SPATIAL AND TEMPORAL PATTERNS OF DECAPOD LARVAE IN THE STRAIT OF GEORGIA, BRITISH COLUMIA

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ABSTRACT

The abundance and dispersal of meroplankton play a fundamental role in determining spatial and temporal patterns of benthic organisms in marine systems. Field studies that quantify abundance patterns are heavily dependent on, and often limited by, proper identification resources. In the present study, diagnostic features of laboratory reared *Glebocarcinus oregonensis* zoeae were described to facilitate identification of cancrid zoeae in the Salish Sea. The larval community was then described from two surveys spanning the Strait of Georgia that were conducted in consecutive spring seasons in 2009 and 2010. Interannual variability in larval abundance, diversity (Shannon index), and similarity between revisited stations was quantified to compare assemblages between years. Finally, the species- and stage-specific abundance and horizontal distribution of three cancrid species including *Cancer productus, G. oregonensis*, and *Metacarcinus magister*, were described from surveys conducted in consecutive spring and summer seasons in 2010.

The zoeae of *G. oregonensis* exhibited much shorter and acutely angled lateral exospines on the telson and much longer posterolateral abdominal spines than other local cancrid species. Other morphological features used to identify *G. oregonensis* in previous studies were found to be misleading. In both years the reptantian decapod larval community consisted of at least 10 families but was dominated by cancrid larvae (approximately 80 % of total larval abundance). Although the relative abundance of the different families was generally consistent with reproductive potential and timing, overall measures of larval abundance, diversity, and similarity between samples were significantly different between years. Large variation in total abundance, possibly caused by heavy mortality in 2009 or increased reproductive output in 2010, could result in a large variation in the year class strength of adult crab populations. Spatial patterns of both total larval abundance and diversity also contrasted between years, and although they were sometimes moderately correlated with environmental variables, these correlations were found not to be consistent enough to function as good predictors of total larval abundance (all species and stages combined). Larvae of *C. productus* were apparently released later than those of *G. oregonensis* and *M. magister*. Larval distributions of these cancrid species did not change dramatically from stage to stage, indicating that transport did not occur rapidly. The distribution of larvae and environmental variables indicated the potential for nearshore retention and/or alongshore larval transport within the central Strait's eastern margin and cross-strait transport in the southern region. Fresh water input from the Fraser River appeared to play an important role in shaping larval distributions, especially for *M. magister*.

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CHAPTER 1

Introduction

Many benthic marine species have complex life cycles that include a planktonic larval phase. The dispersal and survival of larval and early post-settlement stages has been recognized as critical to the abundance and distribution of these organisms (Roughgarden et al., 1988; Cushing, 1990; Hunt and Mullineaux, 2002). While the adult phase is often limited in motility, larvae have the potential to disperse long distances in the pelagic environment. It follows that larval dispersal can facilitate exchange of individuals between populations separated by distances exceeding most adult migratory ranges. Population maintenance is dependent on larval supply (Roughgarden et al., 1988); therefore, the degree of larval connectivity between populations is a major determinant of demographic sustainability and an important consideration for the design of marine protected areas (Kritzer and Sale, 2004). Research on larval distributions is an important step in order to understand how benthic (adult) patterns are maintained and how they can be managed.

The Strait of Georgia (SoG hereafter) is a large semi-enclosed ocean basin situated between Vancouver Island and mainland British Columbia. Its oceanography is primarily influenced by freshwater input and tides and is modulated by wind and basin topography (Thomson, 1981; Masson and Cummins, 2004). This inland sea is highly productive (Masson and Peña, 2009), and is home to a diverse array of crab species (Hart, 1982). This system is also subjected to a range of human impacts (Johannessen and McCarter, 2010), including the commercial exploitation of the Dungeness crab, *Metacarcinus magister* (Fisheries and Oceans, 2010a). Although the distribution and composition benthic stages of crab species is relatively well known in British Columbia on a regional scale (Hart, 1982), the spatial and temporal patterns in terms of larval composition and abundance remain largely unexplored. Crab larvae are typically released in the spring (Knudsen, 1964) and develop over a period of weeks to months (Nyblade, 1987; Strathmann, 1987; Sulkin and McKeen, 1996). However, information on larval abundance patterns and their processes is scarce and larval crab assemblages have not been described.

Field studies are heavily dependent on resources that can be used for proper larval identification (Moser and Smith, 1993; Pardo et al., 2009). Of the near 60 crab species known to reside in the Salish Sea (SoG and surrounding ocean basins), the larval stages of only about two thirds have some form of documented morphological description. These identification resources are typically provided in the form of identification guides (e.g. Puls, 2001) or individual morphological descriptions (e.g. Duguid and Page, 2009). However, in many instances investigators are required to rear larvae in the laboratory in order to confirm diagnostic features (e.g. Shanks, 1986a). Consequently, the first objective of this study was to contribute to the identification of cancrid larvae in the SoG by describing diagnostic morphological features of laboratory reared *Glebocarcinus oregonensis* zoeae. This morphological work was most useful for the differentiation of *G. oregonensis* zoeae from those of *Cancer productus,* and allowed for proper quantification of the larval abundance and distribution of these species.

Quantifying larval abundance and describing community composition provide a basic understanding of the reproductive timing and output of several species. In addition, larval assemblage research can be used to investigate the impact of a common environmental scenario on the distribution and abundance of multiple species (Oliver et al., 2010). Hence, the second objective of this study was to characterize larval crab assemblages from surveys conducted in the spring seasons of 2009 and 2010, compare assemblages between years, and investigate the relationship between abundance, diversity, similarity, and environmental conditions. This research provides the only larval crab assemblage information available in the SoG.

Horizontal larval abundance patterns can be used to test dispersal predictions using prior knowledge of transport processes, or to develop hypotheses describing how dispersal processes potentially generated the observed patterns (Sale and Kritzer, 2003). Species- and stage-specific patterns of larval abundance can then be analyzed for indications of potential dispersal pathways or regions of larval retention, especially when analyzed in concert with distributional patterns of hydrographic variables (e.g. Smith et al., 1999a). With that purpose, the third objective of the present study was to describe spatial patterns of stage-specific larval abundance of the three best represented cancrid species: *M. magister*, *C. productus*, and *G. oregonensis* from surveys conducted in late April and June, 2010. This approach allowed for analysis of all larval stages from these three species within a single year.

These three general objectives are fully developed as Chapters 3, 4, and 5, respectively, and are preceded by a review concerning several aspects relevant to larval distributions, the SoG, and the importance of larval connectivity the design of marine protected areas (Chapter 2).

CHAPTER 2

Literature Review

2.1. Introduction

Factors that influence the displacement and ultimately the distribution of meroplankton are reviewed, as well as statistical methods that may be used to quantify spatial patterns. Planktonic larvae are subjected to multiple processes, interlinked over a range of scales that affect their trajectory and distribution in a given system (Bradbury and Snelgrove, 2003). In this review, transport mechanisms are reviewed in the context of physical forcing; however, larval dispersal is inherently biophysical. For example, biological processes such as swimming/sensory capability and planktonic larval duration interact with physical forcing to influence larval trajectories and dispersal distance respectively (Kingsford et al., 2002; Shanks, 2009).

The physical oceanography of the Strait of Georgia (SoG hereafter) was also reviewed to provide pertinent information on the scale of the study system, as well as circulation patterns and water column characteristics to which larvae may be exposed. Furthermore, because research in the present study is applicable to future management by marine protected areas (MPAs), the importance of larval dispersal to the design and placement of MPAs was reviewed, as well as marine protected areas in Canada and their status in British Columbia. Finally, information on the reproductive timing and larval development of crab species present in the SoG and surrounding waters were compiled to provide information relevant to the interpretation of data on larval community composition and abundance.

2.2. Larval Transport

Larval transport may occur at spatial and temporal scales that range from meters to hundreds of kilometers and seconds to months respectively (Pineda et al., 2007). The terms larval dispersal and larval transport are sometimes confused. Larval dispersal is defined herein as the spread of larvae from the release location to the settlement site (Cowen and Sponagule, 2009), and is a function of larval transport, survival, spawning and settlement (Pineda et al., 2007). Larval transport refers to the horizontal translocation of planktonic larvae between two locations, and is facilitated by interplay between physical transport (advection and diffusion) and larval behaviour (Pineda et al., 2007).

Larval behaviour is essentially the product of swimming, orientation, and sensory abilities (Leis, 2006a). Most larvae are unable to swim against currents, but are capable of migrating vertically (Metaxas, 2001). Because currents can change with depth, larvae can of change their trajectory indirectly by regulating their vertical position. Several field and biophysical modelling studies have illustrated the importance of vertical positioning and vertical migration of larval transport from near shore environments (DiBacco et al., 2001; Paris and Cowen, 2004; Yannicelli et al., 2006; Peliz et al., 2007).

Larval transport is often discussed as along-shore or cross-shelf. Along-shore transport may be an important mechanism of larval exchange between populations situated along a coastline (Wing et al., 1998). On the other hand, cross-shelf transport is tremendously important for larvae that must migrate from off-shore waters to nurseries and estuaries (Epifanio and Garvine, 2001). Cross-shelf transport can have a substantial effect on observed larval distributions because physical gradients that may concentrate or disperse larvae are strongest in the cross-shore direction (Pineda et al., 2007).

The majority of larval transport studies assess mesoscale mechanisms in a coastal environment. There is a need for more studies that address small scale nearshore transport mechanisms that may determine spatial patterns of local recruitment (Bradbury and Snelgrove, 2001; Shanks and Spearman, 2009). Also, less is known about flow regimes and transport mechanisms within enclosed bays and ocean basins. Larval transport has been discussed in contributions provided by Pineda et al. (2007), Queiroga et al. (2007), Queiroga and Blanton (2005), Epifanio and Garvine (2001) and Shanks (1995). In this section, I review how physical forcing and larval behavior facilitate larval transport by categorizing discussion in relation to relevant physical mechanisms.

2.2.1. Wind stress

On the planetary scale, wind and the Coriolis force determine the oceanic surface currents (Levinton, 2001). Friction between wind and the ocean's surface induces horizontal and vertical circulation (Epifanio and Garvine, 2001). An Ekman spiral is produced when wind-induced flow is deflected by the Coriolis force and momentum is transferred from the surface to deeper water. The surface layer is diverted to the right in the northern hemisphere and the left in the southern hemisphere. The net flow in this direction (to the right or left) is referred to as Ekman transport. Upwelling occurs when surface water is deflected offshore by the coriolus force in occurance with alongshore winds. Wind from the opposite direction causes water to downwell near shore (Shanks, 1995; Levinton, 2001).

Upwelling-associated larval transport may be significantly important in certain geographical areas because meroplankton are diverse and abundant during the upwelling season (Shanks and Eckert, 2005). Many studies have supported the notion that upwelling currents transport larvae offshore from their release point and that downwelling currents, or upwelling relaxation events, facilitate the return of larvae residing in an offshore larval pool (Goodrich et al., 1989; Farrell et al., 1991; Little and Epifanio, 1991; Connolly et al., 2001; Queiroga et al., 2006)

This upwelling-downwelling paradigm may be expected if larvae reside near the surface; however, different vertical positioning will yield different transport scenarios if subsurface flow is in the reverse direction (Shanks and Brink, 2005). This is supported by evidence from particle-tracking biophysical models and field observations during upwelling and downwelling events (Shanks et al., 2002; Shanks et al., 2003; Marta-Almeida et al., 2006).

In fact, recent studies suggest that upwelling and downwelling induced cross-shelf flow does not explain larval distributions and recruitment of many marine invertebrate species (Morgan et al., 2009; Shanks and Spearman, 2009; Yoshinaga et al., 2010). One hypothesis reasons that daily vertical migrations facilitate larval retention nearshore (Queiroga et al., 2007). Alternatively, larvae may be capable of avoiding offshore transport due to the retentive nature of shallow nearshore hydrodynamics (Largier, 2003; Shanks and Spearman, 2009). For example, cross-shelf water movement is less pronounced at shallow depths because the surface and bottom mixing layers converge, subjecting the water column to friction and diffusion (Epifanio and Garvine 2001; Austin and Lentz, 2002).

In addition to upwelling, other wind-generated currents can induce different transport scenarios. For example, northerly winds in the mid Atlantic bight play an important role in retaining Blue Crab (*Callinectes sapidus*) larvae within the region while they develop offshore (Epifanio and Garvine, 1989). Crab settlement has also been associated with onshore wind events (Hobbs et al., 1992; Eggleston and Armstrong, 1995, Eggleston et al., 1998); however, the hypothesis that onshore wind actually transported larvae towards shore was not tested. In addition, sea and land breezes have been identified as potential transport mechanism because they coincide with daily vertical migratory behavior (Shanks, 1995). Landward sea breezes occur during the day, when warm air that rises on land is replaced by cold air offshore. The opposite occurs when seaward land breezes are generated at night. Tapia et al. (2004) found that onshore sea breezes are variable in magnitude, but can generate surface current velocities up to 10 cm/s, and noted their potential for nearshore retention and larval transport.

2.2.2. Tidal currents

The gravitational fields of the sun and moon cause oscillatory sea level fluctuations and tidal currents. The extent of unidirectional transport from tidal currents depends on the vertical position of larvae in the water column (Dibacco et al., 2001). A non-linear decrease in tidal current velocity occurs with increasing depth due to friction with the sea bottom. It follows that organisms that reside in the boundary layer on the ocean floor maintain their horizontal position. Because tidal currents behave in a consistent and predictable pattern over evolutionary time, they could facilitate the adaptation of certain larval behaviours (Hill, 1991).

The most effective way for swimming organisms to utilize tidal currents for horizontal movement is to undergo vertical migrations that match the tidal cycle.

Meroplankton that use selective tidal stream transport (STST) ascend from the boundary layer during flood or ebb tidal currents and are carried in a single direction (reviewed by Forward and Tankersley, 2001). Ichthyoplankton that utilize estuaries for nursery habitats may use STST to migrate into and remain within estuaries (Forward et al. 1998), and certain crab larvae that develop offshore use STST to leave and reinvade estuaries (Queiroga et al., 1997; Dibacco et al., 2001). Moreover, decapods are known to release their larvae in relation to light, lunar and tidal cycles (reviewed by Forward, 1987 and Christy, 2011). Larval release has been observed with large amplitude, nocturnal ebb tides that probably facilitate offshore transport of larvae (Morgan and Christy, 1995).

Larvae may also undergo combined tidal and diel vertical migrations, and this interaction likely influences their horizontal displacement (Schwamborn et al., 2008). For example, fish and crab larvae often use the flood tide at night to invade estuaries (DeVries et al., 1994; Christy and Morgan, 1998; Forward et al., 1998). Adding to the complexity, the degree of tidal and diel migratory behaviour can vary with ontogeny. For example, Tamaki et al. (2010) documented that ghost shrimp (*Nihonotrypaea harmandi*) zoeae ascend to the surface during the sunset flood tide, possibly to remain within a bay, whereas megalopae underwent regular diel vertical migrations with no ebb or flood preference.

2.2.3. Internal waves and tidal bores

When water is pulled away from the coast by the ebbing tide across a topographic gradient, such as a canyon, reef or continental shelf break, a "lee wave" is formed. At the subsequent slack tide the wave is released as a shoreward moving internal wave. A large amplitude internal wave will then break as it moves cross-shelf towards the shore, resulting in an internal bore (Shanks, 1995). Water column stratification increases the energy, frequency and vertical structure of internal waves and bores (Pineda and Lopez, 2002). Water over each internal wave trough is characterized by a region of convergence and downwelling that forms a glassy surface slick. These regions are about 30-50 meters wide, can be several kilometers long, and are separated by 100-300 meters of rippled water (Shanks and Wright, 1987; Shanks, 1988).

The "internal wave slick hypothesis" predicts that neustonic meroplankton, capable of maintaining their vertical position in surface slicks, accumulate and are transported towards the shore with the internal wave (Shanks and Wright 1987; Pineda, 1994). Surface slicks have been shown to contain elevated concentrations of flotsam, small fish, holoplankton and meroplankton (Shanks, 1983; Kingsford and Choat, 1986; Shanks, 1988). In some cases, these slicks appear to propagate shoreward, and this movement has been correlated with crab and barnacle settlement (Shanks, 1983; Shanks and Wright, 1987). However, in other cases surface slicks have not accumulated larvae and were unable to transport surface drifters shoreward (Shanks, 1983; Shanks and Wright 1987; Shanks 1988). Although supported by multiple studies, the surface slick hypothesis is largely based on observations and requires in-depth water column measurements for further exploration (Pineda, 1999).

Internal bores are known to have two phases. In the first phase, cold subsurface water is transported nearshore and can be detected by diurnal or semi-diurnal near-bottom temperature drops (Pineda, 1991; Pineda, 1994). Such temperature anomalies as well as changes in water column stratification have been correlated with high barnacle settlement. This evidence supports the "internal bore hypothesis" that predicts onshore transport of subsurface larvae via internal bores (Pineda, 1991; Pineda and Lopez, 2002).

In the second phase, cold subsurface water introduced by an internal bore displaces warmer nearshore water to form a surface thermal front, or warm bore front, that can accumulate larvae and move towards shore (Pineda, 1994; Pineda, 1999). Pineda (1994) argued that warm-bore fronts better explain observed larval transport and settlement patterns than the internal wave slick hypothesis. The author further stated that frontal regions may be misinterpreted as internal wave generated surface slicks.

2.2.4. Density driven transport and fronts

Water density is determined by its temperature and salinity, with cold saline water being denser than warm less saline water. Higher salinity water sinks, leaving low-salinity water at the surface where it can be warmed by the sun, further increasing stratification. Less dense surface water tends to ride over deeper more dense water. Consequently, circulation in estuaries is largely influenced by the offshore transport of discharged freshwater (Queiroga and Blanton, 2005).

Fronts are commonly defined as the boundary between water masses that differ in density (Garvine, 1974; Clancy and Epifanio, 1989; Franks, 1992), and are visible at the surface as a sharp colour contrast, surface slick, or line of foam (Clancy and Epifanio, 1989). Mixing between opposing water masses at the frontal boundary creates a region of intermediate density that sinks (Bakun, 2006). As this water downwells, a surface convergence current is created that can accumulate particles (Garvine, 1974; Franks, 1992; Eggleston et al., 1998). Flow at fronts can exist in the along-front direction as well as the cross-front direction (Franks, 1992). It is generally agreed that zooplankton become concentrated in fronts by swimming upward against downwelling water to maintain a preferred depth (Pineda, 1999; Shanks et al. 2000; Bakun; 2006); therefore, relative swimming capability may dictate whether larvae become concentrated in fronts (Franks, 1992).

The cross-shelf movement of fronts due to density-driven flow provides a potentially important mechanism for larval transport (Pineda, 1994; Shanks et al., 2000). Winds that drive warm, less dense water offshore cause upwelling of cold dense water nearshore and produce an "upwelling front" where the two water masses meet. When winds relax, the displaced warm water rides over the denser upwelled water and the upwelling front moves towards shore. Shanks et al. (2000) demonstrated that a shoreward moving upwelling front contained elevated concentrations of meroplankton, and suggested this to be an important cross-shore transport mechanism. Additionally, Wing et al. (1998) provided evidence suggesting that warm water, retained in a gulf during upwelling, migrated alongshore as a thermal front upon upwelling relaxation. The warm water had high concentrations of crab larvae and its arrival was associated with increased crab settlement. This provides an alternative mechanism for previous observations of increased larval settlement during upwelling relaxation.

Pineda (1994) also found an increased concentration of meroplankton in warm cross-shelf fronts moving onshore; however the author suggested these fronts were a consequence of internal tidal bores. This occurs when tidally generated internal bores introduce cold, dense water nearshore and a warm bore front is established. Hours after this event, the dense nearshore water apparently sinks, creating shoreward movement of the warm bore front (Pineda, 1994). Warm fronts may be diagnosed by temperature measurements and diurnal or semidiurnal periodicity matching the periodicity of internal bores (Pineda, 1999).

Alternatively, fronts have been proposed to act as a dispersal barrier by trapping larvae in frontal convergences, preventing cross-frontal dispersion (Wolanksi and Hamner, 1988; Egglston et al., 1998). Islands, reefs or headlands can interact with currents to generate frontal features that trap buoyant particles in their convergence, and prevent a “normal” dispersion (Wolanksi and Hamner, 1988). Furthermore, Wing et al. (1998) postulated that an array of fronts produced by the interaction of upwelling currents and a headland could restrict distributions of crab larvae within a gulf.

2.2.5. Rotary currents

Rotary currents can affect larval distributions by increasing the residence time of associated water parcels (Mullineaux and Mills, 1997). Eddies are rotary currents ranging from centimeters to kilometers in diameter (Bradbury and Snelgrove, 2001). Particles can be concentrated by eddies in convergent currents at their centre and/or at their outer edge where fronts form (Olson and Backus, 1985; Wolanksi and Hamner, 1988; Bakun, 2006). The convergent properties of eddies depend on their rotary direction and whether or not they are being constantly forced (for discussion on eddy dynamics see Bakun, 2006).

Eddies can be created from the interaction of ocean currents with topographic features such as islands and headlands (Wolanksi and Hamner, 1988). Downstream eddies are apparent retention zones and have been associated with increased larval concentrations and settlement (Wing et al., 1995, 1998; Mace and Morgan, 2006).

Retention zones containing meroplankton in the lee of coastal headlands may supply larvae to more intense upwelling regions that experience advective loss from offshore transport (Wing et al., 1995, 1998). Large eddies known as warm core rings, that can be hundreds of kilometers wide, can arise from coastal current meanders that become 'pinched off' (Olson and Backus, 1985). It has been suggested that warm core rings play a crucial role in transport of fish larvae to nearshore waters from the Gulf Stream (Hare et al., 2002).

A different rotary current, known as a Taylor cap, may form when water flows over elevated topography (Bradbury and Snelgrove, 2001). Benthic organisms in patchy or isolated environments, such as seamounts, may be adapted to exploit this rotary current for self recruitment (Parker and Tunnicliffe, 1994).

2.3. Larval Distributions

2.3.1. Vertical distributions

The ocean's water column is characterized by vertical changes in physical, chemical, and biological parameters. Accordingly, the characteristics of the occupied vertical habitat have important implications for the growth, survival, and transport of meroplankton (Shirley and Shirley, 1988; Ficksen et al., 2007). The vertical distribution of meroplankton is most often studied with reference to larval transport when currents vary with depth (e.g. Tamaki et al., 2010) or in shallow environments (bays and estuaries) where larvae may exploit the directionality of tidal currents by migrating to and from the bottom boundary layer (e.g. DiBacco et al., 2001). Instantaneous vertical positioning is dictated by hydrodynamics and larval behavior (Metaxas, 2001). Few meroplankton appear to be capable of swimming at speeds greater than 3 cm s^{-1} (Chia et al., 1984), and therefore, most larvae are thought to be unable to swim against horizontal currents (but see Sponagule et al., 2002; Leis, 2006a). However, in the vertical field of the water column, even weak swimming larvae are capable of regulating their position in most scenarios (Sameoto et al., 2010).

Decapods are among the strongest invertebrate swimmers with the highest sensory capabilities (Chia et al., 1984; Kingsford et al., 2002). It follows that larval behaviour could potentially play a major role in determining vertical positioning. Field studies have shown considerable interspecific variability in vertical distribution and migratory patterns (Lindley, 1986; Lindley et al., 1994; Wing et al., 1998; Abelló and Guerao, 1999; Park and Shirley, 2005; Yannicelli et al., 2006) and larval behaviour is probably a major contributor to this variability.

In general, meroplankton behaviour changes from an initial upward swimming to a downward migration prior to settlement (Metaxas, 2001). The behaviour of decapod zoeae is indeed characterized by positive phototaxis and negative geotaxis (Sulkin 1975; Bigford, 1979; Jacobey, 1981; Shirley and Shirley, 1988; Adams and Paul, 1999). Abrupt behavioural changes typically occur during the megalopal stage, when these larvae may become non-responsive to light (Forward and Costlow, 1974; Epelbaum et al., 2007) and develop positive geotaxis (Sulkin, 1973; Sulkin 1975).

In some instances, larvae appear to undergo a gradual ontogenetic migration into deeper water. The depth preference of different stages can be tested using experimental columns in the absence of light. Sulkin (1973) demonstrated that later larval stages of two xanthid crab species exhibited deeper vertical distributions compared to earlier stages.

Similarly, Ouelette and Allard (2006) showed that later larval stages of *Pandalus borealis* selected colder temperatures at greater depths compared to earlier stages. Field observations have indicated that ontogenetic migrations appear to be common among decapod larvae, with early stages being located nearest the surface and later stages distributed over a range of depths (see review by Queiroga and Blanton, 2005). However, true ontogenetic migrations may be difficult to resolve in the field because they may reflect spatial variability in mortality (Irrison et al., 2010), and because larvae may also undergo high frequency rhythmic migrations (Tamaki et al., 2010).

Diel and tidal migratory behaviour can be driven by exogenous cues (e.g. light, salinity) and endogenous rhythms (Cohen and Forward, 2009). Tidal migrations and their implications for transport, particularly in estuarine environments, are discussed in section 2.2 of this review. Nocturnal diel vertical migrations occur when zooplankton reside in deep waters during the day and migrate to the surface to feed at night. This behaviour is widespread among zooplankton in aquatic environments, and the literature strongly supports the hypothesis that it is an adaptive response to avoid visual predators (reviewed by Hays, 2003; Cohen and Forward, 2009). Other less frequently encountered forms of daily vertical migrations include twilight vertical migrations and reverse diel vertical migrations (Cohen and Forward, 2009).

Field observations suggest that many different meroplankton undergo diel vertical migrations, including decapod larvae (Tremblay and Sinclair, 1990; Lough and Potter, 1993; Park and Shirley, 2005; dos Santos et al., 2008). Nocturnal migrations appear to be the most frequently observed among decapod species (Lindley, 1986; Wing et al., 1998; dos Santos et al., 2008) but other migratory patterns have been observed (Park and

Shirley, 2005) that can vary with ontogeny (Tamaki et al., 2010). Given the swimming speed of crab zoeae in still water is between 0.5 to 1 cm s^{-1} (Chia et al., 1984), and a migratory period of approximately 2 hours (Shanks, 1986a; Marta-Almeida et al., 2006) zoeae could travel a distance of 36 to 72 m. This is consistent with several studies conducted in deep environments that have found most taxonomic groupings were present above 60 to 80 m regardless of the time of day (Lindley, 1986; Shanks, 1986a; Lindley et al., 1994; Wing et al., 1998). Queiroga and Blanton (2005) also concluded, after reviewing several studies, that decapod larvae are rarely found below 70 m.

Megalopae are typically stronger swimmers than zoeae. In still water, swimming speeds have been estimated to be between 1 and 10 cm s^{-1} (Chia et al., 1984; Shanks, 1986b). However, when challenged with flow, horizontal swimming speeds can increase dramatically. For example, *Metacarcinus magister* megalopae are capable of increasing their swimming speed from 8 cm s^{-1} in still water to almost 45 cm s^{-1} in strong flow (Fernandez et al., 1994). Strong swimming speeds may facilitate large amplitude vertical migrations. For example, Jamieson and Phillips (1993) found high concentrations of *M. magister* megalopae at approximately 160 m in the Strait of Georgia and suggested that this species migrates from this depth to the surface on a diel basis.

Vertical migratory patterns may be altered by the physical structure of the water column and the vertical distribution of other plankton (Clay et al., 2004; Holliday et al., 2010; but see dos Santos et al., 2008). High plankton concentrations often occur near density discontinuities. Examples of this phenomenon are available for phytoplankton (Dekshenieks et al., 2001; Bochdansky and Bollens, 2009; Masson and Peña, 2009), holoplankton (Tiselius et al., 1994; McManus et al., 2005; Holliday et al., 2010), and meroplankton (Thiébaut et al., 1992; Raby et al., 1994; Sánchez-Velasco et al., 2007). These vertical patches are sometimes referred to as biological thin layers. Planktonic particles are expected to form thin layers when convergence forces such as shear, particle buoyancy, and particle motility (with proper orientation) are stronger than turbulent diffusion (Stacey et al., 2007).

The vertical distribution of decapod larvae is most often studied in relation to the thermocline rather than the pycnocline or halocline. Decapod larvae have been shown to exhibit a variety of vertical distributional patterns. However, in the majority of cases, these larvae are most abundant at or above the thermocline in the upper layer of the water column (Lindley, 1986; Wing et al., 1998; Ouellette and Allard, 2006; Yannicelli et al., 2006; Yoshinaga et al., 2010).

Laboratory experiments have demonstrated that larvae of various species and with various swimming abilities, including decapods, tend to aggregate near vertical salinity discontinuities (Harder, 1968; Mann et al., 1991; Lougee et al., 2002; Breckenridge and Bollens, 2010). In the presence of a halocline, experimental vertical distributions can be modulated by halocline strength (Roberts, 1971; O'Conner and Epifanio, 1985), vertical shear (Metaxas et al., 2009), light availability (Breckenridge and Bollens, 2010), food availability (Sameoto and Metaxas, 2008a), and dietary conditioning (Metaxas and Young, 1998). The behavioural response of zooplankton to the presence of vertical discontinuities likely depends on sensory capabilities, physiological limitations, and selective pressure on behavioural responses to proximate cues, such as salinity (Frost et al., 2010). Although salinity tolerance is surely a contributing factor (Sameoto and Metaxas, 2008b), zooplankton still tend to aggregate at haloclines when the salinity of both water layers does not appear to be physiologically limiting (Bochdansky and Bollens, 2009; Frost et al., 2010). Accordingly, it has been suggested that some larvae use these salinity gradients as a proximate cue for food availability (Clay et al., 2004).

It is difficult to determine the relative role of behaviour and hydrodynamics in the formation of vertical distributions. Observations of interactions between larvae and different environmental cues in laboratory experiments provide valuable information; however, these experiments are probably not good predictors for natural conditions. For example, these experiments are almost always conducted in the absence of flow (Metaxas, 2001, but see Metaxas et al., 2009) and cannot account for the numerous sensory cues present at any given time (Fuchs et al., 2010). Furthermore, because field observations of vertical distributions are usually based on relatively few observations, they are only valid under identical environmental conditions to those in which they were observed (Vikebo et al., 2007). Moreover, even in the same environmental conditions, organisms may behave differently based on their individual physiological condition (Metaxas and Young, 1998; Hays et al., 2001).

2.3.2. Horizontal distributions

A central goal in ecology is to understand the processes that shape ecological patterns (Jenkins and Ricklefs, 2011). Spatial patterns can provide information about their underlying processes (Sale and Kritzer, 2003), but first must be properly characterized at relevant scales. The distribution of organisms can be detected at a hierarchy of scales wherein “trends” can be detected at large scales, “patches” at mesoscales, and “noise” at the smallest scales (Fortin and Dale, 2005). Interpretation of spatial structure is fundamentally dependent on the extent and morphology of the true pattern, sampling resolution, grain size (size of sampling unit), and appropriate spatial analysis (Fortin and Dale, 2005). Several physical and biological processes operate at various spatial and temporal scales to shape the spatial distribution of zooplankton (Mackas et al., 1985).

Many studies have used horizontal larval distributions to provide evidence supporting the role of relevant transport processes such as wind forcing (Hobbs et al., 1992), density driven transport (Wing et al., 1995), or oriented horizontal swimming (Chiswell and Booth, 1999) on larval dispersal. Larval distributions can also be used to test transport hypotheses. For example, Morgan et al. (2009) provided evidence against the hypothesis that cross-shelf Ekman transport reduces the supply of many crustacean larvae to coastal environments characterized by strong upwelling. Furthermore, the distribution of different larval stages could also be used to infer locations of larval release and larval supply. Spatial variability in abundance of both larvae and settlers has been measured to investigate the relationship between larval supply and settlement (Poulin et al., 2002; Moreira et al., 2007). Finally, horizontal distributions have utility as validation tools for biophysical particle tracking models (e.g. Paris and Cowen, 2004; Peliz et al. 2007) that have become frequently used to predict larval transport, dispersal distance, and population connectivity (Miller, 2007; Metaxas and Saunders, 2009).

Larval distributions are tightly linked to transport caused by the combined effect of physical forcing and vertical swimming behaviour. Additional factors that influence horizontal distributions include the timing and location of larval release, spatial variation in mortality, and larval behaviour. The location and timing of larval release is expected to influence the distribution of early larval stages (Natunewicz and Epifanio, 2001; Kerr and Duffus, 2006). These factors may also affect the distribution of later stages, as demonstrated by biophysical particle tracking models (e.g. Huret et al., 2007). Spatial variation in mortality may also influence the spatial pattern of larval abundance (Frank et al., 1993, Bradbury et al., 2003). Sources of larval mortality include predation, starvation, and advective loss (Rumrill, 1990; Morgan 1995). Little is known about the spatial and temporal variability of larval mortality (Gallego et al, 2007), and even global estimates of mortality are scarce for benthic invertebrates (Metaxas and Saunders, 2009). Furthermore, the late larval stages of some decapod and many fish species appear to be capable of making headway against ambient currents by swimming horizontally (Fernandez and Armstrong, 1994; Leis, 2006a). Experimental evidence indicates that these larvae are also capable of oriented swimming (Leis, 2006a; Houser and Epifanio, 2009), which has been suggested to explain observed distributions (Bradbury et al, 2003; Chiswell and Booth, 1999; 2005). Megalopae of some crab species have been observed in localized swarms at the surface (e.g. Miner et al., 2000) or rafting on jellyfish medusae (Wickham, 1979; Towanda and Thuesen, 2006). These behaviours likely contribute to spatial heterogeneity in their horizontal distribution and may bias the estimation of larval abundance. For example, *Metacarcinus gracilis* megalopae can reach densities of up to 326 individuals on a single *Phacellophora camtschatica* medusa, suggesting that most *M. gracilis* megalopae actually ride on jellyfish (Towanda and Thuesen, 2006).

Larval distributions are often characterized by many zero or low abundance observations and a few very high abundance observations. Consequently, the variance-to-mean ratio is higher than expected if individuals were randomly distributed. This phenomenon is known as "patchiness". Larval patches can be detected on scales ranging from 10 m to 100 km for zooplankton (Mackas et al., 1985). For example, fine resolution sampling at tens of meters has detected patches sizes ranging from hundreds of meters to kilometers for crab larvae (Natunewicz and Epifanio, 2001) and 1 to 10 km for copepods (Molinero et al., 2008). Physical processes that contribute to patchiness include turbulent advection, which can create spatially heterogeneous filament-like patterns of passive tracer (e.g. dye) (Abraham, 1998), and convergent currents (e.g. Langmuir cells, fronts, surface slicks), which can concentrate zooplankton and flotsam (Franks, 1992; Shanks, 1995). Biological mechanisms that can contribute to patchiness include synchronized larval release (Natunewicz and Epifanio, 2001), aggregative swimming behaviour, and spatial variation in mortality (Mackas et al., 1985; Bradbury et al., 2003).

Patchiness can be quantified using the Lloyd's index of patchiness (Lloyd, 1967), which has been used to describe the distributions of fish eggs and larvae (Stabeno et al., 1996; Bradbury et al., 2003; Maynou et al., 2008 and others). This method determines the number of times more "crowded" an average individual is when taken from the observed distribution compared to a random distribution with the same mean value. The index is described by the following equation:

$$P = 1 + \frac{(\delta^2 - m)}{m^2}$$

where δ^2 is the population variance and m is the population mean (Lloyd, 1967; Benz, 2000). The logic for subtracting the mean and variance is that, if taken from a random spatial configuration, the mean and variances are expected to be equal.

Consequently, indices larger than one indicate over-dispersion (Benz, 2000). This statistic is advantageous in that it is not dependent on density or the scale of sampling (Bradbury et al., 2003); however, it is intended for individual counts rather than density per unit volume. This problem can be overcome by adopting alternative indices of aggregation. Although patchiness indices are capable of describing an organism's distribution, they are technically not spatial statistics (Benz, 2000).

2.3.3. Quantifying spatial structure: spatial statistics and geostatistics

Spatial statistics quantify the extent and intensity of spatial covariance between neighbouring sample locations. A central principle of spatial statistics is that values tend to become increasingly similar with decreasing separation distance across geographical space. This phenomenon is referred to as positive spatial dependence and is present in most ecological data (Fortin and Dale, 2005). Spatial dependence is referred to as anisotropic when its intensity varies with direction. In the absence of anisotropy, spatial dependence is referred to as isotropic (Fletcher and Sumner, 1999). Quantitative detection of spatial dependence is fundamental to the analysis and interpretation of spatial data because it can determine the presence of a non-random pattern (Boots, 2002), often taking the form of patches or gradients (Legendre, 1993). In addition, the presence or absence of spatial dependence provides information about the scale of the underlying processes. In fact, studies that have quantified larval patch size have done so by analyses of spatial dependence (Natunewicz and Epifanio, 2001; Jones and Epifanio, 2005; Moreira et al., 2007). The absence of spatial dependence indicates that the sample design or analysis may have not been conducted at the appropriate resolution or the presence of erroneous data (Olea, 2006). Negative spatial autocorrelation (small values with large values at neighbouring locations and vice versa) may naturally occur under certain circumstances, but has received little attention in the literature (Griffith and Arbia, 2010).

Spatial dependence may be caused by induced and/or inherent processes. Spatial autocorrelation refers to inherent spatial dependence and occurs when a variable is correlated with itself (e.g. larval dispersal by diffusion). In contrast, induced spatial dependence is a result of a variable's response to an underlying process that itself is spatially autocorrelated (e.g. larval dispersal by ocean currents) (Fortin and Dale, 2005). The term spatial autocorrelation is often used interchangeably with spatial dependence. However, in this review spatial autocorrelation will only refer to inherent spatial dependence. In the presence of spatial dependence, the assumption of independence required for standard statistical tests is violated (Legendre, 1993). In contrast to classical statistics, spatial statistics assume that the process driving the pattern are stationary. A process is stationary when its properties are independent of location and direction. Under this assumption, the mean and variance should be the same throughout the study area and in all directions. This assumption is often violated in analyses of large spatial extents (Fortin and Dale, 2005).

Global spatial statistics (e.g. Moran's *I*, Geary's *c*) estimate the degree of spatial dependence over the entire study area by computing a single value at a predefined distance class (Fortin and Dale, 2005). The relationship between global spatial statistics and distance can be described by calculating the statistic at multiple distance classes, and can be illustrated by plotting a correlogram in one or many directions (Legendre, 1993). Because these statistics rely on the assumption of stationarity, they are only relevant when spatial dependence is roughly uniform over the entire study area (Boots, 2002), and may be deceptive when multiple processes act at various levels of intensity in different regions (Fortin and Dale, 2005). Furthermore, global statistics are sensitive to skewed distributions (Fortin and Dale, 2005) that often characterize biological spatial patterns, especially those of planktonic organisms (Mackas et al., 1985). Although the Moran's I statistic has recently been used to analyze spatial structure of larval fish distributions (Maynou et al., 2008), global spatial statistics alone are probably inappropriate for examining the spatial structure of meroplankton over large spatial extents in most instances.

Local spatial statistics were developed in response to the limitations associated with global statistics (Unwin and Unwin, 1998). These local statistics are advantageous because they are calculated for each location and can be mapped to characterize structural components within the dataset (Boots, 2002). Two common local spatial statistics are the local Moran's I_i, and the Getis-Ord G_i^* (Getis and Ord, 1992; Anelsin, 1995). These statistics detect spatial clustering of extreme values within a defined neighbourhood by essentially essentially comparing local and global averages. In doing so, they test the null hypothesis that the observed pattern occurred by chance (Nelson and Boots, 2008). Details regarding significance testing can be found in Boots (2002), Mitchell (2005), and Nelson and Boots (2008). In addition, local spatial statistics can be applied to evaluate the assumption of stationarity, detect unusual events, and help identify biological patches (Unwin and Unwin, 1998; Boots, 2002). The local Moran's I_i statistic can detect both positive and negative spatial dependence, whereas the Getis-Ord G_i^* statistic can only detect positive spatial dependence (Nelson and Boots, 2008). However, the Getis-Ord G_i^*

statistic is unique in that it is capable of distinguishing between clustering of high ("hotspot") and low ("cold spot") values (Fortin and Dale, 2005). The disadvantage of local spatial statistics is that they are sensitive to global spatial dependence because they are calculated with reference to the global average. For example, the probability of a type one error increases in the presence of large regions of high or low values (Getis and Ord, 2001). Consequently, it has been recommended that global measures of spatial dependence be presented along with local measures (Nelson and Boots, 2008).

Geostatistics is a type of spatial analysis based on the "regionalized variable theory" (Fortin and Dale, 2005). This theory considers the value of a variable z at location x, a realization of a random function $Z(x)$, wherein the function $z(x)$ is determined by the following:

$$z(x) = m(x) + \varepsilon(x) + \varepsilon'$$

Here, $m(x)$ is the structural functional component (e.g. trend, or overall average in the absence of trend) at location x, $\varepsilon(x)$ is the spatially dependent residual of $m(x)$ (e.g. spatial variance), and ε' is the normally distributed independent residual (e.g. noise) (Fortin and Dale, 2005). Geostatistics also assume "intrinsic" stationarity and ergodicity. Intrinsic stationarity is satisfied when the variance of any two observations separated by the vector (distance and direction are considered) h is equal and changes only with h. Ergodicity assumes that the average of all realizations is equal to the average of a single realization. The latter cannot be tested; however, the former can be analyzed by trend or drift analysis (Zuur et al., 2007).

