THREAD DRIFTING BY JUVENILE BIVALVES IN THE COOS BAY ESTUARY, OREGON: SPECIES IDENTIFICATION AND THE INFLUENCE OF ESTUARINE HYDRODYNAMICS AND DIEL MIGRATION

by

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THESIS APPROVAL PAGE

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THESIS ABSTRACT

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Title: Thread Drifting by Juvenile Bivalves in the Coos Bay Estuary, Oregon: Species Identification and the Influence of Estuarine Hydrodynamics and Diel Migration

From September 2009 to July 2011 I collected vertically stratified zooplankton samples and recorded estuarine water parameters on a monthly basis in the Coos Bay estuary, Oregon during flood and ebb tides. I identified five taxa of juvenile bivalves in the plankton: *Macoma* spp., *Siliqua* spp., *Clinocardium nuttallii*, *Mytilus* spp. and individuals from the superfamily Tellinoidea. The presence/absence of juvenile bivalves in the plankton was influenced by Julian Day, a result of reproductive cycles. The abundance of *Macoma* spp. was significantly higher during ebb tides while *Mytilus* spp. were significantly more abundant during flood tides. Estuarine hydrodynamic data suggested that other taxa were more abundant during ebb tides. An interaction between diel variation and tidal cycle was observed during the twenty-four hour cruises. Juvenile *Mytilus* spp. were more abundant in the plankton during flood tides during the day, and all other taxa were more abundant during ebb tides at night likely a result of predator avoidance. Thread drifting during ebb tides was more favorable than during flood tides due to the increased current speed.

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CHAPTER I

GENERAL INTRODUCTION

Complex life cycles are a common trait among many marine invertebrate phyla including Echinodermata, Arthropoda, Annelida, and Mollusca. The cycle begins with eggs and sperm being shed into the water, fertilization occurs and the embryo develops in the water column. In some cases internal fertilization occurs and the embryo is brooded until a later stage of development and then released. Once in the water column larvae can be lecithotrophic, subsisting off yolk reserves, or planktotrophic in which they spend time feeding in the water column. Larvae go through a metamorphic process and settle onto the benthos and occupy these habitats as adults.

Some species have the ability to re-enter the plankton as juveniles. For example, Armonies and Hartke (1995) collected juvenile *Hydrobia ulvae,* a European mud snail, in the plankton. Several species of juvenile gastropods including *Lacuna* spp., *Littorina* spp. and *Nucella* spp. were collected above the benthos in Vancouver Island, British Columbia (Martel and Chia 1991). During laboratory experiments juvenile *Nereis diversicolor* and *Streblospio benedicti,* polychaetes, were observed emigrating from the benthos (Armonies 1988; Stocks 2002). Bivalves are common among species that have the ability to re-enter the plankton as juveniles. Baggerman (1953) observed post-metamorphic *Cerastoderma edule,* the European cockle, in areas which had been previously cleared and Bayne (1964) documented large populations of post-larval *Mytilus edulis* entering the water column.

The mechanism of how juvenile clams, with no swimming organ, enter the water column became better understood about a decade later. Sigurdsson *et al.* (1976) observed post-larval bivalves drifting in the water column via a long mucous thread and since this time this behavior has been referred to as byssus drifting or thread drifting. This is analogous to a dispersal technique used by young spiders (Humphrey 1987). Tiny arachnids climb to the top of a tall object (i.e. blade of grass, twig), release a silk thread and are transported by wind. The mucous thread secreted by bivalves is very thin and difficult to see with the naked eye; however, it can be observed by pulling a fine probe through the water which results in movement of the attached bivalve (Beaumont and Barnes 1992, pers obs).

Several studies have investigated this secondary mode of dispersal in juvenile bivalves and certain species have received great attention. The most well studied bivalve is probably *Macoma balthica* and topics have included distribution (Beukema and de Vlas 1989; Beukema 1993; Armonies 1996) and migratory rhythms (Armonies 1992; Hiddink 2002) and behavior (Sörlin 1988). Other well studied species include *Mytilus* spp. (Bayne 1964; de Bolk 1977; Lane *et al.* 1982; Board 1983; Lane *et al.* 1985; Shanks and Shearman 2011), *Mya arenaria* (Roegner *et al.* 1995; Strasser *et al.* 1999; LeBlanc and Miron 2006) and *Cerastoderma edule* (Yankson 1986; de Montaudouin *et al.* 2003).

As pointed out by Baker and Mann (1997) over 48 species of bivalves are known to drift with mucuos threads: consequently, it is not unlikely that bivalves in the Coos estuary (Coos Bay, Oregon) also exhibit thread drifting behavior. However, the assumption should not be made that all local species display secondary dispersal and that they follow the same patterns as other taxa in different parts of the world.

The first objective of this study was to determine which local species drift with mucous threads. In order to address this first objective I collected bivalves from the plankton and identified them to the lowest possible taxonomic level. Taxonomic identification using conventional methods is difficult due to a lack of distinct morphological features at the juvenile stage. It is conceivable that in the laboratory I could rear juveniles collected in plankton until they reach a stage that morphological features would be useful, but this is time consuming and often difficult. In recent years molecular techniques have been employed to identify marine larvae (Hart *et al.* 2003; Barber and Boyce 2006; Heimeier *et al.* 2010). I used molecular techniques in combination with phylogenetic analysis and morphological features to identify juvenile bivalve.

Following determination of which local species may exhibit thread drifting behaviors I investigated how estuarine hydrodynamics influence the behavior. Beukema and de Vlas (1989) indicated juvenile *Macoma balthica* were more abundant during the ebb phases of the tidal cycle. The influence of tidal cycle was also observed for this species on the US east coast; however, abundance was higher at a during the flood phase (Garrison and Morgan 1999). Cummings *et al.* (1992) observed variations in the number of juvenile bivalve drifters depending on food availability. Diurnal migration patterns were observed for *Cerastoderma edule*, *Ensis directus*, and *M. balthica* (Armonies 1992). I investigated similar factors to determine whether observed patterns are species or locale specific.

This thesis provides the first evidence of five taxa of bivalves that exhibit thread drifting behaviors in Coos Bay estuary (Chapter II) and investigates the size of thread

drifters and the influence of tidal cycles, salinity, temperature and chlorophyll *a* levels (Chapter III). The results of the second chapter warranted a further investigation of tidal cycles and this was accomplished with differently sampling methods which also provided an opportunity to look at diel variation (Chapter IV). This thesis provides insight into an important phase in the life cycles of bivalves and the information presented will be useful for the management of commercial and recreational important species.

CHAPTER II

MORPHOLOGIC, MOLECULAR AND PHYLOGENETIC ANALYSIS TO IDENTIFY JUVENILE BIVALVES IN THE PLANKTON IN COOS ESTUARY, OREGON

INTRODUCTION

Identification of organisms is an extremely important aspect in a number of scientific fields. Historically taxonomists identified specimens primarily by morphological traits; however, in recent years technological advancements have provided other means for identification. The use of molecular techniques in combination with traditional morphological identification could aid in uncovering species diversity (Hebert *et al.* 2003a).

Many marine invertebrates have complex life cycles, meaning the larval forms are morphologically distinct from their adult form (*i.e.* pluteus larvae and adult sea urchins, bipinnaira larvae and adult sea stars, pilidium larvae and adult nemerteans, nauplii and adult barnacles, etc.). This difference in body plans at species stages makes larval identification difficult, and as a result larval identification keys are few in number compared to adult guides. One method to identify larvae is to collect them in the plankton, rear them through metamorphosis and keep them alive until they reach a stage at which adult morphological features can be used. Another option is to collect adults, spawn them in the laboratory, rear the larvae, and try to match their larvae with unidentified larvae (Shanks 2001). Both of these options are often time consuming and

involve raising larvae in a laboratory setting, which is often difficult; however, molecular methods provide an alternative.

In the last two decades molecular techniques have been used in various areas around the world to help identify marine invertebrate larvae and uncover cryptic species diversity. In the Coral Triangle, Barber and Boyce (2006) used DNA barcoding to identify five larvae to species level and in the process discovered three species whose adult forms are unknown. Molecular analysis indicated Australian populations of the asteroid *Patiriella pseudoexigua* were composed of individuals with unique mitochondrial DNA sequences and reproductive strategies (Hart *et al.* 2003). Heimeier *et al.* (2010) used a combination of molecular techniques and morphological taxonomic methods to identify nearly 700 Antarctic larvae from four different phyla. The present study investigated the use of molecular techniques to identify juvenile marine bivalves from the southern Oregon coast.

Bivalves are a group of marine invertebrates that also have complex life cycles. Similar to other marine invertebrates, the larvae spend a period of time in the water column feeding on plankton until competent to metamorphose. During the process of metamorphosis, larvae settle into an appropriate habitat. It was previously thought that after this initial settlement the dispersal stage was over. A study by Sigurdsson *et al.* (1976) indicated that bivalves have the ability and potential to disperse during post-larval and juvenile phases using a method referred to as "byssus drifting." It is characterized by the secretion of a very thin mucous thread which leads to an increase in viscous drag allowing the organism to be carried long distances by relatively weak currents

(Sigurdsson *et al.* 1976; Lane *et al.* 1985; Yankson 1986). This is analogous to a behavior exhibited by young spiders (Humphrey 1987).

Over the last three to four decades numerous studies have documented mucous thread drifting in a wide variety of bivalve taxa. Data compiled by Baker and Mann (1997) indicated the occurrence of post-larval byssal drifting in at least 48 species across 16 families. This behavior has been documented in species from the North Sea (Armonies 1992), the Wadden Sea (Beukema and de Vlas 1989; Armonies 1996; Hiddink *et al.* 2002), New Zealand (Cummings *et al.* 1992), and Asia (Wang and Xu 1997). However, along the southwest Oregon coast few studies have occurred, thus warranting an investigation of what species in the local area exhibit this secondary dispersal behavior.

Species identification was a key component of this investigation. As mentioned earlier, identification of organisms at early stages is often difficult. Even at the juvenile stage, using morphological features to distinguish species is not ideal. In this study, rather than attempt to rear juveniles from the plankton in a laboratory setting, molecular techniques were used, in combination with morphology, to identify juvenile bivalves collected in the plankton in Coos Bay estuary.

METHODS

Stratified plankton tows were taken in Coos Estuary, Oregon (N 43°25’16’’, W 124°16’19’’) using a 500 μm net from September 2009 to July 2011. Only samples collected from April 2011 to March 2011 were preserved in ethanol (all others were preserved in 5% buffered formalin) and could be used in this analysis. In the laboratory

juvenile bivalves were sorted into five groups based on similar morphology. The groups were classified as A, B, C, *Clinocardium nuttallii*, and *Mytilus* spp. (Figure 1). Specimens were placed in vials filled with 95% ethanol and stored at room temperature. In October 2011 students from the Estuarine Biology course at the Oregon Institute of Marine Biology collected adults of nine species of bivalves from a mudflat in Charleston, OR. Small pieces of the mantle were clipped from live adult specimens and stored at -80°C.

Figure 1. Juvenile bivalves: Juvenile bivalves collected in the Coos Bay plankton depicting a representative from each of the five groups. From left to right, *Clinocardium nuttallii*, Group A, Group B, Group C, and *Mytilus* spp.

I extracted DNA from 33 juvenile specimens and 9 adult tissue samples with DNeasy Blood and Tissue (Qiagen). I used primers 16SarL (5'-CGCCTGTTTATCAAAAACAT-3') and 16SbrH (5'-CCGGTCTGAACTCAGATCA CGT-3') from Palumbi *et al.* (1991) to amplify a ~ 500 bp region of the 16SrRNA gene. PCR parameters were as follows: initial denaturation at 95°C for 2 minutes, 35 cycles at 95°C for 40 seconds, 52°C for 40 seconds, 72°C for 1 minute, and a final extension of 72°C for 2 minutes. For some samples the annealing temperatures were set higher (55°C) or lower (49°C) to allow for single product amplification. I used primers LCO1419 (5'-GTCAACAAATCATAAAGATATTGG-3') and HCO2198 (5'-TAAACTTCAGGGTGACCAAAAAATCA-3') from Folmer *et al.* (1994) to amplify the ~ 650 bp "barcoding" region of the cytochrome oxidase *c* subunit I gene (COI). PCR

parameters were as follows: 95°C for 2 minutes, 35 cycles at 95°C for 40 seconds, 45°C for 40 seconds, 72°C for 1 minute, and a final extension at 72°C for 2 minutes. PCR products were viewed on a 1% agarose gel. I purified samples that had a single bright band with SV Wizard Gel and PCR clean up Kit (Promega) and quantified on 1% agarose gels with Low Mass DNA ladder (Promega). I sent a total of 25 16S rRNA amplicons and 11 COI amplicons to Sequetech DNA sequencing service (http://sequetech.com/) for sequencing in one direction using one of the PCR primers.

I viewed chromatograms in Codon Code Aligner 3.7.1 and clipped off low-quality ends and primers. I performed a NCBI blastn, and in one instance a blastp, search for initial sequence identification and to check for contamination or mislabeling. I aligned sequences with ClustalX 2.1 and created Neighbor-Joining (NJ) distance trees and viewed these in TreeView X 0.5.0. I analyzed phylogenetic relationships with PAUP 4b10 using maximum parsimony as optimality criterion. When juvenile samples did not match to an adult sample I created a distance tree with "BLAST." See Appendix 1 for GeneBank Accession numbers of sequences included in the phylogenetic analysis.

RESULTS AND DISCUSSION

Amplification success for 16S was 100% for adults and 24.2% for juveniles and for COI was 66.6% for adults and 18.2% for juveniles. Overall the 16S region amplified better than the COI region and adults samples amplified better than juveniles. The reason for low amplification success of juveniles could be a result of too little tissue in the sample. Another possibility may be a result of poor preservation. It is possible the bivalve shells were tightly closed and the ethanol could not reach the tissue fast enough.

Overall lower amplification success for COI may be due to primer mismatch. Using mollusk or bivalve-specific PCR primers may increase amplification success for COI.

I successfully obtained 16S rRNA sequences from eight juvenile samples: one from group A, five from group B, one from group C, and one from *Mytilus* spp. group (Table 1). A distance tree suggests that these represent 5 different types (or taxa) (Figure 2). Samples from groups A, C, and *Mytilus* spp. were each represented by a single specimen, and the five samples from group B formed a monophyletic clade with two subclades. The COI amplification was successful for six juvenile samples: one from group C, three from *Mytilus* spp. group, and two from *Clinocardium nuttallii* group (Table 1). A distance tree for COI samples placed these six juveniles into four different clades (Figure 2). The two juvenile samples provisionally identified as *C. nuttallii* were identical and formed a clade with the sequence derived from the adult of *C. nuttallii*. The three *Mytilus* spp. samples formed two sister clades. Amplification for both genes was only successful for one juvenile sample, a *Mytilus* sp. Overall, results indicate at least five, possibly eight, different taxa of juvenile bivalves from Coos Bay plankton exhibit thread-drifting behavior.

The main purpose of this study was to determine the identity of juvenile bivalves collected in the Coos Bay plankton to the lowest possible taxonomic level. One way I accomplished this was to match up sequences of juvenile samples to adult samples with known identities. Using 16S sequences I determined that the successfully amplified sample from group A belonged to *Macoma inquinata* (0% sequence divergence) (Figure 2). Due to a lack of other sequences from group A samples, I was unable to determine whether all individuals from this group belonged to the same species. The locally

occurring species of *Macoma, M. inquinata, M. balthica*, and *M. nasuta*, are difficult to distinguish, therefore it is very possible that group A includes multiple *Macoma* species.

Table 1. Successfully amplified samples: Samples successfully amplified, whether they were juvenile or adults, identity prior to this study, and genes successfully amplified. Samples not shown were not successfully amplified.

Sample	**Life Stage**	**Identity Prior to Study**	**Gene Amplified**
B1	Adult	*Mya arenaria*	16S and COI
B2	Adult	*Tresus capax*	16S and COI
B3	Adult	*Clinocardium nuttallii*	16S and COI
B4	Adult	*Saxidomus gigantean*	16S and COI
B5	Adult	*Macoma nasuta*	16S
B6	Adult	*Macoma inquinata*	16S
B7	Adult	*Macoma balthica*	16S
B8	Adult	*Cryptomya californiensis*	16S and COI
B9	Adult	*Leukoma staminea*	16S and COI
B18	Juvenile	Group C	COI
B20	Juvenile	Group B	16S
B23	Juvenile	Group C	16S
B26	Juvenile	*Mytilus* spp.	16S and COI
B27	Juvenile	Group A	16S
B29	Juvenile	Group B	16S
B30	Juvenile	Group B	16S
B33	Juvenile	Group B	16S
B34	Juvenile	Group B	16S
B35	Juvenile	*Clinocardium nuttallii*	COI
B37	Juvenile	*Clinocardium nuttallii*	COI
B38	Juvenile	*Mytilus* spp.	COI
B40	Juvenile	*Mytilus* spp.	COI

The two juvenile samples initially identified as *Clinocardium nuttallii* matched exactly to the sequence derived from the adult *C. nuttallii* (0% sequence divergence) confirming my initial identification (Figure 2). Radial ridges and the spherical shape of the shell made this bivalve very different from other juveniles. No other individuals from the *C. nuttallii* group were successfully amplified; however, the distinct morphology indicated all individuals in this group likely belonged to *C. nuttallii*. In the local area, the only other bivalve with radial ridges is *Leukoma stamina*; however, this species also has concentric ridges and our sample did not match the adult tissue from *L. stamina*.

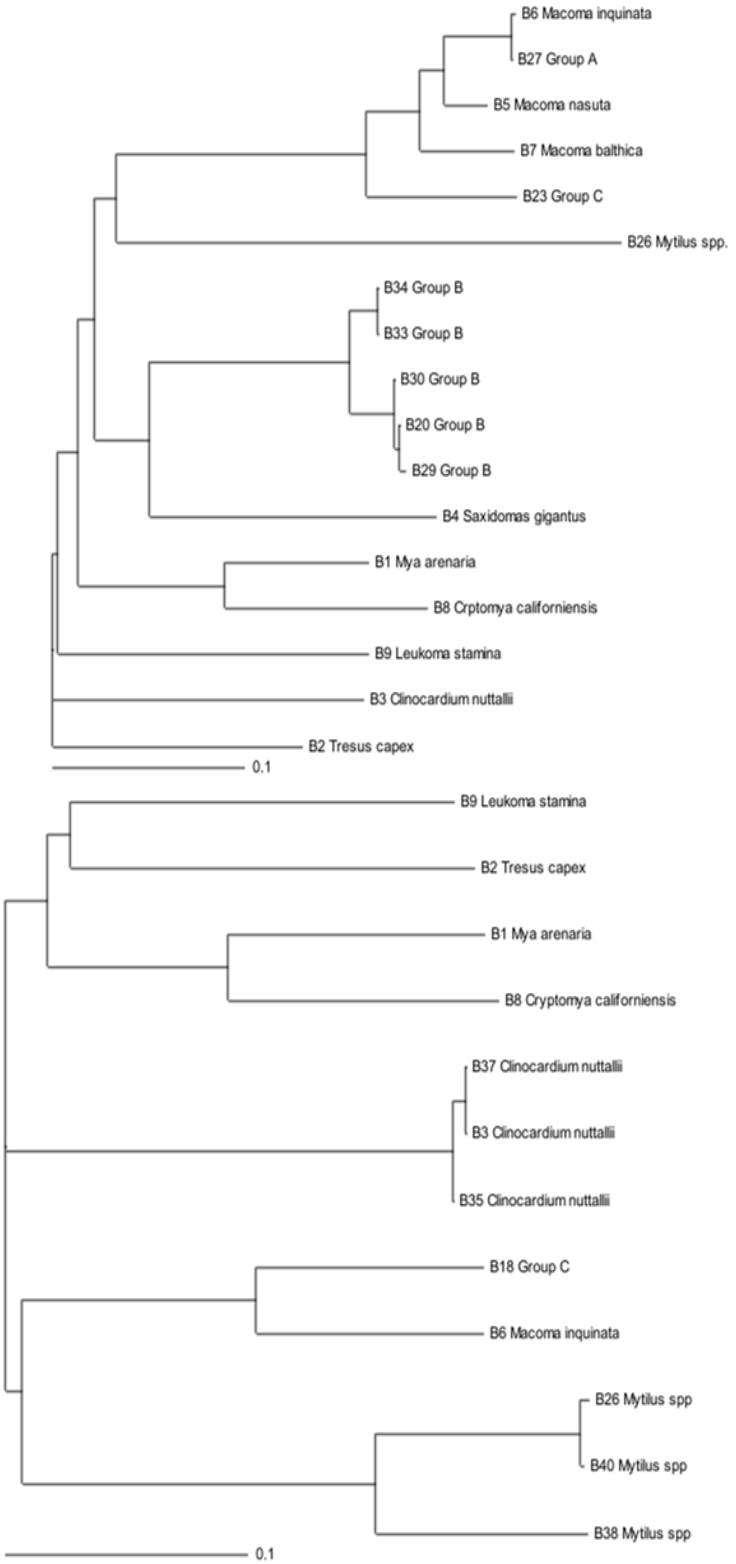


Figure 2. Distance trees (NJ) of samples from this study: Distance (NJ) tree of 16S rRNA (upper) and COI rRNA (lower) sequences of juvenile and adult samples from this study. Samples B1-B9 are adult samples. The remaining samples are juveniles collected from plankton.

