PATTERNS IN THE LARVAL VERTICAL DISTRIBUTION OF MARINE BENTHIC INVERTEBRATES IN A SHALLOW COASTAL EMBAYMENT

by

Michelle J. Lloyd

Submitted in partial fulfilment of the requirements
for the degree of Master of Science

at

Dalhousie University
Halifax, Nova Scotia
September 2011

DALHOUSIE UNIVERSITY

DEPARTMENT OF OCEANOGRAPHY

The undersigned hereby certify that they have read and recommend to the Faculty of Graduate Studies for acceptance a thesis entitled "PATTERNS IN THE LARVAL VERTICAL DISTRIBUTION OF MARINE BENTHIC INVERTEBRATES IN A SHALLOW COASTAL EMBAYMENT" by Michelle J. Lloyd in partial fulfilment of the requirements for the degree of Master of Science.

Dated: September 20, 2011

Supervisor: _____

Readers: _____

_____

_____

_____

Departmental Representative: _____

DALHOUSIE UNIVERSITY

DATE: September 20, 2011

AUTHOR: Michelle J. Lloyd

TITLE: PATTERNS IN THE LARVAL VERTICAL DISTRIBUTION OF MARINE BENTHIC INVERTEBRATES IN A SHALLOW COASTAL EMBAYMENT

DEPARTMENT OR SCHOOL: Department of Oceanography

DEGREE: MSc CONVOCATION: May YEAR: 2012

_____

Signature of Author

To my family for instilling in me a love of the outdoors, and a passion to conserve it.

Table of Contents

List of Tables

List of Figures

Abstract

Processes during the meroplanktonic phase regulate population dynamics for many marine benthic invertebrates. I examined changes in vertical distribution of different meroplanktonic larvae in a coastal embayment during a stable period, at high temporal frequencies and spatial resolutions. Plankton samples were collected at 6 depths (3, 6, 9, 12, 18, 24 m) using a pump, every 2-h over a 36- and a 25-h period, during a spring and neap tide, respectively, concurrently with measures of temperature, salinity, fluorescence and current velocity. For 10 gastropod taxa, larval vertical distribution was mostly related to the thermal structure of the water column. Each of 7 taxonomic groups was found either exclusively near the surface, associated with the fluorescence maximum, or showed diel changes in distribution. These larvae that occupy different depths in the water column exhibit different dispersal potentials.

List of Abbreviations and Symbols Used

Abbreviation/ Symbol	Definition	Unit
ADCP	Acoustic Doppler Current Profiler	
ANOVA	Analysis of variance	
CTD	Conductivity-Temperature-Depth recorder	
D	Diel period (e.g. day, night, dawn, dusk)	
df	Degrees of freedom	
F	Fluorescence	
F	F-value	
i	Depth interval	
j	Sampling time	
HSD	Honestly Significant Difference	
L	Lunar phase (e.g. full moon, quarter moon)	
MDD	Mean Depth Distribution	m
MDD_j	Mean Depth Distribution at sampling time *j*	m
MHHW	Mean Higher High Water	m
MLLW	Mean Lower Low Water	m
N.S.	Not Significant	
N^2	Buoyancy frequency	s^{-2}
N_j	Total number of larvae sampled at sampling time j	Larvae m^{-3}
n_{ij}	Number of larvae collected at depth *i* at sampling time *j*	Larvae m^{-3}
n	Sample size	
n	Sample	
P_{ij}	Proportional abundance at depth interval *i* at sampling time *j*	
p	p-value	
R^2	Coefficient of determination	

Ri	Richardson numbers	
r	Pearson correlation	
S	Salinity	
SD	Standard Deviation	
spp.	Species (plural)	
sp.	Species (singular)	
T	Temperature	°C
Ti	Tidal State (e.g. ebb, flood, high, low)	
t	t-value	
U	Scale for horizontal velocity	mm s^{-1}
u	East-West velocity	mm s^{-1}
v	North-South velocity	mm s^{-1}
w	Vertical velocity	mm s^{-1}
z	Depth	m
z_i	Mean depth of interval *i*	m
α	alpha-value	
ρ	Density (σ_t)	kg m^{-3}- 1000
ΔS	Change in salinity	
ΔT	Change in temperature	° C
Δz	Change in depth	m
+	Positive relationship	
–	Negative relationship	

Acknowledgements

First and foremost, I would like to recognize and thank my supervisor, Anna Metaxas. She has truly exceeded the high expectations I had for a supervisor when I started this journey. She has helped me to build on my strengths and overcome my weaknesses, taught me to be a better scientist, writer and person and above all, she has always been there to support me and provide wise guidance and understanding, in a deeply caring personal and professional manner. Anna you have become a friend and the mentor that I will always hold in high esteem. Thank you to my committee members, Claudio DiBacco, Tetjana Ross and Paul Snelgrove for providing essential direction and advice.

I want to acknowledge and thank, Remi Daigle, Jessie Short, Stacey Henderson, Donny Ross, Ryan Stanley, Jack Foley and Janelle Hrycik for their assistance during the fieldwork phase of this study; Mark Merrimen, John Lindley, Walter Judge, Doug Shillinger, Chris Taggart and Jon Grant for providing and assisting with equipment and technical support; and Amy Roy and Ryan Horricks for help in the laboratory. I could not have completed the ADCP and CTD processing, and learned Matlab without assistance and guidance from Tetjana Ross, Keir Colbo, Brad deYoung, Marielle Lesperance, Eric Oliver, Clark Richards and Kim Davis. Thanks to faculty and staff of the Department of Oceanography for your thoughtful conversations and for sharing your wisdom.

In particular, I want to recognize my good friend, and graduate colleague Remi Daigle for his patience, cheerfulness, advice, editorial support, philosophical and scientific discussions, and for constantly being there for me, even when it wasn't his priority.

Thank you to Metaxas, Scheibling, Taggart and Grant labs (Remi, Jessie, Amy, Myriam, Megan, Alana, Shana, Kristen, Kira, Collette, Janelle, Julie, Kim, Jeff, Lindsey, Ramón) and friends from Oceanography, Biology, Earth Sciences and the climbing community, for your assistance, support, encouragement, laughter and friendship.

This research was funded by grants from the NSERC Strategic Network Canadian Healthy Oceans Network (CHONe) to Anna Metaxas and Brad deYoung, and by the National Sciences and Engineering Research Council (NSERC) Discovery Grant to Anna Metaxas. I am also grateful for the substantial financial support provided by the NSERC Canada Graduate Scholarship, and fellowships from CHONe, and the Faculty of Graduate Studies, Dalhousie University.

Finally, this accomplishment would not have been possible without the inspiration, encouragement and unwavering support of my family and friends, thank you.

CHAPTER 1

Introduction

The life cycle of many marine benthic invertebrates includes a meroplanktonic phase, and dispersal while in the plankton is an important process in regulating population dynamics (Roughgarden et al. 1994). Meroplankton reside in the water column for hours to months before settling on suitable habitat, often dispersing 10's to 1000's of km from their source population (Metaxas & Saunders 2009). This dispersive phase enables larvae of benthic parents to successfully colonize new habitats and/or maintain existing populations (Metaxas & Saunders 2009). In turn, connectivity between populations is critical for the stability, resilience and persistence of a species and their ecosystem (Roughgarden et al. 1994; Pechenik 1999; Metaxas & Saunders 2009). For management and protection (e.g. population resiliency to exploitation, understanding invasive species, establishment of marine protected areas), we need to resolve the mechanisms that regulate larval transport, retention and supply, as well as obtain accurate measures of distance travelled, and direction and frequency of dispersal. To date, modeling of dispersal and connectivity has been hindered, since the processes controlling larval transport continue to remain unresolved (Cowen et al. 2007; Pineda et al. 2007).

Meroplanktonic larvae are small (<2 mm) and weak swimmers (~1-15 mm s^{-1}), and consequently assumed to be incapable of sustained movement against mesoscale horizontal currents (Metaxas 2001). As a result, patterns in their horizontal dispersal have mainly been attributed to advection along dominant directions of flow (Metaxas 2001). However, larvae may influence the magnitude and direction of horizontal

transport by sinking or swimming between water layers of different velocities; their sinking and swimming speeds are greater than the vertical current velocities (1-2 mm s^{-1}) (Young 1995; Metaxas 2001). Laboratory studies have shown larval vertical displacement in response to a suite of abiotic (temperature, salinity, light intensity, pressure, flow regimes etc.) and biotic (food, predators, conspecifics) cues that are common in the water column (Young 1995). Some larvae also respond to cues linked to predictable periodic cycles such as tidal states, diel periods and lunar phases, and these responses can vary among ontogenetic stages (Brookins & Epifanio 1985; Young & Chia 1987; Manuel & O'Dor 1997; DiBacco et al. 2001). Currently, the relationship between horizontal advection and larval behaviour remains elusive, and the conditions under which larvae may actively regulate their depth versus passively drift are poorly understood (Metaxas & Saunders, 2009).

Most studies of larval vertical distribution and migration have focused on a single species or taxonomic group, and many have primarily focused on commercially important (crustaceans, bivalves) species. Consequently, little is known about gastropods, polychaetes, bryozoans, asteroids, and carideans. In this thesis, I extend previous knowledge significantly by examining changes in vertical distribution of several different meroplanktonic larvae in a coastal embayment during a stable period, at high temporal frequencies and spatial resolutions. In Chapter 2, I examine changes in the larval vertical distribution of 10 gastropod taxa with similar morphology and swimming abilities, but different nutritional, habitat requirements and life-history strategies. Through these comparisons, I address whether taxon-specific characteristic can be related to differences in larval distribution in the water column. In Chapter 3, I examine the vertical distribution

of 7 different taxonomic groups (gastropods, bivalves, polychaetes, bryozoans, asteroids, carideans, and brachyurans), with contrasting life-history strategies, morphologies and swimming abilities, under similar environmental conditions. I attempt to resolve factors that are important in regulating larval vertical distributions in the field, and consequent dispersal potential. Chapters 2 and 3 are intended as standalone manuscripts for publication in the primary literature. Consequently, there is some repetition among chapters, particularly in the Methods. Brad deYoung, a CHONe co-investigator, provided the processed ADCP and thermistor data, and figures of current velocities. Consequently, he is a co-author of Chapters 2 and 3. Lastly, in Chapter 4, I summarize the finding of Chapters 2 and 3, recommend areas for future investigations, and provide context for the relevance of my finding to our understanding of larval dispersal.

CHAPTER 2

Patterns in the Vertical Distribution of Larvae of Marine Benthic Gastropods in a Shallow Embayment in Nova Scotia, Canada

2.1 Abstract

The meroplanktonic phase regulates population dynamics for many marine benthic invertebrates, including gastropods. Gastropods are a diverse taxonomic class, yet little is known about the factors that affect their larval distribution and abundance. I investigated the larval vertical distribution and abundance of 10 meroplanktonic gastropod taxa (*Margarites* spp., *Crepidula* spp., *Mitrella lunata*, *Diaphana minuta*, *Littorina littorea*, *Polinices heros*, *Aporrhais occidentalis*, *Nassarius* spp., *Bittium alternatum*, Nudibranchia), with similar morphology and swimming abilities, but different adult habitats and life history strategies. I explored the role of physical and/or biological factors and periodic (lunar phase, tidal state, diel period) cycles in the field in regulating larval vertical distribution. Plankton samples were collected at 6 depths (3, 6, 9, 12, 18, 24 m) using a pump, at each tidal state over a 36- and a 25-h period, during a spring and neap tide, respectively, concurrently with measures of temperature, salinity, fluorescence (proxy for food), and current velocity. Larval vertical distributions varied among gastropod taxa: they were related to the location of the thermocline or the fluorescence maximum, and/or varied on each of the measured cycles. Larval abundance was most strongly related to temperature, except for *Littorina littorea* and *Crepidula* spp. which were most strongly related to fluorescence. All gastropod taxa, except *Polinices*

heros and *Aporrhais occidentalis,* exhibited either diel or reverse-diel vertical migration during one or both lunar phases. The key factors determining the vertical distribution of gastropod larvae were temperature, fluorescence, and light. Differences in vertical distribution may enable these larvae to partition their habitat during the dispersal phase, and expose them to a wide range of potential habitats for settlement.

2.2 Introduction

Dispersal strongly influences the distribution, abundance and survival of marine benthic invertebrates (Roughgarden et al. 1994). Meroplanktonic larvae can reside in the water column for hours to months before settling on suitable habitat, enabling them to successfully exploit new habitats and/or recolonize others (Metaxas & Saunders 2009). Most studies of larval distribution and abundance have primarily focused on commercially important (crustaceans, bivalves), invasive (tunicates, bryozoans) or model (echinoids) species (McEdward 1995).

Gastropods are a diverse class within the molluscs, occupying a wide range of habitats (e.g. rocky intertidal, mudflats, abyssal plains), filling many ecological niches (e.g. predators, grazers, suspension feeders), and following different life history strategies (Shanks 2001). Gastropod larvae exhibit a range of planktonic larval durations (days to months), and feeding (feeding, non-feeding, facultative) and developmental (direct, lecithotrophic, planktotrophic) modes (Strathmann 1987; Shanks 2001), and likely exhibit a variety of behaviours (Young 1995). Such taxon-specific characteristics enable these gastropods to utilize a variety of strategies as plankton. For growth and survival,

they must swim, feed (in some species), and defend against predators (Pechenik 1987). After dispersal, they locate suitable habitat for settlement (Chia & Young 1987). For example, larvae found deeper in the water column are more likely to be retained near source populations, because of weaker currents at depth. Thus, contrasting requirements by the different larval taxa may result in variation in distributional range in the water column to maximize survival, growth and settlement rates. However, little is known about the patterns in larval distribution and abundance of gastropods in the plankton.

Many meroplanktonic larvae alter their vertical position, through changes in buoyancy and/or by ciliary or muscular activity, in response to abiotic (temperature, salinity, pressure, gravity, currents, light, turbulence) and biotic (predators, food, conspecifics) cues (Young 1995). Sensory detection of these cues can affect larval direction of movement and swimming behaviour (acceleration, deceleration, cessation). For example in Sevastopol Bay (Black Sea), gastropod larvae responded to the absence of light by swimming upwards (Petipa 1955 in Russian, as cited in Mileikovsky 1973). Gastropod larvae have the physiological capabilities to detect many of these cues (odour, light, temperature, salinity, pressure and gravity) (Kingsford et al. 2002), however, their behavioural responses to these cues are mostly unknown.

Physical (thermoclines, haloclines, pycnoclines) and biological (food patches) discontinuities in the water column can affect larval vertical distribution (Tremblay & Sinclair 1990b; Raby et al. 1994; Metaxas & Young 1998; Sameoto & Metaxas 2008a, b; Daigle & Metaxas in press). For example, thermoclines, haloclines and pycnoclines often restrict bivalve larvae to a particular layer (Tremblay & Sinclair 1990b; Gallager et al. 1996) due to changes in buoyancy. Alternatively, larvae may actively alter their position

in response to stratification (Metaxas, 2001). Bivalve and echinoderm larvae have also been observed to aggregate around the chlorophyll (food) maxima (Raby et al. 2004; Metaxas & Young 1998), unless prevented by a physical discontinuity (Gallager et al. 1996; Metaxas & Young 1998). However, the effect of discontinuities on gastropod larval distribution remains unknown.

Some meroplanktonic taxa appear to respond to cues linked to predictable periodic cycles such as tidal states, diel periods and/or lunar phases. Some taxa (most notably crustaceans) vertically migrate in relation to tidal changes, possibly to enhance their transport away from estuaries and nearshore areas, and to return for settlement (DiBacco, et al. 2001; Young 1995). Many larvae respond to diel cues, exhibiting either a diel (towards the surface at night and deeper waters during the day) or a reverse-diel migration pattern (Daro 1974; Forward 1988; Pennington & Emlet 1986; Garland et al. 2002; Poulin et al. 2002). Lastly, some larvae respond to lunar cues, which are generally linked to light intensity and/or tidal and diel cues (Manuel & O'Dor 1997; Manuel et al. 1997). The response of larval gastropods to changes in tidal state and lunar phases is unknown, and only a few studies have documented their diel vertical migration in the field; in these studies however, the direction of migration varied among species (Daro 1974; Petipa 1955 in Russian, as cited in Mileikovsky 1973; Garland et al. 2002; Poulin et al. 2002).

This study describes changes in the vertical distribution of larval gastropods relative to changes in the structure of the water column in St. George's Bay, Nova Scotia, Canada, over a 36- and a 25-h period, during a spring (full moon: 6-7 Aug 2009) and neap (quarter moon: 12-13 Aug 2009) tide. Specifically, I examined whether changes in

larval vertical distribution varied: 1) with a suite of physical (temperature, salinity, current velocities, turbulence) and biological (fluorescence as proxy for food) factors; and 2) over predictable cycles (lunar phase, diel period, and tidal state). By examining changes in larval vertical distribution for a variety of taxa with similar morphology and swimming abilities, but different nutritional and habitat requirements and life-history strategies, I can address whether taxon-specific characteristics relate to differences in larval distributions in the water column.

2.3 Materials and Methods

2.3.1 Study Site

The study was conducted in St. George's Bay, Nova Scotia, Canada (45°46' N, 51°43' W), a coastal embayment on the Northumberland Strait that is approximately 45 x 45 km. The tides in St. George's Bay are weak mixed diurnal/semidiurnal, with a tidal range from MHHW to MLLW of ~1.5 m (Canadian Hydrographic Service**)**. The mean circulation in St. George's Bay is mainly clockwise, and only occasionally counter clockwise, and is hydrographically stable in the centre of the gyre (Petrie & Drinkwater 1974). Generally in the summer, the bay is vertically stratified, with a thermocline occurring at ~10 m until October when mixing occurs (Petrie & Drinkwater 1974). A single sampling location was used on the west side of the bay (45.78°N, 61.80°W; depth = 25 m).

2.3.2 Sampling of Physical Characteristics

Temperature, salinity, pressure, fluorescence, and current velocities [vertical (*w*), North-South (*v*) and East-West (*u*)] were measured in the water column, averaged to 1 m depths from 1 to 23-25 m depth, with a Seabird 25 Conductivity-Temperature-Depth (CTD) recorder, a SCUFA fluorometer and an RDI Acoustic Doppler Current Profiler (ADCP) with a chain of VEMCO thermistors, respectively. Two CTD casts were made every 2-h over a 36- (6-7 Aug) and a 25-h (12-13 Aug) sampling period, associated with the plankton sampling (see below). At the beginning of each plankton sampling time, temperature, salinity, pressure and fluorescence were measured with the first CTD cast. The CTD was attached to the pump intake, allowing for a second cast for temperature and pressure measurements concurrent with plankton sampling. Some malfunctioning of the CTD and the SCUFA fluorometer resulted in incomplete data sets. The ADCP was moored on the seafloor, and sampled over 1 m depth bins from just above the bottom to just below the surface, every 20 min from 11 Jul to 22 Aug 2009. The thermistors were attached to the ADCP mooring and distributed throughout the water column, approximately every 3 m from 3 to 24 m depth. Light intensity was measured at the sea surface at the beginning of each plankton sampling time with a LI-COR Terrestrial Quantum Sensor (LI-190SA).

2.3.3 Plankton Sampling

On 6-7 and 12-13 Aug 2009, plankton samples were collected with a cast iron, high volume (~0.85 $m^3 min^{-1}$), 7.6-cm diameter portable trash pump (Gorman-Rupp: Model 3S5HCR) with a two-vane semi-open, 3.2-cm solid handling impeller and a 7.6-

cm diameter, 27-m length hose, a T-shaped intake head and a 5-m discharge hose. The discharge from the pump was directed into a submerged 200-μm mesh plankton net to prevent damage to the larvae. Volume flow rates were determined by measuring the time required to fill a known volume at each sampling depth (e.g. 0.94 and 0.75 m^3 min^{-1}, at 3 and 24 m respectively), and used to standardize plankton abundance per unit volume. While sampling, the intake was moved vertically through a depth interval of ~1 m, for 5 min for a sample volume of ~4.4 m^3. Plankton were sampled at 3, 6, 9, 12, 18 and 24 m every 2-h (10:00, 12:00, 14:00, 16:00, 18:00, 20:00, 22:00, 00:00, 02:00, 04:00, 06:00, 08:00), over a period of ~36- (6-7 Aug) or 25-h (12-13 Aug). The net and codend were washed down with filtered seawater to concentrate larvae for preservation, and samples were preserved in 90% ethanol. Prior to sampling, water was pumped for a minimum of 2 min to clear the hose.

2.3.4 CTD Data Processing

For each CTD cast, only data collected during the down-casts were used and any outliers in temperature, salinity and fluorescence were removed using a moving average. Temperature measurements were averaged between the two casts (before and during plankton sampling), unless the CTD failed to record during one of the casts. Temperature, salinity and fluorescence were averaged into 1-m depth bins, and density (σ_t, kg m^{-3}-1000) calculated for each depth using the 'swstate' function in Matlab 7.1 (The Mathworks Co.) for each sampling time. Vertical temperature gradients for each sampling time were calculated as $\Delta T/\Delta z$, where T is temperature (°C) and z is depth (m), at 1 m intervals. For each sampling time, the depth of the thermocline, in a vertically

stratified water column, was identified as the depth where the vertical temperature gradient over 1 m was >0.54°C m^{-1}; and the depth of fluorescence maximum was where the maximum fluorescence value was recorded.

2.3.5 ADCP Data Processing

For both the ADCP and thermistor data, missing or unreliable data were either replaced by linearly interpolated values from surrounding points if there were sufficient data (typically 1-2 points) or were removed entirely. The ADCP current data from the upper 1 m of the water column were discarded due to backscatter effects. The current velocity and the temperature data were filtered using a 5thorder forward-and-reverse Butterworth lowpass digital filter, with a cut-off frequency of 2-h. The Richardson number for each sampling time was calculated as

$$Ri = \frac{N^2}{(\frac{\partial U}{dz})^2}$$

where

$$\frac{\partial U}{dz} = \left(\frac{\partial u}{dz}\right)^2 + \left(\frac{\partial v}{dz}\right)^2$$

[N^2 = buoyancy frequency, z = depth, u = North-South velocity, v = East-West velocity, U = scale for horizontal velocity]. To calculate density, the 'polyfit' function in Matlab 7.1 (The Mathworks Co.) was used to determine the relationship between temperature and salinity from the CTD casts; density was extrapolated from the thermistor data.

2.3.6 Plankton Sample Processing

In the laboratory, plankton were sorted, identified to the lowest possible taxon, and enumerated, using a Nikon SMZ 1500 dissecting microscope. Plankton samples were serially divided using a Folsom plankton splitter (Wildlife Supply Company), and sub-samples (down to 1/16, depending on larval abundance) sorted until the smallest of either 50 larvae of each taxa or the entire sample was counted. For each taxon at each sampling time and depth for both periods, larval abundance was calculated and standardized to number of larvae m^{-3}. Also, the vertical distribution for each taxon at each sampling time was characterized using mean depth distribution (MDD) calculated for each sampling time *j* as the weighted average:

$$MDD_j = \frac{1}{N_j} \sum_{i=1}^{n} z_i \, n_{ij}$$

where z_i = mean depth of interval *i*, n_{ij} = number of larvae collected at depth *i* at sampling time *j*, and N_j = total number of larvae sampled at sampling time *j* (Tapia et al. 2010). For each larval taxon, the MDD reflects the larval concentration at the mean depth of any given profile. Lastly, the proportional abundance was calculated at each depth interval (3, 6, 9, 12, 18 or 24 m) for each sampling time *j* using

$$P_{ij} = \frac{n_{ij}}{N_j}$$

where P_{ij} = proportional abundance at depth interval *i* at time j, n_{ij} = number of larvae collected at depth *i* at sampling time *j*, and N_j = total number of larvae sampled at sampling time *j*. The proportional abundance was used to standardize larval concentrations for each taxon within and among sampling periods.

2.3.7 Statistical Analysis

I examined changes in the vertical distributions of larvae in response to lunar phase, diel period and tidal state, as manifested by the interaction terms between depth and either diel period, lunar phase or tidal state, respectively. Samples taken at different sampling times were pooled into two diel categories (day and night), and four tidal categories (ebb, flood, high, low). Based on sunset and sunrise times published by Environment Canada, I identified 18 day (8:00, 10:00, 12:00, 14:00, 16:00, 18:00) and 6 night (22:00, 00:00, 02:00) samples for both sampling periods combined. Samples collected at transition times were excluded (dusk: 20:00 and dawn: 4:00, 6:00). There were 10 ebb (decreasing tidal height), 9 flood (increasing tidal height), 6 high tide, and 6 low tide samples for both sampling periods combined, as inferred from published tidal heights. Because there were not enough replicates to test the effects of all four factors (depth, tidal state, diel period, and lunar phase), I simultaneously performed, two 3-way analyses of variance (ANOVA) followed by Tukey's HSD post hoc tests to test the effects on proportional larval abundance of (1) lunar phase, diel period and depth; and (2) lunar phase, tidal state and depth. Also, student's t-test was used to examine the effect of Richardson number (stable: $Ri > 0.25$ or unstable: $Ri < 0.25$) on the proportional abundance of each gastropod taxon. The relationship between temperature [correlated to salinity and density (see Appendix A)], fluorescence, w, v and u, and the proportional larval abundance were examined with simple and multiple (backward stepwise) regressions. Because the proportionality data failed to meet the assumptions of normality and heterogeneity, as determined by examining the residuals, proportional larval abundances were arcsine square root transformation. The relationships between the

depths of the thermocline and maximum fluorescence, tidal height, and light levels, with larval MDD were also examined with simple and multiple (backward stepwise) regressions. Given the large number of comparisons and statistical tests, an α-value of 0.01 was used as an indicator of non-significance. All statistical analyses were conducted with SPSS 17.0.

2.4 Results

2.4.1 Physical Structure of the Water Column

The structure of the water column remained relatively constant at the sampling station across the sampling period on both dates (Fig. 2.1). The temperature generally ranged between ~20°C at the surface and ~4°C at 25 m, and salinity ranged between 29 and 31 (Fig. 2.1). The water column was stratified, with the thermocline located at ~10-17 m (Fig. 2.1). Fluorescence ranged between 0.09 and 0.35, peaking between 13 and 18 m depth (Fig. 2.1). Overall, no clear circulation pattern was detected in summer of 2009 (11 Jul to 22 Aug), and mean currents within St. George's Bay were variable and tended to be depth-dependent (Lesperance et al. 2011; Chapter 3). In general, mean current velocity was 5 times stronger in the mixed layer than at 20 m over the 43-d period at my sampling site, and flowed to the southwest and east, respectively (Lesperance et al. 2011; Chapter 3). The horizontal current velocities were relatively weak (<150 mm s^{-1}), but were stronger during the full moon than the quarter moon (Fig. 2.1). These velocities changed direction during shifts in tidal state, but the shift was lagged among depths. The vertical velocities were weak (most <2 mm s^{-1}) and variable, and patterns were likely due

to noise (Fig. 2.1). Based on the Richardson numbers, there was potential for instability ($Ri < 0.25$) in the mixed layer of the water column, resulting in turbulent conditions (Fig. 2.1). Below the thermocline, the water remained in a relatively stable state ($Ri > 0.25$).

