Arcadia Beach, Oregon

Trypanites Ichnofacies

Economy Point, Nova Scotia

The Ecology, Neoichnology and Sedimentology of Siliciclastic Hardground Communities: Implications for *Trypanites* Assemblages in the Rock Record

by

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ABSTRACT

The paleoecology of rocky substrates in the rock record is commonly interpreted based on ichnology (the *Trypanites* ichnofacies) and is frequently associated with a biotic assemblage with low diversity. However, analyses of two modern, siliclastic, intertidal hardground community at Lion Rock, located at Arcadia Beach State Park, Oregon, and Thomas Cove at Upper Economy, Nova Scotia (Bay of Fundy), reveal diverse communities of boring, encrusting and squatting/clinging organisms. Through observations and descriptions of organism distribution and abundance, up to 45 species of flora and fauna are reported to inhabit the study areas. At Lion Rock, organisms reside within five littoral zones (supra-, upper-, middle-, and lower littoral zones, and a newly established sublittoral zone) on the sea stack. Borings are produced by *Adula californiensis*, *Hiatella arctica*, *Penitella penita*, and *Zirfaea pilsbryi* and are identified as *Gastrochaenolites*-type traces. At Thomas Cove, organisms inhabit eleven depositional sub-environments and borings are formed by *Petricola pholadiformis* and *Zirfaea pilsbryi*, and are also identified as *Gastrochaenolites*-type traces. Within the two studied localities, substrate, sediment type and thickness, water presence during low tide and water velocity control boring location and abundance. It is likely that ancient *Trypanites* communities had considerably higher diversity and faunal abundance than their ichnological record indicates. Comparisons with modern assemblages are thus crucial in assessing these environments in ancient successions.

PREFACE

This thesis is an original work by Carolyn Marie Furlong. Chapter 2 of this thesis has been submitted for publication as C.M. Furlong, M.K. Gingras and J.P. Zonneveld, "Oregon Sea Stack: Ecological Diversity of a Modern Trypanites Ichnofacies" in PALAIOS. The manuscript has yet to be peer reviewed and accepted. I was responsible for data collection, analysis and manuscript composition. M.K. Gingras and J.P. Zonneveld were supervisory authors and were involved with concept formation and manuscript edits. Additionally, a collection permit (Appendix A) was obtained through Oregon State Parks and Recreation (permit number #031-13) to ensure the preservation of the sea stack substrate and the biotic community within the studied area. No further ethics approval was needed from the University of Alberta Research Ethics Board to conduct this research.

DEDICATION

This thesis is dedicated to my family, John, Mary Lou and Jack Furlong. My accomplishments would not have been possible without their endless love and support. You have all been there for me, even when you didn't understand anything I was talking about, and have lovingly supported my ever-changing academic and life goals. Your patience and encouragement has helped me through these two years and I am forever grateful.

ACKNOWLEDGMENTS

Four years ago, I was an undergraduate student in my second year at the State University of New York College at Cortland. At the start of the term, I had added an extra independent study course to my already packed schedule to gain research experience. While looking at a few specimens, I came across one brachiopod that had borings in its shell. Little did I know that questioning small holes within a brachiopod shell would lead me to publish my undergraduate research and pursue a Master's degree in geology. I would like to thank the Geology Department at SUNY Cortland, especially Dr. Christopher McRoberts, Dr. Robert Darling, Dr. Gayle Gleason and Dr. David Barclay, for establishing my love of geology and for always challenging me to do my best. Thanks to Dr. Steven Broyles, Dr. Rena Janke, Dr. Jeremiah Donovan and Jacqueline Scallan for their positive influence in my academic and personal life. I would also like to thank the *Geology Girls* and the *Girls of 9 James* for being loving and supporting friends and for making our four years together one wild and crazy adventure.

Since being at the University of Alberta, I have learned many new aspects of geology and have further enhanced my passion for research. I would foremost like to thank Dr. John Paul Zonneveld for taking me on as a Master's student and providing me with the opportunity to travel to many beautiful places to do field work and to pursue research on "boring" geology. I would also like to thanks Dr. Murray Gingras for adding himself to my supervisorial committee and letting me revisit previous research topics that needed further exploration. I would like to thank Dr. George Pemberton and Dr. Brian Jones for their advice and support inside and outside the classroom. Finally, I would like to thank Dr. John Acorn and Dr. Duane Froese for being apart of my defense committee.

The past two years have been filled with many amusing memories with the Iconology Research Group (IRG). Firstly, I would like to thank Sarah Schultz for being a great field assistant and fellow *Sassy Girl*. We managed to survive DCOD and thunderstorms, rent cars, ship crates, not make friends with Grrr Dog or Harry, make informational videos of Magnetic Mountain, loose and find scales in the mud flats, drown two cameras and become good friends along the way. Thanks to Cheryl Hodgson for being my field assistant and showing me the ropes of neoichnological field techniques, and teaching the border police about marine organisms. Thanks to Alina Shchepetkina for being my field assistant, letting me work with her in some very muddy places and for always having time to talk about everything and anything in the office. Thanks to Tiffany Playter for being one of the best role models within the lab and for her help and suggestions in my research. Thanks to Reed Myers for his useful comments and advice, and never letting me forget about my stamp-sized Illustrator figures. Thanks to David Herbers and Eric Timmer for providing amusing banter within the lab and being the youngest old men I know. Thanks to Scott Botterill for his suggestions in my research and always going out of his way to help me and others. Thanks to Gord Campbell for his support and for never letting me forget that the horrible historical events that happened on my defense date. Thanks to Ryan King for providing me with endless amounts of help, advice and knowledge; I can always count on him to eat any baked goods I bring to lab. Thanks to Rares Bistran, Brad Bobey, Shelby Sanders, Dawn Tobey and Shimeng Zhang for all their useful advice, comments and discussions within the lab. Thanks to "Evil" Eric Webb for keeping the lab amusing by hiding devious beeping devices in cabinets, creating gastropod coquina in the furnace and making the back of the rental car seats, and therefore the whole car, smell like the tidal flats. Thanks to Steven Kolenosky and Shafer Montgomery for your amusing conversations and antics over the summer and school year. Thanks very much, once again, to all of the people that I have mentioned and to the countless others at the University that I was unable to acknowledge.

Thank you to Mark Labbe and Martin von Dollen for making thin sections and providing assistance with shipping and storing samples. Thanks to Igor Jakab for helping with printing, scanning and computer inquiries. Thanks to David Chesterman for his support and assistance with lab equipment. And thanks to the staff of the main office, especially Matthew Barnett, Shyra Craig and Rene Gobeil, who have greatly assisted me with paperwork and printing needs.

I would also like to thank Oregon Fishery and Wildlife for providing a collecting permit for Arcadia Beach. Thanks to Kendra's Kitchen and Tillamook Cheese Factory for providing my field assistants and me with delicious seafood and Marion Berry Pie ice cream, which we always looked forward to after the long days in the field. I would also like to thank Warren and Maureen from the Four Seasons Retreat in Upper Economy, NS for their hospitality and generosity. I am endlessly grateful for their patience while dealing with the shipping crate nightmare and going out of their way to get my samples back to the UofA.

I would finally like to thank the Government of Alberta, University of Alberta and the Department of Earth and Atmospheric Sciences for supporting and funding this research.

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Lithology
- Sandstone
- Basalt

Boring Density (per 15 X 15 cm area)
- Low (<5 borings)
- Moderate (<20 borings)
- High (20-80 borings)

Littoral Zones
- Supralittoral Zone
- Upper Littoral Zone
- Middle Littoral Zone
- Lower Littoral Zone
- Sublittoral Zone
- --- Approx. base of sublittoral zone

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DEPOSITIONAL SUB-ENVIRONMENTS

UP	Upper Platforms	ITSF	Intertidal Sand Flat
ITMF	Intertidal Mud Flat	R	Ridge
LP	Lower Platform	LER	Leading Edge of Ridge
DC	Drainage Channel	TP	Tide Pool
CF	Channel Flank	TPD	Tide Pool Drainage System
DCOD	Main Channel		

FIGURE 2: DEPOSITIONAL SUB-ENVIRONMENT

- Terrestrial
- High Tide Water Level
- UP
- ITMF
- LP
- DC
- CF
- DCOD
- ITSF
- R
- LER
- TP
- App. Location of TPD
- Unstudied Area in the Bay Cahnnel
- App. Location of DC
- Corners of Study Area
- Study Area Boundary

FIGURE 5: BORING DENSITY AND DISTRIBUTION

Boring Bivalve Distribution
- *Petricola pholadiformis*
- *Petricola pholadiformis* and *Zirfaea pilsbryi*

Boring Density (per 1-square meter)
- 10 borings
- 100 borings
- 1000 borings

LIST OF SYMBOLS
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FIGURE 6, 9 & 20: BORING AND TRANSECT SCHEMATIC

Lithology and Sediment

- Bedrock
  - Sandstone
  - Silty mudstone
- Sand
- Gravel
- Mud
- Water

Biogenic Structures

- *Gastrochaenolites*
- *Skolithos*
- *Areonicolites*
- *Poykladichnus; Psilonichnus*
- *Siphonichnus*

Fauna

- *Petricola pholadiformis*
- *Zirfaea pilsbryi*
- *Macoma balthica*
- *Mya arenaria*
- *Heteromastus* sp.
- *Cerebratulus* sp.
- *Nereis* sp.
- *Corophium volutator*
- *Pagurus* sp.
- *Lunatia heros*
- *Littorina saxatilis, Buccinum undatum, Nassarium trivittau*
- *Chthamalus fragilis*
- *Flustra foliacea*

Flora

- *Ascophyllum nodosum*
- *Chondrus crispus*
- *Corallina officinalis*
- *Cystoclonium purpureum*
- *Fucus* sp.
- *Palmaria palmata*
- *Spongomorpha* sp.
- *Ulva lactuca*

CHAPTER 1: INTRODUCTION

The *Trypanites* ichnofacies was defined by Frey and Seilacher (1980) as a bored, consolidated, marine littoral and sublittoral omission surface or organic substrate (Fig. 1-1). Traces are characterized by cylindrical to vase-, tear- or U-shaped to irregular domiciles, which are oriented normal to substrate surfaces (Frey and Seilacher, 1980). Common traces include *Trypanites*, *Gastrochaenolites*, *Entobia*, *Rogerella*, *Uniglobites*, *Maeandropolydora*, *Circolites*, *Caulostrepsis*, polychaete borings and echinoid grooves (Frey and Seilacher, 1980; MacEachern et al., 2010; Gibert et al. 2012). Ichnotaxa diversity is generally low and several of the above ichnogenera may be absent (Frey and Seilacher, 1980). Paleontological studies have aimed to reconstruct the evolution and distribution of hard-substrate biota and traces (Fig. 1-2; Goldring and Kaźmierczak, 1974; Johnson and Baarli, 1999; Bromley, 2004). However, intertidal rocky shore communities consist not only of boring animals, but also encrusting and squatting/clinging organisms that have low preservation potential within the rock record. As such, most paleoecological

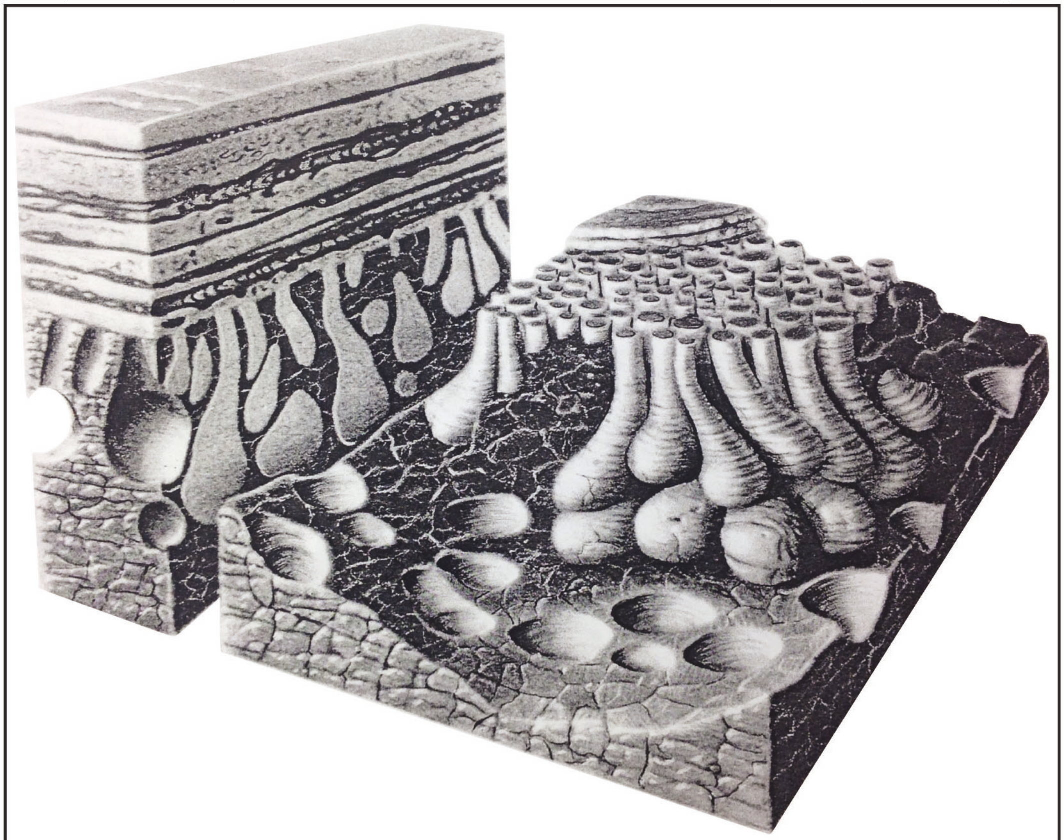


Figure 1-1. Drawing of a *Trypanites* ichnofacies. Image courtesy of Thomas Saunders.

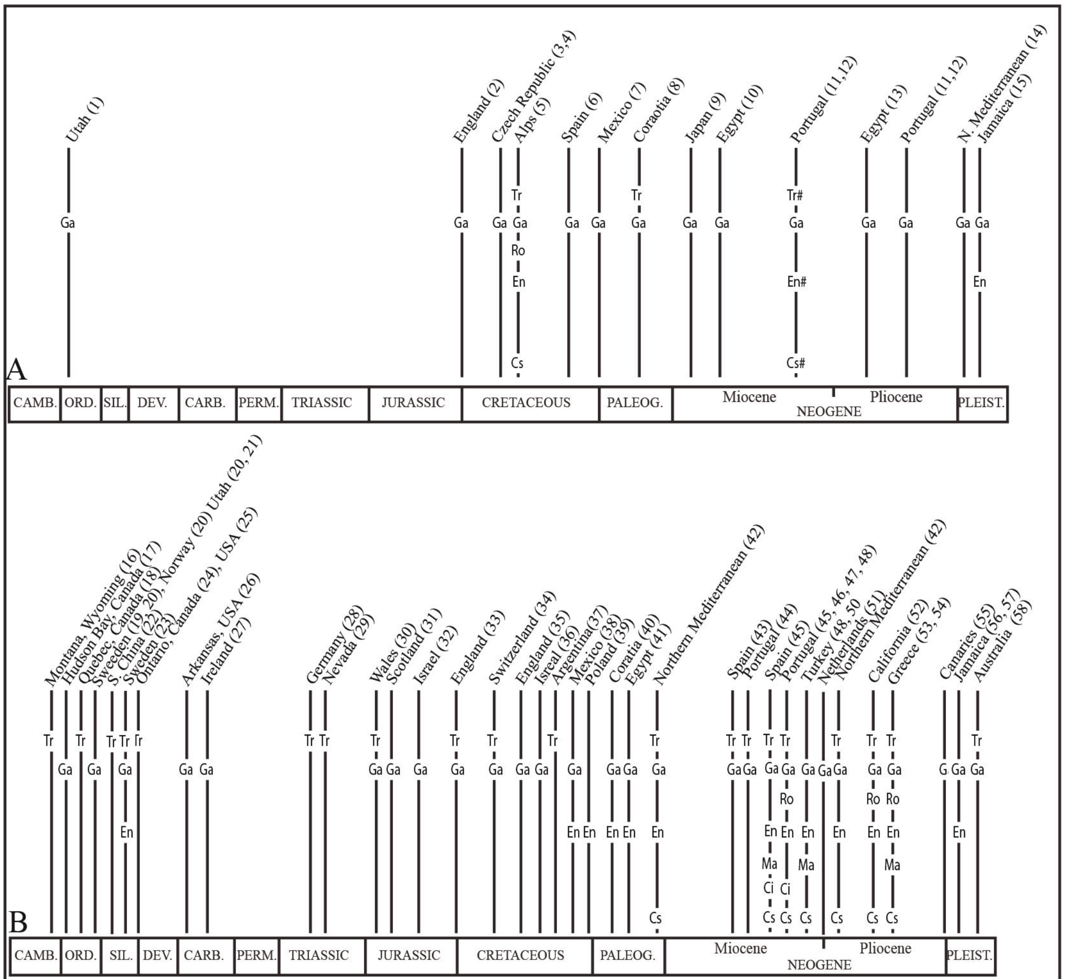


Figure 1-2. *Trypanites* ichnofacies throughout time. (**A**) Composition of clastic rocky-shore tracefossils assemblages throughout time based on bibliographic data. Adapted from Gibert et al. (2012). References used: (1) Banner et al. (2004), (2) Gallois and Goldring (2007), (3) Mikulas and Zitt (2003), (4) Zitt and Mikulas (2006), (5) Delamette (1989), (6) Garcia-Garcia et al. (2013), (7) Ledesma-Vazquez and Johnson (1994), (8) Babic and Zupanic (2000), (9) Suzuki and Hiranaka (2008), (10) Malpas et al. (2005), (11) Silva et al. (1996), (12) Silva et al. (1999), (13) Aigner (1983), (14) Gibert et al. (1998) and (15) Mitchell et al. (2001). (**B**) Composition of carbonate rocky-shore tracefossils assemblages. Adapted from Gibert et al. (2012). References used: (16) Brett et al. (1982), (17) Lescinsky et al. (1991), (18) Desrochers and James (1988), (19) Ekdale and Bromley (2001), (20) Ekdale et al. (2002), (21) Banner et al. (2004), (22) Rong and Johnson (1996), (23) Cherns (1982), (24) Pemberton et al. (1980), (25) Wilson and Palmer (1988), (26) Wilson and Palmer (1998), (27) Trudgill and Crabtree (1987), (28) Bertling (1999), (29) Carter and Stanley (2004), (30) Johnson and McKerrow (1995), (31) Farris et al. (1999), (32) Wilson et al. (2005), (33) Cole and Palmer (1999), (34) Bover-Arnal et al. (2011), (35) Gallois and Goldring (2007), (36) Lewy (1985), (37) Mangano and Buatois (1991), (38) Lescinsky et al. (1991), (39) Bromley et al. (2009), (40) Babić and Zupanič (2000), (41) Aigner (1983), (42) Gilbert et al. (1998), (43) Domènech et al. (2001), (44) Santos et al. (2008), (45) Santos et al. (2010), (46) Silva et al. (1996), (47) Silva et al. (1999), (48) Cachão et al. (2009), (49) Demircan (2012), (50) Donovan and Hensley (2006), (51) Watkins (1990), (52) Uchman et al. (2002), (53) Bromley and Asgaard (1993a), (54) Bromley and Asgaard (1993b), (55) Mayoral et al. (2013), (56) Mitchell et al. (2001), (57) Perry (2000) and (58) Semeniuk and Johnson (1985). Traces include: Ga = *Gastrochaenolites*; Tr = *Trypanites*, Ro = *Rogerella*, En = *Entobia*, Mn = *Maeandropolydora*, Ci = *Circolites*, Cs = *Caulostrepsis*.

assemblages of *Trypanites* ichnofacies are reconstructed based on trace fossils. Therefore, neoactualism may provide important insight for interpreting ancient successions and marine communities.

Additionally, the *Trypanites* ichnofacies is useful for paleogeography and sequence stratigraphy, and may help identify paleoshoreline location, flooding surfaces and omission surfaces that have experienced burial, lithification, exhumation and exposure lengthy enough to allow significant boring to occur (Gibert et al., 1998; Silva et al., 1999; Pemberton and MacEachern, 2005; MacEachern et al, 2010). A variety of studies describe *Trypanites*-demarcated discontinuities throughout geologic time, but most are reported from carbonate successions (Fig. 1-1; Brett, 1988; Gibert et al., 2012). It is likely that the bias in preservation is linked to the ontogeny of the surface; bored surfaces in clastic settings are more frequently associated with erosional exhumed substrates and erosional disconformities, whereas in carbonate settings, hardground surfaces can be autogenic and associated with non-depositional breaks, as well as erosional exhumation (Bromley, 1975; Pemberton, 2003). This suggests that clastic *Trypanites* ichnofacies occur in erosional setting and are more rarely preserved, which makes it important to investigate modern bored hardgrounds to better reconstruct the poorly preserved substrates.

Neoichnology plays an important role in understanding ancient sedimentary strata and biotic communities. Many studies have focused on soft sediment and firmground neoichnology (e.g. Seilacher, 1967; Gingras et al., 2004; Dashtgard and Gingras, 2012) but few have studied the neoichnology of bored hardgrounds and rocky shores in an effort to relate the ichnofacies to ancient successions (i.e. Bromley, 2004; Schiaparelli et al., 2005; Gibert et al., 2012; Baarli et al., 2013; Donovan, 2013; Wilson, 2013). Therefore, more observations are needed within modern settings to fully evaluate biotic and environmental parameters of the bored ichnofacies. This study investigates siliciclastic *Trypanites*-type assemblages within two localities in North America (Fig. 1-3A), to better understand the biotic diversity and environmental conditions surrounding *Trypanites*-type ichnofacies.

Chapter 2 focuses on a *Trypanites*-type ichnofacies at Lion Rock at Arcadia Beach State Park, Oregon (Fig. 1-3B, 1-3C). Lion Rock is a wave exposed sea stack within an upper microtidal, foreshore setting with marine salinity. The headland is composed of Eocene bedrock of the Astoria Formation sandstone (Angora Peak Member) and the Columbia Flood Basalt (Grande Ronde Basalt, Ortley Unit) (Niem, 1975; Reidel et al., 1989; Wells et al., 2009). Borings are limited to the sandstone portions of the sea stack and are produced by *Adula californiensis*,

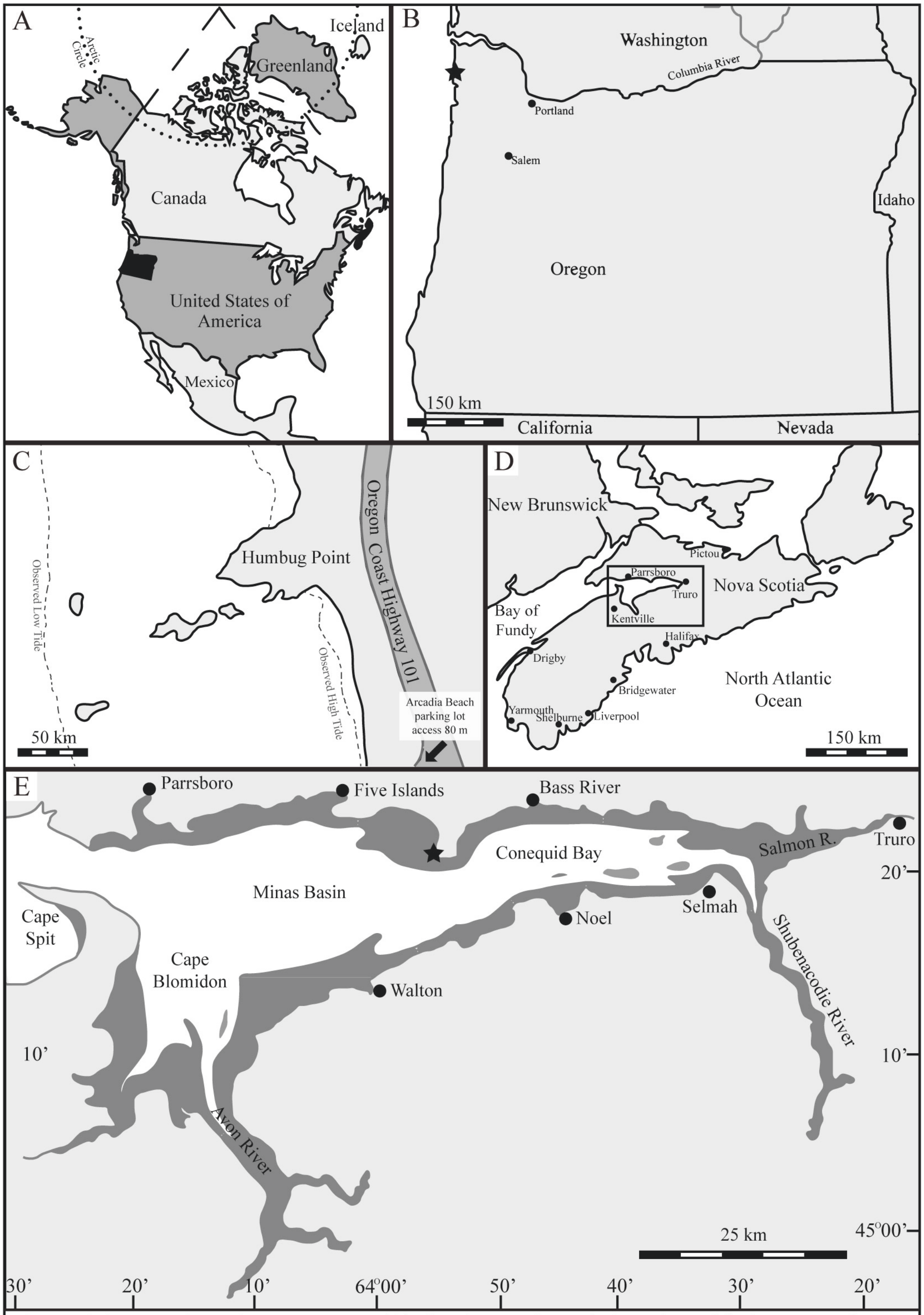


Figure 1-3. Location of study areas. (**A**) Continent of North America with Oregon and Nova Scotia highlighted in black. (**B**) Location map of study area in northern Oregon, USA. Study area located is indicated by a star. (**C**) Zoomed in map of Lion Rock, located at the northern limit of Arcadia Beach State Park. Approximate locations of high tide and low tide are indicated. (**D**) Map of the Bay of Fundy within Nova Scotia and New Brunswick, Canada. (**E**) Inset of the Minas Basin with Nova Scotia, with the extent of the intertidal zone denoted in dark gray. Study area located is indicated by a star. Map modified from Yeo and Risk (1981) and Dalrymple et al. (1990).

Hiatella arctica, *Penitella penita*, and *Zirfaea pilsbryi*. Traces resemble the ancient forms of *Gastrochaenolites turbinatus* and *Gastrochaenolites* cf. *G. lapidicus* (see Kelly and Bromley, 1984). In addition to boring organisms, the biotic community is composed of over 40 species of encrusting and squatting/clinging organisms, which commonly use the borings as isolated, macro-habitats. Five littoral zones are observed and are constructed as a result of environmental and biological parameters.

Chapter 3 focuses on a *Trypanites*-type ichnofacies within the Bay of Fundy, near Thomas Cove, Economy Point, Nova Scotia (Figs. 1-3D, 1-3E). The study area is located within intertidally-exposed, wave-cut and tidally modified platforms and salinity is fully marine. The bored hardground is located within poorly lithified sandstone and silty mudstone, wave-cut benches of poorly lithified Triassic sandstone and silty mudstone (Wolfville Formation) within the macrotidal, estuarine embayment. Borings are produced by *Petricola pholadiformis*, and *Zirfaea pilsbryi* and form traces similar to the ancient forms *Gastrochaenolites turbinatus* and *Gastrochaenolites ornatus* respectively (see Kelly and Bromley, 1984). In addition to boring bivalves, the biotic community is composed of over 30 species of burrowing, encrusting and squatting/clinging organisms. The study area is divided into eleven depositional sub-environments, which each have environmental and sedimentological conditions that dictate settlement and colonization of distinct biota.

In summary, this thesis aims to characterize two very different occurrences of modern colonized hardgrounds. Two goals will be focused upon. (1) Documenting the biotic assemblages associated with modern *Trypanites*-type ichnofacies in an effort to understand the potential biotic diversity of ancient bored hardgrounds. (2) Documenting sedimentation processes associated with the bored substrates, which provides the opportunity to better understand the process ichnology and sedimentology of ancient *Trypanites* ichnofacies. The sedimentological and neoichnological data obtained from the two localities will help expand the overall ecological and stratigraphic importance of ancient silicicilastic *Trypanites* ichnofacies.

CHAPTER 2: OREGON SEA STACK: ECOLOGICAL DIVERSITY OF A MODERN *TRYPANITES* ICHNOFACIES

INTRODUCTION

The *Trypanites* ichnofacies encompasses borings that penetrate into hardgrounds or fully lithified substrates. Common traces include *Trypanites*, *Gastrochaenolites*, *Entobia*, *Rogerella*, *Uniglobites*, *Maeandropolydora*, *Circolites*, *Caulostrepsis*, polychaete borings and echinoid grooves (Frey and Seilacher, 1980; MacEachern et al., 2010; Gibert et al. 2012). The ichnofacies is significant for paleogeography and sequence stratigraphy, and may reveal paleoshoreline location and flooding surfaces that experienced burial, lithification, exhumation and exposure lengthy enough to allow significant boring to occur (Gibert et al., 1998; Silva et al., 1999; Pemberton and MacEachern, 2005). *Trypanites*-demarcated discontinuities are present throughout geologic time and are commonly reported from carbonate successions, but have also been described within siliciclastic lithologies (Fig. 2-1; Brett, 1988; Gibert et al., 2012).

Paleontological studies have aimed to reconstruct the evolution and distribution of hard-substrate biota and traces (Fig. 2-1; Johnson and Baarli, 1999, Bromley, 2004). However, intertidal rocky shore communities are composed not only of boring animals, but also of encrusting and squatting/clinging organisms that have low preservation potential. Thus, most paleoecological reconstructions of *Trypanites* ichnofacies communities are based solely on trace fossil assemblages.

Modern rocky intertidal shores provide analogs for hardground substrates within the rock record and provide insight to ancient biotic assemblages and environmental conditions. Many studies have been conducted on ancient (i.e. Pemberton et al., 1980; Cole and Palmer, 1999; Banner et al., 2004; Demircan, 2012) and modern (i.e. Ricketts, et al., 1985; Donovan, 2013) *Trypanites* ichnofacies and rocky shores, but few (i.e. Baarli et al., 2013) have tried to compare the two within a paleoecological scope. Many have also determined ecological and physical parameters effecting distribution and zonation of organisms on modern rocky shores (Lawson, 1956; Southward, 1958; Hayward, 1971; Bolton, 1981; Ricketts, et al., 1985; Petraitis et al., 2008; Robles, 2008; Troncoso and Sibaja-Cordero, 2011; Gibert, 2012; Wilson, 2013), but a gap in research is present for relating the controls to ancient

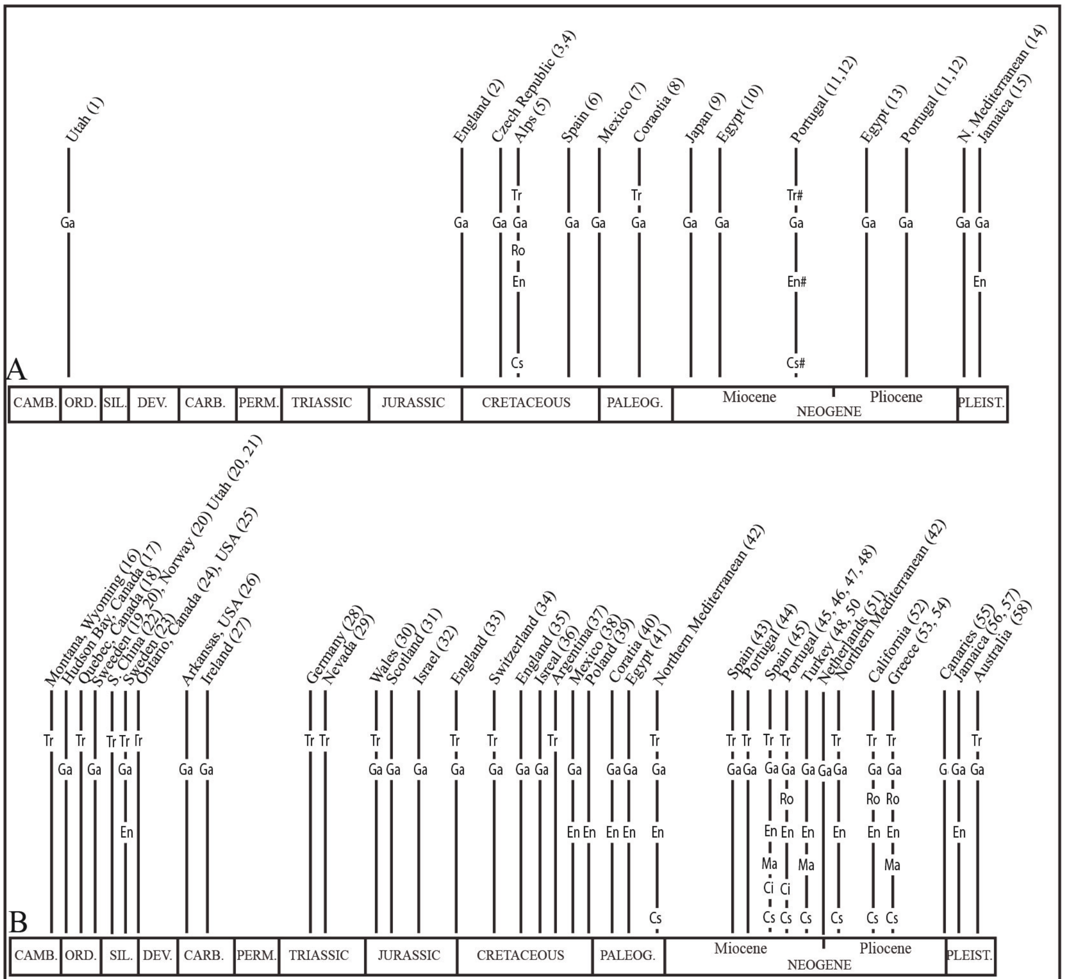


Figure 2-1. *Trypanites* ichnofacies throughout time. (**A**) Composition of clastic rocky-shore tracefossils assemblages throughout time based on bibliographic data. Adapted from Gibert et al. (2012). References used: (1) Banner et al. (2004), (2) Gallois and Goldring (2007), (3) Mikulas and Zitt (2003), (4) Zitt and Mikulas (2006), (5) Delamette (1989), (6) Garcia-Garcia et al. (2013), (7) Ledesma-Vazquez and Johnson (1994), (8) Babic and Zupanic (2000), (9) Suzuki and Hiranaka (2008), (10) Malpas et al. (2005), (11) Silva et al. (1996), (12) Silva et al. (1999), (13) Aigner (1983), (14) Gibert et al. (1998) and (15) Mitchell et al. (2001). (**B**) Composition of carbonate rocky-shore tracefossils assemblages. Adapted from Gibert et al. (2012). References used: (16) Brett et al. (1982), (17) Lescinsky et al. (1991), (18) Desrochers and James (1988), (19) Ekdale and Bromley (2001), (20) Ekdale et al. (2002), (21) Banner et al. (2004), (22) Rong and Johnson (1996), (23) Cherns (1982), (24) Pemberton et al. (1980), (25) Wilson and Palmer (1988), (26) Wilson and Palmer (1998), (27) Trudgill and Crabtree (1987), (28) Bertling (1999), (29) Carter and Stanley (2004), (30) Johnson and McKerrow (1995), (31) Farris et al. (1999), (32) Wilson et al. (2005), (33) Cole and Palmer (1999), (34) Bover-Arnal et al. (2011), (35) Gallois and Goldring (2007), (36) Lewy (1985), (37) Mangano and Buatois (1991), (38) Lescinsky et al. (1991), (39) Bromley et al. (2009), (40) Babić and Zupanič (2000), (41) Aigner (1983), (42) Gilbert et al. (1998), (43) Domènech et al. (2001), (44) Santos et al. (2008), (45) Santos et al. (2010), (46) Silva et al. (1996), (47) Silva et al. (1999), (48) Cachão et al. (2009), (49) Demircan (2012), (50) Donovan and Hensley (2006), (51) Watkins (1990), (52) Uchman et al. (2002), (53) Bromley and Asgaard (1993a), (54) Bromley and Asgaard (1993b), (55) Mayoral et al. (2013), (56) Mitchell et al. (2001), (57) Perry (2000) and (58) Semeniuk and Johnson (1985). Traces include: Ga = *Gastrochaenolites*; Tr = *Trypanites*, Ro = *Rogerella*, En = *Entobia*, Mn = *Maeandropolydora*, Ci = *Circolites*, Cs = *Caulostrepsis*.

environments.

This paper documents a modern *Trypanites*-type assemblage within a siliciclastic substrate at Lion Rock at Arcadia Beach State Park, Oregon, in an effort to (1) identify borings and their originators, (2) define controls affecting borings, and (3) describe the diversity and abundance of organisms throughout the sea stack. Lion Rock is used here as a modern analog to describe the diverse ecological potential of *Trypanites* ichnofacies of the past and to assess the oceanographic and sedimentological controls that govern the development and nature of these assemblages.

STUDY AREA AND GEOLOGICAL CONTEXT

Arcadia Beach State Park is located within the northeast Oregon Coastal Region between Cannon Beach and Arch Cape (Figs. 2-2A, 2-2B) and is 3.4 miles (5.5 km) south of Cannon Beach along U.S. highway 101. The beach resides between two headlands, with Humbug Point to the north and Hug Point to the south. Lion Rock is a sea stack located east of Humbug Point and is the main study area for the *Trypanites* ichnofacies (Figs. 2-2 B-D). Two smaller, basalt sea stacks are located approximately 60 m seaward from Lion Rock and provide additional data to the study.

Arcadia Beach is upper microtidal, with a maximum tidal range of 2.04 m (-0.12 m to 1.92 m). During low tide, Lion Rock is partially to fully exposed and at high tide the base is completely surrounded by water. The two small, seaward basalt sea stacks are exposed only during the lowest of spring tides.