The primary application of geostatistics is for predicting values at unsampled locations based on the spatial variation present in the data (Cressie, 1993; Fortin and Dale, 2005; Zuur et a., 2007). This is accomplished in a series of steps by constructing a semivariogram (referred to herein as variogram), fitting a variogram model, and executing an appropriate kriging interpolation procedure (Olea, 2006). A variogram is created by plotting the relationship between spatial dependence of the attribute z at locations x and $x + h$. This is accomplished by calculating the spatial variance between $z(x)$ and $z(x + h)$ for all locations and plotting the average spatial variance at defined distance classes (Fletcher and Sumner, 1999).

In the presence of spatial dependence, semivariance values gradually increase with distance before leveling off at the distance where spatial dependence no longer exists. This pattern is often best modelled by an asymptotic curve that is characterized by three main parameters: the range, sill, and nugget. The range refers to the distance at which spatial dependence degrades and the sill represents the semivariance at this distance. The nugget is the semivariance at the y intercept and is considered a result of random effects or sampling error (Fortin and Dale, 2005). These parameters are ultimately used to determine the relative weights used to predict the variable of interest (e.g. "z") at unsampled locations by linear kriging equations that minimize estimation error.

Unfortunately variography requires a relatively large sample size, with a minimum of 50 sampling locations (Fortin and Dale, 2005). This is often difficult to accomplish due to logistical limitations (Reay-Jones, 2010). Furthermore, the assumption of stationarity is violated in the presence of drift (also known as a trend) which occurs when the global mean is not constant. In the presence of drift, the data must be detrended for subsequent analysis of the residuals (Olea, 2006). However, decisions regarding trend analysis and detrending techniques are often ambiguously made (Blackwell et al., 2008). When kriging is not suitable, alternative interpolative techniques include inverse distance weighting and voronoi polygons. These techniques rely on distance and point proximity respectively to estimate the value of unsampled locations (Fortin and Dale, 2005).

Despite the large number of studies that have described larval distributions across geographical space, very few have attempted to incorporate quantitative measures of spatial structure. Such quantification is necessary in order to demonstrate the presence of non-random patterns that may be of biological significance, and because it offers information on the scale of the underlying processes. Kriging interpolations have been used, but variogram parameters and model assumptions are rarely discussed (e.g. Bradbury et al., 2003; Grigoryeva, 2009). In many studies, the type of interpolation is not even specified (e.g. Peliz et al. 2007; Sokolovskii and Sokolovskaya, 2008; Hoffmeyer et al., 2009). Other studies have illustrated spatial pattern by the use of proportional symbols instead of interpolated surfaces (e.g. Wing et al., 1995; Abelló and Guerao, 1999; Chiswell and Booth, 2005; Bas et al., 2009). Regardless, interpretation of spatial patterns solely by visualization can be misleading because the number and classification scheme of contours or symbols can be arbitrarily chosen.

In summary, analyses of horizontal meroplankton distributions contribute to the understanding of larval dispersal by generating hypotheses or validating predictions about dispersal processes (Sale and Kritzer, 2003). Planktonic distributions are often characterized by patches that can be detected at different scales (Mackas et al., 1985).

The extent and magnitude of these non-random patterns, caused by induced and/or inherent spatial dependence, can be quantified using different spatial analyses. Global spatial statistics are not recommended for large spatial extents because horizontal larval distributions are often skewed and characterized by high spatial heterogeneity. In addition, local spatial statistics may be particularly useful as exploratory tools for evaluation of stationarity and detection of potential patches. Finally, variography and geostatistical techniques have great potential in determining overall spatial structure and predicting larval abundance at unsampled locations (e.g. Fletcher and Sumner, 1999; Díaz-Avalos et al., 2006), provided that sample size requirements are met and the data are properly detrended in the presence of drift.

2.4. Study area: the Strait of Georgia

The Strait of Georgia (SoG hereafter) is a large and deep semi-enclosed ocean basin situated between Vancouver Island and mainland British Columbia. It is approximately 222 km long and 28 km wide, with an average and maximum depth of 155 m and 420 m, respectively (Thomson, 1981). Its deepest region is situated almost directly in the basin's geographical centre. The shoreline is primarily composed of steep rocky inclines, gentle rocky slopes, and gravel and sandy beaches (Levings et al., 1983; Zacharias et al., 1998).

The SoG communicates with the Pacific Ocean through inter-island passages at its northern and southern extents. To the north, a series of narrow channels between several interlocking islands eventually merge to form the Johnstone Strait. To the south, channels between the Gulf and San Juan Island groups connect the SoG and Juan de Fuca

Strait (hereafter JdF) (Thomson, 1981; Masson and Cummins, 2004). The main source of ocean-basin exchange occurs through the southern channels, as the cross-sectional area of the northern channels makes up only 7% of all exits (Waldichuk, 1957). The SoG also communicates with Puget Sound, an enclosed estuarine fjord south of the San Juan Islands, characterized by a double sill at its main entrance and three large interconnected basins (Moore et al., 2008). The entire SoG-JdF-Puget Sound complex is collectively known as the Salish Sea (Cummins, 2006).

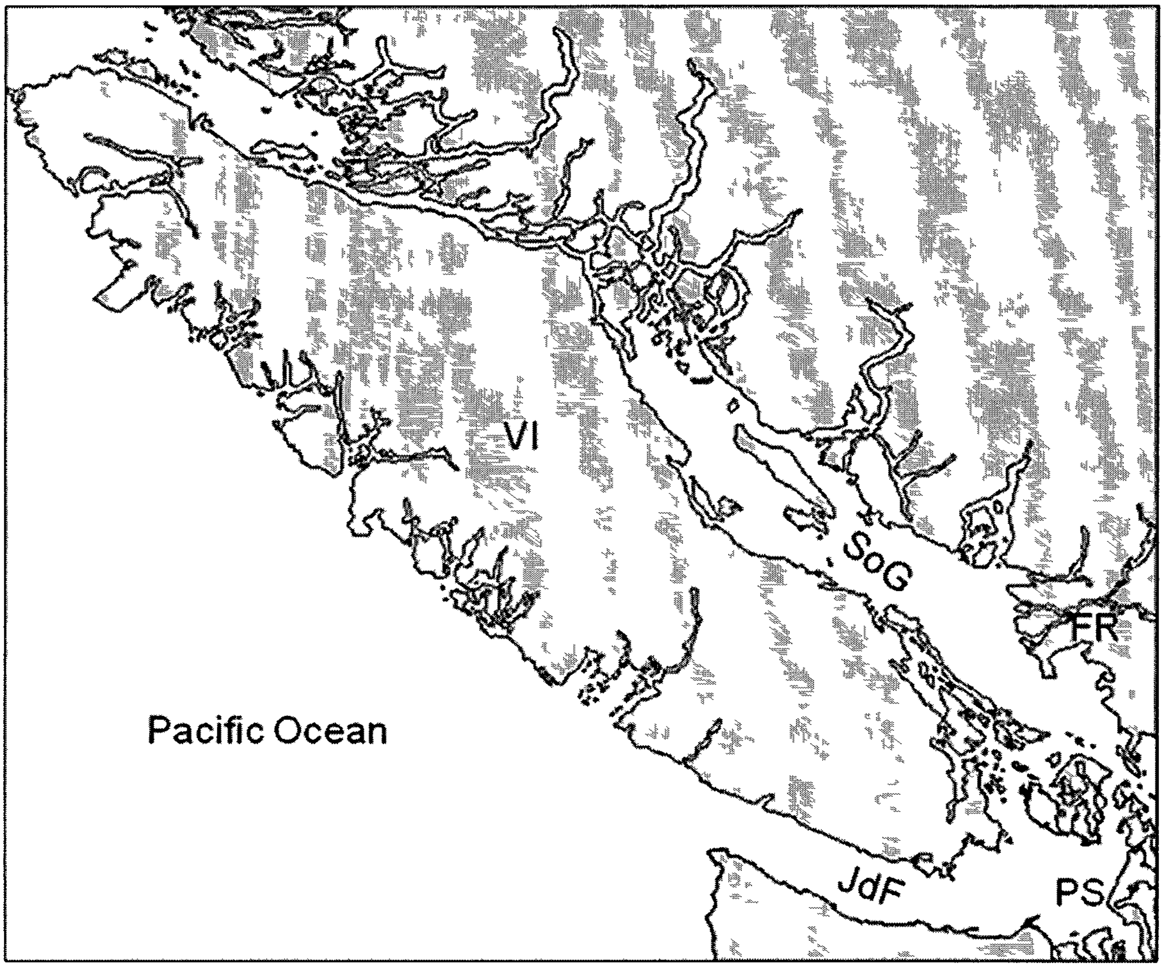

Figure 2.1. Vancouver Island and surrounding water bodies. FR, Fraser river; JdF, Juan de Fuca Strait; PS, entrance to Puget Sound; SoG, Strait of Georiga; VI, Vancouver Island.

2.4.1 Physical Oceanography

The physical oceanography of the SoG has been reviewed by Waldichuk (1957), Thomson (1981; 1994), and LeBlond (1983). Subsequent studies have focused on describing low-frequency currents (e.g. Stacey et al., 1986; 1987), deep water renewal (LeBlond et al., 1991; Masson, 2002) and estuarine exchange between the SoG and JdF basins (LeBlond et al, 1991; Masson and Cummins, 2000; Masson, 2002). More recently, seasonal variations of salinity fields and basin circulation, as well as inter-annual temperature variability, have been described (Masson and Cummins, 2004; 2007). Ocean models have been developed to provide quantitative estimates of deep water renewal and residence time (Masson and Cummins, 2007; Pawlowicz et al., 2007), describe low frequency current trajectories (Marinone et al., 1996; Masson and Cummins, 2004) and investigate the importance of different factors affecting circulation (Masson and Cummins, 2004; Pawlowicz et al., 2007).

Environmental Forcing

For simplicity, further discussion of the SoG in this review will refer to its northern, central and southern regions as illustrated by Thomson (1981). The SoG is essentially a large estuary (Waldichuk, 1957). Its oceanography is primarily influenced by seasonal river runoff and is further modulated by tidal currents, wind stress, and basin topography (Masson and Cummins, 2004). Complex topographical features such as sills, headlands, and valleys interact with ocean hydrodynamics to generate water property and circulation patterns (LeBlond, 1983). A detailed map illustrating the bathymetery of the entire SoG from multibeam surveys has been illustrated by Burd et al. (2008).

Numerous rivers empty into the basin, but approximately 75% of the freshwater input is from the Fraser River (Thomson, 1981). Fraser River runoff may reach a minimum of 300 $m^3 s^{-1}$ during the winter and can exceed 10,000 $m^3 s^{-1}$ during the height of freshet (increased river flow from snowmelt) that usually occurs in June (Masson and Cummins, 2004). Both the central and southern regions are directly influenced by this freshwater input that drives positive estuarine circulation. Circulation is characterized as "estuarine" when a low salinity surface layer is exported as it rides over a deeper more saline layer that is imported. A conspicuous 2 to 10 m thick sediment-laden brackish plume is emitted from the river mouth that can stretch across the central and southern regions (Leblond, 1983). Pawlowicz et al. (2007) estimated that at peak flow, this plume can have an area as large as 600 km^2. In the plume, surface salinity can be as low as 5 PSU and form extreme horizontal gradients with surrounding waters that have surface salinities between 25 and 30 PSU (Pawlowicz et al., 2007).

Because the surface layer is highly stratified, wind stress can have a pronounced effect on transport of the surface layer in the central and southern regions (Thomson, 1981). South-to-southeasterly winds prevail during the winter, whereas weaker northwesterly winds prevail in the summer (Thomson, 1981). The tides are mixed and semidiurnal. The strength of tidal currents varies with proximity to the southern channels where most tidal exchange occurs (Thomson, 1981).

Low-frequency surface and subsurface currents

Most studies that describe the velocity and trajectory of currents have taken place in the central SoG. There is particular interest in energetic low-frequency currents (also known as residual currents), defined by Marione et al. (1996) as the mean current velocity and directionality after higher frequency movements (2-3 days) have been filtered out. In the SoG, low frequency currents have been estimated to have a periodicity of about 10-30 days and a spatial extent of approximately 10 km (Stacey et al., 1987 and references therein). Stacey et al. (1987) measured current velocity and trajectory for six months at a series of depths in the south-central SoG. These authors attributed low-frequency surface currents to wind forcing, and bottom currents to non-linear interactions between tides and topography. These bottom currents were later interpreted as gravity currents from deep water renewal events (LeBlond et al. 1991) as discussed in the next section. The vertical structure of these currents was consistent with what would be expected from wind induced Ekman spirals (Stacey et al., 1986; 1987).

Subsequent modelling efforts have demonstrated to variable degrees that the south-central region is characterized by one or more rotary currents (Marinone et al., 1996; Masson and Cummins, 2004). Masson and Cummins (2004) simulated two counter rotating baroclinic gyres in this region using a three-dimensional ocean model. The size and current velocity of the southernmost gyre was consistent with observations by Stacey et al. (1987), but was positioned approximately 10 km farther south. Early investigations using drift drogues and current meters suggested an "average" northward surface flow along SoG's eastern margin, and southward flow along the western margin. Based on these results it has been suggested that a counterclockwise circulation pattern prevails in the central SoG during the spring and summer months (see reviews by Waldichuk, 1957; Thomson, 1981). These interpretations must be taken with caution as they are based on few observations often made on relatively short time scales (Thomson, 1981; LeBlond, 1983).

The water column in the northern region does not exhibit extensive stratification as a consequence of its greater distance from the Fraser River. The area is generally characterized by weak tidal currents, although a strong tidal jet from Discovery Passage is present during flood tide along the northeast coast of Vancouver Island (Thomson, 1981; Burd et al., 2008). Hydrodynamics in the northern region are not well studied and often neglected due to its relatively low contribution of surface area and volume (Pawlowicz et al., 2007) and minimal exchange with the Pacific Ocean (Leblond et al., 1991). Early observations of surface drifter paths, that have shown westward movement at the northern extent and southward movement along the east coast of Vancouver Island, suggest a counterclockwise surface circulation pattern (Thomson, 1981).

Ocean-Basin exchange and residence time

There has been considerable interest in understanding the estuarine exchange that occurs between water masses of the SoG and JdF (Waldichuk, 1957; LeBlond, 1991; Masson and Cummins, 2000; Masson, 2002; Masson, 2006; Masson and Cummins, 2007; Pawlowicz, 2007). Knowledge of the residence time of water within coastal seas provides a basis for understanding observed seasonal cycles of different water properties (Masson and Cummins, 2007; Pawlowicz et al., 2007), the flushing of pollutants (LeBlond et al., 1991), and even larval retention (c.f. Jamieson and Phillips, 1993). Of the various southern channels, most exchange is thought to occur through the Haro Strait which is the deepest and widest exit from the SoG (Waldichuk, 1957; LeBlond et al., 1991). Tidal currents, sills, and narrow inter-island channels interact to induce vertical mixing where the SoG and JdF meet (Masson and Cummins, 2000; Masson, 2002). The extent of this vertical mixing influences the degree of estuarine exchange and ultimately the water properties within the deeper layers of the SoG and surface layer of the JdF (Masson, 2006; Masson and Cummins, 2007).

The vertical structure of the water column in the central and south-central SoG is organized into the following three layers: a surface layer (0-50 m), intermediate layer (50-200 m), and the deep layer (below 200 m). The surface layer is well oxygenated and its temperature and salinity respond to seasonal variation in heat flux and freshwater input. In the intermediate layer, temperature and oxygen also undergo seasonal cycles that are attributed to cold and warm intrusions from the Pacific Ocean. Finally the bottom layer is characterized by cooling in the summer and (sometimes) warming in the winter (Masson and Cummins, 2007; Pawlowicz et al., 2007). Irregular oxygen peaks also occur in the spring and late summer that coincide with low-frequency currents detected by Stacey et al. (1987). These signals are thought to represent deep water renewal events (LeBlond et al., 1991; Masson, 2002).

Pawlowicz et al. (2007) proposed that the intermediate layer is continuously renewed by intrusions from Pacific Ocean waters present in the JdF, and argued that once inside the SoG, the intermediate layer eventually upwells, mixes with the low salinity surface layer, and exists via estuarine circulation. Using a box-model, Pawlowicz et al., (2007) estimated surface and intermediate layer residence times of less than 80 days and approximately 160 days, respectively. Water mass analysis has shown that while passing through the Haro Strait (and associated channels), mixing between surface SoG layer and deeper JdF layer re-introduces surface water into the SoG at depth (Masson, 2006). Consequently, Pawlowicz et al., (2007) predicted that the residence time of Pacific Ocean source water is longer than that of the intermediate layer (residence time of approximately 1.7 years).

Renewal of the deepest layer requires dense, unmixed water from the JdF to spill into the SoG and cascade to the deep central basin (LeBlond et al., 1991; Masson, 2002). This scenario occurs in late summer and occasionally in spring (Pawlowicz et al., 2007) when upwelling along the west coast of Vancouver Island overlaps with relatively low Fraser River runoff. During these periods, dense water introduced into the JdF basin from upwelling events does not become sufficiently diluted by Fraser River runoff to prevent deep water renewal. Renewal events then occur at every second neap tide when tidal mixing is reduced and water is sufficiently dense at the Boundary Pass sill to replace the bottom waters of the SoG (Masson, 2002). These studies have clearly shown that ocean-basin exchange is heavily influenced by tidal mixing and estuarine circulation from the Fraser River, and can be limited for relatively long time periods.

Climatic influence

Inter-annual variability of temperature trends in the SoG appears to be linked to large scale atmospheric patterns over the entire Northeast Pacific. Open ocean temperature anomalies have been detected within the southern SoG after a time lag sufficient for transport from the open ocean into the SoG (approximately 4 months) via the JdF (Masson and Cummins, 2007). The SoG's temperature in the intermediate and bottom layer is related to that of the upper 100 m of the Pacific Ocean due to the presence of sills (~100 m depth) that restrict deep water exchange. Consequently, deep waters of the SoG have higher temperatures than those recorded at the same depth off the west coast of Vancouver Island and are more sensitive to increasing atmospheric temperatures associated with climate change (Masson and Cummins, 2007). Furthermore, entrainment of the surface layer directly affected by atmospheric warming with the intruding bottom layer over the Boundary Pass sill may magnify warming at depth (Masson and Cummins, 2007).

The effects of climate change appear to be already evident in the SoG. For example, temperature has increased at all depths between 1970 and 2005 by a depth-averaged value of 0.024 °C/year (Masson and Cummins, 2007). Climate change is also expected to have an effect on the timing and volume of the Fraser River runoff. Inter-annual variability of freshwater flow from the Fraser River is directly associated with changes in rainfall and/or snowmelt (Forman et al., 2001; Pawlowicz et al., 2007). Analysis of flow measurements from Hope, British Columbia dating back to 1912 provide evidence that peak flow is occurring earlier each year and this has been attributed to earlier spring snowmelt (Forman et al., 2001). In the next century, peak flow is expected to decrease slightly (approximately 5%) and occur on average 24 days earlier in the year (Morrison et al., 2002). In accordance with increasing atmospheric temperature, rainfall (rather than snowfall) between November and April is expected to increase during the winter and reduce the magnitude of the freshet in the spring and summer (Johannessen and McCarter, 2010). The effects of climate change on the physical oceanography of the SoG are still unknown but will likely affect the seasonal periodicity of temperature and salinity. Both are expected to have substantial impacts on dynamics of physical and biological patterns within the SoG system (Johannessen and McCarter, 2010).

2.4.2. Marine Protected Areas

Marine protected areas (MPAs) are management tools implemented to restrict human use of the marine environment within a defined area (Hoagland et al., 2001). MPAs are implemented for purposes of conservation, fisheries management, and other uses, such as education and research (Roberts et al., 2003). Conservation objectives include protecting threatened species (Mora et al., 2006) and preventing declines in biodiversity (Klein et al., 2008; 2010). Fisheries management objectives include preventing stock depletion (Murawski et al., 2000) and generating stock yield in unprotected areas by density-dependent “spillover” (Hoskin et al., 2011) and larval seeding (Christie et al., 2010).

MPAs are internationally recognized as important conservation tools and are growing in numbers worldwide (Mora et al., 2006; Wood et al., 2008), but their ability to single-handedly restore depleted fisheries has been questioned (Kaiser, 2005; Jones, 2007). Accordingly, MPA implementation has been perceived as a trade-off between maintaining biodiversity and reducing fisheries yield (Klein et al., 2008). On the other hand, both conservation and ecosystem services are thought to depend on the functionality of common ecological processes (Roberts et al., 2003). Ultimately, MPAs have potential in maintaining such processes when combined with other strategies in an ecosystem-based management approach (Halpern et al., 2010).

The utility of MPAs is highly dependent on their design and objectives (Hoagland et al., 2001). Because the presence of no-take MPAs is expected to create spatial variability in mortality, the movement of life history phases (larvae, juveniles, and adults) must be considered when deciding the size and inter-reserve spacing (Martell, 2000; Botsford et al., 2009). For example, MPAs are suspected to be less useful for protection of widespread highly motile organisms (Kaiser, 2005), and may select for reproductive success of organisms with low dispersal distance (Botsford et al., 2001). Before MPA implementation, managers should also consider socio-economic consequences (NRC, 2000; Hoagland et al., 2001) and the environmental impact of fishing displacement (Botsford et al., 2009). Herein, further discussion of MPA design will only be focused on the importance of the larval phase in the life history of benthic marine species, as other factors are outside of the scope of this review.

MPA design

Managers must consider the size of local populations, the spatial scale of dispersal, and larval exchange between subpopulations when designing size and placement of MPAs. In the context of fisheries management, an overall objective is to protect the largest populations with the highest reproductive output (Kritzer and Sale, 2004). Successful MPA design facilitates demographic sustainability (by individual replacement) within a single MPA; therefore, organisms with greater dispersal distances require larger MPAs (Botsford et al., 2001; Shanks et al., 2003). It follows that the sustainability of populations within small (<10 km^2), isolated MPAs are probably dependent on recruits from unprotected areas in many cases. Consequently, MPA networks have generally been accepted as the best alternative to single very large MPAs (Gaines et al., 2010), although a few large MPAs do exist (Wood et al., 2008).

The minimum requirement of self-recruitment within a MPA has been estimated to be 35% to achieve population sustainability. This is based on approximations of the lifetime egg production required for average recruits to achieve population sustainability (that ranged from 30% up to 70 %) in several conventionally managed fisheries (Botsford et al., 2001 and references therein). Accordingly, it has been proposed that over 35% of the total coastline be protected to ensure population sustainability within an MPA network (Botsford et al., 2001). Other estimates from numerous authors range from 20% to 50% network coverage for both conservation and fisheries management objectives (reviewed by NRC, 2000).

Strategic placement of MPAs within a reserve network is critical in a metapopulation context, wherein the persistence of subpopulations situated in different locations is dependent upon various levels of self-recruitment and larval exchange (Kritzer and Sale, 2004). Demographic modelling has demonstrated that it is necessary to protect "source" locations (areas of net export) as opposed to "sink" locations (areas of net import) (Crowder et al., 2000). The optimal distribution of inter-reserve spacing distances within a MPA configuration is difficult to determine as the upper limit is hindered by dispersal distance uncertainty, whereas the lower limit is hindered by vulnerability to local disturbances (Roberts et al., 2003). It follows that using a variety of inter-reserve distances has been suggested (Roberts et al., 2003). Leis (2006b) proposed that there be an equal number of inter-reserve spacing distances within predefined small, moderate, and large distances classes. This strategy may be especially useful when management objectives are to protect several species with a range of dispersal distances. Based on numerous empirical measures of dispersal distance, Shanks et al. (2003) suggested that spacing distances ranging from 10 to 20 km should facilitate connectivity between MPAs.

Unfortunately, it is difficult to determine the larval contribution of each local population. This limits the ability of managers to make informed decisions when implementing MPA networks (Kritzer and Sale, 2004). However, several tools are being refined to better understand larval exchange within MPA networks. Tools used to quantify dispersal distance and population connectivity include genetic parentage analysis (Planes et al., 2009; Christie et al., 2010), biophysical modeling (Robinson et al., 2005), geochemical signature tracing (Miller and Shanks, 2004; Thorrold et al., 2007), and artificial tags (Jones et al., 2005; Kuroki et al., 2010).

Marine Protected Areas in British Columbia and the SoG

Canada has made both national and international commitments to establish a "national network" of marine reserves (Jessen et al., 2011). In Canada there are a variety of marine protection initiatives that are implemented federally and provincially. The title "Marine Protected Area" (MPA) is only used to describe protected areas established by Fisheries and Oceans Canada under the Oceans Act (Fisheries and Oceans Canada, 2010b). Therefore, protected areas implemented by other agencies require the use of different names. For example, National Marine Conservation Areas (NMCAs) are implemented by Parks Canada under the Canada National Marine Conservation Areas Act (Parks Canada, 2010), and Marine Wildlife Areas (MWAs), an extension of National

Wildlife Areas, are implemented by Environment Canada under the Canada Wildlife Act (Environment Canada, 2010). In British Columbia, provincially implemented protected areas may be referred to as marine parks, sanctuaries, reserves, ecological reserves or wildlife areas. Such reserves have been established under several different types of legislation (c.f. Jamieson and Levings, 2001).

To some extent, most protected areas listed above aim to conserve rare, endangered or vulnerable species and/or communities and their associated habitats. Marine protected areas can also be designed for resource protection, including fisheries management (e.g. Fisheries and Oceans Canada, 2006). National Marine Conservation Areas are established to protect marine habitats and ecosystems that are representative of Canada's natural and cultural heritage (Parks Canada, 2010), whereas MWAs are designed for conservation, interpretation, and research of Canadian wildlife, and appear to focus primarily on marine migratory birds (Jamieson and Levings 2001; Environment Canada, 2010). Finally, protected provincial sites within British Columbia are defined as land and resources that cannot be sold, and where industrial extraction of non-renewable resources is prohibited (Jamieson and Levings, 2001). A comprehensive list of mandates for each type of protected area is provided by Jamieson and Levings (2001) and is also listed online (Fisheries and Oceans Canada, 2010b; Environment Canada, 2010; Parks Canada, 2010). Clearly not all marine reserves are governed by the same restrictions; federally implemented MPAs and NMCAs appear to be best qualified for establishing "no-take" reserves. The Canadian Parks and Wilderness Society, in conjunction with numerous Canadian scientists, proposed that at least 30% of each Canadian "bioregion" be protected by a no-take reserve network that prohibits the use of industrial use and development (Jessen et al., 2011).

The biodiversity and productivity of marine life off the coast of British Columbia is considered to be among the highest of temperate marine environments in the world. The province's expansive coastal region houses unique marine communities, such as sponge reefs (Chu and Leys, 2010), supports several commercial, aboriginal, and recreational fisheries (e.g. Fisheries and Oceans Canada, 2010a), and contributes to recreation and tourism. Accordingly, there have been strong incentives to manage and protect British Columbia's marine environment from future human impacts, and over 100 provincial reserves have been established (Jamieson and Levings, 2001). In the SoG, freshwater input from the Fraser River creates strong near surface stratification and entrains nutrients from subsurface waters at sea. This creates ideal conditions for high levels of primary productivity in the spring and into the summer (Yin et al., 1997; Masson and Pẽna, 2009). This productive inland sea contributes towards several of British Columbia's valuable fisheries (e.g. Fisheries and Oceans Canada, 2010b) and is an important nursery area for marine fish such as Pacific salmon (Melnychuck et al., 2010) and herring (Ware and Schweigert, 2002). Because the SoG is surrounded by several growing municipalities, this system is also heavily impacted by human activities such as fishing, pollution, habitat destruction, ship traffic, introduction of invasive species, and escape of hatchery reared fish (Johannessen and McCarter, 2010). Future human influences and climate change are projected to put added pressure on this system, and together may already be responsible for recent changes to its physical and biological oceanography (Johannessen and McCarter, 2010).

Over 40 provincially protected areas currently exist within the SoG, and Parks Canada has been evaluating the potential for implementation of a NMCA near the Gulf Islands in the southern region of the SoG (Jamieson and Levings, 2001; Parks Canada, 2005). Although no MPAs have been created for shellfish (e.g. crabs), Fisheries and Oceans Canada implemented over 80 rockfish conservation areas in the SoG and surrounding inlets and channels in which rock fish mortality from recreational and commercial fishing is prohibited (Fisheries and Oceans Canada, 2006).

2.4.3. Life histories of crabs (Anomura, Brachyura, Axiidea and Gebiidea) of the Salish Sea

The Northeast Pacific Ocean (southern Oregon north to Alaska) is home to over 90 crab species (Hart, 1982), approximately 60 of which are known to reside in the Salish Sea. About one third of the latter group lack larval descriptions. Although there appears to be potential for larval exchange between the SoG and the outer coast, several species only reside on the open coast and are seldom seen as far east as Victoria, British Columbia (Hart, 1982; Jensen, 1995). Many of these species prefer cool, high current environments (Nyblade, 1987; Jensen, 1995) that occur in the SoG's southern region, but tend to decrease with increasing latitude (Thomson, 1981). In the following, I review the life history and reproductive timing of crabs that occur within the JdF, SoG, and Puget sound. This information is organized by infraorder and subsequently family, using taxonomy adopted from De Grave et al. (2009) and is summarized in Table 2.1.

Table 2.1. Reproductive timing and citation for larval description of crab (Anomura, Brachyura, Axiidea, Gebiidea) species found in the Strait of Georgia, British Columbia and/or Puget Sound, Washington. For reproductive timing citations see text. Taxonomic classification as per De Grave et al. (2009); Z, zoea; M, megalopa; * symbol indicates average number of broods per year from Nyblade (1987). Table format adopted from Strathmann (1987).

Taxonomic classification	**Brood /year**	**Months ovigerous**	**Hatch period**	**Larval Description**
Infraorder Anomura				
Family Diogenidae				
Paguristes turgidus	1	Nov-Sept	Aug-Sept	Hart (1937)
Galatheidae				
Munida quadrispina	---	---	---	---
Family Hapalogastridae				
Acantholithodes hispidus	--	--	--	Hong et al. (2005)
Hapalogaster mertensi	1	Nov-Apr	Apr-?	Miller and Coffin (1961)
Oedignathus inermis	---	---	---	---
Placetron wosnessenskii	1	---	---	Crain and McLaughlin (2000a)
Family Lithodidae				
Cryptolithodes typicus	1	Year round?	Spring	Hart (1965)
Lopholithodes foraminatus	0.5	Year round	Jan-Jun	Duguid and Page (2009)
L. mandtii	1	---	Mar-May	Crain and McLaughlin (2000b)
Phyllolithodes papillosus	1	---	---	---
Rhinolithodes wosnessenskii	1	---	---	Haynes (1984)
Family Paguridae				
Discorsopagurus schmitti	1	Jan-May	Mar-May	Gherardi and McLaughlin (1995)
Elassochirus cavimanus	---	---	---	---

E. gilli	1	Sept-May	April-May	---
E. tenuimanus	1	Aug-May	Mar-May	---
Labidochirus splendescens	1	Jul-April	Mar-Apri	Nyblade and McLaughlin (1975)
Pagurus aleuticus	1	---	Mar-May	---
P. armatus	2.6*	Oct-Sept	Feb-Sept	McLaughlin and Gore (1992)
P. beringanus	1.8*	Nov-Sept	Feb-Sept	Hart (1937)
P. capillatus	1	Jan-May	Mar-May	---
P. caurinus	5.2*	Dec-Sept	Mar-Sept	Bidle and McLaughlin (1992)
P. dalli	1	Nov-Apr	Mar-Apr	---
P. granosimanus	3	Oct-Sept	Feb-Sept	Ko and McLaughlin (2008)
P. hirsutiusculus	4.9*	Nov-Sept	Feb-Sept	McLaughlin et al. (1988)
P. kennerlyi	1	Jan-May	Mar-May	McLaughlin, et al. (1989)
P. ochotensis	2.5*	?Mar-Sept	Mar-Sept	McLaughlin et al. (1992)
P. setosus	---	---	---	---
P. stevensae	1	Dec-April	Mar-April	---
Family Porcellanidae				
Petrolisthes eriomerus	2	Feb-Aug	May-Oct	Goner and Goner (1973)
Pachycheles rudis	2-3	Dec-Sep?	Mar-?	Goner and Goner (1973)
Pachycheles pubenscens	---	---	---	Goner and Goner (1973)
Infraorder Brachyura				
Family Cancridae				
Cancer productus	2?	Oct-?	Mar-Jun	Trask (1970)
Glebocarcinus oregonensis	1-2	Nov-May	Feb-Jun	---

Metacarcinus gracilis	2	Dec-Jul	Mar-Sep	Ally (1975)
M. magister	1	Oct-June	Dec-Jun	Poole (1966)
Romaleon antennarius	?	---	---	Roesijadi (1976)
R. branneri	?	---	---	---
Family Cheiragonidae				
Telmessus cheiragonus	---	---	---	Kurata (1963)
Epialtidae				
Chorilia longipes	---	---	--	---
Pugettia gracilis	>1	Year round	Year round?	Oh and Ko (2007) Z1
P. product	>1	Year round	Apr-Aug	---
Scyra acutifrons	>1	Year round	Dec-Aug	Oh and Ko (2010)
Family Oregoniidae				
Chionoecetes bairdi	1	Year round	Dec-Mar?	Haynes (1973; 1981); ZI-ZII; Jewett and Haight (1977); M
Hyas lyratus	---	Year round	Mar-?	Hart (1960)
Oregonia gracilis	---	?Mar-Sep?	April-?	Hart (1960)
Family Pinnotheridae				
Fabia subquadrata	1	Nov-Feb	Feb-?	Irvine and Coffin, (1960)
Pinnixa eburna	---	---	---	---
P. faba	2	Dec-Jun	Apr-Sept	---
P. littoralis	---	Nov; Apr-May	Mar-May; Jul	---
P. schmitti	---	---	---	---
P. tubicola	---	---	---	---
Pinnotheres pugettensis	---	---	---	---

P. taylori	---	---	---	Hart (1935)
Scleroplax granulate	---	---	---	---
Family Varunidae				
Hemigrapsus nudus	1	Jan-Apr	May-Jun	Hart (1935)
H. oregonensis	1	Feb-Apr	May-Jul	Hart (1935)
Family Xanthidae				
Lophopanopeus bellus	2	Jan-Apr	May-Aug	Hart (1935), Knudson (1959)
Infraorder Axiidea				
Family Axiidae				
Calocarides spinulicauda	---	---	---	---
Family Callassinidae				
Neotrypaea californiensis	1?	?-Aug	Mar-Aug	McCrow, 1972; ZI-ZV
N. gigas	---	---	---	---
Infraorder Gebiidea				
Family Upogebiidae				
Upogebia pugettensis	1	Oct-May	Feb-May	Hart (1937)

Infraorder Anomura

The following six anomuran families have been observed in the Salish Sea: Diogenidae, Galatheidae, Hapalogastridae, Lithodidae, Paguridae, and Porcellanidae. Fertilization is external and females molt, mate, and extrude their egg masses in rapid succession (Nyblade, 1987; Molenock, 1975); however it is unknown if this applies to galatheid decapods as information on this family is scarce (Almerão et al., 2010). The anomuran decapodid stage (last larval stage) is sometimes referred to as a glaucothoe (rather than megalopa), especially for the pagurid, diogenid and lithodid families. However, in this review the decapodid stage will be referred to as a megalopa.

Family Diogenidae

The larval development of the only Diogenid species, *Paguristes turgidus*, is entirely lecithotrophic. Females produce large eggs in late fall that do not hatch until August (Nyblade, 1987). There are only three zoeal stages and a megalopal stage. The zoeal stages develop up to four times faster than pagurid zoeae (Nyblade, 1987). All larval stages are described by Hart (1937).

Family Galatheidae

Munida quadrispina is the only local galatheid species, although Hart (1982) has suggested that extensive examination of this species may reveal an additional undescribed species. *Munida quadrispina* is the dominant mobile invertebrate on cliffs of inlets that communicate with the SoG (Burd and Brinkhurst, 1984). Although this species is a widespread subtidal inhabitant in British Columbia (Hart, 1982), information about its natural history and reproductive timing is scarce.

The larvae molt through 4 to 5 zoeal stages and a megalopal stage (J. F. L. Hart, pers. comm. in Nyblade, 1987). The fourth zoeal stage of other galatheid species may also either molt to a fifth zoeal stage or the megalopa in laboratory culture (Gore, 1979; Christiansen and Anger, 1990). The juvenile phase is pelagic and apparently may last up to one year (Burd, 1983). Off the coast of Oregon, larvae have been taken in highest abundance in late spring and summer, and pelagic juveniles were observed during late summer and fall (Lough, 1975). In British Columbia, pelagic juveniles have been observed in plankton samples in the summer months (R. Larson, pers. comm. in Burd and Brinkhurst, 1984) and both reproduction and recruitment apparently occur during the spring (Burd, 1983). However, settlement of pelagic juveniles has also been observed in the fall (Burd and Brinkhurst, 1984).

Family Hapalogastridae

There are four local hapalogastrid species. *Acantholithodes hispidus* has been noted as a common resident in the SoG (Hart, 1982). *Hapalogaster mertensii* is listed as occurring in "widespread in suitable habitats" in British Columbia (Hart, 1982) and its reproductive timing has been documented by Knudsen (1964). *Placetron wosenessenskii* is known to occur within Puget Sound (Jensen, 1995), although no records could be found for either of the latter species in the SoG. *Oedignathus inermis* has apparently been observed (once) at Porlier Pass in the SoG (Hart, 1982); however, its distribution is thought to be restricted to the open coast (Nyblade, 1987; Jensen, 1995). An additional species, *Hapalogaster grebnitzkii* has been observed only from a single record in northern British Columbia (Hart, 1982) and is not considered a local to the Salish Sea.

Species within this family have been recently removed from the family Lithodidae. Although less is known about the reproductive and larval biology of hapalograstrid species, they share several life history characteristics with lithodid species. For example, hatching occurs over an extended time period (days for *H. mertenssii* [Miller and Coffin, 1961] and weeks for *P. wosenenskii* [Nyblade, 1987; Crain and McLaughlin, 2000a]). The larval phase consists of four zoeal stages and a megalopal stage (Crain and McLaughlin, 2000a; Hong et al., 2005) that may be non-feeding (c.f. Miller and Coffin, 1961).

Family Lithodidae

There are five local lithodid species. *Lopholithodes foraminatus* is known to exist within the SoG (c.f. Duguid and Page, 2009) where there has been interest in the development of a fishery (Zhang et al., 1999). *Rhinolithodes wosnessenskii* has been listed as widespread in British Columbia. Other species including *Lopholithodes mantii, Phyllolithodes papillosus*, and *Cryptolithodes typicus* are also widespread or common in British Columbia (Hart, 1982), and appear to prefer high current areas (Jensen, 1995). An additional species, *Cryptolithodes sitchensis* is not uncommon in British Columbia, but is only found on the outer coast, particularly in cold waters (Hart, 1982; Jensen, 1995). The distribution of several additional lithodid species including *Lithodes aequispina, L. couesi, Paralithodes camtchaticus*, *Paralomis multispina*, and *P. verrilli* appears to be limited to either the outer coastal region or northern British Columbia (Hart, 1982), and are therefore not considered local species herein.

Most local lithodid species appear to produce one brood each year that hatches throughout the spring (c.f. Nyblade, 1987). However, recent evidence suggests that at least one species (*L. foraminatus*) reproduces biennially (Duguid and Page, 2011). As in the Hapalogastridae, a single brood may hatch over an extended time period (Nyblade, 1987; Duguid and Page, 2011 and references therein). Larvae progress through four zoeal stages and a non-feeding megalopal stage. Zoeal durations of 20 to 50 days have been recorded for different species reared at temperatures between 8-10 °C (Nyblade, 1987; Duguid and Page, 2009).

Family Paguridae

Fifteen pagurid species can be found within the San Juan Archipelago at the southern extent of the SoG (Nyblade, 1974); it is unclear if the geographic range of two additional species (*Pagurus setosus* and *Elassochirus cavimanus*) extends into the Salish Sea. *Pagurus hirsutiusculus* is a ubiquitous intertidal inhabitant in the region. Other commonly occurring species include *Elassochirus tenuimanus*, *Pagurus kennerlyi, P. armatus*, *P. ochotensis*, *P. granosimanus,* and *P. beringanus*. *Elassochirus gilli* is also common, but most likely to be encountered in areas characterized by high currents (Hart, 1982; Jensen, 1995).

Although females of many species only carry one brood per year, some species can produce several broods (Table 2.1). For all local pagurids, at least one brood is produced between late summer and winter and larvae are then released in the spring. Additional broods are generated over the spring and summer months, and hatching may extend into September (Nyblade, 1987). Pagurid larvae progress though four zoeal stages and a megalopal stage. At 10 °C, the zoeal duration is consistent among local species, ranging from around 50 to 60 days (Nyblade, 1987). The megalopal stage persists for approximately 20 days (Nyblade, 1987); however, their swimming ability is lost near the midpoint of their duration due to reabsorption of the pleopod muscles (Nyblade, 1974). Complete larval descriptions are only available for nine local species (Table 2.1).

Family Porcellanidae

Petrolisthes eriomerus is the only porcellanid species common to the SoG (Hart, 1982). Although Hart (1982) mentioned that two other species, *Pachycheles pubenscens* and *P. rudis*, were rarely observed as far east as Victoria, they have been observed in high current areas within Puget Sound (Jensen, 1995). In Puget Sound, ovigerous female *P. eriomerus* have been observed from February to May. Two broods are produced that are thought to hatch from May to August and August to October, respectively (Knudsen, 1964). Knudsen (1964) observed that *P. rudis* carry at least two broods from December through August, the first of which hatched between March and April. Off the Oregon coast, both *Petrolisthes* and *Pachycheles* zoeae were present year round and were most abundant between May and June, January and February, and October and November (Lough, 1975). Larvae progress through two zoeal stages and a megalopal stage, with larval descriptions available for each species (Table 2.1).

