

SALINITY AS A REFUGE FROM PREDATION IN A NUDIBRANCH-HYDROID
RELATIONSHIP WITHIN THE GREAT BAY ESTUARY SYSTEM

BY

David J. Blezard
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This thesis has been examined and approved.

Thesis Director, Larry G. Harris
Professor of Zoology

John Sasner, Professor of Zoology

Marianne K. Litvaitis, Assistant Professor of Zoology

Date

DEDICATION

To my father,
John Raymond Blezard
1936-1991

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TABLE OF CONTENTS

DEDICATION.....	iii
ACKNOWLEDGEMENTS.....	iv
TABLE OF CONTENTS.....	v
LIST OF TABLES.....	vii
LIST OF FIGURES.....	viii
ABSTRACT.....	ix
INTRODUCTION.....	1
METHODS.....	7
Fouling Panel Study.....	7
Field Surveys.....	10
<i>Cordylophora</i> Colony Growth.....	10
<i>Cordylophora</i> Field Trial.....	13
<i>Tenellia</i> Growth and Reproduction.....	14
RESULTS.....	18
Fouling Panel Study.....	18
Field Surveys.....	28
<i>Cordylophora</i> Colony Growth.....	30
<i>Cordylophora</i> Field Trial.....	34
<i>Tenellia</i> Growth and Reproduction.....	35
DISCUSSION.....	41
Population Distributions and Dynamics.....	41
Species Interactions.....	43

Effects of Salinity on <i>Cordylophora</i> Growth.....	46
Effects of Salinity on <i>Tenellia</i> Growth and Reproduction.....	48
The Effects of Salinity on the <i>Cordylophora–Tenellia</i> Relationship.....	52
The <i>Cordylophora–Tenellia</i> Relationship within the Great Bay Estuary System.....	55
CONCLUSIONS	61
LITERATURE CITED	63

LIST OF TABLES

Table 1. Retrieval and replacement schedule for fouling panels.....	9
Table 2. Two-factor design for the <i>Tenellia adspersa</i> survival and fecundity experiment.	16
Table 3. Pearson correlation coefficients of the percent cover of hydroids with the number of mussels at Stations 1 and 2 for each month.	24
Table 4. Pearson correlation coefficients of the percent cover of hydroids with the number of barnacles at Station 3 for each month.....	25
Table 5. Observations of <i>Cordylophora lacustris</i> colonies.	30
Table 6. Size and growth rates of <i>Cordylophora lacustris</i> colonies at 4 different salinities.	32
Table 7. Repeated measures ANOVA for the effect of salinity on the number of polyps of a <i>Cordylophora lacustris</i> colony.....	32
Table 8. Repeated measures ANOVA for the effect of salinity on the length of the stolon of a <i>Cordylophora lacustris</i> colony.....	33
Table 9. Results from the <i>Cordylophora lacustris</i> field experiment.	34
Table 10. Two factor ANOVA for the effect of salinity on the number spawn masses produced by an individual <i>Tenellia adspersa</i>	37
Table 11. Two factor ANOVA for the effect of salinity on the number eggs produced by an individual <i>Tenellia adspersa</i>	37
Table 12. Observed fecundity measures for <i>Tenellia adspersa</i> with respect to developmental salinity and adult salinity.....	39
Table 13. Two factor ANOVA for the effect of salinity on the life span of <i>Tenellia adspersa</i>	40
Table 14. Comparison of mean fecundity measures for <i>Tenellia adspersa</i> from this study with previously reported values when fed <i>Cordylophora lacustris</i>	49

LIST OF FIGURES

Figure 1. Map of the Great Bay Estuary system showing stations for the fouling panel study.	7
Figure 2. Wooden array with fouling panels.	8
Figure 3. Salinity and temperature at each station for the fouling panel study...	19
Figure 4. Distribution of colonial invertebrates at each station during the five months of the fouling panel study.....	21
Figure 5. Distribution of solitary invertebrates at each station during the five months of the fouling panel study.....	22
Figure 6. Weekly recruitment of hydroids at each station during the fouling panel study	23
Figure 7. Abundances of <i>Tubularia</i> spp. and its predators at Station 1 in July.....	25
Figure 8. Abundances of campanularid hydroids, <i>Tenellia adspersa</i> , and <i>T. adspersa</i> spawn masses at Stations 1, 2, and 3 in June.	27
Figure 9. Map of the Great Bay Estuary system showing where <i>Cordylophora lacustris</i> and <i>Tenellia adspersa</i> were found in 1993 to 1998.	28
Figure 10. Growth of <i>Cordylophora lacustris</i> at four salinities as measured by the number of polyps (top) and the length of the stolon (bottom).....	31
Figure 11. Effect of salinity on the maximum height of <i>Cordylophora lacustris</i>	33
Figure 12. Box plots showing the number of veligers and juvenile <i>Tenellia adspersa</i> surviving development at 6, 12, 18, and 24‰.	36
Figure 13. Effects of salinity on the fecundity of <i>Tenellia adspersa</i>	38
Figure 14. Life span of <i>Tenellia adspersa</i> at different salinities.....	40
Figure 15. Salinity of the Great Bay Estuary system at low and high tide in May.	59
Figure 16. Salinity of the Great Bay Estuary system at low and high tide in July.	60

ABSTRACT

SALINITY AS A REFUGE FROM PREDATION IN A NUDIBRANCH-HYDROID RELATIONSHIP WITHIN THE GREAT BAY ESTUARY SYSTEM

by

David J. Blezard
University of New Hampshire, May 1999

Hydroids are important early colonists in fouling communities. They are among the first occupiers of space and have been shown to affect the course of succession in the community by facilitating the recruitment of some later colonists while inhibiting others. Predators, especially aeolid nudibranchs, rapidly recruit to hydroid colonies and can provide sufficient predation pressure to remove hydroids from the community potentially altering the successional process. Data from a study of the recruitment and interactions of early fouling community organisms within the Great Bay Estuary system, NH, USA, illustrate these principles. In some cases, hydroid colonies are not removed and occupy space for longer periods. Understanding the interactions between nudibranch predators and hydroid prey is an important component in understanding the development of fouling communities.

The hydroid *Cordylophora lacustris* is a common species in the upper reaches of the Great Bay Estuary system. Colonies of *C. lacustris* can reach large sizes effectively occupying space, and populations persist in the same locations from year to year. The nudibranch *Tenellia adspersa* is the primary predator of *C. lacustris*. *T. adspersa* has very short generation times (21 days) and life spans

(36 days) and can produce large numbers of offspring. In laboratory conditions, the nudibranch populations overwhelm the hydroid prey.

Salinity is an essential factor in the relationship between these two species as revealed by studies of their growth and reproduction at 6, 12, 18, and 24‰ salinities. *C. lacustris* grows at all of these conditions but increases most rapidly at 6‰. Adult *T. adspersa* can survive in this salinity range but show increased stress and reduced fecundity at or below 12‰. Fecundity is highest at 24‰. Development of *T. adspersa* fails at both 6‰ and 12‰, and survival of metamorphosis is reduced at 18‰ compared to 24‰. Low salinity environments are a refuge from predation for the hydroid because the nudibranch population cannot increase in size to overwhelm the prey population. The salinity tolerances of these two species along with the seasonal variations in salinity may explain the natural distributions of *C. lacustris* and *T. adspersa*.

INTRODUCTION

Predation is a major factor in determining the distribution and size of populations of organisms. Prey species are a resource for predators leading to increases in the predator population while predatory acts that consume all or part of a prey organism lead to reductions in the prey population. This basic interaction between predator and prey species has been the focus of numerous studies and models to understand the ecological consequences of predation (Lotka, 1925; Volterra, 1926; reviewed in May, 1981a; Crawley, 1992).

In reality, the situation in which a predator and prey interact is much more complex than the strict isolation enforced by mathematical models. Other species can compete with and predate on both the predator and prey, and physical factors in the environment can either augment or depress the rate of predation (see Chesson, 1978; May, 1981b; Malcolm, 1992). One special circumstance is when the physical environment provides a means for some or all of the prey population to hide from or otherwise avoid predators. In such a situation, the prey have a refuge. If a refuge exists, it can lead to the persistence of a prey population that otherwise would be overwhelmed by its predators (see Crawley, 1992).

Beyond the direct determination of populations of the two species, predation is a highly significant factor in determining the development and the structure of a community. As succession takes place, early colonists may be preyed upon by later arrivals and removed from the system, or established predators may prevent new species from colonizing an area by removing the

new arrivals before they become established (e.g., Lubchenco and Menge, 1978; Ayling, 1981; Day and Osman, 1981; Harris and Irons, 1982; Harris, 1987). These processes can have further consequences to the course of succession. Early colonists can facilitate, inhibit, or tolerate later arrivals (Connell and Slayter, 1977). For both the facilitation and inhibition models, the presence of a predator could reduce or even reverse the effect; a species that would have been inhibited by earlier arrivals might now be able to recruit into an area or vice versa. An established predator may also indirectly benefit other non-prey species by preventing a superior competitor from out competing them (Paine, 1966).

Both facilitation and inhibition interactions have been shown to take place in marine benthic and fouling communities (Dayton, 1971; Standing, 1976; Dean and Hurd, 1980; Harris et al., 1984). In these communities, hydroids are often early colonists of open space but may be ephemeral with other species such as mussels, barnacles, and tunicates replacing them over time (Clark, 1975; Harris and Irons, 1982; Lovely, 1995). Early hydroid colonies have been shown to facilitate the arrival of mussels and tunicates (Standing, 1976; Dean and Hurd, 1980; Dean, 1981; Okamura 1986) and to inhibit the recruitment of barnacles (Standing, 1976; Harris and Irons; 1982).

Aeolid nudibranchs are common predators on hydroid colonies (Clark, 1975; Todd, 1981; 1983). Predation by nudibranchs is a significant factor in determining the fate of a population of hydroids. Predation can create open patches within the colony, or, at high predator densities, the nudibranchs can completely consume the colony removing it from the community (Lambert, 1985; Harris, 1987). Thus, high levels of predation by nudibranchs could change the

inhibition and facilitation effects of early hydroid colonists on later successional species.

The hydroid, *Cordylophora lacustris* Allman, 1853, is a gymnoblastic colonial hydroid of the family Clavidae. The colonies grow attached to hard substrates and consist of branching stolons with periodic uprights bearing one to several feeding polyps. Individual colonies are often small, less than 100 cm², but can grow to cover more than a square meter of substrate (personal observation). The uprights with the polyps reach a maximum height of approximately 5 cm (Pollock, 1998). Under appropriate conditions, the uprights also bear gonophores for sexual reproduction.

C. lacustris is unique among hydroids in its ability to tolerate extremely low salinities including fresh water. In fact, *C. lacustris* has been located in freshwater systems in New York, Ohio, Texas, and Florida (Pennak, 1978; Hubschman and Kishler, 1972; Streever, 1992; Kelly and Franks, 1995). Laboratory studies using artificial seawater show that *C. lacustris* colonies grow most rapidly in conditions with a Cl⁻ concentration of 0.07 M (equivalent to 4.5‰ based on 0.545 M Cl⁻ in 35‰ seawater (Kalle, 1971)) but that the hydroid can grow in conditions ranging from nearly 0‰ to 35‰ (Fulton, 1962). Growth rate of the related (and possibly synonymous (Pollack, 1998; SERC, 1998)) *C. caspia* is highest at 16.7‰. *C. caspia* grew in conditions ranging from fresh water to 30‰ although abnormalities were noted at salinities over 24‰ (Kinne, 1956; 1971). Natural populations of *Cordylophora* spp. are reported only in brackish or fresh water (Calder, 1976; Jormalainen et al., 1994). Calder (1976) reported salinities between 0‰ and 7‰ as the range in which the hydroid was found in a South Carolina estuary. Within the Great Bay Estuary system of Maine and New

Hampshire, *C. lacustris* is only previously reported from low salinity areas (Crocker, 1972).

The nudibranch, *Tenellia adspersa* (Nordmann, 1845), is a major predator of *Cordylophora lacustris*. *T. adspersa* is a small (5-7 mm) aeolid nudibranch of the family Cuthonidae. Like *C. lacustris*, *T. adspersa* is unique among nudibranchs in its tolerance of estuarine conditions. Harris et al. (1980) cultured *Tenellia fuscata* (= *Tenellia adspersa*) in a variety of salinities and temperatures, finding that the nudibranch did best at 20°C and 30‰ but that the nudibranch could survive and reproduce at 10‰. Adult nudibranchs survived and produced eggs at a much reduced rate at 5‰, but these eggs did not develop. Conspecific *T. pallida* was able to reproduce at both 20‰ and 12‰ (Rasmussen, 1944).

Tenellia adspersa is also distinct among nudibranchs in that it is a generalist, feeding on a wide variety of hydroid species in addition to *C. lacustris*. A literature review by McDonald and Nybakken (1997) lists over 20 distinct species as prey items for *T. adspersa* including *Bougainvillia* spp., *Campanularia* spp., *Gonothyrea lovenii*, *Ectopleura dumortieri*, *Eudendrium* spp., *Obelia* spp., and *Tubularia* spp. as well as *C. lacustris*. This same review, however, lists only three North American species of nudibranchs (*Eubranchius exiguus*, *E. pallidus*, and *Facelina bostoniensis*) other than *T. adspersa* as feeding on *C. lacustris*, and each of these three is commonly associated with other prey (Pollack, 1998). While *T. adspersa* will feed on a variety of hydroids, it appears that *C. lacustris* is a preferred prey item and that *T. adspersa* is the main predator for *C. lacustris*. *T. adspersa* is often described in association with *C. lacustris* (Moore, 1964; Clark, 1975). In addition, a study by Chester (1996) found that *T. adspersa* grew more

rapidly and reached maturity at an earlier date when raised on a diet of *C. lacustris* compared with either *Obelia commiseralis* or *Hydractinia echinata*.

When *T. adspersa* is maintained in a laboratory situation, the nudibranchs grow and reproduce rapidly enough to overwhelm any size *C. lacustris* colonies (personal observation). When fed on *C. lacustris*, *T. adspersa* has a short life cycle and generation time and exhibits very high fecundity. Harris et al. (1980) found a generation time of 16 to 20 days with a life span of 28 to 30 days. Fecundity ranged from 682 to 2687 eggs per individual. Other results are similar with a generation times of 17 days, life span of 24 days, and fecundity of 1301 eggs per individual (Chester, 1996). Although *C. lacustris* does respond to low levels of predation by *T. adspersa* by changing the growth form of the colony, a change that presumably helps defend the colony (Gaulin et al., 1986), the rate at which *T. adspersa* reproduces means that the nudibranch population will increase very rapidly and consume any conceivably sized colony within a few weeks time.

In order for *C. lacustris* populations to avoid extinction, one or more factors must exist that limit the predation by *T. adspersa* in the natural environment. Salinity is a likely candidate as the two species appear to have differing tolerances for salinities. Based on past studies, *C. lacustris* can tolerate, and is often found, at very low salinities within an estuary whereas *T. adspersa* grows best at higher salinities. Both species, however, appear to be able to survive over a wide range of conditions.

Low salinity may function as a refuge for *Cordylophora lacustris* from predation by *Tenellia adspersa*. This study examines this hypothesis with evidence from natural populations of both species within the Great Bay Estuary system and from laboratory studies of the two species under directly comparable

conditions. It also presents data about the interactions between hydroids, nudibranchs, and other species in early fouling communities.

METHODS

Fouling Panel Study

In June through October 1993, a study was conducted to examine the recruitment and interactions of early fouling community organisms at different locations within the Great Bay Estuary system, NH, USA (Figure 1). Acrylic panels measuring 13 cm x 8 cm were suspended in wooden arrays with four replicates per location (Figure 2).

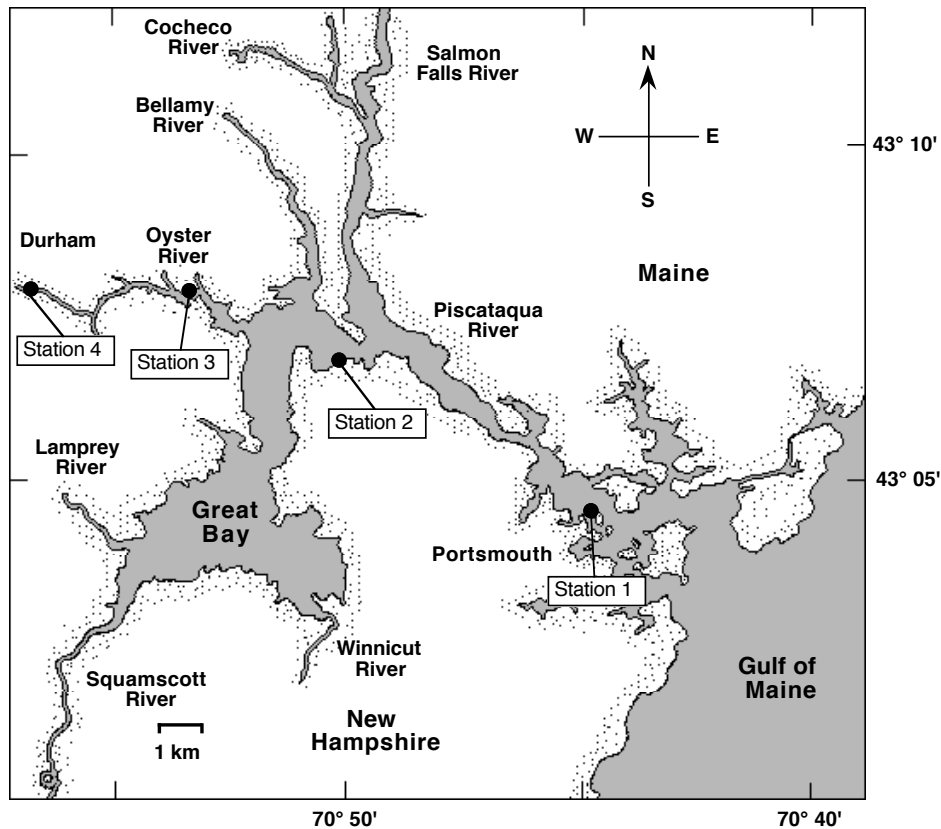


Figure 1. Map of the Great Bay Estuary system showing stations for the fouling panel study.