None of the *Mytilus* spp. samples matched to the adults. This was expected because I did not sequence any adult mussels. The NCBI blastn indicated samples B26 and B40 were *Mytilus trossulus* (100% sequence similarity), a locally abundant intertidal species. When I performed a nucleotide blastn search *Mytilus* spp. sample (B38) no COI match was found; however, a blastp search matched the juvenile sequence to several *Mytilus* spp. all with 90% similarity. I created a distance tree with the three *Mytilus* spp. samples from this study and all available *Mytilus* spp. and *Modiolus* spp. (another mytilid) sequences from NCBI Genbank (Figure 3). Sample B38 nested within a clade that contained only species of *Mytilus*. A phylogenetic analysis that included local *Mytilus* spp. indicated the genus is monophyletic; however, this study did not include all known *Mytilus* species (Distel 2000). It appeared sample 38 was a *Mytilus* spp., but without knowing for sure whether the genus is monophyletic there was some uncertainty.

Previous studies indicate southern latitudes are dominated by *Mytilus galloprovincialis,* while northern latitudes are dominated by *M. trossulus* (Suchanek *et al.* 1997), and these two species are sympatric between Monterey Peninsula and Cape Mendocino (Rawson *et al.* 1999). Braby and Somero (2006) found that 100% (n=93) of mussels collected from the Charleston boat basin, near Coos Bay, OR, were *M. trossulus;* however, both *M. trossulus* and *M. galloprovincialis* were collected from Isthmus Slough in Coos Bay (Suchanek *et al.* 1997). I obtained sequences from GenBank for *M. trossulus* and *M. galloprovincialis,* but sample 38 does not match either of these. The current study sequenced mitochondrial DNA, and if this sample was a hybrid of *M. trossulus* and *M. galloprovincialis* it would have matched to one of these two sequences.

A possible explanation for these results is that sample 38 is an introduced species. Geller *et al.* (1993) indicated *M. galloprovincialis* was very abundant in ballast water of ships that came into ports along the North American west coast and it is likely ballast water acts as a means of transport for all species of *Mytilus.* Extensive sampling and DNA extraction of individuals near our study site would provide more insight.

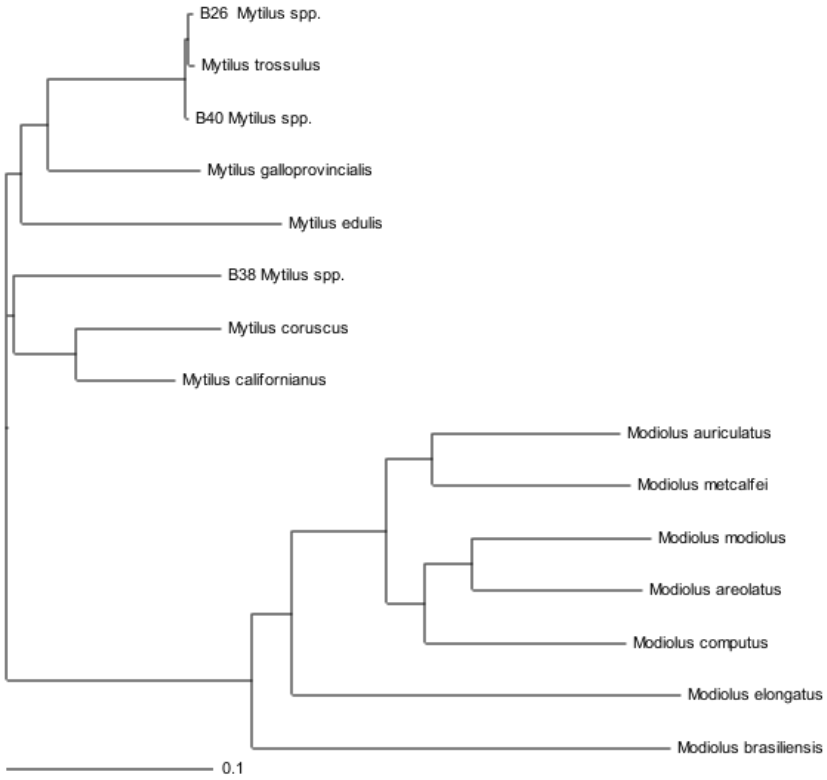


Figure 3. Distance tree (NJ) of *Mytilus* spp. samples: Distance tree created from COI sequences of juvenile *Mytilus* spp. samples (B26, B38, and B40) from this study and NCBI GenBank sequences of Mytilidae species (Appendix A).

The five samples from group B that were successfully amplified formed two different clades (Figure 2). Samples 33 and 34 had zero divergence between each other and likewise did samples 20, 29 and 30, thus I used only one sample from each group, sample 20 and 34, for the remaining analysis. Neither Group B sample matched any adult sequence. The closest blastn match was *Sinonovacula rivularis* (92% similarity).

The distance tree created from the blastn search revealed group B samples were nested within the superfamily Solenoidea. Using two group B samples, B20 and B34, and NCBI Genbank sequences of Solenoidea spp. I created a maximum parsimony tree (Figure 4). The phylogenetic analysis indicated group B samples grouped together forming a sister clade with the razor clam *Siliqua minima*. This clade was sister to a clade containing other razor clams *Ensis* spp. and *Phaxas pellucidus*. *S. minima*, *Ensis* spp., and *P. pellucidus* are all members of the family Pharidae, thus, it is very likely the group B samples are also within this family.

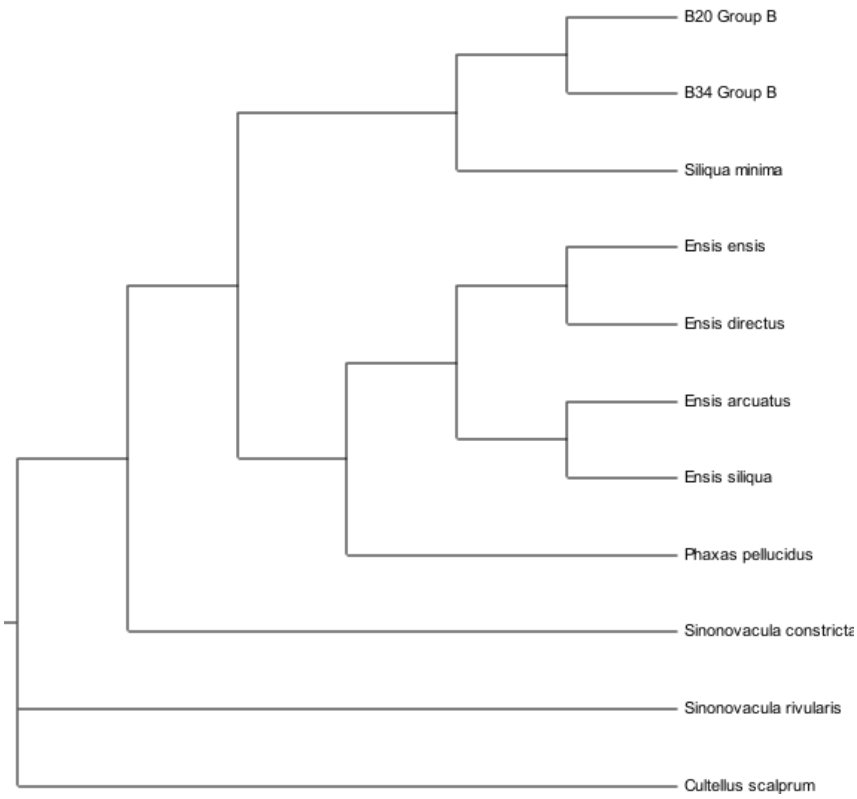


Figure 4. Maximum parsimony tree of group B samples: Maximum parsimony tree created from 16S sequences of juvenile samples (B20 and B34) from this study and NCBI Genbank sequences of Solenoidea species (Appendix A).

I wanted to further investigate this result. Local Pacific razor clams can be collected from intertidal flats in the lower part of the estuary, but due to time constraints I obtained a specimen from a local seafood store. The specimen from the seafood store was not collected locally but shipped frozen from Alaska. According to the Alaska Department of Fish and Game their commercial razor clam is *Siliqua patula* (Alaska Department of Fish and Game. Accessed 9 Feb. www.adfg.alaska.gov), and this species is the same species found in the local area (Coan *et al.* 2000; Coan and Valentich-Scott 2007). Terra Heibert, a fellow graduate student, sequenced the specimen and it matched with 100% sequence similarity to sample 20 from this study (Figure 5). Sample 34 was most closely related to *S. patula* but without known divergence rates I am unable to determine whether it is the same species or another species of the same genus.

Two samples from group C were successfully amplified, however, for sample B18 only COI amplification was successful and for sample B23 only 16S amplification was successful. Neither sample matched to any of my sequences from local adults. The closest blastn match for B18 COI was *M. balthica* (83%) and for B23 16S was *Abra longicallus* (87%). Both of these species belong to the superfamily Tellinoidea. I created a maximum parsimony tree for COI and 16S sequences (Figure 6) including group C samples from this study and NCBI GenBank sequences for selected members of Tellinoidea. The maximum parsimony tree for COI sequences places C18 sister to a clade containing *Semele solida* and *A. longicallus*, both of the family Semelidae. The 16S results indicated sample C23 was sister to a clade containing *Macoma* spp. (Tellinidae) and *A. longicallus* (Semelidae). This indicated samples from group C most likely belong to the superfamily Tellinoidea. Data at hand are insufficient to determine

whether both samples from group C belong to the same species or not, and to identify them to a lower taxonomic level. However, a juvenile illustration identification guide suggested, based on morphology, that group C species might be *Tellina modesta* (Dethier and Catton (2001) unpublished), which is local species that belongs to the superfamily Tellinoidea.

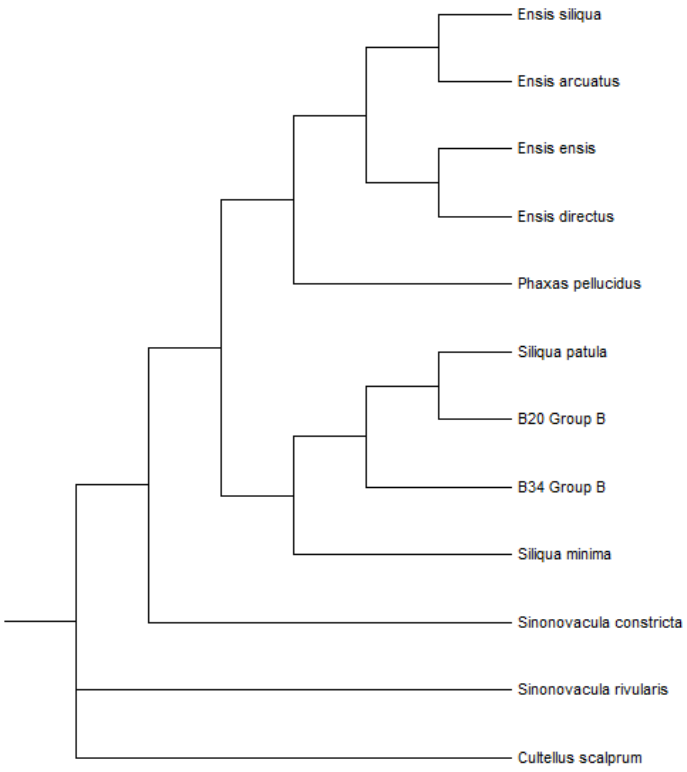


Figure 5. Maximum parsimony tree of group B samples II: Maximum parsimony tree created from 16S sequences of juvenile samples (B20 and B34) from this study, local razor clam sample, and NCBI Genbank sequences of Solenoidea species (Appendix A).

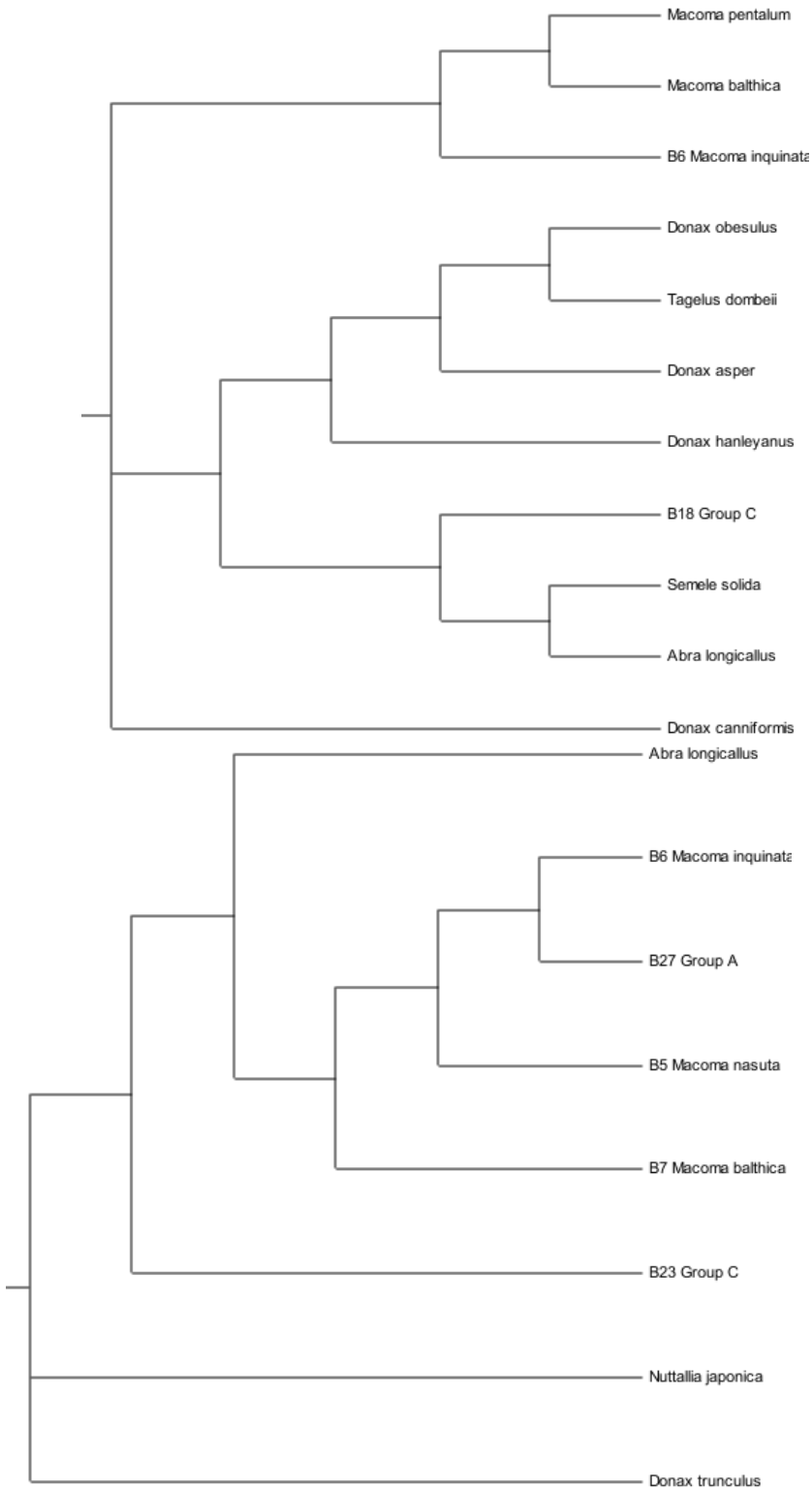


Figure 6. Maximum parsimony trees of group C samples: Maximum parsimony tree created from COI sequences of group C juvenile samples (B18) (upper) and 16S sequences of group C juvenile sample (B23) (lower) from this study and NCBI Genbank sequences of Tellinoidea species (Appendix A).

For this study, the overall amplification success of the juvenile bivalves was low; however, this is not uncommon. Webb *et al.* (2006) attempted to identify Antarctic larvae but had only 22% success (14/64) and only two of the fourteen were identified to species level. The success from my study was partly due to the sequences obtained from adult bivalves in the local area, and a more exhaustive collection of local adults could provide more insight into this study.

A combination of morphological characteristics, sequence data and phylogenetic analysis allowed me to identify juvenile bivalves. Results indicated that *Macoma* spp., *Siliqua* spp., *Mytilus* spp. and *Clinocardium nuttallii* juvenile bivalves were found drifting in the Coos Bay plankton. Individuals from the superfamily Tellinoidea were also collected in plankton tows. This was the first study in which molecular techniques were used to identify juvenile bivalves from the Coos estuary. These local juveniles are exhibiting a behavior that has been observed in other areas of the world. The next step is to determine how environmental factors such a tidal cycle, salinity, and chlorophyll influence the drifting behavior.

CHAPTER III

THREAD DRIFTING BY JUVENILE BIVALVES IN COOS ESTUARY, OREGON: INFLUENCE OF ESTUARINE HYDRODYNAMICS ON SECONDARY DISPERSAL

INTRODUCTION

Larval dispersal is an important aspect of life history in many marine organisms, including bivalves. The majority of bivalve larvae are planktotrophic meaning they spend time in the water column feeding on plankton until competent to metamorphose. During the process of metamorphosis, larvae settle into an appropriate habitat. It was previously thought that after this initial settlement the dispersal stage was over. A study by Sigurdsson *et al* (1976) indicated that many types of bivalve larvae have the ability and potential to disperse during post-larval and juvenile phases using a method referred to as "byssus drifting." It is characterized by the secretion of a very thin mucous thread which leads to an increase in viscous drag allowing the organism to be carried long distances by relatively weak currents (Sigurdsson *et al.* 1976; Lane 1985; Yankson 1986).

Over the last three to four decades several studies have documented byssal drifting in a wide variety of bivalve taxa. Data compiled by Baker and Mann (1997) indicated the occurrence of post-larval byssal drifting in at least 48 species across 16 families. The size of bivalves which exhibit thread drifting behavior varies across taxa. Lane *et al.* (1985) observed *Mytilus edulis* post-larval individuals up to two mm exhibiting drifting behavior. In the lagoon cockle, *Cerastoderma glaucum,* byssal threads were observed on individuals between two to four mm in length (Yankson 1986).

Macoma balthica juveniles up to ten mm in length were captured using plankton nets (Beukema and de Vlas 1989). The length of time after metamorphosis during which drifting occurs appears to be species specific. Yankson (1986) indicated that in the laboratory *C. glaucum* continued to display drifting behavior until the individuals were 77 days old. In contrast, a bivalve native to Asia, *Sinonovacula constricta,* was observed to exhibit drifting behavior nine to 30 days after metamorphosis (Wang and Xu 1997).

Both biotic and abiotic factors are thought to influence bivalve thread drifting behavior. Laboratory experiments indicated when adult densities were high *Cerastoderma edule* juveniles drift to avoid intraspecific competition (de Montaudouin and Bachelet 1995). A diurnal pattern for *Macoma balthica, C. edule,* and *Ensis directus* was observed in the field with these species occurring in the water column in greater abundance at night (Armonies 1992). In the Wadden Sea, *M. balthica* was collected in higher numbers during ebb tides compared to flood tides (Beukema and de Vlas 1989). A lunar periodicity was observed in *C. edule* and *E. directus* with a higher abundance of individuals in the water column during spring tides compared to neap tides (Armonies 1992). Laboratory experiments indicated that when burned sand, denuded of any organics, was the provided substrate *Macomona liliana* readily emerged and exhibited drifting behavior (Cummings *et al.* 1992).

Many of these studies were conducted in coastal waters around Europe and little is known about this behavior on the west coast of the US. This study focused on how physical factors influenced presence, absence and abundance of multiple species of juvenile bivalves found drifting in the plankton in Coos Bay, Oregon.

METHODS

Data Collection

I took monthly plankton tows from September 2009 to July 2011 during flood and ebb tides. From September to November 2009 I sampled the flood and ebb tides on separate days. To increase the efficiency of sampling, I sampled the flood and ebb tide samples on the same day, starting in December 2009. Sampling started about three hours before the tide changed. The plankton tows were in the Coos Estuary, OR near the Southwest Oregon Regional Airport (N 43°25'16'', W 124°16'19'').

I collected plankton with a 1 m Tucker trawl with 0.5 mm mesh. The Tucker trawl was equipped with two nets that could be opened and closed at different depths. Vertically stratified oblique tows were made with each net. On each tow, one net sampled from within 2 meters of the bottom to mid-depth and the second net sampled from mid-depth to the surface. The duration of each tow at each depth was 10 minutes and I measured flow through the nets with a mechanical flowmeter. I took three replicate sets of tows with each net during the flood and ebb tide. Depending on the tidal height water depth ranged from 13 m to 15 m.

