

**DISPERSAL AND COLONIZATION OF *Limnodrilus hoffmeisteri*  
IN A HUDSON RIVER TIDAL MARSH COVE**

A Final Report of the Tibor T. Polgar Fellowship Program

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## ABSTRACT

I investigated how dispersal of the oligochaete, *Limnodrilus hoffmeisteri*, by water movement may influence the large degree of spatial variation in population densities in South Cove, a tidal freshwater cove-marsh system, in the Hudson River. Another reason to investigate the dispersal is the possibility that immigrating worms, not resistant to cadmium, displaced the cadmium-resistant worm population in nearby Foundry Cove, once it had been dredged of cadmium-rich sediment. I measured dispersal by two approaches. First emergence traps were employed to estimate the number of worms that swim into the water column and, second, colonization trays were used to estimate arrival of worms from another location. Emigration of *L. hoffmeisteri* was modest although another species showed more dispersal. Sequencing and independent identification by an expert demonstrated the dispersing species to be *Dero* sp. In a second approach, I placed plankton nets at the Foundry Cove Railroad trestle on the rising tide, in order to capture immigrating worms. No *L. hoffmeisteri* was found. Overall, my results show low intersite movement and no immigration of *L. hoffmeisteri* from outside the system.

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## INTRODUCTION

Tidal freshwater cove-marsh complexes are a common feature of many estuaries and they act as a significant baffle between upstream terrestrial and downstream coastal ecosystems (Simpson et al. 1983, Odum, 1988). Despite the importance of tidal freshwater habitats ecologically and economically, they are poorly studied compared with non-tidal freshwater wetlands (Weinstein and Kreeger 2000). Studies of the spatial patterns of benthic macroinvertebrate populations are especially lacking. Benthic organisms provide food for higher trophic levels, such as fish and birds (Herman et al. 1999, Malmqvist 2002). The sensitivity to environmental disturbances of macrobenthos is also a useful tool for monitoring the ecological changes of the tidal freshwater cove-marsh system (Zajac and Whitlatch 2001, Strayer et al. 2003).

Dispersal of benthic organisms by current movement may influence and even determine the large degree of spatial variation in population densities in a tidal freshwater marsh cove. Soft-sediment freshwater communities are dominated by burrowing organisms of relatively small body size, usually less than 10-20mm in length. A previous study of South Cove (Hudson River, Highlands region) tidal freshwater cove benthos suggests that there is strong spatial variation in population densities at many spatial scales (Allen et al. submitted for publication). The prior investigation did not suggest a strong correlation between benthic abundance and sediment type, which calls into question local effects on population growth due to local sediment parameters. So the question is raised whether dispersal between sites influences the spatial variance in abundance. Water motion and erosion caused by tidal motion, combined with the phenomenon of burrowing organisms emerging from sediment (Palmer and Gust 1998, Nilsson et al. 2000) can be a

possible factor in the strong spatial variation. Erosion of surface sediment by tidal currents may carry benthic organisms to another location. Emergence of burrowing organisms may be followed by transport by water currents.

Our study sites were South Cove and Foundry Cove (Figure 1), which are both located on the east side of the Hudson River, New York, in the vicinity of the villages of Cold Spring and Garrison. Both have been extensively studied since the early 1980s. Before a Superfund cleanup in 1994-1995, Foundry Cove was severely polluted with nickel-cadmium wastes (Knutson et al. 1987), whereas South Cove was relatively clean. In both coves, soft sediments are dominated by benthic larvae of the family Chironomidae and also by tubificid and nauid oligochaetes. The tubificid oligochaete *Limnodrilus hoffmeisteri* is the most common macrobenthic species in both coves (Kelaher et al. 2003). In this study, we focused on this species because its life cycle is well known (Kennedy 1966) and it has strong spatial variation in abundance at all spatial scales according to previous studies and especially according to recent results (B. Allen personal communication).

Another interesting reason to focus our study on *Limnodrilus hoffmeisteri* is the loss of resistance to cadmium after the Superfund cleanup of Foundry Cove of battery waste pollution in 1994-1995 (Levinton et al. 2003). By 2002, the population of the oligochaete in Foundry Cove was as vulnerable to cadmium as was the population in South Cove (Junkins 2002, Levinton et al. 2003).

