VARIATION IN THE POPULATION DYNAMICS OF THE INVASIVE BRYOZOAN *Membranipora membranacea* ALONG A 450-KM LATITUDINAL GRADIENT IN NEWFOUNDLAND AND LABRADOR, CANADA

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Variation in the population dynamics of the invasive bryozoan *Membranipora membranacea* along a 450-km latitudinal gradient in Newfoundland and Labrador, Canada

by

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ABSTRACT

The overall objective of this study was to quantify and compare seasonal (June to November) and inter-annual (2008 and 2009) variation in settlement, recruitment, and colony cover of the invasive bryozoan *Membranipora membranacea* on the kelp *Saccharina longicruris* across eight sites spanning a 450-km latitudinal gradient between the southwestern tip of Newfoundland and southeastern tip of Labrador. Thermal histories were calculated for each site to determine the extent that the observed variation was explained by sea temperature. Analysis of settlement data (Chapter II) indicated that (1) settler abundance varied both seasonally and annually with a sharp increase between August and September at warmer sites, and spatially with differences of up to three orders of magnitude between sites, (2) settler abundance and sea temperature were strongly correlated (r^2=0.577), with maxima at mid-latitudes and minima at the northernmost and southernmost sites, and (3) exposure to waves, degree of kelp blade corrugations, and surface area of colonies of *M. membranacea* on kelp had little explanatory power on settler abundance across the study sites compared to sea temperature. Analysis of recruitment and colony cover data (Chapter III) indicated that (4) recruitment and colony cover varied seasonally, though variation generally decreased with increasing latitude, (5) temperature in the 76 days preceding measurements explained most [>60%] of the variation in recruitment within each month from late summer [September] to late fall [November] with the highest predictive capability (97%) in late fall, and (6) colony cover was strongly correlated (r^2=0.524) to recruit abundance from late summer to late fall. Consistently low abundances of settlers, recruits, and colonies at the two northernmost sites suggested that *M. membranacea* is nearing its northern distribution limit in the northwest Atlantic. This study provides the first quantitative analysis of spatial and temporal variation in the abundance of *M. membranacea* in Newfoundland and Labrador since its introduction in the early 2000s. It strongly supports the general hypothesis that temperature is a key factor in regulating the population dynamics of this species, while suggesting that oceanographic phenomena such as upwelling and downwelling, which act on larval transport, also affect the dynamics at different spatial and temporal scales. A few inconsistencies both within the system studied and between the system studied and that of Nova Scotia indicate additional long-term observational and experimental studies are required to elucidate factors that regulate local and regional variation in the abundance of *M. membranacea* in cold temperate and subarctic environments.

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CHAPTER I

GENERAL INTRODUCTION

Kelp beds are highly productive (globally 120 to 2000 g C m^{-2} yr^{-1}) shallow coastal communities found in temperate and polar zones worldwide (Mann 1973, 1982, Dayton 1985). One of the most common kelp species in the northwest Atlantic (from Rhode Island Sound to the west coast of Greenland) is *Saccharina longicruris* de la Pylaie (formally *Laminaria longicruris* Lane et al. 2006) (Gerard & Mann 1979, Brady-Campbell et al. 1984, Smith 1985, Chapman 1987, Patten & Yarish 1993). This species is particularly abundant in eastern Canada, and especially along the coasts of Nova Scotia and Newfoundland and Labrador, where it often forms dense beds (Mann 1972, Gerard & Mann 1979, South 1983, Chapman 1987, Patten & Yarish 1993). Historically, shallow, rocky, subtidal communities in eastern Canada have alternated between two states, kelp beds and urchin barrens, as a result of cyclical changes in the abundance and grazing of the omnivorous green see urchin, *Strongylocentrotus droebachiensis* (Mann 1977, Scheibling et al. 1999, Gagnon et al. 2004). The introduction of two invasive species, the cheilostome bryozoan *Membranipora membranacea* Linnaeus and the green alga *Codium fragile* ssp. *fragil*e Suringar (formally *Codium fragile* ssp. *tomentosoides* Provan et al. 2008) to Nova Scotia in the late 1980s and early 1990s, has disrupted the dynamic equilibrium between kelp beds and urchin barrens through the formation of locally abundant beds of *C. fragile* (Scheibling et al. 1999, Chapman et al. 2002, Scheibling & Gagnon 2006).

Membranipora membranacea exhibits a life cycle alternating between a free swimming, planktotrophic, cyphonautes larval stage, and a benthic, colonial adult stage (Ryland 1970, Brusca & Brusca 2002). Cyphonautes larvae can spend up to eight weeks in the water column before settling and metamorphosing into the first benthic stage called the ancestrula that gives rise to the first two zooids of any colony (Atkins 1955, Yoshioka 1973, Stricker 1988, Temkin 1994). New zooids are produced asexually at the margin of a developing colony, resulting in concentric rows of zooids extending from the ancestrula. Colonies are typically circular and consist of up to several thousands of box-shaped, hermaphroditic zooids each measuring <1 mm in length. *Membranipora membranacea* colonizes both natural and artificial substrates, though is most frequently encountered on seaweeds, in particular kelp on which it can form thick crusts that cover the entire surface of blades (Yoshioka 1982, Harvell et al. 1990, Lambert et al. 1992, Harris & Jones 2005, Scheibling & Gagnon 2009, Matson et al. 2010). Cyphonautes larvae in *M. membranacea* settle preferentially on younger, meristematic kelp tissues (Seed & O'Connor 1981), whereas colonies are generally more abundant on blade margins (Saier & Chapman 2004). Pervasive effects of colonies of *M. membranacea* on kelp range from reduced growth rates and reproduction to erosion and fracturing of kelp tissues leading to seasonal declines in kelp biomass as documented in the last two decades in the northwest Atlantic (Lambert et al. 1992, Chapman et al. 2002, Saier & Chapman 2004, Saunders & Metaxas 2008, Scheibling & Gagnon 2009).

Thought to originate from the northwest Pacific, *M. membranacea* is now widely distributed along the Atlantic coasts of Europe and North America (Eggleston 1972, Lambert et al. 1992, Schwaninger 2008). The first report of the occurrence of *M. membranacea* in the northwest Atlantic was in the mid-1980s in the Gulf of Maine (presumably introduced in the ballast waters of trans-Atlantic ships, Schwaninger 1999, 2008) where it became the dominant epibiont on kelp in less than two years (Berman et al. 1992, Lambert et al. 1992). The current distribution of *M. membranacea* in eastern

Canada includes the Atlantic coast of Nova Scotia (Chapman et al. 2002, Watanabe et al. 2009), south shore of Québec (Gendron et al. 2007), and the coast of Newfoundland and Labrador (R. Hooper, personal communication).

Temperature can have a profound effect on reproduction, settlement, recruitment, and growth of marine invertebrates, especially in short-lived species that grow on ephemeral substrates (Brown 1984, Bowman & Lewis 1986, Kendall & Lewis 1986, Lewis 1986, Amui-Vedel et al. 2007, Saunders & Metaxas 2007). Colonies of *M. membranacea* exhibit faster growth in warm than cold water (Menon 1972, Saunders & Metaxas 2009a) yet must grow fast enough to reach sexual maturity and reproduce before their algal substrate dies or fragments (Bernstein & Jung 1979, Harvell & Grosberg 1988). Current understanding of the population dynamics of *M. membranacea* in the northwest Atlantic is based on a few studies between 1992 and 2007 in central Nova Scotia. An 11-year survey (1992-2002) in St. Margarets Bay and Mahone Bay showed that inter-annual variation in the peak cover of *M. membranacea* on *S. longicruris* is correlated to thermal history during summer and fall (Scheibling & Gagnon 2009). A two-year survey (2005 and 2006) of settlement, recruitment, and colony cover of *M. membranacea* on the kelp *Saccharina longicruris* in St. Margarets Bay showed that (1) settlers and recruits are seasonally abundant between May and November, with peak abundances in September and October, (2) temporal variation in the abundance of settlers is correlated to thermal history, and (3) recruitment can occur earlier in the spring and the abundance and cover of colonies can be higher following a warmer winter (Saunders & Metaxas 2007, 2008, Saunders et al. 2010). Substantial variation in the onset of settlement in *M. membranacea* can occur over larger spatial domains as shown in the northeast Pacific, where settler abundances generally peak during winter in California, and during summer and fall in Washington (Bernstein & Jung 1979, Yoshioka 1982, Harvell et al. 1990). Such variation has been attributed in part to geographic differences in the vertical position of cyphonautes larvae in the water column during periods of thermohaline stratification (Yoshioka 1982, Saunders & Metaxas 2010).

In general, variation in settler and recruit abundance in marine invertebrates with planktonic larvae such as *M. membranacea* is largely determined by microhabitat availability and predation at small spatial scales (tens to hundreds of meters) and by larval supply at larger scales (tens to hundreds of kilometers) (Connell 1961b, Paine 1974, Pineda 1991, Pawlik 1992, Morgan & Fisher 2010). Hydrodynamic conditions operate across these scales, affecting larval supply, attachment of settlers, and recruitment (Pawlik & Butman 1993, Zacherl et al. 2003, McQuaid & Lindsay 2005, Pratt 2008). In particular, high current energy negatively affects growth and feeding rates in *M. membranacea* and is thought to interfere with settlement and recruitment (Eckman & Duggins 1993, Okamura & Partridge 1999, Pratt 2008). The importance of adult fecundity in regulating recruitment over large spatial scales is increasingly recognized (Cowen et al. 2000, Swearer et al. 2002, Hughes et al. 2008). Since fecundity in *M. membranacea* is positively related to growth and colony surface area (Yoshioka 1973), high current energy may limit the supply of larvae. Therefore, patterns of settlement, recruitment, and growth in *M. membranacea* are most likely a result of interactions between biological, physical (in addition to temperature), and chemical factors that vary in time and space.

The recent (2002; R. Hooper, personal communication) invasion of *M. membranacea* to Newfoundland and Labrador provides an excellent opportunity to test the generality of and refine relationships between temperature, settlement, recruitment, and colony cover on kelp in studies in Nova Scotia, the Gulf of Maine, and California. The west coast of Newfoundland stretches over 500 km across a roughly north-south axis. Temperature (and other oceanographic variables) along this highly heterogeneous coast varies in space and time. In northern Newfoundland, cold arctic water of the Labrador Current flows southward through the narrow Straight of Belle Isle (18 km at the narrowest point) which may form a natural barrier to the northward dispersal of *M. membranacea* (Han 2004). At the southwestern tip of Newfoundland periodic upwelling during the late summer and early fall cause rapid cooling of surface waters (Mouland 2004, 2005, 2006), and likely the offshore transport of cyphonautes larvae. Lastly, current strength and flushing rates of variably sized bays may affect the retention of larvae and the abundance of settlers and recruits. Given the putative importance of sea temperature in regulating the abundance of *M. membranacea* in southeastern Canada, a corollary hypothesis is that its population dynamics in northern, colder environments of the northwest Atlantic differs due to preponderance of suboptimal (or lethal) thermal conditions.

This thesis uses kelp from eight sites along the entire west coast of Newfoundland and southern tip of Labrador to extend our knowledge of spatial and temporal variation in settlement, recruitment, and cover of *M. membranacea* colonies and its relationship with thermal conditions in cold temperate and subarctic environments. The term "settler" refers to a pre-ancestrula (with larval shells still present) or a fully metamorphosed ancestrula (with first two calcified zooids). The term “recruit” refers to a fully developed ancestrula with at least one daughter zooid (three zooids in total) and any cluster of zooids with a diameter <5 mm. A "colony" of *M. membanacea* is any cluster of at least six rows of zooids with a diameter ≥5 mm. Chapter II examines how the abundance of settlers varies temporally within and between sites as well as how thermal integrals for different time periods explain the observed variation. Moreover, it determines whether exposure to waves, kelp blade morphology and the surface area of colonies on kelp can be used to predict settler abundance across the latitudinal gradient. Chapter III investigates spatial and temporal variation in the abundance of recruits and colony cover on kelp and its relationship with the most relevant thermal integral identified in Chapter II. In particular, it provides a temporal breakdown of predictive capabilities of temperature for recruit abundance and colony cover, as well as of recruit abundance for colony cover. Both Chapters II and III are written in a format compatible with the publication of research articles, which explains the repetition of information where appropriate, as well as the use of first-person plural pronoun (“we”) and possessive determiner (“our”) throughout. Chapter IV presents a summary of main findings while briefly discussing their contribution to our knowledge of the structure and function of shallow marine ecosystems of Newfoundland and Labrador.

Co-authorship statement

The work described in this thesis was conducted by Scott Caines with guidance from Patrick Gagnon, Cynthia McKenzie, and Robert Hooper. Scott Caines was responsible for field and laboratory data collection (with assistance by Patrick Gagnon) and analysis and contributed to modifications brought to the original design by Patrick Gagnon. All chapters were written by Scott Caines with intellectual and editorial input by Patrick Gagnon. Publication(s) in the primary literature resulting from this work will be co-authored by Scott Caines and Patrick Gagnon.

CHAPTER II

Seasonal and inter-annual variation in settlement of the invasive bryozoan *Membranipora membranacea* along a 450-km latitudinal gradient in Newfoundland and Labrador, Canada

2.1 INTRODUCTION

Marine benthic invertebrates often exhibit a complex life cycle that involves a dispersing, pelagic larval stage (Thorson 1950). For example, planktotrophic larvae in the barnacle *Semibalanus balanoides*, the blue mussel *Mytilus edulis*, and the green sea urchin, *Strongylocentrotus droebachiensis*, remain in the water column from a few days to up to several weeks, where they are dispersed by currents operating at various spatial and temporal scales (Barnes & Barnes 1958, Strathmann 1974, 1978, Pechenik et al. 1990). Settlement in marine benthic invertebrates with pelagic larvae is defined as the process whereby a competent larva searches for a suitable substratum, attaches to it, and metamorphoses into its benthic form (Keough & Downes 1982, Rodriguez et al. 1993). Processes that regulate the onset and magnitude of settlement and how settler abundance varies spatially and temporally are often complex as a result of interactions between multiple factors and mechanisms (e.g. Hawkins & Hartnoll 1982, Pawlik 1992, Rodriguez et al. 1993, Lagos et al. 2005, Stebbing 2009). At small spatial scales (tens to hundreds of meters), changes in settler abundance can result from variation in bathymetric distribution of larvae, substrate and microhabitat selection by larvae, space availability, and the abundance of predators and competitors (Denley & Underwood 1979, Grosberg 1982, Keough & Downes 1982, Gaines & Roughgarden 1985). At large spatial scales (tens to hundreds of kilometers), variation in settlement can arise from processes that affect the number of individuals within larval pools (Barnes 1956, Menge et al. 2009), larval transport (Shanks 1983, Pineda 1991), and retention or offshore wastage of larvae (Roughgarden et al. 1988, Poulin et al. 2002, Menge et al. 2003, Morgan & Fisher 2010).

Sea temperature affects survival and reproduction in many marine invertebrates, and hence can be a key determinant of their northern and southern distribution limits (Hutchins 1945, Zacherl et al. 2003). Low, sporadic settlement and recruitment at a species northern limit can result in small populations consisting of larger, older individuals (Kendall & Lewis 1986, Lewis 1986). Successful recruitment into these populations is limited to warmer years when sea temperature exceeds a minimum threshold value for survival of juveniles stages (Kendall & Lewis 1986, Zacherl et al. 2003). Larval supply is greatly affected by water circulation and its interaction with temperature (Connolly & Roughgarden 1998, Gaylord & Gaines 2000, Connolly et al. 2001, Zacherl et al. 2003). In particular, coastal upwelling and downwelling, which cause marked changes in water temperature, can displace larvae offshore and inshore, respectively (Yoshioka 1982, Connolly et al. 2001, Saunders & Metaxas 2010). High current energy may promote the transport of larvae to an area (McKindsey & Bourget 2000, McQuaid & Lindsay 2005), while limiting settlement if too high (Crisp 1955, Pawlik & Butman 1993).

The bryozoan *Membranipora membranacea* (Lophophorate: Chelistomata) exhibits a life cycle alternating between a pelagic larval stage (cyphonautes) that can remain in the water column several weeks before settling and metamorphosing (Yoshioka 1973, Temkin 1994) and a benthic, colonial, adult stage. Colonies typically develop on the surface of macroalgae, including large brown seaweeds of the order Laminariales (kelp), though also occur on animals and artificial substrates (Dixon et al. 1981, Ellison & Harvell 1989, Berman et al. 1992, Pratt & Grason 2007, Saunders & Metaxas 2009b). Each colony consists of several to thousands of box-shaped individuals (zooids) measuring less than 1 mm in length. *Membranipora membranacea* was introduced to the Gulf of Maine in the mid-1980s, presumably through discharge of ballast waters from transoceanic vessels (Schwaninger 2008), where it rapidly invaded shallow subtidal kelp habitats (Berman et al. 1992, Lambert et al. 1992). Current known distribution of *M. membranacea* in eastern Canada includes the Atlantic coast of Nova Scotia (Chapman et al. 2002, Watanabe et al. 2009), south shore of Québec (Gendron et al. 2007), and the coast of Newfoundland and Labrador (R. Hooper, personal communication).

