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

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ABSTRACT

The concentration and composition of the larval fish assemblage in the Strait of Georgia (British Columbia, Canada) has changed between the early 1980s (1980 and 1981) and the late 2000s (2007, 2009 and 2010). During both periods, the spring larval fish assemblages were dominated by pelagic species: *Clupea pallasi* (Pacific herring), *Merluccius productus* (Pacific hake), *Leuroglossus schmidti* (northern smoothtongue) and *Theragra chalcogramma* (walleye Pollock). The average concentration of *Merluccius productus*, *Theragra chalcogramma*, *Leuroglossus schmidti*, and *Sebastes* spp. declined between the early 1980s and the late 2000s; in contrast, the absolute concentration and proportion of Pleuronectidae and several demersal fish taxa increased in the spring larval assemblage. Examination of the associations between larval fish assemblages and environmental fluctuations suggests that large-scale climate processes are potential contributors to variations in overall larval concentrations of the dominant taxa and assemblage composition in the Strait of Georgia.

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 concentration 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 supporting marine 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 suggest that large-scale climate indices are more important in explaining interannual and decadal variations in larval fish concentration 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 northeast and the California Current turns to the southeast (Tully, 1938; Thomson, 1981). The bifurcation

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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. 1) 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 that supports commercial, recreational, and aboriginal fisheries. It provides spawning, nursery, and rearing areas for many fish taxa including *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.

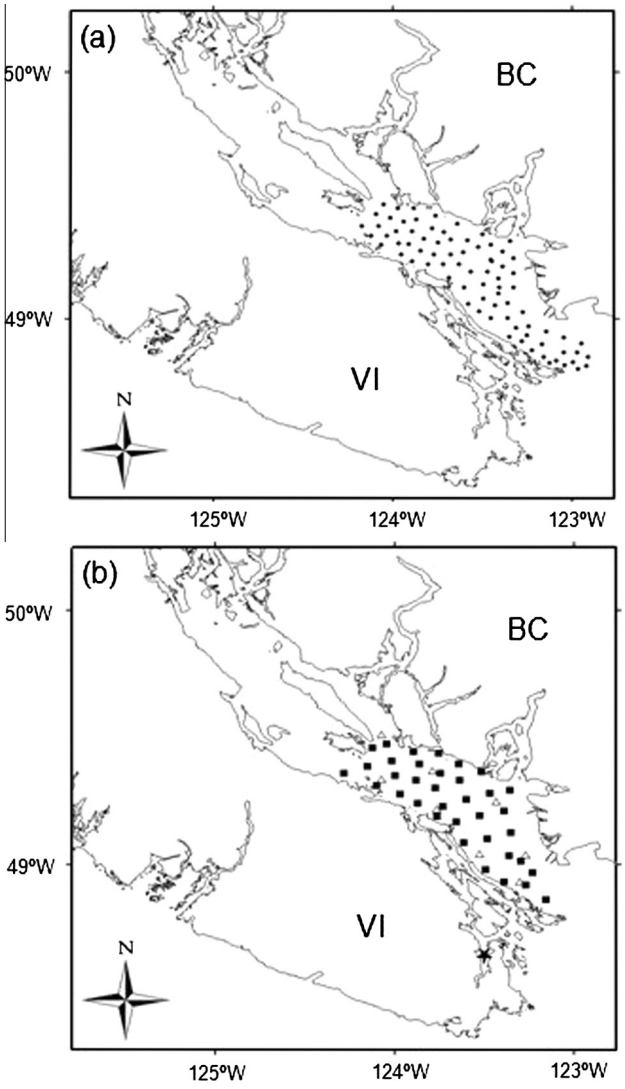

Fig. 1. Map showing the location of ichthyoplankton surveys conducted in the Strait of Georgia (SoG) off mainland British Columbia (BC) and Vancouver Island (VI). Maps show (a) sites sampled in 1980 and 1981, and (b) sites sampled in 2007, 2009 and 2010. Solid circles in (a) are sites sampled in 1980 and 1981. Open triangles in (b) are sites sampled in 2007, while sites samples in 2009 and 2010 are denoted by solid squares. The solid star in (b) marks the location of our gear intercalibration experiment.

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 concentration 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 were available, the present study therefore focuses on comparing SoG ichthyoplankton assemblages between these two periods, nearly three decades apart, and exploring the influence of marine environmental fluctuations. Our specific objectives were to: (i) quantify differences in larval concentration and species composition of the spring larval fish assemblages in the SoG between the early 1980s and 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 concentrations and assemblage structure.

2. Materials and methods

2.1. Ichthyoplankton sampling procedures

The spring ichthyoplankton assemblage in the SoG was sampled from 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 late April (i.e. the time of highest larval fish concentration 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. 1a, Table 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 descended to within 20 m 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 (Table S1).

Table 1
Sampling summary of ichthyoplankton surveys in the central and southern Strait of Georgia during spring of early-1980s and 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 20 m from sea floor
	1981	Apr 28–May 2	80	Bongo sampler	351 μm	
2000s	2007	Apr 25–26	8	Tucker trawl	1 mm	Surface – ~50 m
	2007	Apr 28–29	8	Tucker trawl	1 mm	Surface – ~50 m
	2009	Apr 25–28	32	Tucker trawl	1 mm	Surface – ~50 m
	2009	Apr 29–May 1	34	Tucker trawl	1 mm	Surface – ~50 m
	2010	Apr 24–27	36	Tucker trawl	1 mm	Surface – ~50 m

Five surveys were conducted in the latter half of April in 2007, 2009, and 2010 (Table 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. 1b). At each station, a Seabird SBE-19 conductivity–temperature–depth sensor (CTD) was deployed to record water column properties from the surface to within ~5 m from the sea floor. Next, a 15 min oblique tow using a 1 m^2 Tucker trawl equipped with 1 mm mesh size net was made within the upper ~50 m 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 (Table S1), but larvae of *Sebastes* spp. (rockfishes) and *Liparis* spp. (snailfishes) could only be identified to genus based on meristics and pigmentation patterns. Larval concentration 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. 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 concentration and make direct comparisons difficult. With only limited ship-time available, we therefore conducted a separate field experiment in Saanich Inlet (British Columbia, Fig. 1b), a well studied fjord opening to the SoG on the east of Vancouver Island, to develop intercalibration coefficients between the Bongo 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 depth towed by Bongo net and Tucker trawl were 182 m and 51 m, 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). 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). Furthermore, to compensate for the small sample size and provide a more reliable range for this intercalibration factor, a bootstrapped regression coefficient of 3.3 with its 95% confidence interval of (2.9, 3.7) 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 concentration 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); while, only the large and wide larvae of *Plectobranchus evides* (bluebarred prickleback) were relatively more abundant in the Tucker trawl ($p < 0.001$, Table 2). The average concentrations of all other species did not differ statistically between the two procedures (Table 2). Therefore, *L. exilis* was excluded from subsequent assemblage analyses because its concentration was likely underestimated during recent surveys. However, *P. evides* was included in analyses as Stichaeidae were only identified to family level in the 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 concentrations (0.14, 0.03, and 0.00 individuals/1000 m^3 in 2007, 2009, and 2010, respectively). For the other seven fish species collected in the gear inter-comparison experiment, the original larval concentrations were used in decadal comparisons as no significant differences in larval concentration were detected (Table. 2). For species that occurred in the ichthyoplankton surveys but which were not collected in the inter-comparison experiment,

Table 2
Mean larval abundance (±1 SE) of common species collected by both the "Historical Bongo" and "Recent Tucker" sampling procedures. Bold indicates statistical significance at $\alpha = 0.05$ for the Mann–Whitney *U* test.

