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June 2, 1998
Into the Mystic: Ascidians and Ecosystems in an Age of Biological Invasions

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Introduction

In late March of this year, an unfamiliar green crab was found beneath the Highway 101 bridge in Coos Bay, engaged in the activity that occupies much of its time: devouring a juvenile oyster. This seemingly commonplace discovery, however, has been the cause of excitement and alarm among shellfish-harvesters and biologists alike. The species to which this individual belongs, *Carcinus maenas*, is native not to the southern Oregon coast, but rather to the shores of the Mediterranean Sea. Over the course of two centuries, *Carcinus* has spread far from its origins: South Africa, Australia, New England, California, and most recently southern Oregon (Perlman 1997). Its predatory habits alter the species composition and abundances of each nearshore community it invades. The green crab’s story is but a single example of a global trend of exotic species invasions. The expansion of human enterprise and mobility in recent decades has been accompanied by a species diaspora, at a magnitude and rate unrivaled in previous millennia. Human activity, inadvertently and by design, has created new avenues for dispersal across vast distances and natural barriers. The biological and social consequences of this “homogenization” of the world’s biota are not all clear, but in many instances have and will be unfavorable and widespread.

I spent the summer months of 1997 as a research intern at the University of Connecticut investigating the recent invasions of several marine invertebrates into the waters of Long Island Sound. Measured on the grand scale of a global process, the work I completed seems as insignificant and obscure as the creatures I studied, the implications of my findings frustratingly local and specific. This is the nature of the problem. Just as many localities comprise a region, and many regions the world, many individual species invasions summed across all localities become a global trend. Generalizations are rare in invasion biology; each invasion occurs under a different set of environmental and temporal circumstances. Instead, we are left with a common set of questions regarding the origins, processes, and impacts of any given invasion. The work I did as an intern addresses these questions in regard to but a few species inhabiting a short stretch of New England coastline, but provides as good a vehicle as any for examining the larger problem of biological invasions.

Background: the Prevalence of Biological Invasions

The number of recent invasions around the world is difficult to estimate. All that is known is that the number is vast. Invasion biologist James Carlton estimates that within the single vector of transport in
ships' ballast water, some 3000 species may be on the move around the world every day (Carlton and Geller 1993). Consequently, the waters of a major port or estuary like the San Francisco Bay may now support over 300 species of exotic or unknown origin (Carlton 1996). Several centuries after James Cook arrived on Oahu (undoubtedly carrying the Island's first modern introducer), the Hawaiian Islands now support as many exotic species as natives (Vitousek 1986). Some 20% of the world's endangered vertebrate species are threatened with extinction as a result of invasions (Baskin 1996). Taken together, these statistics provide a fragmentary but conclusive picture of the prevalence of biological invasions as a global phenomenon.

Invasions are not always human caused. The fossil and living biological records contain evidence of an ongoing process of species migration and range-shifting. The bulk of recent invasions, however, fall into the category of introductions: invasions directly related to human activity. Introductions can take a multiplicity of forms, and occur under any imaginable circumstance. They are often intentional: agricultural and livestock species of plants and animals around the world are largely introduced. Fisheries in many seas rely on introduced species, or, as in the case of most salmon hatcheries, the introduction of genetically distinct populations to maintain catch quotas. The introduction of predators has often been attempted as a means of pest control in agriculture. The intended introduction of exotic species has been common practice, and continues today. Unintended introductions occur in similarly diverse circumstances.

As humans travel and migrate, they carry with them a host of uninvited passengers, species that, like humans themselves, readily invade new regions. These stowaways range from shipboard rodents to the larvae of marine invertebrates, from insects to microscopic bacteria and viruses. The seeds of exotic plants disperse far and wide in the intestines of livestock, and within a short span of years, can transform entire landscapes. Particularly vulnerable are those regions whose natural systems have already suffered under human stewardship. The common and oftentimes necessary activities of modern civilizations, from economic development to agriculture, draw upon and weaken natural ecosystems, undermining their resistance to potential invaders. Exotic species tend to capitalize on disturbance.

Background: Impact of invasions

In practical terms, how detrimental to the environment, and especially the human condition, are biological invasions? This question begs an answer, if only to justify the expenditure of effort and energy
on the part of society that will be required to control what some see as a perfectly natural process. Not all introduced species negatively impact the communities they invade, a fact that complicates the answer to this question. The introduced marine invertebrates I studied this summer, for instance, have had the noticeable effect of increasing the diversity and biomass of their recipient community, with few other short-term impacts. To assess the magnitude of the current global problem, then, we must examine the fraction of invasions that have proven disruptive.

The bulk of damaging equations fall loosely into three, non-exclusive categories: (1) those that force biodiversity decline, (2) those that affect ecosystem function, (3) and those that directly impact social or economic systems. The overlap among these categories is great—biodiversity decline can result from changes in an ecosystem, and vice versa, while most invasions that impinge on the human world do so through one or both of the biological mechanisms. While the impacts on biodiversity may in the end prove the most permanent (from an evolutionary standpoint), examples of invasions that have harmed humans directly argue convincingly that biological invasions deserve our attention and concern.