Most of our understanding of population dynamics of *M. membranacea* in the northwest Atlantic is based on recent studies in central Nova Scotia. Two-year surveys of settlement and recruitment of *M. membranacea* on the kelp *Saccharina longicruris* in St. Margarets Bay showed that: (1) changes in the abundance of settlers and recruits follow an annual cycle with peak abundances in fall, (2) settlement is correlated to thermal history, and (3) recruitment can occur earlier, and the abundance of juvenile and adult colonies can be higher, in months following a warmer winter (Saunders & Metaxas 2007, 2008, Saunders et al. 2010). A 10-year survey in St. Margarets Bay and Mahone Bay showed that changes in the cover of *M. membranacea* on *S. longicruris* are seasonal and that inter-annual variation in peak cover is correlated to thermal history during summer and fall (Scheibling & Gagnon 2009). Thermo-haline stratification during one fall in St. Margarets Bay was also found to affect the distribution of cyphonautes larvae in the water column, with possible onshore transport of larvae during wind-driven downwelling events (Saunders & Metaxas 2010). Overall, these pioneering studies conducted in a relatively small area (all study sites were located within a range <50 km) have helped elevate the importance of sea temperature in affecting local patterns of settlement, recruitment, and growth of *M. membranacea*. Given the putative importance of sea temperature in regulating the abundance of *M. membranacea* in southeastern Canada, a corollary hypothesis is that population dynamics of this bryozoan in northern, colder environments of the northwest Atlantic differs due to suboptimal (or lethal) temperature.

This chapter examines seasonal and inter-annual variation in the timing and magnitude of settlement of *M. membranacea* on the kelp *Saccharina longicruris* and how it relates to changes in sea temperature during two consecutive years (2008 and 2009) at eight sites spanning a 450-km latitudinal gradient in subarctic and temperate Newfoundland and Labrador, where *M. membranacea* was recently (<10 years) introduced and low sea temperatures predominate. Specifically, we 1) test the hypothesis that settler abundance is positively correlated with temperature, being generally higher and lower at warmer and colder sites, respectively, 2) examine how the relationship between settler abundance and temperature varies with different temporal windows over which settlement and temperature data are aggregated, and 3) determine whether variation in settler abundance relates to exposure to waves, kelp blade morphology, and the surface area of *M. membranacea* colonies on kelp.

2.2 MATERIALS AND METHODS

2.2.1 Study sites

This study was conducted at eight sites spanning ~450 km between southwestern Newfoundland (47°34'N) and southeastern Labrador (51°43'N): (1) Port aux Basques [southernmost site], (2) Lark Harbour, (3) Norris Point, (4) Daniel's Harbour, (5) Port au

Choix, (6) Bird Cove, (7) Green Island Cove, and (8) Red Bay [northernmost site, located in Labrador] (Fig. 2.1). The shallow (0 to 20 m deep) rocky seabed in southwestern Newfoundland consists of sedimentary (sites 1 and 3) and igneous (sites 2 and 4) boulders and bedrock outcrops. Sedimentary bedrock outcrops and ledges predominate north of $50^{o}1$'N (sites 5, 6 and 7) in Newfoundland, whereas granitic boulders and bedrock prevail in southeastern Labrador (site 8) (Colman-Sadd & Scott 1994). Kelp beds occurred at all sites within the 5-20 m depth range (chart datum), especially in sheltered and moderately exposed locations. The shallow portion of the beds was generally dominated by the kelps *Saccharina longicruris*, and to a lesser extent *Alaria esculenta*, *Laminaria digitata*, and *Saccorhiza dermatodea*. Those species were gradually replaced with increasing depth by the grazing-resistant and shade-tolerant kelp, *Agarum clathratum* (Vadas 1968, South 1983).

2.2.2 Collection of kelp blades

To investigate spatial and temporal variation in the abundance of *Membranipora membranacea* settlers on kelp, blades of the kelp *Saccharina longicruris* were collected by fish harvesters once every month between August and October 2008 at all sites (1 to 8) and between August and October 2009 at sites 3 and 7. Although we originally aimed to obtain blades in the third week of each month, rough seas at certain sites occasionally prevented collection, therefore resulting in blades being collected within a period of 8 to 14 days in each month in 2008 and up to 7 days in 2009. Likewise, no blades were available for August 2008 at sites 3 and 8 and for September 2008 at sites 1 and 2 (Table 2.1). On each collection day, fish harvesters collected a minimum of eight kelp blades at a depth of approximately 6 m. Kelp blades were collected from fishing vessels

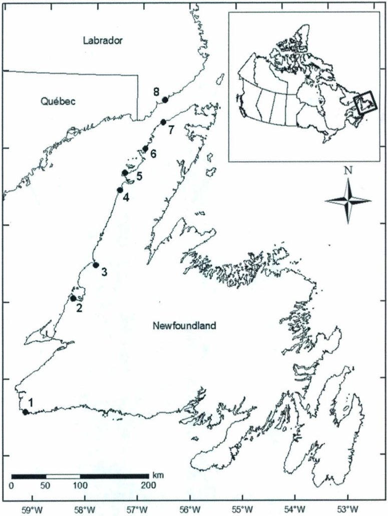

Figure 2.1 Location of the eight study sites on the west coast of Newfoundland and southern tip of Labrador (Canada): (1) Port aux Basques, (2) Lark Harbour, (3) Norris Point, (4) Daniel's Harbour, (5) Port au Choix, (6) Bird Cove, (7) Green Island Cove, and (8) Red Bay. Sampling was done at all sites in 2008 and at sites 3 and 7 in 2009.

Table 2.1: Geographic location (degrees-minutes-seconds) of each study site and corresponding dates of kelp collection, degree of exposure to waves, and depth of temperature logger (chart data).

Study site (number)	Geographic location (N, W)	Sampling year	Kelp collection date (number of kelp blades)						Degree of exposure to waves[1]	Depth of temperature logger (m)
			June	July	August	September	October	November		
Port aux Basques (1)	47°34'43" 59°05'28"	2008	10 (8)	-	26 (10)	-	26 (10)	-	3	4.7
Lark Harbour (2)	49°06'25" 58°21'23"	2008	12 (8)	-	19 (10)	-	27 (10)	1 (5)[2]	7	4.8
Norris Point (3)	49°30'10" 57°53'32"	2008	7 (8)	-	-	17 (9)	14 (10)	25 (5)	2	6.7
		2009	17 (8)	14 (10)	17 (10)	14 (10)	13 (8)	12 (10)		5.5
Daniel's Harbour (4)	50°14'29" 57°35'20"	2008	4 (8)	-	19 (10)	9 (10)	14 (10)	29 (5)	14	4.5
Port au Choix (5)	50°43'56" 57°18'44"	2008	5 (8)	-	18 (8)	23 (10)	21 (10)	25 (5)	9	5.4
Bird Cove (6)	51°03'19" 56°56'25"	2008	5 (8)	-	19 (10)	14 (10)	13 (10)	26 (5)	8	5.2
Green Island Cove (7)	51°22'36" 56°36'28"	2008	-	-	18 (8)	15 (10)	14 (10)	26 (5)	15	2.2
		2009	16 (8)	-	11 (10)	21 (10)	13 (10)	11 (10)		4.1
Red Bay (8)	51°43'35" 56°25'44"	2008	-	9 (10)	-	23 (10)	13 (10)	-	0	3.5

[1] The higher the value, the greater the exposure (see Materials and methods for calculations).

[2] Kelp blades were collected on 1 December, 2008 and analyzed as part of the November data (see Materials and methods).

using a device designed for this research that cut stipes, leaving blades intact (see Appendix A for a description of the kelp collection device and how it was used). Blades were rolled and sealed in plastic bags, placed on ice within sealed plastic coolers, and shipped using expedite courier to the Ocean Sciences Centre (OSC). Upon arrival at the OSC (within 72 h from shipping date) blades were placed in large (330 L) holding tanks supplied with cold, flow through seawater pumped in from a depth of 10 m in Logy Bay. All blades were analyzed (see below) within one to five days of receipt. There were no obvious signs of blade deterioration (e.g. missing portions, production of mucilage, and softening of tissues) resulting from collection, shipping, and maintenance of blades in the tanks (Appendix A). Those few blades with some necrotic tissues were discarded prior to analysis.

Most fish harvesters could not collect kelp blades before August or after October in each year due to seasonal closure of fisheries. To supplement the 2008 series, we used scuba diving to haphazardly collect five to ten blades between 4 and 12 June 2008 at all but the two northernmost sites (7 and 8), on 9 July 2008 at site 8, and at all but the southernmost (1) and northernmost (8) sites between 25 November and 1 December 2008 (Table 2.1). Blades obtained on 9 July and 1 December 2008 were analyzed as part of the June and November sampling months, respectively (see analysis below). We supplemented the 2009 series by collecting eight to ten kelp blades on 17 June, 14 July, and 12 November 2009 at site 3, and on 16 June and 11 November 2009 at site 7 (Table 2.1). Blades collected by divers were packaged and transported to the OSC using the same technique as fish harvesters (see above). They were also maintained in holding tanks with cold, flow through seawater and processed within one to five days.

2.2.3 Abundance of *M. membranacea* settlers on kelp

In this study, the term "settler" refers strictly to a pre-ancestrula (with larval shells still present) or a fully metamorphosed ancestrula (with first two calcified zooids) (Yoshioka 1986, Stricker 1988, 1989). To quantify the abundance of settlers of *M. membranacea* on kelp blades, each blade was divided into three contiguous portions along its length: (1) bottom [the lower or proximal third of the blade including the meristem], (2) centre [the middle third of the blade], and (3) top [the upper or distal third of the blade]. Within each zone we cut with a scalpel three square pieces of kelp tissue of 16 (for kelp blades ≤80 cm in length) or 25 cm^2 (blades >80 cm) each, one in the center and the two others on the left and right margins of the blade. The vertical position of each piece in each zone was determined based on the occurrence of colonies of *M. membranacea*. Pieces were taken halfway through the length of each zone when they contained no colony with a diameter >1 cm (pieces with larger colonies did not appear to offer enough bare surface for settlers), or they were taken up or down the center until this criterion was met. Damages to or heavy infestation of kelp blades by *M. membranacea* in certain months at a few sites limited the sampling to less than nine pieces in 43.2% of the kelp blades. The density of settlers on each sample was obtained by dividing the number of settlers (determined by visual count with a stereomicroscope set at 15x magnification) by the surface area of the sample. Settler density for each kelp blades was determined by averaging densities obtained from each tissue sample (up to nine samples per blade).

2.2.4 Collection and integration of temperature and wave exposure data

To test the hypothesis that spatial and temporal variation in settlement of *M. membranacea* is correlated with sea temperature while determining if exposure to waves (used as a proxy of overall current energy), kelp blade morphology, and the surface area of *M. membranacea* colonies on kelp affect this relationship (see below), we recorded sea temperature in 2008 and 2009 at each site with one temperature logger (HOBO Pendent by Onset Computer Corporation, ± 0.5°C accuracy). Each logger was attached to an eyebolt secured to the seabed with marine epoxy (Z-Spar) at a mean depth of 4.7 ± 1.2 (SD) m (chart datum) (Table 2.1). Loggers were located within 4 km of kelp collection sites except at site 8 where the logger was approximately 22 km from the collection site due to a change in kelp harvester and location of collection site between August and September 2008. In 2008, temperature was recorded every hour from 13 June to 24 November at sites 1 to 7, and from 10 July to 24 November at site 8. All loggers were retrieved by 1 December. In 2009, temperature was recorded every hour from 13 June to 11 November at site 3 and from 16 June to 11 November at site 7. The mean daily temperature for each site was calculated from hourly recordings (Fig. 2.2).

Studies in eastern Canada used integrated indices of thermal history to relate sea temperature to settlement and cover of *M. membranacea* colonies on kelp (Saunders & Metaxas 2007, Scheibling & Gagnon 2009). In those studies, thermal histories were constructed by adding daily average temperature over a given period of time. We used the same approach to construct thermal integrals (hereafter TI_N, where N is the number of days over which the thermal history was calculated) over the 14, 21, 28, and 76 days that preceded every kelp collection day between September and November 2008 and 2009 (period of year when we observed peak settlement values). Those four thermal integrals (76 d was the longest period of time with temperature data available for all months simultaneously) were used to try to determine which one, if any, best explained variation

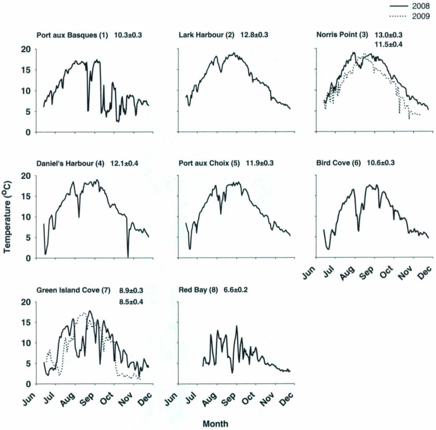

Figure 2.2: Change in mean daily sea temperature at each study site (ordered horizontally from south to north) between June and November 2008 (sites 1 to 7), July and November 2008 (site 8), and June and November 2009 (sites 3 and 7) (see Table 2.1 and Fig. 2.1 for location of sites). Values are mean (±SE) temperature calculated over the entire dataset for 2008 and 2009 (lower values at sites 3 and 7). Note the major drops in temperature in August at all but sites 2 and 3.

in settlement of *M. membranacea* on kelp (see below). Thermal integrals were obtained by adding mean daily averages of hourly records.

We used the Baardseth index (1970) to estimate the relative degree of exposure to waves of each kelp collection site. The centre of a transparent circular disk divided into 36 sectors of 10° each was placed on top of a satellite image (Google Earth 1:50 000) of each collection site. The number of sectors encompassing sea surface only (no landmass) within a radius of 7.5 km from the centre of the disk (collection site) was counted. Accordingly, the degree of exposure to wave action ranged from 0 (minimum exposure) to 36 (maximum exposure).

2.2.5 Kelp blade morphology and surface area of *M. membranacea* colonies on kelp

Factors other than temperature may also contribute to variation in settlement of *Membranipora membranacea* on kelp. Field and laboratory observations in Britain and California suggested that blade texture and corrugations affect settlement of bryozoan larvae on seaweeds, including kelp (Ryland 1959, Yoshioka 1973). In general, *M. membranacea* settles preferentially on younger kelp tissues (close to the meristem), and colonies are usually more abundant on blade margins (Yoshioka 1973, Bernstein & Jung 1979, Saier & Chapman 2004). Blade morphology in *Saccharina longicruris* typically varies with the wave environment with smaller, flatter individuals, and larger, corrugated individuals in high- and low-wave-energy environments, respectively (Gerard & Mann 1979). Our preliminary observations of kelp blades suggested differences in the degree of blade corrugations between sites. To determine the possible contribution of blade corrugations to spatial and temporal variation in settlement of *M. membranacea* on

S. longicruris, we developed a blade corrugation index (hereafter BCI) for each site sampled from August to November in 2008 and June to November in 2009. After assessing the abundance of *M. membranacea* settlers (see above) each kelp blade was laid on a white surface and photographed from above with a digital camera (Canon Powershot A720). The blade was cut into pieces that were flattened on the white surface and photographed again. We used the image analysis software ImageJ (v. 1.43d) to calculate the surface area of both the intact blade and flattened pieces. Each blade was assigned a BCI value expressing the ratio of surface areas of flattened pieces to intact blade, therefore providing an estimate of the degree of corrugation. Accordingly, the degree of corrugation was minimal when BCI=1 (i.e. a perfectly flat blade where intact and flattened surface areas are equal) and increased with increasing BCI value.