The arrays were anchored such that the panels would always remain submerged at the lowest tide. The vertical panels were allowed to rotate freely with the current so that both surfaces of the panel received equal exposure to current while reducing the effects of sedimentation. The top of the wooden array provided shade to the panels to reduce the growth of algae.

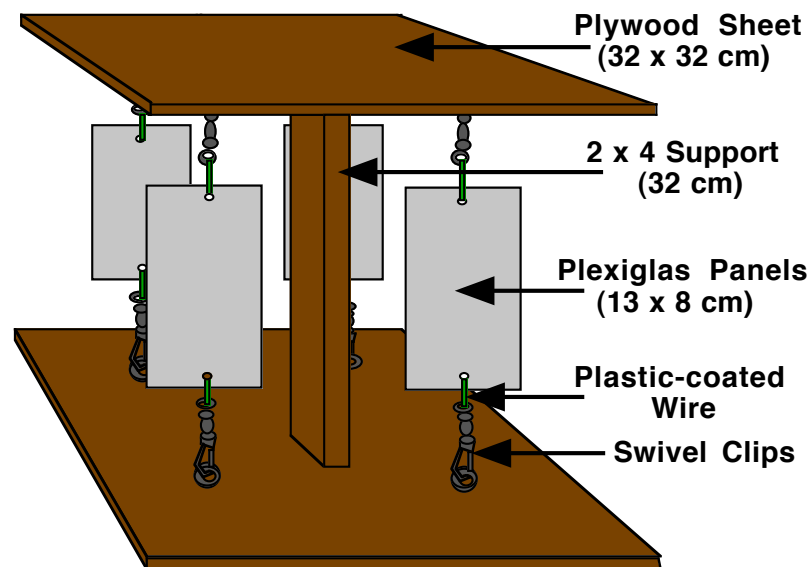


Figure 2. Wooden array with fouling panels.

Each array's four panels were numbered 1 through 4 corresponding to the number of weeks that the panels were exposed before retrieval. At low tide each week, the appropriate set of panels were removed, sealed in individual plastic bags, and replaced with fresh panels. Table 1 shows the retrieval and replacement schedule. Salinity and temperature measurements were taken as the panels were changed.

Table 1. Retrieval and replacement schedule for fouling panels

Panel	Week								
	0	1	2	3	4	5	6	7	8
1	S	C	C	C	C	C	C	C	C
2	S		C		C		C		C
3	S			R	S			R	S
4	S				C				C

S = Set out new panel.

C = Change panel (retrieve and replace).

R = Retrieve panel only.

The retrieved panels were examined in the lab. All organisms present were identified under a dissecting microscope to the lowest possible taxon using keys to local fauna (Frazer, 1944; Smith, 1964; Crocker, 1972). As measures of abundance, numbers of individuals or colonies were counted, and the percent cover of non-motile species was measured using a grid of 100 random points.

The design of the replacement schedule for the panels allowed examination of both temporal variations in recruitment and early successional changes in the community structure. By comparing panels that have been exposed for the same duration (across a row of Table 1), one can examine the changes in the abundance of species throughout the season. Panels that were put in place on the same date and were removed one per week for the four-week period (down a diagonal of Table 1) illustrate the interactions and succession of the community members.

Statistical analysis of the data was performed using StatView (SAS Institute, Inc., Cary, NC). Pearson correlation coefficients were calculated to examine the relationships between the abundances of hydroids and other

organisms. All percent cover data were normalized using an arcsine transformation before use in statistical calculations (Sokal and Rohlf, 1981).

Field Surveys

As the fouling panel study results (see page 18) contained no information about the distribution of *C. lacustris* and only reflect the conditions at the four study sites, a series of field surveys was begun in May 1994. The goal of the surveys was to examine other locations with floating docks, pilings, or other suitable substrate in the Great Bay Estuary system that were likely to have either *C. lacustris* or *T. adspersa*. When either organism was found, salinity and temperature of the water were measured. Any locations where either species had been found were checked at two-week intervals throughout the summer. Informal surveys continued through the summer of 1998.

Cordylophora Colony Growth

Fragments from several colonies of the hydroid, *Cordylophora lacustris*, were collected in July, 1997 from the Bellamy River, Dover, NH within 100 m downstream of the dam that separates the estuarine and fresh water portions of the river. These pieces of colonies were placed into an aquarium as the start of a laboratory culture. The hydroids in the stock culture were fed daily with one-day-old *Artemia salina* nauplii hatched from resting cysts (Aquatic Lifeline, Inc., Lehi, UT) at approximately 15‰.

The aquarium was maintained at 15‰ salinity and approximately 20°C. To obtain water at the desired salinity, unfiltered seawater collected from the Piscataqua River at the state fishing pier in Portsmouth, NH was combined with

the available well-drawn tap water. These same water sources were used throughout all laboratory cultures and experiments.

To produce a sufficient number of colonies in the stock culture, pieces of hydroid colony with one to a few polyps were secured to a glass microscope slide with monofilament line. The slides were suspended from wooden hangers resting on the top of the aquarium walls. Within a few days, the colony produced new stolon tissue that attached to the glass slide. These culture techniques are similar to those used previously to culture hydroids (Crowell, 1953; Fulton, 1960; 1962; Gaulin et al., 1986).

To assess the effects of salinity on the growth rate of *C. lacustris* colonies, 31 colonies were trimmed back to the point that only two uprights, each with a single polyp, connected by an unbranched length of stolon remained. These colony slides were returned to the stock tank for five days, after which time, all of the colonies had recovered from the trimming procedure and had grown new tissue at each end of the cut stolon. Twenty-four of these colonies were randomly selected and assigned into four groups of six replicates. Each group represented one of the treatment salinities of 6, 12, 18, and 24‰. These salinities were selected because they represented a range of conditions over which both *C. lacustris* and *T. adspersa* were likely to be able to survive based upon past studies (Kinne, 1956; 1971; Fulton, 1962; Harris et al., 1980; Chester, 1996).

The monofilament line was removed from around the glass slide before each slide was placed into its own separate dish, hydroid colony facing up. Each dish was filled with approximately 250 ml of water at a salinity of 15‰. After two hours, one-half of the water in each dish was removed and replaced with a like volume of water at the appropriate treatment salinity. After another hour,

the procedure was repeated. After an additional hour, the entire volume of water was siphoned off and was replaced with water at the treatment salinity. The purpose of these steps was to reduce or increase the salinity gradually to protect the colony from damage due to a sudden change in water chemistry.

To maintain these experimental colonies, each dish was supplied with an air tube to slowly aerate and circulate the water. The colonies were fed daily with concentrated *Artemia salina* nauplii. The nauplii were concentrated by placing them in an elongated dish with a light at one end for several minutes then siphoning off the ones that swam to the light. This technique provided a high amount of food with a minimum of water or unhatched cysts to pollute the dishes. The dishes were kept at a temperature of approximately 20°C. Water in the dishes was changed once each week to remove waste and uneaten food.

The growth of the colonies was monitored by photographing each colony every two days using a 35 mm camera equipped with a macro lens set at a ratio of 1:3. The color negative film was developed into Kodak Photo CD. The images on the compact disc were examined using both NIH Image 1.61 and Graphic Converter 3.3.1 on a Macintosh computer system. From the images, both the number of polyps per colony and the total length of the colony's stolon were measured. For length measurements taken with NIH Image, the long edge of the glass slide provided a convenient size reference.

The colonies were maintained and monitored for a total of 20 days. On the last day, in addition to the routine photographing, each colony was examined under a dissecting microscope. The total number of polyps was counted as a check of the accuracy of the numbers that would later be obtained from the digital images. Comparison of the two sets of data revealed that careful counts

made from the images are a very accurate measure of the true number of polyps with an mean difference of 1.5 polyps between the counts and no difference in 12 of the 24 cases. Also on the final day, the longest upright from each colony was removed at its base and measured as an additional indicator of colony size.

The remaining seven *C. lacustris* that had been trimmed down, but not used in the experiment, remained in the stock tank for the three-week duration of the experiment. At the end of the experiment, these seven colonies were also examined under a dissecting microscope, and the total number of polyps per colony was counted. A comparison of these colonies to those used in the experiments provided some measure of whether or not the conditions in the small dishes had negative effects on the colonies.

Statistical analysis of the data was performed using StatView. The measurements taken at two-day intervals throughout the growth study were compared using a repeated measures model analysis of variance (ANOVA). The date of the measurement acted as the *within* factor and salinity as the *between* factor. The Scheffe's F test was used *a posteriori* to compare the paired salinity treatments; this test was chosen due to the unequal cell *n*'s resulting from the exclusion of one replicate (see page 31). For measurements taken only once, a one-factor ANOVA was used (SAS Institute, 1998).

Cordylophora Field Trial

To assess whether or not *Cordylophora lacustris* can survive in areas of the estuary with higher salinities than those where it is regularly located, three groups of *C. lacustris* colonies were placed at different locations in the Great Bay Estuary system in June, 1998. Nine dense, well established colonies were taken

from the aquarium culture and were randomly assigned to three groups. Each glass slide was secured to the side of a brick with several windings of monofilament line.

Each group of three bricks was placed in the water at a subtidal depth at one of the same locations as Stations 2, 3, and 4 of the fouling panel study (see Figure 1). The bricks were placed on the bottom and oriented in such a way that the hydroid colony was attached to the vertical surface of the brick. This was intended to reduce the effects of sediment covering the colony.

After six weeks, the bricks and attached slides were retrieved. The slides were removed from the bricks and were examined under a dissecting microscope to determine the health of the hydroid colony and to see if any nudibranch predators were present.

Tenellia Growth and Reproduction

Tenellia adspersa were collected from the floating dock of the Jackson Estuarine Laboratory on Adams Point, Durham, NH on June 24, 1998. The nudibranchs were found feeding on the hydroid *Gonothyraea integra* at a salinity of 13‰. The nudibranchs were released into a laboratory stock culture of *Cordylophora lacustris* at a salinity of 15‰ and a temperature of approximately 20°C.

On August 11, several adult nudibranchs were removed from the culture and were randomly assigned to one of four groups each consisting of five individuals. Each group was placed in a separate dish with approximately 125 ml of water at the same temperature and salinity as the stock aquarium. One *Cordylophora lacustris* colony was added to each dish.

After five days, the number of nudibranchs in each dish was reduced to four to keep the numbers balanced because of some mortality. The hydroid colony and all spawn masses that had been produced were removed, and a new *C. lacustris* colony was added to the dish. Each dish was assigned one of the same four salinities as used in the hydroid colony growth study (6, 12, 18, and 24‰). To reduce any effects caused by a sudden change in salinity, the water was changed slowly over several hours using the same procedure as for growth experiments on *C. lacustris* (see page 11).

Thirty-six hours after the final water change, all spawn masses were collected from the four dishes. The adult nudibranchs were returned to the culture aquarium while six spawn masses were randomly selected from each salinity. Each spawn mass was each placed in its own dish with approximately 125 ml of water at the same salinity as the dish from which it has been removed resulting in six replicate spawn masses at each treatment salinity. As all of the adult *Tenellia adspersa* died in the 6‰ salinity dish and had produced only a single, malformed spawn mass, spawn masses from the 12‰ dish were used to provide the replicates at 6‰. The number of eggs per spawn mass and the stage of development of each of the masses was recorded.

Every day, each spawn mass was examined under a dissecting microscope to record the stages of development. On the fifth day, as veliger larvae began to hatch and metamorphose, a colony of *C. lacustris* was added to each dish that still contained viable embryos. The volume of water in each dish was also doubled, and an air hose was placed in each dish to assure adequate aeration. Following metamorphosis, the number of eggs that did not complete development was

recorded. On the twelfth day, the experiment was concluded by counting the number of surviving juvenile nudibranchs in each dish.

To determine the fecundity of *Tenellia adspersa* under these same four salinities, a new experiment was begun at the conclusion of the development experiment using the surviving juvenile nudibranchs from the 18‰ and 24‰ salinities. (No juvenile nudibranchs survived at the other two salinities.)

Twenty-four individuals were randomly selected from the 33 nudibranchs in the 18‰ treatment (Group A) and from the 37 nudibranchs in the 24‰ treatment (Group B). Pairs of nudibranchs were randomly assigned to the same four treatment salinities as had been used previously. There were three pairs per salinity from each group resulting in a two-factor experimental design as illustrated in Table 2.

Table 2. Two-factor design for the *Tenellia adspersa* survival and fecundity experiment.

Treatment Salinity	Group A (Developed at 18‰)	Group B (Developed at 24‰)
6‰	3 replicate pairs	3 replicate pairs
12‰	3 replicate pairs	3 replicate pairs
18‰	3 replicate pairs	3 replicate pairs
24‰	3 replicate pairs	3 replicate pairs

Each pair was provided with one *C. Incustris* colony in a volume of approximately 250 ml of water with aeration. The water was changed every two weeks. The pairs of nudibranchs were monitored. As spawn masses were produced, the number of eggs per mass was recorded, and the masses were removed from the dish. The date of death for each individual nudibranch was

recorded. By the 27th day, all of the nudibranchs had either died or ceased producing new spawn masses so the experiment was ended.

All data were analyzed using StatView. As the initial number of eggs in a spawn mass may, in part, determine the number completing development, this factor was examined for inclusion as a covariate in an analysis of covariance (ANCOVA) model. The results, however, indicate that it is not meaningful to include (see page 35). Therefore, a one-factor analysis of variance (ANOVA) was used to compare the number of veliger larvae and juvenile nudibranchs surviving from the spawn masses at different salinities. The data measuring fecundity at the different salinities were compared using a two-factor ANOVA to include both the salinity used in the experiment and the salinity in which the nudibranchs had initially been raised. Post hoc comparisons of means were performed using the Tukey-Kramer test (SAS Institute, 1998).

RESULTS

Fouling Panel Study

The four stations differed in temperature and salinity as would be expected for sites within an estuary (Figure 3). The highest mean salinity (29.2‰) and the lowest mean temperature (14.2°C) occurred at Station 1 closest to the open ocean. Average salinities decreased and average temperatures increased further up the estuary. Station 2 had a mean salinity of 27.8‰ and a mean temperature of 16.4°C. Station 3 had mean values of 23.7‰ and 19.4°C while at Station 4, the salinity was the lowest (mean = 13.1‰) and the temperature was the highest (mean = 20.2°C).

The four sites also differed greatly in the amount of variability in both the salinity and temperature conditions as indicated in Figure 3. Conditions at Station 1 were the least variable. Standard deviations for the salinity and temperature values were 1.2 and 3.2, respectively. These increased to 1.3 and 3.8, respectively, at Station 2, and to 5.7 and 5.7 at Station 3. Station 4 was the most variable in its conditions with standard deviations of 8.2 for salinity and 6.0 for temperature. It should also be noted that on one occasion at Station 3 and twice at Station 4, the salinity measured 0‰. Temperatures increased slightly in the early summer and decreased in the late summer and fall. Salinity remained level or slightly decreased over the four-month period at each station.

