Vertical Zonation and Seasonality of the Intertidal Hydroid *Dynamena pumila* in the Passamaquoddy Bay Region, New Brunswick

by

Lea-Anne Henry

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Graduate Department of Zoology
University of Toronto

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**ABSTRACT**

Size, distribution, and fertility of the hydroid *Dynamena pumila* were examined along desiccation, water movement, and seasonal gradients on five rocky shores in the Passamaquoddy Bay region of Atlantic Canada. Size generally peaked between 50 and 62.5% of the shore height, at sites with strong water movement during the summer. The frequency of occurrence peaked between 37.5 and 50% at all sites except at the second most exposed station. Colony frequency increased with strong water movements and peaked during the fall. Mortality of transplants increased at higher elevations, while transplants at lower levels experienced mortalities not significantly different from the controls. Lower limits were likely set by larval preference for settling near conspecifics. Reproduction rates were greatest in summer, peaking at the most exposed site. Hydroid abundance did not explain much of the variance in colony stem height. A highly predictive relationship was found between abundance and percent occupancy.
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1. INTRODUCTION

1.1 Zonation Patterns on Rocky Shores

Rocky shores exist within a continuum of several principal environmental gradients: among these are a vertical gradient (from low shore to high shore), a horizontal gradient (from sheltered waterways to exposed coasts), and a salinity gradient (from brackish estuaries to fully oceanic sites). Thus, the marine rocky intertidal environment provides a "natural laboratory" within which researchers may develop and test ecological concepts about factors that regulate populations and communities.

Research on rocky intertidal zonation began with qualitative descriptions of the vertical distribution patterns of organisms, primarily on the coasts of France (Audouin and Milne-Edwards, 1832; Vaillant, 1891) and the United Kingdom (Colman, 1933). Doty (1946) observed that organisms of the rocky intertidal on the Pacific coast of the United States were sharply zoned into seven discrete areas that were highly correlated with tidal levels. The upper and lower limits of many organisms appeared to be established by "critical" tide levels.

General trends in the characterization of intertidal biotic vertical zonation emerged only after Stephenson (1936) made observations about common features in the zonation patterns on shores as distant from each other as Scotland and South Africa. This observation led to the conception and development of the Stephensons' "universal classification scheme of zonation" (Stephenson and Stephenson, 1949, 1972), which they later renamed their "general zonation scheme". The scheme proposed that a rocky shore could be divided into three zones: the supralittoral (upper shore), midlittoral (mid-shore), and the infralittoral (lower shore) zones. The distinction of this scheme from previous
ones was that it divided the shore into areas based on biological patterns instead of physical parameters such as critical tide levels. Researchers from different parts of the world could easily compare their studies to those of others because it was no longer necessary to first convert a tidal elevation in one study area to the appropriate level at another study area. For example, Southward (1958a) used the Stephensons’ general scheme to compare zonation patterns on rocky shores with very different tidal regimes, such as those of North and South America, Jamaica, South Africa, and Australia. A slightly modified version of the Stephensons’ scheme was proposed by Lewis (1955, 1964), who preferred the term “eulittoral” to the Stephensons’ “midlittoral” zone.

Not every rocky shore ecologist adopts the Stephensons’ general classification scheme. Critical tide levels are still used to delineate zones in the rocky shores of the Pacific coast of the United States (Foster et al., 1988, 1991). Another classification method developed for Mediterranean rocky shores identifies four main zones (Pérès, 1967): the supralittoral, mediolittoral, infralittoral, and circalittoral zones. A third alternative identifies a boundary "litus" line at the lower limit of the supralittoral that can be used to discriminate assemblages of intertidal organisms (Russell, 1972; Bolton, 1981). Different schemes conceived for different areas suggests that site-specific factors modify the effects of the tides to produce upper and lower limits of shore organisms.

1.2 Physical Factors

Many physical forces affect the distribution of shallow-water marine organisms. These include substrate size (Raffaelli and Hughes, 1978; Brown and McLachlan, 1990) type (Chapman, 1990; Benedetti-Cecchi and Cinelli, 1992) and complexity (Crisp and Barnes, 1954; Lubchenco, 1983), water salinity (Broekhuysen, 1941; Calder, 1976) and
temperature (Naylor, 1965; Thorhaug et al., 1979; Jokiel and Coles, 1990), gradients of oxygen (Meyers et al., 1987) and light (Palmer and Round, 1965).

Two main physical factors that modify the distribution of intertidal organisms are wave exposure (Ballantine, 1961; Foster, 1969; Dayton, 1971; Menge and Sutherland, 1987; Crothers and Hayns, 1994) and desiccation (Southward, 1958b; Ballantine, 1961; Connell, 1961a; Foster, 1969; Landenberger, 1969). The extent to which zonation is affected by desiccation is itself modified by factors such as wind, humidity, precipitation, temperature and emersion periods. A major conclusion from these studies is that organisms are able to expand their upper limits on wave exposed coasts. Increased wave action creates more wave splash, effectively reducing the stress of desiccation on intertidal organisms during periods of emersion. Therefore, physical factors interact with each other and with the tides to influence the distribution of organisms in the rocky intertidal.

1.3 Biological Factors

However, Connell (1961a,b) observed that the settlement and recruitment of some species of cyprid barnacle larvae did not always coincide with apparently optimal conditions at lower shore levels. It appeared that other environmental forces must interact with physical factors to modify rocky intertidal organism distribution.

The importance of biological factors in structuring rocky shore habitats was recognized in two classic accounts by Connell (1961a, 1961b). He examined the dynamics of competition between two species of barnacles, Chthamalus stellatus and the larger Semibalanus balanoides on the Isle of Cumbrae in Scotland. Semibalanus balanoides was removed from experimental plots at mid-shore, resulting in a
considerably higher proportion of *C. stellatus* surviving. Within the upper shore, however, removal of *S. balanoides* showed no significant effect on the survival of *C. stellatus*. Thus, the lower limit of *C. stellatus* was likely determined by competition for space with *S. balanoides* (Connell, 1961a). However, addition of *S. balanoides* to lower shore levels by Connell did not increase the effectiveness of *S. balanoides* as a competitor of *C. stellatus*. This was presumably due to increased predation effects by the dog whelk *Nucella lapillus* on *S. balanoides* at these lower levels (Connell, 1961b). Therefore, predation may interact with competition for space to produce the structural patterns of rocky shore communities.

Paine (1974) identified the dynamics of predation-competition interactions on the Pacific coast of the United States. Manual removal of the "top predator", the starfish *Pisaster ochraceus*, allowed the mussel *Mytilus californianus* to out-compete and exclude other space-limited species in the lower intertidal. Removal of *P. ochraceus* seemed to permit increased competitive effects that "cascaded" from the top trophic levels to those further down. This produced an intertidal community that was dramatically different from the one observed before *P. ochraceus* was removed. This experiment led to Paine’s (1974) conception of the "keystone-species-hypothesis," which suggested that community regulation can be controlled primarily by one species, usually a top predator.

In more recent years, the importance of "bottom-up" effects such as herbivory (Paine and Vadas, 1969; Breen and Mann, 1976; Estes *et al.*, 1978; Lubchenco, 1978; Lubchenco and Gaines, 1981) and productivity (Bosman and Hockey, 1986; Gibbons and Griffiths, 1986; Glynn, 1988) on intertidal community regulation have been investigated. One of the most significant findings was that herbivore diversity, food preference, and
algal competitive abilities are at least as important in regulating intertidal communities as is the density of herbivores (Lubchenco, 1978; Lubchenco and Gaines, 1981). This was an interesting discovery as it explained why areas with a relatively high density of herbivores could sustain relatively high algal density and diversity.

Another noteworthy discovery was that Central and South American populations of marine mammals, iguanas, birds and invertebrates collapsed following the 1986 El Niño event (Glynn, 1988). Glynn attributed these population reductions to decreased primary productivity as a result of reduced nutrient upwelling.

Top-down and bottom-up biological factors can therefore not be treated as mutually exclusive from one another or from the continuum of physical factors that exists on vertical, horizontal and salinity gradients. Ultimately, models that integrate these factors will greatly expand the general understanding of intertidal community regulation.

1.4 Modelling Community Regulation

Synthesis of "multifactorial" models that integrates physical and biological factors into shallow marine community regulation is becoming more prevalent in the primary literature (Dayton, 1971; Underwood et al., 1983; Dayton et al., 1984; Sebens, 1985, McQuaid and Branch, 1985, Sebens, 1986; Robles, 1987). The most comprehensive accounts of intertidal community regulation have been by Menge et al. (Menge, 1976, 1978a, 1978b, 1991, 1992; Menge and Sutherland, 1976, 1987; Menge et al., 1986; Menge and Farrell, 1989). These accounts have resulted in the conception and development of models that explain and predict previously unresolved spatial and temporal variations in community regulation within and among rocky shores. For example, Menge (1992) sought to explain the presence of two very different low shore
communities that shared a similar range of wave exposure along the coast of central Oregon. He predicted that predation by *Pisaster ochraceus* would be more intense in communities with elevated nutrients because increased primary production rates would likely increase the recruitment and growth of benthic species having planktonic larvae. In short, bottom-up factors are linked to top-down factors. A model that permits this link should be supported by experiments that test differences in predation rates, prey recruitment, and prey growth between sites. Menge empirically tested these predictions and found significantly greater prey mortality rates at the site with the higher abundance of prey items. This site also supported significantly higher prey growth rates and recruitment. He concluded that higher prey abundance supported greater predator abundance that in turn created increased predation intensity. Although primary production was not quantitatively measured, it is likely the factor responsible for increased prey growth at this site. Therefore, increased productivity effectively increased predation intensity, resulting in a very different low shore community from that at a different site with slower prey growth and recruitment processes. Thus, Menge's model predicted and empirically tested the relative importance of factors responsible for the regulation of intertidal communities in this area. Future research should likewise pursue the multifactorial dynamics of community regulation over a variety of spatial and temporal scales.

1.5 Conservation

Rocky intertidal ecology has developed into a science that seeks to explain the spatial and temporal dynamics of rocky shore biota over small to large scales. The predictive value of this science is also a noteworthy goal of rocky shore ecology,
especially in light of potential and apparent anthropogenic threats to marine habitats worldwide. At a local scale, acute threats to the rocky intertidal include trampling by humans (Hockey and Bosman, 1986; Bally and Griffiths, 1989; Povey and Keough, 1991), collection of ornamental species (Rubec, 1988; Newton et al., 1993), and increased eutrophication and other kinds of pollution in the form of industrial and human wastes (Rafaelli and Hawkins, 1996). Over a larger spatial scale, acute threats to the intertidal environment include oil spills (Sanders, 1977; Southward and Southward, 1978; Thomas, 1978) and their associated "remediation" techniques (Southward and Southward, 1978). Chronic small scale impacts include the exploitation of commercial and ornamental species (Rubec, 1988), the introduction of exotic species through the release of ballast water (Crisp and Chipperfield, 1948) or by the construction of man-made canals (Hildebrand, 1939; Ben-Tuvia, 1973) and the slow but consistent release of toxic industrial chemicals (Rafaelli and Hawkins, 1996). The largest scale threats to the marine rocky intertidal are likely attributable to the effects of global warming and rising sea temperature (Glynn, 1988, 1991; Southward et al., 1995). Once the dynamics of patterns and processes in the rocky intertidal are identified, models that predict the outcomes of threats as well as restoration measures can be developed and evaluated for their reliability and accuracy.

1.6 The Bay of Fundy

The ecology of rocky intertidal shores has been studied most extensively in areas such as the Pacific coast of the United States, the United Kingdom, South Africa, and Australia. Paradoxically, very little is known about the dynamics of rocky shores in the area of the world with the largest intertidal zone, the Bay of Fundy ("Fundy") in the
boreal Northwest Atlantic. Tidal ranges extend over 20 meters in some areas of the bay, resulting in the most extensive rocky intertidal environment in the world.