Infraorder Brachyura

The following brachyuran families can be found in the Salish Sea: Cancridae, Cheiragonidae, Epialtidae, Origoniidae, Pinnotheridae, Varunidae, and Xanthidae. Brachyuran reproduction differs from their anomuran counterparts in that fertilization is internal and females are capable of storing sperm (Hartnoll, 1969). In some cases, such as for *Chionoecetes bairdi*, females can successfully fertilize an egg mass with sperm that has been stored for up to two years (Paul, 1984).

Family Cancridae

The following four cancrid species, previously all within *Cancer* but now assigned to different genera (Schweitzer and Feldmann 2000), are common in the Salish Sea (Orensanz and Gallucchi, 1988): *Metacarcinus magister, Metacarcinus gracilis, Cancer productus*, and *Glebocarcinus oregonensis*. Two additional species, *Romaleon antennarius* and *Romaleon branneri*, are frequently encountered on the outer coast (Hart, 1982; Jensen, 1995). Recently, both species have been observed deep inside the Juan de Fuca strait (Lamb and Hanby, 2005; W. Duguid, Pers. Comm.). *Romaleon branneri* is morphologically similar to *G. oregonensis* (DeBrosse et al., 1990a); therefore the presence of this species in the Salish Sea may be underreported due to misidentification. The life history of local cancrids has received considerable attention compared to other groups because of their economic importance as a fishery resource (*M. magister*) (Fisheries and Oceans, 2010a) and their ecological importance as predators (Dudas et al., 2005).

In Puget Sound, *M. gracilis, M. magister, C. productus,* and *G. oregonensis* produce a primary brood during the fall and winter that hatches in the spring (Knudsen, 1964; Strathmann, 1987; Orensanz and Galluchi, 1988). Each species may produce a smaller second brood in the spring or summer that does not require additional mating (Strathmann, 1987). Within the San Juan Islands, settlement of *M. gracilis* has been suggested to occur during late summer and early fall, whereas peak settlement events of *M. magister, G. oregonensis*, and *C. productus* have been observed in July and August (Orensanz and Galluchi, 1988). Additional *M. magister* settling events observed in May and early June in the Juan de Fuca strait and San Juan Islands have been attributed to larval intrusions from coastal populations (Dinnel et al., 1993). In Puget Sound, *Metacarcinus gracilis* megalopae have been observed from May through October (Towanda and Thuesen, 2006), whereas megalopae of *M. magister* and *G. oregonensis* have been observed from May to August (Orensanz and Galluchi, 1989; Miner et al., 2000). At 10 °C the mean zoeal duration of these four species is between 60 to 70 days (Sulkin and McKeen, 1994). The natural duration the entire *M. magister* larval phase has been estimated at approximately 130 days off the coast of Oregon (Lough, 1976) and 105-125 days off the Coast of California (Reilly, 1983). Formal larval descriptions are not available for *G. oregonensis* and *R. branneri.*

Family Cheiragonidae

Telmessus cheiragonus is the only local cheiragonid species (Hart, 1982). In British Columbia, this species is listed as "common in suitable areas" (Hart, 1982) and has been recorded in surveys conducted both in southern and northern regions of the SoG (Burd et al., 2009). Although some information does exist on the timing and ethology of mating in this species from Japanese populations (Kamio et al., 2002 and references therein), life history information of Northeast Pacific populations is virtually non-existent. In British Columbia, mating has been observed in early spring (Hart, 1982) and megalopae have been collected from surface swarms in May from the San Juan Islands (Miner et al., 2000). In Glacier Bay, Alaska, peak zoeal abundance and the presence of megalopae have been observed in April and between May and June, respectively (Fisher, 2006). There are no local larval descriptions but all larval stages have been described from a Japanese population (Kurata, 1963).

Family Epialtidae

Chorilia longipes, *Pugettia gracilis, Pugettia producta*, and *Scyra acutifrons* are the four epialtid species local to the Salish Sea. Virtually nothing is known about the life history of *C. longipes*, but in Puget Sound, *P. gracilis, P. producta* and *S. acutifrons* have been noted to carry broods throughout the year (Knudsen, 1964). Hatching observations by Knudsen (1964) are detailed in Table 2.1. At lower latitudes, *P. producta* and *S. acutifrons* females are capable of producing new broods every 1 to 2 months (Hines, 1982). Temporal trends of larval abundance off the Oregon coast suggest hatching of epialtid larvae occurs year round, with peak hatching between May and June (Lough, 1975). Larvae of all epialtid species are morphologically distinct from other majoid groups and have two zoeal and one megalopal stage (Oh and Ko, 2007; 2010).

Family Oregoniidae

There are three local oregoniid species including *Chionoecetes bairdi*, *Hyas lyratus*, and *Oregonia gracilis*. Ovigerous *C. bairdi* females have been observed year round and it is thought that broods are produced annually (C. Staude, pers. comm. in Strathmann, 1987; Paul, 1984). Observations in Rivers Inlet, north of Vancouver Island, have indicated that larvae are released primarily in the early spring (Fong and Dunham, 2007). Ovigerous *H. lyratus* have been observed year round, and broods extruded in late summer appear to hatch in February and March (Hart, 1960). Ovigerous *O. gracilis* have been observed between March and September and eggs ready to hatch have been observed in March and April (Hart, 1960). Larvae progress through two zoeal stages and a megalopal stage.

Family Pinnotheridae

There are at least nine pinnotherid species that reside in British Columbia. However, the geographic range of many of these species is unknown. Pinnotherid crabs (species name in parentheses) live symbiotically with different benthic invertebrates, including bivalves (*Fabia subquadrata*, *Pinnixa faba, Pinnixa littoralis*), tunicates (*Pinnotheres pugettensis, Pinnotheres taylori*), mud shrimp (*Pinnixa schmitti*, *Scleroplax granulata*) and tube dwelling polychaetes (*Pinnixa eberna, Pinnixa tubicola*) (Hart, 1982). The following three species have been not been observed near the SoG, but are listed as widespread or common in British Columbia (Hart, 1982; Jensen, 1995): *P. schmitti*, *P. tubicola*, *S. granulata.*

Because many of these species are not easily encountered, there is little information available on their respective life histories. A detailed account of the *F. subquadrata* life cycle was provided by Pearce (1966a). In Puget Sound, ovigerous *F. subquadrata* were first observed in November until hatching which occurred in February. Also in Puget Sound, females of *P. faba* and *P. littoralis* are ovigerous from winter to early spring, and again between spring and late summer (Pearce, 1966b). Larvae of both species are thought to hatch once in the spring, and again later in the summer (Strathmann, 1987). Larvae collected from one ovigerous *P. taylori* specimen in March hatched in May (Hart, 1935). Pinnotherid larvae progress through a two to five zoeal stages, depending on the species, and a megalopal stage. A reliable larval description is available only for *Pinnotheres taylori* (Table 2.1).

Family Varunidae

Hemigrapsus nudus and *Hemigrapsus oregonensis* are two varunid species common intertidally in British Columbia (Hart, 1982). In Puget Sound, *H. nudus* and *H. oregonensis* females have been observed depositing eggs in January and February, respectively. By April almost all females of both species were ovigerous, and hatching occurred from May to June for *H. nudus* and extended into July for *H. oregonensis* (Knudsen, 1964). Similar, but less extensive observations have been made by Hart (1935) from Departure Bay, Nanaimo, British Columbia. These observations are consistent with these species producing one brood per year, although Knudsen (1964) did note that <1% of *H. nudus* produced a second brood. The larvae progress through four zoeal stages and a megalopal stage.

Family Xanthidae

Two xanthid subspecies of *Lophopanopeus bellus* reside in British Columbia including *L. bellus bellus*, common in the intertidal zone, and *L bellus diegensis*, less frequently encountered in the subtidal zone (Hart, 1982). In Puget Sound, *L. bellus bellus* females produce two broods per year. The first brood has been observed in January and eventually hatched in May (Knudsen, 1964). In British Columbia, Hart (1935) observed hatching from May to August. The second brood is extruded soon after which presumably hatches in September (Knudsen, 1964). There is virtually no information available for *L. bellus diegensis* in the region. Xanthid larvae progress through four zoeal stages and a megalopal stage. Hart (1935) described the larval stages of *L. bellus bellus*, whereas a larval description of *L. bellus diegensis* was provided by Knudsen (1959).

Infraorder Axiidea

Members of this infraorder are mud burrowing shrimp-like decapods categorized within the group Reptantia (Hart, 1982). These organisms are heavily dependent on their burrow for shelter, feeding, and reproduction (Coelho et al., 2000).

Family Axiidae

Calocarides spinulicauda is the only local axiid species and has been reported from the SoG (Hart, 1982; Burd et al., 2009). Virtually nothing is known about this species other than that it is mostly collected in fjords (Hart, 1982).

Family Callianassidae

Two callianassid species, *Neotrypaea califroniensis* and *N. gigas* are common in British Columbia (Hart, 1982). Considerably less information is available for *N. gigas* compared to its congener *N. californiensis*, probably because these species are difficult to separate morphologically (as juveniles and adult females) (Pernet et al., 2010). It is therefore possible that studies on *N. californiensis* may include *N. gigas* individuals.

In Willapa Bay, Washington, ovigerous and spent *N. californiensis* females have been observed from April through August, and from June to August respectively, whereas recruitment has been observed from August to October (Dumbauld et al., 1996). In a recent study, *N. californiensis* zoeae have been observed in Willapa Bay from March through September with peak abundance between May and August (Graham and Bollens, 2010).

Infraorder Gebiidea

Family Upogebiidae

Upogebia pugettensis is the only local upogebiid species. This once common species has recently declined dramatically along the Pacific coast in association with an increased prevalence of a castrating parasitic bopyrid isopod, *Orthione giffenis*, thought to be introduced from Japan (Griffen, 2009; Dumbauld et al, 2011). In Willapa Bay, Washington, ovigerous and spent females have been observed from October to May and February to May respectively, whereas recruitment occurred from April to June (Dumbauld et al., 1996). Ovigerous females have been observed from January to April in British Columbia and in late winter, spring, and summer in Puget Sound (Hart, 1937). Hart (1937) also noted that larvae may be found in plankton samples from February through May.

CHAPTER 3

A description of stage-specific diagnostic characters of laboratory reared zoeae of *Glebocarcinus oregonensis* (Decapoda: Brachyura: Cancridae)

3.1. Abstract

A series of morphological characters were identified from laboratory reared *Glebocarcinus oregonensis* zoeae that can be used to readily distinguish this species from other cancrids in the Salish Sea, North East Pacific. Carapace length and a detailed description of the abdomen and telson were provided for the five zoeal stages of this species. Other features previously considered for cancrid identification were also discussed. Descriptions were supplemented with estimates of stage duration and mortality of zoeae reared at a mean temperature of 13.34 ˚C (± 0.02 SE). Stage-specific duration and mortality were generally consistent with previous estimates for larvae of this species reared at different temperatures. The length and angle of lateral exospines projecting from the telson as well as the length of posterolateral spines projecting from the abdominal somites were identified as the most suitable features for larval identification.

3.2. Introduction

The life cycle of many benthic marine invertebrates includes a dispersive planktonic larval phase. Larval dispersal is an important determinant of population connectivity (Pineda et al., 2007), and the supply and settlement of larvae can be influential to the dynamics of adult populations (Gaines et al., 1985). Field studies investigating the dispersion and recruitment of crab larvae are often limited by issues regarding species and stage identification (Jensen et al., 1992; Abelló and Guerao, 1999; Lindley and Batten, 2008; Pardo et al., 2009). Such issues have been addressed with identification studies based on morphological descriptions of laboratory reared specimens. Laboratory rearing has also been utilized to quantify the duration of larval stages which, in the absence of field data, has been used to estimate or model dispersal distance (Shanks et al., 2003; Metaxas and Saunders, 2009).

The following four carcinid species, previously all within *Cancer* but now assigned to different genera (Schweitzer and Feldmann 2000), are commonly found in the Salish Sea (Orensanz and Galluchi, 1988): *Metacarcinus magister*, *Metacarcinus gracilis*, *Cancer productus*, and *Glebocarcinus oregonensis*. The range of two additional cancrid species, *Romaleon antennarius* and *R. branneri*, that are frequently encountered on the outer coast (Hart, 1982; Jensen, 1995) has extended deep into the Juan de Fuca Strait (Lamb and Hanby, 2005; W. Duguid, pers. comm.). Cancrid crabs are common predators in intertidal and subtidal habitats in the region (Knudsen, 1964; Smith et al. 1999b; Dudas et al., 2005) and their larvae are among the most abundant in plankton samples from the Northeast Pacific (Fisher, 2006; Daly and Konar, 2008; Lindley and Batten, 2008). Moreover, the Dungeness crab (*M. magister*) is one of the main commercially fished crab species along the Northeast Pacific coastline (Helliwell, 2009; Fisheries and Oceans, 2010a); therefore, cancrid larvae have been of interest in field studies that describe community composition and abundance of larval crabs (Lough, 1976; Reilly, 1983). Identification, however, has been problematic due to morphological similarities between certain congeners (e.g. Puls, 2001). To date, complete larval descriptions are available for each cancrid species except *G. oregonensis*, and *R. branneri*

(Poole, 1966; Trask, 1970; Ally, 1975; Roesijadi, 1976). Illustrations of *G. oregonensis* zoeae are available only from field-collected larvae tentatively identified from external characters and setal counts (Lough, 1975); although Debrosse et al. (1990b) claimed that *G. oregonensis* larvae were laboratory reared by Lough (1975).

In many cases, identification of congeneric species can rely on a single morphological feature (Jensen et al., 1992). In the case of cancrid species, the armature and setation of the telson are among the most frequently used diagnostic characteristics (Lough, 1975; Puls, 2001; Rice and Tsukimura, 2007). Puls (2001) summarized some unique features from previous descriptions of cancrid species, and Rice and Tsukimura (2007) provided an identification key for the first zoeal stages of *C. magister*, *M. productus*, *M. gracilis*, and *R. antennarius*, but not *G. oregonensis* or *R. branneri*. The megalopal stage of *G. oregonensis* can be readily identified by overall size and absence of spines projecting from the ventral surface of the pereopods (Debrosse et al., 1990a; 1990b).

Based on descriptions available in the literature cited above, a few studies have identified cancrid zoeae *G. oregonensis* (e.g. Park and Shirley, 2005; Fisher, 2006). However, the morphological features necessary to do so have not been unambiguously identified. This study provides key morphological information that will facilitate identification of *G. oregonensis* larvae with respect to sympatric cancrids, and will improve the resolution and reliability of field studies investigating larval dynamics of Cancridae.

3.3. Materials and Methods

3.3.1. Husbandry and culture

Two ovigerous female *G. oregonensis* crabs were collected from the shoreline in the vicinity of Victoria, British Columbia. The crabs were held at the University of Victoria in a re-circulating seawater system with regular input of fresh seawater collected from the ocean. The water was continually sand-filtered, UV treated and chilled to maintain a temperature between 10 ˚C and 14 ˚C. Female crabs were placed in a 20 L plastic container with continuous flow of seawater and a thick bottom layer of sand and rock substrate until their broods hatched on March 17 (Female A) and March 20, 2010 (Female B). Hatched zoeae passed through an overflow pipe and entered a 750 mL container with a 400 µm Nitex ® mesh bottom, suspended in a 1 L beaker. All larvae hatched at night and were collected the following morning. Only active swimming zoeae were kept for subsequent culture.

Zoeae were cultured in 1 L glass beakers immersed in a sea-table. The beakers were filled to approximately 800 mL with seawater from taps connected to the re-circulating system described above. A single culture from Female A consisted of 36 zoeae. Five cultures were obtained from Female B. Four of these cultures were allocated 39-40 larvae and were used to quantify stage duration and stage-specific mortality. A fifth culture, initially containing approximately 100 zoeae, was maintained as an alternative source of larvae and exuviae for morphological description.

Cultures were fed *Artemia* nauplii daily (newly hatched to 1 day old) at a density that would result in nearly all individuals being consumed within 24 hours. Temperature was initially measured at a mid-depth from at least one culture each day. When a partial vertical stratification was detected within the cultures, temperature readings were recorded both at the surface and bottom of each culture. The mean temperature measured on a daily basis, and over the zoeal duration, was calculated by pooling all temperature measurements (middle, surface, and bottom) across Female B cultures (Fig. 3.1).

Zoeae were transferred to a beaker with fresh seawater and a new supply of *Artemia* on a daily basis. In the process, live zoeae were counted and the exuviae and dead larvae were removed and enumerated for estimation of stage duration and mortality. The mean stage duration was calculated as the difference between the average number of days required to reach the subsequent stage from the average number of days to reach the stage of interest ± the standard error of the time required to reach the subsequent stage (Duguid and Page, 2009). Stage-specific mortality was calculated as the number of dead zoeae in the stage of interest divided by the total number of larvae that successfully molted to that stage. Observations from each of the four cultures were pooled to provide an estimate of duration and mortality for each stage. Unidentified filamentous shoots (bacteria or fungus) were observed on the exoskeleton of first stage zoeae. Although zoeae appeared to shed the filaments with their exoskeleton upon molting, the filaments reappeared near the end of their subsequent stage. This pattern persisted in all cultures for the larval duration. A 50 mg/L Streptomycin solution was initially added to affected cultures, but its use was discontinued when filaments reappeared in the second zoeal stage.

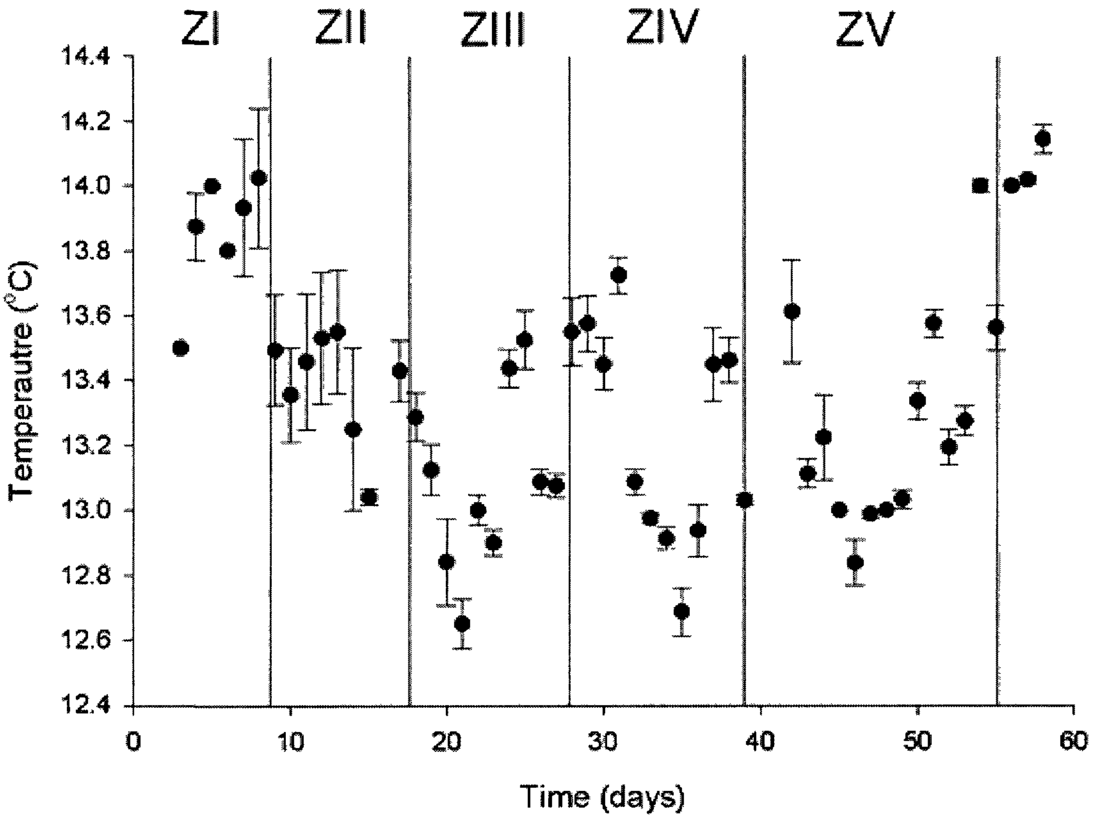

Figure 3.1. Variation of mean temperature (±1 SE) recorded daily from four *G. oregonensis* cultures hatched from female B over the entire zoeal duration. Spacing between the vertical bars represent the average stage duration. Temperature data were not available for days 1, 2, 16, 41, and 42. ZI-ZV, zoeal stages one to five.

3.3.2. Morphological analysis

Larval material was fixed and preserved in a borate buffered 4-5% solution of formalin in seawater. Larvae from both females were used for morphological analysis, except for carapace length (CL), which was measured only from Female B cultures. The CL of zoeae (n = 10) and megalopae (n = 7) were measured, primarily from preserved exuviae, as illustrated by Pohle (1991). To measure CL, images were acquired from a PixeLINK 1394 camera mounted on a Zeiss Stemi 2000-CS stereoscope. Images were then captured using PixeLINK Capture SE software and measurements were obtained using the ruler tool in Adobe Photoshop CS5 Extended software. The ruler tool was calibrated using slide micrometer images captured at the appropriate magnification (50x, 32x, 25x and 20x). The number of maxilliped natatory setae was also enumerated for each zoeal stage.

Illustrations were initially drawn from a preserved zoea that had recently hatched or molted to the stage of interest. The abdomen was removed from each specimen, mounted under a coverslip supported by plasticine feet, and viewed with an Olympus BH-2-BHT microscope. Images were acquired from a Leica DC480 camera and captured using Leica IM50 software. To illustrate each stage, images from multiple focal planes were overlaid and traced using the Brush Tool from Adobe Photoshop CS5 Extended software. Five exuviae from each female at each stage were used to examine variability of morphological features. This study was not intended to be a comprehensive morphological description for the larvae of *G. oregonensis*. Instead, we focused primarily on characteristics of the abdomen and telson as they were considered the most useful for differentiating *G. oregonensis* zoeae from those of sympatric cancrids.

3.4. Results

3.4.1. Stage duration and mortality

The mean stage duration gradually increased from the first (8.59 d ± 0.13) to the fourth zoeal stage (11.00 d ± 0.21) and then abruptly increased in the fifth stage (15.81 d ± 0.44) (Fig. 3.2A). No mean stage duration was available for the megalopal stage due to 100% mortality. Percent mortality fluctuated between 0.8% and 5.7% through the first four zoeal stages, and then increased dramatically (in three of the four cultures) up to an overall value of 61.0% in the fifth zoeal stage (Fig. 3.2B). Virtually all mortality during the fifth zoeal stage occurred when zoeae failed to molt successfully to megalopae. In these cases, zoeae shed only parts of their exoskeleton, sometimes successfully removing part of the carapace, but failed to emerge from the abdomen and maxilliary appendages. Other larvae successfully shed their exoskeleton but became disfigured; these abnormal larvae died within 1-4 days after attempting to molt.

3.4.2. Zoea morphology

The average carapace length increased from one zoeal stage to the next; however there was less pronounced increase from the fourth to fifth zoeal stage that was also associated with increased variability in carapace length (Table 3.1). The number of natatory setae on the first and second maxillipeds increased from 4 to 10 by increments of two from the first to fourth zoeal stage. In the fifth zoeal stage, 11 natatory setae were present on the first maxilliped; the exopod of the second maxilliped had 11 apical

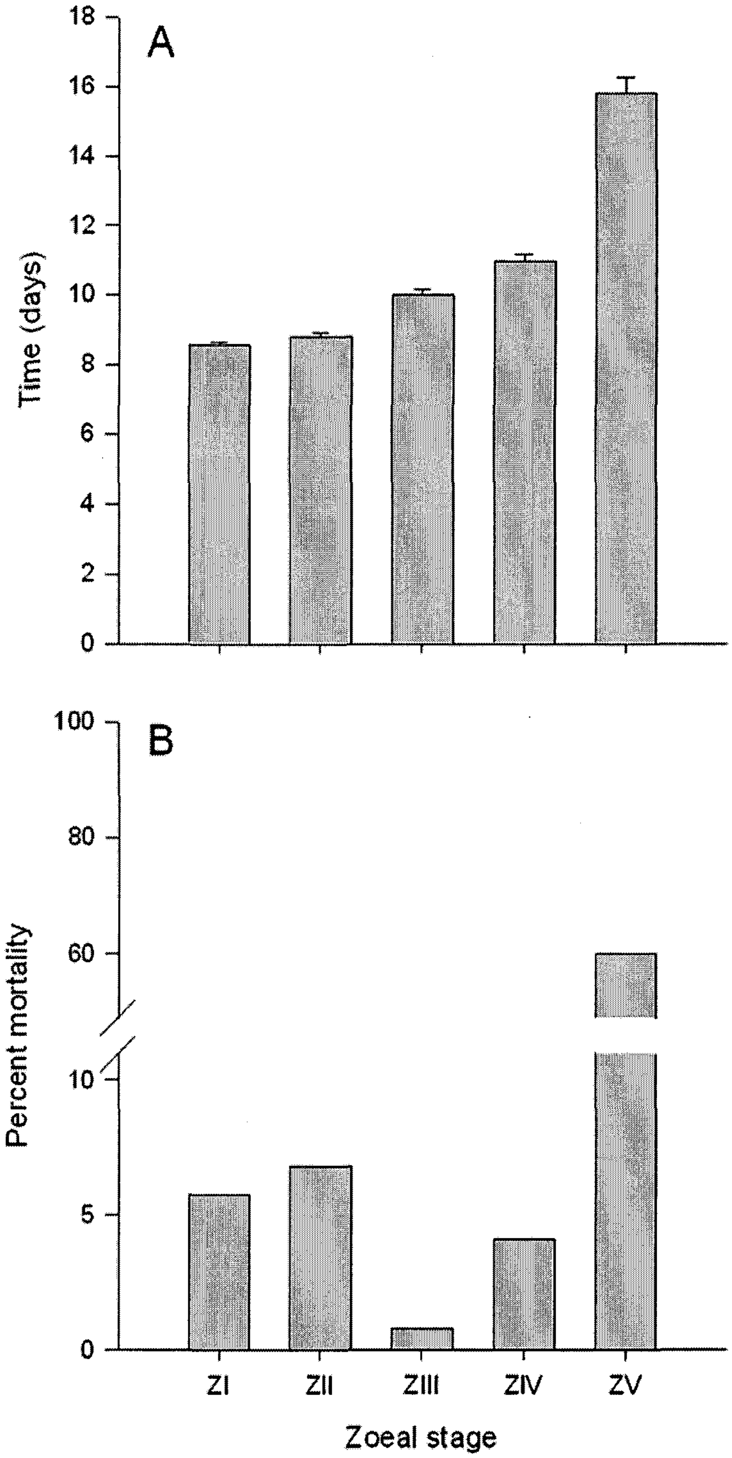

Figure 3.2. A) Mean stage durations (+1 SE) and B) percent mortality calculated from pooled observations taken from four cultures of larvae released by female B. ZI-ZV, zoeal stages one to five.

Table 3.1. Morphological features of *G. oregonensis*, from zoeae of two females. Average carapace length (mm) ± 1 SE were only measured from female B and are compared to those reported from Lough (1975). NS, natatory setae; FAS, number of simple setae on first abdominal somite; CL, carapace length; ZI-ZV, zoeal stages 1-5; M, megalopal stage.

Stage	NS	FAS	CL ± 1 SE	CL (Lough, 1975a)
ZI	4	0	1.75 ± 0.02	1.64
ZII	6	0	2.31 ± 0.01	2.60
ZIII	8	0-1	3.01 ± 0.02	3.36
ZIV	10	2-3	3.91 ± 0.02	4.48
ZV	12-13	3-4	4.54 ± 0.04*	5.28
M	----	----	2.61 ± 0.06*	3.36

*ZV measurements included two whole zoeae (preserved live)

*M measurements were all obtained from whole megalopae (preserved live)

natatory setae and a 12th sub-apical seta. An additional (13th) sub-apical seta appeared on one of the second maxillipeds on a single specimen.

The abdomen was composed of several somites and a bifurcate telson (Fig. 3.3). Five somites were present in the first and second zoeal stages, and a sixth somite was added in the third stage between the fifth somite and the telson. The relative length of posterolateral spines located on somites three to five increased substantially from the first to the third zoeal stage. These spines extended to the distal end of the subsequent abdominal segment from the third to fifth zoeal stage (and sometimes beyond in the third zoeal stage). Pleopod buds appeared on the ventral surface of the abdomen in the fourth zoeal stage, becoming larger in the fifth stage. Small simple setae were present on the dorsal surface of the abdomen and telson as illustrated in Fig. 3.3. The number of these setae on the first abdominal somite varied between specimens (Table 3.1). The number and configuration of the small simple setae and pleopod buds are included here for completeness but are not considered as important features for identification. A lateral and

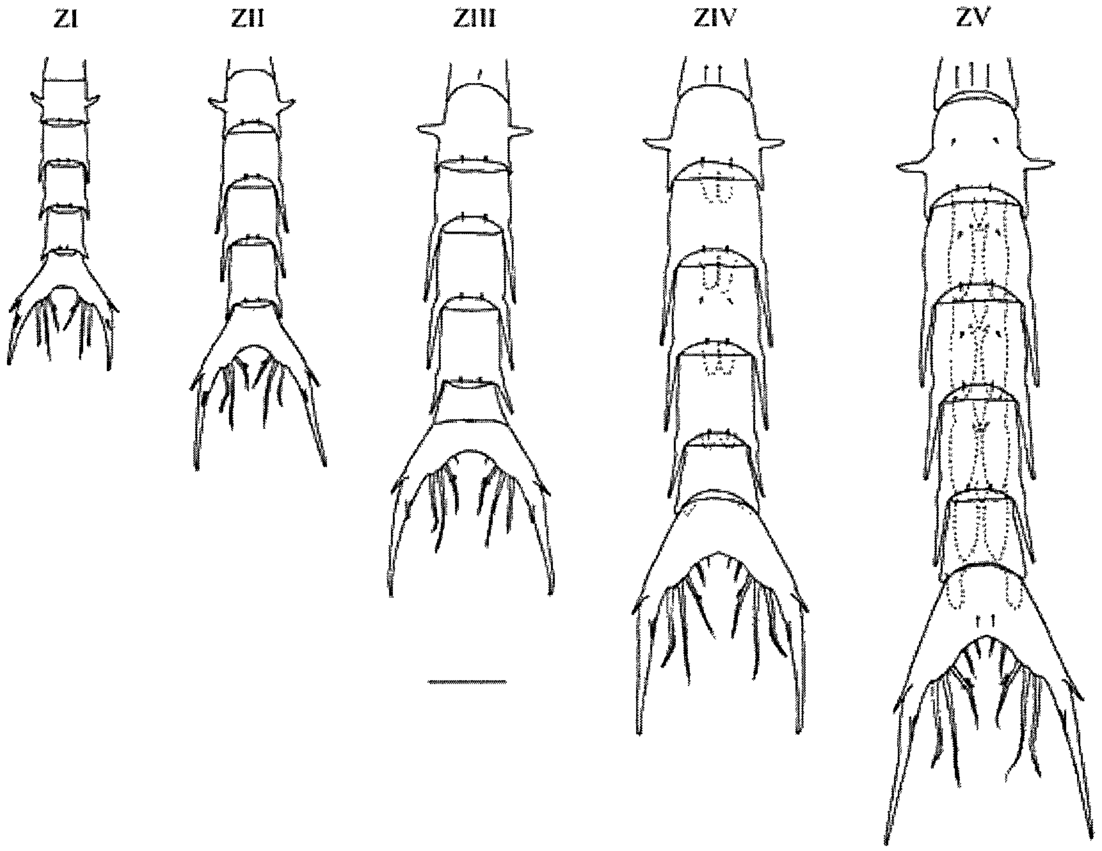

Figure 3.3. Dorsal view of the abdomen and telson of each *G. oregonensis* zoeal stage. Scale bar = 300 µm. Structures on ventral surface are illustrated by stippled lines. ZI-ZV, zoeal stages one to five.

dorsal exospine were present on each furca of the telson. The lateral exospine was approximately one fourth to one fifth the length of the furca. On a single third zoea, an additional (smaller) lateral process was observed on the right furca of the telson located posterior to the lateral exospine. In the first two zoeal stages, three long plumodenticulate setae projected from the inner furcal margin. Fourth and fifth smaller setae were added medially in the third and fourth zoeal stages respectively.

3.5. Discussion

3.5.1. Stage duration and mortality

Zoeae of *G. oregonensis* have been observed hatching between February and May (Orensanz and Gallucci, 1988; Knudsen, 1964), a period at which the mean temperature in the Southern Strait of Georgia is approximately 9.8 ˚C (Fisheries and Oceans Canada, 2009). The duration of the zoeal phase has been determined to be approximately 70 days at a similar temperature (10 ˚C) (Sulkin and McKeen, 1994), which was below the temperature that the larvae experienced in the present study (~13 ˚C). It is well known that developmental stage duration in crab larvae decreases with increasing temperature (Anger et al., 2003; 2004; Hamasaki, 2003; Duguid and Page, 2009), and the stage-specific durations of zoeae described herein were therefore consistent with those reported for *G. oregonensis* by Sulkin and McKeen (1994) at temperatures of 10 ˚C and 15 ˚C.

Stage-specific larval mortality also resembled patterns previously reported for *G. oregonensis* by Sulkin and McKeen (1994). However, in the present study, an unexpectedly wide range of mortality levels occurred in the fifth stage, which is puzzling considering that the cultures were independent from each other but were subjected to near identical rearing conditions. High larval mortality in the fifth zoeal stage may have been a result of a nutritional deficiency. For example, Baylon (2009) demonstrated that the terminal zoeal stage of the mud crab, *Scylla tranquebarica*, endured heavy mortality when fed *Artemia* nauplii only, compared to larvae fed a more diverse diet (rotifers + *Artemia*).

3.5.2. Morphology and Identification

Except for the first zoeal stage, carapace lengths measured in the present study were shorter than those previously reported by Lough (1975). Furthermore, megalopae obtained from the present study were below or near the lowest size limit previously described for samples taken from the Salish Sea (Debrosse et al., 1990b). Thus, carapace lengths from zoeae collected from the field are likely somewhat longer than those reported herein. Laboratory rearing conditions may partially dictate such differences, as water quality, temperature, diet, and/or bacterial or fungal infections may all play a role in the growth of zoeae. The variation in temperature experienced over the zoeal duration was briefly described (Fig. 3.1.), but overall, there appeared to be no serious issues regarding larval growth.

Long posterolateral spines on the abdominal segments and short acutely angled lateral spines on the telson were the most remarkable features for the diagnosis of *G. oregonensis* zoeae. These morphological characteristics are roughly consistent with illustrations provided by Lough (1975). However, Lough (1975) did not acknowledge the length of the abdominal spines, which is an important diagnostic feature for some zoeal stages as described below. The abdominal spines become particularly useful when the telson spines are damaged or missing. Lough (1975) also reported that the second maxillipeds of the fifth zoeal stage had only 11 natatory setae, whereas the fifth zoeae reared in the present study had 12 and once even 13 of these setae. In addition, and contrary to what was described by Puls (2001), there was no evidence of the presence of two pairs of lateral exospines on the telson. A second lateral process on one side of the telson was detected on a single specimen, but this was presumably an abnormality.

In all stages, the telson morphology of *G. oregonensis* zoeae resembled that of *M. gracilis* and *R. antennarius*. However, zoeae of *M. gracilis* and *R. antennarius* are noticeably smaller in size (Rice and Tsukimura, 2007), and have shorter posterolateral spines projecting from abdominal somites three, four, and five (Ally, 1975; Roesijadi, 1976). The first zoeal stage of *M. magister* has lateral exospines that are longer and flare farther out from the telson furca than those described herein for *G. oregonensis* (Poole, 1966; Lough, 1975). In addition, the second and third zoeal stages of *M. magister* have shorter posterolateral spines projecting from abdominal somites three, four, and five, and an additional pair of setae on the telson's inner furcal margin (Poole, 1966; Lough, 1975). The fourth and fifth zoeal stages of *M. magister* are also noticeably larger than those of *G. oregonensis.*

Among the four cancrid species, larvae of *C. productus* and *G. oregonensis* appear to be the most difficult to separate (Lough, 1975; Puls, 2001). Based on previous descriptions of laboratory reared *C. productus* zoeae by Trask (1970), and field caught first zoeae by Rice and Tsukimira (2007), a few features can be used to unambiguously distinguish these species. For example, the lateral exospines projecting from the telson of *G. oregonensis* zoeae are shorter and angled more acutely to each furca than those of *C.*

productus. These differences appear to become less obvious in the fifth zoeal stage (Trask, 1970). In addition, substantially longer posterolateral spines project from the third and fourth abdominal somites in the first to fourth zoeal stage of *G. oregonensis*.

Furthermore, in the third zoeal stage, the inner margin of the telson of *G. oregonensis* has 4+4 setae compared to 5+5 setae in *C. productus*. And in the fifth zoeal stage, the exopod of the second maxilliped of *C. productus* has been described as having 13 apical natatory setae (Trask, 1970), whereas that of *G. oregonensis* has 11 apical natatory setae plus an additional subapical seta. An extensive field study off the Central Oregon coast that used these latter two criteria as diagnostic features was unable to positively identify *C. productus* zoeae (Lough, 1975), leaving the utility of these features in question.

A summary of differences between larval cancrid descriptions (Puls, 2001) revealed that a dorsal exopsine on the telson was neither mentioned nor illustrated in Trask's (1970) description of *C. productus* zoeae. However, the absence of this feature is not recommended for identification of *C. productus*, as it is present on the first zoeae illustrated by Rice and Tsukimura (2007). Such ambiguity may have arisen from oversight or morphological variation. The size, setation, and armature of *C. productus* megalopae reared from the coast of Washington and British Columbia (Debrosse et al., 1990a; 1990b) have been shown to differ from the previously described megalopal stage reared from Californian coast (Trask, 1970). Latitudinal variation in the morphology of *M. magister* zoeae has also been noted, which has been attributed to different temperatures experienced during embryological development (Shirely et al., 1987). Furthermore, the megalopae of *M. magister*, collected off the outer Pacific coast have been demonstrated to be significantly larger in size than those collected from within the SoG and Puget Sound basins (Debrosse et al., 1990b).

Given this morphological variation, preparation of a parallel description of the development of local *C. productus* larvae is encouraged. Such a description would complement the information provided herein for *G. oregonensis*, and would constitute the logical step forward in the discrimination of both species. Furthermore, the larval development of *R. branneri* also requires a morphological description before all cancrid larvae from the Salish Sea can be properly distinguished.

The present study described morphological features that should facilitate the diagnosis of zoeae of *G. oregonensis* with respect to the most common sympatric cancrid species in the Salish Sea. As indicated above, the data provided on stage durations and stage-specific mortality are consistent with previous reports for *G. oregonensis* reared at comparable temperature ranges. Ultimately the morphological features summarized here will improve the resolution of field studies investigating the larval dynamics of cancrid species.

CHAPTER 4

Characterization and inter-annual comparison of larval crab (Decapoda: Reptantia) assemblages from the Strait of Georgia, British Columbia

4.1. Abstract

Larval crab assemblages were characterized for the first time from the Strait of Georgia, British Columbia from two surveys conducted in the spring seasons of 2009 and 2010. Measures of larval abundance, Shannon diversity, and similarity between sampling stations were used to describe and compare the assemblages. Furthermore, the relationship between these measures and environmental variables was explored. Cancrid larvae dominated the assemblages, in both years (approximately 80% of larval abundance). Larvae of the commercially important *Metacarcinus magister* were the most abundant, followed by either *Munida quadrispina* (in 2009) or *Cancer productus* (in 2010). Measures of average larval abundance (352 larvae/100 m^3 in 2009 and 1821 larvae/100 m^3 2010), average Shannon diversity (1.23 in 2009 and 1.03 in 2010), and similarity between stations indicated that larval assemblages were significantly different between years. Potential explanations for this variation that include larval mortality, reproductive output, and reproductive timing are dicussed. Spatial patterns of total larval abundance and diversity also appeared to differ between surveys. In 2009, the distribution of larvae was more closely linked to environmental conditions than in 2010. In addition, elevated sea surface temperatures during the late winter and spring of 2010 may have caused higher abundances at later stages for multiple species, including *M. magister*. Overall, these results indicated that even when the relative abundance at the family level

may be similar between years, absolute measures of larval abundance can undergo large interannual fluctuations in the Strait of Georgia that could impact the year class strength of several species.

4.2. Introduction

The larvae of many demersal species with complex life cycles undergo a period of pelagic development before settling to the benthos. Throughout their larval duration, meroplankton are subjected to various environmental conditions that can affect their distribution, survival, and recruitment (Govoni, 2005; Ouellete et al., 2011). The importance of the larval stage to population dynamics was not sufficiently recognized until the seminal studies on supply-side ecology published by Roughgarden and collaborators during the 1980's (Gaines and Roughgarden, 1985; Gaines et al., 1985; Roughgarden et al., 1988). Recruitment variability is thought to be an important factor that may drive inter-annual fluctuations of benthic populations, stocks and communities (Roughgarden et al., 1988; Connelly et al, 2001). Accordingly, understanding processes affecting the movement and abundance of early life history stages has been a major objective in the field of fisheries oceanography (Govoni, 2005).

In addition to providing baseline data on the developmental timing and larval abundance of multiple species, research on larval assemblages can be used to identify environmental variables (e.g. climatic or oceanographic) that may be responsible for shaping patterns of larval abundance and community composition (Smith et al., 1999a; Rodriguez et al., 2009; Hsieh et al., 2010; Magris and Fernandes, 2011). A primary avenue of this research is to determine whether the pelagic environment has a common effect on larvae of multiple species that may otherwise be confined to different habitats and environmental conditions in their adult phase (Oliver et al., 2010). Accordingly, analyzing larval assemblages allows for insight into the ecological processes and evolutionary adaptations (e.g. reproductive strategies) that may influence the spatial and temporal patterns of different life history phases (Moser and Smith, 1993; Isari et al., 2008).

