Spatial and Temporal Dynamics of Larval Fish Assemblages in the Strait of Georgia

by

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B.Sc., Ocean University of China, 2004
M.Sc., Memorial University of Newfoundland, 2007

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Supervisory Committee

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Abstract

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For marine fishes, the early larval phase is considered a critical stage for survivorship and recruitment. The spatial and temporal dynamics of larval fish assemblages can influence their success and trophic structure of marine communities and entire ecosystems. This thesis will provide the first characterization of larval fish assemblage in the Strait of Georgia (SoG) in terms of diversity, abundance and composition, and their variability over multiple temporal scales, as well as the first quantification of variability in larval fish distribution in the SoG across multiple spatial scales. On the interdecadal scale, a significant decrease in larval abundance of several dominant fish taxa (Pacific hake, walleye Pollock, northern smoothtongue and rockfishes) contributed to a decline in total larval abundance and turnover in the composition structure between the early 1980s and the late 2000s. In contrast, both abundance and the relative composition of flatfishes and several demersal forage fish taxa increased during the same period. On interannual scales, abundance, diversity and community structure of the spring larval assemblages varied dramatically through 2007-2010, a period which alternated between strong La Niña and El Niño events. Higher overall larval concentrations were associated with warm conditions in the SoG in 2007 and 2010, while the lowest larval concentration was associated with cooler condition in 2009. Examination of associations between larval fish assemblages and environmental fluctuations suggests a potential influence of large-scale climate processes between the early 1980s and the late 2000s, but a primary association with local environmental factors on interannual scales. Spatial patterns in larval density of three dominant fish taxa (Pacific herring, Pacific hake and northern smoothtongue) were mostly structured on predefined broad (> 40km) and medium (20~40km) scales. Although their scale-dependent associations with environmental factors varied interannually, larval distributions in the central-southern SoG were generally associated with salinity, temperature and vertical stability of water column in the upper layer (0-50m). Our results emphasize the role of local estuarine circulation in structuring hierarchical spatial distributions of planktonic fish larvae in the SoG. These findings will provide considerable implications in fisheries resource management and conservation strategies.

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Dedication

This thesis is dedicated to my parents, Xinqi and Qingsheng, and my husband Jiejun and our son Lucas.

Chapter 1

Introduction

1.1 General Introduction

The larval stage of most marine fishes represents a very short period of their whole life cycle which lasts from hatching until the fish transform into juveniles, and this stage is planktonic for most teleosts. Since Hjort's landmark research in 1914, the larval stage has been considered as a critical period in the overall reproductive success of marine fishes, because the survival of individuals through this early stage and their eventual transport to nursery areas favourable for survival and growth, are important determinants of recruitment and adult population size (Bailey and Houde, 1989; Houde, 1997). Also, this pelagic early life stage represents the only time that many fish species inhabit the same marine ecosystem, but with different life histories and adult habitats, associate together in the upper layer of the ocean to form multispecies larval assemblages (Ahlstrom and Moser, 1976; Moser and Smith, 1993). Examination of the abundance and composition of such assemblages can provide valuable information for fishery-independent estimation of spawning biomass, reproductive effort and future recruitment success in adult fish stocks of major fishery species (Govoni, 2005; Hsieh *et al.*, 2005; Brodeur *et al.*, 2008; Auth, 2008; Auth *et al.*, 2011).

At the beginning of the twentieth century, Hjort (1914) developed a paradigm to explain the recruitment of young fishes based on the observation of poor relationship between egg production and recruitment of Atlantic herring. Hjort's paradigm expounded that recruitment variation of fish populations depended on varying survival of young fishes, and that the two primary elements affecting early survival are: (1) success at first feeding due to availability of suitable food, and (2) advective transport of fish propagules away from or to nursery areas favorable for their survival and further development. Following the second element of Hjort's recruitment paradigm, one central goal in fisheries oceanography is to describe the patterns of abundance and distribution of fish propagules during their early life-history stages, and to understand the factors driving variations in these patterns (Bradbury and Snelgrove, 2001; Govoni, 2005; Cowen *et al*, 2002; Ciannelli *et al*, 2008).

This thesis aims to quantify variability in various characteristics of larval fish assemblages in the Strait of Georgia (48°50´- 50°00´N, SoG), British Columbia, Canada. More specifically, this thesis assesses differences in the abundance and composition of larval fish assemblages over different temporal scales (interdecadal and interannual) and quantifies variability in geographic distributions of larval fish across multiple spatial scales. This work will provide baseline information on the recent status of the SoG larval fish assemblage, contribute significantly to our knowledge of the dynamics of fish populations in the SoG and their relationship to the varying marine environment. It will also provide valuable information for the application of fisheries management strategies using Marine Protected Areas (MPA), which are presently considered to be potentially one of the most important tools for conserving biodiversity and abundance of marine fishes (Conover, *et al*., 2000; Leis, 2006; Cowen *et al*., 2007).

This research was conducted as part of the Canadian Healthy Oceans Network (CHONe). CHONe was an NSERC strategic network, involving university researchers across Canada and government laboratories (predominantly Fisheries and Oceans Canada), which was established to address the need for scientific criteria for conservation and sustainable use of marine biodiversity resources in Canada's three oceans. CHONe's three main themes were: i) marine biodiversity; ii) ecosystem function, and iii) population connectivity. The research undertaken for this thesis fits under the theme of population connectivity, which is to understand how dispersal of reproductive propagules, typically represented by the early life stages of marine organisms such as eggs and larvae, influences patterns of diversity, resilience and source/sink dynamics of adult marine species and of communities. Within this theme, the principal goal of my research is to quantify mesoscale patterns of spatiotemporal variability and to explore dispersal patterns in the planktonic larval fish community in the Strait of Georgia through field investigations.

1.2 Variations in larval fish assemblages over time

A larval fish assemblage is a collection of fish species whose larvae occur together in space and time. As the year class strength and dynamics of fish populations are widely held to be regulated primarily by survival during early life history stages, studies of the patterns and variations in larval fish assemblages will improve our understanding of recruitment and provide insights into the processes and factors regulating recruitment (Miller, 1999). In addition, the patterns and dynamics of larval fish assemblages can affect the trophic structure of the entire ecosystem (Auth and Brodeur, 2006). Recently, global climate change, environmental fluctuations, and anthropogenic activities have been widely recognized as major threats to larval fishes and their supporting marine ecosystem, as both abiotic and biotic factors from these threats may cause distinct changes in the abundance and structure of the entire larval fish assemblage over multiple temporal scales.

A number of studies have examined long-term (e.g. decadal scale) variations in larval fish populations and ichthyoplankton communities, and their association with environmental fluctuations and fishing activities, in several large marine ecosystems in the Northeast Pacific Ocean. Research in the Gulf of Alaska and the northern California Current region suggests that large-scale climate indices are more important in explaining variations in larval fish abundance than are local environmental factors (Doyle *et al.*, 2009; Auth *et al.*, 2011). In the southern California Current region, studies of larval fish, collected continuously since 1950 through the

California Cooperative Oceanic Fisheries Investigation (CalCOFI) program, shows that climate change has had significant effects on the abundance and distribution of oceanic fishes in this region (Hsieh, *et al*., 2009). Moreover, it appears that fishing has enhanced the sensitivity of marine fishes to climatic variation since unexploited taxa apparently tracked climate trends more closely than did exploited taxa (Hsieh *et al*., 2005; 2008). Nevertheless, environmental fluctuations can also have profound effects on marine fish populations and communities over short time scales (e.g. interannual scale, seasonal scale). For example, a study of spatiotemporal occurrence of fish eggs and larvae in Conception Bay (Newfoundland) showed that interannual and seasonal differences in both species composition and abundance appear to be associated with differences in environmental conditions, particularly temperature (Laprise and Pepin, 1995). Understanding the response of planktonic larval fish assemblages to major external factors such as environmental fluctuations and fishing pressures is thus of paramount importance in fishery resource management and conservation.

1.3 Spatial variability in larval abundance

1.3.1 Spatial heterogeneity of plankton

Understanding the spatial distribution of plankton populations and the underlying processes shaping the patterns is an important focus in biological oceanography (Yamazaki *et al*., 2002). Marine planktonic organisms tend to accumulate together in certain areas (Reese and Brodeur, 2006; Dower and Brodeur, 2004) and form certain non-random spatial patterns over a broad range of spatial scales (Haury *et al*., 1978; Mackas *et al*., 1985). The development of plankton spatial ecology is rooted in the idea of spatial homogeneity. This ideal perspective that plankton are distributed randomly and uniformly in space persisted during the early decades of the twentieth century (Pinel-Alloul, 1995). Since the 1940s and 1950s, however, the phenomenon of spatial heterogeneity in plankton distributions has been broadly recognized. Contrary to homogenous distributions, most planktonic organisms exist in forms of patches, gradients, swarms, aggregates, or schools (Hardy and Gunther, 1935; Cassie 1963; Haury *et al*., 1978; Mackas *et al*., 1985). In recent decades, most investigations have therefore concentrated on the quantification of heterogeneity.

Numerous methods such as mean crowding, index of patchiness, variance:mean ratio and spatial analysis tools have been developed for detecting and describing spatial pattern in the plankton. For example, Lloyd's index of patchiness (Lloyd 1967) has been used frequently in studies of ichthyoplankton distribution (Hewitt, 1981; Stabeno *et al*., 1996; Bradbury *et al*., 2003). Since the 1980s, the research focus has been extended gradually from simply measuring spatial heterogeneity towards exploring the factors and processes responsible for generating and maintaining the spatial structure. It is now evident that the spatial heterogeneity of planktonic organisms is of great ecological significance as their distribution patterns and degree of aggregation will strongly affect their population dynamics, inter-organism relations (e.g. reproduction, competition and predation) and interactions with other planktonic and nektonic compartments in the ecosystem (Avois-Jacquet, 2002; Pinel-Alloul, 1995; Verdy, 2001).

1.3.2 Spatial scales

Spatial scale is defined as the space over which the quantity of a pattern remains the same before significantly changing (Daly and Smith, 1993; Denman and Powell, 1984); it is an intrinsic component that must be considered in most consideration of spatial heterogeneity. Patterns of planktonic organisms have been observed at different spatial scales varying from a few centimeters to thousands of kilometers; and their physical and biological generative processes also vary across a hierarchical range of scales in space (Haury, *et al*. 1978; Pinel-Alloul, 1995; Palacios, *et al*., 2006; Mackas *et al*., 1985). Haury *et al*. (1978) divided the spatial scale continuum into six categories: mega-scale, macro-scale, meso-scale, coarse-scale, fine-scale and micro-scale. It is within the mesoscale, however, which ranges from meters to tens of kilometers horizontally, that spatial heterogeneity of zooplankton, including larval fish, and its physical and biological forcing mechanisms have been most intensively studied (Haury *et al*., 1978; Yamazaki *et al*., 2002; Avois-Jacquet, 2002). This is mainly because the horizontal point sampling methods used in field studies are most effective at this scale, whereas logistical constraints begin to limit field measurements at larger and smaller scales (Mackas *et al*., 1985). Thus, investigating and quantifying scale-dependent spatial heterogeneity and associated generation processes requires multi-scale approaches.

1.3.3 Generation of larval fish spatial patterns

Embedded in a three dimensionally moving fluid, plankton are closely affected by the inherent variability of fluid dynamics (Mackas, *et al*., 1985; Daly and Smith, 1993; Visser and Thygesen, 2003; Franks, 1992). This also applies to early life stages of marine fishes, and has led to various physical characteristics of the marine environment being considered as primary factors affecting patterns in larval fish populations. Physical oceanographic processes occur and interact across a range of scales with different forces dominating at certain scales (Daly and Smith, 1993). At the mesoscale, processes such as currents, tides, density driven fronts, wind induced forces and interactions with seafloor topography (e.g. canyons, sills, seamounts and banks) provide the mechanisms that disperse fish larvae in the planktonic environment.

Prior to the late 1990s, the extent to which larval fishes can influence their dispersal and distribution remained an area of considerable debate (Bellwood *et al*., 1998). Fish larvae had been long considered as passive drifters whose distribution patterns were affected purely by physical processes (Roberts, 1997; Leis, 2006). However, numerous field and modeling studies also showed that physical processes alone were insufficient to explain or predict observed spatial distribution patterns (Stobutzki and Bellwood, 1997). Recent studies have provided strong evidence that active behaviour of larval fish during the pelagic period can significantly contribute to their open water distribution patterns (Fisher *et al*., 2000; Leis, 2006; Guan *et al*., 2008). The most extensively studied larval behaviours which have direct or indirect influence on larval dispersal and spatial distributions include active swimming behaviour (with considerable speed and endurance), feeding, predator avoidance, active schooling, orientation and navigation by using a suite of sensory information such as auditory, olfactory, chemosensory and celestial cues (Kingsford, 2002; Leis, 2006; Cowen and Sponaugle, 2009).

It is evident now that larval fish spatial patterns are likely caused by interactions between the effects of passive drift by physical forcing and active larval behaviour. Multiple physical and biological driving processes will thus operate at various scales to shape the larval distributions: at larger scales, physical processes are relatively more important in structuring biological patterns; whereas at smaller scales, biological processes are likely to be the dominant drivers (Daly and Smith, 1993; Pinel-Alloul, 1995). Additionally, spatial variation in larval mortality due to predation and starvation can also contribute to the spatial distribution of larval abundance (Frank *et al*., 1993; Bradbury *et al*., 2003).

1.4 Study area - the Strait of Georgia

1.4.1 Oceanographic conditions

Off the west coast of Canada, the eastward flowing North Pacific Current splits into two branches: the Alaska Current curves to the north, and the California Current turns to the south (Tully, 1938; Thomson, 1981). The bifurcation region along the British Columbia coast is subject to the variability of both coastal currents (Cummins and Freeland, 2007). The Strait of Georgia (SoG) is a coastal basin located between Vancouver Island and the British Columbia mainland. The average depth of the basin is approximately 155m with 67% of the area over 100m deep. The maximum depth is ~420m in the central SoG off the south end of Texada Island (Thomson, 1981; Thomson and Foreman, 1998; Mackas *et al*., 2013). Connection and water exchange between the SoG and open NE Pacific Ocean occurs mainly through narrow passages including Haro Strait and Juan de Fuca Strait at the southeast end of the strait, and (to a lesser extent) through Johnstone Strait and Discovery Passage to the north (Thomson, 1981; Li *et al*., 1999; Masson, 2006). A sill, located south of Victoria within the Juan de Fuca Strait (~95m) and a northern sill at Boundary Pass (~135m), cause vertical mixing to occur in these passages, and then restrict the depth of estuarine exchange and affect the properties of deep water entering from the outer coast (Masson, 2006).

A large volume of freshwater, mostly from the snow-fed Fraser River (~ 75% of the total river discharges into the SoG, Thomson, 1981), enters the upper layer of the Strait with the freshet generally occurring in June (Masson and Cummins, 2004). This freshwater mixes with saltier water beneath, and drives an estuarine circulation with seaward outflow near the surface (~30-50m) and a nutrient-rich offshore water inflow at depth (Waldichuck, 1957). This freshwater input has a direct influence in the central and southern regions of the Strait, where it plays a key role in supporting patterns of stratification and water column stability and contributes to high biological productivity. The positive estuarine circulation is further modulated by local wind forcing and strong tidal mixing (LeBlond, 1983; Li *et al*., 1999; Masson, 2006). The prevailing winds in the SoG are generally weak (< 2.5m/s) and predominantly from the northwest in summer (Jun - Sep) but stronger and southeast in winter (Oct – Mar, Thomson, 1981). Tides in the Strait are mixed semidiurnal, and the intensity of vertical mixing induced by tidal currents within the SE and NW entrance passages fluctuates on a fortnightly spring-neap cycle (Thomson, 1981). Based on the “drift bottle” approach, Waldichuk (1957) suggested a roughly counterclockwise circulation in the surface layer of the central SoG with northward and southward surface flow along eastern margin and western margin of the SoG, respectively. Subsequent studies have described and characterized currents such as low-frequency currents (also known as residual currents, Stacey *et al*., 1987), gravity currents from deep water renewal events (LeBlond *et al*., 1991) and rotary currents (Marinone *et al*., 1996; Masson and Cummins, 2004), which affect circulation in the central-southern SoG.

The vertical structure of the water column in the central-southern SoG has been described as a three-layered structure: a near-surface layer (0-50 m), an intermediate layer (50-200 m), and a deep layer (below 200 m); the characteristics and dynamics of each layer are quite different (Pawlowicz *et al*., 2007). Water in the near-surface layer is always well oxygenated. Water temperature and salinity within this layer varies seasonally in response to heat exchange and freshwater input. The intermediate and deep water layers of the Strait are renewed when mid-density water, which has been mixed in the entrance passages, flows over the sills at both ends of the Strait and into the interior basin (Masson, 2002; Pawlowicz *et al*., 2007). Intermediate water is continually renewed year round, but deep water renewal events usually occur at the beginning and end of the coastal upwelling season, following a neap tide when the density near the bottom of the sill peaks. Usually, intruding offshore water is cold and rich in oxygen in late winter, but warm with low in oxygen in late summer (Masson, 2002). Residence times of water in the SoG are short, about one day for the Fraser River plume, a few months at most for near-surface water, about 160 days for intermediate water, and approximately one year for deep water (Pawlowicz *et al*., 2007).

1.4.2 Biological characteristics of the Strait of Georgia

The SoG is a highly productive and diverse ecosystem displaying seasonal variation in biological production (phytoplankton, zooplankton and ichthyoplankton) with peak production in spring (Harrison *et al*., 1983). The phytoplankton community is primarily dominated by diatoms from fall through spring, while the summer community is dominated by dinoflagellates (Stockner *et al*., 1979; Harrison *et al*., 1983). The annual spring bloom usually occurs in March or early April in the SoG, followed by occasional short-lived summer blooms in late June or July (Stockner *et al*., 1979). The initiation of the spring bloom is controlled primarily by wind mixing, and has been shown to covary with the North Pacific Gyre Oscillation (NPGO, Yin *et al*., 1997; Collins *et al*., 2009; Allen and Wolfe, 2013). The magnitude of the spring bloom is regulated through both "bottom-up" control by nutrient concentrations and "top-down" control by zooplankton grazing (Yin *et al*., 1996).

The zooplankton community in the near-surface layer of the SoG is dominated by copepods. Mid- and deep- water communities are dominated by the euphausiid *Euphasia pacifica* and dormant stages of large copepods (e.g. *Neocalanus plumchrus*, *Calanus marshallae*, *Calanus pacificus and Metridia pacifica*), respectively (Harrison *et al*., 1983). During the winter, small copepods, particularly *Pseudocalanus spp*., dominate the surface waters. Following the onset of the spring bloom, newly hatched nauplii and early copepodite stages of *N. plumchrus* migrate from deep water to the surface for feeding and further development, and become abundant in the spring community (Fulton, 1973; Mackas *et al*., 1998). At the beginning of the summer around May-June, stage V *N. plumchrus* descend to depth when they have accumulated sufficient lipid stores for dispause (Mackas *et al*., 1998; Campbell and Dower, 2008). This results in the accelerated growth and increased production of the smaller copepods which dominate the surface zooplankton community again in the fall (Harrison *et al*., 1983). As the larvae of most marine fish species graze predominantly on the fraction of small zooplankton with a size around 500 μm, microzooplankton (which generally consist of the egg and naupliar stages of copepods) are their major dietary items in this system (LeBrasseur *et al*., 1969; Parsons and LeBrasseur, 1970; Parsons, *et al*., 1970). In the past two decades, the zooplankton community in the mid- strait has displayed a dominant low-frequency decadal fluctuation in biomass; declining from 1990-1995, increasing to a maximum ~ 1999-2002, declining to a minimum in 2005-2007, and then recovering to near-average levels by 2010. This pattern of interannual variation correlates positively with the NPGO climate index, but negatively with temperature anomalies throughout the water column (Mackas *et al*., 2013).

The SoG is an important spawning, nursery and rearing ground for many fish species, and supports commercial (e.g. Pacific herring, Pacific hake, walleye Pollock, Salmon and several flatfishes), recreational and aboriginal fisheries (Ketchen *et al*., 1983). Previous studies on economically valuable species such as Pacific hake and walleye pollock have suggested the existence of resident stocks within the SoG and a lack of exchange with migratory stocks from outer coast (McFarlane and Beamish, 1985; King and McFarlane, 2006; Mason, 1985).

Our knowledge of the early life history stages of fish in the SoG is still very limited, with only a few studies existing for some dominant species (Mason *et al*., 1981; Mason, 1985; Mason and Philips, 1985; McFarlane and Beamish, 1985). In contrast to neighbouring regions on the outer NE Pacific coast where routine ichthyoplankton surveys have been conducted for many years (e.g. Gulf of Alaska, northern and southern California Current regions), the lack of data from consistent long-term monitoring limits our understanding of the SoG ichthyoplankton community in terms of their community structure, population dynamics, distribution patterns, phenology, biophysical coupling and response to external pressures.

1.4.3 Recent changes in the Strait of Georgia

The SoG ecosystem has been undergoing notable changes under cumulative pressures from accelerating global climatic changes and anthropogenic activities. In recent decades, temperature through the entire water column has been increasing gradually (Masson and Cummins, 2007), while pH and O_2 have declined (Johannessen and Macdonald, 2009). In addition to the general warming trend, the system has also been experiencing frequent El Niño and La Niña events which produce episodic warming on an interannual scale (DFO, 2011). Climate changes have also induced variations in the seasonal pattern of freshwater discharge, such as earlier timing and reduced volume of the summer freshet (Morrison *et al*., 2002). A shift towards earlier development timing of predominant copepod *N. plumchrus* has also been observed, and the shift has been accelerating during the early 2000s (Bornhold *et al*., 2000; Johannessen and Macdonald, 2009). Meanwhile, the various marine resources in this coastal basin have been intensively used by humans, and the marine ecosystem has been disrupted by numerous threats from commercial and recreational fishing, discharge of contaminants, habitat destruction through urbanization and construction, increasing marine traffic and invasive species (Johannessen and Macdonald, 2009). All of these changes may affect biological production in the SoG, including the early life history stage of fish species, by altering their physical habitat. To understand the natural variations in the ecosystems and how they respond to the listed natural and anthropogenic stresses, the status of physical (e.g. temperature, oxygen, nutrients and pH) and biological (e.g. spring bloom) oceanographic conditions, and certain important fishery resources (e.g. Pacific herring) in the SoG have been monitored by Fisheries and Oceans Canada (DFO, hereafter). Unfortunately, the early life history stages of local fisheries resources are still a missing component in the monitoring.

1.5 Thesis objectives and structure

This thesis includes three primary objectives:

(1) To quantify interdecadal differences in the SoG larval fish assemblage (Chapter 2)

A comprehensive evaluation of long-term changes in fish resources on both population and community level is needed in the SoG for conservation and management purposes. In the early-1980s, egg and larval fish surveys were carried out through winter and spring in the SoG by the Groundfish Program of the Pacific Biological Station, DFO, but detailed analysis of the results was never completed. After that, the SoG larval fish community was not sampled quantitatively again until the current research was initiated in 2007. To obtain new baseline knowledge about the current status of SoG larval fish community and to quantify mesoscale patterns of spatiotemporal variability in larval fish community, we conducted surveys in spring of 2007 - 2010 as part of Canadian Healthy Oceans Network (CHONe). Chapter 2 of this thesis describes differences in larval abundance and structure of spring larval fish assemblages in the SoG between the early 1980s and the late 2000s, and investigates the potential contributions of both regional and local environmental factors. This study is the first in the Canadian region of Northeast Pacific Ocean to assess changes in the local fish production and community structure through information during early life history of marine fishes. Results from this chapter have been presented at several international conferences, and are currently in review at *Progress in Oceanography* (co-authored by Guan, L., Dower, J.F., McKinnell, S.M., Pepin, P., Pakhomov, E.A. and Hunt, B.P.V)

(2) To quantify interannual variability in the SoG larval fish community (Chapter 3)

In addition to the gradual warming pattern over recent decades, the SoG has also been experiencing frequent shifts between El Niño and La Niña events (DFO, 2011). The study period through 2007 - 2010 was especially dynamic, experiencing alternating strong La Niña and El Niño events. This chapter describes interannual variations in diversity, abundance and composition structure of the spring larval fish assemblages in the SoG during late-April of 2007, 2009 and 2010. We test for regional differences in larval fish concentration and assemblage structure between the northern SoG and the central-southern SoG, and identify linkages between variations in larval fish assemblages and their physical living environment. This study provides baseline information about the recent status of larval fish community in the SoG, and brings a better understanding of short-term larval fish dynamics in a rapidly changing environment and associated driving factors. This chapter has been presented in international conferences, and is currently being prepared for submission to *Progress in Oceanography*.

(3) To quantify variability of larval fish distributions across multiple spatial scales (Chapter 4)

In this chapter, a new and powerful multiscale approach – principal coordinate neighborhood matrices (PCNM) is applied to investigate the larval distribution patterns of several dominant fish species in the SoG over a range of spatial scales with respect to environmental heterogeneity, and to understand the mechanisms and processes that contribute to the generation and maintenance of multiscale spatial variability. Our results emphasize the critical role of the local estuarine circulation in structuring hierarchical spatial distributions of planktonic fish larvae in the central-southern SoG. This study represents the first account of the spatial structuring of larval fishes and environmental relationships in the SoG across multiple spatial scales, and provides new insights on the role of the environmental variability in the spatial dynamics of local fishery resources. This manuscript will shortly be submitted to the *Journal of Plankton Research* (co-authors Guan, L., Dower, J.F., McKinnell, S.M. and Pepin, P.).

The thesis concludes with Chapter 5, a brief summary section which synthesizes the major findings of chapters 2-4, provides an overview of the “big picture” in terms of larval fish dynamics in the SoG and beyond, and offers some suggestions for future research directions.

1.6 Statement of authorship

I am the first author on all three manuscripts included within this thesis (e.g. Chapters 2-4), as I designed the studies, collected field samples, processed and identified the samples, analyzed and interpreted the data, and prepared the manuscripts. Dr. John Dower and Dr. Pierre Pepin are co-authors on all manuscripts as they provided advice on data analysis, result interpretation, and editorial input. Dr. Skip McKinnell is also a co-author on all manuscripts – he provided the historical dataset of ichthyoplankton surveys in the SoG (1980 and 1981) for this thesis, and also provided advice on results interpretation and editorial assistance. Dr. Evgeny Pakhomov is a co-author on the first two manuscripts - he contributed larval fish data collected in 2007 for analyses needed in the first two manuscripts. Dr. Brian Hunt is a co-author on the first manuscript because of his contributions mainly in the field collection and identification of larval fish specimens in 2007.

Chapter 2

A comparison of spring larval fish assemblages in the Strait of Georgia (British Columbia, Canada) between the early 1980s and late 2000s

2.1 Introduction

The egg and larval stages of most marine fishes are short periods of the life cycle during which these animals experience rapid growth and high mortality (Cushing, 1975; Bailey and Houde, 1989; Houde, 1997). The early life stages are often the only period during which fish species with different life histories and adult habitats form multispecies assemblages in the upper layer of the ocean (Ahlstrom and Moser, 1976; Moser and Smith, 1993). Quantifying the abundance and composition structure of these ichthyoplankton assemblages can provide valuable, fishery-independent estimates of spawning biomass, reproductive effort and future recruitment success in major fishery species (Govoni, 2005; Hsieh *et al*., 2005; Brodeur *et al*., 2008; Auth, 2008; Auth *et al*., 2011).

Fish populations and assemblage composition vary on a range of temporal scales. Over decadal scales, at which strong environmental changes usually occur, variations can be attributed to both external forcing and internal biological processes (e.g. population dynamics, species interactions) of the fish assemblages (Collie *et al*., 2008). External perturbations are linked primarily to anthropogenic exploitation and environmental fluctuations, particularly climate changes, and their influences are usually intertwined. Recently, these factors have received increasing attention and been identified as major threats to fish populations and their ecosystems (Govoni, 2005; Hsieh *et al*., 2008). A number of studies have examined long-term variations in larval fish populations and ichthyoplankton assemblages in the Northeast Pacific Ocean, and explored their association with environmental fluctuations and fishing. For example, research in the Gulf of Alaska and the northern California Current region suggests that large-scale climate indices are more important in explaining interannual and decadal variations in larval fish abundance than are local environmental factors (Doyle *et al*., 2009; Auth *et al*., 2011). In the southern California Current region, where the California Cooperative Oceanic Fisheries Investigation (CalCOFI) program has collected ichthyoplankton data since 1950, unexploited taxa tracked climate trends more closely than did exploited taxa (Hsieh *et al*., 2005). Similar research is lacking in the Canadian portion of the Northeast Pacific coast, however, due primarily to limited ichthyoplankton surveys in this region.

Geographic Setting: Off the west coast of Canada the eastward flowing Subarctic Current splits into two branches: the Alaska Current curves to the north and the California Current turns to the south (Tully, 1938; Thomson, 1981). The bifurcation region along the British Columbia coast is subject to the variability of these coastal currents (Cummins and Freeland, 2007). The Strait of Georgia (SoG hereafter, Fig.2.1a) is a semi-enclosed coastal basin on Canada's west coast between Vancouver Island and mainland British Columbia. This basin is connected to the Pacific Ocean via two passages. The major connection is through Haro Strait and Juan de Fuca Strait in the south, with a narrower connection via Johnstone Strait at the north (Thomson, 1981; Li *et al*., 1999; Masson, 2006). The SoG is dominated by seasonal changes in estuarine circulation driven primarily by the large seaward discharge from the Fraser River near the surface and nutrient-rich deep water flowing inward at depth (Waldichuk, 1957). This general pattern is further modulated by local wind forcing and strong tidal mixing (Li *et al*., 1999; Masson, 2006). The SoG is a highly productive ecosystem (~280 gC/m^2/year by Harrison *et al*., 1983; ~ 220gC/m^2/year by Pawlowicz *et al*., 2007) that supports commercial, recreational, and aboriginal fisheries. It provides spawning, nursery, and rearing areas for many resident fish taxa including

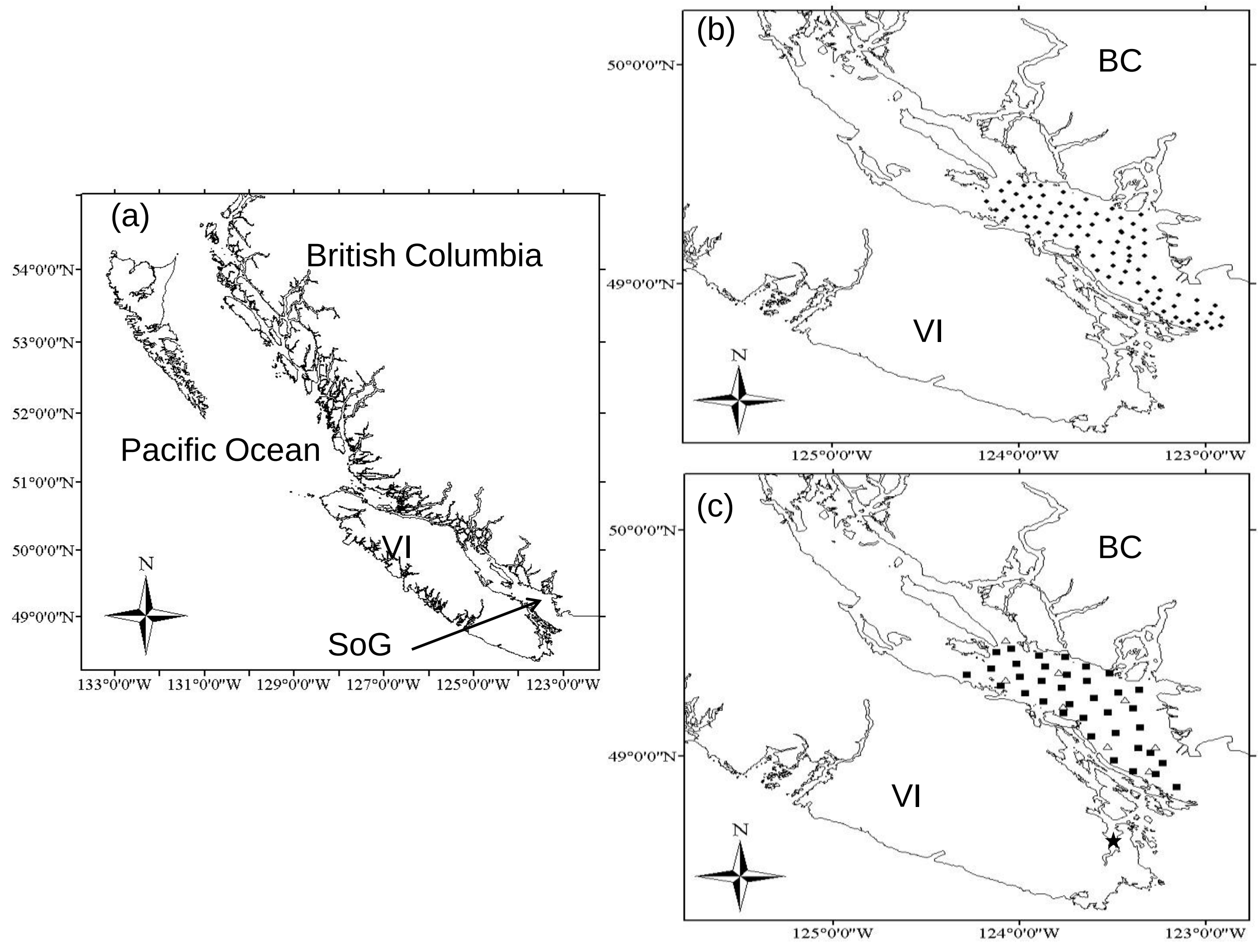


Figure 2.1. Map showing the location of ichthyoplankton surveys conducted in the Strait of Georgia (SoG) off mainland British Columbia (BC) and Vancouver Island (VI). Maps show (a) the Strait of Georgia, (b) sites sampled in 1980 and 1981, and (c) sites sampled in 2007, 2009 and 2010. Solid circles in (b) are sites sampled in 1980 and 1981. Open triangles in (c) are sites sampled in 2007, while sites samples in 2009 and 2010 are denoted by solid squares. The solid star in (c) marks the location of the gear intercalibration experiment.

Merluccius productus (Pacific hake) and *Theragra chalcogramma* (walleye pollock), which have been recognized as resident populations (Mason, 1985; McFarlane and Beamish, 1985; King and McFarlane, 2006). In recent decades, water temperatures in the SoG have increased (Masson and Cummins, 2007), while pH and O_2 have decreased (Johannessen and Macdonald, 2009). In addition, fishing, and habitat destruction have increased the threats to local fish populations (Johannessen and Macdonald, 2009). A comprehensive evaluation of long term changes in fish resources in this marine system at both the species and assemblage levels can help inform the needs of ecosystem-based management.

In the early-1980s, intensive ichthyoplankton surveys were carried out through winter and spring of 1980 and 1981 in the SoG by the Groundfish Program of the Pacific Biological Station, Fisheries and Oceans Canada (DFO). The principal purpose of these surveys was to estimate the recruitment potential and total biomass of resident *M. productus* and *T. chalcogramma* stocks (Mason *et al.*, 1981). Unfortunately, the program was terminated before any analyses were undertaken. These surveys also provide data for co-occurring species which now allows for an evaluation of the historical status of the abundance and species composition of ichthyoplankton assemblages in the SoG. To characterize spatiotemporal variability in larval fish distributions and establish current baseline conditions about the status of SoG ichthyoplankton assemblages, we conducted similar ichthyoplankton surveys in the spring from 2007 to 2010. As no other data was available, the present study therefore focuses on comparing SoG ichthyoplankton assemblages between these two periods, nearly three decades apart, and explores the influence of marine environmental fluctuations. My specific objectives were to: i) quantify differences in larval abundance and species composition of the spring larval fish assemblages in the SoG between the early 1980s and the late 2000s; ii) identify associations of co-varying fish species; and iii) investigate links between trends in larval fish data and both regional and local environmental variables. This study will contribute to an improved understanding of the dynamics of fish populations in the SoG, and their relation to the varying marine environment by providing fishery-independent indices of population abundances and assemblage structures.

2.2 Materials and methods

2.2.1 Ichthyoplankton sampling procedures

The spring ichthyoplankton assemblage in the SoG was sampled in the early 1980s (1980, 1981) and the late 2000s (2007, 2009, 2010). Spatially and temporally intensive sampling was carried out at two week intervals from February to June in 1980 and 1981, while the late-2000 cruises were conducted in the late April (i.e. the time of highest larval fish abundance and diversity in the SoG based on examination of bi-weekly changes in larval production in the early 1980s).

In 1980 and 1981, daytime sampling occurred in the central and southern SoG at 90 and 80 stations, respectively (Fig. 2.1b, Table 2.1). Stations were located approximately 5 km apart and ichthyoplankton samples were collected using a 60 cm diameter Bongo net equipped with 351 μm mesh Nitex net and a General Oceanics center-mounted flowmeter. The Bongo net was descended to within 20m of the sea floor at a rate of 50 m min^{-1}, and was retrieved at 20 m min^{-1} with a ship speed of two knots. Corresponding environmental data (e.g. temperature, salinity) were not collected during these surveys. Ichthyoplankton samples were preserved in 5% buffered seawater formaldehyde (Mason *et al*., 1981). Fish larvae were subsequently sorted and identified to the lowest possible level that taxonomic knowledge permitted during the 1980s. This included some species-level information, but many larvae were only identified to family or genus (Appendix 1).