I collected measurements of estuarine water parameters with a SeaBird model 19 CTD equipped with a WetStar fluorometer to measure chlorophyll *a*. I made three CTD casts during each flood and ebb tide sample collection. I made the first cast before the first tow and the second and third casts after the second and third tow, respectively. The CTD records measurements every half-second throughout the entire water column.

I preserved samples on the boat using borax buffered 5% formalin and preserved samples collected from April to July 2011 in 95% ethanol to allow for molecular

analysis. In the laboratory, using a dissecting microscope, I enumerated bivalves and measured the length from the anterior to the posterior with an ocular micrometer to one-tenth mm. I placed bivalves into groups based on similar morphological features and adult identification guides (Coan *et al.* 2000; Mikkelsen *et al.* 2006; Coan and Valentich-Scott 2007).

Data Analysis

I analyzed the data with the statistical program R™ version 2.13.1. I analyzed the relationships between the explanatory variables, the presence and abundance, log(Ab+1) of bivalve thread drifters for each of the taxa identified using General Additive Models (GAM) as implemented in the mgcv library, a non-parametric regression package, of R (R Development Core Team 2010). GAMs are similar to stepwise regressions in that initially all variables are included and the least significant variables are removed on a step-by-step basis until all variables remaining are significant. GAMs, however, allow the exploration of non-linear functional relationships between dependent and explanatory variables, fitting predictor variables by smooth functions (Guisan *et al*. 2002). The general model form of a GAM is

$$\mathrm{E}(Y) = \alpha + \sum_{j=1}^{p} f_j\left(\mathrm{X}_j\right) + \varepsilon$$

Where E(Y) is the estimated value of the response variable, α is the population intercept, X_j are the covariates, f_j are the smooth unknown functions estimated for each covariate, and $\mathcal{E}$ is the error term (Wood 2006).

Abundance data were characterized by many zero-valued observations and a long right tail. Zero-inflated data are a common feature in species abundance studies, which

prevents the use of common assumptions of data distribution for modelling (Barry and Welsh 2002). Therefore, data were modelled in two steps. The first step modelled the association between the presence and absence of bivalves and the available covariates and the second step modelled the relationship between abundance and the covariates, conditionally on the presence of the organism (Barry and Welsh 2002).

I reported the abundance of bivalves as number/m^2 or number/100 m^2 and to calculate this divided the raw number of bivalves by the volume of water filtered and multiplied by the depth of water sampled (i.e. if the tow was from the surface to 7 meters the depth was 7). I multiplied by 100 for number/100 m^2. I introduced tidal cycle (flood or ebb) and depth (upper or lower net) as fixed factors. I considered continuous variables (salinity, temperature, chlorophyll *a*, and date in Julian Days) as smoothed terms in the model and estimated with thin plate regression splines (Guisan *et al*. 2002). I divided the water column in half creating an upper and lower portion. I averaged the CTD data collected to obtain a single measurement for each portion of the water column for every cast and used these values in the statistical analysis of the biological data. To look at temperature, salinity and chlorophyll *a* patterns over the two-year sampling period, I averaged the values for each tow to obtain a single measurement for each monthly sampling.

The presence-absence data were modelled using a binomial distribution with a logit-link and Akaike's information criterion (AIC) was used to select the optimal set of variables for inclusion in the models (Zurr *et al.* 2009). Model validation included the verification of homogeneity, normality and independence assumptions (Zuur *et al*. 2009).

RESULTS

Estuarine Hydrographic Data

The CTD recorded salinity, temperature and chlorophyll *a* along the sampling transect. The average water temperature, integrated across depth, over the two-year sampling period ranged from approximately 9°C to 17°C; however, in December 2009 the temperature dropped to 6.9°C (Figure 1A). Water temperature was highest during July through September. Average salinity ranged from 21.5 to 32.4 with highest salinities during July through October (Figure 1A). Chlorophyll *a* varied little from September 2009 to June 2010 (ranging from 0.5 to 0.8 µg/L). It peaked in August 2010 (5.9 µg/L); decreased and leveled out from December 2010 to March 2011; then peaked again in April 2011 (6.5 µg/L) and reached its highest concentration (7.4 µg/L) in June 2011 (Figure 1B).

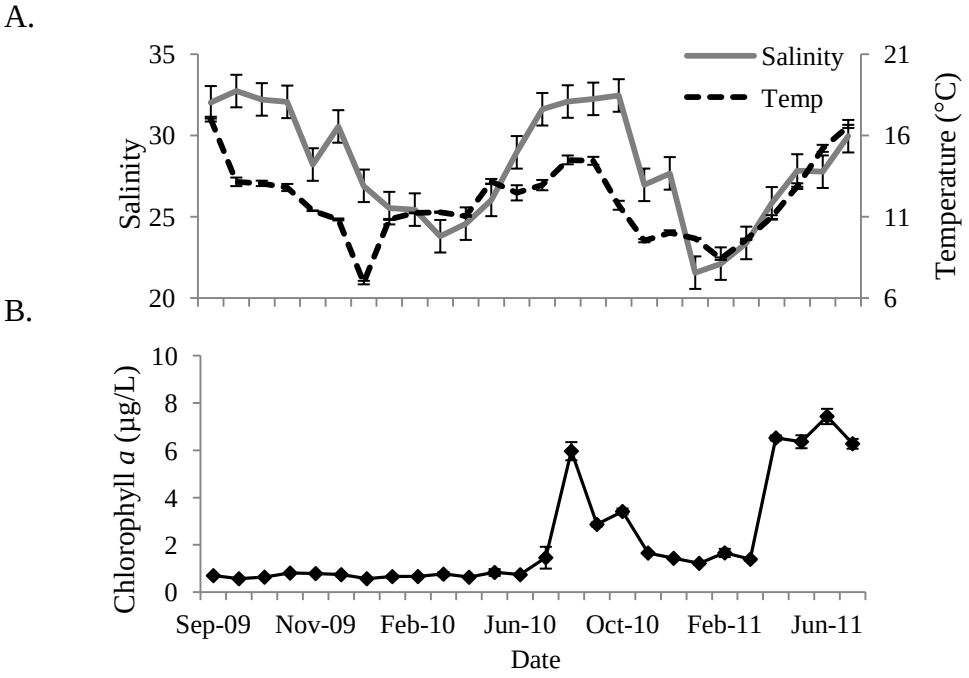


Figure 1. Temperature, Salinity, and Chlorophyll *a:* Average (±SE) of A) water temperature (°C) and salinity and B) chlorophyll *a* (µg/L) for the entire sampling period, September 2009 through July 2011.

Bivalve Species

I recorded five taxa of bivalves from plankton samples collected in Coos estuary from September 2009 to 2011. Morphology and molecular techniques (Chapter II) indicated juvenile bivalves collected included *Clinocardium nuttallii, Macoma* spp., *Siliqua* spp., and *Mytilus* spp. One taxon could not be identified to genus level, but molecular analysis indicated it grouped with the superfamily Tellinoidea (Chapter II).

Size and Abundance Data

The smallest bivalve collected during this study was a 0.6 mm *Mytilus* spp.; however, over 80% of the *Mytilus* spp. collected were 1.0 mm or larger. Ninety-nine percent of *Macoma* spp. and *Clinocardium nuttallii* bivalves collected and 100% of *Siliqua* spp. and Tellinoidea individuals were >1.5 mm in length. The average size (±SE) of *Macoma* spp. was 2.24 mm ± 0.02, of *Siliqua* spp. was 2.52 mm ± 0.24, of Tellinoidea was 2.21mm ± 0.06, of *C. nuttallii* was 2.33 mm ± 0.04 and of *Mytilus* spp. was 1.57 mm ± 0.04. Size frequency data indicated the majority of bivalves collected in the plankton were in the middle of the size range and the smaller and larger individuals were less frequent (Figure 2).

I found juvenile bivalves in the upper (surface to 7 m depth) and lower (7 to 14 m depth) part of the water column. There was a significant difference in bivalve length between the upper and lower parts of the water column for two of the five taxa (Figure 3). *Macoma* spp. juveniles collected with the lower net were larger than those collected with the upper net (ANOVA test, $p<0.005$, $F=10.11$, $n=981$). *Clinocardium nuttalli* juveniles showed a different trend with larger individuals in the upper net compared to those collected with the lower net (ANOVA test, $p<0.001$, $F=18.72$, $n=281$).

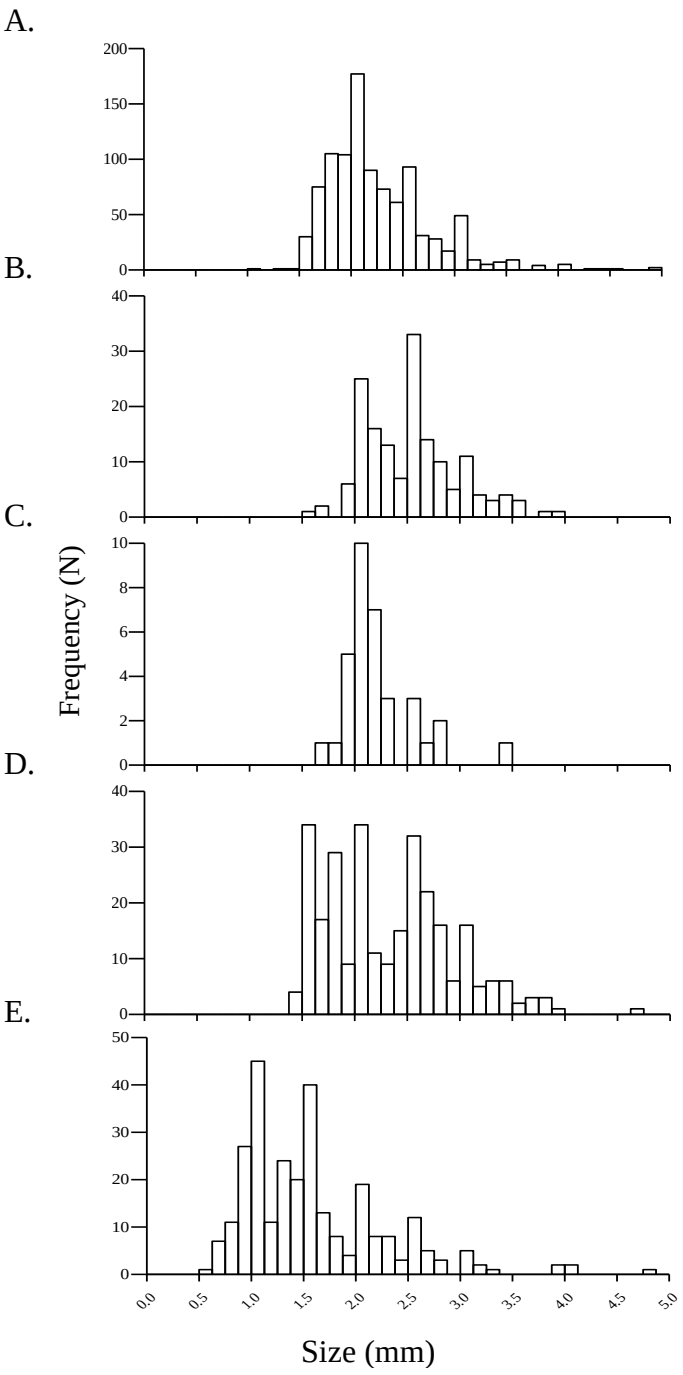


Figure 2. Length frequency distributions: Length (mm) frequency distributions for A) *Macoma* spp. (n=981), B) *Siliqua* spp. (n=159), C) Tellinoidea (n=34), D) *C. nuttallii* (n=281), and E) *Mytilus* spp. (n=282).

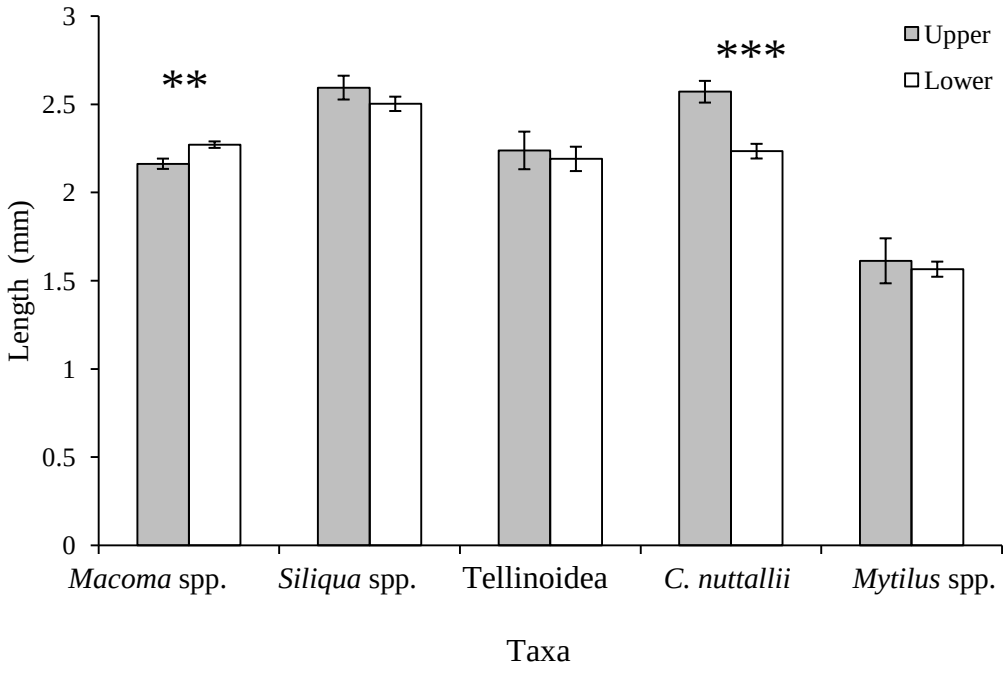


Figure 3. Average bivalve length (posterior to anterior): Length (mm ±SE) in the upper (gray) and lower (white) part of the water column for *Macoma* spp. (ANOVA: F=10.11; df=1; p <0.005; n=981), *Siliqua* spp. (ANOVA: F=1.21; df=1; p=0.27; n=159), Tellinoidea (ANOVA: F=0.16; df=1; p=0.70; n=34), *C. nuttalli* (ANOVA: F=18.72; df=1; p<0.001; n=281), and *Mytilus* spp. (ANOVA: F=0.16; df=1; p=0.69; n=282).

The abundance of juvenile bivalves (all taxa summed) collected in the plankton varied over the two year sampling period. It peaked during early spring and summer of 2010 and there was a smaller peak in late winter and early spring of 2011 (Figure 4A). The most abundant taxon was *Macoma* spp. with the highest average (±SE) abundance for a single sampling day of 86.7/100 m^2 ± 22.4 (Figure 4B). The average abundances for *Siliqua* spp., *Clinocardium nuttallii,* and *Mytilus* spp. taxa were all similar, 25.6/100 m^2 ± 24.6, 15.1/100 m^2 ± 6.0, 18.5/100 m^2 ± 4.23, respectively (Figure 4C, D, and F). Tellinoidea was the least abundant taxon collected with an average of 3.0/100 m^2 ± 1.23 (Figure E).

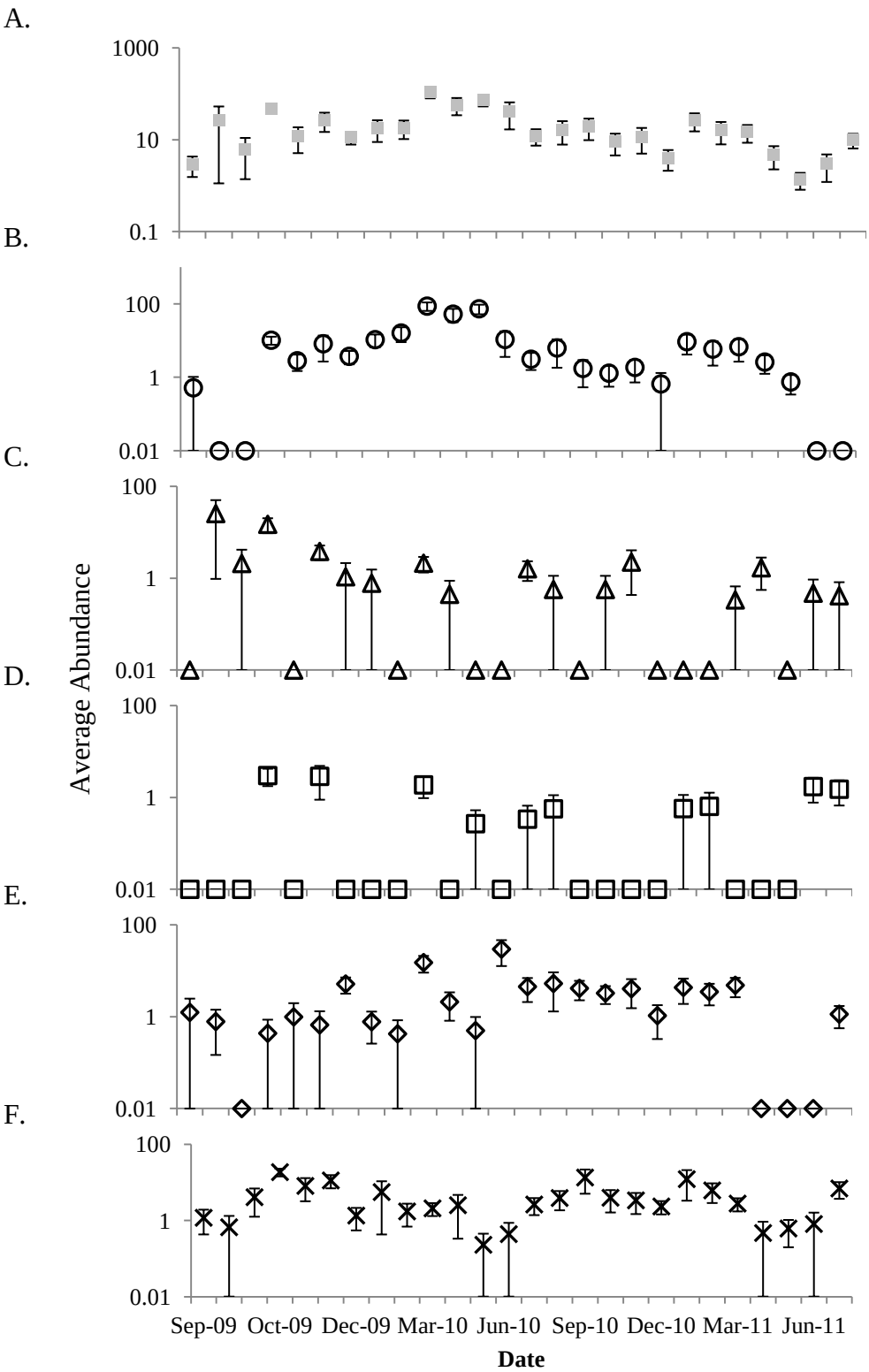


Figure 4. Average abundance of bivalves. Log of the average (log #/100 m^2 +.01) ± SE of A) all taxa summed B) *Macoma* spp., C) *Siliqua* spp., D) Tellinoidea, E) *C. nuttallii*, and F) *Mytilus* spp. from the entire sampling period, September 2009 through July 2011.

General Additive Models

Macoma spp.

Presence/Absence: The GAM model that included depth, Julian Day, and chlorophyll *a* concentration explained 23.9% of the observed deviance (Table 1A – Tables are located in Appendix B). The probability of *Macoma* spp. being present in the lower part of the water column was 3.8 times higher than in the upper part of the water column. The highest probability of catching *Macoma* spp. was from April through early June when the probability of their being present was > 80%, (Figure 5A). The probability of their being present decreased as chlorophyll *a* concentration increased; however, once concentrations reached approximately 7 µg/L, the probability increased (Figure 5B).

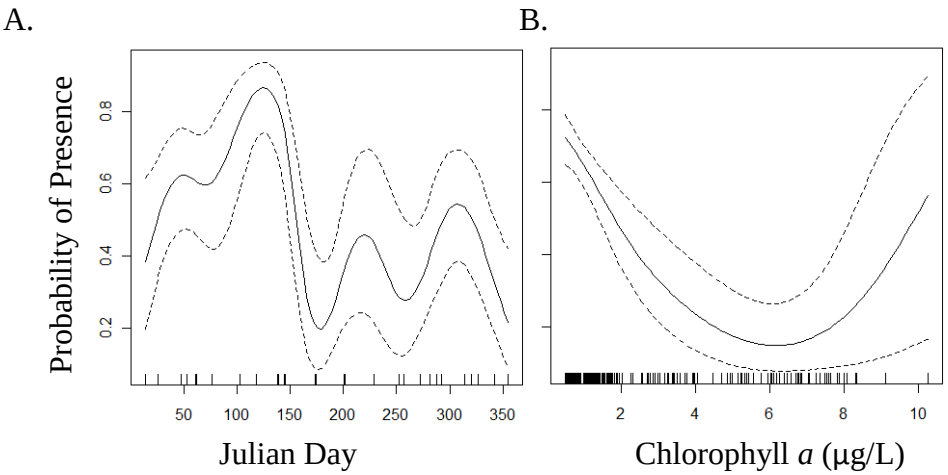


Figure 5. Generalized additive model (GAM) plots for probability of presence of *Macoma* spp.: Influence of A) day of the year (Julian Day) and B) chlorophyll *a* (µg/L) on the probability of presence of *Macoma* spp. GAM results: see Table 1 (A). Solid line is the mean probability, dashed lines are the 95% CI and inner ticks are the data points.