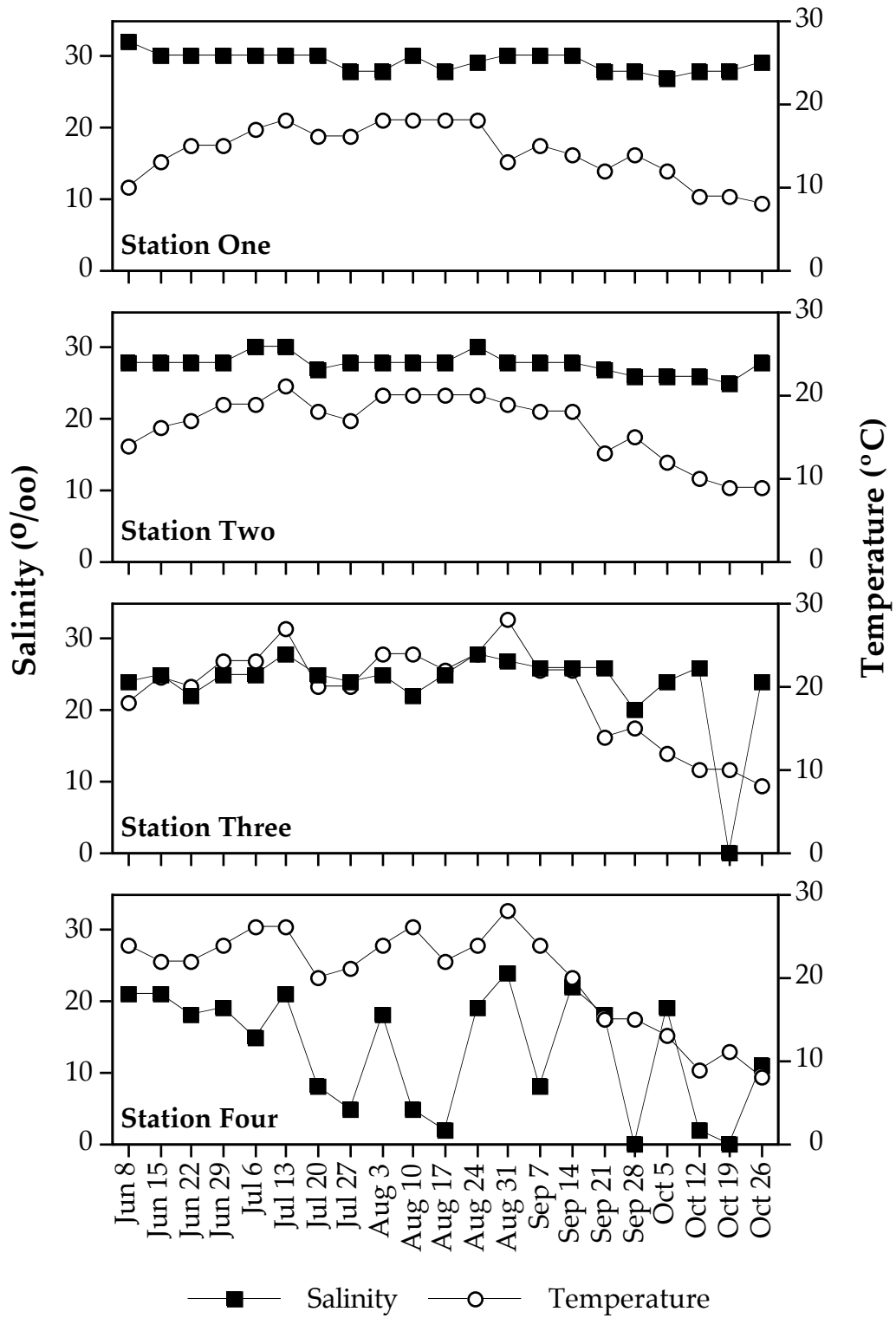


Figure 3. Salinity and temperature at each station for the fouling panel study.

A total of 42 species of invertebrates were identified upon examination of the fouling panels. The species were divided evenly between colonial organisms and solitary species (Figure 4 and Figure 5). The highest number of species, 28, was found at Station 1 with 25 at Station 2, 20 at Station 3, and 9 at Station 4.

The hydroid species recruiting to the panels are of particular interest. A total of eight hydroid species were observed. The gymnoblastic hydroids that were found were *Tubularia crocea*, *T. indivisa*, *T. larynx*, and *Eudendrium* sp. These species have been grouped together as *Tubularia* spp. for analysis purposes as they are structurally and ecologically similar. *Tubularia* spp. were most frequently observed at Stations 1 and 2 in July, but they were also seen in the other months at these location. Only rarely were *Tubularia* spp. found at Stations 3 or 4 (Figure 6).

Four species of calyptoblastic hydroids also recruited to the panels. These were *Campanularia flexulosa*, *C. gelatinosa*, *Gonothyraea lovenii*, and *Obelia commiseralis*. As with the gymnoblastic hydroids, these species are very similar and often difficult to distinguish, especially when the colonies are very small. These have been grouped together as *campanularid hydroids* for analysis. The recruitment of the campanularid hydroids peaked in June. They were only found sporadically during the remaining months. Campanularid hydroids were found at Stations 1, 2, and 3 in similar numbers (Figure 6).

The hydroid *Cordylophora lacustris* was conspicuous by its absence from all of the fouling panels. *C. lacustris* was expected to be found at least at Station 4. In fact, a sexually reproductive colony of *C. lacustris* was observed within 50 meters upstream of the fouling panel array at this location during June.

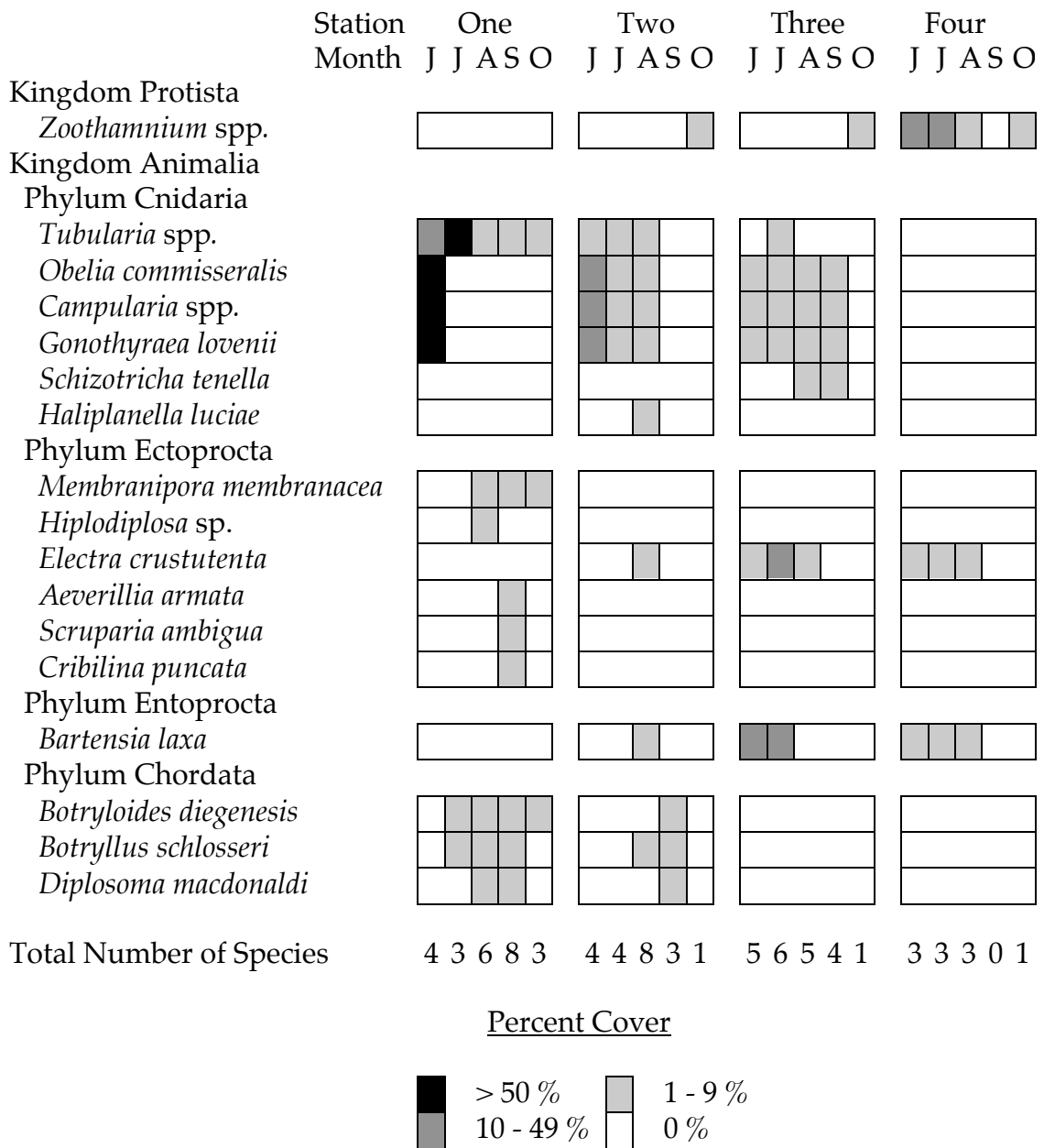
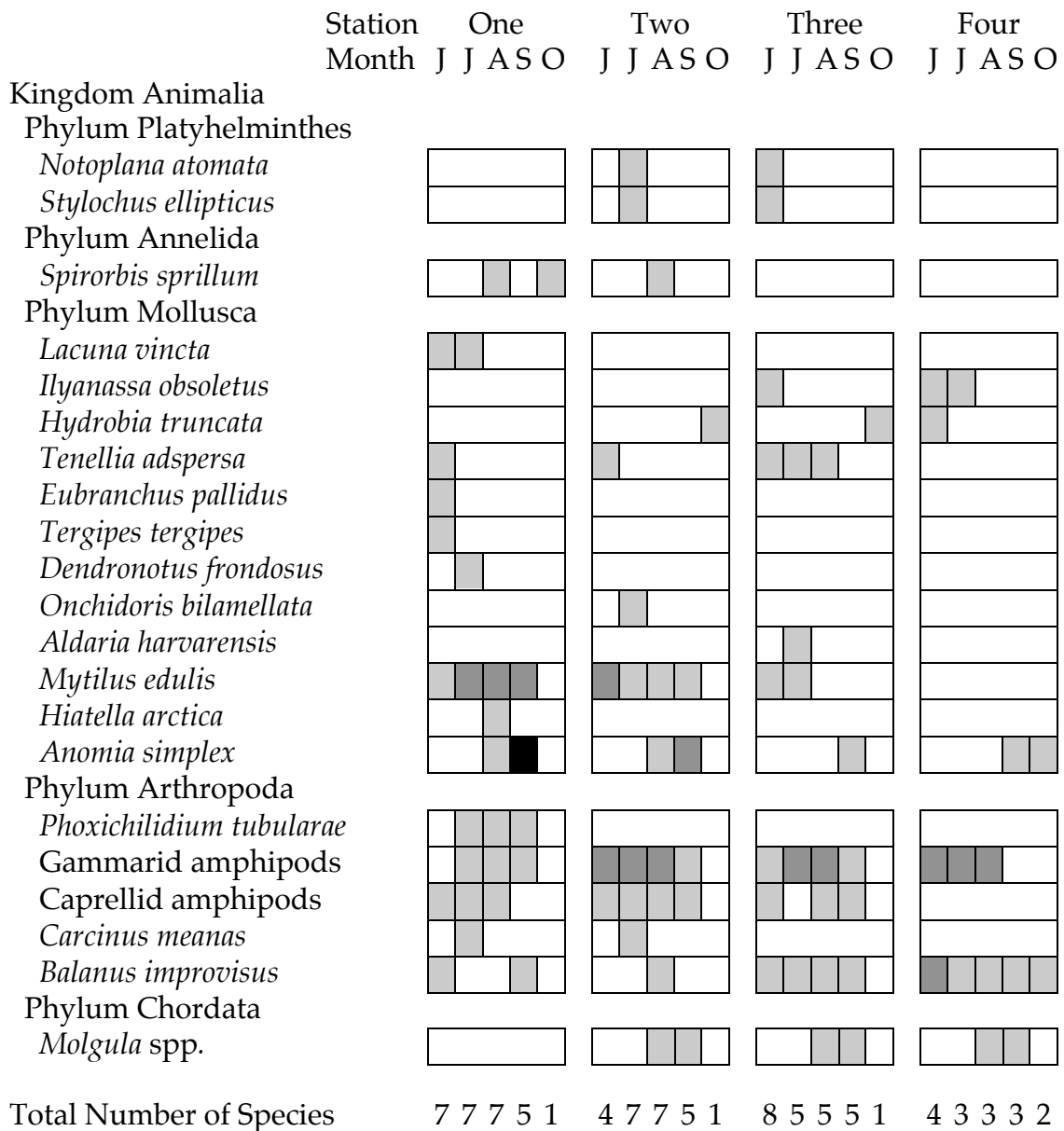


Figure 4. Distribution of colonial invertebrates at each station during the five months of the fouling panel study. Abundance data taken from the panels which had been exposed for four weeks. Total Number of Species is the number of species found at a station in a given month.



Number of Individuals

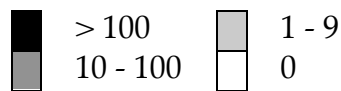


Figure 5. Distribution of solitary invertebrates at each station during the five months of the fouling panel study. Abundance data taken from the panels which had been exposed for four weeks. Total Number of Species is the number of species found at a station in a given month.

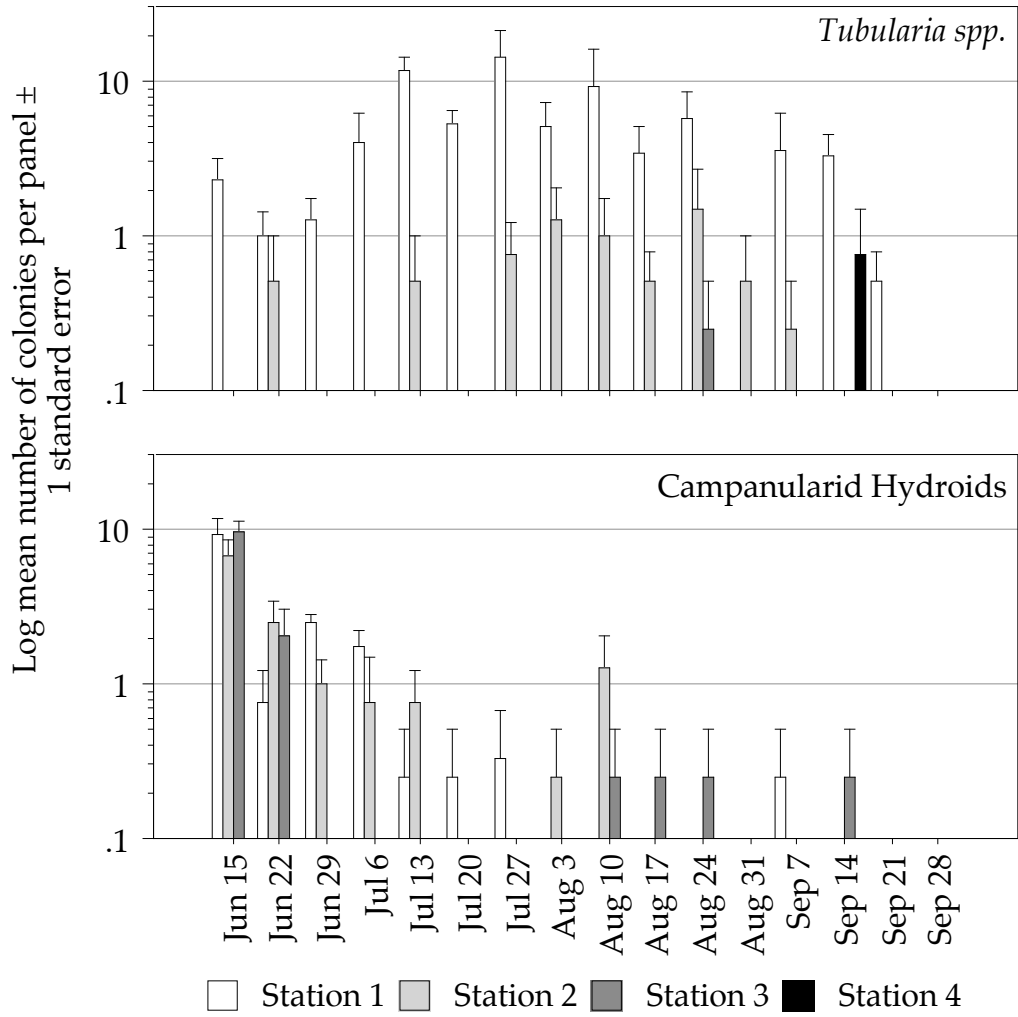


Figure 6. Weekly recruitment of hydroids at each station during the fouling panel study

The abundances of both *Tubularia* spp. and the campanularid hydroids were correlated with the abundances of other species at certain times and locations. The number of juvenile mussels, *Mytilus edulis*, significantly correlated to the percent cover of *Tubularia* spp. at Station 1 in June, July, and September. Similarly, *M. edulis* and campanularid hydroids were significantly correlated in June at Station 1. Table 3 summarizes the correlation coefficients for these relationships at Stations 1 and 2. The data regarding these species in many cases were insufficient for meaningful analysis including all months at the other stations.

Table 3. Pearson correlation coefficients of the percent cover of hydroids with the number of mussels at Stations 1 and 2 for each month.

	Station 1		Station 2	
	<i>Tubularia</i>	Campanularid	<i>Tubularia</i>	Campanularid
June	.54*	.50*	.24	NR
July	.90***	NR	NR	NR
August	.26	NR	NR	NR
September	.56**	NR	NR	NR
October	NR	NR	NR	NR

(* \square $p < 0.01$, ** \square $p < 0.001$, *** \square $p < 0.0001$, NR \square no results)

The abundances of campanularid hydroids and the barnacle, *Balanus improvisus*, also were correlated. Again, limited data prevents analysis in all but two cases, Station 3 in both June and August. In both cases, a strong positive correlation exists (Table 4). No correlations were found between *Tubularia* spp. and *B. improvisus* at any station in any month. Low abundances of other groups of species such as colonial tunicates, bryozoans, tube-dwelling annelids, and other bivalve molluscs do not allow for useful comparisons to be made.

Table 4. Pearson correlation coefficients of the percent cover of hydroids with the number of barnacles at Station 3 for each month.