Five surveys were conducted in the latter half of April in 2007, 2009, and 2010 (Table 2.1). Sixty stations spaced approximately 8-10 km apart and covering the entire SoG were sampled through both day and night during cruises in 2009 and 2010. A subset of 8 stations was sampled twice in 2007 in an exploratory study (Fig. 2.1c). At each station, a Seabird SBE-19 conductivity-temperature-depth sensor (CTD) was deployed to record water column properties from the surface to within ~5m from the sea floor. Next, a 15 minute oblique tow using a 1 m^2 Tucker trawl equipped with 1 mm mesh size net was made within the upper ~50m of the water column at a ship speed of two knots. A calibrated TSK flowmeter measured the volume of seawater filtered and the sampling depth was recorded by a Vemco Minilog-12TX data logger. Samples were preserved in 95% ethanol. All preserved fish larvae were sorted, counted, and identified to the lowest taxonomic level possible following Matarese *et al*. (1989) and the Ichthyoplankton Information System (2011). Species identifications were possible for most taxa (Appendix 1), but larvae of *Sebastes* spp. (rockfishes) and *Liparis* spp. (snailfishes) could only be identified to genus based on meristics and pigmentation patterns. Larval abundance was estimated as the number of individuals 1000 m^{-3} and the standard length of each larva was measured to the nearest millimeter.

2.2.2 Comparison and intercalibration between historical and recent ichthyoplankton sampling methodologies

Differences in sampling gear, tow depth, and net mesh size applied in historical and recent ichthyoplankton surveys were expected to affect estimates of larval fish abundance and make direct comparisons difficult. With only limited ship-time available, a separate field experiment was conducted in Saanich Inlet (British Columbia, Fig. 2.1c), a well studied fjord opening to the SoG on the east of Vancouver Island, to develop intercalibration coefficients between the Bongo

Table 2.1. Sampling summary of ichthyoplankton surveys in the central and southern Strait of Georgia during spring of the early-1980s and the late-2000s.

Decade	Year	Dates	No. of sites	Gear type	Net mesh size	Sampling depth
1980s	1980	Apr 27-May 7	90	Bongo sampler	351 µm	Surface - within 20m from sea floor
	1981	Apr 28-May 2	80	Bongo sampler	351 µm	
2000s	2007	Apr 25-26	8	Tucker trawl	1mm	Surface – ~50m
	2007	Apr 28-29	8	Tucker trawl	1mm	Surface – ~50m
	2009	Apr 25-28	32	Tucker trawl	1mm	Surface – ~50m
	2009	Apr 29-May 1	34	Tucker trawl	1mm	Surface – ~50m
	2010	Apr 24-27	36	Tucker trawl	1mm	Surface – ~50m

net and the Tucker trawl. During the daytime of April 17-18, 2011, a total of eight pairs of ichthyoplankton samples were collected with each gear type at the same site (48 °35.565' N, 123 ° 39.239' W) using the procedures described for each survey era. The average depths towed by Bongo net and Tucker trawl were 182m and 51m, respectively. A nonparametric Mann-Whitney *U* test revealed that the mean total catch of fish larvae from the Bongo net (449 larvae 1000 m^{-3}) was significantly greater than that of the Tucker trawl (137 larvae 1000 m^{-3}, $p = 0.001$, Table 2.2). To facilitate comparison of the two procedures for total larval catch, a Bongo net/Tucker trawl intercalibration factor of 3.3 ($p = 0.001$) was developed using linear regression (Fig. 2.2). Furthermore, to compensate for the small sample size and provide a more reliable range for this intercalibration factor, a bootstrapped regression coefficient of 3.8 with its 95% confidence interval of (2.1, 7.2) were estimated by nonparametric resampling procedure based on 5000 samples. The intercalibration factor, together with the lower and upper bootstrap limits, was then applied to estimate total larval abundance in the late 2000s for comparisons between decades. Among the nine most common species caught by both procedures, only *Lyopsetta exilis* (slender sole) larvae, which has a small thin body shape, was significantly more abundant in the Bongo net than the Tucker trawl ($p= 0.001$, Table 2.2); while, only the large and wide larvae of *Plectobranchus evides* (bluebarred prickleback) were relatively more abundant in the Tucker trawl ($p < 0.0001$, Table 2.2). The average abundances of all other species did not differ statistically between the two gear types (Table 2.2). Therefore, *L. exilis* was excluded from subsequent assemblage analyses because its abundance was likely underestimated during recent surveys. However, *P. evides* was included in analyses as Stichaeidae were only identified to family level in historical dataset, and separation by species within this family was therefore impossible. The inclusion of *P. evides* would not largely affect analysis results as this species was only rarely collected in recent surveys and at very low abundances (0.14, 0.03, and 0.00

Table 2.2. Mean larval abundance (±1 SE) of common species collected by both the "Historical Bongo" and "Recent Tucker" sampling procedures. Bold indicates statistical significant at α = 0.05 for the Mann-Whitney *U* test.

Species name	Common name	Mean abundance by Bongo (no. / 1000m^3)	Mean abundance by Tucker (no. / 1000m^3)	*p*-Value
Lyopsetta exilis	Slender sole	**341.62 (52.27)**	**65.95 (12.22)**	**0.001**
Sebastes spp.	Rockfishes	65.15 (16.42)	36.87 (6.25)	0.208
Theragra chalcogramma	Walleye pollock	6.21 (3.15)	3.18 (1.49)	0.370
Liparis spp.	Snailfishes	4.22 (2.77)	9.29 (2.04)	0.125
Ronquilus jordani	Northern ronquil	1.91 (1.25)	1.25 (0.74)	0.898
Parophyrs vetulus	English sole	1.77 (1.77)	1.92 (1.11)	0.370
Artedius harringtoni	Scalyhead sculpin	2.53 (1.71)	2.05 (1.01)	0.546
Icelinus borealis	Northern sculpin	2.25 (2.30)	1.14 (0.58)	0.370
Plectobranchus evides	Bluebarred prickleback	**1.67 (1.67)**	**6.73 (1.52)**	**<0.0001**
	Total larvae	**448.85 (58.22)**	**137.08 (14.27)**	**0.001**

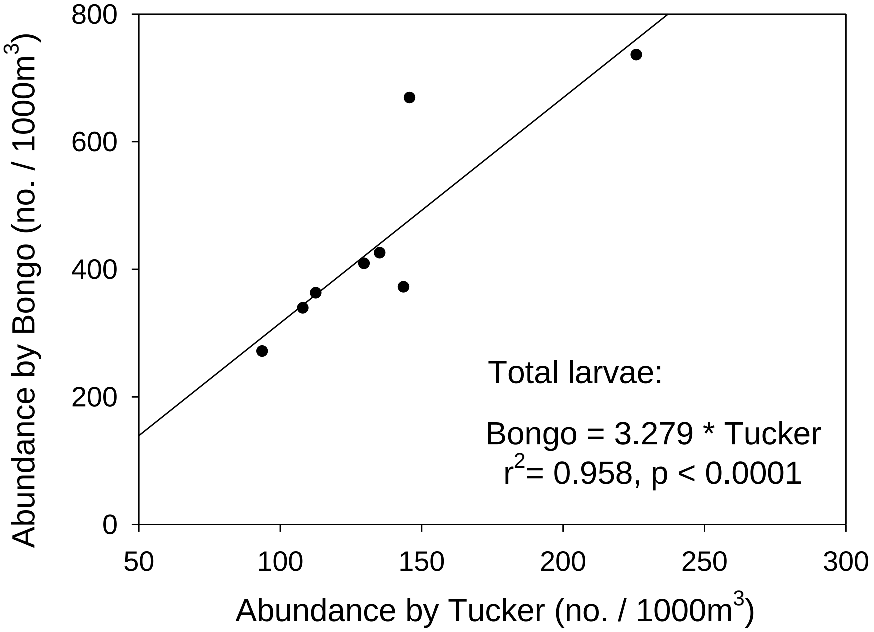


Figure 2.2. Intercalibration of larval fish abundance estimates (no. /1000m^3) from paired tows of “Historical Bongo” and “Recent Tucker” sampling procedures by least squares linear regression. Solid line: regression line.

individuals /1000m^3 in 2007, 2009, and 2010, respectively). For the other seven fish species collected in the gear inter-comparison experiment, the original larval abundances were used in decadal comparisons as no significant differences in larval abundance were detected (Table. 2.2). For species that occurred in the ichthyoplankton surveys but which were not collected in the inter-comparison experiment, the lower and upper limits of the bootstrapped regression coefficient based on total larvae would be applied for further comparisons.

2.2.3 Data processing and analysis on assemblage variations

A total of 288 samples, including 170 from the 1980s and 118 from the 2000s (80 and 38 day and night samples, respectively), were collected during seven late-April cruises covering the central and southern SoG (Table 2.1). Despite lower sampling density, the assemblage information from 2007 was considered in the interdecadal comparisons as the larval diversity in 2007 was comparable to that in 2009 and 2010 (Chapter 3). The taxonomic resolution achieved during the historical and contemporary surveys differed; species which were not consistently identified through time were combined at the level of family or genus to allow comparisons between decades (Appendix 1).

The mean annual total larval abundance and mean annual abundance of each taxon were estimated by averaging across stations for each cruise. The relative mean abundance indicated the percentage abundance of each taxon over total larvae. The occurrence of taxa was calculated as the percentage of sampling sites where a species occurred. Analysis of variance (ANOVA) was performed on ln(N+1) transformed larval abundances to test for significant differences between the 1980s and 2000s. For total larvae and for larvae of taxa not collected during the gear comparison experiment, four intercalibration treatments (no adjustment, adjusted by the intercalibration coefficient of 3.3, and by its lower (2.1) and upper (7.2) bootstrap limits) were applied to abundance estimates and tested for decadal differences by ANOVA respectively, and then the results were compared for consistency. The ratio of pelagic to demersal taxa (Collie *et al*., 2008) was calculated as the total abundance of all pelagic species divided by the total abundance of all demersal species excluding *L. exilis* (for reasons described above). Additionally, diel differences in larval abundance of each taxon were compared through ANOVA for recent surveys in 2009 and 2010 separately.

Larval assemblage structure was analyzed using multivariate statistical methods. Only taxa with a frequency of occurrence higher than 5% were included (14 taxa in total, Table 2.3). Larval abundance for each taxon at each site was standardized by total larval abundance, then fourth-root transformed to reduce the influence of both highly abundant and rare species, and then converted to a Bray-Curtis dissimilarity matrix as the basis for subsequent analyses (Clarke and Gorley, 2006). Firstly, to visualize the patterns of decadal assemblages in a two-dimensional ordination space, an unconstrained ordination method – principal coordinates analysis (PCO) was performed to project the samples onto Euclidean axes which minimize residual variation in the space defined by the original dissimilarities (Anderson *et al*., 2008). PCO analyses were conducted both including and excluding *M. productus* and *Leuroglossus schmidti* (northern smoothtongue) in consideration of issues associated with their vertical distribution and abundance (see 2.4.2 in Discussion). Secondly, permutational multivariate analysis of variance (PERMANOVA) was used to test for significant differences in species composition of the larval fish assemblages between the two periods. Assuming a hypothesis of differences between the two periods, PERMANOVA partitioned the Bray-Curtis dissimilarity matrix into within-decade and between-decade dissimilarities, developed a distribution-free pseudo-*F* statistic and tested for significance using 9999 random permutations (Anderson *et al*., 2008). Because of the sensitivity of PERMANOVA to differences in multivariate dispersion between compared periods, the

Table 2.3. Average total larval abundance and average larval abundances of individual species in the 1980s (1980 and 1981) and 2000s (2007, 2009 and 2010), and the results of ANOVA analysis on decadal comparisons in larval abundances. Bold indicates a significant difference ($p < 0.5$) in larval abundance between two periods in ANOVA test under different intercalibration treatments.

Taxa			1980s Mean abundance (no./1000 m^3)	Relative mean abundance (%)	2000s Mean abundance (no./1000 m^3)	Relative mean abundance (%)	Frequency abundance (%)
Family	Species name	Common name					
Agonidae		Poachers[c]	**0.02**	0.002	**0.69**	0.588	12.847
Ammodytidae	*Ammodytes hexapterus*	Pacific sandlance[c]	**0.52**	0.043	**1.00**	0.855	12.500
Bathylagidae	*Leuroglossus schmidti*	Northern smoothtongue[c]	**128.66**	10.733	**20.00**	17.047	86.111
Bathymasteridae	*Ronquilus jordani*	Northern ronquil[c]	0.27	0.022	0.21	0.180	6.250
Bythitidae	*Brosmophycis marginata*	Red brotula	0.05	0.004	0.06	0.052	2.811
Clinidae	*Hetrostichus rostratus*	Giant kelpfish	0.00	0.000	0.03	0.028	0.694
Clupeidae	*Clupea pallasi*	Pacific herring[c,d]	20.13	1.679	14.49	12.350	70.139
Cottidae		Sculpins[c]	2.13	0.178	1.18	1.002	28.819
	Scorpaenichthys marmoratus	Cabezon	0.05	0.004	0.08	0.069	2.431
Cryptacanthodidae	*Crytacanthodes aleutensis*	Dwarf wrymouth	**0.00**	0.000	**0.10**	0.086	2.778
Cyclopteridae		Lumpsuckers[c]	0.97	0.081	0.41	0.350	13.542
Liparidae	*Nectoliparis pelagicus*	Tadpole snailfish	0.07	0.006	0.00	0.000	1.042
	Liparis spp.	Snailfishes[c]	**0.00**	0.000	**1.37**	1.165	18.403
Gadidae	*Theragra chalcogramma*	Walleye pollock[c]	**140.51**	11.721	**10.59**	9.027	89.931
	Gadus macrocephalus	Pacific cod	0.00	0.000	0.06	0.047	0.694
	Microgadus proximus	Pacific tomcod	**0.51**	0.042	**0.00**	0.000	4.514
Gobiidae		Gobies[c]	0.26	0.022	0.14	0.121	6.250
Hexagrammidae		Greenlings	0.02	0.002	0.00	0.000	0.347
Merlucciidae	*Merluccius productus*	Pacific hake[c]	**829.32**	69.183	**27.07**	23.563	87.847
Myctophidae		Lanternfishes	0.06	0.005	0.00	0.000	0.694
Osmeridae		Smelts	**0.00**	0.000	**0.13**	0.109	1.736
	Thaleichthys pacificus	Eulachon	**0.96**	0.080	**0.00**	0.000	1.736
Pholidae		Gunnels	0.19	0.016	0.07	0.060	3.819
Pleuronectidae		Righteye flounders[c]	**3.56**	0.297	**8.50**	7.245	49.306
	Lyopsetta exilis	Slender sole	**0.60**	0.050	**10.11**	8.611	41.319
Ptilichthyidae	*Ptilichthys goodie*	Quillfish	**0.00**	0.000	**0.10**	0.084	2.778
Scorpaenidae	*Sebastes* spp.	Rockfishes[c]	**65.03**	5.425	**20.12**	17.145	82.986
Stichaeidae		Pricklebacks[c]	**1.84**	0.153	**0.13**	0.106	14.236
	Anoparchus purpurescens	High cockscomb	0.00	0.000	0.01	0.010	0.347
Zoarcidae	*Lycodapus mandibularis*	Pallid eelpout	0.04	0.003	0.00	0.000	0.694
		Total larvae	**1197.49**	--	**117.35**	--	--
		Total larvae exclude 3 sp[a]	**240.15**	--	**59.59**	--	--
		Total larvae exclude 6 major sp[b]	14.48	--	14.38	--	--

[a] Overall larval abundance calculated by excluding *L. exilis, L. schmidti* and *M. productus*.[b] Overall larval abundance calculated by excluding *L. exilis, L. schmidti*, *M. products*, *C. pallasi*, *T. chalcogramma* and *Sebastes spp.* [c] Fish taxa were included in multivariate analyses. **[d]** Abundance was similar between two perioed based on original data, but was significantly higher in the late 2000s after intercalibration.

homogeneity of dispersions was tested separately using PERMDISP (with 9999 permutations). If significant heterogeneity in dispersion and significant differences in assemblage composition were detected simultaneously, a further examination of the position of the multivariate data cloud (centroid ± SE) from the two periods in PCO space would be needed to uncover the nature of the detected differences. To determine major taxa responsible for the multivariate patterns, all included taxa were overlaid onto PCO ordination space according to Spearman rank correlations between species-standardized abundances and the PCO scores (Anderson *et al*., 2008). In addition, potential "species associations", within which species varied in similar fashion, were also identified via hierarchical cluster analysis of species (Clark and Warwick, 2001).

2.2.4 Linking assemblage variations to environmental fluctuations

Relationships between the larval fish assemblages and the SoG environmental fluctuations were evaluated by considering both local physical and chemical oceanographic conditions and large-scale atmosphere and climate variations. The local environmental variables selected were April averages for: SoG sea surface temperature (SST) and salinity (SSS), Fraser river discharge, and a wind mixing index (wind speed cubed). SST and SSS data were acquired from the DFO lighthouse at Entrance Island (49.13 °N 123.48 °W). Fraser River discharge data were measured at Hope (British Columbia) and obtained from the Water Survey of Canada. Wind speed data measured at Vancouver International Airport (YVR) were obtained from Environment Canada. Three large-scale climatic indices were examined: the Pacific Decadal Oscillation Index (PDO, Mantua *et al*., 1997) obtained from JISAO, University of Washington, the Multivariate El Nino-Southern Oscillation Index (MEI, Wolter and Timlin, 1998) obtained from the NOAA Earth System Research Laboratory, and the Northern Oscillation Index (NOI, Schwing *et al*., 2002,) from the NOAA Pacific Fisheries Environmental Laboratory. Values in Jan-Apr, May-Aug, and

Sep-Dec were averaged to indicate seasonal status in winter-spring, spring-summer, and fall-winter, respectively. Seasonal averages, with lags of up to one year, were used to account for delayed effects between physics and biology. Examination of multicollinearity among selected environmental variables using both pair-wise correlations with Bonferroni correction and variance inflation factor resulted in exclusion of SSS and MEI from subsequent analyses.

Relationships between annual average larval abundance (total larvae and dominant taxa) and environmental variables were investigated using forward-stepwise multiple regressions. The environmental variables that produced the best regression model were selected based on the Akaike Information Criterion (AIC). Distance-based linear models (DistLM), which partition variance in multivariate data based on a dissimilarity matrix using multiple regression models (Anderson *et al*., 2008), were applied to assess the relationship between the structure of larval assemblages and environmental variables. Standardized and fourth-root transformed annual average larval abundance of each taxon constituted the units for the dissimilarity matrix; a pseudo-*F* statistic was calculated and tested for significance by 9999 permutations. To visualize the results in a reduced dimensional space, distance-based redundancy analysis (dbRDA) was then used to perform a constrained ordination of fitted values from the given multivariate regression model. Partial correlations between statistically significant environmental predictors and dbRDA ordination scores were calculated as the basis for overlaying these predictors in the dbRDA space. Univariate analyses were performed using SYSTAT (Version No.12.02), while multivariate analyses were performed using PRIMER version 6 (PRIMER-E) and PERMANOVA+ for PRIMER.

2.3. Results

2.3.1 Environmental conditions

Large-scale climatic indices (PDO, MEI, and NOI) and local environmental variables (SST and Fraser River discharge) exhibited both decadal scale variation and large interannual fluctuations. During 1980-1981, the SoG experienced weak El Niño conditions with variable but positive values of both PDO and MEI (Fig. 2.3a); monthly SST anomalies fluctuated around the long term average with relatively small amplitudes, but larger fluctuations and higher average SST anomalies were apparent during the late 2000s (Fig. 2.3b). Meanwhile, fluctuations in both PDO and MEI indicated an oscillating pattern between El Niño and La Niña events from 2006 to 2010. Similarly, the NOI revealed decadal differences between the two periods, more pronounced inter-annual fluctuations in the 2000s, and comparable spring conditions between 2010 and the early 1980s (Fig. 2.3c). The average discharge of the Fraser River increased from 1979 to 1981, but decreased from 2007 to 2010. Interannual variation in April discharge reflected interannual variation in annual average discharge, except for the abrupt decline from 2007 to 2008 (Fig. 2.3d).

2.3.2 Taxonomic composition of ichthyoplankton assemblages

The SoG larval fish assemblages were dominated by a few species/families. During the early 1980s, 20 families were collected but only 24 taxa were identified to species level. The five families accounting for most (98.8%) of the total abundance were: Merlucciidae (69.2%), Gadidae (11.8%), Bathylagidae (10.7%), Scorpaenidae (5.4%), and Clupeidae (1.68%) (Table 2.3). Among these families, five taxa (*Merluccius productus*, *Leuroglossus schmidti*, *Theragra chalcogramma*, *Sebastes* spp. [rockfishes], and *Clupea pallasi* [Pacific herring]) accounted for 98.7% of the total abundance, within which *M. productus* alone contributed ~70%. Larvae of Cottidae (sculpins), Stichaeidae (pricklebacks), and Pleuronectidae (flatfishes) were collected at relatively high frequency but low abundance. Eight species occurred exclusively in the 1980s: *Nectoliparis pelagicus* (tadpole snailfish), *Microgadus proximus* (Pacific cod), *Thaleichthys*

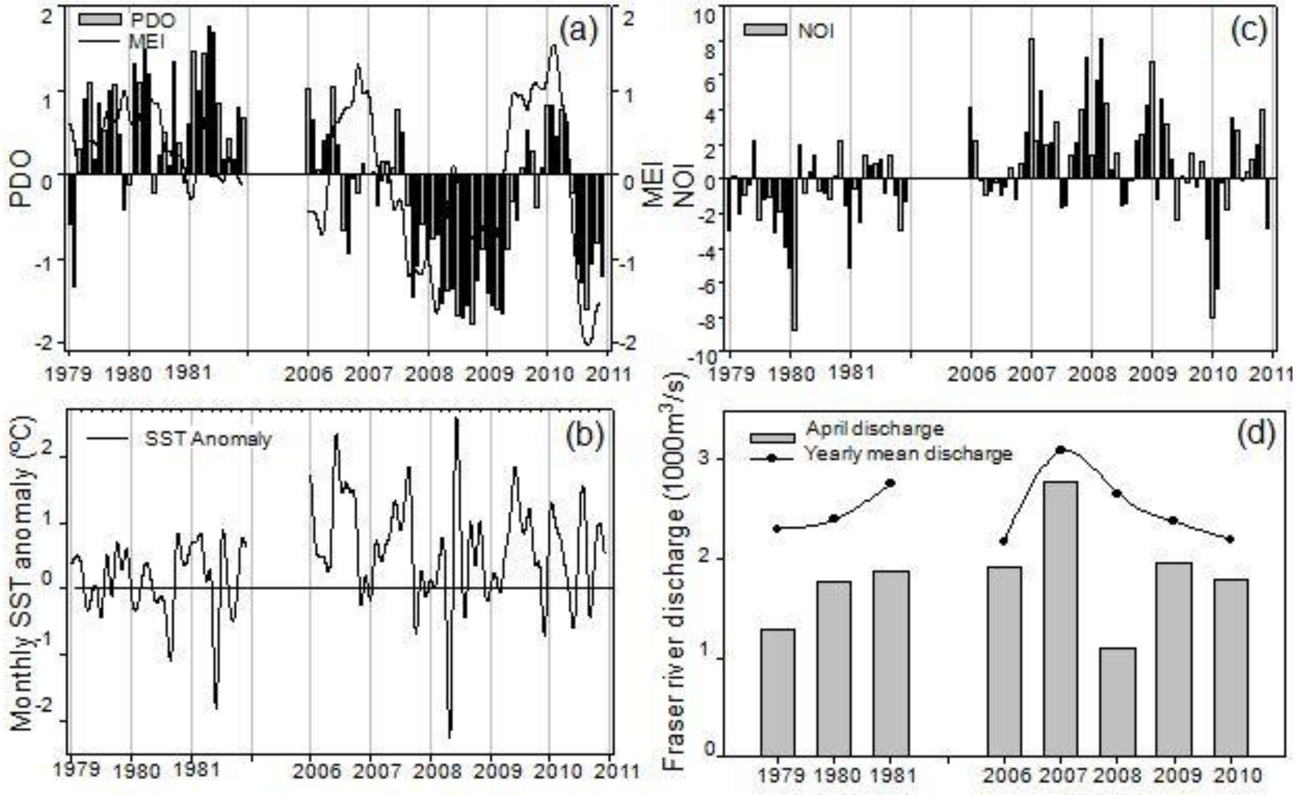


Figure 2.3. Time series of environmental variables and annual runoff from the Fraser River in the early-1980s and the late-2000s. Data are based on monthly averages of (a) the Pacific Decadal Oscillation (PDO) and Multivariate ENSO Index (MEI), (b) the Northern Oscillation Index (NOI), (c) sea surface temperature (SST) anomalies from lighthouse data at Entrance island, and (d) annual averages and April values of Fraser River discharge ($1000 m^3/s$).

pacificus (eulachon), and the flatfishes: *Atheresthes stomias* (arrowtooth flounder), *Reinhardtius hippoglossoides* (Greenland halibut), and *Inopsetta ischyra* (forkline sole), along with the deep water species of *Lycodapus mandibularis* (pallid eelpout) and Myctophidae (lanternfishes).

During the late-2000s surveys, 23 families represented by 65 species were collected and identified. The larval assemblage was characterized by six dominant families which accounted for 95.1% of total larval abundance: Merlucciidae (23.6%), Scorpaenidae (17.2%), Bathylagidae (17.1%), Pleuronectidae (15.9%), Clupeidae (12.4%), and Gadidae (9.1%). The dominant species were the same as the early 1980s, the exception being *L. exilis* which became more dominant in recent years. However, the six dominant species accounted for a smaller proportion (87.7%) of the total larval abundance compared to the 1980s. *Ammodytes hexapterus* (Pacific sandlance), snailfishes, and the flatfishes: *Hippoglossoides elassodon* (flathead sole), *Lepidopsetta bilineata* (rock sole), and *Parophrys vetulus* (English sole), along with a variety of agonids (poachers) and cottids, were collected at relatively high frequency but low abundances.

2.3.3 Interdecadal differences in larval abundance

Changes in the mean abundance of total larvae in late April revealed significantly higher larval abundance in the early 1980s than in the late 2000s (Fig. 2.4, Table 2.3). This trend was consistent among the different intercalibration treatments. Excluding *M. productus*, *L. schmidti*, and *L. exilis*, whose abundances were likely underestimated in recent surveys (see 2.4.2 in Discussion), the significant decadal decline in the total larval abundance remained for the rest of the larval assemblage (p < 0.0001, Table 2.3). The overall abundance of rare taxa remained similar (~14.0 larvae 1000 m^{-3}) in both periods (Table 2.3).

For taxa (except *C. pallasi*) to which I applied intercalibration coefficient, the interdecadal trends displayed in original larval abundances remained consistent across all intercalibration

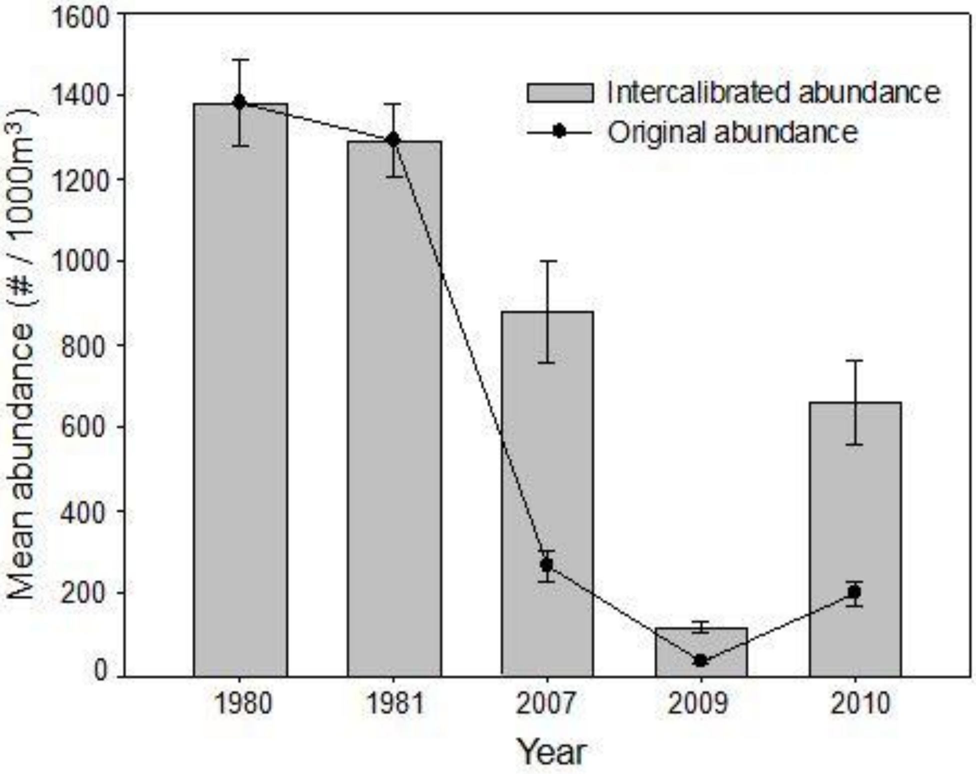


Figure 2.4. Original and calibrated total larval abundance (error bars ±1 SE) in late April of 1980, 1981, 2007, 2009 and 2010. Original total larval abundances were based on averages over all samples collected from each survey. Calibrated abundances were calculated by multiplying original abundance by an intercalibration factor of 3.3. Points indicate the original abundances. Bars indicate estimates after intercalibration.

treatments. In contrast, *C. pallasi* showed similar original larval abundances between two study periods (Fig. 2.5, Table 2.3), but higher abundances in the late 2000s with the application of any intercalibration treatment. Larvae of the other dominant fish species (*T. chalcogramma*, *M. productus*, *L. schimidti*, and *Sebastes* spp.) were more abundant in the early 1980s (Fig. 2.5, Table 2.3), although *M. productus* and *L. schimidti* may have been underestimated in recent surveys because their diel vertical migration may have exceeded the sampling depth (see 2.4.2 in Discussion). Large interannual variability in larval abundance of these species was also evident within each time period, with the lowest abundance occurring in 2009. In contrast, Pleuronectidae larvae were more abundant in the late 2000s. Among rare species, although the larvae of Agonidae and *A. hexapterus* were low in abundance, their decadal trends were similar to the Pleuronectidae. Furthermore, Cottidae, Cyclopteridae (lumpsuckers), Gobiidae (gobies), and Pholidae (gunnels) did not show any significant change in larval abundance between the two decades (Table 2.3).

Larval fish assemblages in the SoG were dominated by pelagic species, which were less diverse but more abundant than demersal species. Only six pelagic species were found in the ichthyoplankton samples and four of these were dominant species. All other species were demersal, except for the anadromous *Thaleichthys pacificus* (eulachon, Table 2.3). Overall, the total abundance of larval pelagics decreased from the 1980s to 2000s, as did larval demersals. Among the six pelagic species, only the Osmeridae (smelts) experienced an increase in abundance between the 1980s and the 2000s. Among demersal species, only three taxa: *Sebastes* spp., Stichaeidae, and *Microgadus proximus* (Pacific tomcod) showed a decrease in abundance. The abundance of other demersal species either increased or did not change.

The pelagic/demersal abundance ratio decreased from 14.8 in the early 1980s to 2.1 in the late 2000s when taking all comparable species and families into account. If the two dominant

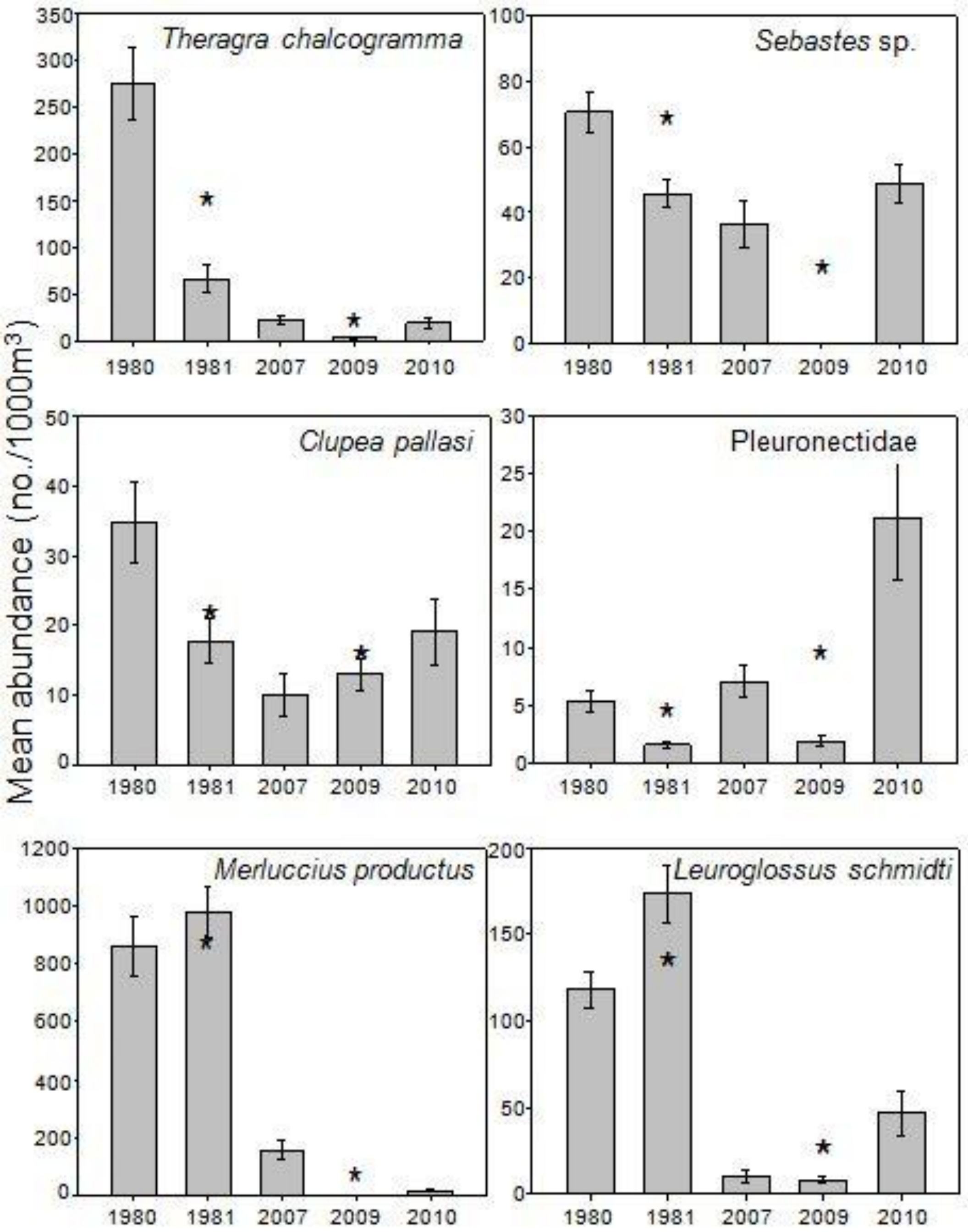


Figure 2.5. Average larval abundance (error bars ±1 SE, no intercalibration applied) of the most abundant fish taxa/groups in late April of 1980, 1981, 2007, 2009 and 2010. Asterisks indicate the average larval abundance within each of the two sampling periods (early-1980s and late-2000s).

species (*M. productus* and *L. schmidti*) are excluded, this ratio drops to 2.1 and 0.7 in the two periods, respectively. In summary, the overall fraction of the SoG larval assemblages represented by demersal species has increased compared to three decades ago.