According to Yoshioka (1986), the abundance of *M. membranacea* recruits on *Macrocystis pyrifera* is positively related to the number of zooids on a kelp blade. Since the number of zooids in colonies increases proportionally with colony size (Yoshioka 1973) the reproductive potential of a colony should be positively related to its surface area. To determine the contribution of the surface area (used as a proxy for fecundity) of *M. membranacea* colonies to spatial and temporal variation in the abundance of settlers on *S. longicruris*, blades of *S. longicruris* with colonies were laid under a large (183 x 62 cm), rectangular sheet of transparent acrylic mounted on a wooden frame. The contours of each kelp blade and associated colonies with a diameter >5 mm were traced on the sheet with markers. The sheet was placed above a white background to highlight kelp and colony contours and photographed. The total surface area of colonies on one side (chosen randomly) of each kelp blade was calculated by analyzing photographs with the image analysis software Sigma Scan Pro 5. Portions of certain colonies were located within folds and corrugations of kelp margins, and hence could not be marked on the sheet. Therefore, the visible portion of the surface area of only those colonies of *M. membranacea* that extended within kelp folds and corrugations was multiplied by the corresponding BCI value (see above) to estimate their actual area. We averaged total surface areas of colonies of all kelp blades for each site in each month. The average total colony surface area per blade and not the percentage of kelp tissues covered (colony cover; Chapter III) was used as a measure of reproductive potential, as standardizing the surface area of colonies to available kelp tissues may obscure the relationship.

2.2.6 Statistical analysis

The absence of data for at least one site in June, August, September, and November 2008 (Table 2.1) precluded the use of a two-way ANOVA (Zar 1999) to analyze variation in the abundance of *M. membranacea* settlers on kelp across all sites and collection months simultaneously. Therefore, we used two separate one-way ANOVAs, one with the factor Site (sites 1 to 8), the other with the factor Month (June, August, September, October, and November), to analyze variation in the abundance of settlers over the largest possible spatial and temporal domains. No transformation corrected the lack of homoscedasticity in the data in both analyses, and hence the ANOVAs were also run with the rank transformed data. Because analyses on both raw and ranked transformed data gave similar results, we presented the results from analyses of the raw data as suggested by Conover (1980). To analyze spatial and temporal variation in the abundance of settlers simultaneously, data in June and August at all sites, and September and November at sites 1, 2, and 8 were removed and the remaining data were analyzed using a two-way ANOVA with the factors Month (September, October, and November) and Site (sites 3 to 7). Although data were cube root transformed (raw data fit a gamma distribution) to correct for the lack of homoscedasticity, residuals were not normally distributed. The ANOVA is generally robust to deviation from normality (Underwood 1997). Therefore, we presented results from the analysis of the cube root transformed data. Inter-annual variation in the abundance of settlers at the two sites sampled in 2008 and 2009 was analyzed using a three-way ANOVA with the factors Year (2008 and 2009), Month (September, October, and November), and Site (sites 3 and 7). Although data were cube root transformed to obtain homoscedasticity, residuals were not normally distributed. Again, we presented results from the analysis of cube root transformed data.

We examined relationships between the mean abundance of *M. membranacea* settlers on kelp and sea temperature (thermal integrals) using simple linear regression analysis (Whitlock & Schluter 2009). Firstly, we performed four separate analyses, one for each of the four thermal integrals (TI_N, calculated over 14, 21, 28, and 76 d prior to each collection day) to determine which thermal integral, if any, best explained variation in the mean abundance of settlers at all sites in September, October, and November (peak settlement period) of 2008 and 2009 (data pooled across months and years). Secondly, we performed twelve separate analyses, one for each thermal integral (TI_{14}, TI_{21}, TI_{28}, and TI_{76}) within each of September, October, and November of 2008 and 2009 (years pooled), to determine which thermal integral best explained settler abundance within each month and how these relationships possibly differed between months. We used log (x +1) transformed data for all regressions to obtain homoscedasticity and normality. TI_{76}

emerged as the best explanatory thermal integral in both sets of analyses (see results), and hence it was used to examine the combined contribution of thermal history, exposure to waves, kelp blade corrugations, and the surface area of *M. membranacea* colonies to variation in the abundance of settlers on kelp between September and November (2008 and 2009). This was done by running a multiple linear regression analysis (Sokal & Rohlf 1995) with TI_{76}, Exp (exposure to waves), BCI (blade corrugation index values), and SA (total surface area of *M. membranacea* colonies on kelp) at each site in both years as independent variables. The assumptions of homoscedasticity and normality were met with the raw data and none of the four independent variables were correlated as shown by low Pearson's correlation coefficient and variance inflation factor.

In the above analyses, normality was verified using the Shapiro-Wilk's statistics and homoscedasticity of the variance by examining the graphical distribution of the residuals and by applying the Levene test (Snedecor & Cochran 1989). The factors Site, Month, and Year in the ANOVAs described above were fixed as they represented specific levels of interest and it was predicted that each site, month, and year would be characterized by unique sea temperature and hydrodynamic conditions affecting settler abundance. To detect differences among levels within a factor, we used Tukey-Kramer multiple comparison tests (comparisons based on LS Means; Sokal & Rohlf 1995). All statistical analyses were conducted using Minitab 16 statistical software and a significance level of 0.05.

2.3 RESULTS

2.3.1 Seasonal variation in *M. membranacea* settlers on kelp

Analysis of the 2008 data indicated that the abundance of *Membranipora membranacea* settlers on the kelp *Saccharina longicruris* varied markedly across the eight study sites (Table 2.2, Fig. 2.3). Changes in settler abundance and sea temperature generally followed a similar pattern, with maxima at mid-latitudes (site 3) and minima at the two geographical extremes (sites 1 and 8) (Fig. 2.3). One major exception was the dramatic decline in settlement from site 3 to site 4, which was accompanied by a decline of only 0.8°C. Mean sea temperature was remarkably similar at sites 4, 5, and 6 as shown by a difference of only 1.4° C between sites 4 and 6. Likewise, settler abundance at those sites was comparable and intermediate compared to the other sites. The steady decrease in settler abundance north of site 5 coincided with a pronounced drop in temperature (Fig. 2.3). Lowest settlement values along the west coast of Newfoundland were at sites 1 and 7 (33.9 ± 17.6 [SE] and 38.5 ± 9.5 settlers m^{-2}, respectively), which were not different than on the southeastern tip of Labrador (site 8). These low values corresponded to lowest temperatures among sites (Fig. 2.3).

The abundance of *M. membranacea* settlers on kelp between June and November 2008 also varied substantially (Table 2.3, Fig. 2.4), being lowest throughout most of the summer with a maximum of 15.1 ± 7.1 settlers m^{-2} in June and August (Fig. 2.4). Settler abundance increased by more than one order of magnitude between August and September (LS Means, $p<0.001$) and remained high (>800 settlers m^{-2}) in October. Settlement declined in late fall as shown by a (non significant) reduction of 53% in the

Table 2.2: Summary of one-way ANOVA (applied to raw data) showing the effect of Site (eight study sites: 1 to 8) on the abundance of *Membranipora membranacea* settlers on kelp pooled over five sampling months (June, August, September, October, and November) in 2008 (see Table 2.1 and Fig. 2.1 for location of sites).

Source of variation	df	MS	*F*	p
Site	7	7.3×10^6	11.7	<0.001
Error	275	6.3×10^5		
Corrected total	282			

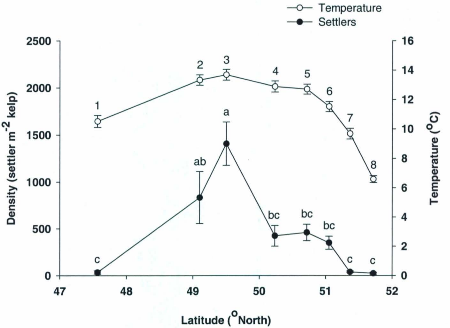

Figure 2.3: Change in mean (±SE) abundance of *Membranipora membranacea* settlers on kelp and sea temperature pooled over five sampling months (June, August, September, October, and November) across the eight study sites in 2008. Values sharing the same letter are statistically similar (LS Means, $p<0.05$; $n = 28$ to 43 kelp blades). Each temperature data point is the average of mean daily temperatures between 10 July and 24 November 2008 ($n = 137$). Values above temperature data points represent study site numbers (see Table 2.1 and Fig. 2.1 for location of sites and dates of kelp collection in each month).

Table 2.3: Summary of one-way ANOVA (applied to raw data) showing the effect of Month (five sampling months: June, August, September, October, and November) on the abundance of *Membranipora membranacea* settlers on kelp pooled across the eight study sites (1 to 8) in 2008 (see Table 2.1 for dates of kelp collection in each month).

Source of variation	**df**	**MS**	***F***	**p**
Month	4	9.9×10^6	14.9	<0.001
Error	278	6.6×10^5		
Corrected total	282			

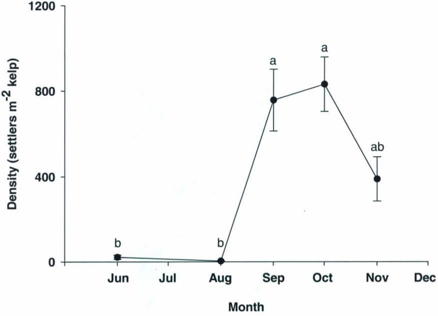

Figure 2.4: Change in mean (±SE) abundance of *Membranipora membranacea* settlers on kelp over five sampling months (June, August, September, October, and November) pooled across the eight study sites in 2008. Values sharing the same letter are statistically similar (LS Means, $p<0.05$; n = 30 to 80 kelp blades) (see Figure 2.1 and Table 2.1 for location of sites and dates of kelp collection in each month).

number of settlers between October and November (Fig. 2.4). Interestingly, settlement in June was restricted to the three southernmost sites (1, 2, and 3) and none of the kelp blades at all sites had colonies of *M. membranacea*. Settlement did not occur before August at site 4 and September at sites 5 to 8. Analysis of the 2008 data for September, October, and November at sites 3 to 7 indicated that spatial variation in settlement of *M. membranacea* on kelp differed between months (Table 2.4, Fig. 2.5). In general, there was a south to north decline in settler abundance, with larger variation between sites in September than in October and November (Fig. 2.5).

The highest settler abundance (2603 ± 498 [SE] settlers m^{-2}) was in September at the southernmost site (3) and was two orders of magnitude greater than at the northernmost site (7) for the same month (LS Means, $p<0.001$; Fig. 2.5). The abundance of settlers in each month at sites 4, 5, and 6 was intermediate relative to the two geographical extremes and did not differ statistically. Although settler abundance decreased from September to November at sites 3 and 4, there seemed to be a shift in peak settlement (the highest number of settlers across months) from September to October at sites 5 to 7 (Fig. 2.5). Settlement was consistently low (and null in November) throughout fall at site 7. Again, the general decrease in settlement from southern to northern sites was accompanied by a simultaneous decline in mean sea temperature, from $13.0 \pm 0.4^{\circ}$ to $9.0 \pm 0.4^{\circ}$ C at sites 3 and 7, respectively (Fig. 2.5).

2.3.2 Inter-annual variation in *M. membranacea* settlers on kelp

Analysis of the 2008 and 2009 data at sites 3 and 7 indicated that variation in settlement of *Membranipora membranacea* on kelp followed similar annual patterns at the two sites, though the overall abundance of settlers differed between sites and years as

Table 2.4: Summary of two-way ANOVA (applied to cube root transformed data) showing the effect of Site (five study sites: 3, 4, 5, 6, and 7) and Month (three sampling months: September, October, and November) on the abundance of *Membranipora membranacea* settlers on kelp in 2008 (see Table 2.1 and Fig. 2.1 for location of sites and dates of kelp collection in each month).

Source of variation	**df**	**MS**	***F***	**p**
Site	4	260.0	49.5	<0.001
Month	2	62.1	11.8	<0.001
Site x Month	8	10.7	2.0	0.048
Error	109	5.3		
Corrected total	123			

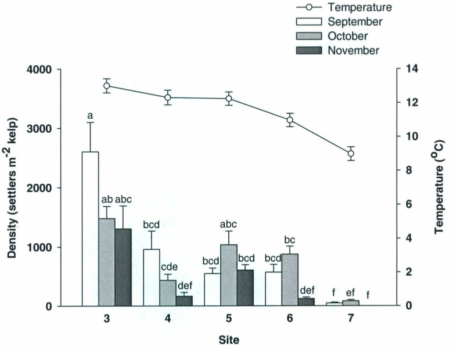

Figure 2.5: Change in mean (+SE) abundance of *Membranipora membranacea* settlers on kelp in September, October, and November at five study sites (3 to 7) in 2008. Values sharing the same letter are statistically similar (LS Means, $p<0.05$; n = 5 to 10 kelp blades). Each temperature data point is the average (±SE) of mean daily sea temperatures between 1 September and 24 November, 2008 (n = 84; see Table 2.1 and Fig. 2.1 for location of sites and dates of kelp collection in each month).

shown by the significant interaction between the two factors in the corresponding three-way ANOVA (Table 2.5, Figs. 2.6 and 2.7). In both years settlement was low ($\leq 46.1 \pm 23.1$ settlers m^{-2}) between June and August, increased by two orders of magnitude between August and September, and decreased to intermediate values in October and November (Fig. 2.6). Settler abundance in September, October, and November at site 3 was more than 1.5 times higher in 2009 than 2008 (LS Means, $p=0.001$) and at least 35 times greater in both years at site 3 than site 7 (LS Means, $p<0.001$ for each site comparison in each year; Fig. 2.7). The overall settler abundance (two sites pooled) was 75.6% higher in 2009 than 2008 ($p=0.001$, Table 2.5) despite a drop of 2.6°C in mean sea temperature (data pooled over September, October, and November) in 2009 compared to 2008 (Fig. 2.2).

2.3.3 Relationships between settler abundance, sea temperature, exposure to waves, kelp blade morphology, and the surface area of colonies on kelp

Analysis of data for sites sampled in September, October, and November 2008 and 2009 indicated that spatial and temporal variation in the abundance of *Membranipora membranacea* settlers on kelp was positively correlated with sea temperature (Table 2.6, Fig. 2.8). The longest thermal integral, TI_{76}, was the strongest predictor of settler abundance for data pooled over the three months (Table 2.6). Specifically, TI_{76} explained 57.7% of the overall variation in settler abundance, a difference of 23% with TI_{21}, the second strongest predictor (Table 2.6). The predictive capability of TI_{76} increased by at least 17.1% when measured for each of the three months individually, explaining up to 91.6% of the variation in November (Table 2.6 and Fig. 2.8). Within each month, the

Table 2.5: Summary of three-way ANOVA (applied to cube root transformed data) showing the effect of Site (two study sites: 3 and 7), Month (three sampling months: September, October, and November), and Year (two sampling years: 2008 and 2009) on the abundance of *Membranipora membranacea* settlers on kelp (see Table 2.1 and Fig. 2.1 for location of sites and dates of kelp collection in each month of each year).

Source of variation	**df**	**MS**	***F***	**p**
Site	1	2747.7	524.2	<0.001
Month	2	121.1	23.1	0.001
Year	1	57.2	10.9	0.001
Site x Month	2	14.6	2.8	0.067
Site x Year	1	27.6	5.3	0.024
Month x Year	2	13.5	2.6	0.081
Site x Month x Year	2	1.5	0.3	0.757
Error	95	5.2		
Corrected total	106			

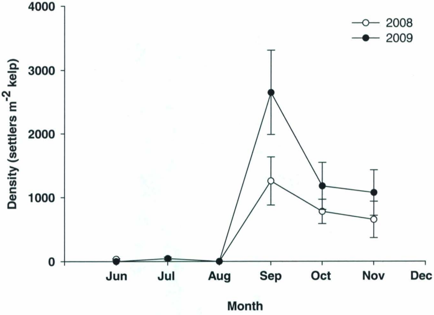

Figure 2.6: Change in mean (±SE) abundance of *Membranipora membranacea* settlers on kelp over six sampling months (June to November) pooled across study sites 3 and 7 in 2008 and 2009 (n = 8 to 20 kelp blades) (see Figure 2.1 and Table 2.1 for location of sites and dates of kelp collection in each month).

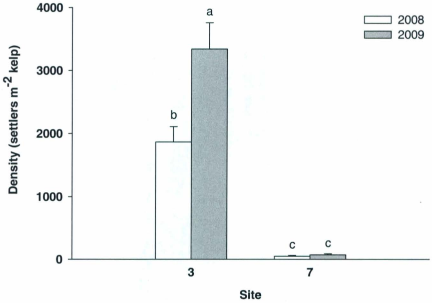

Figure 2.7: Change in mean (+SE) density of *Membranipora membranacea* settlers on kelp at study sites 3 and 7 pooled over September, October, and November in 2008 and 2009 (n = 24 to 30 kelp blades) (see Table 2.1 and Fig. 2.1 for location of sites and dates of kelp collection in each month).

