**Master of Science Thesis**

# THE RELATIONSHIP BETWEEN GENETIC DIVERSITY OF AN ANNELID WORM, *PYGOSPIO ELEGANS*, AND LOCAL INVERTEBRATE SPECIES DIVERSITY

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## ABSTRACT

Biodiversity research is mainly based on studying the numbers and relative abundances of different biological variants. For the field of population genetics, these variants are genes or alleles within a species; and for the field of community ecology, they are species within a community. Both of these biodiversity levels – genetic diversity and species diversity – are affected by similar ecological and evolutionary processes, which in turn are shaped by characteristics of the environment. Several studies have shown that responses to the environmental characteristics are linked to variable relationships between the two levels of diversity. Notably, theory predicts a positive relationship due to similar forces acting in similar ways on both of the levels. Studies of these relationships have mainly focused on terrestrial systems, and have remained largely unexplored in marine environments. Finding a covariation between the diversity levels outside of terrestrial conditions and linking it to the characteristics of the environment would outline the similarities between processes controlling genetic and species diversities. In this study, a relationship between the genetic diversity of a worm *Pygospio elegans* and the species diversity of the local invertebrate community was examined with different environmental characteristics (sediment characteristics, salinity, and temperature) that could explain the observed patterns. Samples of *P. elegans* and local macrofauna were collected from four different sites and three different times within a year at Isefjord-Roskilde Fjord estuary complex in Denmark. A strong positive relationship was found, which indicates that both the genetic diversity within this species, and the species diversity within these communities, react similarly to the mechanisms acting through their environment. The environmental characteristics that seemed to affect the patterns most were the sediment quality and its organic content for the genetic diversity, and the quality of the sediment, the water salinity and its fluctuation for the species diversity. Although implicit processes, such as competition, cannot be excluded from the interpretation, the positive correlation found in this study implies that it could be possible to predict one level of diversity based on the other, or based on one of environmental characteristics that affects both levels. For example, time consuming taxonomic analyses could be substituted by genetic analyses of *P. elegans* alone, from which the level of species richness could be estimated. This would be a valuable approach for research and conservation, and more studies of the topic with different species and environmental properties are needed to advance this field of unified biodiversity research.

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## TIIVISTELMÄ

Ympäristön monimuotoisuutta mitataan pääasiassa erilaisten biologisten yksiköiden lukumäärinä. Populaatiogenetiikassa ne ovat geenejä tai alleeleja yhden lajin sisällä, yhteisöekologiassa puolestaan lajeja eliöyhteisöjen sisällä. Molemmat näistä monimuotoisuuden tasoista – lajin sisäinen ja lajien välinen monimuotoisuus – muokkautuvat ekologisten ja evolutiivisten prosessien kautta, jotka puolestaan syntyvät ympäristön olosuhteista. Ympäristön ominaisuuksien ja niistä syntyvien prosessien tiedetään vaikuttavan molempiin monimuotoisuuden tasoihin samankaltaisesti: tämän teorian mukaan niiden välillä tulisi siten löytyä positiivinen korrelaatio. Tässä tutkimuksessa pyrin etsimään laajalti huomiotta jääneestä ympäristöstä, vesistöstä, positiivista yhteyttä hiekkaputkimadon (*Pygospio elegans)* geneettisen monimuotoisuuden, sekä sen elinympäristön pohjaeläinlajien monimuotoisuuden välillä. Samalla halusin selvittää, onko tutkituilla ympäristön ominaisuuksilla (sedimentin ominaisuudet, veden suolaisuus, ja sen lämpötila) osuutta havaittuihin tuloksiin. Tanskan Isefjord-Roskilde Fjord murtovesistöstä kerättiin neljältä eri paikalta kolmena eri aikana näytteitä hiekkaputkimadosta sekä paikallisista lajeista. Niiden väliltä löytyi vahva, positiivinen korrelaatio, joka kertoo siitä että sekä geneettinen monimuotoisuus lajin sisällä, että lajien välinen monimuotoisuus eliöyhteisössä reagoivat samalla tavalla ympäristönsä kautta toimiviin prosesseihin. Hiekkaputkimadon sisäistä monimuotoisuutta selittäviä ympäristön ominaisuuksia olivat sedimentin laatu ja sen sisältämän orgaanisen aineksen määrä, ja lajien välistä monimuotoisuutta sedimentin laatu sekä veden suolaisuus ja sen vaihtelu. Vaikka havaittuun suhteeseen vaikuttaisivat myös epäsuorat tekijät, kuten lajien välinen kilpailu, positiivisen korrelaation havaitseminen merkitsee että yhden monimuotoisuuden tason ennustaminen toisen tason, tai jonkin ympäristön tekijän kautta, voisi olla mahdollista. Esimerkiksi tutkimalla pelkästään hiekkaputkimadon sisäistä monimuotoisuutta voitaisiin pyrkiä määrittämään myös paikallista lajien monimuotoisuutta ilman lajikartoitusta. Tämä voisi osoittautua edistykselliseksi lähestymistavaksi monimuotoisuuden tasojen yhtenäiselle tutkimukselle ja suojelulle, joiden edistämiseksi tarvitaan lisää tietoa erilaisten lajien ja ympäristön ominaisuuksien vaikutuksista.

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## 1. INTRODUCTION

Biodiversity – the variety of life on Earth – consists of different biological variants within and between species, and all of their interactions with the non-living environment around them (e.g. Wilson & Peter 1988, Wilson 1992, Harper & Hawksworth 1994, Gaston 1996, Laverty et al. 2008). This currently existing hierarchy of diversity has resulted from evolution over the course of life, and continues to be created and maintained by ecological and evolutionary processes. These processes in turn are shaped by the local environment through its different characteristics, ranging from the size and connectivity of the habitat, to the heterogeneity and variable resources it provides, to individual organisms and communities living in it. This leads to increasing concerns about the state of biodiversity as a consequence of rapid environmental changes. The amount of diversity in all of its levels has been shown to contribute to the health and function of ecosystems: for example, higher diversity is often related to higher productivity (Naeem et al. 1994, Tilman et al. 1996, Loreau et al. 2001), resilience of ecosystems (Mori et al. 2013), and more stable communities (Tilman 1987, Folke et al. 2004). These factors are fundamental to properly functioning ecosystems that provide us with ecosystem services (Peterson & Lubchenco 1997), including nutrient recycling, clean drinking water and waste decomposition, along with scientific and medicinal benefits. It is important to further understand the underlying mechanisms that create and shape biodiversity in order to create effective methods in conserving it.

It is useful to try to simplify complex phenomena, such as biodiversity, by dividing it into components with repeatable and consistent patterns in order to aid our understanding. We can break biodiversity down to three main levels: genetic diversity within a species, taxonomical species diversity within a community, and ecological diversity of the communities and their abiotic environments (Norse et al. 1986). Ecological diversity in its broadest sense includes all of the biological diversity, from the variety of species to the number of trophic levels, the range of life cycles, and the diversity of biological resources (Harper & Hawksworth 1994). This approach can be very difficult in practice to describe biodiversity in its entirety, and often measurements of population- and community-level diversities are used instead. There are two distinct research fields that aim to explain the numbers and relative frequencies of different biological variants: in the field of population genetics, the variants are genotypes or alleles (Hartl & Clark 2007, Mahoney & Springer 2009), and in the field of community ecology, the variants are species (Chave 2004, Magurran 1988, 2004). Theories of diversity in these fields are similar enough for the same models to be equally well applied to both the species composition of a community and to the genetic composition of a population (Antonovics 1976, Amarasekare 2000, Vellend 2005). Despite the fact that since the 1970's there have been studies showing that these two fields are connected, genetic diversity and species diversity have been, and often continue to be, treated independently (Vellend 2005, Vellend & Geber 2005). Only relatively recently has there been a rising interest in integrative studies as an aim to unify the two fields towards community genetics, which aims to explain the relationships of genetic- and species-level diversities (e.g. Amarasekare 2000, Bell 2001, Wares 2002, Agrawal 2003, Neuhauser et al. 2003, Vellend 2003, 2005, Etienne & Olff 2004, Bernhardsson et al. 2013). To understand the factors that create and shape the population and community patterns, and how they are connected, a further look to the evolutionary and ecological processes and what lies behind them is necessary.

### 1.1. Processes that create and shape local biodiversity

Biodiversity can be measured at three different scales: $\alpha$ diversity refers to the diversity of a particular area, community or ecosystem; β diversity refers to diversity between different ecosystems; and γ diversity sums the overall diversity for different ecosystems within a region (Whittaker 1972). Here, diversity is considered within a single locality ($\alpha$ diversity), because at large spatial scales (i.e. latitudinal gradients) it is not possible even in theory to adequately determine the relationships between different diversity levels, as variation in species diversity is often accompanied by complete turnover in their composition (i.e. none of the species can be found at all localities) (Vellend 2005).

Biodiversity at its local scale is the result of interplay between birth, death, and migration of different biological variants. In its entirety, it is based from genetic diversity within an individual organism as variation in nucleotides, genes, chromosomes, and whole genomes (Maynard Smith 1989, Laverty et al. 2008, Mahoney & Springer 2009). From a single individual, it leads to the variation between different individuals of a single population, between different populations of a single species, and between different species in the environment. The primary mechanism for creating completely new genes happens through mutations. Correspondingly, at the species level, the new variants are formed through speciation. However, mutation and speciation have commonly been neglected in context of $\alpha$ diversity, as they are thought to act too slowly compared with ecological processes (Vellend & Geber 2005; but see Losos & Schluter 2000, Hartl & Clark 2007, Laroche et al. 2015). Therefore, there remain three processes that in most cases are more likely to shape and explain $\alpha$ diversity at the two levels: drift, migration, and selection (Vellend & Geber 2005).