2.4.2 General Trends in the Abundance of Gastropods

I identified 10 taxa of gastropods (*Margarites* spp., *Crepidula* spp., *Mitrella lunata*, *Diaphana minuta*, *Littorina littorea*, *Polinices heros*, *Aporrhais occidentalis, Nassarius* spp., *Bittium alternatum*, and Nudibranchia), and of these *Margarites* spp. was the most abundant, comprising of 51-55% of total numerical abundance. The next 3 numerically dominant taxa were *Crepidula* spp., *M. lunata* and *D. minuta* (5-17%), while the remaining taxa comprised < 3% of total abundance. Although, the proportional abundance of each taxon remained relatively similar, larval concentration changed between sampling periods (Fig. 2.2). The concentration of *Margarites* spp., *D. minuta*, *A. occidentalis*, *Nassarius* spp. and Nudibranchia increased between sampling periods, whereas that of *Crepidula* spp., *M. lunata*, *P. heros*, *L. littorea* and *B. alternatum* concentrations remained relatively unchanged (Fig. 2.2).

2.4.3 Patterns in Vertical Distribution in Relation to Features in the Water Column

The larvae were not uniformly distributed over the water column (Fig. 2.3). *Margarites* spp. was present throughout the water column, but the greatest proportion was below the thermocline (Fig. 2.3). *Littorina littorea, Polinices heros* and Nudibranchia were mostly found below the thermocline, and *Aporrhais occidentalis,*

Nassarius spp. and *Bittium alternatum* above the thermocline (Fig. 2.3). Lastly, the greatest proportions of *Crepidula* spp., *Mitrella lunata* and *Diaphana minuta* was near the thermocline (12m) (Fig. 2.3). *L. littorea* was the only gastropod species to be found in highest proportions around the fluorescence maximum at 18 m (Fig. 2.3).

The vertical distributions of most gastropods were related (linearly) to temperature, salinity and density, except *Littorina littorea* (Fig. 2.3a, Table 2.1 & Appendix B). The abundances of *Margarites* spp., *Polinices heros* and Nudibranchia were negatively related to temperature (Table 2.1), whereas that of *Crepidula* spp., *Mitrella lunata*, *Diaphana minuta*, *Aporrhais occidentalis*, *Nassarius* spp. and *Bittium alternatum* were positively related to temperature (Table 2.1). The opposite pattern was recorded for salinity and density, which correlated significantly with temperature (Appendix A). The abundance of *L. littorea* showed a quadratic relationship with temperature, which was stronger than the linear one, with abundance low at both low and high temperatures [adj. $R^2 = 0.583$, $F_{(2,160)} = 114.2$, $p < 0.001$].

The vertical distributions of several taxa (*Crepidula* spp., *Mitrella lunata*, *Diaphana minuta*, *Littorina littorea*, and *Polinices heros*) were linearly related to fluorescence, which reflects a potential food source; however, a large proportion of variance in abundance was explained by fluorescence only for *Crepidula* spp. and *L. littorea* (Fig. 2.3b, Table 2.1 & Appendix B). The abundance of *Margarites* spp. and Nudibranchia showed significant, although weak, quadratic relationships with fluorescence, where abundance was higher at both low and high fluorescence [*Margarites* spp.: adj. $R^2 = 0.177$, $F_{(2,98)} = 11.77$ $p < 0.001$; and Nudribranchia: adj. $R^2 = 0.228$, $F_{(2,98)} = 10.71$, $p < 0.001$].

Unlike temperature (salinity and density) and fluorescence, current (*u*, *v*, *w*) velocity only accounted for a small percentage (0-5%) of the variation observed in larval abundance. The abundance of *Mitrella lunata* was negatively related to *u*, and the abundance of *Diaphana minuta* was positively related to *w* (Table 2.1 & Appendix B).

In some cases, a larger proportion of the variance in larval abundance was explained when a combination of factors (temperature, fluorescence, *w* and *u*) was examined (Table 2.1). Of all gastropod taxa, only the variation in the abundance of *Crepidula* spp., *Littorina littorea* and *Polinices heros* was better explained by a combination of temperature and fluorescence (Table 2.1).

The stability of the water column could potentially affect larval vertical distribution, particularly in the mixed layer (3-12 m), where instabilities ($Ri < 0.25$) occurred intermittently throughout the two sampling periods. For *Margarites* spp., *Littorina littorea*, *Polinices heros*, and Nudibranchia, the highest proportional abundance occurred where the water column was stable ($Ri > 0.25$), whereas the opposite was the case for *Nassarius* spp. and *Bittium alternatum* (Table 2.2). The stability of the water column had no effect on the proportional abundance of *Crepidula* spp., *Mitrella lunata*, *Diaphana minuta* and *Aporrhais occidentalis* (Table 2.2).

2.4.4 Patterns in Weighted Mean Vertical Distributions

Mean depth distributions (MDD) were significantly linearly related to the light intensity, and the depths of thermocline and the fluorescence maximum, but only for a few taxa (Fig. 2.4 & Appendix C). No relationships were recorded with either tidal height or the change in tidal height. Specifically, the MDD of *Mitrella lunata* and *Diaphana*

minuta was negatively related to light intensity [*M. lunata*: adj. $R^2 = 0.240$, $F_{(1,27)} = 9.844$, $p = 0.004$; and *D. minuta*: adj. $R^2 = 0.200$, $F_{(1,27)} = 7.986$, $p = 0.009$] (Fig. 2.4). The MDD of *Bittium alternatum* was positively related to the depth of the thermocline [adj. $R^2 = 0.235$, $F_{(1,26)} = 9.291$, $p = 0.005$] (Fig. 2.4). Lastly, the MDD of *Margarites* spp. and Nudibranchia were negatively related to the depth of the fluorescence maximum [*Margarites* spp: adj. $R^2 = 0.425$, $F_{(1,17)} = 12.818$, $p =0.003$; and Nudibranchia: adj. $R^2 = 0.534$, $F_{(1,17)} = 19.342$, $p =0.001$] (Fig. 2.4).

2.4.5 Periodicity in Larval Vertical Distribution

The vertical distribution of most taxa varied periodically with lunar phase and/or diel period, but not with tidal state. Lunar phase influenced the distributions of all gastropod taxa (Fig. 2.5, 2.6), except *Margarites* spp. and *Aporrhais occidentalis*. In addition, the distributions of all gastropod taxa varied dielly (Fig. 2.5), except *Polinices heros*, *Aporrhais occidentalis*, and *Bittium alternatum*. Some taxa exhibited a diel or reverse-diel vertical migration during one lunar phase, but not both.

In general, *Margarites* spp., Nudibranchia and *Crepidula* spp. appeared to exhibit diel vertical migration during one or both lunar phases (Fig. 2.5). The highest proportion of *Margarites* spp. was found at 24 m during the day and between 12-18 m at night (Fig. 2.5 & Table 2.3, 2.4). Even though the vertical distribution of *Margarites* spp. did not vary significantly with lunar phase, a higher proportion of *Margarites* spp. occurred at 24 m at night during the quarter moon than the full moon (Fig. 2.5). The highest proportions of Nudibranchia occurred at 24 m in the daytime and at 18 m at night, during the full moon, but there was no diel period difference during the quarter moon (Fig. 2.5 & Table

2.3, 2.4). For *Crepidula* spp., the highest proportions occurred at 12-18 m in the daytime and at 9 m at night, during the full moon; but during the quarter moon, the highest proportion occurred at 12 m, both at day and night (Fig. 2.5 & Table 2.3, 2.4).

The vertical distribution of *Mitrella lunata*, *Nassarius* spp., and *Diaphana minuta* varied with both the lunar phase and diel period (Fig. 2.5), exhibiting a reverse-diel migration during one lunar phase, but not both. *M. lunata* were deeper (12 m) at night than in the daytime (3-6 m) during the quarter moon, but did not significantly alter their vertical position during the full moon (Fig. 2.5 & Table 2.3, 2.4). Similarly, *Nassarius* spp. was most abundant between 3 and 6 m during the day and 9 and 18 m at night, but only during the quarter moon (Fig. 2.5 & Table 2.3, 2.4). *D. minuta* were more abundant at 3-6 m during the day and 9-12 m at night during the full moon, but during the quarter moon more abundant at 12 m at night and day (Fig. 2.5 & Table 2.3, 2.4). *D. minuta* were also deeper (12 m) at night during the quarter moon than during the full moon (~9 m). The vertical distribution of *Bittium alternatum* appeared to vary with diel period (Fig. 2.3), although the interaction between diel period and depth factors was not significant ($p = 0.046$) (Fig. 2.5 & Table 2.3, 2.4). This species was most abundant at 3-6 m during the day and at 12 m at night during the quarter moon, while, during the full moon, they were most abundant at 3 m during the day and 6 m at night (Fig. 2.5 & Table 2.3, 2.4).

Although the vertical distribution of *Littorina littorea* varied periodically with both the lunar phase and diel period (Fig. 2.5), abundance was consistently greatest at 18 m. During the full moon, *L. littorea* were mostly found at 18 m during the day, but at night their vertical distribution was more even above and below this depth (Fig. 2.5 &

Table 2.3, 2.4). During the quarter moon, *L. littorea* were most abundant at 12 and 18 m in the daytime, and at 18 m at night.

Only the vertical distribution of *Polinices heros* and *Bittium alternatum* varied with lunar phase (Fig. 2.6). For *P. heros*, the highest proportions were found at 18 m for both lunar phases; however, larvae of this species were more abundant at 24 m during the full moon than during the quarter moon (Table 2.3, 2.4, 2.5). In comparison, *B. alternatum* were found slightly deeper (3, 6, and 12 m) in the water column during the quarter moon than the full moon (3-6 m) (Table 2.3, 2.4, 2.5).

Margarites spp. was the only gastropod taxon whose vertical distribution varied with tidal state (Fig. 2.7), although the interaction between tidal state and depth factors was not significant ($p = 0.020$) (Table 2.5a). *Margarites* spp. was most abundant at 24 m during the ebb, and slightly shallower (<24 m) during the flood, low and high tides (Table 2.5b).

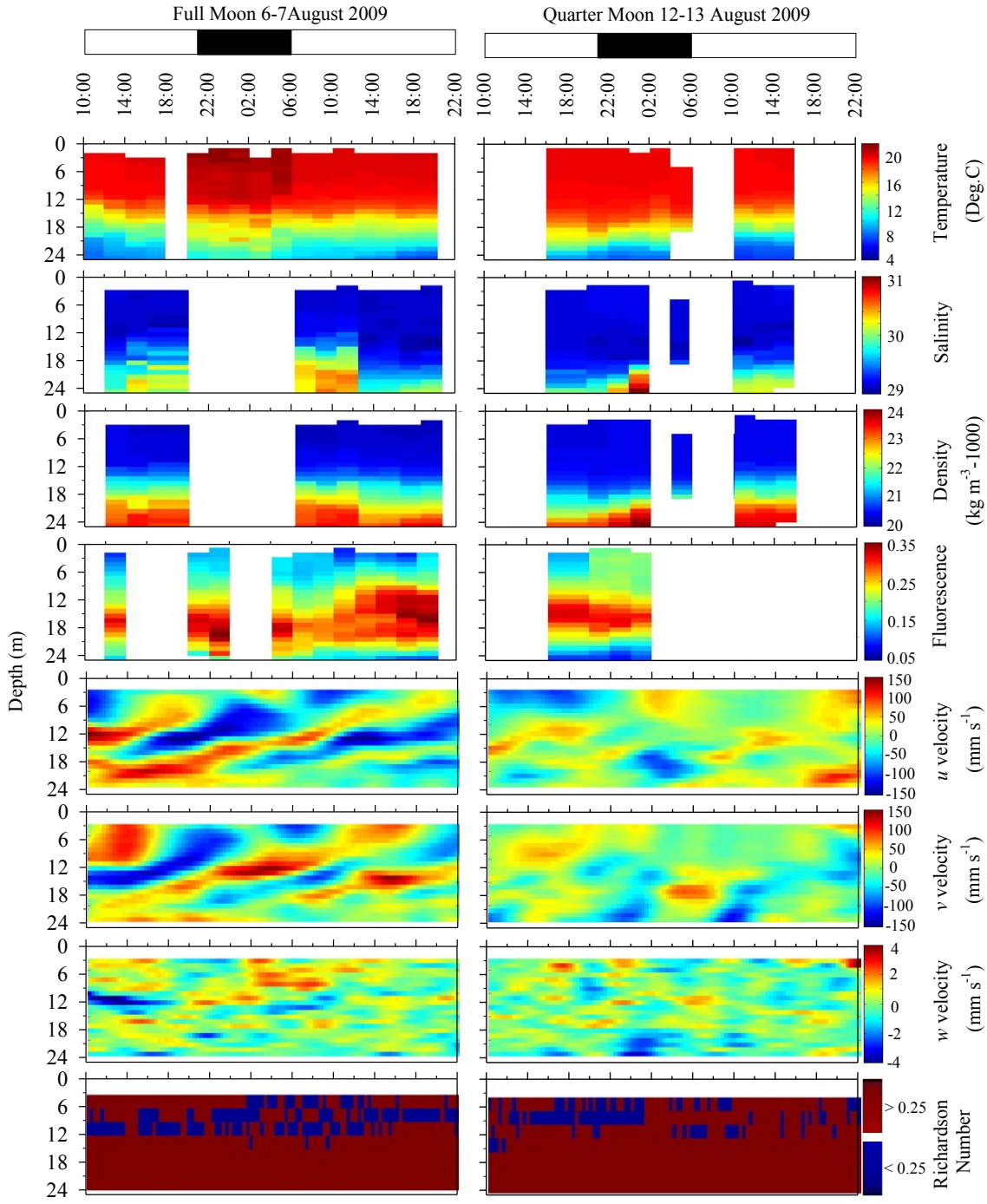


Figure 2.1 Time series of the physical and biological variables measured at a single station (z = 25 m) in St. George's Bay, Nova Scotia, Canada, over a 36- and 25-h period, during a spring (full moon: 6-7 Aug 2009) and neap (quarter moon: 12-13 Aug 2009) tide, respectively. CTD casts were made every 2-h, and an ADCP moored on the sea floor sampled every 20 min (see Methods for details).

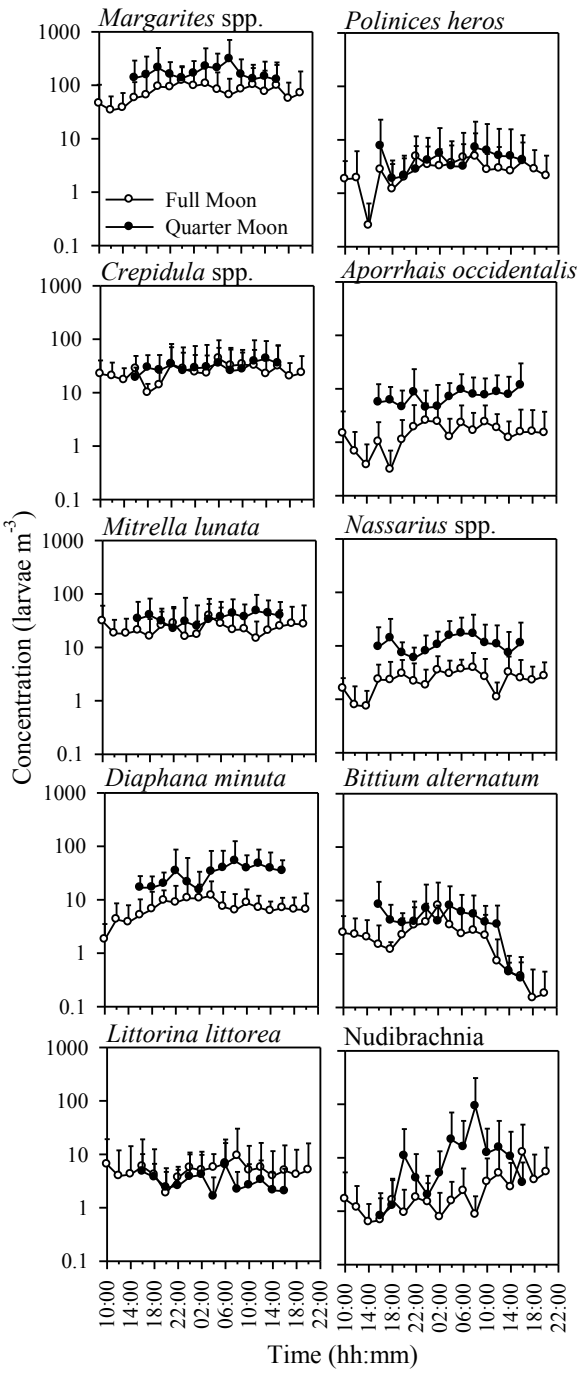
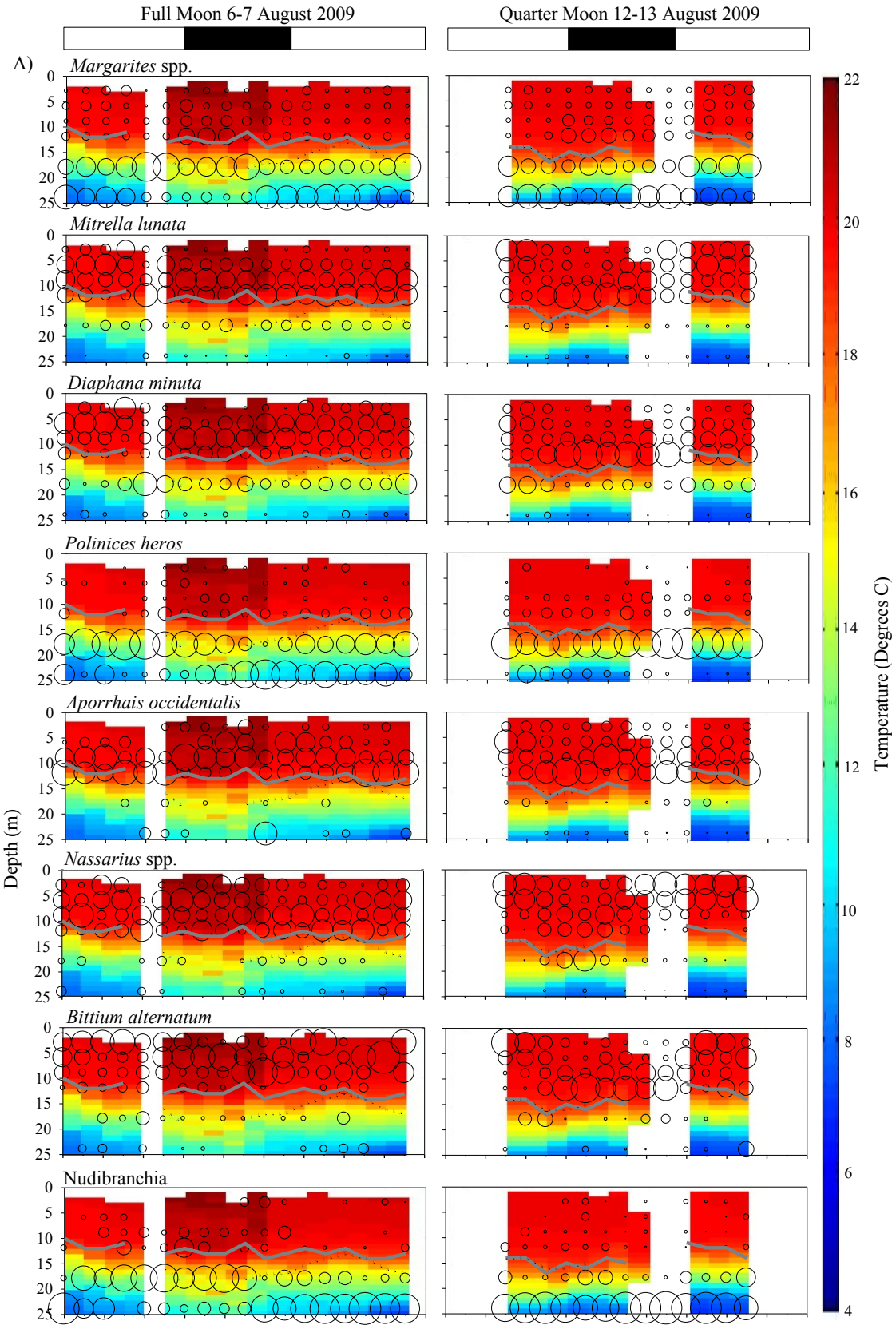


Figure 2.2 Concentrations (mean ± SD, n = 6) of all identified taxa of gastropods in St. George's Bay, Nova Scotia, Canada, over a 36- and a 25-h sampling period, during a spring (full moon: 6-7 Aug 2009) and neap (quarter moon: 12-13 Aug 2009) tide, respectively.


Full Moon 6-7 August 2009
Quarter Moon 12-13 August 2009
A)
Margarites spp.
Mitrella lunata
Diaphana minuta
Polinices heros
Aporrhais occidentalis
Nassarius spp.
Bittium alternatum
Nudibranchia
Depth (m)
0
5
10
15
20
25
Temperature (Degrees C)
22
20
18
16
14
12
10
8
6
4

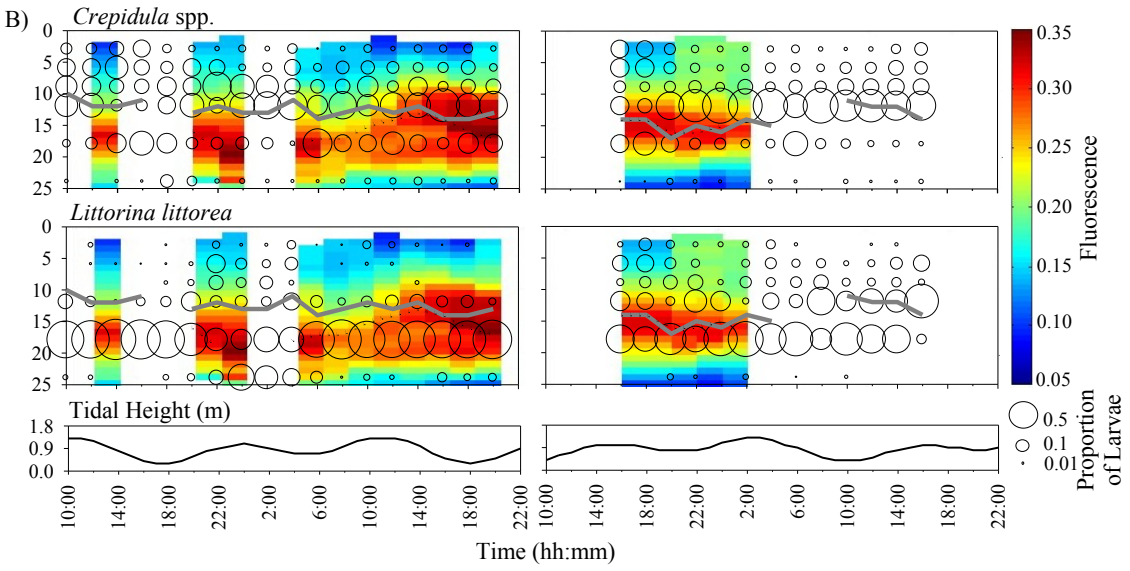


Figure 2.3 Vertical distribution of all identified gastropod taxa, in St. George's Bay, Nova Scotia, Canada, over a 36- and 25-h period, during a spring (full moon: 6-7 Aug 2009) and neap (quarter moon: 12-13 Aug 2009) tide, respectively. Circle size indicates the proportional abundance of larvae for a particular sampling time. ⎯ = thermocline, and ●●● = fluorescence maximum, □ = day and ■ = night. The colored contours represent either A) temperature (*Margarites* spp., *Mitrella lunata*, *Diaphana minuta*, *Polinices heros*, *Aporrhais occidentalis*, *Nassarius* spp., *Bittium alternatum* and Nudibranchia), and B) fluorescence (*Crepidula* spp. and *Littorina littorea*). Only the dominant factors are shown for each gastropod taxon, as determined by simple linear regressions.

Table 2.1 Results of simple and multiple (backwards stepwise) linear regression explaining patterns in the larval abundance of different gastropod taxa in relation to different physical and biological variables. T = temperature, S = salinity, ρ = density, F = fluorescence, w = vertical velocity, v = North-South velocity, u = East-West velocity; -/ + = negative or positive relationship; N.S. = not significant ($p > 0.01$); df for each regression are shown in parentheses below each factor.

		Simple Regression							**Multiple Regression**		
Taxon		***T*** (1,161)	***S*** (1,114)	***ρ*** (1,114)	***F*** (1,99)	***w*** (1,153)	***v*** (1,153)	***u*** (1,153)			
Margarites spp.	direction	-	+	+	N.S.	N.S.	N.S.	N.S.	*T* (1,161)	adj. R^2	0.586
	adj. R^2	0.586	0.503	0.717						F-value	230.1
	F-value	230.1	117.3	292.0						p-value	<0.001
	p-value	<0.001	<0.001	<0.001							
Crepidula spp.	direction	+	-	-	+	N.S.	N.S.	N.S.	*T,F* (2,98)	adj. R^2	0.381
	adj. R^2	0.152	0.126	0.117	0.300					F-value	31.78
	F-value	30.07	17.54	16.21	43.85					p-value	<0.001
	p-value	<0.001	<0.001	<0.001	<0.001						
Mitrella lunata	direction	+	-	-	+	N.S.	N.S.	-	*T,F,u* (3,81)	adj. R^2	0.312
	adj. R^2	0.386	0.305	0.397	0.099			0.050		F-value	13.681
	F-value	102.7	51.46	76.68	12.03			9.100		p-value	<0.001
	p-value	<0.001	<0.001	<0.001	0.001			0.003			
Diaphana minuta	direction	+	-	-	+	+	N.S.	N.S.	*T,F,w* (3,81)	adj. R^2	N.S.
	adj. R^2	0.231	0.322	0.314	0.087	0.037				F-value	
	F-value	49.57	55.63	53.70	10.51	6.871				p-value	
	p-value	<0.001	<0.001	<0.001	0.002	0.010					
Littorina littorea	direction	-	N.S.	+	+	N.S.	N.S.	N.S.	*T,F* (2,98)	adj. R^2	0.514
	adj. R^2	0.054		0.051	0.408					F-value	53.894
	F-value	10.21		7.171	69.93					p-value	<0.001
	p-value	0.002		0.009	<0.001						

Taxon		Simple Regression							Multiple Regression		
		T (1,161)	***S*** (1,114)	***ρ*** (1,114)	***F*** (1,99)	***w*** (1,153)	***v*** (1,153)	***u*** (1,153)			
Polinices heros	direction	-	+	+	+	N.S.	N.S.	N.S.	*T,F* (2,98)	adj. R^2	0.562
	adj. R^2	0.330	0.151	0.324	0.088					F-value	65.054
	F-value	80.84	21.48	56.23	10.62					p-value	<0.001
	p-value	<0.001	<0.001	<0.001	0.002						
Aporrhais occidentalis	direction	+	-	-		N.S.	N.S.	N.S.	N.S.	*T* (1,161)	adj. R^2	0.235
	adj. R^2	0.235	0.190	0.234						F-value	50.79
	F-value	50.79	28.01	36.13						p-value	<0.001
	p-value	<0.001	<0.001	<0.001							
Nassarius spp.	direction	+	-	-		N.S.	N.S.	N.S.	N.S.	*T* (1,161)	adj. R^2	0.451
	adj. R^2	0.451	0.306	0.430						F-value	133.9
	F-value	133.9	51.62	87.84						p-value	<0.001
	p-value	<0.001	<0.001	<0.001							
Bittium alternatum	direction	+	-	-		N.S.	N.S.	N.S.	N.S.	*T* (1,161)	adj. R^2	0.265
	adj. R^2	0.265	0.129	0.203						F-value	59.56
	F-value	59.56	17.98	30.38						p-value	<0.001
	p-value	<0.001	<0.001	<0.001							
Nudibranchia	direction	-	+	+		N.S.	N.S.	N.S.	N.S.	*T* (1,161)	adj. R^2	0.693
	adj. R^2	0.693	0.632	0.753						F-value	366.9
	F-value	366.9	198.7	351.2						p-value	<0.001
	p-value	<0.001	<0.001	<0.001							

Table 2.2 Results of Student's t-test examining the effect of Richardson number (unstable: $Ri < 0.25$, stable: $Ri > 0.25$) on the proportional abundance (arcsine square root transformed) for all gastropod taxa ($p < 0.01$, indicated in bold).