Species name	Common name	Mean abundance by Bongo (no./1000 m^3)	Mean abundance by Tucker (no./1000 m^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)**	**<0.001**
	Total larvae	**448.85 (58.22)**	**137.08 (14.27)**	**0.001**

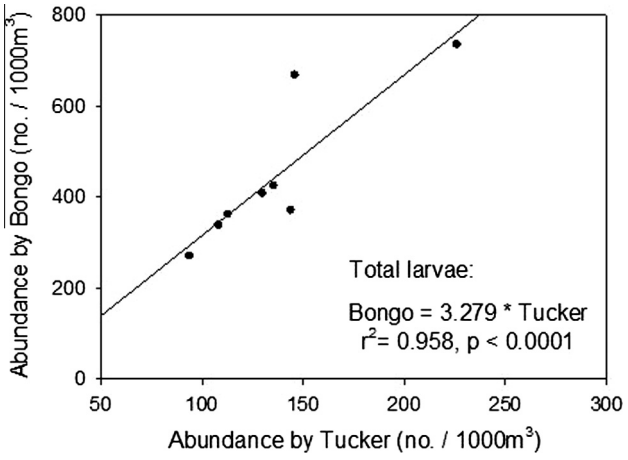

Fig. 2. Intercalibration of larval fish concentration estimates (no./1000 m^3) from paired tows of "Historical Bongo" and "Recent Tucker" sampling procedures by least squares linear regression. Solid line: regression line.

the lower and upper limits of the bootstrapped regression coefficient based on total larvae were applied for further comparisons.

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 1). Despite lower sampling density, the assemblage information from 2007 was considered in our inter-decadal comparisons as the larval diversity in 2007 was comparable to that in 2009 and 2010 (Guan, 2015). The taxonomic resolution achieved during the historical and present surveys differed; species which were not consistently identified through time were combined at the level of family or genus to allow comparisons between decades (Table S1).

The mean annual total larval concentration and mean annual concentration of each taxon were estimated by averaging across stations for each cruise. The relative mean concentration indicated the percentage concentration 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 concentrations 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 (2.9) and upper (3.7) bootstrap limits) were applied to concentration 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 concentration of all pelagic species divided by the total concentration of all demersal species excluding *L. exilis* (for reasons described above). Additionally, diel differences in larval concentration 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 3). Larval concentration for each taxon at each site was standardized by total larval concentration, and 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 (Clark 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 by both including and excluding *M. productus* and *Leuroglossus schmidti* (northern smoothtongue) in consideration of issues associated with their vertical distribution and concentration (see Section 4.4). 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 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 concentrations 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).

2.4. 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 concentration (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

Table 3
Average total larval concentration and average larval concentrations of individual species in the 1980s (1980 and 1981) and 2000s (2007, 2009 and 2010), and the results of ANOVA analysis of decadal comparisons. Bold indicates a significant difference ($p < 0.05$) in larval concentration between the two periods in ANOVA test under different intercalibration treatments.

Taxa		Common name	1980s mean concentration (no./1000 m^3)	1980s relative concentration (%)	2000s Mean concentration (no./1000 m^3)	2000s relative concentration (%)	Frequency occurrence[e] (%)
Family	Species 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 goodei*	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 concentration calculated by excluding *L. exilis*, *L. schmidti* and *M. productus*.
[b] Overall larval concentration 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] Concentration was similar between the two period based on original data, but was significantly higher in the late 2000s after intercalibration.
[e] Frequency occurrence from 1980s to 2000s.

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 concentration 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.

3. Results

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. 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. 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. 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 total annual discharge, except for the abrupt decline from 2007 to 2008 (Fig. 3d).

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 concentration were: Merlucciidae (69.2%), Gadidae (11.8%), Bathylagidae (10.7%),

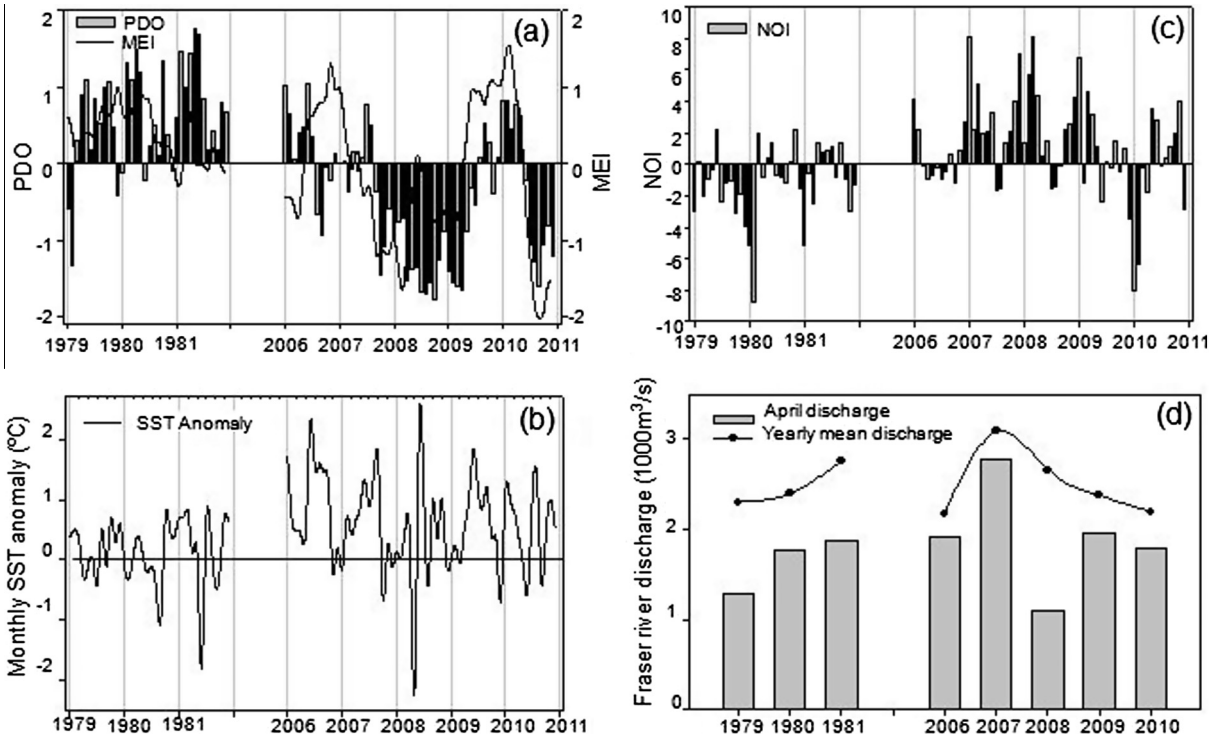

Fig. 3. Time series of environmental variables and annual runoff from the Fraser River in the early-1980s and late-2000s. Data are based on monthly averages of (a) the Pacific Decadal Oscillation (PDO) and Multivariate ENSO Index (MEI), (b) the Northern Oscillation Index (NOI), (c) Sea Surface Temperature (SST) anomalies from lighthouse data at Entrance island based on monthly SST averages during 1956–1999, and (d) annual averages & April values of Fraser River discharge (1000 m^3/s).