Although Stephenson and Stephenson (1954a, b) recognized general patterns in the zonation of rocky intertidal biota between the northwestern Atlantic and rocky shores elsewhere, the Fundy rocky intertidal zone is structurally unique. Research investigating the forces that regulate these communities is patchy: consequently, factors that are important in determining rocky community organization in the Fundy region are simply unknown.

Ecological research in the Fundy region has largely been directed toward the health and sustainability of regional fisheries. For example, overexploitation of the American lobster, *Homarus americanus*, in shallow subtidal environments has been accompanied by an increase in density of the voracious echinoid algal grazer, *Strongylocentrotus droebachiensis* (Breen and Mann, 1976). Along the coasts of Newfoundland and Nova Scotia, the response of algal communities to grazing varies biogeographically as well as with local ecological factors (Himmelman and Steele, 1971; Miller *et al.*, 1971; Breen and Mann, 1976; Chapman, 1981; Chapman and Johnson, 1990; Keats, 1991; Keats *et al.*, 1991). Alternatively, lobster productivity is limited by lower trophic levels such that increasing algal density and production could increase lobster production (Miller *et al.*, 1971).

The high tides of the Fundy region have also been the focus of proposals for the development of tidal power projects. The intertidal zone would be influenced ecologically by such development, and local studies have examined some of the potential impacts it would have on rocky shores (Gordon and Longhurst, 1979; Dadswell *et al.*, 1979).
1986; Gordon, 1994). Major shifts in rates of primary production and abundances of invertebrates, fishes and shorebirds are predicted as a result of tidal power development (Gordon, 1994). Currently, interest in the development of large scale tidal power project in the Fundy region remains dormant for economic reasons (Gordon, 1994).

Accounts by Thomas and colleagues (Hughes and Thomas, 1971a, 1971b; Thomas, 1975, 1983, 1994) are by far the most recent and comprehensive investigations of flora and fauna in the Fundy region. Thomas preferred to use the Stephensons' general zonation scheme to describe patterns in the intertidal biota, although like Lewis he used the term "eulittoral" in place of "midlittoral". Thomas' examination of intertidal biota in the Quoddy region quantified biomass diversity and evenness indices, and the upper and lower limits of the most abundant floral and faunal species. His accounts were exceptional in that they are the only quantitative assessments of intertidal biota and their biomass and diversity patterns, on Fundy rocky shores.

Although Thomas (1994) delineated upper and lower limits of major intertidal species in the Quoddy region, the influence of intertidal gradients and associated modifying factors on rocky shore dynamics of the area can only be inferred from studies performed elsewhere. Thus, factors responsible for zonation and seasonality of most intertidal organisms in the Fundy region have not been determined.

1.7 The Intertidal Hydroid *Dynamena pumila*

*Dynamena pumila* (Linnaeus, 1758; Cnidaria: Hydrozoa) is a colonial leptothecate hydroid that is ubiquitously distributed throughout the rocky intertidal of the boreal North Atlantic (Fraser, 1944, Naumov, 1969; Rasmussen, 1973; Boaden *et al.*, 1975; Cornelius, 1979, 1995; Hughes, 1992). It is commonly found attached to the base
of algal stipes, including *Ascophyllum nodosum* and *Fucus* spp., although colonies are found attached directly to rocky substrates on more exposed coasts (Cornelius, 1979). *Dynamena pumila* is a euryhaline species, with optimal conditions of salinity in the 20-35% range (Burykin, 1980a, b, 1989). Specimens have been observed in estuaries and fjords (Broch, 1918; Kramp, 1929; Rasmussen, 1973). Although a specimen has been collected at a depth of 270 meters (Naumov, 1969), *D. pumila* is almost strictly intertidal: the former record may simply have been a case in which a colony had broken off from an intertidal substrate and sunk with it to bathyal depths.

Being ubiquitously distributed, the biology of *Dynamena pumila* has been examined on both sides of the North Atlantic. Colonies arise from a creeping stolon ("hydrorhiza") and exhibit an upright growth form reaching about 75mm high (Lewis, 1964). Gross phenotypic variation in colony forms has been recorded in response to several environmental factors. Along a vertical gradient, colonies at the lowest shore levels have been found to exhibit more branches (Broch, 1918), greater colony heights (Wood and Seed, 1980), and higher percentages with (reproductive) gonophores (Cornelius, 1979). Populations on exposed coasts generally have shorter stem heights (Seed *et al.*, 1983), and exhibit thicker perisarc and stouter hydranthus (Cornelius, 1979) than those found at more sheltered sites. In fact, the correlation between presence of *D. pumila* and increased wave exposure was sufficiently high (Cornelius, 1979; Seed *et al.*, 1983) that Thomas (Thomas, 1983) proposed using *D. pumila* (reported as *Sertularia pumila*) as a biological indicator species of wave exposure in the Quoddy region. Increased wave action and water currents appear to favour the occurrence of *D. pumila* (Seed *et al.*, 1983), but their effects on hydroid colony height remain unclear: increased
Hydroid abundance resulted in an overall decrease in mean height (Seed et al., 1983) in the Strangford Lough area of Ireland, although Wood and Seed (1980) observed the opposite at higher elevations and no correlation at all in the lower tidal elevations in the Menai Straits of North Wales. Increased food availability increased hydorhizal growth and branching and the number of hydranths (Marfenin and Burykin, 1979; Burykin, 1980a). A resting dormant stage of *D. pumila* has been reported (Haddow, 1937) that allows the hydroid to survive adverse weather conditions and to regenerate during favourable periods.

The upper and lower distribution limits of *Dynamena pumila* in the rocky intertidal have been qualitatively recorded in the Quoddy region (Thomas, 1994). Notably, these do not coincide with limits recorded in the boreal northeastern Atlantic (Wood and Seed, 1980; Orlov, 1996a). Thomas observed the lower limit to be slightly above the intertidal-subtidal interface, although his study did not examine factors that may have determined this distribution. Wood and Seed noted that colonies were most abundant at the intertidal-subtidal interface, and attributed the upper limit to desiccation stress. Orlov noted that colonies from the White Sea area were found predominantly at the intertidal-subtidal interface. Initial experiments by Orlov demonstrated that despite being able to survive at depths to 15 meters, the actual distribution of *D. pumila* only extended to a depth of 8 meters. He investigated the importance of settlement behaviours in the planula larvae of *D. pumila* in determining this lower limit. From preliminary studies, planulae were released during slack water at low tidal emersion and would disperse no more than 5 meters from maternal colonies. Furthermore, larvae were induced to settle and metamorphose by a microbial film covering intertidal fucoid algae.
To resolve the discrepancy in reported lower limits of *D. pumila* from northwestern and northeastern Atlantic regions, the abundance of *D. pumila* should first be quantified and not simply recorded qualitatively. Secondly, the importance of physical and biological factors in determining the lower distribution limits of *D. pumila* needs to be established. The dynamics of *D. pumila* populations may then be understood under a variety of environmental conditions.

An autoecological study of *Dynamena pumila*, and its zonation and seasonality, provides information on dynamics of Fundy rocky shores. *Dynamena pumila* is not only one of the few marine organisms largely restricted to the intertidal zone, but it is also an ideal species for experimental work and an ecologically important component of the biota of Fundy rocky shores.

*Dynamena pumila* can easily be sampled during periods of tidal emersion because it is sessile and benthic, abundant, and widespread on Fundy rocky shores at all times of the year. Thus, data should be easily compiled for several sites throughout several seasons.

Hydroids, including *Dynamena pumila*, are known to exhibit broad phenotypic variation in response to physical gradients. For example, dramatic variation in hydroid form has been observed over water velocity (Riedl, 1966; Boero, 1981; Mergner, 1987; Piraino and Morri, 1990) and salinity gradients (Kinne, 1971; Kinne and Paffenhöfer, 1966, Burykin, 1989). Variation in hydroid form and fertility associated with fluctuations in water temperatures has also been documented for several hydroid species (Ralph, 1956; Kinne, 1963; Calder, 1971, 1990). Significant variation in hydroid height, the number of branches, and the frequency of gonophore production has been quantified
across vertical, water depth, and wave exposure gradients for the closely related warm-water species, *Dynamena crisioides* from the Twin Cays region of Belize (Calder, 1991a). Therefore, effects of environmental factors on hydroid distribution should be relatively easier to distinguish and quantify than on organisms that are simply present or absent under variable physical conditions.

Space is a limiting factor in the settlement and growth of sessile invertebrates on rocky intertidal shores. Therefore, biological factors such as competition should also be considered for their relative importance in determining the distribution of *Dynamena pumila*. Seed et al. (1983) found that *Dynamena pumila* was more sensitive to competition with the bryozoans *Electra pilosa* and *Flustrellida hispida* than another intertidal hydroid, *Gonothyraea loveni*. Other potential competitors such as encrusting bryozoans, sponges, and tunicates can often smother hydroids. However, interference between these animals and *D. pumila* appears unlikely because the abundance and diversity of these animals are greatly reduced in the intertidal zone of the Quoddy region. Furthermore, the opportunity for competition is likely reduced by the upright growth form exhibited by *D. pumila*: erect stems are placed high above competitors, putting the hydranths in unobstructed positions to feed on plankton (Stebbing, 1973). Interspecific competition with other hydroids is also unlikely to influence the distribution of *D. pumila* in any significant way because there are few other hydroids found intertidally. Thus, the likelihood of interspecific competition modifying occurrence and morphology of *D. pumila* is potentially diminished such that hydroid distribution should be attributed to fewer environmental factors.
*Dynamena pumila* is an abundant and ecologically important element of the Fundy rocky intertidal biota. Benthic suspension feeders have been shown to have significant impacts on the plankton communities from which they feed (Dame *et al.*, 1980; Officer *et al.*, 1982; Cohen *et al.*, 1984; Jørgensen, 1990). Recent investigations into benthic-pelagic coupling systems in marine habitats demonstrate the potential for hydroids to significantly contribute to energy flow. Prey capture rates as high as 800 000 prey items per meter squared per day were recorded for the hydroid *Campanularia everta* (Coma *et al.*, 1995), and estimates of mass-specific ingestion rates for other hydroid species are comparable to those estimated for active suspension feeders such as tunicates and bivalves (Gili *et al.*, 1998). This ranks hydroids among the most voracious suspension feeders of shallow-water marine ecosystems (Klumpp, 1984; Griffiths and Griffiths, 1987; Barange and Gili, 1988; Gili *et al.*, 1996; Gili *et al.*, 1998). Quantifying suspension feeder biomass along environmental gradients is therefore a preliminary step in understanding the dynamics of benthic-pelagic coupling in the rocky intertidal.

Notably, hydroid reproduction often coincides with periods of increased prey density (Gili *et al.*, 1998). This is ecologically interesting because it adds a temporal component to the way in which plankton communities are impacted by hydroids and vice-versa. Understanding benthic-pelagic coupling mechanisms requires that the reproductive periodicities and seasonality of hydroids and factors that modify these cycles be quantified.

Hydroids are extremely efficient suspension feeders and zooplankton predators, considering their negligible contributions to the total benthic community biomass (Boero, 1984). Factors that influence the distribution and growth of hydroids in the Quoddy
region will ultimately affect rocky shore food webs, the distribution of plankton communities that contribute energy to intertidal and subtidal habitats, and even regional fisheries.

1.8 Objectives

The primary goal of this study is to relate distribution and growth patterns of *Dynamena pumila* in the Quoddy region to environmental factors. This goal incorporates two research objectives: (1) establishing the seasonal distribution and growth of *D. pumila* over vertical and horizontal intertidal gradients and (2) determining the statistical and biological significance of physical and biological factors as they relate to *D. pumila* and its overall distribution.

1.9 Systematic account

*Dynamena pumila* (Linnaeus, 1758)

(Figure 1)

*Sertularia pumila* (Linnaeus, 1758), *Cellularia bursaria* (Ellis, 1768),

*Dynamena pumila* (Lamoureux, 1812), *Nigellastrum pumilum* (Oken, 1815)

*Type locality:* "Habitat in Oceano" (Linnaeus, 1758); type locality of neotype restricted to Rattingdean, near Brighton, U.K. (Cornelius, 1979).