For every introduced species as useful as the Monterey Pine, a species once endemic to California now grown commercially in the southern hemisphere, there is one as damaging as the Asian clam (*Potamocorbula amurensis*), a rapidly reproducing, voracious planktonivore that invaded the San Francisco Bay Delta in 1988 and now dominates the bottom-dwelling (benthic) community. Its consumption of zooplankton is such that it alters the structure of the estuary’s food web, depleting the amount available to young fish. The clam has been implicated in the decline of the Bay’s once-rich salmon and bass fisheries. For every introduced grass species that replaces a native without obvious impact on ecosystem function, there is a case like the Cape Province fynbos ecosystem, in which exotic Mediterranean grasses and shrubs have increased vegetation biomass from 50 to 1000%. The relatively large water demands of the exotic grasses have depleted natural runoff (and the supply available to humans) by some 30-80% (Daily 1997). The introduction of the water fern *Salvinia molesta* into tropical rivers around the world has had significant impact on local ecosystem productivity, water chemistry, and fishery yields (Vitousek 1986). The economic and societal importance of introduced crops in this country is undeniable, yet it is estimated that introduced pests inflict economic losses of nearly $7.5 billion on American agriculture and forestry each year (Daily 1997). The intestinal bacterium Cyclospora, introduced

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1 A “negative” impact is, of course, defined as such through human systems of valuation, which have traditionally emphasized the direct economic benefits culled from a resource above other factors. More recently, the relevance of any particular invasion has come to be evaluated using broader criteria, including its impacts on ecosystems.
to the U.S. on berries imported from Mexico and Guatemala, has been the cause of several recent disease
scarese (Baskin 1996). This “global anecdote” of disruptive biological invasions leaves little doubt as to the
seriousness and ubiquity of the problem.

**Practical and Philosophical Bases of the Internship**

The pervasiveness and potential importance of the invasion phenomenon never occurred to me
until I was introduced to the marine communities of Long Island Sound during my participation in the
Williams College-Mystic Seaport Maritime Studies Program⁷ in the fall of 1996. Under the tutelage of
respected ecologist Jim Carlton and biological oceanographer Jimmy McKenna, some of my unexamined
assumptions about the nature of biological communities began to erode. If ecology helped me exchange a
two-dimensional, still-frame view of the natural world (seen from a suburban window) for a three-
dimensional conception of habitat, niche, and cyclical interaction, then my new concern with exotic species
contributed a fourth element to the picture—time. Not only was each member of a community inextricably
related to its surroundings, biological and environmental, but on a certain timescale each member was in
constant motion, each relationship in perpetual flux. My excitement came from the perception of motion
where it had been undetectable, my concern from the knowledge that human activities lay at the root of this
unprecedented acceleration in the movement of species.

Anyone who spends a few moments pondering the concept of a “biological invasion” will sense a
certain pejorative leaning in the phrase itself. The word “invasion” implies violation, a forcible disruption
of the natural order. An invader is something that has inserted itself, perhaps destructively, where it has
no right to be. It is with this implicit understanding of what it means to be an invader that many people
approach the problem of species invasions. Argentinean *pampas* grass is changing the appearance of
California coastal scrublands before our very eyes. It looks alien, and we mistrust the speed with which it
seems to spread; clearly it should not be here, let alone be allowed to spread further.

A closer look reveals this sort of thinking as simplistic. Under the less condemning moniker of
“migration.” species (as well as populations, sub-populations and individuals) have been invading new
regions since the early history of life on earth. Such mobility is the key to long term survival, a
fundamental mechanism of evolution. Wave after wave of migration, invasion by a different name, have

⁷ This unique interdisciplinary program is based in Mystic, CT, a small town at the eastern end of Long Island
Sound, renowned for oysters (now toxic), ice cream, and Julia Robert’s breakthrough film “Mystic Pizza.” The
pizza, incidentally, is not that good.
contributed to the creation of the biosphere as we know it today. The coastal terraces on which pampas grass has gained its strongest foothold were long ago invaded by the European annual grasses that now give California its characteristic golden brown color. The mythical "original California" lies far beyond the reach of living memory, and on anything but a human timescale never existed.

In confronting the notion of humanity as a vector for biological invasions, I am presented with a philosophical quandary. The strictest practice of natural science, as well as current wilderness philosophy, urge us to abandon the anthropocentrism that seeks to separate humankind from the rest of the living world. From this perspective, human vectors for invasion are as "natural" as any others, and my objection to the recent species diaspora on the grounds that it is anthropogenic conflicts with other principles that I hold dear. Any environmentalist aspiring towards philosophical consistency would either have to quit worrying about species invasions or discard the notion that humans are intrinsically embedded in the global ecosystem.