Scorpaenidae (5.4%), and Clupeidae (1.68%) (Table 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 concentration, within which *M. productus* alone contributed ~70%. Larvae of Cottidae (sculpins), Stichaeidae (pricklebacks), and Pleuronectidae (flatfishes) were collected at relatively high frequency but low concentration. Eight species occurred exclusively in the 1980s: *Nectoliparis pelagicus* (tadpole snailfish), *Microgadus proximus* (Pacific cod), *Thaleichthys 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 concentration: 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 concentration 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 concentrations.

3.3. Interdecadal differences in larval concentration

Changes in the mean concentration of total larvae in late April revealed significantly higher larval concentration in the early 1980s than in the late 2000s (Fig. 4, Table 3). This trend was consistent among the different intercalibration treatments (Table S3). Excluding *M. productus*, *L. schmidti*, and *L. exilis*, whose concentrations were likely underestimated in recent surveys (see Section 4.2), the significant decadal decline in the total larval concentration remained for the rest of the larval assemblage ($p < 0.001$, Table 3). The overall concentration of rare taxa remained similar (~14.0 larvae 1000 m^{-3}) in both periods (Table 3).

For taxa (except *C. pallasi* and Cottidae) to which we applied intercalibration coefficients the interdecadal trends displayed in the original larval concentrations remained consistent across all intercalibration treatments (Table S3). In contrast, *C. pallasi* and Cottidae showed similar original larval concentrations between the two study periods (Fig. 5, Table 3), but higher concentrations in the late 2000s with the application of intercalibration treatments (three and two treatments for *C. pallasi* and Cottidae, respectively, Table S3). Larvae of the other dominant fish species (*T. chalcogramma*, *M. productus*, *L. schmidti*, and *Sebastes* spp.) were more abundant in the early 1980s (Fig. 5, Table 3), although *M. productus* and *L. schmidti* may have been underestimated in recent surveys because their diel vertical migration may have exceeded our sampling depth (see Section 4.2). Large interannual variability in larval concentration of these species was also evident within each time period, with the lowest concentration 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 concentration, their decadal trends were similar to the Pleuronectidae. Furthermore, Cyclopteridae (lumpsuckers), Gobiidae (gobies), and Pholidae (gunnels) did not show any significant change in larval concentration between the two decades (Table 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*

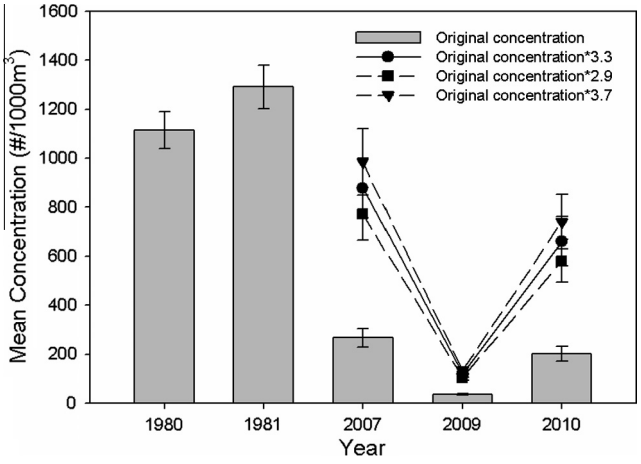

Fig. 4. Original and calibrated total larval concentration (error bars ±1 SE) in late April of 1980, 1981, 2007, 2009 and 2010. Original total larval concentrations were based on averages over all samples collected from each survey. Calibrated concentrations were calculated by multiplying original concentrations by an intercalibration factor of 3.3. Points indicate the original concentration. Bars indicate estimates after intercalibration.

(eulachon, Table 3). Overall, the total concentration 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 concentration between the 1980s and the 2000s. Among demersal species, only three taxa: *Sebastes* spp., Stichaeidae, and *Microgadus proximus* (Pacific tomcod) showed a decrease in concentration. The concentration of other demersal species either increased or did not change. The pelagic/demersal concentration 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 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.

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. 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 inter-annual variation in species composition. A PERMDISP test verified the different dispersions of data clouds from two study periods (Pseudo-$F = 197.3$, $p_{perm} = 0.0001$); meanwhile, the PERMANOVA test also suggested significant interdecadal differences in assemblage composition (Pseudo-$F = 101.24$, $p_{perm} = 0.0001$). 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) revealed the real 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. 6b). *Merluccius 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 concentration between decades (Fig. 6b). In contrast, *C. pallasi* ($r = -0.87$) and Pleuronectidae ($r = -0.66$) had the largest increases in relative concentration 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.

3.5. Species associations

Two significant species associations were detected by cluster analysis (Fig. 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 A2 (Table S2). Group B consisted principally of demersal species that produce adhesive demersal eggs and which are not subject to directed commercial exploitation (Table S2). Larval concentration 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 concentrations between decades.

3.6. Larval concentration and assemblage composition in relation to environmental variables

Multiple regression analyses revealed that the spring concentration of the dominant species consistently displayed strong correlations with the Northern Oscillation Index (NOI) (Table 4). The concentration 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 and larval concentrations between 2010 and the early 1980s (Fig. 8a). The concentration of *M. productus* and *L. schmidti* larvae were also correlated negatively with this index but with a lag of one year (Fig. 8b and c). The concentration of *T. chalcogramma*, *Sebastes* spp., and total larvae were all negatively correlated with average NOI during fall–winter lagged by one year, and was strongest for *Sebastes* spp. (Table 4, Fig. 8d–f). Fluctuations in larval concentration 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 4).