*Description:* Colonies erect, up to 75mm high, with cormidia arising from a creeping hydrorhiza. Hydrocaulus monosiphonic, divided into internodes, unbranched or with one or more branches. Hydrothecae nearly cylindrical, opposite to sub-opposite, 2 hydrothecae per internode, separated front and back, curving outward distally. Hydrothecal margin with two large, lateral teeth, and a small, median adcauline tooth. Operculum with 2 valves. Gonophores fixed sporosacs, with planulae brooded in an
external acrocyst. Gonothecae ovoid, somewhat rugose, with wide aperture and very narrow collar, and arising from front of hydrocaulus.

**Habitat:** Predominantly intertidal, typically attached to fucoids and directly to rocky substrates. Eurytopic, tolerating reduced salinities to about 5‰ salinity and water temperatures between 2-20° Celsius.

**Recorded distribution:** (Atlantic Canada) Nova Scotia, Labrador, Passamaquoddy Bay, Canso, Seven Islands, Eastern Harbour, Cheticamp, Gulf of St. Lawrence (Fraser, 1944). (Western Atlantic) Southern Labrador to New Jersey (Fraser, 1944). (Worldwide) Boreal North Atlantic (Cornelius, 1995).

**Remarks:** Cornelius (1979) regarded *Sertulardia pumila* Linnaeus, 1758 and *Sertulardia bursaria* Linnaeus, 1758 as synonyms. In the interests of nomenclature stability, he chose the more familiar specific name *pumila* as having precedence over *bursaria* under the First Reviser Principle in nomenclature (I.C.Z.N., Art. 24). However, Cornelius (1995) later reported that *Sertulardia bursaria* Linnaeus, 1758 was actually a bryozoan, now under the genus *Epistomia*. Hydrothecal shape varies in *Dynamena pumila*, such that this character can be used as a biological indicator of wave exposure. Couch (1844) reported that agitation or slight heating caused specimens of *Dynamena pumila* to bioluminesce, probably due to adhering “Entomostraca and Acalephae”.
Figure 1: Colonies of the hydroid *Dynamena pumila*. (a) (Actual size.) *Ascophyllum nodosum* fouled by several cormoids of *D. pumila* showing stoloniferous network connecting hydroid plumes. (b) (Actual size.) A large, branched single cormoid of *D. pumila* with gonophores attached. (c) (Scale shows 1 millimeter.) Erect hydrocaulus with alternately to sub-oppositely paired tricusped hydrothecae and attached gonophore.
1.10 Description of Study Area

Events that followed the Pleistocene glaciation have strongly influenced the present day geology and biology of the Quoddy region. As glaciers retreated 16,000 years ago, bedrock shores eroded, releasing large quantities of sediment deposited in the form of sand flats, mud flats, and salt marshes (Gordon, 1994). Sea levels also began to rise as a direct result of glacial retreat, and flooded much of Atlantic Canada. The sea level of the Gulf of Maine increased substantially, resulting in a mean tidal amplitude of about 5.5 meters in height throughout the Quoddy region.

The amplitude of the semi-diurnal tidal flow in the Quoddy region remains unusually large for two reasons. First, the Bay of Fundy is funnel shaped, so that water is moved to the progressively narrower head of the bay during periods of high tide and away from it during low tide. Secondly, the natural period of oscillation in the bay coincides with and amplifies that of the gravitational effects exerted on the tides.

The Quoddy region is influenced by the cold Labrador Current, and by mixing of waters due to the extreme tidal range. As a result, waters of the Quoddy region remain cold even during summer months. Annually, water temperatures may range from -2 to 13°Celsius throughout the year. This has profound biological effects on the biota of the region, including that of its rocky shores. For example, areas of significant upwelling are created where deep and cold nutrient rich waters are vertically mixed with layers above. Nutrients are brought to the surface waters by interaction of the large tidal ranges and the main current, thereby increasing rates of biological productivity (Rafaelli and Hawkins, 1996).
According to one hypothesis, rocky shores of the boreal northwestern Atlantic have been colonized by European flora and fauna that escaped the effects of the Pleistocene glaciation (Ingolfsson, 1992). This hypothesis was based on observations that species on the coasts of northeastern North America are to a considerable extent the same as those found in northwestern Europe. Notably, the diversity of biota in the eastern Atlantic is greater than on western Atlantic shores.

The fringe of the supralittoral zone of Fundy rocky shores consists mainly of *Fucus spiralis* and populations of lichens (*Verrucaria* spp. and *Calothrix* spp.). Dominant fauna in the supralittoral fringe includes barnacles (*Semibalanus balanoides*) and littorinid snails (*Littorina saxatilis*). The eulittoral zone is characterized by a broad zone of fucoid algae, primarily knotted wrack (*Ascophyllum nodosum*) and rockweed (*Fucus vesiculosus*). Dominant fauna in the eulittoral includes the common periwinkle (*Littorina littorea*, also found throughout the entire intertidal zone), the tortoise shell limpet (*Notoacmea testudinalis*), the blue mussel (*Mytilus edulis*), and the Atlantic dogwinkle (*Nucella lapillus*). The infralittoral fringe is usually dominated by red and green algae, including Irish moss (*Chondrus crispus*), sea lettuce (*Ulva lactuca*), the feathery coralline alga (*Corallina officinalis*), and hollow green weeds (*Enteromorpha intestinalis*). Laminarian kelps (*Alaria* and *Laminaria* spp.) are usually found no higher than this zone. Pink encrusting coralline algae (*Phymatolithon lenormandii*) often form quite extensive patches from the infralittoral fringe into the sublittoral zone. Fauna associated with the infralittoral fringe and the sublittoral zone include the green crab (*Carcinus maenus*), the green sea urchin (*Strongylocentrotus droebachiensis*), the common starfish (*Asterias vulgaris*) and a periwinkle (*Littorina obtusata*).
The rocky intertidal habitat of the Quoddy region has commercial and intrinsic value, not mutually exclusive from one another. This habitat supports high primary productivity, and also provides nursery and refuge grounds for juvenile fish and invertebrates. These features contribute to productive herring, lobster, and urchin fisheries in the Quoddy region. The shore is visited by dogshark, pollock, sticklebacks and sculpins at high tide (Sean Corrigan, personal communication). It is also an optimal breeding habitat and foraging ground for migratory shorebirds and eider ducks.

2. MATERIALS AND METHODS

2.1 Experimental procedures

The effects of vertical elevation on Dynamena pumila were assessed at five stations by sampling at fixed shore heights.

During the summer season (July 1998), a temporary transect line running at right angles to the shoreline was set at each site from mean low water (MLW) to mean high water (MHW). Levels at each site were defined by the 1998 and 1999 Canadian Tide and Current Tables for the Bay of Fundy. These Tables include predicted standard times at which low and high tides occur at primary ports in the Bay of Fundy. They also include the predicted daily tidal range at each port, given as the height above and below Canadian chart datum (CD). With respect to the five selected sites, Saint John, New Brunswick, is considered to be the primary port from which these two parameters were referenced. Several corrections to these references from the primary port had to be made in order to apply the predicted times and ranges to the five "secondary" ports in this study. One hour was added to the predicted tide times during the summer due to Daylight Savings Time. Additional time corrections were made during every season for each secondary port, as
tidal movement and the times of high and low tides vary throughout the Bay of Fundy. Height corrections were also necessary for each secondary port because sites in narrower parts of the Fundy region have higher tidal ranges. As an example, Holmes Cove Point was visited on July 21, 1998. According to the 1998 Canadian Tide and Current Tables, low tide was predicted to occur at 15:50 in Saint John. An hour was added to this time because of Daylight Savings Time, and six minutes were subtracted because Holmes Cove Point experiences its low tide before Saint John does. Thus, MLW at this site on July 21, 1998 occurred at 16:44. The predicted height above MLW for Saint John was one meter. The tidal height for Holmes Cove Point is 1.3 meters different from CD. Therefore, MLW at Holmes Cove Point was found 0.3 meters above the water level at exactly 16:44. These latter two corrections have been taken and adapted from Thomas (Thomas, 1983) and are summarized below.

Table 1: Summary of tidal corrections made to secondary ports (adapted from Thomas, 1983).

<table>
<thead>
<tr>
<th>Site</th>
<th>Time correction (min)</th>
<th>Height correction (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Holey Point</td>
<td>+16</td>
<td>+1.3</td>
</tr>
<tr>
<td>Holmes Cove Point</td>
<td>-6</td>
<td>+1.3</td>
</tr>
<tr>
<td>Green’s Point Station #1</td>
<td>-6</td>
<td>+1.3</td>
</tr>
<tr>
<td>Green’s Point Station #2</td>
<td>-6</td>
<td>+1.3</td>
</tr>
<tr>
<td>Pea Point</td>
<td>-5</td>
<td>+1.1</td>
</tr>
</tbody>
</table>

Using the cross-staff methodology suggested by Thomas (Thomas, 1983), each shore was surveyed and profiled to note dominant flora and fauna at different vertical elevations. Starting at MLW at Green’s Point Station 1, vertical elevations were fixed at increments of 12.5% of the total shore height to the MHW level of the shore. Thus, 8
elevations (to 100% of the shore height) in total were fixed with flagging tape and
dominant biota were noted at each site.

The 5 sites were visited at low tide during each season, in July 1998, October
1998, February 1999 and April 1999. Water temperature and salinity were recorded at
times of low and high tides, and the mean taken for each. The air temperature at the
surface of each elevation was recorded, and water velocity was estimated twice and
averaged during mid-tide using a water current meter. Mean water temperature was then
averaged across sites to establish a seasonal temperature gradient. Mean current velocity
was averaged within a site across seasons to establish a gradient of water movement. A
biological index of wave exposure was estimated by measuring the vertical height of the
supralittoral “black” zone (due to its colouration) of lichens (Verrucaria) (Thomas,
1983). This zone often extends above the 100% tidal elevation and well into the
eulittoral. The height of this zone did not change throughout the period of this study;
consequently, there was only one estimate of this physical variable for each site for all
four seasons. Site locations and shore profiles are given below in Figure 2, and Tables 2
and 3.
Figure 2: A map of the five sampling sites in the Quoddy region. HLY=Holey Point, HLM=Holmes Cove Point, GR1=Green's Point Station #1, GR2=Green's Point Station #2, PEA=Pea Point.
Table 2: Summary of transect physical parameters at the five sampling sites in the Quoddy region.

<table>
<thead>
<tr>
<th></th>
<th>Holey Point</th>
<th>Holmes Cove Point</th>
<th>Green's Point Station #1</th>
<th>Green's Point Station #2</th>
<th>Pea Point</th>
</tr>
</thead>
<tbody>
<tr>
<td>longitude/latitude</td>
<td>67° 05.25'W, 45° 05.45'N</td>
<td>67° 51.25'W, 45° 02.70'N</td>
<td>67° 51.30'W, 45° 02.40'N</td>
<td>67° 51.20'W, 45° 02.30'N</td>
<td>67° 56.38'W, 45° 02.36'N</td>
</tr>
<tr>
<td>slope of shore (°)</td>
<td>10.3</td>
<td>9.3</td>
<td>9.5</td>
<td>9.7</td>
<td>13.7</td>
</tr>
<tr>
<td>mean tidal range (m)</td>
<td>7.68</td>
<td>6.40</td>
<td>6.40</td>
<td>6.40</td>
<td>6.40</td>
</tr>
<tr>
<td>exposure (m)</td>
<td>3.0</td>
<td>3.3</td>
<td>5.1</td>
<td>7.2</td>
<td>7.7</td>
</tr>
</tbody>
</table>

Table 3: Summary of seasonal changes in physical parameters at the five sampling sites in the Quoddy region.