Abundance: The GAM model that included depth, tide, salinity, temperature, and chlorophyll *a* explained 55.1% of the observed deviance (Table 1B). Juvenile *Macoma* spp. abundance was higher in the lower part of the water column compared to the upper and they were more abundant during ebb than flood tides. There was significant

interaction between tidal cycle and depth: there was a larger difference in abundance between the upper and lower parts of the water column during flood tide than during ebb tide. Abundance was influenced by temperature, salinity, and chlorophyll *a* with higher abundance at warmer temperatures, lower salinities, and lower chlorophyll *a* concentrations (Figure 6A, B and C).

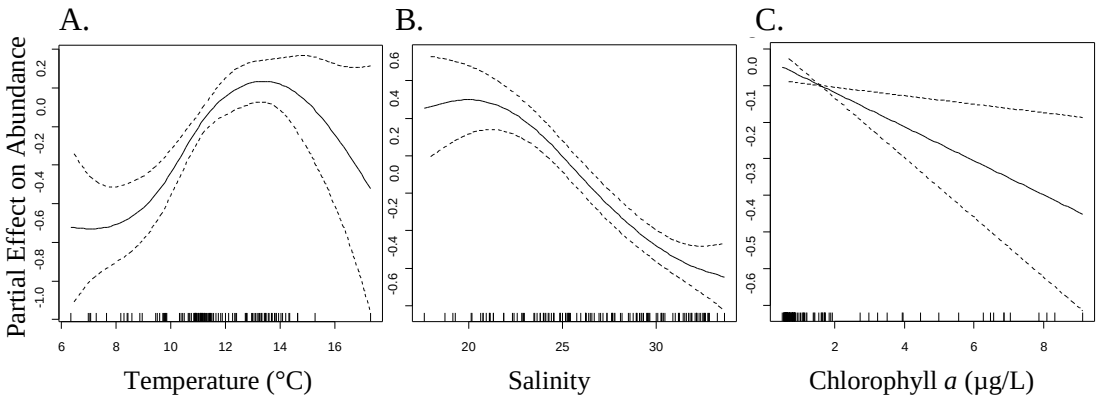


Figure 6. Generalized additive model (GAM) plots for abundance of *Macoma* spp. Partial effect of A) temperature (°C), B) salinity, and C) chlorophyll *a* (µg/L) on *Macoma* spp. abundance (log number/m^2). GAM results: see Table 1 (B). Solid line is the mean partial effect, dashed lines are 95% CI and inner ticks are data points.

***Siliqua* spp.**

Presence/Absence: Similar to the *Macoma* spp. analysis, initially I determined how estuarine hydrodynamics affect the presence and absence of the *Siliqua* spp. species. The GAM model that included depth, Julian Day and chlorophyll *a* concentration explained 21.0% of the observed deviance (Table 2A). It was 3.1 times more likely that *Siliqua* spp. were present in the lower part of the water column than the upper part. During late winter, February and early March, the probability of presence was approximately 75%, which was the highest throughout the year (Figure 7A). The probability that *Siliqua* spp. were present decreased as chlorophyll *a* concentration increased; however, once concentrations reached approximately 4 µg/L the probability increased (Figure 7B).

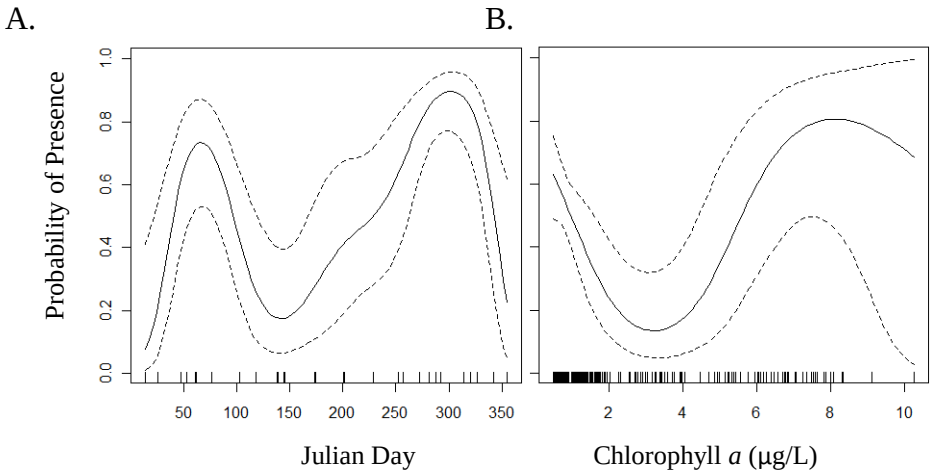


Figure 7. Generalized additive model (GAM) plots for probability of presence for *Siliqua* spp. Influence of A) day of the year (Julian Day) and B) chlorophyll *a* (µg/L) on the probability of presence for *Siliqua* spp. GAM results: see Table 2 (A). Solid line is the mean probability, dashed lines are the 95% CI and inner ticks are the data points.

Abundance: When *Siliqua* spp. were present, estuarine hydrodynamics influenced their abundance. The model that included depth and salinity explained 44.3% of the observed deviance (Table 2B). The GAM indicated *Siliqua* spp. abundance was affected by salinity with highest abundance above salinity 32 (Figure 8) which occur during the rainy season usually early fall to late spring.

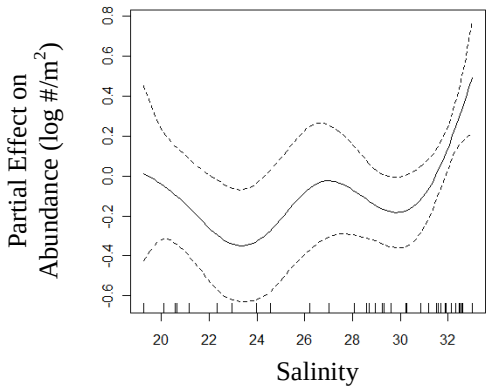


Figure 8. Generalized additive model (GAM) plots for abundance of *Siliqua* spp. Partial effect of salinity on *Siliqua* spp. abundance (log number/m^2). GAM results: see Table 2 (B). Solid line is the mean partial effect, dashed lines are the 95% CI and inner ticks are the data points.

Superfamily Tellinoidea

Presence/Absence: These bivalves were rare compared to the other taxa. Tide and depth were included in the GAM model that explained 9.23% of deviance (Table 3). There was a 4 times greater chance of their being found in the lower water column and a 3.4 greater chance of their being present during ebb compared to flood tides. Other variables tested were not significant.

Abundance: The analysis for abundance indicated none of the variables tested were significant.

Clinocardium nuttallii

Presence/Absence: The presence and absence of *Clinocardium nuttallii* was influenced by estuarine hydrodynamics. The model that included depth, Julian Day and salinity explained 15.4% of the observed deviance (Table 4A). There was a 3.5 times greater chance of finding juvenile *C. nuttallii* in the lower part of the water column than the upper part of the water column. The presence of this species appeared to have a seasonal trend indicated by the high probability of presence during late July and early August (Figure 9A). The presence of *C. nuttallii* varied with salinity with lower probabilities of their being present as salinity increased (Figure 9B).

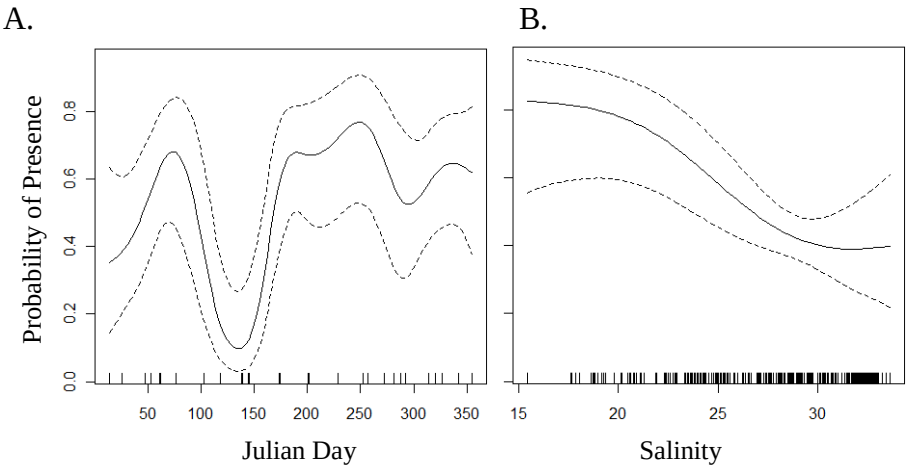


Figure 9. Generalized additive model (GAM) plots for probability of presence for *C. nuttallii.* Influence of A) day of the year (Julian Day) and B) salinity on the probability of presence for *C. nuttallii*. GAM results: see Table 4 (A). Solid line is the mean partial effect, dashed lines are the 95% CI and inner ticks are the data points.

Abundance: Estuarine hydrodynamics played a role in the abundance of *Clinocardium nuttallii* when it was present. The model that included depth, day, salinity and chlorophyll *a* explained 27.1% of the observed deviance (Table 4B). The results of the GAM indicated juvenile *C. nuttallii* abundance was higher in the lower part of the water column and abundance decreased as salinity increased (Figure 10).

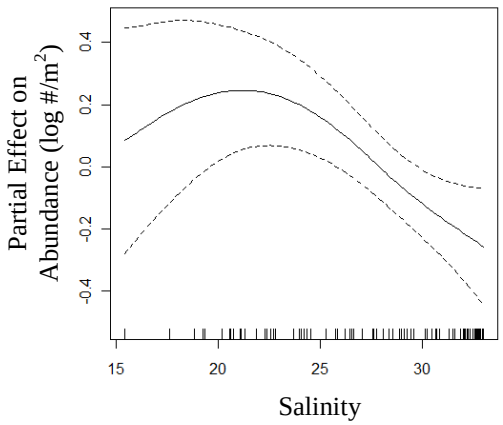


Figure 10. Generalized additive model (GAM) plots for abundance for *C. nuttallii.* Partial effect of salinity on *C. nuttallii* abundance (log number/m^2). GAM results: see Table 4 (B). Solid line is the mean partial effect, dashed lines are the 95% CI and inner ticks are the data points.

Mytilus spp.

Presence/Absence: For this species the GAM model that included depth, tide and Julian Day explained 22.8% of the observed deviance (Table 5). The model indicated the chance of finding juvenile *Mytilus* spp. in the lower part of the water column was 7.2 times higher than in the upper water column and a 2.2 times greater chance of their being present during flood than ebb tides. The highest probability of presence, approximately 85%, was during fall, specifically late September and early October (Figure 11).

Abundance: The model that included depth explained 11.7% with higher abundance in the lower part of the water column. None of the variables were significant.

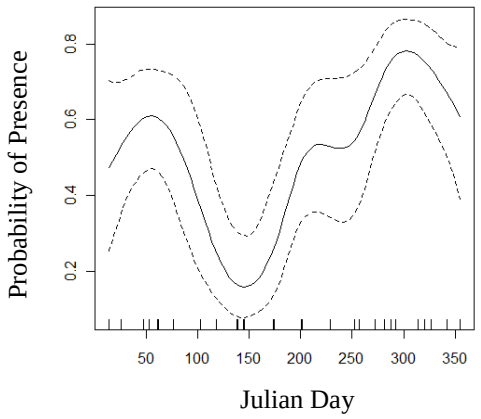


Figure 11. Generalized additive model (GAM) plots for probability of presence of *Mytilus* spp. Influence of day of the year (Julian Day) on the probability of presence for *Mytilus* spp. GAM results: see Table 5. Solid lines are mean probability, dashed lines are the 95% CI and inner ticks are the data points.

DISCUSSION

Juvenile bivalves collected in the Coos estuary included *Clinocardium nuttallii, Macoma* spp., *Mytilus* spp., *Siliqua* spp., and individuals from the superfamily Tellinoidea. Morphological features and molecular techniques were used to confirm the taxonomic identification (Chapter II). Size data indicated the bivalves collected during

this study were well over the size of bivalves at the time of metamorphosis. The length of metamorphosis for *Macoma* spp. is between 255-330 µm (Brink 2001), for *Siliqua* spp. is about 300 µm (Breese and Robinson 1981), for *C. nuttallii* is less than 1.0 mm (Liu *et al.* 2009), and for *Mytilus* spp. is 320-330 µm (Strathmann 1987; Brink 2001). The size of metamorphosis for the Tellinoidea individuals is not reported due to the uncertainty of species or genus identification. Size at metamorphosis varies depending on species and the temperature, salinity, and food availability during larval development; however, the majority of bivalves reach metamorphosis and settle well before they reach 1 mm in length (Strathmann 1987; Brink 2001; Gosling 2003). Bivalves caught in the plankton during this study were much larger than the size at metamorphosis. These individuals were much too large to be larvae or even newly settled larvae. Their size indicates that they were juveniles that had spent time as settled individuals growing on the bottom. Determining the age of the juvenile bivalves is quite difficult but they were likely between a few months to one-year post-metamorphosis.

During this study *Macoma* spp. was the most abundant species collected from the plankton with almost 3.5 times as many individuals compared to the other four taxa. The reason for this is not clear. *Macoma* spp. are a fairly abundant taxon in Coos Bay mudflats, but *Clinocardium nuttallii* is also abundant (personal observation) and both are recreationally harvested. It is likely the *Macoma* spp. complex is a mixture of *M. inquinata*, *M. balthica*, and *M. nasuta*.

Depth was an important factor for all five taxa of bivalves and I observed a higher probability of presence (for all five taxa) and higher abundance (for three taxa) in the lower part of the water column. Juveniles settle on the benthos, and have the ability to

secrete a thread, which provides an opportunity for lift, and, once lifted off the bottom horizontal currents carry the drifting juvenile clam. As a result of being lifted off the bottom, they would occur more frequently and more abundantly near the bottom. What was surprising is that juveniles were collected in the upper part of the water column, which sampled from the surface to approximately 7 meters depth; a significant number of thread drifters were caught between 7 and 15 m off the bottom. During larval stages, bivalves possess a velum which is used for swimming; however, at the juvenile stage they no longer have this structure. Without swimming capability, vertical movement is more difficult, but apparently not impossible. To try to determine how they are being transported into the surface waters I looked at a terrestrial animal with a similar behavior.

Juvenile spiders exhibit a behavior, similar to thread drifting, known as ballooning in which they use wind currents and silk threads for transport. Humphrey (1987) reported that ballooning occurs when forces on the spider and the silk thread, spider-filament system (SFS), are able to overcome the weight of the spider and the thread, plus the force of attachment to the substratum. SFS will continue to rise as long as the vertical component of wind is greater than the system's free-fall terminal velocity. Basically without lift the SFS will sink, but it lift continues the system will continue to rise. Juvenile bivalves are likely exposed to forces which are greater than the weight of the bivalve and the thread. Shanks and Shearman (2011) collected juvenile *Mytilus* spp. 40 m from the bottom and found they were significantly more abundant during downwelling/relaxation events compared to upwelling events. This is an offshore example of physical processes in the marine environment that generate lift that allows the bivalves to reach more shallow waters. A different physical process occurring in the

estuary could have the same effect. The bottom topography can result in separations of flow at a crest and reattachments at a trough which can lead to the formation of a mixing layer and depending on the turbulence and the amount of flow a boil can be generated (Müller and Gyr 1986). These boils are difficult to study in the field, but using infrared imaging and Chickadel *et al.* (2009) captured surface eruptions of meter sized boils in the Snohomish River estuary in Washington. These localized upwelling events could provide the lift that allows the juvenile bivalves to move from depths to higher surface waters.

The maximum size of individuals collected was 4.9 mm and in general larger individuals were less frequent. The spider study indicated individuals have to be exposed to forces greater than their own weight; thus as bivalves grow the shell thickens, increasing their weight, which makes it harder to obtain initial lift from the bottom. For two of the taxa there was also a relationship between their size and whether they were in the upper or lower part of the water column. *Macoma* spp. collected in the lower net were larger than those collected in the upper net; however, the opposite trend was found for *Clinocardium nuttallii.* These two species have quite different shell morphologies (personal observation). If measuring the width from the dorsal side to the ventral side juvenile *C. nuttallii* is much wider than *Macoma* spp. *C. nuttallii* is spherical in shape while *Macoma* spp. is more flattened. There was no significant size difference between nets for *Mytilus* spp. but the body shape for this species is kind of a mixture between the two previously mentioned species; it is normally wider than *Macoma* spp., but not round like *C. nuttallii.*

For all taxa, except the Tellinoidea, the probability of being present was significantly influenced by Julian Day and this was most likely due to reproductive seasonality. The results from the statistical analysis revealed each taxon had more than one peak of probability of presence throughout the year. If the probability of presence corresponds with the reproductive cycle then multiple peaks would be consistent with bivalve reproductive biology. In England *M. balthica* was reported to have two spawning occurrences, a major pulse in April-May and a minor pulse in November (Caddy 1969). *Siliqua patula*, the Pacific razor clam, has a spawning period of May-June and another peak in late fall (Lassuy and Simmons 1989). *M. edulis* has a partial spawning event in the spring and a second event in the fall after gonad recovery (Gosling 2003). Histological samples from *C. nuttallii* in Garrison Bay, Washington revealed mature bivalves had an extended period, six months, during which their gonads were ripe, which could indicate two spawning events (Gallucci and Gallucci 1982). *C. nuttallii* along the Oregon coast also display an extending spawning period, June through October, (Robinson and Breese 1982).

I attempted to match up peaks in probability of finding drifters with post spawning periods documented in the literature; however, this is quite difficult. Exact spawning times for taxa in this study are unknown, even for the well-studied *M. balthica*. Rae (1978) reported in central California *Macoma* spp. were ripe from February through August. A study in British Columbia by McGreer (1983) found *M. balthica* spawning occurred during June and July. Strathmann (1987) reported spawning occurs over an extended period, spring-summer. In addition to variability in reproduction, *M. balthica* growth rates of all stages vary with environmental factors specifically faster growth in

warmer temperature (Gilbert 1973; McGreer 1983). I was unable to determine when the drifters were spawned and how long they were in the plankton. The data suggested that the probabilities of finding them in the plankton increases during certain times of the year which is likely a result of reproductive cycle.

Macoma spp. abundance was significantly affected by tidal cycle with higher abundances occurring during ebb tides. The estuarine hydrodynamic data supported this pattern. Abundance was higher at warmer temperature, lower salinities and lower chlorophyll *a* concentrations which are all characteristics of ebb tides. Roegner and Shanks (2001) found that chlorophyll *a* was transported into the estuary from the nearshore ocean which resulted in higher concentrations during flood tides compared to ebb tides. A possible explanation for this observed pattern are that *Macoma* spp. are trying to leave the estuary or move to a lower part of the estuary. In the Wadden Sea, Beukema and de Vlas (1989) found drifting *M. balthica* abundance was higher during ebb tides suggesting initial settlement was in the estuary and secondary dispersal was directed toward the North Sea. Another possibility is juveniles are displaying an ontogenetic shift. If initial settlement occurs in the high intertidal, *Macoma* spp. may be moving to lower intertidal and subtidal habitats and this would be done most efficiently during ebb tides. In the North Sea, higher growth rates, higher annual survival, and lower parasite infections for juveniles were found in the lower intertidal compared to higher intertidal populations (Hulscher 1973; Beukema *et al*. 1977; Moorsel 1979 in Beukema *et al.* 1977).

The individuals from the superfamily Tellinoidea were influenced by tidal cycle with a higher probability of presence during ebb tides. It is somewhat difficult to

determine why this pattern was observed without knowing to which species or genus these individuals belong. While the exact identification is not certain, knowing the superfamily may allow some general conclusions to be drawn. *Macoma* spp. are also a member of the superfamily Tellinoidea, and *Macoma* spp. collected in this study were more abundant during ebb tides. It is possible bivalves from the same superfamily have a similar life history, thus, maybe these unidentified Tellinoideas initially settle in the upper intertidal and move to the lower area, during ebb tides, for similar reasons as the *Macoma* spp.

The probability of presence of *Mytilus* spp. was influenced by tidal cycle with higher probabilities of being present during flood tides compared to ebb tides. This is different than the pattern observed for *Macoma* spp. One reason for the difference could be the variation in life histories for the two genera. *Macoma* spp. are benthic bivalves that live solitarily in a burrow while *Mytilus* spp. are gregarious bivalves, that primarily live attached to substrate in the intertidal or wave exposed areas. *Mytilus* spp. are thought to normally occur in the intertidal zone; however, *M. trossulus* populations occur in subtidal habitats as well (Selin and Lysenko 2006). Shanks and Shearman (2011) collected *M. trossulus* juveniles at depth and these individuals had not been in the intertidal as indicated from the lack of darkening on their shell (Trevelyan and Chang 1987). The juveniles I collected during flood tides were possibly from a subtidal population and they were drifting to a more suitable habitat.

