higher proportions of deposit feeders compared to suspension feeders. Since this pioneering study, this idea has been examined in other environments such as Louisiana in Gaston and Nasci (1988), Mananaku Harbor, New Zealand with Grange (1977) and Pridemore et al. (1990), and has permeated marine ecology textbooks (Bertness, 1999; Bertness et al., 2013; Levinton, 2021).

Studies that have attempted to document this pattern in other locations produced mixed results. Explanations for this divergence include differences in larval settling, facultative feeding, and trophic group amenalism (Macdonald et al., 2012; Rhoads & Young, 1970; Snelgrove & Butman, 1994). A more fundamental question is whether the relationship between sediment grain size and feeding mode first documented by Sanders (1958) is an anomaly or a more general pattern. Given that sediment grain size may be directly or indirectly connected to the food supply for deposit feeders and suspension feeders, I hypothesized that the correlation between feeding modes and sediment grain size would covary with food availability in the water column. A higher food availability would result in deposit feeders being less restricted to sediments with a high proportion of fine sediment sizes and suspension feeders would not be restricted to areas of higher flow and consequently larger sediment grain size. In areas with low food availability, the grain-size distribution might become more important in determining spatial variation in feeding modes.

To achieve this, a meta-analysis using a random-effects model was conducted to determine whether the correlation between sediment grain size and feeding mode (deposit feeders versus suspension feeders) holds across different regions and whether water column chlorophyll concentrations as a measure of food availability can explain discrepancies in this pattern.

Methodology:

Following the general procedure for a meta-analysis from Ferriss et al (2019) criteria for study inclusion were created before starting the literature review. Papers in this meta-analysis study met these criteria for inclusion in the study. The criteria were at least different 5 stations within the study area, sediment grain size as a percent silt-clay (< 63-µm diameter), and data relating percent silt-clay and the proportion of deposit feeders and suspension feeders.

Literature review:

The literature review was primarily done by using Google Scholar. Two sets of search terms were used in two rounds of literature review. The first round of the literature review used the search terms; “deposit”, “suspension”, “feeding”, and “grain-size”. From this search, four out of the nine included studies were found. The second round of the literature review used the search terms; “trophic structure”, “macro-benthic”, and “soft bottom.” Five out of the nine included studies were found from this second round of search terms.

Data Collection

Once each paper passed the criteria, the data for percent silt/clay or fine sediment and percent deposit feeders were found within each study. In some studies, this information was conveyed in figures and graphs, so the automeris.io web plot digitizer was used to extract data points. Once all the information was collected into one document, Excel’s Pearson function was used to calculate the Pearson correlation coefficient between the percent deposit feeders and percent silt-clay.

To estimate food availability at each study location, the annual average chlorophyll-a concentration at each study location was calculated using satellite data from NASA’s National Earth Observatory (NEO). Chlorophyll concentrations were averaged for the year 2021, a year that included monthly chlorophyll-a estimates for all study sites. Even though the studies had been conducted in different years, this exercise enabled comparisons among stations during the same year.

Statistical Analysis

Using R-studio's “meta” and “metafor” packages, a random effects model meta-analysis was performed. The metacor function was used to find between-study heterogeneity and the associated p-value. This same function also provided the general effect size of percent fine sediments on the proportion of deposit feeders and the associated p-value for statistical significance.

After the general effect size was found, a meta regression was used to determine if chlorophyll concentration could explain between-study heterogeneity.

Results:

