

## Flow modifies the effect of biodiversity on ecosystem functioning: an in situ study of estuarine sediments

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### Abstract

The effect of flow and biodiversity on ecosystem functioning was investigated in an estuarine system using in situ benthic chambers. Macrofaunal communities were artificially assembled to manipulate both species richness and functional trait richness. In addition, naturally occurring communities were sampled in order to determine the effect of macrofaunal and sediment disruption. Ecosystem functioning was assessed by measurement of nutrient release ( $\text{NH}_4\text{-N}$ ) from the sediment, a process essential for primary production. Natural and assembled communities were found to differ significantly, demonstrating the effect of experimental manipulation on the system. Flow was found to have a highly significant effect on ecosystem functioning in both natural and assembled communities in treatments containing macrofauna. No significant difference between static and flow treatments was found in macrofaunal-free controls, indicating that flow generates an effect through promoting changes in bioturbatory activity of the infauna causing greater disruption to the sediment. In assembled communities, functional richness significantly increased ecosystem functioning. Species richness had no influence in assembled communities.

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**Keywords:** Benthic; Biodiversity; Ecosystem functioning; Flow; In situ; Species richness

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## 1. Introduction

With increasing world-wide extinction rates (Pimm et al., 1995), the effects of biodiversity on ecosystem functioning have been the focus of much research and debate (Hector, 1998; Tilman, 1999; Naeem et al., 2000; Snelgrove et al., 2000; Loreau et al., 2001). The majority of controlled, experimental investigations of the relationships between species richness and ecosystem functioning have so far been carried out in terrestrial ecosystems (Tilman et al., 1997; Hooper and Vitousek, 1997; Wardle et al., 1997). A limited number of similar studies have been done in marine systems, usually involving artificially constructed communities containing several levels of species richness and maintained under laboratory conditions (e.g. Emmerson and Raffaelli, 2000; Emmerson et al., 2001; Solan and Ford, in press). While these experiments have been a necessary and valuable contribution to biodiversity-functioning research, the full range of environmental factors to which communities would normally be exposed are tightly controlled. In order to minimise this problem, Duffy et al. (2001) used a series of outdoor mesocosms to incorporate the effects of ambient conditions of light, temperature and weather in an artificially assembled sea grass community. Clearly, there still remains an urgent need to examine biodiversity relationships under real field conditions (Raffaelli et al., in press); only one marine study to date has manipulated species diversity in situ (Parker et al., 2001). Here, we report the results of experiments carried out in the field using macrofaunal communities subject to realistic conditions of light, temperature and overlying water, in particular flow, which is an important element missing from most laboratory experiments. Flow is known to affect feeding and bioturbation methods used by several macrofaunal taxa, including the polychaete *Nereis diversicolor* (Riisgård and Kamermans, 2001) and the bivalve *Macoma balthica* (Olafsson and Persson, 1986), both of which are important numerical and biomass dominant components at the study site (see below). The ecosystem process of interest in our study is nutrient release from the sediment to the water column (specifically  $\text{NH}_4\text{-N}$ ), due to its importance in primary production (Heip et al., 1995) and because the effect of benthic invertebrates on sediment–water exchange is well-documented (Fry, 1982; Henriksen et al., 1980). The processes and mechanisms of nutrient release and flow are well known (Berner, 1976; Huettel and Gust, 1992; Jahnke et al., 1999), but have yet to be addressed within the context of biodiversity-ecosystem functioning issues. Using benthic chambers, in which flow can be controlled, we explore the relationship between species richness and ammonium release from sediments containing artificially constructed macrofaunal communities maintained in the field. The specific biodiversity issue being tested is species richness per se, and not (for example) whether the loss of certain keystone species might lead to changes in ecosystem functioning. The results are compared with the release of ammonium under static and flow conditions in adjacent mudflat communities containing a more limited range of species richness, but which are undisturbed and are therefore closer to the natural system.