Taxon	Unstable		Stable		t-test			Conclusions
	Mean	SD	Mean	SD	t	df	p	
Margarites spp.	13.89	4.85	24.06	12.95	-8.198	156.7	**< 0.001**	Unstable < Stable
Crepidula spp.	20.47	8.04	22.07	13.71	-0.920	94.82	0.360	Unstable = Stable
Mitrella lunata	24.28	9.97	20.54	13.70	1.882	73.69	0.064	Unstable = Stable
Diaphana minuta	22.93	10.12	21.39	12.82	0.682	184.0	0.496	Unstable = Stable
Littorina littorea	7.98	7.99	21.92	20.35	-6.569	150.5	**< 0.001**	Unstable < Stable
Polinices heros	5.88	6.49	21.95	20.78	-8.003	175.7	**< 0.001**	Unstable < Stable
Aporrhais occidentalis	23.47	12.97	18.58	17.02	1.921	70.25	0.059	Unstable = Stable
Nassarius spp.	30.61	8.70	18.45	13.63	6.704	85.59	**< 0.001**	Unstable > Stable
Bittium alternatum	28.62	17.95	17.73	15.73	3.666	184.0	**< 0.001**	Unstable > Stable
Nudibranchia	5.64	7.55	20.92	22.70	-6.834	170.3	**< 0.001**	Unstable < Stable

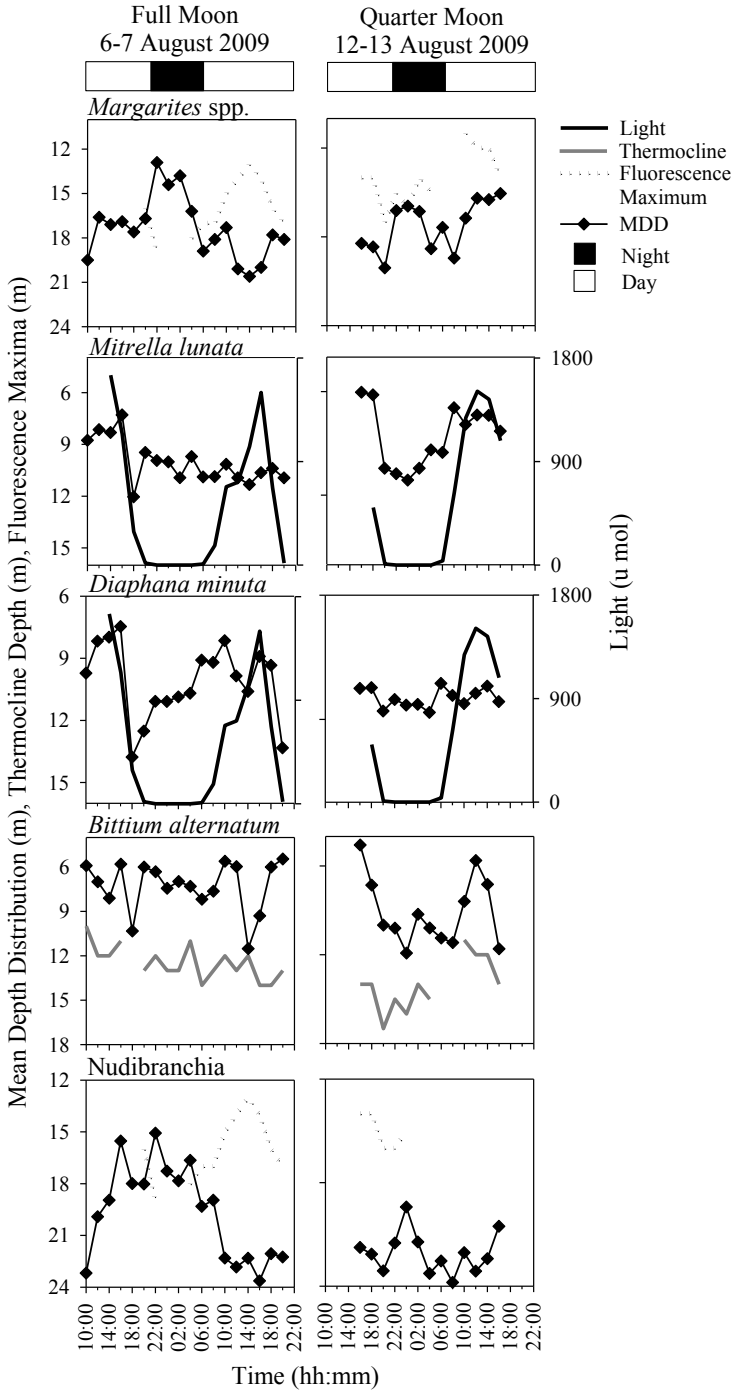


Figure 2.4 Temporal patterns in larval mean depth distribution (MDD) of *Margarites* spp., *Mitrella lunata*, *Diaphana minuta, Bittium alternatum*, and Nudibranchia, in St. George's Bay, Nova Scotia, Canada, over a 36- and 25-h sampling period, during a spring (full moon: 6-7 Aug 2009) and neap (quarter moon: 12-13 Aug 2009) tide, respectively. Patterns in depths of thermocline and fluorescence maximum, and light intensity are also shown. Only factors that are significant are shown.

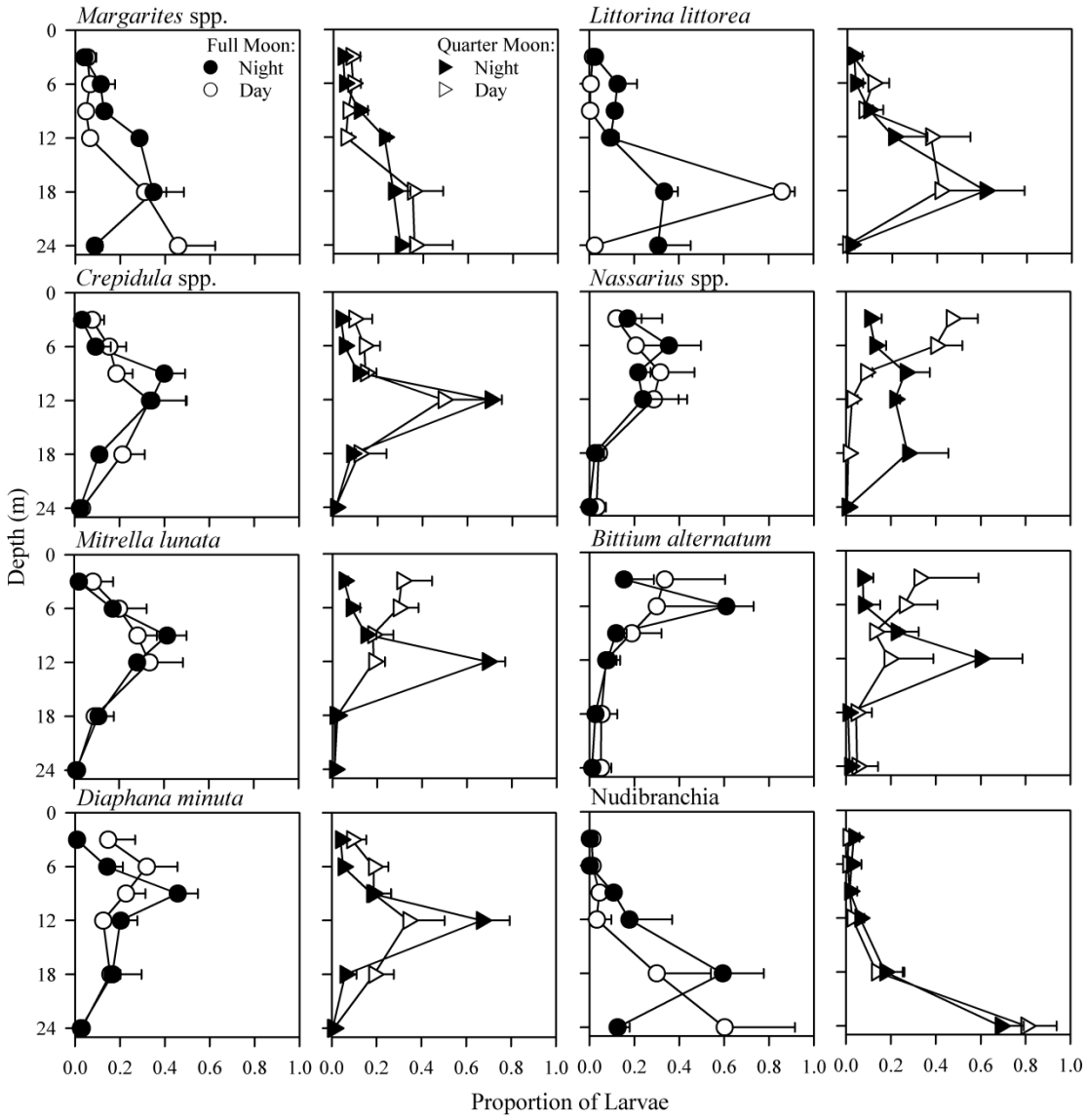


Figure 2.5 Larval vertical distribution of gastropod taxa, at each of 2 diel periods and 2 lunar phases (mean ± SD, n = 3 to 11) in St. George's Bay, Nova Scotia, Canada.

Table 2.3 Results of Analysis of Variance (ANOVA) examining the effect of lunar phase (full moon, quarter moon), diel period (day, night), and depth (3, 6, 9, 12, 18, 24 m) on the proportional abundance (arcsine square root transformed) for all gastropod taxa ($p < 0.01$, indicated in bold).

Taxon	**Source**	**Lunar Phase (*L*)**	**Diel Period (*D*)**	**Depth (*z*)**	***L* x *D***	***L* x *z***	***D* x *z***	***L* x *D* x *z***	**Error**
	df	1	1	5	1	5	5	5	120
Margarites spp.	F-ratio	0.066	0.602	38.32	0.055	0.991	12.612	3.859	
	p-value	0.787	0.439	**<0.001**	0.816	0.426	**<0.001**	**0.003**	
Crepidula spp.	F-ratio	0.606	0.327	55.46	0.002	7.598	3.112	2.177	
	p-value	0.438	0.568	**<0.001**	0.964	**<0.001**	**0.011**	0.061	
Mitrella lunata	F-ratio	0.473	0.698	66.59	0.436	11.15	11.153	9.831	
	p-value	0.493	0.405	**<0.001**	0.51	**<0.001**	**<0.001**	**<0.001**	
Diaphana minuta	F-ratio	0.231	0.855	37.00	0.249	11.85	8.306	3.06	
	p-value	0.632	0.357	**<0.001**	0.619	**<0.001**	**<0.001**	**0.012**	
Littorina littorea	F-ratio	0.001	4.931	106.00	4.087	12.61	10.326	20.106	
	p-value	0.952	0.028	**<0.001**	0.045	**<0.001**	**<0.001**	**<0.001**	
Polinices heros	F-ratio	0.534	0.727	75.11	0.337	8.658	0.585	0.922	
	p-value	0.467	0.395	**<0.001**	0.563	**<0.001**	0.712	0.469	
Aporrhais occidentalis	F-ratio	0.68	0.002	41.07	0.258	1.574	2.108	1.691	
	p-value	0.411	0.963	**<0.001**	0.613	0.172	0.069	0.142	
Nassarius spp.	F-ratio	0.005	0.246	32.59	1.48	6.032	4.790	12.963	
	p-value	0.942	0.621	**<0.001**	0.226	**<0.001**	**<0.001**	**<0.001**	
Bittium alternatum	F-ratio	0.024	0.000	10.71	0.046	4.593	2.340	2.529	
	p-value	0.876	0.985	**<0.001**	0.831	**0.001**	0.046	0.033	
Nudibranchia	F-ratio	0.116	0.671	50.06	0.053	8.404	5.080	1.859	
	p-value	0.734	0.414	**<0.001**	0.818	**<0.001**	**<0.001**	0.107	

Table 2.4 Results of multiple comparisons for 3-way ANOVA [lunar phase, diel period, depth (Table 2.3)] that identified significant differences for each taxon using Tukey's test. Numbers represent depths (3, 6, 9, 12, 18 and 24 m). Only significant differences are shown. Depths separated by commas, are ordered sequentially (3 to 24 m), not according to relative larval abundance at each depth.

Taxon	Factors	Multiple Comparison Low ——————> High Abundance
Margarites spp.	Full Moon - Day	3, 6, 9, 12 < 18 < 24
	Full Moon - Night	3, 6, 9, 24 < 18; 3, 24 < 12
	Quarter Moon - Day	3, 6, 9, 12 < 18, 24
	Quarter Moon - Night	3, 6, 9 < 24; 3, 6 < 12, 18
Crepidula spp.	Full Moon - Day	3, 6, 9, 24 < 12; 3, 24 < 6, 9, 18
	Full Moon - Night	3, 6, 18, 24 < 9; 3, 6, 24 < 12
	Quarter Moon - Day	3, 6, 9, 18 < 12; 24 < 6, 9, 18
	Quarter Moon - Night	3, 6, 9, 18, 24 < 12
Mitrella lunata	Full Moon - Day	3, 6, 18, 24, < 12; 3, 18, 24 < 9; 24 < 3, 18
	Full Moon - Night	3, 6, 18, 24, < 9; 3, 24 < 6,12
	Quarter Moon - Day	18, 24 < 3, 6, 12, 9
	Quarter Moon - Night	3, 6, 9, 18, 24 < 12; 18, 24 < 9
Diaphana minuta	Full Moon - Day	3, 12, 18, 24 < 6; 24 < 3, 9, 12, 18
	Full Moon - Night	3, 6, 18, 24 < 9; 3, 24, < 12; 3 < 18
	Quarter Moon - Day	3, 24 < 12; 24 < 3, 6, 9, 18
	Quarter Moon - Night	3, 6, 9, 18, 24 < 12; 24 < 9
Littorina littorea	Full Moon - Day	3, 6, 9, 24 < 12 < 18
	Full Moon - Night	3, 6, 9, 12 < 18; 3, 12 < 24
	Quarter Moon - Day	3, 6, 9, 24 < 12, 18; 3, 24 < 6, 9
	Quarter Moon - Night	3, 6, 9, 12, 24 < 18; 3, 6, 24 < 12
Nassarius spp.	Full Moon - Day	3, 18, 24 < 9, 12; 18, 24 < 6; 24 < 3
	Full Moon - Night	18, 24 < 6, 9, 12; 24 < 3
	Quarter Moon - Day	9, 12, 18, 24 < 3, 6; 18, 24 < 9
	Quarter Moon - Night	24 < 9, 12, 18
Nudibranchia	Full Moon - Day	3, 6, 9, 12 < 18 < 24
	Full Moon - Night	3, 6, 9, 12, 24 <18
	Quarter Moon - Day	3, 6, 9, 12, 18 < 24; 6 < 18
	Quarter Moon - Night	3, 6, 9, 12, 18 < 24
Bittium alternatum	Full Moon - Day	12, 18, 24 < 3, 6
	Full Moon - Night	9, 12, 18, 24 < 6
	Quarter Moon - Day	18, 24 < 3, 6
	Quarter Moon - Night	3, 6, 18, 24 < 12

Taxon	Factors	Multiple Comparison Low ——————> High Abundance
Polinices heros	Full Moon	3, 6, 12 < 24 < 18
	Quarter Moon	3, 6, 9, 12, 24 < 18
Bittium alternatum	Full Moon	12, 18, 24 < 6, 3
	Quarter Moon	18, 24 < 3, 6, 12
Aporrhais occidentalis	Depth	3, 6, 18, 24 < 9, 12; 3, 18, 24 < 6

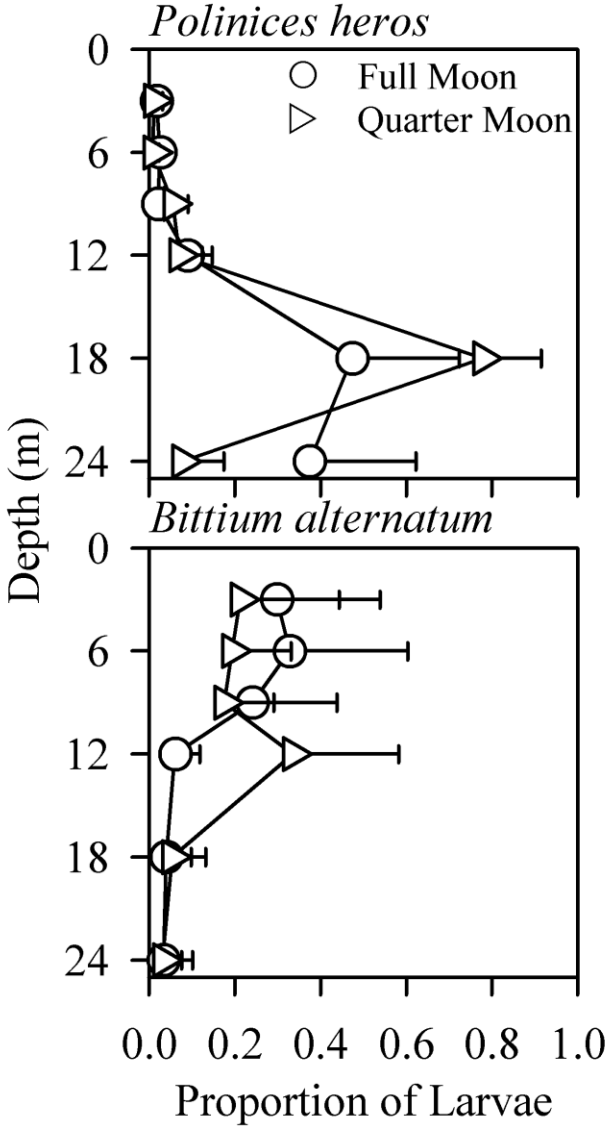


Figure 2.6 Larval vertical distribution of gastropod taxa with a significant interaction between depth and lunar phase (mean ± SD, n = 13 to 18) in St. George's Bay, Nova Scotia, Canada.

Table 2.5a Results of 3-way ANOVA examining the effect of lunar phase (full moon, quarter moon), tidal state (ebb, flood, high, low), and depth (3, 6, 9, 12, 18, 24 m) on the proportional abundance (arcsine-transformed) for all gastropod taxa ($p < 0.01$, indicated in bold).
A.

Taxon	**Source**	**Lunar Phase (*L*)**	**Tidal State (*Ti*)**	**Depth (*z*)**	***L* x *Ti***	***L* x *z***	***Ti* x *z***	***L* x *Ti* x *z***	**Error**
	df	1	3	5	3	5	15	15	138
Margarites spp.	F-ratio	0.149	0.074	58.786	0.096	0.903	1.984	0.945	
	p-value	0.700	0.974	**<0.001**	0.962	0.481	0.02	0.517	
Crepidula spp.	F-ratio	0.467	0.093	62.494	0.003	5.388	0.888	0.734	
	p-value	0.495	0.964	**<0.001**	1	**<0.001**	0.578	0.746	
Mitrella lunata	F-ratio	0.002	0.142	54.388	0.742	6.32	0.742	0.427	
	p-value	0.967	0.935	**<0.001**	0.974	**<0.001**	0.738	0.969	
Diaphana minuta	F-ratio	0.009	0.122	39.61	0.11	11.707	1.637	1.045	
	p-value	0.925	0.947	**<0.001**	0.954	**<0.001**	0.071	0.414	
Littorina littorea	F-ratio	0.979	0.013	93.681	0.076	9.657	0.544	0.43	
	p-value	0.324	0.998	**<0.001**	0.973	**<0.001**	0.911	0.968	
Polinices heros	F-ratio	0.267	0.096	95.114	0.284	13.709	0.313	0.635	
	p-value	0.606	0.962	**<0.001**	0.837	**<0.001**	0.993	0.842	
Aporrhais occidentalis	F-ratio	1.702	0.053	45.737	0.082	1.285	1.248	0.535	
	p-value	0.194	0.984	**<0.001**	0.97	0.274	0.244	0.917	
Nassarius spp.	F-ratio	0.095	0.135	35.109	0.071	0.516	8.754	0.601	
	p-value	0.963	0.717	**<0.001**	0.975	**<0.001**	0.928	0.87	
Bittium alternatum	F-ratio	0.147	0.148	13.714	0.094	3.994	1.04	0.615	
	p-value	0.702	0.931	**<0.001**	0.964	**0.002**	0.419	0.859	
Nudibranchia	F-ratio	0.011	0.212	85.501	0.041	7.835	1.069	1.101	
	p-value	0.917	0.888	**<0.001**	0.989	**<0.001**	0.39	0.361	

Table 2.5b Results of multiple comparisons for 3-way ANOVA that identified significant differences for each taxon using Tukey's test. Numbers represent depths (3, 6, 9, 12, 18 and 24 m). Only significant differences are shown. Depths separated by commas, are ordered sequentially (3 to 24 m), not according to relative larval abundance at each depth.

B.

Taxon	**Factors**	**Multiple Comparison** **Low ----------> High Abundance**
Margarites spp.	Ebb	3, 6, 9, 12 < 18 < 24
	Flood	3, 6, 9, 12 < 18, 24
	High	3, 6, 9, 12 < 18, 24
	Low	3, 6, 9, 12 < 18, 24

*Multiple comparisons that identified significant difference from 3-way ANOVA (*L*, *Ti*, *z*) for *L* x *z* and *z* are the same as those for 3-way ANOVA (*L*, *D*, *z*) shown in Table 2.4.

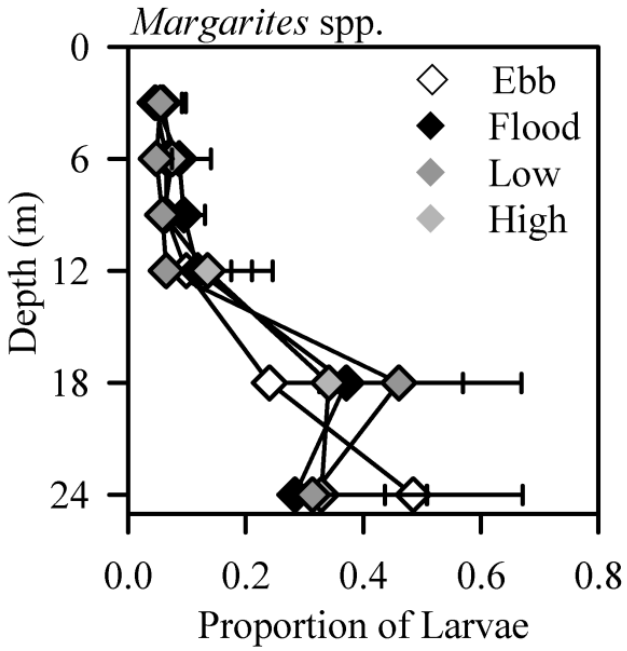


Figure 2.7 Larval vertical distribution of *Margarites* spp. with a significant interaction between depth and tidal state (mean ± SD, n = 3 to 6) in St. George's Bay, Nova Scotia, Canada.

2.5 Discussion

2.5.1 Patterns in Vertical Distribution

In this study, the vertical distribution of gastropod larvae in the water column was strongly related to physical and biological ocean features. The thermocline strongly influenced the distributions of most taxa. Because the density structure of the water column was primarily a function of temperature, temperature accounted for most of the variation in larval abundance for most taxa (Table 2.6). The presence of larvae in a particular water layer may be the result of changes in their buoyancy and changes in water density (Tremblay & Sinclair 1990b; Gallager et al. 1996). The role of buoyancy in the vertical distribution of gastropod larvae is not known. However, bivalve (e.g. *Placopecten magellanicus*) larvae in stratified regions tend to aggregate around the pycnocline, whereas, in mixed regions, they are evenly distributed throughout the water column (Tremblay & Sinclair 1990b; Raby et al. 1994; Gallager et al. 1996). It has been suggested that a minimum gradient in pycnocline is required for larval vertical distribution to be modified (Tremblay & Sinclair 1990b). For example, a density (σ_t) change >0.007 prevented larval movement in Georges Bank (z < 60 m) (Tremblay & Sinclair 1990b). In the laboratory, the vertical distribution of giant scallop larvae (*P. magellanicus*) was restricted either above or below the thermocline (ΔT = 7 °C m^{-1}), and only larvae >200 μm could penetrate it (Gallager et al. 1996). In my study, the vertical structure of instabilities (i.e. mixing or turbulence) in water column was intrinsically confounded with the thermal structure. Instabilities may also influence the vertical distribution of larvae, given that gastropod larvae may sink in response to turbulence (Fuchs et al. 2004; Young & Chia 1987).

Table 2.6 Summary of factors that explain the vertical distribution of gastropod larvae. *T* = temperature, *F* = fluorescence, *w* = vertical velocity, *v* = North-South velocity, *u* = East-West velocity. In all cases ● = no effect on vertical distribution. For lunar phase: ● = difference between the full and quarter moon. For diel period: ● = diel, ● = reverse-diel, ● = disaggregating at night. For depth: ● = above thermocline, ● = at thermocline, ● = below thermocline. For structure (*T*, *F*, *w*, *v*, *u*): ● = positive relationship, ● = negative relationship, and the numbers represent in decreasing order the relative importance of each variable on larval distribution: 1 = explained most and 3 = least amount variance in larval abundance based on simple linear regressions.

Taxon	Periodic				Structure				
	Lunar Phase	Diel Period	Tidal State	Depth	*T*	*F*	*w*	*v*	*u*
Margarites spp.	●	●	●	●	1	●	●	●	●
Nudibranchia	●	●	●	●	1	●	●	●	●
Crepidula spp.	●	●	●	●	2	1	●	●	●
Littorina littorea	●	●	●	●	2	1	●	●	●
Mitrella lunata	●	●	●	●	1	2	●	●	3
Diaphana minuta	●	●	●	●	1	2	3	●	●
Nassarius spp.	●	●	●	●	1	●	●	●	●
Bittium alternatum	●	●	●	●	1	●	●	●	●
Polinices heros	●	●	●	●	1	2	●	●	●
Aporrhais occidentalis	●	●	●	●	1	●	●	●	●

Temperature and salinity are known to affect the abundance, as well as development and survival rates, of many meroplanktonic species (Pechenik 1987); however, the effect of these physical factors on gastropod larvae is not well known. Growth rates increase with temperature, such as for *Ilyanassa* (*Nassarius*) *obsolete* and *Crepidula plana* (Lima and Pechenik 1985; Scheltema 1967). In my study, *Margarites* spp., *Polinices heros* and Nudibranchia were found in greater abundance in the cooler waters below the thermocline, and may develop more slowly than taxa found predominantly in waters at or above the thermocline. Many larvae have a salinity and temperature tolerance limit beyond which conditions become stressful or lethal (Pechenik 1987).