The spatial variability in larval assemblages is dependent on species-specific larval distributions, which may be influenced by the timing and location of spawning or larval release (Natunewicz and Epifanio, 2001), transport from the release location (Wing et al., 1998), spatial variation in larval mortality (Frank et al., 1993), and swimming behaviour (Chiswell and Booth, 1999). In comparison, interannual fluctuations in assemblage composition may be caused by variation in larval mortality, reproductive timing, and reproductive output (Isari et al., 2008 and references therein). Although the majority of larval assemblage research has been focused on larval fish (see above citations), common processes are expected to affect the movement (Bradbury and Snelgrove, 2001) and survival (Platt et al., 2003; Koeller et al., 2009) of invertebrate and fish larvae in the water column. This is especially true for decapod larvae that have the most advanced invertebrate swimming and sensory capabilities, rivalling those of larval fish (Kingsford et al., 2002).

Numerous crab species reside along the coast of southern British Columbia (Hart, 1982). In this temperate region, crab larvae develop in the water column for a period of weeks to months (Nyblade, 1987; Strathmann, 1987; Duguid and Page, 2009), and are an important food source for higher trophic levels (Duhnam and Duffus, 2001;

Schabetsberger et al., 2003). The monitoring of ovigerous female crabs has made possible the documentation of reproductive timing of several species throughout the inland waters of the Salish Sea (Knudsen, 1964; Orensenz and Galluchi, 1988; Duguid and Page, 2011). Nevertheless, information on the early life history of many Northeast Pacific crab species remains scarce. To date, very few studies have focused on the distribution and abundance of crab larvae in the Salish Sea (but see Jamieson and Phillips, 1993), and virtually no studies have described larval assemblages from this region.

Within the Salish Sea, the Strait of Georgia (SoG hereafter) is a deep semi-enclosed ocean basin situated between Vancouver Island and mainland British Columbia. Within the SoG, the distribution of crab larvae likely depends on ocean circulation, which is primarily influenced by seasonal river runoff from the Fraser River, tidal currents, wind stress, and basin topography (Thomson, 1981). Although the oceanography of the SoG has been relatively well studied (Thomson, 1981; Leblond, 1983; Masson and Cummins, 2004; Pawlowicz et al, 2007), information on the strength and direction of low frequency horizontal ocean currents that could potentially transport larvae is scarce and spatially limited (Thomson, 1981; Stacey et al., 1987; Masson and Cummins, 2004). Furthermore, the influence of these physical characteristics on the diversity and abundance of larval assemblages remains unclear.

In the present study, the composition, abundance, and spatial pattern of larval crab assemblages from the SoG were described for the first time from the spring seasons of 2009 and 2010. Interannual variation in composition and abundance is discussed and the relationship between larval assemblages from each year, the annual variation in sea surface temperature, and a series of hydrographic properties was also explored.

4.3. Methods and Materials

4.3.1. Plankton sampling and larval identification

Crab larvae were collected from surveys conducted during two consecutive spring seasons (April 25-29 in 2009 and April 24-27 in 2010). Samples were collected from a grid of 57 stations spaced approximately 8 km apart that covered the majority of the SoG. Sampling took place continuously throughout the day and night, following an order of consecutive stations that largely depended on weather conditions and ship time constraints (Fig. 4.1). During each survey, vertical profiles of environmental variables (temperature, fluorescence, salinity, and oxygen) were logged immediately before each plankton tow using a Sea-Bird Electronics 19*plus* Seacat CTD equipped with an oxygen sensor and fluorometer. Also, in order to assess potential temperature differences between years, hourly recorded sea surface temperatures were obtained from the Halibut Bank meteorological buoy (property of Environment Canada) located in the central SoG (see Fig. 1A). Data were retrieved from January 2008 to December 2010 and averaged for each day.

At each station, plankton samples were obtained using a Tucker Trawl (1.5 m^2 frame, 1 mm mesh size) equipped with a flowmeter. The duration of the each plankton tow was approximately 15 minutes at a speed of 2 knots with a targeted maximum depth between 30 and 50 m. In 2009, the Tucker Trawl was towed primarily within the 30-50 m

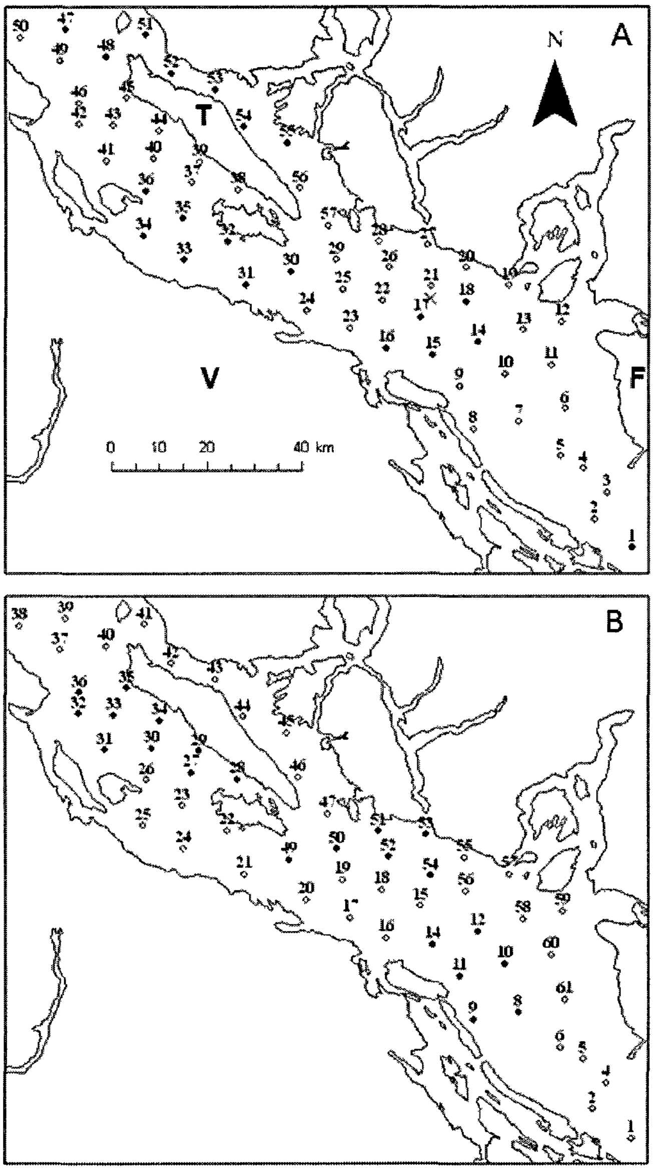

Figure 4.1. Location of sampling stations from surveys conducted during A) April 25-29, 2009 and B) April 24-27, 2010. Labels indicate the order in which samples were taken. Filled and empty dots indicate that the stations were sampled at night or day respectively. In A: F, Fraser River delta; T, Texada Island; V, Vancouver Island, X , location of Halibut Bank weather buoy (just below Station 21).

depth range, whereas in 2010, samples were collected by oblique tows that covered depths between 50 m and the surface more evenly. Depth profiles were verified from a Vemco Minilog-12TX data logging device attached to the Tucker Trawl. Plankton samples were preserved in 95% ethanol, and subsequently subsampled with a Folsom splitter and sorted for crab larvae.

A minimum of approximately 200 crab larvae were identified and enumerated for each sample that required splitting. Larval abundance was standardized to larval concentrations per 100 m^3 of filtered seawater using flowmeter readings. Two highly unusual recorded volumes of filtered seawater (stations 4 and 34 in 2009) were replaced with the average volume filtered from all other stations sampled for that survey.

Crab larvae were identified to stage and to the lowest taxonomic level possible using relevant identification guides (Lough, 1975; Puls, 2001; Rice and Tsukimura, 2007) and larval descriptions, as well as laboratory reared specimens of *Glebocarcinus oregonensis* (c.f. Chapter 3). Morphologically distinct larvae that could not be identified based on published larval descriptions (e.g., Pagurid sp. A, Pagurid sp. C, Lithodid sp. A, Lithodid sp. B) were readily distinguished by the shape of the carapace. Although anomuran larvae identified as *Pagurus beringanus, P. caurinus*, *P. granosimanus* and *Hapalogaster mertensii* were consistent with published descriptions, their identification should be considered tentative as all local pagurid, hapalogastrid, and lithodid species have not yet been described and several species within these families closely resemble one another. The fourth and fifth stages of *Telmessus cheiragonus* were grouped together due to the large proportion of damaged zoeae that made proper distinction between stages impossible. Zoeae that could not be identified to genus or species with certainty were labelled as "unidentified" within pagurid, lithodid and cancrid families.

4.3.2. Comparison of larval assemblages and spatial analysis

Larval composition and abundance were used to determine levels of similarity between the April 2009 and April 2010 larval communities. Such similarity was visually explored using nonmetric multidimensional scaling ordination and tested using Analysis of Similarities (ANOSIM). A two-way ANOSIM was conducted in an attempt to separate the potential effect of sampling during the day and night from changes in community composition between years. For these comparisons and all other multivariate statistics, abundance per species (all stages combined) were fourth-root transformed to create Bray-Curtis similarity matrices using PRIMER 6 v. 6.1.13 routines. The contribution (%) of each species to the dissimilarity observed between 2009 and 2010 was examined using the Similarity Percentage function (SIMPER). Species abundances were also used to estimate taxa diversity using the Shannon index (Magurran, 1988), and total abundances per station. A Paired Samples T-Test was used to assess the difference in overall abundance and diversity between years using SPSS v.15.0 software. For the abundance comparison, total larval concentrations were log transformed to meet the assumption of normality of differences between paired samples.

Mapping and spatial analyses of diversity and total abundance were carried out in ArcMap v. 9.3 using the WGS 1984 coordinate system and UTM Zone 10N projection. The British Columbia base map was obtained online from the North American Atlas (Natural Resources Canada, 2007). Horizontal patterns of larval diversity and total abundance were visualized by creating continuous surfaces from an inverse distance weighting interpolation. The data classification contours for total abundance were modified from a log scale of abundance covering the range of values for both surveys, whereas classification of diversity contours was formed from an equal interval. The G_i* statistic (Getis and Ord, 1992) was used to determine if high and low abundance sampling locations clustered spatially. This statistic was calculated in its standardized form as:

$$G_i^* = \frac{\sum_{j=1}^{n} w_{i,j}\, x_j - \bar{X} \sum_{j=1}^{n} w_{i,j}}{s \sqrt{\frac{\left[n \sum_{j=1}^{n} w_{i,j}^2 - \left(\sum_{j=1}^{n} w_{i,j}\right)^2\right]}{n-1}}}$$

Where x_j is the neighbouring value for the feature j, $w_{i,j}$ is the spatial weight between features i and j, $\bar{X}$ is the sample mean, and s is the sample standard deviation. This version of the G_i* statistic is normally distributed when sampling stations have at least eight neighbours, an assumption met here, and is considered a Z-score (Ord and Getis, 1995). Z-scores were calculated based on the null hypothesis that the observed spatial pattern is one of numerous random spatial configurations (Ord and Getis, 1995; Mitchell, 2005), and were considered significant at values > 2 or < -2 to emphasise that local values are different than the mean (Nelson and Boots, 2008), and to reduce the chance of obtaining a type 1 error. The latter can be caused by spatial dependence and the use of many of the same neighbours for different features (Mitchell, 2005). Normality of the data points is not required; however, significance testing may be misleading when data are strongly skewed (Zhang, 2008). Accordingly, abundance data for both years were log transformed prior to the analysis to reduce the potential effect of the heavily skewed distributions. For both abundance and diversity analyses, the spatial weight was set to one within a distance band of 20 km, and zero outside that distance band. A fixed distance of 20 km was chosen as it was the minimum distance that allowed the majority of sampling locations to have at least eight neighbours. Larger distances were not used as they would have produced irrelevant local measures for the sampling resolution used and size of the study area. Z-scores for stations with less than 8 neighbours (stations 1-5, 12, 48-50 [Fig. 3.1A]) were not considered. Also, stations 51-56 (Fig. 3.1A) were excluded to reduce the effect of Texada Island on distance between stations.

4.3.3. Correlations between larval assemblages and environmental variables

Both diversity and total abundance were used to explore the relationship between larval communities and environmental data. Because plankton tows were not depth stratified, the relationship between larval crab assemblages and environmental variables was analyzed using measurements of environmental variables at the following depths: 1 m, 10 m, 20 m, 30 m, 40 m and 50 m. For each station, temperature, salinity, oxygen, and fluorescence readings at each depth ± 0.5 m were averaged using Sea-Bird Electronics Data Processing software. The Spearman rank correlation (SPSS v. 15.0) was employed to assess the degree of correlation between environmental variables and both taxonomic diversity and total abundance at each depth. A BEST analysis was carried out using PRIMER 6 v. 6.1.13 software with normalized values for each environmental variable. This analysis was used to determine the environmental variable(s) that best explained the structure of larval assemblages based on the maximum Spearman Rank correlation coefficient between similarity matrices of larval composition and environmental variables (Clarke and Ainsworth, 1993).

4.4. Results

4.4.1. Larval abundance and assemblage composition

The composition of larval assemblages from late April 2009 and 2010 is illustrated in Fig. 4.2 at the family level, and detailed in Tables 4.1 and 4.2 at the level of lowest taxonomic classification. At the family level, cancrid larvae dominated the assemblages, making up approximately 80 % of the total abundance in both years. Galatheid larvae were the only other family that were present in substantial numbers (between 10% and 20%) as all remaining families were present at relative abundances of less than 4% (Fig. 4.2). With the exception of the families Upogebiidae, Varunidae, and Axiidae, all reptantian decapod families known to reside within or near the SoG were collected in both surveys. Larvae from the families Xanthidae (*Lophopanopeus bellus*) and Callassinidae (*Neotrypaea californiensis*) were only present in 2010. The numerically dominant species in both surveys was *Metacarcinus magister*, followed by *Munida quadrispina* (in 2009) and *Cancer productus* (in 2010). In both surveys, the majority of the larvae (with four zoeal stages or more) were in the second or third zoeal stage. Exceptions include *Telmessus cheiragonus*, and several lithodid and pagurid species (Tables 4.1 and 4.2).

Despite overall similarities in percent composition at the family level, the relative abundance of several species changed between years. For example, in 2010 the relative abundance of *M. magister* and *M. quadrispina* decreased in comparison to 2009 by 19%

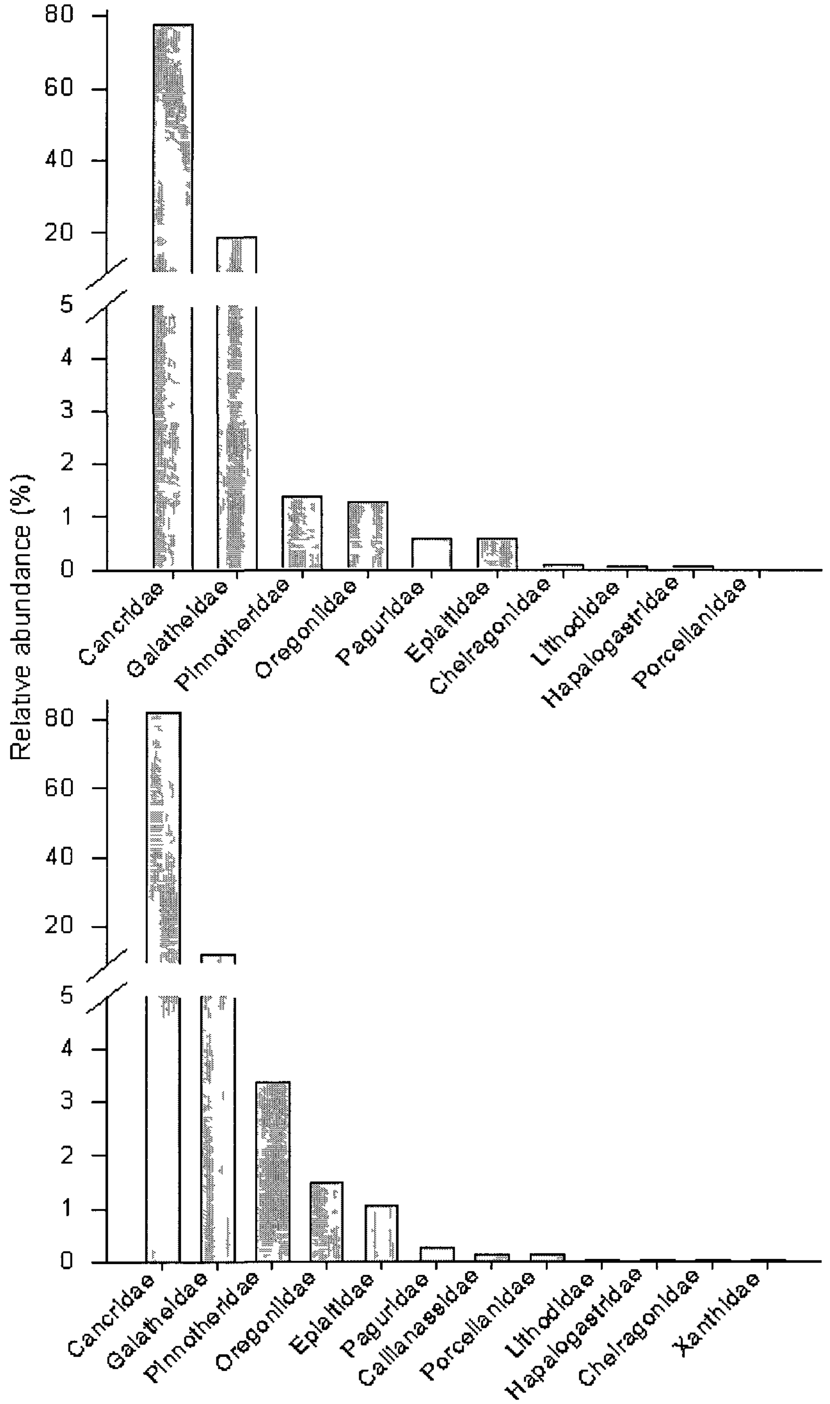

Figure 4.2. Relative abundance of reptantian decapod families in decreasing order of abundance from surveys conducted in A) 2009 B) 2010.

Table 4.1. Cumulative stage-specific larval abundance from the 2009 survey expressed as the number of larvae per 100 m^3 filtered seawater. The relative abundance of all stages combined is detailed in parentheses in the 'Total' column. Z, number of zoeal stages; I-V, zoeal stages one through five; M, Megalopa. The asterisk symbol * is used to mark tentative species identifications.

Infraorder	Family	Identification	Z	I	II	III	IV	V	M	Total
Brachyura	Cancridae	*Cancer productus*	5	815.5	900.1	110.6	3.2	0	0	1,838.6 (9.16)
		Glebocarcinus oregonensis	5	26.9	178.6	68.1	4.4	0	0	279.3 (1.39)
		Metacarcinus gracilis	5	0	1.1	0.3	0	0	0	1.3 (0.01)
		Metacarcinus magister	5	376.5	5,357.5	6,198.7	568.7	0	0	12,563.6 (62.59)
		Unidentified Cancridae	5	96.0	409.7	415.6	23.9	0	0	949.9 (4.73)
	Cheiragonidae	*Telmessus cheiragonus*	5	0	0.6	2.2	11.1	-	1.1	15.2 (0.08)
	Epialtidae	Epialtidae sp.	2	56.9	49.0	-	-	-	7.7	114.1 (0.57)
	Oregoniidae	Oregoniidae sp.	2	137.2	114.3	-	-	-	5.7	258.5 (1.29)
	Pinnotheridae	Pinnotheridae sp.	2-5	0.7	150.9	117.2	7.6	0	0	277.8 (1.38)
Anomura	Galatheidae	*Munida quadrispina*	4-5	293.1	1,369.5	1,513.9	489.5	50.8	0	3,735.4 (18.61)
	Hapalogastridae	*Acantholithodes hispidus*	4	0.6	3.6	0.8	0	-	0	5.1 (0.03)
		*Hapalogaster mertensii**	4	1.4	2.7	0.6	0	-	0.3	5.0 (0.02)
	Lithodidae	*Lopholithodes foraminatus*	4	1.1	1.0	1.0	0.1	-	0	3.2 (0.02)
		Lopholithodes mantii	4	8.0	0.2	0.1	0	-	0	8.4 (0.04)
		Rhinolithodes wosenessenskii	4	0	0.4	0	0	-	0	0.4 (<0.01)
		Lithodidae sp. B	4	0.1	0.4	0	0	-	0	0.5 (<0.01)
		Unidentified Lithodidae	4	0	0	0	0	-	0.7	0.7 (<0.01)
	Paguridae	*Discorsopagurus schmitti*	4	0.5	8.0	34.9	15.2	-	-	58.9 (0.29)
		*Pagurus beringanus**	4	0	0	0.1	0	-	-	0.1 (<0.01)
		*Pagurus caurinus**	4	0	0	0.6	2.2	-	-	2.8 (0.01)
		*Pagurus granosimanus**	4	0	0	0.2	0.6	-	-	0.8 (<0.01)
		Pagurus hirsutiusculus	4	0	0	0.5	2.7	-	0.2	3.4 (0.02)
		Paguridae sp. A	4	16.9	5.2	7.5	2.7	-	-	32.5 (0.16)
		Unidentified Paguridae	4	2.8	8.0	3.8	2.6	-	0.4	17.7 (0.09)
	Porcellanidae	*Petrolisthes eriomerus*	2	0.3	0	-	-	-	0	0.3 (<0.01)

Table 4.2. Cumulative stage-specific larval abundance from the 2010 survey expressed as the number of larvae per 100 m^3 filtered seawater. The relative abundance of all stages combined is detailed in parentheses in the 'Total' column. Z, number of zoeal stages; I-V, zoeal stages one through five; M, Megalopa. The asterisk symbol * is used to mark tentative species identifications.

Infraorder	**Family**	**Identification**	**Z**	**I**	**II**	**III**	**IV**	**V**	**M**	**Total**
Brachyura	Cancridae	*Cancer productus*	5	7974.2	16233.2	3918.1	136.3	0	0	28287.3 (25.46)
		Glebocarcinus oregonensis	5	251.8	1369.5	2444.4	570.5	0	0	4640.4 (4.18)
		Metacarcinus gracilis	5	23.2	74.1	90.7	20.6	0	0	208.8 (0.19)
		Metacarcinus magister	5	3624.4	9131.0	30646.2	5675.2	0	0	49120.8 (44.21)
		Unidentified Cancridae	5	1085.2	4055.5	3069.6	410.0	0	0	8628.0 (7.77)
	Cheiragonidae	*Telmessus cheiragonus*	5	0	0	0	19.5	-	0	19.5 (0.02)
	Epialtidae	Epialtidae sp.	2	416.0	715.7	-	-	-	40.5	1173.2 (1.06)
	Oregoniidae	Oregoniidae sp.	2	714.0	928.1	-	-	-	0	1643.6 (1.48)
	Pinnotheridae	Pinnotheridae sp.	2-5	111.6	2101.4	1377.6	134.0	0	0	3728.0 (3.36)
	Xanthidae	*Lophopanopeus bellus*	4	11.4	3.1	0	0	-	0	14.5 (0.01)
Anomura	Galatheidae	*Munida quadrispina*	4-5	1302.7	6379.4	5032.2	397.1	0	0	13123.3 (11.81)
	Hapalogastridae	*Acantholithodes hispidus*	4	0	2.6	10.3	3.7	-	0	16.7 (0.02)
		*Hapalogaster mertensii**	4	0	0	2.0	1.1	-	0	3.1 (<0.01)
	Lithodidae	*Lopholithodes foraminatus*	4	6.1	3.9	6.6	0	-	0	16.6 (0.01)
		Lopholithodes mandtii	4	0	1.1	0	0	-	0	1.1 (<0.01)
		Rhinolithodes wosenessenskii	4	0	0	5.0	0	-	0	5.0 (<0.01)
		Lithodid sp. A	4	0	0	1.1	0	-	0	1.1 (<0.01)
		Lithodid sp. B	4	0.5	0	0.0	0	-	0	0.5 (<0.01)
	Paguridae	*Discorsopagurus schmitti*	4	0	13.6	48.2	14.8	-	0.5	77.1 (0.07)
		*Pagurus beringanus**	4	2.3	0	2.6	4.7	-	0	9.6 (0.01)
		*Pagurus caurinus**	4	0	0	3.1	0	-	0	3.1 (<0.01)
		*Pagurus granosimanus**	4	0	0	0	6.2	-	0	6.3 (0.01)
		Pagurus hirsutiusculus	4	0	0	0	38.1	-	0	38.2 (0.03)
		Pagurid sp. A	4	13.2	43.1	5.5	2.0	-	0	64.0 (0.06)
		Pagurid sp. B	4	4.7	0	2.0	0	-	0	6.8 (0.01)
		Unidentified Paguridae	4	51.5	11.8	19.5	1.0	-	1.0	84.8 (0.08)
	Porcellanidae	*Petrolisthes eriomerus*	2	126.4	0	-	-	-	0	126.5 (0.11)
Axiidea	Callassinidae	*Neotrypaea californiensis*	5	5.2	35.6	116.4	0	0	0	157.4 (0.14)

and 7% respectively, whereas that of *C. productus* increased by 16% (Tables 4.1 and 4.2). The percent contribution of each stage to total abundance also varied between years for several taxa. Three notable examples are presented in Fig. 4.3. In 2010 the relative abundance of the third zoeal stage of *M. magister* increased by 13%, the second and third zoeal stages of *C. productus* increased by 9% and 8% respectively, and the second zoeal stage of Epialtidae larvae increased by 15%.

A nonmetric multidimensional scaling plot based on assemblage composition and abundance, identified distinctive larval communities during April 2009 and 2010 (Fig. 4.4). Based on ANOSIM, these communities were significantly different (R = 0.408; P = 0.001). Samples collected under darkness and daylight conditions also appeared to group together (Fig. 4.4.); however, their differences were not significantly different (R = 0.051; P = 0.078). The individual contribution of species to the dissimilarity between years (Table 4.3) is consistent with the inter-annual changes in the relative abundance of the most abundant taxa. *Cancer productus* contributed most to the dissimilarity between years, followed by *M. magister* and *M. quadrispina*, together accounting for approximately 39% of cumulative dissimilarity.

Average diversity values of 1.23 and 1.03 in 2009 and 2010 respectively were significantly different (T(56) = 3.233; P = 0.002). Average total larval concentrations in of 352/100 m^3 and 1821 larvae/100 m^3 also differed significantly between years (T(56) = 7.552; P < 0.001). During late April 2009, regions of high larval diversity were primarily restricted to the northwest region, between Vancouver Island and Texada Island, and the SoG's western margin (Fig. 4.5). That year, significant spatial clustering of high and low

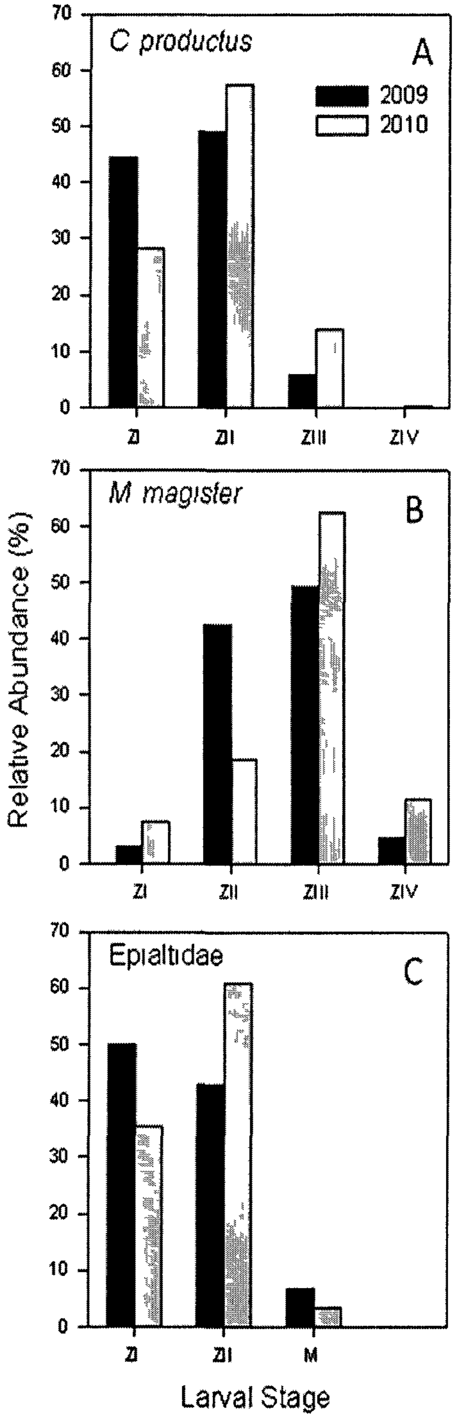

Figure 4.3. Relative abundance of larval stages in 2009 and 2010 for A) *C. productus* B) *M. magister* and C) Epialtid larvae. Z1-ZIV, first to fourth zoeal stages; M, megalopa

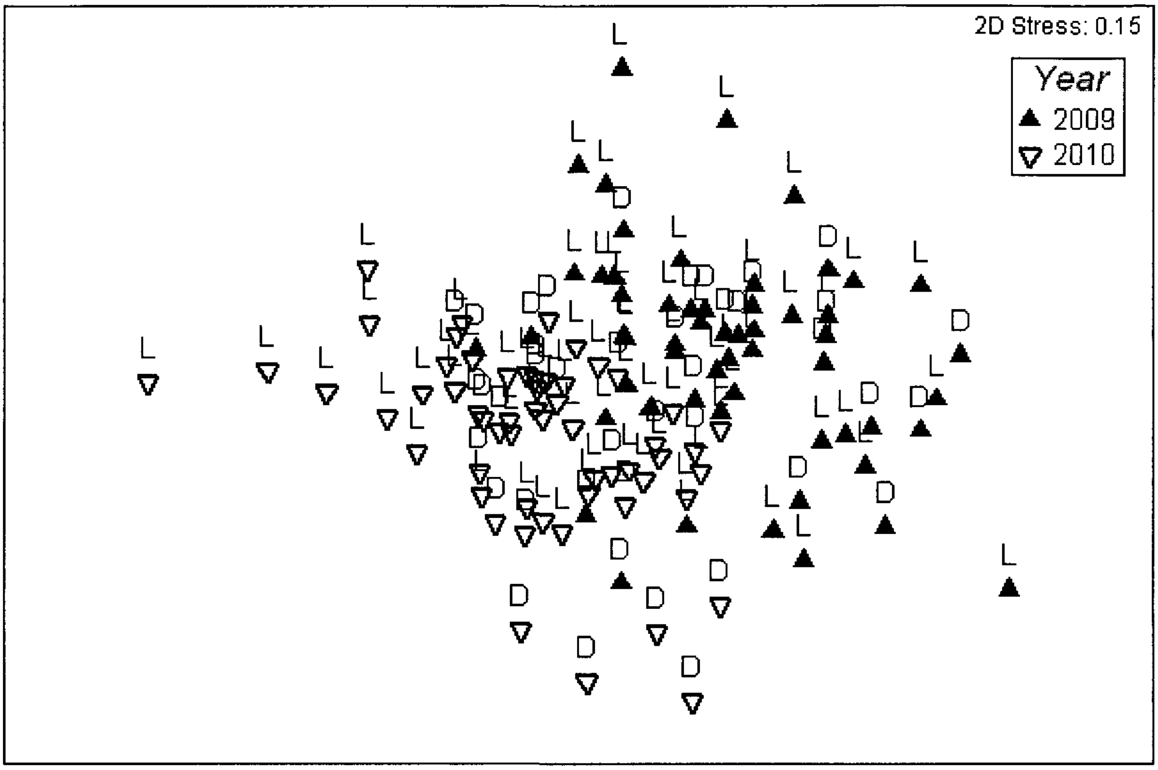

Figure 4.4. Non-metric multidimensional scaling ordination illustrating similarity between samples collected during 2009 and 2010. D, sample collected during darkness; L, sample collected during daylight.

Table 4.3. The percent contribution of taxa to Bray-Curtis dissimilarity between 2009 and 2010 assemblages listed in descending order.

Taxonomic classification	Percent contribution	Cumulative Percent
C. productus	17.48	17.48
M. magister	12.35	29.83
M. quadrispina	9.29	39.12
G. oregonensis	7.90	47.02
Epialtidae	6.98	54.01
Pinnotheridae	6.86	60.87
M. gracilis	6.15	67.02
Oregoniidae	5.59	72.61
D. schmitti	4.25	76.86
Paguridae	4.17	81.03
Pagurid sp. A	4.09	85.12
T. cheiragonus	2.15	87.27
P. eriomerus	1.89	89.16
A. hispidus	1.58	90.74

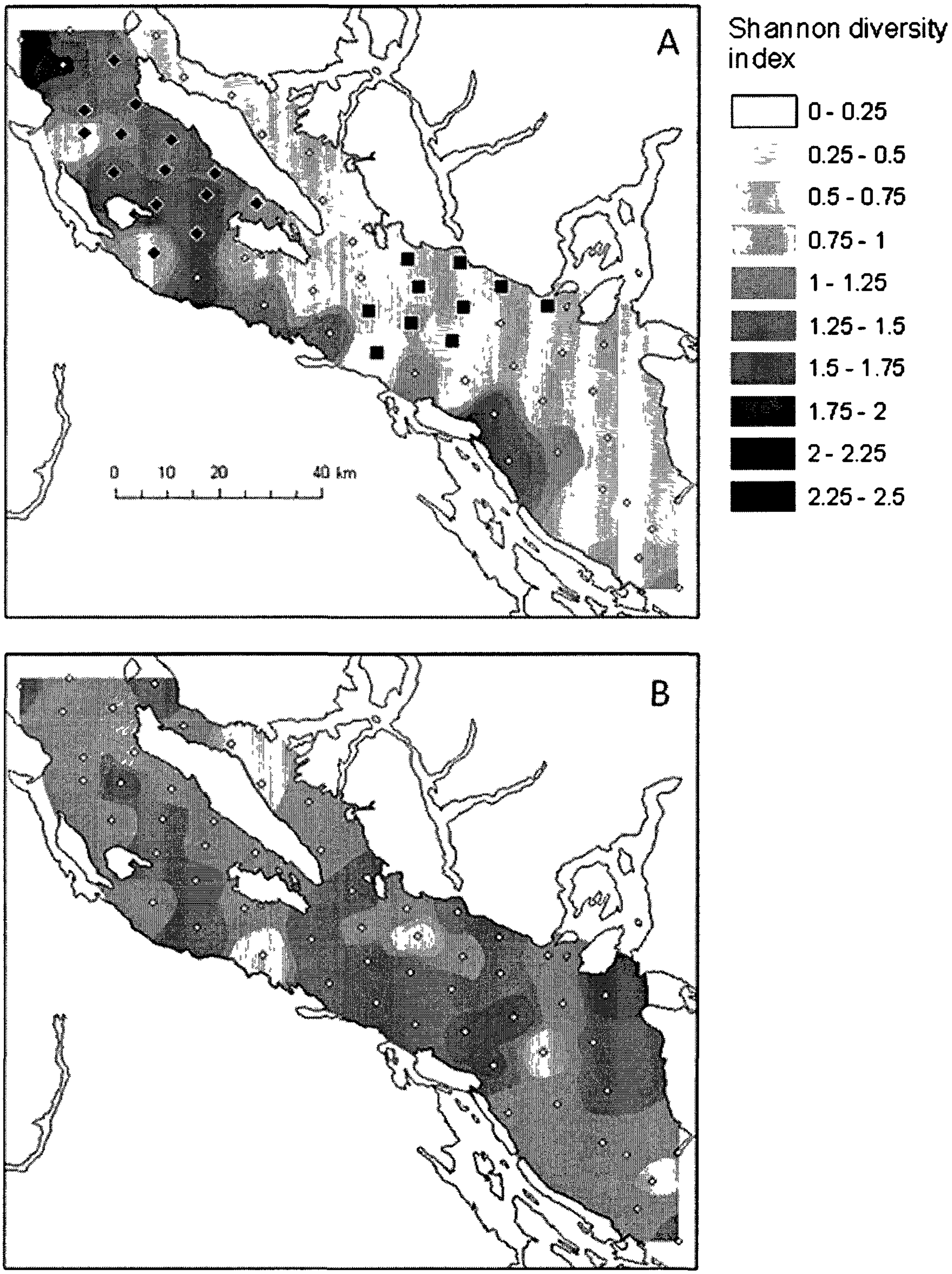

Figure 4.5. Spatial pattern of the Shannon diversity index during the A) 2009 and B) 2010 surveys. Significant Gi* statistics are shown for clusters of high (filled diamond) and low (filled square) diversity locations.

diversity values was detected throughout the SoG's northwest and central regions respectively. During 2010, the highest diversity values were widespread in the central SoG with additional localized areas of high diversity in the SoG's northwest and southeast region. No significant clustering of high or low diversity values was detected during this survey. With respect to total abundance (Fig. 4.6), during 2009 a significant spatial clustering of low and high abundance was detected in the SoG's northwest and central regions respectively. Other highly localized regions of high and low abundance were widespread. In 2010, no significant spatial clustering was detected, but the highest larval abundance occurred primarily along the SoG's eastern margin and most southern region (Fig. 4.6).

4.4.2. Relationship between larval assemblages and environmental variables

Records of sea surface temperature from the Halibut Bank weather buoy, located in the central SoG, indicated that temperatures were higher in 2009 compared to 2008 during late spring/summer and late summer/fall, and lower in 2009 for a short period in December. Moreover, temperatures were higher in 2010 comapared to 2009 between January and April (Fig. 4.7).

The degree to which larval crab diversity correlated with environmental variables is summarized in Table 4.4. The distribution of temperature, fluorescence, salinity and oxygen are illustrated in Appendix 1. In 2009, diversity was significantly correlated with all the environmental variables measured at depths between 20 and 50 m. Within this depth range, diversity was positively correlated with temperature, fluorescence, and

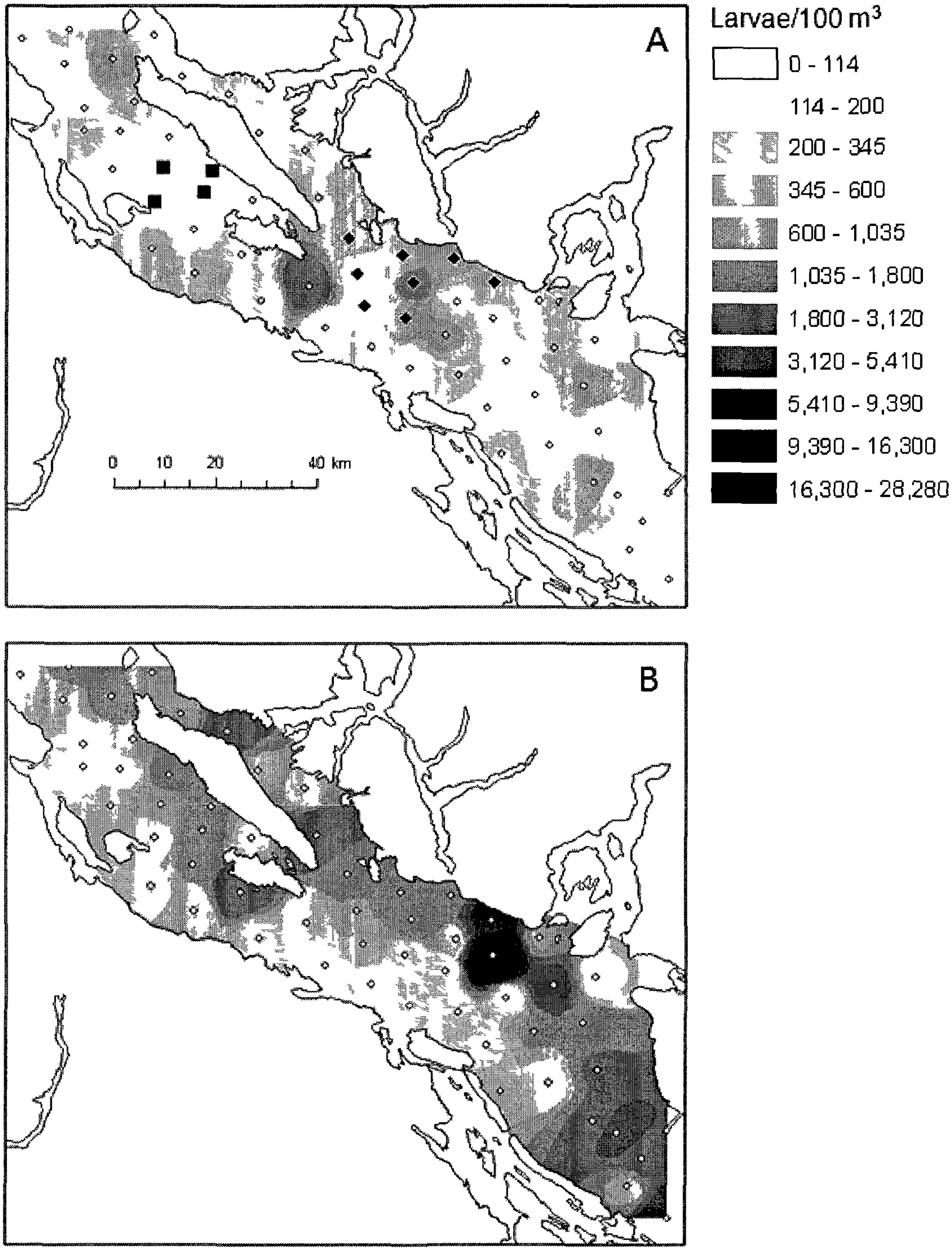

Figure 4.6. Spatial pattern of total larval abundance during the A) 2009 and B) 2010 surveys. Significant Gi* statistics are shown for clusters of high (filled diamond) and low (filled square) abundance locations.