	Station 3	
	<i>Tubularia</i>	Campanularid
June	NR	.57**
July	NR	NR
August	NR	.69***
September	NR	NR
October	NR	NR

(** \square $p < 0.001$, *** \square $p < 0.0001$, NR \square no results)

A variety of hydroid predators was observed on the panels. Predators on *Tubularia* spp., the nudibranch *Dendronotus frondosus* and the pycnogonid *Phoxichilidium tubularae*, were seen only at Station 1. Both species were most abundant in July corresponding to the peak abundance of *Tubularia* spp. The predators were first seen in the second week and rise in number as *Tubularia* spp. becomes more dense to a high of 7.33 per panel by week four (Figure 7).

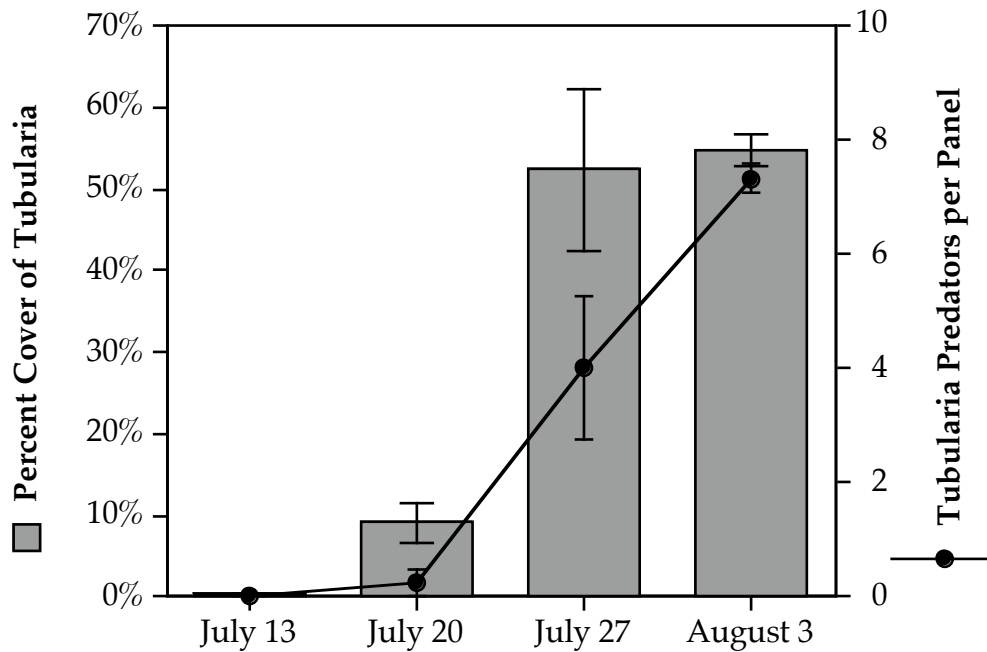


Figure 7. Abundances of *Tubularia* spp. and its predators at Station 1 in July. Error bars show ± 1 standard error.

Predators on the campanularid hydroids included three nudibranch species, *Eubranchus pallidus*, *Tergipes tergipes*, and *Tenellia adspersa*. The first two of these species were found only at Station 1 in June. *T. adspersa* was seen at Stations 1, 2 and 3 in the months of June, July, and August. Numerous spawn masses of *T. adspersa* were observed as well.

Examining the sequences of panels over the four weeks in June showed a similar relationship between the campanularid hydroids and *T. adspersa* to the relationship seen between *Tubularia* spp. and its predators. The abundance of *T. adspersa* increased with the density of the hydroids. No nudibranchs were found after one week, but they appeared after two weeks at Station 3, after three weeks at Station 1, and after four weeks at Station 2. The number of spawn masses on the panels followed the same pattern. Of particular interest is the pattern seen at Station 3 where the number of *T. adspersa* increased along with their hydroid prey during the first three weeks to a high of 2.7 nudibranchs and 12.3 spawn masses per panel, but by the fourth week, almost no living hydroids were found. The fourth week panels, however, still had the dead perisarcs of hydroid colonies along with fewer nudibranchs and spawn masses than the previous week (Figure 8).

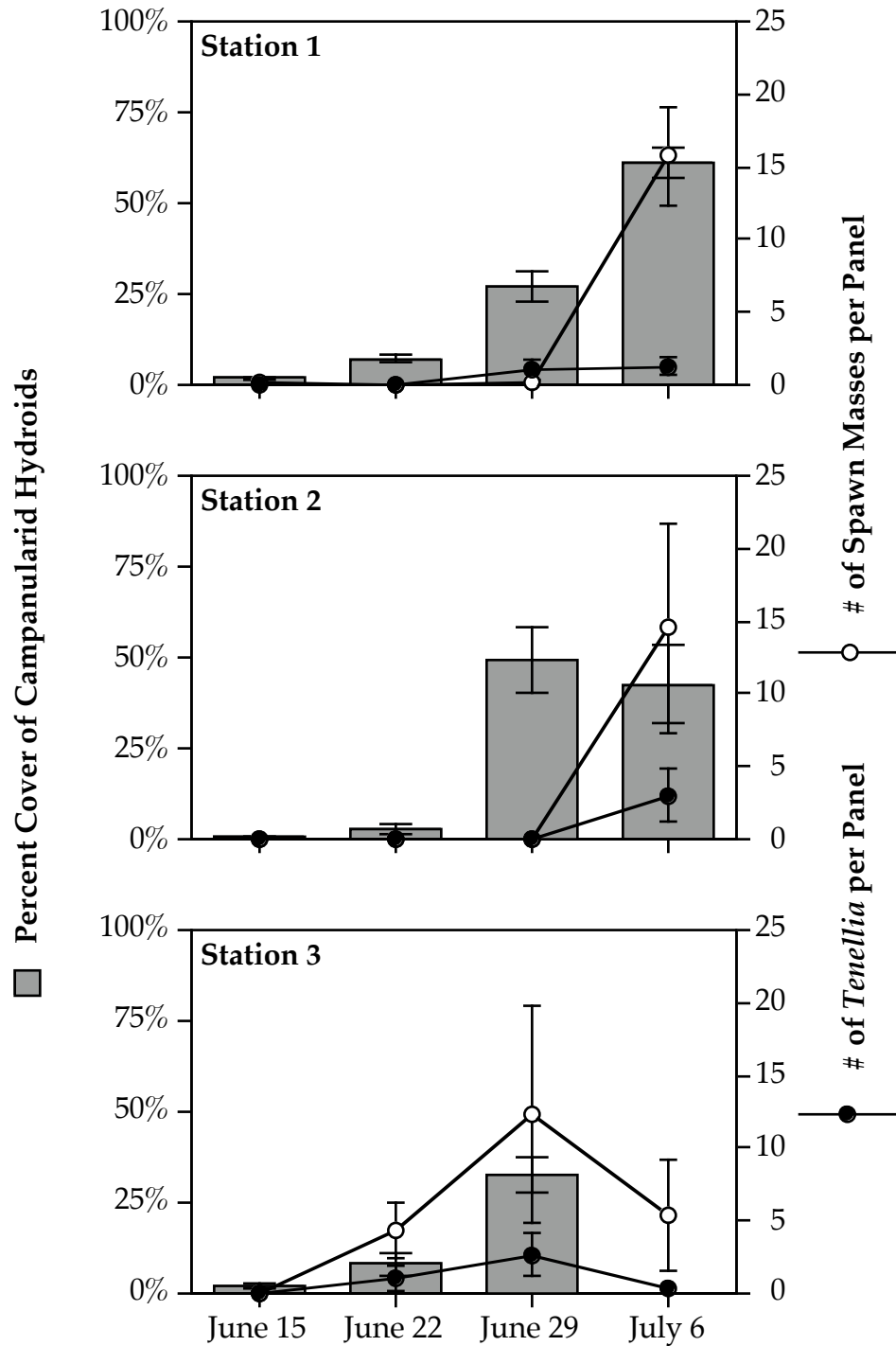


Figure 8. Abundances of campanularid hydroids, *Tenellia adspersa*, and *T. adspersa* spawn masses at Stations 1, 2, and 3 in June. Error bars show ± 1 standard error.

Field Surveys

The field surveys to locate *Cordylophora lacustris* and *Tenellia adspersa* within the Great Bay Estuary system revealed a consistent pattern. *C. lacustris* was only seen in the upper portions of the rivers leading into the estuary while *T. adspersa* was found primarily in the mid to low regions (Figure 9).

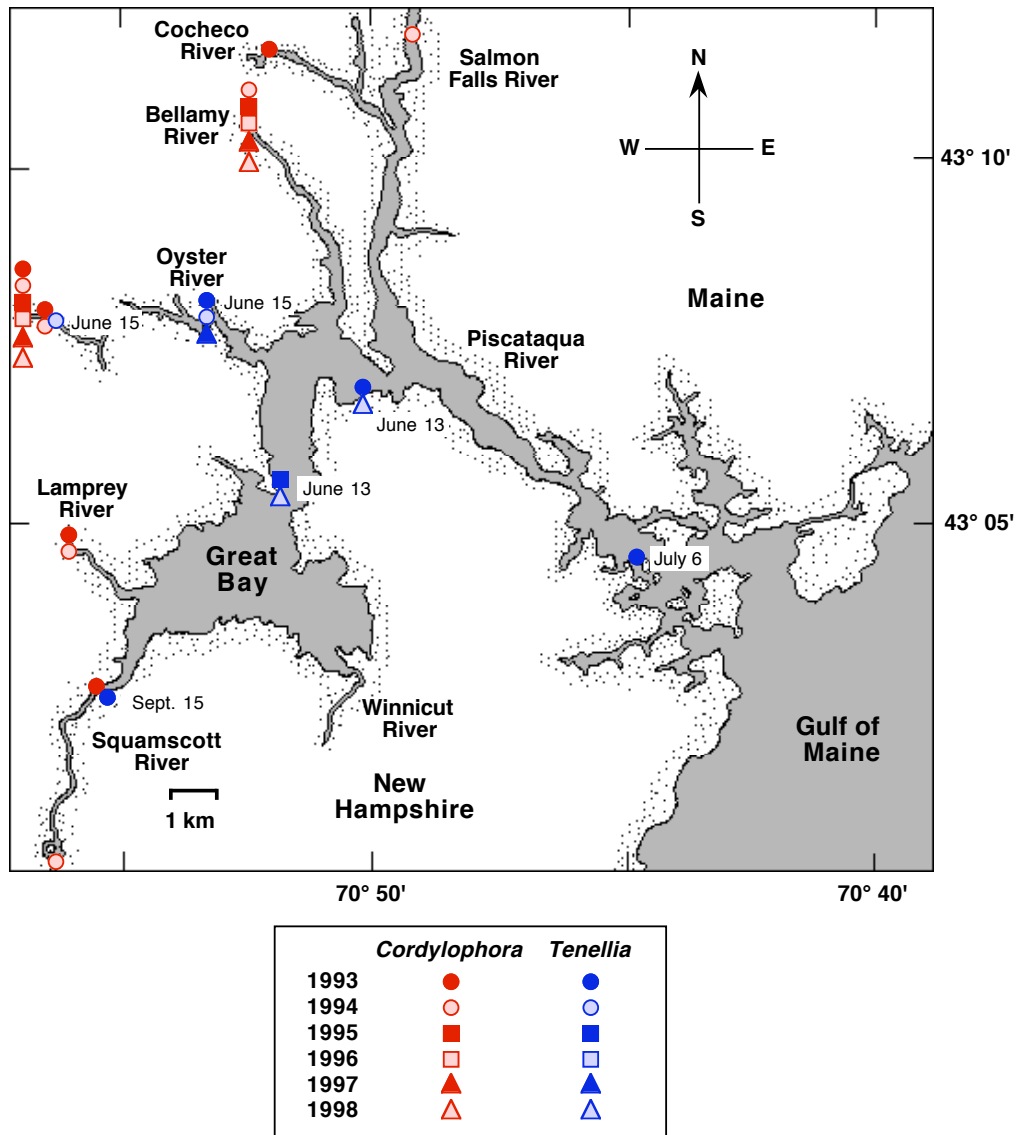


Figure 9. Map of the Great Bay Estuary system showing where *Cordylophora lacustris* and *Tenellia adspersa* were found in 1993 to 1998. Dates shown are the earliest date on which *T. adspersa* was found at that location.

C. lacustris colonies were found in all of the rivers of the Great Bay Estuary system that were examined. The salinity measured in the vicinity of the hydroids was usually quite low and often measured 0‰. Only in the mid to late summer were higher salinities seen, and the hydroids were in poor condition in these cases.

Although colonies were found in the Lamprey River, Cocheco River, and Squamscott River, these hydroids were on floating docks that were subsequently removed. The *C. lacustris* seen in the Salmon Falls River was growing on bridge pilings that were very difficult to access even at the lowest tides. In these cases, long term monitoring was not possible. The colonies in the Bellamy River and Oyster River were growing on natural rock substrate. These populations persisted from May 1994 through at least August 1998.

Observations of colonies in these two locations reveal that *C. lacustris* overwinters as small amounts of stolon tissue with no feeding polyps. A colony that appeared to be completely dead in early May was observed to regenerate into a colony with numerous feeding polyps in only a few weeks time. The colonies persisted throughout the summer, but as salinities and temperature rose and the flow of water declined in the mid summer, the condition of the colonies deteriorated with missing polyps and a high degree of slit and other debris covering the hydroids' perisarc. Table 5 details observations of the colonies throughout 1994. Similar patterns were observed in subsequent years.

Nudibranchs were found on few occasions and in fewer locations than the hydroids. With the exception of the *T. adspersa* seen in the upper portion of Oyster River, at a salinity of 8‰, all of the locations where *T. adspersa* were

Table 5. Observations of *Cordylophora lacustris* colonies.

Location	Date	Salinity (‰)	Temperature (°C)	Notes
Bellamy River	5/4/94	0	14	Undersides of rocks, few to no polyps, strong water flow
	5/24/94	0	15	Many polyps
	6/15/94	0	25	Sexually reproductive
	7/20/94	18	26	Poor condition, heavily silted, low water flow
Oyster River	5/4/94	0	12	On rock surfaces, no polyps
	6/15/94	8	21	Sexually reproductive, <i>T. adspersa</i> present
	7/20/94	25	25	Poor condition, heavily silted

found were in the mid to low regions of the estuary including Great Bay, Little Bay, and near the mouth of the Piscataqua River (Figure 9). In these locations, *T. adspersa* were found feeding on various species of campanularid hydroids. Only the nudibranchs from the upper Oyster River and from the Squamscott River were found feeding on *C. lacustris*. Unlike *C. lacustris*, the populations of *T. adspersa* were not persistent over the long term. For example, locations where nudibranchs could be found in the late summer usually had no nudibranchs present the following spring. *T. adspersa* were never found earlier than mid-June.

Cordylophora Colony Growth

Cordylophora lacustris colonies grew at different rates at the four salinities tested, but all of the colonies did increase in their number of polyps, stolon length, and upright height. As measured both by the number of feeding polyps per colony and the total stolon length, the colonies at 6‰ grew the fastest

followed by those at 12‰, 18‰, and 24‰ (Figure 10 & Table 6).

One colony from the 6‰ treatment was damaged during handling on or around the ninth day of the experiment. Although the colony did continue to grow, it did so at a much slower rate. The data from this colony are clear statistical outliers and were removed before all analyses were performed.

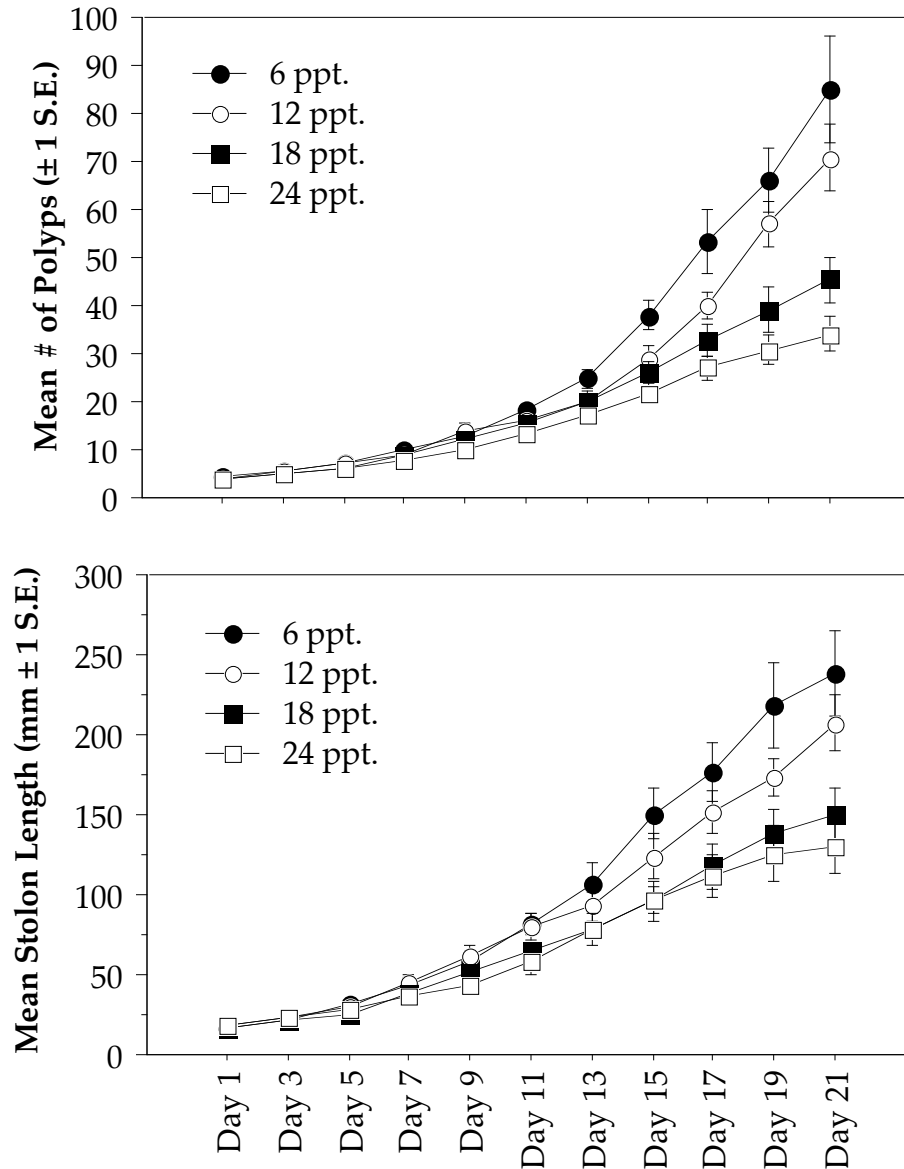


Figure 10. Growth of *Cordylophora lacustris* at four salinities as measured by the number of polyps (top) and the length of the stolon (bottom).