Table 2.6: Results of simple and multiple linear regression analyses examining relationships between the abundance of *Membranipora membranacea* settlers on kelp and thermal history (TI_{14} to TI_{76}), exposure to waves (Exp), kelp blade corrugation index (BCI), and surface area (SA) of colonies of *M. membranacea* on kelp at all sites between September and November 2008 and 2009. Refer to materials and methods for calculations of TI_n, Exp, BCI, and SA.

Sampling month	Explanatory variable	Equation for log (settlers m^{-2} kelp + 1)	r^2	$F_{(df)}$	p
Sep to Nov	TI_{14}	$2.678 + 0.021*TI_{14}$	0.314	$11.0_{(1,24)}$	0.003
Sep to Nov	TI_{21}	$2.462 + 0.015*TI_{21}$	0.347	$12.8_{(1,24)}$	0.002
Sep to Nov	TI_{28}	$2.481 + 0.010*TI_{28}$	0.317	$11.1_{(1,24)}$	0.003
Sep to Nov	TI_{76}	$-1.622 + 0.008*TI_{76}$	0.577	$37.7_{(1,24)}$	<0.001
Sep	TI_{14}	$-1.750 + 0.039*TI_{14}$	0.742	$17.3_{(1,6)}$	0.006
Sep	TI_{21}	$-1.863 + 0.026*TI_{21}$	0.791	$22.7_{(1,6)}$	0.003
Sep	TI_{28}	$-3.350 + 0.022*TI_{28}$	0.752	$18.2_{(1,6)}$	0.005
Sep	TI_{76}	$-3.996 + 0.009*TI_{76}$	0.836	$30.6_{(1,6)}$	0.002
Oct	TI_{14}	$0.0988 + 0.039*TI_{14}$	0.557	$10.1_{(1,8)}$	0.013
Oct	TI_{21}	$0.0363 + 0.028*TI_{21}$	0.592	$11.6_{(1,8)}$	0.009
Oct	TI_{28}	$0.716 + 0.018*TI_{28}$	0.485	$7.54_{(1,8)}$	0.025
Oct	TI_{76}	$-1.940 + 0.008*TI_{76}$	0.748	$23.7_{(1,8)}$	0.001
Nov	TI_{14}	$-1.980 + 0.093*TI_{14}$	0.463	$5.18_{(1,6)}$	0.063
Nov	TI_{21}	$-2.214 + 0.062*TI_{21}$	0.543	$7.13_{(1,6)}$	0.037
Nov	TI_{28}	$-2.684 + 0.047*TI_{28}$	0.616	$9.62_{(1,6)}$	0.021
Nov	TI_{76}	$-15.239 + 0.029*TI_{76}$	0.916	$65.1_{(1,6)}$	<0.001
Sep to Nov[1,2]	TI_{76}, Exp, BCI, SA	$2.42 + 0.0062*TI_{76} - 0.12*Exp - 1.78*BCI + 0.0029*SA$	0.662	$9.3_{(4,19)}$	<0.001

[1] No BCI estimate available for sites 3 and 7 in November 2008

[2] No SA estimate available for site 3 in November 2008

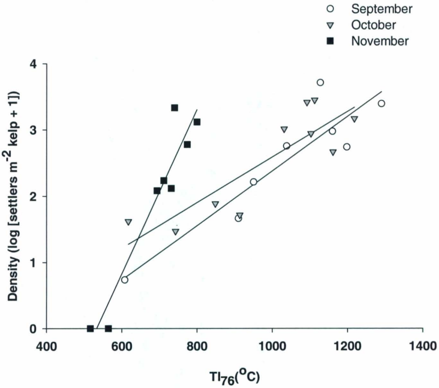

Figure 2.8: Relationship between the abundance of *Membranipora membranacea* settlers on kelp and thermal integral (TI$_{76}$) across sites in each of September, October, and November (2008 and 2009 data pooled). The lines are the linear fit to these data (r^2=0.836, 0.748, and 0.916 for September, October, and November, respectively; see Table 2.6 for details of regression analyses).

difference in predictive capability between TI_{76} and the second best predictor (TI_{14}, TI_{21}, or TI_{28}) varied between 4.5 (September, TI_{21}) and 30% (November, TI_{28}) (Table 2.6).

Indices of exposure to waves ranged from 0 (minimal, site 8) to 15 (intermediate, site 7) (Table 2.1). Kelp blade corrugation index (BCI) values ranged from 1.0 (perfectly flat) to 2.5 (highly corrugated) across sites in both 2008 and 2009, being generally highest and lowest in August (1.5±0.04) and November (1.2±0.06), respectively. Yet, multiple regression analysis showed that the abundance of *M. membranacea* settlers on kelp between September and November 2008 and 2009 (data pooled) was not significantly related to Exp ($p=0.11$), BCI ($p=0.52$), and SA ($p=0.39$), which altogether increased the predictive capability of the model with TI_{76} by 8.5% only (Table 2.6). Overall, these results indicate that thermal history is a strong predictor of spatial and temporal variation in the abundance of *M. membranacea* settlers on kelp along the coast of Newfoundland and Labrador.

2.4 DISCUSSION

We examined variation in the timing and magnitude of settlement of the invasive bryozoan *Membranipora membranacea* on the kelp *Saccharina longicruris* and how it relates to changes in sea temperature during two consecutive years (2008 and 2009) at eight sites spanning a latitudinal gradient of 450 km in Newfoundland and Labrador. Inspection of the 2008 data revealed differences of up to three orders of magnitude in settler abundance among sites, with highest abundances at mid-latitudes (site 3), where mean sea temperature was highest, and lowest abundances at the two geographical extremes (sites 1 [southernmost] and 8 [northernmost]), where temperature was lowest. Settler abundance did not vary steadily throughout the latitudinal gradient (i.e. form south to north) but rather in conjunction with local temperature regimes along the coast, which strongly supports our general hypothesis that settler abundance throughout the west coast of Newfoundland is positively correlated with temperature, being generally higher and lower at warmer and colder sites, respectively. Yet, the dramatic decline in settlement from site 3 to site 4, despite only a slight decrease in temperature (0.8°C), suggests that the effect of one or more factor(s) on settlement in this area is more important than that of temperature (see below). Very low settler abundances at sites 7 and 8 suggest that *M. membranacea* is nearing its northern distribution limit in the northwest Atlantic. This limit could be imposed by the combined effects of low temperature on settlement and the natural dispersal barrier represented by the Labrador Current, which flows southward along the Labrador side of the Strait of Belle Isle. (Han 2004).

Settlement across the eight sites followed a strong seasonal cycle with virtually no settlers during summer (June to August), a sharp increase in September and October, and subsequent decline to intermediate values in November. This pattern is generally consistent with that observed in central Nova Scotia in 2005 and 2006 (Saunders & Metaxas 2007) with the exception that settlement at our warmest sites appeared to decline earlier during fall (i.e. September and early October instead of late October and November). Interestingly, settler abundance in September at our most productive site (site 3) was more than 500 settlers m^{-2} kelp higher than the most productive site in Nova Scotia (Lodge, located in St. Margarets Bay) where settler abundance peaked to approximately 2000 settlers m^{-2} kelp (Saunders & Metaxas 2007). A comparison of temperature regimes during fall suggests that water temperature was on average higher and less variable at site 3 than at Lodge (Saunders & Metaxas 2007). Patterns of change in settler abundance between September, October, and November varied from sites 3 to 7 (logistical considerations did not allow us to track monthly changes at sites 1 and 2), with a general decrease from September to November at the two southernmost (warmest) sites and a 2- to 3-week delay in peak settlement values at the northern (coolest) sites. Altogether, these results strongly support the notion that lower temperature at more northerly latitudes can severely limit settlement in *M. membranacea*.

Comparison of the 2008 and 2009 data from sites 3 and 7 indicated monthly changes in the overall abundance of settlers on kelp between June and November followed similar trajectories, with sudden increases in September and gradual declines thereafter. However, the abundance of settlers at site 3 was 1.5 times higher in 2009 than 2008 and more than 30 times higher in both years than at site 7. Settlement at site 3 was higher than at site 7 in both years, whereas settlers first appeared in June at sites 1 to 4 and as late as September in more northerly sites (e.g. site 7) in 2008. Thus, those results are consistent with the idea that settlement was generally higher in areas with warmer sea temperature. However, settlement at site 3 was delayed (July instead of June) but still substantially higher in the cooler of two years (2009), which also suggests that inter-annual changes in the timing and magnitude of settlement of *M. membranacea* on kelp arise from interactions between sea temperature and some other factors. This finding contradicts that of Saunders and Metaxas (2007, 2008) whereby both settlement and recruitment of *M. membranacea* in Nova Scotia occurred earlier and were higher following the warmer of two consecutive winters. Temperature often largely regulates spawning and settlement in marine invertebrates such as mollusks, echinoderms, and crustaceans (Allen 1955, Brown 1984, Lewis 1986, Waddy & Aiken 1992, Matsuda et al. 2002, Hernández et al. 2010). Several studies showed that growth in *M. membranacea* colonies is positively correlated with temperature and can occur as low as 4°C (Menon 1972, Saunders & Metaxas 2009a, Caines & Gagnon unpublished data). Yet, the physicochemical factors (including temperature) that regulate settlement of cyphonautes larvae and sexual development of zooids are unclear. The delayed occurrence of settlers of *M. membranacea* at northern compared to southern sites in our study could be related to longer periods of time required at higher latitudes to achieve threshold temperatures that trigger settlement, growth, and reproduction.

Inter-annual differences in the timing and magnitude of settlement and recruitment in *M. membranacea* in Nova Scotia are, presumably, partly caused by differences in winter temperature affecting the survival of overwintering colonies (Saunders & Metaxas 2007, 2008). Settlement and recruitment in any given year could also depend on other factors such as the cover and abundance of colonies in that year, as well as the frequency and strength of winter storms and kelp growth and defoliation in the preceding year. In the northwest North Atlantic, *M. membranacea* colonies can cover up to ~80% of kelp blade surface, which can cause dramatic declines in kelp biomass and associated colonies (Lambert et al. 1992, Saunders & Metaxas 2008, Scheibling & Gagnon 2009). Therefore, years of high kelp survival could favor the survival of overwintering colonies, resulting in higher settlement and recruitment in subsequent years. Our data suggest that settlement of *M. membranacea* during summer is affected by temperature in late spring and early summer, whereas inter-annual differences in settler abundance are caused by factors that interact with temperature during winter.

Settlement of *M. membranacea* on *S. longicruris* during two consecutive years at two sites separated by a few kilometers in Nova Scotia was positively correlated to sea temperature (Saunders & Metaxas 2007). Our study, conducted over a much larger spatial domain encompassing cold temperate and subarctic environments with differences of up to 6.4°C between sites, provided an opportunity to test the generality of this relationship. Regression analysis indicated that TI_{76}, the sum of daily average sea temperature over the 76 days preceding measurement of settler abundance, explained 58% of the variation in settlement in September, October, and November across all sites in both years. Interestingly, this value is only slightly lower than the 62% obtained by Saunders and Metaxas (2007) using thermal integrals calculated over much longer periods (up to ten months) than in this study. Exposure to waves was not a significant variable in the multiple regression analysis of the contribution of thermal history, exposure to waves, kelp blade corrugation, and surface area of colonies of *M. membranacea* on kelp to the abundance of settlers on kelp with all sites included. Nevertheless, it is possible that part of the unexplained variation in settler abundance at a few sites was due to differences in hydrodynamic conditions (e.g. currents and waves, see below). This could help explain why settlement at site 4 was 76% lower than the adjacent site 3 despite a difference of only 0.8°C between these sites. Exposure to waves at site 4 was 7-fold higher than at site 3. Laboratory studies showed that strong currents can interfere with settlement in marine invertebrate larvae (Crisp 1955, Pawlik & Butman 1993, Fuchs et al. 2007), which could have been the case at site 4. Comparisons of regression analyses with TI_{76} and thermal integrals calculated over shorter periods of time (14, 21, and 28 days) indicated that TI_{76} was by far the best predictor of variation in settler abundance (a difference of 23% in r^2 with TI_{21}, the second best predictor) when pooling data over September, October, and November 2008. The explanatory power of TI_{76} further increased to up to 92% (November) when analyzing recruitment for each month individually. Again, such a strong relationship suggests that during warmer months (September and October) sea temperature interacts with other factors to influence settlement, whereas the effect of sea temperature may supersede that of the other factors in November when temperature is lower. TI_{21} explained only slightly less (4.5%) of the variation in September than TI_{76}, therefore indicating that the sharp increase in settler abundance between August and September at most sites (see above) could be largely predicted uniquely from thermal history in the preceding three weeks.

Inspection of daily mean sea temperature revealed that sudden, marked drops and subsequent rises in temperature occurred in late August and early September 2008 at all sites, with most pronounced changes in the southernmost and two northernmost sites. These sudden shifts in temperature coincided with sharp seasonal increases in settler abundance across sites. Although sea temperature at each site was recorded at a single depth, these marked shifts were indicative of sudden changes in the vertical structure of the water column, which could have enabled deeper larval populations to move in shallow water and settle on kelp. This suggestion is supported by pioneering observations of cyphonautes larvae of *M. membranacea* congregating in deep (20 to 80 m) water during periods of vertical stratification, while exhibiting a shallower distribution when the water column became cooler and well mixed in the Irish Sea and along the coast of California (Yoshioka 1982, Scrope-Howe & Jones 1986). Mean sea temperature and settler abundance in 2008 were highest at sites 2 and 3, which were both located in large, semi-enclosed bays where cyphonautes larvae possibly had longer residence times, and hence opportunities to settle, than at the other sites. Both our data and independent historical records of temperature (Mouland 2004, 2005, 2006) suggested that upwelling is frequent during fall at site 1, which likely resulted in the offshore transport of cyphonautes larvae and low settler abundance as observed in California and proposed for Nova Scotia (Yoshioka 1986, Saunders & Metaxas 2010). More research addressing the connections between temperature, larval transport, and ocean currents (e.g. vertical mixing, upwelling, and downwelling) is needed to better understand settlement and recruitment in *M. membranacea*.

Several studies suggested that settlement of bryozoan larvae on kelp varies with blade morphology and texture (Ryland 1959, Yoshioka 1973). In particular, Saier & Chapman (2004) reported higher abundances of *M. membranacea* colonies on ruffled margins of *S. longicruris* blades than on flatter blade portions. Despite marked differences in the degree of kelp blade corrugations across the eight study sites (BCI values ranged from 1.0 to 2.5), the multiple regression analysis refuted our hypothesis that settlement of *M. membranacea* on *S. longicruris* varies with the degree of kelp blade corrugations. The absence of a relationship between the two variables indicates that kelp blade morphology has very little effect, if any, on settlement in *M. membranacea* at large spatial and temporal scales. Asexual reproduction of zooids, and hence colony growth, in marine bryozoans including *M. membranacea* are strongly affected by temperature, being generally higher in warmer water (Menon 1972, Amui-Vedel et al. 2007, Saunders & Metaxas 2009a, Yorke 2010). Each mature zooid can produce both male and female gametes, and hence contribute to the larval pool. Therefore, it is assumed that fecundity in *M. membranacea* is correlated to the surface area of colonies (Yoshioka 1973), which should be at least partly regulated by spatial and temporal variation in temperature. Like kelp blade morphology, colony surface area explained only a small proportion of the variation in settlement of *M. membranacea*, suggesting that larval supply in *M. membranacea* is decoupled from local fecundity (Roughgarden et al. 1985, Caley et al. 1996).

This study is the first to examine spatial and temporal variation in the timing and magnitude of settlement of the invasive bryozoan *Membranipora membranacea* on kelp along the coast of Newfoundland and Labrador. We provide clear evidence that (1) settler abundance varied both seasonally and annually with a sharp increase between August and September at warmer sites, and spatially with differences of up to three orders of magnitude between sites, (2) settler abundance and sea temperature were strongly correlated (r^2=0.577), with maxima at mid-latitudes and minima at the northernmost and southernmost sites, and (3) exposure to waves, degree of kelp blade corrugations, and surface area of colonies of *M. membranacea* on kelp had very little explanatory power on settler abundance across the study sites compared to sea temperature. These findings are based on measurements of settlement and temperature over a large spatial domain encompassing areas of cold and warm water, which further elevates the importance of temperature in regulating populations of *M. membranacea* in the northwest Atlantic. However, a few inconsistencies both within our system and between our system and that of Nova Scotia indicate additional experimental and long-term, observational studies are required to elucidate factors that regulate local and regional variation in the abundance of this invader. In particular, temporal changes in recruitment and colony cover on kelp and their connections with temperature and settler abundance should also be assessed over large spatial domains to provide insights on regulatory processes that may otherwise go unnoticed, as well as to increase our capacity to identify areas of low and high vulnerability to kelp defoliation, an important aspect in the development of sustainable fisheries.