The coastal region of northern Oregon consists of a structurally and geologically complex mosaic of Tertiary sedimentary and igneous strata (Wells et al., 2009, fig. 21). Humbug Point and Lion Rock contain the Astoria Formation (Angora Peak Member sandstone) and the Columbia Flood Basalt (Grande Ronde Basalt, Ortley Unit) (Fig. 2-2; Niem, 1975; Reidel et al., 1989; Wells et al., 2009). The Astoria Formation has been interpreted as inter-woven strata of wave-dominated deltaic (or river mouth) and deep-water delta slope forearc deposits of the ancestral early Miocene Columbia River (Cressy, 1974; Smith, 1975; Wells et al., 2009). The Angora Peak Member of the Astoria Formation consists of thick layers of laminated and cross-bedded, feldspathic and lithic sandstone interbedded with minor layers of well-laminated, carbonaceous and micaceous siltstone, and pebble conglomerate (Niem, 1975; Smith, 1975). Lion Rock is composed of well-cemented, massive

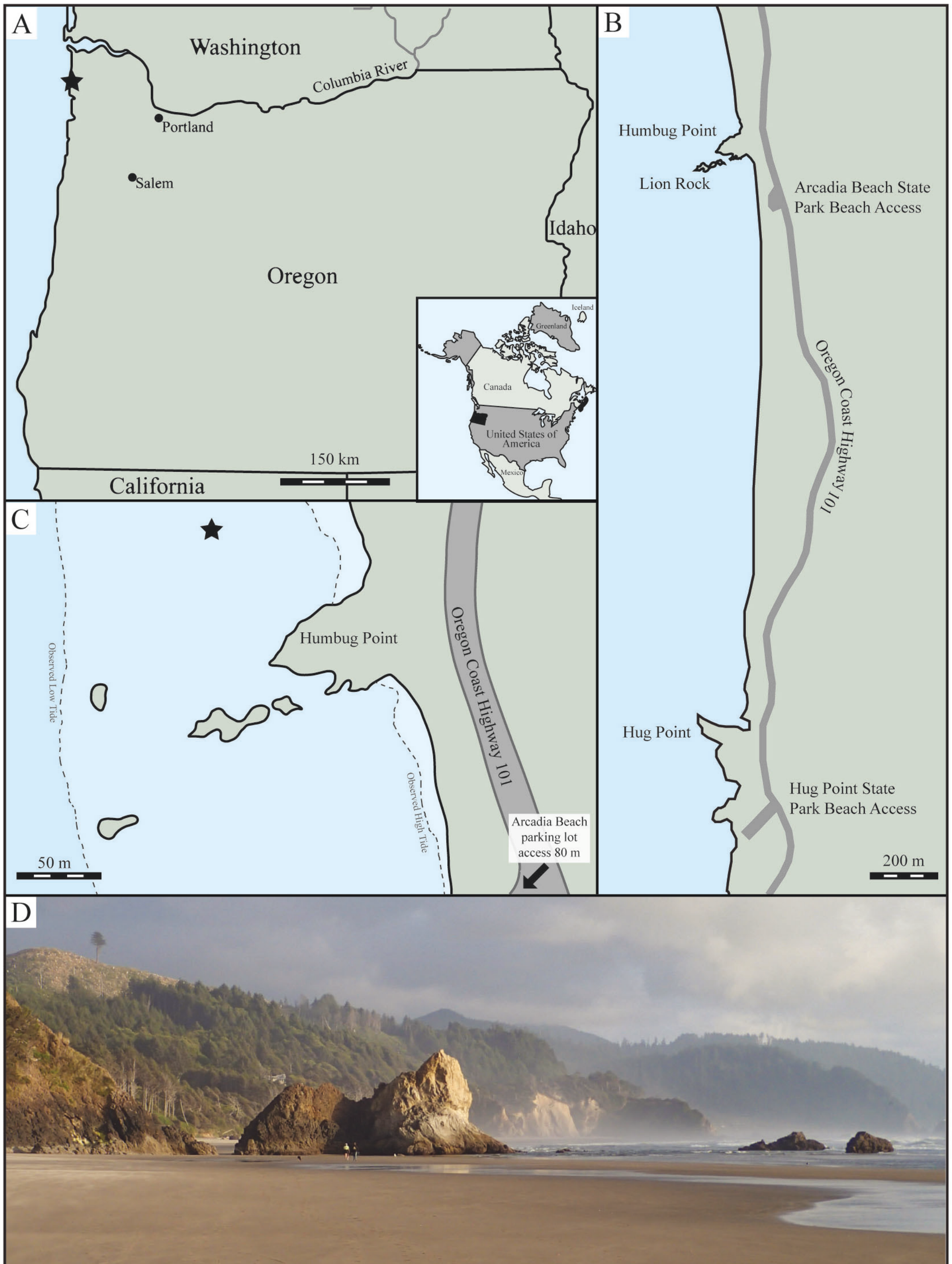


Figure 2-2. Study area locality. (**A**) Location map of study area (denoted by a star) in northern Oregon, USA. Inset shows location Oregon within North America. (**B**) Northern Oregon coastline of Arcadia Beach State Park, which is located between Humbug Point and Hug Point. (**C**) Zoomed in map of Lion Rock, located at the northern limit of Arcadia Beach State Park. Approximate locations of high tide and low tide are indicated. The star represent approximate location where photograph was taken for D. (**D**) Photograph of northern face of Lion Rock.

sandstone that has been intruded with a dark-gray to black, fine grained basalt dike, which is most likely equivalent to the Ortley Unit of invasive peperite dikes present at Humbug point (Wells et al., 2009). Borings discussed herein occur solely within the sandstone substrate of the sea stack and represent a modern *Trypanites*-type ichnocoenosis.

METHODS

Key aspects of this study include: (1) identification and distribution of organisms within the intertidal zone of Lion Rock, (2) description of the morphology, density and distribution of the borings and boring organisms, (3) identification of specialized habitats generated by the borings and fractures within the sea stack, and (4) identification of the controls on boring patterns and organism distribution. To do this, data was collected a vertical transects every 5 m along the perimeter of the sea stack, giving a total of 18 transects studied. Substrate type, organism distribution, organism abundance and littoral zone thickness were observed and documented along the vertical transects throughout the exposed faces of Lion Rock.

Additionally, borings within the sandstone hardground of Lion Rock were observed, photographed and documented along the exposed substrate and along the transects. Small pieces of rock were broken off using a chisel and hammer to describe and photograph the inner, bored portion of the sea stack. Boring densities were assessed using a grid with a 15 cm by 15 cm outline; a larger grid size was ineffective since multiple zones were frequently present within the larger sized outline. Boring density was only assessed on the exposed substrate surface, and the complex three-dimensional assemblage of traces was not assessed due to the unpermitted removal of large amounts of rock.

INTERTIDAL ECOLOGICAL ZONATION

Rocky shores are vertically divided into littoral zones based on environmental conditions including elevation within the intertidal range, degree of exposure to wave energy, the magnitude of the tidal range and lithological characteristics (Lawson, 1956; Ricketts, et al., 1985; Wilson, 2013). Fundamental biologic parameters affecting the distribution of organisms include the organisms' ability to resist desiccation, competition between species, larval recruitment and larval attachment (Gibert et al., 2012). The boundaries of zones may be abrupt or gradational; however archetypal/universal zone schemes have proven difficult to apply due to high variability of physical and biological constraints across localities (Gibert et al., 2012).

Zonations based on physical parameters vertically divide rocky shores into three or four zones including the supralittoral, upper littoral (optional), middle littoral and lower littoral zones (Table 2-1). An additional sublittoral zone has been added within this study to describe a horizontal zone, which is greatly influenced by shifting sediment. Each zone has specific environmental conditions that organisms must tolerate in order to survive (Table 2-1). Organisms may either span several different littoral zones or may be limited to a specific littoral zone (Lawson, 1956; Troncoso and Sibaja-Cordero, 2011), thus adding to the complexity of biological zonation schemes.

Littoral zones	Other common names	Elevation	Environmental conditions	Organism tolerance	Population
Supralittoral zone	Supralittoral fringe, supratidal zone, splash zone	Uppermost region; rarely to never submerged below water	Effected by the highest waves, storm waves, ocean spray and rain water	Must be able to retain moisture and tolerate extreme salinity and temperature changes	Low diversity; low to high abundance
Upper littoral zone	High intertidal zone	Only submerged within water during high tide	Effected by tidal changes, high energy wave action, sea spray and rain water	Must attach themselves to the substrate and tolerate salinity changes	Low diversity; high abundance
Middle littoral zone	Mid intertidal zone, eulittoral zone	Covered and uncovered by water twice a day	Effected by tidal changes, fluctuating wave energy	Must withstand energy fluctuations and slight changes in salinity	High diversity; high abundance
Lower littoral zone	Sublittoral fringe, low intertidal zone, infralittoral zone	Submerged except for a limited time at the lowest tides	Effected slightly by tidal changes; almost constant fully marine conditions	Must withstand only slight time periods of exposure	High diversity; high abundance
Sublittoral zone		Submerged except for a limited time at the lowest tides	Effected slightly by tidal changes; greatly affected by sedimentation and erosion	Must withstand periods of complete sediment cover	Low diversity; low abundance

Table 2-1. Littoral zones. Zone descriptions summarized from Lawson (1956), Robles (2008), Gilbert et al. (2012), Wilson (2013), with the addition of the sublittoral zone. The upper littoral zone is not always included within described littoral zonation, but is applicable to the zonation scheme at Lion Rock, Oregon.

ECOLOGICAL ZONATION OF LION ROCK

Lion Rock reflects previously described littoral zonation patterns (e.g., Lawson, 1956; Ricketts, et al., 1985; Robles 2008; Gibert et al., 2012; Wilson, 2013) and is divided into five zones (supra-, upper-, middle-, lower- and sublittoral zones). Each zone has an observable, distinct band of dominant biota (Figs. 2-3E, 2-3F, 2-4, 2-5), which is a product of biological response to environmental parameters. Ricketts et al. (1985) suggested that littoral zones are not a fixed thickness and tend to be narrower, and overall lower, in protected settings and spread wider and higher with increased wave exposure. Littoral zone thicknesses vary around Lion Rock and form an overall wedge-shape (Figs. 2-3E, 2-3F), with the thickest zones located at the head, or seaward side, of the sea stack. General littoral zones are present irrespective of lithology and are primarily a result of water energy, wave action and tidal activity; however, specific organisms, such as the boring bivalves, may be absent from specific littoral zones due to lithology. Each littoral zone is described below and organism diversity, distribution and abundance are summarized within Figure 2-5, Table 2-2 and Appendix B.

Supralittoral zone

The supralittoral zone is a harsh environment for invertebrate colonization and is affected by the highest waves (storm waves), ocean spray and rainwater. Organisms that live here must be able to retain moisture and tolerate extreme changes in salinity and temperature. Diversity and abundance are low (Figs. 2-5, Table 2-2), with small, isolated barnacles (*Balanus glandula*) (Fig. 2-6A) as the dominant organism. Limpets (*Lottia digitalis*, *Lottia pelta*, *Lottia scutum* and other *Lottia* species) and gastropods (*Littorina sitkana*, *Nucella lamellose, Nucella ostrina* and other *Littorina* and *Nucella* species) are present within the lowermost part of the zone (Fig. 2-6B). Small, black limpets (3 mm to 1 cm in length) are present in the supralittoral zone (Fig. 2-6B), as well as all the lower zones, but remain unassigned to a genus or species due to the likelihood of them being juveniles of multiple limpet species. Yellow seaweed (*Mazzaella parksii*) is sparse within this zone and no other plant life is present.

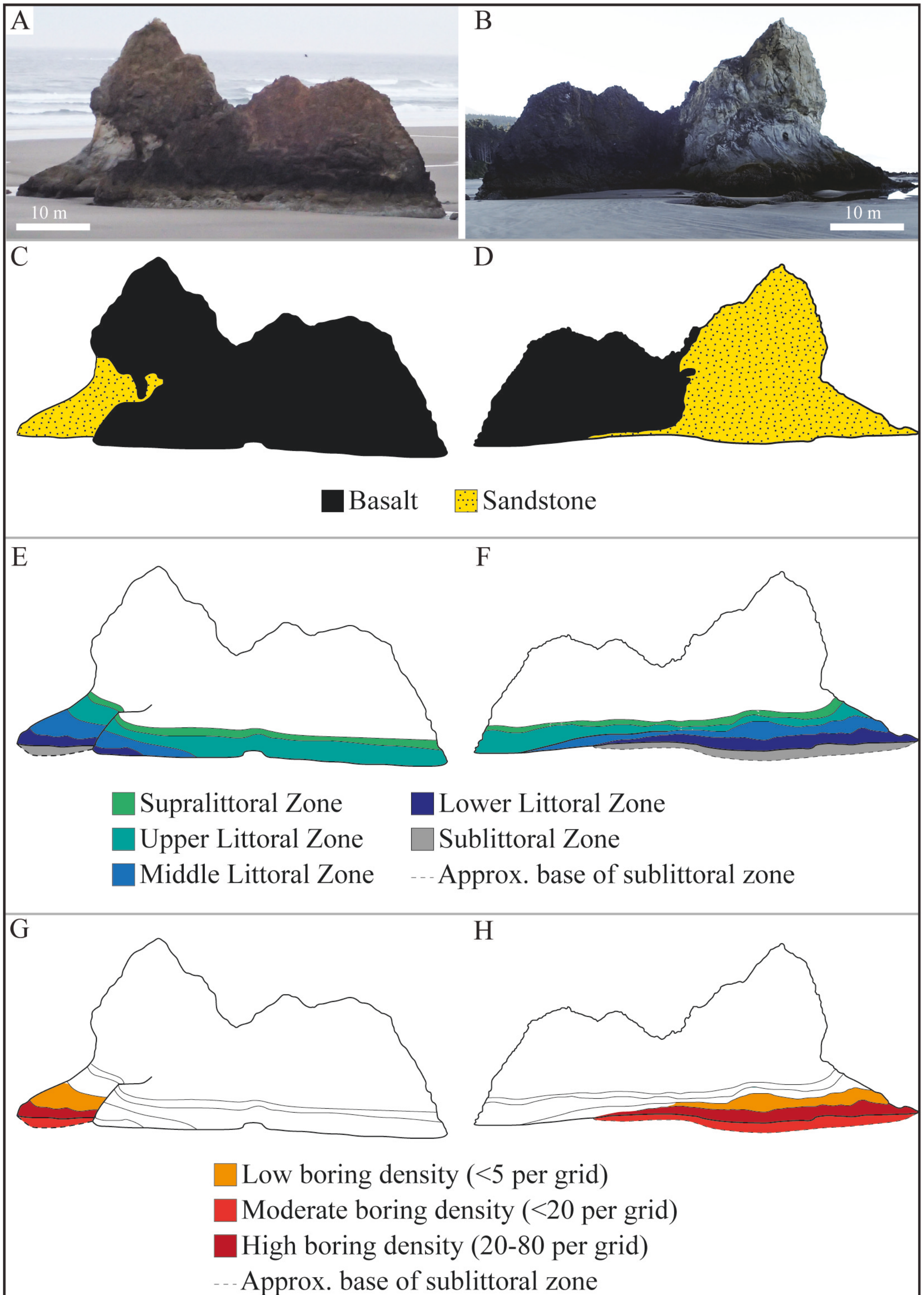


Figure 2-3. Lion Rock. (**A**) South face of Lion Rock. (**B**) North face of Lion Rock. (**C**) Lithology of the south face. (**D**) Lithology of the north face. Basalt and sandstone identified within C and D. (**E**) Littoral zonation of the south face. (**F**) Littoral zonation of the north face. Supralittoral, upper-, middle-, lower littoral and sublittoral zones. The approximate base of the sublittoral zone is indicated by a dashed line within E and F. (**G**) Boring density within the south face. (**H**) Boring density within the north face. Low, moderate and high boring densities and the approximate base of the bored zone are indicated within G and H. Vertical exaggeration = 1x.

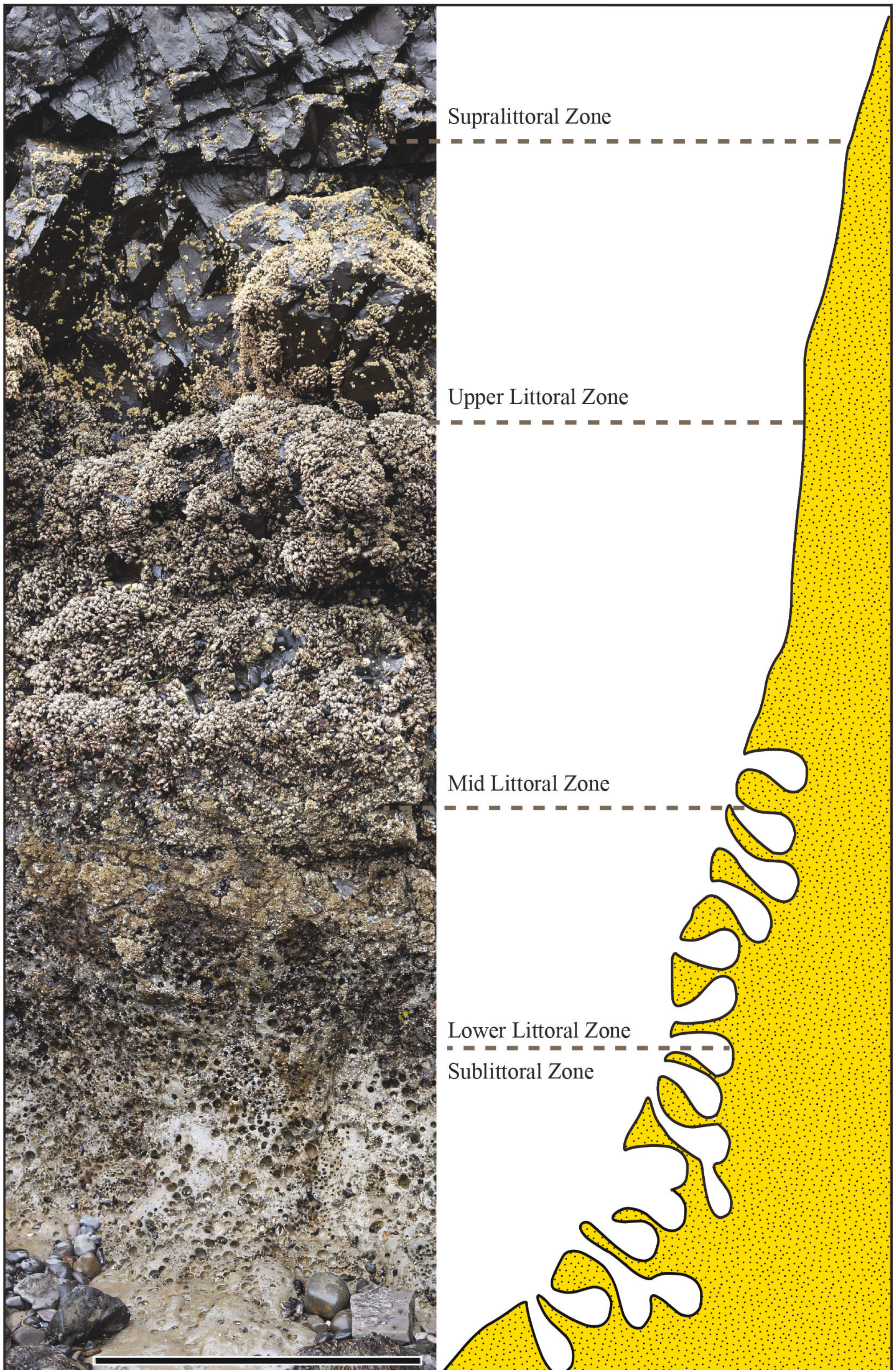
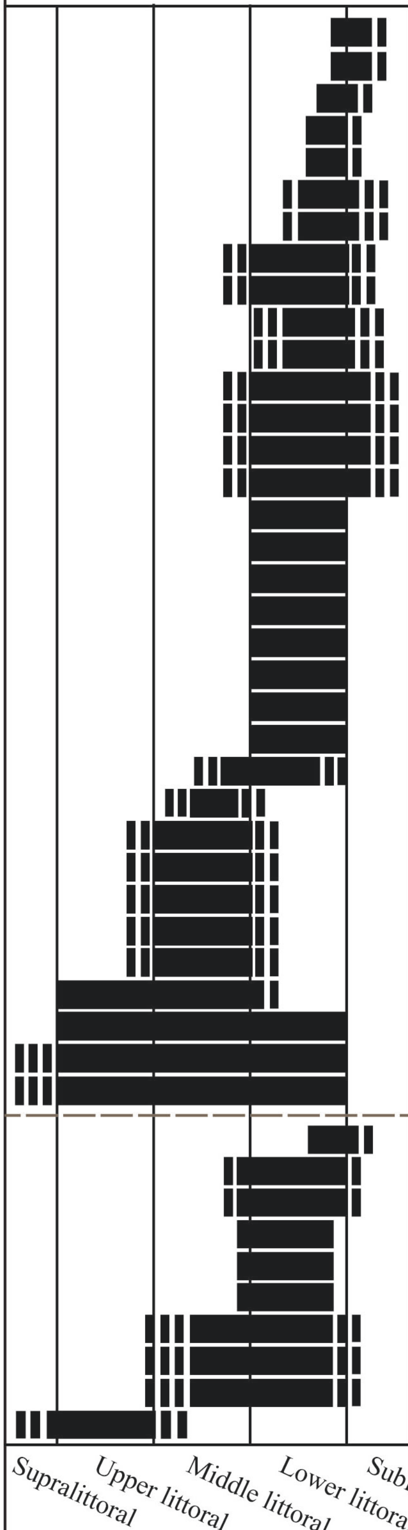


Figure 2-4. Transect and schematic of Lion Rock. *Gastrochaenolites* traces located within sublittoral zone, lower littoral zone and the lower middle littoral zone. Littoral zones indicated by dashed lines. Transect scale bar = 1 m, vertical exaggeration = 1x. Schematic not to scale.



Scientific Name	Common Name
Fauna	
Carcinus maenas	Green crab*
Oligocottus maculosus	Tidepool sculpin*
Pagurus hirsutiusculus	Hairy hermit*
Pentidotea wosnesenskii	Vosnesensky's isopod
Phylloplana viridis	Green flatworm
Lirabuccinum dirum	Dire whells
Pisaster ochraceus	Purple star
Anthopleura elegantissima	Aggregating anemone
Anthopleura xanthogrammica	Green surf anemone
Katharina tunicata	Black katy chiton
Mopalia muscosa	Mossy chiton
Adula californiensis	California datemussel
Hiatella arctica	Artic hiatella
Penitella penita	Flat-tip piddock
Zirfaea pilsbryi	Rough piddock
Acanthodoris nanaimoensis	Rufus tipped nudibranch
Aeolidia papillosa	Shag rug nudibranch
Amphiporus imparispinosus	Pink-frosted ribbon worm
Hermissenda crassicornis	Opalescent nudibranch
Ligia pallasii	Rock louse
Serpula columbiana	Red trumpet calcareous
Styela montereyensis	Long-stalked sea squirt
Tubulanus polymorphus	Red ribbon worm
Encrusting bryozoan	Unidentified bryozoan
Eudistylia vancouveri	Northern feather-duster worm
Hesperibalanus hesperius	Shell barnacle
Mytilus californianus	California mussel
Mytilus trossulus	Pacific blue mussel
Pollicipes polymerus	Gooseneck barnacles
Semibalanus cariosus	Thatched baranacles
Chthamalus dalli	Little brown barnacles
Lottia sp., Diodora sp.	Limpets
Balanus glandula	Acorn barnacle
Littorina sp., Nucella sp.	Gastropods
Flora	
Mazzaella splendens	Iridescent seaweed
Mastocarpus papillatus	Papillate seaweed
Hedophyllum sessile	Sea cabbage
Lithothamnion sp.	Encrusting coralline algae
Calliarthron sp.	Branching coralline algae
Endocladia muricata	Nail brush seaweed
Cladophora sp.	Sea moss
Ulva intestinalis	Maiden-hair sea lettuce
Ulva lactuca	Common sea lettuce
Mazzaella parksii	Yellow seaweed

* Limited to tide pools

Figure 2-5. List of species inhabiting Lion Rock. Distribution of organisms within the different littoral zones is indicated by a solid bar. Dashed bars represent areas where specific organisms may be present or are present in relatively low population. Common names are limited to names used within Oregon and do not reflect other common names used elsewhere along the Pacific coast.

Littoral zones	Thickness (cm)	Organisms	Population	Boring density
Supralittoral zone	-	*Balanus glandula* (o) *Littorina* sp. (o) *Nucella* sp. (o)	Low diversity; low abundance	0
Upper littoral zone	78.0 (30.5-182.8)	*Balanus glandula* (a) *Chthamalus dalli* (o) *Diodora aspera* (o) Encrusting bryozoan (o) *Eudistylia vancouveri* (o) *Hesperibalanus hesperius* (o) *Littorina* sp. (a) *Lottia* sp. (a) *Nucella* sp. (a) *Mytilus californianus* (o) *Mytilus trossulus* (o) *Semibalanus cariosus* (o)	Low diversity; high abundance	0
Middle littoral zone	121.9 (91.44-182.8)	*Adula californiensis* (o) *Anthopleura elegantissima* (o) *Anthopleura xanthogrammica* (o) *Balanus glandula* (d) *Chthamalus dalli* (o) *Diodora aspera* (o) Encrusting bryozoan (o) *Eudistylia vancouveri* (d) *Heptacarpus brevirostris* (r) *Hesperibalanus hesperius* (a) *Hiatella arctica* (r) *Katharina tunicata* (o) *Lirabuccinum dirum* (r) *Littorina* sp. (a) *Lottia* sp. (a) *Mopalia muscosa* (r) *Mytilus californianus* (d) *Mytilus trossulus* (d) *Nucella* sp. (a) *Pagurus hirsutiusculus* (r) *Penitella penita* (a) *Pentidotea wosnesenskii* (r) *Phylloplana viridis* (r) *Pollicipes polymerus* (d) *Semibalanus cariosus* (d) *Zirfaea pilsbryi* (o)	High diversity; high abundance	0-5

Table 2-2. Littoral zone descriptions at Lion Rock, Oregon. Thickness of each zone include average (minimum-maximum) thicknesses. Thickness for the supratidal extends to the upper height of the sea stack. Average thickness of the sublittoral zone variable due to shifting sand substrate burying and exposing the zone. Organisms encrusting, squatting and boring into the substrate are identified as being dominant (d), abundant (a), occasional (o) or rare (r) based on relative abundance within each littoral zone. Boring densities were tabulated within a 15 cm by 15 cm outline and is only reflective of the density within sandstone surfaces.

Littoral zones	Thickness (cm)	Organisms	Population	Boring density
Lower littoral zone	59.7 (33.3-85.4)	*Acanthodoris nanaimoensis* (r) *Adula californiensis* (a) *Aeolidia papillosa* (r) *Anthopleura elegantissima* (d) *Anthopleura xanthogrammica* (d) *Amphiporus imparispinosus* (o) *Balanus glandula* (a) *Chthamalus dalli* (o) *Diodora aspera* (o) Encrusting bryozoan (o) *Eudistylia vancouveri* (o) *Heptacarpus brevirostris* (r) *Hermissenda crassicornis* (r) *Hesperibalanus hesperius* (o) *Hiatella arctica* (a) *Katharina tunicata* (a) *Ligia pattasii* (r) *Lirabuccinum dirum* (r) *Littorina sp.* (a) *Lottia sp.* (a) *Mopalia muscosa* (a) *Mytilus californianus* (o) *Mytilus trossulus* (o) *Nucella sp.* (a) *Pagurus hirsutiusculus* (r) *Penitella penita* (d) *Pentidotea wosnesenskii* (r) *Phylloplana viridis* (r) *Pisaster ochraceus* (a) *Pollicipes polymerus* (o) *Semibalanus cariosus* (o) *Serpula Columbiana* (o) *Styela montereyensis* (r) *Tubulanus polymorphus* (o) *Zirfaea pilsbryi* (a)	High diversity; high abundance	20-80
Sublittorial	(0-200)	*Adula californiensis* (o) *Anthopleura elegantissima* (a) *Anthopleura xanthogrammica* (a) *Hiatella arctica* (o) *Katharina tunicate* (o) *Lirabuccinum dirum* (r) *Mopalia muscosa* (o) *Oligocottus maculosus* (r) *Pagurus hirsutiusculus* (r) *Penitella penita*(o) *Pentidotea wosnesenskii* (r) *Phylloplana viridis* (r) *Pisaster ochraceus* (a) *Zirfaea pilsbryi* (o)	Low diversity; low abundance	0-20

Table 2-2 continued. Littoral zone descriptions at Lion Rock, Oregon.

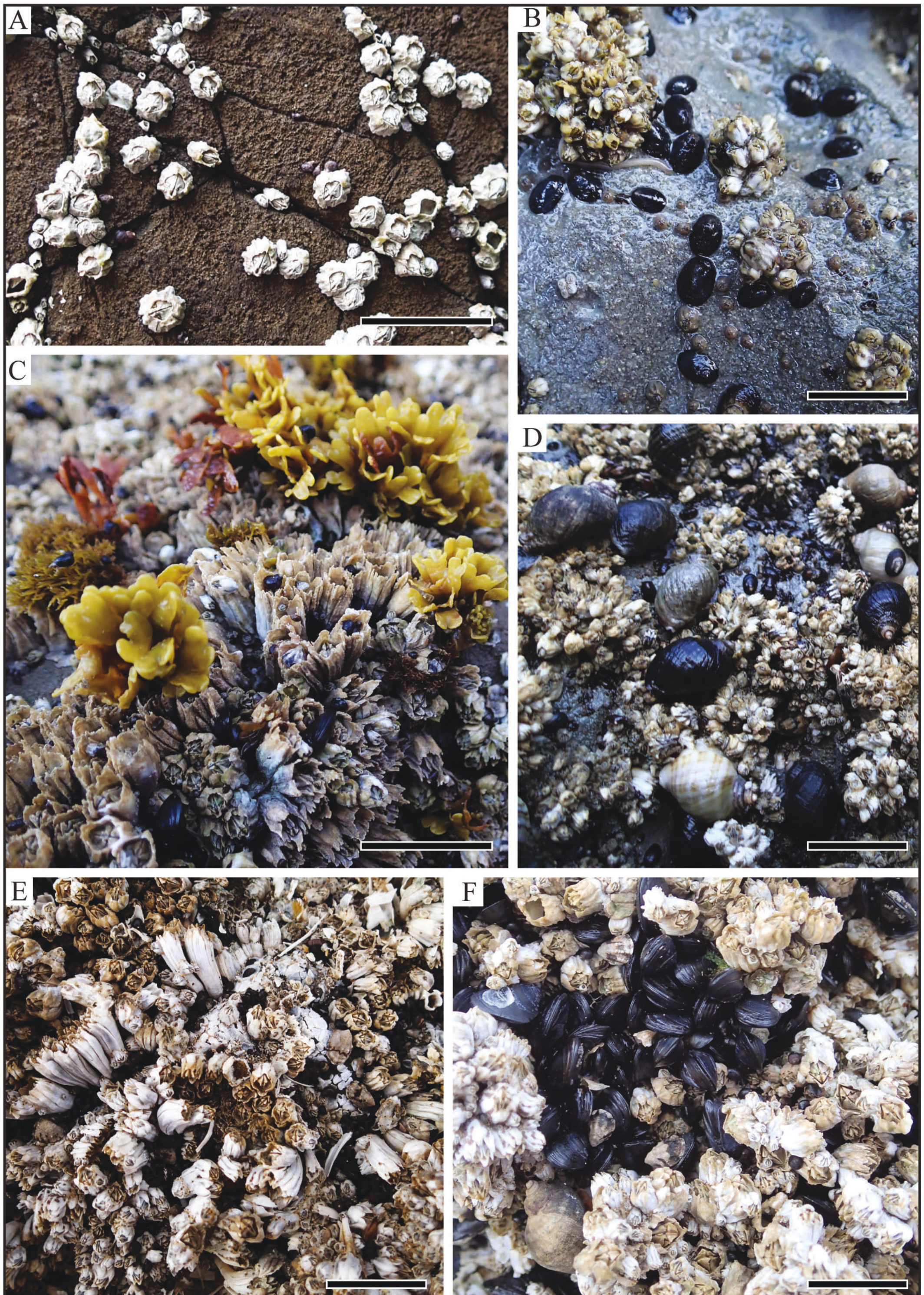


Figure 2-6. Supralittoral and upper littoral zones. (**A**) *Balanus glandula* encrusting on basalt of the supralittoral zone. Scale bar = 2 cm. 2. (**B**) *B. glandula* and unidentified, small black limpets within the transition zone between the supralittoral and upper littoral zones. Scale bar = 1 cm. (**C**) *Mazzaella parksii* within the upper littoral zone. Scale bar = 2 cm. (**D**) *Littorina sp.*, *Nucella sp.* and *B. glandula* within the upper littoral zone. Scale bar = 1 cm. (**E**) Dense encrustation of *B. glandula* within the upper littoral zone. Scale bar = 2 cm. (**F**) Small *Mytilus trossula* and *B. glandula* within the upper littoral zone. Scale bar = 2 cm.

Upper littoral zone

The upper littoral zone is submerged only at the highest tides and forms an environment that is subject to high wave energy and long periods of exposure. This zone possesses a similar species richness as the supralittoral zone, but with a greater abundance of individuals (Figs. 2-5, 2-6, Table 2-2). Acorn barnacles, limpets and gastropods are the major biota present within the zone, and the abundance of acorn barnacles is such that 80%-100% of the substrate is encrusted (Figs. 2-6 C-E). The limpet, *Diodora aspera*, and the little brown barnacle, *Chthamalus dalli*, also occur here. Limpets, gastropods and little brown barnacles occur in isolation throughout. Plant life is limited to small, isolated clusters of yellow seaweed (*Mazzaella parksii*) (Fig. 2-6C).

The base of the upper littoral zone is gradational with the middle littoral zone (Fig. 2-6F) and organisms located along the transitional fringe (about 10-15 cm in thickness) include mussels (*Mytilus trossulus* and *Mytilus californianus*), barnacles (*Hesperibalanus hesperius*) and feather-duster worms (*Eudistylia vancouveri*). The distribution of individual organisms within the transitional zone is abundant, patchy or isolated, but about 70% to 100% of the lithic substrate is colonized.

Middle littoral zone

Owing to the semidiurnal tides, the middle littoral zone is exposed and submerged twice a day, and thus is subject to large fluctuations in water energy. Diversity and abundance are very high (Figs. 2-5, 2-7, Table 2-2) and overgrowth of encrusting organisms is common, with the majority (90-100%) of the surface being encrusted. Barnacles (*Balanus glandula*, *Pollicipes polymerus*, *Chthamalus dalli* and *Hesperibalanus hesperius*), mussels (*Mytilus trossulus* and *Mytilus californianus*), feather-duster worms (*Eudistylia vancouveri*), and a variety of limpets (*Lottia* sp. and *Diodora* sp.) and gastropods (*Littorina* sp. and *Nucella* sp.) are among the most common organisms inhabiting the zone (Figs. 2-7 A-F), but more than 20 other species of organisms reside here (Table 2-2). Plant life includes sea moss (*Cladophora* sp.; Fig. 2-7A), common sea lettuce (*Ulva lactuca*) and maiden-hair sea lettuce (*Ulva intestinalis*). The transition to the lower littoral zone is gradational and organisms are typically smaller and more sporadically distributed.

Gastrochaenolites-type traces are present within this zone (discussed further within the *Trypanites*-type Ichnofacies section). Determining boring abundance is

Figure 2-7. Middle littoral zone. (**A**) *Cladophora sp.*, *Mytilus trossulus* and *Balanus glandula* within the transition zone between the upper and middle littoral zones. Scale bar = 3 cm. (**B**) *M. californianus* encrusted with *B. glandula*. Scale bar = 2 cm. (**C**) *M. californianus* and *Pollicipes polymerus*. Scale car = 5 cm. (**D**) *Eudistylia vancouveri* and *M. californianus* within the middle littoral zone. Scale bar = 1.5 cm. (**E**) *B. glandula*, *P. polymerus*, *Chthamalus dalli*, H*esperibalanus hesperius* and *M. trossulus*. Scale bar = 4 cm. (**F**) *B. glandula*, *Littorina sp.* and *Nucella sp*. Scale bar = 2 cm.

problematic due to the high level of encrustation, making it difficult to observe the underlying substrate. Where borings were observed (i.e. areas where encrusting organisms had been removed by waves or rock exfoliation), abundance is low (0 to 5 borings per 15 cm by 15 cm area) and borings appear unoccupied. A more precise boring density was unable to be obtained due to collection permit restrictions preventing the removal of a significant number of organisms from the substrate.

Lower littoral zone

The lower littoral zone is exposed only at the lowest of low tides and is otherwise completely submerged. Most organisms herein can survive out of the water for only short periods of time. The greatest diversity and abundance of organisms is present, with a species richness of over 40 species of plants and animals residing here (Fig. 2-5, Table 2-2). The most abundant organisms include anemones (*Anthopleura xanthogrammica* and *Anthopleura elegantissima*) and chitons (*Katharina tunicata* and *Mopalia muscosa*) (Figs. 2-8 A-E). Also present, although less abundant, are an unidentified encrusting bryozoan (Fig 2-8F), nudibranchs (*Acanthodoris nanaimoensis*, *Aeolidia papillosa*, and *Hermissenda crassicornis*), tubeworms (*Serpula columbiana*; Fig. 2-8G), flatworms (*Phylloplana viridis*) and hermit crabs (*Pagurus hirauriusculus*). Flora include nail brush sea weed (*Endocladia muricata*), common sea lettuce (*Ulva lactuca*), papillate seaweed (*Mastocarpus papillatus*), branching and encrusting coralline algae (*Calliarthron* sp. and *Lithothamnion* sp.) (Figs. 2-8B, 2-8D).

The sandstone substrate within this zone is subject to the boring activity of four boring bivalve taxa (*Penitella penita*, *Adula californiensis*, *Hiatella arctica* and *Zirfaea pilsbryi*), which produce *Gastrochaenolites*-type traces. It is difficult to determine the density of live boring bivalves due to their endolithic nature and clavate structure. However, many borings are sufficiently eroded to permit observation of the boring morphology. Unoccupied borings also provide shelters for other encrusting and squatting/clinging organisms (discussed further within the *Trypanites*-type Ichnofacies: Specialized macro-habitat section) and allow a diverse assemblage of biota to reside within a relatively small area (Figs. 2-8 E-G).

Figure 2-8. Lower littoral zone. (**A**) *Anthopleura xanthogrammica*, *A. elegantissima*, *Pisaster ochraceus* and *Gastrochaenolites*-type traces. Scale bar = 6 cm. (**B**) *Calliarthron sp.* and *Lithethamnion sp.* encrusting within and around *Gastrochaenolites*-type traces. Scale bar = 2 cm. (**C**) *A. xanthogrammica*, *A. elegantissima*, *Calliarthron sp.*, *Lithethamnion sp.*, *Mopalia muscosa* and *Gastrochaenolites*-type traces. Scale bar = 3 cm. (**D**) *A. elegantissima*, *Ulva lactuca* and *Mastocarpus papillatus*. Scale bar = 5 cm. (**E**) *A. xanthogrammica*, *A. elegantissima*, *M. muscosa* and *Gastrochaenolites*-type traces. (**F**) Encrusting bryozoan within a *Gastrochaenolites*-type trace. Scale bar = 1 cm. (**G**) *Serpula columbiana* within a *Gastrochaenolites*-type trace. Scale bar = 1 cm.