In my mind, this sort of dichotomized thinking hides several flaws. One can argue that the accumulation of anthropogenic carbon dioxide in the atmosphere is the logical extension of respiration (a process intrinsic to heterotrophic life) in human ecology, and be indisputably correct. The error occurs when we use this argument to abdicate responsibility for facing the issue of global warming. If every environmental problem resulting from human activity were dismissed as natural, unavoidable, and therefore unimportant, much of the natural order we’re supposedly a part of would eventually disappear, perhaps taking us along a parallel path to extinction. The problem with species invasions, as with global warming, is essentially one of timescale. Carbon dioxide plays a vital role the earth’s climatic system, and the system has evolved slow-acting mechanisms to keep this vital but potentially destabilizing component in balance. The trebling of carbon dioxide input to the atmosphere over the last 200 years has occurred on a far shorter timescale than the larger earth system operates on. If the old, apparent equilibrium is to be restored, it will take time; meanwhile, the biosphere’s ability to adapt to rapid environmental change is likely to be severely stressed. A similar conceptual model can be constructed for species invasions: over millennia, ecosystems have become adapted to absorb invasions occurring at some average rate—they may have come to depend on them. If the expansion of the human vector has accelerated invasion rates to unprecedented levels, then the possibility of catastrophic ecosystem change must be considered. This seems like idle speculation until one considers that invasions are but one of many stresses modern biological systems must endure. It is like a game of ecological roulette\(^3\) in which the odds are unknown.

\(^3\)I owe the apt phrase "ecological roulette" to Jim Carlton. I have encountered its use in several of his papers, and have heard him use it in conversations as well.
For anyone who sees value in a biosphere not entirely controlled by human ecology, it is crucial to realize that seeking to impose limits upon our own ecological niche is as "natural," as ignoring our impacts. The ability to exert a measure of control over our actions is a defining if not exclusively human trait.

Applying this ability to the problem of biological invasions entails learning to monitor the various dispersal vectors we offer to potential invaders.

It was with some precursor of the above attitude that I scanned an e-mail from my friend Jim McKenna last spring, regarding an opportunity to study marine invasions in the Mystic area for the summer. Motivated by the desire to gain experience in scientific research, learn more about a topic that had caught my attention the previous fall, and renew old friendships, I applied for the job and got it (I also managed to alleviate a vague sense of anxiety stemming from the knowledge that I had to get an internship at some point!).

By mid-June I was back in Connecticut, ready to begin an internship with Robert B. Whitlatch, a colleague of Carlton's, in his lab at UConn's Avery Point campus near Mystic.

Setting the Stage: Land and Sea

The Connecticut coastline presents a striking contrast to the California coast I call home. Epitomizing a passive tectonic margin, the Connecticut coast lacks strong relief. Rocky headlands abound (with lots of potassium feldspar-rich granites), but where rivers cut to the sea or the coastline is sheltered, marshes or beaches can be found. The land slopes gently towards the water, a trend that continues beneath the waves; far out into Long Island Sound, the water remains relatively shallow. Within the protected confines of the Sound, wave energy is low, and even the waves on the Rhode Island coast, on the open Atlantic, make for disappointing surfing. It is impossible to travel in a straight line near the coast in southern New England, for your path will undoubtedly intersect one of the many drowned river valleys that make this stretch of coast appear so convoluted on nautical charts. The town of Mystic lies on one such inlet, and the Avery Point campus at the mouth of another. Formed during Pleistocene ice ages when sea level was substantially lower than it is today, these river valleys gradually filled with the rising sea as the present interglacial epoch progressed. Glaciers have contributed other important features to the seascape: a portion of Long Island itself is the terminal moraine of the farthest extent of the great Laurentide ice sheet that began to retreat some 21,000 years ago (Lewis 1995).
Setting the Stage: The Lab

Dr. Whitlatch’s lab has accumulated an impressive body of knowledge and wide coverage in the field of benthic (ocean bottom) ecology. Past research has focused on polychaete worms, or on the deep benthos of the Caribbean trenches as seen from the submersible Alvin. His graduate students have studied topics as diverse as the invasion ecology of the Japanese crab Hemigrapsus in Atlantic intertidal communities and the sulfide biogeochemistry of eelgrass. Whitlatch’s current research, however, has focused on benthic fouling communities, that is, the assemblage of sessile (immobile) invertebrate species that can be found attached to any hard surface (“substrate”) in the nearshore environment: rocks, pilings, docks, kelp, and boat bottoms. In particular, research has focused on several species of introduced ascidians, more commonly known as sea squirts or tunicates.

Ascidians

Ascidians are small, filter-feeding animals common to nearshore marine and estuarine environments around the world. The class is divided between two basic morphologies, solitary and colonial (see Figures 1&2). The globular, irregularly-shaped solitary ascidians look as though they were specifically designed for eating. Their most striking features are two siphons, one incumbent, the other excursive, at either terminus of a two-stage digestive tract. From its position at the head of the intestine (often externally visible), a fibrous “basket” filters plankton, larvae, and other organic debris from the stream of water siphoned through the organism. These and other internal organs are sheathed in a protective “tunic” (hence the name “tunicate”) of a strength and thickness that varies among species. Solitary ascidians attach to hard substrates by means of basal threads or stalks. Colonial tunicates occur as flat, sheet-like “systems” of semi-autonomous animals (known as “zooids”), linked by a common vascular system and contained within a shared gelatinous tunic. Each zooid is made up of several individual animals, in some species arranged in a star-like pattern. Each zooid shares a single excursive siphon, but each individual retains its own incumbent siphon (Carlton 1996, unpublished). Ascidians are among a handful of invertebrate members of our own phylum (Chordata). As larvae they resemble small tadpoles.