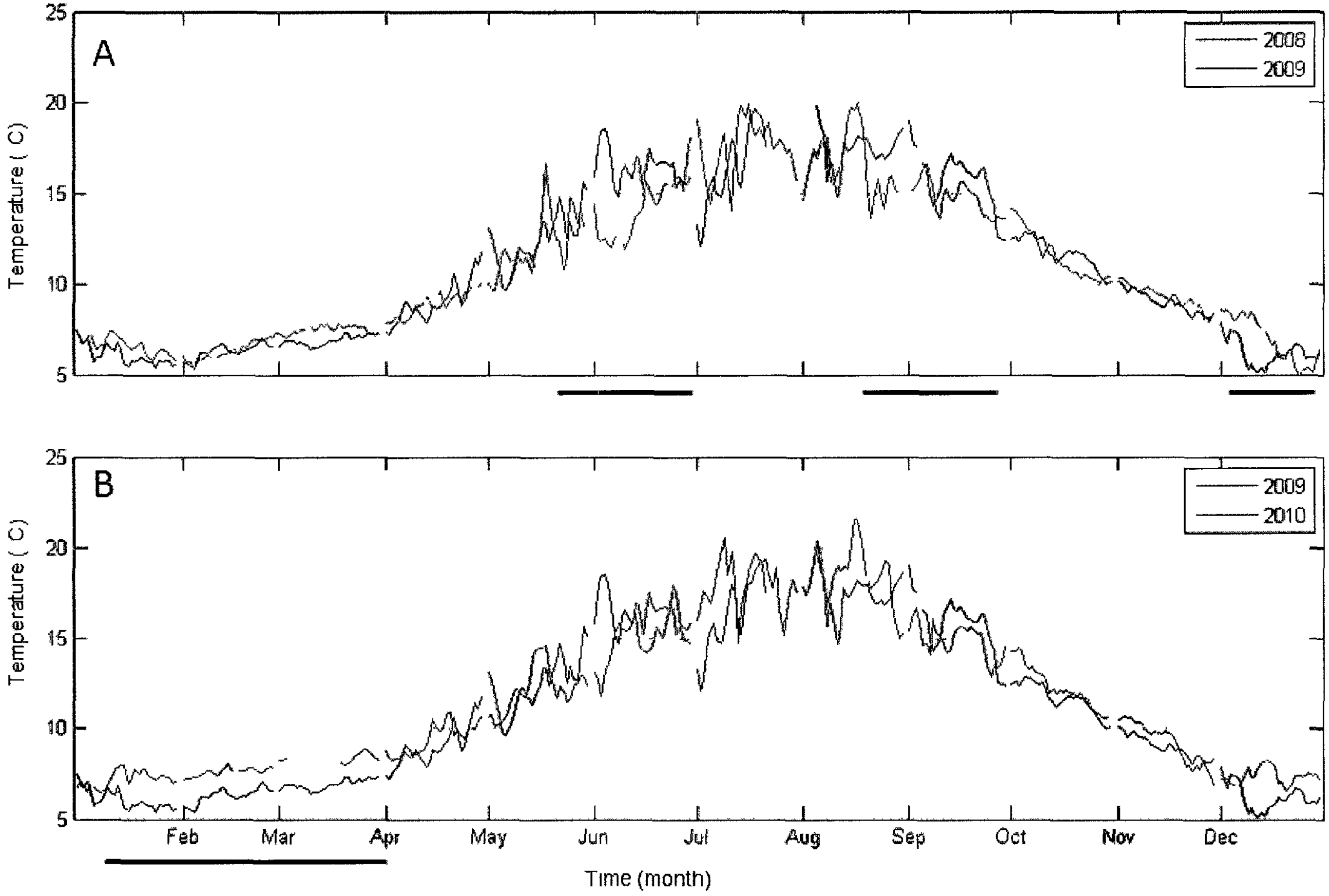

Figure 4.7. Daily averaged temperature fluctuations from Halibut Bank for years A) 2008 and 2009 and B) 2009 and 2010. Bars below the x-axis indicate notable interannual temperature variations. Gaps indicate periods of missing data from buoy records.

Table 4.4. Spearman rank correlation coefficients between Shannon diversity and environmental variables of temperature, fluorescence, salinity, and oxygen at depths of 1 to 50 m (10 m intervals) for 2009 and 2010 surveys. * and ** represent significance at P = 0.05 and P = 0.01 respectively.

Year	Depth (m)	Temperature	Fluorescence	Salinity	Oxygen
2009	1	0.091	-0.219	0.572**	0.057
	10	0.18	-0.036	0.346**	0.381**
	20	0.526**	0.385**	-0.324*	0.502**
	30	0.564**	0.536**	-0.470**	0.611**
	40	0.569**	0.623**	-0.542**	0.669**
	50	0.574**	0.699**	-0.554**	0.491**
2010	1	0.126	-0.023	-0.134	0.06
	10	0.137	0.155	-0.116	0.045
	20	-0.075	0.216	-0.043	-0.131
	30	-0.303*	-0.077	0.002	-0.111
	40	-0.248	-0.029	-0.073	-0.009
	50	-0.171	-0.124	-0.072	-0.084

Table 4.5. Spearman rank correlation coefficients between total larval abundance and environmental variables of temperature, fluorescence, salinity and oxygen at depths of 1 to 50 m (10 m intervals) for 2009 and 2010 surveys. * and ** represent significance at P = 0.05 and P = 0.01 respectively.

Year	Depth (m)	Temperature	Fluorescence	Salinity	Oxygen
2009	1	0.285*	0.177	-0.338*	0.112
	10	0.055	0.092	-0.251	-0.160
	20	-0.290*	-0.191	0.214	-0.266*
	30	-0.268*	-0.258	0.317*	-0.316*
	40	-0.330*	-0.325*	0.377**	-0.420**
	50	-0.329*	-0.314*	0.361**	-0.381**
2010	1	0.22	0.15	-0.118	-0.116
	10	0.315*	-0.139	-0.431**	0.262*
	20	0.37*	-0.06	-0.231	0.199
	30	0.321*	0.041	0.048	0.16
	40	0.172	-0.012	0.192	0.138
	50	0.133	-0.022	0.256	0.201

oxygen, but negatively correlated with salinity. In 2010, diversity was only significantly correlated with temperature at 30 m depth.

With respect to total larval abundance (Table 4.5), in 2009 significant correlations were detected at 40 and 50 m for all environmental variables. For most depths, correlation coefficients were negative for temperature, fluorescence, and oxygen, but positive for salinity; the opposite trend was observed at 1 m for salinity and temperature. In 2010, total abundance was significantly positively correlated with temperature between 10 and 30 m, and significantly correlated with salinity and oxygen at 10 m.

Results from the BEST analysis (Table 4.6) indicated that the environmental variables responsible for the maximum Spearman correlation coefficients were temperature in 2009, and temperature and salinity in 2010. Maximum correlation coefficients occurred at 50 m in 2009 and 2010. In general, correlation coefficients were higher in 2009 than 2010, particularly between 20 and 50 m.

Table 4.6. Maximum Spearman correlations between larval and environmental similarity matrices from BEST analysis at depths of 1 to 50 m for 2009 and 2010 surveys. Bolded values indicate the highest correlation coefficient for each survey. Symbols adjacent to each coefficient indicate the variable(s) responsible for maximum correlation. T, temperature; F, fluorescence, S, salinity; O, oxygen. Symbols are arranged in order of importance.

Depth	**Year**	
	2009	**2010**
1	SO (0.114)	FTO (0.138)
10	ST (0.082)	TO (0.111)
20	TOF (0.187)	S (0.159)
30	T (0.313)	SO (0.127)
40	T (0.318)	TS (0.16)
50	**T (0.337)**	**ST (0.194)**

4.5. Discussion

4.5.1. Larval assemblage composition

The composition of a larval assemblage is dependent on processes associated with the adult and larval phases (Isari et al., 2008). Adult-regulated processes include the distribution of adults, the magnitude of the reproductive output, and the timing of larval release. On the other hand, larval-related processes are more closely regulated by hydrodynamics (Bakun, 2006) and include larval transport, growth, and survival.

The reproductive output of crab populations is a function of the number of successfully fertilized females and their individual fecundity (Sato et al., 2007). Cancrid crabs are capable of producing large broods, especially *M. magister* and *C. productus* (Hines, 1991). It was therefore not surprising that *M. magister* dominated the larval assemblage as females of this species are very abundant, especially in the Southern SoG (Jamieson and Phillips, 1993; Palsson et al., 2001) and have an exceptionally high fecundity (1 million eggs per brood at 155 mm carapace width) (Hines, 1991). *Cancer productus* is also considered common throughout British Columbia (Hart, 1982; Jensen, 1995) and females can produce a comparable brood size (Hines, 1991). The fecundity of other local species is much lower (Knudsen, 1964; Somerton and Meyers, 1983; Nyblade, 1987; Hines, 1991), which is consistent with their overall lower larval abundances reported herein.

The occurrence of crab larvae reflected the reported species-specific hatching periods in the Salish Sea. For example, *Lophopanopeus bellus bellus, Hemigrapsus* spp. and *Petrolisthes eriomerus* begin hatching in May (Knudsen, 1964), and were either absent or rarely collected in the present study. In contrast, only late larval stages of *T.*

cheiragonus were collected in this study, consistent with reports describing the occurrence of swarms of *T. cheiragonus* megalopae in early May in the San Juan Archipelago (Miner et al., 2000). Epialtid crabs do not appear to conform to a strict temporal pattern of reproductive timing (Knudsen, 1964), and their larvae have been observed in plankton samples year round with peak larval abundance observed in the spring off the coast of Oregon (Lough, 1975). This is consistent with the presence of all epialtid larval stages during the surveys. For the remaining species, the onset of hatching occurs between December and April (MacKay, 1942; Knudsen, 1964; Nyblade, 1987; Strathmann, 1987; Fong and Dunham, 2007; Duguid and Page, 2011) so, not surprisingly, zoeal stages one through four of many species in the samples which were collected in late April.

There is limited information on the life history of *M. quadrispina* despite this species' widespread geographic range in British Columbia (Hart, 1982) and its numeric dominance in suitable habitat (Burd and Brinkhurst, 1984). In the present study, the majority of larvae had already progressed to the second and third zoeal stages by late April, suggesting that larvae hatched in early spring. Bi-monthly sampling off the coast of Oregon in 1970-71 indicated that the onset of *M. quadrispina* hatching occurred in early May, and that the second zoeal stage was most abundant by mid-June (Lough, 1975). The samples collected in the present study suggest a timing of development somewhat different and unexpected, considering that crab larvae typically hatch at a later date and develop at a slower rate at higher latitudes (Fisher, 2006).

Neotrypaea californiensis and *L. bellus* larvae were present in 2010 but absent in 2009. This could have been a result of the slightly different sampling methodologies used between years, or interannual variation in reproductive timing. In Willipa Bay, Washington, *N. californiensis* zoeae were first observed in March, with peak abundance in either May or July, depending on the year (Graham and Bollens, 2010). Larvae of another mudshrimp, *Upogebia pugettensis* were entirely absent in both years despite a hatching period thought to occur by February in British Columbia (Hart, 1937). This may be related to the recent collapse of this species along the Pacific Northwest (Griffen, 2009; Dumbauld et al, 2011) or an unusually deep vertical distribution.

Field studies have demonstrated that crab larvae undergo daily vertical migrations with considerable interspecific variability in terms of preferred distribution and migratory behaviour (Lindley 1986; Lindley et al. 1994; Park and Shirely, 2005; Queiroga and Blanton, 2005; Yannicelli et al., 2006; dos Santos et al., 2007). However, crab zoeae are typically most abundant in the upper water column (above 70 m) and are only rarely present below 100 m (Queiroga and Blanton, 2005). Such evidence suggests that the sampling methodology used in this study was most likely effective in collecting representative numbers of species and stages. Communities collected during darkness and daylight conditions were not significantly different; however, this result must be taken cautiously considering the relatively low ANOSIM P-value. This was likely a result of collecting samples from consecutive sites in either condition (samples obtained in daylight or darkness were clustered spatially) (Fig. 4.1).

Detailed records of vertical distributions of larvae in the Northeast Pacific are scarce. Depth stratified samples off the California coast have demonstrated that cancrid zoeae are most abundant in the upper 30 to 40 m of the water column (Shanks, 1986a; Wing et al., 1998). Although larvae of *C. productus*, *G. oregonensis*, and *M. magister* all appear to undergo daily vertical migrations (Park and Shirley, 2005), their zoeae have not been observed below 80 m (Shanks, 1986a). In addition, pinnotherid zoeae have been shown to be most prevalent in the upper 30 m during the night and from 30 to 60 m during the day off the coast of California (Wing et al., 1998). Although all this information suggests that the sampling range used in this study is appropriate, one must take caution when generalizing vertical distribution patterns from studies conducted in the past or elsewhere (Vikebo et al., 2007).

It was difficult to interpret results for some families due to identification problems and minimum size ranges that were close to the 1 mm mesh size used to collect samples. For example, the number of zoeal stages is not consistent across pinnotherid species, ranging from two to five (Hart 1935; Bousquette, 1980; Pohle, 1989). As larval descriptions are not available for many local species, their identity could not be determined with certainty, and therefore, interpretation of their relative stage-specific abundance became problematic. The small size of many zoeae further prevented proper interpretation as some taxa were almost certainly undersampled in their early stages. For example, first stage pinnotherid zoeae identified as *Pinnixa* sp. by Lough (1975) measured as little as 1.02 mm. Similarly, the carapace lengths of the first zoeal stage of *M. gracilis* (1.1 mm) and *Hemigrapsus* spp. (1.1 – 1.2 mm) are likely also small enough to be undersampled (Hart, 1937; Ally, 1975). Furthermore, the carapace length and body width of many pagurid species are probably also small enough to avoid retention by 1 mm mesh in their early stages.

4.5.2. Interannual comparison

With the exception of *T. cheiragonus*, pagurid, and lithodid larvae, the significant differences detected between the April 2009 and 2010 assemblages were consistent with the large differences in the abundance of multiple species. Considerable changes in the abundance of two numerically dominant species, *C. productus* and *M. magister*, contributed the most towards the Bray-Curtis dissimilarity measured between years. Major inter-annual fluctuations in marine zooplankton and benthic populations are not uncommon and may be associated to climatic events, habitat alteration or overfishing (deYoung et al., 2008).

Lough (1976) attributed large inter-annual variation in abundance of *M. magister* larvae to within-year larval mortality from temperature and precipitation anomalies. Mismatch between the timing of larval release and food availability may also decrease the survival of meroplankton, resulting in low levels of recruitment and reduced year class strength (Cushing, 1990). The mismatch hypothesis has been supported by recent evidence suggesting that temporal fluctuations in temperature and phytoplankton availability cause inter-annual variability in recruitment of decapod and fish larvae (Koeller et al. 2009; Kristiansen et al., 2011; Oulette et al., 2011). Variation in year class strength from previous years could also have decreased the abundance of sexually mature individuals in 2008, resulting in less larvae being released in 2009. Finally, the larvae of some species may have been most abundant in surface water layers (up to 20 m deep), and therefore partially underrepresented in tows conducted in 2009, when samples were collected primarily between 30 and 50 m. Although this could explain shifts in the relative abundance of taxa between years, it is unlikely that the difference in sampling depth alone could have produced abundance differences of the magnitude recorded in this study. This argument is supported by a similar average overall larval abundance (1659 larvae/100 m^3) measured from the SoG between April 25-29, 2007, wherein plankton samples were obtained with methodology virtually identical to that in 2009 (see Appendix 2).

It is also unlikely that the differences in community composition and abundance observed in April 2009 and 2010 were primarily due to variation in reproductive timing. Reproductive timing is expected to be influenced by temperature which is known to affect the timing of mating (Christy et al., 2011) and the rate of embryological and larval development (Wear, 1974; Anger et al., 2004). Elevated sea surface temperatures in late spring and late summer/early fall in 2009 and in late winter/early spring in 2010 may have caused larvae to hatch earlier in the year, and develop at an increased rate in 2010. Under these conditions, it is possible that the peak hatching period for *C. productus*, which typically occurs in late March (Knudsen, 1964), did not occur until after sampling in late April 2009. However, given the same scenario, the absolute abundance of *M. magister* larvae, which normally hatch in late winter and early spring, should be lower in late April 2010 than 2009 (due to a longer period of exposure to larval mortality). This is not consistent with the results from the present study.

Although temperature variation does not appear to explain the major differences in larval abundance between years, it may be responsible for a slightly earlier hatching period for several species in 2010. This may explain the absence of *L. bellus* and *N. californiensis* in April 2009 and the low abundance of *P. eriomerus* in the same survey. Cold winter and spring temperatures have also been linked to later larval release dates for several crab species off the Oregeon coast (Lough, 1975). In the present study, temperature may be responsible for the interannual differences in the relative stage-specific abundance of *C. productus*, *M. magister* and epialtid larvae, all of which were more abundant in later stages during April 2010. Sulkin and McKeen (1996) demonstrated that a temperature difference of less than 2 °C has measurable effects on zoeal duration of *M. magister* under laboratory conditions. Although laboratory conditions cannot be readily extrapolated to the field, the higher temperatures recorded in the SoG between January and April 2010 are consistent with and most likely related to fluctuations in the relative abundance of larval stages reported herein.

Spatial patterns of abundance and diversity resulted from differences in the horizontal distribution of individual species and the overall abundance of each taxon. In the present study, significant spatial clustering of larval abundance and diversity was detected only in 2009. The absence of significant clustering in 2010 may have been due in part to a combination of the sampling resolution, the shape of the pattern, and the size of the study area. For example, relatively large regions of high and low abundance appeared to be present, especially along the margins of the central SoG, but were not detected by the Getis-Ord hotspot analysis.

Because cancrid zoeae accounted for nearly 80% of the larvae collected during both years, the spatial pattern of total larval abundance and diversity was largely influenced by species within this family. For example, the large increase in the abundance of *C. productus* larvae in April 2010 may be an important contributor to variation in spatial patterns of total abundance observed between years. *Metacarcinus magister* was the most abundant species in both years; therefore, its spatial configuration was likely the most important influence on observed patterns of total abundance and diversity. For example, high abundances generally occurred along the eastern side of the central SoG and near the Fraser River mouth, whereas low abundance regions occurred in the SoG's northwestern region and along its western margin. This pattern is consistent with the distribution of *M. magister* inferred from fishing landings, wherein the highest landings have come from fishing areas encompassing the entire southern region and the eastern margin of the central strait (Fisheries and Oceans, 2010a). Furthermore, adult abundance of *M. magister* is known to be particularly low in the northwest region, possibly due to elevated temperatures that have been shown to reduce the survival of juveniles under laboratory conditions (Sulkin et al., 1996).

4.5.3. Relationship between larval assemblages and environmental variables

Environmental conditions were probably not capable of influencing larval survival directly. For example, the range of temperatures observed in both years is not lethal to cancrid zoeae under laboratory conditions (Sulkin and McKeen, 1994; 1996). Furthermore, many localities characterized by low surface salinity, which could possibly cause physiological problems for zoeae, were actually associated with elevated larval abundance. Regardless, these variables could collectively depict oceanographic conditions that could influence larval survival, advection, or retention. For example, eddies can cause upwelling, downwelling, and frontal boundaries that can then influence the distribution of temperature, salinity, and phytoplankton (fluorescence) (Bakun, 2006).

The high correlation coefficients observed in the present study were probably related to processes affecting the distribution of both larvae and water column characteristics. For example, adult *M. magister* individuals are commonly found in estuarine environments characterized by low surface salinity, and are known to be highly concentrated near the mouth of the Fraser River (Fisheries and Oceans, 2010a), where large larval release events likely occur. Ocean currents may then disperse estuarine water and larvae together resulting in a spatial association between low salinity and larval abundance.

Correlations between environmental variables and different larval attributes (diversity, abundance, and assemblage similarity matrices) differed between April 2009 and 2010. In general, the relationship between larval abundance, diversity, and community composition with environmental variables was stronger in 2009. The highest correlation coefficients were detected between 30 and 50 m in 2009 and between 10 and 30 m in 2010, which may reflect the difference in sampling protocol between years. The BEST analysis selected temperature in 2009 and salinity and temperature in 2010 as the best explanatory variables for the larval assemblages. However, correlation coefficients were generally modest, and it is difficult to unambiguously determine the relative importance of each environmental variable as they were correlated to each other to different extents at different depths.

There is no clear explanation for the differences in the correlations observed between years. Interannual variation in the abundance and distribution of the dominant species (*M. magister, C. productus*, and *M. quadrispina*) was probably a major contributor. It is also possible that a combination of processes (e.g. wind, fresh water input) is capable of affecting the distribution of environmental variables and larvae in a similar fashion, but only under certain conditions (e.g. in April 2009, but not in 2010).

The present study has demonstrated that substantial variability can occur in temporal and spatial patterns of larval assemblages within the SoG. Interannual variability in larval abundance may have been caused by large mortality events or variation in reproductive output. In addition, temperature differences between years appeared to influence the stage-specific abundance for multiple species. Fluctuations in the abundance and distribution of *M. magister*, *C. productus*, and *M. quadrispina* between years likely contributed to interannual variability in the spatial patterns of total larval abundance and diversity, as well as correlations with environmental variables. Consequently, an analysis of species-specific distributions is required to fully understand the spatial patterns of abundance and diversity and their association with hydrographic conditions.

Further studies in the SoG should consider using oblique tows with a smaller mesh size (at least 500 μm) to ensure proper representation of early larval stages of all resident crab species. Additional research is needed to determine the precise vertical distribution of these species and their stages from depth stratified sampling, as vertical distributions may be different in the SoG compared to the open coast (e.g. Jamieson and Phillips, 1993). Furthermore, diagnostic features of larvae from many resident species are required to increase taxonomic resolution in the region upon which field studies are heavily dependent.

CHAPTER 5

Horizontal larval distributions of three cancrid species (*Cancer productus*, *Glebocarcinus oregonensis*, and *Metacarcinus magister*) from the spring and summer seasons in the Strait of Georgia, British Columbia

5.1. Abstract

Spatial and temporal patterns of larval crab abundance from the three cancrid species, *Cancer productus*, *Glebocarcinus oregonensis*, and *Metacarcinus magister*, were described from plankton surveys conducted during the spring and summer of 2010 in the Strait of Georgia, British Columbia. In both surveys, larvae of *M. magister* were most abundant, followed by *C. productus* and *G. oregonensis*, and the majority of *C. productus* larvae occurred at an earlier larval stage compared to the other two species. In the spring, the distribution of the first zoeal stage was noticeably different among species, which likely reflected the distribution of adults. The total abundance of each species (all larval stages combined) was highest along the eastern side of the Strait's central and northern regions, where larvae may have been retained nearshore or transported alongshore. In contrast, in the southern region larvae were widespread, indicating potential for cross-strait transport. In the summer, megalopae were most abundant throughout the Strait's most southern region for *G. oregonensis*, but along the Strait's southwestern margin for *M. magister*. *Cancer productus* megalopae were most abundant in an area characterized by high levels of fluorescence, located just below Lasqueti Island in the Strait's central region, where localized patches of *G. oregonensis* and *M. magister* megalopae were also detected. In both surveys, stage- and species-specific larval abundance was frequently

correlated with the distribution of different environmental variables measured at each station. Relatively high correlation coefficients between larval abundance and temperature and salinity in the upper water column indicated that the dynamics of the Fraser River plume could strongly influence the distribution of *M. magister* larvae, and to a lesser extent, the distribution of *C. productus* and *G. oregonensis* larvae.

5.2. Introduction

In marine systems, the dispersal of planktonic larvae plays a fundamental role in determining the exchange of individuals between populations (Cowen and Sponaugle, 2009), and is an important consideration for the strategic design of marine protected areas and their networks (Kritzer and Sale, 2004). The horizontal distribution of larvae can be used to test predictions based on dispersal processes or to develop hypotheses about dispersal pathways (Sale and Kritzer, 2003). Larval distributions have also been employed as validation tools for biophysical models (e.g. Peliz et al. 2007) that have been recurrently used to predict the probability of larval exchange between locations (Metaxas and Saunders, 2009).

In the pelagic environment, several physical and biological processes operate at various spatial and temporal scales that shape the distribution of plankton, which is often characterized as "patchy" (Mackas et al., 1985). The distribution of meroplankton is highly influenced by larval transport (Hobbs et al., 1992; Wing et al., 1998) resulting from physical forcing by ocean currents and vertical swimming behaviour (Pineda et al., 2007). Additional factors that affect larval distributions include the timing and location of larval release (Natunewicz and Epifanio, 2001; Kerr and Duffus, 2006), spatial variation in mortality (Frank et al., 1993; Bradbury et al., 2003), and horizontal swimming by late pre-settlement stages (Chiswell and Booth, 1999).

The Strait of Georgia (SoG hereafter) is a deep semi-enclosed ocean basin situated between Vancouver Island and mainland British Columbia (Thomson, 1981). The SoG communicates with Puget Sound to the south and the Juan de Fuca Strait to the west. These ocean basins are collectively referred to as the Salish Sea (Cummins, 2006). The following six cancrid species, previously all within *Cancer* but now assigned to four different genera (Schweitzer and Feldmann 2000), co-occur off the coast of southern British Columbia: *Cancer productus*, *Glebocarcinus oregonensis, Metacarcinus gracilis*, *M. magister*, *Romaleon antennarius*, and *R. branneri* (Lamb and Hanby, 2005). Only the first four species commonly occur in the Salish Sea's inland waters (Orensanz and Galluchi, 1988). The range of *Romaleon* spp. extends into the Juan de Fuca Strait (Lamb and Hanby, 2005; W. Duguid Pers. Comm.); however, it remains unclear if these species reside within the SoG.

Cancrid crabs are common predators in intertidal and subtidal habitats (Knudsen, 1964; Smith et al. 1999b; Dudas et al., 2005) and their larvae are collectively among the most abundant in plankton samples from the Northeast Pacific (Lough, 1975; Fisher, 2006). *Metacarcinus magister* (Dungeness crab) populations support a valuable commercial fishery in British Columbia, a substantial portion of which comes from landings in the SoG (Fisheries and Oceans, 2010a). *Cancer productus* (Red Rock crab) is also eligible for commercial exploitation (Fisheries and Oceans, 2010a).

Despite their economical and ecological importance, information on the distribution of adult cancrid species in the SoG is scarce. Jamieson and Phillips (1993) mention that the largest aggregation of *M. magister* occurs in the SoG's most southern region, where commercial landings are highest (Fisheries and Oceans, 2010a). Local cancrid species occupy both intertidal and subtidal habitats (Jensen, 1995), but prefer different substrates. *Metacarcinus magister* is usually found on sandy substrate, *C. productus* in and around gravel and boulders, and *G. oregonensis* nestled in small holes or crevices (Knudsen, 1964; Jensen, 1995).

The larval duration of *M. magister* has been estimated to be approximately 130 days off the coast of Oregon (Lough, 1976). Laboratory rearing at 10°C has also indicated that the zoeal durations among cancrid species are relatively similar, although *C. productus* appeared to have a slightly shorter duration (Sulkin and McKeen, 1994). Given their relatively long larval duration, there is potential for cancrid larvae to be transported large distances and generate spatial patterns that reflect the circulation within the SoG.

The oceanography of the SoG is primarily influenced by seasonal river runoff and is further modulated by tidal currents, wind stress and basin topography (Thomson, 1981). The majority of studies that have described the trajectory of low frequency currents, capable of displacing larvae, have taken place in the SoG's central and southern regions. These studies suggest that alongshore currents prevail on either side of the SoG's central region and that a rotary current exists between the Fraser River delta and Gulf Islands (Waldichuk, 1957; Tabata, 1972; Thomson, 1981; Stacey et al., 1987), where subsequent ocean modeling has simulated two baroclinic counter-rotating gyres (Masson and Cummins, 2004).

This study describes mesoscale stage-specific larval distributions for *C. productus*, *G. oregonensis*, and *M. magister* from consecutive spring and summer seasons of 2010. The relationship between environmental variables and the larval distribution of these species is also explored by correlative analysis and potential dispersal pathways are hypothesized and discussed. Apart from a single study (Jamieson and Phillips, 1993), there is virtually no information available on the distribution or dispersal of crab larvae in the SoG. Such information can ultimately contribute to the establishment of marine protected areas for management of the crab fisheries and marine communities in this inland sea.

5.3. Methods and materials

5.3.1. Plankton sampling and larval identification

Crab larvae were collected from surveys conducted in the spring (April 24-27) and summer (June 27-29) of 2010 in the SoG, British Columbia. A total of 61 stations were sampled in the spring that spanned the majority of the SoG (57 of these stations were used for analysis in Chapter 4 of this thesis), whereas 34 stations were sampled in the summer covering the SoG's central and southern regions (Fig. 5.1). The stations were arranged in a grid and spaced approximately 8 km apart. Sampling took place throughout the day and night, following an order of consecutive stations that largely depended on weather conditions and ship time constraints.

At each station, plankton samples were obtained using a Tucker Trawl (1.5 m^2 frame, 1 mm mesh size) equipped with a flowmeter. Samples were collected by oblique plankton tows with a duration of approximately 15 minutes at a speed of 2 knots and a

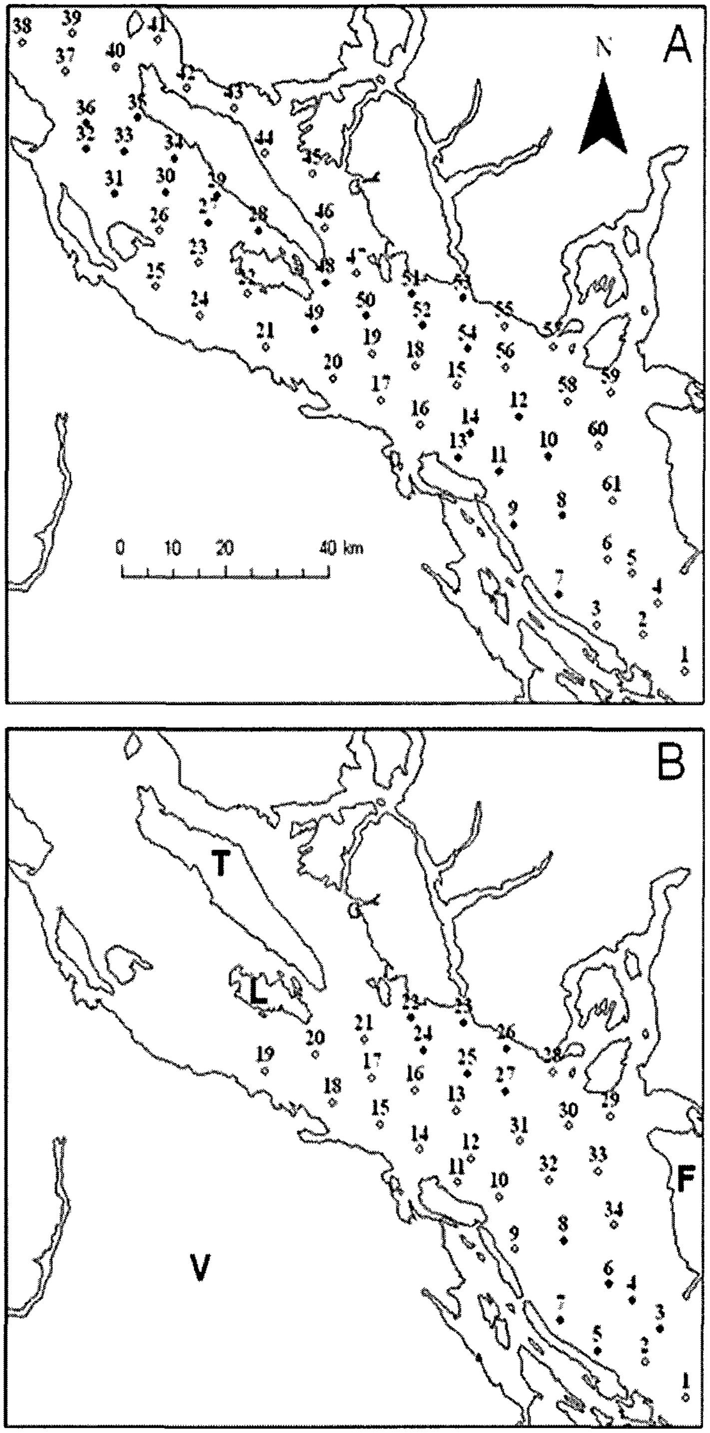

Figure 5.1. Locations of samples from surveys conducted in A) April 23-27 and B) June 27-29, 2010. Labels indicate the order in which samples were taken. Filled and empty dots indicate that the stations were sampled at night or day respectively. In B: F, Fraser River delta; L, Lasqueti Island; T, Texada Island; V, Vancouver Island.

targeted maximum depth between 30 and 50 m. Depth profiles were verified from a Vemco Minilog-12TX data logging device attached to the Tucker Trawl. In each survey, vertical profiles of different water properties (temperature, fluorescence, salinity and oxygen) were logged from CTD casts conducted at the starting location of each plankton tow using a Sea-Bird Electronics 19*plus* Seacat CTD equipped with an oxygen sensor and fluorometer.

Plankton samples were preserved in 95% ethanol, subsampled with a Folsom splitter, and sorted for crab larvae. Approximately 200 crab larvae were enumerated for each sample that required splitting. Larval abundance was standardized to larval concentrations per 100 m^3 of filtered seawater from flowmeter readings. Crab larvae were identified to stage and species using relevant identification guides (Lough, 1975; DeBrosse et al., 1990a; Puls, 2001; Rice and Tsukimura, 2007) and larval descriptions (Poole, 1966; Trask, 1970; Ally, 1975) as well as laboratory reared specimens of *G. oregonensis* (c.f. Chapter 3 of this thesis). The megalopae of *M. gracilis* and *C. productus* were distinguished by size only (*M. gracilis* carapace length < 3 mm), as coxal spines were present on the ventrodistal surface of the second pereopod on all cancrid megalopae observed (c.f. DeBrosse et al., 1990a). *Metacarcinus gracilis* was not included in this study as it its abundance was very low, making spatial patterns difficult to interpret. The larval development of *R. branneri* has not been described and it was assumed that larvae from this species were not collected.

5.3.2. Data analysis

Larval abundance was mapped and analyzed using the WGS 1984 coordinate system and UTM Zone 10N projection in ArcMap v. 9.3. The base map of British Columbia was obtained online from the North American Atlas (Natural Resources Canada, 2007). Horizontal patterns of total and stage-specific abundance for each species were visualized by creating continuous surfaces from an inverse distance weighting interpolation. The larval abundance classification contours were modified from a log scale that covered the entire range of values observed for all species for each individual survey. The G*i** statistic (Getis and Ord, 1992) was used to determine if high and low total abundance (all stages combined) locations clustered spatially (c.f. section 4.3.2. of this thesis for more information on the G*i** statistic). A fixed distance of 20 km was chosen as it was the minimum distance that allowed the majority of sampling locations to have at least eight neighbours. Larger distances were not used as they would have produced irrelevant local measures for the sampling resolution used and size of the study area. Z-scores for stations with less than 8 neighbours (Late April: stations 1-4, 37-39, 59; Late June: stations 1-4, 21, 49) were not considered. Stations 41-46 (Fig 5.1A) from the spring survey were also excluded from the analysis to prevent the effect of Texada Island on distance between stations. Although normality of the data points is not required for this analysis, significance testing may be misleading when the data is strongly skewed (Zhang, 2008). Therefore, this statistic could only be used with log transformed total abundance measures [e.g. log(abundance+1)], as a high number of zero counts for several larval stages prevented analysis on stage-specific spatial patterns.

Although plankton tows were not depth stratified, the relationship between the abundance of each species and environmental variables was analyzed using measurements of temperature, salinity, oxygen, and fluorescence at the following depths: 1 m, 10 m, 20 m, 30 m, 40 m and 50 m. For each station, readings of each environmental variable were averaged at each depth ± 0.5 m using Sea-Bird Electronics Data Processing software. The Spearman rank correlation (SPSS v. 15.0) was used to assess the degree of correlation between the environmental variables and the abundance at each depth for each species and stage. The large number of correlations computed increased the probability of obtaining a type I error; therefore, significance results were only used as indicators of potential relationships and only the highest correlations were taken into consideration when interpreting results. The horizontal distribution of each environmental variable was mapped at each depth to visualize the relationship between the distribution of larval abundance and environmental variables (Appendix 1). The inverse distance weighting interpolation was used to map the distribution of each environmental variable.

5.4. Results

5.4.1. Larval abundance

Metacarcinus magister was the most abundant species in both surveys. In the spring, only the first four zoeal stages were present, and the third stage was most abundant. During the summer, all larval stages were present and the megalopal stage was most abundant (Fig. 5.2). *Cancer productus* was the second most abundant species in both surveys. The second and third zoeal stages were the most abundant in the spring and summer surveys respectively (although abundance was more evenly distributed

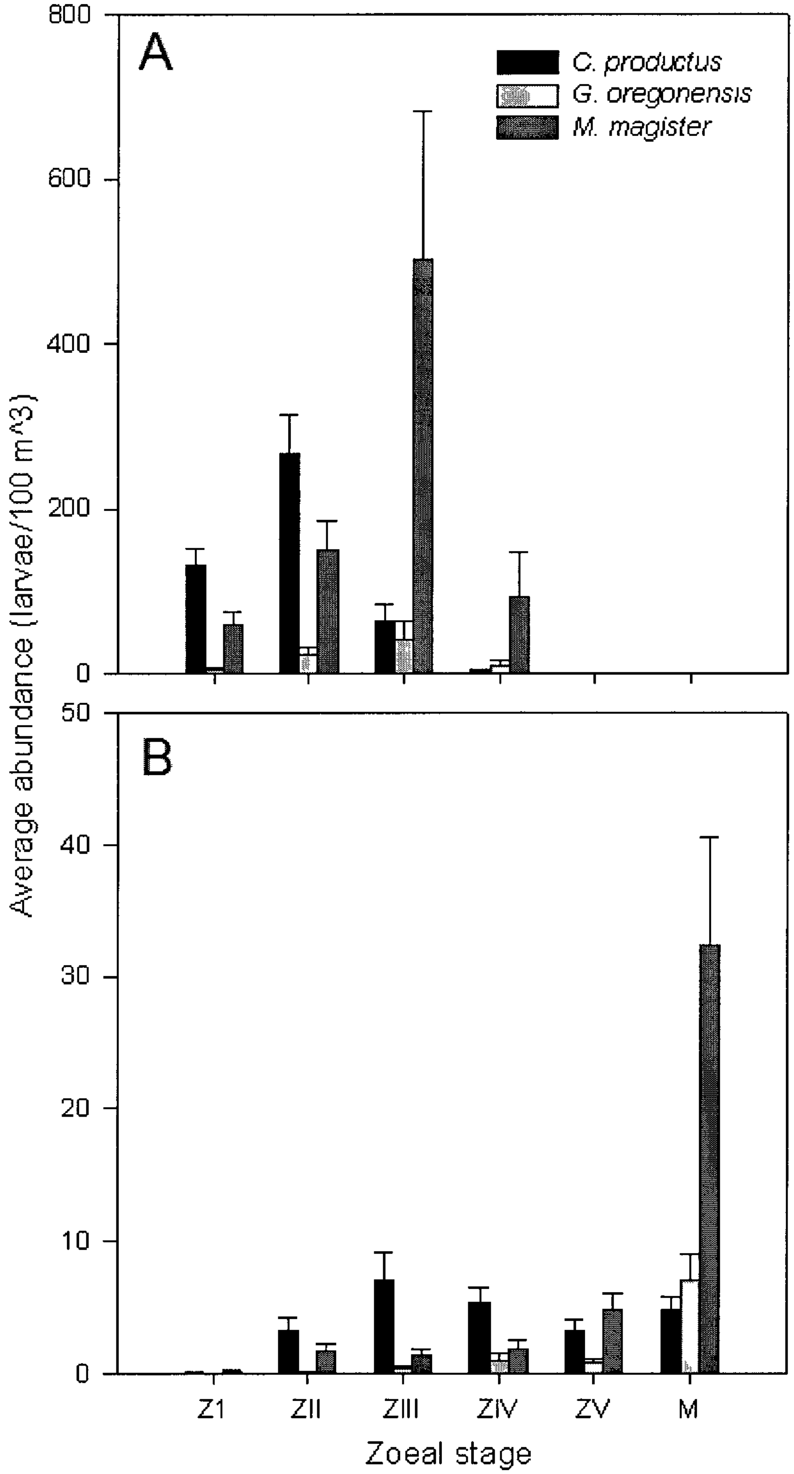

Figure 5.2. Stage-specific average abundance (+/- standard error) of *C. productus*, *G. oregonensis* and *M. magister* larvae from A) April and B) June 2010.

among stages during the summer). In the spring, only the first four zoeal stages were present, whereas all larval stages were present in the summer. *Gleobocarcinus oregonensis* was the third most abundant cancrid and the occurrence and abundance of its larval stages followed the same pattern as *M. magister*, although the first zoeal stage was absent during the summer.

5.4.2. Horizontal distributions

Metacarcinus magister

In the spring, spatial clustering of high total abundance was detected in the SoG's southern region and along the eastern margin, whereas clustering of low abundance was detected in the northwest region, between Vancouver Island and Texada Island (Fig. 5.3A). In the summer, spatial clustering of high and low abundance occurred in the SoG's southern and western-central regions respectively (Fig. 5.4A). With respect to zoeal stages during the spring, the first stage was most abundant in the SoG's southern region and along the eastern side, but almost entirely absent in the northwest region (Fig. 5.5). The remaining zoeal stages were more widespread; however, the highest abundances were restricted to the SoG's eastern side, especially in the SoG's central and northern regions. For all stages, a high abundance anomaly was detected at station 56 in the central SoG.