Sublittoral zone

The sublittoral zone is greatly influenced by shifting sand surrounding Lion Rock, which is highly mobile and acts as a primary source of abrasive material. The sand is entrained within waves on a daily basis and aggrades and degrades on a seasonal basis. Due to this dynamic environment, organisms have a difficult time settling, attaching and growing here. Diversity and abundance is low and the rocky substrate itself is frequently devoid of any living macrofauna. Organisms, including chitons (*Katharina tunicate* and *Mopalia muscosa*), anemones (*Anthopleura elegantissima* and *Anthopleura xanthogrammica*), asteroids (*Pisaster ochraceus*) and boring bivalves (*Penitella penita*, *Adula californiensis*, *Hiatella arctica* and *Zirfaea pilsbryi*), as well as other taxa (Fig. 2-5 and Table 2-2), can survive within the uppermost area of the sublittoral zone. Organisms here must be able to survive episodes of burial by the shifting foreshore sand (maximum length of time unknown). Boring occurrence within the sublittoral zone is variable (0-20 per 15 cm by 15 cm grid) and no occupied borings are observed. The majority of borings are cross cut with the chamber of the clavate forms being exposed, suggesting that the rock was substantially eroded (as much as 2 cm) post-boring production (Figs. 2-9, 2-10).

The sublittoral zone in the study area provides an analog of how *Trypanites* ichnofacies commonly appear when preserved within the rock record. The substrate has been eroded to reveal the chambers of many of the *Gastrochaenolites*-type forms. Shells of the boring bivalves are dissolved or transported shortly after the death of the organism, leaving the borings vacant or in-filled with sediment. Encrusting organisms are not commonly preserved and have been washed or eroded away.

ECOLOGICAL ZONATION OF HUMBUG POINT AND BASALT SEA STACKS

Humbug Point is located landward of Lion Rock and possesses only the supralittoral zone. Small barnacles (*Balanus glandula*) and maiden-hair sea lettuce (*Ulva intestinalis*) are present (Figs. 2-11A, 2-11B). Although the majority of the substrate that is influenced by water at high tide is sandstone, the time length of exposure is evidently too long for boring organisms to survive within this area.

The two small basalt sea stacks located seaward of Lion Rock are exposed only at the lowest spring tides. The sea stacks reside within the break zone and are

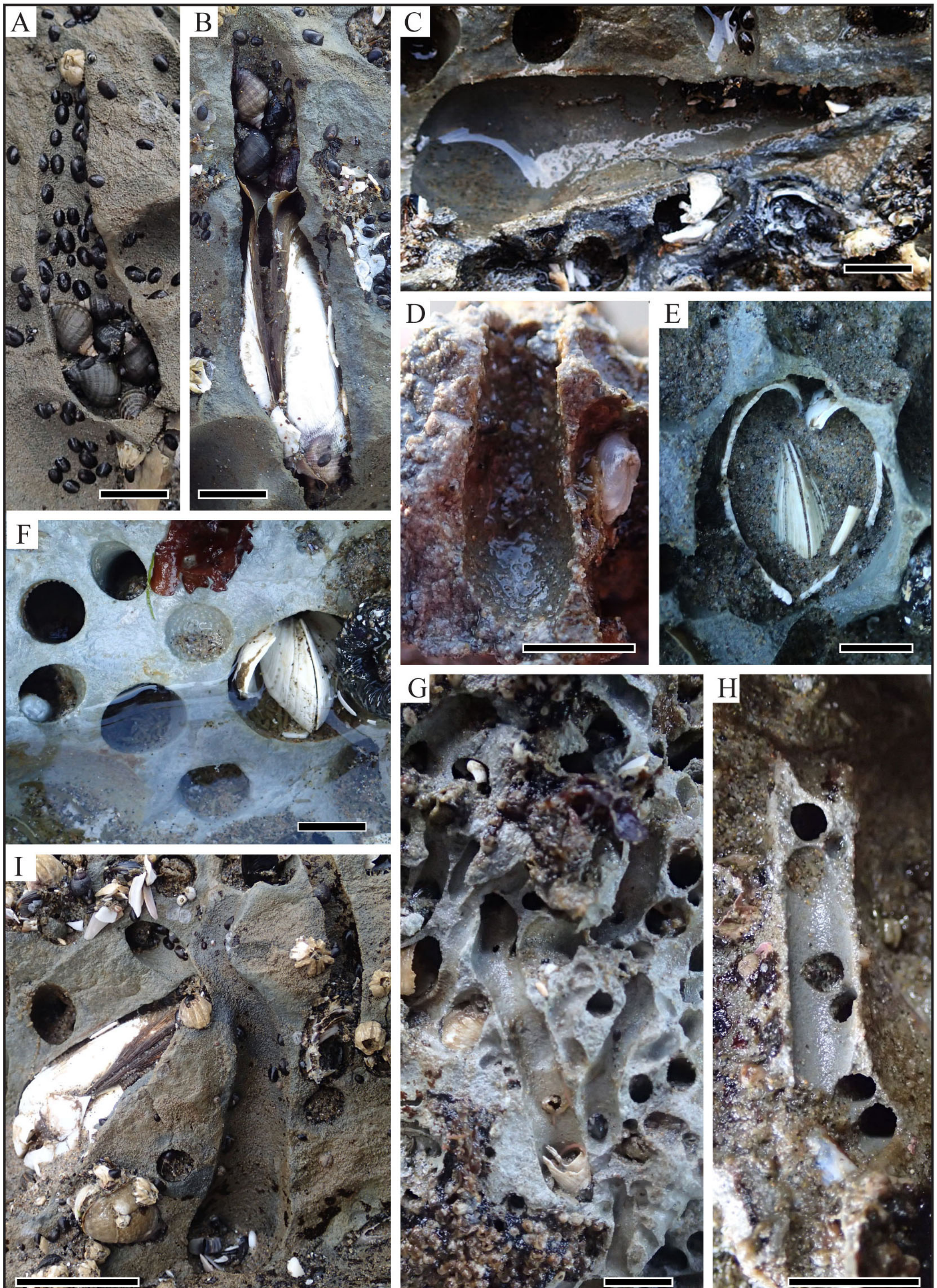


Figure 2-9. *Gastrochaenolites*-type traces. All imaged within the sublittoral zone due to exceptional exposure and lack of encrusting and squatting organism. (**A**) *Gastrochaenolites turbinatus* occupied by limpets and gastropods. (**B**) *Penitella penita* within *G. turbinatus*. (**C**) Empty *G. turbinatus*. (**D**) *G. turbinatus* produced by *Adula californiensis*. Scale bar = 0.5 cm. (**E**) Stacked shells of *H. arctica*. (**F**) *Hiatella arctica* within *Gastrochaenolites* cf. *G. lapidicus*. (**G**) *Gastrochaenolites* with various orientations. (**H**) Three vertical *Gastrochaenolites* extending from horizontal *Gastrochaenolites* tunnel. Scale bar = 5 cm. (**I**) Occupied and unoccupied *G. turbinatus*. All scale bars = 1 cm unless otherwise noted.

Figure 2-10. Sublittoral zone. (**A**) *Trypanites* ichnofacies composed of *Gastrochaenolites*-type traces. Scale bar = 5 cm. (**B**) Same. Scale bar = 5 cm. (**C**) Same. Scale bar = 15 cm.

Figure 2-11. Littoral zones and organisms on Humbug Point and the two seaward, basalt sea stacks. (**A**) *Balanus glandula* within the supralittoral zone of Humbug Point. Scale bar = 2 cm. (**B**) *Ulva intestinalis* and *B. glandula* within the supralittoral zone of Humbug Point. Scale bar = 5 cm. (**C**) The northern basalt sea stack; a clear biological division is present between the middle and lower littoral zones. Scale bar = 75 cm. (**D**) Middle littoral zone of the basalt sea stacks. Organisms present include *Mytilus trossulus*, *M. californianus*, *B. glandula*, *Pollicipes polymerus*, *Chthamalus dalli*, *Hesperibalanus hesperius*, *Eudistylia vancouveri*, *Lottia sp.*, *Diodora sp.*, *Littorina sp.* and *Nucella sp*. Scale bar = 20 cm. (**E**) Lower littoral zone of the basalt sea stack. Organisms present include *Anthopleura xanthogrammica* and *Pisaster ochraceus*. Scale bar = 10 cm.

subject to high-energy conditions. The combination of these factors allow organisms to grow much larger in size compared to their counterparts on Lion Rock; for example, mussels reach up to 20 cm in length on the basalt sea stacks, as compared to 12 cm on Lion Rock. The lower and middle littoral zones are present (Figs. 2-11 C-E) and organisms encrust 90%-100% of the substrate. Organisms present within the middle littoral zone include mussels (*Mytilus trossulus* and *Mytilus californianus*), barnacles (*Balanus glandula*, *Pollicipes polymerus*, *Chthamalus dalli* and *Hesperibalanus hesperius*), feather duster worms (*Eudistylia vancouveri*), limpets (*Lottia* sp. and *Diodora* sp.) and gastropods (*Littorina* sp. and *Nucella* sp.). Organisms observed within the lower littoral zone include anemones (*Anthopleura xanthogrammica* and *Anthopleura elegantissima*), asteroid (*Pisaster ochraceus*), limpets (*Lottia sp.* and *Diodora* sp.), gastropods (*Littorina* sp. and *Nucella* sp.), sea cabbage (*Hedophyllum sessile*) and sea lettuce (*Ulva lactuca*). No borings are present within the two sea stacks due to their basalt lithology. The lack of borings prevents macro-habitats from being present to protect more fragile organisms thereby eliminating them from residing on the basalt sea stacks. A lower population of squatters/clingers is observed due to the greater wave exposure conditions of the sea stacks and the deficiency in borings providing protective macro-habitats.

TRYPANITES-TYPE ICHNOFACIES

Macroborings, identified here as *Gastrochaenolites*-type traces, are produced by the boring bivalves, *Adula californiensis*, *Hiatella arctica*, *Penitella penita*, and *Zirfaea pilsbryi* (Fig. 2-12), and demonstrate a modern example of a *Trypanites*-type ichnofacies. Boring bivalves present at Lion Rock use mechanical means to penetrate the substrate and the overall shape of the borings is indicative of taxonomic affiliation, age and growth patterns of the originator. Many boring bivalves are rotating borers and use their muscles to slowly rotate themselves to

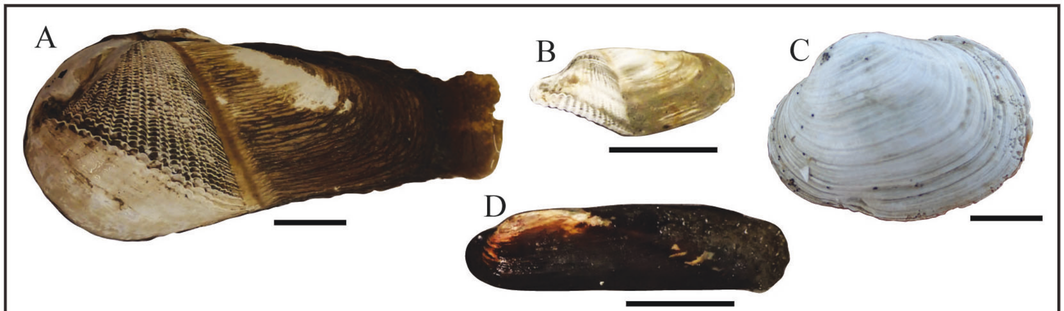


Figure 2-12. Boring bivalves. (**A**) *Penitella penita*. (**B**) *Zirfaea pilsbryi*. (**C**) *Hiatella arctica*. (**D**) *Adula californiensis*. All scale bars = 1 cm.

excavate boreholes (Gosling, 2003; Savazzi, 2005). Additionally, the sharp-edged ridges along the anterior face of their shell assist in abrading the substrate (Gosling, 2003). Non-rotating borings open and close their valves to penetrate the rock and frequently nest within persisting void spaces or weakly byssally attach to the substrate (Savazzi, 2005). It is likely that *Penitella penita* and *Zirfaea pilsbryi* are rotating borers, whereas *Hiatella artica* and *Adula californienis* are non-rotating borers. All boring bivalves, regardless of boring mechanics, are permanently locked within their borings and are not capable of leaving their traces and reestablishing a new boring (Gosling, 2003).

Traces produced by the boring bivalves are similar to the ancient form *Gastrochaenolites*. *Gastrochaenolites* Leymerie, 1842 are teardrop-shaped or clavate borings that have been primarily associated with bivalve originators. The apertural region and neck are circular, oval or dumb-bell shaped and are narrower than the main chamber (Kelly and Bromley, 1984). The main chamber varies from subspherical to elongate, with a rounded to parabolic base, and is circular to oval in cross section (Kelly and Bromley, 1984). Borings may be straight, curved or irregular and possess walls that are smooth or ornamented (Kelly and Bromley, 1984).

The most prevalent forms at Lion Rock are similar to the ancient forms of *Gastrochaenolites turbinatus* Kelly and Bromley, 1984 (Figs. 2-9 A-D) and are produced by *Penitella penita*, *Zirfaea pilsbryi*, and *Adula californiensis*. The forms vary in size with respect to the taxon and age of the originator, but producers cannot be differentiated when the boring organism is not present within the trace. The aperture and chamber reach 0.5 cm and 4 cm in diameter respectively and the overall length reaches 7 cm. *Hiatella arctica* produces traces similar to the ancient forms of *Gastrochaenolites* cf. *G. lapidicus* Kelly and Bromley, 1984 (Fig. 2-9 E-F), however the ichnospecies is uncertain due to the inability to observe the full form along the axis of the boring and only being able to observe the form from a planar perspective. Kelly and Bromley (1984) suggested that different species of modern *Lithophaga* and *Hiatella* produce *G. lapidicus*-type traces.

All *Gastrochaenolites*-type traces within Lion Rock are morphologically variable. The morphology of individual examples reflects the age and growth patterns of the originator as well as taxonomic affinity. Crowding, siphon action and marine erosion have been proposed by Evans (1968) to greatly affect boring morphology, causing traces to cross, intersect, avoid each other and be isolated from one another. No preferred orientation is present among borings within the study area, either with reference to a horizontal or vertical plane. Borings occur parallel to, perpendicular to and at various angles to the substrate surface, as well as oriented towards variable azimuths, thereby forming a complex three-dimensional network of traces (Figs. 2-9, 2-10). Borings are not limited to a single lineation or axial plane and frequently bend and curve around other traces, making the clavate morphology of the borings irregular (Figs. 2-9 G-I, 2-10). Traces are frequently truncated as a result of marine erosion.

The ichnocoenosis at Lion Rock is produced by multiple generations of boring bivalves and results in traces crossing and intersecting (Figs. 2-9 G-I, 2-10). Individual borings are commonly re-inhabited after the original borer died, resulting in complex crosscutting relationships, with younger borings branching off of older forms (Fig. 2-9H). Erosion of the sea stack surface aids in exposing different bored substrates, allowing re-colonization and thereby producing a mosaic of old, eroded borings mixed with new traces (Fig. 2-10). Stacked shells (Fig. 2-9E) also support the hypothesis of a complex, multigenerational ichnocoenose; shell stacking occurs when one bivalve originally bored into the substrate, perished, and subsequently another bivalve bores into the same space and 'inhabits' the shell of the previous borer. The few examples of shell stacking reveal that the shell of the original borer remained unaltered and was not penetrated or broken by the secondary boring organism. Little in known about the biological conditions surrounding the occurrence of stacked shells, and further research from Lion Rock and other localities may provide insight onto the mechanics and potential reasoning for bivalves residing within a stacked shell pattern.

Boring density (occupied and unoccupied borings) within the exposed substrate varies by ecological zone (Figs. 2-3G, 2-3H). Borings within the sublittoral zone ranged from 0-20 traces within a 15 x 15 cm area; the lower littoral zone is characterized by 20-80 borings per area; the middle littoral zone is characterized by 0-5 borings per area and the upper- and supralittoral zones are devoid of all borings. It must be noted that the middle littoral zone is heavily encrusted by a variety of taxa, rendering it difficult to determine if boring bivalves are present without removing a significant number of biota. Boring densities are highest on the west (seaward) side as compared to the east (landward) side of Lion Rock, which results from variable water depth, wave energy exposure and lithology of the sea stack (i.e. more sandstone preserved on the seaward side of the stack).

The distribution and comparison of occupied versus unoccupied borings is nearly impossible to tabulate due to the endolithic nature of the boring bivalves. The middle-, lower- and sublittoral zones possess observable unoccupied and eroded borings. Occupied borings were only present within the lower- and sublittoral zones and were identifiable when siphons extending to the surface and were observed. Larger populations of live boring bivalves reside within the lower littoral zone, as compared to the highly eroded sublittoral zone, but exact ratios are unobtainable.

Clastic *Trypanites* ichnofacies, both within the rock record and in equivalent modern environments, are associated with erosional processes and unconformities. Weathering and associated alteration of the eroded surface commonly results in complications to ichnotaxonomic identification, making it difficult to identify traces to the ichnospecies level. Erosion of the substrate may reveal numerous possible cross sectional profiles of the forms (Figs. 2-9, 2-10), further complicating identification of trace and potential trace makers. Sand often infills borings, which conceals the internal structure of the forms. The complexities of the borings and bored substrates therefore have the potential to be under appreciated and under represented within both modern and ancient *Trypanites* ichnofacies.

Specialized macro-habitats

Eroded *Gastrochaenolites*-type traces generate rounded and bowl-shaped cavities within the rock that provide protected maco-habitats for many organisms. The eroded borings increase the surface area of the sea stack and provide a more favorable location for larval attachment and growth by providing relatively protected area from oncoming tidal and wave energy. Unoccupied traces can collect water and act as small oases during low tide, thus preventing the desiccation of organisms. Boring intersections form high points where organisms can extend parts of their bodies to have better access to water movement for feeding or reproductive purposes. Each *Gastrochaenolites* macro-habitat may contain one or several animals (Figs. 2-8F, 2-8G, 2-9A, 2-9B) and allow a diverse assemblage of organisms to reside within a very small area.

Tidal pools, vugs and fractures within the sea stack also allow sheltered areas for organisms to inhabit. Water pools in these areas during low tide and allow organisms from lower littoral zones to inhabit areas of higher elevations. Within the middle littoral zone, the anemones, *Anthopleura elegantissima* and *Anthopleura xanthogrammica*, are typically very small (0.5-1 cm in diameter) and isolated, but when sheltered within tide pools, vugs and fractures the anemones are much larger in size (4-5 cm in diameter). These areas are less frequently inhabited by organisms that can withstand strong currents or need strong currents for suspension feeding, like *Mytilus trossulus*, *Mytilus californianus*, *Pollicipes polymerus*, *Hesperibalanus hesperius*. With less competition for space, organisms such as anemones can grow to sizes comparable to those within lower littoral zones.

Terminology discrepancies

Borings are defined as structures produced by organisms, which cut across all grains besides the most impenetrable (Gallois and Golding, 2007). Within the rock record, this is essential to identify borings in order to recognize an assemblage as a *Trypanites* ichnofacies. However, thin sections of borings at Lion Rock (Fig. 2-13) show that the very fine, quartz grains of the Angora Peak sandstone are not cross cut. There is also no evidence of chemical alteration of cement surrounding the borings. Although grains are not cut by the boring organism, the forms cannot be considered burrows, which are restricted to soft grounds, nor pseudo-"borings," which cross-cut softer grains and avoid harder grains. In fact, in these examples, the bivalves bore by scissoring their valves and abrade the rock using sand grains that are lodged in grooves on their shells. This is not consistent with burrowing behavior, which consist of advection, compaction or excavation by an animal (Simpson, 1975; Ekdale et al., 1984;). Moreover, Lion Rock is fully lithified and therefore the term "borings" must be used for the observed traces.

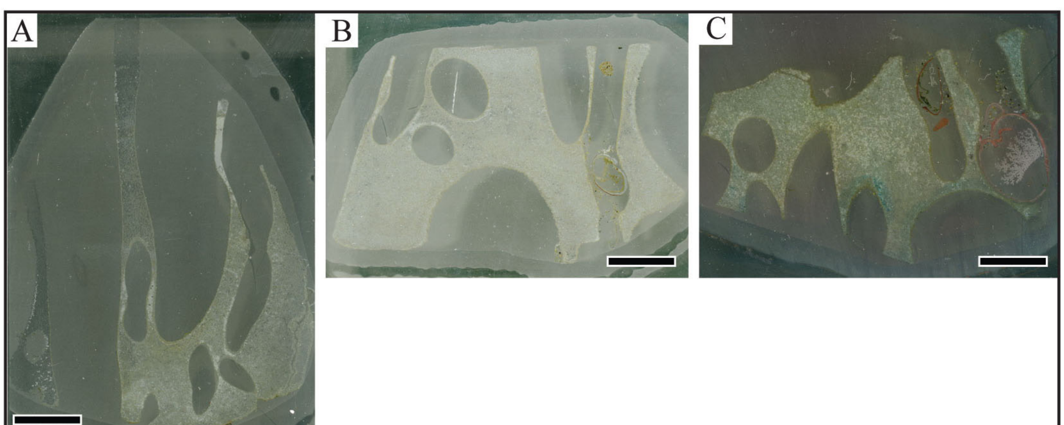


Figure 2-13. Thin sections through borings. (**A**) Thin section through a longitudinal profile of multiple borings. (**B**) Thin section through a longitudinal profile through multiple borings alongside cross sectional view of borings. (**C**) Thin section double carbonate stained with Alizarin Red S and Potassium Ferricyanide. Two bivalve shells are present within the borings (stained red). All scale bar = 1 cm.

CONTROLS ON BORINGS AND ORGANISM DISTRIBUTION

Different environmental factors affect the boring patterns of the four boring bivalves identified in the study area. Those discussed herein include lithology, water depth/wave energy, and sediment dynamics (i.e. movement of sediment within the system).

Lithology

Lion Rock is composed of two distinct lithologies: sandstone assigned to the Angora Peak Member of the Astoria Formation and basalt from the Ortley Unit of the Columbia Flood Basalt (Figs. 2-3C, 2-3D). Both of these lithologies are exposed to encrusting and squatting/clinging organisms, however the basalt is too hard for the bivalves to penetrate. Thus, the bivalves are limited to exposures of Angora Peak Sandstone. Other studies have documented traces within basalt (Santos et al., 2011, 2012), but within this study boring bivalves traces are limited to the sandstone substrate.

On the south side of Lion Rock, the boundary between sandstone and basalt can be traced from the lower- and supralittoral zones to the top of the sea stack (Fig. 2-14A). The borings within the sandstone closest to the boundary are unoccupied and have a low abundance (8-15 borings per 15 cm by 15 cm area) (Fig. 2-14B), whereas the basalt has no borings (Fig. 2-14C). The boundary between the sandstone and basalt on the north side of Lion Rock is more difficult to trace due to the boundary being covered by a high degree of encrusting organisms within the middle and lower littoral zones (Fig. 2-14E). Here, the basalt does not reach the base of the sea stack and extends only as low as the uppermost region of the lower littoral zone. The sandstone substrates within the sublittoral and lower littoral zones are highly bored (up to 80 borings per 15 cm by 15 cm area).

Water depth and wave energy

Marginal marine environments are subject to tidal influences creating a cyclical pattern of exposure and submergence. The maximum tidal range of Arcadia Beach is 2.04 m (-0.12 to 1.92 m). As a result, Lion Rock is completely exposed during the lowest of low tides and is entirely surrounded by water during all high tides (Fig. 2-2B). The water depth and tidal energy results in littoral zones on the rocky shore

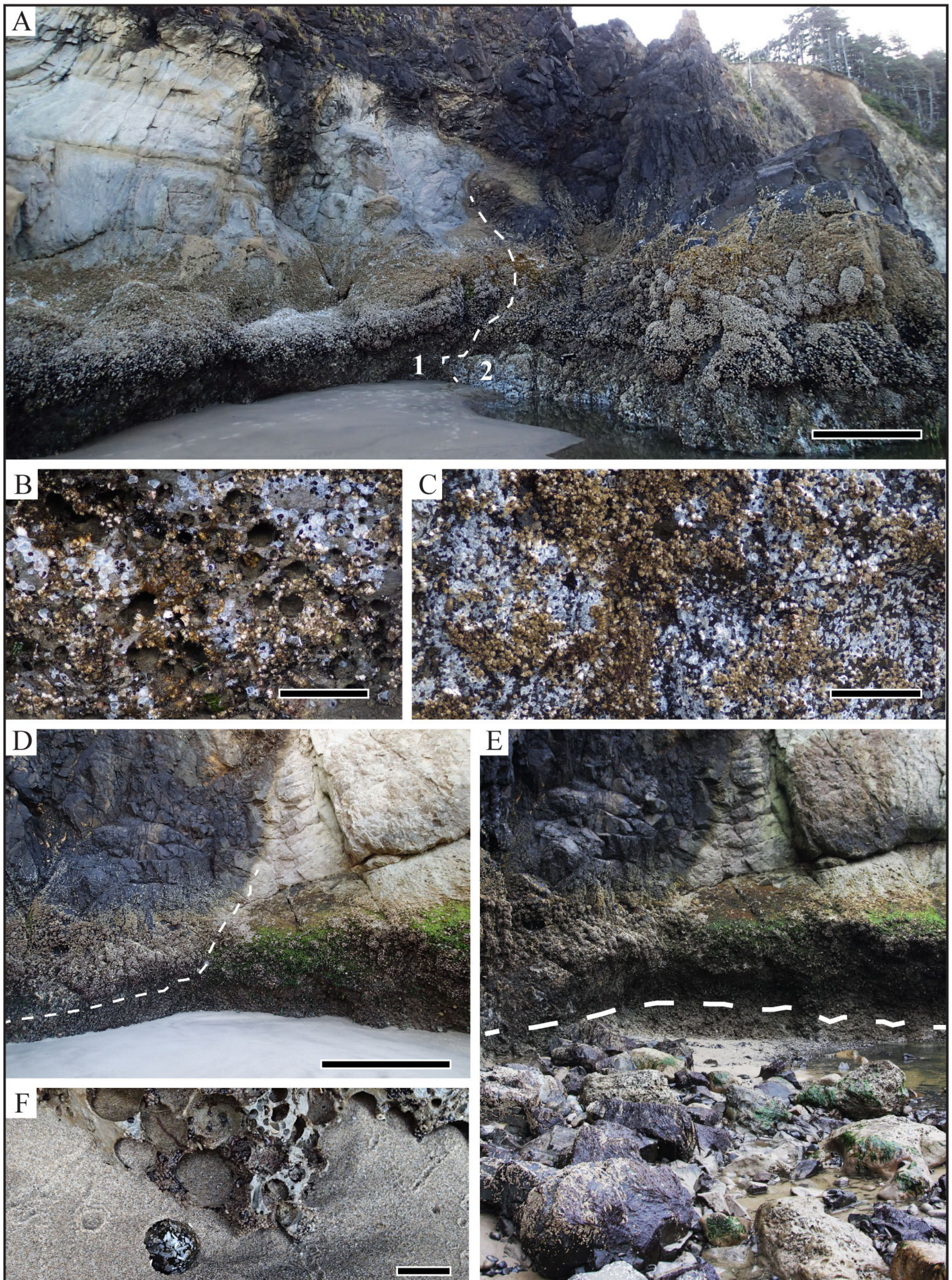


Figure 2-14. Lithology of Lion Rock. (**A**) South face of Lion Rock with dashed line separating sandstone (right) and basalt (left); 1 and 2 correspond to B and C respectively. Scale bar = 2 m. (**B**) Zoomed in view of bored sandstone at location 1. Scale bar = 5 cm. (**C**) Zoomed in view of basalt without borings at location 2; encrusting *Balanus glandula* abundant. Scale bar = 6 cm. (**D**) North face of Lion Rock with dashed like separating sandstone from basalt; foreshore sand present within the foreground; photo taken in August 2013. Scale bar = 2 m. (**E**) North face of Lion Rock with foreground, foreshore sand eroded; photo taken in April 2013. Same scale as D. (**F**) Contact between foreshore sand and bored sandstone; anemone generated tunnel through sand to maintain exposure to the surface; depth of tunnel is 2 cm. Scale bar = 3 cm.

faces, where organisms reside within zones of acceptable conditions. The boring bivalves are limited to the sublittoral zone, lower littoral zone and the lowermost portion of the middle littoral zone of the sandstone substrate. This is where exposure is limited to short periods of time (maximum 6 hours of continuous exposure), allowing bivalves to become dormant during low tides.

Shifting sediment

During our first research visit in April of 2013, a thick bored succession was exposed at the base of Lion Rock. During a subsequent visit in August of 2013, over a meter of sand had accumulated within the northern alcove of Lion Rock (Figs. 2-14D, 2-14E), and is hypothesized here to be related to seasonal storm activity. This area, classified as the sublittoral zone, possesses vacant *Gastrochaenolites*-type traces and has few to no living organisms present due to the shifting sand. In addition to seasonal aggradation and degradation, sediment shifts daily and exposes and covers portions of the sea stack substrate. Sea anemones (*Anthopleura elegantissima* and *Anthopleura xanthogrammica*,), chitons (*Katharina tunicate* and *Mopalia muscosa*), asteroids (*Pisaster ochraceus*) and boring bivalves (*Adula californiensis*, *Hiatella arctica*, *Penitella penita*, and *Zirfaea pilsbryi*) were observed to survive during short periods of burial (maximum time length unknown). Anemones, in particular, can move sediment in the outgoing tide to generate tubular excavations allowing them to be exposed to water while being located below more than a centimeter of sand (Fig. 2-14F). During periods of long exposure, mobile organisms can move to areas previous buried, where competition for ecospace is decreased. The maximum and minimum depths of sediment surrounding Lion Rock is unknown since many factors affect sedimentation and erosion within this area. Although *Trypanites* ichnofacies are typically associated with prolonged sedimentary hiatuses, environmental conditions here suggest that shortened periods of deposition and erosion can occur along the hardground ichnofacies.

IMPLICATIONS FOR THE ROCK RECORD

Based on the analog of Lion Rock, modern *Trypanites*-type communities are characterized by a much higher diversity and abundance of organisms than exemplars described within the rock record (e.g. Palmer, 1982; Gibert et al., 1998). Although paleontology commonly relies on neoactualism in the interpretation of ancient successions, many organisms have a low preservation potential, making it difficult to determine the true diversity of many ancient marine communities. Although inferences have been made by Goldring and Kaźmierczak (1974, fig. 3) Palmer (1982, fig. 5), and Johnson and Baarli (1999, fig. 1) to suggest an evolution of rocky shore organisms through geologic time, it is difficult to define the biodiversity of most ancient hardgrounds when few body fossils are found. However, within this study, the diversity and abundance of taxa clearly illustrates that ancient bored rocky shores are areas of potentially high biodiversity with organisms possessing low preservation potential, instead of the low diversity ecosystems that are commonly associated with the *Trypanites* ichnofacies.

Trace makers are frequently overlooked when describing preserved *Trypanites* ichnofacies and other marine ichnofacies due to the complexity of making a clear association between traces and trace makers. Occasionally a phylum of biota is assigned to a trace, but lower taxonomic assignment is commonly impossible, as skeletal detritus of boring organisms is not commonly preserved. Multiple boring organisms may also be responsible for producing the same trace or very similar traces within a very small area, as is exemplified by the occurrence of the four boring bivalve taxa within Lion Rock.

Boring, encrusting and squatting/clinging organisms that reside within the rocky intertidal zone have specific environmental conditions that are most favorable. *Gastrochaenolites*-type traces are limited to the sublittoral and lower littoral zones, but non-boring organisms extend to higher elevations. Since the traces have the highest preservation potential, the rock record of rocky shores can possess bored and unbored surfaces. Thus unbored surfaces have the potential to be under-appreciated, over-generalized or overlooked as being associated with *Trypanites* ichnofacies.

Lion Rock is an exceptional example of a siliciclastic rocky shore. *Trypanites* ichnofacies have been described throughout the world and throughout the geologic timescale, but few examples have been reported from siliciclastic substrates (Fig. 2-1). It is unclear why there is a significant lack of preserved siliciclastic *Trypanites* ichnofacies compared to those in carbonates and there is no clear geographic or longitudinal restriction to the two lithologies. The preservation of rocky shores has been suggested to be linked to sea level and tectonic margin types (see Johnson et al., 1988). Bored substrates in clastic settings are more frequently associated with erosionally exhumed substrates and erosional disconformities, whereas in carbonate settings, hardground surfaces can be autogenic and associated with non-depositional breaks as well as erosional exhumation (Bromley, 1975; Pemberton, 2003). Carbonate successions therefore have a higher likelihood of preservation within the rock record, whereas clastic substrates are more likely to be cannibalized.

CONCLUSIONS

A modern example of a *Trypanites*-type community occurs at Lion Rock at Arcadia Beach State Park, Oregon. Four species of bivalves, *Adula californiensis*, *Hiatella arctica*, *Penitella penita*, and *Zirfaea pilsbryi*, produce an ichnocoenosis of *Gastrochaenolites*-type traces produced by multiple generations of borers. Traces similar to the ancient forms of *Gastrochaenolites turbinatus* and *Gastrochaenolites* cf. *G. lapidicus* have been identified within this modern environment, however, the identification of an ichnospecies is difficult due to erosion, inability to observe entire forms and multiple generations of borings crosscutting one another. The clavate forms are limited to the sandstone substrate of the sublittoral zone, lower littoral zone and the lowermost portion of the middle littoral zone. Boring, encrusting and squatting/clinging organisms are divided into five littoral zones (supralittoral, upper littoral, middle littoral, lower littoral and sublittoral) based on physical and biological parameters including wave energy, water depth, exposure period, resistance to desiccation and predation. The sublittoral zone, as described herein, includes the lowermost area of the sea stack that is exposed only at the lowest tides, which experiences prolonged periods of burial by surrounding foreshore sand and is absent of many organisms residing on higher zones. The diversity of the entire sea stack exceeds 40 species of flora and fauna, with the majority of biota having a low preservation potential within the rock record. *Trypanites* ichnofacies are typically associated with a low diversity and abundance of organisms due to the low preservation potential of many organisms. The modern analog of a *Trypanites*-type ichnofacies at Lion Rock reveals that bored hardground assemblages within the rock record represent communities that are potentially much higher in diversity and abundance than previously described.

CHAPTER 3: EXTENSIVE *TRYPANITES*-TYPE ICHNOFACIES AT THE BAY OF FUNDY, NOVA SCOTIA, CANADA

INTRODUCTION

The *Trypanites* ichnofacies includes suites of trace fossils that occupy hardgrounds or fully lithified substrates (Frey and Seilacher, 1980). Organisms, which excavate the traces included in this ichnofacies, are uniquely adapted to penetrate rocky substrates, either through chemical dissolution or mechanical abrasion. Most trace fossil included in the *Trypanites* ichnofacies are domiciles, and common traces include *Trypanites*, *Gastrochaenolites*, *Entobia*, *Rogerella*, *Uniglobites*, *Maeandropolydora*, *Circolites*, *Caulostrepsis*, polychaete borings and echinoid grooves (Frey and Seilacher, 1980; MacEachern et al., 2010; Gibert et al. 2012). Trace fossil diversity is generally low and some ichnogenera may be completely absent within localities and throughout time (Frey and Seilacher, 1980; Gibert et al. 2012). The ichnofacies is frequently associated with palaeoshoreline locations and significant stratal surfaces and can provide significant insight into paleogeography and sequence stratigraphy (Gibert et al., 1998; Silva et al., 1999; Pemberton and MacEachern, 2005). Paleoecological communities (body fossils and trace fossils) associated with *Trypanites* ichnofacies are typically low due to the low preservation potential of organisms and unpredictable conditions associated with the erosional, high-energy environment (Gibert et al. 2012). However, biotic assemblages of modern bored surfaces suggest that *Trypanites* ichnofacies have a diverse assemblage of boring, encrusting and squatting/clinging organisms (see Chapter 2).

This paper documents a modern *Trypanites*-type assemblage within an extensively-exposed siliciclastic substrate near Thomas Cove, Economy Point, Nova Scotia, Canada. The bored surface occurs within exposed, wave-cut benches of Triassic bedrock (Wolfville Formation). The focus of the study is to (1) identify borings and trace makers, (2) define the controls affecting boring distributions and (3) describe the diversity and abundance of borings. Sedimentological and environmental conditions are also evaluated within the multiple terraced, wave-cut benches. Thomas Cove is used here as a modern analog to describe the diverse ecological potential of *Trypanites* ichnofacies of the past and to assess the oceanographic and sedimentological controls that govern the development and nature of these assemblages.

STUDY AREA AND GEOLOGICAL CONTEXT

The Bay of Fundy is a large, megatidal estuarine embayment bordered primarily by the provinces of New Brunswick and Nova Scotia, Canada (Fig. 3-1). The Fundy Basin is a product of a series of early Mesozoic rifting along the Atlantic margin as a result of the breakup of Pangaea (Olsen and Schlische, 1990; Wade at al., 1996; Leleu et al., 2009, 2010; Leleu and Hartley, 2010). The Fundy Basin splits into two smaller sub-basins, with Chignecto Basin to the northeast and the Minas Basin to the east. The Minas Basin is a transtensional rift, with northwest-southeast extension forming a main half graben in the early Mesozoic where continental clastic deposits accumulated (Klein, 1962; Olsen and Schlische, 1990). The basal and basin-margins of the Minas Basin are comprised of Wolfville Formation and is overlade by the Blomidon Formation (Klein, 1962, Olsen and Schlische, 1990; Wade at al., 1996; Leleu et al., 2009, 2010; Leleu and Hartley, 2010). Locally the Wolfville Formation is intersected with extrusions of the McKay Head Basalt (Klein, 1962). Today, the Minas Basin is an active embayment incised into Triassic bedrock and unconsolidated Pleistocene outwash with Modern sedimentary deposits consisting of tidally deposited gravel, sand and mud, which are identical in color and mineral composition to the underlying bedrock (Klein, 1964).