## 2. Methods

The study was carried out on the Ythan Estuary (N 57°20.085', W 02°0.206'), Scotland. Incubations using natural sediments with existing infaunal communities took

place over the course of two tidal cycles, each with 10 chambers (20 cm diameter, 25 cm deep) (Fig. 1). All incubations were carried out within a 5-m<sup>2</sup> area. For each incubation, flow was generated in five chambers using a revolving skirt (12-cm diameter) located at the top of the chamber. The skirt ensures a constant and laminar, annular flow. In addition, five identical chambers were static. Chambers were placed in the sediment to a depth of 12 cm, 4 h prior to low tide and filled with ambient seawater. Flow was initiated at 6 cm/s, comparable to ambient velocities, and the chambers were sealed. Oxygen concentrations were measured throughout the experiment and all tanks remained supersaturated. Water column samples for nutrient analysis were taken after 1 and 7 h, filtered (Nalgene, 0.45 µm) and frozen for later analysis using an FIA star 5010 series flow injection autoanalyser with an artificial seawater carrier solution. The sediment from the chambers was recovered and sieved through a 500-µm mesh to remove all macrofauna. Macrofauna were later identified and biomass and abundance quantified.

For the assembled communities, chambers were emplaced in the sediment to a depth of 12 cm over the course of four tidal cycles, each with 10 chambers. Natural sediment was removed and replaced with defaunated sediment, i.e. sediment sieved through a 500-µm mesh to remove macrofauna. Macrofaunal treatments included five locally abundant species (*Nereis diversicolor*, (N.d.), *Hydrobia ulvae* (H.u.), *Mytilus edulis* (M.e.), *Macoma balthica*, (M.b.) and *Corophium volutator* (C.v.)) used to manipulate biodiversity, with a total fixed biomass of 4 g in each treatment (Table 1). This eliminates the need to examine the effect of species evenness. To avoid ‘hidden treatment’ effects (Huston, 1997) and minimise pseudo-replication, species richness treatments were replicated using different species permutations. Because of the limited species pool in estuarine systems, this cannot be done at the highest level of species richness although we recognise that certain combinations of species may produce different outcomes. Wet weight (in grams) was determined to four decimal places and all bivalve and gastropod molluscs were weighed within their shells. Species combinations were selected to maximise variation in functional richness. A 300-µm mesh cover was used on the top and base of each chamber to prevent faunal immigration and emigration. The chambers were filled with seawater and were subject to one tidal immersion before sampling. The top mesh cover was removed 4 h prior

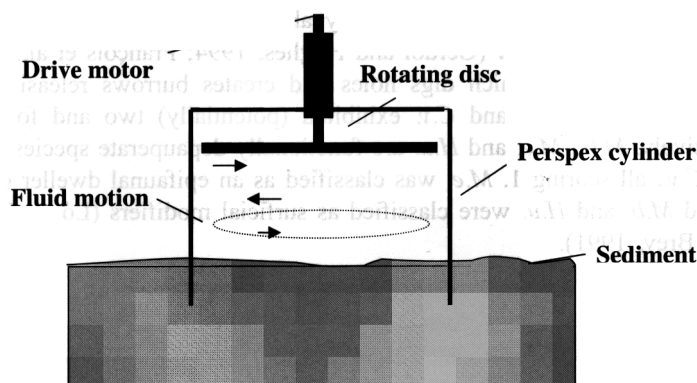


Fig. 1. Benthic chamber in situ showing flow facility.

Table 1

Species combinations used in assembled macrofaunal treatments

Species treatment	Number of replicates (static or flow)
Control (number of macrofauna)	3
<i>N.d.</i>	1
<i>C.v.</i>	
<i>H.u.</i>	
<i>M.b.</i>	
<i>M.e.</i>	
<i>C.v.</i> and <i>N.d.</i>	
<i>M.b.</i> and <i>M.e.</i>	
<i>N.d.</i> and <i>H.u.</i>	
<i>C.v.</i> , <i>N.d.</i> and <i>M.e.</i>	1
<i>H.u.</i> , <i>M.b.</i> and <i>M.e.</i>	1
<i>C.v.</i> , <i>N.d.</i> and <i>H.u.</i>	1
<i>C.v.</i> , <i>N.d.</i> , <i>H.u.</i> and <i>M.b.</i>	2
<i>N.d.</i> , <i>H.u.</i> , <i>M.b.</i> and <i>M.e.</i>	1
<i>N.d.</i> , <i>C.v.</i> , <i>H.u.</i> , <i>M.b.</i> and <i>M.e.</i>	3