DistLM analyses were used to investigate relationships between the environmental variables and composition of the larval fish assemblages based on annual average larval concentrations (Fig. 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

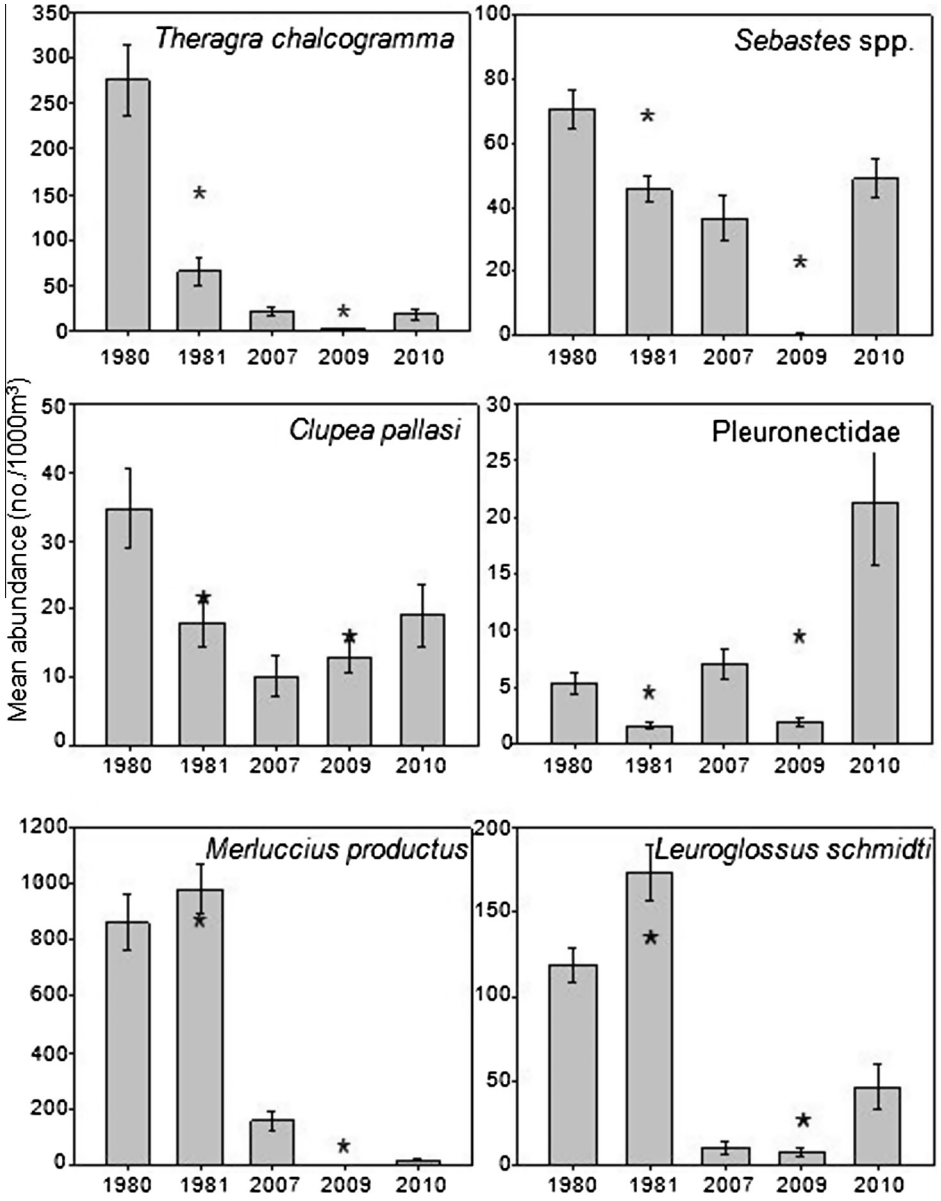

Fig. 5. Average larval concentration (error bars ±1 SE, no intercalibration applied) of the most abundant fish taxa/groups in late April of 1980, 1981, 2007, 2009 and 2010. Asterisks indicate the average larval concentration for each of the two sampling periods (early-1980s and late-2000s).

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 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.

4. Discussion

4.1. Interdecadal variation in larval concentration and assemblage composition

Our analyses of the SoG larval fish assemblages revealed notable differences in concentration and composition of spring assemblages between the early 1980s and late 2000s. In general, the SoG larval assemblages are dominated by a few pelagic fish species that consistently make up a majority of the overall larval concentration. In the early 1980s, the dominant species was *M. productus*, followed by another 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 (Table S2). In the late 2000s, a drop in larval concentration of these dominant species, particularly some pelagic species, contributed significantly to a dramatic decline in overall larval concentration and a shift in assemblage composition. Meanwhile, demersal Pleuronectids became much more abundant, accompanied by an increasing proportion of several non-dominant demersal forage species including *A. hexapterus*, *Liparis* spp., and Agonidae, while the concentration 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 our study

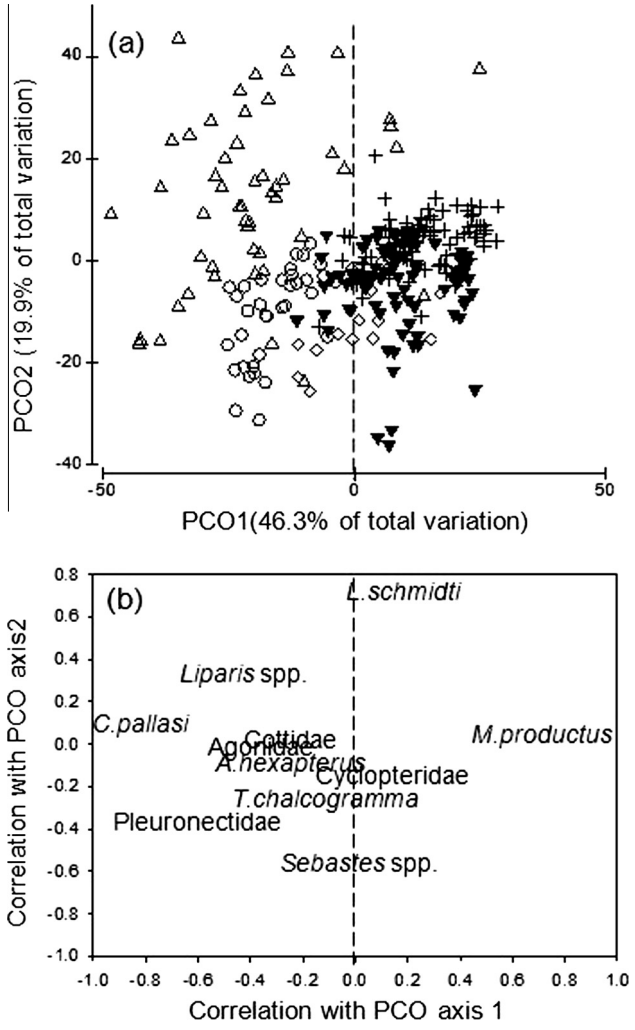

Fig. 6. (a) Principal coordinates (PCO) ordination of larval fish assemblages based on all samples from 1980s and 2000s with all species (frequency of occurrence >5%) including *Merluccius productus* and *Leuroglossus schmidti*, (b) Correlations of individual species with the first two PCO axes. Solid triangles: samples collected during early 1980s. Open triangles: samples collected in late 2000s.