Clinocardium nuttallii was influenced by salinity in way similar to *Macoma* spp. with a decrease in drifters as salinity increased. Unlike *Macoma* spp., *C. nuttallii* was not influenced by tidal cycle. There are a few possibilities for this pattern: lower salinities

create an unfavorable habitat increasing the likelihood of drifting or exposure to increased salinities in the water column is unfavorable and the juveniles prefer to stay on the substrate. Both of these possibilities are related to salinity tolerances. The European cockles, *Cerastoderma* spp., have different shell morphologies depending on the salinity of their environment suggesting they are able to adapt to variations in physical parameters (Mariani *et al*. 2002). If this were also true for the species in this study this could indicate a range of salinity tolerances and changes in salinity may not have a direct effect. It is possible *C. nuttallii* also is more abundant during falling tides despite the lack of significance of the statistical analysis.

Siliqua spp. were also influenced by salinity and abundance was highest at very high salinities. Razor clams normally occur on the open coast and in high surf areas which are normally higher in salinities. It is possible these juvenile clams are being brought into the estuary from the outer coast during flood tides; however, tidal cycle was not significant. Chlorophyll *a* concentrations were important for the presence and absence of *Siliqua* spp. The results suggested they are more likely to drift at low (<2 µg/L) and high (>4 µg/L) chlorophyll *a* concentrations. Previous studies concluded lack of food can lead to an increase in drifting behavior in *Cerastoderma glaucum*, *C. edule* (Yankson 1986) and *Macomona liliana* (Cummings *et al.* 1992), but when particle concentration is high filter feeders have been shown to decrease ingestion rates (Iglesias *et al.* 1996; Denis *et al.* 1999; Gosling 2003). This suggests there is an optimal chlorophyll *a* concentration level and *Siliqua* spp. may be leaving their habitat when conditions vary from this level. The reason this pattern was not observed in *Macoma* spp. could be due to the differences in feeding techniques. *Macoma* spp. have long split

siphons allowing them to switch to deposit feeding while *Siliqua* spp. have a relatively short fused siphon limiting them to filter feeding.

This study suggested bivalves in the Coos estuary disperse during juvenile stages and focused on how several factors, including size, tidal cycle, seasonality, depth in the water column, temperature, salinity, and chlorophyll *a*, influence the behavior. Analysis of physical estuarine water parameters strongly suggested the juvenile abundance of drifters, with the exception of *Mytilus* spp., increased during ebb tides; however, differences in tidal cycle, specifically, were only observed for *Macoma* spp. and Tellinoidea. Other studies which have detected variations in abundance as a result of tidal cycle sampled over a period which encompassed a full ebb and flood cycle (Beukema and de Vlas 1989; Hiddink *et al.* 2002).

The tides in Coos Bay are categorized as mixed, semi-diurnal meaning there are two highs and two lows every 24 hours, but there is variation in heights of the two highs and the two lows. While the bay is about 20 km long, the tidal influence extends 43 km from the mouth upstream in the South Fork Coos River (ACOE 1975). Coos Bay has the 2nd largest tidal prism, the amount of water that leaves the estuary between the highest high tide and the lowest low tide, out of 12 Oregon estuaries excluding the Columbia River (ACOE 1994). Substantial tidal currents are generated as a result of the tidal flow (ACOE 1994). During this two year period I also sampled over a twenty-four hour period which encompasses two full tidal cycles. Analyzing these data will provide more insight on the effect of tidal cycles on juvenile bivalve thread drifting.

CHAPTER IV

TIDAL TRANSPORT AND DIEL MIGRATION OF FIVE TAXA OF JUVENILE BIVALVES IN COOS ESTUARY, OREGON

INTRODUCTION

Bivalve dispersal occurs during the planktonic larval stages, but for many species it continues in the post-larval stages. After initial settlement, secondary dispersal occurs by secretion of a mucous thread which increases viscous drag resulting in the potential for a juvenile clam to be carried along even via relatively weak currents (Sigurdsson *et al.* 1976). This dispersal mechanism is analogous to a techniques used by juvenile spiders in which they climb to the top of a blade of grass, release a silk thread, and use wind currents to transport and disperse them (Humphrey 1987). For juvenile bivalves, the duration of dispersal stage and the size of the individuals that display the behavior varies depending on the species (Yankson 1986; Beukema and de Vlas 1989; Wang and Xu 1997).

There is evidence that the likelihood of bivalves displaying this behavior is dependent on biological conditions and the physical environment. Previous studies have tested the effects of predator interactions (Hiddink *et al.* 2002), food concentrations (Cummings *et al.* 1992) and the physical parameters such as tidal cycles (Garrison and Morgan 1999) or diel migrations (Armonies 1992) on thread drifting. A majority of the previous studies examined tidal cycles and diel migration separately. Armonies (1992) found a trend in regard to the diel rhythm for *Macoma balthica, Cerastoderma edule* (the European cockle), and *Ensis directus* with higher abundance during the night. The

plankton nets were stationary and samples were only retrieved during low tide, thus, there was no way to determine if drifting bivalves were entering the plankton net during the flood or ebb tide. Beukema and de Vlas (1989) found nearly ten times more *M. balthica* drifters during flood tides compared to ebb tides; however, their study did not consider diel variation.

Like many behaviors in the marine environment, the act of thread drifting is likely influenced by more than one factor and it is also likely that these factors interact with one another. The Coos estuary is characterized by mixed semi-diurnal tides, two high tides and two low tides within a twenty-four hour period. By sampling over this period I was able to investigate whether tidal cycle or diurnal variation had an influence on thread drifting behavior and whether an interaction between the two occurs.

METHODS

Data Collection

From October 2009 until May 2011, I took plankton tows on a ca. quarterly basis. I sampled in October 2009, March, May, July, and October of 2010, and February and May 2011. I made plankton tows in the Coos Estuary, Coos Bay, Oregon near the airport (N 43°25’16’’, W 124°16’19’’). Depending on the tidal height water depth ranged from 13 m to 15 m. I used a 1 m Tucker trawl with 0.5 mm mesh equipped with two nets that could be opened and closed at different depths. Vertically stratified oblique tows were made with each net. On each tow, one net was sampled from within 2 meters of the bottom to mid-depth and the second net was sampled from mid-depth to the surface. I towed at each depth for 10 minutes and measured flow through the nets with a

mechanical flowmeter. During each sampling day tows were taken every two hours for twenty-four hours or until a total of 12 samples, for each net, were collected.

Samples were preserved using borax buffered 5% formalin. Samples collected in May 2011 were preserved in 95% ethanol to allow for molecular analysis. In the laboratory, using a dissecting microscope, I enumerated bivalves and measured the length from the anterior to the posterior with an ocular micrometer to one-tenth mm. I identified juveniles with adult identification guides (Coan *et al.* 2000; Mikkelsen *et al.* 2006; Coan and Valentich-Scott 2007) and molecular techniques (Chapter II).

I obtained tidal information and sunrise/sunset times for Empire, Coos Bay (about 1.5 miles south of the sampling site) from Nobeltec® Tides and Currents version 3.7. To indicate whether it was a flood or ebb tide, I multiplied the tidal heights by -1, thus all negative values represented an ebb tide while all positive values represented a flood tide. In the data analysis I refer to this term as tidal height. I considered the hour before sunset and the hour after sunrise as night time to account for low light levels experienced under water.

During the May 2011 cruise I deployed an Argonuat XR Acoustic Doppler Current Profiler (ADCP) near the study site and it remained there during the 24 hour sampling period. The ADCP was attached to a small platform, with lead weights, that allowed the device to set about .25 m off the estuary bottom. I used a winch equipped with a trigger mechanism to lower the ADCP to the bottom. I set the ADCP sampling parameters to divide the water column into six cells and to take measurements every 15 minutes. I averaged cells 4 and 5 to obtain a speed for the upper part of the water column and averaged cells 2 and 3 for the lower part of the water column.

Data Analysis

To analyze the results I used the statistical program R™ version 2.13.1. I analyzed the relationships between the explanatory variables and the log transformed abundance of bivalve thread drifters, log (Ab +1), for each of the taxa identified using General Additive Models (GAM) as implemented in the mgcv library, a non-parametric regression package of R (R Development Core Team 2010). GAMs are similar to stepwise regressions in that initially all variables are included and the least significant variables are removed on a step-by-step basis until all variable remaining are significant. GAMs, however, allow the exploration of non-linear functional relationships between dependent and explanatory variables, fitting predictor variables by smooth functions (Guisan et al. 2002). The general model form of a GAM is

$$\mathrm{E}(Y) = \alpha + \sum_{j=1}^{p} f_j\left(\mathrm{X}_j\right) + \varepsilon$$

Where E(Y) is the estimated value of the response variable, α is the population intercept, *Xj* are the covariates and *fj* are the smooth unknown functions estimated for each covariate, and $\mathcal{E}$ is the error term (Wood 2006).

I reported the abundance of bivalves as number/100 m^2 and to calculate this divided the raw number of bivalves by the volume of water filtered and multiplied by the depth of water sampled. For example, if the tow was from the surface to 7 meters the depth was 7. I multiplied by 100 to obtain number/100 m^2. I introduced depth (upper or lower net) and diel variation (day or night) as factors and considered the continuous variable tidal height as smoothed terms in the model and estimated with thin plate regression splines. I tested for interactions between tidal height and diel variation.

Akaike's information criterion (AIC) was used to select the optimal set of variables for inclusion in the models. Model validation included the verification of homogeneity, normality and independence assumptions (Zuur *et al*. 2009). Initially I attempted to combine all seven cruises in a single analysis; however there was high variation in abundance between cruises (Figure 1), most likely a result of the species seasonal pattern of spawning (Chapter III), and the data did not meet the above mentioned assumptions. To overcome this I analyzed each cruise separately. During a number of the cruises some of the taxa were not collected in any of the samples or were only collected in one sample. Due to the extremely low abundance these taxa were not analyzed for that specific cruise.

RESULTS

I collected five types of bivalves from the Coos Bay plankton during October 2009 through July 2011. Morphological features and molecular techniques indicated juvenile bivalves collected included *Clinocardium nuttallii*, *Macoma* spp., *Siliqua* spp., *Mytilus* spp. and individuals from the group Tellinoidea, possible *Tellina modesta* (Chapter II). The size data indicated the bivalves collected during this study were well over the size of bivalves at the time of metamorphosis, confirming they were definitely juveniles and not larvae (Chapter III).

The average abundance of each taxa varied between cruises (Figure 1). The maximum average (±SE) abundance for *Macoma* spp. was 310.3/100 m^2 ± 55.7 and occurred during at night during the March 2010 cruise. *Siliqua* spp. and *C. nuttallii* were most abundant during the July 2010 cruise at night with an average (±SE) of 290.3/100 m^2 ± 115.2 and 379.3/100 m^2 ± 150.3, respectively. The highest abundance for Tellinoidea was in the October 2009 night samples with an average (±SE) of 33.1/100 m^2

± 18.0. *Mytilus* spp. was also most abundant during the October 2009 cruise but during the day. The average (±SE) was 36.7/100 m^2 ± 6.6. During the May 2011 cruise overall bivalve abundance was extremely low.

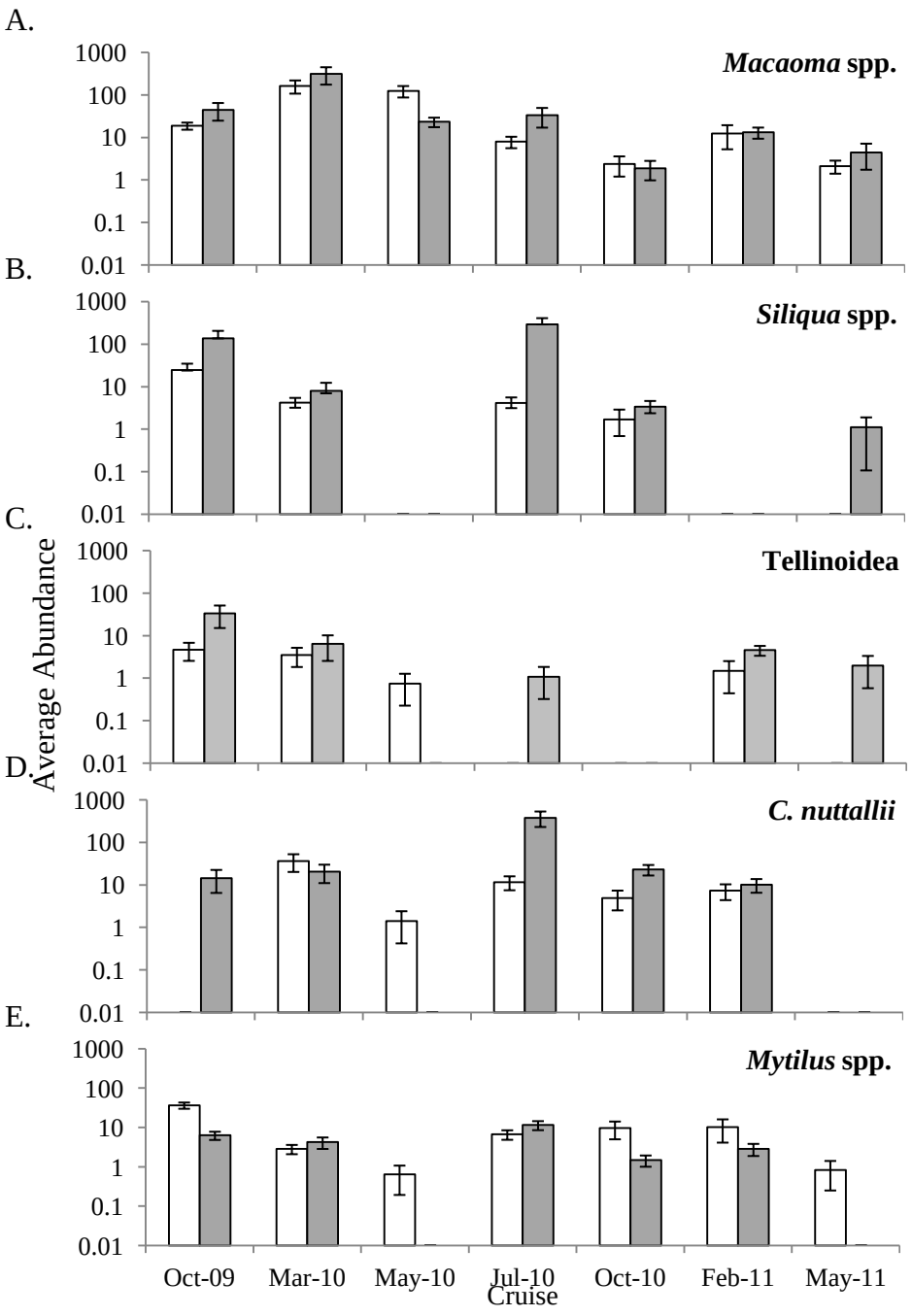


Figure 1. Average abundance of bivalves: Average abundance (log #/100 m^2 +.01) ±SE for each cruise during the day (white) and night (gray).

Acoustic Doppler Current Profiler

Data from the ADCP indicated that maximum current speeds were during ebb tide and minimum speeds were during slack tide (Figure 2). This pattern was true for the upper and lower part of the water column. There was a difference in speed between the upper and lower part of the water column and the largest difference occurred after slack high tide as water began leaving the estuary.

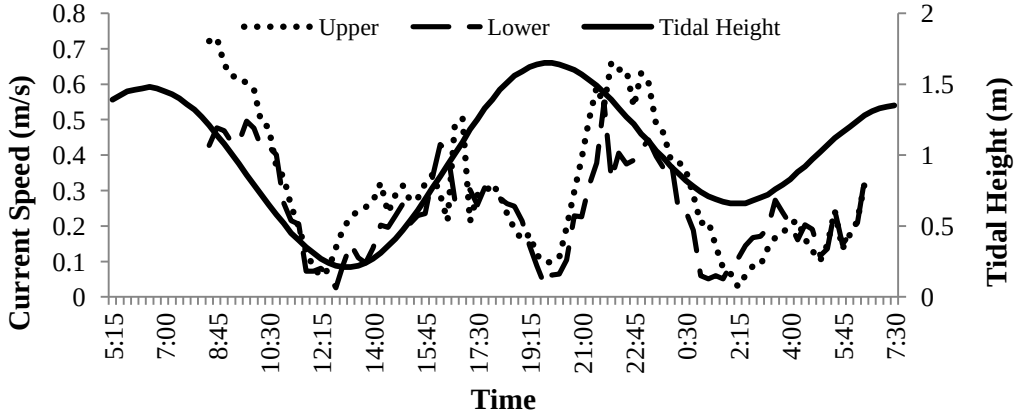


Figure 2. ADCP Data for May 2011 Cruise. Tidal height (m) and average current speed (m/s) in the upper and lower part of the water column over the 24 hour sampling period. The tidal height is plotted pre and post sampling period to show more of the tidal cycle.

October 2009

During the October 2009 cruise *Macoma* spp., *Siliqua* spp., *Clinocardium nuttallii* and Tellinoidea abundances higher during falling tide at night (Fig 3A). For each of these taxa the GAM model that included tidal height and diel variation explained >70% of the observed deviance (Table 1A-D – All tables in Appendix C). For these taxa there was a significant interaction between tidal height and diel variation. During the day there was no difference in abundance between flood and ebb tide; however, during the night there was a maximum in abundance during falling tide (Figure 3B-E). The pattern for *Mytilus* spp. was different (Figure 4A). The GAM model that included depth and diel

variation explained 59.8% of the observed deviance (Table 1E). *Mytilus* spp. abundance was higher during the day and in the lower part of the water column.

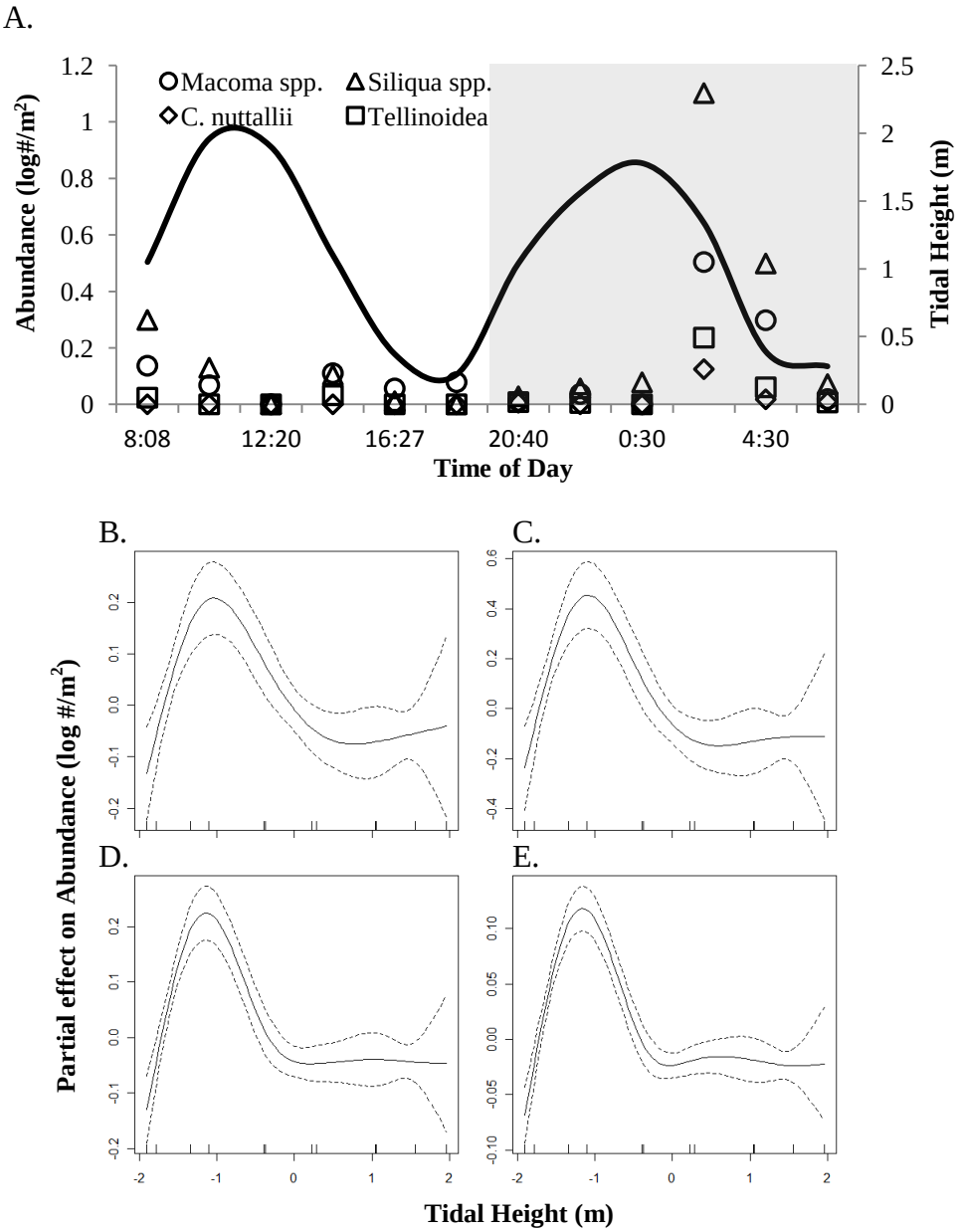


Figure 3. October 2009 Cruise *Macoma* spp., *Siliqua* spp., Tellinoidea, *C. nuttallii*: A) Abundance (log number/m^2) during the 24 hour sampling period. The black line represents tidal height (m) and the shaded box represents night. Partial effect of tidal height (m) on abundance (log number/m^2) of B) *Macoma* spp., C) *Siliqua* spp., D) Tellinoidea, and E) *C. nuttallii* at night. Negative tidal heights represent ebb tides and positive tidal heights represent flood tides. Solid line is the mean partial effect, dashed lines are the 95% CI and inner ticks are the data points.