### 1.2. Mechanisms connecting genetic diversity and species diversity

Drift is the random fluctuation in the relative frequencies of genes and species, and migration is their movement between gene and species pools. Drift and migration are called neutral processes, as unlike selection, they do not target any specific allele or species based on their success. The effects of these processes independently on either genetic diversity or species diversity are relatively well understood (Rosenzweig 1995, Frankham 1996, 1997), but the simultaneous response of the two levels of diversity to them is not. Based on the theories of island diversity (island biogeography by MacArthur and Wilson, 1967, and the island model of population genetics by Sewall Wright, 1940) Vellend (2003) proposed that species diversity within a community, and genetic diversity within a single species, might be positively correlated as the result of processes that influence the two levels of diversity in the same way. Island biogeography predicts that there is a balance between immigration and local extinction in regulating species diversity in the same way as Wright's model predicts a balance between gene flow and genetic drift in regulating genetic diversity. This kind of a positive correlation (termed as SGDC, a species-genetic diversity correlation, by Vellend 2005) would therefore be theoretically expected, since the two levels of diversity are affected by similar processes in similar ways. Although this has been the case for the majority of studies (e.g. Morishima & Oka 1978, Antonovics 1992, Huston 1994, Vellend 2003, 2005, Etienne & Olff 2004, Cleary et al. 2006, He et al. 2008, Derry et al. 2009), many have also found negative relationships (e.g. Marshall & Camp 2005), while others have not found relationships of any kind (Hughes et al. 1997, Puşcaş et al. 2008, Silvertown et al. 2009, Struebig et al. 2011).

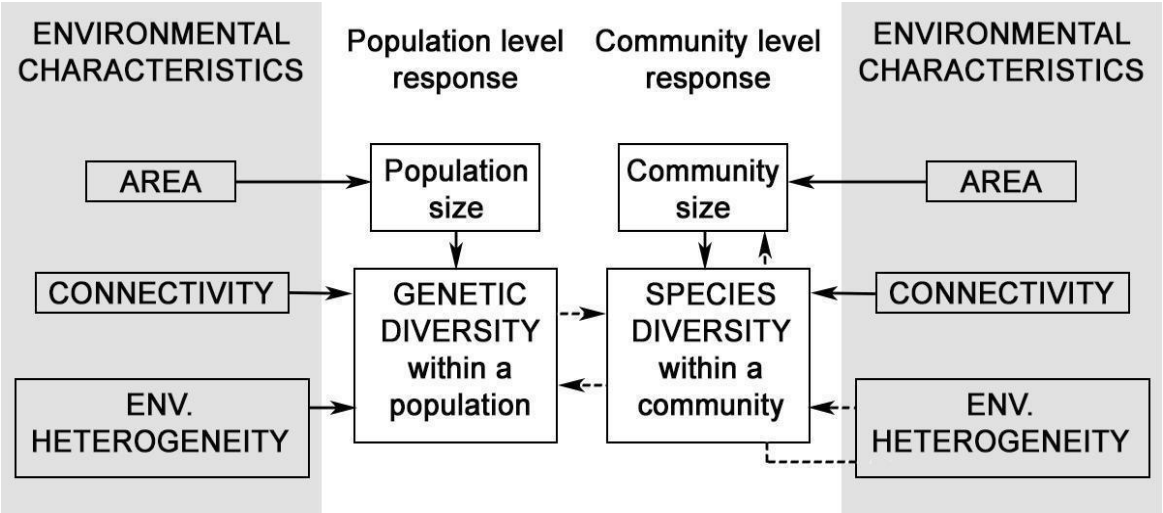


Figure 1. A representation of how environmental characteristics (grey) influence both the genetic diversity within a species and the species diversity within a community (modified from Kahilainen et al. 2014). Continuous lines indicate positive (parallel) connections, and dashed lines indicate ambiguous connections.

These results suggest that genetic and species diversities are not always regulated by processes acting similarly on both levels. In addition to the environmental characteristics directly affecting both of the diversity levels in parallel, the levels might also be related to each other by one of the levels acting causally on the other. The different ways in which the two levels of diversity are affected by their environment or by the other level of diversity is visualized in Figure 1, and further explained in the next two sections.

### 1.2.1. Parallel effects

The primary prediction for a positive relationship between genetic diversity and species diversity is based on local environmental characteristics having a similar, parallel influence on both levels of diversity through similar ecological and evolutionary processes. The parallel influence could be the result of neutral processes of drift and migration (Hubbell 2001, Vellend & Geber 2005) or spatially varying non-neutral selection (Antonovics 1992, Huston 1994, Vellend 2003, Vellend & Geber 2005, Etienne & Olff 2004). The founding study of species-genetic diversity correlations by Vellend (2005) resulted most commonly in moderate to strong positive relationships between genetic diversity and species diversity in a simulation where communities were surveyed under different environmental conditions. Certain local environmental characteristics have been pointed out as strong candidates for having parallel effects and therefore creating the positive relationships: the size of an area influences both diversity levels through drift; geographic connectivity through immigration (Foster & Tilman 2003, Vellend 2003, 2005), and exogenous heterogeneity through spatially or temporally varying selection (Levene 1953, Morishima & Oka 1978, Chesson 2000, Marshall & Camp 2005). There can also be other non-neutral environmental characteristics that act in parallel to genetic diversity and species diversity. For example, productivity or available resources can be linked to the population and community sizes and therefore can lead to positive relationships (e.g. Marshall & Camp 2005, He et al. 2008). Regardless of whether the underlying mechanisms are neutral or not, there is a good basis for expecting positive correlations between diversity at the two levels based on these studies.

The area of a suitable habitat affects the number of communities and populations it can contain: larger areas can contain larger populations and communities, and therefore support both higher genetic and higher species diversities. Connectivity of a habitat to the global gene and species pool in turn determines the amount of gene flow and species migration. Small, poorly connected areas can be expected to lose genes and species more frequently, and gain less back through immigration, while better connected localities receive more immigrants from more species as well as more alleles. Therefore better connected habitats also allow for both higher genetic and species diversities (Hubbell 2001, Lamy et al. 2013). Empirical studies have proved this to be true, so as the two environmental characteristics affect both levels of diversities in a parallel manner, a positive relationship between the two levels of diversity can be expected based on the area and connectivity of the habitat (Foster & Tilman 2003, Vellend 2003, 2005).

Niche variation theory (Van Valen 1965) predicts that populations with broader niches contain greater genetic diversity, which in turn favours coexistence among species. Environmental heterogeneity therefore leads to a prediction of a positive relationship between genetic diversity and species diversity. This theory has also been supported by empirical experiments (Levene 1953, Morishima & Oka 1978, Chesson 2000, Marshall & Camp 2005), but the relationship has proven more complex than that. For example, predictions of positive relationships may fail if individual fitnesses depend strongly on community context (Vellend 2005). In addition, local environmental heterogeneity does not only impose varying selection, but causes changes in population sizes and therefore their genetic diversity. These processes acting together might lead to no correlation or even a negative one between the two levels of diversity in some cases.

A positive relationship may be absent if there is a varying response to environmental characteristics between the diversity levels (Vellend 2003, 2005, Derry et al. 2009, Silvertown et al. 2009). For example, a study by Wei and Jiang (2011) aimed to find SGDCs and their underlying mechanisms in forests that were either natural (undisturbed) or disturbed by human activity (e.g. roads). They found that in the natural forests, a significant positive correlation between the genetic diversity of their study species *E. pleiospermum* and the local species diversity existed – but it was absent in the disturbed forests. They concluded that, in their case, a positive relationship was driven by altitude. In the disturbed forests, the lack of a significant positive correlation was thought to be because species diversity had been reduced due to disturbance, but genetic diversity was unaffected. Similarly, no correlations were found in a study by Derry and others (2009) on zooplankton, in which genetic diversity corresponded with topographical lake structure, whereas species diversity varied with lake acidity.

### 1.2.2. Causal effects

Environmental characteristics do not always influence the two levels of diversity directly, but may have an indirect effect through the other level of diversity (Vellend 2005, Vellend & Geber 2005). This could be due to one level occupying a majority of niche space, so that it constrains the space for the other. Genetic diversity may causally influence species diversity, if it affects population's viability, or if a dominant species determines the biotic environment experienced by the rest of the community. Conversely, species diversity of a community may causally influence the genetic diversity within a species if it affects the set of selective pressures it experiences. For example, if species diversity increases by immigration causing population sizes to shrink due to the relative space available for each population, therefore also reducing genetic diversity, a negative relationship between the

two levels may form. Empirical patterns and theoretical frames still argue, however, that negative correlations between genetic and species diversities are rare in nature and unlikely to occur. While positive correlations are expected in general, what is found in a particular environment will depend on the mechanisms influencing each level of diversity and the relationship between them in the specific environment, making it difficult to predict the direction and strength of the possible correlation.

### 1.3. Are species-genetic diversity correlations universal?

Observational or experimental studies can shed light on how specific environmental characteristics drive diversity correlations, and should be further pursued. Continuing research is necessary for better knowledge of the interplay between the ecological and evolutionary processes in determining community structure and dynamics, which is critical for effective strategies on conservation and research on biodiversity at all of its levels. Diversity within and between species could be simultaneously taken into account in conservation if a positive SGDC occurs, and on the contrary, a negative correlation might imply a conflict between them (Kahilainen 2014, Cleary et al. 2015). The nature of this relationship in a given habitat provides essential information when planning conservation. Applications of the knowledge could help in predicting the overall response of biodiversity to the changes in environment. Generalization of the relationship would possibly allow predictions of one level based on the other, based on environmental characteristics, or even based on a community foundation species (a species that has a strong role in structuring a community). There is strong evidence that the genetic diversity within a single species that has a dominant or foundational role in the ecosystem, could affect the diversity of a whole community (Treseder & Vitousek 2001, Whitham et al. 2003). Evidence of genetic diversity of a single species being tightly connected to the whole species diversity of the community could mean that the species might be used to predict it instead of time-consuming and costly whole-community analyses (Chatzigeorgiou et al. 2014).