Table 6. Size and growth rates of *Cordylophora lacustris* colonies at 4 different salinities. Polyp and length values are means \pm 1 standard error at 20 days. Doubling Time is the time for the number of polyps in a colony to double. It is calculated as $T = \ln 2 / k$ where k is the exponential growth rate in $N_t = N_0 e^{kt}$.

Salinity	Number of Polyps	Total Stolon Length (mm)	Length of Longest Upright (mm)	Doubling Time (Days)
6‰	85.2 \pm 11.1	238.7 \pm 26.9	22.8 \pm 2.1	4.7
12‰	70.8 \pm 6.8	207.5 \pm 17.7	24.3 \pm 2.1	5.0
18‰	45.3 \pm 4.9	150.5 \pm 15.5	12.3 \pm 3.0	5.7
24‰	34.0 \pm 3.7	129.8 \pm 16.9	9.5 \pm 1.6	6.3

Repeated measures analysis of variance (ANOVA) showed that salinity, time, and the interactive effect between the two were all highly significant for both the number of polyps and the total stolon length (Table 7 & Table 8). The colonies grown at 6‰ had more polyps than those grown at 18‰ and 24‰, and the colonies grown at 12‰ also had more polyps than the colonies from the 24‰ treatment (Scheffe's F test, $p < 0.05$). For the stolon length measurements, only the hydroids from 6‰ and 24‰ differed (Scheffe's F test, $p < 0.05$).

Table 7. Repeated measures ANOVA for the effect of salinity on the number of polyps of a *Cordylophora lacustris* colony.

	DF	Sum of Squares	Mean Square	F-Value	P-Value
Salinity	3	6388.677	2129.559	9.488	.0005
Subject (Group)	19	4264.588	224.452		
Time	10	79928.630	7992.863	236.436	<.0001
Time * Salinity	30	10210.091	340.336	10.067	<.0001
Time * Subject (Group)	190	6423.079	33.806		

Table 8. Repeated measures ANOVA for the effect of salinity on the length of the stolon of a *Cordylophora lacustris* colony.

	DF	Sum of Squares	Mean Square	F-Value	P-Value
Salinity	3	51259.129	17086.376	4.975	.0103
Subject (Group)	19	65251.289	3434.278		
Time	10	783539.572	78353.957	202.936	<.0001
Time * Salinity	30	52155.907	1738.530	4.503	<.0001
Time * Subject (Group)	190	73359.338	386.102		

Colonies grown at lower salinities also produced longer uprights (Figure 11 & Table 6). The longest uprights of colonies at the two lower salinities were longer than those of the two higher salinities (Scheffe's F test, $p < 0.05$).

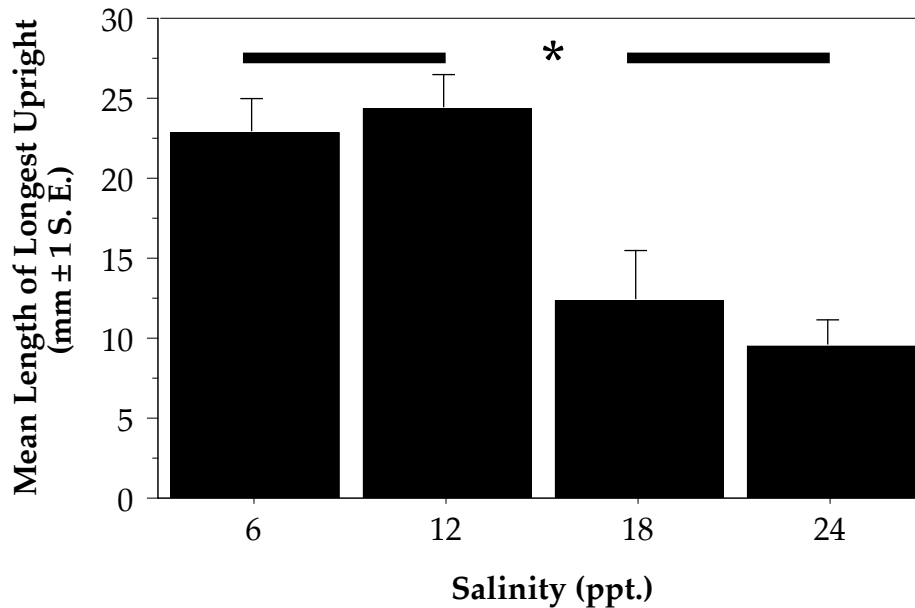


Figure 11. Effect of salinity on the maximum height of *Cordylophora lacustris*. (* \square significantly different, $p < 0.05$; line \square not significantly different)

The seven colonies not used experimentally also grew over the course of the 20 days. These colonies had 40.6 ± 11.0 polyps compared to 57.7 ± 5.3 polyps for all of the colonies used in the experiment. This difference was not significant (ANOVA: $F_{1,28} = 2.3$, $p = 0.14$). The doubling time for those colonies was 6.5 days compared to 5.3 days for the experimental colonies.

Cordylophora Field Trial

Table 9 lists the complete results from the field trial in which *Cordylophora lacustris* colonies were placed at three locations within the Great Bay Estuary. Unfortunately, one colony at Station 2 and two colonies at Station 4 were lost so the data is limited. Note that adult *Tenellia adspersa* or their egg masses were found on colonies from Station 2 but no where else. Colonies at Station 3 were in very poor condition with much of the original colony gone, but there was no evidence of nudibranch predators. This site was very muddy, and a great deal of mud was found on the recovered slides.

Table 9. Results from the *Cordylophora lacustris* field experiment.

Location	Replicate 1	Replicate 2	Replicate 3
Station 2	Colony severely damaged, no polyps <i>T. adspersa</i> present	Colony severely damaged, no polyps <i>T. adspersa</i> present	Lost
Station 3	Colony severely damaged, lots of mud on colony	Colony severely damaged, lots of mud on colony	Colony severely damaged, lots of mud on colony
Station 4	Colony damaged in some portions with no polyps left, other portions have new growth and are sexually reproductive	Lost	Lost

Tenellia Growth and Reproduction

Unlike *Cordylophora lacustris*, *Tenellia adspersa* developed and grew distinctly differently at the lower and higher salinities. Adult nudibranchs all died within 36 hours of the salinity being lowered to 6‰ from the initial concentration of 15‰, and only a single, malformed spawn mass was produced. The spawn masses that were taken from the 12‰ treatment and transferred to 6‰ to provide replicates for that treatment fared no better. Only a few developed beyond the single cell stage, and all ceased dividing and began to disintegrate within 48 hours. Spawn masses raised at 12‰ did develop further than those at lower salinity. In four out of the six replicates, embryos at least reached the early veliger stage by the fourth or fifth day. Only a single embryo, however, formed a complete veliger that metamorphosed into a juvenile nudibranch on day eight, and the juvenile did not survive more than two days beyond metamorphosis.

At the higher salinities, 18 and 24‰, five out of the six spawn masses had at least some of their embryos complete development into surviving juvenile nudibranchs. These embryos developed faster compared to those at 12‰ with the veliger stage being reached around day three or four and metamorphosis taking place, on average, by the seventh day. On average, 77.7% and 78.8% of the eggs at 18‰ and 24‰, respectively, reached the veliger stage. A total of 39 juvenile nudibranchs at 18‰ and 43 juveniles at 24‰ completed metamorphosis and survived to become adults, averages of 32.1% and 43.3%, respectively. The box plots in Figure 12 summarize the results for all salinities. Note that in all treatments, at least one spawn mass failed to develop.

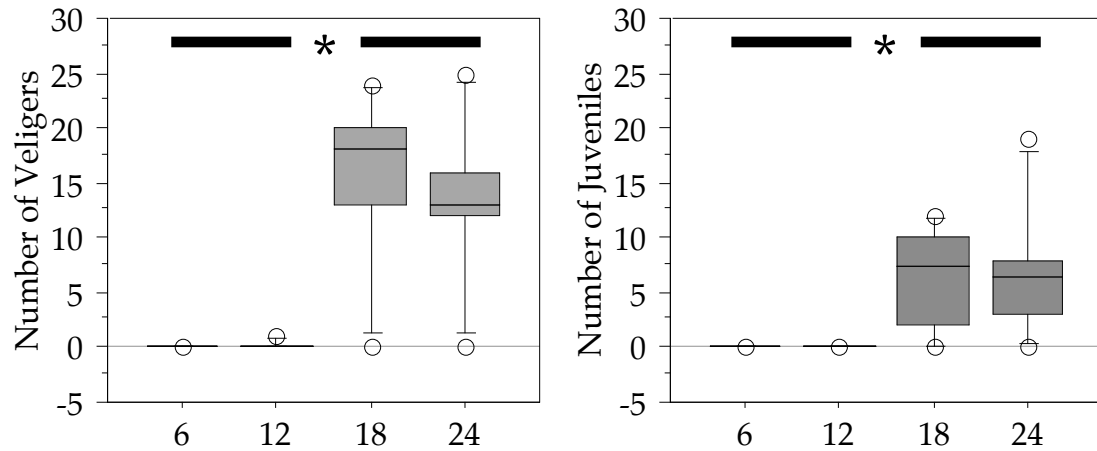


Figure 12. Box plots showing the number of veligers and juvenile *Tenellia adspersa* surviving development at 6, 12, 18, and 24‰. (* □ significantly different, $p < 0.05$; line □ not significantly different)

Analysis of variance tests indicated a highly significant effect of salinity for both the number of eggs developing to the veliger stage (ANOVA: $F_{3,20} = 12.2$, $p \leq 0.0001$) and the number of surviving juveniles (ANOVA: $F_{3,20} = 5.8$, $p = 0.005$). The results from the two lower salinities differed from those at the two higher salinities in both cases with no difference between the two lower or between the two higher salinities (Tukey-Kramer: $p \geq 0.05$).

The fecundity of *T. adspersa* also varied with salinity. The salinity at which the adult nudibranchs were kept (adult salinity) and the interaction between this salinity and the salinity at which the nudibranchs had originally completed their development (developmental salinity) both had significant effects on the number of spawn masses and total number of eggs that an individual *T. adspersa* produced in its lifetime. The developmental salinity alone was not a significant factor (Table 10 & Table 11).

Table 10. Two factor ANOVA for the effect of salinity on the number of spawn masses produced by an individual *Tenellia adspersa*.

	DF	Sum of Squares	Mean Square	F-Value	P-Value
Adult Salinity	3	2698.031	899.344	9.652	.0007
Developmental Salinity	1	231.260	231.260	2.482	.1347
Adult * Developmental	3	2198.365	732.788	7.864	.0019
Residual	16	1490.833	93.177		

Table 11. Two factor ANOVA for the effect of salinity on the number of eggs produced by an individual *Tenellia adspersa*.

	DF	Sum of Squares	Mean Square	F-Value	P-Value
Adult Salinity	3	8475256	2825085	23.620	<.0001
Developmental Salinity	1	20126	20126	.168	.6871
Adult * Developmental	3	3183948	1061316	8.873	.0011
Residual	16	1913689	119606		

Table 12 lists the mean values for the number of spawn masses and the total number of eggs produced by *T. adspersa* under each set of conditions. The group of nudibranchs that were transferred from the developmental salinity of 24‰ to an adult salinity of 6‰ clearly stands out from the other groups. Within this treatment, one pair of nudibranchs died before any reproduction took place, and the remaining pairs produced far fewer spawn masses and eggs than the others did. The number of spawn masses produced was fairly consistent across all other groups. Egg production exhibits a trend to increase with the adult salinity for the nudibranchs from the developmental salinity of 24‰, whereas

the ones from the developmental salinity of 18‰ show lower fecundity at 6‰ and equivalent egg production at the three higher salinities (Figure 13).

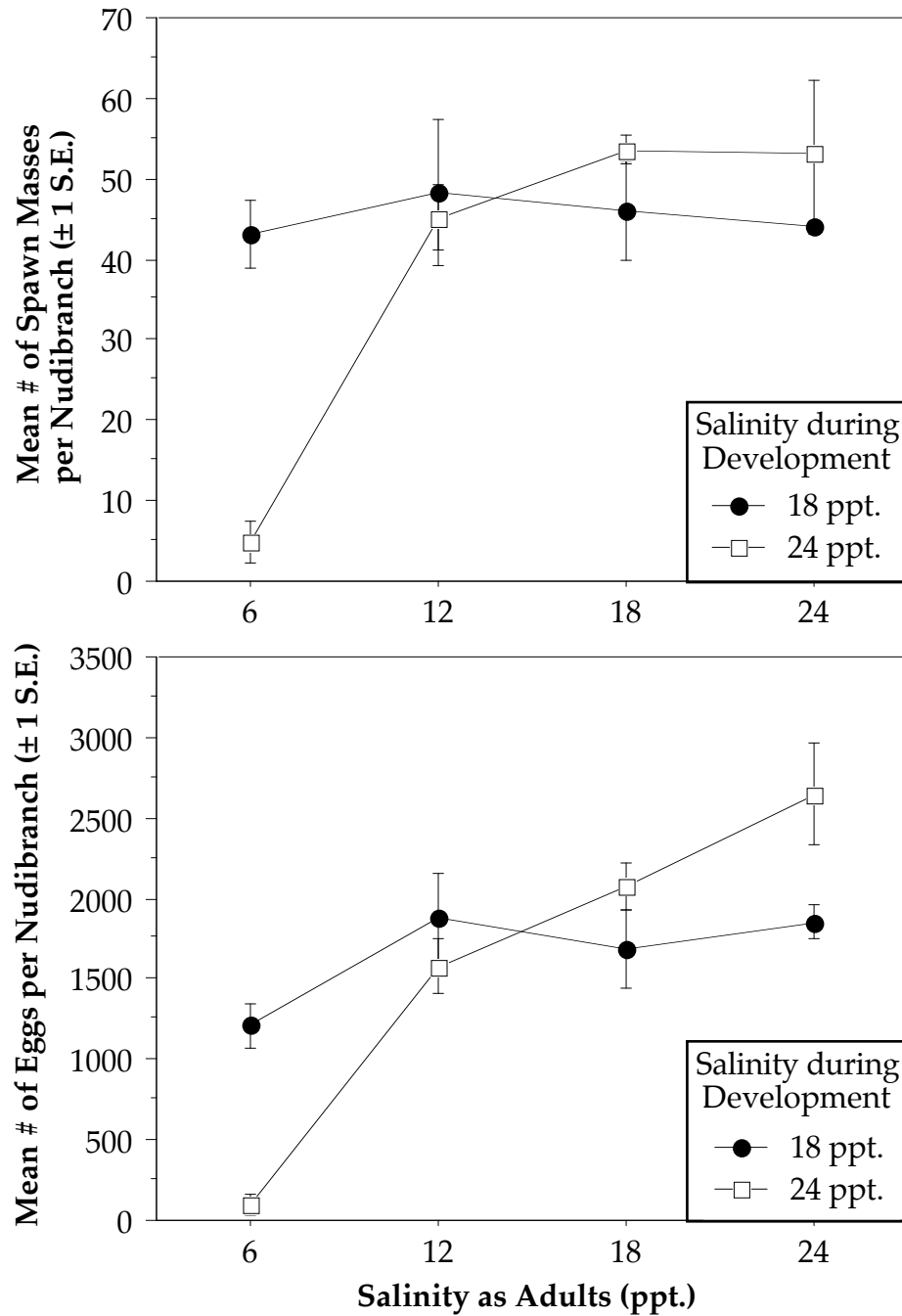


Figure 13. Effects of salinity on the fecundity of *Tenellia adspersa* as measured by the number of spawn masses and number of eggs produced by each nudibranch.

Table 12. Observed fecundity measures for *Tenellia adspersa* with respect to developmental salinity and adult salinity. Values are means \pm 1 standard error.