The study area is located south of Thomas Cove on Economy Point, Nova Scotia (Figs. 3-1, 3-2). Economy Point is located on the northern shore of the Minas Basin where Wolfville Formation red rock outcrops extensively. The Wolfville Formation within the Minas Basin has been interpreted as representing a variety of depositional environments including braided river, alluvial fan, lacustrine and aeolian (Klein, 1962, Hubert and Mertz, 1980; Olsen, 1981; Olsen and Schlische, 1990; Wade at al., 1996; Leleu et al., 2009, 2010; Leleu and Hartley, 2010). In the study area, the Triassic bedrock commonly preserves cross-stratified bed forms (Fig. 3-3A) and is made up of sandstone and silty mudstone (Figs. 3-3B, 3-3C). Triassic traces were observed by Leleu et al. (2010, fig. 4H) and are herein identified as *Thalassinoides* (Fig. 3-3D). Isolated areas of bedrock possess a marbled texture of green and red colored sandstone and mudstone as a result of oxidation condition during the Triassic (Fig. 3-3E). The Wolfville Formation outcrops within the study areas as a series of platforms descending stepwise basinward from the two headland cliffs at

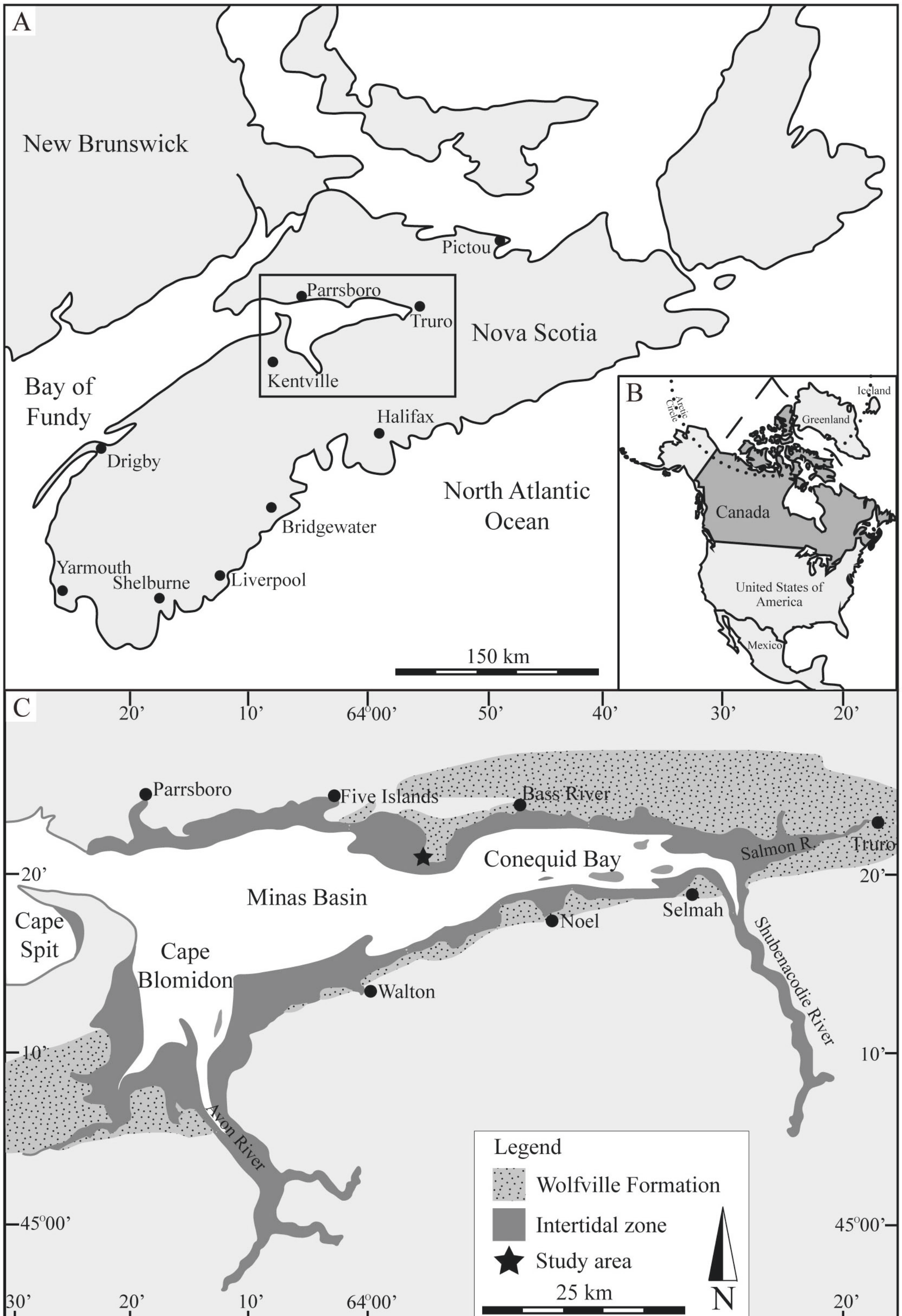


Figure 3-1. Economy Point, Nova Scotia study area location map. (**A**) Bay of Fundy within Nova Scotia and New Brunswick. (**B**) Insert showing location of the Bay of Fundy within eastern Canada. (**C**) Inset of the Minas Basin with Nova Scotia, with the extent of the intertidal zone and Wolfville Formation denoted. Map modified from Yeo and Rish (1981), Dalrymple et al. (1990) and Leleu (2010).

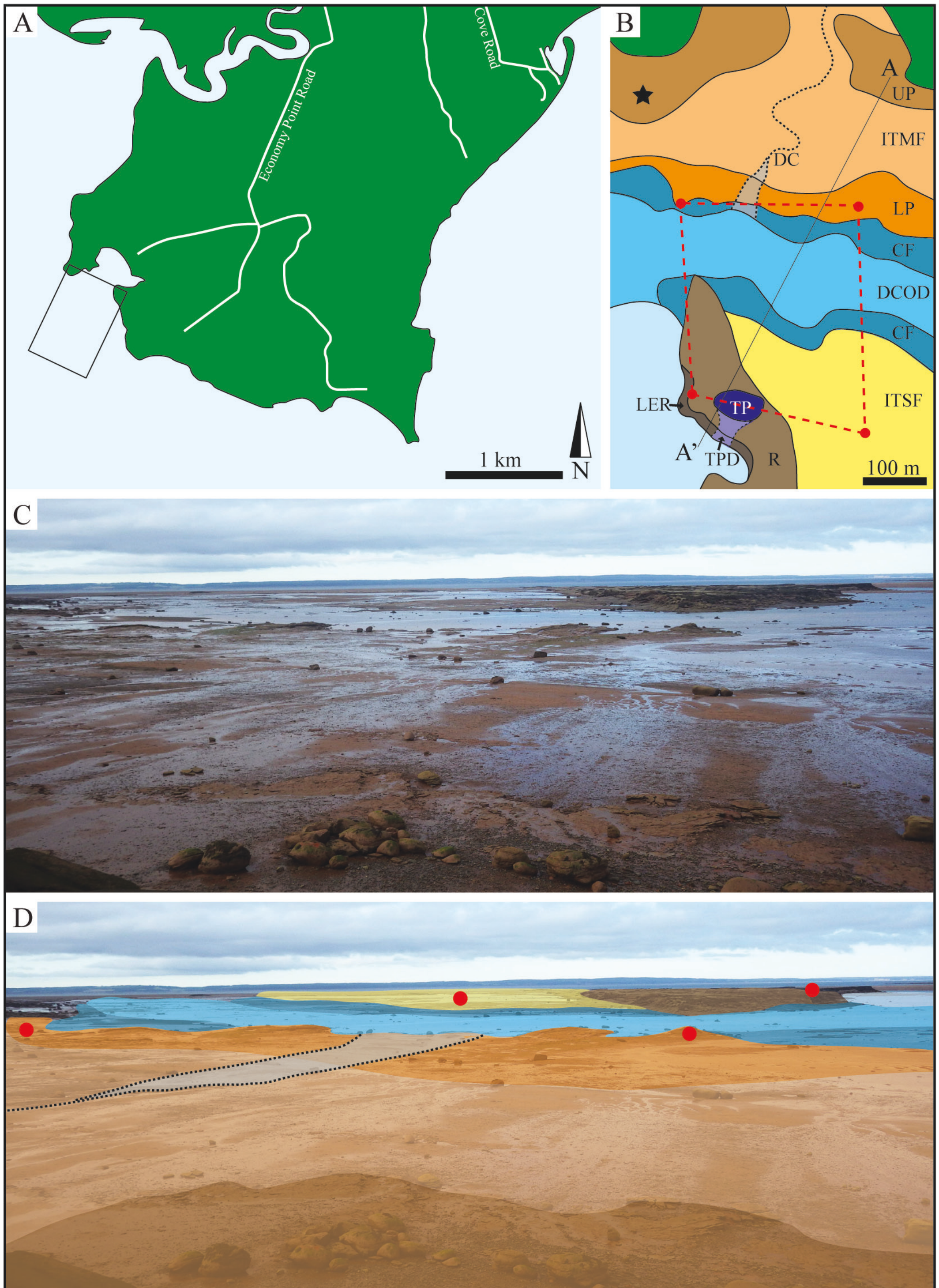


Figure 3-2. Economy Point, Nova Scotia study area location map and depositional sub-environments. (**A**) Economy Point, Nova Scotia. Box represents location area of B. (**B**) Locations of interpreted depositional sub-environments within and around the study area. Study area boundaries indicated by red, dashed line. Depositional sub-environments along transect A-A' was used to construct a schematic cross section (see Fig. 9). The star represents location where image was taken for C and D. Scale bar = 100 m. (**C**) Photograph of study area. (**D**) Photograph of study area in C, with interpreted depositional sub-environments. All symbols and colors used in B and D are listed within "List of Symbols" section of this thesis.

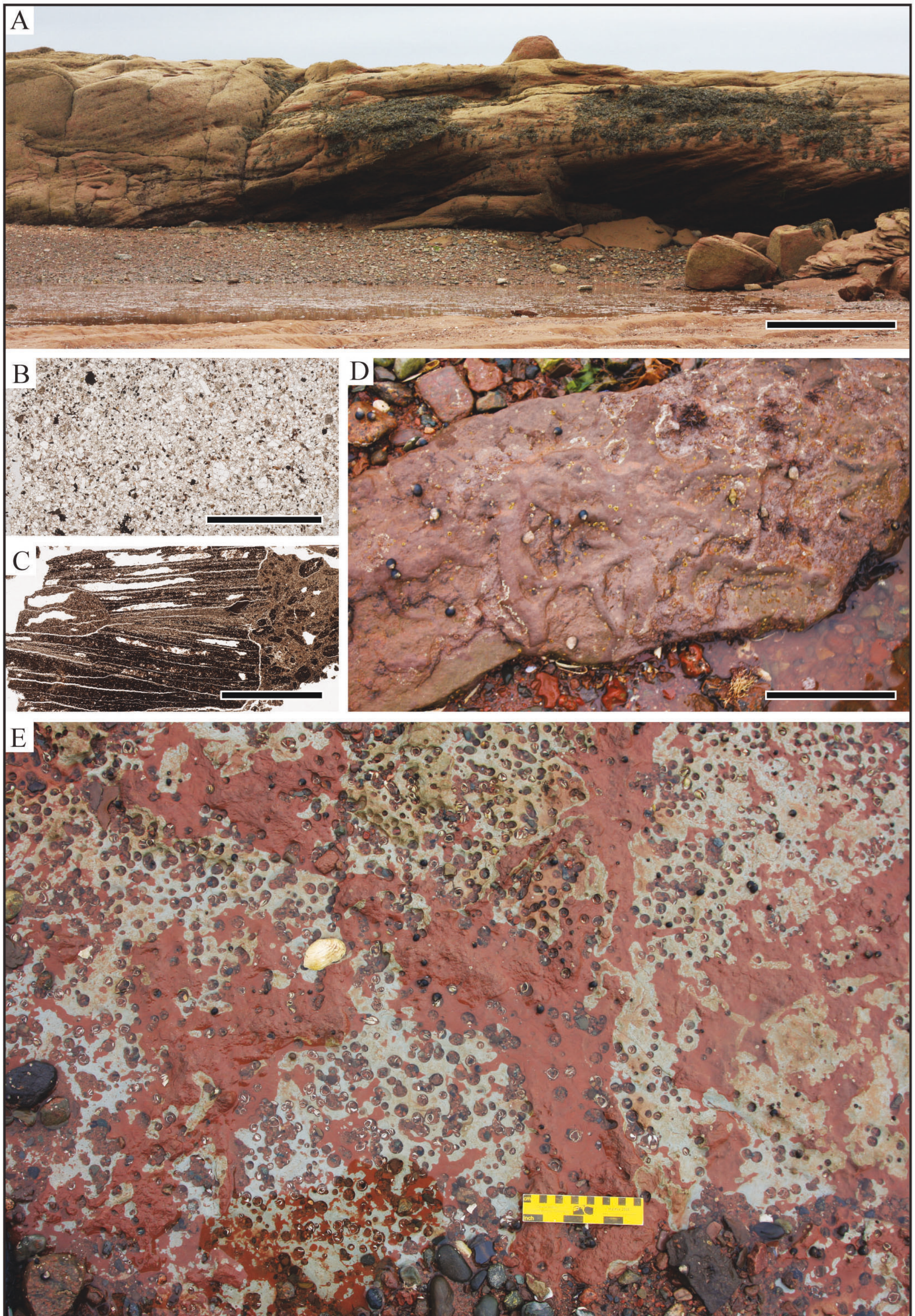


Figure 3-3. Triassic bedrock. (A) Cross stratified bedforms within the Triassic bedrock on the ridge. Scale bar = 1 m. (B) Thin section of sandstone that makes up the majority of the bedrock substrate within the study area. Scale bar = 1 cm. (C) Time section of silty mudstone, which outcrops as on bed within the study area. Scale bar = 1 cm. (D) Thalassinoides formed within the original bedrock. (E) Marbled texture of bedrock with green and red colored silty mudstone. Scale bar = 15 cm.

the edge of Thomas Cove.

Modern depositional environments of the Minas Basin have been divided into four categories: wave-cut benches, estuarine clay flats, tidal flats on lee of bedrock islands and salt marshes (Klein 1963, 1964). Although the study area is characterized as a wave-cut bench environment, eleven different depositional sub-environments are superimposed on the benches (Fig. 3-2). In addition, modern *Trypanites*- and *Skolithos*-type ichnofacies occur within specific dispositional sub-environments, creating a complex ichnocoenosis. The study area is completely submerged at high tide and almost fully exposed during low time as a result of a maximum tidal range that exceeds 13 m. Water accumulates within the topographic lows and forms tide pools, which provide many organisms with refuge during low tide.

METHODS

Key aspects of this study include: (1) identification and distribution of Modern organisms within the Triassic bedrock, (2) description of the morphology, density and distribution of the borings and boring organisms, (4) identification, description and distribution of depositional sub-environments, and (4) identification of the controls on boring patterns and organism distribution. To do this, data was collected along 7 transects throughout the study area, with data points being 30 m apart. A total of 63 data points studied. At each data point lithology, sediment veneer thickness, sediment size, sedimentary structures, water salinity (if water was present, salinity was measured with a salinity meter) was assessed. Distribution of depositional sub-environments was mapped using observed sedimentologic data along the transects. Biotic diversity and species richness of boring, encrusting, squatting/clinging and swimming organisms was identified at each data point. Additionally, boring densities were assessed through counting observed boring within a grid with a 1 m^2 outline. Smaller grids were used (15 cm by 15 cm area) in regions that were smaller than 1 m square in area (i.e. near vertical surfaces of the platform and ridge). For the sake of clarity, all results are reported in square meters. Bored samples of rock were broken off using a chisel and hammer to describe and photograph the inner, bored portion of bedrock. Thin sections of collected rock were made at the University of Alberta to further assess biologic and sedimentologic parameters. Location of transects and raw data collected at each point are described within Appendix C. All invertebrate taxa observed on, or in the bored surfaces were identified to the lowest taxonomic level possible (Appendix D).

Macroborings, identified here as *Gastrochaenolites*-type traces, are produced by the boring bivalves, *Petricola pholadiformis*, and *Zirfaea pilsbryi* (Fig. 3-4), and demonstrate a modern example of a *Trypanites*-type ichnofacies. *Gastrochaenolites* Leymerie, 1842 are teardrop-shaped or clavate borings that have been primarily associated with bivalve originators. The form is made up of an apertural region and neck, which are circular, oval or dumb-bell shaped, and a larger main chamber, which varies from subspherical to elongate, with a rounded to parabolic base, and a circular to oval cross section (Kelly and Bromley, 1984). Borings may be straight, curved or irregular and possess walls that are smooth or ornamented (Kelly and Bromley, 1984). The overall morphology of individual borings reflect the taxonomic affiliation, age and growth patterns of the originator.

The boring bivalves mechanically bore into the lithified substrate and each species produce distinctive forms of *Gastrochaenolites*-type traces. *Petricola pholadiformis* produce traces similar to the trace fossil *Gastrochaenolites turbinatus* Kelly and Bromley, 1984 (Figs. 3-4A, 3-4C). These forms have an aperture less than 0.5 cm in diameter with a chamber less than 4 cm in diameter, and all surfaces of the boring are smooth. *Zirfaea pilsbryi* produces traces similar to the ancient form of *Gastrochaenolites ornatus* Kelly and Bromley, 1984 (Fig. 3-4B). These forms are similar in size to *G. turbinatus*, but within well-preserved traces, spiral-shaped bioglyphs are observed on the base of the chamber and all other surfaces are smooth (Fig. 3-4B). These bioglyphs are products of the mechanical, rotational boring activity as the bivalves penetrate deeper into the substrate throughout their lives. Bioglyphs are frequently not present due to erosion of the surface of the traces after the deceased bivalve shells are eroded or dissolved away. When bioglyphs are erosionally removed, all forms resemble *Gastrochaenolites turbinatus*-type traces.

Boring orientations are similar throughout the study area. The majority of traces penetrate horizontal or slightly sloped surfaces, where bivalves can easily penetrate perpendicularly to the substrate surface (Fig. 3-4). Borings deviate from this orientation when substrates are oriented vertically or sloped at high angles. In these cases, the traces are oriented at various angles to the substrate surface, but occur near vertical with respect to gravitational up. Angular boulders along the bed of the main channel (DCOD) are commonly bored on numerous surfaces, suggesting that the boulders were bored at different time intervals between clast mobilizations. Borings within these boulders are frequently oriented perpendicular to the outside surfaces

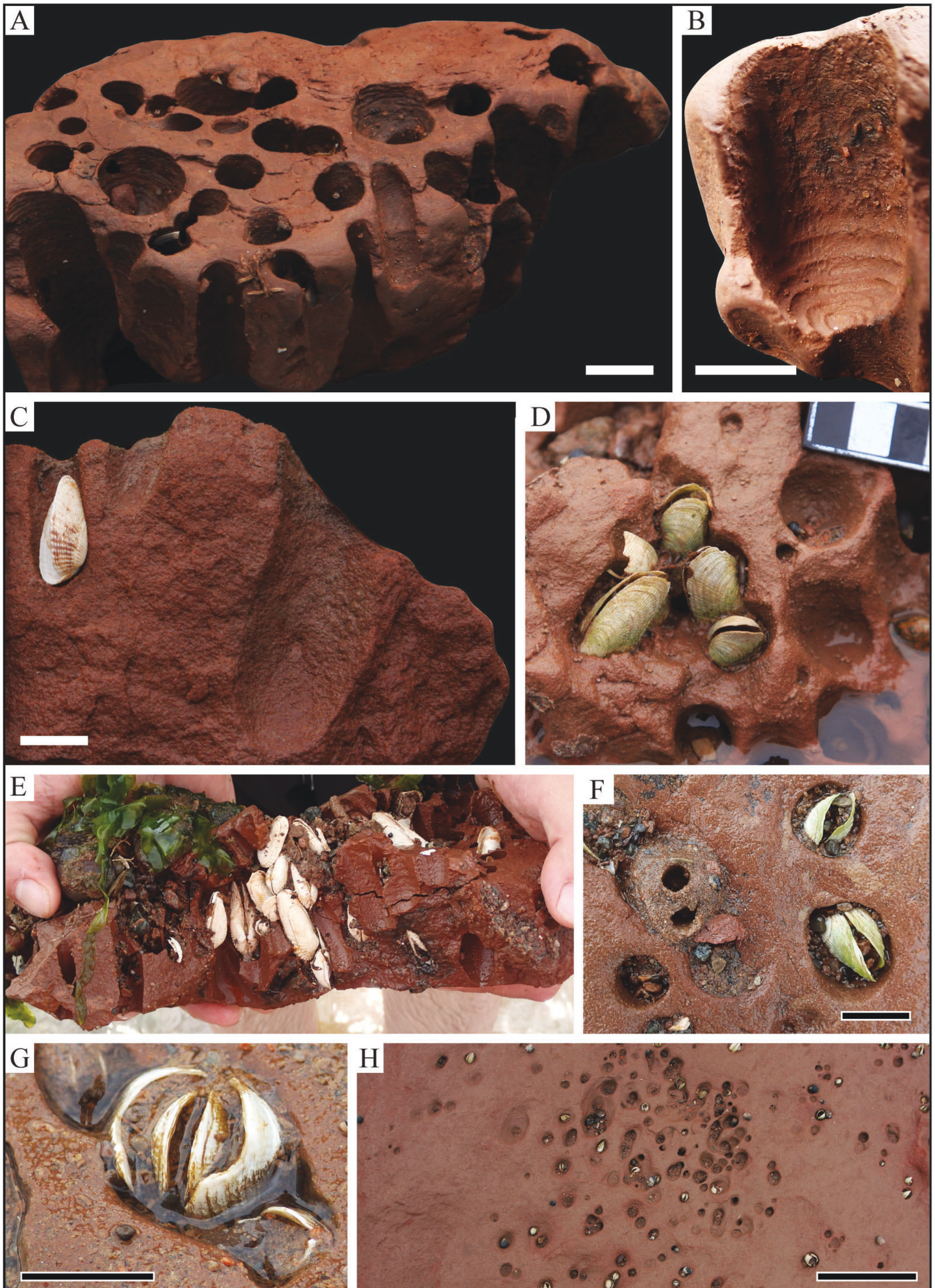


Figure 3-4. *Gastrochaenolites*-type traces. (**A**) *Trypanites* ichnofacies made up of *Gastrochaenolites*-type traces. Scale bar = 1 cm (**B**) *Gastrochaenolites ornatus*-type trace produced by *Zirfaea pilsbryi*. Scale bar = 1 cm. (**C**) *Gastrochaenolites turbinatus*-type traces produced by *Petricola pholadiformis*. Sclae bar = 1 cm. (**D**) Partially eroded traces with *P. pholadiformis*. Scale bar = 3 cm. (**E**) Cluster of *P. pholadiformis* within DCOD bed block. Hands for scale. (**F**) Partially eroded traces with *Z. pilsbryi* and a sediment mound over an occupied boring. Scale bar = 1 cm. (**G**) Stacked shells. Scale bar = 1 cm. (**H**) Hydrodynamically eroded *Gastrochaenolites*-type traces. Scale bar = 15 cm.

and can have dense populations of bivalves (Fig. 3-4E). Traces are commonly cross cut via hydrodynamic erosion and reveal open, unoccupied borings to the surface (Figs. 3-4A, 3-4 D-H).

Borings are present within the bayward sub-environments, including the lower platform (LP), channel fringe (CF), main channel (DCOD), intertidal sand flat (ITSF), ridge (R), leading edge of the ridge (LER), tide pools on ridge (TP) and tide pool drainage system (TPD) (Table 3-1). The density of borings within the depositional sub-environments is variable (Table 3-1, Fig. 3-5, Appendix C) and can be patchy to continuous, with abundance ranging from 0 to 1500 borings per 1m^2 area. Both occupied and unoccupied borings were observed (Fig. 3-6), however ratios of unoccupied versus occupied borings could not be assessed due to the endolithic nature of the bivalves. Shells of deceased bivalves are common within the substrate and are exposed at the surface when the surrounding substrate has been partially eroded (Figs. 3-4D, 3-4F, 3-4G, 3-6E, 3-6F). Living organisms occur within the substrate in different ways and can either have soft body parts or shell material exposed at the surface or be fully confined within the substrate (Fig. 3-6).

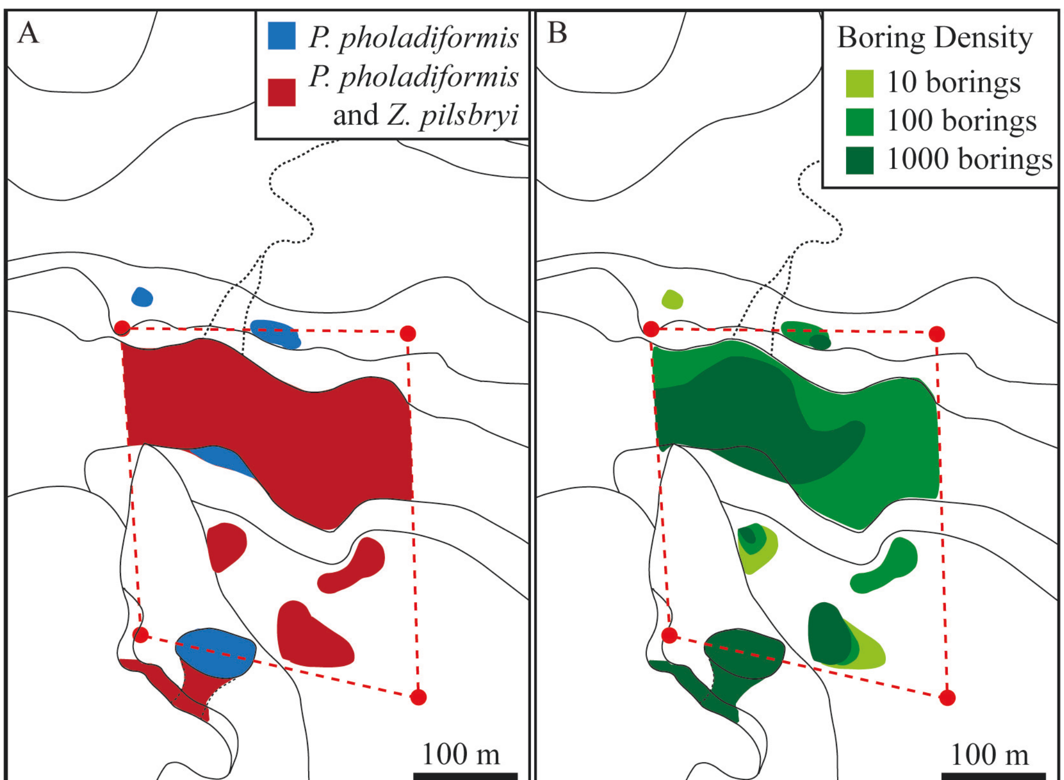


Figure 3-5. Boring density and distribution. (**A**) Distribution of *Petricola pholadiformis* and *Zirfaea pilsbryi* across the depositional sub-environments. (**B**) Boring density irrespective of boring bivalve species. Density is measured in number of borings / m^2. Raw data for boring density is reported in Appendix C

Depositional sub-environment	Trace Fossil Equivalent to Modern Trace Forms	Burrow Density	Boring Density	Observed Tracemakers	Other Organisms Observed
Upper Platforms (UP)	*Arenicolites, Skolithos*, *Gordia*, *Aulichnites*	0-10000	--	*Corophium volutator*, *Heteromastus* sp., *Littorina saxatilis*	*Fucus sp.*, *Spongomorpha* sp.
Intertidal Mud Flat (ITMF)	*Arenicolites, Skolithos, Siphonichnus Polycladichnus, Psilonichnus, Aulichnites, Gordia, Coenobichnus, Coenobichnus/Diplichnites*	0-100000	--	*Corophium volutator*, *Heteromastus* sp., *Macoma baltica*, *Mya arenaria, Cerebratulus* sp., *Nereis* sp., *Littorina saxatilis, Pagurus* sp.	
Drainage channel (DC)	*Arenicolites, Aulichnites*	0-100000	--	*Corophium volutator, Littorina saxatilis*, *Buccinum undatum*, *Nassarius trivittatus*	*Ulva lactuca*, *Palmaria palmata*
Lower Platform (LP)	*Gastrochaenolites, Aulichnites, Coenobichnus/Diplichnites, Polykladichnus*	0-20	0-600	*Petricola pholadiformis, Littorina saxatilis*, *Buccinum undatum*, *Pagurus* sp., *Nereis* sp.	*Chthamalus fragilis*, *Ulva lactuca*, *Fucus* sp., *Lanice sp.*, *Lysianopsis alba*
Channel Fringe (CF)	*Gastrochaenolites, Aulichnites Coenobichnus/Diplichnites*	0-5	0-1500	*Petricola pholadiformis, Littorina saxatilis*, *Buccinum undatum*, *Nassarium trivittaus*, *Urosalpinx cinerea, Lunatia heros*, *Pagurus* sp.	*Chthamalus fragilis*

Table 3-1. Summary of biotic components and associated traces of the depositional sub-environments. Burrow and boring densities are tabulated for a 1-square meter area. Trace fossil equivalent to modern forms, trace makers and other organisms are listed based on observed relative appearance from highest to lowest abundance.

Depositional sub-environment	Trace Fossil Equivalent to Modern Trace Forms	Burrow Density	Boring Density	Observed Tracemakers	Other Organisms Observed
Main Channel (DCOD)	*Gastrochaenolites, Aulichnites, Coenobichnus/Diplichnites*	0-5	100-1500	*Petricola pholadiformis, Zirfaea pilsbryi, Pagurus* sp., *Littorina saxatilis*, *Buccinum undatum*, *Nassarium trivittaus*, *Urosalpinx cinerea, Lunatia heros*	*Ulva lactuca*, *Chondrus crispus*, *Spongomorpha* sp., *Cystoclonium purpureum, Palmaria palmate, Corallina officinalis*, *Flustra foliacea, Chthamalus fragilis*, *Acmaea testudimalis*, *Eualus sp*., *Glycera sp., Enchytraeus sp*, *Didemnum* sp., *Microclona plolifera*, *Haliclona oculata*, *Flustra foliacea*, *Clathromorphum* sp., *Lanice* sp., *Carcinus maenas*, *Libinia dubia*, *Cancer irroratus, Myoxocephalus scorpius*
Intertidal Sand Flat (ITSF)	*Gastrochaenolites, Aulichnites Coenobichnus/Diplichnites*	0-5	0-1500	*Petricola pholadiformis, Zirfaea pilsbryi*, *Littorina saxatilis*, *Buccinum undatum*, *Nassarium trivittaus*, *Pagurus* sp.	*Chondrus crispus*, *Clathromorphum* sp., *Flustra foliacea*, *Cystoclonium purpureum, Lanice* sp., *Glycera* sp., *Enchytraeus* sp.
Ridge (R)	*Gastrochaenolites*	--	0-5	*Petricola pholadiformis*	*Chthamalus fragilis*, *Littorina saxatilis*, *Ascophyllum nodosum Fucus vesiculous*
Leading Edge of Ridge (LER)	*Gastrochaenolites*	--	0-500	*Petricola pholadiformis, Zirfaea pilsbryi*	*Chthamalus fragilis*, *Littorina saxatilis*, *Pagurus* sp.
Tide Pool on Ridge (TP)	*Gastrochaenolites*	--	500-750	*Petricola pholadiformis*	*Chthamalus fragilis Pagurus* sp., *Littorina saxatilis, Buccinum undatum*, *Clathromorphum* sp., *Spongomorpha* sp., *Chondrus cripus, Cystoclonium purpureum, Corallina officinalis*, *Flustra foliacea*, *Crepidula fornicate*, *Glycera* sp., *Enchytraeus* sp.
Tide Pool Drainage System (TPD)	*Gastrochaenolites*	--	0-350	*Petricola pholadiformis, Zirfaea pilsbryi*	*Chthamalus fragilis*, *Littorina saxatilis*, *Pagurus* sp., *Carcinus maenas*

Table 3-1. Summary of biotic components and associated traces of the depositional sub-environments continued.

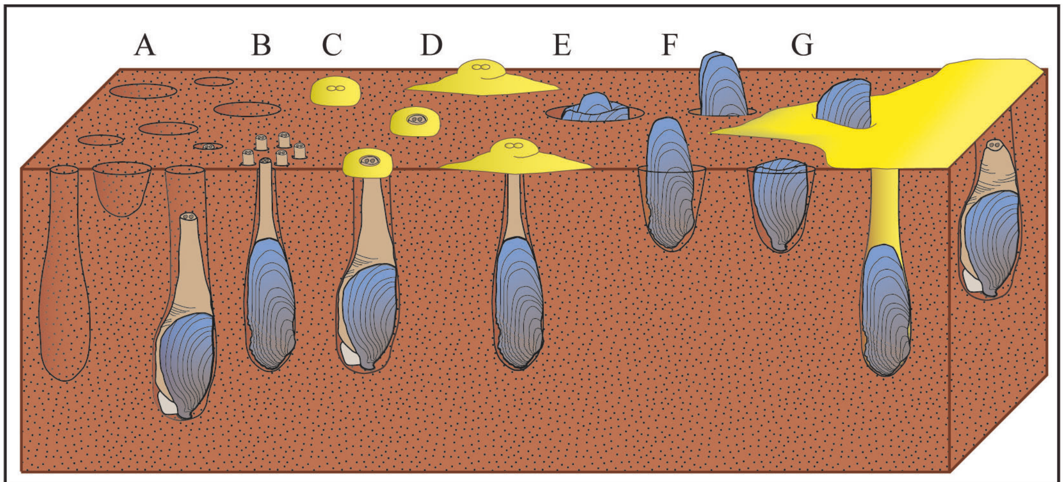


Figure 3-6. Bivalve orientation and appearance within *Gastrochaenolites*-type traces. (**A**) Empty and eroded *Gastrochaenolites*-type traces of various sizes and ages. (**B**) *Petricola pholadiformis* and *Zirfaea pilsbryi* occupying *Gastrochaenolites*-type traces, with their siphons retracted or extending to the surface. No sediment is present on the surface. (**C**) Boring bivalves within traces that are capped with a sediment mound. The sediment mound is limited to the opening of the borings. (**D**) Boring bivalves within traces that are capped with a sediment mound. Sediment mounds extend beyond the opening of the trace. (**E**) Eroded *Gastrochaenolites*-type traces with stacked shells. (**F**) Eroded *Gastrochaenolites*-type traces with bivalve shell sticking out of the substrate. (**G**) *Gastrochaenolites*-type traces that are covered in sediment. Shells may be partially covered, completely covered and can be occupied or unoccupied.

Mounds of sediment held together by mucus occasionally occur above occupied borings when patches of fine to very coarse sand are present on the surface of the substrate (Figs. 3-4F, 3-6C, 3-6D). Mounds do not exceed 4 cm in height and 2 cm in diameter, and are limited to the opening of *Gastrochaenolites*-type traces. Two holes are typically present within the sediment mounds (Fig. 3-4F), which correspond to the inhalant and exhalent openings of the siphon. Sediment mounds are limited to areas that have thin sediment veneer (< 4 cm thick) or areas that have no sediment. It is postulated that, within areas devoid of a loose sediment veneer, the sediment that comprises the sediment mounds was transported across the surface via tidal currents. Sediment mounds are located on the bedrock surface or on top of the thin sediment layer (Figs. 3-6C, 3-6D) and are only associated with living bivalves, but no distinct pattern or preference was observed. The structures can occur, either within close proximity of each other, as isolated examples or adjacent to occupied borings without sediment mounds.

The ichnocoenosis near Thomas Cove is produced by multiple generations of bivalves residing within a variety of sub-environments and at a variety of elevations of exposed bedrock surfaces. The presence of occupied and unoccupied borings suggests different periods of settlement and growth. Crosscut and eroded borings suggest that a period, or periods, of erosion (time length unknown) occurred after the substrate was populated. Stacked shells (Figs. 3-4G, 3-6E) support the hypothesis that this ichnocoenosis was produced by multiple generations of bivalves. Shell stacking occurs when one bivalve originally bored into the substrate, perishes and subsequently another bivalve penetrates the shell of the older boring. No evidence was observed to suggest that the secondary bivalve damaged the shell material of the original bivalve and the secondary bivalve appears to nest within the shell of the primary bivalve. The stacked shells can be either *Petricola pholadiformis* or *Zirfaea pilsbryi* and there is no species preference to stacked shell sequence.

SOFTGROUND ICHNOCOENSIS

Soft sediment traces are restricted to areas where sediment overlies the hardground bedrock. Various organisms produce a wide range of traces and make a moderately complex, three-dimensional network of forms (Table 3-2). The amphipod, *Corophium volutator*, makes *Arenicolites*-type traces and *Gordia*-type surface traces (Figs. 3-7 A-E). The bivalves, *Macoma balthica* and *Mya arenaria*, form *Siphonichnus*-type trace (Figs. 3-7 D-F). Similar forms have been attributed to burrowing bivalves by Zonneveld and Gingras (2013) within both ancient and modern settings. The worms *Heteromastus* sp. produce *Skolithos*-type traces, *Cerebratulus* sp. make *Psilonichnus*-types traces (Fig. 3-8A) and *Nereis* sp. make *Polykladichnus*-type traces and *Coenobichnus*-type surface traces (Figs. 3-8 B-D). *Nereis* sp. and *Macoma balthica* also produce stellet interface deposit feeding traces on the substrate surface (Figs. 3-8E, 3-8F). Gastropods (*Littorina saxatilis*, *Buccinum undatum Buccinum undatum*, *Nassarium trivittaus*, *Urosalpinx cinerea Lunatia heros*,) and hermit crabs (*Pagurua* sp.) produce *Aulichnites*- and *Coenobichnus*/*Diplichnites*-type surface traces respectively (Figs. 3-8G, 3-8H). Traces produced by hermit carbs within the study area resemble *Diplichnites*-type traces (Hagadorn et al., 2011) but hermit crabs have also been described to produce *Coenobichnus*-type traces within modern setting of the Bahamas (Walker et al., 2003). Many of the soft sediment traces found at Thomas Cove have also been described within the muddy tidal flats of the Chignecto Bay (Dashtgard et al., *in press*) and other softground settings (Dashtgard and Gingras, 2012). Soft sediment traces in the study area comprise a mix of locomotory and domicile structures, and would closely correlate to a *Skolithos*- type ichnofacies.