Most studies on the relationships between genetic diversity and species diversity have focused on terrestrial systems, and SGDCs remain largely unexplored in marine environments (Messmer et al. 2012). Oceans are environments of high connectivity and allow great dispersal both within and among populations (Cowen & Sponaugle 2009). Since $\alpha$ diversity correlations are thought to be more commonly positive in island-like systems, and for aquatic environments area is much harder to define than for terrestrial habitats, it could be that a positive correlation might be less likely to exist in aquatic environments than in terrestrial environments. Also, as it is the different environmental characteristics that are linked to the variable relationships, it is of interest to pursue studies in marine environments as they have many unique characteristics. The structure of diversity in marine environments can be affected by its abiotic conditions, such as water salinity (Bekkevold et al. 2005) and temperature (Banks et al. 2007), as well as different biotic factors (Kesäniemi et al. 2014a). There are some studies that have focused in either full marine waters (e.g. Chatzigeorgiou et al. 2014) or freshwater systems (e.g. Blum et al. 2012, Lamy et al. 2013), but very few exist where an environment such as brackish water has been studied (Robinson et al. 2010). The study by Robinson and others (2010) investigated the correlation between the genetic diversity of eight different invertebrate species and the species richness of their local fauna in salt marshes, where the water salinity can vary from fully marine to fresh water and are considered as estuarine ecosystems. A positive correlation was found when their whole dataset was analyzed simultaneously, but there were no statistically significant correlations in the analyses of

each species separately. Because the invertebrates they studied were rare or nonexistent in the areas of lower salinity, they had to exclude them from their study and concentrate on the marine areas. This means that they could not make proper conclusions about the effect of the salinity on the diversity correlations. They listed a number of limitations to their study, and stressed the importance of studying the diversity levels of local communities in naturally varying environments in order to determine the driving forces behind relationships of these two levels.

Marine benthos is the most widespread habitat on Earth, and it has a major role in supporting key ecosystem services (Snelgrove 1999). Benthic invertebrate taxa would be good species groups to study in terms of looking for a positive SGDC, as they usually have limited dispersal potential as adults, but many species disperse in their larval stage (Weersing & Toonen 2009). Many environmental factors and life history traits, such as the duration of the larval stage, can lead to a variety of distribution patterns with significant differences even at close geographic distances (Hohenlohe 2004, Hart & Marko 2010, Derycke et al. 2013). Studying the SGDCs of benthic fauna in a brackish water system would be of interest in order to find out if these systems show similar patterns as previously discovered positive correlations in terrestrial and either fully marine or freshwater systems, and what kind of environmental characteristics could be driving them.

The aim of this study is to investigate possible correlations between the genetic diversity of a community foundation species *Pygospio elegans* and the species diversity of the local invertebrate benthic macrofauna community, and whether the observed patterns could be explained by certain environmental characteristics. My main hypothesis is that a positive correlation between the two levels of diversity exists. The environmental characteristics that support more niches and allow larger population sizes should lead to higher species diversity within communities and greater genetic diversity within *P. elegans.* The most crucial features of the environment that are thought to affect the studied macrofauna both on the genetic and species levels are the temperature and salinity of the water and the characteristics of the sediment they live in.

### 1.4. Study species and location

*Pygospio elegans* is a species from the spionid family of annelid polychaete worms. It can reach 15 mm in length and has a lifespan of one to two years (Anger et al. 1986), which it spends living a sedentary life in sand-tubes it constructs in shallow sandy or muddy sediments (Rasmussen 1973, Anger et al. 1986). *P. elegans* is a cold adapted, widely spread species distributed in the temperate waters of the Northern hemisphere, and commonly found in subtidal and intertidal habitats (Rasmussen 1973, Morgan et al. 1999, Boström & Bonsdorff 1997). It has been described as opportunistic (Morgan et al. 1999, Desprez et al. 1992) and has a wide environmental tolerance i.e. in terms of salinity: high abundance of individuals has been found at salinities as low as 2 ppt (Anger et al. 1986). *P. elegans* is poecilogonous, which means that it expresses polymorphism in its developmental and reproductive strategies by sexually producing either a planktotrophic, benthic, or intermediate larvae; or asexually through fragmentation (Rasmussen 1973, Wilson 1985, Anger et al. 1986, Kesäniemi et al. 2012b).

*P. elegans* can reach high densities especially in nutrient rich waters (Bolam 2004, Bolam & Fernandes 2003), and is the main tube-building polychaete worm in Northern European waters. The dense tube-beds are conspicuous structural features of many marine soft-bottom habitats that affect community structure (Sanders et al. 1962, Woodin 1981, Trueblood 1991). There is evidence that even small patches of *P. elegans* can have a

significant effect on species abundance and community composition by increasing the number of species and small-scale spatial heterogeneity (Bolam & Fernandes 2003). This species was chosen because it is very widespread, and it has a major effect on the environment other species experience. Correlations between diversity levels have been reported to be more easily identified when the species from which the genetic diversity is measured is relatively common (Vellend 2005). *P. elegans* has also been used in a variety of studies before, and its genetic structure is well known (e.g. Kesäniemi et al 2012a, 2012b, 2012c, 2014a, 2014b). If the genetic diversity of *P. elegans* seems to be correlated positively with the local macrofauna, it would mean that its genetic diversity might be used as an indicator for the species richness of an area.

Larval developmental mode and the stochastic environment of adults have been shown to affect temporal genetic variation of *P. elegans* (Kesäniemi et al. 2012c). Some populations are reported to produce only one type of larvae (Anger 1984, Bolam 2004), but *P. elegans* show a greater variability of developmental modes and reproductive strategies in Danish estuaries. Populations in Denmark are polymorphic, showing all types of developmental and reproductive modes either simultaneously or seasonally (Rasmussen 1973, Kesäniemi et al 2012c, Thonig, personal communication). The study took place in the Isefjord (305 $km^2$) and Roskilde Fjord (123 $km^2$) estuary complex that is connected to the Kattegat sea area in the southern Baltic Sea, where *P. elegans* is commonly found.

## 2. METHODS

The data used for this study was based on samples collected from four different locations in Denmark: Lynaes, Lammefjord, Vellerup, and Herslev (abbreviated LYN, LAM, VEL, and HER) (Figure 2) and transported to Jyväskylä for analyses. Samples of *Pygospio elegans* for the measures of genetic diversity and samples of benthic macrofauna for the measures of species diversity were collected from each location at three different times during the year 2014 (17.–20.3.; 12.–14.5.; and 19.–20.8.). I participated in the August sampling. From now onwards, the sampling times will be referred to either by name or number of the month when sampling took place (March = 3, May = 5, and August = 8).

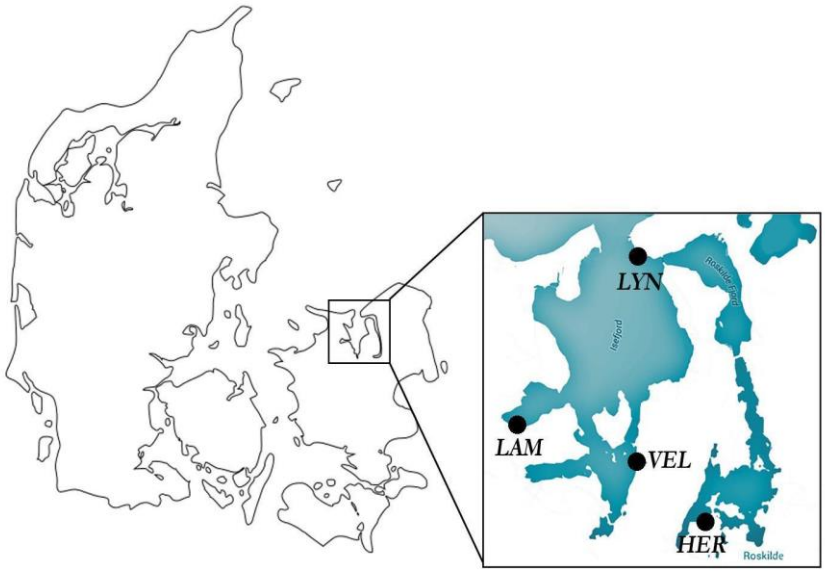


Figure 2. The four sampling locations, Lynaes, Lammefjord, Vellerup, and Herslev, located in the Isefjord-Roskilde Fjord estuary complex in Denmark.

Environmental data from the same locations were collected for another project (Thonig et al., MS in review) and made available for me to use in order to assess whether the diversity patterns were related to the different environmental characteristics. Data used in this study included water and sediment variables that are thought to most likely define the habitat conditions for the studied benthic fauna. The salinity and temperature of the water were recorded continuously using automatic data loggers at the sites. During the sampling, sediment was also collected for measuring its particle size, its sorting, porosity, organic content, and the carbon/nitrogen ratio of the organic matter, which gives an indication of how much of the organic matter is usable for production. Methods used and data handling are described in Thonig et al. (MS in review).

### 2.1. Genotyping *Pygospio elegans*

The genetic diversity of *P. elegans* within a population was measured as allelic richness (the number of different alleles) at five different genetic loci (Table 1). Microsatellite loci were used as they are commonly reported in other studies that measure SGDCs (Cleary et al. 2006, He et al. 2008, Struebig et al. 2011, Blum et al. 2012, Lamy et al. 2013). Samples of *P. elegans* were collected by shoveling the sediment and sieving (1 mm mesh size) on site. The sand-tubes of the worms were picked from the sieved material with forceps and placed in a container filled with seawater. Approximately 50–100 sand-tubes were collected each time to guarantee there would be enough material given that some sand-tubes are empty. The worms were then taken to the laboratory where they were placed on trays with seawater and left undisturbed. In these conditions, the worms will leave their sand-tubes and are easily sampled. The worms were preserved in 95% EtOH. 27–45 individuals per location and collection time were sampled and genotyped for robust estimates of allelic richness.