During the summer, the first zoeal stage was only collected at five locations, whereas stages two through five were widespread; abundances increased near the northern extent of the sampling grid as zoeal stages progressed (Fig. 5.6). The megalopal stage was most abundant in the SoG's southern region, especially along the southwest

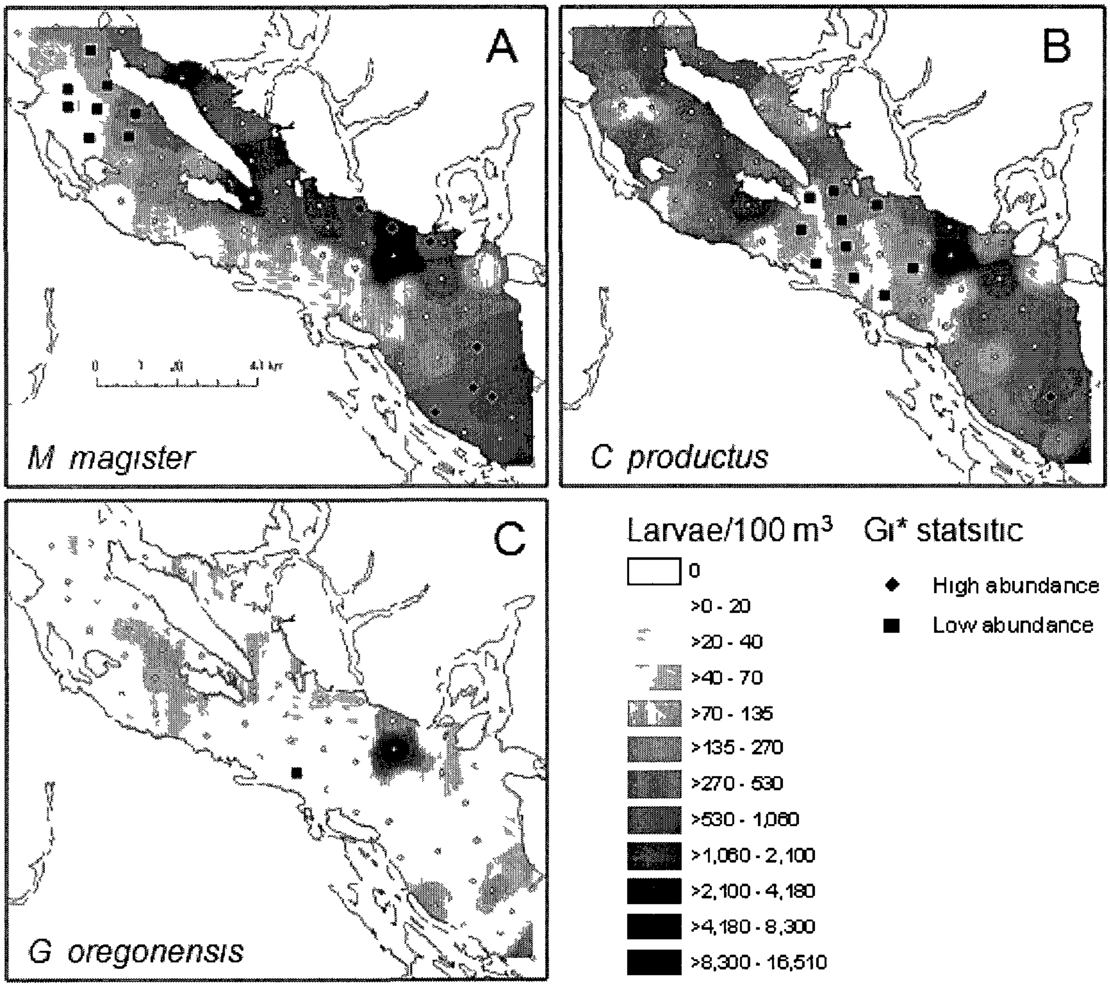

Figure 5.3. Spring horizontal distribution of total abundance and Gi* statistics for A) *M magister*, B) *C productus,* and C) *G. oregonensis* zoeae.

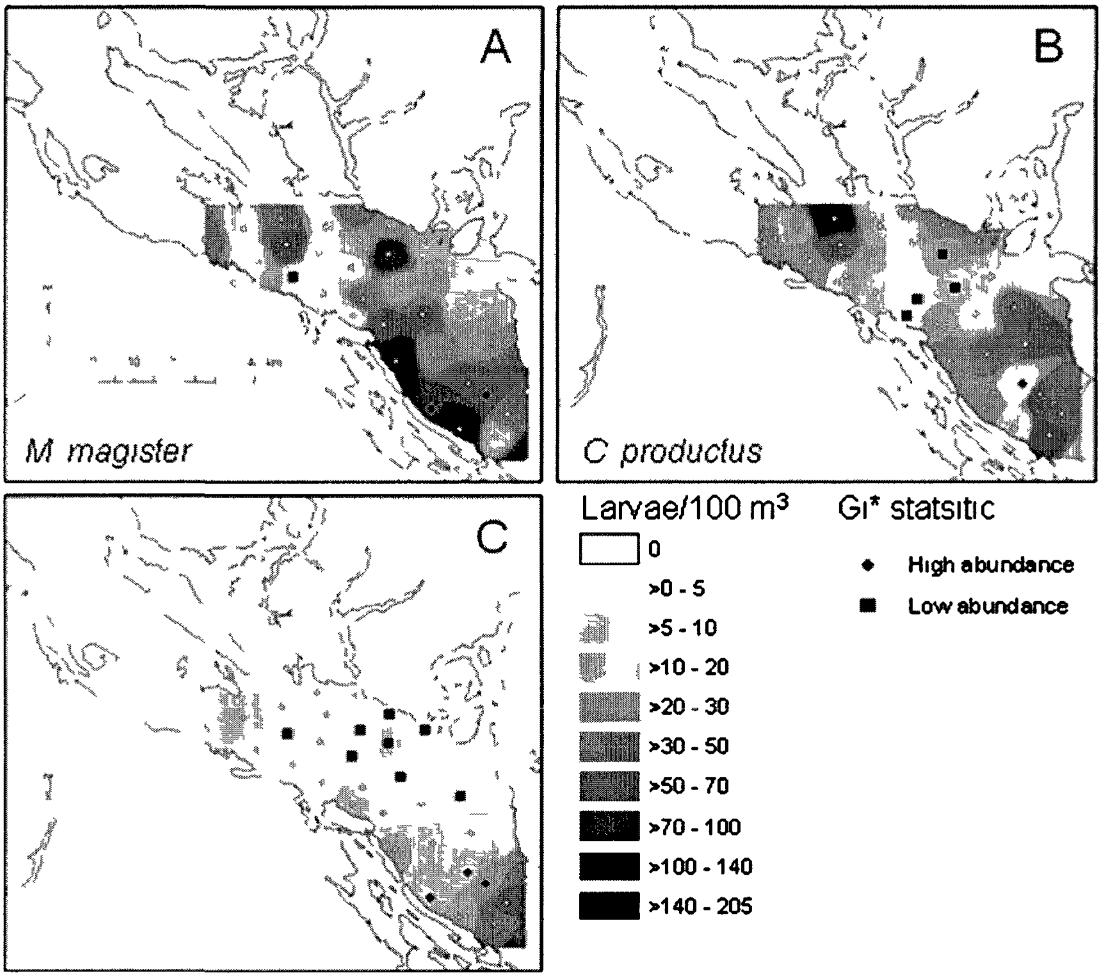

Figure 5.4. Summer horizontal distribution of total abundance and Gi* statistics for A) *Metacarcinus magister*, B) *Cancer productus,* and C) *Glebocarcinus oregonensis* zoeae.

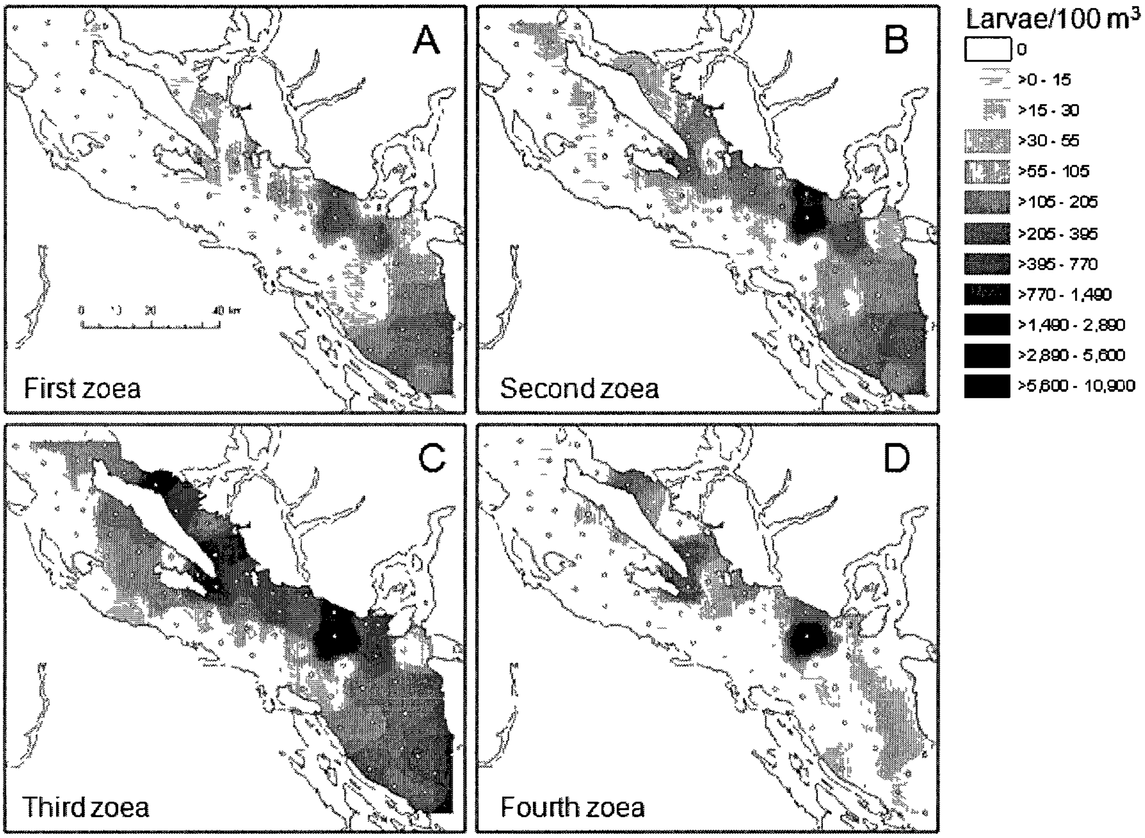

Figure 5.5. Spring horizontal distribution of *M. magister* larval stages for A) first zoea, B) second zoea, C) third zoea, and D) fourth zoea.

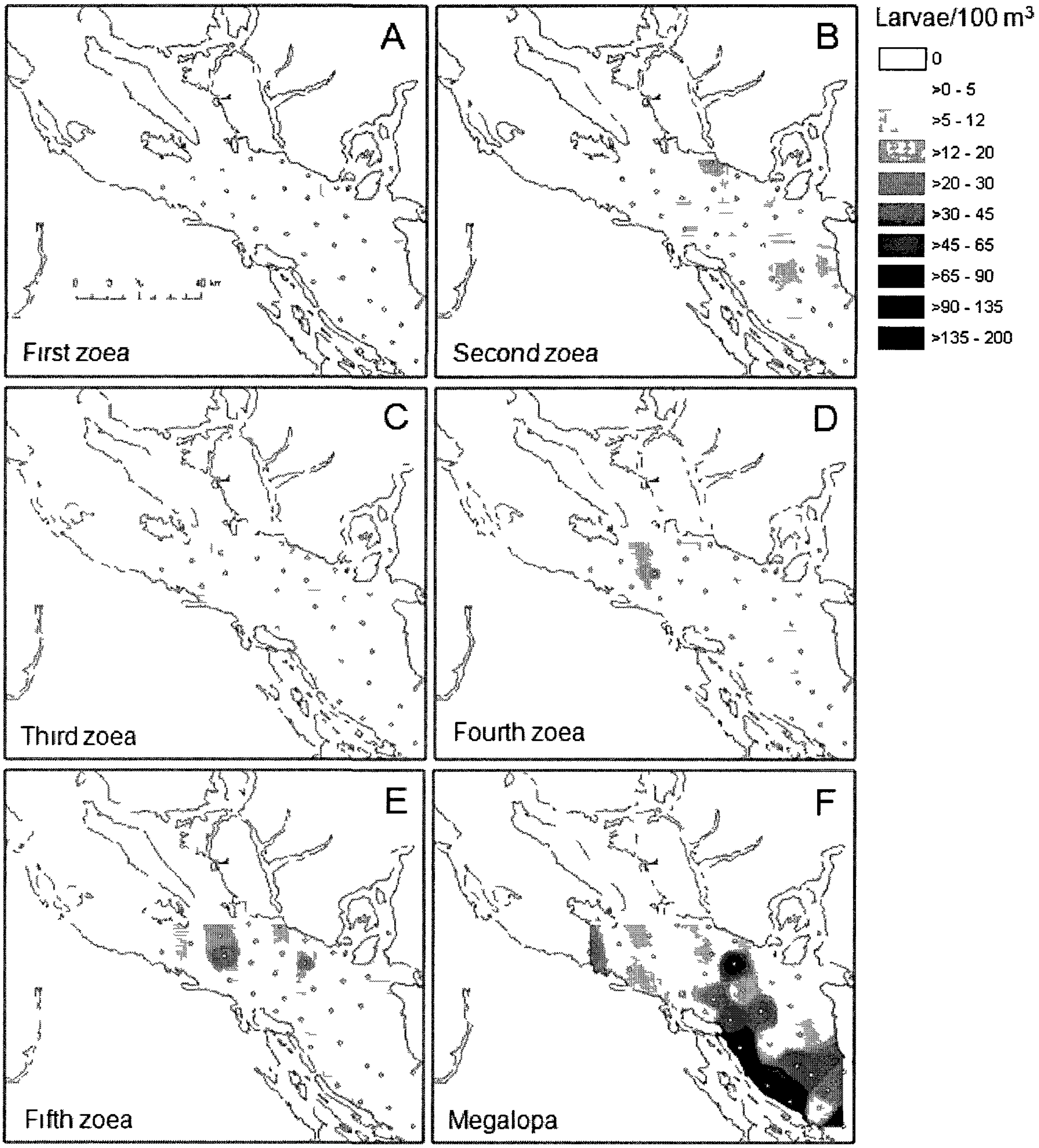

Figure 5.6. Summer horizontal distribution of *Metacarcinus magister* larvae for larval stages for A) first zoea, B) second zoea, C) third zoea, D) fourth zoea, E) fifth zoea, and F) megalopa.

margin, but was also present in high concentrations at stations 56 (eastern margin of central SoG) and 21 (southwest of Texada and Lasqueti Island) (Fig. 5.1A).

Cancer productus

In the spring and summer, clustering of high abundances was detected in the SoG's southern region, whereas clustering of low abundances was spread across the SoG's central region (Figure 5.3B and 5.4B). During spring, the distribution of the first zoeal stage was characterized by elevated larval abundances in large portions of the SoG's southeast and northwest regions separated by a prominent region of low abundance in the central region, south of Texada Island (Fig. 5.7). High abundances of the second zoeal stage were more widespread, but abundance remained low in the SoG's central region, especially along the western margin. The third zoeal stage was largely restricted to the SoG's eastern margin. The fourth zoeal stage was almost entirely absent, but most frequently detected in the SoG's central region. As in the case of *M. magister*, the highest abundance of all larval stages was detected at station 56.

During the summer, the first zoeal stage was only detected at four stations, whereas the remaining zoeal stages were present throughout the study area (Fig. 5.8). The third and fourth zoeal stages were most abundant in three different areas: the southern region in proximity to the Fraser River delta, along the eastern margin of the central SoG, and just south of Texada Island. The second and fifth zoeal stages were only present in elevated concentrations at individual stations. The megalopal stage was most abundant in the northwest region of the study area on the western margin of the central SoG.

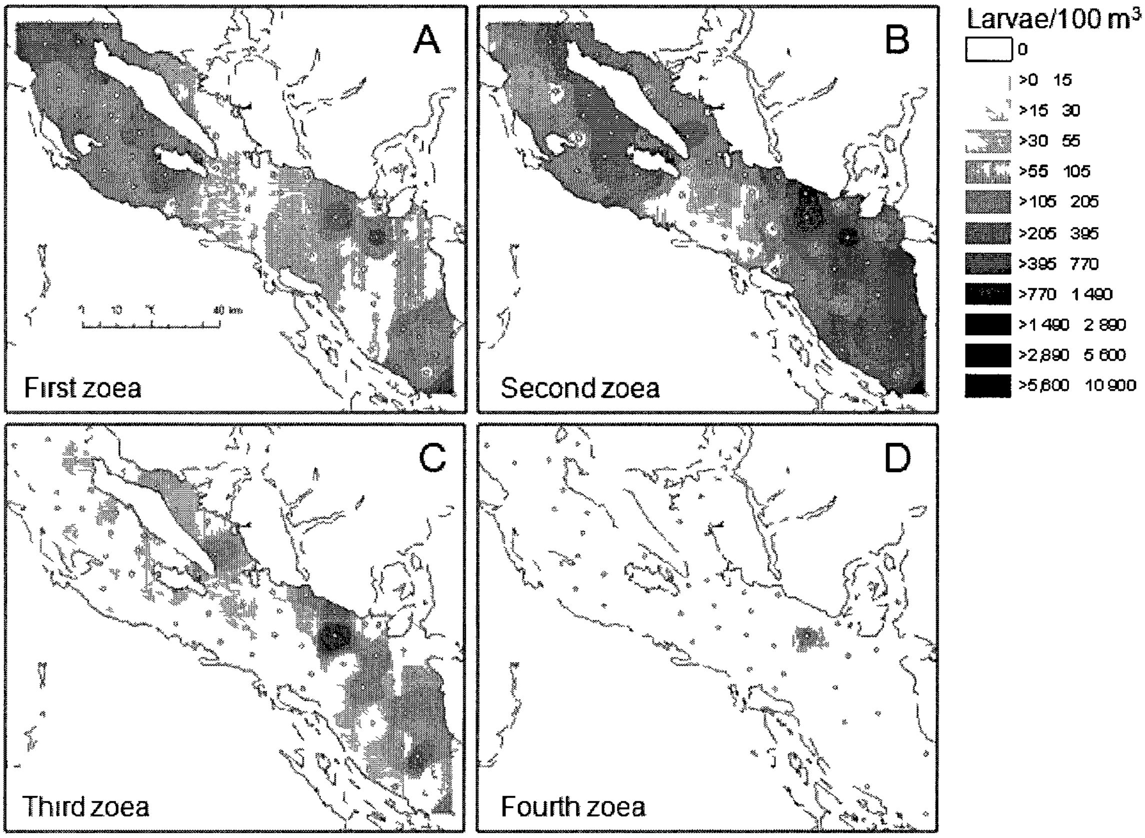

Figure 5.7. Spring horizontal distribution of *C productus* larval stages for A) first zoea, B) second zoea, C) third zoea, and D) fourth zoea.

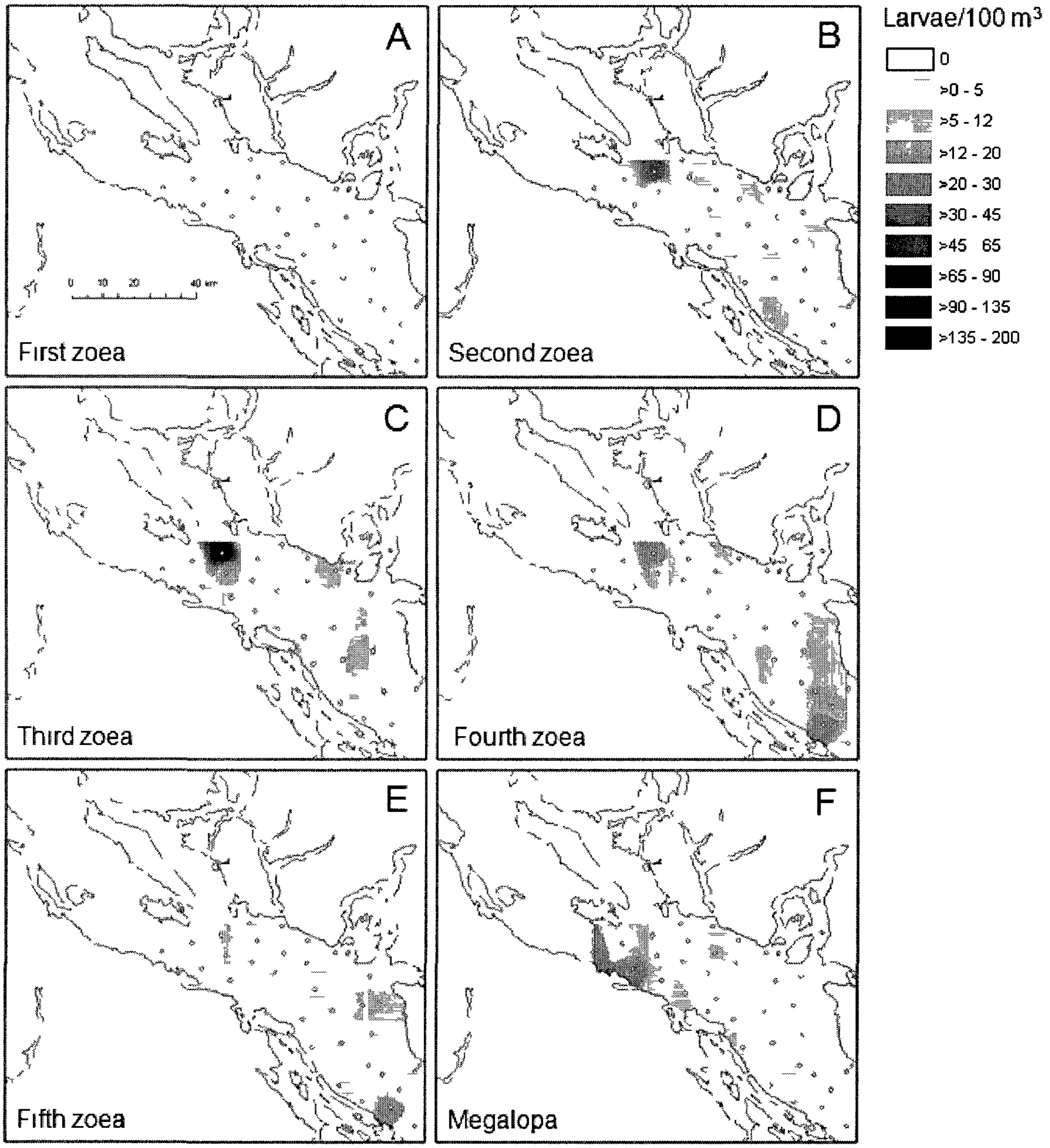

Figure 5.8. Summer horizontal distribution of *C productus* larvae for larval stages for A) first zoea, B) second zoea, C) third zoea, D) fourth zoea, E) fifth zoea, and F) megalopa.

Glebocarcinus oregonensis

During the spring, spatial clustering of low abundance was only detected near the western margin of the central SoG (Fig. 5.3C). In contrast, during the summer, spatial clustering of high abundance was detected in the SoG's southern region, whereas a large region of low abundance was detected in the centre of the study region, especially on the SoG's eastern side (Fig. 5.4C). With respect to zoeal stages during spring, the first stage was largely absent along the SoG's eastern margin and in other localized areas. In contrast, the second and third stages were present throughout the SoG, with high abundances in localized areas situated in the SoG's southern region, along the eastern margin, and in the northern region (Fig. 5.9). The fourth stage was largely restricted to the eastern side of the SoG and was absent at many locations throughout the northwest region. During the summer, all larval stages were consistently most abundant in the SoG's most southern region (Fig. 5.10). The megalopal stage was also abundant in localized patches along the central SoG's western margin.

5.4.3. Relationship between larval abundance and environmental variables

During the spring, the abundance of all larval stages of *M. magister* was best (negatively) correlated with salinity at 10 m depth (Table 5.1). During summer, the abundance of zoeal stages was best correlated with temperature (positive) or salinity (negative) at either 1 or 10 m. In contrast, megalopal abundance was negatively correlated with temperature at 1 m and positively correlated with salinity at 10 m deep (Table 5.2).

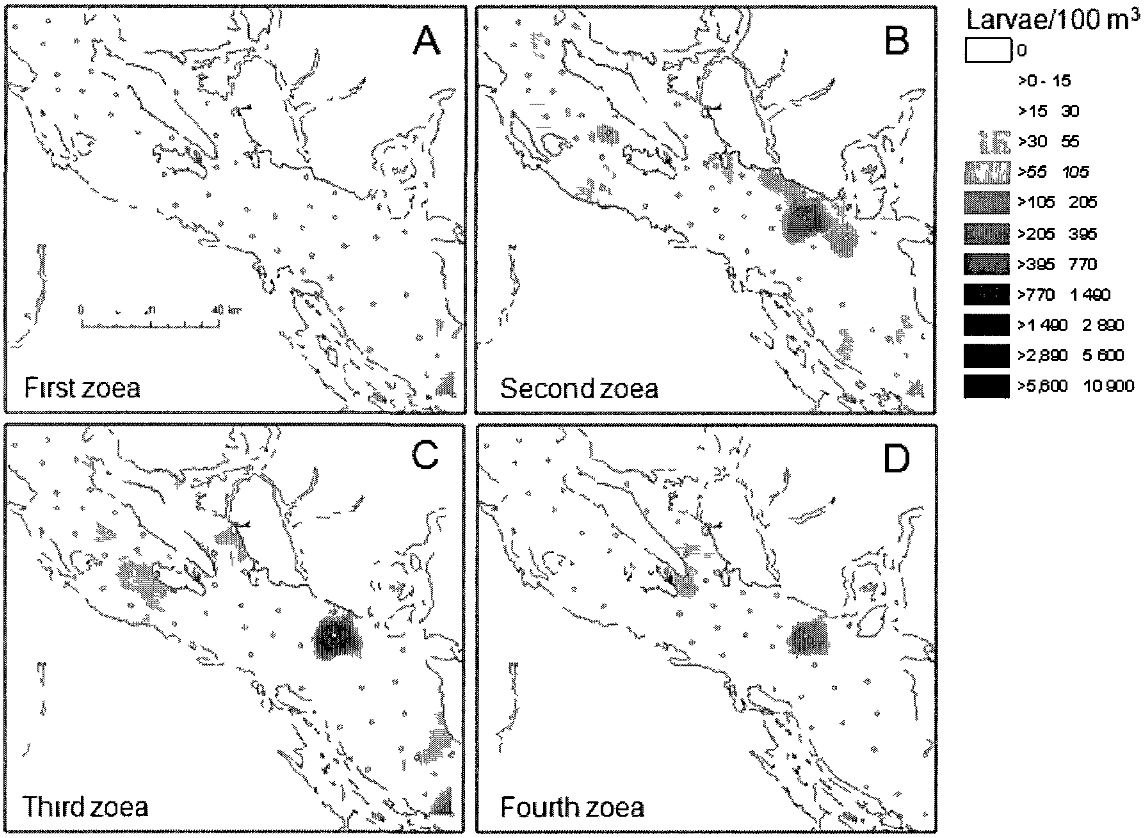

Figure 5.9. Spring horizontal distribution of *G oregonensis* larval stages for A) first zoea, B) second zoea, C) third zoea, and D) fourth zoea.

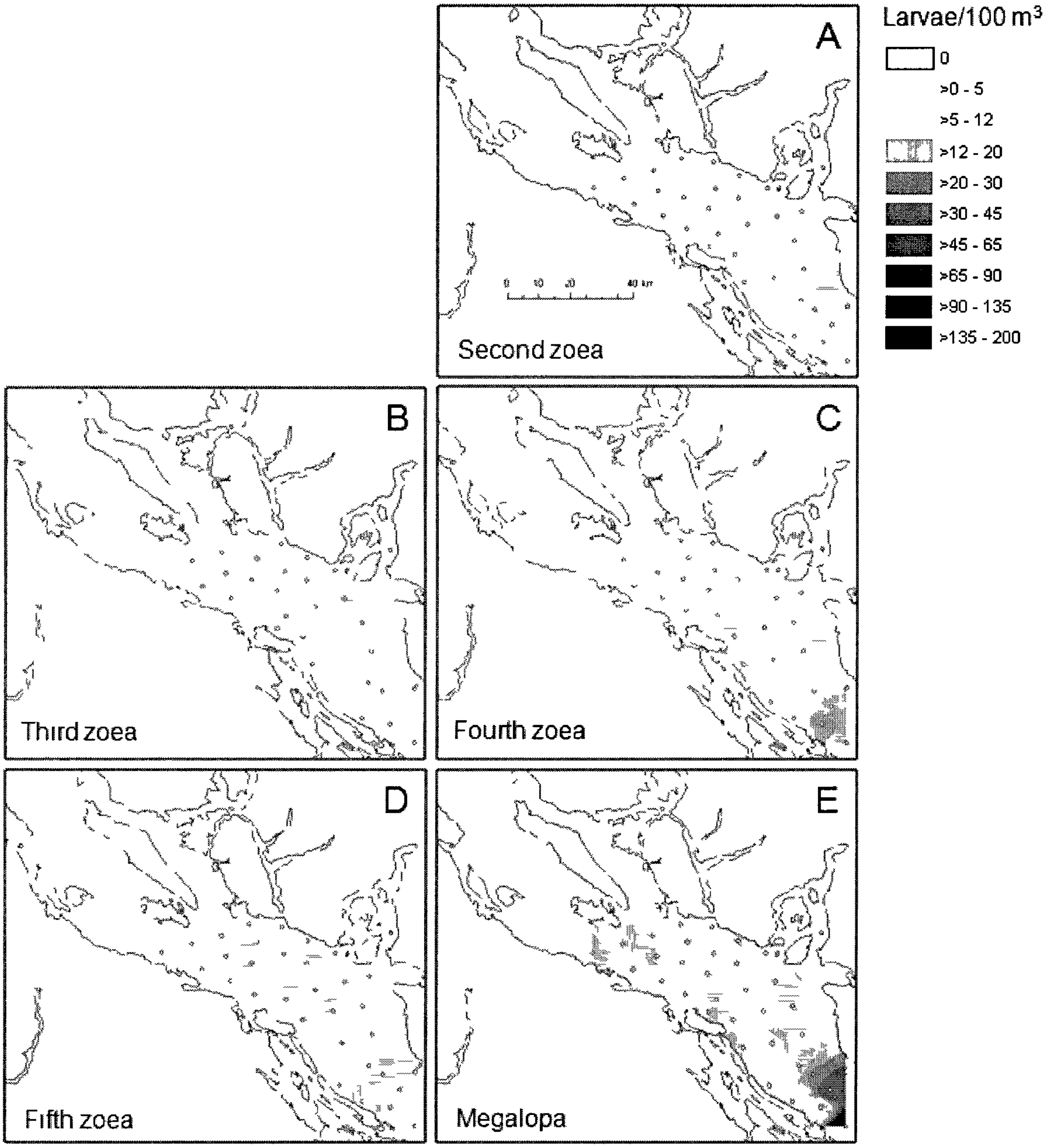

Figure 5.10. Summer horizontal distribution of *G oregonensis* larvae for larval stages for A) second zoea, B) third zoea, C) fourth zoea, D) fifth zoea, and E) megalopa.

Table 5.1. Spearman rank correlation coefficients from the spring survey between *M. magister* larval abundance and temperature, fluorescence, salinity and oxygen at depths 1 m-50 m (10 m intervals) for zoeal stages one to four (ZI-ZIV) and all stages combined (Total). * and ** represent significance at P = 0.05 and P = 0.01, respectively.

Stage	**Depth (m)**	**Temperature**	**Flourescence**	**Salinity**	**Oxygen**
Z1	1	0.194	0.145	-0.396**	-0.256*
	10	0.118	-0.006	-0.532**	-0.064
	20	0.054	-0.161	-0.073	0.062
	30	0.257*	-0.121	0.095	0.195
	40	0.281*	-0.183	0.412**	0.406*
	50	0.190	-0.232	0.451**	0.463**
ZII	1	0.238	0.087	-0.266*	-0.379**
	10	0.275*	-0.167	-0.570**	0.095
	20	0.288*	-0.087	-0.254*	0.198
	30	0.294*	0.038	-0.016	0.259*
	40	0.194	-0.077	0.285*	0.297*
	50	0.102	-0.089	0.435**	0.334**
ZIII	1	0.225	0.101	-0.150	-0.370**
	10	0.344*	-0.195	-0.502**	0.178
	20	0.395**	-0.056	-0.317*	0.246
	30	0.302*	0.108	-0.030	0.210
	40	0.155	-0.040	0.234	0.181
	50	0.085	-0.031	0.420**	0.209
ZIV	1	0.277*	0.132	-0.183	-0.391**
	10	0.379**	-0.196	-0.490**	0.181
	20	0.406**	-0.055	-0.361**	0.261
	30	0.270*	0.113	-0.084	0.214
	40	0.015	-0.009	0.124	0.122
	50	-0.043	0.007	0.305	0.159
Total	1	0.235	0.091	-0.196*	-0.373**
	10	0.307*	-0.189	-0.526**	0.151
	20	0.363**	-0.098	-0.293*	0.236
	30	0.307*	0.079	-0.026	0.236
	40	0.182	-0.053	0.256*	0.239
	50	0.188	-0.070	0.437**	0.274*

Table 5.2. Spearman rank correlation coefficients from the summer survey between *M magister* larval abundance and temperature, fluorescence, salinity and oxygen at depths 1 m-50 m (10 m intervals). ZI-ZV, zoeal stages one to five; M, megalopal stage; Total, all stages combined. * and ** represent significance at P = 0.05 and P = 0.01, respectively.

Stage	**Depth (m)**	**Temperature**	**Flourescence**	**Salinity**	**Oxygen**
ZI	1	0.364*	-0.003	-0.358*	-0.051
	10	-0.244	0.019	0.014	-0.185
	20	-0.146	0.069	0.134	-0.209
	30	-0.073	0.110	0.103	-0.182
	40	0	0.090	0.041	-0.083
	50	0.153	0.114	0.010	0.032
ZII	1	0.495*	0.088	-0.422*	0.285
	10	0.120	0.161	-0.305	-0.219
	20	-0.040	0.052	-0.011	0.142
	30	-0.012	0.070	-0.134	0.285
	40	-0.023	-0.070	-0.069	0.229
	50	-0.083	-0.047	-0.038	0.235
ZIII	1	0.468**	0.259*	-0.218	0.257
	10	0.369*	0.375*	-0.501**	0.042
	20	0.092	0.195	-0.164	0.288
	30	0.029	0.222	-0.171	0.266
	40	-0.005	0.171	-0.037	0.196
	50	0.010	0.193	-0.002	0.335
ZIV	1	0.400*	0.035	-0.221	0.411*
	10	0.227	0.164	-0.436*	-0.023
	20	-0.054	-0.001	-0.077	0.285
	30	-0.213	-0.101	0.064	0.266
	40	-0.166	-0.168	0.238	0.302
	50	-0.187	0.033	0.224	0.257
ZV	1	0.108	0.199	0.093	0.271
	10	0.500**	0.375*	-0.496**	-0.023
	20	0.327	0.277	-0.400*	0.395*
	30	0.118	0.218	-0.249	0.223
	40	-0.012	0.174	-0.195	0.121
	50	-0.113	0.189	-0.130	0.094
M	1	-0.510**	-0.204	0.109	-0.353*
	10	-0.201	-0.171	0.381*	-0.094
	20	-0.202	-0.176	0.281	-0.148
	30	-0.021	-0.164	0.172	0.105
	40	0.141	0.036	0.037	0.189
	50	0.306	0.012	0.053	0.346*
Total	1	-0.323	-0.261	0.003	-0.234
	10	-0.156	0.002	0.222	-0.144
	20	-0.081	-0.075	0.141	0.040
	30	0.060	-0.059	0.009	0.371*
	40	0.213	0.097	-0.012	0.387*
	50	0.348	0.115	0.056	0.572**

In the case of *C. productus*, during the spring the abundance of first and third zoeal stages were best correlated with temperature at 50 m and salinity at 10 m respectively. On the other hand, the abundance of the second and fourth zoeal stages were all best (positively) correlated with oxygen at 10 m deep (Table 5.3). During the summer, abundance of the first zoeal stage and megalopal stage were best (positively) correlated with fluorescence at 1 and 40 m, respectively. On the other hand, abundance of the second to fourth zoeal stages were best (positively) correlated with oxygen levels at either 40 or 50 m deep (Table 5.4).

In the case of *G. oregonensis*, during spring 2010 abundance of the first zoeal stage was best correlated with fluorescence at 50 m, whereas all the other zoeal stages were best correlated with temperature at 1 or 10 m (Table 5.5). During the summer, the highest correlations were less consistent and the abundance of each stage best correlated to different variables at different depths. However, temperature was highly correlated with the abundance of third and forth zoeal stage and the megalopal stage (Table 5.6).

In the spring survey, the highest total abundance for each species was located at station 56. In comparison to adjacent stations, station 56 was characterized by a lower temperature at 1 m and 20 m depths, a substantially higher fluorescence concentration only present in the upper 15 m, higher salinity at 20 m depth, and a slightly lower oxygen concentration at 20 m depth (Fig. 5.11).

Table 5.3. Spearman rank correlation coefficients from the spring survey between *C productus* larval abundance and temperature, fluorescence, salinity and oxygen at depths 1 m-50 m (10 m intervals) for zoeal stages one to four (ZI-ZIV) and all stages combined (Total). * and ** represent significance at P = 0.05 and P = 0.01, respectively.

Stage	Depth (m)	Temperature	Flourescence	Salinity	Oxygen
Z1	1	-0.163	0.099	0.244	0.287*
	10	-0.090	-0.014	0.170	0.163
	20	0.076	-0.066	0.072	0.022
	30	0.190	-0.085	0.020	0.099
	40	0.333**	-0.007	-0.083	0.102
	50	0.376**	0.097	-0.191	0.007
ZII	1	0.191	0.023	-0.095	0.043
	10	0.342*	-0.212	-0.376**	0.435**
	20	0.402**	0.049	-0.286*	0.287*
	30	0.250	0.070	-0.093	0.323*
	40	0.231	0.071	0.059	0.293*
	50	0.227	0.072	0.065	0.259*
ZIII	1	0.291*	0.001	-0.160	-0.187
	10	0.411**	-0.287*	-0.488**	0.314*
	20	0.351**	0.022	-0.277*	0.240
	30	0.230	0.110	-0.052	-0.275*
	40	0.114	0.008	0.150	0.225
	50	0.074	-0.045	0.258*	0.223
ZIV	1	0.103	0.055	-0.150	0.069
	10	0.253*	0.053	-0.258*	0.323*
	20	0.091	0.166	-0.127	0.025
	30	-0.074	0.073	-0.060	-0.001
	40	-0.109	0.169	-0.051	-0.141
	50	-0.064	0.053	0.021	-0.142
Total	1	0.088	0.110	0.036	0.128
	10	0.213	-0.156	-0.198	0.350**
	20	0.310*	-0.014	-0.161	0.185
	30	0.287*	0.008	-0.028	0.233
	40	0.316*	0.040	0.042	0.220
	50	0.322*	0.073	-0.003	0.183

Table 5.4. Spearman rank correlation coefficients from the summer survey between *C. productus* larval abundance and temperature, fluorescence, salinity and oxygen at depths 1 m-50 m (10 m intervals) for zoeal stages one to four (ZI-ZIV) and all stages combined (Total). * and ** represent significance at P = 0.05 and P = 0.01, respectively.