2.3.4 Interdecadal differences in species composition of spring larval fish assemblages

PCO analysis revealed strong differences between the two time periods in spring larval fish assemblages in the SoG. The first and second PCO axes explained 46.3% and 19.9%, respectively, of the total variance in the original resemblance matrix, suggesting that a two-dimensional projection captures the salient patterns of the full data cloud. Samples from the early 1980s clustered closely together in the ordination space, showing high similarity in species composition (Fig. 2.6a). Samples from the late 2000s displayed a clear separation from the 1980s samples along the first PCO axis, but with relatively broader dispersion along the second PCO axis, indicative of greater variation in species composition in contemporary samples. PERMDISP test verified the different dispersions of data clouds from two study periods (Pseudo-$F = 197.3$, $p_{\text{perm}} = 0.0001$); meanwhile, the PERMANOVA test also suggested significant interdecadal differences in assemblage composition (Pseudo-$F = 101.24$, $p_{\text{perm}} = 0.0001$). A further ANOVA test comparing PCO1 values of data cloud centroids between the early 1980s and late 2000s (11.5 ± 0.67 and -18.4 ± 1.7, respectively) confirmed the significant differences in assemblage composition ($F = 356.3$, $p < 0.0001$). Species showing correlations >|0.2| with the first two PCO axes (11 of 14) were overlaid onto the PCO ordination space (Fig. 2.6b). *M. productus* displayed the highest positive correlation (r = 0.79) with the PCO1 axis, while the correlation for *L. schmidti* (r = 0.19) was much weaker. Both species experienced a notable decline in relative abundance between decades (Fig. 2.6b). In contrast, *C. pallasi* (r = -0.87) and Pleuronectidae (r =

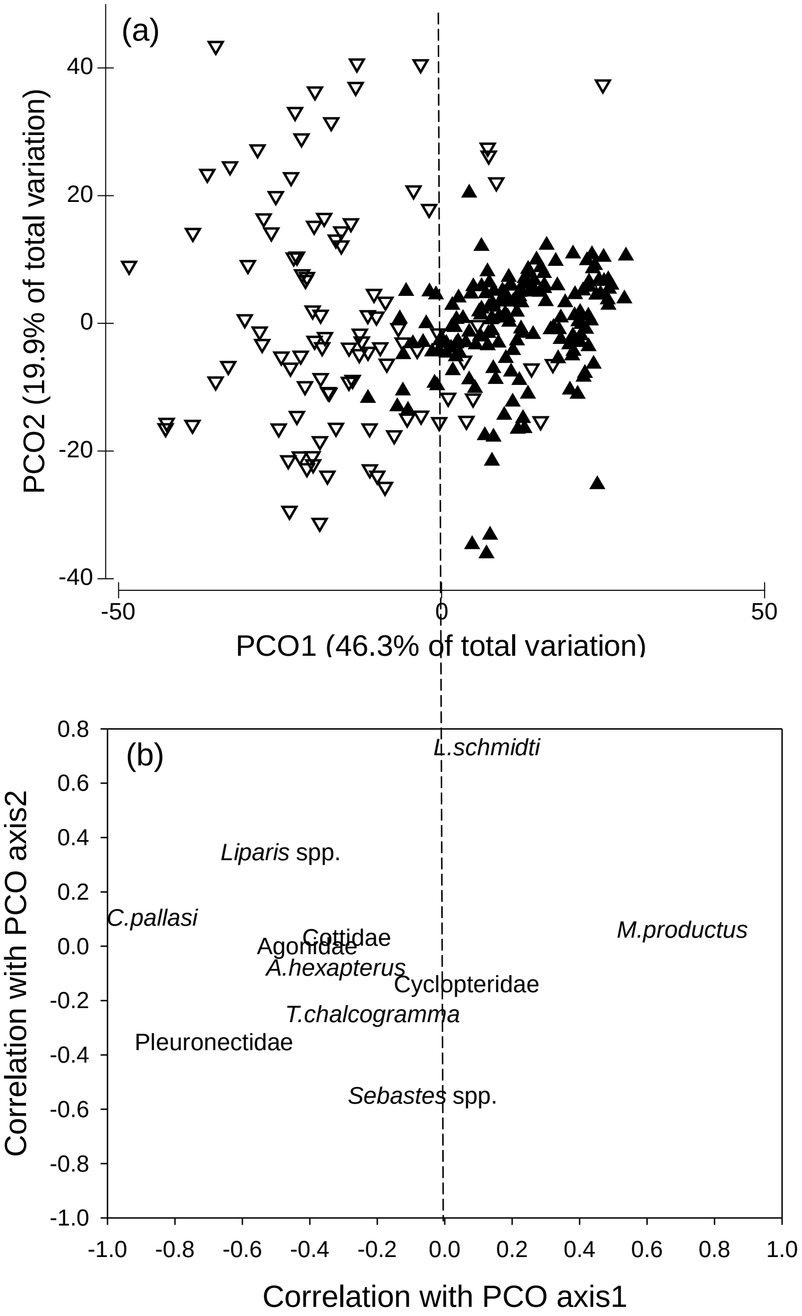


Figure 2.6. (a) Principal coordinates (PCO) ordination of larval fish assemblages based on all samples from 1980s and 2000s with all species (frequency of occurrence > 5%) including *Merluccius productus* and *Leuroglossus schmidti*; (b) Correlations of individual species with the first two PCO axes. Solid triangles: samples collected during early 1980s. Open triangles: samples collected in late 2000s.

-0.66) had the largest increases in relative abundance on the decadal scale. *Liparis* spp. (r = -0.50), *A. hexapterus* (r = -0.25), Agonidae (r = -0.34), and Cottidae (r = -0.25) displayed similar but weaker trends. *T. chalcogramma* (r = -0.15) and *Sebastes* spp. (r = -0.04) displayed weak loadings on the PCO1 axis. Similar patterns remained evident when *M. productus* and *L. schmidti* were excluded from the analysis.

2.3.5 Species associations

Two significant species associations were detected by cluster analysis (Fig. 2.7). Group A was the most distinct species cluster and was divided into two subgroups. Group A2 was composed of the most abundant taxa, which were also the local commercially valuable species, plus *L. schmidti*. Most of the species within Group A2 were pelagic taxa. The two nearshore bottom dwellers in Group A1 were less similar in temporal variation patterns compared to the tightly clustered taxa within A1 (Appendix 2). Group B consisted principally of demersal species that produce adhesive demersal eggs and are not species subject to directed commercial exploitation (Appendix 2). Larval abundance of these species increased from the 1980s to the 2000s. The remaining taxa including Gobiidae, Cyclopteridae, and *Ronquilus jordani* (northern ronquil) were also demersal species but showed similar larval abundances between decades.

2.3.6 Larval abundance and assemblage composition in relation to environmental variables

Multiple regression analyses revealed that the spring abundance of the dominant species consistently displayed strong correlations with the Northern Oscillation Index (NOI) (Table 2.4). The abundance of *C. pallasi* larvae was correlated negatively with NOI during winter-spring, showing stronger interannual variation within the late 2000s and comparable values in both NOI

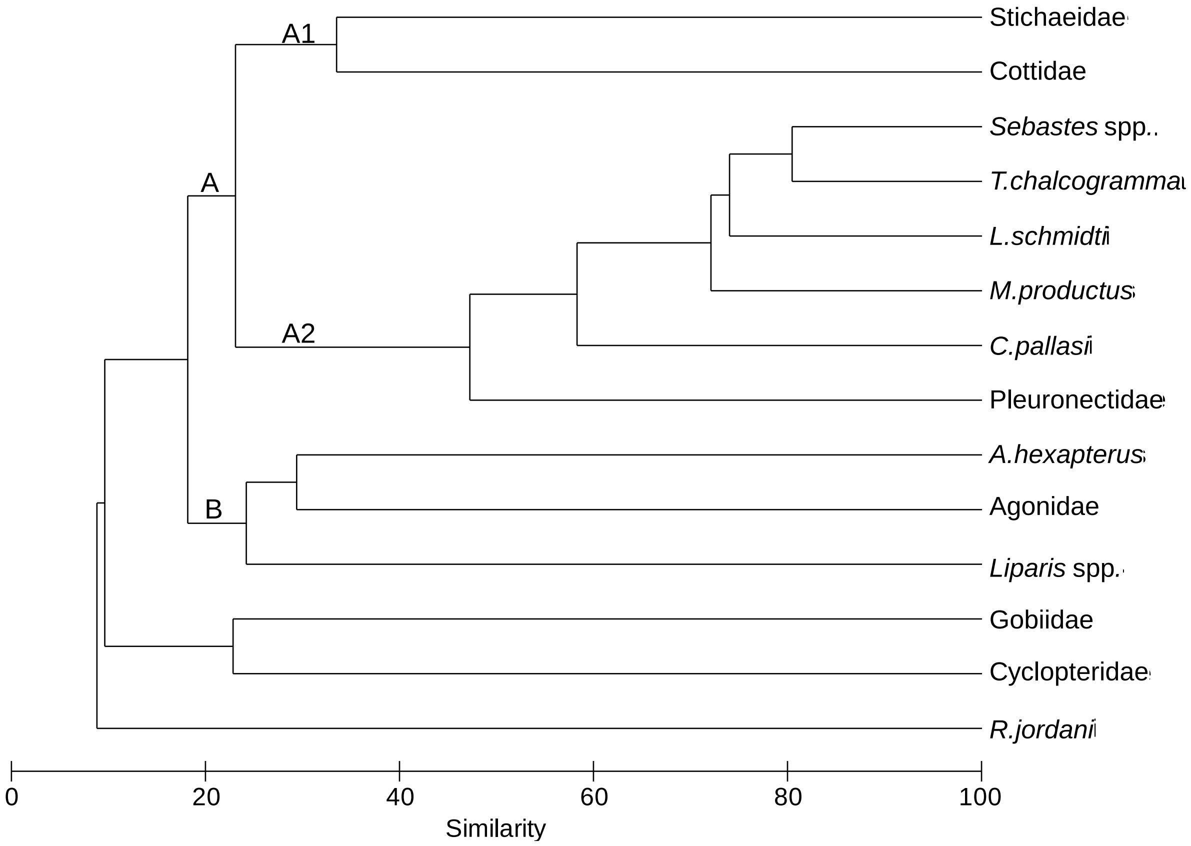


Figure 2.7. Relations among species shown by cluster analysis of taxa based on species relative abundance data. Species groups were labeled A and B, group A was split into two subgroups: A1 and A2.

Table 2.4. Best selected environmental variables and correlation coefficients from the multiple regression models for larval abundance (dominant taxa and total larvae) and environmental variables. Numbers in parentheses indicate the correlation coefficient, sign (+) and (-) indicate significant positive and negative correlation respectively. Bold indicates statistical significant at α = 0.05 for least squares linear regression analysis. (NOI: Northern Oscillation Index. PDO: Pacific Decadal Oscillation. FD_{Apr}: Fraser River discharge in April)

Species	**Selected variable**
Clupea pallasi	**$NOI_{Jan\text{-}Apr}$ (-0.943)**,
Theragra chalcogramma	**$NOI_{Sep\text{-}Dec}$ lag1(-0.884)**,
***Sebastes* spp.**	**$NOI_{Sep\text{-}Dec}$ lag1(-0.998)**, FD_{Apr} (0.145)
Merluccius productus	**$NOI_{Jan\text{-}Apr}$ lag1(-0.965)**, $PDO_{May\text{-}Aug}$ lag1 (-0.489)
Leuroglossus schmidti	**$NOI_{Jan\text{-}Apr}$ lag1(-0.668)**, $NOI_{May\text{-}Aug}$ lag1 (0.498)
Total larvae	**$NOI_{Sep\text{-}Dec}$ lag1(-0.976)**,

and larval abundances between 2010 and the early 1980s (Fig. 2.8a). The abundances of *M. productus* and *L. schmidti* larvae were also correlated negatively with this index but with a lag of one year (Fig. 2.8b, c). The abundance of *T. chalcogramma*, *Sebastes* spp., and total larvae were all negatively correlated with average NOI during fall-winter lagged by one year, and the association was strongest for *Sebastes* spp. (Table 2.4, Fig. 2.8d, e, and f). Fluctuations in larval abundance along with strong interannual NOI variations, especially within the late 2000s, existed for all examined species. In addition, the regression analysis indicated no statistically significant associations of the dominant species with the PDO index or Fraser River discharge (Table 2.4).

DistLM analysis was used to investigate relationships between the environmental variables and composition of the larval fish assemblages based on annual average larval abundances (Fig. 2.9). The first and second dbRDA axes captured 90.7% and 9.3% of the variance in the fitted model, which corresponds to 59.7% and 6.1% of the total variance in the original Bray-Curtis dissimilarity matrix. Analogous to the results of PCO analysis, strong decadal differences in assemblage composition between 1980s and 2000s were evident along the first axis in the constrained dbRDA plot; while interannual differences, particularly within the late 2000s, became apparent along the second axis. The marginal tests showed that among all the large scale and local environmental variables only two indices - winter-spring NOI lagged by one year, and winter-spring PDO, significantly explained 59.1% and 54.1% of the total variance in the data cloud when considered alone (p = 0.026 and 0.034, respectively). When considered together, the two variables explained 66.0% of the variance in the assemblage structure. The multiple partial correlations showed that the first dbRDA axis was strongly negatively correlated with winter-spring NOI lagged by one year (r = -0.943), but positively correlated with winter-spring PDO (0.334). The high correlation between dbRDA1 and NOI reflected the influence of large-scale climate changes on decadal differences in composition structure of larval fish

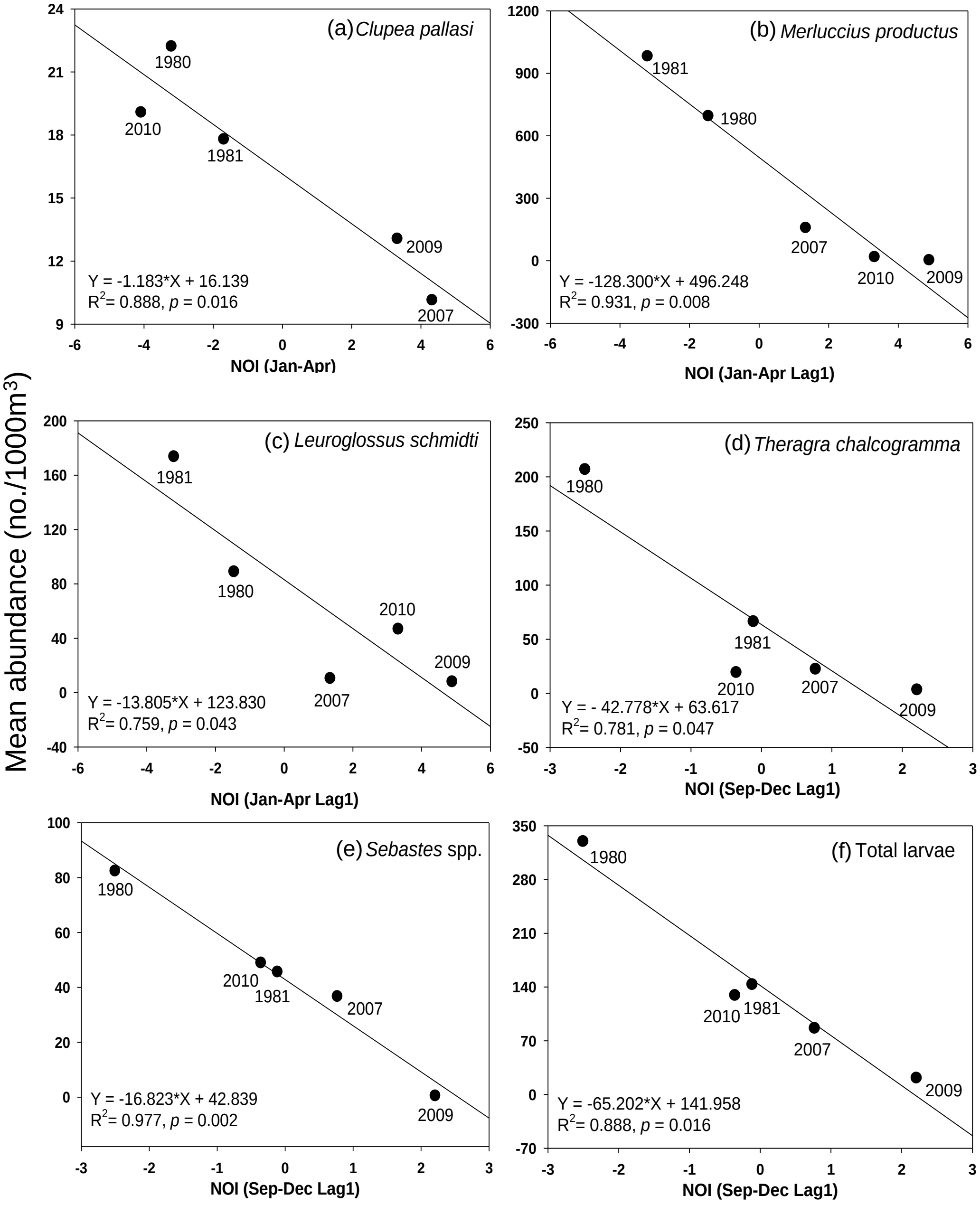


Figure 2.8. Relationship between larval abundance and Northern Oscillation Index for (a) *Clupea pallasi*, (b) *Merluccius productus*, (c) *Leuroglossus schmidti*, (d) *Theragra chalcogramma*, (e) *Sebastes* spp., (f) Total larvae. Larval abundances were based on averages over all samples collected in each sampling year. Climate indices were based on seasonal averages of Jan-Apr and Sep-Dec. Lag 1: with a lag of one year. NOI: Northern Oscillation Index. Linear regression statistics and fitted lines are shown in each panel.

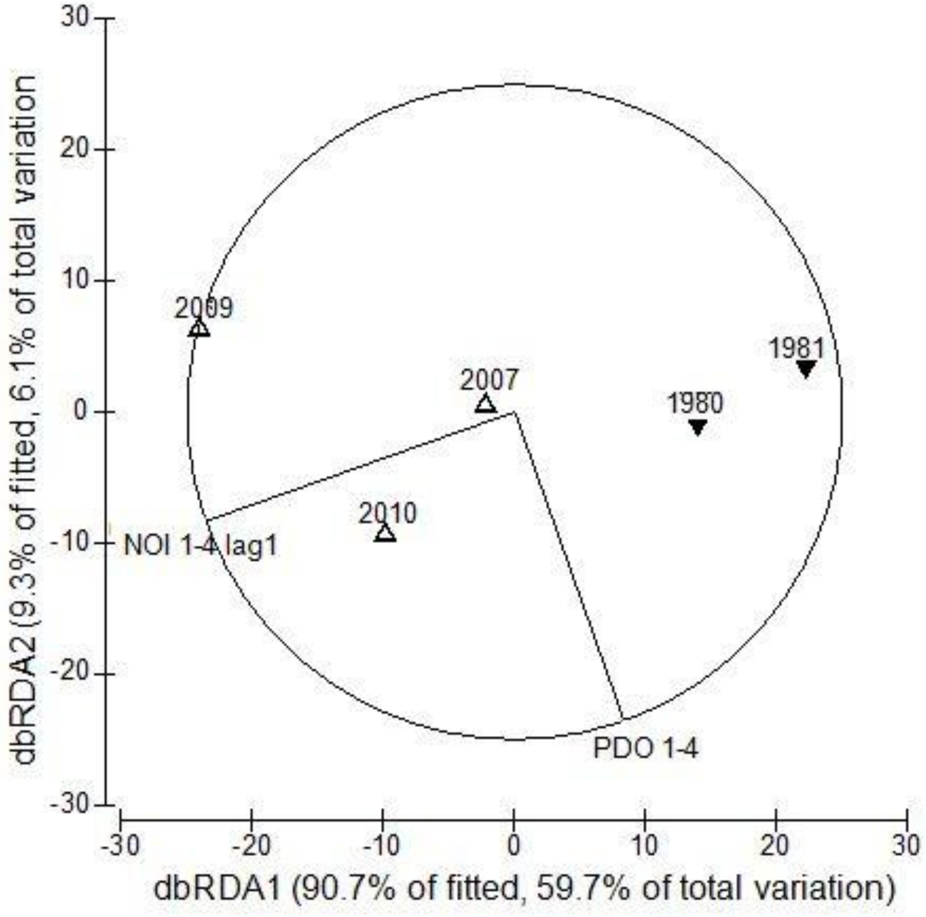


Figure 2.9. Constrained dbRDA ordination of larval fish assemblages with significant environmental variables based on average larval abundance over all samples collected in late April of each sampling year. Vectors display partial correlations of environmental variables with the first two dbRDA axes. NOI_{1-4} lag1: mean value of Northern Oscillation Index from January to April with lag of one year. PDO_{1-4}: mean value of Pacific Decadal Oscillation from January to April. Solid triangle: samples from early 1980s. Open triangle: samples from late 2000s.

assemblages. Similarly, the second dbRDA axis displayed its strongest correlation with winter-spring PDO (r = -0.943) which reflected the associations between climate fluctuations and interannual variations in the composition of larval fish assemblages.

2.4 Discussion

2.4.1 Interdecadal variation in larval abundance and assemblage composition

Analyses of the SoG larval fish assemblages revealed notable differences in abundance and composition of spring assemblages between the early 1980s and late 2000s. In general, the SoG larval assemblages were dominated by a few pelagic fish species that consistently make up a majority of the overall larval abundance. In the early 1980s, the dominant species was *M. productus*, followed by three pelagic species (*T. chalcogramma*, *L. schmidti*, and *C. pallasi*), and demersal *Sebastes* spp. to a lesser extent. According to the SoG commercial fishery records (Fisheries and Oceans Canada, unpublished), all of these taxa, with the exception of *L. schmidti*, were fished commercially in the 1980s (Appendix 2). In the late 2000s, a drop in larval abundance of these dominant species, particularly some pelagic species, contributed significantly to a dramatic decline in overall larval abundance and a shift in assemblage composition. Meanwhile, demersal Pleuronectids became much more abundant in the ichthyofauna, accompanied by an increasing proportion of several non-dominant demersal forage species including *A. hexapterus*, *Liparis* spp., and Agonidae, while the abundance of their predators (e.g. adult rockfishes etc.) decreased. Interestingly, a recent study in the Gulf of St. Lawrence (Quebec, Canada) comparing ichthyoplankton assemblage composition between the same decades as this study (mid-1980s and mid-2000s) reported similar decadal declines in total ichthyoplankton abundance and long-term species turnover, with a decrease in the larvae of commercial fishes and an increase in the larvae of non-commercial, small, demersal fishes (Bui *et al*., 2010).

Fluctuations in the dominant fish species in the SoG seem to have been affected by both fishing and environmental variations, the effects of which are intertwined and difficult to separate. The most prominent changes among the pelagic species in the SoG between the early 1980s and late 2000s were the decreased absolute and relative abundance of *M. productus* and the corresponding relative increase of *C. pallasi*. Note that the average absolute abundance of *C. pallasi* larvae did not decline in the 2000s, consistent with a recent stock assessment indicating that the *C. pallasi* stock in the SoG was relatively stable, and that its biomass remained well above the fishing cutoff (DFO, 2008; 2011). Commercial removal of *C. pallasi* in the SoG was also comparable between the early-1980s and late-2000s, although there have been fluctuations during each period (Fig. 10a).

M. productus has been considered an important contributor to ecosystem dynamics in the SoG as a result of its relatively high abundance and high trophic level. Although an increase in *M. productus* abundance has been documented in recent years (Beamish *et al*., 2008), my data show dramatically lower larval *M. productus* abundance in the 1980s compared to the 2000s. Similar decreases were observed for two other midwater species: *T. chalcogramma* and *L. schmidti*. Unfortunately, stock assessments are lacking for these species in the SoG. If the adult populations of these species declined (as suggested by my observations), higher fishing pressure from commercial catches of *M. productus* and *T. chalcogramma* in the early 1980s than the late 2000s may have been a contributor (Fig. 2.10 a, b); in addition, decreased abundance of *M. productus*, *T. chalcogramma* and *L. schmidti* could have positively affected the herring population by reducing predation pressure.

Sebastes spp. and Pleuronectids, which are long-lived, slow-growing, benthic carnivores, experienced the most pronounced changes within the demersal fish assemblages. Based on very limited biological observations and catch data, inshore *Sebastes* spp. in the SoG have experienced

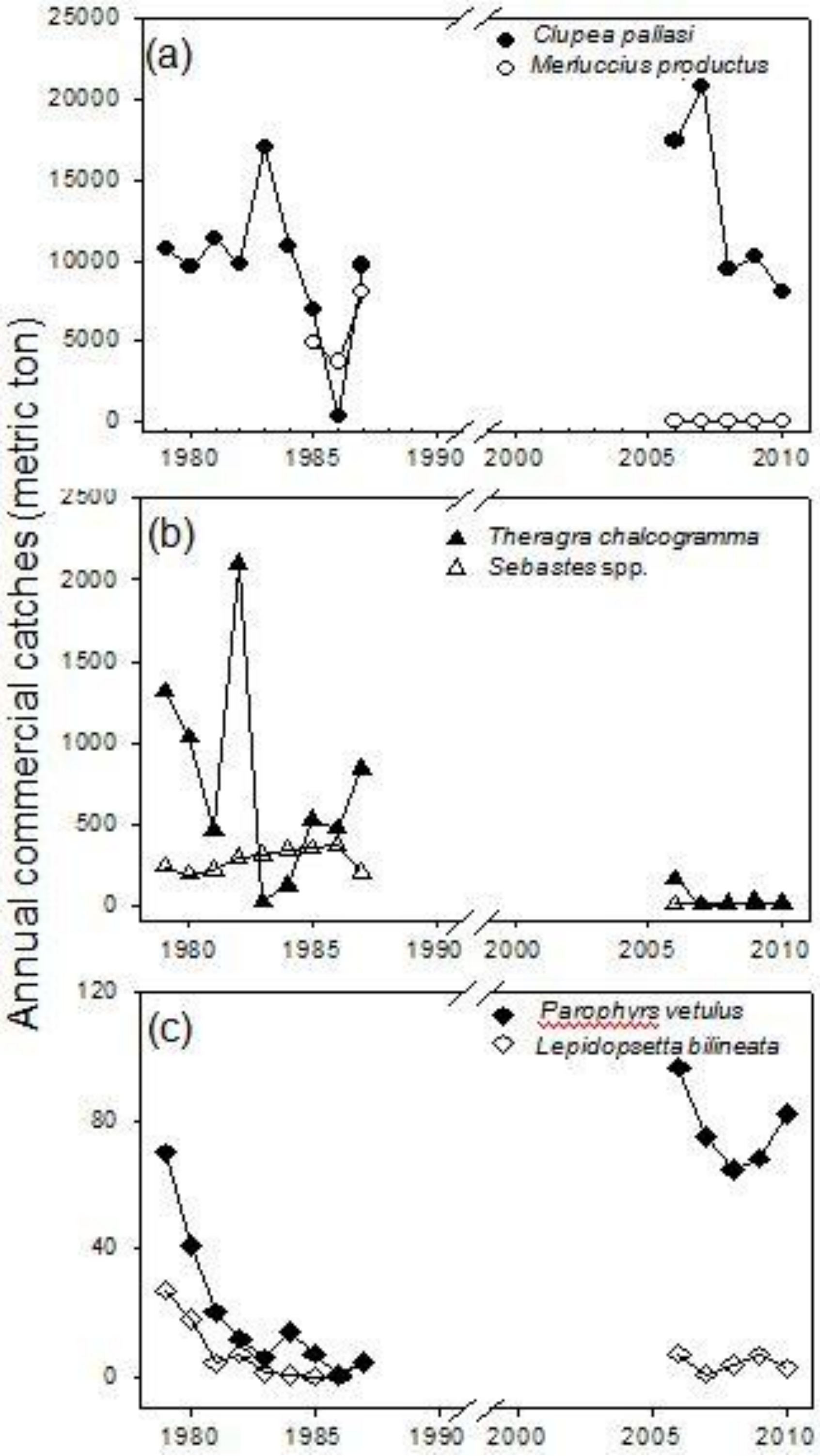


Figure 2.10. Annual commercial catches during the 1980s (1979-1987) and the late-2000s (2006-2010) in the Strait of Georgia. (a) *Clupea pallasi* and *Merluccius productus*, (b) *Theragra chalcogramma* and *Sebastes* spp., (c) *Parophyrs vetulus* and *Lepidopsetta bilineata*. Catch statistics data were provided by Regional Data Services Unit, Fisheries and Oceans Canada.

dramatic declines in abundance, mainly as a result of an expanded and unrestricted fishery during the 1970s and 1980s (Yamanaka and Lacko, 2001; Yamanaka and Logan, 2010). Compared to the late 2000s, higher commercial catches of *Sebastes* spp. in the early 1980s could put more pressure, and even threats, on SoG rockfish populations (Fig. 2.10b). Currently, several *Sebastes* spp. in the SoG are considered to be threatened species and species of special concern (Yamanaka and Logan, 2010). In contrast, Pleuronectids, which are important predators in benthic communities, increased dramatically in recent years. Similar trends were also observed for Pleuronectids along the west coast of Vancouver Island in 2010 (Crawford and Irvine, 2011). Along with population increase, harvesting pressure on these fishes, particularly the *Parophrys vetulus* (English sole), rose correspondingly in the 2000s (Fig. 2.10c).

2.4.2 Larval fish and environmental conditions

Relationships between larval fish dynamics and environmental variability are complex, usually non-linear, and involve multiple environmental factors and pathways (Hsieh *et al*., 2005; Auth *et al*., 2011). Analyses indicate that fluctuations in larval production in the SoG were significantly affected by changes in large-scale climatic conditions, especially their interannual variations. Although the NOI displayed the strongest and broadest negative associations with larval production, it is difficult to specify this causal relationship based on very limited years of observations.

Large-scale climate variability in the North Pacific likely affects the water properties and surface currents in the SoG via physical processes such as changes in sea level pressure (SLP) and atmosphere-ocean interaction, thereby indirectly affecting larval fish survival and growth through multiple mechanisms simultaneously. More specifically, changes in SLP are closely linked to changes in surface winds, an important component of atmosphere-ocean interaction and heat exchange, and will affect the variability in SST, upper ocean temperature, mixed layer depth, and direction and strength of near surface wind-driven currents in the SoG directly (Schwing *et al*., 2002). Variations in the intensity of local winter and spring wind mixing can also modify the timing of the SoG spring phytoplankton bloom (Allen and Wolfe, 2013). Furthermore, climate-associated fluctuations in the timing and amount of precipitation and snowmelt influence Fraser River discharge and the timing and magnitude of the summer freshet, which in turn influence the entrainment of nutrients and the magnitude of phytoplankton production (Yin *et al*., 1997) and hydrodynamic features of estuarine circulation. The composition of the phytoplankton community can also be affected by the entrained nutrients. Taken together, these factors all contribute to the variability of survival and growth of zooplankton in the SoG (El-Sabaawi *et al*., 2009). In addition, SLP-associated changes in the strength of trade winds and coastal upwelling-favorable winds will modify the intensity of upwelling offshore, and thus influence the level of nutrients supply of deep estuarine inflow to the SoG via the Strait of Juan de Fuca. For instance, negative NOI periods, such as the early-1980s and 2010, were generally associated with El Niño events, with weaker than normal SLP over the Northeast Pacific, weaker trade winds, weaker coastal upwelling winds, warmer upper ocean temperatures, and associated with high larval abundance within the SoG. In summary, large-scale climate variability in the North Pacific can affect larval fish production in the SoG by altering water temperature, nutrients levels, the production and composition of phytoplankton and zooplankton communities, and the degree of timing match-mismatch between consecutive trophic levels.

Recent studies of biological production in the SoG not only indicated that variations in the timing of the spring bloom and zooplankton biomass are significantly correlated with the North Pacific Gyre Oscillation index (NPGO, DiLorenzo, *et al*., 2008) which indicates fluctuations in the mechanisms driving plankton dynamics in the Northeast Pacific (DiLorenzo, *et al*., 2008;

Mackas *et al*., 2013; Allen and Wolfe, 2013), but also suggested that the extratropical-based Southern Oscillation Index (SOIx, Schwing *et al*., 2002) as the best single indicator of changes in zooplankton community composition (Li *et al*., 2013). Similarly, studies on the continental shelf of the Northeast Pacific have linked large-scale climate forcing factors to variations in larval fish abundance. For example, using generalized additive models, Auth *et al*. (2011) found that large-scale climate indices, particularly the PDO, explained more variability in larval fish abundance than did local environmental factors. In the southern California Current region, Hsieh *et al*. (2005) showed that variations in the abundance of most oceanic taxa also tracked the PDO. In contrast, the PDO showed only a weak association with zooplankton in the SoG (Mackas *et al*., 2013; Li *et al*., 2013).

2.4.3 Factors affecting larval abundance estimates

Differences in sampling protocols between the early 1980s and late 2000s could have affected larval abundance estimates in several ways. First, the Bongo net (351 µm mesh) used in 1980s was more efficient in capturing small larvae than was Tucker trawl (1mm mesh) used in 2000s. Gear intercalibration indicated that more of the small and slender larvae were extruded through the Tucker trawl because of its larger mesh size (Pepin and Shears, 1997; Guan and Dower, unpublished data). In contrast, larger and older larvae could likely escape from the Bongo net because of its smaller mouth area and so larval abundance could be underestimated in both cases.

Second, the whole water column was sampled in 1980s whereas only the upper layer (50m to surface) was sampled in 2000s. The shallower sampling depth in the recent surveys could also induce negative bias in larval abundance estimates. However, several studies conducted in Northeast Pacific have suggested that the greatest abundances of fish larvae were consistently near the thermocline in regions ranging from California to the Gulf of Alaska (Ahlstrom, 1959; Boehlert *et al*., 1985; Brodeur and Rugen, 1994). For example, off the Oregon coast (87.5% of fish larvae were found within the top 50m of the water column, with peak abundance centered near the thermocline at 20-30m (Boehlert *et al*., 1985; Auth *et al*., 2007). In the SoG, the average depth of the thermocline was 20-25m in late April of 2009 and 2010, which is similar to the depth off the Oregon coast. Thus, the vertical distribution of fish larvae in the SoG is likely analogous to the records from that region suggesting that Tucker trawl was sampling a high fraction of the ichthyoplankton community. *M. productus* larvae, on the other hand, were abundant through 200-250m in the SoG during April and at shallower depths as they developed (McFarlane and Beamish, 1985). Newly-hatched *L. schmidti* larvae were also found with hake larvae in the deeper layer, but the majority of the older larvae were located between 40-90m (Mason and Phillips, 1985). Therefore, the recent sampling of the upper 50m of the water column should be sufficient to characterize pelagic larval abundance of the majority of fish taxa in the SoG, with the possible exception of *M. productus* and *L. schmidti*. Underestimation of larval abundance of these two species, especially their newly hatched larvae, in the recent period could be possible due to their deeper vertical distribution which extends below the sampling depth ~50m in the SoG.

Finally, ichthyoplankton samples were collected during day and night in recent surveys, but only during daytime in 1980s. Examination of diel variability in 2010 showed significantly fewer *M. productus* and *L. schmidti* larvae in the upper layer at night compared to day. Haldorson *et al*. (1993) also found *L. schmidti* larvae to be less abundant near the surface at night, presumably due to a reverse diel vertical migration. However, Alverson and Larkins (1969) found *M. productus* larvae to be more abundant near the surface at night, presumably due to a regular diel vertical migration. Taken together, these results suggest an underestimation of the average abundance of *L. schmidti* larvae in recent surveys, especially at night.

2.4.4 Phenology and match-mismatch

In temperate marine ecosystems, zooplankton and larval fish have adapted to typical seasonal cycles of seawater temperature, but remain highly sensitive to changes in baseline temperatures. Rapid changes of ecological characteristics such as demographic timing, development rate, and species composition in response to temperature variation, particularly in the upper water column, have been suggested for zooplankton in various studies (Mackas *et al*., 1998; Bornhold, 2000; Mackas *et al*., 2007; Mackas *et al*., 2012). Developmental timing of *Neocalanus plumchrus*, historically the dominant copepod in the Northeast Pacific, shifted ~60 days earlier during 1990s compared to the early 1970s due to the warming trend in the upper-ocean temperatures (Mackas *et al*., 1998). A more recent study (Mackas *et al*., 2007) revealed a shift of several weeks to earlier seasonal peaks in biomass of *N. plumchrus* in warm years in both oceanic and coastal regions in the Northeast Pacific. Similar phenomena have been documented in the SoG from the 1960s to the 1990s whereby the developmental timing of *N. plumchrus* shifted gradually toward an earlier peak (~25 days) during a period characterized by a 1-2 ℃ increase in surface water temperature (Bornhold *et al*., 2000). Observations of stage composition of this species in the early-2000s (2002-2005) revealed a similar but accelerated early shifting trend (Fig. 13b in Johannessen and Macdonald, 2009).

Unlike the situation for copepods, very few studies on the phenology of larval fish assemblages exist. In the North Sea, a study of ichthyoplankton based on observation over 7 years and across 27 species showed that the timing of larval fish abundance was significantly negatively correlated with winter-spring SST in weeks 1-10 (Greve *et al*., 2005). The explanation proposed was that the gonadal development rate of adults is faster under higher temperatures, thereby leading to earlier spawning in warmer years. If the same mechanism applies in the SoG, the similar winter mean SST during Jan – Mar (7.4 ℃ and 7.5 ℃ in early-1980s and late-2000s, respectively) would suggest that the observed interdecadal differences are probably not due to phenology. On the other hand, direct observations of changes in phenology of fish in the SoG are limited. *C. pallasi* is the only species for which a long-term phenology time series is available. The mean spawning date was very similar between the two study periods: approximately the 15th and 18th of March in the early-1980s and the late-2000s, respectively (*C. pallasi* spawn and catch records, Fisheries and Oceans Canada). Furthermore, as part of an unrelated project we measured otolith microstructure of *M. productus* larvae from recent surveys in the SoG and constructed an age:length relationship (Age = 6.68*Length – 21.9). Back-calculation of the mean hatch date of *M. productus* larvae was in early April in the late 2000s (Dower, unpublished data). In the early 1980s, we estimated a similar peak hatch time based on my examination of annual changes in the abundance of stage IV *M. productus* eggs from historical ichthyoplankton surveys in 1980 and 1981, and inspecting the annual abundance-at-date curve to calculate the date of peak abundance (Dower and Guan, unpublished data). Together, data from these two sampling periods suggests that there has not been a significant change in the phenology of spawning for Pacific hake in the SoG. Unfortunately, we have no comparable data for any other fish species. However, if phenological effects are manifest across the entire SoG assemblage (i.e. as in the North Sea), the lack of any such effects for two of the dominant species (*C. pallasi* and *M. productus*) suggests that the interdecadal differences in the abundance and species composition of the SoG ichthyoplankton assemblages that we detected are in fact real changes and not merely phenological artefacts.