Adult Salinity	Developmental Salinity			
	18‰		24‰	
	Spawn Masses	Eggs	Spawn Masses	Eggs
6‰	43.2 \pm 4.2	1213 \pm 136	4.8 \pm 2.6	93 \pm 66
12‰	43.3 \pm 9.0	1879 \pm 270	45.2 \pm 3.8	1577 \pm 174
18‰	46.0 \pm 6.3	1685 \pm 245	53.5 \pm 1.8	2080 \pm 147
24‰	44.0 \pm 0.8	1852 \pm 106	53.2 \pm 9.1	2648 \pm 317

T. adspersa in the 6‰ and 12‰ treatments showed signs of shock from the initial decrease in salinity. When a *C. lacustris* colony was added for food, nudibranchs at the higher salinities immediately approached the hydroids. Individuals at the lower salinities did not, and they exhibited little movement from the location where they were placed in the dish for approximately the first hour.

On average, the nudibranchs in the study lived to an age of 36 days (\pm 1.0). There was, however, a high degree of variability with life spans ranging from 21 days to 42 days. Adult salinity, developmental salinity, and the interaction between the two all had significant effects on the life span of the nudibranchs (Table 13). The shortest-lived group were those nudibranchs that were transferred from a developmental salinity of 24‰ to an adult salinity of 6‰, but those transferred from 18‰ to 6‰ were one of the longest-lived groups (Figure 14). The fact that nudibranchs at an adult salinity of 24‰, a group with high fecundity, were one of the shortest lived groups suggests that there might be an inverse relationship between the number of eggs a nudibranch produced and the

length of its life span. Regression analysis, however, does not support this hypothesis (Linear regression: $r^2 = 0.08$).

Table 13. Two factor ANOVA for the effect of salinity on the life span of *Tenellia adspersa*.

	DF	Sum of Squares	Mean Square	F-Value	P-Value
Adult Salinity	3	321.562	107.188	3.736	.0186
Developmental Salinity	1	196.021	196.021	6.833	.0126
Adult * Developmental	3	459.896	153.299	5.344	.0034
Residual	40	1147.500	28.687		

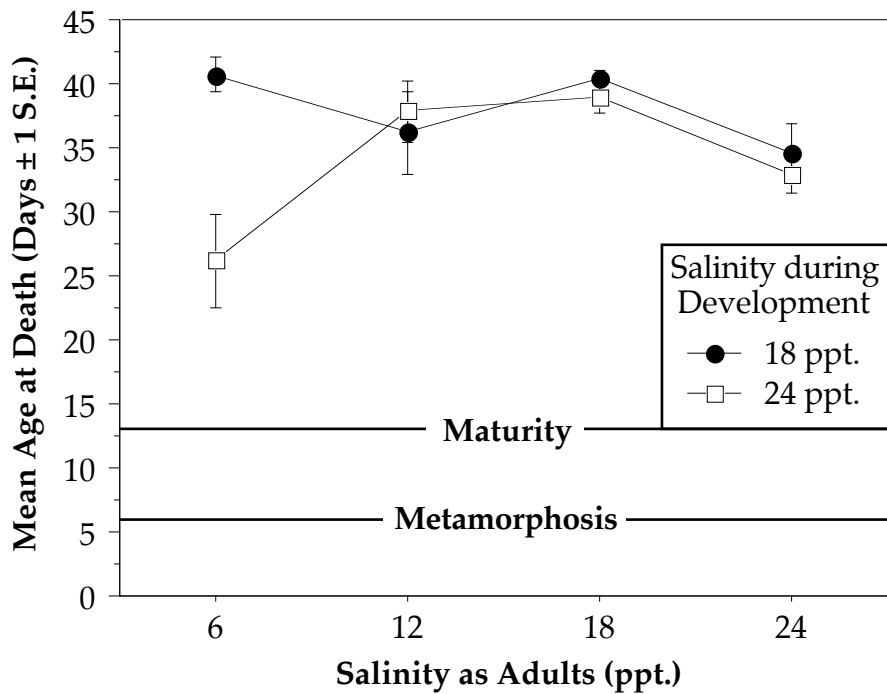


Figure 14. Life span of *Tenellia adspersa* at different salinities.

DISCUSSION

Population Distributions and Dynamics

The distribution of *Cordylophora lacustris* within the Great Bay Estuary system displays a consistent pattern. The hydroid is only found within the rivers that flow into the estuary system and often is found in the most upstream tidal regions of these rivers (Figure 9). Published descriptions of the habit of *C. lacustris* consistently cite low salinity as characteristic (Gosner, 1971; Crocker, 1972; Pollack, 1998), and *C. lacustris* is the only known species of hydroid that lives in freshwater (Pennak, 1978). Although the salinity in areas where *C. lacustris* is found is usually low, under some circumstances, the salinity can be much higher than the usually cited 5‰. For example, in this study, colonies that were in locations with salinities at or close to 0‰ in the early summer where at salinities of 18‰ and 25‰ by the end of July. This coincided with a period of summer drought with temperatures 1.4°C and 1.7°C higher than normal for June and July, 1994, respectively (NCDC, 1999). Reduced flow of freshwater into the rivers allowed the salt water to penetrate further upstream.

C. lacustris colonies are persistent from year to year in locations where they have favorable conditions and stable substrate. Colonies in both the Oyster River and Bellamy River have been present for at least five years (Figure 9). Either the individual colonies themselves are able to persist for several seasons, or hydroid larvae are recruiting to the same location leading to a sustained population. Unfortunately, little is known about the recruitment of *C. lacustris*

larvae within the Great Bay estuary system. Although sexually mature hydroid colonies are regularly present, neither the fouling panel study described herein nor any other observations made during these studies provide data about the distribution and settlement of *C. lacustris* larvae. A study of the growth and reproduction of *C. caspia* colonies in Finland describes the settlement of larvae in the same area as the mature colonies. Recruitment occurred exclusively during the month of July with rates reaching as high as 200 settling larvae per square meter per day (Jormalainen et al., 1994). Considering my own observations and previous descriptions (Kinne, 1956; Jormalainen et al., 1994) of *Cordylophora* spp. colonies that had survived the winter as stolon tissue in a dormant phase, it is quite possible that both long term survival of colonies and replacement of colonies by new recruits are occurring simultaneously.

Unlike *C. lacustris*, the populations of the nudibranch *Tenellia adspersa* within the Great Bay Estuary system are much more dynamic. The results from both the fouling panel study (Figure 8) and the *C. lacustris* field trials (Table 9) show that *T. adspersa* can recruit to previously uninhabited hydroid colonies within only a few weeks. Like many aeolid nudibranchs, *T. adspersa* has a life history with short generation times and high reproductive output. This combination results in the ability to opportunistically take advantage of new food sources when they become available (Thompson, 1964; Clark; 1975; Harris et al., 1980). *T. adspersa* has the ability to utilize many different hydroid species as food (Clark, 1975). In fact, *T. adspersa* exhibits plasticity in the development and subsequent dispersal of offspring. When food supplies are plentiful, the nudibranch produces larger eggs that have an increased likelihood of metamorphosing in the egg capsule directly into benthic juveniles. Under

conditions of scarce food such as when a hydroid colony has been overwhelmed by nudibranch predation, the smaller eggs nearly all develop into lecithotrophic veligers that disperse in the plankton thus distributing the offspring to new food resources (Chester, 1996).

A consequence of the opportunistic nature of *T. adspersa* is that populations of the nudibranch are not stable over the long term. Locations where no nudibranchs are seen may have a substantial population a few weeks later, and locations where nudibranchs are abundant one month may not have any only a few weeks later. Chambers (1934) describes a population of *T. adspersa* in Barnegat Bay, NJ from which several hundred individuals were collected in mid-November only to have the entire population vanish two weeks later. Despite the volatility of the distribution, *T. adspersa* were found within a consistent range of the estuary. In most cases, the nudibranchs were present in the mid to low estuary (Figure 9). Only when salinities increased in the upper portions of the rivers did the nudibranchs penetrate into these regions. As with *C. lacustris*, this distribution of *T. adspersa* is consistent with previously published data (Rasmussen, 1944; Crocker, 1972; Clark, 1975; Harris et al., 1980).

Species Interactions

The distributions and population dynamics of both these species are important to understand when examining the larger issue of the distribution of all of the benthic organisms within the estuary. As shown by the fouling panel study, recruitment of species is staggered in time with the peaks in recruitment of some species coinciding while others do not (see Figure 4 & Figure 5). For example, campanularid hydroids and the barnacle *Balanus improvisus* both had

peaks in recruitment in the month of June while *Tubularia* spp. and *Mytilus edulis* recruitment were highest in July and August. This pattern means that new recruits will be interacting with both the new recruits of other species and with populations of already established species.

Coinciding patterns of recruitment such as the correlations seen here between hydroids and mussels and between barnacles and campanularid hydroids could be caused simply by a synchrony in the reproductive patterns of these species, or it may be an example of the presence of one species facilitating the recruitment of another. Settlement of *Mytilus edulis* larvae has been repeatedly shown to preferentially occur on substrates that have filamentous structure (Bayne, 1964; Seed; 1969; 1976; Dean and Hurd, 1980; Okamura, 1986). The filamentous structure of a hydroid colony may provide such a preferred substrate leading to facilitation. For example, Okamura (1986) described the hydroid *Tubularia crocea* and the barnacle *Balanus improvisus* facilitating the recruitment of mussels, and Dean and Hurd (1980) found facilitation of mussel recruitment by the hydroid *T. crocea* in conjunction with the tunicate *Molgula manhattensis*. The recruitment of solitary tunicates has also been shown to be facilitated by the presence of the hydroid *Obelia dichomata* (Standing, 1976). The correlations observed in this study might constitute another example.

On the other hand, hydroids can also prevent the recruitment of other species. The hydroids may prey on settling larvae, or a dense enough colony may physically block space preventing attachment. For example, both Standing (1976) and Harris and Irons (1982) found the presence of hydroids on fouling panels was negatively correlated with the abundance of barnacles. The barnacle in this study, *Balanus improvisus*, which was positively correlated with the

presence of campanularid hydroids, is a different species than those described in the previous studies. *Balanus improvisus* may behave differently, or these results may simply be synchronized reproductive and settlement patterns.

In the case of *C. lacustris*, since the hydroid was not present on any of the fouling panels, there is no direct evidence of it facilitating or inhibiting other species. There are, however, at least three species that are likely to interact with established *C. lacustris* colonies during settlement. The tunicate *Molgula* sp., the bivalve *Anomia simplex*, and the barnacle *Balanus improvisus* all recruited to the fouling panels at the Station 4 study site which was in the vicinity of established *C. lacustris* colonies. The structure of a *C. lacustris* colony provides a similar filamentous structure to that seen in other hydroid species. If it is this structural feature, and not a chemical or some other cue that induces preferential larval settlement to *Obelia* spp. or *Tubularia* spp., the same should apply to *Cordylophora* sp. My own observations of very dense *C. lacustris* colonies also suggest that a well-established population of *C. lacustris* can effectively occupy space and block other recruits.

The role *Tenellia adspersa* plays in these recruitment interactions is that of a predator which could potentially remove the hydroid colonies and thereby change any inhibition or facilitation of the recruitment of other species. Nudibranchs can overwhelm their hydroid prey leading to the removal of the hydroid colony (Harris, 1987). In comparing the predation rates of *T. adspersa* with the growth rates of *C. lacustris*, Chester (1996) concluded that hydroid colonies above 10 to 15‰ will be removed in two to three weeks after being colonized by *T. adspersa* while colonies at lower salinities may be able to survive predation. In this study, *T. adspersa* recruited to young campanularid hydroid

colonies. In approximately two weeks time, the nudibranchs were able to reduce the density of or eliminate the campanularid hydroids on the fouling panels (Station 2 and 3, respectively, on Figure 8).

Nudibranchs that feed on hydroid colonies either graze on the polyps or penetrate the perisarc and suck out the tissue inside (Nybakken & MacDonald, 1981; Lambert, 1991). *T. ādispersa* feeds in both fashions (Chester, 1996; personal observation). Even when predation is sufficient to remove all of the polyps or consume all of the hydroid tissue, the hydroid colony may still have effects on the recruitment of other organisms. If predation is limited to just the polyps, the colony can regenerate new polyps. If predation is more complete, reducing the colony to a point at which its stored resources are not sufficient to regenerate, the perisarc skeleton remains. The skeleton alone may provide the same preferred habitat for settling larvae, and as there are no feeding polyps to consume the larvae, it is possible that recruitment could even be higher in this situation.

Effects of Salinity on *Cordylophora* Growth

The laboratory study of the growth of *Cordylophora lacustris* reveals that this hydroid can survive and increase in size over a wide range of salinities. The hydroids did grow most rapidly both in terms of the production of new polyps and in terms of the extension of the colony's stolon at the lowest salinity tested, 6‰ (Figure 10 & Table 6). Under all conditions, the number of polyps increased exponentially with doubling times ranging from 4.7 days for the 6‰ group to 6.3 days for the 24‰ group. These results compare favorably to other studies. Fulton (1960) achieved a doubling time of 3 days using an optimal defined media instead of diluted seawater, and other studies by Fulton (1962) of the growth of

C. lacustris report doubling times ranging from 2.3 to 6.3 days with a mean of 3.0 days. Chester (1996) reports growth rates equivalent to doubling times ranging from 2.5 days at 5‰ to 4 to 5 days at 10, 15, and 20‰ to more than 17 days at 25‰. The growth rates seen in this study far exceed those seen by Kinne (1956; 1971); calculated doubling times based on his results range from 9.0 to 12.0 days.

The colonies at the two lower salinities also produced longer uprights than those at 18 and 24‰ (Figure 11). This fact is significant not only as another indicator of better growth in lower salinity environments but also because the uprights branch as they increase in length. Each side branch will bear an additional polyp. The net result is a more dense colony with more feeding polyps reaching further off the substrate. Therefore, salinity may also be altering the form of the colony, which may lead to other effects such as changes in water flow around and through the colony. Changes in the structure of colonies at different salinities have been previously reported (Kinne, 1971).

It is of note that the colonies used in the experimental treatments as a group grew at a faster rate than identical colonies not used in the experiments and returned to the stock culture (see page 33). Also, considering the stock culture was kept at approximately 15‰, the doubling time of 6.5 days for those colonies is poor compared to the 5.0 and 5.7 day doubling times for the 12‰ and 18‰ experimental treatments when one would expect an intermediate value. I believe the cause of the difference is the amount of food available to the two sets of colonies. Whereas the experimental treatments were receiving a concentrated amount of *Artemia salina* nauplii in a small container, the food in the stock culture was dispersed throughout the 10-gallon aquarium in which several colonies containing thousands of feeding polyps all competed for it. Food availability is

likely to be an important factor in fast growing species such as hydroids (e.g., Crowell, 1934).

Effects of Salinity on *Tenellia* Growth and Reproduction

In order to assess the effects of salinity on *Tenellia adspersa*, it is necessary to examine the changes to adult survival, fecundity, and development at the various conditions. Adult nudibranchs show the greatest tolerance of different salinities compared to other life history stages. Adult *T. adspersa* can live at all four salinities used in the experiments, and while life span did vary with salinity, nearly all of that variability was due to the group of nudibranchs that were initially raised at 24‰ before being transferred to 6‰. All other groups exhibited essentially equal life spans with a mean of 37 days (Figure 14). Past studies report shorter life spans of 27 to 33 days for *T. adspersa* when feed *C. lacustris* (Harris et al., 1980; Chester, 1996). Changes in salinity, however, do appear to have profound effects on adult *T. adspersa* survival. Nudibranchs that were transferred from 15‰ and from 24‰ salinities to 6‰ suffered increased mortality (see pages 35 & 37).

Fecundity of *T. adspersa* decreased with salinity (Table 12). Excluding the nudibranchs which were transferred from 24‰ to 6‰, all groups produced similar numbers of spawn masses which means that the nudibranchs at the higher salinities were laying more eggs in each spawn mass than were the nudibranchs at lower salinities. Table 14 lists the fecundity measures for this study in comparison with previous life history studies of *T. adspersa*. The data from this study match those from past studies. The combined data also illustrates the trend of increased egg production with increased salinity. Again,

changes in salinity affect *T. adspersa*. Nudibranchs that were transferred from a developmental salinity of 24‰ to the lower salinities of 12‰ and 6‰ exhibited marked decreases in fecundity compared to nudibranchs transferred from a developmental salinity of 18‰ to those same adult salinities.

Table 14. Comparison of mean fecundity measures for *Tenellia adspersa* from this study with previously reported values when fed *Cordylophora lacustris*. Values from this study are the averages of the pooled 18‰ and 24‰ developmental salinity treatments.

Salinity	Eggs per Individual	Spawn Masses per Individual	Eggs per Spawn Mass	Reference
5‰	79	8.0	9.9	Harris et al., 1980
6‰	653	24.0	27.2	This study
10‰	1015	35.0	29.0	Harris et al., 1980
12‰	1728	44.3	39.0	This study
18‰	1883	49.8	37.8	This study
20‰	2073	43.5	47.7	Harris et al., 1980
24‰	2250	48.6	46.3	This study
25‰	1302	36.2	36.0	Chester, 1996
30‰	2687	70.5	38.1	Harris et al., 1980

The development of *T. adspersa* from egg to veliger larva and then through metamorphosis is the stage of the nudibranch's life cycle where the effects of salinity are seen most strikingly (Figure 12). At 6‰, eggs fail to develop. At 12‰, nearly all eggs fail to develop into veligers, and those that do either do not metamorphose or die soon thereafter. Harris et al. (1980) found very similar results with eggs failing to cleave at 5‰, and at 10‰, development continued but larvae died before metamorphosis. The threshold necessary for *T. adspersa* to complete development appears to be at, or very close to, 12‰. It is not unusual for eggs and early developmental stages of marine and estuarine invertebrates to

have more limited tolerances for wide ranges of salinity compared to adult forms (e.g., Fox, 1941; Rao, 1951; Barnes, 1953; Dybern, 1967; Wright et al, 1996).