Most of these traces are on the surface or are located within the top 10 cm of the soft substrate. Softground traces were not observed to penetrate into the underlying

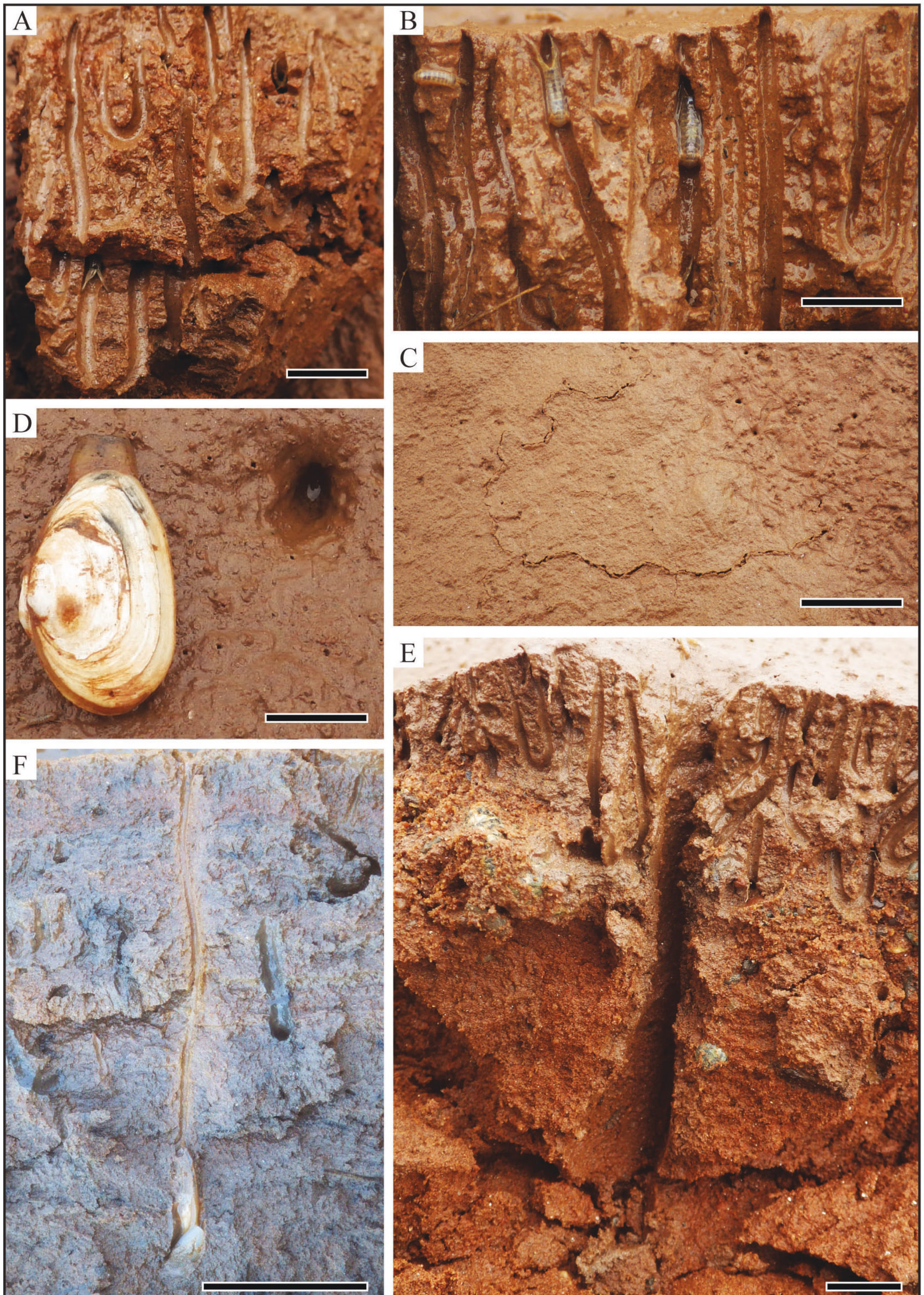


Figure 3-7. Soft sediment traces within inter tidal mud flat. (**A & B**) *Arenicolites*-type traces formed by *Corophium volutator*. Scale bars = 1 cm. (**C**) *Gordia*-type surface trace produced by *C. volutator*. Scale bar = 5 mm. (**D**) Small openings on the substrate surface correlate to the openings of *Arenicolites*-type traces formed by *C. volutator*. Larger, singular opening is produced by *Mya arenaria*. Scale bar = 1.5 cm. (**E**) *C. volutator* produced *Arenicolites*-type traces and deeper penetrating *Siphonichnus*-type trace form produced by *M. arenaria*. Scale bar = 1 cm. (**F**) *Siphonichnus*-type trace produced by *Macoma balthica*. Scale bar = 3 cm.

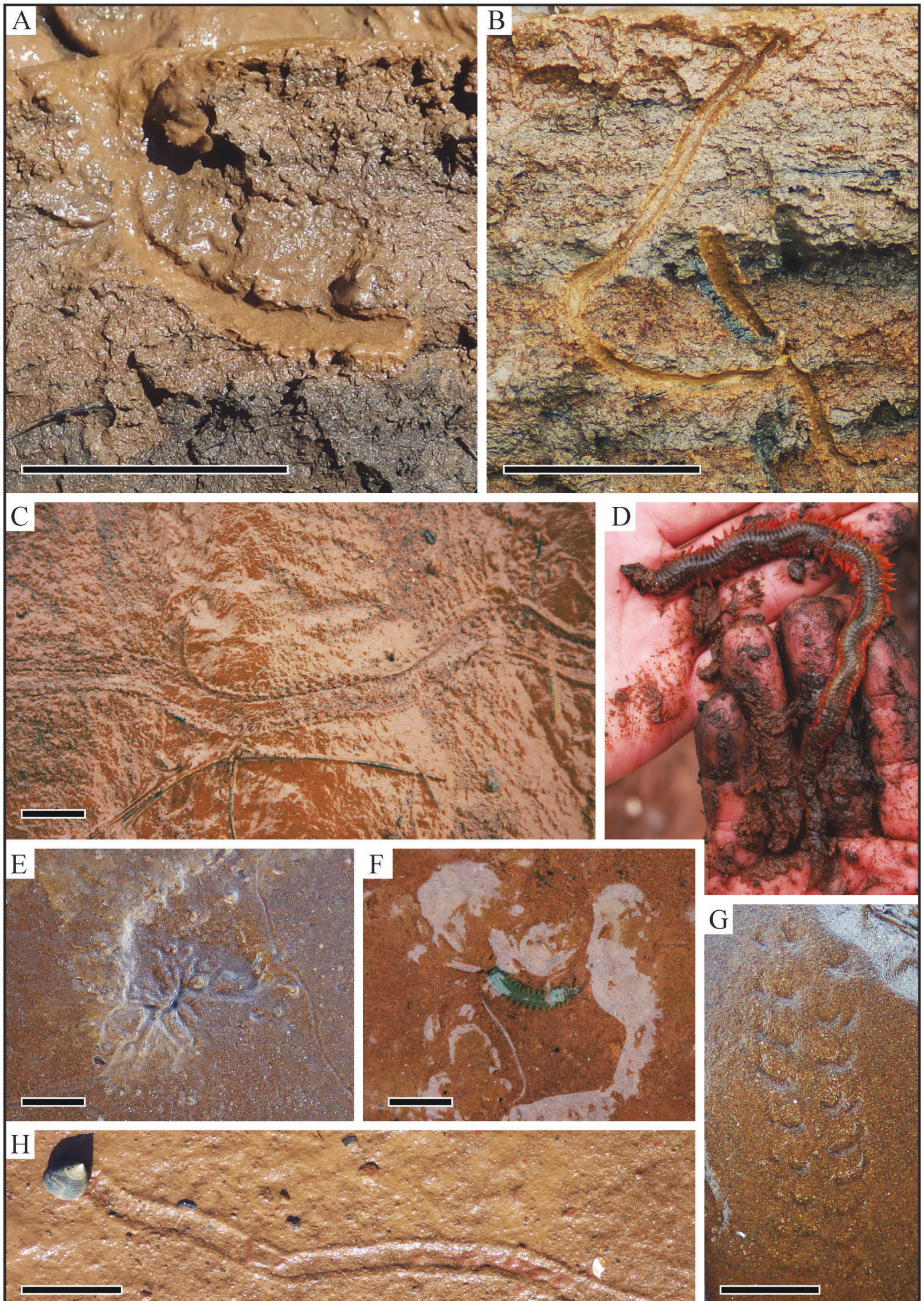


Figure 3-8. Soft sediment traces continued. (**A**) *Psilonichnus*-type trace formed by unknown trace maker. Scale bar = 5 cm. (**B**) *Polykladichnus*-type trace produced by unknown trace maker. Scale bar = 2.5 cm. (**C**) *Coenobichnus*-type surface trace produced by *Nereis sp*. Scale bar = 1 cm. (**D**) *Nereis sp*. Hands for scale. (**E**) Stellet interface deposit feeding trace produced by *Nereis* sp. Scale bar = 2 cm. (**F**) *Nereis* sp. producing surface trace of E. Scale bar = 1 cm. (**G**) *Coenobichnus/Diplichnites*-type trace going up the crest of a ripple produced by hermit crabs. Scale bar = 2 cm. (**H**) *Aulichnites*-type trace produced by a gastropod. Scale bar = 3 cm.

	Observed Tracemaker	Trophic Behavior	Trace Fossil Equivalent	Sub-environmental occurrence
Mollusca	*Petricola pholadiformis*	Suspension feeder	*Gastrochaenolites turbinatus*	LP, CF, DCOD, ITSF, R, LER, TP, TPD
	Zirfaea pilsbryi	Suspension feeder	*Gastrochaenolites ornatus*	DCOD, ITSF, LER, TPD
	Macoma baltica,	Suspension feeder	*Siphonichnus* Stellet interface deposit feeding trace	ITSF
	Mya arenaria	Suspension feeder, interface deposit feeder	*Siphonichnus*	ITSF
	Gastropoda (*Littorina saxatilis*, *Buccinum undatum*, *Nassarium trivittaus*, *Urosalpinx cinerea, Lunatia heros*)	Surface deposit feeders	*Aulichnites*	UP, ITSF, DC, LP, CF, DCOD, ITSF (Different species of gastropoda reside within different depositional sub-environments)
Crustacea	*Pagurus* sp.	Scavenger	*Coenobichnus*/*Diplichnites*	ITMF, LP, CF, DCOD, ITSF
	Corophium volutator	Deposit feeder, suspension feeder	*Areonicolites*	UP, ITMF, LP
Vermiforms	*Heteromastus* sp.	Deposit feeders	*Skolithos*	UP, ITMF, LP
	Cerebratulus sp.	Deposit feeder, suspension feeder	*Psilonichnus*	ITMF
	Neries sp.	Deposit feeders	*Polykladichnus*, *Coenobichnus*, Stellet interface deposit feeding trace	ITMF, LP

Table 3-2. Summary of trace making organisms and associated traces.

hardground or firmground. All traces are observed within the intertidal mud flat (ITMF); however, the majority of the traces are not seen elsewhere. *Arenicolites*- and *Gordia*-type traces are present within the upper platform (UP) and the lower platform (LP). *Aulichnites*- and *Coenobichnus*/*Diplichnites*-type surface traces are the only traces that span across almost all sub-environments where a thin layer or veneer of sand or mud is present.

SEDIMENTOLOGY, NEOICHNOLOGY AND ECOLOGY OF DEPOSITIONAL SUB-ENVIRONMENTS

Eleven different depositional sub-environments (Tables 3-1, 3-3, Figs. 3-2, 3-9) were identified within the study area within the intertidal zone of the Bay of Fundy:

Sub-environment 1: Upper Platforms (UP)

The upper platform (UP) consists of a series of step-like terraces and cliffs cut into the Triassic bedrock. The terraces are located between the landward salt marsh and the bayward intertidal mudflat (Figs. 3-10 A-C). Mud and silt vary in thickness and form a thin veneer on the relative highs and thin, structureless layers (3 cm thick) within the relative lows of the terraces (Fig. 3-10A). Water pools within natural lows and is the main habitat for organisms residing on the UP (Fig. 3-10C). Trace producing organisms include amphipods (*Corophium volutator*), which make *Arenicolites*-type traces and *Gordia*-types surface traces, threadworms and red worm (*Heteromastus* sp.), which produce *Skolithos*-type traces, and gastropods (*Littorina saxatilis*), which form *Aulichnites*-type surface traces. Amphipods are limited to layers of mud and silt that are at least 0.25 cm thick and increase in abundance when sediment is thicker, with *Arenicolites*-type traces can exceed 10,000 burrows / m^2. The abundance of *Skolithos*-type traces was not established due to their small size. Surface trace abundance is moderately low, with 0-10 *Gordia*- and *Aulichnites*-type traces / m^2. Several seaweed taxa (*Spongomorpha* sp. and *Fucus* sp.) (Fig. 3-10D) occur on the most bayward terraces, but the distribution is patchy throughout the UP. Borings are absent and, other than isolated potholes, no sedimentary structures were observed.

A slight transitional zone occurs between the UP and the intertidal mud flat (ITMF). This area possesses poorly sorted sediment ranging in size from mud to cobble. Most of the larger clasts occur close to the UP and consist of broken pieces of bedrock. Isolated areas of exposed bedrock are common and small drainage channel systems occur throughout the zone. Organism assemblages are similar to the other regions of within the UP, with abundance increasing towards the ITMF.

Interpretation: The UP is made up of wave-cut platforms and is a harsh environment for organisms to inhabit. This area has the longest exposure time of the sub-environments and there are only thin patches of mud and silt for burrowing organisms to inhabit. The majority of biotas are limited to thin layers of mud

Sub-environment	Common Sedimentary Features	Sediment Analysis	Salinity (PSU)	Figure
Upper Platforms (UP)	Triassic bedrock outcropping in step-like terraces. Mud and silt covers bedrock in a thin veneer and thin (3 cm), structureless beds. Isolated potholes are present within exposed bedrock. Traces are present within mud and silt layers at least 0.25 cm thick.	Mud and silt; exposed bedrock Well sorted	-	3-10
Intertidal Mud Flat (ITMF)	Dominated by planar-bedded mud and silt. Sediment (3-11.5cm thick) overlies bedrock and muddy firmground. Lunate, linguoid, sinuous and continuous wave and current ripples are common, with dominant current ripples oriented in the flood direction. Ripples are commonly mud draped. Ebb- and floor-oriented horseshoe-shaped scours are present around large boulders. Substrate highly bioturbated within the uppermost 3 cm; traces are present within the 10 cm of the substrate.	Mud, silt and fine sand Well sorted	-	3-7 3-8 3-11A
Drainage channel (DC)	Runoff and drainage channel from the landward saltmarsh. Channel cuts through planar-bedded muds of the intertidal mud flat until reaching the bedrock. Channel bed contains isolated patches of exposed bedrock. Soft sediment traces are present within shallowly sloping point bars and slumping cut banks. The channel mouth open onto the LP and contains a fan of soupy, organic rich mud (1-8 cm thick) with small distributary channels. Wash over debris, shell fragments and a wide range of grain sizes (mud to cobbles) are present.	Mud to cobbles; exposed bedrock Well to poorly sorted	10	3-11B 3-11C
Lower Platform (LP)	Mud to coarse sand layers (0 to 7 cm thick) overly bedrock. Shell debris and organic debris frequently washed onto substrate. Ebb- and flood-oriented ripples (0.75 cm high, 10 cm long) are superimposed on flood-oriented dunes (6.5 cm high by 1 m long) where sediment is thickest. Flat-topped ripples and flood-oriented horseshoe scours are present. Exposed bedrock commonly possesses furrows. Surface traces are common in troughs of ripples and dunes. Borings and sediment mounds are present in areas where sediment thickness is < 4 cm thick, including areas within the horseshoe scours. Borings are both occupied and unoccupied.	Mud to coarse sand; shell debris; boulders; exposed bedrock Well to poorly sorted	31	3-12
Channel Fringe (CF)	Exposed bedrock with areas of gravel veneer (0.5-5 cm thick). Winnowing of finer grains is common. Sheltered areas adjacent to platform form depositional shadows where coarse sand accumulates; ebb-oriented ripples can be present within sand. Soft sediment surface traces are present within sand. Borings are limited to exposed bedrock and forms are occupied and unoccupied, and sediment mounds are present.	Medium to very coarse sand, gravel and boulders; exposed bedrock Poorly sorted	30	3-13

Table 3-3. Summary of sedimentological and environmental characteristics of the depositional sub-environments.

Sub-environment	Common Sedimentary Features	Sediment Analysis	Salinity (PSU)	Figure
Main Channel (DCOD)	Exposed bedrock and thin veneer of sediment along channel base. Large boulders (up to 1.5 m in length and height) are present. Bedrock channel base is frequently bored and form angular blocks that are easily transported; some individual cobbles are bored on all exterior surfaces. Boring density is high and vacant borings are commonly infilled with coarse and very coarse sand.	Coarse sand to boulders; exposed bedrock Well sorted	30	3-14
Intertidal Sand Flat (ITSF)	Coarse to vary coarse sand, pebbles, cobbles and shell debris (2-5 cm in length and width) overlying bedrock. Ebb-oriented dunes (< 1 m in length and < 30 cm high) with ebb-oriented ripples (< 8 cm in length and < 1 cm high), interference ripples, drainage ripples and drainage splays are common in thick, sandy areas. Ebb-oriented horseshoe scours are common. Isolated areas of bedrock are exposed through the surrounding sand and possess borings and furrows. Gravel veneer, similar to CF, occurs in isolated patches along the margin of the area.	Coarse to vary coarse sand, pebbles, cobbles; exposed bedrock Poorly sorted	31	3-15
Ridge (R)	Exposed bedrock creates an elevated high within the basin. The bedrock is composed of a thin silty mudstone layer (0.5-1 m thick), with sandstone above and below. Sandstone is exposed on the upper surface of the ridge and is covered with a thin, mud veneer. Fine sand is common within relative lows and fractures. Potholes, tide pools, furrows and reduction spheres are common. Borings are rare and commonly unoccupied and eroded.	Mud veneer, fine grained sand; exposed bedrock Well sorted	-	3-16
Leading Edge of Ridge (LER)	The ocean-ward side of the ridge comprised of exposed bedrock and boulders. The bedrock is a fissile, silty mudstone that outcrops between layers of sandstone. Large boulders (up to 1.5 m in length and width), cobbles and gravel veneer bedrock in isolated areas. Borings are limited to areas of exposed bedrock and are not present under gravel veneers. Borings are mainly unoccupied and are frequently eroded.	Gravel to boulders; exposed bedrock Poorly sorted	30	3-17
Tide Pool on Ridge (TP)	Located within the topographic lows on upper surface of the ridge. Water depth is < 1.5 m throughout the tide pools. Little to no sediment is present within the tide pools. Borings and the majority of biota are limited to areas of submerged bedrock.	Exposed bedrock -	30	3-18
Tide Pool Drainage (TPD)	Area southerly adjacent to LER and is the main location for water to drain from R and TP. Substrate is made up of sandstone with an underlying thick layer (1.5 m thick) of silty mudstone. No sediment is present. Borings are limited to areas where water is present at low tide.	Exposed bedrock -	30	3-19

Table 3-3. Summary of sedimentological and environmental characteristics of the depositional sub-environments.

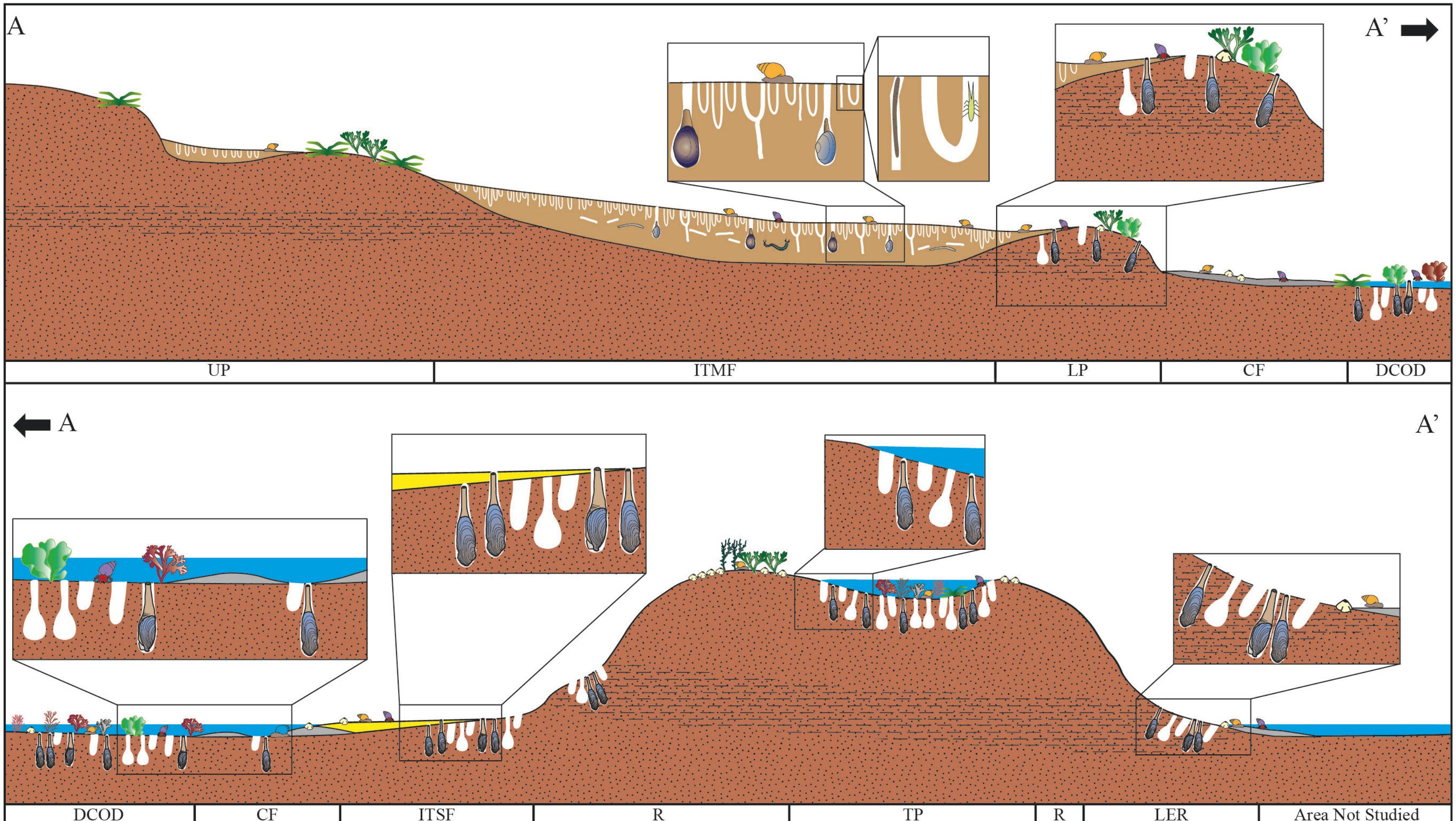


Figure 3-9. Schematic of transect A-A’. Schematic of depositional sub-environments along transect A-A’ in Figure 3-2. Insets provide detailed view of each depositional sub-environment. Soft sediment, borings, biota, sediment and lithology are listed within “List of Symbols” section of this thesis. Drawing not to scale.

Figure 3-10. Upper platform (UP) sub-environment. (**A**) Rocky terraces of UP with thin mud within horizontal surfaces of steps. (**B**) Rocky terrace. Shovel for scale (105 cm in length). (**C**) Bedrock terraces. Person in for scale. (**D**) *Spongomorpha* sp. and *Fucus* sp. attached to bedrock. Scale = 8cm.

and tide pool areas, which trap water as the tide falls. *Aulichnites*-type traces are commonly oriented in a converging direction towards the tide pools, suggesting that the grazing gastropods prefer to remain in or near water, likely to prevent desiccation. Deposition of the mud and silt veneer is connected to the calm, slow moving water conditions associated with the sheltered area of Thomas Cove, which is protected from fast moving water by the surrounding cliffs. Mud and silt settle out of suspension and drape the platforms and collect within the relative lows, producing a mud veneer and thin mud layers. No boring organisms are able to inhabit the UP due to the long periods of exposure and low water energy during high tide.

The transition zone between the UP and the ITMF represents a mixing of the two depositional sub-environments and possess distinct characteristics of both areas. The variation in grain size is indicative of multiple depositional processes. Gravels and cobble accumulations consist of the parent rock and were produced by the mechanical and chemical break down of the bedrock, whereas the fine-grained material settles out of suspension as a result of daily tidal water movement. As the muddy substrate gets thicker, the abundance of burrowing amphipods and gastropods increase. Small drainage channels collect excess water within the area and funnel it to the drainage channel (DC) sub-environment.

Sub-environment 2: Intertidal Mud Flat (ITMF)

The intertidal mud flat (ITMF) consists of well-sorted, planar-bedded, silty mud, with sand content increasing bayward (Fig. 3-11A). Bedrock is exposed in isolated patches throughout the area. Thinly layered, compacted mud occurs within areas that have been exposed by the cutting and erosion of the drainage channel (DC) (Fig. 3-11B). The surface is typically structureless or planar bedded (Fig. 11-3A), but isolated sedimentary structures, including lunate, linguoid, sinuous and continuous wave and current ripples, may occur near the bayward base of the ITMF. The dominant current ripple orientation is to the east (i.e. flood tide current direction). Ripples are larger and more prevalent bayward and are commonly mud draped. Horseshoe-shaped scours, in both floodd and ebb-tidal orientation, occur around large boulders (Discussed later within Horseshoe Scours: Specialized Habitats section). These scours form tide pools that are more favorable environment for many organisms to inhabit.

Bioturbation is high and traces are formed by numerous taxa (discussed above).

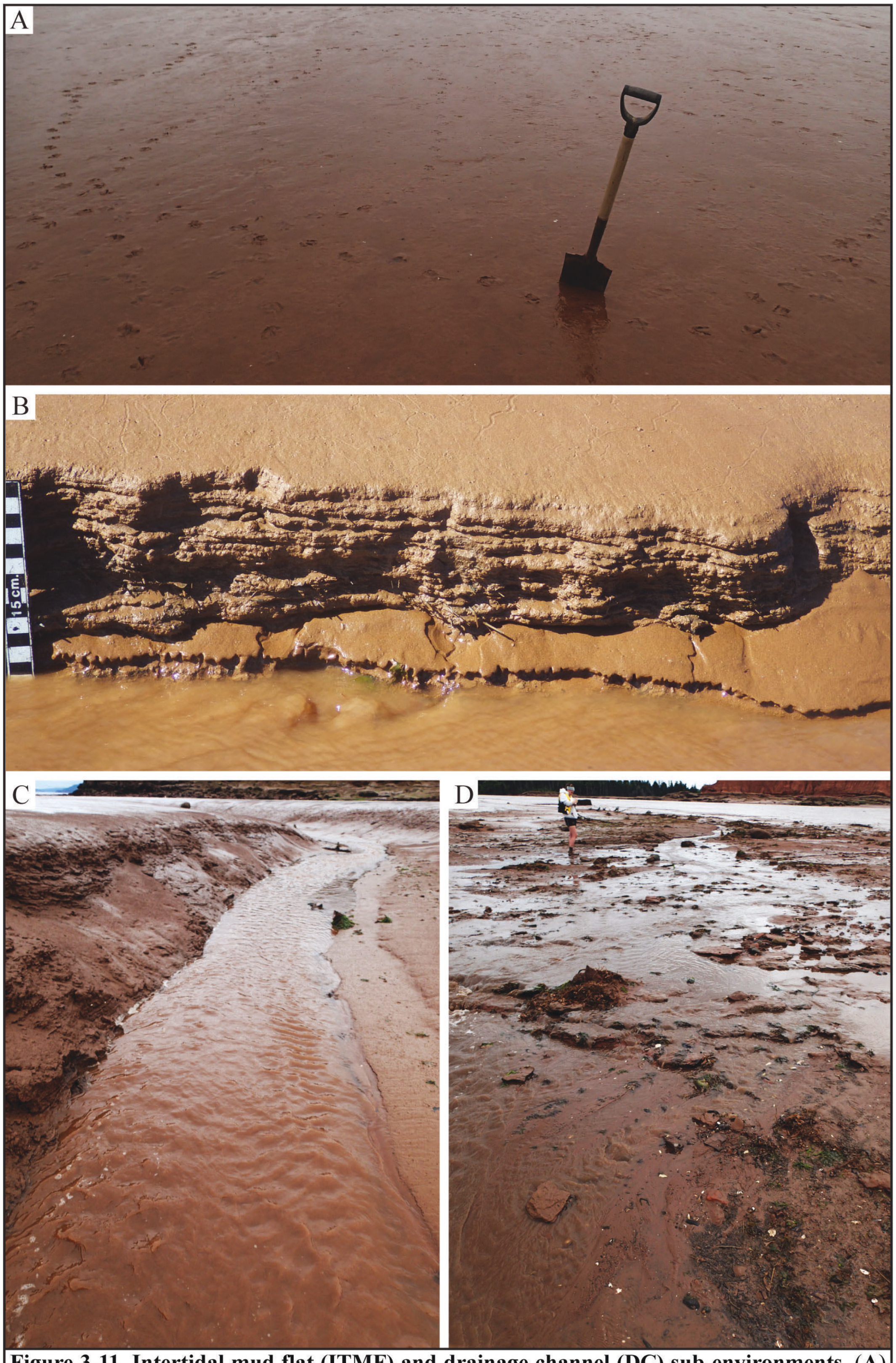


Figure 3-11. Intertidal mud flat (ITMF) and drainage channel (DC) sub-environments. (**A**) Intertidal mud flat with bird foot prints. Shovel for scale. (**B**) Bank of channel showing laminated muds of the ITMF. Scale bar = 15 cm. (**C**) Channel cutting though the upper part of the ITMF. Channel width approximately 1 m. (**D**) Mouth of the channel draining across LP. Person for scale.

The uppermost 3 cm of substrate is dominated by *Arenicolites* and *Skolithos*-type traces (Figs. 3-7A, 3-7B, 3-7E) and has a high abundance of traces (exceeding 100,000 burrows / m^2). Other traces extend to deeper depths (up to 10 cm deep), including *Siphonichnus*- (Figs. 3-7E, 3-7F), *Psilonichnus*- (Fig. 3-8A) and *Polykladichnus*-type traces. (Fig. 3-8B), and are more sporadically distributed, with trace abundance ranging from 5 to 50 / m^2. Surface traces include *Gordia*- (Fig. 3-7C), *Coenobichnus*- (Fig. 3-7C), *Coenobichnus*/*Diplichnites*- (Fig. 3-7G), *Aulichnites*-type traces (Fig. 3-7H) and stellet interface deposit feeding traces (Figs. 3-7E, 3-7F), with abundance varying from 0-20 / m^2. Surface traces are most abundant near tide pools, areas of relative low relief, horseshoe scours and within troughs of ripples. *Gastrochaenolites*-type traces are present in low numbers (0-50 borings / m^2) within the exposed bedrock.

A transition zone occurs between the ITMF and the lower platform (LP) and possesses depositional features characteristic of both sub-environments. This area has a decreased amount of mud and increased amount of silt, sand and larger grain sized sediment. Sediment also thins towards the LP and bedrock is exposed sporadically, with isolated areas having a thin sediment veneer. Sedimentary structures are similar to the ITMF and become more dominant bayward. Organism abundance and bioturbation decrease bayward, due to the thinning of sediment (from over 20 cm thick to less than 1 cm thick).

Interpretation: The ITMF exhibits multiple depositional processes that form an environment that is inhabitable by multiple species of burrowing organisms. The ITMF is almost completely sheltered between the bedrock cliffs of Thomas Cove (Fig. 3-2), which allows the area to be protected from faster moving water within the bay and allows thick accumulation of mud. Ripples are predominantly oriented in the flood direction, suggesting that flooding processes possess flow dynamics with higher velocities. The ebbing water has only localized effects on the sediment and modifies limited area of the ITMF. The occurrence of wave ripples suggests that wave modification occurs even though tidal currents dominate. The multidirectional current ripples and wave ripples suggest multidirectional flow patters of water, which shifts with daily water movement. Many of the ripples are mud draped suggesting sedimentation also occurs during slack tide, when mud can settle out of suspension from water that has pooled within the troughs of the ripples.

A moderately high diversity of organisms resides within the muddy substrate of the ITMF. Distribution ranges from 0-100,000 traces /m^2 suggesting that environmental conditions (sediment thickness, grain size, salinity, etc.) are ideal for a diverse assemblage of organisms. The ITMF has the highest bioturbation of all of the depositional sub-environments.

Under the silty mud of the ITMF is bedrock and compressed layers of firm mud, which can exceed 1 m in thickness when exposed along the banks of DC. The firmground is made up of slightly bayward dipping, planar beds of mud with varying in thicknesses (1-5 cm thick). Soft sediment burrows do not penetrate the firmground and no preexisting fabric or bioturbation is observed within the exposed layers. Compaction of the mud by the overlying sediment and water is a suggested hypothesis for the formation of the firmground. However, an extensive examination of the substrate was outside the scope of this project, and further investigation may reveal significant insight into previous environmental conditions surrounding the firmground.

The transition zone between the ITMF and LP is less protected by the surrounding cliffs of Thomas Cove and possesses less mud and more silt, sand and larger sized grains, as well as exposed bedrock. These features relate to the relative topographic high of the bedrock and higher velocity of water flowing over the transition zone when the tide ebbs and floods. Less organisms and traces are present due to the decease in sediment thickness, increase in sediment size and increase in water velocity.

Sub-environment 3: Drainage channel (DC)

The drainage channel (DC) collects runoff from the landward sub-environments including terrestrial areas, the ITMF and the UP, and has a salinity of 10 ppt. The DC is fed by a small creek flowing into Thomas Cove and divides the UP, ITMF and LP into two separate regions. DC is variable in size, with 1 m as an average width and 10 cm as an average depth. The channel cuts down through the ITMF and reveals firm layer of mud that makes up the ITMF (Fig. 3-11B). The base of the channel is variable in composition and includes patches of exposed and mud covered bedrock. Broken shells and gravel-sized clasts (1-3 cm in length) of bedrock occur in isolated areas of the channel floor. Slumping of the layered ITMF along the banks is common (Fig. 3-11C), and amphipods (*Corophium volutator*), creating *Arenicolites*-type traces, frequently reside within the shallowly sloped surfaces. Similar traces and organisms are present within shallowly sloping channel point bars. Gastropods (*Littorina saxatilis*, *Buccinum undatum* and *Nassarius trivittatus*) are also present within shallow sloped surfaces and channel base, and produce *Aulichnites*-type traces. *Arenicolites*- and *Aulichnites*-type traces can exceed 100,000 and 10 traces / m^2 respectively. Vertically oriented surfaces of the channel banks are unoccupied by any trace producing organisms. Borings are not present within the exposed bedrock in this sub -environment. Sea lettuce (*Ulva lactuca*) and ribbon weed (*Palmaria palmata*) are isolated and small in size within the channel base, where mud is limited.

The mouth of the DC empties onto the LP and further into the main channel (DCOD) (Fig. 3-11D). A small, shallow fan of soupy, organic rich mud (1-8 cm thick) and small distributary channels are formed here. Distributary channels frequently shift as a result of the fluctuating discharge of the ITMF and landward sub-environments. Sediment within the drainage fan includes mud and sand, over-wash debris including shell fragments (1-2 cm in length), gravels and cobbles (3-15 cm in length) and unattached vegetation. The underlying bedrock is covered by 1-8 cm of soupy mud and debris. Organism abundance is low, with isolated gastropods and amphipods residing in areas with little to no flowing water.

Interpretation: The DC gathers runoff from landward terrestrial and intertidal sub-environments and brings water, sediment and organic material into the bay. The constantly flowing channel is fed by a small terrestrial stream and interstitial water draining from the ITMF. The low water salinity (10 ppt) indicates that mixing of marine and fresh water occurs within the DC. Organisms within the channel must deal with daily fluctuations in salinity, from fully marine conditions during high tide to brackish conditions at low tide and fresh water during periods of precipitation. Seaweed and isolated gastropods occur within the base of the DC, but most organisms live within the sediment that makes up the channel banks. Slumped ITMF layers and point bars provide relatively horizontal surfaces for amphipods and gastropods to reside and make burrows. The vertical banks of the DC are too steep for colonization by available burrowing organisms. Water velocity through the DC is unknown, but water energy is enough to produce isolated patches of exposed and mud covered bedrock. Shell fragments and gravel-sized grains of bedrock make a channel lag within isolated areas of the DC.

The mouth of the DC subdivides into minute, shallow, shifting channels across the LP. A thin (1-8 cm), soupy, organic rich mud overlies the bedrock of LP and shifts in size with fluctuating discharge from DC. The fan overprints the LP and ITMF and forms a water-saturated, sediment rich environment unfavorable to many organisms. The absence of amphipods and gastropods, and their traces, indicates that environmental conditions at the mouth of the DC are inimical to life. Although isolated amphipods and gastropods occur throughout the area, most/all were likely washed in from the surrounding ITMF. The mouth of DC is a transitional zone between the DC and the ITMF, PL and DCOD, where the mixing of sediment, sedimentary processes and water dynamics occurs.

Sub-environment 4: Lower Platform (LP)

The LP is the most bayward terrace of bedrock that is exposed within the study area. It is subdivided into two zones: the top horizontal surface and the vertical leading edge. The top horizontal surface of the LP consists of a mosaic of isolated patches of exposed bedrock and thin layers of silt to coarse sand, which thin bayward (thickness varies from 0-7 cm) (Figs. 3-12A, 3-12B). A thin (>1cm thick) sheet of water covers the surface and has a salinity of 31 ppt. Shell debris consisting of bivalve and gastropod fragments (1-4 cm in length and width) and organic material are common. Sedimentary structures are diverse and vary across the LP. Lunate and continuous ebb- and flood-oriented ripples (0.75 cm high, 10 cm long) are superimposed on flood-oriented dunes (6.5 cm high by 1 m long), where sediment is thickest (Fig. 3-12A). Large grained sediment and shell debris (<10 cm in length and width) accumulate within troughs of dunes. Flat-topped ripples are also present (Fig. 3-12C). Large boulders (up to 2 m in length and height) are scattered throughout the horizontal surface of LP and possess flood-oriented horseshoe scours. Within the horseshoe scours, sediment is typically removed, exposing the underlying bedrock and forming habitats favorable for boring bivalves and other organisms. Isolated areas of exposed bedrock are present and commonly possess both erosional furrows and *Gastrochaenolites*-like traces (Fig. 3-12B).