Genomic DNA was extracted from the worms using the Qiagen DNeasy kit (Qiagen Nordic, Helsinki) following the manufacturer's protocol. Five microsatellite loci were amplified in multiplex reactions using reagents from Qiagen's Multiplex PCR kit (Qiagen Nordic, Helsinki). Multiplex reactions contained 1X Qiagen Multiplex Master mix and 0.2 µM each primer. All amplification reactions were carried out in BioRad C1000 or S1000 thermocyclers (Bio-Rad Laboratories, Helsinki) with the following thermocycling program: 95 $^{o}$C for 15 min followed by 30 cycles of 94 $^{o}$C for 30 sec, 60 $^{o}$C for 90 sec and 72 $^{o}$C for 60 sec, terminating with a 30 min incubation at 60 $^{o}$C. 1 µL of the amplification products were separated together with 0.09 µL GeneScan Liz500 size standard using the ABI PRISM 3130xl machine (both Applied Biosystems; Thermo Scientific, Helsinki). Fragments were sized and genotypes assigned using GeneMapper v.3.7. software (Applied Biosystems; Thermo Scientific, Helsinki) and manually checked for errors.

Table 1. Primers used for the measurements of genetic diversity in *P. elegans* for each locus.

| Locus | Forward Primer (5' to 3') | Reverse Primer (5' to 3') |
|---|---|---|
| pe307 | AGCTAAATCTTGACACTGGCCT | GAAGTCAGCCATCTTGGATTCT |
| pe309 | CCAGAGGAAATGATGTAGGCTC | ATTCACACTTGACCATGACCAC |
| pe385 | TCAATAGGAGAAGCACAACGAA | CGCTGGTTATTTTAGGGATGAG |
| pe6 | ACTACGGAAACTGCCTGCAC | ATATGGCCACCGAAACCTCT |
| pe7 | CTCACCCTTTACACCCAAGG | AGCGTCTGTTATGGGGTACAG |

### 2.2. Benthic faunal surveys

Species diversity was measured as the number of different species (species richness) at each sampling. Three sediment cores were collected using a hand corer (⌀ = 15 cm; ca. 30 cm depth) from each of the four locations at the three different times, adding to 36 sediment cores in total. Sediment from the samples was sieved (1 mm mesh size) on site, and the remaining material was then fixed in 5% formaldehyde solution. In the laboratory, the formaldehyde was drained from the samples with the help of a sieve (1 mm mesh size), and the sample was rinsed several times with deionized water. The rinsed samples were then covered with deionized water and ca. 5 ml of Rose Bengal (2g/L concentration), which is a protein stain that dyes the organic material pink. After letting the colour stain overnight, the samples were rinsed and sieved again and the remaining material was sorted under a dissecting microscope. Organisms, now visible as pink, were placed in their own containers and identified to species. For identification, I used the keys provided in Barnes (1994) and Hayward and Ryland (1995). When exact species identification was not possible, the samples were identified to the lowest reliable level (e.g. *Hydrobia* spp.).

### 2.3. Statistical analyses

The genetic data was first tested for linkage equilibrium and conformity to Hardy-Weinberg expectations using Fstat v.2.9.3.2. (Goudet 1995). With the same software, allelic richness was then calculated based on a minimum sample size of 25, allowing for comparison of the differently sized samples. Species richness was calculated with PRIMER-E v.6.1.16. (Clarke & Warwick 2001) using a rarefaction method which adjusted the number of species to the smallest sample size (9 species observed). The rarefaction method is analogous to the calculating allelic richness based on a minimum sample size, making the two values comparable. For the rest of the analyses, species data was transformed by taking the 4th root, a very strong transformation, to reduce the influence of very high numbers of a single species (*Hydrobia* spp.) which would have otherwise dominated the results.

The allelic and faunal data for the different samples were compared in a similarity matrix using the Bray-Curtis coefficient calculated in PRIMER-E. Based on the counts at each sampling location, matrices were created with similarity values of 0–1, where 0 means no difference in allelic or species composition (the two sites share the same alleles or the same number of individuals of the same species), and 1 means they are completely different (no alleles or species shared). These matrices were then used to create two-dimensional MDS (non-metric MultiDimensional Scaling analysis) scatter plots using PRIMER-E. This analysis plots the samples based on how similar they are to each other, allowing for a visual comparison of e.g. how similar are the temporal samples from the same location, and whether there is overlap between the different locations. MDS plots are more commonly used for visualizing species composition, but since the allelic richness is comparable to species richness, it can also be used as a tool for both the genetic and species compositions, allowing a visual comparison of the two. Based on the Bray-Curtis similarity matrix, an ANOSIM (analysis of similarities) global test was done to see whether there were significant spatial and/or temporal differences in the faunal community compositions and the allelic compositions of populations between different sampling times and locations using PRIMER-E. ANOSIM uses permutation (randomization) methods on a similarity matrix to explore differences between groups of community samples. The test was done for differences between sampling times and for sampling locations in a 2-way crossed design (without replicates) using 9999 permutations. To find out which of the

groups differed from each other, a follow-up ANOSIM pairwise test was done for the species data. A similar test that compares the groups of alleles was performed with Fstat.

To find which of the studied environmental characteristics would best explain the population and community patterns a BEST BIO-ENV analysis with 9999 permutations was done using PRIMER-E. Euclidean distance matrix from the environmental data was formed for it and compared to the similarity of the fauna data based on Bray-Curtis. BIO-ENV analysis provides the best match to the observed biodiversity patterns using Spearman's correlation, linking environmental variables to the community structure by comparing the distance matrices of allele/species data to a similar distance matrix based on the environmental data. The main hypothesis of a species-genetic diversity correlation was tested by plotting allelic richness and species richness in a Pearson's correlation using IBM SPSS Statistics v.22.0 (IBM Corp., NY). This was done across the sampling locations for each collection time separately, but because of the small number of replicate sites for each sampling time (N = 4), it was, however, unlikely to find any statistically significant results. Therefore, the data for all three times was combined and an overall correlation across all sampling times and locations was also tested. This is not usually done, as there is a possibility to mix effects of time and space, which could lead to incorrect interpretations of the results. In this case, however, there did not seem to be conflicts that would prevent pursuing the correlation across all sampling times and locations (see discussion).

## 3. RESULTS

436 *P. elegans* worms were used for the genotyping, from which only 10 were excluded from the data due to amplification failures in more than two of the loci. From the remaining 426 individuals, amplifications were completely successful for loci pe307 and pe6. Most failures occurred in locus pe309, in which the amplifications for 24 individuals across the samples failed; amplifications of pe385 and pe7 each failed in seven individuals. The numbers of genotyped worms and alleles found for each sample are shown in Table 2.

Table 2. The number of genotyped worms and the number of alleles found for each sample and locus (N = number of individuals genotyped, Na = number of alleles). Asterisks (*) indicate which of the loci vary in the sample size due to null alleles (failed amplifications).

| | Na | | | | |
|---|---|---|---|---|---|
| Sample/locus | pe307 | pe309 | pe385 | pe6 | pe7 |
| LYN3 (N = 31) | 2 | 2 | 5 | 5 | 16 |
| LYN5 (N = 45) | 2 | 2* | 5 | 5 | 19 |
| LYN8 (N = 43) | 6 | 5* | 10 | 12 | 24* |
| LAM3 (N = 34) | 3 | 3* | 5 | 3 | 12 |
| LAM5 (N = 36) | 3 | 2* | 7* | 5 | 17 |
| LAM8 (N = 27) | 3 | 3 | 7 | 5 | 18* |
| VEL3 (N = 32) | 2 | 4 | 5 | 3 | 18 |
| VEL5 (N = 37) | 3 | 3* | 6* | 3 | 18* |
| VEL8 (N = 31) | 8 | 7* | 10* | 6 | 18 |
| HER3 (N = 41) | 2 | 4* | 6 | 3 | 17 |
| HER5 (N = 39) | 3 | 4* | 5* | 2 | 18* |
| HER8 (N = 40) | 2 | 4* | 5* | 2 | 14 |

No signs of genotypic linkage disequilibrium in any of the 120 possible pairwise comparisons of the five different loci were found from the allelic data (data not shown), meaning that all of the loci were independent from each other and therefore inherited randomly. The population inbreeding coefficient of individuals relative to the population ($F_{IS}$), a value that measures the extent to which each of the populations deviate from Hardy-Weinberg expectations, is presented for each population and locus in Table 3. Low $F_{IS}$ values are indicators of random mating, whereas high values closer to 1 are indicators of inbreeding: most of the values were close to zero, but the samples showed some variation, and in 30 cases out of possible 60 statistically significant deviations from Hardy-Weinberg conformity were observed. Especially for locus pe7, all except one of the samples had a significant result, and for the loci pe309 and pe385, the number of significant results was also high (more than half of the populations). Only loci pe307 and pe6 showed signs of Hardy-Weinberg equilibrium in most of their samples.

Allelic richness in *P. elegans* based on a minimum sample size of 25 and averaged over loci for the different sampling locations and times is shown in Figure 3 as scatter plots. In Lynaes, allelic richness was lowest in March and increased over time from May to August. In the same manner, Lammefjord and Vellerup had noticeably higher allelic richness in August compared to other sampling times, but there was virtually no difference between the allele samples collected in May and March. Herslev in turn had a completely opposite pattern compared to the genetic diversity in Lynaes: allelic richness in Herslev decreased over time from May to August. In addition, Herslev differed from all of the other sampling locations in that the lowest amount of diversity was found in the August samples. In Herslev the samples from May and March had a very slight difference in the same manner as in Vellerup and Lammefjord, May having slightly lower allelic richness, leaving Lynaes to the only sampling location that shows noticeable difference in the allelic richness between May and March samples, and where May is substantially higher in allelic richness than March.