Food availability is a key determinant of larval fish survival and somatic growth (Leggett and DeBlois, 1994). As larvae of most fish feed primarily on zooplankton <500 µm in size, copepod eggs, nauplii, and some small copepods (e.g. *Pseudocalanus*) are their major dietary components (LeBrasseur *et al.*, 1969). An advance in timing of the dominant copepod *N.*

plumchrus has been observed in the SoG, but evidence from the SoG for other copepods is lacking. If such a temperature-driven temporal advance also exists for other co-existing copepod species, the lack of phenological change in the larval fish assemblages could create the opportunity for a timing mismatch between these two consecutive trophic levels. However, the potential effect of a predator-prey mismatch in time could also be compensated for by high abundances of microzooplankton (Durant *et al*., 2005). Although the SoG is generally considered to be a very productive ecosystem, at least one previous study found evidence that microzooplankton abundance in the SoG was at marginal abundances and could restrict the survival of larval fish (LeBrasseur *et al*., 1969). Therefore, the possibility that a mismatch between larval fish assemblages and microzooplankton may have contributed to the declines in larval fish production cannot be ruled out. Unfortunately, my analysis is data-limited, and evidence from further investigations will be needed to clarify this point.

The ichthyoplankton data analyzed in this study were collected during the last week of April in each sampling year. As such, they provide only a snapshot of the annual pattern of larval fish production. For instance, larvae of species with spawning periods in summer and autumn would have been missed in our samples. Moreover, we were unable to examine seasonal patterns of several important species (e.g. *M. productus*, *T. chalcogramma* and *L. exilis*) in recent years and the long-term variability in seasonal patterns among the sampling years as a result of the limited sampling time. Although a temporal mismatch between fish larvae hatching times and their zooplankton prey was discussed as one contributor to the recent declines in overall larval fish abundance, examinations of other crucial factors affecting early larval survival such as match or mismatch in the spatial distribution with their prey and predators in the SoG, or shifts in the composition and nutritional condition of the zooplankton community are still lacking. In addition to the significant interdecadal differences in the spring ichthyoplankton assemblages presented in this study, considerable interannual variability among recent sampling years was evident in our data. Investigating these changes and possible climate and oceanographic driving forces will provide additional information for assessing changes in ichthyoplankton assemblages through time.

Chapter 3

Interannual variability in spring larval fish assemblages in the Strait of Georgia in response to the 2007 - 2010 ENSO events

3.1 Introduction

Being both predators on microzooplankton and the prey of zooplanktivorous fish, the early life stages of marine fishes represent a crucial trophic linkage in marine food chains, and their temporal dynamics can therefore influence the trophic structure of the entire marine ecosystem. At an early stage of development, larval fish production can be used as a primary indication of reproductive success of spawning adults (Hsieh *et al*., 2005), and can be used to monitor the status of commercially and ecologically important fish stocks, and predict the future recruitment potential of these stocks (Houde, 1997). In the pelagic marine environment, larvae of different fish taxa, which share the same habitat and spawning period, usually form multispecies assemblages (Doyle *et al*., 1993). The co-occurrence of different species of larval fish potentially reflects similar responses to the variable environmental conditions. Features of these assemblages such as abundance, composition and distributions are sensitive to short-term changes in the environment, and their variations have been suggested as potential “ecosystem indicators” of environmental shifts (Brodeur *et al*., 2008). In the Strait of Georgia (SoG), ichthyoplankton surveys have been conducted occasionally since 1960s to study a few dominant and commercially valuable species such as *Merluccius productus* (Pacific hake, McFarlane and Beamish, 1985), *Clupea pallasi* (Pacific herring, Hay and McCarter, 1997) as well as *Leuroglossus schmidti* (northern smoothtongue, Mason and Phillip, 1985). However, the recent status of the SoG ichthyoplankton assemblage, and its relation to environmental influences is still largely unexplored.

The SoG ecosystem has been undergoing notable changes under cumulative pressures from accelerating global climatic changes and anthropogenic activities. A gradual warming trend has been observed since 1970 throughout the entire water column (Masson and Cummins, 2007). In addition to the decadal warming trend, the SoG system has been experiencing more frequent shifts between El Niño and La Niña events which produced episodic warming on interannual scales. Climate-change induced variations in seasonal patterns of freshwater discharge from the Fraser River (such as earlier timing and reduced volume of the summer freshet) can also affect the SoG ecosystem (Morrison *et al*., 2002). On the other hand, living marine resources in this coastal basin have been intensively used by humans and the ecosystem has been disrupted by numerous threats from commercial and recreational fishing, contamination from local sewage discharges, habitat destruction through urbanization and construction, increasing marine traffic and the introduction of invasive species via ballast water or hull fouling. All of these changes can potentially induce stress on larval fish assemblages in the SoG by altering the physical environment. Therefore, understanding how local fishes respond to distinct short-term environmental fluctuations during their early life stage is of great need for conservation and fishery resource management purposes.

Ichthyoplankton surveys were conducted recently (2007, 2009 and 2010) in the SoG with the principal purpose to characterize the spatiotemporal variability in larval distribution. During the period from 2007-2010, the Northeast Pacific Ocean experienced distinct El Niño-Southern Oscillation (ENSO) weather patterns from the typical La Niña state, which lasted through 2007 and 2008, towards the El Niño state at the beginning of 2009, and then this warm condition continued until the summer of 2010 (Crawford and McKinnell, 2009; Crawford *et al*., 2010; Crawford and Rober, 2011). In response to this 2009-2010 regime shift, zooplankton off the Vancouver Island continental margin displayed a shift in community dominance from cool-water species to warm-water species by the late summer of 2009 (Crawford *et al*., 2010). Meanwhile, a series of changes in the oceanographic environment have also been observed over this period in the SoG. For example, from 2008 to 2010, the temperature throughout entire water column has experienced the most dramatic changes over the past 25 years (Fig. 3.1). However, the reaction of biological entities to the sudden environmental changes is still unclear.

In this chapter, I examined interannual variations in the SoG larval fish assemblages in late-April of 2007, 2009 and 2010 to explore the response of larval fish to the rapid and dramatic environmental changes during this period. The specific objectives were: i) describe larval fish diversity, abundance and assemblage structure in the SoG and quantify interannual variability; ii) test for differences in larval fish abundance and assemblages structure between the northern and central-southern regions of the SoG; iii) for 2009 and 2010, develop a number of variables based on *in situ* measured water properties to describe the physical environment of fish larvae, and identify linkages between these variables and patterns of assemblage structures. Through this study, I will obtain baseline information about the recent status of the larval fish community in the SoG, gain a better understanding of short-term larval fish dynamics and their relation to environmental fluctuations, and provide valuable information for estimation of future recruitment success of dominant fishery species.

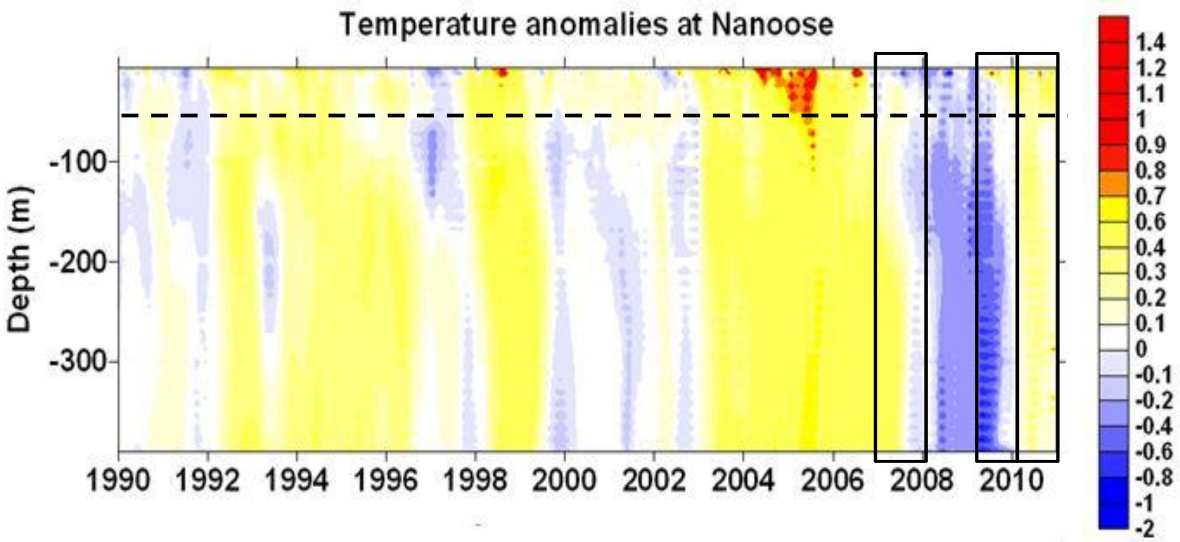


Figure 3.1. Time series of temperature anomalies over the entire water column measured at Nanoose Bay in the Strait of Georgia; figure provided by Mackas, D. (Institute of Ocean Sciences, Fisheries and Oceans Canada). Dash line indicates 50m. Frames highlight sampling years in this study: 2007, 2009 and 2010.

3.2 Materials and methods

3.2.1 Field sampling procedure

The SoG was divided into two regions – the northern SoG and central-southern SoG at the southern tip of Texada Island and Lasqueti Island (Fig. 3.2a). Larval fish samples used in the present study were collected in 2007, 2009 and 2010. A total of 57 sites was sampled during April 25-28, 2009, and 60 sites were sampled during April 24-27, 2010 (Fig. 3.2b). Only 12 of these sites were sampled twice in two continuous cruises during April 25-29 in 2007 (Fig. 3.2c). Sites sampled in 2009 and 2010 were largely consistent in geographic position. Sampling sites were spaced around 8-10km apart and sampled continuously through both day and night. At each site, a Seabird -19 conductivity-temperature-depth sensor (CTD) was deployed to measure physical properties of water column from the surface to ~5m from the sea floor. Next, a 1 m^2 Tucker trawl equipped with 1mm mesh size net was rapidly lowered ~50m depth and then towed back to surface obliquely for approximately 15 minutes at a ship speed of 1m/s. Water volume filtered by the Tucker trawl was measured by a calibrated TSK flowmeter placed at the center of the net mouth. The depth of the Tucker trawl was tracked by an attached Vemco Minilog-12TX depth logger. On the deck, the Tucker trawl was rinsed, and samples were washed into the cod-end and immediately preserved in 95% Ethanol. After the cruise all preserved larvae were sorted, counted and identified to the lowest taxonomic level possible, according to Matarese *et al*. (1989) and the Ichthyoplankton Information System (2011). Species-level identifications were possible for most taxa except the larvae of *Sebastes s*pp. (rockfishes) and *Liparis* spp. (snailfishes) which were identified to a generic level based on meristics and pigmentation patterns. Larval size was measured to the nearest 1 mm in standard length.

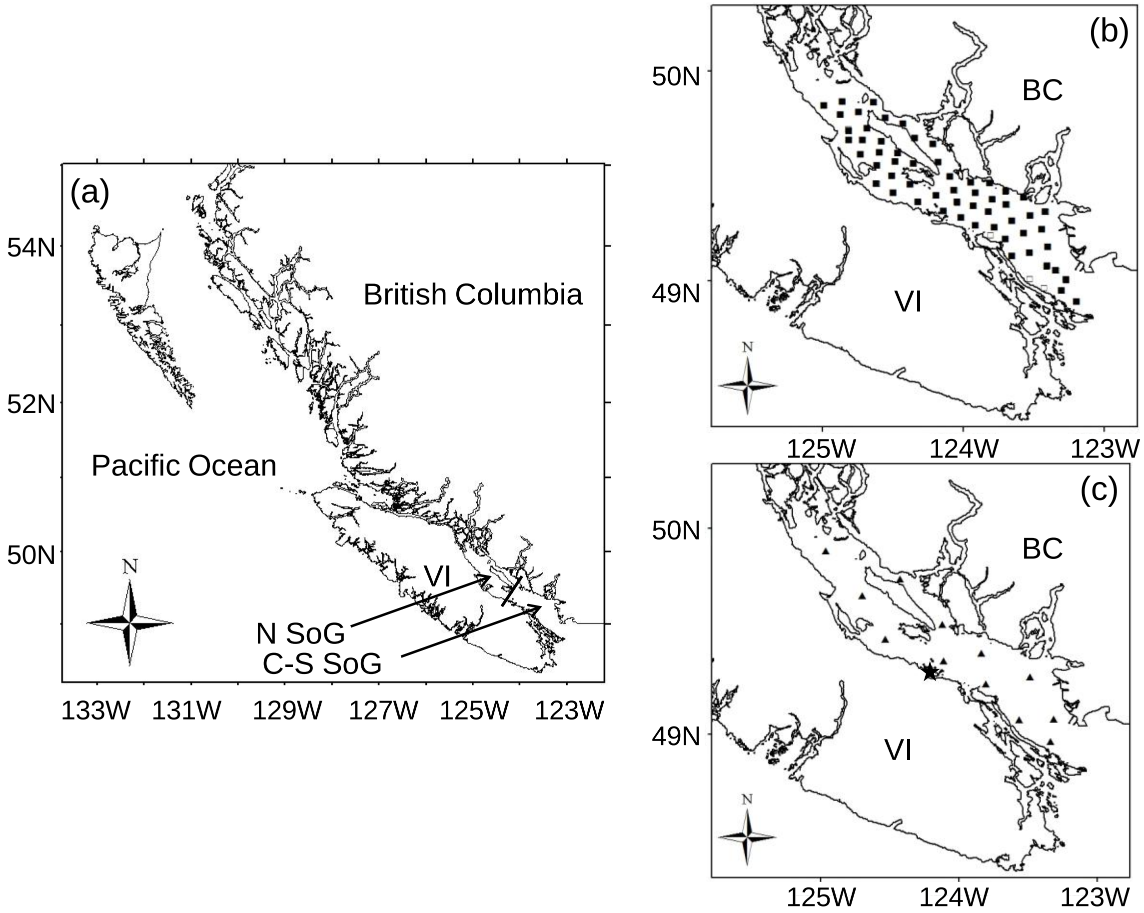


Figure 3.2. Map showing sampling locations of ichthyoplankton surveys in the Strait of Georgia (SoG) off mainland British Columbia (BC) and Vancouver Island (VI). Maps show (a) the Strait of Georgia, (b) sites sampled in 2009 and 2010, represented by solid squares in figure, and extra three sites added in 2010 are represented by open squares, (c) sites sampled in 2007, represented by solid triangles. The Nanoose Bay station is represented by the solid star in figure (c).

3.2.2 Environmental indices

To characterize changes in the environmental conditions over the sampling period (2007-2010), I examined time series of two regional climatic indices: the Pacific Decadal Oscillation Index (PDO), Mantua *et al*. (1997), obtained from JISAO, University of Washington, (http://jisao.washington.edu/pdo/PDO.latest) and the Multivariate El Nino-Southern Oscillation Index (MEI), Wolter and Timlin (1998), obtained from NOAA Earth System Research Laboratory (http://www.esrl.noaa.gov/psd/enso/mei/table.html). The PDO is based on the sea surface temperature variability in North Pacific and usually shifts on inter-decadal scales (Mantua *et al*., 1997). In contrast, the MEI is used to monitor the ENSO events which usually vary on interannual time scales. I also examined monthly changes of three local environmental indices representing conditions within the SoG over 2007-2010: sea surface temperature (SST), the temperature at the lower limit of the sampling layer (~ 50m), and the Fraser River discharge. SST was recorded from the DFO lighthouse at Entrance Island (49.130 °N 123.480 °W, http://www.pac.dfo-mpo.gc.ca/science/oceans/data-donnees/index-eng.htm). Temperature at 43m was obtained from Fisheries and Oceans Canada (DFO) buoy weather data at Halibut Bank (49 ° 20.4 ´N, 123 ° 43.6 ´ W, http//www.pac.dfo-mpo.gc.ca/science/oceans/data-donnees/buoydatadonneebouee/index-eng.htm). Volume of freshwater discharged from Fraser River was measured at Hope, British Columbia and obtained from the Water Survey of Canada (www.ec.gc.ca/rhc-wsc/).

Based on the habitat descriptors developed in Pepin *et al*. (2011), I used a series of indices based on the CTD profiles from each site to characterize important physical properties (temperature, salinity, oxygen and fluorescence) of the water column from which the samples were taken. These indices also included:

- latitude (Lat), longitude (Long) and bottom depth (D_{Bot}) which provided the geographic position and bathymetry information;
- temperature, salinity and oxygen at surface (T_{sur}, S_{sur}, O_{sur}), at bottom (T_{Bot}, S_{Bot}, O_{Bot}), at 50m which was the lower limit of the sampling layer (T_{50}, S_{50}, O_{50}) and their vertical averages over the sampling layer ($T_{0\text{-}50}$, $S_{0\text{-}50}$, $O_{0\text{-}50}$);
- the minima and maxima of temperature and oxygen over entire water column (T_{min}, T_{max}, O_{min}, O_{max}), and the depth where the extremes occurred (Z_{Tmax}, Z_{Tmin}, Z_{Omax}, Z_{Omin});
- the differences in water temperature and salinity between surface and 50m which indicated stratification (Delta_$T_{0\text{-}50}$, Delta_$S_{0\text{-}50}$);
- chlorophyll fluorescence values at surface, fluorescence maxima, and vertical average from surface to 20m (F_{sur}, F_{max}, $F_{0\text{-}20}$) which represented the amount of phytoplankton.

Water property indices were only developed for stations sampled in 2009 and 2010 due to the limited sampling effort in 2007. Similarly, analyses based on these indices were limited to 2009 and 2010. In addition, $T_{0\text{-}50}$, $S_{0\text{-}50}$, $F_{0\text{-}20}$, Delta_ $T_{0\text{-}50}$ and Delta_ $S_{0\text{-}50}$ were averaged across all stations sampled within each year to describe the average state of the SoG over the survey periods. Normalization and principal component analysis (PCA) were performed on the above 25 water property indices to seek the existence of general patterns in the multivariate ordination space. The PCA scores on the first five PCA axes (which explained 76% of total variance) for each observation were used as the base for later multivariate analyses linking assemblage structures to environmental predictors.

3.2.3 Data processing and analysis

Larval abundance was estimated three ways: (i) the total number of larvae per 1000m^3, (ii) the average abundance of individual taxa across all sites and (iii) across sites within each region (northern and central-southern) for each year. Relative abundance was estimated as the percentage abundance of each species over the total larval abundance, and the occurrence of taxa was estimated as the percentage of sampling sites at which a given species occurred. The pelagic:demersal ratio was calculated as total larval abundance of all pelagic species divided by total abundance of all demersal species (Collie *et al*., 2008). This index indicates the extent to which the ichthyoplankton community was dominated by either pelagic or demersal species.

Margalef's richness index, Shannon's diversity index and Pielou's evenness index were calculated for each sample based on the collected taxa, and then averaged across all sites for annual mean values. Annual averages of larval size measurements and size frequency distributions were also calculated for four dominant fish species (*M. productus, L. schmidti, C. pallasi* and *Theragra chalcogramma* [walleye pollock]) and four flatfishes (*Lyopsetta exilis* [slender sole], *Parophrys vetulus* [English sole], *Lepidopsetta bilineata* [rock sole] and *Hippoglossoides elassodon* [flathead sole]).

A total of 141 larval fish samples representing 23 fish families were collected, and 49 taxa was identified to species level. Rare species within the families Agonidae, Cottidae, Gobiidae and Stichaeidae were combined at the family level to reach the 5% threshold for abundance comparison and community analysis. Analysis of Variance (ANOVA) and pairwise comparisons were performed on ln(N+1) transformed larval abundance data to test for significant differences among sampling years and geographic regions. ANOVA was also applied on diversity, richness, evenness and larval length to test for significant interannual differences. All ANOVAs were performed using SYSTAT (Version No.12.02) software.

Larval assemblages were analyzed using a series of multivariate approaches. Only species/families with a frequency of occurrence higher than 5% (21 species/families in total) were included in the analyses. For each sample unit, larval abundance for each taxon was standardized by total larval abundance, fourth-root transformed to reduce the influence of a few highly abundant and rare species, and then converted to a Bray-Curtis dissimilarity matrix as the basis for further analyses (Clarke and Gorley, 2006).

To test for significant interannual and regional differences in species composition of larval fish assemblages, permutational multivariate analysis of variance (PERMANOVA), a variance partitioning method analogous to ANOVA (but based on the Bray-Curtis dissimilarity matrix) was performed, first using pairwise test with 9999 random permutations to test for significance (Anderson *et al*., 2008). Next, canonical analysis of principal coordinates (CAP) was performed to discriminate samples from three annual groups (2007, 2009 and 2010), and to assess how distinct these groups were from one another in the multivariate space. As a constrained ordination approach, CAP serves to find axes through the multivariate data cloud that maximize the differences and best separate groups, and which might not have been easily discriminated by unconstrained ordination methods such as MDS and PCO (Anderson *et al*., 2008). Cross-validation was performed to assess the CAP model by removing one sample at a time and checking the ability of the model to reassign that sample back to the correct group. To explore which species best characterized annual patterns, fish taxa/families were overlaid in the CAP ordination space to examine their associations with the first two CAP axes according to a Spearman rank correlation between standardized abundance and the CAP ordination scores (Anderson *et al*., 2008). A dendrogram created by hierarchical cluster analysis based on Bray-Curtis dissimilarity matrix was then used to determine which regions or years were most similar in species composition (Clark and Warwick, 2001). Annual average larval abundance of each taxon across all sites within each region (northern and central-southern SoG) constituted the sampling units for the dissimilarity matrix.

Distance-based linear models (DISTLM) were used to analyze the relationship between larval assemblage structures and environmental variables based on data collected in 2009 and 2010. Analogous to traditional regression analysis, DISTLM partitions the variance in a multivariate data cloud based on a dissimilarity matrix (according to a regression or multiple regression model), and then calculates a pseudo-*F* statistic and tests for significance by permutation (Anderson *et al*., 2008). Distance-based redundancy analysis (dbRDA) was then used to perform a constrained ordination of fitted values from the given multivariate regression model to look for linear combinations of environmental variables which explain the greatest variation in the data cloud. Partial correlations between significant environmental predictors and dbRDA ordination scores along the first two axes were calculated as the base of overlaying these predictors in the ordination space (Anderson *et al*., 2008). Analyses were first applied to 25 water property indices to determine the specific variables that could significantly explain some portion of the variance. The same analyses were then performed again but using different sets of environmental predictors - PCA scores (PC1-PC5) from PCA analysis on water property indices for verification and comparison. All of the multivariate analyses were performed through PRIMER statistical software version 6 (PRIMER-E) and PERMANOVA+ for PRIMER.

3.3 Results

3.3.1 Environmental conditions

The large-scale climatic indices (PDO and MEI) exhibited strong interannual fluctuations over the late-2000s (Fig. 3.3a). Both indices decreased dramatically from late 2006 to mid 2008, but then recovered from early 2009 to early 2010, reflecting shifts between El Niño-Southern Oscillation (ENSO) events during 2006-2010. The thermal status of the whole water column in the SoG roughly followed the patterns in the climate indices but with delays: the SoG shifted

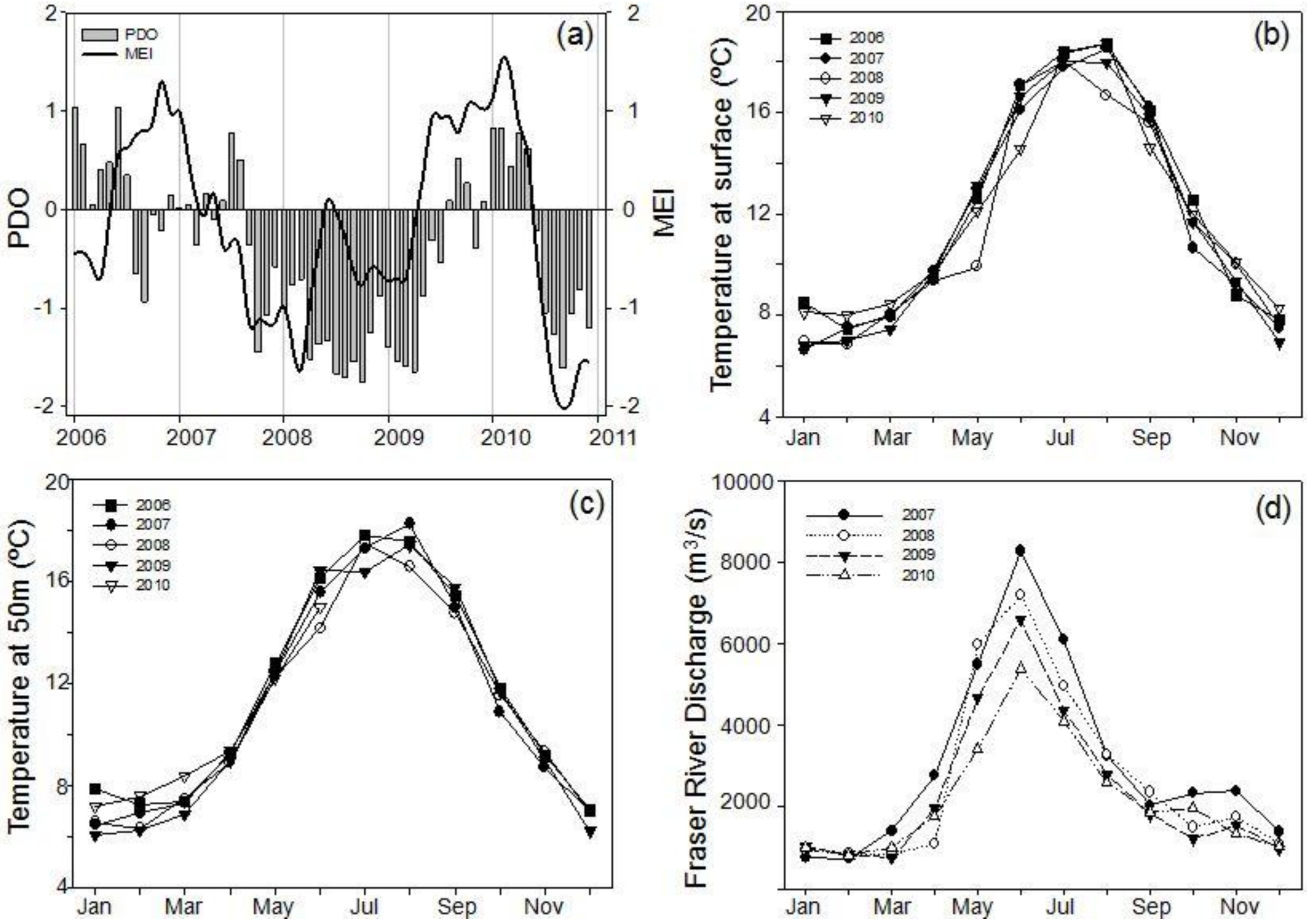


Figure 3.3. Time series of climate indices and monthly changes of environmental variables during 2006-2010. Data shown are based on monthly averages of (a) the Pacific Decadal Oscillation (PDO) and the Multivariate ENSO Index (MEI), (b) sea surface temperature (SST) measured from lighthouse at Entrance Island, (c) seawater temperature at 50m measured from the DFO buoy (46146; 49 °20.4´N, 123 °43.6´W) at Halibut Bank, and (d) the Fraser River discharge (m^3/s).

from a warm oceanic phase towards a colder phase in 2007, this cold status lasted throughout 2008 into early 2009, before shifting back in late 2009 to finally return to warmer conditions by early 2010 (Fig. 3.1). During the early portion of the year from January to March, surface waters were consistently more than 1 ℃ warmer in 2010 compared to 2009, with 2007 in between; and temperatures in April were very similar across years (Fig. 3.3b). The same patterns existed for water temperatures at 50m, representing the interface between the upper and deeper layers (Fig. 3.3c). However, seawater in the upper layer was colder in the previous November and December of 2010 than 2009 (Fig. 3.3b and c). Freshwater discharge from the Fraser River generally peaked in June (Fig. 3.3d), and the discharge in 2009 was slightly higher than in 2010 (from January to April) with the exception of March 2009 (Fig. 3.3d).

The first two principal components (PC1 and PC2) of the 25 water property indices for the samples collected in 2009 and 2010 explained 29.7% and 22.2% of the total variance (Fig. 3.4), with the third, fourth and fifth components explaining 10.2%, 7.6% and 6.3% of total variance, respectively. Salinity indices, followed to a lesser extent by fluorescence and oxygen indices, generally displayed negative values on PC1 showing an inverse relationship with temperature indices (which loaded positively). These loadings along PC1 mainly reflected interannual variations in water properties, with cold saltier waters rich in phytoplankton and oxygen in 2009 (Fig. 3.5, Table 3.1). On PC2 axis, positive loadings of salinity indices along with negative loadings of fluorescence, oxygen and stratification were more indicative of within SoG variations in water properties which were mainly affected by the Fraser River discharge and horizontal mixing (Fig. 3.4). Water temperature and salinity in the surface layer increased gradually along a latitudinal gradient towards northern SoG, with stronger vertical thermal stratification evident in 2009 (Fig. 3.5, Table 3.1). The influence of Fraser River discharge was more evident in 2010 with warm and less saline waters occurring in the vicinity of the estuary and

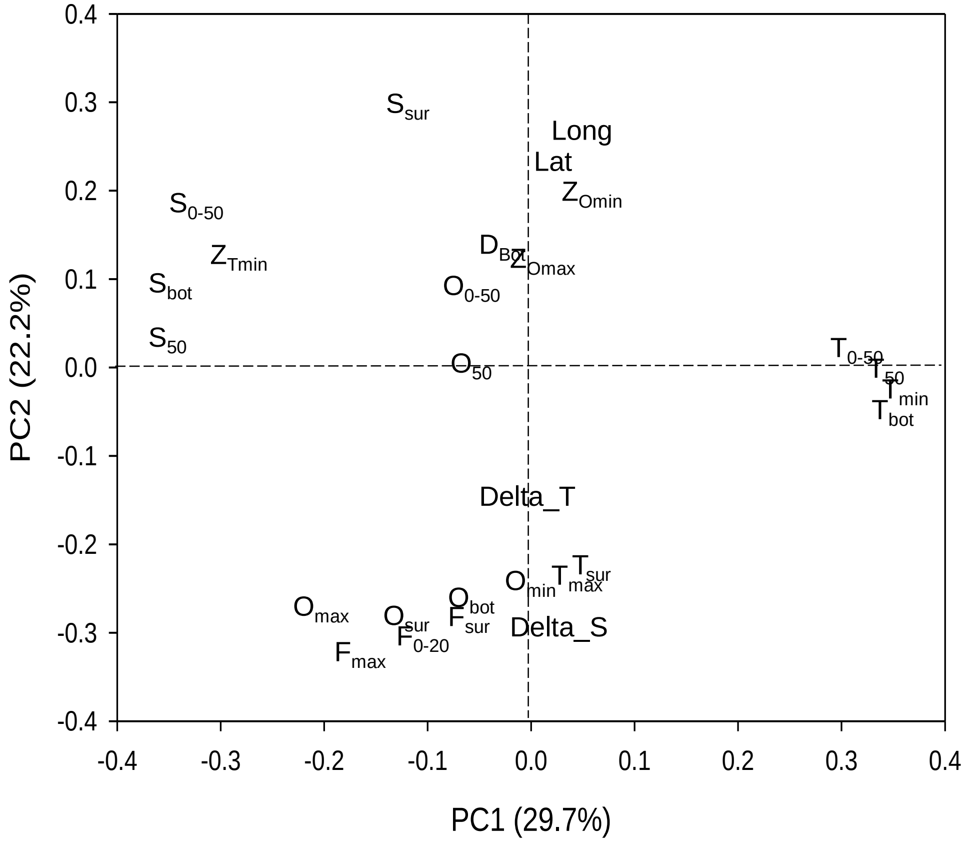


Figure 3.4. Principal component analysis (PCA) of 25 environmental variables representing geographic position, bathymetry information and water property indices, based on data collected during surveys in 2009 and 2010. Lat: latitude; Long: longitude; D_{Bot}: bottom depth; T_{sur}, T_{Bot}, T_{50} & $T_{0\text{-}50}$: temperature at surface, bottom, 50m, vertical average over 0-50m; S_{sur}, S_{Bot}, S_{50} & $S_{0\text{-}50}$: salinity at surface, bottom, 50m, vertical average over 0-50m; O_{sur}, O_{Bot}, O_{50} & $O_{0\text{-}50}$: oxygen at surface, bottom, 50m, vertical average over 0-50m; T_{min}, T_{max}, O_{min} & O_{max}: the minima and maxima of temperature and oxygen over entire water column; Z_{Tmax}, Z_{Tmin}, Z_{Omax} &Z_{Omin}: the depth where the extremes of temperature and oxygen occurred; Delta_$T_{0\text{-}50}$ & Delta_$S_{0\text{-}50}$: differences in water temperature and salinity between surface and 50m; F_{sur}, F_{max} & $F_{0\text{-}20}$: chlorophyll fluorescence values at surface, fluorescence maxima, and vertical average over 0-20m (details see 3.2.2 Environmental indices).

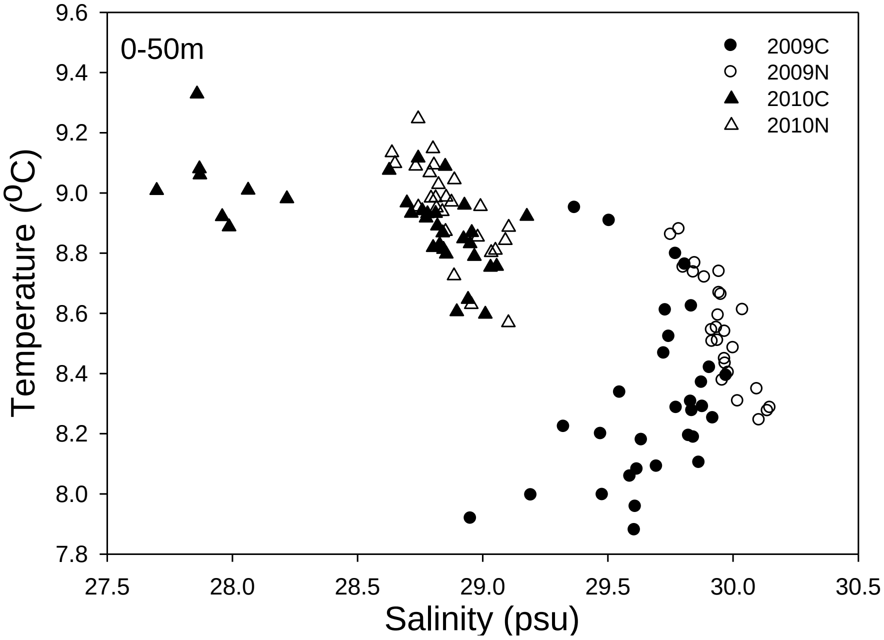


Figure 3.5. Temperature-Salinity plot of average measurements over the surface layer (0-50m) based on field observations in April of 2009 and 2010. Solid circle: TS data collected in central-southern SoG in 2009; open circle: TS data collected in northern SoG in 2009; solid triangle: TS data collected in central-southern SoG in 2010; open triangle: TS data collected in southern SoG in 2010.

Table 3.1. Spatially-averaged measurements of principal physical environmental variables in the upper layer (0-50m) over all observations from the entire SoG, based on field observations from the 2009 and 2010 surveys. T_{0-50} indicates average temperature over 0-50m; S_{0-50} indicates average salinity over 0-50m; ΔT_{0-50} indicates differences in water temperature between surface and 50m; ΔD_{0-50} indicates differences in water density between surface and 50m; F_{0-20}indicates average chlorophyll fluorescence values over 0-20m.

	T_{0-50} (℃)	S_{0-50} (psu)	$\Delta T_{0\sim50}$ (℃)	$\Delta D_{0\sim50}$ (Kg/m^3)	F_{0-20} (ug/L)	Wind mixing (m^3/s^3)
2009	8.4	29.8	0.034	0.036	11.5	73.1
2010	8.9	28.7	0.028	0.037	10.4	285.6

separated from other water masses mixed by the stronger winds (Fig. 3.5, Table 3.1). In addition, the strongest loadings for the oxygen indices were generally on the third and fourth PC axes which led to the complex relationships with other indices.

3.3.2 Biodiversity measures of spring larval assemblages

The Margalef's richness and Shannon's diversity of the larval fish assemblages displayed similar interannual patterns: their values were similar in the late-April of 2007 and 2009, but were significantly higher ($p < 0.001$) during the same period in 2010 (Fig. 3.6). Species evenness increased significantly from the lowest value in 2007 to the highest value in 2009, before a modest decline in 2010 (Fig. 3.6).