That the rapid loss of genetically-based resistance loss happened so quickly might be explained by two different hypotheses. First, after the cleanup non-resistant *L. hoffmeisteri* from outside Foundry Cove might have immigrated and swamped out the

local dominant resistant genotypes. I tested this hypothesis with two studies. First, I did an experimental study to see if there is a potential for dispersal of worms between sites within a cove. Second, I estimated the potential for *L. hoffmeisteri* to immigrate from distant habitats by sampling the water during the incoming tide into Foundry Cove. If worms immigrated into Foundry Cove and there also was extensive potential for dispersal within a cove, then we should seriously consider the hypothesis of dilution of locally resistant genotypes by immigration of vulnerable genotypes from outside areas.

A second hypothesis for the rapid loss of resistance to cadmium is that resistance is energetically expensive. As a consequence, non-resistant genotypes now have an advantage since Foundry Cove is no longer polluted. I will not, however, be testing this hypothesis directly in this project. This hypothesis was investigated in a previous Polgar report (Montero 1996).

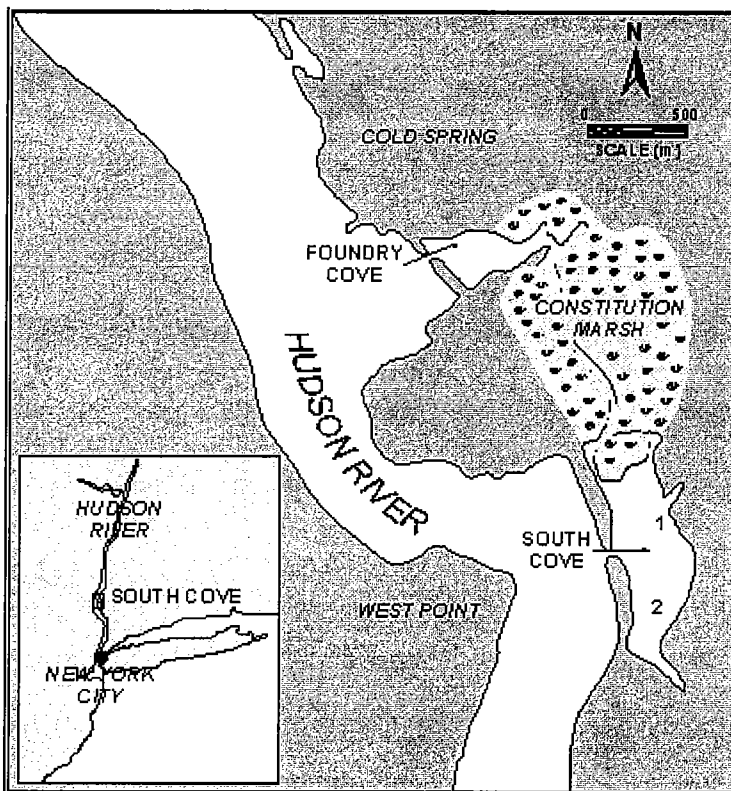
## METHODS

### *Study Site*

South Cove is a part of a tidal freshwater cove-marsh system in the Hudson River about 50 miles North of Manhattan, New York (41° 23' 94'' N, 73 ° 56' 41'' W) (Figure 1). The cove is separated from Foundry Cove to the north by Constitution Marsh, a nearly freshwater tidal marsh-creek system. Both Foundry and South Cove soft sediments are almost fully covered by Hudson River water in each tidal cycle. For the June 2004 sampling, a mudflat near the opening of Indian Brook, which enters South Cove from the east, was chosen to determine dispersal variability of *Limnodrilus hoffmeisteri*. For the following month's sampling, an additional site about 1 km

southeast was selected to compare the difference of population density and dispersal of the oligochaetes with the original site. They were both situated in the intertidal zone, but the second site had a higher density of water chestnuts.

**Figure 1:** Map of Foundry Cove and South Cove, showing sampling sites used for within-cove dispersal studies within South Cove.



### *Field Work*

Three types of samplers were employed in the field: emergence traps, colonization trays, and plankton nets. Modified emergence traps (Thistle 2003) were used to see if *L. hoffmeisteri* would swim into the water column (Figure 2A). A cylinder of PVC pipe (10 cm diameter by 15.2 cm high) was placed into the sediment to a depth of 9.5 cm. Within the cylinder was the top of a 2-liter plastic soft drink bottle, which



divided the trap into a lower chamber above the sediment and an upper chamber. Worms emerging from the sediment swam upwards through the mouth of the soft drink bottle. The constricted top guided worms into the upper chamber and trapped them. Each trap was covered by a 63-micron mesh cloth to prevent the oligochaetes that emerged from the sediment to escape from the traps. At each site, four groups (subsites) of five replicate emergence traps were placed 10 meters apart; traps in each site were spaced about one meter away from each other. Traps were placed in the sediment at the time of low tide and then worms were collected in the upper trap chamber 48 hours later. The trap nets were replaced and were sampled again 48 hours later. This sampling regime gave us data for the emergence over a 4-day period. At the end of the 4 days, four 2.5 cm diameter cores were taken to a depth of 5 cm within the sediment inside each trap.