<table>
<thead>
<tr>
<th></th>
<th>Holey Point</th>
<th>Holmes Cove Point</th>
<th>Green's Point Station #1</th>
<th>Green's Point Station #2</th>
<th>Pea Point</th>
</tr>
</thead>
<tbody>
<tr>
<td>current velocity, mid-tide (m/s)</td>
<td>summer=0.040 fall=0.079 winter=0.045 spring=0.060</td>
<td>summer=0.050 fall=0.084 winter=0.075 spring=0.090</td>
<td>summer=0.100 fall=0.116 winter=0.110 spring=0.125</td>
<td>summer=0.150 fall=0.169 winter=0.165 spring=0.195</td>
<td>summer=0.800 fall=0.749 winter=0.950 spring=1.150</td>
</tr>
<tr>
<td>water temperature (°C)</td>
<td>summer=13.0 fall=11.0 winter=2.0 spring=7.0</td>
<td>summer=10.5 fall=10.5 winter=2.5 spring=8.0</td>
<td>summer=11.0 fall=11.0 winter=2.5 spring=7.5</td>
<td>summer=10.5 fall=11.0 winter=2.0 spring=8.0</td>
<td>summer=12.0 fall=11.5 winter=2.0 spring=7.0</td>
</tr>
<tr>
<td>water salinity (‰)</td>
<td>summer=30.0 fall=29.0 winter=29.0 spring=20.5</td>
<td>summer=33.5 fall=34.0 winter=34.0 spring=24.5</td>
<td>summer=35.0 fall=34.5 winter=35.0 spring=23.5</td>
<td>summer=35.0 fall=33.5 winter=35.0 spring=23.5</td>
<td>summer=33.8 fall=35.0 winter=35.0 spring=23.0</td>
</tr>
</tbody>
</table>
Sampling for hydroids was undertaken at each site using a stratified random sampling methodology. This technique involves partitioning a study site into smaller stations, then sampling within each. In the present study, each site was divided into eight vertical elevations or "strata" where between five and ten 0.25 m² square quadrats were randomly thrown to sample hydroids. This stratified sampling technique was used to partially offset the risk of collecting spatially autocorrelated samples.

Within each quadrat, hydroid abundance was visually inspected. Each live erect hydroid stem was considered to constitute a hydroid "cormoid" (a single plume of a hydroid colony). Hydroid percent occupancy was estimated using a 0.25 m² square quadrat with a grid of one hundred equally sized smaller squares. If one or more cormoids were observed under one of the smaller squares, the count was one percent occupancy. No cormoids of *Dynamena pumila* were observed at the lowest two elevations during the summer, and therefore these elevations were not re-sampled until the spring.

On the opposite side of the transect, this same stratified random methodology was used so that at least five hydroid colonies could be removed from each of five quadrats at every elevation. This produced a sample of at least 25 colonies from no more than five elevations. Specimens were preserved in 70% ethanol or 5% formaldehyde and returned to the lab. Five cormoids were examined from each of the sampled quadrats. Stem height, the number of primary and secondary branches and the presence of full reproductive gonophores were recorded for each cormoid. Specimens were individually patted dry to obtain estimates of fresh weights. Each cormoid was then dried in a forced air oven for 24 hours at 70° Celsius to obtain its dry weight. Stolons were not included in
the fresh and dry weights because it was difficult to determine which stoloniferous network belonged to which hydroid cormoid. To avoid pseudoreplication of samples, a quadrat mean for each response variable (mean stem height, dry weight, number of branches in each quadrat) was determined and used in subsequent analyses.

To assess the effects of wave exposure and water velocity on *Dynamena pumila*, the five sites were selected in the Quoddy region along a horizontal gradient from sheltered bays, with little wave action, to exposed coasts, having stronger surf. The selection of sites (Figure 2) was standardized by choosing rocky shores that were of similar salinity and those consisting mainly of moderately sloped and freely draining bedrock substrates.

To determine whether desiccation limits the upper distribution of *Dynamena pumila* on Quoddy rocky shores, transplantation experiments were performed in July 1999 at Green’s Point Station #1. Ten thalli of *Ascophyllum nodosum* colonized by *D. pumila* were transplanted from the fourth lowest elevation (50-62.5% of the tidal range) to each of the four higher elevations (to 100% of the tidal range). An equal number of control treatments were created by removing ten thalli from the fourth elevation and replanting them at that same elevation. Thus, 40 experimental and ten control treatments were established. At the time of transplantation, the number of live cormoids and the total number were recorded for each transplant. The transplants were left 72 hours, after which time the number of live cormoids and the total number were re-measured to obtain estimates of percent mortality for each elevation.
The importance of biological factors in determining the lower distribution limit of *Dynamena pumila* was examined using transplantations, larval behaviour studies, and feeding preference experiments with notable hydroid predators, the nudibranchs.

Concomitant with the desiccation experiments, 10 algal thalli colonized by *Dynamena pumila* were transplanted from the lowermost marked elevation with colonies to each of the three lower elevations (down to 0% of the tidal range). The control treatments for this experiment were created in the same manner as those for the desiccation experiments. Thus, 30 experimental and 10 control treatments were created. The number of live and total cormoids was recorded for each treatment. These measurements were recorded once more after three weeks time to obtain estimates of percent mortality for each elevation.

Laboratory feeding preference tests were undertaken in July 1999. Twenty specimens of *Dendronotus frondosus* were collected by hand from the intertidal zone at Green’s Point Station #1. Sixteen of the nudibranchs were placed in a common aquarium with dense colonies of *Dynamena pumila*. Each of the remaining 4 nudibranchs were placed in its own separate glass finger bowl containing nothing else. All 4 bowls were placed in a large plastic tray with running seawater. The 4 nudibranchs were starved and acclimatized in their respective bowls for 24 hours. Colonies of about 10 *Dynamena pumila* and 10 *Laomedea flexuosa* (another intertidal hydroid) were then placed in each bowl. The predators were observed for 6 hours, and the frequency of time spent consuming each hydroid was recorded. The experiment was repeated for the remaining 16 nudibranchs in sets of 4.
To examine whether larval choice determines the lower limit of *Dynamena pumila*, planula larvae were obtained in the laboratory. Fertile colonies were collected, brought into the lab, and placed in petri dishes containing shallow water (no more than one centimeter) of 35%/₀₀ salinity and 12° Celsius. Over the next 72 hours, over 150 planulae were collected.

Each of 20 larvae was placed in a separate petri dish containing a piece of *Ascophyllum nodosum* already colonized by *Dynamena pumila* and an approximately equal sized fragment devoid of cormoids. In a separate experiment, each of 20 larvae were placed in a separate petri dish containing pieces of *A. nodosum* fouled by *D. pumila* and pieces fouled by *Laomedea flexuosa*. In a third experiment, each of 20 larvae were placed in a separate petri dish containing equally sized pieces of *A. nodosum, Fucus vesiculosus*, and *Laminaria saccharina*. In all experiments, dishes were left for 48 hours, after which the number of larvae that had settled on each substrate was recorded. No larvae settled on the petri dishes.

### 2.2 Statistical procedures

The analysis of data was divided into three parts: the testing of specific hypotheses about *Dynamena pumila* and other hydroids; the testing of hypotheses about factors that organize intertidal organisms in general; statistics relating to an exploratory analysis.

Most response variables of interest (stem height, number of branches, dry weight, abundance, and percent occupancy) were grouped using principal components analysis (PCA) to create new composite variables for subsequent analyses. PCA grouped the
variables into two components that summarized “size” (stem height, number of branches, dry weight) and “distribution” (abundance, percent occupancy) measures.

Percent fertility was not included in the PCA because it is not really an estimate of hydroid morphology or distribution. Therefore, fertility was treated separately using two separate one-way parametric ANOVAs to examine how treatment effects (elevation and water movement) structured hydroid reproductivity in the rocky intertidal.

A “water movement” component was also generated using PCA. This component was a composite variable of the wave action and water current velocity estimates made at a given site during a given season.

The following analyses involve two-way ANOVAs that consider first and second order interactions. Although there were actually three main gradients (vertical, horizontal, and temporal), results from a three-way ANOVA would be difficult to interpret and demonstrate, given the possibility of statistically significant first, second, and third order interactions. It would be necessary to interpret the way in which the biological effects of a given physical factor are affected by a second and third factor, in addition to the biological effects of the interaction of these physical factors. In order to demonstrate the effects that desiccation and water movement had on Dynamena pumila, it was simpler to interpret a second order interaction. Therefore, the highest order multiple classification ANOVA that was performed was a two-way, to determine if the effects of one physical variable depended on the effects of another. In this way, it was possible to test previous hypotheses while incorporating the possibility that hydroid populations are organized by other (previously untested) physical forces.
2.2.1 Specific hypotheses about Dynamena pumila and other hydroids

Previous work in the boreal northeastern Atlantic demonstrated that stem height (Cornelius, 1979; Wood and Seed, 1980), the number of branches (Broch, 1918), proportion of fertile cormoids (Cornelius, 1979), and abundance (Wood and Seed, 1980) of Dynamena pumila are greatest at the lowest tidal elevation because this level is believed to provide optimal conditions for growth of this hydroid.

In addition to these hypotheses, studies of hydroids including Dynamena pumila have demonstrated that growth appears reduced in areas with increased wave action and current speeds (Ralph, 1956; Riedl, 1966; Boero, 1981; Seed et al., 1983; Piraino and Morri, 1990). Furthermore, it is unresolved as to how abundance of Dynamena pumila is affected by this gradient of water movement. Thus, the effects of exposure to waves and rapid currents on the size and distribution of Dynamena pumila needs to be addressed.

Anecdotal observations suggest that Dynamena pumila, like many other hydroid species (Morse, 1909; Huxley and De Beer, 1923; Strehler, 1961, 1963; Toth, 1969; Calder, 1971, 1990; Boero et al., 1986; Crowell, 1991) resorb the coenosarc and become dormant during unfavourable weather conditions and regenerate this tissue during favourable weather periods. It is expected that the size of D. pumila should be drastically reduced during the winter in the Quoddy region. Therefore, the seasonality of hydroid size should also be considered in the following analyses of the effects of water movement and elevation on hydroid size and distribution.

2.2.1.1 Hydroid size

The general hypothesis that cormoids of Dynamena pumila are largest at the lowest elevation at more sheltered sites was tested using a two-way ANOVA that tested
for differences in the size component across fixed vertical (elevation) and horizontal 
(water movement) gradients. This analysis was performed for each season to determine if 
there was a temporal (seasonal) component to how population size is structured on the 
rocky shore.

2.2.1.2 Hydroid distribution

The general hypothesis that cormoids of *Dynamena pumila* are most abundant at 
the lowest elevation at sites with increased water movement (wave action and current 
velocity) was tested using a two-way ANOVA that tested for differences in the 
distribution component across fixed vertical (elevation) and horizontal (water movement) 
gradients. The two-way analysis was performed for each season to determine if there was 
a temporal (seasonal) component to how hydroid distribution is organized on the rocky 
shore.

2.2.1.3 Hydroid fertility

Differences in the proportion of fertile cormoids among elevations were evaluated 
during the summer using a one-way ANOVA. This analysis was also used to determine 
if there was a horizontal (water movement) component to the way in which hydroid 
fertility is affected.

2.2.1.4 Relationship between hydroid stem height and abundance

Wood and Seed (1980) and Seed *et al.* (1983) demonstrated that stem heights of 
*Dynamena pumila* were affected by hydroid density. This hypothesis was tested with 
samples from the Quoddy region by determining the relationship between the mean 
hydroid abundance at a given elevation and the quadrat mean stem height within that 
elevation using a simple linear regression analysis.
2.2.2 Expectations from hypotheses about other intertidal organisms

The upper limit of most intertidal organisms is determined by desiccation, and the lower limit is often set by biological factors, especially predation. These hypotheses were tested for *Dynamena pumila* using two separate one-way ANOVAs, each with an *a posteriori* Bonferroni multiple comparison. The percent mortality of cormoids on each transplanted algal thallus was taken as one observation, and observations were compared across elevations at Green's Point Station #1 in July 1999.