3.3.3 Composition, abundance and size of spring larval fish assemblages

The larval fish assemblage in the SoG was typically dominated by a few families and species through the sampling years. The six families accounting for most (~94%) of the total abundance were: Merlucciidae (21.78%), Scorpaenidae (22.85%), Bathylagidae (10.91%), Pleuronectidae (19.53%), Clupeidae (10.23%) and Gadidae (9.07%). However, the composition of these dominant families varied among the sampling years (Fig. 3.7). Pleuronectidae and Cottidae were the two families with the highest diversity. At the species level, six dominant species/group including *M. productus*, *L. schmidti*, *L. exilis*, *C. pallasi*, *T. chalcogramma* and *Sebastes spp*. accounted for 86.5% of the total abundance. The larvae of *Ammodytes hexapterus* (Pacific sand lance), *Liparis spp*. and several flatfishes – *H. elassodon*, *L. bilineata* and *P. vetulus*, along with a variety of Agonids and Cottids were collected at relatively high frequency but low abundance (Table 3.2). Among flatfishes, dominance of slender sole larvae was apparent in all sampling years.

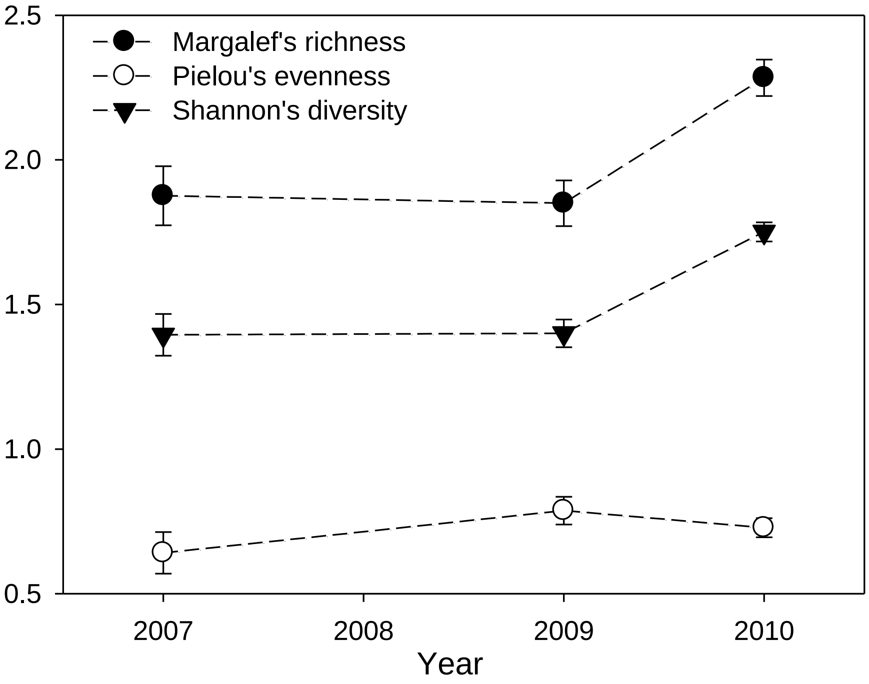


Figure 3.6. Interannual trends in biodiversity measures (±1 SE) in 2007, 2009 and 2010.

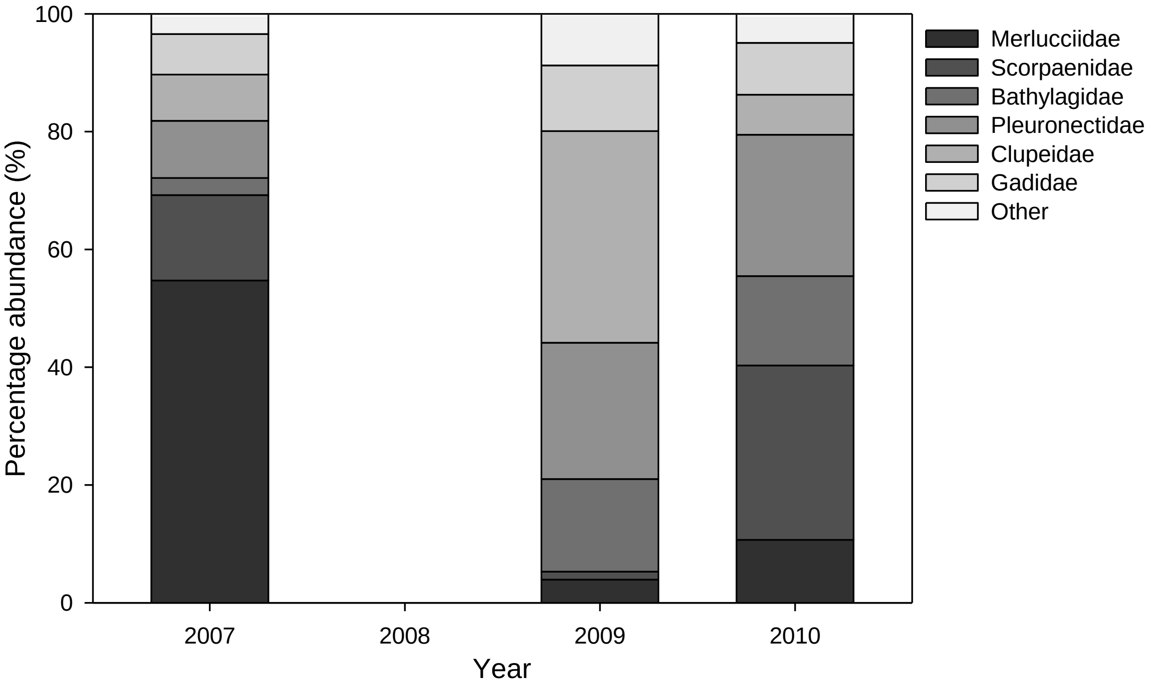


Figure 3.7. Percentage abundance of the six dominant fish families within the Strait of Georgia in late-April of 2007, 2009 and 2010.

Changes in the mean abundance of total larvae in late-April of 2007, 2009 and 2010 revealed remarkable interannual variability. The catch of total larvae in 2007 (249.0 per 1000m^3) was similar to 2010 (201.7 per 1000m^3, $P = 0.484$), and both were over 5-fold greater than the catch in 2009 (32.0 per 1000m^3, $P < 0.0001$, Table 3.2 and 3.3), reflecting an abrupt drop in larval abundance during this time period of 2009. More specifically, the interannual changes in larval abundance of commercially fished and bycatch species showed three major patterns.

First, larval abundance of the dominant fished and bycatch species – *T. chalcogramma*, *M. productus*, *Sebastes* spp. and *L. exilis* decreased significantly from 2007 to 2009, before increasing dramatically again in 2010 (Table 3.3). Also, the abundance of *M. productus* larvae was remarkably higher in 2007 than the other two years. A second group of species including *L. schmidti*, *A. hexapterus* (a major forage species, plus five commercially fished Pleuronectids and Agonids (by-catch species) displayed similar larval abundance in 2007 and 2009, but then also followed a significant increase in 2010 (Table 3.3). Finally, the only fished species showing no change in larval abundance through the whole study period was *C. pallasi* (Table 3.3). Altogether, late-April larval abundances of all the fished and bycatch species, (with the exception of *C. pallasi*) experienced significant increases simultaneously from 2009 to 2010; whereas larval abundances of most unfished species and species with unknown fishing status were relatively stable (Table 3.3). Moreover, the pelagic/demersal abundance ratio decreased from 2.6 in 2007 to 1.9 in 2009, and then down to 0.7 in 2010. These drops suggest that the SoG larval fish assemblage shifted from dominance by pelagic species towards dominance by demersal species from 2007 to 2010.

Similar interannual patterns in mean larval size existed for the four dominant fish species (*C. pallasi*, *T. chalcogramma*, *M. productus* and *L. schmidti*) and four major flatfishes (*L. exilis*, *P. vetulus, H. elassodon* and *L. bilineata*). In general, larvae caught in late April of 2009 were the

Table 3.2. Annual mean larval abundance, relative abundance and frequency of occurrence for all fish taxa collected in the Strait of Georgia in late-April 2007, 2009 and 2010.

Taxa		Common name	2007 Mean abundance (no./1000m^3)	2009 Mean abundance (no./1000m^3)	2010 Mean abundance (no./1000m^3)	Relative abundance (%)	Frequency occurrence (%)
Family	Species name						
Agonidae		Poachers	0.89	0.52	1.36	0.81	40.85
	Agonopsis vulsa	Northern spearnose poacher	0.00	0.14	0.32	0.16	9.16
	Bathyagonus pentacanthus	Bigeye poacher	0.00	0.02	0.06	0.03	2.11
	Bathyagonus alascanus	Gray starnout	0.00	0.00	0.14	0.05	4.23
	Bathyagonus nigripinnis	Blackfin poacher	0.00	0.00	0.22	0.08	4.23
	Odontopyxis trispinosa	Pygmy poacher	0.00	0.15	0.53	0.25	18.31
	Podothecus acipenserinus	Sturgeon poacher	0.00	0.08	0.00	0.01	0.70
	Xeneretmus latifrons	Blacktip poacher	0.89	0.19	0.09	0.24	14.09
Ammodytidae	*Ammodytes hexapterus*	Pacific sand lance	0.38	0.30	0.91	1.42	33.10
Bathylagidae	*Leuroglossus schmidti*	Northern smoothtongue	7.27	5.04	30.64	10.91	59.86
Bathymasteridae	*Ronquilus jordani*	Northern ronquil	0.38	0.07	0.19	0.15	7.75
Bythitidae	*Brosmophycis marginata*	Red brotula	0.00	0.00	0.25	0.09	4.87
Clinidae	*Heterostichus rostratus*	Giant kelpfish	0.16	0.00	0.00	0.02	1.41
Clupeidae	*Clupea pallasi*	Pacific herring	19.56	11.51	13.70	10.23	86.62
Cottidae		Sculpins	3.12	0.53	1.86	1.29	42.96
	Artedius spp.		2.10	0.19	0.84	0.64	25.35
	Ruscarius meanyi	Puget Sound sculpin	0.34	0.11	0.21	0.17	11.27
	Ascelichthys rhodorus	Rosylip sculpin	0.00	0.03	0.04	0.02	2.11
	Enophrys bison	Buffalo sculpin	0.00	0.00	0.07	0.03	1.41
	Gilbertidia sigalutes	Soft sculpin	0.00	0.06	0.10	0.06	3.52
	Gymnocanthus spp.		0.00	0.02	0.00	0.01	0.70
	Icelinus borealis	Northern sculpin	0.00	0.00	0.07	0.02	2.11
	Leptocottus armatus	Pacific staghorn sculpin	0.00	0.00	0.14	0.05	2.82
	Malacocotus zonurus	Darkfin sculpin	0.00	0.05	0.00	0.02	1.41
	Myoxocephalus spp		0.53	0.02	0.00	0.08	4.23
	Paricelinus hopliticus	Thornback sculpin	0.00	0.00	0.14	0.05	4.23
	Radulinus asprellus	Slim sculpin	0.15	0.04	0.07	0.06	4.23
	Scorpaenichthys marmoratus	Cabezon	0.00	0.00	0.18	0.07	4.23
	Triglop pingedi	Ribbed sculpin	0.00	0.02	0.00	0.01	0.70
Hemitripteridae	*Nautichthys oculofasciatus*	Sailfin sculpin	0.00	0.00	0.10	0.04	2.82
Psychrolutidae	*Dasycottus setiger*	Spinyhead sculpin	0.00	0.00	0.05	0.02	1.41
Cryptacanthodidae	*Crytacanthodes aleutensis*	Dwarf wrymouth	0.00	0.12	0.15	0.10	7.75

Table 3.2. Continue

Cyclopteridae		Lumpsuckers	2.14	0.00	0.00	0.30	9.86
Liparidae	*Liparis spp.*	Snailfishes	0.08	1.06	1.61	0.95	38.73
Gadidae	*Theragra chalcogramma*	Walleye Pollock	16.80	3.55	17.76	9.01	85.21
	Gadus macrocephalus	Pacific cod	0.37	0.02	0.00	0.06	2.11
Gobiidae		Gobies	0.60	0.00	0.09	0.13	6.34
	Coryphopterus nicolsii	Blackeye goby	0.54	0.00	0.09	0.12	5.63
	Lepidogobius lepidus	Bay goby	0.05	0.00	0.00	0.01	0.70
Hexagrammidae	*Oxylebius pictus*	Painted greenling	0.12	0.00	0.00	0.02	0.70
Merlucciidae	*Merluccius productus*	Pacific hake	136.25	1.26	21.53	21.78	76.06
Osmeridae	*Mallotus villosus*	Capelin	0.43	0.00	0.08	0.09	3.52
Pholidae		Gunnels	0.00	0.03	0.05	0.03	2.11
Pleuronectidae	*Glyptocephalus zachirus*	Rex sole	0.00	0.02	0.00	0.01	0.70
	Hippoglossoides elassodon	Flathead sole	0.80	0.13	6.58	2.32	45.07
	Hippoglossoides stenolepis	Pacific halibut	0.08	0.00	0.00	0.01	0.70
	Isopsetta isolepis	Butter sole	0.68	0.00	0.25	0.19	8.45
	Lepidopsetta bilineata	Rock sole	2.05	0.69	3.46	1.54	53.52
	Lyopsetta exilis	Slender sole	17.69	5.51	29.29	11.72	92.96
	Microstomus pacificus	Dover sole	0.00	0.00	0.06	0.02	1.41
	Parophyrs vetulus	English sole	2.50	1.06	8.31	3.51	65.49
	Platichthys stellatus	Starry flounder	0.35	0.00	0.46	0.21	7.75
Ptilichthyidae	*Ptilichthys goodie*	Quillfish	0.00	0.07	0.14	0.07	5.63
Scorpaenidae	*Sebastes spp.*	Rockfishes	36.12	0.43	59.75	22.85	71.13
Stichaeidae		Pricklebacks	0.21	0.11	0.10	0.10	7.04
	Anoparchus purpurescens	High cockscomb	0.00	0.00	0.02	0.01	0.70
	Anoplarchus insignis	Slender cockscomb	0.00	0.02	0.00	0.01	0.70
	Phytichthys chirus	Ribbon prickleback	0.00	0.02	0.00	0.01	0.70
	Plectobranchus evides	Blubarred prickleback	0.14	0.03	0.00	0.03	2.11
	Poroclinus rothrocki	Whitebarred prickleback	0.00	0.00	0.02	0.01	0.70
Stichaeidae		Unidentified ricklebacks	0.07	0.05	0.05	0.05	2.11
		Total larvae	249.03	32.04	201.74	--	--

Note: Species belongs to family Agonidae, Cottidae, Gobiidae and Stichaeidae are also combined at family level and indicated in grey shade.

Table 3.3. Inter-annual trends in mean larval abundance of fish taxa with frequency of occurrence >5% in late-April of 2007, 2009 and 2010; fishing status and selected life history traits of examined taxa. Bold indicates significant difference ($p < 0.05$) in larval abundance between years in ANOVA test.

Species	ANOVA test *p*-Value		Inter-annual trend in larval abundance	Fishing status	Type of eggs	Adult Ecology
	2007 VS. 2009	2009 VS. 2010				
Lyopsetta exilis	< **0.0001**	< **0.0001**	2007 > 2009, 2009 < 2010	Bycatch	Pelagic	Epi-, meso- and bathbenthal
Theragra chalcogramma	< **0.0001**	< **0.0001**	2007 > 2009, 2009 < 2010	Fished	Pelagic	Epi-, meso- and bathpelagic
Merluccius productus	< **0.0001**	< **0.0001**	2007 > 2009, 2009 < 2010	Fished	Pelagic	Epi- and mesopelagic
Sebastes spp	< **0.0001**	< **0.0001**	2007 > 2009, 2009 < 2010	Fished	Ovoviviparous	Epi- and mesobenthal
Cottidae	**0.001**	**0.002**	2007 > 2009, 2009 < 2010	Unknown	Demersal	Nearshore shelf demersal
Leuroglossus schmidti	0.66	**0.001**	2007 = 2009, 2009 < 2010	Unfished	Pelagic	Epi-, meso- and bathypelagic
Isopsetta isolepis	0.135	**0.001**	2007 = 2009, 2009 < 2010	Fished	Pelagic	Epi- and mesobenthal
Hippoglossoides elassodon	0.293	< **0.0001**	2007 = 2009, 2009 < 2010	Fished	Pelagic	Epi-, meso- and bathybenthal
Parophrys vetulus	0.154	< **0.0001**	2007 = 2009, 2009 < 2010	Fished	Pelagic	Benthal, intertidal
Platichthys stellatus	0.317	**0.016**	2007 = 2009, 2009 < 2010	Fished	Pelagic	Epi- and mesobenthal
Lepidopsetta bilineata	0.230	< **0.0001**	2007 = 2009, 2009 < 2010	Fished	Demersal adhesive	Epi-, meso- and bathdemersal
Ammodytes hexapterus	0.999	< **0.0001**	2007 = 2009, 2009 < 2010	Fished	Demersal adhesive	Epi- and mesodemersal
Agonidae	0.589	**0.001**	2007 = 2009, 2009 < 1010	Bycatch	Probably demersal	Epi- and mesodemersal
Clupea pallasi	0.259	0.420	2007 = 2009 = 2010	Fished	Demersal adhesive	Nearshore shelf pelagic
Ronquilus jordani	0.195	0.722	2007 = 2009 = 2010	Unfished	Unknown	Nearshore shelf demersal
Stichaeidae	0.637	0.958	2007 = 2009 = 2010	Unknown	Demersal	Nearshore shelf demersal
Crytacanthodes aleutensis	0.408	0.945	2007 = 2009 = 2010	Unknown	Demersal	Epi- and mesobenthal
Ptilichthys goodie	0.771	0.403	2007 = 2009 = 2010	Unknown	Unknown	Nearshore shelf demersal
Gobiidae	< **0.0001**	0.571	2007 > 2009 = 2010	Unknown	Demersal adhesive	Nearshore shelf demersal
Liparis spp.	**0.011**	0.886	2007 < 2009 = 2010	Unfished	Demersal adhesive	Epi- and mesodemersal, intertidal
Total larvae	**<0.0001**	**<0.0001**	2007 > 2009, 2009 < 2010	--		

Note: “Fished” represents species that have been fished commercially in the SoG since the early 1980s, based on DFO records.

largest and larvae caught in late April of 2007 were the smallest (Table 3.4), all the comparisons are statistically significant except for differences in larval size of *P. vetulus* between 2007 and 2010. Larval size frequency distributions were also compared for the same species but only for samples collected in 2009 and 2010 (Fig. 3.8). Larvae collected in 2010 were significantly smaller than those from 2009, and the differences in midpoint of size frequency between the two years were relatively small for *C. pallasi* and *L. bilineata*.

3.3.4 Interannual variations in larval fish assemblage structure

The species composition of the late–April larval fish assemblages varied on an interannual scale (Pseudo-F = 26.475, $p_{perm} = 0.0001$). Three clear distinguishable patterns in the constrained CAP ordination space displayed the differences detected by this discriminate – type canonical analysis (Fig. 3.9a). Smaller differences in the species composition of larval fish assemblages between 2007 and 2009 ($t = 0.445$, $P_{perm} = 0.0001$) compared to the differences between 2009 and 2010 ($t = 5.887$, $P_{perm} = 0.0001$) revealed a relatively abrupt change from 2009 to 2010. The first two squared canonical correlations were $\delta^2{}_1 = 0.791$ and $\delta^2{}_2 = 0.461$. The first canonical axis principally separated the larval assemblages in late-April of 2009 from those sampled during the same periods in 2007 and 2010; whereas the second canonical axis mainly separated the samples between 2007 and 2010. The greater dispersion of observation points from 2009 compared to the other two years reflected larger variation in species composition among the samples collected within this year. Furthermore, I examined species that characterized the differences among the yearly groups found by CAP analysis. Species showing correlations between relative larval abundance and the first two CAP axes greater than 0.2, were overlaid on the CAP ordination space (Fig. 9b). In late-April, the typical warmer water species in the Northeast Pacific, *M. productus* was found principally in 2007. *C. pallasi*, *L. exilis, Liparis spp.* and the typical cold

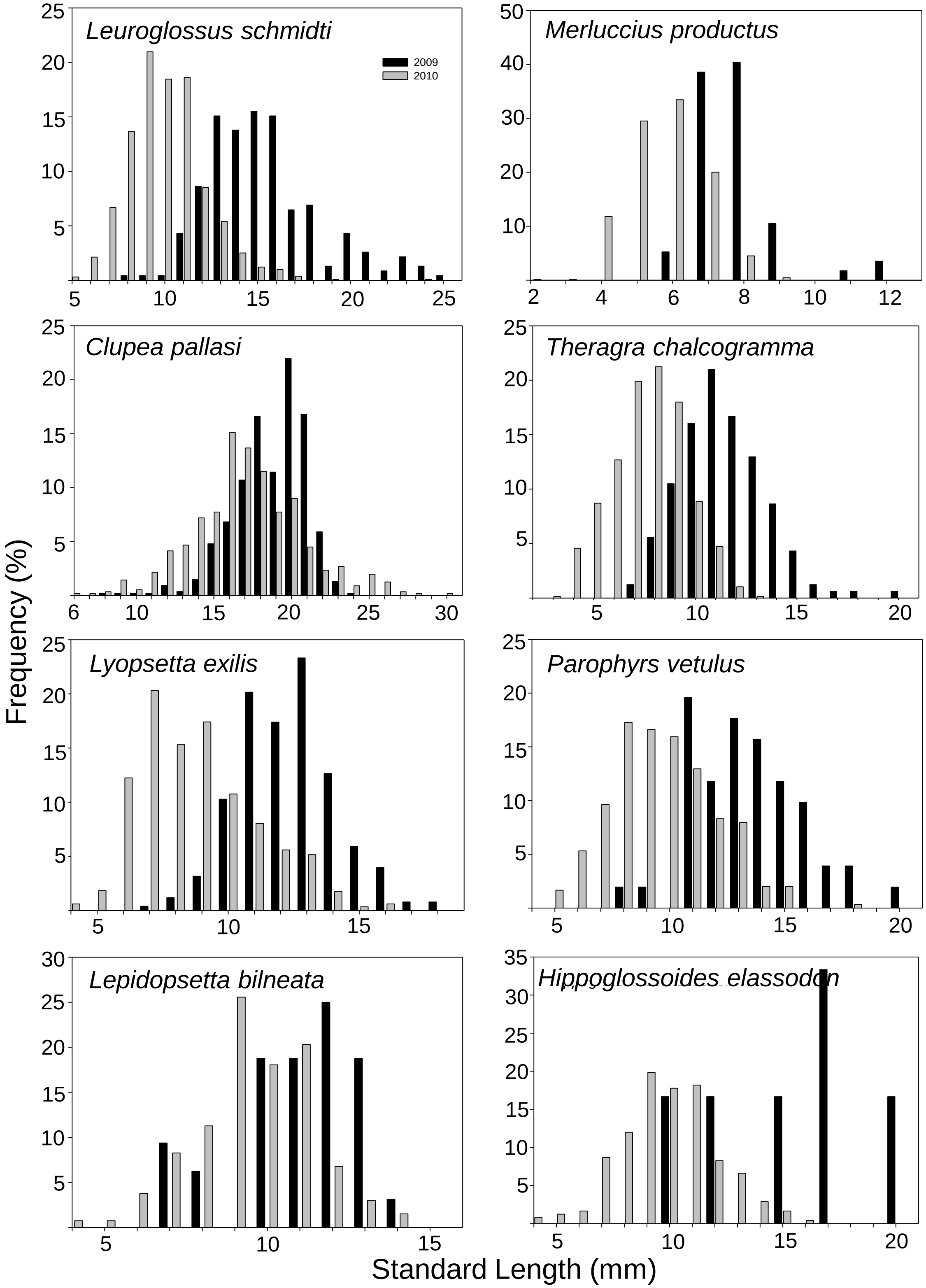


Figure 3.8. Length-frequency distributions of larvae of four locally dominant fish species and four flatfishes collected in 2009 and 2010. Solid bar: 2009; Grey bar: 2010.

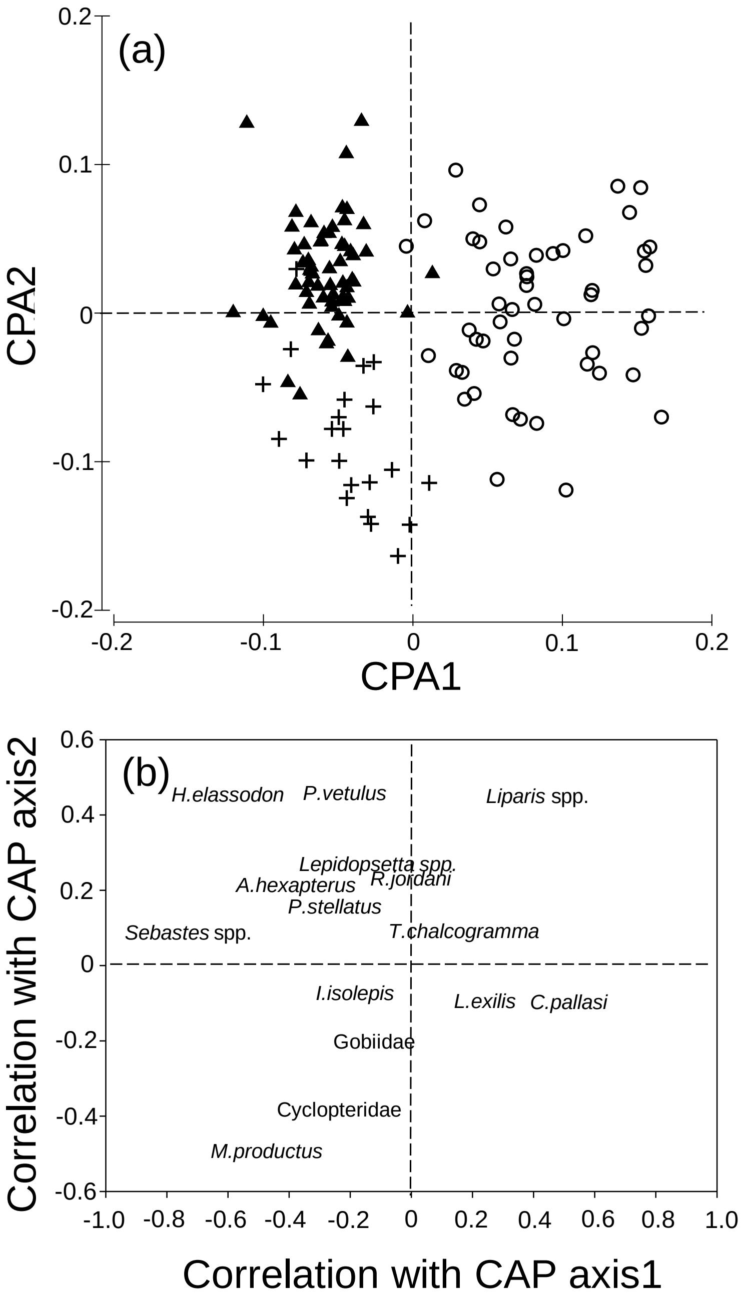


Figure 3.9. (a) Canonical analysis of principal coordinates (CPA) ordination of larval fish assemblages based on all samples from 2007, 2009 and 2010 for species >5% frequency of occurrence; (b) Correlations of individual species with two CAP axes. Solid cross: samples collected in 2007. Solid triangle: samples collected in 2010. Open circles: samples collected in 2009.

Table 3.4. Mean standard length (in mm, SE in parentheses) of larvae for four locally dominant fish species (*Clupea pallasi*, *Theragra chalcogramma*, *Merluccius productus*, *Leuroglossus schmidti*) and four flatfishes (*Lyopsetta exilis*, *Parophyrs vetulus*, *Hippoglossoides elassondon*, *Lepidopsetta bilineata*), and the results of inter-annual comparison through ANOVA test. Bold indicates significant difference ($p < 0.05$) in larval size among years in ANOVA test.

	2007	2009	2010	Comparison
Clupea pallasi	14 (0.0)	19 (0.1)	17 (0.2)	**2009 > 2010 > 2007**
Theragra chalcogramma	5 (0.1)	11 (0.2)	7 (0.1)	**2009 > 2010 > 2007**
Merluccius productus	5 (0.0)	8 (0.2)	6 (0.0)	**2009 > 2010 > 2007**
Leuroglossus schmidti	9 (0.4)	15 (0.2)	10 (0.1)	**2009 > 2010 > 2007**
Lyopsetta exilis	7 (0.2)	12 (0.1)	9 (0.1)	**2009 > 2010 > 2007**
Parophyrs vetulus	10 (0.8)	13 (0.3)	10 (0.1)	**2009 > 2010** = 2007
Hippoglossoides elassondon	7 (0.8)	15 (1.5)	10 (0.1)	**2009 > 2010 > 2007**
Lepidopsetta bilineata	7 (0.5)	11 (0.3)	10 (0.2)	**2009 > 2010 > 2007**

water species – *T. chalcogramma* were relatively abundant in 2009. Various demersal species in families of Scorpaenidae, Agonidae and Pleuronectidae were more associated with 2010 data cloud. Cross-validation results of the above CAP analysis yielded a misclassification rate of 8.1%, with the greatest error occurring between samples from 2009 and the other two years, followed by errors in distinguishing samples between 2007 and 2010.

3.3.5 Linkages between assemblage structure and environmental variables

Relationships between the larval fish assemblage structure and water property indices were examined through Distance-based linear models (DISTLM) based on observations from 2009 and 2010, and results were displayed in a distance-based redundancy analysis (dbRDA) ordination space (Fig. 3.10a). Together the first two dbRDA axes explained 75.5% of the model fitted variation and 37.7% of the total variation. Clear interannual separation was displayed along the first dbRDA axis, whereas the second dbRDA axis represented a latitudinal gradient. The results of sequential tests suggested that four of the 25 water property indices (minimum water column temperature, mean salinity of the surface layer, surface and maximum fluorescence) collectively explained 34.3% of the variation in community structure (21.9%, 7.9%, 2.0% and 2.5% of the variation, respectively). Multiple partial correlations showed that the first dbRDA axis was strongly correlated with minimum temperature (r = -0.349) and mean salinity (r = 0.304), reflecting their associations with the interannual variations in assemblage structure between 2009 and 2010. Mean surface salinity (r = -0.218) and maximum fluorescence (r = 0.297) displayed relatively stronger associations with the second dbRDA axis, suggesting their utility in explaining along-strait variations in assemblage structure within each year.

To verify the relationship between the assemblage structure and environmental variables, principal components scores were used in the same analyses (DISTLM and dbRDA) instead of

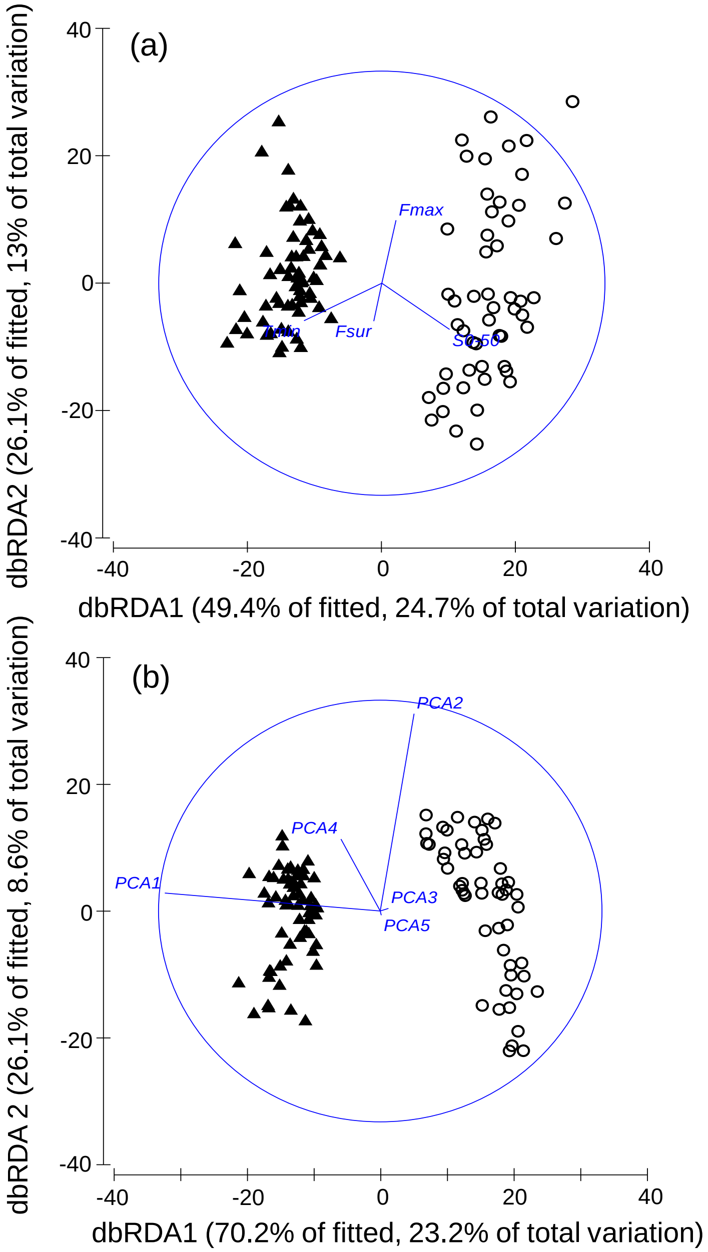


Figure 3.10. Constrained dbRDA ordination of larval fish assemblages based on samples collected in late-April of 2009 and 2010. (a) Correlation of significant water property indices with two dbRDA axes. Indices displayed were: maximum fluorescence (F_{max}), fluorescence at surface (F_{sur}), minimum temperature over water column (T_{min}) and average salinity over the surface layer (S_{0-50}); (b) Correlation of PC scores with two dbRDA axes. Solid triangle: samples collected in 2010. Open circle: samples collected in 2009.

the 25 water property indices. Together, the first two dbRDA axis explained 96.3% of the model fitted variation and 31.8% of the total variation (Fig 3.10b). The first dbRDA axis was strongly negatively correlated with PCA1(r = -0.972), reflecting strong associations between interannual variations in assemblage structure and PCA1 of the water property indices. Similarly, the second dbRDA axis was positively correlated with the PCA2 (r = 0.936) which reflected the latitudinal gradient in assemblage structure in response to salinity and fluorescence in the surface layer.

3.3.6 Regional variations between the Northern and Central-Southern SoG

Total larval abundances were similar in the northern and central-southern SoG for each sampling year (Table 3.5). *L. exilis* was the only species that showed significantly greater abundance in the northern SoG consistently, whereas larvae of *L. schmidti* were significantly more abundant in the central-southern SoG. No consistent difference in larval abundance was observed between the two regions for any other fish species. PERMANOVA testing based on 9999 permutations revealed that the composition of larval fish assemblages between the northern and central-southern SoG were significantly different in 2007, 2009 and 2010 (Pseudo-F = 4.226, 10.253 and 3.159, respectively; P_{perm}= 0.0005, 0.0001 and 0.0017, respectively). The regional differences were relatively greater in 2009 than in 2010, suggesting the larval assemblages were more similar between regions in 2010. However, the regional differences in larval assemblage structures within each year were smaller and negligible compare to the interannual differences in community structure (Fig. 3.11).

3.4 Discussion

3.4.1 Interannual variation in larval abundance and diversity

The period from 2007 - 2010 alternated between strong La Niña and El Niño events. The

Table 3.5. Mean larval abundance of fish taxa collected within the Northern and Central-Southern Strait of Georgia in late-April of 2007, 2009 and 2010, and results of ANOVA analyses on regional comparison in larval abundances.