Where more than one species was used, all species were in equal proportions (*N.d.*, *Nereis diversicolor*, *C.v.*, *Corophium volutator*, *H.u.*, *Hydrobia ulvae*, *M.b.*, *Macoma balthica*, *M.e.*, *Mytilus edulis*).

to low tide, flow started (6 cm/s) and the chambers sealed. Water column samples were collected under replicated flow and static conditions. All measurements were carried out within a single 10 tidal cycle period during July 2001. Weather remained calm and sunny throughout the sampling period.

Species were classified into different functional groups based on their known effects on the sediment. The variety of different behaviours exhibited by each species was accounted for using a point scoring system. *N.d.* has been classified as a surficial modifier (i.e. a species whose activities occur within the surface sediment layers of 1 to 10 mm) and a biodiffuser (i.e. activities result in the diffuse movement of sediment particles in and around the system) (Rönn et al., 1988; François et al., 1997; Christensen et al., 2000). *C.v.* was classified as an epifaunal dweller (i.e. species which impact the sediment surface, though activity is primarily above the sediment–water interface), a surficial modifier, a biodiffuser (Gerdol and Hughes, 1994; François et al., 1997) and a regenerator (i.e. a species which digs holes and creates burrows releasing sediments locked at depth). Both *N.d.* and *C.v.* exhibited (potentially) two and four functional traits, respectively. *M.b.*, *M.e.* and *H.u.* are functionally depauperate species with respect to *N.d.* and *C.v.*, all scoring 1. *M.e.* was classified as an epifaunal dweller (Widdows et al., 1998) and *M.b.* and *H.u.* were classified as surficial modifiers (López-Figueroa and Niell, 1987; Brey, 1991).

### 3. Data analysis

To analyse the effects of flow, species richness, functional richness and biomass, Analysis of Covariance (ANCOVA) was applied to  $\text{NH}_4\text{-N}$  concentration after 7 h.

Table 2  
Summary of ANCOVA results

	<i>df</i>	MS	<i>F</i>	<i>p</i>
Biomass		2.041e–07		0.997
Community assembly		0.288		0.001
Flow		0.974		0.001
Community assembly* Flow		6.345e–03		0.567
Error		1.914e–02		
Total				

Community assembly and flow as fixed factors and biomass as a co-variate.

Four different ANCOVAs were performed, firstly using natural versus assembled communities (community assembly) and flow regime as main factors, with biomass as a co-variate. Although biomass was fixed at 4 g in our assembled communities, we recognise that biomass would vary slightly between treatments due to difficulties in assembling groups that weighed exactly 4 g. ANCOVA was also applied to  $\text{NH}_4\text{-N}$  concentrations of assembled communities in three separate tests, each using biomass

Table 3  
Summary of ANCOVA results

	<i>df</i>	MS	<i>F</i>	<i>p</i>
(a) Species richness (SR) and flow as fixed factors and biomass as a co-variate				
Biomass	1	0.171	6.188	0.019
SR	5	4.028e–02	1.458	0.236
Flow	1	0.465	16.822	0.001
SR* Flow	5	2.856e–02	1.0033	0.418
Error	27	2.763e–02		
Total	40			

(b) Functional richness (FR) and flow as fixed factors and biomass as a co-variate

	<i>df</i>	MS	<i>F</i>	<i>p</i>
Biomass	1	0.171	8.120	0.008
FR	4	6.718e–02	3.190	0.027
Flow	1	0.483	22.948	0.001
FR* Flow	4	4.810e–02	2.284	0.084
Error	29	2.106e–02		
Total	40			

(c) Species richness (SR) and flow as fixed factors and biomass and functional richness (FR) as co-variables