A.

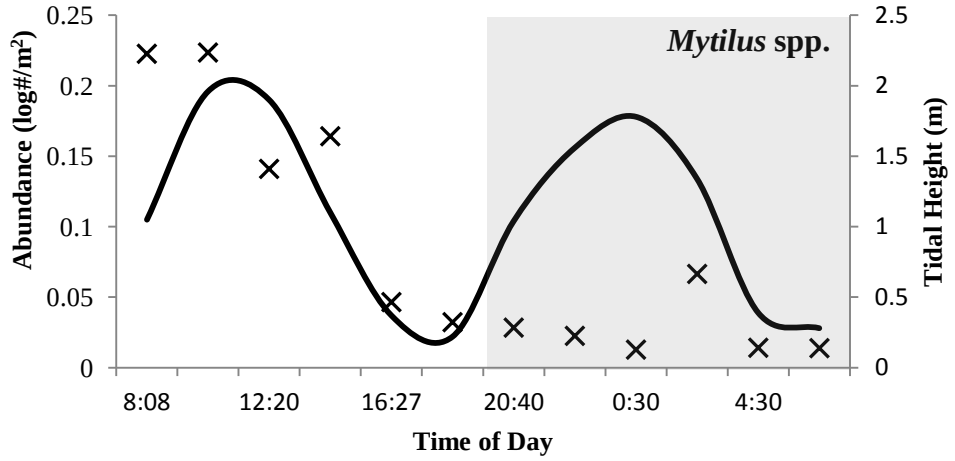
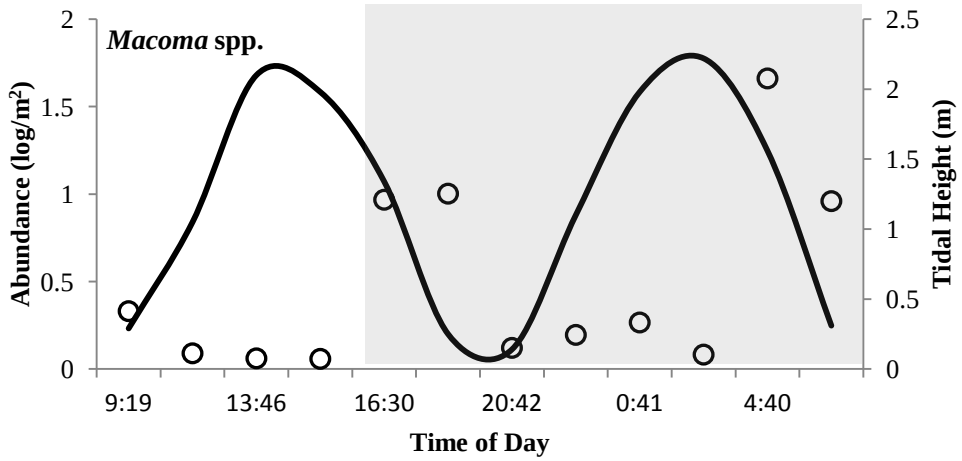


Figure 4. October 2009 Cruise *Mytilus* spp.: A) Abundance (log number/m^2) of *Mytilus* spp. during the 24 hour sampling period. The black line represents tidal height (m) and the shaded box represents night.

March 2010

The pattern of abundance of *Macoma* spp., Tellinoidea, and *Clinocardium nuttallii* was similar in October 2009 and March 2010 (Figure 5A, 6A, and 7A). For these species the GAM model that included tidal height and diel variation explained >60% of the observed deviance (Table 2A, B, and C). Abundance was highest during ebb tides at night (Figure 5A, 6B, and 7C). The results for *Siliqua* spp. and *Mytilus* spp. indicated none of the variables were significant; however, the data suggested juvenile bivalve abundance was higher at night (Figure 8A and B).

A.



B.

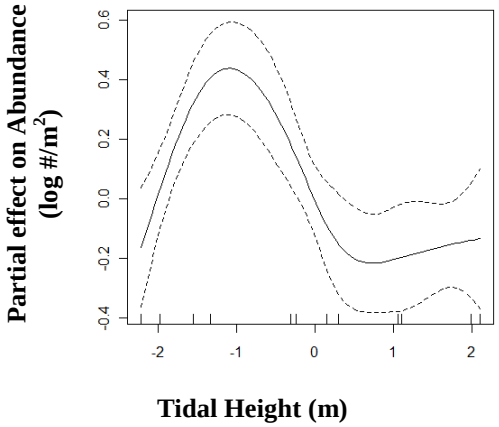
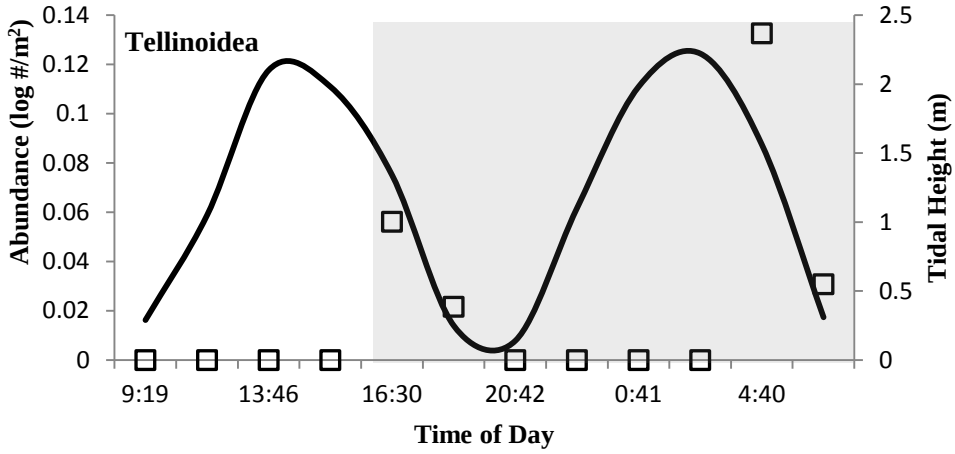


Figure 5. March 2010 Cruise *Macoma* spp.: A) Abundance (log number/m^2) of *Macoma* spp. during the 24 hour sampling period. The black line represents tidal height (m) and the shaded box represents night. Partial effect of tidal height (m) on abundance (log number/m^2) of *Macoma* spp. and night. Negative tidal heights represent ebb tides and positive tidal heights represent flood tides. Solid line is the mean partial effect, dashed lines are the 95% CI and inner ticks are the data points.

A.



B.

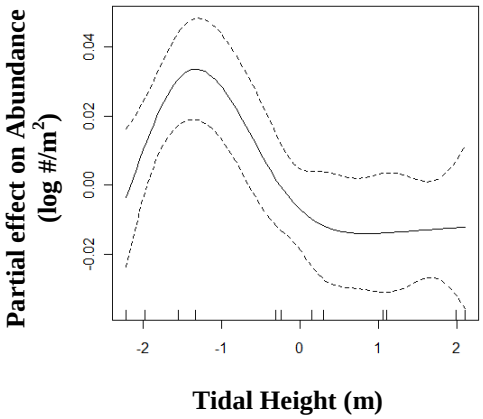


Figure 6. March 2010 Cruise Tellinoidea: A) Abundance (log number/m^2) of Tellinoidea during the 24 hour sampling period. The black line represents tidal height (m) and the shaded box represents night. B) Partial effect of tidal height (m) on abundance (log number/m^2) of Tellinoidea at night. Negative tidal heights represent ebb tides and positive tidal heights represent flood tides. Solid line is the mean partial effect, dashed lines are the 95% CI and inner ticks are the data points.

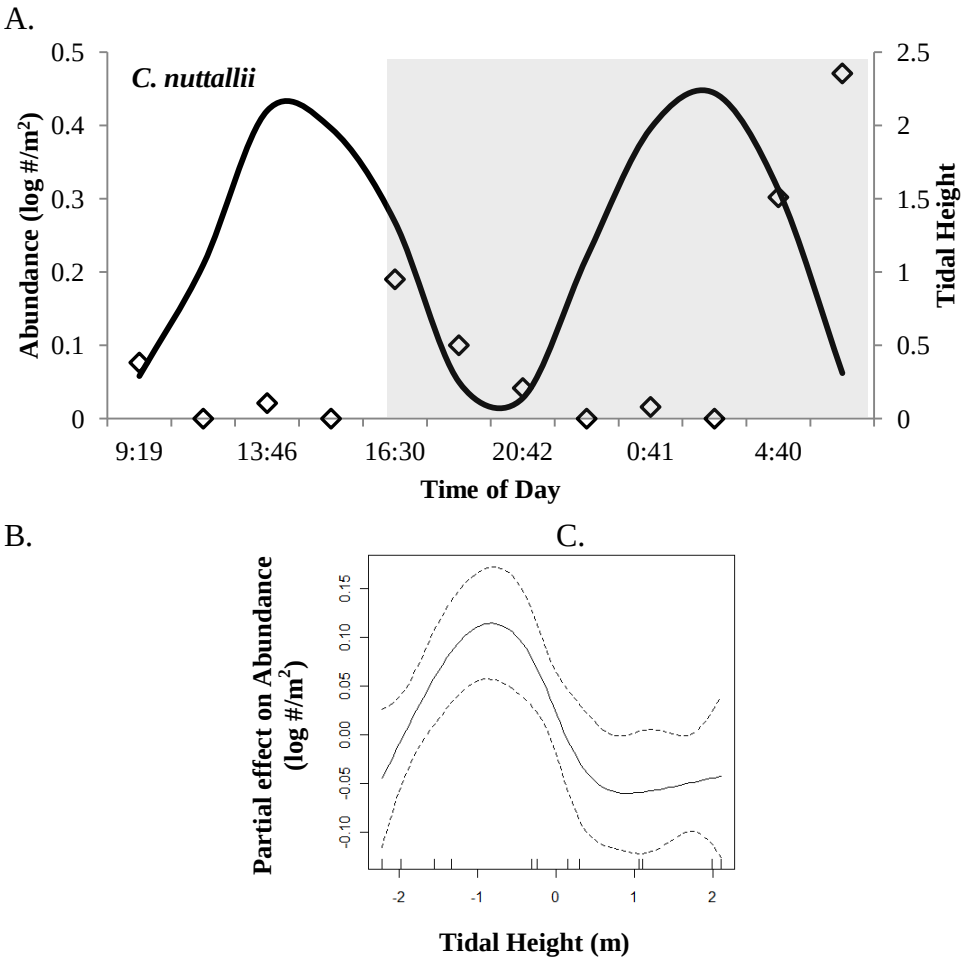
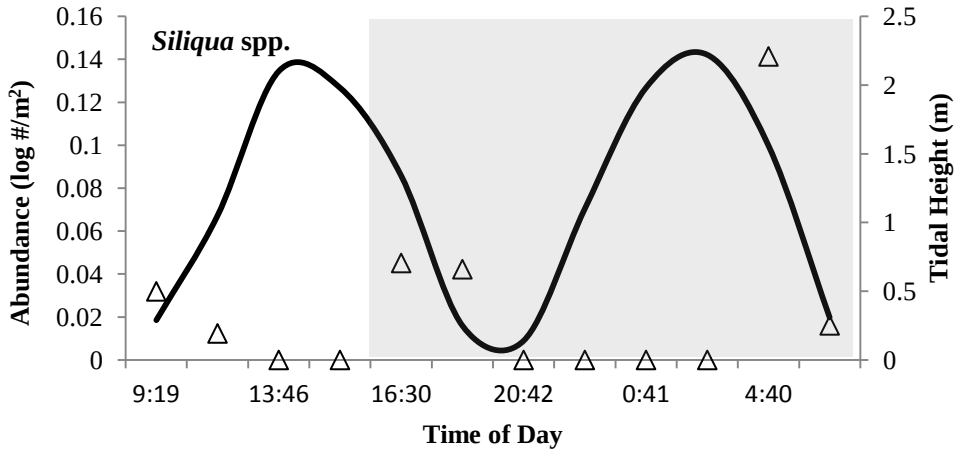


Figure 7. March 2010 Cruise *Clinocardium nuttallii*: A) Abundance (log number/m^2) of *C. nuttallii* during the 24 hour sampling period. The black line represents tidal height (m) and the shaded box represents night. B) Partial effect of tidal height (m) on abundance (log number/m^2) of *C. nuttallii* during at night. Negative tidal heights represent ebb tides and positive tidal heights represent flood tides. Solid line is the mean partial effect, dashed lines are the 95% CI and inner ticks are the data points.

A.



B.

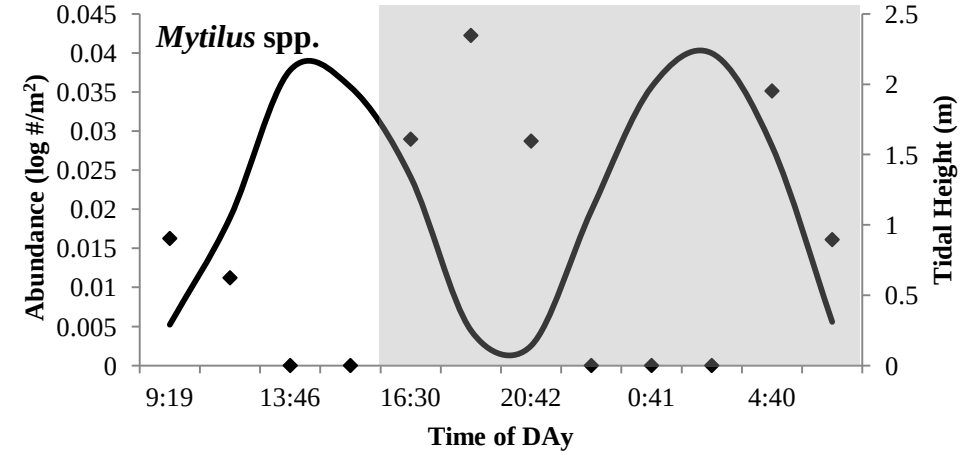


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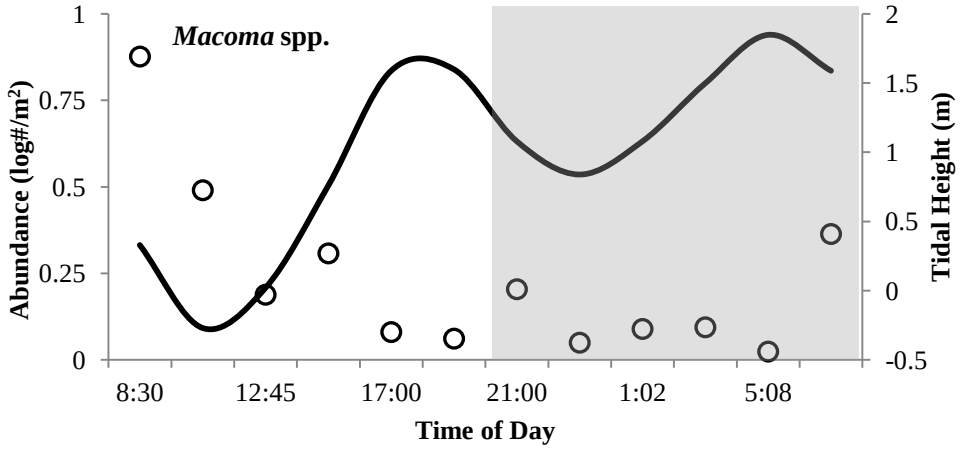
Figure 8. March 2010 Cruise *Siliqua* spp. and *Mytilus* spp.: Abundance (log number/m^2) of A) *Siliqua* spp. and B) *Mytilus* spp. during the 24 hour sampling period. The black line represents tidal height (m) and the shaded box represents night.

May 2010

During this cruise there were no *Siliqua* spp. in any of the twelve samples, and *Clinocardium nuttallii* and *Mytilus* spp. were only collected in one sample, therefore, these three taxa were not analyzed. For *Macoma* spp. although they were again more abundant during ebb tides, during this cruise they were more abundant during the day (Figure 9A). The GAM model that included day/night, tidal height and depth explained

70.5% of the observed deviance (Table 3). There was a significant interaction between diel variation and tidal height. During the day there was a greater abundance of juveniles during ebb tides than during the flood tides (Figure 9B). During the night there was no difference between ebb and flood tides.

A.



B.

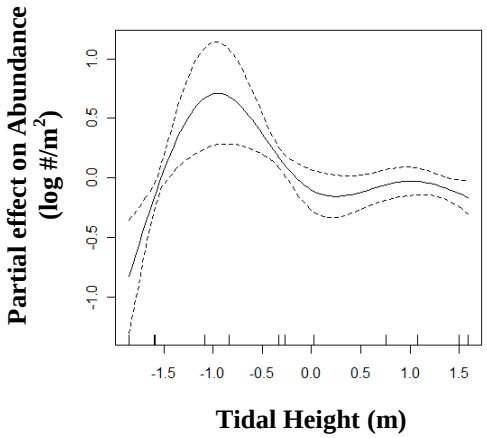


Figure 9. May 2010 Cruise *Macoma* spp.: A) Abundance (log number/m^2) during the 24 hour sampling period. The black line represents tidal height (m) and the shaded box represents night. Partial effect of tidal height (m) on abundance (log number/m^2) of *Macoma* spp. during the day. Negative tidal heights represent ebb tides and positive tidal heights represent flood tides. Solid line is the mean partial effect, dashed lines are the 95% CI and inner ticks are tge data points.

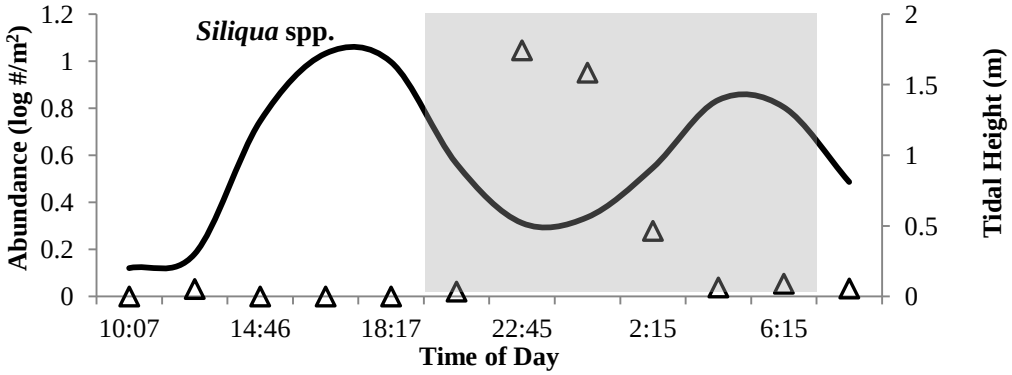
July 2010

During this cruise, only one sample had Tellinoidea bivalves, thus this taxon was not analyzed. For *Siliqua* spp. abundance was higher again during the night, but during low slack tide (Figure 10A). The GAM model that included tidal height, diel variation and depth explained 66.5% of the observed deviance (Table 4A). There was a significant interaction between tidal height and day/night. While there was no difference in abundance between the two tides during the day, at night there was greater abundance during slack tide (Figure 10B). For *Macoma* spp., *Clinocardium nuttallii* and *Mytilus* spp. there were no clear patterns related to tidal height or day/night (Figure 11A, B and C). The GAM model for *C. nuttallii* that included day/night explained 23% of the observed deviance (Table 4B) and indicated abundance was higher at night. *Mytilus* spp. was significantly more abundant in the lower part of the water column, and the GAM model that included depth explained 33% of the observed deviance (Table 4C).