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4 The term “fouling” has very logical roots: these organisms tend to colonize, or “foul” ropes and boat surfaces that people would rather keep free of debris.
and have a dorsal notochord that disappears upon settlement and maturation.

**Fouling Communities**

The fouling community at Avery Point includes seven species of ascidians, four of which have been introduced in the last 25 years. It also includes many species of bryozoans—colonies of tiny, filter-feeding organisms, that to the naked eye look like some sort of siliceous crust—several types of molluscs (mussels, oysters, barnacles), various polychaete tube-worms, small anemones, and a diverse flora of red, green, and brown algae. Associated with these communities are several snail species, and at least two types of fish, that prey on larvae or recently-settled juvenile fouling organisms. The fouling community is an easily overlooked but important component of the larger ecosystem: great numbers of these diminutive creatures can consume a large fraction of an area’s primary and secondary planktonic productivity.

Although water temperature is perhaps the ultimate biophysical limit on a fouling community’s areal extent, in a shallow water system like the Sound, the availability of settlement surfaces proves more limiting. The rocky, island-dotted coast at Avery Point offers suitable habitat within the first few tens of meters out from shore. Further out to sea, the rocks become sparser, and soft-sediment bottoms dominate. At the mouths of rivers, wide “fields” of eelgrass grow out of the silty bottom. These dense pastures graduate into dispersed stands of kelp out beyond the reach of the estuaries. Where rocks are abundant, the fouling community is populous and diverse. Because fouling species cannot settle on the sandy flats away from shore, the offshore community is much reduced, consisting of a few ascidian colonies attached to narrow stems of eelgrass, or bryozoans encrusting the leaves of kelp.

Unlike other biological communities, which for the most part have suffered as a result of contact with humankind, fouling communities have often had their habitat extended as a result of human activities. Thousands of sheltered embayments and harbors have been carved out of rough-water coasts, creating the calm water conditions these communities thrive in. Likewise, long stretches of soft-sediment coastline have been lined with rock and concrete, providing hard settling substrate where once it did not exist. Innumerable pilings, docks, and vessel bottoms have trebled the amount of habitat available to benthic species. The protected embayment at the mouth of the drowned river valley adjacent to Avery Point is no exception: the fouling community supporting the bulk of the research in the Whitlatch lab is centered on the University’s floating docks and a nearby breakwater.
The Internship

Opportunistic fouling species have capitalized on human mobility to spread from their native regions to other likely regions around the world. Ballast water transport is the most common but by no means the only mechanism of dispersal. As is the case for most marine invasions, fouling species tend to insert themselves most easily into disturbed or otherwise depauperate communities (Carlton 1996). At Avery Point, introduced ascidians are particularly prevalent. Dr. Whitlatch’s studies of these ascidians have branched along two general pathways: (1) identifying the ecological factors that control the establishment and persistence of the invaders; (2) uncovering the impacts of the ascidian invasions on the survival of co-occurring benthic species, and on the ecosystem at large.

The projects I became involved in focused on two species in particular. The first, the colonial tunicate Botrylloides diegensis (known as the Pacific colonial tunicate or the “Orange Scourge,” depending on one’s politics) is an opportunist and fast growing ascidian easily identified by its bright orange color. Proving that even science plays its role in global change, Botrylloides was accidentally introduced to the New England coast by biologists at Woods Hole in 1973. It has since spread as far south as western Connecticut and as far north as the Gulf of Maine (Whitlatch et al. 1995) Botrylloides has received the bulk of the attention from the Whitlatch lab. The second species of concern, the large (up to 7 cm in length) solitary tunicate Ascidia aspera, first appeared in eastern Long Island Sound in 1990 and 1991, and has gradually increased its population density to the present day (Berger and Whitlatch 1995). If nothing else, this recent invasion has provided an opportunity to examine the mechanisms by which a newcomer becomes established in an extant community, and to document any early-stage impacts it might have. My individual research project on Ascidia recruitment dynamics (discussed later) addressed both these concerns.

Project 1: Population Biology of Botrylloides

The last several field seasons in Dr. Whitlatch’s lab have been spent uncovering the basic characteristics of Botrylloides’ population biology. My arrival in Groton coincided with a shift in the focus of the Botrylloides project. Past efforts had centered on uncovering the larger controls on the species’ reproduction, larval settlement and survival, and adult populations. This summer’s goal was to

\footnote{Ascidia is a native of western European coastlines (Carlton 1996).}
flesh out the general trends with more specific data on a smaller temporal and spatial scale.

It had been well-established that Botrylloides produces two distinct cohorts (a "cohort" is a "batch" of larvae released within a discrete time period) per year. The first is a sparse, early-summer cohort made up of the offspring of those few colonies which have survived the low temperatures of winter, and the second a more abundant generation whose recruitment peaks in late August (Whitlatch et al. 1995). The next desired piece of information along this line of investigation was the day-to-day timing of larval release, relative to daily fluctuations in water temperature and to tidal cycles.