Temperature and salinity are scalar cues, which can elicit larval behavioural responses (Young & Chia 1987). For example, contact with a rapid change in density (temperature/salinity) causes some larvae to stop swimming and sink into denser water (e.g. crustaceans, echinoids, ascidians, bryozoans), or swim upwards (crabs, bivalves) (Young & Chia 1987). Behavioural responses to changes in temperature, salinity and density have yet to be studied in larval gastropods; however, gastropods, like bivalves, possess the sensory ability to detect changes in temperature and salinity (Kingsford et al. 2002). In the laboratory, when giant scallop larvae (*Placopecten magellanius*) contact a temperature gradient, they appeared to move away from it (Gallager et al. 1996), possibly altering their swimming direction in a thermokinetic response to a rapid change in temperature (Young & Chia 1987; Kingsford et al. 2002). This response may have evolved as a mechanism to avoid lethal or stressful temperatures. Thus, the larval gastropods found above the thermocline in my study may have been responding to the

thermocline by swimming upwards in order to remain in the mixed layer, where temperature changes are minimal (~1°C). The actual behavioural mechanisms regulating the response of these taxa to particular temperatures should be examined through controlled experiments.

The larval abundances of only 2 (*Crepidula* spp. and *Littorina littorea*) of 5 gastropod taxa, both of which were planktotrophic (Lebour, 1937), were strongly related to fluorescence, in turn indicating the presence of food. The other 3 gastropods (*Mitrella lunata*, *Diaphana minuta*, *Polinices heros*) also are likely planktotrophic, as relatives in the same genus have planktotrophic veligers (Strathmann 1987; Shanks, 2001). The vertical distribution of planktotrophic larvae is often related to the presence of food patches (Raby et al. 1994; Metaxas & Young 1998). Many larvae have chemosensory mechanisms to detect food (Kingsford et al. 2002), and laboratory studies have shown directed movement towards food patches (Metaxas & Young, 1998). Once within the food patch, larvae modify their position and swimming behaviour to remain within the patch (Metaxas & Young, 1998). As *Littorina littorea* were most abundant around the fluorescence maximum, they may be more efficient at feeding at high food concentrations than other gastropod taxa (Strathmann 1987). In order to remain within that layer, *L. littorea* would likely have to modify their swimming behaviour to counteract any effect of vertical currents on their vertical position. Taxa that do not aggregate around the fluorescence maximum, may be lecithotrophic or facultative feeders (Strathmann 1987), or may be avoiding the chlorophyll maximum to avoid predators which also tend to aggregate around prey fields (Morgan, 1995).

Although often both increased chlorophyll and larval aggregations are located at pycnoclines (Tremblay & Sinclair 1990b; Raby et al. 1994; Young 1995), in my study, the layer of chlorophyll maximum was located below the thermocline. Many of the gastropod taxa were found either at or below the thermocline, potentially taking advantage of high fluorescence (food) concentrations. However, the thermocline may also be potentially acting as a barrier to accessing the layer of maximum fluorescence for larvae found above the thermocline. In the laboratory, giant scallop (*Placopecten magellanicus*) and mussel (*Mytilus edulis*) larvae did not cross the thermocline and halocline, respectively, into a layer with higher food concentrations (Gallager et al. 1996; Pearce et al. 1996; Sameoto & Metaxas 2008b). However, more mussel (*M. edulis*) larvae were observed at the halocline when algae were present than absent above the halocline (Sameoto & Metaxas 2008b). In the Baie des Chaleurs (Quebec, Canada), bivalve larvae were more abundant at the chlorophyll maximum at night in a stratified water column, than during the day or in a mixed water column (Raby et al. 1994). It is unknown whether gastropod larvae respond as bivalves do to the presence of food layers or patches, but they may as most are planktotrophic, and require sufficient and nutritionally adequate food to develop and survive (Pechenik 1987; Strathmann 1987).

The vertical position of larvae can affect their direction and distance of dispersal, since current velocity generally varies with depth. In St. George's Bay, currents measured over a 43-d period were depth-dependent and fastest at the surface. Thus, larvae above the thermocline may have been transported farther than larvae near the seafloor, which in turn may be more likely to be retained near their source. The taxa that were more abundant below the thermocline (*Margarites* spp., *Polinices heros*, Nudibranchia) were

experiencing currents moving away from shore (east). Many of these taxa settle in rocky- and/ or soft-bottom habitat, in the infralittorial to bathyal zone (Brunel et al. 1998). In contrast, larvae (*Mitrella lunata*, *Bittium alternatum*, *Nassarius* sp.) above the thermocline were being transported shoreward (southwest), where many would settle in the intertidal or shallow subtidal (hard and soft substrate, algae or eelgrass beds) (Brunel et al. 1998).

2.5.2 Changes in Larval Vertical Distribution on Periodic Cycles

Three gastropod taxa exhibited diel migration, but the depth range of migration varied among taxa. *Margarites* spp. and Nudibranchia migrated from the seafloor to the fluorescence maximum layer at night, presumably when predation risk is low. Larvae of *Crepidula* spp., known planktotrophic, may be feeding below the thermocline during the day, migrating into the mixed layer at night. The diel vertical migration by *Crepidula fornicata* in a sluice dock of Ostend (1.5 m) was attributed to negative phototaxis, since chlorophyll concentrations were minimal at the surface at night (Daro 1974). Similarly, gastropod larvae in Sevastopol Bay (Black Sea) swam upwards towards the surface in response to a reduction in light during a solar eclipse (Petipa 1955 in Russian, as cited in Mileikovsky 1973). In contrast, diel vertical migration of gastropods in an offshore region was attributed to predator avoidance (Garland et al. 2002). Both Scyphozoans and fishes feed on gastropods in St. George's Bay (Short et al. in revision). Thus, gastropods may undertake diel migration to reduce predation risk from visual predators; it is unknown whether light and/or predation are the drivers of the patterns observed. *Crepidula* spp. by vertically migrating from below the thermocline into the mixed layer at

night, are also potentially altering the magnitude of shoreward transport, compared to *Margarites* spp. and Nudibranchia which remain below the thermocline. However, it is unknown whether species migrate dielly in order to alter their horizontal position, or whether this change is a consequence of periodic vertical migration.

Four gastropod taxa found at or above the thermocline exhibited reverse-diel migration. *Diaphana minuta*, *Mitrella lunata*, *Nassarius* spp., and *Bittium alternatum* may undertake reverse-diel migration to avoid diel-migrating predators, as do some copepods (Ohman et al. 1983). On the central coast of Chile, higher concentrations of competent larvae of abalone *Concholepas concholepas* were found at the surface during the day, but not at night (Poulin et al. 2002). This reverse-diel migration was suggested as a mechanism utilized to prevent offshore transport (Poulin et al. 2002). However, in my study, the taxa that undertake reverse-diel migration remained within the same (mixed) layer. *D. minuta* exhibited this change in distribution during both lunar phases. Manuel and O'Dor (1997), using a tidal/diel model showed that most vertical migration patterns appear at different model lunar phases, and suggested that larvae may actively alter their horizontal transport by responding to the combination of tidal and diel cues. *M. lunata*, *Nassarius* spp. and *B. alternatum*, may only vertically migrate during the quarter moon, as a mechanism to increase shoreward transport, thus avoiding strong eastward currents, given that all 3 species are commonly found in intertidal flats and eelgrass beds as adults (Brunel et al. 1998; Appeltans et al. 2011). In contrast, *D. minuata* are generally found deeper, in the circalittoral (20-200 m) and bathyal (200-500 m) zones (Brunel et al. 1998), and vertically migrate during both lunar phases; thus, their change in vertical distribution is likely in response to light rather than currents. Controlled experiments in

the laboratory can unconfound the scale of different potential cues (light, currents, predation etc.) to which larvae may be responding, and determine the behaviours associated with the vertical patterns observed in the field.

In this study, only *Margarites* spp. showed evidence of a tidally timed migration, and was more abundant deeper during the ebbing than the flooding and slack tides. Garrison and Morgan (1999) found the bivalve *Macoma* spp. was more abundant near the surface during flood tides. Molluscs are known to respond to pressure changes (Kingsford et al. 2002), swimming upwards in response to increases in hydrostatic pressure (Garrison & Morgan 1999), such as those that result from changes in tidal state. Larvae in estuaries/embayments can use tidally timed migration to increase transport away from their source population or towards a settlement site (DiBacco et al. 2001). For example, migration to deep waters during the ebb tide can result in retention and migration to shallow water during the flood tide increases transport towards a settlement site. The opposite migration pattern would lead increase offshore transport (DiBacco et al. 2001). Thus, *Margarites* spp. are likely retained.

2.5.3 Conclusion

In this study, I have shown that although patterns in larval vertical distribution vary among gastropod taxa, they are most strongly related to the location of the thermocline or the fluorescence maximum, and/or the diel period and/or lunar phase. Our knowledge of the ecology of larval gastropods is limited, and has primarily focused on commercially important (e.g. *Concholepas concholepas*, *Strombus gigas*) and invasive (e.g. *Crepidula fornicata*) species. This is the first study to document the relationship

between larval abundance and physical and biological factors in the water column, and vertical migration for gastropod larvae with respect to both diel period and lunar phase. I found that temperature (and consequently water column structure), fluorescence (food), and diel period are the key factors in determining the vertical distribution of these larvae. However, variation in the vertical distribution may result from larvae responding to more than one cue. The specific responses to different cues (temperature, chlorophyll, light, currents, stratification etc.) should be explored in laboratory studies. By associating changes in larval vertical distribution in the field with measured behavioural responses in the laboratory, we could quantify the role of larval behaviour in the natural setting.

CHAPTER 3

Patterns in Larval Vertical Distribution Affect Dispersal Potential of Marine Benthic Invertebrates in a Shallow Embayment in Nova Scotia, Canada

3.1 Abstract

Recruitment of benthic invertebrate populations is limited by larval supply, and quantification of the mechanisms that drive larval transport, retention and supply are necessary for their management and protection. Consequently, measurements of larval vertical distributions at high temporal frequencies and spatial resolutions and their behavioural responses to environmental characteristics are needed in order for bio-physical models to accurately simulate larval dispersal. In this study, I measured larval vertical distribution for 7 taxonomic groups (gastropods, bivalves, polychaetes, bryozoans, asteroids, carideans, brachyurans), with different morphology, swimming abilities and life-history strategies, and examined whether these vary with physical and/or biological factors and periodic (diel period, tidal state) cycles in the field. Plankton samples were collected at each of 6 depths (3, 6, 9, 12, 18, 24 m) using a pump, at each tidal state over a 36- and a 25-h period, during a spring and neap tide, respectively, concurrently with measures of temperature, salinity, fluorescence (proxy for food), and current velocity. Larval vertical distribution varied among taxonomic groups, but all patterns can be grouped under one of the 3 categories: (1) larvae found exclusively in the mixed layer (asteroids), (2) larvae associated predominantly with fluorescence maximum

(bryozoans and carideans), and (3) larvae with varying diel distributions (gastropods, bivalves, polychaetes, carideans and brachyurans). Based on flow velocities and depending on distribution, asteroid larvae were likely to be more dispersive than bryozoans and carideans, while gastropods, bivalves, polychaetes, carideans and brachyurans varied in their direction of transport, most likely resulting in retention. For most taxonomic groups where data exist, behaviour observed in the field agreed with measured laboratory responses to relevant cues. For these groups, asteroids and bivalves simple behavioural parameters can be generated that can be used to parameterize bio-physical models. By quantifying the role of larval behaviour in the field, we can augment the quality of estimates of dispersal potential of different larval taxonomic groups.

3.2 Introduction

For marine benthic invertebrates with a meroplanktonic phase, larval dispersal is critical for the establishment and maintenance of adult populations (Roughgarden et al. 1994). Meroplanktonic larvae can reside in the water column for periods from hours to months before settling on suitable habitat, thus enabling them to both exploit new habitats and/or recolonize old ones (Metaxas & Saunders 2009). The degree of larval exchange between populations can regulate the stability and resilience of species (Roughgarden et al. 1994; Pechenik 1999; Metaxas & Saunders 2009). Thus, quantification of the mechanisms that drive larval transport, retention, and supply, as well as accurate measures of distance travelled, and direction and frequency of dispersal are necessary for management and protection of species and their ecosystems.

Meroplanktonic larvae are typically small (<2 mm) and weak swimmers (~1 to 15 mm s^{-1}) (Metaxas 2001; Strathmann 1987; Young 1995) and are consequently considered incapable of sustained horizontal movement against large-scale horizontal currents (velocities >100 cm s^{-1}). As a result, horizontal dispersal patterns have been mainly attributed to advection along dominant directions of flow. Horizontal currents can advect larvae of coastal species offshore, leading to failure of recruitment to nearshore habitats (Shanks 1995).

It is well accepted that meroplankton are capable of movement against vertical currents, as their swimming or sinking speeds are greater than the weak vertical current velocities (mm s^{-1}; Chia et al. 1984; Metaxas 2001). Larval movement (swimming or sinking) between layers of different velocities can alter the horizontal direction and magnitude of larval transport and dispersal (Young & Chia 1987; Young 1995; DiBacco et al. 2001; Metaxas 2001). Through changes in buoyancy and/or propelled by ciliary or muscular activity, some crustacean and bivalve larvae are capable of moving large distances vertically, in some cases many times a day (Forward 1988; Manuel et al. 1996; Manuel & O'Dor 1997; dos Santos et al. 2008). These change can occur possibly through an innate behavioural response to physical and chemical stimuli. Consequently, sensory detection of the environment can potentially affect larval direction of movement and/or swimming behaviour (acceleration, deceleration, cessation) (Kingsford et al. 2002). Currently, the role of larval behaviour in affecting their horizontal advection remains elusive, and the conditions under which larvae may actively regulate their depth versus passively drift are poorly understood (Metaxas & Saunders 2009).

The vertical distribution of meroplankton in the water column can be related to physical and biological discontinuities. Many larvae respond to abiotic (e.g. temperature, salinity, density, pressure, gravity, light, flow regimes, tides, waves) and biotic (predators, food, conspecifics) cues that can in turn be related to features in the water column (Young 1995), thus possibly shaping larval vertical distributions. For example, larval aggregations of bivalves at the chlorophyll maxima (Raby et al. 1994) and pycnocline (Tremblay & Sinclair 1990b) have been observed in the field. In the laboratory, larvae (e.g. echinoderms, bivalves, crustaceans) respond to food patches (Metaxas & Young 1998), changes in temperature (McConnaughey & Sulkin 1984; Daigle & Metaxas in press) and salinity (Mann et al. 1991; Sameoto & Metaxas 2008a, b), and the presence of predators (Metaxas & Burdett-Coutts 2006). In the laboratory, larval response to cues can be measured through changes in vertical or horizontal distribution, or swimming speeds. However, in the field, behaviour is typically inferred from spatial and temporal patterns in abundance and distribution on a number of scales. Because patchy larval distributions can confound these patterns (Pineda 2000), our understanding of larval behaviour is based mainly on laboratory studies.

Some larval taxa appear to respond to cues linked to predictable cycles (tidal states, diel periods, lunar phases, ontogenetic stages). For example, crustacean larvae time their movement in relation to changes in the tide, and as a result increase the probability of import or export in or out of bays (DiBacco et al. 2001; Garrison 1999). Some larval gastropods, bivalves, polychaetes, echinoids, and crustaceans respond to diel cues either by diel (toward the surface at night and deeper waters during the day) or reverse-diel migration (Daro 1974; Young & Chia 1987; Pennington & Emlet 1986;

Forward 1988; Poulin et al. 2002). Some bivalve larvae are thought to respond to lunar cues, which are generally linked to light intensity and/or tidal and diel cues (Manuel & O'Dor 1997; Manuel et al. 1997). In addition, ontogenetically, older larvae of bivalves and decapods tend to be more abundant near the seafloor than younger larvae, presumably due to an increase in specific gravity, and change in morphology or behaviour (Brookins & Epifanio 1985; Mann et al. 1991; Baker and Mann 2003; Gallager et al. 1996; Tamaki et al. 2010). Near-bottom distribution presumably enhance the probability of locating a suitable site for settlement. Larval movement in response to these periodic cues has been suggested as a mechanism to avoid predation, optimize feeding, and increase/ decrease dispersal (Young 1995).

Quantifying larval dispersal in the field is difficult due to small larval size and prolonged (days to months) planktonic duration. Consequently, biophysical models are increasingly being used to quantify larval transport and supply to the benthos. However, the ability of models to predict larval distributions and transport depends on the accuracy of estimates of the physical and biological parameters in the field, and often these are location-, species- and life-history stage-specific (Metaxas & Saunders 2009). Larvae are often modeled as passive (non-swimming) particles, thus dispersal is mainly attributed to physical processes. Often these models cannot account for observed larval distributions (Metaxas & Saunders 2009), possibly because parameterizations of biological variables are based mainly on laboratory studies, where larval behaviors are often measured on small scales (cm) and in the absence of flow (Metaxas 2001; Kingsford et al. 2002; Metaxas & Saunders 2009). As more biological parameters (e.g. vertical migration, larval behaviour, growth, mortality, settlement behaviour) are incorporated into these models,

the outputs can change significantly (Levin, 2006; Metaxas & Saunders, 2009). Thus, to accurately model larval transport, we need accurate measures of biological parameters in the field. Spatial and temporal measures (continuous, or at least are at high frequency) of changes in larval vertical distribution relative to associated changes in the structure of the water column in the field should prove useful in quantifying larval behaviour in the field.

To date, most studies of vertical distribution or migration in the field have focused on a single species or taxonomic group. Less than a handful of studies have examined changes in vertical distribution concurrently for multiple taxonomic groups (e.g. gastropods, bivalves, crustaceans, polychaetes) with different of swimming abilities, morphologies, and life histories (Daro 1974; Garland et al. 2002). In these studies, changes in vertical distribution were measured in an upwelling/ downwelling region in the outer Banks of North Carolina (depth: 20-25 m) (Garland et al. 2002) and in an artificial lagoon at sluice dock Ostend (depth: 1.5 m) (Daro 1974). My study extends previous knowledge significantly by examining changes in the larval vertical distribution for different taxonomic groups in a coastal embayment during a stable period, at high temporal (h) frequencies and spatial (m) resolutions. I examined whether changes in larval vertical distribution in St. George's Bay, Nova Scotia, Canada, over a 36- and a 25-h period, during a spring (full moon: 6-7 Aug 2009) and neap (quarter moon: 12-13 Aug 2009) tides, respectively, varied: 1) with a suite of physical (temperature, salinity, density, current velocities), and biological (fluorescence, a proxy for food) characteristics; and 2) at periodic cycles (diel period, tidal state). I examined distributions of 7 different taxonomic groups (gastropods, bivalves, polychaetes, bryozoans, asteroids, carideans, brachyurans), with contrasting life histories, morphologies (size and form) and

swimming abilities (weak to strong), under similar environmental conditions. This approach allowed the assessment of factors important in regulating larval vertical distributions in the field. Since behavioural responses to cues (e.g. temperature, salinity, density, food, light etc.) for some of these taxonomic groups have been measured in laboratory studies, I can associate changes in their vertical distribution in the field with published behavioural responses observed in the laboratory. Thus, I begin to quantify the role of larval behaviour in the field, which in turn can improve the parameterization of biological variables for biophysical models, and ultimately improve the quality of estimates of dispersal potential for different taxonomic groups of larvae.

3.3 Materials and Methods

3.3.1 Study Site

The study was conducted in St. George's Bay, Nova Scotia, Canada (45°46' N, 51°43' W), a coastal embayment on the Northumberland Strait that is approximately 45 x 45 km. The tides in St. George's Bay are weak mixed diurnal/semidiurnal, with a tidal range from MHHW to MLLW of ~1.5 m (Canadian Hydrographic Service). A single sampling location was used on the west side of the bay (45.78°N, 61.80°W; depth = 25 m).

3.3.2 Sampling of Physical Characteristics

Temperature, salinity, pressure, fluorescence, and current velocities [vertical (*w*), North-South (*v*) and East-West (*u*)] were measured in the water column, averaged to 1 m depths from 1 to 23-25 m depth, with a Seabird 25 Conductivity-Temperature-Depth (CTD) recorder, a SCUFA fluorometer and an RDI Acoustic Doppler Current Profiler (ADCP) with a chain of VEMCO thermistors, respectively. Two CTD casts were made every 2-h over a 36- (6-7 Aug) and a 25-h (12-13 Aug) sampling period, associated with each sampling time (see plankton sampling below). At the beginning of each sampling time, temperature, salinity, pressure and fluorescence were measured with a CTD cast. The CTD was also attached to the pump intake, allowing for a second cast for temperature and pressure measurements concurrent with plankton sampling. Some malfunctioning of the CTD and the SCUFA fluorometer resulted in incomplete data sets. The ADCP was deployed on the seafloor, sampling over 1 m depth bins from just above the bottom to just below the surface, every 20 min from 11 Jul to 22 Aug 2009. The thermistors were attached to the ADCP mooring and distributed throughout the water column, approximately every 3 m from 3 to 24 m depth. Light intensity was measured at the sea surface at the beginning of each plankton sampling time with a LI-COR Terrestrial Quantum Sensor (LI-190SA).

3.3.3 Plankton Sampling

On 6-7 and 12-13 Aug 2009, plankton samples were collected with a cast iron, high volume (~0.85 $m^3 min^{-1}$), 7.6-cm diameter portable trash pump (Gorman-Rupp: Model 3S5HCR) with a two-vane semi-open, 3.2-cm solid handling impeller and a 7.6-

cm diameter, 27-m length hose, a T-shaped intake head and a 5-m discharge hose. The discharge from the pump was directed into a submerged 200-μm mesh plankton net to prevent damage to the larvae. Volume flow rates were determined by measuring the time required to fill a known volume at each sampling depth (e.g. 0.94 and 0.75 m^3 min^{-1}, at 3 and 24 m respectively), and used to standardize plankton abundance per unit volume. While plankton sampling, the intake was moved vertically through a depth interval of ~1-m, for 5 min for a sample volume of ~4.4 m^3. Plankton were sampled at 3, 6, 9, 12, 18 and 24 m every 2-h (10:00, 12:00, 14:00, 16:00, 18:00, 20:00, 22:00, 00:00, 02:00, 04:00, 06:00, 08:00), over a period of ~36- (6-7 Aug) or 25-h (12-13 Aug). The net and codend were washed down with filtered seawater to concentrate larvae for preservation, and plankton samples were preserved in 90% ethanol. Prior to plankton sampling, water was pumped for a minimum of 2 min to clear the hose.

3.3.4 CTD Data Processing

For each CTD cast, only data collected during the down-casts were used and any outliers in temperature, salinity and fluorescence were removed using a moving average. Temperature measurements were averaged between the two casts (before and during plankton sampling), unless the CTD failed to record during one of the casts. Temperature, salinity and fluorescence were averaged into 1-m depth bins, and density (σ_t, kg m^{-3}-1000) calculated for each depth using the 'swstate' function in Matlab 7.1 (The Mathworks Co.) for each sampling time. Vertical temperature gradients for each sampling time were calculated as $\Delta T/\Delta z$, where T is temperature (°C) and z is depth (m), at 1 m intervals. For each sampling time, the depth of the thermocline, in a vertically

stratified water column, was identified as the depth where the vertical temperature gradient over 1m was >0.54 °C m^{-1}; and the depth of fluorescence maximum was where the maximum fluorescence value was recorded.

3.3.5 ADCP Data Processing

For both the ADCP and thermistor data, missing or unreliable data were either replaced by linearly interpolated values from surrounding points if there were sufficient data (typically 1-2 points) or were removed entirely. The ADCP current data from the upper 1 m of the water column were discarded due to backscatter effects. The current velocity and the temperature data were filtered using a 5^{th}order forward-and-reverse Butterworth lowpass digital filter, with a cut-off frequency of 2 h. Progressive vector plots were constructed where the distance travelled was calculated at 20 min intervals for a 38-h period, at 3, 12 and 23 m depth, over both sampling periods.

3.3.6 Plankton Sample Processing

In the laboratory, plankton were sorted, and enumerated to major taxonomic group (gastropods, bivalves, bryozoans, polychaetes, asteroids, brachyurans, carideans), using a Nikon SMZ 1500 dissecting microscope. Plankton samples were serially divided using a Folsom plankton splitter (Wildlife Supply Company), and sub-samples (down to 1/16, depending on larval abundance) sorted until the smallest of either 50 larvae of each taxonomic group or the entire sample was counted. For each taxon at each sampling time and depth for both periods, larval abundance was calculated and standardized to number

of larvae m^{-3}. Also, the vertical distribution for each taxon at each sampling time was characterized using mean depth distribution (MDD) calculated for each sampling time *j* as the weighted average:

$$MDD_j = \frac{1}{N_j} \sum_{i=1}^{n} z_i \, n_{ij}$$

where z_i = mean depth of interval *i*, n_{ij} = number of larvae collected at depth *i* at time *j*, and N_j = total number of larvae sampled at time *j* (Tapia et al. 2010). For each larval taxon, the MDD reflects the larval concentration at the mean depth of any given profile. Lastly, the proportional abundance was calculated at each depth interval (i.e. 3, 6, 9, 12, 18 or 24 m) for each sampling time *j* using

$$P_{ij} = \frac{n_{ij}}{N_j}$$

where P_{ij} = proportional abundance at depth interval *i* at time j, n_{ij} = number of larvae collected at depth *i* at time *j*, and N_j = total number of larvae sampled at time *j*. The proportional abundance was used to standardize larval concentrations for each taxon within and among sampling periods.

3.3.7 Statistical Analysis

The relationships between temperature [correlated to salinity and density (Appendix A)], fluorescence, *w*, *v* and *u*, and the proportional larval abundance were examined with simple and multiple (backwards stepwise) regressions. Because the proportionality data failed to meet the assumptions of normality and heterogeneity, as determined by examining the residuals, they were arcsine square root transformed. The

relationships between tidal height and light intensity, with larval MDD were also examined with simple regressions. I examined temporal changes in the vertical distributions of larvae using ANOVA, as manifested by the interaction terms between depth, and either diel period or tidal state. Samples taken at different sampling times were pooled into four diel categories (dawn, day, dusk, night), and four tidal categories (ebb, flood, high, low). Based on sunset and sunrise times published by Environment Canada, I identified 4 dawn (4:00, 6:00), 18 day (8:00, 10:00, 12:00, 14:00, 16:00, 18:00), 3 dusk (20:00), and 6 night (22:00, 00:00, 02:00) samples for both sampling periods combined. Based on tidal height, there were 10 ebb tide (decreasing tidal height), 9 flood tide (increasing tidal height), 6 high tide, and 6 low tide samples for both sampling periods combined. Because there were not enough replicates to test all 3 factors (depth, tidal state, and diel period) simultaneously, two 2-way analyses of variance (ANOVA) were performed followed by Tukey's HSD post hoc tests to test the effects on proportional larval abundance of: (1) diel period and depth; and (2) tidal state and depth. Given the large number of comparisons and statistical tests, an α-value of 0.01 was used as an indicator of non-significance. All statistical analyses were conducted with SPSS 17.0.