Colonization trays (Figure 2B) were placed on the sediment surface to examine the possible settlement of *L. hoffmeisteri* from the water column. One 61 cm X 96.5 cm bare Plexiglass plate was placed on top of the mudflat next to each group of emergence traps and eight settlement dishes were attached in the center of the plate and 20 cm away from the sediment surface (Kelaher and Levinton 2003). Each settlement plate was a 9-cm diameter petri dish, 1 cm in depth, that was packed with South Cove sediment that had been sieved and frozen. The colonization trays were collected at the end of the 4-day colonization period.

We used plankton nets to test the movement of *L. hoffmeisteri* into Foundry Cove through a narrow passage beneath the Metro-North Railroad bridge, where strong tidal currents transport water and suspended materials into Foundry Cove on the rising tide. Two 63-micron plankton nets with a 20 cm diameter circular opening were placed two

meters apart under the bridge of the opening of Foundry Cove for a 30-minute interval, which was repeated three times during a rising tide on August 23, 2004. Captured material was thoroughly washed from the net into a jar and organisms were preserved with 5% formalin. The velocity of water currents was recorded for each interval by using a stopwatch to record the movement of floating material past a ca. 2 m-long floating bar. We used the mean of ten replicates for each of the three 30-minute sampling, recorded mid-way during the plankton sampling.



**Figure 2:** (A) Emergence Trap (Left) with top net removed and (B) Colonization Trays (Right)

#### *Laboratory Work*

The sediment cores were washed in a 297-micron sieve and preserved in 37% formalin which was tinted with Rose Bengal. The colonization tray samples were rinsed through a 297-micron sieve and identified as above. The plankton net samples were washed in a 63-micron sieve; I identified oligochaetes in these samples. The emergence trap samples were placed under a binocular microscope to count and identify existing *L. hoffmeisteri*. In the June sampling, without considering the possible presence of other species of oligochaetes, all oligochaetes that had similar morphology with *L. hoffmeisteri* were considered as one species. In the July sampling, different species of oligochaetes

had been recognized and were sorted separately. Moreover, a small-sized oligochaete was found that resembled *L. hoffmeisteri* morphologically, but behaved differently and was smaller. After samples being sent to a taxonomic expert for analysis (Alexa Bely, written communication) we keyed the unknown worm to be the naiid *Dero* sp. (also called fluted oligochaete in some contents below).

### *Genetic Analysis*

As discussed below, there were uncertainties in the identification of oligochaetes found in the emergence traps. One especially common worm was troublesome to identify. It was small, with a fluted posterior segment. We were uncertain whether the worm (later identified as *Dero* sp.) was a juvenile morph of *L. hoffmeisteri* or a distinct species. To answer this question we analyzed DNA nucleotide data of a subset of oligochaetes. Sequenced data from the mitochondrial 16S ribosomal subunit has been provided for a number of oligochaetes, demonstrating the usefulness of this gene for distinguishing known and ‘cryptic’ (genetically but not morphologically divergent) species in oligochaetes (Sturmbauer et al. 1999). We compared the 16S sequences of three *Dero* sp. (collected and preserved during sampling in July) and one other ‘unknown’ found in the emergence trap. The nucleotide data were compared with sequences of *L. hoffmeisteri* sampled in the Hudson River at South Cove and nearby Foundry Cove (in 1997: Sturmbauer, unpublished data), including a sequence of mature *L. hoffmeisteri* individual collected at Foundry Cove (800m north of the South Cove) in 2004 (Mackie, unpublished data). Sequences representing other oligochaete species, available in the GenBank database; <http://www.ncbi.nih.gov/Genbank/>), were included to provide a point of reference for variation.

The DNA extraction, using Chelex-100 (Biorad), PCR and sequencing steps were conducted by Dr. Joshua Mackie using established protocols (Bastrop et al. 1998). 16S rDNA sequences (a total of 296 sites including gaps) were aligned using Clustal W software (available online: <http://www.ebi.ac.uk/clustalw>). A tree was constructed with Mega 2.0 (Kumar et al. 2001) using the Neighbor Joining algorithm to sequentially group nearest pairs of sequences. The robustness of this phylogeny was tested using the bootstrap resampling of the data set, which is a statistical method of testing the reliability of a tree. Ten thousand bootstrap iterations were run.