Borings in this sub-environment are produced by *Petricola pholadiformis*. Occupied and unoccupied borings are present, and some of the occupied borings are identified based on the presence of sediment mounds. Boring are limited to exposed bedrock and bedrock that has a < 4 cm sediment veneer (Fig. 3-12B). Boring abundance reaches 600 borings / m^2 within exposed bedrock areas and 440 borings / m^2 area within horseshoe scours. Other traces observed include the soft sediment surface traces *Aulichnites*- and *Coenobichnus*/*Diplichnites*-type traces, which can reach up to 20 surface traces / m^2, *Aulichnites*- and *Coenobichnus*/*Diplichnites*-type traces, produced by gastropods (*Littorina saxatilis* and *Buccinum undatum*) and hermit crabs (*Pagurus* sp.). These increase in abundance around areas of relative lows (i.e. horseshoe scours, troughs of ripples and dunes) where

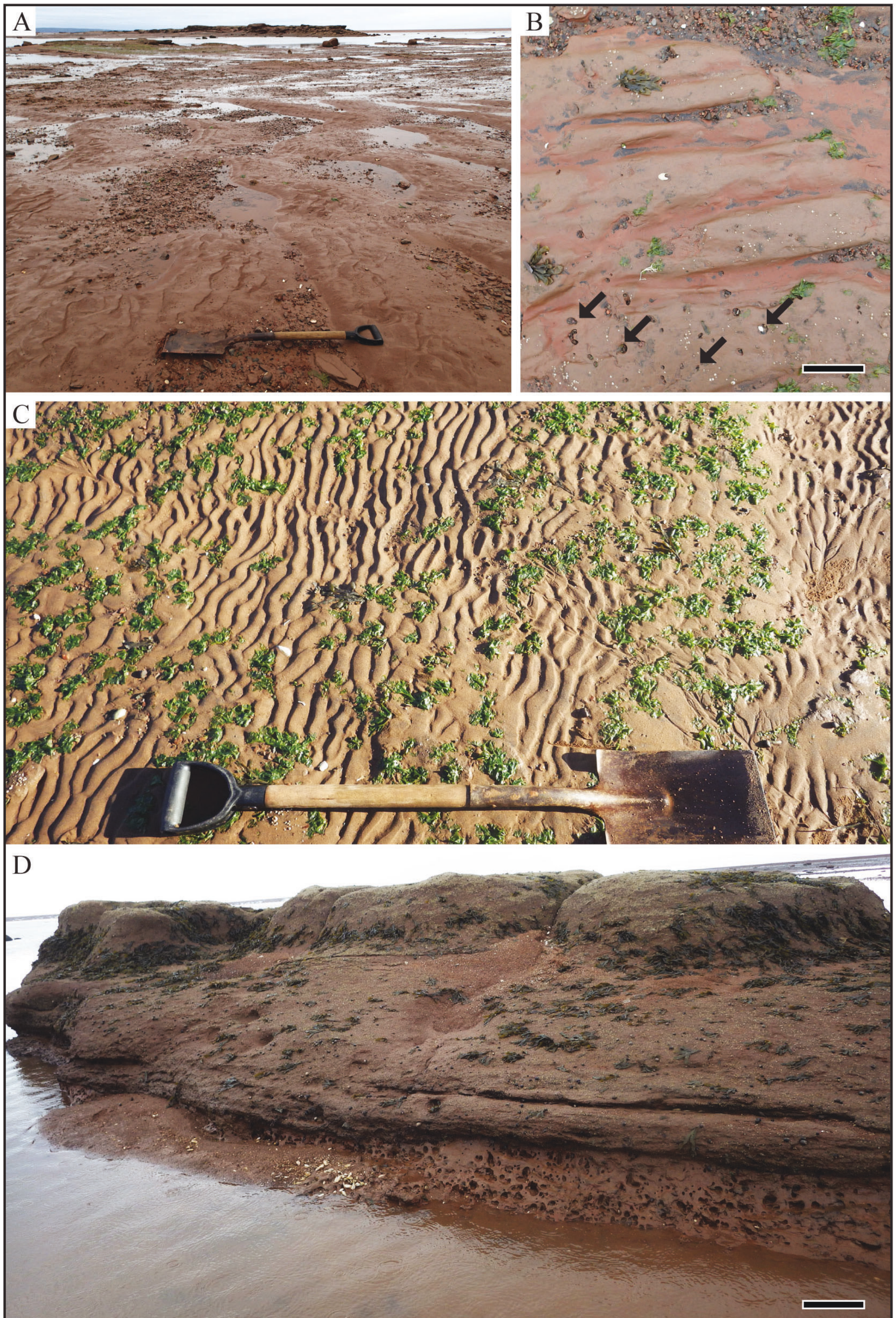


Figure 3-12. Lower platform (LP) sub-environment. (**A**) Flood oriented dunes with flood-oriented ripples. Shovel for scale. (**B**) Furrows within the bedrock. *Gastrochaenolites*-type traces indicated by arrows. Scale bar = 9 cm. (**C**) Flat topped ripples within fine-grained sand with attached Ulva lactuca. Shovel for scale. (**D**) LP at the northeast corner of the study area. Borings present within the vertical surfaces. Scale bar = 45 cm.

water pools. The distribution of borings and surface traces are very patchy and are dependent on the presence or absence of sediment and water. *Nereis* sp. (which produce *Polykladichnus*-type traces) are very isolated with only two being observed within the LP during the study.

Other residents of this sub-environment are barnacles (*Chthamalus fragilis*), amphipods (*Lysianopsis alba*) and seaweed (*Ulva lactuca* and *Fucus* sp.). Little gray barnacles are limited to areas of exposed bedrock with little or no sediment veneer (i.e. the sediment layer is thinner than the height of the barnacle shell) and are present on the exposed upper surface of small and large boulders (7-100 cm in length and width). Amphipods (*Lysianopsis alba*) abundance is low, with less than 20 individual observed epifaunally within the study. Both species of seaweed also attach to the bedrock and are limited to areas near the northwest corner of the study area, where the platform extends into the main channel (DCOD) (Fig. 3-12C, 3-12D).

About 1 m of bedrock is exposed on the nearly vertical surface of the leading edge of LP (Fig. 3-12D). The bedrock consists of a layer of silty mudstone (~60 cm thick) with layers of sandstone above and below. Oxidation has resulted in green and red marbling (Fig. 3-2B). *Petricola pholadiformis* occurs within the leading edge of the LP and produces *Gastrochaenolites*-like traces. The abundance of borings increases within the silty mudstone layer (880 borings per 1 m^2 area), but borings are also present within the overlying and underlying sandstone layers (up to ~ 400 boring per 1 m^2 area). Occupied borings (evidenced by exposed siphons and sediment mounds) and empty borings are present. Tubeworms (*Lanice* sp.) also occur in this area although their colonies are rare (i.e. only a single colony of about 100 tubes was observed).

Interpretation: Environmental conditions of the LP are more dynamic than the landward sub-environments (UP, CD and ITMF). Both flood and ebb tides possess fluid velocities capable of producing large ripples. Sedimentary structures in this depositional sub-environment preserve evidence of multiple flow orientations underscoring that the depositional sub-environment is influenced by both flood and ebb tidal currents. Flood tides clearly possess greater velocities in comparison to ebb tides, based on the occurrence of meter scale flood oriented dunes within isolated areas (whereas ebb oriented dunes are not present). Flat-topped ripples also suggest fluctuating velocities and form as a result of current scouring (Klein, 1963, 1964, Dalrymple et al., 1990). In areas where sediment is completely removed, furrows and *Gastrochaenolites*-like traces are present. Erosional furrows are topographic lows within the bedrock that are formed by erosional processes and erosional vortices. The variety of sedimentary features suggests diverse depositional processes.

Boring bivalves are limited to areas of exposed bedrock and bedrock that is covered with < 4 cm of sediment. This suggests that if sediment veneer is too thick, boring bivalves cannot extend their siphons through the sediment to feed. Boring abundance is higher (~ 880 borings / m^2 area) within the silty-mudstone of the vertical leading edge of LP as compared to the sandstone layers (vertical surfaces: 0-200 borings; horizontal surfaces: 0-660 borings / 1 m^2 area). However, the horizontal surface of the LP provides a more expansive area for bivalves to bore resulting in diminished intraspecific ecospace competition. Horseshoe scours also provide a unique sediment free area for bivalves to settle (see Horseshoe Scour: Specialized Habitat section for further discussion). Other organisms that reside in the PL include gastropods, hermit crabs, tubeworms, little gray barnacles and seaweed, similar to organisms within the landward sub-environment. This suggests that these species have adapted to a variety of sub-environments. However, amphipods (*Corophium volutator*), worms (*Nereis* sp. and *Cerebratulus* sp.) and their traces are absent within the LP, which reflect the higher water energy conditions, mobile substrates, lack of mud-sized sediment and lack of thick mud layers, which are all present within the LP sub-environment.

Sub-environment 5: Channel Fringe (CF)

The CF flanks either side of the main channel (DCOD) and mainly consists of poorly sorted, gravel overlying bedrock. The gravel overlay layer is 0.5-5 cm thick and consists of sub-angular grains that are 0.5-10 cm in length and width (Figs. 3-13 A-C). Small, isolated patches of exposed bedrock are present (Fig. 3-13 C). Fine-grained sediment has been winnowed from the gravel layer. Shell debris, consisting of broken bivalve shells and numerous species of gastropods (*Littorina saxatilis*, *Buccinum undatum*, *Nassarium trivittatus*, *Urospapinx cinerea* and *Lunatia heros*), is scattered throughout the gravel layer. Areas within close proximity to the LP are located within depositional shadows and have a high concentration of coarse-grained sand superimposed with ebb-oriented ripples. Coarse sand is most abundant in the northwest corner of the study area where the LP extends furthest into the DCOD (Fig. 3-13D). Large boulders (up to 2 m in length and height) are scattered within the CF. Boulders are typically characterized by faint flood-oriented horseshoe scours that consist of exposed bedrock surrounded by gravel. Standing

Figure 3-13. Channel fringe (CF) sub-environment. (**A**) Clast rich gravel vaneer. Scale bar =15 cm. (**B**) Clast poor gravel vaneer. Scale bar = 15 cm. (**C**) Area of bored exposed bedrock surrounded by gravel vaneer. Scale bar = 10 cm. (**D**) Depositional shadow east of the lower platform located at the north west corner of the study area. Shovel handle for scale.

water, with salinities of ~ 30 ppt, occurs in relative lows within the gravel.

Gastrochaenolites-like traces are limited to areas of exposed bedrock (Fig. 3-13C) and do not occur underneath the gravel veneer. Abundance is relatively low (with the majority of the surface possessing no boring), but can reach up to 1500 borings / m^2 when bedrock is exposed in close proximity to DCOD. The traces are produced only by *Petricola pholadiformis*. Borings are both occupied and unoccupied, and sediment mounds are present. Gastropods (*Littorina saxatilis*, *Buccinum undatum*, *Nassarium trivittaus*, *Urosalpinx cinerea* and *Lunatia heros*) and hermit crabs (*Pagurua* sp.) are isolated throughout the CF and little gray barnacles (*Chthamalus fragilis*) frequently encrust the upper surface larger cobbles and boulders. *Aulichnites*- and *Coenobichnus*/*Diplichnites*-type traces are uncommon (<5 / m^2) and are limited to areas where coarse sand is deposited. No plant life was observed within the CF.

Interpretation: The CF is formed as a channel lag as a result of fast moving water around the edges of the DCOD. Water is fast enough to entrain and deposit large gravel-sized sediment and winnow the fine-grained matrix. Sheltered areas behind the LP that extends into the DCOD form shadows where coarse-grained sand accumulates (Fig. 3-13D). Borings are limited to exposed bedrock but do not occur beneath the gravel veneer, suggesting that the gravel prevents bivalve settlement and growth, and that the occurrence (and limits) of the gravel veneer is semi-permanent. Other organisms are isolated within the CF, suggesting that the gravel does not provide an adequate substrate for deposit feeding organisms. Little gray barnacles solely encrust on the upper, exposed surfaces of cobbles and boulder, indicating that the substrate is immobile for sufficient time to allow for larval settlement and growth. The lack of a diverse assemblage of organisms supports the hypothesis that the CF is too harsh of a sub-environment for organisms to survive.

Sub-environment 6: Channel (DCOD)

The DCOD is the main tidal channel in the study area. It runs in an east-west direction within the study area and is about 100 m wide at its largest width (Fig. 3-14A). Water depth at low tide during the study did not exceed 30 cm and the channel is commonly waterless during spring tides. Water salinity remains at 30 ppt throughout low tide, even in isolated pools. The base of the channel consists of highly bored bedrock. Numerous, large, loose boulders (10-30 cm in length

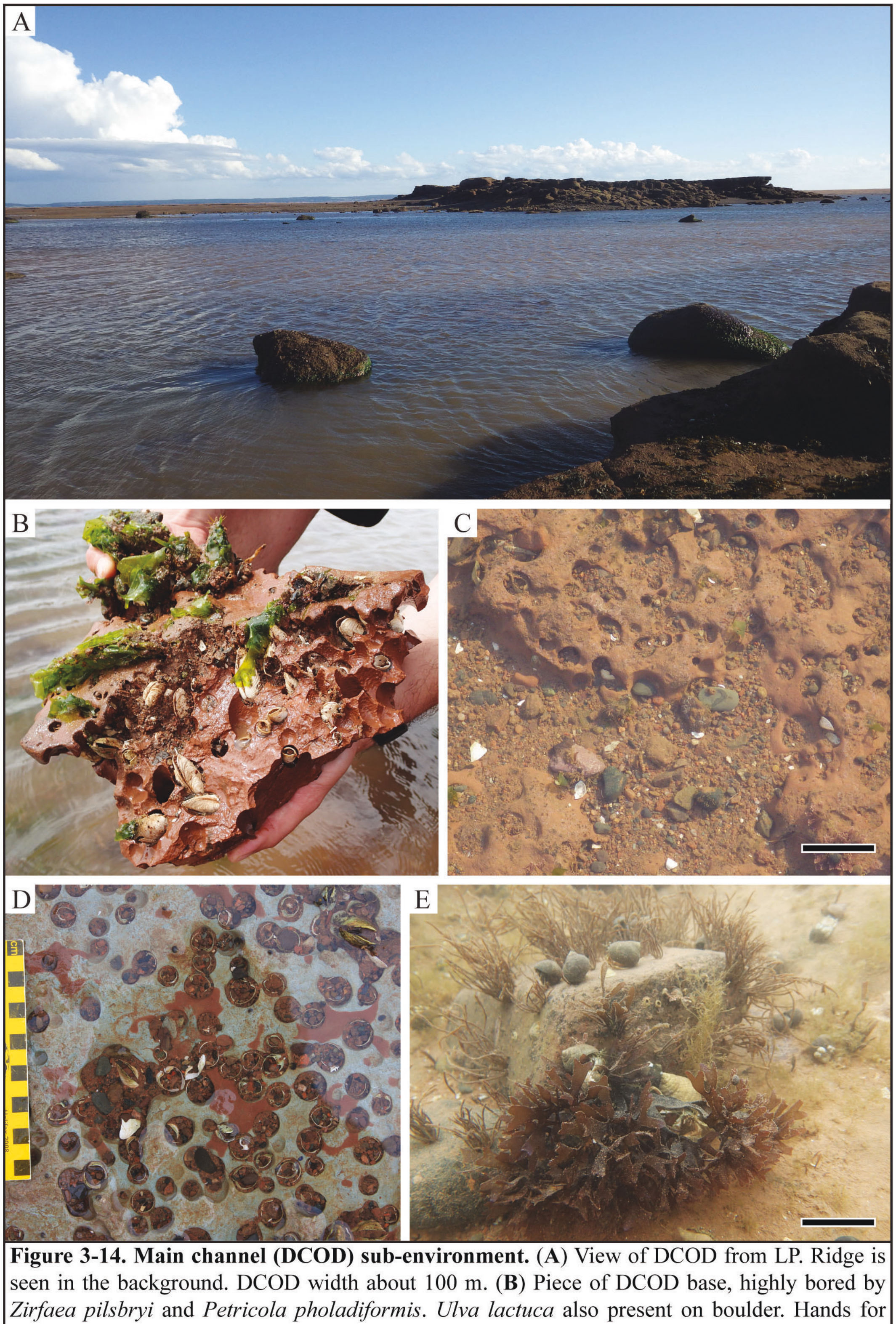


Figure 3-14. Main channel (DCOD) sub-environment. (**A**) View of DCOD from LP. Ridge is seen in the background. DCOD width about 100 m. (**B**) Piece of DCOD base, highly bored by *Zirfaea pilsbryi* and *Petricola pholadiformis*. *Ulva lactuca* also present on boulder. Hands for scale. (**C**) Base of channel, with areas of bored and unbored surfaces. Scale bar = 4 cm. (**D**) Base of channel with marbleized texture of bedrock. *Gastrochaenolites*-like traces cut distribution is not dependent on the bedrock texture. Scale bar = 15 cm. (**E**) Small boulder within DCOD with *Littorina saxatilis, Buccinum undatum, Pagurus* sp., *Chondrus crispus, Spongomorpha* sp. and *Cystoclonium purpureum*. Scale bar = 2 cm.

and width) occur and have borings on multiple sides (Figs. 3-14 B-E). Borings are produced by both *Petricola pholadiformis* and *Zirfaea pilsbryi* and abundance varies from 100-1500 / m^2, with the majority of bored surfaces containing 1000-1500 borings / m^2. Boring density is highest on the western end of DCOD (700-1500 borings / m^2) and lowest on the eastern end of DOCD (100-930 borings / m^2) (Fig. 3-5). The ratio of borings that are occupied versus unoccupied, and the proportional abundance of the two boring bivalve species is uncertain due to the endolithic nature of the bivalves. Sediment mounds are not common and are only present on the eastern end of DCOD (< 10% of borings exhibit sediment mounds) where sediment accumulates. A thin veneer of coarse-grained sand is present within isolated patches of the eastern end, but most of the channel bed is exposed bedrock. Throughout the DCOD, borings are infilled with coarse and very coarse-grained sand. No sedimentary structures are present within the sand or bedrock. Large boulders (< 1.5 m in length) are isolated throughout the DCOD and do not possess horseshoe scours due to the lack of sediment.

The DCOD possesses the highest diversity of organisms of all the sub-environments. In addition to the two species of boring bivalves, over 20 invertebrate species were identified (Table 3-1). Organism distribution is patchy, but abundance is higher on the western part of the channel. Organisms here must be tolerant of high ebb- and flood-tidal water velocities on a substrate with minimal unconsolidated sediment. *Aulichnites*- and *Coenobichnus*/*Diplichnites*-type traces are present within thin sediment veneer patches, with abundances reaching up to 5 traces / m^2.

Interpretation: The western and eastern ends of the DCOD within the study area have different environmental conditions that effect boring bivalve abundance. The western side of the DCOD has a higher number of borings (700-1500 / m^2). None of the borings were observed to possess sediment mounds. The more oceanward side has a thin layer of water that remains present within this area throughout low tide. The eastern part of the DCOD has a lower number of borings (100-930 / m^2) and possesses sediment mounds. This side is upslope of the western side and is commonly fully subaerially exposed during the lowest tides. This suggests that bivalves prefer areas that remain submerged (even with only a thin veneer of) water during low tide and prefer the western end of DCOD.

A high diversity of organisms occurs within the DCOD. The diversity is directly related to the high water energy that results from water funneling through the DCOD. The fast velocity allows the majority of DCOD to remain sediment free and provides a steady food supply to organisms. Water remains within the channel for the majority of low tide, which prevents the desiccation of organisms and facilitates feeding throughout the tidal cycle.

Sub-environment 7: Intertidal sand flat (ITSF)

The intertidal sand flat (ITSF) is located east of the ridge (R). The ITSF consists of a mosaic of gravel veneer, exposed bedrock and one large sand deposit (Fig. 3-15). Topographic lows remain water-filled and have salinities of ~ 31 ppt. The gravel veneer is compositionally similar to the CF and is limited to areas around the margin of the ITSF, areas closest to the R and the CF (Fig. 3-15A) and within the troughs of dunes (Fig. 3-15D). Isolated patches of gravel veneer cover areas of about 5 m^2. No plants, organisms or borings are present in the bedrock underlying the gravel or within the gravel veneer.

Areas of exposed bedrock have little to no sediment (Fig. 3-15B); a thin veneer of sand and mud or isolated pebbles (0.5-5 cm in length) and isolated fragments of shell debris (0.5-8 cm in length and width) are present where sediment is deposited. Continuous and lunate, ebb-oriented ripples are occasionally present within thin layers of sediment, but are not common. Furrows are present on isolated areas of exposed bedrock and ebb-oriented horseshoe scours are common (Fig. 3-15B). Water frequently pools in areas of exposed bedrock and form small (1 m^2 area) and large (15 m^2 area) tidal pools. Gastropods (*Littorina saxatilis*, *Buccinum undatum* and *Nassarium trivittaus*), hermit crabs (*Pagurus* sp.), worms (*Glycera* sp. and *Enchytraeus* sp.), tubeworms (*Lanice* sp.), Irish moss (*Chondrus crispus*), bushy red weed (*Cystoclonium purpureum*), encrusting algae (*Clathromophum* sp.) and a white branching bryozoan (*Flustra foliacea*) are all present within these tide pools. The boring bivalves, *Petricola pholadiformis* and *Zirfaea pilsbryi*, are present within the areas of exposed bedrock and abundance can reach up to 1500 borings / m^2. Borings are occupied and unoccupied, and sediment mounds are present on top of some occupied borings.

The large sand deposit consists of poorly sorted coarse to vary coarse sand, pebbles, cobbles and shell debris (2-5 cm in length and width) that covers a 75 m^2 area. Meter scale ebb-oriented dunes (< 1 m in length and < 30 cm high), with coarse sediment filled troughs, are commonly overprinted with ebb ripples (< 8 cm in length and < 1 cm high), drainage ripples and drainage splays on the lee side of the dunes (Figs. 3-15C-E). Drainage ripple refers to ripples that are oriented perpendicular to the strike of the lee side of the dunes (Fig. 3-15E). Faint

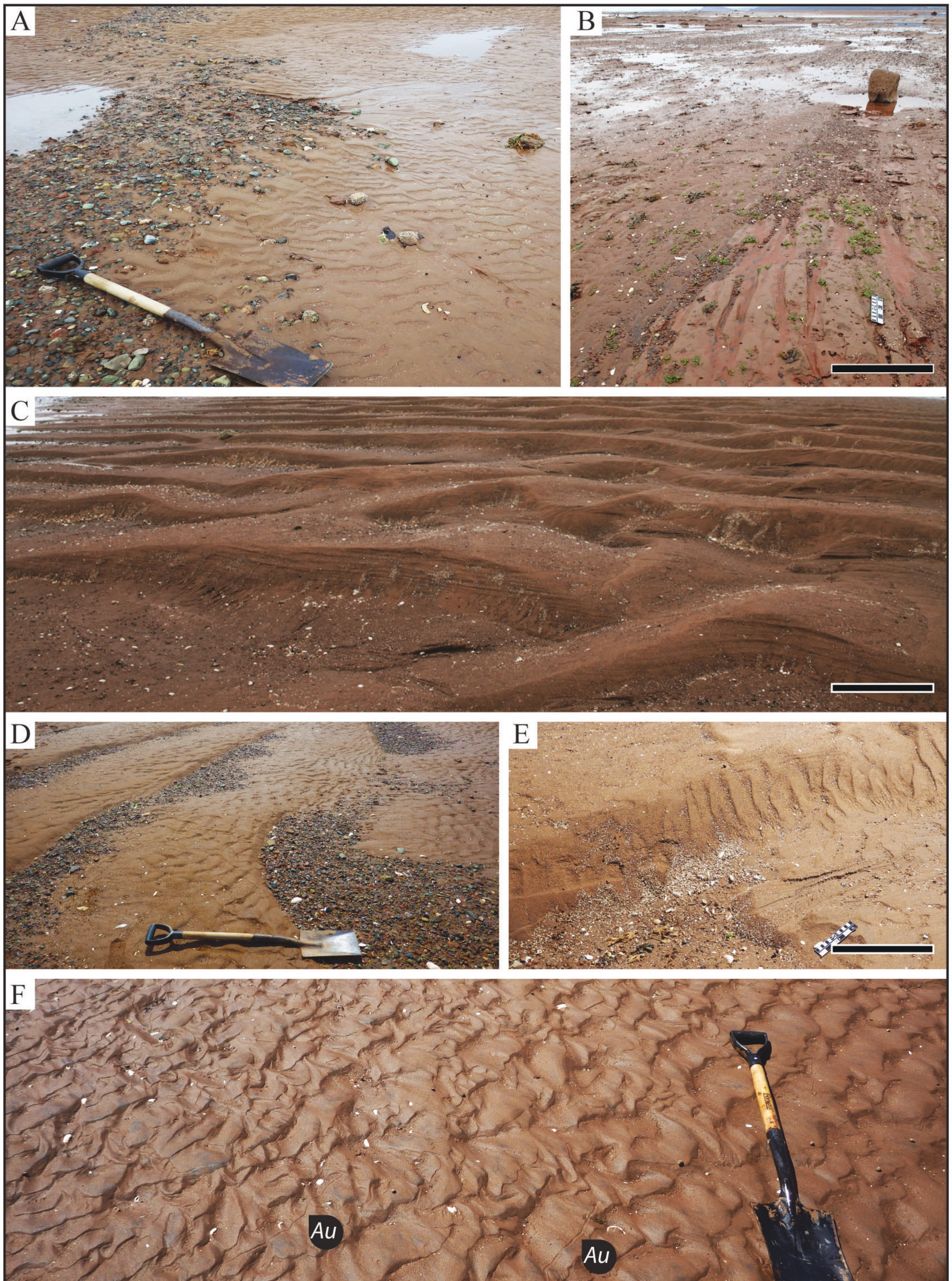


Figure 3-15. Intertidal sand flat (ITSF) sub-environment. (**A**) Patches of gravel vaneer, sand with faint ebb-oriented ripples. Shovel for scale. (**B**) Patches of thin, structureless, sand layers and exposed bedrock with borings and furrows. Ebb-oriented horseshoe scour associated with large bounder in background. Scale bar = 45 cm. (**C**) Large sand deposit with ebb-oriented dunes. Drainage ripples and faint horizontal drainage marks on the lee side of the dunes. Scale bar = 30 cm. (**D**) Ebb-oriented dunes overprinted with ebb-oriented ripples. Gravel and shell debris concentrated within the troughs of the ripples. Shovel for scale. (**E**) Drainage ripples superimposed on lee side of a dune. Drainage splay within the trough. Scale bar = 30 cm. (**F**) Interference ripples within sand. Au = *Aulichnites*-type traces. Shovel for scale.

horizontal lines are also present on the lee side of dunes (Fig. 3-15C). Interference ripples are common within the sand deposit where dunes do not occur (Fig. 3-15F). Gastropods (*Littorina saxatilis*) and hermit crabs (*Pagurus* sp.) and their traces (*Aulichnites*- and *Coenobichnus*/*Diplichnites*-type traces respectively) are present within the troughs of the dunes and within the interference ripples (Fig. 3-15F). The abundance of surface traces does not exceed 5 traces / m^2. No plant life is present within the thick sand layer. Boring bivalves (*Petricola pholadiformis* and *Zirfaea pilsbryi*) are rare and are limited to the outer fringes of the sand deposits, where sand is < 4 cm think.

Interpretation: The ITSF is located within a flood-oriented, depositional shadow of the R and many depositional processes occur here. Areas of exposed bedrock and gravel veneer suggest high-energy water condition, which are capable of transporting and depositing gravel and preventing deposition within other areas. Water velocity is high enough to form furrows in bedrock and winnow fine-grained sediment from the gravel veneer.

Within the large sand deposit the majority of sedimentary features are ebb-oriented and suggest a change in water velocity as the features formed. Meter scale dunes and large grained gravels and shell debris in the troughs of the dunes suggest high water velocities. As the tide continues to ebb and drain, water velocity decreases and forms ebb-oriented ripples that are superimposed on the dunes. Many of the dunes also have current ripples superimposed on their lee side surface, suggesting that water is channeled through the troughs of the dunes as the ITSF drains. Drainage splays where water breached dunes or ripples, and flooded over their crests. The faint horizontal lines on the lee sides of the dunes suggest that water slowly drains from the ITSF dunes creating levee-like deposits along the surface of the lee side of the dunes. Interference ripples indicate multi-directional currents (Klein, 1963). The different sedimentary structures preserved in this sub-environment indicate frequent changes in water velocity and direction. Similar features occur throughout the Minas Bay (Klein, 1962, 1963, 1964).

Biotic distribution is complex and is limited to specific areas within the ITSF (Fig. 3-5). No organisms were noted in the gravel veneer suggesting that the substrate does not provide adequate supply of food resources and the substrate, which is likely mobile during peaks in tidal current velocity, may be harmful to invertebrates (i.e. larger grains crush parts of organisms). The large sand deposit is inhabited solely by gastropods and hermit crabs, suggesting that other organisms cannot survive within the relative thick, shifting substrate. Boring bivalves are limited to exposed bedrock and the fringes of the large sand deposit, where sediment is < 4 cm thick. The bivalves prefer exposed lithic substrates but are tolerant of burial beneath a thin layer of sediment. The highest diversity and abundance of organisms are within areas of exposed bedrock where water pools and remains throughout low tide. Species within the ITSF are similar to those within the DCOD, suggesting that similar environmental conditions occur in both sub-environments.

Sub-environment 8: Ridge (R)

The ridge (R) is a local topographic high within the study area. Its elevation reaches ~ 5 m above the DCOD level (Figs. 3-16 A-C). It extends outside of the southern portion of the study area for almost 1 km south into the Minas Basin. The R consists of sandstone and has a layer (~ 0.5-1 m thick) of fissile, silty mudstone that outcrops on the eastern edge of the R and the southern portion of the leading edge of the ridge (LER). The upper, planar surfaces of the R consist of sandstone, which commonly has a very thin, overlying mud veneer. Fine sand is common within the sheltered topographic lows and infill fractures. Boulders (30 cm to 1 m in length) of bedrock are scattered along the surface and sides of the R. Potholes, tide pools, furrows and reduction spheres are common (Figs. 3-16 D-E). Gastropods (*Littorina saxatilis*) occur in high abundance within the potholes, but also occur scattered across the upper surface. Little gray barnacles (*Chthamalus fragilis*) encrust the majority of the surface (90-100% of the exposed surface) and seaweed (*Fucus vesiculous* and *Ascophyllum nodosum*) is isolated to relative topographic highs and reduction spheres (Figs. 3-16 D-E). Borings are rare (0-5 borings / m^2) and are commonly unoccupied. *Petricola pholadiformis* shells are the only observed bivalves residing within the borings and many borings are eroded, making it difficult to determine the originator trace-maker taxon. The upper surface of the R also possesses depositional sub-environments, which are formed due to topography controls and include the tide pools (TP) and tide pool drainage (TPD) sub-environments. Both of these sub-environments have unique biologic assemblages (discussed later) that are more diverse than R.

On the vertical sides of the R, a bed of fissile silty mudstone occurs. On the eastern edge of the R, the silty mudstone layer is about 30 cm thick and is located about 2 m from the top of the ridge. This small surface is bored solely by *Petricola pholadiformis*, and abundance reaches 600 borings / m^2 area (Fig. 3-16F). The overlying and underlying sandstone layers are not bored. Silty mudstone also

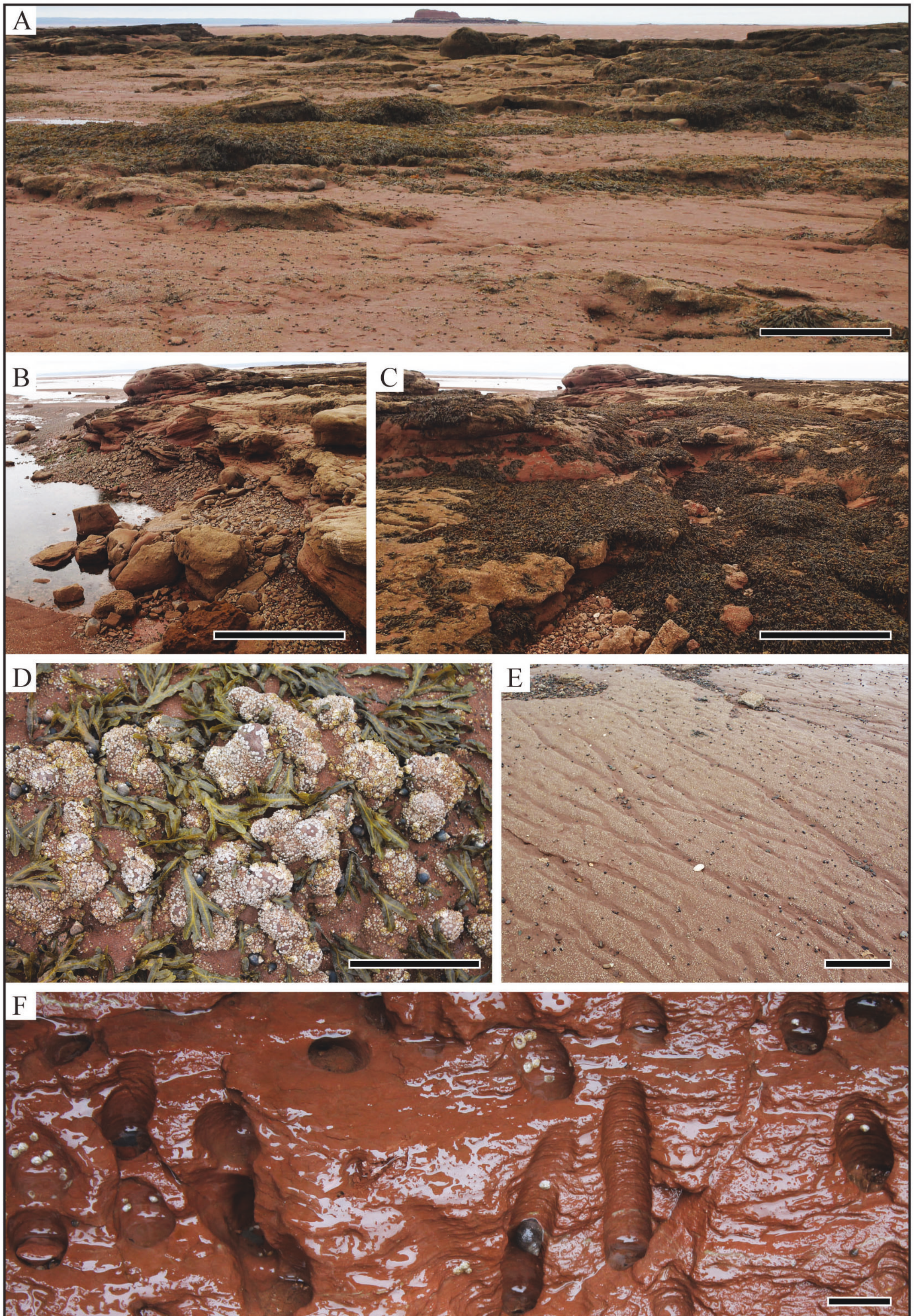


Figure 3-16. Ridge (R) sub-environment. (**A**) Upper surface of R. Scale bar = 50 cm. (**B**) Eastern edge of R. Scale bar = 1 m. (**C**) Upper surface of R covered by a high density of *Fucus vesiculosus* and *Ascophyllum nodosum*. Scale bar 40 cm. (**D**) Reduction spheres with *F. vesiculosus* and encrusting *Chthamalus fragilis*. Scale bar = 15 cm. (**E**) Furrows on R's upper surface. *Chthamalus fragilis* encrust areas surrounding the furrows. Scale bar = 15 cm. (**F**) *Gastrochaenolites*-like traces within the fissile silty mudstone bed within the east vertical face. Scale bar = 2 cm.

outcrops on the LER, is much thicker (about 150 cm thick) and is highly bored (see LER sections for more details of the sub-environment). Gastropods (*Littorina saxatilis*) are the only other organisms that reside here.

Interpretation: The topographic high of the R forms a desolate environment that is exposed daily for much of the low tide interval. Organisms in this sub-environment must be able to survive multiple stresses (i.e. salinity and temperature fluctuations, desiccation). Little gray barnacles, gastropods and two species of seaweed are the only organisms capable of thriving under these conditions. Barnacles encrust over much of the surface and become more abundant and larger in size on reduction spheres. Gastropods are limited to topographic lows and are commonly found in high abundance within potholes and other areas where water collects during low tide. Seaweed commonly attaches to edges of bedrock and relative topographic highs. Erosional structures on the upper surface are limited to erosional furrows, potholes and reduction spheres. Depositional sedimentary structures are uncommon due the high water velocity around the R during high tide.

Borings are located primarily within the silty mudstone layers within the margins of the R. The silty mudstone is fissile and much softer than the surrounding sandstone. The high abundance of boring bivalves within this layer suggests that bivalves prefer to bore into softer substrates when it is available. However, bivalves will bore into the sandstone when environmental conditions are favorable (i.e. TP and TPD).

Sub-environment 9: Leading Edge of the Ridge (LER)

The leading edge of the ridge (LER) is located along the sloped face and lower horizontal surface on the ocean-ward side of ridge. The area is divided into two zones, which are differentiated by the slope of the substrate. The vertically sloped zone is located on the northern extent of the LER and made up of large bedrock boulders (< 1.5 m in height and width). Sediment (very coarse sand to boulder sized) and shell debris (1-5 cm in length and width) are present between the large boulders. Boulders have a high concentration of encrusting little gray barnacles (*Chthamalus fragilis*), but are devoid of any other flora or fauna.

The horizontal surface is located within the southern portion of the LER and is within a slightly sheltered area. Boulders, sediment and shell debris occur but areas of exposed bedrock are prevalent (Figs. 3-17A, 3-17B). A gravel veneer is present, which is compositionally similar to gravel within the CF. A thin sheet of water

Figure 3-17. Leading edge of the ridge (LER) sub-environment. (**A**) Bored fissile silty mudstone. Bedrock boulders in the background. Shovel for scale. (**B**) Bored silty mudstone, sediment debris and bedrock boulders. Scale bar = 24 cm. (**C**) Fissile silty mudstone with exposed *Petricola pholadiformis* and *Zirfaea pilsbryi shells* within *Gastrochaenolites*-like traces. Pencil for scale.

(salinity 30 ppt) is common on the surface. The bedrock is composed primarily of fissile silty mudstone with sandstone layers at the uppermost and lowermost elevated areas. This silty mudstone is compositionally similar to the layer on the other side of the R. Borings are limited to this lithology and are not present under the gravel veneer. Borings are produced by both *Petricola pholadiformis* and *Zirfaea pilsbryi.* The distribution is patchy, with abundance can reach up to 500 borings / m^2 area. Many borings contain empty shells or are completely empty, with no shell remaining. Many are also widened through erosion (Fig. 3-17C). However, live boring organisms can be found. Hermit crabs (*Pagurus* sp.) and gastropods (*Littorina saxatilis*) are also present along the exposed bedrock surface, however surface traces are not present due to the lack of sand and mud.

Interpretation: The LER is a relatively harsh environment and is the first major obstacle water faces in the flooding direction. Large boulders in this setting are frequently surrounded by sediment deposits and are colonized solely by barnacles. Boring bivalves, gastropods and hermit crabs are limited to more sheltered, horizontally-oriented areas where softer, fissile silty mudstone outcrops without a sand and gravel veneer. This suggests that the bivalves prefer the softer substrate and that the gravel veneer hinders larval settlement and growth. The thin sheet of moving water that is present in some areas facilitates. The distribution of borings on the exposed outcrop is patchy and reflects the location of flowing and standing water at low tide.