CHAPTER III

Thermal histories across a 450-km latitudinal gradient in the northwest Atlantic explain variation in recruitment and colony cover in the invasive, marine bryozoan *Membranipora membranacea*

3.1 INTRODUCTION

Recruitment, broadly defined as the transition from the larval stage to the benthic juvenile stage, is a key process regulating populations in a number of marine benthic invertebrates with planktonic larvae (Hughes 1990, Caley et al. 1996, Connolly & Roughgarden 1999, Jenkins et al. 2009). Marine benthic invertebrates with long-lived pelagic larvae often form open populations in which larvae are supplied from distant pools, and hence recruitment is, to various extent, decoupled from local larval production (Roughgarden et al. 1988, Caley et al. 1996). The abundance of recruits can vary highly in space and time (Menge 1991, Minchinton & Scheibling 1991, Connolly et al. 2001, Broitman et al. 2008) as a result of factors affecting post settlement growth and survival (Thorson 1950, Barnes 1956, Caley et al. 1996, Jenkins et al. 2009). At small spatial scales (centimeters to hundreds of meters), variation in recruitment is mainly related to physical disturbance, predation, and competition (Connell 1961a, b, Keough 1983, Connell 1985, Raimondi 1990, Skinner & Coutinho 2005), whereas at larger scales variation arises principally from effects of temperature on the growth and survival of juvenile stages (Kendall & Lewis 1986, Zacherl et al. 2003)

Sea temperature often determines the distribution limits of marine invertebrates by creating thermal conditions unfavorable for settlement and recruitment (Hutchins 1947, Thorson 1950, Brown 1984, Bowman & Lewis 1986, Lewis 1986). Near or at their polar limits, populations of marine invertebrates are generally constrained by short reproductive periods and recruitment failure is frequent, whereas populations near or in the middle of a species distribution range benefit from longer reproductive periods while exhibiting a higher stability (Bowman & Lewis 1986, Kendall & Lewis 1986, Lewis 1986). Effects of sea temperature on recruitment, growth, and ultimately population abundance in marine invertebrates are particularly manifest in short-lived, sessile species that utilize ephemeral substrates. One good example are marine bryozoans that form colonies of tens to hundreds of zooids (individuals) on the surface of seaweeds and in which the addition and growth of new zooids are positively correlated with sea temperature, being generally faster in warm than cold water (Menon 1972, Atkinson et al. 2006, Amui-Vedel et al. 2007, Saunders & Metaxas 2009a). Fecundity in these bryozoans is a function of the abundance of zooids (Yoshioka 1973), and hence abundances of planktonic larvae, settlers, recruits, and colonies are interrelated and, to some extent, controlled by spatial and temporal variation in sea temperature (Yoshioka 1982, 1986, Saunders & Metaxas 2007, 2008).

The pioneering work of Yoshioka (1982, 1986) on the cheilostome bryozoan *Membranipora membranacea* in California, suggests that spatial and temporal variation in recruit abundance on kelp (large brown seaweeds of the order Laminariales) is regulated by a set of factors that include larval abundance, upwelling, sea temperature, and predator abundance. This colonial bryozoan was introduced to shallow marine ecosystems of the northwest Atlantic (Gulf of Maine, USA) in the mid-1980s (Lambert et al. 1992), presumably through the release of cyphonautes larvae in ballast water of ships traveling from Europe (Schwaninger 1999). In the northwest Atlantic, *M. membranacea* commonly settles and grows on kelp and other seaweeds (Harris & Jones 2005, Pratt 2008, Saunders & Metaxas 2009b, Yorke 2010). In eastern Canada it is abundant in shallow subtidal kelp habitats from Nova Scotia to southern Labrador (Chapman et al.

2002, Gendron et al. 2007, Watanabe et al. 2009, Chapter II). Effects of *M. membranacea* colonies on kelp range from reduced growth rates and release of spores, to dramatic, autumnal declines in kelp biomass (Lambert et al. 1992, Saier & Chapman 2004, Saunders & Metaxas 2008, Scheibling & Gagnon 2009).

Recent studies showed that in eastern Canada spatial and temporal variation in the abundance of settlers of *M. membranacea* on the common kelp *Saccharina longiruris* are correlated with sea temperature from spring to fall, with geographic differences in the strength of relationships (Saunders & Metaxas 2007, Chapter II). In particular, settlement on the west coast of Newfoundland and southern tip of Labrador does not occur before June at the warmest locations and generally peaks in September or October depending on latitude (Chapter II). Likewise, in Nova Scotia, inter-annual variation in peak cover of *M. membranacea* on kelp is correlated to thermal history during the summer/fall period (Scheibling & Gagnon 2009, Saunders et al. 2010). This pattern is most likely due to the positive effect of higher sea temperature at that time on growth of *M. membranacea* (Menon 1972, Saunders & Metaxas 2009a, Caines & Gagnon unpublished data). Direct and indirect observations in both Nova Scotia and Newfoundland and Labrador suggest that peaks in settlement during late summer and early fall can coincide with oceanographic events such as upwelling and downwelling that cause changes in the vertical structure of the water column, which in turn increase vertical and horizontal transport of cyphonautes larvae to kelp habitats (Saunders & Metaxas 2010, Chapter II). Yet, the relationship between recruitment and colony cover of *M. membranacea* has not been formally quantified, nor has the generality of relationships between sea temperature, settlement, recruitment, and colony cover in southeastern Canada been tested in northern, colder environments.

The recent introduction of *M. membranacea* to Newfoundland and Labrador provides a unique opportunity to test temperature-based relationships between recruitment and colony cover over an extensive latitudinal gradient that includes both cold- and warm-water environments. Relationships between sea temperature and settlement of *M. membranacea* on *S. longicruris* over two consecutive years (2008 and 2009) at eight sites with contrasting thermal conditions (on average between <7°C and >13°C during summer and fall) and spanning a 450-km latitudinal gradient from Port aux Basques (southwestern tip of Newfoundland) to Red Bay (southeastern tip of Labrador) were presented in Chapter II. This study examines seasonal and inter-annual variation in the abundance of recruits and colony cover of *M. membranacea* on *S. longicruris* and its relationship to changes in sea temperature over the same spatial and temporal domains as in Chapter II. Specifically, we 1) test the general hypothesis that recruitment and colony cover are positively correlated with thermal history, 2) identify temporal windows over which temperature explains smallest and largest proportions of variation in recruit abundance and colony cover, and 3) determine whether recruit abundance can be used to predict colony cover across the entire latitudinal gradient.

3.2 MATERIALS AND METHODS

3.2.1 Study sites and collection of kelp blades

This study was part of a larger research project examining spatial and temporal variation in population dynamics of *Membranipora membranacea* in Newfoundland and

Labrador. A more comprehensive description of study sites and methods of collection of kelp blades and integration of temperature data is provided elsewhere (refer to Chapter II and especially Table 2.1 and Fig. 2.1). Essentially, eight sites spanning ~450 km between the southwestern tip of Newfoundland and southeastern tip of Labrador and containing shallow (<20 m deep) kelp (primarily *Saccharina longicruris*) beds were used: (1) Port aux Basques [southernmost site], (2) Lark Harbour, (3) Norris Point, (4) Daniel's Harbour, (5) Port au Choix, (6) Bird Cove, (7) Green Island Cove, and (8) Red Bay [northernmost site, the only one in Labrador]. Sites 1 to 6 were located along the eastern edge of the Gulf of St. Lawrence, whereas sites 7 and 8 were in the Strait of Belle Isle through which the cold Labrador Current flows along the coast of Labrador and into the Gulf of St. Lawrence along the coast of Québec (Han 2004).

To investigate spatial and temporal variation in the abundance of recruits and cover of *Membranipora membranacea* colonies on kelp, fish harvesters collected at least eight blades of the kelp *S. longicruris* monthly between August and October 2008 at sites 1 to 8, and between August and October 2009 at sites 3 and 7. In each month, blades at all sites were collected within eight to fourteen days in 2008 and within less than eight days in 2009. In 2008, rough seas prevented collection at sites 3 and 8 in August and sites 1 and 2 in September. Kelp blades were rolled and sealed in plastic bags, placed on ice inside insulated rigid containers, and shipped using expedite courier to the Ocean Sciences Centre (OSC). Upon arrival at the OSC (within 72 h from shipping date), blades were transferred to 330-L holding tanks supplied with ambient, flow-through seawater pumped in from Logy Bay. All blades were analyzed within one to five days of receipt.

To supplement the 2008 data we used scuba diving to haphazardly collected five to ten blades between 4 and 12 June at all but sites 7 and 8, on 9 July at site 8, and between 25 November and 1 December at all but sites 1 and 8. Samples obtained on 9 July and 1 December were included in the June and November data, respectively (Table 2.2). We supplemented the 2009 data by using scuba diving to collect eight to ten blades on 17 June, 14 July, and 12 November at site 3, and on 16 June and 11 November at site 7. Blades collected by divers were packaged and transported to the OSC using the same technique as fish harvesters (see above). They were also maintained in holding tanks with cold, flow through seawater and processed within one to five days.

3.2.2 Abundance of *M. membranacea* recruits on kelp

In this study, we use the term "recruit" to refer to a fully developed ancestrula with at least one daughter zooid (three zooids in total) and any cluster of zooids with a diameter <5 mm. Clusters of 5 mm typically have five or six rows of zooids and an estimated maximum age of three weeks when grown at temperatures between 10 and 14°C (Saunders & Metaxas 2008). To quantify the abundance of recruits of *M. membranacea* on kelp we divided the blade of each kelp specimen into three contiguous portions that each extended one third of total blade length. Up to three square pieces (16 and 25 cm^2 for blades $\leq$80 and >80 cm in length, respectively) of kelp tissues were removed from each portion - one in the center and one along the left and right margins of the blade. Pieces were systematically taken from blade areas with no colonies >1 cm (pieces with larger colonies did not appear to offer enough bare surface for settlers), generally halfway through the length of each portion. Recruits on each piece were enumerated by visual inspection with a stereomicroscope (15x magnification). The density of recruits on each piece was determined by dividing the number of recruits by the surface area of the piece, and for each kelp blade by averaging densities of all (up to nine) pieces. Damages to or heavy infestation of kelp tissues by *M. membranacea* in certain months at a few sites limited the sampling to less than nine pieces in 43.2% of blades.

The lack of data for at least one site in June, August, September, and November 2008 (see Chapter II for details) prevented the use of a two-way ANOVA for analysis of the abundance of recruits of *M. membranacea* on kelp across all sites and months. Consequently, we used two one-way ANOVAs (Zar 1999) with factors Site (sites 1 to 8) or Month (June, August, September, October, and November) to investigate separately spatial and temporal variation in recruit abundance. Because no transformation corrected the lack of homoscedasticity in the data in both analyses, we ran each ANOVA with the ranked transformed data. Analyses of raw and ranked transformed data gave similar results, and hence we reported the results from analyses of raw data as per Conover (1980). To investigate spatial and temporal variation in recruit abundance in 2008 simultaneously, data in September and November at sites 1, 2 and 8, and all data in June and August were discarded and the remaining data were analyzed using a two-way ANOVA with the factors Site (sites 3 to 7) and Month (September, October and November). Although data were log (x+1) transformed to correct for the lack of homoscedasticity, residuals were not normally distributed. Given that the ANOVA is generally robust to deviation from normality (Underwood 1997) we presented results from the analysis of the log (x+1) transformed data. Inter-annual variation in the abundance of recruits at sites 3 and 7 were examined using a three-way ANOVA with the factors Site (sites 3 and 7), Month (September, October, and November), and Year (2008 and 2009). Although data were log (x+1) transformed to obtain homoscedasticity, residuals were not normality distributed. Therefore, we presented results from the analysis of the log (x+1) transformed data.

3.2.3 Cover of *M. membranacea* colonies on kelp

We use the term "colony" to refer to any *Membranipora membranacea* cluster with a diameter ≥ 5 mm and at least six rows of zooids. To quantify spatial and temporal variation in the cover of *M. membranacea* colonies on kelp, a sheet of translucent acrylic was placed atop each blade of the kelp *S. longicruris*. Contours of kelp blade and each colony were traced onto the sheet with markers. The sheet was then placed above a white countertop and photographed. Surface areas of the kelp blade and each colony were determined by analyzing photographs with the image analysis software Sigma Scan Pro 5. Certain colonies extended within folds and corrugations of kelp blades, which resulted in partial marking of their margins on the sheet. To correct surface areas of those partly visible colonies, each kelp blade was subsequently cut into pieces that were flattened on the white surface and photographed. The total surface area of blade pieces was calculated for each blade with the image analysis software Image J (v. 1.43d). Each blade was assigned a numerical value (BCI, see Chapter II) expressing the ratio of total surface area of blade pieces to surface area of the intact (uncut) blade, therefore providing an estimate of the degree of blade corrugations. This value was multiplied by the surface area of only those colonies that were partly visible. Total colony cover on each kelp was obtained by dividing the total surface area of all colonies (i.e. the sum of corrected surface areas of partly visible colonies and raw surface areas of fully visible colonies) by the total surface area of blade pieces multiplied by 100. Those few, smaller colonies completely hidden within kelp folds could not be measured reliably, and hence were not included in the analyses described below.

Here again, the lack of data for at least one site in June, August, September and November in 2008 precluded analyzing spatial and temporal variation in *M. membranacea* colony cover simultaneously with two-way ANOVAs. Therefore, we used separate one-way ANOVAs with the factors Site (sites 1 to 8) or Month (June, August, September, October and November). No transformation corrected for the lack of homoscedasticity in colony cover data. Analyses of raw and ranked transformed data gave similar results, and hence we presented the results from analyses of raw data (Conover 1980). Data in August and November for all sites and September and October for sites 1 and 2 were discarded to investigate spatial and temporal variation in colony cover with a two-way ANOVA with the factors Site (sites 3 to 8) and Month (September and October). Data in November were not included due to missing data at site 3 (a key site for settlement as shown in Chapter II), where deterioration of kelp blades prevented accurate measurement of colony cover. Colony cover data were arcsine ($\sqrt{x}$) transformed, which corrected for the lack of homoscedasticity but not normality of residuals. Yet, we presented the results from analyses of the arcsine ($\sqrt{x}$) transformed data (Underwood 1997). Inter-annual changes in colony cover at the two sites sampled in 2008 and 2009 were analyzed using three-way ANOVAs with the factors Site (sites 3 and 7), Month (September and October) and Year (2008 and 2009). No transformation corrected for the lack of homoscedasticity in colony cover data. Yet, we presented the results from the analysis on the arcsine ($\sqrt{x}$) transformed data since analysis of ranked transformed data is not recommended for ANOVAs with more than two factors (Conover, 1980).

3.2.4 Collection and integration of temperature data

To test the hypothesis that spatial and temporal variation in the abundance of recruits and cover of colonies of *Membranipora membranacea* on kelp are correlated with temperature, we recorded sea temperature in 2008 and 2009 at each site with a Hobo Pendant (Onset Computer Corporation) logger installed at a depth between 2.2 and 6.7 m (chart datum). In 2008, temperature was recorded every hour between 13 June and 24 November at sites 1 to 7 and between 10 July and 24 November 2008 at site 8. In 2009, temperature was recorded between 13 June and 11 November at site 3, and between 6 June and 11 November at site 7 (see Chapter II for temperature patterns at each site in both years). We used these data to construct thermal integrals (Chapter II) for each site in each year. Each thermal integral, referred to as TI_{76}, is the sum of daily mean temperatures over the 76 days preceding kelp collection in September, October, and November. We used thermal integrals calculated over 76 days because this was the longest period of time with temperature data concurrently available for each month and it best explained relationships between temperature and settlement in *M. membranacea* in Newfoundland and Labrador among shorter thermal integrals (Chapter II).

3.2.5 Relationships between temperature, recruit abundance, and colony cover

We examined relationships between sea temperature (TI_{76}, see above) and the abundance of recruits and colony cover of *M. membranacea* on kelp across sites using simple regression analysis (Whitlock & Schluter 2009). The relationship between sea temperature and the abundance of recruits (log [density+1]) was firstly determined using all data pooled (September, October, and November 2008 and 2009) and again for each of September, October, and November with both years pooled since the three-way ANOVA of inter-annual changes in the abundance of recruits indicated patterns differed between months but not years (see results). Relationships between sea temperature and colony cover (arcsine [$\sqrt{x}$]) and recruit abundance and colony cover were firstly investigated using simple linear regression with data pooled over September, October, and November 2008 and 2009 and again for each of September, and October and November pooled to determine whether those relationships varied in time. Data in October and November were pooled since >98% of colonies in each of those two months were small (≤ 10 cm^2), and hence the relationship between recruit abundance and colony cover was unlikely to change between those two months (see section results).