#### *Statistical Analysis*

All counts from individual emergence traps and colonization trays were transformed into numbers of worms per 100 cm<sup>2</sup> for comparison. The mean number of oligochaetes in each plot was used for comparison and tests of differences of proportions of emerging and colonizing oligochaetes were performed using a Chi-Square test.

## **RESULTS**

### *Oligochaetes in Sediment and in Emergence Traps*

In the June sampling period, the means of the total oligochaetes in sediment (calculated from counts of the cores) among four groups (subsites) showed relatively little spatial variability at location 1 (Figure 3A). In the July sampling, the numbers of oligochaetes in the sediment decreased by nearly half. Examinations of densities of samples from location 2 (collected only in July) showed that all groups had high spatial variability within this site. The oligochaetes that were trapped in the emergence traps also had considerable variability among groups at each site (Figure 3B). I found more

oligochaetes in the emergence traps in the June sampling than in the July sampling (Figure 3B). I found oligochaetes in the emergence traps in all groups from the June sampling, but there was one group in each location in the July sampling where I found no oligochaetes at all. The oligochaete population densities in the sediment and in emergence traps declined from June to July and the variability increased between groups and among sites. The means of the total numbers of oligochaetes in sediment and in emergence traps pooled over two sampling dates and one additional location (Figure 4) showed an overall strong positive correlation between numbers of worms in the sediment and numbers of worms that were found in the emergence traps. Overall, a linear approximation suggests an emergence rate of about one percent per day.

#### *Oligochaetes in Colonization Trays*

The oligochaetes that settled on the colonization trays had strong spatial variation among each group in both sampling dates and locations (Figure 3C). On average, location 1 in the June sampling had at least double the numbers of oligochaetes that were found in the July sampling except the similar count of worms from group 2 in the June colonization trays. When densities from each sampler type (emergence and colonization) were corrected to numbers per 100 cm<sup>2</sup>, it is possible to compare rate of colonization (numbers per 4 days) with rate of emigration (Fig. 3 B, C and Figure 5). The relationship