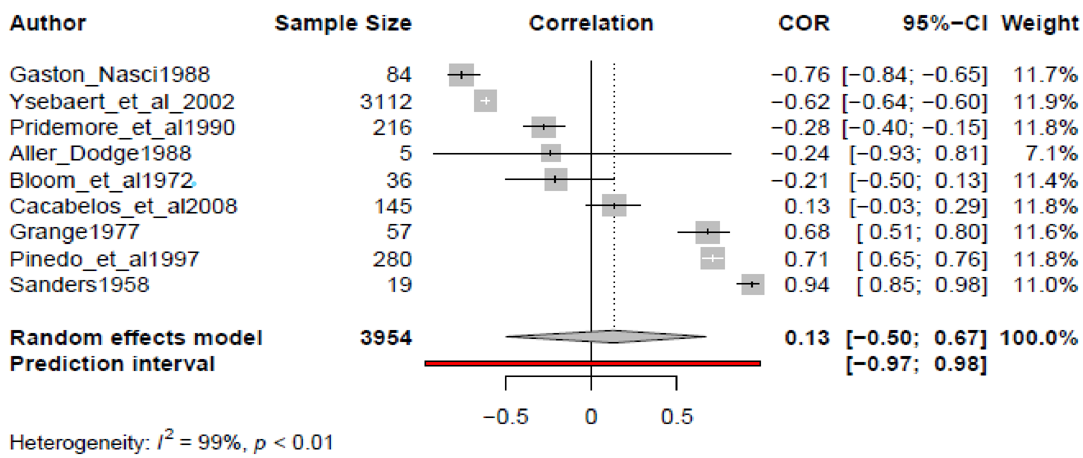

Figure 1: Forest plot showing the study, sample size, the Pearson correlation, and the weight of the study. The analysis was done using a random effects model and determined if there was significant between-study heterogeneity. The p-value for the determination of between-study heterogeneity was <0.01, which indicates significant variation across studies. The overall study effect size is 0.13, which is not a strong correlation.

The random effects meta-analysis model met a p-value <0.01, indicating that the effect grain size on the proportion of deposit feeders varied among the studies. The Pearson correlation coefficient, our measure of study effect size, ranged from -0.76 to 0.94. The Sanders (1958) study had the strongest positive correlation between the proportion of fine sediments and the proportion of deposit feeders. The study by Gaston and Nasci (1988) had the strongest negative correlation. Other studies showed positive, negative, or no correlations (*Figure 1*). The overall effect size was determined to be 0.13 with a p-value of 0.67, indicating no significant correlation between the proportion of fine sediment and the proportion of deposit feeders across these studies.

This variation in effect size across studies is not explained by variation in food availability. There is no significant correlation between effect size and average chlorophyll concentration, although the slope of the trendline is negative, as would be expected if food

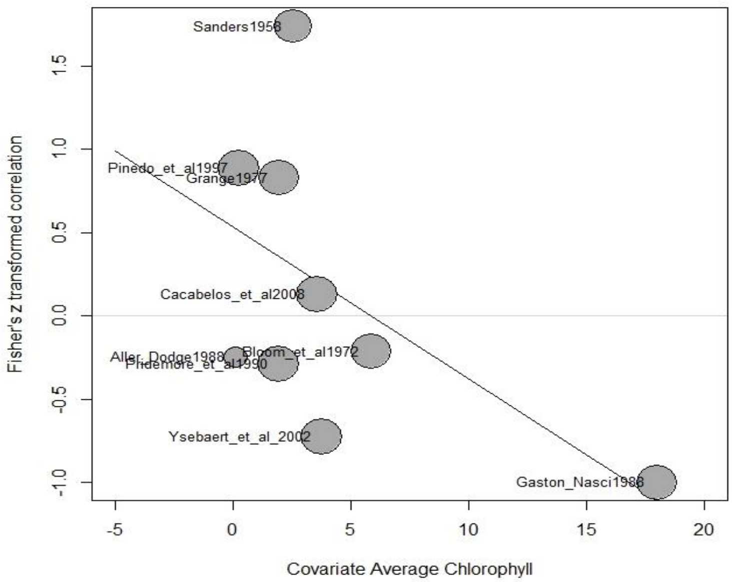

Figure 2: A bubble plot following a meta-regression of the effect size of the study and the chlorophyll concentration. The sizes of the bubbles indicate relative weight within the meta-analysis. This graph indicates that there is not a significant relationship between the study effect size and chlorophyll concentration.

availability drove this relationship *(Figure 2).* Gaston & Nasci (1988) and Cacabelos et al (2008) were the only studies that fell near the regression line, the other studies fell away from the regression line. Sanders (1958) showed an effect size larger than would be expected if chlorophyll was the variable that overrides the grain-size distribution, and the effect observed by Ysebaert et al (2002) was below what would be expected.