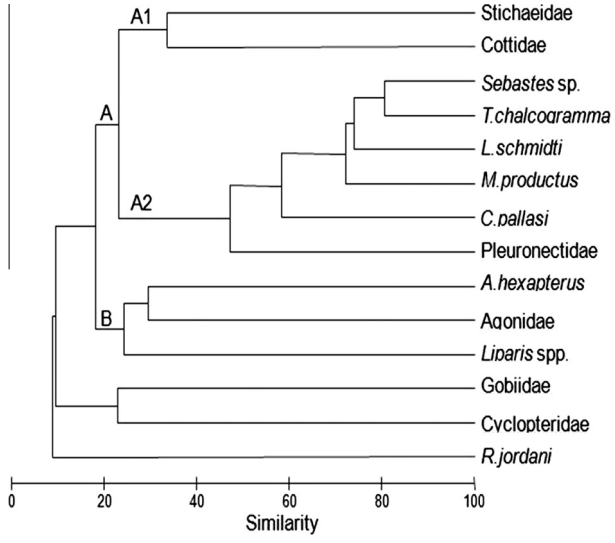

Fig. 7. Relations among species shown by cluster analysis of taxa based on species relative concentration data. Species groups were labeled A–C, group A was split into two subgroups: A1 and A2.

Table 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 significance at $\alpha = 0.05$ 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	**$NOI_{Jan-Apr}$ (−0.943)**
Theragra chalcogramma	**$NOI_{Sep-Dec}$ lag1(−0.884)**
Sebastes spp.	**$NOI_{Sep-Dec}$ lag1(−0.998)**, FD_{Apr} (0.145)
Merluccius productus	**$NOI_{Jan-Apr}$ lag1(−0.965)**, $PDO_{May-Aug}$ lag1(−0.489)
Leuroglossus schmidti	**$NOI_{Jan-Apr}$ lag1(−0.668)**, $NOI_{May-Aug}$ lag1(0.498)
Total larvae	**$NOI_{Sep-Dec}$ lag1(−0.976)**

(mid-1980s and mid-2000s) reported similar decadal declines in total ichthyoplankton concentration 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 can be 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 concentration of *M. productus* and the corresponding relative increase of *C. pallasi*. Note that the average absolute concentration 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 concentration and high trophic level. Although an increase in *M. productus* concentration has been documented in recent years (Beamish et al., 2008), our data show dramatically lower larval *M. productus* concentration 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 populations of these species declined (as suggested by our 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 non-trivial contributor (Fig. 10a and b). In addition, decreased concentration 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 available biological observations and catch data, inshore *Sebastes* spp. in the SoG have experienced dramatic declines in concentration, 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. 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

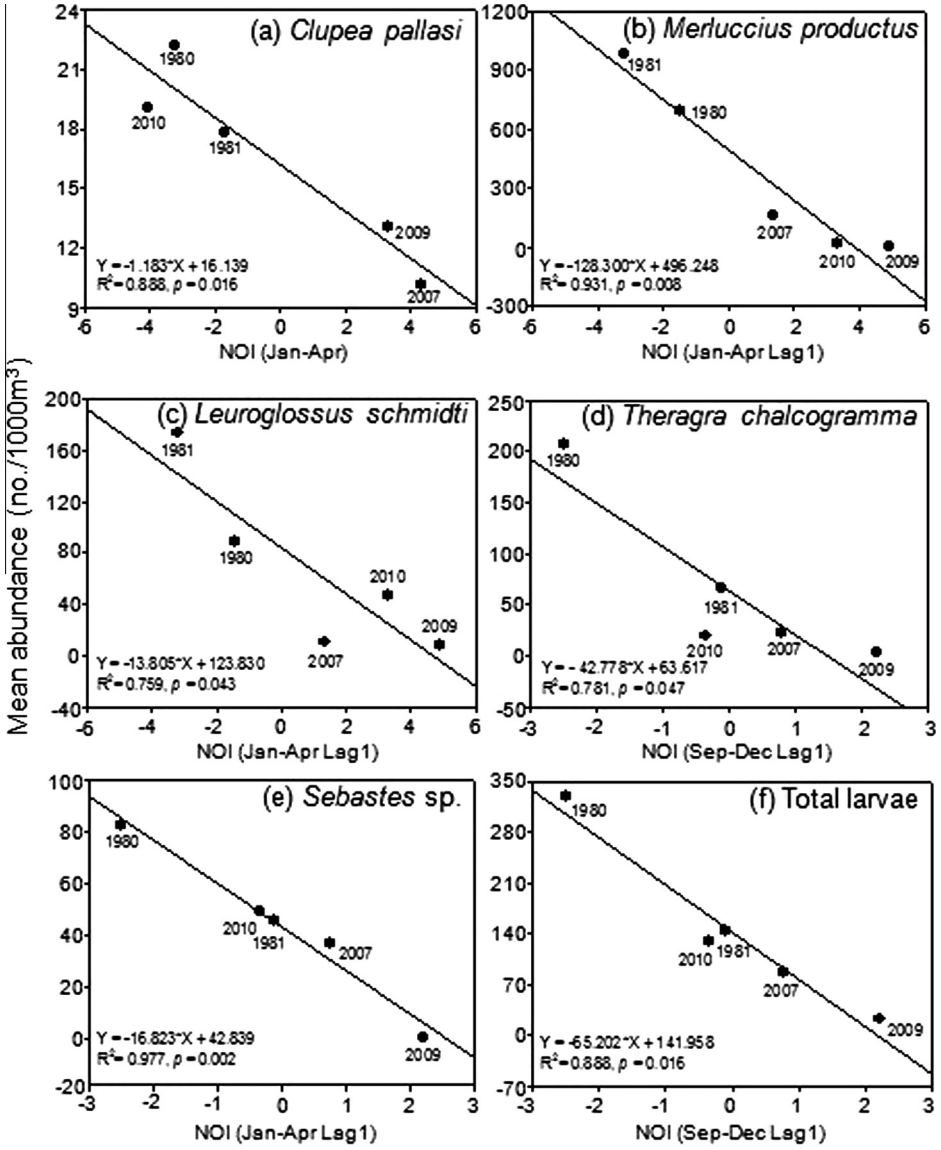

Fig. 8. Relationship between larval concentration and environmental variables by regression for (a) *C. pallasi* (b) *M. productus*. (c) *Sebastes* spp. (d) *T. chalcogramma*. (e) *L. schmidti*. (f) Total larvae. Larval concentrations were based on averages over all samples collected in each sampling year. Climate indices were based on seasonal averages of Jan–Apr and Sep–Dec. Lag 1: with one year lag. NOI: Northern Oscillation Index.

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. 10c).