Taxon	2007 Mean abundance (no./1000m^3)		2009 Mean abundance (no./1000m^3)		2010 Mean abundance (no./1000m^3)		Comparison results
	North	Central-Southern	North	Central-Southern	North	Central-Southern	
Agonidae	1.67	0.50	**0.89**	**0.21**	1.34	1.38	--
Ammodytes hexapterus	0.36	0.39	**0.62**	**0.04**	5.17	2.97	--
Leuroglossus schmidti	**1.20**	**10.31**	**0.38**	**8.94**	**8.03**	**47.43**	**N < C-S**
Ronquilus jordani	0.47	0.34	0.10	0.04	0.07	0.28	N = C-S
Brosmophycis marginata	0.00	0.00	0.00	0.00	0.32	0.21	N = C-S
Hetrostichus rostratus	0.00	0.24	0.00	0.00	0.00	0.00	N = C-S
Clupea pallasi	**38.41**	**10.13**	12.80	10.43	**6.07**	**19.37**	--
Cottidae	3.32	3.09	0.77	0.34	1.69	1.99	N = C-S
Nautichthys oculofasciatus	0.00	0.00	0.00	0.00	0.13	0.07	N = C-S
Dasycottus setiger	0.00	0.00	0.00	0.00	0.00	0.09	N = C-S
Crytacanthodes aleutensis	0.00	0.00	0.14	0.11	0.07	0.21	N = C-S
Cyclopteridae	**0.38**	**3.03**	0.00	0.00	0.00	0.00	--
Liparidae	0.00	0.12	0.75	1.32	0.82	2.20	N = C-S
Theragra chalcogramma	**6.12**	**22.14**	**4.99**	**2.35**	15.73	19.27	--
Gadus macrocephalus	0.38	0.36	0.05	0.00	0.00	0.00	N = C-S
Gobiidae	0.38	0.70	0.00	0.00	0.00	0.16	N = C-S
Oxylebius pictus	0.36	0.00	0.00	0.00	0.00	0.00	N = C-S
Merluccius productus	94.42	157.17	**0.67**	**1.76**	27.51	17.09	--
Mallotus villosus	0.00	0.65	0.00	0.00	0.00	0.13	N = C-S
Pholidae	0.00	0.00	0.00	0.05	0.05	0.05	N = C-S
Glyptocephalus zachirus	0.00	0.00	0.00	0.04	0.00	0.00	N = C-S
Hippoglossoides elassodon	0.00	1.21	0.10	0.16	5.46	7.41	N = C-S
Hippoglossoides stenolepis	0.00	0.12	0.00	0.00	0.00	0.00	N = C-S
Isopsetta isolepis	1.31	0.37	0.00	0.00	0.00	0.44	N = C-S
Lepidopsetta bilineata	1.82	2.16	0.54	0.82	3.77	3.22	N = C-S
Lyopsetta exilis	**28.15**	**12.46**	**7.29**	**4.02**	**44.40**	**18.08**	**N > C-S**
Microstomus pacificus	0.00	0.00	0.00	0.00	0.13	0.00	N = C-S
Parophyrs vetulus	2.45	2.52	**1.54**	**0.66**	5.97	10.05	--
Platichthys stellatus	0.00	0.52	0.00	0.00	0.32	0.57	N = C-S
Ptilichthys goodei	0.00	0.00	0.11	0.04	0.13	0.15	N = C-S
Sebastes spp.	35.08	36.64	0.51	0.37	73.78	49.33	N = C-S
Stichaeidae	0.42	0.10	0.25	0.00	0.00	0.17	N = C-S
Total larvae	216.72	265.19	32.22	31.69	200.96	202.32	N = C-S

Note: Bold indicates a significant difference ($P < 0.05$) in larval abundance between northern and central-southern SoG in ANOVA test. N: northern SoG, C-S: central – southern SoG.

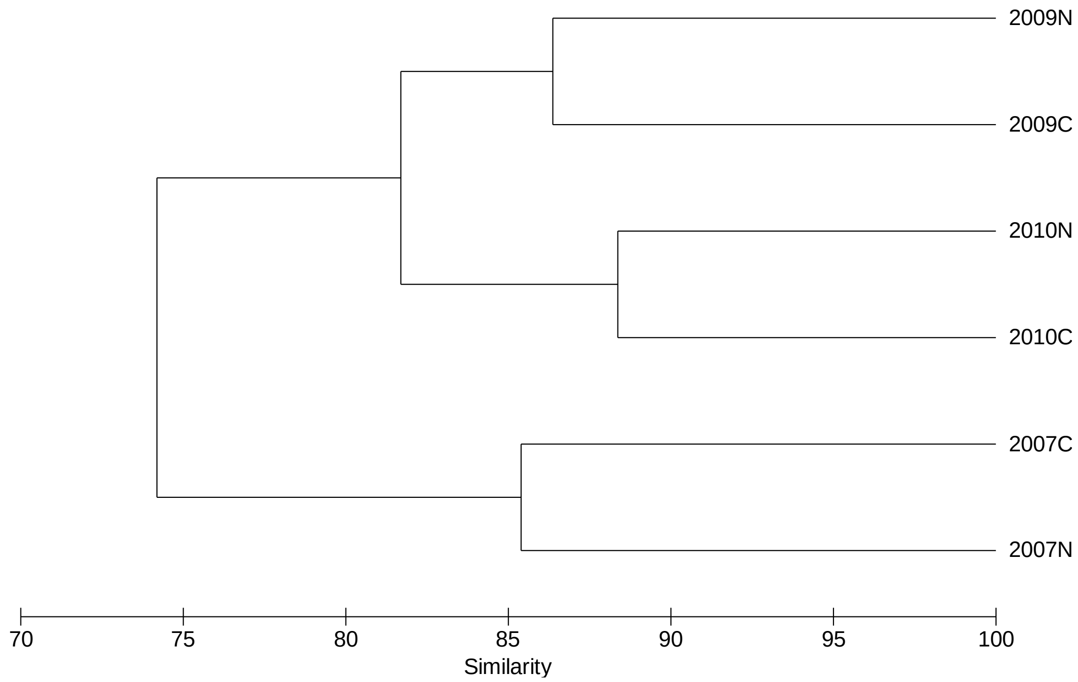


Figure 3.11. Dendrogram by cluster analysis based on average larval abundances of individual species in the northern and central-southern SoG in late April of 2007, 2009 and 2010. Only species with frequency of occurrence >5% were included.

SoG had been in a relatively warm condition since mid-2003. This warm state lasted until 2007 when the SoG started shifting toward a cooler La Niña state associated with a dramatic decline in PDO and water temperatures (DFO, 2008). The unusually cool conditions lasted through 2008 until the spring of 2009, before reversing again. By 2010, waters in the SoG had warmed at most depths in response to an strong El Niño condition in the beginning of the year (Crawford and Irvine, 2010; 2011).

The early life history stages of marine fishes are very sensitive to changes in water temperature (Green and Fisher, 2004; Bradbury *et al*., 2000; Guan *et al*., 2008); larval abundance and biodiversity measures in this study exhibited significant variations in response to the recent environmental fluctuations. Higher overall larval abundances and lower species evenness in 2007 and 2010, along with the highest species diversity and richness in 2010, were associated with warm conditions in the SoG. In contrast, the lowest larval abundance and species diversity occurred in 2009 (along with the highest species evenness), and were associated with a cooler environment which suggested less favorable conditions for adult spawning and larval survival. The relatively low species diversity in 2007 may be attributed to the reduced sampling effort in this year. The positive relationship between larval fish abundance and water temperature, and the fact that that fish larvae are generally more abundant in warmer years has also been discussed in studies elsewhere along the Northeast Pacific coast (Hsieh *et al*., 2005; Auth, 2008; Auth and Brodeur, 2006; Siddon *et al*., 2011). Similar interannual variations in production have been detected for crab larvae in the SoG with higher abundances in late-April of 2007 and 2010, but lower abundances in late-April of 2009 (Sorochan, 2011; Sorochan and Quijon, 2014).

Larval abundance of demersal fishes in the SoG, especially several major flatfishes, increased in 2010. Similarly, on the west coast of Vancouver Island an increase in biomass was also observed for key flatfish species in May of 2010 (Crawford and Irvine, 2011). *Gadus* *macrocephalus* (Pacific cod), a species which used to be abundant in the SoG, was found at extremely low larval abundance during recent years, and no larva was collected at all in 2010. *G. macrocephalus* is a typical cold water species which reaches its southern distribution limit in British Columbia. Its seemingly dramatic decline can probably be attributed to the gradual warming of the SoG (Beamish, 2008). This species usually produces demersal eggs around February and March, and the eggs do not survive well when the bottom temperature is over 8.5 ℃ (Beamish, 2008). The warmer temperature over the entire water column during January-March in 2010, compared to the other two sampling years, might therefore have limited the larval occurrence of this species in 2010. Therefore, this species can be considered as a potential indicator of temperature change in the SoG due to its sensitivity and vulnerability to warmer waters.

Over the period of 2007 -2010, the entire water column of the SoG experienced the most dramatic and rapid temperature changes over the past 25 years (Fig. 3.1), although only minor temperature differences (~ 1 ℃) were detected at sea surface. The current study showed that fish species that produce pelagic eggs all exhibited an abrupt increase in larval abundance along with the temperature shift from the cold-2009 to warm-2010, which probably suggested that the pelagic spawners were more sensitive to the environmental fluctuations. However, time series studies based on longer-term observations will be needed to verify this hypothesis built on limited data from narrow time window.

3.4.2 Are there possible phenology changes and "match-mismatch" between trophic levels?

Larval fish sampling for this study was consistently conducted in the last week of April across years. Each survey only lasted for three to four days which is relatively short compared to the temporal duration of the early life history events, including adult spawning and larval hatching. Therefore, temperature mediated changes in the timing of fish spawning and larval hatching could be one possible mechanism for the substantial interannual differences in larval fish abundance and species diversity. Based on weekly observation of ichthyoplankton over a 7-year period in southern North Sea, Greve *et al*. (2005) have suggested a negative correlation between the timing of the larval fish occurrence and winter SST from January to early April, with early appearance of fish larvae in warm winter due to faster gonadal development. In contrast, a more recent study in the Western English Channel (UK) related the timing of larval appearance of the spring spawning fishes to the sea temperature in the previous November and December, with earlier appearance in cooler waters (Genner *et al*., 2010).

In the SoG, the upper ocean was consistently around 1 ℃ warmer from January to March in 2010 compared to 2009; but was cooler in the previous November and December of 2010. Temperatures in 2007 were intermediate to these two years for both time periods. An earlier timing of larval appearance in 2010 might be expected according to the temperature comparisons, something which was confirmed by the SoG *C. pallasi* spawning dates from Fisheries and Oceans Canada (http://www.pac.dfo-mpo.gc.ca/science/species-especes/pelagic-pelagique/herring-hareng/herspawn). The average spawning date of *C. pallasi* across all spawning areas in the SoG was earliest in 2010 (69 Day of Year, DOY hereafter), followed by 2007 (77 DOY), and latest in 2009 (85 DOY). However, as a multiple spawner, the spawning of *C. pallasi* usually occurs in several different areas with different spawning time periods around the SoG; the extended spawning period for this species would help explain the similar larval abundance for the three sampling years. For co-occurring species within the spring larval assemblages, the timing mismatch between the fixed sampling dates and larval production could be one of the factors contributing to the low larval abundance in 2009. Furthermore, colder water temperatures in 2009 might be expected to have reduced larval growth rates and prolonged the pelagic larval phase.

This could, in turn, have increased larval mortality due to extended temporal overlap between fish larvae and their predators, and thus led to the unusually low larval abundance seen in 2009.

In temperate waters, the spring bloom is a key oceanographic phenomenon. The bloom usually occurs around late March in the SoG when phytoplankton receive enough sunlight for growth to exceed losses, and its timing is believed to be important to the growth and survival of higher trophic level species (Stockner *et al*., 1979; Allen and Wolfe, 2013). In the SoG, winter wind stress has been found to be the primary factor to control the timing of spring bloom: in years with strong winter winds the mixing-layer is deepened, breaking down stratification and postponing the bloom (Yin, *et al*., 1996; Yin, *et al*., 1997; Collins *et al*., 2009; Allen and Wolfe, 2013). Ocean colour satellite imagery and prediction of the bloom peak via coupled bio-physical model suggest that the spring bloom started particularly early in 2009 - around late February (56-58 DOY), peaking in early April (97 DOY). In contrast, strong wind mixing appears to have pushed the bloom back by about one month in 2010 (82-84 DOY), with the peak not occurring until mid-April (104 DOY) (Allen and Wolfe, 2013).

An early spring bloom can cause a timing mismatch between primary production and the production of microzooplankton (e.g. copepod nauplii) which are the most important prey for larval fish especially during their first-feeding stage, thus leading to unfavorable feeding conditions for larval survival and growth (Cushing, 1969, 1975; Sastri and Dower, 2009; El-Sabaawi *et al*., 2009). Biomass of large- and medium-sized copepods in the SoG in 2007 was close to the recent minima observed in the early 2000s, which might hint at poorer feeding conditions for larvae in 2007 (i.e. relative to 2009 and 2010) and explain the observed smallest larval size associated with this year (Mackas *et al*., 2013). In addition, temperature should also have a direct effect on the timing of microzooplankton production and affect the degree of overlap or mismatch with their predators - larval fish. Unfortunately, there have been few studies on microzooplankton production and timing in the SoG, and their relationship to larval fish; further studies are definitely needed to address the questions about temporal “match-mismatch” among trophic levels.

3.4.3 Why were larvae largest in the coldest year?

Larvae of the four dominant species plus four other flatfish species were all larger in late-April 2009 compared to 2010. Mackas *et al*. (1998) has suggested three mechanisms to explain the interdecadal changes in developmental timing of the large copepod *Neocalanus plumchrus* at Ocean Station P: i) timing of spawning; ii) development rate of individuals; and iii) differential survival among the portions of the annual cohort. Similar mechanisms are discussed for possible interpretations of the consistently distinct interannual differences in larval size between 2009 and 2010. First, earlier adult spawning in 2009 could have resulted in earlier larval development into larger size. However, this is unlikely to have been the case in the cold spring of 2009 as herring spawning in the SoG was reportedly late in 2009 (section 3.4.2). It therefore seems be reasonable to assume that co-occurring fish species might also have spawned later in 2009 than normal.

A second possibility is that favorable feeding conditions could have accelerated larval growth in 2009, resulting in the observed larger larval size. However, given that the water temperature was lower in 2009, one might have predicted that this would slow larval development (Guan *et al*., 2008). Otolith microstructure examination could be utilized to verify the interannual differences in larval fish growth between 2009 and 2010.

Differences in larval survival between early and late portions of the annual larval production between the two years would be another reasonable interpretation. Most of the species examined in this study including *C. pallasi*, *L. schmidti* (Mason and Phillips, 1985) and several flatfishes (Auth and Brodeur, 2006; Brodeur *et al*., 2008) have prolonged spawning periods and extended larval durations. It is possible that in the colder spring of 2009, the earlier portion of the entire larval production (or annual cohort) was associated with better survival, and led to the development of larger size by late April. Whereas in the warm spring of 2010, the latter portion of the larval production may have been more successful, and resulted in the late-April collection dominated with a large number of smaller larvae.

3.4.4 Variations in assemblage structure and linkage to environmental factors

The composition of the SoG larval fish assemblage varied interannually, likely reflecting species-specific responses to the rapidly changing environmental conditions. The 2007 assemblage was dominated by *M. productus* which is a typical southern species characteristic of warm waters. Similarly in 2010, the assemblage was again dominated by *Sebastes* spp. and several southern benthic taxa including *P. vetulus* and *H. elassodon*. Together, the warmer spring water temperatures in these years were associated with southern species living in the deep-water and benthic habitat. In contrast, the nearshore fishes including *C. pallasi* and *Liparis* spp., and the typical "cold water indicator" fish species – *T. chalcogramma* were relatively more abundant in the cooler spring of 2009. Although based on limited observations over only three years, my results are largely consistent with the species alternation pattern suggested by a long-term study of fish larvae in the Oregon upwelling zone (Brodeur *et al*., 2008), which found that cool PDO years were dominated by northern or nearshore fish taxa, while warmer years were dominated by more southern or offshore species.

In addition, adult spawning behavior may also affect larval assemblage structure. The present study found that larvae of fish species producing pelagic eggs were more abundant in warmer years when warm water would shorten their pelagic egg and larval stage, which might also have reduced the mortality caused by predation and thus enhance survival. In contrast, cooler water temperatures should prolong the egg incubation duration and increase the chance of loss of pelagic eggs and larvae. DISTLM analysis revealed that the interannual patterns of larval assemblage composition in the SoG were primarily affected by the minimum temperature of the water column, and secondly related to the salinity in the upper ocean (which was controlled by the timing and volume of Fraser River discharge). As a result, the compositional structure of the larval fish assemblage can also be considered as an effective indicator of climate-induced temperature change in the SoG.

Along-strait variations in larval assemblage structure appeared to be primarily related to a strong horizontal salinity gradient in the surface layer, and the pattern of phytoplankton production. As the primary source of freshwater input for the SoG, the Fraser River has a major influence on the properties of the surface layer. The outflow of freshwater spreads from the river mouth, enters the general counter-clockwise circulation of the SoG, mixes gradually with seawater in the surface layer, and forms a horizontal salinity gradient in the central-southern region of the SoG. The northern SoG is less affected by this estuarine circulation (Thomson, 1981). The extent of this horizontal salinity gradient is determined by the moving and mixing of surface water which is largely driven by the variable winds and tides. Therefore, the association between larval assemblage structure and patterns of salinity and phytoplankton in the surface layer is closely tied to the estuarine circulation. In contrast, different environmental determinants have been suggested for ichthyoplankton assemblages in a relatively open region such as the continental shelf. For example, several studies in the Gulf of Alaska, eastern Bering Sea shelf and southeastern Bering Sea all showed the importance of large-scale bathymetric features in determining assemblage structures. (Doyle *et al*., 2002; Lanksbury *et al*., 2005; Duffy-Anderson *et al*., 2006; Siddon *et al*., 2011).

3.4.5 Regional differences between the Northern and Central-Southern SoG

No significant differences in larval abundance between the northern and central-southern region of the SoG were observed for most of the fish species during this study. The between regional similarities suggest that the local hydrodynamic circulation in the surface layer promote horizontal mixing of drifting larvae throughout the entire SoG. The only species that showed consistent regional differences in larval abundance were *L. schmidti* and *L. exilis*. Significantly more *L. schmidti* larvae were collected in central-southern SoG, primarily reflecting concentrated spawning activity in this area which has been identified in a previous study (Mason and Phillips, 1985). Advection to the southern SoG has also been suggested as major mechanism for enhancing larval retention in the central-southern region (Mason and Phillips, 1985). Similarly, a significantly higher abundance of *L. exilis* larvae in the northern SoG may reflect the potential spawning aggregation and larval retention in this area. Unfortunately, my study cannot identify the species- specific spawning ground and larval dispersal trajectories to clarify the larval exchange between the northern and central-southern SoG. Further studies on the dispersal and spatial distribution of larval fish in the SoG will be needed to address these questions.

3.5 Conclusions

In summary, the three springs sampled in this study represented contrasting environmental conditions in the SoG, including the end of an El Niño period (2007), a strong La Niña spring (2009), followed by a swing back to an El Niño spring (2010). Significant interannual variations were detected in characteristics of larval assemblages including larval abundance, diversity and composition. We demonstrated that these interannual variations were primarily related to the minimum temperature of the water column, and (to a lesser extent) the salinity of the surface layer, while the horizontal pattern within each year was more related to the estuarine circulation.

Due to the sensitivity of fish larvae and their assemblages to the changes in water properties such as temperature and salinity, they can be considered as potential indicators for detecting and monitoring the effect of environmental and climate changes within the marine ecosystem. However, this study only provided a snap-shot of the larval fish assemblages at a certain short period of the entire year. Further investigations on spatial patterns of larval fish in relation to the physical and biological oceanographic processes would enhance the understanding of the larval dynamics in this region, and thus gradually build up comprehensive knowledge background to assist in management and conservation planning of fishery resources in the SoG, such as the design and evaluation of marine protected areas.

Chapter 4

Multiscale spatial structures and relationships with environmental factors: an application of principal coordinates of neighbour matrices (PCNM) to larval fish assemblages in the Strait of Georgia

4.1 Introduction

Spatial structure of planktonic fish larvae, formed when the presence and abundance of a variety of species are distributed non-randomly in space, is of great importance in affecting larval feeding and survival and is one of the fundamental features of planktonic marine ecosystems (Legendre, 1993). Identifying these spatial distribution patterns and understanding the underlying mechanisms and processes responsible for the generation and maintenance of these patterns remains a major issue in marine ecology (Legendre, 1993; Legendre and Legendre, 1998, Fortin and Dale, 2005; Dray *et al*., 2006). By the very nature of the early life history stages of marine fishes, such as possessing very limited active mobility capability, the processes structuring their spatial variations are usually complex, and can be largely distinguished into two categories: exogenous and endogenous processes (Fortin and Dale, 2005). The horizontal distribution of fish larvae is strongly affected by advection, and further modulated by the distribution of various environmental factors that determine habitat suitability (Legendre, 1993; Fortin and Dale, 2005). Meanwhile, inherent biological processes such as growth, mortality, predation and interspecies competition can also induce spatial dependence (Legendre and Legendre 1998, Fortin and Dale, 2005). In most situations, both exogenous and endogenous processes act simultaneously to structure larval fish distributions. However, the relative importance of the two processes varies at different larval developmental stages. More specifically, exogenous processes are usually more important during the very early larval stage when active behavior of fish larvae is very limited. The relative importance of endogenous processes gradually increases with larval growth.

A key component which must be considered in the analysis and interpretation of spatial patterns is the scale (Legendre and Legendre, 1998; Pinel-Alloul, 1995). In marine environments, the structure of spatial variability has been shown to occur across a hierarchical range of scales (Mackas *et al*., 1985). The physical and biological mechanisms that induce spatial variations also operate over a variety of characteristic scales (Legendre *et al*., 1986), and contribute to the generation of multiscale patterns in the distribution of marine organisms (Platt and Denman, 1975; Bellier *et al*., 2007; de Souza Moraes *et al*., 2012). Thus multiscale approaches are required for investigating and quantifying the spatial variability of populations and modeling their spatial-environmental relationships.

Building on earlier methods which had incorporated space as a predictor in models of ecological data (i.e. in terms of either geographic coordinates or a Euclidean distance matrix), Borcard and Legendre (2002) developed a powerful new approach - principal coordinates of neighbour matrices (PCNM) to identify spatial structures across a complete series of spatial scales within a study dataset. The method starts with building a Euclidean distance matrix using geographic locations of sampling sites. A principal coordinate analysis is then performed on the distance matrix and results in a set of principal coordinates as PCNM variables with progressively decreasing eigenvalues representing hierarchical spatial scales from largest to smallest. Subsequently, the constructed PCNM variables can be applied *post hoc* as spatial descriptors in quantitative models serving different study purposes (e.g. regression, ordination analysis, variance partitioning).

This new form of multiscale analysis has been successfully applied in spatial ecology studies in various types of ecosystems, including the planktonic marine environment. For example, a study examining the spatial variability of tropical zooplankton biomass and abundance in a coastal reef lagoon in Guadeloupe revealed a multiscale spatial relationship between zooplankton variability and environmental processes and identified the importance of local hydrodynamics, phytoplankton availability and zooplankton behavior in the generation and maintenance of the observed spatial patterns (Avois-Jacquet, 2002). In the Southeastern Brazilian Bight, a study of the spatial structure of sardine spawning and nursery habitats found that the spatial distributions of eggs and larvae were associated with distributions of seawater properties including surface temperature and salinity, and also suggested mesoscale and local hydrodynamic processes as possible driving forces (de Souza Moraes *et al.*, 2012). Through a spectral decomposition of spatial variance into a set of independent orthogonal spatial components, PCNM allows the study of spatial structures and correspondent processes on predefined spatial scales.

The Strait of Georgia (SoG) is a highly productive coastal basin between mainland British Columbia and Vancouver Island on the west coast of Canada (Fig. 4.1). To date, there has been little research on the spatial dynamics of the early life stages of fish species in this temperate estuarine ecosystem. In the spring of 2009 and 2010, two spatially intensive ichthyoplankton surveys were conducted in the SoG to characterize the spatiotemporal variability in larval distribution and to investigate the resent status, including diversity, abundance and spatial variability, of larval fish assemblages. The previous chapter in this thesis has revealed that both the physical and biological oceanographic conditions in the SoG differed between these two survey years. Specifically, the SoG had experienced the most significant temperature changes throughout the entire water column over the past 25 years, with an unusually cool condition starting in 2008and persisting into the spring of 2009, followed by a shift toward a warmer phase in late 2009 and into the spring of 2010 (Figure 3.1, Chapter 3). Furthermore, significantly more

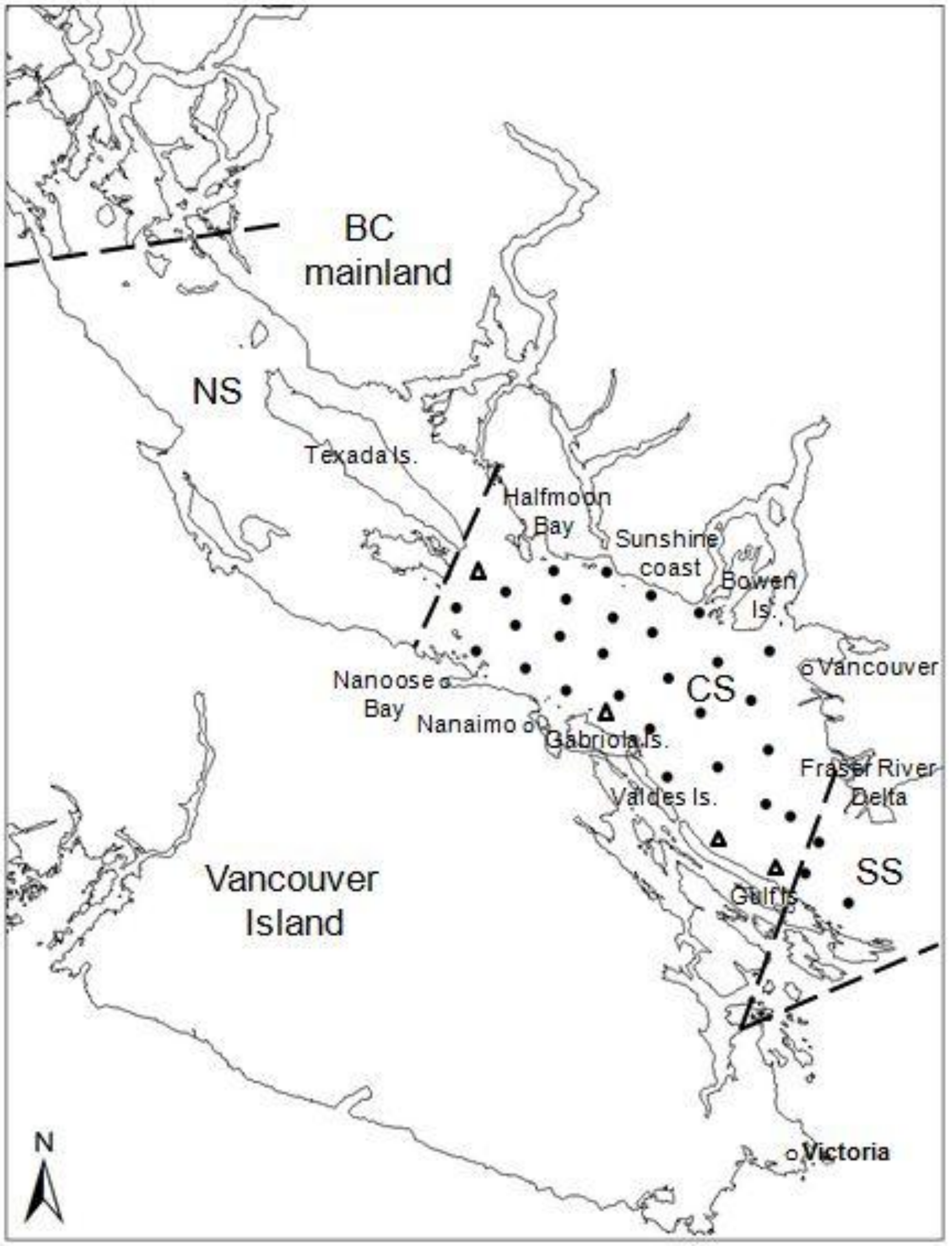


Figure 4.1. Sampling sites in the Strait of Georgia, British Columbia, Canada. Solid circles: locations sampled in late-April of 2009 and 2010; open triangles: additional four locations sampled in 2010. The Strait of Georgia was divided into three sections by the dashed lines: NS - Northern SoG, CS – Central SoG, SS – Southern SoG.

larvae were caught in 2010 than the previous year (201.7 and 32.0 larvae per 1000m^3, respectively), but the higher larval abundance in 2010 was associated with smaller body size compared to the larvae caught in 2009 (Chapter 3).

Based on existing knowledge, the present study is primarily intended to investigate the differences in the spatial variability of larval fish in the SoG over a range of spatial scales with respect to environmental heterogeneity under contrasting oceanographic conditions. By applying PCNM, the dominant scales at which the spatial variability is structured are identified, and the relations between spatial distributions of environmental variables and the observed larval distributions at multiple scales are explored for interannual comparisons. In addition, the relative importance of environmental and spatial variables in explaining spatial variability at different early life history stages of fish larvae is assessed and compared between years. Finally, the importance of fish life history traits (e.g. demersal spawner vs. pelagic spawner) in the generation and variation of larval spatial structures is also discussed. This study provides the first account of the spatial heterogeneity of larval fishes and environmental relations in the SoG across multiple spatial scales, and will provide insights on the influence of changing environmental conditions on the spatial and population dynamics of local fisheries resources in this temperate estuarine ecosystem.

4.2 Materials and Methods

4.2.1 Study area:

The Strait of Georgia (48°50´ - 50°00´N), on the western coastline of Canada, is approximately 222km in length and 28km in width with a total surface area of 6800km^2 (Fig. 4.1). The average depth of this semi-enclosed basin is around 155m, and the maximum depth recorded is 420m just south of Texada Island (Thomson, 1981). This coastal basin connects to the open

Pacific Ocean in two directions: northward, via the narrow and constricted Johnstone Strait and Discovery Passage, and southward via two comparatively wider passages - Haro and Juan de Fuca Straits (Thomson, 1981; Li *et al*., 1999; Masson, 2006). The water mass exchanges occurs mainly through the southern passages with the continuous seaward movement of low salinity water near the surface and a landward movement of nutrient-rich water from the continental shelf at depth (LeBlond, 1983; King and McFarlane, 2006).

The SoG can be generally divided into two layers: the upper layer, within 50m from the surface, and the lower layer beneath. A large volume of freshwater, mostly from the snow-fed Fraser River, enters this upper layer seasonally with the maximum volume occurring during early summer, and sets up an estuarine circulation which is modulated by strong tides and generally weak wind forcing (LeBlond, 1983; Li *et al*., 1999; Masson, 2006). This freshwater input also plays an important role in structuring most of the spatial variation in water temperature and salinity within the upper layer (Thomson, 1981), affecting the seasonal variation in the stratification of the water column and thus the biological productivity in the SoG. In contrast, the lower layer is less affected by the freshwater input and remains relatively stable with nearly uniform temperature (8-10 ℃) and salinity (29.5‰ - 31‰) throughout the year. The prevailing winds in the SoG are generally less than 2.5m/s, and predominantly from the northwest in summer (Jun to Sep) and southeast in winter (Oct to Mar) (Thomson, 1981). A roughly counterclockwise circulation in the surface layer of the SoG has been suggested using the “drift bottle” approach (Waldichuk, 1957; reviewed by Thomson, 1981).

Based on surface circulation and differences in the relative importance of driving mechanisms, the SoG can be divided into three main regions: northern, central and southern sectors (Fig. 4.1). The central and southern SoG, south of Texada and Lasqueti Islands, is under more direct influence of the Fraser River runoff and is characterized by strong tidal currents; the northern SoG is characterized by weak and variable tidal currents, and is less affected by the Fraser River (Thomson, 1981).

4.2.2 Biological data: field sampling procedure

In late-April of 2009 and 2010, ichthyoplankton were collected from the central and southern SoG. A total of 31 and 35 sites were sampled during April 25-28 2009 and April 24-27 2010, respectively (Fig. 4.1). Geographic coordinates of sampling sites were largely consistent in these two study years except for four additional sites that were added in 2010. Sampling sites were spaced around 8-10km apart and sampled continuously throughout the day and night in both surveys. At each sampling site, a 1 m^2 Tucker trawl with 1000 μm mesh size Nitex net was lowered quickly to a depth of ~50m then towed back to surface obliquely for approximately 15 minutes at a ship speed of 1m s^{-1}. Water volume filtered was recorded by a calibrated TSK flowmeter placed at the center of the mouth. The sampling depth of the Tucker trawl was tracked by a Vemco Minilog-12TX depth logger. In addition, a Seabird -19 conductivity-temperature-depth sensor (CTD) equipped with a WETLabs fluorometer and an SBE 43 oxygen sensor was used to record the physical properties of the water column from the surface to ~5m from the bottom at each site. Upon retrieval, the net was rinsed and plankton samples were bulk-preserved in 95% ethanol. In the laboratory after the cruise, all larvae were sorted, counted and identified to the lowest taxonomic level possible following Matarese *et al*. (1989) and the Ichthyoplankton Information System (2011). The size of each larva was measured to the nearest 1 mm in standard length, and larval density was estimated as the number of larvae per $1000m^3$.

4.2.3 Environmental descriptors

The vertical structure of water properties in the upper surface layer (0-50m) of the SoG varies in both space and time as a result of the strong influence of estuarine circulation driven by the Fraser River. Nine descriptors based on onsite CTD measurements were developed to characterize the water masses in this upper layer from where the samples were collected:

- temperature and salinity at surface (T_{sur}, S_{sur}), and their vertical averages over surface layer ($T_{0\text{-}50}$, S_{0_50}) were used to represent the upper layer of water column;
- temperature and salinity at the lower limit of surface layer (~ 50m, T_{50}, S_{50}) were used to characterize the interface between surface layer and the layer beneath;
- vertical average of chlorophyll fluorescence from surface to 20m ($F_{0\text{-}20}$) represented the amount of phytoplankton;
- depth at which a change in density (sigma-t) from surface of 0.125 had occurred ($Z_{D0\text{-}0.125}$) served as a measure of mixed layer depth (Levitus, 1982);
- bottom depth (D_{Bot}) provided basic bathymetry information of the sampling sites over central-southern SoG.

Pair-wise correlations were used to avoid high levels of multicollinearity ($r \geq |0.8|$) which may affect the accuracy of the estimated model parameters (Legendre and Legendre 1998). For 2009, all variables were included in subsequent analyses although moderate correlations displayed between S_{50} and $T_{0\text{-}50}$ (-0.75), S_{0_50} and S_{sur} (0.73); while, for 2010, S_{sur} was excluded due to strong correlations with T_{sur} and S_{0_50} (-0.83 and 0.85, respectively).

4.2.4 Spatial descriptors

Spatial patterns of larval fish distribution were examined and quantified over a wide range of scales following the PCNM method described in Borcard and Legendre (2002) and Borcard *et* *al*. (2004). Geographic coordinates of sampling sites were recorded during field sampling, and then converted into Universal Transverse Mercator (UTM) coordinates to construct a matrix of Euclidean distances among sites. We then identified a threshold value, the largest distance between any two contiguous sites, to truncate the distance matrix and retain only the distances among neighboring sites. The Euclidean distances under the threshold value were kept as measured, but the distances above this value were replaced by an arbitrary large value equal to four times the threshold value, as beyond this value the principal coordinates would remain the same (Borcard and Legendre, 2002). Next, a principal coordinate analysis (PCoA, Gower, 1966) of the truncated distance matrix was performed and only the coordinates with positive eigenvalues, which indicate positive autocorrelation (Dray *et al*., 2006), were kept as a matrix of spatial variables for use as spatial explanatory descriptors. Each principal coordinate represented a spatial variable that characterized a particular spatial scale, with higher eigenvalues representing broader-scale variations, and smaller eigenvalues representing finer-scale variations. The PCNM analyses resulted in 12 and 15 PCNM variables in 2009 and 2010, respectively. As shown in Figure 4.4, these PCNMs were classified into three subsets according to their eigenvalues and the scales of the spatial patterns they represent: a “broad-scale” subset with eigenvalues $> 2.5*10^9$ and a range > 40km, including PCNM1-4 for both years; a “medium-scale” subset ranging from $1.2*10^9$ to $2.5*10^9$ in eigenvalues and from 20 to 40km in distance, containing the PCNM5-10 for 2009 but PCNM5-12 for 2010; and a “fine-scale” subset with eigenvalues $< 1.2*10^9$ and a range of < 20 km corresponding to PCNM12-13 for 2009 but PCNM13-15 for 2010 (Fig. 4.2).

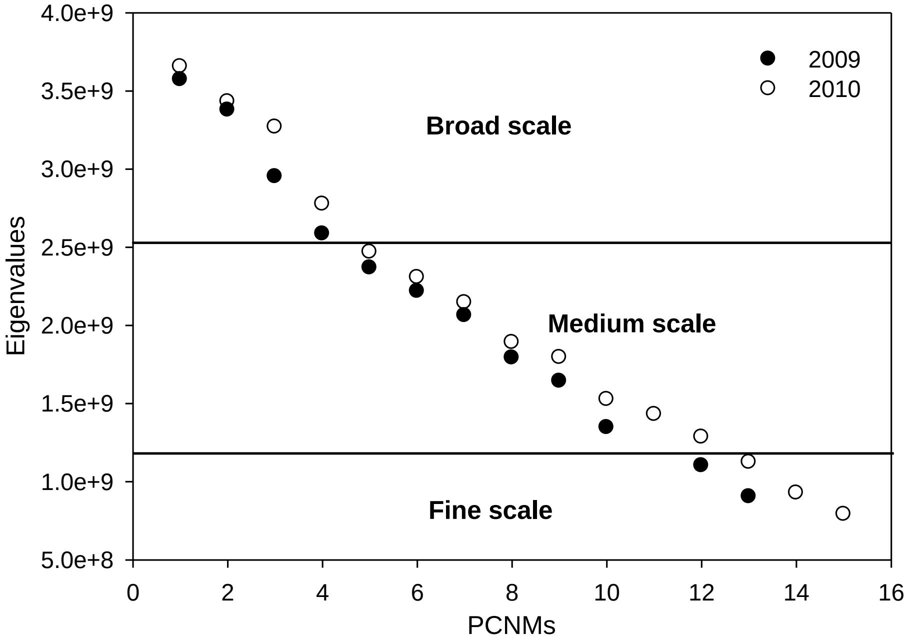


Figure 4.2. Eigenvalues of PCNM variables in 2009 and 2010, and classifications of submodels. “Broad scale”: eigenvalue > $2.5*10^9$; “Medium scale”: $1.2*10^9$ < eigenvalue < $2.5*10^9$; “Fine scale”: eigenvalue < $1.2*10^9$. Solid circle: 2009; open circle: 2010.