Table 3. Inbreeding coefficients ($F_{IS}$) of each locus across populations, where asterisks (*) indicate samples that deviate significantly from Hardy-Weinberg expectations ($P < 0.05$).

| | $F_{IS}$ | | | | |
|---|---|---|---|---|---|
| Population/locus | pe307 | pe309 | pe385 | pe6 | pe7 |
| LYN3 | -0.15 | 0.61* | 0.34* | -0.03* | 0.50* |
| LYN5 | 0.17 | 0.76* | 0.29* | 0.00 | 0.25* |
| LYN8 | 0.13 | 0.29* | 0.36* | 0.00 | 0.31* |
| LAM3 | -0.17 | 0.47* | 0.13 | 0.17 | 0.15* |
| LAM5 | 0.04 | 0.12 | 0.10 | -0.02 | 0.32* |
| LAM8 | 0.10 | 0.19 | 0.40* | 0.08 | 0.68* |
| VEL3 | 0.32* | 0.25 | 0.33* | -0.01 | 0.09 |
| VEL5 | 0.19 | 0.48* | 0.33* | -0.03 | 0.20* |
| VEL8 | 0.46* | 0.40* | 0.22* | -0.04 | 0.37* |
| HER3 | 0.28 | 0.23 | 0.20* | -0.02 | 0.19* |
| HER5 | 0.46* | 0.43* | 0.17 | -0.01 | 0.39* |
| HER8 | 0.16 | 0.13 | 0.08 | -0.05 | 0.38* |

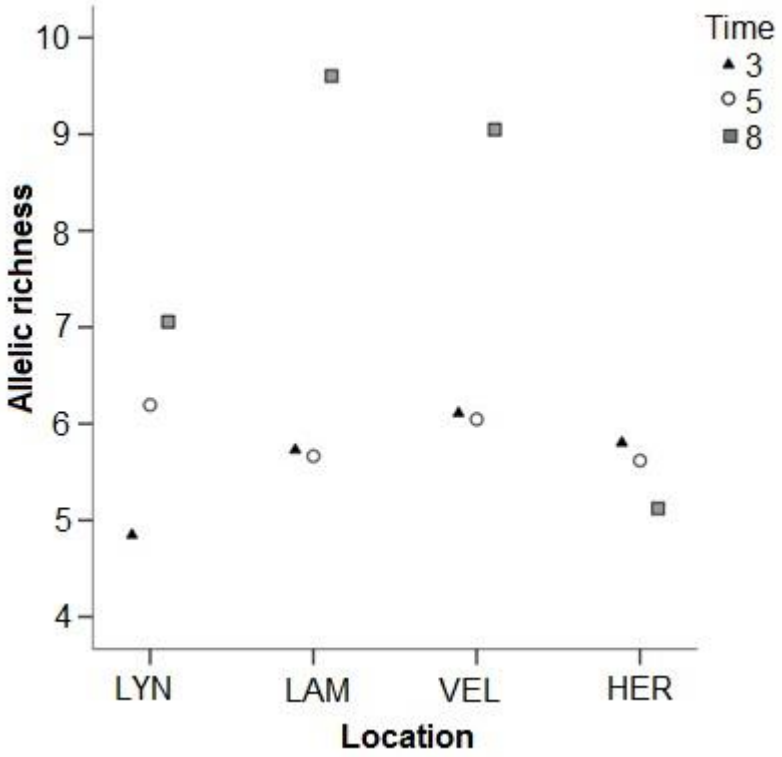


Figure 3. A scatter plot of the allelic richness averaged over loci in *P. elegans* show the differences in genetic diversity between each of the sampling locations, and its changes over time.

Overall, faunal samples contained 16 281 individuals, from which a total number of 46 different species were identified (a complete species list is provided in the Appendix). The number of individuals found in each replicate sample ranged from 128 to 1198, and the number of species ranged from 5 to 29. For each sample time and location overall, the number of individuals ranged from 497 to 2560, and the number of species ranged from 13 to 41. Community structures of each location are depicted in Figure 4 as boxplots, which show the abundances of major species groups (worms [which includes annelids and flatworms], crustaceans, bivalves, and molluscs) across the sampling times. Some variation in the community structures was evident in the abundances of different species groups between the sites. The amount of crustaceans and bivalves were similar to each other in all of the locations, but the abundances of worms and gastropods differed between Lynaes and Lammefjord compared to Vellerup and Herslev. While Lynaes and Lammefjord had higher numbers of gastropods, there were higher numbers of worms in Vellerup and Herslev. The rarefied species richness with error bars across the different locations during each sampling time is shown in Figure 5. Species richness increased over time from March to August in all locations except in Herslev, which had an opposite pattern.

Visualizations of the genetic composition of populations and species composition of communities are shown as MDS plots in Figure 6. For both cases, stress values were less than 0.1, which means that the pictures represent the populations and communities relatively well (for *P. elegans* populations: 2D stress = 0.08, and for macrofauna communities: 2D stress = 0.09). The MDS scatter plots showed that the similarities among populations and communities were clustered based on their location, though there were some overlapping between Lynaes and Lammefjord especially in the allelic data. In addition, Vellerup and Lammefjord allelic samples collected at August were somewhat separated from their clusters.

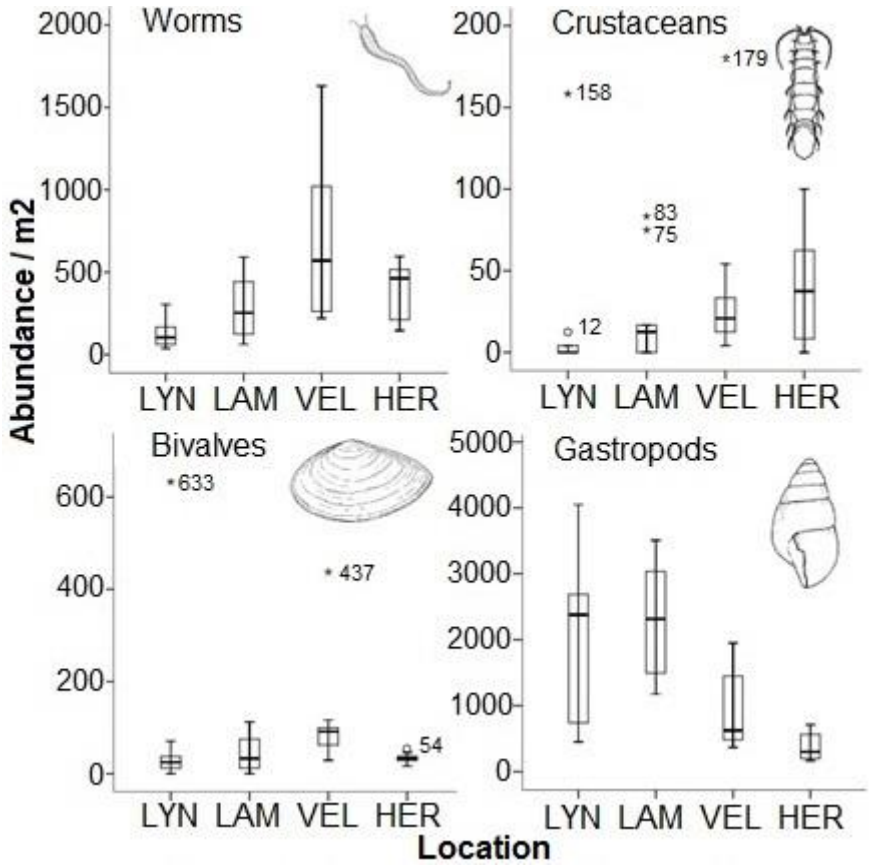


Figure 4. Boxplots of the number per square meter ($m^2$) of individuals found at each site for four major taxa (worms, crustaceans, bivalves, and gastropods).

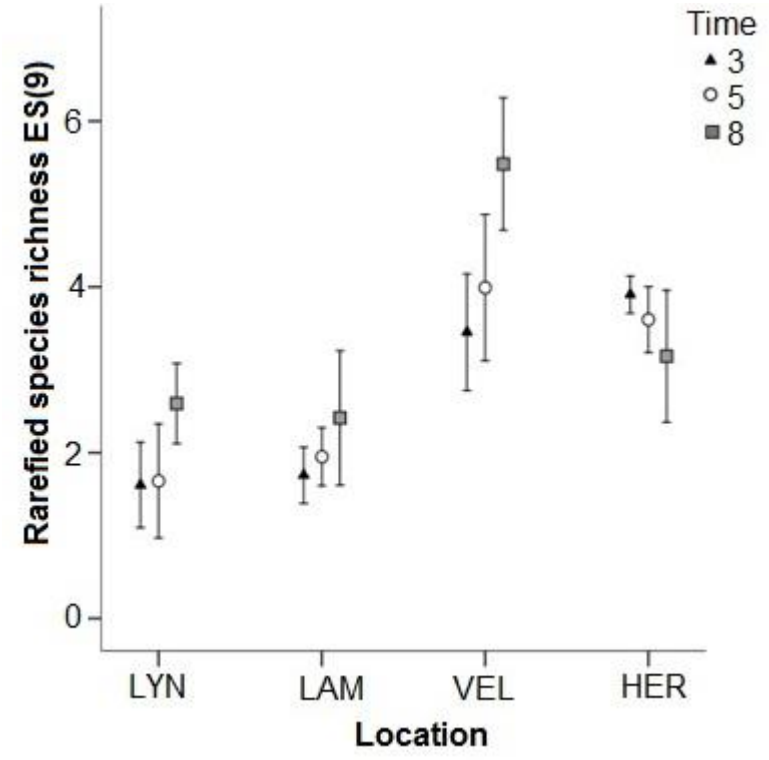


Figure 5. Rarefied species richness based on a minimum sample of 9 species, ES(9), with error bars (SE 95%) across each sampling location and time.