3.4 Results

3.4.1 Physical Structure of the Water Column

The structure of the water column remained relatively constant at the sampling station across both sampling periods (Fig. 3.1). The temperature generally ranged between ~20°C at the surface and ~4°C at 25 m, and salinity ranged between 29 and 31

(Fig. 3.1). The water column was stratified, with the thermocline located at ~10-17 m (Fig. 3.1). Fluorescence ranged between 0.09 and 0.35, peaking between 13 and 18 m depth (Fig. 3.1). Overall, no clear circulation patterns were detected in summer 2009, and mean currents within St. George's Bay were variable and tended to be depth-dependent (Fig. 3.2). Over a long temporal scale (43-d), mean current velocities at 6 and 10 m were 2-5 times stronger than at 20 m (Fig. 3.2). At most locations, mean currents over a 43-d period at 6 and 10 m were generally directed shoreward, and at 20 m the mean currents flowed clockwise in the southern portion of St. George's Bay (Fig. 3.2). During my sampling periods, the horizontal current velocities were relatively weak (<150 mm s^{-1}), but were stronger during the full moon than the quarter moon (Fig. 3.1). These velocities changed direction during shifts in tidal state, but the shift was lagged among depths. The vertical velocities were weak (most <2 mm s^{-1}) and variable, and patterns were likely due to noise (Fig. 3.1).

Progressive vector diagrams showed the path a hypothetical passive particle would travel over a 38-h period (short temporal scale), which varied among depths and between sampling periods. During the full moon, particles at 3 and 12 m would have been displaced ~3.4 and 5.3 km, respectively, westward of the start position, whereas, at 23 m, they would have been displaced ~3.1 km northeast (Fig. 3.3). During the quarter moon, passive particles at 3 m would have been displaced ~1.9 km to the northwest, and at 12 and 23 m ~2.3 km and 3.8 km to the southeast (Fig. 3.3). Although, excursions were greatest at 12 m during the full moon, net displacement was short (Fig. 3.3).

3.4.2 General Trends in the Abundance, Composition, and Stage of Different Taxonomic Groups

I identified 7 numerically dominant taxonomic groups, with different life histories and swimming abilities (gastropods, bivalves, polychaetes, bryozoans, asteroids, carideans and brachyurans). Of these, bivalves were the most abundant, comprising 59% of total numerical abundance. The next two numerically dominant taxonomic groups were gastropods and bryozoans (10-30%), while the remaining taxonomic groups comprised less than 3.5% of total abundance. The mean abundance of each taxonomic group remained relatively similar across time within each sampling period (Fig. 3.4). The mean abundance of gastropods, bivalves, bryozoans, asteroids, carideans and brachyurans also remained relatively constant between sampling periods, whereas that of polychaetes decreased from 6-7 to 12-13 Aug (Fig. 3.4).

Gastropods were the most diverse taxonomic group, being composed of 10 taxa, with *Margarites* spp. being the most abundant (~53% of total gastropods) (Fig. 3.4) (see Chapter 2). Bivalves were composed of at least 2 taxa (possibly more), but only *Anomia simplex* (30% full moon or 49% quarter moon of the total bivalves) could be reliably identified (Fig. 3.4). Polychaetes were composed of at least 4 Families, and bryozoans were composed of 2 species, *Electra pilosa* being the most abundant (Fig. 3.4). Brachyurans were composed of at least 4 taxa, with *Cancer irroratus* being the most abundant (91%) (Fig. 3.4). Asteroids and carideans could only be reliably identified to class and infraorder, respectively.

Different ontogenetic stages were present throughout the water column over both sampling periods. Both early and late larval stages, as well early juveniles were observed

for polychaetes, brachyurans and carideans; however, only later stages were observed for asteroids. Also, some meroplankton that lack clear ontogenetic features varied in size. For example, gastropods ranged in size from 200 to 900 μm, and bivalves from 200 to 400 μm.

3.4.3 Spatial and Temporal Patterns in Vertical Distribution

Gastropods were found throughout the water column, but the greatest proportion was below the thermocline (Fig. 3.5a). Variation in their abundance was explained mostly by a negative relationship with temperature, but also a positive one with fluorescence (Fig. 3.5a & Table 3.1). Gastropods also exhibited diel vertical migration (Fig. 3.6). The highest proportion was found at ~18-24 m during the day, at 18 m at dusk, at 12 m at night, and between 9 and 24 m at dawn (Fig. 3.6 & Table 3.2). Gastropods were also the only taxonomic group to exhibit tidally-timed migration (Fig. 3.7). They were most abundant at 24 m during ebb, at 18 m at low tide, and at 12-18 m during flood and at high tide (Fig. 3.7 & Table 3.3).

Like gastropods, bivalves were found throughout the water column with the greatest proportion below the thermocline (Fig. 3.5b & Tables 3.2, 3.3). Most of the variation in their abundance was explained by the thermal structure of the water column (Fig. 3.5b & Table 3.1). Bivalves also showed diel migration; the highest proportional abundance occurred at 18-24 m at dawn, day and dusk, but was shallower at night (Fig. 3.6 & Table 3.2).

Polychaetes were found almost exclusively below the thermocline (Fig. 3.5c & Tables 3.2, 3.3) and most of the variance in their proportional abundance was explained

by a negative relationship with temperature (Fig. 3.5c & Table 3.1). They were found at shallower depths at night than during the remainder of the diel cycle (Fig. 3.6 & Table 3.2).

Bryozoans were concentrated at ~ 18 m, where fluorescence was highest and most of the variation in their proportional abundance was explained by positive relationship with fluorescence (Fig. 3.5d & Table 3.1). Bryozoan abundance did not vary temporally on either a tidal or diel cycle (Tables 3.2, 3.3).

Asteroids were found almost exclusively above or near the thermocline, and much of the variation in their abundance was explained by temperature (Fig. 3.5e & Table 3.1). Like bryozoans, asteroids abundance did not vary temporally on either a tidal or diel cycle (Tables 3.2, 3.3).

Although the vertical structure of carideans varied over the sampling period, their abundance was most often greatest around the fluorescence maximum (Fig. 3.5f & Table 3.3). The variation in their abundance was explained by the combination of temperature and fluorescence (Fig. 3.5f & Table 3.1). The highest proportion of carideans was found primarily at 18 m; however, at night, their vertical distribution was slightly more even throughout the water column (Fig. 3.6 & Table 3.2).

The proportional abundance of brachyurans was greatest above or near the thermocline, but was variable over time (Fig. 3.5g). Only 4 % of the variation in their abundance was explained by the thermal structure. Their MDD was negatively related to tidal height [$R^2 = 0.216$, $F_{(1,29)} = 9.257$, $p = 0.005$], indicating that brachyurans were found at shallower depths at high tide than at low tide (Fig. 3.8). They did exhibit diel vertical migration within this upper mixed layer (Fig. 3.6). The highest proportional

abundance was at 12 m during the day and at 3 and 9 m at night; they were more evenly distributed throughout the water column at dusk and dawn (Fig. 3.6 & Table 3.2).

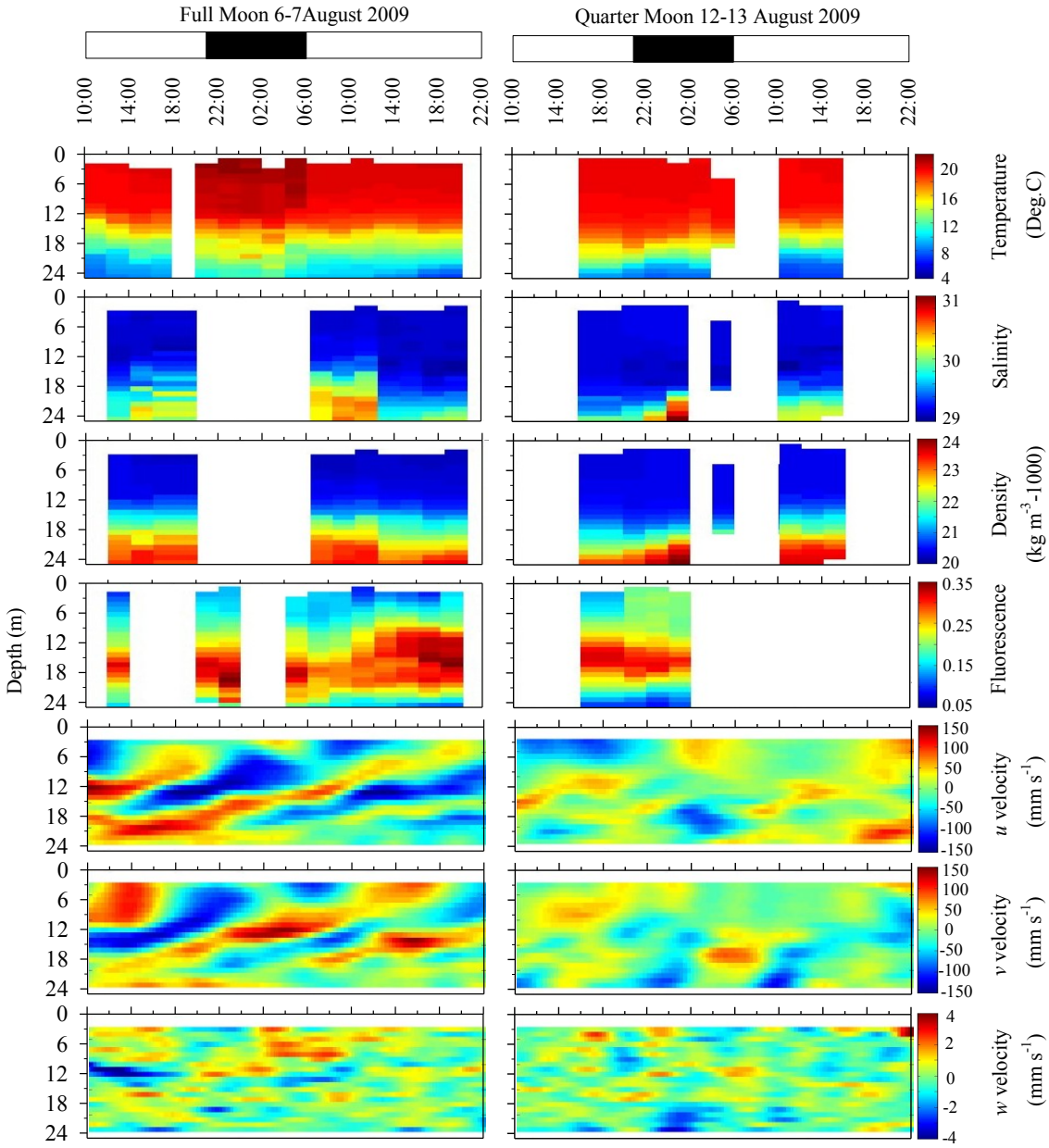


Figure 3.1 Time series of the physical and biological variables measured at a single station (z = 25 m) in St. George's Bay, Nova Scotia, Canada, over a 36- and 25-h period, during a spring (full moon: 6-7 Aug 2009) and neap (quarter moon: 12-13 Aug 2009) tide, respectively. CTD casts were made every 2-h, and an ADCP moored on the sea floor sampled every 20 min (see Methods for details).

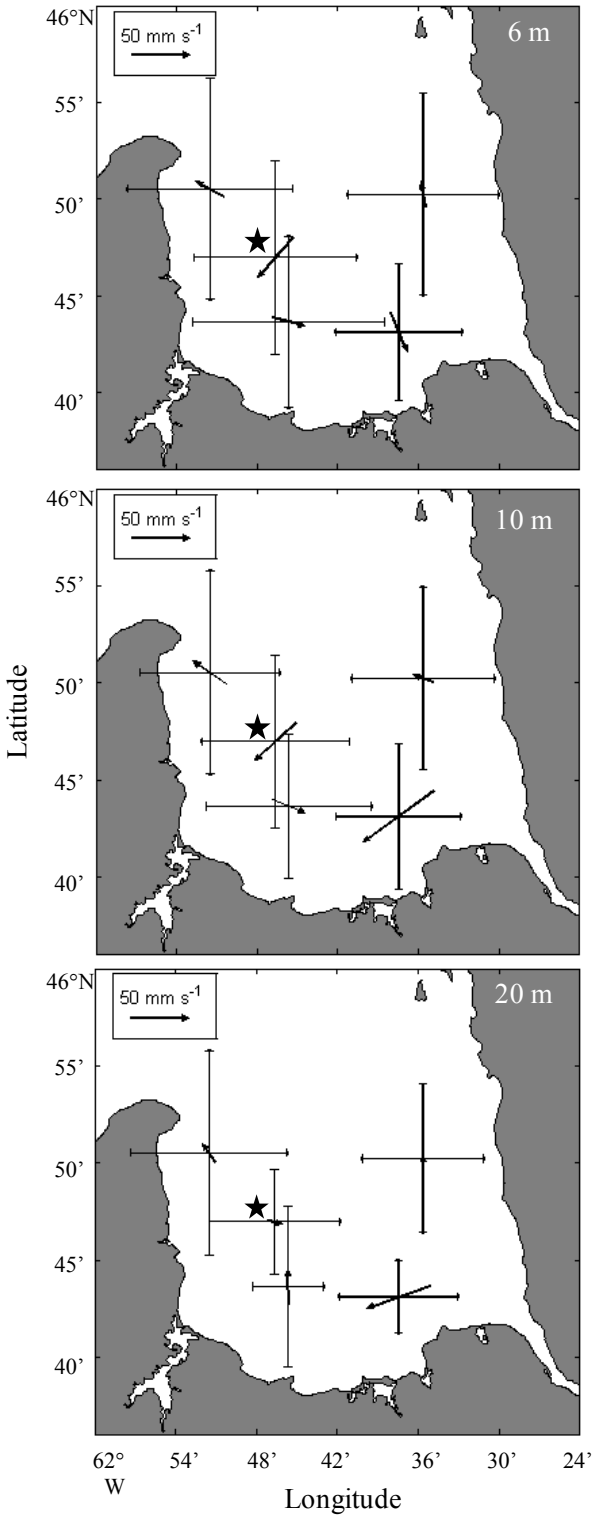


Figure 3.2 Current velocities (mean ± SD) at 6, 10 and 20 m depth in St. George's Bay, Nova Scotia, Canada, over a 43-d period (11 Jul to 22 Aug 2009). → = mean current velocity, ★= sampling location (z = 25 m) (modified from Lesperance et al. 2011).

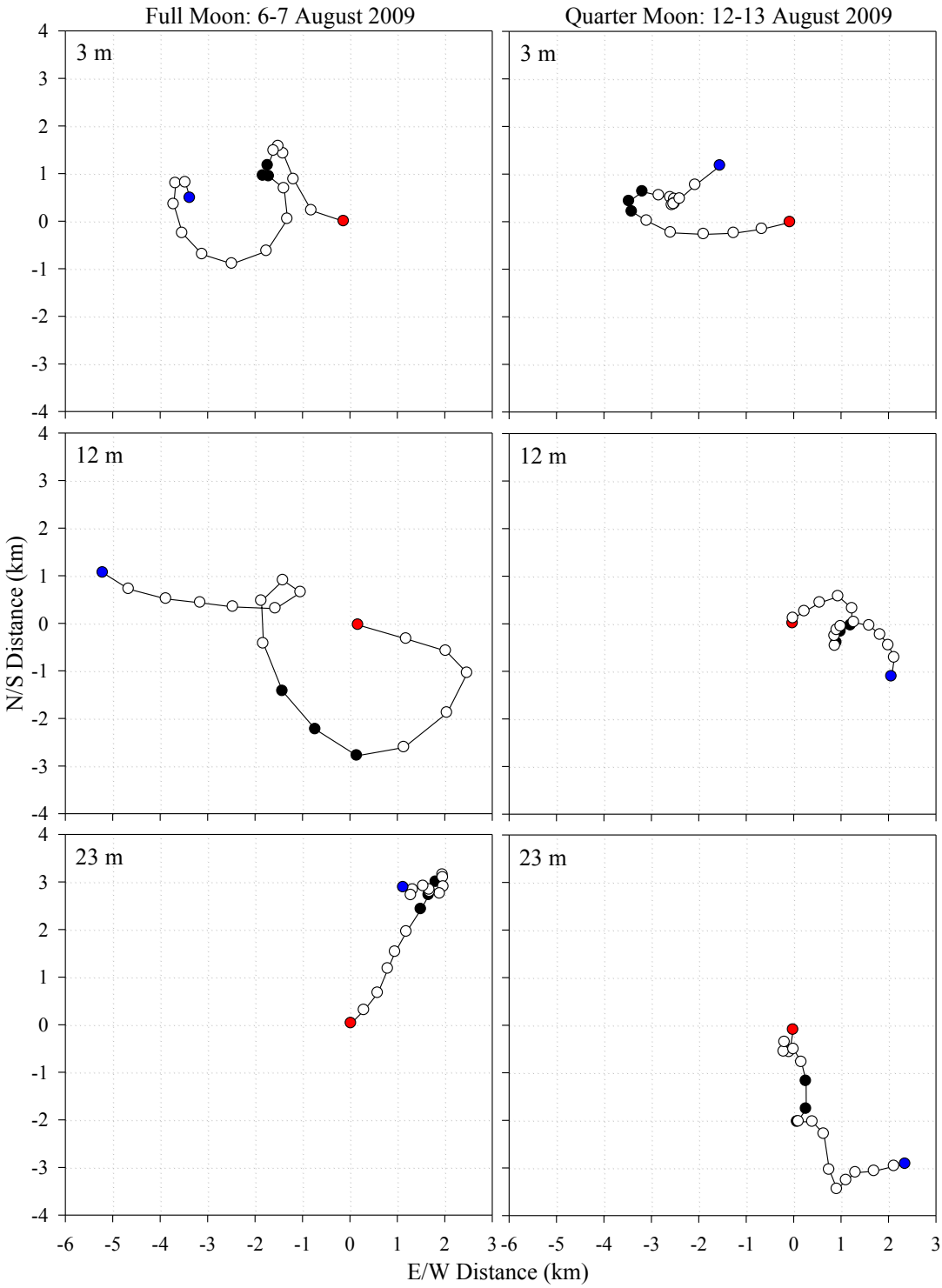


Figure 3.3 Progressive vector diagram at 3, 12 and 23 m depth in St. George's Bay, Nova Scotia, Canada, over a 36- and a 25-h sampling period, during a spring (full moon: 6-7 Aug 2009) and neap (quarter moon: 12-13 Aug 2009) tide, respectively. ● = start position, ● = end position, and in between, ○ = day and ● = night displacement.

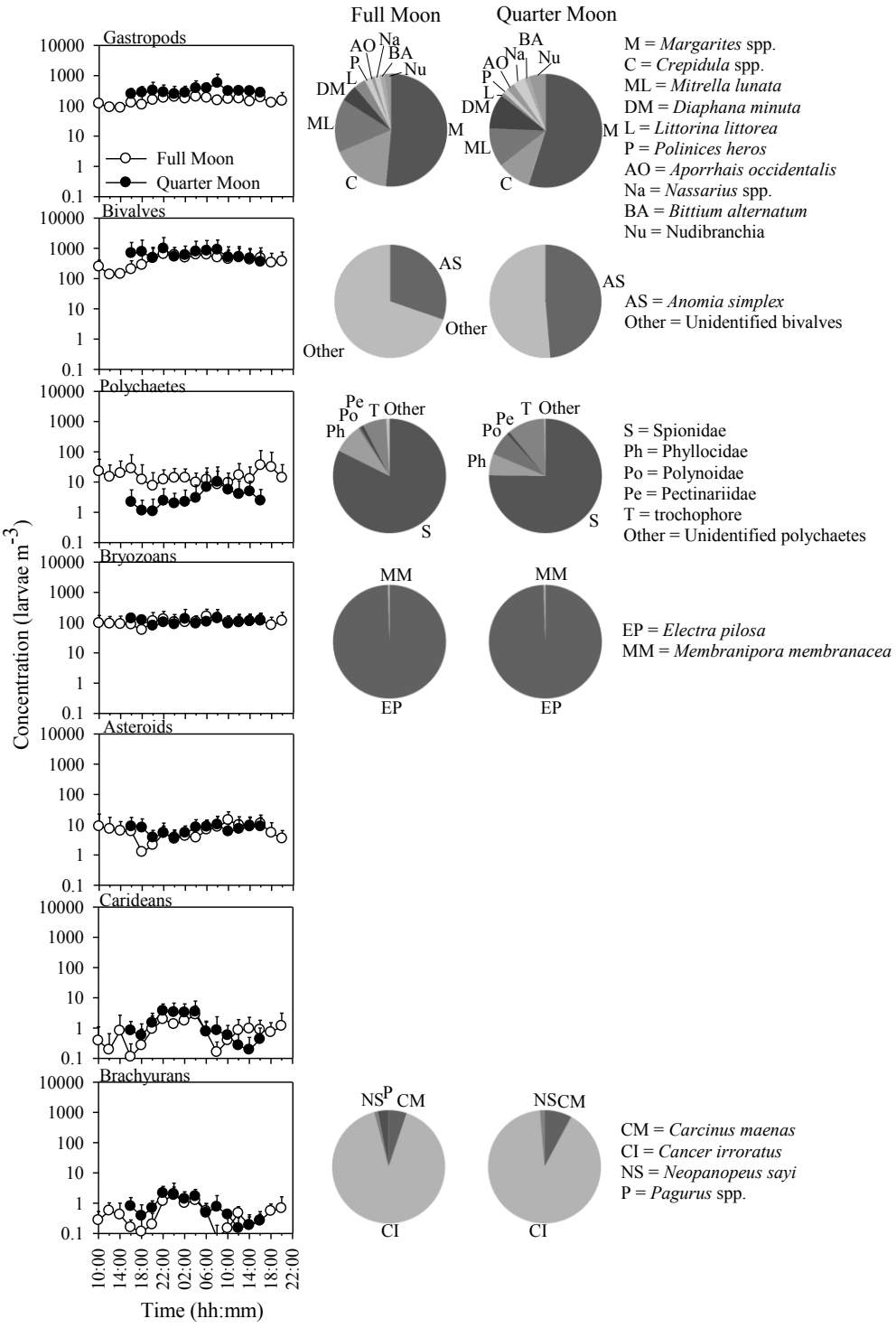
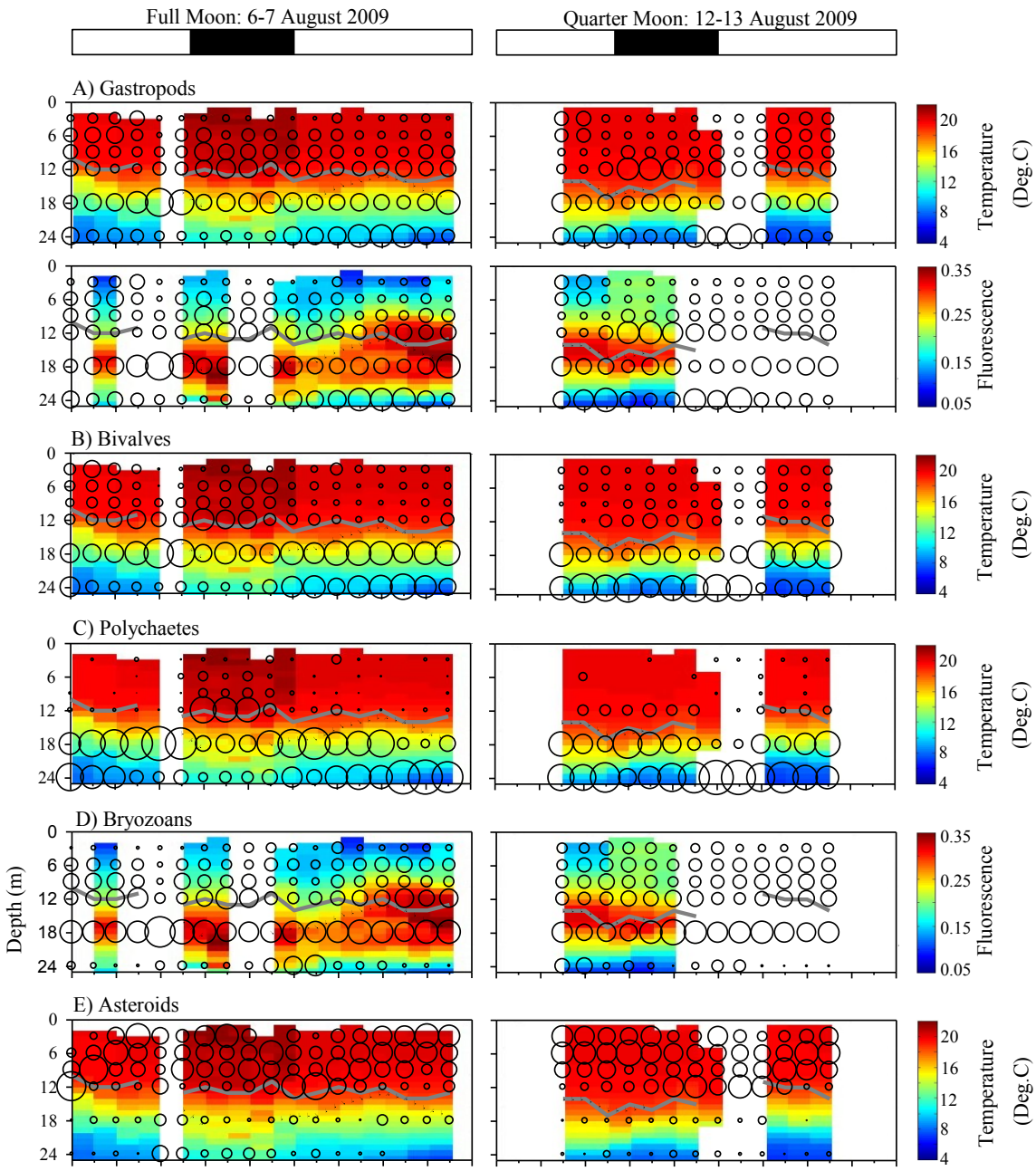


Figure 3.4 Concentrations (mean ± SD, n = 6) of 7 taxonomic groups in St. George's Bay, Nova Scotia, Canada, over a 36- and a 25-h sampling period, during a spring (full moon: 6-7 Aug 2009) and neap (quarter moon: 12-13 Aug 2009) tide, respectively. The pie charts represent proportional abundance of each species/taxon within each taxonomic group, where discrimination was possible.