The "Elvis" Experiment

To this end, the lab constructed a unique piece of equipment, affectionately dubbed "Elvis." Elvis possesses three main components (see Figure 3): (1) a circular plastic base of 2-ft radius, punctured with four, evenly-spaced circular holes; (2) on top of the disk, a mechanized carousel that rotates sixteen PVC plastic settlement surfaces in a circle, such that four settlement surfaces are exposed through the holes in the disk at any one time; (3) operating the carousel, a motor and computer sealed in a water-tight cylinder. The whole apparatus is designed to be suspended from a large tripod and placed on the seafloor. Elvis' internal computer could be programed to expose different sets of four settlement surfaces to the water column for any length of time. The apparatus can also be rigged with a thermometer that periodically measures the surrounding water temperature and records it in the computer's memory. When fully deployed, Elvis is suspended with its base and settlement surfaces facing downward (larval recruitment is highest on upside-down surfaces) with reproductive adult tunicates strapped onto the tripod nearby. In theory, at least some of the larvae released by the nearby tunicates would settle on the surfaces Elvis provided; in practice, recruits settled in low numbers, requiring many replicates of the experiment before trends became obvious. It was our task (the graduate students' and my own) to deploy Elvis and collect any data it might yield.

We programmed the machine to expose a different set of settlement panels to larvae in the water column during each phase of the mixed, semi-diurnal tidal regime operating at Avery Point: incoming tide, slack tide, and out-going tide. Elvis also recorded a temperature reading during each phase. In this way, we hoped to correlate larval release and settlement with particular temporal and tidal phases, as well as water temperature. We dropped the entire apparatus in relatively deep offshore water, amidst a wide swath of sandy bottom, where our dock-grown reproductive ascidians would be isolated from their wild
counterparts, and the experiment tightly controlled. With this set-up we also hoped to minimize the chance of introducing genes from the decidedly unnaturally-selected research dock population into less altered populations.

As the junior member of the team, it was my dubious task to “garden” sets of PVC collection panels for settlement of ascidian larvae, maintaining a continuous population of reproductive Botrylloides (and for comparative purposes, the native colonial ascidian Botryllus schlosseri) for deployment on the Elvis apparatus and in other experiments. I spent many hours staring through a microscope or lying on the research dock, locating recruits of the proper species and removing unwanted settlers. I felt not unlike a dental hygienist, picking away at heavy deposits of “marine plaque.” In return for this drudgery, however, I became intimately familiar with the animals’ developmental stages, and was exposed to a unique brand of microscopic beauty. When a set of panels was covered with reproductive ascidians (you could see eggs and sperm pouches embedded in the tunics), we were ready to run the “Elvis experiment.” Two or three times a month we’d strap on our SCUBA (in my case snorkeling) equipment to redeploy the experiment and collect the previous fortnight’s settlement panels. These would then be taken to the lab, where the number of recruits settled on panels corresponding to each tidal phase would be counted under a microscope.

Although I left before all data sets had been collected, preliminary results indicate that both Botrylloides and the indigenous Botryllus release their larvae in highest abundance at slack tide (the period of relatively quiet water after the peak high or low, but before the tide begins to turn), and when the water is relatively warm. Although the latter finding merely reconfirms earlier studies, the former came as somewhat of a surprise. Because of the lack of water movement during this phase, a slack tide larval release point is a potential limit on Botrylloides’ dispersal. In other words, Botrylloides cannot depend on tidal currents to spread its larvae far from a point of origin. The species’ rapid spread along the New England coast requires another explanation.

The key element in explaining and limiting the extent of any biological invasion, of course, is knowing how a species spreads after its initial introduction. The Elvis experiments tested one possible mechanism, and indicated that others must be involved. As mentioned previously, many aquatic species with prolonged larval stages become entrained in the ballast water of cargo vessels, and so are spread from one coastal zone to another along shipping lanes. Although one might reasonably suggest this vector to explain the spread of Botrylloides, this does not appear to be the case. Data gathered by the Whitlatch lab the past several summers all but eliminates the possibility.
**Undersea Columns: The Piling Experiment**

*Botrylloides* larvae seldom remain in the water column for more than 1 hour (Osman and Whitlatch 1995), another characteristic that should limit their dispersal capability. A second large experiment performed by our team this summer sought to confirm this prediction and determine how far larvae actually do disperse before settling. 3-foot high, 10-inch diameter PVC pilings were constructed and affixed with 20 evenly spaced settlement panels (Figure 4). One was chosen as the central or source piling, placed at another sandy, offshore site, and affixed with panels of reproductive *Botrylloides* (or, for comparison, *Botryllus*) for which larval densities had been estimated. The remaining pilings were placed in two concentric rings of radii one meter and three meters surrounding the source piling (Figure 5).

Sufficient space was left between the pilings in each ring to prevent a fencing effect, in other words, so that the 1-meter pilings didn’t block larval access to the 3-meter pilings and skew our results. Recruitment was allowed to take place for once week, after which the pilings were surfaced, and the panels removed and recruits counted. The overwhelming majority of the recruits that found their way to a piling settled on the central piling or on the 1-m pilings (personal observations). This result implies that *Botrylloides* relies on some vector other than larval phase transport in its spread from Woods Hole. One likely but unproven dispersal mechanism is the transport of adults attached to the bottoms of pleasure boats and other coastal craft (Whitlatch, personal communication).