A second hypothesis derived from the latter is that the lower distribution limit is set by predation because the ubiquitous nudibranch *Dendronotus frondosus* prefers to feed on *Dynamena pumila* over other hydroids that proliferate from the intertidal to well within the subtidal. This was tested using a one-tailed t-test to determine if *D. frondosus* spent significantly more time feeding on *D. pumila* than on another hydroid, *Laomedea flexuosa*, also found in the intertidal and subtidal zone.

Alternatively, the lower limit of *Dynamena pumila* may be set by larval behaviour, such as preference for *Ascophyllum nodosum* over other dominant shallow water algae, *Fucus vesiculosus* and *Laminaria saccharina*. This hypothesis was tested by noting the significance of Pearson's likelihood statistics between the larvae and each alga. However, larvae of *D. pumila* may prefer to settle on or near conspecifics instead of on bare substrates, or on one already fouled by another hydroid, *Laomedea flexuosa*, thereby indirectly creating what appears to be a strictly intertidal distribution in the Quoddy region. These two hypotheses were tested by noting the significance of likelihood ratio probabilities.
2.2.3 Exploratory analysis

Sampling hydroid density requires much effort. A more rapid estimate of the quantity of hydroids would be percent occupancy as it requires much less effort to sample than abundance. The correlation is expected to be fairly high, as the PCA grouped these response variables together. Therefore, the relationship between density and occupancy was evaluated using a simple linear regression analysis to determine whether hydroid density could accurately be predicted from percent occupancy.

3. RESULTS

Most of the estimated response variables were ordinated into groups by principal component analysis (PCA). Varimax-rotated components with eigenvalues greater than one were selected as the new, main factors (Table 4). This resulted in 2 new variables that summarized hydroid "size" and "distribution" in order that the effects on all response variables could be examined.

Table 4: The selection of response variable summary components from the PCA with varimax rotation.

<table>
<thead>
<tr>
<th>Component</th>
<th>Eigenvalue</th>
<th>% of variance explained</th>
<th>Cumulative % explained</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>2.035</td>
<td>40.698</td>
<td>40.698</td>
</tr>
<tr>
<td>2</td>
<td>1.780</td>
<td>35.607</td>
<td>76.305</td>
</tr>
</tbody>
</table>

Recall that the size response variables were obtained from 5 hydroids in each quadrat. Thus, these 5 samples would not actually be independent replicates. Therefore, the mean values of the size component for each quadrat were taken as replicates for all statistical procedures that required the use of this variable. The factor plot shown below in Figure 3 demonstrates the way in which the PCA ordinat ed the response variables.
Figure 3: Ordination of principal components “size” and “distribution”. Note the abbreviations, mean occupancy = “avoccup”, mean abundance = “avabund”, stem height = “stemht”, dry weight = “drywt”, number of branches = “totbranc”.

Likewise, most of the physical variables measured were ordinated into groups using PCA with varimax rotation. This analysis generated two new variables, one that summarized mass water movement at a given site, and one that summarized seasonal changes in abiotic factors. Components with eigenvalues greater than one (displayed in Table 5) were selected as the new main variables.

Table 5: The selection of physical variable summary components from the PCA with varimax rotation.

<table>
<thead>
<tr>
<th>Component</th>
<th>Eigenvalue</th>
<th>% of variance explained</th>
<th>Cumulative % explained</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1.704</td>
<td>42.608</td>
<td>42.608</td>
</tr>
<tr>
<td>2</td>
<td>1.087</td>
<td>27.175</td>
<td>69.784</td>
</tr>
</tbody>
</table>
Figure 4 demonstrates the way in which the PCA ordinated these physical variables.

Figure 4: Ordination of principal “water movement” and “seasonal” components. Note the abbreviation, water temperature = “watertem”.

3.1 Specific hypotheses about *Dynamena pumila* and other hydroids

The general hypotheses that *Dynamena pumila* should be larger and more abundant at lowermost elevations at locations with significant water movement were tested using two-way ANOVAs (vertical elevation and water movement were fixed factors). This was repeated for each of 4 seasons to determine if there was a temporal component to the importance of these two physical factors. The ANOVA results are in Table 6 and 7.
Table 6: Summary of ANOVA statistics for main and interaction effects of vertical elevation and water movement on hydroid size across four consecutive seasons.

<table>
<thead>
<tr>
<th>Season</th>
<th>Effect</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Summer</td>
<td>elevation</td>
<td>4</td>
<td>13.108</td>
<td>16.183</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>water movement</td>
<td>4</td>
<td>45.776</td>
<td>56.515</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>elevation*water movement</td>
<td>13</td>
<td>10.603</td>
<td>13.090</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Fall</td>
<td>elevation</td>
<td>4</td>
<td>1.539</td>
<td>28.245</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>water movement</td>
<td>4</td>
<td>3.499</td>
<td>64.218</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>elevation*water movement</td>
<td>13</td>
<td>1.706</td>
<td>31.311</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Winter</td>
<td>elevation</td>
<td>4</td>
<td>1.293</td>
<td>35.616</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>water movement</td>
<td>4</td>
<td>11.499</td>
<td>316.653</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>elevation*water movement</td>
<td>12</td>
<td>2.694</td>
<td>74.193</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Spring</td>
<td>elevation</td>
<td>4</td>
<td>7.563</td>
<td>131.716</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>water movement</td>
<td>4</td>
<td>8.491</td>
<td>147.883</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>elevation*water movement</td>
<td>12</td>
<td>3.801</td>
<td>66.208</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

Table 7: Summary of ANOVA statistics for main and interaction effects of vertical elevation and water movement on hydroid distribution across four consecutive seasons.

<table>
<thead>
<tr>
<th>Season</th>
<th>Effect</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Summer</td>
<td>elevation</td>
<td>4</td>
<td>10.975</td>
<td>342.476</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>water movement</td>
<td>4</td>
<td>8.303</td>
<td>259.108</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>elevation*water movement</td>
<td>13</td>
<td>5.470</td>
<td>170.109</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Fall</td>
<td>elevation</td>
<td>4</td>
<td>70.606</td>
<td>7850.609</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>water movement</td>
<td>4</td>
<td>37.863</td>
<td>4209.920</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>elevation*water movement</td>
<td>13</td>
<td>34.419</td>
<td>3826.972</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Winter</td>
<td>elevation</td>
<td>4</td>
<td>50.861</td>
<td>4697.384</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>water movement</td>
<td>4</td>
<td>19.655</td>
<td>1815.254</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>elevation*water movement</td>
<td>12</td>
<td>13.436</td>
<td>1240.922</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Spring</td>
<td>elevation</td>
<td>4</td>
<td>62.643</td>
<td>6238.282</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>water movement</td>
<td>4</td>
<td>21.433</td>
<td>2134.427</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>elevation*water movement</td>
<td>12</td>
<td>18.844</td>
<td>1876.608</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

To examine the general effects of vertical, horizontal, and seasonal gradients on hydroid populations, bar graphs showing two standard error deviations from the means were created for each response variable (size, distribution, and fertility).
3.1.1 Effects of the vertical gradient:

Figure 5: Trends in the vertical zonation of hydroid size. Bars represent 2 standard errors of the mean for this and every figure.

Figure 6: Trends in the vertical zonation of hydroid distribution.
The zonation of fertility was highly significant ($F=23.913$, $df=4$, $p<0.001$) according to the one-way ANOVA analysis with an elevation treatment effect.

3.1.2 Effects of the horizontal gradient:

Figure 8: Horizontal zonation of hydroid size.
During field sampling, it was noted that hydroids at more exposed sites tended to be shorter with more branches. This observation does not corroborate the trends seen in Figure 8. Patterns in the individual components of "size" (number of branches, dry weight, stem height) were examined in finer detail to identify what aspect of hydroid size truly increased at sites with greater water movement.

![Figure 9: Effect of water movement on the number of branches.](image)

![Figure 10: Effect of water movement on the dry weight of Dynamena pumila.](image)
Individual components of hydroid size appeared to be affected differently by the horizontal gradient. The effects of water movement on each of these variables will therefore be discussed separately from one another.

Figure 11: Effects of water movement on hydroid stem height.

Figure 12: The horizontal zonation of hydroid distribution.
Figure 13: Effects of water movement on hydroid fertility.

Treatment effects of water movement were highly significant ($F=80.247$, $df=4$, $p<0.001$) on fertility according to the one-way ANOVA analysis.

3.1.3 The effects of the seasonal gradient:

Figure 14: Seasonal trends in hydroid size.
3.2 The relationship between hydroid stem height and abundance

The specific hypothesis that stem height of *Dynamena pumila* was related to hydroid abundance was also tested. The relationship between the response variable “stem height” (a mean was taken for each quadrat) and mean abundance is demonstrated below in Figure 16.

A simple linear regression analysis was performed to evaluate the statistical significance and predictive value of this relationship. Although the regression was statistically significant (df=1, F=157.665, p<0.001), a very low r-squared value was noted (R²=0.143). The equation was Y=0.0023X+8.941.
Figure 16: The relationship between stem height and mean abundance of *Dynamena pumila*. Observations were grouped over elevations, sites, and seasons. Both variables were log$_{10}$ transformed to reduce residual heteroscedasticity, and a value of one was added to the mean abundance estimates as some observations contained zero hydroids. The equation for the regression is $Y=0.0023X+8.941$, $\text{R}^2=0.143$, $p<0.001$.

### 3.3 Expectations from hypotheses about intertidal organisms

#### 3.3.1 The importance of desiccation

The effects of desiccation on mortality of transplanted hydroid cormoids were statistically significant among elevations according to a one-way ANOVA analysis ($\text{df}=4$, $\text{F}=528.914$, $p<0.001$). Figure 17 illustrates the results of the algal transplantation experiment.
Figure 17: Hydroid percent mortality on transplants of *Ascophyllum nodosum* to higher elevations at Green's Point Station #1 in July 1999. Note that percent mortality did not differ significantly between the control elevation (50-62.5% of the mean tidal range) and the next higher elevation (62.5-75% of the mean tidal range) according to a non-significant Bonferroni statistic (p=1.000).

The highest mean percent mortality was observed at the highest elevation (Figure 17) (μ=100.00%), and this was statistically different from the percent mortality at all other elevations according to the Bonferroni statistic (p<0.001). Percent mortality increased exponentially from the elevation closest to the control, up to the greatest vertical height (87.5-100% of the mean tidal range).
3.3.2 The importance of predation

The effects of predation by *Dendronotus frondosus* on hydroids transplanted to lower elevations were not statistically significant among elevations (df=3, F=0.379, p=0.769). The results of this experiment are illustrated below in Figure 18.

![Figure 18: Hydroid percent mortality at lower elevations on site at Green’s Point Station #1 in July 1999. Percent mortality within the experimental transplants never differed significantly from that recorded for the control (50-62.5%) elevation according to non-significant Bonferroni statistics (p=1.000 for all).](image)

There was statistical significance in prey choice made by *Dendronotus frondosus*. According to the one-tailed t-test (df=19, t=7.107, p=0.001), *D. frondosus* spent significantly more of the experimental time of six hours feeding on the hydroid
Laomedea flexuosa (mean time spent feeding=54.9%) than it did on Dynamena pumila (mean time spent feeding=30.7%).

3.3.3 The importance of planulae behaviour

Planular larval settlement and metamorphosis of Dynamena pumila was observed in vitro, and was found to occur as previously described (Orlov, 1996a).

There was no statistical significance in substrate choice by larvae of Dynamena pumila given the choice between the fucoids (Ascophyllum nodosum and Fucus vesiculosus) and Laminaria saccharina according to Pearson's likelihood ratios (Table 8).

Table 8: Likelihood ratio probabilities for larval settlement preferences on intertidal and subtidal algae.