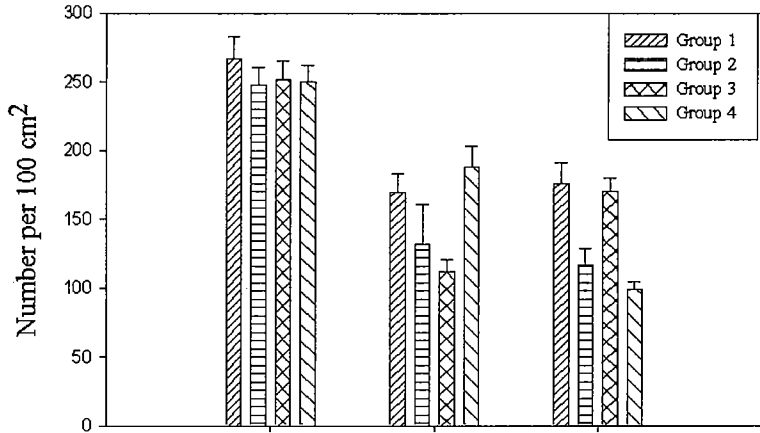


Fig. 3A

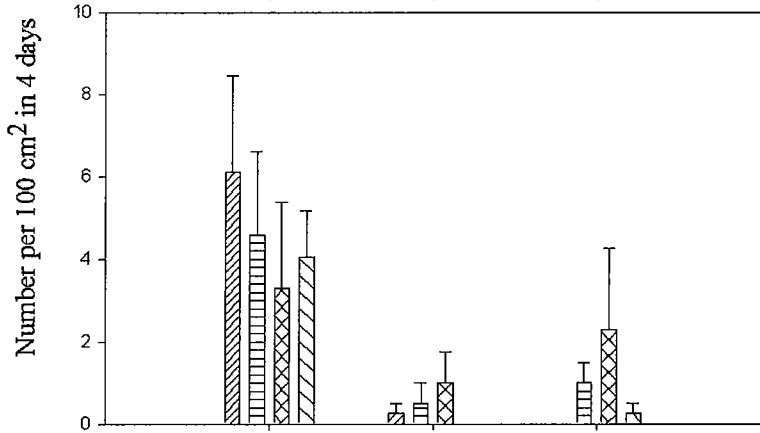


Fig. 3B

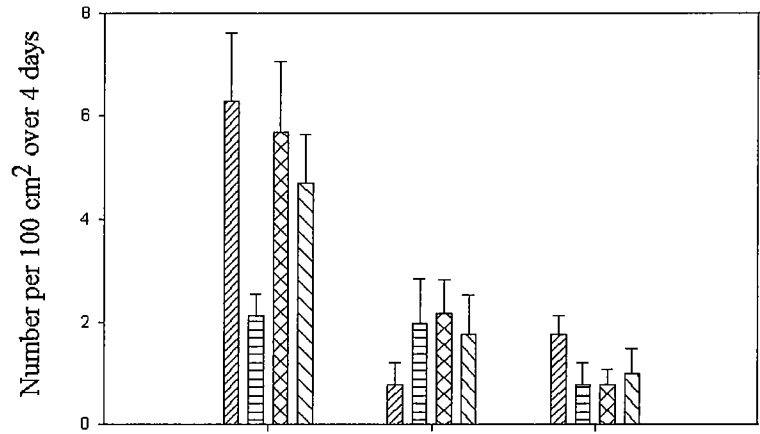
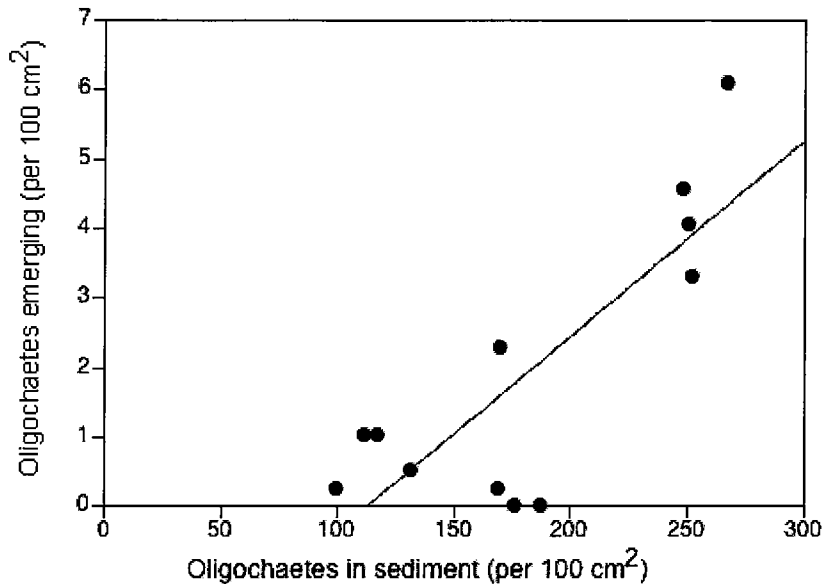


Fig. 3C

June 25, Location 1 July 26, Location 1 July 26, Location 2

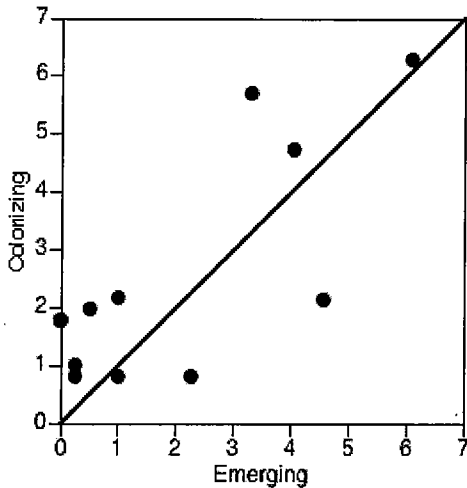
Times and Locations

**Figure 3:** Number of Oligochaetes (mean  $\pm$  1 SE) in (A) Sediment, (B) Emergence Traps and (C) on Colonization Trays. The experiments were done on two separate dates with additional location on the later date.



**Figure 4:** The means of the total numbers of oligochaetes in emergence traps and oligochaetes in sediment pooled over two sampling dates and additional location in later date.