In the above analyses, normality was verified using the Shapiro-Wilk's statistics and homoscedasticity of the variance by examining the graphical distribution of the residuals and by applying the Levene test (Snedecor & Cochran 1989). The factors Site, Month, and Year in the ANOVAs described above were fixed as they represented specific levels of interest and it was predicted that each site, month, and year would be characterized by unique sea temperature and hydrodynamic conditions affecting recruitment and colony cover. We used Tukey-Kramer multiple comparison tests (based on LS Means; Sokal & Rohlf 1995) to detect differences among levels within a factor. All statistical analyses were conducted using Minitab 16 statistical software and a significance level of 0.05.

3.3 RESULTS

3.3.1 Seasonal variation in recruit abundance and colony cover

Analysis of 2008 data indicated the abundance of recruits of *Membranipora membranacea* on the kelp *Saccharina longicruris* varied markedly across the eight study sites (Table 3.1, Fig. 3.1). Variation in recruit abundance and mean sea temperature followed similar trends, with highest and lowest values near the middle (site 3; 2500±432 [SE] recruits m^{-2} kelp and 13.7±0.4°C) and extremes of the latitudinal gradient (sites 1, 7, and 8; <22±6 recruits m^{-2} kelp and 10.5±0.4°C) of the latitudinal gradient, respectively (Fig. 3.1). Although the abundance of recruits increased by two orders of magnitude between sites 1 and 2 (LS Means p=0.004) and by more than 100% between sites 2 and 3 (LS Means p<0.001), it markedly decreased, by 94%, between sites 3 and 4 (LS Means p<0.001) and remained relatively low (<581±138 recruits m^{-2} kelp) north of site 4 (Fig. 3.1). Like recruit abundance, mean sea temperature from July to November peaked at site 3, and decreased from site to site both southward and northward. Continuous decreases in recruit abundance north of site 5 were accompanied by a sharp drop in sea temperature, down to 6.6°C at site 8. Interestingly, the major drop in recruitment from site 3 to site 4 was accompanied by a decrease of only 0.8°C between the two sites.

The abundance of *M. membranacea* recruits on kelp also varied substantially between June and November 2008 (Table 3.2, Fig. 3.2). Recruitment was null at all sites in June and had increased only slightly in August to <30 recruits m^{-2} kelp. The dramatic increase in recruitment from August to October (LS Means p<0.001), when there was 1290±222 recruits m^{-2} kelp, was followed by a decline to intermediate values in

Table 3.1: Summary of one-way ANOVA (applied to raw data) showing the effect of Site (eight study sites: 1 to 8) on the abundance of *Membranipora membranacea* recruits on kelp pooled over five sampling months (June, August, September, October, and November) in 2008 (see Table 2.1 and Fig. 2.1 for location of sites).

Source of variation	**df**	**MS**	***F***	**p**
Site	7	2.4×10^6	19.8	<0.001
Error	275	1.2×10^5		
Corrected total	282			

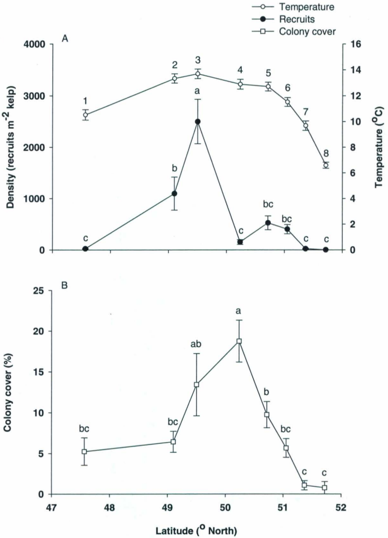

Figure 3.1: Change in mean (±SE) (A) recruitment and (B) colony cover of *Membranipora membranacea* on kelp and sea temperature pooled over five sampling months (June, August, September, October, and November) across the eight study sites in 2008. Values sharing the same letter are statistically similar (LS Means, $p<0.05$; $n = 27$ to 43 kelp blades). Each temperature data point is the average of mean daily temperatures between 10 July and 24 November 2008 ($n = 137$). Values above temperature data points represent study site numbers.

Table 3.2: Summary of one-way ANOVA (applied to raw data) showing the effect of Month (five sampling months: June, August, September, October, and November) on the abundance of *Membranipora membranacea* recruits on kelp pooled across the eight study sites (1 to 8) in 2008 (see Table 2.1 for dates of kelp collection in each month).

Source of variation	**df**	**MS**	***F***	**p**
Month	4	2.0×10^6	13.0	<0.001
Error	278	1.5×10^5		
Corrected total	282			

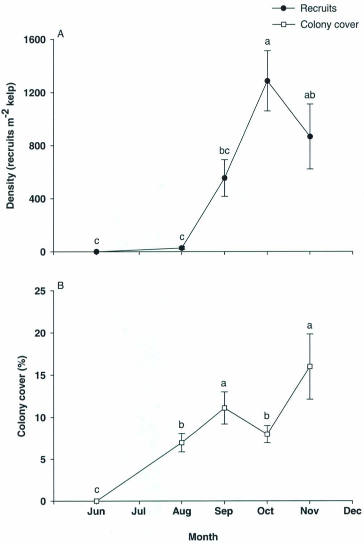

Figure 3.2: Change in mean (±SE) (A) recruitment and (B) colony cover of *Membranipora membranacea* on kelp over five sampling months (June, August, September, October, and November) pooled across the eight study sites in 2008. Values sharing the same letter are statistically similar (LS Means, $p<0.05$; n = 25 to 80 kelp blades).

November (Fig. 3.2). Analysis of the 2008 data for September, October, and November at sites 3 to 7 indicated that monthly changes in recruit abundance were not consistent among sites as shown by the significant interaction between the factors Site and Month (Table 3.3, Fig. 3.3). Here again, recruit abundance was highest (up to 5039 recruits m^{-2} in October) at the most southerly site (3) and relatively low at the other sites. There were no significant differences in recruit abundance between months within all sites except for site 3 where values in November were at least 46.7% smaller than in September and October (Fig. 3.3).

Changes in the cover of *M. membranacea* colonies on kelp across the eight sites generally followed the same pattern as recruit abundance with highest (up to 18.9%) cover values in the centre (sites 3 and 4) of the latitudinal gradient (Table 3.4, Fig. 3.1). Yet, changes in cover between adjacent sites appeared more gradual than those in recruit abundance as shown by the lack of statistical differences in cover values between the three southernmost sites. Interestingly, colony cover peaked at site 4 which is also where recruitment values were among the lowest of all sites (Fig. 3.1). Here again, changes in colony cover from one site to another coincided relatively well with changes in mean sea temperature, with lowest cover values at the coldest sites (e.g. <2% cover at sites 7 and 8). The only noticeable exception to this pattern was the substantial drop of 50.6% in colony cover between sites 4 and 5 (LS Means $p=0.0023$) which was accompanied by a decrease in temperature of only 0.2° C (Fig. 3.1).

The significant pattern of changes in colony cover between June and November 2008 (Table 3.5) differed somewhat from that of recruit abundance during the same period (Fig. 3.2). Indeed, colony cover increased more gradually than recruit abundance

Table 3.3: Summary of two-way ANOVA (applied to log [x+1] transformed data) showing the effect of Site (five study sites: 3, 4, 5, 6, and 7) and Month (three sampling months: September, October, and November) on the abundance of *Membranipora membranacea* recruits on kelp in 2008 (see Table 2.1 and Fig. 2.1 for location of sites and dates of kelp collection in each month).

Source of variation	**df**	**MS**	***F***	**p**
Site	4	141.8	51.6	<0.001
Month	2	7.00	2.5	0.083
Site x Month	8	16.5	6.0	<0.001
Error	109	2.8		
Corrected total	123			

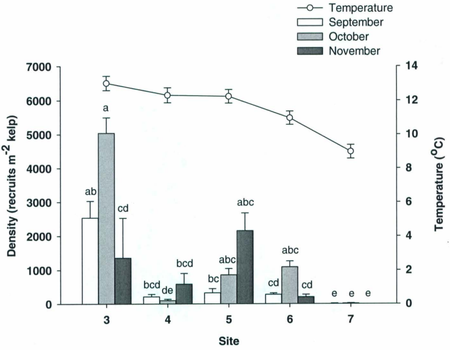

Figure 3.3: Change in mean (+SE) abundance of *Membranipora membranacea* recruits on kelp in September, October, and November at five study sites (3 to 7) in 2008. Values sharing the same letter are statistically similar (LS Means, $p<0.05$; n = 5 to 10 kelp blades). Each temperature data point is the average (±SE) of mean daily sea temperatures between 1 September and 24 November 2008 (n = 84).

Table 3.4: Summary of one-way ANOVA (applied to raw data) showing the effect of Site (eight study sites: 1 to 8) on the cover of *Membranipora membranacea* colonies on kelp pooled over five sampling months (June, August, September, October, and November) in 2008 (see Table 2.1 and Fig. 2.1 for location of sites).

Source of variation	**df**	**MS**	***F***	**p**
Site	7	1425	11.7	<0.001
Error	270	121		
Corrected total	277			

Table 3.5: Summary of one-way ANOVA (applied to raw data) showing the effect of Month (five sampling months: June, August, September, October, and November) on the cover of *Membranipora membranacea* colonies on kelp pooled across the eight study sites (1 to 8) in 2008 (see Table 2.1 for dates of kelp collection in each month).

Source of variation	**df**	**MS**	***F***	**p**
Month	4	1763	13.5	<0.001
Error	273	131		
Corrected total	277			

between June and September, as well as decreased from 13.4 to 8.0% between September and October (LS means, p=0.048) while recruit abundance increased (see above). This drop in colony cover was followed by a twofold increase between October and November (LS Means p=0.02), when cover peaked to 16%. The decrease in cover between September and October was accompanied by a 52% drop in the proportion of large ($\geq$50 cm^2) colonies (Fig. 3.4), which suggests that erosion or fragmentation of kelp tissues and associated colonies occurred. Results of the two-way ANOVA of the 2008 data for sites 3 to 8 indicated differences in colony cover between September and October were less important than those in recruit abundance, while following the same general south-to-north decrease as sea temperature (Table 3.6, Figs. 3.3 and 3.5). Yet, there were no significant differences in colony cover between September and October within each sampling site (Fig. 3.5). Like recruitment, colony cover was highest (27.3% in September) at the southernmost site (3) and lowest (<0.1% in both September and October) at the northernmost site (8). In each of September and October 2008 sea temperature differed by as much as 2.2°C and the abundance of recruits by up to two orders of magnitude among sites 3 to 6 (Fig. 3.3). Yet, there were no significant differences in colony cover among those sites despite a general trend towards decreasing cover with increasing latitude (Fig. 3.5).

3.3.2 Inter-annual variation in recruit abundance and colony cover

Analysis of the 2008 and 2009 data at sites 3 and 7 indicated that patterns of monthly changes in the abundance of *M. membranacea* recruits on kelp differed between years (Table 3.7, Fig. 3.6). In both 2008 and 2009, the abundance of recruits was low (<25.3±14.8 recruits m^{-2} kelp) in June, July, and August and increased by three orders of

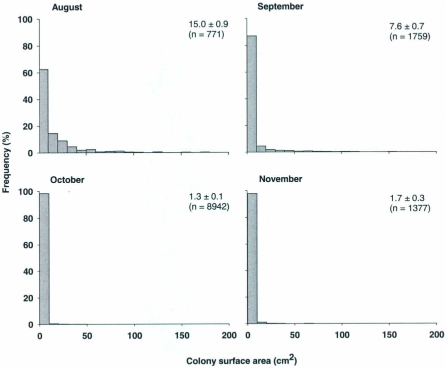

Figure 3.4: Size-frequency distributions of *Membranipora membranacea* colonies on kelp across the eight study sites (1 to 8) in August, September, October, and November 2008. Data are mean colony surface area ±SE (sample size in parentheses).

Table 3.6: Summary of two-way ANOVA (applied to arcsine [√x] transformed data) showing the effect of Site (six study sites: 3, 4, 5, 6, 7, and 8) and Month (two sampling months: September and October) on the cover of *Membranipora membranacea* colonies on kelp in 2008 (see Table 2.1 and Fig. 2.1 for location of sites and dates of kelp collection in each month).

Source of variation	**df**	**MS**	***F***	**p**
Site	5	0.6	25.1	<0.001
Month	1	0.1	5.1	0.026
Site x Month	5	0.07	2.7	0.023
Error	107	0.03		
Corrected total	118			

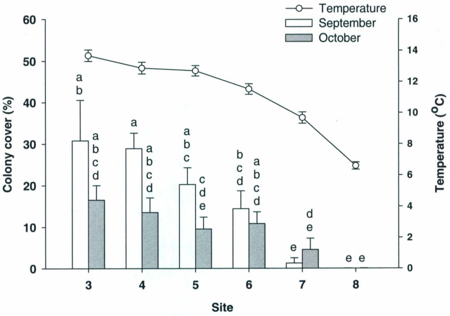

Figure 3.5: Change in mean (+SE) cover of *Membranipora membranacea* colonies on kelp in September and October at six study sites (3 to 8) in 2008. Values sharing the same letter are statistically similar (LS Means, p<0.05; n = 9 or 10 kelp blades). Each temperature data point is the average (±SE) of mean daily sea temperatures between 10 July and 24 November 2008 (n = 137).

Table 3.7: Summary of three-way ANOVA (applied to log [x+1] transformed data) showing the effect of Site (two study sites: 3 and 7), Month (three sampling months: September, October, and November), and Year (two sampling years: 2008 and 2009) on the abundance of *Membranipora membranacea* recruits on kelp (see Table 2.1 and Fig. 2.1 for location of sites and dates of kelp collection in each month of each year).

Source of variation	**df**	**MS**	***F***	**P**
Site	1	1151.4	523.2	<0.001
Month	2	34.5	15.7	<0.001
Year	1	7.6	3.5	0.065
Site x Month	2	6.1	2.8	0.067
Site x Year	1	19.5	8.9	0.004
Month x Year	2	9.1	4.1	0.019
Site x Month x Year	2	3.2	1.5	0.240
Error	95	5.2		
Corrected total	106			

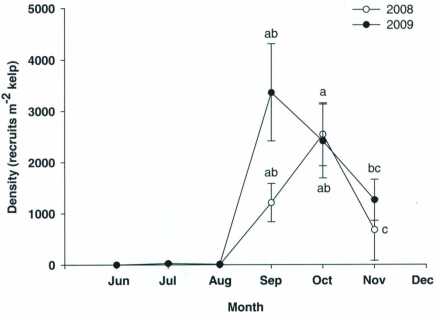

Figure 3.6: Change in mean (±SE) abundance of *Membranipora membranacea* recruits on kelp over six sampling months (June to November) pooled across study sites 3 and 7 in 2008 and 2009. Values sharing the same letter are statistically similar (LS Means, $p<0.05$; $n = 8$ to 20 kelp blades). Data from June, July, and August were not included in the statistical analysis (see materials and methods).

magnitude between August and September (Fig. 3.6). Recruit abundance decreased steadily by 63% between September and November in 2009 (LS Means, p=0.21), though increased by an additional 110% between September and October 2008, followed by a 73% decrease in November (LS Means p=0.027, Fig. 3.6). The overall recruitment at site 3 was at least two orders of magnitude greater than at site 7 in both 2008 and 2009, yet was 45.2% higher in 2009 than 2008 (Fig. 3.7) despite a decrease of 2.6°C in mean sea temperature between September and November from 2008 to 2009 (Fig. 2.2).

Results of the tree-way ANOVA of colony cover data at sites 3 to 8 in 2008 and 2009 indicated a significant interaction between the factors Site and Year, where changes in cover within site 3 were dependent on the sampling year (Table 3.8). Patterns of monthly changes in the cover of *M. membranacea* colonies on kelp at sites 3 and 7 were similar in 2008 and 2009 (Table 3.8, Fig. 3.8), while slightly different than those in recruit abundance (Figs. 3.6 and 3.8). In both years colony cover was low (<1%) in June, July, and August and increased by at least 8 times between August and September (Fig. 3.8). Although recruitment increased between September and October 2008 (Fig. 3.6), colony cover decreased from 13.5 to 8.6%, whereas in 2009 recruitment decreased between October and November while colony cover slightly increased from 8.5 to 10.5% (Figs. 3.6 and 3.8). Colony cover pooled over September and October was 7 times greater at site 3 (warmest site) than site 7 in 2008 (LS Means p<0.001), yet was not different between the two sites in 2009 (Fig. 3.9). Overall colony cover (two sites pooled) in 2008 (11.0%) was only slightly higher than in 2009 (9.4%), a non significant difference (Table 3.8).