	<i>df</i>	MS	<i>F</i>	<i>p</i>
FR	1	0.258	9.743	0.004
Biomass	1	8.086e–03	0.306	0.585
SR	5	3.107e–02	1.174	0.348
Flow	1	0.471	17.810	0.001
SR* Flow	5	2.914e–02	1.101	0.384
Error	26	2.646e–02		
Total	40			

as a co-variate. Species richness and flow were fixed factors in the first test and functional richness and flow were fixed factors in the second test. The third ANCOVA used species richness and flow as fixed factors and functional richness as a co-variate. Biomass was used as a co-variate throughout. Analysis of variance (ANOVA) was also performed between static and flow chambers in assembled communities, separately for treatments with and without macrofauna using flow as a factor.

It should be noted that the most rigorous way to separate any effects of species richness and functional richness is through an orthogonal design, whereby different levels of functional richness are nested within each level of species richness (e.g. Jonsson and Malmqvist, 2000). This was not possible in our own experiments due to the limited species pools available. An alternative procedure is to carry out sequential analysis where each diversity level is given priority in the analysis (e.g. Hector et al., 1999) and we have attempted to do this by assigning different diversity terms as main factors and co-variables alternatively. This approach has its limitations compared to an orthogonal design and the results should be viewed as indicative rather than conclusive.

Overyielding, where the mixture performs better than the corresponding monocultures (Loreau, 1998), was examined using the metric  $D_{\text{Max}}$ .  $D_{\text{Max}}$  compares the observed

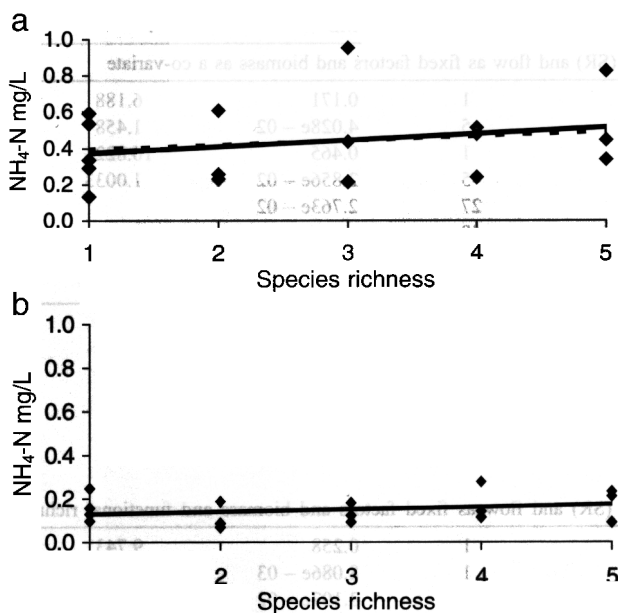


Fig. 2. Scatter graphs of  $\text{NH}_4\text{-N}$  production with increasing species richness. Solid line shows linear regression of data, dotted line shows linear regression with the co-varying effects of biomass removed. (a) Assembled communities with flow conditions. (b) Assembled communities with static conditions.

values of the mixture to the maximally yielding individual species in separate treatments (Hector, 1998).

$$D_{\text{Max}} = \frac{O_T - \text{Max}(M_i)}{O_T}$$

where  $O_T$  is the observed value of the mixture and  $\text{Max}(M_i)$  is the maximally yielding species in monoculture.

$D_{\text{Max}}$  was calculated for  $\text{NH}_4\text{-N}$  concentrations, overyielding occurring when  $D_{\text{Max}} > 0$ . There are other measures of overyielding (Hector, 1998; Hooper, 1998; Loreau, 1998; Loreau and Hector, 2001), but their calculation requires quantification of the contribution of each species to the overall measure of function, which is not appropriate to nutrient concentration (Emmerson and Raffaelli, 2000).