Discussion:

The meta-analysis showed no significant general effect of grain size on the proportion of deposit feeders in the community. There was a wide range of correlation coefficients found in each study indicating that grain size is not a reliable measure for determining trophic distribution. Interestingly, two studies, Grange (1977) and Pridemore et al. (1990), were conducted in Manukau Harbour, New Zealand and had different Pearson correlation coefficients. Grange (1977) observed a strong positive correlation of 0.68 whereas Pridmore et al. (1990) had a weak negative correlation of –0.28 (*Figure 1).* Both locations were estimated to have similar chlorophyll concentrations and neither fell on the regression line (Figure 2). This suggests that this pattern is not location specific and does not persist at a given location.

This lack of a general pattern is not connected to food availability, as measured by average chlorophyll concentration. Most studies had weak correlations between sediment grainsize and proportion of deposit feeders, and those with strong correlations were either significantly above or below the regression line (Figure 2). Only three of the nine studies fell close to the regression, so while there is no general pattern associated with grain size and deposit feeder distribution chlorophyll concentration does not appear to influence this variability.

Several explanations have been proposed to explain the discrepancies from Sanders (1958) observation of grain size as an indicator of deposit feeder abundance. One explanation is that many species employ facultative feeding, or more than one feeding mode (Macdonald et al., 2012). Many species of polychaetes and some bivalves exhibit facultative feeding, which would broaden the potential range of their distribution. Another theory is trophic group amensalism, where deposit feeders inhibit suspension feeders from settling in the larval stage due to a lack of sediment stability (Rhoads & Young, 1970). Flow fields that influence sediment grain size might also change patterns of larval settlement, which could obscure the effects of sediment grain size on spatial variation in trophic groups (Snelgrove & Butman, 1994).

Examining interactions with other trophic levels may provide additional insight as well. The focus on deposit and suspension feeders ignores interactions with predators and scavengers. Increases of predation pressure has been connected to changes in behavior in order to increase chances of survival (Bertness, 1981; Cousyn et al., 2001). An example being observations shown that tropical gastropod species do not tend to forage during high tide due to higher predation by fish, while gastropod species in temperate waters experience less fish predation do the majority of their foraging during high tides (Bertness, 1981). It is likely that similar pressures influence spatial feeding mode variation, so expanding the examination of benthic trophic distribution to include predation pressure may reveal patterns not previously observed. Additionally, there may be a pattern associated with the mobility of the organisms being studied. Suspension feeders are often sessile, whereas many deposit feeders are mobile. Population distribution is likely to be connected to the difference in lifestyle. Once settlement occurs for sessile organisms, the likelihood of the individual moving to a different place, even if another location is more ideal, is low. However, deposit feeders tend to be more mobile than suspension feeders, allowing for greater freedom to move to more suitable conditions (Jumars and Fauchald 1977).

Potential caveats for this analysis primarily center around the chlorophyll data. An aggregated mean was used for the meta-regression and in general aggregated means are not recommended for this kind of analysis. We assumed that because each study focused on a particular body of water that was relatively small geographically, the aggregated mean would still be representative of the study region. Additionally, chlorophyll content at the water surface is an imperfect indicator of food availability since the rate of export of food from the surface to the seafloor likely varies among stations. The total abundance or biomass of benthic macrofauna could potentially be a better indicator of food availability; however, abundance was not consistently reported in our studies, whereas satellite chlorophyll data was readily available. The number of studies in this meta-analysis was also small due to incompatible data representation across studies. Despite the small number of studies included, the wide range of effect sizes (both positive and negative) we observed indicates that the addition of more studies to the meta-analysis would not likely change our findings.

The effect of sediment grain size on the proportion of deposit feeders is not generalizable. It is interesting that the earlier study by Sanders (1958) was conducted at a location where a very strong relationship occurred, but subsequent studies have shown different patterns. For this reason, the idea that grain-size is directly related to deposit feeder abundance should be retired from textbooks. Most studies in this meta-analysis either did not show a strong correlation between grain size and deposit feeder presence or showed the opposite trend. While I hypothesized that the variation of the effect of grainsize on the proportion of deposit feeders was a result in varying surface chlorophyll concentrations, this was shown not to be the case. There are several additional theories proposed that may better explain this variation, and more study into unexplored relationships may reveal additional patterns previously overlooked.

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