Full Moon: 6-7 August 2009
Quarter Moon: 12-13 August 2009
A) Gastropods
B) Bivalves
C) Polychaetes
D) Bryozoans
E) Asteroids
Depth (m)
0
6
12
18
24
Temperature (Deg.C)
20
16
12
8
4
Fluorescence
0.35
0.25
0.15
0.05

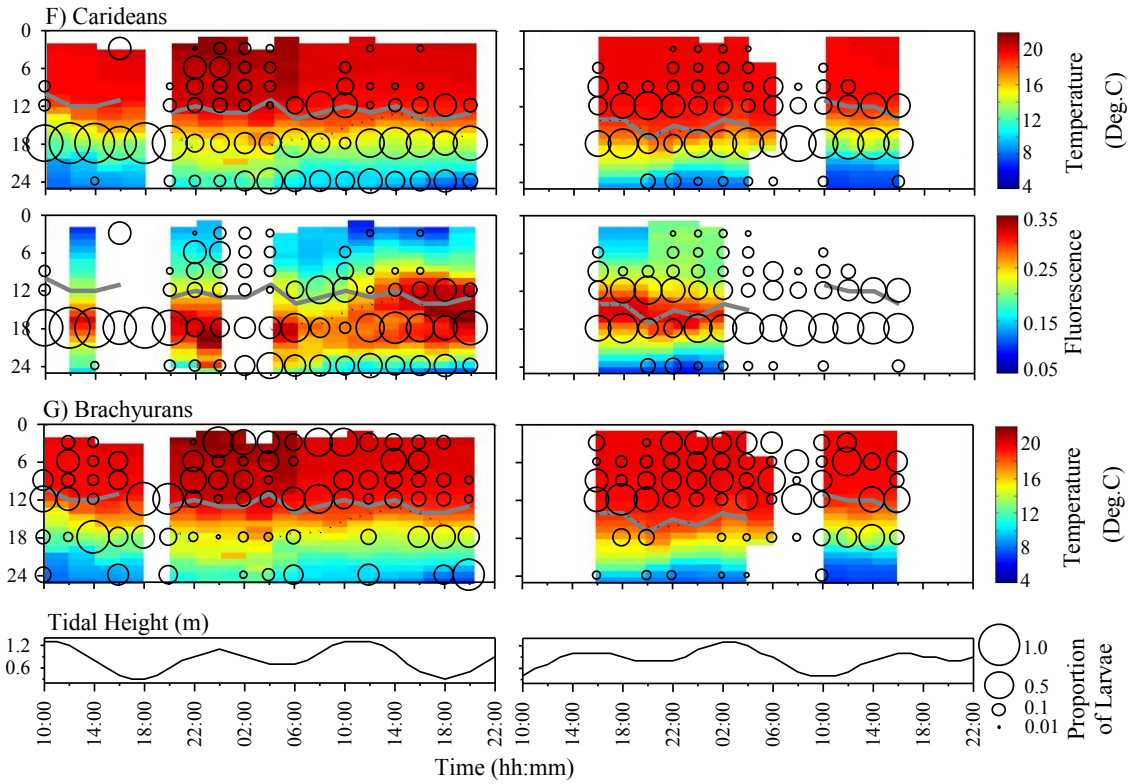


Figure 3.5 Vertical distribution of 7 taxonomic groups [(A) gastropods, (B) bivalves, (C) polychaetes, (D) bryozoans, (E) asteroids, (F) carideans, (G) brachyurans], over a 36- and 25-h period, during a spring (full moon: 6-7 Aug 2009) and neap (quarter moon: 12-13 Aug 2009) tide, respectively. Circle size indicates the proportional abundance of larvae for a particular sampling time. —— = thermocline, and ●●● = fluorescence maximum, □ = day and ■ = night. The colored contours represent: temperature and fluorescence. Only the significant factors are shown for each taxonomic group, as determined by simple and multiple (backwards stepwise) linear regressions.

Table 3.1 Significant relationships [simple or multiple (backwards stepwise) linear regression] that explained most of the variance in patterns of larval abundance of different taxonomic groups with different physical and biological variables (*T* = temperature, *F* = fluorescence, *w* = vertical velocity, *v* = North-South velocity, *u* = East-West velocity).

Taxon	Relationship with Larval Abundance	adj. R^2	$F_{(df)}$	p	Part Correlation Coefficient
Gastropods	= 23.22 - 5.172*T* + 2.699*F*	0.414	$36.37_{(2,98)}$	**<0.001**	*T*: -0.605 , *F*: 0.317
Bivalves	= 22.14 - 7.866*T*	0.461	$139.3_{(1,161)}$	**<0.001**	*T*: -0.681
Polychaetes	= 18.36 - 14.99*T*	0.646	$296.0_{(1,161)}$	**<0.001**	*T*: -0.805
Bryozoans	= 22.99 +6.442*F*	0.542	$119.3_{(1,99)}$	**<0.001**	*F*: 0.739
Asteroids	= 21.34 + 8.810*T*	0.469	$144.2_{(1,161)}$	**<0.001**	*T*: 0.687
Carideans	= 19.65 - 8.683*T* +10.57*F*	0.517	$54.43_{(2,98)}$	**<0.001**	*T*: -0.486, *F*: 0.594
Brachyurans	= 20.572 + 3.059*T*	0.04	$7.760_{(1,161)}$	**0.006**	*T*: 0.214

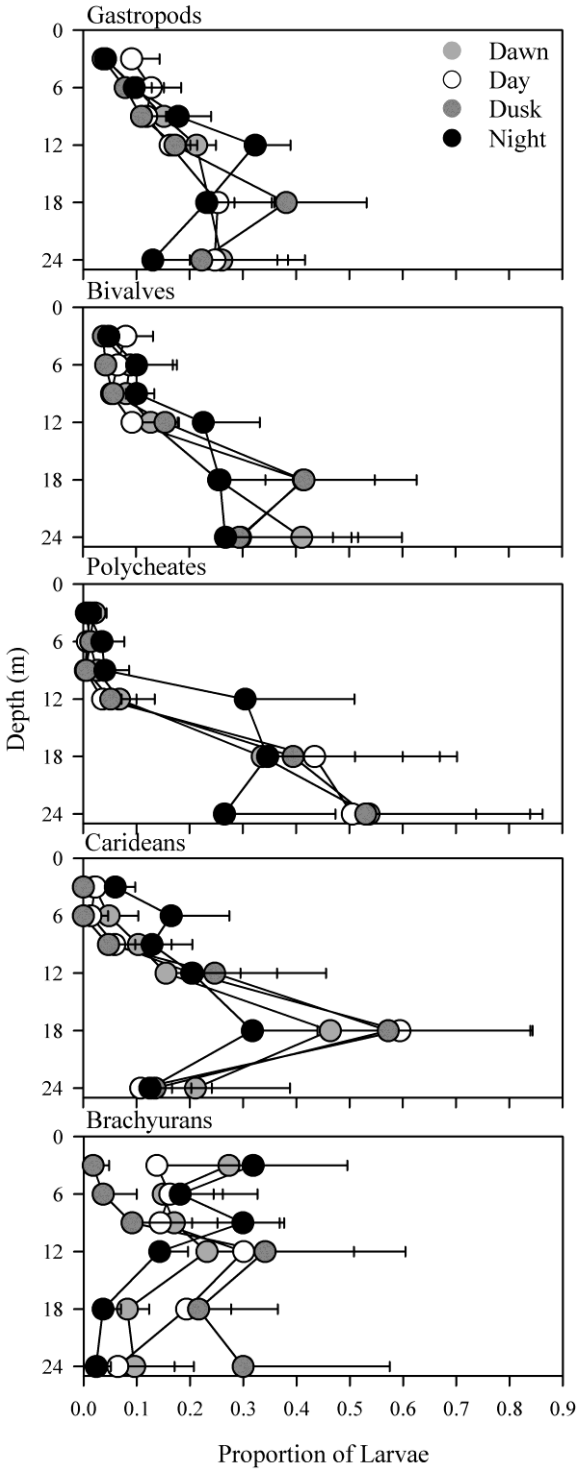


Figure 3.6 Larval vertical distribution of the proportional abundance of which 5 taxonomic groups (gastropods, bivalves, polychaetes, brachyurans and carideans) exhibited a significant interaction between depth and diel period (mean ± SD, n = 3 to 18) in St. George's Bay, Nova Scotia, Canada.

Table 3.2 Results of ANOVA examining the effects of diel period (dawn, day, dusk, night), and depth (3, 6, 9, 12, 18, 24 m) on the proportional abundance (arcsine square root transformed) of 7 taxonomic groups ($\alpha = 0.01$, significant p-valves indicated in bold). Numbers in multiple comparisons (Tukey's tests) represent depths (3, 6, 9, 12, 18 and 24 m). Only significant differences are shown. Depths separated by commas, are ordered sequentially (3 to 24 m), not according to relative larval abundance at each depth.

	Source	Diel Period (*D*)	Depth (*z*)	*D* x *z*	Error	Multiple Comparisons	
Taxon	df	3	5	15	162	**Factor**	**Low ——————————> High Abundance**
Gastropods	F-ratio	0.136	29.80	3.301		Dawn	3, 6 < 24; 3 < 9, 12, 18
	p-value	0.938	**<0.001**	**<0.001**		Day	3, 6, 9, 12 < 18, 24; 3 < 12
						Dusk	3, 6, 9, 12 <18; 3 < 12, 24
						Night	3, 6, 9, 24 < 12; 3, 6 < 18; 3 < 9
Bivalves	F-ratio	0.105	34.08	2.279		Dawn	3, 6, 9, 12 < 24; 3 < 18
	p-value	0.957	**<0.001**	**0.006**		Day	3, 6, 9, 12 < 24 < 18
						Dusk	3, 6, 9 < 18, 24
						Night	3, 6 < 18; 3 < 12, 24
Polychaetes	F-ratio	0.383	57.03	2.674		Dawn	3, 6, 9, 12 < 18, 24
	p-value	0.765	**<0.001**	**0.001**		Day	3, 6, 9, 12 < 18, 24
						Dusk	3, 6, 9, 12 < 18, 24
						Night	3, 6, 9 < 12, 18, 24
Bryozoans	F-ratio	0.150	51.00	1.599		Depth	3, 6, 9, 24 < 12 < 18; 3, 24 < 6, 9
	p-value	0.930	**<0.001**	0.079			
Asteroids	F-ratio	0.282	24.22	1.308		Depth	3, 9, 12, 18, 24 < 6; 12, 18, 24 < 3, 9; 18, 24 < 12
	p-value	0.838	**<0.001**	0.202			
Carideans	F-ratio	2.159	29.98	2.369		Dawn	3,6, 9 < 18
	p-value	0.095	**<0.001**	**0.004**		Day	3, 6, 9, 12, 24 < 18; 3, 6, 9 < 12
						Dusk	3, 6, 9, 12, 24 < 18; 3, 6 < 12
						Night	3 < 18
Brachyurans	F-ratio	0.356	2.436	2.759		Day	3, 24 < 12; 24 < 18
	p-value	0.785	0.037	**0.001**		Night	12, 18, 24 < 3, 9

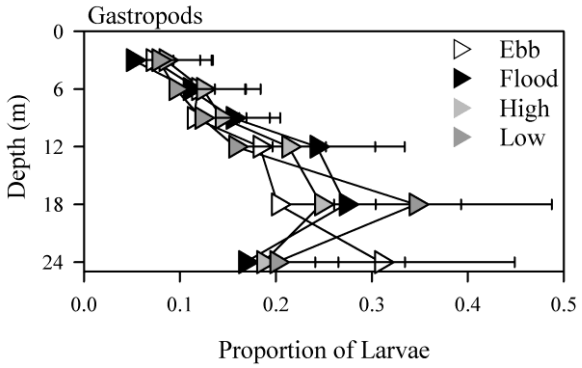


Figure 3.7 Larval vertical distribution of the proportional abundance of which 1 taxonomic group (gastropods) exhibited a significant interaction between depth and tidal phase (mean ± SD, n = 6 to 10) in St. George's Bay, Nova Scotia, Canada.

Table 3.3 Results of ANOVA examining the effects of tidal (ebb, flood, high, low) state and depth (3, 6, 9, 12, 18, 24 m) on the proportional abundance (arcsine square root transformed) of 7 taxonomic groups ($p < 0.01$, indicated in bold). Numbers in multiple comparisons (Tukey's tests) represent depths (3, 6, 9, 12, 18 and 24 m). Only significant differences are shown. Depths separated by commas, are ordered sequentially (3 to 24 m), not according to relative larval abundance at each depth.

Taxon	Source	Tidal Phase (*Ti*)	Depth (*z*)	*Ti* x *z*	Error		Multiple Comparisons
	df	3	5	15	162	**Factor**	**Low ———> High Abundance**
Gastropods	F-ratio	0.047	29.73	2.241		Ebb	3, 6, 9, 12 < 24; 3 < 12, 18
	p-value	0.986	**<0.001**	**0.007**		Flood	3, 6, 9 < 18; 3, 6 < 12; 3 < 9, 24
						High	3 < 12, 18
						Low	3, 6, 9, 12, 24 < 18; 3 < 24
Bivalves	F-ratio	0.005	50.44	1.429		Depth	3, 6, 9, 12 < 18, 24; 3 < 12
	p-value	1.000	**<0.001**	0.139			
Polychaetes	F-ratio	0.086	80.50	0.960		Depth	3, 6, 9, 12 < 18, 24; 3, 6, 9 < 12
	p-value	0.968	**<0.001**	0.500			
Bryozoans	F-ratio	0.099	75.60	0.434		Depth	3, 6, 9, 24 < 12 < 18; 3, 24 < 6, 9
	p-value	0.960	**<0.001**	0.967			
Asteroids	F-ratio	0.055	36.49	0.358		Depth	12, 18, 24 < 6; 18, 24 < 3, 9, 12
	p-value	0.983	**<0.001**	0.987			
Carideans	F-ratio	0.160	44.64	1.160		Depth	3, 6, 9 < 18; 3, 6, 9 < 12; 3, 6 < 24
	p-value	0.923	**<0.001**	0.308			
Brachyurans	F-ratio	0.273	4.790	1.189		Depth	24 < 9, 12
	p-value	0.845	**<0.001**	0.285			

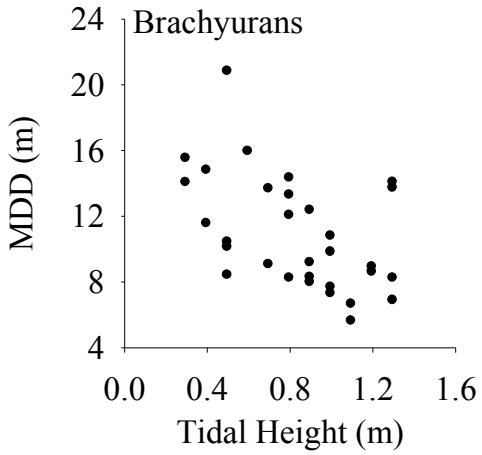


Figure 3.8 Relationships of larval mean depth distribution (MDD) of 1 taxonomic groups, brachyurans with tidal height, in St. George's Bay, Nova Scotia, Canada. Only significant relationships are shown.

3.5 Discussion

3.5.1 Spatial and Temporal Patterns in Vertical Distribution

I have demonstrated that the vertical distribution of larvae varies among taxonomic groups. All patterns can be grouped under one of the 3 categories: (1) larvae found exclusively in the mixed layer, (2) larvae associated predominantly with fluorescence maximum, and (3) larvae with dielly varying distributions. As a consequence, larvae in each of these categories experience different flow regimes, particularly where current intensity or direction are depth-dependent (Table 3.4).

Late-staged larval asteroids were the only taxonomic group to be found almost exclusively in the mixed layer. In general, echinoderm larvae (e.g. asteroid*, Odontaster validus*) are found to aggregate in the surface layer in field (Pearse and Bosh 1986; Greenwood et al. 2010) and laboratory studies (Young & Metaxas 1998; Sameoto & Metaxas 2008 a, b; Daigle & Metaxas in press). Even though larval asteroids are weak swimmers (e.g. *Asterias rubens*: 0.3 mm s^{-1}) (Chia et al. 1984), they may be able to actively regulate their vertical position within the water column. For example, early-stage larval asteroids (*Asterias rubens*) are known to swim to the surface, regardless of thermal structure of the water column (Daigle & Metaxas in press). Once within the surface layer, asteroid larvae may be able to actively maintain their position. A consequence of remaining within the mixed layer in my study may be a shortened planktonic duration, as a result of the warm temperatures there (~20 °C). However, the mixed layer in St. George's Bay has limited food, and most asteroids require food in order to develop and survive (Strathmann 1987). A shortened planktonic duration usually corresponds to

increased survival rate and potentially shorter dispersal time (Pechenik 1987). Asteroid dispersal is most likely the result of advection in the surface layer, potentially transporting larvae ~ 3.4 km westwards and ~1.9 km to the northwest of the sampling site during the full and quarter moons sampling period, respectively (Table 3.4). Over longer temporal scales, asteroids would be advected towards shore at most locations within the bay, promoting transport of these late-staged larvae towards potential settlement sites.

Larvae of bryozoans and carideans differ greatly in life histories, morphologies and swimming abilities, yet both were found to aggregate around the fluorescence maximum. Many bryozoans and carideans are planktotrophic, and while bryozoans feed exclusively upon phytoplankton (Strathmann 1987), only caridean stages I and II feed on phytoplankton (see Ouellet & Allard 2006). The vertical distribution of planktotrophic larvae is often related to the presence of food patches (Raby et al. 1994; Metaxas & Young 1998). Both bryozoan and caridean larvae have the chemosensory ability to detect food (Kingsford et al. 2002), and laboratory observations have shown directed movement towards food supply for the decapod, *Nihonotrypaea harmandi* (Tamaki et al. 2010). Once within the food patch, larvae may modify their swimming to remain within the patch (Metaxas & Young 1998), optimizing their feeding potential (Young 1995). In St. George's Bay, for bryozoans and carideans to remain within the layer of fluorescence maximum would require a combination of swimming and buoyancy. Bryozoans are small and weak swimmers compared to carideans (Chia et al. 1984), but probably less dense. Increased feeding opportunity can shorten planktonic larval duration, increasing their survival and potentially decreasing dispersal distance (Pechenik 1987). Larval bryozoans may be transported ~3.1 km to the northeast and ~3.8 km to the southeast of the sampling

site during the full and quarter moons, respectively (Table 3.4). Below the thermocline current velocities are relatively weak over longer temporal scales and bryozoans may be recirculated (i.e. retained) around the southern portion of St. George's Bay. Carideans would experience similar transport to the bryozoans, however, their horizontal transport pattern will also be affected by diel vertical migration (see below).

Diel vertical migration was exhibited by larval gastropods, bivalves, polychaetes, carideans and brachyurans, suggesting a potential adaptive significance to their migration. Light has been inferred as the cue that drives vertical migration for all these taxonomic groups (Petipa 1955 in Russian, as cited in Mileikovsky 1973; Daro 1974; Forward 1985), often as a result of negative phototaxis. This response may have evolved as a mechanism by which larvae may avoid predation (particularly visual predators such as fish) (Cronin & Forward 1986; Garland et al. 2002; dos Santos et al. 2008) and/or optimize feeding (as suggested for bivalves, Raby et al. 1994), increasing survival (Hays 2003). In St. George's Bay, fishes (*Gasterosteus aculeatus* and *Merluccius bilinearis*) are known to feed on larval gastropods, bivalves and crustaceans (Short et al. in revision). In my study, the mechanism driving the migratory behaviour is uncertain. However, gastropods, bivalves and polychaetes are known planktotrophic herbivores. These larvae may either feed below the thermocline during the day and migrate into the mixed layer at night, or migrate from the seafloor to the fluorescence maximum layer (13-18 m depth) at night to potentially feed.

The magnitude of diel vertical migration varied among taxonomic groups, potentially leading to differences in dispersal distance and direction. Gastropods, bivalves and polychaetes migrated a distance of ~6-12 m, from the seafloor to just above the

thermocline at night, while carideans and brachyurans migrated a distance >12 m, from below the thermocline to the surface. This difference in magnitude may result from differences in size, ontogenetic stage, or swimming abilities. Due to their small size and weak swimming abilities, larval gastropods, bivalves and polychaetes may be unable to migrate the total water column depth. Decapod larvae are known to vertically migrate the greatest distances (20-50 m; dos Santos et al. 2008), whereas bivalve vertical migrations tend to be short (~5 m; Tremblay & Sinclair 1990a). As a consequence, these taxonomic groups experience different flow regimes and may have very different dispersal patterns and pathways. In St. George's Bay below the thermocline during the day, all taxonomic groups would experience slow, direct transport either to the northeast during the full moon or to the southeast during the quarter moon. When brachyurans and carideans vertically migrate to the surface at night, they would encounter currents at the surface that generally flow westwards or to the northwest during the full and quarter moon, respectively. Thus, this vertical migration would promote retention in the vicinity of the sampling site. Gastropods, bivalves and polychaetes migrated to just above the thermocline at night, also promoting retention in the vicinity of the sampling site during the full moon. At this time, transport during the day would be ~ 2.2 km to the northeast and at night ~3.9 km to the northwest (Table 3.4). Over longer temporal scales, the dispersal potential of all taxonomic groups may be similar since current velocities above the thermocline (i.e. mixed layer) are similar in magnitude (Table 3.4). Since current velocities in the mixed layer are 2-5 times stronger than below the thermocline, gastropod, bivalve, polychaete, brachyuran and caridean larvae may be retained during

the day, and advected clockwise around the southern portion of St. George's Bay at night (Fig. 3.2 & Table 3.4).

In addition to performing diel migration, gastropods and brachyurans appeared to alter their vertical position in relation to changes in tidal state. Tidally timed migration has been attributed to perceived cues of changes in pressure (Forward & Wellins 1989), and both mollusc and brachyuran larvae are known to swim upwards in response to increases in hydrostatic pressure (Forward & Wellins 1989; Kingsford et al. 2002). However, gastropod and brachyuran larvae are also known to respond to light, and there may be interactions between light and tidal cues which cannot be resolved within the sampling periods in this study. In general, gastropods appeared near the seafloor during ebbing tide and shallower in the water column during other tidal states, potentially promoting retention. The mean depth distribution of brachyurans indicated that larvae were in the mixed layer during high tide and below the thermocline during low tide, perhaps modifying the direction of their horizontal transport to also promote retention.

Table 3.4 Summary of all taxonomic groups larval transport over short (38-h) and long (43-d) temporal scales based on their vertical distribution at my sampling site in St. George's Bay, Nova Scotia, Canada. Short and long temporal scale estimates are based on Fig. 3.3 and 3.2, respectively. N = north, S = south, W = west, E = east.

Category	Taxonomic Group	Larval Transport		
		Short Temporal Scale		Long Temporal Scale
		38-h (Full Moon)	38-h (Quarter Moon)	43-d
In the Mixed Layer	Asteroids	3.4 km W	1.9 km NW	SW
Associated with Fluorescence Maximum	Bryozoans Carideans	3.1 km NE	3.8 km SE	NE
Vary with Diel Period	Gastropods Bivalves Polychaetes	2.2 km NNE at day 3.9 km NW at night 5.5 km NW (net)	3.0 km SE at day 0.5 km SWW at night 3.0 km SE (net)	NE at day SW at night
	Carideans Brachyurans	2.2 km NNE at day 1.4 km SE at night 1.5 km NE (net)	3.0 km SE at day 0.8 km NE at night 3.4 km SE (net)	NE at day SW at night

3.5.2 Linking Behavioural Responses to Field Vertical Distributions

Laboratory studies are often used to provide first order estimate of larval behaviour in the field, and field larval distributions measured at high temporal frequencies can be used to test the validity of these first order estimates. I observed vertical distributions of bivalve and asteroid larvae in the field that are similar to those reported in laboratory studies (Gallager et al. 1996; Sameoto & Metaxas 2008b; Daigle & Metaxas in press). For example asteroids, swim upwards and remain in the upper layers of the water column (Sameoto & Metaxas 2008b; Daigle & Metaxas in press). Larvae remain below a discontinuity, when temperatures above the thermocline exceed 24 °C (Daigle & Metaxas in press) or the halocline is strong ($\Delta S > 8$; Sameoto & Metaxas 2008b). I observed planktotrophic herbivores aggregated around or within the fluorescence maximum in the field, that are explained by behaviours observed in laboratory studies (Metaxas & Young 1998; Burdett-Coutts & Metaxas 2004; Sameoto & Metaxas 2008b). In the laboratory, bivalves migrated towards the food when it was present (Sameoto & Mataxas 2008b). Changes in the vertical distribution of bivalves with respect to diel period is observed both in the field and laboratory (Tremblay & Sinclair 1990a; Gallager et al. 1996), and the range of migration observed in both settings appears to coincide with the discontinuity layer. For example the bivalve *Placopecten magellunicus* was found in high abundance at the surface at night, and at the thermocline during the day, regardless of vertical position of food (Tremblay & Sinclair 1990b; Gallager et al. 1996). In agreement with the studies, I observed bivalve migration from the seafloor to the thermocline at night. Therefore, simple behaviours of bivalves and asteroids measured in laboratory studies can be used to explain general patterns observed

in the field, and used to derive biological parameters. To my knowledge, there have been no studies examining responses of gastropods, polychaetes, bryozoans and carideans to physical (temperature, salinity, current velocity, light) and biological (food) cues, with the exception of one study examining carideans response to thermal gradients (Ouellet & Allard 2006).

Unlike bivalves and asteroids, few generalizations can be made about the behaviour of brachyurans. Most brachyurans respond to light and pressure cues in field and laboratory studies (Forward 1985; Cronin & Forward 1986; Forward & Wellins 1989; Garrison 1999), which concurs with my observations. However, the response varies among species and developmental stages (Forward 1985; Cronin & Forward 1986; Forward & Wellins 1989; Garrison 1999). In the laboratory, early- and late-stage behavioural responses were different (Cronin & Forward 1986), while field studies have shown different species and larval stages (zoea and megalopae) exhibiting different vertical distributions under the same environmental conditions (Brookins & Epifanio 1985; Cronin & Forward 1986; Garrison 1999; DiBacco et al. 2001). For example, megalopae were found near the surface at flooding tide, while zoea were at the surface during ebbing tide (Brookins & Epifanio 1985). Also zoea of *Pachygrapsus crassipes* exhibited vertical migration while those of *Lophopanopeus* spp. did not under the same tidal state and flow regime (DiBacco et al. 2001). The complexity of responses by brachyurans requires the collection of species-, stage- and system- specific information that can be used in the parameterization of their behaviour.

3.5.3 Summary and Conclusion

I found that the vertical distribution of each taxonomic groups could be described either as (1) found exclusively in the mixed layer, (2) being associated predominantly with fluorescence maximum, or (3) varying with diel period. Larvae in the mixed layer are likely to be more dispersive than those associated with the fluorescence maximum, and diel vertical migration between layers may increase retention and decrease transport (Table 3.4). For all taxonomic groups for which data exist (e.g. bivalves, asteroids), the behaviours observed in the field agree with those measured in the laboratory, except for brachyurans, where the response is species-, stage-, and/or system-specific. For most taxonomic groups, simple field measurements of water-column structure (e.g. temperature and fluorescence profile) in the field linked to behavioural responses in the laboratory, can be used to improve the parameterization of biological components of bio-physical models. For each taxonomic group, the behavioural component of the model can be relatively simple. With valid biological parameters, we can ultimately improve the quality of dispersal estimates generated using biophysical models for different taxonomic groups.

CHAPTER 4

Discussion

This thesis documents that patterns in larval vertical distribution vary among taxa within the gastropods, and among taxonomic groups of different benthic invertebrates. However, general patterns emerged from this variation. The vertical distributions of larval gastropods are most strongly related to the location of the thermocline or the fluorescence maximum, and/or the phases of the diel period and/or lunar phase. For different taxonomic groups, larval distributions fell into one of 3 categories: (1) larvae found exclusively in the mixed layer; (2) larvae associated predominantly with fluorescence maximum; and (3) larval distributions varying with diel period. For bivalves and asteroids, association of field observations with behavioural responses obtained in laboratory studies can point to specific behavioural components that can be incorporated into bio-physical models. For brachyurans, field observations could not be associated with behavioural responses obtained in the laboratory, because the complexity of their responses requires the collection of species-, stage- and system-specific information. For gastropods, polychaetes, bryozoans and carideans, measurements of specific responses to cues (temperature, food, light etc.) in the laboratory are currently lacking and field observations therefore cannot be linked at the moment to quantified behavioural responses.