Stage	**Depth (m)**	**Temperature**	**Flourescence**	**Salinity**	**Oxygen**
Z1	1	0.200	0.345*	-0.217	-0.207
	10	-0.197	-0.162	0.031	-0.227
	20	-0.054	0.006	0.045	-0.003
	30	-0.115	-0.174	0.058	0.173
	40	-0.074	-0.242	0.153	0.161
	50	-0.011	-0.228	0.076	0.207
ZII	1	0.191	0.139	-0.212	0.105
	10	0.007	0.057	-0.133	0.007
	20	0.041	0.198	-0.124	0.222
	30	-0.204	-0.044	-0.042	0.251
	40	-0.097	-0.082	0.088	0.277
	50	-0.075	-0.092	0.072	0.342*
ZIII	1	0.302	-0.095	-0.295	0.052
	10	-0.208	0.021	0.090	-0.120
	20	-0.119	0.095	0.083	0.025
	30	-0.182	-0.066	0.030	0.371*
	40	0.033	-0.126	0.209	0.424*
	50	-0.021	-0.097	0.169	0.406*
ZIV	1	0.221	-0.024	-0.170	0.033
	10	-0.087	0.103	-0.020	-0.083
	20	-0.101	0.059	0.099	0.093
	30	-0.133	-0.092	0.072	0.417*
	40	0.089	-0.155	0.181	0.503**
	50	0.082	-0.017	0.161	0.512**
ZV	1	0.282	-0.068	-0.255	0.094
	10	-0.104	0.003	0.002	-0.003
	20	-0.029	-0.039	0.013	0.124
	30	-0.143	-0.183	0.013	0.461**
	40	0.014	-0.248	0.231	0.480**
	50	-0.077	-0.188	0.165	0.417*
M	1	-0.250	-0.101	0.290	-0.092
	10	0.360*	0.411*	-0.096	0.330
	20	0.325	0.295	-0.232	0.109
	30	0.372*	0.396*	-0.183	0.167
	40	0.344*	0.463*	-0.282	-0.069
	50	0.382*	0.390*	-0.257	0.141
Total	1	0.205	-0.074	-0.090	0.087
	10	-0.030	0.226	0.038	0.050
	20	0.162	0.277	-0.095	0.201
	30	0.139	0.121	-0.149	0.520**
	40	0.308	0.034	-0.029	0.428*
	50	0.244	0.082	-0.106	0.351*

Table 5 5. Spearman rank correlation coefficients from the spring survey between *G oregonensis* larval abundance and temperature, fluorescence, salinity and oxygen at depths 1 m-50 m (10 m intervals) for zoeal stages one to four (ZI-ZIV) and all stages combined (Total) * and ** represent significance at P = 0 05 and P = 0.01, respectively

Stage	**Depth (m)**	**Temperature**	**Flourescence**	**Salinity**	**Oxygen**
Z1	1	-0.251	-0.058	0.261*	0.086
	10	-0.208	-0.064	0.112	-0.065
	20	-0.013	0.070	0 010	0.020
	30	-0.031	0.184	-0.095	0.086
	40	-0.052	0.164	-0.133	0.131
	50	-0.099	0.297*	-0.113	-0.013
ZII	1	0 135	0 134	-0 100	0 045
	10	0 340**	0 128	-0 301*	0 322*
	20	0 271*	0 187	-0 260*	0 142
	30	0 048	0 113	-0 073	0 036
	40	-0 097	-0 040	-0 009	0 024
	50	-0 037	0 028	-0 040	-0 071
ZIII	1	0 268*	0.086	-0.068	-0 089
	10	0 454**	-0 154	-0.350**	0 289*
	20	0.370**	0.035	-0.222	0.073
	30	0 115	0.052	0.083	-0 068
	40	0 058	0.122	0.117	-0.039
	50	0 030	-0 052	0.139	0.035
ZIV	1	0 312*	-0 005	-0 275*	-0 295*
	10	0 200	-0 250	-0 281*	0 041
	20	0 086	-0 186	0 063	0 006
	30	0 196	-0 020	0 050	0 029
	40	0 069	-0 111	0 167	0
	50	0 004	-0 262*	0 287*	0 087
Total	1	0.265*	0.108	-0.032	-0.134
	10	0.473**	-0.118	-0 336**	0.310*
	20	0.411**	0.109	-0.268*	0.151
	30	0.160	0.158	-0.035	0.020
	40	0.031	0.163	0.031	-0.013
	50	0	0.022	0.121	-0 065

Table 5.6. Spearman rank correlation coefficients from the summer survey between *G. oregonensis* larval abundance and temperature, fluorescence, salinity and oxygen at depths 1 m-50 m (10 m intervals) for zoeal stages one to four (ZI-ZIV) and all stages combined (Total). * and ** represent significance at P = 0.05 and P = 0.01, respectively.

Stage	Depth (m)	Temperature	Flourescence	Salinity	Oxygen
ZII	1	-0.062	-0.127	0.013	0.120
	10	-0.220	-0.270	0.220	-0.56
	20	-0.191	-0.257	0.139	-0.052
	30	-0.370*	-0.451**	0.319	0.029
	40	-0.192	-0.329	0.359*	0.203
	50	0.014	-0.157	0.408*	0.221
ZIII	1	-0.416*	-0.188	0.365*	-0.290
	10	-0.265	-0.037	0.385*	-0.139
	20	-0.280	-0.060	0.231	-0.119
	30	-0.162	-0.027	0.121	0.042
	40	0.065	0.033	0.150	0.261
	50	0.147	0.185	0.243	0.312
ZIV	1	-0.451**	-0.307	0.257	-0.346*
	10	0.418*	-0.088	0.526**	-0.236
	20	-0.310	0.036	0.410*	-0.275
	30	-0.157	-0.005	0.187	0.092
	40	0.154	0.151	0.025	0.321
	50	0.182	0.171	0.099	0.221
ZV	1	-0.298	-0.145	0.277	-0.088
	10	-0.122	0.068	0.267	-0.008
	20	0.018	0.128	0.067	0.094
	30	0.106	0.042	-0.037	0.446**
	40	0.248	0.059	-0.014	0.469**
	50	0.174	0.166	0.004	0.240
M	1	-0.462**	-0.112	0.208	-0.338
	10	-0.156	0.050	0.268	-0.250
	20	-0.084	-0.023	0.141	-0.007
	30	0.099	-0.020	0.049	0.410*
	40	0.271	0.061	-0.025	0.334
	50	0.398*	0.202	0.052	0.502**
Total	1	-0.512**	-0.174	0.288	-0.386*
	10	-0.172	0.056	0.316	-0.209
	20	-0.063	0.040	0.138	0.011
	30	0.126	-0.011	-0.007	-0.459**
	40	0.323	0.049	-0.080	0.398*
	50	0.408*	0.184	0	0.476**

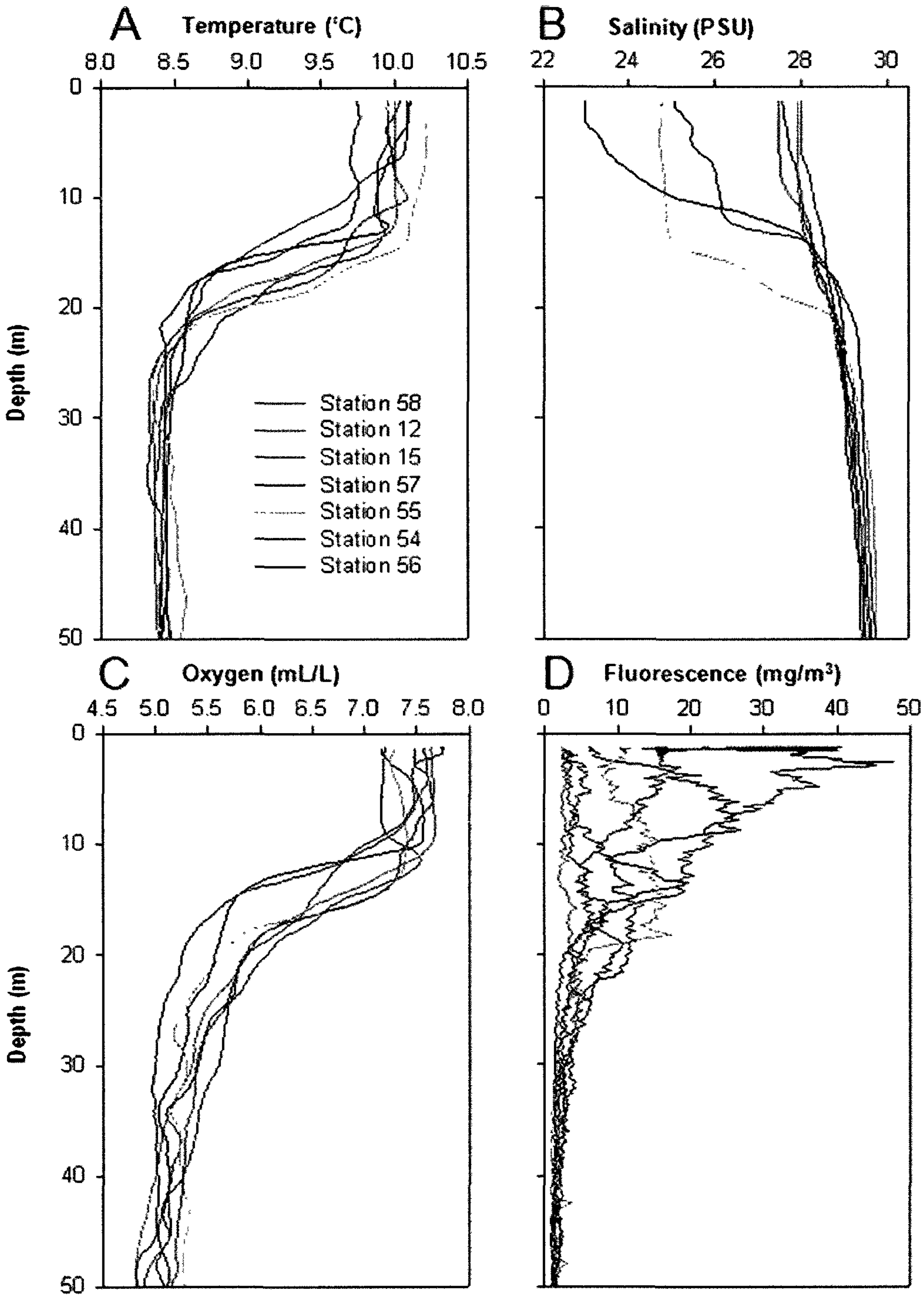

Figure 5.11. Vertical profiles of A) temperature B) salinity C) oxygen and D) fluorescence at station 56 (Fig. 5.1A) and surrounding stations during the spring survey.

5.5. Discussion

5.5.1. Larval abundance

In both surveys, larvae of *M. magister* were the most abundant, followed by *C. productus* and *G. oregonensis*. Larval abundance may be influenced by several factors, including the fecundity and number of females, the rate of fertilization success, and the rate of larval mortality. It has been demonstrated that *M. magister* and *C. productus* have a much higher fecundity than *G. oregonensis* (Hines, 1991), and the abundance of *M. magister* in the SoG's southern and central regions is indeed high enough to sustain commercial fishing (Fisheries and Oceans, 2010a). Apart from a single study that quantified the sex ratio and abundance of *M. magister* in the SoG's most southern region (Palsson et al., 2003), there is virtually no information on additonal factors that may influence larval abundance.

The overall larval abundances of each species were substantially lower in the summer compared to the spring survey. This can be attributed to the following three factors: a decreasing number of larvae being released, an increasing level of cumulative mortality, and an early settlement of megalopae prior to sampling in late June (peak settlement typically occurs in July and August [Orensanz and Galluchi, 1988]).

The relative stage-specific abundances of *M. magister* and *G. oregonensis* were almost identical, whereas earlier stages were far more abundant for *C. productus*. This is consistent with the reproductive timing for each species in the San Juan Islands. Peak hatching has been observed in February for *M. magister* (Armstrong et al., 1986) and *G. oregonensis* (Knudsen, 1964), but appears to occur in late March and early April for *C. productus* (Knudsen, 1964). Moreover, synchrony in the progression of *M. magister* and

G. oregonensis larval stages has been observed in British Columbia and Alaska (Jamieson and Phillips, 1988; Park and Shirley, 2005; Fisher, 2006), which is consistent with their similar zoeal durations under laboratory conditions (Sulkin and McKeen, 1994). The higher megalopal abundance of *M. magister* and *G. oregonensis* was also consistent with reports of the occurrence of this stage in the Salish Sea between May and August (Orensenz and Galluchi, 1988), and peak abundance (of *M. magister*) between July and August (Jamieson and Phillips, 1993).

In the summer, the abundance of late zoeae was lower than expected. Lough (1976) had also noted that late zoeal stages of *M. magister* "disappear", without apparently affecting the abundance of the impending megalopal stage. As proposed in Lough's (1976) study, late zoeae may have been undersampled due to either an exceptionally deep vertical distribution, transport away from the study area, or increased dispersion across geographic space. Unfortunately, information on the vertical distribution and migratory patterns of crab larvae in the SoG is scarce. In Alaska, high abundance of the three cancrid species' zoeae has been observed near the surface at night or near twilight (Park and Shirley, 2005). Similarly, off the California coast cancrid zoeae are most abundant in the upper 30 to 40 m of the water column and entirely absent below 80 m regardless of the time of day (Shanks, 1986a; Wing et al., 1998). Based on these observations, it appears that the maximum sampling depth of 50 m covered the depth range of zoeal vertical migrations of these species. However, it should be noted that vertical distributions may vary in different environmental conditions (Vikebo et al., 2007).

High abundances of *M. magister* megalopae have been frequently observed in the neuston at night but not during the day (Jamieson et al., 1989; Hobbs and Botsford, 1992; Jamieson and Phillips, 1988; 1993). Off the coast of Vancouver Island, *M. magister* megalopae have been found to reside within the upper 30 m of the water column regardless of the time of day (Jamieson et al., 1989; Jamieson and Phillips, 1993). Jamieson and Phillips (1993) also noted that in deep (> 200 m) regions of the central SoG, megalopae were more abundant below 150 m during daylight and may migrate to the surface from this depth on a diel basis. Such a migratory pattern could affect the interpretation abundance and distribution of megalopae taken from the upper water column. Observations on the vertical distribution of megalopae of other cancrid species are scarce. *Glebocarcinus oregonensis* megalopae also appear to be most abundant at the surface at night (Jamieson and Phillips, 1988) when "surface swarms" have been observed (Miner et al., 2000).

5.5.2. Larval distributions

The shape and structure of horizontal larval distributions can be influenced by several factors, including the timing and location of larval release (Natunewicz and Epifanio, 2001), larval transport (Wing et al., 1998), larval behaviour (Chiswell and Booth, 1999), and spatial variation in mortality (Frank et al., 1993). The sampling resolution can also dictate and bias the shape of the observed patterns (Fortin and Dale, 2005). For example, at a sampling resolution of approximately 8 km, patches that may have occurred at scales of hundreds of meters to a few kilometers (e.g. Natunewicz and Epifanio, 2001) may be missed entirely or simply increase variability in spatial structure.

Larvae were subjected to different environmental conditions in late April and June, which may explain, at least in part, the differences between larval distributions. Therefore, they are discussed separately.

Spring Survey (April 24-27, 2010)

The distribution of the first zoeal stage was noticeably different among species, and appeared to reflect what is known about the distribution of adults. For example, *M. magister* crabs are found throughout the SoG, but are most abundant in the southern-most region, between Vancouver, British Columbia and Anacortes, Washington (Jamieson and Phillips, 1993). First zoeae were absent from the northwest region, where adults may be less abundant due to high temperatures that have been demonstrated to inhibit the development of juveniles (Sulkin et al, 1996). *Cancer productus* and *G. oregonensis* crabs are probably less restricted to substrate types than *M. magister*, which is consistent with the more widespread distribution of their first zoeae. For each species, the distribution of subsequent larval stages generally matched that of the preceding stage. This suggests that larvae were not rapidly transported over their stage duration estimated to be approximately 3 to 4 weeks (Sulkin and McKeen, 1996). Instead, it appeared that larvae were largely retained near their release points. Larval "spreading" that did occur from one stage to the next may be caused by larval transport or undetected release events that had occurred during peak hatch, months before this survey was conducted.

In the SoG's central and northern regions, the highest total abundance (all stages combined) of each species was largely restricted to the eastern side, along the mainland coast and west coast of Texada and Lasqueti Islands. This suggests that nearshore retention and/or alongshore transport were more prominent than cross-strait transport in these areas. Previous studies have identified along-shore surface circulation in the SoG's central region by tracking passive surface drifters (see reviews by Waldichuck, 1957; Thomson, 1981). In the present study, the distribution of salinity was consistent with these reports (Fig. A7, Appendix 1), as it suggests that some Fraser River outflow was transported north along the mainland coast. However, it should also be noted that several small streams and creeks empty into the central SoG from the mainland that may have produced low salinities in their immediate area. The possibility of westerly winds transporting larvae east and subsequently causing nearshore retention was not supported by wind data from the Halibut Bank weather bouy in the central SoG (not shown).

The strong relationship between the larval abundance of *M. magister* and salinity at 10 m could indicate potential for transport of larvae associated with the Fraser River plume. Indeed, an along-shore surface and subsurface current could have transported *M. magister* zoeae released in the southern region into the central and northern regions of the SoG. *Metacarcinus magister*, *C. productus* and *G. oregonensis* larvae were also positively correlated with temperature at 1 to 20 m (except for the first zoea), indicating that larvae were more abundant in thermally stratified waters. Furthermore, all zoeal stages of *M. magister* and *C. productus* (and the second and third zoeae of *G. oregonensis*) were also significantly positively correlated with oxygen at either 1 or 10 m. Although it is unclear why larvae were most prevalent in waters characterized by elevated temperature and oxygen, these conditions could be beneficial for larval growth. Higher temperatures are likely to increase the rate of growth, and more stratified conditions are often associated with high concentrations of phytoplankton (see discussion in Masson and Peña, 2009) which larvae may utilize as food.

Widespread larval abundance of each species in the SoG's southern region could have been caused by strong tidal currents, mesoscale rotary currents (Tabata, 1972; Thomson, 1981; Stacey et al., 1987), or the movement of the fraser river plume across the SoG. If the rotary current described by Stacey et al. (1987) is persistent throughout the spring and summer, it could also retain larvae within the SoG's southern region. High larval abundances were also detected at a single station (56), located off the mainland coast in SoG's central region. Larvae may have been concentrated there by a small-scale (meters to kilometres) physical convergence mechanism. Potential mechanisms include an internal wave slick (Shanks and Wright, 1987), an eddy (Wolanksi and Hamner, 1988) and/or a frontal formation (Shanks et al., 2000). In the SoG, surface manifestations resembling internal waves appear to occur most frequently in the southern region between the Fraser River delta and Vancouver Island; however, they have been observed as far north as station 58 (Fig. 5.1A) (Tabata, 1972). Station 56 was characterized by slightly different water properties than its neighbouring stations, but they did not provide compelling evidence for the previously proposed convergence mechanisms, such as a variability in the depth of the thermocline from an internal wave (Criales et al., 2007) or upwelling from an eddie (Bakun, 2006). Small scale hydrographic anomalies that may explain larval abundance at this station may not have been detected as water properties were measured near the starting point of plankton tows that were approximately 0.5 km in length.

Summer Survey (June 27-29)

Freshwater input from the Fraser River is a primary factor influencing circulation within the SoG's southern and central regions, and its volume is considerably higher in June than April (Thomson, 1981). As a consequence, a much larger spatial extent of low salinity waters emanating from the Fraser River was observed in June (Fig. A11, Appendix 1). Although the size and shape of the Fraser River plume changed between surveys, the distribution of salinity at 1 m depth still showed an overall pattern of northward surface circulation along the SoG's eastern side. Significant correlations between the abundance of *M. magister* larvae and salinity and temperature at 1 or 10 m suggest that the dynamics of the Fraser River plume influenced the larval horizontal distribution of this species.

As in the spring survey, the distribution of zoeae was usually similar to the subsequent stage, and this continued into the megalopal stage for *G. oregonensis*, but not for *M. magister* and *C. productus*. For the latter two species, megalopae exhibited patterns of distribution essentially different from those of zoeae, and their correlations with environmental variables changed as well. In the case of *M. magister*, the relationship between larval abundance and both salinity and temperature was opposite for zoeae compared to megalopae. This contrast between zoeae and megalopae was not surprising considering that zoeae are much weaker swimmers than megalopae (Chia et al., 1984) and that they respond differently to environmental stimuli, such as light and gravity (Sulkin, 1973; Forward and Costlow, 1974; Sulkin 1975; Epelbaum et al., 2007). Therefore, behavioural differences between the zoeal and megalopal stage may have contributed to differences in their spatial patterns of abundance.

Cancrid juveniles require shallow coastal habitat when settlement occurs in the summer months (Orensenz and Galluchi, 1988; Jamieson et al., 1989; Eggleston and Armstrong, 1995). Accordingly, Jamieson et al. (1989) found that late-stage *M. magister* megalopae were closely associated with the shoreline, which was consistent with the distributional pattern of megalopae in the present study. In addition, *Cancer productus* megalopae were not as abundant in the SoG's southern region as *M. magister* and *G. oregonensis*. The distribution of *C. productus* has also contrasted with the latter two species off the west coast of Vancouver Island (Jamieson et al., 1989). This may have been caused by unique behavioural characteristics of *C. productus* megalopae or the difference in timing of larval release between species. Regardless, localized high densities of *C. productus* megalopae overlapped with those of *M. magister*, *G. oregonensis*, and flourescence. In these locales, the megalopae may have been taking advantage of large patches of phytoplankton, either as direct consumers or as consumers of grazing zooplankton. Information on the natural diet of decapod larvae is scarce, although they are known to ingest both phytoplankton and zooplankton under laboratory conditions (e.g. Schwamborn et al., 2006).

Incidentally, *M. magister* megalopae have been observed below 150 m during daylight in the deep central region of the SoG and may migrate to the surface from this depth at night (Jamieson and Phillips, 1993). Although many stations with high abundance were sampled at night, several locations were also sampled during the day. Even so, the potential for large amplitude vertical migrations must not be disregarded when interpreting the megalopal distributions.

Although the presence of elevated larval abundance at station 56 (Fig. 5.1A) was not as obvious as in the spring survey, this did occur for both *M. magister* and *G. oregonensis*. As in the spring, station 56 was characterized by a surface temperature lower than its immediate neighbours and was located near a frontal boundary (not shown). If the same mechanism was acting to concentrate larvae at this location in both surveys, the convergent flow must be persistent or occur at a high frequency. Unfortunately, this does not rule out other convergence mechanisms such as internal wave slicks, eddies, or fronts. However, because this station was observed near a strong density gradient in both surveys, larval concentration associated to a frontal formation is a likely explanation.

In summary, as observed in other areas of the Northeast Pacfic, the stage-specific larval abundance of *M. magister* and *G. oregonensis* were similar, but both differed from that of *C. productus*. In the spring survey, the analysis of larval distributions and their association with environmental variables suggested that the distribution of zoeae was influenced by the location of larval release and hydrographic conditions, but also ontogentic differences in larval behaviour, especially between the zoeal and megalopal phases.

Moreover, spatial patterns of larval abundance did not appear to change substantially from stage to stage, suggesting that larvae are not rapidly transported within this system. The distribution of larvae, temperature, and salinity indicated the potential for along-shore surface circulation near the mainland coast to be an important mechanism for larval transport in this system. Similarly, tidal currents and rotary circulation in the southern region may transport larvae across the SoG and retain larvae within the southern region. In both surveys, the larval abundance of *M. magister* was strongly correlated with low salinity and high temperature signals that emanated from the Fraser River. This suggests that the transport of fresh water input from the Fraser River plume is important in shaping the distribution of these larvae in the SoG's southern and central regions.

Based on the results obtained in the present study, future research should consider a detailed description of the vertical distribution of cancrid larvae in relation to surface and subsurface currents. A precise dissection of the vertical distribution of larvae would contribute enormously to the understanding of larval transport in the SoG and the interpretation of larval abundance patterns from plankton tows. In conjunction with empirical observations, the study of dispersal patterns of "virtual larvae" from a biophysical model could be extremely valuable in determining dispersal pathways that exist in the SoG (c.f. Metaxas and Saunders, 2009). A combination of both empirical evidence and theoretical models would provide essential information that could be used to forecast the influence of oceanographic conditions on larval movements that would ultimately contribute the management of the SoG's Dungeness crab fishery.

CHAPTER 6

Discussion

The information gathered in this thesis provides the first analysis of spatial and temporal variability of decapod larvae in the Strait of Georiga, British Columbia (SoG hereafter). This information was used to develop hypotheses regarding the effects of environmental conditions on the timing of larval release, the rate of larval development, and the nature of larval transport. Ultimately, it is expected that this research will contribute to a better understanding of patterns of larval abundance and its governing processes that are fundamentally important to the distribution and abundance of adult decapods (Roughgarden et al., 1988, Cushing, 1990; Govoni, 2005).

This research also provides the basis for more applied studies regarding larval dispersal, management of the crab fishery, and proper implementation of conservation sites such as Marine Protected Areas (MPAs) in the SoG (Sale and Kritzer, 2003). Particular emphasis was placed on the Dungeness crab, *Metacarcinus magister*, a well-studied and commercially exploited species in British Columbia (Fisheries and Oceans, 2010a) that also plays an important ecological role as a benthic mobile predator (Dudas et al., 2005).

Field studies are heavily dependent on reliable tools for larval identification (Pardo et al, 2009). In Chapter 3, a morphological description of diagnostic characteristics facilitated identification of four commonly encountered cancrid zoeae in the region. *Glebocarcinus oregonensis* zoeae were found to differ from *C. productus, M. gracilis*, and *M. magister* by having much shorter and acutely angled lateral exospines on the telson and much longer posterolateral abdominal spines projecting from the abdominal somites. The results of that chapter also indicated that other morphological features previously used to identify *G. oregonensis* and *C. productus* (e.g. Lough, 1975) could be misleading, and therefore, future surveys on this and related species should abandon the use of these features. These findings may become particularly useful with the arrival of new species (invaders or not) whose larvae have not been properly described or whose descriptions overlap to some extent with the description of resident cancrids.

For instance, two additional cancrid species of the genus *Romaleon*, commonly encountered on the west coast of Vancouver Island (Jensen, 1995; Hart, 1982), have been recently observed within the Juan de Fuca Strait (but not the SoG) (Lamb and Hanby, 2005; W. Duguid, Pers. Comm.). The morphology of *Romaleon antennarius* is almost identical to that of *M. gracilis* (Rice and Tsukimura, 2009) and no description is available for the larval stages of *R. branneri*. Although, the adult phase of these species has not been observed within the SoG, there is potential for *Romaleon* larvae to enter the SoG from the Juan de Fuca basin. Further research should focus, on the comparative description of laboratory reared larvae of each cancrid species, in order to provide an identification resource for laboratory and field studies in this area.

Patterns of species and stage-specific abundance from surveys conducted in late April in 2009 and 2010 were, for the most part, consistent with the reproductive potential and timing for most species. These observations contribute substantially to life history knowledge that is scarce for multiple species, most noteably *Munida quadispina*, a dominant benthic invertebrate in deep water habitats (Burd and Brinkhurst, 1984).

Results also suggest that elevated sea surface temperatures in late winter and early spring may increase the rate of embroyonic or larval development. Large differences in larval abundance between 2009 and 2010 indicated either heavy mortality in 2009 or an increase in the reproductive output in 2010. This may cause considerable variability in the year class strength for many species and consequently affect the *M. magister* fishery. An assessment of the abundance of benthic crab stages in subsequent seasons in the SoG could be used to determine how large fluctuations in larval abundance impact juvenile or adult abundance.

Spatial patterns of total larval abundance and diversity were associated with different environmental variables. However, because these relationships were not consistent between years, and several correlation coefficients were rather modest; therefore, individual environmental variables are not necessarily useful predictors for the horizontal distribution of total larval crab abundance and diversity. An analysis of the species-specific larval distributions would aid in the interpretation of the patterns of total abundance and diversity and their relationship with environmental conditions. Future studies should also determine the relationship between larval abundance and environmental conditions using vertically stratified samples to confirm the relationships detected in this study.

In the spring and summer seasons of 2010, the species-specific larval abundances of *C. productus*, *G. oregonensis*, and *M. magister* were consistent with information available on the reproductive output of each species (Hines, 1991). Stage-specific abundance measures indicated that *C. productus* larvae were released later in the year than *G. oregonensis* and *M. magister*, which was consistent with observations of reproductive timing in the Salish Sea (Knusden, 1964) and the stage-specific abundance of each species reported at higher latitudes (Park and Shirley, 2005; Fisher, 2006). However, the abundance of late zoeal stages for each species was unexpectedly low, which may have been caused by ontogenetic changes in their vertical distribution (c.f Lough, 1976). The distribution of the first zoeal stage most likely reflected the distribution of reproductive females, whereas the distribution of megalopae may have indicated potential settlement locations. The distribution of subsequent stages was similar to that of the preceding stages, suggesting that these larvae are not rapidly transported in this system.

During the spring, distributions of larvae and environmental variables indicated potential for nearshore retention and/or alongshore transport of larvae along the central SoG's eastern margin and cross-strait transport in the southern region. Larval distributions appeared to be most associated with either temperature or salinity in the upper water column, which are strongly regulated by the dynamics of Fraser River outflow (Thomson, 1981). In the summer, behavioural differences between zoeae and megalopae of *M. magister* and *C. productus* may explain the strong contrast in their distribution and relationship with environmental variables.

Future high resolution plankton surveys would be helpful in determining the variability in species-specific larval distributions and their association with environmental variables at larger temporal scales. Although time constraints may severely limit the resolution of these surveys, samples should be collected from bottom to surface using oblique plankton tows with a mesh size of no greater than 500 μm to ensure that all species and stages are equally represented in samples. To better understand larval transport in the SoG, further research is required to document the stage-specific vertical distribution of several species and describe baroclinic circulation patterns. Knowledge of the vertical distribution of larvae would also aid in the interpretation of observed horizontal patterns of abundance. Finally, a morphological description of the larval stages of several species present or likely present in the SoG is required. Currently, a lack of identification tools is a major limitation in the interpretation of field results. For example, in the present study correlation coefficients between total larval abundance and environmental variables were much stronger in Chapter 5, when analyzed for certain species and their stages, than in Chapter 4, when analyzed for all species and stages combined.

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8.1. Appendix 1. Environmental variables: 2009 and 2010 surveys

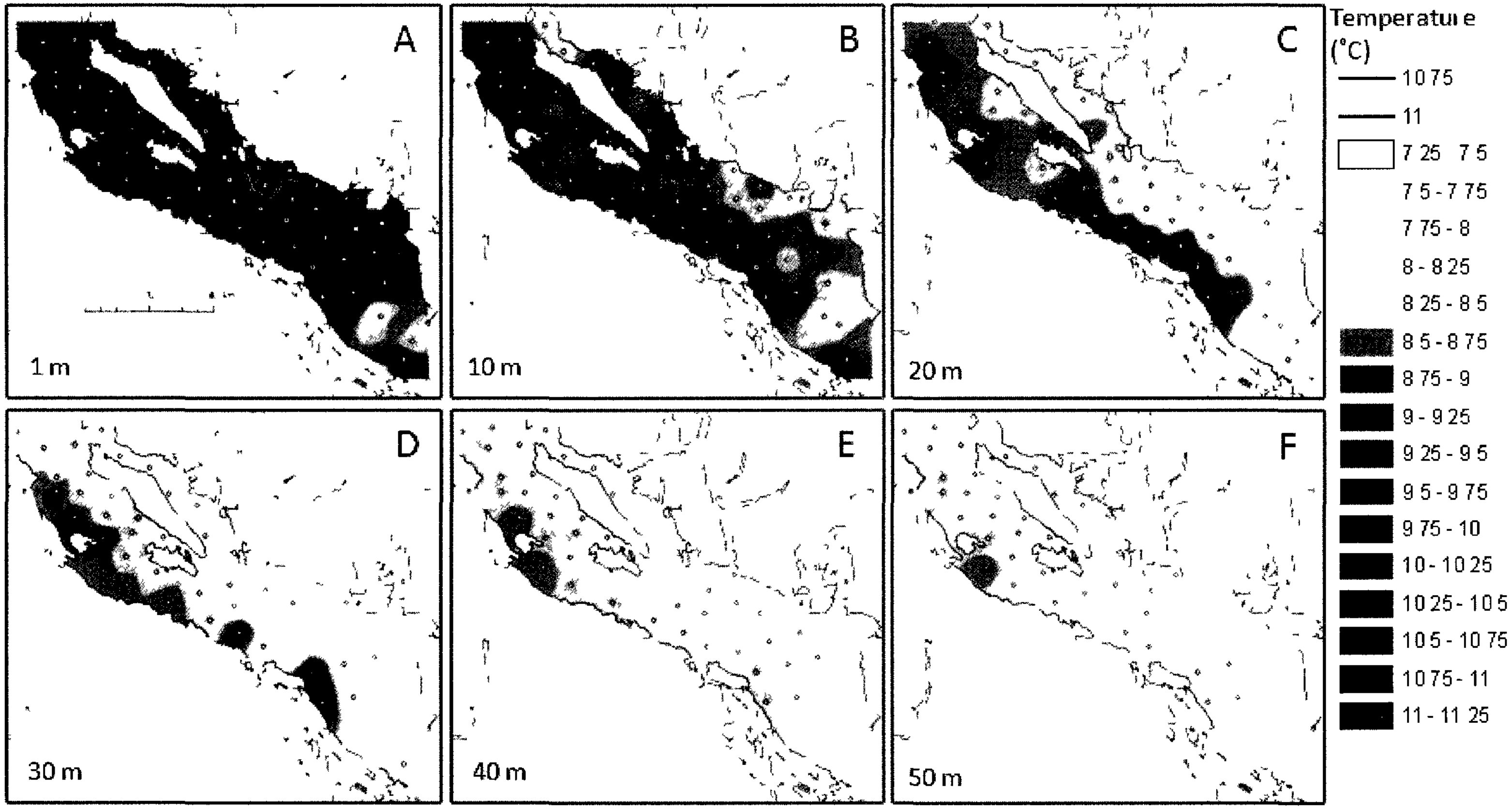

Figure A1 April 2009 horizontal distribution of temperature for depths A) 1 m B) 10 m C) 20 m D) 30 m E) 40 m F) 50 m. Contour lines were used to distinguish the last two classification intervals

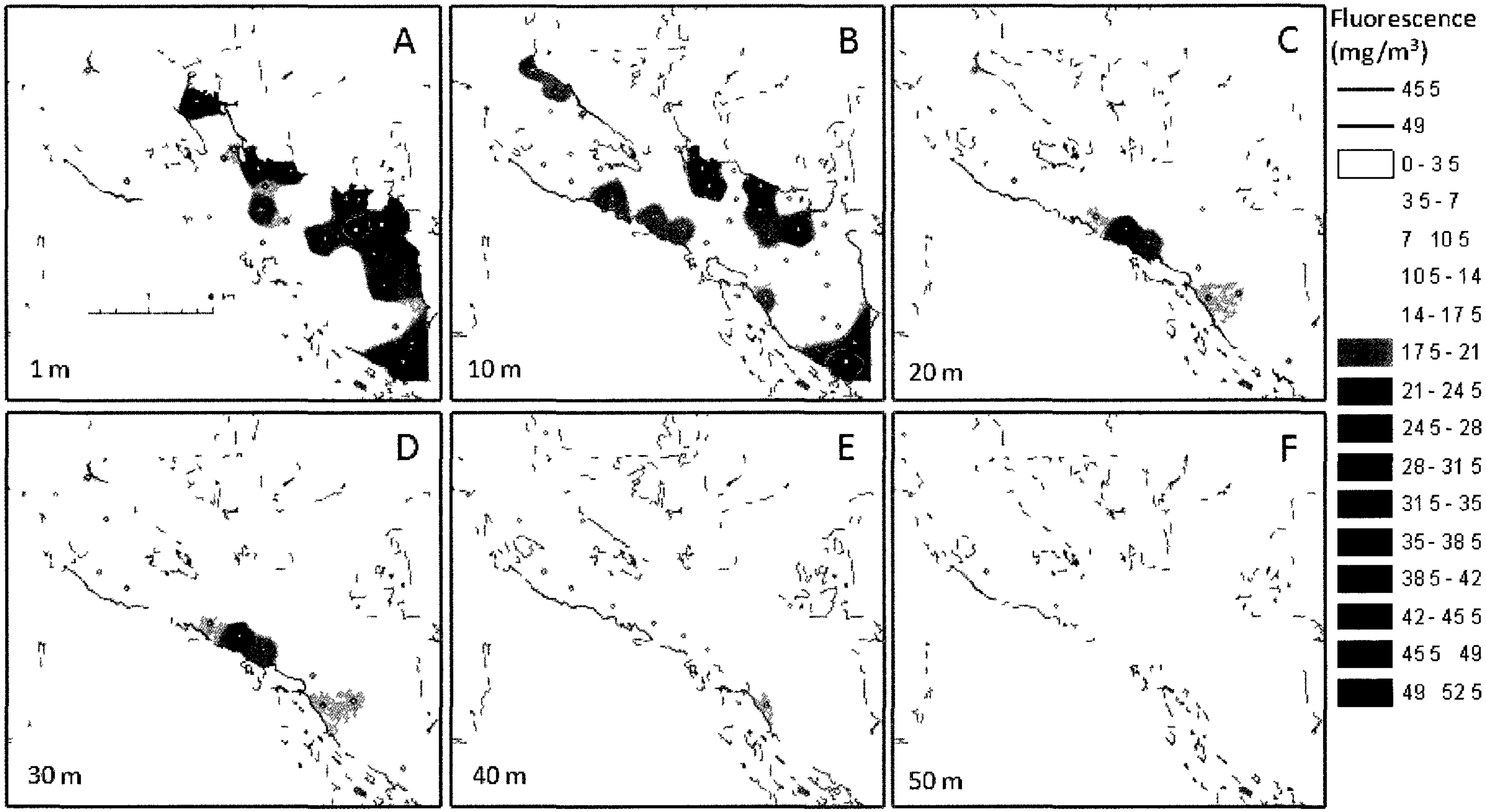

Figure A2 April 2009 horizontal distribution of fluorescence for depths A) 1 m B) 10 m C) 20 m D) 30 m E) 40 m F) 50 m Contour lines were used to distinguish the last two classification intervals

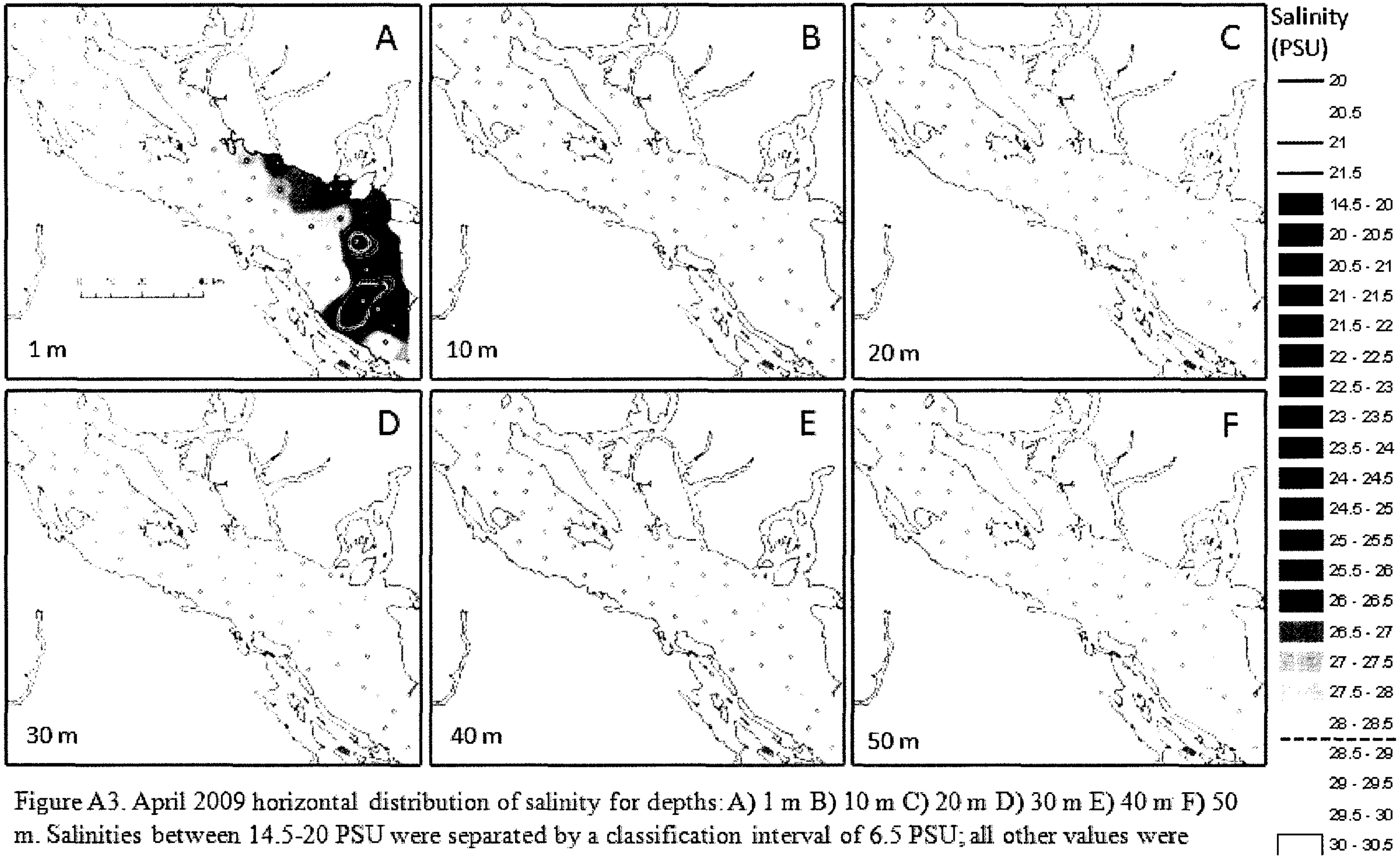

Figure A3. April 2009 horizontal distribution of salinity for depths: A) 1 m B) 10 m C) 20 m D) 30 m E) 40 m F) 50 m. Salinities between 14.5-20 PSU were separated by a classification interval of 6.5 PSU; all other values were separated by 0.5 PSU. The colour ramp was reversed from all other maps and contour lines were used to distinguish the four five classification intervals. Contours after 1 m depth are marked below the horizontal stippled line.