#### 4. Results

As expected, natural communities contained a limited range of (8–10) species. A total of 14 species were recorded and 8 of these were present in all samples

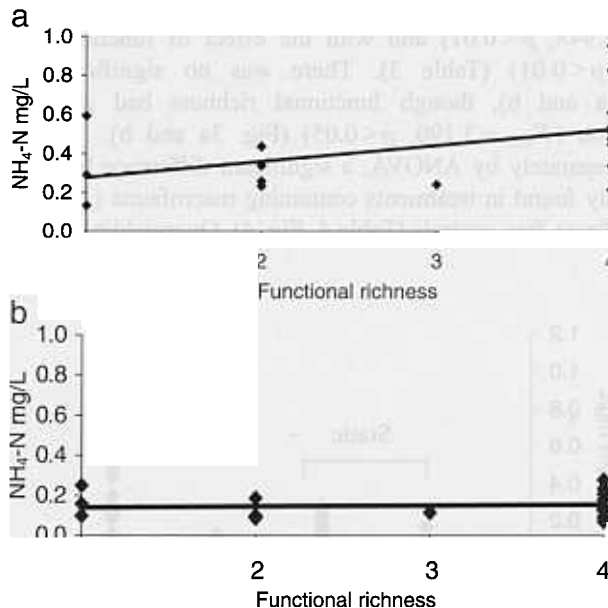


Fig. 3. Scatter graphs of  $\text{NH}_4\text{-N}$  production with increasing functional richness. Solid line shows linear regression of data, dotted line shows linear regression with the co-varying effects of biomass removed. (a) Assembled communities with flow conditions. (b) Assembled communities with static conditions.

Table 4  
Summary of ANCOVA results

	<i>df</i>	<i>MS</i>	<i>F</i>	<i>p</i>
Flow (a)		0.285	14.168	
Error	32	2.011e – 02		
Total	34			
Flow (b)		6.357e – 04	0.646	0.467
Error	4	9.847e – 04		
Total	6			

Flow as a fixed factor, testing separately treatments with macrofauna (a) and macrofauna-free controls (b) in assembled communities.

(Appendix A). Due to the limited range of species, the effects of species richness were not analysed using data from natural communities. Communities were equally functionally rich, all containing epifaunal dwellers, surficial modifiers, biodiffusers, regenerators, upward conveyors and downward conveyors and consequently functional richness could not be considered in the analysis of natural communities.

Assembled communities had significantly higher  $\text{NH}_4\text{-N}$  release than natural communities ( $F_{1,55} = 15.042$ ,  $p < 0.001$ ). Flow also significantly increased  $\text{NH}_4\text{-N}$  release ( $F_{1,55} = 50.889$ ,  $p < 0.001$ ) (Table 2).

Assembled communities had significantly greater  $\text{NH}_4\text{-N}$  release under flow conditions ( $F_{1,27} = 16.822$ ,  $p < 0.01$ ), with functional richness instead of species richness as a factor ( $F_{1,29} = 22.948$ ,  $p < 0.01$ ) and with the effect of functional richness removed ( $F_{1,26} = 17.810$ ,  $p < 0.01$ ) (Table 3). There was no significant effect of species richness (Fig. 2a and b), though functional richness had a significant effect on  $\text{NH}_4\text{-N}$  production ( $F_{4,29} = 3.190$ ,  $p < 0.05$ ) (Fig. 3a and b).

When tested separately by ANOVA, a significant difference between flow and static chambers was only found in treatments containing macrofauna ( $F_{1,32} = 14.168$ ,  $p < 0.01$ ) and not in macrofauna-free controls (Table 4, Fig. 4). Overyielding occurred with  $\text{NH}_4\text{-N}$

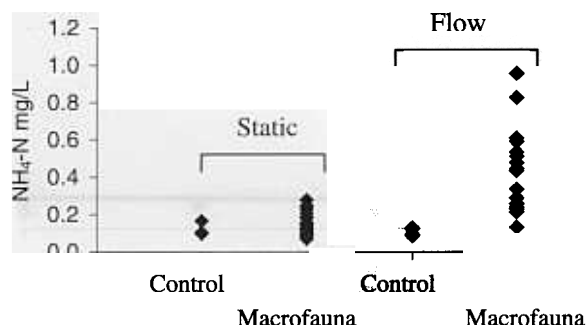


Fig. 4. Scatter graph of  $\text{NH}_4\text{-N}$  production in assembled communities in flow and static conditions. Control describes treatments without macrofauna.