4.2.5 Statistical analysis:

Densities of total larvae and larvae of three dominant fish species (Pacific herring [*Clupea pallasi*], Pacific hake [*Merluccius productus*] and northern smoothtongue [*Leuroglossus schmidti*]) were ln(N+1) transformed to achieve normality in frequency distribution and improve linear relationships. Transformed larval density data were checked for linear trends, which would have indicated the presence of spatial structure at a scale broader than the sampling extent. To make the response variables (larval density here) stationary and retain the more complex structures which could be more optimally modeled by PCNM analysis, linear regression was applied to model and remove the linear trend if a significant trend was identified (Legendre and Legendre 1998; Borcard and Legendre, 2002). The residuals (i.e. detrended data) of the response variables were used in the subsequent analyses. The same linear trend examination and detrending processes were also applied to environmental descriptors.

Multiple linear regressions of detrended density data were performed through constructed spatial submodels to decompose the response data onto broad, medium and fine scales. Significance of spatial patterns at each scale was tested by permutation. Next, the predicted values of multiple regression analysis were regressed against the detrended environmental descriptors using a second multiple linear regression with a forward selection procedure to identify which environmental descriptors had significant effects on the larval distribution at the spatial scales identified as statistically significant. The *F*-statistic of the multiple regression coefficients and *t*-statistic for the individual regression coefficients were tested for significance via permutation. In addition, fitted scores of identified linear trends in larval distribution were also regressed on the environmental descriptors to determine associations.

Variance partitioning analysis (Borcard *et al*., 1992) was performed following multiple regressions to fractionate the variation in larval density data and quantify the relative importance of various unique and combined fractions of variations explained by environmental conditions, trends, plus broad- and medium-scale spatial structures as shown in Figure 4.3. Fine-scale spatial structures were not included in the variance partitioning analysis as neither environmental variables nor larval abundance distributions displayed any significant spatial structure on this scale. Prior to variance partitioning, forward selection was performed on the geographical coordinates, the environmental variables and the PCNM variables independently, and the selected significant PCNM variables were clustered into a broad and a medium scale component. The adjusted R^2 (R^2_{adj}) provides unbiased estimates of the variation in the response data explained by each of the explanatory variables (Peres-Neto *et al*., 2006). Negative R^2_{adj} values, which correspond to explanatory variables that explain less variation than expected by chance, were interpreted as zeros (Borcard *et al*., 2011). Finally, we tested the significance of each unique fraction (environmental, trend, broad and medium spatial scale fractions ([a] to [d])) by permutation of the reduced model (Borcard *et al*. 1992; Legendre and Legendre, 1998). All data manipulation and statistical analyses were performed in the R-language environment (R Core Team 2012, http://cran.r-project.org/). Packages included: *PCNM* version 2.1-2 (Legendre *et al*., 2012); *packfor* version 0.0-8 (Dray *et al*., 2011) and *vegan* version 2.0-4 (Oksanen *et al*., 2012). In addition, the spatial distributions of three environmental descriptors (T_{sur}, S_{sur}, F_{0_20}) and larval densities (total larvae and dominant fish species) were represented in distribution maps for visualization purposes using kriging - an interpolation approach commonly used in the geostatistics which takes into account the spatial structure of the variables to provide optimal, unbiased linear predictions at unsampled locations. These kriging maps are highly simplified approximations to the real patterns based on the data collected over a span of 3-4 days. Maps were created through ArcGIS v10.1 and displayed in projection GCS WGS 1984.

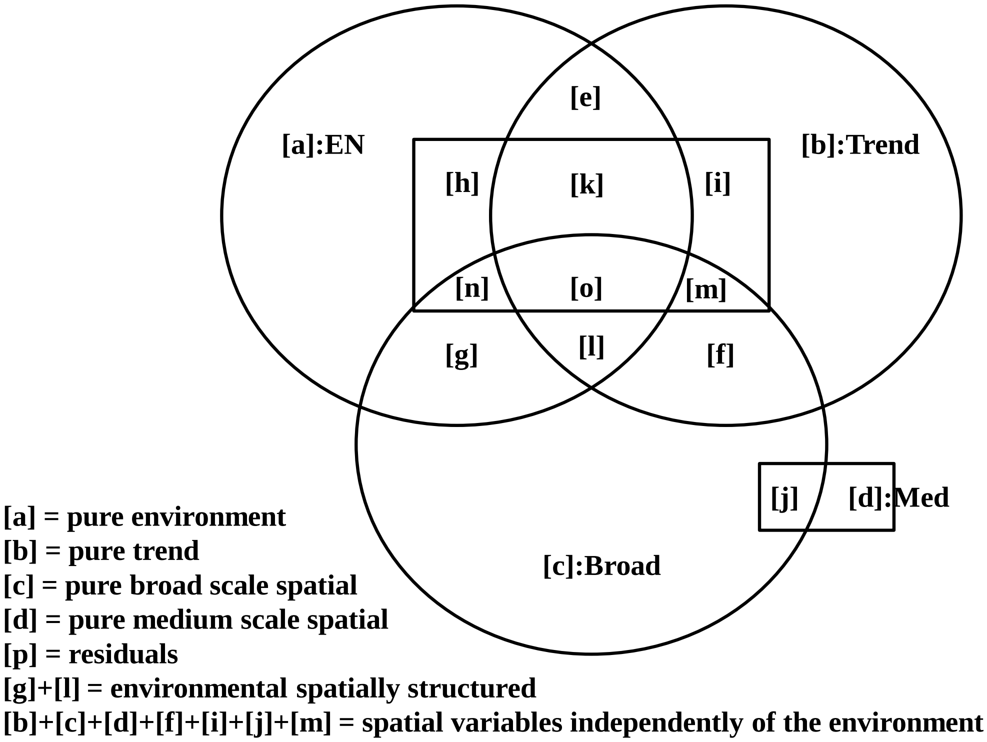


Figure 4.3. Variance partitioning of non-detrended larval fish abundance into an environmental component, a linear trend, a broad-scale and medium-scale PCNM spatial components.

4.3 Results

4.3.1 Multiscale patterns - environmental factors

The SoG experienced different oceanographic conditions in late-April of 2009 and 2010. During the survey days in 2009, winds were blowing predominantly from the southeast, but occasionally from northwest or northeasterly directions, with an average speed of 3.9m/s (Fig. 4.4a). Wind mixing (characterized by cubed wind speed) over the two weeks prior to field survey was relatively strong with an average of 189.1 m^3/s^3. The surface plume with lighter and colder brackish water was adjacent to the Fraser River estuary in the southern SoG. The temperature and salinity of the surface water displayed an along-strait gradient increasing toward the north under the forces of the predominantly southeasterly winds (Fig. 4.5a, b). Surface water temperature varied from 7.6 ℃ to 11.0 ℃ over the central-southern SoG with an average of 9.7 ℃; and surface salinity varied from 16.4psu to 29.6psu with an average of 27.1psu. In contrast, during the 2010 field survey, the stronger northwesterlies (averaged 6.0m/s) prevailed (Fig. 4.4b). The average wind mixing over the two weeks prior to the surveys was weaker (143.3 m^3/s^3) in 2010 compared to 2009. The lighter but warmer surface brackish water that flowed from Fraser River was spread around the Fraser River delta and a narrow band of low salinity water extending along the mainland shore of the SoG, resulting in a cross-strait gradient in the central and southern SoG, with saline but colder water along the western coast (Fig. 4.5d, e). The average values of surface water properties in 2010 were 9.9℃ in temperature and 26.8psu in salinity. Phytoplankton biomass estimated as chlorophyll fluorescence was greater in 2009 than in 2010 with averages of 15.7 mg/m^3 and 10.2 mg/m^3, respectively. Observed phytoplankton spatial distributions were very different between years, displaying significant spatial structure on the medium scale in 2009 (Fig. 4.5c and Table 4.1), but on a broader scale in 2010 (Fig. 4.5f, Table. 4.1). However, the area in proximity to the Sunshine Coast in the northeastern central SoG had higher phytoplankton

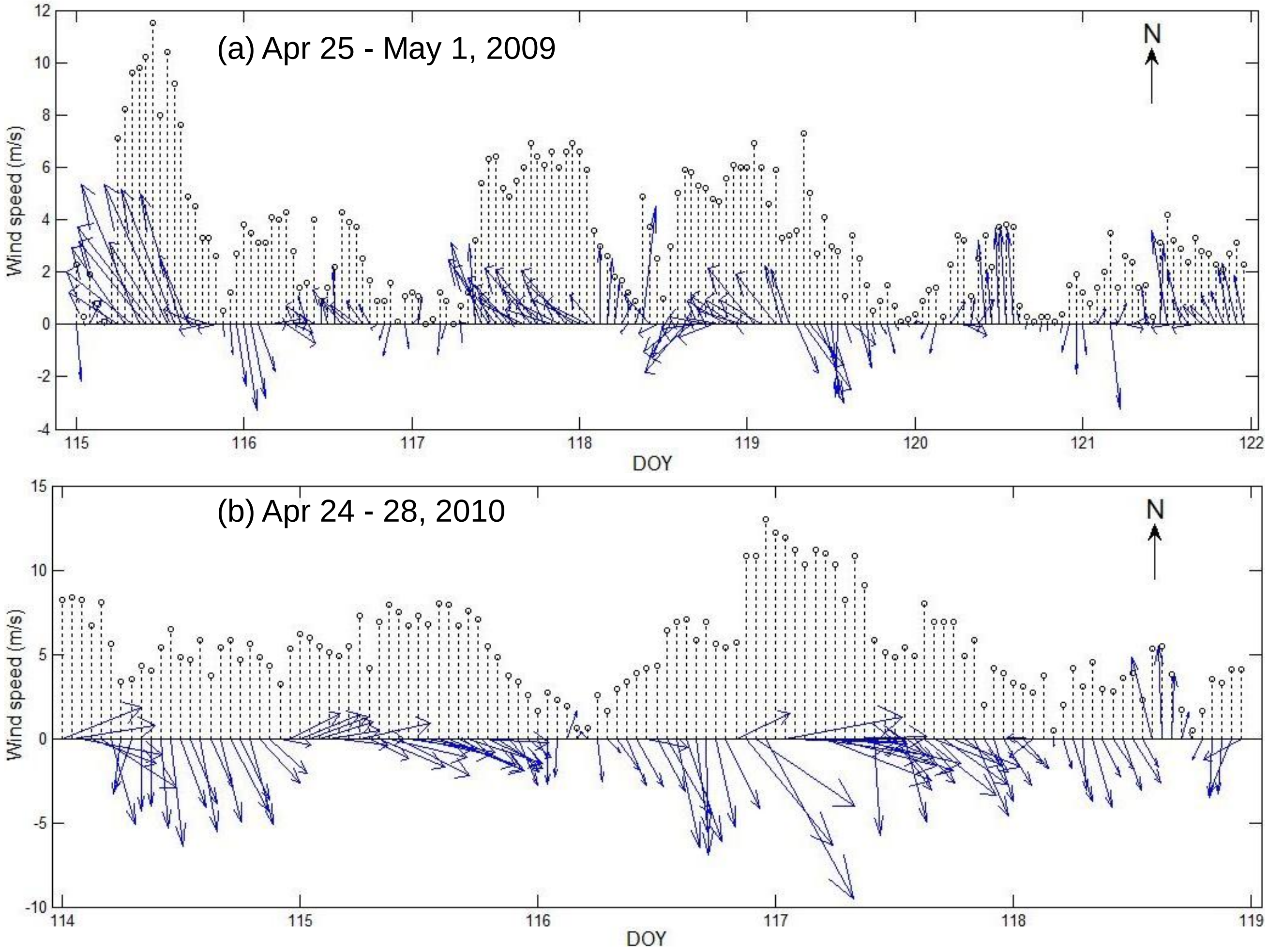


Figure 4.4. Hourly variations in wind direction and speed (m/s) during ichthyoplankton surveys: (a) April 25 – May 1, 2009 and (b) April 24-28, 2010. Solid arrow indicates the vector of wind including the wind direction and speed (m/s). The dash stem indicates the absolute value of wind speed. Wind speed and direction data were obtained from Buoy weather data at Halibut Bank (49.340 °N 123.730 °W, http://www.pac.dfo mpo.gc.ca/science/oceans/data-donnees/buoydata-donneebouee/index-eng.htm).

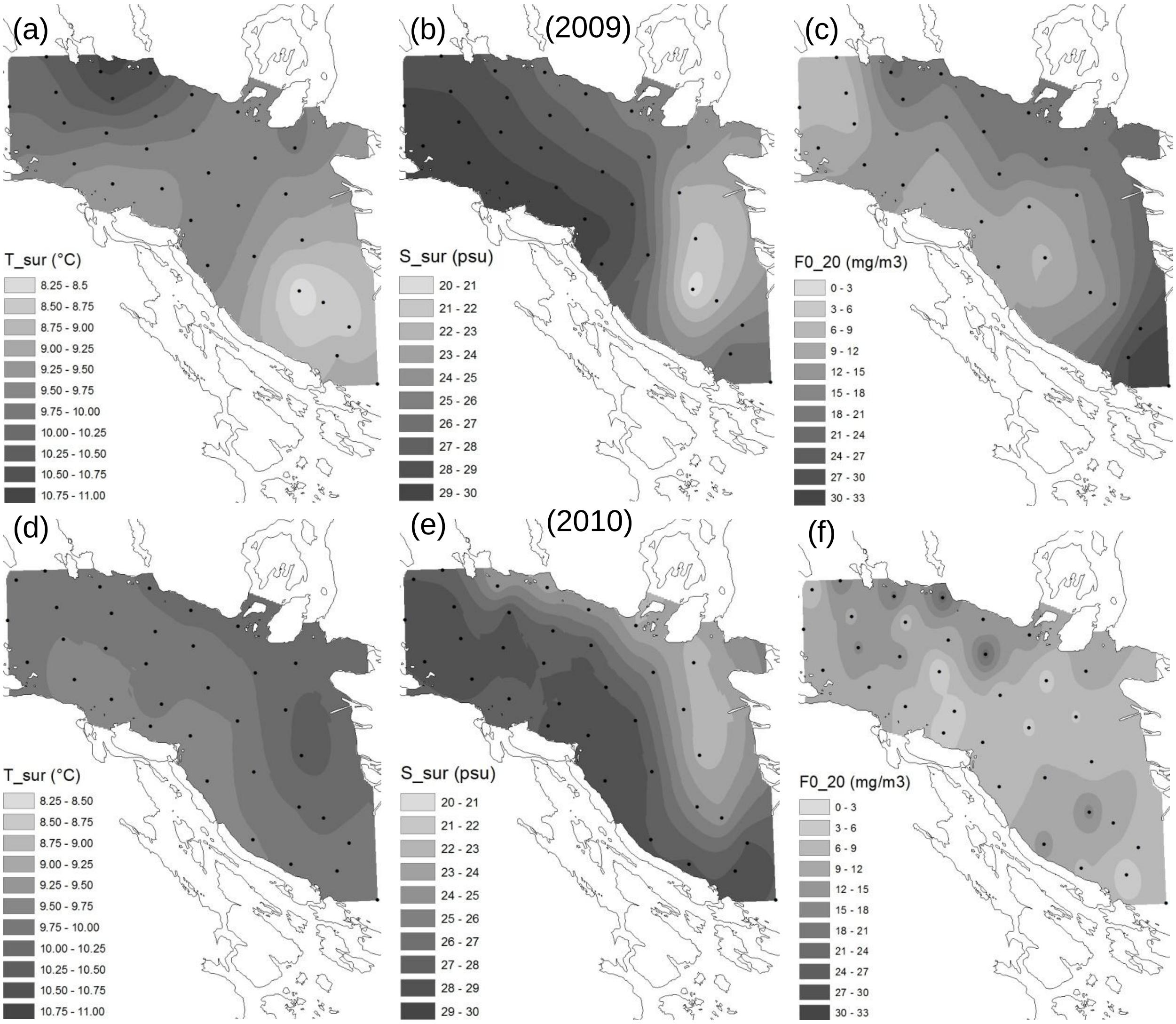


Figure 4.5. Spatial distributions of surface water characteristics measured through surveys in 2009 and 2010: (a) surface temperature in 2009; (b) surface salinity in 2009; (c) mean fluorescence in 2009; (d) surface temperature in 2010; (e) surface salinity in 2010; (f) mean fluorescence in 2010. $T_{\_sur}$ indicates surface temperature, $S_{\_sur}$ indicates surface salinity, F_{0_20} indicates mean fluorescence from surface to 20m.

Table 4.1. Significant spatial structures (as *p*-values) of ten environmental descriptors on multiple spatial scales in 2009 and 2010.

	Depth	**T_{sur}**	**T_{50}**	**T_{0_50}**	**Z_{DMIX}**	**S_{sur}**	**S_{50}**	**S_{0_50}**	**F_{0_20}**
2009									
Trend	0.005	0.005	0.005	0.005	0.024	0.005	0.005	0.005	0.013
Broad	0.042			0.015			0.020		
Medium				0.010		0.005	0.017		0.041
Fine									
2010									
Trend	0.037	0.005	0.005	0.010	0.030	0.005		0.005	0.025
Broad	0.027		0.025						0.026
Medium					0.010	0.005	0.010	0.005	
Fine									

Note: only *p*-values of significant spatial patterns are shown, blank indicates non-significant pattern.

concentrations in both years. A horizontal linear trend was a common feature that existed for all environmental descriptors with the exception of salinity measured at 50m in 2010 (Table. 4.1). Interannual variations in multiscale spatial patterns were also evident. In 2009, spatial variability was mostly structured on both broad and medium scales for temperature (T_{0_50}) and salinity (S_{50}), but only on the medium scale for surface salinity (S_{sur}, Table 4.1). In 2010 the spatial variability was mostly structured on a broad scale for temperature (T_{50}), but on a medium scale for all salinity relevant indices and the depth of the mixed layer (Z_{DMIX}, Table 4.1). No spatial variability was detected for any environmental variables at a fine scale in either 2009 or 2010.

4.3.2 Multiscale patterns – total larvae

2009: Two distinct patches of high total larval density were detected close to the Sunshine Coast (northeastern) and Valdes Island (southwestern) in 2009 (Fig. 4.6a). More larvae occurred in warm and saline water with salinity between 26 – 30psu (Fig. 4.7b). Observed spatial patterns of total larvae were significantly structured on medium scales ($p = 0.01$), which independently explained 11.3% of the total variation (Table 4.2), and reflected negative relationships with salinity at 50m (S_{50}) and the depth of mixing layer (Z_{DMIX}) at this spatial scale (Table 4.3a). However, environmental factors alone did not explain any significant amount of variance (Table 4.2).

2010: A single patch with high total larval density was observed adjacent to the Sunshine Coast on the eastern side of the SoG in late April of 2010 (Fig. 4.6b), forming a significant cross-strait trend that decreased from the eastern to the western shoreline (Fig 4.8, $p = 0.01$, Table 4.2) and which was strongly associated with patterns of surface water salinity ($p = 0.004$). Unlike 2009, however, high larval density was more closely associated with the warm plume water where salinity was ranging from 22psu to 26psu (Fig. 4.7b). Taken together, the environmental

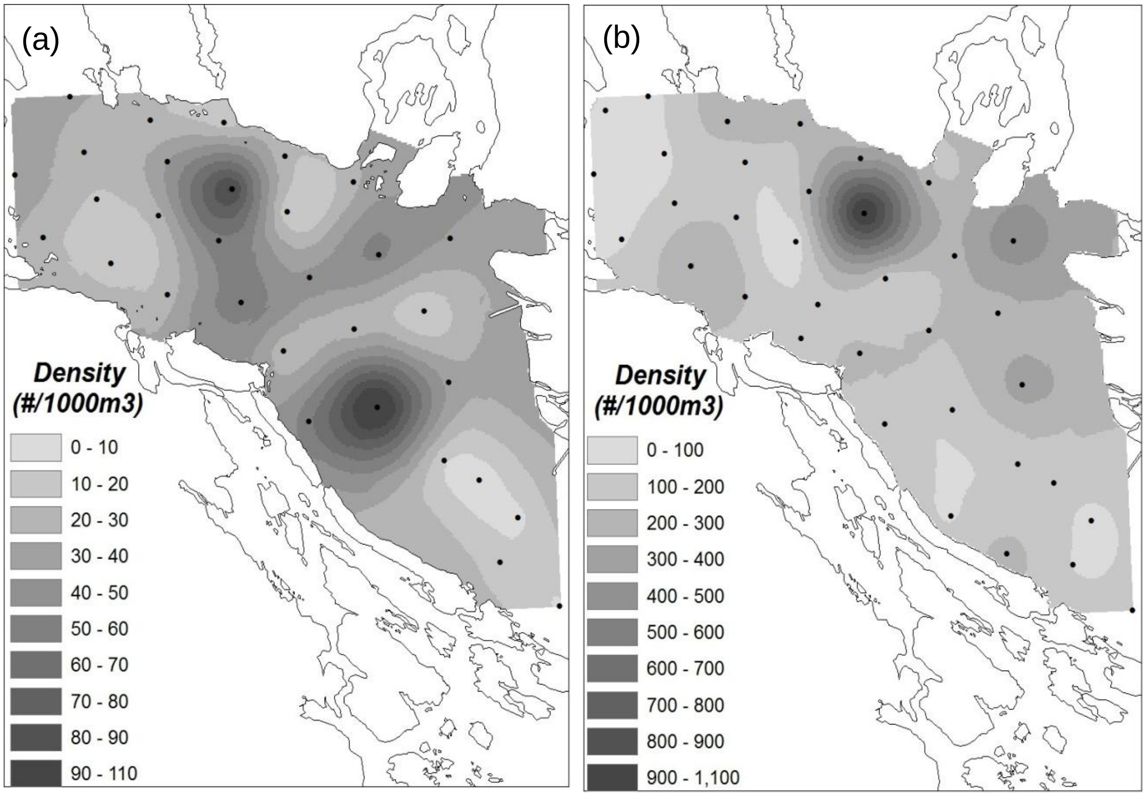


Figure 4.6. Observed spatial distribution of total larval abundance (larvae /1000m^3) in the Strait of Georgia during late-April of: (a) 2009 (b) 2010. Different scales in larval density are applied in 2009 and 2010 for better visualization of larval fish spatial distribution within each survey year.

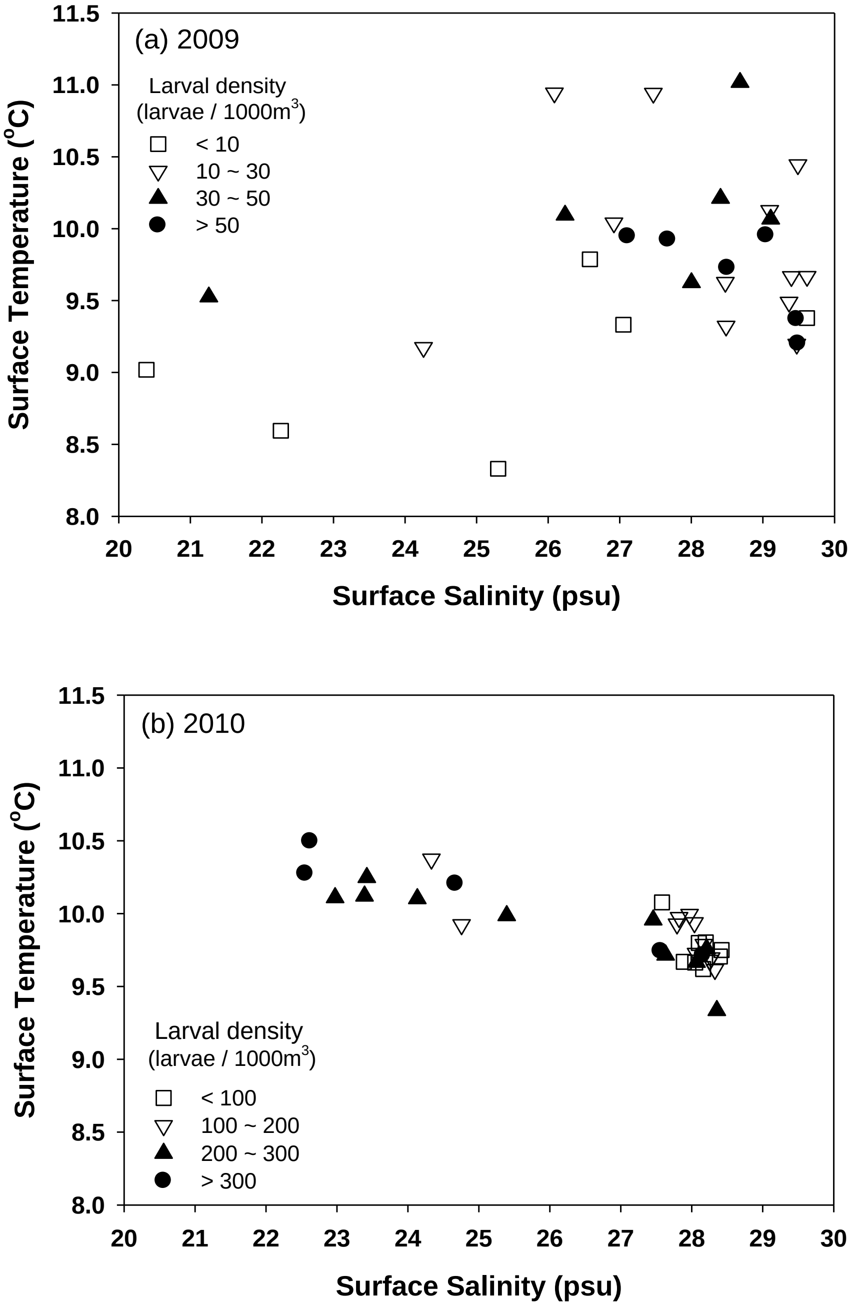


Figure 4.7. Total larval abundances in surface temperature – salinity space for all sampling stations in (a) 2009 and (b) 2010.

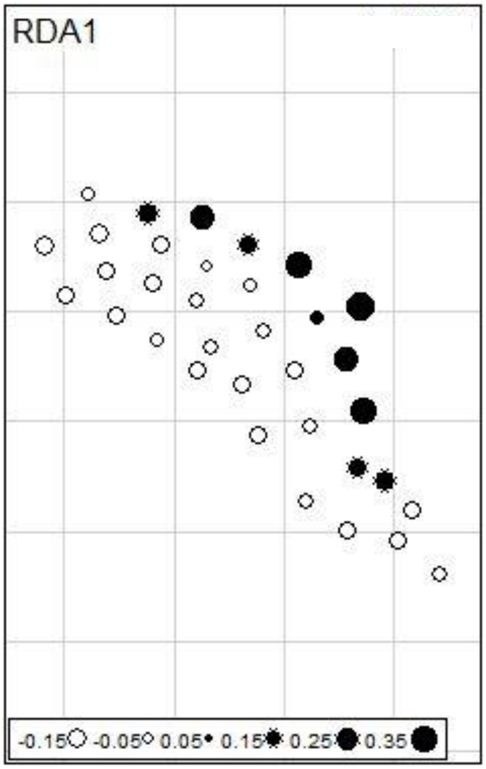


Figure 4.8. Decomposition of linear trends in distribution of total fish larvae in 2010. Values presented are fitted site scores of the first RDA axis.

Table 4.2. Variance partitioning of non-detrended larval fish data in 2009 and 2010.

	Total larvae		***Clupea pallasi***		***Merluccius productus***		***Leuroglossus schmidti***	
	2009	2010	2009	2010	2009	2010	2009	2010
Trend (*p*-value)	--	0.041	--	--	--	--	--	--
Coordinate	--	--	--	--	--	--	--	--
EN Variables	T_{sur}	Z_{DMIX}		T_{50}	T_{sur}			Z_{DMIX}
Variance Partition								
A	-0.022	**0.141**	-0.126	**0.105**	-0.017			**0.090**
B	-0.033	0.016	0.024	0.010	0.015			-0.038
C	-0.010	0.014	**0.170**	0.077	0.007			**0.060**
D	**0.113**	-0.124	0.036	**0.234**	**0.425**			**0.095**
ALL	0.315	0.193	0.253	0.497	0.572			0.397

Note: significant fractions of variation ($p < 0.05$) are marked in bold. X and Y represent longitude and latitude, respectively. ALL: total variance explained by all components, a: pure environment fraction, b: pure trend fraction, c: pure broad-scale spatial fraction, d: pure medium scale spatial fraction.

and spatial variables explained 19.3% of the total variance, of which the only significant environmental variable identified by forward selection - Z_{DMIX} (p = 0.005) alone explained a relatively large portion ~14.1% (p = 0.049). In contrast, almost none of the variance was explained by the spatial variables independent of the environment. No significant spatial structure was detected on any predefined scale.

For the density of total larvae, the spatial variation on the medium-scale was notable in 2009; while the horizontal linear trend (both across and along the SoG) and environmental impact were relatively more important in 2010. Among all measured environmental descriptors, Z_{DMIX} was associated to the variation in total larval density in both years.

4.3.3 Multiscale patterns – larvae of dominant fish species

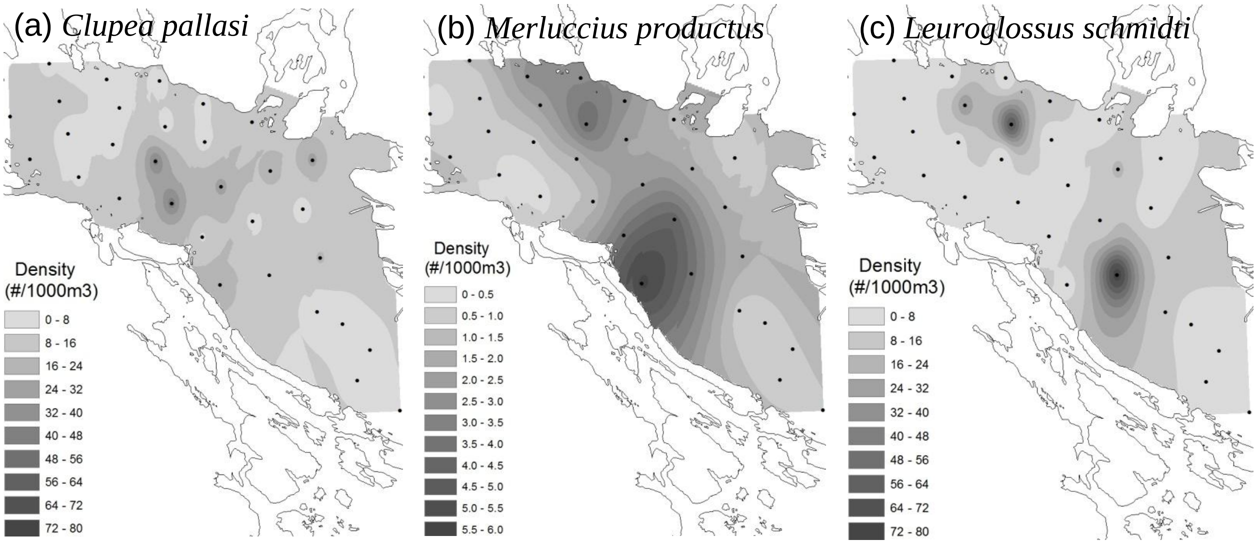
In late April of 2009, herring larvae were more abundant in the central section of the SoG near Gabriola Island (Fig. 4.9a), while the density of hake larvae was highest along the northeastern and southwestern shores of the central SoG near the Sunshine Coast and Valdes Island (Fig. 4.9b). Spatial patterns of larval herring and hake varied significantly at both broad and medium scales (Table 4.3a). Similar to the distribution of larval hake, northern smoothtongue larvae were more abundant in two patches (Fig. 4.9c), but no significant spatial structure was detected at any scale for this species in 2009. In 2010, larvae of northern smoothtongue were distributed along the eastern side of the central SoG (Fig. 4.9f), and was the only species with larval distributions structured at both broad and medium scales in this year (p = 0.020 and 0.026, respectively, Table 4.3b). The density of larval herring was highest around the northeastern part of the central SoG and (to a lesser extent) around Gabriola Island and showed a significant medium-scale pattern (Fig. 4.9d). Although Pacific hake larvae displayed a patchy distribution, no significant spatial structure was detected at either broad or medium scales for this species in

2010 (Fig. 4.9e, Table 4.3b). In addition, no fine-scale structure was detected for any species in 2009 and 2010.

The relative importance of broad-scale and medium-scale spatial structures varied among species within each study year, but the medium-scale structures of different species were consistently associated with the same environmental factor for each year. In 2009, the broad-scale spatial structure, which significantly explained 17.0% of the total variation (p = 0.037), was more remarkable for herring compared to the medium-scale spatial structure which only explained 3.6% of the variation (Table 4.2). In contrast, the spatial structure of hake larvae was more evident at medium scales, explaining 42.5% of the total variance significantly (Table 4.2). Broad-scale distribution of herring larvae was significantly negatively associated with average salinity in the surface layer (b = -0.581); but a similar distribution- environment relationship was not detected for hake larvae on this scale. On the medium scale, larval distribution patterns were consistently negatively related to salinity at 50m for both species (b = -0.415 and b = -0.775 for herring and hake, respectively), and also negatively related to depth of mixing layer (b = -0.448) for hake. In 2010, the observed distributions of herring and smoothtongue larvae were both mostly structured on the medium scale, which explained 23.4% and 9.5% of total variance, respectively (Table 4.3b); their medium-scale patterns were each related to average water temperature in the surface layer, but with opposite effects (b = 0.488 for herring and for b = -0.490 northern smoothtongue, Table 4.3b). In addition, broad-scale distributions of larval smoothtongue, which was less notable compared to their medium-scale spatial variations, was positively associated with bathymetric characteristics of the sampling sites (Table 4.3b).

The portions of total variance explained by pure environmental effects were quite different between the two study years. Environmental factors barely explained any variance for either Pacific herring or Pacific hake in 2009 (0% for both species, Table 4.2), but significantly explained a considerable portion of total variance for both herring and smoothtongue in 2010 (10.5% and 9%, respectively, Table 4.2).

2009:



2010:

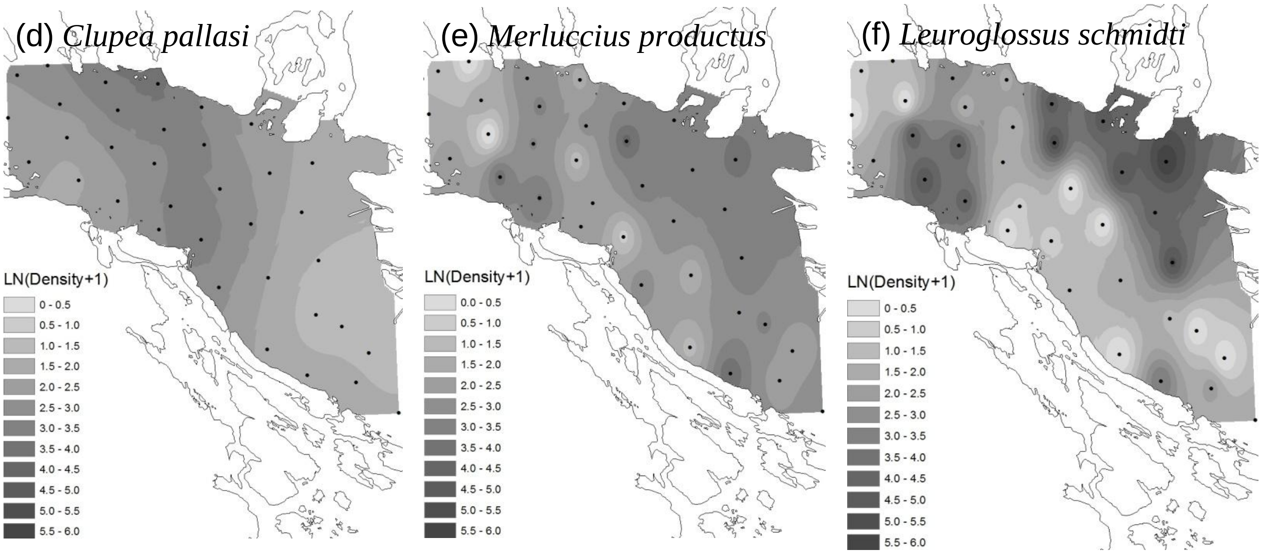


Figure 4.9. Spatial distribution maps of larval density of six major fish species in 2009 and 2010 for illustration. Larval density is mapped and expressed in number of larvae per 1000m^3 for 2009, while LN(Density +1) is mapped for 2010.