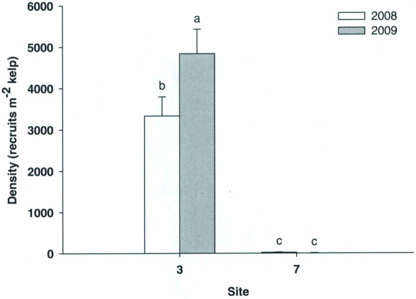

Figure 3.7: Change in mean (+SE) abundance of *Membranipora membranacea* recruits on kelp at study sites 3 and 7 pooled over September, October, and November in 2008 and 2009 (n = 24 to 30 kelp blades).

Table 3.8: Summary of three-way ANOVA (applied to arcsine [√x] transformed data) showing the effect of Site (two study sites: 3 and 7), Month (two sampling months: September and October), and Year (two sampling years: 2008 and 2009) on the cover of *Membranipora membranacea* colonies on kelp (see Table 2.1 and Fig. 2.1 for location of sites and dates of kelp collection in each month of each year).

Source of variation	**df**	**MS**	***F***	**P**
Site	1	0.29	12.8	0.001
Month	1	0.01	0.6	0.440
Year	1	0.02	0.75	0.388
Site x Month	1	0.08	3.5	0.066
Site x Year	1	0.15	6.5	0.013
Month x Year	1	0.03	1.3	0.253
Site x Month x Year	1	0.02	0.9	0.340
Error	66	1.5		
Corrected total	73			

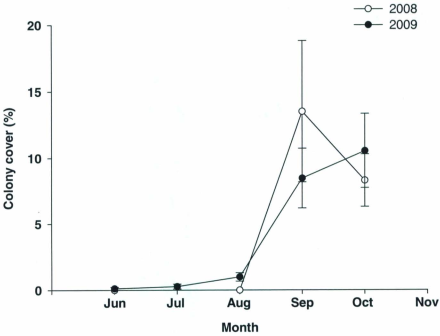

Figure 3.8: Change in mean (±SE) cover of *Membranipora membranacea* colonies on kelp over six sampling months (June to November) pooled across study sites 3 and 7 in 2008 and 2009 (n = 8 to 20 kelp blades).

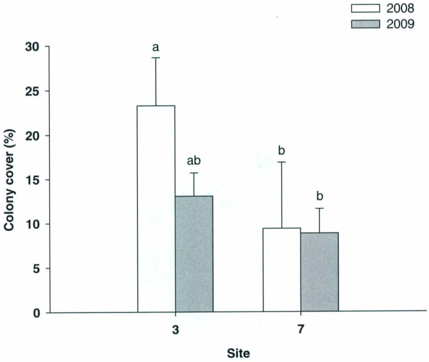

Figure 3.9: Change in mean (+SE) cover of *Membranipora membranacea* recruits on kelp at study sites 3 and 7 pooled over September and October in 2008 and 2009 (n = 18 to 20 kelp blades).

3.3.3 Relationships between temperature, recruit abundance, and colony cover

Regression analyses with data from sites sampled in September, October, and November 2008 and 2009 indicated that changes in both the abundance of recruits and colony cover of *Membranipora membranacea* on kelp were positively correlated to sea temperature patterns over the 76 days (TI_{76}) preceding measurements (Table 3.9). Up to 33.9% of the variation in recruit abundance was explained by TI_{76} when using data in all three months (Table 3.9). Predictive capabilities of TI_{76} increased by at least 31.4% when considering each month separately, peaking at 96.5% in November (Fig. 3.10). Likewise, 27.7% of the variation in colony cover across September, October, and November was explained by TI_{76} (Table 3.9). Examination of size-frequency distributions of colonies in each month indicated that >98% of colonies in both October and November were small ($\leq 10 cm^2$), and hence that most colonies at that time had formed from newly recruited larvae (Fig. 3.4). This pattern coupled with our observations that those small colonies accounted for 42 and 49% of total colony surface area in October and November, respectively, suggest that recruitment is a strong predictor of colony cover. Accordingly, recruit abundance explained 52.4% of the variation in colony cover for all data in 2008 and 2009 (Fig. 3.11). Restricting the analysis to shorter periods of time did not affect this relationship as shown by virtually identical correlation coefficients in September, and October and November pooled (Table 3.9). Interestingly, in September sea temperature explained 24.5% more of the variation in colony cover than recruit abundance, whereas in October and November recruit abundance explained 37.6% more of the variation in colony cover than temperature, i.e. a reverse trend (Table 3.9, Fig. 3.12). Multiple linear regression analysis showed sea temperature and recruit

Table 3.9: Results of simple linear regression analyses examining relationships between the abundance of *Membranipora membranacea* recruits on kelp, colony cover on kelp, and thermal history (TI_{76}) from all sites between September and November 2008 and 2009 ($p<0.05$ for all regressions). Refer to materials and methods for calculation of TI_{76}.

Response variable (sampling month)	**Explanatory variable**	**Equation for log (recruits + 1) or arcsine (√cover)**	**r^2**	**$F_{(df)}$**
Recruits (Sep to Nov)	TI_{76}	$= -1.59 + 0.0070\ TI_{76}$	0.339	$12.3_{(1,24)}$
Recruits (Sep)	TI_{76}	$= -5.33 + 0.010\ TI_{76}$	0.674	$12.4_{(1,6)}$
Recruits (Oct)	TI_{76}	$= -5.02 + 0.012\ TI_{76}$	0.653	$15.0_{(1,8)}$
Recruits (Nov)	TI_{76}	$= -18.82 + 0.035\ TI_{76}$	0.965	$168.6_{(1,6)}$
Cover (Sep to Nov)	TI_{76}	$= -0.065 + 0.0004\ TI_{76}$	0.277	$8.8_{(1,24)}$
Cover (Sep)	TI_{76}	$= -0.59 + 0.0009\ TI_{76}$	0.852	$34.4_{(1,6)}$
Cover (Oct and Nov)	TI_{76}	$= 0.058 + 0.0003\ TI_{76}$	0.132	$2.3_{(1,15)}$
Cover (Sep to Nov)	Recruits	= 0.070 + 0.050 Recruits	0.524	$25.3\ _{(1,23)}$
Cover (Sep)	Recruits	= 0.37 + 0.35 Recruits	0.607	$9.3_{(1,6)}$
Cover (Oct and Nov)	Recruits	= 0.077 + 0.046 Recruits	0.508	$15.5_{(1,15)}$

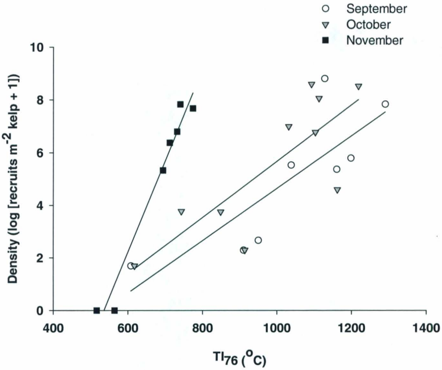

Figure 3.10: Relationship between the abundance of *Membranipora membranacea* recruits on kelp and thermal integral (TI_{76}) across sites in each of September, October, and November (2008 and 2009 data pooled). The lines are the linear fit to these data (r^2=0.674, 0.653, and 0.965 for September, October, and November, respectively; see Table 3.9 for details of regression analyses).

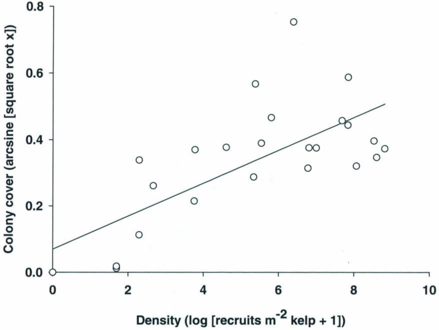

Figure 3.11: Relationship between the cover of colonies and abundance of recruits of *Membranipora membranacea* on kelp for sites sampled in September, October, and November 2008 and 2009. The line is the linear fit to these data (r^2=0. 524, see Table 3.9 for details of regression analysis).

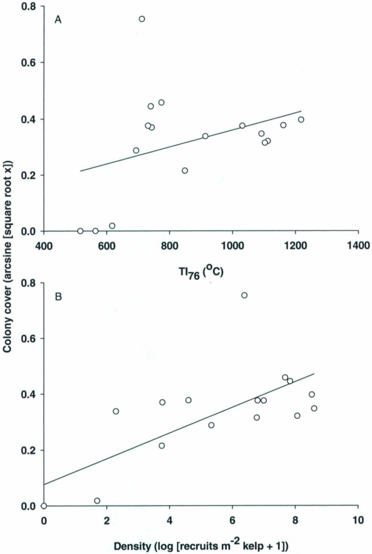

Figure 3.12: Relationship between the cover of *Membranipora membranacea* colonies on kelp and (A) thermal history (TI_{76}) and (B) the abundance of recruits for sites sampled in October and November 2008 and 2009. The lines are the fit to these data (r^2=0.132 and 0.508 for [A] and [B], respectively; see Table 3.9 for details of regression analyses).

abundance explained 52.3% of the variation in colony cover altogether in September, October, and November ($F_{(2,22)}$=12.7, p<0.001), which is only slightly higher than the 52.4% obtained with recruit abundance alone (Table 3.9). Therefore, those results suggest that sea temperature and recruit abundance are both strong predictors of *M. membranacea* colony cover on kelp, though their relative importance varies over time with temperature being more critical than recruit abundance in late summer and early fall.

3.4 DISCUSSION

We investigated seasonal (June to November) and inter-annual (2008 and 2009) variation in the abundance of recruits and colony cover of the invasive bryozoan *Membranipora membranacea* on the kelp *Saccharina longicruris* and its relationship to thermal history at eight sites spanning a latitudinal gradient of 450 km between the southwestern tip of Newfoundland and southeastern Labrador. Monthly changes (all sites pooled) in recruitment followed a strong seasonal pattern in 2008, with very low recruit abundance from June to August, dramatic increases in September and October, and slight decreases in November. Yet, this pattern was largely determined by recruitment at the warmest sites, which was much higher (by up to three orders of magnitude) than at the coldest sites. Both recruit abundance and mean sea temperature were lowest at the southernmost (1) and northernmost (7 and 8) sites, while peaking at mid-latitudes (site 3). Although those patterns suggest a relationship between recruitment and temperature exist along the coast of Newfoundland and Labrador, the strength of this relationship undoubtedly varies locally as shown by the 16-fold drop in recruit abundance from sites 3 to 4 despite the relatively small distance (85 km) and difference (<1°C) in mean sea temperature between the two sites. Interestingly, spatial and temporal changes in recruitment were remarkably consistent with those in settlement, including a marked decline in settler abundance from site 3 to site 4 (Chapter II). Such similarity in the changes in settler and recruit abundances across sites despite obvious differences in sea temperature strongly supports the idea that temperature is a key factor in regulating larval supply in *M. membranacea*, whereas the magnitude of recruitment is largely driven by settler abundance and to a much lesser extent by changes in temperature.

Many factors affect recruitment success in marine invertebrates, including predation (Keough & Downes 1982), inter- and intraspecific competition (Connell 1961b), siltation (Hunt & Scheibling 1997), and temperature and salinity (Chen & Chen 1993). In this study, recruitment was about 30% higher than settlement at half the sites (2, 3, 5, and 6), yet was at least 60% lower at the other sites (1, 4, 7, and 8). This finding suggests that both pre- and post-settlement processes affect recruitment in *M. membranacea*, while suggesting that the nature and relative importance of those processes vary geographically. There are only a few predators of *M. membranacea* in the northwest Atlantic, including the snail *Astyris lunata*, and the nudibranchs *Onchidoris muricata* and *Doridella obscura*, with no demonstrated ability to control its populations (Harris & Mathieson 2000, Harris & Dijkstra 2007, Pratt & Grason 2007). According to patterns described above and our analysis of relationships between temperature, recruit abundance, and colony cover, we propose that changes in the physical environment exert the largest influence on population dynamics of *M. membranacea* along the coast of Newfoundland and Labrador. This suggestion is further supported by largest ratios of settler to recruit abundances (an indication of lower recruitment success) at sites with a mean sea temperature (July to November) <11°C. Likewise, in Europe, recruitment in barnacles and gastropods is generally lower in northern than southern populations, a difference likely due to suboptimal sea temperature at higher latitudes (Bowman & Lewis 1986, Lewis 1986). The apparent paradox created by site 4 where mean sea temperature (12.9°C) was almost as high as in the two warmest sites (2 and 3), yet settlement and recruitment were comparatively much lower, is interesting. Site 4 was located on an entirely exposed coastline and kelp blades at this site were consistently smaller and flatter than at the other sites (Chapter II). This pattern, along with previous reports of decreases in kelp size with increasing exposure to waves (Gerard & Mann 1979, Gerard 1987) provide a good indication that wave energy was high at that site. Possibly, the relatively low abundances of settlers and recruits at site 4 and associated 56% reduction in recruit abundance compared to settler abundance were due to current and wave patterns affecting both larval supply to the site and subsequent survival of settlers.

August and September marked the initiation of major increases in both settlement and recruitment at the warmest sites (Chapter II and this chapter). However, settler abundance generally peaked earlier (September) than recruit abundance (October). The relatively low, though increasing abundance of recruits in September, when settlement was highest, indicates that cyphonautes larvae had achieved competency and began to settle out of the water column between August and September. In 2007, Saunders and Metaxas (2010) found large numbers of competent larvae of *M. membranacea* in the second half of September in St. Margarets Bay (Nova Scotia). Numbers were still large at the beginning of October, yet had decreased substantially in mid-November. Such highs and lows in the abundance of competent larvae coincided well with periods of increasing and decreasing abundances of juvenile colonies (which are equivalent to recruits in this study), respectively, in the two preceding years (2005 and 2006) (Saunders & Metaxas 2008, 2010). Analysis of changes in recruitment in September, October, and November indicated that the abundance of recruits at site 3 (the warmest site) was four times higher in October than November. Yet, at sites 4 and 5 (slightly colder sites) settlement decreased while recruitment increased from October to November, i.e. a small delay compared to southern, warmer sites. Low temperature can increase development times in larvae of crustaceans, gastropods, and echinoderms (Brenko & Calabrese 1969, Calabrese 1969, Harms 1986, Thiyagarajan et al. 2003, Asha & Muthiah 2005). Accordingly, we propose that lower sea temperature at sites 4 and 5 increased the development time of cyphonautes larvae, which delayed recruitment. The absence of settlers and recruits in November at site 7, where sea temperature averaged only 8.9°C throughout summer and fall, suggests that further decreases in sea temperature combined with relatively high exposure to waves (Chapter II) resulted in complete recruitment failure at that site. More research is needed to elucidate effects of low sea temperature on behavior, growth, and survival of *M. membranacea* larvae.

Changes in the cover of *M. membranacea* colonies on kelp across sites in 2008 generally paralleled those in recruit abundance, with differences in cover of more than three orders of magnitude between warmest and coldest sites and the notable exception that cover increased while recruit abundance decreased from sites 3 to 4. The unexpectedly high colony cover at site 4 could be partly due to an artificial increase in cover values caused by a preponderance of small kelp individuals compared to the other sites (Chapter II). Colony cover followed a strong seasonal cycle that was somewhat different than that of recruitment. Indeed, there were no recruits in June and August, yet growth of June settlers resulted in intermediate colony cover values (on average 7%) by August. Moreover, the sharp increase in recruit abundance between September and October coincided with a significant decrease in colony cover, which subsequently rebounded to September values while recruitment decreased. Such reverse trends in recruit abundance and colony cover during fall suggest kelp defoliation occurred. Short- and long-term studies in the northwest Atlantic showed that decreases in kelp cover during fall are related to the degree of infestation by *M. membranacea* (Lambert et al. 1992, Saunders & Metaxas 2008, Scheibling & Gagnon 2009). In September 2008, kelp blades from sites 1, 3, 4, 5, and 6 had numerous large (>50 cm^2) colonies on the middle and distal portions of blades. Conceivably, those colonies weakened kelp tissue (Dixon et al. 1981, Saunders & Metaxas 2008), causing their own fragmentation and loss. This suggestion is well supported by the 52% decrease in the abundance of large colonies between September and October. Continued colony growth and recruitment caused increases in colony cover from October to November.