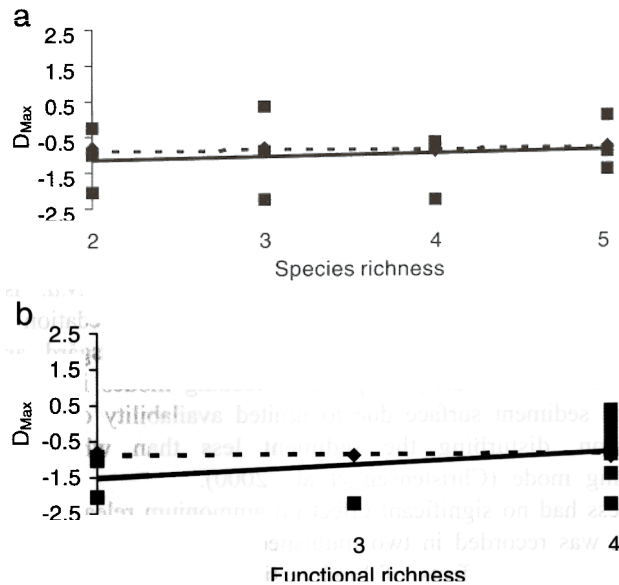


Fig. 5. (a) Scatter graph of  $D_{Max}$  in assembled communities in both flow and static conditions with increasing species richness. Square symbols show data from flow treatments and diamond symbols show data from static treatments. Solid line shows linear regression of data from flow treatments, dotted line shows linear regression of data from static treatments. (b) Scatter graph of  $D_{Max}$  in assembled communities in both flow and static conditions with increasing functional richness. Square symbols show data from flow treatments and diamond symbols show data from static treatments. Solid line shows linear regression of data from flow treatments, dotted line shows linear regression of data from static treatments.

in both static and flow treatments (Fig. 5a and b), occurring more frequently in flow than static treatments.

## 5. Discussion

In assembled communities, the effects of diversity are more easily assessed than in natural communities as both species richness and functional richness differed between treatments. Increasing functional richness was found to significantly increase nutrient production, confirming previous work using laboratory maintained static mesocosms that species role, rather than number has an important influence on sediment chemistry (Emmerson et al., 2001).

The significant effect of community assembly is revealing, almost certainly due to disruption of the sediment by sieving. Clearly, the absolute concentrations of nutrients generated by macrofauna in sediments thus treated are not equivalent to those generated naturally. Other experiments in marine sediment systems have used freezing instead of sieving as a method of defaunation (e.g. Emmerson et al., 2001; Raffaelli et al., in press). This procedure might also be expected to generate

unnatural concentrations but between treatment (species richness) comparisons remain valid since the procedures were common to all treatments; this is the case for our own artificially constructed systems.

Perhaps the most important outcome from our experiments is the marked effect of flow. Significant differences were found between flow and static chambers for macrofaunal treatments but not in control chambers without macrofauna, also consistent with laboratory maintained systems reported elsewhere (Raffaelli et al., in press). This strongly suggests that flow may have its greatest effect through influencing species behaviour. For instance, the polychaete *N.d.* is capable of a variety of feeding modes including grazing, scavenging, predation and suspension feeding that may be modified by flow (Vedel, 1998; Riisgård and Kamermans, 2001). Static conditions are likely to promote feeding modes involving collection of deposits from the sediment surface due to limited availability of particulate matter in the water column, disturbing the sediment less than when the more active suspension feeding mode (Christensen et al., 2000).