Combining these separate effects of salinity on various aspects of the life history of *T. adspersa*, one can see that while *T. adspersa* can tolerate a range of salinities, there are limits and that *T. adspersa* survives and reproduces best at higher salinities. At and below 6‰, survival of the nudibranch is poor, and fecundity is low. While it can survive, grow, and spawn between 6‰ and 12‰, the eggs in these conditions will not develop. Therefore, for a population of *T. adspersa* to be able to persist, the salinity must be above 12‰. Considering only the salinities used in this study, population growth rates will be the highest at 24‰. Based on past research (Harris et al, 1980) and the salinities at which *T. adspersa* was found within the Great Bay Estuary system in this study, I believe that the growth and reproduction rates of *T. adspersa* are likely to achieve maxima around 30‰.

Population growth will be most rapid at higher salinities because of increased fecundity and increased survival of the eggs through development and metamorphosis (see page 35). At 24‰, an individual nudibranch producing an average 2250 eggs will produce 1773 veligers, and of these 974 will survive to become juvenile nudibranchs compared with 1883 eggs, 1463 veligers, and 604 juveniles at 18‰. It is interesting to note the high levels of mortality during development even under laboratory conditions and that nudibranchs are more likely to die in the process of hatching and metamorphosing than in the earlier stages of development. Chester (1996) also notes that hatching and metamorphosis is the critical survival period for *T. adspersa* with only 18% to 35% of nudibranchs surviving metamorphosis.

In nature, it is quite likely that the number surviving metamorphosis will be even lower. *T. ādispersa* has a plastic mode of development with either capsular metamorphic development or pelagic lecithotrophic development possible based, in part, on the amount of food available to the adults. The majority of nudibranchs (87-93%) undergo pelagic lecithotrophic development, and when food is scarce, this percentage increases to as much as 100% (Chester, 1996). With such high percentages of offspring developing as planktonic larvae which will have to survive predation and potentially unfavorable conditions and have to find a suitable food source before metamorphosing, it is quite likely that survival rates will be much lower than those seen here.

It is tempting to attribute the ability of *Cordylophora lacustris* populations to persist to these high mortality rates of nudibranch larvae. After all, if nine out of ten veligers leave the colony and only a fraction of these will survive to metamorphose anywhere, let alone in the same colony as their parents, this will greatly slow the rate of increase in the nudibranch population. Consider, however, the one out of ten that remains in the colony. Given a pair of nudibranchs reproducing at the highest rates seen in this study, that pair will release over 3700 veligers into the plankton, while 530 will remain to develop directly. Even after losses at metamorphosis, this will result in 229 juvenile nudibranchs in the colony in approximately 30 days from the time the pair began reproducing. This still results in an incredibly rapid increase in population size even ignoring the fate of the remaining thousands of veligers. Of course, the second generation will also begin reproducing only a week or so after metamorphosis!

The Effects of Salinity on the *Cordylophora*–*Tenellia* Relationship

Comparison of the salinity tolerances of *Cordylophora lacustris* and *Tenellia adspersa* reveals a distinct difference between prey and predator. *C. lacustris* can live in salinities from nearly 0‰ through at least 24‰ (Figure 10) although survival at or above 30‰ is unlikely (unpublished data). The hydroid grows most rapidly at lower salinities. *T. adspersa*, on the other hand, can survive and feed as an adult in salinities greater than 6‰ up to 30‰, but for reproduction and development to be successful, the salinity must be greater than 12‰. A salinity of 12‰, therefore, appears to be a critical value in this system. At or below that salinity, *C. lacustris* grows rapidly while *T. adspersa* populations cannot increase due to developmental failure; populations must consist solely of a low number of adults which will not replace themselves at the end of their life span.

Chester (1996) measured the predation rate of *T. adspersa* on *C. lacustris*. He reported increasing amounts of both stolon tissue and polyps consumed as the nudibranch grows in size. The maximum rate is 6.6 polyps and 18.01 mm³ of stolon tissue consumed per day, which applies to nudibranchs over 4 mm in length or 16 to 28 day old individuals. Chester used these rates and growth rates of *C. lacustris* to simulate the predation of a single nudibranch on a colony. The simulation indicates that only a colony at 5‰ could grow rapidly enough to survive predation by a single nudibranch. There are problems with this simulation, however, as Chester incorrectly modeled the increase in the number of polyps in a *C. lacustris* colony as a linear function. His own data and descriptions, as well as past descriptions (Fulton, 1962), clearly show that the number of polyps in a colony increases exponentially. An exponential growth

model will lead to much greater colony sizes. Taking this into consideration, colonies at salinities greater than 5‰ may also survive predation.

Still, these simulations only reflect predation by a single individual. Given the rates of reproduction described above under favorable conditions, a second-generation population of 200 individuals is a very conservative estimate. A population that size consuming 1320 polyps per day as full sized adults would require a colony of more than 17000 polyps during the 30 day life cycle. A *C. lacustris* colony growing at 18‰ and a doubling time of 5.7 days that started with ten polyps would take 63 days to reach that size, assuming no limitation from other factors such as food or space. The nudibranch population would have completed the third generation and begun a fourth in that same time. At higher salinities, the population growth rate for the nudibranch can swamp any conceivably sized hydroid colony.

Crawley (1992) states “A prey refuge exists when the predators are unable to drive the prey to extinction.” Clearly then, low salinity is a refuge for *C. lacustris*. Spatial variation in the physical environment within the estuary, specifically the gradient of salinity, is providing a range of habitat where the predator population cannot increase to great enough numbers to drive the hydroid to extinction. Outside of the low salinity range, extinction of the prey population is inevitable.

This author knows of only a few prior examples where salinity has been shown to provide a refuge for organisms in estuarine benthic or fouling communities. Burkenroad (1931) describes predation by the snail *Thais haemastoma* on the mussel *Mytilus clava* and notes that mussels are more abundant in lower salinities and that the snail is apparently unable to tolerate the

low salinity, but no experimental evidence is given. Similarly, Seed (1976) states that *Mytilus* species can survive reduced salinities and that this provides protection against predators, yet again, no experiments are reported. The best substantiated case, and one very similar to the relationship presented here, is that of the polyclad flatworm *Stylochus inimicus* which parasitizes oysters in Florida (Pearse and Wharton, 1938). Here, the adult flatworms cannot tolerate salinities below 6‰, and they cannot reproduce below 15‰ because the developing eggs die. Reproductive rates are highest at 33‰. An important difference, however, is that the flatworm does not cause the extinction of the oysters at higher salinities, merely increased rates of parasitism. The role that salinity plays in predator-prey relationships involving two estuarine species should be considered in future studies.

Sih (1987) discusses the use of physically severe habitats by stress-tolerant prey as one of evolutionary strategy to reduce predation pressure under the general category of “avoiding encounters”. Within this category, Sih states that different defense strategies have evolutionary consequences. For example, cryptic prey or ones which spend a great deal of time hiding to avoid detection are not able to move freely through their habitat so they pay a penalty in terms of being able to search for and take advantage of available resources. The resulting low activity and low energetic rates he terms a “slow lifestyle”. By contrast, prey using ephemeral habitats must feed, grow, and reproduce rapidly before the habitat is lost or invaded by predators. This he terms a “fast lifestyle”. In discussing the evolutionary tradeoffs of using a physically severe habitat, Sih states that these habitats select for a very slow life-style because of the metabolic

stress and that prey using this strategy have low growth and reproductive rates as well as late maturity.

Cordylophora lacustris is clearly stress tolerant and using a habitat that is physically severe by most marine and estuarine organisms' standards, yet the hydroid definitely has the fast lifestyle characterized by very rapid growth. From the perspective of the hydroid, low salinity regions of an estuary are the optimum habitat. All hydroid species originated in marine environments. At one point in the evolution of *C. lacustris* as the species moved from marine to estuarine conditions, the penalties of the stressful environment must have applied. Over time, the hydroid has apparently been able to evolve the physiological adaptations to escape from the penalties.

The *Cordylophora*–*Tenellia* Relationship within the Great Bay Estuary System

The salinity tolerances of the two species and the refuge at low salinities can explain the natural distributions of *Cordylophora lacustris* and *Tenellia adspersa* seen within the Great Bay Estuary system, but the relationship between salinity and the organisms is more complex than it may seem at first glance. It is important to remember that estuaries are temporally variable environments on many scales with both daily and seasonal changes to the physical environment (Caspers, 1967). Temporal variability in salinity will impact the relationship between the nudibranch and hydroid. The experiments reported here were all conducted at constant salinities. In nature, organisms must also deal with daily fluctuations in salinity due to tides, seasonal fluctuations due to precipitation patterns, and stochastic fluctuations due to individually significant weather events.

Since 1990, the Great Bay Watch program has monitored the water quality at low and high tide at various locations in the Great Bay Estuary system every two weeks from April through November (Great Bay Watch, 1995a; 1995b). The salinity data reveal the temporal variability of salinity within the Great Bay Estuary system. On a daily scale, some study sites vary only slightly between high and low tide while others vary 5 to 6‰, and one site in southern Great Bay varies 12‰ on average. This kind of slow, cyclic variation in salinity is something to which both *C. lacustris* and *T. adspersa* must be adapted as estuarine organisms. Only when the organisms were living in conditions near the limits of their tolerances is this variation likely to be a significant stress. Stochastic variations, on the other hand, may have major effects. For example, precipitation from hurricane Bob in August 1991 drastically reduced the salinity throughout the estuary between 12‰ and 30‰ at both high and low tide, and the effects, in some cases, lasted for several weeks. An event such as this would have significant impact on *T. adspersa* populations by causing nearly complete failure of all eggs as well as likely increases in adult mortality.

It is the seasonal changes in salinity, however, that have the greatest significance to the observed distributions of *C. lacustris* and *T. adspersa*. The maps in Figure 15 and Figure 16 display the average low tide and high tide salinities in the Great Bay Estuary System in May and July based on the Great Bay Watch data for 1990 through 1995 (Great Bay Watch, 1995a;1995b) and on additional data from this study. In May, nearly the entire estuary is below 25‰ at low tide, and the majority still is at high tide meaning that in the absence of *T. adspersa*, *C. lacustris* could survive in nearly all portions of the estuary (Figure 15). The presence of *T. adspersa*, however, restricts the hydroid to its refuge. At

low tide, the salinity is such that all of the tributary rivers, except for the lower thirds of the Bellamy River and Oyster River are unsuitable habitat for *T. adspersa*.

As the summer progresses, the estuary becomes more saline. By July, the majority of the estuary is at salinities greater than 25‰ at low tide (Figure 16). Only the tributary rivers are lower. At high tide, the higher salinities penetrate into all but the uppermost portions of the rivers except for the Lamprey River and Squamscott River, which appear to remain completely below 25‰. These two rivers may be more protected because of their greater distance from the mouth of the estuary. Thus, much of the estuary that would have been possible habitat for *C. lacustris* in May is too saline by mid-summer. The salinities have also increased to the point *T. adspersa* can successfully reproduce in nearly all portions of the estuary except, again, for portions of the Lamprey and Squamscott Rivers. By July, nudibranchs should be able to become established and to multiply in most all of the *C. lacustris* colonies within the estuary. Thus, the refuge that *C. lacustris* has in low salinity conditions is both spatial (only the most upstream locations within the estuary) and temporal (only during the early summer) in nature.

A *C. lacustris* colony emerging from winter dormancy requires four to six weeks to grow to the point that it can produce gonophores and reproduce sexually. Jormalainen et al. (1994) observed *C. caspia* colonies emerging from dormancy in early June. These colonies produced mature gonophores by July 1 and had their reproductive peak on July 15. In this study, colonies observed just emerging from dormancy in the first week of May were sexually reproductive by June 15, and in one case, *T. adspersa* was already present by that date (Table 5).

The largest, most luxurious colonies of *C. lacustris* have been found in the Squamscott River (Chester, personal communication; personal observations). Considering the extra protection this river appears to receive from higher salinities, and therefore nudibranchs, this pattern makes sense. For a *C. lacustris* colony to be successful, either it must reproduce itself sexually, or it must obtain enough resources to be able to survive the winter dormancy and be able to regenerate the following spring. The window of opportunity for the hydroids to grow free from predation is short, and only in the uppermost regions of the estuary do they receive the necessary protection long enough for the populations to be able to persist from year to year.

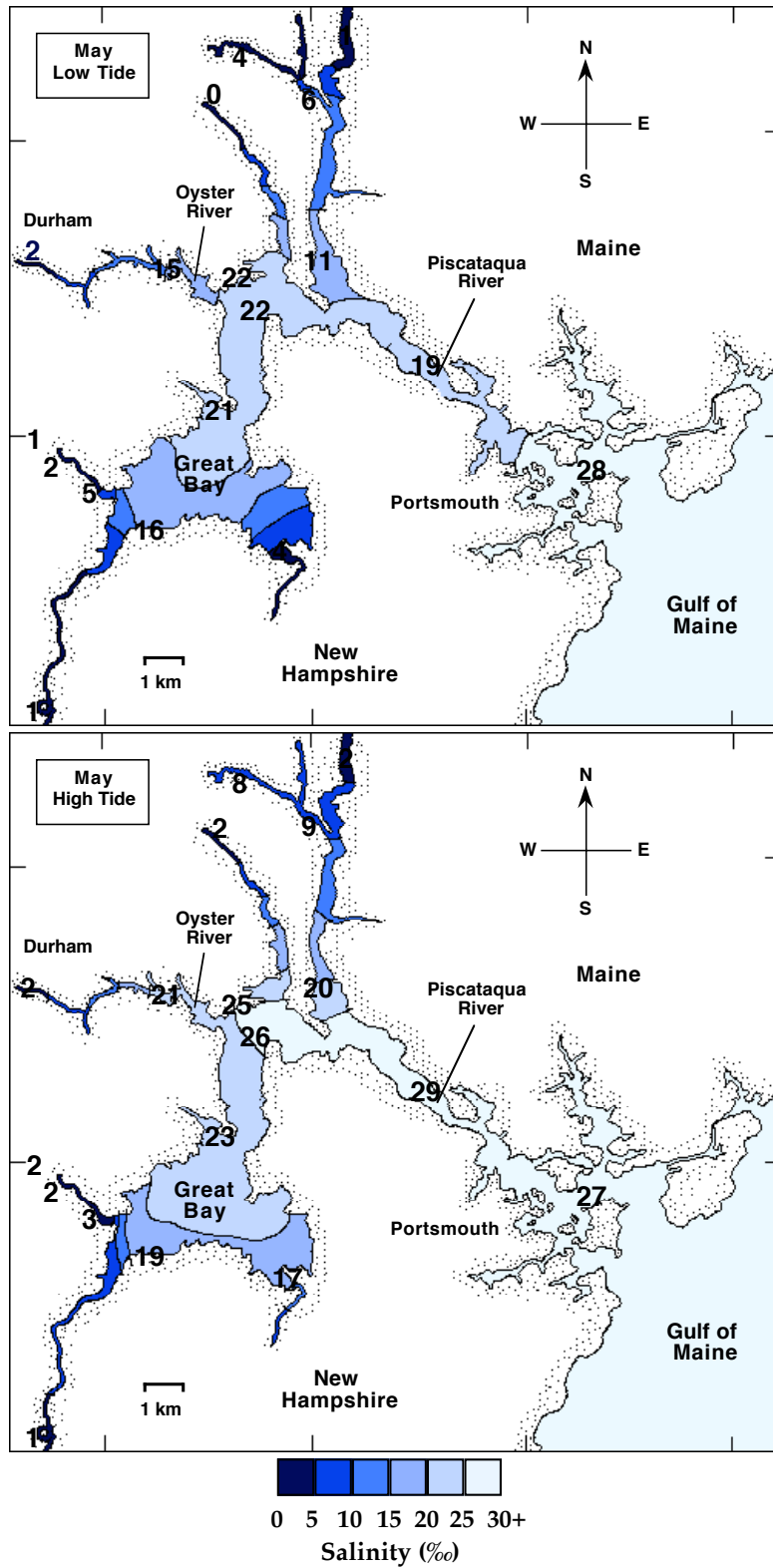


Figure 15. Salinity of the Great Bay Estuary system at low and high tide in May. The maps are based on data from this study and measurements taken by the Great Bay Watch 1990-1995 (Great Bay Watch, 1995a; 1995b).