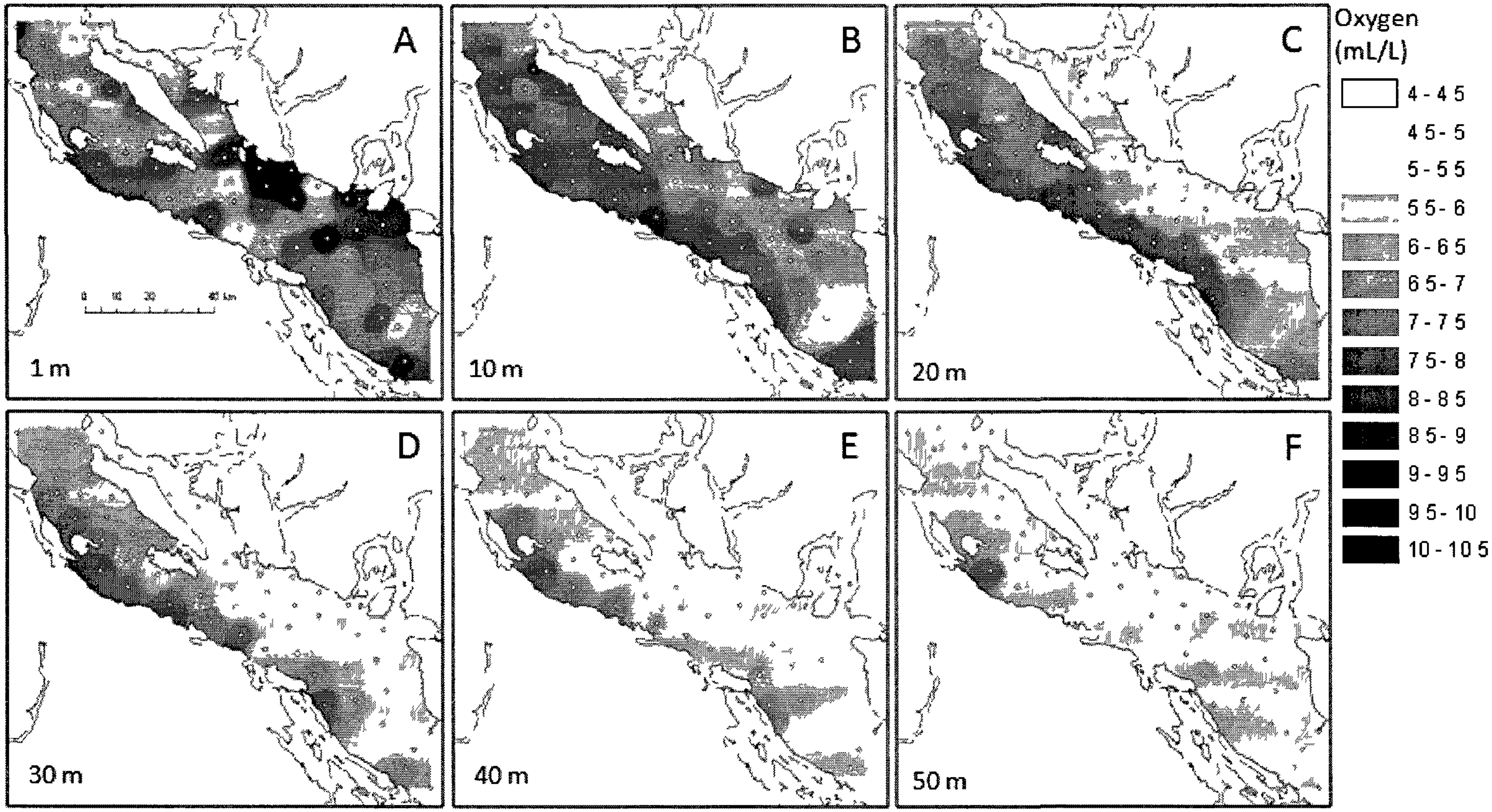

Figure A4 April 2009 horizontal distribution of oxygen for depths A) 1 m B) 10 m C) 20 m D) 30 m E) 40 m F) 50 m Contour lines were used to distinguish the last two classification intervals

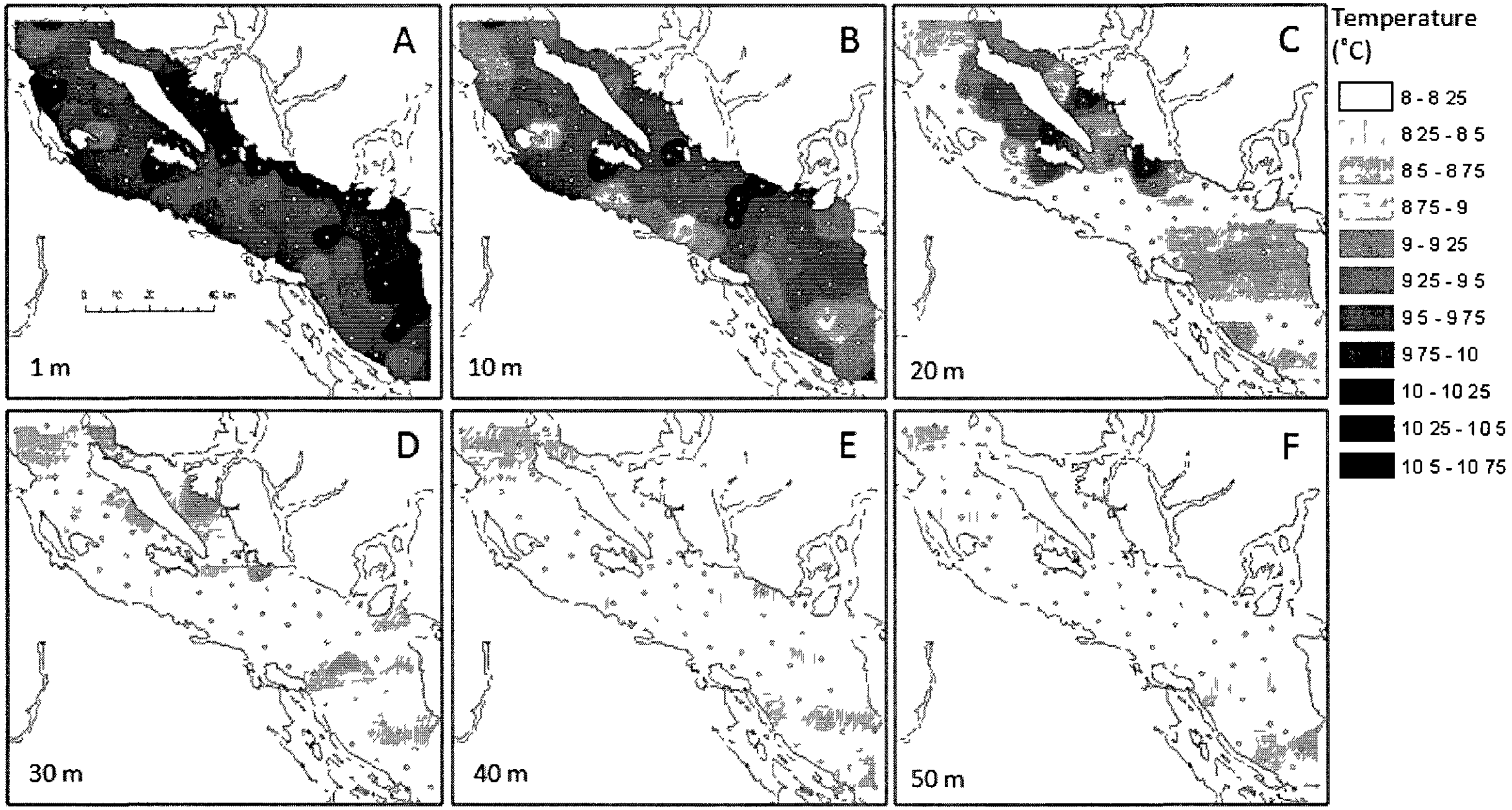

Figure A5: April 2010 horizontal distribution of temperature for depths: A) 1 m B) 10 m C) 20 m D) 30 m E) 40 m F) 50 m

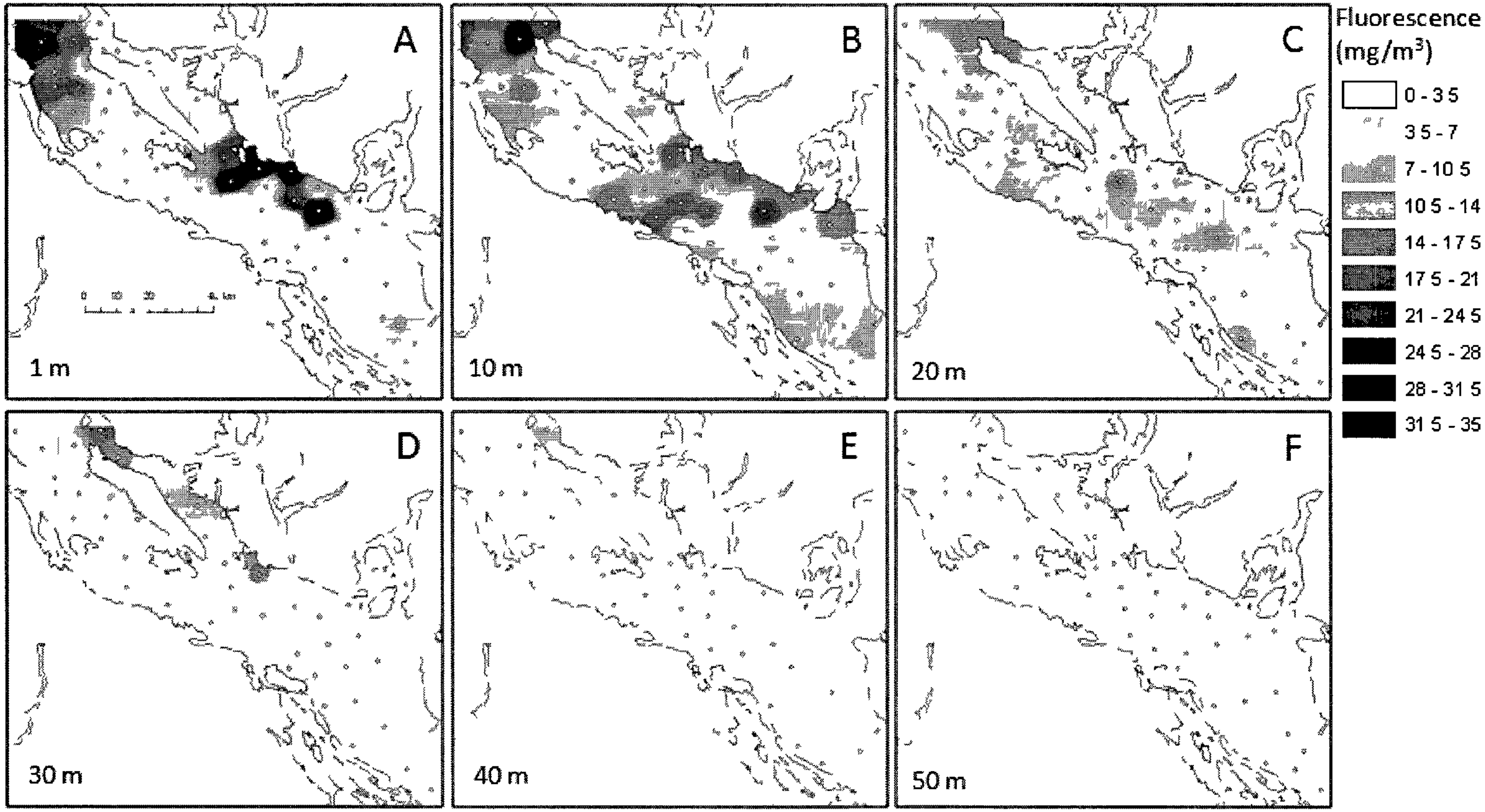

Figure A6 April 2010 horizontal distribution of fluorescence for depths A) 1 m B) 10 m C) 20 m D) 30 m E) 40 m F) 50 m

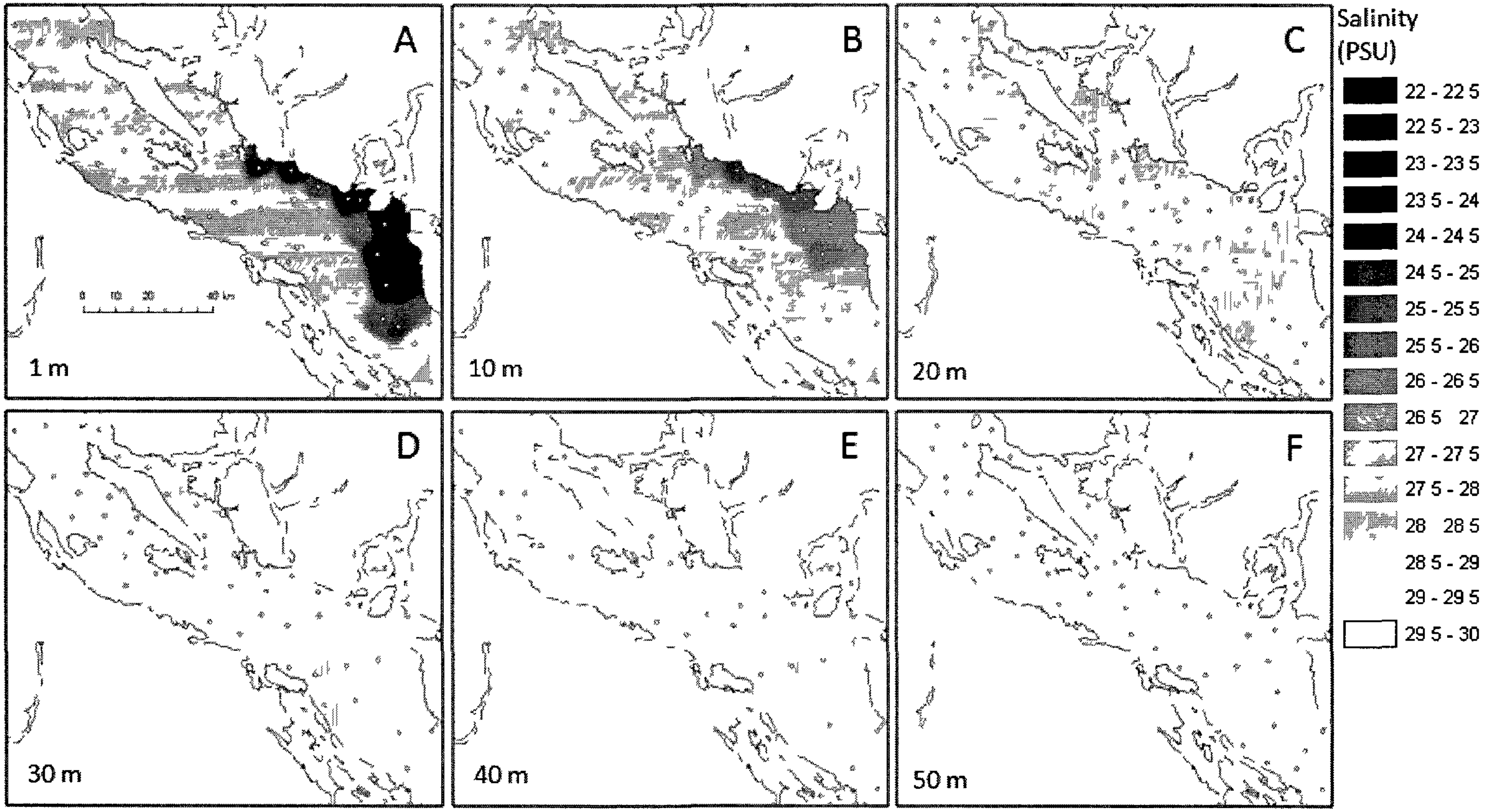

Figure A7 April 2010 horizontal distribution of salinity for depths A) 1 m B) 10 m C) 20 m D) 30 m E) 40 m F) 50 m (note to improve visualization the colour ramp is reversed from all other maps)

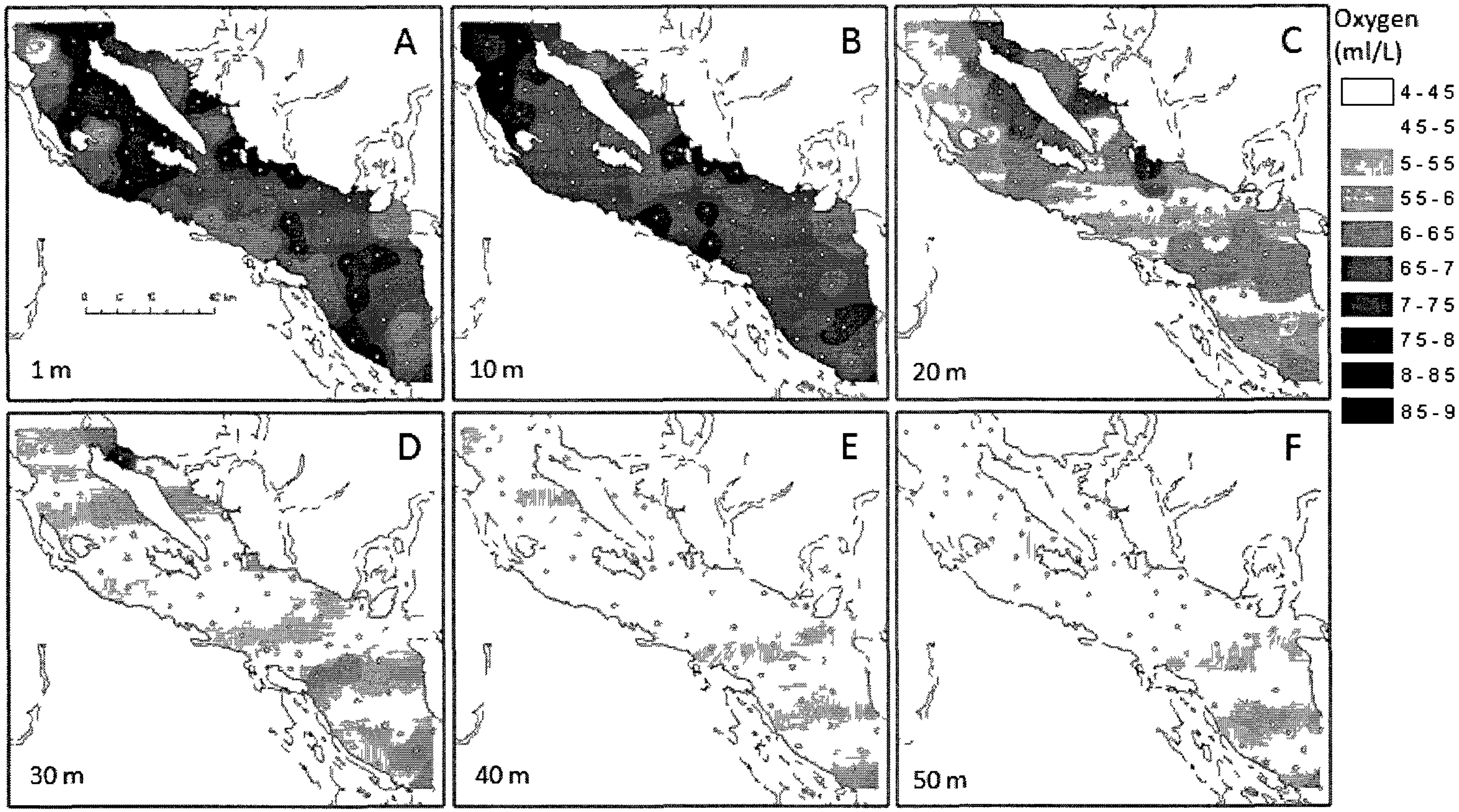

Figure A8 April 2010 horizontal distribution of oxygen for depths A) 1 m B) 10 m C) 20 m D) 30 m E) 40 m F) 50 m

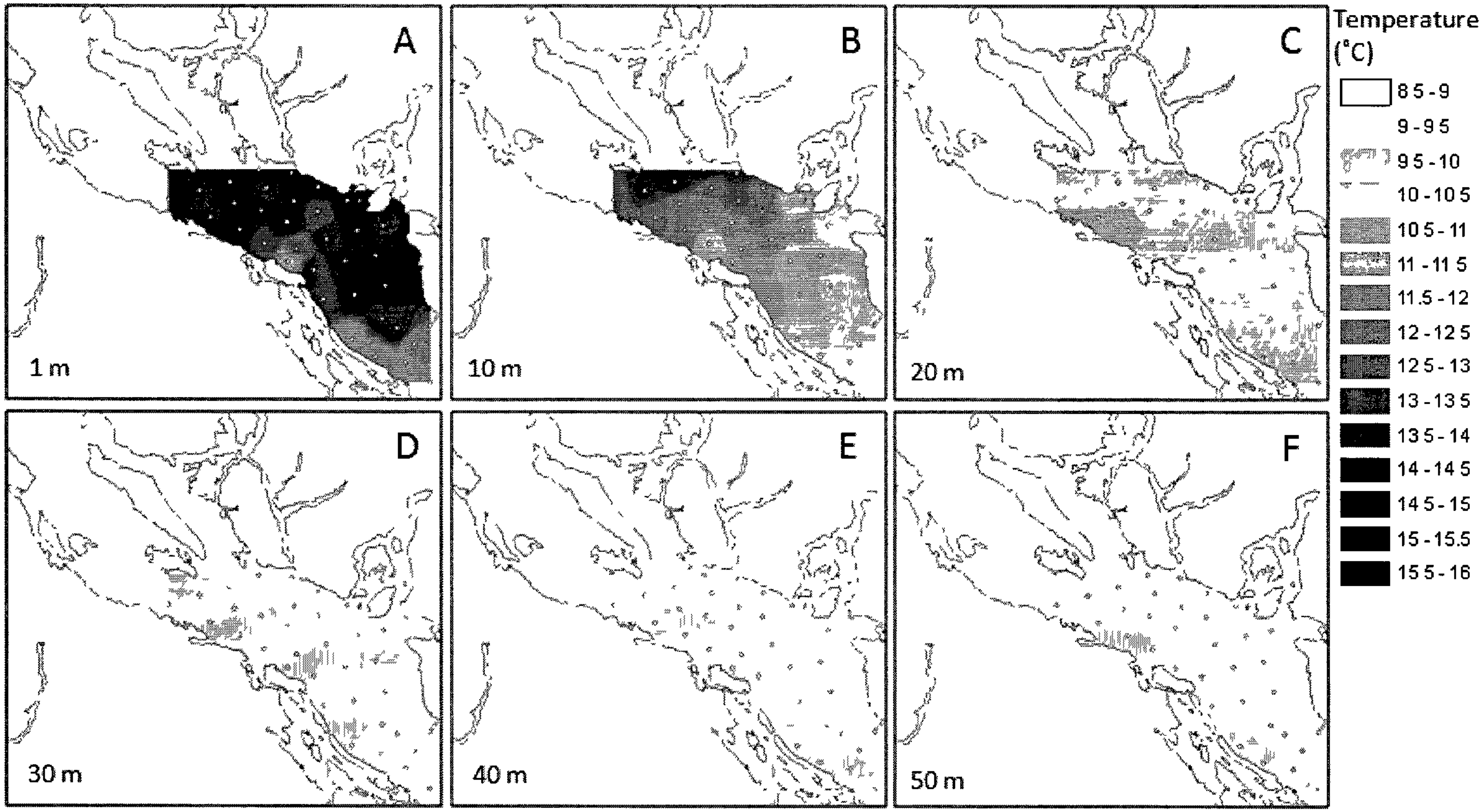

Figure A9. June 2010 horizontal distribution of temperature for depths: A) 1 m B) 10 m C) 20 m D) 30 m E) 40 m F) 50 m

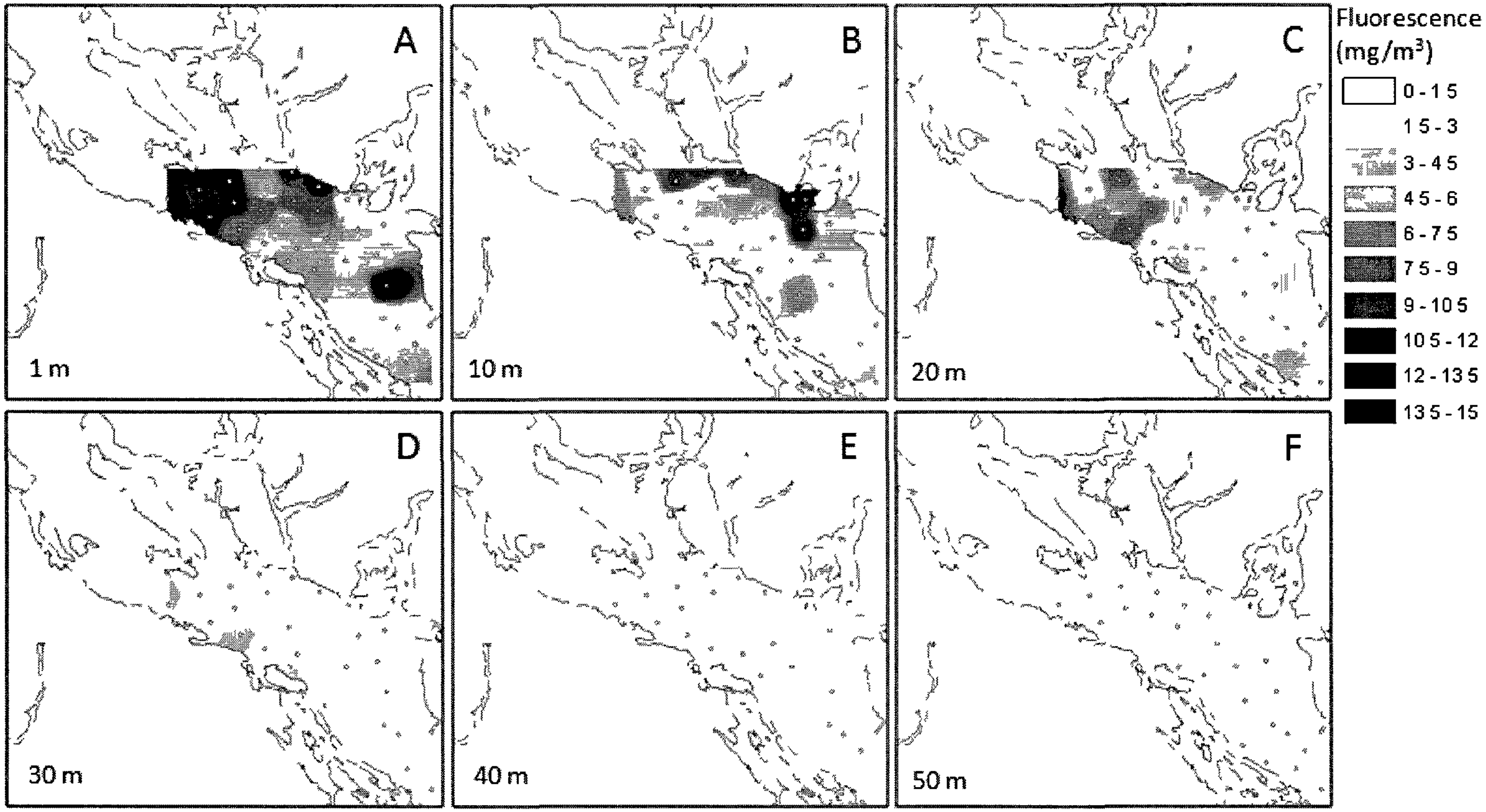

Figure A10 June 2010 horizontal distribution of fluorescence for depths A) 1 m B) 10 m C) 20 m D) 30 m E) 40 m F) 50 m

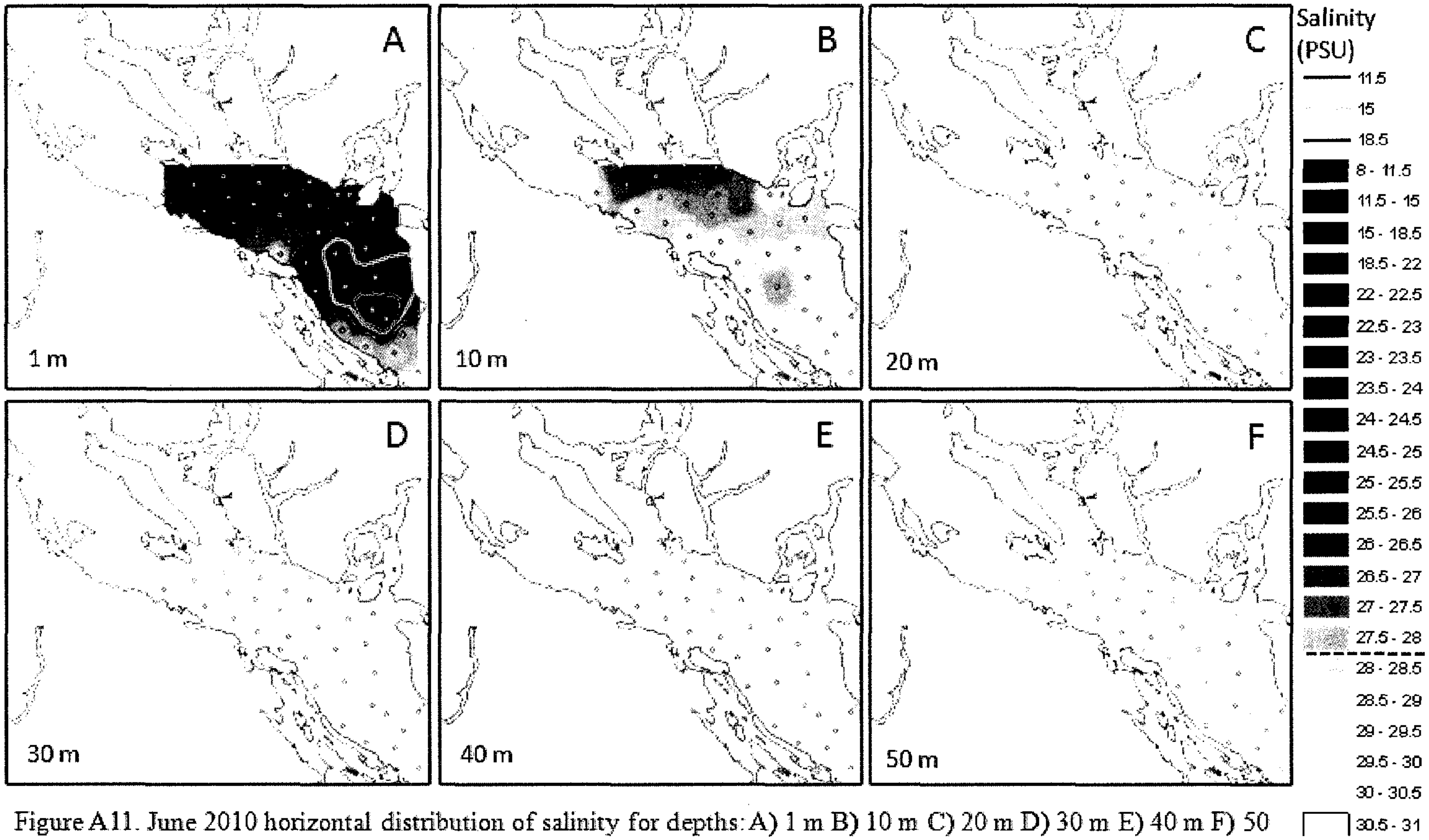

Figure A11. June 2010 horizontal distribution of salinity for depths: A) 1 m B) 10 m C) 20 m D) 30 m E) 40 m F) 50 m. Salinities between 8-22 PSU were separated by a classification interval of 3.5 PSU; all other values were separated by 0.5 PSU. The colour ramp was reversed from all other maps and contour lines were used to distinguish the first three classification intervals. Relevant contours after 10 m depth are represented below the horizontal stippled line.

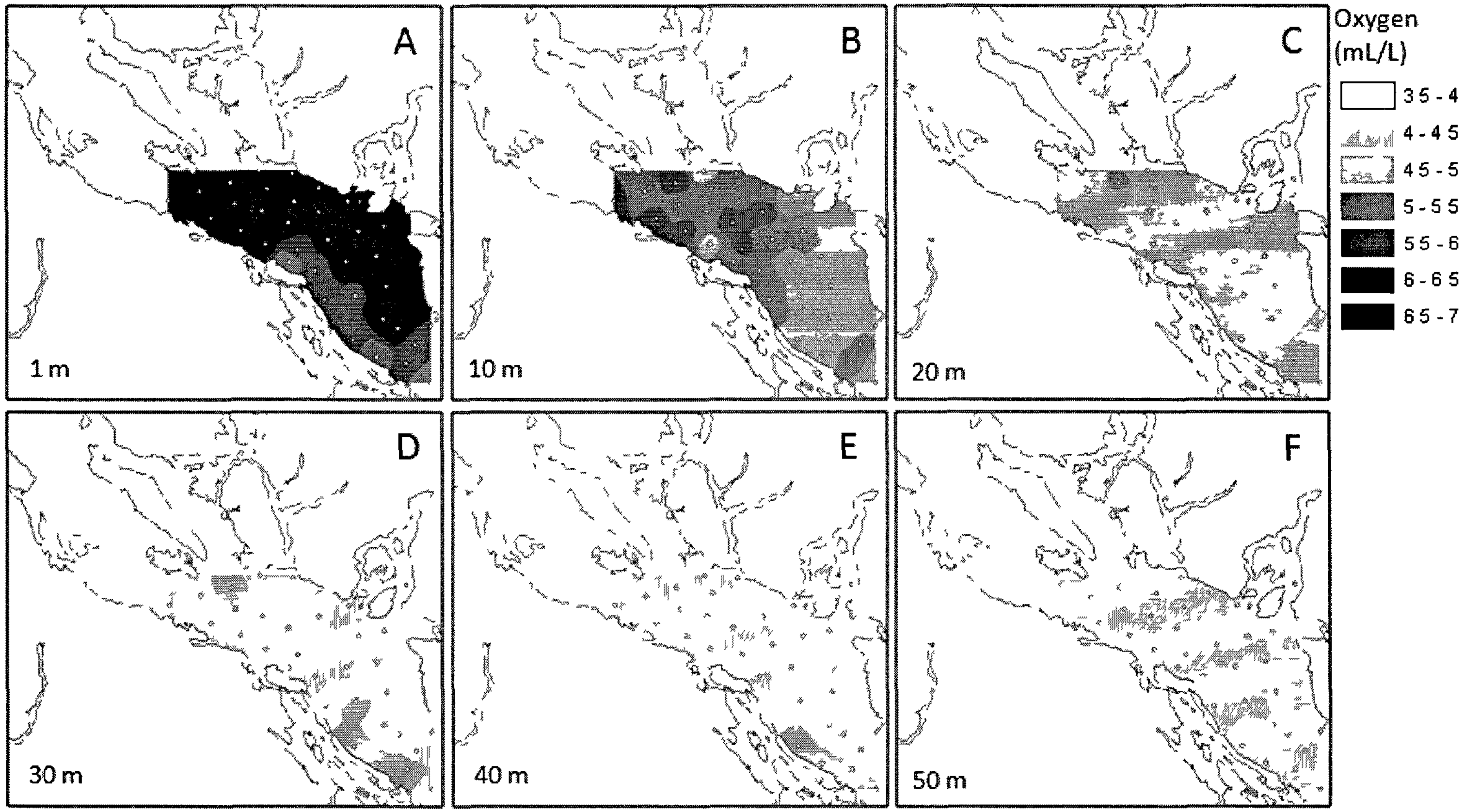

Figure A12 June 2010 horizontal distribution of oxygen for depths A) 1 m B) 10 m C) 20 m D) 30 m E) 40 m F) 50 m

8.2. Appendix 2. Larval abundance and composition: 2007 survey

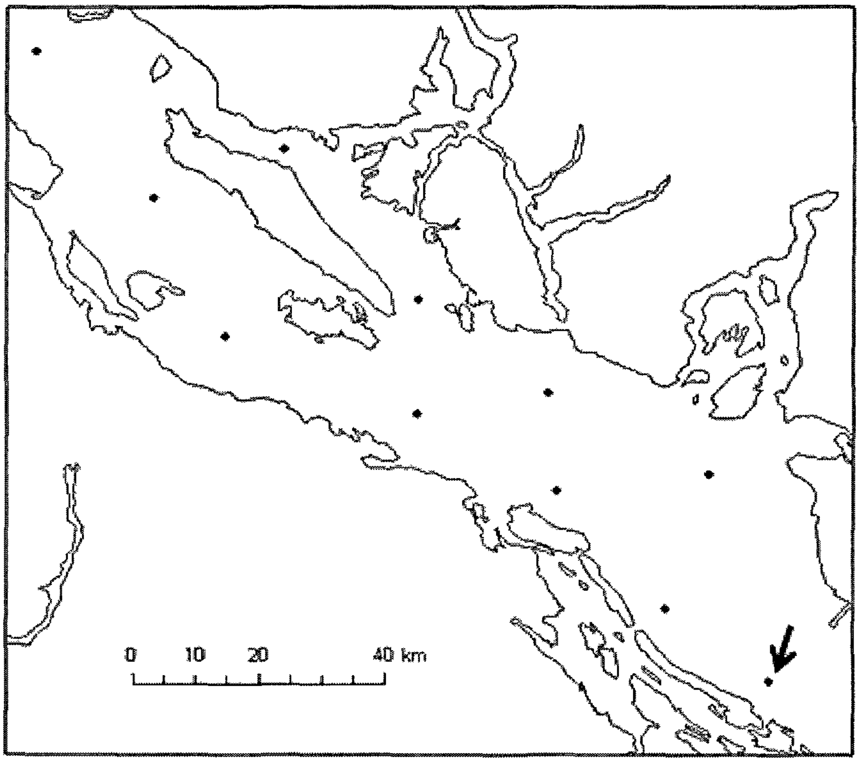

Figure A13. Location of stations sampled from April 25-29, 2007. All stations were visited twice except the southern-most station marked by an arrow which was sampled only once.

Table A1. Stage-specific abundance of crab larvae combined from two surveys conducted in Late April 2007 (see Fig. A1). Larval concentrations are expressed as the number of larvae per 100 m^3 filtered seawater. The relative abundance of all stages combined is detailed in parentheses in the 'Total' column. Z: number of zoeal stages; I-V: zoeal stages one through five; M: Megalopa.

Infraorder	**Family**	**Identification**	**Z**	**I**	**II**	**III**	**IV**	**V**	**M**	**Total**
Brachyura	Cancridae	*Cancer productus*	5	8608.7	4509.4	647.1	33.4	0	0	13789.6 (41.58)
		Glebocarcinus oregonensis	5	103.7	765.1	585.6	21.6	4.3	0	1480.4 (4.46)
		Metacarcinus gracilis	5	88.2	13.1	2.7	0	0	0	104.0 (0.31)
		Metacarcinus magister	5	1318.3	5417.3	5535.4	458.3	18.6	0	12747.8 (38.42)
		Unidentified Cancridae	5	894.4	597.4	703.7	51.1	0	0	2246.6 (6.77)
	Epialtidae	Epialtidae sp.	2	194.7	25.4	-	-	-	18.6	238.7 (0.72)
	Oregoniidae	Oregoniidae sp.	2	109.0	0	-	-	-	-	109.0 (0.32)
	Pinnotheridae	Pinnotheridae sp.	2-5	253.3	417.9	81.2	16.3	0	0	768.8 (2.31)
	Xanthidae	*Lophopanopeus bellus*	4	24.3	0	0	0	-	0	24.3 (0.07)
Anomura	Galatheidae	*Munida quadrispina*	4-5	423.9	601.6	363.6	47.4	0	0	1436.6 (4.32)
	Paguridae	Pagurid sp	4	92.4	19.1	29.0	74.0	-	0	214.5 (0.65)
	Porcellanidae	*Petrolisthes eriomerus*	2	5.0	0	-	-	-	0	5.0 (0.01)
Axiidae	Callassinidae	*Neotrypaeae californiensis*	5	8.2	0	0	0	0	0	8.2 (0.02)

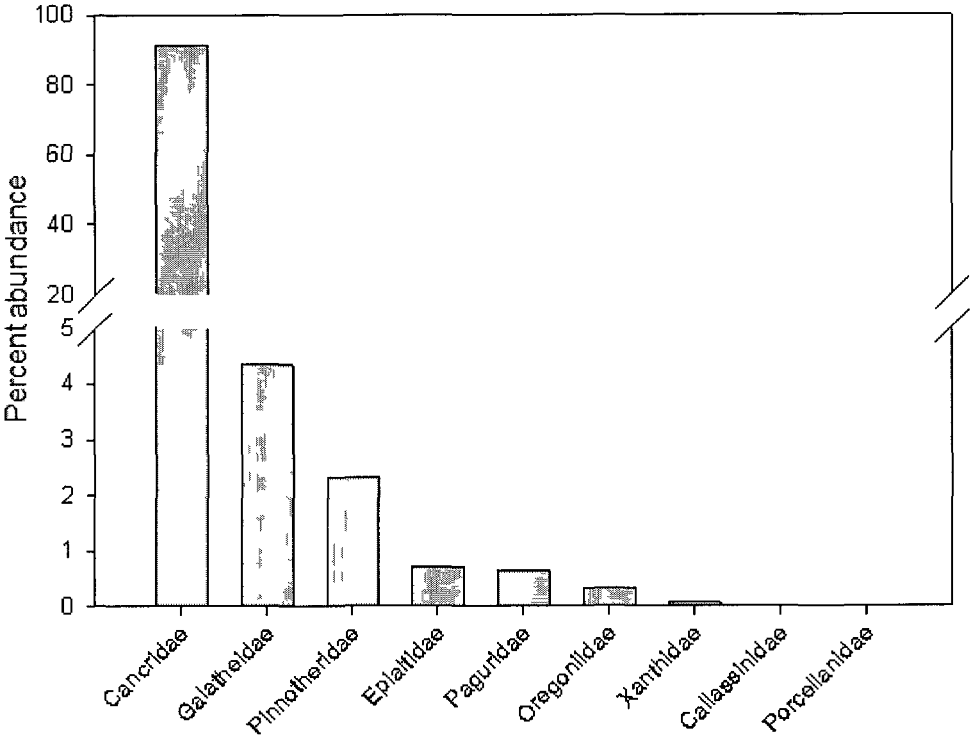

Figure A14. Relative abundance of crab larvae organized by family from samples collected during April 25-29, 2007.