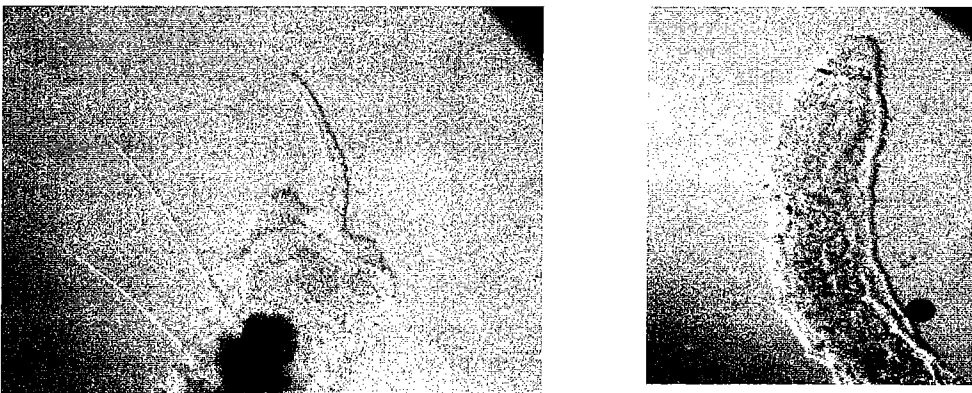
between emergence-emigration and colonization-immigration was striking (Figure 5). If the best least-squares fit is forced through the origin slope is 0.99 ( $r = .76$ ), it suggests an approximate equality of emigration and immigration to microsites. These data are combined from the first and second sampling periods. The four points with emergence greater than 3 are from the first sampling period, suggesting that the two groups are a combination of two different populations. The emergence rate (per four days per 100 cm<sup>2</sup>) for the June samples was 4.5, which closely matched the colonization rate of 4.7. This was not true for the July samples (lower left points in Figure 5), where emergence was 0.5 and colonization was 1.2. These latter data, however, were based on rather low numbers, including some zeros.



**Figure 5:** The Means of the Total Numbers of Oligochaetes in Emergence Traps (rescaled to numbers per 100 cm<sup>2</sup>) and Oligochaetes on Colonization Trays Pooled over Two Sampling Dates and Additional Location in Later Date. Line is expectation when emergence and colonization are equal.

#### *Immigration From Outside Foundry Cove*

There were no *Limnodrilus hoffmeisteri* found in the plankton nets with an average total water sampling volume of about 22 m<sup>3</sup> in August. However, several other oligochaete species, such as *Stylaria lacustris* and *Nais pseudobscura*, were discovered in the nets (Figure 6). This shows that oligochaetes can enter the cove through the tidal entrance at the railroad bridge, but that no *L. hoffmeisteri* was found in this case.



**Figure 6:** Oligochaetes Found in Plankton Nets: *Stylaria lacustris* (Left) and *Nais pseudobscura* (Right). Under 200 magnification by Josh Mackie.



*Proportions of Swimmers and Settlers of Limnodrilus hoffmeisteri and Dero sp.*

In the first sampling I did not identify oligochaetes to species in each emergence trap or colonization tray, but I did look at the aggregate sample of oligochaetes from the total combined worms found in the emergence traps and colonization trays, respectively. I attempted to make broad classifications of the oligochaetes in the combined samples. The proportions of swimmers (from emergence traps) and colonizers of *L. hoffmeisteri* and *Dero* sp. were not significantly different in the first sampling period, according to the Chi-Square test ( $df = 2, X^2 = 0.009, P = 0.926$ ) (Table 1). This was also true for the second sampling period ( $df = 2, X^2 = 2.06, P = 0.259$ ).

**Table 1:** Numbers and Proportions of *Limnodrilus hoffmeisteri*, *Dero* sp. and other oligochaetes in Emergence Traps and in Colonization Trays. Analysis of first sample period in June.

	<i>Limnodrilus hoffmeisteri</i>	<i>Dero</i> sp.	Other Oligochaetes
Emerging	21	15	35
	29.58%	21.13%	49.30%
Colonizing	29	19	48
	30.21%	19.79%	50.00%

Note that large numbers of other oligochaetes were found in each group in both sampling dates and locations. Unfortunately, the oligochaete samples, especially the worms counted from the sediment cores had not been completely saved in the June sampling so that we cannot examine the samples again.

*Identification of worms in emergence traps*

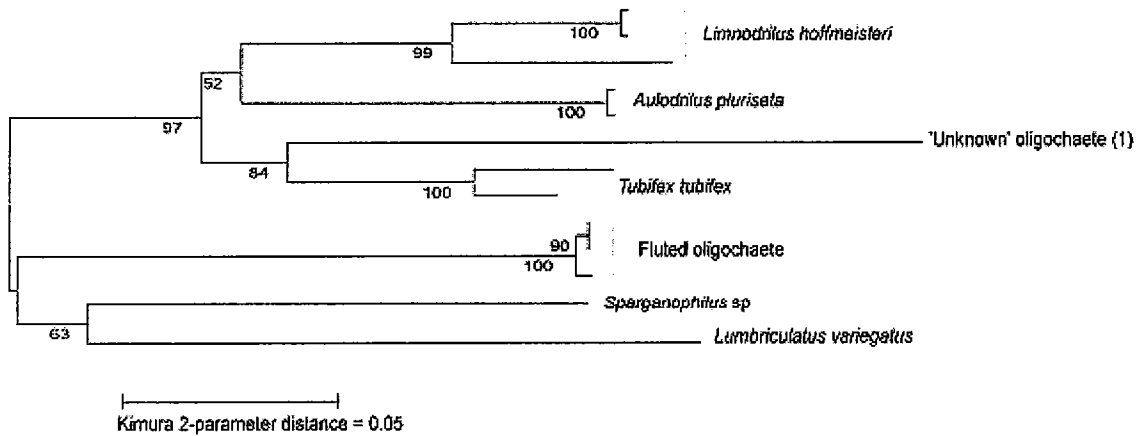
Some of the oligochaetes found in emergence traps were smaller than worms collected in the colonization trays, or in the sediment core samples. We had difficulties identifying these individuals to species. Setae structure and gonadal differentiation, the taxonomic characters that are typically used for defining aquatic oligochaetes (Brinkhurst, 1986), were not apparent. We asked Dr. Alexandra Bely (Biology Department, University of Maryland) to identify the unknown individuals, which were preserved in 85% ethanol (samples from sampling in July and September).