Experiments showed that colony growth in *M. membranacea* is positively correlated to temperature, at least within the range of 6 to 18°C (Menon 1972, Saunders & Metaxas 2009a), which is compatible with temperature ranges in this study. Colony cover in September and October 2008 (November was excluded from the statistical analysis due to missing data at a few sites) gradually decreased with increasing latitude (and temperature), from 27% at site 3 (September) to <10% at sites 5 and 6 (October). Cover values did not exceed 5% at the two northernmost sites, 7 and 8. Low temperature combined with low settlement and high recruit mortality (see above) most likely accounted for such low cover at higher latitudes. The highest mean colony cover (46% at site 4 in November 2008) noted in this study is much lower than the >75% peak cover values reported in years of heavy infestation (1993, 1997, and 1999) in central Nova Scotia (Scheibling & Gagnon 2009). Massive kelp defoliations following infestation by *M. membranacea* have been reported in California, the Gulf of Maine, and Nova Scotia (Dixon et al. 1981, Lambert et al. 1992, Saunders & Metaxas 2008, Scheibling & Gagnon 2009). Observational and experimental studies suggested that such sudden kelp removals may facilitate the establishment of other invasive species, including the green alga *Codium fragile* spp. *fragile* (Levin et al. 2002, Scheibling & Gagnon 2006, Saunders & Metaxas 2008, Scheibling & Gagnon 2009). Although the cover of *M. membranacea* on kelp along the coast of Newfoundland was consistently lower than values observed elsewhere in the northwest Atlantic and northeast Pacific (Dixon et al. 1981, Berman et al. 1992, Lambert et al. 1992, Saunders & Metaxas 2008, Scheibling & Gagnon 2009), we witnessed marked declines in kelp abundance during our dives at sites 3 and 5 in November 2008.

Patterns of monthly (June to November) changes in recruitment (sites 3 and 7 pooled) differed between 2008 and 2009, with recruit abundances peaking earlier in 2009 (September) than 2008 (October). Recruit abundance at site 3 was 45% higher in 2009 than 2008 and did not differ between years at site 7. Changes in colony cover from September to October were contrary to those in recruit abundance in both years. In addition, colony cover at site 3 did not differ between years even though sea temperature in 2009 was on average 2.6°C lower than in 2008. Such similarity in cover between years may have been caused by the substantial increase in recruitment in 2009 compared to 2008. These findings contradict patterns at two sites within a bay in Nova Scotia whereby recruitment and colony cover in *M. membranacea* occurred earlier and were higher following the warmer of two consecutive winters (Saunders & Metaxas 2007, 2008). Globally, our results from multiple sites with contrasting thermal histories indicate that relationships between temperature, settlement, recruitment, and colony cover in *M. membranacea* is more complex than previously thought, with variables operating over distinct spatial and temporal windows.

We showed that in Newfoundland and Labrador settlement of *M. membranacea* on *S. longicruris* is strongly correlated to spatial and temporal variation in thermal history over the 76 days preceding measurements (TI_{76}), being generally higher at warmer sites (Chapter II). This study further elevates the importance of temperature for both early and late life stages of *M. membranacea* by documenting reduced recruitment success at colder sites and relatively strong, time-sensitive relationships between temperature, recruitment, and colony cover. Simple regression analysis indicated that TI_{76} explained 34% of the variation in recruit abundance during late summer and fall (September, October, and November) across all sites in 2008 and 2009, which is considerably less than the 58% correlation coefficient for the relationship between TI_{76} and settler abundance (Chapter II). The explanatory power of TI_{76} nearly doubled when restricting the analysis to each of September and October, yet peaked to 97% in November. Such differences in explanatory power suggest that temperature has a greater impact on settlement than recruitment, and that the greatest effect of temperature on recruitment is in late fall, when sea temperature is colder. Like recruitment, spatial and temporal variation in colony cover was only moderately related (r^2=0.28) to TI_{76} in September, October, and November across all sites in both years, yet was largely explained (r^2=0.85) by TI_{76} in September. In fact, temperature explained 25% more of the variation in colony cover than recruitment in September, whereas recruitment explained nearly 40% more of the variation in colony cover than temperature in October and November, a reverse trend.

Growth stops at contacting margins of adjacent colonies of *M. membranacea* (Harvell et al. 1990). Presumably, space was not limiting for the few colonies that formed and grew between June and August at the warmest sites, yet crowding gradually occurred as those colonies grew into September under the predominant influence of temperature. Conversely, the lesser influence of temperature on colony growth (and hence colony cover) in October and November was likely due to large increases in the abundance of recruits in those months which monopolized the space at the expense of fewer, smaller colonies. Relationships between recruitment and colony cover were invariably strong (with r^2 values between 0.51 and 0.61) regardless of the temporal window over which data were aggregated. In California, sea temperature and the abundance of *M. membranacea* cyphonautes larvae in the water column explained 55 and 70% of the variation in recruitment on kelp, respectively, and up to 79% when analyzed together (Yoshioka 1982, 1986). Likewise, in Nova Scotia, temperature patterns explained 83% of inter-annual variation in peak cover of *M. membranacea* on kelp (Scheibling & Gagnon 2009). Differences in the way temperature was aggregated in this and those studies prevent direct comparisons of the absolute effect of temperature on recruitment and colony cover. Overall, our findings indicate that temperature strongly affects spatial and temporal differences in recruitment and colony growth within a same year, while suggesting that inter-annual differences are governed by interactions between temperature and some other environmental factors.

This study is the first to examine spatial and temporal variation in recruitment and colony cover of the invasive bryozoan *Membranipora membranacea* on kelp along the recently invaded coast of Newfoundland and Labrador. We showed that (1) recruitment and colony cover varied seasonally, though variation generally decreased with increasing latitude, (2) temperature in the 76 days preceding measurements explained most [>60%] of the variation in recruitment within each month from late summer [September] to late fall [November] with the highest predictive capability (97%) in late fall, and (3) colony cover was strongly correlated (r^2=0.524) to recruit abundance from late summer to late fall. Our findings extend our knowledge of population dynamics of *M. membranacea* in the northwest Atlantic by demonstrating the complex nature of relationships between thermal history, settlement, recruitment, and colony cover. Working at different spatial and temporal scales enabled both generalization and refinement of patterns seen in Nova Scotia, the Gulf of Maine, and California. Future research should experimentally address effects of low temperature on growth and survival of larvae, settlers, and colonies to gain fuller understanding and increase our predictive capability of population dynamics of *M. membranacea* and its impacts on cold temperate and subarctic marine ecosystems.

CHAPTER IV

SUMMARY

4.1 Overall objective of the study

Studying effects of environmental variability on populations of marine organisms is key to our understanding and predictive capability of changes in the structure and function of marine ecosystems and the fisheries that depend on them. Many biological and physicochemical factors affect to various degrees population dynamics in marine invertebrates. In particular, settlement, recruitment, and growth in marine benthic invertebrates with pelagic larval stage(s) can vary substantially in time and space, especially when larvae spend large amounts of time drifting in the water column, therefore creating open populations in which larval supply is, to some extent, decoupled from local larval production. The overall objective of this study was to quantify and compare seasonal (June to November) and inter-annual (2008 and 2009) variation in settlement, recruitment, and cover of the invasive, colonial bryozoan *Membranipora membranacea* on the kelp *Saccharina longicruris* across eight sites spanning a 450-km latitudinal gradient between the southwestern tip of Newfoundland and southeastern tip of Labrador, and to what extent the observed variation is explained by thermal histories at these sites. Sites were, in order of increasing latitude: (1) Port aux Basques [southernmost site], (2) Lark Harbour, (3) Norris Point, (4) Daniel's Harbour, (5) Port au Choix, (6) Bird Cove, (7) Green Island Cove, and (8) Red Bay [northernmost site, the only one in Labrador]. Interestingly, mean sea temperature did not decrease from south to north, but rather with increasing and decreasing latitude north and south of site 3, respectively. This particular pattern provided ideal conditions to test temperature-related hypotheses.

4.2 Settlement

Chapter II examined spatial variation in the timing and magnitude of settlement of *M. membranacea* and how it relates to changes in sea temperature. I showed that (1) settler abundance varied both seasonally and annually with a sharp increase between August and September at warmer sites, and spatially with differences of up to three orders of magnitude between sites, (2) settler abundance and sea temperature were strongly correlated (r^2=0.577), with maxima at mid-latitudes and minima at the northernmost and southernmost sites, and (3) exposure to waves, degree of kelp blade corrugations, and surface area of colonies of *M. membranacea* on kelp had little explanatory power on settler abundance across the study sites compared to sea temperature. Specifically, patterns of changes in the abundance of settlers closely matched latitudinal differences in sea temperature. As hypothesized, settlement was generally highest at the warmest sites (2 and 3), and lowest at the coldest sites (1, 7, and 8). Settlement was highest at two sites (2 and 3) located within large, semi-enclosed bays where water circulation likely favored larval retention and settlement. Temperature patterns suggested that annual upwelling in late summer and fall caused consistently lower settlement at the southernmost site (1). Settlement did not occur before June 2008 at the three southernmost sites (1, 2 and 3) and was delayed by up to three months at the northernmost site in Newfoundland (7). Settlement began later (July) in 2009 and was substantially greater than in 2008, despite lower mean sea temperature (2.6°C colder) in 2009 than 2008. Settlement was positively correlated to sea temperature, with up to 92% of the variation explained by TI_{76} (the sum of mean daily temperature over the 76 days preceding measurement) in November. Yet, settler abundance in September was strongly related to a shorter thermal integral, TI_{21}, suggesting again that settlement in late summer and early fall may have been caused by changes in the vertical structure of the water column. The extent of colonies on kelp explained up to 46% of spatial and temporal variation in settlement, whereas kelp blade morphology had no significant effect on those relationships.

4.3 Recruitment and colony cover

Chapter III examined spatial and temporal variation in the abundance of recruits and colony cover of *M. membranacea* and its relationship to changes in sea temperature over the same spatial and temporal domains as in Chapter II. I showed that (1) recruitment and colony cover varied seasonally, though variation generally decreased with increasing latitude, (2) temperature in the 76 days preceding measurements explained most [>60%] of the variation in recruitment within each month from late summer [September] to late fall [November] with the highest predictive capability (97%) in late fall, and (3) colony cover was strongly correlated (r^2=0.524) to recruit abundance from late summer to late fall. As predicted, recruit abundance was highest at the warmest site (3), and lowest at coldest sites (7 and 8). Yet, colony cover was highest at the third warmest site (4) and equally low at the two coldest sites (7 and 8). Interestingly, settlement and recruitment were remarkably low at one site (4) located midway through the latitudinal gradient and where high wave and current energy most likely prevailed as show by the particular morphology of kelp blades at that site. Comparison of data with Chapter II indicated that spatial and temporal changes in settlement and recruitment were generally similar, suggesting that larval supply is a key factor affecting recruitment of *M. membranacea.* Spatial and temporal variation in recruitment and colony cover across the eight sites in September, October, and November 2008 and 2009 were moderately correlated (34 and 28%, respectively) to thermal histories. Yet, the strength of the relationship between temperature and recruitment increased to 97% in October, indicating that sea temperature has the greatest effect on recruitment during late fall. Sea temperature had its greatest influence on colony cover in September, whereas colony cover was strongly related to recruit abundance in October and November. Therefore, results indicated that spatial and temporal variation in settlement, recruitment, and cover of *M. membranacea* on kelp in Newfoundland and Labrador is not merely a function of temperature, but depends also on other factors that most likely act at different spatial and temporal scales.

4.4 Importance of the study

This study provides the first quantitative analysis of spatial and temporal variation in the abundance of the invasive bryozoan *Membranipora membranacea* in Newfoundland and Labrador. It strongly supports the overall hypothesis that temperature is a key factor in regulating the population dynamics of this species. Like for other species of bryozoans in California, the United Kingdom, and Antarctica, our study indicated that the abundance of *M. membrancea* settlers and recruits can vary greatly spatially and temporally. Findings support studies of *M. membranacea* along the Atlantic coast of Nova Scotia by showing that colony cover on kelp correlates generally well with sea temperature patterns in summer and fall. They also provide new insights into other factors that may or may not affect population dynamics by showing that settlement cannot be reliably predicted from changes in exposure to waves, kelp blade morphology, and surface area of colonies of *M. membranacea* on kelp, whereas colony cover is strongly related to spatial and temporal changes in recruit abundance. Consistently low abundances of settlers, recruits, and colonies at site 8 suggest that *M. membranacea* is nearing its northern distribution limit in the northwest Atlantic. This limit is likely imposed by the pervasive effects of low temperature on settlement, recruitment, and growth of colonies as well as the likely natural barrier to dispersal created by the Labrador Current, which flows southward along the Labrador side of the Strait of Belle Isle. These findings extend our knowledge of population dynamics of *M. membranacea* in the northwest Atlantic and east Pacific by demonstrating the complex nature of relationships between thermal history, settlement, recruitment, and colony cover. Patterns outlined in this thesis will likely change with increases in sea temperature predicted to result from climate change.

4.5 Future directions

Working at different spatial and temporal scales enabled both generalization and refinement of patterns of settlement, recruitment and colony cover of *M. membranacea* on kelp seen in Nova Scotia, the Gulf of Maine, and California. However, a few inconsistencies both within the system studied and between the system studied and that of Nova Scotia indicate additional long-term observational and experimental studies are required to elucidate factors that regulate local and regional variation in the abundance of this invader. In particular, temporal changes in recruitment and colony cover on kelp and their connections with temperature and settler abundance were assessed over a large spatial domain encompassing a wide range of temperature regimes. This time-consuming, yet effective approach provided new insights on the effect of temperature and its possible interactions with other physical variables and phenomena such as exposure to waves and upwelling on the dynamics of *M. membranacea* in the northwest Atlantic. It also increased our capacity to identify areas of low and high vulnerability to kelp defoliation, an important aspect in the development of sustainable fisheries. It appears that kelp communities located in and around the Bonne Bay area are currently the most vulnerable to the invasion by *M. membranacea* as shown by dramatic declines in kelp biomass following relatively mild infestations in late fall 2008. Conversely, those kelp communities located in the Port aux Basques, Green Island Cove, and Red Bay areas are not likely to experience significant changes due to the invasion. Future research should also experimentally address effects of low temperature on growth and survival of larvae, settlers, and colonies of *M. membranacea* to gain fuller understanding and increase our predictive capability of population dynamics of *M. membranacea* and its impacts on cold temperate and subarctic marine ecosystems. Lastly, it is worth mentioning that most of the results presented in this thesis originate from the collective workforce provided by fish harvesters at each site who simultaneously collect kelp blades when they were needed. Such collaborations between researchers and fish harvesters are strongly encouraged to increase the range of scientific questions that can be addressed.

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APPENDIX A

Description of kelp collection device and procedure for kelp collection

The device that was provided to each fish harvester to collect kelp blades consisted of the head of an iron garden rake welded to two 61-cm horizontal steel rods and two 61-cm vertical steel bars (Fig. A.1). A PVC pipe (5 cm in diameter) was added to strengthen the device. A jointer blade was screwed to the base of the rake tines to cut kelp stipes as the device was pulled across kelp stands with a 16-m long nylon rope. Detaching kelp specimens gradually accumulated in the collection basket made up of 2.5-cm mesh, nylon fishing net. Cast lead dive weights were secured with plastic cable ties to the front (3.6 kg) and back (1.8 kg) ends of the bottom of the device for increased stability on the seabed.

The device was lowered from the boat to the seabed at a depth of approximately 6 m (as indicated by a marker on the rope), pulled manually over a distance of approximately 5 m, and brought to the surface for extraction of kelp blades trapped in the collection basket. This procedure was repeated until at least eight blades with undamaged blades measuring 70 to 150 cm in length were obtained (Fig. A.2), which usually required between 30 and 60 min of work. Kelp blades were kept in a 25-L plastic container filled with cold seawater until they were packaged in hermetic plastic bags and shipped on ice in rigid coolers to the OSC.

Figure A.1: Side view of one of the kelp collection devices that were provided to each fish harvester to collect kelp blades from their fishing boats.

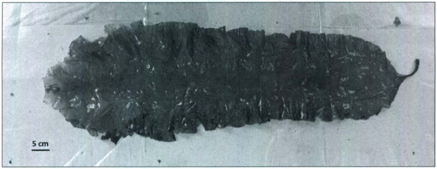

Figure A.2: Top view of a kelp blade collected by one of the fish harvesters with the kelp collection device and received at the Ocean Sciences Centre for analysis.