**Interlude: Other projects**

My involvement as an intern was not always so focused. In between the periods of frantic activity surrounding the major projects, there were moments of more relaxed duty. In addition to “gardening” the ascidian stocks for use in experiments, regular tasks included counting settlers on a set of recruitment panels, maintained year-round, for all the members of the fouling community. These panels provide an important baseline of recruitment abundance for all the species that could potentially be studied. Early on, I spent several days at the library delving into the obscure literature of benthic ecology, attempting to answer various unknowns impeding the major experiments. For example, I was able to uncover a paper on the reproductive ecology of *Botryllus schlosseri* that described how to recognize a reproductively mature colony. This information allowed us to correctly select the animals ready to be included in the experiments of a given week. I also spent considerable time assisting Dr. Whitlatch’s graduate students
inhibited by the presence of native species on shared substrate (Osman and Whitlatch 1995). Taken together, these ecological characteristics offer a plausible explanation for the success of Botrylloides as an invader. The ascidian appears to have become a firmly entrenched member of the nearshore fouling community.

**Impacts Associated with Ascidian Invasions**

The effects of invasions (incl. Botrylloides”) on the fouling communities of the Sound have proven more difficult to establish than the actual mechanisms of invasion. Unlike the freshwater zebra mussel, which has invaded the Great Lakes on a massive scale, out-competing native filter-feeders and clogging water intakes, the ascidian invaders have for the most part quietly inserted themselves into the existing community structure. This is not to say that the invasions have had no impact. What effects they have had (and potentially could have) must be teased from the background noise of a complex and highly variable system.

Whitlatch and others have have adopted several approaches to this question. Initially, and not surprisingly, the impetus was economic. Early studies examined the impacts of the introductions of Botrylloides and another invasive tunicate, Styela clava, on the larval settlement and post-settlement mortality of the American oyster, a species still harvested commercially in New England. It was revealed that Styela has the capacity to ingest oyster larvae, and that competition with Botrylloides for substrate and food reduces the post-settlement survivorship and growth of oysters (Whitlatch et al. 1995). Although this information could prove useful in the management of commercial oyster beds, it is unknown whether oyster populations have been impacted by the ascidians outside the experimental setting.

During the short time period that ascidian invasions in Long Island Sound have been examined, the consequences of successive invasions have been relatively minor. Some introduced species, notably Botrylloides, have been shown to reduce the larval settlement of other ascidian and bryozoan species—but only when the density of the invasive adults is high. This effect could result from either competition for space or from the ingestion of small larvae by actively-feeding adult invader. The importance of this impact, however, appears limited: in many cases, it is not even observed; certain species settle thickly on top of preexisting animals, circumventing the space shortage problem. In 1995, a sickly-green colonial ascidian Diplosoma maldonaldi appeared at many sites in great abundance, resulting in local displacements of both native and introduced ascidian populations. By the next year, however, Diplosoma itself had
with their own projects, in the process learning about topics as diverse as the predatory behavior of invasive crabs, the surveying and mapping of beach profiles, and anoxia in the bottom waters of local estuaries. These peripheral activities added variety to an otherwise narrow research experience.

**An Unpleasant Mouthful: Botrylloides' Competitive Advantage**

The primary thrust of the internship, of course, was the experimental study of invasive ascidians, to which I made several individual contributions aside from the group work. The lesser of these individual projects provided a simple but important clue in the mystery of *Botrylloides'* successful invasion. A major control on the populations of most ascidians at Avery Pt., native and exotic alike, is the predation of the tiny snails *Anachis lafresnayi* and *Mitrella lunata*, and the fish *Tautogolabrus adspersus* (common name: cunner) (Osman and Whitlatch 1995). Dr. Whitlatch had suspected that the successful invasion of *Botrylloides* could be partially attributed to a chemical defense that protects it from predators and endows it with a competitive advantage over other species, and asked me to devise a short experiment to test this idea. My approach proved as effective as it was simple. In separate trials in the lab, I fed a population of food-deprived cunner either plain mussel flesh or a pulverized mixture of mussel and *Botrylloides*. The mussel was consumed greedily, while in the vast majority of trials, the mixture was violently rejected. This suggests that while the populations of other tunicate species suffer from predation, *Botrylloides'* bad taste defends it against at least some of the predators in the community. This could measurably increase its chance of successful settlement and maturation.

**A Successful Invasion**

A gradual accumulation of information has begun to expose *Botrylloides* as a model for successful invasion. Rather than being an especially rapid disperser, the species' success seems to stem from the ability to build abundant, concentrated populations of reproductive adults. With their short range dispersal, *Botrylloides* recruits can settle a single site in high densities. Because of their unpleasant taste, the recruits enjoy a high survival rate relative to other species, which only increases the relative density of *Botrylloides* in the community as a whole. Compared to the indigenous colonial ascidians present at Avery Point, *Botrylloides* develops rapidly, reaching adult size and reproductive maturity ahead of its competitors (personal observation). This allows *Botrylloides* to monopolize space and to turn out new generations in quick succession. In addition, the species' recruitment has not been found to be strongly
disappeared from some sites, and now appears to be on the wane as an invader. Other than this one episode, ascidian invasions have had no negative impact on biodiversity. No extinctions have occurred, and few declines in native populations have been observed. It may be the case that the Sound’s fouling communities will continue to prove resilient under this constant barrage; deeper impacts of repeated invasion, however may only become apparent with the passage of time.