In the emergence traps we found a number of worms that, based on setae and gonadal characters alone, do not appear to be distinguishable from juveniles of *Limnodrilus hoffmeisteri*.

The common worm found in the emergence trap has an abdomen that is flared or fluted. The abdomen of mature individuals of *L. hoffmeisteri*, which were abundant in sediment in this experiment, is not flared but rather tapers to a blunt end point. In the laboratory we observed individuals of this species, identified by Dr. Bely as *Dero* sp., swimming with a wiggling motion, resembling the movement of a fly larva.

#### *Genetic Analysis*

The analysis of 16S sequence data indicated that the fluted oligochaete (*Dero* sp.) is distinct from *L. hoffmeisteri*. Sequences of three fluted individuals formed a distinct clade in the phylogenetic tree (Figure 7). Sequences were separated by an average genetic distance of 27% from the *Limnodrilus hoffmeisteri* (Table 2). Bootstrap support for the fluted clade was 100%. The sequence of one unknown oligochaete, collected after the two sampling times in September (neither a fluted oligochaete, nor *L. hoffmeisteri*), was also divergent.



**Figure 7:** Neighbor-joining tree of 16S rDNA sequences of a number of oligochaetes sampled from South Cove, as compared with sequences of *L. hoffmeisteri* determined by Christian Sturmbauer (unpublished).

**Table 2:** 16S sequence data. Average pairwise distances between selected oligochaete taxa and two species that were collected in swimmer traps (labeled\*). Distances in the lower left of the matrix are the raw number of sites that varied between taxa in the 296-base pair 16S fragment. Proportional distances corrected with the Kimura (1980) 2 parameter model are shown in upper right of the table. The averages are based on groups of one or more taxa, shown in the tree (Figure 6)

	1.	2.	3.	4.	5.	6.	7.
1. <i>Limnodrilus hoffmeisteri</i>	-	0.27	0.30	0.28	0.33	0.19	0.20
2. 'Unknown' oligochaete (1)*	66.67	-	0.34	0.37	0.43	0.28	0.23
3. Fluted oligochaete*	74.22	81.67	-	0.26	0.36	0.27	0.28
4. <i>Sparganophilus</i> sp.	70.00	87.00	65.00	-	0.31	0.27	0.29
5. <i>Lumbriculatus variegatus</i>	78.67	97.00	84.33	76.00	-	0.36	0.32
6. <i>Aulodrilus plurisetata</i>	49.50	70.00	67.00	67.00	84.50	-	0.20
7. <i>Tubifex tubifex</i>	52.67	58.00	68.50	71.00	77.00	51.00	-

Our initial attempt to discriminate worm species in the emergence traps leads us to conclude that there may be differences between the swimming abilities of different species of oligochaetes. *Dero* sp. comprised approximately 20 % of the number of worms combined with *L. hoffmeisteri* found in the emergence traps. *Dero* sp. were apparently more mobile in the water column than *L. hoffmeisteri*, which were also found in the emergence traps but in lower abundance. In the lab, *Dero* sp. responded to touch by a probe and swam rapidly away. This was not the case for *L. hoffmeisteri*.

## DISCUSSION

### *Population Densities and Spatial Variation of Oligochaetes*

The results of this study indicate that the emergence and colonization of oligochaetes are correlated with population densities within the sediment. The higher the number of oligochaetes within the sediment, the more oligochaetes swim in the water column and possibly settle in a new location (although the dispersal distance is not clear). It may be that dispersal by emergence and colonization is very short-range. Our results do not suggest that either emigration or immigration is contributing significantly to larger-scale variation in density, although it is clear that movement occurs, perhaps at smaller scales. A repeat of this study would involve larger numbers of replicates to see if emigration was proportional to immigration at local spatial scales (i.e., within sites).