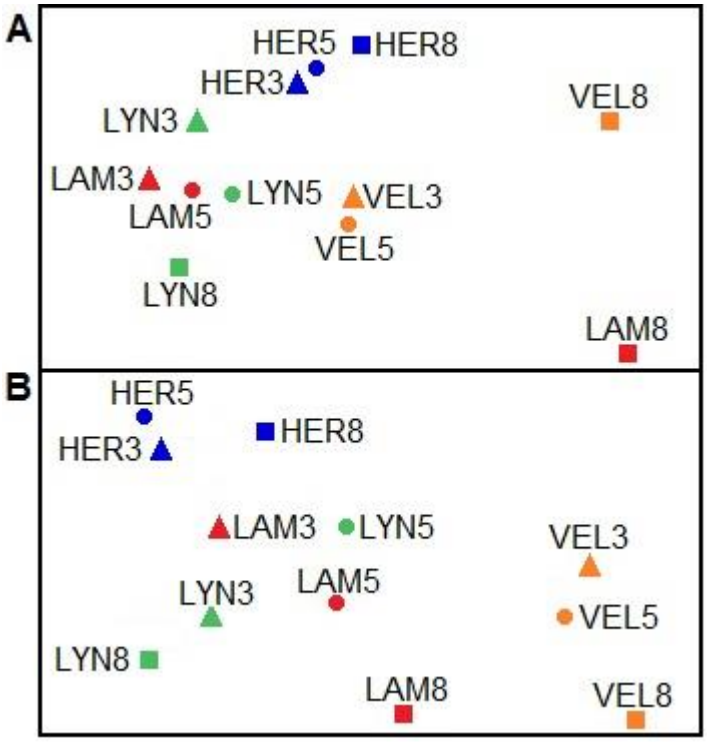


Figure 6. Two-dimensional MDS (a non-metric Multi-Dimensional Scaling analysis) scatter plots for alleles (A) and for species (B).

ANOSIM analysis was used to test the differentiation of the different locations and sampling times for both the allele and species compositions. In these analyses, the overall test gives an R value ranging from 0 to 1, with a higher number indicating greater separation between the factors. For allele compositions between different sites, there was no significant result ($R = -0.01$, $n = 12$, $P = 0.57$), but for different sampling times an overall difference was found ($R = 0.75$, $n = 12$, $P = 0.04$). The results for species compositions were significant both across sampling locations ($R = 0.508$, $n = 12$, $P < 0.001$) and times ($R = 0.809$, $n = 12$, $P < 0.001$). Despite the fact that for allele compositions there was no significant result in the overall pattern among sites for all times, the pairwise test done with Fstat found that all of the sites differed from each other significantly (Table 4). The pairwise test for differences between sampling times showed that there was statistically significant variation in the allelic composition of the August samples compared to those collected in May and March. The same was true for the species composition, which also showed that all of the sites differed from each other significantly and that August differed from both March and May samples.

According to the BEST BIO-ENV analysis, the best explaining environmental characteristics for the genetic composition of *P. elegans* were the degree of the sediment sorting and its organic content (Spearman's correlation: $r_s = 0.709$, $P = 0.004$). A significant result was also found for the species composition, where the best explaining environmental characteristics were the particle size, its degree of sorting, the mean value of salinity, and its standard deviation (Spearman's correlation: $r_s = 0.549$, $P = 0.008$). The environmental data that the BEST BIO-ENV analysis highlighted as the most likely contributors to the genetic and species compositions is shown in Table 5.

Pearson's correlation for the allelic richness within *P. elegans* and the species richness of the local macrofauna community for each sampling time across the sampling locations were all positive, but not significant (Figure 7). The correlation across all

sampling times and locations was, however, positive and statistically significant (Pearson's r = 0.723, n = 12, P = 0.008) (Figure 8).

Table 4. ANOSIM pairwise tests all sampling times and between all sampling locations points out differences between groups of different sampling times and between groups of different sampling locations, asterisks (*) indicating the significant results (R values were not available for the allele data due to lack of replicate samples).

| | Alleles | Species | |
|---|---|---|---|
| Groups | P | R | P |
| 3, 5 | 0.883 | 0.139 | 0.1270 |
| 3, 8 | 0.017* | 0.796 | 0.0003* |
| 5, 8 | 0.017* | 0.556 | 0.0002* |
| LYN, LAM | 0.008* | 0.568 | 0.0030* |
| LYN, VEL | 0.008* | 0.889 | 0.0010* |
| LYN, HER | 0.008* | 0.840 | 0.0010* |
| LAM, VEL | 0.008* | 0.864 | 0.0010* |
| LAM, HER | 0.008* | 0.778 | 0.0010* |
| VEL, HER | 0.008* | 1.000 | 0.0010* |

Table 5. The environmental characteristics that were most likely to contribute to the genetic composition of the *P. elegans* populations (sediment median size and organic content) and the species composition of the communities (sediment median size, sediment sorting, salinity mean, and salinity SD) throughout all the sampling times and locations. Sediment median size median and sorting are measured in Φ scale: for the sediment median size, higher Φ indicates finer sediment; and for sediment sorting, higher Φ indicates more poorly sorted sediment (Gray & Elliott 2009). Organic content is measured as the carbon content of the sediment as percentages. (%) The mean salinity of the month is measured as parts per thousands (ppt), and salinity fluctuation as its standard deviation of the month (SD).

| Population | Sediment median size (Φ) | Sediment sorting (Φ) | Organic content (%) | Salinity mean (ppt) | Salinity fluctuation (SD) |
|---|---|---|---|---|---|
| LYN3 | 2.50 | 0.63 | 1.00 | 19.32 | 0.66 |
| LYN5 | 2.50 | 0.52 | 0.98 | 15.97 | 1.68 |
| LYN8 | 2.50 | 0.49 | 0.90 | 16.02 | 1.11 |
| LAM3 | 2.50 | 0.65 | 0.92 | 19.87 | 2.76 |
| LAM5 | 2.30 | 0.75 | 0.90 | 17.22 | 3.29 |
| LAM8 | 1.80 | 1.20 | 1.29 | 17.74 | 1.84 |
| VEL3 | 1.10 | 1.36 | 0.89 | 20.89 | 0.51 |
| VEL5 | 0.70 | 1.36 | 1.08 | 17.02 | 2.00 |
| VEL8 | 0.80 | 2.16 | 0.60 | 15.71 | 0.90 |
| HER3 | 1.50 | 1.02 | 0.72 | 11.88 | 2.48 |
| HER5 | 2.00 | 0.55 | 0.75 | 11.46 | 2.65 |
| HER8 | 1.60 | 0.86 | 0.80 | 13.50 | 1.45 |

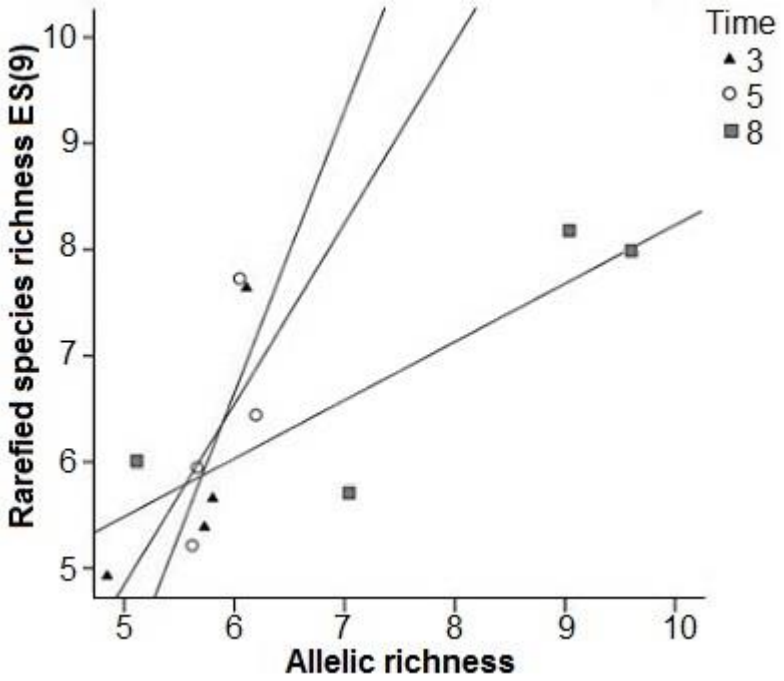


Figure 7. The non-significant Pearson's correlations across all sampling locations at each sampling time separately showed positive trends (March: r = 0.772, n = 4, P = 0.228; May: r = 0.713, n = 4, P = 0.287; August: r = 0.869, n = 4, P = 0.131).

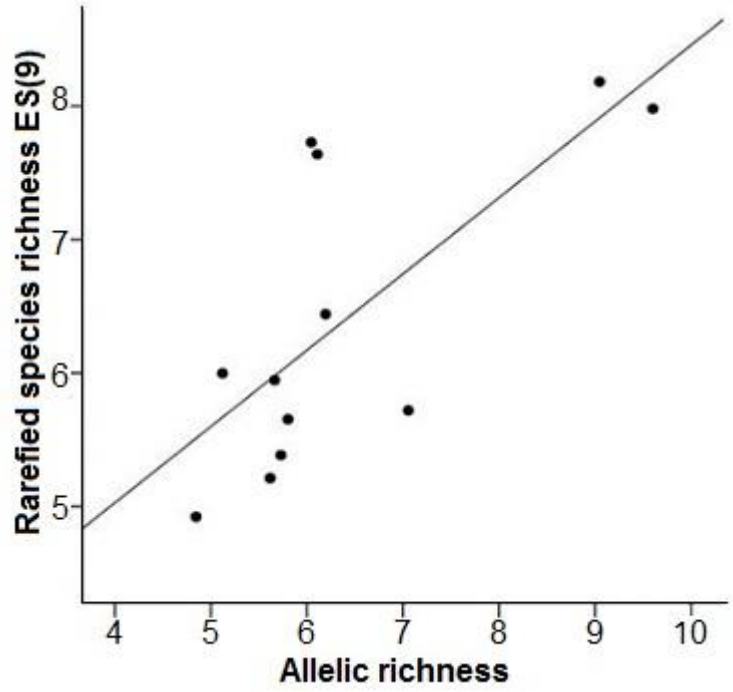


Figure 8. A positive correlation between the allelic richness of *P. elegans* and the species richness of the local macrofauna communities across all sampling locations and times.