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). Our 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 concentration, 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 survival and growth of zooplankton in the SoG (El-Sabaawi et al., 2009). In addition, SLP-associated changes in the strength of trade

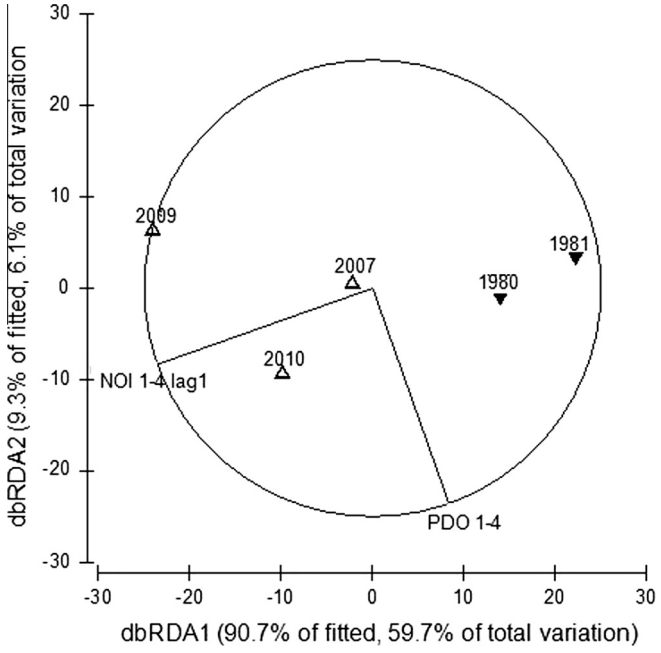

Fig. 9. Constrained dbRDA ordination of larval fish assemblages with significant environmental variables based on average larval concentration over all samples collected in late April of each sampling year. Vectors display partial correlations of environmental variables with the first two dbRDA axes. 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.

winds and coastal upwelling-favorable winds will modify the intensity of upwelling offshore, and thus influence the level of nutrient 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 concentration 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 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 concentration. 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 concentration than did local environmental factors. In the southern California Current region, Hsieh et al. (2005) showed that variations in the concentration 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).

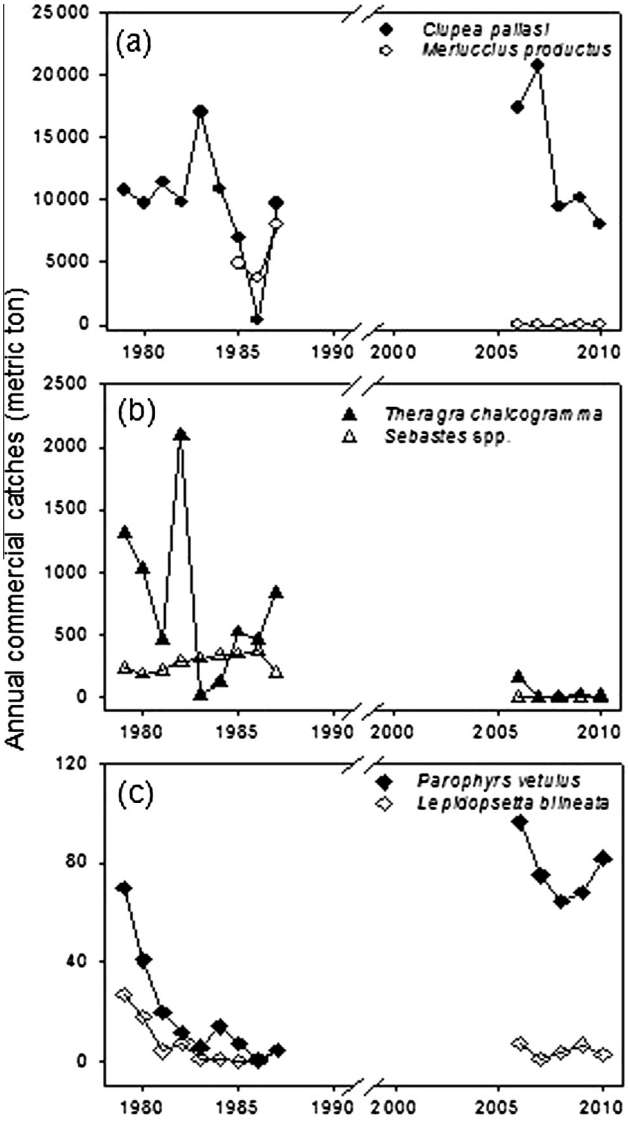

Fig. 10. Annual commercial catches during 1980s (1979–1987) and the late-2000s (2006–2010) in the Strait of Georgia. (a) *Clupea pallasi* and *Merluccius productus*, (b) *Theragra chalcogramma* and *Sebastes* spp., (c) *Parophyrs vetulus* and *Lepidopsetta bilineata*. Catch statistics data were provided by Regional Data Services Unit, Fisheries and Oceans Canada.

4.3. Phenology

In temperate marine ecosystems, zooplankton, including 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 have been suggested for zooplankton in various studies (Mackas et al., 1998, 2007, 2012; Bornhold, 2000). For example, the developmental timing of *Neocalanus plumchrus* in the SoG shifted gradually toward an earlier peak (~25 days) during a period characterized by a 1–2 °C increase in surface water temperature from the 1960s to the 1990s (Bornhold, 2000). A similar but accelerated early shifting trend continued in the early-2000s (2002–2005) (Fig. 13b in Johannessen and Macdonald, 2009).

Unlike copepods, very few studies on the phenology of larval fish assemblages exist. In the North Sea, a study of ichthyoplankton

based on observation across 27 species over 7 years showed that the timing of larval fish concentration was significantly negatively correlated with winter–spring SST in weeks 1–10 because of faster gonadal development rate of adults under higher temperatures and thus earlier spawning in warm years (Greve et al., 2005). If the same mechanism applies in the SoG, the similar winter mean SST during Jan–Mar (7.4 °C and 7.5 °C 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. *Clupea 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 SoG surveys. 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 examination of annual changes in the concentration of stage IV *M. productus* eggs from historical ichthyoplankton surveys in 1980 and 1981 (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 concentration and species composition of the SoG ichthyoplankton assemblages that we detected are in fact real changes and not merely phenological artefacts.

4.4. Limitations to present analysis and suggestions for future study

Differences in sampling protocols between the early 1980s and late 2000s could have affected our larval concentration estimates in several ways. First, the Bongo net (351 μm mesh) used in 1980s was more efficient in capturing small larvae than was our Tucker trawl (1 mm mesh). Our gear intercalibration indicated that more 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 concentration could be underestimated in both cases.