<table>
<thead>
<tr>
<th>Algal species</th>
<th>df</th>
<th>Pearson’s likelihood ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ascophyllum nodosum</td>
<td>19</td>
<td>0.107</td>
</tr>
<tr>
<td>Fucus vesiculosus</td>
<td>19</td>
<td>0.180</td>
</tr>
<tr>
<td>Laminaria saccharina</td>
<td>19</td>
<td>0.180</td>
</tr>
</tbody>
</table>

According to the likelihood ratio probabilities, there appeared to be a statistically significant component to the way in which larvae of Dynamena pumila chose to settle on algal substrates already colonized by conspecifics. Larvae of D. pumila preferred to settle on substrates already colonized by conspecifics rather than settling on a bare substrate (likelihood ratio p=0.048) or one fouled by another hydroid Laomedea flexuosa (likelihood ratio p=0.048).

3.4 Exploratory analysis

Measuring hydroid abundance in the field is time consuming, and requires much effort as cormoids are often small, colonial, and in the case of Dynamena pumila,
intertwined with other individuals in a population. A simple linear regression analysis was used to determine whether hydroid abundance could be accurately predicted from an alternate measurement of distribution. Percent occupancy requires much less time to estimate, and does not require as much effort to distinguish between individuals. The relationship between the two variables is illustrated below in Figure 19.

Figure 19: The relationship between hydroid percent occupancy and abundance. A value of one was added to each variable because many quadrats contained zero hydroids. Variables were then \( \log_{10} \) transformed to reduce residual heteroscedasticity. The relationship is positively linear relationship, with the equation \( Y=1.634X+0.309 \) and a relatively high \( R^2 \) value of 0.841.

The linear regression (Figure 19) was highly significant (df=1, \( F=6458.978 \), \( p<0.001 \)), with the equation for the regression line \( Y=1.634X+0.309 \).
4. DISCUSSION

4.1 General

This autoecological examination of the intertidal hydroid *Dynamena pumila* has evaluated forces that organize populations of a sessile rocky shore organism in the Quoddy region of the Bay of Fundy. Estimates of seasonal trends in hydroid size, distribution, and fertility have been determined in relation to physical and biological factors. Most interesting is the accumulation of new information regarding settlement preferences exhibited by larvae of *D. pumila*.

4.2 Size and fertility in *Dynamena pumila*

4.2.1 Vertical gradient

4.2.1.1 Hydroid size

Trends in the size of *Dynamena pumila* were assessed over small (vertical gradients) and large (horizontal gradients) spatial scales. On a small local scale, size in *D. pumila* was affected by the vertical (elevation) gradient (Figure 5) throughout the seasons (see Table 6). Cormoids of *D. pumila* higher up on the rocky shore were generally shorter, had fewer branches, and weighed less than those lower down. In contrast to previous observations made by Wood and Seed (1980) and Broch (1918), cormoids at the elevation closest to the water line were not consistently the largest ones in the Quoddy region. There was always a significant interaction between elevation and the water component variable (Table 6). Therefore, the way in which elevation affected hydroid size depended on the site where the hydroids were located. In addition to this interaction, there was a seasonal component to the way in which elevation and wave exposure affected hydroid size. The effects of this horizontal gradient will be discussed
under the heading "Horizontal gradient" to address the discrepancy between the findings of Broch (1918) and Wood and Seed (1980) with those reported in the present study. The temporal component to hydroid size will also be discussed separately, under the heading "Temporal gradient". However, the change in the effects of space and time suggests considerable variation in the importance of site-specific factors organizing hydroid populations within the Quoddy region, and across the boreal North Atlantic in general. This observation provides evidence for the need for researchers to adopt a "multifactorial" approach before generalizing about forces that are important in structuring a community.

Cormoids of Dynamena pumila were hypothesized to be larger at the lowermost distribution limits of hydroids on the rocky shore. Generally, this was the case at the most exposed sites in the Quoddy region, where the largest hydroids were found between 37.5 and 50% of the mean tidal range (Figure 5 and Figures IV and V in the Appendix). This position on the shore offers sufficient feeding time, as cormoids remain immersed in the plankton-rich water throughout most of the tidal cycle, and minimal exposure to desiccation and extremes of temperature and salinity. Therefore cormoids of D. pumila are largest between 37.5 and 50% of the mean tidal range because this position provides optimal food availability and feeding time for this hydroid.

At the more sheltered sites, cormoids were largest at the second lowest elevation between 50 and 62.5% of the mean tidal range (Figures I through III in the Appendix). Rocky shore ecological literature suggests that sites with little to no physical disturbance or high degrees of habitat stability will be structured by biological forces more than physical factors. Therefore, a sheltered site with minimal exposure to shearing forces
created by waves or strong water currents, should experience increased predatory and competitive interactions. As a mostly epiphytic macro-organism, *Dynamena pumila* is particularly susceptible to predation by nudibranchs because of its conspicuous position on intertidal algae. In addition to the risk of predation, *D. pumila* may not be able to escape competition for food when its feeding hydranths are smothered by the fast growing epiphytic filamentous algae that are so prominent on sheltered shore in the Quoddy region. Therefore, two possible (and not mutually exclusive) explanations for observing the largest hydroids between 50 and 62.5% at more sheltered sites include reduced predation by hydroid predators and reduced competition for space or food. Larger hydroids would be more conspicuous to predators at lower elevations, and would also have to compete more for food and space at lower elevations, resulting in sub-optimal growth. *Dynamena pumila* may grow optimally at this elevation because this position offsets predation and competition risks while moderating desiccation stresses associated with positions higher up on the shore.

Cormoids of *Dynamena pumila* generally decreased in size beyond 62.5% of the mean tidal range (Figure 5).

### 4.2.1.2 Hydroid fertility

At a small, local scale, fertility in *Dynamena pumila* varied significantly. Cormoids are most fertile at the lowermost shore elevations (Figure 7). This observation is congruent with that made by Cornelius (1979) in the boreal northeastern Atlantic, and suggests that the lowermost elevations provide optimal environmental conditions for the sexual maturity of adults and the release of larvae.
4.2.2 Horizontal gradient

4.2.2.1 Hydroid size

At a larger spatial scale, the growth of *Dynamena pumila* appears to be affected by water movement. There were highly statistically significant differences in the size of cormoids across sites (Table 6), with hydroid size decreasing with exposure to waves and rapid water currents (Figure 8). At first this contrasts with field observations that cormoids from exposed sites were more branched with greater dry weights. To determine which aspects of hydroid size truly increased with water movement, the size component was decomposed to its original response variables (number of branches, dry weight, and stem height) then re-plotted against the water movement component. The number of branches on a hydroid and its dry weight are positively related with water movement (Figures 9 and 10 respectively), while stem height is negatively related (Figure 11).

The length of other hydroids has been found to increase substantially in slow moving waters. This would initially be expected to translate into an increase in dry weight, however Cornelius (1979) noted that in *Dynamena pumila*, colonies from wave exposed sites exhibited a thicker perisarc. This would necessarily contribute to increased dry weight, and therefore to a "size component".

Branching in hydroids is affected by the direction of current flow (Reidl, 1966; Bandel and Wedler, 1987; Da Silveira and Migotto, 1991), however the response differs from species to species. Increased branching in *Dynamena pumila* would allow the hydroid to maximize feeding under turbulent water conditions. Having only a simple upright stem would cause *D. pumila* to capture food in one plane, despite plankton being carried in the water column in many directions under increased flow conditions. For the
present study, hydroid dry weight was highly correlated with the number of branches
\(R^2=0.895, p<0.001\).

The vertical gradient (elevation) and horizontal gradient (water movement) interact to control the size of *Dynamena pumila* (Table 6). The interaction was highly significant throughout the seasons (p was always less than 0.001). As noted earlier, hydroids were generally largest between 37.5 and 62.5% of the mean tidal range, depending on the degree of exposure water at a given site. If the effects of elevation and water movement are considered concomitantly, it may be concluded that the effect of elevation on size of *D. pumila* is site specific in the Quoddy region.

### 4.2.2.2 Hydroid fertility

At a larger scale it seemed that exposure to waves and rapid water currents were very important forces in determining the reproductive state of *Dynamena pumila*. Fertility increased significantly as the values of the water movement increased (Figure 13).

Theories of life history predict that under stressful environmental conditions, sexual reproduction is favoured over asexual strategies (Ridley, 1996) to increase the genetic variation in a population. Thus, under more harsh, wave exposed conditions, hydroids may increase reproductive effort in order to increase the genetic variation of those populations (Gili and Hughes, 1995). *Dynamena pumila* appeared to respond in this manner, as noted by the dramatic increase in fertility along a gradient of wave exposure and water currents in the Quoddy region.

Alternatively, the rapid movement of water experienced at Pea Point may provide optimal feeding conditions for benthic sessile filter-feeders such as hydroids, sponges,
and bryozoans. Reproduction effort in *Dynamena pumila* may be elevated at wave
exposed sites with rapid currents as a result of sufficient food availability, much as it is at
a smaller (vertical) spatial scale.

### 4.3 Temporal gradient

In addition to small and large spatial scales, there also appears to be a temporal
(seasonal) component to the way in which the size of *Dynamena pumila* is affected
(Table 6). Cormoids were largest during the summer and progressively decreased in size
as the seasons cooled (Figure 14). This was probably in response to the unfavourably
cooler water temperatures experienced by the hydroids.

A dormant cyst stage has been reported for *Dynamena pumila* that enables this
hydroid to survive adverse environmental conditions (Haddow, 1937). Although this
stage was not directly observed over the period of this study, the consistent reduction in
the size response variable across seasons suggests that some resorption of the coenosarc
had been occurring during the cooler seasons. Tissue resorption (and even dormancy) has
been reported for several other hydroid species (Morse, 1909; Huxley and De Beer, 1923;
Seasonal cycles of coenosarc resorption appear to be much more apparent in shallow
water species, due to greater seasonal differences in temperature (Gili and Hughes, 1995).
Seasonal reductions in the size of *Dynamena pumila* may likewise be caused by changes
in water temperature, and future work could involve the *in vitro* test of this hypothesis.

Size of *Dynamena pumila* is also affected by biological factors such as food
quality and availability (Marfenin and Burykin, 1979). Thus, the reduction in size of *D.
pumila* may be attributed to seasonal fluctuations in the abundance and quality of
plankton in the Quoddy region (Murison and Gaskin, 1988). However it is uncertain as to whether mean size of cormoids would actually decrease as a response to changes in the plankton. It is more likely that cormoids would simply arrest any additional growth in the stem height, number of branches, or weight of the cormoid. Thus, size reduction in *D. pumila* in the Quoddy region is probably an attribute of dormancy processes evolved to survive unfavourable decreases in water temperature.

4.3 Distribution of *Dynamena pumila*

4.3.1 Vertical gradient

4.3.1.1 Vertical zonation

Cormoids generally decrease in abundance as their position on the shore increases (Figure 6). However, contrary to previous observations made by Cornelius (1979), Wood and Seed (1980), and Seed *et al.* (1983), hydroid abundance generally peaked at the second or third lowermost elevations where cormoids were found. This discrepancy will be discussed after site to site differences in hydroid zonation of distribution are explained.

On finer examination of site to site differences in distribution, there is an effect of the horizontal gradient on the vertical elevation factor (Table 7). At sites with less wave action and slower moving water currents, the greatest mean distribution component remains greatest at the second lowest elevations, between 50 and 62.5% of the mean tidal range (Figures VI through VIII in the Appendix). As exposure and water currents increased (i.e.: at Green's Point Station #2), abundance and occupancy of hydroids peaked at higher elevations, between 62.5 and 75% of the mean tidal range, except in the spring when the mean peaked at the next lower elevation (Figure IV in the Appendix). However at the most wave exposed site with the most rapid currents (Pea Point), the
distribution component values peaked at lower elevations once more (between 37.5-50% of the mean tidal range in the summer and fall, or at 50-62.5% of the mean tidal range during the winter and the spring) (Figure X in the Appendix). Therefore, it appears that zonation of hydroid distribution may be regulated differently across the horizontal gradient.

Site to site variation in hydroid zonation of distribution may be explained by considering that the importance of environmental factors can change in space and time (Hunter and Price, 1992).