## 4. DISCUSSION AND CONCLUSIONS

The main goal of this study was to investigate whether a theoretically expected positive correlation would be found between the allelic richness of *Pygospio elegans* and the species richness of local macrofauna communities. The second aim was to determine if the studied environmental characteristics could explain the observed diversity patterns. The species genetic diversity correlations over locations for each of the sampling times separately showed strong positive correlations, but no statistical significance due to the low number of samples (i.e. only four sampling locations). After combining the data to create one common correlation across the sampling times and locations, a strong, positive, and statistically significant correlation was found. As the same pattern was found when studying the data both separately and when time and space scales were combined – a clear, positive trend in all of the correlations – I expect that the same mechanisms are likely acting over both scales to create the correlation and that it was justified to combine the data without risking misinterpretation of temporal and spatial effects. The results showed that of the studied environmental characteristics, sediment sorting and its organic content were most likely to drive the diversity patterns in allelic richness; and particle size of the sediment, its sorting, average salinity of the water and its fluctuation were most likely to drive the diversity patterns in species richness.

Neutral theories of molecular evolution (Kimura 1984) and of biodiversity (Hubbell 2001) predict that the main drivers of diversity patterns are drift and migration, which affect the carrying capacities and immigration rates of individuals and of species. A positive SGDC should then arise as a consequence of any external factor, such as abiotic environmental characteristics, causing variation in carrying capacity and immigration. This study is consistent with the theoretical models and empirical experiments that suggest a positive correlation to exist between the genetic diversity of a foundation species and the species richness of the local community (Vellend 2005, Vellend & Geber 2005). The only other known study that has focused on brackish waters by Robinson and others (2010) resulted in a positive, but weaker correlation (Pearson's $r = 0.37$) than what was found in my research (Pearson's $r = 0.723$). In both of the cases, the initial correlations done separately had no significance due to lack of power caused by small sample sizes, but the general trend supported positive correlations. Although the correlations that have been reported in previous studies have varied greatly, this study shows that it can reach similar strengths in brackish water as has been observed from terrestrial (e.g. Pearson's $r = 0.98$ between space and $r = 0.96$ over time by Cleary et al. 2006) and freshwater (e.g. Pearson's $r = 0.53$ by Blum et al. 2012) systems, and can is comparable to them.

As the positive correlation is more likely to be found in island-like systems, these results would indicate that in this estuary different locations behave to some extent in a similar way as expected from more isolated terrestrial systems. Despite an apparent large degree of connectivity that is expected in marine environments with species that have a highly dispersive life stage (Roughgarden et al. 1985), there could be factors that limit the area and connectivity, such as environmental tolerances (Mann & Harding 2003) and larval retention (Swearer et al. 1999). A positive SGDC is a sign that the processes acting behind genetic diversity and species diversity work in the same direction for each. However, the interpretation of a positive SGDC may always not indicate that these processes are neutral (Laroche et al. 2015). For example, there might be interactions between the species used for genetic analyses, *P. elegans* in this case, and the rest of the community that are not taken into account. The distribution of abundance data for the major taxonomic groups shows that Lynaes and Lammefjord share higher abundances of gastropods, and similarly,

Vellerup and Herslev share higher abundances of worms. Different kinds of distributions in different locations could mean that there might be interactions between different species groups that could lead to the mentioned causal effects, but other explanations for the distributions will also be discussed.

The observed diversity patterns were explained by some of the studied environmental characteristics, which differed slightly for the allelic richness within *P. elegans* populations and the species diversity of the communities. Characteristics of the sediment in which the species live explained both of the observed diversity patterns. This could be simply due to the possibility that certain kinds of sediment provide a more suitable habitat for *P. elegans*, allowing larger population sizes; and for more species, allowing higher species richness. Indeed, *P. elegans* has been reported to perform better in sandy, heterogeneous sediments (Smidt 1951, Armitage 1979, Thonig et al. MS in review). Grain sizes of the sampling locations varied from medium sized to very coarse sand, from which *P. elegans* seemed to be slightly more abundant in Vellerup and Herslev which shared more coarse sediment compared to Lynaes and Lammefjord (see Appendix 1 for *P. elegans* abundances). The species compositions of communities are also known to be influenced by sediment grain sizes (Gray 1974), and different species have their own preferences of it (Fenchel et al. 1975, Whitlatch 1981). This could explain the differing community compositions of the major taxa between Vellerup and Herslev compared to Lynaes and Lammefjord. The presence of *P. elegans* has been found to increase the abundance of benthic organisms by approximately 40% (Reise 1983), and its abundance has been shown to correlate with especially other annelid species even in very small patches (Morgan 1997, Bolam & Fernandes 2003). The reason for Vellerup and Herslev to have a more annelid based community could be explained by this. The organic content of the sediment, which explained diversity for *P. elegans*, could be an indicator of the amount of resources available for *P. elegans*: more energy available for the population would allow for larger population size, and therefore higher allelic richness within the population (Waide et al. 1999).

Benthic macrofaunal species richness in Danish estuaries has been previously connected positively to the salinity of the water (Edgar et al. 1999, Josefson & Hansen 2004). This was the expected result, as the studied brackish water area is connected to the salty Kattegat from where new individuals and species spread to the estuary. Therefore more species spreading to the area are expected to be adapted to the fully salty water, allowing for more diverse species compositions in areas of higher salinity. On the contrary to the previous observations and the theoretical expectation, species diversity in Vellerup and Herslev decreased as salinity increased in the temporal samples, and likewise for Lynaes and Lammefjord, when there were highest salinity values, there were also the lowest measured species diversities. This result implies that in an estuarine system, peaks in salinity might cause species diversity to drop. This could also be due to salinity reflecting seasonality, where other factors related to it that are not taken account for could be affecting the diversity. In addition, the fluctuation of the salinity was also an explaining factor to the species diversity. As salinity itself strongly affects the suitability of the environment to certain species, it is expected that fewer species can tolerate fluctuations in salinity compared to the number tolerating more stable environments (Levinton 2001).

Allelic richness and rarefied species richness had very similar patterns through time in each of the sampling locations. With the exception of Herslev, the two levels of diversity increased from May to August, with the latter being clearly higher in diversity. In Herslev, however, the opposite pattern was seen. The difference in Herslev's diversity

patterns compared to the other sites could be due to its location in more isolated Roskilde Fjord, while the rest of the sites are located in or near Isefjord which is more open to the Kattegat (see map, Figure 2). The more distant and isolated location of Herslev compared to the others could cause it to have less diverse populations and communities as it is harder for new larvae and species to spread there, while the overall genetic and species diversities between the other sites were similar to each other. Isefjord might have different temporal patterns compared to Roskilde fjord, but more study locations would be needed in the area and in both estuaries to confirm this general pattern. Distance to full marine waters (and presumably larvae sources) has been shown to be correlated to patterns of diversity for benthic fauna in Danish estuaries (Josefson & Hansen 2004). The difference in hydrology of the inner Roskilde Fjord, such as longer residence time, leads to a different salinity pattern compared to the other sites (e.g. Primo et al. 2009). This would be in line with the observation that Herslev had noticeably lower salinities overall, and was at its highest during August, whereas for the other sites salinity was highest in March.

There are some methodological issues in this study that should be taken into account and discussed. In the genetic analyses, some variation in the sample sizes of different loci was found due to null alleles. The missing data is not concentrated on any one location or time, but is relatively evenly distributed and should not contribute greatly to any one sample showing differences in the analyses. The amplification failures could be caused by several reasons, such as errors during the DNA extractions or when setting up the amplification reactions. Another reason could be due to *P. elegans* individuals varying greatly in their size, and the smallest ones could have contained too little DNA and therefore might have required longer amplification periods to work. Another problem with the genetic data were the deviations from Hardy-Weinberg expectations. They can arise from several factors and could be due to technical artifacts, such as limited sampling sizes and null alleles at the loci. Most of the null alleles were in the loci pe309, in which case it could explain the deviations from Hardy-Weinberg observed in it. The deviations might also have biological explanations. For example, there could be inbreeding in the populations, the samples could be composed of individuals from genetically distinct populations (indicating a Wahlund effect), or the loci could have very high mutation rates (Waples 2015). Locus pe7, which showed the most consistent deviation from Hardy-Weinberg expectations in most populations also had the largest number of alleles, indicating that mutation rate of this locus might be particularly high.

The sampling of the faunal surveys might not have resulted in even samples sizes, as the device used for taking the sediment core was easier to use in soft, finer sediment, compared to rough, harder sediment. Because of this, all of the samples did not contain the same amount of sediment. Sample sizes varied from full cores to partial ones, and these differences could potentially cause the data to show some sampling effects (the larger the sample, the more species and individuals it will likely contain). Still, the upper layers of the sediments (15 cm) were sampled in all cases and the majority of individuals and species are found there, hence the variation in sample sizes were not likely to cause any bias to the data. All of the species that were identified are commonly found in estuarine habitats (Barnes 1994). There were only few species in the samples that could not be identified accurately due to the samples missing a feature essential for identification, and problems in species identifications are unlikely to affect the results in this study. As was expected, one species group dominated the abundance data, as *Hydrobia* spp. could reach over 900 individuals per sample. This is not uncommon and is often reported for estuarine habitats (e.g. Dolbeth et. al 2007), and was considered in the treatment of the faunal data.