Second, the whole water column was sampled in 1980s whereas only the upper layer (50 m to surface) was sampled in 2000s. The shallower sampling depth in the recent surveys could also induce negative bias in larval concentration estimates. However, several studies conducted in Northeast Pacific have suggested that the greatest concentrations 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 (adjacent to the SoG) 87.5% of fish larvae were found within the top 50 m of the water column, with peak concentration centered near the thermocline at 20–30 m (Boehlert et al., 1985; Auth et al., 2007). In the SoG, the average depth of the thermocline was 20–25 m 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 our Tucker trawl was sampling a high fraction of the ichthyoplankton community. *Merluccius productus* larvae, on the other hand, were abundant through 200–250 m 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 and 90 m (Mason and Philips, 1985). Therefore, our recent sampling of the upper 50 m of the water column should be sufficient to characterize pelagic larval concentration of the majority of fish taxa in the SoG, with the possible exception of *M. productus* and *L. schmidti*. Underestimation of larval concentrations of these two species, especially their newly hatched larvae, in our recent surveys could be possible due to their vertical distribution below our sampling depth of 50 m in the SoG.

Finally, ichthyoplankton samples were collected during both day and night in recent surveys, but only during daytime in the 1980s. Examination of diel variability in our 2010 surveys 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 concentration of *L. schmidti* larvae in our recent surveys, especially at night.

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. Also, examinations of crucial factors affecting early larval survival such as temporal and spatial match or mismatch with their prey (e.g. microzooplankton) and predators in the SoG 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.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.pocean.2015.09.006.

References

Ahlstrom, E.H., 1959. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. United States Fish and Wildlife Services. Fishery Bulletin 60, 107–146.

Ahlstrom, E.H., Moser, H.M., 1976. Eggs and larvae of fishes and their role in systematic investigations and in fisheries. Revue des Travaux de l'Institut des Pêches Maritimes 40 (3–4), 379–398.

Allen, S.E., Wolfe, M.A., 2013. Hindcast of the timing of spring phytoplankton bloom in the Strait of Georgia, 1968–2010. Progress in Oceanography 115, 6–13.

Alverson, D.L., Larkins, H.A., 1969. Status of knowledge of the Pacific hake resource. CalCOFI Report 13, 24–31.

Anderson, M.J., Gorley, R.N., Clark, K.R., 2008. PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. PRIMER-E, Plymouth, UK.

Auth, T.D., 2008. Distribution and community structure of ichthyoplankton from the northern and central California Current in May 2004–06. Fisheries Oceanography 17 (4), 316–331.

Auth, T.D., Brodeur, R.D., Fisher, K.M., 2007. Diel variation in vertical distribution of an offshore ichthyoplankton community off the Oregon coast. Fishery Bulletin 105, 313–326.

Auth, T.D., Brodeur, R.D., Soulen, H.L., Ciannelli, L., Peterson, W.T., 2011. The response of fish larvae to decadal changes in environmental forcing factors off the Oregon coast. Fisheries Oceanography 20 (4), 314–328.

Bailey, K.M., Houde, E.D., 1989. Predation on eggs and larvae of marine fishes and the recruitment problem. Advances in Marine Biology 25, 1–83.

Beamish, R.J., King, J.R., McFarlane, G.A., 2008. Canada. In: Beamish, R.J. (Ed.), Impacts of Climate and Climate Change on the Key Species in the Fisheries in the North Pacific. PICES Scientific Report No. 35, pp. 15–52.

Boehlert, G.W., Gadomski, D.M., Mundy, B.C., 1985. Vertical distribution of ichthyoplankton off the Oregon coast in spring and summer months. Fishery Bulletin 83 (4), 611–621.

Bornhold, E.A., 2000. Interannual and Interdecadal Patterns in Timing and Abundance of Phytoplankton and Zooplankton in the Central Strait of Georgia, BC: With Special Reference to *Neocalanus plumchrus*. M.Sc. Thesis, University of British Columbia.

Brodeur, R.D., Rugen, W.C., 1994. Diel vertical distribution of ichthyoplankton in the northern Gulf of Alaska. Fishery Bulletin 92, 223–235.

Brodeur, R.D., Peterson, W.T., Auth, T.D., Soulen, H.L., Parnel, M.M., Emerson, A.A., 2008. Abundance and diversity of coastal fish larvae as indicators of recent changes in ocean and climate conditions in the Oregon upwelling zone. Marine Ecology Progress Series 366, 187–202.

Bui, A.O.V., Ouellet, P., Castonguay, M., Brethes, J., 2010. Ichthyoplankon community structure in the north-west Gulf of St. Lawrence (Canada): past and present. Marine Ecology Progress Series 412, 189–205.

Clark, K.R., Gorley, R.N., 2006. Primer v6: User Manual/Tutorial. PRIMER-E, Plymouth, UK.

Clark, K.R., Warwick, R.M., 2001. Changes in Marine Communities: An Approach to Statistical Analysis and Interpretation, second ed. PRIMER-E, Plymouth.

Collie, J.S., Wood, A.D., Jeffries, H.P., 2008. Long-term shifts in the species composition of a coastal fish community. Canadian Journal of Fisheries and Aquatic Sciences 65, 1352–1365.

Crawford, E.R., Irvine, J.R., 2011. State of Physical, Biological, and Selected Fishery Resources of Pacific Canadian Marine Ecosystems in 2010. DFO Canadian Science Advisory Secretariat Report No. 2011/054.

Cummins, P.F., Freeland, H.J., 2007. Variability of the North Pacific Current and its bifurcation. Progress in Oceanography 75 (2), 253–265.

Cushing, D.H., 1975. Marine Ecology and Fisheries. Cambridge University Press, Cambridge, UK.

DFO, 2008. Stock Assessment Report on Strait of Georgia Pacific herring. DFO Canadian Science Advisory Secretariat Report No. 2008/014.

DFO, 2011. Stock Assessment Report on Pacific Herring in British Columbia in 2011. DFO Canadian Science Advisory Secretariat Report No. 2011/061.

DiLorenzo, E., Schneider, N., Cobb, K.M., Chhak, K., Franks, P.J.S., Miller, A.J., McWilliams, J.C., Bograd, S.J., Arango, H., Curchitser, E., Powell, T.M., Rivere, P., 2008. North Pacific Gyre Oscillation links ocean climate and ecosystem change. Geophysical Research Letters 35, L08607.

Doyle, M.J., Picquelle, S.J., Mier, K.L., Spillane, M.C., Bond, N.A., 2009. Larval fish abundance and physical forcing in the Gulf of Alaska, 1981–2003. Fisheries Oceanography 80, 163–187.

El-Sabaawi, R., Dower, J.F., Kainz, M., Mazumder, A., 2009. Interannual variability in fatty acid composition of the copepod *Neocalanus plumchrus* in the Strait of Georgia, British Columbia. Marine Ecology Progress Series 382, 151–161.

Govoni, J.J., 2005. Fisheries oceanography and the ecology of early life histories of fishes: a perspective over fifty years. Scientia Marina 69 (Suppl. 1), 125–137.

Greve, W., Prinage, S., Zidowitz, H., Nast, J., Reiners, F., 2005. On the phenology of North Sea ichthyoplankton. ICES Journal of Marine Science 62, 1216–1223.

Guan, L., 2015. Dynamics, Structure and Distribution of Larval Fish in the Strait of Georgia. Ph.D Thesis, University of Victoria.