October 2010

There were no Tellinoidea individuals collected during any of the tows during this cruise. The abundance of *Clinocardium nuttallii* suggested juveniles were more abundant during ebb tides at night time (Figure 12); however, neither tidal cycle nor diel variation were significant. The GAM models for *C. nuttallii* only included depth as a significant variable and explained 18% of the observed deviance (Table 5). For *Macoma* spp., *Siliqua* spp., and *Mytilus* spp. no clear patterns were observed (Figure 13 A, B, and C) and none of the variables included in the GAM were significant.

A.



B.

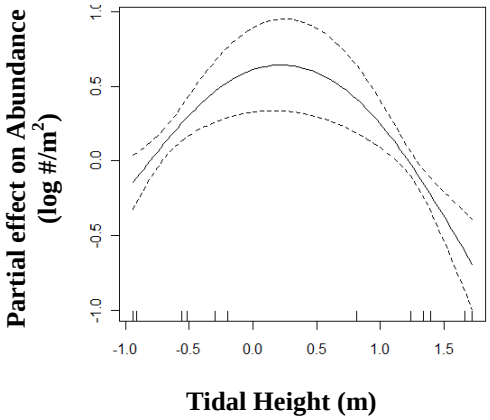


Figure 10. July 2010 Cruise *Siliqua* spp.: A) Abundance (log number/m^2) during the 24 hour sampling period. The black line represents tidal height (m) and the shaded box represents night. B) Partial effect of tidal height (m) on abundance (log number/m^2) of *Siliqua* spp. during the night. Negative tidal heights represent ebb tides and positive tidal heights represent flood tides. Solid line is the mean partial effect, dashed lines are the 95% CI and inner ticks are the data points.

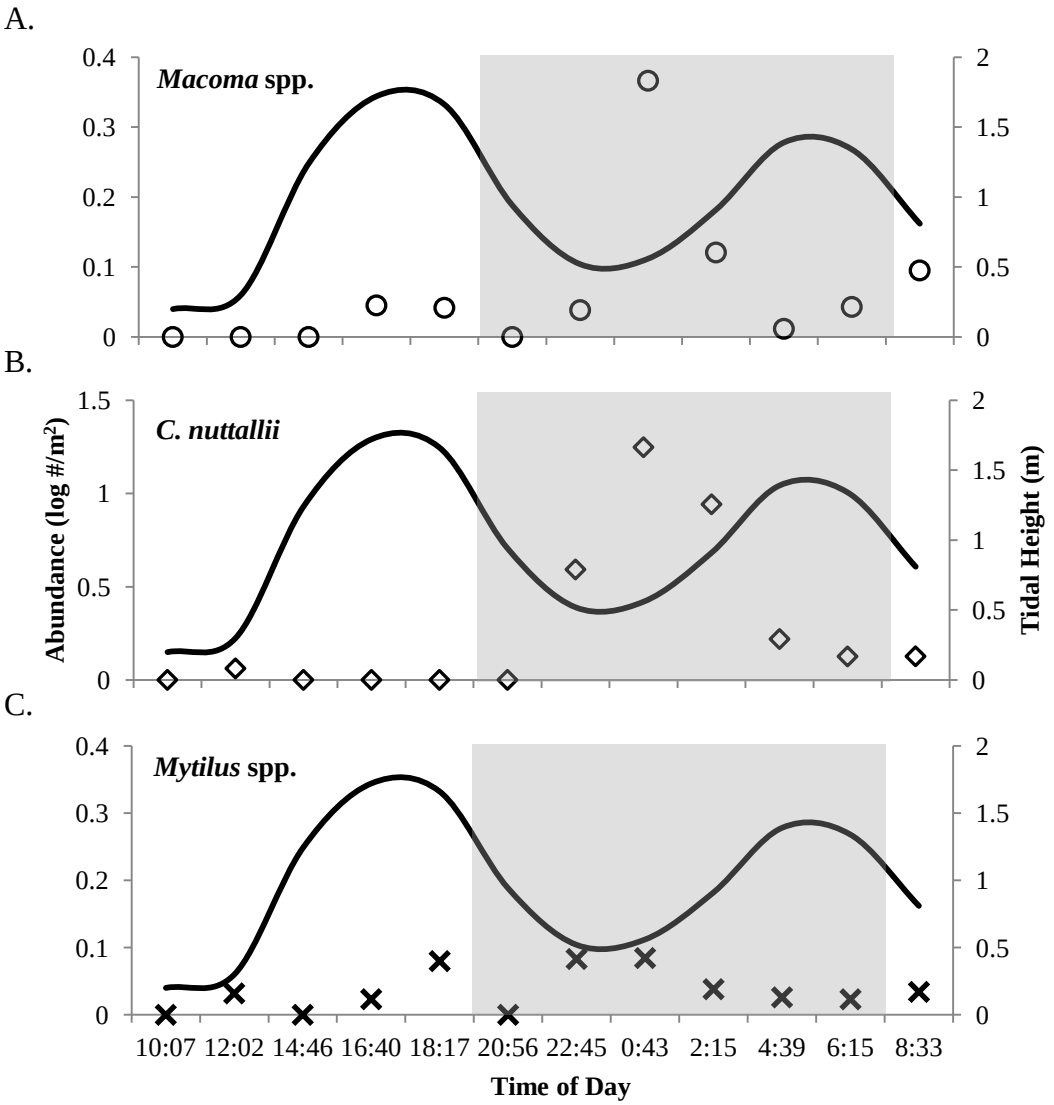


Figure 11. July 2010 Cruise *Macoma* spp., *C. nuttallii*, *Mytilus* spp.: Abundance (log number/m^2) during the 24 hour sampling period. The black line represents tidal height (m) and the shaded box represents night.

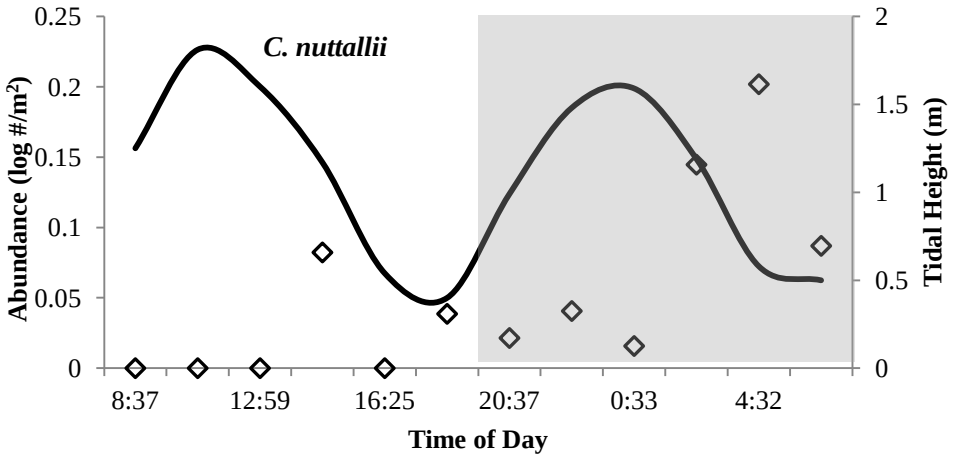


Figure 12. October 2010 Cruise *C. nuttallii*: Abundance (log number/m^2) during the 24 hour sampling period. The black line represents tidal height (m) and the shaded box represents night.

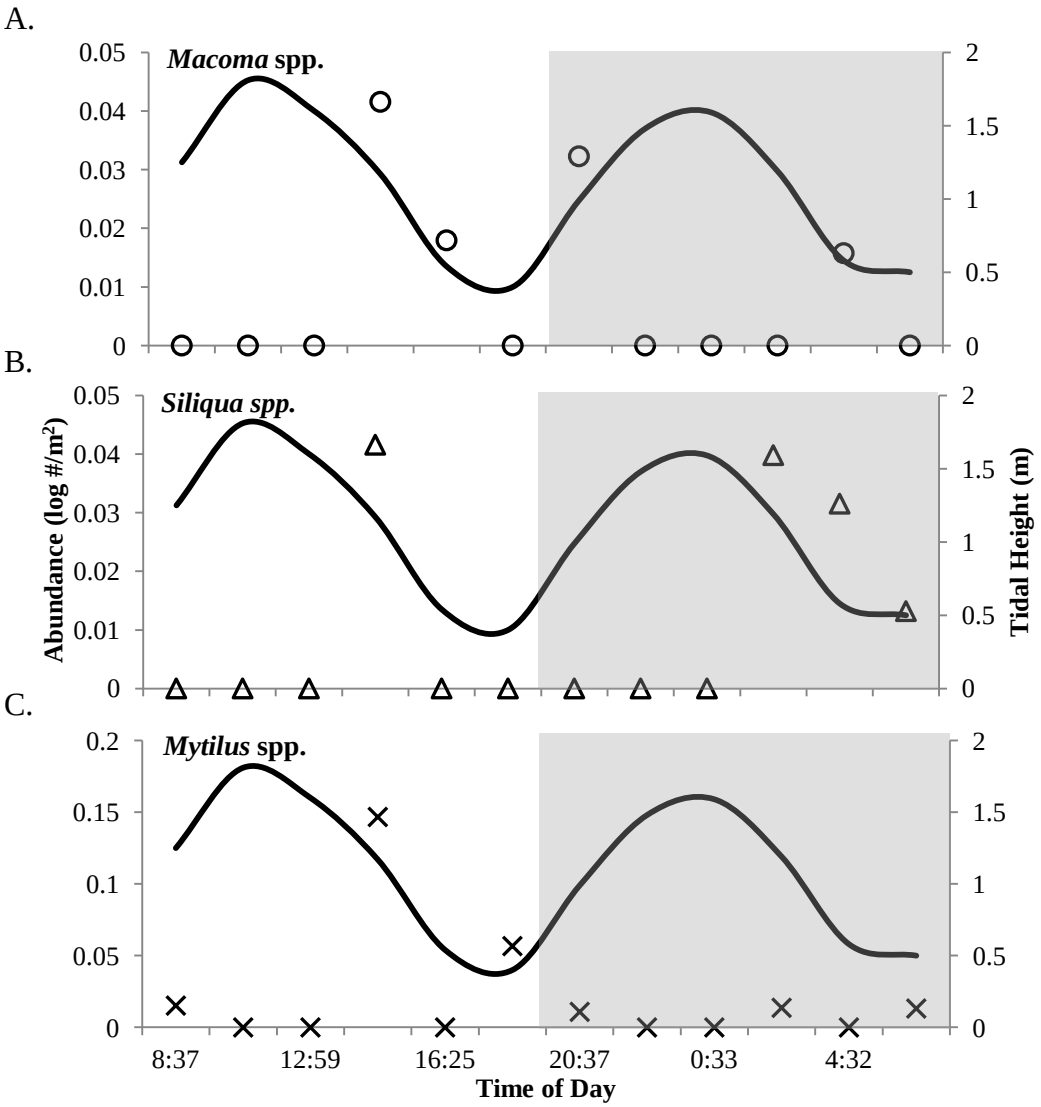


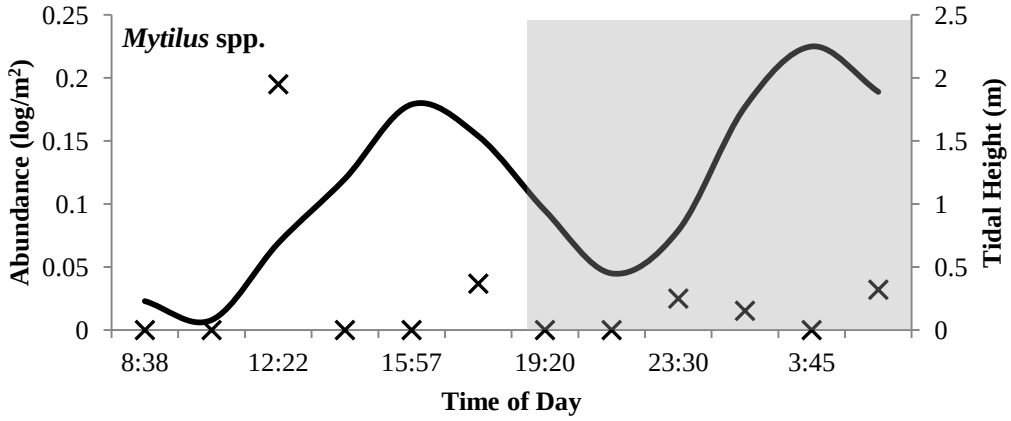
Figure 13. October 2010 Cruise *Macoma* spp., *Siliqua* spp., *Mytilus* spp.: Abundance (log number/m^2) of during the 24 hour sampling period. The black line represents tidal height (m) and the shaded box represents night.

February 2011

No *Siliqua* spp. individuals were collected during this cruise. The abundance of *Mytilus* spp. was highly variable and they were most abundant during the day (Figure 14A). The GAM model that included tidal height, day/night and depth explained 76.8% of the observed deviance (Table 6A). There was a higher abundance during flood tides compared to ebb tides during the day (Figure 14B), but no difference during tides at

night. *Mytilus* spp. was significantly more abundant in the lower part of the water column. I observed no clear patterns relating abundance and tidal height or day/night for *Macoma* spp., Tellinoidea and *C. nuttallii* (Figure 15A, B, and C). *Macoma* spp. and Tellinoidea were more abundant in the lower part of the water column, but this was the only significant variable for these taxa. The GAM models that included depth explained 21.9% and 24.4% of the observed deviance, respectively (Table 6B and C).

A.



B.

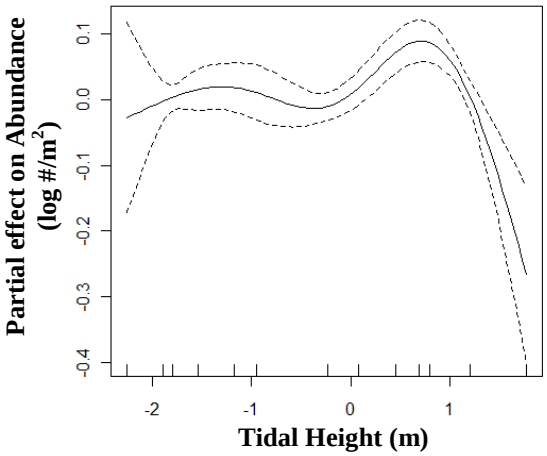


Figure 14. February 2011 Cruise *Mytilus* spp.: A) Abundance (log number/m^2) during the 24 hour sampling period. The black line represents tidal height (m) and the shaded box represents night. B) Partial effect of tidal height (m) on abundance (log number/m^2) of *Mytilus* spp. during the day. Negative tidal heights represent ebb tides and positive tidal heights represent flood tides. Solid line is the mean partial effect, dashed lines are the 95% CI and inner ticks are the data points.

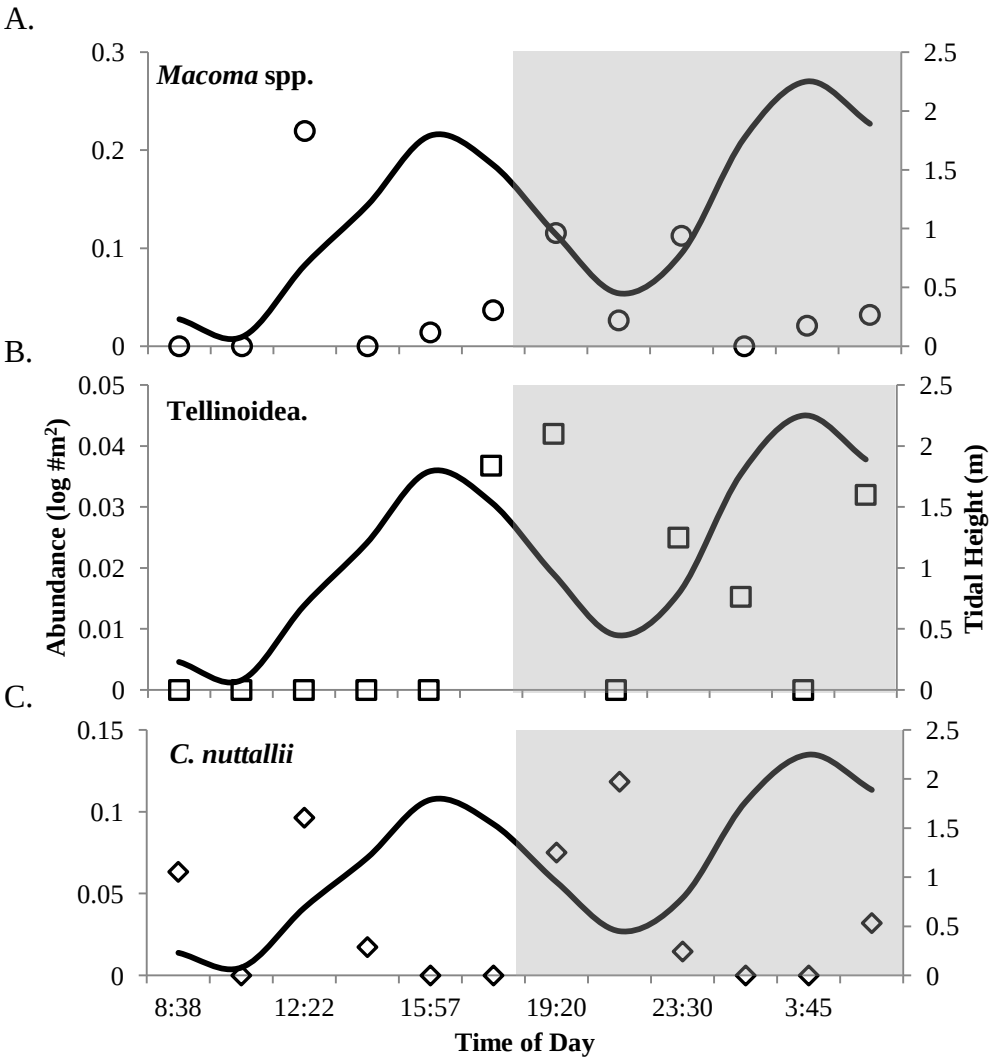


Figure 15. February 2011 Cruise *Macoma* spp., Tellinoidea, *C. nuttallii* spp.: Abundance (log number/m^2) of A) *Macoma* spp., B) Tellinoidea and *C. nuttallii* spp. during the 24 hour sampling period. The black line represents tidal height (m) and the shaded box represents night.

May 2011

During this cruise no *C. nuttallii* were collected and *Siliqua* spp., Tellinoidea and *Mytilus* spp. were only collected in one sample. The data suggested that *Macoma* spp. was more abundant at night during rising tides (Figure 16). However, the GAM model for *Macoma* spp. indicated none of the variables were significant.

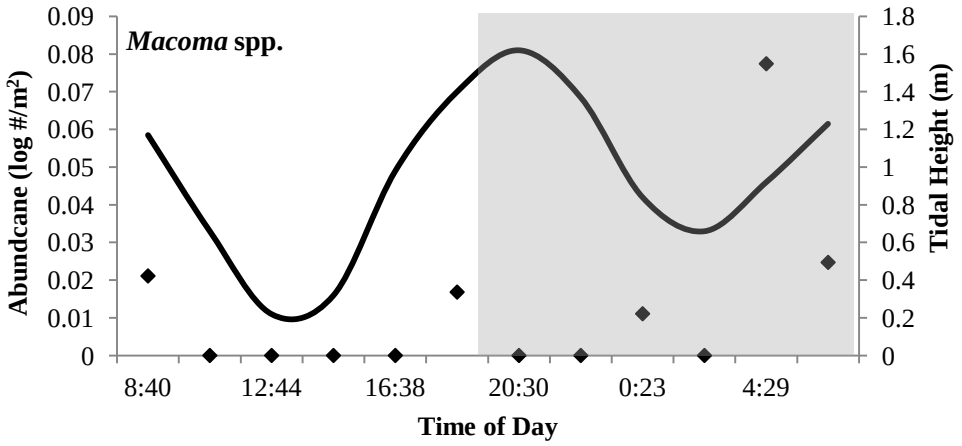


Figure 16. May 2011 Cruise *Macoma* spp.: Abundance (log number/m^2) of *Macoma* spp. during the 24 hour sampling period. The black line represents tidal height (m) and the shaded box represents night.

DISCUSSION

During this one and one-half year study I caught five taxa of juvenile bivalves in the plankton of the Coos estuary: *Macoma* spp., *Siliqua* spp., *Clinocardium nuttalli, Mytilus* spp., and individuals from Tellinoidea. Throughout the study bivalve abundance was extremely variable. This may be partly due to the seasonality of their reproductive cycle and is discussed in detail in Chapter III.

The maximum abundance of *Macoma* spp., *Siliqua* spp., *Clinocardium nuttallii,* and Tellinoidea usually occurred at night during ebb tides and there was no difference in their abundance between tides during the day. This pattern could be a result of predator avoidance. Laboratory experiments by Hiddink *et al.* (2002) observed flatfish, gobies, whiting and crab feeding on thread drifting *Macoma balthica. Pleuronectes platessa*, a species of flatfish, consumed significantly more juvenile bivalves during the day compared to the night. Experiments that examined predation between light and dark were conducted during the day, suggesting the observed behavior is a result of visual

stimuli rather than circadian rhythm (Hiddink *et al.* 2002). If juvenile bivalves were able to avoid predators by thread drifting at night this would be highly advantageous.