On sheltered shores, larval preference for settling on or near a bacterial film could act concomitantly with larval choice to settle at a level that limits desiccation. Planulae larvae of *Dynamena pumila* settle significantly more frequently on algae that are covered by a thick, bacterial film (Orlov, 1996a). Thus, in the Quoddy region, it can be reasoned that hydroid distribution peaks between 50 and 62.5% on sheltered shores because this elevation supports the greatest biomass of film-covered algae.

At Green’s Point Station #2, a more exposed site, distribution is probably regulated by competition for space with other benthic filter-feeders, in addition to larval preference and desiccation. Abundance and occupancy were usually greatest between 62.5-75% of the mean tidal range (Figure VIV in the Appendix). This was probably due to increasing competition experienced by *Dynamena pumila* with other benthic filter-feeders such as sponges, mussels, and bryozoans that exist at lower shore levels, as well as the need to limit desiccation. These findings corroborate with those observed in the past (Lewis, 1964; Stephenson and Stephenson, 1972; McQuaid and Branch, 1985). For example, McQuaid and Branch examined the effects of wave action on the intertidal
fauna on the coast of South Africa. They found an overall increase in biomass of filter-feeders as a direct effect of strong wave action, relative to sheltered sites. Across this gradient of exposure, they concluded that biomass of filter-feeders increased because exposed sites have less biomass of algae and thus act as “net importers” of energy. Therefore, exposed shores can support a higher biomass of filter-feeders that require a large input of energy from the water column. The highest rates of successful larval settlement and metamorphoses for D. pumila may occur between 62.5 and 75% of the mean tidal range at Green’s Point Station #2 because this level compromises the abundance and diversity of competitors, with larval preferences and desiccation stress.

At Pea Point, the most exposed site, regulation by competition, larval preference, and desiccation is likely modified by surface topography. The greatest mean distribution component peaked at the lowermost distribution limit for Dynamena pumila at the most wave exposed site, Pea Point (Figure X in the Appendix). Although wave battering had increased the space availability for mussels, barnacles, sponges, and bryozoans to attach at lower levels, this phenomenon may have also created a gradient that was not accounted for in this study. The long-term severity and stressful action of the waves at this site appeared to have eroded crevices and concave surfaces into the bedrock. Therefore, a "third-dimension" gradient was created that increased habitat complexity for which sessile benthic invertebrates such as hydroids may attach (recall that although care was taken to not sample cryptic or crevice-dwelling hydroids, it is not possible to confirm that specimens in concave surfaces were not incorporated into this study). At Pea Point, hydroids were rarely collected from algal substrates. Most hydroids were collected directly from the rock itself. Much like the situation at sheltered sites, the upper limit of
larval settlement remains determined by desiccation forces. Intertidal algae at Pea Point exist consistently only very high up on the shore, past 62.5% of the mean tidal range. Therefore, hydroid larvae choose to settle at very low elevations to offset desiccation, despite increased competitor biomass and diversity, because they can settle in crevices and depressions created by the mass movement of water itself.

The discrepancy between boreal northwestern and northeastern Atlantic distributions may be explained by the difference in zonation of the primary substrates of *Dynamena pumila*. On Quoddy shores, rocky shores are dominated by the fucoids *Fucus vesiculosus* and *Ascophyllum nodosum* in the lower to middle intertidal. Therefore, settlement might preferentially occur at this position because larvae are attracted to the copious amounts of bacterial film exuded by the algae at this elevation (Orlov, 1996a).

In the boreal northeastern Atlantic, *Dynamena pumila* also appears predominantly at lower shore levels as well into the subtidal. However *Ascophyllum nodosum* and *Fucus vesiculosus* are found higher up on the shore, while *Laminaria saccharina* and *Fucus serratus* contribute to most of the algal biomass on the lower shore and into the subtidal. Following Orlov's findings that planulae of *D. pumila* preferred to settle on these latter algae in the White Sea, the discrepancy may be resolved by considering the spatial variation in how larvae choose settlement sites. Instead of choosing a specific alga, *D. pumila* may have evolved a preference for settling on algae that offered the greatest biomass (and attracted by the great amounts of bacterial film) at lower shore levels. Evolving a co-existence with large, macrophytic algae may have evolved as a way to escape predation and/or to prevent intense desiccation in the intertidal zone. In the boreal northwestern Atlantic, *A. nodosum* contributes the most to lower shore algal
biomass whereas in the northeastern Atlantic, F. serratus and L. saccharina contribute the most.

The consistent absence of Dynamena pumila from the lower two elevations (between 0 and 25% of the mean tidal range) at all 5 sites was unexpected. In the boreal northeast Atlantic, D. pumila has been recorded to a depth of about 10 meters below MLW (Orlov, 1996a). From the previous discussion, the presence of D. pumila in the subtidal in the boreal northeastern Atlantic is probably a result of larval choice for settling on or near the greatest biomass of algae. However previous qualitative observations made by Thomas (1994) determined that the lower limit of D. pumila extended down to about 14% of the mean tidal range in the Quoddy region. The differences between past observations and those made here may reflect spatial and/or temporal components to the way in which rocky shore macroalgae communities are controlled in the Quoddy region.

Assuming that larvae of D. pumila still prefer to settle on algae covered by a bacterial film, the distribution of this hydroid is truly set by the zonation of biomass of the latter. Therefore, if algal zonation were to vary in space and/or time, it can be conceived that distribution of D. pumila should vary. Alternatively, these differences may reflect the presence of different structuring forces at different times and/or in different areas. Predation may be more important than larval preference at different times, or in different areas. By allowing the relative roles of ecological forces to vary, the discrepancy between reported lower limits of D. pumila and other intertidal organisms can be reasoned (Hunter and Price, 1992; Menge, 1976; Menge and Sutherland, 1976).
4.3.1.2 Upper and lower limits

The upper limit of cormoids appears to be regulated by desiccation (Figure 17), as it is for most other intertidal organisms (Southward, 1958b; Ballantine, 1961; Connell, 1961a; Foster, 1969; Landenberger, 1969), while the lower limit appears to be set by larval behaviour, notably settling on certain algae (Orlov, 1996a) and significantly more often near conspecifics (Pearson’s likelihood ratio p=0.048).

Transplanted hydroid colonies were used to assess whether desiccation determined the upper distribution limit of *Dynamena pumila*. After 72 hours, mortality of transplants was highest in the uppermost hydroid transplants, and declined exponentially toward the MLW mark (Figure 17). Transplants at the 3 highest elevations experienced significantly higher mortalities than the control treatments (Bonferroni statistic p was always less than 0.001). Fewer cormoids exist in the upper intertidal because it is more difficult to withstand the drying effects of tidal emersion at these elevations.

The lower distribution limit appears to be set by larval preference for settling near substrates harbouring conspecifics. This finding was not expected, as it was thought that predation by the nudibranch *Dendronotus frondosus* was the most important factor determining the lower distribution limit of *Dynamena pumila* in the Quoddy region, a situation common to many intertidal organisms (Connell, 1961b; Estes et al., 1978; Menge 1976, 1978a, b; Calder, 1991a). However hydroid transplants to the lower intertidal, where *D. pumila* was not naturally found, experienced zero percent mortality (Figure 18). Perhaps the transplants were not left long enough for the nudibranchs to discover, yet after three weeks, no nudibranchs were even observed near the transplants despite the ubiquitous presence and peak abundance of *D. frondosus* (Clark, 1975).
nudibranch simply was observed feeding at locations where food was very abundant (i.e.: between 37.5 and 50% of the mean tidal range) and it did not need to migrate to lower elevations in search of additional hydroid prey. Thus, *D. frondosus* does not appear to limit the lower distribution of *D. pumila* in the Quoddy region. Furthermore, *D. frondosus* spent more time feeding on another intertidal hydroid, *Laomedeia flexuosa* (df=19, t=7.101, p<0.001) rather than *D. pumila*. Therefore, predation by this nudibranch cannot be implicated as the direct cause for the strictly intertidal distribution of *D. pumila* on Quoddy rocky shores.

Alternatively, the importance of planula larval behaviour exhibited by *Dynamena pumila* should be revisited as an important factor in determining the lower distribution limit. Larval behaviour in *D. pumila* and other hydroids has been previously examined in relation to such factors as surface inclination, substrate roughness, the presence of conspecifics and microbial films, light, gravity, and emersion (Williams, 1965; Müller et al., 1976; Hughes, 1977; Burykin and Marfenin, 1978; Sommer, 1992; Orlov, 1996b).

Orlov (1996a) found that larvae of *Dynamena pumila* settled most intensively on *Fucus serratus* (an alga predominantly at the intertidal-subtidal interface) and *Laminaria saccharina* (an alga that is predominantly shallow-subtidal), less so on *Fucus vesiculosus*, and even less infrequently on *Ascophyllum nodosum*. Therefore, the predominance of *D. pumila* at the intertidal-subtidal in the White Sea area may be explained by larval preference for settling and metamorphosizing within elevations that contained the highest proportion of *F. serratus*. Recall from earlier discussion that this preference may have evolved as a way to avoid predators or prevent desiccation.
However, on Quoddy shores, *Ascophyllum nodosum* covers most of the intertidal zone, and *Fucus vesiculosus* replaces *F. serratus* as the lower intertidal fucoid (*Laminaria saccharina* occurs predominantly in the shallow-subtidal much as it does in the White Sea area, but no coralline algae of *Dynamena pumila* were ever observed on laminarians). If larval preference created the high abundance of *D. pumila* between 37.5 and 62.5% of the mean tidal range, then larvae were expected to prefer *A. nodosum* over *F. vesiculosus* and *L. saccharina* because of the abundance of *A. nodosum* at these elevations. However, larvae collected for a substrate choice test did not show a significant preference for settling on *A. nodosum*, *F. vesiculosus*, or *L. saccharina* (Table 8). Given the significant attraction by larvae for microbial films discovered by Orlov (for which the molecular mechanism is being examined by Orlov), the 3 algal species may have exhibited similar quantities and/or qualities of bacterial film. The majority of larvae seem to settle between 37.5 and 62.5% of the mean tidal range because this elevation roughly corresponds with the elevation wherein the greatest biomass of these algae exists on Quoddy region rocky shores (Thomas, 1994).

This study also provides evidence that larvae prefer to settle on areas already colonized by *Dynamena pumila*, rather than on bare substrates or algae fouled by another hydroid (*Laomedea flexuosa*) (p=0.048 for both). The settlement of larvae near conspecifics would not appear to benefit *D. pumila*, as increased intraspecific competition for space and food may occur if these resources are limited. Orlov (1996b) demonstrated that planula larvae of the solitary hydroid *Clava multicornis* would actively choose settlement points along the algae that were devoid of conspecifics, however he did not test whether the larvae would have preferred a bare substrate or one at least partly
colonized by other *C. multicornis*. *Dynamena pumila* settles intensively at the base of fucoid algae, but in dense populations it has been noted to extend to the tip of the algal frond (personal observation). In addition to the ability of *D. pumila* to colonize most parts of fucoid algae, the benefits of gregarious settlement include protection from the wind as more water can be retained in the center of the aggregation, and protection from predation.

Other benthic marine organisms prefer to settle on or near conspecifics, or specific substrates, including tube worms, oysters, polychaetes, ascidians, barnacles, (Knight-Jones, 1951; Crisp, 1967; Scheltema et al, 1981; Marsden 1987; Svane et al, 1987; McGee and Targett, 1989; Marsden et al, 1990; references within Pawlik, 1992). Chemical cues have been implicated that induce the settlement and metamorphosis of these organisms, while inhibiting these processes in other organisms. These cues may likewise occur in *Dynamena pumila* as they do for other colonial hydroids, and future work should consider the biological and ecological consequences of these chemicals.