### *Emergence-Swimming and Colonization*

The data demonstrate that oligochaetes will emerge from the sediment, swim up to the water column, and settle in a new location. Generally, the oligochaetes in the water column will settle down elsewhere. The positive correlation of numbers of emerging and settling oligochaetes supports the idea that small benthos are able to move from one location to another. Given our results, approximately 15-30% emerge and emigrate each month. However, we cannot determine why the oligochaetes move away, how far they travel and where they will settle. It should also be noted that all of the metamorphosing chironomids leave local sites to develop into nymphs and, eventually, flies. Thus, oligochaete emigration is a major feature of soft sediment tidal mud flats of the lower Hudson River.

The loss rate is about one percent per day. On the other hand, there is also a considerable rate of recolonization at the same sites. In June, the loss of 4.5 average worms per 100 cm<sup>2</sup> per day is balanced approximately by the colonization rate of 4.7 worms per 100 cm<sup>2</sup> per day. For the July sampling, low numbers reduce our confidence, but emergence was at a rate of 0.67 and colonization was about double at 1.37 worms per 100 cm<sup>2</sup> per day. The June sampling dominates emigration-immigration numbers, so a balance is suggested.

The slope of the relationship between colonizers and emerging oligochaetes was approximately unity, which indicates a balance of emigration and immigration. But the number of colonizers is also strongly positively related to the number within the sediment locally, as is the relationship of emergers and numbers in the sediment. Given the strong local spatial variation in densities of worms in the sediment, this suggests that worms

travel only very short distances. Otherwise one would expect colonizers to not be correlated with numbers within the sediment in the same microsite. This argues for very short distance dispersal, even if emergence occurs. A problem with this interpretation, is that we are mixing two successive sampling periods, which involve two different sets of conditions and average densities (much higher density in June). Further work with denser samples within sites would be necessary to confirm the idea of local dispersal.

*Proportions of Swimmers and Settlers of Limnodrilus hoffmeisteri and Dero sp.*

Our results suggest that some of the worms emerging (ca. 20 percent) into the traps have the morphology corresponding to a species of the naiid genus *Dero*. Aside from the identification on the basis of morphological characters, the 16S rDNA sequencing results suggest that this is another species, and not juvenile *L. hoffmeisteri*. The remaining worms in the emergence traps are a combination of *L. hoffmeisteri* (ca. 30 percent) and other oligochaete species (ca. 50 percent). We thus can conclude that *L. hoffmeisteri* emerges from the sediment, but that emergence and dispersal is dominated by at least one other oligochaete species. Unfortunately, the number of worms emerging or colonizing the settling trays were both small in the July sampling period. The results, however, at least demonstrate that dispersal is proportional to abundance of worms in the sediment (high in the June sampling), and that dispersal is probably seasonal.

*Immigration from other locations*

It is unlikely that *L. hoffmeisteri* can enter Foundry Cove or South Cove from other locations since we did not find any evidence in the plankton nets. However, the

fact that other oligochaetes were found in the nets shows that certain species are capable of swimming into the water column, being entrained, and traveling for a distance to enter the cove from other locations. Two previous samplings with plankton nets also failed to find *L. hoffmeisteri* entering the cove via the tidal channel. Because the nets were deployed near the surface, we cannot be sure about possible movement of worms from the Hudson River (actually West Foundry Cove) near the bottom.

#### *Genetic Analysis*

The genetic divergences indicate that conservative grouping of oligochaete taxa by means of morphological characters is likely to underestimate species diversity. The *Dero* sp. is clearly a different species, not juvenile *L. hoffmeisteri*, as we thought previously. The data indicate that *L. hoffmeisteri* was less abundant in the emergence traps than would have been expected based on our initial inspection. There were *L. hoffmeisteri* in the emergence traps, but I can now estimate that 20% of the worms in the emergence traps were *Dero* sp.

## CONCLUSIONS

In summary, there is no evidence of *Limnodrilus hoffmeisteri* emerging from locations outside of Foundry Cove and immigrating into the cove in significant numbers. Therefore, our results do not support the hypothesis of immigrating *L. hoffmeisteri* invading and displacing numerically the resistant genotypes in Foundry Cove. However, our study shows *L. hoffmeisteri* has strong spatial variation in tidal freshwater cove-marsh systems. Emergence and colonization does occur within a cove but it is not clear that this involves significant dispersal beyond a few meters. Further study of macrobenthos is strongly encouraged for this ecologically and economically important habitat.

## ACKNOWLEDGEMENTS

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