Species richness had no significant effect on ammonium release but it is noteworthy that overyielding was recorded in two multispecies treatments, both of which were in flow conditions. Why the effects of biodiversity should be more pronounced under flow is not clear, but the underlying mechanism is likely to be associated with changes in behaviour, promoting macrofauna to bioturbate the sediment more rigorously in flow conditions. Whatever the mechanism, our results demonstrate the necessity of simulating the natural system as closely as possible when carrying out biodiversity experiments. The high degree of control normally employed in such experiments, including zero flow, could significantly weaken our ability to interpret the real relationship between biodiversity and ecological functioning in marine sediments. We have shown that functional traits are not immutable and can be affected by the behavioural responses of species to external stimuli. Moreover, our findings suggest that species behaviour may be a more important determinant of ecosystem function than species richness, functional type and external environmental factors. Separating the effects of species diversity from the effects of species–environment interactions is an important step in understanding the mechanisms that underlie the biodiversity–ecosystem functioning issue. Although it will be difficult to manipulate species richness at large scales in the field, the experiments described here involving in situ chambers incorporating flow are a significant advance in attempting to explore biodiversity effects under natural conditions.

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**Appendix A.** Biomass (and abundance) per m<sup>2</sup> in each incubation using natural communities (*C.v.*, *Corophium volutator*; *H.u.*, *Hydrobia ulvae*; *M.b.*, *Macoma balthica*; *P.e.*, *Pygospio elegans*; *O.sp.*, *Oligochaeta sp.*, *M.a.*, *Manayunkia aestuarina*; *N.d.*, *Nereis diversicolor*; *E.sp.*, *Eleone sp.*; *N<sup>1</sup>*, *Nematoda sp.*; *N<sup>2</sup>*, *Nemertea sp.*; *R.*, *Renusa sp.*; *C.c.<sup>1</sup>*, *Capitella capitata*; *C.c.<sup>2</sup>*, *Crangon crangon*; *C.e.*, *Cerastoderma edule*)