An important note to consider is the importance of physical disturbance on the horizontal (from sheltered, slow moving currents, to exposed, rapid currents) zonation of macroalgae on rocky shores in the northwest Atlantic. Sheltered sites with little water movement are dominated by *Ascophyllum nodosum*, and as the exposure to waves and water currents increases, *Fucus vesiculosus* and fast-growing epiphytic algae (*Ulva lactuca, Gigartina stellata, Chondrus crispus, Enteromorpha intestinalis*) replaces *A. nodosum*. Thus, larvae of *Dynamena pumila* might be expected to settle most heavily at Holey Point because this relatively undisturbed shore exhibits the greatest biomass of *A. nodosum* (Thomas, 1994). However the greatest distribution component values for *D.
*pumila* recorded here were from Holmes Cove Point and Green's Point Station #1 (sites exposed to moderate wave action). Site to site variation in hydroid zonation was discussed earlier, and will now be elaborated to explain large scale trends in distribution.

### 4.3.2 Horizontal gradient

At a small scale, larvae of *Dynamena pumila* prefer to settle at elevations with the greatest biomass of fucoid algae, near conspecifics. Thus, at larger spatial scales, the greatest abundance of *D. pumila* should occur at sites with the greatest biomass of fucoid algae because there would presumably be a larger amount of the bacterial film that attracts larvae. In the boreal northwestern Atlantic, the greatest biomass of fucoids exists in sheltered bays with slow moving water currents (i.e.: at Holey Point in the Quoddy region).

However, the greatest mean distribution components of *Dynamena pumila* occur at sites with moderate amounts of water movement (Holmes Cove Point and Green's Point Station #1; Figure 12 and Figures VII and VIII in the Appendix). Mean values of the distribution component are reduced at Holey Point (Figure VI in the Appendix) despite the high biomass of fucoid algae typically found at sheltered sites (Thomas, 1994) and at sites with higher exposure and faster water currents (Figures IV and X in the Appendix). The "optimal" distribution at Holmes Cove Point and Green's Point Station #1 is likely due to a balance that exists between larvae settling in areas with sufficient water flow, in addition to preferentially settling in areas with high algal biomass. Reduction of water movement may be accompanied by the smothering of many shallow-water benthic filter-feeders. In conditions of reduced water movement, hydroids are smothered by sediments that are not being swept away by the currents. Much less food is
supplied to filter-feeders under conditions of reduced water movement. Therefore, hydroids are usually more abundant in areas with moderate to strong water currents. However, much as there is a lower tolerance limit with respect to water flow, there also appears to be an upper limit. Beyond 0.09 m/s, larvae of D. pumila have difficulty settling (Orlov, 1996a), and will quickly be swept away by the currents. Thus, although the localized (vertical) zonation of D. pumila is mostly controlled by desiccation, algal zonation, and habitat complexity, the larger scale (horizontal) distribution in the Quoddy region appears to be organized by gradients of water flow.

4.3.3 Temporal gradient

There was also a temporal component in population distribution of Dynamena pumila (Table 7). Surprisingly, the greatest mean distribution components were observed during the fall (Figure 15). Furthermore, all sites supported significantly fewer hydroids during the winter (Figures VI through X in the Appendix). This was especially noticeable at the most wave exposed site with the strongest currents (Figure X in the Appendix).

Hydroid abundance was expected to be maximal in summer. However, with the exception of the most sheltered site (i.e.: Holey Point), the highest mean distribution component was consistently observed during fall (Figures VII through X in the Appendix). These trends can be explained by the observation that cormoids were reproductive during the summer sampling season (July 1998), and that recruitment into the autumn was high. By fall (October 1998), almost all hydroids had completed gonophore production. Furthermore, the abundance of Dendronotus frondosus was drastically reduced by the fall (e.g.: only 2 nudibranchs were observed at all 5 sites
during this time). Thus, the distribution component of *Dynamena pumila* increased during the fall because of heavy summer recruitment. Meanwhile, predation by nudibranchs was no longer a significant determinant of hydroid mortality.

All 5 sites experienced significant reductions in hydroid distribution during winter (Figures VI through X in the Appendix). In some cases, elevations that supported hydroids during summer and fall no longer did so in February 1999 (Figures VII, VIV, and X in the Appendix). Seasonal fluctuations in hydroid distribution were expected, and can be explained by high recruitment during summer and fall followed by high mortality as well as ice-shearing forces during the winter. The fertile period of *Dynamena pumila* in the northwestern Atlantic is between April and October (Hincks, 1868; personal observation). Planulae are released during periods of spring tidal emersion and settle within 72 hours (Orlov, 1996a). Recruitment of hydroids should therefore be maximal during this period. The decline in hydroid density in the winter is best explained by mortality from the thick ice layers that cover the shore during periods of tidal emersion. As the tide rises, the ice layers are sheared off, scraping organisms along with them. The result is a drastic reduction in the abundance of epiphytic organisms. In addition to mortality, it is possible that some colonies of *D. pumila* may have resorbed tissue and formed dormant cysts during this unfavourable season, a phenomenon reported by Haddow (1937). With spring and summer comes a new fertile period, growth of old colonies that survived by encysting, and corresponding increases in distribution of *D. pumila* (Figures VI through X in the Appendix).

The abundance and percent occupancy of *Dynamena pumila* are dependent on both the season and exposure. This finding is congruent with that determined by
Stephenson and Stephenson (1972), who observed that many sessile intertidal organisms, including barnacles, mussels, and epiphytic algae, experienced drastic reductions in abundance during the winter months on temperate and boreal rocky shores. They reasoned that during tidal emersion in the winter, the rocky shore retains water long enough for it to freeze, given low enough air temperatures. Thus, in the Quoddy region, the upper intertidal may be left covered in ice for up to 12 hours, twice a day, and the lower intertidal for up to about one hour a day, twice a day. Stephenson and Stephenson noted that at the more exposed sites they visited, strong wave action scraped away at the ice layers on the shore, carrying away any organisms attached underneath. Therefore, this "ice-scouring" effect was hypothesized to have significant impacts on the distribution of these organisms. In Figure X (c) and (d) (from the Appendix) for example, hydroids were lacking between 37.5 and 50% of the mean tidal range, and the greatest mean distribution component was no longer between 62.5 and 75% of the mean tidal range. The combined effects of waves, currents, and ice probably account for the drastic winter reductions in hydroid populations at Pea Point, more so than at the other sites.

4.4 Hydroid stem height and abundance

Wood and Seed (1980) demonstrated a significant relationship between colony height and abundance in *Dynamena pumila*. Although morphometric parameters were sampled on opposite sides of the transect from distribution parameters, the nature of this relationship in the Quoddy region was investigated.

Although a simple linear regression analysis was highly significant (df=1, F=157.665, p<0.001) with the equation $Y=0.0028X+8.941$, a very low r-squared value
was noted $R^2=0.144$. Therefore, hydroid abundance affects colony height, but the predictive value of this relationship is not very useful (Figure 16).

Hydroid stem height may increase in relation to colony abundance in order to maintain food capture rates. In a sparse population, *Dynamena pumila* may continue hydorhizal growth. In this way, the newly formed stolon can place cormoids in new areas not currently being exploited. However in a dense population, *D. pumila* may continue food capture rates by growing upwards, and placing its hydranths above other individuals to exploit food sources there. Therefore, as hydroid abundance increases in *D. pumila*, stem heights may be expected to increase to maintain feeding efficiency.

4.5 Exploratory analysis

Hydroids are difficult to quantify, given the small, colonial nature of most species. Yet these measurements are required to assess the ecological importance of hydroids in terms of biomass, secondary productivity, and benthic-pelagic coupling processes in the marine environment. Few studies have described hydroid distribution by means other than presence-absence estimates (True, 1970; Gili and Ros, 1985; Calder, 1991b; Bourget *et al.*, 1994). This study explored the relationship between abundance of *Dynamena pumila* and its percent occupancy to determine an accurate predictor variable of abundance that could be more easily sampled.

The high correlation between percent occupancy and abundance was expected (Pearson correlation coefficient = 0.916). Over the small scale that was used in the sampling design, a large number of hydroids would necessarily occupy a greater amount of space.
Using both parameters to quantify distribution was justified, because it was unknown that abundance would vary significantly among elevations. If it was found that densities were fairly similar among elevations but that the occupancy varied, then inferences may have been made about the distribution habits of *Dynamena pumila*. For example, a large number of hydroids in a small space suggests a more clumped distribution than a large number distributed over a greater space.

There appeared to be a positive linear relationship between hydroid abundance and percent occupancy by *Dynamena pumila* (Figure 19). A regression analysis was performed to determine whether occupancy would be a good predictor of abundance. If occupancy does predict abundance reasonably well, more time could be dedicated to sampling larger areas or more species, as less time is required to estimate occupancy than hydroid abundance (personal observation). The regression was noted to be highly significant, and the model $Y=1.634X+0.309$ had a high R-squared ($R^2=0.841$). Therefore, in future analyses of *D. pumila* and other hydroids, occupancy may be used to estimate abundance fairly well.

The ecological importance of *Dynamena pumila* in this region may also be determined using these quantified measurements together with dry weights to obtain estimates of hydroid biomass and secondary productivity. Future work could see these biomass and productivity estimates incorporated with consumption regimes of *D. pumila* into a model that estimates the contribution of this hydroid to benthic-pelagic coupling systems in marine habitats.
5. SUMMARY

The size and distribution of the colonial leptothecate hydroid *Dynamena pumila* (Hydrozoa: Sertulariidae) were found to vary significantly across vertical, horizontal, and temporal gradients in the Passamaquoddy ("Quoddy") Bay region of the boreal northwestern Atlantic. Desiccation forces appear to determine the upper distribution limit of *D. pumila* much as they do for most intertidal organisms. The lower limit of *D. pumila* in the Quoddy region is likely set by larval substrate selection (fucoid algae and near conspecifics) more so than by predation although this hypothesis should be tested in situ.

The effects of hydroid abundance on cormoid height were found to increase stem height perhaps to maintain feeding efficiency. Finally, it was determined that hydroid abundance and percent occupancy were highly correlated so that future sampling protocols could use occupancy as an accurate predictor of abundance.

The largest hydroids were found during the summer. In general, the lowermost elevation (usually between 37.5 and 50% of the mean tidal range) on exposed rocky shores of the Quoddy region supported hydroids with the greatest dry weights, the most branches, but shorter stems. At sheltered sites, the largest hydroids were found between 50 and 62.5% of the mean tidal range. The smallest hydroids were consistently found during winter at the highest elevations (between 75 and 87.5% of the mean tidal range) on these rocky shores.

Patterns in hydroid fertility were strongly related to season. Cormoids were found to be reproductively mature from July to October (although records indicate gonophore production in May) (Hincks, 1868), and almost exclusively during the summer. There is a significant negative relationship between vertical elevation and
fertility of hydroids. Mean fertility was highest at the most wave exposed site with the fastest water currents.

The greatest abundance and percent occupancy of hydroids were usually found during the fall, and at rocky shores with moderate exposure to wave action and water currents. At sheltered sites, most hydroids were observed at the second lowest elevation from the lowermost distribution limit of *Dynamena pumila*. However at the more exposed sites with faster water currents, most hydroids were found at the lowermost vertical shore position.

A highly significant and predictive log-linear relationship exists between hydroid abundance and percent occupancy. Thus, a new protocol that requires less effort for sampling the density of *Dynamena pumila* and other colonial hydroids may include estimating occupancy in order to obtain abundance estimates.
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7. APPENDIX

(a)=summer, (b)=fall, (c)=winter, (d)=spring
Bars around the mean are +/- 2 standard errors.

Figure 1: Vertical zonation of hydroid size at Holey Point.
Figure II: Vertical zonation of hydroid size at Holmes Cove Point.
Figure III: Vertical zonation of hydroid size at Green’s Point Station #1.
Figure IV: Vertical zonation of hydroid size at Green's Point Station #2.
Figure V: Vertical zonation of hydroid size at Pea Point.
Figure VI: Vertical zonation of hydroid distribution at Holey Point.
Figure VII: Vertical zonation of hydroid distribution at Holmes Cove Point.
Figure VIII: Vertical zonation of hydroid distribution at Green's Point Station #1.
Figure VIIV: Vertical zonation of hydroid distribution at Green's Point Station #2.
Figure X: Vertical zonation of hydroid distribution at Pea Point.