Using high temporal frequencies and spatial resolution of field distributions of larvae, this thesis tested the validity of some of the first order estimates of larval behaviour based on laboratory studies. However, more studies on larval vertical

distribution both in the laboratory and field are needed. Controlled laboratory experiments examining behavioural responses of gastropod, polychaete, bryozoan and caridean larvae to physical (e.g. temperature, salinity, discontinuities, pressure, light, etc.) and biological (food, predators, conspecifics) cues, as well as combinations of these cues (e.g. diel period and tidal state cues) should be performed. In the field, studies over long sampling periods (>36 h), and at high temporal frequency (e.g. 2 h) and spatial resolution (e.g. 2-3 m) sampling, encompassing multiple diel periods and tidal states, may resolve the interactions between diel and tidal cues. In particular, differences in vertical distributions between early and late larval stages are needed, in particular for crustaceans. Laboratory studies show that many larvae modify their vertical position in the presence of stratification, however parallel studies are lacking for many species in the field.

In recent years a shift from single species to ecosystem-based management (e.g. understanding invasive species, establishment of marine protected areas, resiliency of population to human exploitation) has occurred, fuelling the need to understand how larval dispersal influences patterns of diversity, resilience, and source/sink dynamics of species and communities. The Population Connectivity theme of the Canadian Healthy Oceans Network (CHONe) is attempting to partially address these questions, using a multidisciplinary approach and a model system (St. George's Bay, Nova Scotia). My thesis provides high temporal frequency and spatial resolution of the vertical distribution of a variety of meroplanktonic larvae, and simple behavioural responses for use in a bio-physical model. Associated studies include: (1) bay- and small-scale resolution of horizontal distributions of larvae; (2) biological null model to validate hydrodynamic models and assess the purely passive component of biological connectivity; and (3) a

hydrodynamic circulation model in St. George's Bay. The combination of these studies will eventually help us to understand how metapopulations of key species are interconnected, and resolve the role of larval behaviour in dispersal.

References

Appeltans W, Bouchet P, Boxshall GA, Fauchald K, Gordon DP, Hoeksema BW, Poore GCB, van Soest RWM, Stöhr S, Walter TC, Costello MJ. (eds) (2011). World Register of Marine Species. Accessed at http://www.marinespecies.org on 2011-10-06.

Baker P and Mann R (2003) Late stage bivalve larvae in a well-mixed estuary are not inert particles. Estuaries and Coasts 26:837-845

Brookins KG and Epifanio CE (1985) Abundance of brachyuran larvae in a small coastal inlet over 6 consecutive tidal cycles. Estuaries 8:60-67

Brunel P, Bossé L, Lamarche G (1998) Catalogue of the marine invertebrates of the estuary and gulf of Saint Lawrence. Can Spec Publ Fish Aqua Sci 126:1-1-391

Burdett-Coutts V and Metaxas A (2004) The effect of the quality of food patches on larval vertical distribution of the sea urchins *Lytechinus variegatus* (lamarck) and *Strongylocentrotus droebachiensis* (mueller). J Exp Mar Ecol 308:221-236

Chia FS, Buckland-Nicks J, Young CM (1984) Locomotion of marine invertebrate larvae - a review. Can J Zool Rev Can Zool 62:1205-1222

Cowen RK, Gawarkiewic G, Pineda J, Thorrold SR, Werner FE (2007) Population connectivity in marine systems an overview. Oceanography 20:14-21

Cronin TW and Forward RB (1986) Vertical migration cycles of crab larvae and their role in larval dispersal. Bull Mar Sci 39:192-201

Daigle RM and Metaxas A (in press) Vertical distribution of marine invertebrate larvae in response to thermal stratification in the laboratory. J Exp Mar Biol Ecol

Daro MH (1974) Study of nycthemaral migrations of zooplankton in a shallow marine biotope. Hydrobiologia 44:149-160

DiBacco C, Sutton D, McConnico L (2001) Vertical migration behavior and horizontal distribution of brachyuran larvae in a low-inflow estuary: Implications for bay-ocean exchange. Mar Ecol Prog Ser 217:191-206

dos Santos A, Santos AMP, Conway DVP, Bartilotti C, Lourenco P, Queiroga H (2008) Diel vertical migration of decapod larvae in the portuguese coastal upwelling ecosystem: Implications for offshore transport. Mar Ecol Prog Ser 359:171-183

Forward RB (1988) Diel vertical migration - zooplankton photobiology and behavior. Oceanogr Mar Biol 26:361-393

Forward RB (1985) Behavioral-responses of larvae of the crab *Rhithropanopeus harrisii* (Brachyura, Xanthidae) during diel vertical migration. Mar Biol 90:9-18

Forward RB and Wellins C (1989) Behavioral responses of a larval crustacean to hydrostatic pressure: *Rhithropanopeus harrisii* (Brachyura: Xanthidae). Mar Biol 101:159-172

Fuchs HL, Mullineaux LS, Solow AR (2004) Sinking behavior of gastropod larvae (*Ilyanassa obsoleta*) in turbulence. Limnol Oceanogr 49:1937-1948

Gallager S, Manuel J, Manning D, O'Dor R (1996) Ontogenetic changes in the vertical distribution of giant scallop larvae, *Placopecten magellanicus*, in 9-m deep mesocosms as a function of light, food, and temperature stratification. Mar Biol 124:679-692

Garland ED, Zimmer CA, Lentz SJ (2002) Larval distributions in inner-shelf waters: The roles of wind-driven cross-shelf currents and diel vertical migrations. Limnol Oceanogr 43:803-817

Garrison LP (1999) Vertical migration behavior and larval transport in brachyuran crabs. Mar Ecol Prog Ser 176:103-113

Garrison LP and Morgan JA (1999) Abundance and vertical distribution of drifting, post-larval *Macoma* spp. (Bivalvia : Tellinidae) in the York River, Virginia, USA. Mar Ecol -Prog Ser 182:175-185

Greenwood A, O'Riordan R, Barnes D (2001) Seasonality and vertical zonation of zooplankton in a semi-enclosed sea lough. J Mar Biol Assoc UK 81:213-220

Hays GC (2003) A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. Hydrobiologia 503:163-170

Kingsford MJ, Leis JM, Shanks AL, Lindeman KC, Morgan SG, Pineda J (2002) Sensory environments, larval abilities and local self-recruitment. Bull Mar Sci 70:309-340

Lebour MV (1937) The eggs and larvae of the British prosobranchs with special reference to those living in the plankton. J Mar Biol Assoc U K 22:105-166

Lesperance M, deYoung B, Foley J (2011) Analysis of physical oceanographic data from St. George's Bay, NS July-August 2009. Physics and Physical Oceanography Data Report 2011-1:1-23 (http://www.physics.mun.ca/~bdeyoung/2009report_8feb2011.pdf)

Levin LA (2006) Recent progress in understanding larval dispersal: New directions and digressions. Integr Comp Biol 46:282-297

Lima GM and Pechenik JA (1985) The influence of temperature on growth-rate and length of larval life of the gastropod, *Crepidula plana* Say. J Exp Mar Biol Ecol 90:55-71

Mann R, Campos BM, Luckenbach MW (1991) Swimming rate and responses of larvae of 3 mactrid bivalves to salinity discontinuities. Mar Ecol Prog Ser 68:257-269

Manuel JL and O'Dor RK (1997) Vertical migration for horizontal transport while avoiding predators: I. A tidal/diel model. J Plankton Res 19:1929-1947

Manuel JL, Pearce CM, O'Dor RK (1997) Vertical migration for horizontal transport while avoiding predators: II. evidence for the tidal/diel model from two populations of scallop (*Placopecten magellanicus*) veligers. J Plankton Res 19:1949-1973

Manuel JL, Gallager SM, Pearce CM, Manning DA, ODor RK (1996) Veligers from different populations of sea scallop *Placopecten magellanicus* have different vertical migration patterns. Mar Ecol Prog Ser 142:147-163

McConnaughey RA and Sulkin SD (1984) Measuring the effects of thermoclines on the vertical migration of larvae of *Callinectes sapidus* (Brachyura: Portunidae) in the laboratory. Mar Biol 81:139-145

McEdward L (ed) (1995) Ecology of marine invertebrate larvae CRC Press, Inc., Boca Raton, Florida, USA, p.464

Metaxas A (2001) Behaviour in flow: Perspectives on the distribution and dispersion of meroplanktonic larvae in the water column. Can J Fish Aqua Sci 58:86-98

Metaxas A and Saunders MI (2009) Quantifying the "bio-" components in biophysical models of larval transport in marine benthic invertebrates: Advances and pitfalls. Biol Bull 216:257-272

Metaxas A and Burdett-Coutts V (2006) Response of invertebrate larvae to the presence of the ctenophore *Bolinopsis infundibulum*, a potential predator. J Exp Mar Ecol 334:187-195

Metaxas A and Young CM (1998) Responses of echinoid larvae to food patches of different algal densities. Mar Biol 130:433-445

Mileikovsky S (1973) Speed of active movement of pelagic larvae of marine bottom invertebrates and their ability to regulate their vertical position. Mar Biol 23:11-17

Morgan SG (1995) Life and death in the plankton: Larval mortality and adaptation. In: McEdward L (ed) Ecology of Marine Invertebrate Larvae. CRC Press, Boca Raton, Florida, USA, p. 279-322

Ohman MD, Frost BW, Cohen EB (1983) Reverse diel vertical migration - an escape from invertebrate predators. Science 220:1404-1407

Ouellet P and Allard JP (2006) Vertical distribution and behaviour of shrimp *Pandalus borealis* larval stages in thermally stratified water columns: Laboratory experiment and field observations. Fish Oceanogr 15:373-389

Pearce CM, Gallager SM, Manuel JL, Manning DA, ODor RK, Bourget E (1996) Settlement of larvae of the giant scallop, *Placopecten magellanicus*, in 9-m deep mesocosms as a function of temperature stratification, depth, food, and substratum. Mar Biol 124:693-706

Pearse JS and Bosch I (1986) Are the feeding larvae of the commonest antarctic asteroid really demersal? Bull Mar Sci 39:477-484

Pechenik JA (1999) On the advantages and disadvantages of larval stages in benthic marine invertebrate life cycles. Mar Ecol Prog Ser 177:269-269–297

Pechenik JA (1987) Environmental influences on larval survival and development. In: Giese AC, Pearse JS and Pearse VB (eds) Reproduction of Marine Invertebrates, IX, General Aspects: Seeking Unity in Diversity. The Boxwood Press, Pacific Grove, CA, USA, p. 551-551-608

Pennington JT and Emlet RB (1986) Ontogenic and diel vertical migration of a planktonic echinoid larva, *Dendraster excentricus* (eschscholtz) - Occurrence, causes, and probable consequences. J Exp Mar Biol Ecol 104:69-95

Petipa TS (1955) Observations on zooplankton behavior during the solar eclipse. Dokl Akad Nauk SSSR 104:323-323-325

Petrie B and Drinkwater K (1977) Physical oceanographic measurements in St. George's Bay, Nova Scotia. Report Series BI-R-77-5 June 1977.. 1-78

Pineda J (2000) Linking larval settlement to larval transport: Assumptions, potentials, and pitfalls. Oceanogr East Pacific 1:84-105

Pineda J, Hare JA, Sponaugle S (2007) Larval transport and dispersal in the coastal ocean and consequences for population connectivity. Oceanography 20:22-39

Poulin E, Palma AT, Leiva G, Narvaez D, Pacheco R, Navarrete SA, Castilla JC (2002) Avoiding offshore transport of competent larvae during upwelling events: The case of the gastropod *Concholepas concholepas* in central chile. Limnol Oceanogr 47:1248-1255

Raby D, Lagadeuc Y, Dodson JJ, Mingelbier M (1994) Relationship between feeding and vertical distribution of bivalve larvae in stratified and mixed waters. Mar Ecol Prog Ser 103:275-275

Roughgarden J, Pennington T, Alexander S (1994) Dynamics of the rocky intertidal zone with remarks on generalization in ecology. Philos Trans R Soc Lond Ser B-Biol Sci 343:79-85

Sameoto JA and Metaxas A (2008a) Can salinity-induced mortality explain larval vertical distribution with respect to a halocline? Biol Bull 214:329-338

Sameoto JA and Metaxas A (2008b) Interactive effects of haloclines and food patches on the vertical distribution of 3 species of temperate invertebrate larvae. J Exp Mar Biol Ecol 367:131-141

Scheltema RS (1967) Relationship of temperature to larval development of *Nassarius obsoletus* (Gastropoda). Biol Bull 132:253-265

Shanks AL (ed) (2001) An identification guide to the larval marine invertebrates of the Pacific Northwest. Oregon State University Press, Corvallis, Oregon, USA, p.314

Shanks AL (1995) Mechanisms of cross-shelf dispersal of larval invertebrates and fish. In: McEdward LR (ed) Ecology of marine invertebrate larvae. CRC Press, Inc., Boca Raton, Florida, p. 323-367

Short J, Metaxas A, Daigle RM (in revision) Predation of larval benthic invertebrates in St. George's Bay, Nova Scotia.

Strathmann MF (1987) Reproduction and development of marine invertebrates of the Northern Pacific coast: data and methods for the study of eggs, embryos, and larvae. University of Washington Press, Seattle, USA, p. 670

Strathmann RR (1987) Larval feeding. In: Giese AC, Pearse JS and Pearse VB (eds) Reproduction of Marine Invertebrates, IX, General Aspects: Seeking Unity in Diversity. The Boxwood Press, Pacific Grove, CA, USA, p. 465-550

Tamaki A, Mandal S, Agata Y, Aoki I, Suzuki T, Kanehara H, Aoshima T, Fukuda Y, Tsukamoto H, Yanagi T (2010) Complex vertical migration of larvae of the ghost shrimp, *Nihonotrypaea harmandi*, in inner shelf waters of Western Kyushu, Japan. Estuar Coast Shelf Sci 86:125-136

Tapia FJ, DiBacco C, Jarrett J, Pineda J (2010) Vertical distribution of barnacle larvae at a fixed nearshore station in southern California: Stage-specific and diel patterns. Estuar Coast Shelf Sci 86:265-270

Tremblay MJ and Sinclair MM (1990a) Diel vertical migration of sea scallop larvae *Placopecten-magellanicus* in a shallow embayment. Mar Ecol Prog Ser 67:19-25

Tremblay MJ and Sinclair MM (1990b) Sea scallop larvae *Placopecten-magellanicus* on Georges Bank - vertical-distribution in relation to water column stratification and food. Mar Ecol Prog Ser 61:1-15

Young CM (1995) Behavior and locomotion during the dispersal phase of larval life. In: McEdward L (ed) Ecology of marine invertebrate larvae. CRC Press, Boca Raton, Florida, USA, p. 249-278

Young CM and Chia FS (1987) Abundance and distribution of pelagic larvae as influenced by predation, behavior, and hydrographic factors. In: Giese AC, Pearse JS and Pearse VB (eds) Reproduction of Marine Invertebrates, IX, General Aspects: Seeking Unity in Diversity. The Boxwood Press, Pacific Grove, CA, USA, p. 385-464

Appendix A

Pearson Correlation Coefficients

Table A.1 Pearson correlation coefficients for all pairs of physical variables: T = temperature (°C), S = salinity, ρ = density (kg m-3), F = fluorescence, w = vertical velocity (mm s^{-1}), v = North-south velocity (mm s^{-1}), and u = East-West velocity (mm s^{-1}). Bold values indicate significantly correlated variables; n = sample size.

		T	S	ρ	F	w	v	u
T	r	1	-0.884	-0.992	0.124	0.132	0.017	-0.167
	p		**<0.001**	**<0.001**	0.218	0.123	0.848	0.051
	n	163	116	116	101	137	137	137
S	r		1	0.931	-0.335	0.004	0.104	0.082
	p	-		**<0.001**	**0.002**	0.965	0.307	0.424
	n		116	116	83	98	98	98
D	r			1	-0.230	-0.079	-0.051	0.087
	p	-	-		0.037	0.438	0.619	0.395
	n			116	83	98	98	98
F	r				1	-0.092	-0.032	0.077
	p	-	-	-		0.402	0.770	0.482
	n				101	85	85	85
w	r					1	0.326	-0.350
	p	-	-	-	-		**<0.001**	**<0.001**
	n					155	155	155
v	r						1	-0.068
	p	-	-	-	-	-		0.398
	n						155	155
u	r							1
	p	-	-	-	-	-	-	
	n							155

Appendix B

Larval Vertical Distributions of Gastropods in Relation to Structure

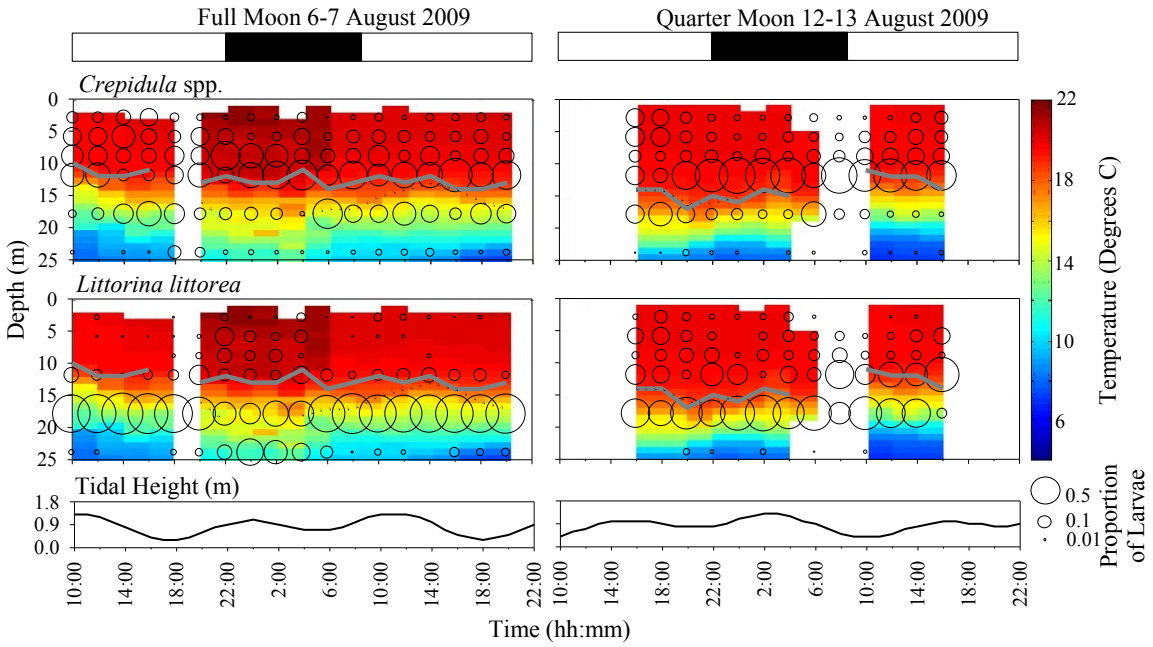
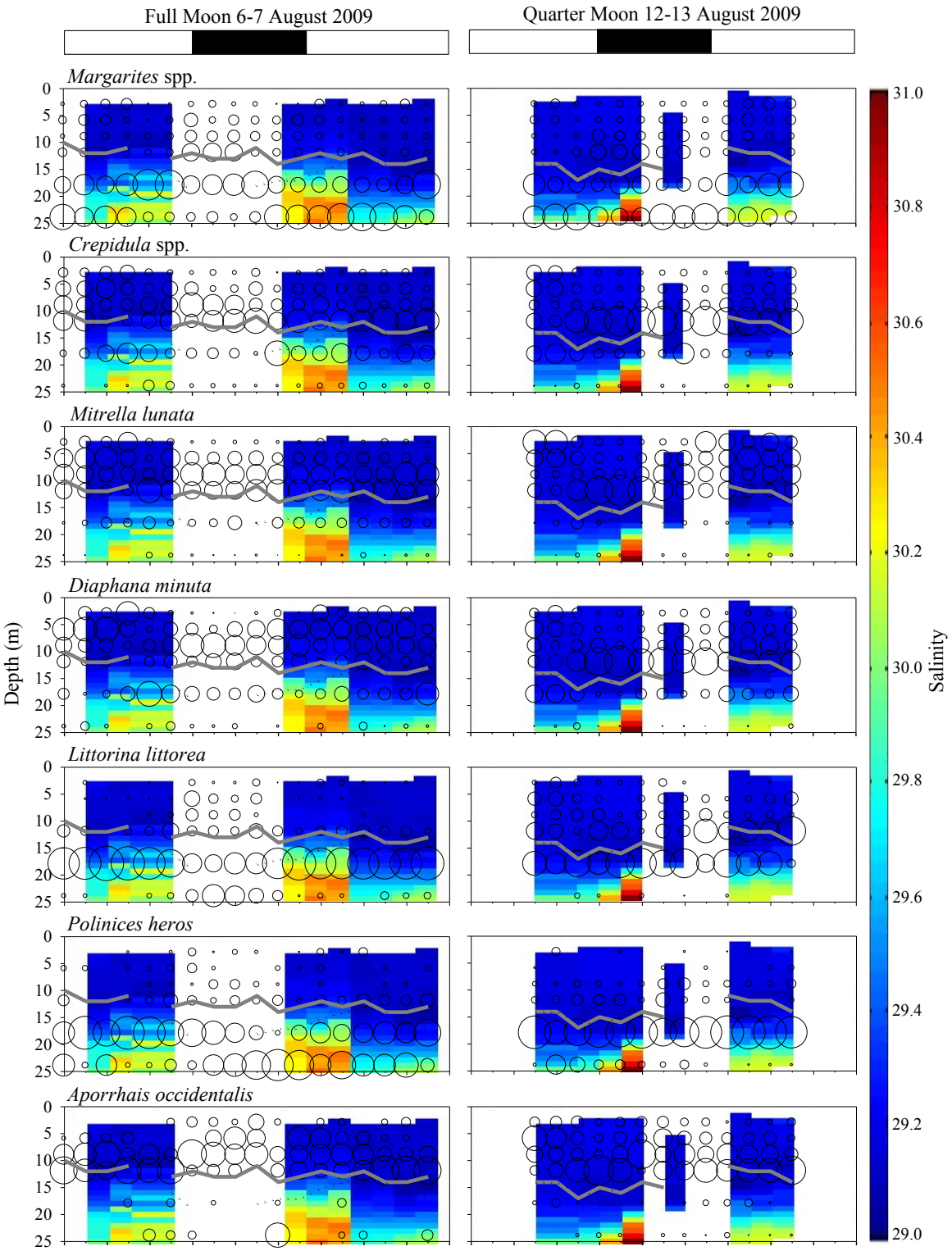


Figure B.1 Vertical distribution of *Crepidula* spp. and *Littorina littorea* in relation to the structure in temperature in St. George's Bay, Nova Scotia, Canada, over a 36- and 25-h period, during a spring (full moon: 6-7 Aug 2009) and neap (quarter moon: 12-13 Aug 2009) tide, respectively. Circle size indicates the proportional abundance of larvae for a particular sampling time. — = thermocline, and ●●● = fluorescence maximum, ☐ = day and ■ = night. The colored contours represent temperature.


Full Moon 6-7 August 2009
Quarter Moon 12-13 August 2009
Margarites spp.
Crepidula spp.
Mitrella lunata
Diaphana minuta
Littorina littorea
Polinices heros
Aporrhais occidentalis
Depth (m)
0
5
10
15
20
25
Salinity
31.0
30.8
30.6
30.4
30.2
30.0
29.8
29.6
29.4
29.2
29.0

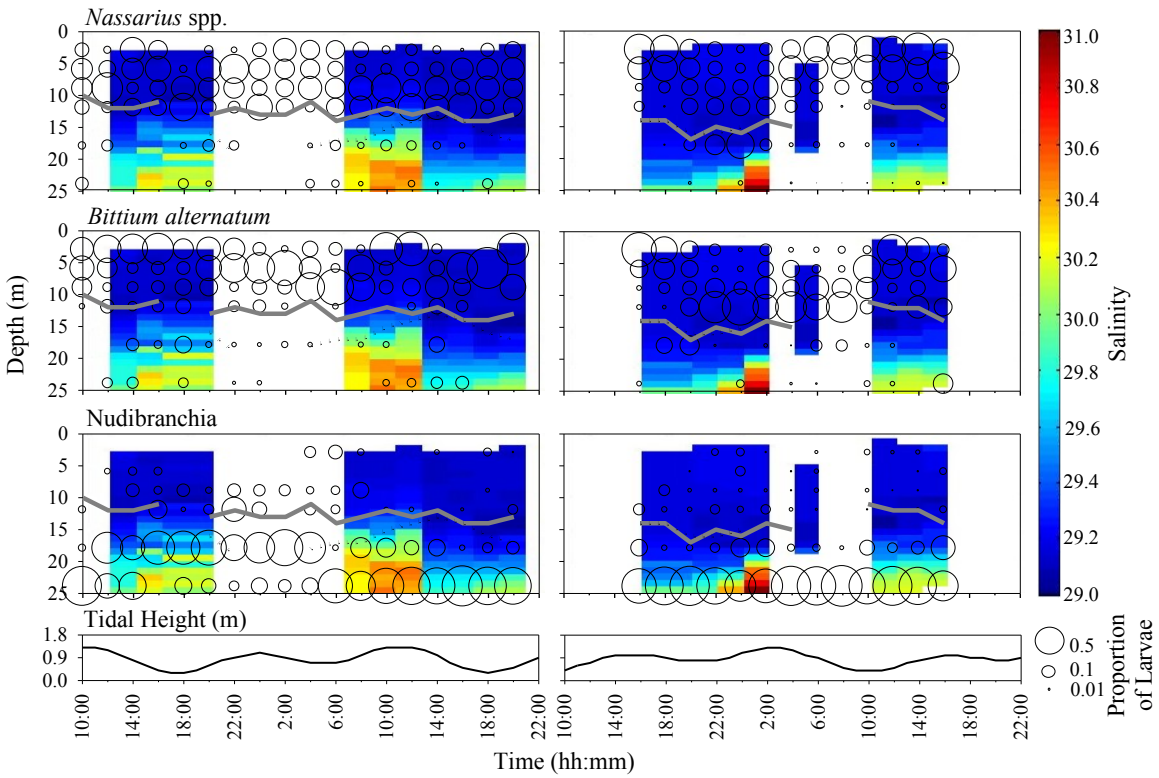


Figure B.2 Vertical distribution of all identified gastropod taxa in relation to the structure in salinity in St. George's Bay, Nova Scotia, Canada, over a 36- and 25-h period, during a spring (full moon: 6-7 Aug 2009) and neap (quarter moon: 12-13 Aug 2009) tide, respectively. Circle size indicates the proportional abundance of larvae for a particular sampling time. ⎯ = thermocline, and ●●● = fluorescence maximum, ☐ = day and ■ = night. The colored contours represent salinity.