Individual Project: the Impact of *Asciidiella*

For reasons no longer clear to me, I began this internship assuming that I would be researching the impacts of introduced tunicates on the local ecosystem, with the specific intent of finding methods to halt the flow of invasions. That the impacts would be serious enough to warrant some form of mitigation was implicit in my thinking. It came as somewhat of a shock to realize that the scientists I was to work with maintained at best a neutral attitude towards invasions.\(^6\) Not only would research be focused on more traditional topics in population ecology (albeit with the long term goal of understanding invasion processes to aid in invasion prediction), but the impacts of the *Botrylloides* invasion, already assessed and deemed minor, would not be touched on at all. I hid my disappointment, and swiftly discarded my earlier assumptions, but retained the notion of exploring the impacts of an invasion as an individual project. The opportunity presented itself the on the third day of the internship, in the midst of a whirlwind tour of the many species and genera I would have to learn to identify under the microscope. What at first appeared to be an off-white speck of gelatinous crud, barely visible under a microscope set at 6.5X magnification, turned out to be the an early recruit of the solitary tunicate *Asciidiella aspersa*, one of the species most recently introduced to the system. One of the students I worked with, Mike Berger, had undertaken the initial study of the species’ reproductive ecology and community impacts several years earlier, and had extracted the surprising result that, in low densities, the presence of adult *Asciidiella* on settlement surfaces actually increased the settlement densities of other fouling species.

Suddenly, my mind latched onto a completely different conception of what could qualify as an “impact.” I had been locked into thinking that an invader would cause the decline of native species, or otherwise have no impact at all; now I realized that it could also work in the opposite direction. Mike’s talk of an invader stimulating settlement in the benthic community brought to mind the concept of the

\(^6\) At one point, I overheard one of the graduate students voice the opinion that perhaps invasions are a good thing, given the amount one can learn about ecology in their aftermath. I saw his point, but couldn’t help but feel that there was something flawed in his reasoning.
positive feedback loop. I imagined an *Ascidiiella*-impacted community becoming more and more crowded with animals of all species, until it reached a point where its consumption of resources limited its growth, forced the decline of some species, or began to impact the larger ecosystem. I kept this wild, indefensible train of thought to myself, but my interest was piqued to learn more. Eventually, I decided to attempt an independent project with more modest objectives, given the multiplicity of tasks I was expected to perform as an intern.

I chose to build upon Mike's research, and attempt to tease out the mechanism of *Ascidiiella*'s curious effect on the fouling community. My hypothesis was that the observed effect is biological, that the tunicate releases some sort of chemical cue that is sensed by larvae, causing them to settle nearby. To call this a "chemical cue" is perhaps misleading, for the effect Mike observed included but was not limited to *Ascidiiella* recruits. Whether or not *Ascidiiella* actively secretes a cue to aid its own larvae, inadvertently aiding other species as well, is a question one step beyond the scope of my project. The alternative to my hypothesis was that the observed effect is hydrodynamic—that is, that the tunicate’s profile in the water column creates a pocket of calm water in which larvae are more likely to try to settle.

To test these possibilities, it was necessary to produce three different settling "environments," or, more formally, treatments, to be used in the experiment. The first, of course, was one in which larvae could settle among a low-density assemblage of adult *Ascidiiella*. Following Mike's earlier procedure, I drilled small holes in the lab's standard 100 cm² PVC settlement panels, and attached two adult animals, harvested from the local waters, to each one by means of gently-tied monofilament line. The more difficult task was to devise an environment that mimicked the hydrodynamic profile of *Ascidiiella* without the biological effects of a living organism. I eventually settled on carving *Ascidiiella* "dummies" out of polystyrene, and spent one messy night at home with a pocket-knife, fashioning replicas to specifications that a small survey indicated were the average dimensions of the adult tunicate. The dummies (2 per panel) were easily affixed to the panels with a chemically-inert silicon-based aquarium sealant. The final treatment, a control of blank panels, was necessary in order to reconfirm Mike's findings. If I could not show that a low-density *Ascidiiella* treatment collected a higher density of recruits than a blank panel, then the comparison with the "dummy" panels would carry less weight. Once eight panels of each treatment had been prepared, they were randomly attached upside down to a mobile of horizontal PVC pipes (figure), and suspended off the Avery Point research dock, in the midst of a virile fouling community. After being exposed to recruitment for a week, I retrieved the panels, and, under the microscope, the counted the recruits of each species. I repeated this sequence several times before perfecting the
experiment to the point where I could gather usable data. I culled the two trials with the fewest technical problems (e.g. dead tunicates, tunicates that mysteriously disappeared, faulty glue-jobs, etc.) for analysis.

Given the number of late nights I spent in the lab, counting tiny specks and wearing out my favorite cassettes long after all but the most disturbed graduate students had gone home, my results seem modest. For most species, recruitment densities were significantly higher on the live-Asciidiella panels than on either of the other two treatments (see Figures 6 & 7). In other words, I reconfirmed Mike’s finding, and in addition determined that for many species, the presence of Asciidiella adults exerts a strong biological effect on larval settlement. My original notion of a biological positive-feedback loop was not so foolish after all; unfortunately, I’d managed to take only one small step towards understanding Asciidiella’s impact as an invader.