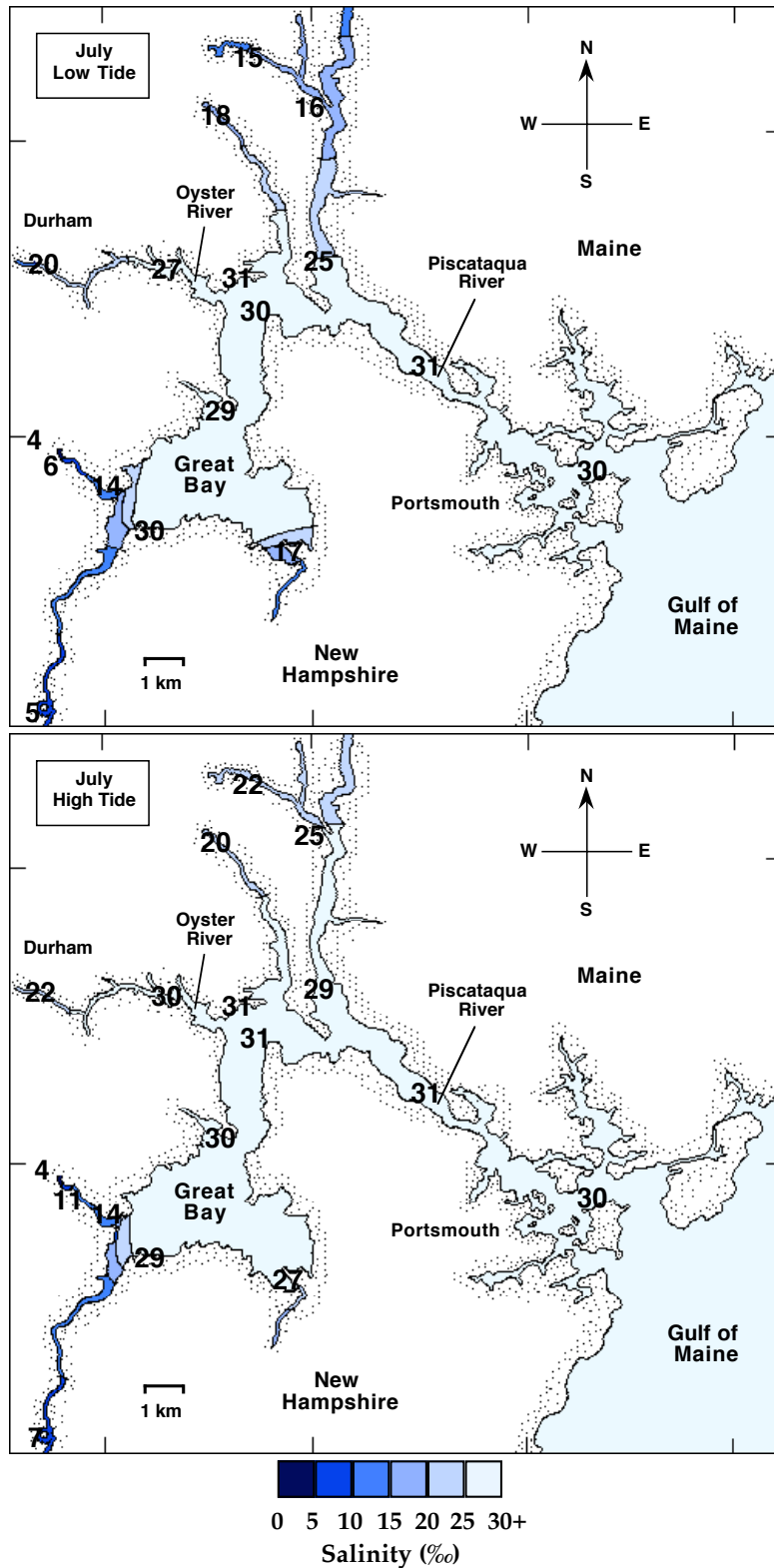


Figure 16. Salinity of the Great Bay Estuary system at low and high tide in July. The maps are based on data from this study and measurements taken by the Great Bay Watch 1990-1995 (Great Bay Watch, 1995a; 1995b).

CONCLUSIONS

1. Hydroids are seen as early colonists of free space in fouling communities. Timing of recruitment differs between species with campanularid hydroids being most abundant in June while *Tubularia* spp. dominate in July and August. Predators rapidly recruit to hydroids and can decrease the abundance of or completely remove colonies in less than a month after settlement of the hydroid.
2. The hydroid *Cordylophora lacustris* is consistently found in the upper portions of the rivers of the Great Bay Estuary system at low salinities. Populations in these locations can persist for several years.
3. The location of populations of the nudibranch *Tenellia adspersa* within the Great Bay Estuary system is highly variable, and the populations do not persist from year to year.
4. *Cordylophora lacustris* grows most rapidly at low salinities, but colonies can survive salinities at least as high as 24‰.
5. *Tenellia adspersa* can tolerate salinities as low as 6‰ as an adult, but in order for the development of eggs to be successful, the salinity must be greater than 12‰. The fecundity of *Tenellia adspersa* is greater at higher salinities.
6. Low salinity regions are a refuge from predation for *Cordylophora lacustris* due to the inability of *Tenellia adspersa* to produce offspring in these conditions. At salinities in which *Tenellia adspersa* can successfully reproduce, the nudibranch population will increase to the point that it will drive the hydroid to local extinction.

7. The observed distributions for both *Cordylophora lacustris* and *Tenellia adspersa* within the Great Bay Estuary system can be explained based on the salinity tolerances of the two species and the increase in salinity seen in the estuary during the summer months.

LITERATURE CITED

- Barnes, H. 1953. The effects of lowered salinity on some barnacle nauplii. *Journal of Animal Ecology*. 22:328-330.
- Bayne, B. L. 1964. Primary and secondary settlement in *Mytilus edulis* L. (Mollusca). *Journal of Animal Ecology*. 33:512-523.
- Burkenroad, M. D. 1931. Notes on the Louisiana conch, *Thais haemastoma* Linn., in its relation to the oyster, *Ostrea virginica*. *Ecology*. 12:656-664.
- Calder, D. R. 1976. The zonation of hydroids along salinity gradients in South Carolina estuaries. In: G. O. Mackie, ed. *Coelenterate Ecology and Behavior*. Plenum Publishing Corp., New York, 165-174.
- Caspers, H. 1967. Estuaries: analysis of definitions and biological considerations. In: G. H. Lauff, ed. *Estuaries*. American Association for the Advancement of Science, Washington, D. C., 6-8.
- Chambers, L. A. 1934. Studies on the organs of reproduction in the nudibranchiate mollusks, with special reference to *Embletonia fuscata* Gould. *Bulletin of the American Museum of Natural History*. 66:599-641.
- Chesson, P. L. 1978. Predator-prey theory and variability. *Annual Review of Ecology and Systematics*. 9:323-347.
- Chester, C. M. 1996. Life history and reproductive biology of the estuarine nudibranch *Tenellia adspersa* (Nordmann, 1845). Ph. D. Dissertation, University of New Hampshire.
- Clark, K. B. 1975. Nudibranch life cycles in the northwest Atlantic and their relationship to the ecology of fouling communities. *Helgoländer Meeresuntersuchungen*. 27:28-69.
- Connell, J. H. and R. O. Slayter. 1977. Mechanisms of succession in natural communities and their roles in community stability and organization. *American Naturalist*. 111:1119-1144.
- Crawley, M. J. 1992. Population dynamics of natural enemies and their prey. In: M. J. Crawley, ed. *Natural Enemies*. Blackwell Scientific Publications, Oxford, 40-89.
- Crocker, R. A. 1972. Checklist with habitat notes, of some common intertidal estuarine, and nearshore invertebrate animals of New Hampshire and Southern Maine. Jackson Estuarine Laboratory, Durham.

- Crowell, S. 1953. The regression-replacement cycle of hydranths of *Obelia* and *Campanularia*. *Physiological Zoology*. 26:319-327.
- Dayton, P. K. 1971. Composition, distribution, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs*. 41:351-389.
- Dean, T. A. 1981. Structural aspects of sessile invertebrates as organization forces in an estuarine fouling community. *Journal of Experimental Marine Biology and Ecology*. 53:163-186.
- Dean, T. A. and L. E. Hurd. 1980. Development in an estuarine fouling community: the influence of early colonists on later arrivals. *Oecologia*. 46:295-301.
- Dybern, B. I. 1967. The distribution and salinity tolerance of *Ciona intestinalis* (L.) f. *typica* with special reference to the waters around southern Scandinavia. *Ophelia*. 4:207-226.
- Fox, D. L. 1941. Changes in the tissue chloride of the Californian mussel in response to heterosmotic environments. *Biological Bulletin*. 80:111-129.
- Frazer, C. M. 1944. *Hydroids of the Atlantic Coast of North America*. University of Toronto Press, Toronto.
- Fulton, C. 1960. Culture of a colonial hydroid under controlled conditions. *Science*. 132:473-474.
- Fulton, C. 1962. Environmental factors influencing the growth in *Cordylophora*. *Journal of Experimental Zoology*. 151:61-78.
- Gaulin, G., L. Dill, J. Beaulieu, and L. Harris. 1986. Predation-induced changes in growth form in a nudibranch-hydroid association. *The Veliger*. 28:389-393.
- Gosner, K. L. 1971. *Guide to Identification of Marine and Estuarine Invertebrates*. Wiley-Interscience, New York.
- Great Bay Watch. 1995a. The Great Bay Watch Five Year Report, 1990-1994. UNH Sea Grant Extension, Durham, NH, UNHMP-AR-SG-95-1.
- Great Bay Watch. 1995b. The Great Bay Watch Annual Report, January-December 1995. UNH Sea Grant Extension, Durham, NH, UNHMP-V-SG-95-13.
- Harris, L. G. 1987. Aeolid nudibranchs as predators and prey. *American Malacological Bulletin*. 5:387-392.
- Harris, L. G., A. W. Ebeling, D. R. Laur, and R. J. Rowley. 1984. Community recovery after storm damage: a case of facilitation in primary succession. *Science*. 224:1336-1338.

- Harris, L. G. and K. P. Irons. 1982. Substrate angle and predation as determinants in fouling community succession. In: J. Cairns, ed. *Artificial Substrates*. Ann Arbor Science Publishers, Inc, Ann Arbor, 131-174.
- Harris, L. G., M. Powers, and J. Ryan. 1980. Life history studies of the estuarine nudibranch *Tenellia fuscata* (Gould, 1870). *The Veliger*. 23:70-74.
- Hubschman, J. H. and W. J. Kishler. 1972. *C. sowerbii* Lankester 1880 and *Cordylophora lacustris* Allman 1871 in Western Lake Erie (Coelenterata). *Ohio Journal of Science*. 72:318-332.
- Jormalainen, V., T. Honkanen, T. Vuorisalo, and P. Laihonen. 1994. Growth and reproduction of an estuarine population of the colonial hydroid *Cordylophora caspia* (Pallas) in the northern Baltic Sea. *Helgoländer Meeresuntersuchungen*. 48:407-418.
- Kalle, K. 1971. Salinity: General Introduction. In: O. Kinne, ed. *Marine Ecology*. Wiley-Interscience, New York, 683-688.
- Kelly, J. P. and J. L. Franks. 1995. *Cordylophora lacustris* (Cnidaria: Clavidae) from Livingston Reservoir in east Texas. *Texas Journal of Science*. 47:319-321.
- Kinne, O. 1956. Über den Einfluß des Salzgehaltes und der Temperatur auf Wachstum, Form und Vermehrung bei dem Hydroidpolypen *Cordylophora caspia* (Pallas), Athecata, Clavidae. *Zool. Jahrb., Abt. Physiol.* 66:565-638.
- Kinne, O. 1971. Salinity: Invertebrates. In: O. Kinne, ed. *Marine Ecology*. Wiley-Interscience, New York, 821-995.
- Lambert, W. J. 1985. The influence of predators on early colonists in a fouling community. Master's Thesis, University of New Hampshire.
- Lambert, W. J. 1991. Coexistence of hydroid eating nudibranchs: do feeding biology and habitat use matter?. *Biological Bulletin*. 181:248-260.
- Lotka, A. J. 1925. *Elements of Physical Biology*. Williams and Wilkins, Baltimore.
- Lovely, E. C. 1995. Coexistence of hydroid predators and persistence of prey, *Tubularia larynx* and *Tubularia indivisa* (Hydrozoa: Tubulariidae) in shallow fouling communities. Master's Thesis, University of New Hampshire.
- Lubchenco, J. and B. A. Menge. 1978. Community development and persistence in a low rocky intertidal zone. *Ecological Monographs*. 59:67-94.
- Malcolm, S. B. 1992. Prey defense and predator foraging. In: M. J. Crawley, ed. *Natural Enemies*. Blackwell Scientific Publications, Oxford, 458-475.

- May, R. M. 1981a. Models for two interacting populations. In: R. M. May, ed. *Theoretical Ecology: Principles and Applications*, 2nd ed. Sinauer Associates, Inc., Sunderland, MA, 78-104.
- May, R. M. 1981b. Patterns in multi-species communities. In: R. M. May, ed. *Theoretical Ecology: Principles and Applications*, 2nd ed. Sinauer Associates, Inc., Sunderland, MA, 197-227.
- McDonald, G. and J. Nybakken. 1997. A worldwide review of the food of nudibranch mollusks. *The Veliger*. 40: Supplement 1-000. URL: <ftp://ucmp1.berkeley.edu/pub/mollusca/>.
- Moore, G. M. 1964. Shell-less opisthobranchs. In: R. I. Smith, ed. *Key to Marine Invertebrates of the Woods Hole Region*. Systematics-Ecology Program, Marine Biological Laboratory, Woods Hole, Contribution No. 11.
- NCDC, 1999. National Climate Data Center: Climate Division Drought Data. URL: <http://www.ncdc.noaa.gov/onlineprod/drought/main.html>.
- Nybakken, J. and G. McDonald. 1981. Feeding mechanisms of west American nudibranchs feeding on Bryozoa, Cnidaria, and Ascidiacea, with special respect to the radula. *Malacologia*. 20:439-449.
- Okamura, B. 1986. Formation and disruption of aggregations of *Mytilus edulis* in the fouling community of San Francisco Bay. *Marine Ecology Progress Series*. 30:275-282.
- Paine, R. T. 1966. Food web complexity and species diversity. *American Naturalist*. 100:65-75.
- Pearse, A. S. and G. W. Wharton. 1938. The oyster "leech" *Stylochus inimicus* Palombi, associated with oysters on the coasts of Florida. *Ecological Monographs*. 8:605-655.
- Pennak, R. W. 1978. *Fresh-water Invertebrates of the United States*, 2nd. ed. Wiley, New York.
- Pollock, L. W. 1998. *A Practical Guide to the Marine Animals of Northeastern North America*. Rutgers University Press, New Brunswick.
- Rao, K. V. 1951. Observations on the probable effects of salinity on the spawning, development and setting of the Indian backwater oyster, *Ostrea madrasensis* Preston. *Proceedings of the Indian Academy of Sciences (Section B)*. 33:231-256.
- Rasmussen, E. 1944. Faunistic and biological notes on marine invertebrates. I. The eggs and larvae of *Brachystomia rissoides* (Hanl.), *Eumella nitidissima* (Mont.), *Retusa trunculata* (Brog.), and *Embletonia pallida* (Alder and Hancock) (Gastropoda marina). *Vedensk. Medd. Dansk Naturhist. Foren.* 102:207-233.

- SAS Institute. 1998. StatView Reference. SAS Institute, Cary, NC.
- Seed, R. 1969. The ecology of *Mytilus edulis* (Lamellibranchiata) on exposed rocky shores. I. Breeding and settlement. *Oecologia*. 3:277-316.
- Seed, R. 1976. Ecology. In: B. L. Bayne, ed. *Marine Mussels: Their Ecology and Physiology*. Cambridge University Press, Cambridge, 13-65.
- SERC, 1998. Smithsonian Environmental Research Center: Marine Invasions Research Lab. URL: <http://www.serc.si.edu/invasions/cordylophora.htm>.
- Smith, R. J. (ed.). 1964. Keys to marine invertebrates of the Woods Hole region. Systematics Ecology Program, Marine Biological Laboratory, Woods Hole.
- Sokal, R. R. and F. J. Rohlf. 1981. *Biometry*. W. H. Freeman and Company, New York.
- Standing, J. D. 1976. Fouling community structure: effects of the hydroid, *Obelia dichotoma*, on larval recruitment. In: G. O. Mackie, ed. *Coelenterate Ecology and Behavior*. Plenum Publishing Corp., New York, 155-164.
- Streever, W. J. 1992. First record of the colonial cnidarian *Cordylophora lacustris* within a flooded cave system. *NSS Bulletin*. 54:77-78.
- Thompson, T. E. 1964. Grazing and life-cycles of British nudibranchs. In: D. J. Crisp, ed. *Grazing in Terrestrial and Marine Environments*. Blackwell, Oxford, 275-297.
- Todd, C. D. 1981. The ecology of nudibranch molluscs. *Annual Review of Oceanography and Marine Biology*. 19:141-234.
- Todd, C. D. 1983. Reproductive and trophic ecology of nudibranch molluscs. In: W. D. Russell-Hunter, ed. *The Mollusca, Volume 6, Ecology*. Academic Press, New York, 225-259.
- Volterra, V. 1926. Variations and fluctuations of the numbers of individuals in animal species living together. In: R. N. Chapman, ed. *Animal Ecology*. McGraw-Hill, New York, 409-448.
- Wright, D. A., E. M. Setzler-Hamilton, J. A. Magee, V. S. Kennedy, and S. P. McInch. 1996. Effect of salinity and temperature on survival and development of young zebra (*Dreissena polymorpha*) and quagga (*Dreissena bugensis*) mussels. *Estuaries*. 19:619-628.