Sub-environment 10: Tide Pool on Ridge (TP)

One large tide pool is located on the middle of the portion of the R within the study area and is about 75 m long and 50 m wide (Fig. 3-18A). The TP bed occurs on sandstone bedrock in an area with no sediment veneer and possesses small (1-5 cm^2) pieces of bored rock that have been broken off of the bedrock. The water is 1.5 m at its deepest and has a salinity of 30 ppt. Other smaller (1-5 m^2) tide pools are located north of the large tide pool and are all connected with a system of small (5-10 cm wide) drainage channels. The water drains from the tide pools over the edge of R in the tide pool drainage (TPD) sub-environment near the LER. The small tide pools and drainage systems occasionally possess borings (Fig. 3-18B) and isolated gastropods (*Littorina saxatilis*), however, the large tide possesses a diverse assemblage of biota. The bottom surface of the large tide pool is highly bored by *Petricola pholadiformis* with density reaching 750 borings / m^2

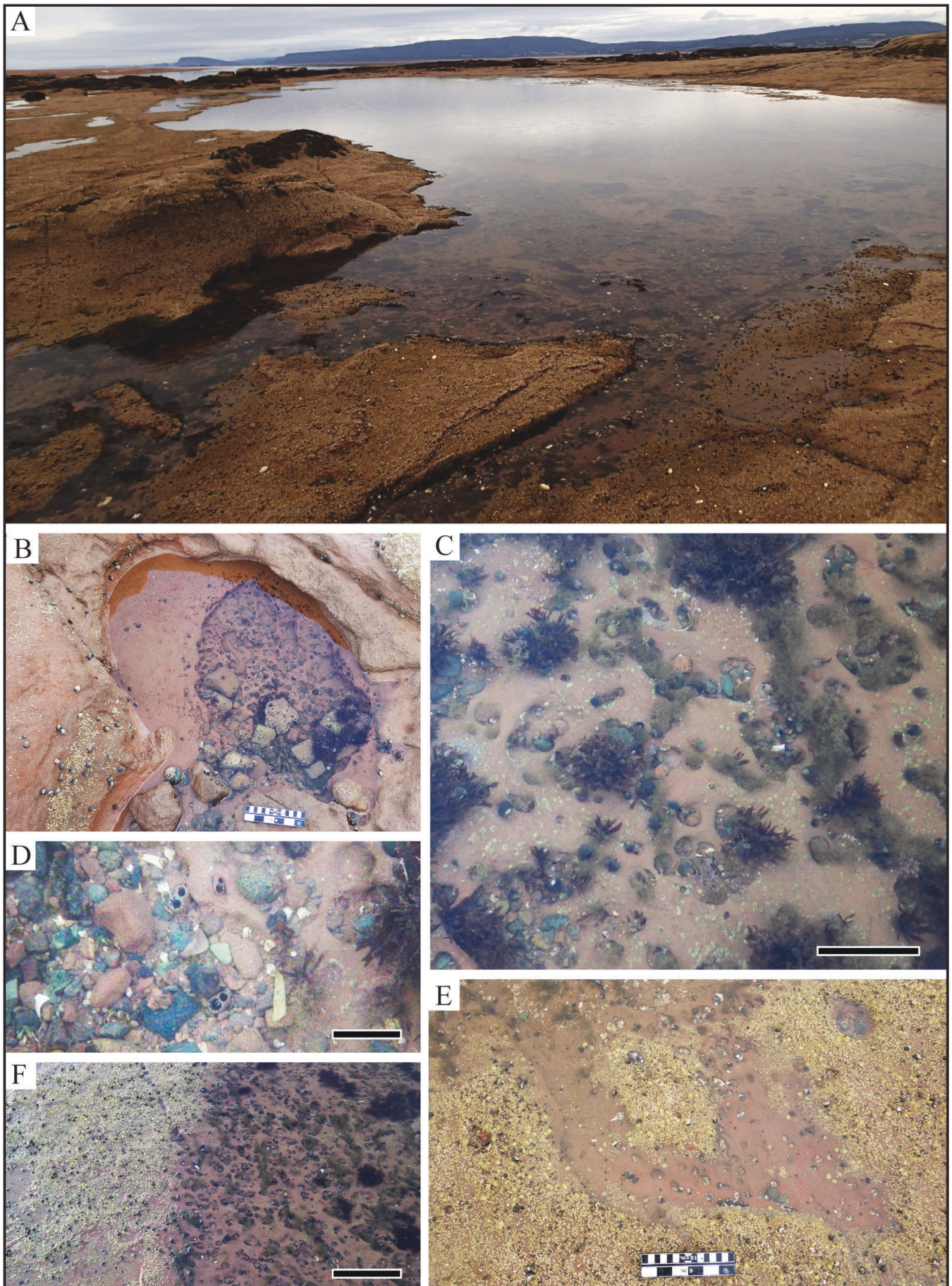


Figure 3-18. Tide pool (TP) on ridge sub-environment. (**A**) Large tide pool in the middle of the ridge. Tide pool width ~ 50 m. (**B**) Small tide pool with *Gastrochaenolites*-like traces within the substrate under the deepest water. Scale bar = 15 cm. (**C**) Base of tide pool with *Gastrochaenolites*-like traces, *Chondrus crispus* and *Codium fragile*. Scale bar = 8 cm. (**D**) Three *Petricola pholadiformis* with siphons extended outside of the substrate. Scale bar = 3 cm. (**E**) Area along side a tide pool, with *C. fragilis* encrusting over area above water and *Gastrochaenolites*-like traces within substrate below water level. Scale bar = 15 cm. (**F**) Edge of tide pool with *Chthamalus fragilis* encrusting over area above water and *Gastrochaenolites*-like traces within substrate below water level. Scale bar = 20 cm.

(Fig. 3-18C). Both occupied and unoccupied borings occur although no sediment mounds were observed. The bivalves frequently extend their siphons 1-2 cm past the substrate surface into the water (Fig. 3-18D). Borings are limited to areas that are covered with water, forming a distinct line between bored and unbored surfaces that correlate to the water's edge (Figs. 3-18E, 3-18F). Twelve other invertebrate taxa were identified within the TP (Table 3-3). All organisms, other than little gray barnacles (*Chthamalus fragilis*) and isolated gastropods and hermit crabs, are limited to submerged areas. Organism diversity, abundance and composition are very similar to that of the DCOD.

Interpretation: The TP provides a sediment free sub-environment that remains submerged throughout the low tide interval. The constant presence of water provides nutrients and protection from desiccation for organisms. All organisms, other than little gray barnacles and the isolated gastropod and hermit crab, are limited to the submerged substrate suggesting that the majority of organisms prefer to be submerged in water. The distinct line between bored and unbored surfaces correlating to the edge of the water in the TP suggests that the boring bivalves must stay submerged under at least a thin sheet of water to survive. A similar distinct boundary, between bored and unbored surfaces, was noted by Moura et al (2012). Salinity at low tide is ~30 ppt. Thus, the TP provides a stable marine environment where biota can reach high population levels with minimal stress. Due to their high abundance, boring bivalves significantly weaken the substrate which can break off, producing small pieces of the bedrock that are transported within the study area, exposing new substrate to the surface.

Sub-environment 11: Tide Pool Drainage (TPD)

The tide pool drainage (TPD) sub-environment consists of a gently sloping surface adjacent to the LER and is the area where most of the water drains from the R and TP sub-environments (Fig. 3-19A). A series of waterfalls and pools are formed as the water (with a salinity of 30 ppt) continuously drains off of the R and TP throughout the low tide interval, forming a thin sheet of water that flows over the horizontal surfaces (Fig. 3-19B). The substrate consists of sandstone along the upper surface (ie. upper edge of the ridge), which becomes a fissile silty mudstone 50 cm below the top surface of the R. Borings are produced by *Petricola pholadiformis* and *Zirfaea pilsbryi* and are present irrespective of substrate (Figs. 3-19C, 3-19D). Borings are occupied and unoccupied, and are highly eroded due to

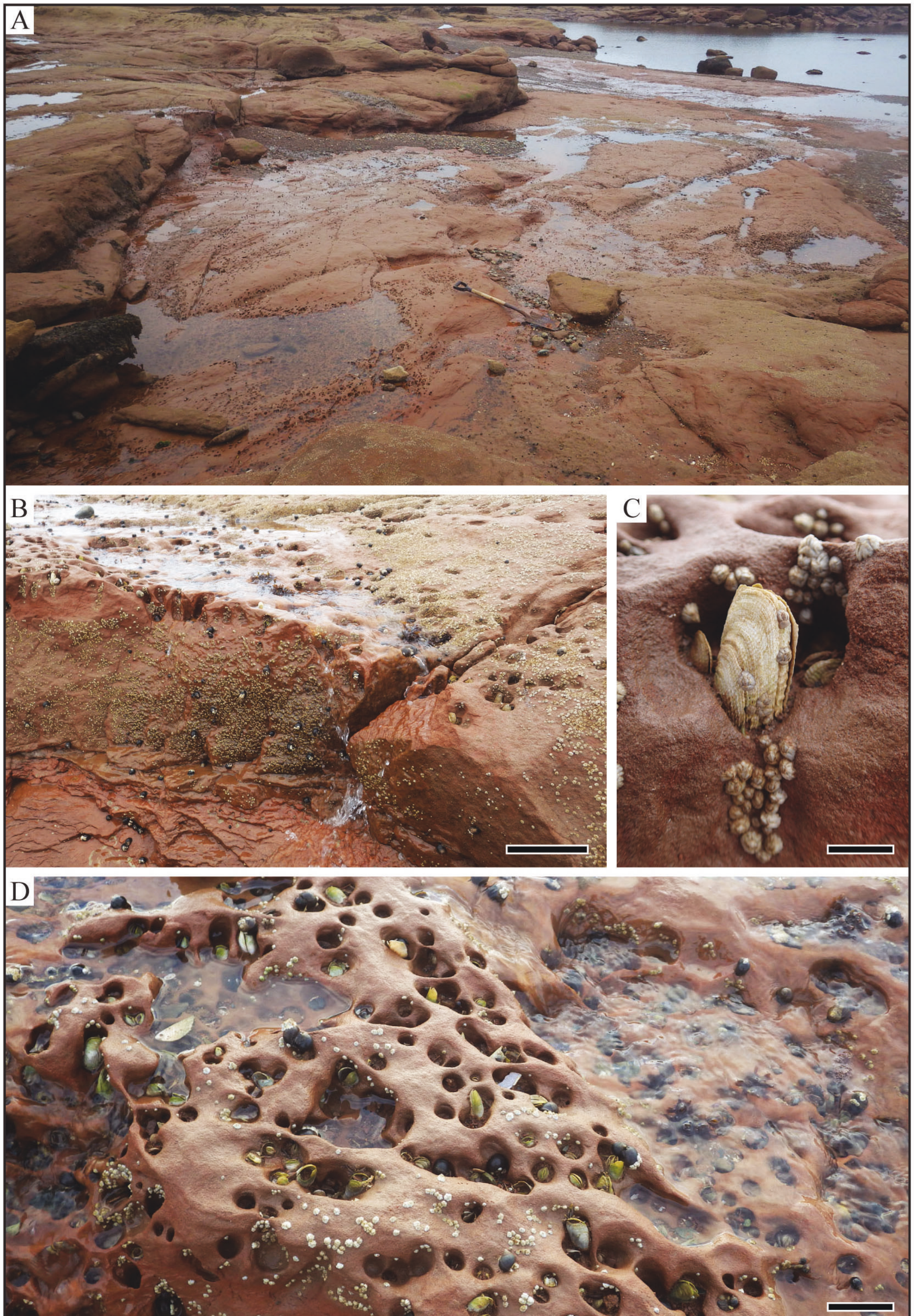


Figure 3-19. Tide pool drainage (TPD) sub-environment. (**A**) Tide pool drainage system. Water drains to the upper right corner of the photograph. Shovel for scale. (**B**) Small waterfall with *Gastrochaenolites*-like traces and encrusting *Chthamalus fragilis*. Scale bar = 12 cm. (**C**) *Petricola pholadiformis* within a hydrodynamically eroded *Gastrochaenolites*-like traces. *Chthamalus fragilis* encrusts within and around the trace. Scale bar = 1 cm. (**D**) Hydrodynamically eroded *Gastrochaenolites*-like traces. Scale bar = 5 cm.

the water flow, which exposes living and dead bivalve shells (Figs. 3-19C, 3-19D). Traces are limited to areas were water flows over the substrate. A sharp boundary occurs between bored and unbored surfaces, which clearly correlates to the presence or absence of continuous submersion. Boring abundance is about 350 borings / m^2. Other organisms that live within this area include little gray barnacles (*Chthamalus fragilis*), isolated gastropods (*Littorina saxatilis*) and hermit crabs (*Pagurus* sp.). On one occasion, a green crab (*Carcinus maenas*) was observed within an area where water pools.

Interpretation: The TPD provides a depositional sub-environment that has water running over the substrate surface throughout the low tide interval. Although it is unclear if the stream water provides an adequate food supply to biota during low tide, the water prevent desiccation and ease respiration for subaqueous taxa. Borings are not substrate controlled within this area. Rather the presence/absence of a continuous water covers dictates the presence or absence of hardground infaunal organisms. Hydrodynamic erosion occurs along the surface and removes substrate from around the bivalve shells, which modifyies the morphology of the borings. Many/most of the exposed bivalves are dead with only their shells remaining, suggesting that either erosion occurred post mortem, or that substrate erosion interfered with bivalve survival. It is possible that when too much of the substrate is removed, structural stability and protection is eliminated.

Biotas are limited to encrusting little gray barnacles, boring bivalves, gastropods and hermit crabs. The mobile organisms gather where water depth is greatest and avoid both areas of fast flowing water as well as areas covered in a thin sheet of water, suggesting that the thicker layers of calm water provide optimal environmental conditions and food supply for the organisms. Little gray barnacles encrust sporadically over the substrate (Figs. 3-19 B-D). The presence of organisms such as the green crab, suggests that organisms throughout the Bay of Fundy have the potential to be washed up within different sub-environments and may remained trapped there until the tide floods the area. These organisms can survive for short periods of times within non-optimum sub-environments.

HORSESHOE SCOURS: SPECIALIZED HABITATS

Horseshoe vortices around large, isolated boulders produce localized windows of exposed lithic substrate throughout the study area (Fig. 3-20). It has been suggested that the large boulders were distributed throughout the Bay of Fundy

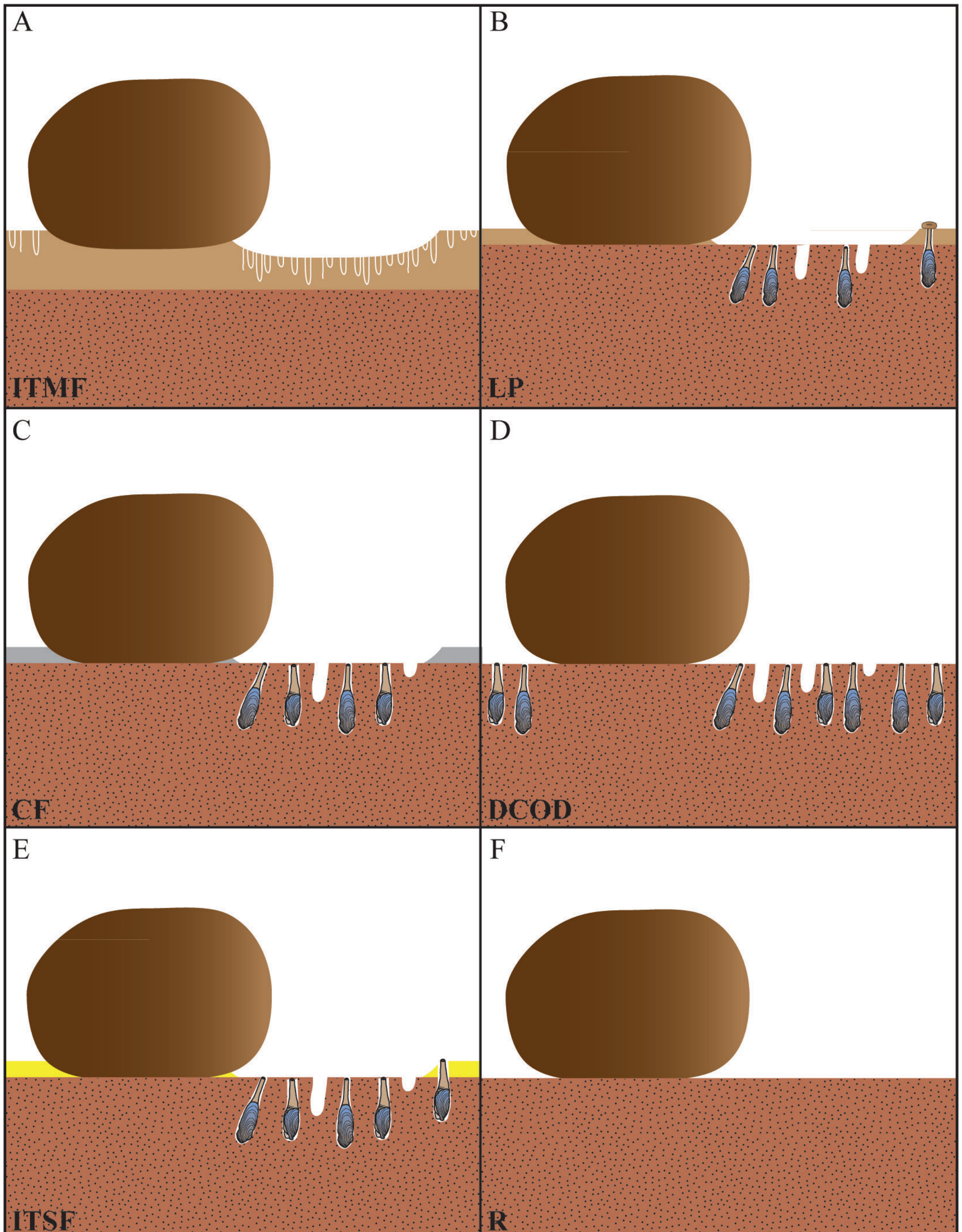


Figure 3-20. Horseshoe scour formation. (**A**) Horseshoe scour within the ITMF. *Arenicolites*- and *Skolithos*-type traces are present within and around the boulder. (**B**) Horseshoe scour intersecting bedrock within the LP. *Gastrochaenolites*-like traces are occupied and unoccupied, and sediment mounds are present. (**C**) Horseshoe scour intersecting bedrock within the CF. Occupied and unoccupied *Gastrochaenolites*-like traces are present. (**D**) Large boulder within DCOD. Horseshoe scour not produced due to the lack of sediment. Occupied and unoccupied *Gastrochaenolites*-like traces are present within all substrate surrounding the boulder. (**E**) Horseshoe scour intersecting bedrock within the ITSF. Occupied and unoccupied *Gastrochaenolites-l*ike traces are present. (**F**) "Horseshoe scour" intersecting bedrock within the R. Due to the lack of sediment, a true scour is not formed. No *Gastrochaenolites*-like traces are present. Drawings are not to scale.

during the winter via ice rafting (Dalrymple et al., 1990). Boulder size, water current direction, duration and velocity, substrate thickness and sediment size within the depositional sub-environments affect the morphology of the horseshoe scours and dictate colonization patterns of boring organisms. The size of the horseshoe scours is directly related to the size of the boulder and the velocity of water surrounding the boulder. The scours are oriented in flood and ebb directions within and across the different depositional sub-environments, suggesting that water moving in both tidal directions has sufficient velocity to produce horseshoe scours. These scours remained consistent in shape, size and orientation throughout the duration of this study. In some areas of the ITMF, horseshoe scours, which do not penetrate to bedrock, are formed within the silt and mud substrate (Fig. 3-20A). In other sub-environments (LP, CF and ITSF) horseshoe scours can intersect the underlying bedrock and expose the hard substrate to the colonization of boring bivalves (Figs. 3-20B, 3-20C, 3-20E). Boring densities range from 0 to 900 borings / m^2 within the horseshoe. Areas that do not have any sediment overlying the bedrock, like in DCOD and R, do not form horseshoe scours and boring density remains consistent between exposed areas and those adjacent to boulders (Figs. 3-20D, 3-20F).

CONTROLS ON SEDIMENTATION AND BIOTIC DISTRIBUTION

Controls on sedimentary structures

Tide direction and water velocity play major roles in the formation of sedimentary structures, where sediment overlies bedrock within the study area. Within the different depositional sub-environments flooding and ebbing tides form distinct sedimentary features (Table 3-3). Both tidal orientations have velocities sufficient to produce ripples and meter scale dunes in different depositional areas. However, sedimentary structures indicating an ebb-oriented flow direction are considerably more common. The dominance of ebb-oriented sedimentary features may be a result of the study area being investigated during low tide and ebb processes overwriting flood sedimentary structures. Therefore, it is unclear how the sediment shifts during high tide.

Ebb-oriented ripples and/or dunes occur within the ITMF, LP and ITSF, however flood-oriented sedimentary features occur within the ITMF and LP. The ITMF contains both flood- and ebb- oriented ripples suggesting influence by both tidal orientations. The ITSF is completely dominated by ebb-oriented dunes and ripples, as well as other drainage features (drainage ripples and drainage splays) indicating that the ebbing tide has sufficient strength to rework any features produced by the flooding tide. The LP also possesses ripples superimposed on dunes, but ripples are both flood- and ebb-oriented, whereas the dunes are solely flood-oriented. Superimposed ripples on dunes are common, regardless of the direction of water flow, and suggest that multiple water velocities produce sedimentary structures and are preserved during low tide. Similar superimposed features are common and have been documented elsewhere in the Bay of Fundy (Klein 1963; 1964; Dalrymple, 1984; Dalrymple et al., 1990).

Controls on borings

Salinity: Salinity is close to fully marine across nearly all the sub-environments (~30 ppt), with the exception of the DC, which has a salinity of 10 ppt. The brackish water of DC is indicative of fresh water within the landward stream mixing with marine water within the ITMF. Salinity of the remaining sub-environments remain within 1 ppt of each other and is reasonably within the mechanical error of the salinity meter. The strong tidal currents within the Minas Basin form a well-mixed water column, both laterally and vertically, with respect to salinity, water temperature and suspended sediment content (Knight, 1980; Amose and Long 1980, Dalrymple et al., 1990). Boring bivalves and their traces are not present within the reduced salinity area of the DC, as well as the drainage fan produced over the lower position of the ITMF and LP, suggesting that the boring organisms prefer depositional sub-environments with normal marine salinity. However, not all depositional sub-environments with fully marine water salinity possess boring bivalves, suggesting that salinity is not the only control on boring distribution.

Water energy: The velocity of water is variable across the different depositional sub-environments and varies throughout the flooding and ebbing tides. The DCOD and CF depositional sub-environments are the last areas to drain as the ebbing tide and the first to fill during the flooding tide. Water is channeled through the DCOD and overflows onto the LP and eventually to higher elevated sub-environments as the tide floods. Water velocity decreases as elevation increases due to the water expanding over a broader area. Similar water velocities are present with the ebbing tide. Water velocities across the study area are unknown during high tide.

Within the study area, boring bivalves prefer areas that experience higher water velocities. Boring densities reach up to 1500 / m^2 area within DCOD, whereas areas that have slow flowing water have lower boing densities (i.e. density in TP reaches up to 750 / m^2 area) (Fig. 3-5B). *Zirfaea pilsbryi* are located within areas that have a higher maximum energy level, such as DCOD and TPD, whereas *Petricola pholadiformis* reside both in areas that have fast flowing water as well as areas of standing or sluggish flowing water (Fig. 3-5A). Although all depositional sub-environment are completely submerged during high tide and many of the depositional sub-environments possessing both bivalve taxa are devoid of water during low tide, there are still depositional sub-environments that do not possess both species. This suggests that the conditions during flooding, ebbing and high tides play a major role in where the bivalves can settle and grow.

Substrate: The Wolfville Formation has been interpreted as being deposited within a braided river system, alluvial fan, eolian and lacustrine depositional environments, which produces interbedded sandstone and silty mudstone (Klein, 1962, Hubert and Mertz, 1980; Olsen, 1981; Olsen and Schlische, 1990; Wade at al., 1996; Leleu et al., 2009, 2010; Leleu and Hartley, 2010). Bivalves prefer to bore within the silty mudstone layers, but also bore within sandstone when the silty mudstone is absent. Borings can reach 440 borings / 1 m^2 within the silty mudstone, but reach up to 310 borings / 1 m^2 within nearby sandstone. However, some sandstone surfaces can reach higher boring abundances (DCOD = 1500 borings / 1 m^2), but other sandstone surfaces are uninhabitable by boring bivalves, which suggests that substrate plays a role in bivalve distribution, but it is not the sole factor.

Boring bivalves prefer areas and depositional sub-environments with minimal sediment overlying the bedrock. The ITMF is vacant of *Gastrochaenolites*-like traces due to the thick layer of silty mud. The unconsolidated mud is too thick for the siphons of bivalves to extend through. However, along transitional areas where mud is thinner, substrate with muddy sediment veneer can possess borings. The LP, DCOD and ITSF have borings where sediment overlying the bedrock is <4 cm thick. It is uncertain why there is a 4 cm threshold for the borings bivalves, but no borings were found under thicker sediment layers. Boring bivalves also do not reside within areas of gravel veneer. The gravel is interpreted herein to be harmful to the bivalves; it may prevents settlement and growth, the shifting gravel likely damages protruding siphons during intervals of maximum flow, and the siphons are insufficiently muscular to penetrate a gravel layer should burial occur.

Additional factors: Climatic influences and food-resource parameters also may play vital roles in the distribution and abundance of borers and burrowers (below).

Controls on biotic distribution

Water and sediment abundance: The distribution of organisms is dependent on various environmental and sedimentological controls within each depositional sub-environment. Organisms prefer depositional sub-environments (ITMF, LP, CF, DCOD, ITSF, TP and TPD) that are submerged in water through the low tide interval. Areas that are better drained (UP, R and LER) have a lower abundance and diversity of organisms. This suggests that the organisms that are in these sub-environments must withstand extended periods of exposure and must be able to prevent desiccation. *Chthamalus fragilis*, *Fucus* sp. and *Spongomorpha* sp. are most common organisms within the exposed sub-environments. Areas that are submerged or have flowing water over the substrate can have a biotic community of 10 to 20 species, which include boring, encrusting and squatting/clinging organisms. Communities are most diverse within the DCOD and TP, and possess similar biotic components, suggesting that organisms and their larva can be redistributed during high tide.

The majority of organisms that are present within the ITMF are not present in other sub-environments and rely of the soupy, silty mud substrate to burrow. The substrate that accumulates has a thickness of 11.5 cm and allows a diverse assemblage of organisms to make traces. No other depositional sub-environment has silty mud layers of that thickness, which limits burrowing biota to the ITMF.

Climatic influences: The Bay of Fundy is considered a sub-polar environment, and ice develops during winter and has major impacts on sedimentology, ichnology and infaunal communization (Dionne 1972; Knight and Dalrymple, 1975, 1976; Hicklin et al., 1980; Gordon and Desplanque, 1983; Desplanque and Bray, 1986; Woodworth-Lynas, 1995; Desplanque and Mossman, 1998, Dionne, 1998; Pearson and Gingras, 2006; Dalrymple et al., 2011; Dashtgard et al., *in press*). Due to ice development, sedimentation is low and many invertebrates either hibernate or are killed in a mass die-off at the onset of winter (Hicklin et al., 1980; Dashtgard et al, *in press*). It is likely that all biota, including *Petricola pholadiformis* and *Zirfaea pilsbryi*, are greatly influenced by the seasonal changes within the Bay of Fundy, and determining the how biota are effected by seasonal changes is a potential avenue for future research.

Food-resources: Food-resources may play a distinct role in biota (and thereby borings and burrow) abundance and distribution. The megatidal setting produces a daily flux of nutrient input from the ocean into the estuarine embayment.

Additionally, algal and diatom blooms within fluvial systems feeding into the Bay of Fundy also influence food-resource distribution within the embayment system. No research was found to support or reject this hypothesis, and further research on a regional scale may provide insight onto the food-resource availability throughout the Bay of Fundy.

COMPARISON TO *TRYPANITES*-TYPE ICHNOFACIES AT ARCADIA BEACH STATE PARK, OREGON

The modern examples of *Trypanites*-type ichnofacies at Lion Rock, Arcadia Beach State Park, Oregon (discussed within Chapter 2 of this thesis) and near Thomas Cove, Nova Scotia (discussed herein) represent two different examples of bored siliciclastic hardground. Both localities exhibit high densities of borings, with a maximum of ~3560 borings / m^2. A diverse assemblage of encrusting and squatting/clinging organisms also occurs on the bored surfaces. Over 40 species of organisms were identified at Lion Rock and over 30 occur at Thomas Cove. The distributions of these organisms differ greatly between the two localities based on four fundamental environmental differences. First, Lion Rock is located along the Pacific Coast within a microtidal, intertidal, foreshore setting, whereas Thomas Cove occurs within the megatidal, estuarine embayment of the Bay of Fundy along the Atlantic coast. The difference in oceanic and tidal settings dictates what species of organisms can reside within the two localities. Secondly, Lion Rock is located within a temperate environment and does not experience winter freezing that is seem in the Bay of Fundy (sub-polar environment). The lack of ice during the winter at Lion Rock prevents a mass die-off to occur, making the biotic community more stable and consistent throughout the year. The environmental differences of the two localities may greatly influence food-resources and impact organism distribution. Thirdly, Thomas cove has a significant amount of suspended sediment within the water column during high tide as compared to Lion Rock. This can prevent suspension feeding organisms with delicate feeding apparatuses from residing within the Bay of Fundy. Lastly, Lion Rock is a sea stack and provides a vertically oriented substrate for biotic settlement, whereas Thomas Cove is an expansive horizontal surface of multiple terraces of different elevations. Distinct littoral zones are formed at Lion Rock due to the vertical nature of the substrate and the environmental condition within the microtidal setting. However, the *Trypanites*-type ichnofacies at Thomas Cove lack distinct littoral zonation and organism distribution is dependent on water energy and sediment veneer. The Bay of Fundy is megatidal and all depositional subenvironments are submerged and exposed twice a day, thus preventing distinct littoral zones from forming. Although significant environmental differences dictate the distribution of biota, the diversity at both localities greatly exceeds reported diversity of ancient *Trypanites* ichnofacies communities (Palmer, 1982; Gibert et al., 1998; Johnson and Baarli, 1999; Bromley, 2004).

IMPLICATIONS FOR THE ROCK RECORD

The modern analog near Thomas Cove demonstrates an extensive *Trypanites*-type community characterized by a much higher diversity and abundance than examples within the rock record (e.g. Palmer, 1982; Gibert et al., 1998). This study documented over 30 species of encrusting and squatting/clinging organisms and two boring bivalves that reside along the surfaces. Similar findings are found within other modern settings (see Chapter 2). Although paleontology and ichnology frequently rely on neoactualism for interpreting ancient successions, many organisms have a low preservation potential, which conceals the true diversity of many ancient marine communities. *Trypanites* ichnofacies are typically associated with erosive processes in high-energy environments, which do not favor biotic preservation processes (Gibert et al., 2012). Therefore, organisms that modify the substrate are most likely to be preserved whereas those that encrust upon the substrate have much lower preservation potential.

Few species of organisms can bore within fully lithified substrates (Johnson and Baarli, 1999; Taylor and Wilson, 2003; Bromley, 2004; Gibert et al., 2012). Of those that do, similar traces are commonly produced and thus ichnotaxonomic diversity makes a poor proxy for assessing biotic diversity. Within this study, two species of bivalves, *Petricola pholadiformis* and *Zirfaea pilsbryi*, mechanically produce *Gastrochaenolites*-type traces. Within similar modern studies, up to four species of boring bivalves can produce similar traces and reside within close proximity to each other (Chapter 2). When organisms are not preserved as body fossils, interpretations of biotic diversity are based solely on traces fossil diversity, which in *Trypanites*-type communities grossly underrepresents the true diversity associated with the surface. Additionally, eroded *Gastrochaenolites* borings preserved within the rock record may resemble other described traces. Taxonomic variance of clustered *Gastrochaenolites* may appear similar to remnant or eroded *Balanoglossites*-type sacs, but this would be a secondary interpretation at best. Thus, further complicating the identification of traces and tracemakers associated with *Trypanites* ichnofacies.

The *Trypanites*-type assemblage near Thomas Cove is an exceptional exemplar of an extensive, bored siliciclastic hardground, few of which been reported from the rock record (further discussed within Chapter 2). Extensive *Trypanites* ichnofacies are rarely documented (i.e. Ledesma-Vázquez and Johnson, 1994; Cachão, 2009) and bored surfaces are frequently limited to a few outcrops within relative small geographic area. At Thomas Cove, the *Trypanites*-type assemblage extends over a 120,000 m^2 (0.12 km^2) area within the studied area and is made up of multiple surfaces of various elevations. Bored surfaces of multiple elevations result from different bedrock and environmental characteristics and have the potential to be preserved within the rock record as one or multiple surfaces. Additionally, *Trypanites*-type surfaces may coexist with soft ground ichnofacies, forming complex ichnocoenose.

This study provides a specific glimpse in time for describing *Trypanites*-type ichnofacies. It is uncertain how this study area would change on the scale of decades and centuries. Currently, eleven depositional sub-environments are present within the study area and some have distinct boundaries between areas of bored and unbored substrate (CF, DCOD, ITSF, TP, etc.), whereas other areas have more gradual boundaries (UP, ITMF, LP). Abrupt facies boundaries, sporadic boring distribution, multiple levels of bored substrates and ichnocoenosis are common throughout the study area. The migration and preservation of the depositional sub-environments remains unknown and the identification of depositional sub-environments may be impossible within the rock record. However, it is important to recognize the biotic and sedimentologic potential of *Trypanites* ichnofacies

CONCLUSIONS

Thomas Cove is a modern example of an extensive, siliciclastic *Trypanites*-type ichnofacies. Two species of bivalves, *Petricola pholadiformis* and *Zirfaea pilsbryi*, produce an ichnocoenosis of *Gastrochaenolites*-type traces produced by multiple generations of borers on multiple surfaces of different elevations. Forms produced are similar to the ancient traces of *Gastrochaenolites turbinatus* and *Gastrochaenolites ornatus* and are produced by *P. pholadiformis* and *Z. pilsbryi* respectively. Extensive hydrodynamic erosion widens and exposes boring chambers to the surface. Borings have a patchy distribution within multiple elevations inside a small geographic area, and have the potential to be preserved as multiple surfaces within the rock record. Over 30 species of boring, encrusting and squatting/clinging organisms occur within the eleven depositional sub-environments within the study area and each exhibits distinctive sedimentary structures, soft sediment traces, borings and biota, which are dependent upon physical parameters of the different sub-environments. The modern analog of a *Trypanites*-type ichnofacies at Thomas Cove reveals that bored hardground ichnofacies within the rock record can be made up of multiple surfaces and represent communities with higher diversity and abundance of biotic communities than previously described.

CHAPTER 4: SUMMARY AND CONCLUSIONS

This thesis investigates *Trypanites*-type ichnofacies at two North American localities, to identify the ecology, neoichnology, sedimentology and environmental conditions surrounding siliciclastic, bored hardgrounds. *Trypanites* ichnofacies throughout geological time have been hypothesized as having a generally low biological diversity and are frequently associated with erosional exhumed substrates and erosional disconformities (Bromley, 1975; Frey and Seilacher, 1980; Brett, 1988; Pemberton, 2003; Gibert et al., 2012). However, this study provides deeper insights into the variety of biota and sedimentary processes associated with these ichnofacies. A summary of major findings from the two localities is provided as Table 4-1.

Lion Rock is a sea stack composed of Eocene age Astoria Formation sandstone (Angora Peak Member) and Columbia Flood Basalt (Grande Ronde Basalt, Ortley Unit), which is located within the foreshore of Arcadia Beach State Park, Oregon. Exposed tide- and wave-wetted sandstones are bored and the exposed basalts are not. Borings are produced by *Adula californiensis*, *Hiatella arctica*, *Penitella penita* and *Zirfaea pilsbryi*. All bivalves produce traces similar to the trace fossils *Gastrochaenolites turbinatus*, except *Hiatella arctica*, which produces forms similar to the ancient trace of cf. *Gastrochaenolites lapidicus*. Five littoral zones are present (supra-, upper-, middle-, lower- and sublittoral), whereupon over 40 species of boring, encrusting and squatting/clinging biota reside. The newly established sublittoral zone is described here as being the lowermost littoral zone and is greatly influenced by shifting foreshore sand, which prevents the majority of biota from residing within this area. *Gastrochaenolites*-type traces are present within the sublittoral and lower littoral zones, and infrequently within the lower portion of the middle littoral zone. Occupied traces are present within the sublittoral and lower littoral zones, but the distribution of occupied *versus* unoccupied borings cannot be determined due to the endolithic nature of the boring bivalves. Where *Gastrochaenolites*-type traces are eroded, the internal chamber can be exposed to the surface. The bowl shaped, eroded chambers provide macro-habitats, wherein multiple species and multiple individual organisms can be present. It is hypothesized that the *Gastrochaenolites*-type traces increase the surface area in which organisms can inhabit, provide a smooth surface for attachment and offer

	Lion Rock	Thomas Cove
Location	Pacific Coast; Oregon	Atlantic Coast; Bay of Fundy, Nova Scotia
Climatic Zones	Temperate	Sub-polar
Environmental Setting	Wave exposed, sea stack on the intertidal foreshore	Multiple elevated terraces of exposed bedrock within an estuarine embayment
Tidal Setting	Microtidal	Megatidal
Salinity	Fully marine	Fully marine
Bedrock Substrate	Astoria Formation sandstone (Angora Peak Member)	Wolfville Formation; Sandstone and silty mudstone
Boring Bivalves	*Adula californiensis* *Hiatella arctica* *Penitella penita* *Zirfaea pilsbryi*	*Petricola pholadiformis* *Zirfaea pilsbryi*
Ancient equivalent to modern forms	*Gastrochaenolites turbinatus* *Gastrochaenolites lapidicus?*	*Gastrochaenolites turbinatus* *Gastrochaenolites ornatus*
Maximum Density of Borings within a 15 cm by 15 cm area	80	20
Controls on borings	Lithology Water depth Water energy Shifting sediment	Salinity Water energy Substrate type
Diversity of encrusting and squatting/clinging organisms	42 species	35 species
Soft sediment traces (ancient equivalent to modern forms)	N/A	*Arenicolites* *Aulichnites* *Coenobichnus* *Coenobichnus/Diplichnites* *Polykladichnus* *Psilonichnus* *Siphonichnus* *Skolithos* Stellet interface deposit feeding traces

Table 4-1. Major conclusions from Lion Rock and Thomas Cove.

protection to the organisms from breaking waves. The presence of these exposed *Gastrochaenolites*-associated chambers allow specific species of encrusting and squatting/clinging organisms (i.e. nudibranch, chitons, calcareous tube worms) to be present, whereas within areas of unbored substrate (i.e. two seaward, basalt sea stacks), macro-habitats are not present.

The *Trypanites*-type ichnofacies near Thomas Cove is located at Economy Point, Nova Scotia, within the Bay of Fundy. The ichnofacies is formed within the multiple elevated terraces of Triassic sandstone and silty mudstone of the Wolfville Formation. Traces produced are similar to the trace fossils *Gastrochaenolites turbinatus* and *Gastrochaenolites ornatus* and are produced by *P. pholadiformis* and *Z. pilsbryi* respectively. The ichnocoenosis is produced by multiple generations of borers on multiple surfaces of different elevations. In addition, over 30 species of boring, encrusting and squatting/clinging organisms are found within the eleven depositional sub-environments of the study area. Distinct littoral zones, which are present at Lion Rock, are absent due to the Bay of Fundy being megatidal and the study area being completely submerged and completely exposed on a daily basis. However, each sub-environment has distinctive sedimentary structures, soft sediment traces, borings and biota, which are resulted from physical parameters of the different sub-environments. Observations here suggest that shifting sediment thickness, sediment grain size, substrate type, water energy, water depth and salinity are all important parameters in determining where organisms can reside. Showing statistical interdependence of these parameters is a promising avenue of future investigation.