Table 4.3. Patterns of total fish larvae and larvae of dominant fish species over different spatial scales and coefficients of multiple regression with explanatory environmental variables in (a) 2009 and (b) 2010.

(a). 2009

2009	**Depth**	**T_{sur}**	**T_{50}**	**T_{0_50}**	**Z_{DMIX}**	**S_{sur}**	**S_{50}**	**S_{0_50}**	**F_{0_20}**
Total larvae									
Broad-scale									
Medium-scale**					**-0.347**		**-0.671**		
C. pallasi									
Broad-scale*		-0.411						**-0.581**	
Medium-scale*							**-0.415**		
M. productus									
Broad-scale*									
Medium-scale**					**-0.448**		**-0.775**		
L. schmidti									
Broad-scale									
Medium-scale									

(b) 2010

2010	**Depth**	**T_{sur}**	**T_{50}**	**T_{0_50}**	**Z_{DMIX}**	**S_{sur}**	**S_{50}**	**S_{0_50}**	**F_{0_20}**
Total larvae									
Broad-scale									
Medium-scale									
C. pallasi									
Broad-scale									
Medium-scale**				**0.488**					
M. productus									
Broad-scale									
Medium-scale									
L. schmidti									
Broad-scale**	**0.341**								
Medium-scale*				**-0.490**					

Note: Scales with significant pattern are indicated by stars with level of significance: *: $0.01 < p < 0.05$, **: $0.001 < p < 0.01$, ***: $p < 0.001$. Significant correlations ($p < 0.05$) are shown in bold.

4.4 Discussion

The interannual variations in the distributions of seawater properties revealed differences between years in the underlying physical oceanographic processes. Generally, current patterns in the SoG are primarily attributed to the interaction of the Fraser River discharge with tides and the prevailing winds, and further adjusted by basin bathymetry and other physical effects such as the Coriolis force (Thomson, 1981). Freshwater from the Fraser River is initially directed southwesterly toward the Gulf Islands by the momentum of the river water flowing out, and discharged into the middle of the southern SoG (Stronach, 1981; Thomson, 1981). In the presence of strong southeasterly wind and predominantly ebb tides during 2009 field survey, the surface plume maintained its southwest direction, spread toward southern region, and formed the observed along-strait pattern of decreasing surface salinity from north to south. In contrast, during the 2010 survey, the plume turned sharply northward under the forces of a flood tide and light northwest winds, resulting in a cross-strait gradient of decreasing surface salinity from west to east. Compared to the weak wind effect in 2010, the strength of wind mixing in 2009 was more prominent in affecting current patterns in the surface layer, thus the depth of mixing layer and TS distributions within this layer. These dominant physical oceanographic processes contributed significantly not only in structuring the distribution of abiotic factors, but also in driving biotic spatial heterogeneity on multiple scales in the SoG.

Analysis of variability at three predefined spatial scales suggested that significant variations in larval fish distributions occurred at broad- and medium-scales for both years. The broad-scale spatial pattern in the SoG characterized along-strait variations. The decomposed larval spatial variations on this scale reflected not only the effect of basin bathymetry but also the influence of external environmental factors. The broad-scale distribution of northern smoothtongue larvae in 2010 was associated with bathymetry in central-southern SoG with more larvae occurring around deeper regions in the central SoG. This probably reflected the bathypelagic life history and deep-water reproductive activity of the adults centered in the central SoG, as most of smoothtongue larvae collected in this year were still in their early pre-flexion stage (Mason and Phillips, 1985). In contrast, the distribution of Pacific herring larvae on broad-scales in 2009 was mainly associated with the spatial structure of salinity within the upper layer. Their negative association suggested larval aggregation in less saline water. The salinity-related environmental descriptors played crucial roles in explaining spatial variations not only at broad-scales but also on medium-scales in the SoG. The mechanisms underlying these patterns will be detailed in the following discussion.

The spatial dependency of the dominant larval fish species in the SoG was primarily structured on medium-scales ranging from 20 to 40 km. Spatial variation at this scale likely represented the influence of oceanographic processes interacting with the estuarine circulation in the central-southern SoG, but the specific explanatory environmental factors associated with the variations differed between years. In 2009, densities of total larvae and larvae of Pacific herring and Pacific hake displayed medium-scale spatial dependency and negative co-dependence relationship with salinity at the interface between the upper layer and the deeper layer. Indication of more larvae aggregating in the plume water with lower salinity emphasized the importance of freshwater input in regulating the spatial distribution of larvae in this estuarine system. The brackish water and associated saline fronts, which are formed when two water masses with different salinity or density meet, are considered an important concentrating mechanism and would enhance plankton retention due to the strong density gradients (Mackas, 1985; Daly and Smith, 1993; Bakun, 2006). Previous studies on the distribution and aggregation of zooplankton within the SoG reported that very high abundances of different copepods had been observed frequently in the upper layer at the margin of the Fraser River plume, and also suggested a strong and direct link to the pattern of surface salinity in the SoG (Parsons *et al*., 1969b; Mackas *et al*., 1980, Mackas and Louttit, 1988). From another perspective, these saline frontal zones concentrating high zooplankton biomass will also provide ideal feeding environments for fish larvae which may promote higher survival during their early-life-history stages. A similar negative correlation with salinity and association with local estuarine outflows has also been reported for the spatial structure of early life stages of the Brazilian sardine (*Sardinella brasiliensis*) in a tropical marine ecosystem – Southeastern Brazilian Bight (de Souza Moraes *et al*., 2012).

In addition to the association with salinity, a negative relationship between the depth of the mixed layer and larval densities was detected for total larvae and hake larvae on the medium-scale. The mixed layer of the upper ocean is a boundary layer for atmosphere-ocean interaction and energy transfer via turbulent diffusion, and the physical properties of seawater (e.g. salinity and temperature) throughout this layer are nearly constant (Daly and Smith, 1993). The depth of the mixed layer usually reflects the strength of wind stress which is the primary mechanism driving turbulent mixing at the sea surface (Kantha and Clayson, 2003). Compared to 2010, the much stronger wind mixing two weeks prior to the field survey in 2009, and its direct impact on the depth and intensity of the mixed layer became another significant factor influencing the distribution of larvae within the upper ocean on the medium scale. More larvae existing in the water column with a shallower mixed layer depth suggested that physical processes favoring vertical stability of water column probably also enhance the larval aggregation. Furthermore, an upper water layer associated with less vertical mixing and stronger stability would enhance the growth of phytoplankton which may promote the production of young herbivores such as copepods, and thus increase the possibility of larval fish survival (Pinel-Alloul *et al*., 1999).

In 2010, the observed medium-scale larval spatial patterns were associated with average temperature in the upper layer, which also displayed a moderately negative relation to average salinity. The co-dependent relationship with temperature was not consistent across species, with higher densities of herring larvae mostly related to the presence of warmer surface water, but inversely for smoothtongue larvae. The direct influence of water temperature could be due to different thermal requirements for metabolism and growth of early life stages of various fish taxa (Houde, 1989; Pepin, 1991).

The generation of larval fish spatial patterns takes place from spawning, and develops through dispersal and then re-aggregation by either endogenous processes (e.g. spatially variable mortality) or directed larval behavioral interaction (e.g. schooling behaviour, Matsuura and Hewitt, 1995). Therefore, basic life history traits of fish species such as adult spawning locations and the characteristics of eggs and larvae play important roles in the formation and variation of spatial structures. Among the fish species examined, Pacific herring which produce demersal eggs was the only species that consistently displayed significant spatial structures, particularly on medium scales, in both 2009 and 2010. Pacific herring is a nearshore pelagic species, and usually produces demersal adhesive eggs attached to vegetation and substrates in intertidal or shallow subtidal water (Hay, 1985). The distribution of herring spawning in the SoG has documented for many years, but most of the spawning activity has been confined to a number of relatively discrete locations along the western coastline between Saltspring and Denman islands in recent years (Hay and McCarter, 1997; Therriault *et al.*, 2009). After hatching from demersal eggs and staying within the upper surface layer, the dispersal of herring larvae is largely affected by the surface circulation. From an early age of around 6 days post-hatch, these larvae start to perform diel vertical migration, actively adjusting their vertical position and possibly using the appropriate currents to stay around nearshore nursery areas with more food available for better survival (Hourston and Haegele, 1980).

Pacific hake and northern smoothtongue are the dominant mid-water schooling fish in the SoG (Mason and Phillips, 1985). These species are pelagic spawners which produce pelagic eggs at deeper layer in the central SoG, but their pelagic larvae usually develop at shallower depth (Mason and Phillips, 1985; McFarlane and Beamish, 1985). For these species, dispersal is a complex process starting from spawning, and then lasting through the entire egg and larval stages during which they ascend from the deep spawning layer to shallow depth. Their dispersal is subject to varying hydrodynamic conditions throughout the entire water column with deep currents, such as low frequency current fluctuations which produce deep gyre with cross-strait currents, in the deeper layer (>50m) but currents primarily driven by wind in the upper layer (0-50m) (Snauffer, 2013). Compared to these pelagic spawners, the relatively shorter passive dispersal process of Pacific herring (i.e. starting from roughly consistent spawning areas) is more favorable for generation of consistent spatial patterns.

The development of active larval behavior at different stages of the early life history is an often overlooked factor that can affect the “re-aggregation” of fish larvae later in their development. The two ichthyoplankton surveys in this study were both conducted during the last week of April (in 2009 and 2010). However, the phenology of the fish taxa examined differed interannually, with significantly larger and presumably older larvae consistently collected in 2009 than in 2010 (Table 3.3, Figure 3.8 in Chapter 3). Larvae in their early developmental stage usually display very limited mobility capability and can be considered as passive drifters. Their spatial pattern is first determined by the adult spawning locations, and subsequently modified by hydrodynamic processes. However, physical processes alone are often insufficient to explain the spatial structure of older/larger larvae which possess stronger directed larval behavior and interaction (Guan *et al*., 2008). The contributions of biological processes such as active swimming, food searching, predator avoidance and habitat selection are prominent, and the spatial distribution of the larger (presumably older) larvae are the result of a combination of biological and physical processes (Cowen *et al*., 1993; Leis, 2006; Cowen and Sponaugle, 2009). As a result, the relative contribution of environmental factors and biological processes in structuring spatial distribution of fish larvae varies at different developmental stages of their early life history (Leis, 2006).

Finally, the variance partitioning analysis also revealed that environmental descriptors alone barely explained any spatial variance in larval distributions in 2009 and only a small portion (< 15%) in 2010. One possibility is that part of the variation in larval distribution could be explained by environmental factors that have not been included in analyses. For example, as one of the major factors modulating the estuarine circulation (Li *et al*., 1999; Masson, 2006), wind can alter distributions of water properties through transporting and mixing water masses in the upper layer (LeBlond, 1983), and thus should be considered as an important forcing agent to affect the transport and distribution of fish larvae. A recent study simulating larval dispersal of herring in the SoG using a regional circulation model and a particle tracking model has verified that the distribution of herring larvae is significantly influenced by local winds (Snauffer, 2013). In present study, however, wind forcing has been only considered in the form of wind mixing strength (characterized by cubed wind speed) for interannual comparison, but was not included in the variance partitioning analysis. In addition, the portion of variance in larval distribution explained by pure environmental variables was consistently lower than the portion explained by pure spatial (PCNM) variables for both study years. This is probably attributed to a mismatch between the scale of field observations and the particular scale at which larval fishes respond to surrounding environmental variability (de Knegt *et al*., 2010).

By applying the multi-scale PCNM approach, larval fish distributions in the central–southern sector of the SoG were decomposed onto three predefined spatial scales ($\geq$40 km, 20-40 km and $\leq$ 20 km). Spatial variations in larval density of three dominant fish species were mostly structured on broad and medium scales, and their scale-dependent distributions were generally associated with salinity, temperature and vertical stability of water column in the upper layer. These findings emphasize the importance of the local estuarine circulation in structuring spatial distributions of planktonic fish larvae in the SoG, and suggest a role for fundamental differences in life history traits in influencing the formation and development of larval spatial structures. The results also indicate the relative contributions of physical oceanographic processes and active larval behavior in structuring larval distributions at different developmental stages of the early life history.

Chapter 5

Conclusions and Future Research

The primary objective of this thesis was to provide the first characterization of spatiotemporal variability of spring larval fish assemblages in the Strait of Georgia (SoG). Based on several spatially intensive field investigations in the late 2000s (2007, 2009 and 2010) and previously unanalyzed ichthyoplankton data from the early 1980s (1980 and 1981), Chapter 2 revealed differences in the characteristics of larval fish assemblages between two periods nearly three decades apart. Chapter 3 presented comprehensive baseline information on the recent status of the larval fish community in the SoG in terms of its diversity, abundance and compositional structure, and evaluated interannual variations in larval fish assemblages with respect to fluctuating environmental conditions. Chapter 4 characterized spatial variations in larval distributions of several dominant fish species across multiple spatial scales and explored their relationships to environmental heterogeneity. This thesis will ultimately contribute to a better understanding of spatial and temporal dynamics in larval production of individual fish species and their assemblages in the SoG, and the primary exogenous factors and processes governing such variations in space and time.

5.1 Temporal dynamics of the SoG larval fish assemblages

5.1.1 Overview

In Chapter 2, differences in the absolute abundance and relative composition of the SoG larval fish assemblages were compared between the early 1980s and late 2000s. The most remarkable finding of this chapter was the significant decline in total larval abundance and the differences in assemblage composition in the late 2000s compared to the early 1980s. In the early

1980s, the spring larval fish assemblage in the SoG was dominated by a few pelagic fish species including Pacific herring, Pacific hake, northern smoothtongue and walleye pollock. The dramatic decline in larval abundance of three of these pelagics (Pacific hake, northern smoothtongue and walleye pollock) and rockfishes contributed significantly to the decline in overall larval abundance in the late 2000s. In contrast, the larval abundance and the relative contribution of flatfishes and several demersal forage fish taxa increased in the late 2000s. Notable differences in larval production between the early 1980s and late 2000s, especially for commercially valuable species (e.g. Pacific hake and rockfishes), likely reflect corresponding declines in their adult populations; unfortunately, no stock assessment information is available in the SoG for further verification.

On interannual scales, features of larval fish assemblages (abundance, diversity and assemblage structure) in the SoG displayed remarkable variations during the springs of 2007, 2009 and 2010, which represent contrasting environmental conditions including the end of an El Niño period (2007), a strong La Niña spring (2009), and a strong El Niño spring (2010), respectively. Higher overall larval abundances in 2007 and 2010 were associated with somewhat warmer conditions, while the lower larval abundance in 2009 was associated with a cooler environment. This suggests a positive relationship between larval fish abundance and water temperature, as has been demonstrated by several other recent time-series studies of larval fish in the NE Pacific (Hsieh *et al*., 2005; Auth, 2008; Auth and Brodeur, 2006; Siddon *et al*., 2011). In addition, assemblage composition varied dramatically from (i) dominance by Pacific hake in 2007, to (ii) dominance by Pacific herring and walleye pollock in 2009, followed by a shift to (iii) dominance of benthic species, including rockfishes and several flatfishes, in 2010. Similar to fluctuations in larval fish production, the observed inter-annual variability in assemblage structure was primarily related to the temperature of the water column, possibly reflecting species-specific responses of adult spawning population to the rapidly changing environment.

Chapters 2 and 3 have demonstrated that larval fish assemblages in the SoG can vary dramatically on both inter-decadal and inter-annual scales. Over the shorter time span, variations detected in larval fish production and assemblage structure likely suggest prompt responses of adult spawning population to environmental fluctuations, as these external changes were usually directly and rapidly reflected in the changes of water properties, especially water temperature. Although this study demonstrated that over longer time-scales large-scale climate processes were only one potential contributor to variations in SoG larval fish assemblages, strong associations between variations in larval fish production and large-scale climate forcing factors have also been emphasized by several other recent time-series studies in Northeast Pacific (Hsieh *et al.*, 2005; Auth *et al*., 2011). Variation in water temperature is also a primary (albeit indirect) pathway by which large-scale climate variability influences larval fish production. In addition, temperature variations can potentially trigger a series of changes in larval fish phenology (e.g. timing of larval appearance), pelagic larval duration, larval development rate, phytoplankton productivity, zooplankton production and timing, and the degree of match-mismatch between consecutive trophic levels, which all will indirectly contribute to fluctuations in larval fish productions (Greve *et al*., 2005; Guan *et al*., 2008; Genner *et al*., 2010; Mackas *et al*., 1998, 2007, 2013).

In addition to environmental fluctuations, anthropogenic activity such as fishing may also have contributed to the observed long-term decline in larval fish production of the SoG. Pacific herring, a dominant forage species in the SoG (Therriault *et al*., 2009), is a typical example. Pacific herring have been exploited as one of the major fisheries off Canada's west coast, including the SoG, over the past century. The population collapsed in the mid-1960s under the combined pressure from severe overfishing and reduced recruitment (Beamish *et al*., 2004). After a short period of closure of the fishery from 1967 to 1970, the stock recovered (Beamish *et al*., 2004). According to commercial fishery records (DFO, unpublished), several other pelagic fish species including Pacific hake, walleye Pollock, and demersal rockfishes and flatfishes were also fished commercially in the SoG in the past. Unfortunately, stock assessments are lacking for most of these species and so we cannot quantify any causal relationship between fishing pressure and larval fish production with the limited data available.

5.1.2 Suggestions for future research

Although examination of the associations between larval fish assemblages and environmental fluctuations in the present study suggests that large-scale climate processes are potential contributors to variations in overall larval production and assemblage composition in the SoG, the underlying mechanisms through which climate processes mediate variations in larval fish assemblage are still unclear. One potential mediation pathway is that changes in water properties (e.g. water temperature), induced by climatic effects, could affect the early survival and growth of fish larvae via altering their prey production and composition.

5.1.2a Examination of prey availability and composition of fish larvae

Understanding the mechanisms regulating recruitment success and variations in fish populations has been a focus in fisheries oceanography for a century (Hjort, 1914; Govoni, 2005). One of the key factors affecting larval fish survival is whether larvae acquire sufficient and appropriate food. Although the SoG has long been recognized as a highly productive ecosystem, a comprehensive examination of food availability for larval fish is still lacking. A natural follow-up to the work presented in this thesis would be to examine the variations in larval fish prey production and composition under varying environmental conditions and to explore their influence on early survival of larval fish.

Previous studies on the SoG zooplankton community have focused on a few dominant mesozooplankton species such as copepod *Neocalanus plumchrus* and the euphausiid *Euphasia pacifica*, but little attention has been paid to the abundance of eggs and naupliar stages of copepods, and other microzooplankton which represent the major prey items of most fish larvae. In addition to the classic marine food chain represented by diatoms – copepods – zooplanktivorous fish, the protozooplankton-ichthyoplankton link has recently been emphasized as another key component within marine food webs (Montagnes *et al*., 2010). Studies have demonstrated the consumption of protozoa by larval fish, especially during their early feeding stages (Russell, 1976; Watson and Davis, 1989; Nagano *et al*., 2000; Hunt von Herbing *et al*., 2001), because of their features such as small size, easy digestibility and high abundance. Investigations on the production and composition of larval fish prey including both microzooplankton and protozooplankton, their temporal variability in relation to environmental fluctuations, and temporal match-mismatch with fish larvae will help improve our understanding of mechanisms linking climate changes and potential variations in larval fish assemblages.

5.1.2b Examination of the early growth of fish larvae

In Chapter 3, examination of interannual variations in larval fish assemblages revealed smaller larval size of the dominant fish species and several flatfishes in the warmer environmental condition of 2010 compared to the cooler conditions of 2009. However, recorded spawning dates of the SoG Pacific herring from Fisheries and Oceans Canada shows an earlier timing of herring spawning in 2010 than in 2009 (69 DOY and 85 DOY, respectively). The earlier adult spawning but smaller larval size suggests a possible slower larval growth of Pacific herring in 2010, a trend which might be expected to occur across other co-occurring fish species within the assemblage. The suggested potential differences in larval growth may be related to feeding conditions; more specifically, insufficient appropriate prey supply or increased competition for food in the year with higher larval abundance could be associated with slower larval growth. One suggested follow-up study would therefore be to examine the influence of climate-induced environmental fluctuations on variations in larval fish growth. Early larval growth can provide a good indication of larval stage duration, development of active larval behavior (e.g. swimming capability, Fisher and Bellwood, 2001; Guan *et al*., 2008), vulnerability to predation, survivorship (Searcy and Sponaugle, 2001) and, ultimately, recruitment to the juvenile stage. Thus, understanding the association between larval growth and environmental conditions would improve our prediction strength regarding larval fish dynamics and subsequent recruitment success. In terms of approach, the analysis of otolith microstructure (e.g. the width of individual daily rings) of larval fish can be utilized to age individual larvae collected from the field and used to reconstruct their daily growth history (Chambers and Miller, 1995; Pepin *et al*., 2001; Campana, 2005).

5.1.2c Long-term monitoring of the larval fish community

The SoG ecosystem has been undergoing notable changes under cumulative pressures from accelerating global climatic changes and anthropogenic activities. In the present study, the association between environmental fluctuations and variations in larval fish assemblages over multiple temporal scales has been suggested. However, an accurate quantification of the causal relationships has been somewhat constrained by the paucity of ichthyoplankton data in the region. Long-term monitoring of the diversity, abundance and composition of the larval fish community in the SoG is essential for detecting long-term fluctuations and trends in the ecosystem under natural and anthropogenic stresses, identifying the specific mechanisms driving the variations, and predicting future changes in relation to climate and ecosystem changes. In addition, larval fish data can provide fishery-independent information on the spawning population size of adult fish for both commercially exploited and unexploited species. Thus, such time-series data can be used to monitor trends, and especially to detect declines, in adult population size which also provide an indication of the health of marine ecosystems.

5.1.2d Regional differences in larval fish assemblages

In this thesis, features of larval fish assemblages and their spatiotemporal dynamics were characterized for the first time in the SoG. However, studies of larval fish at either the species-level or community-level are still lacking off the west coast of Canada where the Subarctic Current splits into the northeastward Alaska Current and southeastward California current (Tully, 1938; Thomson, 1981). Specifically, the Vancouver Island continental margin sits in a transition area sharing the biological and physical characteristics of both coastal currents. Compared to the SoG, which displays estuarine circulation involving fresh water input and exchange with coastal waters, biological entities along the Vancouver Island continental margin are directly subject to the interannual variability of these coastal currents (Cummins and Freeland, 2007). Annual zooplankton surveys have been carried out consistently along the west coast of Vancouver Island for nearly thirty years (Mackas *et al*., 2001), and these surveys also provide larval fish data in recent years which allow for an evaluation on basic characteristics of the larval fish assemblage (e.g. abundance and species composition) on the continental margin, and quantification of their spatiotemporal variability in relation to ocean climate fluctuations. In addition, a regional comparison on larval fish assemblages and their spatiotemporal dynamics between the SoG and Vancouver Island continental margin will contribute to an understanding of whether larval fish from the two ecosystems with very different oceanographic background (open vs. semi-enclosed area) display synchrony in response to ocean climate fluctuations, show similar magnitude of variations, and respond to similar governing mechanisms (large-scale climate index vs. local environmental factors). Addressing these questions will help improve our ability to understand the functioning of contrasting ecosystems.

5.2 Spatial dynamics of larval fish in the SoG

5.2.1 Overview

Spatial heterogeneity of zooplankton, including pelagic fish larvae, is one of the fundamental features of planktonic marine ecosystems. In Chapter 4, mesoscale (1-100km) distributions of larval fish were quantified for the first time in the SoG to understand their relationship to environmental heterogeneity. My results showed that spatial patterns in the larval abundance of the dominant taxa were mostly structured on pre-defined broad and medium scales, which represented >40km and 20~40km, respectively, in the SoG. Although co-dependence with environmental factors varied interannually and among pre-defined scales, larval fish distributions were generally more closely associated with salinity, temperature and the vertical stability of water column in the surface layer (0-50m). These results emphasize the critical role of estuarine circulation in structuring mesoscale spatial distributions of planktonic fish larvae in the SoG. Consequently, the primary physical forces driving and modulating the estuarine circulation (i.e. the amount of Fraser River discharge, the direction and strength of wind, and the frequency and strength of tides) would also contribute to spatial variability in larval distributions.

Passive transport by local hydrodynamic processes is just one aspect involved in the formation and variation of larval fish spatial patterns. Larval distributions are ultimately determined by a complex interaction of physical transport mechanisms with biological processes. Multiple biological factors including the location and timing of adult spawning, species-specific life history traits (e.g. demersal eggs or pelagic eggs), planktonic larval duration and the development of active larval behavior (e.g. active swimming behavior, food searching, predator avoidance and habitat selection) will all contribute to the variability in horizontal patterns of larval fish distribution, and increase the difficulty in understanding these patterns at the same time.

As part of the NSERC Canadian Healthy Oceans Network (CHONe), the original purpose of this study was to utilize ichthyoplankton field surveys to look for consistent spatial patterns in larval fish distribution including “hotspot” areas and potential “dispersal pathways”, which are basic and important components which can assist the design of new marine protected areas (MPAs) and the evaluation of existing MPAs. Based on the analyses presented in this thesis, the existence of consistent spatial patterns across years is not likely for the SoG, as both the physical oceanographic and biological factors influencing the formation and variation of spatial patterns are highly variable from year from year. In addition, as larval fish spatial structure exists and varies continuously in time, the examination of spatial patterns through field surveys can only provide periodic snapshots of larval distribution. Our ichthyoplankton surveys in 2009 and 2010 are the most spatially intensive and frequent surveys in the SoG since the early 1980s. Nonetheless, the snapshots of larval fish distributions still showed only limited strength in identifying and characterizing consistent spatial patterns.

5.2.2 Suggestions for future study

Understanding the spatial dynamics of larval fish and the underlying governing processes has considerable implication in the conservation and management of regional fisheries resources. The present study has shown that larval fish production in the SoG is highly variable in space and that no consistent larval fish “hotspots”, in terms of either abundance or diversity, were observed. Therefore, establishing general MPAs to protect multiple fish species is unlikely to be an effective approach in the SoG. In contrast, planning protected areas based on species-specific spatial characteristics (e.g. spawning areas, dispersal pathway and nursery areas) could offer a better conservation strategy for the SoG. Pacific herring and rockfishes will be used as examples to help clarify this point.

Pacific herring, a nearshore pelagic species, produces demersal adhesive eggs, and their spawning locations in the SoG have been confined to a number of locations along the western coastline between Saltspring and Denman islands in recent years (Hay, 1985; Hay and McCarter, 1997; Therriault *et al.*, 2009). Hatched from relatively consistent areas and staying within the upper surface layers, the dispersal pathway of herring larvae should be explored to determine the existence of consistent nursery areas of this species. Conservation planning for Pacific herring, when needed, should focus specifically on adult spawning areas and early juvenile nursery areas. Another example to demonstrate the application of species-specific conservation strategy is rockfishes. Studies have showed that several rockfish species in the SoG have experienced dramatic population declines due to overfishing and are consequently of special concern (Yamanaka and Lacko, 2001; Yamanaka and Logan, 2010). A network of small rockfish conservation areas (RCAs) has already been implemented in and around the SoG in response to the unrecovered declines. However, the effectiveness of these existing conservation areas has not been evaluated yet. A key prerequisite for such effectiveness evaluation is to explore larval dispersal pathways for the determination of whether these RCAs consistently represent sources or sinks of larval supply and the extent to which these RCAs are self-sustaining.

The present study emphasizes the importance of physical oceanographic mechanisms in driving and modulating the SoG estuarine circulation with respect to distributing larval fish. That said, the limited strength of ichthyoplankton field surveys in describing continuously varying spatial distributions is also acknowledged. Therefore, more accurate and efficient approaches such as coupled biological-physical models which could establish real-time predictions on larval fish dispersal and characterize larval fish spatial dynamics are in great need. In the Salish Sea, including the Strait of Georgia and Juan de Fuca Strait, the Regional Ocean Modeling System (ROMS) has been well developed to model the three-dimensional estuarine circulation and the deep currents in the central SoG. Driven by ROMS model output, a particle tracking model – a Lagrangian TRANSport model (LTRANS) (North *et al*., 2011) could incorporate advection, mixing and larval behavior (e.g. drifting and diel vertical migration) to simulate the trajectories of fish "particles" to predict larval distributions. Therefore, coupled biophysical model combining a regional circulation model (ROMS) and a particle tracking model (LTRANS) could be a powerful tool to predict the transport and dispersal of fish larvae from spawning to nursery areas (Miller, 2007). Meanwhile, field surveys can be utilized to determine the starting point (e.g. distribution of spawning areas) and verify the results of model simulation. A combination of field observation and biophysical modeling is therefore likely the most effective way to study spatial dynamics and dispersal of larval fishes.

In summary, this thesis has demonstrated that larval fish assemblages in the SoG display spatial and temporal dynamics across multiple spatiotemporal scales. The temporal variability was directly and indirectly attributed to the changes in characteristics of water masses on interannual and interdecadal scales, respectively. The meso-scale spatial variability was closely associated with the estuarine circulation within the SoG. Understanding the spatial and temporal dynamics of larval fish and underlying governing processes has considerable implications in conservation and management of regional fisheries resources.

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Appendix

Appendix 1: Fish taxa identified in the Strait of Georgia ichthyoplankton surveys in early 1980s and late 2000s.

Family	Species	Common Name	Families and species identified in 1980s	Families and species identified in 2000s
Agonidae		Poachers	X	X
	Agonopsis vulsa	Northern spearnose poacher		X
	Bathyagonus pentacanthus	Bigeye poacher		X
	Bathyagonus alascanus	Gray starnout		X
	Bathyagonus nigripinnis	Blackfin poacher		X
	Odontopyxis trispinosa	Pygmy poacher		X
	Podothecus acipenserinus	Sturgeon poacher		X
	Xeneretmus latifrons	Blacktip poacher		X
Ammodytidae	*Ammodytes hexapterus*	Pacific sand lance	X	X
Bathylagidae	*Leuroglossus schmidti*	Northern smoothtongue	X	X
Bathymasteridae	*Ronquilus jordani*	Northern ronquil	X	X
Bythitidae	*Brosmophycis marginata*	Red brotula	X	X
Clinidae	*Heterostichus rostratus*	Giant kelpfish		X
Clupeidae	*Clupea pallasi*	Pacific herring	X	X
Cottidae		Sculpins	X	X
	Scorpaenichthys marmoratus	Cabezon	X	X
	Artedius spp.			X
	Ruscarius meanyi	Puget sound sculpin		X
	Ascelichthys rhodorus	Rosylip sculpin		X
	Enophrys bison	Buffalo sculpin		X
	Gilbertidia sigalutes	Soft sculpin		X
	Gymnocanthus spp.			X
	Icelinus borealis	Northern sculpin		X
	Leptocottus armatus	Pacific staghorn sculpin		X
	Malacocotus zonurus	Darkfin sculpin		X
	Myoxocephalus spp			X
	Paricelinus hopliticus	Thornback sculpin		X
	Radulinus asprellus	Slim sculpin		X
	Triglop pingedi	Ribbed sculpin		X
Hemitripteridae	*Nautichthys oculofasciatus*	Sailfin sculpin		X
Psychrolutidae	*Dasycottus setiger*	Spinyhead sculpin		X
Cryptacanthodidae	*Crytacanthodes aleutensis*	Dwarf wrymouth		X
Cyclopteridae		Lumpsuckers	X	
Liparidae	*Liparis spp.*	Snailfishes		X
		Tadpole snailfish	X	

Appendix 1. Continue

Family	Species	Common Name	Families and species identified in 1980s	Families and species identified in 2000s
Gadidae	*Theragra chalcogramma*	Walleye pollock	X	X
	Gadus macrocephalus	Pacific cod		X
		Pacific tomcod	X	
Gobiidae		Gobies	X	X
	Coryphopterus nicolsii	Blackeye goby		X
	Lepidogobius lepidus	Bay goby		X
Hexagrammidae		Greenlings	X	X
	Oxylebius pictus	Painted greenling		X
Merlucciidae	*Merluccius productus*	Pacific hake	X	X
		Laternfishes	X	
Osmeridae		Smelts		
		Eulachon	X	
	Mallotus villosus	Caplin		X
Pholidae		Gunnels	X	X
Pleuronectidae		Righteye flounders	X	X
	Lyopsetta exilis	Slender sole	X	X
	Glyptocephalus zachirus	Rex sole		X
	Hippoglossoides elassodon	Flathead sole		X
	Hippoglossoides stenolepis	Pacific halibut		X
	Isopsetta isolepis	Butter sole		X
	Lepidopsetta bilineata	Rock sole		X
	Microstomus pacificus	Dover sole		X
	Parophyrs vetulus	English sole		X
	Platichthys stellatus	Starry flounder		X
Ptilichthyidae	*Ptilichthys goodie*	Quillfish		X
Scorpaenidae	*Sebastes spp.*	Rockfishes	X	X
Stichaeidae		Pricklebacks	X	X
	Anoparchus purpurescens	High cockscomb		X
	Anoplarchus insignis	Slender cockscomb		X
	Phytichthys chirus	Ribbon prickleback		X
	Plectobranchus evides	Blubarred prickleback		X
	Poroclinus rothrocki	Whitebarred prickleback		X
		Pallid eelpout	X	

Note: Species belongs to family Agonidae, Cottidae, Gobiidae Hexagrammidae, and Stichaeidae are only identified at family level in 1980s and indicated in grey shade.

Appendix 2. Ecology, spawning mode, egg type and exploitation status of examined fish taxa

Taxa			Ecology	Spawning mode	Egg type	Exploitation status
Family	Species name	Common name				
Agonidae		Poachers	Epi- and mesodemersal		Probably demersal	Bycatch
Ammodytidae	*Ammodytes hexapterus*	Pacific sandlance	Epi- and mesodemersal		Demersal, adhesive eggs	Bycatch
Bathylagidae	*Leuroglossus schmidti*	Northern smoothtongue	Epi, meso and bathypelagic		Pelagic eggs	Unfished
Bathymasteridae	*Ronquilus jordani*	Northern ronquil	Nearshore shelf demersal			Unfished
Bythitidae	*Brosmophycis marginata*	Red brotula	Epi- and mesobenthal		Probably ovoviviparous	Unfished
Clinidae	*Hetrostichus rostratus*	Giant kelpfish	Nearshore shelf demersal	Pairs, males guard nests	Adhesive, attached eggs	Unknown
Clupeidae	*Clupea pallasi*	Pacific herring	Nearshore shelf pelagic	Schools	Demersal, adhesive eggs	Fished
Cottidae		Sculpins				Unknown
	Scorpaenichthys marmoratus	Cabezon	Neashore shelf demersal		Demersal, adhesive eggs	Fished
Cryptacanthodidae	*Crytacanthodes aleutensis*	Dwarf wrymouth	Epi- and mesobenthal		Demersal eggs	Unknown
Cyclopteridae		Lumpsuckers		Males guard eggs	Demersal, adhesive eggs	Unfished
Liparidae	*Nectoliparis pelagicus*	Tadpole snailfish	Nearshore shelf demersal			Unfished
	Liparis spp.	Snailfishes	Epi- and mesodemersal	Egg masses		Unfished
Gadidae	*Theragra chalcogramma*	Walleye pollock	Epi-, meso and bathypelagic	Schools	Pelagic eggs	Fished
	Gadus macrocephalus	Pacific cod	Epi-, meso and bathybenthal	Schools	Demersal eggs	Fished
	Microgadus proximus	Pacific tomcod	Epi-, and meso benthal		Demersal eggs	
Gobiidae		Gobies	Nearshore shelf demersal	Pairs, males guard nests	Demersal, attached eggs	Unknown
Hexagrammidae		Greenlings				Unknown
Merlucciidae	*Merluccius productus*	Pacific hake	Epi-, meso-, and bathypelagic	Schools	Pelagic eggs	Fished
Myctophidae		Lanternfishes	Epi/meso pelagic		Eggs probably pelagic	Unfished
Osmeridae		Smelts	Nearshore shelf pelagic		Demersal eggs	
	Thaleichthys pacificus	Eulachon	Anadromous			Fished
Pholidae		Gunnels	Intertidal; nearshore demersal	Adhesive egg masses	Demersal, adhesive eggs	Unfished
Pleuronectidae		Righteye flounders	Epi-, meso and bathybenthal			Fished
	Lyopsetta exilis	Slender sole	Epi-, meso and bathybenthal		Pelagic eggs	Bycatch
Ptilichthyidae	*Ptilichthys goodei*	Quillfish	Nearshore shelf demersal			
Scorpaenidae	*Sebastes* spp.	Rockfishes	Epi-, meso, bathybental		Ovoviviparous	Fished
Stichaeidae		Pricklebacks	Demersal, or benthal			Unknown
	Anoparchus purpurescens	High cockscomb	Nearshore shelf demersal	Pairs, egg in masses	Demersal, adhesive eggs	Unfished
Zoarcidae	*Lycodapus mandibularis*	Pallid eelpout	Bathypelagic			