Core	Flow	<i>C.v.</i>	<i>H.u.</i>	<i>M.b.</i>	<i>P.e.</i>	<i>O.sp.</i>	<i>M.a.</i>	<i>N.d.</i>	<i>E.sp.</i>	<i>N<sup>1</sup></i>	<i>N<sup>2</sup></i>	<i>R.sp.</i>	<i>C.c.<sup>1</sup></i>	<i>C.c.<sup>2</sup></i>	<i>C.e.</i>	Total
		10.1 (16965)	107.7 (20881)	5.5 (414)	9.1 (318)	3.2 (2578)	0.2 (3661)	10.0 (987)	0 (1273)	0.1 (1273)	0 (1273)	0 (1273)	0 (1273)	0 (1273)	0 (1273)	136.9 (47077)
		4.5 (13305)	121.1 (23140)	6.9 (382)	0.05 (223)	2.3 (2196)	0.6 (6939)	10.4 (1146)	0.09 (32)	0.1 (1528)	0 (1528)	0 (1528)	0 (1528)	0 (1528)	0 (1528)	145.9 (48891)
		6.6 (11109)	110.5 (23172)	13.0 (382)	0.01 (32)	0.9 (828)	0.1 (1878)	17.4 (1019)	0 (1019)	0.01 (414)	0 (414)	0 (414)	0 (414)	0 (414)	0 (414)	148.5 (38833)
		2.0 (3342)	152.3 (31926)	16.6 (668)	0.04 (223)	4.1 (2737)	1.2 (15660)	35.4 (1464)	0 (1464)	0.03 (796)	1.4 (32)	0 (32)	0.1 (32)	0 (32)	0 (32)	214.6 (56912)
		7.2 (17920)	130.0 (24605)	5.6 (382)	0.1 (159)	1.2 (1337)	0.2 (3151)	9.6 (700)	0.02 (32)	0.02 (1655)	0 (1655)	0 (1655)	0 (1655)	0 (1655)	0 (1655)	153.9 (49941)
		2.8 (8308)	140.1 (26992)	9.2 (573)	0.02 (382)	2.3 (2387)	0.6 (6748)	22.8 (1019)	0 (1019)	0.04 (1528)	0 (1528)	0.1 (32)	0 (32)	0 (32)	0 (32)	177.9 (47968)
		1.9 (3278)	138.1 (28647)	5.8 (414)	0.02 (32)	1.2 (1337)	0.4 (4074)	20.4 (1328)	0 (1328)	0.01 (509)	0 (509)	0 (509)	0 (509)	0 (509)	0 (509)	167.8 (39819)
		12.0 (13719)	112.7 (23204)	14.7 (541)	0.2 (828)	2.7 (4838)	0.5 (5157)	37.4 (1496)	0.05 (64)	0.02 (1178)	0 (1178)	0 (1178)	0 (1178)	0 (1178)	0 (1178)	180.3 (50992)
		10.7 (12700)	113.7 (23363)	11.5 (478)	0.04 (287)	3.0 (2483)	0.1 (2992)	32.6 (1305)	0 (1305)	0.06 (1082)	0.9 (32)	0 (32)	0 (32)	0 (32)	0 (32)	173.6 (44753)
0		5.5 (18398)	132.2 (25942)	6.3 (414)	0.003 (32)	2.4 (1560)	0.1 (3979)	16.2 (891)	0 (891)	0.04 (1082)	0 (1082)	0 (1082)	0 (1082)	0 (1082)	0 (1082)	162.6 (52297)
1	*	9.4 (4584)	150.9 (28965)	29.5 (255)	0.06 (191)	0.8 (1241)	0.1 (3661)	34.6 (1369)	0 (1369)	0.003 (159)	0 (159)	0 (159)	0 (159)	0 (159)	5.2 (32)	230.6 (40456)
2	*	4.0 (3374)	123.4 (23331)	26.0 (637)	0.01 (32)	1.5 (2196)	0.02 (3724)	21.8 (1273)	0.02 (64)	0.006 (382)	0 (382)	0 (382)	1.5 (64)	0 (64)	0 (64)	178.2 (35077)
3	*	0.3 (318)	134.5 (28679)	8.8 (350)	0.08 (159)	2.9 (2610)	0.07 (5347)	18.4 (1114)	0 (1114)	0.003 (255)	0 (255)	0 (255)	0 (255)	0 (255)	0 (255)	165.0 (38833)
4	*	13.1 (10854)	119.1 (24127)	18.1 (446)	0.01 (127)	1.7 (1496)	0.1 (4647)	19.2 (1019)	0 (1019)	0.006 (191)	0 (191)	0 (191)	0 (191)	0 (191)	0 (191)	171.5 (42907)
5	*	6.9 (6239)	138.2 (27788)	8.7 (318)	0.01 (96)	2.2 (2546)	0.1 (3151)	28.8 (1082)	0.01 (32)	0.003 (159)	0 (159)	0 (159)	0 (159)	0 (159)	0 (159)	184.9 (41411)
6		3.6 (3469)	147.5 (28201)	8.1 (382)	0.003 (127)	3.5 (2801)	0.2 (4934)	18.0 (1082)	0.006 (32)	0.003 (350)	0 (350)	0 (350)	0 (350)	0 (350)	0 (350)	181.1 (41379)
7		1.1 (1146)	166.8 (32339)	10.3 (509)	0.05 (191)	2.6 (2897)	0.4 (9867)	21.2 (1209)	0 (1209)	0.006 (796)	0 (796)	0 (796)	0 (796)	0 (796)	0 (796)	202.3 (48955)
8		0.6 (859)	162.9 (30780)	6.5 (287)	0.02 (318)	3.4 (2706)	0.1 (3247)	31.9 (1368)	0 (1368)	0.003 (127)	0 (127)	0 (127)	0 (127)	0 (127)	0 (127)	205.5 (39692)
9		17.4 (9040)	114.3 (21835)	31.2 (382)	0.01 (32)	0.7 (1019)	0.2 (2897)	22.2 (1241)	0 (1241)	0.006 (159)	0 (159)	0 (159)	0 (159)	1.0 (64)	0 (64)	186.9 (36668)
20		7.3 (7989)	128.6 (24255)	7.4 (350)	0.05 (350)	1.5 (1241)	0.1 (2960)	14.8 (859)	0 (859)	0.003 (541)	0 (541)	0 (541)	0 (541)	0 (541)	0 (541)	159.7 (38546)

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