My findings may actually be most applicable to understanding the apparent success of the Asciidiella invasion: a species that, through its own presence, can increase the recruitment success of its own larvae (Asciidiella recruitment abundances were highest for the live-animal treatment in both trials) is well-equipped to establish itself in a new community. There is a limit to this effect I have dubbed a “biological positive feedback.” The recruitment-augmentation effect only occurs when a low density of Asciidiella adults reside on the recruitment panels. As the number of adult tunicates on the panels increase, the effect dissipates, presumably as a result of increased competition for the limited supply of substrate and food resources (Berger 1995). Even with this reservation, it is safe to suggest that the presence of Asciidiella can facilitate the rapid early development of a fouling community; by the same token, the tunicate’s positive effect on its own recruitment when adult density is low may be a favorable trait in the early stages of invasion.

The Internship in the Eyes of the Intern

The Asciidiella project emerged a success, yielding intelligible results, and providing me with the independent research experience I had desired. After a short period of grovelling, I was granted a key role in the larger research activities of Dr. Whitlatch’s lab, which enjoyed a relatively productive summer. My co-workers accepted me into the close-knit fold of their small research team, and the backslaps and casual “so longs” exchanged on my last day disguised some real regret at the separation. Even my seldom-seen supervisor, Bob Whitlatch, seemed to appreciate my efforts, and on the occasions I had the opportunity to chat with him, offered friendly and valuable insights into science and the life of a scientist. On what
grounds could I claim dissatisfaction?

From my present vantage point, removed from the internship by thousands of miles and several months, I can look back and recognize the value of the experience with a certain detached objectivity. I can play the pragmatist and reassure myself that this intense exposure to experimental science looks great on my resume, that I'm a solid nine units nearer to a university degree thanks to the summer's activities. I can play the intellectual, and revel in having gained the basis for a new area of expertise. The reward-seeker in me can find validation in having completed another independent project with a certain amount of competence. I can simply be thankful I didn't spend the summer taking physics at Foothill or mopping up spilled lattes in a dark Santa Cruz cafe. I am all these things (pragmatic, intellectual, pathetic, thankful), but I am also hard to please. I felt and still feel a certain amount of disappointment because my internship fell short in one crucial aspect: it was not consistently the most enjoyable and engaging part of my summer.

Lounging on the deck of the research skiff Tautog on a sunny afternoon, riding the incoming swells and listening to the gentle gurgle of the divers' air rising through the surface, I'd dread the inevitable hours to be spent in the lab, counting the small specks we called research subjects. During moments like these, I could not help but feel that I'd gain more through listening and seeing, by simply absorbing my surroundings, than by collecting and analyzing any number of data sets. I'm not talking just about laziness or lack of discipline, although these certainly contributed to my malaise. The tedium of repeated tasks, and the slow, incremental accumulation of results often left me frantic, convinced that the work I was doing was pointless. It wasn't, of course, but it did conflict with my present temperament on a very basic level.

This vague feeling of disappointment may in fact be the most valuable piece of information imparted by the internship. I have emerged from the experience still committed to environmental science and the natural world, but far less sure that I want to play the role of a scientist (or, more accurately, a benthic ecologist). I proved to myself that I capable of doing so, but suspect that I would find more fulfillment elsewhere.

In this paper I have traced a jagged line from my original interest in the global phenomenon of biological invasions to the past summer's immersion in the study of a few localized invasions. Despite this recent and rapid narrowing of focus, I have tried to keep the larger problem in the periphery of my vision. I retain my original belief, tempered by gained knowledge and a bit more judgment, that humans
accelerate the natural processes of species invasion and spread at their own peril. The potential for damage to both human and natural systems exists. If I have learned one thing, it is that even the most obscure corners of the natural world are dizzyingly complex. This complexity alone requires that humans learn to look at the world with respectful, cautious eyes.
**Figure 1**

**Prototypical Solitary Ascidian**

- Incurrent (buccal) siphon
- Excurrent (atrial) siphon
- Internal pharyngeal basket (filters food)
- Intestine
- Tunic
- Basal threads
- Hard substrate

**Figure 2**

**Colonial Ascidian**

- The colony attaches like a thick film or slime to any hard substrate
- Tunic
- Matrix
- "Systems" of zoid systems
- All zoid systems are connected by a common vascular system, and blood circulates throughout the colony

**Detail of a zoid**

- Incurrent siphons
- Excurrent siphon
- Each zoid is made up of 6 to 7 semi-autonomous members

Modelled from Carlton (1996), unpublished
"Elvis" Apparatus: Simplified Side-View

(several mechanical support structures are excluded, as well as the arms from which the apparatus is hung)
Recruitment piling for larval dispersal distance experiment
Piling experiment with Botrylloides

Deploy: 8 July 97
Retrieve:
Census:

Piling # placement map

clump

7 39 44 31 12

current direction

93

40

- adult Botrylloides colonies were allowed to re-attached to panels
- panels #1-5 will always face towards the central piling
- the piling were set up to be along a perpendicular and parallel transect with regard to the current controls

37 6
Literature Cited