All of the sampling locations differed from each other both in their allelic and species compositions according to the MDS plots and the pairwise tests, and could be treated as separate populations and communities. However, there was no significant overall pattern in allelic compositions among sampling locations for each time. The reason for the lack of an overall pattern cannot be objectively tested, as there are no replicate samples for each sampling location and time in the case of allelic composition. I addition, it could be argued whether May and March samples deserve to be treated as their own points in the correlation, because they might not be independent from each other as they did not differ statistically. It should be considered that the dataset used in this study is small – more sampling locations and dates with a longer study overall would provide more convincing results. To get this thesis to the standards of a research article, some improvements could be made. First, there is one more data set collected during November that was not included in this study because of time restrictions, but it would be of interest to add this data and see if it affects the results and in which ways. Second, only one species was used for measuring allelic richness. This approach might not give results that represent the whole community. Using more than one species from different taxonomic orders would provide more comprehensive results, as if a single process is the driver of the patterns in both diversity levels of an area, it would be easier to detect if seen across multiple taxa (Vellend & Geber 2005). For example, if dispersal would be the underlying cause for the correlations between genetic and species diversities, different taxa with comparable dispersal potentials should show the relationship. This way causal effects could also be detected: if, for example, genetic diversity of a foundation species drives the local species diversity, correlations may not exist for genetic diversity in other species of the community. Alternatively, this study could be refocused to one taxonomic group only. The statistical analyses could be repeated using only other annelid species to avoid using too broad taxonomic scale for the species richness of the community. In addition, the genetic data could be supplemented by using more loci for calculating allelic richness. When studying SGDCs, mutation and selection are generally excluded. There have been, however, studies that imply that especially mutations should be taken into account because the genetic markers that are commonly used in studies of SGDCs are highly mutable (Jarne & Lagoda 1996, Laroche et al. 2015). Other environmental characteristics not included in this study could prove to have a greater influence on the diversity patterns, for example, saltwater flux which can contribute to the dispersal of species (Josefson & Hansen 2004), the degree of openness to the adjacent sea area (Teske & Wooldridge 2001), and the water depth (Snelgrove 1999).

One of the major implications this study shows, is since the genetic diversity within *P. elegans* is linked to the species diversity, it might be possible that the presence of this community foundation species could very well be used in identifying SGDCs (Papadopoulou et al. 2011). In addition, by studying only the genetic richness of *P. elegans* (or some other species), the species richness of the local area could be predicted based on it. From the environmental characteristics, I suggest that the sediment grain size would potentially be the most useful indicator for predicting diversities on both genetic and species levels in this brackish water system. These results give possible tools for future studies and research efforts for more efficiently measuring the overall diversity of an area. More studies of the species-genetic diversity correlations and the mechanisms behind them are needed with different species and in variable environments to find more about the response of the diversity levels to certain environmental characteristics in different conditions (Struebig et al. 2008, Bergmann et al. 2013, Cleary et al. 2015).

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**APPENDIX 1**

| | AVERAGE ABUNDANCE OF A SAMPLE | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **SPECIES NAME** | LYN3 | LYN5 | LYN8 | LAM3 | LAM5 | LAM8 | VEL3 | VEL5 | VEL8 | HER3 | HER5 | HER8 |
| *Arenicola marina* | 0 | 0.33 | 0.33 | 0 | 0 | 0 | 0.33 | 0.33 | 0.33 | 0 | 0 | 0.33 |
| *Capitella capitata* | 1.64 | 1.35 | 0 | 0 | 0.44 | 0.94 | 0.89 | 1.35 | 0.98 | 0.64 | 0 | 0 |
| *Eteone picta/longa* | 0 | 0 | 0 | 0 | 0 | 0 | 0.4 | 1.26 | 0.73 | 0 | 0 | 0 |
| *Glysera capitata* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.47 | 0 | 0 | 0 | 0 |
| *Heteromastus filiformis* | 0.33 | 0.44 | 1.57 | 0 | 0.73 | 0.8 | 0.67 | 1.23 | 1.23 | 0 | 0 | 0 |
| *Lepidonotus squamatus* | 0 | 0.56 | 0 | 0 | 0 | 0.33 | 0 | 0.92 | 0 | 0 | 0 | 0 |
| *Marenzelleria viridis* | 0 | 0 | 1.23 | 0 | 0 | 0 | 0.33 | 0.73 | 0.92 | 0 | 0 | 0 |
| *Nereis diversicolor* | 1.23 | 1.59 | 1.44 | 2.27 | 1.5 | 0.97 | 0 | 0.88 | 0.8 | 2.78 | 2.22 | 2.26 |
| *Nereis succinea* | 0 | 0 | 0 | 0 | 0.47 | 1.03 | 0 | 0 | 0.44 | 0 | 0 | 0 |
| *Nereis virens* | 0.33 | 0.33 | 0 | 0 | 0.67 | 1.17 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Pectinaria belgica* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.33 | 0 | 0 | 0 | 0 |
| *Perinereis cultifera* | 0 | 0.47 | 0 | 0 | 0.4 | 0.33 | 0 | 1.5 | 1.48 | 0 | 0 | 0 |
| *Phyllodoce maculata* | 0 | 0 | 0 | 0 | 0.4 | 0.33 | 0 | 0.33 | 0 | 0 | 0 | 0 |
| *Platynereis dumerilii* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.84 | 0 | 0 | 0 |
| *Polydora ciliata* | 0 | 0 | 0 | 0 | 0 | 1.26 | 0 | 0.67 | 1.14 | 0 | 0 | 0.77 |
| *Pygospio elegans* | 1.08 | 1.41 | 0.77 | 1.31 | 2.96 | 0.77 | 1.79 | 3.31 | 1.74 | 2.42 | 2.99 | 1.43 |
| *Scoloplos armiger* | 0 | 0 | 0 | 0 | 0 | 0 | 1.65 | 1.7 | 1.75 | 0 | 0 | 0 |
| *Tubificid* | 1.93 | 1.01 | 1.31 | 1.46 | 1.69 | 1.82 | 2.76 | 2.96 | 2.65 | 1.66 | 1.27 | 1.54 |
| *UNID: Annelid | 0 | 0 | 0 | 0 | 0 | 0 | 0.33 | 0 | 0 | 0 | 0 | 0 |
| *Prostomatella obscura* | 0 | 1.03 | 0.44 | 0.87 | 0.33 | 1.65 | 1.54 | 1.27 | 0.4 | 0 | 0 | 1.33 |
| *UNID: Flatworm | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.4 | 1.68 | 0.94 |
| *Leptoplana tremellaris* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1.17 | 0 | 0 | 0 |
| *Corophium sp.* | 0 | 0.54 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Cyathura carinata* | 0 | 0.62 | 0 | 0 | 0 | 0.73 | 0 | 0 | 0 | 0 | 0 | 0.33 |
| *Ericthonius difformis* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.33 | 0 | 0.33 | 0.73 |
| *Gammarus locusta* | 0 | 0 | 0 | 0 | 0.4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Idotea balthica* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.4 | 1.45 |
| *Idotea chelipes* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.33 | 0 |
| *Idotea granulosa* | 0 | 0 | 0 | 0 | 0 | 0.89 | 0.4 | 0.33 | 1.69 | 0 | 0 | 0 |
| *Lekanesphaera rugicauda* | 0 | 0.33 | 1.38 | 0.4 | 0.67 | 1.64 | 0 | 0.4 | 1.35 | 0.44 | 0.4 | 0.33 |
| *Sphaeroma serratum* | 0 | 0 | 0 | 0 | 0 | 0 | 0.84 | 0.88 | 2.01 | 0 | 0 | 0 |
| *UNID: Amphipod | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.58 | 0 | 0 | 0 |
| *Cerastoderma sp.* | 0 | 0.33 | 0.4 | 0.67 | 1.37 | 0.92 | 0.87 | 0.56 | 1.79 | 0 | 1.11 | 0.5 |
| *Lepidochitona cinereus* | 1.04 | 1.27 | 1.11 | 0.33 | 0.77 | 0.4 | 0 | 0.92 | 1.08 | 1.39 | 1.41 | 1.64 |
| *Macoma balthica* | 0 | 1.55 | 0 | 0 | 0.4 | 0.58 | 1.88 | 1.59 | 1.33 | 0 | 0 | 0.33 |
| *Mya arenaria* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.5 | 0 | 0 | 0 |
| *Mytilus edulis* | 0 | 0 | 0 | 0.33 | 0 | 0.69 | 0 | 0 | 1.09 | 0.83 | 0.33 | 0.44 |
| *Parvicardium ovale* | 0 | 0 | 0 | 0 | 0 | 0 | 0.33 | 0.33 | 0.77 | 0 | 0 | 0 |
| *Parvicardium sp.* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.67 | 0.33 | 0 | 0 | 0 |
| *Hydrobia sp.* | 4.92 | 5.21 | 3.36 | 4.67 | 5.19 | 4.46 | 3.63 | 3.77 | 3.26 | 2.65 | 2.85 | 3.53 |
| *Bittium reticulatum* | 0.44 | 0.33 | 0.47 | 0 | 0 | 0 | 0.77 | 0.52 | 0.87 | 0 | 0.33 | 0.44 |
| *Hinia reticulata* | 0 | 0 | 0 | 0 | 0.4 | 1.11 | 0.77 | 0.88 | 0.79 | 0 | 0 | 0 |
| *Rissoa membranacea* | 0 | 0.4 | 0 | 0 | 0 | 0 | 0.52 | 0.47 | 1.83 | 0 | 0 | 0.33 |
| *Pusillina sarsi* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.44 | 1.73 | 0 | 0 | 0 |
| *Theodoxus fluviatilis* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.4 |
| *Littorina littorea* | 0 | 0.52 | 0 | 0.77 | 0.98 | 0.83 | 1.23 | 1.19 | 1.64 | 0.5 | 0 | 0 |

- UNID. = identified as separate species (none of the previously identified), but further classification was not possible