Haldorson, L., Prichett, M., Paul, A.J., Ziemann, D., 1993. Vertical distribution and migration of fish larvae in a Northeast Pacific bay. Marine Ecology Progress Series 101, 67–80.

Houde, E.D., 1997. Patterns and trends in larval-stage growth and mortality of teleost fish. Journal of Fish Biology 51, 52–83.

Hsieh, C., Reiss, C., Watson, W., Allen, M.J., Hunter, J.R., Lea, R.N., Rosenblatt, R.H., Smith, P.E., Sugihara, G., 2005. A comparison of long-term trends and variability in populations of larvae of exploited and unexploited fishes in the Southern California region: a community approach. Progress in Oceanography 67, 160–185.

Hsieh, C., Reiss, C.S., Hewitt, R.P., Sugihara, G., 2008. Spatial analysis shows that fishing enhances the climatic sensitivity of marine fishes. Canadian Journal of Fisheries and Aquatic Sciences 65, 947–961.

Ichthyoplankton Information System, 2011. National Oceanic and Atmospheric Administration. <http://access.afsc.noaa.gov/ichthyo/index.cfm>.

Johannessen, S.C., Macdonald, R.W., 2009. Effect of local and global change on an inland sea: the Strait of Georgia, BC, Canada. Climate Research 40, 1–21.

King, J.R., McFarlane, G.A., 2006. Shift in size at age of the Strait of Georgia population of Pacific hake (*Merluccius productus*). California Cooperative Oceanic Fisheries Investigations Reports 47, 111–118.

Li, M., Gargett, A., Denman, K., 1999. Seasonal and interannual variability of estuarine circulation in a box model of the Strait of Georgia and Juan de Fuca Strait. Atmosphere–Ocean 37 (1), 1–19.

Li, L., Mackas, D., Hunt, B., Schweigert, J., Pakhomov, E., Perry, I., Galbraith, M., Pitcher, T.J., 2013. Zooplankton communities in the Strait of Georgia, British Columbia, track large-scale climate forcing over the Pacific Ocean. Progress in Oceanography 115, 90–102.

Mackas, D.L., Goldblatt, R., Lewis, A.G., 1998. Interdecadal variation in developmental timing of *Neocalanus plumchrus* populations at Ocean Station P in the subarctic North Pacific. Canadian Journal of Fisheries and Aquatic Sciences 55, 1878–1893.

Mackas, D.L., Batten, S., Trudel, M., 2007. Effects on zooplankton of a warmer ocean: recent evidence from the Northeast Pacific. Progress in Oceanography 75, 223–252.

Mackas, D.L., Greve, W., Edwards, M., Chiba, S., Tadokoro, K., Eloire, D., Mazzocchi, M.G., Batten, S., Richardson, A., Johnson, C., Head, E., Converssi, A., Peluso, T., 2012. Changing zooplankton seasonality in a changing ocean: comparing time series of zooplankton phenology. Progress in Oceanography 97–100, 31–62.

Mackas, D., Galbraith, M., Faust, D., Masson, D., Young, K., Shaw, W., Romaine, S., Trudel, M., Dower, J., Campbell, R., Sastri, A., Pechter, E.A.B., Pakhomov, E., El-Sabaawi, R., 2013. Zooplankton time series from the Strait of Georgia: results from year-round sampling at deep water locations, 1990–2010. Progress in Oceanography 115, 129–159.

Mantua, N.J., Hare, S.R., Zhang, Y., Wallace, J.M., Francis, R.C., 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. Bulletin of the American Meteorological Society 78, 1069–1079.

Mason, J.C., 1985. The fecundity of the walleye Pollock, *Theragra chalcogramma*, spawning in Canadian waters. Journal of Fish Biology 27, 335–346.

Mason, J.C., Philips, A.C., 1985. Biology of the Bathylagid fish, *Leuroglossus schmidti*, in the Strait of Georgia, British Columbia, Canada. Canadian Journal of Fisheries and Aquatic Sciences 42, 1144–1153.

Mason, J.C., Kennedy, O.D., Phillips, A.C., 1981. Canadian Pacific Coast Ichthyoplankton Survey. 1980. Ichthyoplankton. Cruise Four (April 15–23). Canadian Data Report of Fisheries and Aquatic Sciences 278.

Masson, D., 2006. Seasonal water mass analysis for the Strait of Juan de Fuca and Georgia. Atmosphere–Ocean 44 (1), 1–15.

Masson, D., Cummins, P.F., 2007. Temperature trends and interannual variability in the Strait of Georgia, British Columbia. Continental Shelf Research 27, 634–649.

Matarese, A.C., Kendall Jr., A.W., Blood, D.M., Vinter, B.M., 1989. Laboratory guide to early life history stages of northeast Pacific fishes. NOAA Technical Reports NMFS 80, 1–652.

McFarlane, G.A., Beamish, R.J., 1985. Biology and fishery of Pacific whiting, *Merluccius productus*, in the Strait of Georgia. Marine Fisheries Review 47 (2), 23–34.

Moser, H., Smith, P.E., 1993. Larval fish assemblages and ocean boundaries. Bulletin of Marine Science 53 (2), 283–289.

Pepin, P., Shears, T.H., 1997. Variability and capture efficiency of bongo and Tucker trawl samplers in the collection of ichthyoplankton and other macrozooplankton. Canadian Journal of Fisheries and Aquatic Sciences 54, 765–773.

Schwing, F.B., Murphree, T., Green, P.M., 2002. The Northern Oscillation Index (NOI): a new climate index for the northeast Pacific. Progress in Oceanography 53, 115–119.

Thomson, R.E., 1981. Oceanography of the British Columbia coast. Canadian Special Publication of Fisheries and Aquatic Sciences 56.

Tully, J.P., 1938. Some relations between meteorology and coast gradient-currents off the Pacific coast of North America. Transactions American Geophysical Union, Nineteenth Annual Meeting, pp. 176–183.

Waldichuk, M., 1957. Physical oceanography of the Strait of Georgia, British Columbia. Journal of the Fisheries Research Board of Canada 14, 321–486.

Wolter, K., Timlin, M.S., 1998. Measuring the strength of ENSO events: how does 1997/98 rank? Weather 53 (9), 315–324.

Yamanaka, K.L., Lacko, L.C., 2001. Inshore Rockfish Stock Assessment for the West Coast of Canada and Recommendations for Management. DFO Canadian Science Advisory Secretariat Report No. 2001/139.

Yamanaka, K.L., Logan, G., 2010. Developing British Columbia's inshore rockfish conservation strategy. Marine and Coastal Fisheries: Dynamics, Management and Ecosystem Sciences 2 (1), 28–46.

Yin, K., Harrison, P.J., Beamish, R.J., 1997. Effect of a fluctuation in Fraser River discharge of primary production in the central Strait of Georgia, British Columbia, Canada. Canadian Journal of Fisheries and Aquatic Sciences 54 (5), 1015–1024.