During the May 2010 cruise *Macoma* spp. abundance peaked during the daytime ebb tide. This indicated there was likely another variable playing an important role. Beukema and de Vlas (1989) collected the highest number of *Macoma* spp. at maximum current speeds, and during slack tide juveniles were mostly absent. In the laboratory, de Montaudouin *et al.* (2003) observed a higher percentage of *Cerastoderma edule* drifting from an unsuitable habitat at higher (24 cm s^{-1}) than at lower (10 or 20 cm s^{-1}) current speeds. The ADCP was not deployed during this cruise but the data from May 2011 when the ADCP was deployed is still informative. Current speed data indicated that fastest current speeds occurred right after slack tide and through the ebbing tide. During the May 2010 cruise the maximum bivalve abundance was during the middle of the ebb tide. It would be interesting to analyze the May 2011 abundance data with the ADCP current speed data. Unfortunately, only one taxa of bivalve was present during that cruise, it was present in less than half the samples, and in the samples it was present it was 10 times less abundant than on the May 2010 cruise.

As discussed in Chapter III thread drifters require a physical force, a current, great enough to overcome their weight and thus, lift them from the benthos. The strength of the tidal current, or current speed, depends on the volume of water that moves in and out of the estuary (Gross 1993). Coos Bay is an "ebb dominated" estuary (Steve Rumrill, pers comm) meaning more water moves out during ebb tides than comes in during flood tides. This suggests the current speed is highest during ebb tides and this is what the

ADCP data from May 2011 indicated. Therefore, if higher velocities are needed to lift juveniles from the bottom then bivalves would be lifted more easily during ebb tides.

The physical characteristics of an ebb tide could make drifting more likely, but thread drifting during this portion of the tidal cycle could also have biological significance. Garrison and Morgan (1999) indicated drifting *Macoma* spp. displayed selective tidal transport in the York River, Virginia with higher abundances during nocturnal flood and high tides indicating upstream dispersal. Their results are similar to the present study with respect to diel variation; however, in this study there was no indication of upstream dispersal. Juvenile bivalves in Coos Bay estuary, with the exception of *Mytilus* spp., were drifting during ebbing tides. One possibility is that *M. balthica* initially settle into the high intertidal and later move into the lower intertidal similar to a pattern observed for this species in the Wadden Sea (Beukema and de Vlas 1989). Initial spat fall of *M. balthica* was found to be much higher in upper tidal flats compared to lower in the intertidal zone (Armonies and Armonies 1992). However, as the bivalves grow the higher intertidal area becomes unfavorable. In the lower intertidal the percent of time immersed is greater than in the higher intertidal, allowing for longer durations for feeding and thus increased *M. balthica* growth rates (Beukema *et al.* 1977). Hulscher (1973) found that *M. balthica* trematode infection was higher in the upper intertidal and larger individuals were infected more often than smaller individuals. This could indicate that as settled bivalves become larger their risk of infection increases, thus there is a benefit to moving to the lower intertidal. There appear to be a number of potential benefits resulting from relocating to the lower intertidal.

Four of the bivalve taxa, *Macoma* spp., *Siliqua* spp., *Clinocardium nuttallii* and Tellinoidea, had similar behaviors during many of the cruises, but *Mytilus* spp. tended to respond differently. *Mytilus* spp. were often more abundant during the daytime flood tides, and this was consistent over the two year study (Chapter III). Drifting on a flood tide could indicate transport from the subtidal into the intertidal or up the estuary. Mussels are viewed as an intertidal species. Local subtidal populations of *Mytilus* spp. have not been surveyed; however, subtidal populations do exist in other parts of the world, such as, from Baja California to Washington (Chan 1973; Paine 1976; Love *et al.* 1999), the Kamchatka Peninsula (Selin and Lysenko 2006) and Lough Hyne Marine Reserve, Ireland (pers obs.). The present study site is located in the portion of the estuary that is dredged on a regular basis to allow large ships to enter. Dredging could limit the amount of available substrate which mussels need for attachment, thus, they may be drifting to the intertidal to obtain a more suitable habitat.

Thread drifting during increased current speeds did not appear to be as important for *Mytilus* spp. as it was for the other four taxa. The average size of *Mytilus* spp. was smaller than the other taxa of clams (Chapter III). Laboratory experiments indicated smaller *C. edule* required less current speed to obtain lift off from the benthos (de Montaudouin *et al.* 2003). Due to their smaller size the *Mytilus* spp. may be able to be lifted by lower current speeds that are present during rising tides. It is unclear why *Mytilus* spp. abundance did not increase at night. Hiddink *et al.* (2002) found small *M. edulis* in the stomachs of sprat indicating they are preyed on by visual predators.

Five taxa of juvenile bivalves were found in the plankton suggesting they were drifting via mucous threads. Four of the taxa displayed this secondary dispersal method

during ebb tides suggesting they may have been migrating from the upper intertidal to the shallow subtidal or migrating to lower parts of the estuary. Ontogenetic shifts have been documented for *M. balthica;* however, this is the first study on the west coast of the United States that suggests local species could be actively changing their habitat. The timing of their migration is based on both physical and biological parameters. Juveniles may be taking advantage of increased current speeds which occur during ebb tides, but this is done most often at night perhaps to avoid visual predators.

CHAPTER V

CONCLUSION

In this study I found five taxa of juvenile bivalves, *Macoma* spp., *Siliqua* spp., Tellinoidea, *Clinocardium nuttallii* and *Mytilus* spp., in Coos estuary, Coos Bay, OR, USA displaying a method of secondary dispersal known as thread drifting. While thread drifting has been well studied in other parts of the world, this thesis is the first documentation of juvenile bivalves in the plankton of the local nearshore environment. This also appears to be the first record of juveniles of the genus *Siliqua* thread drifting. This identification was surprising because at this size the shape of the shell does not resemble the rectangular shape of the adult razor clams. Drifting has been documented in other razor clam species, but not this genus.

During this study I also discovered a novel species of *Mytilus* spp. It is possible this "unknown" mussel is an invasive species. Mussels are well-known invaders and can colonize new areas quickly as exemplified by the fresh water zebra mussel. It will be important to determine if a new species of mussel has been transported into Coos Bay.

This research suggested tidal transport may carry juvenile bivalves into different habitats, such as into the lower intertidal or further down the estuary. To understand community ecology and population structure it is important to know them. Some of the bivalves I found in the plankton, *Clinocardium nuttallii*, are of commercial importance and all of the taxa I found are harvested recreationally. From 1989-1999 Coos Bay was responsible for 23% of clams commercially harvested in Oregon, and *C. nuttallii* made up 70% of the catch (ODFW 2001). In 1985 recreational catch for the Pacific razor

clams along the Oregon coast was approximately 26,308 kg and valued at $115,000 (Lassuy and Simmons 1989); however, these harvest levels have dropped considerable over the last few years. In 1971 ODFW estimated that in eleven Oregon estuaries 1.8 million clams were recreationally harvested (ODFW 2001). Bivalves are economically important and thus it is important to understand their life history in full to help maintain and manage populations.

Lastly, this research demonstrated that aspects of thread drifting are species specific. The time during the year in which thread drifters are found in the plankton depends on reproductive cycle of the taxa, but more interesting is the difference in abundance of thread drifters depending on tidal cycles and the time of day. Current speed appeared to be playing an important role, but was more important for some species than others and this is possible due to the size of the thread drifting clams. Bigger clams need more force to be lifted from the bottom, but bivalves of smaller size require less force. The results in this study differed from an east coast study that found *Macoma* spp. juveniles more abundant during rising tides. This indicates that the same taxa can behave differently in different locations and this is likely due to the physical processes of the environment. When trying to understand the biology of the organisms in an area it is important to consider the hydrodynamics.

APPENDIX A

SAMPLES FROM NCBI GENBANK

Sample Name	GenBank Acquisition #	Gene	Length (bp)
Abra longicallus	JF496754.1	16S	478
Cultellus scalprum	EU169033.1	16S	479
Donax trunculus	EF417553.1	16S	470
Ensis arcuatus	AJ586446.1	16S	471
Ensis directus	GQ166561.1	16S	470
Ensis ensis	AJ548775.1	16S	470
Ensis siliqua	AJ586469.1	16S	470
Nuttallia japonica	AB476462.1	16S	482
Phaxas pellucidus	DQ2800361.1	16S	473
Siliqua minima	EU169034.1	16S	460
Sinonovacula constricta	EU169035.1	16S	472
Sinonovacula rivularis	EU169036.1	16S	476
Abra longicallus	JF496762.1	COI	431
Donax asper	GQ868451.1	COI	567
Donax canniformis	AY673020.1	COI	463
Donax hanleyanus	GQ8684481.1	COI	567
Donax obesulus	GQ868484.1	COI	567
Macoma balthica	EF044126.1	COI	573
Macoma pentalum	EF044136.1	COI	573
Modiolus arelatus	DQ917604.1	COI	614
Modiolus auriculatus	GQ480317.1	COI	658
Modiolus brasiliensis	DQ264392.1	COI	610
Modiolus computus	GQ480316.1	COI	658
Modiolus elongatus	GQ480318.1	COI	661
Modiolus metcalfei	GQ480322.1	COI	658
Modiolus modiolus	FJ890501.1	COI	579
Mytilus californianus	GQ902240.1	COI	661
Mytilus coruscus	GQ480295.1	COI	661
Mytilus edulis	JN241970.1	COI	638
Mytilus galloprovincialis	JF912374.1	COI	572
Mytilus trossulus	GQ902685.1	COI	661
Semele solida	JF301888.1	COI	636
Tagelus dombeii	JF301916.1	COI	645

APPENDIX B

RESULTS FROM THE GENERALIZED ADDITIVE MODELS FOR CHAPTER III

Table 1. Results of the GAM for A) presence versus absence and B) abundance of *Macoma* spp.

A.

Parametric coefficients				
Parameter	Estimate	S.E.	z	P
Intercept	-1.325	0.212	-6.255	<0.001
Net	1.352	0.278	4.867	<0.001
Smooth terms (non parametrics)				
Parameter	e.d.f.	χ^2	P	
Julian Day	7.653	33.91	<0.001	
Chlorophyll a	2.249	34.45	<0.001	
n = 324	R^2 adjusted: 0.261		% Deviance explained: 23.9	

B.

Parametric coefficients				
Parameter	Estimate	S.E.	z	p
Intercept	-1.342	0.081	-16.513	<0.001
Net	0.688	0.101	6.782	<0.001
Tide	0.430	0.116	3.720	<0.001
Net*Tide	-0.369	0.142	-2.594	0.0107
Smooth terms (non parametrics)				
Parameter	e.d.f.	F	P	
Salinity	2.263	25.364	<0.001	
Temperature	3.816	8.830	<0.001	
Chlorophyll a	0.856	7.068	0.009	
n = 126	R^2 adjusted: 0.512		% Deviance explained: 55.1	

Table 2. Results of the GAM for A) presence versus absence and B) abundance of *Siliqua* spp.

A.

Parametric coefficients				
Parameter	Estimate	S.E.	z	P
Intercept	-3.170	0.380	-8.332	<0.001
Net	1.127	0.408	2.762	0.006
Smooth terms (non parametrics)				
Parameter	e.d.f.	χ^2	P	
Julian Day	4.831	23.19	<0.001	
Chlorophyll a	3.474	13.42	0.011	
n = 324 R^2 adjusted: 0.156 % Deviance explained: 21.0				

B.

Parametric coefficients					
Parameter	Estimate	S.E.	z	p	
Intercept	-1.190	0.093	-12.835	<0.001	
Net	0.207	0.112	1.847	0.074	
Smooth terms (non parametrics)					
Parameter	e.d.f.		F	P	
Salinity	4.638		3.601	0.009	
n = 38 R^2 adjusted: 0.343 % Deviance explained: 44.3					

Table 3. Results of the GAM for presence versus absence of Tellinoidea.

Parametric coefficients				
Parameter	Estimate	S.E.	Z	P
Intercept	-4.205	0.587	-7.166	<0.001
Tide	1.223	0.494	2.476	0.013
Net	1.394	0.528	2.666	0.008
n = 324 R^2 adjusted: 0.0355 % Deviance explained: 9.23				

Table 4. Results of the GAM for A) presence versus absence and B) abundance of *Clinocardium nuttallii*.

A.

Parametric coefficients				
Parameter	Estimate	S.E.	z	P
Intercept	-2.068	0.255	-8.133	<0.001
Net	1.239	0.310	3.993	<0.001
Smooth terms (non parametrics)				
Parameter	e.d.f.	χ^2	P	
Julian Day	7.446	18.47	0.017	
Salinity	1.540	8.96	0.013	
n = 324	R^2 adjusted: 0.139		% Deviance explained: 15.4	

B.

Parametric coefficients				
Parameter	Estimate	S.E.	z	P
Intercept	-1.230	0.074	-17.454	<0.001
Net	0.385	0.093	4.131	<0.001
Smooth terms (non parametrics)				
Parameter	e.d.f.	F	P	
Julian Day	2.082	2.699	0.061	
Salinity	1.937	3.290	0.033	
n = 77	R^2 adjusted: 0.22		% Deviance explained: 27.1	

Table 5. Results of the GAM for presence versus absence of *Mytilus* spp.

Parametric coefficients				
Parameter	Estimate	S.E.	z	P
Intercept	-1.884	0.278	-6.781	<0.001
Tide	-0.786	0.290	-2.709	0.007
Net	1.967	0.310	6.343	<0.001
Smooth terms (non parametrics)				
Parameter	e.d.f.	χ^2	P	
Julian Day	6.054	28.18	<0.001	
n = 324	R^2 adjusted: 0.238		% Deviance explained: 22.8	

APPENDIX C

RESULTS FROM THE GENERALIZED ADDITIVE MODELS FOR CHAPTER IV

Table 1. October 2009 Cruise: Results of the GAM for A) *Macoma* spp., B) *Siliqua* spp., C) Tellinoidea, D) *Clinocardium nuttallii*, E) *Mytilus* spp.

A.

Parametric coefficients				
Parameter	Estimate	S.E.	z	P
Intercept	0.036	0.016	2.23	0.040
Day/Night	0.038	0.022	1.72	0.104
Smooth terms (non parametrics)				
Parameter	e.d.f.	F	P	
Tidal Height (Day)	1.000	0.495	0.491	
Tidal Height (Night)	4.404	7.744	<0.001	
n = 24	R^2 adjusted: 0.629	% Deviance explained: 73.2		

B.

Parametric coefficients				
Parameter	Estimate	S.E.	z	P
Intercept	0.053	0.029	1.793	0.092
Day/Night	0.090	0.040	2.211	0.042
Smooth terms (non parametrics)				
Parameter	e.d.f.	F	P	
Tidal Height (Day)	1.000	1.296	0.271	
Tidal Height (Night)	4.59	10.202	<0.001	
n = 24	R^2 adjusted: 0.703	% Deviance explained: 78.8		

C.

Parametric coefficients				
Parameter	Estimate	S.E.	z	P
Intercept	0.011	0.010	1.155	0.265
Day/Night	0.037	0.014	2.628	0.018
Smooth terms (non parametrics)				
Parameter	e.d.f.	F	P	
Tidal Height (Day)	1.00	0.012	0.915	
Tidal Height (Night)	4.848	17.564	<0.001	
n = 24	R^2 adjusted: 0.803	% Deviance explained: 86.2		

Table 1 Continued

D.

Parametric coefficients				
Parameter	Estimate	S.E.	z	P
Intercept	<0.001	0.004	0.000	1.000
Day/Night	0.024	0.006	4.07	<0.001
Smooth terms (non parametrics)				
Parameter	e.d.f.	F	P	
Tidal Height (Day)	1.000	0.00	1	
Tidal Height (Night)	4.923	28.34	<0.001	
n = 24 R^2 adjusted: 0.873 % Deviance explained: 91.1				

E.

Parametric coefficients				
Parameter	Estimate	S.E.	z	P
Intercept	0.102	0.013	7.795	<0.001
Day/Night	0.067	0.014	-4.680	<0.001
Net	-0.043	0.014	-3.063	0.005
n = 24 R^2 adjusted: 0.56 % Deviance explained: 59.8				

Table 2. March 2011 Cruise: Results of the GAM for A) *Macoma* spp., B) Tellinoidea and C) *Clinocardium nuttallii*

A.

Parametric coefficients				
Parameter	Estimate	S.E.	z	P
Intercept	0.067	0.058	1.162	0.261
Day/Night	0.204	0.071	2.869	0.011
Smooth terms (non parametrics)				
Parameter	e.d.f.	F	P	
Tidal Height (Day)	1.000	0.000	0.999	
Tidal Height (Night)	4.102	7.435	<0.001	
n = 24 R^2 adjusted: 0.661 % Deviance explained: 75.1				

B.

Parametric coefficients				
Parameter	Estimate	S.E.	z	P
Intercept	<0.001	0.006	0.000	1.000
Day/Night	0.012	0.007	1.709	0.105
Smooth terms (non parametrics)				
Parameter	e.d.f.	F	P	
Tidal Height (Day)	1.000	0.000	1.000	
Tidal Height (Night)	3.814	4.81	0.008	
n = 24 R^2 adjusted: 0.505 % Deviance explained: 63.0				

C.

Parametric coefficients				
Parameter	Estimate	S.E.	z	P
Intercept	0.011	0.020	0.514	0.614
Day/Night	0.044	0.025	1.741	0.099
Smooth terms (non parametrics)				
Parameter	e.d.f.	F	P	
Tidal Height (Day)	1.000	0.016	0.902	
Tidal Height (Night)	4.094	4.047	0.015	
n = 24 R^2 adjusted: 0.472 % Deviance explained: 61.2				

Table 3. May 2011 Cruise: Results of the GAM for *Macoma* spp.

Parametric coefficients				
Parameter	Estimate	S.E.	z	P
Intercept	0.256	0.044	5.772	<0.001
Day/Night	-0.133	0.049	-2.721	0.015
Net	-0.114	0.039	-2.891	0.011
Smooth terms (non parametrics)				
Parameter	e.d.f.	F	P	
Tidal Height (Day)	3.889	5.709	0.005	
Tidal Height (Night)	1.0	0.326	0.576	
n = 24	R^2 adjusted: 0.579	% Deviance explained: 70.5		

Table 4. July 2011 Cruise: Results of the GAM for A) *Siliqua* spp., B) *Clinocardium nuttallii* and C) *Mytilus* spp.

A.

Parametric coefficients				
Parameter	Estimate	S.E.	z	P
Intercept	0.078	0.061	1.280	0.217
Day/Night	0.206	0.073	2.835	0.011
Net	-0.051	0.027	-1.910	0.072
Smooth terms (non parametrics)				
Parameter	e.d.f.	F	P	
Tidal Height (Day)	1.000	0.006	0.940	
Tidal Height (Night)	1.943	10.457	<0.001	
n = 24	R^2 adjusted: 0.573	% Deviance explained: 66.5		

B.

Parametric coefficients				
Parameter	Estimate	S.E.	z	P
Intercept	0.016	0.067	0.235	0.816
Day/Night	0.244	0.095	2.562	0.018
n = 24	R^2 adjusted: 0.195	% Deviance explained: 23		

C.

Parametric coefficients				
Parameter	Estimate	S.E.	z	P
Intercept	0.033	0.006	4.905	<0.001
Net	-0.031	0.009	-3.290	0.003
n = 24	R^2 adjusted: 0.299	% Deviance explained: 33		

Table 5. October 2011 Cruise: Results of the GAM for *C. nuttallii.*

Parametric coefficients				
Parameter	Estimate	S.E.	z	P
Intercept	0.046	0.013	3.559	0.002
Net	-0.040	0.01821	-2.196	0.039
n = 24	R^2 adjusted: 0.143	% Deviance explained: 18.0		

Table 6.February 2011 Cruise: Results of the GAM for A) *Mytilus* spp., B) *Macoma* spp. and C) Tellinoidea.

A.

Parametric coefficients				
Parameter	Estimate	S.E.	z	P
Intercept	<0.001	0.018	0.012	0.990
Day/Night	0.16	0.018	0.909	0.377
Net	-0.018	0.008	-2.292	0.036
Smooth terms (non parametrics)				
Parameter	e.d.f.	F	P	
Tidal Height (Day)	3.888	6.787	0.002	
Tidal Height (Night)	1.00	0.011	0.919	
n = 24	R^2 adjusted: 0.669	% Deviance explained 76.8		

B.

Parametric coefficients				
Parameter	Estimate	S.E.	z	P
Intercept	0.049	0.013	3.629	0.001
Net	-0.043	0.018	-2.426	0.024
n = 24	R^2 adjusted: 0.175	% Deviance explained: 21.1		

C.

Parametric coefficients				
Parameter	Estimate	S.E.	z	P
Intercept	0.013	0.003	3.693	0.001
Net	-0.013	0.005	-2.611	0.016
n = 24	R^2 adjusted: 0.202	% Deviance explained: 23.7		

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