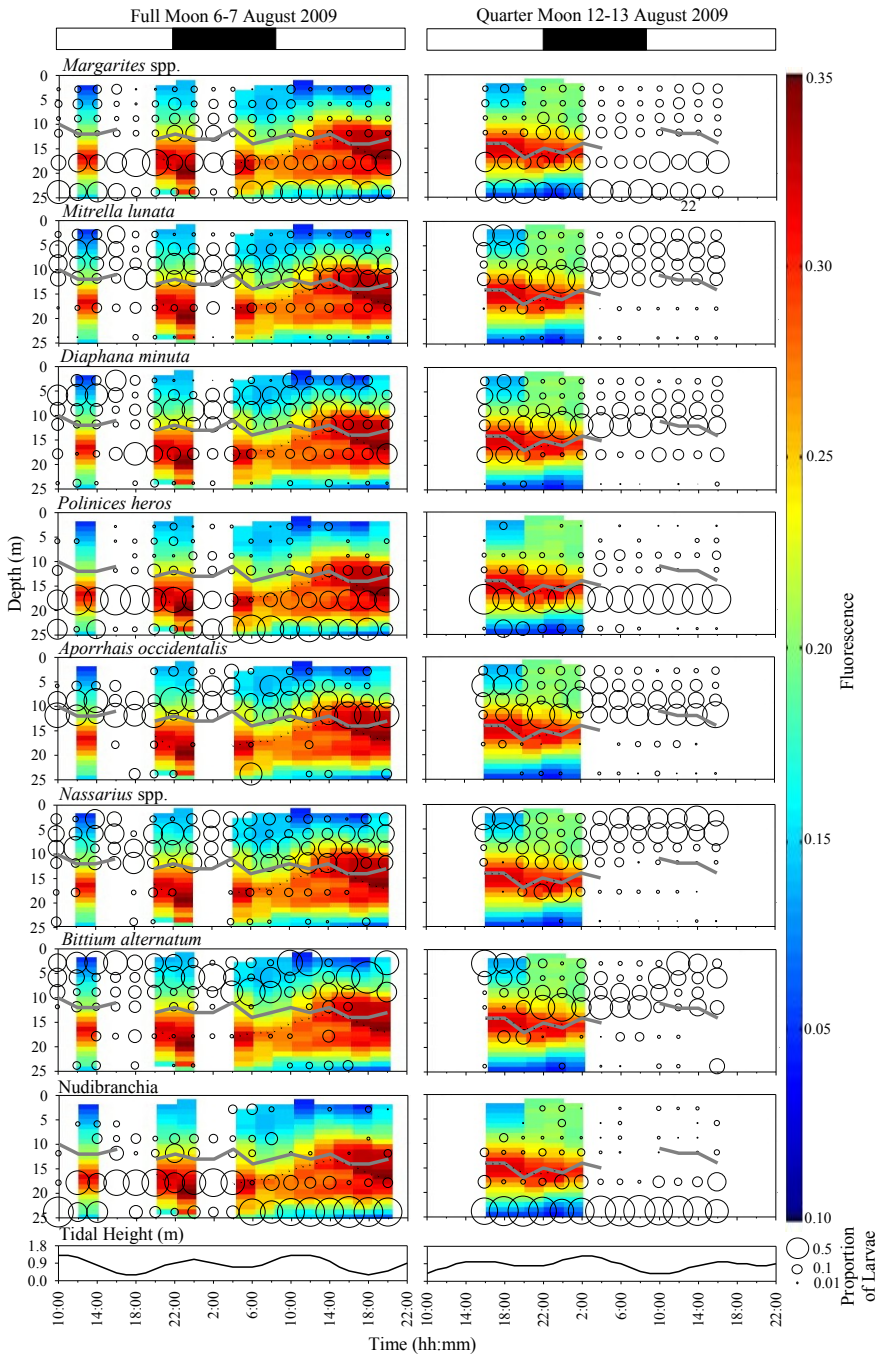
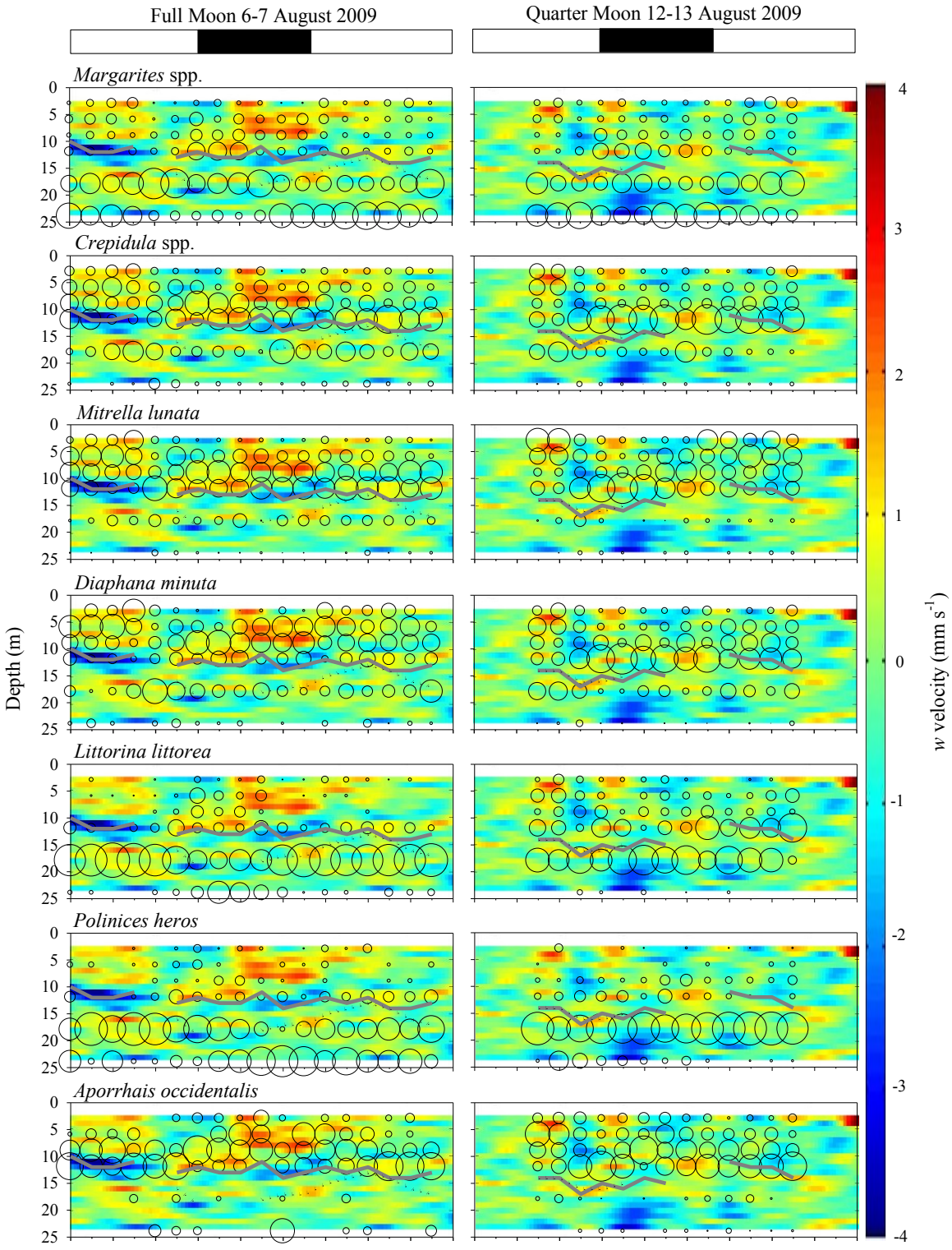


Figure B.3 Vertical distribution of *Margarites* spp., *Mitrella lunata*, *Diaphana minuta*, *Polinices heros*, *Aporrhais occidentalis*, *Nassarius* spp., *Bittium alternatum* and Nudibranchia in relation to the structure in fluorescence in St. George's Bay, Nova Scotia, Canada, over a 36- and 25-h period, during a spring (full moon: 6-7 Aug 2009) and neap (quarter moon: 12-13 Aug 2009) tide, respectively. Circle size indicates the proportional abundance of larvae for a particular sampling time. —— = thermocline, and ●●● = fluorescence maximum, □ = day and ■ = night. The colored contours represent fluorescence.


Full Moon 6-7 August 2009
Quarter Moon 12-13 August 2009
Margarites spp.
Crepidula spp.
Mitrella lunata
Diaphana minuta
Littorina littorea
Polinices heros
Aporrhais occidentalis
Depth (m)
0
5
10
15
20
25
w velocity (mm s-1)
4
3
2
1
0
-1
-2
-3
-4

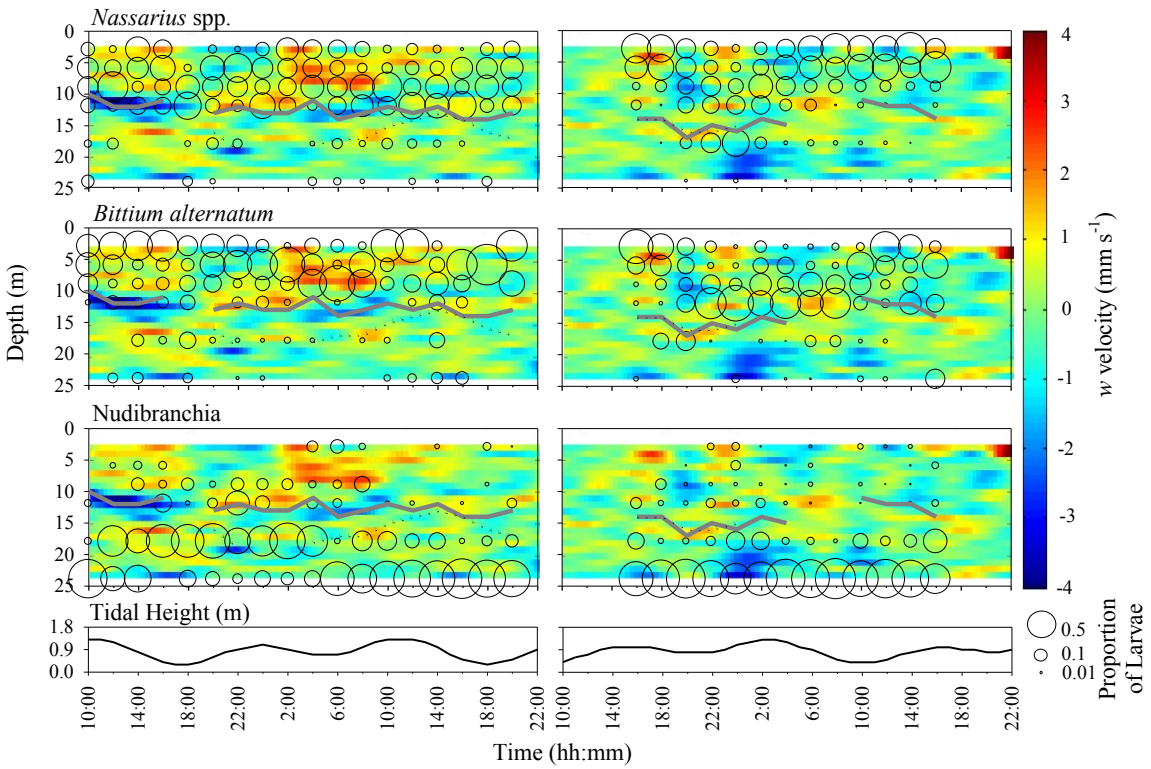
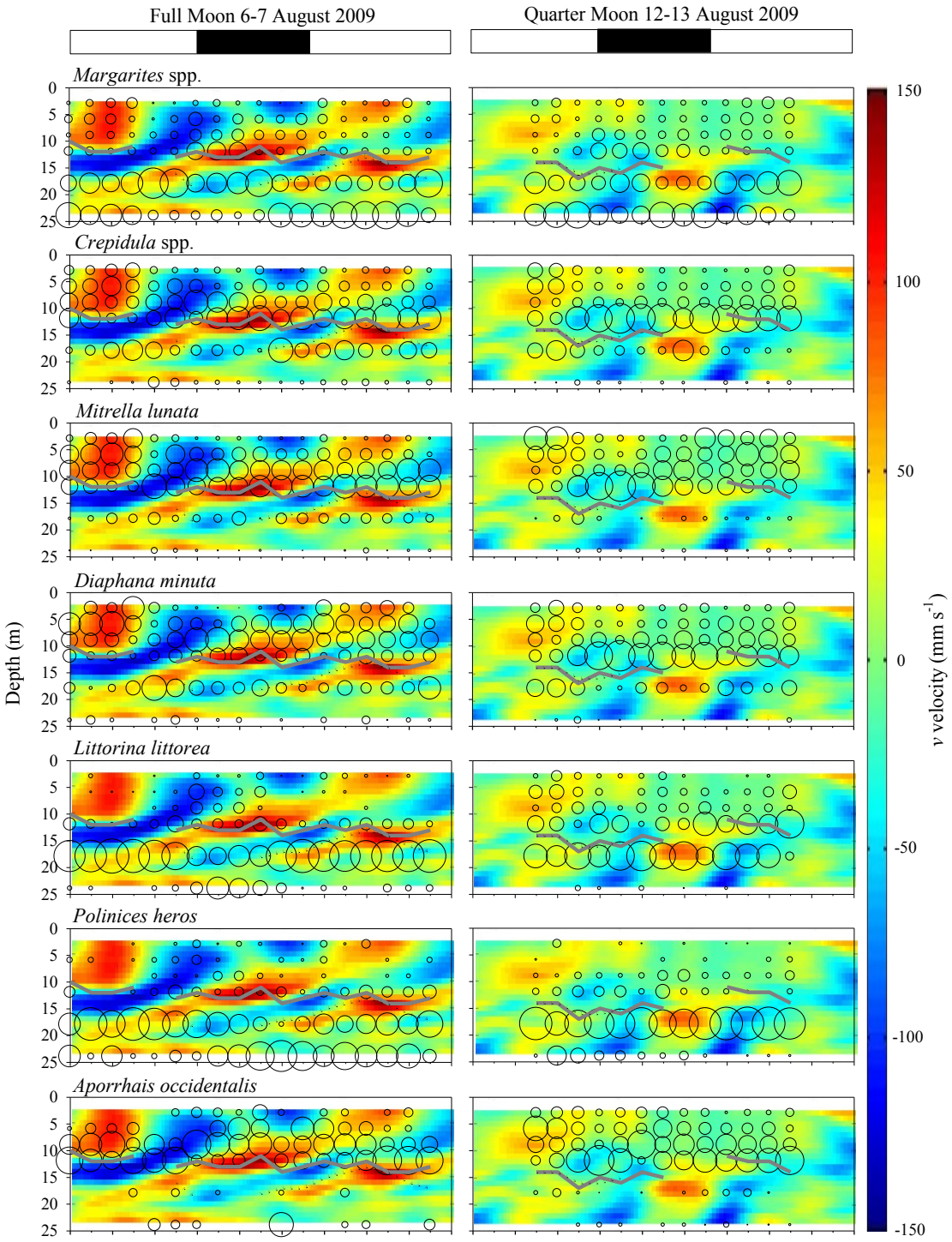


Figure B.4 Vertical distribution of all identified gastropod taxa in relation to the structure in vertical velocity (*w*) in St. George's Bay, Nova Scotia, Canada, over a 36- and 25-h period, during a spring (full moon: 6-7 Aug 2009) and neap (quarter moon: 12-13 Aug 2009) tide, respectively. Circle size indicates the proportional abundance of larvae for a particular sampling time. —— = thermocline, and ●●● = fluorescence maximum, □ = day and ■ = night. The colored contours represent *w*.


Full Moon 6-7 August 2009
Quarter Moon 12-13 August 2009
Margarites spp.
Crepidula spp.
Mitrella lunata
Diaphana minuta
Littorina littorea
Polinices heros
Aporrhais occidentalis
Depth (m)
0
5
10
15
20
25
150
100
50
0
-50
-100
-150
v velocity (mm s-1)

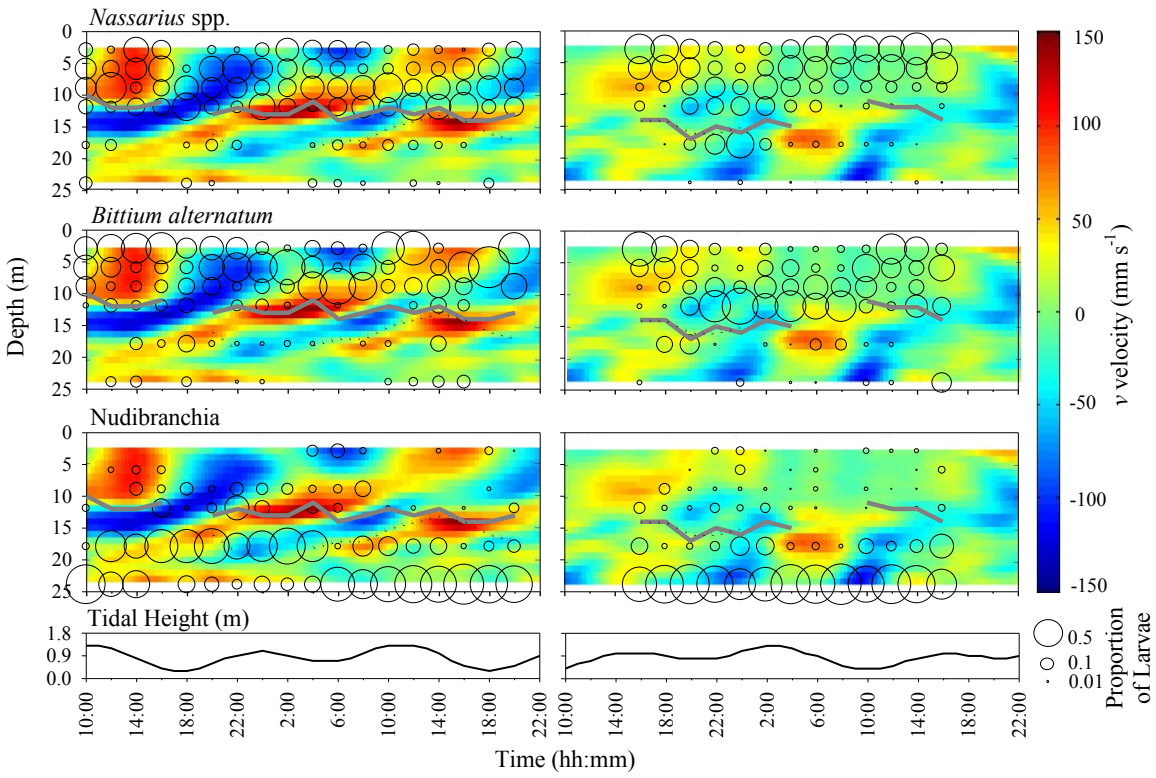
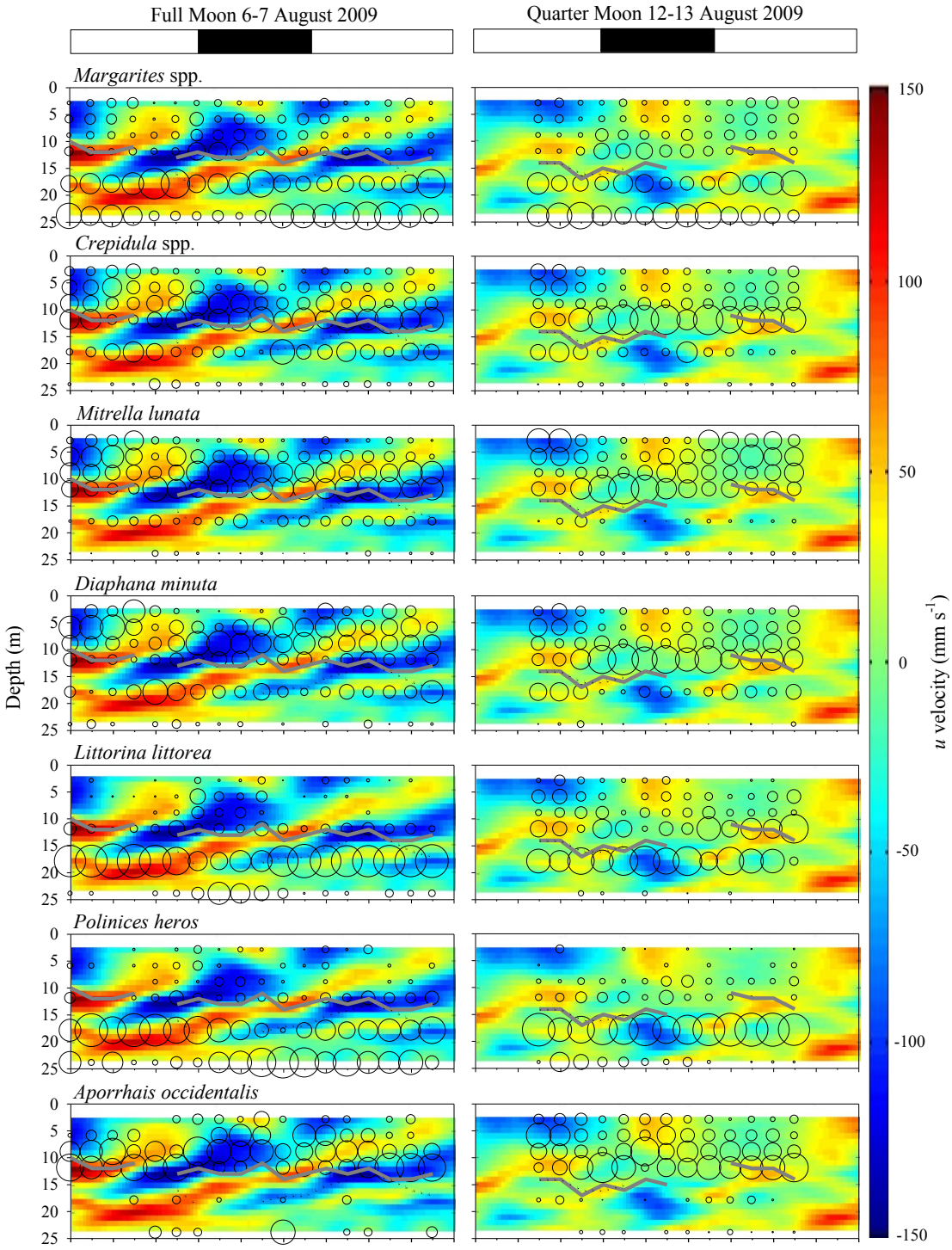


Figure B.5 Vertical distribution of all identified gastropod taxa in relation to the structure in North-South velocity (*v*) in St. George's Bay, Nova Scotia, Canada, over a 36- and 25-h period, during a spring (full moon: 6-7 Aug 2009) and neap (quarter moon: 12-13 Aug 2009) tide, respectively. Circle size indicates the proportional abundance of larvae for a particular sampling time. ⎯ = thermocline, and ●●● = fluorescence maximum, □ = day and ■ = night. The colored contours represent *v*.


Full Moon 6-7 August 2009
Quarter Moon 12-13 August 2009
Margarites spp.
Crepidula spp.
Mitrella lunata
Diaphana minuta
Littorina littorea
Polinices heros
Aporrhais occidentalis
Depth (m)
0
5
10
15
20
25
150
100
50
0
-50
-100
-150
u velocity (mm s-1)

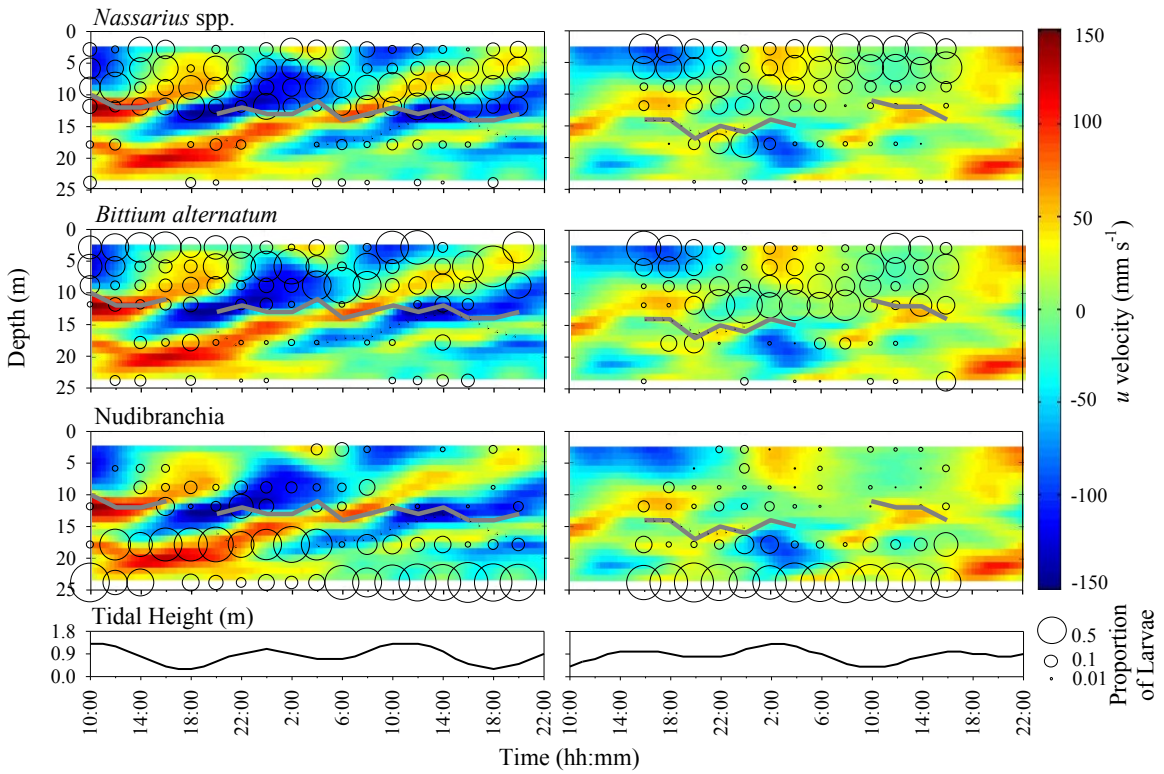


Figure B.6 Vertical distribution of all identified gastropod taxa in relation to the structure in East-West velocity (*u*) in St. George's Bay, Nova Scotia, Canada, over a 36- and 25-h period, during a spring (full moon: 6-7 Aug 2009) and neap (quarter moon: 12-13 Aug 2009) tide, respectively. Circle size indicates the proportional abundance of larvae for a particular sampling time. —— = thermocline, and ●●● = fluorescence maximum, ☐ = day and ■ = night. The colored contours represent *u*.

Appendix C

Surface Light Intensity

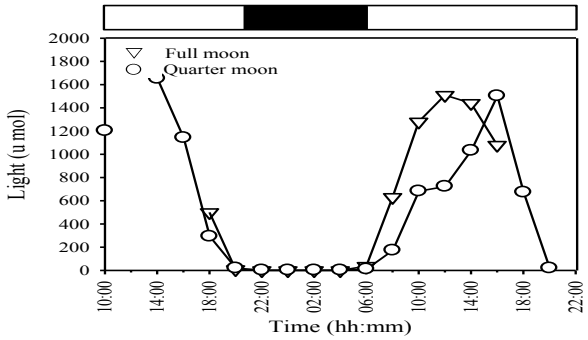


Figure C.1 Time series of the surface light intensity measured in St. George's Bay Nova Scotia, Canada, over a 36- and 25-h period, during a spring (full moon: 6-7 Aug 2009) and neap (quarter moon: 12-13 Aug 2009) tide. On 6-7 Aug 2009, cloudy from ~18:00 to ~8:00 (weather record incomplete), and 12-13 Aug 2009, sunny during the day and partially cloudy at night.