The two localities are environmentally very different (see Table 4-1) and three main factors render dissimilarities in the two *Trypanites*-type ichnofacies. Firstly, Thomas Cove has more shifting sediment over the studied area than seen at Lion Rock. Shifting sediment veneers form sedimentary structures and sediment thickness, which likely mitigates larval recruitment. Areas covered by sediment can be unbored, as seen at Thomas Cove, or can be previously bored, like at Lion Rock. Although *Trypanites* ichnofacies are associated with erosional processes, shifting sediment can be locally present. Secondly, climatic controls associated with the two localities ascribe to differences in temperature and seasonal patterns. The Bay of Fundy is considered a sub-polar environment, and ice develops during winter and has major impacts on sedimentology, ichnology and infaunal communization (Dionne 1972; Knight and Dalrymple, 1975, 1976; Hicklin et al., 1980; Gordon and Desplanque, 1983; Desplanque and Bray, 1986; Woodworth-

Lynas, 1995; Desplanque and Mossman, 1998, Dionne, 1998; Pearson and Gingras, 2006; Dalrymple et al., 2011; Dashtgard et al., *in press*). Due to ice development, sedimentation is low and many invertebrates either hibernate or are killed in a mass die-off at the onset of winter (Hicklin et al., 1980; Dashtgard et al, *in press*). Whereas, the Oregon coast has a temperate climate and no ice forms within the foreshore and sea stack environment to influence colonization and sedimentation. However, it is likely that the shifting foreshore sand at Arcadia Beach is greatly influenced by winter storms, which may greatly influence biotic assemblages. Collecting data and observations on this would also be a promising avenue of future investigation. Lastly, coastal blooms of diatoms and algae provide a substantial food-recourse for organisms on the Oregon coast. This allows for a high diversity of organisms (46 reported species) to reside within and upon the sea stack. Food-resources are very different within the Bay of Fundy and it is uncertain if they are better or worse than that of the Pacific coast of Oregon. However, it is most likely that food-resources come from the ocean and are influenced with the tides and seasonal fluctuations. Thomas Cove has a slightly lower diversity of organisms (37 species observed), which may be reflective of food availability. This idea has yet to be tested by the science community and may lead to data, which supports this and other research projects. In the rock record, then, boring distributions and biotic diversities may be influenced by many of the aforementioned factors, and it is still unclear how to resolve this multidimensional interdependency.

The overall biotic diversity is moderately high within the two study areas (Table 4-2), but the majority of organisms have a low preservation potential within the rock record, which makes the identification of ancient *Trypanites* assemblages be based solely on trace fossils. The diversity of trace fossils associated with the modern bored hardground is variable, but multiple organisms make very similar traces. Within this study, *Adula californiensis*, *Hiatella arctica*, *Penitella penita*, *Petricola pholadiformis* and *Zirfaea pilsbryi* all produce *Gastrochaenolites*-type traces, and can reside within close proximity to one another within their respective localities. At ancient localities, it is almost impossible to identify the boring taxon beyond class where body fossils are not present, which diminishes our ability to assess the biodiversity represented by the fossil assemblage. Likewise, encrusting and squatting/clinging organisms are rarely preserved, which further hinders the evaluation of diversity of ancient *Trypanites*-associated assemblages.

The modern *Trypanites*-type ichnofacies studied within this thesis demonstrate that bored hardgrounds represent a much more vibrant and dynamic environment

	Lion Rock	Thomas Cove
Annelid	*Amphiporus imparispinosus* *Eudistylia vancouveri* *Phylloplana viridis* *Serpula columbiana* *Tubulanus polymorphus*	*Cerebratulus lacteus* *Enchytraeus* sp. *Glycera* sp. *Heteromastus* sp. *Lanice* sp. *Nereis* sp.
Arthropod	*Balanus glandula* *Carcinus maenas* *Chthamalus dalli* *Hesperibalanus hesperius* *Ligia pallasii* *Pagurus hirsutiusculus* *Pentidotea wosnesenskii* *Pollicipes polymerus* *Semibalanus cariosus*	*Cancer irroratus* *Carcinus maenas* *Chthamalus fragilis* *Corophium volutator* *Eualus* sp. *Libinia dubia* *Lysianopsis alba* *Pagurus* sp.
Bryozoan	Encrusting bryozoan	*Flustra foliacea*
Chordate	*Oligocottus maculosus* *Styela montereyensis*	*Myoxocephalus scorpius*
Cnidarian	*Anthopleura elegantissima* *Anthopleura xanthogrammica*	
Echinoderm	*Pisaster ochraceus*	
Mollusca	*Acanthodoris nanaimoensis* *Adula californiensis* *Aeolidia papillosa* *Diodora* sp. *Hermissenda crassicornis* *Hiatella arctica* *Katharina tunicata* *Lirabuccinum dirum* *Littorina* sp. *Lottia* sp. *Mopalia muscosa* *Mytilus californianus* *Mytilus trossulus* *Nucella* sp. *Penitella penita* *Zirfaea pilsbryi*	*Acmaea testudinalis* *Buccinum undatum* *Crepidula fornicata* *Littorina saxatilis* *Lunatia heros* *Macoma balthica* *Mya arenaria* *Nassarius truvuttatus* *Petricola pholadiformis* *Zirfaea pilsbryi*
Porifera		*Didemnum* sp. *Microciona prolifera*
Plants	*Calliarthron* sp. *Cladophora* sp. *Endocladia muricata* *Hedophyllum sessile* *Lithothamnion* sp. *Mastocarpus papillatus* *Mazzaella parksii* *Mazzaella splendens* *Ulva intestinalis* *Ulva lactuca*	*Ascophyllym nodosum* *Chondrus crispus* *Clathromophum* sp. *Corallina officinals* *Cystoclonium purpureum* *Fucus vesiculosus* *Palmaria palmata* *Spingomorpha* sp. *Ulva lactuca*

Table 4-2. Flora and fauna from Lion Rock and Thomas Cove.

than inferred from the rock record. A high diversity and abundance of boring, encrusting and squatting/clinging organisms can reside within and on the hardground, and multiple species of bivalves can produce seemingly similar traces within a relatively small area. Sedimentation can also occur on the erosive surface and influence settlement and growth of organisms. From these modern analogs, a higher diversity and abundance of organisms and sedimentary traces can be affiliated with *Trypanites* ichnofacies within the rock record.

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Appendix A: Collection Permit

Oregon Parks and Recreation Department
Scientific Research Permit Application
Instructions

Nature
HISTORY
Discovery

The Oregon Parks and Recreation Department (OPRD) welcomes interest in conducting scientific research on lands owned and managed by the department. Scientific studies designed to increase the understanding of ecological processes and resources on state park lands are a valuable source of information for park and resource managers.

OPRD intends to cooperate with organizations and institutions when their scientific research is compatible with the department's mission of land stewardship through the protection of ecological processes and natural resources.

A scientific research permit is required for most scientific activities pertaining to natural and cultural resources that involve specimen collection, field work, or that may have the potential to disturb natural and cultural resources on OPRD owned or managed lands.

All requests for permit to conduct scientific research and/or collection must be submitted on a current "Oregon Parks and Recreation Department Scientific Research Permit Application" form (Available in Adobe or Microsoft Word formats).

Instructions:

- Complete all appropriate blocks/lines. Applications must be typewritten with original signatures. A complete application prevents delays!
- Sign the application in ink and send an original to the address at the bottom of the application. Faxed copies will not be accepted.
- Attach to application a USGS topographic map and aerial photo with precise location of proposed work.
- We recommend that applications be submitted at least 60 days in advance of the first planned field activity.
- Permits may be issued for multiple years.

Mail Applications to:
Oregon Parks and Recreation Department
Attention: Natural Resource Section
725 Summer Street, NE Suite C
Salem, Oregon 97301

For further Information Contact:
Sara Griffith, Natural Resource Assistant
(503) 986-0737
sara.griffith@state.or.us

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Permit # Permit #031-13 Permit Expires: August 31, 2014

Oregon Parks and Recreation Department
Scientific Research Permit Application

Instructions: Applications must be typewritten with original signatures. The precise location of the proposed work must be shown on an USGS topographic map and aerial photo. Application should be sent to the department's Salem office.

Please allow for a minimum of 30 days to process the permit application.

Applicant's Name:	Carolyn Furlong
Title:	Graduate Student
Affiliation:	University of Alberta
Address:	114 Street 89 Ave NW Edmonton, AB P6G 2M7
City/State/Zip:	Edmonton, AB P6G 2M7
Telephone Number:	780-700-8055
Fax Number:	
E-mail address:	cfurlong@ualberta.ca

Names of others involved in project/study, including names and phone numbers of all collectors:

Carolyn Furlong, 780-700-8055	
Sarah Schultz, 780-868-4340	
John Paul Zonneveld, 780-492-3287	

☒ Resume or curriculum vitae for principal investigator and all field staff attached (required)

Permit # 031-13 Permit Expires: August 31, 2014

PROJECT DESCRIPTION:

Include: Purpose, method of investigation, method of collection, species to be investigated and/or collected, steps to be taken to minimize impact, location and duration of project. Please include a project proposal if available. However, please do not simply say, "see attached", include a brief project summary in the space provide below.

The project to be done at Arcadia State Park, Oregon (between the dates of October 1 and 15, 2013) is to analyze, observe and describe the boring bivalves, *Adula californiensis* and *Penitella penita*, within Lion Rock and use this environment as a modern analog for the rock record. Bored rock (hardground) surfaces, known as a *Trypanites* ichnofacies, within the rock record have been described as representing environments with low diversity. However, Lion Rock reveals a bored surface with high diversity, with many organisms that are not typically preserved within the rock record. The goal of this research is to provide an ecological analysis of Lion Rock and to describe the diversity of organisms living there. Methods used within this study include photography, written description and observations, and counting organisms within a specific sized area (1 square foot). Collection of rocks and organisms will be needed to analyze the size and shape of the borings, but collecting will be limited to pieces of rock previously broken from the main sea stack itself. Collection of organisms will be limited to the boring bivalves *Adula californiensis* and *Penitella penita*, however the study will examine all organisms living on Lion Rock, which have been listed on an attached Specimen Collection sheet. A surplus of plants and animals will not be removed or relocated in order to minimize the impact of the study.

SAMPLE/SPECIMEN COLLECTION:

☒ Plant ☐ Soils ☐ Fungi ☐ Seeds ☐ Water ☒ Animal ☒ Rock
☐ Other (specify): ______

If Plant/Animal – Identify the Species to be researched or collected:

Name of Species See attached Specimen Collection list

Is/are the species a:

Federal endangered or threatened species?	Yes ☐ No ☒	
Federal candidate species?	Yes ☐ No ☒	
State endangered or threatened species?	Yes ☐ No ☒	
State sensitive or candidate Species?	Yes ☐ No ☒	

Voucher specimens will be deposited at: The University of Alberta

Permit # 031-13 Permit Expires: August 31, 2014

Will the project involve ground disturbance: Yes ☐ No ☒

Additional Permits:

Are additional federal or state permits required? Yes ☐ No ☒

If so, please list and provide a copy of each permit:

Area for Proposed Study:

Please note that OPRD's jurisdiction includes all state parks AND that portion of Oregon's coastal zone from extreme low tide to the statutory or actual vegetation line, whichever is most landward and ¼ mile on each side of the river of all state designated Scenic Waterways.

The area of interest within this study is Lion Rock on Arcadia Beach, Oregon. The sea stack is located at the northern most end of Arcadia Beach. Here, the boring bivalves, *Adula californiensis* and *Penitella penita*, resides within cavities that the organism forms by mechanically digging, grinding and boring into the rocks.

Dates of Proposed Study: Project Begin Date/Project End Date

October 1 – 15, 2013	August 31, 2014	

Permit # 031-13 Permit Expires: August 31, 2014

Scientific Research Permit

Standard Permit Conditions and Restrictions

Nature
HISTORY
Discovery

By acceptance of this permit, Permittee agrees to abide by the following conditions:

1. All activities shall comply with applicable federal, state, and local laws, regulations, and ordinances. Any necessary federal, state, or local permits shall be obtained prior to the beginning of the activity. Copies of those permits must be provided to the Park Manager before work begins.
2. The Permittee assumes full responsibility and liability for any damages or injury to any member of the public arising out of the activity, including personal injury and property damage, and for any damage to park property.
3. The Permittee shall indemnify and hold harmless the State of Oregon, its Parks and Recreation Commission and members thereof, the State Parks and Recreation Department, and its officer, agents, and employees against any and all damages, claims, or causes of action arising from or in connection with the activity.
4. The study shall be completed only in those areas identified in the permit application and as identified on a 1:24,000 scale USGS map with a circle drawn around the proposed study area.
5. The Permittee shall carry a copy of this permit at all times while on OPRD property, and must be able to show the permit to OPRD staff upon request.
6. The collections allowed under this permit shall be used for scientific purposes only, shall be dedicated to the public benefit, and shall not be used for commercial purposes.
7. Except for the resources indicated in the permit, the taking or disturbing of resources is specifically prohibited.
8. Any holes dug must be refilled. All holes must be dug with a shovel or a hand auger.
9. The collection of plants shall not occur within 200 feet of any road, parking lot, trail, campground, picnic area, or restroom, unless the collecting site is completely screened from view, in which case 100 feet will be the minimum distance.
10. No more than 1% of the population will be collected (i.e., one out of every hundred individuals). Permittee will use scientific judgment and will collect specimens only from populations that can tolerate collection without jeopardizing the viability of that population.
11. The Permittee shall submit a summary of the information gathered to the Park Manager where the investigations took place, and to the OPRD Natural Resource Section in Salem, Oregon. The Department further requires that the Permittee shall provide to the Department any materials published because of this permit.
12. Contact the Park Manager(s) at least 24 hours prior to each occurrence of the permitted activity.
13. OPRD reserves the right to cancel this permit for any reason.
14. For activities on the ocean shore, a special drive-on-beach permit is needed for any areas closed to motor vehicles.
15. If any cultural material is discovered during a project, all work and operations must stop immediately and the OPRD archeologist must be contacted to assess the discovery. Contact Nancy Nelson-OPRD Archeologist @ (503) 986-0578.

Permit # 031-13 Permit Expires: August 31, 2014

Special Conditions

[X] Special conditions apply: [X] As follows [ ] See attached

Make sure ODFW has been contacted to see if you need a permit to remove living invertebrates.

I, the undersigned, have read and hereby agree to the conditions and restrictions listed above. I further understand that the department may impose special conditions. I hereby agree to abide by any special conditions if this permit is granted.

Carolyn M Furlong	Carolyn M Furlong	9/5/13
Signature of Applicant	Printed Name of Applicant	Date

This permit has been [X] approved with conditions [ ] denied

Sara Griffith	Sara Griffith, Stewardship Admin	11/19/13
OPRD Staff Signature (NR Staff)	Printed Name and Title	Date
Matt	Matt Rippee, Park Manager	11/19/13
OPRD Staff Signature (Park Manager)	Printed Name and Title	Date

Applicant must carry this permit at all times while on state park owned or managed properties

Return to:
Oregon Parks and Recreation Department
Attn: Natural Resource Section
725 Summer Street NE, Suite C
Salem, OR 97301

Updated 01/2010

Appendix B: Oregon Organisms

Preface

Identification of organisms present within this appendix do not necessary represent a rigorous taxonomic investigation. Thus, the appendix should be used as a reference and not a taxonomic assessment of biota present at Arcadia Beach State Park, Oregon.

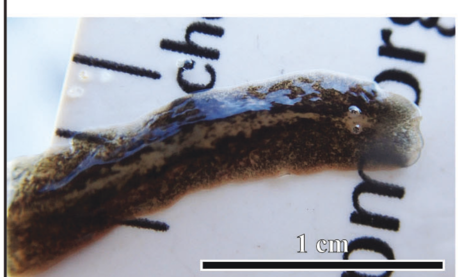
Appendix B: Oregon Organisms

Annelid

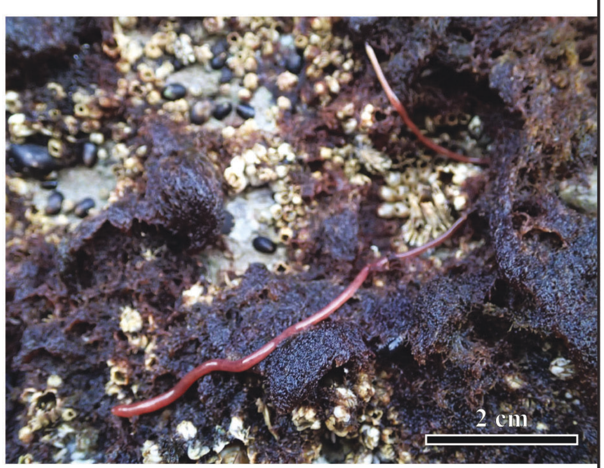
Northern feather-duster Worm
Eudistylia vancouveri

Red trumpet calcareous
Serpula columbiana

Pink-frosted ribbon worm
Amphiporus imparispinosus

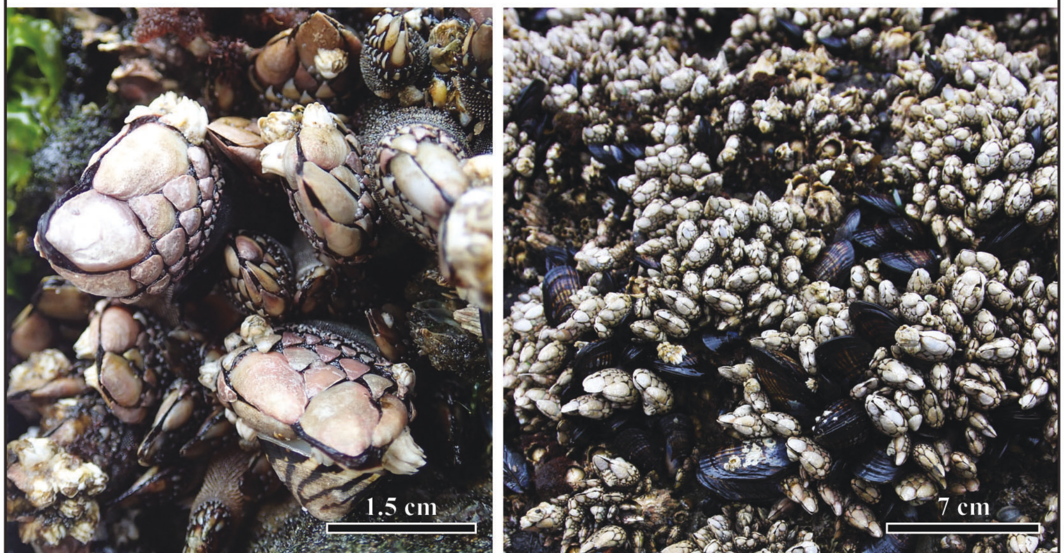


Green flatworm
Phylloplana viridis

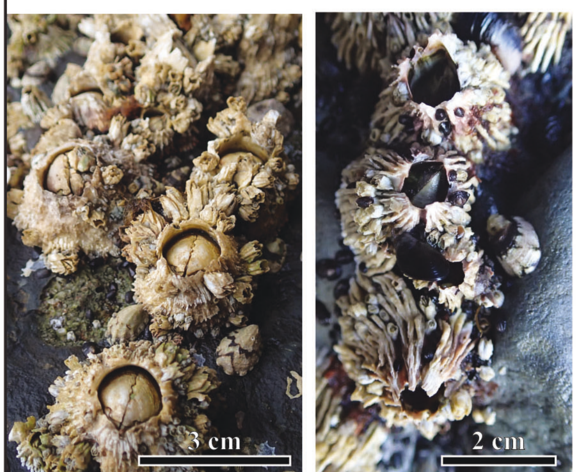


Red ribbon worm
Tubulanus polymorphus

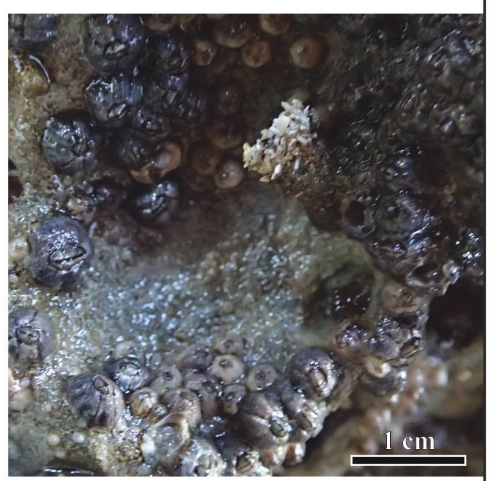
Arthropod



Gooseneck barnacles
Pollicipes polymerus



Thatched baranacles
Semibalanus cariosus



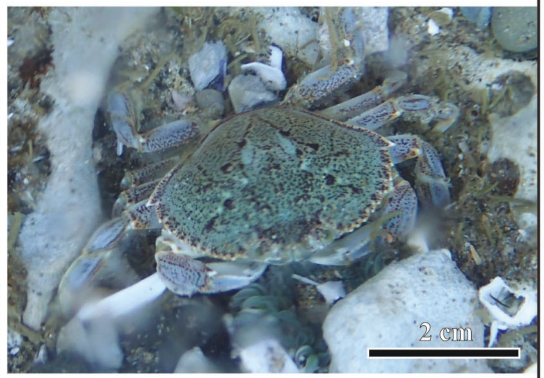
Little brown barnacles
Chthamalus dalli

Shell barnacle
Hesperibalanus hesperius

Acorn barnacle
Balanus glandula

Arthropod

Hairy hermit
Pagurus hirsutiusculus



Green crab
Carcinus maenas

Rock louse
Ligia pallasii

Vosnesensky's isopod
Pentidotea wosnesenskii

Bryozoan

Encrusting bryozoan

Chordate

Tidepool sculpin
Oligocottus maculosus

Long-stalked sea squirt
Styela montereyensis

Cnidarian

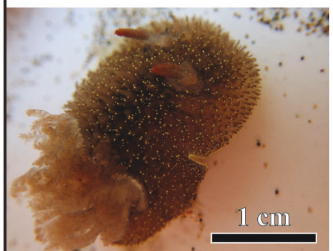
Aggregating anemone
Anthopleura elegantissima

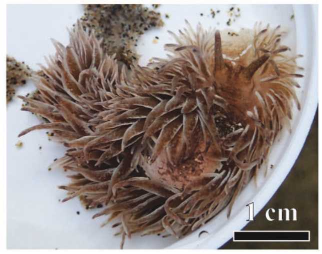
Green surf anemone
Anthopleura xanthogrammica

Echinoderm

Purple Star
Pisaster ochraceus

Mollusca

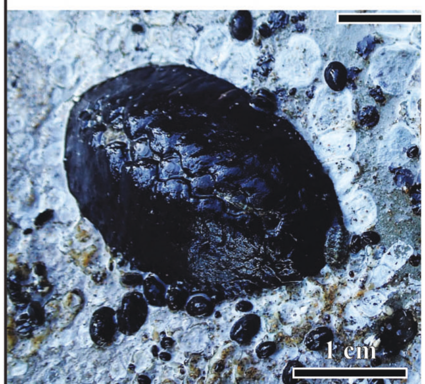


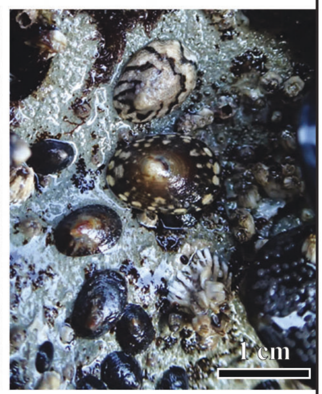


Rufus tipped nudibranch
Acanthodoris nanaimoensis

Shag rug nudibranch
Aeolidia papillosa

Opalescent nudibranch
Hermissenda crassicornis





Black katy chiton
Katharina tunicata

Mossy chiton
Mopalia muscosa

Limpets
Lottia sp., *Diodora* sp.

Gastropods
Littorina sp., *Nucella* sp.

Dire whells
Lirabuccinum dirum

Gastropods
Littorina sp., *Nucella* sp.

Mollusca

California mussel
Mytilus californianus

Pacific blue mussel
Mytilus trossulus

Artic hiatella
Hiatella arctica

California datemussel
Adula californiensis

Rough piddock
Zirfaea pilsbryi

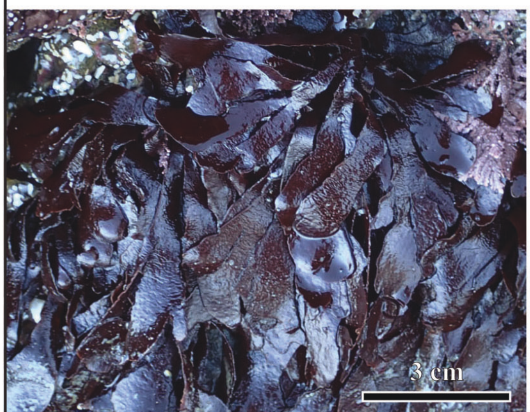
Flat-tip piddock
Penitella penita

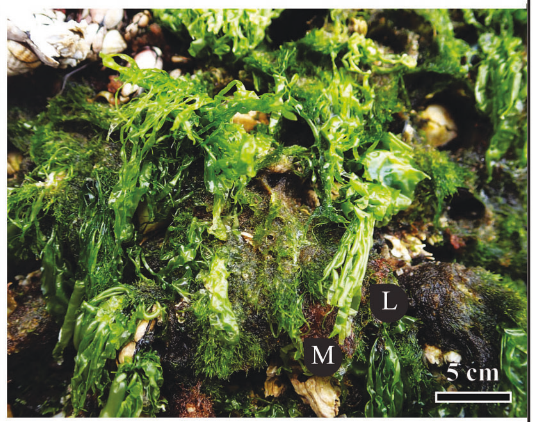
Siphons of boring bivalve (specific taxa unknown)

Flora

Yellow seaweed
Mazzaella parksii

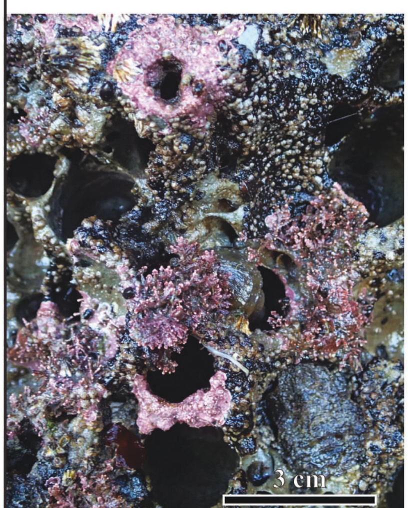
Nail brush seaweed
Endocladia muricata





Iridescent seaweed
Mazzaella splendens

Maiden-hair sea lettuce (L) & Sea moss (M)
Ulva intestinalis & *Cladophora* sp.

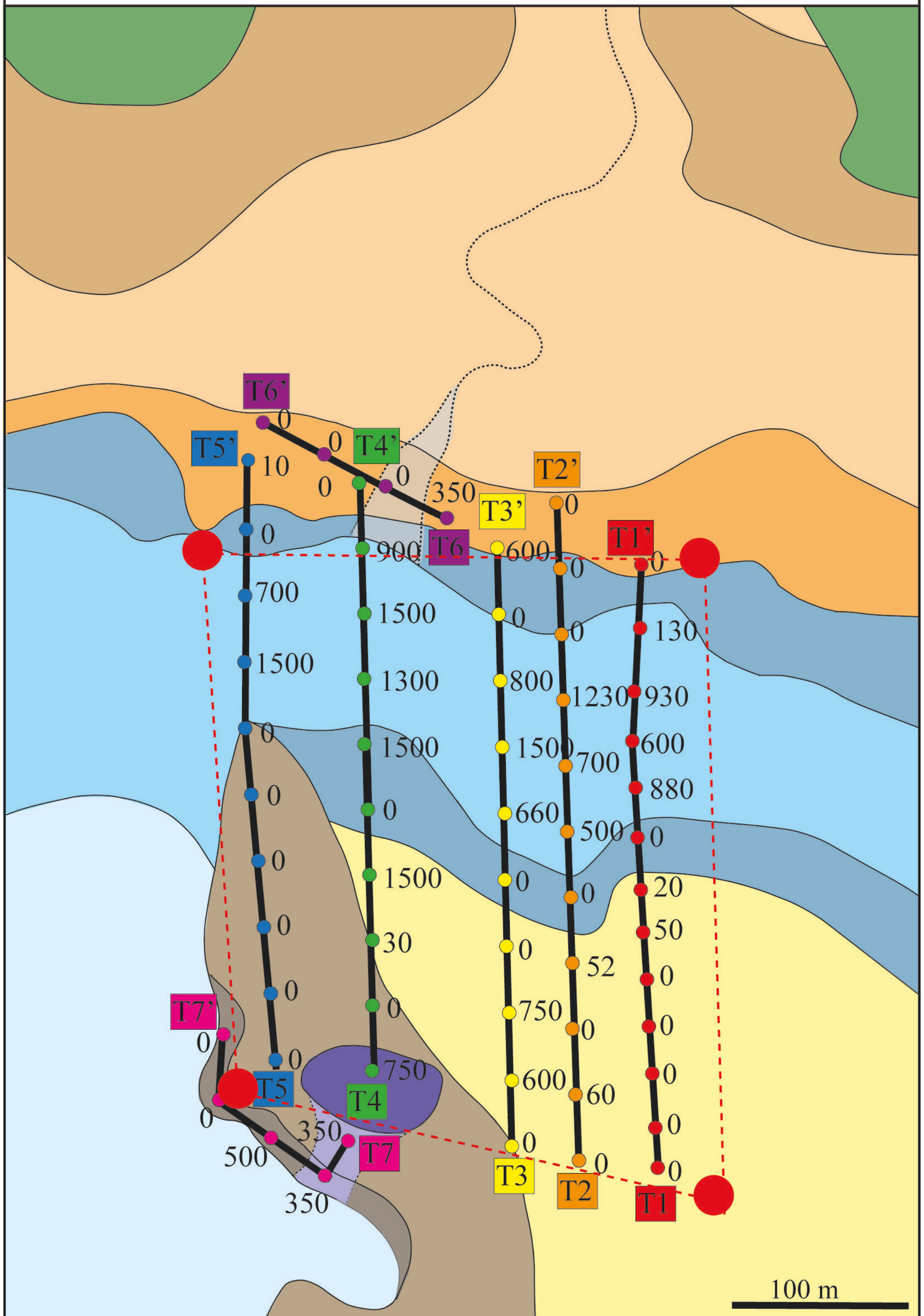


Coralline algae
Lithothamnion sp. & *Calliarthron* sp.

Common sea lettuce (C) & Papillate seaweed (P)
Ulva lactuca & *Mastocarpus papillatus*

Sea cabbage (S)
Hedophyllum sessile

Appendix C: Bay of Fundy Transect Data



Appendix Figure C1. Bay of Fundy study area and associated transects. All transect data collection points are 30 m apart, beside Transect 1, points 1-10, which has data points 25 m apart. Data collected at each point is recorded in Appendix Table C1. Depositional sub-environment colors and symbols used are listed within "List of Symbols" section of this thesis.

Transect	Point	Depositional sub-environment	Boring taxa	Number of borings per $1m^2$
T1	1	ITSF	--	--
	2	ITSF	--	--
	3	ITSF	--	--
	4	ITSF	--	--
	5	ITSF	--	--
	6	ITSF	P & Z	50
	7	ITSF	P & Z	20
	8	CF	--	--
	9	DCOD	P & Z	880
	10	DCOD	P & Z	600
	11	DCOD	P & Z	930
	12	DCOD	P & Z	130
T1’	13	LP	--	--
T2	14	ITSF	--	--
	15	ITSF	P & Z	60
	16	ITSF	--	--
	17	ITSF	P & Z	52
	18	CF	--	--
	19	DCOD	P & Z	500
	20	DCOD	P & Z	700
	21	DCOD	P & Z	1230
	22	CF	--	--
	23	CF	--	--
T2’	24	LP	--	--
T3	25	ITSF	--	--
	26	ITSF	P & Z	600
	27	ITSF	P & Z	750
	28	ITSF	--	--
	29	CF	--	--
	30	DCOD	P & Z	660
	31	DCOD	P & Z	1500
	32	DCOD	P & Z	800
	33	CF	--	0
T3’	34	LP	P	600

Appendix Table C1. See next page for table caption.

T4	35	TP	P	750
	36	R	--	--
	37	R	--	--
	38	ITSF	P	1500
	39	CF	--	--
	40	CF	P	1500
	41	DCOD	P & Z	1300
	42	DCOD	P & Z	1500
	43	DCOD	P & Z	900
T4’	44	LP	--	--
T5	45	R	--	--
	46	R	--	--
	47	R	--	--
	48	R	--	--
	49	R	--	--
	50	R	--	--
	51	DCOD	P & Z	1500
	52	DCOD	P & Z	700
	53	CF	--	--
T5’	54	LP	P	10
T6	55	LP	P	350
	56	DC	--	--
	57	LP	--	--
T6’	58	LP	--	--
T7	59	TPD	P & Z	350
	60	TPD	P & Z	350
	61	LER	P & Z	500
	62	LER	--	--
T7’	63	LER	--	--

Appendix Table C1. Data collected from transects within the study area at Thomas Cove, Economy, Nova Scotia, Canada. Transect and data points depicted in study area figure of Appendix C. Depositional sub-environments acronyms are denoted within “List of symbols” section of this thesis. Boring bivalve species include *Petricola pholadiformis* (P) and *Zirfaea pilsbryi* (Z). Boring densities are tabulated for abundance within a 1 m^2 area.

Appendix D: Bay of Fundy Organisms

Preface

Identification of organisms present within this appendix do not necessary represent a rigorous taxonomic investigation. Thus, the appendix should be used as a reference and not a taxonomic assessment of biota present at Thomas Cove, Economy Point, Nova Scotia.

Appendix D: Bay of Fundy Organisms

Annelid

Common clam worm
Nereis sp.

Milky ribbon worm
Cerebratulus lacteus

Murray Gingras
Homo sapiens (Chordate)

Sand worm
Lanice sp.

Photographs of *Enchytraeus* sp., *Glycera* sp. and *Heteromastus* sp. were not obtained.

Arthropod

Little gray barnacles
Chthamalus fragilis

Shrimp
Eualus sp.

Amphipod
Lysianopsis alba

Mud shrimp
Corophium volutator

Hermit Crabs
Pagurus sp.

Rock Crab
Cancer irroratus

Green Crab
Carcinus maenas

Common spider crab
Libinia dubia

Bryozoan

Leafy bryozoan
Flustra foliacea

Chordate

Short fin sculpin
Myoxocephalus scorpis

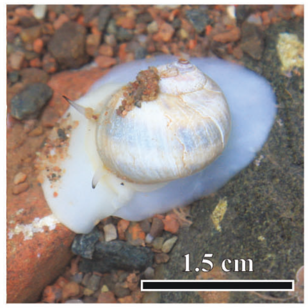
Porifera

White crust
Didemnum sp.

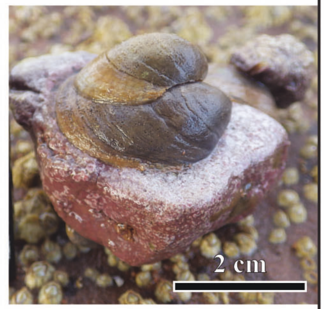
Red beard sponge
Microciona prolifera

Mollusca

Rough periwinkle
Littorina saxatilis

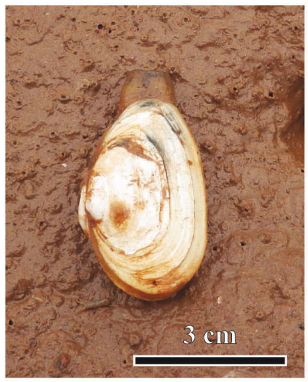


Moon snail
Lunatia heros



Common slipper shell
Crepidula fornicata

Baltic clam
Macoma balthica



Soft shell clam
Mya arenaria

False angel wing piddock
Petricola pholadiformis

Siphons of bivalves (specific taxa unknown)

Rough piddock
Zirfaea pilsbryi

Gastropod shell overlay
Littorina saxatilis, Nassarius trivittus, Buccinum undatum

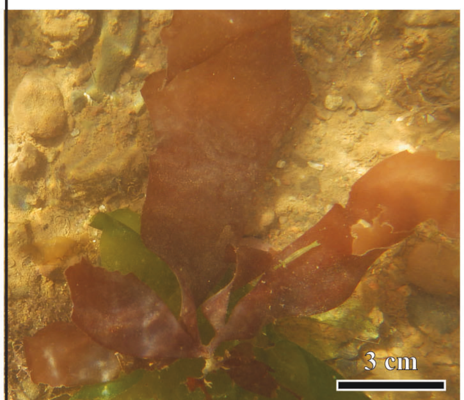
Photographs of *Acmaea testudinalis* were not obtained.

Flora

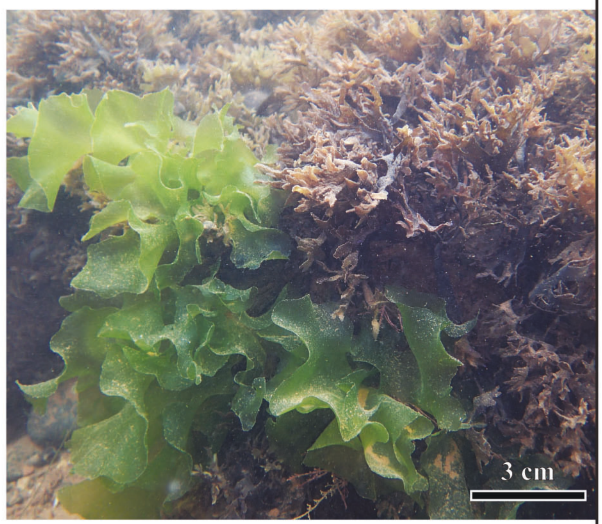
Sea moss
Spingomorphia sp.

Rock Weed
Fucus vesiculosus

Knotted wrack
Ascophyllum nodosum

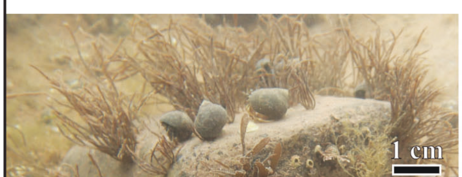


Ribbon weed
Palmaria palmata



Common sea lettuce
Ulva lactuca

Irish moss
Chondrus crispus



Bushy red weed
Cystoclonium purpureum

Branching corraline algae
Corallina officinalis

Corraline red algae
Lithothamnion sp.